Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae

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Synopsis

Members of the ammonite family Gaudryceratidae occur widely in the South African Cretaceous, and are locally common. The earliest representative of the group, *Eogaudryceras* (*Eogaudryceras*), appears in the Upper Aptian, and species of *Gaudryceras* range to the Campanian. In all, twenty species referred to seven genera have been recognized; thirteen of the species represent new records for the area. The following species are described: *E.* (*Eogaudryceras*) *hertleini* (Wiedmann), *E.* (*E.*) *shimizui* Breistroffer, *Eogaudryceras* (*Eotetragonites*) *raspaili raspaili* Breistroffer, *E.* (*Eotetragonites*) *umbilicostriatus* Collignon, *Gaudryceras* cf. *varagurense* Kossmat, *G. stefaninii* Venzo, *G. varicostatum* van Hoepen, *G. denseplicatum* (Jimbo), *G. tenuiliratum* Yabe, '*Gaudryceras*' *sigcau* van Hoepen, '*Gaudryceras*' spp., *Anagaudryceras buddha* (Forbes), *A. subsacya* (Marshall), *A. politissimum* (Kossmat), *A. subtilineatum* (Kossmat), *A. pulchrum* (Crick), *Vertebrites kayei* (Forbes), *Zelandites odiensis* (Kossmat), *Zelandites* spp., *Kossmatella marut* (Stoliczka) and *Kossmatella* aff. *romana* Wiedmann. Lectotypes of *Anagaudryceras subtilineatum* (Kossmat) and *Vertebrites kayei* (Forbes) are selected. The collections allow illustration of the ontogeny and intraspecific variation in *Anagaudryceras buddha* and *A. pulchrum*, and show *Gaudryceras cinctum* Spath to be a synonym of *G. varicostatum*, '*G.*' *tenuiliratum* van Hoepen to be a synonym of *Anagaudryceras subtilineatum* and *G. amapondense* van Hoepen to be a synonym of *G. denseplicatum*. Several of the species are adequately illustrated for the first time.

Introduction

The superfamily Tetragonitaceae Hyatt, 1900 is a group of long-ranging forms conservative in external morphology, but the most advanced of ammonites in terms of sutures. They have a sexlobate primary suture, with a formula E LU_2 U_3 U_1, and a septal lobe, Is (p. 123). As Wiedmann (1963, 1973) and Kullman & Wiedmann (1970) have demonstrated, this progressive septal pattern suggests that, had the ammonites weathered the Cretaceous/Palaeocene crisis, the tetragonitids would be the group which would probably still be with us. The group evolved from the Lytoceratacea during the Barremian, although no forms with intermediate sutures are known (Wiedmann 1962*a*: 147). There has been considerable disagreement as to the subdivision of the superfamily, and we have adopted Wiedmann's conclusions in dividing the superfamily into two families, the Gaudryceratidae, South African representatives of which are described here, and the Tetragonitidae, to be described subsequently.

The Gaudryceratidae range from Barremian to Maastrichtian, and have a world-wide distribution. They are, however, rare in the boreal areas of north-west Europe and the Soviet Union, and the western interior of North America, being best known from the circum-Pacific area, north, east and west Africa, Madagascar and Antarctica. Typical gaudryceratids (*Gaudryceras*, *Vertebrites*) are evolute, many-whorled, depressed at first, becoming compressed as size increases, with an ornament of coarse to fine lirae, and bearing constrictions. The sutures are typically lytoceratinid, with more or less symmetrical bifid saddles, and a prominent septal lobe. Departures from this type include compressed genera such as *Mesogaudryceras* Spath, 1927 and *Zelandites* Marshall, 1926 or coronate forms with a keel-like lateral angle – *Jaubertella* Jacob, 1908 and *Gabbioceras* Hyatt, 1900.

There have been a number of attempts to subdivide the family. *Kossmatella* Jacob, 1907 has been placed in a subfamily Kossmatellinae Breistroffer, 1953, *Vertebrites* Marshall, 1926 in a subfamily Vertebritinae Wiedmann, 1962 and *Gabbioceras* Hyatt, 1900 and *Jauberticeras* Jacob, 1907 in a subfamily Gabbioceratinae Breistroffer, 1953.

All of the gaudryceratids appear to be intimately related, and species of individual genera often develop, at some stage in ontogeny, features which typify one or other of these subfamilies, as will be clear from our subsequent discussions and those of Wiedmann (1962*a*, *b*), Henderson (1970) and others. We do not, therefore, subdivide the family here.

In South Africa, gaudryceratids first appear in the Upper Aptian, with representatives of *E.* (*Eogaudryceras*). *E.* (*Eogaudryceras*) and *E.* (*Eotetragonites*) occur in the Middle Albian; the Upper Albian yields *Kossmatella* and abundant *Anagaudryceras* at some levels, and we have a few examples of the latter genus from the Upper Cretaceous. *Gaudryceras* appears in the Lower Cenomanian and occurs rarely up to the Campanian.

Most described collections of gaudryceratids consist of relatively few specimens. We have large collections of two species, *Anagaudryceras buddha* and *A. pulchrum*, which allow description of the range of intraspecific variation and ontogenetic changes within the group, whilst redescription of van Hoepen's material (1920, 1921) clarifies the relationships and nomenclatoral problems associated with the five gaudryceratids described by him.

Location of specimens

The following abbreviations are used to indicate the repositories of the material studied:

BM(NH)	British Museum (Natural History), London.
MHNG	Musée d'Histoire Naturelle, Geneva.
EMP	École des Mines, Paris.
MHNP	Muséum d'Histoire Naturelle, Paris.
SAS	South African Geological Survey, Pretoria.
TM	Transvaal Museum, Pretoria.
UND	University of Natal, Durban.
DM	Durban Museum.
SAM	South African Museum, Cape Town.
UPE	University of Pretoria, Pretoria.

Field localities

Outline details of field localities referred to in this paper are given in Kennedy & Klinger (1975); full descriptions of sections are deposited in the Palaeontology Library of the British Museum (Natural History).

Dimensions of specimens

Dimensions of specimens are given below in millimetres; abbreviations are as follows:

D = Diameter
Wb = Whorl breadth
Wh = Whorl height
U = Umbilical diameter

Figures in parentheses are dimensions as a percentage of the total diameter.

Suture terminology

The suture terminology of Wedekind (1916, see Kullman & Wiedmann 1970) is followed in the present work:

Is = Internal lobe with septal lobe
U = Umbilical lobe
L = Lateral lobe
E = External lobe

Systematic palaeontology

Class **CEPHALOPODA** Cuvier, 1797

Subclass **AMMONOIDEA** Zittel, 1884

Order **LYTOCERATIDA** Hyatt, 1899

Superfamily **TETRAGONITACEAE** Hyatt, 1900

Family **GAUDRYCERATIDAE** Spath, 1927

Genus ***EOGAUDRYCERAS*** Spath, 1927

Eogaudryceras is the root stock of all the younger gaudryceratids. Current treatment of the genus is sharply divided between those authors who would restrict it to forms without constrictions

(e.g. Spath 1927, Wright 1957, Murphy 1967*a*, *b*) and others (e.g. Wiedmann 1962*a*, *b*) who point to the presence of intermediates between the type species, *E. numidum*, and the type species of *Eotetragonites* Breistroffer, 1947, *E. raspaili* Breistroffer, and divide *Eogaudryceras* into two subgenera. *Eogaudryceras* s. str. gave rise to the gaudryceratids and *E.* (*Eotetragonites*) to the tetragonitids. A further complication arises from the view of Murphy (1967*a*, *b*), who places *Eotetragonites* within the Tetragonitidae because of its phylogenetic position. For our present purposes, we are impressed by Wiedmann's arguments, and have adopted a subdivision of *Eogaudryceras* into subgenera, as described below.

Subgenus ***EOGAUDRYCERAS*** Spath, 1927

TYPE SPECIES. *Ammonites numidus* Coquand 1880 : 22, by original designation.

DIAGNOSIS. Moderately evolute, whorl section initially trapezoidal, becoming rounded and in some cases laterally compressed when adult. Ornament consists of fine, flexuous lirae; mould smooth, constrictions absent or only weakly developed, typically confined to inner whorls. Suture with symmetrically bifid saddles and a large suspensive lobe.

DISCUSSION. *Eogaudryceras* was originally separated from *Eotetragonites* on the basis of the presence of strong constrictions throughout development and a suture with irregularly bifid saddles in the latter genus. Whilst these differences separate the type species, Wiedmann (1962*b* : 35) has pointed to the occurrence of *Eogaudryceras* with constrictions (*E. llosetaense* Breistroffer), *Eotetragonites* without constrictions (*E. blieuxiensis* Breistroffer) or with symmetrical saddles (e.g. Fallot 1920). The two subgenera are thus better separated on the basis of the intially trapezoidal and subsequently rounded whorl and the fine, moderately curved striae of *Eogaudryceras*, as opposed to the square whorl section and general absence of curved striae in *Eotetragonites*. These points stress the similarities and close relationships between the two subgenera, and their critical position in tetragonitid phylogeny.

Eogaudryceras also shows superficial similarities with *Anagaudryceras* Shimizu, 1934, but the fine lirae and frequent collar-ribs and constrictions of that genus differentiate juveniles, whilst adult ornament clearly differentiates the two. *Gaudryceras* Grossouvre, 1894 and *Vertebrites* Marshall, 1926 develop their distinctive ornament at such an early stage that confusion is unlikely.

The following are the chief *Eogaudryceras* (*Eogaudryceras*) species and varieties currently recognized: *Eogaudryceras numidum numidum* (Coquand 1880 : 22) and *E. numidum* (Coquand) *besavoaensis* Collignon (1962 : 13; pl. 221, fig. 956), Aptian-Albian; *E. turgidum* Breistroffer (1947 : 58), Aptian; *E. vocontianum* (Fallot 1920 : 233; pl. 2, fig. 2; text-fig. 4), Albian; *E. muntaneri* Wiedmann (1962*b*: 42; pl. 2, fig. 5; text-fig. 14), Albian; *E. llosetaense* Breistroffer (1947 : 58), Albian; *E. elegans* Basse (1928 : 134; pl. 8, fig. 8; text-figs 11–12), Albian; *E. inequale* Breistroffer (1947 : 58), Albian; *E. shimizui shimizui* Breistroffer (*in* Besairie 1936 : 175–176), Albian; *E. shimizui skoenbergense* Collignon (1949 : 50; pl. 21, figs 2, 3), Albian; *E. shimizui gaonai* Wiedmann (1962*a* : 153; pl. 8, fig. 4; text-fig. 13), Albian; *E. bourritianum bourritianum* (Pictet 1848 : 298; pl. 4, fig. 1a–c), Albian; *E. bourritianum hispanicum* Wiedmann (1962*a* : 155; pl. 12, fig. 6; text-fig. 15), Albian; *E. italicum* Wiedmann & Dieni (1968 : 34; pl. 1, fig. 8; text-fig. 6), Albian; *E. hertleini* (Wiedmann 1962*c* : 16, 18, 19; pl. 1, fig. 3), Aptian.

OCCURRENCE. *E.* (*Eogaudryceras*) ranges from the Upper Aptian to Upper Albian. Species are best known from the western Mediterranean area (southern France, Balearics, Sardinia) but also occur in northern Spain, England, central Europe, north Africa, Madagascar, California and South Africa (Zululand).

Eogaudryceras* (*Eogaudryceras*) *shimizui Breistroffer ***skoenbergense*** Collignon

1949 *Eogaudryceras skoenbergense* Collignon : 50; pl. 21, figs 2, 3.
1960 *Eogaudryceras shimizui* Breistroffer; Casey : 9; pl. 1, fig. 2.
1962*a* *Eogaudryceras shimizui* Breistroffer *skoenbergense* Collignon; Wiedmann : 151 et seqq.
1968 *Eogaudryceras shimizui* Breistroffer *skoenbergense* Collignon; Wiedmann & Dieni : 33 et seqq.

DISCUSSION. Collignon (1949) introduced *Eogaudryceras skoenbergense* in discussions of *E. shimizui*, basing the species on two figured specimens (1949 : pl. 21, figs 2–2b, 3–3b) said to be from the Skoenberg, Zululand. Wiedmann (1962*a* : 151), in his detailed discussion of *Eogaudryceras*, divided *E. shimizui* into three successive subspecies as follows:

High Upper Albian: *Eogaudryceras shimizui gaonai*, with a depressed oval whorl section.
Low Upper Albian: *Eogaudryceras shimizui shimizui*, with a compressed oval whorl section.
Middle Albian: *Eogaudryceras shimizui skoenbergense*, with a rounded whorl section.

Although we have collected no further specimens which can be referred to *E. shimizui skoenbergense*, otherwise than the South African material known only very doubtfully from southern England, comment is needed because of the type locality given for the subspecies. No Middle Albian sediments outcrop on the Skoenberg, and the specimens are therefore of either Upper Albian or Cenomanian age, and *E. shimizui skoenbergense* would thus be the *latest* known *Eogaudryceras*. Alternatively the specimens in fact come from Middle Albian sediments exposed along the Mzinene, well to the west (Kennedy & Klinger 1975), perhaps in the area of our Locality 53, on the farm Izwehelia (1975 : 288).

Eogaudryceras (*Eogaudryceras*) *hertleini* (Wiedmann)
(Pl. 1, fig. 1)

1938 *Lytoceras* (*Gabbioceras*) *wintunium* Anderson : 150 (pars); pl. 15, fig. 5, *non* pl. 16, figs 2–5.
1962*c* *Gabbiocerus hertleini* Wiedmann : 16, 18, 19; pl. 1, fig. 3.
1967*b* *Eogaudryceras hertleini* (Wiedmann) Murphy : 9; pl. 1, figs 2–5.

HOLOTYPE. California Academy of Sciences no. 8767, from the Upper Aptian of Shasta County, California.

MATERIAL. A single specimen, BM(NH) C78755 from the Makatini Formation at Loc. 37, Mzinene River, Zululand (Aptian IV).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
BM(NH) C78755	39·5	18·0 (46)	16·4 (42)	1·1	12·2 (31)

DESCRIPTION. The coiling is relatively involute, over 50% of the previous whorl being covered, with a depressed whorl section (whorl breadth/height ratio varies from 1·2 to 1·1, decreasing as diameter increases) with greatest breadth close to mid-flank. The umbilicus is small, with a subvertical wall and abruptly rounded shoulder. The sides are flattened with a broadly rounded venter during the early growth stages, the whorl section becoming rounded as diameter increases.

The shell surface is covered by fine, flexuous striae which arise at the umbilical seam, and sweep forwards across the ventrolateral shoulders to form a broad, shallow ventral peak. Occasional groups of striae become stronger to produce incipient collar ribs, associated with faint constrictions (Pl. 1, fig. 1a).

The sutures are not fully visible in our specimen, but include a large bifid first lateral saddle (E/L), a smaller bifid second lateral saddle (L/U_2) and a suspensive lobe with a large first auxiliary saddle.

DISCUSSION. Species of *Eogaudryceras* are differentiated chiefly on relative proportions, whorl section, form of growth striae and nature of constrictions, if present. Our specimen thus most closely resembles *Eogaudryceras hertleini*, in particular the specimens figured by Murphy (1967*b* : pl. 1, figs 2–5). These specimens differ, however, in having some well-formed collar ribs, a feature poorly developed in our specimen. Murphy notes some variation in this feature, however, and reference of our material to *E. hertleini* seems acceptable.

Other species can be differentiated from *Eogaudryceras hertleini* as follows. *Eogaudryceras bourritianum bourritianum* (neotype refigured by Wiedmann 1962*a* : pl. 13, figs 2a–b, and by Murphy 1967*b* : pl. 5, fig. 11) has a very depressed whorl section. *E. bourritianum hispanicum* Wiedmann (1962*a* : pl. 12, fig. 6; text-fig. 16) has a depressed, trapezoidal whorl section with a flattened venter. *Eogaudryceras shimizui shimizui*, *skoenbergense* and *gaonai* all have differing

whorl sections and are also easily distinguished by the presence of three conspicuous collar-like ribs per whorl. *Eogaudryceras elegans* Basse has a trigonal whorl section and lirae rather than striae; in *E. llosetaense* and *E. muntaneri* there are obvious constrictions, *E. muntaneri* having a trapezoidal whorl section. *E. turgidum* is depressed (whorl breadth/height ratio up to 1·4) with a trapezoidal whorl section. *Eogaudryceras numidum numidum* and *besavoaensis* have differing whorl sections, becoming trigonal and distinctly compressed at large diameters, with an abruptly rounded umbilical shoulder.

OCCURRENCE. *Eogaudryceras hertleini* is known only from the Upper Aptian of California and Zululand.

Subgenus ***EOTETRAGONITES*** Breistroffer, 1947

TYPE SPECIES. *Eotetragonites raspaili* Breistroffer, by original designation.

DIAGNOSIS. Moderately evolute, with a rectangular whorl section, even when young. Shell surface smooth, or finely striate; constrictions typically strong, and present throughout ontogeny. External suture line with asymmetrically bifid saddles; internal suture with an incipient second lateral saddle.

DISCUSSION. The relationship between *Eogaudryceras* and *Eotetragonites* is discussed above. There are also difficulties in separating some *Eotetragonites* from *Tetragonites* species, as might be expected from their phylogenetic relationship. In general, however, the constrictions are deeper in *Eotetragonites* (although unconstricted forms are known) and straight or convex on the flanks with a strong ventral peak. The close relationship of the two taxa remains, however, as is clear from the reference of the same specimen to both in the most recent reviews, one by Wiedmann (1962*b*) and the other by Murphy (1967*a*, *b*).

The chief *Eogaudryceras* (*Eotetragonites*) species are: *E.* (*Eot.*) *raspaili raspaili* Breistroffer (1947 : 47), Aptian; *E.* (*Eot.*) *raspaili jacobi* (Kilian) (*in* Fallot 1920 : 237; pl. 2, fig. 7; text-fig. 6), Aptian; *E.* (*Eot.*) *jallabertianus* (Pictet 1848 : 302; pl. 4, figs 2a–b), Albian; *E.* (*Eot.*) *plurisulcatus* Breistroffer (1947 : 57), Aptian; *E.* (*Eot.*) *umbilicostriatus* Collignon (1949 : 48; pl. 13, figs 4a–b; pl. 21, fig. 5), Albian; *E.* (*Eot.*) *duvalianum duvalianum* (d'Orbigny 1841 : 158; pl. 50, figs 4–6), Aptian; *E.* (*Eot.*) *duvalianum* (d'Orbigny) *cheinourense* Breistroffer & Mahmoud (1956 : 81), Aptian-Albian; *E.* (*Eot.*) *kossmatelliformis* (Fallot 1920 : 240; pl. 2, figs 4a–c), Aptian; *E.* (*Eot.*) *gainesi* (Anderson 1938 : 153; pl. 20, figs 3, 4, 5), Albian; *E.* (*Eot.*) *wintunius* (Anderson 1938 : 150; pl. 16, figs 2–5, *non* pl. 15, fig. 5, = *Eogaudryceras hertleini* (Wiedmann)), Aptian; *E.* (*Eot.*) *shoupi* Murphy (1967*b* : 22; pl. 3, figs 7, 8, 9), Aptian; *E.* (*Eot.*) *crudus* Drushchits (1956 : 105; pl. 8, fig. 29), Lower Albian; *E.* (*Eot.*) *gardneri* Murphy (1967*a* : 75; pl. 1, figs 6–9), Aptian.

OCCURRENCE. *Eotetragonites* ranges from the Upper Aptian to Middle Albian. Species are best known from the western Mediterranean (southern France, Balearics), and also occur in central Europe, Bulgaria, the Caucasus, north Africa, South Africa (Zululand), Madagascar and California.

Eogaudryceras* (*Eotetragonites*) *raspaili raspaili Breistroffer
(Pl. 1, fig. 6)

1866 *Ammonites depressus* Raspail : 29; pl. 2, fig. 9 (non *Ammonites depressus* Bruguière 1789).
1913 *Lytoceras* (*Tetragonites*) *depressus* (Raspail) Kilian : 329; pl. 11, fig. 3a–b.
1920 *Tetragonites depressus* (Raspail); Fallot : 239; pl. 2, fig. 8; text-fig. 7.
1947 *Eotetragonites depressus* (Raspail) Breistroffer : 56.
1947 *Eotetragonites raspaili* Breistroffer : 83.
1962*b* *E.* (*Eotetragonites*) *raspaili* Breistroffer; Wiedmann : 44.

HOLOTYPE. Original of *Lytoceras* (*Tetragonites*) *depressus* (Raspail) Kilian (1913 : 329; pl. 11, fig. 3), from the Aptian of southern France.

MATERIAL. One specimen only, BM(NH) C78772 from the Mzinene Formation at Loc. 175, Ndumu, Zululand (Albian III).

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78772	30·0	–	10·8 (36)	–	11·5 (38)

Description. The coiling is moderately evolute, slowly expanding, and distinctly polygonal on the outer whorl. The umbilicus is of moderate size (26% of diameter), shallow, with an outward-sloping wall and an abruptly rounded shoulder. The flanks are flattened and subparallel, the ventrolateral shoulders abruptly rounded, and the venter flattened. The surface of the shell is virtually smooth, save for fine, straight prorsiradiate striae on the flanks, which flex forwards across the ventrolateral shoulders to form a broad ventral peak. There are eight constrictions on the outer whorl; these are shallow on the shell, but deep and prominent on the internal mould, which is otherwise smooth. Constrictions arise at the umbilical seam, are strongly prorsiradiate on the flank, straight at first, but becoming faintly convex as diameter increases. They pass straight up the umbilical wall, sweep forwards across the inner flank and are markedly prorsiradiate, flex backwards across the mid-flank to pass straight across the upper flank, faintly backwards across the ventrolateral shoulder and forwards across the venter to form a very shallow, broad ventral peak. Occasional striae are strengthened into low ribs (? 3 on the outer whorl), perhaps corresponding to the constrictions on the internal mould.

The suture includes a large assymetrically bifid first lateral saddle (E/L) and a smaller but otherwise similar second lateral saddle (L/U_2) separated by a large, deeply incised, bifid lateral lobe (L).

Discussion. The limited number of constrictions on our specimen, their course, at first straight but later slightly convex, and the rectangular whorl section compare well with published figures of *Eotetragonites raspaili*. The rounded ventrolateral shoulders further suggest our specimen is closer to the restricted form than to *Eotetragonites raspaili jacobi*, where the shoulders are markedly angular.

Other species, including *Eotetragonites jallabertianus* (see Murphy 1967*b*: pl. 5, figs 7–8 for photographs of the type material), *E. plurisulcatus* (= *Tetragonites duvali* Anthula 1899: pl. 7, figs 3a–b), *E. duvalianum duvalianum* and *cheinourense*, *E. kossmatelliformis*, *E. umbilicostriatus*, *E. gainesi*, *E. shoupi* and *E. wintunius* all have far more constrictions, and these are generally curved or flexuous.

Occurrence. Upper Aptian of the western Mediterranean; Middle Albian of Zululand.

Eogaudryceras (*Eotetragonites*) *umbilicostriatus* Collignon
(Pl. 1, fig. 3)

1949 *Eotetragonites umbilicostriatus* Collignon: 48; pl. 8, fig. 4; pl. 21, fig. 5.
1963 *Eotetragonites umbilicostriatus* Collignon; Collignon: 17; pl. 248, fig. 1060.

Holotype. Original specimen figured by Collignon (1949: pl. 8, fig. 4; pl. 21, fig. 5) from the Lower Albian of Ambarimaninga, Madagascar.

Material. A single specimen, BM(NH) C78830 from the Mzinene Formation at Loc. 36 on the Mzinene River, Zululand (Albian III).

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (from Collignon 1949: 48)	21·0	9 (43)	8 (38)	1·13	8 (38)
Collignon 1963: 17	71·0	32 (45)	32 (42)	1·00	25 (35)
BM(NH) C78830	38·0	–	14·6 (38)	–	15·2 (40)

Description. The specimen is poorly preserved, one side being abraded; it retains recrystallized test, so the sutures are not visible although the specimen is wholly septate. The coiling is fairly evolute, the whorls expanding at a moderate rate, with a ? depressed subrectangular whorl section, the greatest breadth being close to mid-flank. The umbilicus is broad and shallow, with a rounded, outward-sloping wall and an abruptly rounded shoulder. The sides are flattened and subparallel, the ventrolateral shoulder rounded, and the venter flattened. The test is weathered,

and growth striae, if once present, are no longer preserved. Instead, there are closely-spaced shallow, flexuous constrictions on the outer whorl. These arise at the umbilical seam, pass straight up the umbilical wall, flex gently forwards and are slightly convex on the flanks, flex gently backwards across the upper flank, and gently forwards across the shoulder to connect across the venter with a weak ventral peak.

So far as can be seen, the inner whorls bore fewer, broader, straighter constrictions, ? 6 per whorl.

DISCUSSION. Collignon (1949) based *Eotetragonites umbilicostriatus* on a juvenile specimen with four to five strong constrictions and a curious umbilical ornament. Subsequently (1963 : 17; pl. 248, fig. 1060) he figured an adult showing denser constrictions, with which our specimen closely agrees.

Eotetragonites umbilicostriatus can be separated from other species of the subgenus on the basis of the curious juvenile ornament, but when this is not preserved, the closely-spaced constrictions are diagnostic, being far less flexed than those of *Eotetragonites duvalianum*, *E. plurisulcatus*, *E. wintunius* or *E. gardneri*. The constrictions of *E. balmensis* are straight on the flank, and the proportions are quite different; adult *E. jacobi* and *E. blieuxiensis* lack prominent constrictions, *E. raspaili* has far fewer constrictions and a squarer whorl section, whilst the poorly-known *E. jallabertianus* has rather more, flexuous constrictions.

OCCURRENCE. Lower Albian of Madagascar and South Africa (Zululand).

Genus *GAUDRYCERAS* de Grossouvre, 1894

TYPE SPECIES. *Ammonites mitis* von Hauer, 1866, by the subsequent designation of Boule, Lemoine & Thévenin (1906).

SYNONYMY. *Epigaudryceras* Shimizu, 1934 (type species *Gaudryceras striatum* Jimbo 1894, by original designation); *Pseudogaudryceras* Shimizu, 1934 (type species *Gaudryceras tenuiliratum* var. *infrequens* Yabe 1903, by original designation); *Hemigaudryceras* Shimizu, 1934 (type species *Lytoceras* (*Gaudryceras*) *denmanense* Whiteaves 1901, by original designation); *Neogaudryceras* Shimizu, 1934 (type species *Gaudryceras tenuiliratum* Yabe 1903, by original designation).

DIAGNOSIS. Typically evolute, early whorls depressed, slowly expanding, later whorls compressed, expanding more rapidly. Ornament consists of lirae, flexuous or branched, fine and wire-like throughout ontogeny or coarsening and bunching on the outer whorl. Constrictions are present on the internal mould, being marked on the shell by faint collars and depressions. Suture with large bifid lobes and saddles, suspensive lobe typically retracted, with several auxiliaries.

DISCUSSION. This genus has been reviewed at some length by Wright & Matsumoto (1954 : 111–113), Matsumoto (1959*a* : 141) and Howarth (1965 : 360). Wiedmann (1962*a* : 156) provides a detailed synonymy for the genus, but we feel that, given currently accepted generic divisions of the gaudryceratids, *Anagaudryceras* Shimizu, 1934 and *Mesogaudryceras* Spath, 1927 bear separation as either genera or subgenera.

About thirty specific names have been given to gaudryceratids which can be placed in the genus with certainty, as listed by Collignon (1956 : 67–69) and Howarth (1965 : 360), to which can be added *Gaudryceras anomatum* Collignon 1966 and *Gaudryceras yokoyamaiforme* Collignon 1969.

Species of the genus fall into three subgroups, which may be differentiated on characters of adult ornamentation. They probably do not merit subgeneric separation:

1. The group of *Gaudryceras mite* von Hauer, where fine, equal ribs are present throughout ontogeny. The chief species are: *Gaudryceras mite* von Hauer (1866 : 6; pl. 2, figs 3, 4), Santonian to Campanian; *Gaudryceras varagurense* Kossmat (1895 : 122; pl. 17, fig. 9; pl. 18, fig. 2) Turonian to Campanian; *Gaudryceras analabense* Collignon (1956 : 54; pl. 6, figs 1–3), Coniacian; *Gaudryceras beantalyense* Collignon (1956 : 53; pl. 5, figs 1–3), Coniacian; *Gaudryceras varicostatum* van Hoepen (1921 : 7; pl. 2, figs 10–12); *Gaudryceras devallense* Anderson (1958 : 183; pl. 41, fig. 4), Coniacian or Santonian; *Gaudryceras striatum* Jimbo (1894 : 181; pl. 6, fig. 6), Santonian to Maastrichtian; *Gaudryceras stefanini* Venzo (1936 : 21; pl. 2, figs 3, 4), Cenomanian.

2. The group of *Gaudryceras denseplicatum* Jimbo, in which coarse, fold-like ribs appear in the adult in addition to finer lirae (= *Neogaudryceras* Shimizu, 1934). The chief species are: *Gaudryceras denseplicatum* (Jimbo 1894 : 182; pl. 23, figs 1–1a), Turonian to Campanian; *Gaudryceras glannegense* Redtenbacher (1873 : 119; pl. 27, figs 3a–b), Coniacian; *Gaudryceras lauteli* Collignon (1956 : 57; pl. 7, figs 1–1a), Santonian; *Gaudryceras vascogoticum* Wiedmann (1962*a* : 159; pl. 9, figs 2, 6; text-fig. 17), Coniacian; *Gaudryceras amapondense* van Hoepen (1920 : 142; pl. 24, figs 1–3), Santonian to Campanian.

3. The group of *Gaudryceras tenuiliratum* Yabe with finely ribbed inner and coarsely ribbed outer whorls. This includes *Gaudryceras tenuiliratum* Yabe (1903 : 19; pl. 3, figs 3, 4), Coniacian to Campanian; and *Gaudryceras denmanense* Whiteaves (1903 : 329), Campanian.

In addition there is almost a score of juvenile gaudryceratids described in the literature which may be valid species or mere inner whorls of well-known forms. Many of these are listed by Collignon (1956 : 70).

Gaudryceras is readily separable from the more closely related gaudryceratid genera as follows. *Anagaudryceras* Shimizu, 1934, is typically very finely lirate, with widely-spaced constrictions and collars when young, and has adult whorls which may or may not develop coarse folds (= *Paragaudryceras* auctt.) by approximation of constrictions. *Mesogaudryceras* Spath, 1927, is compressed, involute, and finely lirate, without constrictions. *Vertebrites* Marshall, 1926, is small, very evolute, serpenticone, with depressed whorls and an ornament of strong lirae on the flank which split into hair-like striae over the venter. Some *Gaudryceras* (e.g. *G. stefaninii*) develop this feature when young, foreshadowing the persistence of the feature in adult *Vertebrites*.

OCCURRENCE. *Gaudryceras* has a time range extending from Upper Albian to Maastrichtian; the geographical range includes Antarctica, New Zealand, Madagascar, South Africa (Zululand and Natal), Angola, north Africa, the Middle East, central and southern Europe, southern India, Japan, Sakhalin, Kamchatka, Alaska, British Columbia, California, Chile and southern Patagonia.

Gaudryceras cf. *varagurense* Kossmat
(Pl. 1, figs 4, 7)

cf. 1895 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat : 122; pl. 17, fig. 9; pl. 18, figs 2a–c.
cf. 1965 *Gaudryceras varagurense* Kossmat; Howarth : 36; pl. 4, fig. 5; pl. 5, figs 1–2 (with synonymy).
cf. 1965*a* *Gaudryceras varagurense* Kossmat; Collignon : 2; pl. 376, fig. 1635.
cf. 1965*b* *Gaudryceras varagurense* Kossmat; Collignon : 2; pl. 415, fig. 1712.
cf. 1966 *Gaudryceras varagurense* Kossmat; Collignon : 2, 3; pl. 455, fig. 1852.
cf. 1966 *Gaudryceras varagurense* Kossmat; Howarth : 4; pl. 1, figs 6, 7 (with synonymy).

MATERIAL. Two specimens. SAS SM/2 from the St Lucia Formation at Loc. 63, Skoenberg, Zululand (Coniacian I); BM(NH) C78825 from the St Lucia Formation at Loc. 85, False Bay (Santonian I).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
SAS SM/2	31·8	11·6 (36)	10·8 (34)	1·07	15·6 (49)

DESCRIPTION. The smaller specimen, SAS SM/2, is wholly septate, and retains recrystallized test. The coiling is very evolute, the whorls slowly expanding, depressed, but becoming less so as diameter increases. The greatest breadth is some way below mid-flank. The umbilicus is broad and shallow, with a low, subvertical wall, abruptly rounded shoulder, somewhat flattened, rounded, convergent flanks and a broad, arched venter.

Ornament consists of fine dense lirae, which typically arise at all points from the umbilical seam to mid-flank; many branch at various points on the flank. The lirae pass forwards across the umbilical wall, are markedly prorsiradiate on the lower flank, but flex backwards at mid-flank only to flex forwards across the ventrolateral shoulder to form a distinct if shallow ventral peak. There are ? six strong collar-like ribs on the outer whorl, preceding shallow, narrow constrictions. The sutures are not visible.

The larger specimen, BM(NH) C78825, is a mere fragment, with a maximum whorl height of

18 mm. At this size, the whorls appear to have been slightly compressed, with convergent flanks. Typical flexuous lirae are present on the test, but the internal mould is smooth, save for constrictions. The suture line is poorly exposed, but includes an asymmetrically bifid first lateral saddle (E/L), a smaller second lateral saddle (L/U_2) and a weakly retracted suspensive lobe.

DISCUSSION. The dense, even lirae and relative proportions of our two specimens clearly place them in the group of *Gaudryceras varagurense*; the ornament of our smaller specimen matches closely the inner whorls of Kossmat's type.

The taxonomy of this species has been clarified by Howarth (1965 : 362). As he notes, *Gaudryceras mite* is too poorly understood at present for satisfactory interpretation, whilst there are three names applied to forms matching our material in the Indian Ocean area: *G. varagurense* known from Cenomanian to Campanian, and *Gaudryceras analabense* and *G. beantalyense* both from the Coniacian of Madagascar, where they occur with *G. varagurense*. From the published figures, we doubt, however, that these species bear separation, although our material does not allow comment on the problem. *G. analabense* is said to possess markedly flexuous fine lirae with a strong ventral projection; *G. beantalyense* has less flexuous lirae and lacks a projection.

OCCURRENCE. *Gaudryceras varagurense* ranges from Turonian to Campanian, and there are records from Spain, southern India, Madagascar, Antarctica and Angola in addition to our present Zululand occurrences.

Gaudryceras stefaninii Venzo
(Pl. 1, figs 2, 5, 8; Pl. 2)

1936 *Lytoceras* (*Gaudryceras*) *stefaninii* Venzo : 21; pl. 2, figs 3, 4.
1956 *Gaudryceras stefaninii* Venzo; Collignon : 67.
1963 *Gaudryceras stefaninii* Venzo; Collignon : 16; pl. 247, fig. 1057.
1964 *Gaudryceras stefaninii* Venzo; Collignon : 4; pl. 318, fig. 1352.

TYPE. In a letter dated 15.5.1974, Dr Ladini Walter of the Museo di Paleontologica of the University of Pisa informed us that part or all of Venzo's collection may have been destroyed during the 1939–45 war. We have therefore refrained from designating a lectotype, since neotype designation may be necessary when the condition of the Venzo collection is known.

MATERIAL. Eight specimens, all from the Lower to Middle Cenomanian, Mzinene Formation of Loc. 62, Skoenberg, Zululand: SAS A834, SM/1, A1086; BM(NH) C78758–61, C78765.

Plate 1 × 1, except Figs 2d–e

Fig. 1 *Eogaudryceras* (*Eogaudryceras*) *hertleini* (Wiedmann). BM(NH) C78755, Makatini Formation, Aptian IV, Loc. 37, on Mzinene River, Zululand.

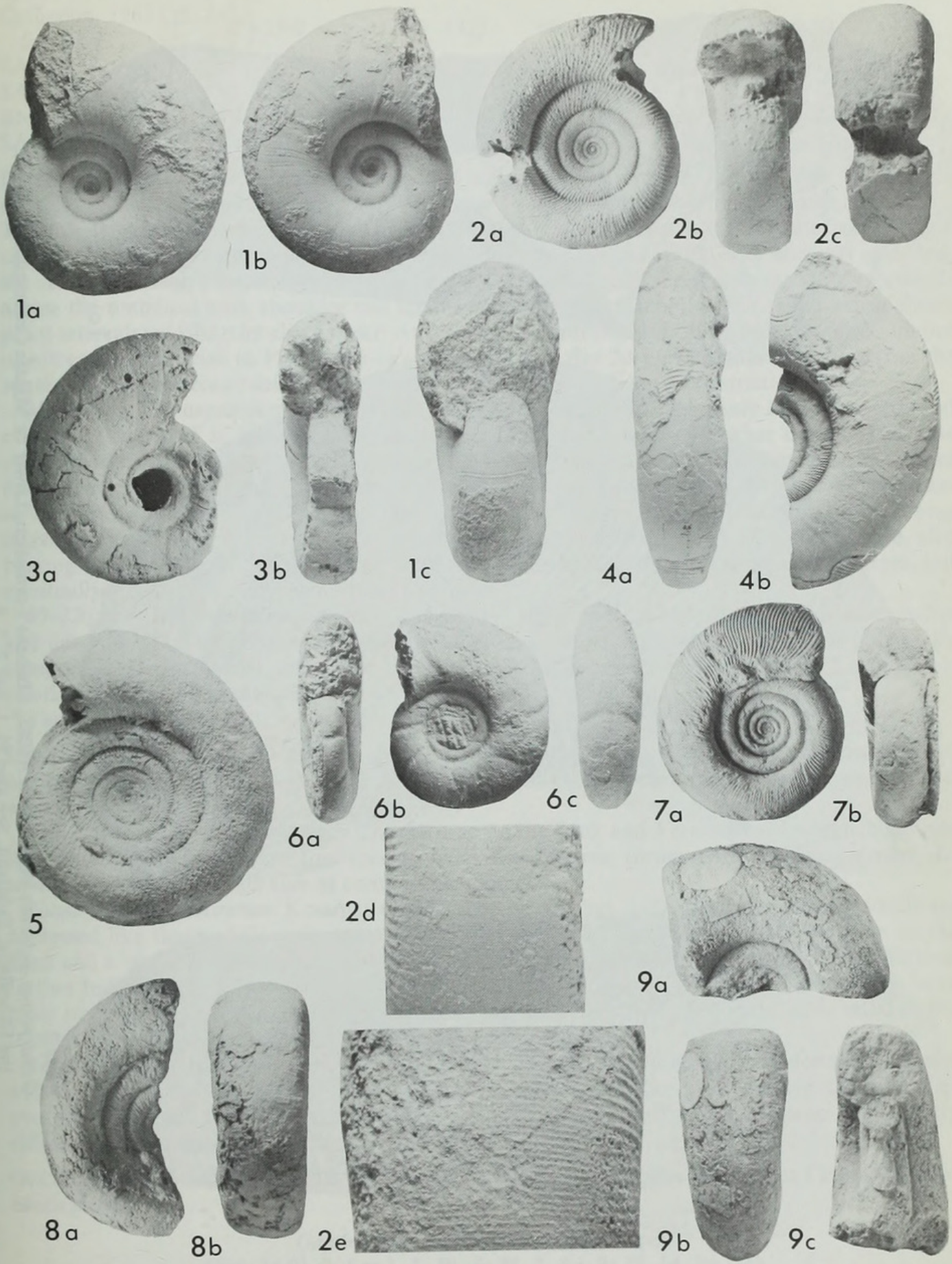
Figs 2, 5, 8 *Gaudryceras stefaninii* Venzo. Fig. 2, SAS A834, Figs 2d–e × 3 to show details of ribbing on venter; Fig. 5, BM(NH) C78759; Fig. 8, SAS SM/1; all Lower to Middle Cenomanian Mzinene Formation at Loc. 62, the Skoenberg, Zululand. See also Plate 2.

Fig. 3 *Eogaudryceras* (*Eotetragonites*) *umbilicostriatus* Collignon. BM(NH) C78830, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand.

Figs 4, 7 *Gaudryceras* cf. *varagurense* Kossmat. Fig. 4, BM(NH) C78825, St Lucia Formation, Santonian 1, Loc. 85, False Bay, Zululand; Fig. 7, SAS SM/2, St Lucia Formation, Coniacian I, Loc. 63, the Skoenberg, Zululand.

Fig. 6 *Eotetragonites* (*Eotetragonites*) *raspaili raspaili* Breistroffer. BM(NH) C78772, Mzinene Formation, Albian III, Loc. 175, Ndumu, Zululand.

Fig. 9 *Anagaudryceras* aff. *sacya* (Crick) (*non* Forbes). BM(NH) C18140, figd Crick (1907*a* : pl. 10, fig. 13), Mzinene Formation, presumably Albian or Cenomanian, Skoenberg area, Zululand. See p. 148.


1a
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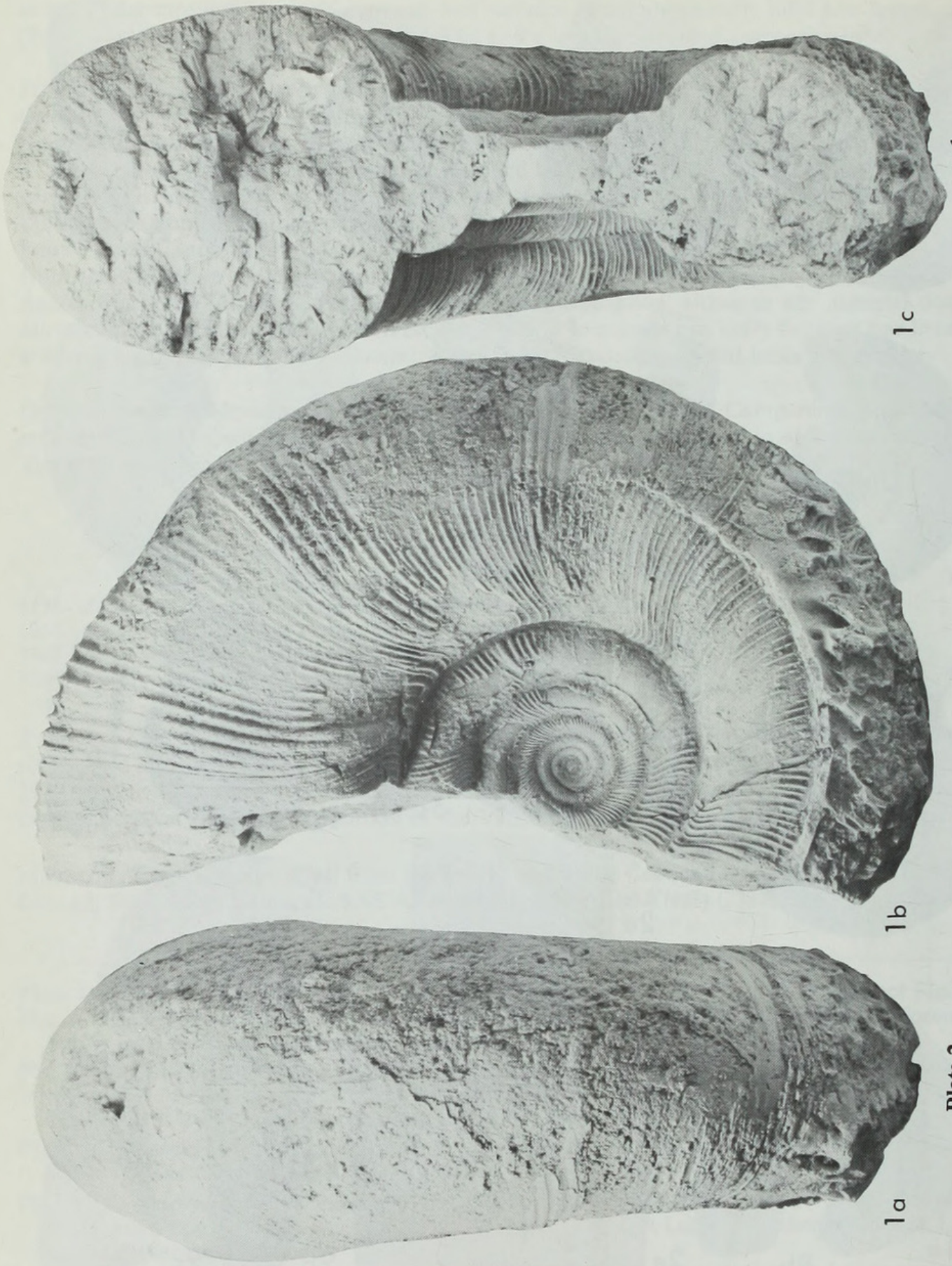

Plate 2
Gaudryceras stefaninii Venzo. SAS A1086, Mzinene Formation, Lower or Middle Cenomanian, Loc. 62, the Skoenberg, Zululand. See also Pl. 1, figs 2, 5, 8. ×1

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Syntype (Venzo 1936)	29	12 (41)	9 (31)	1·33	15 (51)
Collignon, 1963 : pl. 247, fig. 1057	19·0	80 (42)	60 (32)	1·33	90 (47)
SAS A834	34·5	14·6 (42)	9·5 (28)	1·53	17·2 (50)
SAS SM/1	36·2	14·9 (41)	10·1 (28)	1·47	17·4 ? (48)
BM(NH) C78759	43·8	16·1 (37)	12·3 (28)	1·30	22·9 (52)
SAS A1086	c. 120	50·3 (41)	52·8 (44)	0·95	43·0 (36)

Description. *Early whorls, up to 35 mm.* The coiling is very evolute, serpenticone, the whorls slowly expanding, the whorl section very depressed (whorl breadth/whorl height ratio up to 1·53). The umbilicus is broad, shallow, with a low outward-sloping umbilical wall. The sides are strongly curved, with the greatest breadth at mid-flank. The ventrolateral shoulder is abruptly rounded, the venter flattened. Fine, dense, subequal lirae arise at the umbilical seam, sweep gently forwards across the umbilical wall, shoulder and flanks, sometimes branching low on the flank, at which point intercalated ribs may also appear. At the ventrolateral shoulder, lirae break up into bundles of extremely fine striae in *Vertebrites*-like fashion (Pl. 1, figs 2d–e), and pass straight across the venter. There are occasional straight, prorsiradiate, shallow, narrow constrictions.

35–60 mm. The expansion rate increases, the whorls become progressively less depressed, and eventually as broad as high. The umbilicus becomes smaller, and somewhat deeper. The lirae progressively coarsen, sweep forwards over the umbilical shoulder but are flexed on the lower flank, then pass straight across the upper flank and venter. Some branch, and occasional intercalated lirae appear low on the flank. Periodic prorsiradiate constrictions are present, becoming increasingly closely spaced as diameter increases; behind each is a thickened, collar-like rib, also bearing lirae. When visible, the venter shows that lirae at first divide into twos and threes, but eventually pass across the venter without division.

60–120 mm. The expansion rate increases, so that the umbilicus becomes progressively smaller and deeper. Whorl height increases, and at the largest diameter preserved, the whorl is laterally compressed. Lirae coarsen, and collar-like ribs, bearing lirae, become frequent (Pl. 2, figs 1a–b); in other respects, the ornament is like that of the middle growth stages.

The sutures are not fully exposed.

Discussion. Our collections provide the first detailed ontogenetic series for this curious species; our largest specimen is still wholly septate at 120 mm, and bears traces of a further septate half whorl.

The depressed early whorls, with straight lirae on the flank and *Vertebrites*-like branching over the venter, readily separate this species from *Gaudryceras varagurense*, *G. beantalyense*, *G. analabense* and *G. multiplexum* at comparable diameters.

Gaudryceras vertebratum Kossmat (1895 : 126; pl. 15, figs 4–5) has inner whorls which are depressed like those of *G. stefaninii*, show a flattened venter, straight prorsiradiate lirae on the flank and a 'smooth' venter, but the outer whorl shows finer lirae than in our specimens. Without further Indian material it is not possible to assess the significance of these minor differences, or to place *stefaninii* in synonymy with *vertebratum*; the two species thus stand in the same relationship to each other as *Gaudryceras varagurense* does to *G. analabense*.

Gaudryceras isovokyense Collignon (1964 : 31; pl. 324, fig. 1447) is a further Cenomanian species with a similar whorl section to *G. stefaninii*. The ribs do not, however, develop fine branches over the venter so far as can be seen from the figure, but this may reflect no more than slightly different rates of ontogenetic change.

Occurrence. Lower and Middle Cenomanian of Zululand, Albian and Lower Cenomanian of Madagascar.

Gaudryceras varicostatum van Hoepen

(Fig. 1; Pl. 3, figs 1–3; Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11)

1921 *Gaudryceras varicostatum* van Hoepen: 7; pl. 2, figs 10–12; text-figs 3, 4.

1921*b* *Gaudryceras kayei* (Forbes); Spath : 50 (table).

1922 *Gaudryceras varicostatum* van Hoepen; Spath : 117.
1922 *Gaudryceras cinctum* (Crick ms) Spath : 118; pl. 9, figs 3a–3b.
? 1926 *Gaudryceras propemite* Marshall : 142; pl. 20, fig. 4; pl. 28, figs 3, 4.
1931 *Lytoceras* (*Gaudryceras*) *varicostatum* (van Hoepen); Collignon : 12; pl. 2, figs 1–4; pl. 8, fig. 3.
1956 *Gaudryceras* sp. aff. *cinctum* (Crick) Spath; Collignon : 55; pl. 5, figs 4, 5.
1956 *Gaudryceras varicostatum* van Hoepen; Collignon : 56.
1965 *Gaudryceras varicostatum* van Hoepen; Howarth : 362.
1965 *Gaudryceras cinctum* Spath; Howarth : 362.
1966 *Gaudryceras varicostatum* van Hoepen; Collignon : 3; pl. 456, fig. 1854.
? 1970 *Gaudryceras propemite* Marshall; Henderson : 15; pl. 2, fig. 6.

HOLOTYPE. By monotypy, TM 538, the original of van Hoepen 1921 : 7; pl. 2, figs 10–12, from the Umzamba Formation, Loc. 1, Pondoland (Santonian to Campanian).

MATERIAL. Five specimens. The holotype TM 538, SAS P1418 and the holotype of *Gaudryceras cinctum* BM(NH) C19415, all from the late Santonian to early Campanian, Umzamba Formation, at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland). SAS Z999 from the St Lucia Formation at Loc. 93 on the farm Ncedomhlope, ESE of Hluhluwe, Zululand (Coniacian II). SAS FB11 from the St Lucia Formation in the southern part of False Bay (age unknown). SAS Z1157 from the St Lucia Formation (Campanian II) the Nibela, Lake St Lucia, Zululand.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
TM 538	39·6	14·7 (37)	13·7 (35)	1·07	17·2 (43)
BM(NH) C19415 (a)	65·3	–	25·3 (38)	–	22·3 (34)
(b)	49·0	18·2 (37)	17·2 (35)	1·1	18·5 (37)
SAS P1418	29·3	10·7 (36)	9·8 (33)	1·09	14·0 (47)

DESCRIPTION. *Early whorls, up to 40 mm* (Pl. 3, figs 1–3). The coiling is evolute, slowly expanding, with a depressed whorl section (whorl breadth/height ratio 1·1), the greatest breadth being close to the umbilicus. The whorl sides and venter are rounded, the latter being a little flattened. The umbilicus is broad and of moderate depth, with a rounded wall and abruptly rounded shoulder. Fine, dense, prorsiradiate flexuous lirae arise at the umbilical seam, sweep forwards across the shoulder and inner flanks, and gently backwards across mid-flank. A few lirae branch at the umbilicus and some intercalate on the flanks. The ventrolateral shoulders and venter are covered in fine dense striae, invisible to the naked eye, and produced by the splitting of the lirae at a position corresponding approximately to the umbilical seam of the succeeding whorl (Pl. 3, figs 3c–d). Occasional strengthened collar-like ribs are present on the test, corresponding to the site of shallow constrictions on the otherwise smooth internal mould.

Middle and later growth stages (Pl. 3, fig. 2; Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11). The expansion rate increases markedly, the umbilicus becomes proportionately smaller (34% of diameter). The umbilicus is relatively deep, with a subvertical wall and abruptly rounded shoulder. The sides are flattened and convergent, the venter arched. Ornament consists of fine, dense lirae which arise at the umbilical seam, pass forwards across the umbilical wall, shoulder and lower flank where they may branch, or where intercalated ribs may be inserted. The lirae flex gently backwards at mid-flank and forwards over the ventrolateral shoulders to form a broad shallow peak over the siphonal area. Shallow constrictions are present (? four per whorl), and each has a collar-like thickened rib parallel to it, and bearing lirae. The mould is smooth, save for constrictions. The suture line (Fig. 1) with large, incised, bifid lobes and saddles is of typical gaudryceratid type.

What may be an adult of this species is represented by a partially crushed specimen SAS FB11, 140 mm in diameter (Pl. 4). This shows a relative increase in whorl height and decrease in relative umbilical diameter. Ornament consists of strong wiry lirae which branch into twos and threes near the umbilical shoulder, and become very flexuous across the flanks.

DISCUSSION. The fragmentary specimen SAS Z999 demonstrates very clearly that *Gaudryceras cinctum* is no more than the adult of *Gaudryceras varicostatum*, as Spath suspected in 1922. The distinctive features of *G. varicostatum* are thus the *Vertebrites*-like inner whorls together with

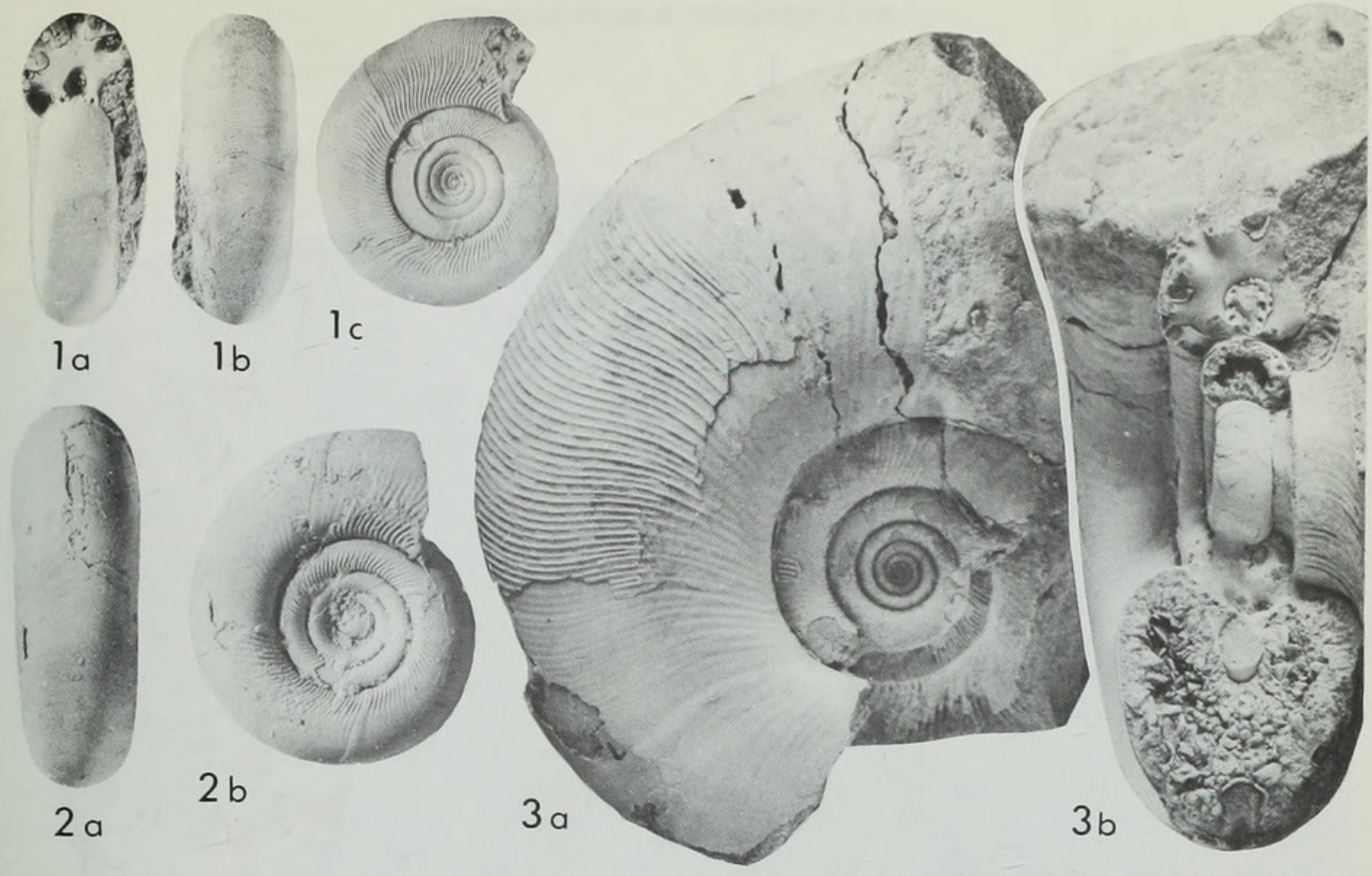

Plate 3 × 1, except Figs 3c–d

Figs 1–3 *Gaudryceras varicostatum* van Hoepen. Fig. 1, SAS P1418; Fig. 2, the **holotype**, TM 538; both late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). Fig. 3, SAS Z999, St Lucia Formation, Coniacian II, Loc. 93, on farm Ncedomhlope, ESE of Hluhluwe, Zululand; Figs 3c–d × 3 to show details of juvenile ornament. See also Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11.

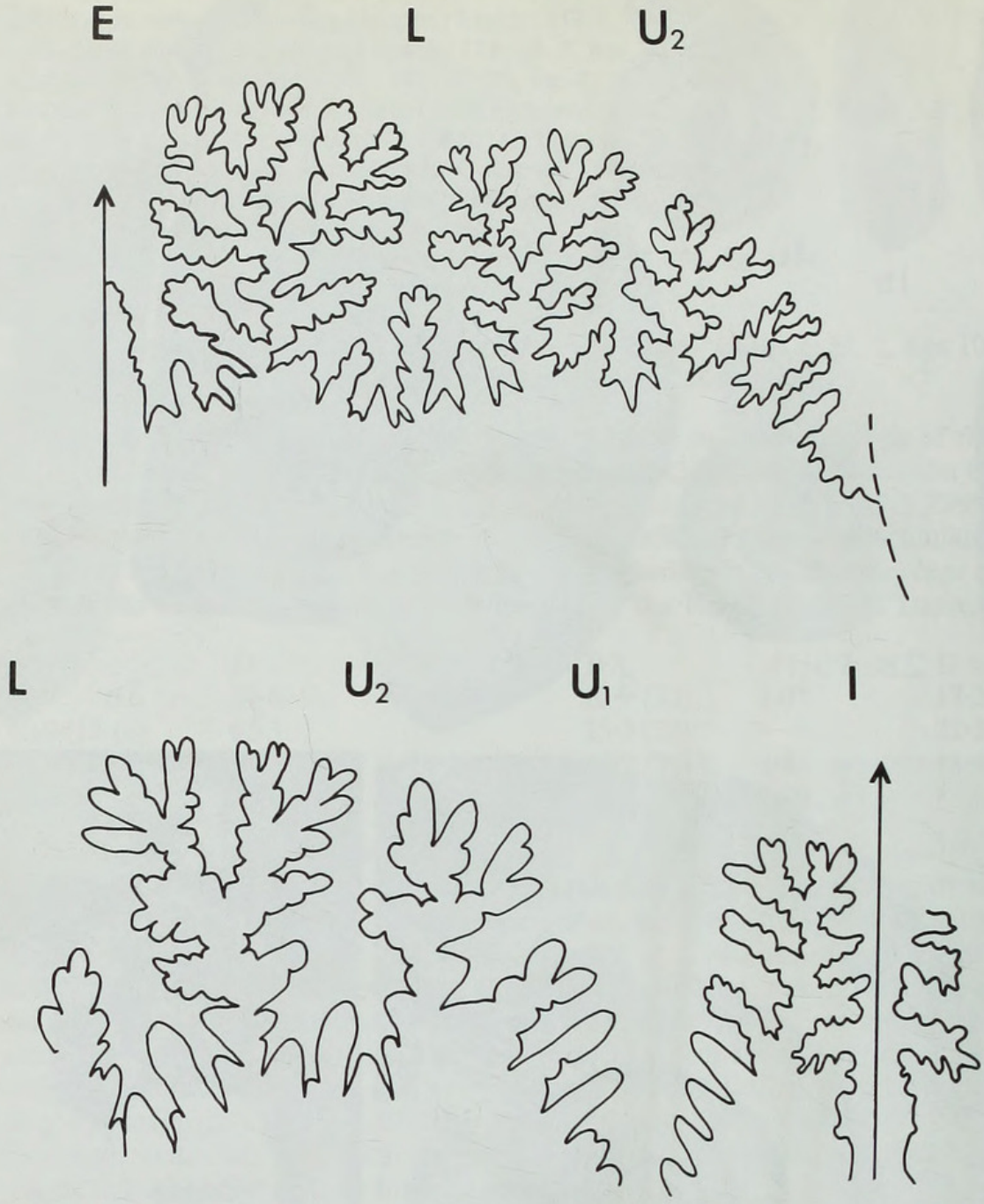

Fig. 1 Sutures of *Gaudryceras varicostatum* van Hoepen. TM 538, × 7½ approx.

typical *Gaudryceras*-like subsequent ornament, which place it clearly within the group of *G. mite*. There are obvious comparisons with *Gaudryceras stefaninii*, from which this species may well be descended, but there are more constrictions and a completely different whorl section in that species. Similar features separate *G. varicostatum* from *Gaudryceras varagurense*, as does the presence of more constrictions (six to eight per whorl), more evolute coiling and finer lirae in the latter. Differing relative proportions and coarseness of ornament also allow separation of medium-sized specimens from the superficially similar *Gaudryceras beantalyense* and *G. analabense*. *Gaudryceras striatum* Jimbo (1894 : pl. 6, fig. 6) and var. *pictum* Yabe (1903 : 33; pl. 4, fig. 6) are very finely ribbed and have many more collars and constrictions per whorl.

The poorly-known *Gaudryceras propemite* is said to have depressed whorls up to diameters of

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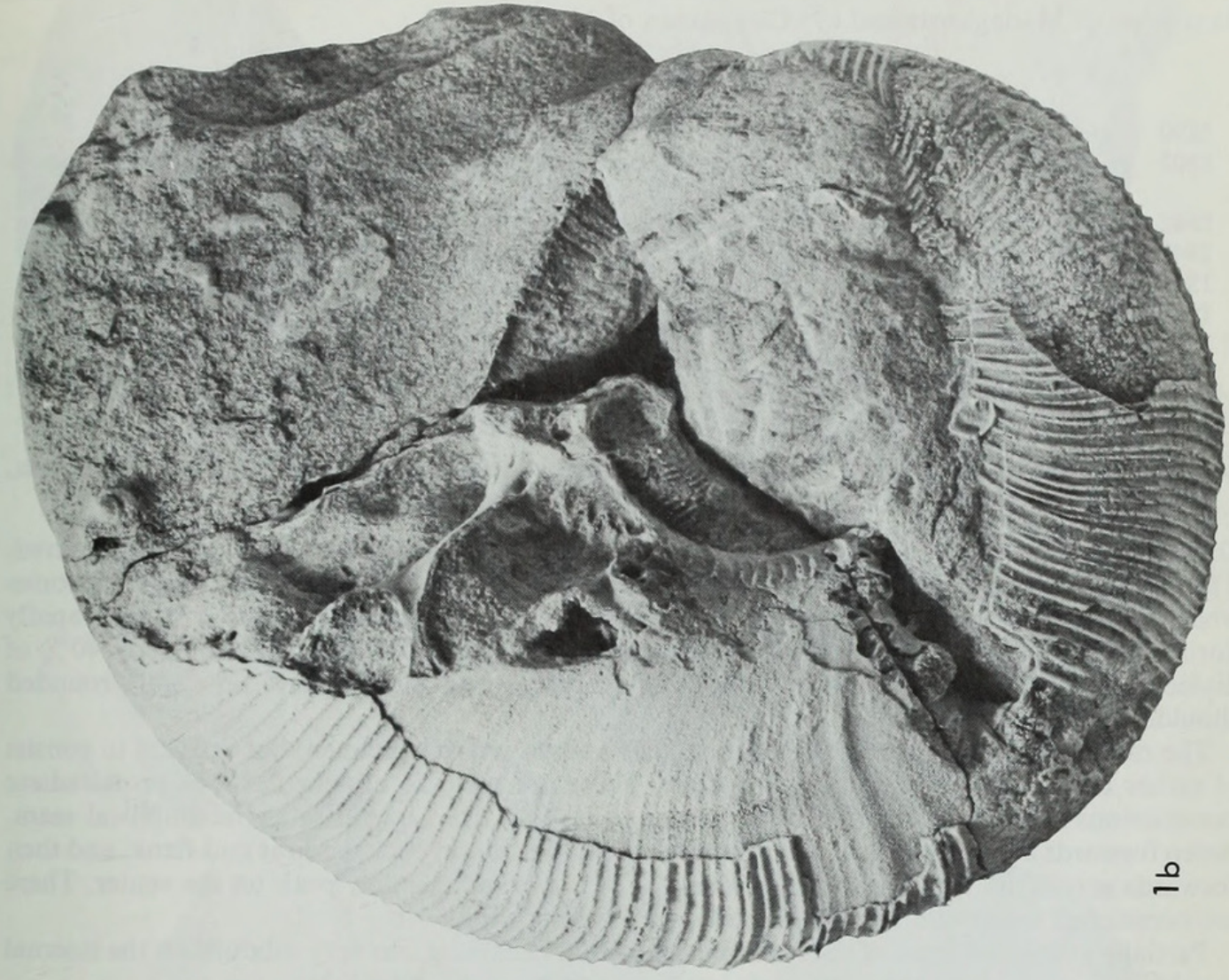
Plate 4 ×1

Gaudryceras varicostatum van Hoepen. SAS FB11, St Lucia Formation, southern part of False Bay, Zululand (precise horizon unknown, probably Coniacian or Santonian). See also Pl. 3; Pl. 7, fig. 2; Pl. 14, fig. 11.



1b

1a

60 mm; it is, however, probably a synonym of *G. cinctum*. *Gaudryceras anomalum* Collignon (1966 : 21; pl. 436, fig. 1891) is too poorly illustrated for comparison.

OCCURRENCE. Coniacian of Zululand, and late Santonian or early Campanian of Pondoland, Santonian of Madagascar and (?) Campanian of New Zealand.

Gaudryceras tenuiliratum Yabe

1890 *Lytoceras sacya* Forbes; Yokoyama : 178; pl. 18, figs 12, 13.
1903 *Gaudryceras tenuiliratum* Yabe : 19; pl. 3, figs 3–4; *non* var. *intermedia*: 27; pl. 3, fig. 1 (= *Gaudryceras denseplicatum*); ? var. *ornata*: 24; pl. 3, figs 2; ? var. *infrequens*: 28; pl. 4, figs 3a–3b.
1942 *Gaudryceras tenuiliratum* Yabe; Matsumoto : 667, fig. 1.
1942 *Gaudryceras tenuiliratum* Yabe var. *substriata* Matsumoto : 666 (nom nud).
1956 *Neogaudryceras tenuiliratum* (Yabe) Collignon : 69.
1963 *Gaudryceras tenuiliratum* Yabe; Jones : 26; pl. 9; pl. 10, figs 1–3; text-fig. 12.
? 1966 *Neogaudryceras* aff. *tenuiliratum* (Yabe); Collignon : 21; pl. 463, fig. 1891.

LECTOTYPE. Designated by Jones (1963 : 28), the original of *Lytoceras sacya* Yokoyama 1890 : 178, pl. 18, fig. 12.

MATERIAL. A single specimen, SAS Z1906, from the north-western part of the Nibela Peninsula, Lake St Lucia, Zululand, at 27° 57′ 00″ S, 32° 25′ 00″ E, and of Santonian age.

DESCRIPTION. The coiling is moderately evolute, less than 40% of the previous whorl being covered. The whorl section is rounded, slightly depressed during the early growth stages, becoming somewhat compressed as growth proceeds. Whorls expand slowly during early growth and rapidly during middle to late growth stages. The umbilicus is of medium size (approximately 40% of diameter) with a subvertical, outward-sloping umbilical wall merging into an evenly rounded shoulder.

The ornament of the early whorls is not well exposed in our specimen, but appears to consist of rather coarse, flexuous prorsiradiate lirae. There are periodic narrow flexuous prorsiradiate constrictions behind each of which is a strong collar-like rib. Lirae arise at the umbilical seam, sweep forwards across umbilical wall, shoulder and lower flank, backwards at mid-flank, and then forwards across the ventrolateral shoulders to form a broad, shallow peak on the venter. There are occasional constrictions, each preceded by a strong simple rib.

Partially exfoliated areas of the specimen show that ornament was very subdued on the internal mould. The suture line is not exposed, but there is a massive septal lobe.

DISCUSSION. The finely lirate inner and coarsely lirate outer whorls separate *G. tenuiliratum* from members of the *varagurense* and *denseplicatum* groups. The closest species is thus *Gaudryceras denmanense*, known from the Campanian of Vancouver Island, Alaska and Madagascar. Juveniles of the two species are said to be indistinguishable (Jones 1963 : 28) and the only obvious difference between adults is the development of coarse, simple ribs on the body chamber of *denmanense* which are never as flexuous as those of *tenuiliratum* and do not branch. These are trivial differences, whilst the species have overlapping geographic and stratigraphic ranges; large collections may show that they are no more than variants of a single species.

The position of *Gaudryceras tenuiliratum* vars *infrequens* and *ornata* is uncertain, as they are based on juveniles.

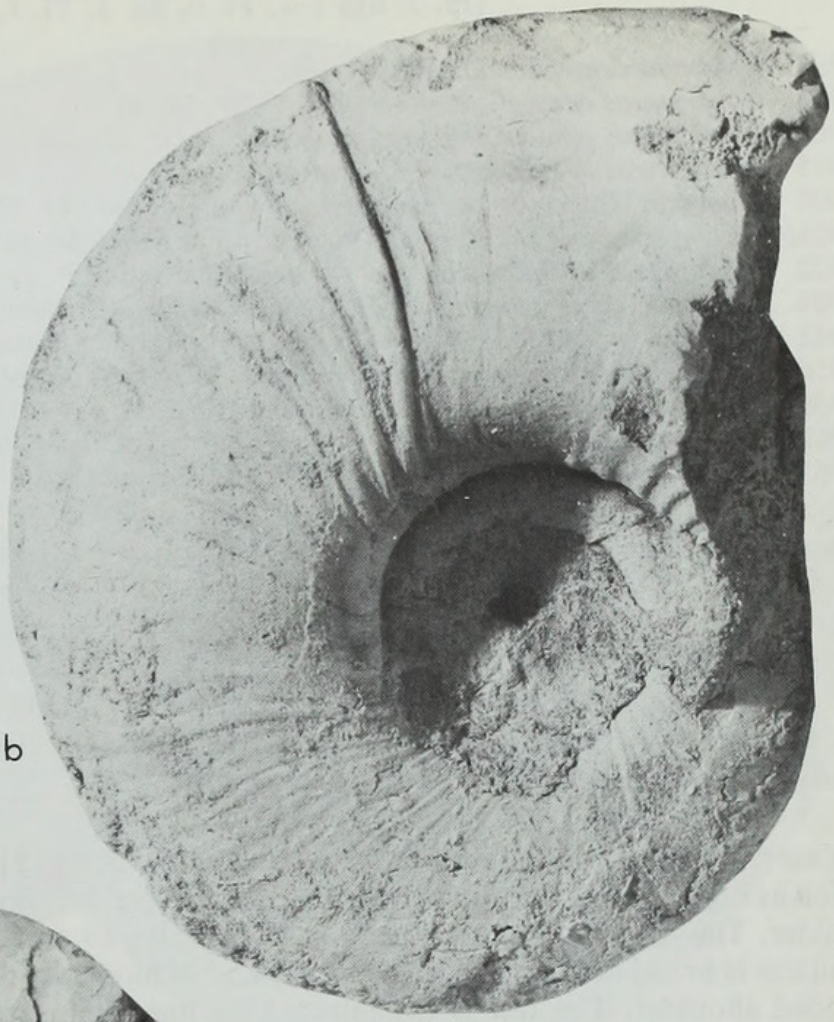
OCCURRENCE. Coniacian to Campanian of Japan, Santonian of Madagascar, Campanian of Alaska and Sakhalin, Santonian of South Africa (Zululand).

Plate 5 ×1

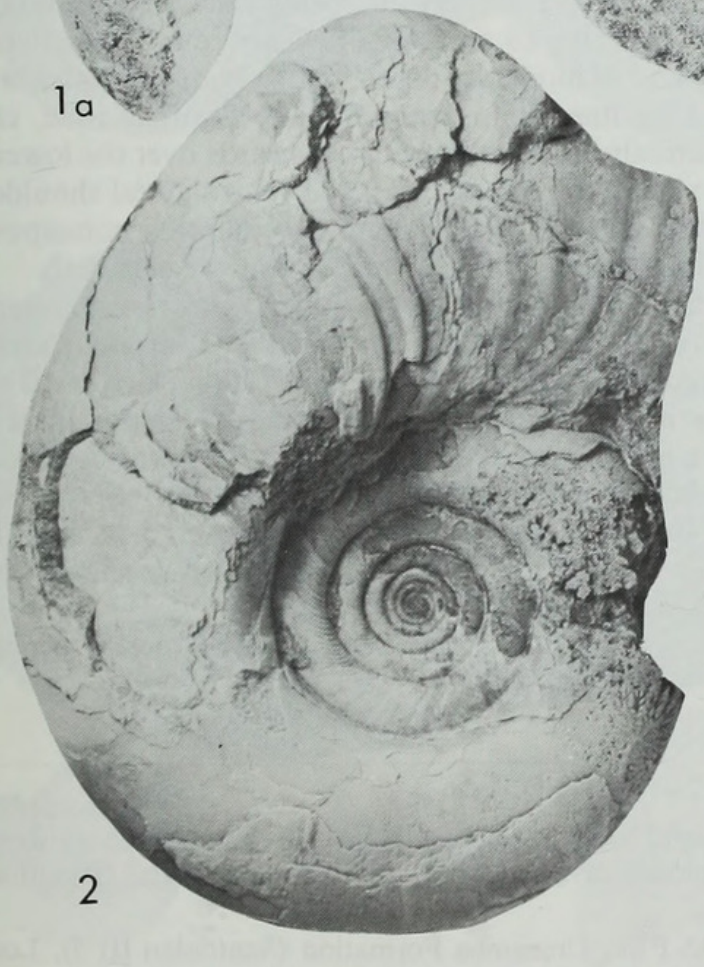
Figs 1–2 *Gaudryceras denseplicatum* (Jimbo). Fig. 1, TM 551, holotype of *Gaudryceras amapondense* van Hoepen, Umzamba Formation, late Santonian to early Campanian, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). Fig. 2, SAS H31, St Lucia Formation, Loc. 101, Hluhluwe River, Zululand (Santonian I–III). See also Pl. 6, fig. 2; Pl. 7, fig. 1.

Fig. 3 *Anagaudryceras politissimum* (Kossmat). SAS H202/1, St Lucia Formation, Loc. 87, False Bay, Lake St Lucia, Zululand (Santonian I–II).

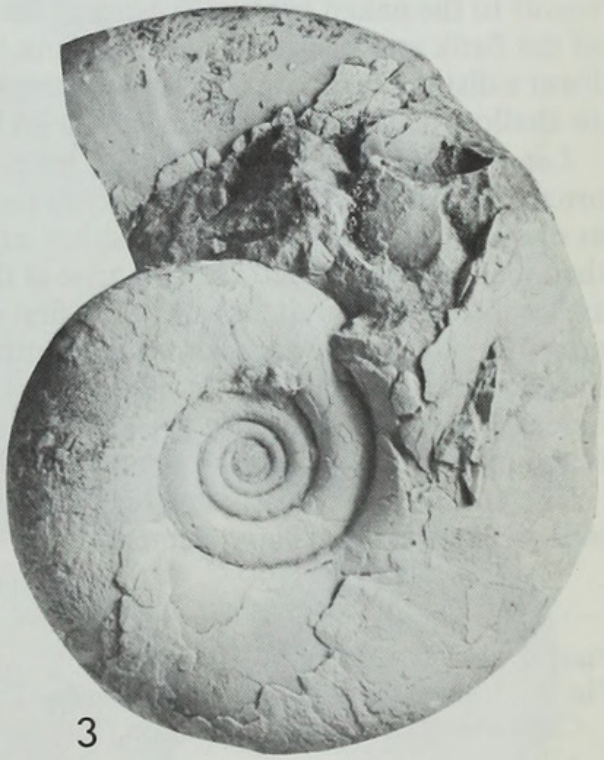
1a



1b



2



3

Gaudryceras denseplicatum (Jimbo)
(Pl. 5, figs 1–2; Pl. 6, fig. 2; Pl. 7, fig. 1)

1894 *Lytoceras denseplicatum* Jimbo : 182; pl. 23, fig. 1.
1903 *Gaudryceras denseplicatum* (Jimbo) Yabe : 16, 30.
1903 *Gaudryceras tenuiliratum* var. *intermedia* Yabe : 27; pl. 3, figs 1a–1b.
1915 *Gaudryceras denseplicatum* (Jimbo); Yabe : 13.
1920 *Lytoceras* (*Gaudryceras*) *amapondense* van Hoepen : 42; pl. 24, figs 1–3.
1921*b* *Gaudryceras amapondense* van Hoepen; Spath : 50 (table).
1922 *Gaudryceras amapondense* van Hoepen; Spath : 118.
? 1924 *Neogaudryceras denseplicatum* (Jimbo) *nonstriata* Yehara : 35; pl. 2, fig. 1.
? 1942 *Neogaudryceras denseplicatum* (Jimbo) var. *kawadai* Matsumoto : 666 (nom. nud).
1956 *Neogaudryceras denseplicatum* (Jimbo); Collignon : 60; pl. 9, fig. 1.
1959 *Gaudryceras glaneggense* (Redtenbacher); Wiedmann : 715.
1962*a* *Gaudryceras vascogoticum* Wiedmann : 159; pl. 9, figs 2, 6; text-fig. 17.
1965*b* *Neogaudryceras denseplicatum* (Jimbo); Collignon : 6; pl. 416, fig. 1719.

MATERIAL. Seven specimens. TM 551 (the holotype of *Gaudryceras amapondense* van Hoepen), TM 558, SAS P7/1 and SAM 7094, from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland); SAS H-30-3 from Loc. 100 and SAS H31 from Loc. 101 on the Hluhluwe River, Zululand (Santonian I–III); SAS Z1154 from Loc. 114 on the Nibela Peninsula, Zululand (Campanian II) and Z337 from the west bank of the Hluhluwe River at 28° 05′ 00″ S, 32° 15′ 00″ E (Upper Coniacian ?). All the Zululand material is from the St Lucia Formation.

DESCRIPTION. *Early growth stages, up to 60 mm* (Pl. 5, fig. 2). The coiling is evolute, the whorl section as high as broad, or slightly compressed, the greatest breadth being just above the umbilical shoulder. The flanks are gently rounded, converging to an arched, evenly rounded venter. The umbilicus is broad (about 50% of diameter) and of moderate depth, with a high wall and abruptly rounded shoulder. The test is ornamented by fine, dense, prorsiradiate flexuous lirae, clearly visible to the naked eye, and arising at the umbilical seam. They flex forwards over the lower part of the flank and backwards at mid-flank to sweep forwards across the ventrolateral shoulders to form a distinct peak over the siphonal region. There are periodic strengthened ribs, corresponding to shallow prorsiradiate constrictions on the internal mould, which is otherwise smooth.

Later growth stages (Pl. 5, fig. 1; Pl. 6, fig. 2). At diameters greater than 60 mm, the type of ornament described above gives way to narrow, rounded, flexuous ribs which increase in strength as diameter increases. These are rather irregularly spaced, with interspaces typically much wider than the ribs themselves. The ribs arise at the umbilical seam, strengthen across the umbilical wall, are prorsiradiate on the lower flank, first sweep gently forwards, then flex backwards across the upper flank and forwards across the ventrolateral shoulder to form a strong ventral peak, where they are thickened into a lip-like process. Both ribs and interspaces are covered in fine, dense lirae, like those of the early growth stages, when shell is preserved. Exfoliated specimens or internal moulds show only the strong ribs (Pl. 5, fig. 2).

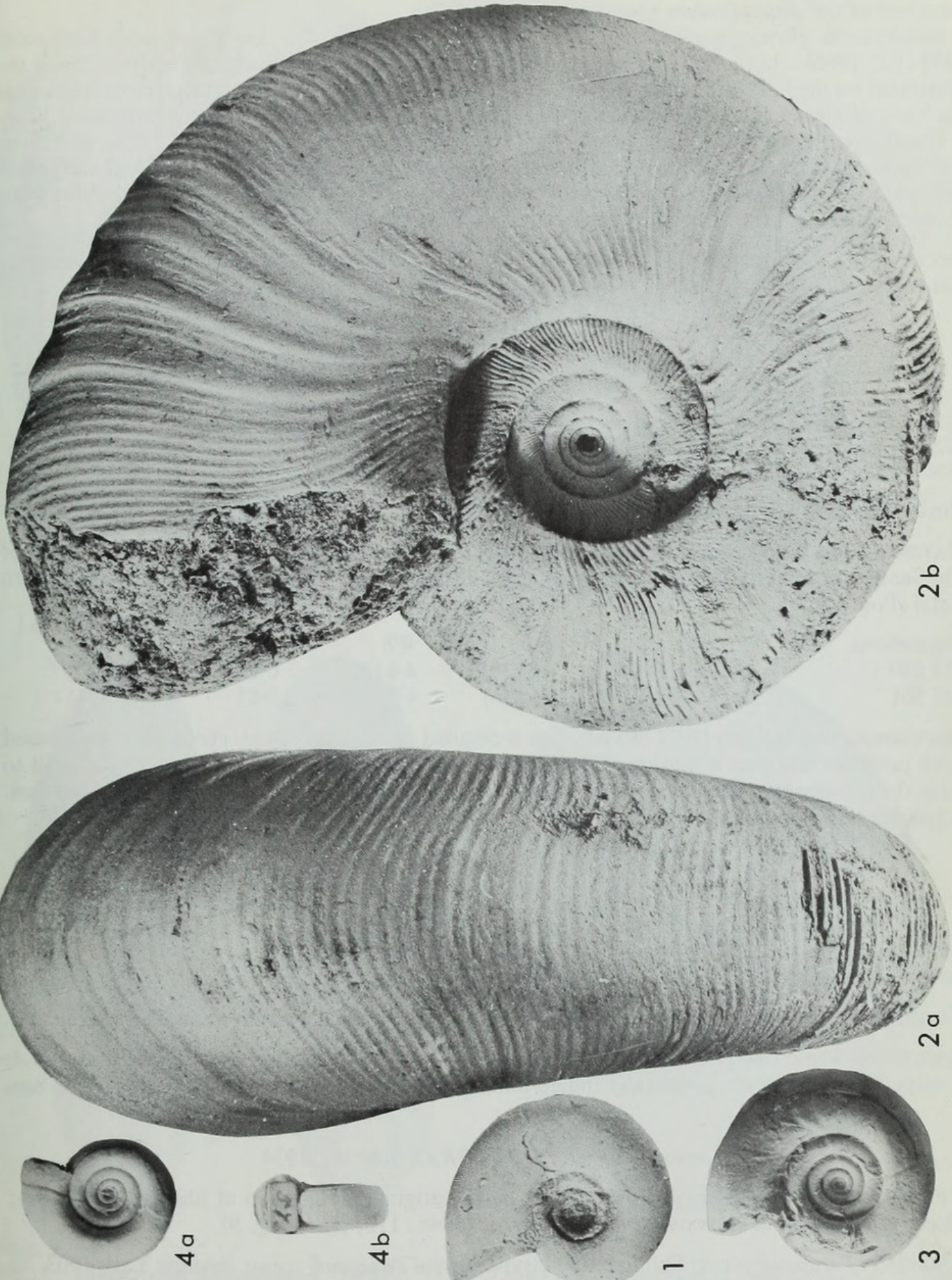
The suture line consists of deeply incised bifid lobes and saddles, and a retracted suspensive lobe with several auxiliary elements.

Plate 6 × 1, except Fig. 1

Fig. 1 '*Gaudryceras*' *sigcau* van Hoepen. Lateral view of **holotype**, TM 560, late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland), × 2·5.

Fig. 2 *Gaudryceras denseplicatum* (Jimbo). SAS P7/1, Umzamba Formation (Santonian III ?), Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). See also Pl. 5, figs 1–2; Pl. 7, fig. 1.

Figs 3–4 *Anagaudryceras pulchrum* (Crick). Fig. 3, SAS U1; Fig. 4, SAS 57; both Mzinene Formation (Albian V ?), Mzinene River, Zululand. See also Pl. 12, figs 1–3, 5–10; Pl. 13.


2b
2a
4a
4b
1
3

DISCUSSION. The striking change from juvenile to adult ornament clearly separates *Gaudryceras denseplicatum* from members of the *mite* and *tenuiliratum* groups. Comparisons with other members of the *denseplicatum* group are as follows.

Gaudryceras glaneggense (Redtenbacher 1873 : 119; pl. 28, figs 3a–b; see also Collignon 1956 : 62; 1965*b* : 4; pl. 414, fig. 1716) is a rather poorly known European species, since re-illustrated on the basis of specimens from Madagascar. It is separated from the present species on the basis of stronger, more widely spaced, more flexuous ribs, with far more intermediate lirae.

Gaudryceras lauteli (Collignon) by contrast develops only occasional fold-like ribs, and these only on the last part of the body chamber. *Gaudryceras tenuiliratum* var. *intermedia*, *Gaudryceras vascogoticum* Wiedmann and the crushed and poorly-preserved *Gaudryceras amapondense* (van Hoepen) are clear synonyms of *G. denseplicatum*.

OCCURRENCE. Coniacian to Campanian of Zululand and Pondoland, Coniacian of Madagascar, Turonian to Coniacian of Japan, Coniacian of northern Spain.

'Gaudryceras' sigcau van Hoepen
(Pl. 6, fig. 1)

1921 *Gaudryceras sigcau* van Hoepen : 9; pl. 2, figs 13–16; text-fig. 5.
1922 *Gaudryceras sigcau* van Hoepen; Spath : 118.
1956 *Gaudryceras sigcau* van Hoepen; Collignon : 170.

HOLOTYPE. TM 560, figured by van Hoepen (1921) as pl. 2, figs 13–16.

MATERIAL. The holotype TM 560 and paratype TM 561, both from the Umzamba Formation of late Santonian to early Campanian age, at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wh/Wb*	*U*
TM 560	11·6	4·5 (39)	4·6 (40)	0·99	3·9 (39)
TM 561	11·1	4 (36)	4·7 (42)	0·85	4 (36)

DISCUSSION. Van Hoepen (1921 : 9) provides a detailed description of this species, which is based upon juveniles just over a centimetre in diameter. As a result of their small size, it is difficult to place the specimens with certainty in any gaudryceratid genus, or to discuss their actual position. A specimen is refigured as Pl. 6, fig. 1.

'Gaudryceras' spp.
(Pl. 12, figs 4, 11)

1907*b* *Gaudryceras* sp. Crick : 238; pl. 15, figs 4, 4a.
1907*b* *Gaudryceras* sp. Crick : 239.

MATERIAL. Two specimens, BM(NH) C18271 and C18269, from the Munywana Creek, Zululand.

DISCUSSION. These two indeterminate fragments cited by Crick are here figured as Pl. 12, figs 4, 11 respectively. They are generically indeterminate. Both specimens are probably of Albian age.

Genus *ANAGAUDRYCERAS* Shimizu, 1934

TYPE SPECIES. *Ammonites sacya* Forbes 1846, by the original designation of Shimizu (1934 : 67); subjective synonym of *Ammonites buddha* Forbes (1846 : 112; pl. 14, fig. 9).

SYNONYMY. *Paragaudryceras* Shimizu, 1934 (type species *Paragaudryceras limatum* Yabe 1903, by original designation); *Murphyella* Matsumoto, *in* Matsumoto, Muramoto & Takahashi 1972 (type species *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi 1972, by original designation).

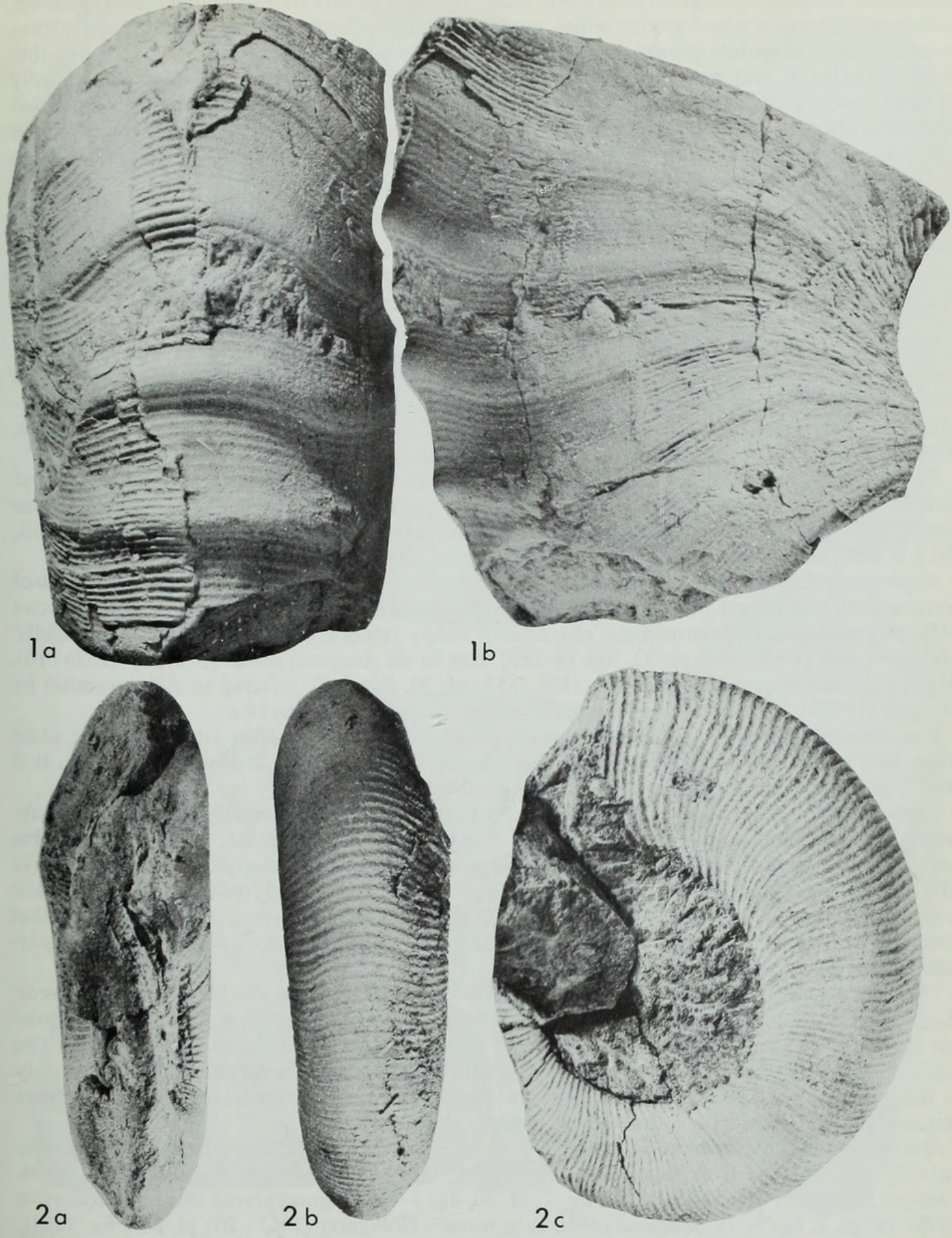


Plate 7 ×1

Fig. 1 *Gaudryceras denseplicatum* (Jimbo). SAS 337, St Lucia Formation (Upper Coniacian ?), west bank of Hluhluwe River at 28° 05′ 00″ S, 32° 15′ 00″ E. See also Pl. 5, figs 1–2, Pl. 6, fig. 2.

Fig. 2 *Gaudryceras varicostatum* van Hoepen. SAS Z1157, St Lucia Formation, close to Loc. 114, SW tip of Nibela Peninsula, Zululand (Campanian II). See also Pls 3, 4; Pl. 14, fig. 11.

DIAGNOSIS. Medium-sized gaudryceratids in which the early growth stages show an evenly rounded, circular to depressed whorl section which may become compressed in later growth stages. Ornament of early and middle growth stages typically consists of very fine radial lirae, often invisible to the naked eye, and periodic rounded, collar-like radial ribs. Internal moulds are typically smooth, save for radial constrictions corresponding to the site of the periodic ribs. Ornament frequently changes on the body chamber, where constrictions become closely spaced and fold- or scale-like ribs develop between them. Suture line gaudryceratid, with deeply incised, bifid lobes and saddles and a retracted suspensive lobe.

DISCUSSION. Nomenclatoral problems associated with the erection of *Anagaudryceras* have been reviewed by Wright & Matsumoto (1954 : 111–113) and the interpretation of the genus is discussed by Matsumoto (1959*a* : 138; 1959*b* : 73), Wiedmann (1962*a* : 156–158) and Howarth (1965 : 357). The difficulty stems mainly from the fact that the type specimen of *Anagaudryceras sacya* (Pl. 8, fig. 3) is a poorly-preserved juvenile which could conceivably be referred to a number of other genera. If current interpretations of *Ammonites buddha* Forbes as the adult of this species are valid, then *Anagaudryceras* is in our view sufficiently different from other gaudryceratids to be given generic status. If, however, this is found not to be the case when topotype material is redescribed, then most of the forms described here will be referable to *Paragaudryceras* Shimizu, 1934.

Of the most similar genera, *Gaudryceras* de Grossouvre, 1894, is characterized by fine but distinct sigmoid lirae or riblets which are strongly projected on the venter. *Mesogaudryceras* Spath, 1927, is very compressed, with flexuous lirae and no constrictions. *Zelandites* Marshall, 1926, is compressed with many constrictions and virtually no ornament at any stage.

Kossmatella Jacob, 1907, can normally be distinguished by its smaller size and the presence of constrictions and lateral fold-like ribs throughout ontogeny. There are, however, some species with morphologically intermediate characters, which require comment. Thus '*Kossmatella*' *whitneyi* Gabb (1869 : 134; pl. 22, figs 14–14b) may be an *Anagaudryceras* (Murphy 1967*b* : 16), whilst *Kossmatella gainesi* Anderson (1938 : 153; pl. 20, figs 3–5), referred to *Eotetragonites* by Murphy (1967*b* : 23), also shows features recalling *Anagaudryceras buddha*.

Jauberticeras Jacob, 1907, has a depressed whorl section with a sharp lateral angle at some stage, very evolute coiling, slowly expanding whorls, and is typically ornamented by lirae. It is readily distinguished from *Anagaudryceras* (Murphy 1967*c*).

Matsumoto (*in* Matsumoto, Muramoto & Takahashi 1972) has recently introduced the subgenus *Kossmatella* (*Murphyella*), type species *K.* (*M.*) *enigma* Matsumoto, Muramoto & Takahashi (1972 : 210; pl. 33, figs 1–3; text-fig. 1), for gaudryceratids characterized by *Kossmatella*-like ribs on their inner whorls, relatively smooth middle growth stages, and fold-like ribs on the adult whorl. It is quite clear from the material referred below to *Anagaudryceras buddha* (Forbes) that these same ontogenetic changes are seen in typical *Anagaudryceras*, and we would regard *Murphyella* as a synonym of *Anagaudryceras*.

The currently-held view on the origin of *Anagaudryceras* is that it evolved from *Eogaudryceras* (*Eogaudryceras*) during the early Albian; it is therefore of some interest that our collections contain large numbers of specimens of low Middle Albian age, amongst the earliest records of the genus. *Eogaudryceras* (*Eogaudryceras*) differs from *Anagaudryceras* in having constrictions only on the inner whorls, and lacking fold-like ribs when adult. *Eogaudryceras* (*Eotetragonites*) bears frequent oblique constrictions throughout ontogeny.

About twenty-five species of *Anagaudryceras* or '*Paragaudryceras*' have been proposed; the majority are listed by Collignon (1956 : 68–70), to which can be added *Anagaudryceras particostatum* Marshall (1926 : 143; pl. 20, fig. 7; pl. 30, figs 3–4), *Anagaudryceras tennanti* Henderson (1970 : 10; pl. 2, figs 4, 7), *Anagaudryceras coagmentum* Collignon (1963 : 20; pl. 249, fig. 1064), *Anagaudryceras pulvinatum* Collignon (1964 : 12; pl. 324, fig. 1445) and *Anagaudryceras yokoyamaiforme* Collignon (1966 : 12; pl. 516, fig. 2031).

Many of these are based upon juveniles at the *sacya* stage, and their reference to *Anagaudryceras* rather than *Gaudryceras* is questionable; others are based upon only a few specimens, so that intraspecific variability is poorly understood. Howarth (1965 : 358) provides an excellent

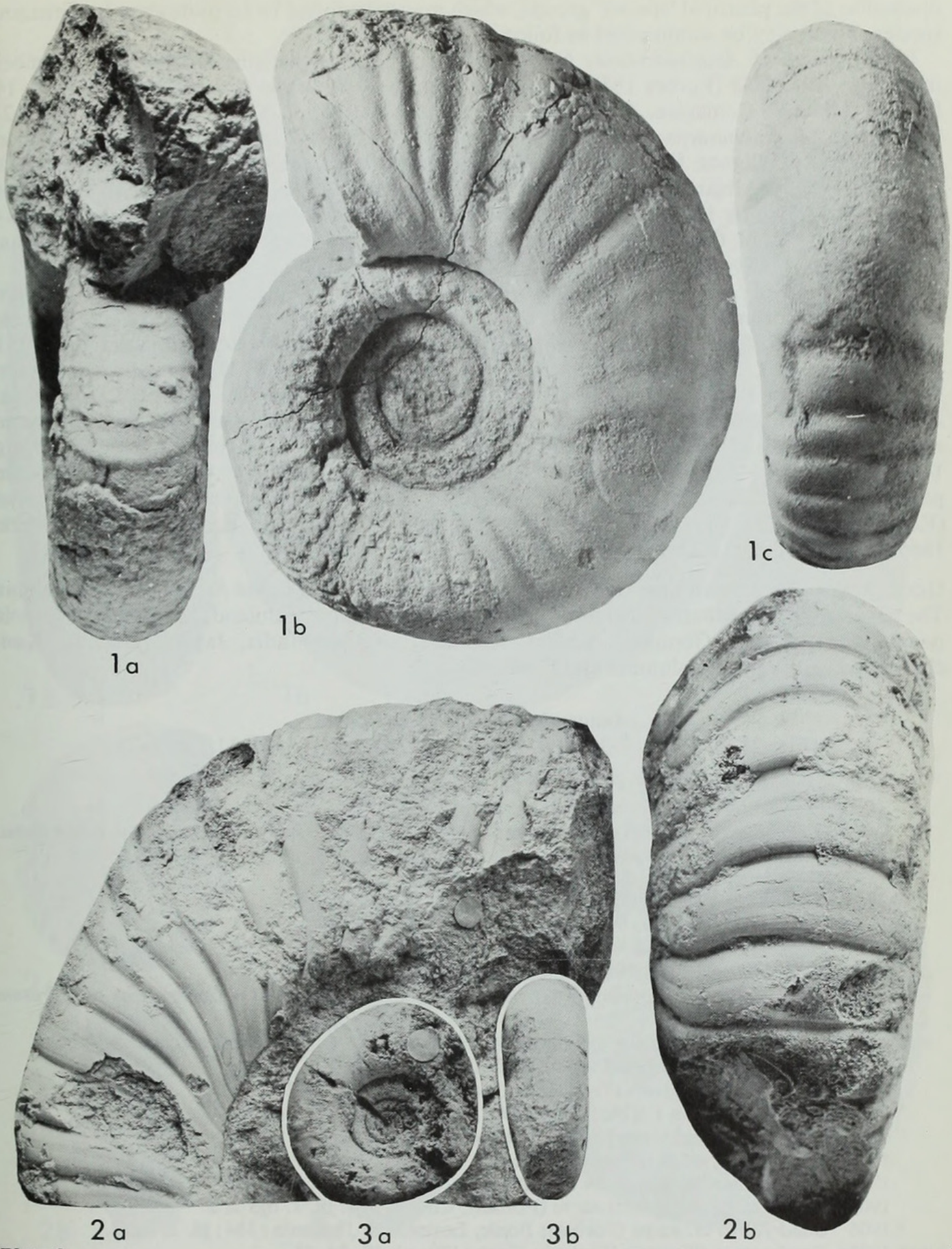


Plate 8 ×1

Figs 1, 2, 3 *Anagaudryceras buddha* (Forbes). Fig. 1, SAS A1402, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand. Fig. 2, the **holotype,** BM(NH) C22673, Utatur Group of Verdachellum, southern India, figd Forbes (1846 : pl. 14, fig. 9). Fig. 3, holotype of *A. sacya* (Forbes), BM(NH) C51067, from the same formation, also figd Forbes (1846 : pl. 14, fig. 10). See also Pls 9, 10; Pl. 11, figs 1–2.

discussion of the principal 'species' groups, which may correspond to no more than long-ranging species. These may be summarized as follows.

1. The group of *Anagaudryceras buddha*, with strong, fold-like ribs on the body chamber, including: *A. buddha* (Forbes 1846 : 112; pl. 14, fig. 9) [= *A. sacya* (Forbes 1846 : 113; pl. 14, fig. 10)], Albian to Coniacian. *A. subsacya* Marshall (1926 : 144; pl. 20, figs 8–8a; pl. 29, figs 1–2), Campanian. *A. mokharaense* (Collignon 1950 : 67; pl. 11, figs 1–2; pl. 12, fig. 5), Upper Albian. *A. sakalavum* (Collignon 1949 : 51; pl. 7, figs 3–3b), Albian. *A. aurarium* (Anderson 1938 : 151; pl. 20, figs 1, 2), Albian. *A. coagmentum* (Collignon 1963 : 20; pl. 249, figs 1064), Albian. *A. luneburgense* (Schlüter 1872 : 62; pl. 18, figs 8–9), Campanian. *A. limatum* (Yabe 1903 : 34; pl. 14, fig. 2; pl. 5, fig. 2; pl. 6, figs 3a–b). *A. revelatum* (Stoliczka 1865 : 152; pl. 75, figs 3–3b), Albian–Cenomanian. *A. salinarium* (Douvillé 1931 : 42; pl. 1, fig. 3; text-fig. 5), Cenomanian.

2. The group of *Anagaudryceras involvulum*, typically compressed during later growth and retaining weak ornament apparently throughout ontogeny, including: *A. involvulum* (Stoliczka 1865 : 150; pl. 75, figs 1–1b), Cenomanian–Turonian. *A. madraspatanum* (Stoliczka 1865 : 151; pl. 75, figs 2–2c), Albian–Cenomanian. *A. utaturense* (Shimizu 1935) [= *Ammonites sacya* Forbes; Stoliczka 1865, pars], Cenomanian. *A. pulchrum* (Crick 1907b : 237; pl. 15, figs 1–1a), Albian. *A. politissimum* (Kossmat 1895 : 128; pl. 15, figs 7–7c), Turonian–Santonian. *A. yamashitai* (Yabe 1903 : 38; pl. 4, fig. 7), Santonian. *A. mikobokoense* (Collignon 1956 : 59; pl. 8, figs 1–1b), Campanian. *A. particostatum* (Marshall 1926 : 143; pl. 20, fig. 7; pl. 30, figs 3, 4), Campanian. *A. tennanti* Henderson (1970 : 19; pl. 2, figs 4–7; text-fig. 5b), Campanian. *A. subtilineatum* (Kossmat 1895 : 123; pl. 19, figs 1a–c, 2a–b), Santonian–Campanian. *A. multiplexum* (Stoliczka 1865 : 154; pl. 76, fig. 1–1b), Cenomanian.

OCCURRENCE. The known time range of *Anagaudryceras* is from Middle Albian to Maastrichtian. The geographical distribution includes Antarctica, New Zeland, Zululand, Madagascar, Angola, north Africa, France, Germany, Austria, Romania, southern India, Japan, Sakhalin, Kamchatka, Alaska, British Columbia and California.

Anagaudryceras buddha (Forbes)

(Fig. 2; Pl. 8, figs 1–3; Pl. 9, figs 1–3; Pl. 10, figs 1–6, Pl. 11, figs 1–2)

1846 *Ammonites buddha* Forbes : 112; pl. 14, fig. 9.
1846 *Ammonites sacya* Forbes : 113; pl. 14, fig. 10.
1865 *Ammonites sacya* Forbes; Stoliczka : 154; pl. 75, figs 5–7 (*non* pl. 76, figs 2–3, = *Gaudryceras multiplexum* (Kossmat).
1865 *Ammonites revelatus* Stoliczka : 152; pl. 75, fig. 3.
1869 *Ammonites whitneyi* Gabb : 134; pl. 22, figs 14–14b.
1876 *Ammonites filicinctus* Whiteaves : 43; pl. 2, figs 2a–c, 3.
1879 *Ammonites filicinctus* Whiteaves; Whiteaves : 104 (footnote).
1884 *Lytoceras sacya* (Forbes) Whiteaves : 203; pl. 25.
non 1890 *Lytoceras sacya* (Forbes); Yokoyama : 178; pl. 8, figs 12, 13 (= *Gaudryceras tenuiliratum* Yabe).
non 1894 *Lytoceras sacya* (Forbes); Jimbo : 34; pl. 6, fig. 1 (= *Gaudryceras tenuiliratum* Yabe).
1895 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Kossmat : 119.
1895 *Lytoceras* (*Gaudryceras*) *revelatum* (Stoliczka) Kossmat : 128.
? 1897 *Ammonites sacya* Forbes; Simionescu : 271.
? 1902 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Anderson : 82.
1903 *Gaudryceras sacya* (Forbes); Yabe : 17.
1903 *Gaudryceras limatum* Yabe : 34; pl. 4, fig. 2; pl. 5, fig. 2; pl. 6, fig. 3.
1903 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Choffat : 14; pl. 1, figs 2, 3.
? 1906 *Gaudryceras* cf. *sacya* (Forbes); Boule, Lemoine & Thévenin : 184; pl. 2, fig. 2.
? non 1907*a* *Gaudryceras* aff. *sacya* (Forbes); Crick : 170; pl. 10, fig. 13.
? 1913 *Gaudryceras* cf. *sacya* (Forbes); Petković : 51; pl. 1, figs 1–2.
? 1917 *Gaudryceras sacya* (Forbes); Woods : 170; pl. 10, figs 13–13A) (= *Anagaudryceras* sp. nov. according to Henderson 1970 : 19).
1921*b* *Paragaudryceras buddha* (Forbes) Spath : 41.
1934 *Anagaudruceras sacya* (Forbes) Shimizu : 67.

Plate 9 ×1

Figs 1–3 *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78746; Fig. 2, BM(NH) C78742; Fig. 3, SAS A2118; all Mzinene Formation, Albian III, Loc. 35, Mzinene River, Zululand. See also Pls 8, 10; Pl. 11, figs 1–2.

1935 *Gaudryceras choffati* Shimizu : 116.
1936 *Gaudryceras* (*Paragaudryceras*) *buddha* (Forbes); Breistroffer *in* Besairie : 167, fig. 10a.
non 1936 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Venzo : 78; pl. 5, figs 5a–5b (= *Anagaudryceras pulchrum* Crick).
1938 *Lytoceras* (*Kossmatella*) *whitneyi* (Gabb) Anderson : 152; pl. 31, figs 1, 2.
1950 *Gaudryceras* (*Paragaudryceras*) *buddha* (Forbes); Collignon : 38; pl. 6, fig. 5.
? 1950 *Gaudryceras* (*Paragaudryceras*) *mokharaense* Collignon : 67; pl. 11, figs 1–2; pl. 12, fig. 5.
1953 *Paragaudryceras buddha* (Forbes); Spath : 10.
1953 *Anagaudryceras* sp. nov. Spath : 10–11.
1954 *Anagaudryceras sacya* (Forbes); Wright & Matsumoto : 112.
1957 *Anagaudryceras sacya* (Forbes); Wright : L200, fig. 230, 4.
1959*b* *Anagaudryceras sacya* (Forbes); Matsumoto : 72; pl. 22, figs 4, 5a–c.
1960 *Kossmatella cappsi* Imlay : 99; pl. 12, figs 17–22.
? 1963 *Paragaudryceras coagmentum* Collignon : 20; pl. 249, fig. 1064.
1964 *Gaudryceras sacya* auctt.; Collignon : 4; pl. 318, fig. 1351.
1965 *Paragaudryceras buddha* (Forbes); Thomel : 138, table 2.
1965 *Anagaudryceras sacya* (Forbes); Howarth : 358.
1967 *Anagaudryceras sacya* (Forbes); Jones : 23; pl. 1, figs 5–7, 13–15.
1967*b* *Anagaudryceras* sp. Murphy : 15; pl. 2, figs 1, 2, 4.
1967*b* *Anagaudryceras whitneyi* (Gabb) Murphy : 16; pl. 2, figs 3, 5, 6.
1972 *Anagaudryceras sacya* (Forbes); McLearn : 28; pl. 5, figs 3a–b, 4; pl. 6, fig. 4; pl. 16, figs 2, 3, 4; pl. 17, figs 1–2; pl. 43, figs 1a–c.
1972 *Anagaudryceras* cf. *sacya* (Forbes); McLearn : 33; pl. 6, figs 3a–b; pl. 40, figs 2a–c.
1972 *Anagaudryceras filicinctum* (Whiteaves) McLearn : 33, 34; pl. 17, fig. 3, 4a–c; pl. 19, figs 1–2; pl. 36, fig. 2.
1972 *Anagaudryceras* sp. McLearn : 35; pl. 19, figs 3a–b.
1972 *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi : 210; pl. 33, figs 1–3; text-fig. 1.

HOLOTYPE. Forbes' original specimen, BM(NH) C22673, from Verdachellum in southern India, refigured here as Pl. 8, figs 2a–b.

MATERIAL. We have a large number of specimens: SAS A13, A1218, A1323–4, A1326–8, A1410, A1417, A1428, A1586, A1616 and BM(NH) C78719–C78747 from the Mzinene Formation at Loc. 35 and BM(NH) C78748–C78752 from Loc. 36 on the Mzinene River (Albian III); BM(NH) C78753–4 from Bed 11 or 12 of the Mzinene Formation, Loc. 51 on the Mzinene (Albian V) and SAS Z36 from the same locality (previous horizon unknown, Albian IV–V). BM(NH) C18140 referred to and figured by Crick (1907*a*) as *Gaudryceras* aff. *sacya* Forbes appears to belong to some other species (Pl. 1, fig. 9).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C51067 (holotype of *A. sayca*)	32·0 ?	13·0 (41)	11·2 (35)	1·16	13·1 (41)
BM(NH) C78742	35·8	14·3 (39)	11·9 (33)	1·20	16·0 (44)
BM(NH) C78743	47·7	17·6 (37)	17·3 (36)	1·02	19·7 (41)
SAS A1404	47·8	19·3 (40)	16·2 (34)	1·19	20·0 (42)
BM(NH) C78744	50·0	18·7 (37·4)	17·8 (35·6)	1·05	20·3 (41)
BM(NH) C78745	51·0	20·0 (39)	19·4 (38)	1·03	19·7 (39)
SAS A1403	55·0	22·0 (40)	22·0 (40)	1·0	19·4 (35)
SAS A1402	79·0	31·0 (39)	31·5 (40)	0·98	29·4 (37)
SAS 1218	80·5	–	30·8 (38)	–	28·3 (35)
BM(NH) C78746	101·0	–	37·8 (37)	–	38·0 (38)
BM(NH) C78747	102·0	37·7 (37)	38·5 (38)	0·98	36·4 (36)

DESCRIPTION. *Early growth stages, up to 30–40 mm diameter.* The coiling is very evolute, with a slightly depressed whorl section (whorl breadth/height ratio up to 1·20), the greatest breadth being a little way below mid-flank. The umbilicus is broad (up to 44% of diameter) with a low, rounded

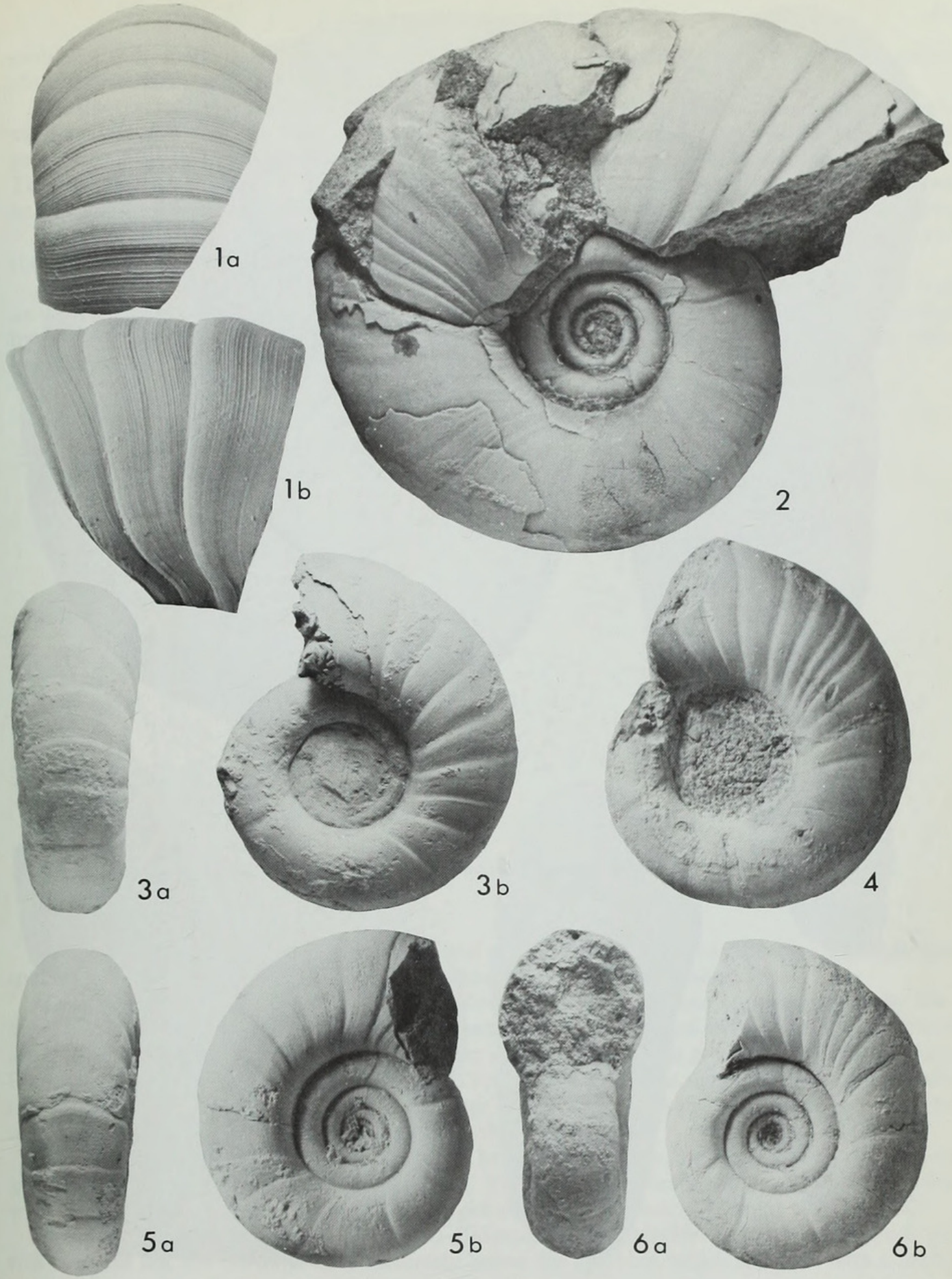


Plate 10 × 1, except Fig. 1

Figs 1–6 *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78753, Mzinene Formation, Albian V, Loc. 51, Bed 12 or 13, Mzinene River, Zululand: × 2 to show details of lirae on shell surface. Fig. 2, SAS Z36 from same locality; Albian IV–V, precise horizon unknown. Fig. 3, BM(NH) C78745; Fig. 4, SAS A1403; Fig. 5, BM(NH) C78744; Fig. 6, BM(NH) C78743; all Mzinene Formation, Albian III, Loc. 35, Mzinene River, Zululand. See also Pls 8, 9; Pl. 11, figs 1–2.

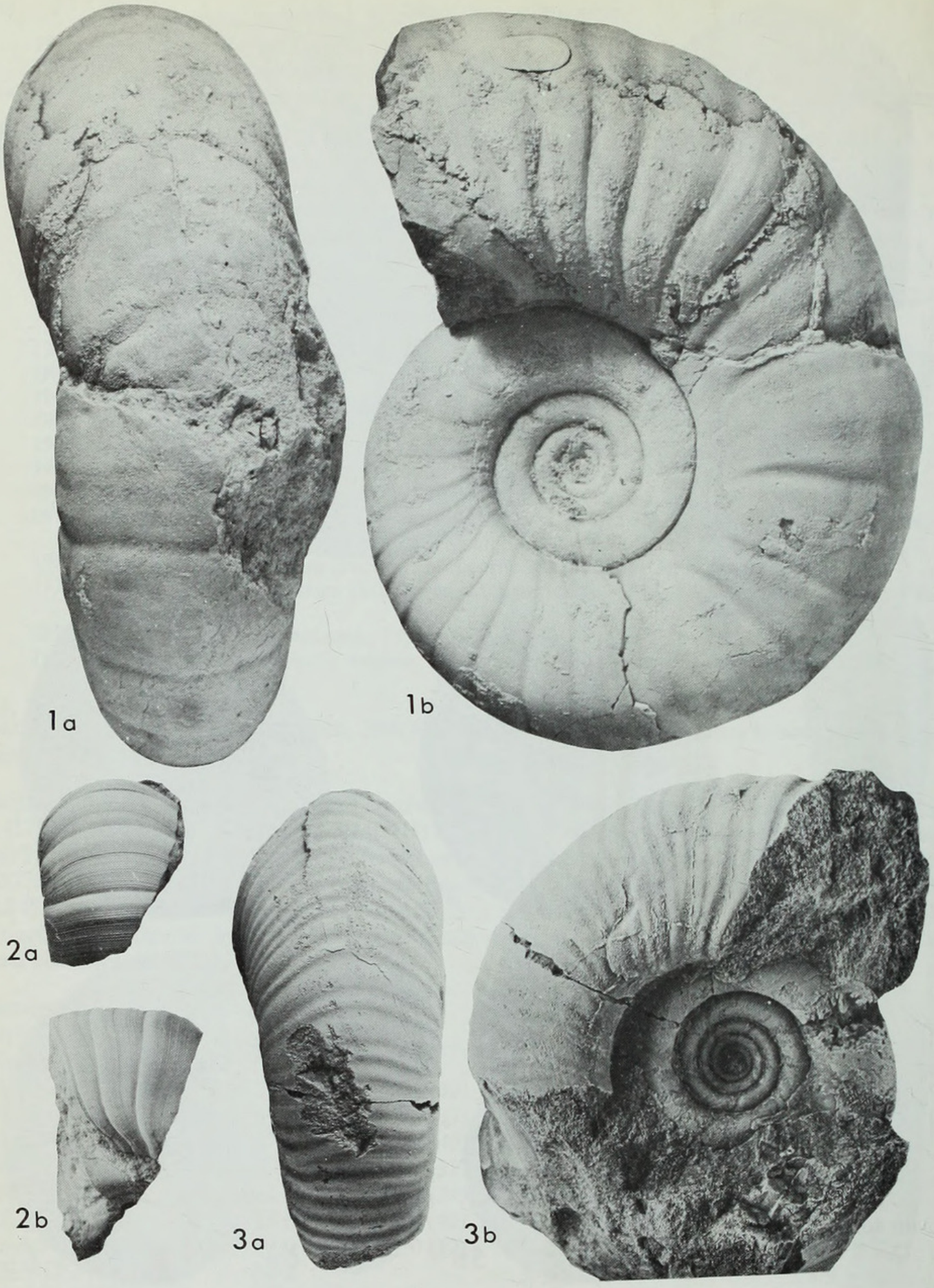


Plate 11 ×1

Figs 1–2. *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78747, Mzinene Formation, Albian III, Loc. 35; Fig. 2, BM(NH) C78753, Mzinene Formation, Albian V, Loc. 51, Bed 12 or 13, Mzinene River, Zululand. See also Pls 8–10.

Fig. 3 *Anagaudryceras subsacya* (Marshall). UND 635, Umzamba Formation, Santonian or Campanian, Loc. 4, Sometsu Road, Durban.

umbilical wall, merging with rounded, convergent flanks. The ventrolateral shoulders are rather abruptly rounded, and the venter somewhat flattened.

The shell surface is ornamented by very fine lirae which arise at the umbilical seam, pass straight up the umbilical wall, are markedly prorsiradiate and weakly convex across the flank, flexing gently backwards across the ventrolateral shoulder to cross the venter with a shallow broad peak. There are up to six broad, low, rounded collar-like ribs per whorl, running parallel to the lirae, and in front of each is a shallow constriction. Both collar and constriction are covered in lirae.

Internal moulds are smooth, save for low swellings, corresponding to the site of collars, and shallow constrictions, rather more prominent than those on the shell surface.

Middle growth stages, 30–50 mm. As size increases, the whorl section tends to become as high as wide, and as a result the umbilicus becomes proportionately smaller. The test is ornamented by fine lirae and periodic collars and constrictions as in the early growth stages, but the latter become progressively more closely spaced and distinctly flexuous.

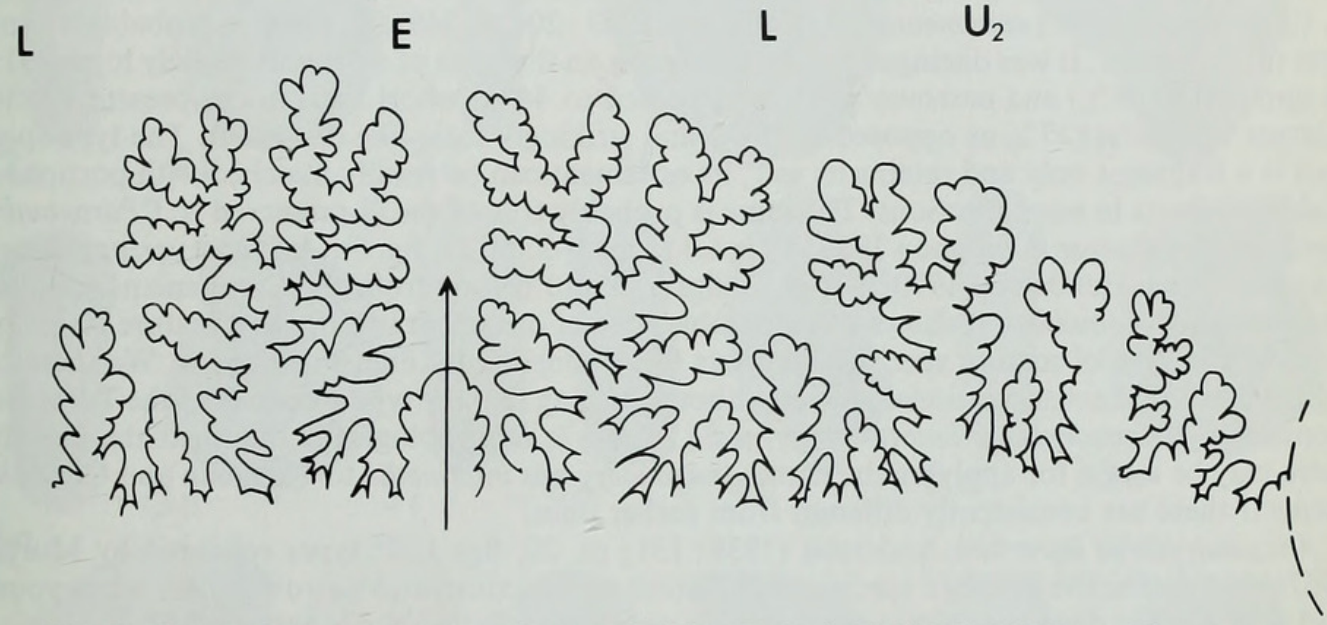


Fig. 2 External suture of *Anagaudryceras buddha* (Forbes). BM(NH) C78721, × 3½ approx.

These changes take place at different rates and at different diameters in different specimens, and spacing of constrictions is irregular; there is thus wide intraspecific variability.

Mature ornament, 50 mm onwards. Outer whorls and body chamber are ornamented by low, broad, straight, prorsiradiate to gently flexed band-like ribs separated by narrow furrows which are clearly derived from the constrictions present on early and middle growth stages. On the shell, the ribs are typically flattened, with a flattened apertural face so that they appear distinctly scale-like, whilst the whole shell surface bears fine lirae (Pl. 10, fig. 1). On the internal mould, ribs tend to be rounded and furrows broader than when shell is preserved.

Ornament is, however, enormously variable. In some specimens, close-spaced regular furrows give a *Kossmatella*-like appearance (Pl. 9, fig. 3); other individuals show very irregular ribs, with some broad segments of almost smooth whorl between constricted areas (Pl. 10, fig. 2).

Our specimens are adult at diameters of 90–100 mm, and typically show crowded, narrow flexed ribs over the last few centimetres immediately before the aperture, which is simple with a gently projected ventral peak.

The suture line (Fig. 2) is deeply incised with a lanceolate ventral lobe, a large, bifid, deeply-incised first lateral saddle (E/L), a smaller, bifid second lateral saddle (L/U_2), a bifid lateral lobe (L) which is shallower than the ventral lobe (E), and a retracted suspensive lobe with a large asymmetrically bifid first auxiliary lobe; the number of auxiliaries is not clear. The internal suture is not well exposed, but some specimens show a well-developed septal lobe.

DISCUSSION. Our collections are the largest known for this species; the presence of specimens with and without test, and at various ontogenetic stages, show that there is great intraspecific variability.

The problems of nomenclature associated with *A. buddha* stem from the description by Forbes (1846) of successive ontogenetic stages of the same species under different names, *Ammonites sacya* for the juvenile and *Ammonites buddha* for the adult. Our collections confirm the view that these are indeed synonymous, but contrary to common usage the name *buddha* has page priority, as Breistroffer (*in* Besairie 1936) has indicated.

There are a large number of names available for specimens at both the *sacya* and *buddha* stages, but we feel fairly confident that *Anagaudryceras limatum*, *A. limatum obscura*, *A. revelatum*, *A. utaturense*, *A. choffati*, *A. filicinctum*, '*Kossmatella*' *whitneyi*, '*Kossmatella*' *cappsi* and '*Murphyella*' *enigma* fall within the range of intraspecific variability. The Albian species *A.* ('*Paragaudryceras*') *sakalavum* (Collignon 1949 : 51; pl. 7, figs 3, 3a, 3b) differs from *A. buddha* in the subdued nature of the ornament of the outer whorls, together with differing proportions, which place it outside the range of variation seen in our material. It probably represents no more than the unornamented end member of variability within the species group. A further Albian species from Madagascar, *A.* ('*Paragaudryceras*') *coagmentatum* (Collignon 1963 : 20; pl. 249, fig. 1064) is probably a synonym of *A. buddha*. It was distinguished by Collignon on the basis of a proportionately lower (41% as opposed to 46%) and narrower (40% as opposed to 44%) whorl than in the present species, a larger umbilicus (37% as opposed to 29%) and strikingly scale-like ornament. The type specimen is a fragment only and retains its test; its ornament can be readily matched with portions of *buddha* variants in our collections. The same is probably true of the ill-preserved *A.* ('*Paragaudryceras*') *mokarahaense* (Collignon 1950 : 67; pl. 11, figs 1–2; pl. 12, fig. 5). *Anagaudryceras subsacya* (Marshall) (see Henderson 1970 : 18; pl. 2, figs 5, 6 and below) from the Campanian is a direct descendant of *A. buddha*. It shows a comparable style of ornament in early and mature stages,but the fold-like ribs of mature specimens appear to be consistently finer in *subsacya*. We therefore regard it as a distinct successional species, although noting that the type specimen of the Turonian–Coniacian *Anagaudryceras limatum intermedia* (Yabe) is morphologically intermediate, and that there may be a case for applying the name *Anagaudryceras intermedia* to Turonian and Coniacian forms if these are consistently different from earlier ones.

Anagaudryceras aurarium Anderson (1938 : 151; pl. 20, figs 1, 2; types refigured by Murphy 1967*b*) is a distinctive involute species, with distant constrictions and narrow collars when young, and with distant deep constrictions separating very broad flattened ribs when adult.

Other *Anagaudryceras* species either belong to the *involvulum* group, or are juveniles at the *sacya* stage. Most of these (see Collignon 1956 : 69, sections K, L for a fairly complete summary) are too poorly characterized for profitable discussion, and their relations to species known as adults is not determinable.

OCCURRENCE. Middle and Upper Albian of Zululand; Middle Albian, Cenomanian and Turonian of Madagascar, Cenomanian of Mozambique, Cenomanian of New Zealand, Cenomanian to Coniacian of Japan, Cenomanian of Alaska, Albian of British Columbia and California, Albian and Cenomanian of central and southern Europe, Albian of the Balkans.

Anagaudryceras subsacya (Marshall)
(Pl. 11, fig. 3)

1917 *Lytoceras* sp. Marshall : 445; pl. 33, fig. 3; text-fig. 4.

Plate 12 × 1, except Figs 1c–d

Figs 1–3, 5–10 *Anagaudryceras pulchrum* (Crick). All Mzinene Formation, Albian V, Mzinene–Munywana areas, Zululand. Fig. 1, BM(NH) C78782, Bed 12 or 13, Loc. 51: × 2 in figs 1c–d to show details of lirae and collars. Fig. 2, BM(NH) C78815, Loc. 65; Fig. 3, BM(NH) C78797, Bed 12, Loc. 51; Fig. 5, SAS 56, Loc. 51; Fig. 6, BM(NH) C78781, Bed 9 or 10, Loc. 51; Fig. 7, BM(NH) C78793, Bed 12, Loc. 51; Fig. 8, BM(NH) C78818, Loc. 66; Fig. 9, BM(NH) C78774, Bed 6, Loc. 51; Fig. 10, BM(NH) C78796, Bed 12, Loc. 51. See also Pl. 6, figs 3–4; Pl. 13.

Figs 4, 11 '*Gaudryceras*' spp. Fig. 4, BM(NH) C18271; Fig. 11, BM(NH) C18269. Specimens mentioned by Crick (1907*b* : 238, 239), from Munywana Creek; presumably Albian.


1a
1b
1c
1d
2a
2b
2c
3a
3b
3c
4a
4b
5a
5b
6a
6b
7a
7b
7c
8
9a
9b
10a
10b
11a
11b

1926 *Gaudryceras subsacya* Marshall : 144; pl. 20, figs 8–9; pl. 29, figs 1–2.
1965 *Anagaudryceras subsacya* (Marshall) Howarth : 358.
1970 *Anagaudryceras subsacya* (Marshall); Henderson : 18; pl. 2, figs 5–6; text-fig. 5a.
1972 *Anagaudryceras subsacya* (Marshall); Kennedy, Kauffman & Klinger : 100; pl. 3, figs 1a–b.

LECTOTYPE. Designated by Henderson (1970 : 18), the original of Marshall 1926 : pl. 29, figs 1–2, from the Mata Series of North Auckland, New Zealand, and probably of Lower–Middle Campanian age.

MATERIAL. Two specimens, UND 6545 and 6546 from the Umzamba Formation at Loc. 4, Sometsu Road, Durban, and of Santonian or Campanian age.

DESCRIPTION. Our best-preserved specimen is an internal mould, too fragmentary for measurement. The coiling is evolute, with an evenly-rounded whorl section, depressed (whorl breadth/height ratio up to 1·33) when young, becoming progressively less depressed as diameter increases (ratio decreases to almost 1·0). The expansion rate is moderately high. The umbilicus is broad, up to 45% of diameter when young, falling to just over 30% when adult, and shallow. As in *Anagaudryceras buddha*, two distinct types of ornament are present. Up to a diameter of about 40 mm, the test bears fine, dense striae which sweep gently forwards across flanks and venter, as do periodic collar-like ribs, five per whorl, in front of each of which is a narrow, shallow constriction. The mould is smooth, save for subdued collars and rather more conspicuous constrictions. On the mould of the body chamber, ornament consists of fine, irregular, narrow, band-like ribs separated by shallow, rounded furrows. The ribs are gently flexed on the flanks and slightly projected on the venter. The transition zone between the two types of ornament is not fully preserved.

The suture line is incompletely exposed, but includes a long, moderately subdivided, lanceolate ventral lobe, a large, deeply-incised bifid first lateral saddle (E/L), and a smaller, ? bifid second lateral saddle (L/U_2). The suspensive lobe is strongly retracted, with at least three auxiliary lobes, the first large and asymmetrically bifid.

DISCUSSION. As noted above, the species with which *Anagaudryceras subsacya* shows closest similarities is *Anagaudryceras buddha*, from which it is descended. The inner whorls of the two species are virtually identical, but with the appearance of adult ornament, the band-like ribs of *subsacya* appear to be consistently finer and more regular than those of *buddha*.

OCCURRENCE. Lower to Middle Campanian of New Zealand, Santonian/Campanian of Durban, Natal.

Anagaudryceras politissimum (Kossmat)
(Pl. 5, fig. 3)

1895 *Lytoceras* (*Gaudryceras*) *politissimum* Kossmat : 128 ; pl. 15, figs 7a–c.
non 1909 *Gaudryceras politissimum* Kossmat; Kilian & Reboul : 14; pl. 1, figs 7, 8.
? 1926 *Gaudryceras politissimum* Kossmat; Marshall : 145; pl. 28, figs 1, 3; text-fig. 3 (= *Anagaudryceras particostatum* Marshall according to Henderson 1970 : 17).
non 1938 *Gaudryceras politissimum* Kossmat; Collignon : 42; pl. 7, figs 2–2a (= *Anagaudryceras mikobokoense* Collignon).
1956 *Anagaudryceras politissimum* (Kossmat); Collignon : 58; pl. 8, figs 2a–c.

HOLOTYPE. Kossmat's original specimen from the Upper Trichinopoly group of Varagur, southern India.

MATERIAL. A single specimen, SAS H202/1, from the St Lucia Formation at Loc. 87, False Bay, Lake St Lucia, Zululand (Santonian I–II).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (after Kossmat)	89	28 (31)	33 (37)	0·85	34 (38)
Collignon 1956 : pl. 8, fig. 2	97	30 (31)	37 (38)	0·81	36 (37)

Dimensions.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
Collignon 1956 : 59	105	31 (30)	38 (36)	0·82	37 (35)
SAS H202/1	61·2	21·5 (35)	21·8 (36)	0·98	22·4 (37)
Anagaudryceras involvulum (after Stoliczka)	44·0	16·0 (36)	19·0 (43)	0·84	14·6 (30)
Anagaudryceras madraspatanum (after Stoliczka)	30	13 (43)	12·0 (40)	1·08	10·8 (36)
Anagaudryceras yamashitai (after Yabe)	88	33 (37)	44 (50)	0·75	22 (25)
Anagaudryceras mikobokoense (after Collignon)	92	35 (38)	39 (42)	0·9	35 (38)

Description. The coiling is relatively evolute, about 30% of the previous whorl being covered. The whorl section is slightly compressed (whorl breadth/whorl height ratio 0·98), the greatest breadth being some way below mid-flank. The umbilicus is fairly wide (37% of diameter), shallow, with a low rounded umbilical wall and shoulder which merge into the moderately inflated, rounded and convergent flanks. The ventrolateral shoulders are rounded, merging with an arched, rounded venter.

The shell surface is not well preserved in our specimen, but appears to have borne very fine, flexuous, prorsiradiate lirae, projected on the venter as a shallow broad peak. There appear to have been four or five flexuous, rounded collar-like ribs per whorl, parallel to the lirae, and followed by shallow constrictions.

The internal mould is smooth, save for the low collar-like ribs and constrictions. The suture line is poorly visible, but is made up of moderately incised, bifid lobes and saddles.

Discussion. As Howarth (1965, 1966) has noted, the second species group recognizable within *Anagaudryceras* listed above (p. 146) includes a large number of named forms based either on juveniles or geographically and stratigraphically isolated individuals. It is thus not at present possible to assess intraspecific variability nor to decide upon valid interspecific criteria, although it seems clear that *Anagaudryceras involvulum* (of which *A. utaturense* Shimizu is a synonym), *A. madraspatanum*, *A. yamashitai* and *A. mikobokoense* (of which *Gaudryceras aenigma* Haas and *G. aureum* Anderson are synonyms) can be differentiated from our specimen on the basis of differing relative proportions, as summarized in the table above. It is clearly distinguished from *Anagaudryceras pulchrum* and *A. subtilineatum*, discussed below, on similar criteria, whilst *A. particostatum* and *A. tennanti* are based on juveniles too small for proper comparison.

Our specimen thus finds its closest similarities with *Anagaudryceras politissimum* in terms of style of ornament and proportions, although less compressed than Kossmat's type.

Occurrence. *Anagaudryceras politissimum* is known from the Turonian to Santonian of southern India, the Maastrichtian of Madagascar and the Santonian of Zululand.

Anagaudryceras subtilineatum (Kossmat)
(Fig. 3; Pl. 14, figs 3, 12)

1895 *Lytoceras* (*Gaudryceras*) *subtilineatum* Kossmat : 123; pl. 10, figs 1a–c, 2a–b.
1921 *Gaudryceras tenuilineatum* van Hoepen : 5; pl. 2, figs 7–9; text-fig. 2.
? 1921*b* *Gaudryceras* sp. juv. Spath : 41.
1922 *Gaudryceras tenuilineatum* van Hoepen; Spath : 117.
1956 *Anagaudryceras subtilineatum* (Kossmat) Collignon : 68.
1956 *Gaudryceras tenuilineatum* van Hoepen; Collignon : 70.
1965 *Anagaudryceras subtilineatum* (Kossmat); Howarth : 358.

Lectotype. Herein designated, the original of Kossmat 1895 : pl. 19, figs 1a–c, from the Arialoor Group of Karapady, southern India.

MATERIAL. We have five specimens, the holotype of *Gaudryceras tenuilineatum* TM 559, SAM 7036, a further two fragments in the Durban Museum (unregistered) and a doubtful fragment BM(NH) C78757, all from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
TM 559	26·5	10·8 (41)	7·3 (28)	1·48	13·4 (51)

DESCRIPTION. The coiling is evolute, about 30% of the previous whorl being covered, the whorls expanding rather slowly. The whorl section is depressed, the greatest breadth being close to mid-flank. The umbilicus is broad (51% of diameter) and of moderate depth, with a rounded umbilical wall. The whorl section is depressed, evenly rounded, with a broad venter. The shell surface appears smooth to the naked eye, but is in fact covered in very fine, dense lirae. These arise at the umbilical seam, or from a point some way up the wall or flank. The lirae at first run normal to the umbilical seam, but sweep forwards across the umbilical shoulder and lower flank, are rectiradiate at mid-flank, and sweep forwards over the shoulder to produce a shallow, broad, ventral peak.

There are four shallow constrictions on the outer whorl; behind each is a low, rounded collar. Both rib and collar run parallel to the lirae and are themselves lirate.

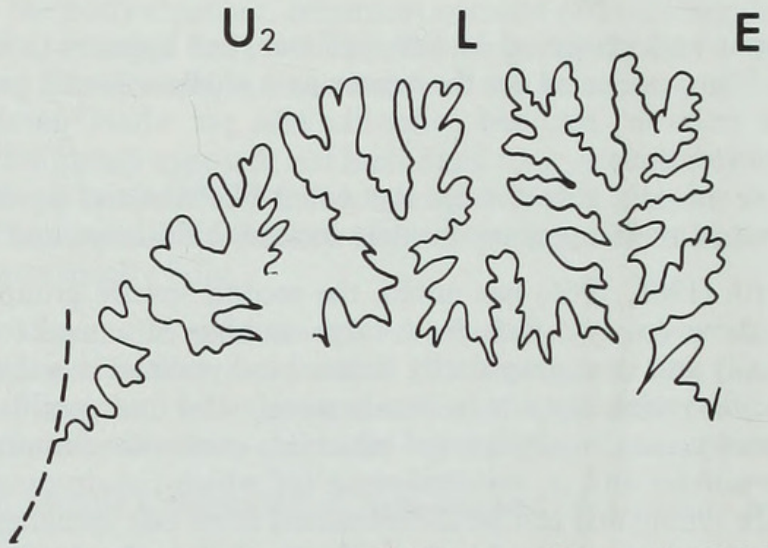


Fig. 3 External suture of *Anagaudryceras subtilineatum* (Kossmat). TM 559 (holotype of *Gaudryceras tenuilineatum* van Hoepen), × 7½ approx.

The suture (Fig. 3) consists of a quite deeply divided ventral lobe (E) with a lanceolate ventral saddle extending for half its height, a large, bifid first lateral saddle (E/L) and a smaller bifid second lateral saddle (L/U_2), a lateral lobe (L) which is symmetrically bifid and shallower than the ventral lobe, plus a retracted suspensive lobe with bifid auxiliaries.

DISCUSSION. *Anagaudryceras subtilineatum* is a poorly-known species, being based upon a large fragment of an individual with a maximum whorl height of 24 mm and a septate nucleus only 25 mm in diameter. The fine ornament indicates, however, that it is clearly an *Anagaudryceras*.

Van Hoepen (1921) separated his *Gaudryceras tenuilineatum* from Kossmat's species on the basis of slightly differing relative proportions. The figures of Kossmat show, however, that proportions vary enormously with age, whilst the identical ornament of the two groups of specimens leads us to place them in synonymy.

The evolute coiling, depressed whorl section, fine ornament and limited number of constrictions serve to distinguish *Anagaudryceras subtilineatum* from species such as *A.* '*sacya*' and *subsacya* at comparable diameters, and from *A. mikobokoense*, *A. politissimum*, *A. madraspatanum*, *A. involvulum*, *A. yamashitai* and *A. tennanti* at large diameters. The closest comparisons are clearly with *Anagaudryceras pulchrum*, but in this Albian species the umbilicus is proportionally

smaller, the expansion rate greater, the ornament coarser and the constrictions and collar ribs more conspicuous.

OCCURRENCE. Campanian? of southern India, Santonian or Campanian of southern Natal (Pondoland).

Anagaudryceras pulchrum (Crick)

(Fig. 4; Pl. 6, figs 3, 4; Pl. 12, figs 1–3, 5–10; Pl. 13, figs 1–9)

1907*b* *Gaudryceras pulchrum* Crick : 237; pl. 15, figs 1, 1a.
1936 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Venzo : 78; pl. 5, figs 8a–b; pl. 6, figs 5a–b.
1956 *Anagaudryceras pulchrum* (Crick) Collignon : 68.
1964 *Anagaudryceras pulvinatum* (Crick); Collignon : 30; pl. 324, fig. 1445.

HOLOTYPE. BM(NH) C18266 from the 'south branch of the Manuan Creek, Zululand', figured by Crick (1907*b* : pl. 15, figs 1–1a), and of Upper Albian age.

MATERIAL. In addition to the holotype, there are two paratypes, BM(NH) C18267–8, also from the Munywana, and a large number of additional specimens. SAS GSO 1–4, SAS 55–57, A3056, A3061–2 and SAS U1–3 are from the Mzinene Formation at Loc. 51 (Albian IV–V, precise horizon unknown); BM(NH) C78774–5 are from Bed 6, C78776–7, C78779–80 from Bed 8, C78781–3 from Beds 9 or 10, C78784 from Bed 10 or 11, C78785–78797 from Bed 12, C78799–78801 from Bed 12 or 13 at the same locality (Albian V); BM(NH) C78802 from Loc. 52, BM(NH) C78803–13 from Loc. 54 (Albian V), BM(NH) C78816, C78820–2 from Loc. 56 (Albian V), all on the Mzinene. BM(NH) C78814 is from Bed 4 of the Mzinene Formation at Loc. 64, C78815 from Loc. 65 and C78817–9 from Loc. 66, all Mzinene Formation (Albian V) on the Munywana and its tributaries.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Paratype, BM(NH) C18268	21·8	9·9 (45)	6·5 (30)	1·52	10·4 (48)
Paratype, BM(NH) C18267	34·8	14·5 (41)	11·0 (32)	1·32	15·5 (45)
Holotype, BM(NH) C18266	39·0	15·5 (38)	12·5 (32)	1·24	16·8 (43)
BM(NH) C78797	27·3	11·3 (41)	9.3 (34)	1·22	12·0 (44)
BM(NH) C78793	29·0	11·8 (41)	10·8 (37)	1·1	13·2 (45)
BM(NH) C78794	30·3	12·7 (42)	10·0 (33)	1·27	14·0 (46)
BM(NH) C78802	44·4	16·7 (38)	15·7 (35)	1·06	17·3 (39)
BM(NH) C78776	48·2	–	17·2 (36)	–	19·2 (40)

DESCRIPTION. The coiling is very evolute, slowly expanding, with a broad shallow umbilicus. The umbilical wall is low and slopes outwards, merging with the inflated flanks. The whorl section is depressed at first (whorl breadth/height ratio 1·5–1·3), but as diameter increases the whorls become less depressed, and eventually almost as broad as high. The venter, initially rather flattened, becomes first broadly rounded, and then somewhat arched. When well preserved, the surface of the test is covered in fine dense striae. These arise at the umbilical seam, pass slightly forwards across the wall and shoulder, and are distinctly prorsiradiate on the flanks, where they are gently flexed, forwards to mid-flank, backwards across the upper flank, thence passing across the venter with the shallowest of ventral peaks.

There are four or five collar ribs and associated constrictions per whorl during the early growth stages, increasing to seven or more when fully grown. These collars are parallel to the lirae, and have a gently rounded apical slope and a steep, abrupt apertural slope, giving them a distinctly scale-like appearance. The constrictions are narrow, and both collar and constriction are lirate.

The internal mould is smooth, save for periodic collars and constrictions which are broader and shallower than on the test.

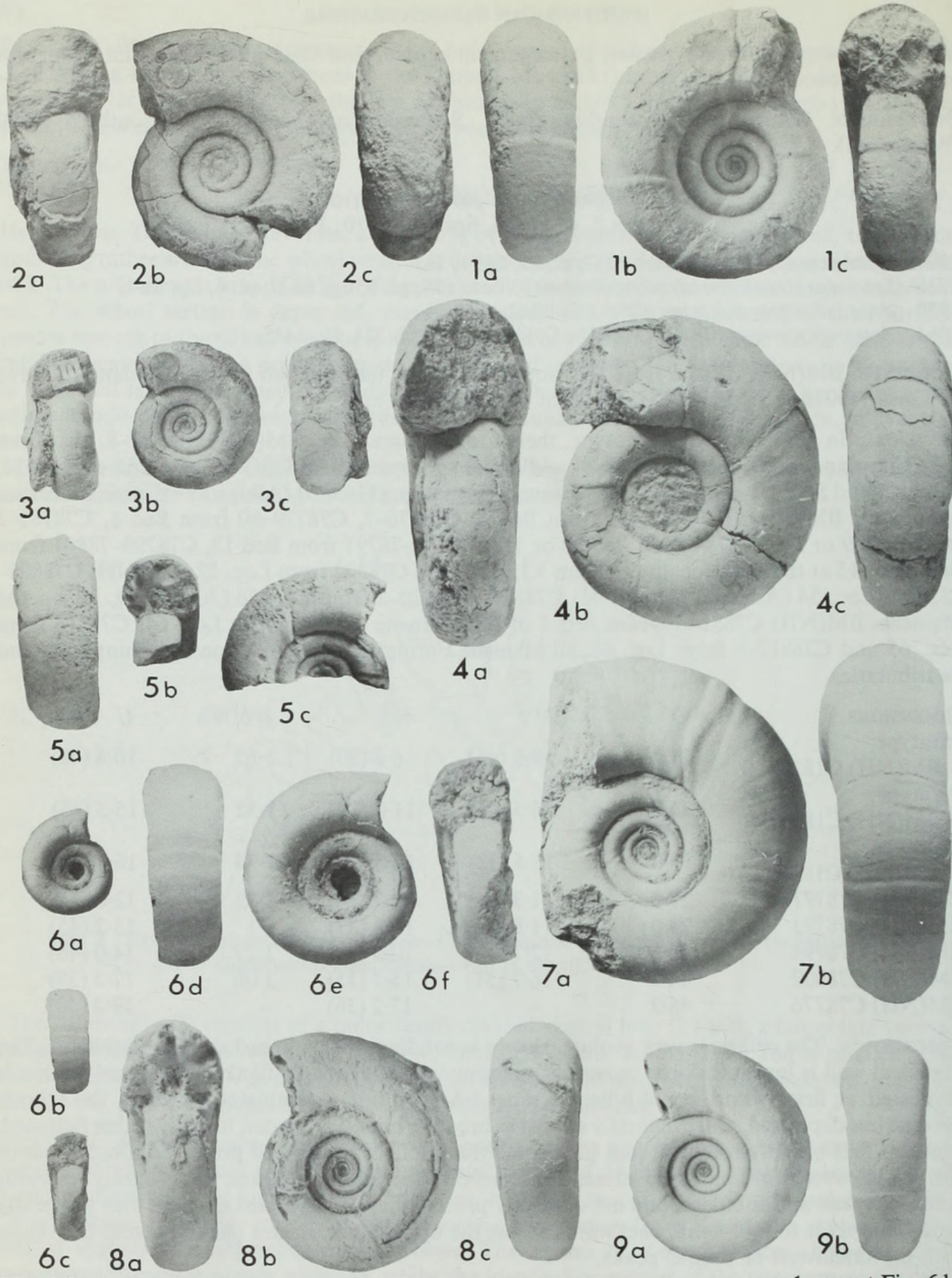


Plate 13 × 1, except Figs 6d–f

Figs 1–9 *Anagaudryceras pulchrum* (Crick). All from Mzinene Formation, Albian V, Mzinene–Munywana area, Zululand. Fig. 1, the **holotype,** BM(NH) C18266; Fig. 2, paratype, BM(NH) C18267; Fig. 3, paratype, BM(NH) C18268; Fig. 4, BM(NH) C78802, Loc. 52; Fig. 5, BM(NH) C78816, Loc. 56; Fig. 6, BM(NH) C78783, Bed 9 or 10, Loc. 51, Figs 6d–f × 2 to show juvenile features; Fig. 7, BM(NH) C78776, Bed 8, Loc. 51; Fig. 8, SAS VI and Fig. 9, SAS A55, both Loc. 51 (precise horizon unknown), Fig. 8 showing a well-preserved septal lobe. See also Pl. 6, figs 3–4; Pl. 12, figs 1–3, 5–10.

The suture (Fig. 4) consists of a large, moderately incised, bifid ventral lobe (E) with a narrow lanceolate ventral saddle extending to half its height, a large bifid first lateral saddle (E/L) and a smaller second lateral saddle (L/U_2), both symmetrically bifid, and separated by a bifid lateral lobe (L) with a large, slender central foliole. The suspensive lobe is retracted, with five auxiliary saddles, the first large and asymmetrically bifid. There is a deep and narrow internal lateral lobe (I) flanked by a large lateral saddle, and a large, horseshoe-shaped septal lobe.

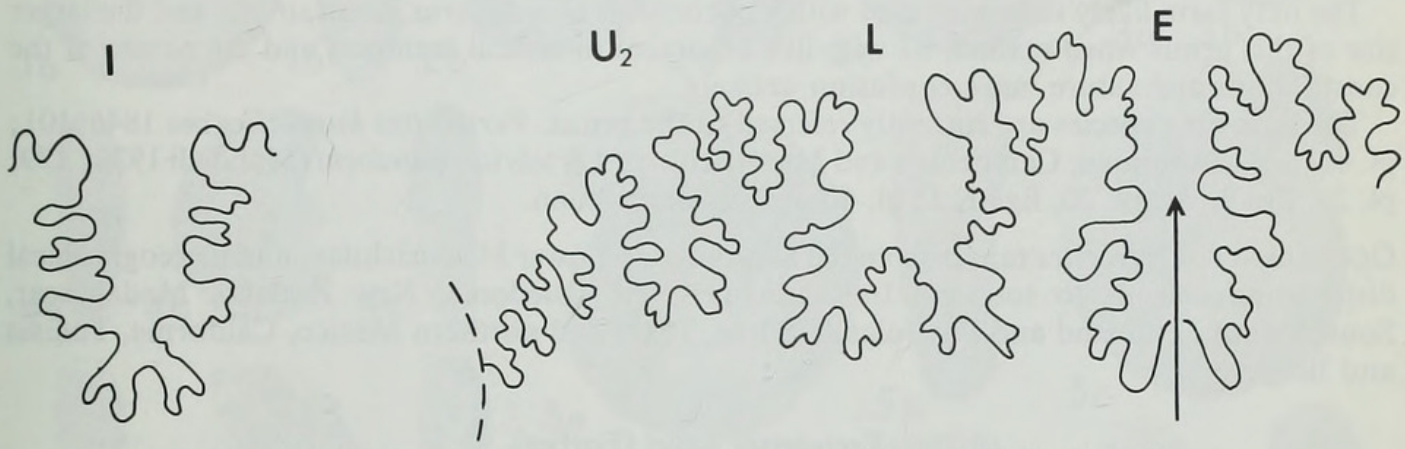


Fig. 4 External and internal sutures of *Anagaudryceras pulchrum* (Crick). SAS 56, ×7 approx.

Discussion. *Anagaudryceras pulchrum* closely resembles *A. buddha* when young, but the two species can be separated on the basis of the coarser lirae of *pulchrum*, scale-like collars, less depressed whorl section and more evolute coiling. Adults of the two species are clearly distinguished by the fold-like ribs of *buddha*. *Anagaudryceras subtilineatum*, a close ally from a somewhat higher horizon, appears to be more depressed when young and to possess more markedly flexed lirae; it bears the same relationship to *A. pulchrum* as *Anagaudryceras subsacya* does to *A. buddha*.

Gaudryceras pulvinatum Collignon (1964 : 30; pl. 324, fig. 1445) was separated from *Anagaudryceras pulchrum* on the basis of its Cenomanian age and differing proportions (at 48 mm diameter, *Wb* = 40%, *Wh* = 40%, *U* = 31%), plus a change from a depressed to a compressed whorl section as diameter increases and a consequent decrease in proportionate umbilical width; it is best regarded as a synonym of *A. pulchrum*.

Anagaudryceras cassisianum (d'Orbigny 1850), from Cassis in the south of France, appears to be a close relation of *A. pulchrum*. From the figures of Fabre (1940 : 15; pl. 5, figs 8, 9) this species seems to have a smaller umbilicus than *pulchrum* at comparable diameters (30% as opposed to over 40%), slowly expanding whorls which are strikingly depressed when young, more prominent lirae, and scale-like collars. More material is needed to determine its true affinities.

Occurrence. Upper Albian of Zululand; Lower Cenomanian of Madagascar.

Genus *VERTEBRITES* Marshall, 1926

Type species. *Vertebrites murdochi* Marshall 1926.

Diagnosis. Very evolute, many-whorled serpenticone gaudryceratids retaining a depressed, subrectangular whorl section throughout ontogeny. Ornament consists of fine prorsiradiate lirae which are simple and rather prominent on the flank, dividing into many finer lirae over the venter. Internal suture with several saddles which increase in size from the dorsal lobe towards the umbilical seam.

Discussion. Treatment of *Vertebrites* has varied from its acceptance as merely a subgenus of *Gaudryceras* (Matsumoto 1959*a*) to separation as the sole member of a subfamily Vertebritinae (Wiedmann 1962*a*), on the basis of the presence of a greater number of umbilical lobes than in the

Gaudryceratinae *sensu stricto*. Henderson (1970 : 22) noted, however, that forms such as *Anagaudryceras tennanti* Henderson (1970 : 19; pl. 2, figs 4, 7; text-fig. 5b) and *Gaudryceras varicostatum* (van Hoepen) (= *Anagaudryceras subtilineatum* Kossmat) are transitional to *Vertebrites* in shell form and proliferation of umbilical lobes, whilst Matsumoto (1959*a* : 141) noted that some juvenile *Gaudryceras, sensu stricto*, e.g. *Gaudryceras tenuiliratum* Yabe, resemble *Vertebrites* in both shell form and ornament. We would also draw comparisons to juveniles of *Gaudryceras stefaninii* and *G. varicostatum* described and figured here (Pl. 1, figs 2, 8; Pl. 3, figs 3a-d) in this respect. We have followed a conservative course, and treat *Vertebrites* as an independent genus.

The only form likely to be confused with *Vertebrites* is *Gaudryceras, sensu stricto*, and the larger size of this genus when mature, its wire-like ornament in typical members and the nature of the constrictions and suture make confusion unlikely.

The following species are currently referred to the genus. *Vertebrites kayei* (Forbes 1846 :101; pl. 8, fig. 3), Santonian, Campanian and Maastrichtian. *Vertebrites murdochi* (Marshall 1926 : 139; pl. 20, figs 9, 9a; pl. 30, figs 1, 2; pl. 40, fig. 3), Campanian.

OCCURRENCE. *Vertebrites* ranges from the Santonian to Lower Maastrichtian, and its geographical distribution extends to southern India, Japan, New Caledonia, New Zealand, Madagascar, South Africa (Zululand and Pondoland), Chile, Texas and northern Mexico, California, Tunisia and Belgium.

Vertebrites kayei (Forbes)
(Fig. 5; Pl. 14, fig. 2)

1846 *Ammonites kayei* Forbes : 101; pl. 8, fig. 3.
1865 *Ammonites kayei* Forbes; Stoliczka : 156; pl. 87, figs 1, 1a.
1871 *Lytoceras kayei* (Forbes) Griesbach : 63.
1895 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Kossmat : 124, 162; pl. 16, figs 5a–b; pl. 17, figs 2a–b.
1895 *Lytoceras kayei* (Forbes); Steinmann : 86; pl. 15, figs 5a–b; text-fig. 8.
1906 *Gaudryceras kayei* (Forbes); Woods : 335; pl. 41, fig. 8; pl. 42, fig. 1.
1907 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Pervinquière : 69; pl. 3, figs 2a–b.
? 1908 *Gaudryceras kayei* (Forbes); de Grossouvre : 34; pl. 9, fig. 4.
1927 *Gaudryceras kayei* (Forbes); Böse : 269; pl. 10, figs 10–14; pl. 11, figs 5–10.
1956 *Vertebrites kayei* (Forbes) Collignon : 64; pl. 6, figs 4a–c.
? 1958 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Anderson : 182.

Plate 14 × 1, except Figs 6d–e

Fig. 1 *Zelandites* sp. 2. SAM 7100, late Santonian or early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland).

Fig. 2 *Vertebrites kayei* (Forbes). BM(NH) C78756, St Lucia Formation (Campanian), Loc. 14, Mfolozi River, Zululand.

Figs 3, 12 *Anagaudryceras subtilineatum* (Kossmat). Fig. 3, SAM 7036; Fig. 12, TM 559, holotype of *Gaudryceras tenuilineatum* van Hoepen; both from late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland).

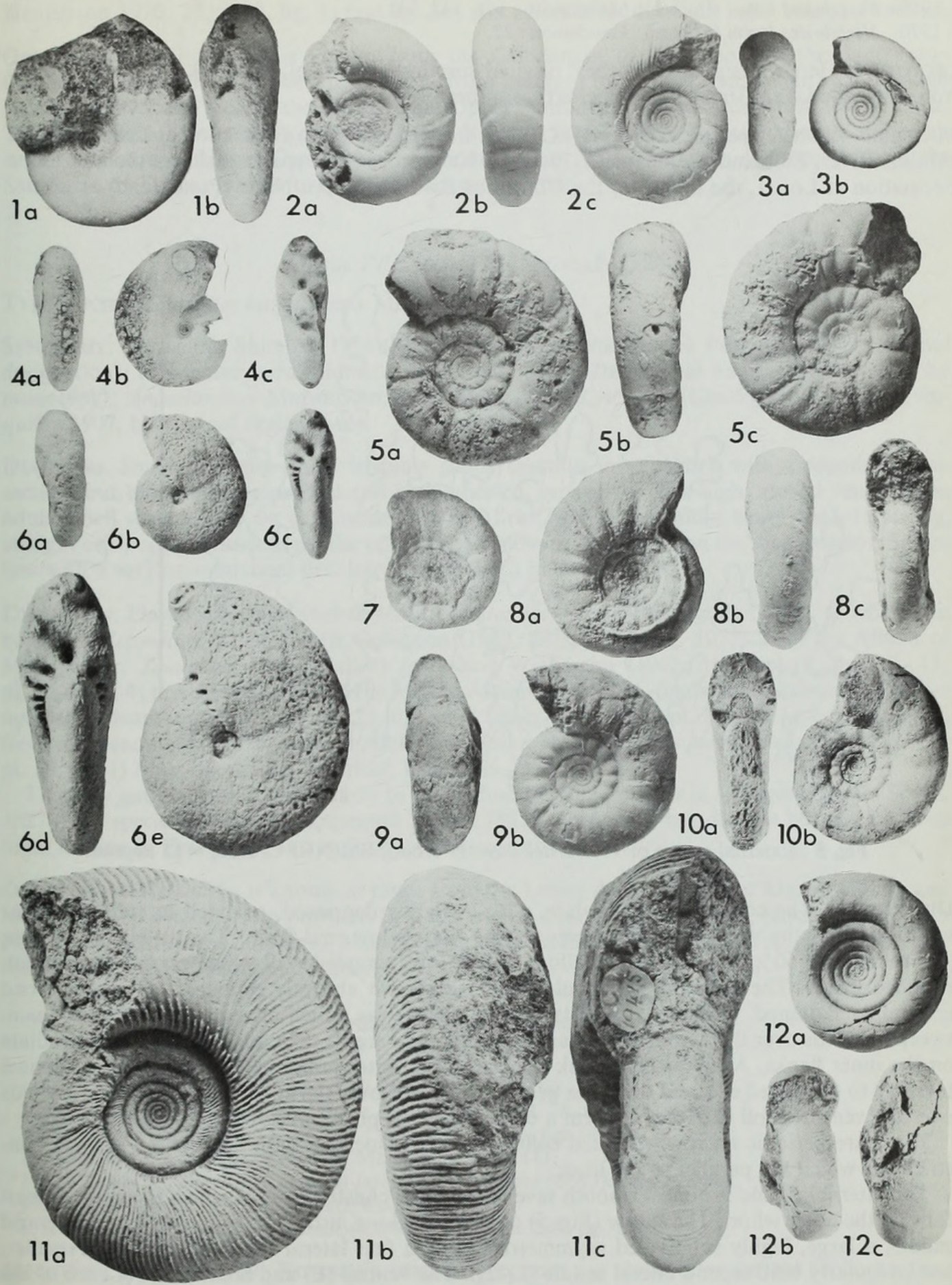
Fig. 4 *Zelandites odiensis* (Kossmat). BM(NH) C18141, Lower or Middle Cenomanian Mzinene Formation, Skoenberg area, Mzinene River, Zululand.

Figs 5, 7, 9, 10 *Kossmatella* (*Kossmatella*) aff. *romana* Wiedmann. Fig. 5, BM(NH) C78764; Fig. 7, SAS Z539b; Fig. 9, BM(NH) C78763; Fig. 10, SAS Z539a; all from Mzinene Formation, Albian V, Loc. 56, Mzinene River, Zululand.

Fig. 6 *Zelandites* sp. 1. BM(NH) C78864, Mzinene Formation, Middle Cenomanian, Loc. 62, the Skoenberg, Zululand, Figs 6d–e × 2 to show constrictions.

Fig. 8 *Kossmatella* (*Kossmatella*) *marut* (Stoliczka). BM(NH) C78762, Bed 12, Mzinene Formation, Albian V, Loc. 51, Mzinene River, Zululand.

Fig. 11 *Gaudryceras varicostatum* van Hoepen. Holotype of *Gaudryceras cinctum* Spath, BM(NH) C19415, late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). See also Pls 3, 4; Pl. 7, fig. 2.


1a
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8c
6d
6e
9a
9b
10a
10b
11a
11b
11c
12a
12b
12c

1958 *Lytoceras* (*Gaudryceras*) *coalingense* Anderson : 184; pl. 68, fig. 1.
1958 *Lytoceras* (*Gaudryceras*) *birkhaueseri* Anderson : 185; pl. 68, figs 4–4a.
1959*a* *Vertebrites kayei* (Forbes); Matsumoto : 141, 142, 145.
1970 *Vertebrites kayei* (Forbes); Henderson : 22.

LECTOTYPE. Herein designated, Forbes' original specimen (1846 : pl. 8, fig. 3), BM(NH) C51050 from the Valudayar Group of Pondicherry, southern India.

MATERIAL. A single specimen, BM(NH) C78756, from the St Lucia Formation at Loc. 14 on the Mfolozi River, Zululand (Campanian). Woods (1906) records four specimens from the Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

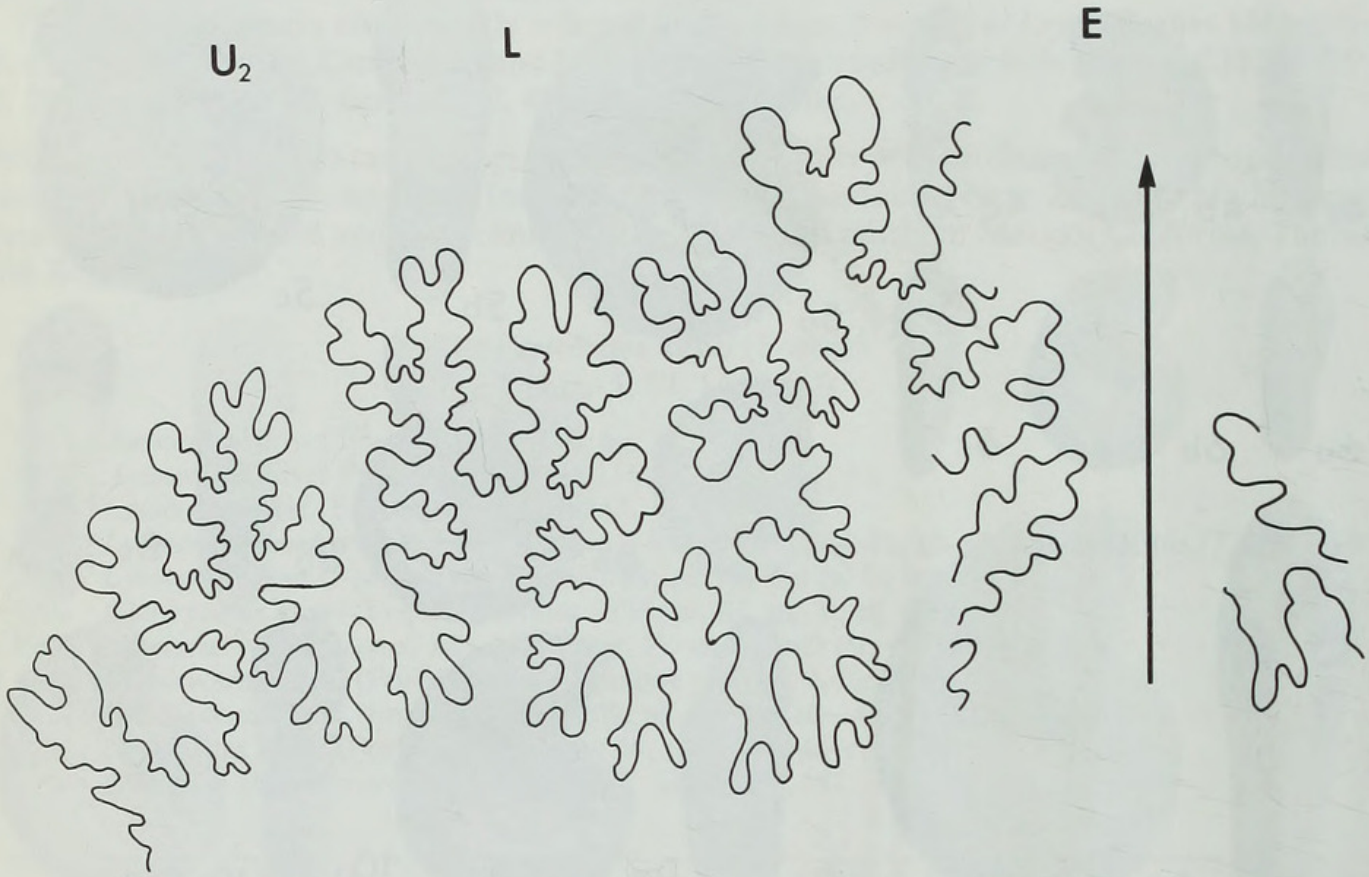

Fig. 5 External suture of *Vertebrites kayei* (Forbes). BM(NH) C78756, × 15 approx.

DESCRIPTION. The coiling is very evolute, with a slightly depressed, rounded to subrectangular whorl section, the greatest breadth being some way below mid-flank. The umbilicus is large (approximately 50% of diameter), shallow, with a low, rounded wall which merges into broad, rounded flanks. The ventrolateral shoulders are somewhat abruptly rounded, the venter broad and rather flattened. Ornament consists of fine, dense lirae which arise at the umbilical seam, sweep forwards over the umbilical wall and shoulder, and are straight and markedly prorsiradiate on the inner flanks. At about mid-flank they subdivide into numerous fine dense striae, almost invisible to the naked eye, and these flex gently backwards over the upper flank and then forwards over the ventrolateral shoulder to form a distinct peaked projection over the siphonal area.

There are periodic narrow, rounded collar-like ribs associated with narrow but distinct constrictions which are parallel to the lirae.

The internal mould is almost smooth save for shallow constrictions of which there are at least four on the outer whorl. The suture (Fig. 5) consists of a long, little subdivided, lanceolate ventral saddle, a large, highly subdivided asymmetrically bifid first lateral saddle (E/L) and a smaller, less irregularly bifid second lateral saddle (L/U_2). The ventral (E) and lateral lobe (L) are of the same length, the latter being bifid. There are three distinct auxiliaries on a retracted suspensive lobe. The first and largest auxiliary saddle is subtrifid.

DISCUSSION. *Vertebrites kayei* can be readily separated from the type species, *Vertebrites murdochi*, in that the latter species is consistently more depressed at corresponding growth stages (e.g. Henderson 1970 : 22; pl. 3, fig. 1; text-fig. 5c), the whorl breadth/height ratio being up to 2·25.

OCCURRENCE. This species is known from the Campanian of Zululand and the Santonian–Campanian of Pondoland. The type material, from southern India, is of Campanian age, although Kossmat (1895 : 86) records the species from Upper Santonian to Maastrichtian strata. In Chile, Texas, northern Mexico and perhaps Belgium, it occurs in the Lower Maastrichtian; Californian occurrences are of Upper Campanian to Maastrichtian age whilst there are records from the Santonian of Tunisia and an unspecified horizon in Japan.

Genus *ZELANDITES* Marshall, 1926

TYPE SPECIES. *Zelandites kaiparaensis* Marshall 1926.

SYNONYMY. *Varunaites* Shimizu, 1926 (type species *Ammonites varuna* Forbes 1846, by original designation); *Hypogaudryceras* Shimizu, 1934 (type species *Desmoceras kawanoi* Jimbo 1894, by monotypy); *Anazelandites* Matsumoto, 1938 (type species *Lytoceras* (*Gaudryceras*) *flicki* Pervinquière 1907, by original designation).

DIAGNOSIS. Small, typically rather involute gaudryceratids, inner whorls with a rounded cross-section, but becoming compressed and high-whorled, typically with a high, arched venter when adult. Shell surface may be ornamented by fine lirae, whilst the mould bears weak to strong, straight or sinuous constrictions, the position of which may be visible on the shell exterior. Suture line with a very asymmetrical first lateral lobe (E/L) in adults.

DISCUSSION. Eleven species or varieties of *Zelandites* are listed by Collignon (1956), to which can be added *Zelandites befamontensis* Collignon (1963 : 24; pl. 250, fig. 1075) from the Albian of Madagascar, *Zelandites dozei* (Fallot) *schroederi* Wiedmann (1962*a* : 161; pl. 8, figs 12, 13; pl. 13, figs 3, 4; text-figs 18–20) from the Middle Albian of Navarra, Spain and Sardinia, *Zelandites inflatus* Matsumoto (1959*b* : 74; pl. 23, figs 2a–d, 3a–c, 4a–c, 5a–d; pl. 24, figs 1a–c; text-fig. 14) from the Cenomanian of Japan and Albian of Alaska and *Zelandites perezi* McLearn (1972 : 40; pl. 37, fig. 1) from the Albian of British Columbia.

The only gaudryceratid genus likely to be confused with *Zelandites* is *Mesogaudryceras* Spath, 1927 (type species *Ammonites leptonema* Sharpe 1855). This genus has distinct but fine flexuous lirae, lacking in *Zelandites*, and is quite without constrictions.

OCCURRENCE. *Zelandites* is known to range from the Lower Albian to Lower Maastrichtian, and its distribution extends from northern Spain, southern France, the Balearics, Sardinia and north Africa to South Africa (Zululand), Madagascar, southern India, Japan, California, British Columbia, Alaska, New Zealand and Chile.

Zelandites odiensis (Kossmat)
(Pl. 14, fig. 4)

1865 *Ammonites varuna* Forbes; Stoliczka : 111; pl. 58, fig. 1.
1895 *Lytoceras* (*Gaudryceras*) *odiense* Kossmat : 129; pl. 18, fig. 1; pl. 19, fig. 3.
1907*a* *Gaudryceras odiense* Kossmat; Crick : 171; pl. 10, figs 14–14a.
1938 *Zelandites odiensis* (Kossmat) Matsumoto : 140, 141.
? 1942 *Zelandites odiensis* (Kossmat) *japonica* Matsumoto : 666 (*nomen nudum*).
1956 *Zelandites odiensis* (Kossmat); Collignon : 66.
1963 *Zelandites odiensis* (Kossmat); Collignon : 20; pl. 249, fig. 1066.

HOLOTYPE. By monotypy, Kossmat's original specimen (= *Ammonites varuna* Stoliczka (*non* Forbes) 1865 : pl. 58, fig. 1) from the Utatur group of Odium, southern India, and probably of Cenomanian age.

MATERIAL. A single specimen in William Anderson's collection, BM(NH) C18141, clearly from the Mzinene Formation of the Skoenberg area of Zululand and of Lower to Middle Cenomanian age.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (after Kossmat)	19	6·4 (34)	8·5 (45)	0·75	4·5 (24)
BM(NH) C18141	22·3	7·2 (32)	11·0 (49)	0·65	4·0 (17)
Collignon 1963 : 20	38	14 (37)	17 (45)	0·82	11 (29)

DESCRIPTION. The coiling is involute, with a small, deep, conical umbilicus (17% of diameter). The whorl section is compressed (whorl breadth/height ratio 0·65), with the greatest breadth close to mid-flank. The umbilical wall slopes outwards, to merge with the broadly rounded, flattened flanks, which converge to the high, rather narrow, arched venter. The specimen retains corroded test, and none of the original ornament remains, nor are any constrictions visible. The suture is not exposed.

DISCUSSION. Our specimen is poorly preserved, but the involute coiling, compressed whorl section with greatest breadth at mid-flank, and lack of constrictions and lirae clearly place it in Kossmat's species. *Zelandites odiensis* may be separated from other members of the genus as follows.

Z. dozei (Fallot 1885 : 235; pl. 4, figs 3–3b) from the Albian to Cenomanian of France, Spain, Sardinia, Japan and Madagascar is a more evolute, inflated species, and bears distinct constrictions, as does *Z. dozei schroederi* Wiedmann (1962*a* : 161; pl. 8, figs 12, 13; pl. 13, figs 3, 4; text-figs 18–20), an Upper Albian species from Spain and Sardinia, which also has an almost trigonal whorl section. *Z. flicki* (Pervinquière 1907 : 65; pl. 3, fig. 16) from the Upper Albian of Tunisia is more evolute, and has closely-spaced prorsiradiate constrictions which are very prominent across the lower flank. *Z. befamontensis* Collignon (1963 : 24; pl. 250, fig. 1074) from the Lower Albian of Madagascar is a less compressed species (whorl breadth/height ratio 0·92) with a subtrigonal whorl section and weak, distant constrictions. *Z. busnardoi* Collignon (1956 : 62; pl. 6, figs 4–4a; text-figs 10–11) from the Santonian of Madagascar has subparallel flanks, is more evolute, and bears strong constrictions. *Z. kaiparaensis* Marshall (1926 : 147; pl. 19, figs 9–9a; pl. 31, fig. 12; Henderson 1970 : 21; pl. 2, fig. 8) from the Campanian of New Zealand and California is more inflated, with strong prorsiradiate constrictions. The presence of constrictions also serves to distinguish *Z. mihoensis* Matsumoto (1938 : 144; pl. 14, figs 2a–c) from the Cenomanian of Japan; *Z. inflatus* Matsumoto (1959*b* : 74; pl. 23, figs 2a–d, 3a–c, 4a–c, 5a–d; pl. 24, figs 1a–c; text-fig. 14) from the Albian of Alaska and Cenomanian of Japan, and *Z. kawanoi* (Jimbo 1894 : 281; pl. 1, fig. 7) from the Santonian to Maastrichtian of Japan.

Zelandites varuna (Forbes 1846 : 107; pl. 8, figs 5a–c) and *Z. varuna japonica* Matsumoto (1938 : 140; pl. 14, figs 5a–b, 6a–b, 7a–b; text-fig. 1a–d) from the Campanian–Maastrichtian of southern India, Japan and Chile (Steinmann 1895 : 84; pl. 5, figs 2a–b; text-fig. 7) are perhaps the most closely comparable species, but in these forms the greatest whorl breadth is closer to the umbilicus, whilst there are distinct lirae and constrictions which are particularly well marked on the lower flank.

OCCURRENCE. Cenomanian of southern India and South Africa (Zululand); Albian of Madagascar, and perhaps Cenomanian of Japan (Matsumoto 1942).

Zelandites sp. 1

(Pl. 14, fig. 6)

MATERIAL. A single specimen, BM(NH) C78864, from the Middle Cenomanian Mzinene Formation at Loc. 62, the Skoenberg, Zululand.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78864	21·5	12·1 (56)	11·5 (53)	1·05	2·0 (9)

DESCRIPTION AND DISCUSSION. This corroded specimen from the same general locality as the specimen of *Zelandites odiensis* noted above is very badly preserved, but nevertheless retains

traces of constrictions in the umbilical region, indicating that a further species is present in the area. It is specifically indeterminate.

OCCURRENCE. Cenomanian III, Zululand.

Zelandites sp. 2
(Pl. 14, fig. 1)

MATERIAL. A single specimen, SAM 7100 from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

DISCUSSION AND OCCURRENCE. M. R. Cooper of the South African Museum has kindly sent us photographs (Pl. 14, figs 1a–b) of a further *Zelandites*, from the Umzamba Formation. The whorl section and coiling recall *Zelandites varuna* (Forbes) although constrictions appear to be absent.

Genus *KOSSMATELLA* Jacob, 1907

Subgenus *KOSSMATELLA* Jacob, 1907

TYPE SPECIES. *Ammonites agassizianus* Pictet 1848, by original designation.

DIAGNOSIS. The coiling is moderately involute, the whorl section depressed to compressed. The flanks bear deep constrictions, between which are radial folds varying from mere swellings to massive protruberances. The surface of the test is finely lirate.

DISCUSSION. Two subgenera are recognized in *Kossmatella*, *K.* (*Kossmatella*) and *K.* (*Guderianites*) Wiedmann, 1962, with *Kossmatella costata* Douvillé (1916) as type species. *Guderianites* is typified by the invariable presence of more than one swelling between constrictions. The subgenus *K.* (*Murphyella*) Matsumoto, 1972 (type species *K.* (*M.*) *enigma* Matsumoto, Muramoto & Takahashi, 1972 : 210; pl. 33, figs 1–3; text-fig. 1) is regarded as a synonym of *Anagaudryceras* Shimizu 1934.

Wiedmann (1962*a*, *b*) and Wiedmann & Dieni (1968) provide an extensive review of the genus and subgenus, and the following arrangement has been proposed on the basis of ornamentation.

1. The group of *Kossmatella agassiziana*, with radial folds, sometimes weakly bullate, including: *K. agassiziana* (Pictet) (Wiedmann 1962*a* : pl. 13, figs 9–11), Middle to Upper Albian of southern Europe. *K. romana* Wiedmann (1962*a* : 164; pl. 8, figs 6–7; pl. 13, fig. 12; text-figs 21–24), Middle and Upper Albian of southern France, the Balearics, northern and south-eastern Spain, and possibly South Africa (Zululand). *K. jacobi jacobi* Wiedmann (1962*a* : 167, *nom. nov.* for *K. agassiziana* var. II of Jacob 1908 : pl. 2, fig. 4), and *K. jacobi quenstedti* Wiedmann (1962*b* : 59; pl. 5, fig. 5; text-fig. 20), both Lower Albian of southern France and the Balearics. *K. marut* (Stoliczka 1865 : 162; pl. 17, figs 3–3c), Upper Albian of southern India and South Africa (Zululand), and the Middle Cenomanian (?) of Madagascar. *K. sublaevis sublaevis* Wiedmann (1962*b* : 52; pl. 4, fig. 7; text-fig. 17), *K. sublaevis pachys* Wiedmann, 1962*b* : 54; pl. 4, figs 2, 8; text-fig. 18) and *K. sublaevis involuta* Wiedmann (1962*b* : 56), all Lower to Upper Albian of southern France, the Balearics, Sardinia and Zacatecas (Mexico). *K. muhlenbecki* (Fallot 1885 : 233; pl. 4, fig. 1), Upper Albian of southern France, northern Spain and Sardinia.

2. The group of *Kossmatella ventrocincta*, with strong umbilical nodes, including: *K. ventrocincta* (Quenstedt 1847–8 : 223; pl. 17, figs 14a–b) and *K. ventrocincta gignouxi* Breistroffer (1931 : 193), both Middle Albian of southern France. *K. oosteri oosteri* Breistroffer (1936*a* : 1492) and *K. oosteri passendorferi* Wiedmann & Dieni (1968 : 41), Upper Albian of Switzerland, southern France, Sardinia and Poland. *K. schindewolfi* Wiedmann & Dieni (1968 : 41; pl. 3, fig. 13; pl. 4, figs 1–3; text-figs 11–12), Upper Albian of southern France, Sardinia and Poland.

All our Zululand specimens belong to *Kossmatella* (*Kossmatella*), and to the *agassiziana* group.

OCCURRENCE. *K.* (*Kossmatella*) ranges from the ? Upper Aptian to Lower and ? Middle Cenomanian. Its chief occurrences are in the western Mediterranean region, the distribution covering southern France, Spain, the Balearics, Sardinia, Italy, Poland, north Africa, southern India,

Madagascar, South Africa (Zululand), Mexico, California and Alaska. *K.* (*Guderianites*) occurs in the Albian of Sinai and possibly the Lower Albian of the Balearics.

Kossmatella (*Kossmatella*) *marut* (Stoliczka)
(Pl. 14, fig. 8)

1865 *Ammonites marut* Stoliczka : 162; pl. 79, figs 1–1b.
1895 *Lytoceras* (*Gaudryceras*) *marut* (Stoliczka) Kossmat : 130; pl. 17, figs 3–3c.
1956 *Kossmatella marut* (Stoliczka) Collignon : 66.
1963 *Kossmatella* aff. *marut* (Stoliczka); Collignon : 20; pl. 249, fig. 1065.

Holotype. By monotypy, Stoliczka's original specimen (1865 : pl. 79, figs 1–1b) from the Upper Albian of Odium, southern India.

Material. One specimen, BM(NH) C78762 from Bed 12 of the Mzinene Formation at Loc. 51 on the Mzinene River, Zululand (Albian V).

Dimensions.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*	*Folds*
Holotype (after Stoliczka)	14·0	4·8 (35)	5·5 (39)	0·88	6·3 (45)	17
Kossmat 1895 : 130	19·5	6·0 (31)	6·5 (33)	0·92	8·0 (41)	17
BM(NH) C78762	31·1	9·8 (32)	11·2 (36)	0·88	11·1 (36)	17/18
	23·5	8·0 (34)	8·6 (37)	0·93	9·0 (38)	–

Description. The coiling is moderately involute, about 50% of the previous whorl being covered. The umbilicus is of moderate size (36–38% of diameter) with a low, sloping, rounded wall, which merges imperceptibly with the flanks. The whorl section is compressed, the greatest breadth being some way below mid-flank. The flanks are gently rounded and merge, via broad, gently rounded shoulders, into an evenly rounded venter.

Ornament consists of broad, band-like radial lateral folds separated by narrower constrictions; there are seventeen folds on the outer whorl. These arise as broad swellings at the umbilical seam, and pass straight across the flanks, broadening and weakening as they do so, and eventually merging with the flanks at the ventrolateral shoulder.

The constrictions are narrow and rectiradiate. Most are clearly visible only on the flanks, but some continue over the venter to form a distinct peaked constriction over the siphonal area.

The test surface of the available specimen is corroded, and no trace of lirae remains. The sutures are not visible.

Discussion. Our specimen clearly matches Stoliczka's small holotype and the rather larger specimen figured by Kossmat, apart from minor differences in relative proportions. When compared with other members of the *agassiziana* group, differences are clear, if subtle; given larger populations a reduction of the large number of species names currently in use may be possible. Comparisons are as follows.

Kossmatella agassiziana itself (Wiedmann 1962*a* : pl. 13, figs 9–11) has rather similar relative proportions, but has fewer (12) and narrower lateral folds, which flex backwards on the flanks. *K. romana* Widemann (1962*a* : 164; pl. 8, figs 6, 7; pl. 3, fig. 12; text-figs 21–24; 1962*b* : 50; pl. 3, fig. 8; pl. 4, figs 1, 5; pl. 5, fig. 3) is a depressed form with coarser folds and a lower expansion rate than *K. marut* – as is *K. jacobi* Wiedmann (1962*a* : 167; 1962*b* : 56, 57; pl. 4, fig. 4; text-fig. 19; 1962*b* : 59; pl. 5, fig. 5; text-fig. 20). *K. muhlenbecki* (Fallot) (Wiedmann 1962*a* : 168; pl. 8, figs 5–8; text-figs 27–29) is a depressed slowly expanding species with 15 coarse lateral bulges per whorl, and a test ornamented by very coarse lirae. *K. sublaevis sublaevis* Wiedmann, *pachys* Wiedmann and *involuta* Wiedmann (1962*b* : 52; pl. 4, figs 2, 7, 8; text-figs 17–18) are slowly expanding forms, ornamented by faint, irregular bulges separated by broad constrictions.

Occurrence. Upper Albian of South Africa (Zululand) and southern India. Middle ? Cenomanian of Madagascar.

Kossmatella (*Kossmatella*) aff. *romana* Wiedmann
(Pl. 14, figs 5, 7, 9, 10)

1962*a* *Kossmatella romana* Wiedmann : 114; pl. 8, figs 6–7; pl. 13, fig. 12; text-figs 21–24.
1962*b* *Kossmatella* (*Kossmatella*) *romana* Wiedmann : 50; pl. 3, fig. 8; pl. 4, figs 1, 5; pl. 5, fig. 3.
1968 *Kossmatella* (*Kossmatella*) *romana* Wiedmann : Wiedmann & Dieni : 38; pl. 1, figs 10, 11; pl. 2, fig. 7; pl. 3, fig. 10.

MATERIAL. Four specimens, SAS Z539a–b and BM(NH) C78763–4 from the Mzinene Formation at Loc. 56 on the Mzinene River, Zululand (Albian V).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78763	27·8	9·5 (34)	9·4 (34)	1·01	10·8 (39)
BM(NH) C78764	35·0	12·0 (34)	12·0 (34)	1·0	13·5 (38·5)
SAS Z539a	27·0	9·5 (35)	9·7 (36)	0·98	9·7 (36)

DESCRIPTION. The coiling is evolute, about 20% of the previous whorl being covered. The whorl section varies from slightly depressed during early growth stages to slightly compressed later. The umbilicus is broad, 36–39% of diameter, and shallow. The umbilical wall is low, rounded and gently sloping; the flanks are weakly inflated, the greatest breadth being a little below mid-flank. The ventrolateral shoulder is rounded, merging into a broad, evenly rounded venter. The flanks bear 17–19 lateral bulges per whorl; these arise at the umbilical seam, are at their maximum strength on the lower flank, declining on the upper flank, and disappearing by the ventrolateral shoulder. The intervening constrictions are quite narrow, rectiradiate to slightly prorsiradiate, and distinctly peaked on the venter; up to seven of these per whorl are deeply incised on the internal mould, although all are relatively weak where shell is preserved.

The surface of the test, when preserved, is covered in fine dense lirae. The sutures are not seen.

DISCUSSION. The striking features of our specimens are the presence of strong lateral bulges, a wide umbilicus, the deep incision of occasional constrictions and the rather broad whorl section. *Kossmatella marut* is more compressed, with weaker bulges, as is *K. agassizianum*, where the lateral bulges are fewer (12 per whorl) and flexed. *K. jacobi* and its variety *quenstedti* are more inflated and more robustly ornamented. *K. muhlenbecki* has a markedly tabulate venter and other distinctive characters, whilst forms such as *K. laevis* and its varieties are even more distinctive, as noted above.

The most obvious comparisons are thus to be made with *Kossmatella romana* Wiedmann. The published figures show a range of variability in specimens referred to the species; in general, specimens retaining their test have somewhat stronger lirae and coarser lateral bulges than our specimens, whilst internal moulds lack the occasional deeply-incised constrictions of our material. The Zululand specimens may represent a new species, or a subspecies of *K. romana*, but we would hesitate to introduce a new name on the basis of the present limited material.

OCCURRENCE. *Kossmatella romana* occurs in the Middle and Upper Albian of France, the Balearics, south-eastern and northern Spain, and Sardinia; our Zululand material is of Upper Albian age.

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