

On the ammonite genus *Ophryoceras* van Hoepen, 1942, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, from the Upper Albian of KwaZulu-Natal, South Africa

WILLIAM JAMES KENNEDY¹ and HERBERT CHRISTIAN KLINGER†

¹ Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, U.K.;
e-mail: jim.kennedy@oum.ox.ac.uk
†deceased

ABSTRACT:

Kennedy, W.J. and Klinger, H.C. 2025. On the ammonite genus *Ophryoceras* van Hoepen, 1942, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, from the Upper Albian of KwaZulu-Natal, South Africa. *Acta Geologica Polonica*, **75** (2), e46.

The type, figured and cited material of thirteen species assigned by van Hoepen (1942, 1946) to his genus *Ophryoceras*, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910, are described and illustrated, and shown to be a single variable Late Albian ammonite species. *Pervinquieria salebrosa* van Hoepen, 1942 is a further synonym. Van Hoepen (1946) referred a series of fragments to *Ophryoceras* sp. under four separate entries. We have not seen this material which we refer to as ?*Ophryoceras* spp. (a)–(d); they may be further synonyms of *salebrosa*.

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

HERBIE KLINGER – AN APPRECIATION

Herbert Christian Klinger died unexpectedly on the 5th of July 2024. We first met in the summer of 1970, and this marked the beginning of a friendship and collaboration that was to extend over 54 years. I had become interested in the Cretaceous faunas of KwaZulu-Natal (Zululand and Natal as they were then known) from encountering specimens in the London Natural History Museum described by Baily, Crick, Spath, and others. Of particular interest was cephalopod material collected by F.W. Anderson, the one-man Geological Survey of Natal and Zululand from what was described as “*the deposit at the north end of False Bay, Zululand.*” This included a range of Cenomanian ammonites clearly related to material from the Lower Chalk of southern England I had studied as part of my doctoral thesis. Field work in KwaZulu-Natal and Western Cape Province (then the

Transkei) in 1970 and 1971 led to our documenting over 150 localities spanning intervals from Barremian to Cenomanian and Coniacian to Maastrichtian (the Turonian is absent at outcrop).

Field work, much of it carried out in game reserves and on the cliffs of Lake St Lucia was not without incident, including encounters with crocodiles, hippos, and wart hogs and near encounters with Black Rhinos.

In all, our names appear together on over 80 publications, with coauthors including Jost Wiedmann and Mikhail Kakabadze on ammonites, Niall Mateer on a theropod dinosaur (bits of which we discovered in the bed of Lake St Lucia) and Irek Walaszczyk on inoceramids. Major contributions with Herbie as first author provided comprehensive accounts of the global species record of Placenticeratidae, Texanitinae and others; the 2001 account of the Baculitidae, with its annotated list of species referred to the family is a standard source.



Herbie began his career with the Geological Survey of South Africa in Pretoria, thereafter moving to the South African Museum in Cape Town, where he devoted his time to research, curation, editing, reviewing, and much else, as well as University teaching. I last met him there in late March and early February 2011, when we began the revision of the ammonites of the Subfamily Pervinquierinae of which this is a part.

It was a privilege to have known and worked with Herbie, without whose collaboration and friendship I would never have had the experiences and memories of exploring the Cretaceous rocks and fossils of the Zululand littoral, half a century ago now.

INTRODUCTION

In this contribution we continue our revision of the Upper Albian ammonites from northern KwaZulu-Natal, dealing with the species of *Ophryoceras* van Hoepen, 1942, a synonym of *Pervinquieria* (*Pervinquieria*) Böhm, 1910.

Repository of specimens

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).

Species	13	14	ERW	W	624
<i>Ophryoceras obesum</i>	*				
<i>Ophryoceras costatum</i>		*	*		
<i>Ophryoceras undosum</i>			*		
<i>Ophryoceras jugosum</i>				*	
<i>Ophryoceras tenuicostatum</i>				*	
<i>Ophryoceras annaalida</i>					*
<i>Ophryoceras crassinodatum</i>					*
<i>Ophryoceras crassum</i>					*
<i>Ophryoceras liberta</i>					*
<i>Ophryoceras obsoletum</i>					*
<i>Ophryoceras opimum</i>					*
<i>Ophryoceras spinosum</i>					*
<i>Ophryoceras tereticostatum</i>					*

Table 1. Distribution of species of *Ophryoceras* described by van Hoepen (1942) in his banks 13 and 14 at locality 51 of Kennedy and Klinger (1975) and successively stratigraphically higher localities to the east as cited by van Hoepen. Explanations: ERW – “Extension of Ridge West of Beacon 624, to the West into the valley and gradually higher westward”; W – “Ridge West of Beacon 624”; 624 – Beacon 624 and Runlet that joins the Umsinene River at Beacon 624.

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 *Pervinquieria* Böhm, 1910

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

DIAGNOSIS: See Kennedy and Klinger (2023b, p. 550).

DISCUSSION: The distinguishing features of *Pervinquieria sensu stricto* are the presence of umbilical and ventrolateral tubercles throughout ontogeny, and lateral tubercles for part or all of ontogeny, as discussed previously (Kennedy *et al.* 1998; Kennedy in Gale and Kennedy 2020; Kennedy and Klinger 2023b). In this account we describe and discuss the 13 species that van Hoepen (1942, 1946) assigned to his genus *Ophryoceras*, together with *Pervinquieria salebrosa* van Hoepen, 1942, which we regard as a further synonym. They come from the following localities as described by van Hoepen, and located by him in relation to Beacon 624 on the Mzinene (Umsinene) River, which corresponds to locality 54 of Kennedy and Klinger (1975, p. 288; see Kennedy and Klinger 2023a, text-fig. 1), and summarised in Table 1:

- *annaalida*: “at Beacon 624”;
- *costatum*: bank 14 at locality 51 of Kennedy Klinger (1975); “Extension of Ridge West of Beacon 624 to the West into the valley and gradually higher westward”;

- *crassum*: “loose near Beacon 625”; “Lower End of Runlet which joins the Umsinene River at Beacon 624”;
- *crassinodatum*: “Upper End of Runlet which joins the Mzinene River at Beacon 624”;
- *jugosum*: [ridge west of Beacon 624];
- *liberta*: “at Beacon 624”;
- *obesum*: bank 13 at locality 51 of Kennedy and Klinger (1975);
- *obsoletum*: “Upper End of Runlet which joins the Umsinene River at Beacon 624”;
- *opimum*: “Upper End of Runlet which joins the Umsinene River at Beacon 624”;
- *salebrosum*: “at Beacon 624”; this species was originally referred to *Pervinquieria* by van Hoepen;
- *spinsum*: “Upper End of Runlet which joins the Umsinene River at Beacon 624”;
- *tenuicostatum*: “Ridge West of Beacon 624”;
- *tereticostatum*: “at Beacon 624”; “Lower End of Runlet which joins the Umsinene River at Beacon 624”;
- *undosum*: “Extension of Ridge West of Beacon 624 to the West into the valley and gradually higher towards the West”.

It will be seen that these species come from a limited number of localities that are close to each other. Given the very low regional dips, they are interpreted as coming from a limited stratigraphic interval.

Van Hoepen (1946, pp. 237–237) also described, under four separate entries as *Ophryoceras* sp. what he regarded as four further species, based on fragments. We have not seen this material, which may represent further synonyms of *Pervinquieria* (*Pervinquieria*) *jugosa*; in the interests of clarity, we refer to these citations in the synonymy below as *Ophryoceras* sp. (a), (b), (c), and (d).

Ophryoceras was treated as a possible synonym of *Mortoniceras* (*Mortoniceras*) Meek, 1876, by Wright (1957, p. 406), and as an undoubted synonym by Wright (1996, p. L141) and more recently by Klein (2018), without discussion. This we provide.

The type species of *Ophryoceras*, by original designation, is *Ophryoceras jugosum* van Hoepen, 1942 (p. 93, text-figs 56–58). A translation of van Hoepen’s original diagnosis (1942, p. 91) is as follows:

“Family Drepanoceratidae van Hoepen 1941.

Genus *Ophryoceras* n. g.

Juvenile stages unknown. The earliest whorls present have weakly convex, high whorls with umbilical tubercles at the umbilical edge. Spiral ornament. No

old apertures seen on the available material. Ribs with umbilical tubercles on the early whorls, which can become weaker on older whorls. Furthermore, they have a weak tubercle on the flanks of old whorls. At the ventral side the ribs form a large, widened tubercle elongated in a spiral direction. Ribs and tubercles on the juvenile whorls fine; coarse on the older whorls.

Type *Ophryoceras jugosum* n.sp.

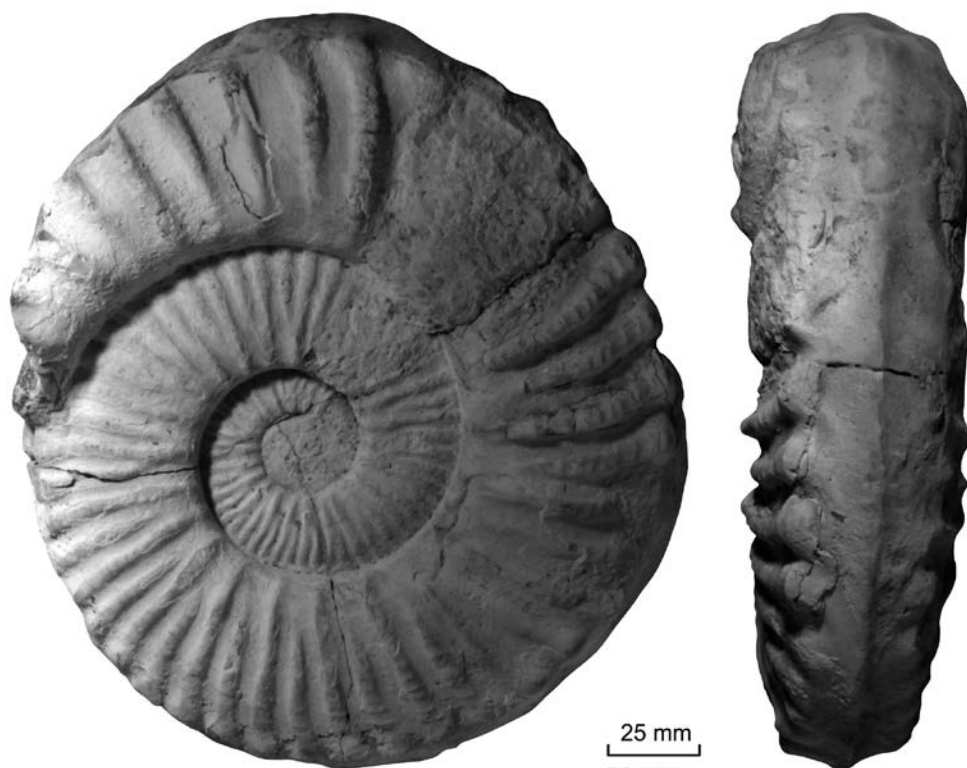
Seeing that the early whorls are not present there is no certainty that this genus belongs to the Drepanoceratidae, but there is no other group that has early whorls as flat, and minute tubercles at the edge of the umbilicus.

Differs from *Drepanoceras* by its ventral tubercles and its weakly convex flanks. Differs from *Angolaites* Spath by the tubercle-like thickening of the ribs at mid flank and by the presence of only a single ventral tubercle.”

The presence of spiral ridges indicates to us that *Ophryoceras* is distinct from *Mortoniceras* Meek, 1876; their presence is a feature of *Pervinquieria*, as discussed elsewhere (Kennedy in Gale and Kennedy 2020, p. 30; Kennedy and Klinger 2023b, p. 550). The presence of umbilical, lateral, and a single row of ventrolateral tubercles corresponds to the arrangement in *Pervinquieria* (*Pervinquieria*), rather than bituberculate *P.* (*Deiradoceras*) or quadrituberculate *P.* (*Subschloenbachia*), as discussed previously (Kennedy and Klinger (2023b, p. 550).

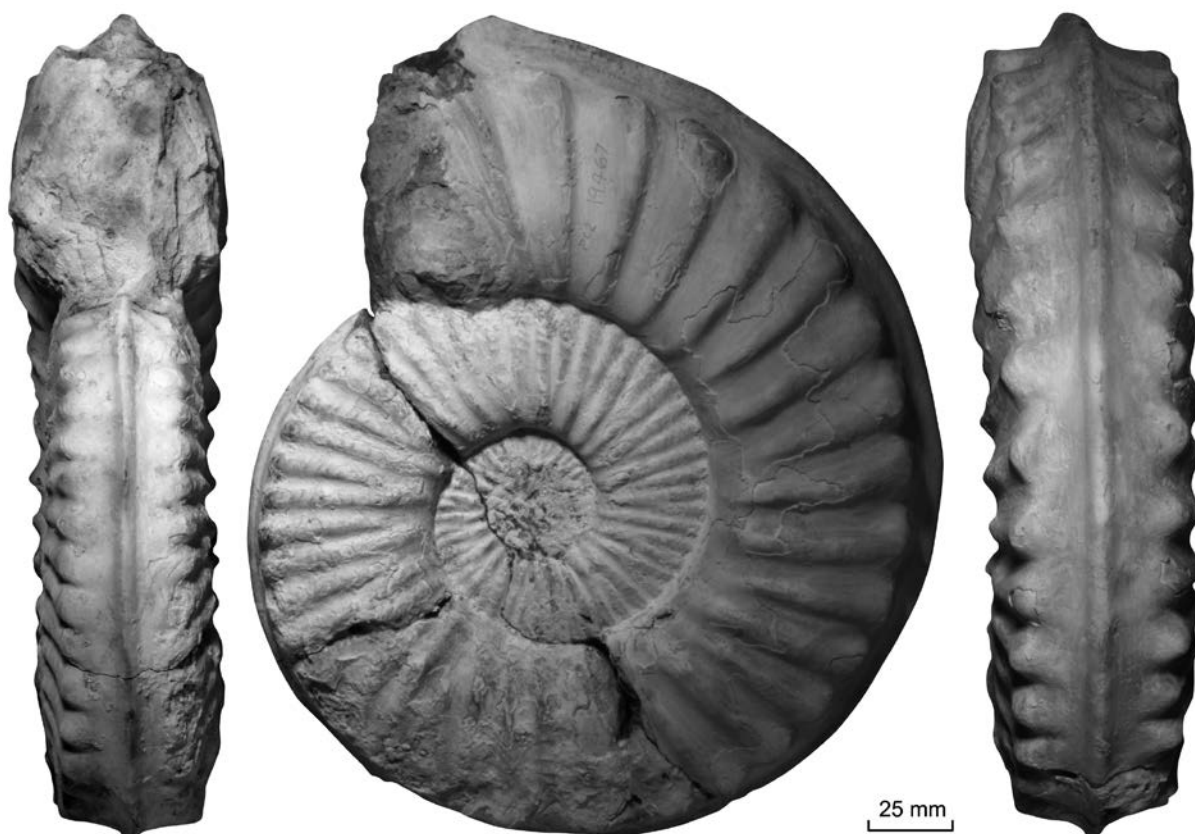
Pervinquieria (*Pervinquieria*) *jugosa*
(van Hoepen, 1942)
(Text-figs 1–17)

- ?1936. *Mortoniceras* (*Pervinquieria*) *curvatocostatum* Venz, p. 91 (33), pl. 8 (4), fig. 5, pl. 12 (8), fig. 2.
- 1942. *Ophryoceras jugosum* van Hoepen, p. 93, text-figs 56–58.
- 1942. *Ophryoceras costatum* van Hoepen, p. 93, text-figs 59, 60.
- 1942. *Pervinquieria salebrosa* van Hoepen, p. 113, text-figs 96–98.
- 1946. *Ophryoceras jugosum* van Hoepen; van Hoepen, p. 216, text-figs 200–204.
- 1946. *Ophryoceras costatum* van Hoepen; van Hoepen, p. 217.
- 1946. *Ophryoceras tenuicostatum* van Hoepen, p. 217, text-figs 205, 206.
- 1946. *Ophryoceras crassinodatum* van Hoepen, 1946, p. 219, text-figs 207, 208.



Text-fig. 1. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The holotype, SAM PCZ 19285 (ex D.789), the original of van Hoepen (1942, p. 93, text-figs 56–58), from the “Ridge West of Beacon 624”.

1946. *Ophryoceras crassum* van Hoepen, p. 221, text-figs 209, 210.
1946. *Ophryoceras spinosum* van Hoepen, p. 222, text-figs 211–215.
1946. *Ophryoceras anna-alida* van Hoepen, p. 225, text-figs 216–219.
1946. *Ophryoceras liberta* van Hoepen, p. 227, text-figs 220–222.
1946. *Ophryoceras opimuim* van Hoepen, p. 229, text-figs 223–225.
1946. *Ophryoceras tereticostatum* van Hoepen, p. 231, text-figs 226, 227.
1946. *Ophryoceras obsoletum* van Hoepen, p. 233, text-figs 228, 229.
1946. *Ophryoceras undosum* van Hoepen, p. 235, text-figs 230–232.
- ?1946. *Ophryoceras* sp. (a) van Hoepen, p. 237, text-figs 233, 234.
- ?1946. *Ophryoceras* sp. (b) van Hoepen, p. 237.
- ?1946. *Ophryoceras* sp. (c) van Hoepen, p. 237.
- ?1946. *Ophryoceras* sp. (d) van Hoepen, p. 238.
1963. *Mortoniceras* (*Ophryoceras*) *hoepeni* Collignon, p. 158, pl. 305, fig. 1309.
1963. *Mortoniceras* (*Ophryoceras*) *crassinodatum* van Hoepen var. *nicolaiae* Collignon, p. 164, pl. 308, fig. 1314.
1979. *Mortoniceras* (*Ophryoceras*) *liberta* van Hoepen; Collignon, p. 29, pl. 12, fig. 2, pl. 17, fig. 1.
2018. *Mortoniceras* (*Mortoniceras*) *annaalida* (van Hoepen, 1946); Klein, pp. 98, 103.
2018. *Mortoniceras* (*Mortoniceras*) *costatum* (van Hoepen, 1942); Klein, pp. 98, 105.
2018. *Mortoniceras* (*Mortoniceras*) *jugosum* (van Hoepen, 1941); Klein, p. 100.
2018. *Mortoniceras* (*Mortoniceras*) *crassinodatum crassinodatum* (van Hoepen, 1946); Klein, pp. 98, 105.
2018. *Mortoniceras* (*Mortoniceras*) *crassinodatum nicolaiae* Collignon, 1963; Klein, pp. 98, 105.
2018. *Mortoniceras* (*Mortoniceras*) *liberta* (van Hoepen, 1946); Klein, pp. 102, 116.
2018. *Mortoniceras* (*Mortoniceras*) *obsoletum* (van Hoepen, 1946); Klein, pp. 101, 118.
2018. *Mortoniceras* (*Mortoniceras*) *opimum* (van Hoepen, 1946); Klein, pp. 101, 118.
2018. *Mortoniceras* (*Mortoniceras*) *spinosum* (van Hoepen, 1946); Klein, pp. 102, 125.
2018. *Mortoniceras* (*Mortoniceras*) *tenuicostatum* (van Hoepen, 1946); Klein, pp. 102, 126.



Text-fig. 2. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). Paratype SAM PCZ 19467 (ex D.2590), the original of van Hoepen (1946, p. 216, text-figs 200–204), from the “Lower End of Runlet which runs into the Umsinene River at Beacon 624”.

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

TYPE: The holotype of *Ophryoceras jugosum*, by original designation, is SAM PCZ 19285 (ex D.789), the original of van Hoepen (1942, p. 93, text-figs 56–58) (Text-fig. 1), from the “Ridge West of Beacon 624”.

DESCRIPTION: As will be seen from the synonymy, we regard all of the species assigned to *Ophryoceras* by van Hoepen as a single variable species, the basic characters of which are: early whorls with crowded ribs that arise in pairs (occasionally in threes) from umbilical bullae, with additional ribs intercalating, stronger ventrolateral tubercles and an outer lateral tubercle that varies between individuals from poorly to well-differentiated. On the outer whorl, bullate primaries and long intercalated ribs alternate, and are prorsiradial and concave on the outer flanks. Towards the adult aperture the ribs become increasingly concave, and are predominantly bullate and non-bullate primaries.

The holotype of *Ophryoceras jugosum* (Text-fig. 1) is worn away on one side and on the venter; the body chamber extends to 240°. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ19285	210 (100)	– (–)	76.0 (36.2)	–	87.0 (41.4)

Coiling is very evolute, the umbilicus broad, comprising 41.4% of the diameter, of moderate depth, the umbilical wall vertical and feebly convex, the umbilical shoulder broadly rounded. The inner flanks are feebly convex, the outer flanks converging to broadly rounded ventrolateral shoulders, the venter fastigate, with a strong siphonal keel. The greatest breadth is at the umbilical bullae in costal section. An estimated 26 ribs per whorl arise at the umbilical seam and pass backwards across the umbilical wall and straight across the umbilical shoulder, where they strengthen into weak, elongate umbilical bullae. The bullae give rise to pairs of ribs (occasionally three), and additional ribs intercalate low on the flanks to

give a total of 50–54 at the ventrolateral shoulder, the ribs strengthening and broadening across the flanks. There are indications of a feeble outer lateral tubercle. On the outer whorl, the ornament modifies. Long, feebly bullate primary ribs alternate with long intercalated ribs that arise low on the flanks. The ribs strengthen across the flanks, and are prorsiradate, straight on the inner flank, flexing forwards and concave on the middle to outer flank. All ribs bear well-differentiated conical to feebly clavate ventrolateral tubercles. These give rise to a broadening and weakening rib that effaces before reaching the siphonal keel. Towards the adapertural end of the outer whorl the ribs become increasingly concave, and are predominantly primaries, both bullate and non-bullate. Spiral ridges are well-developed on flanks and ventrolateral shoulders.

SAM PCZ 19467 (ex D.2590) (Text-fig. 2), from the “Ridge West of Beacon 624”, is a paratype of *jugosum* (van Hoepen 1946, p. 216, text-figs 200–204). It is a near-complete adult with a maximum preserved diameter of 265 mm, a 180° sector of body chamber with the base of the terminal rostrum pre-

served. It retains extensive areas of shell material. The dimensions are:

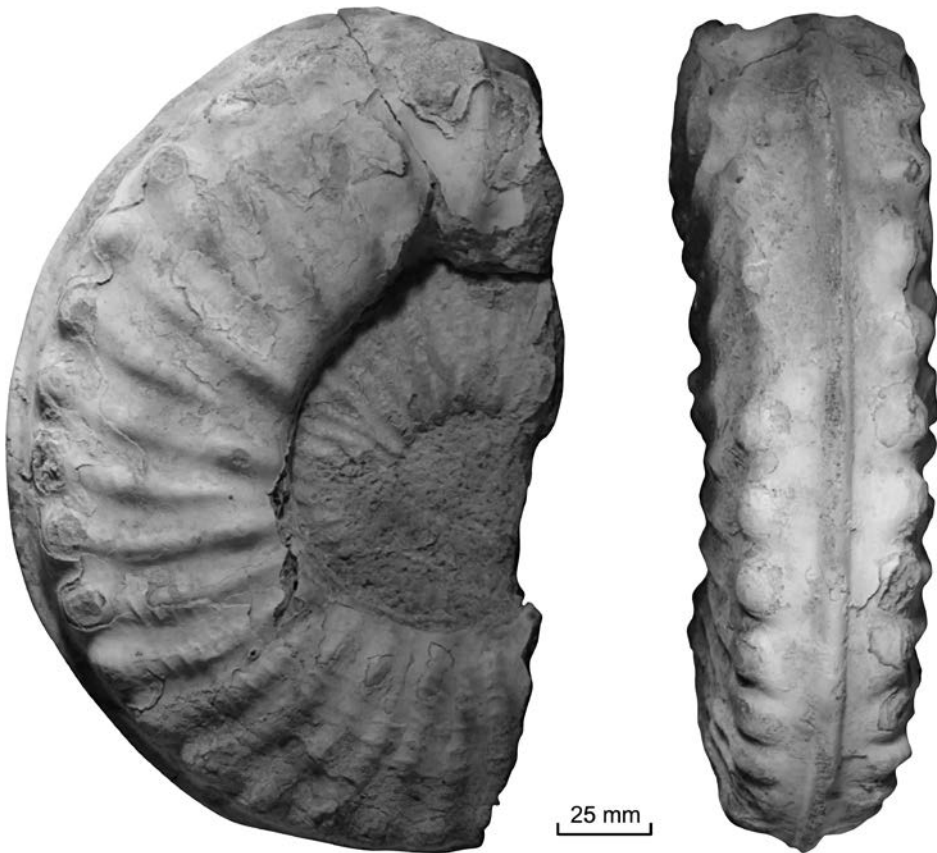
	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19467	At 216.0 (100)	64.2 (29.7)	86.9 (40.2)	0.74	111.5 (51.6)

It differs in no significant respects from the holotype.

SAM PCZ 19466 (ex D.644); SAM PCZ 19463 (ex D.2592) and SAM PCZ 19464 (ex D.2591) are further specimens from this general area.

SAM PCZ 19465 (ex D. 2595) (Text-fig. 3) found “loose on the Ridge West of Beacon 624”, was described by van Hoepen (1946, p. 217); it is no more than a coarsely ribbed variant, with a distinct thickening of the ribs into very elongate bullae on the outer flank.

The holotype, by original designation, of *Ophryoceras costatum*, SAM PCZ 19284 (ex D.644) is the original of van Hoepen (1942, p. 93, text-figs 59, 60), from bed 14 at locality 51. Only a part of the specimen survives (Text-fig. 4) of what was once a near-complete adult with a maximum preserved



Text-fig. 3. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). SAM PCZ 19465 (ex D.2595) “found loose on the Ridge West of Beacon 624”/locality 54, described by van Hoepen (1946, p. 217).



Text-fig. 4. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The surviving fragment of the holotype of *Ophryoceras costatum* van Hoepen, 1942, SAM PCZ 19284 (ex D.644), the original of van Hoepen (1942, p. 93, text-figs 59, 60), from bank 14 at locality 51.

diameter of 290 mm. It differs in no significant respects from specimens assigned to *jugosum* by van Hoepen, other than clearer accentuation of the ribs at mid-flank, a feature incipient in the type of *jugosum*. SAM PCZ 19462 (ex D.2596) mentioned in 1946 (p. 217) come from the “Extension of Ridge West of Beacon 624 to the West into the valley and gradually higher westward”, and is one of four fragments mentioned by van Hoepen; it is a phragmocone fragment with a maximum preserved whorl height of 57 mm.

The holotype of *Ophryoceras tenuicostatum* van Hoepen (1946, p. 217, text-figs 205, 206), SAM PCZ 19120 (ex D. 2597) is from the “Ridge West of Beacon 624”. It is a sector of the penultimate whorl and the apertural end of the body chamber with part of the ventral rostrum preserved (Text-fig. 5). It differs in no significant respects from SAM PCZ 19467 (ex D.2590) (van Hoepen 1946, text-fig. 200), assigned

to *jugosum* by van Hoepen, other than its greater original size, with a whorl height 95.3 mm before the increased whorl height associated with the development of the rostrum, versus 80 mm, perhaps a reflection of dimorphism.

The holotype of *Ophryoceras crassinodatum* van Hoepen, 1946 (p. 219, text-figs 207, 208), SAM PCZ 19119 (ex D.2598), is a superb specimen with silicified shell with indications of the former presence of a further 300° whorl sector (Text-fig. 6). It is from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”/locality 54. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19119 costal	195.0 (100)	58.1 (29.8)	67.9 (34.8)	0.86	71.3 (36.6)

The slight differences from other *Ophryoceras* species introduced by van Hoepen, the flatter venter and coarser tubercles, are regarded as within the limits of intraspecific variation.

The holotype of *Ophryoceras crassum* van Hoepen, 1946 (p. 221, text-figs 209, 210), is SAM PCZ 19118 (ex D.978), collected “loose near Beacon 625”. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19118	162.0 (100)	53.5 (33.0)	55.1 (34.0)	0.97	71.3 (44.0)



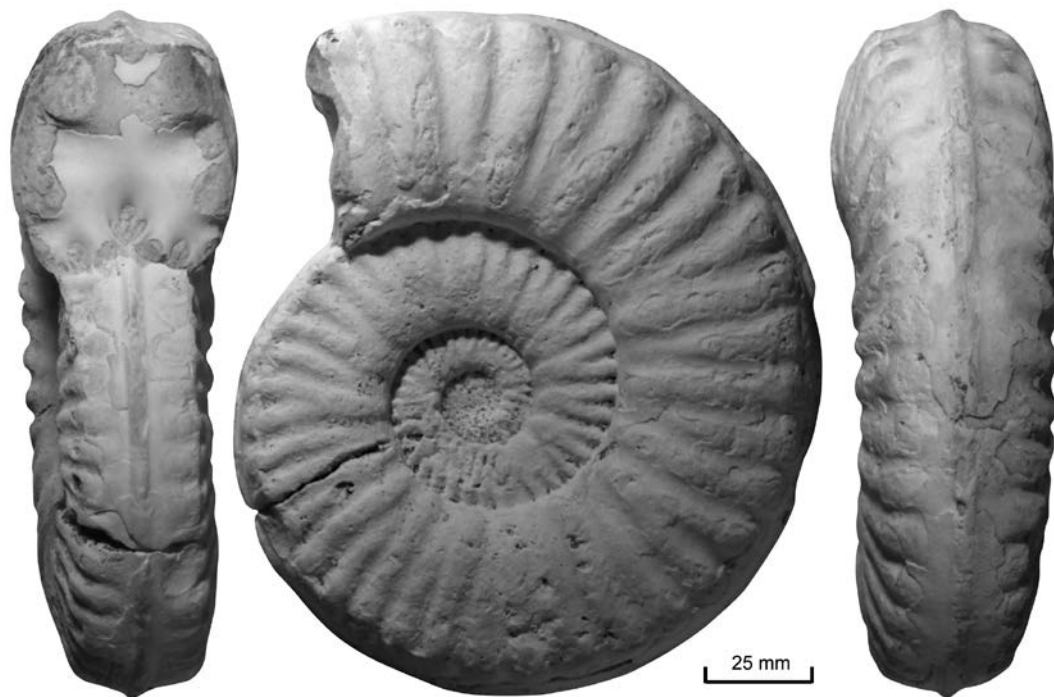
Text-fig. 5. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The holotype of *Ophryoceras tenuicostatum* van Hoepen, 1946 (p. 217, text-figs 205, 206), SAM PCZ 19120 (ex D.2597) from the “Ridge West of Beacon 624”.



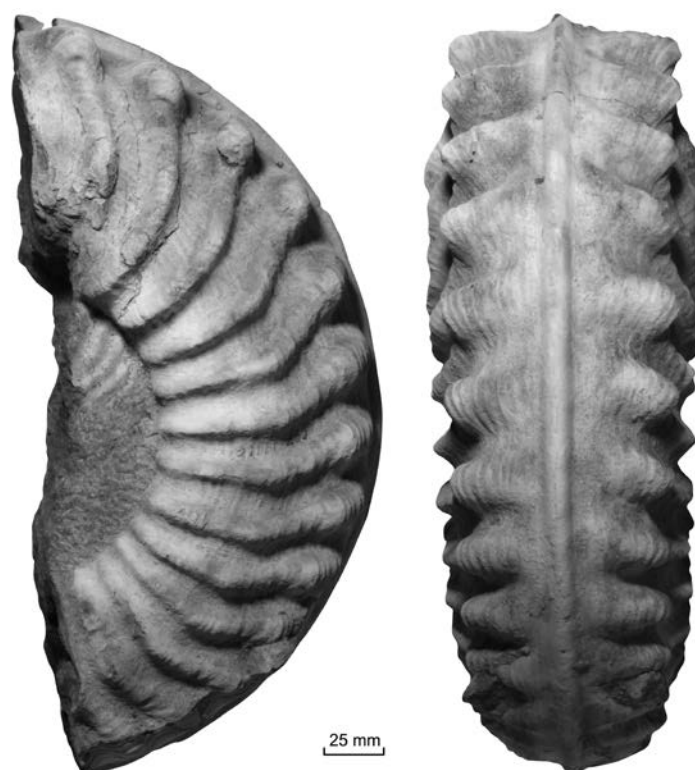
Text-fig. 6. *Pervinqueria (Pervinqueria) jugosa* (van Hoepen, 1942). The holotype of *Ophryoceras crassinodatum* van Hoepen, 1946 (p. 219, text-figs 207, 208), SAM PCZ 19119 (ex D.2598), from "The Upper End of Runlet which joins the Umsinene River at Beacon 624".

This very worn specimen (Text-fig. 7) differs in no significant respects from the holotype of *jugosum*.

The holotype of *Ophryocera annaalida*, SAM PCZ 19116 (ex D.2601), is the original of van Hoepen (1946, p. 225, text-figs 216–219), from "Beacon 624". The surviving fragment is a half whorl (Text-fig. 8) with a maximum preserved whorl height of 119 mm before the ventral rostrum develops. The intercostal whorl breadth to height ratio is 0.92; the costal whorl breadth to height ratio 1.07. The umbilicus is broad, of moderate depth, the umbilical wall convex and outward-inclined, the umbilical shoulder broadly rounded. The slightly compressed intercostal whorl section has the greatest breadth below mid-flank, the inner flanks broadly rounded, the outer flanks converging to broadly rounded ventrolateral shoulders and venter. There are 15 ribs per half whorl. They arise on the umbilical wall, strengthen across the umbilical shoulder without developing into a clearly differentiated bulla (one is present on the penultimate whorl of the missing fragment, as shown in van Hoepen 1946, text-fig. 219). They are distant, coarse, concave, strengthening progressively across the flanks, with a well-developed outer lateral bulla and a massive ventrolateral tubercle that broadens and effaces across the venter. There is strong siphonal keel. Spiral ridges are present over all of the surface of the shell. It is interpreted as a coarsely ornamented variant of the species.



Text-fig. 7. *Pervinqueria (Pervinqueria) jugosa* (van Hoepen, 1942). The holotype of *Ophryoceras crassum* van Hoepen, 1946 (p. 221, text-figs 209, 210), SAM PCZ 19118 (ex D.978), collected "loose near Beacon 625".



Text-fig. 8. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The surviving fragment of the holotype of *Ophryoceras annaalida*, SAM PCZ 19116 (ex D.2601), the original of van Hoepen (1946, p. 225, text-figs 216–219), from “Beacon 624”.

The holotype of *Ophryoceras salebrosum* (van Hoepen, 1942) (p. 113, text-figs 96–98) is SAM PCZ 19521 (ex D.739), from “Beacon 624”. It is a huge fragmentary macroconch with all of one flank worn away, retaining a 180° sector of body chamber (Text-fig. 9). The approximate dimensions are:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 21951	320 (100)	– (–)	96.0 (30.0)	–	139.5 (43.6)

On the penultimate whorl, well-developed bullae perch on the umbilical shoulder and give rise to pairs of coarse, straight, recti- to feebly prorsiradiate ribs. On the outer whorl, the broad umbilicus is of moderate depth, with a feebly convex wall and broadly rounded umbilical shoulder. The intercostal whorl section appears to have been compressed, with broadly convex inner and convergent outer flanks, broadly rounded ventrolateral shoulders and a broad, feebly convex venter with a strong siphonal keel. There are fifteen ribs on the 90–270° sector of the outer whorl. Eight of these arise at the umbilical seam and strengthen into well-developed umbilical bullae. These give rise to pairs of ribs, the adapical one recti- to feebly prorsiradiate, the adapertural one



Text-fig. 9. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942), the holotype of *Pervinquieria salebrosum* van Hoepen 1942 (p. 113, text-figs 96–98), SAM PCZ 19521 (ex D.739), from “Beacon 624”.



Text-fig. 10. *Pervinqueria* (*Pervinqueria*) *jugosa* (van Hoepen, 1942). A fragment of the holotype of *Ophryoceras liberta* van Hoepen, 1946 (p. 227, text-figs 220–222), SAM PCZ 19117 (ex D.1385), from “Beacon 624”.

only weakly linked to the bulla, and more markedly prorsiradiate. The ribs are distant, strengthen across the flanks and develop into an incipient lateral bulla, and a strong ventrolateral tubercle that gives rise to a broad, forwards-directed rib that broadens and declines, effacing before reaching the siphonal keel. On the 90° final sector the seven ribs preserved are single; six arise from strong umbilical bullae; one is a long intercalated rib. There is a weakly expressed lateral bulla on some ribs. Spiral ridges are well-developed over all of the external shell surface.

The holotype of *Ophryoceras liberta* van Hoepen, 1946 (p. 227, text-figs 220–222) is SAM PCZ 19117 (ex D.1385), from “Beacon 624”. Only two of the original three fragments survive (Text-figs 10, 11) of a huge macroconch, 360 mm in diameter at the beginning of the rostrum, and over 400 mm including

the rostrum. Coiling is very evolute, the umbilicus of moderate depth, with a feebly convex umbilical wall and broadly rounded umbilical shoulder. The intercostal whorl breadth to height ratio is 0.84; the costal ratio 0.93. On the penultimate whorl fragment, ornament is of primary ribs that are single or bifurcate at mid-flank, with incipient umbilical bullae only, although the pattern cannot be established with confidence because of the poor preservation. The ribs are crowded, prorsiradiate, and bear clearly differentiated outer lateral bullae. There are well-developed spiral ridges where shell is preserved. There are 12 ribs on the associated outer whorl fragment, all primaries. They arise at the umbilical seam, sweep back across the umbilical wall and strengthen into coarse, distant, prorsiradiate bullae, perched on the umbilical shoulder. The ribs are distant and prorsiradiate, and develop strong outer lateral bullae, linked by a broad, weak rib to massive, conical ventrolateral tubercles that give rise to broad ribs that efface before reaching the strong siphonal keel. The last two ribs are weaker, closer together, and lack a bulla.

The lectotype, here designated, of *Ophryoceras opimum* van Hoepen, 1946 (p. 229, text-figs 223–225), is SAM PCZ 19123 (ex D.2602) (Text-fig. 12),



Text-fig. 11. *Pervinqueria* (*Pervinqueria*) *jugosa* (van Hoepen, 1942). A further fragment of the holotype of *Ophryoceras liberta* van Hoepen, 1946 (p. 227, text-figs 220–222), SAM PCZ 19117 (ex D.1385), from “Beacon 624”.

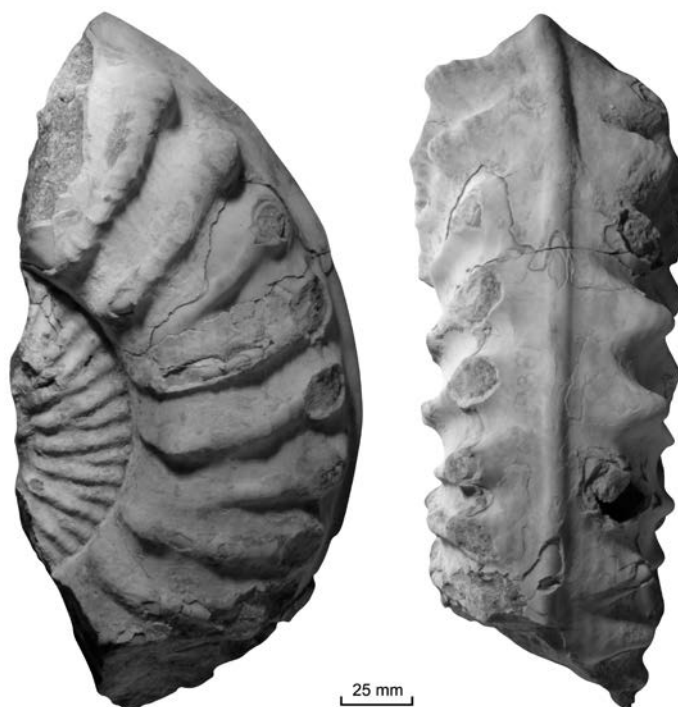


Text-fig. 12. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The lectotype of *Ophryoceras opimum* van Hoepen, 1946 (p. 229, text-figs 223–225), SAM PCZ 19123 (ex D.2602), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

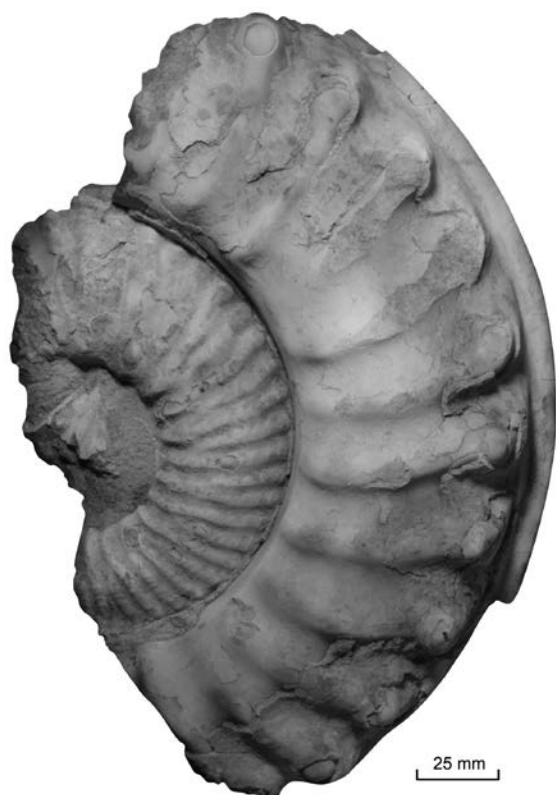
from “The Upper End of Runlet which joins the Umsinene River at Beacon 624”. SAM PCZ 19381 (ex D.2603) is a paralectotype, from “Beacon 624”. The dimensions of the lectotype are as follows:

	D	Wb	Wh	Wb;Wh	U
SAM PCZ 19123 costal	200.0 (100)	78.6 (39.3)	74.4 (37.0)	1.1	83.2 (41.6)

Coiling is evolute, with 45% of the previous whorl covered. The whorl section is slightly depressed, rounded-trapezoidal, the umbilicus broad and of moderate depth, the umbilical shoulder broadly rounded. On the penultimate whorl, primary ribs arise on the umbilical wall and strengthen into small bullae, perched on the umbilical shoulder. They give rise to pairs of straight prorsiradiate ribs. On the outer whorl there are 25 small umbilical bullae that give rise to pairs of ribs, with some intercalated ribs on the adapical 180° sector, beyond which the ribs are predominantly single, mostly bullate, straight and prorsiradiate on the inner flank, flexed forwards and concave on the outer flank, sweeping forwards to well-developed ventrolateral tubercles that give rise to a broad rib that effaces before reaching the siphonal keel. There are incipient lateral bullae, and prominent spiral ridges are present on the flanks and ventrolateral shoulders. Paralectotype SAM PCZ 19381 (ex D.2603) (Text-fig. 13) is a much better preserved 120°



Text-fig. 13. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The paralectotype of *Ophryoceras opimum* van Hoepen, 1946, SAM PCZ 19381 (ex D.2603), from “the Umsinene River at Beacon 624”.



Text-fig. 14. *Pervinqueria* (*Pervinqueria*) *jugosa* (van Hoepen, 1942). The holotype of *Ophryoceras tereticostatum* van Hoepen, 1946 (p. 231, text-figs 226, 227), SAM PCZ 19121 (ex D.2604), from "Beacon 624".

whorl fragment with a maximum preserved whorl height of 89.5 mm. The penultimate whorl fragment bears crowded prorsiradiate ribs that arise in pairs from small umbilical bullae, and bear an incipient lateral tubercle. There are eight ribs on the outer whorl fragment, six primaries with strong bullae, and two long intercalatories. The ribs are prorsiradiate and markedly concave, with a well-developed lateral bulla and a massive ventrolateral tubercle; spiral ridges are very prominent. The specimen links the types of *liberta* and *salebrosum* in terms of tuberculation, and links to *annaalida* in terms of rib concavity, although the ribs in *annaalida* are all bullate primaries, the lateral bulla weaker, the ribs closer together, with stronger spiral ridges.

The holotype of *Ophryoceras tereticostatum* van Hoepen, 1946 (p. 231, text-figs 226, 227) is SAM PCZ 19121 (ex D.2604) (Text-fig. 14), from "Beacon 624". It is a 180° sector of the penultimate whorl and a 120° sector of body chamber with a maximum preserved whorl height of 102 mm. One flank is worn

away; the other retains traces of recrystallized shell. The penultimate whorl fragment is 160 mm approximately in diameter, the umbilicus comprising 40% approximately of the diameter. Coarse ribs arise at the umbilical seam, sweep back across the umbilical wall and shoulder and strengthen into weak umbilical bullae. These give rise to pairs of ribs, while there are additional long intercalated ribs to give a total of 26 ribs at the ventrolateral shoulder of the fragment, the ribs low, broad, strengthening across the flanks, prorsiradiate and straight on the inner flank and feebly concave on the outer flank. Some of the ribs at the adapertural end of the fragment bear a weak lateral bulla. There are 12 ribs on the 120° outer whorl sector. All but one are primaries with well-developed umbilical bullae, weakened on the last two ribs. The ribs are concave and prorsiradiate, with well-developed lateral bullae and a long conical-clavate ventrolateral tubercle. The inner whorls of this specimen compare well with those of the type material of *jugosum*, well-developed lateral tubercle apart.



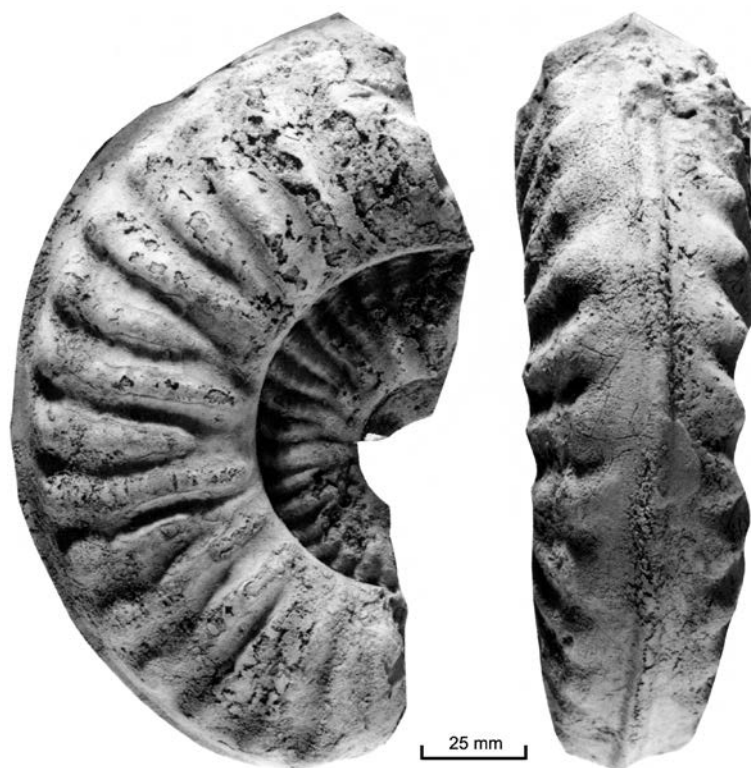
Text-fig. 15. *Pervinqueria* (*Pervinqueria*) *jugosa* (van Hoepen, 1942). The holotype of *Ophryoceras obsoletum* van Hoepen, 1946 (p. 233, text-figs 228, 229), SAM PCZ 19182 (ex D.2605), from the "Upper End of Runlet which joins the Umsinene River at Beacon 624".

The holotype of *Ophryoceras obsoletum* van Hoepen, 1946 (p. 233, text-figs 228, 229) is SAM PCZ 19182 (ex D.2605), from “Upper End of Runlet which joins the Umsinene River at Beacon 624”. It is a battered and worn half whorl of a macroconch phragmocone 225 mm in diameter, with a part of the penultimate whorl preserved (Text-fig. 15). The ornament of the penultimate whorl is of primary ribs that arise in pairs from weak umbilical bullae, with some intercalated ribs, the ribs crowded, straight, and prorsiradiate. On the outer whorl fragment there are 15 umbilical bullae and 22 ribs at the ventrolateral shoulder. Ribs arise in pairs from bullae at the adapical end of the fragment, but are single primaries or long intercalatories over most of it. There is a well-developed lateral bulla and strong ventrolateral tubercle on all ribs.

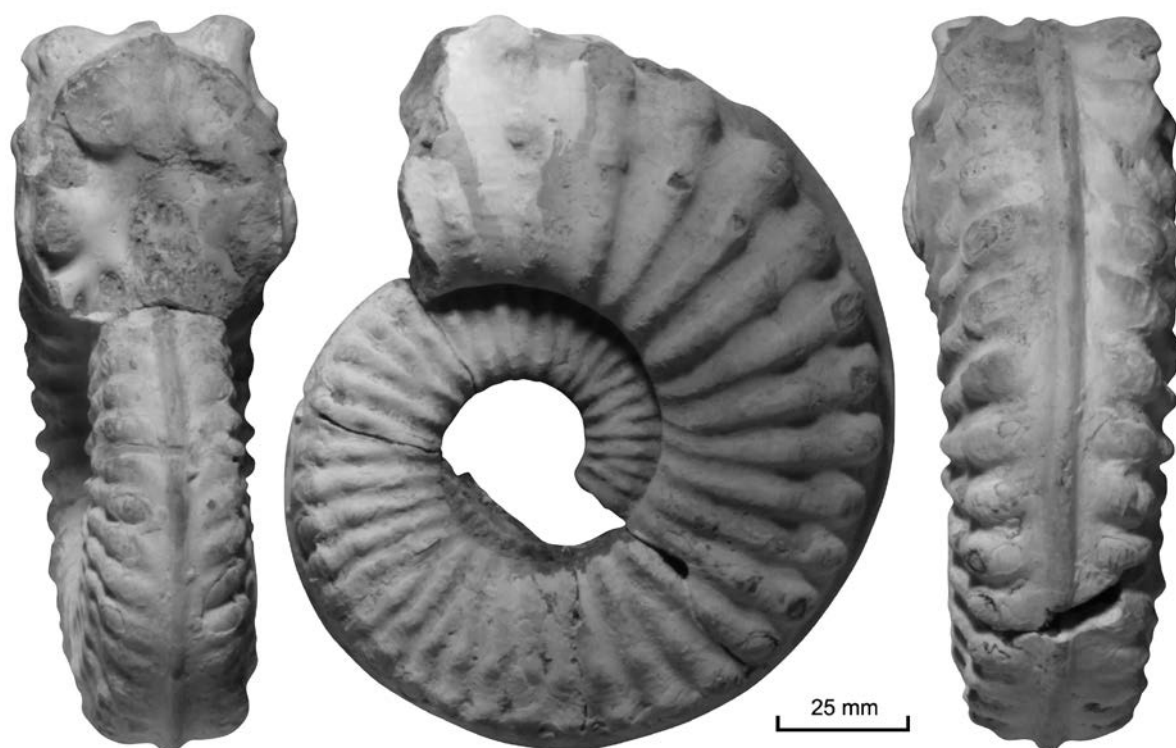
The holotype of *Orphyroceras undosum* van Hoepen, 1946 (p. 235, text-figs 230–233) is SAM PCZ 19181 (ex D.2608), from the “Extension of Ridge West of Beacon 624 to the West and into the valley and gradually higher towards the West”. It is a worn and battered half whorl 180 mm in diameter with parts of the two preceding whorls preserved (Text-fig. 16). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19181 costal	180.0 (100)	57.0 (31.7)	63.8 (35.4)	0.89	78.7 (43.7)

Coiling is very evolute, the umbilicus comprising 43.7% of the diameter, of moderate depth, with a flattened to feebly convex wall, the umbilical shoulder broadly rounded, the whorl section compressed with feebly convex subparallel flanks, broadly rounded ventrolateral shoulders and a flattened venter in intercostal section, with a strong siphonal keel. Extensive traces of recrystallized shell are preserved on one flank. On the innermost whorl fragment primary ribs arise at the umbilical seam and bifurcate at the umbilical shoulder without developing into a bulla; there are additional single primaries, the ribs straight and rectiradiate on the flanks. A similar rib pattern is developed on the penultimate whorl, with a weak umbilical bulla at the largest preserved diameter. On the outer whorl fragment, nine weak bullae give rise to single ribs, while there are additional non-bullate primaries and long intercalated ribs to give a total of 16 ribs at the ventrolateral shoulder. The ribs broaden markedly across the flanks, and are straight and prorsiradiate on the inner to middle flank, flexing



Text-fig. 16. *Pervinqueria* (*Pervinqueria*) *jugosa* (van Hoepen, 1942). The holotype of *Orphyroceras undosum* van Hoepen, 1946 (p. 235, text-figs 230–233), SAM PCZ 19181 (ex D.2608), from the “Extension of Ridge West of Beacon 624 to the West and into the valley and gradually higher towards the West.”



Text-fig. 17. *Pervinquieria* (*Pervinquieria*) *jugosa* (van Hoepen, 1942). The holotype, by monotypy, of *Ophryoceras spinosum* van Hoepen, 1942 (p. 222, text-figs 211–215), SAM PCZ 19122 (ex D.2600), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”.

forwards and concave on the ventrolateral shoulder where they link to a blunt ventrolateral tubercle that gives rise to a weak, effacing rib. There is a strong siphonal keel. Spiral ridges are prominent, notably on the outer flank and ventrolateral shoulder. There are slight indications of a lateral bulla on some ribs.

The holotype, by monotypy, of *Ophryoceras spinosum* van Hoepen, 1942 (p. 222, text-figs 211–215) is SAM PCZ 19122 (ex D.2600), from the “Upper End of Runlet which joins the Umsinene River at Beacon 624”/locality 54. The dimensions are as follows:

	D	Wb	Wh	Wb;Wh	U
SAM PCZ 219122 costal	144.4 (100)	50.5 (35.0)	53.4 (37.0)	0.95	55.4 (38.4)
SAM PCZ 219122 intercostal		46.1 (31.9)	52.0 (36.0)		

The holotype, a near-complete macroconch, has a maximum preserved diameter of 224 mm approximately. The early whorls (Text-fig. 17) retain recrystallized shell. Coiling is very evolute, with 31% of the previous whorl covered, the umbilicus broad, comprising 38.4% of the diameter, of moderate depth, with a feebly convex subvertical wall. Twenty eight ribs arise at the umbilical seam and strengthen across the

umbilical wall, developing into weak to incipient umbilical bullae. These give rise to predominantly single ribs, with only occasionally pairs of ribs on the 120° adapical sector of the outer whorl, and exclusively single ribs on the adapertural 120° sector. The ribs are slightly concave on the umbilical shoulder and straight and prorsiradiate across the flanks, strengthening progressively and bearing well-developed outer lateral tubercles and massive ventrolateral tubercles that give rise to low, broad, near-transverse effacing ribs. The fragment of outer whorl extends to a maximum preserved whorl height of 70 mm, with distant primary ribs with umbilical, lateral, and ventrolateral tubercles. The holotype shows a more conspicuous development of a lateral bulla, incipient in *jugosum*, and feebly expressed in *costatum*, notably on the outer whorl.

The suture (van Hoepen 1946, text-fig. 204) is quite deeply incised, with a deep median incision in bifid E/A and U2, with A narrow.

DISCUSSION: The ontogenetic changes outlined above separate *jugosum* from all other *Pervinquieria* (*Pervinquieria*) from northern KwaZulu-Natal.

Mortoniceras (*Pervinquieria*) *curvatocostatum* Venzo, 1936 [p. 91 (33), pl. 8 (4), fig. 5, pl. 12 (8),

fig. 2], from “Ndabana-Umsinene”, is based on a 120° body chamber fragment with a maximum preserved whorl height of 100 mm according to Venzo (1936). It bears eight feebly prorsiradiate feebly convex ribs, the adapertural two very widely spaced when compared with the adapertural six. There are small umbilical bullae, an incipient lateral bulla and a strong ventrolateral tubercle on all ribs. It may be conspecific with the present material, the name *curvatocostatum* having priority over *jugosum*, but in the absence of the early ontogenetic stages we reserve judgement.

Mortonicer (*Ophryoceras*) *hoepeni* Collignon, 1963 (p. 158, pl. 305, fig. 1309), from the Upper Albian of Mont Raynaud, Madagascar, was described as “voisine de plusieurs espèces rapportées par van Hoepen a son genre *Ophryoceras*, en particulier de *O. crassum* van Hoepen, *O. costatum* van Hoepen, et surtout *O. obsoletum* van Hoepen..... En diffère par sa section plus régulièrement trapézoïdale et par la force considerable des tubercles externes.” The holotype is 195 mm in diameter, and is interpreted as the phragmocone of a macroconch. The ornament differs in no significant respects from that of the penultimate whorl of the holotype of *liberta* (Text-fig. 10) and the lectotype of *opimum* (Text-fig. 12) at the same whorl height, and it is a synonym of *jugosa*, as is *Mortonicer* (*Ophryoceras*) *crassinodatum* var. *nicolaiae* Collignon, 1963 (p. 164, pl. 308, fig. 1314) from “Ouest de la Manamana (Ankazoabo)”, Madagascar. Collignon (1963) distinguished it from *crassinodatum* on the basis of the presence of a lateral tubercle in his variety, but there is in fact a lateral tubercle in the type of *crassinodatum* (Text-fig. 6).

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

Acknowledgements

WJK acknowledges the support of the staff of the Earth Collections of the Oxford University Museum of Natural History and David Sansom 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. HJK 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 Francis Amédéo and Markus Wilmsen for their comments on the original manuscript, and Anna Żylińska for editorial guidance.

REFERENCES

- Böhm, J. 1910. Review of ‘Etudes de Paléontologie Tunisienne’ by L. Pervinquier. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **1910**, 149–155.
- Collignon, M. 1963. Atlas des fossiles caractéristiques de Madagascar (Ammonites). X. Albién, 1–184. Service Géologique; Tananarive.
- Collignon, M. 1979. Ammonites du Crétacé Moyen-Supérieur de l’Angola. *Reconhecimento Científico de Angola: Estudos de Geologie et Paleontologica e de Micologia*. Lisbon, 1–75 (misdated 1978).
- Gale, A.S. and Kennedy, W.J. 2020. Upper Albian ammonites from north-east Texas. *Revue de Paléobiologie*, **39**, 1–139.
- Hoepen, E.C.N. van 1941. 3. Die gekielde ammonitie van die Suid-Afrikaanse Gault. 1. Dipoloceratidae, Cechenoceratidae en Drepanoceratidae. *Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein*, **1**, 55–90.
- Hoepen, E.C.N. van 1942. 4. Die gekielde ammonitie van die Suid-Afrikaanse Gault. II. Drepanoceratidae, Pervinquieridae, Arestoceratidae, Cainoceratidae. *Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein*, **1**, 91–157.
- Hoepen, E.C.N. van 1946. 6. Die gekielde Ammoniete van die Suid-Afrikaanse Gault. IV. Cechenoceratidae, Dipoloceratidae, Drepanoceratidae, Arestoceratidae. *Paleontologiese Navorsing van die Nasionale Museum, Bloemfontein*, **1**, 199–270.
- Hyatt, A. 1884. Genera of fossil Cephalopoda [2nd part]. *Proceedings of the Boston Society of Natural History*, **22** (1883), 337–412.
- Hyatt, A. 1889. Genesis of the Arietidae. *Smithsonian Contributions to Knowledge*, **673**, 1–239.
- Kennedy, W.J., Cobban, W.A., Gale, A.S., Hancock, J.M. and Landman, N.H. 1998. Ammonites from the Weno Limestone (Albian) in northeast Texas. *American Museum Novitates*, **3236**, 1–46.
- Kennedy, W.J. and Klinger, H.C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bulletin of the British Museum (Natural History) Geology*, **25**, 263–315.
- Kennedy, W.J. and Klinger, H.C. 2023a. The ammonites *Dipoloceras*, *Diplasioceras*, *Euspectroceras*, and *Rhytidoceras* from the Upper Albian of KwaZulu-Natal, South Africa. *Acta Geologica Polonica*, **73**, 505–548.
- Kennedy, W.J. and Klinger, H.C. 2023b. The ammonite *Pervinquieria* (*Deiradoceras*) van Hoepen, 1931 from the Upper Albian of KwaZulu-Natal, South Africa. Part 1. *Acta Geologica Polonica*, **73**, 549–569.
- Klein, J. 2018. Lower Cretaceous Ammonites, XI. Acanthoceratoidea: Leymeriellidae, Brancoceratidae, Lyelliceratidae, Flickiidae, Forbesiceratidae, including Upper Cretaceous representatives. *Fossilium Catalogus, I: Animalia*, pars 158, 333 pp. Backhuys Publishers; London.

- Korn, D., Ebbighausen, V., Bockwinkel, J. and Klug, C. 2003. The A-mode ontogeny in prolecanitid ammonites. *Palaeontology*, **46**, 1123–1132.
- Kullmann J. and Wiedmann J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas, Paleontological Contributions*, **42**, 1–32.
- Meek, F.B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country. In: Hayden, F.V. (Ed.), Report of the United States Geological Survey of the Territories, 9, 629 pp. Government Printing Office; Washington.
- Sowerby, J. 1812–1822. The Mineral Conchology of Great Britain, 1, pls 1–9 (1812), pls 10–44 (1813), pls 45–78 (1814), pls 79–102 (1815); 2, pls 103–114 (1815), pls 115–150 (1816), pls 151–186 (1817), pls 187–203 (1818); 3, pls 204–221 (1818), pls 222–253 (1819), pls 254–271 (1820), pls. 272–306 (1821); 4, pls. 307–318 (1821), pls 319–383 (1822). The Author; London.
- Spath, L.F. 1926. On new ammonites from the English Chalk. *Geological Magazine*, **63**, 73–83.
- Spath, L.F. 1934. A monograph of the Ammonoidea of the Gault, Part 11. *Monograph of the Palaeontographical Society*, 443–496. Palaeontographical Society; London.
- Venzo, S. 1936. Cefalopodi del Cretaceo medio-superiore dello Zululand. *Palaeontographica Italica* (new series), **3**, 59–133 (1–75).
- Wright, C.W. 1957. Cretaceous Ammonoidea. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology. Part L, Mollusca 4, Cephalopoda, Ammonoidea, 490 pp. Geological Society of America and The University of Kansas Press; New York and Lawrence.
- Wright, C.W. 1996. Treatise on Invertebrate Paleontology. Part L, Mollusca 4: Cretaceous Ammonoidea (with contributions by J.H. Calloman (sic) and M.K. Howarth), 362 pp. Geological Society of America and The University of Kansas Press; Boulder, Colorado and Lawrence, Kansas.
- Zittel, K.A. von 1884. Handbuch der Palaeontology. 1, Abt. 2; Lieferung 3, Cephalopoda, 329–552. R. Oldenbourg; Munich and Leipzig.

Manuscript submitted: 3rd January 2025

Revised version accepted: 19th March 2025