

On the ammonite genus *Rusoceras* van Hoepen, 1946, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, from the Upper Albian of KwaZulu-Natal, South Africa

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ABSTRACT:

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The genus *Rusoceras* van Hoepen, 1946, is revised and interpreted as a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, while the five species from KwaZulu-Natal described by van Hoepen are interpreted as a single variable species for which we select the name *notha* van Hoepen, 1946.

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

INTRODUCTION

In this contribution we revise the Upper Albian ammonite genus *Rusoceras* van Hoepen, 1946, which we interpret as a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910. The five KwaZulu-Natal species referred to *Rusoceras* by van Hoepen are described, and interpreted as a single variable species.

Repositories of specimens

BMNH – The Natural History Museum, London, UK;
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, 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 van Hoepen, his D numbers, are given in parentheses.

SYSTEMATIC PALAEONTOLOGY

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Acanthoceratoidea Zittel, 1884
Family Brancoceratidae Spath, 1934
Subfamily Pervinquieriinae Spath, 1926
Genus and Subgenus *Pervinquieria* Böhm, 1910



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

DISCUSSION: The type species, by original designation, of *Rusoceras* van Hoepen, 1946 (p. 238), is *Rusoceras nothum* van Hoepen, 1946 (p. 238, text-figs 235–242). The original diagnosis is as follows:

“Keeled forms of the Gault, the young of which are higher than broad; dorsally they are broader than over the shoulders. At first the flanks are flat, later they are slightly convex from the umbilicus to beyond the middle of the flank, while the remainder is more or less concave. Old mouth edges have not been observed. From the first stage that ribs are known they already possess umbilical tubercles. The ribs are round, slightly S-shaped to straight or even slightly concave forwards. The umbilical tubercles are strong, radially elongated but short. There are apparently no ventral tubercles in young forms, at any rate the ribs here so broad and flat that they do not form tubercles that are worth mentioning; later the ribs become thicker on the shoulder and finally a strong tubercle is formed, especially on the shoulder. The ribs are slightly thickened on the middle of the flank. This weak flank “tubercle” is already visible from a very young stage. The ribs are coarse and short on the young whorls and are often forking in a wide V-shape; later the ribs stand closer together. They are either single and long (with or without umbilical tubercle) or narrowly bifurcating from the umbilical tubercle or the middle of the flank, or single and short (only from the middle of the flank). Sometimes the ribs are weaker on the middle of the flank of later whorls or on a portion of the young whorls. Umbilical surface vertical. Keel of medium height.”

Van Hoepen described five species of *Rusoceras* from a small area in the environs of Beacon 624 (locality 54 of Kennedy and Klinger 1975, p. 288): *Rusoceras nothum* van Hoepen, 1946 (p. 238, text-figs 235–242); *Rusoceras gibberum* van Hoepen, 1946 (p. 241, text-figs 243, 244); *Rusoceras densecostatum* van Hoepen, 1946 (p. 243, text-figs 245–247); *Rusoceras corpulentum* van Hoepen, 1946 (p. 244, text-figs 248, 249), and *Rusoceras sufflatum* van Hoepen, 1946 (p. 245, text-figs 250–252). They are described below, and interpreted as a single variable species.

Pervinquieria (*Pervinquieria*) is diagnosed (Kennedy and Klinger 2023b, p. 550) as being characterised as a subgenus by the presence of umbilical, lateral and ventrolateral tubercles. This ornament, combined with well-developed spiral ridges, charac-

terise what is to us a variable species, *Pervinquieria* (*Pervinquieria*) *notha*.

Van Hoepen referred three other species to his new genus: *Elobiceras browni* Haas, 1942 [p. 120, pl. 31, figs 2, 3; pl. 32, fig. 1; text-fig. 12e (p. 241)]; *Elobiceras oxytropidoceratoides* Haas, 1942 [p. 107, pl. 26, figs 2–5; pl. 27, fig. 1; pl. 28, fig. 5 (p. 244)], and *Schloenbachia neuparthi* Choffat, 1905 [p. 38, pl. 2, fig. 1; pl. 3, fig. 1; ?pl. 4, fig. 4 (p. 247)]. In our view, *browni* and *oxytropidoceratoides* are *Elobiceras* (*Elobiceras*) Spath, 1921, and *neuparthi* is an *Elobiceras* (*Craginites*) Young, 1957 (see Kennedy in Gale and Kennedy 2020, p. 19).

Pervinquieria (*Pervinquieria*) *notha* (van Hoepen, 1946)
(Text-figs 1–5)

1946. *Rusoceras nothum* van Hoepen, p. 238, text-figs 235–242.

1946. *Rusoceras gibberum* van Hoepen, p. 241, text-figs 243, 244.

1946. *Rusoceras densecostatum* van Hoepen, p. 243, text-figs 245–247.

1946. *Rusoceras corpulentum* van Hoepen, p. 244, text-figs 248, 249.

1946. *Rusoceras sufflatum* van Hoepen, p. 245, text-figs 250, 251.

1971. *Mortoniceras* (*Rusoceras*) *nothum* van Hoepen; Renz, p. 606, pl. 9, fig. 1; text-fig. 5a.

1982. *Mortoniceras* (*Rusoceras*) *nothum* van Hoepen; Renz, p. 55, pl. 12, fig. 6; text-fig. 39.

1982. *Rusoceras nothum* van Hoepen, 1946; Matsumoto and Obata, p. 34.

?1997. *Mortoniceras* groupe *pricei* Spath cf. forme *nothum* van Hoepen; Delamette *et al.*, pl. 16, fig. 4.

2018. *Mortoniceras* (*Mortoniceras*) *densecostatum* (van Hoepen, 1946); Klein, pp. 99, 105.

2018. *Mortoniceras* (*Mortoniceras*) *gibberum* (van Hoepen, 1946); Klein, pp. 99, 110.

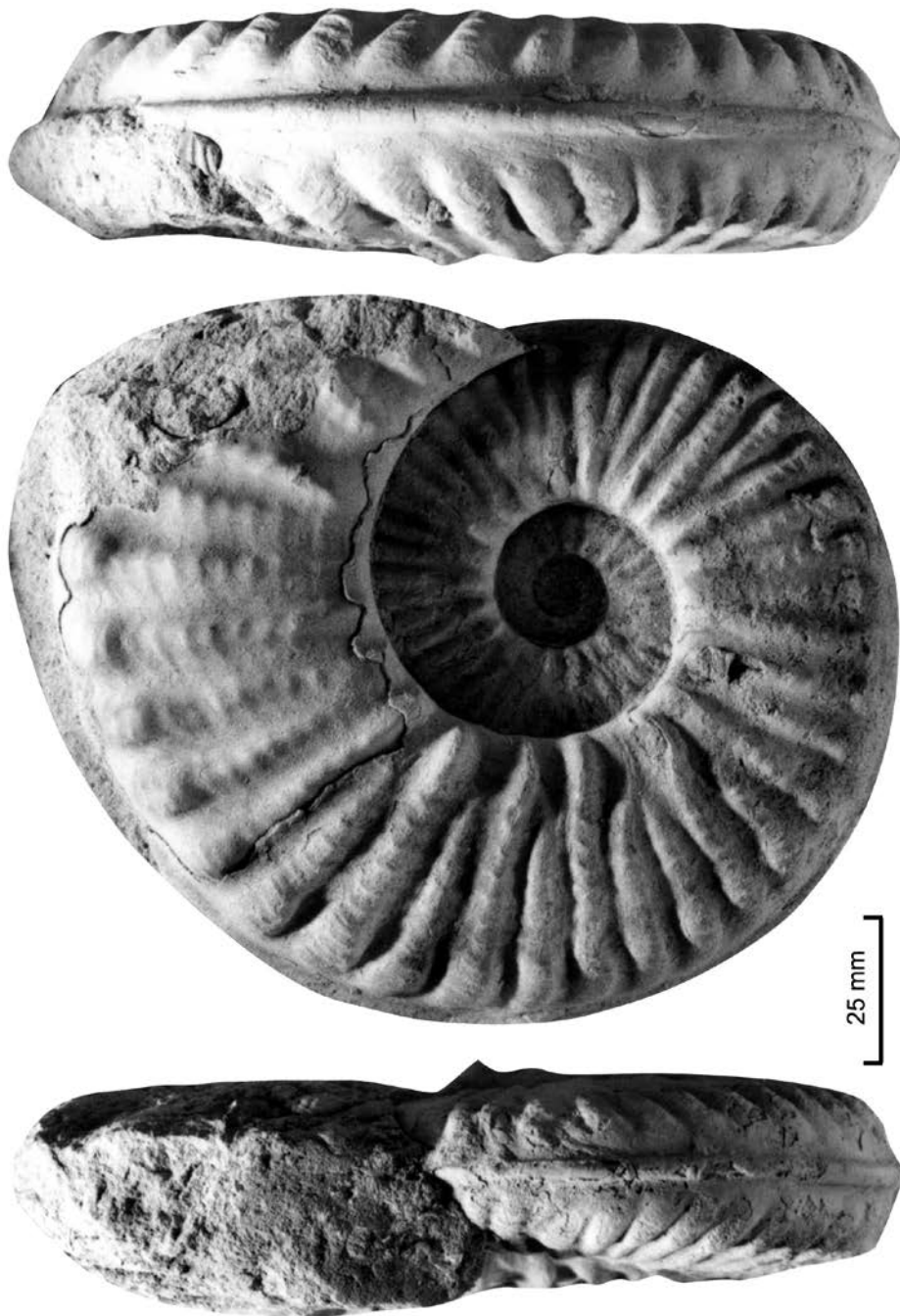
2018. *Mortoniceras* (*Mortoniceras*) *nothum* (van Hoepen, 1946); Klein, pp. 100, 117.

2018. *Mortoniceras* (*Mortoniceras*) *corpulentum* (van Hoepen, 1946); Klein, pp. 98, 105.

2018. *Mortoniceras* (*Mortoniceras*) *sufflatum* (van Hoepen, 1946); Klein, pp. 102, 125.

NAME OF THE SPECIES: As first revising authors we select the name *notha* for the species.

TYPE: The holotype, by original designation, is SAM PCZ 19180 (ex D. 2620) (Text-fig. 1), the original of van Hoepen (1946, p. 238, text-figs 235, 236,



Text-fig. 1. *Pervinquieria* (*Pervinquieria*) *notha* (van Hoepen, 1946). The holotype, SAM PCZ19180 (ex D.2620), the original of van Hoepen (1946, text-figs 235, 236, 238, 241), from the “Lower End of Runlet which joins the Umsinene river at Beacon 624”.

238, 241), from the “Lower End of Runlet which joins the Umsinene river at Beacon 624”.

MATERIAL: Specimens assigned to *nothum* by van Hoepen (1946), i.e., SAM PCZ 19211 (ex D. 2624) from the “Extension of Ridge West of Beacon 624

to the West into the valley and gradually higher towards the West”; and SAM PCZ 19212 (ex D. 2622), from the “Ridge West of Beacon 624”. SAM PCZ 19176 (ex D. 2623), the holotype of *Rusoceras gibberum* van Hoepen, 1946 (p. 241, text-figs 243, 244), from the “Upper End of Runlet which joins the

Umsinene River at Beacon 624". SAM PCZ 19177 (*ex* D. 2625), the holotype of *Rusoceras densecostatum* van Hoepen, 1946 (p. 243, text-figs 245–247), from the "Lower End of Runlet which joins the Umsinene river at Beacon 624" and a second specimen from the upper end of the runlet. SAM PCZ 19213 (*ex* D. 2626), from the "Extension of Ridge West of Beacon 624 to the West into the valley and gradually higher towards the West". SAM PCZ 19178 (*ex* D. 2628), the holotype of *Rusoceras sufflatum* van Hoepen, 1946 (p. 245, text-figs 248, 249), from the "Upper End of Runlet which joins the Umsinene river at Beacon 624." OUMNH KX.1411, from locality 56 of Kennedy and Klinger (1975).

DESCRIPTION: The dimensions of the holotype of *notha* (Text-fig. 1) are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19180 costal, at	132.9 (100)	45.8 (34.5)	54.5 (41.0)	0.84	43.2 (32.5)

It retains extensive areas of recrystallized shell and has a maximum preserved diameter of 145 mm; there are indications of the former presence of a further 30° whorl sector. Coiling is evolute, the umbilicus comprising 32.5% of the diameter, of moderate depth, with a feebly convex subvertical wall and quite narrowly rounded umbilical shoulder. The whorl section is compressed, rectangular to feebly trapezoidal in intercostal section with the greatest breadth just outside the umbilical shoulder, the ventrolateral shoulders broadly rounded, the venter flattened, with a strong siphonal keel. The costal section is compressed trapezoidal with the greatest breadth at the umbilical bullae. On the penultimate whorl, 21 ribs arise at the umbilical seam, pass straight up the umbilical wall and across the umbilical shoulder, where they strengthen into a small umbilicolateral bulla. The bullae give rise to single ribs that bifurcate around mid-flank or are single, while there are additional long intercalated ribs, to give a total of 44 ribs per whorl. On the outer whorl, 23–24 ribs arise at the umbilical seam and flex back across the umbilical wall, strengthen across the umbilical shoulder and develop into elongate umbilical bullae. Ribs and bullae strengthen progressively as size increases, and the bullae migrate out onto the inner flank. They give rise to single ribs, with only occasional pairs of ribs and intercalatories to give a total of 38–40 at the ventrolateral shoulder. The ribs are feebly prorsiradiate, and broaden and coarsen across the flanks, developing into a feebly prorsiradiate blunt bulla that extends across the ventrolat-

eral shoulders and venter, efface, leaving a smooth zone on either side of the siphonal keel. Thirteen rows of spiral ridges are well-developed on both shell and internal mould, becoming increasingly conspicuous across flanks and venter. Two rows of ridges on the outer flank are borne on a slight elevation – an incipient bulla. The suture (van Hoepen 1946, text-fig. 241) is deeply incised, with a bifid E/A with a deep median incision and narrow stem, narrow A, and narrow bifid A/U2.

SAM PCZ 19212 (*ex* D. 2622) (Text-fig. 2) is the original of van Hoepen's (1946) text-fig. 242, and has the following dimensions:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19212	137.5 (100)	43.4 (31.6)	54.1 (39.3)	0.8	47.8 (34.8)

The ribs on the phragmocone are markedly flexuous at one point towards the adapertural end of the penultimate whorl, but the ribbing style otherwise agrees closely with that of the holotype. There are 41 ribs at the ventrolateral shoulder of the outer whorl.

SAM PCZ 19217 (*ex* D. 264) (Text-fig. 3I, J) is the original of van Hoepen's (1946) text-figs 239–240, a specimen retaining limonitised shell. The dimensions are as follows:

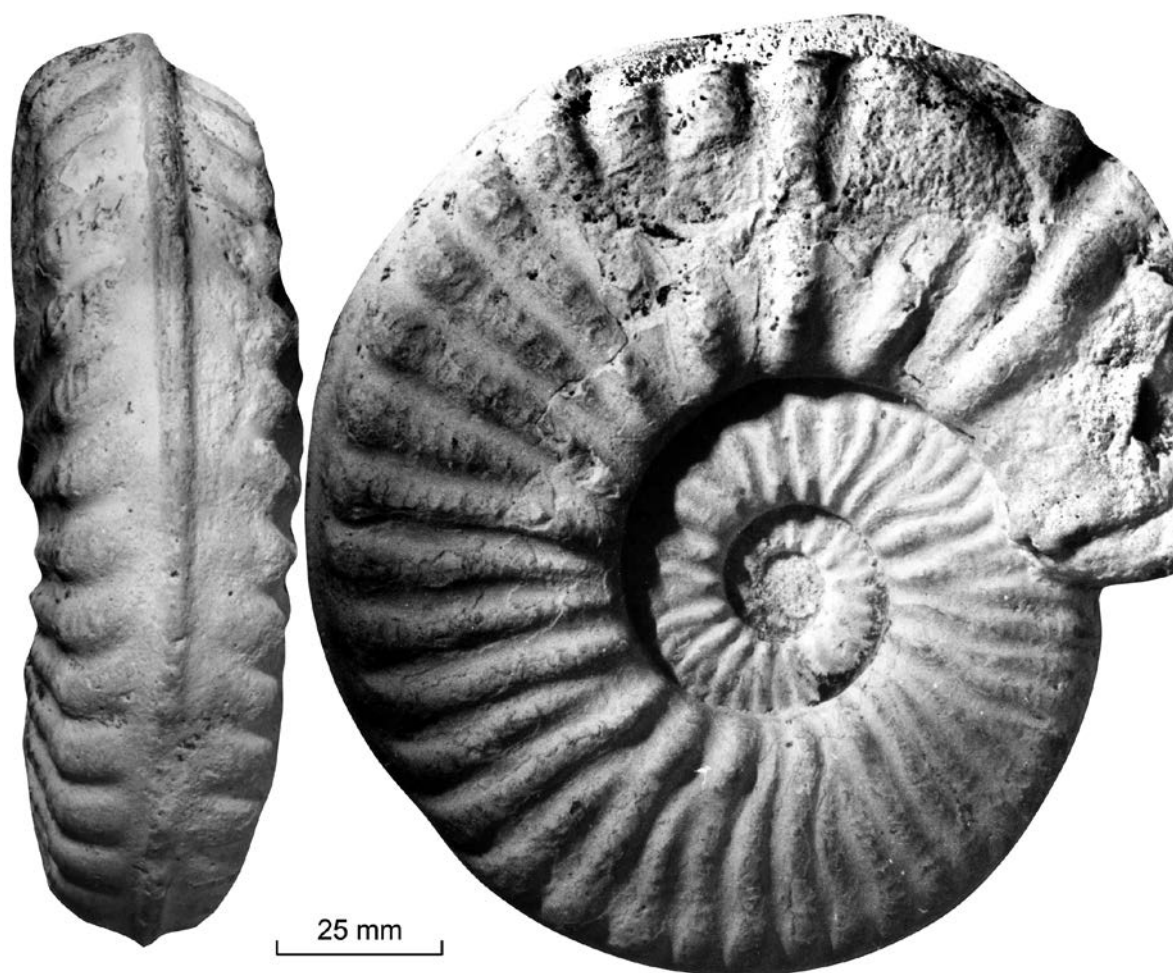
	D	Wb	Wh	Wb:Wh	U
SAM PCZ 18217 c	85.1 (100)	39.1 (46.0)	44.0 (51.7)	0.89	47.2 (55.5)

It differs in no significant respects from the holotype at the same diameter.

The holotype, by original designation, of *Rusoceras gibberum* van Hoepen, 1946 (p. 241, text-figs 243, 244) is SAM PCZ 19176 (*ex* D. 2623) (Text-fig. 4), a worn individual, now in fragments. All but a short sector of the outer whorl is phragmocone. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19176	127.6 (100)	39.1 (30.6)	44.0 (34.5)	0.89	47.2 (37.0)

Twenty-four ribs arise at the umbilical seam of the outer whorl. They strengthen across the umbilical wall and bear small, pointed oblique bullae that give rise to pairs of relatively coarse ribs on the adapertural 240° sector of the outer whorl, with additional single bullate primaries and intercalated ribs. From a diameter of 98 mm the ribs are variably bullate primaries and long intercalated ribs that are recti- to feebly prorsiradiate and strengthen across the flanks, developing into a blunt bulla that projects forward across the ventrolateral shoulder. It is interpreted as a coarsely ornamented variant of *notha*.



Text-fig. 2. *Pervinquieria* (*Pervinquieria*) *notha* (van Hoepen, 1946). SAM PCZ 19212 (ex D. 2622), the original of *Rusoceras nothum* van Hoepen, 1946 (text-fig. 242), from the “Ridge West of Beacon 624”.

SAM PCZ 19177 (ex D. 2625) (Text-fig. 3E, F, G, K) is the holotype of *Rusoceras densecostatum* van Hoepen, 1946 (p. 244, text-figs 245–247); the nucleus and part of the outer whorl survive. The dimensions of the former are as follows:

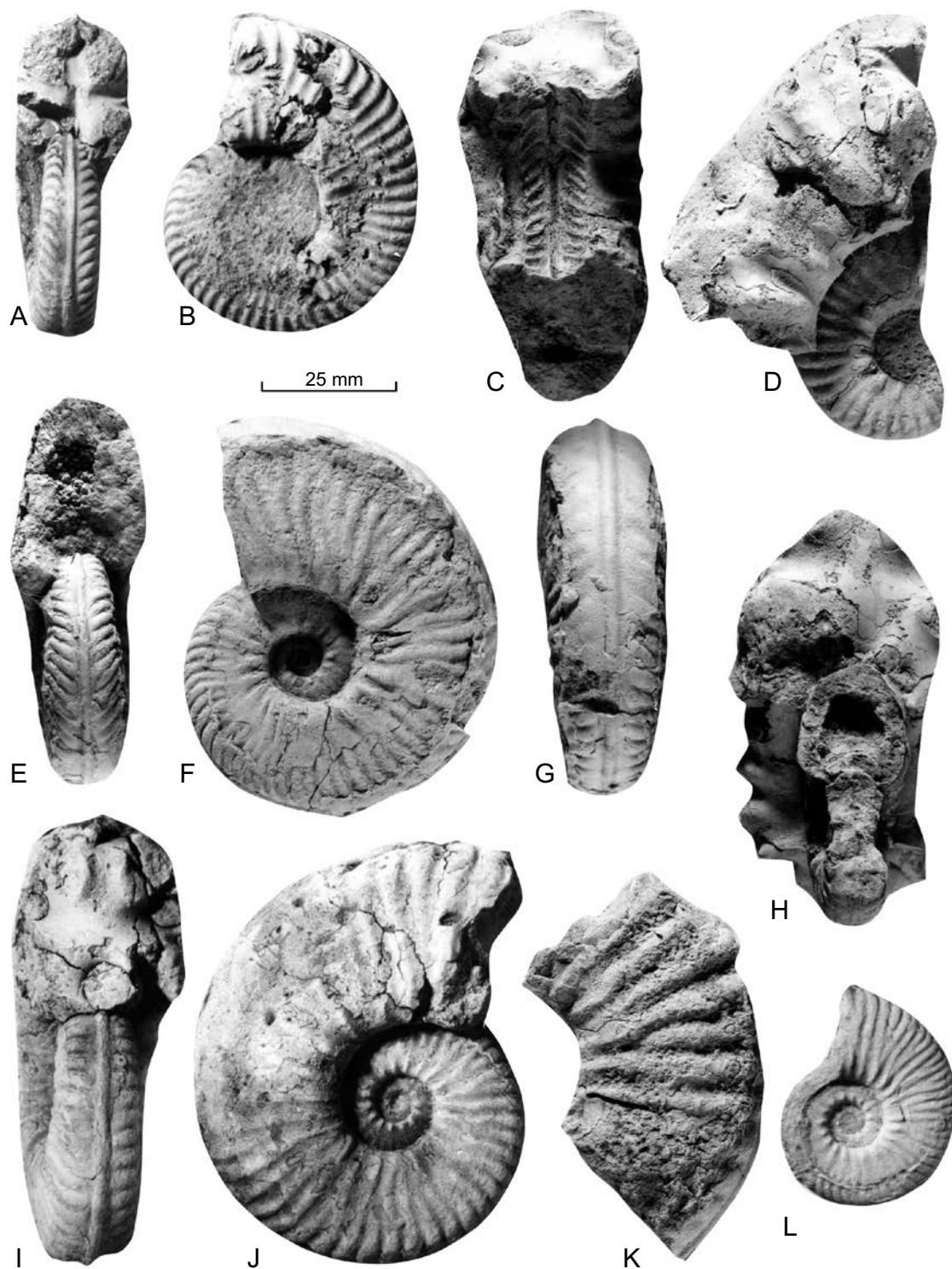
	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19177	81.8 (100)	– (–)	36.4 (44.5)	–	25.1 (30.7)

There are 24 ribs on the umbilical wall of the nucleus and an estimated 54 at the ventrolateral shoulder. The ribs strengthen across the umbilical shoulder and develop into small umbilicolateral bullae that give rise to pairs of ribs, which occasionally bifurcate, and there are numerous long intercalated ribs. The ribs are prorsiradial, feebly flexuous, convex at mid-flank and concave on the outer flank. They

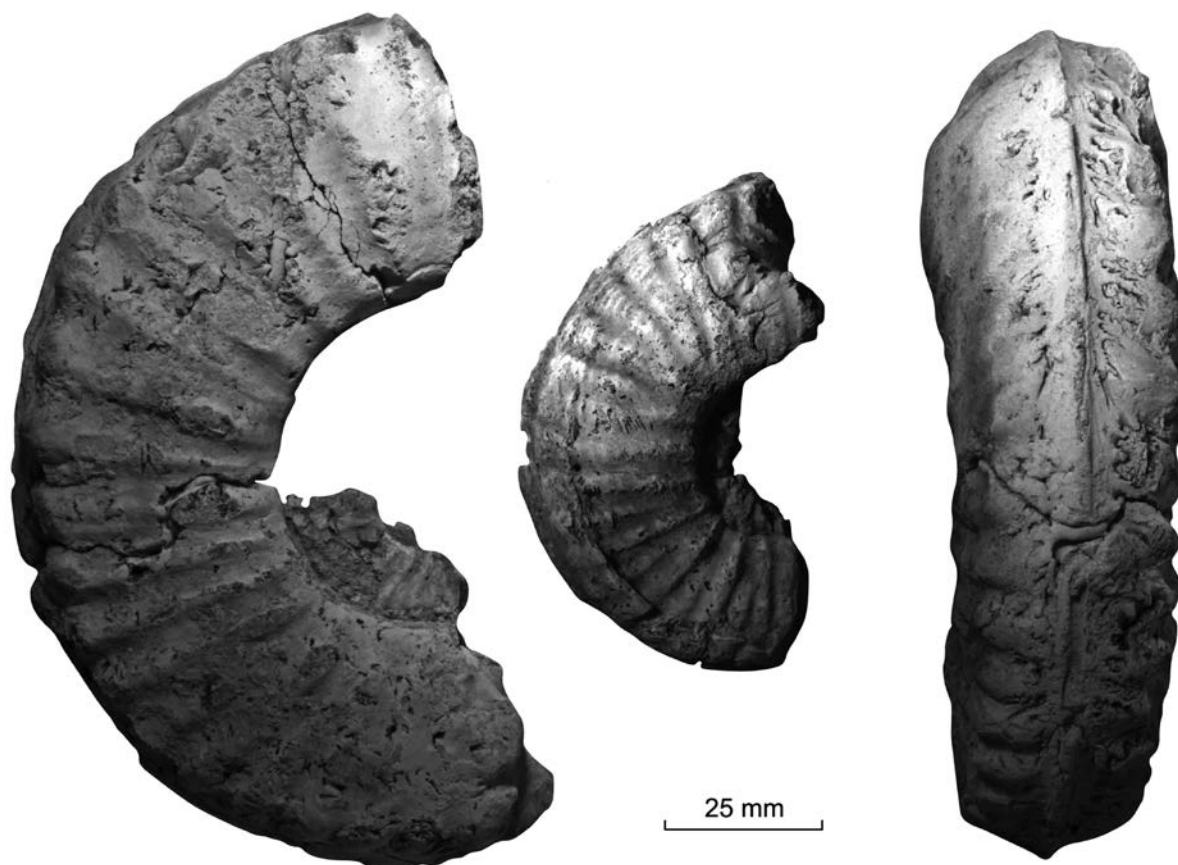
sweep forwards across the ventrolateral shoulder to form an obtuse ventral chevron, without developing into a distinct bulla. A weak bulla develops on the outer whorl fragment, which has a maximum preserved whorl height of 39 mm approximately; it is interpreted as a densicostate variety of *notha*.

SAM PCZ 19213 (ex D. 2626), cited by van Hoepen (1946, p. 244, text-fig. 247) (Text-fig. 3A, B) as a specimen of *densecostatum*, is a beautifully preserved internal mould of a phragmocone 63.1 mm in diameter with 50 ribs on the outer whorl at the ventrolateral shoulder, again without strengthening into a bulla.

The holotype, by original designation, of *Rusoceras corpulentum* van Hoepen, 1946 (p. 245, text-figs 248, 249) is SAM PCZ 19178 (ex D. 2627) (Text-fig. 3C, D, H). The surviving fragments are wholly septate, and comprise a 180° sector of the penultimate



Text-fig. 3. *Pervinqueria (Pervinqueria) notha* (van Hoepen, 1946). A, B – SAM PCZ 19213 (ex D. 2626), the original of *Rusoceras densecostatum* van Hoepen, 1946 (text-fig. 247), from the “Upper End of Runlet which joins the Umsinene river at Beacon 624”. C, D, H – SAM PCZ 19178 (ex D. 2627), the holotype of *Rusoceras corpulentum* van Hoepen, 1946 (p. 244, text-figs 248, 249), from the “Extension of Ridge West of Beacon 624”. E, F, G, K – SAM PCZ 19177 (ex D. 2625), the holotype of *Rusoceras densecostatum* van Hoepen, 1946, the original of van Hoepen (1946, p. 244, text-figs 245, 246), from the “Lower End of Runlet, which joins the Umsinene river at Beacon 624”. I, J – SAM PCZ 19180 (ex D. 21620), the original of *Rusoceras nothum* van Hoepen, 1946 (text-figs 239, 240), from the “Extension of Ridge West of Beacon 624”. L – OUMNH PAL-KX.11411, from locality 56 of Kennedy and Klinger (1975, p. 288) on the north side of the Mzinene River.



Text-fig. 4. *Pervinquieria* (*Pervinquieria*) *notha* (van Hoepen, 1946); SAM PCZ 19176 (ex D. 2623), the holotype of *Rusoceras gibberum* van Hoepen, 1946 (p. 241, text-figs 243, 244), from the “Lower End of Runlet which joins the Umsinene river at Beacon 624”.

whorl and a 60° sector of the succeeding whorl. The dimensions of the penultimate whorl fragment are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19178 c	52.0 (100)	23.5 (45.2)	25.3 (48.7)	0.93	14.5 (27.9)

The whorl section is compressed trapezoidal in intercostal section, with the greatest breadth close to the umbilical shoulder, the flanks feebly convex, the ventrolateral shoulders broadly rounded, the venter flattened. The costal whorl section is trapezoidal, with the greatest breadth at the umbilical bullae. There is a well-developed siphonal keel. Nine umbilicolateral bullae per half whorl give rise to pairs of ribs, and additional ribs intercalate to give a total of 22 per half whorl at the ventrolateral shoulder, across which they strengthen into blunt bullae. The ribs are near-transverse on the venter, and do not extend to the siphonal keel. The outer whorl fragment bears four coarse ribs on the umbilical wall that strengthen

into prominent umbilicolateral bullae. The best-preserved of the bullae gives rise to a pair of coarse prorsiradial ribs bearing well-developed spiral ridges. The ornament of the outer whorl fragment is coarser than in the holotype of the type species, but there are no significant differences.

The holotype, by original designation of *Rusoceras sufflatum* van Hoepen, 1946 (p. 245, text-figs 250–252), is SAM PCZ 17178 (ex D. 2628) (Text-fig. 5). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 17179	185.0 (100)	71.1 (38.4)	72.8 (39.4)	0.98	65.6 (35.5)

The specimen retains recrystallized shell and is in part body chamber, although the position of the final septum cannot be established. The surface has been extensively pitted during preparation. Coiling is very evolute, with 34% of the previous whorl covered, the umbilicus of moderate depth, with a feebly convex subvertical wall and a broadly rounded umbilical

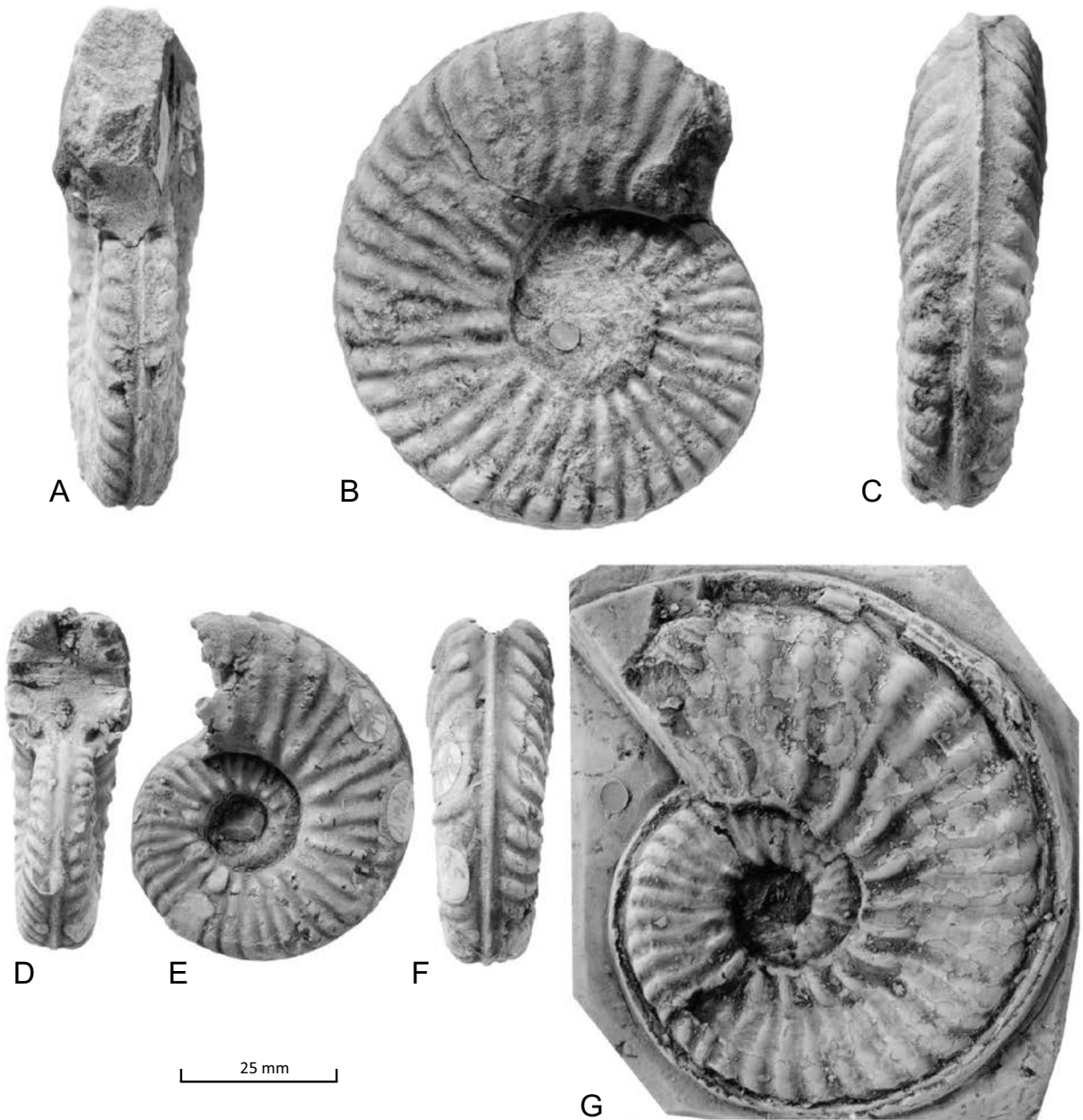


Text-fig. 5. *Pervinqueria* (*Pervinqueria*) *notha* (van Hoepen, 1946); SAM PCZ 19178 (ex D. 2628), the holotype of *Rusoceras sufflatum* van Hoepen, 1946 (p. 245, text-figs 250–252), from the “Upper End of Runlet which joins the Umsinene river at Beacon 624”.

shoulder. The whorl section is trapezoidal, with the greatest breadth just outside the umbilical shoulder in intercostal section and at the umbilical shoulder in costal section. The inner flanks are feebly convex, the outer flanks flattened and convergent, the ventrolateral shoulders broadly rounded, the venter flat in intercostal section, with a strong siphonal keel. The venter is concave between the ventrolateral bullae and keel in costal section. On the penultimate whorl, 34 ribs arise on the umbilical wall and strengthen into weak umbilical bullae, little more than a thickened rib. The bullae give rise to straight primary ribs that bifurcate low on the flank in some cases, although most of the ribs are single. There are additional long intercalated ribs. The ribs are crowded, broadening across the flanks, and numbering an estimated 50

per whorl at the ventrolateral shoulder. On the outer whorl, there are 35 ribs on the umbilical wall and 52 at the ventrolateral shoulder. Most ribs are single, a few branch and there are long intercalated ribs. The ribs broaden across the flanks and are straight to feebly concave, developing into an ill-defined bulla on the ventrolateral shoulder, forming an obtuse chevron, the ribs effacing before reaching the siphonal keel. Spiral ridges are well-developed, and there is a distinct mid-to outer lateral bulla that first appears at the very end of the penultimate whorl and strengthens around the outer whorl.

DISCUSSION: As here interpreted, specimens of van Hoepen’s *Rusoceras* are the end member, in terms of weakness and variable development of tubercles,



Text-fig. 6. *Pervinqueria* (*Pervinqueria*) *pricei* (Spath, 1922). A–C – BMNH C.77674 (ex 88720a), the original of *P. (P.) pricei intermedia* Spath, 1922 (pl. 38, fig. 5), from the Upper Albian Potterne Rock of Potterne, Wiltshire; D–F – BMNH C.7617 (ex C.790e), the original of Spath (1932, pl. 36, fig. 12), from bed x of the Upper Albian Gault Clay at Folkestone, Kent, UK; G – the holotype, BMNH C.12488, the original of Spath (1932, text-fig. 131), from bed x of the Upper Albian Gault Clay at Folkestone, Kent, UK.

within *Pervinqueria* (*Pervinqueria*). What is debatable is whether they are a distinct species in their own right, or simply the weakly tuberculate variants of one or more co-occurring species.

Pervinqueria (*Pervinqueria*) *pricei* (Spath, 1922) (p. 101; 1932, p. 391, pl. 36, figs 11, 12; pl. 37, fig. 3; text-figs 130c, 131, 132, 137c), a lower Upper

Albian zonal index in Western Europe is a comparable form. The holotype, BMNH C.12488 (Text-fig. 6G) is a crushed individual retaining traces of aragonitic shell. It has umbilical bullae that give rise to pairs of ribs on the penultimate whorl; on the outer whorl the bullae migrate outwards to an inner lateral position. The ribs have expanded spatulate terminations,

and there are well-developed spiral ridges, with, in places, incipient lateral bullae. In other specimens assigned to the species by Spath (1932), for example BMNH C.77617 (*ex* C. 790e) (Text-fig. 6D–F), the original of his pl. 36, fig. 12, there is a suggestion of a feeble outer lateral tubercle in places, and this tubercle is well-developed in his var. *intermedia* (BMNH C.77674 (*ex* 88720a) (Text-fig. 6A–C).

There are also comparisons with *Pervinqueria* (*Pervinqueria*) *fissicostata* (Spath, 1932) (p. 396, pl. 38, fig. 6; pl. 47, fig. 1; text-fig. 111); see revision in Kennedy in Gale and Kennedy (2020, p. 48, pl. 15, figs 5, 6; text-fig. 31), interpreted as both a valid species and as a gracile variant of *P. (P.) inflatum* (Amédéo *et al.* 2004, pl. 2). We retain *notha* as a separate, variable species at this time, as none of the material assigned to *pricei* or *fissicostata* by previous authors shows the same range of variation as the present material, which includes very finely ribbed individuals (Text-fig. 3E–G), those with pronounced flexuous ribbing on nuclei (Text-fig. 2), and the coarse adult ornament shown by the holotype (Text-fig. 1).

OCCURRENCE: Lower Upper Albian, KwaZulu-Natal, South Africa, Venezuela, and, possibly, Haute-Savoie, France.

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