Cretaceous faunas from Zululand and Natal, South Africa. The ammonite subgenus *Hauericeras* (*Gardeniceras*) Matsumoto & Obata, 1955[‡]

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Four species of the distinctive desmoceratid ammonite *Hauericeras* (*Gardeniceras*) Matsumoto & Obata, 1955, are described from KwaZulu-Natal and the Eastern Cape Province: the type species, *H.* (*G.*) *gardeni* (Baily, 1855), from the Santonian to Lower Campanian, *H.*(*G.*) *pseudoangustum* Collignon, 1961, and *H.* (*G.*) *madagascariense* Collignon, 1961, from the Lower Campanian, and *H.* (*G.*) *rembda* (Forbes, 1846) from the upper Upper Maastrichtian.

Keywords: ammonites, *Hauericeras* (*Gardeniceras*), Santonian, Campanian, Cretaceous, KwaZulu, Eastern Cape Province, South Africa.

INTRODUCTION

Hauericeras (*Gardeniceras*) *gardeni* (Baily, 1855) is one of the most distinctive and immediately recognizable ammonites from the Santonian–Campanian Mzamba Formation of the coastal outcrops in the northeast of the Eastern Cape Province. In the cliff outcrops of the St Lucia Formation on the northwestern shores of False Bay, in KwaZulu-Natal, the species is abundant, sometimes occurring as imbricate stacks of individuals lying inclined at a low angle to bedding, and overlapping like roof tiles. The distinctive keel of the genus led Matsumoto (1938) to introduce a subfamily Hauericeratinae, supported in more extensive discussions by Matsumoto & Obata (1955) and Matsumoto *et al.* (1990); the subgenus *Gardeniceras* was introduced by Matsumoto & Obata (1955, p. 134) for the 'Fairly evolute and fairly widely umbilicate subgroup of *Hauericeras*' and later (Matsumoto *in* Matsumoto *et al.* 1990, p. 456) redefined as 'a subgroup of *Hauericeras* in which ventral or ventrolateral riblets or nodes disappeared completely'. Wright (1957, p. L371; 1996, p. 85) retained the subfamily, and defined it as follows (the phrase in italics was our addition to the 1996 account): 'Rather evolute to rather involute; whorl section high, with flat sides, venter rounded (at least initially), then typically fastigiate, and later with high sharp septicarinate keel. Smooth or with weak tubercles on the shoulders. *Microconchs with lappets.* Suture with suspensive lobe retracted or not.… Origin is doubtful, either in Desmoceratinae close to point of origin of Muniericeratidae or *Parapuzosia* of Puzosiinae.' Wright defined *Hauericeras* as having 'characters as for subfamily', and noted that 'Separation of *Gardeniceras* for the less involute forms seems unnecessary.' Apart from *Hauericeras,* the genera *Mossamedites* Cooper, 2003a, and *Oiophyllites* Spath, 1953, have been referred to the Hauericeratinae. The latter is based on tiny desmoceratoidean nuclei and is best treated as a *nomen dubium.*

In introducing his new genus *Hauericeras,* de Grossouvre (1894, p. 219) stated that '…Je donne ce nom à la série de formes se rattachant à *Ammonites gardeni…*', but took *Ammonites pseudogardeni* Schlüter, 1872, p. 54, pl. 16, figs 3–6, as type species. *Hauericeras* (*Hauericeras*) *pseudogardeni* has been revised in detail by Kaplan & Kennedy (1995, p. 18, pls 1–4, pl. 5, figs 1–2; pl. 6, figs 1, 7; pls 7, 8) and Kaplan *et al.* (2006, p. 31, pl. 1, figs 4, 7, 9, 11–12). These authors redescribed the type material from Dülmen in Westphalia, and additional specimens from Braunschweig in Lower Saxony, Germany. From the material available it seems that internal moulds may be virtually smooth (but for constrictions), whereas the shell surface and composite moulds bear ribs/tubercles on the outer flanks and ventrolateral shoulders. But even some composite moulds are virtually smooth, although this might be due to postmortem effects. If this interpretation is accepted, variety *nodatum* of Schlüter (1899) and *Hauericeras buszii* Wegner, 1905 (p. 209, pl. 8, fig. 1a, b) are synonyms of *pseudogardeni.* The illustrations of the species in Müller & Wollemann (1906) of material from Braunschweig, included constricted ribbed/nodate phragmocones up to 160 mm diameter (1906, pl. 4, fig. 1; pl. 8, fig. 3) as well as smooth, delicately constricted juveniles. Matsumoto *in* Matsumoto *et al.* 1990 (p. 451) thought *Ammonites mengedensis* Schlüter, 1876 (p. 154, pl. 40, fig. 9) might be the microconch of *H.* (*H.*) *pseudogardeni,* but this is a significantly older species (Kaplan & Kennedy 1994) and does not co-occur with *H.* (*H.*) *pseudogardeni* in any of the collections studied by Kaplan & Kennnedy, who were unable to conclusively demonstrate dimorphism.

Hauericeras (*H.*) *pseudogardeni* is firmly dated as Upper Santonian to Lower Campanian in Western Europe. Matsumoto *et al.* (1990) and Kaplan & Kennedy (1995) suggested that *Hauericeras* (*H.*) *antiquum* Collignon, 1961

[‡]In current geopolitical terminology Zululand and Pondoland now form parts of the provinces of KwaZulu-Natal and the Eastern Cape, respectively. For the sake of continuity we retain the names Zululand and Natal in the title of our series of systematic descriptions of the invertebrate faunas from these regions from 1975 onwards.

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(p. 75, text-fig. 12) known from a single specimen from the Lower Coniacian of Madagascar might be the stock ancestral to *H.* (*H.*) *pseudogardeni,* having the shell shape of *Hauericeras* plus delicate ventral ribs, but no constrictions. It is transitional to the Middle Turonian *Puzosia* (*Puzosia*) *serratocarinata* Kennedy & Cobban 1988 (p. 595, text-fig. 2; text-fig. 4, figs 1–3), from northern Mexico and Angola, the type species of *Mossamedites* Cooper, 2003 (p. 115) with a fastigiate venter but no well-differentiated keel.

Gardeniceras first appears in the Middle Coniacian, with *Ammonites lagarus* Redtenbacher, 1973, from the Middle Coniacian of Austria and southeastern France (see revision in Kennedy *in* Kennedy *et al.* 1995, p. 397, pl. 4, fig. 17), and ranges to the upper Upper Maastrichtian, with *Gardeniceras rembda* (Forbes, 1846) (see revision in Kennedy & Henderson 1992, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H). *Gardeniceras* thus appears a little later than *Hauericeras sensu stricto* if *antiquum* is accepted as a *Hauericeras*: Middle versus Lower Coniacian. When compared to *Hauericeras sensu stricto*, *Gardeniceras* lacks outer flank and ventrolateral ribs/tubercles, has a keel that is present on the shell from an early ontogenetic stage, hollow when first secreted, but thereafter filled in by additional shell material so that it is solid over the phragmocone, as a result of which internal moulds of phragmocones have a rounded venter, rather than the sharply fastigiate venter with solid keel of *H.* (*H.*) *pseudogardeni.* The venter of internal moulds of *Gardeniceras* body chambers retains a rounded venter, with a keel that remains hollow. If *Hauericeras* and *Gardeniceras* are closely related, the stratigraphic evidence suggests the former gave rise to the latter during the Coniacian. Interestingly, the juvenile *Mossamedites serratocarinatus* figured by Kennedy (1988, pl. 2, figs 8–10) has the overall proportions of *Gardeniceras.*

In conclusion, we accept *Gardeniceras* as a subgenus of *Hauericeras* in the absence of evidence to the contrary, but note that a keel has appeared more than once in the Desmoceratidae; in *Damesites* Matsumoto, 1942, *Moremanoceras* Cobbban, 1972, and in an as yet undescribed form from the Lower Cenomanian of Nigeria. It may well be that *Hauericeras* and *Gardeniceras* are homoeomorphs that acquired a keel independently. The only distinctive feature to justify Hauericeratinae is the presence of a keel, and as noted, this feature has appeared more than once in the evolution of the Desmoceratidae and we regard Hauericeratinae as unnecessary, and place *Hauericeras* in Puzosiinae – contrary to the views of Matsumoto (1938, pp. 6–7)

Crick (1907, p. 242–3; pl. 15, fig. 5) referred two poorly preserved fragments of compressed ammonites from the southern branch of the Manuan Creek in northern KwaZulu-Natal to *Hauericeras.* They are illustrated here as Fig. 10 I–L, and appear to be fragments of an Albian or Cenomanian puzosiine, possibly *Bhimaites* Matsumoto, 1954.

FIELD LOCALITIES

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

SYSTEMATIC PALAEONTOLOGY

Superfamily Desmoceratoidea Zittel 1895
Family Desmoceratidae Zittel, 1885
Subfamily Puzosiinae Spath, 1922
(= Hauericeratinae Matsumoto, 1938)

Genus *Hauericeras* de Grossouvre, 1894
Schlueteria Rollier, 1922, p. 359, *non* Fritsch in Fritsch & Kafka, 1887, p. 33; *Pseudogardenia* Tomlin, 1930, p. 23.

Type species
Ammonites pseudogardeni Schlüter, 1872, p. 54, pl. 16, figs 3–6, by original designation by de Grossouvre, 1894, p. 219.

Subgenus *Gardeniceras* Matsumoto & Obata, 1955

Type species
Ammonites gardeni Baily, 1855, p. 450, pl. 11, fig. 3, by original designation by Matsumoto & Obata, 1955, p. 134.

Hauericeras* (*Gardeniceras*) *gardeni Baily, 1855,
Figs 1A–C, 2, 3A–D, 4A–F, 5A–H, 6, 7, 10M–O

1855	*Ammonites gardeni* Baily, p. 450, pl. 11, fig. 3.
non 1865	*Ammonites gardeni* Baily; Stoliczka, p. 61, pl. 33, fig. 4. (= *H.*(*G.*) *angustum* Yabe, 1904.
non 1869	*Ammonites Gardeni* Baily; Favre, p. 12, pl. 4, fig. 1 (= *Hauericeras* (*Gardeniceras*) *sulcatum* (Kner, 1850)).
1871	*Ammonites rembda* Forbes; Griesbach, p. 63, pl. 3, figs 2–3.
?*non* 1879	*Ammonites Gardeni* Baily; Whiteaves, p. 102.
non 1890	*Desmoceras gardeni* (Baily); Yokoyama, p. 184, pl. 20, fig. 10 (=*Hauericeras* (*Gardeniceras*) *angustum* Yabe, 1904).
1894	*Hauericeras gardeni* (Baily); de Grossouvre, p. 219.
?*non* 1895	*Desmoceras Gardeni* (Baily); Whiteaves, p. 131.
non 1898	*Hauericeras Gardeni* (Baily); Kossmat, p. 123 (188), pl. 18 (24), fig. 7.
?*non* 1903	*Hauericeras gardeni* (Baily); Whiteaves, p. 352.
1906	*Hauericeras Gardeni* (Baily); Woods, p. 332.
?*non*1907	*Hauericeras* cf. *Gardeni* (Baily); Pervinquière, p. 166, pl. 7, fig. 1, 3–6.
?1908	*Desmoceras* (*Hauericeras)* cf. *Gardeni* (Baily); Kilian & Reboul, p. 18.
non 1913	*Hauericeras gardeni* (Baily); Nowak, p. 371, pl. 41, fig. 12; pl. 43, fig. 34; pl. 45, figs 44, 45 (= *Hauericeras* (*Gardeniceras*) *sulcatum* (Kner, 1850)
1921	*Hauericeras gardeni* (Baily); Van Hoepen, p. 27, fig. 15.
1921	*Hauericeras gardeni* (Baily); Spath, p. 238, text-fig. A-1 to A-9.
1922	*Hauericeras gardeni,* Baily sp.; Spath, p. 129.
1925	*Hauericeras gardeni* (Baily); Diener, p. 95 (*pars*).
1930	*Hauericeras gardeni* Baily; Besairie, p. 220, pl. 20, fig. 3.

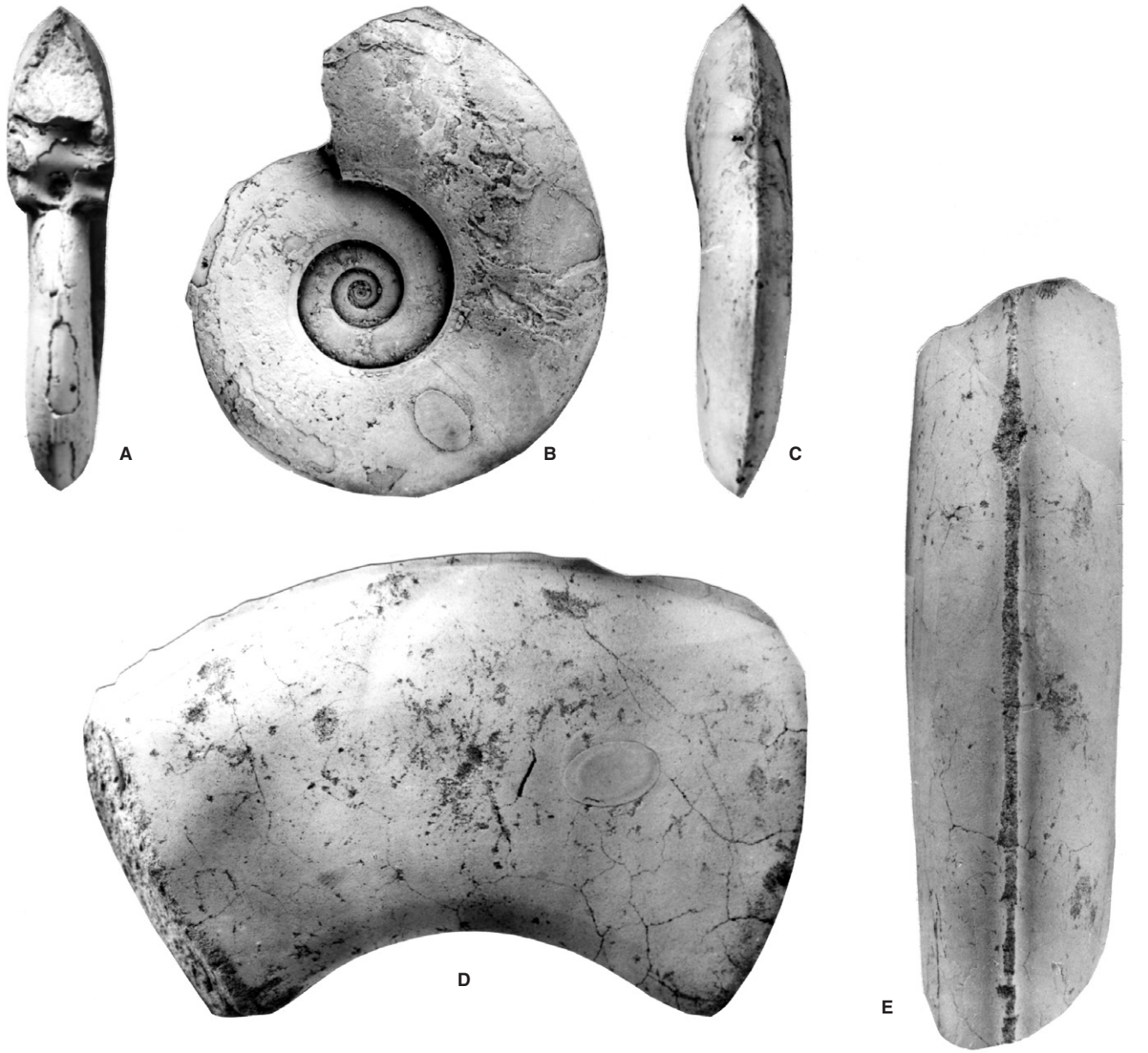

Figure 1. **A–C**, *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). The lectotype, BMNH C72219, the original of Baily 1855, p. 456. pl. 11, fig. 3a, b. **D**, **E**, *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, 1961, BMNH C35621, a paralectotype of *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). Both specimens are from " 'White-mens houses', coast of S. Africa near the Umzambani River", that is to say the Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

1931	*Hauericeras Gardeni* Baily; Basse, p. 23, pl. 4, figs 2–4, pl. 10, fig. 8; pl. 11, fig. 1.
1932	*Hauericeras gardeni* (Baily); Collignon, p. 17, pl. 3, fig. 3.
1938	*Hauericeras Gardeni* (Baily); Collignon, p. 74.
non 1942	*Hauericeras gardeni* (Baily); Matsumoto, p. 25 (=*Hauericeras* (*Gardeniceras*) *angustum* Yabe, 1904).
?*non* 1952	*Hauericeras gardeni* (Baily); Usher, p. 65, pl. 5, figs 1, 2; pl. 21, fig. 10.
1955	*Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Matsumoto & Obata, p. 140 *et seq.*; text-figs 8–10.
1961	*Hauericeras gardeni* (Baily); Collignon, p. 76, pl. 28; pl. 29; pl. 30, figs 1, 2; text-figs 13–14.
1969	*Hauericeras* (*Gardeniceras*) *gardeni* Baily; Collignon, p. 66, pl. 539, fig. 2114.
1973	*Hauericeras* cf. *H. gardeni* (Baily); Kennedy & Klinger *in* Kennedy, Kauffman & Klinger, p. 101, p. 6, fig. 2.
1975	*Hauericeras gardeni* (Baily); Kennedy & Klinger, p. 279, 280.
1977	*Hauericeras gardeni* (Baily, 1855); Klinger & Kennedy, p. 80, text-figs 7A–C, 8A.
non 1979	*Hauericeras* (*Gardeniceras*) *gardeni* (Baily); Summesberger, p. 133, pl. 6, fig. 27; text-fig. 19.
1982	*Hauericeras gardeni* (Baily); Immel, Klinger & Wiedmann, p. 16 (*pars*), pl. 6, figs 2, 3, *non* pl. 5, figs 1–4; *non* pl. 6, figs 1,4; *non* text-fig. 5.
non 1982	*Hauericeras* (*Gardeniceras*) aff. *gardeni* (Baily); Renz, p. 106, pl. 35, figs 2–4.
non 1987	*Hauericeras gardeni* (Baily); Immel, p. 91.
1990	*Hauericeras gardeni* (Baily, 1855); Matsumoto, Toshimitsu & Kawashita, p. 451.
1995	*Hauericeras* (*Gardeniceras*) cf. *gardeni* (Baily, 1855); Kennedy in Kennedy, Bilotte & Melchior, p. 396.
2003b	*Hauericeras* (*Gardeniceras*) *gardeni* (Baily1855); Cooper, p. 159, figs 6A–D.

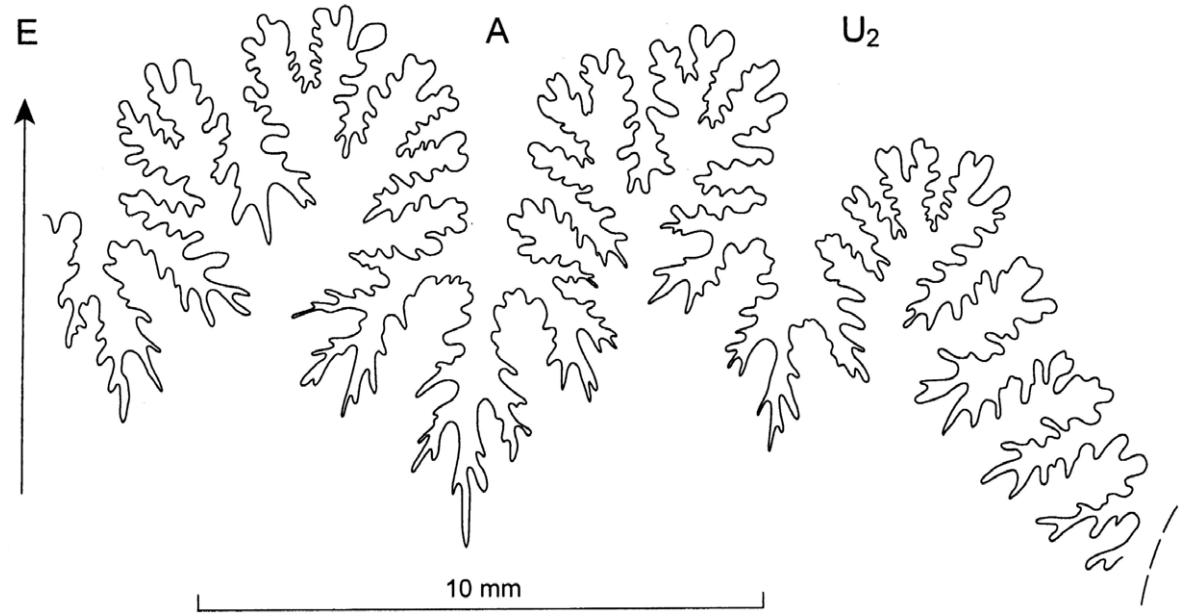

Figure 2. External suture of *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855), based on OUM KX10843.

Types

Spath (1921, p. 238) refers to 'Baily's type (BM Geol. Soc. Coll., no. 11370) and the larger of the two fragmentary cotypes (No. 11371) from which Baily's figure of the suture line was taken,' and subsequently (1922, p. 131) refers to BMNH 11371 as 'Baily's paratype'. This does not constitute a valid lectotype designation in our view. Accordingly, we designate BMNH C72219 (Geological Society Collection no. R11370) lectotype. It is the original of Baily 1855, pl. 11, figs 3a,b, and is illustrated here as Fig. 1A–C. The locality is given on an attached contemporary paper label as 'White-mens houses Umzambani River.' Paralectotype BMNH C35621 (Geological Society Collection no. R11369) is figured here as Fig. 1D,E, and is referred to *Hauericeras pseudoangustum* Collignon, 1961, below. It has an associated grey-blue paper label: '*Ammonites gardeni* nov. sp. Cretaceous Formation Amzamba River Port Natal. Presd. By Captain Garden D.B. p. 237.' Paralectotype BMNH C35622 (Geological Society Collection no. R11370) has the same associated information, and is illustrated here as Fig. 3A,B; it provided the basis for Baily's illustration of the suture line of the species (1855, pl. 11, fig. 3c).

Garden (1855, p. 453) gave the following account, 'About three miles to the southward of the river commence certain excavations in the cliffs, formed by the actions of the sea, and called by the natives 'Izinhuluzabalungu … the houses of the white men' so called probably from the caverns having once been occupied by shipwrecked sailors.' This clearly identifies the locality of the types as locality 1 of Kennnedy & Klinger (1975), illustrated as text-figs 1–3 in Klinger & Kennedy (1980), the Izinhluzabalungu Caves of Griesbach (1871, fig. 5) and the Umzamba Cliff of Plows (1921), on the north side of the Mzamba estuary.

Material

BMNH C8516 and C18517 (both mentioned by Spath 1922, p. 130), C18518 (mentioned by Spath 1922, p. 130, figured by Matsumoto & Obata 1955, p. 141, text-fig. 10), C18519, C18520 (both mentioned by Spath 1922, p. 130, the latter figured by Matsumoto & Obata 1955, p. 140, text-fig. 9), C18521 and C18522 (both mentioned by Spath 1922, p. 130), C18523–7, C18528 (the original of Spath 1921, p. 238, fig. A1–7) (Fig. 3C), C18530, C18531 (the original of Spath 1921, p. 238, text-fig. A-8 (Fig. 3D herein), C18532, C18534, C18535 (mentioned by Spath 1922, p. 131), C18536, C18537 (mentioned by Spath 1922, p. 130), C18538, C18539, C18540 (mentioned by Spath 1922, p. 130), C18541, C18544–18549, C18531. All of these specimens are from the Mzamba Formation of locality 1 of Kennedy & Klinger (1975) although the details on associated labels vary slightly. OUM KX90, SAM-PCZ* all from locality 1 of Kennedy & Klinger (1975), where the species ranges from Santonian III to Campanian I (Klinger & Kennedy 1980, fig. 4). SAM BH9/120/22, BH9/124, BH9/127, 80, from the St Lucia Formation, Santonian III, in the BH9 borehole, 14 km west of Richards Bay in northern KwaZulu-Natal. OUM KX10671–1076 and SAM-PCZ* from the St Lucia Formation, Campanian I, at locality 14 of Kennedy & Klinger (1975) south of Mtubatuba, northern KwaZulu-Natal. OUM KX5353, 5356, 10838, 10839, 10841, 10843, 10845, SAM-PCZ* from the St Lucia Formation, Santonian I, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. OUM KX4970a–b, SAM-PCZ* from the St Lucia Formation, Campanian I at locality 105 of Kennedy & Klinger (1975; see also Klinger & Kennedy 1980a, fig. 130) on the southeastern shores of False Bay, lake St Lucia, northern KwaZulu-Natal. OUM KX12818, 12872–12876, 12880, 12881, 12891–12923, 13037, 13057–13060, 13078, SAM-PCZ* from locality 74 of Kennedy & Klinger (1975), Die Rooiwalle, northwestern False Bay, Lake St Lucia, northern KwaZulu-Natal. The species has been collected *in situ* from beds 2–22 of the section, spanning the Santonian I–Campanian I interval.

*Unregistered.

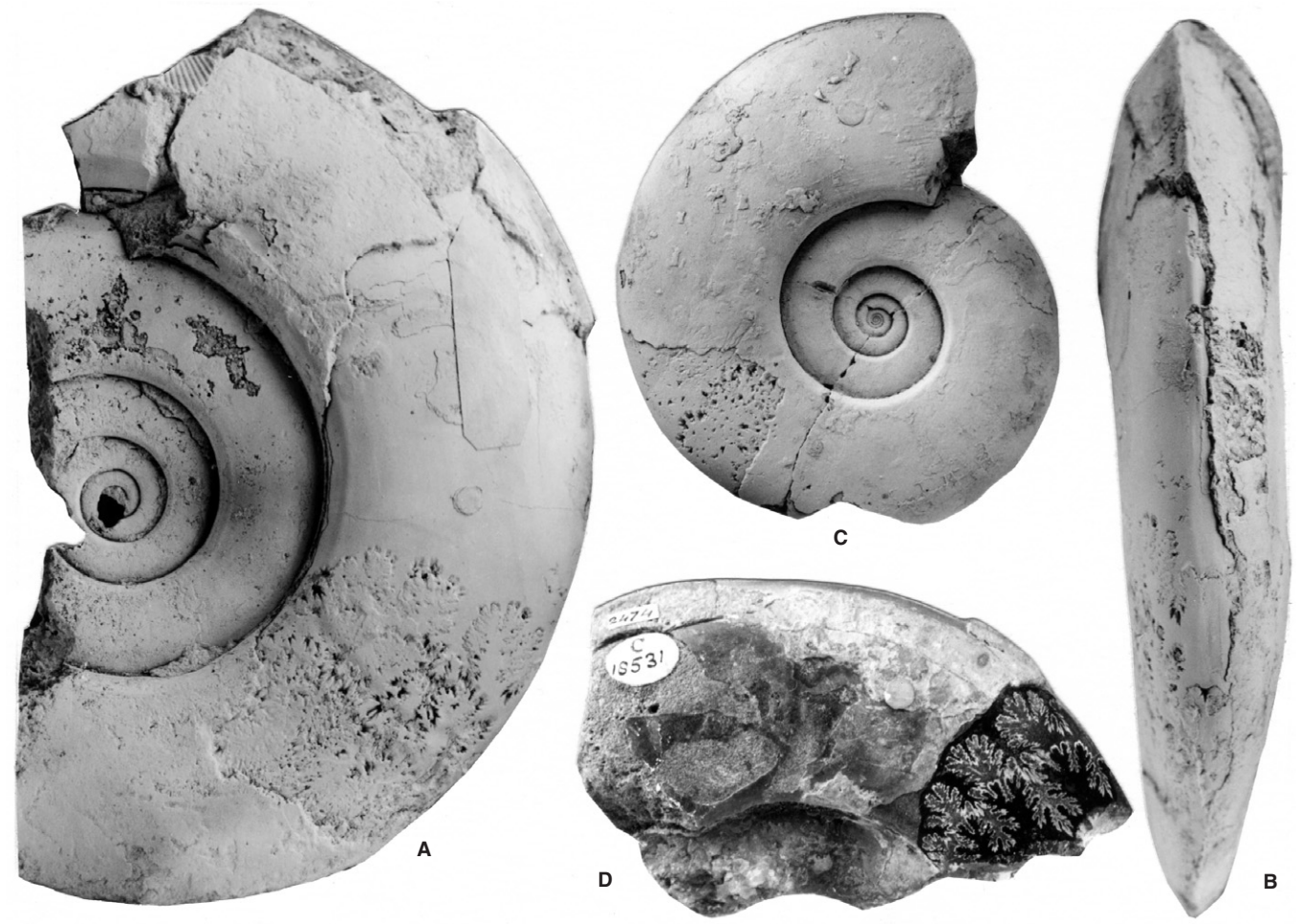

Figure 3. **A–D.** *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A**, **B**, paralectotype BMNH C35622, the original of Baily, 1855, pl. 11, fig. 3c (suture), from " 'White-mens houses', coast of S. Africa near the Umzambani River", that is to say the Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. **C**, BMNH C18528, the original of Spath 1921, p. 238, text-fig. A-1-7, 9. **D**, BMNH C18531, the original of Spath 1921, p. 238, text-fig. A-8, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

Dimensions

	D	Wb	Wh	Wb:Wh	U
KX10844	75.0 (100)	15.2(20.3)	25.5 (34.0)	0.60	31.3 (41.7)
C72219	77.9 (100)	16.4 (21.0)	29.0 (37.2)	0.57	29.5 (37.9)
C18547	81.3 (100)	16.2 (19.9)	30.4 (37.4)	0.53	28.7 (35.3)
KX5350	82.3 (100)	16.1 (19.6)	29.2 (35.5)	0.55	33.0 (40.1)
C18527	87.0 (100)	18.0 (20.7)	32.2 (37.0)	0.55	35.3 (40.6)
KX10843	89.3 (100)	16.8 (18.8)	31.7 (35.5)	0.53	37.1 (41.5)
C18526	93.1 (1000	18.0 (19.8)	33.0 (35.4)	0.55	34.6 (37.2)
C18522	93.5 (100)	19.0 (20.3)	31.6 (33.8)	0.6	38.6 (41.3)
C18538	105.8 (100)	21.4 (20.2)	37.4 (35.3)	0.57	41.0 (38.7)
KX5349	111.1 (100)	20.8 (18.7)	39.5 (35.5)	0.53	47.3 (42.6)
KX90	124.8 (100)	20.1 (16.1)	42.5 (34.1)	0.47	53.2 (42.6)
C18540	130.5 (100)	22.8 (17.5)	42.6 (32.6)	0.53	58.1 (44.5)
C18518	130.7 (100)	28.0 (21.4)	43.3 (33.1)	0.65	53.6 (41.0)
C18523	131.6 (100)	22.2 (16.8)	42.3 (32.1)	0.52	56.7 (43.1)

Description

The inner septate whorls are well represented by the lectotype, BMNH C72219 (Baily 1855, p. 456, pl. 11, fig. 3a, b; Fig. 1A–C herein) which is partially exfoliated, retaining original aragonitic shell layers. There are indications of the former presence of at least one further whorl. Coiling is very evolute, the umbilicus very broad and shallow, comprising 37.9% of the diameter, with 41% of the previous whorl covered. The low umbilical wall is flattened and outward-inclined with a shallow groove just below the umbilical shoulder. The umbilical shoulder is sharp on the penultimate whorl, becoming rounded on the outer whorl. The whorl section is compressed, with a whorl breadth to height ratio of 0.57, the greatest breadth low on the flanks, the inner flanks flattened and feebly convergent, the outer flanks convex and converging to the acutely fastigiate venter. A strong siphonal keel is present where shell is preserved, but absent on the internal mould. There is no ornament preserved on the surface of the exfoliated shell. Part of a single constriction is visible on the internal mould on one flank. The delicate growth lines shown in Baily's figure are not detectable.

Paralectotype BMNH C35622 is the basis of Baily's figure of the suture (1855, pl. 11, fig. 3c; Matsumoto & Obata

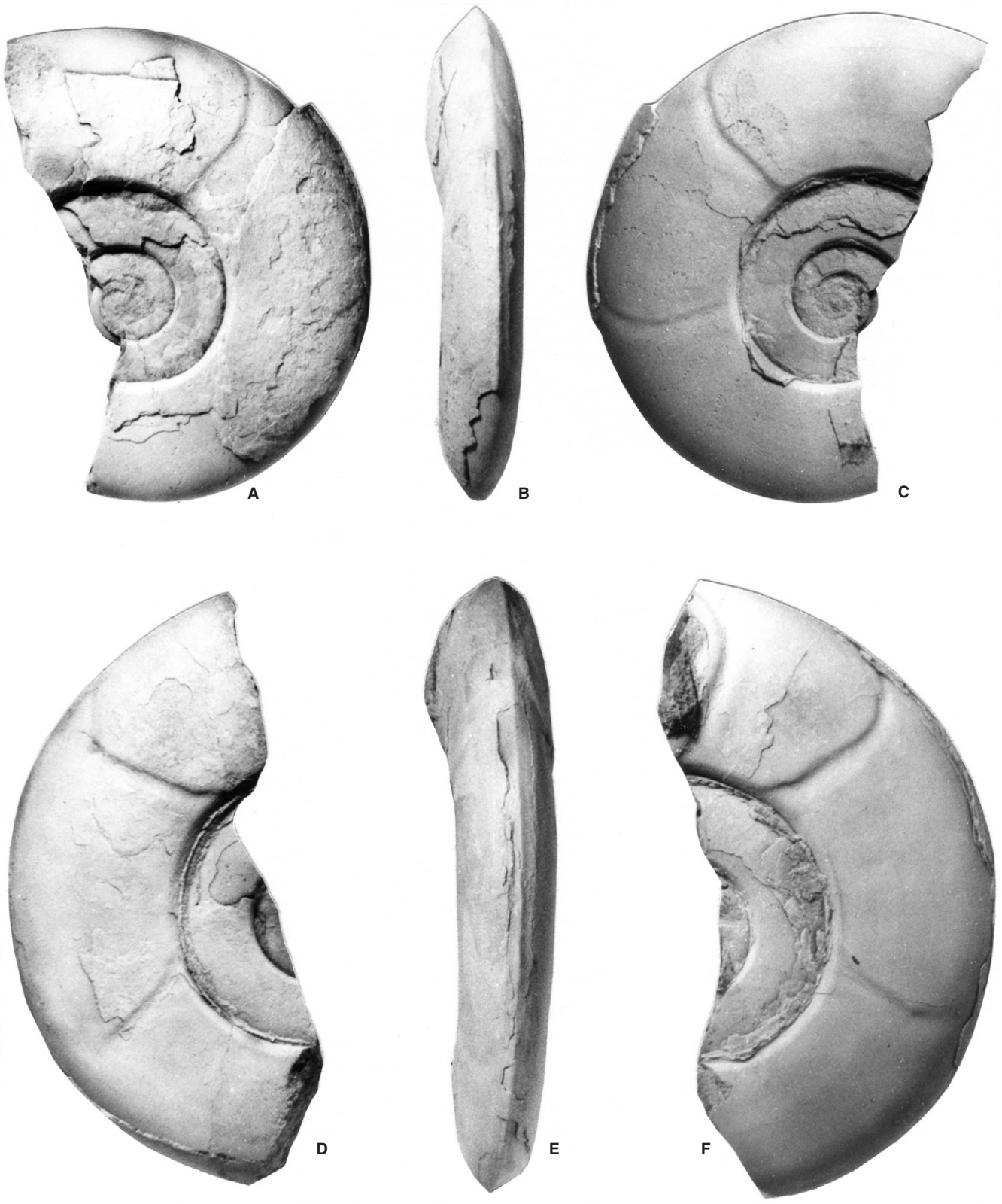

Figure 4. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A–C**, OUM KX10843; **D–F**, OUM KX10840, from the St Lucia Formation, Santonian III, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. Figures are ×1.

1955, text-fig. 8; Fig. 3A,B). It comprises fragmentary inner whorls and a 180° sector of outer whorl; the estimated maximum diameter is 130 mm. The adapertural 90° sector is body chamber. The specimen retains partially exfoliated shell in places. Constrictions are not detectable on the early phragmocone whorls. A weak constriction is present at the adapertural end of the phragmocone, and there is a single constriction on the body chamber fragment. The constrictions are concave, projecting strongly forwards on the ventrolateral shoulders and venter. The constrictions are far less conspicuous than is suggested by the sketch in Matsumoto & Obata (1955, text-fig. 8a).

BMNH C18518 (Fig. 7) is the 'thickest form' mentioned by Spath (1922, p. 130), and figured by Matsumoto &

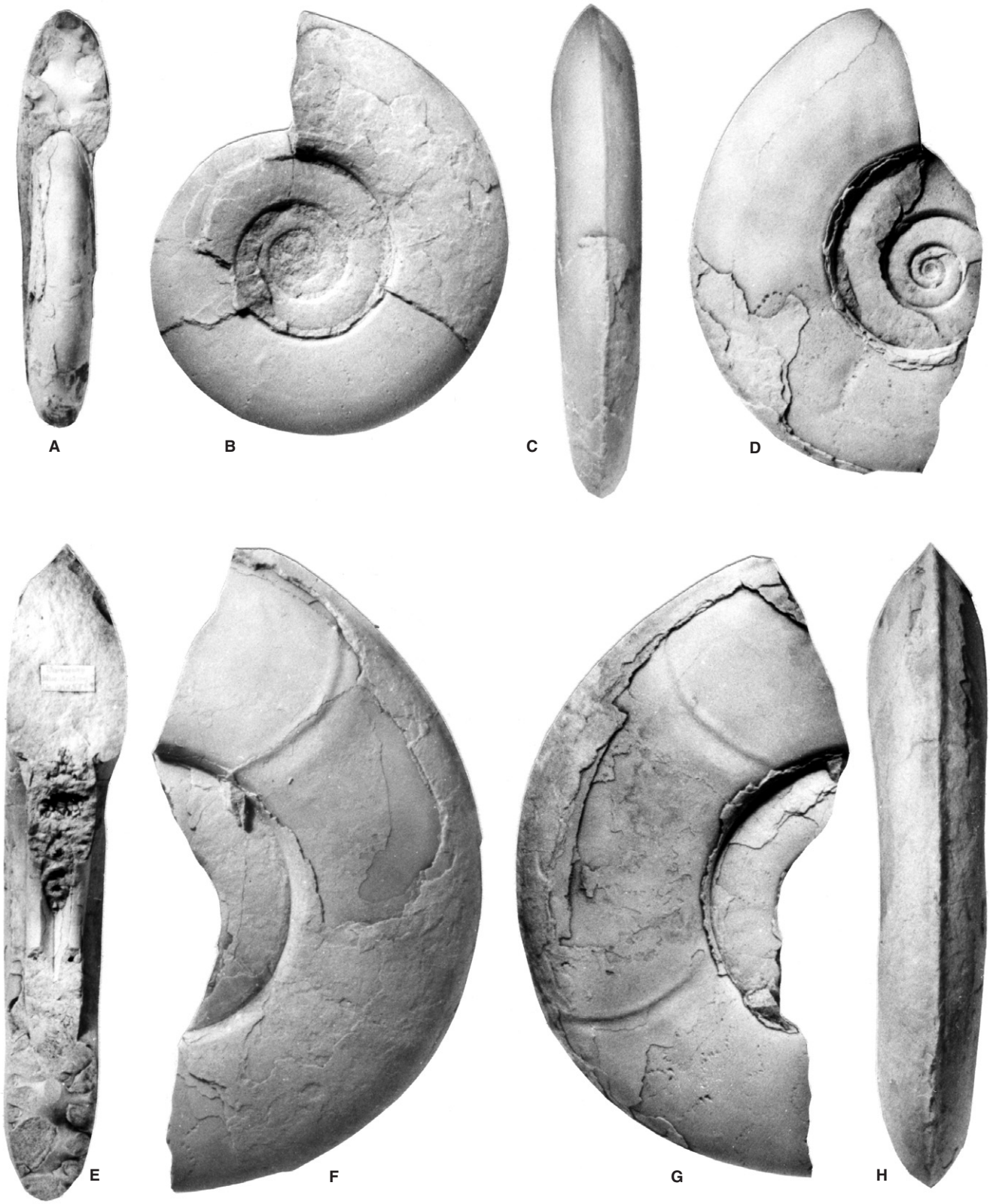

Figure 5. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). **A**, **B**, OUM KX10844; **C**, **D**, OUM KX5350; **E–H**, OUM KX5349, all from the St Lucia Formation, Santonian III, locality 17 of Kennedy & Klinger (1975), southeast of Mtubatuba, northern KwaZulu-Natal. Figures are ×1.

Obata (1955, text-fig. 10). The specimen has a maximum preserved diameter of 130.7 mm, and retains extensive areas of shell. Coiling is very evolute. The wide, shallow umbilicus comprises 41% of the diameter, the umbilical wall low, the umbilical shoulder very narrowly rounded. The whorl breadth to height ratio is 0.65, the flanks feebly convex, and feebly converging, the greatest breadth just outside the umbilical shoulder. The ventrolateral shoulders are broadly rounded, the venter acutely fastigiate with a strong sharp keel where shell is preserved on both phragmocone and body chamber, and on the internal mould of the body chamber. The internal mould of the phragmocone lacks a keel. The shell surface is smooth on the phragmocone, apart from delicate growth lines that

Figure 6. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). OUM KX 90, from the Mzamba Formation, Santonian III, at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

are feebly prorsiradiate on the inner flank, concave on the middle to outer flank and projected strongly forwards on the ventrolateral shoulders and venter, indicating the presence of a long ventral rostrum at the aperture. The adapertural 240° sector is body chamber, with four constrictions that become increasingly prominent as size increases. They are concave across the flanks and project strongly forwards on the ventrolateral shoulders and venter. The adapertural edge of the constrictions is marked by a feeble collar-rib. The final constriction appears to be just before a damaged apertural margin that bears a ventral rostrum.

OUM KX 90 (Fig. 6) is 120 mm in diameter, and retains extensive traces of partially exfoliated shell. Six constrictions are detectable on both the outer whorl and the penultimate whorl. Very well-preserved body chambers from locality 17 (Figs 4A–F, 5A–H) show the presence of strong constrictions, three per half whorl, with an adapical collar-rib on the internal mould. There is little or no indication of the constrictions where shell is preserved on the opposite flank of the same individual (OUM KX10843: compare Figs 4A and C; OUM KX5349: compare Figs 5F and 5G).

An unexplained feature of partially exfoliated specimens is particularly well-shown by BMNH C18520 (Fig. 10M–O, the original of Spath 1922, p. 130, and Matsumoto & Obata 1955, text-fig. 9). The translucent layers of replaced shell material show a pattern of deeply concave, narrow dark bands (much more deeply concave than the constrictions) separated by wider white bands. This feature is largely within the shell material, being scarcely indicated on the surface, as can be seen from the whitened and unwhitened picture of the specimen (Fig. 10N, uncoated; Fig. 10O, coated with ammonium chloride). These patterns presumably relate to the accretion pattern of the shell material; similar structures are shown by BMNH C18535 and C18539.

A keel is present on phragmocones and body chambers with shell preserved, and on internal moulds of body chambers. The keel was thus initially hollow and open to the interior of the shell, and thereafter infilled with shell material and solid on the phragmocone, but remained hollow on the body chamber. (See also Matsumoto & Obata 1955, text-figs 8–10; Klinger & Kennedy 1977, figs 7a,c, 8a.)

The suture (Fig. 2) is deeply incised, with asymmetrically bifid E/A and A/U2, deep asymmetrically trifid A (=L) and U2, the suspensive lobe strongly retracted.

Discussion

Hauericeras (*Gardeniceras*) *gardeni*, as interpreted from the lectotype, paralectotype BMNH C35622 and the abundant Mzamba material referred to the species, has a compressed whorl section with whorl breadth to height ratios

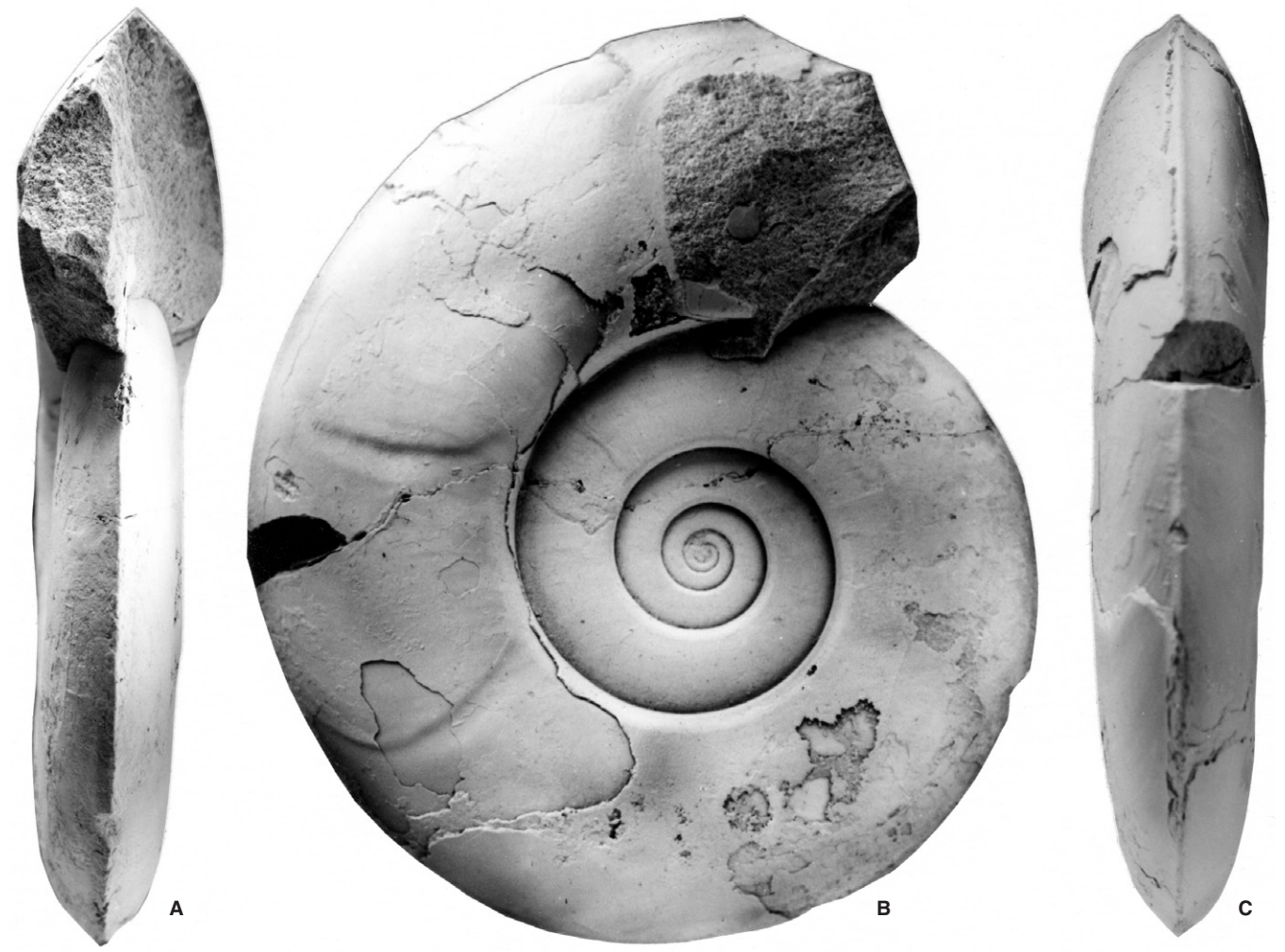

Figure 7. *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). BMNH C18518, the original of Spath 1922, p. 130 and Matsumoto & Obata, 1955, text-fig. 10, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. Figures are ×1.

of 0.47–0.6, the majority falling between 0.53 and 0.57, the umbilicus comprising between 35.3% and 47.0% of the diameter, the majority falling between 37.2% and 44.5%. Concave growth lines are only occasionally discernible, perhaps as a result of the partial exfoliation of most specimens. Concave constrictions are weak or imperceptible on the surface of the shell, but conspicuous on the internal mould, and are markedly strengthened on the body chamber, with an associated adapertural collar rib. On this basis, *H.* (*G.*) *gardeni* can be distinguished from the closely allied *H.* (*G.*) *angustum* Yabe, 1904 (p. 33, pl. 5, figs 5, 6) which was carefully revised by Matsumoto & Obata (1955, p. 137, pl. 24, fig. 6; pl. 28, figs 1, 2; pl. 29, figs 1–5; text-figs 5, 7) and Matsumoto *et al.* (1990, p. 443, text-figs 2–7). On the basis of the observations of these authors, and specimens in the Natural History Museum, London (BMNH C47749–50, mentioned by Spath, 1922 p. 131) *H.* (*G.*) *angustum* has sinuous growth lines and constrictions that are concave on the innermost flank, convex on the inner to middle flank, and concave on the outer flank. Body chambers of *gardeni* have strengthened ribs on the body chamber, with a collar rib; they are weak on body chambers of *angustum,* some specimens of which develop what appear to be coarse inner flank ribs on the body chamber (Matsumoto & Obata 1955, pl. 28, fig. 2). Dimorphism has been recognized in *H.* (*G.*) *angustum*. Matsumoto *et al.* (1990, text-fig. 2) figured what they regarded as a macroconch 225 mm in diameter with a sinuous, biconcave mouth border (1990, text-fig. 3) and microconchs, the best preserved of which (1990, text-figs 6, 7) is 113 mm in diameter, with a long lappet at mid-flank, and longer ventral rostrum. Matsumoto *et al.* (1990, p. 451) thought that BMNH C18518, figured here as Fig. 7, was the macroconch of *H.* (*G.*) *gardeni.* This specimen is 135 mm in maximum preserved diameter, with an estimated 230° sector of body chamber, what appears to be a long ventral rostrum, but no trace of a lappet. Matsumoto *et al.* (1990, p. 452) then proposed that the two large figured specimens of *H.* (*G.*) *gardeni* from Madagascar figured by Collignon (1961, pls 28, 29) were macroconchs. These appear to lack the final sector of body chamber and are preserved to diameters of 183 and 195 mm. They are far larger than any material from Mzamba or KwaZulu-Natal that we have seen, and we are unable to confirm dimorphism in the material before us.

Hauericeras (*Gardeniceras*) *pseudoangustum* Collignon, 1961 (p. 83, text-fig. 18) is smooth, with weak sinuous constrictions that are restricted to the body chamber.

Hauericeras (*Gardeniceras*) *madagascariense* Collignon,

Figure 8. *Hauericeras* (*Gardeniceras*) *madagascariense* Collignon, 1961. SAM-7043, from the uppermost beds of the Lower Campanian of the Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in the Eastern Cape Province. Figure is ×0.9.

1961 (p. 81, pl. 31, fig. 1; pl. 32, fig. 1; text-figs 15–17) differs from *H.* (*G.*) *gardeni* in its much broader whorl section, with whorl breadth to height ratios of up to 0.76, and sinuous, biconcave constrictions.

If the strength and course of the constrictions is regarded as a key feature, then material with sinuous rather than simple concave constrictions must be excluded from *H.* (*G.*) *gardeni.* These include material from Tunisia (Pervinquière 1907), Austria (Summesberger 1979; Immel *et al.* 1982; Immel 1987) and Venezuela (Renz 1982).

Occurrence

In South Africa, *H.* (*G.*) *gardeni* first appears in Santonian I and ranges into Campanian I of Kennedy & Klinger (1975), with records from the Mzamba Formation of the coastal outcrops in northeastern Eastern Cape Province, and the St Lucia Formation of northern KwaZulu-Natal. In Madagascar it ranges from Upper Santonian through all of the Lower Campanian. There are also records from the Santonian of southeastern France and Angola. Records of *H.*(*G.*) *gardeni* from the Santonian–Campanian of south India and Vancouver Island, British Columbia, Canada are best referred to *H.*(*G.*) *angustum* as pointed out by Matsumoto & Obata (1955, p. 144) and Matsumoto (1959, p. 25)

Hauericeras pseudoangustum Collignon, 1961,
Figs 1D,E; 9

1961 *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, p. 83, text-fig. 18

Type

The holotype, by original designation, is no. 2795 in the collections of the Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris, the original of Collignon. 1961 text-fig. 18, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of

Figure 9. *Hauericeras* (*Gardeniceras*) *pseudoangustum* Collignon, 1961. The holotype, no. 2795 in the collections of the Laboratoire de Paléontologie of the Musém d'Histoire Naturelle, Paris, the original of Collignon. 1961, text-fig. 18, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Triribihina), Madagascar. Figures are ×1.

Collignon 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar, illustrated here as Fig. 9.

Material

BMNH C35621 (Fig. 1D,E), a paralectotype of *Ammonites gardeni* Baily, 1855, from the Mzamba Formation at the mouth of the Mzamba River, Eastern Cape Province, corresponding to locality 1 of Kennedy & Klinger (1975).

Description

BMNH C35621 is an internal mould of a body chamber fragment with a maximum preserved whorl height of 63.2 mm and a whorl breadth to height ratio of 0.52. There are traces of a single feeble constriction that is convex on the inner flank, concave on the outer flank, and projected strongly forwards on the outermost flank and ventrolateral shoulder. The estimated total original diameter of the present specimen is 170 mm.

Discussion

Whorl section and course of the single constriction separate this specimen from *Hauericeras* (*Gardeniceras*) *gardeni,* but correspond to that of *Hauericeras* (*Gardeniceras*) *pseudoangustum,* to which it is referred. Collignon's (1961, pp. 83–84) description leaves no doubt as to the affinities of the specimen: 'Coquille très plate, discoidale, à tours élevés, se recouvrant d'un peu plus de 2/5; flancs plats, parallèles au voisinage de l' ombilic et jusque vers leur milieu, puis s'abaissent doucement vers la région externe arrondie d'abord, puis devenant ogivale avec carène. Versant ombilical relativement élevé, vertical, limité par une arrête mousse. Ombilic moyennement large dégeant les tours internes plats, en escalier. Aucune ornamentation; seule un constriction est visible très nettement au début de la chambre d'habitation, immédiatement en avant de la dernière cloison. Elle est légèrement tordue en S étiré, très allongé. Sur le plus grand exemplaire … il y a 3 constrictions visibles, toutes sur la chambre d'habitation.'

Occurrence

Uppermost Santonian or Lower Campanian, Mzamba Formation at locality 1 of Kennedy & Klinger (1975); Lower Campanian Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Madagascar.

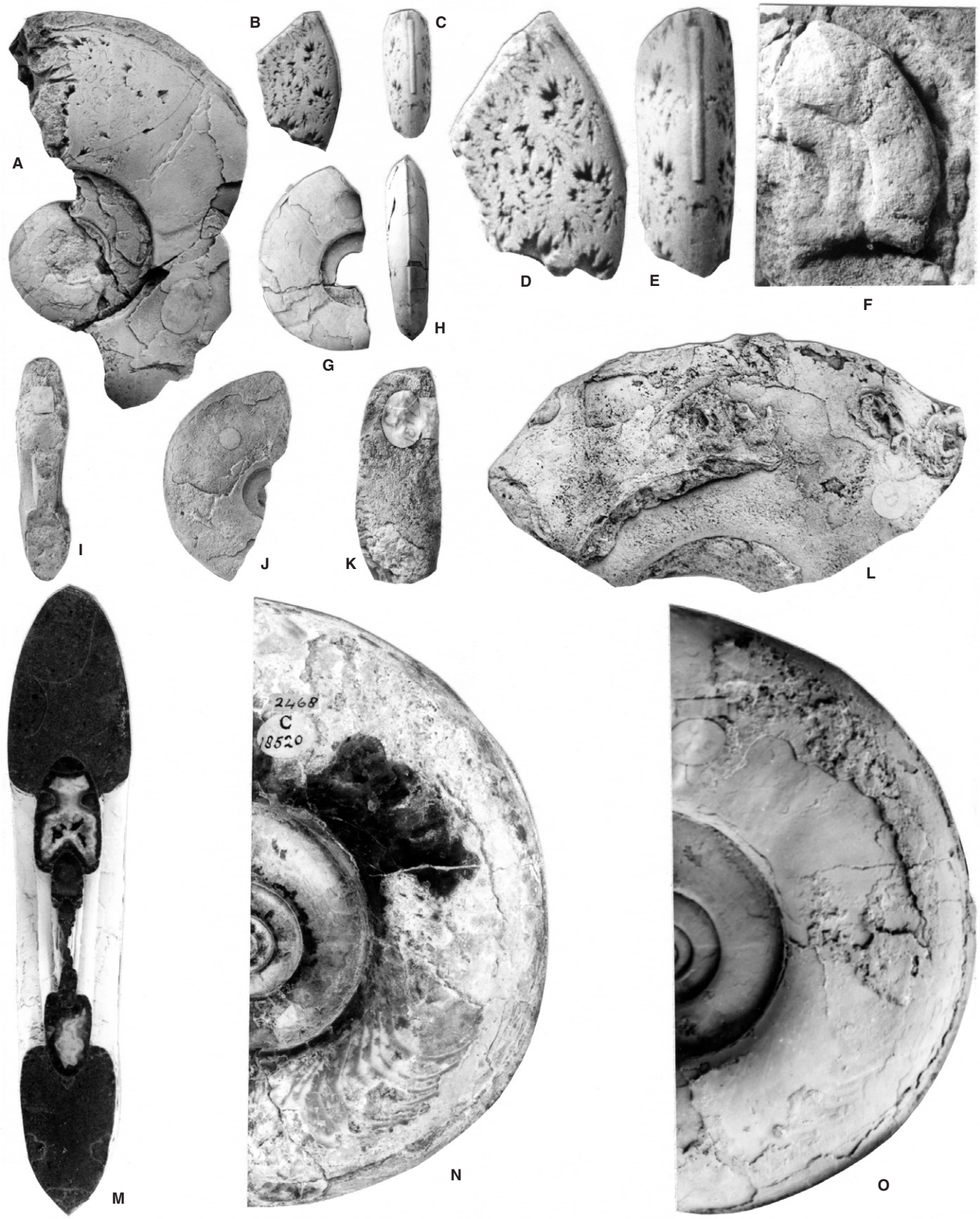

Figure 10. **A–H**. *Hauericeras* (*Gardeniceras*) *rembda* (Forbes, 1846). **A**, BMNH C51023, a paralectotype; **G**, **H**, BMNH C51024, the lectotype. Both specimens are from the Upper Maastrichtian Valudavur Formation of Pondicherry, south India. **B–E**, OUM KX6973, from the St Lucia Formation, Maastrichtian II, upper Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone of locality 20 of Kennedy & Klinger (1975), east-southeast of Mtubatuba, northern KwaZulu-Natal. **F**, OUM KX8906, from the St Lucia Formation, Maastrichtian III, upper Upper Maastrichtian of locality 128 of Kennedy & Klinger (1975), Lake St Lucia, northern KwaZulu-Natal. **I–L**, indeterminate Puzosiinae. **I**, **J**, BMNH C18275, the original of *Hauericeras* sp. of Crick, 1907, p. 242, pl. 15, fig. 5; **K**, **L**, BMNH C18276, the original of *Hauericeras* sp. of Crick, 1907, p. 243. Both specimens were described as being from the southern branch of the Manuan Creek. **M–O**, *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855). BMNH C18520, the original of Spath 1922, p. 130 (table) and Matsumoto & Obata, 1955, text-fig. 9, from the Upper Santonian to Lower Campanian Mzamba Formation at locality 1 of Kennedy & Klinger (1975), in Eastern Cape Province. The specimen is uncoated in Figs M and N; the latter shows the distinctive colour banding within the partially exfoliated shell material. Figures A, D, E are ×2; B, C, F–O are ×1.

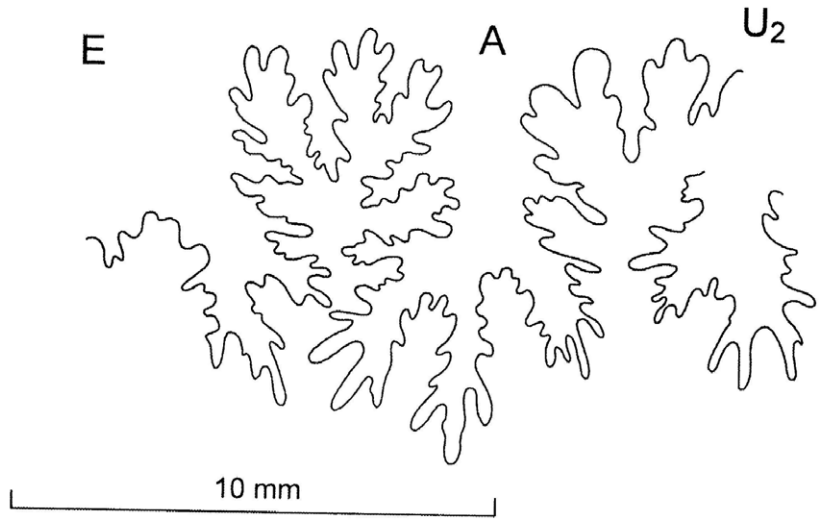

Figure 11. External suture of *Hauericeras* (*Gardeniceras*) *rembda* (Forbes, 1846), based on OUM KX6937.

Hauericeras (Gardeniceras) madagascariense Collignon, 1961, Fig. 8

1961 *Hauericeras* (*Gardeniceras*) *madagascariense* Collignon, p. 81, pl. 31, fig. 1; pl. 32, fig. 1; text-figs 15–17.
1969 *Hauericeras* (*Gardeniceras*) *madagascariense* Coll.; Collignon, p. 66, pl. 539, fig. 2115.
1980b *Hauericeras madagascariense* Collignon, 1961; Klinger & Kennedy, p. 219, text-fig. 5B.
?1996 *Hauericeras* (*Gardeniceras*) *gardeni* (Baily, 1855); Cooper & Greyling, p. 23, fig. 7m–n.

Type

The holotype by original designation, is the orignal of Collignon, 1961, pl. 31, fig. 1, no. 2848 in the collections of the Muséum National d'Histoire Naturelle, Paris, from the Lower Campanian Zone à *Anapachydiscus arrialoorensis* (= the Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969) of Iampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar.

Material

SAM-7043 from the Mzamba Formation, probably bed A15 of Klinger & Kennedy (1980, text-fig. 4) (Bed T2 of Gevers 1923; see also Gevers 1977) at locality 1 of Kennedy & Klinger (1875), Eastern Cape Province. OUM KX1781, from the St Lucia Formation, Campanian II at locality 109 of Klinger & Kennedy (1975) on the southwestern corner of the Nibela Peninsula, Lake St Lucia, northern KwaZulu-Natal.

Description

SAM-7043 (Fig. 8) is a large specimen (D = *c.*160 mm) embedded in a concretion with specimens of *Baculites sulcatus* Baily, 1855 on the reverse side (Klinger & Kennedy 1997, fig. 64a). Part of the last septum is exposed. The body chamber occupies a sector of slightly more than 180°. Four concave constrictions are visible on the body chamber; the most prominent one near the adapical part. The umbilicus is wide, *c.* 45 % of the total diameter)

OUM KX1781 is an internal mould of a phragmocone 190 mm in diameter, the umbilicus shallow, comprising 47.5% of the diameter, with a low, feebly convex, outward-inclined umbilical wall and narrowly rounded umbilical shoulder. The whorl breadth to height ratio is 0.64, the inner and middle flanks flattened and feebly convergent, the outer flanks broadly rounded, converging to the narrowly rounded, arched venter of the internal mould. This is smooth, with no indication of constrictions. In places, traces of recrystallized shell on the venter demonstrate the presence of a sharp siphonal keel. The suture is very deeply and intricately incised, the saddles narrow-stemmed, bifid, with deep asymmetrically trifid A (=L).

Discussion

Hauericeras (*Gardeniceras*) *madagascariense* differs from *Hauericeras* (*Gardeniceras*) *gardeni* in its greater size, broader whorls, slightly larger umbilical diameter and feebly convex rather than narrowly rounded venter. The constrictions, well seen in SAM-7043, are concave, rather than sinuous as they are in *Hauericeras pseudoangustum.*

Occurrence. According to Collignon (1961, p. 82) *H.* (*G.*) *madagascariense* is restricted to the upper part of the Lower Campanian, zone of *Anapachydiscus arrialoorensis* redefined as the upper Lower Campanian Zone à *Menabites boulei* et *Anapachydiscus arrialoorensis* of Collignon, 1969 of Madagascar. Campanian II of KwaZulu-Natal. At Mzamba in the Eastern Cape, it has only been found in the topmost beds of the Mzamba Formation, above the level of abundant *H.* (G.) *gardeni.*

Hauericeras rembda (Forbes, 1846), Figs 10A–H, 11

1846 *Ammonites Rembda* Forbes, p. 111, pl. 7, fig. 3.
1846 *Ammonites Durga* Forbes, p. 104, pl. 7, fig. 11.
non 1871 *Ammonites rembda* Forbes; Griesbach, p. 63, pl. 3, figs 2–3 (= *Hauericeras gardeni*)
?1978 *Hauericeras* sp. cf. *H.* (*Gardeniceras*) *rembda* (Forbes); Matsumoto, Okada & Sakurai, pp. 323–324, fig. 3.
1992 *Hauericeras rembda* (Forbes, 1846); Kennedy & Henderson, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H (with full synonymy).

Types

The lectotype, by the subsequent designation of Matsumoto & Obata (1955, p. 145), is BMNH C51024, the

original of Forbes 1846, pl. 7, fig. 3; paralectotypes are BMNH C51023 and C51025. The figured syntype of *Ammonites Durga* Forbes, 1846, p. 104, pl. 7, fig. 11 is BMNH C51021. All of these specimens are from the Upper Maastrichtian Valudavur Formation of Pondicherry, south India.

Material

OUM KX6973, from the St Lucia Formation, Maastrichtian II, upper Upper Maastrichtian '*Inoceramus*' *ianjonaensis* Zone of locality 20 of Kennedy & Klinger (1975), ESE of Mtubatuba, northern KwaZulu-Natal. OUM KX8906, from the St Lucia Formation, Maastrichtian III, upper Upper Maastrichtian of locality 128 of Kennedy & Klinger (1975), Lake St Lucia, northern KwaZulu-Natal.

Description

OUM KX6937 (Fig. 10B–E) is a well-preserved phosphatized phragmocone fragment of a 60° whorl sector with a maximum preserved whorl height of 15.3 mm and a whorl breadth to height ratio of 0.64, the greatest breadth well below mid-flank. The inner and middle flanks are feebly convex, the outer flank and ventrolateral shoulders converge to the broadly rounded venter. The surface of the internal mould is smooth. A sector of a solid calcite replaced siphonal keel is present. The suture is deeply incised, with a large trifid A (= L) (Fig. 11).

OUM KX8906 (Fig. 10F) is a composite mould of a 120° sector of two successive whorls with a maximum preserved whorl height of 14.8 mm. Coiling is very evolute, the umbilicus broad and shallow, with a feebly convex outward-inclined umbilical wall and more narrowly rounded umbilical shoulder. The specimen is partially embedded in matrix, but the whorl section and proportions correspond to those of the previous specimen. A poorly preserved constriction is present toward the apertural end of the fragment. It is markedly prorsiradiate, feebly sinuous (?) and strongly projected forwards on the ventrolateral shoulders and venter.

Discussion

The type material of *Hauericeras rembda* was revised by Kennedy & Henderson (1992, p. 408, pl. 6, figs 10–24; pl. 17, fig. 1; text-fig. 3H). Given the Upper Maastrichtian horizon of the present material, the whorl section, and apparent course of the constriction on OUM KX 8906, reference to *rembda* seems appropriate; the lectotype and largest paralectotype are illustrated here as Fig. 10A, G, H for comparison. The other Maastrichtian species, *Hauericeras sulcatum* (Kner, 1848) (see revision in Kennedy & Summesberger 1987, p. 27, pl. 1, figs 1–7; pl. 13, fig. 2) has six or seven constrictions per whorl, and these are concave.

The two specimens from the type locality of the Mzamba Formation described by Griesbach (1871, p. 63, pl. 3, figs 2–3) as *Ammonites rembda* do not belong here and are probably *H. (G.) gardeni*. We have not been able to examine Griesbach's material – it is presumed to have been destroyed during aerial bombardment in World War II. (Klinger 1995).

Occurrence

Upper Maastrichtian of India and northern KwaZulu-Natal. Maastrichtian of Madagascar.

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ABBREVIATIONS

Institutional

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

Anatomical

[Dimensions are given in millimetres]
D diameter
Wb whorl breadth
Wh whorl height
U umbilicus
c costal dimension
ic intercostal dimension
(Figures in brackets are dimensions as a percentage of the diameter.)

The suture terminology is that of Korn *et al.* (2003):
E external lobe
A adventive lobe (= lateral lobe, L, of Kullmann & Wiedmann 1970)
U umbilical lobe
I internal lobe.

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