

Cretaceous faunas from Zululand and Natal, South Africa.

The ammonite subfamily

Acanthoceratinae de Grossouvre, 1894

William James Kennedy

Oxford University Museum of Natural History, Parks Road, Oxford, OX1 3PW, U.K.

E-mail: jim.kennedy@oum.ox.ac.uk

&

Herbert Christian Klinger

Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa
and

Department of Geological Sciences, University of Cape Town, Private Bag, Rondebosch, 7701 South Africa

E-mail: hklinger@iziko.org.za

(with 63 figures)

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Ammonites of the subfamily Acanthoceratinae occur in abundance at a single locality in KwaZulu, the eastern part of the Skenberg, on the lower reaches of the Mzinene River, north-northeast of Hluhluwe. This is the classic locality from which William Anderson collected the material described by G.C. Crick in 1907 as being from the 'deposit at the north end of False Bay.' The fossils occur weathered out on the surface; there is no section. The ammonites described below are predominantly Middle Cenomanian, with indications of the presence of lower Upper Cenomanian on the basis of records elsewhere. The following species are described: *Acanthoceras flexuosum* Crick, 1907 (of which *Acanthoceras crassiornatum* Crick, 1907, *Acanthoceras munitum* Crick, 1907, *Acanthoceras expansum* Crick, 1907, *Acanthoceras robustum* Crick, 1907, *Acanthoceras quadratum* Crick, 1907, *Acanthoceras hippocastanum* Crick, non J. de C. Sowerby, and *Acanthoceras latum* Crick, 1907, are synonyms), *Acanthoceras cornigerum* Crick, 1907, *Protacanthoceras subwaterloti* (Venzo, 1936), *Cunningtoniceras?* sp. a and sp. b, *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart, 1822) (of which *Acanthoceras paucinodatum* Crick, 1907 is a synonym), *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894), *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897), *Calycoceras* (*Newboldiceras*) cf. *asiaticum hunteri* (Kossmat, 1897), *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897), *Calycoceras* (*Newboldiceras*) *laticostatum* (Crick, 1907), *Calycoceras* (*Newboldiceras*) *breistrofferi* (Collignon, 1937) and *Pseudocalycoceras harpax* (Stoliczka, 1864).

Key words: ammonites, Acanthoceratinae, Cenomanian, Mzinene Formation, KwaZulu-Natal, South Africa.

CONTENTS

Abstract	1	Subgenus <i>Calycoceras</i> (<i>Gentoniceras</i>)	9
Introduction	1	<i>Calycoceras</i> (<i>G.</i>) <i>gentoni</i>	9
Repositories of specimens	2	Subgenus <i>Calycoceras</i> (<i>Newboldiceras</i>)	10
Conventions	2	<i>Calycoceras</i> (<i>N.</i>) <i>asiaticum asiaticum</i>	10
Systematic palaeontology	2	<i>Calycoceras</i> (<i>N.</i>) <i>asiaticum spinosum</i>	12
Genus <i>Acanthoceras</i>	2	<i>Calycoceras</i> (<i>N.</i>) cf. <i>asiaticum hunteri</i>	13
<i>Acanthoceras flexuosum</i>	3	<i>Calycoceras</i> (<i>N.</i>) <i>planecostatum</i>	14
<i>Acanthoceras cornigerum</i>	6	<i>Calycoceras</i> (<i>N.</i>) <i>laticostatum</i>	16
Genus <i>Protacanthoceras</i>	7	<i>Calycoceras</i> (<i>N.</i>) <i>breistrofferi</i>	16
<i>Protacanthoceras subwaterloti</i>	7	Genus <i>Pseudocalycoceras</i>	18
Genus <i>Cunningtoniceras</i>	8	<i>Pseudocalycoceras harpax</i>	18
<i>Cunningtoniceras?</i> sp. a	8	Acknowledgements	19
<i>Cunningtoniceras?</i> sp. b	9	References	19
Genus <i>Calycoceras</i>	9	Figures 1–63	21

INTRODUCTION

The ammonite subfamily Acanthoceratinae de Grossouvre, 1894, is a cosmopolitan group, members of which range from the upper Lower Cenomanian into the Lower Turonian. The

composition of the group adopted here follows that of Wright (1996) apart from the exclusion of *Hourcquiceras* Collignon, 1939, and *Tunesites* Pervinquier, 1907, which should be referred to Euomphaloceratinae. Members of the group are

important stratigraphic indicators throughout their range. Representatives of *Acanthoceras* Neumayr, 1875, *Protacanthoceras* Spath, 1923, *Cunningtoniceras* Collignon, 1937, *Calycoceras* (*Gentonoceras*) Thomel, 1972, *Calycoceras* (*Newboldiceras*) Thomel, 1972, and *Pseudocalycoceras* Thomel, 1972, are described below. These genera/subgenera are reviewed in detail by Wright & Kennedy (1981, 1987, 1990) and others, and we have nothing to add to previous accounts. Accordingly, the diagnoses given below are based on the work of these authors, to whom reference should be made.

The KwaZulu Acanthoceratinae recorded below come from a very restricted area in the Skoenberg region, north-northeast of Hluhluwe. The Skoenberg (Afrikaans for 'Shoe Mountain') is a crescentic hill that lies between the Mzinene and the Munywana rivers. The steep northern face rises to a height of over 30 m at the western end; to the east it falls away to the level of the flood plain. It is the abandoned river cliff of the Munywana, which is now located 700 m to the north. This richly fossiliferous locality was discovered by William Anderson in 1907 (p. 60), who described it as situated 'near the junction of the Manuan and Umsinene Rivers. The exposure shows a thicker series of beds than in any other locality from which I have collected. There are from 70 to 100 feet of strata exposed, chiefly calcareous sandy shales and sandstones, the whole being capped by a very hard calcareous sandstone full of broken shells. The beds are exposed almost continuously where the bank is precipitous. They are exceedingly prolific in fossils, chiefly Mollusca, Cephalopoda and Gasteropoda. The Cephalopoda are extremely abundant, and range from half an inch to over a yard in diameter. The fossils weather out from the shales in perfect condition, but from long exposure on the surface to the atmosphere, rains, and tropical bush fires, they are largely composed of casts. Some good specimens however were obtained. These are described by Mr G.C. Crick, of the British Museum, in this Report, under the title of the "North End of False Bay Deposit".'

The Skoenberg is the type locality of the Skoenberg Beds of Van Hoepen (1926, 1929). It was visited during the 1929 International Geological Congress (Du Toit & Van Hoepen 1929), and specimens collected by a number of those attending (see Heinz 1930; Besairie 1930; Venzo 1936; Dietrich 1938; Socin 1939; Montanaro & Lang 1937); they survive in a number of European collections (for example those of the Sorbonne, now housed in the Université Pierre et Marie Curie-Paris 6). Venzo (1936) described and illustrated a number of acanthoceratines from the locality.

Kennedy & Klinger (1975) revised the stratigraphy of the Skoenberg area. They recognized an upper Upper Albian to Lower Cenomanian succession of Mzinene Formation silts with calcareous concretions at their locality 61, west of the western 'horn' of the Skoenberg, continued in their locality 62, the Skoenberg itself, and the source of the material described below. Fossils derived from the upper part of the Mzinene Formation littered the slopes of the Skoenberg, but exposures were inadequate to establish an actual succession. The Cenomanian succession is terminated by an unconformity, overlain by a thin *Pterotrionia* conglomerate of Coniacian date that marks the base of the St Lucia Formation (Kennedy & Klinger 1975, p. 289, fig. 7). The actual

boundary was exposed to the south of the Skoenberg, on the north bank of the Mzinene, at locality 60 of Kennedy & Klinger (1975). Here the Coniacian *Pterotrionia* conglomerate capped up to 10 m of deeply weathered buff silts. Those immediately below the unconformity yielded acanthoceratids that we identified as *Calycoceras* aff. *choffati* (Kossmat, 1897), but now regarded as variants of *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). These *in situ* records provide only an imprecise upper Middle or Lower Upper Cenomanian horizon for the top of the Mzinene Formation here. The ammonites collected from the surface of the slopes of the Skoenberg occasionally occur as composite moulds in yellow-buff siltstones. The majority, however, commonly retaining recrystallized calcite, or silicified shell material, such that the sutures are rarely exposed. The overwhelming majority are phragmocones, their chambers infilled by sparry calcite and chalcedonic silica.

This weathered-out material is of more than one age, with Lower Cenomanian *Mantelliceras*, *Sharpeiceras* and *Hypoturrites*, together with abundant Middle Cenomanian elements including the Acanthoceratinae described below, together with rare *Turrilites scheuchzerianus* Bosc, 1801, rare *Turrilites costatus* Lamarck, 1801, and more common *Turrilites acutus* Passy, 1832. There is a specimen of the lower Upper Cenomanian *Pseudocalycoceras harpax* (Stoliczka, 1864) from this locality in the collections of the South African Museum (SAM-PCZ22194; Fig. 63) that confirms the presence of lower Upper Cenomanian here.

REPOSITORIES OF SPECIMENS

The following abbreviations are used to indicate the repositories of specimens cited in the text:

BMNH: The Natural History Museum, London.

OUM: Oxford University Museum of Natural History.

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

CONVENTIONS

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in brackets are dimensions as a percentage of diameter. The suture terminology is that of Korn *et al.* (2003): E = external lobe; A = adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann 1970); U = umbilical lobe; I = internal lobe.

SYSTEMATIC PALAEOONTOLOGY

Order **AMMONOIDEA** Zittel, 1884

Suborder **AMMONITINA** Hyatt, 1889

Superfamily **ACANTHOCERATOIDEA** de Grossouvre, 1894

Family **ACANTHOCERATIDAE** de Grossouvre, 1894

Subfamily **ACANTHOCERATINAE** de Grossouvre, 1894

Genus ***Acanthoceras*** Neumayr, 1875

Type species

Ammonites rhotomagensis Brongniart, 1822, pp. 83, 391, pl. 6, fig. 2, by the subsequent designation of de Grossouvre, 1894, p. 27.

Diagnosis

Large, up to 300 mm diameter; the few known adult microconchs are about half the size of macroconchs. Early whorls with rounded to rectangular intercostal whorl section, with umbilical, inner and outer ventrolateral and siphonal tubercles, the latter two generally clavate, with or without distinct ribs; where present at this stage the ribs are irregularly long and short or branch from umbilical bullae. Later the ribs may become uniformly long, or short ribs may persist; they are normally broad and rounded and they may strengthen or weaken; umbilical tubercles may enlarge, one or the other of the ventrolaterals may disappear and the other enlarge; the whorl section is slightly compressed to depressed, generally square, rectangular or trapezoidal in section.

The suture is rather simple with broad, more or less symmetrical, squarish trifold or bifid elements (Wright & Kennedy 1987, p. 153).

Occurrence

Middle Cenomanian, northern and southern Europe, North, West and southern Africa, Madagascar, south India, Japan, northern Australia, the U.S. Western Interior and western seaboard, Peru, Japan.

Acanthoceras flexuosum Crick, 1907

Figs 1D–I, 2–25, 34A–C

- 1907 *Acanthoceras flexuosum* Crick, p. 184, pl. 12, fig. 1.
- 1907 *Acanthoceras crassiornatum* Crick, p. 185.
- 1907 *Acanthoceras munitum* Crick, p. 187.
- 1907 *Acanthoceras expansum* Crick, p. 188.
- 1907 *Acanthoceras robustum* Crick, p. 189.
- 1907 *Acanthoceras quadratum* Crick, p. 192, pl. 13, fig. 2.
- 1907 *Acanthoceras hippocastanum* J. de C. Sowerby sp.; Crick, p. 194, pl. 13, fig. 4.
- 1907 *Acanthoceras latum* Crick, p. 195, pl. 12, fig. 2.
- 1936 *Acanthoceras flexuosum* Crick; Venzo, p. 84 (26), pl. 7 (3), fig. 6.
- 1936 *Acanthoceras hippocastanum* Sow; Venzo, p. 85 (27), pl. 7 (3), fig. 2.
- non 1971 *Acanthoceras latum* Crick; Kennedy, p. 89 (*pars*), pl. 57, fig. 1.
- 1975 *Acanthoceras flexuosum* Crick; Förster, p. 294, pl. 16, fig. 2; pl. 17, figs 2, 5.
- 1975 *Acanthoceras rhotomagense confusum* (Guéranger); Förster, p. 248, figs 3, 4.
- 1978 *Acanthoceras flexuosum* Crick; Kennedy, pl. 2, fig. 1.
- 1978 *Acanthoceras quadratum* Crick; Kennedy, pl. 2, fig. 6.
- 1978 *Acanthoceras latum* Crick; Kennedy pl. 3, fig. 1.
- 1978 *Acanthoceras* sp. Kennedy, pl. 3, fig. 6.
- ?1985 *Acanthoceras robustum* Crick, 1907; Zaborski, p. 33, fig. 37a, b.
- 1987 *Acanthoceras crassiornatum* Crick, 1907; Wright & Kennedy, p. 189, text-fig. 72a, b.
- 1987 *Acanthoceras flexuosum* Crick, 1907; Wright & Kennedy, p. 189, text-figs 72c, 73a.
- 1987 *Acanthoceras robustum* Crick, 1907; Wright & Kennedy, p. 189, text-fig. 73b, c.
- 1987 *Acanthoceras latum* Crick, 1907; Wright & Kennedy, p. 189, text-figs 66h, i, 72d, e.

Name of the species

As first revising authors we select the name *flexuosum* for the species.

Types

The holotype of *Acanthoceras flexuosum* Crick, 1907, p. 184, pl. 12, fig. 1, is BMNH C18174 (Fig. 1G–I).

The holotype of *Acanthoceras crassiornatum* Crick, 1907, p. 185, is BMNH C18175 (Fig. 1D–F).

The lectotype, here designated, of *Acanthoceras munitum* Crick, 1907, p. 187, is BMNH C18182 (Fig. 2D–F); paralectotypes are BMNH C18183–5.

The holotype of *Acanthoceras expansum* Crick, 1907, p. 188, is BMNH C18187 (Fig. 2G–I).

The lectotype, here designated, of *Acanthoceras robustum* Crick, 1907, p. 189, is BMNH C18189 (Fig. 2A–C); paralectotypes are BMNH C18188 (figs 2J, 3) and 18190.

The lectotype, here designated, of *Acanthoceras quadratum* Crick, 1907, p. 192, pl. 13, fig. 2, is BMNH C18194 (Fig. 4). Paralectotype BMNH C18195 is a *Cunningtoniceras*.

The holotype of *Acanthoceras latum* Crick, 1907, p. 195, pl. 12, fig. 2, is BMNH C18197 (Fig. 5).

Material

We have studied several hundred specimens, including SAM-PCZ 13474, 13489–99, 13501–13515, 13517–28, 13531, 13534; OUM KX1749, 1750, 4371–4583. BMNH C90252–79. BMNH C18196 is the original of *Acanthoceras hippocastanum* Crick (1907, p. 194, pl. 13, fig. 4) *non* J. de C. Sowerby. BMNH C18176–81, C18191, C18192, C18199, C18231, C18232.

Dimensions

See Table overleaf.

Description

The majority of specimens are phragmocones, often partially silicified, with replaced shell present in many.

Coiling is evolute during middle and later growth, with less than 20% of the previous whorl covered, to just below the level of the inner ventrolateral tubercle. The umbilicus is of moderate width (19.6–27.7% of the diameter), and depth. The umbilical wall is flattened to feebly convex, the umbilical shoulder narrowly rounded. The whorl section is generally depressed in both costal and intercostal whorl section; costal whorl breadth to height ratios vary from 0.76 to 1.3. The greatest breadth is just outside the umbilical shoulder in intercostal section, and at the umbilical bullae in costal section. The intercostal section is rounded-trapezoidal, with a broad, flattened venter, broadly rounded umbilical and ventrolateral shoulders.

In our smallest specimens, at diameters of 5–7 mm, the ornament consists of seven conical inner ventrolateral tubercles per half whorl, with associated ribs on the outer flank, and feeble outer ventrolateral clavi. From around 8 mm diameter, the ornament of the middle growth stage appears, with from 8–10 umbilical bullae per whorl, perched on the umbilical shoulder. They give rise to single straight to feebly flexuous primary ribs that efface markedly at mid-flank. Short intercalated ribs alternate more-or-less regu-

Dimensions table

	D	Wb	Wh	Wb:Wh	U
PCZ13524c	26.3 (100)	12.6 (47.9)	16.5 (62.7)	0.76	6.2 (23.6)
PCZ13504c	28.6 (100)	14.6 (51.0)	14.8 (51.7)	0.99	5.6 (19.6)
PCZ13525c	37.2 (100)	20.2 (54.3)	17.3 (46.5)	1.17	8.9 (23.9)
PCZ13526c	43.0 (100)	22.8 (53.0)	20.9 (48.6)	1.1	9.9 (23.0)
PCZ13490c	51.5 (100)	26.9 (52.2)	23.6 (45.8)	1.14	11.9 (23.1)
PCZ13495c	46.2 (100)	24.8 (53.6)	22.1 (47.8)	1.0	10.6 (22.9)
PCZ13505c	54.3 (100)	27.2 (50.1)	26.8 (49.4)	1.0	11.6 (21.4)
PCZ13496c	59.1 (100)	32.2 (54.5)	27.7 (46.9)	1.16	14.6 (24.7)
PCZ13521c	64.3 (100)	35.1 (54.6)	30.5 (47.4)	1.16	17.1 (26.6)
PCZ13497c	72.7 (100)	37.2 (51.2)	33.6 (46.2)	1.1	18.3 (25.2)
PCZ13489c	78.6 (100)	36.2 (46.1)	36.5 (46.4)	0.99	19.2 (24.4)
PCZ13498c	79.5 (100)	40.8 (51.3)	36.9 (46.4)	1.1	21.8 (27.4)
PCZ13527c	89.1 (100)	39.4 (44.2)	38.9 (43.7)	1.0	26.2 (29.4)
PCZ13494c	96.4 (100)	48.8 (50.6)	39.4 (40.9)	1.24	27.4 (28.4)
PCZ13492c	102.9 (100)	51.6 (50.1)	46.9 (45.6)	1.1	28.1 (27.3)
PCZ13530ic	107.0 (100)	48.6 (45.4)	48.9 (45.7)	0.99	28.7 (26.8)
PCZ13491	107.5 (100)	53.4 (49.7)	50.1 (47.4)	1.1	28.8 (26.8)
PCZ13514c	108.7 (100)	58.8 (54.1)	49.0 (45.4)	1.2	27.4 (25.2)
PCZ13528c	117.3 (100)	60.2 (51.3)	50.3 (42.9)	1.2	30.8 (26.3)
PCZ13523c	121.6 (100)	58.5 (48.1)	51.8 (42.6)	1.1	36.4 (29.9)
PCZ13512c	136.5 (100)	70.1 (51.4)	57.5 (42.1)	1.2	40.4 (29.6)
PCZ1518c	137.5 (100)	75.9 (55.2)	59.5 (43.3)	1.3	36.9 (26.8)
PCZ13517c	152.8(100)	— (—)	68.9 (45.1)	—	45.4 (29.7)
at	125.5 (100)	68.1 (54.3)	58.0 (46.2)	1.2	34.9 (27.8)

	D	Wb	Wh	Wb:Wh	U
Holotype, <i>flexuosum</i> C18174	74.7 (100)	38.5 (51.5)	36.9 (49.4)	1.04	18.0 (24.1)
Holotype, <i>crassiorum</i> C181765	77.1 (100)	36.8 (47.7)	36.0 (46.7)	1.0	19.7 (25.6)
Lectotype, <i>munitum</i> C18182	65.6 (100)	35.2 (54.3)	31.1 (47.4)	1.1	16.7 (25.5)
Paralectotype, <i>munitum</i> C18183	55.8 (100)	(—)	26.5 (47.5)	—	13.7 (24.6)
Paralectotype, <i>munitum</i> C18184	42.0 (100)	23.8 (56.6)	20.3 (48.3)	1.2	10.9 (26.0)
Paralectotype, <i>munitum</i> C18185	41.9 (100)	22.7 (54.1)	21.1 (50.4)	1.1	10.5 (25.1)
Holotype, <i>expansum</i> C18187	61.7 (100)	33.1 (53.7)	30.2 (49.0)	1.1	18.0 (29.2)
Lectotype, <i>robustum</i> C18189	96.4 (100)	50.0 (51.9)	43.5 (45.1)	1.2	25.6 (27.0)
Paralectotype, <i>robustum</i> C18188	154.0 (100)	~74.3 (—)	68.6 (44.5)	~	45.4 (29.5)
Paralectotype, <i>robustum</i> C18190	95.7 (100)	— (—)	42.7 (44.6)	—	27.7 (28.9)
Lectotype, <i>quadratum</i> C18194c	109.8 (100)	60.1 (54.7)	48.4 (44.1)	1.2	31.2 (28.4)
Lectotype, <i>latum</i> C18197 at c	99.1 (100)	68.3 (68.9)	44.2 (44.6)	1.55	29.2 (29.5)
at ic	99.1 (100)	57.3 (57.8)	44.2 (44.6)	1.3	29.2 (29.5)

larly with the primaries. They arise at mid-flank; some are linked to the umbilical bullae by tenuous striae. There are a total of 17–22 ribs per whorl at the umbilical shoulder. All ribs bear a conical inner ventrolateral tubercle, connected by a broad, low rib to clavate outer ventrolateral and siphonal tubercles. There is some variation in the strength and density of the ornament; depressed individuals are more coarsely ribbed and tuberculate than compressed ones. This style of ornament extends to a diameter of around 70 mm. As size increases beyond this, the intercalated ribs lengthen progressively until all extend to the umbilical shoulder, although not all develop umbilical bullae. As a result the third growth stage is characterized by primary ribs with bullae of very variable strength. This change in ribbing style is accompanied by a marked change in tuberculation. The umbilical bullae strengthen and migrate out to a mid-flank position, the inner ventrolateral tubercles develop into horns, and the siphonal clavi decline. The outer flanks become markedly concave in costal section at this growth stage. As size increases beyond 100 mm diameter, the outer

ventrolateral clavi merge with the ventrolateral horn to produce a single protuberance that initially bears a trace of the clavus, thereafter lost. Ventrolateral ribbing and siphonal tuberculation also decline, so that in the largest phragmocones there are no more than low, broad undulations on the venter and a feeble siphonal ridge. At this stage the costal whorl section is characterized by concave flanks and a feebly convex venter.

We have two fragments of large adults. OUM KX1749 is a phragmocone fragment with a maximum preserved whorl height of 90 mm and an intercostal whorl breadth to height ratio of 1.2, the whorl section reniform, with the greatest breadth below mid-flank. Coarse umbilical bullae give rise to single coarse, broad, straight, prorsiradiate ribs that weaken at mid-flank before strengthening into coarse ventrolateral bullae, linked across the broad convex venter by a low, broad rib that weakens and effaces in the mid-ventral region. OUM KX1750 (Figs 23, 24) is a massive 120° sector of body chamber with a maximum preserved whorl height of 105 mm, with whorl section and coarse

ornament as in the previous specimen. When complete the estimated diameter must have exceeded 200 mm.

The holotype of *Acanthoceras flexuosum* Crick, 1907 (p. 184, pl. 12, fig. 1) is BMNH C18174 (Fig. 1G–I), a wholly septate phragmocone that retains recrystallized shell. Coiling is moderately evolute; the umbilicus comprises 24% of the diameter, and is quite deep, with a broadly convex umbilical wall, the umbilical shoulder more narrowly rounded. The whorl section is slightly depressed, with the greatest breadth at the umbilical bullae in costal section, and just outside the umbilical shoulder in intercostal section. The inner and middle flanks are broadly rounded in intercostal section, the outer flanks flattened, converging to broadly rounded ventrolateral shoulders. The venter is broad and feebly convex. The costal section is rounded-polygonal. Eighteen to 19 primary ribs arise at the umbilical seam, and are weak, narrow, and concave across the umbilical wall. They strengthen across the umbilical shoulder and develop into pinched concave bullae of variable strength. These give rise to feebly flexuous, prorsiradiate primary ribs, either singly or in pairs, while there are occasional non-bullate primaries, to give a total of 24–25 ribs per whorl at the ventrolateral shoulder. All ribs develop a small, conical inner ventrolateral tubercle, linked by a low, broad prorsiradiate rib to a stronger outer ventrolateral clavus; a low, broad, transverse rib connects to a slightly weaker siphonal clavus. Where well preserved, the surface of the replaced shell bears strong growth lines and striae.

The holotype of *Acanthoceras crassioratum* Crick, 1907 (p. 185), is BMNH C18175 (Fig. 1D–F). It is a phragmocone 77.1 mm in diameter, and retains replaced shell, with indications of the former presence of a further half whorl. It is rather worn on one side. The specimen is no more than a more robustly ribbed individual than the holotype of *Acanthoceras flexuosum*, with approximately 15–16 variably developed umbilical bullae per whorl, and approximately 22 ribs per whorl at the ventrolateral shoulder.

The lectotype of *Acanthoceras munitum* Crick, 1907 (p. 187) is BMNH C18182 (Fig. 2D–F). It and paralectotypes BMNH C18183–5 are no more coarsely ornamented than the holotype of *Acanthoceras crassioratum*. The smaller paralectotypes show very regularly alternating long and short ribs; in BMNH C18185 there are ten umbilical bullae on the outer whorl, corresponding to an estimated 22 ribs at the ventrolateral shoulder at a diameter of 22 mm. In the lectotype, this alternation is well developed on the adapical half of the outer whorl, whereas on the adapertural half, there is a transition towards alternately bullate and non-bullate primary ribs.

The holotype of *Acanthoceras expansum* Crick, 1907 (p. 188) is BMNH C18187 (Fig. 2G–I), a phragmocone 64 mm in diameter. It is a more coarsely ribbed and tuberculate variant than the types of *crassioratum*, with umbilical bullae that are subspinose where well preserved. The ribs are regularly long and short throughout, with 13 bullate primary ribs and a total of 21–22 ribs at the ventrolateral shoulder on the outer whorl.

The lectotype, here designated, of *Acanthoceras robustum* Crick, 1907 (p. 189), is BMNH C18189 (Fig. 2A–C), Crick's specimen b. Fifteen bullae of variable strength perch on the umbilical shoulder, with 23–24 ribs per whorl at the

ventrolateral shoulder. The specimen shows a transition from alternately long and short to predominantly long, alternately bullate and non-bullate ribs. It retains replaced shell, and shows a weakening and decline of the siphonal clavi and ventral rib, in part due to wear. Paralectotype BMNH C18190, Crick's specimen c, is a comparable individual, badly corroded on one flank. BMNH C18188 (Figs 2J, 3), Crick's specimen a, is a much larger, wholly septate individual 154 mm in diameter. Bullate and non-bullate primary ribs alternate at the adapical end of the outer whorl, to be replaced by entirely bullate primaries over the adapertural 240° sector. These bear strong inner ventrolateral clavi, linked by a low, broad, transverse rib to smaller outer ventrolateral clavi. The venter is feebly convex in intercostal section, the siphonal clavi effacing progressively.

The lectotype of *Acanthoceras quadratum* Crick, 1907 (p. 192, pl. 13, fig. 2) is BMNH C18194 (Fig. 4), a silicified internal mould of a phragmocone. It is a much more robust individual than the previous specimens, with a very depressed whorl section. The style of ornament and ontogenetic changes correspond to those shown by Crick's other specimens described above, of which it is a further variant. Coiling is very evolute, the umbilicus comprising 28.4% of the diameter, deep, with a feebly convex umbilical wall and broadly rounded umbilical shoulder. The whorl section is rounded-trapezoidal in intercostal section, with the greatest breadth just outside the umbilical shoulder. The greatest breadth is at the umbilical bullae in the polygonal costal section, and the whorl breadth to height ratio is 1.24. Fifteen to 16 primary ribs arise at the umbilical seam on the outer whorl, and develop into umbilical bullae of variable strength. On the penultimate whorl, and the adapical part of the outer whorl, primary and secondary ribs alternate. On the adapertural part of the outer whorl, they are replaced by alternately strongly bullate and weakly to non-bullate primaries. Only the last few ribs have umbilical bullae of variable strength. The primary ribs are straight, feebly prorsiradiate, and broaden progressively across the flanks. All ribs bear conical inner ventrolateral tubercles that strengthen progressively around the outer whorl. At the beginning of the outer whorl, a low, broad, prorsiradiate rib links to a well-developed outer ventrolateral clavus, with a low, broad, transverse rib linking to a subequal siphonal clavus. As size increases, the rib linking the inner and outer ventrolateral tubercle broadens markedly, and changes from prorsiradiate to near transverse. The siphonal clavi are not preserved on the adapertural 120° sector of the outer whorl. Crick referred to *Acanthoceras quadratum* a second specimen, BMNH C18195, which appears to be a *Cunningtoniceras*.

BMNH C18196 (Fig. 11D–F) is the original of *Acanthoceras hippocastanum* Crick (1907, p. 194, pl. 13, fig. 4) *non* J. de C. Sowerby. It is a juvenile coarse-ribbed variant, with 9–10 umbilical bullae and 18 ribs at the ventrolateral shoulder of the outer whorl, which is 33.2 mm in diameter.

The holotype of *Acanthoceras latum* Crick, 1907 (p. 195, pl. 12, fig. 2) is BMNH C18197 (Fig. 5). It is wholly septate, and slightly distorted into an ellipse, 114 mm in diameter, with replaced shell well preserved. Coiling is very evolute, the umbilicus comprising 29.5% of the diameter. The umbilical wall is feebly convex, the umbilical shoulder broadly

rounded. The intercostal whorl section is rounded-trapezoidal, with a whorl breadth to height ratio of 1.3, the greatest breadth below mid-flank. The costal section is depressed-polygonal, and concave between the tubercles. The greatest breadth is at the inner ventrolateral horns. On the penultimate whorl, ten primary ribs arise at the umbilical seam, and strengthen into strong, pointed umbilical bullae. These give rise to one or more strong, broad, straight, prorsiradiate ribs. On the outer whorl, 16 primary ribs arise at the umbilical seam. They strengthen progressively across the umbilical wall, and develop into coarse, progressively strengthening umbilical bullae. These give rise to low, broad, coarse, straight, recti- to feebly prorsiradiate ribs that link to progressively strengthening and ultimately massive inner ventrolateral horns. There are two non-bullate primary ribs at the adapical end of the outer whorl. A broad, transverse rib connects the inner ventrolateral horns to much weaker long outer ventrolateral clavi. A low, broad, near-effaced transverse rib extends across the venter. There is a low continuous siphonal ridge that strengthens where it intercepts the ventral ribs. There are traces of siphonal clavi at the adapical end of the outer whorl, but preservation is imperfect.

What appears to be a further fragment of this form is BMNH C18193 (Fig. 6), the specimen described by Crick (1907, p. 191–192) as *Acanthoceras* sp. It is a sector of penultimate whorl, and a 100° sector of outer whorl of a phragmocone with a maximum preserved whorl height of 80 mm. The intercostal whorl breadth to height ratio is 1; the costal ratio is 1.2. On the penultimate whorl, weakly and strongly bullate primary ribs alternate. On the outer whorl, parts of five ribs are preserved. All are primary ribs that arise at the umbilical seam, where they are concave, strengthen progressively across the wall, and develop into strong umbilical bullae. These give rise to a low, broad, coarse straight primary rib that weakens at mid-flank, thereafter strengthening into strong ventrolateral horns. The costal whorl section is concave between umbilical and ventrolateral tubercles, and across the venter. A pair of low, broad ribs, the adapical one concave, the adapertural one convex, loop across the venter, linking the ventral horns on opposite flanks. There is a low, broad siphonal ridge that strengthens into incipient bullae where it intersects the ribs. Crick (1907, p. 196) mentions two other specimens, BMNH C18198–9.

Discussion

Acanthoceras gortanii Venzo, 1936 (p. 82 (24), pl. 7 (3), fig. 5, reproduced as Fig. 44 A–C herein, appears to be a juvenile *Calycoceras*. *Acanthoceras hippocastanum* Sow. and *flexuosum* of Venzo (1936, p. 85 (27), pl. 7 (3), figs 2, 6 (reproduced here as Fig. 25A–D) are based on specimens from the Skoenberg, and are juvenile *A. flexuosum*. The *Acanthoceras rhotomagense confusum* (Guéranger) of Förster (1975, p. 248, figs 3, 4) is a further synonym.

The early and middle growth stages, characterized by alternate primary and intercalated ribs, followed by a later growth stage characterized by primary ribs only, is a feature shared by *Acanthoceras rhotomagense* (see revision in Wright & Kennedy 1987, p. 156, pl. 42, fig. 8; pl. 44, figs 1–11; pl. 45, figs 1–5; pl. 46, figs 1–4, 6; pl. 47, figs 1, 2; pl. 48, figs 1,

2; pl. 49, figs 1, 5, 6; text-figs 47–54; 63f–j; 64a, b; 65a–d, k; 66d, f, g, j; 67a–g; 68; 69) and *Acanthoceras flexuosum*. Indeed, single examples of juveniles of the one would not stand out as different from the other, distinctive preservation apart. Both species also show a wide range of intraspecific variation. As noted by Wright & Kennedy (1987, p. 189) they can be separated in that in *flexuosum*, specimens around 100 mm diameter show predominantly long ribs on the last half whorl, with umbilical bullae of variable strength. This change to predominantly long ribs is accompanied by a marked change in tuberculation and whorl profile in costal section. It is initially polygonal, a trapezium with truncated corners, but as size increases the umbilical bullae strengthen and migrate outwards to an inner flank position. The inner ventrolateral tubercles develop into horns, and the siphonal clavi decline. The outer flanks become markedly concave in costal section. Beyond 100 mm diameter the inner and outer ventrolateral tubercles progressively merge into a single horn-like protuberance that initially retains traces of the outer ventrolateral clavus (Fig. 5 shows this well), but this is ultimately assimilated (Fig. 6). Ventral ribbing and tuberculation decline so that the largest specimens have only low, broad undulations on the venter, and a low siphonal ridge (Figs 20, 22).

Occurrence

Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289), and southern Mozambique.

Acanthoceras cornigerum Crick, 1907

Fig. 1A–C

- 1907 *Acanthoceras cornigerum* Crick, p. 207, pl. 13, fig. 1.
 1957 *Acanthoceras cornigerum* Crick; Matsumoto, Saito & Fukada, p. 18, text-fig. 5.
 1969 *Acanthoceras cornigerum* Crick; Matsumoto, Muramoto & Takahashi, p. 268, pl. 32, fig. 1; text-fig. 5.
 1978 *Acanthoceras cornigerum* Crick; Kennedy, pl. 2, fig. 5.

Type

The holotype, by monotypy, is BMNH C18230, the original of Crick, 1907, p. 207, pl. 13, fig. 1 (Fig. 1A–C).

Dimensions

	D	Wb	Wh	Wb:Wh	U
C18230c	69.4 (100)	30.8 (44.4)	30.4 (43.8)	1.0	21.4 (30.8)
ic		26.5 (38.2)	23.9 (34.4)	1.1	

Description

The specimen is wholly septate, and retains replaced shell. Coiling is very evolute, the umbilicus broad, and of moderate depth. The umbilical wall and shoulder are broadly rounded. To a diameter of 47 mm, primary ribs arise at the umbilical seam, and are well developed and concave across the umbilical wall, strengthening into sharp bullae on the inner flank. These give rise to feebly flexuous prorsiradiate single ribs that alternate regularly with shorter intercalated ribs. All ribs develop an ill-defined inner ventrolateral tubercle,

linked by a prorsiradiate rib to an equally ill-defined outer ventrolateral tubercle. These tubercles are little more than angulations on the ribs. The ribs are strongly and broadly convex across the venter. There are ill-defined siphonal clavi on all ribs. On the remaining sector of outer whorl, the ribs are all primaries. They all bear a strong, subspinose umbilical bulla that migrates out away from the umbilical shoulder as size increases, ultimately occupying a mid-lateral position. A strong, high, feebly flexuous to straight prorsiradiate rib links to a large, outward- and upward-directed horn, with a strong rib linking the horns across the venter. There are in all 18–19 primary ribs on the outer whorl.

Discussion

Acanthoceras cornigerum is highly distinctive species, differing from all other described *Acanthoceras* species in the ill-defined inner and outer ventrolateral and siphonal tubercles of early growth, the rapid transition to exclusively primary ribs at a small diameter, together with the migration of the umbilical bullae out to mid-flank and the development of large, outward- and upward-directed horns, with a strong rib linking the horns across the venter. So distinctive is the species that it might be considered pathological but for the description of a larger individual from Hokkaido, Japan, that shows comparable distinctive ontogenetic changes (Matsumoto, Muramoto & Takahashi 1969 p. 268, pl. 32, fig. 1; text-fig. 5).

Occurrence

Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Genus ***Protacanthoceras*** Spath, 1923

Type species

Ammonites bunburianus Sharpe, 1853, p. 25, pl. 9, fig. 3, by original designation by Spath 1923, p. 144.

Diagnosis

Dwarf offshoots of *Acanthoceras* reaching adult stage at diameters from 15 to 150 mm. Moderately involute, compressed and flat-sided to inflated with inner and outer ventrolateral and siphonal tubercles; intercalated or branched secondaries bear ventrolateral and siphonal tubercles. Tubercles weaken or disappear towards the end of the adult body chamber, and the ribs become broad and flat. Microconchs are 66–80% of the diameter of macroconchs and tend to have fewer and stronger ribs. In some species the ornamentation on the last whorl weakens. The suture is similar in plan to that of *Acanthoceras*, but simpler in detail (modified after Wright & Kennedy 1987).

Occurrence

Middle and lower Upper Cenomanian, southern England, France, Romania, Bulgaria, KwaZulu in South Africa, Madagascar, south India, and possibly Middle Cenomanian of Hokkaido, Japan.

Protacanthoceras subwaterloti (Venzo, 1936)

Fig. 26

1936 *Acanthoceras* (*Acompsoceras*) *subwaterloti* Venzo, p. 87 (29), pl. 7 93), fig. 11.

Type

The holotype, by monotypy, is the original of Venzo, 1936, p. 87 (29), pl. 7 93), fig. 11, reproduced here as Fig. 26G, H, from the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975).

Material

Two specimens, SAM-PCZ22192 and 22193, from the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975).

Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ22192	25.8 (100)	8.3 (32.2)	11.4 (44.2)	0.73	7.3 (28.3)
PCZ22193	23.4 (100)	8.5 (36.2)	9.7 (41.5)	0.87	7.4 (31.6)

Description

SAM-PCZ22192 (Fig. 26D–F, M, N) is a phragmocone 25.8 mm in diameter, lacking the adapical 120° sector of the outer whorl, and with indications of the former presence of a further whorl. Coiling is moderately evolute, with 40% of the previous whorl covered. The umbilicus comprises 28–32% of the diameter, with a low, subvertical wall and narrowly rounded shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.73, the greatest breadth well below mid-flank. The inner flanks are flattened and subparallel; the outer flanks converge to broadly rounded ventrolateral shoulders and a narrow, feebly convex venter. Primary ribs arise at the umbilical seam, and are low and broad, strengthening into a blunt bulla on the umbilical shoulder, producing a distinctive crenulate margin to the umbilicus. They give rise to low, broad, straight, prorsiradiate ribs that broaden and weaken at mid-flank before strengthening markedly on the outer flank, while additional ribs intercalate between successive primaries to give 20 ribs at the ventrolateral shoulder, corresponding to nine bullae at the umbilical shoulder of the 270° sector of outer whorl preserved. There are traces of a low, rounded, effaced inner lateral bulla at the adapical end of the outer whorl that is rapidly lost. All ribs bear strong, equal outer ventrolateral and weaker siphonal clavi, connected across the venter by a low, broad swelling.

SAM-PCZ22193 (Fig. 26A–C, I–L) has an estimated maximum preserved diameter of 25.5 mm (the venter at the adapertural end of the outer whorl is damaged). It closely resembles the previous specimen, with a total of 12–13 umbilical bullae on the outer whorl, and weak inner ventrolateral tubercles at the adapical end that are thereafter lost. The outer ventrolateral clavi are strong and persistent; the siphonal clavi are somewhat weaker.

Discussion

The very limited material attributed to *Protacanthoceras subwaterloti* most closely resembles the lower Upper Cenomanian *Protacanthoceras bunburianum* (Sharpe, 1853) (p. 25, pl. 9, fig. 3; see revision in Wright & Kennedy 1987 p. 215, pl. 55, figs 10–16; text-figs 83b, c; 84d–h). This differs in the persistence of inner ventrolateral clavi on

phragmocones of individuals of comparable ribbing strength, and the marked concavity and forward projection of the ribs on the ventrolateral shoulders.

The holotype of *subwaterloti* (Fig. 26C, D) is a fragment only, with a maximum preserved whorl height of 14 mm, while both of the present specimens retain indications of the presence of a further whorl, suggesting adults reached a substantially greater size than *P. bunburianum*.

Occurrence

Middle or lower Upper Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Genus ***Cunningtoniceras*** Collignon, 1937

(?Synonym: *Guerangericeras* Thomel, 1972, p. 119)

Type species

Ammonites cunningtoni Sharpe, 1855, p. 35, pl. 15, fig. 2; by the original designation of Collignon, 1937, p. 64(40).

Diagnosis

Large, evolute. Whorl section quadrate to depressed. Flanks typically ornamented by bullate primary ribs only, with inner and outer ventrolateral tubercles, the former commonly developing into horns that eventually assimilate the latter. For part of ontogeny, ventral ribs and siphonal tubercles more numerous than the outer ventrolateral, to which they are linked in pairs or groups of ribs, additional ribs with siphonal clavi intercalating between, the siphonal clavi commonly borne on a siphonal ridge. In later stages all ribs and tubercles except umbilical and fused ventrolateral may disappear and the ventrolateral tubercles extend sideways beyond the umbilical or obliquely upwards and may be excessively enlarged.

Discussion

Wright & Kennedy (1987, p. 193) derived *Cunningtoniceras* from *Acanthoceras* by the development of additional ventral ribs and siphonal tubercles. Subsequent work suggests that *Cunningtoniceras* preceded *Acanthoceras* in North Africa (Amedro in Robaszynski *et al.* 1994) and Western Europe (Gale 1995; Kaplan *et al.* 1998), and the relationships of early *Acanthoceratinae* require reassessment.

Acanthoceras flexuosum commonly show a siphonal ridge, and there are a number of KwaZulu specimens that develop more numerous ventral than flank ribs, and more numerous siphonal clavi. These are referred to here as *Cunningtoniceras?* sp. a and b.

Occurrence

Middle and lower Upper Cenomanian, Europe, Turkmenistan, Middle East, North Africa, Nigeria, Angola, KwaZulu, Madagascar, southern India, Japan, New Guinea, Bathurst Island (northern Australia), U.S. Gulf Coast and Western Interior.

***Cunningtoniceras?* sp. a**

Figs 27A–D, 28, 29

1907 *Acanthoceras quadratum* Crick, p. 193 (*pars*).

Material

OUM KX 1744, 4630–4634; SAM-PCZ13516, BMNH C18193.

Description.

OUM KX4632 (Fig. 27A–D) is a well-preserved 120° sector of phragmocone retaining recrystallized shell. The maximum preserved whorl height is 40.5 mm. Coiling is evolute, the umbilicus deep, with a feebly convex, outward-inclined wall. At the adapical end of the fragment the intercostal whorl section is very depressed oval, with a whorl breadth to height ratio of 1.58, the flanks very strongly convex, the ventrolateral shoulders and venter broadly and evenly rounded. Coarse primary ribs, of which five are preserved on the fragment, arise at the umbilical seam and sweep back across the umbilical wall, strengthening progressively. They strengthen into alternately weak and very strong umbilical bullae that mark the greatest whorl breadth in costal section, with a whorl breadth to height ratio of up to 1.45. A strong bulla on one flank corresponds to a weak bulla on the opposite flank at this stage. The bullae give rise to strong, very coarse recti- to feebly rursiradiate ribs that pass straight across the venter without diminution, and bear a subequal, bullate inner, and weakly rounded outer ventrolateral tubercle, and a weakly rounded to feebly clavate siphonal tubercle.

This growth stage is succeeded by one in which the inner ventrolateral tubercles strengthen markedly into a prominent horn. At the largest preserved diameter the outer ventrolateral tubercle has all but effaced and merged with the inner ventrolateral horn, the venter feebly concave in costal section, with the rib and siphonal tubercle effaced.

A number of very worn fragments (OUM KX4630, 4631, 4633, 4634), with whorl heights of 19.8–38 mm, represent the remarkably depressed early growth stage of the species. The greatest breadth is at the umbilical bulla, and some ribs have a weak and strong bulla in corresponding positions on the opposing flanks. A feeble, low siphonal ridge links the siphonal clavi in some of these specimens. OUM KX4630 (Fig. 28C, D) shows the incipient development of pairs of ribs looping across the venter between outer ventrolateral clavi and a pair of siphonal tubercles corresponding to a single outer ventrolateral at the largest preserved diameter. By contrast, the impression of the venter of the penultimate whorl on the dorsum of the fragment shows equal numbers of outer ventrolateral and siphonal tubercles.

SAM-PCZ13516 (Fig. 29) continues the ontogeny, and is a 120° whorl sector with a maximum preserved whorl height of 57 mm. It bears five very distant coarse primary ribs with blunt umbilicolateral horns, linked to massive inner ventrolateral horns by a low broad rib that effaces on the outer flank. The outer ventrolateral tubercles are near-effaced, and the broad venter concave in costal section, the ventral ribbing effaced. OUM KX1744 (Fig. 28E) is a massive body chamber fragment with a maximum preserved whorl height of 64 mm. Coarse primary ribs arise on the umbilical wall, and strengthen into massive umbilicolateral horns, connected to massive ventrolateral horns by a low, broad rib. The ventrolateral horns are connected across the venter by low, broad ribs. These efface in the middle of the very broad venter. The costal ventral section is concave.

BMNH C18195, the second specimen referred to *Acanthoceras quadratum* by Crick (1907, p. 193), is a 180° sector of the penultimate whorl, and a 120° sector of the outer whorl that are wholly septate, with a maximum preserved whorl height of 55 mm. Parts of nine ribs survive on the penultimate whorl fragment, and parts of seven on the outer whorl.

Discussion

The smaller fragments referred to the species are highly distinctive. The presence of looped ventrolateral ribbing and multiplication of siphonal versus outer ventrolateral tubercles at one point on OUM KX4630 (Fig. 28C, D) suggest reference to *Cunningtoniceras*, but the limited extent of these diagnostic features on the material may be of no taxonomic significance, hence the qualified identification.

Occurrence

Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Cunningtoniceras? sp. b.

Figs 27E–F, 30

1907 *Acanthoceras* sp., Crick, p. 191.

Description

BMNH C18273 (Fig. 30) consists of a 120° sector of two phragmocone whorls, with a maximum preserved whorl height of 60.8 mm. Coiling appears to have been very evolute, the umbilicus deep, with a feebly convex, outward-inclined umbilical wall and broadly rounded shoulder. The whorl section is very depressed, rectangular, with rounded corners. Seven ribs survive on the outer whorl fragment. The ribs are low and broad on the umbilical wall, and strengthen into strong, widely separated bullae, perched on the umbilical shoulder. The ribs are straight and prorsiradiate on the flanks, across which they strengthen progressively and develop into a pinched ventrolateral horn that does not rise above the level of the venter. The horns are linked over the venter by a very broad, transverse rib, which is feebly differentiated into a concave adapical and convex adoral rib. There are low, ill-defined siphonal tubercles.

What may be the inner whorls of this species are represented by OUM KX4574 (Fig. 27E, F), fragment of phragmocone with a maximum preserved whorl height of 46 mm. The whorl section appears to have been depressed trapezoidal in intercostal section. The costal section is depressed, and markedly concave between the umbilical and inner ventrolateral tubercles. Parts of eight ribs are preserved on the fragment. They arise at the umbilical seam, and strengthen across the umbilical wall, developing into well-developed pinched umbilical bullae. These give rise to strong, narrow, recti- to feebly rursiradiate primary ribs that are straight on the flanks and link to pinched inner ventrolateral horns. These are linked to effacing outer ventrolateral tubercles by a strong transverse rib, beyond which the venter is damaged.

Discussion

Feeble development of multiple ventral ribbing is a *Cunningtoniceras*-like feature, hence the questionable

generic assignation. The quadrate costal whorl section, with broad, flattened venter, distinguishes the material from *Cunningtoniceras?* sp. a.

Occurrence

Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Genus *Calycoceras* Hyatt, 1900

(ICZN Generic Name No. 1352)

Type species

By designation under the Plenary Powers (ICZN Opinion No. 557) *Ammonites navicularis* Mantell, 1822, p. 198, pl. 22, fig. 5 (ICZN Specific Name No. 1633).

Diagnosis

Small to large, rather evolute with oval, depressed round, subquadrate or polygonal whorl section. Strong, generally straight ribs cross uninterrupted a rounded or flat venter. There are up to seven rows of tubercles on the primary ribs: umbilical, inner and outer ventrolateral and siphonal. Secondary ribs lack the umbilical and sometimes the inner ventrolateral tubercles. Some or all tubercles may be lost early in ontogeny, or may persist, or be rejuvenated or not on the last part of the mature body chamber. Marked size dimorphism is probably general (from Wright & Kennedy 1987, p. 217).

Occurrence

Lower Middle to middle Upper Cenomanian, Europe, Asia, Africa, North America, Antarctica and possibly Brazil.

Subgenus *Calycoceras* (*Gentoniceras*) Thomel, 1972

Type species

Ammonites gentoni Brongniart, 1822, pp. 83, 392, pl. 6, fig. 6 from the lower Middle Cenomanian of Rouen, Seine-Maritime, France, by original designation by Thomel 1972, p. 65.

Diagnosis

Small to moderate-sized, inner whorls with umbilical, inner, and outer ventrolateral and siphonal tubercles in early growth, later whorls with umbilical bullae and, in some cases, weak outer ventrolateral tubercles on crowded or distant primary and secondary ribs (from Kennedy & Juignet 1994, p. 30).

Occurrence

Middle and lower Upper Cenomanian in Western Europe, South Africa and south India.

Calycoceras (*Gentoniceras*) *gentoni* (Brongniart, 1822)

Fig. 31

1822 *Ammonites gentoni* Brongniart, p. 83, 392, pl. 6, fig. 6.

1907 *Acanthoceras paucinodatum* Crick, p. 203, pl. 13, fig. 3.

1990 *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart, 1822); Wright & Kennedy, p. 219, pl. 56, figs 1–3, 6–8; pl. 57, figs 2, 3, 8; pl. 58, fig. 7; pl. 66, figs 1, 2; text-figs 88a, c; 89a, b; 90a–c (with synonymy).

- 1990 *Calycoceras* (*Gentoniceras*) *subgentoni* (Spath, 1926a); Wright & Kennedy, p. 226, pl. 56, figs 4, 5; pl. 57, fig. 4; pl. 58, figs 5, 6; pl. 59, figs 1–4; text-figs 88k; 90d–f (with synonymy).
- 1990 *Calycoceras paucinodatum* (Crick, 1907); Wright & Kennedy, p. 228, text-fig. 91a, b.
- 1994 *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart, 1822); Juignet & Kennedy, p. 30, figs 1a; 2d, e; 6d, e, j, k; 7a–l; 8a–e; 22a, b.
- 1998 *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart, 1822); Kaplan, Kennedy, Lehmann & Marcinowski, p. 156, pl. 26, figs 3–5.

Type

Lectotype, by the subsequent designation of R. Douvillé (1911), is the original of Brongniart (1822, pl. 6, fig. 6), from the lower Middle Cenomanian of Rouen, Seine-Maritime, France. It was refigured by Wright & Kennedy (1990, text-fig. 90a–c).

Material

BMNH C18214, the holotype of *Acanthoceras paucinodatum* Crick, 1907, p. 203, pl. 13, fig. 3.

Dimensions

	D	Wb	Wh	Wb:Wh	U
C18214	65.1 (100)	– (–)	28.4 (43.6)	– (–)	19.0 (29.2)

Description

BMNH C18214 (Fig. 31), the holotype of *Acanthoceras paucinodatum*, is 65.1 mm in diameter, and very worn and corroded on one side. The adapertural 90° sector of the outer whorl is body chamber. Traces of replaced shell survive on one flank. Coiling is evolute; the umbilicus comprises 29.2% of the diameter. The umbilical wall is flattened, the umbilical shoulder broadly rounded. The whorl section is depressed, rounded-polygonal at the adapical end of the outer whorl, becoming rounded-oval at the adapertural end. The specimen has been mechanically cleaned, and the ribbing 'improved' on the adapical parts of the outer whorl. The penultimate whorl bears alternately long and short ribs, the long ribs with small umbilical bullae, all ribs with inner and outer ventrolateral tubercles. This pattern persists onto the adapical 120° sector of the outer whorl, where the ribs are seen to be straight, prorsiradiate, and crowded. The primary ribs bear umbilical bullae, and both primary and intercalated ribs bear inner and outer ventrolateral tubercles. The preservation of the venter is defective and it cannot be determined with any certainty if a siphonal tubercle was present. On the adapertural 240° sector of the outer whorl, from a diameter of approximately 40 mm onwards, the inner, and then the outer ventrolateral tubercles efface, leaving an evenly and broadly rounded venter, crossed by well-developed transverse ribs. The ribs alternate regularly long and short to the greatest diameter preserved, the umbilical bullae weakening slightly.

Discussion

We follow Kennedy & Juignet (1994, p. 36) in uniting slender-whorled, slowly expanding, paucicostate *C. (G.)*

gentoni (Brongniart, 1822), and *C. (G.) subgentoni* (Spath, 1926), with more rapidly expanding densicostate whorls; Wright & Kennedy (1990, pp. 219–227) treated them as separate species, and regarded *paucinodatum* as a separate species. Comparisons with large new collections from southern England now persuade us that it is a synonym.

Occurrence

C. (G.) gentoni ranges from lower Middle to lower Upper Cenomanian. It is recorded from southern England, Haute-Normandie, Sarthe and Provence in France, Spain, and, possibly, Iran. The present specimen is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Subgenus *Calycoceras* (*Newboldiceras*) Thomel, 1972

Type species

Acanthoceras newboldi Kossmat, 1897, p. 5 (112), by original designation by Thomel 1972, p. 105, = *Acanthoceras rhotomagense* var. *asiaticum* Jimbo, 1894, p. 177, pl. 20, fig. 1.

Diagnosis

Evolute, with polygonal to subcircular or subquadrate whorl section, rapidly expanding in breadth and height, strongly and often densely ribbed with strong and persistent umbilical and outer ventrolateral tubercles and less persistent inner ventrolateral and siphonal; occasionally there is a slight protuberance between the umbilical and inner ventrolateral tubercles. Typically the inner parts of the whorl sides are subparallel or weakly convergent and the outer third or quarter strongly convergent to a more or less flat venter. Known complete macroconchs are up to about 250 mm in diameter; fragments described below suggest macroconch phragmocones of up to 200 mm diameter. Adult microconchs range from 45 mm diameter but are more commonly 60–100 mm (modified after Wright & Kennedy 1990, p. 238).

Occurrence

Middle and lower Upper Cenomanian. Widespread in Europe, Africa, Madagascar, southern India, Japan, California, the U.S. Western Interior, and the James Ross Island Group, Antarctica.

Calycoceras (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894)

- Figs 32, 33A–F, 34J–L, P, Q, 36–38, 44D, E, H, 57A–F
- 1865 *Ammonites Rhotomagensis* DeFrance; Stoliczka, p. 66 (*pars*), including *typicus* (p. 68) (*pars*) and var. *subcompressus* (p. 68), pl. 34, figs 3, 4; pl. 35, fig. 1; pl. 36, fig. 1; pl. 37, figs 1, 2.
- 1894 *Acanthoceras rhotomagense* var. *asiatica* Jimbo, p. 177, pl. 20, fig. 1.
- 1897 *Acanthoceras Newboldi* n.sp. (Typische Form) Kossmat, p. 5 (112), pl. 1 (12), figs 2, 3; pl. 3 (14), fig. 2.
- 1907 *Acanthoceras newboldi* (typical form) F. Kossmat: Crick, p. 197.
- 1907 *Acanthoceras newboldi* var. *spinosa* F. Kossmat: Crick, p. 199 (*pars*), pl. 12, fig. 3.

- 1907 *Acanthoceras nitidum* Crick, p. 201 (*pars*).
 1936 *Acanthoceras newboldi* var. *spinosa* Kossm.; Venzo, p. 82 (24), pl. 7, figs 3, 4.
 1972 *Newboldiceras (Newboldiceras) newboldi* (Kossmat); Thomel, p. 106 (*pars*), pl. 40, figs 1–3; *non* pl. 34, figs 1–3; pl. 38, figs 1, 2; pl. 39, figs 1–3; pl. 41; ?pl. 42, figs 3, 4.
 1990 *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894); Wright & Kennedy, p. 239, pl. 58, fig. 1; pl. 64, figs 1, 2; pl. 65, figs 1–3, 5, 7; pl. 72, fig. 3; text-figs 87a–c; 88f; 97; 98 (with full synonymy).
 1994 *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894); Kennedy, p. 227, pl. 7, figs 7, 8; pl. 8, figs 1, 2.
 1997 *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo); Wilmsen, pl. 16, fig. 1.
 2004 *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894); Kennedy & Jolkičev, p. 275, pl. 3, fig. 1; pl. 4, figs 6, 7; pl. 5, figs 1–4.
 2009 *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894); Lehmann & Herbig, p. 64, pl. 1, figs a, b.

Type

The holotype by monotypy is the original of Jimbo, 1894, pl. 20, fig. 1, no. 1–105 in the Collections of the Geological Institute, Tokyo University, from the Middle Cenomanian *Trigonia* Sandstone of the Ikushumbets, Hokkaido, Japan. A cast is figured here as Fig. 38.

Material

SAM-PCZ 13426, 13431, 13433, 13437, 134441, 13455, 132457, 13460, 13468, 13472, 13473, 13476, 13485, 13486. OUM KX4590, 4591, 4599. BMNH C18200–182002 (the originals of *Acanthoceras newboldi* (typical form) of Crick, 1907, p. 199). BMNM C18204, the original *Acanthoceras newboldi* var. *spinosa* of Crick, 1907, pl. 12, fig. 3. BMNH C18212, specimen b of *Acanthoceras nitidum* of Crick (1907, p. 202).

Costal dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ13472	20.7 (100)	10.4 (50.2)	10.0 (48.3)	1.04	5.5 (20.6)
PCZ13468	38.8 (100)	19.6 (50.5)	17.8 (45.9)	1.1	10.9 (28.1)
PCZ13428	40.0 (100)	22.0 (55.0)	18.7 (46.8)	1.2	– (–)
PCZ13433	35.5 (100)	18.0 (50.7)	15.3 (43.0)	1.17	10.2 (28.7)
PCZ13486	49.6 (100)	27.4 (55.2)	25.3 (51.0)	1.1	13.4 (27.0)
PCZ13431	62.5 (100)	30.3 (48.5)	29.4 (47.0)	1.0	16.7 (26.7)
PCZ13476	68.3 (100)	37.1 (54.3)	32.6 (47.7)	1.14	17.1 (25.0)
PCZ13437	69.2 (100)	36.7 (53.0)	32.0 (46.20)	1.15	19.8 928.6)
PCZ13441	71.4 (100)	35.6 (49.9)	33.5 (46.9)	1.1	18.6 (26.1)

Description

Juvenile phragmocones vary from 17.7–71.4 mm in diameter. All retain recrystallized shell, and the sutures are not seen. Coiling is involute, with 40–44% of the previous whorl covered, the umbilicus of moderate depth, with a subvertical wall and narrowly rounded umbilical shoulder. The costal whorl section is slightly depressed, with a whorl breadth to height ratio of 1.04–1.17, trapezoidal–polygonal, with the greatest breadth at the umbilical bullae. The intercostal whorl section is equidimensional, trapezoidal, with the greatest breadth low on the inner flank. Ornament is variable. The smallest specimens, between 17.7 and 26.2 mm (SAM-PCZ13460: Fig. 32F–I; 13472: Fig. 32A, B, J, K, L; 13473: Fig. 32P–R, 13477: Fig. 33A–F) have 12–14 primary ribs per whorl. They arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and develop into well-developed umbilical bullae of variable strength. These give rise to single straight prorsiradiate ribs that strengthen across the flanks. Single ribs intercalate between successive primaries, and strengthen to match them at the ventrolateral shoulder, where all ribs bear a conical inner ventrolateral tubercle of variable strength. These are linked to feebly clavate outer ventrolateral tubercles by a strong prorsiradiate rib. A low broad transverse rib links the outer ventrolateral tubercles to feeble siphonal clavi.

Somewhat larger individuals are up to 42 mm in diameter (SAM-PCZ13428: Fig. 32P–R; 13433: Fig. 32M–O; 13468: 32S–T), and have up to 40 ribs per whorl. Primary ribs have sharp umbilical bullae of variable strength, and generally sharp subspinose conical inner ventrolateral tubercles at small diameters; in some individuals these decline markedly as size increases. There are one or two long or short intercalated ribs between successive primaries, with inner ventrolateral tubercles that are generally weaker than those on the primary ribs. All ribs bear feebly clavate outer ventrolateral and siphonal tubercles, linked across the venter by a strong transverse rib.

The larger phragmocones vary from 59–72 mm in diameter (SAM-PCZ13431; 13437: Fig. 36D–F; 13441, 13476: Fig. 36A–C; 13485, 13486). SAM-PCZ13431 has 14 primary ribs on the outer whorl. The umbilical bullae are subspinose on the adapical half of the outer whorl, with one or two shorter ribs intercalated between, strong conical inner, and weaker feebly clavate outer ventrolateral and siphonal tubercles. On the apertural half of the outer whorl, the umbilical bullae elongate, the ribs are feebly flexuous, the inner ventrolateral tubercles weaken and efface, outer ventrolateral clavi persist, siphonal clavi are lost, and the venter is convex in costal section, with a strong, feebly convex transverse rib. By contrast, SAM-PCZ13486 (Fig. 32 X, Y) shows the persistence of all rows of tubercles to a diameter 54mm, the siphonal row weakening and offset as a result of damage to the shell and subsequent asymmetric regeneration thereafter. SAM-PCZ13437 (Fig. 36D–F) and 13476 (Fig. 36A–C) are relatively flexuously ribbed individuals with up to 40 ribs per whorl. Subspinose umbilical bullae of variable strength persist to the greatest preserved diameter, as do the outer ventrolateral clavi, the inner ventrolateral and siphonal tubercles effacing.

SAM-PCZ13455 (Fig. 37) is a fragment of a huge

phragmocone with a maximum preserved whorl height of 90 mm. Eight primary ribs with well-developed umbilical bullae of variable strength are preserved on the 120° whorl fragment. They alternate regularly with single intercalated ribs that arise below mid-flank, to give a total of 14 ribs on the fragment at the ventrolateral shoulder. All ribs retain subdued inner and outer ventrolateral tubercles, linked across the venter by a broad transverse rib. This specimen closely resembles the holotype (Fig. 38).

Discussion

Calycoceras (Newboldiceras) asiaticum asiaticum and *C. (N.) asiaticum spinosum* (Kossmat, 1897) are closely allied, and linked by occasional passage forms. They differ in the much more robust tuberculation of the latter, well seen in the present material (compare Fig. 33A–E and G–R, Fig. 37 and Figs 40–43). The *Acanthoceras newboldi* var. *spinosa* Kossmat of Crick, 1907 (p. 199) is in part based on a specimen here referred to *C. newboldi newboldi*: BMNH C18204, the original of Crick, 1907, pl. 12, fig. 3, illustrated here as Fig. 57I. BMNH C18212, specimen b of *Acanthoceras nitidum* of Crick (1907, p. 202; Fig. 23J–L) is a juvenile of the present species. The *Acanthoceras newboldi* var. *spinosa* Kossm. of Venzo (1936, p. 82 (24), pl. 7, figs 3, 4, reproduced here as Fig. 44D, E, H) are interpreted as typical *C. (N.) asiaticum asiaticum*. More problematic is *Acanthoceras gortanii* Venzo, 1936 (p. 82 (24), pl. 7 (3), fig. 5, reproduced here as Fig. 44A–C). The holotype comes from the Skoenberg, and is a juvenile *Calycoceras*, here treated as specifically indeterminate.

Occurrence

Upper Middle Cenomanian, rarer in the lower Upper Cenomanian. Southern England, northern and southern France, Spain, Romania, Bulgaria, Tunisia, Madagascar, south India, and Japan, with possible records from Poland, Israel, and China. The present material is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Calycoceras (Newboldiceras) asiaticum spinosum (Kossmat, 1897)

Figs 33G–R, 34M,O, 35A–J, M–O,R,S, 39–43

- 1897 *Acanthoceras Newboldi* var. *spinosa* Kossmat, p. 7 (114), pl. 2 (13), figs 2, 3; pl. 3 (14), fig. 1.
 1907 *Acanthoceras newboldi* var. *spinosa* F. Kossmat: Crick, p. 199 (*pars*), non pl. 12, fig. 3 (= *C. (N.) asiaticum asiaticum*).
 non 1936 *Acanthoceras newboldi* var. *spinosa* Kossm.; Venzo, p. 82 (24), pl. 7, figs 3, 4.
 1972 *Newboldiceras (Newboldiceras) spinosum* (Kossmat); Thomel, p. 110, pl. 42, figs 1, 2; pl. 46, figs 1–3.
 1978 *Calycoceras newboldi-choffati* Crick (*non* Kossmat); Kennedy, pl. 4, fig. 4.
 1990 *Calycoceras (Newboldiceras) asiaticum spinosum* (Kossmat, 1897); Wright & Kennedy, p. 249, pl. 64, fig. 3; pl. 65, figs 4, 6; pl. 66, figs 3, 4; pl. 69, fig. 1; pl. 70, fig. 3; text-figs 87a–c; 88d, l; 99; 100; 102; 107k (with full synonymy).

- 1994 *Calycoceras (Newboldiceras) asiaticum spinosum* (Kossmat, 1897); Kennedy, p. 228, pl. 9, figs 1–3, 7–9; pl. 10, figs 12, 13.
 1997 *Calycoceras (Newboldiceras) asiaticum spinosum* (Kossmat); Wilmsen, pl. 12, fig. 1; pl. 20, fig. 1.

Types

Lectotype, designated by Wright & Kennedy (1990) is the original of Kossmat's 1897, pl. 2 (13), fig. 2, from the Utatur Group of Odium, South India. Paralectotypes are the originals of Kossmat's pl. 2 (13), fig. 3, and pl. 3 (14), fig. 1. The paralectotype of Stoliczka, 1865, pl. 35, fig. 2 may not belong to this subspecies.

Material

SAM-PCZ13446, 13448, 13451, 13456, 13458, 13463, 13479, 13459, 13460, 13464, 13465, 13469, 13478, 13482; SAM D1005; OUM KX4592, 4601. BMNH C18205–18206, the originals of Crick, 1907, p. 200 (*pars*)

Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ13458	23.1 (100)	14.8 (64.0)	10.5 (45.10)	1.41	5.9 (25.5)
PCZ13446	32.7 (100)	19.6 (59.9)	14.6 (44.6)	1.34	9.2 (28.1)
PCZ13448	37.3 (100)	19.4 (52.0)	16.1 (43.2)	1.2	10.4 (27.9)
PCZ13479	37.8 (100)	23.5 (62.1)	16.6 (43.9)	1.4	10.9 (28.8)
PCZ13464	39.0 (100)	22.2 (57.0)	17.8 (45.6)	1.25	10.4 (26.7)
PCZ13459	45.0 (100)	26.9 (59.8)	21.7 (48.2)	1.24	12.7 (28.2)
PCZ13463	46.2 (100)	28.6 (61.9)	24.5 (53.0)	1.17	12.5 (27.1)

Description

The smallest individual is SAM-PCZ13458 (Fig. 33K–N), 24.8 mm in diameter. Coiling is moderately involute, the umbilicus of moderate depth with a convex, outward-inclined umbilical wall and more narrowly rounded umbilical shoulder that comprises 25.5% of the diameter. The primary ribs arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, where they bear a progressively strengthening spinose umbilical bulla. The bullae give rise to broad, coarse, straight, prorsiradiate single ribs that link to very strong, coarse inner ventrolateral spines. A broad, coarse rib links to strong, subspinose outer ventrolateral clavi. Single shorter ribs intercalate between successive primaries, arising on the outermost flank or ventrolateral shoulder. They generally lack an inner ventrolateral tubercle, and have outer ventrolateral and siphonal clavi only slightly weaker than those on the primary ribs. SAM-PCZ13478 (Fig. 33I, J, O, P) is a coarsely ribbed individual an estimated 33 mm in maximum diameter, with 12 primary ribs on the outer whorl, and strong inner and outer ventrolateral tubercles. SAM-PCZ13446 (Fig. 33G, H, Q, R) has two intercalated ribs separating successive primaries on the

adapertural third of the outer whorl at a diameter of 34.5 mm. SAM-PCZ13463 (Fig. 35D, E), 13464 (Fig. 35A–C), and 13479 (Fig. 33G, H, Q, R) are between 37.8 and 46.2 mm in diameter. The inner whorls are less markedly spinose than those of the previous individuals at the same diameter. The costal whorl sections are depressed polygonal, with the greatest breadth at the umbilical bullae. SAM-PCZ13464 (Fig. 35A–C) is a coarsely ornamented individual with 14 subspinose umbilical bullae on the outer whorl that give rise to single strong, straight, prorsiradiate primary ribs. One or two long or short ribs intercalate between successive bullate primaries; occasional long intercalatories extend to the umbilical shoulder without developing a bulla, to give a total of 27–28 ribs per whorl at the ventrolateral shoulder. All ribs bear strong subspinose inner ventrolateral tubercles and strong, feebly clavate outer ventrolateral tubercles, linked across the venter by a strong transverse rib that bears a slightly weaker siphonal clavus. SAM-PCZ13463 (Fig. 35D, E) has less robust ornament of this type, the inner ventrolateral tubercles of variable strength. SAM-PCZ13479 is a very depressed individual with more subdued tuberculation relative to the ribs.

SAM-PCZ 13459 (Fig. 35M–O) is 45 mm in diameter, with indications of the former presence of a further 180° whorl sector. The adapical half of the outer whorl has comparable flank ornament to that of the previous specimens, with well-developed inner and outer ventrolateral tubercles, and the siphonal row near-effaced. The inner ventrolaterals are lost by a diameter of 42 mm., leaving only strong umbilical bullae and weak outer ventrolateral clavi on either side of the broad, convex venter. This specimen may be an incomplete microconch.

SAM-PCZ13482 is a fragment 70.5 mm in diameter with depressed whorl section, the whorl breadth to height ratio of 1.13, the crowded ribs recti- to feebly rursiradiate with persistent umbilical, inner and outer ventrolateral tubercles.

SAM-PCZ13456 (Fig. 39A, B) is wholly septate to a diameter of 91.2 mm. There are an estimated 40–42 ribs at the ventrolateral shoulder on the outer whorl, with strong umbilical, inner and outer ventrolateral tubercles throughout, the siphonal row surviving to at least 60 mm diameter. It closely resembles the paralectotype, the original of Kossmat, 1897, pl. 2 (13), fig. 3.

SAM-D1005 (Fig. 39C, D) is a rather corroded internal mould, septate to 120 mm diameter. There are 24 ribs at the ventrolateral shoulder on the outer half whorl. Primary ribs have well-developed umbilical bullae, and are separated by single intercalated ribs. All ribs bear strong inner and weaker outer ventrolateral tubercles, the venter broadly convex between. The fragment closely resembles the lectotype (Kossmat, 1897, pl. 2 (13), fig. 2).

SAM-PCZ13451 (Fig. 40) is a phragmocone fragment with a maximum preserved whorl height of 70 mm. There are strong conical umbilical bullae and inner ventrolateral tubercles, the venter broadly convex between, with weaker outer ventrolateral tubercles.

SAM-PCZ13462 (Fig. 41) is a huge phragmocone fragment with a maximum preserved whorl height of 108 mm and a whorl breadth to height ratio of 1.2. Massive umbilical bullae are displaced out to an umbilicolateral position, and are borne on coarse, straight, prorsiradiate primary ribs, sepa-

rated by single intercalated ribs. All ribs bear massive rounded-conical inner ventrolateral tubercles and outer ventrolateral clavi. These are quite closely spaced on either side of the venter when compared to the other specimens studied. They are linked by a strong rib, the costal whorl profile markedly convex.

SAM-PCZ13469 (Fig. 42) is a 120° sector of body chamber with a maximum preserved whorl height of 78 mm. There are eight primary ribs on the fragment. They arise at the umbilical seam and sweep back across the umbilical wall, strengthening progressively, and developing into strong umbilical bullae. The ribs are recti- to feebly rursiradiate on the flanks, and alternate with single long intercalated ribs. All bear strong conical-clavate inner ventrolateral tubercles and outer ventrolateral clavi, the ventral rib linking them strong and transverse. Ribs and umbilical bullae efface at the adapertural end of the fragment, suggesting proximity to the adult aperture.

OUM KX4623 (Fig. 43) is a 180° whorl sector of phragmocone with indications of the former presence of a further whorl. Recrystallized shell is exceptionally well preserved. The maximum preserved whorl height is 55.5 mm, the whorl breadth to height ratio is 1.55; the greatest breadth is at the umbilical tubercle in costal section. Coiling is evolute, the umbilical seam crenulated to accommodate the inner ventrolateral tubercles of the preceding whorl. There are nine coarse primary ribs on the outer whorl fragment. They arise at the umbilical seam, sweep back across the umbilical wall and shoulder, and develop into a strong umbilicolateral bulla. The ribs arise singly or in pairs, and sweep back across the flanks. The inner and outer ventrolateral tubercles are concealed between the recrystallized dorsal shell wall of the succeeding whorl (now lost). The ribs are strong and coarse across the venter.

None of the specimens show the sutures.

Discussion

Calycoceras (*N.*) *asiaticum spinosum* differs from the nominate subspecies in its coarser tuberculation, the inner and outer ventrolateral rows persisting to maturity, as noted above under *C. (N.) asiaticum asiaticum*. See Wright & Kennedy (1990, p. 249) for a discussion of differences from other *Newboldiceras* species.

Occurrence

Upper Middle and lower Upper Cenomanian, southern England, France, Spain, Romania, Bulgaria, Tunisia, Madagascar, South India, Tibet(?), Japan and California. The present material is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Calycoceras (*Newboldiceras*) cf. *asiaticum hunteri* (Kossmat, 1897)

Fig. 45

Compare:

- 1897 *Acanthoceras Hunteri* Kossmat, p. 9 (116), pl. 3 (14), fig. 4.
- 1972 *Newboldiceras* (*Newboldiceras*) *newboldi* (Kossmat); Thomel, p. 106 (*pars*), pl. 34, figs 1–3; pl. 38, figs 1, 2; pl. 39, figs 1–3; pl. 41; *non* pl. 40, pl. 42, figs 3, 4.

1990 *Calycoceras* (*Newboldiceras*) cf. *asiaticum hunteri* (Kossmat, 1897); Wright & Kennedy, p. 251, text-figs 90g, h; 103; 104; 110b.

Types

The lectotype, by the subsequent designation of Wright & Kennedy, 1990, p. 251, is the original of Kossmat (1897, p. 9 (116), pl. 3 (14), fig. 4), no. 1489 in the collections of the Geological Survey of India, from the Utatur Group of Odium, south India. A cast was figured by Wright & Kennedy (1990, text-fig. 103). The second specimen mentioned by Kossmat is a paralectotype.

Material

SAM PCZ13449; OUM KX4622.

Description

SAM-PCZ13449 (Fig. 45) is an internal mould of a 120° sector of phragmocone with a maximum preserved whorl height of 67.4 mm, corresponding to an original estimated diameter of 170 mm. It retains traces of limonitized test. Coiling is moderately evolute, the umbilicus of moderate depth, with a flattened wall and broadly rounded umbilical shoulder. The whorl breadth to height ratio is 1.1, the greatest breadth below mid-flank, the inner to middle flanks broadly rounded, the outer flanks convergent, the ventrolateral shoulders broadly rounded, and the broad venter very feebly convex. Four coarse umbilical bullae perch on the umbilical shoulder and give rise to one or two coarse, straight, prorsiradiate primary ribs. One or two non-bullate long ribs or short ribs intercalate between the bullate primaries. The ribs flex slightly forwards and are very feebly concave on the ventrolateral shoulder, where feeble angulations mark the site of inner and outer ventrolateral tubercles, largely assimilated into the ribs at this diameter. The ribs are strong, coarse, and very feebly convex across the venter. Traces of the suture line are visible, with a large asymmetrically bifid E/A.

OUM KX4622 is a very worn but comparable fragment of phragmocone with a maximum preserved whorl height of 75 mm, with a total of 12 ribs at the ventrolateral shoulder.

Discussion

Ribbing style and effacement of ventrolateral tuberculation separate this specimen from *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* and *C. (N.) asiaticum spinosum*. The fragment compares well with a cast of the holotype of *hunteri* before us.

Occurrence

The present material is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Calycoceras (*Newboldiceras*) *planecostatum* (Kossmat, 1897)

Figs 34D, G, H, 35K, L, P, Q, 44F, G, 46–54, 56A–K, 57H, 61A, B

1897 *Acanthoceras Newboldi* var. *planecostata* Kossmat, p. 9(116), pl. 2(13), fig. 1.

1907 *Acanthoceras Newboldi* var. *planicostata* F. Kossmat; Crick, p. 201.

1907 *Acanthoceras choffati* F. Kossmat; Crick, p. 205, pl. 12, fig. 5.

1978 *Calycoceras newboldi-choffati* Crick (*non* Kossmat); Kennedy, pl. 4, figs 1–3 only.

1990 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Wright & Kennedy, p. 252, pl. 61, figs 2, 3; pl. 67, figs 1–4; text-figs 101c–e (with full synonymy).

1994 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Kennedy, p. 228, pl. 10, figs 2, 3.

1994 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Kennedy & Juignet, p. 50, text-figs 1c; 18a–c; 19a–c.

1996 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Kennedy, Bilotte & Hansotte, p. 314, pl. 40, fig. 3.

1998 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Kaplan, Kennedy, Lehmann & Marcinowski, p. 158, pl. 26, figs 9–11.

2004 *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897); Kennedy & Jolkičev, p. 376, pl. 3, figs 2–6, 8, 9.

Type

Lectotype, by the subsequent designation of Wright & Kennedy (1990, p. 252), is no. 14842 in the Collections of the Geological Survey of India, the original of Kossmat (1897, pl. 2(13), fig. 1), from the Utatur Group of Odium, south India. A cast is illustrated here as Fig. 54.

Material

SAM-PCZ13430, 13432, 13434–6, 13438–40, 13443, 13444, 1345–4, 13467, 13475, 13480–81, 13483, 1348–7, 13449, 13453, 13465 OUM KX4589, 4595, 4597, 4598, 4602, 4603, 4610, 4612, 4615. BMNH C18208–9, the originals of *Acanthoceras newboldi* var. *planicostata* of Crick, 1907, p. 201. BMNH C18215–18228 the originals of *Acanthoceras choffati* of Crick, 1907 (p. 205, pl. 12, fig. 5).

Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ13454	29.4 (100)	16.1 (54.8)	14.7 (50.00)	1.1	16.9 (23.5)
PCZ13432	40.3 (100)	21.1 (52.4)	19.4 (48.1)	1.1	9.9 (24.6)
PCZ13434	48.0 (100)	20.1 (41.8)	21.9 (45.6)	0.92	12.2 (25.4)
PCZ13435	48.4 (100)	22.6 (46.7)	21.1 (43.5)	1.1	12.9 (25.3)
PCZ13487	51.0 (100)	27.6 (54.1)	23.7 (46.5)	1.16	12.9 (25.3)
PCZ13440	55.6 (100)	21.7 (39.0)	26.4 (47.5)	0.82	14.8 (26.6)
PCZ13467	65.3 (100)	29.6 (45.3)	29.0 (44.4)	1.0	17.2 (26.30)
PCZ13436	64.4 (100)	31.4 (48.8)	30.5 (47.4)	1.0	15.6 (24.2)
PCZ13488	74.3 (100)	31.9 (42.9)	33.0 (44.4)	0.96	20.5 (27.50)
PCZ13442	81.4 (100)	32.6 (39.8)	34. (41.8)	0.96	20.9 (25.7)

PCZ13443	92.9 (100)	44.8 (48.4)	40.0 (43.1)	1.1	27.0 (29.0)
PCZ13465	128.0 (100)	64.7 (50.5)	61.0 (47.7)	1.1	33.9 (26.5)

Description

Well-preserved phragmocones vary from 29.4–128 mm in diameter. Coiling is involute, with around 40% of the previous whorl covered, the umbilicus comprising 24–29% of the diameter, and of moderate depth, with a feebly convex vertical wall and narrowly rounded umbilical shoulder. The whorl section varies from slightly compressed to slightly depressed, with whorl breadth to height ratios that range from 0.82 (SAM-PCZ13430: Fig. 49D, F) to 1.2 (SAM-PCZ13487). The flanks are very feebly convex and parallel, the ventrolateral shoulders broadly rounded, the relatively broad venter very feebly convex. There are 37–44 ribs per whorl. Primary ribs arise at the umbilical seam, and sweep back, strengthen progressively, and are concave across the umbilical wall and shoulder, developing into a weak to moderately strong concave umbilical bulla. Successive primary ribs are separated by up to three intercalated ribs that arise at various levels from innermost to outer flank. The ribs are prorsiradiate and straight to feebly flexuous, strengthening progressively across the flanks. The smallest specimens (e.g. SAM-PCZ13454; Fig. 47A–C) have a feeble inner ventrolateral tubercle, lost beyond a diameter of 26 mm in this specimen, linked by a progressively broadening rib to a small outer ventrolateral clavus. The clavi are linked across the venter by a broad, flattened, feebly convex transverse rib that bears a weak siphonal clavus. The outer ventrolateral clavi persist to the greatest preserved diameter in these nuclei, but the siphonal clavi are lost at diameters of 38 mm or less. As size increases the crowded ribs may flatten markedly on the outer flanks and venter, producing the distinctive ventral ornament that characterizes the species. The overwhelming majority of specimens retain recrystallized shell. The suture is partially exposed in SAM-PCZ13435; E/A is broad and moderately incised, A is narrow, and A/U₂ broad with minor incisions.

Discussion

The holotype, is a phragmocone, a cast of which is illustrated here as Fig. 54, falls at the inflated end of the variable KwaZulu assemblage, corresponding closely with specimens such as SAM-PCZ13475 (Fig. 55), 13481 (Fig. 47K–M) and 13483 (Fig. 49A, B). The dimensions of the cast of the holotype are: D = 114 (100); Wb = 52.5 (46.0); Wh = 52.6 (46.00 Wb:Wh = 1.0; U = 30.0 (26.3). The adapertural end of the specimen was crushed, and the whorl breadth to height ratio where undeformed is up to 1.1. The coiling is slightly involute, with 67% of the previous whorl covered, the umbilical wall convex and undercut, the umbilical shoulder more narrowly rounded. Nineteen to twenty primary ribs arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and develop into weak, feebly concave umbilical bullae. These give rise to one or very occasionally two ribs, with single intercalated ribs between that arise at or below mid-flank to give a total of 36 ribs at the ventrolateral shoulder on the outer whorl. The ribs are low, crowded, and broaden across the flanks. They are concave on the inner-

most flank, straight and prorsiradiate on the inner flank, flex back and are very feebly convex at mid-flank, and feebly concave on the outermost flank and ventrolateral shoulder, where they broaden markedly, and link to feeble outer ventrolateral clavi. A low, broad, feebly convex rib links the clavi across the broad, feebly convex venter. The ribs become broad, flat-topped, and ribbon-like on the adapertural half of the outer whorl.

Crick (1907, p. 205, pl. 12, fig. 5) referred a series of 13 specimens (BMNH C18215–18228) to *Acanthoceras choffati* Kossmat, 1897 (p. 12 (119), pl. 15 (4), fig. 1). A number of Crick's specimens are illustrated here (Figs 34D, G–I, 46 A–P, 56 A–K, 57 H). Wright & Kennedy (1990, p. 252) treated these specimens as variants of *planecostatum*, and regarded *choffati* of Kossmat as a separate species, which they referred to *Proeucalycoceras* (p. 221, explanation of fig. 87). A cast of the holotype of *choffati* is illustrated here as Fig. 55. The dimensions are as follows: D = 78.9 (100); Wb = 33.5 (42.5); Wh = 38.3 (48.5); Wb:Wh = 0.87; U = 16.1 (20.4). The cast reveals the original to be an internal mould, with traces of shell preserved, the sutures approximated and interfering, indicating the specimen to be an adult. The adapical 180° sector of the outer whorl is body chamber. On the phragmocone coiling is slightly involute, with 66% of the previous whorl covered, the umbilical wall undercut, feebly convex to flattened, the umbilical shoulder quite narrowly rounded. The whorl section is compressed, with feebly convex, subparallel inner and middle flanks, convergent outer flanks, broadly rounded ventrolateral shoulders and a feebly convex venter in intercostal section. The penultimate whorl shows small elongate prorsiradiate umbilical bullae that give rise to narrow, crowded primary ribs, either singly or in pairs, with up to three long or short ribs intercalated between. On the outer whorl, an estimated 20 umbilical bullae of variable strength perch on the umbilical shoulder. They give rise to one or two ribs, with up to three long or short intercalated ribs separating the bullate ones. The ribs are narrow, crowded, prorsiradiate and very feebly flexuous, strengthening progressively across the flanks, feebly concave on the outermost flank and broadly convex across the ventrolateral shoulders and venter. There are small outer ventrolateral clavi at the adapical end of the outer whorl, connected across the venter by a broad, flattened, ribbon-like rib, with a very feeble siphonal clavus. The siphonal clavi are rapidly lost, the outer ventrolateral clavi weaken, and are replaced by mere angulations on the adapertural end of the body chamber. At the adapertural end of the body chamber the venter and ventrolateral shoulders are rounded, the angulation lost.

The ornament of the phragmocone of the holotype of *choffati* differs in no significant respects from that of compressed variants of *planecostatum* in the present assemblage such as SAM-PCZ 13434 (Fig. 47D, E), 13452 (Fig. 48D, E), and 13480 (Fig. 50H–J). It may well be that *choffati* is no more than a microconch of *planecostatum*, but conclusive evidence is lacking at this time.

Occurrence

Upper Middle and lower Upper Cenomanian, south India, Morocco, Madagascar, KwaZulu, James Ross Island, Antarctica, Iran, Bulgaria, France, Germany and southern

England. The present material is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

***Calycoceras (Newboldiceras) laticostatum* (Crick, 1907)**

Figs 56L, M, 57G, J, K

1907 *Acanthoceras laticostatum* Crick, p. 201.

1978 *Calycoceras* group of *naviculare* (Mantell); Kennedy, pl. 4, fig. 8.

Type

The holotype is BMNH C18210, the original of Crick, 1907, p. 201.

Material

An unregistered specimen in the M.R. Cooper Collection, housed in the Department of Geology and Applied Geology of the University of KwaZulu-Natal (Fig. 57G, J, K) may also belong here.

Description

What may be an early growth stage of this species is represented by a 93 mm diameter phragmocone in the collections of the University of KwaZulu-Natal, Durban (Fig. 57G, J, K). The whorl section is depressed, the greatest breadth below mid-flank. The inner flanks are broadly rounded, the outer flanks convex and convergent. The broad venter is feebly convex. Primary ribs arise from well-developed umbilical bullae, and are separated by one or two intercalated ribs. The ribs are prorsiradial, straight on the inner and middle flanks and feebly concave on the outermost flank. Low, coarse, and rounded, they broaden progressively across the flanks. All ribs bear feebly clavate outer ventrolateral tubercles, and there are feeble indications of inner ventrolateral tubercles on some ribs. The ribs are low, broad, and wider than the interspaces on the venter. There are no siphonal tubercles.

The holotype (Fig. 56L, M) is a 150 mm long phragmocone fragment retaining extensive areas of recrystallized shell. A detached fragment reveals the feebly convex venter of the penultimate whorl. It bears broad flattened ribs separated by narrower interspaces, with outer ventrolateral clavi, as in the specimen described above. The outer whorl fragment lacks most of one flank. The whorl section appears to have been depressed reniform in intercostal section, with the greatest breadth just outside the umbilical shoulder. The umbilical wall and shoulder are broadly rounded, the flanks converging to the feebly convex venter. There are three primary ribs on the fragment. They arise at the umbilical seam, sweep back are straight and across the umbilical wall, strengthening into coarse bullae on the umbilical shoulder. The primary ribs are coarse, broad, flattened and prorsiradial on the flanks, across which they broaden progressively, and link to coarse inner ventrolateral clavi. A low broad prorsiradial rib links these to somewhat weaker outer ventrolateral clavi that are in turn linked across the venter by a broad, ribbon-like transverse rib. Single intercalated ribs arise low on the flanks, and have a ventrolateral and ventral development comparable to that of the primary ribs.

Discussion

Calycoceras (Newboldiceras) laticostatum is most closely allied to *C. (N.) planecostatum*, from which the present material differs in the much more inflated whorl section, apparently late appearance and persistence of the inner ventrolateral tubercles, and the very coarse ribbing. Coarse ribbing characterizes *Calycoceras (Proeucalyoceras) picteti* Wright & Kennedy, 1990 (p. 264, pl. 58, fig. 2; pl. 64, fig. 4; pl. 68, figs 1, 2; pl. 74, fig. 3; pl. 74, figs 2–6; text-figs 110d, g; 113, 114, 116a–d; 117; 119a–c), but here the ribs of the adult whorls are narrower, with wide interspaces, early loss of inner ventrolateral tubercles, and a flat venter (Wright & Kennedy 1990, text-fig. 113).

Occurrence

The present material is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Calycoceras (Newboldiceras) breistrofferi

(Collignon, 1937)

Figs 58–60, 61C–E, 62

1937 *Acanthoceras breistrofferi* Collignon, p. 38, pl. 6, fig. 4; pl. 9, fig. 2.

non 1964 *Acanthoceras breistrofferi* Collignon; Collignon, p. 140, pl. 371, fig. 1616.

Type

The holotype, by monotypy, is the original of *Acanthoceras breistrofferi* Collignon, 1937, p. 38, pl. 6, fig. 4; pl. 9, fig. 2, from the Cenomanian of Ankomaka, Madagascar (Fig. 58).

Material

SAM-PCZ13445, 13450, 13453, 13457, 13461.

Dimensions

	D	Wb	Wh	Wb:Wh	U
Holotype	119 (100)	53.5 (44.9)	42.1 (35.3)	1.27	38.0 (31.9)
PCZ13453	118 (100)	56.9 (48.2)	48.0 (40.7)	1.18	32.2 (27.3)

Description

The holotype (Fig. 58) is an internal mould of a phragmocone 119 mm in diameter. Coiling is very evolute, with 36% of the previous whorl covered; the relatively deep umbilicus comprises 31.9% of the diameter. The umbilical wall is flattened, the umbilical shoulder broadly rounded, the whorl section trapezoidal, the whorl breadth to height ratio 1.27, the greatest breadth close to the umbilical shoulder. The venter is broad, and very feebly convex. An estimated 18 primary ribs arise at the umbilical seam and strengthen across the umbilical wall, developing into sharp umbilical tubercles. Additional non-bullate primaries and short intercalated ribs give a total of an estimated 50 ribs per whorl at the ventrolateral shoulder. The ribs are strong, straight, sharp, and narrower than the interspaces. They broaden and strengthen across the flanks, project slightly forwards across the ventrolateral shoulders and cross the venter near

straight to feebly convex. There are indications of ventrolateral tubercles at the adapical end of the outer whorl, but these efface, and are replaced by a mere angulation in the rib profile.

SAM-PCZ13457 (Fig. 59) is a phragmocone 95 mm in diameter, with recrystallized shell preserved. Coiling is moderately evolute, the deep umbilicus comprising 26% of the diameter, with a feebly convex, outward-inclined wall and broadly rounded umbilical shoulder. The specimen has suffered postmortem crushing, and the original whorl section cannot be established. It appears to have been depressed, with feebly convex subparallel flanks, broadly rounded ventrolateral shoulders, and a broad, feebly convex venter. Parts of the penultimate whorl show primary ribs that arise at the umbilical seam, strengthen across the umbilical wall, and develop into strong spinose umbilical tubercles. There are 11 primary ribs on the adapical half of the outer whorl. They arise at the umbilical seam, and are strong and straight on the umbilical wall and shoulder, where they develop into prominent, sharp, subspinose umbilical tubercles, from which single narrow, strong, prorsiradiate ribs arise and pass straight across the inner and middle flanks, flexing slightly forwards to become very feebly concave on the outermost flank and ventrolateral shoulder. They are near straight to very feebly convex across the venter. Single ribs intercalate between successive primaries. They arise below mid-flank, and strengthen to match the primaries on the outer flanks, ventrolateral shoulders, and venter. The ventral region of the adapical part of the outer whorl is damaged, but there are indications of small inner and outer ventrolateral and siphonal tubercles that are progressively lost, and are absent from the adapertural half of the outer whorl.

SAM-PCZ13453 (Fig. 60) is a half whorl of phragmocone with a maximum preserved diameter of 118 mm, and indications of the former presence of a further whorl. Coiling is moderately evolute on the outer whorl, the umbilicus deep, with broadly convex outward-inclined wall and broadly rounded umbilical shoulder. The whorl section is depressed, rounded-trapezoidal with feebly convex converging flanks, broadly rounded ventrolateral shoulders and a very broad, convex venter. Eight primary ribs arise at the umbilical seam, sweep back and strengthen across the umbilical wall, developing into a weak umbilical bulla, perched on the umbilical shoulder. The bullae give rise to single ribs at the adapical end of the fragment; the two adapertural bullae give rise to pairs of ribs. Long single ribs, arising below mid-flank, intercalate between the single primaries. The ribs strengthen progressively and are prorsiradiate and very feebly flexuous across the flanks, flex forwards and broaden across the ventrolateral shoulders, and are low and feebly convex across the venter. There are no detectable tubercles on the ventrolateral shoulders and venter, or on the impression of the previous whorl preserved in the dorsal impressed zone of the outer whorl. By contrast, the dorsal impressed zone of the penultimate whorl records impressions of outer ventrolateral and siphonal tubercles at small diameters.

SAM-PCZ13461 (Fig. 61C–E) is a 120° sector of phragmocone with a 180° sector of the penultimate whorl preserved to a maximum whorl height of 25.4 mm, with a whorl breadth to height ratio of 1.19. The coiling is moderately evolute, the

umbilical wall high, with a feebly convex, outward-inclined wall. The flanks are feebly convex and subparallel, the ventrolateral shoulders broadly rounded, and the very broad venter feebly convex. There are eight primary ribs on the fragment. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, where they develop into sharp bullae. These give rise to narrow straight primary ribs, separated by single shorter intercalated ribs, giving a total of 18 ribs on the outer flank of the penultimate whorl fragment. An examination of the fractured section gives no indication of ventrolateral or siphonal tubercles. The outer whorl of this fragment has a maximum preserved whorl height of 59.7 mm., with a whorl breadth to height ratio of 1.17. Nine primary ribs arise at the umbilical seam and strengthen across the umbilical wall and shoulder, developing into a sharp umbilical bulla. The ribs become progressively more widely spaced as size increases. The ribs are coarse, straight, and rectiradiate, and strengthen progressively across the flanks, ventrolateral shoulders and venter. They cross the venter in a broad convexity at the adapical end of the fragment, and are near transverse at the adapertural end. Single intercalated ribs separate the primaries at the adapical end; all the ribs are primaries at the adapertural end. There are thus nine ribs at the umbilical shoulder and 12 at the ventrolateral shoulder of the fragment.

SAM-PCZ13445 (Fig. 62A, B) is a 90° sector of phragmocone with a maximum preserved whorl height of 55.8 mm, and a whorl breadth to height ratio of 1.20, bearing four widely separated primary ribs. It differs in no significant respects from the preceding specimen.

SAM-PCZ13450 (Fig. 62C, D) is a large phragmocone fragment with a maximum preserved whorl height of 64.2 mm., and whorl breadth to height ratio of 1.2, the whorl section depressed reniform. Four primary ribs are preserved on the fragment, and bear strong, sharp umbilical bullae. The ribs are straight and rectiradiate on the flanks, and strengthen progressively across flanks, ventrolateral shoulders and venter, where they are very widely separated, strong, and coarse.

The poorly exposed suture of SAM-PCZ13445 has a large, deeply incised bifid E/A, a narrow, bifid A, and a smaller U₂.

Discussion

Calycoceras (N.) *breistrofferi* differs from other *Newboldiceras* in the present collections in the early loss of all but the umbilical tuberculation, and the change from closely spaced to very widely separated ribbing at the largest preserved diameters. Large size and widely spaced ribbing at large diameters separate it from *Calycoceras* (*Gentoniceras*) species.

The distinctive change in rib spacing is also seen in *C.* (N.) *tunetanum* (Pervinquière, 1907) (p. 268, pl. 13, fig. 4; Wright & Kennedy 1990, p. 251, pl. 69, fig. 2; text-figs 105, 106, 107m, 110f; 1996, p. 401, pl. 124, fig. 1), but in that species the inner ventrolateral tubercles persists to maturity, and a size where they are lost in *breistrofferi*.

The *Acanthoceras breistrofferi* of Collignon (1964, p. 140, pl. 371, fig. 1616) appears to have inner and outer ventrolateral tubercles to a diameter of over 90 mm. We are uncertain of its affinities.

Occurrence

Ankomaka, Madagascar, and the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289).

Genus *Pseudocalycoceras* Thomel, 1969

Type species

Ammonites harpax Stoliczka, 1864, p. 72, pl. 39, fig. 1, 2, by the original designation of Thomel, 1969, p. 650.

Diagnosis

'Whorl section slightly compressed to slightly depressed. Ribs flexuous to convex and rursiradiate, more or less regularly branching or alternately long and short, the primaries with umbilical bullae, characteristically twisted, and all ribs with inner ventrolateral nodate or clavate and outer ventrolateral and siphonal clavate tubercles. In some species one or two weak lateral tubercles may appear on primary ribs. Near the aperture the ribs narrow and approximate and the tubercles disappear (Wright & Kennedy 1981, p. 36).

Occurrence

Lower and middle Upper Cenomanian, England, France, Spain, Romania, Algeria, Tunisia, Israel, Lebanon, Angola, KwaZulu, Madagascar, south India, central and west Texas, New Mexico and the U.S. Western Interior.

Pseudocalycoceras harpax (Stoliczka, 1864)

Fig. 63

- 1864 *Ammonites harpax* Stoliczka, p. 72 (*pars*), pl. 39, fig. 1 only.
- 1864 *Ammonites morpheus* Stoliczka, p. 80, pl. 38, fig. 1.
- 1897 *Acanthoceras harpax* (Stoliczka); Kossmat, p. 13 (120), pl. 4 (15).
- non 1920 *Acanthoceras harpax* Taubenhau, p. 16, figs 1, 2; pl. 5, fig. 6.
- 1931 *Acanthoceras harpax* (Stoliczka); Basse, p. 38, pl. 5, figs 17, 18.
- 1937 *Protacanthoceras harpax* Stol.; Collignon, p. 32, pl. 1, figs 1–4, pl. 8, figs 1, 2, including varieties *ramondaensis*, *ankomakaensis*, and *tulearensis*.
- non 1940 *Calycoceras harpax* Stol.; Basse, p. 451.
- non 1962 *Calycoceras harpax* (Stol.); Avnimelech & Shores, p. 532.
- 1964 *Protacanthoceras harpax* Stol.; Collignon, p. 145, pl. 373, fig. 1620.
- 1964 *Protacanthoceras harpax* Stol. var. *ankomakaensis* Coll.; Collignon, p. 145, pl. 373, fig. 1621.
- 1964 *Protacanthoceras harpax* Stol. var. *talinoensis* Coll.; Collignon, p. 145, pl. 373, fig. 1622.
- non 1966 *Eucalycoceras harpax* (Stol.) var. *lattensis* Thomel, p. 429, pl. 10, figs 1, 2 (= *Thomelites sornayi* (Thomel, 1966)).
- non 1966 *Eucalycoceras harpax* (Stol.) var. *tulearensis* (Coll.); Thomel, p. 429, pl. 9, figs 1–3 (= *Thomelites sornayi* (Thomel, 1966)).
- 1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax* (Stoliczka); Thomel, p. 88.

non 1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax tulearensis* (Collignon); Thomel, p. 89 (= *Thomelites sornayi* (Thomel, 1966)).

non 1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax lattense* (Thomel); Thomel, p. 89, pl. 32, figs 1, 2 (= *Thomelites sornayi* (Thomel, 1966)).

non 1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax moustierensis* Thomel, p. 90, pl. 31, figs 4, 5 (= *Thomelites sornayi* (Thomel, 1966)).

non 1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *morpheus* (Stoliczka); Thomel, p. 91, pl. 32, figs 3, 4.

1972 *Pseudocalycoceras* (*Pseudocalycoceras*) *harpax talinoensis* (Collignon); Thomel, p. 90, pl. 29, fig. 3.

1975 *Pseudocalycoceras harpax* (Stoliczka); Matsumoto, in Matsumoto & Kawano, p. 8, text-fig. 1.

1975 *Pseudocalycoceras morpheus* (Stoliczka); Matsumoto in Matsumoto & Kawano, p. 10, text-fig. 2.

1981 *Pseudocalycoceras harpax* (Stoliczka, 1864); Wright & Kennedy, p. 36, text-fig. 14a, b.

1996 *Pseudocalycoceras harpax* (Stoliczka); Wright, p. 164, text-fig. 123, 5.

Name of the species

We regard *Ammonites morpheus* Stoliczka, 1864 (p. 80, pl. 38, fig. 1), as a pathological individual, and a variant of *harpax*; as first revising authors we select the name *harpax* for the species.

Type

The lectotype, by the subsequent designation of Matsumoto in Matsumoto & Kawano, 1975, p. 8, is no. 169 in the collections of the Geological Survey of India, a cast of which was figured by Wright & Kennedy, 1981, text-fig. 14a, b.

Material

SAM-PCZ22194 (SAM A640).

Description

The specimen (Fig. 63) is an internal mould of a 180° sector of body chamber with a maximum preserved diameter of 55.8 mm. Coiling is moderately evolute, the shallow umbilicus comprising an estimated 30% of the diameter. The umbilical wall is flattened and subvertical, the umbilical shoulder narrowly rounded. The whorl section is compressed, with a costal whorl breadth to height ratio of 0.8, the greatest breadth at the umbilical bullae. The inner to middle flanks are flattened and subparallel, the outer flanks converging to the broadly rounded ventrolateral shoulders and feebly convex venter. There are eight primary ribs on the fragment. They arise at the umbilical seam, and are well developed on the umbilical wall and shoulder, where they develop into a prominent prorsiradiate umbilical bulla. These give rise to a single rib, with one or two longer short ribs intercalated between successive primaries to give a total of 18 ribs on the fragment. The ribs are prorsiradiate on the inner flank, flex back and are convex on the middle to outer flank, linking to rounded inner ventrolateral tubercles. A broadening rib sweeps forwards over the ventrolateral shoulder and passes straight across the venter and links to well-developed equal outer ventrolateral and siphonal clavi.

Discussion

The fragment compares well with material from south India of comparable size that we have studied. The species most closely resembles *Pseudocalycoceras angolaense* (Spath, 1931) (p. 316) (see revisions in Kennedy, 1988, p. 42, pl. 4, figs 1, 2, 6–9; pl. 5, figs 1–12; pl. 8, figs 7, 8; pl. 22, figs 8, 9; text-figs 10h, 11b, e, and Cobban, Hook & Kennedy, 1989, p. 29, figs 29, 73e–o, 74a–g). In their discussion of differences from *Pseudocalycoceras dentonense* (Moreman, 1942) (here regarded as a synonym of *angolaense*), Wright & Kennedy (1981, p. 38) noted the more narrowly arched venter of *harpax*, the five rows of ventrolateral and ventral tubercles more closely approximated, higher and sharper ribbing on the body chamber, and traces of lateral tubercles on primary ribs. *Pseudocalycoceras alaouitense* (Basse, 1940) (p. 419, pl. 8, figs 1, 4, 5) and *paralaouitense* (Basse, 1940) (p. 449, pl. 7, fig. 4; pl. 8, fig. 2; pl. 9, fig. 3) have as few as 12–16 strongly convex rursiradiate, predominantly primary ribs on what appear to be an adult microconch (Basse 1940, pl. 8, fig. 3) and macroconch (Basse 1940, pl. 8, fig. 6) body chamber.

Occurrence

Where well dated, the species is lower Upper Cenomanian. The geographic distribution is southeast France, Morocco, south India, KwaZulu, and Madagascar. The present specimen is from the Middle Cenomanian (or lower Upper Cenomanian?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289)

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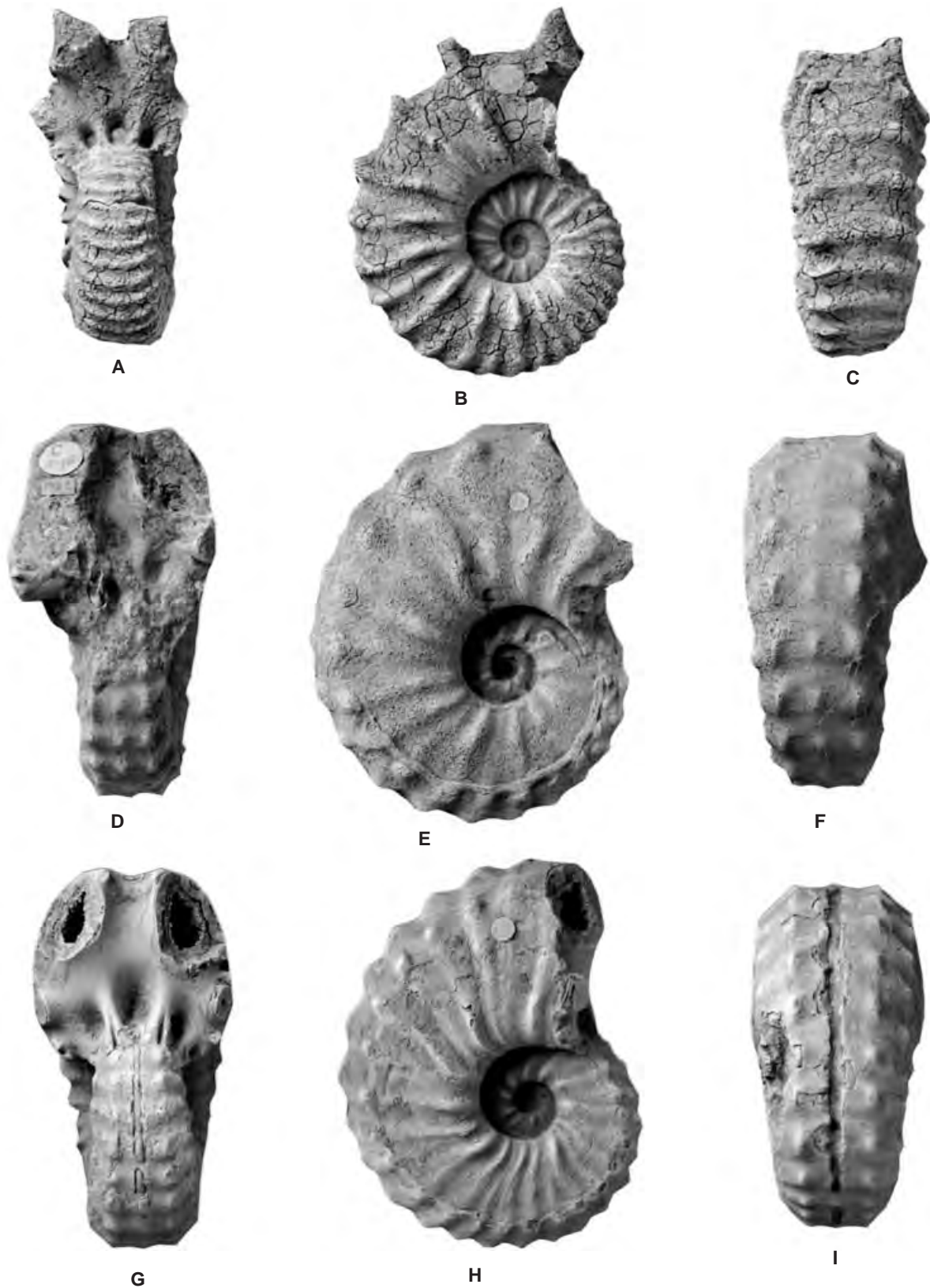


Fig. 1. A–C, *Acanthoceras cornigerum* Crick, 1907. The holotype, BMNH C18230, the original of Crick, 1907, pl. 13, fig. 1. D–I, *Acanthoceras flexuosum* Crick, 1907; D–F, BMNH C18175, the holotype of *Acanthoceras crassiornatum* Crick, 1907, p. 185; G–I, BMNH C18174, the holotype of *Acanthoceras flexuosum* Crick, 1907, pl. 12, fig. 1. All specimens are from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 0.90$.

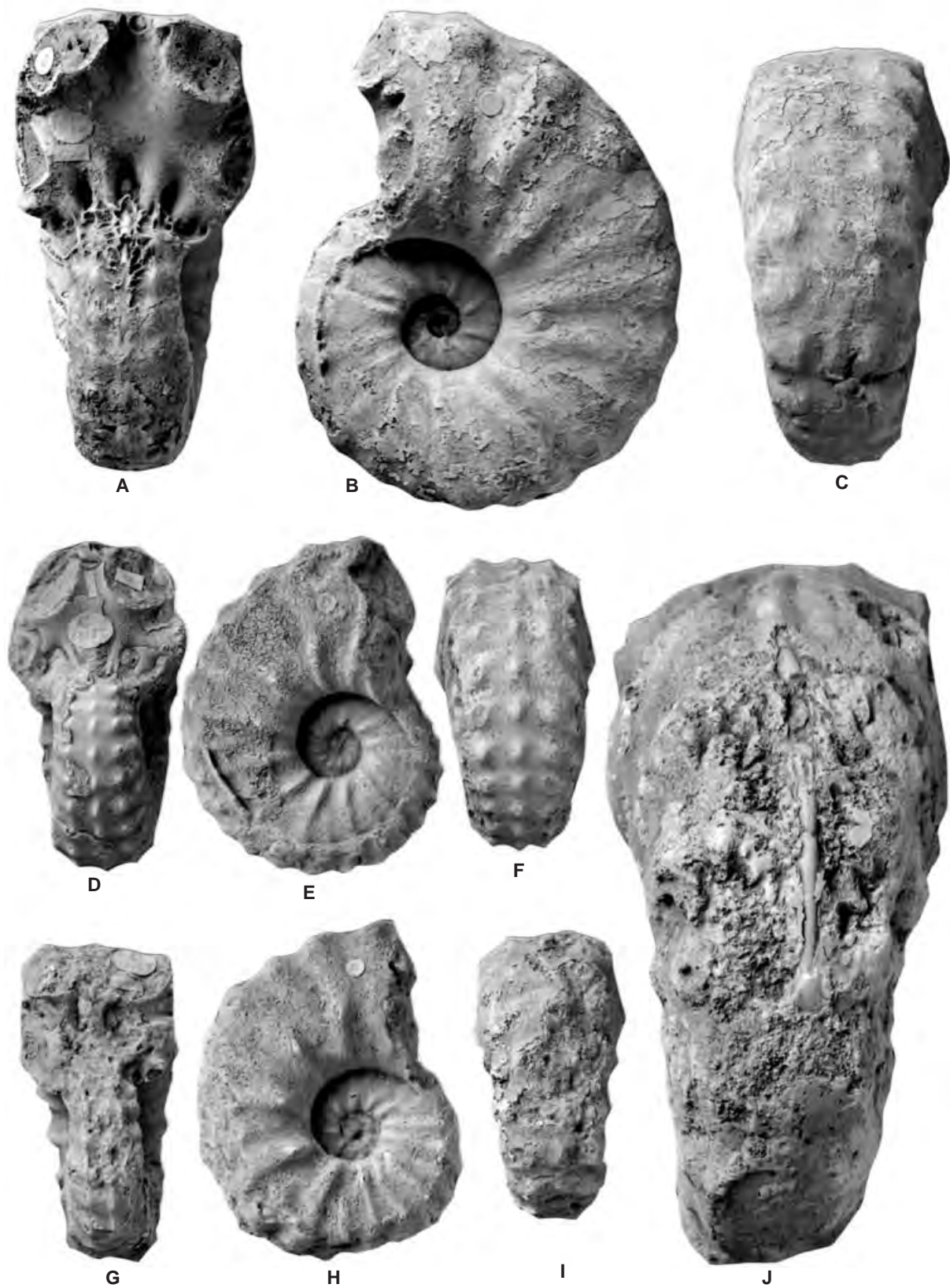


Fig. 2. A–J, *Acanthoceras flexuosum* Crick, 1907. A–C, BMNH C18189, the lectotype of *Acanthoceras robustum* Crick, 1907, p. 189; D–F, BMNH C18182, the lectotype of *Acanthoceras munitum* Crick, 1907, p. 187; G–I, BMMH C18187, the holotype of *Acanthoceras expansum* Crick, 1907, p. 188; J, BMNH C18188, a paralectotype of *Acanthoceras robustum* Crick, 1907. All specimens are from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 0.90$.



Fig. 3. BMNH C18188, a paralectotype of *Acanthoceras robustum* Crick, 1907, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are x1.



Fig. 4. *Acanthoceras flexuosum* Crick, 1907. BMNH C18194, the lectotype of *Acanthoceras quadratum* Crick, 1907, the original of Crick, 1907, pl. 13, fig. 2, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 5. *Acanthoceras flexuosum* Crick, 1907. BMNH C18197, the holotype of *Acanthoceras latum* Crick, 1907, the original of Crick, 1907, pl. 12, fig. 2, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 6. *Acanthoceras flexuosum* Crick, 1907. BMNH C18193, the original of *Acanthoceras* sp. of Crick, 107, p. 191, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.

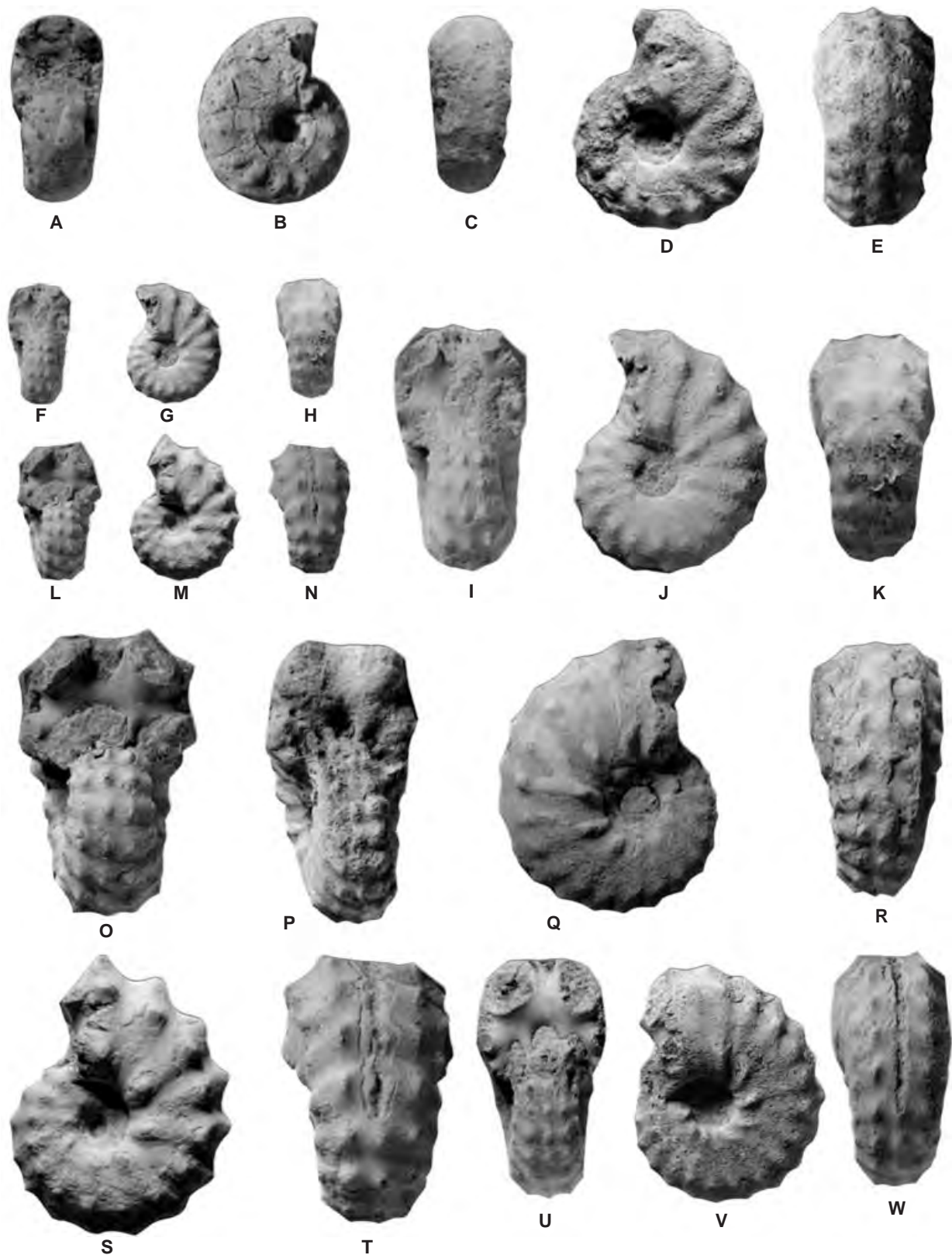


Fig. 7. A–W, *Acanthoceras flexuosum* Crick, 1907. A–C, SAM-PCZ13524; D–E, SAM-PCZ13474; F–K, SAM-PCZ13503; L–N, O, S, T, SAM-PCZ13524; P–R, SAM-PCZ13490; U–W, SAM-PCZ13459, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–E are $\times 3.6$; F–H, L–N, P–R, U–W are $\times 0.90$; I–K, O, S, T, are $\times 1.8$.

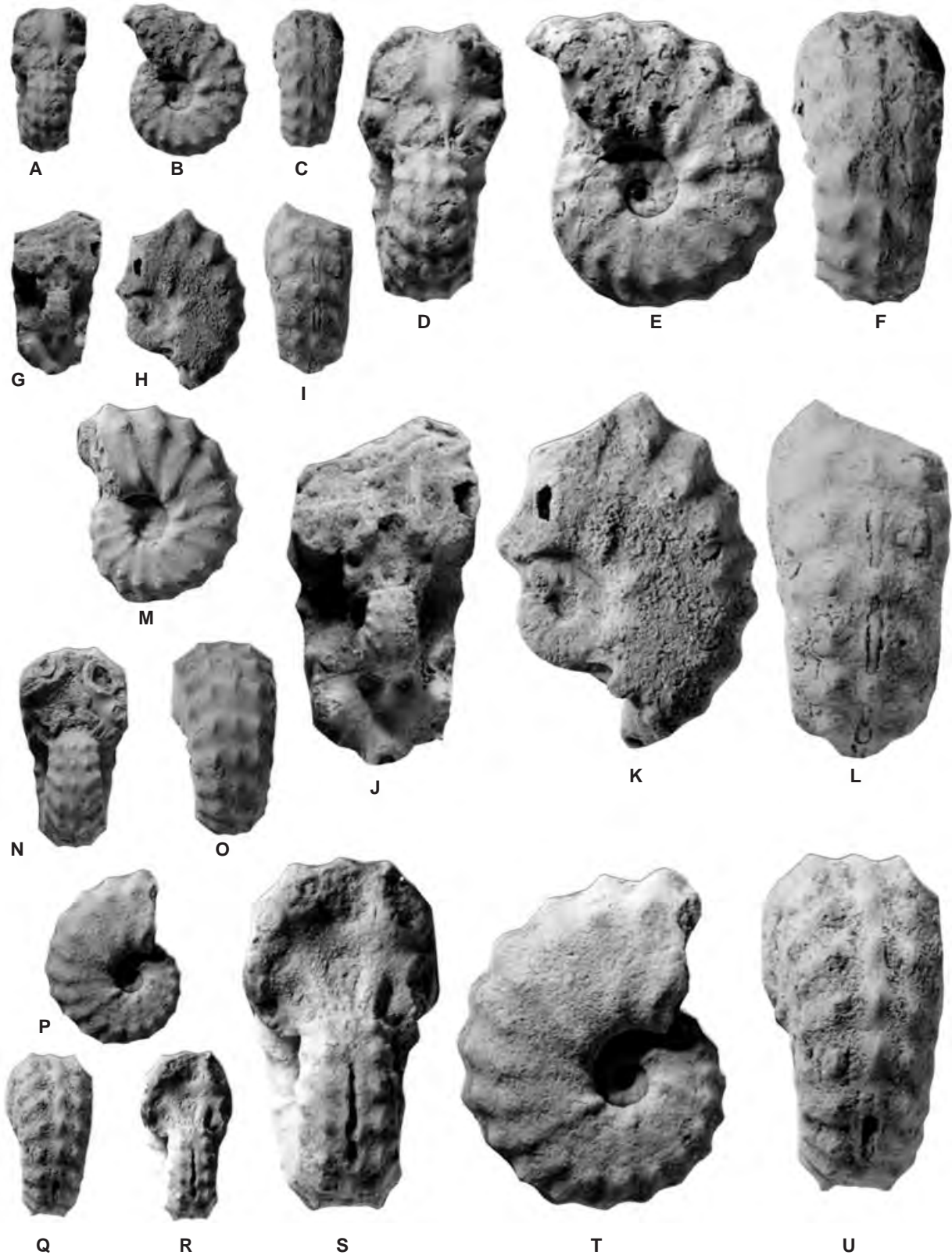


Fig. 8. A–U, *Acanthoceras flexuosum* Crick, 1907. A–F, SAM-PCZ13501; G–L, SAM-PCZ13515; M–O, SAM-PCZ13525; P–U, SAM-PCZ13507, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–C, G–I, M–R are $\times 0.90$; D–F, J–L, S–U are $\times 1.8$.

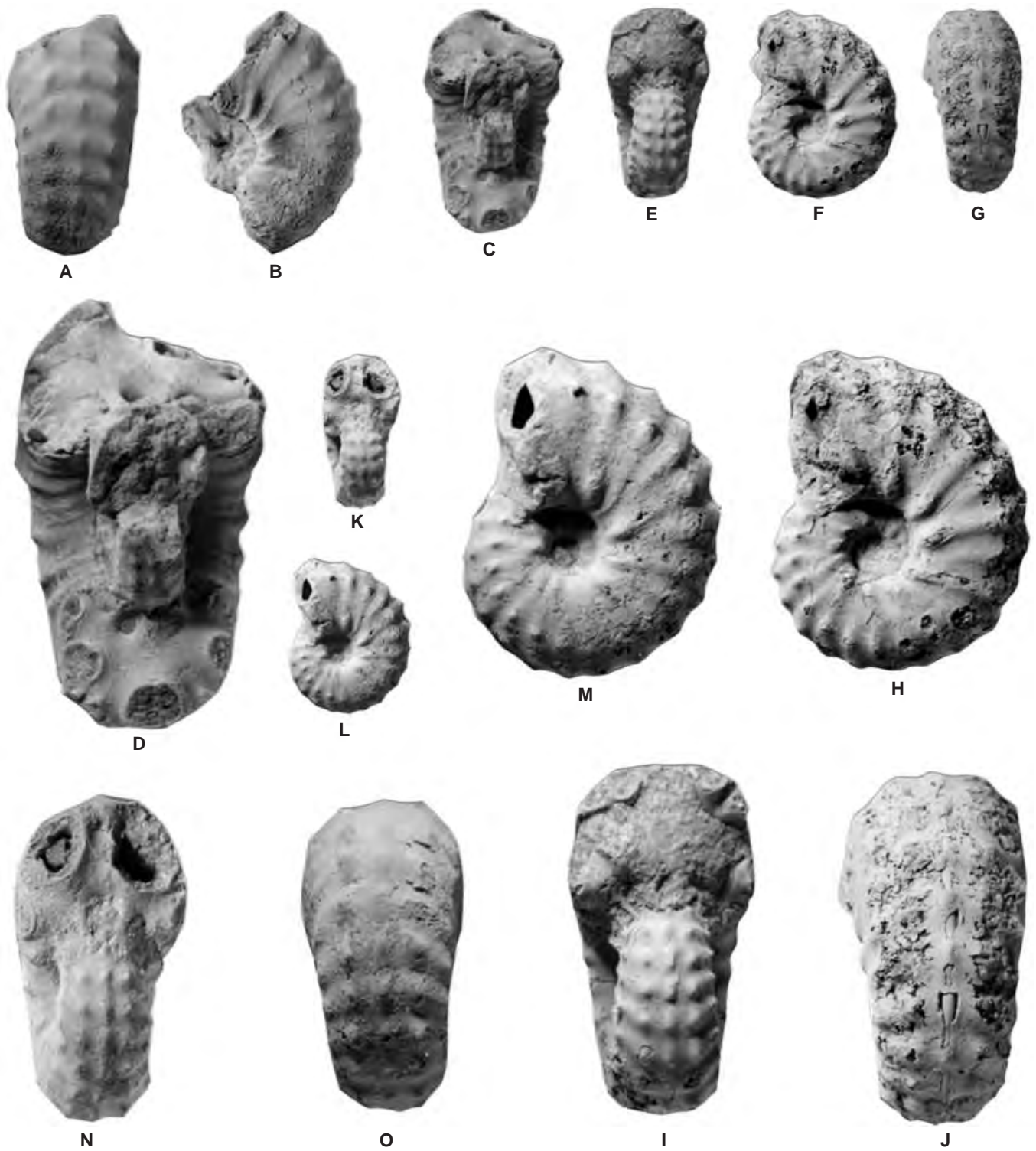


Fig. 9. A–O, *Acanthoceras flexuosum* Crick, 1907. A–D, SAM-PCZ13520; E–J, SAM-PCZ13506; K–O, SAM-PCZ13504, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–C, E–G, K, L, are $\times 1$; D, H–J, M–O are $\times 2$.

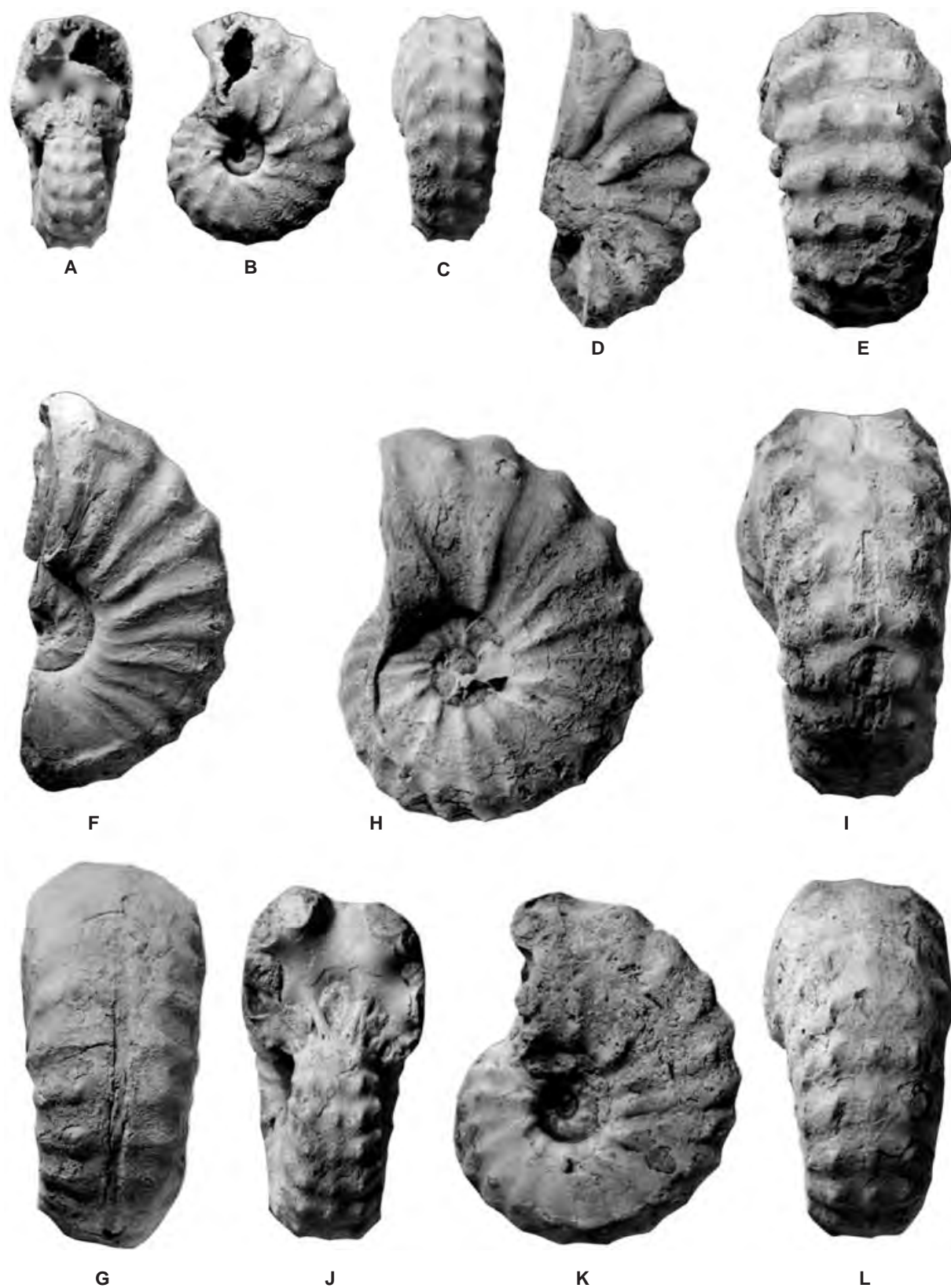


Fig. 10. A–L, *Acanthoceras flexuosum* Crick, 1907. A–C, SAM-PCZ13526; D, E, SAM-PCZ13522; F, G, SAM-PCZ4435; H, I, SAM-PCZ13497; J–L, SAM-PCZ13521, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.90$.

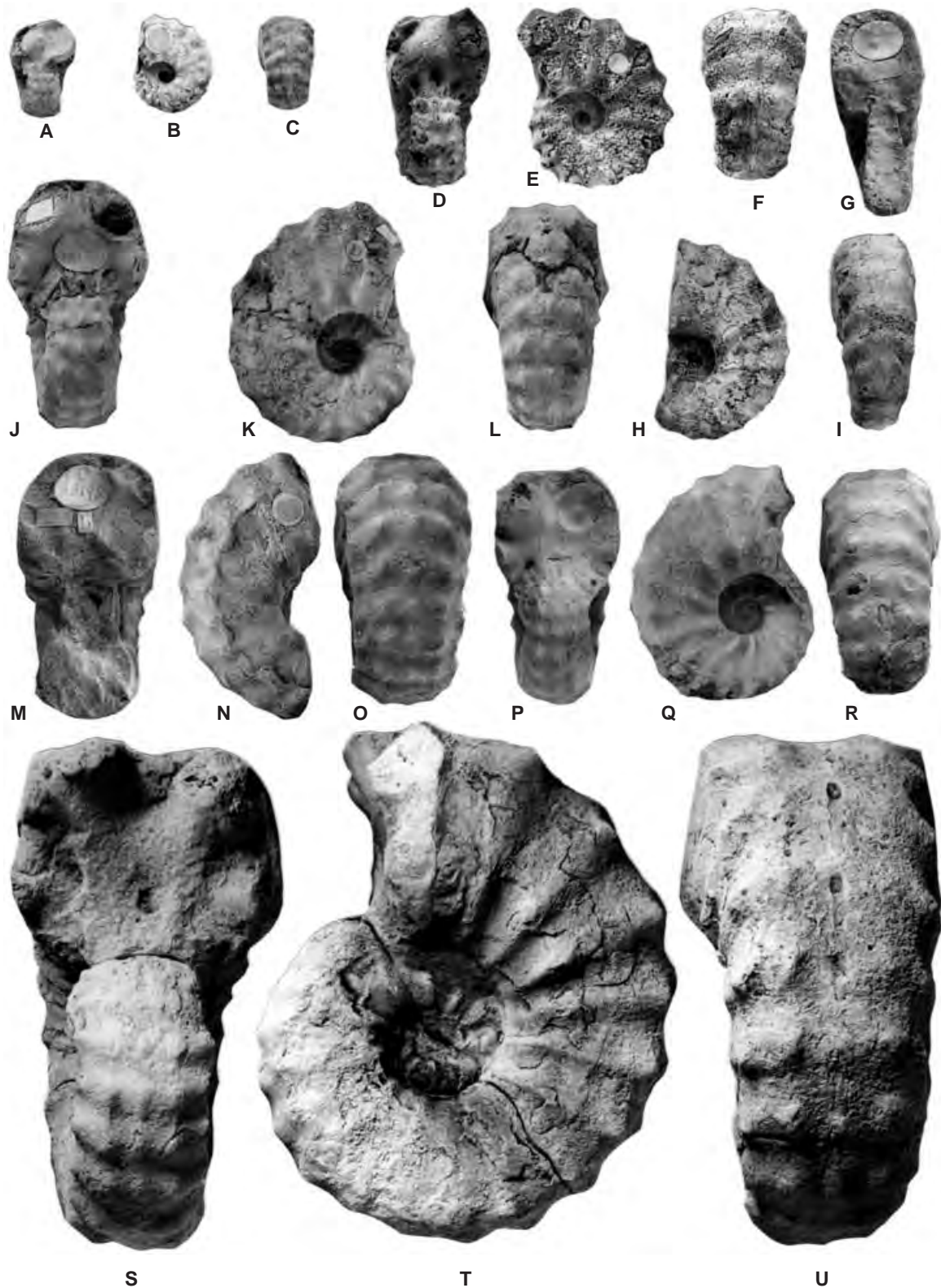


Fig. 11. A–U, *Acanthoceras flexuosum* Crick, 1907. A–C, BMNH C18199, the original of *Acanthoceras latum* Crick, 1907, p. 196 ('The young of this species'); D–F, BMNH C18196, the original of *Acanthoceras hippocastanum* of Crick, 1907, p. 194, pl. 13, fig. 4; G–I, BMNH C18176, the original of one of the specimens referred to by Crick (1907, p. 186) as possibly referable to *Acanthoceras crassioratum* Crick, 1907; J–L, BMNH C18184, the original of specimen c of *Acanthoceras munitum* of Crick, 1907, p. 187; M–O, BMNH C18198, the original of specimen b of *Acanthoceras latum* of Crick, 1907, p. 196; P–R, BMNH C18185, the original of specimen d of *Acanthoceras munitum* of Crick, 1907, p. 187; S–U, SAM-PCZ13494, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy and Klinger (1975, p. 289). Figures are $\times 0.85$.



Fig. 12. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13530, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 13. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13492, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 14. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13528, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 15. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13523, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are x0.95.



Fig. 16. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13512, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figure is $\times 1$.



Fig. 17. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13512, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 18. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13517, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figure is $\times 1$.



Fig. 19. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13517, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are x1.



Fig. 20. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13513, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 21. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13518, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figure is $\times 1$.



Fig. 22. *Acanthoceras flexuosum* Crick, 1907. SAM-PCZ13518, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 23. *Acanthoceras flexuosum* Crick, 1907. OUM KX1750, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figure is $\times 0.8$.



Fig. 24. *Acanthoceras flexuosum* Crick, 1907. OUM KX1750, from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figure is $\times 0.8$.

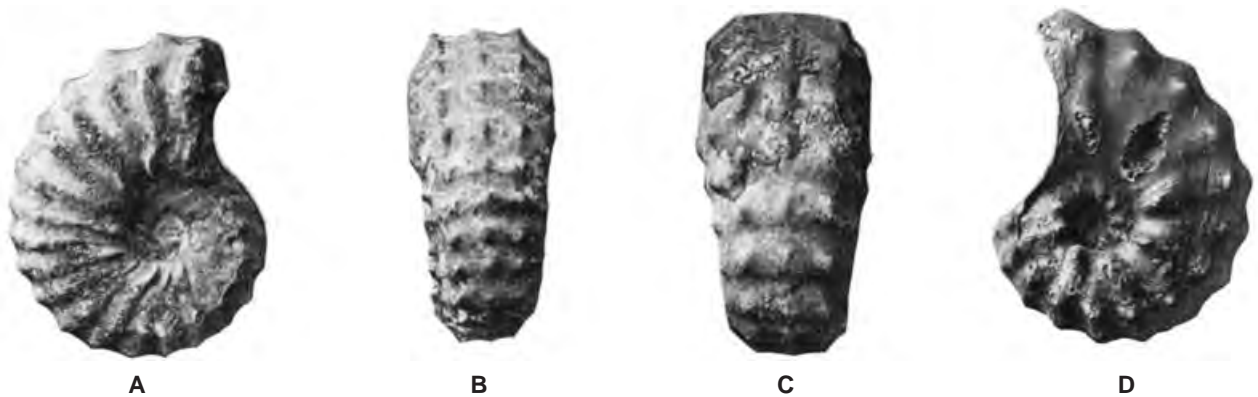


Fig. 25. A–D, *Acanthoceras flexuosum* Crick, 1907. Copies of Venzo, 1936. **A, B,** '*Acanthoceras flexuosum*', pl. 7 (3), fig. 6; **C, D,** '*Acanthoceras hippocastanum*' pl. 7 (3), fig. 2; the original specimens were from the Middle Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.

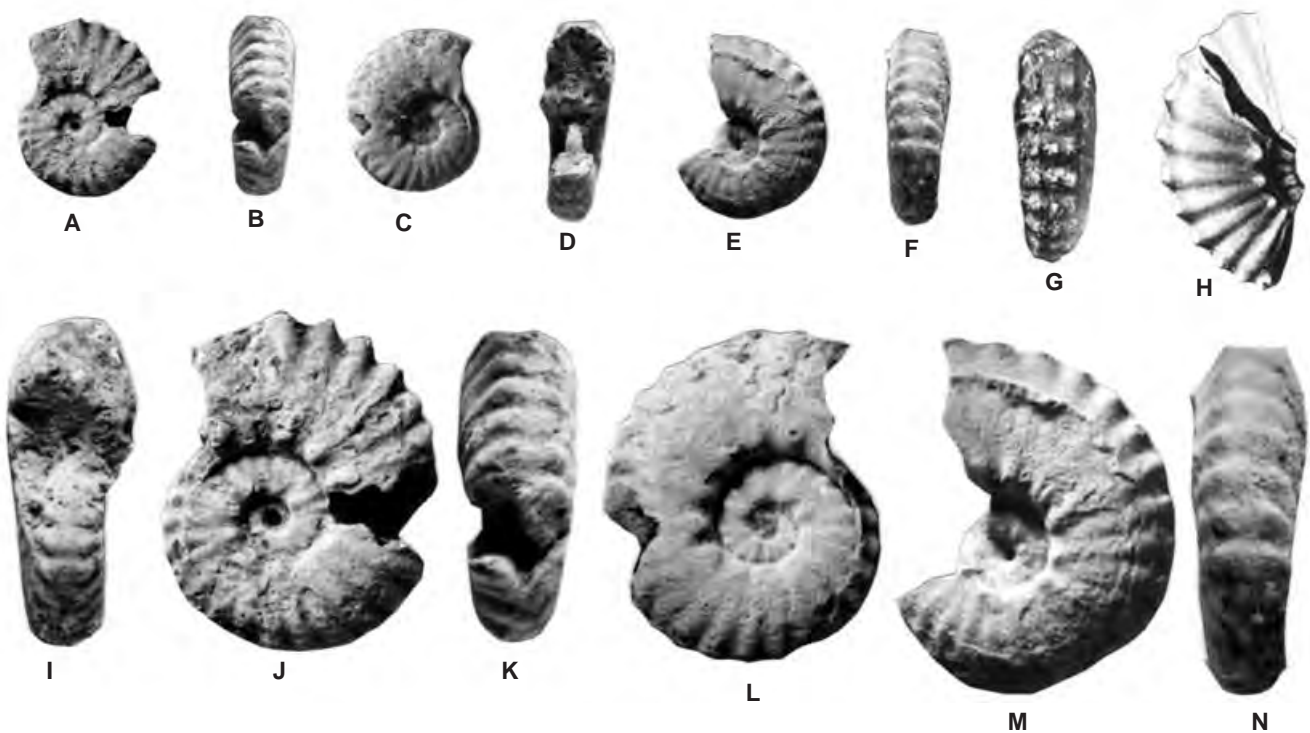


Fig. 26. A–N, *Protacanthoceras waterloti* (Venzo, 1936). **A–C, I–L,** SAM-PCZ22193; **D–F, M, N,** SAM-PCZ22192; **G, H,** the holotype, copy of Venzo, 1936, pl. 7 (3), fig. 11, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–H are $\times 1$; I–N are $\times 2$.

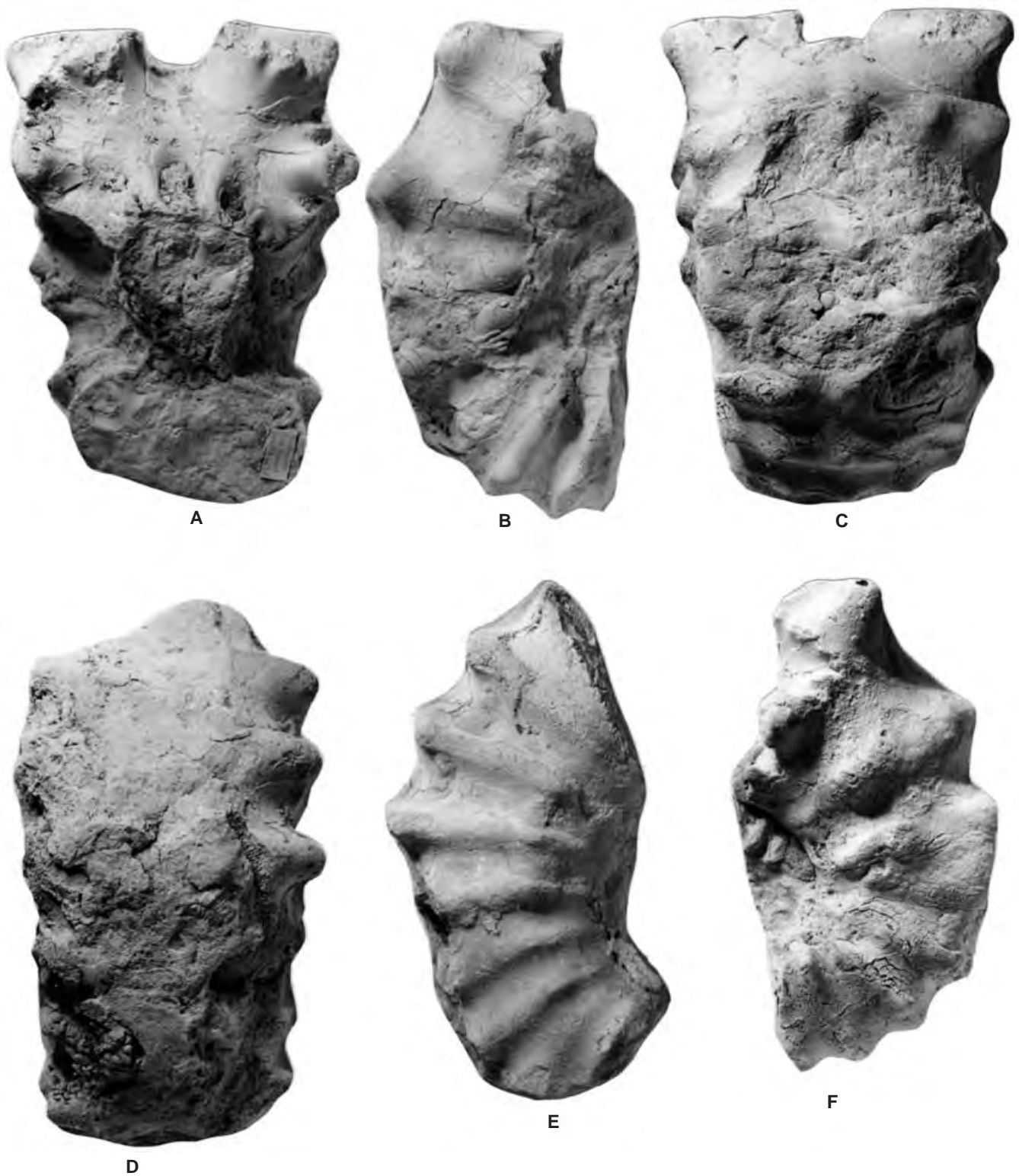


Fig. 27. A–D, *Cunningtoniceras?* sp. a, OUM KX4312. E, F, *Cunningtoniceras?* sp. b, OUM KX4574, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 28. A–E, *Cunningtoniceras?* sp. a. A, B, OUM KX4631; C, D, OUM KX4630; E, OUM KX1744, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.

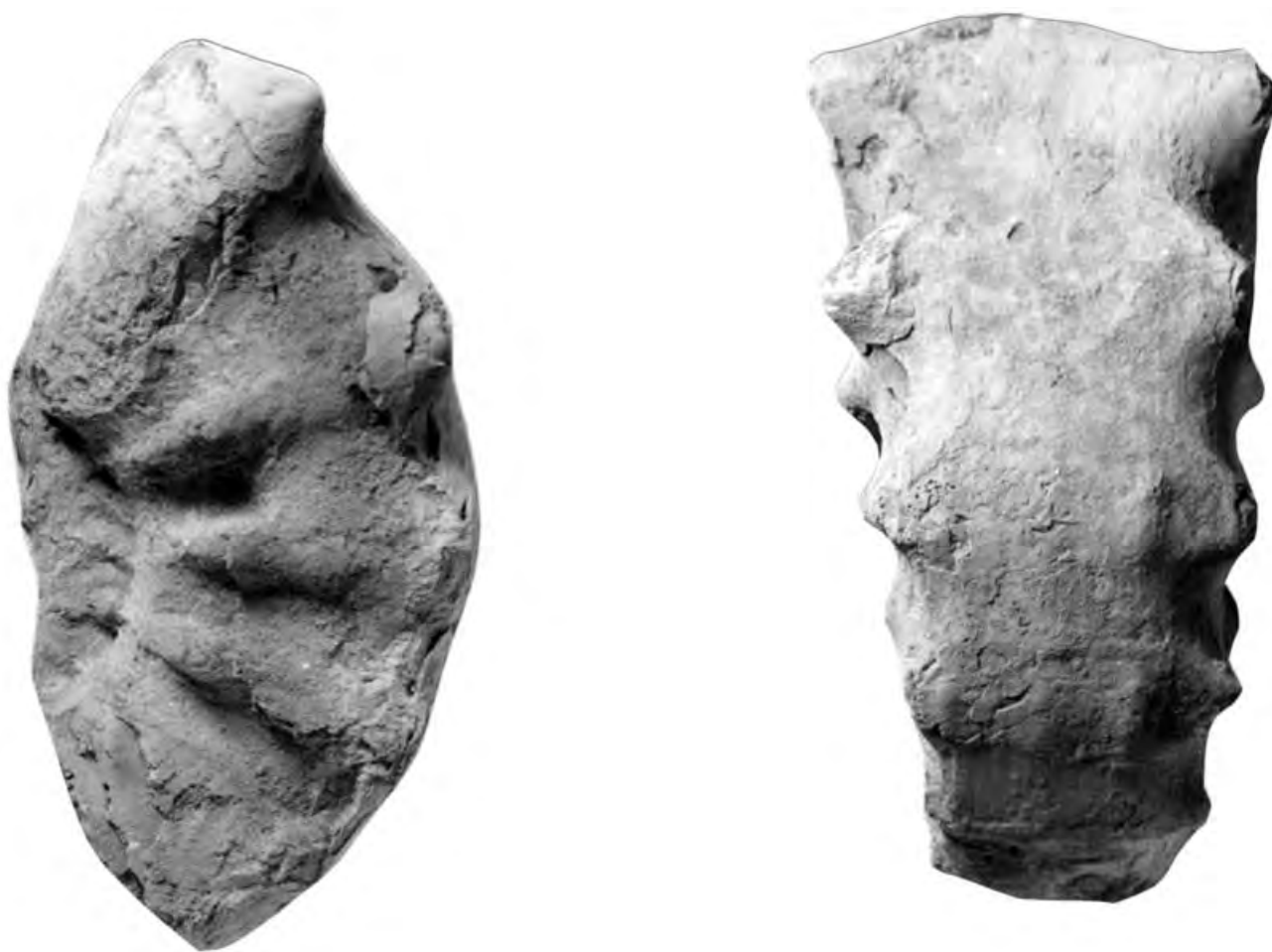


Fig. 29. *Cunningtoniceras?* sp. a. SAM-PCZ13516, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 30. *Cunningtoniceras?* sp. BMNH C18273, the original of *Acanthoceras* sp. of Crick, 1907, p. 241, and said to be from 'the south branch of the Manuan Creek'; preservation suggests the specimen to be from from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 31. *Calycoceras* (*Gentoniceras*) *gentoni* (Brongniart, 1822). BMNH C18214, the holotype of *Acanthoceras paucinodatum* Crick, 1907, pl. 13, fig. 3, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 1$.

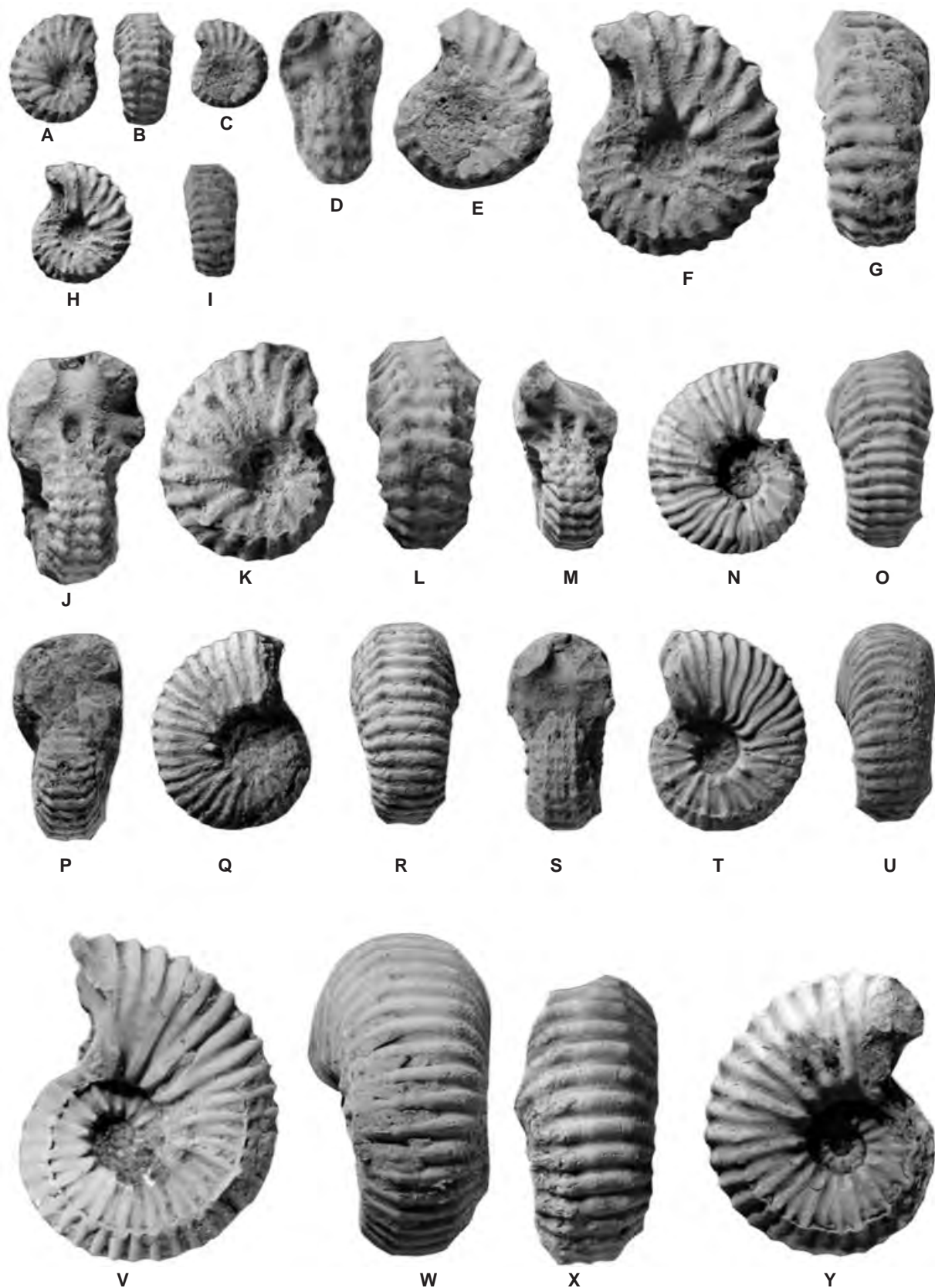


Fig. 32. A–Y, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894). A, B, J–L, SAM-PCZ13472; C–E, SAM-PCZ13473; F–I, SAM-PCZ13460; M–O, SAM-PCZ13433; P–R, SAM-PCZ13428; S–U, SAM-PCZ13468; V, W, SAM-PCZ13485; X, Y, SAM-PCZ13486, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–C, H, I, M–Y are $\times 0.90$; D–G, J–L are $\times 1.8$.

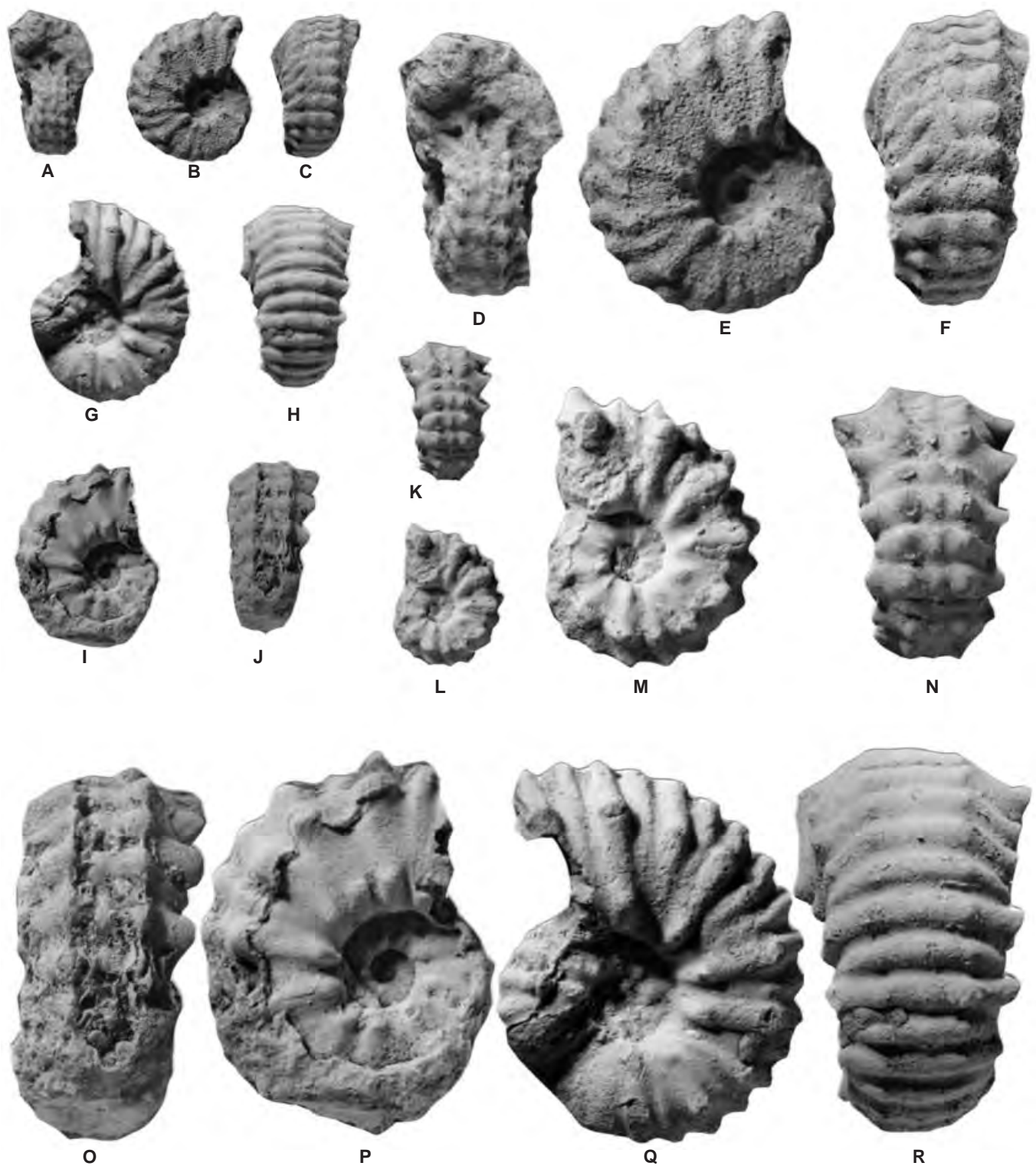


Fig. 33. A–F, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894), SAM-PCZ13477. G–R, *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). G, H, Q, R, SAM-PCZ13446; I, J, O, P, SAM-PCZ13478; K–N, SAM-PCZ13458, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–C, G–L are $\times 1$; D–F, M, N, O–R are $\times 2$.

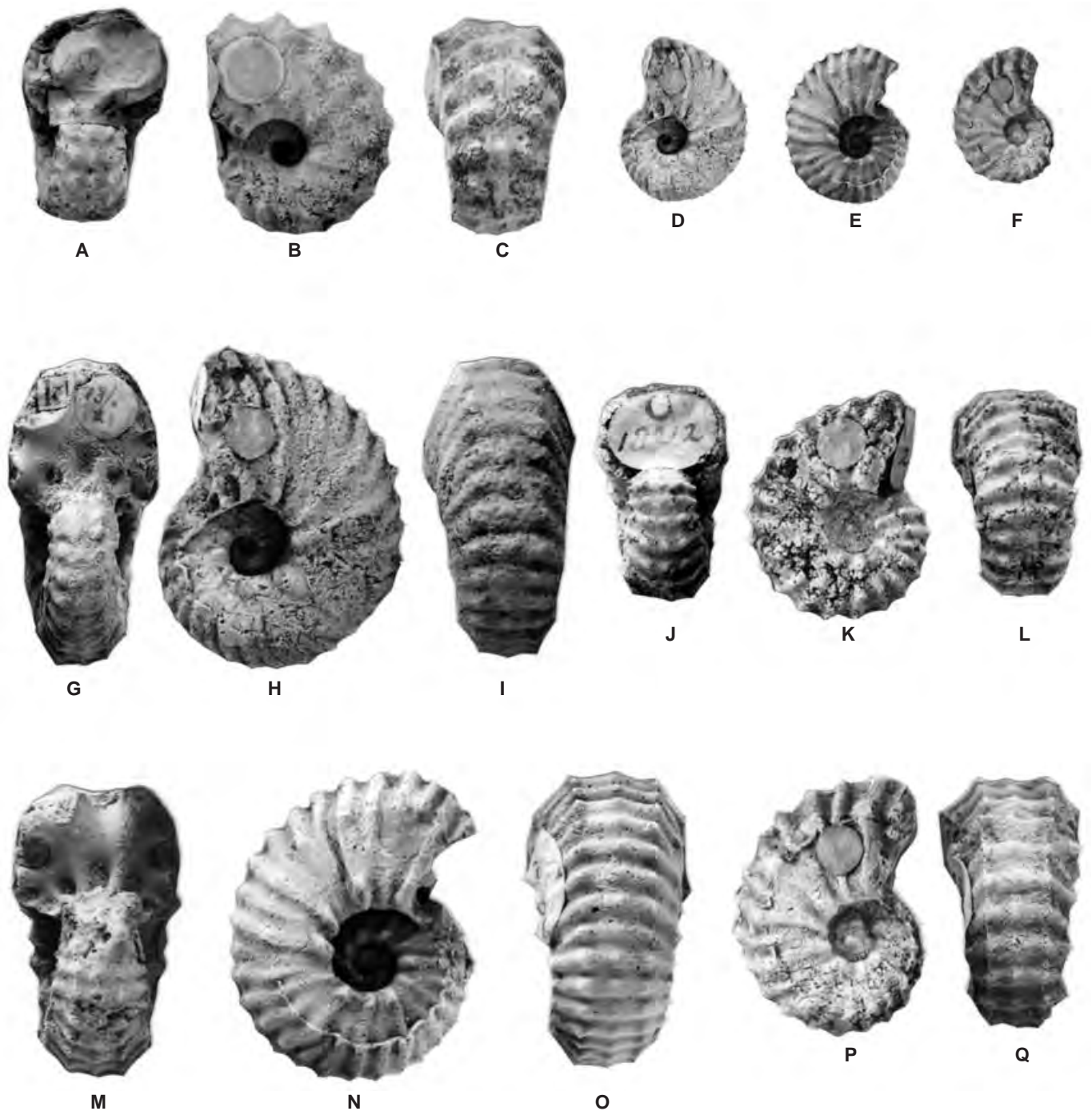


Fig. 34. A–C, *Acanthoceras flexuosum* Crick, 1907, BMNH 18199, the original of *Acanthoceras latum* Crick, 1907 ('young', p. 196). D, G–I, *Calyoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897), BMNH C18225, original of specimen k of *Acanthoceras choffati* of Crick, 1907, p. 206. J–L, *Calyoceras* (*Newboldiceras*) *asiaticum asiaticum* (Kossmat, 1897), original of specimen b of *Acanthoceras nitidum* Crick, 1907, p. 201–2. E, M–O, *Calyoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897), original of specimen c of *Acanthoceras newboldi* var. *spinosum* of Crick, 1907, p. 200. F, P, Q, *Calyoceras* (*Newboldiceras*) *asiaticum asiaticum* (Kossmat, 1897), original of specimen c of *Acanthoceras newboldi*, typical form, of Crick, 1907, p. 198, from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A–C, G–Q are x2; D–F are x1.

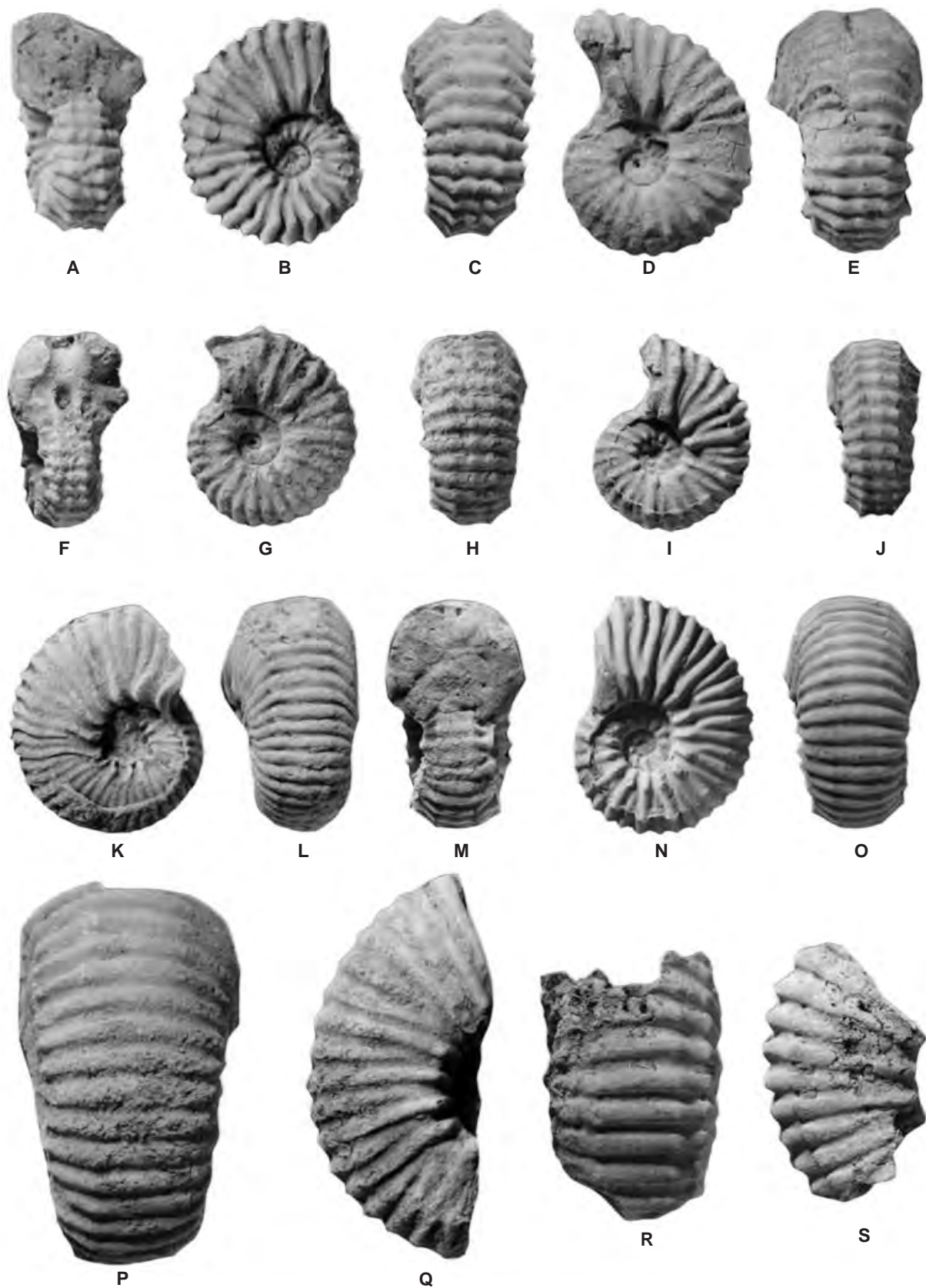


Fig. 35. A–J, M–O, R, S, *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). A–C, SAM-PCZ13464; D, E, SAM-PCZ13463; F–H, SAM-PCZ13446; I, J, SAM-PCZ13448; M–O, SAM-PCZ13459; R, S, OUM KX4592. K, L, P, Q, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). K, L, SAM-PCZ13432; P, Q, SAM-PCZ13482, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 0.90$.

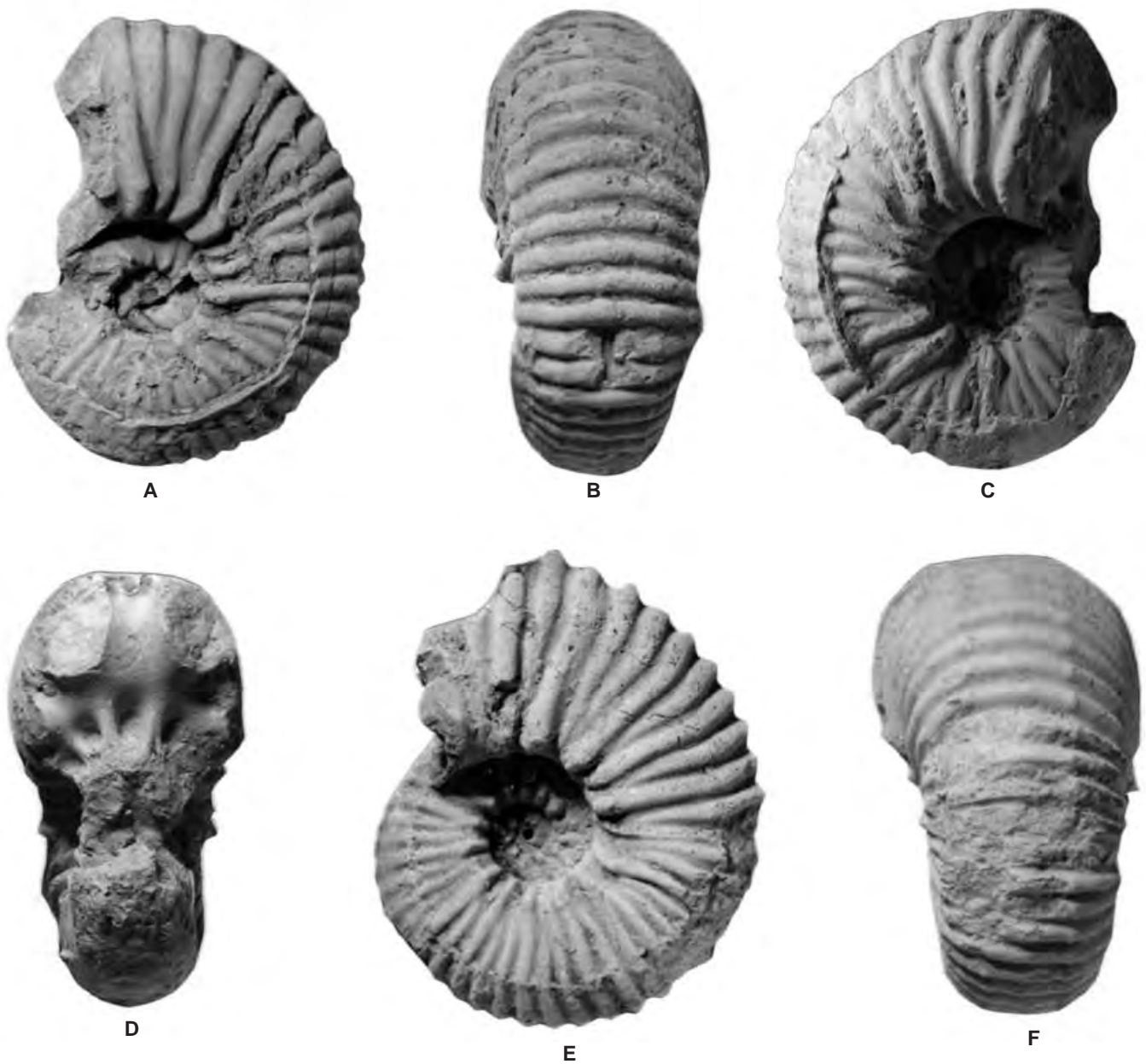


Fig. 36. A–F, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894). A–C, SAM-PCZ13476; D–F, SAM-PCZ13437, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 1$.



Fig. 37. *Calyoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894). SAM-PCZ13455, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 38. *Calycoceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894). Cast of the holotype, the original of Jimbo, 1894, pl. 20, fig. 1, no. 1–105 in the collections of the Geological Institute, Tokyo University, from the Middle Cenomanian *Trigonia* Sandstone of the Ikushumbets, Hokkaido, Japan. Figures are $\times 0.95$.



Fig. 39. A–D, *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). A, B, SAM-PCZ13456; C, D, SAM-D1005, from the Middle Cenomanian (or lower Upper?) Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.90$.



Fig. 40. *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). SAM-PCZ13451, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 41. *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). SAM-PCZ13462, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 42. *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897). SAM-PCZ13469, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.

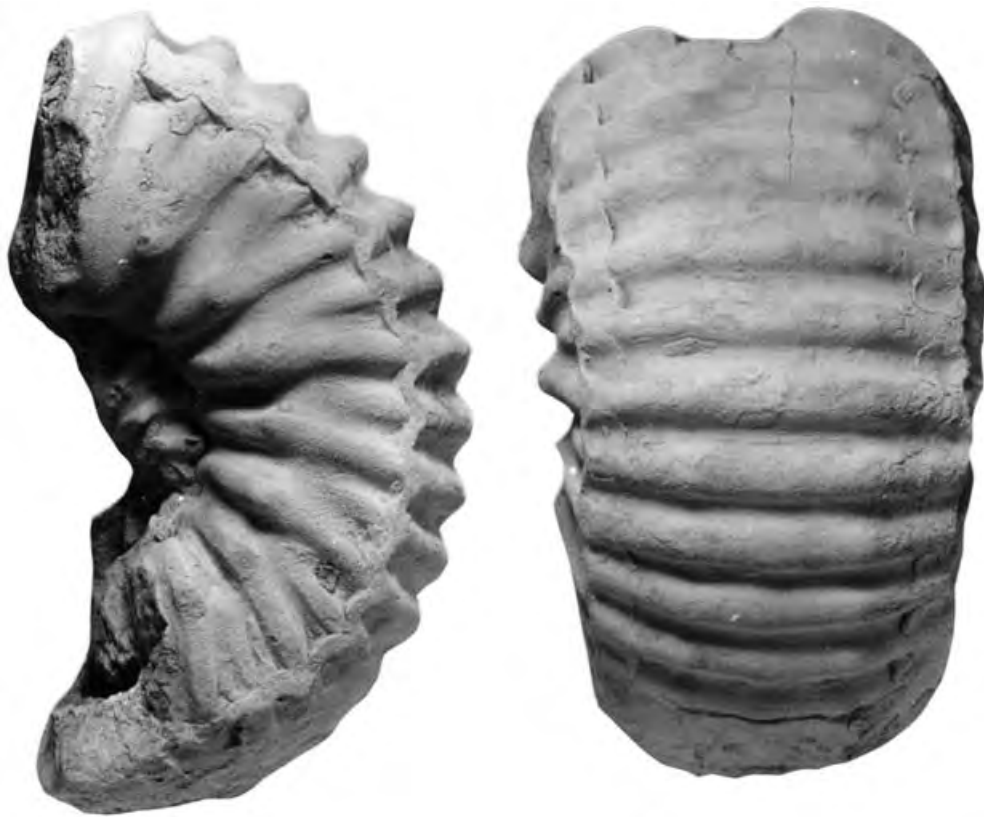


Fig. 43. *Calycceras (Newboldiceras) asiaticum spinosum* (Kossmat, 1897). OUM KX4623, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.80$.

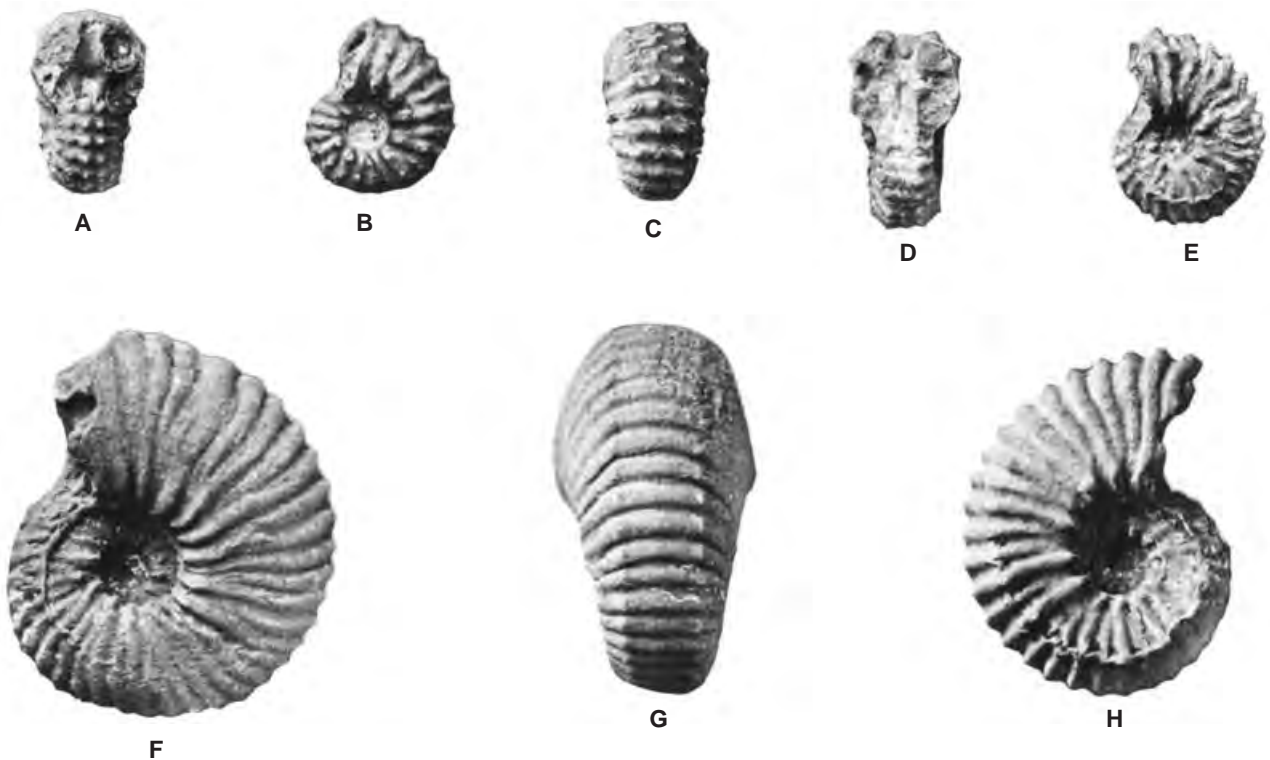


Fig. 44. A–H, copies of acanthoceratines from the Skoenberg figured by Venzo (1936). A–C, *Calycceras* sp. juv., the holotype of *Acanthoceras gortanii* Venzo, 1936, p. 82 (24), copy of pl. 7 (3), fig. 5. D, E, H, *Calycceras (Newboldiceras) asiaticum asiaticum* (Jimbo, 1894), the *Acanthoceras newboldi* var *spinosa* of Venzo, 1936, p. 82 (24), pl. 7 (3), figs 3, 4. F, G, *Calycceras (Newboldiceras) planecostatum* (Kossmat, 1897), the *Acanthoceras choffati* of Venzo, 1936, p. 83 (25), pl. 7 (3), fig. 8. All figures are $\times 1$.

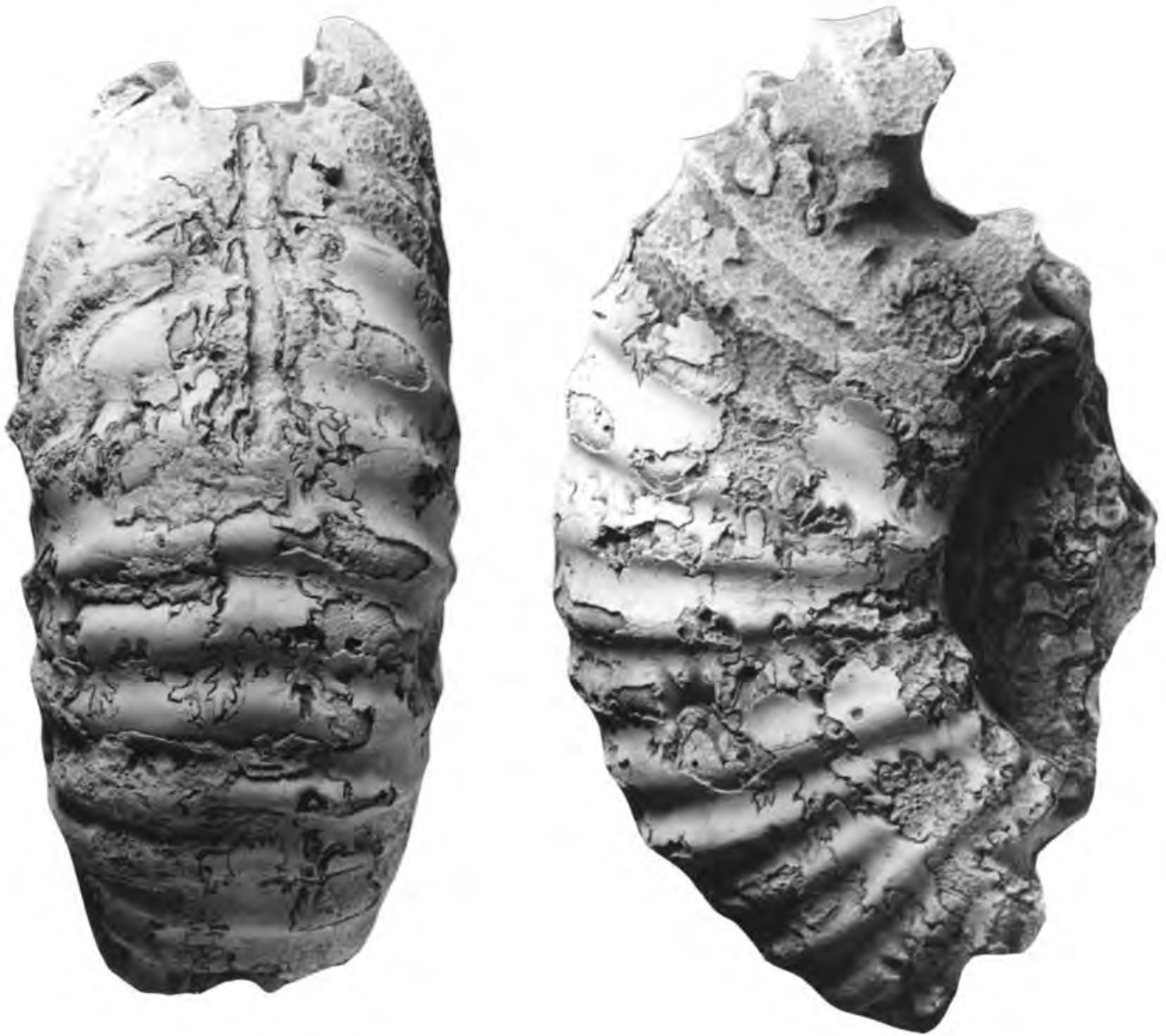


Fig. 45. *Calycoceras* (*Newboldiceras*) cf. *asiaticum hunteri* (Kossmat, 1897), SAM-PCZ13448, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.

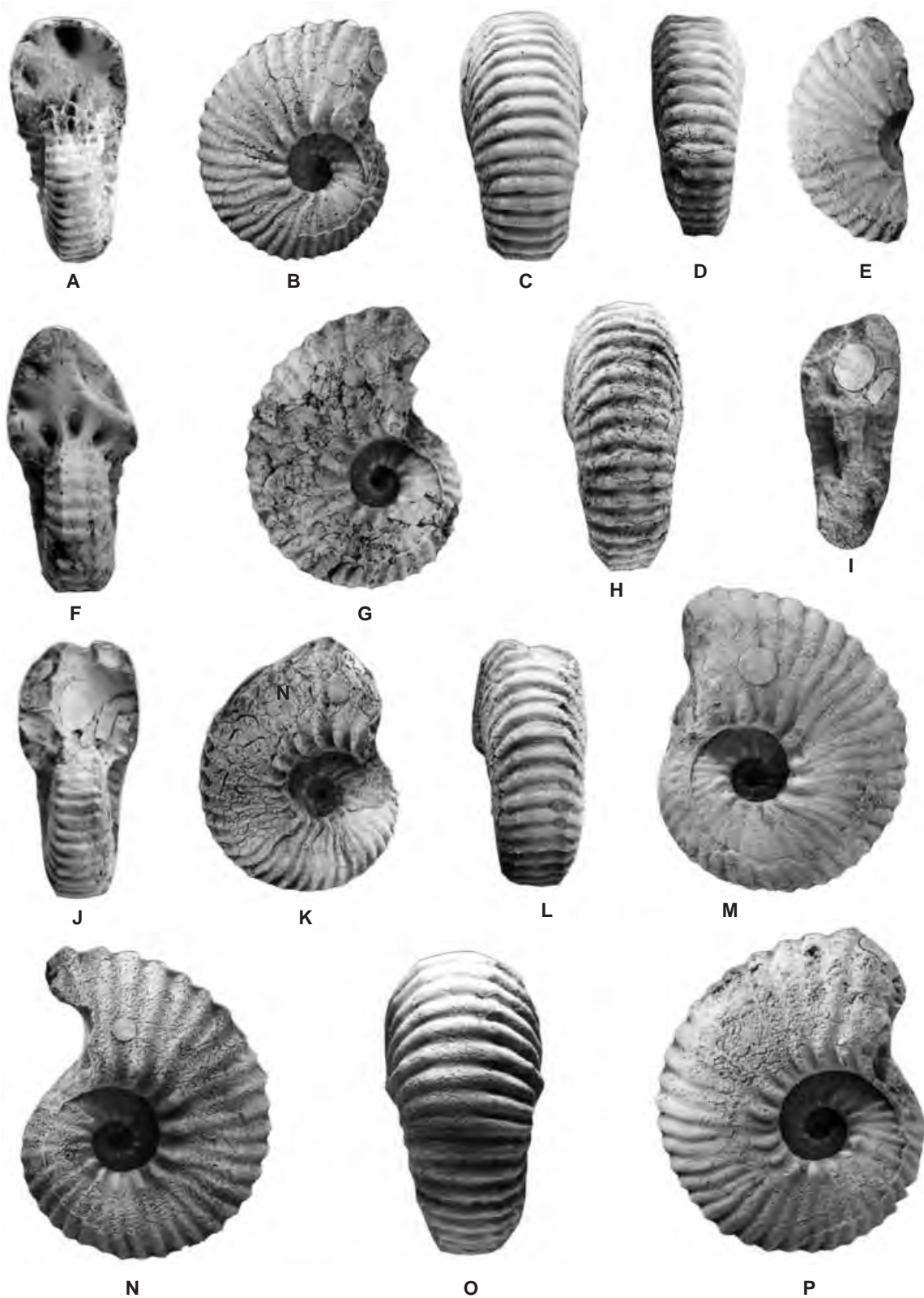


Fig. 46. A–P, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). Specimens described as *Acanthoceras choffati* Kossmat by Crick, 1907, p. 205, pl. 12, fig. 5, and assigned letters on p. 206. **A–C**, BMNH C18223, specimen i; **D, E, I**, BMNH C18228, specimen n; **F–H**, BMNH C18219, specimen e; **J–L**, BMNH C18218, specimen d; **M, P**, BMNH C18216, specimen b, the original of Crick, 1907, pl. 12, fig. 5; **N, O**, BMNH C18220, specimen f, all from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). All figures are $\times 0.85$.

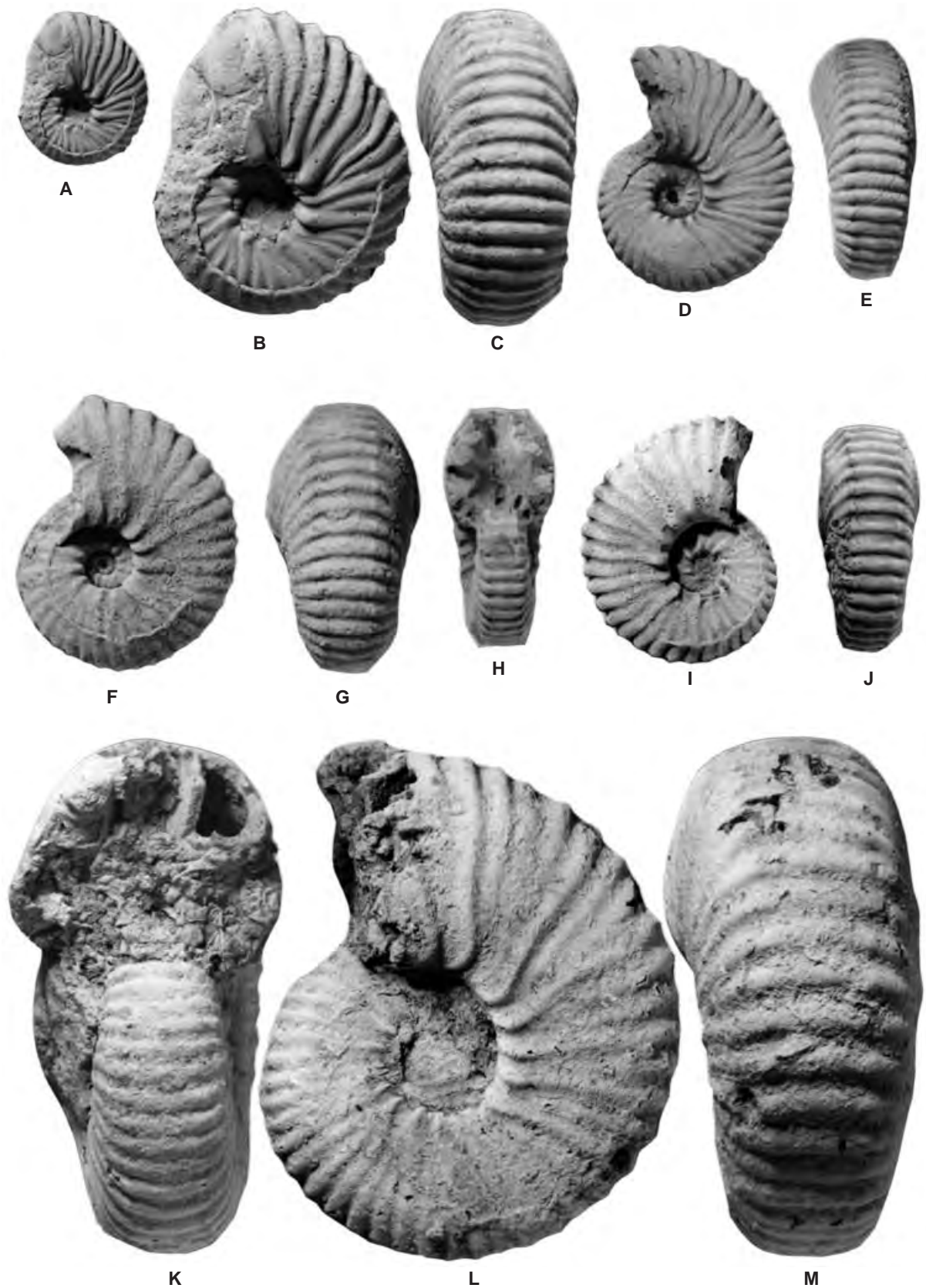


Fig. 47. A–M, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). A–C, SAM-PCZ13454; D, E, SAM-PCZ13434; F, G, SAM-PCZ13484; H–J, SAM-PCZ13435; K–M, SAM-PCZ13481, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A, D–M are $\times 0.90$; Figs B, C are $\times 1.8$.

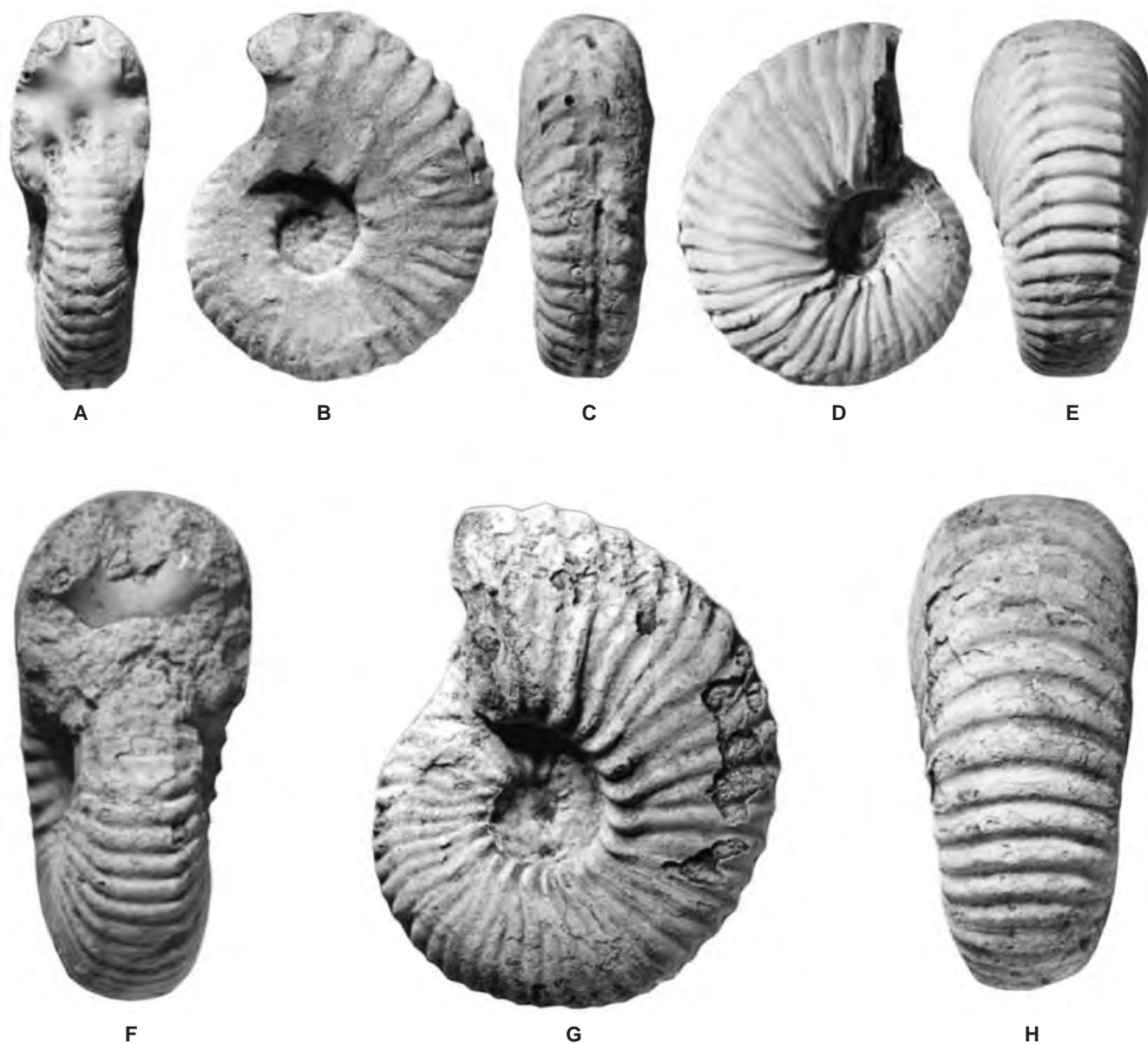


Fig. 48. A–H, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). A–C, SAM-PCZ13440; D, E, SAM-PCZ13452; F–H, SAM-PCZ13439, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are x1.

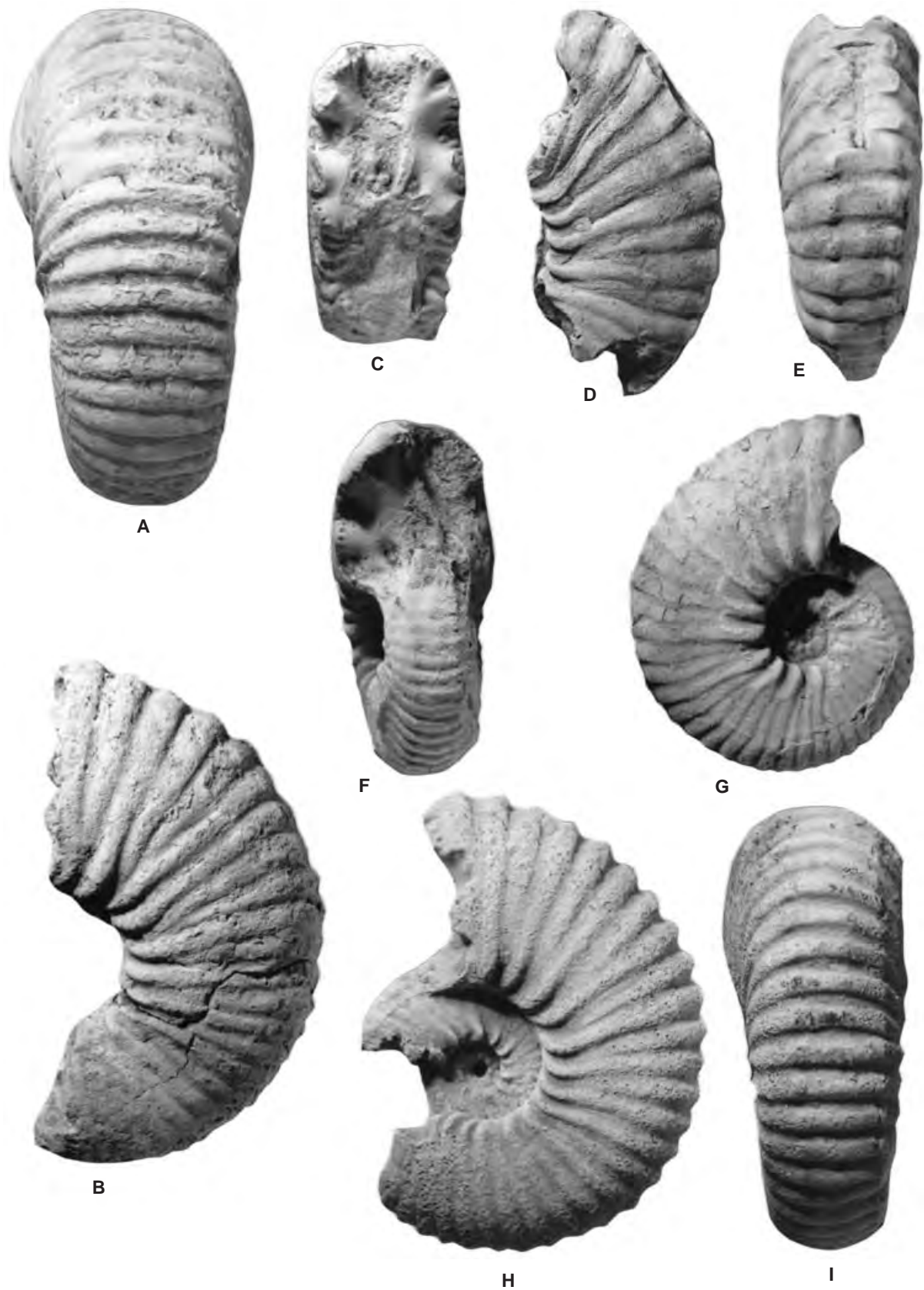


Fig. 49. A–I, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). A, B, SAM-PCZ13483; C–E, SAM-PCZ13430; F, G, SAM-PCZ13456; H, I, SAM-PCZ13442 from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.90$.

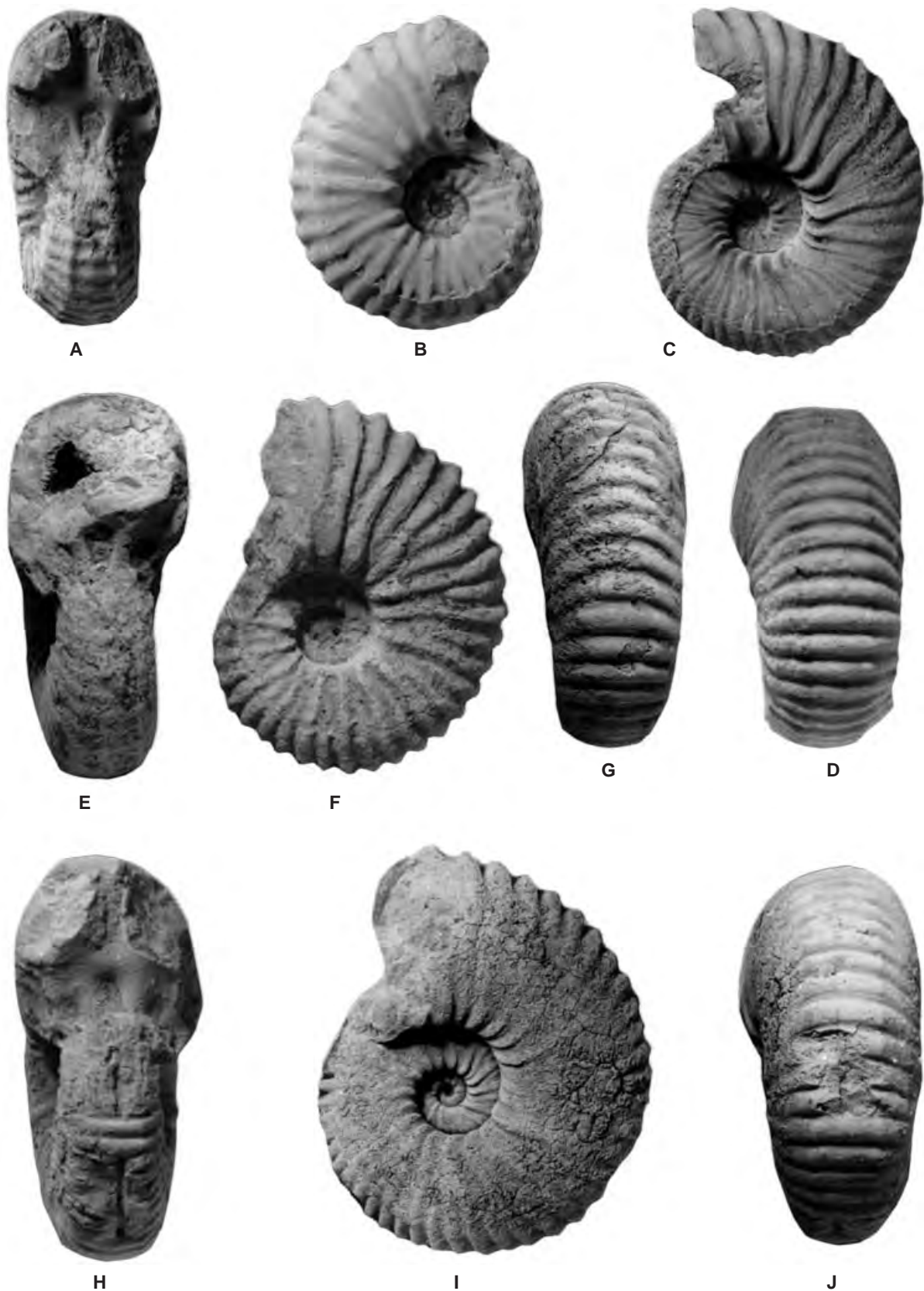


Fig. 50. A, B, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Kossmat, 1897), SAM-PCZ13431. C–J, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). C, D, SAM-PCZ13467; E–G, SAM-PCZ13488; H–J, SAM-PCZ13480, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.90$.



Fig. 51. *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897). SAM-PCZ13475, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 52. *Calycoceras (Newboldiceras) planecostatum* (Kossmat, 1897). SAM-PCZ13443, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 53. *Calyoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). SAM-PCZ13465, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.



Fig. 54. Cast of the lectotype of *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897), the original of Kossmat, 1897, pl. 2 (13), fig. 1, from the Utatur Group of Odium, south India. Geological Survey of India Collections no. 14842. Figures are $\times 1$.



Fig. 55. Cast of the holotype of *Acanthoceras choffati* Kossmat, 1897, pl. 15 (4), fig. 1, from the Utatur Group of Odium, south India. Geological Survey of India Collections no. 14844. Figures are $\times 1$.

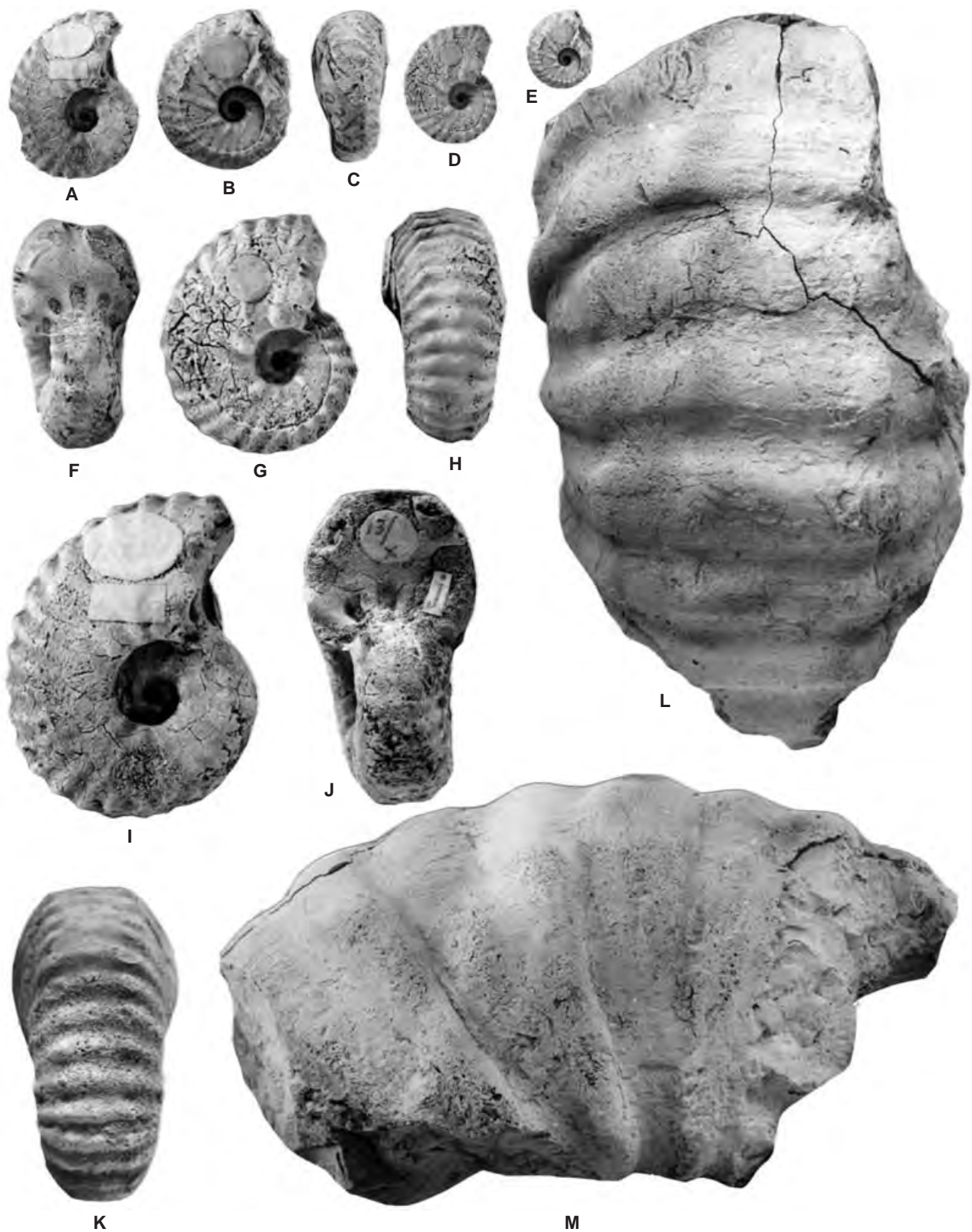


Fig. 56. A–K, *Calyoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897). Specimens described as *Acanthoceras choffati* Kossmat by Crick, 1907, p. 205, pl. 12, fig. 5, and assigned letters on p. 206; **A, I, J, K**, BMNH C18224, specimen j; **B, C, E**, BMNH C18227, specimen m; **D, F, G, H**, BMNH C18226, specimen l. **L, M, *Calyoceras* (*Newboldiceras*) *laticostatum*** (Crick, 1907), the holotype, BMNH C18210, all from the 'deposit at the north end of False Bay' of Crick (1907, p. 164), that is to say the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figs A, D, E, L, M are $\times 0.95$; Figs B, C, F–K are $\times 1.9$.

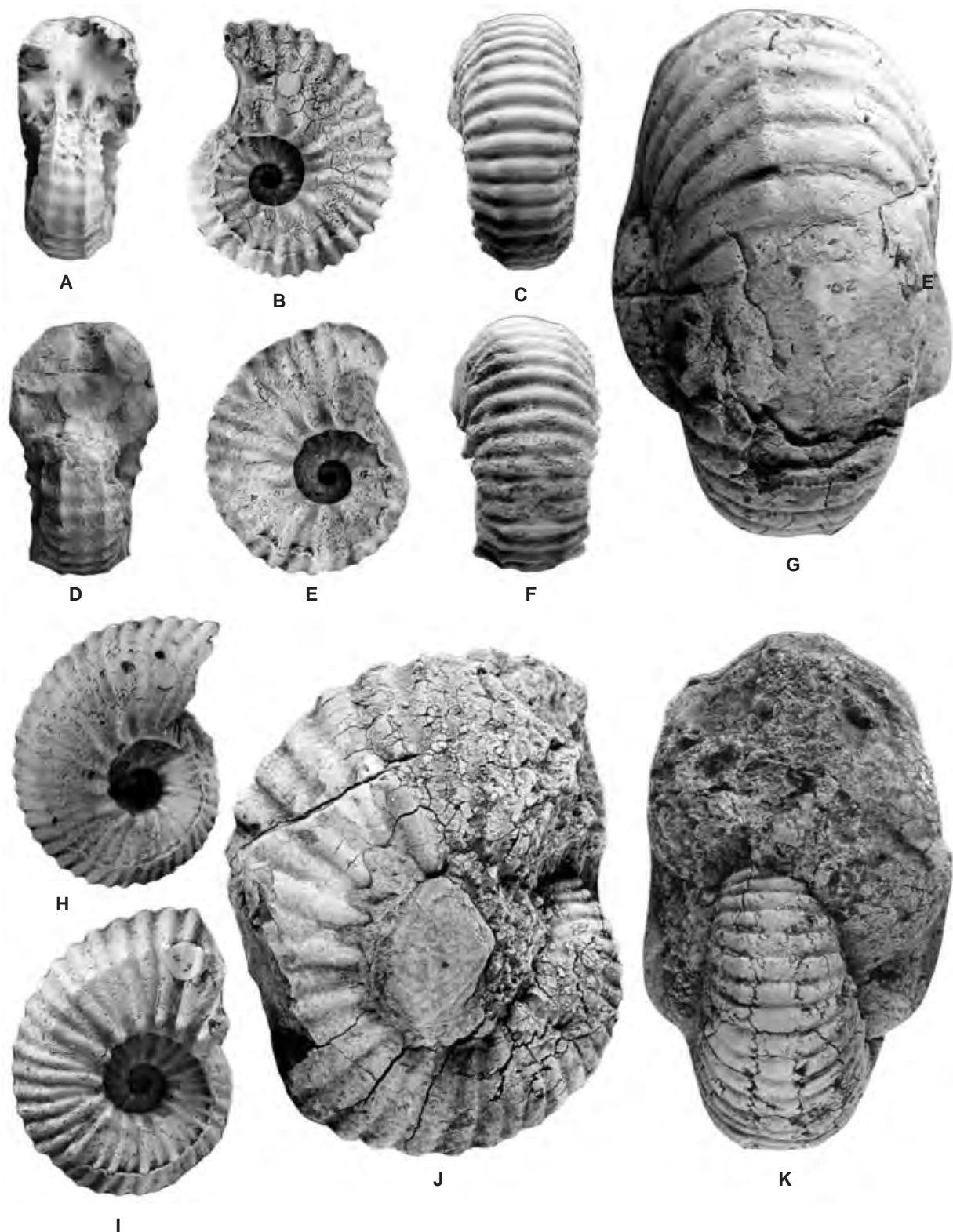


Fig. 57. A–C, I, *Calycoceras* (*Newboldiceras*) *asiaticum asiaticum* (Jimbo, 1894). A–C, BMNH C18201, the original of *Acanthoceras newboldi* typical form, specimen b, of Crick, 1907, p. 198; I, BMNH C18204, original of *Acanthoceras newboldi* var. *spinosa* specimen a of Crick, 1907, p. 206, pl. 12, fig. 3. **D–F, *Calycoceras* (*Newboldiceras*) *asiaticum spinosum* (Kossmat, 1897).** BMNH C18205, original of *Acanthoceras newboldi* var. *spinosa* specimen b of Crick, 1907, p. 200. **H, *Calycoceras* (*Newboldiceras*) *planecostatum* (Kossmat, 1897),** the original of *Acanthoceras choffati* specimen g of Crick, 1907, p. 206. **G, J, K, *Calycoceras* (*Newboldiceras*) *laticostatum* (Crick, 1897),** an unregistered specimen in the M.R. Cooper Collection, housed in the Department of Geology and Applied Geology of the University of KwaZulu-Natal. All specimens are from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289); the originals of A–I were originally described as being from the 'deposit at the north end of False Bay' of Crick (1907, p. 164). All figures are $\times 0.90$.



Fig. 58. *Calycceras (Newboldiceras) breistrofferi* (Collignon, 1937), the holotype, the original of *Acanthoceras breistrofferi* Collignon, 1937, p. 38, pl. 6, fig. 4; pl. 9, fig. 2, from the Cenomanian of Ankomaka, Madagascar, an unregistered specimen currently in the reserve collections of the Université de Bourgogne, Dijon. Figures are $\times 1$.



Fig. 59. *Calycoceras (Newboldiceras) breistrofferi* (Collignon, 1937), SAM-PCZ13457, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.



Fig. 60. *Calycoceras (Newboldiceras) breistrofferi* (Collignon, 1937), SAM-PCZ13453, from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.95$.

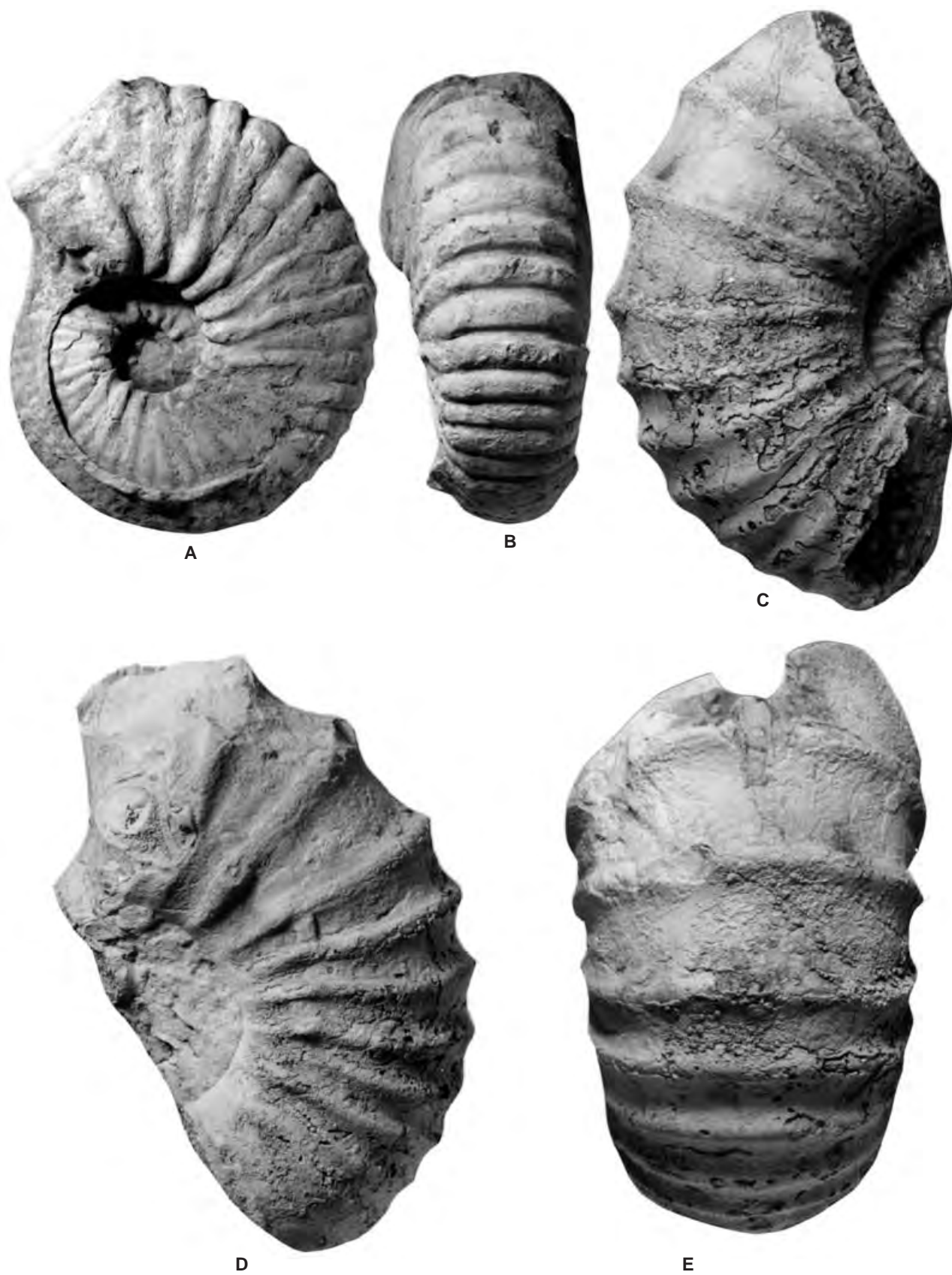


Fig. 61. A, B, *Calycoceras (Newboldiceras) asiaticum asiaticum* (Kossmat, 1897), SAM-PCZ13438. C–E, *Calycoceras (Newboldiceras) breistrofferi* (Collignon, 1937), SAM-PCZ13461, all from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are x0.95.



Fig. 62. A–D, *Calycceras* (*Newboldiceras*) *breistrofferi* (Collignon, 1937). **A, B**, SAM-PCZ13445; **C, D**, SAM-PCZ13450, both from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 0.90$.



Fig. 63. *Pseudocalycoceras harpax* (Stoliczka, 1864), SAM-PCZ22194 (SAM-A640), from the Middle (or lower Upper?) Cenomanian Mzinene Formation of the Skoenberg, KwaZulu, locality 62 of Kennedy & Klinger (1975, p. 289). Figures are $\times 1$.