

Cretaceous faunas from Zululand and Natal, South Africa. The Santonian-Campanian ammonite genus *Eulophoceras* Hyatt, 1903

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(with 19 figures)

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The distinctive Santonian-Campanian ammonite genus *Eulophoceras* Hyatt, 1903, is revised and assigned to the subfamily Lenticeratinae. *Pelecodiscus* Van Hoepen, 1921, and *Spheniscoceras* Spath, 1921, are junior synonyms. *Praelibycoceras* H. Douvillé, 1912, regarded as a junior synonym by previous authors, is regarded as a separate taxon. All seven species previously recorded from the Mzamba Formation of the Eastern Cape Province are assigned to a variable, dimorphic *Eulophoceras natalense* Hyatt, 1903, which is also recorded from the St Lucia Formation of KwaZulu-Natal, as is a second species, *Eulophoceras bererense* Hourcq, 1949. The Madagascan representatives of the genus are described and illustrated for comparison, and the status of other species referred to the genus reviewed.

Key words: Ammonites, *Eulophoceras*, Santonian, Campanian, Cretaceous, KwaZulu-Natal, Eastern Cape Province, South Africa.

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INTRODUCTION

Alpheus Hyatt (1903, p. 86, pl. 11, figs 2–6) introduced his new genus and species *Eulophoceras natalense*, which he referred to his new family Eulophoceratidae Hyatt, 1903 (p. 83), on the basis of a single specimen from ‘Port Natal, South Africa’ in the collections of the Peabody Museum of Yale University (Figs 1–3). Port Natal was renamed Durban on the latter’s foundation in 1835. There are no outcrops of Cretaceous sediments in the environs of Durban (although they are present in the subsurface: Kennedy *et al.*, 1973). The Yale collections also include a series of other ammonites labelled ‘Port Natal’: *Plesiotexanites stangeri* (Baily, 1855) (YPM6250), *Hauericeras gardeni* (Baily, 1855) (YPM1000, 1026), and *Kossmaticeras* (*Karapadites*) *planissimus* Collignon, 1966 (YPM1071, figured by Kennedy & Klinger, 1985, figs 25, 26). The preservation of the material indicates it all to be from the Mzamba Formation, and from outcrops at the mouth of the Mzamba Estuary in the Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980).

REPOSITORIES OF SPECIMENS

OUM: Geological Collections, Oxford University Museum of Natural History, Oxford.
SAM: Natural History Collections Department, Iziko South African Museum, Cape Town.
BMNH: The Natural History Museum, London.
YPM: Peabody Museum of Yale University, Yale.

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, The Natural History Museum, London, and the Natural History Collections Department, Iziko, South African Museum, Cape Town.

CONVENTIONS

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in

brackets are dimensions as a percentage of the diameter. The suture terminology is that of Korn *et al.* (2003): E = external lobe; A = adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann 1970); U = umbilical lobe; I = internal lobe.

SYSTEMATIC PALAEOLOGY

Superfamily **ACANTHOCERATOIDEA** de Grossouvre, 1894
 Family **SPHENODISCIDAE** Hyatt, 1900
 (= Libycoceratinae Zaborski, 1982, p. 306)
 Subfamily **LENTICERATINAE** Hyatt, 1900
 (= Eulophoceratinae Hyatt, 1903, p. 83)

Discussion

Hyatt introduced his family Lenticeratidae validly in 1900 (p. 585), of which Eulophoceratidae Hyatt, 1903 is a junior synonym, notwithstanding the comment in the posthumously published *Pseudoceratites of the Cretaceous* (Hyatt, 1903) by the editor, T.W. Stanton (footnote *b* on p. 84) that 'In Zittel's Text-book of Palaeontology, Vol. 1, p. 590, Professor Hyatt referred this genus [*Lenticeras* Gerhardt, 1897], together with *Paralenticeras* and *Platylenticeras*, to the family Lenticeratidae. Although the statement is not directly made that the family is abandoned, it may be inferred from the reference of *Platylenticeras* to Coilopoceratidae, the remark under *Paralenticeras* about its affinity for *Eulophoceras*, and the fact that the manuscript was arranged as now published with *Lenticeras* and *Paralenticeras* between *Tegoceras* and *Eulophoceras*'.

Genus *Eulophoceras* Hyatt, 1903

(= *Spheniscoceras* Spath, 1921, p. 242; *Pelecodiscus* Van Hoepen 1921, p. 30).

Diagnosis

Oxycone, whorl section lanceolate or with fastigate venter separated from flanks by change in slope. Near-smooth, or with feeble bullae at the umbilical shoulder; ribs arise singly or in pairs at the umbilical shoulder and strengthen progressively across the flanks, straight on the inner flank and flexing back on the outer, where they may efface or strengthen, be feebly concave or feebly convex, and accentuated into an elongate outer lateral bulla. Intercalated ribs, where present, arise around mid-flank. Few, feeble, spiral ridges in some. Suture highly variable, with asymmetrically trifid to subtrifid E/A, and several auxiliary elements; folioles on saddles may be highly elongated.

Discussion

Praelibycoceras H. Douvillé, 1912 (p. 315), type species *Lenticeras jullieni* Pervinquier, 1910, p. 69, pl. 12 (3), fig. 24, text-fig. 34 was regarded as a synonym of *Eulophoceras* by Wright (1957, p. L436; 1996, p. 204); Spath (1922, p. 143) had previously regarded it as belonging to the Coniacian Tissotiidae Hyatt, 1900. *Lenticeras jullieni* is known from the holotype of the type species only, an unregistered specimen in the Sorbonne collections, now housed in the Muséum National d'Histoire Naturelle, Paris. It is a composite mould of a battered, worn, and corroded phragmocone 91 mm in diameter. An oxycone, the original proportions cannot be

established because of the damage. The tiny shallow umbilicus comprises an estimated 5.5% of the diameter, the umbilical wall inclined outward to form a conical pit. An estimated 12 primary ribs arise at the umbilical seam, and are straight and prorsiradiate on the flanks, across which they initially broaden and strengthen progressively, before declining and effacing on the outer flank and not extending to the venter. Most ribs bifurcate around mid-flank. The adapical secondary rib of each pair is markedly rursiradiate, so that the primary and secondary ribs have the form of a reversed letter Y. Some strengthen on the outer flank into a low rounded swelling or incipient bulla before effacing. The suture, as depicted by Pervinquier (1910, text-fig. 34) has broad, only moderately incised bifid saddles, with narrower, little-incised lobes. The specimen is from Les Tamarins, southeast of Batna, Algeria, and was said to be associated with *Tissotia robini* Thiollière (Pervinquier, 1910, p. 71), a junior synonym of the Middle Coniacian *Metatissotia ewaldi* (Von Buch, 1848) (Kennedy, 1984, p. 127). If correctly dated, there is a substantial gap between Middle Coniacian *Praelibycoceras* and Upper Santonian–Lower Campanian *Eulophoceras*, while the suture of the former lacks the distinctive features of the suture of the latter. In fact, the oxycone shell form is the main common feature they share. Accordingly, we see no strong evidence to link *Praelibycoceras* and *Eulophoceras*; the familial position of the former remains uncertain in our view.

Spheniscoceras Spath, 1921, p. 242, was introduced as *Spheniscoceras* Crick MS, but must be attributed to Spath. His comments (footnote on pp. 242–243) on Crick's manuscript are less than positive 'In fact the writer is not convinced that Crick was right in separating the forms he described [*Spheniscoceras africanum*, *minor*, and *tenuis*, G.C. Crick MS] from *Eulophoceras*.' In spite of this doubt, Spath separated *Spheniscoceras* from *Eulophoceras* and designated *S. africanum* (Crick MS) as type species (explanation of text-fig. C, 1921, p. 243) based on a figure of a suture line only (Spath, 1921, p. 243, text-fig. C1a). The holotype of *africanum* (Figs 6, 11A) is from the Mzamba Formation at the mouth of the Mzamba River in the Eastern Cape Province, as is the holotype of *Eulophoceras natalense*. There are no significant differences between the two, as described below, and *Spheniscoceras* is a junior subjective synonym of *Eulophoceras* (Spath continued to use *Spheniscoceras* in his 1922 revision of the ammonite fauna of Pondoland, but it is very much out of respect for Crick '...Hyatt's form [*Eulophoceras natalense*] may only be one and an uncommon type of the development separated by Crick and again by Dr Van Hoepen on account of minute differences in what appears to be a very variable suture-line' (p. 142). No type species was designated for *Pelecodiscus* Van Hoepen, 1921, p. 30; *P. umzambiensis* Van Hoepen, 1921, p. 30, pl. 5, fig. 10, pl. 6, fig. 1, is here designated type species. Van Hoepen separated his new genus from *Eulophoceras* on the basis of details of the suture line, but as described below, sutures are variable both within and between individuals referred to *E. natalense*, and we follow previous authors in regarding *Pelecodiscus* as a synonym of *Eulophoceras*.

Kennedy (1987, p. 776; in Kennedy *et al.*, 1995, p. 425) and Wright (1996, p. 204) regarded *Skoumalia* Summesberger, 1979, p. 141, type species *Skoumalia austriaca* Summesberger,

1979 (p. 141, pl. 9, figs 37–41, text-figs 26–30), from the Upper Santonian of the Gosau Basin, Austria, as a synonym of *Eulophoceras*. Summesberger recognized two morphotypes in *Skoumalia austriaca*. His Form A included the holotype (Summesberger, 1979, pl. 9, figs 37, 38; text-fig. 26–28) an oxycone phragmocone 75 mm in diameter with fastigate venter, strong umbilical bullae that give rise to pairs of straight prorsiradiate ribs that terminate in small ventral bullae. The suture has a broad E/A with a deep median incision. The suture of the holotype (Summesberger, 1979, text-fig. 27) lacks the ventral part, but the second specimen has a bifid E/A (Summesberger, 1979, fig. 28). A is deep and narrow, A/U2 small and bifid. The ornament is that of *Diaziceras* Spath, 1921, while E/A is asymmetrically bifid, rather than trifid as in *Eulophoceras*. Form B of Summesberger (1979, p. 143, pl. 9, figs 39–41; text figs 29, 30) was based on a phragmocone 58.7 mm in diameter; according to Summesberger (1979, p. 143) it differs from form A in its flat, discoidal shell, narrow umbilicus, and lack of umbilical tubercles; also, the lateral ornament is less conspicuous. They were regarded as probable sexual dimorphs. The suture has a broad, subtrifid E/A (Summesberger, 1979, fig. 30). Summesberger (1980, p. 280, pl. 2, figs 5–6; pl. 3, figs 7–8; text figs 5, 6) subsequently described and figured what he believed to be the adult of his Form B, 122 mm in diameter ornamented by delicate umbilical bullae on the phragmocone. The outer whorl bears delicate feebly flexuous growth lines and striae, with ten distant outer lateral bullae (Fig. 4). The suture has a broad subtrifid E/A, deep, narrow A, bifid A/U2, and simplifying auxiliary elements.

Form A closely resembles *Diaziceras guillanoni* Hourcq, 1949, p. 108 (22), pl. 12 (2), fig. 1, from the Upper Santonian of Madagascar according to Hourcq, but actually Lower Campanian (after Collignon, 1969, p. 212) in whorl section, ornament, and may even be conspecific, so that *Skoumalia* should be regarded as a synonym of *Diaziceras*, an hypothesis to be developed elsewhere. In contrast, Form B of Summesberger, with compressed whorl, fastigate venter, near smooth outer whorl, tiny outer lateral bullae in the adult, is close to *Eulophoceras jacobi* Hourcq, 1949, p. 95 (9), pl. 11 (1), fig. 2, text-fig. 7 (Fig. 11D, 12A–C), from the Lower Campanian of Madagascar. They differ in that the outer lateral bullae are prorsiradiate in *austriaca*, but swept back and markedly rursiradiate in *jacobi*. The following species are assigned to *Eulophoceras*:

1. *E. natalense* Hyatt, 1903, of which *E. africanum* (Spath, 1921), *E. minor* (Spath, 1921), *E. tenue* (Spath, 1921), *E. umzambiensis* (Van Hoepen, 1921), *E. capensis* (Van Hoepen, 1921), and *E. amapondensis* (Van Hoepen, 1921), are synonyms.
2. *E. bererensis* Hourcq, 1949, of which *E. miloni* Hourcq, 1949, *E. besairiei* Hourcq, 1949, *E. manambolense* Hourcq, 1949, and *E. hourcqi* Collignon, 1969, are synonyms.
3. *E. jacobi* Hourcq, 1949.
4. *Eulophoceras vautreini* Basse, 1954
5. *Eulophoceras* sp. of Reymont (1955, p. 83, pl. 22, fig. 5; text-fig. 42).
6. *Eulophoceras wollmanae* Young, 1963.
7. *Eulophoceras* sp. (= *Eulophoceras jacobi* Renz, 1982, non

Hourcq, p. 111, pl. 36, figs 10, 11; pl. 37, figs 2, 3; text-fig. 86a–b).

8. *Eulophoceras losaense* Santamaria Zabala, 1995.

Eulophoceras berryi Knechtel, 1947 (p. 125, pl. 43, text-fig. 21) is based upon a single specimen from Rio Cuxiabata, Loreto, in the Peruvian Andes. It occurs in association with three species of *Tissotia* introduced by Knechtel, and is presumably of Coniacian age. It has a distinctive ornament of convex growth lines only, and a suture with an asymmetrically bifid E/A, and very narrow A. We are uncertain as to its generic position.

The generic assignment of *Eulophoceras phansalkari* Ghare, 1969 (p. 165, pl. 4, figs 1–4; text-fig. 1) is problematic in our view. It is based on the holotype only, a half whorl of worn and corroded phragmocone 140 mm in diameter, from the Upper Trichinopoly Group of Iluppakudi in the Trichinopoly District of Tamil Nadu, South India. It was described as having very feeble ornamentation of fold-like ribs of which five or six are just visible round the umbilicus, and differing from *E. natalense* in ‘...not having the ornamentation of weak ribs, crowded sutures with lobes of at least three consecutive sutures telescoping into one another ... the folioles of *E. natalense* are twice longer than those of the present species.’

The *Eulophoceras* sp. of Reymont (1955, p. 83, pl. 22, fig. 5; text-fig. 42) was based on a fragment of phragmocone only, with faint low undulations on the flank, and a suture with a very broad asymmetric E/A with large median element. The poor preservation makes generic assignment questionable. It is from the upper part of the Awgu-Ndeaboh Shale of Onitscha province, Nigeria, and dated as Coniacian by Reymont.

The *Eulophoceras jacobi* Hourcq of Renz (1982, p. 111, pl. 36, figs 10, 11; pl. 37, figs 2, 3; text-fig. 86a–b) from the Coniacian of Venezuela, differs from Hourcq’s species in having radial ribs that flex forwards and are concave on the outermost flank, whereas the ribs flex back and are concave on the outer flank in *jacobi*. The specimens are between 25 and 55 mm in diameter, much smaller than the Madagascan material; they are best referred to as *Eulophoceras* sp. juv. Pattaroyo & Dueñas (2006, p. 504, pl. 1, figs 1–3) described and figured a specimen with a diameter of ca. 150 mm with weak ventrolateral ribs and striae on the inner, lateral flanks as *Eulophoceras jacobi* from the Lower Coniacian of Quebrada Bambucá, Aipe-Huila Colombia, which, judging by their synonymy, they regarded as the same as Renz’s (1982) species and questionably that of Reymont (1955). This Coniacian specimen certainly does not belong to *E. jacobi*, a lower Campanian species. This may belong to a new species, but with no further material, we provisionally regard it as *Eulophoceras* sp.

Eulophoceras grossouvrei Collignon 1983 (p. 205, pl. 7, fig. 5; see Kennedy, Bilotte & Melchior, 1995, p. 426, pl. 25, figs 1–2) is from the Upper Santonian of the Corbières in southern France. It is a worn juvenile 55 mm in diameter, a *nomen dubium* in our view. Referred to as *Eulophoceras* sp. juv. by Kennedy *et al.* (1995) it is without ornament and shows no diagnostic features.

Occurrence

Coniacian of Colombia, and possibly Nigeria. Santonian of

KwaZulu-Natal, South Africa, Austria, southern France, and northern Spain, and Syria? Lower Campanian of KwaZulu-Natal, Eastern Cape Province, Madagascar, and Angola.

Eulophoceras natalense Hyatt, 1903

Figs 5–11, 12A–C

- 1903 *Eulophoceras natalense* Hyatt, p. 86, pl. 11, figs 2–6.
 1906 *Eulophoceras natalense* Hyatt; Woods, p. 337, pl. 42, fig. 3.
 1921 *Eulophoceras natalense* Hyatt; Spath, footnote # on p. 242; text-fig. C-2.
 1921 *Spheniscoceras africanum* Crick MS; Spath, p. 242, footnote # on p. 242, text-fig. C-1a.
 1921 *Spheniscoceras minor* Crick MS; Spath, p. 242, footnote # on p. 242, text-fig. C-1b.
 1921 *Spheniscoceras tenue* Crick MS; Spath, p. 242, footnote # on p. 242, text-fig. C-1c.
 1921 *Eulophoceras natalense* Hyatt; Van Hoepen, p. 30, pl. 6, figs 2, 3.
 1921 *Pelecoidiscus umzambiensis* Van Hoepen, p. 30, pl. 5, fig. 10; pl. 6, fig. 1.
 1921 *Pelecoidiscus capensis* Van Hoepen, p. 32, pl. 5, fig. 11.
 1921 *Pelecoidiscus amapondensis* Van Hoepen, p. 33, pl. 7, fig. 1, 2.
 1921 *Eulophoceras natalense* Hyatt; Van Hoepen, pl. 6, fig. 2 only.
 1922 *Eulophoceras natalense* Hyatt; Spath, p. 142
 1922 *Spheniscoceras africanum* (Crick MS); Spath, p. 143, pl. 6, fig. 1.
 1922 *Spheniscoceras tenue* (Crick MS); Spath, p. 144, pl. 7, fig. 3; pl. 8, fig. 3.
 1922 *Spheniscoceras minor* (Crick MS); Spath, p. 144, pl. 6, fig. 2.
 1922 *Spheniscoceras amapondense* v. Hoepen sp.; Spath, p. 144, pl. 7, fig. 2.
 1922 *Spheniscoceras umzambiense* v. Hoepen; Spath, p. 145.
 1982 *Eulophoceras natalense* Hyatt, 1903; Immel, Klinger & Wiedmann, p. 24, pl. 8, fig. 5.
 1987 *Eulophoceras natalense* Hyatt, 1903; Immel, p. 113.
 1988 *Eulophoceras natalense* Hyatt; Cooper, p. 209, figs 1a, b.
 Non 1995 *Eulophoceras cf. natalense* Hyatt, 1903; Kennedy in Kennedy, Bilotte & Melchior, p. 235, pl. 26, figs 3, 4, 7; text-fig. 32 (= *Eulophoceras losaense* Santamaria Zabala, 1995).

Type

The holotype is YPM 956 (Figs 1–3), the original of Hyatt (1903, pl. 11, fig. 2), from ‘Port Natal. S. Africa.’

Material

From unspecified horizons in the Mzamba Formation at the mouth of the Mzamba Estuary, Eastern Cape Province: BMNH C19421, the holotype of *Spheniscoceras africanum* Spath, 1921, p. 242, footnote # on p. 242, text-fig. C-1a; BMNH C19423, the holotype of *Spheniscoceras minor* Spath, 1921, p. 242, footnote # on p. 242, text-fig. C-1b; BMNH C19423, the holotype of *Spheniscoceras tenue* Spath, 1921, p. 242, footnote # on p. 242, text-fig. C-1c; BMNH C19424, the original of *Spheniscoceras amapondense* of Spath (1922, p. 144, pl. 7, fig. 2); the holotype of

Pelecoidiscus umzambiensis Van Hoepen, 1921, p. 30, pl. 5, fig. 10; pl. 6, fig. 1, and two additional paratype specimens referred to the species by Van Hoepen, the holotype of *Pelecoidiscus capensis* Van Hoepen 1921, p. 32, pl. 5, fig. 11, the holotype of *Pelecoidiscus amapondensis* Van Hoepen, 1921, p. 33, pl. 7, fig. 1, 2, all in the collections of the Ditsong National Museum of Natural History, (formerly the Transvaal Museum; Northern flagship Institution), Pretoria., SAM-PCP019070, PCP006727, 019752, 019749, 019753–019764, 0201244, from bed 7 or 8, PCP20144, 19733, 19750, 19754, 19784 presumably from the same horizon, of the Mzamba Formation, Campanian I at locality 1 of Kennedy and Klinger (1975, p. 281), at the mouth of the Mzamba Estuary, Eastern Cape Province. OUM KX5348 from the St Lucia Formation, Santonian III, in the environs of locality 17 of Kennedy & Klinger (1975, p. 283), southeast of Mtubatuba, KwaZulu – Natal. OUM KX12925, 12926, SAM-PCZ007346, 019750–019752, 019785, 27346 from the St Lucia Formation, Campanian I–II, locality 74 of Kennedy & Klinger (1975, p. 292), Die Rooiwal, western False Bay, Lake St Lucia, KwaZulu-Natal.

Description

The holotype (Figs 1–3) is a phragmocone retaining most of the original shell on one side (Fig. 1). The other side (Fig. 2), that illustrated by Hyatt (1903, pl. 11, fig. 2) with only traces of shell remaining is labelled ‘Port Natal. S. Africa.’ The specimen has been sawn, and the section polished (Fig. 2). It is interpreted as a macroconch phragmocone, with an estimated original diameter of 164 mm. It is oxycone, with a tiny conical umbilicus 4 mm deep, that comprises approximately 2% of the diameter. The shell of the succeeding whorls completely infills the umbilicus of the preceding whorls. The minimum preserved whorl height is 62 mm, where the whorl breadth to height ratio is 0.37; the ratio is 0.38 at a whorl height of 91.3 mm, beyond which the venter is damaged, rendering accurate measurement impossible. The umbilical shoulder is broadly rounded, the whorl section lanceolate. There are eight low, broad, prorsiradiate fold-like ribs on the half whorl preserved. They arise on the umbilical shoulder, broaden and strengthen progressively across the inner three quarters of the flanks, thereafter effacing, leaving the outermost flanks smooth. On the basis of the size ratio of phragmocone to adult shell in other *Eulophoceras*, the complete diameter of this specimen may have been well over 200 mm. None of the specimens has the aperture preserved, but PCP019762 retains the apertural margin, which is concave across the dorsal 75% of the flank.

The sutures (Fig. 3) interfere throughout. E/A is deeply incised and asymmetrically bifid, with elongated folioles; A is broad; U2 is deeply incised with very elongate narrow-necked folioles.

Woods’ specimen of *Eulophoceras natalense* (1906, p. 337 pl. 42, fig. 3; Fig. 5A herein) is embedded in a block of matrix, has a maximum preserved diameter of 131 mm, and retains extensive areas of original shell material. It is almost wholly septate, and is interpreted as the macroconch phragmocone of a feebly ornamented variant of the species, with low, broad, prorsiradiate ribs detectable under oblique light to a diameter of 112 mm.

BMNH C19421, the holotype of *Spheniscoceras africanum* Spath, 1921 (p. 242, text-fig. C-1a; 1922, p. 143, pl. 6, fig. 1; Figs 5B, 6, 11A herein), is an incomplete macroconch just over 142 mm in diameter, with a 180° sector of the incomplete body chamber preserved. The dimensions are as follows:

D:142.0 (100) Wb: 33.7 (23.7) Wh: 84.5 (59.5) Wb:Wh: 0.40 U: 6.4 (4.5)

The specimen retains extensive areas of variably exfoliated shell, and is oxycone, with the greatest breadth low on the flanks, and a whorl breadth to height ratio of 0.40. On the phragmocone, broad distant primary ribs arise on the umbilical shoulder, some of them incipiently bullate. They give rise to low, broad, feebly prorsiradiate ribs that bifurcate low on the flanks, with additional ribs intercalating, the secondary and intercalated ribs low and broad, and strengthening at their termination on the outermost flank: they do not extend to the ventral keel. The ornament is relatively strong on adapical 120° sector of the outer whorl, thereafter declining, so that the adapertural part of the body chamber is near-smooth. The suture (Fig. 11A) has a broad, strongly asymmetric, incipiently trifid E/A with a deep, narrow median incision and moderately elongated folioles. A is narrower, and asymmetrically bifid, U2 plump, bifid, with minor incisions.

BMNH C19422, the holotype of *Spheniscoceras minor* Spath, 1921 (p. 242, text-fig. C-1b; 1922, p. 144, pl. 6, fig. 2; Figs 8A,B, 10A), retains extensive areas of original aragonitic shell, and is septate to a diameter of 86 mm, with indications of the original presence of a 240° sector of body chamber. The last-formed sutures are crowded, indicating the specimen to be adult. The shell is oxycone, with a tiny umbilicus. The whorl breadth to height ratio is 0.44, the greatest breadth is low on the flanks. The dimensions are as follows:

At: D: 97.2 (100) Wb: 27.8 (28.6) Wh: 58.5 (60.2) Wb:Wh: 0.48 U: —(—).

There are five low, broad ribs on the adapertural half whorl of the phragmocone. They arise on the umbilical shoulder and sweep forwards on the inner flanks, weakening at mid-flank and branching into two or three secondary ribs, with additional ribs intercalating between the groups of secondaries to give as many as 20 low, broad ribs that extend to the sharp venter. This ornament declines rapidly and effaces on the body chamber, which is near-smooth.

BMNH C19423, the holotype of *Spheniscoceras tenue* Spath, 1921 (p. 242, text-fig. C-1c; 1922, p. 144, pl. 7, fig. 3; pl. 8, fig. 3; Figs 9, 10C herein), is interpreted as a microconch. It consists of a phragmocone 79 mm in diameter, with a 240° sector of body chamber preserved. The dimensions are as follows:

At: D: 122.6 (100) Wb: 29.0 (23.7) Wh: 71.2 (58.1) Wb:Wh: 0.41 U: —(—)

The shell is oxycone, more compressed than the holotype of *Spheniscoceras minor*, the greatest breadth low on the flanks, with a whorl breadth to height ratio of 0.41 and, with a comparable style of flank ornament, but much weaker. The suture (Fig. 10C) has a broad, deeply incised E/A with a deep, narrow median element and moderately elongated folioles; A is narrow and asymmetrically bifid.

BMNH C19424 (Fig. 8C) was referred to *Spheniscoceras amapondense* Van Hoepen, 1921, by Spath (1922, p. 144,

pl. 7, fig. 2), and is a fragment of the outer flank of a macroconch phragmocone.

The holotype of *Pelecodiscus umzambiensis* Van Hoepen, 1921, is the original of his pl. 5, fig. 10; pl. 6, fig. 1, in the collections of the Ditsong National Museum of Natural History (formerly the Transvaal Museum, Northern flagship Institution). It is 124 mm approximately in diameter, and retains a short section of body chamber. It is a moderately robustly ornamented individual, corresponding in this respect to the holotypes of *natalense* and *tenue* of Spath (Figs 8, 9A,B). The suture (Fig. 11B) also differs in no significant respects.

The holotype of *Pelecodiscus capensis* Van Hoepen, 1921 (p. 32, pl. 5, fig. 11), housed in the collections of the Ditsong National Museum of Natural History (formerly the Transvaal Museum, Northern Flagship Institution), Pretoria is a battered individual just over 50 mm in diameter. Van Hoepen differentiated it on the basis of details of the suture (Fig. 10B), specifically the 'long and narrow saddles and lobes external to the third lateral saddle. The internal portion runs much stronger backwards' (p. 33).

The holotype of *Pelecodiscus amapondensis* Van Hoepen (1921, p. 33, pl. 7, figs 1, 2) is based on a fragment of phragmocone with a whorl height of over 70 mm. It was separated from *umzambiensis* on the basis of details of the suture, but this differs in no significant respects from that of *africanum* of Spath (compare Figs 11A and C).

Discussion

The specimens referred here to *Eulophoceras natalense* all share a common style of weak to near effaced ribbing (Fig. 7), and in this respect clearly belong to a single dimorphic species. The species recognized by Spath (1921, 1922) and Van Hoepen (1921) were all differentiated on details of the external suture line. But as can be seen from Figs 2, 8C, 10, and 11A–C, no two specimens have identical suture lines, and sutures are not a basis for differentiating a series of species within the present material. Even Spath (1922) who recognized one species of *Eulophoceras* and five of *Spheniscoceras* from the Mzamba Formation clearly had considerable doubts on their distinctiveness based on minute differences of suture line: '...the four 'species' of Crick are very close to *Eulophoceras natalense* Hyatt, and it might be held that the development of what may be a thinner keel, and the slight differences in suture line and ornamentation, are not sufficient to justify the creation of even different species.' (1922, p. 142).

His comments on BMNH C19424 (Fig. 8C) a fragment that he referred to *Spheniscoceras cf. amapondense* of Van Hoepen are even more telling:

'...A fragment ... agrees with the smooth outer whorl of the type-species, *S. africanum*, but its suture-line differs from those of the known 'species' of this genus, notably in the external saddle. The suture line of *S. amapondense* is probably nearer than any other to that of the present fragment, but the half of the suture line of *S. africanum*, opposite to that figured [Spath, 1922, pl. 7, fig. 2 is the figure referred to here] is also similar, so that by splitting one of these specimens in two a further 'species' could be established.' In other words, the differences between the sutures on the left and right flanks of this fragment are

as great as that between the 'species' Spath recognized.

Eulophoceras jacobii Hourcq, 1949 (p. 95, pl. 11 (1), fig. 2, text-fig. 7) was based on a number of specimens from south of Berere, Madagascar, which Hourcq assigned to the top of the Santonian. Collignon (1969, p. 204, pl. 600, fig. 2253) figured a specimen from the *Hourcquiella bererensis* Subzone of his Lower Campanian Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobii*. The original of Hourcq's pl. 11 (1), fig. 2, text-fig. 7, an unregistered specimen in the École des Mines Collections, now housed in the Université Claude Bernard, Lyon, is here designated lectotype, and illustrated here as Fig. 12A–C. Its dimensions are as follows:

D: 119 (100) Wb: 25.0 (0.21), Wh: 70.0 (0.59), Wb:Wh: 0.36, U: 2.7 (2.3)

The specimen is an internal mould with traces of recrystallized shell, retaining a 60° sector of body chamber, an oxycone, with a whorl breadth to height ratio of 0.36, the greatest breadth well below mid-flank. Ornament is greatly reduced. Spiral ridges and depressions are prominent on the outer flank of the mould, and where shell is preserved on the phragmocone, delicate growth lines and striae arise in bunches at the umbilical shoulder and sweep forwards across the flanks, together with feeble low, broad, prorsiradiate ribs. These strengthen and flex back on the outer flank, where they are markedly rursiradiate and feebly crescentic, extending across the outer third of the flank, but failing to reach the venter. On the adapical half of the outer whorl the ribs terminate in a feeble bulla. The ribs decline towards the adapertural end of the phragmocone, where the ornament consists of delicate falcoid growth lines and striae, straight and prorsiradiate to mid-flank, thereafter flexed back on the outer two thirds of the flank. The sutures are approximated, and the shell margin is flared at the greatest preserved diameter. If this is an indication of maturity, the body chamber was extraordinarily short. The suture (Fig. 11D) has a very wide subtrifid E/A with a deep median incision, and folioles of moderate length; A is broad and bifid, with numerous minor incisions; U2 is asymmetrically bifid. The species is immediately distinguished from *E. natalense* on the basis of the course of the ribs, which are markedly rursiradiate on the outer flank, and terminate in distinctive bullae.

Eulophoceras bererense Hourcq, 1949, of which *E. miloni* Hourcq, 1949, *E. besairiei* Hourcq, 1949 *E. manambolense* Hourcq, 1949, and *E. hourcqi* Collignon, 1969, are synonyms, is described below. It differs from *E. natalense* in its stouter shell, the body chamber of which broadens markedly with a rounded venter at the aperture. The primary ribs are broader and coarser than those of *natalense*, flex back, coarsen, and are markedly concave on the outer flank.

Eulophoceras vautreini Basse, 1954 (p. 869, pl. 27, figs 1a–c) is based on a single specimen from the Upper Santonian or Lower Campanian of 'Forlos', southeast of Palmyra in Syria. The species is based on a single battered individual 73 mm in diameter, the adapertural 180° sector body chamber. The flanks are ornamented by strong, concave ribs on the outer flank, and the suture has a broad, subtrifid E/A, and an A/U2 with a pair of distinctive narrow-necked bulbous folioles.

Eulophoceras wollmanae Young, 1963 (p. 126, pl. 72, fig. 5; pl. 74, figs 1–3, 6; text figs 11c,g,m,s) from the Lower

Campanian of Texas has a less compressed whorl section, and is described by its author as being smooth throughout its ontogeny, while the poorly preserved sutures are rather different.

Eulophoceras losaense Santamaria Zabala, 1995 (p. 98, pl. 5, figs 3–4; text-fig. 1f), from the Santonian of northern Spain, is distinguished by having ribs that flex back and are markedly rursiradiate and concave on the middle and outer flank.

The *Eulophoceras natalense* of Immel *et al.* (1982, p. 24, pl. 8, fig. 5) from the Gosau Group of Brandenberg Tirol, Austria, was originally described as being from the Lower Santonian, but Immel (1987, p. 113) subsequently suggested it might range into the Lower Campanian. It is a composite mould 77 mm in diameter, with low broad ribs well-developed on the adapertural half whorl, as in the holotype of Spath's *tenuis* (Fig. 9) at a comparable diameter. Specimens referred to as *Eulophoceras cf. natalense* from the Santonian of the Corbières in southern France (Kennedy *in* Kennedy *et al.*, 1995, p. 425, pl. 26, figs 3, 4, 7; text-fig. 32) have ribs that flex back and are markedly concave on the outer flank, and are better referred to *E. losaense*, discussed above.

Occurrence

Eulophoceras natalense occurs at the contact of beds A7 and A8 and in bed A8 of the Mzamba Formation at Mzamba Cliff in Eastern Cape Province (Klinger & Kennedy, 1980, p. 216, text-fig. 4), where it is associated with *Submortonicerus condamyi* (Collignon), and probably *Hauericeras gardeni* (Baily) and *Pseudoschloenbachia umbulazi* (Baily), indicating Campanian I, the lowest division of the Campanian of Kennedy & Klinger (1975). It occurs in the St Lucia Formation, Santonian III, in the environs of locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, associated with *Hauericeras gardeni*, *Pseudoschloenbachia umbulazi* (Baily, 1855), and *Anagaudryceras politissimum* (Kossmat, 1895) At Die Rooiwalle, western False Bay, Lake St Lucia, KwaZulu-Natal, locality 74 of Kennedy & Klinger (1975), it ranges from Santonian III to Campanian I. Records from Austria are Lower Santonian to Lower Campanian (Immel, 1987, p. 113). Lower Campanian of Angola.

Eulophoceras bererense Hourcq, 1949

Figs 12D, 13A–D, 14–19

- 1949 *Eulophoceras Bererense* Hourcq, p. 91 (5), pl. 11 (1), text figs 1, 2.
- 1949 *Eulophoceras Miloni* Hourcq, p. 93 (7), pl. 11 (1), fig. 3; text-fig. 3.
- 1949 *Eulophoceras Besairiei* Hourcq, p. 94 (8), pl. 11 (1), fig. 4; text figs 4, 5.
- 1949 *Eulophoceras Manambolense* Hourcq, p. 96, pl. 13(3), fig. 2; text-fig. 8.
- 1969 *Eulophoceras bererense* Hourcq; Collignon, p. 204, pl. 600, fig. 2254.
- 1969 *Eulophoceras hourcqi* Collignon, p. 206, pl. 601, fig. 2255.
- 1969 *Eulophoceras miloni* Hourcq; Collignon, p. 206, pl. 601, fig. 2256.
- 1969 *Eulophoceras besairiei* Hourcq; Collignon, p. 208, pl. 602, fig. 2257.

Name of the species

As discussed below, we believe that *Eulophoceras bererense* Hourcq, 1949, *Eulophoceras miloni* Hourcq, 1949, *E. besairiei* Hourcq, 1949, and *E. manambolense* Hourcq, 1949, are conspecific. As first revising authors, we select the name *bererense* for the species.

Types

Hourcq mentioned 12 specimens in his account of *E. bererense* (1949, p. 91 (5)), all of which ranked as syntypes. We here designate the original of Hourcq, 1949, pl. 11 (1), fig. 1, lectotype. It is re-illustrated here as Figs 13A, B, 17B, and is an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon. The types are from Berere, Madagascar, and were referred to the top of the Santonian by Hourcq.

Material

OUN KX12924, from the St Lucia Formation, Campanian I–II, at locality 74 of Kennedy & Klinger (1975), Die Rooiwal, False Bay, western Lake St Lucia, KwaZulu-Natal.

Description

The lectotype is an internal mould of an adult microconch with a 240° sector of body chamber preserved. The dimensions are as follows:

D: 125 (100) Wb: 33.0 (26.4) Wh: 66.5 (53.2) Wb:Wh: 0.5 U: 7.9 (6.1)

The phragmocone is oxcone; the body chamber broadens markedly, and develops an obtusely fastigate, rounding venter. On the adapical half of the outer whorl six low broad ribs arise at the umbilical seam, strengthen across the flanks, and bifurcate around mid-flank, while occasional shorter ribs intercalate. The ribs sweep back and are concave and rursiradiate on the outer flank, thicken, and terminate before reaching the venter, to give a total of 13 ribs at the ventrolateral shoulder. Similar but more subdued ornament is present on the adapical half of the body chamber; the adoral half is smooth. Suture (Fig. 17B) moderately incised with short folioles; E/A very wide, asymmetrically bifid, with a large median element; A narrow; A/U2 broad, asymmetrically bifid.

Hourcq mentioned four specimens in his account of *Eulophoceras miloni*, which rank as syntypes. We designate the original of his pl. 11 (1) fig. 3 lectotype, and illustrate it here as Figs 13D, 17A. It is an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon. The types are from Berere, Madagascar, and were referred to the top of the Santonian by Hourcq.

The lectotype is an internal mould of a microconch of a feebly ornamented variant. The dimensions are as follows:

D: 107 (100) Wb: 126.5 (24.8) Wh: 61.5 (57.5) Wb:Wh: 0.43 U: 5.5 (5.1)

Oxycone, with a 120° sector of somewhat stouter incomplete body chamber preserved. Ornament is conspicuous on the phragmocone only. Delicate prorsiradiate primary ribs, riblets and striae arise on the umbilical shoulder and sweep forwards and are prorsiradiate and feebly concave on the

inner 60% of the flanks, thereafter sweeping back, and broadening into concave blunt ribs, 12 per half whorl, that decline before reaching the venter. In some cases two inner flank ribs link to a single outer flank rib. On the body chamber the course of the growth lines remains falcoid, but the outer flank ribs are reduced to mere feeble undulations. Suture (Fig. 17A) with very broad asymmetrically bifid E/A, more deeply incised than in the lectotype of *bererense*.

Hourcq mentioned two specimens in his account of *Eulophoceras besairiei*, which rank as syntypes. We designate the original of his pl. 11 (1) fig. 4 lectotype, and illustrate it here as Fig. 12D. It is an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon. The types are from Berere, Madagascar, and were referred to the top of the Santonian by Hourcq.

The lectotype is an internal mould of a microconch with a 240° sector of body chamber preserved. The dimensions are as follows:

D: 134 (100) Wb: 28.5 (21.3) Wh: 70.5 (52.6) Wb:Wh: 0.4 U: –(–)

The phragmocone is an oxycone, the body chamber somewhat stouter, with an obtusely fastigate venter that rounds towards the adapertural end. The specimen is closely similar to the lectotype of *Eulophoceras bererense*, but with more delicate ornament of an estimated fourteen primary ribs on the inner flank. The ribs increase by bifurcation and intercalation to give an estimated total of 28 ribs per whorl at the ventrolateral shoulder. The suture (Hourcq, 1949, text-fig. 5) is essentially the same as that of the lectotype of *E. bererense*.

The holotype, by monotypy, of *Eulophoceras manambolense* Hourcq, 1949, is the original of his p. 96, pl. 13 (3), fig. 2; text-fig. 8. It is an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon. It is from Berere, Madagascar, and was referred to the top of the Santonian by Hourcq.

The specimen is a small corroded phragmocone, with the following dimensions:

D: 81.0 (100) Wb: 21.5 (26.5) Wh: 47.0 (58.0) Wb:Wh: 0.54 U: 5.3 (6.5)

It is a relatively stout oxycone with a tiny umbilicus. The greatest breadth is just outside the umbilical shoulder, the inner to mid-flank region broadly convex, the outer flanks convergent, and feebly concave on either side of the sharp venter. Seven low, broad, straight prorsiradiate ribs arise at the umbilical shoulder of the outer whorl and bifurcate below mid-flank to give rise to pairs of feebly concave rursiradiate ribs that efface before reaching the venter. Additional ribs intercalate at the level that the primary ribs bifurcate, to give a total of 26–28 ribs on the outer flank of the outer whorl. The suture (Hourcq, 1949, text-fig. 8) differs in no significant respects from that of *E. bererense*.

The holotype of *Eulophoceras hourcqi* Collignon, 1969 (p. 206, pl. 601, fig. 2255) is from the Lower Campanian of Ampamba-Antsirasira (Belo-sur-Tsiribihina), Madagascar (Fig. 15); it is housed in the Collignon Collection in the Université de Bourgogne, Dijon. It is an internal mould of an adult microconch 119 mm in diameter, with a 200° sector of body chamber preserved. As in previous specimens, the phragmocone is oxycone, the body chamber broadening,

with a fastigate venter that rounds at the adapertural end. The ribs are low and broad on the phragmocone, and weaken and efface progressively on the body chamber. The specimen differs in no significant respects from the lectotype of *E. bererense*.

All of the Madagascan specimens described above are interpreted as microconchs. Collignon (1969, p. 208, pl. 602, fig. 2257) described and illustrated a complete adult individual 175 mm in diameter that he referred to *Eulophoceras besairiei* Hourcq, 1949. The specimen (Figs 18, 19) has a maximum phragmocone height of 70 mm. The outer whorl has lost virtually all ornament. The phragmocone is oxycone, while the body chamber broadens markedly, developing a fastigate venter, that broadens and rounds at the adapertural end. We interpret this specimen as an adult macroconch. On this basis, the single KwaZulu specimen, OUM KX12924 (Figs 13C, 14, 17C), with a maximum measurable phragmocone whorl height of 70 mm, and an estimated maximum phragmocone whorl height of 75–80 mm is also a macroconch, adult on the basis of the crowded final sutures, but lacking virtually all of the body chamber. The specimen is an internal mould; the phragmocone has the following dimensions:

At D: 109 (100) Wb: 31.7 (29.1) Wh: 67.8 (62.1) Wb:Wh: 0.47 U: 7.3 (6.7)

A stout oxycone, with a whorl breadth to height ratio of 0.47, the greatest breadth is just outside the umbilical shoulder. Ten primary ribs arise at the umbilical seam of the outer whorl, and strengthen across the umbilical shoulder, where some develop into low bullae, best developed at the adapical end of the outer whorl. Ribs arise either singly or in pairs at the umbilical shoulder. They are low, broad, straight and prorsirdiate on the inner flank, across which they strengthen progressively. The ribs flex back around mid-flank, and may bifurcate, sweeping back and concave on the outer flank, strengthening progressively before effacing, and not extending to the venter. Little but the inner flank of the adapical end of the body chamber survives (Fig. 14), but this shows a marked weakening of the ornament. A suture from some way adapical of the end of the phragmocone (Fig. 17C) has a broad, asymmetrically bifid E/A, with a narrow median incision; A is narrow and subtrifid; U2 is bifid. Both lobes and saddles have only minor, shallow incisions. The sutures crowd markedly towards the end of the phragmocone, with simplifying elements on the inner flank region.

Discussion

The suite of Madagascan specimens, and the single KwaZulu-Natal example referred to the species share a common basic style of ornament of low, falcid weak to coarse ribs, a whorl section in which the body chamber changes from the lanceolate of the phragmocone to fastigate on the adapical part of the body chamber to rounded at the adapertural end. These features separate *bererense* from *natalense*, as noted above. The sutures are also distinctive. Those of *natalense*, albeit variable, are characterized by elongate folioles, seen in extreme form in the lectotype (Figs 2, 3), but also present in others (Figs 10A–C; 11A–C). Those of *bererense* are, by contrast, characterized by minor incisions and, commonly, short, blunt folioles.

As noted above, the *Eulophoceras jacobi* Hourcq of Renz (1982, p. 111, pl. 36, figs 10, 11; pl. 37, figs 2, 3; text-fig. 86a–b) from the Coniacian of Venezuela, has quite different ornament, and is best referred to as *Eulophoceras* sp. juv.; the specimen described by Pattaroya & Duenas (2006) as *E. jacobi* also is best referred to *Eulophoceras* sp.

Occurrence

Hourcq (1949) referred his species to the top of the Santonian. Collignon (1969) recorded 227 *Eulophoceras* from Madagascar, all from his lowest Lower Campanian *Anapachydiscus wittekindi* and *Eulophoceras jacobi* Zone. All those figured came from the upper, *Hourcquiella bererensis* Subzone. The KwaZulu-Natal specimen comes from Campanian I–II of Kennedy & Klinger (1975).

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Fig. 1. *Eulophoceras natalense* Hyatt, 1903. The holotype, YPM 956, from 'Port Natal. S. Africa', that is to say the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980). Figures are $\times 1$.

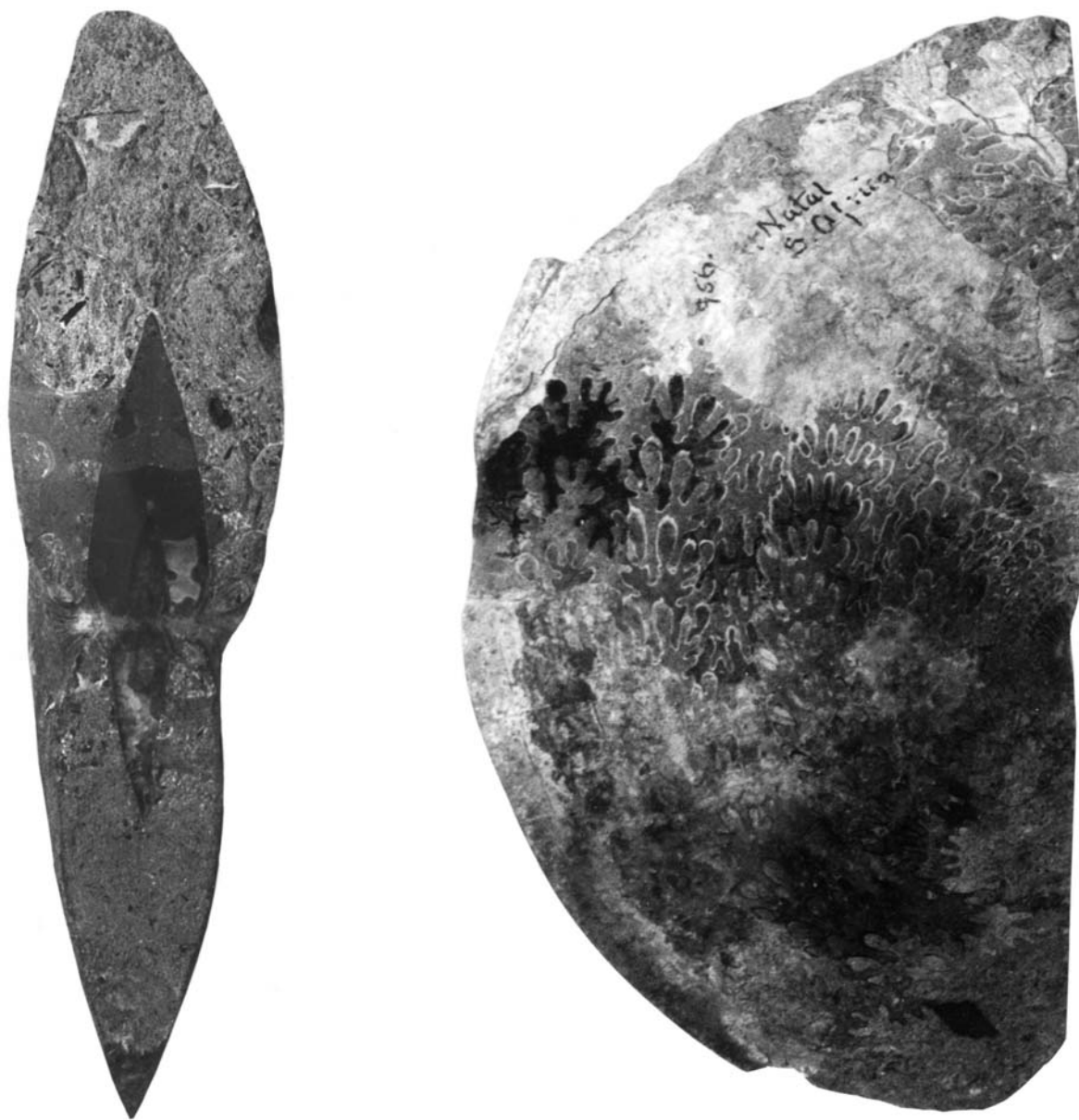


Fig. 2. *Eulophoceras natalense* Hyatt, 1903. The holotype, YPM 956, from 'Port Natal. S. Africa', that is to say the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980). The specimen is uncoated. Figures are $\times 1$.

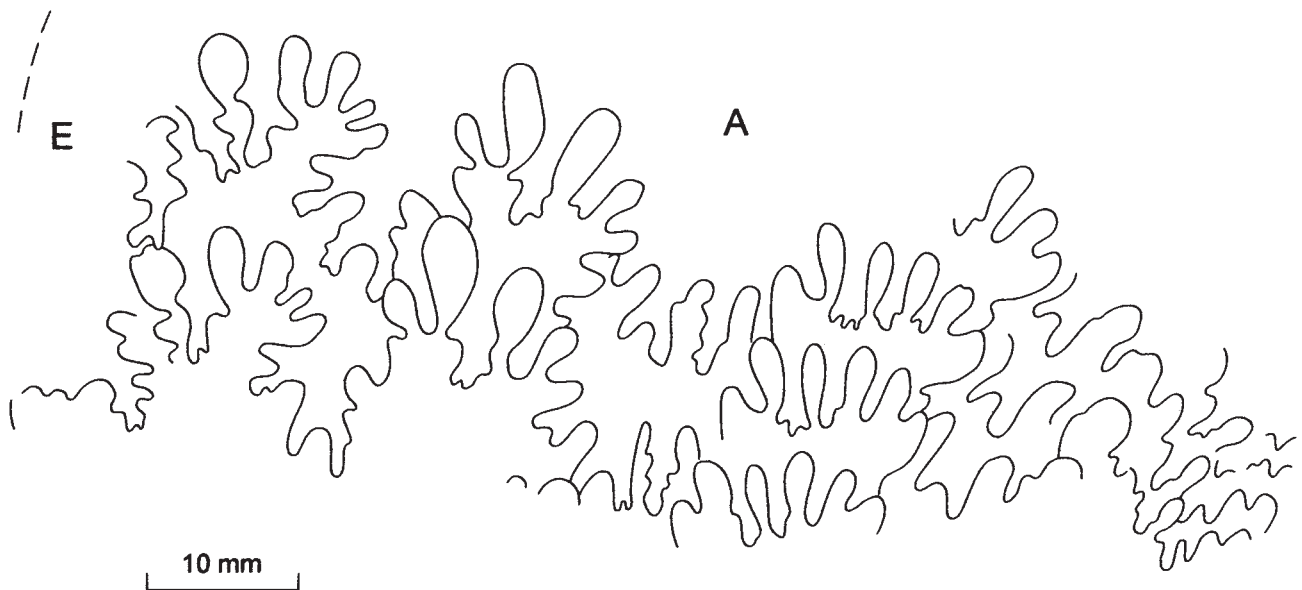


Fig. 3. *Eulophoceras natalense* Hyatt, 1903. External suture of the holotype, YPM 956, from 'Port Natal. S. Africa', that is to say the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980). Scale bar is 10 mm.



Fig. 4. *Skoumalia austriaca* Summesberger, 1979 form B, no. SK 1979/3, housed in the Skoumal Collection, Vienna, the original of Summesberger, 1980, pls 2, 3, text figs 5, 6, from the Upper Santonian of the Sandkalkbank of the Hockmooschichten of the Gosau Basin, Austria. Figures are $\times 1$.

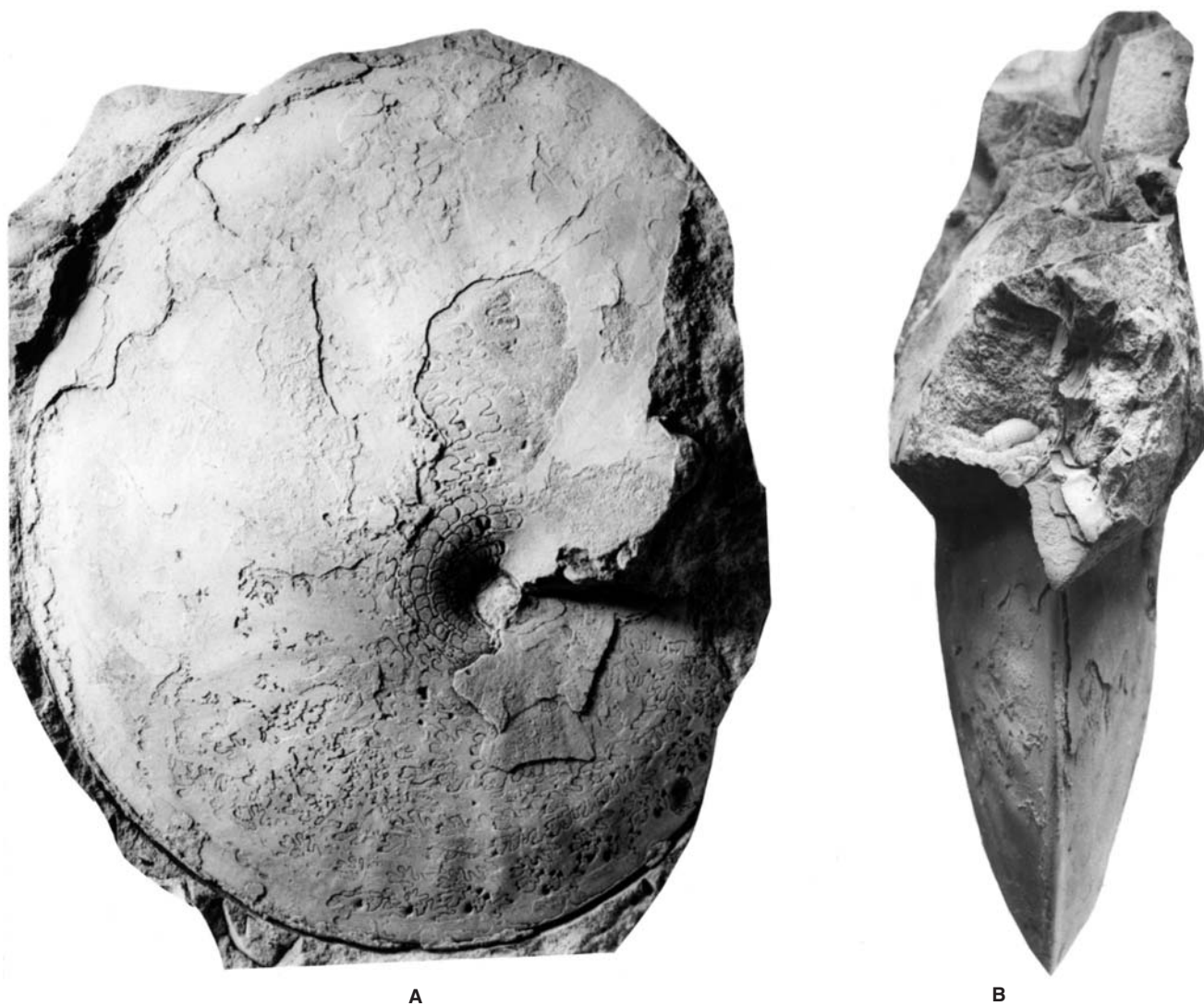


Fig. 5. A, B, *Eulophoceras natalense* Hyatt, 1903. A, SAM-PCZ19079 (formerly 4813), the original of Woods, 1906, pl. 42, fig. 3. B, The holotype of *Spheniscoceras africanum* Spath, 1921, the original of Spath, 1921, text-fig. C, 1a; 1922, pl. 6, fig. 1, BMNH C19421. Both specimens are from the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975 ; see also Klinger & Kennedy, 1980). Figures are $\times 1$.



Fig. 6. *Eulophoceras natalense* Hyatt, 1903. The holotype of *Spheniscoceras africanum* Spath, 1921, the original of Spath, 1921, text-fig. C, 1a; 1922, pl. 6, fig. 1, BMNH C19421, from the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980). Figures are $\times 1$.



Fig. 7. *Eulophoceras natalense* Hyatt, 1903. OUM KX5348, from the St Lucia Formation, Santonian III, at locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. Figures are $\times 1$.

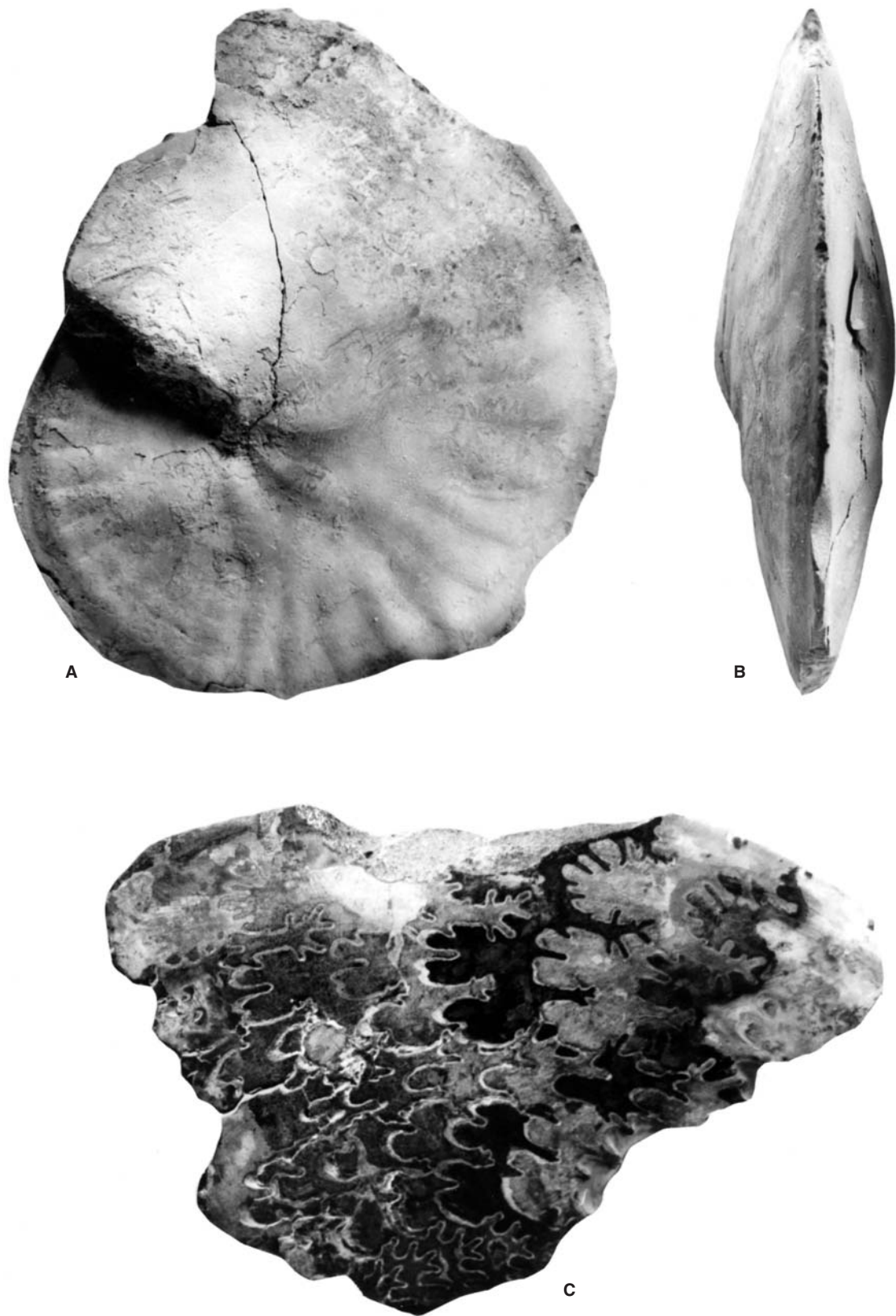


Fig. 8. *Eulophoceras natalense* Hyatt, 1903. **A, B**, the holotype of *Spheniscoceras minor*, Spath, 1921, the original of Spath, 1921, text-fig. C, 1b; 1922, pl. 6, fig. 2; pl. BMNH C19422. **C**, BMNH C19424, the original of *Spheniscoceras cf. amapondense* van Hoepen of Spath, 1922, p. 144, pl. 7, fig. 2. Both specimens are from the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975 see also Klinger & Kennedy, 1980). Figures A, B, are $\times 1$; Fig. C is $\times 2$.

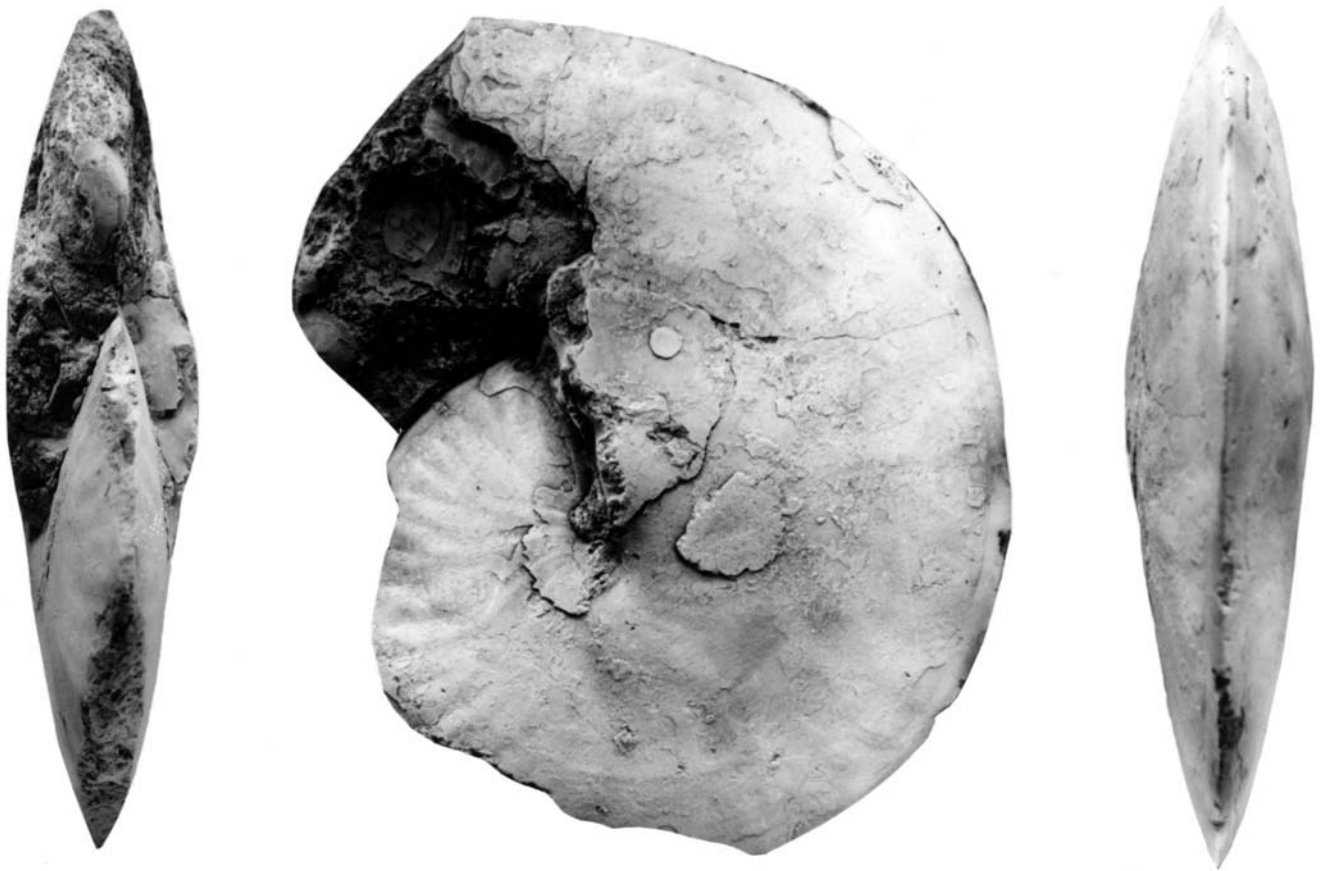


Fig. 9. *Eulophoceras natalense* Hyatt, 1903. The holotype of *Spheniscoceras tenue* Spath, 1921, the original of Spath, 1921, text-fig. C, 1c; 1922, pl. 7, fig. 3; pl. 8, fig. 3, BMNH C19423, from the Santonian-Lower Campanian Mzamba Formation, outcrops at the mouth of the Mzamba Estuary, Eastern Cape Province (locality 1 of Kennedy & Klinger, 1975; see also Klinger & Kennedy, 1980). Figures are $\times 1$.

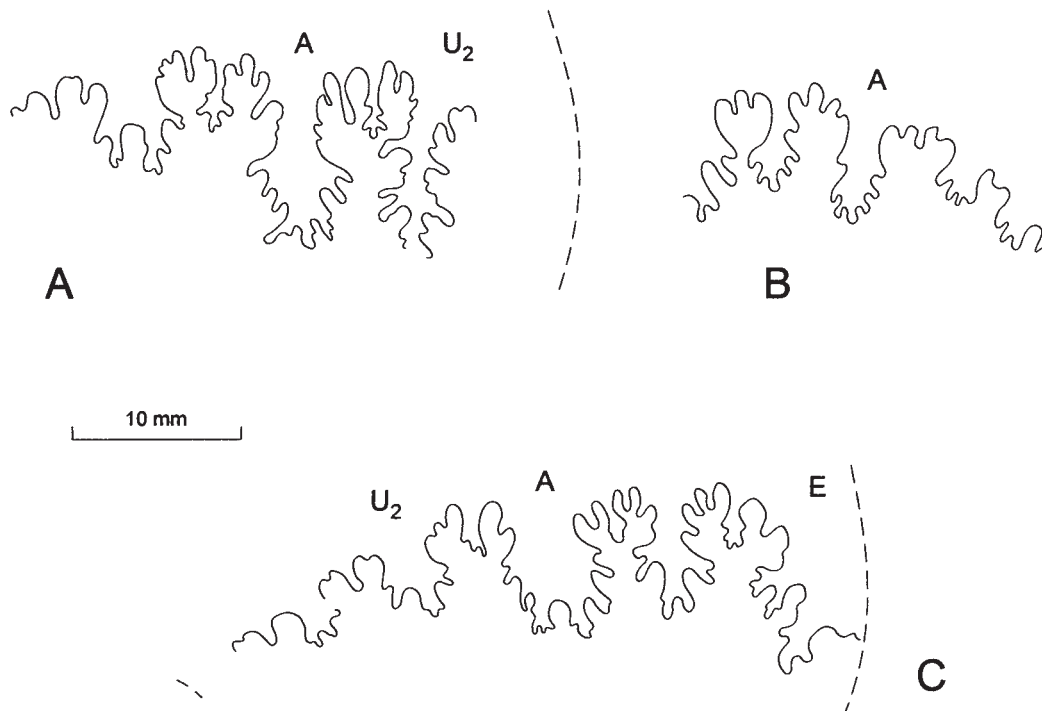


Fig. 10. External sutures of *Eulophoceras natalense* Hyatt, 1903. **A**, the holotype of *Spheniscoceras minor* Spath, 1921 BMNH C19422. **B**, the holotype of *Pelecodyscus capensis* Van Hoepen, 1921, drawn from Van Hoepen 1921, pl. 5, fig. 11. **C**, the holotype of *Spheniscoceras tenue*, Spath, 1921, BMNH C19423. Scale bar is 10 mm.

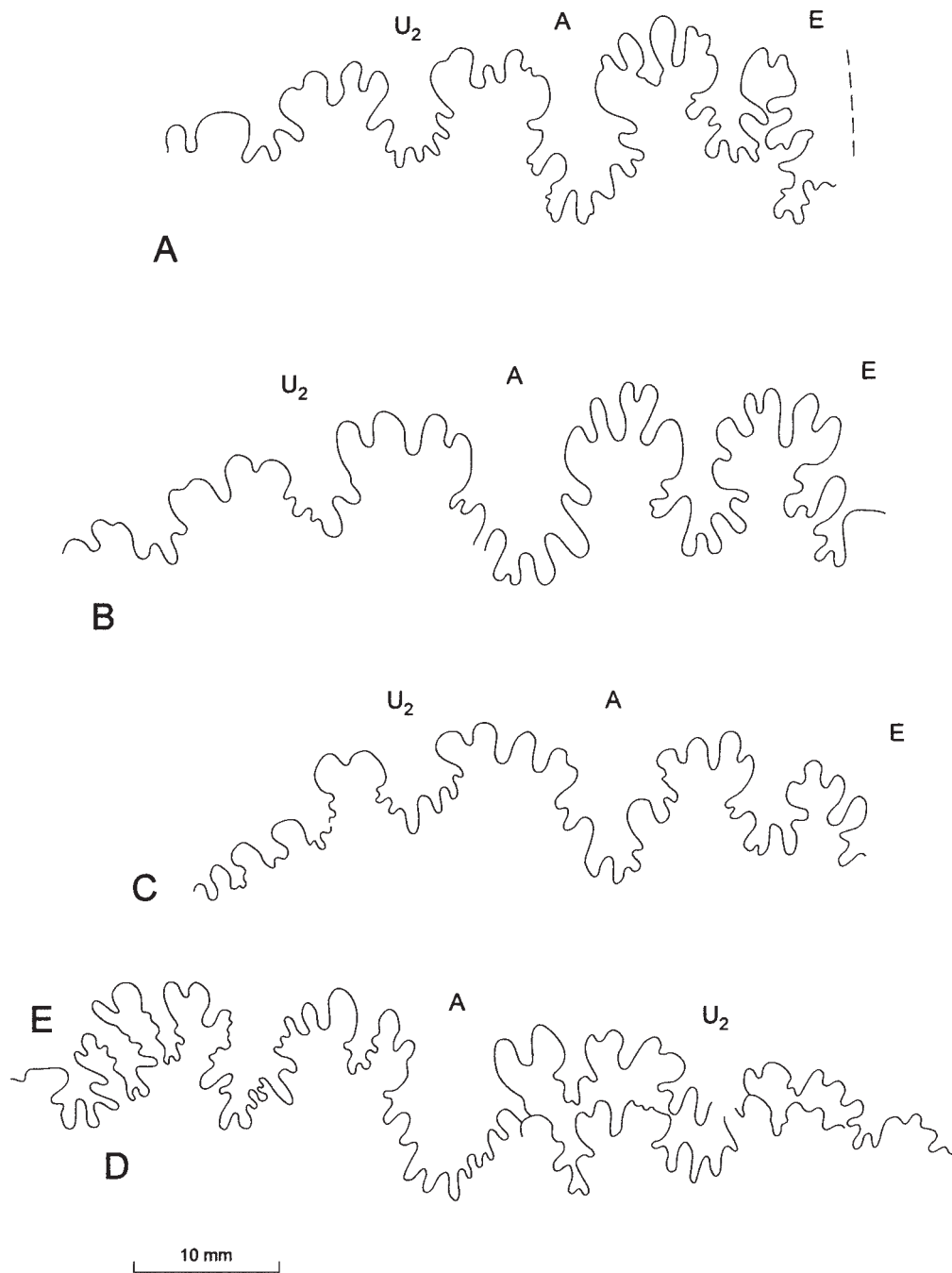


Fig. 11. External sutures. **A–C.** *Eulophoceras natalense* Hyatt, 1903. **A**, the holotype of *Spheniscoceras africanum* Spath, 1921, BMNH C19421. **B**, the holotype of *Pelecodiscus umzambiensis* Van Hoepen, 1921, drawn from Van Hoepen, 1921, pl. 6, fig. 1. **C**, the holotype of *Pelecodiscus amapondensis* Van Hoepen, 1921, pl. 7, fig. 1. **D**, *Eulophoceras jacobi* Hourcq, 1949, the holotype, the original of Hourcq, 1949, pl. 11 (1), fig. 2. Scale bar is 10 mm.

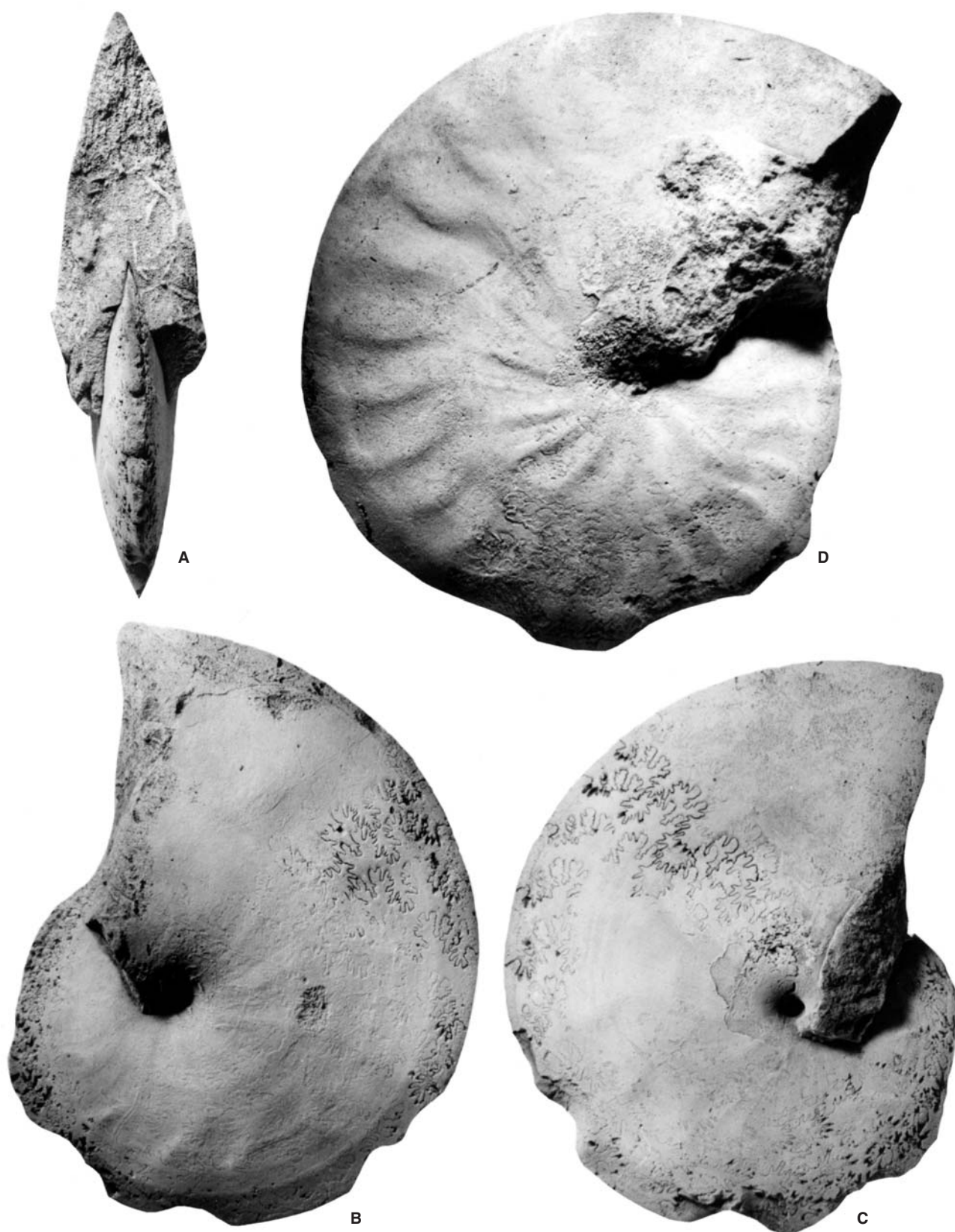


Fig. 12. A–C, *Eulophoceras jacobii* Hourcq, 1949, the lectotype, an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon, the original of Hourcq, 1949, pl. 11 (1), fig. 2. D, *Eulophoceras besairiei* Hourcq, 1949, the lectotype, EMP an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon, the original of Hourcq, 1949, pl. 11 (1), fig. 4. Both specimens are from the Lower Campanian of Berere, Madagascar. Figures are $\times 1$.



Fig. 13. A–D, *Eulophoceras bererense* Hourcq, 1949. A, B, the lectotype, an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon, the original of Hourcq, 1949, pl. 11 (1), fig. 3, from the Lower Campanian of Berere, Madagascar; C, OUM KX12924, from the St Lucia Formation, Campanian I–II, at locality 74 of Kennedy & Klinger (1975), Die Rooiwal, False Bay, Lake St Lucia, northern KwaZulu-Natal. D, the lectotype of *Eulophoceras miloni* Hourcq, 1949, an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon, the original of Hourcq, 1949, pl. 11 (1), fig. 3, from the Lower Campanian of Berere, Madagascar. Figures are $\times 1$.

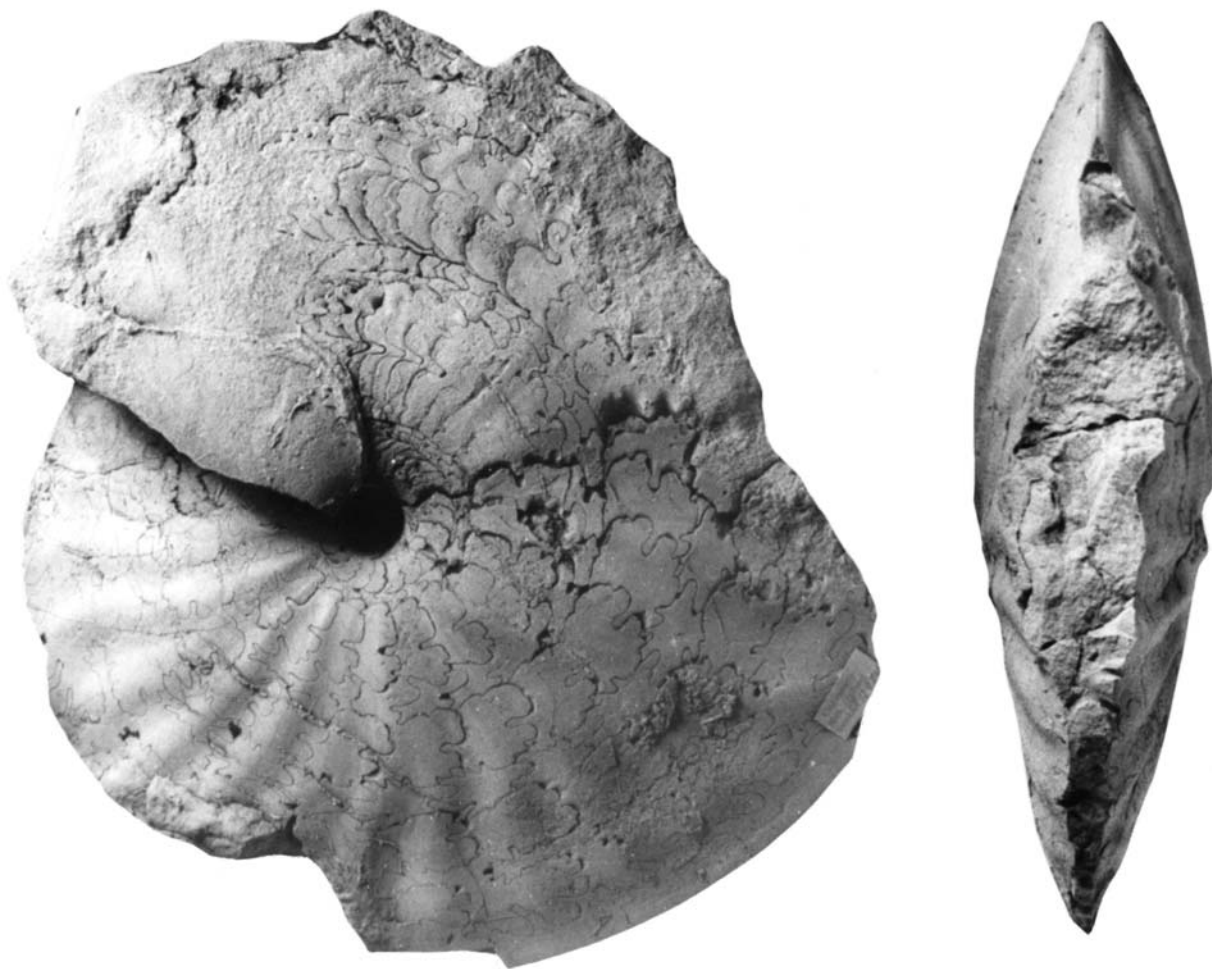


Fig. 14. *Eulophoceras bererense* Hourcq, 1949, OUM KX12924, from the St Lucia Formation, Campanian I–II, at locality 74 of Kennedy & Klinger (1975), Die Rooiwalle, False Bay, Lake St Lucia, northern KwaZulu-Natal. Figures are $\times 1$.



Fig. 15. *Eulophoceras hourcqi* Collignon, 1969. The holotype, the original of Collignon, 1969, pl. 601, fig. 2255, in the collections of the Université de Bourgogne, Dijon, from the Lower Campanian Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi* of Ampamba-Antsirasira (Belo-sur-Tsiribihina), Madagascar. Figures are $\times 1$.



Fig. 16. *Eulophoceras manambolense* Hourcq, 1949. The holotype, the original of Hourcq, 1949, pl. 13 (3), fig. 2, an unregistered specimen in the collections of the École des Mines, Paris, now housed in the collections of the Université Claude Bernard, Lyon from the Lower Campanian of Berere, Madagascar. Figures are $\times 1$.

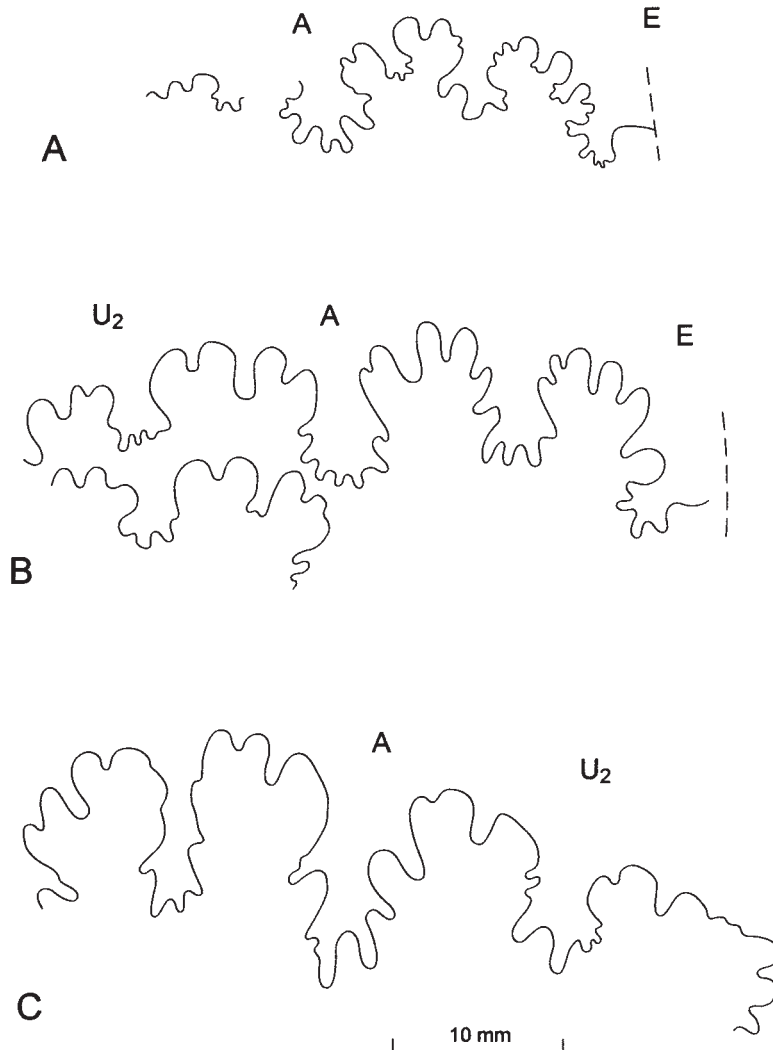


Fig. 17. External sutures. **A**, *Eulophoceras miloni* Hourcq, 1949, the lectotype, the original of Hourcq, 1949, pl. 11 (1), fig. 3. **B**, *Eulophoceras bererense* Hourcq, 1949, the lectotype, the original of Hourcq, 1949, pl. 11 (1), fig. 3. **C**, OUM KX12924. Scale bar is 10 mm.



Fig. 18. *Eulophoceras besairiei* Hourcq, 1949. The original of Collignon, 1969, p. 208, pl. 602, fig. 2257, in the collections of the Université de Bourgogne, Dijon, from the Lower Campanian Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi* of Ampamba-Antsirasira (Belo-sur-Tsiribihina), Madagascar. Figure is $\times 1$.



Fig. 19. *Eulophoceras besairiei* Hourcq, 1949. The original of Collignon, 1969, p. 208, pl. 602, fig. 2257, in the collections of the Université de Bourgogne, Dijon, from the Lower Campanian Zone à *Anapachydiscus wittekindi* et *Eulophoceras jacobi* of Ampamba-Antsirasira (Belo-sur-Tsiribihina), Madagascar. Figures are $\times 1$.