

On the ammonite subgenus *Styphloceras* van Hoepen, 1951, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, from the Upper Albian of KwaZulu-Natal, South Africa

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ABSTRACT:

Kennedy, W.J. and Klinger, H.C. 2026. On the ammonite subgenus *Styphloceras* van Hoepen, 1951, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, from the Upper Albian of KwaZulu-Natal, South Africa. *Acta Geologica Polonica*, 76 (1), e72.

In this contribution we revise the ammonite subgenus *Pervinquieria* (*Styphloceras*) van Hoepen, 1951, and show it to be a synonym of *Pervinquieria sensu stricto*. All of the species assigned to the subgenus by van Hoepen are interpreted as a single variable species, of which *Pervinquieria* (*Collignonia*) *vallifera* van Hoepen, 1951, is a further synonym.

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

INTRODUCTION

In this contribution we revise the species referred by van Hoepen to his subgenus *Pervinquieria* (*Styphloceras*) van Hoepen, 1951, which we interpret as a single variable species, for which we select the specific name *nodosocostata* van Hoepen, 1942.

Institutional abbreviation

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

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 D numbers, assigned to specimens in the original publications by van Hoepen, are given in parentheses.

SYSTEMATIC PALAEOLOGY

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: See Kennedy and Klinger (2023b, p. 550) for a diagnosis and discussion of *Pervinquieria* (*Pervinquieria*). Van Hoepen introduced his subgenus *Pervinquieria* (*Styphloceras*) as follows (van Hoepen 1951, p. 300): “Subgenus *Styphloceras* n. s.g. Type: *Pervinquieria* (*Styphloceras*) *nododoso-costata* v. Hp.

The characteristics of this subgenus are those of the third group of *Pervinquieria* noted above”

“3. *Pervinquieria nodoso-costata* may be taken as the typical form of this group. It is characterised by coarse ribbing and tuberculation. The ventral tubercle may have a nail-like appearance, but is generally inflated above the basis of the keel. It has a prominent shoulder tubercle from which it is usually separated by a concavity. There is a strong flank tubercle on older whorls. Young whorls only have prominent umbilical and ventral tubercles. The latter are divided into a thick ventral portion and a sharp pointed shoulder portion, separated by a more or less deep concavity. Young whorls have no flank tubercle and the ribs are therefore concave outwards. Unusual mouth edges are present from very young stages up to large diameters and the flap in the young stages lies between the umbilical tubercle and the ventral tubercle, covering the flank- and the shoulder tubercle. In later stages the flap lies between the flank- and the ventral tubercles, covering the flank and shoulder tubercles.”

Van Hoepen (1951) assigned the following to *Styphloceras*:

– *Pervinquieria nodoso-costata* van Hoepen, 1942 (p. 101, text-figs 71–76; 1951, p. 300), from Beacon 624, the “Upper End of Runlet which joins the Umsinene River at Beacon 624”, and the “Mouth of the Ndabana Spruit”;

– *Pervinquieria multicostata* van Hoepen, 1942 (p. 99, text-figs 67–70; the originals of figs 69 and 70 were subsequently referred to *Pervinquieria* (*Styphloceras*) *familiaris* van Hoepen, 1951, p. 300), from Beacon 624 and the “Upper End of Runlet which joins the Umsinene River at Beacon 624”;

– *Pervinquieria ordinato-costata* van Hoepen, 1942 (p. 103, text-figs 77–79), from Beacon 624, and the “Mouth of the Ndabana Spruit”;

– *Pervinquieria* (*Styphloceras*) *latidorsata* van Hoepen, 1951 (p. 311, text-figs 350–352), from Beacon 624;

– *Pervinquieria clivosa* van Hoepen, 1942 (p. 107, text-figs 81–85; 1951, p. 301, text-fig. 330), from the

“Upper End of Runlet which joins the Umsinene River at Beacon 624”;

– *Pervinquieria* (*Styphloceras*) *apta* van Hoepen, 1951 (p. 302, text-figs 331–333), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *cognata* van Hoepen, 1951 (p. 304, text-figs 334–337), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *propinqua* van Hoepen, 1951 (p. 306, text-figs 338–340), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *vicina* van Hoepen, 1951 (p. 307, text-figs 341–343), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *familiaris* van Hoepen, 1951 (p. 308, text-fig. 344) [= *Pervinquieria multicostata* van Hoepen, 1942, p. 99 (*pars*), text-figs 69, 70 only], from the “Upper End of Runlet which joins the Umsinene River at Beacon 624” and Beacon 624;

– *Pervinquieria* (*Styphloceras*) *latiumbilicata* van Hoepen, 1951 (p. 309, text-figs 345, 346), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *necessaria* van Hoepen, 1951 (p. 310, text-figs 347–349), from Beacon 624;

– *Pervinquieria* (*Styphloceras*) *bulbifera* van Hoepen, 1951 (p. 313, text-figs 353–356), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

It will be seen that the overwhelming majority of van Hoepen’s *Styphloceras* come from either his Beacon 624, or the “Upper End of Runlet which joins the Umsinene River at Beacon 624” and on the basis of the descriptions given below, we regard them as a single variable species of which we regard *Pervinquieria* (*Collignonia*) *vallifera* van Hoepen, 1951 (p. 297, text-figs 317–319), also from Beacon 624, as a further synonym.

The key features of the species assigned to *Styphloceras* by van Hoepen (1951) is the presence of umbilical, lateral and ventrolateral tubercles throughout most of the ontogeny, the lateral tubercle effacing on adult body chambers; these characters, shared with the type species of *Pervinquieria*, lead us to regard *Styphloceras* a synonym of *Pervinquieria sensu stricto*.

Pervinquieria (*Pervinquieria*) *nodosocostata* van
Hoepen, 1942
(Text-figs 1–16)

1942. *Pervinquieria multicostata* van Hoepen, p. 99. text-figs 67–70.

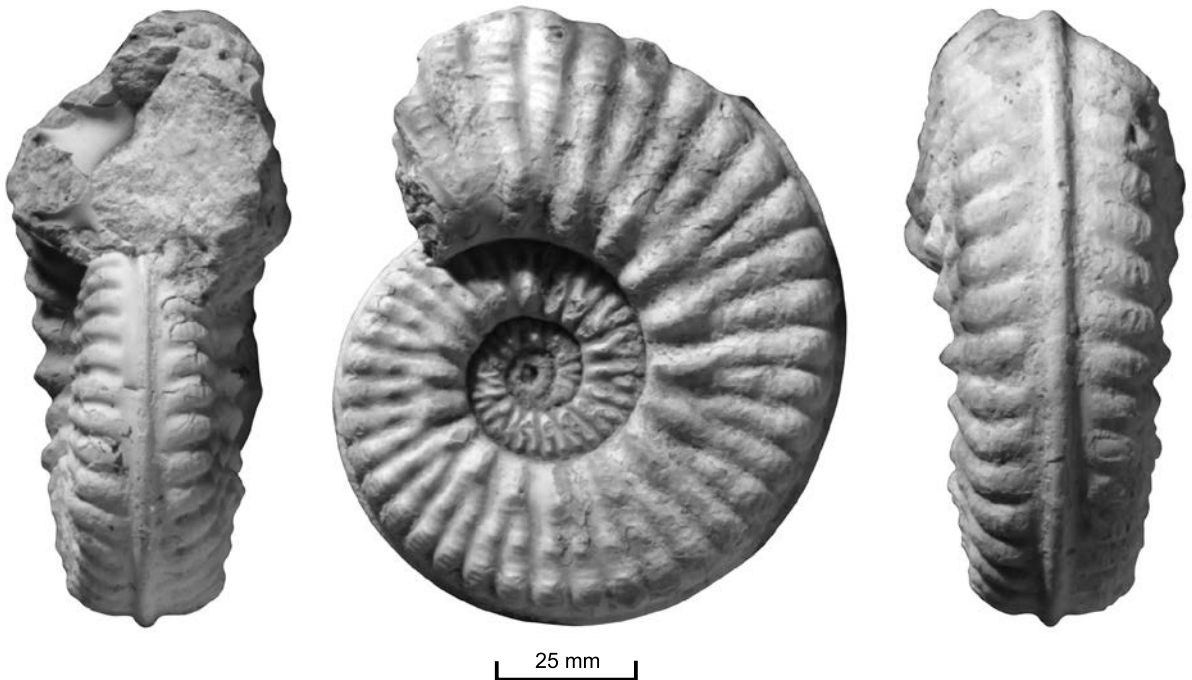
1942. *Pervinquieria nodoso-costata* van Hoepen, p. 101, text-figs 71–76.

1942. *Pervinquieria ordinato-costata* van Hoepen, p. 103, text-figs 77–80.
1942. *Pervinquieria clivosa* van Hoepen, p. 107, text-figs 81–85.
1951. *Pervinquieria (Collignonia) vallifera* van Hoepen, p. 297, text-figs 317–319.
1951. *Pervinquieria (Styphloceras) nodoso-costata* van Hoepen, 1942; van Hoepen, p. 300.
1951. *Pervinquieria (Styphloceras) multicostata* van Hoepen, 1942; van Hoepen, p. 300, text-figs 321–325.
1951. *Pervinquieria (Styphloceras) ordinato-costata* van Hoepen, 1942; van Hoepen, p. 300, text-figs 326–329.
1951. *Pervinquieria (Styphloceras) clivosa* van Hoepen, 1942; van Hoepen, p. 301, text-fig. 330.
1951. *Pervinquieria (Styphloceras) apta* van Hoepen, p. 302, text-figs 331–333.
1951. *Pervinquieria (Styphloceras) cognata* van Hoepen, p. 304, text-figs 334–337.
1951. *Pervinquieria (Styphloceras) propinqua* van Hoepen, p. 306, text-figs 338–340.
1951. *Pervinquieria (Styphloceras) vicina* van Hoepen, p. 307, text-figs 341–343.
1951. *Pervinquieria (Styphloceras) familiaris* van Hoepen, p. 308, text-fig. 344.
1951. *Pervinquieria (Styphloceras) latiumblicata* van Hoepen, p. 309, text-figs 345, 346.
1951. *Pervinquieria (Styphloceras) necessaria* van Hoepen, p. 310, text-figs 347–349.
1951. *Pervinquieria (Styphloceras) latidorsata* van Hoepen, p. 311, text-figs 350–352.
1951. *Pervinquieria (Styphloceras) bulbifera* van Hoepen, p. 313, text-figs 353–356.
1955. *Pervinquieria (Styphloceras) multicostata* v. Hp.; van Hoepen, p. 355, text-figs 1–3.
- ?1955. *Mortoniceras (Mortoniceras) aff. multicostatum* (van Hoepen); Reyment, p. 35.
1955. *Mortoniceras (Mortoniceras) cf. nodoso-costatum* (van Hoepen, 1942); Reyment, p. 35 pl. 6, fig. 1.
- non 1979. *Mortoniceras (Pervinquieria) velliferum* van Hoepen; Collignon, p. 26, pl. 10, fig. 2.
2018. *Mortoniceras (Mortoniceras) aptum* (van Hoepen, 1951); Klein, pp. 98, 104.
2018. *Mortoniceras (Mortoniceras) bulbiferum* (van Hoepen, 1951); Klein, pp. 98, 104.
2018. *Mortoniceras (Mortoniceras) clivosum* (van Hoepen, 1942); Klein, pp. 98, 104.
2018. *Mortoniceras (Mortoniceras) cognatum* (van Hoepen, 1951); Klein, pp. 98, 105.
2018. *Mortoniceras (Mortoniceras) familiare* (van Hoepen, 1951); Klein, pp. 99, 108.
2018. *Mortoniceras (Mortoniceras) latiumblicatum* (van Hoepen, 1951); Klein, pp. 100, 115.
2018. *Mortoniceras (Mortoniceras) latidorsatum* (van Hoepen, 1951); Klein, pp. 100, 116.
2018. *Mortoniceras (Mortoniceras) necessarium* (van Hoepen, 1951); Klein, pp. 100, 117.
2018. *Mortoniceras (Mortoniceras) nodosocostatum* (van Hoepen, 1942); Klein, pp. 100, 117.
2018. *Mortoniceras (Mortoniceras) propinquum* (van Hoepen, 1951); Klein, pp. 101, 121.
- part 2018. *Mortoniceras (Mortoniceras) valliferum* (van Hoepen, 1951); Klein, pp. 102, 126.
2018. *Mortoniceras (Mortoniceras) vicinum* (van Hoepen, 1951); Klein, pp. 102, 127.
2018. *Styphloceras latidorsatum* van Hoepen; Cooper, pl. 23, fig. e.

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

TYPE: The holotype is SAM PCZ 19267 (*ex* D.2397), the original of van Hoepen (1942, p. 101, text-figs 71, 72), from Beacon 624 (Text-fig. 6).

MATERIAL: The holotype of *Pervinquieria ordinatocostata* van Hoepen, 1942, SAM PCZ 19268 (*ex* D.2399). The following specimens assigned to *ordinatocostata* in 1942 (p. 103) and 1951 (p. 300): SAM PCZ 19433 (*ex* D.2791), SAM PCZ 19444 (*ex* D.2792), SAM PCZ 21621 (*ex* D.2793), SAM PCZ 21620 (*ex* D.2805). SAM PCZ 19269 (*ex* D.870), the holotype of *Pervinquieria clivosa* van Hoepen, 1942. SAM PCZ 19437 (*ex* D.2394), the holotype of *Pervinquieria multicostata* van Hoepen, 1942. SAM PCZ 19435 (*ex* D.2791), mentioned by van Hoepen (1951, p. 300) under *Pervinquieria (Styphloceras) nodosocostata* van Hoepen, 1942 from Beacon 624. SAM PCZ 19440 (*ex* D.2795), the holotype of *Pervinquieria (Styphloceras) apta* van Hoepen, 1951. SAM PCZ 19439 (*ex* D.2900), referred to *clivosa* by van Hoepen (1951, p. 301). SAM PCZ 19441 (*ex* D.2796), the holotype of *Pervinquieria (Styphloceras) cognata* van Hoepen, 1951. SAM PCZ 19328 (*ex* D.2804), referred to *cognata* by van Hoepen (1951, p. 306). SAM PCZ 19329 (*ex* D.2729), the holotype of *Pervinquieria (Styphloceras) propinqua* van Hoepen, 1951. SAM PCZ 19330 (*ex* D.2798), the holotype of *Pervinquieria (Styphloceras) vicina* van Hoepen, 1951. SAM PCZ 19442 (*ex* D.2395), the holotype of *Pervinquieria (Styphloceras) familiaris* van Hoepen, 1951. SAM PCZ 19443 (*ex* D.2799), referred to *familiaris* by van Hoepen (1951, p. 308). SAM PCZ 19331 (*ex* D.2802), the holotype of *Pervinquieria (Styphloceras) latiumblicata* van Hoepen, 1951. SAM PCZ 19332 (*ex* D.2807), the



Text-fig. 1. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. The holotype of *Pervinquieria* (*Styphloceras*) *multicostata* van Hoepen, 1942, SAM PCZ 19437 (ex D.2394), the original of van Hoepen [1942, p. 99 (*pars*), text-fig. 67, 68], from Beacon 624.

holotype of *Pervinquieria* (*Styphloceras*) *necessaria* van Hoepen, 1951. SAM PCZ 19444 (ex D.2808), the holotype of *Pervinquieria* (*Styphloceras*) *latidorsata* van Hoepen, 1951. SAM PCZ 19335 (ex D.2810), the holotype of *Pervinquieria* (*Styphloceras*) *bulbifera* van Hoepen, 1951.

DESCRIPTION: The dimensions of the holotype of *P. nodosocostata* (Text-fig. 6) are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19267 c at	87.5 (100)	41.8 (47.8)	34.2 (39.0)	1.2	35.6 (40.7)

The holotype retains recrystallized shell. Coiling is evolute, the umbilicus comprising 40.7% of the diameter, of moderate depth, with a feebly convex, outward-inclined wall and broadly rounded umbilical shoulder. The whorl section is depressed trapezoidal with the greatest breadth below mid-flank, the ventrolateral shoulders broadly rounded, the venter flattened in intercostal section, with a strong siphonal keel. Sixteen ribs arise at the umbilical seam of the penultimate whorl, strengthen across the umbilical wall, sweep forwards, and link to strong conical/bullate tubercles displaced slightly out from the

umbilical shoulder. The tubercles give rise to pairs of coarse, straight, prorsiradiate ribs to give a total of 30 ribs approximately on the outer flank. All ribs bear slightly weaker conical lateral tubercles from the smallest diameter visible. On the outer whorl, there are sixteen progressively strengthening umbilical bullae that migrate outwards to an umbilicolateral position. They give rise to pairs of coarse prorsiradiate ribs that bear coarse rounded/conical lateral tubercles and subequal rounded to feebly clavate inner ventrolateral tubercles. There are also single primary ribs that lack an umbilicolateral tubercle, to give a total of 35 ribs on the ventrolateral shoulder. The ribs are slightly offset across the venter at the beginning of the outer whorl, but become opposite as diameter increases, and near-transverse, forming a very obtuse ventral chevron. The ribs broaden across the venter, terminate abruptly, and are separated from the siphonal keel by a smooth zone. Spiral ridges are well-developed on the flanks and ventrolateral shoulders. SAM PCZ 21621 (ex D.2793), SAM PCZ 21620 (ex D.2805) and SAM PCZ 19433 (ex D.2791) are coarsely ribbed, the ribs becoming single with alternate ribs lacking an umbilicolateral



Text-fig. 2. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19414 (ex D.2398), mentioned by van Hoepen (1942, p. 103), from Beacon 624.

tubercle. SAM PCZ 19414 (ex D.2398) (Text-fig. 2) is crushed, and was originally 140 mm in diameter; the dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19414I c	118.5 (100)	55.3 (46.7)	43.0 (36.3)	1.29	51.3 (43.0)

SAM PCZ19435 (ex D.2791) (Text-fig. 3) has a coarsely ribbed nucleus and retains a fragment of body chamber with single bullate and non-bullate ribs.

SAM PCZ 19445 (ex D.2792) (Text-fig. 4) is 155 mm in diameter, a very coarsely ribbed individual with 17 umbilical tubercles and 33 ribs at the ventrolateral shoulder of the outer whorl.

The holotype of *Pervinquieria (Styphloceras) multicostata* van Hoepen, 1942 (p. 99, text-figs 67, 68) is SAM PCZ 19437 (ex D.2394) (Text-fig. 1). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19437 c at c	107.8 (100)	(-)	41.6 (38.6)	-	40.1 (37.2)
	98.7 (100)	42.7 (43.3)	40.3 (40.8)	1.1	34.7 (35.2)

The holotype is a phragmocone retaining limonitized shell. Coiling is moderately evolute, with 37%

of the previous whorl covered. The umbilicus comprises around 36% of the diameter and is of moderate depth, with a subvertical, feebly convex wall and broadly rounded umbilical shoulder. The whorl section is depressed trapezoidal, with the greatest breadth low on the flanks in intercostal section, the flanks convergent, the ventrolateral shoulders broadly rounded, the venter broad, flattened, with a strong siphonal keel. The maximum whorl breadth is at the umbilical bullae in costal section. On the outer whorl, 20 ribs arise at the umbilical seam, sweep back across the umbilical wall, strengthen markedly across the umbilical shoulder and develop into a rounded/conical umbilical bulla. The bullae give rise to pairs of low, broad, coarse straight, prorsiradiate ribs with small rounded-conical lateral tubercles, conspicuous on the adapical part of the outer whorl, but less conspicuous with increasing size. There is a coarse, blunt inner ventrolateral tubercle that gives rise to a coarse ventral rib that defines a very obtuse ventral chevron, the ribs near-transverse and opposite on either side of



Text-fig. 3. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19435 (ex D.2791), mentioned by van Hoepen (1951, p. 300), from Beacon 624.



Text-fig. 4. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19445 (ex D.2792), mentioned by van Hoepen (1951, p. 300), from the "Upper End of Runlet which joins the Umsinene River at Beacon 624".

the siphonal keel. There is no clearly differentiated outer ventrolateral tubercle. Spiral ridges are well-developed on the flanks and ventrolateral shoulders. When compared with the holotype of *nodosocostata*, the tuberculation is more subdued.

SAM PCZ 19326 (ex D.2808), mentioned by van Hoepen (1951, p. 300), is a smaller individual, 63 mm in diameter, with 22 umbilical bullae on the outer whorl.

SAM PCZ 19438 (ex D.3396) is a battered phragmocone, 160 mm in diameter, with indications of further whorl, indicating that the species reached a large size.

SAM PCZ 19436 (ex D.2794) (Text-fig. 5), the original of van Hoepen (1951, p. 300, text-figs 321–324), has a maximum preserved diameter of 160 mm, and appears to be septate to 143 mm in diameter. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19436 c	160.0 (100)	59.3 (37.1)	57.7 (36.1)	1.03	65.4 (40.9)

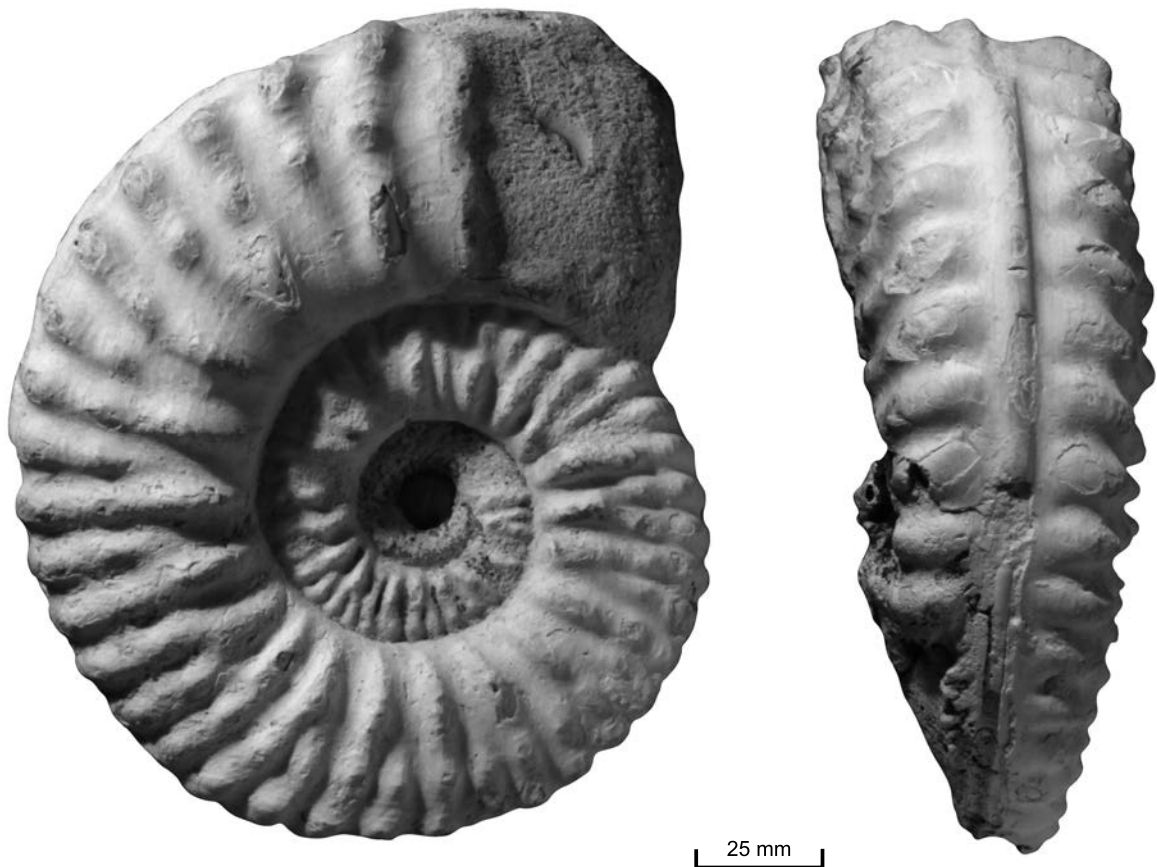
There are 22 umbilicolateral bullae on the outer whorl that migrate progressively outwards. They

give rise to pairs of ribs at the adapical end of the outer whorl; on the adapertural 120° sector they give way to single primaries alternating with long or short intercalated ribs. The ribs are strong and prorsiradiate, and number 39–40 per whorl at the ventrolateral shoulder. The ribs bear progressively strengthening rounded-conical lateral tubercles and strong, blunt inner ventrolateral tubercles. These give rise to a coarse, near-transverse rib, not differentiated into an outer ventrolateral tubercle, and separated from the siphonal keel by a smooth zone. Spiral ridges are prominent on flanks and ventrolateral shoulders. The inner whorls are closely similar to those of the holotype of *nodosocostata*.

The holotype of *Pervinquieria (Styphloceras) ordinatocostata* van Hoepen, 1942 (p. 103, text-figs 77–79), SAM PCZ 19268 (ex D.2399) (Text-fig. 7) is a large individual that lacks part of one flank at the apertural end and retains limonitised shell and a 90° sector of body chamber. The original diameter when complete, was an estimated 175–180 mm. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19268 at c	153.1 (100)	59.5 (38.9)	55.4 (36.2)	1.08	62.3 (40.7)

Coiling is evolute, the umbilicus comprising 40.7%, of the diameter on the outer whorl, of moderate depth, the umbilical wall of the penultimate whorl subvertical, that of the outer whorl inclined outwards. On the penultimate whorl, 20 umbilical bullae give rise to pairs of ribs, and there are 40 ribs at the umbilical seam of the succeeding whorl, all of which bear a rounded-conical lateral tubercle. Twenty ribs arise at the umbilical seam of the outer whorl, strengthen across the umbilical wall and shoulder and develop into strong umbilicolateral bullae. On the adapical half of the outer whorl the bullae give rise to pairs of coarse, straight, prorsiradiate ribs with a strong rounded-conical lateral tubercle and conical to feebly bullate inner ventrolateral tubercle. These give rise to a coarse, prorsiradiate rib with an incipient ventrolateral clavus. The ribs efface before reaching the strong siphonal keel and form an obtuse ventral chevron. On the adapertural half of the outer whorl the ribs are predominantly single bullate primaries with occasional paired ribs; the umbilical bullae decline on the last few ribs, suggesting the specimen to be a near-complete adult. The inner whorls of this specimen have sharper ribbing than those of the holotype of *nodosocostata*, while the ribs form a ventral chevron, rather than being near-transverse. In this respect the specimen compares with SAM PCZ 19445 (ex



Text-fig. 5. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19436 (ex D.2794), the original of *Pervinquieria* (*Styphloceras*) *multicosata* van Hoepen, 1942, original of van Hoepen (1951, p. 300, text-figs 321–324), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

D.2792) (Text-fig. 4), the large, coarsely ornamented individual referred to *nodosocostata* by van Hoepen.

The holotype of *Pervinquieria* (*Styphloceras*) *bulbifera* van Hoepen, 1951 (p. 313, text-figs 353–356), SAM PCZ 19335 (ex D.2810) (Text-fig. 13D–F), is a rather battered individual retaining recrystallized shell; the surface detail is lost. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19335 c	74.6 (100)	31.1 (41.7)	28.1 (37.7)	1.1	28.0 (37.5)

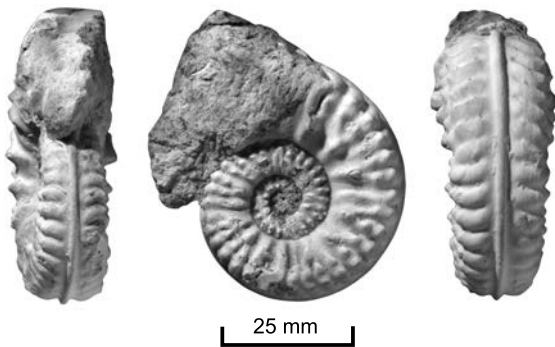
Coiling is evolute, the umbilicus comprising 37.5% of the diameter, of moderate depth, the umbilical wall convex and outward-inclined. Twenty ribs arise at the umbilical seam, and strengthen across the umbilical wall, linking to coarse, pinched umbilical bullae. The bullae give rise to pairs of feebly prorsiradiate straight ribs that strengthen and broaden across the flanks to give a total of 34 ribs at the ventrolateral shoulder; all bear a small lateral tuber-

cle and a large conical to bullate inner ventrolateral tubercle, from which a broad transverse rib extends to a well-developed outer ventrolateral clavus, separated from the siphonal keel by narrow smooth zone.

The holotype of *Pervinquieria* (*Styphloceras*) *latidorsata* van Hoepen, 1951 (p. 311, text-figs 350–352), SAM PCZ 19444 (ex D.2808) (Text-fig. 13A–C) retains well-preserved nacreous shell. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19444 c	71.5 (100)	30.5 (42.7)	25.6 (35.8)	1.2	30.4 (42.5)

Coiling is evolute, the umbilicus, of moderate depth, comprises 42.5% of the diameter. The umbilical wall is convex and outward-inclined, the umbilical shoulder broadly rounded. The whorl section is trapezoidal, the intercostal whorl section with broadly rounded ventrolateral shoulders, a flattened venter and a strong siphonal keel. The greatest breadth is at the umbilical bullae in costal section. The ornament of the penulti-



Text-fig. 6. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19437 (ex D.2394), the holotype, the original of van Hoepen (1942, text-figs 71, 72), from Beacon 624.

mate whorl is poorly preserved. Sharp bullae give rise to pairs of ribs, and there are well-developed lateral tubercles. On the outer whorl, 20 strong ribs arise on the umbilical wall and strengthen into strong, high bullae that migrate outwards progressively to an umbilicolateral position. They give rise to pairs of strong, high, rursiradiate ribs with a well-developed conical-bullate lateral tubercle and an equal to slightly weaker bullate inner ventrolateral tubercle. These give rise to strong ribs that link to a small but well-differentiated outer ventrolateral clavus, separated from the siphonal keel by smooth zone. The ribs are near-transverse on the venter, forming a very obtuse ventral chevron. On the adapertural half whorl, 10 umbilical bullae correspond to 19 ribs at the ventrolateral shoulder. Spiral ridges are best-preserved on the ventrolateral shoulders. The good definition of the outer ventrolateral tubercles is distinctive.

The holotype of *Pervinquieria* (*Styphloceras*) *clivosa* van Hoepen, 1942 (p. 107, text-figs 81–85), SAM PCZ 19269 (ex D.870) (Text-fig. 8), is an adult retaining a 270° of body chamber; when complete it had an estimated diameter of 180–190 mm. The specimen has been coated with emulsion paint by a previous worker, blurring the fine surface detail. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19269 c ic	155.0 (100)	56.3 (36.3)	57.8 (37.3)	0.97	69.6 (44.9)
		49.6 (32.0)	57.8 (37.3)	0.86	

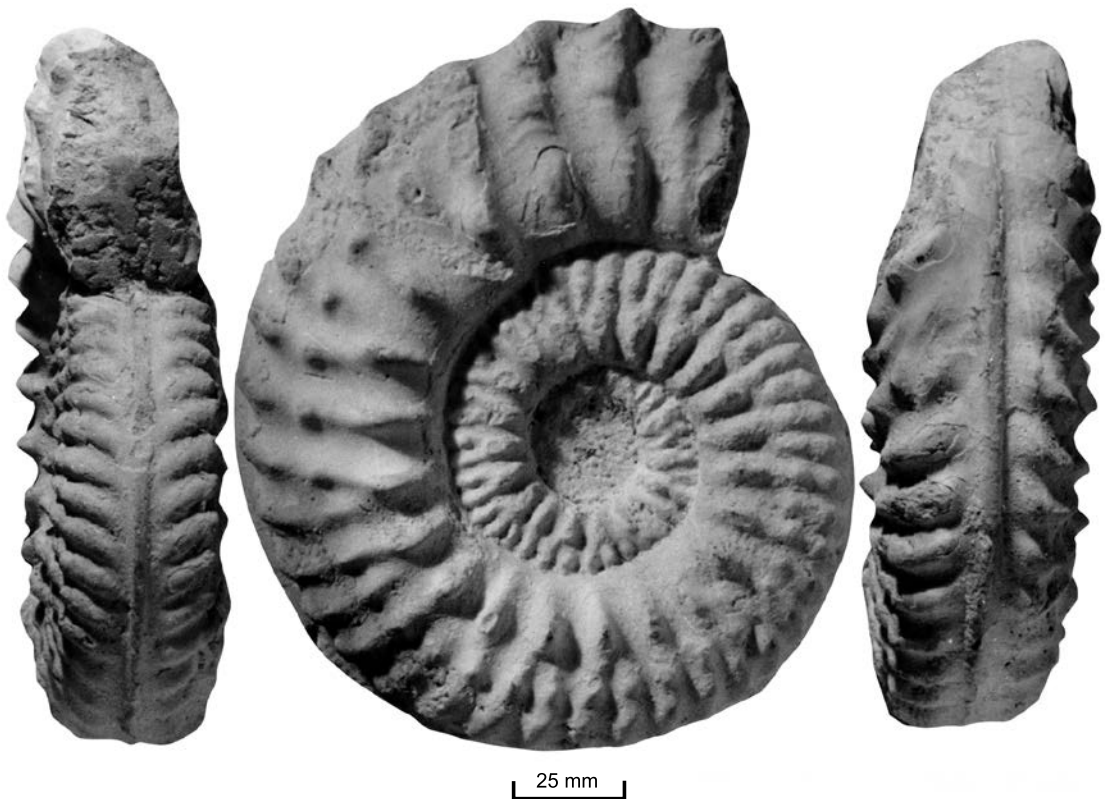
Coiling is very evolute. On the penultimate whorl the umbilicus, of moderate depth, has a feebly convex subvertical wall and broadly rounded umbilical shoulder. Ten ribs arise at the umbilical seam of the

adapertural half whorl, strengthen across the umbilical wall and shoulder, and develop into strong umbilical bullae that give rise to pairs of coarse rursiradiate ribs, 22 on the outer flank, with a well-developed rounded lateral tubercle. On the outer whorl, the intercostal whorl section is slightly compressed, with the greatest breadth low on the feebly convex flanks, the ventrolateral shoulders broadly rounded, the venter feebly convex. The greatest breadth is at the umbilical bullae in costal section. At the adapical end of the outer whorl four coarse primary ribs strengthen across the umbilical wall and shoulder, developing into strong conical-bullate umbilical tubercles that give rise to pairs of coarse ribs. Beyond this, the ribs are predominantly single bullate primaries, together with two non-bullate primaries and a single long intercalated rib, the ribs rursiradiate and straight, with a strong conical-bullate lateral tubercle. At the adapical end of the outer whorl, a coarse conical-rounded inner ventrolateral tubercle gives rise to a broad transverse rib that broadens progressively and terminates without reaching the siphonal keel. On the body chamber there are strong conical ventrolateral tubercles, separated from the keel by a broad smooth zone. There are traces only of spiral ridges, a reflection of the poor preservation and the coating of emulsion paint. To the adapical part of the body chamber this specimen resembles the holotype of *ordinatocostata*, but beyond this, ventrolateral tuberculation is distinctive, transverse, rather than forming an obtuse chevron.

SAM PCZ 19439 (ex D.2900) (Text-fig. 9) is the original of van Hoepen (1951, fig. 330), which he assigned to *clivosa*. It is an adult, complete to the base of the rostrum, and differs in no significant respects from the holotype. On the penultimate whorl, eighteen strong umbilical bullae give rise to pairs of ribs with rounded-bullate lateral tubercles. There are 29–30 rursiradiate ribs at the ventrolateral shoulder of the outer whorl, arising in pairs from the umbilical bullae on the penultimate whorl and adapical part of the outer whorl. On the adapertural part of the outer whorl the ribs are single, with progressively weakening umbilical bullae, the lateral tubercle effacing on the last few ribs.

The holotype of *Pervinquieria* (*Styphloceras*) *apta* van Hoepen, 1951 (p. 302, text-figs 331–333), SAM PCZ 19440 (ex D.2795) (Text-fig. 10D–F) retains limonitised shell, the surface battered and pitted during preparation, obscuring details of the surface ornament. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19440 c	95.8 (100)	39.0 (37.4)	36.8 (38.4)	1.1	37.7 (39.4)



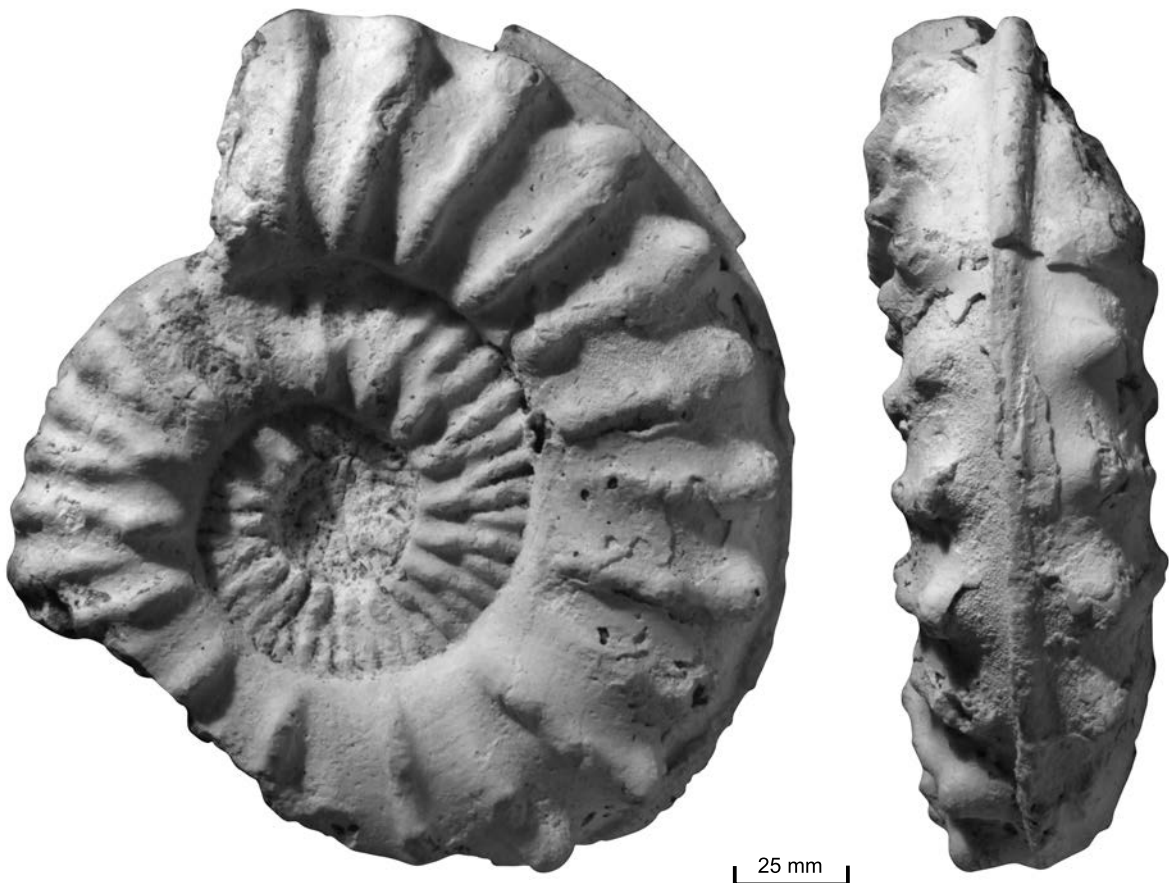
Text-fig. 7. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. The holotype of *Pervinquieria* (*Styphloceras*) *ordinatocostata* van Hoepen, 1942, SAM PCZ 19268 (ex D.2399), the original of van Hoepen (1942, p. 103, text-figs 77–79), from Beacon 624.

Coiling is evolute, the umbilicus comprising 39.4% of the diameter, of moderate depth, with a feebly convex subvertical wall and broadly rounded umbilical shoulder. The whorl section is trapezoidal in intercostal section, with broadly rounded ventrolateral shoulders, a flattened venter, and a strong siphonal keel. The greatest breadth is at the umbilical bullae in costal section. Eighteen to nineteen ribs arise at the umbilical seam of the outer whorl, strengthen across the umbilical wall and shoulder and develop into coarse, conical umbilicolateral bullae. The bullae give rise to pairs of coarse, feebly prorsiradiate primary ribs, and there are additional intercalated ribs to give a total of 40–42 per whorl at the ventrolateral shoulder. The ribs are crowded, straight and prorsiradiate, with a well-developed rounded-conical lateral tubercle and a rounded-bullate inner ventrolateral tubercle. The inner ventrolateral tubercles give rise to a coarse, broad, prorsiradiate expanding rib that declines and effaces before reaching the siphonal keel, from which they are separated by a narrow smooth zone.

The holotype of *Pervinquieria* (*Styphloceras*) *cognata* van Hoepen, 1951 (p. 304, text-figs 334–337), SAM PCZ 19441 (ex D.2796) (Text-fig. 11) retains extensive areas of recrystallized shell and is in part body chamber. Details are obscured by a coating of emulsion paint. The maximum preserved diameter is 175 mm approximately. Dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19441 at	136.1 (100)	55.3 (40.6)	51.2 (37.6)	1.1	56.0 (41.1)

Coiling is evolute, with 37% of the previous whorl covered. The umbilicus comprises 41.1% of the diameter and is of moderate depth with a broadly convex, subvertical umbilical wall and a broadly rounded umbilical shoulder. The whorl section is depressed trapezoidal in intercostal section, with broadly rounded ventrolateral shoulders and a broad, flattened venter with a strong siphonal keel. Eleven ribs arise at the umbilical seam of the adapertural half of the penultimate whorl, strengthen across the umbilical wall and shoulder, developing into strong, conical umbilical bullae. These give rise to pairs of coarse straight ribs,



Text-fig. 8. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. The holotype of *Pervinquieria* (*Styphloceras*) *clivosa* van Hoepen, 1942, SAM PCZ 19269 (*ex* D.870), the original of van Hoepen (1942, p. 107, text-figs 81–85). The locality given by van Hoepen (1942, p. 107) translates as from the “Upper reaches of the creek that flows into the second northerly bend of the Mzinene, east of the causeway (drift)”, i.e., at his Beacon 624.

with occasional single bullate primary ribs, to give a total of 17 ribs on the outer flank, all bearing strong conical to feebly bullate lateral tubercles. There are 24 ribs on the umbilical wall of the outer whorl. They strengthen across the wall and shoulder and develop into strong bullae on the adapertural half of the outer whorl that give rise to pairs of straight, feebly prorsiradiate ribs, with occasional single bullate primaries. On the adapertural half of the outer whorl, paired ribs persist, with single primaries with bullae of variable strength becoming more numerous. The ribs bear progressively strengthening conical-rounded lateral and rounded-bullate inner ventrolateral tubercles. These give rise to a broad, coarse ventral rib, differentiated into a feebly clavate outer ventrolateral tubercle that sweeps forwards in a distinct ventral chevron, effaces, the rib terminations separated from the siphonal keel by a narrow smooth zone. Spiral

ridges are developed over all of the surface of the shell and are most conspicuous on the lateral tubercle and ventrolateral shoulder. It is interpreted as a densicostate variant showing coarsening of ornament on the adult body chamber.

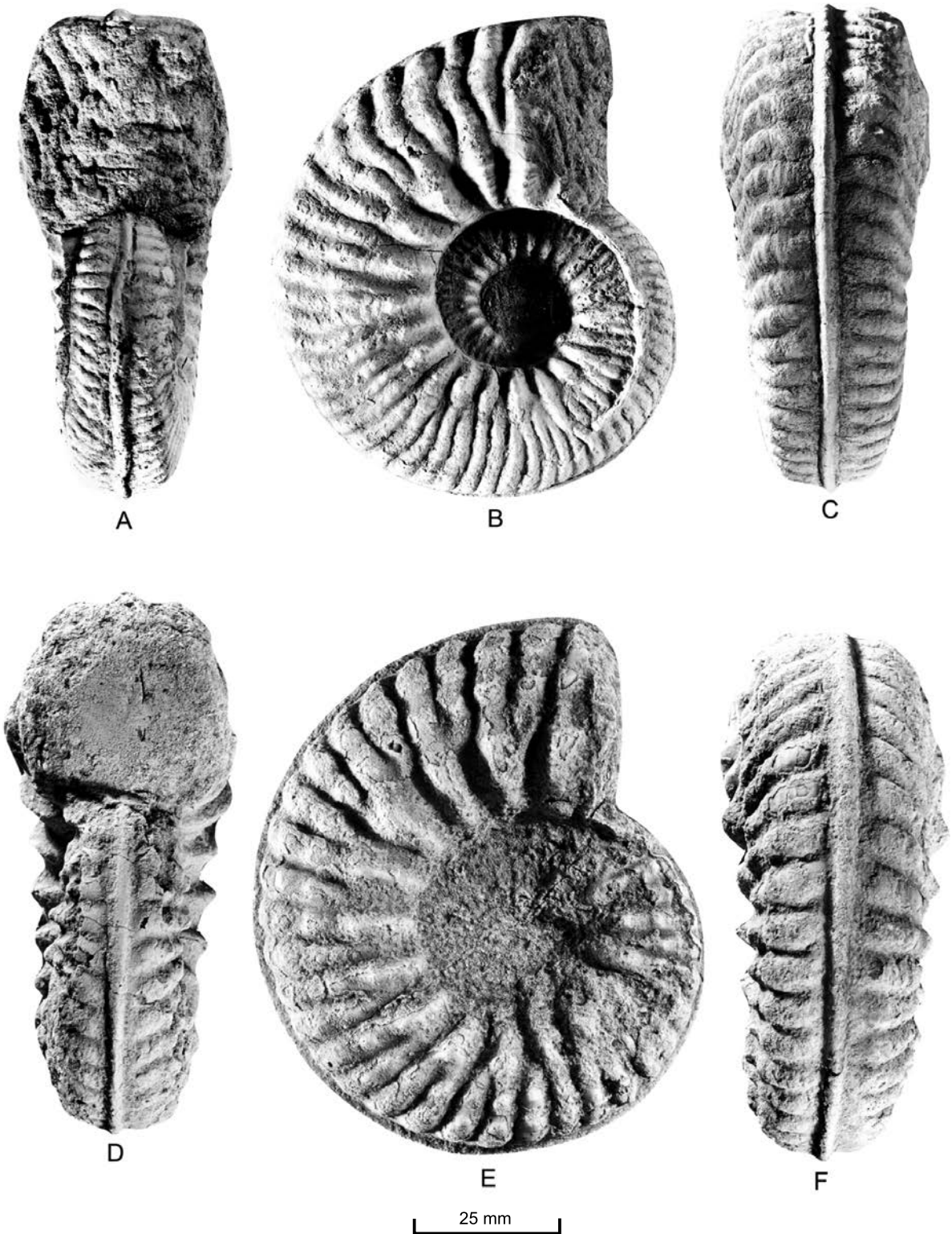
The holotype of *Pervinquieria* (*Styphloceras*) *propinqua* van Hoepen, 1951 (p. 306, text-figs 338–340), SAM PCZ 19329 (*ex* D.2797) (Fig. 12E–G), is a juvenile retaining exfoliated shell material. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19329 c	56.5 (100)	25.0 (44.2)	23.1 (40.9)	1.1	21.2 (37.5)

Coiling is evolute, the umbilicus of moderate depth, comprising 37.5% of the diameter. The umbilical wall is feebly convex and subvertical, the umbilical shoulder broadly rounded. The whorl section is trapezoidal with broadly rounded ventrolateral



Text-fig. 9. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942. SAM PCZ 19439 (ex D.2900), the original of *Pervinquieria* (*Styphloceras*) *clivosa* van Hoepen, 1942, original of van Hoepen (1951, p. 301, text-fig. 330), from the Upper End of Runlet which joins the Umsinene River at Beacon 624.



Text-fig. 10. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. A–C – The holotype of *Pervinquieria (Collignonia) vallifera* van Hoepen, 1951, SAM PCZ 19325 (ex D.2789), the original of van Hoepen (1951, p. 297, text-figs 317–319), from Beacon 624. D–F – SAM PCZ 19440 (ex D.2795), the holotype of *Pervinquieria (Styphloceras) apta* van Hoepen, 1951, the original of van Hoepen (1951, p. 302, text-figs 331–333), from Beacon 624.



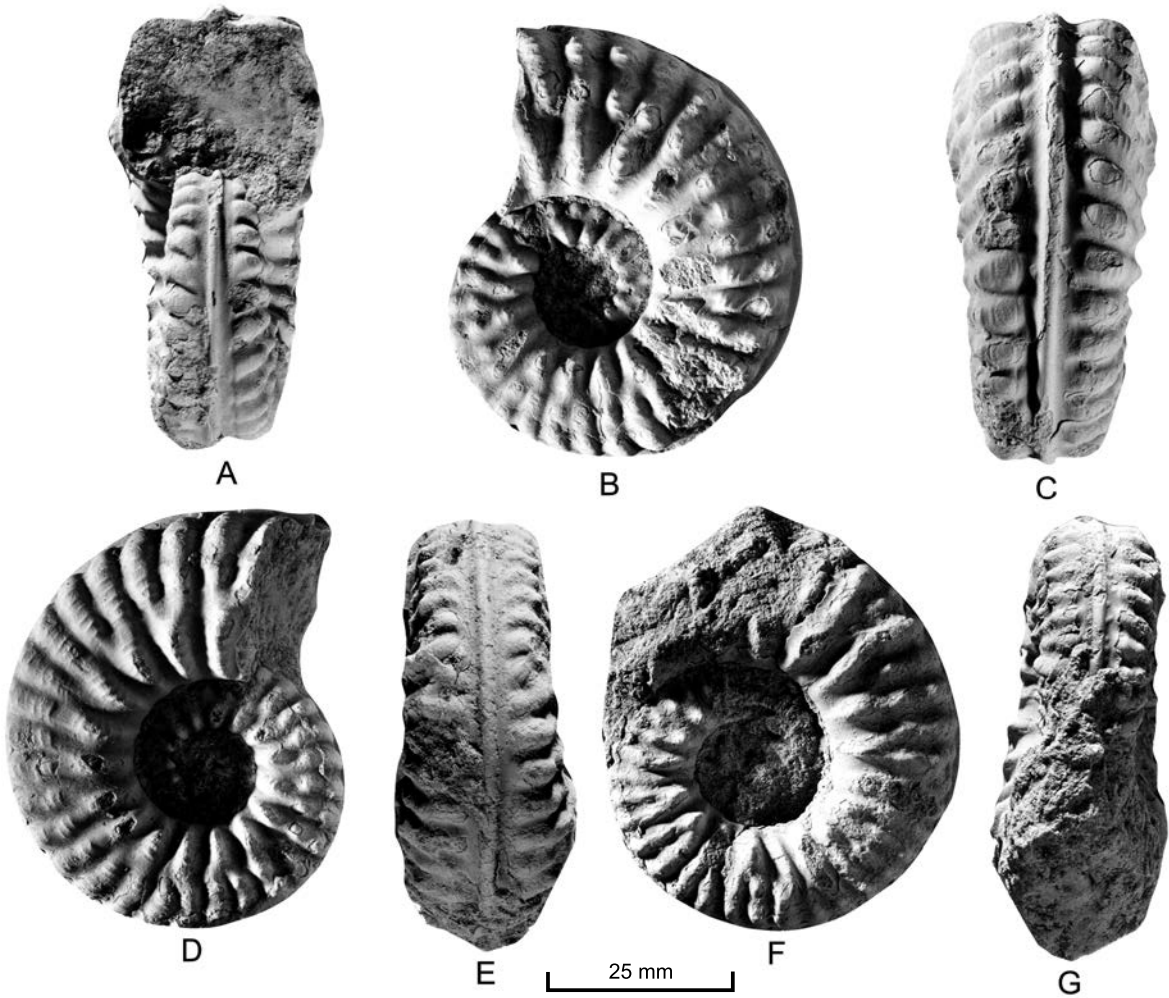
Text-fig. 11. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942. SAM PCZ 19441 (ex D.2796), the holotype of *Pervinquieria* (*Styphloceras*) *cognata* van Hoepen, 1951, the original of van Hoepen (1951, p. 304, text-figs 334–347), from Beacon 624.

shoulders and a broad, flattened venter with a strong siphonal keel. The greatest breadth is at the umbilical bullae in costal section. There are an estimated 20 umbilical bullae on the outer whorl that give rise to pairs of feebly prorsiradiate ribs, together with single bullate primaries and long intercalated ribs. On the adapertural half of the outer whorl there are 11 umbilical bullae and 20 ribs at the ventrolateral shoulder. All ribs bear a rounded-bullate lateral tubercle and an inner ventrolateral tubercle that gives rise to a broad transverse rib that links to a feebly clavate outer ventrolateral tubercle. The siphonal keel is flanked by narrow smooth zones.

The holotype of *Pervinquieria* (*Styphloceras*) *vicina* van Hoepen, 1951 (p. 307, text-figs 341–343) is SAM PCZ 19330 (ex D.2798) (Text-fig. 12A–D). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19330 c	59.1 (100)	28.7 (48.6)	26.9 (45.5)	1.1	20.8 (35.2)

Coiling is evolute, the umbilicus comprising 35.2% of the diameter, of moderate depth, with a feebly convex umbilical wall and broadly rounded umbilical shoulder. The whorl section is depressed trapezoidal, with broadly rounded ventrolateral shoulders, a broad, flattened venter and strong siphonal keel. Eighteen ribs arise at the umbilical seam of the outer whorl and strengthen across the umbilical wall and shoulder, developing into a small umbilicolateral bulla. The bullae give rise to pairs of ribs, with both single bullate primaries and intercalated ribs to give a total of an estimated 32–34 ribs at the ventrolateral tubercle. The ribs are straight and prorsiradiate, broaden across the flanks and bear a coarse rounded lateral and inner ventrolateral tubercle. The inner ventrolateral tubercles give rise to a broad rib that passes straight across the venter, the rib terminations separated from the siphonal keel by a narrow smooth zone. There are no outer ventrolateral tubercles. Spiral ridges are



Text-fig. 12. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942. A–D – The holotype of *Pervinquieria (Styphloceras) vicina* van Hoepen, 1951, SAM PCZ 19330 (ex D.2798), the original of van Hoepen (1951, p. 307, text-figs 341–343), from Beacon 624. E–G – The holotype of *Pervinquieria (Styphloceras) propinqua* van Hoepen, 1951, SAM PCZ 19329 (ex D.2797), the original of van Hoepen (1951, p. 306, text-figs 338–340), from Beacon 624.

well-developed over all of the well-preserved surface of the shell.

The holotype of *Pervinquieria (Styphloceras) familiaris* van Hoepen, 1951 [p. 300, text-fig. 344 = *Pervinquieria multicostata* van Hoepen, 1942, p. 99 (*pars*), text-figs 69, 70], is SAM PCZ 19442 (ex D.2395) a juvenile retaining well-preserved nacreous shell (Text-fig. 15A–C). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19442 c	74.9 (100)	31.2 (41.7)	27.8 (37.1)	1.1	30.4 (40.6)

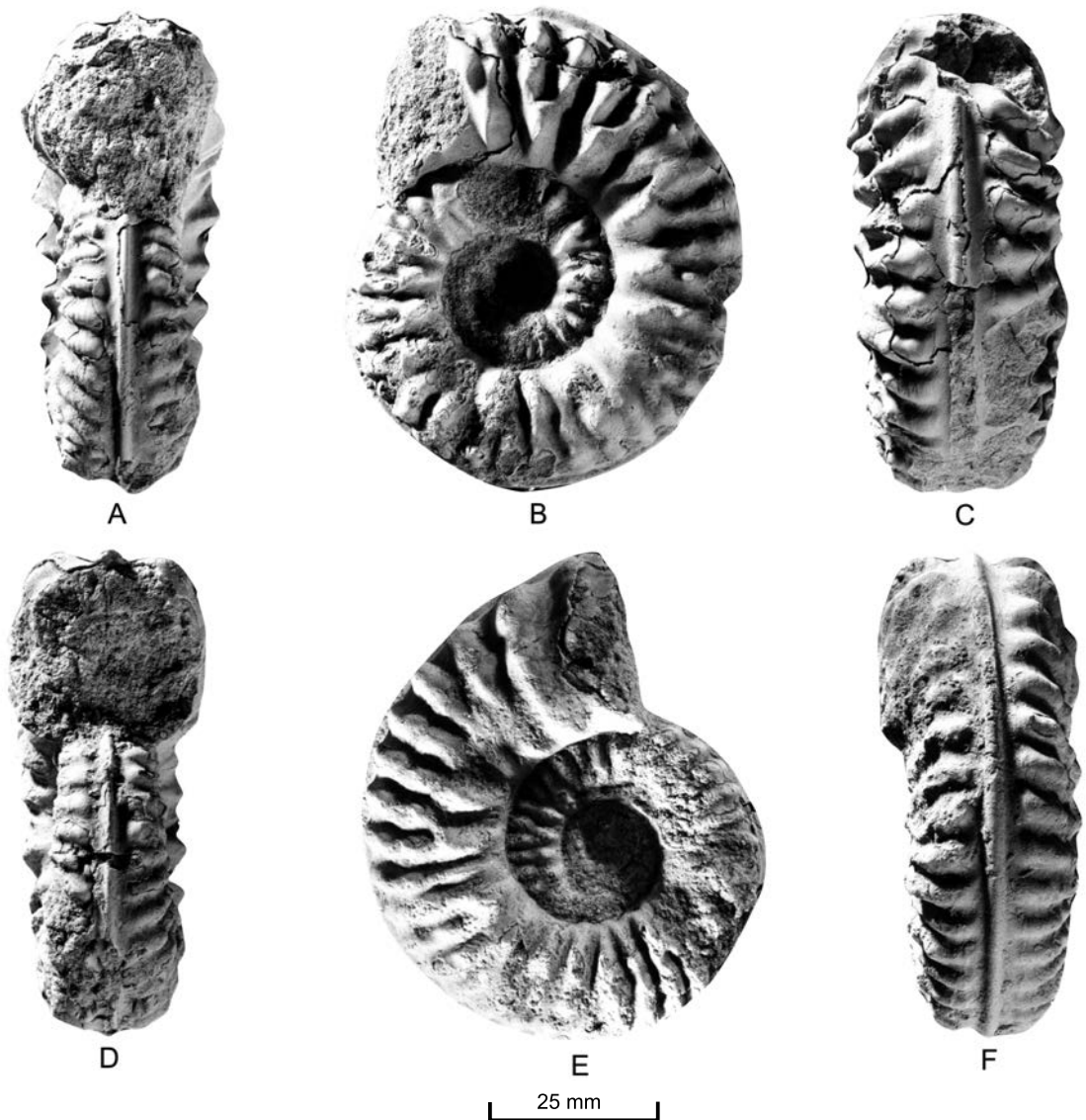
There are 21–22 umbilical bullae on the outer whorl and 38–40 ribs at the ventrolateral shoulder. There is a well-developed rounded-conical lateral tu-

bercle, a well-developed rounded-conical inner ventrolateral tubercle and no, or only an incipient outer ventrolateral tubercle. The surface of the shell is covered in well-developed spiral ridges.

The holotype of *Pervinquieria (Styphloceras) latiumbilicata* van Hoepen, 1951 (p. 309, text-figs 345, 346), SAM PCZ 19331 (ex D.2802) is a badly corroded juvenile the shell surface pitted and detail lost (Text-fig. 14). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19331 c	95.6 (100)	33.9 (35.5)	31.2 (32.6)	1.1	44.1 (46.1)

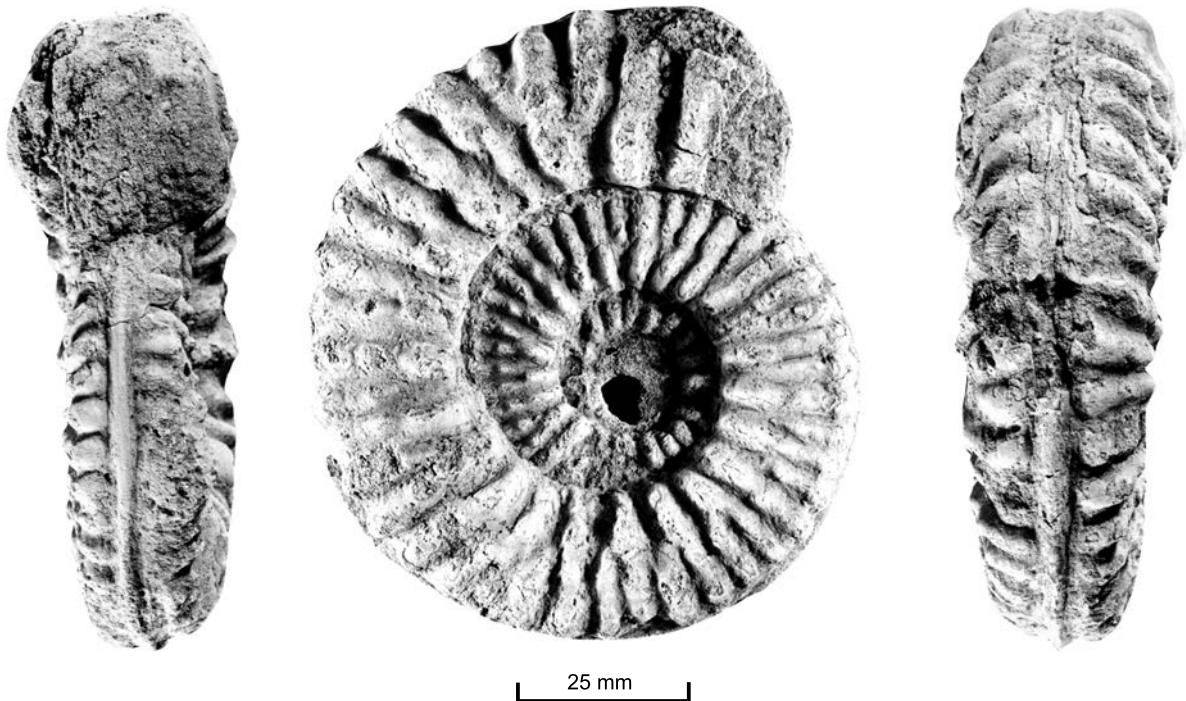
Coiling is very evolute, the umbilicus broad and shallow, comprising 46.1% of the diameter, with a feebly convex umbilical wall and broadly rounded



Text-fig. 13. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. A–C – The holotype of *Pervinquieria (Styphloceras) latidorsata* van Hoepen, 1951, SAM PCZ 19444 (ex D.2808), the original of van Hoepen (1951, p. 311, text-figs 350–352), from Beacon 624. D–F – the holotype of *Pervinquieria (Styphloceras) bulbifera* van Hoepen, 1951, SAM PCZ 19335 (ex D.2810), the original of van Hoepen (1951, p. 313, text-figs 353–356), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

umbilical shoulder. The whorl section is trapezoidal, with broadly rounded ventrolateral shoulders in intercostal section, the costal whorl section depressed, with the greatest breadth at the umbilical bullae. Twelve ribs arise on the umbilical wall of the adapertural half of the penultimate whorl and are strong and crowded on the umbilical wall, strengthening into small bullae, perched on the umbilical shoulder. The bullae give rise to pairs of crowded straight prorsiradiate ribs, 20 on the outer flank of the half

whorl, with well-developed rounded-conical lateral tubercles. On the outer whorl, 24 ribs arise at the umbilical seam, strengthen across the umbilical wall and shoulder, developing into progressively coarsening bullae, perched on the umbilical shoulder. They give rise to pairs of progressively strengthening coarse rounded-conical lateral tubercles. A strong rib links these to a subequal rounded inner ventrolateral tubercle from which a broad rib extends near-transverse across the venter, bearing a moderately differentiated



Text-fig. 14. *Pervinquieria* (*Pervinquieria*) *nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19331 (ex D.2802), the holotype of *Pervinquieria* (*Styphloceras*) *latiumbilicata* van Hoepen, 1951, the original of van Hoepen (1951, p. 309, text-figs 345, 346), from Beacon 624.

outer ventrolateral clavus. The rib terminations are separated from the siphonal keel by a narrow smooth zone. There are also long bullate and non-bullate single ribs, to give a total of 39–40 ribs at the ventrolateral shoulder. The evolute coiling is distinctive, as is the differentiation of the outer ventrolateral tubercles.

The holotype of *Pervinquieria* (*Styphloceras*) *necessaria* van Hoepen, 1951 (p. 310, text-figs 347–349) is SAM PCZ 19332 (ex D.2807) (Text-fig. 15D–F) retains original aragonitic shell; the original estimated diameter is 87 mm. Dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19332 c at	68.4 (100)	30.5 (44.6)	28.9 (42.3)	1.06	24.5 (35.8)

A massive-whorled individual, coiling is evolute, the umbilicus comprising 35.8% of the diameter, the umbilical wall feebly convex, the umbilical shoulder broadly rounded. The whorl section is trapezoidal in intercostal section with broadly rounded ventrolateral shoulders and a broad, flattened venter bearing a strong siphonal keel. Sixteen ribs arise on the umbilical wall of the penultimate whorl, strengthen across the umbilical wall and shoulder and link

to conical bullae, perched on the umbilical shoulder. The bullae give rise to pairs of prorsiradiate ribs that bear well-differentiated lateral tubercles; there are 30 ribs on the outer flanks of the penultimate whorl. On the outer whorl, seventeen primary ribs strengthen into conical-bullate umbilical tubercles that increase markedly in strength around the whorl, and migrate outwards to an umbilicolateral position. The bullae give rise to pairs of ribs that are coarse and rounded, strengthen progressively across the flank and bear progressively strengthening rounded lateral tubercles and rounded inner ventrolateral tubercles. Broad feebly prorsiradiate to near-transverse ribs extend across the ventrolateral shoulders and develop incipient outer ventrolateral tubercles. The ribs are separated from the siphonal keel by a smooth zone. Spiral ridges are conspicuous on outer flanks and ventrolateral shoulders.

The holotype of *Pervinquieria* (*Collignonia*) *valdifera* van Hoepen, 1951b (p. 297, text-figs 317–319), SAM PCZ 19325 (ex D.2789) (Text-fig. 10A–C), retains limonitised shell, and there are indications of the former presence of a further 120° whorl sector.



Text-fig. 15. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. A–C – SAM PCZ 19442 (ex D.2395) The holotype of *Pervinquieria (Styphloceras) familiaris* van Hoepen, 1951, the original of van Hoepen (1942, text-figs 69, 70; where it was regarded as an example of *Pervinquieria multicostata* van Hoepen, 1942; and 1951, p. 308, text-fig. 344), from Beacon 624. D–F – SAM PCZ 19332 (ex D.2807), the holotype of *Pervinquieria (Styphloceras) necessaria* van Hoepen, 1951, the original of van Hoepen (1951, p. 310, text-figs 347–349), from Beacon 624.

Twenty one bullae perch on the umbilical shoulder of the outer whorl, and there are 51–52 ribs at the ventrolateral shoulder. The ribs are crowded, recti-to feebly rursiradiate, arising in pairs from the bullae and occasionally bifurcating; there are additional

long intercalated ribs. The ribs strengthen across the flanks, and bear a conical to feebly bullate lateral tubercle, from which the ribs broaden, thicken and are feebly concave on the outer flanks, linking to a broad spatulate rib termination that is near-transverse on



Text-fig. 16. *Pervinquieria (Pervinquieria) nodosocostata* van Hoepen, 1942 from KwaZulu-Natal, South Africa. SAM PCZ 19443 (ex D.2799), mentioned by van Hoepen (1951, pp. 308, 309) under *Pervinquieria (Styphloceras) familiaris* van Hoepen, 1951, from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

the venter, and differentiated into a conical inner ventrolateral tubercle on the adapertural 90° sector of the outer whorl. Spiral ridges are well-developed, notably on the ventrolateral shoulders.

DISCUSSION: The flank ornament of phragmocones with umbilicolateral bullae giving rise to pairs of ribs in a distinctive Y pattern links coarsely ornamented individuals (Text-figs 2–5) to the holotype of *nodosocostata* (Text-fig. 6), and others with ornament of intermediate strength (Text-fig. 1) to those with crowded, weaker ornament (Text-figs 10, 14). The holotype of *Pervinquieria (Collignonia) vallifera* van Hoepen, 1951 (Text-fig. 10A–C), described above, has exactly this pattern of flank ornament, comes from the same locality as many of van Hoepen’s *Styphloceras* spp., and we regard it as a synonym (compare for example Text-figs 10A–C and 10D–E). The abrupt termination of ribs on the venter at the smooth zones that flank the siphonal keel produces what we have described as an incipient to weak tubercle in some but not all of the specimens we assign to *nodosocostata*. They are very different from the well-developed and consistently developed outer ventrolateral tubercles of *Pervinquieria*

(*Subschloenbachia*) Spath, 1922 (see Kennedy *et al.* 1998; Kennedy and Latil 2008). Such an incipient outer ventrolateral tubercle is also developed for a very short interval at the adapical end of the outer whorl of the holotype of *Pervinquieria (P.) inflata* (J. Sowerby, 1818) (Gale and Kennedy 2020, p. 40, pl. 11, figs 4–6), but this specimen does not develop the striking Y-shaped ribbing of *vallifera* of the same size (Text-fig. 10A–F). Adult *inflata* (Amédro and Matrimon in Amédro *et al.* 2004, p. 16, pls 3–8) do not develop pairs of ribs arising from the umbilical bullae that is such a striking feature of specimens assigned to *vallifera*.

Mortoniceras (Pervinquieria) velliferum van Hoepen of Collignon (1979, p. 26, pl. 10, fig. 2), from Angola lacks the distinctive Y-shaped pattern of flank ribbing and the lateral tubercle of the holotype of *vallifera* (Text-fig. 10A–C), and may be a *Prohysteroceas* Spath, 1921.

OCCURRENCE: Upper Albian of northern KwaZulu-Natal, South Africa.

Acknowledgements

WJK acknowledges the support of the staff of the Earth Collections of the Oxford University Museum of Natural History and David Sansom formerly of the Department of Earth Sciences, Oxford. Field work and museum study in South Africa was supported by the Strakosch Bequest and the Oppenheimer Fund. HCK acknowledges financial assistance from the NRF (South Africa) and technical assistance from Samantha Black, formerly of the Natural History Department, Iziko, South African Museum. We thank reviewers Frank Wiese and Francis Amédro for their comments on the original manuscript, and Anna Żylińska for editorial guidance.

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Manuscript submitted: 4th November 2025

Revised version accepted: 9th February 2026