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ANNALS
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   (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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Major headings of the paper are centred capitals; first subheadings are centred small capitals; second subheadings are shouldered small capitals; third subheadings are shouldered italics; fourth subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations. Footnotes should be avoided unless they are short and essential. All generic and specific names should be underlined or italicized.

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'Smith (1969) described . . .'
'Smith (1969: 36, fig. 16) described . . .'
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'As described (Haughton *et al.* 1927) . . .'

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88**: 100–140.

FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA. THE AMMONITE FAMILY BACULITIDAE GILL, 1871 (EXCLUDING THE GENUS *EUBACULITES*)

By

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&
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Cape Town Kaapstad

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(With 132 figures)

[*MS accepted 17 May 1995*]

ABSTRACT

Representatives of the ammonite family Baculitidae are common faunal elements in the mid- and Upper Cretaceous of Zululand. The genus *Lechites* is rare, being represented by a single species in the Upper Albian, *L. gaudini* (Pictet & Campiche); *Sciponoceras* is represented by rare Cenomanian *S. roto* Cieśliński, *S. baculoides* (Mantell) and common *S. cucullatum* Collignon. *Baculites* is very common, and represented by Coniacian *B. yokoyamai* Tokunaga & Shimizu, Coniacian to Santonian *B. capensis* Woods, Coniacian to Campanian *B. bailyi* Woods, and Campanian *B. sulcatus* Baily, *B. increscens* Collignon, *B. vanhoepeni* Venzo, *B. duharti* Hünicken, *Baculites* sp. aff. *B. rectus* Marshall and *B. nibelae* sp. nov.

CONTENTS

INTRODUCTION

Members of the ammonite family Baculitidae are conspicuous faunal elements in the mid- and Upper Cretaceous of Zululand. Early representatives of the family belonging to the genus *Lechites* are rare, and so far only one species, *L. gaudini* (Pictet & Campiche), represented by two specimens, is known from the Upper Albian of Zululand. *Sciponoceras* is locally common in the Cenomanian; the majority of specimens belong to the Lower Cenomanian *S. cucullatum* Collignon. *Sciponoceras roto* Cieśliński and *S. baculoides* (Mantell) are rare in the Lower and Middle Cenomanian, respectively. Turonian sediments are absent in outcrops in Zululand and there is thus no baculitid record of this stage. The earliest Middle Coniacian baculitids include smooth, or

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only rarely ribbed forms, referable to *B. yokoyamai* Tokunaga & Shimizu and *B. bailyi* Woods. Nodose baculitids of the group of *B. capensis* Woods first appear in the Middle Coniacian, and become very abundant in the Upper Coniacian of Zululand where they, in places, formed the major part of the biomass. Concretions crowded with *B. capensis* are common in parts of the Middle and Upper Coniacian. *Baculites capensis* and *B. bailyi* are common up to the Lower or the Middle Santonian in southern Africa, but both occur as late as the Early Campanian. Ribbed *B. sulcatus* Baily occurs in the Lower Campanian of Pondoland. In Zululand and Natal, ribbed to nodose baculitids referable to *B. increscens* Collignon, *B. vanhoepeni* Venzo and *B. nibelae* sp. nov. occur in the Lower and Middle, and possibly part of the Upper Campanian, respectively. A smooth species, *B. duharti* Hünicken is recorded from the Middle Campanian.

In the Maastrichtian of Zululand, the genus *Eubaculites* replaces *Baculites* completely, and locally forms a major part of the total biomass. Representatives of the genus *Eubaculites* from Zululand have been described earlier by Klinger (1976) and Klinger & Kennedy (1993) and include *E. carinatus* (Morton), *E. labyrinthicus* (Morton), *E. latecarinatus* (Brunnschweiler) and *E. simplex* (Kossmat).

CLASSIFICATION

Fig. 1

Until recently, authorship of the family Baculitidae was ascribed to Meek (1876) (see e.g. Wright 1957: L218; Luppov & Drushchits 1958: 64). However, the name Baculitidae had been introduced five years earlier by Gill, in 1871, and authorship rests with him, as correctly indicated by Wright (1981: 172).

Wiedmann (1962*a*: 179) suggested that Cretaceous ptychoceratitid, polyptychoceratid, hamitid and baculitid heteromorphs could be united as subfamilies into a single family, Baculitidae, and later (Wiedmann 1962*b*: 93) even suggested including bochianitids in this 'super' family Baculitidae. This radical reorganization has found few supporters apart from Scholz (1979). According to a recent review of the higher taxa of Jurassic and Cretaceous Ammonoidea by Besnosov & Michailova (1991), Wiedmann's classification would involve lumping genera of two different orders into a single family! We regard the family Baculitidae as a rather conservative group that probably had its origins in the genus *Hamites* in the Albian, and retained a more or less straight shell throughout its existence right up to the end of the Cretaceous Period.

The earliest baculitid, *Lechites*, arose in the Upper Albian from the genus *Hamites*. The adult shell of *Lechites* consists of a single, straight shaft; as yet, the ammonitella is unknown. Ornament is simple, consisting of circumperipheral ribs. Constrictions are rare. One small branch of *Lechites*, elevated to subgeneric rank as *L. (Tuberolechites)* by Cooper & Kennedy (1977), developed feeble tubercles on the venter. There is considerable variation in the symmetry of the umbilical lobe in *Lechites* (see e.g. Wiedmann & Dieni 1968: 63, text-fig. 36; Scholz 1979: 14, text-fig. 5A); it may differ on either side of the same individual. Recent comprehensive reviews of the genus by Cooper &

Kennedy (1977) and Scholz (1979) differed somewhat in details, but covered most of the taxonomic problems. The distribution of the genus is more or less cosmopolitan.

Baculites (?) (Protobaculites) ambiguus Collignon (1964: 9, pl. 319 (fig. 1375)), recorded from a single specimen from the Lower Cenomanian of Madagascar, was regarded by Collignon as a possible precursor of *Baculites*, as indicated by the etymology. Ornament consists of annular ribs and periodic constrictions between every fifth and sixth rib. The suture line has a trifid umbilical (U) lobe and a large internal (I) lobe. Kennedy & Wright (1994) have shown that *Baculites (?) (Protobaculites) ambiguus* is, in fact, not a baculitid, but a *Hemiptychoceras*.

Lechites gave rise to the next-oldest baculitid genus, *Sciponoceras*, in the Early Cenomanian. The main feature of *Sciponoceras* is the regular occurrence of constrictions. The last representatives of *Sciponoceras* occur in the Upper Turonian. As in *Lechites*, *Sciponoceras* has a more or less cosmopolitan distribution.

The first true *Baculites* occur in the Lower Turonian and differ from contemporary *Sciponoceras* mainly by the loss of regular constrictions. The earliest, Turonian, *Baculites* are cosmopolitan but later representatives become restricted to distinct biogeographic regions. The genus *Baculites* persists up to the end of the Maastrichtian, and is amongst the last ammonite genera before the extinction of the order Ammonoidea at the K/T boundary (see e.g. Birkelund 1979, 1993; Ward & Kennedy 1993).

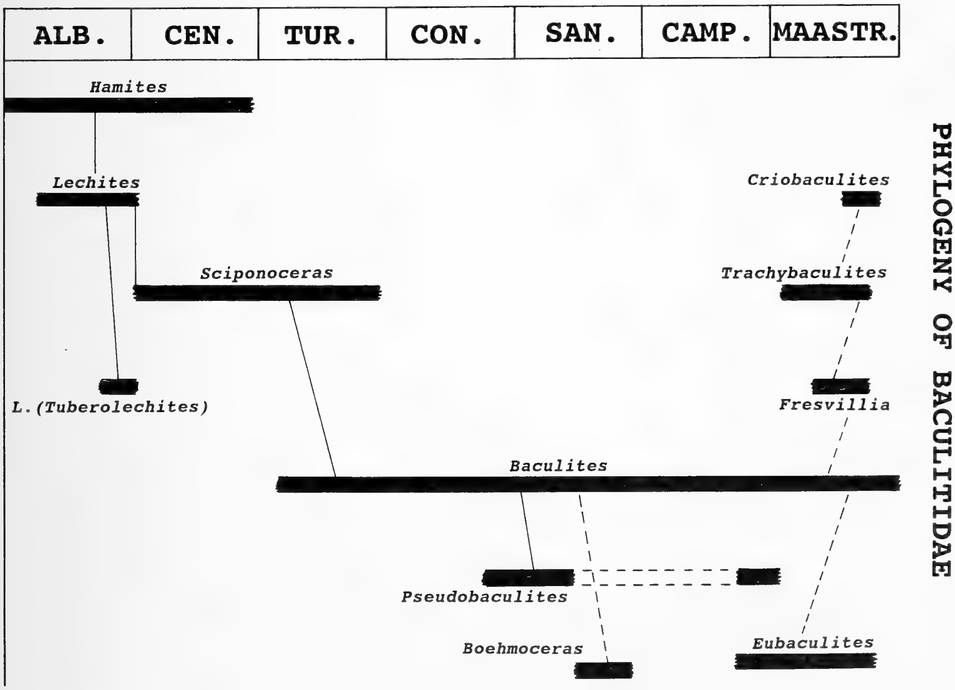

Fig. 1. Suggested phylogeny of the ammonite family Baculitidae Gill, 1871. Time axis not to scale.

During the Late Coniacian, an insignificant baculitid lineage, *Pseudobaculites*, arose from *Baculites* in the United States Western Interior. It differed from contemporary *Baculites* mainly in being larger, having a more rapid rate of taper, and a far more complex suture line. *Pseudobaculites* is an endemic lineage, the last representatives occurring in the Lower Maastrichtian; no representatives are known outside the U.S. Western Interior.

Boehmoceras, another short-lived but apparently slightly more widely distributed lineage, evolved from *Baculites* during the Late Santonian. The shell is coiled in an open criocone, and it is interpreted as a recoiled baculitid. It is so far known only from the Upper Santonian of Germany, Sweden, Austria, France, Mississippi, Alabama and Texas; it is rare in Europe, but common in the Gulf Coast region of the U.S.A.

During the Late Campanian, the genus *Eubaculites* arose from *Baculites*, differing from the latter mainly by the development of a tabulate or acute venter and pyriform whorl section. *Eubaculites* is the dominant baculitid of the Maastrichtian in the Southern Hemisphere, excluding Antarctica and New Zealand. It is rare in Western Europe, and absent or not yet recorded from the Middle East and North and West Africa. It is also absent from the U.S. Western Interior, but occurs in the Pacific, Gulf Coast and Atlantic Seaboard regions of the U.S.A.

A number of aberrant baculitids are known from the Maastrichtian but their origins and relations to *Baculites* are not clear. They all probably merit generic separation and include:

(1) *Fresvillia* Kennedy, 1986, type species *Fresvillia constricta* Kennedy, 1986*a* (p. 62, pl. 14 (figs 39–42), text-fig. 10a) from the Upper Maastrichtian of France. Also included in the genus is *Baculites teres* Forbes, 1846 (p. 115, pl. 10 (fig. 5)), recorded from the Upper Maastrichtian of Southern India and tentatively from the Maastrichtian of California (Matsumoto 1959: 163, pl. 45 (figs 5a–d, 6a–c), text-figs 82a–c, 83) and southern Alaska (Jones 1963: 29, pl. 16 (figs 10–12, 14), text-fig. 14).

(2) *Trachybaculites* Cobban & Kennedy, 1995, type species *Baculites columna* Morton, 1834 (p. 44, pl. 19 (fig. 8)) (see Cobban & Kennedy 1992*c*, 1995) from the Maastrichtian of Alabama, Texas, Mississippi, California and South Dakota. This is a heterochronous homoeomorph of Albian *Lechites* with circumperipheral ribbing, but with apparently simplified sutures.

Baculites lechitides Brunnschweiler, 1966 (p. 23, pl. 1 (figs 1–3), text-fig. 8) from the Upper Maastrichtian of Western Australia probably also belongs here and possibly *B. kegeli* Oliveira (1957: 22, pl. 2 (figs 6–7), text-fig. 1) from the Maastrichtian of Brazil. According to Cobban & Kennedy (1995: 29), *Baculites vicentei* Stinnesbeck, 1986 (p. 203, pl. 9 (fig. 4), pl. 10 (figs 3–6), text-figs 23a–c) from the Maastrichtian of Chile also belongs to *Trachybaculites*.

(3) The group of *Hamites trabeatus* Morton, 1834 (p. 45, pl. 15 (fig. 3)) from the Upper Maastrichtian of Alabama, appears to be an endogastrically recoiled baculitid lineage, homoeomorphic with Santonian *Boehmoceras* but for the position of the siphuncle. *Baculites?* sp. of Cobban & Kennedy (1992*c*: 68, figs 1.1–1.4, 3.1) from the Maastrichtian Fox Hills Formation of South Dakota belongs here.

The name ***Criobaculites*** gen. nov. is here proposed for this group, with type species *Hamites trabeatus* Morton, 1834. ***Diagnosis***: Criocone coiled baculitids with siphuncle inside the curve (i.e. endogastric).

(4) ?The group of *Baculites paradoxus* Pervinquière, 1907 (p. 94, pl. 4 (figs 10–11), text-fig. 24) from the Upper Maastrichtian of Tunisia. We are not certain if this group belongs to the family Baculitidae at all. These are minute, straight shells with trigonal saddles and lobes, reminiscent of some *Sciponoceras*. *Baculites* indét. of Pervinquière (1907: 95, pl. 4 (fig. 12a–b), text-fig. 25) may also belong here. It differs from *B. paradoxus* mainly in possession of constrictions. Both are of very dubious baculitid affinities and are better regarded as allied to *Phylloptychoceras*.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of material referred to in the text.

SAM	South African Museum, Cape Town
NMB	National Museum, Bloemfontein—presently housed in the South African Museum
TM	Transvaal Museum, Pretoria
MRC	Prof. M. R. Cooper Collection, University of Durban-Westville
SAS	Geological Survey, Pretoria—presently housed in the South African Museum
GD	Institut des Sciences de la Terre de l'Université Dijon (ex Collignon Collection)
BMNH	The Natural History Museum, London
MNHP	Muséum National d'Histoire Naturelle, Paris
CPC	Facultad de Ciencias Exactas, Fisicas y Naturales, Universidad Nacional de Córdoba, Argentina
GO	Department of Geological Sciences, University of Bologna

FIELD LOCALITIES

Details of field localities are given in Kennedy & Klinger (1975); fuller descriptions of localities are deposited in the Department of Palaeontology, Natural History Museum, London, Geological Survey of South Africa, Pretoria, and Division of Earth Sciences, South African Museum, Cape Town. Additional localities are referred to in the text.

DIMENSIONS

All dimensions are given in millimetres. MxWb—maximum whorl breadth (in mm); MxWh—maximum whorl height (in mm); MnWb—minimum whorl breadth (in mm); MnWh—minimum whorl height (in mm); D—distance between maximum and minimum whorl height and breadth measurements (in mm); Wb/Wh—ratio of whorl breadth to whorl height; Ri—Rib or tubercle index:

number of ribs or tubercles per whorl height; Ti—taper index (after Matsumoto & Obata 1963: 4) (Ti = MxWh - MnWh / D × 100).

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916) reviewed and discussed by Kullmann & Wiedmann (1970) is followed here: I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1797

Order AMMONOIDEA Zittel, 1884

Suborder ANCYLOCERATINA Wiedmann, 1960

Family **Baculitidae** Gill, 1871

Genus *Lechites* Nowak, 1908

Type species. *Baculites gaudini* Pictet & Campiche (1861: 112, pl. 55 (figs 5–9)) by the original designation of Nowak (1908: 350).

Diagnosis

Shell straight, with simple ornament consisting of prorsiradiate ribs, sometimes grouped in pairs; shallow constrictions may be present. Ventral tubercles present in some. Dimorphic; macroconchs with trumpet-shaped aperture, microconch with down-turned aperture and incipient lappets.

Discussion

Lechites is the oldest of the Baculitidae; it first appeared in the Late Albian and, as Spath (1941: 660) had previously suggested, was presumably derived from *Hamites*. Middle Albian records, as *Baculites Sanctae-Crucis* Pictet & Campiche (1861: 109, pl. 55 (figs 1–4)) are probably misidentified protanisoceratids and not *Lechites* (see e.g. Spath 1939: 572–573; 1941: 661 footnote).

Recent work by Cooper & Kennedy (1977) and Scholz (1979) showed that some specimens of *Lechites* in the Upper Albian and Lower Cenomanian acquire incipient to distinct ventral tubercles, and are homoeomorphs of *Idiohamites* and *Pseudoxybeloceras* fragments to a certain extent. Cooper & Kennedy (1977) separated the tuberculate forms as a separate subgenus of *Lechites*, *Tuberolechites* (type species *Tuberolechites regifex* Cooper & Kennedy, 1977: 654, fig. 8 (1–15)). Initially Scholz also considered separating them at least at subgeneric level. On closer examination, Scholz (1979: 15) found that all transitions occur between simply ribbed *L. gaudini* and tuberculate forms in the condensed sequences he studied. According to Scholz, the tuberculate forms occur in the Upper Albian and again in the 'Vraconnian'; he thus regarded the acquisition of tubercles as an iterative, rather than as a unique monophyletic event. Consequently, Scholz merely separated tuberculate and normally ribbed at subspecific level, as *Lechites gaudini* s.s. and *L. gaudini nodosus* Scholz (1979: 15, pl. 1 (figs 11–16)).

It is important to note that, in spite of their unique morphology, tuberculate forms of *Lechites* are rare. Cooper & Kennedy (1977: 645, 654) examined nearly 200 specimens of *L. gaudini* but found only four tuberculate examples; Scholz (1979: 12, 15) had nearly 700 specimens of *L. gaudini*, of which only 32 from France and nine from Hungary were tuberculate.

From the extensive descriptions of e.g. Spath (1941), Renz (1968), Cooper & Kennedy (1977) and Scholz (1979), it is obvious that there is considerable variation in the shape and density of ribbing, and that transitions occur between most of the different 'species' attributed to the genus. A reduction in the number of names, as suggested by Cooper & Kennedy (1977) and Scholz (1979), is probably justifiable.

Occurrence

Lechites is known with confidence only from the Upper Albian. It has been recorded from Western and Central Europe, North Africa, ?Somalia, Madagascar, Zululand, India, North, Central and South America, Antarctica (Thomson 1984: 88—as *Baculites*; Moncrieff & Kelly 1993: 5) and Japan (Hokkaido).

Lechites gaudini (Pictet & Campiche, 1861)

Figs 2A–C, M, 3

1861 *Baculites Gaudini* Pictet & Campiche, p. 112, pl. 55 (figs 5–9).
1933 *Baculites Gaudini* Pictet & Campiche; Collignon, p. 73, pl. 5 (fig. 8, 8a).
non 1936 *Baculites Gaudini* Pictet & Campiche: Venzo, p. 118 [60], pl. 10 [6] (fig. 3). [= *Sciponoceras ?cucullatum*]
1941 *Lechites gaudini* (Pictet & Campiche); Spath, p. 662, pl. 72 (figs 4–7, 9–10), text-fig. 242. (*cum. synon.*)
1941 *Lechites communis* Spath, p. 666, text-fig. 244.
1947 *Lechites Gaudini* var. *raricosta* Breistroffer, p. 78.
? 1968 *Lechites italicus* Wiedmann & Dieni, p. 64, pl. 6 (fig. 10), text-fig. 37.
1968 *Lechites campichei* Renz, p. 82, pl. 17 (figs 8a–c, 9a–c, 10a–b), text-fig. 29m.
1968 *Lechites vraconensis* Renz, p. 82, pl. 17 (figs 11a–c, 12a–b, 14a–b, 15a–c), text-fig. 29b, g–h, k.
? 1971 *Lechites fasciata* Scholz, p. 431, figs 1–2.
1977 *Lechites gaudini* (Pictet & Campiche); Cooper & Kennedy, p. 644, figs 1 (1–38), 2 (1–30), 3, 4 (1–18), 5 (1–15), 6–7, 8 (16–26). (*cum. synon.*)
1978 *Lechites gaudini* (Pictet & Camp.); Scholz, pl. 3 (figs 1, 8).
1979 *Lechites gaudini gaudini* (Pictet & Campiche); Scholz, p. 12, pl. 1 (figs 1–9), text-fig. 5A–B.
1982 *Lechites* aff. *gaudini* Pictet & Campiche; Renz, p. 59, pl. 20 (fig. 7a–b).
1983 *Lechites gaudini* (Pict. & Camp.); Horvath, pl. 1 (fig. 2).
1984 *Lechites gaudini* (Pict. & Camp.); Mitiu, p. 83, pl. 2 (figs 6–9).
1984 *Lechites gaudini* (Pict. & Camp.) transition to *L. communis* Spath; Mitiu, p. 85, pl. 2 (figs 10–11).
1984 *Lechites communis* Spath; Mitiu, p. 85, pl. 2 (figs 12–13).
1985 *Lechites gaudini* (Pictet & Campiche); Immel & Seyed-Emami, p. 112, pl. 7 (fig. 11).
1991 *Lechites communis* (Pictet & Campiche); Ivanov, pl. 4 (fig. 11).

Type

Lectotype, by subsequent designation of Spath (1941, p. 663) the specimen figured by Pictet & Campiche (1861, pl. 55 (fig. 5a–c)) and refigured by Renz

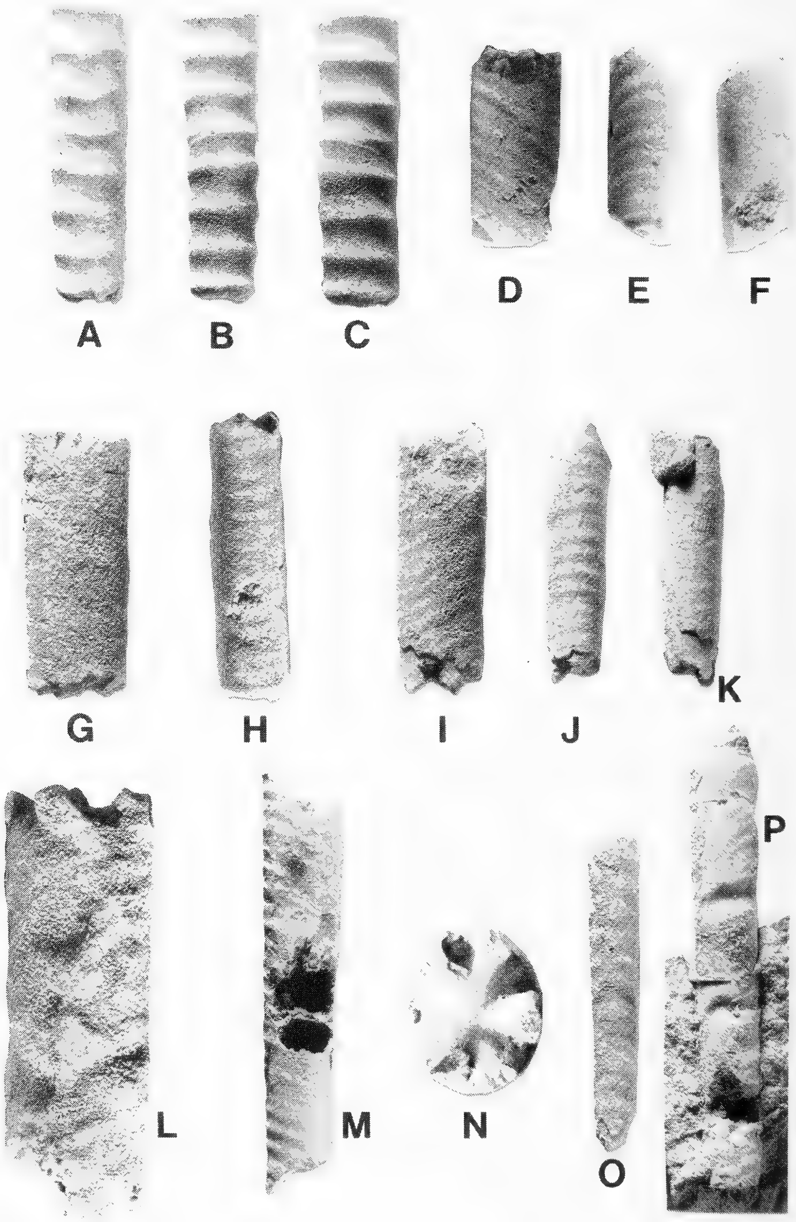

Fig. 2

(1968, pl. 17 (fig. 3)) from the Upper Albian *Stoliczkaia dispar* zone of Sainte-Croix, Kanton Waadt, Switzerland.

Material

SAM–PCZ8766 from locality 182, Zululand, Mzinene Formation. Outcrops here extend from uppermost Albian to Lower Cenomanian; SAS Z19 from Haughton's (1936: 299) locality Z19 on the Pongola River, north of the confluence with the Mfongozi Creek, Zululand, Mzinene Formation, Upper Albian.

Description

SAM–PCZ8766 is part of a phragmocone with parts of the original shell preserved; SAS Z19 is an internal mould of part of the body chamber with the last septum preserved. The whorl section in both specimens is ovoid, higher than wide with Wb : Wh ratios 7.7 : 8.8 = 0.87 and 7.8 : 10.2 = 0.76, respectively. PCZ8766 is finely ribbed, with 5 ribs per whorl height; Z19 is more coarsely ribbed with 3 ribs per whorl height.

The suture is partially exposed in PCZ8766 (Fig. 3); the umbilical lobe (U) is distinctly smaller than the lateral lobe (L) and asymmetric.

Discussion

Lechites gaudini is quite variable as far as density and shape of ribbing is concerned, and several varietal or specific names have been given to extreme morphologies. PCZ8766 could be referred to *Lechites gaudini* s.s., whereas Z19 could be referred to *L. raricosta* Breistroffer, 1947. We follow Cooper & Kennedy (1977: 644), Wiedmann & Dieni (1968: 62) and Scholz (1979: 12) in including these variants within *L. gaudini* s.s. *Lechites antanimangaensis* Collignon (1964: 34, pl. 325 (fig. 1451)) is very similar to our coarsely ribbed specimen (Z19). However, it has been suggested by Cooper & Kennedy (1977: 653) and Wright & Kennedy (1995: 314) that *L. antanimangaensis* may be a *Sciponoceras* body chamber.

Occurrence

The species is common in the Upper Albian, *Stoliczkaia dispar* zone. It has been recorded from England, France, Switzerland, Romania, Hungary, Sardinia, Algeria, Madagascar, southern India, Hokkaido, Mexico, Venezuela and Antarctica.

Fig. 2 *(see facing page).* A–C, M. *Lechites gaudini* (Pictet & Campiche, 1861). A–C. SAS Z19 from Haughton's (1936: 299) locality Z19, Zululand, Mzinene Formation, Albian. M. SAM–PCZ8766 from locality 182, Mzinene Formation; the locality ranges from the Upper Albian to Lower Cenomanian I. D–F. *Sciponoceras baculoides* (Mantell, 1822). SAS A705 from an unspecified horizon on the Skoenberg, Mzinene Formation, Cenomanian. G–L, N–O. *Sciponoceras cucullatum* Collignon (1964). G–H. NMB D1004a. I–K. SAS H210/34. L, N. NMB D1004b. O. NMB D1002a. All from an unspecified horizon on the Skoenberg, Mzinene Formation, Cenomanian. P. *Sciponoceras roto* Cieśliński, 1959. SAS EM191 from an unspecified horizon at locality 181, Zululand, Mzinene Formation, Cenomanian I or II. All × 1.

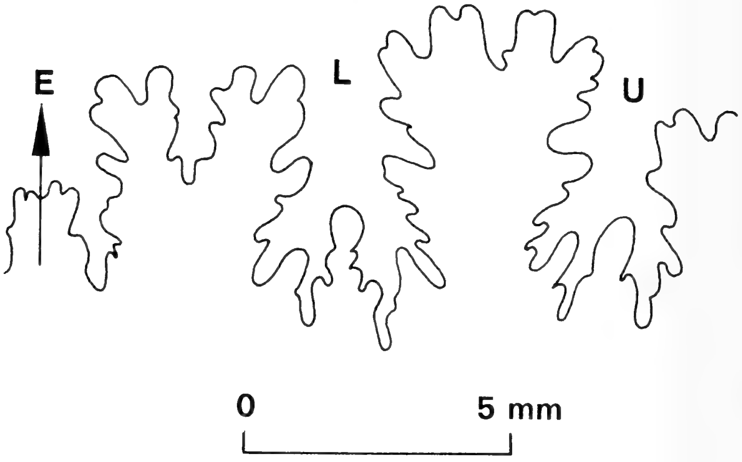

Fig. 3. *Lechites gaudini* (Pictet & Campiche, 1861).
Suture line of SAM–PCZ8766. Scale bar for size.

Genus *Sciponoceras* Hyatt, 1894
(= *Cyrtochilus* Meek, 1876, *non* Jakowlew, 1875; *Cyrtochilella* Strand, 1929)

Type species: *Hamites baculoides* Mantell, 1822: 123, pl. 23 (figs 6–7), by the original designation of Hyatt (1894: 578).

Diagnosis

According to the most comprehensive, recent review by Wright & Kennedy (1981: 112), '*Sciponoceras* is distinguished . . . by its marked constrictions. These are straight and prorsiradiate in early forms but in later ones are rursiradiate on the inner quarter or third of the flank and then turn forward. There are also well-marked, weakly branching ribs on the body chamber or the whole shell, following the same course as the constrictions. The apertural features appear to be of specific as well as sexual significance; some are relatively simple, others have a long rostrum, broad folds and a high collar, others have long lateral lappets.'

Discussion

Extensive discussions on *Sciponoceras* are given by Matsumoto (1959), Matsumoto & Obata (1963), Kennedy (1971), Cobban & Scott (1972), Wright (1979), Wright & Kennedy (1981), Kennedy & Juignet (1983) and Wright & Kennedy (1995), and nothing new can be added to these.

Occurrence

Transitions from *Lechites* to *Sciponoceras* first occur in the Upper Albian *Stoliczkaia dispar* Zone faunas of the Anglo-Paris Basin. The genus extends to the Upper Turonian. The genus has a world-wide distribution (see Matsumoto

1973: 422, fig. 1), including Europe as far east as Transcaspia, the Middle East, North Africa, Madagascar, Zululand, ?Angola, India, northern Australia, New Zealand, various localities in North America in the Western Interior, Gulf Coast and California, Mexico, and in Argentina in South America.

Sciponoceras baculoides (Mantell, 1822)

Fig. 2D–F

1822 *Hamites baculoides* Mantell, p. 123, pl. 23 (figs 6–7).
1959 *Sciponoceras baculoide* (Mantell); Matsumoto, p. 104, pl. 31 (fig. 1a–d), text-fig. 2a–b. (*cum. synon.*)
non 1973 *Sciponoceras baculoide* (Mantell); Henderson, p. 81, text-fig. 4a–d, fig. 6 nos 4a–c, 5a–c, 7a–c.
? 1975 *Sciponoceras baculoides* (Mantell); Förster, p. 166, pl. 4 (fig. 6), text-fig. 36.
1980 *Sciponoceras baculoide* (Mantell); Marcinowski, p. 252, pl. 3 (figs 17–20).
1983 *Sciponoceras baculoides* (Mantell); Kennedy & Juignet, p. 19, figs 11(a)–(y), 12(a)–(bb), 13(a)–(w), 14(a)–(n) (*cum. synon.*)
1983 *Sciponoceras baculoide* (Mantell); Marcinowski & Walaszczyk, pl. 1 (fig. 3).
1983 *Sciponoceras baculoide* (Mantell); Kaplan *et al.* pl. 5 (fig. 2).
1987 *Sciponoceras baculoides* (Mantell); Wright & Kennedy, p. 177, pl. 37 (fig. 13).
1991 *Sciponoceras baculoide* (Mantell); Delamette & Kennedy, p. 462, figs 17.6, 17.7, 17.14, 17.15.
1992 *Sciponoceras baculoide* (Mantell); Thomel, pl. 6 (fig. 7), pl. 10 (fig. 2), pl. 11 (figs 1–3), pl. 19 (fig. 4).
1995 *Sciponoceras baculoides* (Mantell); Wright & Kennedy, p. 317, pl. 95 (figs 1–3, 5–10), pl. 96 (figs 1–7), pl. 97 (figs 1–5), pl. 98 (figs 29–32), text-figs 129H, 132R–S, 133A–C, M–FF. (*cum. synon.*)

Type

Lectotype BMNH 8612, by subsequent designation of Kennedy (1971: 9), is the larger specimen on the block figured by Mantell (1822, pl. 23 (fig. 6)) from the lower Middle Cenomanian of Hamsey, Sussex, refigured by Kennedy (1971, pl. 2 (fig. 5a–b)).

Material

SAS A705 from an unspecified horizon and locality on the Skoenberg, Zululand, Mzinene Formation, Cenomanian.

Description

The specimen is a phragmocone fragment, preserved as an internal mould in glauconitic silt. Part of a constriction is preserved at the smaller end, and faint prorsiradiate ribs are visible on the flanks and over the venter. The whorl section is ovoid, Wb : Wh 10.7 : 11.7 (= 0.91).

Discussion

Extensive descriptions and discussions can be found in Kennedy (1971), Juignet & Kennedy (1976), Kennedy & Juignet (1983) and Wright & Kennedy (1995).

Occurrence

Sciponoceras baculoides has been reported from the Lower to Upper Cenomanian, but many of these records are difficult to substantiate. According to Kennedy & Juignet (1983: 22), the species is abundant only in the lower part of the Middle Cenomanian in southern England and France. It extends to the lower Upper Cenomanian. Other records are from Germany, Poland, Romania, California, North Africa, southern India, Madagascar, Mozambique and Zululand.

Sciponoceras cucullatum Collignon, 1964

Figs 2G–L, N–O, 4–5, 6A–D

? 1936 *Baculites Gaudini* Pictet & Campiche; Venzo, p. 118 [60], pl. 10 [6] (fig. 3).
1964 *Sciponoceras cucullatum* Collignon, p. 38, pl. 326 (fig. 1458).

Type

Holotype by monotypy is the specimen figured by Collignon (1964, pl. 326 (fig. 1458)) from the 'Lower' Cenomanian, Zone of *Mantelliceras mantelli* and *Calycoceras newboldi* of gisement 505, west of the falls of Mahaboboka (Manera), Madagascar; herein refigured in Figure 6A–C.

Material

SAM-PCZ7499, PCZ9137, PCZ9139–9140, NMB D1002, D1002a–b, D1003a–c, D1004, D1004a–i, SAS H210/23, H30–31, H33–35, SAS A106, 1063–1064, 1069, all from an imprecisely located horizon on the Skoenberg at locality 61. Judging by the preservation, the specimens seem to have come from the higher parts of the section. Mzinene Formation, upper Lower or lower Middle Cenomanian.

Dimensions

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Ri*
D1002a	5.1	7.2	0.71	5.1	6.0	0.85	30	4.0	—
D1002b	7.1	8.3	0.85	5.7	7.1	0.80	37	3.24	—
H210/34	8.6	12.0	0.72	7.6	10.6	0.72	25	5.6	—
D1004i	9.9	14.8	0.67	9.7	13.5	0.72	34	3.8	5
H210/23	10.6	12.7	0.83	9.5	11.1	0.86	31	5.2	—
D1004d	12.7	16.4	0.77	10.2	14.7	0.69	38	4.5	—
D1004b	13.6	19.5	0.70	13.0	17.7	0.73	59	3.05	3–4
D1003b	13.8	15.0	0.92	12.0	14.3	0.90	72	0.91	4
D1003c	15.7	19.3	0.81	—	—	—	—	—	—
A1063	16.4	17.2	0.95	16.2	16.2	1.0	40	2.5	—
D1004	18.6	22.9	0.81	—	21.2	—	83	2.0	—
H210/31	19.5	22.6	0.86	18.2	23.4	0.77	46	1.7	—
D1003a	23.0	24.7	0.93	18.5	21.4	0.86	110	3.0	6

Fig. 4 *(see facing page). Sciponoceras cucullatum* Collignon, 1964. A–C. NMB D1003a. D. NMB D1003b, both from an imprecisely located horizon on the Skoenberg at locality 61, Zululand, Mzinene Formation, ?Middle Cenomanian. Arrow points to shallow constriction. Both × 1.

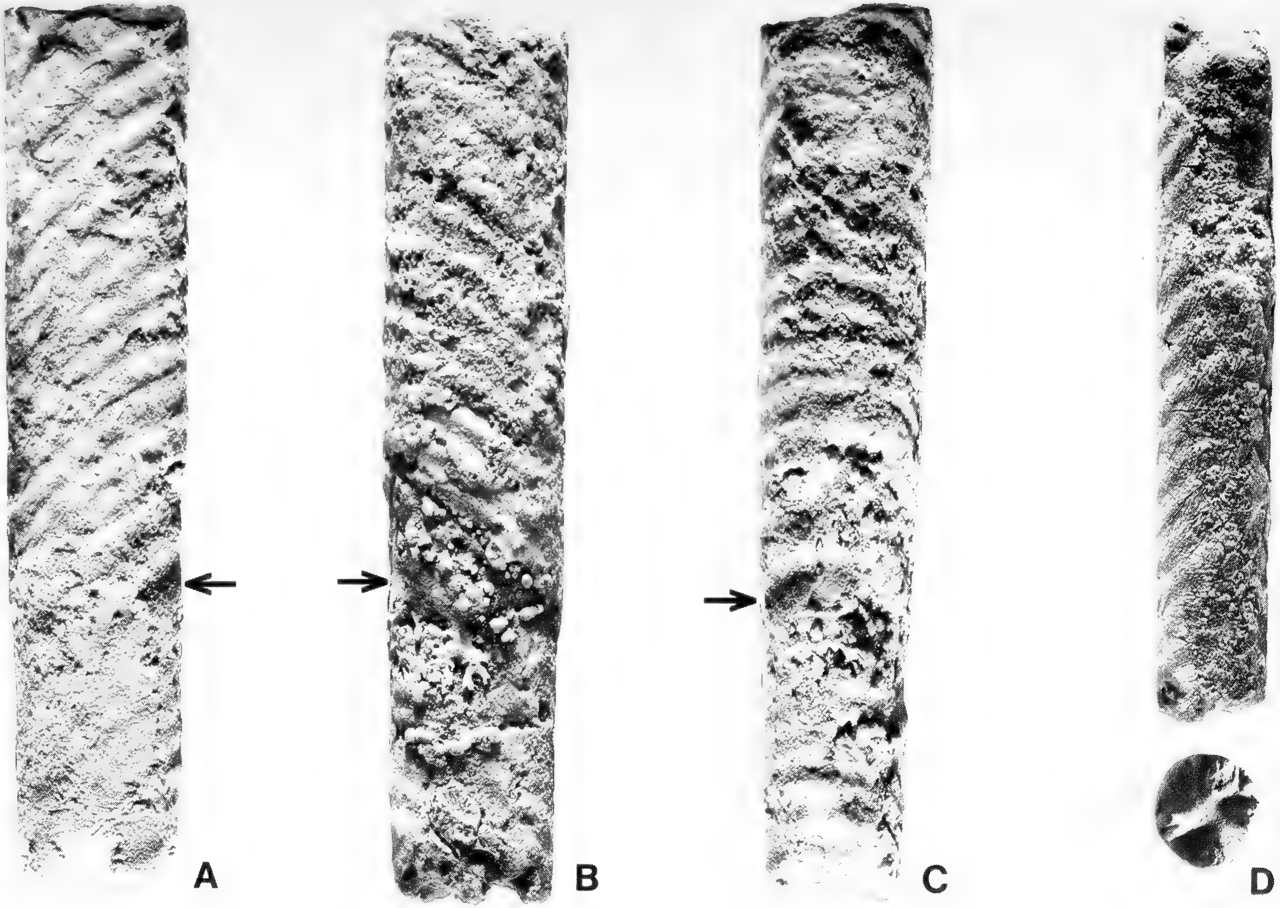

Fig. 4

Description

Preservation of the material from this locality is characteristic: specimens are either preserved as internal moulds in a combination of glauconitic silt and sparry calcite, or with part of the original shell preserved in recrystallized sparry calcite. Unfortunately, recrystallization of the calcite, plus the fact that most specimens were found eroded on the surface, has obliterated most of the surface ornament.

The species reaches large size; the largest Zululand specimen, D1003a (Fig. 4A–C) is still septate at a whorl height of nearly 25 mm. The Madagascan holotype (Fig. 6A–C) is adult with a fully developed, recurved, hooded aperture at Wb = 20.7 mm.

There is considerable variation in whorl shape; it varies from circular, to high oval, with Wb : Wh ratio as little as 0.67. This variation is partially due to ontogenetic change: smaller specimens are generally more compressed laterally than large specimens, which tend to be almost circular in cross section.

Where the shell is preserved, ornament is seen to consist of ribbing that is distinctly prorsiradiate on the flanks, transverse or feebly convex on the venter, and also straight and transverse, but weakened on the dorsum. Density of ribbing is approximately 5 per whorl height. On internal moulds the surface is completely smooth. Constrictions are very rare, e.g. D1003a (Fig. 4A–C); these seem to follow the same direction as the ribs and are strongest over the venter. As a result of the preservation, only parts of the suture are visible.

Discussion

We have not yet been able to examine Venzo's (1936) described material, but the figure and the locality data indicate that it is very probable that his *Baculites gaudini* (Venzo 1936: 118 [60], pl. 10 [6] (fig. 3)) belongs to this species, and not to *Lechites gaudini*. Because of the rare and weak development of constrictions it is quite easy to understand Venzo's error in referring this species to *Lechites* rather than to *Sciponoceras*.

In retrospect, we suspect that our earlier reference to *S. roto* from Zululand (Kennedy & Klinger 1975: 277) may, in part, have been based on this species. As is shown below, *S. roto* lacks the distinctive prorsiradiate ribbing of the present material and has regular constrictions, thus easily distinguishing it from *S. cucullatum*.

As far as the large size is concerned, *S. cucullatum* is close to *S. santacrucense* Leanza (1970: 212, pl. 11 (figs 1–7)) (Fig. 6E herein), a rather poorly known species from Santa Cruz Province, Argentina. This species was initially dated as Cenomanian, but this was based on incorrect stratigraphic information. *Sciponoceras santacrucense* occurs below a level with abundant *Placenticeras* at Puesto el Alamo (Riccardi & Aguirre Urreta 1988; personal observation), which would probably date it as late Turonian. *Sciponoceras santacrucense* has distinct, regular, albeit widely spaced constrictions that easily distinguish it from *S. cucullatum*.

Sciponoceras gracile (Shumard, 1860) (see Kennedy 1988: 108, pl. 20 (figs 1–14, 17–20), text-fig. 38 for the most recent review) from the Upper Cenomanian, grows to similar large size, but the ornament consists of fine ribs

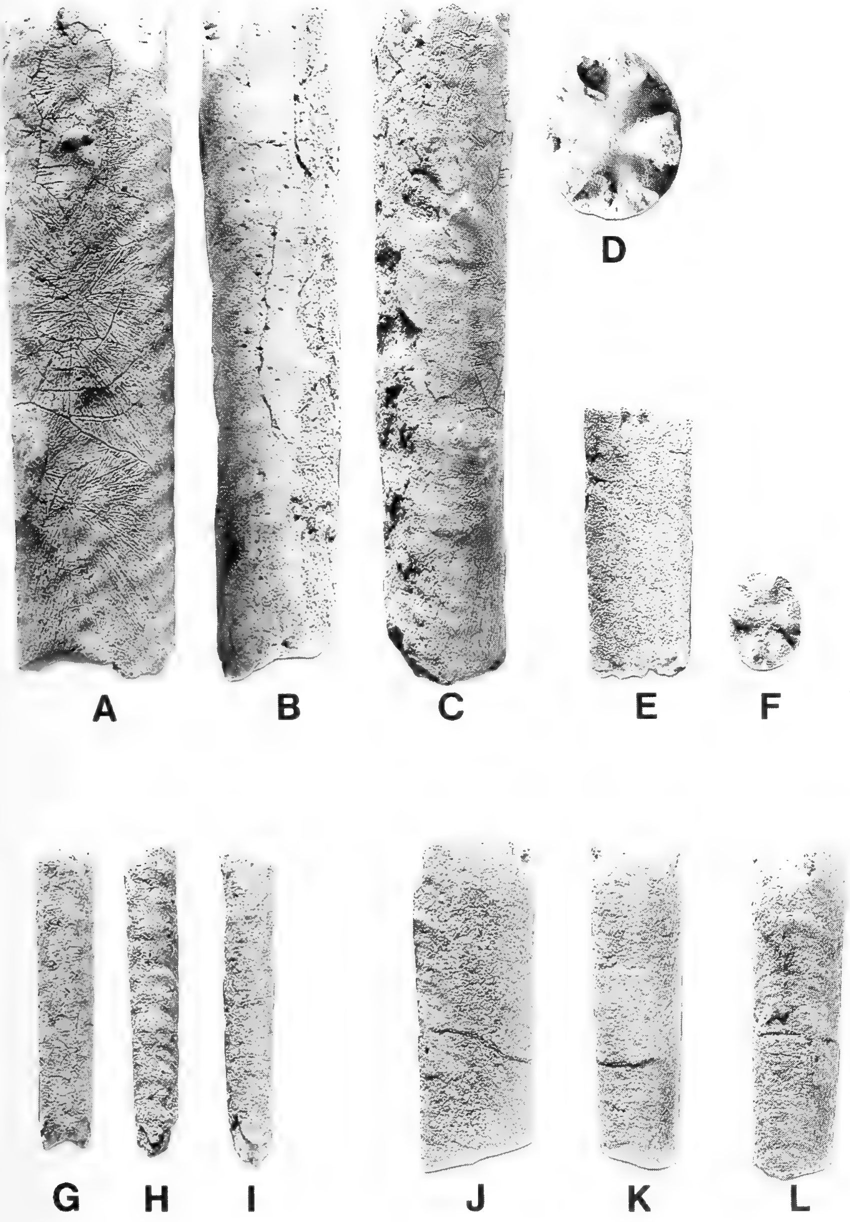

Fig. 5. *Sciponoceras cucullatum* Collignon, 1964. A–D. NMB D1004. E–F. NMB D1004c. G–H. NMB D1002. J–L. NMB D1004d. All from an imprecisely located horizon on the Skoenberg at locality 61, Zululand, Mzinene Formation, ?Middle Cenomanian. All × 1.

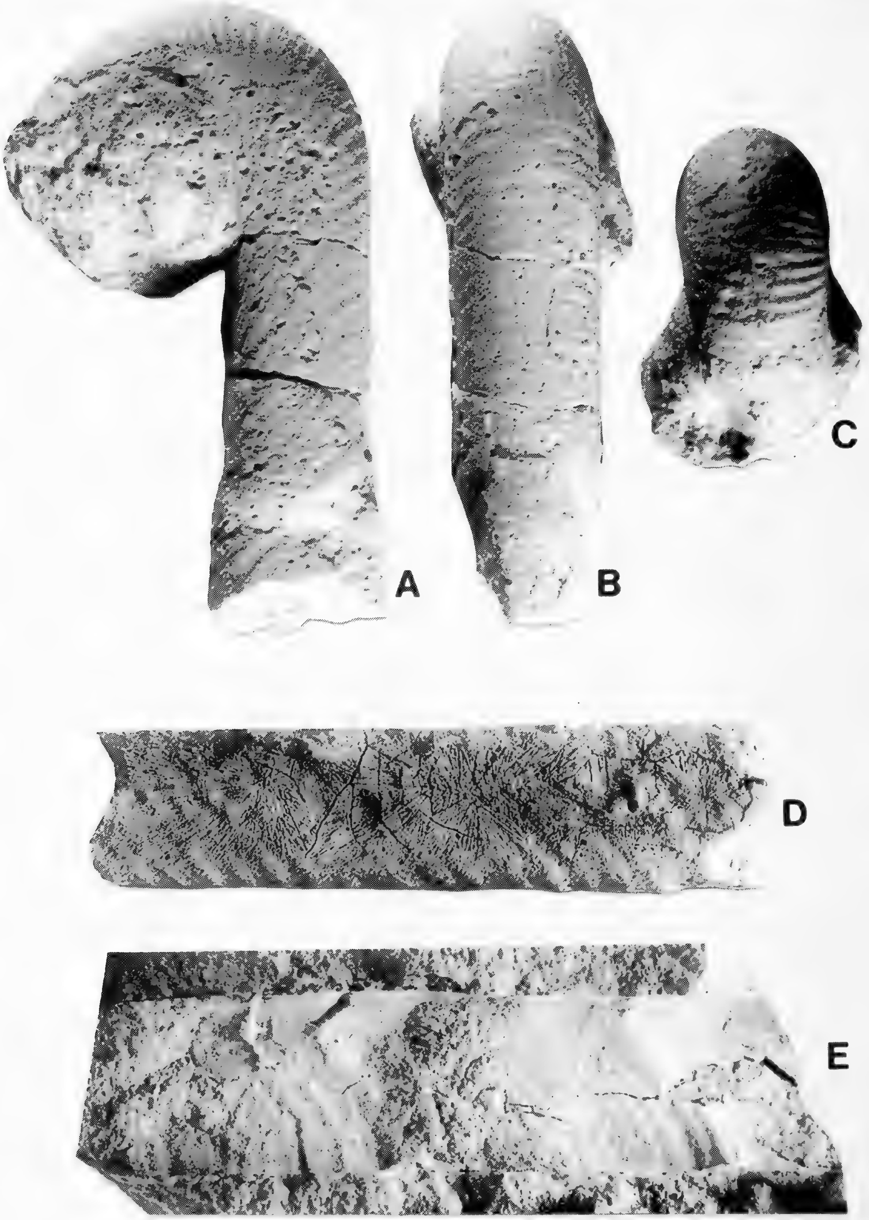

Fig. 6. A–D. *Sciponoceras cucullatum* Collignon, 1964. Plaster cast of the holotype from the Lower Cenomanian zone of *Mantelliceras mantelli* and *Calycoceras newboldi* of gisement 505, west of the falls of Mahaboboka (Manera), Madagascar. D. NMB D1004 from an imprecisely located horizon on the Skoenberg at locality 61, Zululand, Mzinene Formation, ?Middle Cenomanian. E. *Sciponoceras santacrucense* Leanza, 1970. Impression of specimen from the Turonian of Puesta el Alamo, Santa Cruz Province, Argentina. All × 1.

that are strongest on the ventral half of the flanks, and constrictions occur fairly regularly at distances ranging from 1 to 1.5 major diameters, according to Wright & Kennedy (1981: 113).

Sciponoceras kossmati (Nowak, 1908) is difficult to interpret (see Wright & Kennedy 1981: 114), but it appears that most of the material from California and Hokkaido, described by Matsumoto (1959: 106, pl. 31 (figs 2a–b, 3), text-figs 4a–b, 5a–b, 6a–b) and Matsumoto & Obata (1963: 13, pl. 3 (fig. 2), pl. 4 (fig. 1), pl. 5 (figs 1–3), pl. 6 (figs 3–5), text-figs 5–25) as *S. kossmati*, is indistinguishable from *S. gracile*.

Sciponoceras orientale Matsumoto & Obata (1963: 18, pl. 3 (fig. 1), pl. 6 (figs 1–2), pl. 7 (figs 1–6), pl. 9 (fig. 6), text-figs 33–49) from the Lower and Middle Turonian of Hokkaido is also quite large, but is distinguished by the frequent constrictions and coarse ribbing.

The recurved aperture of the holotype of *S. cucullatum* is totally unlike any of the known apertures of other *Sciponoceras* species.

Occurrence

'Lower' Cenomanian of Madagascar, Lower and ?Middle Cenomanian, Zululand.

Sciponoceras roto Cieślinski, 1959

Fig. 2P

1907 *Baculites baculoides* Mantell; Pervinquière, p. 92 (pars), pl. 4 (fig. 8 only), *non* pl. 4 (fig. 7), text-fig. 22.
1940 *Cyrtochilus pervinquierei* Breistroffer, p. 99 (29). (*nomen nudum*)
1959 *Sciponoceras roto* Cieśliński, p. 39, pl. 4 (fig. 10), text-fig. 14 (II).
1971 *Sciponoceras roto* Cieśliński; Kennedy, p. 10, pl. 3 (fig. 7).
1972 *Sciponoceras roto* Cieśliński; Hancock *et al.* pl. 81 (fig. 8).
1975 *Sciponoceras roto* Cieśliński; Kennedy & Klinger, p. 277 (pars).
1979 *Sciponoceras* cf. *roto* Cieśliński; Kennedy *et al.* p. 10, pl. 1 (fig. 4).
1980 *Sciponoceras roto* Cieśliński; Marcinowski, p. 254, pl. 3 (figs 14–15).
1985 *Sciponoceras roto* Cieśliński; Marcinowski & Walaszczyk, pl. 1 (fig. 9).
1991 *Sciponoceras roto* Cieśliński; Delamette & Kennedy, p. 460, figs 17.8–17.13, 17.16–17.23.
1995 *Sciponoceras roto* Cieśliński; Wright & Kennedy, p. 315, pl. 94 (figs 13–19), pl. 95 (fig. 4), pl. 98 (fig. 28), text-figs 131J–L, N. (*cum. synon.*)

Type

Cieśliński based this species on nine syntypes; as yet, no lectotype has been designated.

Material

SAS EM191 from an unspecified horizon at locality 181, Zululand, Mzinene Formation, Cenomanian I–II.

Description

The specimen consists of part of the phragmocone and body chamber. The whorl section is circular; Wb : Wh 9.5 : 9.5 (= 1.0) at the greatest diameter.

Apart from two prominent constrictions spaced at about two whorl heights apart, the surface of the internal mould is nearly smooth. Faint ribs occur on the venter.

Discussion

Sciponoceras roto is easily identified by the circular whorl section and lack of ornament between the constrictions. The specimen from Zululand differs from the European material in having the constrictions slightly closer spaced—twice the whorl height compared to three times. We do not know if this feature is significant.

Breistroffer (1940: 99 (29)) erected a new species, *Cyrtochilus pervinquierei*, for one of Pervinquière's specimens of *Baculites baculoides*. As Wright & Kennedy (1995: 315) have noted, this is a *nomen nudum*. In any case, the specimen is close to, if not identical with, *S. roto*.

As discussed above, earlier records of *S. roto* from Zululand (Kennedy & Klinger 1975: 277) are probably partially based on misidentified *S. cucullatum*.

Occurrence

Sciponoceras roto is rare and known from the Lower Cenomanian of Poland, southern England, France, Germany, Mangyschlak, Iran, Tunisia, Madagascar and Zululand.

Genus *Baculites* Lamarck, 1799

(= *Homaloceratites* Hupsch, 1768 (*non binom.*); *Euhomaloceras* Spath, 1926)

Type species. *Baculites vertebralis* Lamarck, 1799: 80, by subsequent designation of Meek (1876: 80).

Diagnosis

Planispiral ammonitella followed by straight or curved shaft; body chamber may curve in some. Size variable, up to 2 m in length; probably dimorphic. Ornament variable, from nearly smooth with only growth striae around periphery, to crescentic ribs that are strongest on dorsolateral region, but may be circumperipheral, to distinct dorsolateral nodes, which may be round, crescentic or, rarely, longitudinally elongated. In some, the venter may be distinctly corrugated, associated either with or without ventrolateral ribbing. Aperture simple, in line with long axis of shell, short dorsal rostrum, prominent lateral sinus and straight to slightly curved ventral rostrum; may be flared in some species. Suture variable, ranging from simple, subquadrate lobes and saddles with open bases with simple incisions or phylloid folioles, to highly dendritic, with saddles and lobes with slender bases.

Discussion

Of all the heteromorph ammonite genera, the genus *Baculites* probably poses most problems in identification and global stratigraphic correlation. The great number of monotypical and/or endemic *Baculites* species that exist in the literature, as well as gross misidentifications (e.g. *B. ovatus*, typically from the Upper Campanian of North America, allegedly from the Coniacian of Venezuela (Reyment 1958) or *B. inornatus*, typically Campanian but reportedly from the Lower Coniacian of Venezuela (Renz 1982)), all bear testimony to this problem.

Reasons for the taxonomic difficulties are due to a combination of various factors. These include:

(1) Extreme degree of intraspecific variation. This is especially obvious in ornate species; these may vary from completely smooth to heavily ribbed or tuberculate (see e.g. *B. anceps* or *B. capensis*).

(2) Inornate (smooth) species are virtually impossible to identify unless they have a very characteristic whorl section and/or suture line and the stratigraphic position is known.

(3) Apparent endemism of some *Baculites* species and restriction to distinct bio(?)geographic regions, i.e. U.S. Western Interior, Europe and Indo-Pacific regions, as well as possibly the U.S. Gulf Coast–Atlantic region and North Africa–Middle East regions.

Details of these problems are to be discussed fully in our forthcoming synthesis of the family Baculitidae (Klinger & Kennedy in press).

Fortunately, the descriptions and/or revision of the majority of the baculitid faunas of these major regions are the work of a few persons. Consequently, the taxonomic criteria within a certain geographic region are more or less constant.

The baculitid faunas of the U.S. Western Interior were dealt with primarily by Reeside (1927*a*, 1927*b*) and especially Cobban (1951 onwards), and recently with the assistance of Kennedy. The northern extension of the Western Interior region into West Greenland was covered by Birkelund (1965). In the Indo-Pacific region, the baculitids of California, Hokkaido and Honshu were monographed by Matsumoto (1959), Matsumoto & Obata (1963) and Obata & Matsumoto (1963), respectively; Ward (1978) revised the baculitids of Washington State and British Columbia. Those of Madagascar were described virtually single-handedly by Collignon (1931 to 1971). Major contributions from other parts of the Indo-Pacific region include New Zealand (Marshall 1926; Henderson 1970), Antarctica (Olivero 1984, 1992), the Austral Basin of South America (Hünicken 1965; Hünicken *et al.* 1975, 1980) and Argentina (Leanza 1964, 1967).

In contrast, *Baculites* is poorly known in the European and Asian regions. Recent revision of the Upper Cretaceous ammonite faunas of Europe, especially those of France by Kennedy (1984 onwards) and Kennedy & Summesberger (1986, 1987), have clarified the taxonomy of most of the Coniacian, Santonian and Maastrichtian *Baculites* species. The succession and systematics of the majority of *Baculites* species of the Campanian Stage still have to be worked out.

Distribution of *Baculites* on either side of the Atlantic is erratic. The oldest *Baculites* in Angola is an as yet undescribed Late Turonian–Early Coniacian species, which is transitional between *B. yokoyamai* and *B. codyensis* (M. R. Cooper collections, S.A. Museum; herein Fig. 131N—R, 132) or *B. capensis*. Cooper (1988) recorded *B. capensis* from the Lower Campanian. Haughton

(1925, 1926) and Howarth (1965) described *B. subanceps* (Figs 130, 131A–H) from the Upper Campanian or Lower Maastrichtian, and Haas (1943: 13, figs 15–19) described *B. anceps* (herein Fig. 131I–M) from the Lower Maastrichtian. A single baculite species, *B. teicherti* is known from the Maastrichtian of Nigeria.

Baculites from the Atlantic seaboard and the Gulf Coast region of the U.S.A. (see e.g. Adkins 1929; Stephenson 1941; Cobban 1974; Cobban & Kennedy 1991*a*, 1991*b*, 1992*a*, 1992*b*, 1993; Kennedy & Cobban 1993*a*, 1993*b*, 1993*c*, 1993*d*, 1993*e*) bear little resemblance to those of Angola or of the Western Interior.

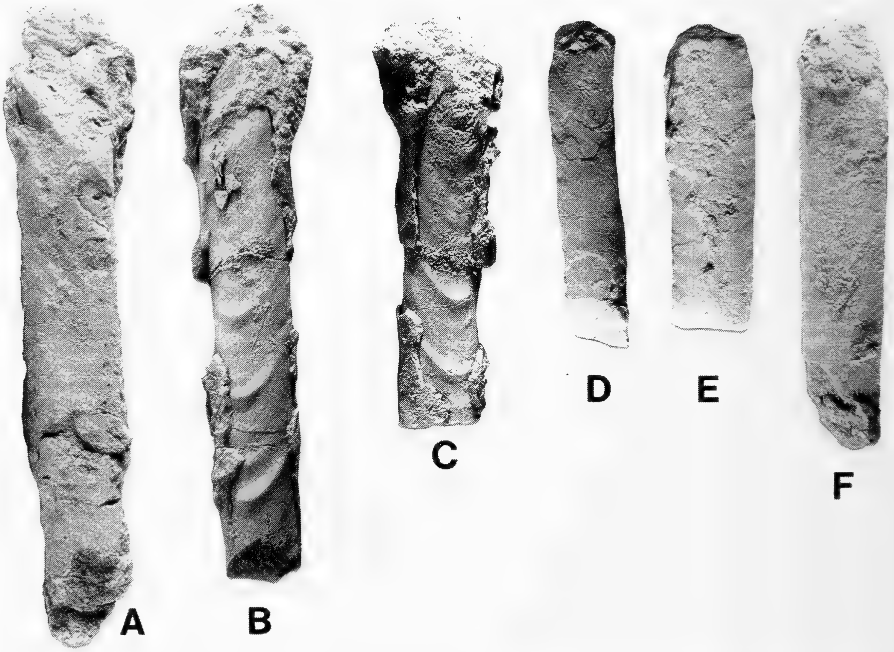

Fig. 7. A–F. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. A. NMB D1158/2. B–C. NMB D1158/3, specimen with distinct ribbing on body chamber. D. NMB D1158/4. E. NMB D1158/1. F. NMB D1158/7. All from a locality on the Msunduzi River, Van Hoepen collection, presumably the equivalent of locality 145 of Kennedy & Klinger (1975: 299), St Lucia Formation, Coniacian II. Scale × 1.

The baculitid records from Central America and Brazil are scant. Only *B. yokoyamai* is known from the Lower Coniacian of Venezuela and *B. kegeli* from the Maastrichtian of Brazil.

The North African baculitids were last studied by Pervinquière (1907, 1910) and, from his descriptions, it appears that *Baculites* is rare. Lefeld & Uberna (1992) recently mentioned *Baculites* in association with *Nostoceras* from Libya.

The baculitids of the Middle East, specifically Israel, appear to contain a mixture of European, Indo-Pacific and U.S. Gulf Coast and Atlantic seaboard elements, as well as some endemics. Dr Z. Lewy (Jerusalem) has shown us an extensive collection of Campanian to Maastrichtian *Baculites*, which he intends to describe. This as yet undescribed collection shows that the older records of Blanckenhorn (1905), Taubenhaus (1920) and Picard (1929) are badly in need of revision. Baculitids from Egypt were recently described by Luger & Gröschke (1989) and Hamama & Kassab (1990). These include *B. subanceps* and *B. ovatus*—Indo-Pacific and Gulf Coast–Atlantic region species. The record of *B. scotti*, a Western Interior species by Hamama & Kassab (1990: 462, pl. 2 (figs 5–9)) is probably incorrect. Alharithi & Ibrahim (1992) also recorded *B. ovatus* from the Maastrichtian of Jordan.

The Upper Coniacian to Lower Maastrichtian *Baculites* fauna of the U.S. Western Interior is mainly endemic (see review by Cobban 1994), but Kennedy (1993) has recently recorded three typical Western Interior species from the Campanian and Maastrichtian of Belgium. Some parallel development of the sutures and ornament occurs in the baculites of the Western Interior and of the Indo-Pacific regions (Klinger & Kennedy in press). Differences between baculites of the European and Indo-Pacific regions appear to be of lesser magnitude, and there seems to have been a much greater amount of faunal interchange between these two regions.

Occurrence

The genus first appears in the Lower Turonian, Zone of *Pseudaspidoceras flexuosum*, of the Western Interior of the U.S.A., as *B. yokoyamai*, and also in the Lower Turonian of Romania as *Baculites* aff. *undulatus* and *Baculites* sp. (Szász 1986); it persists to the end of the Maastrichtian (Birkelund 1979, 1993).

Baculites yokoyamai Tokunaga & Shimizu, 1926

Figs 7–11, 12A–I

1926 *Baculites (Lechites) yokoyamai* Tokunaga & Shimizu, p. 195, pl. 22 (fig. 5a–b), pl. 26 (fig. 11).
1931 *Baculites Besairiei* Collignon, p. 37, pl. 5 (figs 6, 6a, 7, 7a, 8, 8a, 9), pl. 9 (fig. 16).
1931 *Baculites sulcatus* Collignon, *non* Baily, p. 36, pl. 5 (figs 3, 3a, 4, 4a, 5, 5a, 13, 13a), pl. 9 (fig. 15).
1931 *Baculites Roedereri* Collignon, p. 38, pl. 5 (figs 10, 10a), pl. 9 (fig. 17).
1931 *Baculites latelobatus* Collignon, p. 38, pl. 5 (figs 11, 11a, 12, 12a), pl. 9 (fig. 18).
? 1958 *Baculites ovatus* Say?; Reyment, p. 7, pl. 1 (figs 1–2), text-figs 1–2.
1959 *Baculites* aff. *B. yokoyamai* Tokunaga & Shimizu; Matsumoto, p. 118, text-fig. 26.
1963 *Baculites yokoyamai* Tokunaga & Shimizu; Matsumoto & Obata, p. 30, pl. 8 (fig. 5), pl. 10 (figs 1–6), pl. 11 (figs 1, 4, 5), pl. 12 (fig. 3), pl. 14 (fig. 4), text-figs 72–87.
1965 *Baculites besairiei* Coll.; Collignon, p. 18, pl. 420 (figs 1745–1746).
1972 *Baculites* cf. *B. yokoyamai* Tokunaga & Shimizu; Cobban & Scott, p. 48, pl. 20 (figs 15–21).
1975 *Baculites* cf. *B. yokoyamai* Tokunaga & Shimizu; Hattin pl. 8 (figs F, H).
1977 *Baculites* cf. *B. yokoyamai* Tokunaga & Shimizu; Kennedy, p. 271, fig. 17 (1, 2).
1978 *Baculites* cf. *B. yokoyamai* Tokunaga & Shimizu; Hattin & Siemers, text-fig. 7.2.

1980 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban & Hook, p. 13, pl. 4 (figs 9–10).
1982 *Baculites inornatus* non Meek; Renz, p. 105, pl. 34 (figs 3–4, 5a–b, 6), text-fig. 80.
1983 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban & Hook, p. 7, pl. 1 (figs 1–7).
1983 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban, p. 16, pl. 14 (figs 6–8).
1984 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban, p. 14, pl. 1 (figs 5–6).
1986 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban, fig. 3H–I.
1988 *Baculites yokoyamai* Tokunaga & Shimizu; Kennedy, p. 110, pl. 23 (figs 8–10), text-fig. 29c.
1988 *Baculites yokoyamai* Tokunaga & Shimizu; Kennedy & Cobban, p. 608, fig. 3 (1, 2, 7, 13, 14, 18, 19).
1989 *B. yokoyamai* Tokunaga & Shimizu; Kennedy *et al.* p. 101, fig. 31e–h.
1990 *Baculites yokoyamai* Tokunaga & Shimizu; Cobban, p. B11, pl. 9 (figs 16–22).
1991*a* *Baculites yokoyamai* Tokunaga & Shimizu; Kennedy & Cobban, p. 69, pl. 13 (figs 4–10, 17–21, 24–28, 34–37, 41–42), text-fig. 22A.
1992 *Baculites yokoyamai* Tokunaga & Shimizu; Summesberger, p. 124, pl. 8 (figs 10–11).

Type

Holotype, by monotypy, is the specimen figured by Tokunaga & Shimizu (1926, pl. 22 (fig. 5a–b), pl. 26 (fig. 11)) from the lower Futaba Beds in the upper reaches of the Sakurazawa in Orikiri, Hirono-mura, Fukushima prefecture, north-east Honshu. The type was destroyed by fire during World War II. A specimen from the collections of the Kyushu University, GK 4580 from the Bannosawa in Hokkaido, of Coniacian age, zone of *Inoceramus uwajimensis*, was to be designated neotype by Matsumoto & Obata (see Matsumoto & Obata 1963: 30–31).

Material

NMB D1158/1–2, ?3, 4–8, all from a locality on the Msundusi River, collected by E. C. N. van Hoepen in 1923, presumably equivalent to Kennedy & Klinger's (1975: 299) locality 145, St Lucia Formation, Coniacian II (associated with *Forresteria (F.) madagascariensis* Collignon, 1965).

Dimensions

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*
D1158/4	6.4	8.6	0.74	5.7	8.1	0.70	20	2.5
D1158/7	8.4	11.6	0.72	7.9	9.9	0.80	28	6.1
D1158/1	9.3	12.0	0.77	7.9	10.3	0.77	26	6.5
D1158/5	9.3	12.1	0.77	—	—	—	—	—
D1158/2	—	13.0	—	—	—	—	—	—
D1158/3	8.0	11.7	0.68	7.0	9.9	0.70	50	3.6

Description

This species is rare in Zululand, and known from one locality only. It is easily identified by the elliptical whorl section and the very slow rate of taper in adult specimens. Also, the maximum adult size is small compared to later species of *Baculites* in Zululand.

Only one specimen, D1158/1 (Fig. 7E) has faint traces of ribbing over the venter; all the other specimens are perfectly smooth, both on the shell surface and on internal moulds.

One specimen, D1158/3 (Fig. 7B–C)—a body chamber with part of the last two septa preserved, is identical to the above specimens except that it has distinct, crescentic lateral ribs, which appear to originate in a curved, dorsolateral tubercle. Unfortunately we cannot determine on the basis of this specimen whether this ribbing is restricted to the body chamber, or is also present on the phragmocone.

The suture is partially exposed in D1158/4 (Fig. 8A) and D1158/3 (Fig. 8B), showing very simple, open subquadrate saddles and lobes.

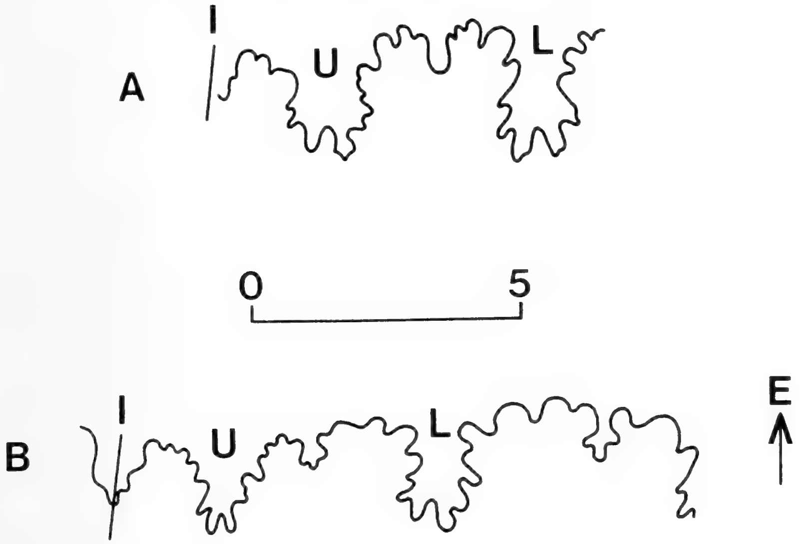

Fig. 8. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. Suture lines. A. NMBD1158/4. B. NMBD1158/3. Scale bar in mm.

Discussion

Baculites yokoyamai is the best documented species in the early history of the genus *Baculites* and appears to have both a wide geographic distribution and long stratigraphic range. It appears to be the root stock from which the majority of later *Baculites* species has evolved.

The name *B. yokoyamai* has been applied to non-tuberculate baculitids with elliptical whorl section, primitive suture and of Turonian to Coniacian age. The Turonian occurrences are best documented in the U.S. Western Interior, where the species ranges throughout the stage, first appearing in the Lower Turonian Zone of *Pseudaspidoceras flexuosum*. It persists into the Lower Coniacian, Zone of *Inoceramus erectus* of the Western Interior, from where it has recently been fully illustrated by Kennedy & Cobban (1991*a*). In Hokkaido it persists through the greater part of the Coniacian, although possibly not into the uppermost part, in the Zone of *Inoceramus uwajimensis*.

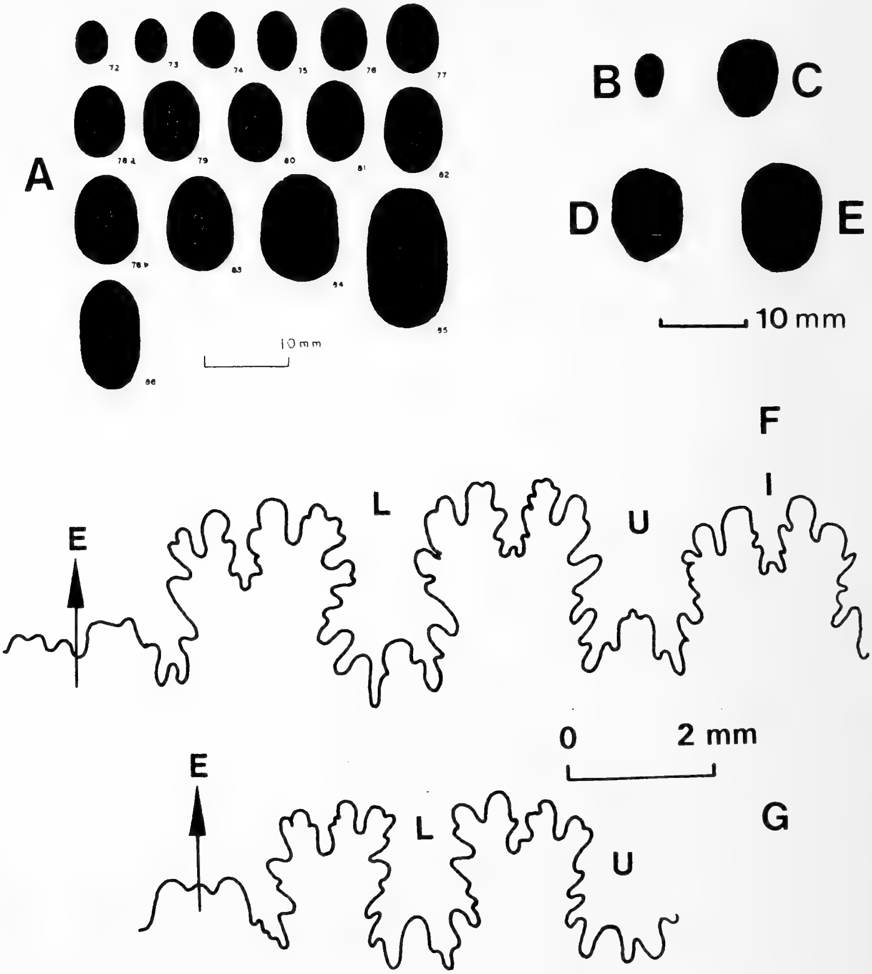

Fig. 9. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. A–E. Whorl sections. A. Japanese specimens (copy of Matsumoto & Obata 1963, text-figs 72–86). B. NMB D1158/8. C. NMB D1158/6. D. NMB D1158/1. E. NMB D1158/5. All × 1. F–G. *Baculites bailyi* Woods, 1906. Suture lines. F. SAM–PCZ8355. G. SAM–PCZ8344.

Our smooth specimens are identical to material described from the U.S. Western Interior and Hokkaido. Kennedy & Cobban (1991*a*) have recently shown that, even though the majority of *B. yokoyamai* in the lower Coniacian of the Western Interior are smooth, some forms occur with fold-like ribs on the upper part of the flanks (e.g. Kennedy & Cobban 1991*a*, pl. 13 (figs 20, 24). D1158/3 (Fig. 7B–C) could possibly be interpreted as a more strongly sculptured variant of *B. yokoyamai*, and we see no need for separating it from the latter at present. Nevertheless, the similarity in ornament between D1158/3 and *B. sweetgrassensis* Cobban (1951: 820, pl. 118 (figs 6–9), text-figs 1–3) (see also Kennedy & Cobban 1991*a*: 70, pl. 14 (figs 24–25, 29–34, 38–42)) is striking. This latter species, however, has a distinctive ovoid whorl section with a narrow venter.

The relationship between ribbed D1158/3 and smooth forms of *B. yokoyamai* is very similar to that of *B. sweetgrassensis* (ribbed) and *B. mariasensis* (smooth) (Cobban 1951: 818, pl. 118 (figs 10–12), text-figs 4–7)—see also Kennedy & Cobban 1991*a*: 69, pl. 13 (figs 11–16, 22–23, 29–33, 38–40), pl. 14 (figs 1–23, 26–28, 43–48), text-fig. 25E). The latter species both occur in the Lower Coniacian Zone of *Inoceramus erectus*, and, according to the original description of Cobban (1951: 820), '*B. sweetgrassensis* is an uncommon species . . . . The types were collected with *B. mariasensis* in the Colorado shale'. Their co-occurrence, as well as the ratio of smooth to ribbed forms suggests that *B. sweetgrassensis* may be no more than a ribbed form of *B. mariasensis*, in the same relation as the ribbed Zululand specimen of *B. yokoyamai* to the majority of smooth specimens.

Cobban (1951: 817) and Cobban & Reeside (1952) initially identified what is now known as *B. yokoyamai* in North America, as *Baculites* cf. *B. besairiei*. Matsumoto (1959: 117) subsequently suggested that *B. besairiei* Collignon (1931: 37, pl. 5 (figs 6–9), pl. 9 (fig. 16)) might be a synonym of *B. yokoyamai*. Later, Matsumoto & Obata (1963: 34) concluded confidently that 'all the described characters of *Baculites besairiei* Collignon are the same as those of *B. yokoyamai*'.

Collignon had 721 baculitid specimens from the apparently condensed or secondarily concentrated ferruginous conglomerate of Mahagaga, initially dated as Santonian (Collignon 1931), but later as Late Coniacian (Besairie & Collignon 1959). Of these, 531 specimens were discarded as being too fragmentary, leaving 190 specimens to be studied. The majority, 150 specimens, were referred to *B. besairiei* Collignon (1931: 37, pl. 5 (figs 6, 6a, 7, 7a, 8, 8a, 9), pl. 9 (fig. 16)); lectotype herein designated, is the largest figured specimen pl. 5 (fig. 6)) (herein Fig. 10A–C). Collignon (1931: 37) described the variation in strength of ribbing over the venter in *B. besairiei* in detail. In typical forms, the ribs are oblique over the flanks and cross the venter in a sharp chevron. In some, ribbing is thin, in others thick, and in some alternating thick and thin.

In addition to *B. besairiei*, Collignon described three other non-tuberculate baculitids from this assemblage. These include *B. sulcatus* Collignon, *non* Baily (Collignon 1931: 36, pl. 5 (figs 3–5, 13), pl. 9 (fig. 15)) (24 specimens) (herein Fig. 11D–L); *B. roedereri* (Collignon 1931: 38, pl. 5 (fig. 10), pl. 9 (fig. 17)) (herein Fig. 12G–I); holotype by monotypy is the figured specimen; *B. latelobatus* (Collignon 1931: 38, pl. 5 (figs 11–12), pl. 9 (fig. 18)) (3 specimens) (herein Fig. 12A–F); lectotype, herein designated, is the largest of the two figured specimens (Collignon 1931, pl. 5 (fig. 11)) (herein Fig. 12A–C).

We have been able to examine the figured and some of the unfigured material and agree with Matsumoto & Obata that *B. besairiei* is probably a synonym of *B. yokoyamai*. Certainly as far as the elliptical whorl section and variation in ornament are concerned, there is no valid reason for maintaining them as separate species.

Furthermore, Collignon's *B. sulcatus* definitely does not belong to this Campanian Pondoland species; it lacks the typical strong lateral ornament. Instead, we regard the 24 specimens described by Collignon under that name as slightly

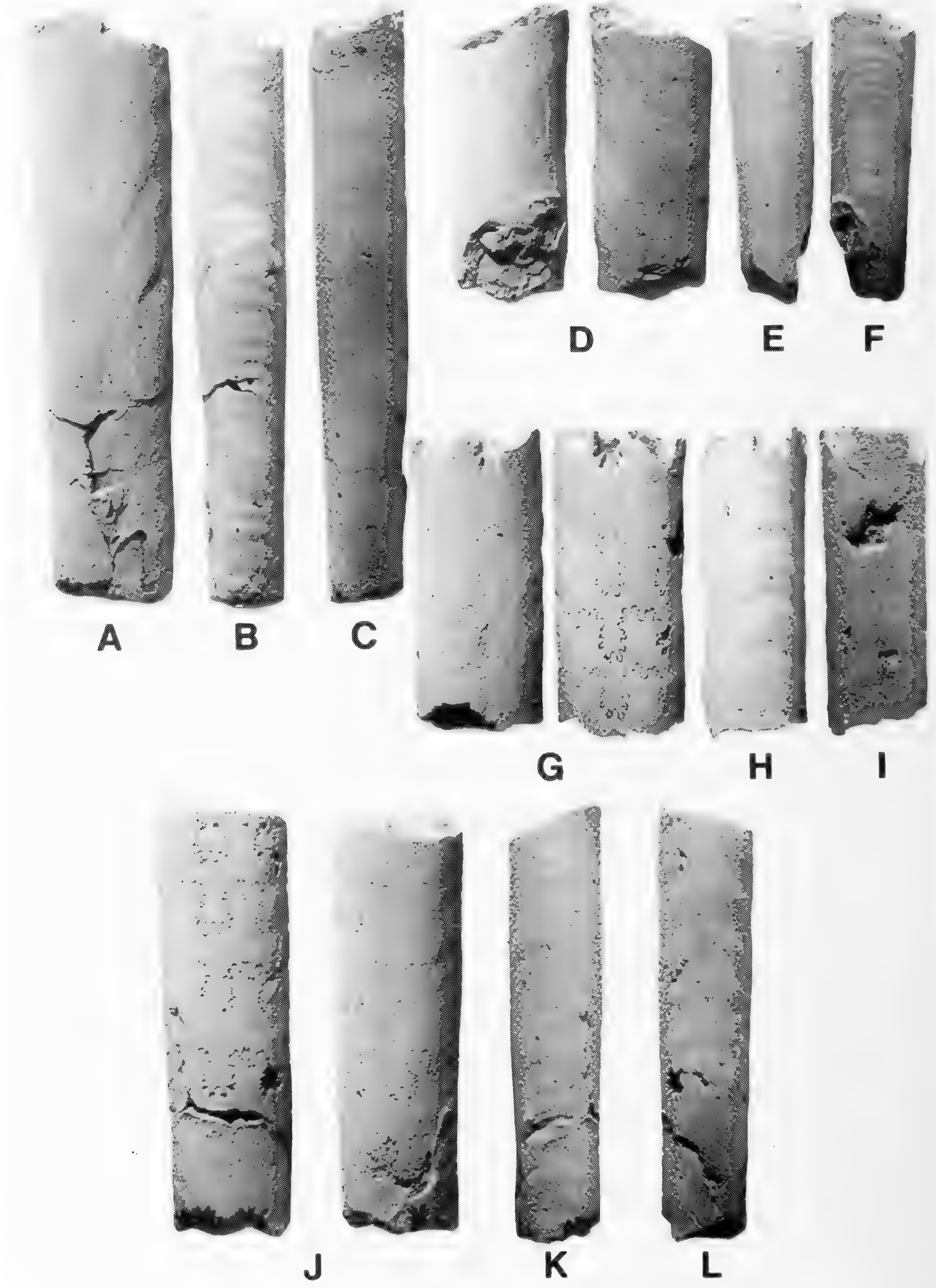

Fig. 10

more strongly ribbed variants of *B. yokoyamai*. Externally, *B. roedereri* is indistinguishable from *B. besairiei*, i.e. *B. yokoyamai*. According to Collignon (1931: 38) it differs in the suture line: the terminations of the lobes are rounded; the first (E/L) saddle is very large and divided by a prominent lobule; the second lateral saddle (L/U) is narrow and much higher than the first; and the antisiphonal saddle (I/U) is very large and very low, divided by a large, pointed lobule. The first lateral lobe (L) is narrow and prominent, the second lateral lobe (U) is smaller than the first and asymmetrical. These differences are trivial and well within the range of variation of *B. yokoyamai* (= *B. besairiei*).

Similarly, *B. latelobatus* was alleged to differ on sutural details. The antisiphonal saddle (U/I) is elongated above the first lateral saddle (E/L), the first lateral lobe (L) is wide, whereas the second lateral lobe (U) is nearly rudimentary. Again, these differences are well within the limits of variation of *B. yokoyamai* (= *B. besairiei*).

The Mahagaga baculitid assemblage is of extreme interest in that it contains the earliest representatives of tuberculate *Baculites* in Madagascar, i.e. *B. boulei* Collignon (1931: 35, pl. 5 (fig. 2, 2a), pl. 9 (fig. 14)) (herein Fig. 12J–L) and *Baculites* cf. *B. brevicosta* Collignon *non* Schlüter (Collignon 1931: 34, pl. 5 (fig. 1, 1a), pl. 9 (fig. 13)), but these are numerically insignificant compared to unornamented *B. yokoyamai*.

It is difficult to separate *B. yokoyamai* from other contemporary Turonian *Baculites* species. In the Western Interior, the name *B. calamus* Morrow, 1935 (p. 473, pl. 49 (fig. 8a–b)) is used for Turonian *Baculites* with weak lateral ribs (*fide* Cobban & Scott 1972: 49). However, as shown by e.g. Cobban & Hook (1983, pl. 1 (figs 3–6)) and recently Kennedy & Cobban (1991*a*), some specimens of *B. yokoyamai* also have weak to prominent lateral ornament, and it is difficult to maintain them as separate species. Compared to *B. yokoyamai*, *B. calamus* is extremely rare. We are not quite sure on how many specimens Morrow based his species; he only mentioned the holotype but, according to Cobban & Scott (1972: 49), 'The species is uncommon; we found it in only one bed at one locality' (in Colorado). According to Cobban & Scott (1972: 32, table 3), *B. yokoyamai* occurs throughout virtually the whole of the Turonian, whereas *B. calamus* occurs only in the Middle Turonian *Collignoniceras woollgari* Zone. Rarity alone can not be a criterion for invalidating the species but, combined with the overlapping morphologies, we doubt that *B. calamus* can be separated satisfactorily from *B. yokoyamai*.

The only other Turonian *Baculites* species is *B. undulatus* d'Orbigny, 1850. Matsumoto & Obata (1963: 28) ascribed authorship of this species to Roman & Mazeran, who indeed first provided a description of this species and designated the lectotype (Roman & Mazeran 1913: 11, pl. 4 (figs 6–8)). Although poorly defined, d'Orbigny's Prodrome species are valid, and authorship of

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Fig. 10 *(see facing page)*. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. The figured specimens of *B. besairiei* Collignon, 1931. A–C. Lectotype, the original of Collignon, pl. 5 (fig. 6). D–F. The original of Collignon, pl. 5 (fig. 9). G–I. The original of Collignon, pl. 5 (fig. 8). J–L. The original of Collignon, pl. 5 (fig. 7). All from the ferruginous conglomerate at Mahagaga, Madagascar. All unregistered and housed in the collections in Dijon. All × 2.

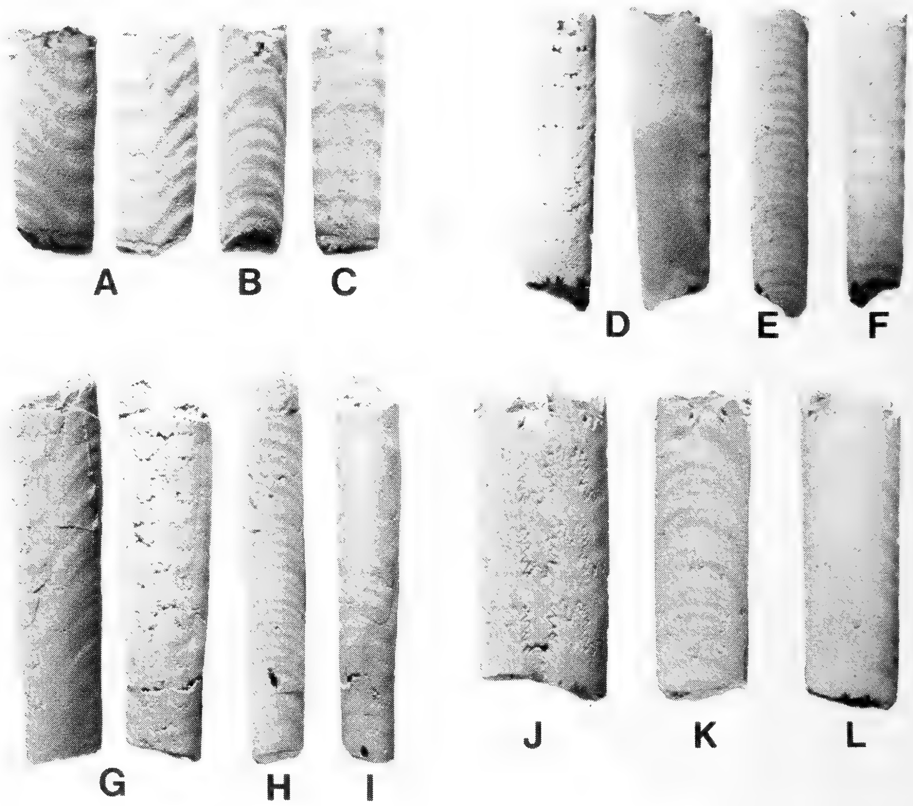

Fig. 11. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. A–C. The original of Collignon (1931, pl. 5 (fig. 13)) *Baculites* aff. *sulcatus*. D–F. The original of Collignon (1931, pl. 5 (fig. 4). G–I. The original of Collignon (1931, pl. 5 (fig. 3)). J–L. The original of Collignon (1931, pl. 5 (fig. 5)), all originally referred to *Baculites sulcatus*. All from the ferruginous conglomerate at Mahagaga, Madagascar. All unregistered and housed in the collections in Dijon. All × 2.

B. undulatus rests with d'Orbigny. The lectotype was refigured and described by Sornay (1955) and Breton & Bavent (1985: 101–102, figs 1–3).

The name *B. undulatus* has generally been applied to Upper Turonian *Baculites* in Western Europe, especially France (d'Orbigny 1850: 19, 21, no. 21; Roman & Mazeran (1913: 11, pl. 4 (figs 6–8)), and the Chalk Rock of England

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Fig. 12 *(see facing page)*. A–I. *Baculites yokoyamai* Tokunaga & Shimizu, 1926. A–C. The lectotype of *B. latelobatus*, the original of Collignon (1931, pl. 5 (fig. 11)). D–F. A paralectotype of *B. latelobatus*, the original of Collignon (1931, pl. 5 (fig. 12)). G–I. The holotype of *B. roedereri*, the original of Collignon (1931, pl. 5 (fig. 10)). J–O. *Baculites capensis* Woods, 1906. J–L. The lectotype of *Baculites boulei* Collignon, the original of Collignon (1931, pl. 5 (fig. 2)). M–O. The original of *Baculites* cf. *B. asperoanceps* of Collignon (1931, pl. 3 (fig. 7)). A–L from the ferruginous conglomerate at Mahagaga; M–O from Mokotibe-Tsianaloky. All unregistered and housed in the collections in Dijon. A–L × 2; M–O × 1.

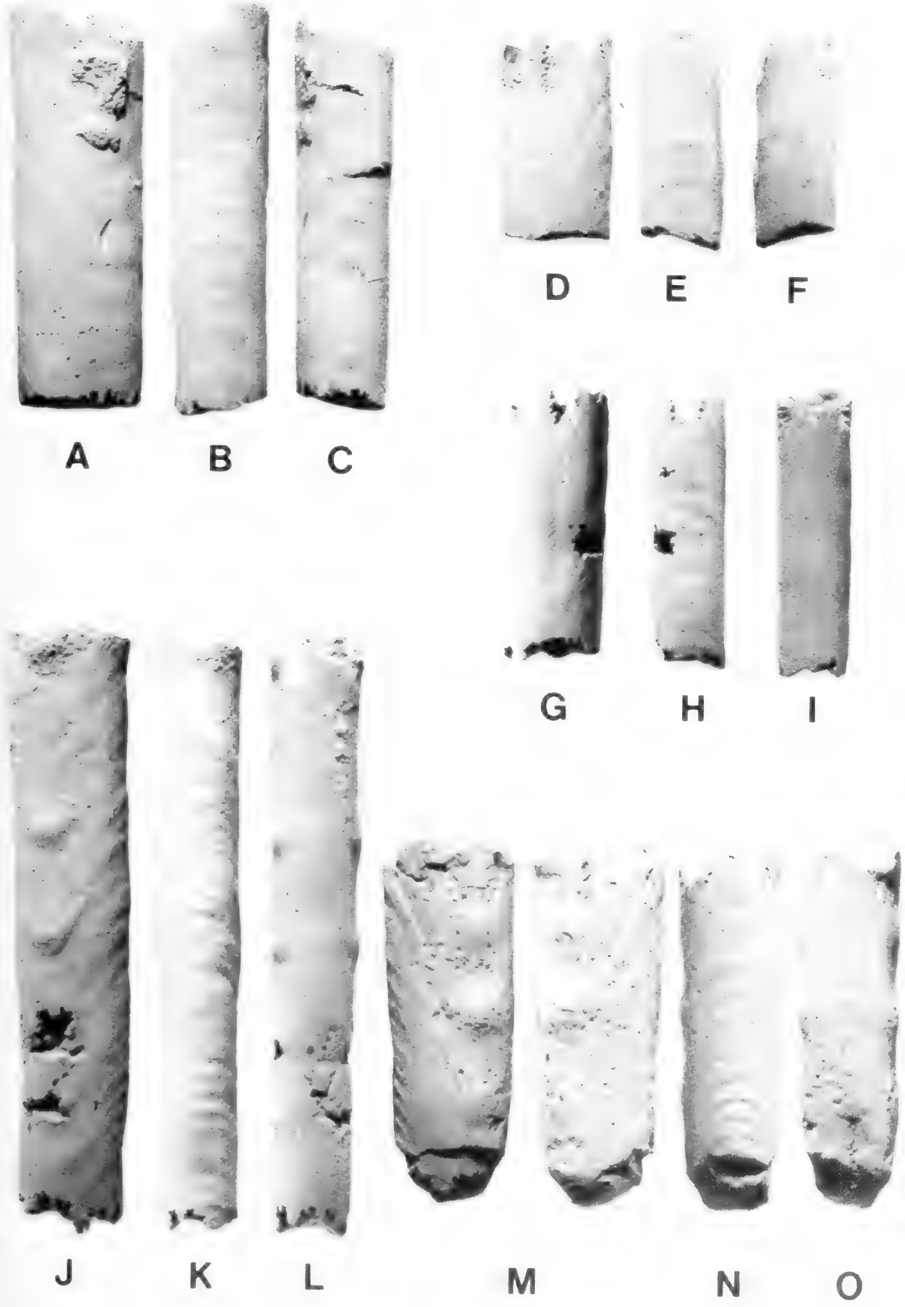

Fig. 12

(Wright 1979: 287, pl. 1 (figs 6–8), pl. 7 (fig. 11)), where it is only known from a few localities; Fritsch & Schloenbach (1872: 49) recorded numerous baculitids from several localities in Bohemia that they considered to probably belong to *B. undulatus*. Unfortunately, the specimens were nearly all secondarily compressed, and none were figured; this makes it difficult to confirm their Bohemian records. That of Jahn (1895: 136, pl. 8 (fig. 8a–c)), as *Baculites* n. sp., however, confirms the occurrence of *B. undulatus* in Bohemia. Matsumoto & Obata (1963: 28, pl. 8 (fig. 4), pl. 9 (figs 1–5), pl. 11 (figs 2–3), text-figs 62–71) recorded *B. undulatus* from the Upper Turonian of Hokkaido.

Kennedy *et al.* (1989: 101, fig. 31i) recently recorded *B. undulatus* from the Upper Turonian *Prionocyclus macombi* and *P. wyomingensis* zones of Trans-Pecos Texas and New Mexico. This figured specimen is very similar to the Middle Turonian *B. calamus*, and we suspect that they may be allied, possibly as a local subspecies or variant of *B. undulatus*.

Szász (1986: 120, pl. 1 (figs 1–2)) recorded *Baculites* aff. *B. undulatus* from the Lower Turonian of Romania, accompanied by a questionable baculitid with ornament very similar to that of *B. calamus*. If the Romanian material is correctly identified as *B. undulatus*, this suggests that *B. yokoyamai* and *B. undulatus* appeared more or less at the same time in Europe and in North America.

Baculites undulatus differs from *B. yokoyamai* mainly in having coarser, less oblique ribbing. Dorsolateral bullae develop in some adult specimens of both *B. undulatus* (see e.g. Wright 1979, pl. 7 (fig. 11)) and *B. yokoyamai* (see above and NMB D1158/3—Fig. 7B–C), and seem to be of little systematic value.

It thus appears that differences between *B. yokoyamai* and *B. undulatus* are found mainly in the ribbing—that of the former being more delicate than that of the latter. In addition, *B. undulatus* has a narrower stratigraphic distribution, being restricted mainly to the Upper Turonian, although it might already occur in the Lower Turonian, whereas *B. yokoyamai* occurs throughout the Turonian, all of the Lower Coniacian and probably persists into the Upper Coniacian.

Differences between *B. yokoyamai* and *B. bailyi* are discussed below.

Feebly ornamented baculitids recorded from the Coniacian of Venezuela, and misidentified as *B. inornatus* Meek (a Campanian species) by Renz (1982: 105, pl. 34 (figs 3–6), text-fig. 80) and as *B. ovatus* Say? (of Late Campanian age) by Reyment (1958: 7, pl. 1 (figs 1–2), text-figs 1–2), are good examples of *B. yokoyamai*, thus extending the geographic range of the species to South America.

Occurrence

Baculites yokoyamai is known from the Turonian and Lower Coniacian of the U.S. Western Interior, Lower Coniacian of Venezuela, and Coniacian of Hokkaido (though apparently not extending to the uppermost part of the stage), Middle Coniacian of Zululand, and Upper Coniacian of Madagascar. Dubious specimens have recently been recorded from the Middle Turonian of Austria (Summesberger 1992: 124).

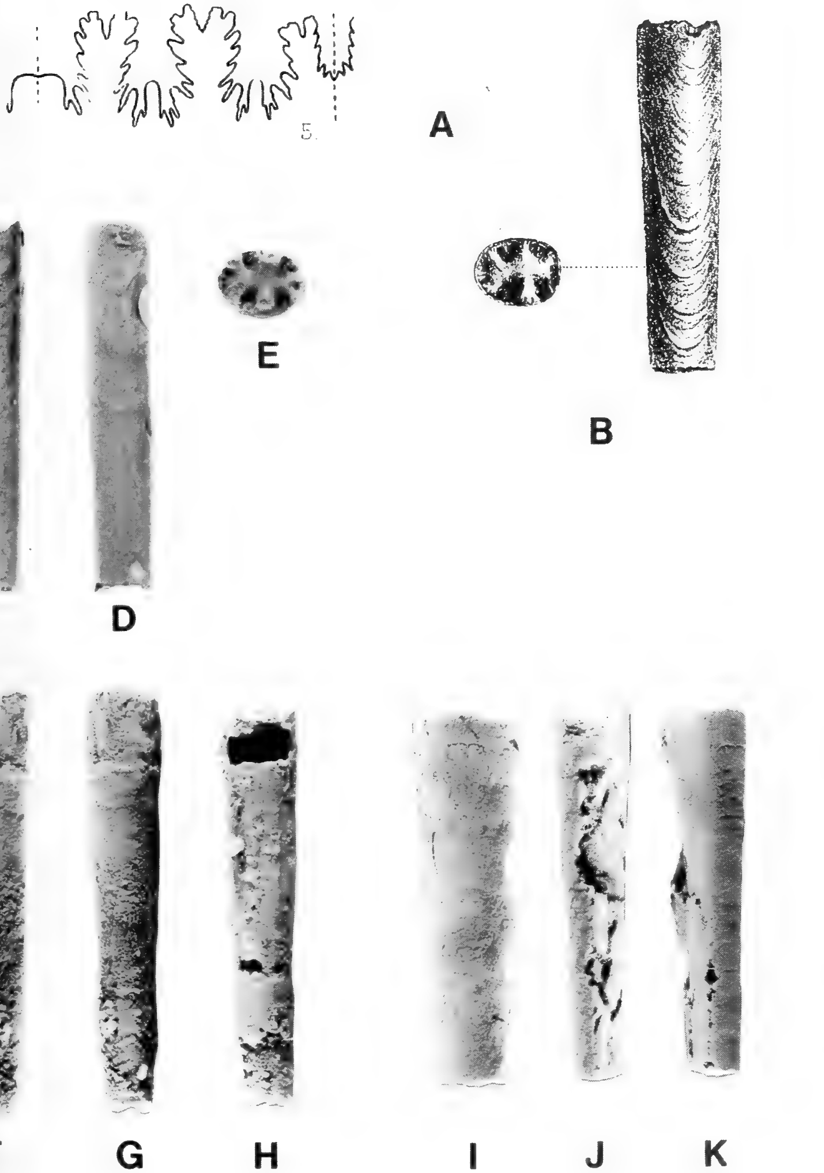

Fig. 13. *Baculites bailyi* Woods, 1906. A. Copy of the suture line figured by Woods (1906, pl. 44 (fig. 5)) based on a paratype in the now missing Griesbach collection. B. Copy of Baily (1855, pl. 11 (fig. 5a–b)) of the holotype of *B. bailyi* (as *B. sulcatus*). C–E. The holotype, BMNH C11372. F–H. SAM-PCO5994a. I–K. SAM-PCO5994b. Both from dredge samples off the Natal South Coast. All except A × 1. Photographs in C–E by courtesy of Natural History Museum, London.

Baculites bailyi Woods, 1906

Figs 13–23, ?34M–R, 67K–Q, 78A–B

	1855	*Baculites sulcatus* Baily, p. 457 (pars), pl. 11 (fig. 5a–b only, *non* 5c).
?	1904	*Baculites* sp. Etheridge, p. 90, pl. 3 (fig. 24).
	1906	*Baculites Bailyi* Woods, p. 341, pl. 44 (fig. 5).
?	1921	*Baculites Bailyi* Woods; van Hoepen, p. 18, pl. 3 (figs 9–10).
	1921	*Baculites bailyi* H. Woods; Spath, p. 261.
	1922	*Baculites bailyi* Woods; Spath, p. 146.
?	1930	*Baculites Bailyi* Woods; Besairie, p. 223, pl. 21 (fig. 7 only, *non* 6).
	1963	*Baculites bailyi* Woods; Matsumoto & Obata, p. 35, pl. 20 (figs 1–2), pl. 21 (fig. 5), text-figs 88–89, 116–120, 140–142.
	1969	*Baculites bailyi* Woods; Collignon, p. 21, pl. 520 (fig. 2051).
	1977	*Baculites bailyi* Woods; Klinger & Kennedy, p. 75, fig. 5D.
	1978	*Baculites bailyi* Woods; Ward, p. 1148, pl. 1 (figs 5–7), text-fig. 5A–D.
	1984	*Baculites bailyi* Woods; Olivero, p. 57, pl. 1 (figs 1–5), text-fig. 1a–b.
	1985	*Baculites bailyi* Woods; Klinger, p. 5, fig. 4E–H.
?	1988	*Baculites* cf. *kirki* Matsumoto; Riccardi & Aguirre-Urreta, p. C389, pl. 3 (figs 4–8).

Types

Holotype, by original designation of Woods (1906: 342) is the specimen figured by Baily (1855, pl. 11 (fig. 5a–b)), BMNH C11372 (herein refigured as Fig. 13C–E), from an unspecified horizon at the type section of the Mzamba Formation, Mzamba Estuary, Pondoland, Transkei. Probable paratypes are SAM–4822 and SAM–13103 (Fig. 67M), both also from an unspecified horizon at the Mzamba Estuary.

Material

We have more than one hundred specimens from the following localities:

(1) Locality 1, Mzamba Formation, Pondoland, Transkei, Santonian II.

(2) Locality 10, Zululand (locality d of Spath 1921: 221–222), St Lucia Formation; the locality extends from Coniacian II at the base to probably as high as Campanian.

(3) Locality 13, Zululand, St Lucia Formation, Coniacian II or III.

(4) Locality 72, Zululand, St Lucia Formation, Coniacian III.

(5) Locality 73, Zululand, St Lucia Formation, Coniacian IV (associated with *Peroniceras (Zuluiceras) modestum*).

(6) Locality 74, Zululand, St Lucia Formation, the section extends from Santonian I to Campanian I.

(7) Locality 77, Zululand, St Lucia Formation, Coniacian V.

(8) Locality 78, Zululand, St Lucia Formation, Santonian I–II.

(9) Locality 80, Zululand, St Lucia Formation, Coniacian V.

(10) The top of the section at locality 92, Zululand, St Lucia Formation, Coniacian III.

Fig. 14 *(see facing page)*. *Baculites bailyi* Woods, 1906. A–I. SAM–PCZ8391. J–Q. SAM–PCZ8357. Both from locality 99, Zululand, St Lucia Formation, Santonian I or II. A–D, J–M × 1, E–H, N–Q × 2, I × 4.

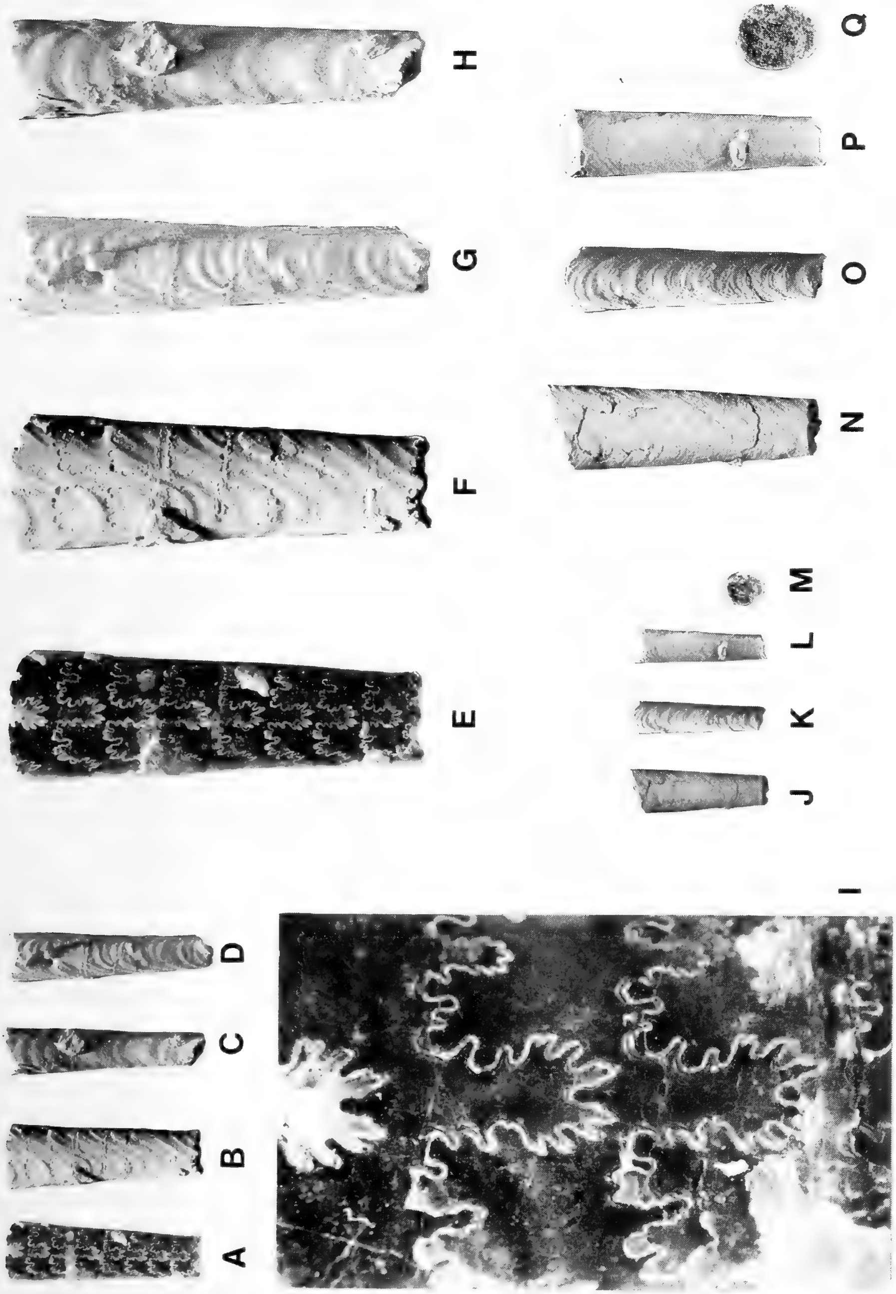

Fig. 14

(11) Locality 96, Zululand, St Lucia Formation, Coniacian V or Santonian I.
(12) Locality 98, Zululand, St Lucia Formation, Santonian ?II.
(13) Locality 99, Zululand, St Lucia Formation, Santonian I or II.
(14) Locality 100, Zululand, St Lucia Formation, Santonian I.
(15) Locality 101, Zululand, St Lucia Formation, Santonian II or III.
(16) Field locality H40, small exposure at pump house on the banks of the Nyalazi River, on Nyalazi Sugar Estate, 2 km east of Nyalazi River Settlement, Zululand, St Lucia Formation, Campanian ?I.
(17) Field locality H135, loose concretions next to railway line, near Lake View siding, Zululand, St Lucia Formation, Coniacian ?V.
(18) Dredge samples off the Natal South Coast.

Dimensions

A list of dimensions is given in the appendix.

Max. Wb. (mm)	*MxWb/MxWh*	*MnWb/MnWh*	*Ti*
0–4.9	0.75	0.71	5.3
5.0–9.9	0.75	0.76	5.4
10.0–14.9	0.76	0.75	4.15
15.0–19.9	0.77	0.76	2.97

Description

Woods's (1906: 341) original description is as follows: 'Shell increasing in diameter very slowly. Section oval, compressed, rather narrower on the siphonal than on the antisiphonal side. A small carina is seen in specimens which have the shell well-preserved. Lobes and saddles narrow and rather deep . . . . Ornamentation consists of small, inconspicuous ribs, which bend rapidly backwards from the siphonal margin; below the middle of the shell they curve round and pass forward over the anti-siphonal margin.'

Our material shows that this is essentially an inornate species with ovoid whorl section, which, in typical specimens, has a venter that is narrower than the dorsum and may even be acute; but in some, the whorl section may be near-circular. Lateral ornament consists of fine striae only, which may strengthen on the ventral half of the flanks and cross the venter with a distinct chevron, and, in the process, form distinct corrugations, which may be present even on internal moulds. Irregularly developed, weak dorsolateral nodes occur in a few specimens.

One of the notable features of *B. bailyi* (and other baculitids as well) is that it often occurs in great concentrations in single concretions, sometimes in more or less parallel arrangement. In some of these concretions, e.g. SAM–PCZ8390 from locality 13, the preservation is exquisite, with original shell material and protoconchs preserved (Figs 17A–B, 18A–B).

Early whorls with protoconchs are preserved in PCZ8390 (Fig. 17A), PCZ8390z (Fig. 18A), PCZ8390m (Fig. 18B), PCZ8390o, PCZ8390e and PCZ7213–4. The small diameter of the early coiled section is less than 0.5 mm, and explains why exposed protoconchs on fracture surfaces of concretions are

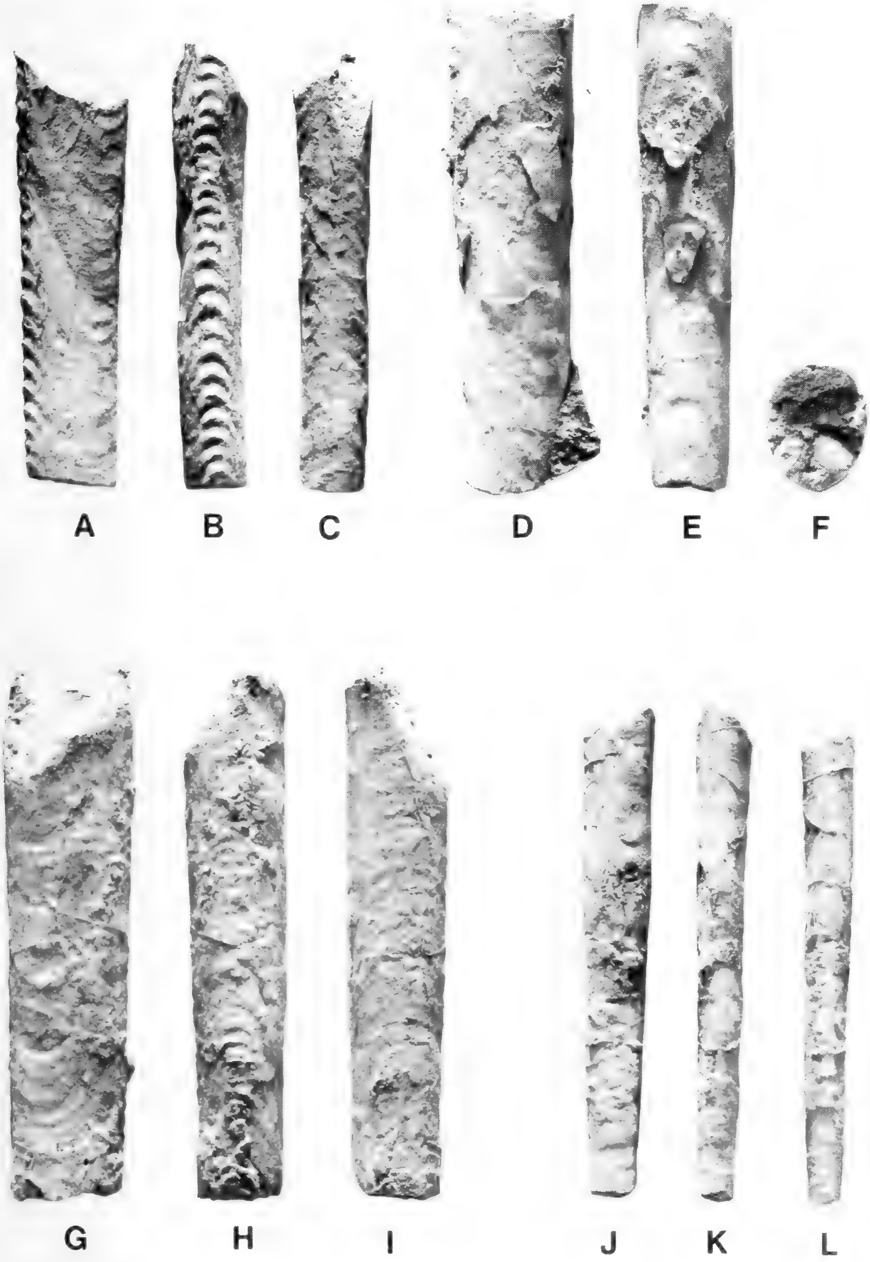

Fig. 15. *Baculites bailyi* Woods, 1906. A–C. SAM-PCZ8359, exact locality unknown, probably Mkweyane (Umkwelane Hill), Zululand. Note distinct ventral corrugation. D–F. SAM-PCZ8346. G–I. SAM-PCZ8345. J–L. SAM-PCZ8344 (microconch), all from locality 99, Zululand, St Lucia Formation, Santonian I or II. All × 1.

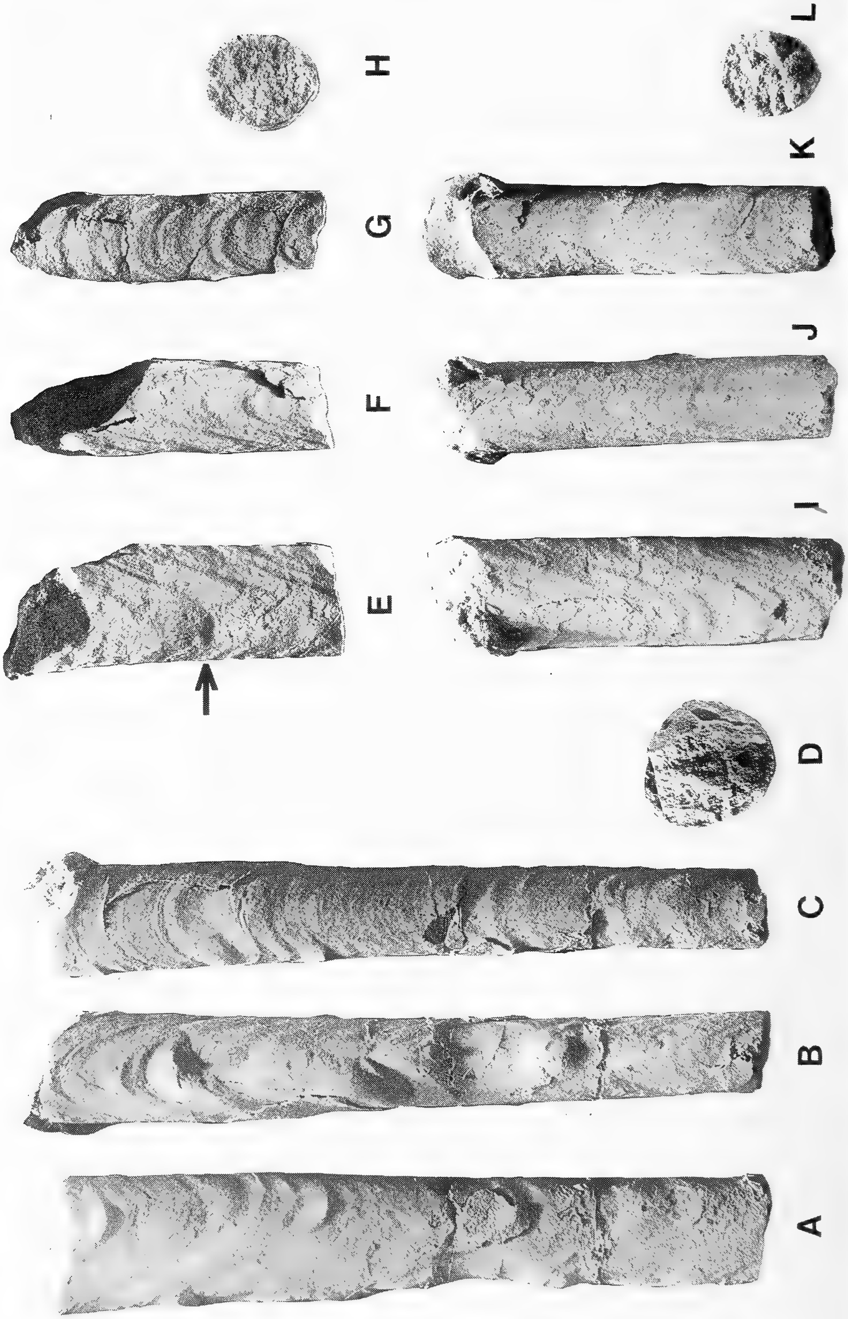

Fig. 16

extremely rare. A slight nick-point in the early shaft is also conspicuous. The presence and preservation of baculitids with protoconchs probably indicate very low energy levels in this depositional environment.

The whorl section is elliptical at very early diameters, *c.* 2 mm, and subsequently becomes ovoid, with a narrow to acute vènter, and maximum whorl breadth just dorsal of mid-flank (Figs 19B–C, F, 20A–I, 21A–I, 22B–E). The whorl section is quite variable. In some, the section is distinctly tear-shaped, with a nearly acute venter, often accentuated by chevron ribbing over, and distinct corrugation of the venter. In others the venter may remain broadly rounded to large diameters, resulting in a near-circular whorl section.

Details of the ornament vary considerably, partly due to preservation. Ornament consists of fine striae which cross the whole periphery of the shell (Fig. 14J–Q), but are generally strongest on the ventral half of the flanks, where they curve and are strongly prorsiradiate. In some, the striae may be raised in sheaves on the dorsal part of the flanks, forming slight, crescentic, incipient tubercles (Fig. 14A–H). Over the venter some striae may thicken periodically, separated by weaker ones, or all may thicken. Both types of ornament produce distinct crenulation and chevron ribbing over the venter (e.g. Figs 15A–C, 16I–L, 23D–G, P–R).

In the majority of specimens, ornament on the body chamber and phragmocone is the same. In some, however, irregularly spaced dorsolateral nodes may appear on the body chamber. In PCZ8350 (Fig. 16A–D), albeit slightly pathologic, crescentic ribs appear on the body chamber. On PZC8353 (Fig. 34H–I) a single pair of tubercles occurs; on PCZ8387 (Fig. 34M–O) two pairs of distantly-spaced tubercles occur. We are not quite sure if these are, indeed, atypical forms of *B. bailyi* or weakly ornamented variants of *B. capensis*—we suspect the former.

Unfortunately preserved apertures are rare, but the disparate sizes of some apparently adult specimens (compare e.g. Figs 15G–I and 15J–L) suggest that the species may be dimorphic.

The suture lines (Figs 19A, D, 22A) of our specimens vary in details, but are relatively simple with open saddles and lobes.

Discussion

For several reasons, *B. bailyi* is difficult to interpret on the basis of the Pondoland material alone. Of the original type series, only the holotype and two very poorly preserved paratypes remain. The exact stratigraphic location of the holotype at the type section of the Mzamba Formation is unknown and, despite being amongst the first ammonites recorded from Mzamba, *B. bailyi* is extremely rare there. Most probably the biggest obstacle in referring smooth Coniacian and Santonian *Baculites* from Zululand and Pondoland to *B. bailyi*, as we had indeed done earlier (Kennedy & Klinger 1975: 278–279), is the seemingly atypical suture line of *B. bailyi* as figured by Woods (1906, pl. 44

Fig. 16 *(see facing page). Baculites bailyi* Woods, 1906. A–D. SAM–PCZ8350 (note irregular ornament on body chamber). E–H. SAM–PCZ8349 (arrow points to lateral tubercle). Both from locality 99, Zululand, St Lucia Formation, Santonian I or II. I–L. SAM–PCZ8356 from locality 100, Zululand, St Lucia Formation, Santonian I. All × 1.

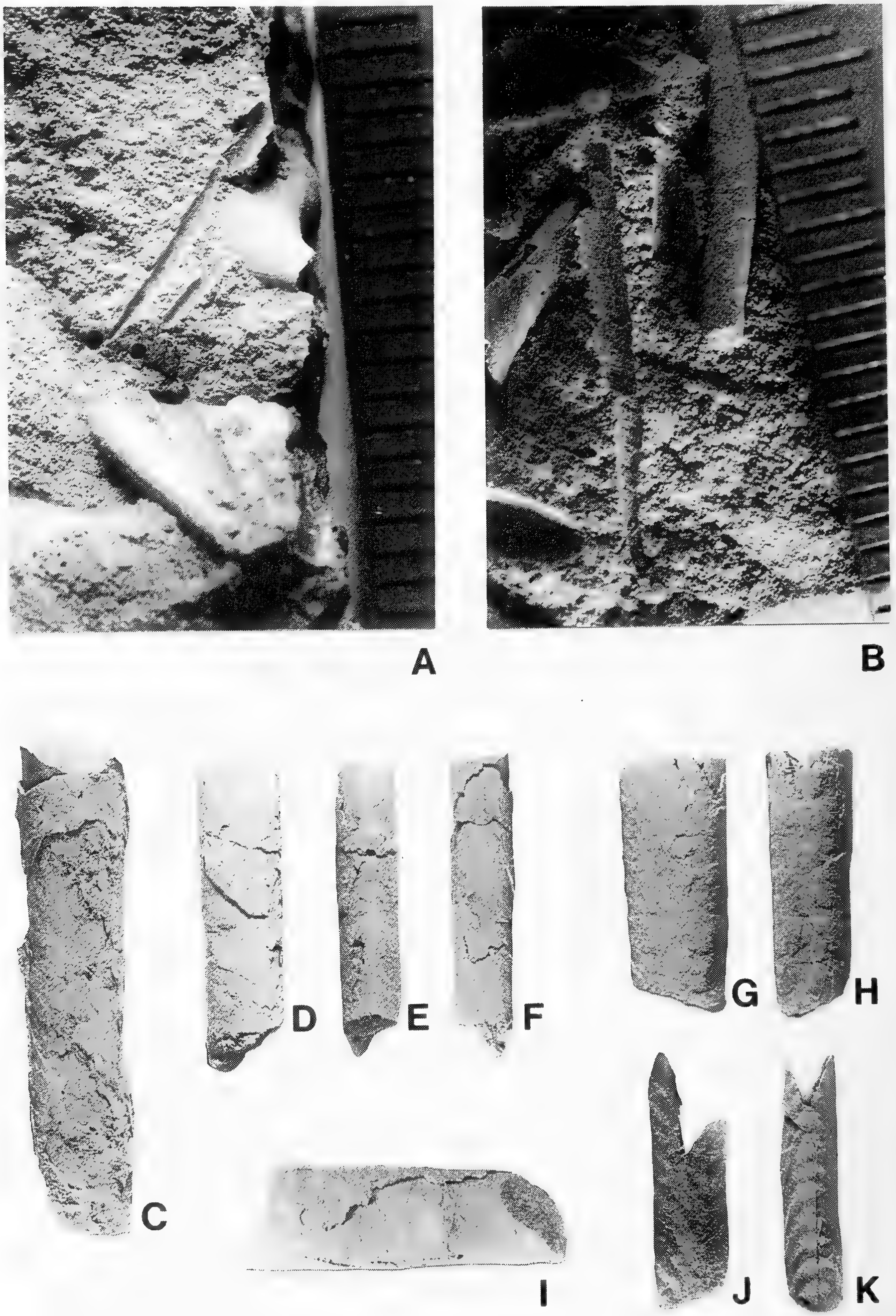

Fig. 17

(fig. 5)) (herein Fig. 13A) and taken from a specimen in the Griesbach collection. None of our smooth *Baculites* from Zululand have as narrow saddles as the specimen in Woods's figure.

The Griesbach collection was originally housed in the Hamburg Museum (Woods 1906: 275). This collection could not be traced and, according to Prof. C. Spaeth (letter 2.2.1992) was probably destroyed during aerial bombardment of the Museum in 1943. There is thus no way of ascertaining whether the suture line figured by Woods was indeed accurate or not. Unfortunately, the holotype, through being septate throughout, still has the shell preserved. Without damaging the shell, it is impossible to determine whether it has a suture like that of the material described here, or of the lost Griesbach specimen.

Woods (1906: 432) also mentioned that 'Several other specimens were collected by the (Cape of Good Hope Geological) Survey.' Only two of the Survey specimens (SAM-13103, 4822) could be traced in the collections of the S.A. Museum. These are poorly preserved internal moulds and do not show the sutures.

As mentioned above, *B. bailyi* is a rarity at Mzamba. All our specimens of *B. bailyi* from Mzamba were collected in the basal beds, where it occurs with *B. capensis*. Most of these specimens are small but we are reasonably confident that these are indeed consistently smooth *Baculites* and not merely smooth forms of *B. capensis*. Those specimens from which sutures could be traced, e.g. PCP6765 (Fig. 19A) and PCP8729 (Fig. 19E), show considerable variation in sutural details, but none are quite like Woods's figure.

Apart from our own material, the largest fossil collection from Mzamba to date was made by Van Hoepen in 1919 and is housed in the Transvaal Museum (Van Hoepen 1921). Unfortunately, no precise stratigraphic data are available for this collection; the locality is merely given as Mzamba Estuary. The Van Hoepen collection is of extreme interest in that it contains a baculitid assemblage that we had not encountered at the type section. Six of these baculites were tentatively referred to *B. bailyi* by Van Hoepen, 'There is, however, still an element of doubt' (Van Hoepen 1921: 18). These are all juvenile specimens with whorl sections varying from circular to elliptical. It is impossible to identify them any more precisely as *Baculites*. All the other baculitids were referred to *B. sulcatus* by Van Hoepen. Details of these are given below (p. 114). What is important, however, is that these differ from typical *B. sulcatus* from the uppermost beds at Mzamba, and can possibly be regarded as early forms connecting with *B. capensis* from the basal beds. Ornament in these specimens of *B. sulcatus* varies from individuals with extremely strong lateral nodes projected forwards over the flanks and over the venter as strong ribs and with

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Fig. 17 *(see facing page)*. *Baculites bailyi* Woods, 1906. A. SAM-PCZ8390. B. SAM-PCZ8390b. Parts of same concretion showing protoconchs. Both from locality 13, Zululand, St Lucia Formation, Coniacian II or III. C. SAM-PCZ8039. D-F. SAM-PCZ8367 from locality 99, Zululand, St Lucia Formation, Santonian I or II. G-H. SAM-PCZ8390j from locality 13, Zululand. I. SAM-PCZ8020 from locality 101, Zululand, St Lucia Formation, Santonian II or III. (Note weak tubercle.) J-K. SAM-PCZ8364b from locality 80, Zululand, St Lucia Formation, Coniacian V. Scale bar for size for A and B; D-F, I-K × 1; G-H × 2.

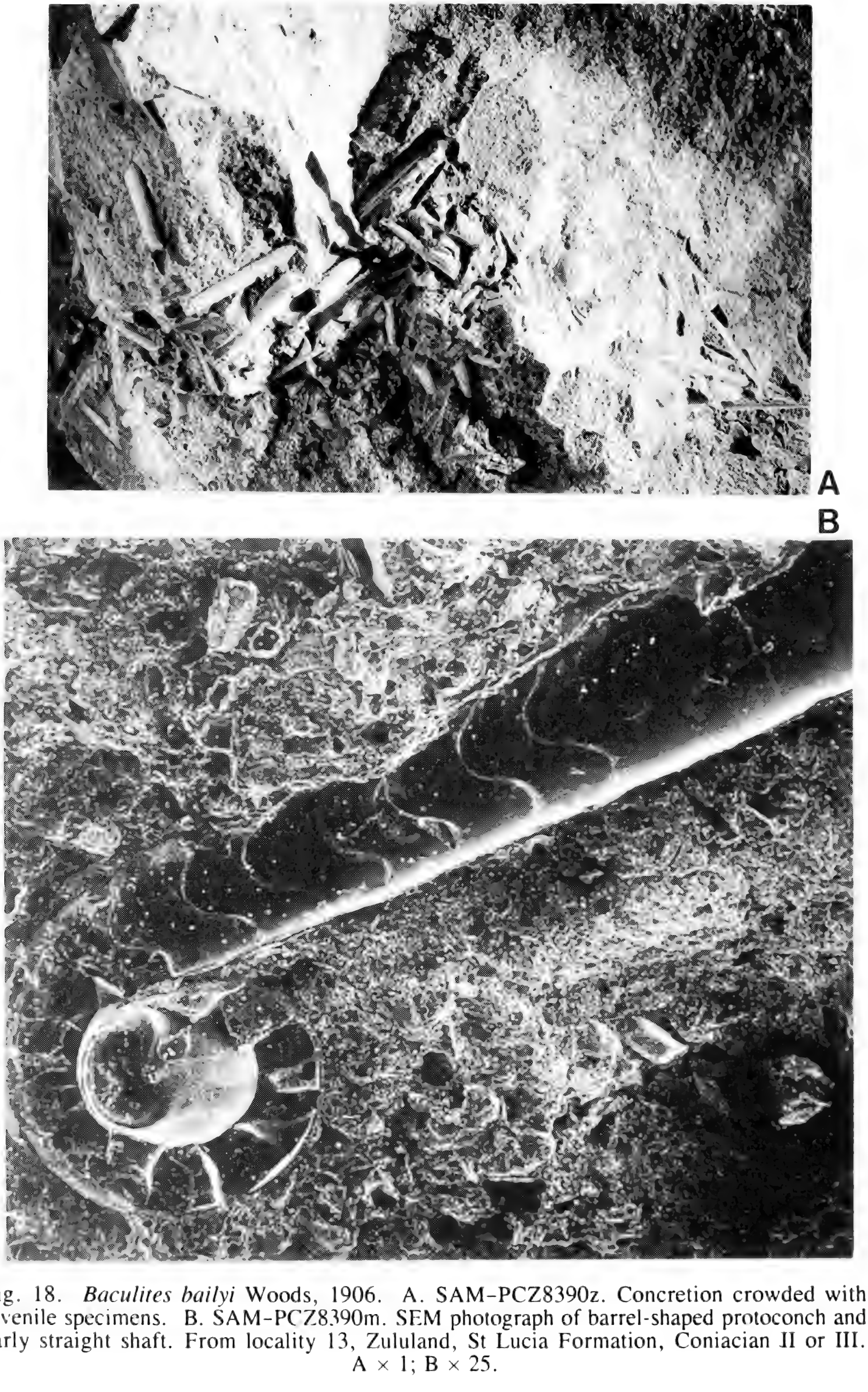

Fig. 18. *Baculites bailyi* Woods, 1906. A. SAM-PCZ8390z. Concretion crowded with juvenile specimens. B. SAM-PCZ8390m. SEM photograph of barrel-shaped protoconch and early straight shaft. From locality 13, Zululand, St Lucia Formation, Coniacian II or III. A × 1; B × 25.

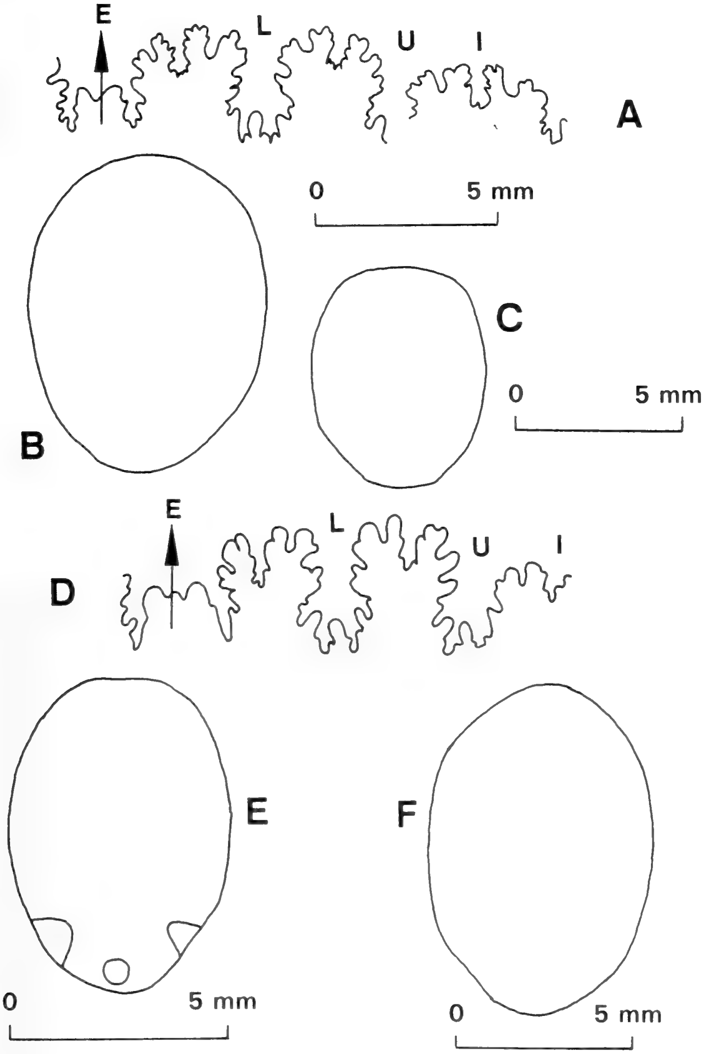

Fig. 19. *Baculites bailyi* Woods, 1906. Whorl section and suture lines. A–B. SAM-PCP6765. C–D. SAM-PCP6766. E. SAM-PCP8729. F. NMBD108. Venter in whorl section pointing downward. Scale bar for size.

numerous ventral intercalatories, to specimens with smooth flanks and only suggestions of ventral corrugations. The suture line of one of the latter (smooth specimens), TM 540m (Fig. 70C) is nearly identical to that figured by Woods of the specimen of *B. bailyi* in the (now lost) Griesbach collection. This suggests—but it is impossible to prove—that the suture line figured by Woods may possibly have been taken from a smooth form of *B. sulcatus*.

Three baculitids (Fig. 13F–K) dredged off the Natal South Coast (Klinger 1985) are derived from what are probably offshore equivalents of the Mzamba Formation. They occur in a faunal assemblage similar to that described from

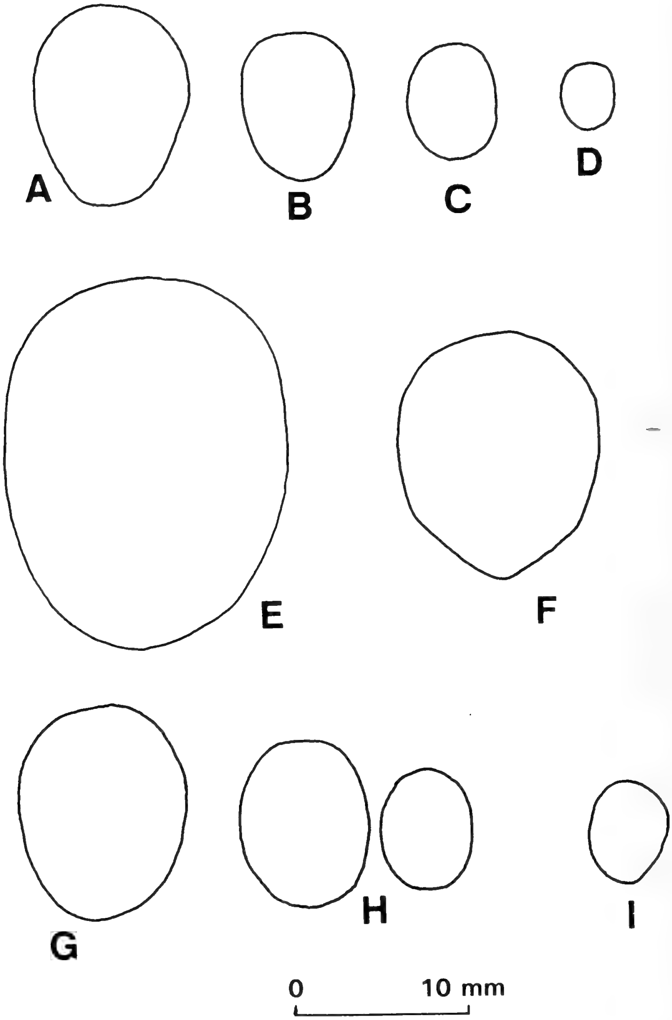

Fig. 20. *Baculites bailyi* Woods, 1906. Whorl sections. A–D. SAM-PCZ8710. E. SAM-PCZ9845. F. SAM-PCZ8356. G. SAM-PCZ8374. H. SAS H28/3. I. SAM-PCZ9943. Venter pointing downward. Scale bar for size.

Mzamba by Van Hoepen (1920, 1921). As far as whorl section and lack of ornament is concerned, they are unmistakably *B. bailyi* when compared to the holotype. Unfortunately only parts of the suture are visible in two of the specimens but the tops of the saddles appear wider than in Woods's figure.

These rather inconclusive data from the type locality of *B. bailyi* indicate that the species is coeval with *B. capensis* in the Middle Santonian, and may occur as late as the early Campanian, where it is partly coeval with *B. sulcatus*. The suture line figured by Woods does not seem to be characteristic of typical *B. bailyi*. In all likelihood, it was either drawn incorrectly, or is from a smooth form of *B. sulcatus*.

This interpretation of *B. bailyi* seems to verify Matsumoto & Obata's (1963: 35), Ward's (1978: 1148) and Olivero's (1984: 57) records of this species from the Upper Santonian of Hokkaido, Upper Santonian to Lower Campanian of British Columbia and Lower Campanian of James Ross Island, respectively. Furthermore, none of the figured suture lines of their specimens has narrow saddles and lobes, as in Woods's figure. Matsumoto & Obata (1963: 37) also commented that the sutures of their specimens of *B. bailyi* differed from the Pondoland material. The two sutures illustrated by Matsumoto & Obata (1963, text-figs 88–89) also show minor differences in the width of the individual elements.

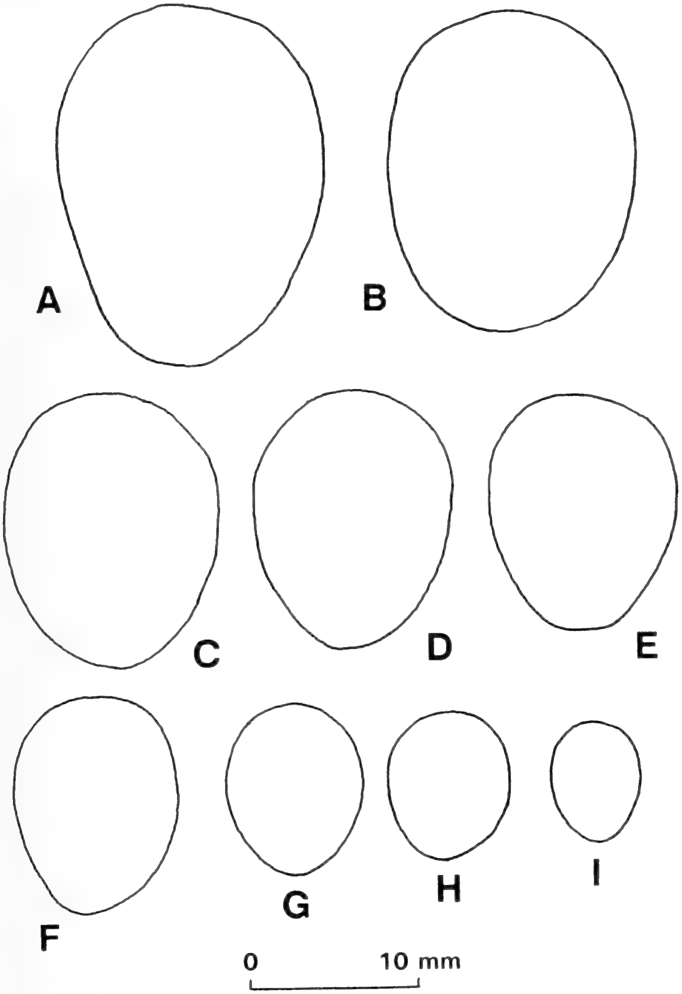

Fig. 21. *Baculites bailyi* Woods, 1906. A. Whorl sections. A. SAM-PCZ8389. B. SAM-PCZ8346. C. SAM-PCZ8345. D. SAM-PCZ8373. E. SAM-PCZ8347. F. SAM-PCZ8375. G. SAM-PCZ8384. H. SAM-PCZ8384. I. SASH135. Venter pointing downward. Scale bar for size.

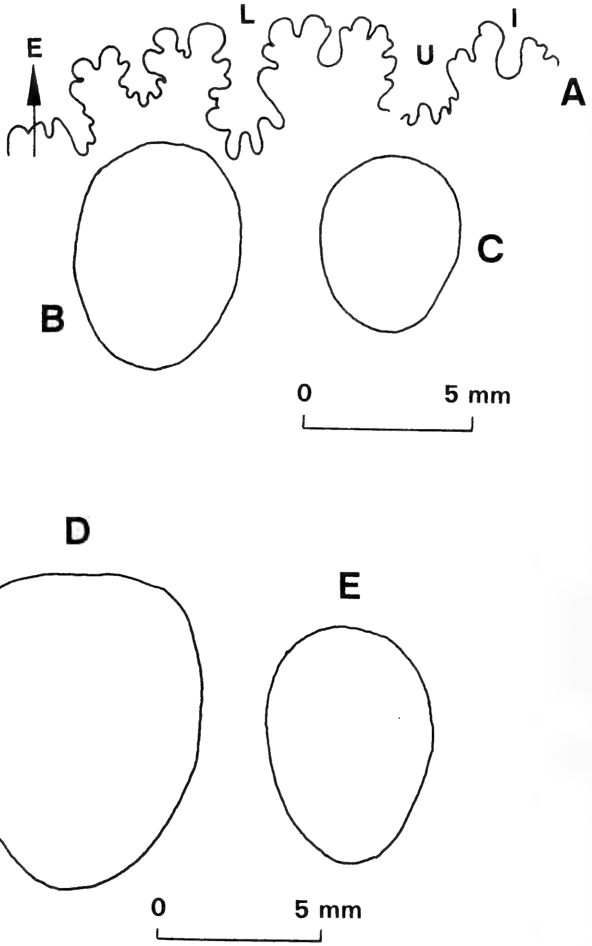

Fig. 22. *Baculites bailyi* Woods, 1906. Suture line and whorl sections. A–C. SAM-PCZ8390i. D–E. SAM-PCZ8390a. Venter in whorl section pointing downward. Scale bar for size.

Collignon (1969: 21, pl. 520 (fig. 2051)) confirmed the rarity of the species in Madagascar, where only two specimens are known, from the Lower Campanian. Earlier records of *B. bailyi* from the Santonian of the Montagne de Français (Madagascar) by Besairie (1930: 223, pl. 21 (figs 6–7)) are probably partially incorrect. One of these specimens (Besairie's fig. 6) has distinct dorsolateral ribbing and definitely does not belong here; the other is probably *B. bailyi*.

Fig. 23 *(see facing page)*. *Baculites bailyi* Woods, 1906. A–C. SAM-PCZ8379. D–G. SAM-PCZ8354. H–I. SAM-PCZ8353. J–M. SAM-PCZ8355. Note lateral tubercle in H. N–O. SAM-PCZ12782, all from locality 98, Zululand, St Lucia Formation, Coniacian ?V. P–R. SAM-PCZ8016 from locality 96, Zululand, St Lucia Formation, Coniacian V or Santonian I. S–U. SAM-PCZ8390 from locality 13, Zululand, St Lucia Formation, Coniacian II–III. All × 1.

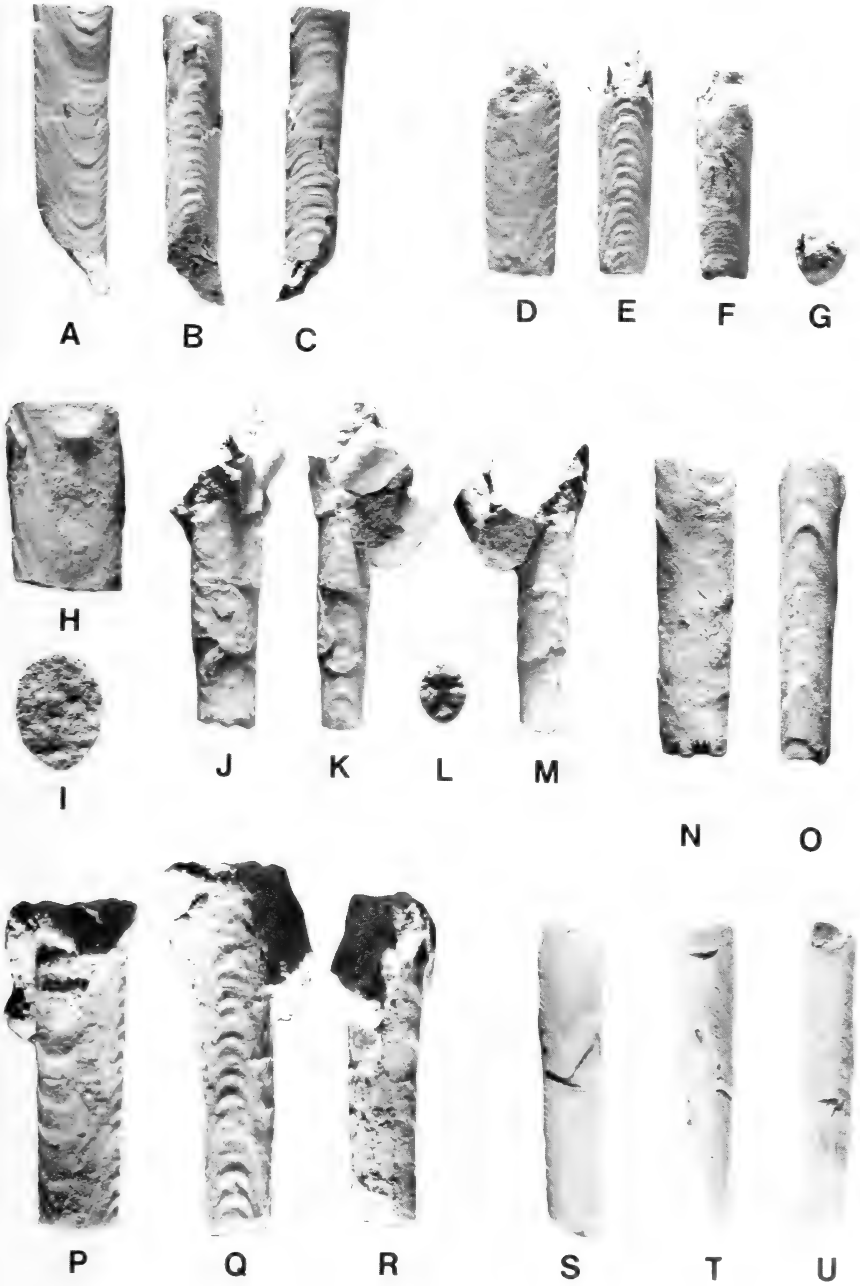

Fig. 23

In contrast to Pondoland, *B. bailyi* is locally very common in Zululand, especially on the north-eastern part of the floodplain of the Hluhluwe River at Nkundusi, where it occurs in the uppermost Coniacian and/or Lower Santonian. Elsewhere in Zululand, *B. bailyi* first occurs in the second or third divisions of the Coniacian. Initially we thought that these smooth Coniacian specimens of *Baculites* were the same as *B. besairiei* from Madagascar. However, as discussed above, *B. besairiei* (including *B. roedereri* and *B. latelobatus*) is a synonym of *B. yokoyamai*. We admit that it is difficult to separate isolated specimens of *B. yokoyamai*, *B. bailyi* and smooth or juvenile *B. capensis*; identification is mainly by association. These three species have overlapping stratigraphic ranges and morphologies in the Coniacian, but they generally do not occur together. The whorl section of *B. yokoyamai* is predominantly elliptical, whereas that of *B. bailyi* is generally ovoid to circular. Completely smooth specimens of *B. capensis* are rare, but can generally be distinguished from *B. bailyi* by the more elliptical whorl section. Juvenile specimens of some early forms of *B. capensis*, where tuberculation only develops in late stages of growth—e.g. Figure 49J, are difficult to impossible to separate from *B. bailyi*.

It is equally difficult or impossible, on external morphology alone, to distinguish between *B. bailyi* and *Baculites* sp. aff. *B. rectus* (see p. 47). Both are completely smooth and have similar whorl sections. Suturally, however, they are totally different. Even small phragmocone fragments of *Baculites* sp. aff. *B. rectus* show the highly complex suture that immediately distinguishes it from *B. bailyi* as figured by Woods (1906), Matsumoto & Obata (1963), Ward (1978) or Olivero (1984).

Baculites uedae Matsumoto & Obata (1963: 40, pl. 20 (figs 5–7), pl. 21 (figs 1, 3, 6), text-figs 91–92, 121–129), from the Santonian of Hokkaido, appears indistinguishable from our Zululand *B. bailyi*. It is virtually identical to some Santonian microconchs of *B. bailyi* (see e.g. Fig. 15J–L) from Zululand and we suspect that they may be synonyms. According to Matsumoto & Obata (1963: 43), *B. bailyi* and *B. uedae* are nearly contemporary in Hokkaido but, in all cases except one, occur at different localities. This seems to fit the general pattern of *Baculites* distribution in Zululand, where individual variants of the same species are generally clustered at different localities but at the same stratigraphic level.

Baculites kirki Matsumoto (1959: 143, pl. 43 (figs 1–3), text-figs 53a–b, 54–57, 58a–b) from the Santonian of California and possibly Hokkaido (Matsumoto & Obata 1963: 65, pl. 18 (fig. 2), text-fig. 114) resembles some of our specimens of *B. bailyi* with an acute venter, but in that species a distinct rounded ventral keel develops. However, the specimens figured by Riccardi & Aguirre Urreta (1988, pl. 3 (figs 4–8)) as *Baculites* cf. *B. kirki* from the Santonian of Cerro Indice in Patagonia are indistinguishable from some of our *B. bailyi* with very narrow venters, e.g. NMB D1075/1, and are probably conspecific, as are probably the Santonian specimens from James Ross Island, figured by Olivero (1992, pl. 1 (figs 1–3)).

Baculites fuchsi Redtenbacher (1873: 134, pl. 30 (fig. 15); see also Summesberger 1979: 113, pl. 1 (figs 2–4), text-figs 2–3; Immel *et al.* 1982: 28, pl. 11 (fig. 8)), from the Santonian of the Gosau Beds of Austria, is indistinguishable from *B. bailyi*. Unfortunately, the Austrian species is too poorly known for definite comments. However, the association of smooth *B. fuchsi* with nodose *B. incurvatus* in the Gosau Beds is remarkably similar to the Pondoland association of *B. bailyi* with *B. capensis*. Given more material, it is possible that these European species may prove to be senior synonyms of *B. bailyi* and *B. capensis* (see also p. 92 onwards).

Baculites nugssuaquensis Birkelund (1965: 48, pl. 4 (fig. 1), pl. 5 (figs 1–4), pl. 6 (figs 1–2), text-figs 35–41), from the Santonian of West Greenland, is a homoeomorph of *B. bailyi*. Some specimens of *B. nugssuaquensis* with smooth flanks and ventral corrugations (e.g. Birkelund 1965, pl. 6 (fig. 2)) are indistinguishable from similarly ornamented *B. bailyi*, e.g. PCZ8359 (Fig. 15A–C). This species, however, belongs to the northern extension of the U.S. Western Interior baculitid lineage and any resemblance is due only to convergence.

Occurrence

Middle Santonian to Lower Campanian of Pondoland, offshore Natal Coast, Coniacian II to Campanian I of Zululand, Lower Campanian of Madagascar, James Ross Island, Antarctica, Upper Santonian of Hokkaido and Upper Santonian to Lower Campanian of British Columbia.

Baculites sp. aff. *B. rectus* Marshall, 1926

Figs 24–26

Compare

1926 *Baculites rectus* Marshall, p. 154, pl. 19 (fig. 1), pl. 32 (figs 9–10).
1953 *Baculites* aff. *rectus* Marshall; Spath, p. 19, pl. 7 (fig. 2a–c).
1970 *Baculites rectus* Marshall; Henderson, p. 23, pl. 3 (figs 2–3), text-fig. 6.
1984 *Baculites rectus* Marshall; Olivero, p. 64, pl. 1 (figs 6–9), text-figs 1c, 2.

Material

SAM–PC5068, glauconitic concretion with numerous baculitid fragments, labelled 'Sugar Terminus Foundations, Durban—Donated'. This locality is probably the same as 'Maydon Wharf Sugar Terminal Site' referred to by Kennedy *et al.* (1973) and later (Kennedy & Klinger 1975: 282) as locality 5 of the Mzamba Formation, and dated as Santonian III and Campanian ?I; several horizons are clearly represented (Kennedy & Klinger 1975: 282).

Description

The concretion contains numerous baculitids with whorl heights ranging from *c.* 2 mm to more than 20 mm. The whorl section (Fig. 25E–F) is typically ovoid, in some with a very narrow venter. Different sizes of body chambers suggest dimorphism. The aperture is slightly flared. The body chambers are all smooth.

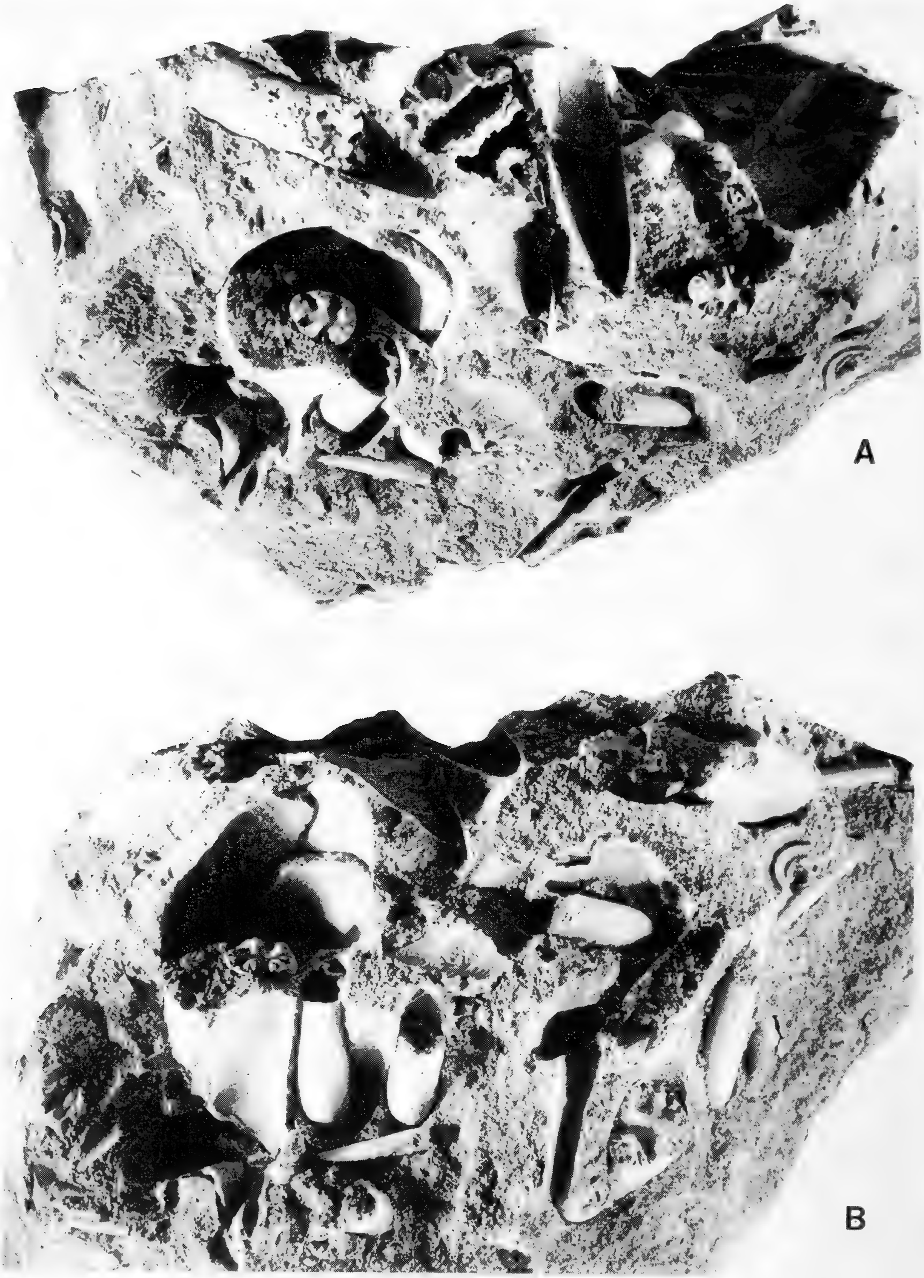

Fig. 24. *Baculites* sp. aff. *B. rectus* Marshall, 1926. A–B. Parts of same concretion, SAM–PC5068 from Maydon Wharf, Sugar Terminal site, locality 5, Mzamba Formation, imprecisely dated as Santonian III–Campanian I. Both × 1.

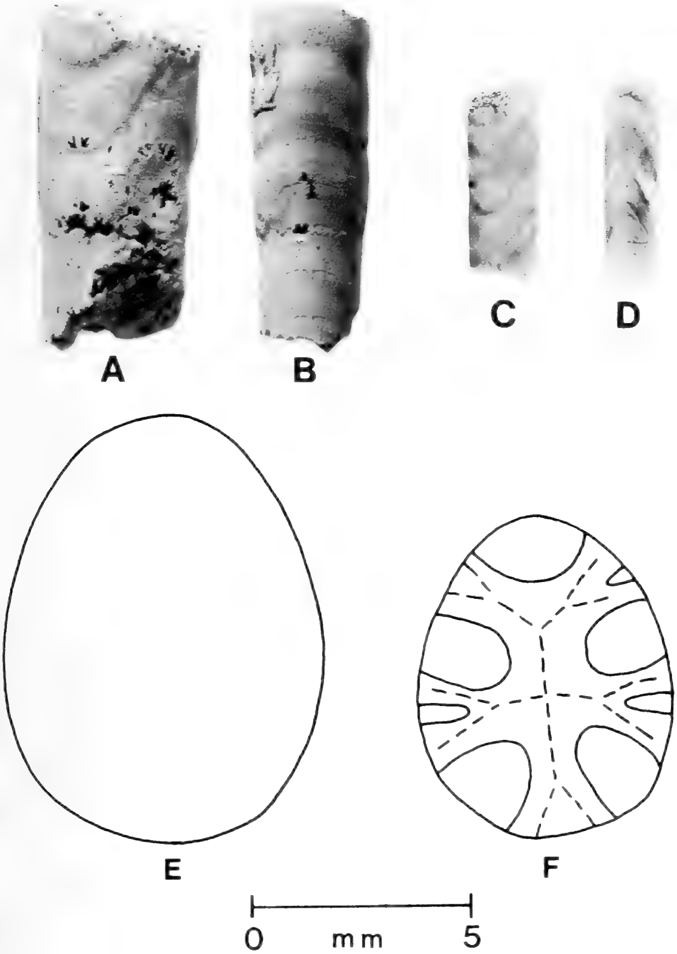

Fig. 25. *Baculites* sp. aff. *B. rectus* Marshall, 1926. A–B. SAM-PC5068b. C–D. SAM-PC5068a. A–B x 2; C–D × 1. E–F. Whorl sections. Venter pointing upward. Scale bar for size.

The majority of specimens are smooth, but several phragmocone fragments have low, rib-like swellings on the dorsal half of the flanks, and distinct, prorsiradiate sulci on the ventral half.

The suture is very complex, dendritic, with saddles and lobes with narrow stems and some phylloid folioles (Fig. 26).

Discussion

We initially thought that this was a concretion with *B. bailyi*, but the complex suture line immediately rules out this identification. Even small specimens can easily be distinguished as being totally different from *B. bailyi* on the basis of the sutural complexity. Unfortunately, we do not have a definite age

Fig. 26. *Baculites* sp. aff. *B. rectus* Marshall, 1926. Suture line of SAM–PC5068. Scale bar for size.

for these specimens but we assume them to be younger than the highest beds exposed at the Mzamba Cliff, above the level of *B. sulcatus*. The association of an inflated pachydiscid nucleus possibly confirms this. At any rate, the degree of complexity of the suture line is greater than that of any of the other smooth baculitids yet known from southern Africa. The origins of this species are obscure. The similar whorl sections suggest derivation from *B. bailyi*,

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Fig. 27 *(see facing page)*. *Baculites capensis* Woods, 1906. A–C. SAM–4825b, paralectotype. D–H. SAM–4823, lectotype. I–K. SAM–PCP8753. L. SAM–PCP8050. All from the basal beds at locality 1, Pondoland, Transkei, Mzamba Formation, Santonian II. All × 1.

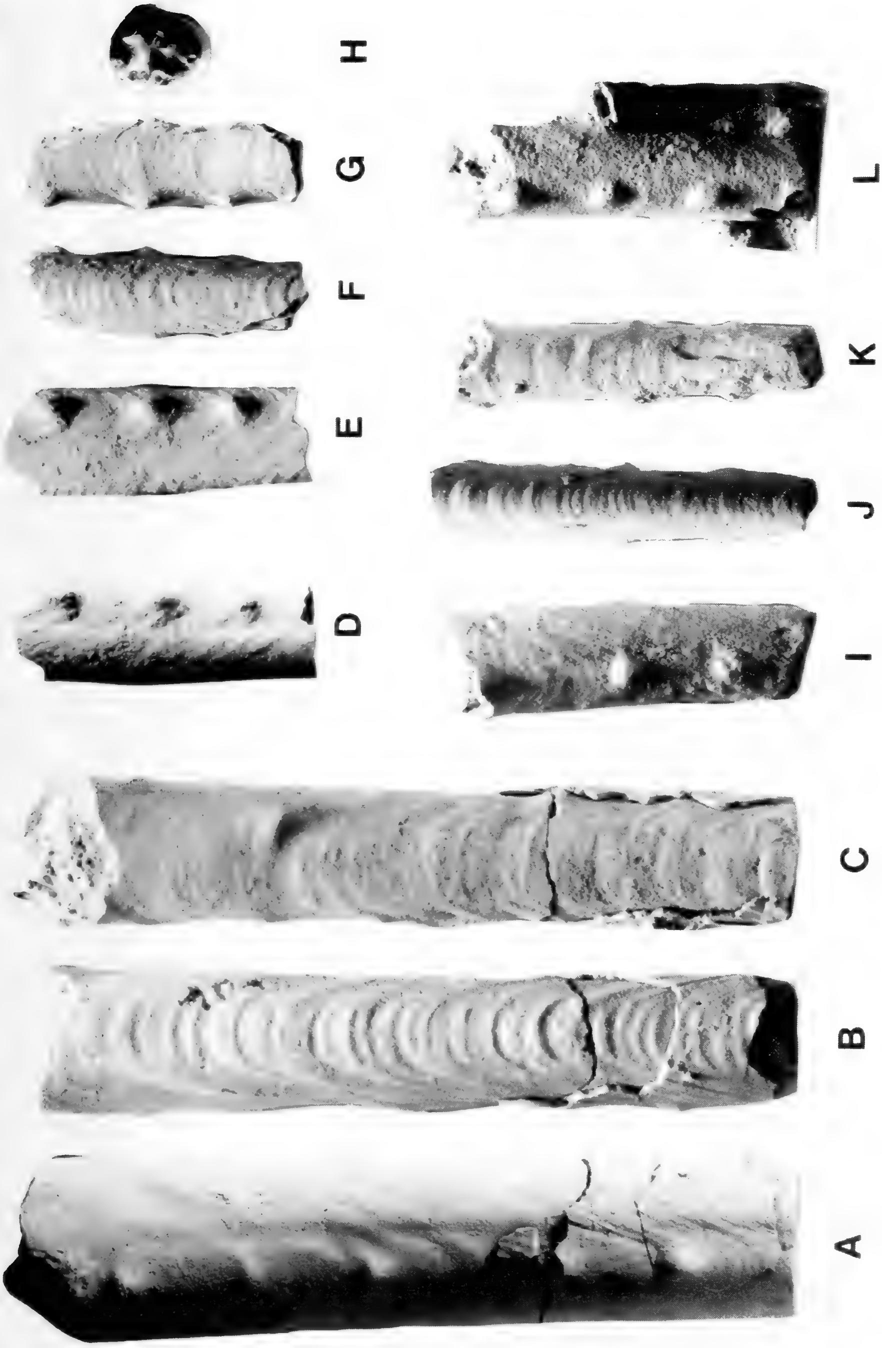

Fig. 27

associated with a sudden increase in sutural complexity. Alternatively, it could be regarded as an immigrant.

There are several smooth baculitid species with complex sutures with which our specimens can be compared.

Closest affinity seems to be with *B. rectus* Marshall (1926: 154, pl. 19 (fig. 1), pl. 32 (figs 9–10)), best known, but imprecisely dated, as Campanian–Maastrichtian from New Zealand (see also Henderson 1970: 23, pl. 3 (figs 2–3), text-fig. 6). Spath (1953: 19, pl. 7 (fig. 2a–e)) also tentatively recorded the species from Graham Land, Antarctica. Olivero (1984: 64, pl. 1 (figs 6–9), text-figs 1c, 2) also reported the species from the Campanian of James Ross Island, Antarctica. Collignon's (1977: 10) *Baculites* sp. indet. from the Campanian of New Caledonia may also belong here. None of these specimens has quite as complex a suture line as the Durban specimens—that figured by Olivero (1984, text-fig. 2) is the closest match. The suture figured by Spath (1953, pl. 7 (fig. 3)) has very narrow saddles, and resembles that of *B. bailyi* as figured by Woods (1906, pl. 44 (fig. 5)), but is more finely incised.

Baculites chicoensis Trask (1856: 85, pl. 2 (fig. 2)) from the Upper Campanian of California and British Columbia, and possibly southern Saghalin (Grabovskaya 1984) has a comparable complex suture line, but the whorl section is different—an incipient ventral keel appears in later growth stages. *Baculites chicoensis yezoensis* Matsumoto & Miyauchi (1984: 70, pl. 25 (figs 1–5), text-figs 11B–C) from the Lower Campanian of Hokkaido is closer to the Durban specimens in retaining a narrow but not perceptibly keeled venter, as in the nominate subspecies.

Baculites rex Anderson (1958: 191, pl. 49 (fig. 2)) from the Upper Campanian and Maastrichtian of California, British Columbia and Hokkaido has a more 'lytoceratine' or jagged suture and apparently grows to enormous size, as the name implies.

Baculites hochstetteri Liebus (1902: 119, pl. 6 (figs 4–6)), imprecisely dated as Upper Senonian of the Silesian Carpathian region, has sutures indistinguishable from our specimens. Unfortunately, this species is known only by the figured syntypes and further comparisons are impossible. The types, originally housed in Munich are lost, presumably destroyed during World War II.

Baculites regina Obata & Matsumoto (1963: 85, pl. 22 (figs 3–6), pl. 23 (figs 1–2), pl. 24 (figs 1–5), pl. 25 (figs 3–5), pl. 27 (figs 1, 6–7, 9), text-figs 191–196, 200–214) from the Campanian of Honshu, has a similarly complex suture line, but the adult, subpentagonal whorl section is immediately distinctive.

Baculites duharti Hünicken (*in* Hünicken *et al.* 1975: 116, pl. 1 (figs 1–4), pl. 2 (figs 1–2), pl. 3 (figs 5–8), text-figs 2a–d, 3a–c, 4–5)), from the Middle and/or Upper Campanian of Tierra del Fuego, and also from the Middle Campanian of Zululand (p. 178), is superficially similar to *Baculites* sp. aff. *B. rectus*, but has a much simpler suture line, and the elliptical whorl section typical of the *B. capensis* group.

Occurrence

Campanian s.l. of Durban.

Baculites capensis Woods, 1906
Figs 27–33, 34A–L, ?34M–R, 35–54

1906 *Baculites capensis* Woods, p. 342, pl. 44 (figs 6–7).
1907 *Baculites vagina* Forbes; Boule, Lemoine & Thevenin, p. 65(45), pl. 15 (fig. 3–3a).
1907 *Baculites* sp. Crick, p. 240.
1921 *Baculites capensis* H. Woods; Spath, p. 257, pl. 24 (figs 6–7).
1921 *Baculites* sp. aff. *capensis* H. Woods; Spath, p. 258.
1921 *Baculites* cf. *aspero-anceps* Lasswitz; Spath, p. 259, pl. 24 (figs 4, 4a).
1921 *Baculites* cf. *brevicosta* Schlüter; Spath, p. 260, pl. 24 (figs 5, 5a).
1921 *Baculites* sp. cf. *sulcatus* Baily; Spath, p. 260.
1922 *Baculites capensis* Woods; Spath, p. 146.
1923 *Baculites capensis* Woods; Spath, p. 13, text-fig. 3d.
? 1925 *Baculites* sp. ind. Spath, p. 31, pl. 1 (fig. 1).
? 1930 *Baculites Bailyi* Woods; Besairie, p. 223 (pars), pl. 21 (fig. 6) only.
1931 *Baculites* cf. *aspero-anceps* Lasswitz; Collignon, p. 22, pl. 3 (figs 7, 7a), pl. 9 (fig. 12).
1931 *Baculites* aff. *capensis* Woods; Collignon, p. 22, pl. 3 (fig. 6).
1931 *Baculites* cf. *brevicosta* Schlüter; Collignon, p. 34, pl. 5 (fig. 1, 1a), pl. 9 (fig. 13).
1931 *Baculites Boulei* Collignon, p. 35, pl. 5 (fig. 2, 2a), pl. 9 (fig. 14).
1932 *Baculites capensis* Woods; Besairie, p. 50.
1936 *Baculites capensis* Woods; Venzo, p. 116 [58].
1936 *Baculites capensis* Woods var. *umsinenensis* Venzo, p. 116 [58], pl. 10 [6] (figs 11–12).
1958 *Baculites buttensis* Anderson, p. 191, pl. 49 (fig. 6, 6a, 6b).
1958 *Baculites* aff. *B. capensis* Woods; Anderson, p. 192, pl. 48 (fig. 8, 8a).
1959 *Baculites schencki* Matsumoto, p. 113, pl. 32 (figs 1a–c, 2a–c, 3a–b, 4a–b, 5a–c, 6a–c), text-figs 12a–b, 13a–c, 14a–b, 15–21, 22a–b, 23a–c, 24–25.
1959 *Baculites boulei* Collignon; Matsumoto, p. 118, pl. 32 (fig. 7a–c), pl. 33 (figs 4a–c, 5a–b, 6a–d, 7a–b), text-figs 27a–b, 28–32.
1959 *Baculites capensis* Woods; Matsumoto, p. 121, pl. 33 (figs 1a–d, 2a–c, 3a–b), pl. 45 (figs 1a–d, 2a–d, 3a–d, 4a–d), text-figs 33a–b, 34a–b.
1963 *Baculites capensis* Woods; Matsumoto & Obata, p. 47, pl. 14 (fig. 2), pl. 15 (figs 3–5), pl. 19 (fig. 2), text-figs 95–96, 147–151.
1966 *Baculites capensis* Woods; Collignon, p. 6, pl. 457 (fig. 1862).
1966 *Baculites capensis* Woods var. *tenuetuberculata* Collignon, p. 6, pl. 457 (figs 1863).
1966 *Baculites malagasyensis* Collignon, p. 7, pl. 457 (fig. 1865).
non 1973 *Baculites* sp. group of *B. capensis* Woods; Kennedy & Klinger, p. 101, pl. 4 (figs 1–5), pl. 5 (fig. 1a–d), pl. 6 (figs 4–5). (= *B. vanhoepeni*)
1977 *Baculites capensis* Woods; Klinger & Kennedy, p. 71, figs 2A–F, 3G.
?*non* 1988 *Baculites capensis* Woods; Cooper, p. 210, fig. 1G–I.
1991*b* *Baculites capensis* Woods; Kennedy & Cobban, p. 182, figs 6: 4,; 8: 1–8; 10: 7–10, 12–14; 12: 2,5.

Types

Woods based this species on at least four syntypes, which survive in the collections of the South African Museum. Lectotype, by subsequent designation of Matsumoto & Obata (1963: 48), is the smaller of the two specimens figured by Woods (1906, pl. 44 (fig. 6a–b)), from an unknown horizon at the type section of the Mzamba Formation at the Mzamba Estuary, Transkei, South Africa, SAM-4823—herein refigured as Figure 27D–H. Paralectotypes are SAM-4824, 4825 and 4825b, all from the same locality.

Material

We have several hundred catalogued and uncatalogued specimens from the following localities:

(1) Basal beds and foreshore exposures at locality 1 at the Mzamba River Estuary, Pondoland, Mzamba Formation, Santonian II.
(2) Locality 6, Zululand, St Lucia Formation, Santonian II–III to Campanian I.
(3) Locality 15, Zululand, St Lucia Formation, Coniacian IV.
(4) Locality 16, Zululand, Coniacian ?III.
(5) Bed B at locality 22, Zululand, St Lucia Formation, Coniacian IV.
(6) Locality 24, Zululand,St Lucia Formation, Coniacian II–V.
(7) Locality 26, Zululand, St Lucia Formation, ?Santonian.
(8) Locality 72, Zululand, St Lucia Formation, Coniacian III.
(9) Locality 73, Zululand, St Lucia Formation, Coniacian IV–V, ?Santonian I.
(10) Locality 80, Zululand, St Lucia Formation, Coniacian V.
(11) Locality 83, Zululand, St Lucia Formation, Coniacian IV.
(12) Locality 85, Zululand, St Lucia Formation, Santonian I.
(13) Locality 88, Zululand, St Lucia Formation, Coniacian IV–V, ?Santonian I.
(14) Localities 89 and 90, Zululand, St Lucia Formation, Coniacian IV.
(15) Locality 91, Zululand, St Lucia Formation, Coniacian IV or V.
(16) Locality 92, Zululand, St Lucia Formation, Coniacian II and III.
(17) Locality 93, Zululand, St Lucia Formation, Coniacian II.
(18) Locality 94, Zululand, St Lucia Formation, Coniacian V–Santonian I.
(19) Locality 98, Zululand, St Lucia Formation, Coniacian ?V.
(20) Field locality H51, Mpisene Creek, east of Nyalazi River Trading Store, Zululand, St Lucia Formation, ?Santonian.
(21) Field locality H40, exposure at pump house on Nyalazi River, west of Nyalazi River Trading Store, Zululand, St Lucia Formation, Campanian ?I.

Dimensions

A full list of dimensions is given in the appendix.

Max Wb (mm)	*MxWb/MxWh*	*MnWb/MnWh*	*Ti*	*Tubs/Wh*
0–4.9	0.63	0.6	7.5	2
5–9.9	0.73	0.74	6.48	2.57
10–14.9	0.73	0.71	3.92	2.29
15–19.9	0.75	0.75	5.64	2.18
20–21	0.77	0.73	—	2

Fig. 28 *(see facing page)*. *Baculites capensis* Woods, 1906. A. Plaster cast of exposed surface of basal beds of Mzamba Formation on south side of the Mzamba River estuary. B–E. SAM-4824, paralectotype figured by Woods (1906, pl. 44 (fig. 7a–c)). F. SAM-4825, unfigured paralectotype. All from the basal beds of the Mzamba Formation at locality 1, Pondoland, Transkei, Santonian II. All × 1.

Fig. 29 *(see overleaf)*. *Baculites capensis* Woods, 1906. All specimens from the basal beds of the Mzamba Formation at locality 1, Pondoland, Transkei, to illustrate the variation in ornament. A–C. SAM-PCP8664. D. SAM-PCP8665. E. SAM-PCP8755. F–H. SAM-PCP8663. I. SAM-PCP8360. J. SAM-PCP8052. K. SAM-PCP8053. L. SAM-PCP8051. M. SAM-PCP8054. N–P. SAM-PCP8241. All × 1.

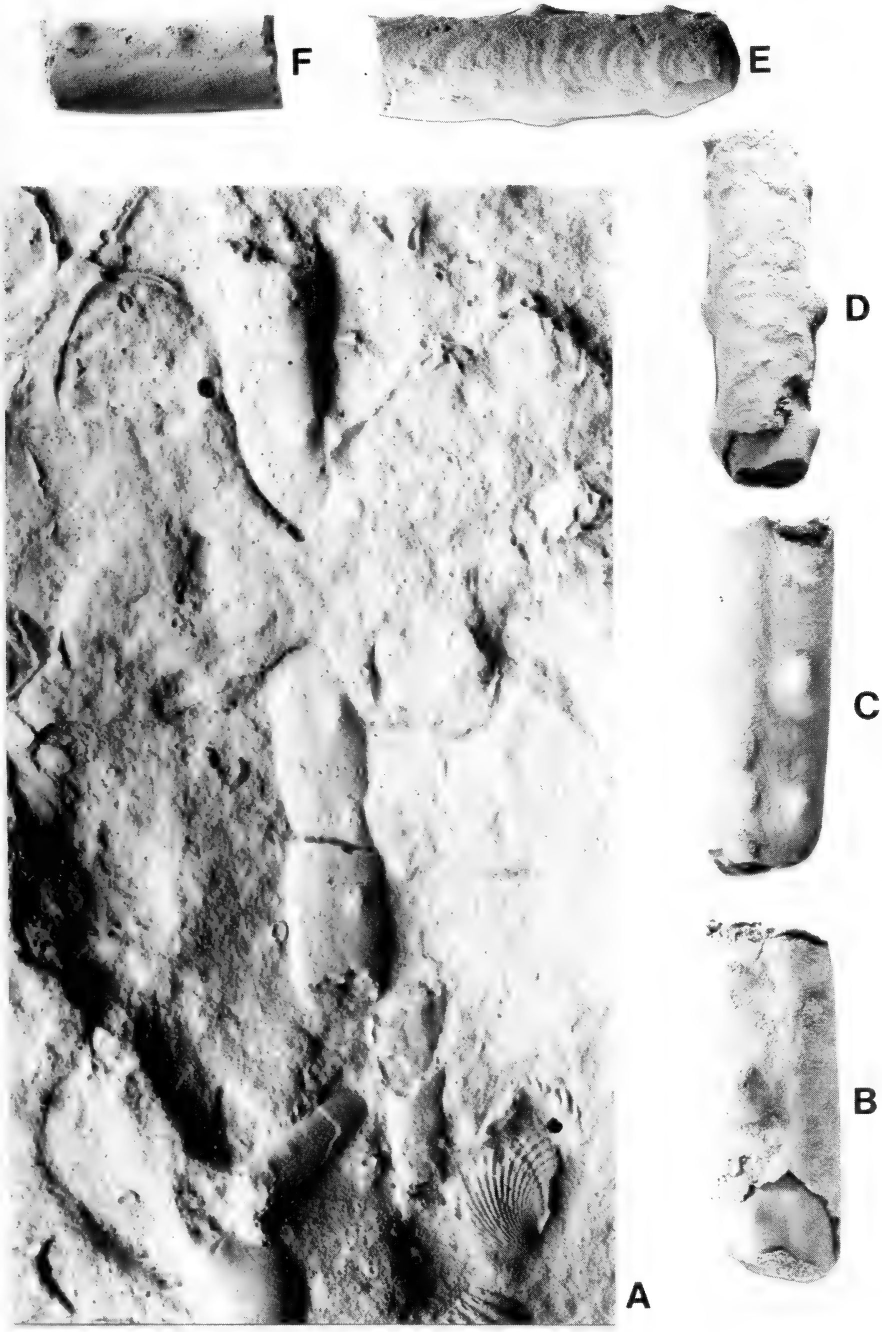

Fig. 28

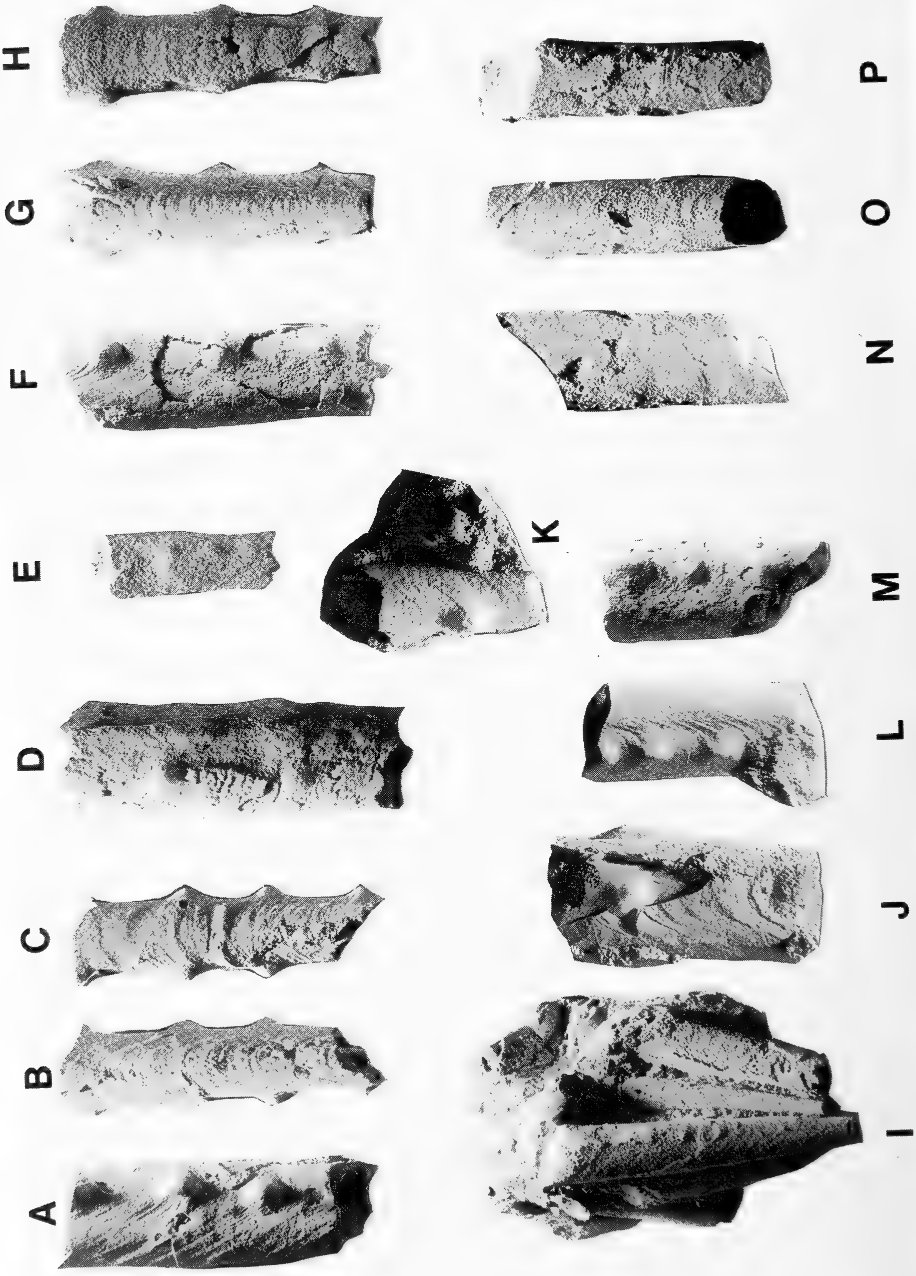

Fig. 29

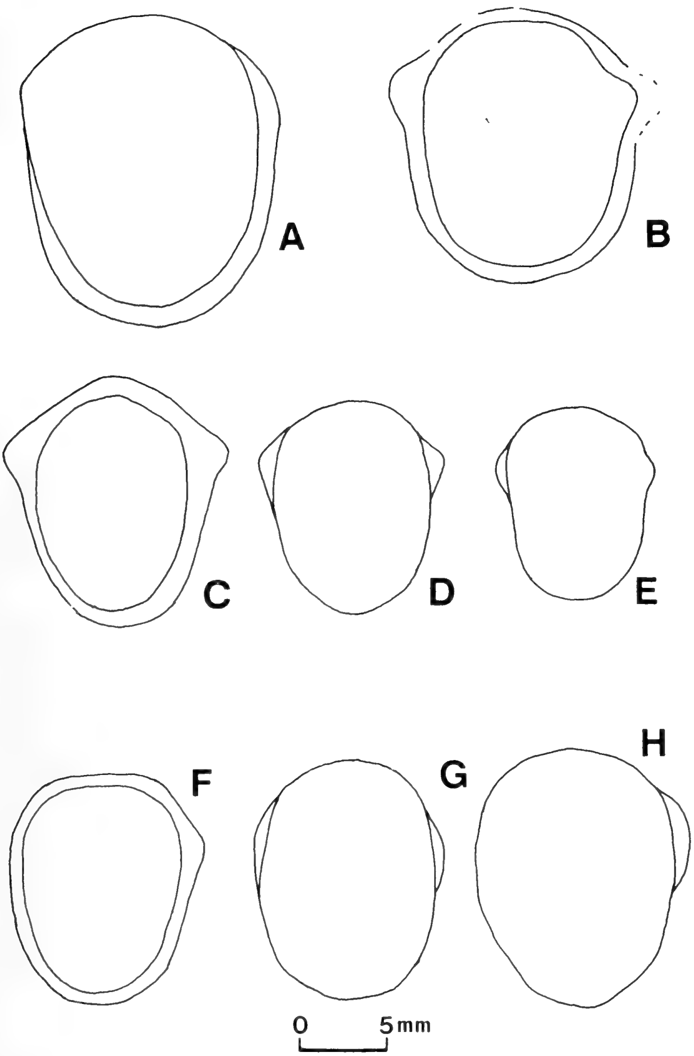

Fig. 30. *Baculites capensis* Woods, 1906. Whorl sections of type series and topotype material. A–B. SAM–4824. C–D. SAM–4823 (lectotype). E. SAM–PCP8754. F. SAM–PCP8756. G. SAM–PCP8662. H. SAM–PCP8665. Venter pointing downward. Scale bar for size.

Description

This is the most common baculitid in Zululand, Natal and Pondoland, and is very variable, as here interpreted. In order to illustrate the variation of the species, we first describe the types and topotype material collected at the type locality, the Mzamba River estuary in Pondoland.

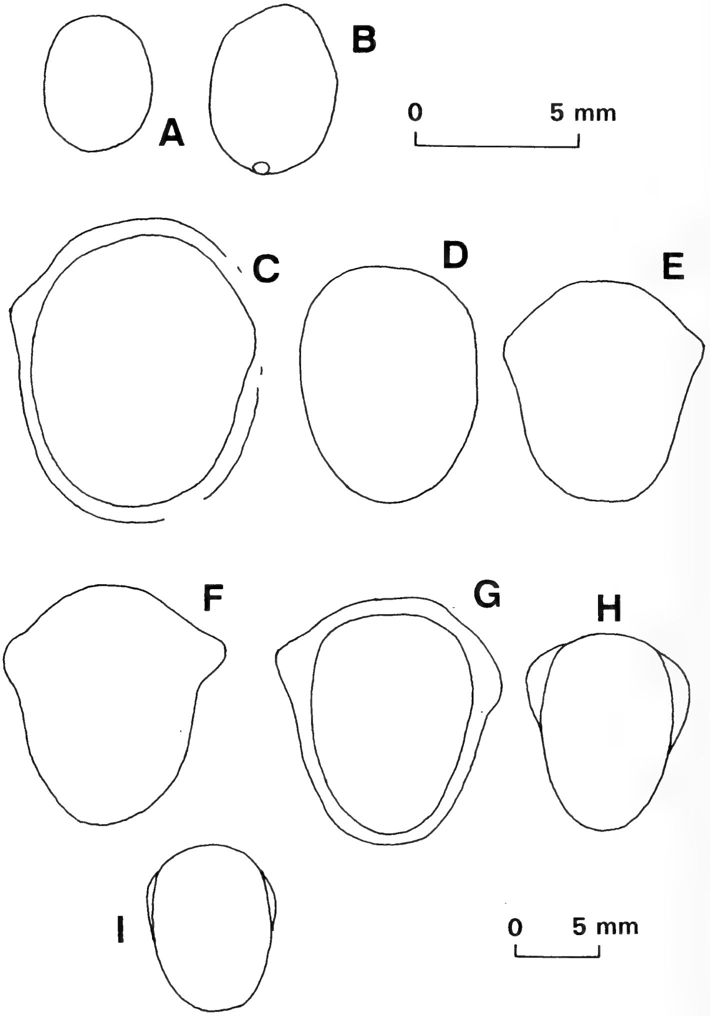

Fig. 31. *Baculites capensis* Woods, 1906. Whorl sections of specimens from the type locality. A. SAM-PCP8360/10. B. SAM-PCP8360/13. C. SAM-PCP8052. D. SAM-PCP8241. E. SAM-PCP8051. F. SAM-PCP8644. G. SAM-PCP8663. H. SAM-PCP8663. I. SAM-PCP6767. Venter pointing downward. Scale bar for size.

Description of type specimens. The lectotype, SAM-4823 (Fig. 27D-H) is part of a phragmocone, partially filled with sparry calcite and glauconitic silt. SAM-4824 (Fig. 28B-E) is non-septate, and, at the larger end, has part of the aperture preserved. SAM-4825 (Fig. 28F) is a fragment of which the one flank is corroded. SAM-4825b (Fig. 27A-C) is a large body chamber and, to date, the largest specimen of *B. capensis* recorded from the Mzamba Formation.

Woods's figures of the lectotype and paralectotype are quite accurate and show the characteristic features of the species—an elliptical whorl section with the venter as wide as, or only slightly narrower than the dorsum, and parallel flanks with a shallow, longitudinal depression situated immediately ventral of the tubercles. This depression is very shallow, as different angles of illumination of the lectotype illustrate (Fig. 27D–E). In the lectotype (SAM–4823) and paralectotypes (SAM–4824, 4825) the tubercles are characteristically pinched and clavate.

Paralectotype SAM–4825b (Fig. 27A–C) is part of an internal mould of a body chamber. As mentioned above, it is the largest specimen of *B. capensis* known to us from the Mzamba Formation and is obviously a macroconch. Here the tubercles are much weaker than on the lectotype and conical to bullate, rather than clavate. The longitudinal depression at midflank is not as prominent as in the other specimens. Distinct, forwardly projected ribs are visible on the venter (on the internal mould).

Decriptions of topotype Pondoland material. We have several specimens of *B. capensis*, all from the basal beds of the Mzamba Formation, at Mzamba Cliff.

Juveniles. The juveniles are fortuitously preserved in a small concretion (SAM–PCP8360) containing about 20 individuals (Fig. 29I) and the impressions of others. The smallest diameter preserved is 1.7 mm. The whorl section in the early stages is oval (Fig. 31A–B), with the venter as wide, or only slightly narrower than the dorsum. The appearance of tubercles is variable. On PCP8360/10 (Fig. 29I), an internal mould, the surface of the flanks is perfectly smooth up to a whorl height of about 5 mm, when weak, crescentic dorsolateral tubercles start appearing. Faint ribbing over the venter starts appearing at a slightly earlier stage. In other, larger specimens, the flanks are still smooth, ornamented by faint striae only. In PCP8360/3 the venter is distinctly crenulated on the internal mould and the flanks bear low, rounded tubercles.

Adult stage. The whorl section shows some variation, depending on whether seen in nodal or internodal view, and also whether taken on an internal mould or on the external surface of the shell (Figs 30–31). They are generally near-elliptical, with parallel flanks and the venter only slightly narrower than the dorsum. In some, however, e.g. PCP8644 (Fig. 31F), the whorl section is trigonal, with a narrowly rounded venter. In others, the venter may be slightly fastigiate, e.g. SAM–4823 (Fig. 27H).

The size, shape and spacing of the tubercles varies considerably; again this is partially determined by whether the shell is preserved, or whether seen on the internal mould. Typical ornament associated with the name *B. capensis* consists of longitudinally elongated, either oblongly rounded or dorsoventrally pinched tubercles, situated near the dorsal quarter of the flanks, e.g. lectotype SAM–4823 (Fig. 27D–E), paralectotype SAM–4824 (Fig. 28B–C)—this shows the tuberculation on the internal mould and in shelly preservation, and Figure 28A—a plaster cast of a large phragmocone. These longitudinally elongated tubercles are generally bordered at mid-flank by a very shallow, longitudinal depression. This depression is hardly visible in transverse (whorl section) view, but is quite clear under oblique, low lighting. Compare, for example, Figure 27D–E of the same (lectotype) specimen under different illumination. In typical *B. capensis*, the spacing of tubercles numbers about two per whorl height.

In some specimens, the tubercles are distinctly conical to rounded, e.g. SAM–8753 (Fig. 27I–K) or PCP8050 (Fig. 27L), and in others low and rounded, e.g. PCP8052 (Fig. 29J) and PCP8665 (Fig. 29D). In a few, e.g. PCP8662 or PCP8241 (Fig. 29N–P), the tubercles are extremely feebly developed, so as to be near-absent. In PCP8054 (Fig. 29M) the tubercles are closer and irregularly spaced.

The surface of the shell bears fine striae, e.g. PCP8050 (Fig. 27L), and PCP8052 (Fig. 29J). In some, e.g. PCP8664 (Fig. 29A–C), these are quite strongly developed, and even visible on internal moulds, e.g. SAM–4825b (Fig. 27A–C). Ventral corrugations are variably developed, ranging from absent to extremely prominent, even on internal moulds.

Parts of the aperture are preserved in paralectotype SAM–4824 (Fig. 28C); paralectotype SAM–4825b (Fig. 27A–C)) is a larger body chamber; both are perfectly straight. PCP8050 (Fig. 27L) is a smaller, slightly curved body chamber. The former two are probably macroconchs; the latter a microconch.

Description of Zululand material. In Zululand, *B. capensis* may be defined as a predominantly nodose baculitid with elliptical to ovoid whorl section; size and shape of nodes varies, from absent, through weakly conical to strongly conical, weakly to strongly crescentic, longitudinally elongated, obliquely elongated, close, widely or irregularly spaced; some with shallow longitudinal depression at midflank. Suture simple.

As can be deduced from this definition, the material is extremely variable (see e.g. Fig. 33) and several morphotypes, based primarily on the presence and shape of the tubercles, can be recognized. Some of these morphotypes appear to be related to stratigraphic occurrence—others are conspicuous at particular

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Fig. 32 *(see facing page). Baculites capensis* Woods, 1906. Two specimens to illustrate extremes of variation in ornament. A–C. NMB D1052/1 from locality 72, Zululand, St Lucia Formation, Coniacian III. D–F. SAS A2101 from locality 73, Zululand, St Lucia Formation, Coniacian IV–V. Both × 1.

Fig. 33 *(see overleaf). Baculites capensis* Woods, 1906. Diverse specimens to illustrate variation in strength and shape of tuberculation. A–C. SAM–PCZ11999 from locality 91, Zululand, St Lucia Formation, Coniacian IV or V. D. SAM–PCZ12000. E. SAM–PCZ8676, both from locality 83, Zululand, St Lucia Formation, Coniacian IV. F. SAM–PCZ12001 from locality 85, Zululand, St Lucia Formation, Santonian I. G. SAM–4832 from locality 1, Pondoland, Mzamba Formation, Santonian II. H. NMB D1028/3. I. SAS A361. J. SAS A333. L. SAM–PCZ8013, all from locality 72, Zululand, St Lucia Formation, Coniacian III. K. SAS Z1795f. M. SAS Z1795g. Both from locality 85. All × 1.

Fig. 34 *(see overleaf).* A–L. *Baculites capensis* Woods, 1906. A–C. SAM–5454. D–F. SAM–5480. G. SAM–5458. H. SAM–5486. I. SAM–5461. J. SAM–5472. K. SAM–PCZ8674b. L. SAS A1610a. All from Mkweyane ('Umkwelane Hill'), probably locality 10, Zululand, St Lucia Formation. All specimens with '*brevicosta*' or '*schencki*' type of ornament. M–R. Two specimens with atypical, widely spaced tubercles. It is uncertain if these are atypical *B. capensis* (form 12) or nodose variants of *B. bailyi*. M–O. SAM–PCZ8387. P–R. SAS PCZ8349. Both from locality 98, Zululand, St Lucia Formation, Coniacian V, associated with typical *B. bailyi* fauna. All × 1.

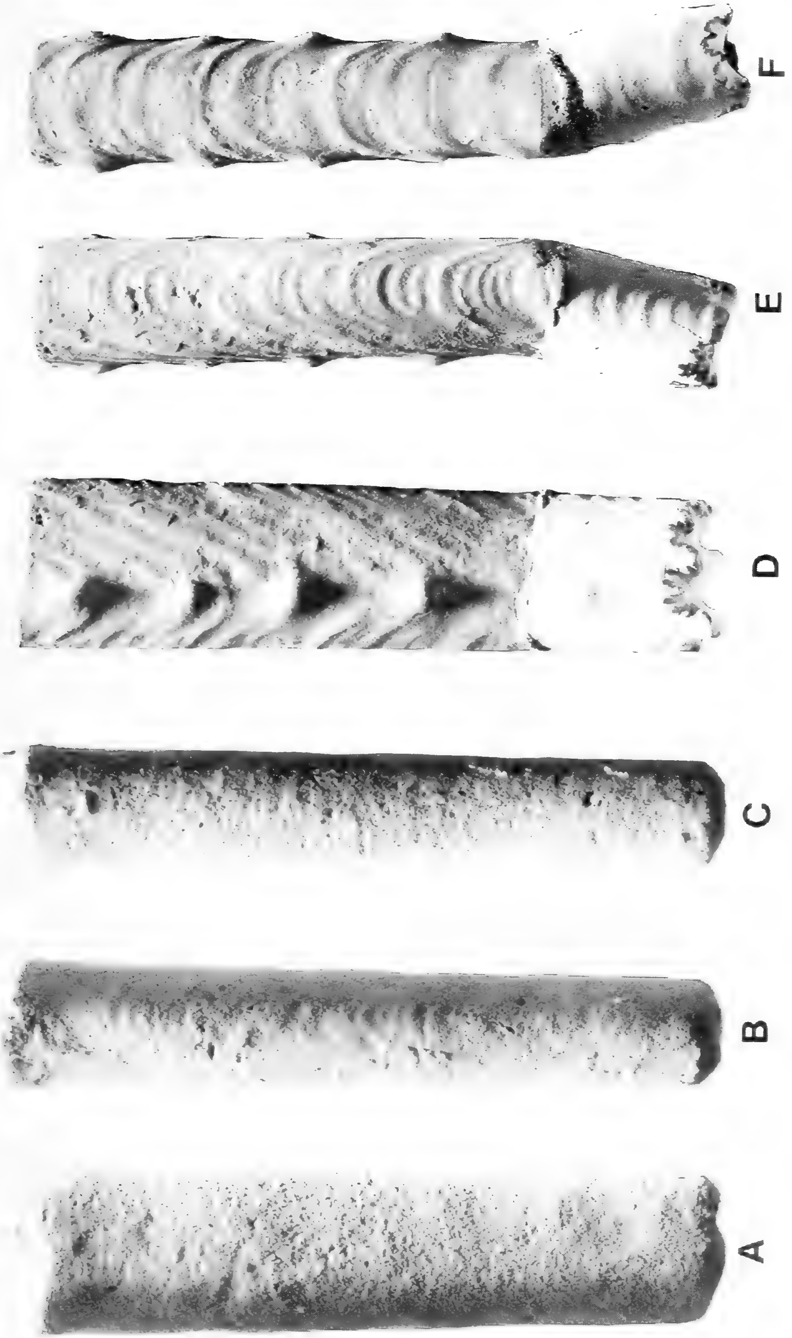

Fig. 32

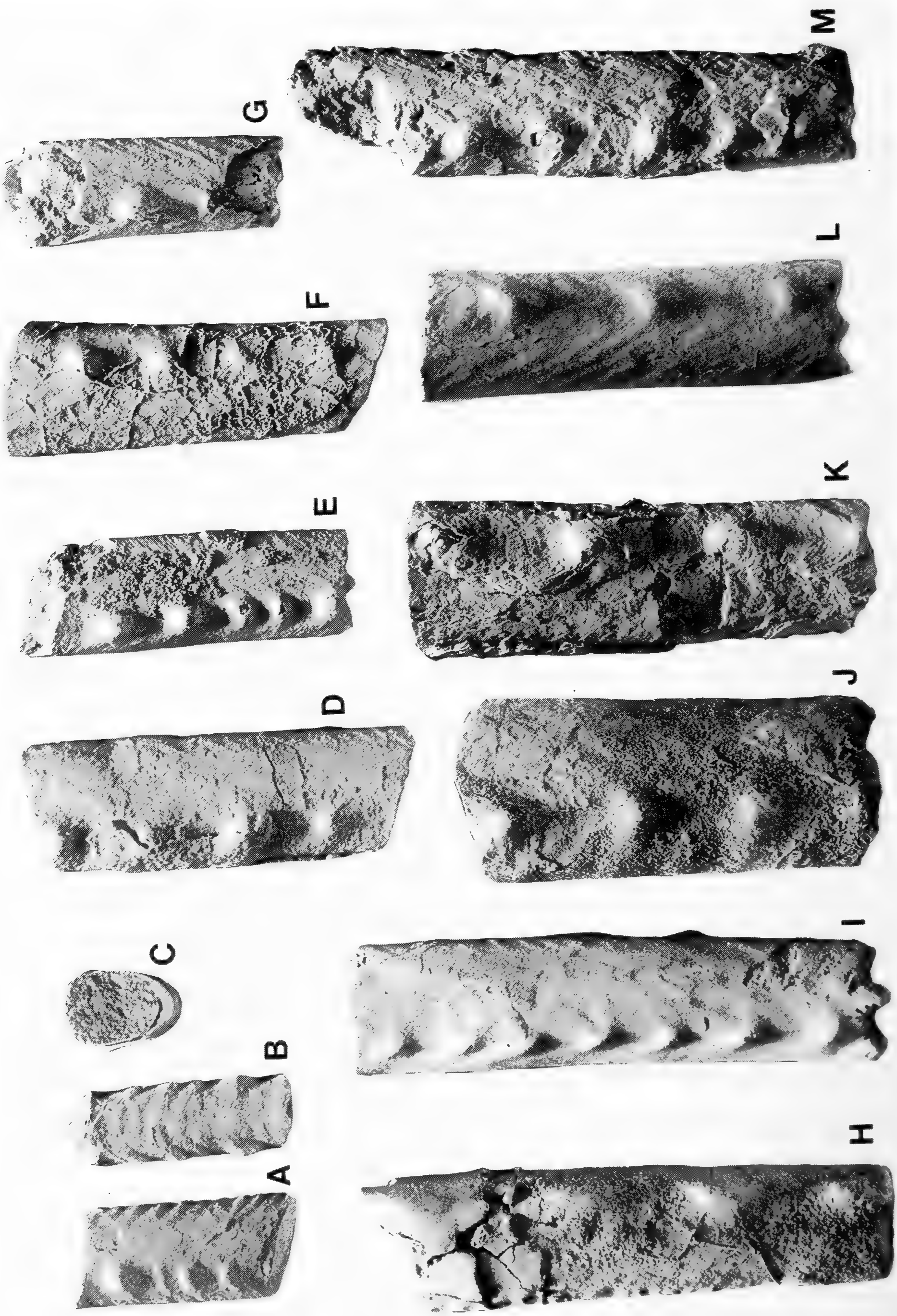

Fig. 33

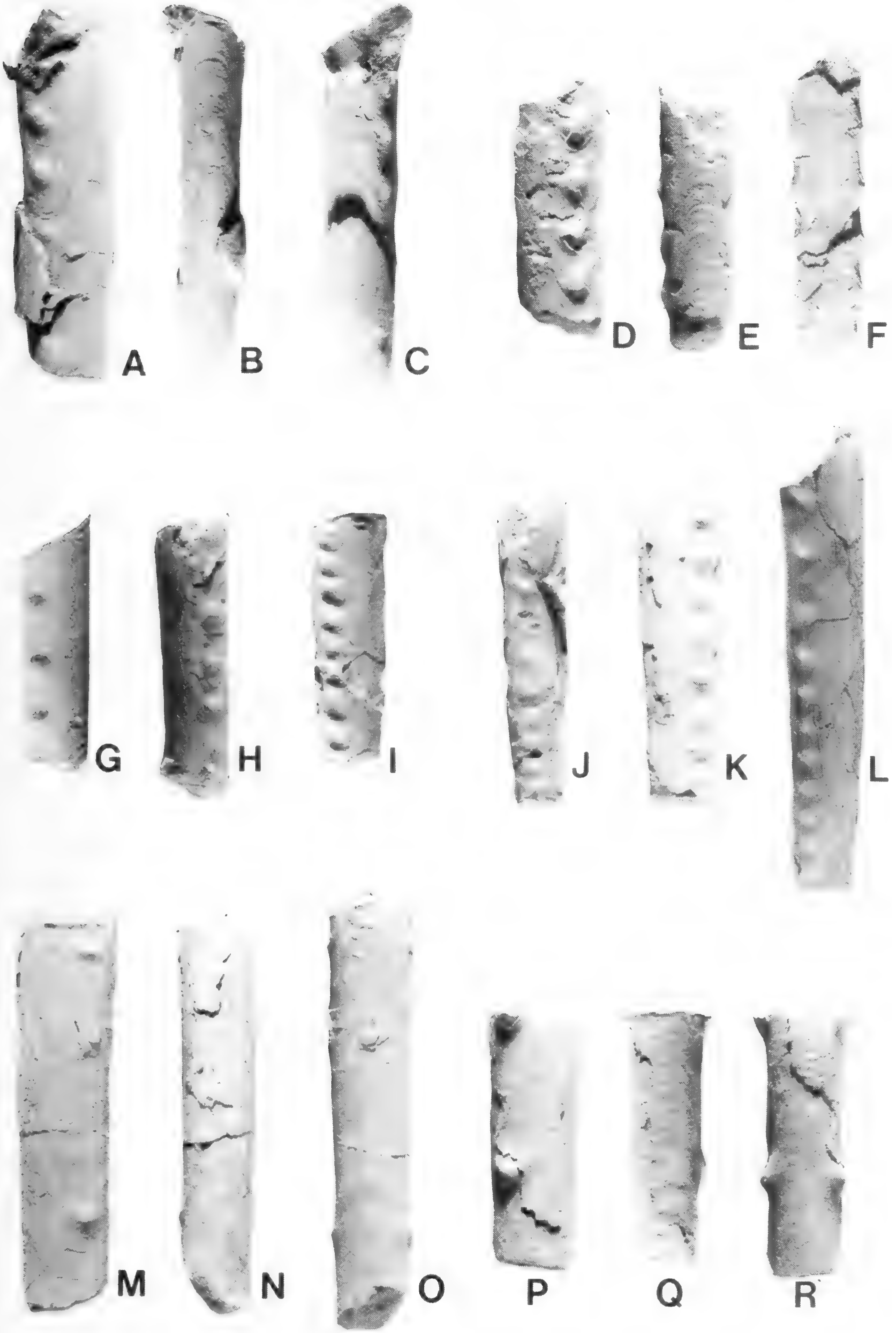

Fig. 34

localities. These morphological types are merely convenient reference points on which to base the descriptions of this material and have no taxonomic status whatsoever. Some have, in the past, been given varietal or specific names, and we try as far as possible to identify our morphotypes with these names. Their stratigraphic and phylogenetic relationships are discussed below.

Form 1 (= *Baculites* sp. aff. *B. capensis* Spath, 1921: 258). Predominantly smooth to feebly ornamented forms. These have the whorl section of typical *B. capensis*, but lack lateral ornament, e.g. NMB D1052/1 (Fig. 32A–C). In some, e.g. SAM-5467 (Fig. 48J), ornament consists of ventral corrugations only (= *Baculites* sp. cf. *sulcatus* of Spath 1921: 260). In others, e.g. SAM-PCZ8760 (Fig. 42I), NMB D1124 (Fig. 42J) and SAM-PCZ8027 (Fig. 42K–M), feeble lateral ornament may occur, as far as can be seen, on the body chamber only. Specimens reach maturity at very different sizes, e.g. SAM-5484c at Wh = 10 mm and PCZ7210 at Wh = 20 mm.

Form 2 (= *Baculites* cf. *brevicosta* Spath, 1921: 260, pl. 24 (fig. 5, 5a)); (= *B. schencki* Matsumoto, 1959: 113, pl. 32 (figs 1a–c, 2a–c, 3a–b, 4a–b, 5a–c, 6a–c), text-figs 12a–b, 13a–c, 14a–b, 15–21, 22a–b, 23a–c, 24–25). Small forms with closely spaced, crescentic tubercles situated near the dorsolateral edge of the flanks and ovoid whorl section (Fig. 34I–L, 36M–N, 42E). The tubercles may be narrow and pinched, or broad and low. Dorsally and ventrally the tubercles fade into fine striae. Whorl section generally ovoid.

Form 3 (= *Baculites* cf. *asperoanceps* Spath, 1921: 259, pl. 24 (fig. 4, 4a)). Small forms with closely spaced, generally conical to low, rounded tubercles situated near the dorsolateral edge of the flanks, e.g. SAM-PCZ8691 (Fig. 35A) and SAM-PCZ8699 (Fig. 35E). Forms with more widely spaced tubercles correspond to *B. boulei* Collignon (1931: 35, pl. 5 (fig. 2), pl. 9 (fig. 14)). A weak longitudinal groove may be visible at mid-flank. e.g. SAM-5480 (Fig. 34D–F), SAM-PCZ8675 (Fig. 35F) and PCZ8674b.

Form 4 (= *'incurvatus'*). Generally large forms with prominent conical to rounded tubercles, situated near the dorsal third of the flanks, e.g. SAM-PCZ9974 (Fig. 42A–D), SAS Z1795a–f (Fig. 44A–F) and SAS Z632a–c (Fig. 45A–E, I–J).

Fig. 35 *(see facing page)*. *Baculites capensis* Woods, 1906. A. SAM-PCZ8691. B. SAM-PCZ8692. C. SAM-PCZ8749. D. SAM-PCZ8682. E. SAM-PCZ8699. F. SAM-PCZ8675. All from locality 83, Zululand, St Lucia Formation, Coniacian IV. G. SAM-PCZ8725. H. SAM-PCZ8720. J–K. SAM—PCZ8715. L. SAM-PCZ8711. M. SAM-PCZ8713. N–P. SAM-PCZ8717. Q. SAM-PCZ8762. R. SAM-PCZ8747. All from locality 85, Zululand, St Lucia Formation, Santonian I. All × 1.

Fig. 36 *(see overleaf)*. *Baculites capensis* Woods, 1906. A–C. SAM-PCZ12002. D–F. SAM-PCZ12003. G–I. SAM-PCZ12004. J–L. SAM-PCZ12005. O. SAS A1493b. All from locality 22, Zululand, St Lucia Formation, Coniacian IV. M. SAM-PCZ12006. N. SAM- 16026, both from Mkweyane ('Umkwelane Hill'), probably locality 10, Zululand. All × 1.

Fig. 37 *(see overleaf)*. *Baculites capensis* Woods, 1906. A–B. SAM-PCZ8674, concretion to show co-occurrence of smooth and weakly nodose (*boulei*) forms of *B. capensis*. From locality 83, Zululand, St Lucia Formation, Coniacian IV. Both × 1.

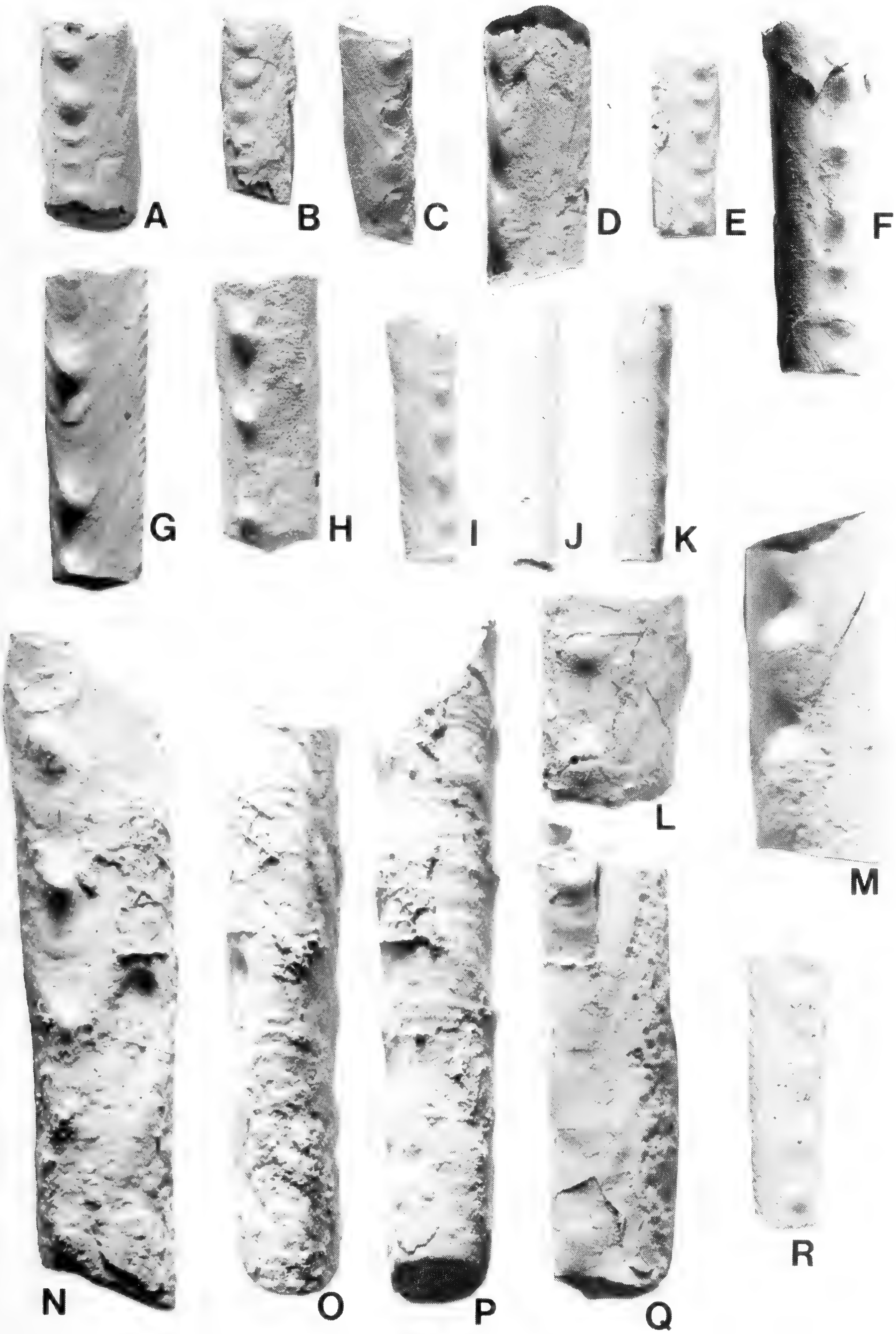

Fig. 35

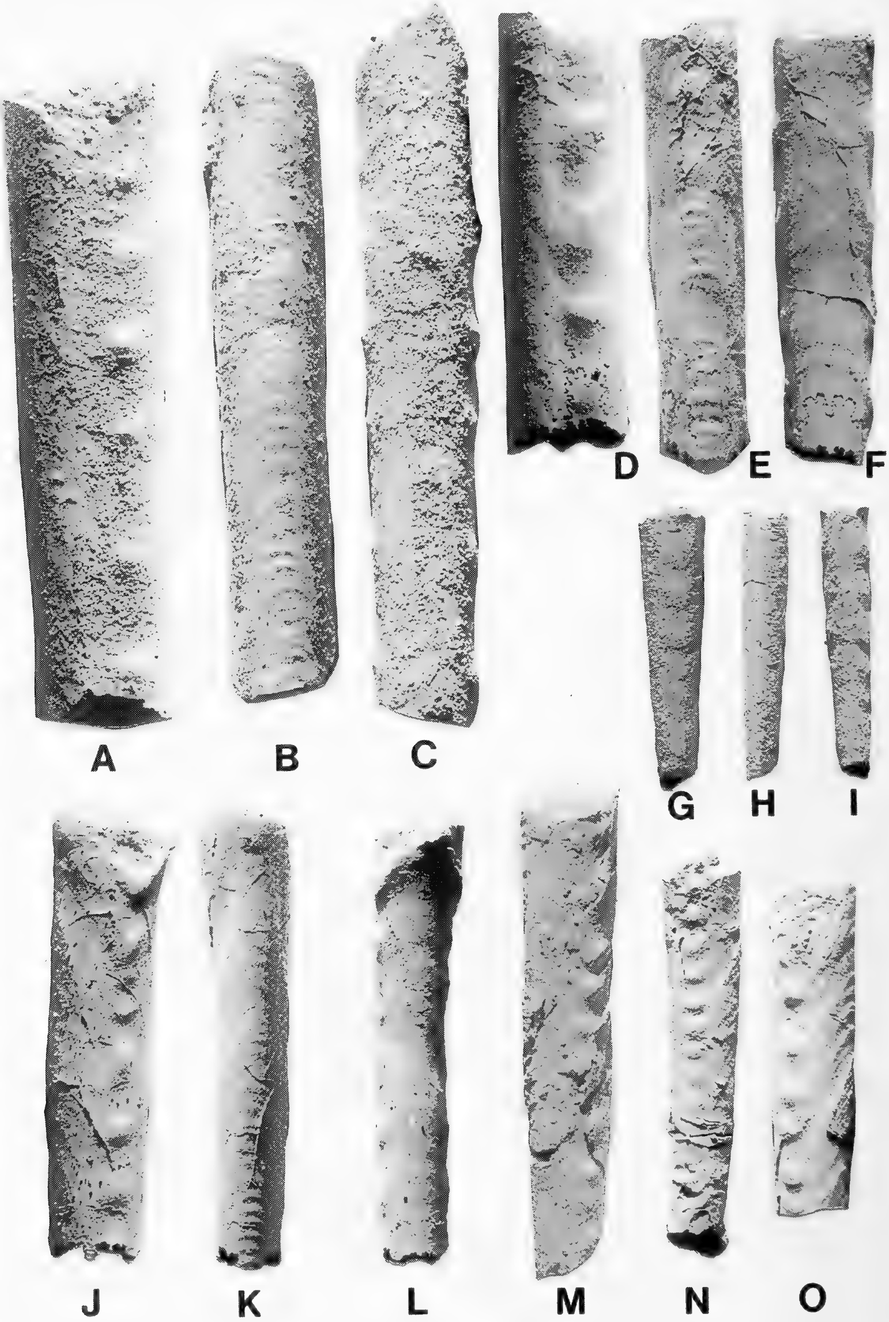

Fig. 36

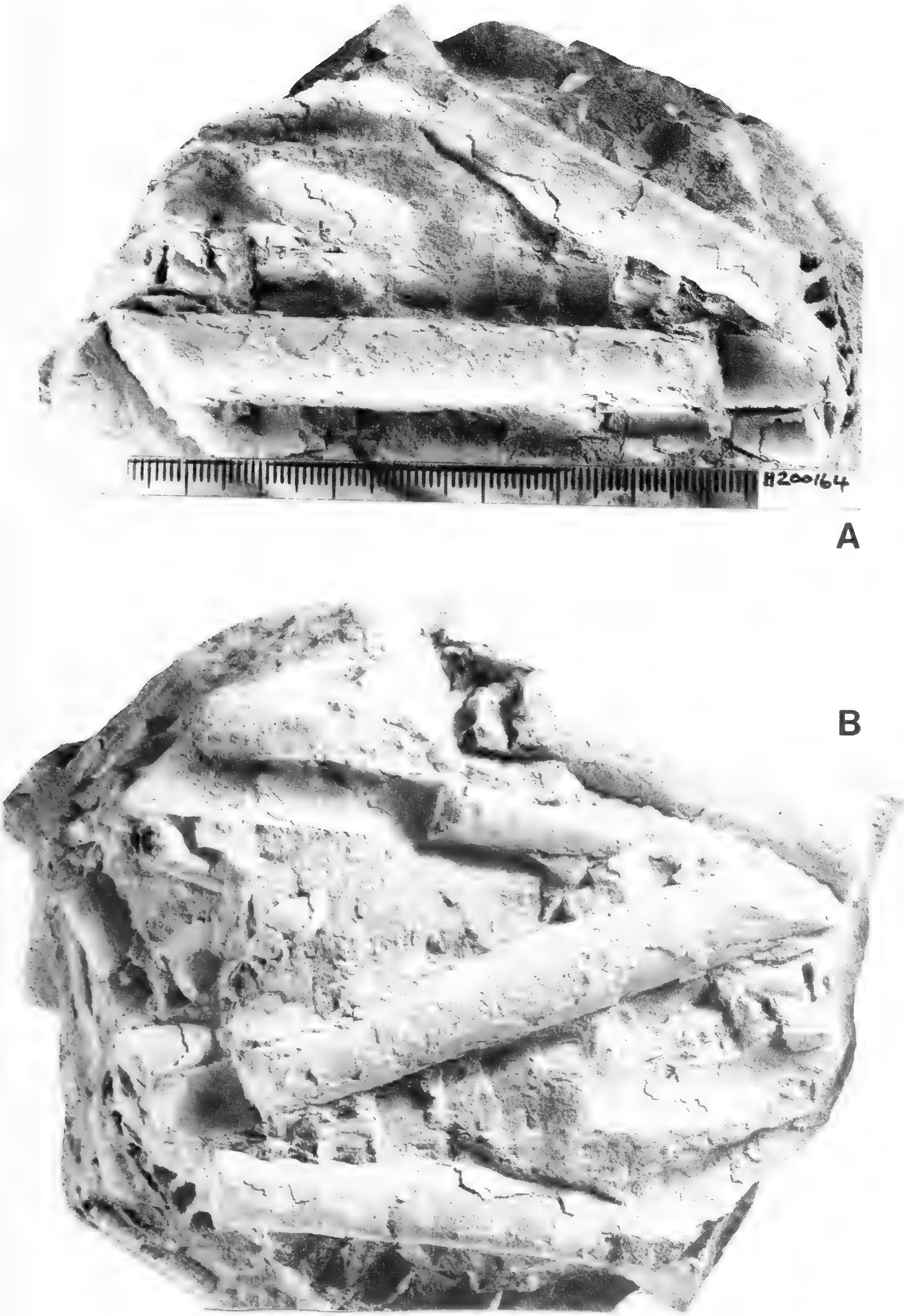

Fig. 37

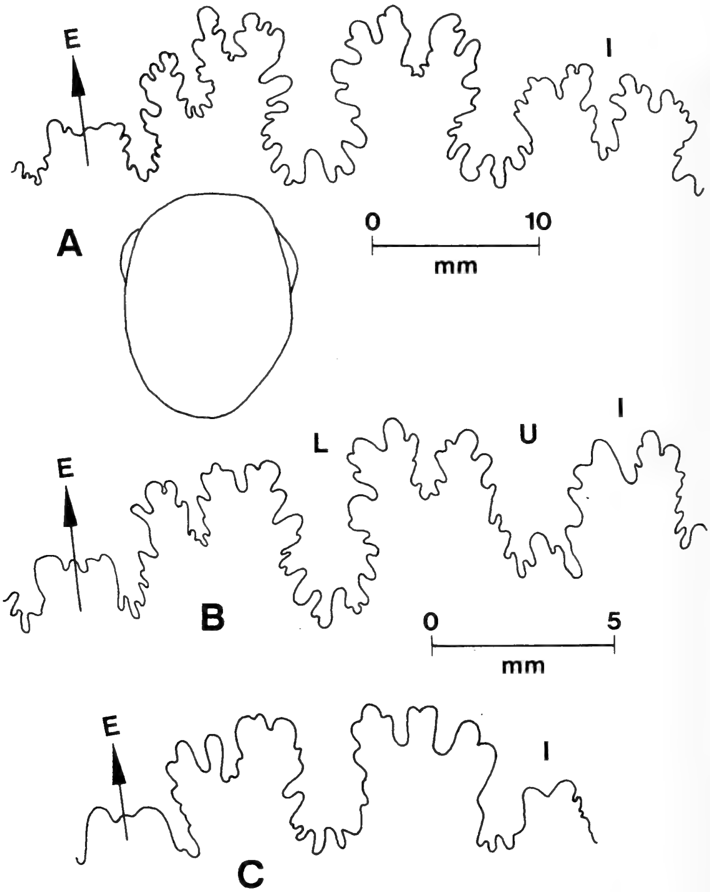

Fig. 38. *Baculites capensis* Woods, 1906. Suture lines and whorl section. A. SAS H13/6. B. SAS A335. C. SAM–1670b. Venter in whorl section pointing downward. Scale bar for size.

Form 5 (= var. *tenuetuberculata* Collignon, 1966: 6, pl. 457 (figs 1863–4). Generally large forms with weak conical to rounded tubercles, e.g. SAM–PCZ12002 (Fig. 36A–C). These are probably only large forms (macroconchs) of form 3.

Form 6. Generally large forms with prominent conical to crescentic, or transversely elongated tubercles, situated near dorsal third of flanks, e.g. NMB D1052a (Fig. 43A–C), NMB D1052c (Fig. 43F–H), SAS Z1795a (Fig. 46A–C) and SAS A353 (Fig. 47A–B).

Form 7 (= *capensis* typical form). Generally large forms with rounded to longitudinally elongated tubercles near the dorsal third of the flanks. Longitudinal depression often present near midflank; whorl section varies from subtrigonal to distinctly elliptical, e.g. SAM–4823 (Fig. 27D–H) and SAM–4824 (Fig. 28B–E). In some, e.g. SAS Z632a (Fig. 45A–C), the transition from conical (*'incurvatus'*) to longitudinally elongated (*capensis*) tubercles can be observed on the same specimen.

Form 8 (= *B. capensis* in Collignon 1966: 6, pl. 457 (fig. 1862)). Tubercles extremely elongated longitudinally, assuming crescentic outline in dorsal view, e.g. NMB D1028/3 (Fig. 50A–C).

Form 9 (= var. *umsinenensis* Venzo, 1936: 116 [58], pl. 10 [6] (figs 11–12)). Tubercles elongated obliquely, some with shallow, longitudinal depression at mid-flank. Tubercles closely or widely spaced, generally situated high on the flank or near the dorsolateral edge, e.g. SAM–PCZ12016 (Fig. 50G–H), SAM–PCZ12017 (Fig. 50M), NMB D1028/12 (Fig. 50N) and SAS A361 (Fig. 33I, 49C–E). Some specimens with very large tubercles, e.g. NMB D1028/3 (Fig. 50A–C), are transitional between forms 8 and 9.

Form 10 (= *B. malagasyensis* Collignon, 1966: 7, pl. 457 (fig. 1865)). Tubercles are of the *capensis* or *incurvatus* type, but irregularly spaced or doubled.

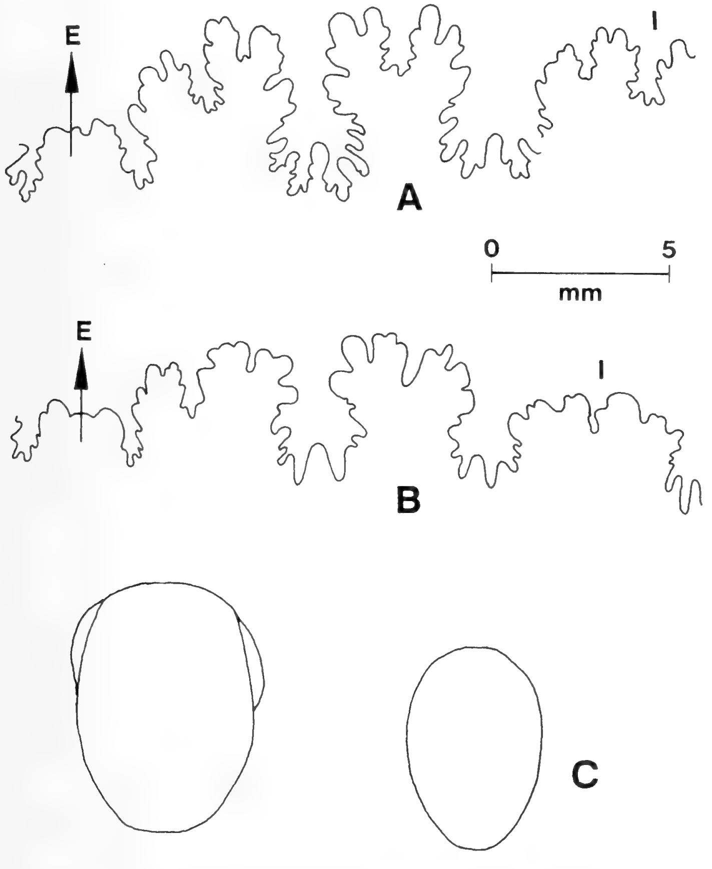

Fig. 39. *Baculites capensis* Woods, 1906. Suture lines and whorl sections. A. SAM-PCZ12007. B. SAM-PCZ12006. C. SAM-PCZ12008. Venter in whorl sections pointing downward. Scale bar for size.

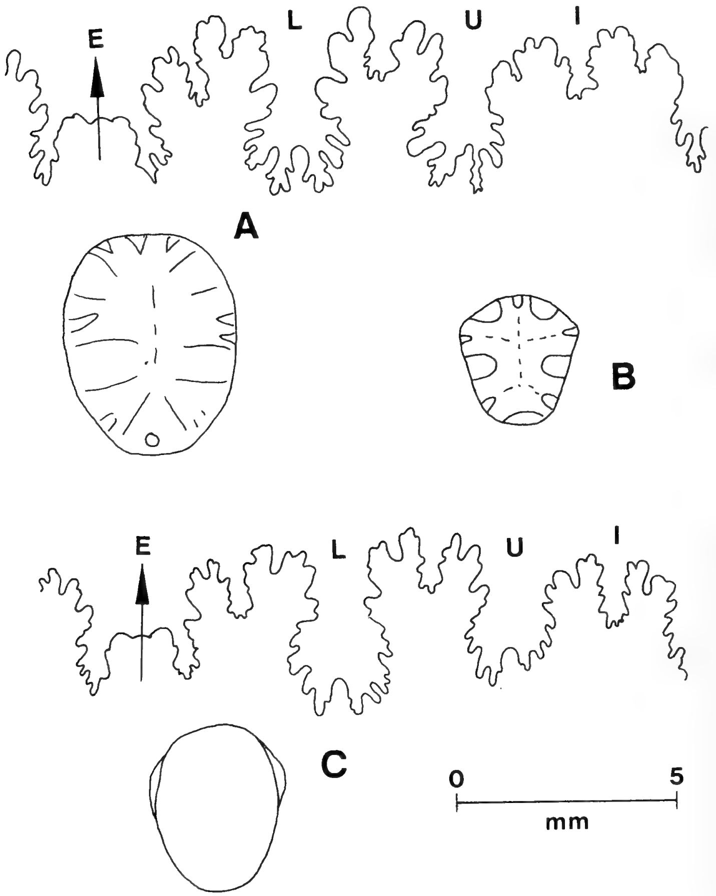

Fig. 40. *Baculites capensis* Woods, 1906. Suture lines and whorl sections. A. SAS A2101. B. SAM-PCZ8039. C. SAM-PCZ12009. Venter in whorl sections pointing downward. Scale bar for size.

Form 11. (= *?B. sparsinodosus* Collignon, 1969: 23, pl. 521 (figs 2052–2054)). Rare, ?Lower Campanian forms with large, rounded, distantly spaced tubercles, e.g. SAM-PCZ8022 (Fig. 54A), SAM-PCZ9971 (Fig. 54B) and SAM-PCZ9972 (Fig. 54C–E).

?Form 12. Rare Santonian specimens with very widely spaced tubercles, e.g. SAM-PCZ8387 (Fig. 34M–O) and SAM-PCZ8349 (Fig. 34P–R). We are not quite sure if these are true *B. capensis* or merely rare, tuberculate *B. bailyi*; faunal association suggests the latter.

Apertures and dimorphism

The aperture, or part thereof, is preserved in numerous (about 35) specimens (Figs 51A–N, 52A–D). It is simple, consisting of a short, rounded dorsal

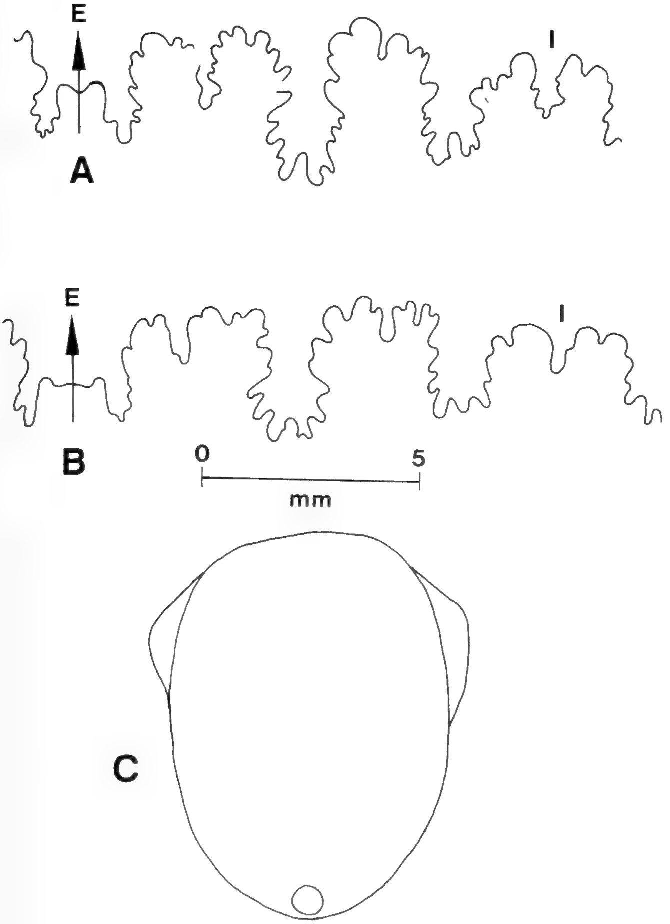

Fig. 41. *Baculites capensis* Woods, 1906. Suture lines and whorl section. A. SAM-PCZ9974. B–C. NMB D1028g. Venter in whorl section pointing downward. Scale bar for size.

rostrum, a prominent lateral sinus and a long, ventral rostrum. The dorsal rostrum may curve slightly outwards, i.e. away from the longitudinal axis of the shell, whereas the ventral rostrum may curve inwards.

The diameter at which apertures are formed and maturity presumably sets in, is quite variable (Fig. 53). The smallest whorl height at which indications of an aperture are present, is 9 mm, whereas some shells reach maximum whorl heights of 31 mm on the body chamber without having formed an aperture. Even though specimens at the smaller and larger ends of the distribution range may be distinguished as micro- and macroconchs respectively, there is no distinct break in size between them. An alternative interpretation is that this indicates a variable range of maturation size.

Most body chambers are perfectly straight, but some (e.g. NMB D1052c) (Fig. 43F–H) are slightly curved.

Suture lines

Details of the sutures are shown in Figures 38A–C, 39A–B, 40A, C, and 41A–B. The suture is very simple with open saddles and lobes.

Discussion

According to our interpretation, *B. capensis* is a predominantly nodose baculitid, which first appears in the second or third division of the Coniacian of Zululand, and persists to the second division of the Santonian in Pondoland and possibly to the first division of the Campanian in Zululand.

From the descriptions above, and the figures, it can be seen that the presence and shape of the lateral tubercles is extremely variable. This variation was already noticed by Spath (1921) in material from Mkweyane (Umkwelane Hill) collected by A. L. du Toit. Even though he referred several of the morphotypes present to extant species in open nomenclature, e.g. *Baculites* sp. aff. *capensis*, *Baculites* cf. *aspero-anceps*, *Baculites* cf. *brevicosta* and *Baculites* sp. cf. *sulcatus*, he admitted that all of these forms were probably only varieties of *B. capensis*. Our material not only confirms, but further illustrates the wide variety of ornament in *B. capensis*.

The ornament of the different morphotypes suggests that *B. capensis* could be derived from smooth *B. yokoyamai* through strengthening of groups or sheaves of striae near the dorsolateral parts of the flanks, thus forming weak, crescentic (*'brevicosta-schencki'*) tubercles, as in form 2. Strengthening of these crescentic nodes could lead to form 3 type of ornament, and further strengthening and wider spacing to type 4. Longitudinal elongation of these tubercles could lead to typical *B. capensis*-type of ornament. Oblique arrangement of typical *B. capensis* tubercles could lead to form 9 *'umsinenensis'*-type of ornament and ultimately to *B. menabensis–B. tanakae* to be discussed below. Alternatively, *'umsinenensis'*-type of ornament could be transitional between form 2 *brevicosta* and form 7 (typical *capensis*). The suggested evolution of *capensis*-type ornament from smooth *B. yokoyamai* is outlined in Figure 55.

Unfortunately, the answer is not that simple. This transition does not involve a simple change from a population of smooth baculitids through crescentic to conically nodose to longitudinally elongated tuberculate baculitids. Instead, the transition seems to involve subtle shifts in proportions of the population. The appearance and disappearance of distinct morphological features are not strictly synchronous. Thus, the first appearance of nodose baculitids does not mean that all smooth forms disappear (see e.g. Figs 29, 37)—instead, smooth forms continue to exist at least until the first appearance of typical *capensis* forms. Typical *capensis* forms first appear together with weakly nodose forms, long before

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Fig. 42 *(see facing page)*. *Baculites capensis* Woods, 1906. A–D. SAM–PCZ9972. E. NMB D1124/4. F–G. NMB D1028. H. SAM–PCZ12010. I. SAM–PCZ8760. J. NMB D1124. K–M. SAM–PCZ8027, all from locality 72, Zululand, St Lucia Formation, Coniacian III. All × 1.

Fig. 43 *(see overleaf)*. *Baculites capensis* Woods, 1906. Body chambers. A–C. NMB D1052a. D–E. NMB D1052d. F–H. NMB D1052c (note slight curvature). All from locality 73, Zululand, St Lucia Formation, Coniacian IV–V. All × 1.

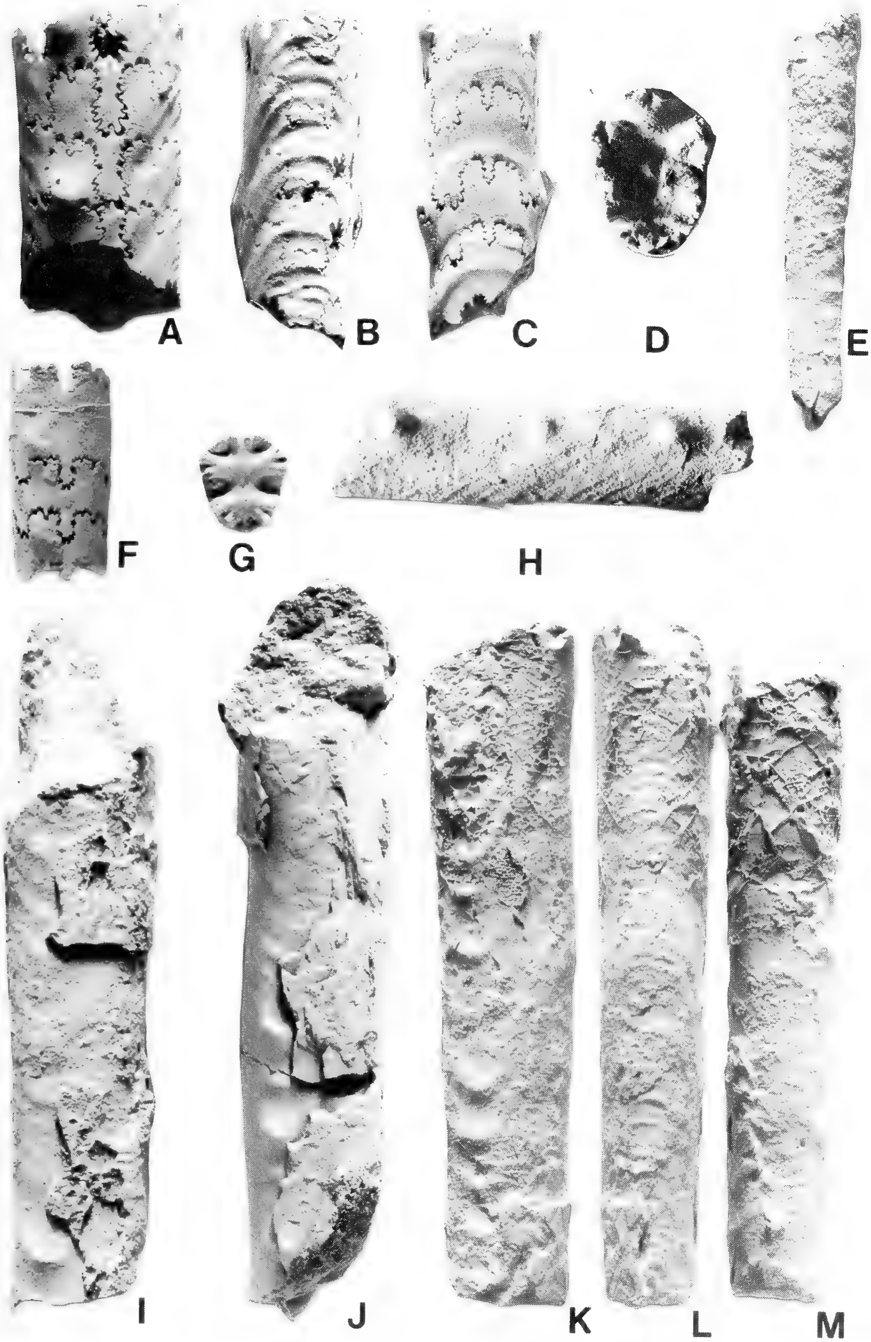

Fig. 42

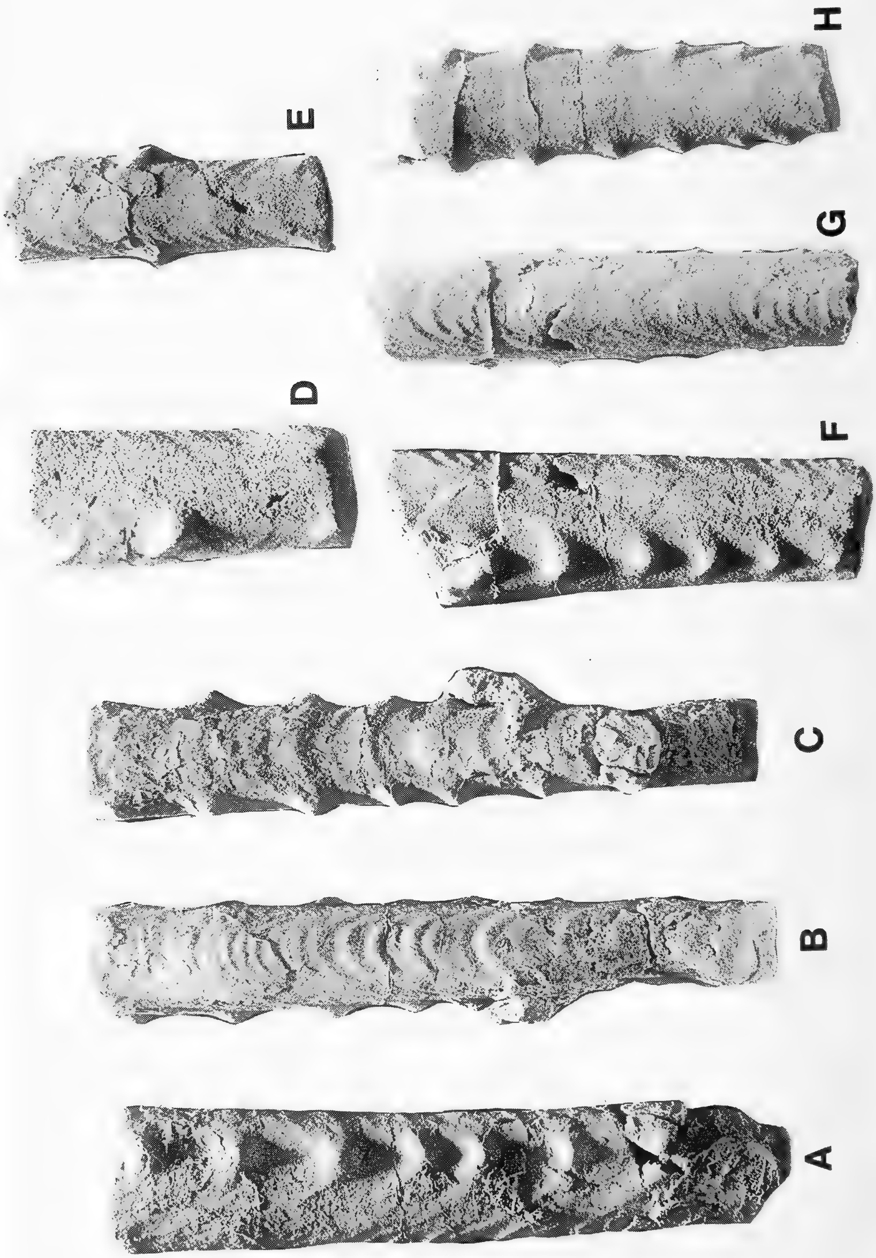

Fig. 43

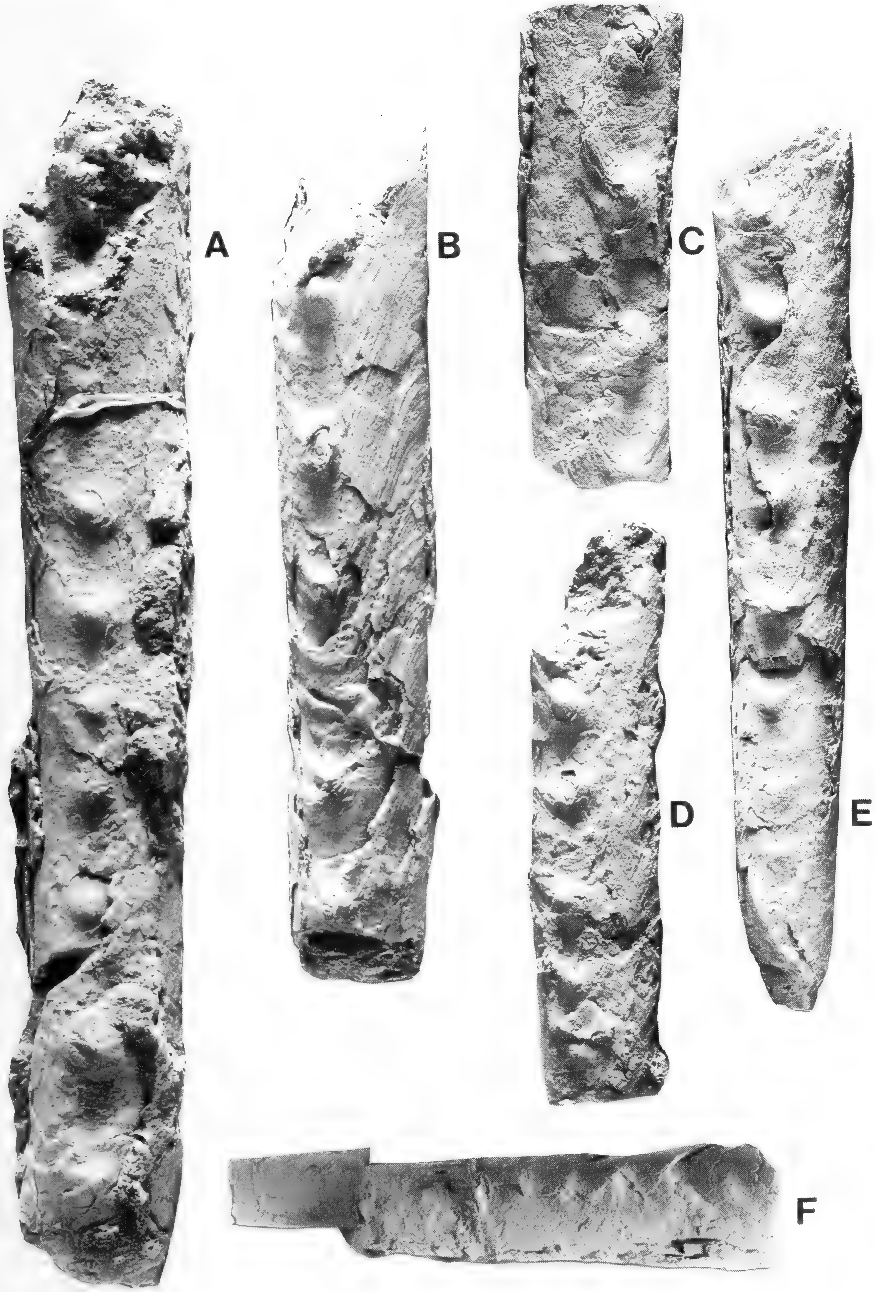

Fig. 44. *Baculites capensis* Woods, 1906. A. SAS Z1795a. B. SAS Z1795c. C. SAS Z1795f. D. SAS Z1795. E. SAS Z1795d. F. SAS Z1795l. All from locality 85, Zululand, St Lucia Formation, Santonian I. All × 1.

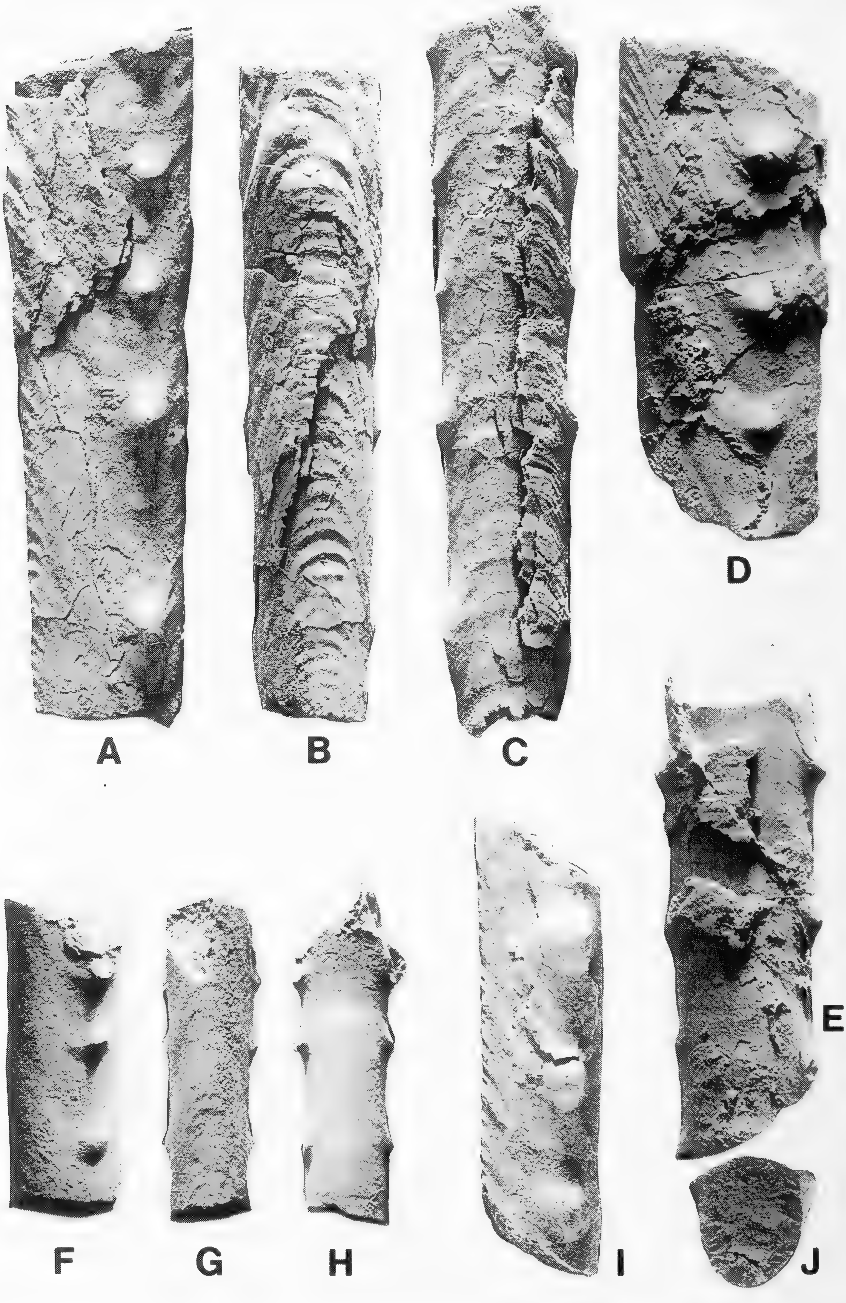

Fig. 45. *Baculites capensis* Woods, 1906. A–C. SAS Z632a. D–E. SAS Z632b. F–H. SAS Z632e. I–J. SAS Z632c. All presumably from locality 91, Zululand, St Lucia Formation, Coniacian IV or V. All × 1.

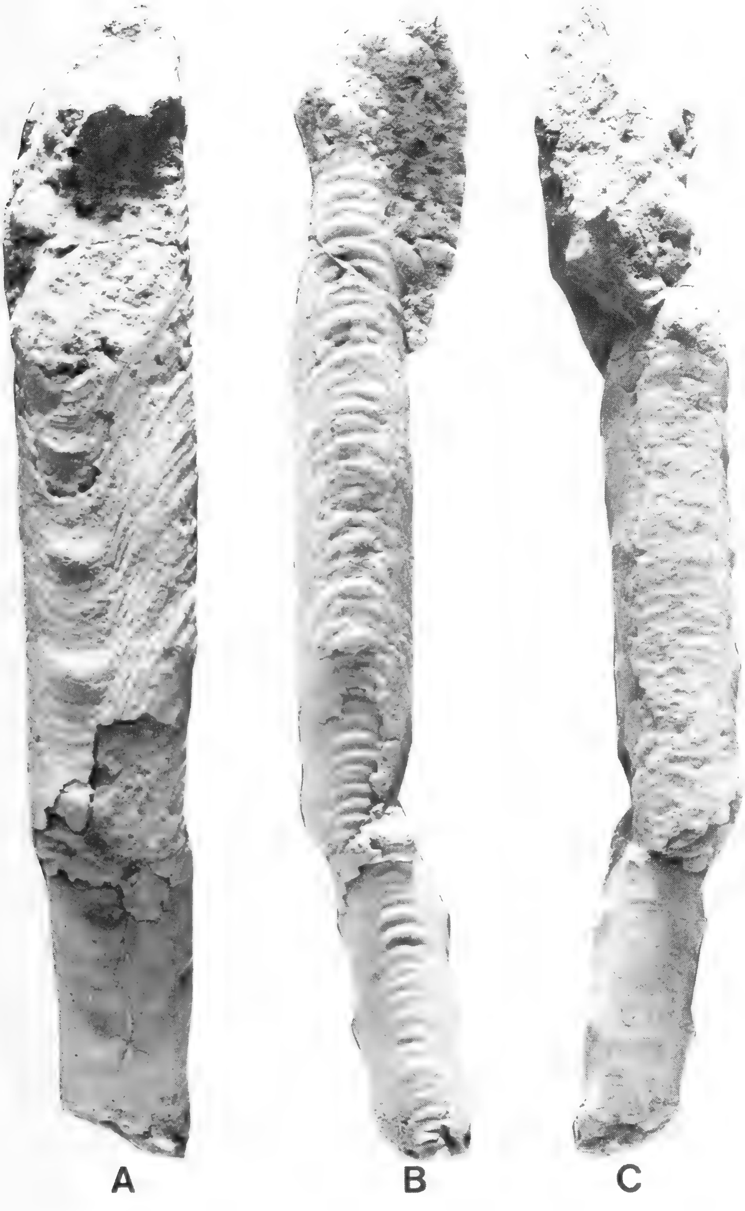

Fig. 46. *Baculites capensis* Woods, 1906. A–C. SAS Z1795a. Macroconch with part of the aperture preserved. From locality 85, Zululand, St Lucia Formation, Santonian I. All × 1.

capensis-type of ornament reaches its peak. Also, many of these different morphological types, even though stratigraphically contemporaneous, seem to be concentrated at different localities (see e.g. Fig. 35 (Coniacian IV), Fig. 43 (Coniacian IV–V), Fig. 44 (Coniacian IV–V), Fig. 45A–E, I–J (Coniacian IV or V), Figs 49C–E, 50A–C, N (Coniacian IV–V), etc.). Thus it is very common for baculitids from a single locality all to be the same, but different from those from another locality at more or less the same stratigraphic level.

Forms 1–3, i.e. smooth or with small crescentic or weakly conical tubercles situated near the dorsolateral edge of the flanks, are most common amongst the first representatives of the species in the second and third divisions of the Coniacian, but typical *capensis* forms with elongated tubercles also occur. This includes most of the baculitids described from Umkwelane Hill (Mkweyane) by Spath (1921). A similar early *capensis* baculitid assemblage occurs at locality 15. In the fourth division of the Coniacian tuberculate forms of group 3 (*boulei*) dominate, but smooth forms still persist, often in the same nodule (Fig. 37); in addition, typical forms of *capensis*, including forms 4–9 occur.

In the later part of the Coniacian and in the first two divisions of the Santonian, forms 4–9 dominate, but weakly ornamented forms still occur. Normally we find that, at a given locality, the baculitids will not occur as a random mixture of the different morphological types, but that one form will be dominant (see e.g. specimens Z1795a, c–f (Figs 44A–F), Z632a–b, e (Fig. 45A–J) and D1052a, c–d (Fig. 43A–H), all from more or less the same stratigraphic level but different localities). Based purely on morphological criteria, each of these morphotypes could be given a different name, but from a stratigraphic point of view, this would be illogical.

One morphotype that seems to be most common at, but not exclusively restricted to, the outcrops along the Mzinene River at localities 71 and 73, is form 9 (*umsinenensis*). Typical forms with distinct obliquely elongated tubercles are best known, and first recorded by Crick (1907: 240) and later by Venzo (1936: 116 [58], pl. 10 [6] (figs 11–12)) from this locality, but similar specimens are also known from localities 22, 91, and 83.

Specimens with extremely elongated tubercles (form 8) are rare (Figs 33H, 50A). Forms with extremely distant tuberculation (form 11) are also rare and have thus far only been found in rubble from excavations at locality 6, which yielded a mixed Santonian II–III and/or Campanian I fauna. We think that these baculitids are from the Campanian section of the excavations, but are not sure. The ornament is comparable to material from the Lower Campanian of Madagascar described by Collignon (1969) as *B. sparsinodosus*.

Form 12 is extremely rare and is mostly found in association with abundant Santonian specimens of *B. bailyi*. Because of this, we suspect that these may rather be atypical, nodose *B. bailyi* than *B. capensis*, but again we cannot be completely sure.

Form 11 (*malagasyensis*) is merely a *capensis* with irregular spacing of the tubercles.

Fig. 47. *Baculites capensis* Woods, 1906. Body chamber specimens. A–B. SAS A353. C. SAM-PCZ8011. D–F. SAM-PCZ12011. All from locality 73, Zululand, St Lucia Formation, Coniacian IV or V. All × 1.

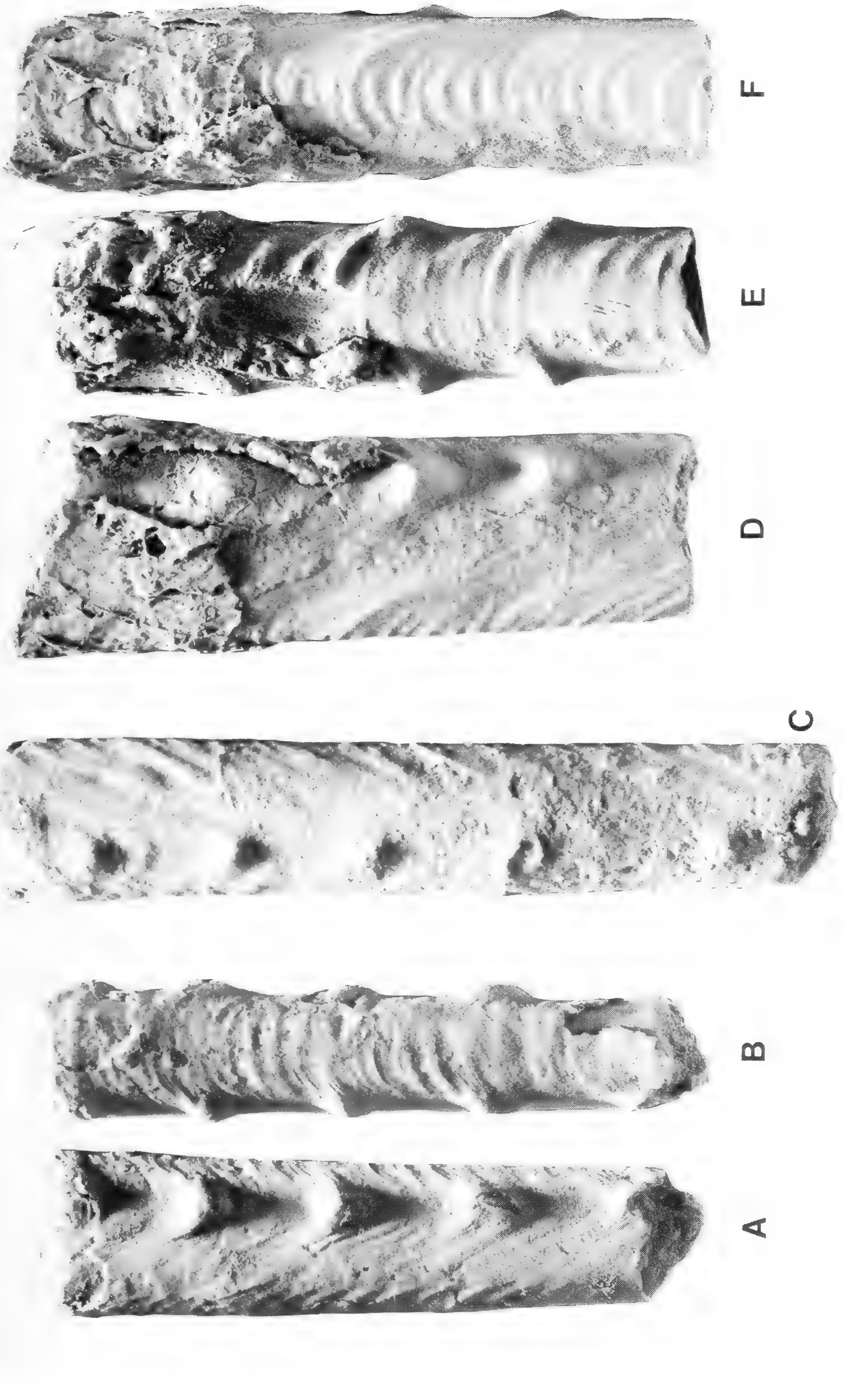

Fig. 47

Affinities and comparisons

Our interpretation of *B. capensis* is very broad, and consequently it is very difficult or in cases impossible to separate it satisfactorily from similar, contemporary species known only from a few individuals and where the range of variation is unknown.

The first problem is separating *B. capensis* from *B. bailyi*. It is easy to name the first nodose specimens *B. capensis*, but what should we call the smooth variants? We consider it expedient to regard these smooth specimens as variants of early *B. capensis*, albeit mainly by their co-occurrence with these nodose forms. Fortunately, these smooth forms of *B. capensis* are generally larger than *B. bailyi*, and have the whorl section of the former species, but separation of isolated specimens remains difficult. Also, in some of the early forms of *B. capensis*, e.g. SAM-PCZ8030 (Fig. 49J), tubercles only appear at a relatively late stage. The early, non-tuberculate parts of these shells are indistinguishable from *B. yokoyamai* or *B. bailyi*.

Contemporary, nodose baculitids appear to be separated into three distinct bio(?)geographic regions:

A. Indo-Pacific Region

i. *Baculites boulei* Collignon (1931: 35, pl. 5 (fig. 2, 2a), pl. 9 (fig. 14)).

ii. *Baculites schencki* Matsumoto (1959: 113, pl. 32 (figs 1–6), text-figs 12a–b, 13a–c, 14a–b, 15–21, 22a–b, 23a–c, 24–25).

B. Western Interior of North America

i. *Baculites codyensis* Reeside (1927: 4, pl. 2 (figs 6–9)).

Fig. 48 *(see facing page)*. *Baculites capensis* Woods, 1906. A. SAM-PCZ7198a from locality 73, Zululand, St Lucia Formation, Coniacian IV or V. B. SAM-PCZ12012 (H200/84), body chamber with part of aperture preserved. From locality 83, Zululand, St Lucia Formation, Coniacian IV. C. SAM-PCZ12013, body chamber showing transition from conical to elongate, *capensis* tuberculation. From locality 16, Zululand, St Lucia Formation, Coniacian ?III. D. SAM-PCZ12014 from locality 22, Zululand, St Lucia Formation, Coniacian IV. E. SAM-PCZ7210, body chamber with hardly perceptible tubercles from locality 72, Zululand, St Lucia Formation, Coniacian III. F–H. SAM-5443 from Mkweyane ('Umkwelane Hill'), Zululand. I. SAM-PCZ12015 from locality 89, Zululand, St Lucia Formation, Coniacian IV. J. SAM-5467, body chamber with no tuberculation; the original of Spath's (1921: 260) *Baculites* sp. cf. *sulcatus* from Mkweyane ('Umkwelane Hill'), Zululand. All × 1.

Fig. 49 *(see overleaf)*. *Baculites. capensis* Woods, 1906. A–B. SAS A334. C–E. SAS A361—specimen with typical '*umsinenensis*' type of ornament. F–I. SAS A137—specimen showing shallow longitudinal groove under oblique lighting. All from locality 73, Zululand, St Lucia Formation, Coniacian IV–V. J. SAM-PCZ8030, microconch, showing transition from smooth to weakly tuberculate '*brevicosta*' type of ornament. From locality 15, Zululand, St Lucia Formation, Coniacian IV. All × 1.

Fig. 50 *(see overleaf)*. *Baculites capensis* Woods, 1906. A–C. NMB D1028/3. D–F. SAS A606. G–I. SAM-PCZ12016. J–L. SAS A335. M. SAM-PCZ12017. N. NMB D1028/12. A–C, G–I, M–N—all specimens with obliquely elongated tubercles of the '*umsinenensis*' form 9 type, but note the variation in strength; A–C is closest to form 8; D–F, with irregularly spaced, incipiently doubled tubercles, as in *B. malagasyensis*. All × 1.

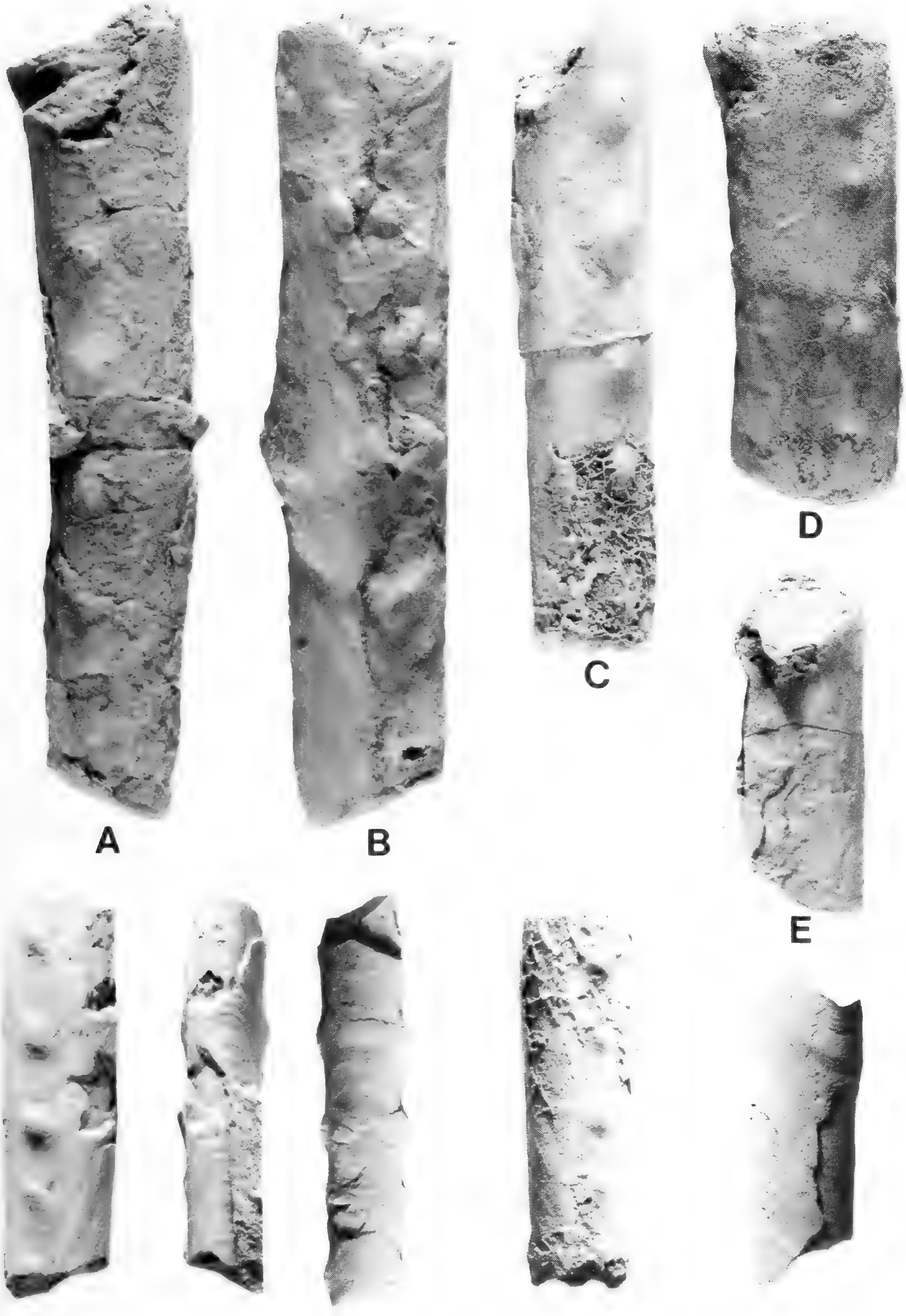

Fig. 48

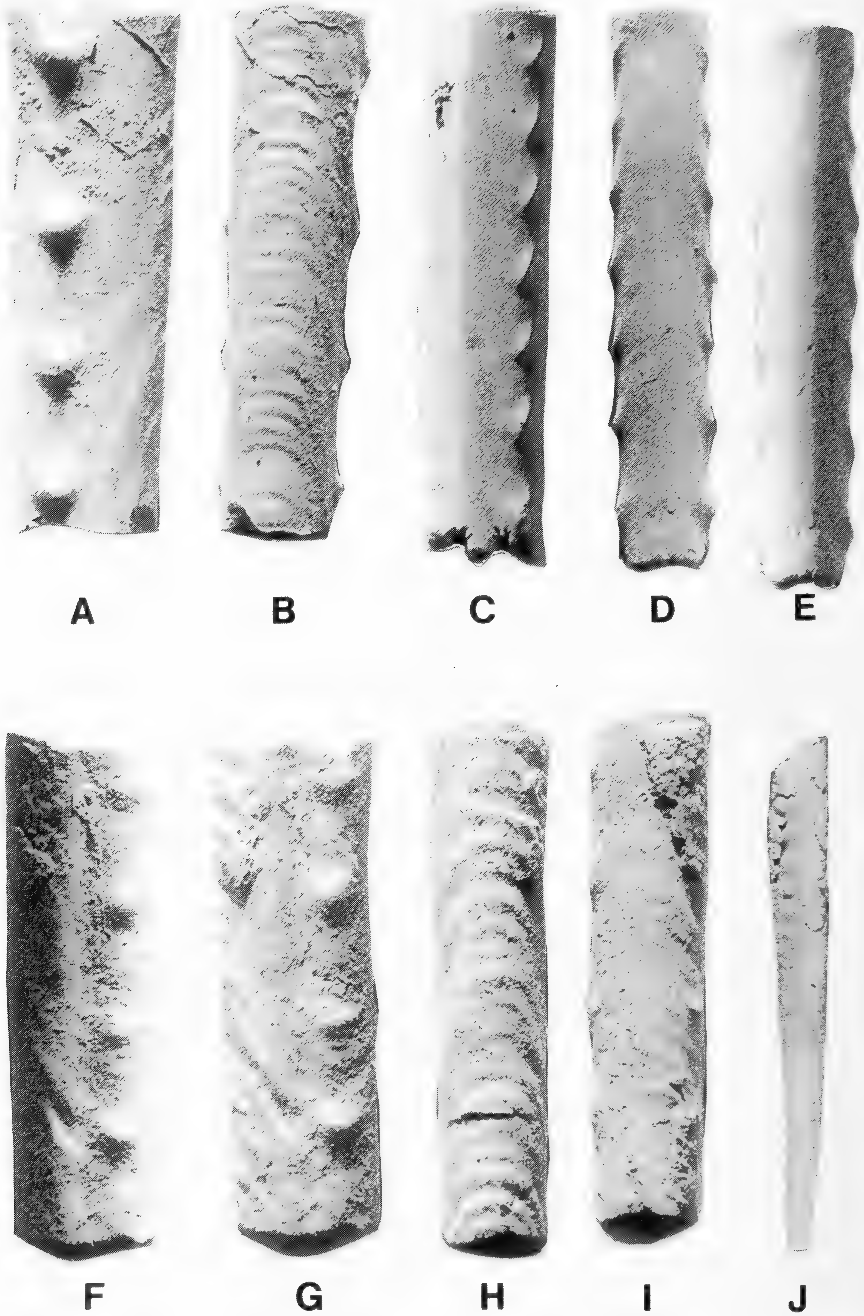

Fig. 49

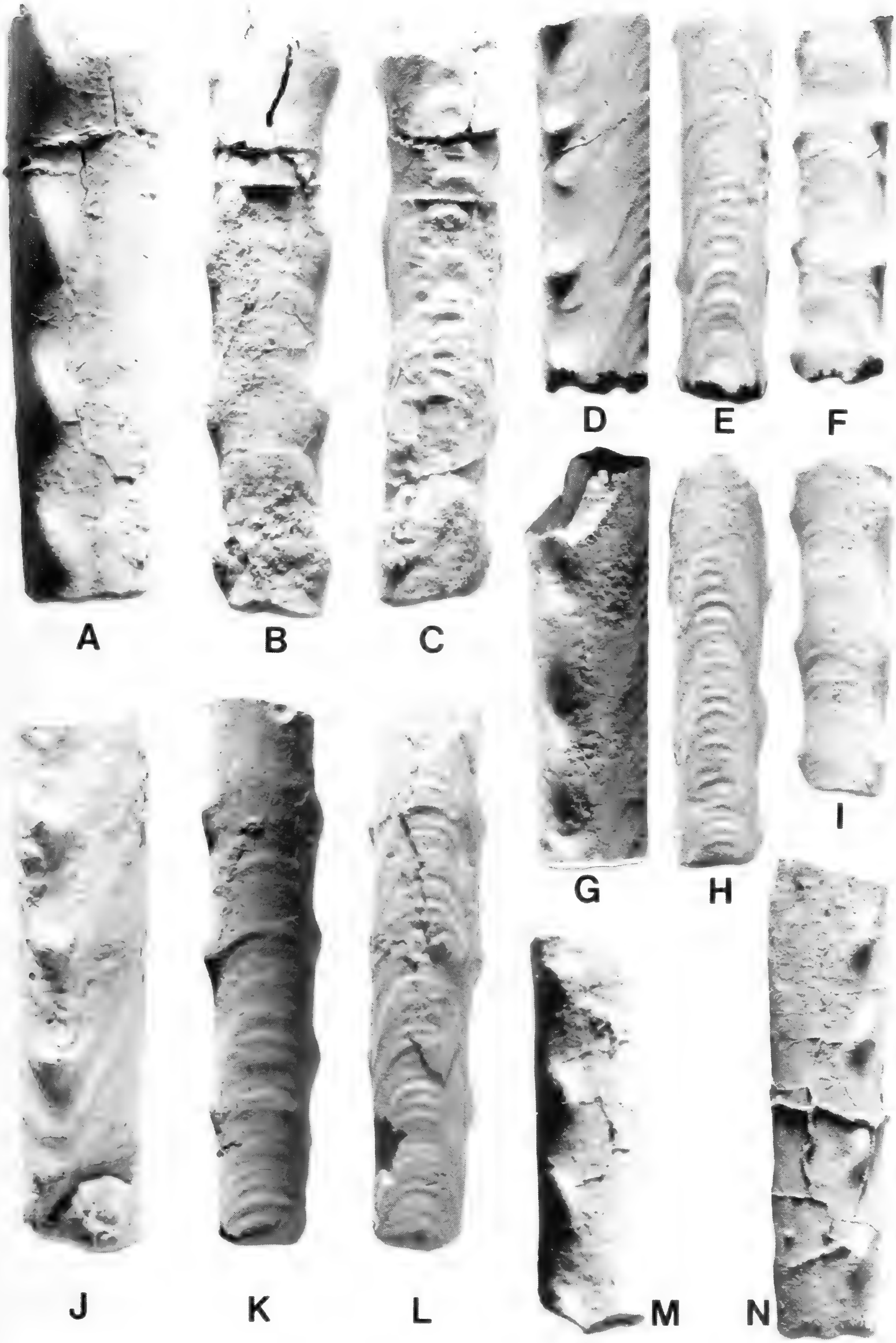

Fig. 50

C. European Tethyan and Boreal Region
i. *Baculites incurvatus* Dujardin (1837: 232, pl. 17 (fig. 13)).
ii. *Baculites brevicosta* Schlüter (1876: 141, pl. 39 (figs 9–10)).

A. Indo-Pacific. *Baculites boulei*—Collignon established this species based on nine syntypes. The lectotype, by subsequent designation of Matsumoto (1959: 118), is the specimen figured by Collignon (1931, pl. 5 (fig. 2, 2a)) (herein Fig. 12J–L) from Mahagaga, Madagascar.

Baculites boulei has been interpreted in various, contradictory ways, including by Collignon himself. As discussed above (p. 27), *B. boulei* was described from a ferruginous conglomerate north-north-east of Mahagaga. Five other 'species' of *Baculites* were found in association with *B. boulei*, one with arcuate lateral tubercles—, *Baculites* cf. *B. brevicosta* Schlüter (Collignon 1931: 34, pl. 5 (fig. 1, 1a), pl. 9 (fig. 13) (3 specimens), and four non-tuberculate 'species': *B. sulcatus* Baily (Collignon 1931: 36, pl. 5 (figs 3–5), pl. 9 (fig. 15)) (24 specimens), *B. besairiei* Collignon (1931: 37, pl. 5 (figs 6–9), pl. 9 (fig. 16)) (150 specimens), *B. roedereri* Collignon (1931: 38, pl. 5 (fig. 10, 10a), pl. 9 (fig. 17)) (1 specimen), and *B. latelobatus* Collignon (1931: 38, pl. 5 (figs 11–12), pl. 9 (fig. 18)) (3 specimens). The latter four smooth 'species' are all considered synonyms of *B. yokoyamai*, as stated above.

According to Collignon's (1931: 35) original diagnosis, *B. boulei* is ornamented every 7–8 mm by a large low tubercle, which is arched and concave, and elongated forward into a thin rib; between two successive tubercles, there are 4–5 intercalatory ribs, which are visible only in the siphonal region and in the immediate vicinity of the flanks. The species is similar to *B. capensis*, but, according to Collignon (1931: 36) differs by its whorl section being distinctly oval.

According to Collignon's description and, judging by the faunal association and age, it is clear that *B. boulei* is an early form of *B. capensis* as here interpreted, thus corresponding to form 3.

Collignon later recorded *B. boulei* (1938: 88, pl. 6 (figs 6–6b)), together with *Baculites incurvatus* (Collignon 1938: 88, pl. 6 (figs 4, 4a–5, 5a)) and *Baculites* cf. *B. aspero-anceps* (Collignon 1938: 89, pl. 6 (fig. 7–7b)) from unequivocal Campanian strata at Andimaka. This is clearly incorrect, as is Förster's (1975: 168, pl. 4 (figs 3, 9), text-fig. 37) record of *B. boulei* from the Lower Campanian of Mozambique. The suture figured by Förster as that of *B. boulei* is more complex than that of Collignon's original figure. *Baculites* cf. *B. asperoanceps* has a trigonal whorl section, and seems close to *B. nibelae* sp. nov. (see p. 162) from the Upper Campanian of Zululand or perhaps *B. increscens*. (True *B. asperoanceps* Lasswitz (1904: 16 (236), pl. 3 (15) (fig. 1a–b)) (lectotype figured herein Fig. 129) is a Campanian species and possibly a synonym of *B. obtusus*.)

Fig. 51 *(see facing page)*. *Baculites capensis* Woods, 1906. Various specimens with parts of the aperture preserved. A–C. NMB D1028/4. F. NMB D1124. K–N. NMB D1024/10, all from locality 72, Zululand, St Lucia Formation, Coniacian II or III. D. SAS Z632e from locality 91, Zululand, St Lucia Formation, Coniacian IV or V. G. SAM-1621b from an unrecorded locality. H–J. SAM-PCZ12018 from locality 83, Zululand, St Lucia Formation, Coniacian IV. All × 1.

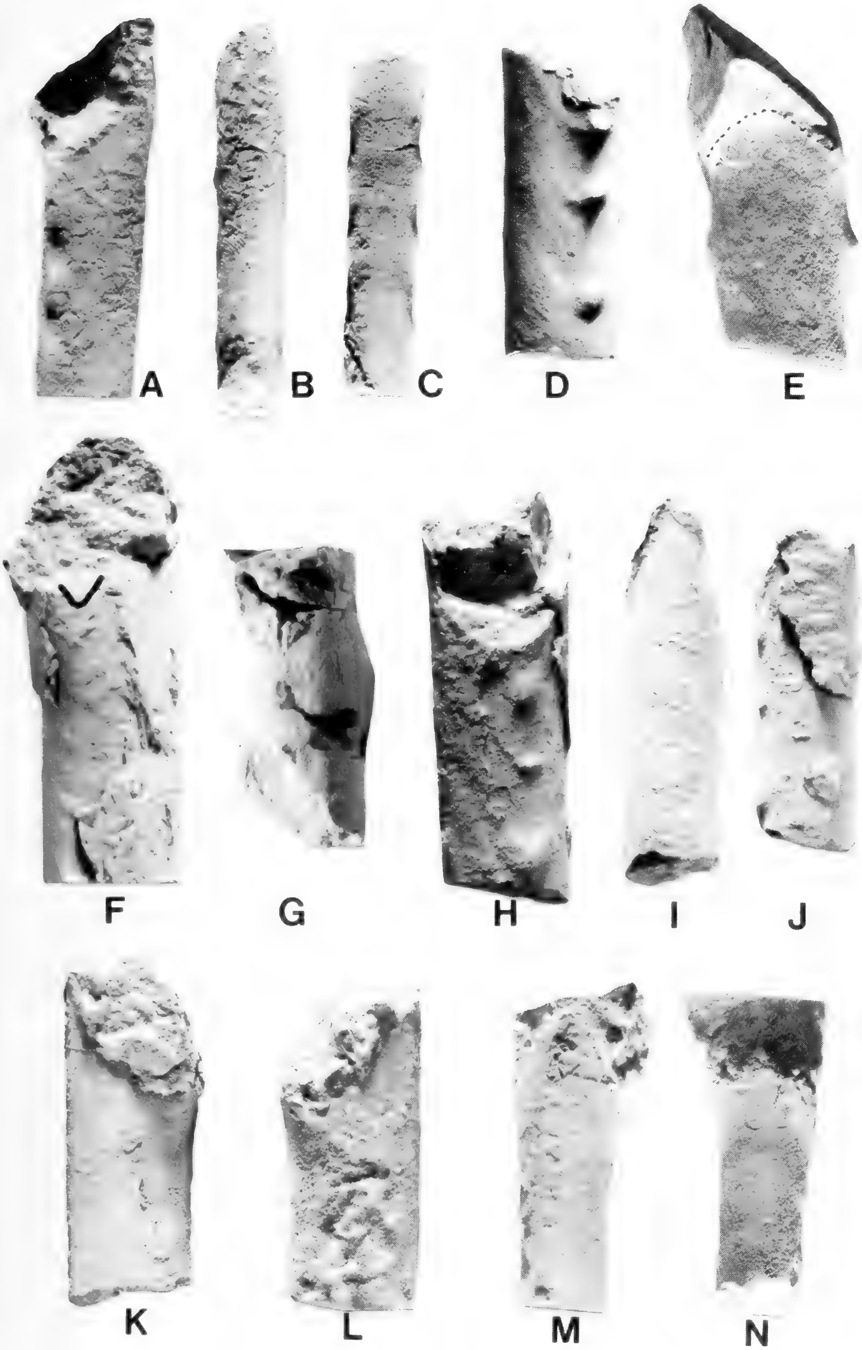

Fig. 51

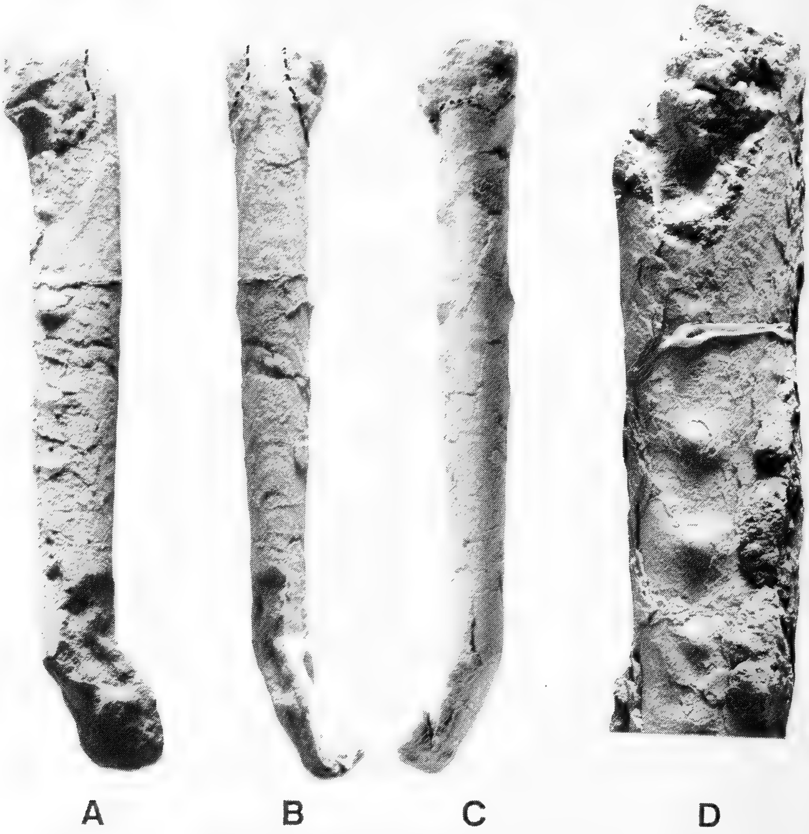

Fig. 52. *Baculites capensis* Woods, 1906. Two specimens with preserved apertures at disparate sizes to illustrate dimorphism. A–C. Microconch. NMB D1075 from locality 73, Zululand, St Lucia Formation, Coniacian IV or V. D. Macroconch. SAS Z1795a from locality 85, Zululand, St Lucia Formation, Santonian I. Both × 1.

Matsumoto (1959: 118, pl. 32 (fig. 7a–c), pl. 33 (figs 4a–c, 5a–b, 6a–d, 7a–b), text-figs 27a–b, 28–32) recorded *B. boulei* from California, the first record of the species outside Madagascar. Some of the Californian specimens were reported together with *B. schencki*, from 'Member V of the Redding area', which was dated as Coniacian. According to Haggart (1984) and Haggart & Ward (1989: 226), however, all the Californian occurrences of *B. boulei* are Santonian.

Haggart & Ward (1989: 226, fig. 3.7–3.10)) recorded a single specimen of *Baculites* cf. *B. boulei* from the Santonian–Campanian of Vancouver Island. Ornament is of the *brevicosta* form 2 type of *B. capensis*, but this is mainly an early Coniacian form. As Haggart & Ward (1989: 226) suggested, the Vancouver specimen resembles *B. tanakae* and is probably a late form of *B. capensis* transitional to *B. tanakae*.

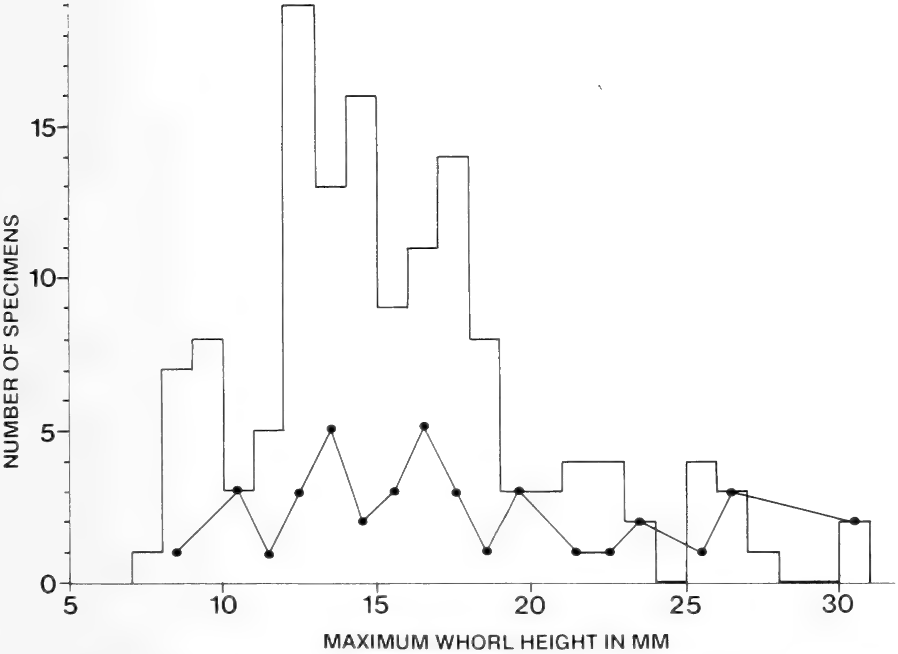

Fig. 53. *Baculites capensis* Woods, 1906. Histogram illustrating distribution of maximum whorl height. Solid circles represent specimens with the aperture preserved. Note the absence of a sharp break between apparent macro- and microconchs suggesting, perhaps, a uniform variable range of maturation sizes.

Matsumoto & Obata (1963: 43, pl. 13 (figs 3, 5), pl. 15 (fig. 6), text-figs 93, 152–155) subsequently described *B. boulei* from Hokkaido, where it is partly coeval with both *B. capensis* and *B. schencki*, i.e. Coniacian and Santonian (Matsumoto & Obata, text-fig. 216).

Kennedy (1986*b*: 112) regarded *B. boulei* as having a stouter whorl section than *B. capensis* and more closely spaced tubercles, which lie nearer to the dorsum than in the latter species.

Baculites schencki Matsumoto (1959: 113, pl. 32 (figs 1a–c, 2a–c, 3a–b, 4a–b, 5a–c, 6a–c), text-figs 12a–b, 13a–c, 14a–b, 15–21, 22a–b, 24–25) typically has an ovoid whorl section, and closely spaced, crescentic lateral nodes. It differs in typical forms from *B. boulei* by the weaker lateral ornament, and the narrower venter, but intermediate forms occur. This is very similar to, or identical with what we regard as form 2 of early *B. capensis*.

According to Matsumoto (1959: 120), the stratigraphic ranges of the two species overlap in California: *B. schencki* is more common in the lower part (of Member IV and V of the Redding area), whereas *B. boulei* is relatively common in the upper part.

In comparing *B. boulei* and *B. schencki* with *B. capensis*, Matsumoto (1959: 125) remarked that in California 'the three species, *B. schencki*, *B. boulei* and *B. capensis* are nearly contemporary, but their stratigraphic positions of the

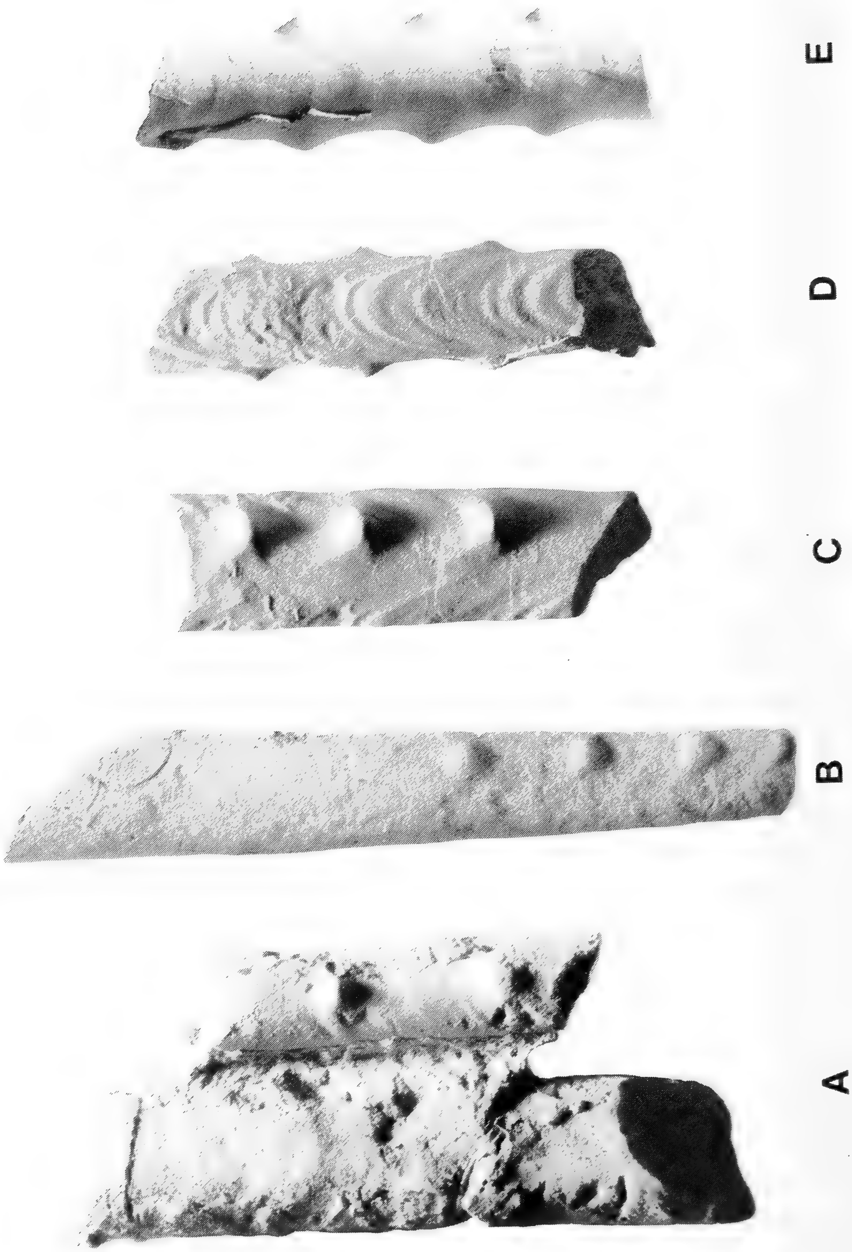

Fig. 54

maximum abundance are arranged in ascending order'. Our Zululand material partially confirms this, although the *B. schencki*-type of ornament is not as common here as in California. (According to Haggart (1984: 232) no further specimens of *B. boulei* or of *B. schencki* were collected in the Chico Formation.) Our material confirms that the stratigraphic ranges of these forms are largely overlapping.

Thus on stratigraphic grounds alone, there is no justification for formally separating *B. schencki*, *B. boulei* and *B. capensis*. We admit that, in some areas, one of the morphologies may be more common, but if different morphologies are to be the criterion for separating *B. schencki* and *B. boulei* from *B. capensis*, then we may as well regard all the varieties of *B. capensis* described above as different species. We thus regard *B. schencki* and *B. boulei* as synonyms of *B. capensis*. A case could be argued to refer to *B. schencki*, *B. boulei* and *B. capensis* as early, intermediate and typical forms but, as noted above, these morphologies are partly co-eval, and this terminology would be confusing.

B. Western Interior of North America. In his original description of *B. capensis*, Woods (1906: 343) remarked on the similarities between the former and *B. asper* Morton (1834: 43, pl. 1 (figs 12–13), pl. 13 (fig. 2)), stating that the latter differed 'in having larger and transversely elongated tubercles'. Spath (1921: 257) also referred to the resemblance between *B. capensis* and *B. asper*. According to Spath, the specimen figured by Meek (1876, pl. 39 (fig. 10a only)) and a specimen from Mississippi in the British Museum 'are close to the South African species in all characters but the suture line'. Matsumoto (1959: 125) also commented on the similarities between *B. capensis* and *B. asper*, concluding that it was 'probably a parallelism between the entirely separated biogeographic provinces'. Similarities between the two species were again referred to by Matsumoto & Obata (1963: 50).

Unfortunately, *B. asper* appears to be uninterpretable at present. According to Morton (1834: 44), *B. asper* was initially discovered by Mr Nuttal at Cahawba, Alabama, and later found by Mr Conrad at Prairie Bluff, also in Alabama. These localities are both appreciably younger than the Coniacian–Santonian range of *B. capensis*. Cahawba is in the Selma Chalk, which is Late Campanian, and the Prairie Bluff Chalk is Maastrichtian.

Reeside (1962: 116) mentioned that only one of Morton's specimens survived. This had a label in Morton's handwriting that states the locality as being Prairie Bluff—i.e. Maastrichtian. Reeside concluded that Conrad's locality data, accepted by Morton, was erroneous, and interpreted *B. asper* as a Coniacian, Santonian and early Campanian species.

Kennedy & Cobban (1991*a*: 72), on the other hand, regarded all the American Coniacian–Santonian records of *'B. asper'* non Morton as *B. codyensis*

Fig. 54 *(see facing page)*. *Baculites capensis*, form 11. Compare with *B. sparsinodosus* Collignon, 1969. A. SAM-PCZ8022. B. SAM-PCZ9971. C–E. SAM-PCZ9972. All from rubble from excavations at locality 6, Zululand, St Lucia Formation, Santonian II–III to Campanian I; presumably from the Campanian. Note the absence of tubercles on the body chambers in A and B. All × 1.

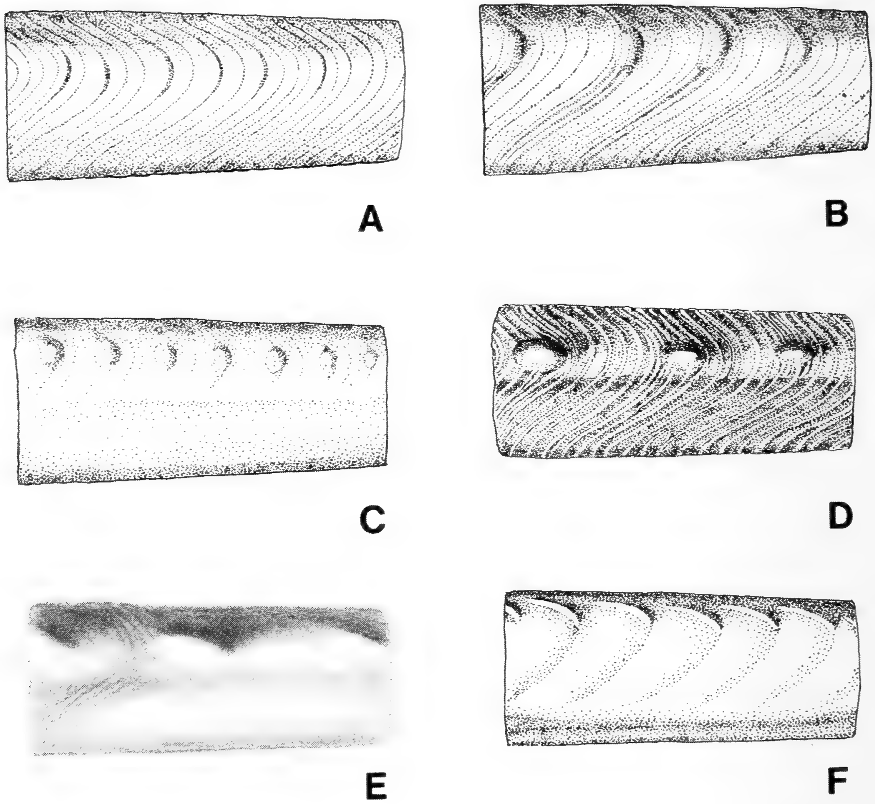

Fig. 55. *Baculites capensis* Woods, 1906. Suggested evolution of ornament, from *B. yokoyamai* (A), through *B. brevicosta* (B), *schencki* (C), *boulei* (D), to typical *capensis* (E) and *umsinenensis* (F), and ultimately to *B. menabensis* type (Fig. 57) (see p. 93).

Reeside (1927*a*: 4, pl. 2 (figs 6–19)). Typical forms of *B. codyensis* are easily distinguished from all varieties of *B. capensis*. These have crescentic, rib-like lateral tubercles, which may be projected prominently over the venter, superficially resembling *B. sulcatus*. Atypical forms of *B. codyensis*, previously misidentified as *B. asper*, have strong, distant bullae and a stouter whorl section (see e.g. Kennedy & Cobban 1991*a*, pl. 16). These are identical to some of our *B. capensis*, referred to as form 6 (see e.g. Fig. 43A–H, 47A–F) by their strong, crescentic dorsolateral tubercles. Even though some representatives of *B. capensis* and *B. codyensis* appear identical, the populations as a whole are very distinctive. No known specimens of *B. capensis* ever develop as strong and regular crescentic lateral ribbing as in typical *B. codyensis*, and no forms of *B. codyensis* ever develop longitudinally elongated lateral tubercles and a slight depression at mid-flank as in typical *B. capensis*.

An as yet unnamed baculitid fauna from the Upper Turonian–Lower Coniacian of Mossamedes, Angola, collected by Dr M. R. Cooper and now in the collections of the S.A. Museum, is of interest in apparently linking smooth

B. yokoyamai and ornate *B. codyensis*. These specimens all have dorsolaterally situated, closely spaced, crescentic tubercles (Figs 131N–R, 132A–F). These are very similar to our form 3 or *B. schencki*, and seem to suggest that acquisition of lateral ornament took place in a similar manner in both *B. codyensis* and

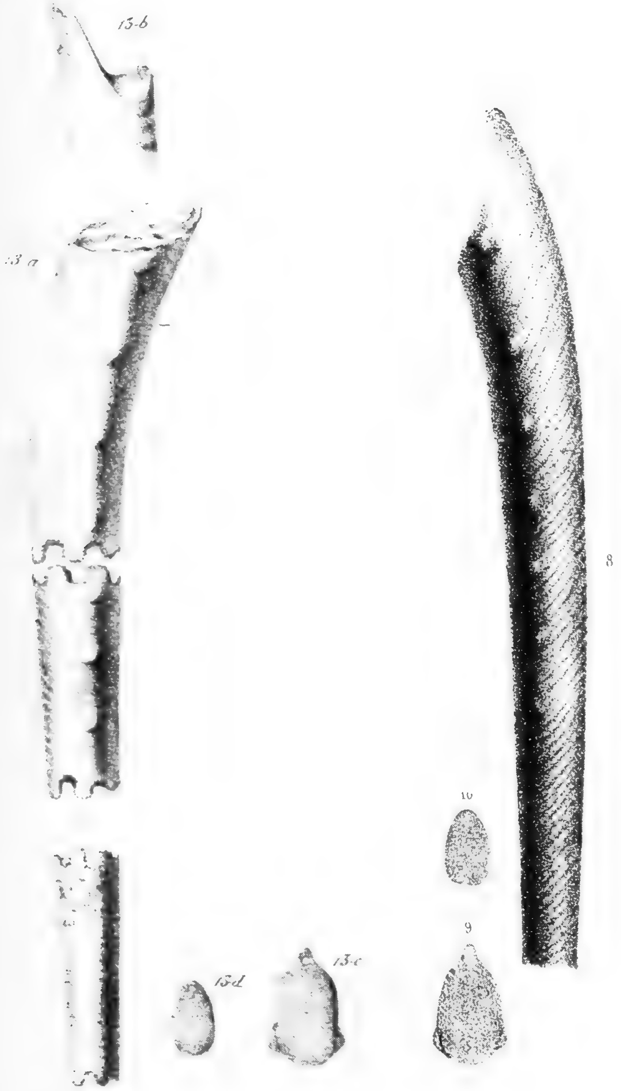

Fig. 56. *Baculites incurvatus* Dujardin, 1837. Numbers 13a–d: copy of Dujardin (1837, pl. 17 (figs 13a–d)). Numbers 8–10: copy of D'Orbigny (1842, pl. 139 (figs 8–10)). Note the apparent ventral keel in both figure 13c of Dujardin and figure 9 of D'Orbigny.

B. capensis, albeit at different times. Lateral ornament in the *B. codyensis* lineage first appears in the Lower Coniacian, whereas that of *B. capensis* occurs later, in the Middle or Upper Coniacian as shown by the Zululand and the Madagascan Mahagaga fauna.

C. European Region. Less easy to resolve are the relationship between the Indo-Pacific and the European nodose baculitids. In contrast to the Western Interior and the Indo-Pacific regions, baculitids are not as common in the European Tethys and are poorly preserved, and consequently the species are poorly known.

The relevant species are *B. incurvatus* Dujardin, 1837, and *B. brevicosta* Schlüter, 1876. The former name has, on occasions, been used indiscriminately for European *Baculites* with widely spaced nodes; the latter has been used for specimens with closely spaced, slightly oblique tubercles near the dorsolateral edge of the flanks.

Baculites incurvatus was recently reviewed by Immel *et al.* (1982), and Kennedy (1984), based on Austrian (Gosau) and French material respectively. Dujardin based this species on a series of fragments. The largest, a curved body chamber, was designated lectotype by Immel *et al.* (1982: 27). The lectotype (MNHP R1025a) and paralectotypes (MNHP R1025b–c (?e in WJK p. 143)) were refigured by Kennedy (1984, pl. 33 (figs 4–6, 15, 19–22)).

It is difficult to reconcile Dujardin's original figures (herein Fig. 56—13a–d) and descriptions on the one hand, and the type material on the other. Dujardin (1837: 232) gave the following diagnosis: 'Testa vaginaeformi, compresa, versus basim aliquantum incurvata; dorso nunc carinato, nunc rotundo, rugoso aut laevi, utrinque tuberculis evanescentibus instructa'. In his illustrations, two whorl sections are figured. The smaller (pl. 17 (fig. 13d)) is distinctly ovoid, but the larger (pl. 17 (fig. 13c)) shows distinct lateral sulci on either side of the venter, suggesting either a ventral keel, or a row of ventral (siphonal) tubercles—although the latter seems to be unlikely. If there were ventral tubercles on the body chamber, surely these would have shown up in the lateral view of the body chamber. The lectotype, MNHP R1025a, however, shows no trace whatsoever of a ventral keel.

Fig. 57 *(see facing page)*. *Baculites menabensis* Collignon, 1969. Plaster cast of the holotype, GD 12036, the original of Collignon (1969, pl. 518 (fig. 2036)) from the Lower Campanian of gisement 307, km 15 600 Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar. x 1.

Fig. 58 *(see overleaf)*. A–C. *Baculites falcatus* Collignon, 1969. Plaster cast of the holotype, GD 12045, the original of Collignon (1969, pl. 520 (fig. 2045)) from the Lower Campanian of gisement 303, km 15 000 Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar. D–F. *Baculites ventroplanus* Collignon, 1969. Plaster cast of the holotype, GD 12048, the original of Collignon (1969, pl. 520 (fig. 2048)) from the same locality as above. Both × 1.

Fig. 59 *(see overleaf)*. A–C. *Baculites antsirasiraensis* Collignon, 1969. Plaster cast of the holotype, GD 12040, the original of Collignon (1969, pl. 519 (fig. 2040)) from the Lower Campanian of gisement 304, km 15 200 Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina) Madagascar. D–F. *Baculites subtilis* Collignon, 1969. Plaster cast of the holotype, GD 12042, the original of Collignon (1969, pl. 519 (fig. 2042)) from the same locality as above. Both × 1.

Fig. 57

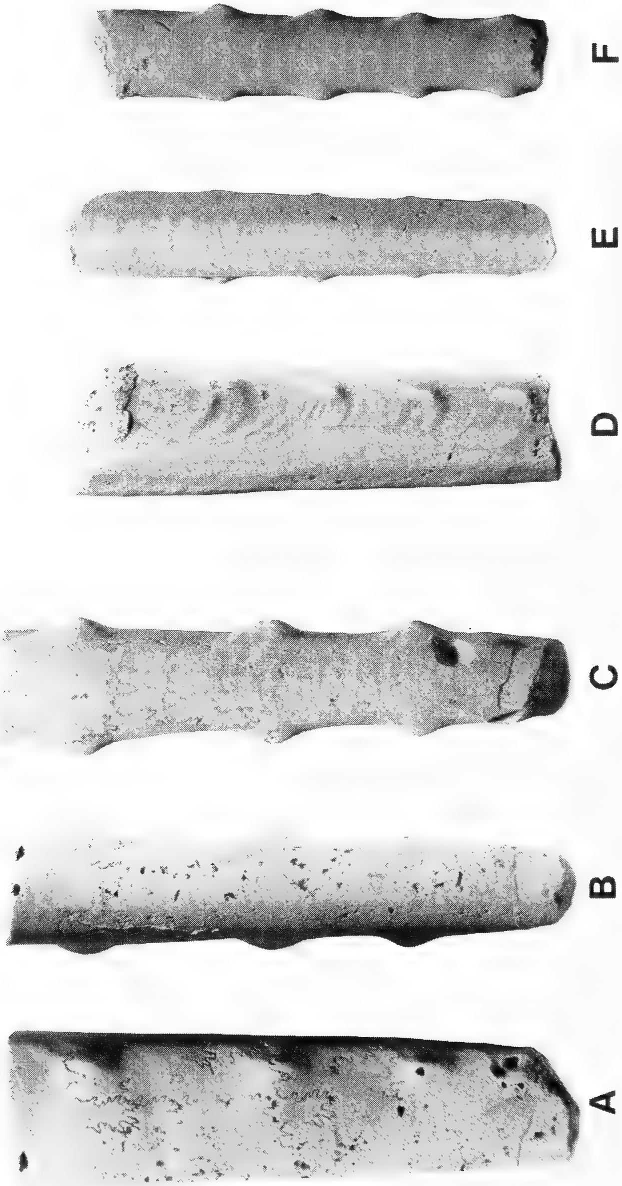

Fig. 58

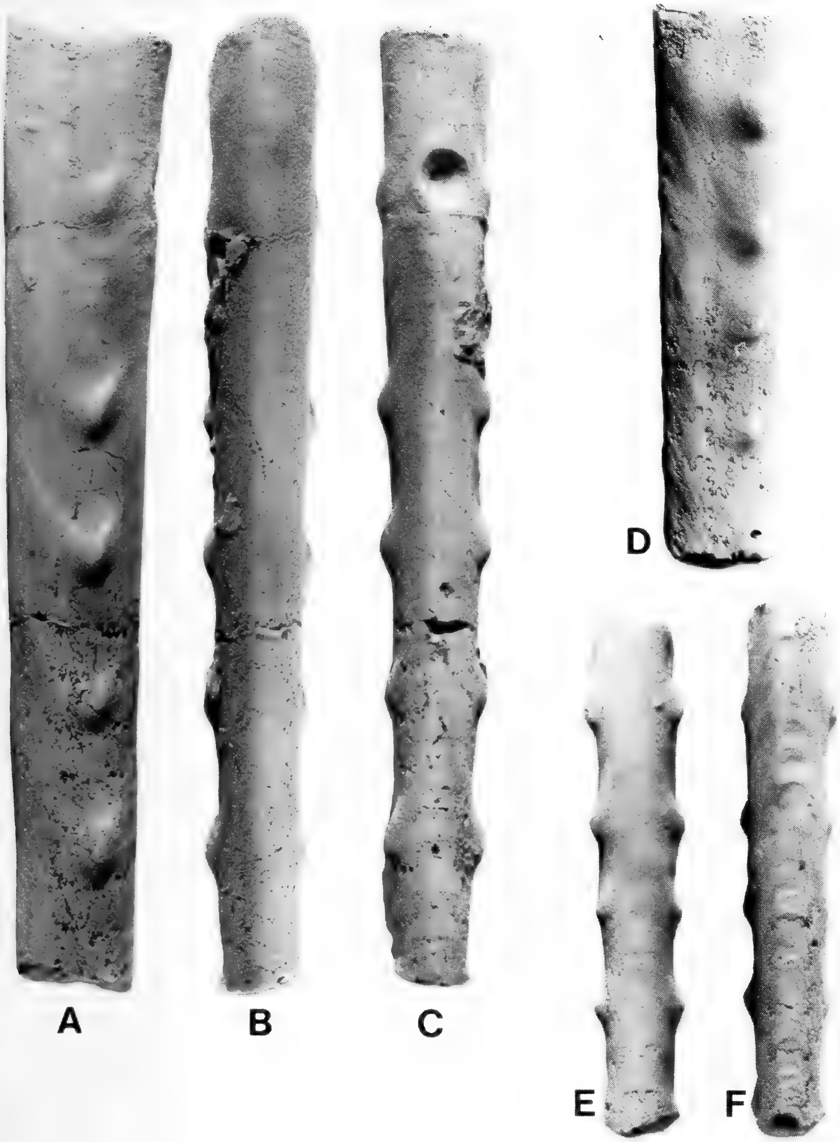

Fig. 59

Fig. 60. *Baculites sparsinodosus* Collignon, 1969. Plaster cast of the holotype, GD 12052, the original of Collignon (1969, pl. 521 (fig. 2052)) from the Lower Campanian of gisement 302, km 14 200, Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar. × 1.

D'Orbigny's (1842: 564, pl. 139 (figs 8–10)) (herein Fig. 56–8–10) subsequent description and illustration of *B. incurvatus* is better known than that of Dujardin. Again, D'Orbigny's figure shows a baculitid with a curved body chamber, and a whorl section that is ovoid on the phragmocone, but distinctly carinate on the body chamber. Two specimens in D'Orbigny's collection, presumably used in his reconstruction of *B. incurvatus*, survive and were refigured by Kennedy (1984, pl. 33 (figs 1–3, 16–18)). Neither shows any trace of a ventral keel. We suspect that D'Orbigny's figure of *B. incurvatus* may have been based more on Dujardin's original figures than on his own material.

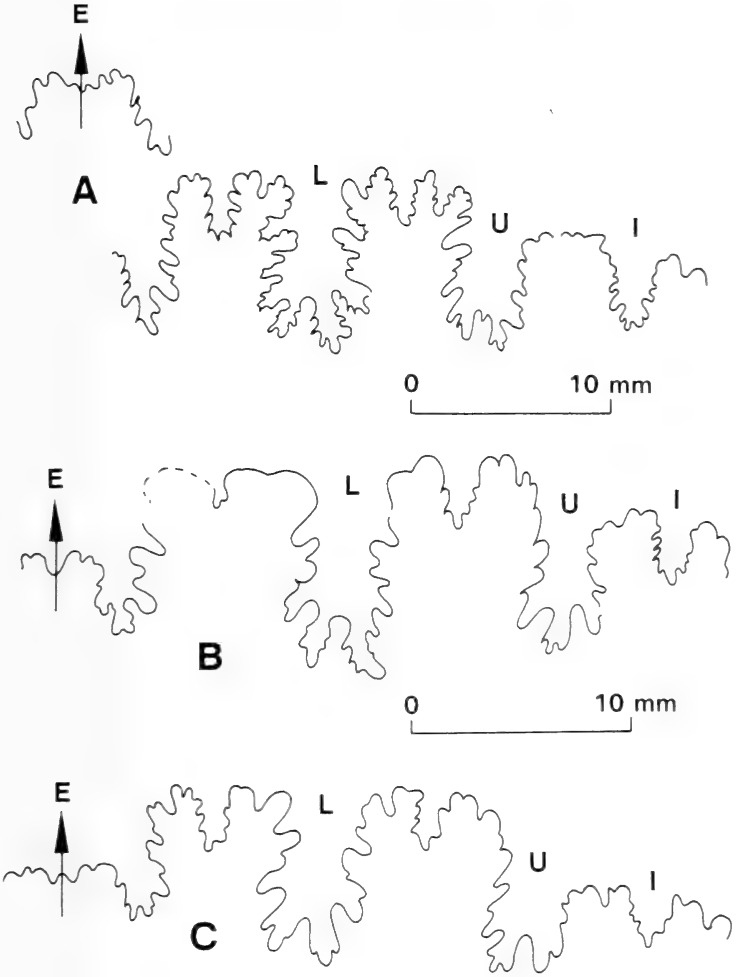

Fig. 61. Suture lines. A. *Baculites sparsinodosus*. Collignon, 1969 (see Fig. 60). B. *Baculites falcatus* Collignon, 1969 (see Fig. 58A–C). C. *Baculites subtilis* Collignon, 1969 (see Fig. 59D–F). Scale bar for size.

Subsequent interpretations of *B. incurvatus* are confused. Meek (1876: 392) divided the genus *Baculites* into two groups. His group b was defined as follows: '?b. Shell straight posteriorly, but with the non-septate part gently arcuate; aperture a little oblique; appendage of siphonal side of lip arching slightly with the general curvature of the non-septate part, but not curving over the aperture—(*B. incurvatus* Dujardin)'. Spath (1926: 80) subsequently introduced the new baculitid genus *Euhomaloceras* as follows: 'the new genus *Euhomaloceras* gen. nov. is proposed for Meek's group b (Invertebr. Cret. and Tert. Fossils, *U.S. Geol. Surv. Territ.*, vol. ix, 1876, p. 392) with *B. incurvatus*

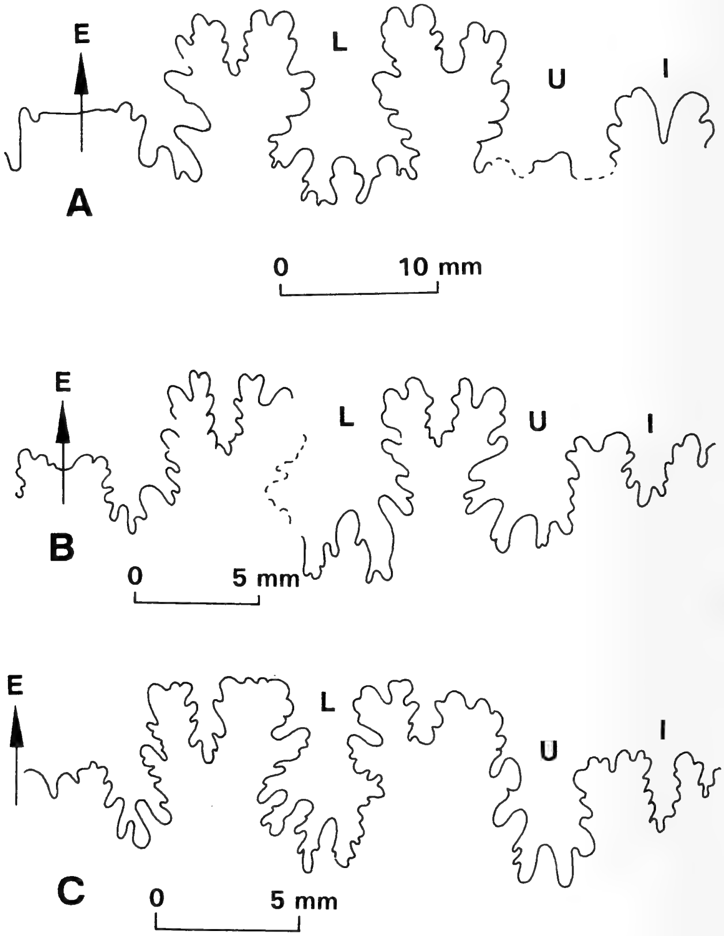

Fig. 62. Suture lines. A. *Baculites ambatryensis* Collignon, 1971 (see Fig. 128). B. *Baculites antsirasiraensis* Collignon, 1969 (see Fig. 59A–C). C. *Baculites menabensis* Collignon, 1969 (see Fig. 57). Scale bar for size.

Dujardin (in D'Orbigny, *Pal. Franc., Terr. Cret.*, vol. 1, 1842, p. 564, pl. 139 (fig. 8)) as genotype.' Spath's concept of *Euhomaloceras* is difficult to interpret. Both Dujardin and D'Orbigny's figures show a curved body-chamber, and it was this feature that defined Meek's group b; Meek did not refer to the whorl section at all. Wright (1957: L218) provided the first, and only diagnosis of *Euhomaloceras* as: 'Bodychamber gently curved with distinct rounded siphonal and laterodorsal tubercles.' The mention of siphonal tubercles is based on a misinterpretation of the cross section in the figures of Dujardin and D'Orbingy.

Fig. 63 *(see facing page)*. *Baculites sulcatus* Baily, 1855. A–B. BMNH C35625, the lectotype, and impression of paralectotype, from an unrecorded horizon at locality 1, Pondoland, Mzamba Formation—presumably from the upper parts of the section, Campanian ?I. × 5. Photograph courtesy of Natural History Museum, London.

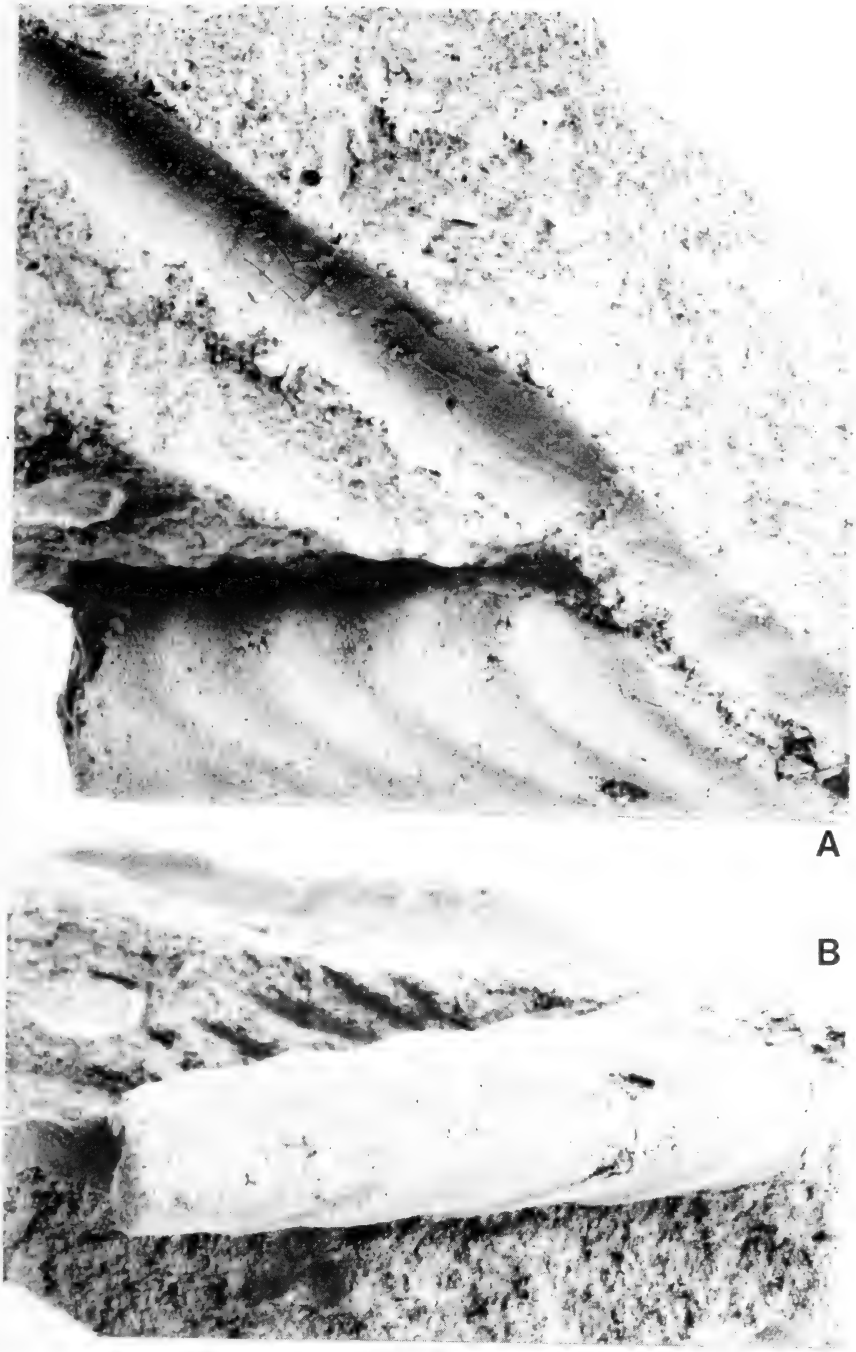

Fig. 63

Subsequent examination of *Baculites* has shown that curvature of the body chamber is a very variable and inconsistent feature, and is certainly not of generic significance. The name *Euhomaloceras* is thus unnecessary as discussed by Immel *et al.* (1982: 27–28).

As mentioned above, none of the surviving specimens on which Dujardin and D'Orbigny based their figures shows any indications of a ventral keel on the body chamber. Why both Dujardin and D'Orbigny figured a ventral keel on the body chamber of *B. incurvatus* remains a mystery. We suspect that Dujardin may have erred, and that D'Orbigny's artist merely copied the error.

In France, *B. incurvatus* first occurs in the Middle Coniacian in Touraine and Aquitaine, and persists through the Upper Coniacian into the Santonian, a stratigraphic range nearly identical to that of *B. capensis*. In Austria it occurs in the Lower Santonian.

Younger Campanian records of *B. incurvatus*, e.g. Holzapfel (1887: 64, pl. 4 (figs 5–6), pl. 5 (fig. 10)) from the Vaals Formation at Aachen, Germany; Müller & Wollemann (1906: 4, pl. 2 (figs 2–5)) from Braunschweig and Broitzem in northern Germany, and Collignon (1938: 88, pl. 6 (figs 4–5)) from the Campanian of Andimaka in Madagascar, are all probably misidentifications. The specimens referred to *B. incurvatus* by Holzapfel and Müller & Wollemann were considered the same as *Baculites* sp. 1 by Kennedy (1986*b*: 110, pl. 17 (figs 7–9, 13–15, 21–23), pl. 18 (figs 18–22), pl. 23 (figs 1, 7), text-fig. 8A–C), from the Upper Campanian of France. However, Müller & Wollemann's specimens show distinct longitudinally to obliquely elongated tubercles, whereas Kennedy's *Baculites* sp. 1 has transversely elongated tubercles. In this respect, the German specimens seem closer to some of the baculitids from the Lower Campanian of Madagascar described by Collignon (1969); all are probably synonyms of *B. menabensis* Collignon or *B. tanakae* Matsumoto & Obata, 1963, as discussed below (p. 109).

The Campanian *B. incurvatus* of Collignon (1938) has a distinct trigonal whorl section and is closer to *B. bassei* Besairie or *B. nibelae* sp. nov., to be described below.

Fig. 64 *(see facing page)*. *Baculites sulcatus* Baily, 1855. Typical forms. A. SAM–7043. Specimen on back of block with *Hauericeras* figured by Klinger & Kennedy (1980, fig. 5b), collected by T. Gevers from the top bed, T2. B–D. SAM–PCP5695. E–G. SAM–PCP5684. H–I. BMNH C35625, the lectotype. J. SAM–PCP8420. K. SAM–PCP8656. L–N. SAM–PCP5684. A–G, J–N, all from the top beds at Mzamba Cliff, Pondoland, Mzamba Formation, Campanian I. A–D, H–N × 1; E–G × 2.

Fig. 65 *(see overleaf)*. *Baculites sulcatus* Baily, 1855. All weakly ornamented forms. A–C. SAM– PCP8653. D–F. SAM–PCP8361. G–H. SAM–PCP8656. I–K. SAM–PCP8153b. L–N. SAM–PCP8422. O–Q. SAM–PCP8153. R. SAM–PCP8660. All from the upper beds at the type section of the Mzamba Formation, Campanian I. All × 1.

Fig. 66 *(see overleaf)*. *Baculites sulcatus* Baily, 1855. Early forms—Van Hoepen collection, Transvaal Museum. A–B. TM 540g. C–E. TM 548c. F. TM 540f. G–I. TM 548a (microconch with part of aperture preserved). J–L. TM 540a. M–O. TM 540b. O–P. TM 540d. All from an unspecified horizon at locality 1, Pondoland, Mzamba Formation, presumably below the level of typical forms figured in Figures 64–65. All × 1.

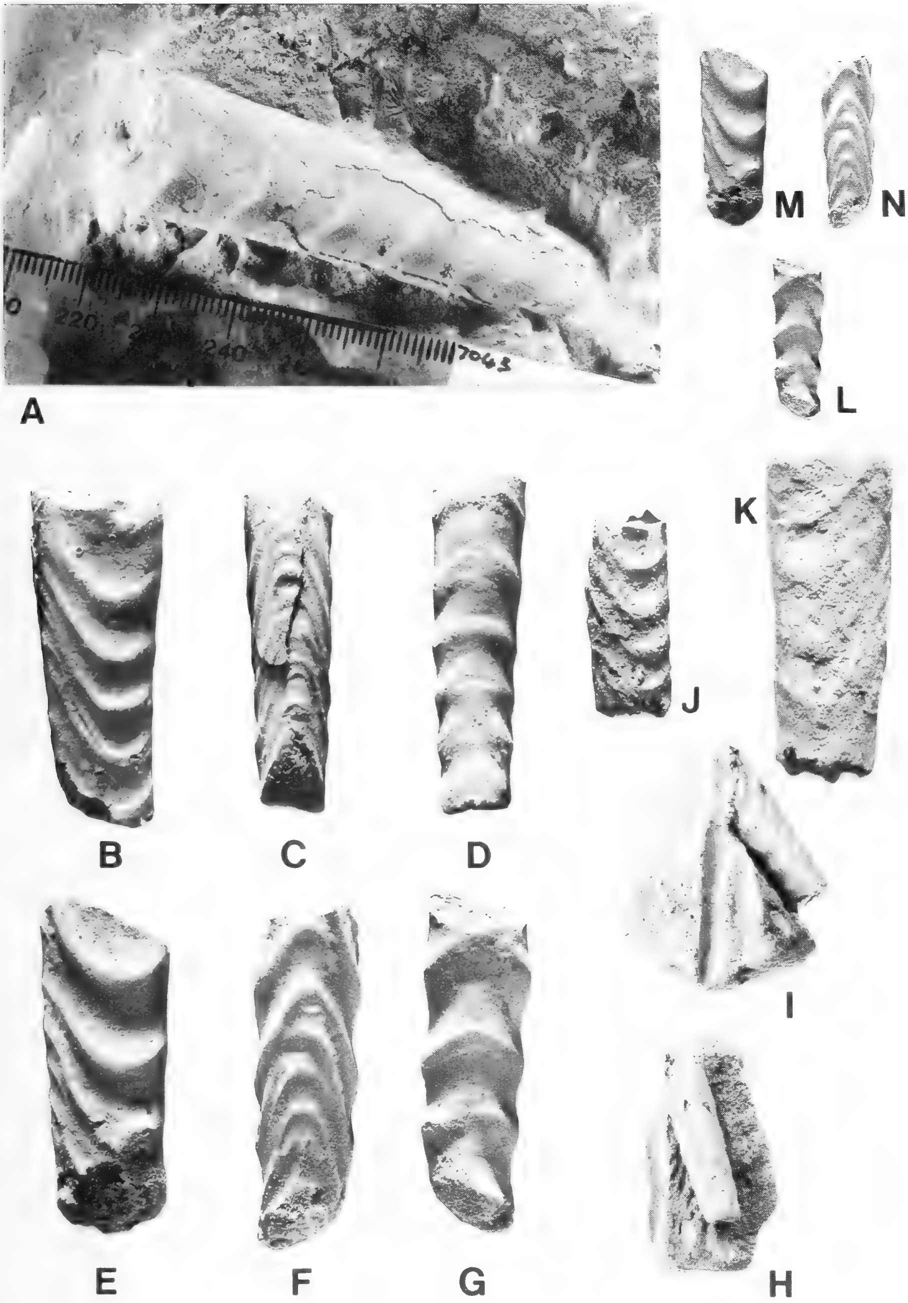

Fig. 64

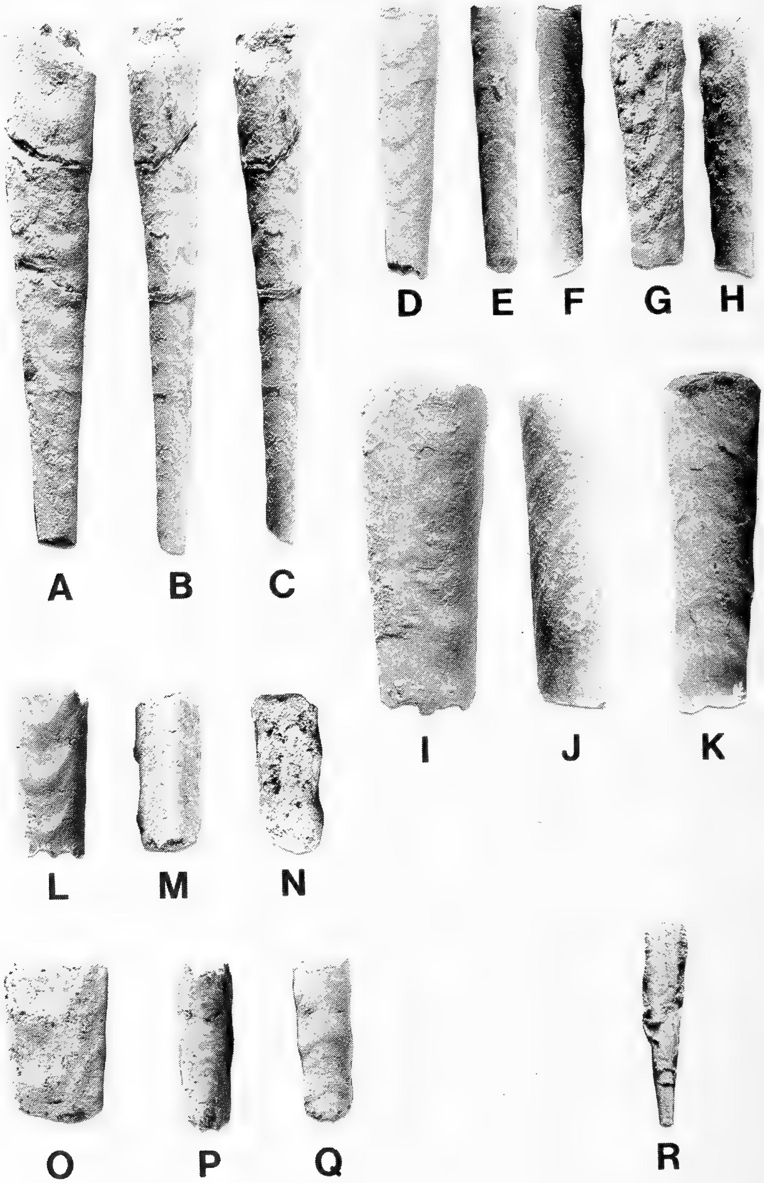

Fig. 65

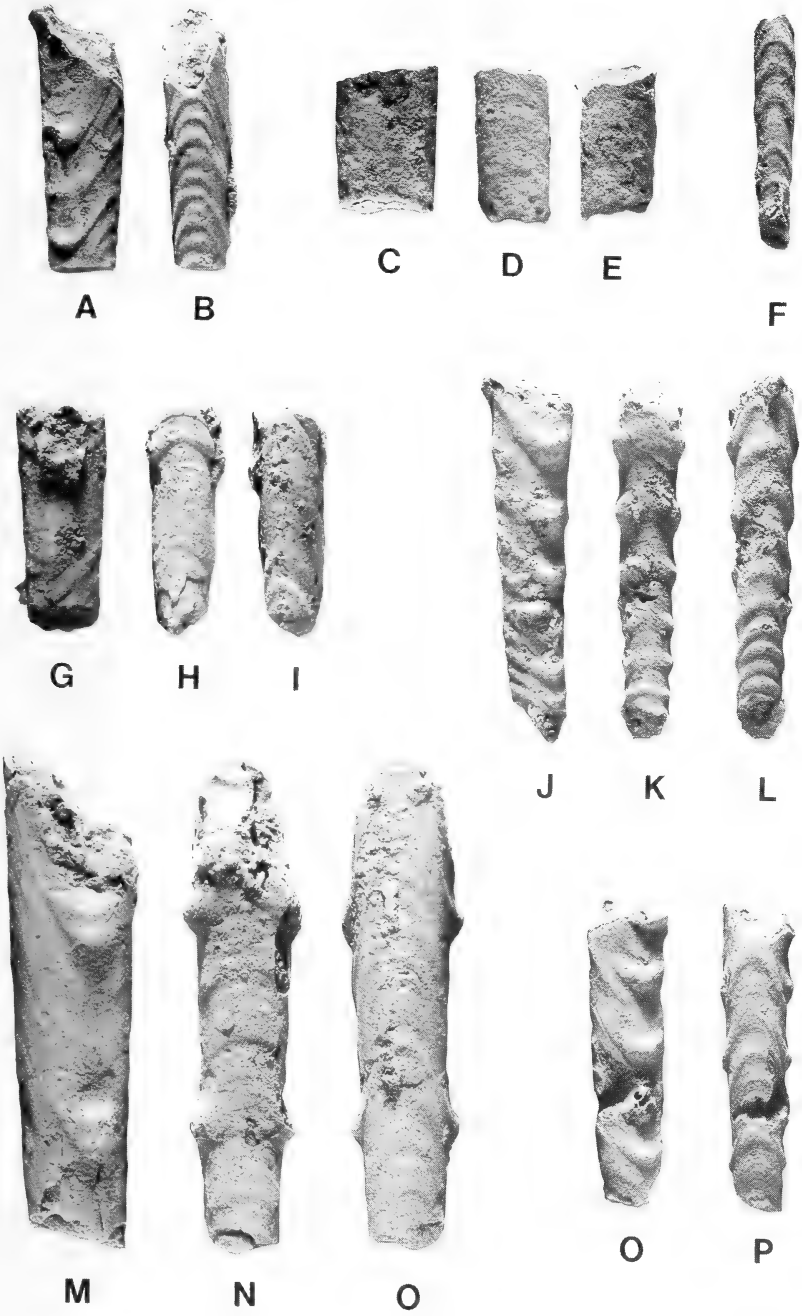

Fig. 66

It is difficult to distinguish satisfactorily between *B. capensis* and *B. incurvatus*. Curvature of the body chamber, initially used to separate *B. incurvatus* (as *Euhomaloceras*) from the other baculitids, is of little significance, and indeed is shown only by the lectotype and by one other specimen figured to date (Kennedy 1984, pl. 33 (figs 4–6, 7–9)). Curved and straight body chambers occur in both species; occurrence of curved body chambers is apparently random.

As Woods (1906: 342) had already noticed, typical *B. capensis* differs from *B. incurvatus* by the longitudinal elongation of the tubercles, and by the presence of a shallow sulcus at mid-flank. A single specimen of *B. incurvatus* figured by Kennedy (1984: 143, pl. 33 (12–14)) has doubled tubercles and a shallow lateral groove, which, apart from being smaller, is very similar to Collignon's (1966: 7, pl. 457 (fig. 1865)) *B. malagasyensis*, here regarded a synonym of *B. capensis* s.s. Apart from this specimen, which was regarded by Kennedy as possibly being pathologic, no specimens of *B. incurvatus* are as yet known with typical *B. capensis* ornament.

However, the majority of specimens of *B. capensis* with rounded, conical or slightly crescentic tubercles are indistinguishable from contemporary *B. incurvatus*.

Woods (1906: 342), Spath (1921: 257–258) and Matsumoto (1959: 125) all commented on minor differences in suture lines of *B. capensis* and *B. incurvatus*. We can see absolutely no significant difference between the sutures of *B. capensis* and *B. incurvatus* (Kennedy 1984, text-fig. 42F–H).

Immel *et al.* (1982: 28) also considered the whorl sections to be different—that of *B. capensis* being more elliptical, with wide venter and flat flanks. Again, typical forms of *B. capensis* do have elliptical whorl sections, but many have whorl sections indistinguishable from those of known *B. incurvatus* (see Figs 30, 31).

It is interesting to note that some specimens of *B. incurvatus* are virtually smooth and lack tubercles, and show a similar range of variation in this respect as *B. capensis*.

Clearly, on the basis of the disparate sizes in population of *B. capensis*—numbering several hundred specimens, and *B. incurvatus*—numbering perhaps 30 specimens, no final decision can be taken as to whether *B. capensis* should be regarded as a junior synonym of *B. incurvatus*. However, given their similar ages, but apparent geographic separation, it might eventually be feasible to regard them as a subspecies (of *B. incurvatus*).

Fig. 67 *(see facing page)*. A–D, H–N. *Baculites sulcatus* Baily, 1855. Early forms. Van Hoepen Collection, Transvaal Museum. Smooth to weakly ribbed specimens. A–B. TM548a. Microconch with aperture. C–D. TM548e. H–J. TM548d. Microconch with complete aperture. Note long, slightly inwardly-curved linguiform ventral rostrum and short, outwardly-curved dorsal rostrum. All from an unspecified horizon at locality 1, Pondoland, Mzamba Formation, presumably below the level of typical forms figured in Figure 64. E–G. *Baculites furcillatus* (Blanckenhorn, 1905). SAM–PCI8573 from the Campanian of Israel (ex Z. Lewy collection). K–Q. *Baculites bailyi* Woods, 1906. K–L. SAM–PCP6766. M. SAM–13103. Specimen from Geological Commission collection, one of Woods' paratypes of *B. bailyi*. N. SAM–PCP6765. O–Q. SAM–PCP8729, all from the basal beds at locality 1, Mzamba Formation, Santonian II. A–J, M × 1; K–L, N–Q × 2.

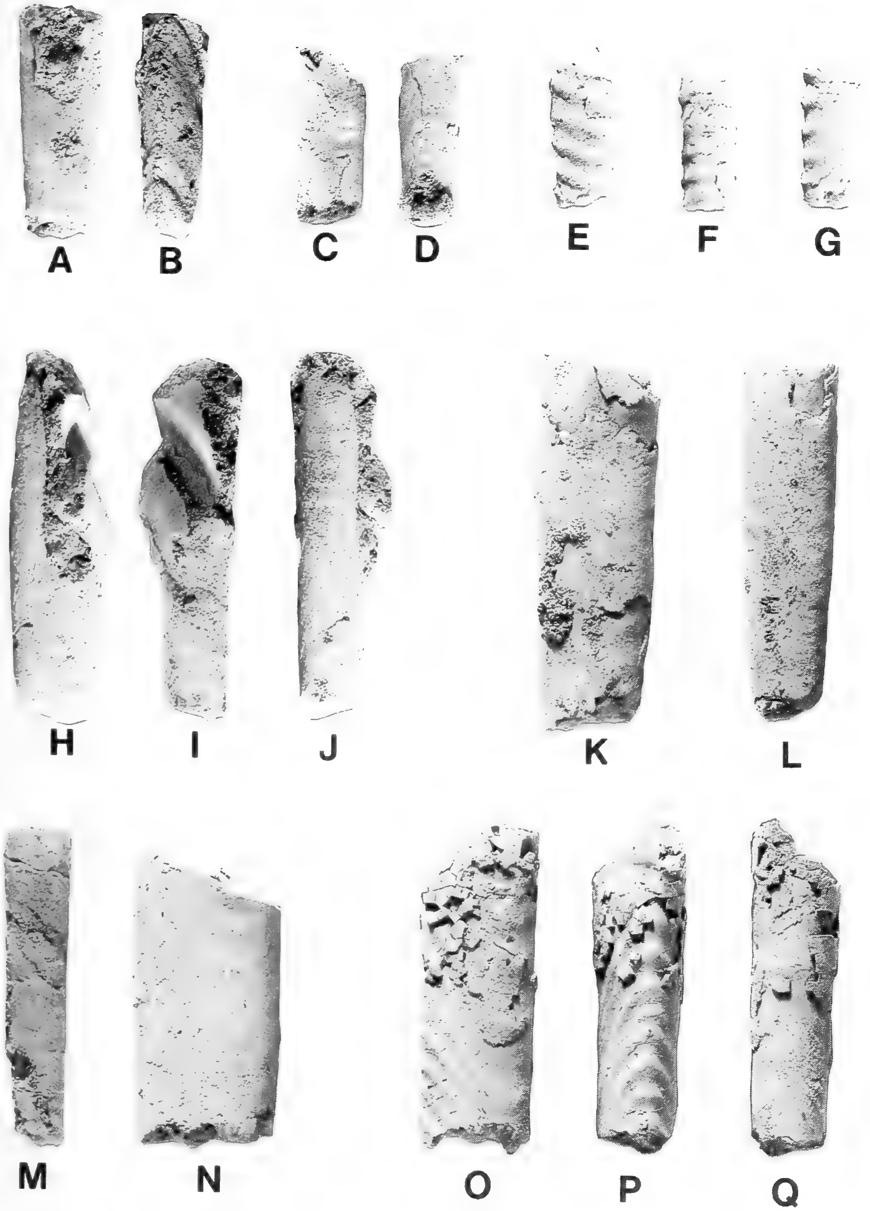

Fig. 67

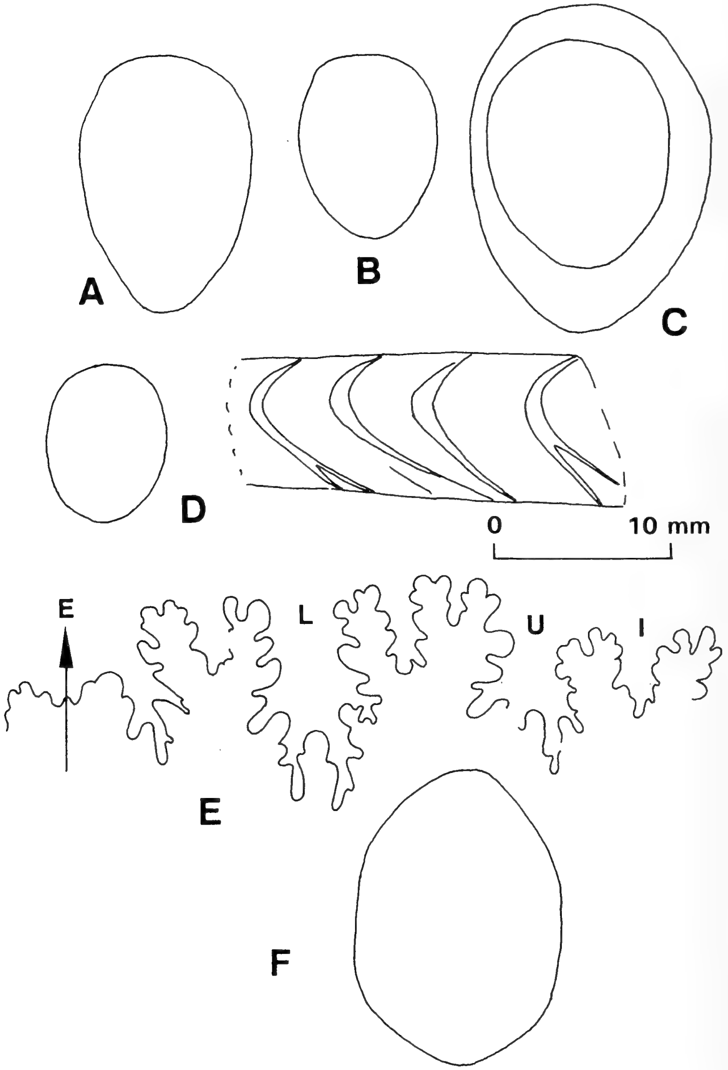

Fig. 68. *Baculites sulcatus* Baily, 1855. Typical form. Whorl sections, suture line and ornament. A. SAM-PCP8421. B. SAM-PCP8420. C. SAM-PCP5685. D. SAM-PCP5684. E. SAM-PCP8421. F. SAM-PCP8419. Venter in whorl sections pointing downward. Scale bar for size.

The other European baculitid that falls within the morphological limits of *B. capensis* is *B. brevicosta* Schlüter. Unfortunately, the only unequivocal record of this species is the original description from northern Germany given by Schlüter (1876: 141, pl. 39 (figs 9–10)). Schlüter based this species on several specimens (not just two as claimed incorrectly by Kennedy 1984: 146). The original of Schlüter (1876, pl. 39 (figs 9–10)) was designated lectotype by

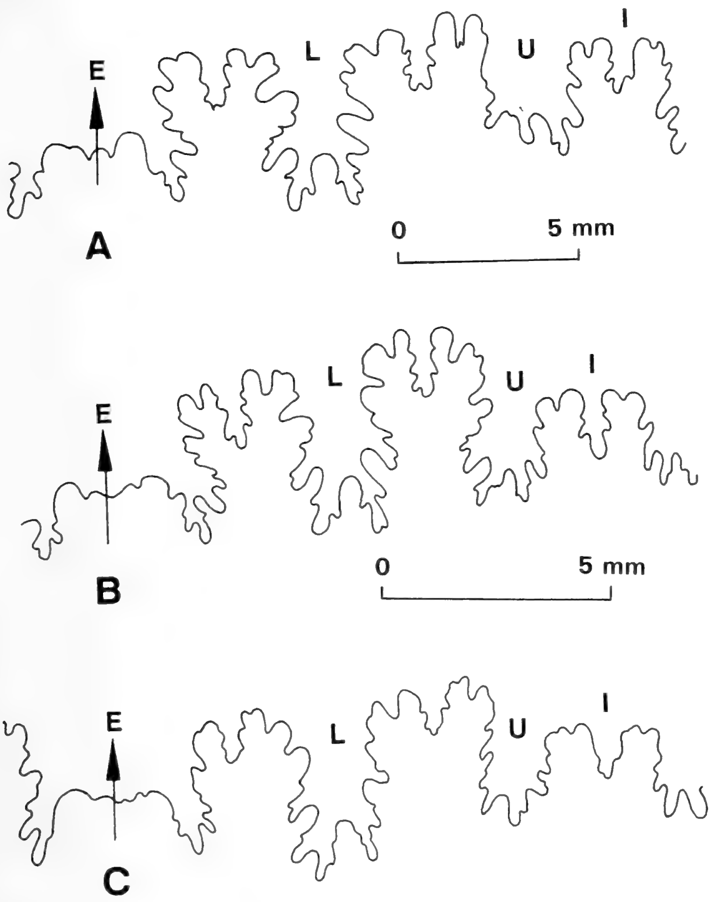

Fig. 69. *Baculites sulcatus* Baily, 1855. Typical form. Suture lines. A. SAM-PCP8152. B. SAM-PCP8153. C. SAM-PCP8661. Scale bar for size.

Kennedy (1984: 146). Unfortunately, neither the lectotype nor any of the other paralectotypes could be traced by us in the collections in Bonn, and we have to assume that they are lost.

Subsequent records of *B. brevicosta* all have to viewed with caution. The specimens from the Lower Senonian of Sweden (with *Actinocamax quadrata*) from Eriksdal, Sweden, described and figured by Moberg (1885: 37, pl. 4 (figs 5–6)) have very weak, crescentic lateral ribs, rather than dorsolaterally situated tubercles as in *B. brevicosta*, and they do not seem to belong to this species.

The specimens from Mkweyane (Umkwelane Hill), Zululand, described and figured by Spath (1921: 146, pl. 24 (fig. 5)) as *Baculites* cf. *brevicosta* are identical to Schlüter's figures, as also noted by Spath (1921: 260) 'since it probably only represents a variety of *B. capensis* . . . its exact agreement with Schlüter's species may be a case of heterochronous homoeomorphy'. The relationship of this (Zululand) specimen to typical *B. capensis* is probably the same as that of European *B. brevicosta* to *B. incurvatus*. Their relative stratigraphic occurrences in France (Kennedy 1984) seem to confirm this.

Kaplan & Kennedy (1994: 59, pl. 40 (figs 15–19)) described and figured alleged *B. brevicosta* from the Coniacian of Westphalia. These show some *B. brevicosta* to have distinct ventral ribbing and weak lateral ornament, which places it closer to *B. undulatus* than to *B. capensis*. Nevertheless, it is still a rare species and the extent of variation is not fully known.

A closer analogue to *B. brevicosta* is *B. schencki* Matsumoto, 1959, as discussed above (see p. 87). *Baculites schencki*, here regarded as an early form of *B. capensis*, was said to differ from *B. brevicosta* merely by the strength of the tubercles (Matsumoto 1959: 117). The association of *B. schencki* and *B. capensis* is the same as that of *B. brevicosta* and *B. incurvatus*, thus further suggesting that the relationship of *B. capensis* and *B. incurvatus* is very close, and that separation at subspecific level only is probably justifiable.

In Zululand and Pondoland, the typical *B. capensis* lineage ends in the Middle Santonian, although some atypical forms (form 11, *B. sparsinodosus*?) may occur in the Lower Campanian of Zululand. These last representatives include typical *B. capensis* forms with longitudinally elongated tubercles, with the middle part of the flanks flat or slightly depressed and with a round or fastigiate venter.

In Pondoland, *B. capensis* is succeeded by *B. sulcatus* in the Lower Campanian, and in Zululand by *B. increscens–B. vanhoepeni* in the Middle Campanian—both with typical rib-like or auricular lateral ornament. Morphologically these seem far removed from the *B. capensis* type of ornament.

Some of the baculitids from Pondoland, described as *B. sulcatus* by Van Hoepen (1921: 18, pl. 3 (figs 7–8)) and later referred to *Baculites vagina* var. *vanhoepeni* by Venzo (1936: 116 [58], pl. 10 [6] (figs 11–12)) (see Fig. 66), could possibly be seen as a link between *B. capensis* and *B. sulcatus* + *B. vanhoepeni* as is to be discussed below (p. 150).

Fortunately, Collignon (1969) has described a rich baculitid fauna from the Lower Campanian of Madagascar that seems to continue the *B. capensis* lineage. This fauna includes: *B. menabensis* Collignon (1969: 15, pl. 518 (figs 2036–7)) (herein Fig. 57); *B. antsirasiraensis* Collignon (1969: 18, pl. 519 (figs 2040–2041)) (herein Fig. 59A–C); *B. subtilis* Collignon (1969: 18, pl. 519 (figs 2043–2044)) (herein Fig. 59D–F); *B. falcatus* Collignon (1969: 20, pl. 520 (figs 2045–2046)) (herein Fig. 58A–C); *B. ventroplanus* Collignon (1969: 20, pl. 520 (figs 2048–2050)) (herein Fig. 58D–F) and *B. sparsinodosus* Collignon (1969: 23, pl. 521 (figs 2052–2054)) (herein Fig. 60). With the exception of *B. sparsinodosus*, all these species have dorsoventrally compressed, longitudinally elongated tubercles of the *B. capensis* type. They differ from typical *B. capensis* mainly in that the tubercles are more pinched, slightly oblique and situated nearer to the dorsum. Also, the whorl section becomes more compressed, and in some, e.g. *B. ventroplanus*, the venter becomes distinctly fastigiate. The ornament of these Lower Campanian Madagascan species is nearly identical to that of form 9 or *'umsinenensis'* type of *B. capensis*, which makes its first appearance in the Upper Coniacian of Zululand.

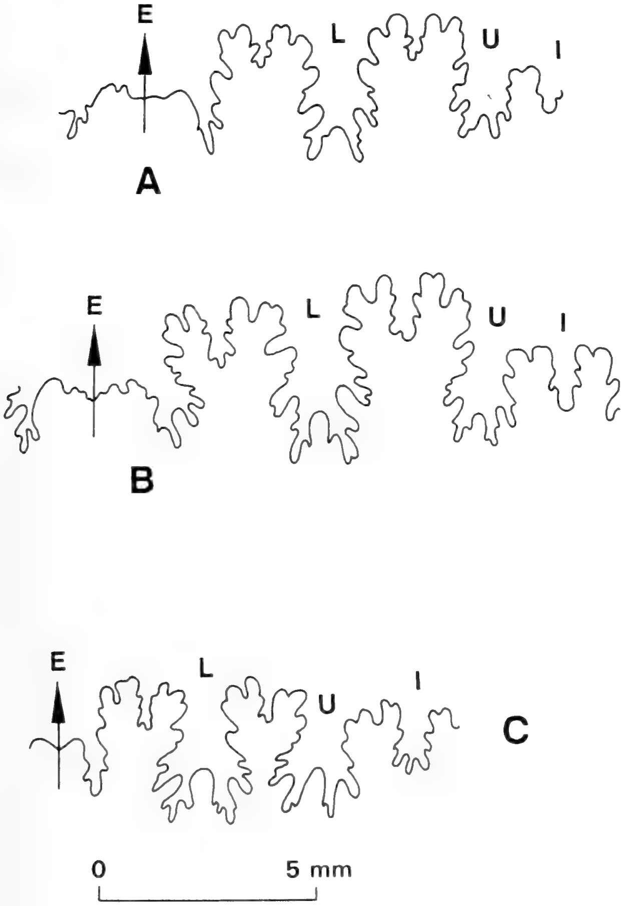

Fig. 70. *Baculites sulcatus* Baily, 1855. Suture lines. A. SAM-PCP12019. B. SAM-PCP8361. C. TM540m—note similarity to Woods' figured suture line of *B. bailyi* (1906, pl. 44 (fig. 5)). Scale bar for size.

With the possible exception of *B. sparsinodosus*, all these Lower Campanian Madagascan *Baculites* are probably synonyms; as first revising authors, we select *B. menabensis* as the name of this species.

As far as lateral ornament is concerned, Madagascan *B. menabensis* is indistinguishable from similarly dated specimens described as *B. incurvatus* from Braunschweig in Germany by Müller & Wollemann (1906: 4, pl. 2 (figs 2–5)) and the Vaals Formation on the Belgian–Dutch border by Holzapfel (1887: 64, pl. 4 (figs 5–6)). More and precisely located material is needed to resolve the true identity of these European specimens.

Baculites tanakae Matsumoto & Obata (1963: 51, pl. 13 (fig. 4), pl. 16 (figs 1–5), pl. 17 (figs 1–5), pl. 18 (figs 1, 3–4), pl. 19 (figs 1, 4), text-figs 97–113, 115)) from the Lower Campanian of Hokkaido is probably a senior synonym of *B. menabensis* as here interpreted. According to Matsumoto & Obata

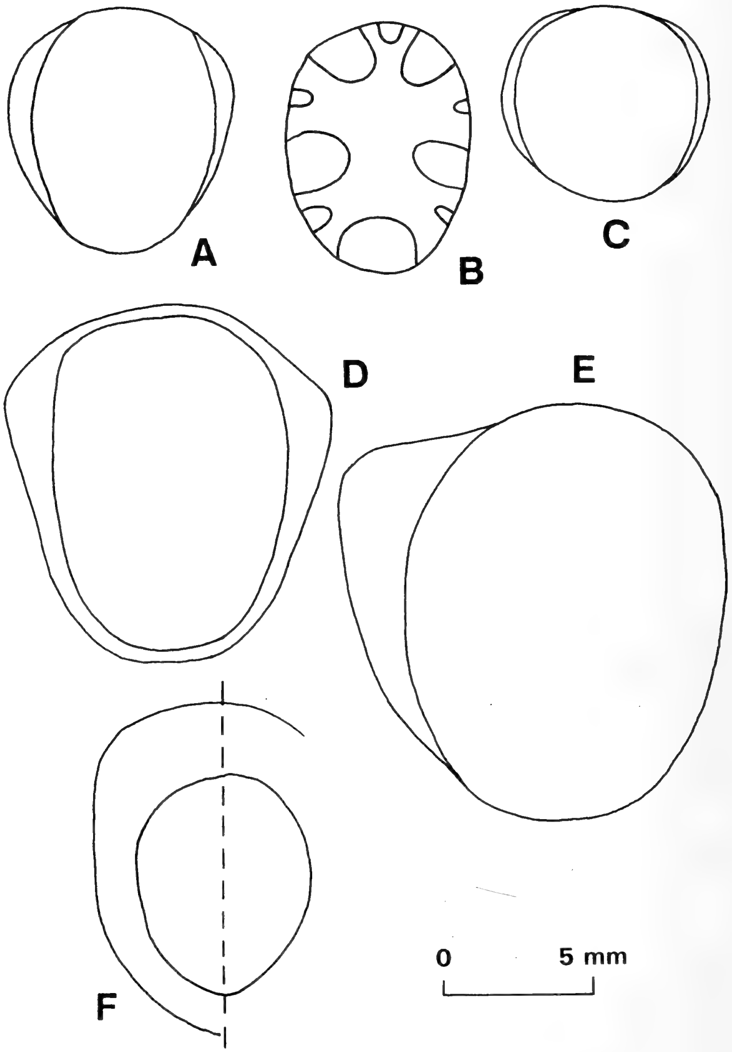

Fig. 71. *Baculites sulcatus* Baily, 1855. Early form. Whorl sections. A–B. TM 540g. C. TM 540h. D. TM 540a. E. TM 540b. F. TM 540c. Venter pointing downward. Scale bar for size.

(1963: 54), *B. tanakae* occurs above the beds with *B. capensis* in Hokkaido. The roof-shaped (fastigiate) venter and the shape of the tubercles that varies from 'asymmetrically crescentic or obliquely elongated to longitudinally elongated, as in *B. capensis*' (Matsumoto & Obata 1963: 52–53) in *B. tanakae* is identical to that of the Madagascan *B. menabensis*. We can see no valid grounds for maintaining *B. tanakae* and *B. menabensis* as separate species.

Baculites tanakae differs from *B. capensis* by the fastigiate venter, and the predominance of obliquely or longitudinally elongated tubercles that are situated higher up on the flanks than in typical *B. capensis*. As mentioned above, this style of ornament is very similar to that of form 9 or var. *'umsinenensis'* in *B. capensis*. This seems to indicate that the first appearance of *B. tanakae–B. menabensis* type of ornament already occurs in the Upper Coniacian, but that dominance of this type of ornament only takes place much later, in the Lower Campanian. Unfortunately, we have no records of *B. capensis* from the Upper Santonian of Pondoland or Zululand, but we suspect that in Hokkaido, where the species occurs throughout the Santonian, specimens with this type of ornament should be found. Alternatively, the occurrence of *'umsinenensis'* type of ornament has to be regarded as iterative; we cannot say for sure.

Occurrence

Mainly Middle Coniacian to Middle Santonian of Zululand, but possibly also Lower Campanian, and Upper Coniacian to Lower Santonian of Madagascar, Middle Santonian of Pondoland, Santonian of Hokkaido and California, Upper Santonian of U.S. Gulf Coast, and, doubtfully, Lower Campanian in Angola.

Baculites sulcatus Baily, 1855

Figs 63–66, 67A–D, H–N, 68–77, 78C

1855 *Baculites sulcatus* Baily, p. 457, pl. 11 (fig. 5c only, *non* 5a–b) (= *B. bailyi* Woods).
1906 *Baculites sulcatus* Baily; Woods, p. 341, pl. 44 (fig. 4).
1921 *Baculites sulcatus* Baily; van Hoepen, p. 18, pl. 3 (figs 7–8).
non 1921 *Baculites* sp. cf. *sulcatus* Baily; Spath, p. 260 (= *B. capensis* Woods).
1922 *Baculites sulcatus* Baily; Spath, p. 146.
? 1930 *Baculites Bailyi* Woods; Besairie, p. 223, pl. 21 (fig. 6 only).
non 1931 *Baculites sulcatus* Baily; Collignon, p. 36, pl. 5 (figs 3, 3a, 4, 4a, 5, 5a, 13, 13a), pl. 9 (fig. 15). (= *?B. yokoyamai* Tokunaga & Shimizu).
non 1963 *Baculites* n. sp. (?) aff. *B. sulcatus* Baily; Matsumoto & Obata, p. 46, pl. 12 (fig. 6), text-figs 94, 130.
1977 *Baculites sulcatus* Baily; Klinger & Kennedy, p. 75, figs 3B–E, J–L.

Type

Baily (1855) apparently based this species on more than one specimen—Woods (1906: 341) refers to (the) ' . . . only specimens seen are the types . . . .' Matsumoto & Obata (1963: 46) claimed that Woods did not designate a lectotype. They accordingly designated the specimen figured in ventral view by Baily (1855, pl. 11 (fig. 5c)) as lectotype. However, Woods (1906, pl. 44 (fig. 4)) referred to this same specimen (which he figured in lateral view) in the plate explanation as 'The Type, Museum of the Geological Society of London'. In our view, this is a perfectly valid lectotype designation.

The lectotype, in the collections of the Natural History Museum, London, BMNH C35625 from an unspecified horizon at the type section of the Mzamba Formation at Mzamba Cliff is here refigured as Figures 63A–B, 64H–I.

Material

In addition to the lectotype, we have SAM–PCP5684, 5686, 8152–8154, 8361a, 8419–8422, 8653–7, 8660, SAM–7043, all from Bed A15 at locality 1 (see Klinger & Kennedy, 1980 figs 1–2), Pondoland, Transkei, Mzamba Formation, Campanian I; NMB D1663 from, an unspecified horizon at the same locality. In addition, we also have examined the material collected by Van Hoepen in 1919 and described in 1921, in the collections of the Transvaal Museum, TM 540a–g, 548a–c, all from an unspecified horizon at this locality. Recent excavations for a car park at the Wild Coast Casino a few kilometres north of the Mzamba Estuary, have yielded additional specimens (Cooper collection, MRC 1–39).

Dimensions

Spec.	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Ri*
PCZ8660	4.0	5.7	0.7	1.5	1.6	0.9	27	15.2	—
PCZ8361	6.2	8.6	0.72	4.1	5.5	0.74	32	9.7	2.5
PCZ5684	6.9	8.7	0.79	5.3	7.4	0.72	17	7.6	2.5
PCZ8656	7.0	10.0	0.7	5.0	6.9	0.73	31	10.0	3
PCZ8654	7.0	9.0	0.78	4.7	6.4	0.73	23	11.3	3
PCZ8153a	7.6	10.2	0.76	6.5	8.1	0.8	19	11.0	2.5
PCZ8421	7.7	9.8	0.79	6.7	8.0	0.84	18	10.0	—
PCZ8152	8.7	12.5	0.7	7.4	10.6	0.7	19	10.0	2–3
PCZ8420	9.0	11.0	0.82	7.5	10.0	0.75	24	4.2	3
PCZ8422	9.0	14.0	0.64	8.8	12.4	0.71	16	10.0	2.5
PCZ8419	11.2	15.3	0.73	8.3	11.7	0.71	38	9.5	—
PCZ8153b	12.3	17.0	0.72	9.1	13.0	0.7	39	10.2	2.5
D1663	10.7	14.9	0.72	8.0	11.0	0.73	34	11.5	3
TM 540e	7.0	8.4	0.83	5.7	7.1	0.8	36	3.6	—
TM 540c	7.2	9.8	0.74	5.6	7.9	0.71	28	6.9	—
TM 540a	8.0	10.6	0.75	6.0	7.2	0.83	38	8.9	2
TM 540g	8.0	11.0	0.73	7.0	9.0	0.78	27	7.4	2
TM 540b	12.6	16.7	0.75	10.0	13.2	0.76	42	8.3	0.5
MRC 6	7.0	11.0	0.64	—	9.0	—	34	5.9	2
MRC 28	8.0	10.0	0.8	6.0	7.0	0.86	24	12.5	2.5
MRC 13	9.3	13.0	0.71	7.7	10.7	0.72	26	8.8	2
MRC 12	11.0	13.0	0.81	—	—	—	—	—	—
MRC 8	11.0	14.9	0.79	8.0	11.0	0.73	35	8.6	0.5
MRC 7	14.0	19.0	0.74	12.0	17.0	0.71	46	4.3	0
MRC 1	19.0	24.0	0.79	14.0	19.0	0.74	67	7.5	2.5

Description

Lectotype. The lectotype is a small individual, 22 mm long with a whorl height of approximately 7 mm, partially embedded in soft, green silty matrix

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Fig. 72 *(see facing page)*. *Baculites sulcatus* Baily, 1855. ?Late forms. A. MRC 24. B. MRC 6. C. MRC 9. D. MRC 18. E–F. MRC 17. G–H. MRC 7. Note slight curvature in A and E. All from excavation for new car park at Wild Coast Casino, Pondoland, Mzamba Formation, Campanian. All × 2.

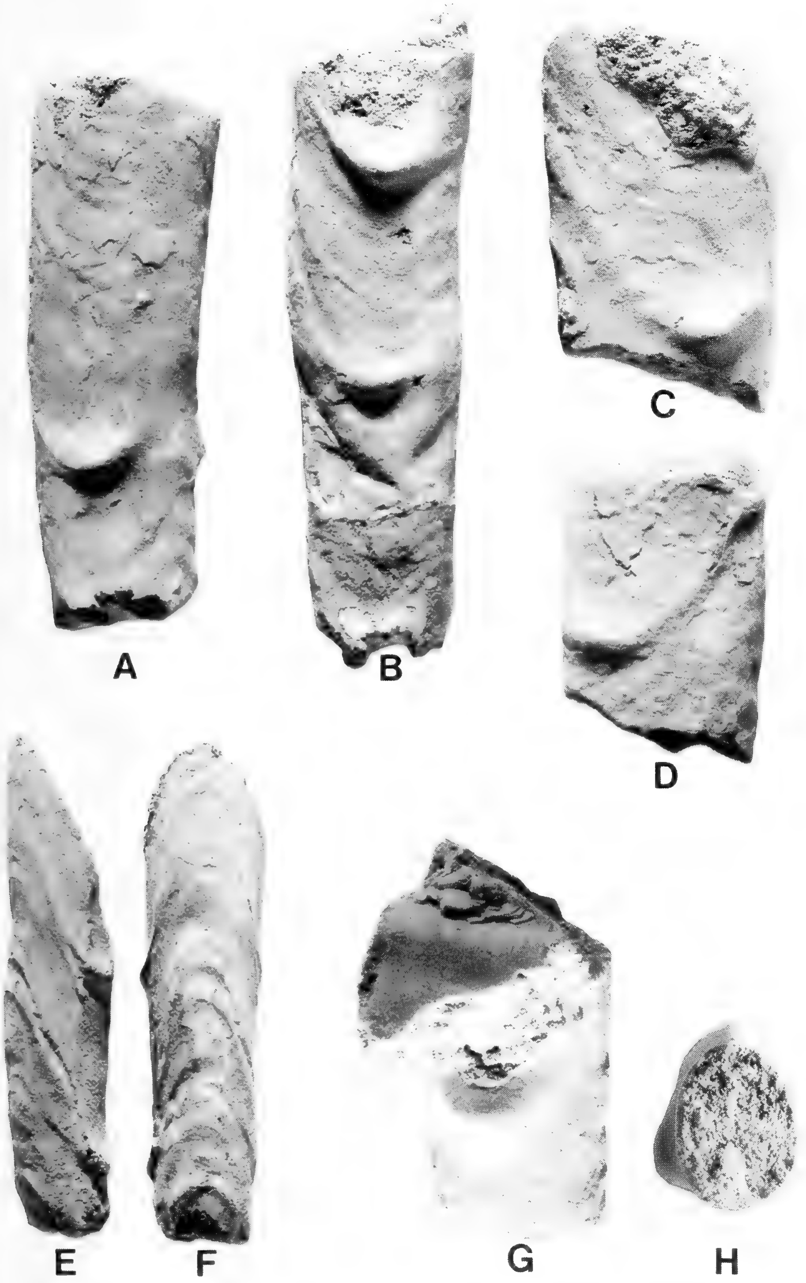

Fig. 72

(Figs 63, 64H–I). The main features are the strong lateral ornament. The ribs are crescentic, strongest on the dorsolateral part of the flanks, weaker on the lower half and sweep forwards over the venter, forming a distinct chevron. The impression of another (paralectotype) individual is present in the block of matrix.

Topotype material. The initial discovery of *B. sulcatus* by Capt. Garden was serendipitous. Detailed collecting by us yielded identical specimens only in the topmost beds at the Mzamba Cliff. However, the underlying beds are difficult to reach at this locality, and it is quite possible that *B. sulcatus* already occurs lower down in the section, probably above the Santonian–Campanian boundary. The following description is based on material from these topmost beds exposed at the Mzamba Cliff, collected by us and the late Prof. T. Gevers, respectively.

SAM–7043 is part of a concretion with a complete specimen of *Hauericeras* on the one side (Klinger & Kennedy 1980, fig. 5B), and a large body chamber and part of a phragmocone of *B. sulcatus* on the other side (Fig. 64A). The phragmocone fragment is identical to the lectotype, and we have no doubts in identifying *B. sulcatus* from this bed. Another phragmocone fragment from the same concretion, SAM–7043a shows the transition from the smooth to the laterally ribbed stage at a whorl height of 7.5 mm.

Ornament in the rest of the material varies considerably—from extremely robust, circumperipheral ribbing to virtually smooth. Ornament associated with typical *B. sulcatus* is shown in PCP5684 (Fig. 64E–G), PCP5695 (Fig. 64B–D) and PCP5684 (Fig. 64L–N), consisting of almost circumperipheral ribbing; ribs strongest on the dorsal half of the flanks, and, in sweeping forwards over the ventral half of the flanks, bifurcate or occur with intercalatories, forming distinct chevrons and loops over the venter (Fig. 68D). Dorsally the ribs weaken and curve broadly forward.

On the body chamber, as shown in SAM–7043 (Fig. 64A), ornament seems to weaken, especially on the ventral half of the flanks. Lateral ornament consists of two to three crescentic ribs per whorl height.

Other specimens have less prominent ornament, e.g. PCP8656 (Figs 64K, 65G–H), and only the upper half of the crescentic lateral ribs is visible and less prominent than in the above-mentioned specimens. D1663 (Fig. 76D–E), a body chamber fragment, also has very weak ribbing.

In the last group, e.g. PCP8361 (Fig. 65D–F) and PCP8653 (Fig. 65A–C), ornament is very faint. PCP8153b (Fig. 65I–K) is a body chamber fragment with part of the last septum preserved. Here, lateral ornament is practically absent and only visible under very oblique, low lighting.

Transvaal Museum, Van Hoepen collection. Van Hoepen (1921: 18, pl. 3 (figs 7–8)) described and figured as *B. sulcatus* part of a collection of 22 specimens. Unfortunately, we do not know exactly where in the Mzamba Cliff these specimens were collected. Judging by the preservation, we presume them to be

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Fig. 73 *(see facing page). Baculites sulcatus* Baily, 1855. ?Late forms. A–C. MRC 23. D. MRC 22. E. MRC 34. F–H. MRC 28. I. MRC 14. J. MRC 30. K. MRC 4. L. MRC 19. M. MRC 39. All from excavations for new car park at Wild Coast Casino, Pondoland, Mzamba Formation, Campanian. All × 2.

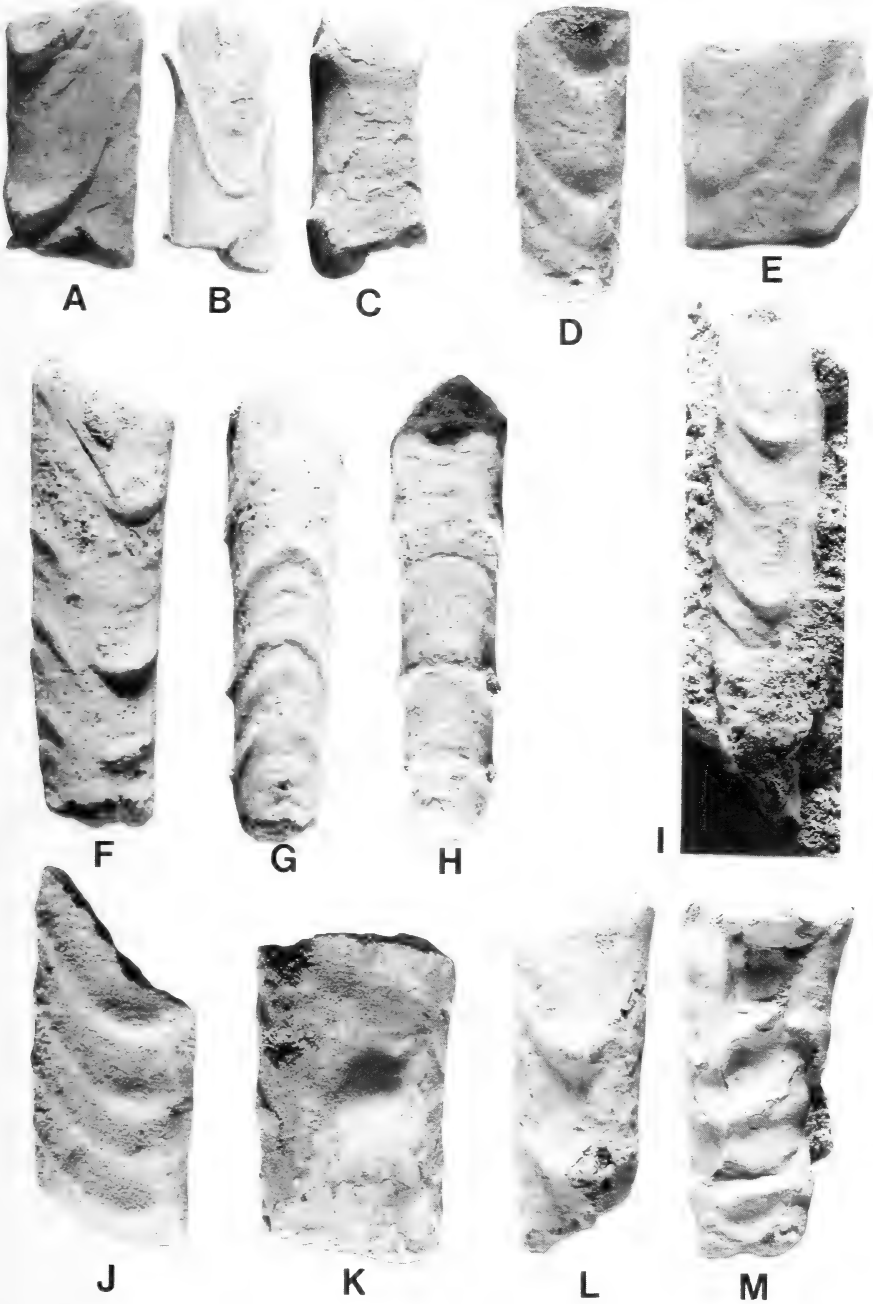

Fig. 73

from below the topmost beds with typical *B. sulcatus*, but also well above the basal beds with *B. capensis*. These specimens differ from typical *B. sulcatus* mainly in that the lateral ribs form a more or less distinct tubercle on the dorsal half of the flanks. In addition, in some of these specimens the whorl section appears to be more elliptical, with the venter as wide as the dorsum and with parallel flanks, reminiscent of *B. capensis* rather than ovoid as in typical *B. sulcatus*.

However, as in typical *B. sulcatus* described above, strength and presence of ornament is extremely variable. TM 540a (Fig. 66J–L) and TM 540d (Fig. 66O–P) have extremely strong ornament; that of TM 540g (Fig. 66A–B) is much weaker, whereas TM 540e, TM 548a (Fig. 66G–I) and TM 548e (Fig. 67C–D) are all practically smooth, save for ventral ribbing. TM 548c (Fig. 67E–G) and TM 548d (Fig. 67H–J) are completely smooth. TM 548d (Fig. 67H–J) and TM 548a (Fig. 66G–I) have parts of the aperture preserved. This consists of a prominent dorsal rostrum, raised by a slight step, a very deep lateral sinus, and a very prominent and long, spoon-shaped ventral rostrum. Part of another aperture is preserved in TM 548b. These are all microconchs. TM 540b (Fig. 66M–O), a body chamber, is a macroconch.

The suture lines of several specimens are exposed, e.g. Figs 68E, 69A–C, 70A–C. These show some variation, but the saddles and lobes are distinctly more incised and complex than those of *B. capensis;* in some, the bases of the saddles and lobes are slightly constricted, resulting in a subtriangular shape. The suture of one of the specimens, TM 540m (Fig. 70C), has rather narrow saddles and resembles the suture of *B. bailyi*—as figured by Woods (1906, pl. 44 (fig. 5)) and as mentioned above (p. 41).

Material from excavations at the Wild Coast Casino. Excavations for a new car park at the Wild Coast Casino, north of the Mzamba River estuary, yielded—amongst others—numerous baculitids best referable to *B. sulcatus*. Again, ornament is quite variable, but in the majority of specimens consists of distinct, widely spaced, crescentic ribs. These are strongest on the upper part of the flanks, decrease in strength and width ventrally, and often cross the venter as distinct lirae. In addition to these latter, intercalatory ribs or lirae may cross the venter, some branching near the venter, forming distinct looped chevrons over the venter (Figs 72–75, 76A–C).

In a few specimens, e.g. MRC 39 (Fig. 73), lateral ornament is as strong as in typical *B. sulcatus*. In another group of about five specimens, lateral ornament consists of obliquely elongated tubercles and ventral ribs, e.g. MRC 12 (Fig. 75A–C), MRC 9, and MRC 4 (Fig. 73K). In others, e.g. MRC 24 (Fig. 72A), MRC 6 (Fig. 72B), MRC 20 (Fig. 74A) and MRC 16 (Fig. 74F), lateral ornament consists of auricular, dorsolateral tubercles, projected ventrally into ribs of variable strength. In a few specimens, e.g. MRC 35 (Fig. 74G), ornament is completely absent.

Fig. 74 *(see facing page)*. *Baculites sulcatus* Baily, 1855. ?Late form. A. MRC 20. B. MRC 25. C. MRC 1a. D. MRC 13. E. MRC 38. F. MRC 16. G. MRC 35. All from excavations for new car park at Wild Coast Casino, Pondoland, Mzamba Formation, Campanian. All × 2, except C × 1.

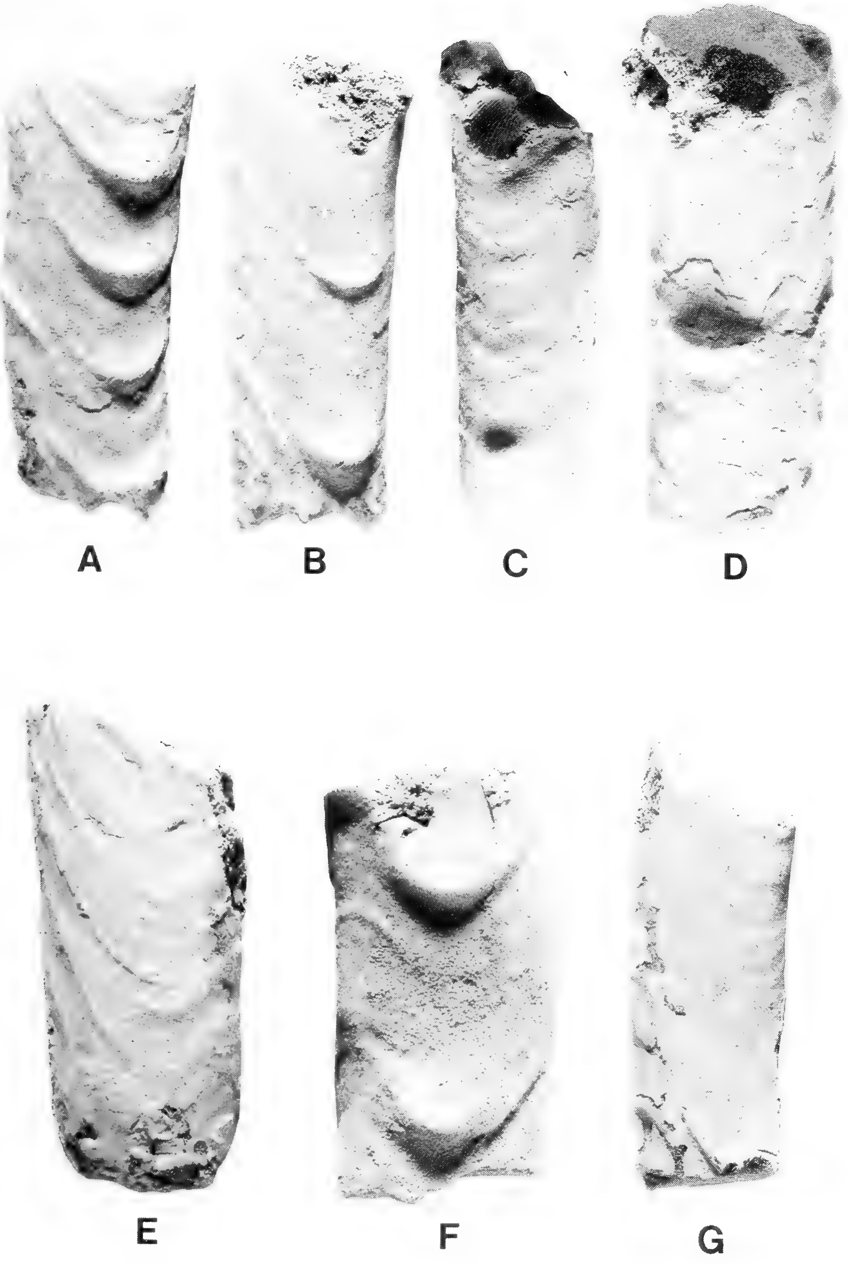

Fig. 74

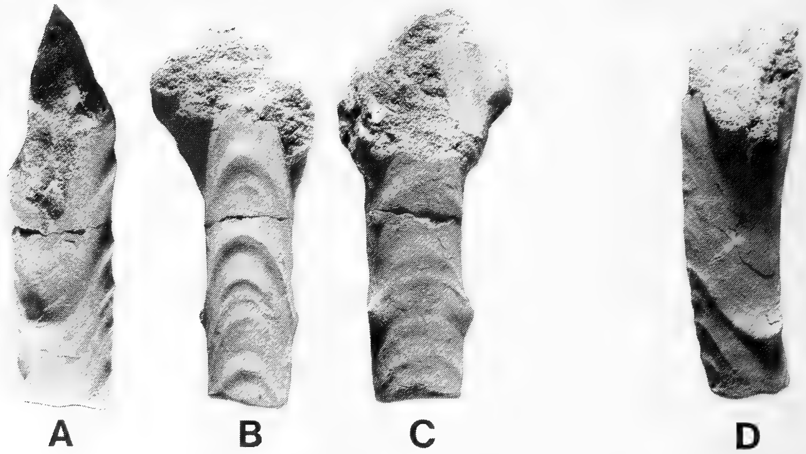

Fig. 75. *Baculites sulcatus* Baily, 1855. ?Late form. A–C. MRC 12. D. MRC 8, body chamber specimen with aperture. Note distinct curvature of latter. Both from excavations for new car park at Wild Coast Casino, Pondoland, Mzamba Formation, Campanian. All × 1.

Two nearly complete apertures are preserved: MRC 1 (Fig. 76A–C) and MRC 2 at maximum whorl heights of 20 mm and 24 mm, respectively. Most of the specimens show a slight to pronounced curvature on the body chamber, e.g. MRC 32, 33, 8 (Fig. 75D), MRC 24 (Fig. 72A), MRC 25 (Fig. 74B), MRC 2, MRC 13, MRC 20 and MRC 1 (Fig. 76A–C). At first we thought that this was due to diagenetic deformation, but it seems to be a primary feature. In others, however, e.g. MRC 12 (Fig. 75A–C), the body chamber is perfectly straight.

For descriptive purposes, the specimens in the Transvaal Museum may be regarded as early forms of *B. sulcatus*; those from the top of Mzamba cliff as typical forms, and those from the Casino site as ?late *B. sulcatus*.

The suture lines and whorl sections of the latter are shown in Figure 77.

Discussion

Klinger & Kennedy (1977: 76) mentioned that *B. sulcatus* was a relatively rare and poorly understood species. So far it is only definitely known from the Campanian of the Mzamba Formation in Pondoland and from borehole material in Richards Bay, Zululand. As yet, we have not found typical *B. sulcatus* in outcrop in Zululand. Reports of *B. sulcatus* from Zululand (Mkweyane (Umkwelane Hill)) by Spath (1921: 260) are incorrect; these are smooth forms of *B. capensis*. Records of *B. sulcatus* from Madagascar (Collignon 1931: 36, pl. 5 (figs 3–5, 13), pl. 9 (fig. 15)) are also wrong. These Madagascan specimens are of late Coniacian age and probably variants of *B. besairiei* (= *B. yokoyamai*).

We (Klinger & Kennedy 1975: 280) initially thought that *B. vanhoepeni* Venzo, best known from Zululand, was a synonym of *B. sulcatus*. Indeed,

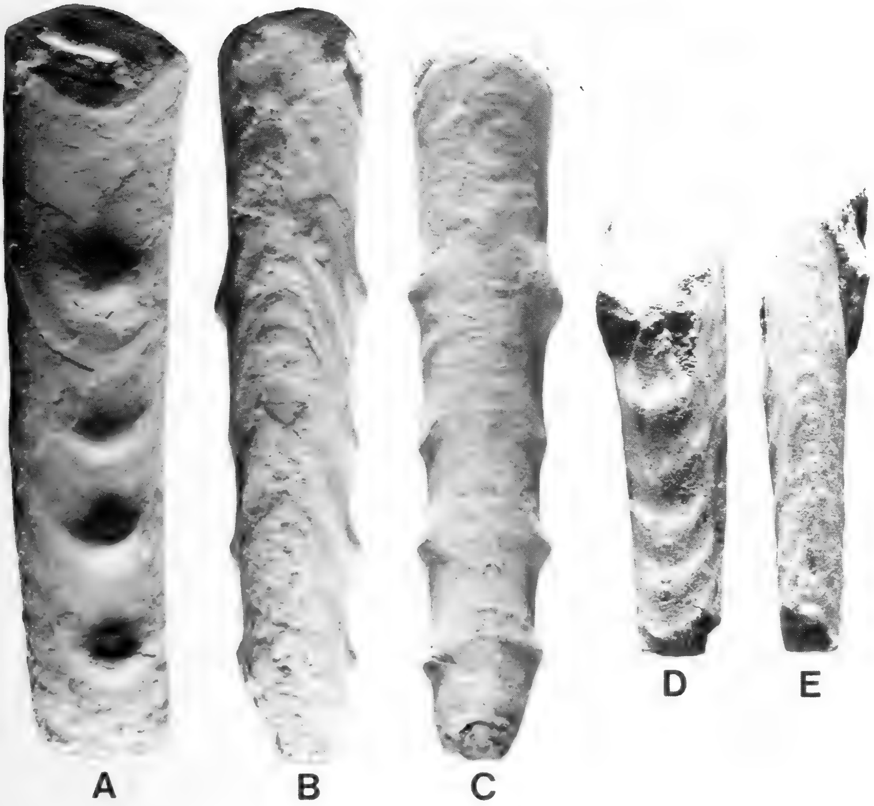

Fig. 76. *Baculites sulcatus* Baily, 1855. A–C. ?Late form. MRC 1, from excavations for car park at Wild Coast Casino, Pondoland, Mzamba Formation, Campanian. D–E. NMB D1663, ex Van Hoepen collection. Typical form from an unrecorded horizon at locality 1, Pondoland, Mzamba Formation, Campanian. Both × 1.

Venzo (1936: 116 [58]) included the specimens described by Van Hoepen (1921: 18, pl. 3 (figs 7–8)) as *B. sulcatus* in the synonymy of *B. vanhoepeni*. Part of the problem in distinguishing between these two species lies in the disparate sizes. Almost all our specimens of *B. sulcatus* are small whereas nearly all our specimens of *B. vanhoepeni* are large. Very few specimens of both species are of equal size for comparison. Small specimens of *B. vanhoepeni*, e.g. Figure 109H, show lateral ornament comparable to that of typical forms of *B. sulcatus*, but none shows as strong ventral or dorsal ribbing as in typical *B. sulcatus*. Adult forms are easily distinguished: *B. vanhoepeni* has typical widely spaced, auricular, lateral tubercles and grows to much larger size than any known *B. sulcatus*. Lateral ornament in typical *B. vanhoepeni* is very similar to that of ?late *B. sulcatus*, but again, none of these late forms of

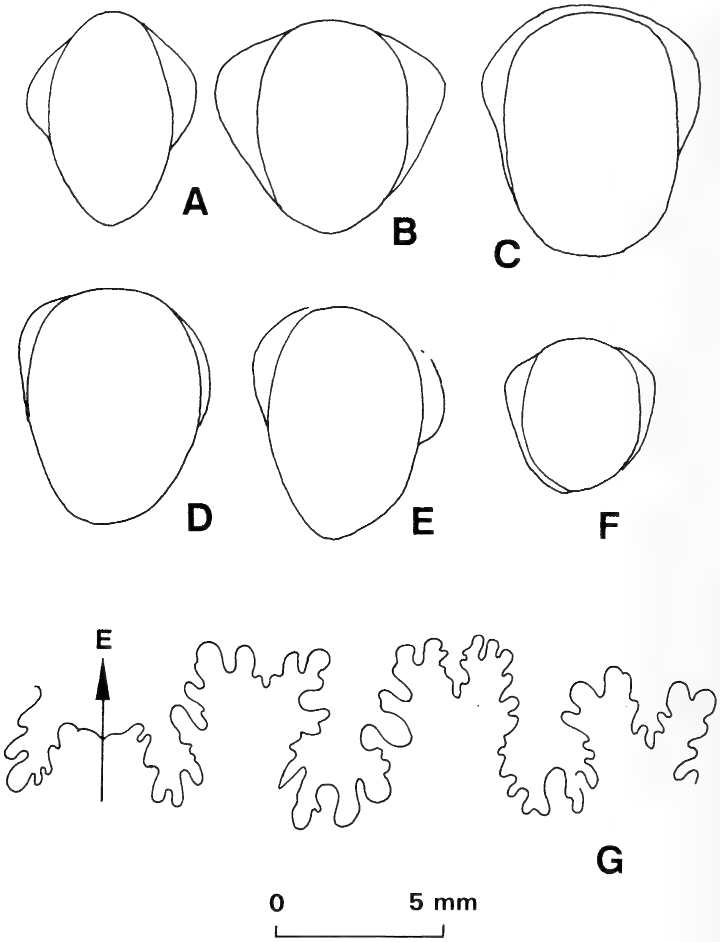

Fig. 77. *Baculites sulcatus* Baily, 1855. ?Late form. Whorl sections and suture line. A–B. MRC 7. C. MRC 6. D. MRC 3. E. MRC 21. F. MRC 23. E. MRC 20. Venter in whorl sections pointing downward. Scale bar for size.

B. sulcatus grows to as large a size as *B. vanhoepeni*, nor is ornament ever as prominent. Also, the two species appear to differ in age: *B. sulcatus* appears restricted to the Lower Campanian, whereas *B. vanhoepeni* is a typical Middle or even partly Upper Campanian species, occurring in association with *Australiella* and *Menabites*.

The origins of *B. sulcatus* are not quite clear. The early forms of *B. sulcatus*, with distinct lateral nodes and elliptical whorl section, are very reminiscent of *B. capensis*. The occurrence of the latter in the basal beds of the Mzamba Formation would support the derivation of *B. sulcatus* from *B. capensis*. It is possible that the transition from *B. capensis* to *B. sulcatus* took place via some of the forms described from the Lower Campanian of

Madagascar by Collignon (1969)—as *B.* cf. *tanakae* (Collignon 1969: 23, pl. 521 (fig. 2055)) or *B. sparsinodosus* Collignon (Collignon 1969: 23, pl. 521 (figs 2056–8 only)), with crescentic dorsolateral tubercles.

Looking at typical forms of *B. sulcatus*, however, especially the weakly ornamented forms, it would alternatively seem possible to derive the former from late forms of *B. bailyi*. Some specimens of *B. bailyi* from the basal beds of the Mzamba Formation, e.g. SAM-PCP8729 (Fig. 67O–Q), look remarkably like weakly ornamented *B. sulcatus*.

The specimens of ?late *B. sulcatus* from the Casino excavations bear a striking resemblance to an Upper Santonian baculitid fauna recently described from the U.S. Gulf Coast region by Kennedy & Cobban (1991*b*) as *B. capensis* and *Boehmoceras arculus*. Kennedy & Cobban used the name *B. capensis* (1991*b*: 182, figs 6: 4, 8: 1–8; 10: 7–10, 12–14; 12: 2.5) for straight baculites with dorsolateral nodes, and *Boehmoceras arculus* (1991*b*: 182, figs 6: 2, 8; 8: 9–15, 18–22; 9: 1–2, 11–52; 10: 20–21, 24–26; 12: 3) (a senior synonym of *Boehmoceras loescheri* Riedel, 1931) for predominantly curved specimens with distinct, crescentic to auricular lateral bullae that extend across the dorsolateral half to two thirds of the flanks.

As far as lateral ornament is concerned, the Pondoland specimens are indistinguishable from the Gulf Coast material. MRC 1 (Fig. 76A–C) or MRC 8 (Fig. 75D) are indistinguishable from specimens assigned to *B. arculus* by Kennedy & Cobban (1991*b*, fig. 9: 50–52 or fig. 9: 46), but none of our specimens has as distinct curvature as the Gulf Coast material to merit assignation to the genus *Boehmoceras*.

It is obvious that in both assemblages we are dealing with a baculitid population morphologically transitional between *Baculites* and *Boehmoceras*, with both having their origins in *B. capensis*. As shown above (p. 71), some specimens of *B. capensis* have slightly curved body chambers. In the majority of the Pondoland specimens, ornament is of the *Boehmoceras arculus* or *Baculites sulcatus* type, but curvature is restricted to the body chamber, as in *B. capensis*, and they still belong to *Baculites* s.s. In the Gulf Coast material, lateral ornament is the same, but the curvature is more distinct and already occurs on the phragmocone, and they are referable to *Boehmoceras*. In both populations, more or less straight specimens with *B. capensis*-like ornament occur associated with the curved specimens, indicating an origin in the latter species. It is tempting to link *B. capensis* to the Gulf Coast *Boehmoceras* fauna via the Pondoland specimens but, lacking a precise date for the latter assemblage, this is not advisable at present. Affinities of ?late *B. sulcatus* with typical forms of *B. sulcatus*, rather suggests that the Pondoland and Gulf Coast faunas have a common origin in the Upper Santonian in *B. capensis*, and subsequently acquired similar ornament, but developed in parallel. The Gulf Coast fauna became progressively more curved and gave rise to true *Boehmoceras*, whereas the Pondoland fauna remained in the strict *Baculites* lineage.

Baculites increscens Collignon (1970: 3, pl. 607 (figs 2266–2268)) from the Middle Campanian of Zululand and Madagascar resembles ?late *B. sulcatus*, but lateral ornament in the former is more prominent, and transitional to the prominent auricular *B. vanhoepeni* type.

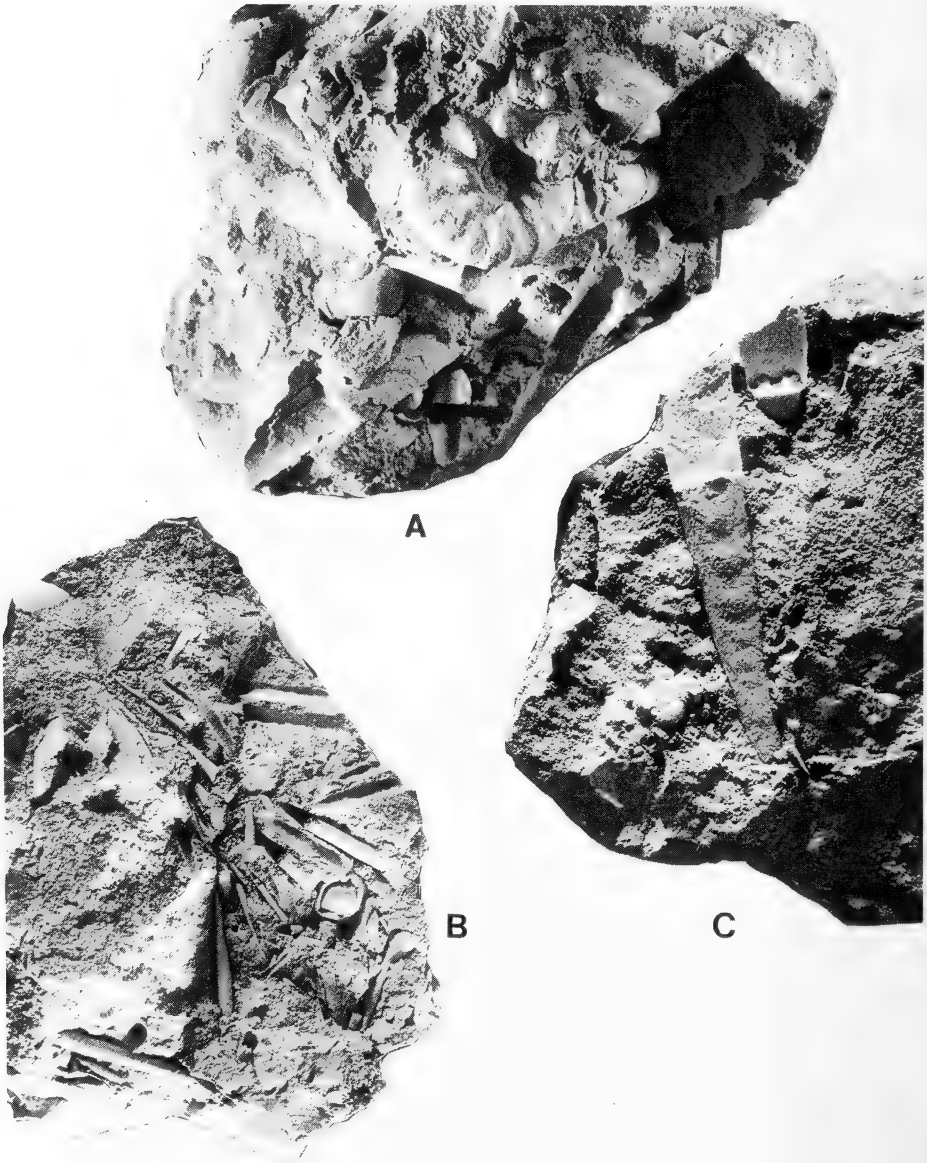

Fig. 78. A–B. *Baculites bailyi* Woods, 1906. A. SAM–PCZ8358, concretion with *B. bailyi* and *Premuniericeras* from locality 98, Zululand, St Lucia Formation, Santonian II. B. SAM–PCZ7214, concretion crammed with juvenile *B. bailyi* from locality 73, Zululand, St Lucia Formation, Coniacian IV or V. C. *B. sulcatus* Baily, 1855. SAM–PCP8361, concretion from locality 1, Pondoland, Mzamba Formation, Campanian I. All × 1.

Strongly ornamented forms of typical *B. sulcatus* bear superficial resemblance to *Trachybaculites columna* (Morton, 1834) (see Cobban & Kennedy 1992*c* for a recent review). *Trachybaculites columna*, however, is a Maastrichtian species known from the Prairie Bluff Chalk of Alabama, the Corsicana Marl of the Navarro Group of Texas, Trail City Member of the Fox Hills Formation in South Dakota, and also from the Ganzas Formation of the San Joaquin Valley, California (Matsumoto 1959: 163). Ribbing seems to be more uniform, and stronger on the dorsum and venter than in *B. sulcatus*. Also, the suture is distinctly simple compared to that of *B. sulcatus*.

Baculites furcillatus (Blanckenhorn, 1905, pl. 6 (fig. 2)) (herein Fig. 67E–F) has ornament similar to that of some *B. sulcatus*. This is a rare species in the Maastrichtian of Israel, and more material is needed for definite comment. According to Picard (1929: 441), *B. furcillatus* 'is only a strongly ribbed form of *B. palestinensis*'. Ribbing in *B. furcillatus* is stronger over the venter and dorsum than in *B. sulcatus*, and thus seems closer to *T. columna*.

Baculites thomi Reeside (1927*b*: 13, pl. 12 (figs 9–14)) from the Elk Basin Sandstone member of the Telegraph Creek Formation of the U.S. Western Interior, is superficially similar to some typical *B. sulcatus* in the strong, circumperipheral ribbing. However, a recent review of the species by Cobban & Kennedy (1991*a*: C1–C8, pls 1–2) showed that Reeside's original figures of the holotype were retouched. According to Cobban & Kennedy (1991*a*), *B. thomi* first appears in the Upper Santonian, where it reaches its peak, and persists into the Lower Campanian. Ornament in *B. thomi* is far more regular than in *B. sulcatus*, with very regular ventral corrugations developing in typical forms. Also, the suture line (Cobban & Kennedy 1991*a*, fig. 2A–B) is less complex.

Some representatives of two baculitid species from the Coniacian of the U.S. Western Interior are very similar to *B. sulcatus*. These are *B. sweetgrassensis* Cobban, 1951 (see Kennedy & Cobban 1991*a*: 70, pl. 14 (figs 24–25, 29–34, 38–42)) and *B. codyensis* Reeside (see Kennedy & Cobban 1991*a*: 72, pl. 15 (figs 1–30), pl. 16 (figs 1–13), pl. 17 (figs 1–8), text-fig. 25F).

Baculites sweetgrassensis is a Middle Coniacian species, and, in typical forms, has widely spaced, crescentic bullae that are projected ventrally into sharp, forwardly direct ribs. Superficially some of these (e.g. Kennedy & Cobban 1991*a*, pl. 14 (fig. 40–41)) resemble early forms of *B. sulcatus*; others, (e.g. Kennedy & Cobban 1991*a*, pl. 14 (figs 30, 38)) resemble ?late *B. sulcatus*.

Baculites codyensis first appears in the Middle Coniacian, and ranges up to the Middle Santonian. Typical forms have regular, concave, concentric ribs, and these, together with the age difference clearly separate *B. codyensis* from *B. sulcatus*. Some of the more coarsely ornamented forms of *B. codyensis* (see e.g. Kennedy & Cobban 1991*a*, pl. 16 (fig. 12)) resemble ?late forms of *B. sulcatus*, but again, this is mere homoeomorphy.

Some specimens of *B. ovatus* Say, recently figured by Kennedy & Cobban (1993*c*, fig. 15. 9–12), are remarkably similar to our ?late *B. sulcatus*, but *B. ovatus* is a younger species, and typically has weaker ornament than *B. sulcatus*.

Baculites oberholzeri Böhm (1909: 52, pl. 1 (fig. 9a–b)), imprecisely dated from the Senonian of Switzerland, appears to have similar lateral ornament, but this species is based on a crushed fragment, about 11 mm long, and is best regarded as a *nomen dubium*.

Some specimens described and figured by Birkelund (1965: 58, pl. 8 (fig. 1), pl. 9 (figs 1–3), pl. 10 (fig. 1), pl. 11 (figs 1–2), pl. 12 (figs 1–2), pl. 13 (figs 1–2), pl. 14 (fig. 1), text-figs 47–52) as *Baculites obtusus* Meek from the Lower Campanian of West Greenland resemble *B. sulcatus*, but none of the specimens develops as strong ornament as typical representatives of the latter.

Typical forms of *B. sulcatus* are also nearly identical with some *B. leopoliensis* Nowak (see e.g. Kennedy 1986*e*, pl. 2 (figs 11–12)); this, however, is an Upper Campanian species, and typical forms have more regular, thin, crescentic ribs.

Occurrence

To date, *B. sulcatus* has only been recorded from the Lower Campanian of Pondoland and in subsurface deposits at Richards Bay, Zululand.

Baculites increscens Collignon, 1970

Figs 79A–L, N–O, 80A–B, 82

1970 *Baculites increscens* Collignon, p. 3, pl. 607 (figs 2266–2268), p. 5, pl. 608 (fig. 2269).
1970 *Baculites tanakaeformis* Collignon, p. 2, pl. 607 (figs 2263–2265).
1970 *Baculites androtsyensis* Collignon, p. 5, pl. 608 (figs 2270–2272).
1970 *Baculites mamillatus* Collignon, p. 7, pl. 609 (figs 2273–2274).

Type

Holotype, by original designation, the specimen figured by Collignon (1970, pl. 607 (fig. 2266)) from the Middle Campanian, Zone of *Pachydiscus grossouvrei*, subzone of *Eupachydiscus lamberti*, gisement 177, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar, housed in the collections of the Institut des Sciences de la Terre, Université de Dijon, GD 12266, here refigured as Figure 82.

Material

SAM–PCZ11986–11996, all from locality 102, Zululand, St Lucia Formation, Campanian II.

Description

All of our material is fragmentary, but the specimens range in size from juveniles to large body chamber sections, covering all the growth stages.

PCZ11992 (Fig. 79I–J) is a juvenile and shows distinct crescentic, dorsolateral nodes. PCZ11995 at similar whorl height has less conspicuous nodes but shows a distinct trigonal whorl section. PCZ11996, at whorl height

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Fig. 79 *(see facing page)*. A–L, N–O. *Baculites increscens* Collignon, 1970. A–D. SAM–PCZ11988. E. SAM–PCZ11991. F–H. SAM–PCZ11997. I–J. SAM–PCZ11992. K–L. SAM–PCZ11987. N–O. SAM–PCZ11993, all from locality 103, Zululand, St Lucia Formation, Campanian ?II. M. *Baculites vanhoepeni* Venzo, 1936. SAM–PCZ11998 from locality 110, Zululand, St Lucia Formation, Campanian II or III. All × 1.

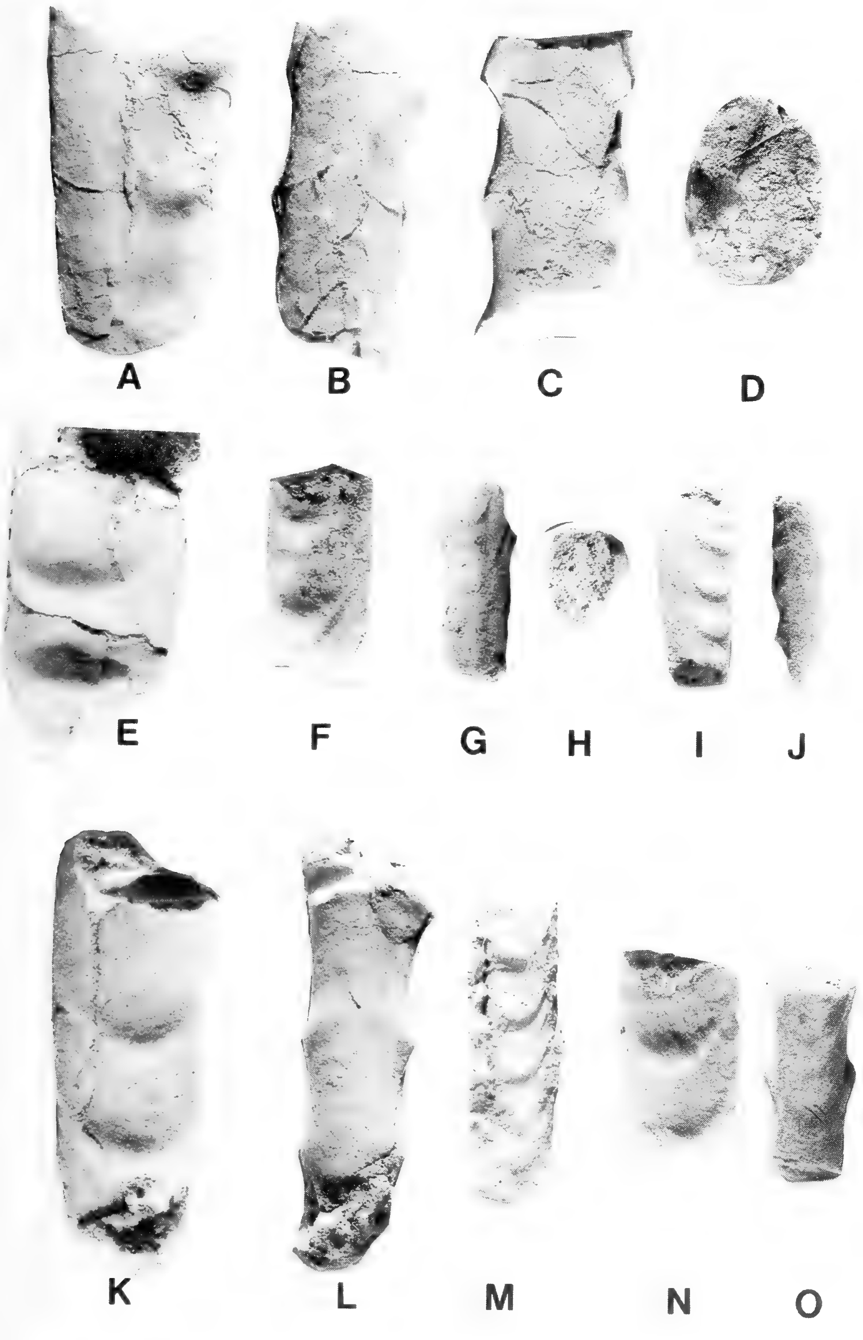

Fig. 79

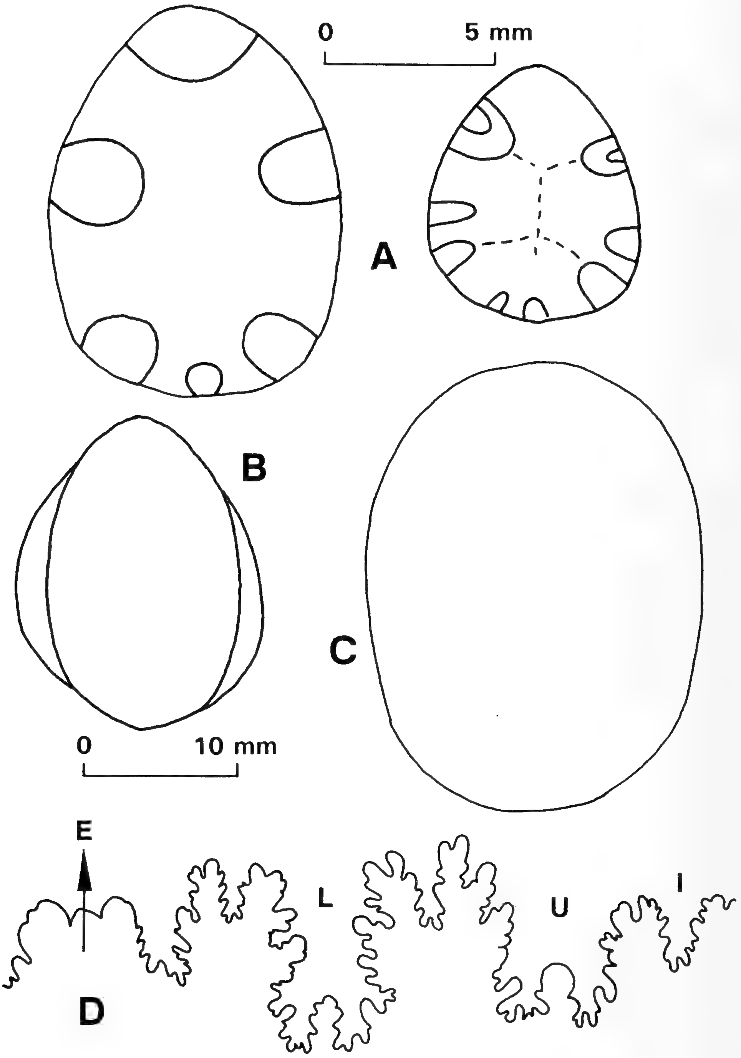

Fig. 80. Whorl sections and suture lines. A–B. *Baculites increscens* Collignon, 1970. A. SAM-PCZ11995. B. SAM-PCZ11986. C–D. *Baculites duharti* Hünicken, 1965. C. SAM-PCZ7685. D. SAM-PCZ7685. Venter in whorl section pointing upward. Scale bar for size.

12 mm, shows a similar rounded, trigonal whorl section. PCZ11993 (Fig. 79N–O) and PCZ11986 show typical phragmocone ornament consisting of prominent, dorsolaterally situated auricular nodes, projected ventrally into thin lirae that cross the venter, accompanied by intercalated lirae. Slightly more than two nodes occur per whorl height. The whorl section is compressed ovoid (Fig. 80A–C)with the dorsum flat to slightly rounded, and the venter narrowly rounded. PCZ11990 is a fragment, and has large, rounded, instead of crescentic dorsolateral nodes.

<table>
<tr><td colspan="4">UPPER CAMPANIAN</td></tr>
<tr><td rowspan="3">MIDDLE CAMPANIAN</td><td colspan="2">Zone of <i>Delawarella subdelawarensis</i>
and
<i>Australiella australis</i></td><td><i>B.</i> cf. <i>taylorensis</i> Adkins
(183)
<i>B. ankilizatensis</i> sp. nov.
(153-159)
<i>B. rectangulatus</i> sp. nov.
(156-157)</td></tr>
<tr><td rowspan="2">Zone of
<i>Pachydiscus grossouvrei</i></td><td>Sub-zone of
<i>Pachydiscus bassae</i></td><td><i>B. ankilizatensis</i> sp. nov.
(first: 153-159)
<i>B. leopoliensis</i> Nowak
(177-156)</td></tr>
<tr><td>Sub-zone of
<i>Eupachydiscus</i>
<i>lamberti</i></td><td><i>B. coagmentatus</i> sp. nov.
(177-156)
<i>B. increscens</i>
(last: 177)
<i>B. androtsyensis</i> sp. nov.
(180 & 327-328-329)
<i>B. mamillatus</i> sp. nov.
(181-326)
<i>B. increscens</i>
(first: 180-181)
<i>B. tanakaeformis</i> sp. nov.
(326-327 & 180-181)</td></tr>
<tr><td colspan="2">LOWER CAMPANIAN</td><td colspan="2">Top of Lower Campanian:
Sub-zone of <i>Termiericeras lenticulare</i></td></tr>
</table>

Fig. 81. Biostratigraphic zonation of the Middle Campanian and distribution of *Baculites* spp. at Menabe, Madagascar after Collignon (1969).

PCZ11991 (Fig. 79E), PCZ11988 (Fig. 79A–C) and PCZ11989 are body chamber fragments. Lateral ornament varies from closely spaced crescentic ribs, to low and rounded nodes. Some fragments appear to have been smooth.

Discussion

Baculites increscens is but one of several baculitids described by Collignon (1970) from the Middle Campanian of Madagascar. Our material fits the description of *B. increscens* best, but several features ascribed to the other Madagascar species are also present, and it is necessary to comment on the latter.

According to Collignon's (1970) stratigraphy of the Middle Campanian of Menabe, Madagascar (Fig. 81) the majority of *Baculites* species occur in the lower part of the substage, in the Zone of *Pachydiscus grossouvrei*, Subzone of *Eupachydiscus lamberti*. These include *B. coagmentatus* Collignon (1970: 7,

Fig. 82. *Baculites increscens* Collignon, 1969. Plaster cast of the holotype, GD12266, the original of Collignon (1970, pl. 607 (fig. 2266)) from the Middle Campanian of gisement 177, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. × 1.

pl. 609 (figs 2275–2276)) (herein Fig. 88); *B. increscens* Collignon (1970: 3, pl. 607 (figs 2266–2268)) (herein Fig. 82); *B. androtsyensis* Collignon (1970: 5, pl. 608 (figs 2270–2272)) (herein Fig. 83), *B. mamillatus* Collignon (1970: 7, pl. 609 (figs 2273–2274)) (herein Fig. 84A–C) and *B. tanakaeformis* Collignon (1970: 2, pl. 607 (figs 2263–2265)) (herein Fig. 84D–F).

The order of their listing below suggests that this is the order of their occurrence, but this is not strictly so. If they are arranged according to their occurrence at the different localities or horizons (Collignon's 'gisements'), it is clear that these species are contemporary to a large extent.

'Gisement'	
183	*Baculites* cf. *B. taylorensis*
153	*Baculites ankilizatensis* *Baculites coagmentatus*
156	*Baculites rectangulatus* *Baculites leopoliensis*
157	*Baculites rectangulatus*
159	*Baculites ankilizatensis*
177	*Baculites leopoliensis* *Baculites coagmentatus* *Baculites increscens*
180	*Baculites androtsyensis* *Baculites increscens* *Baculites tanakaeformis*
181	*Baculites mamillatus* *Baculites increscens* *Baculites tanakaeformis*
329	*Baculites androtsyensis*
328	*Baculites androtsyensis*
327	*Baculites androtsyensis* *Baculites tanakaeformis*
326	*Baculites tanakaeformis* *Baculites mamillatus*

According to Collignon (1970: 2), *B. tanakaeformis* occurs at the base of the Middle Campanian, and *B. androtsyensis* is the oldest of the series of baculitids that dominates the Middle Campanian (Collignon 1970: 5). Both occur together at gisement 327; at gisement 181 they occur together with *B. increscens*; and at 326 and 181 *B. tanakaeformis* occurs with *B. mamillatus*.

On the basis of their co-occurrence, it would seem logical to regard the above-mentioned four species, *B. tanakaeformis*, *B. increscens*, *B. androtsyensis* and *B. mamillatus* as a single, variable species. However, Collignon based these species on large assemblages—*B. tanakaeformis* (87 specimens), *B. androtsyensis* (50 specimens) and *B. increscens* (50 specimens), and they cannot summarily be dismissed as synonyms.

Fig. 83. *Baculites androtsyensis* Collignon, 1969. Plaster cast of the holotype, GD12270, the original of Collignon (1970, pl. 608 (fig. 2270)), from the Middle Campanian of gisement 329, Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar. × 1.

All four species have a subtriangular whorl section in common, with faint indications of longitudinal depressions on either side of the venter, indicating an incipient ventral keel. Lateral ornament varies from strong crescentic to mammiform in *B. increscens*, weaker in *B. androtsyensis* (with more compressed whorl section), distinct mammiform in *B. mamillatus*, conical to obliquely elongated in *B. tanakaeformis*. The suture lines of *B. mamillatus* and *B. androtsyensis* (Figs 85A, C) are very similar.

We do not doubt that these four broad morphological groups can be identified in large collections, and that some morphotypes probably are more common at certain localities than others in Madagascar. However, our Zululand material from locality 102 shows that even though the majority of specimens are identifiable with *B. increscens*, some specimens could be referred to either of the other three species, e.g. PCZ11993 (Fig. 79N–O) and PCZ11986 have a more compressed whorl section as in *B. androtsyensis*; PCZ11988 (Fig. 79A–D) has rounded tubercles as in *B. mamillatus*; those of PCZ11991 (Fig. 79E) are as in *B. tanakaeformis*. Because of this, we doubt if it is justifiable to maintain formal specific names for these different, yet overlapping and co-eval morphotypes and, as first revising authors, we select *Baculites increscens* as the name of this species.

Baculites coagmentatus Collignon (1970: 7, pl. 609 (figs 2275–2276)) (Fig. 88) appears to be slightly younger than most of the baculitids of the group of *B. increscens*, but co-occurs with the last appearance of *B. increscens* at Collignon's locality 177. The whorl section is still subtriangular as in *B. increscens*, but the ornament of *B. coagmentatus* consists essentially of thin, closely spaced, crescentic ribs—a mode of ornament found in some of the Durban specimens of *B. vanhoepeni* to be described below. *Baculites leopoliensis* Collignon (1970: 10, pl. 610 (figs 2277–2278) non Nowak) (herein Fig. 86) has a more ovoid whorl section, but similar lateral ornament as in *B. coagmentatus* and they are probably synonyms. *Baculites leopoliensis* Nowak (1908: 328, pl. 14 (figs 1–5, 10, ?11), text-figs 1–5 on p. 329, ?text-figs 5–10 on p. 331) is a typical Upper Campanian species (see Hancock & Kennedy 1993: 165) and not Lower Maastrichtian as recorded earlier by, for example, Kennedy (1986*c*: 1013). The ornament consists of lateral ribs that break down into riblets and striae on the venter, whereas intercalated ribs develop over the venter. This style of ornament is quite characteristic and unlike that of the Madagascar material. *Baculites leopoliensis* Collignon *non* Nowak is here renamed *B. collignoni* nom. nov. *Baculites coagmentatus* and *B. collignoni* have a style of ornament similar to some forms of *B. vanhoepeni* (see e.g. Fig. 111A–C), and these two species can probably be regarded as ?early forms (and junior synonyms?) of *B. vanhoepeni*.

Fig. 84 *(see overleaf)*. A–C. *Baculites mamillatus* Collignon, 1970. Plaster cast of the holotype, GD12273, the original of Collignon (1970, pl. 609 (fig. 2273)) from the Middle Campanian of gisement 181, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. D–F. *Baculites tanakaeformis* Collignon, 1970. Plaster cast of the holotype, GD12263, the original of Collignon (1970, pl. 607 (fig. 2263)) from the Middle Campanian of gisement 326, Coupe Ampolypoly-Antsirasira-Behamotra (Belo sur Tsiribihina), Madagascar. Both × 1.

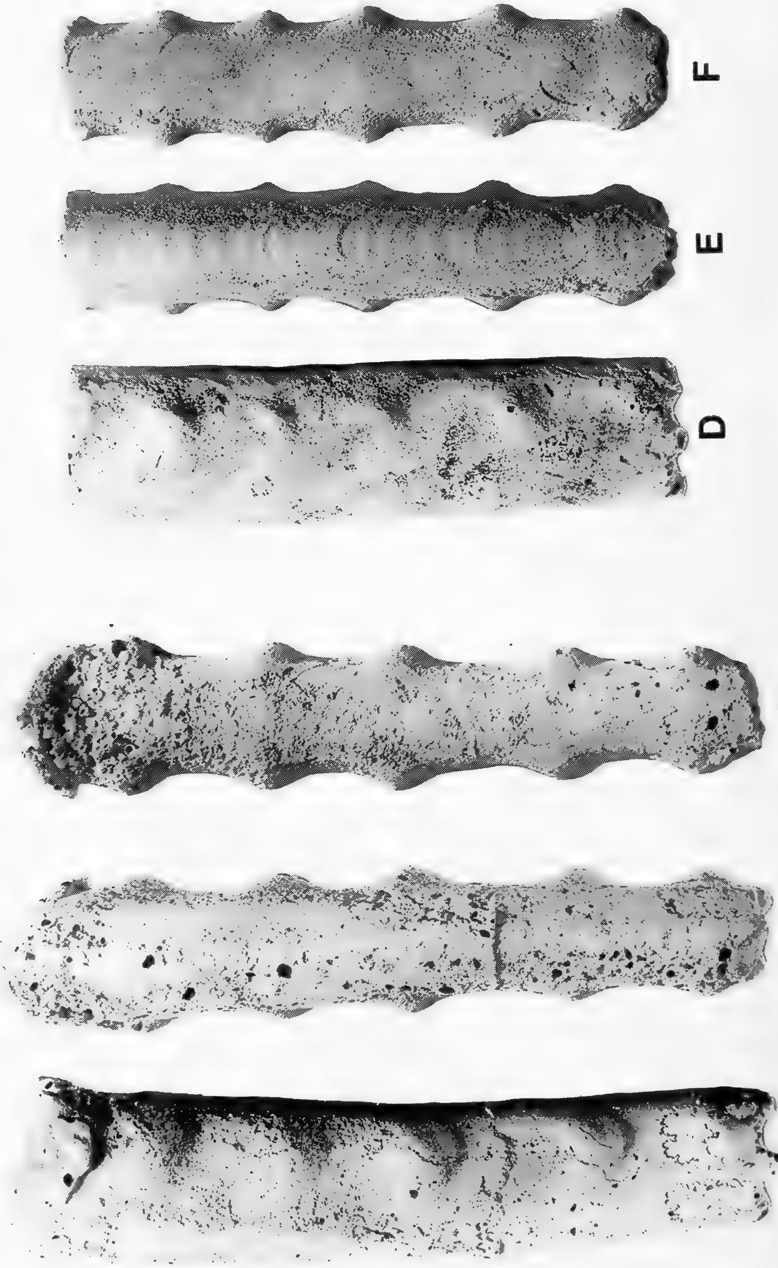

Fig. 84

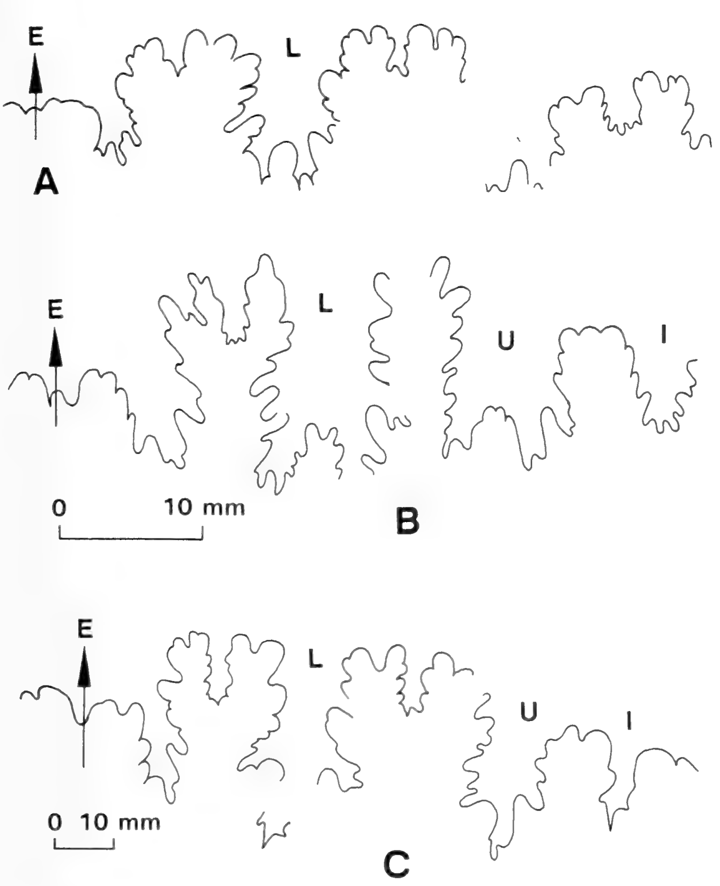

Fig. 85. Suture lines. A. *Baculites mamillatus* Collignon, 1970. GD12273. (see Fig. 84A–C). B. *Baculites ankilizatensis* Collignon, 1970. GD12282 (see Fig. 89). C. *Baculites androtsyensis* Collignon, 1970. GD12270 (see Fig. 83). Scale bars for size.

Baculites rectangulatus Collignon (1970: 12, pl. 611 (figs 2279–2281)) (herein Fig. 87) is a late representative of the group of *B. increscens* as far as ornamentation is concerned. The whorl section, however, is more compressed and subrectangular. *Baculites ankilizatensis* Collignon (1970: 13, pl. 612 (figs 2282–2284)) (herein Fig. 89) is a large baculitid with reduced lateral ornament.

In Zululand, *B. increscens* appears to occupy an intermediate position between *B. sulcatus*, especially the material from the Casino excavations, and *B. vanhoepeni*. Juvenile specimens of *B. increscens* are virtually indistinguishable from ?late *B. sulcatus*. *Baculites increscens* differs from *B. sulcatus* mainly in having stronger lateral ornament in the adult stage, and from *B. vanhoepeni* in being weaker ornamented. To be quite frank, the main reason for separating *B. increscens* in Zululand is probably because of its isolated occurrence at locality 102.

Fig. 86. *Baculites collignoni* nom. nov. Plaster cast of GD12277, the original of *Baculites leopoliensis* non Nowak in Collignon (1970, pl. 610 (fig. 2277)) from gisement 156, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. × 1.

Fig. 87. *Baculites rectangulatus* Collignon, 1970. Plaster cast of the holotype, GD12279, the original of Collignon (1970, pl. 611 (fig. 2279)) from the Middle Campanian of gisement 157 of Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. × 1.

Fig. 88. *Baculites coagmentatus* Collignon, 1970. Plaster cast of the holotype, GD12275, the original of Collignon (1970, pl. 609 (fig. 2275)) from the Middle Campanian of gisement 177, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. × 1.

Fig. 89. *Baculites ankilizatensis* Collignon, 1970. Plaster cast of the holotype, GD12282, the original of Collignon (1970, pl. 612 (fig. 2282)) from the Middle Campanian of gisement 153, Coupe d'Ankilizato (Belo sur Tsiribihina), Madagascar. × 1.

Baculites nibelae sp. nov., described below (p. 162) is younger than typical *B. increscens*, lateral ornament is similar, but the whorl section is characteristically wedge-shaped,trigonal, with a flat dorsum and a narrow venter.

Occurrence

Middle Campanian of Zululand and Madagascar.

Baculites vanhoepeni Venzo, 1936
Figs 79M, 91–115

1936 *Baculites vagina* Forbes var. *van Hoepeni* Venzo, p. 116 [58], pl. 10 [6] (figs 11–12).
1973 *Baculites* sp. group of *Baculites capensis* Woods; Kennedy & Klinger, p. 100, pl. 4 (figs 1–5), pl. 5 (fig. 1a–d), pl. 6 (figs 4–5).
1975 *Baculites sulcatus* (non Baily); Kennedy & Klinger, p. 280.
? 1970 *Baculites coagmentatus* Collignon, p. 7, pl. 609 (figs 2275–2276).
? 1970 *Baculites leopoliensis* non Nowak, Collignon, p. 10, pl. 610 (figs 2277–2278) (= *B. collignoni* nom. nov.)
1977 *Baculites vanhoepeni* Venzo; Kennedy & Klinger, p. 73, figs 2G–K, 3A, H–I, 4A–C, 5C.

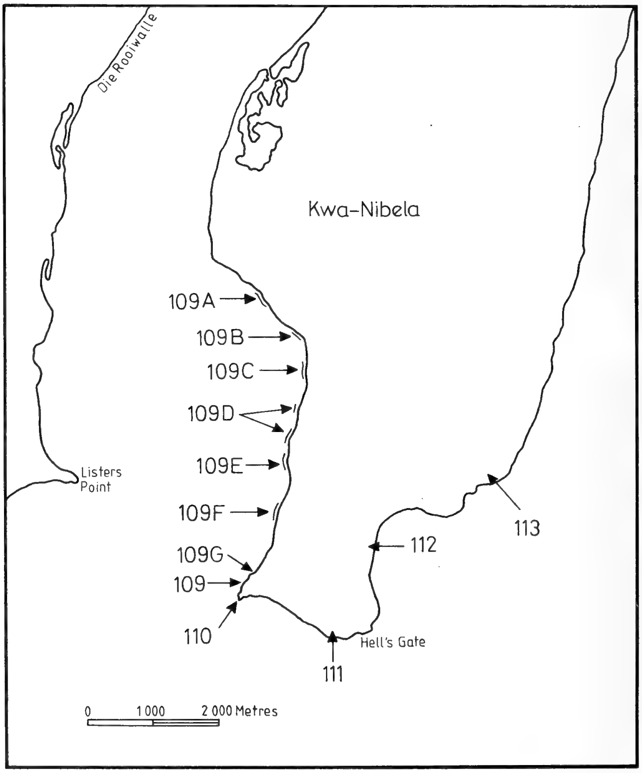

Fig. 90. Localities on Nibela Peninsula referred to in text, but not included in Kennedy & Klinger (1975).

Type

Venzo (1936: 116 [58]) based this species on several specimens. Klinger & Kennedy (1977: 73) designated the larger of the two specimens figured by Venzo (1936, pl. 10 [6] (fig. 11a–b)) from 'False Bay', Zululand, as lectotype. It is housed in the Department of Geological Sciences, University of Bologna, no. 1 GO 243.

Material

We have more than 150 specimens from localities on the Nibela Peninsula (Fig. 90), Zululand, St Lucia Formation, Campanian II–III.

Dimensions

A list of dimensions is given in the appendix.

Max Wb (mm)	*MxWb/MxWh*	*MnWb/MnWh*	*Ti*	*Ri*
10–14.9	0.71	0.69	5.32	0.81
15–19.9	0.71	0.73	4.7	0.8
20–24.9	0.77	0.76	4.9	1.15
25–27.9	0.77	0.79	3.8	1.28
30–34.9	0.77	0.77	6.2	1
37	0.80	—	—	—

Description

This species is conspicuous by its large size; the largest available specimen (D1302b, Fig. 103) has a whorl height of 55 mm. Unfortunately, the early stages are poorly known—almost all our specimens are large. This is probably due to taphonomic and/or diagenetic factors.

Early stages of growth are shown in PCZ7714 (Fig. 109H). Here the whorl section is more or less ovoid, with a narrow venter. Ornament consists of dorsolaterally situated crescentic ribs which are projected ventrally and aperturally over the venter, numbering about 2.5 per whorl height.

All the characteristic features of the species are shown in PCZ8764 (Fig. 91A–C). The bullae are typically crescentic to auricular, with sharp to rounded lateral crests, and are situated on the dorsal half of the flanks. Ventrally, they are projected acutely forwards and over the venter as thin riblets. In addition, a variable number of intercalatories arises on the ventral half of the flanks, and these also cross the venter with distinct, albeit variable corrugation.

Fig. 91 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. A–C. SAM-PCZ8764. D–F. SAM-PCZ7717. G–I. SAM-PCZ7415. J–L. SAM-PCZ7707. M–O. SAM-PCZ7091. Note the irregular occurrence of ventral corrugations. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

Fig. 92 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. A–C. NMB D1467. D. SAS Z1911. E–F. NMB D1467a. G–H. SAS Z1863e. Note the aperture in D and H. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

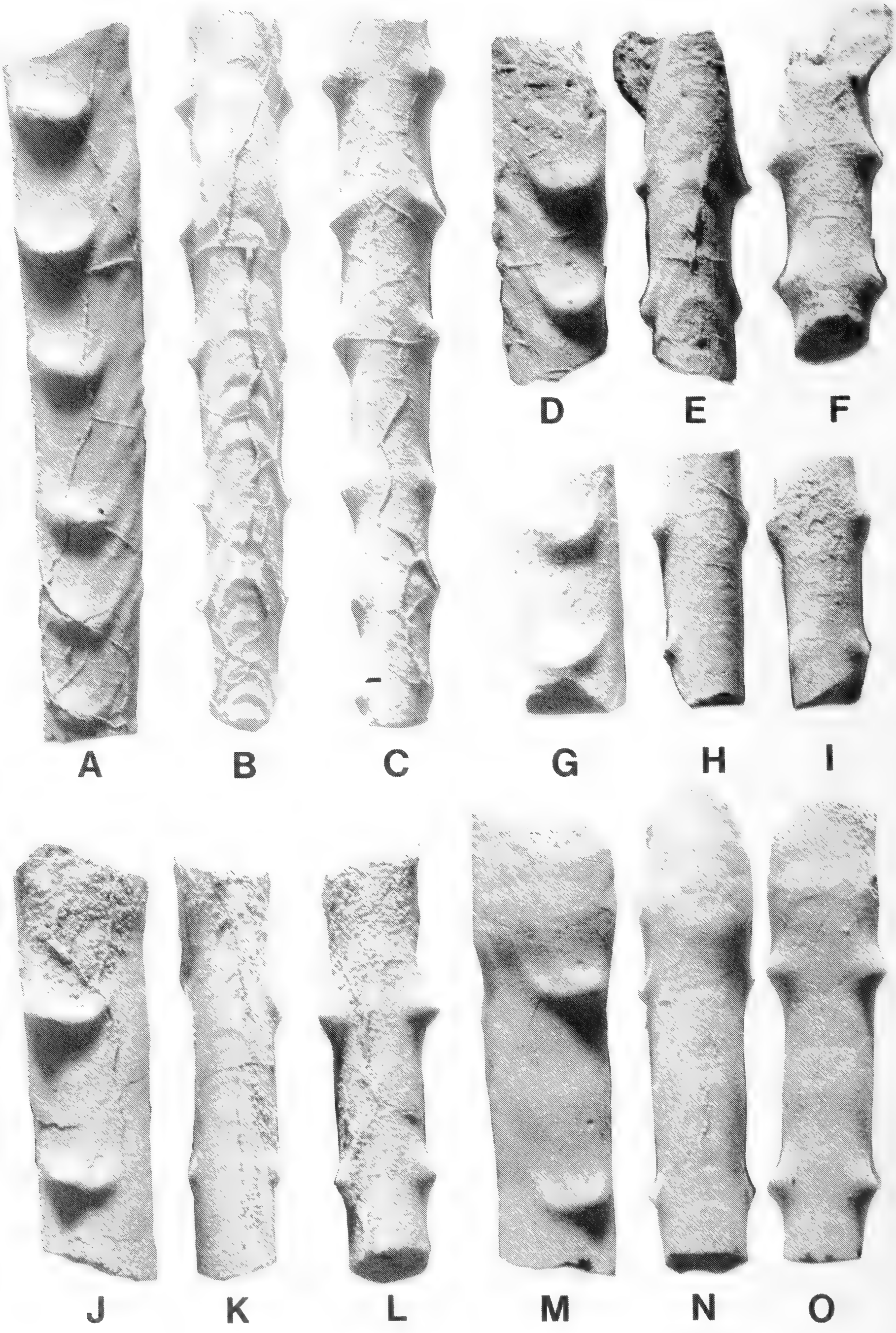

Fig. 91

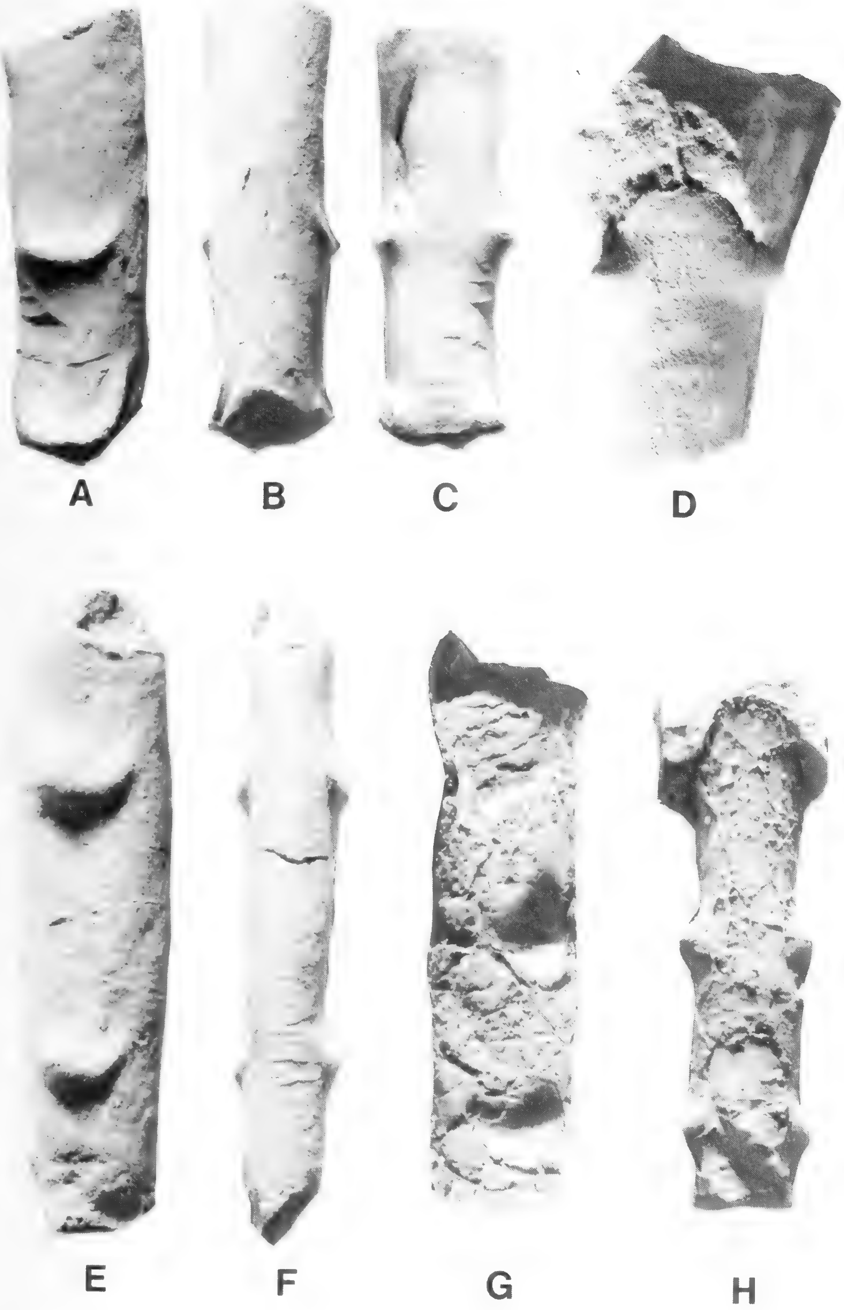

Fig. 92

Fig. 93. *Baculites vanhoepeni* Venzo, 1936. A–C. SAS A2035. Large, adult specimen with typical prominent auricular lateral tubercles. From locality 110, Zululand St Lucia Formation, Campanian II–?III. × 1.

Fig. 94 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. A–C. SAS A2032. D. SAS A477. E. SAM-PCZ7411. F. SAM-PCZ8765. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

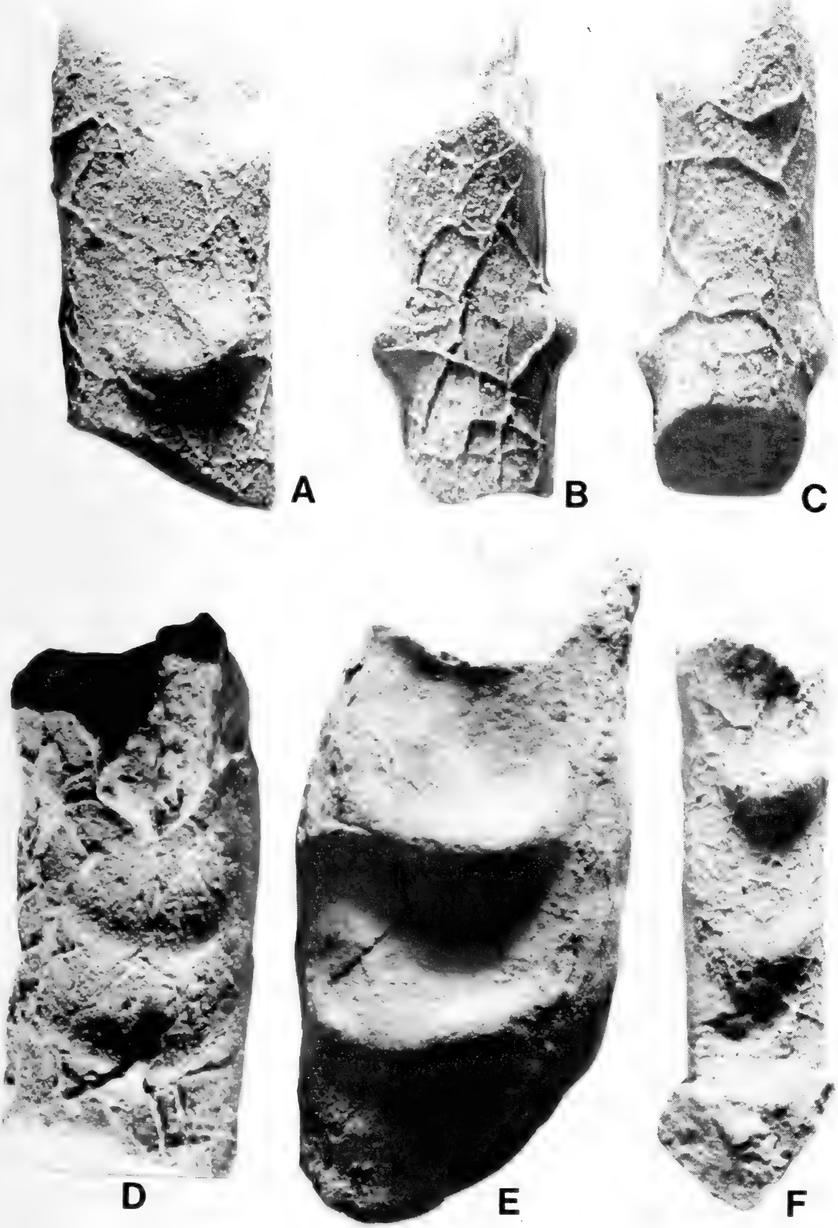

Fig. 94

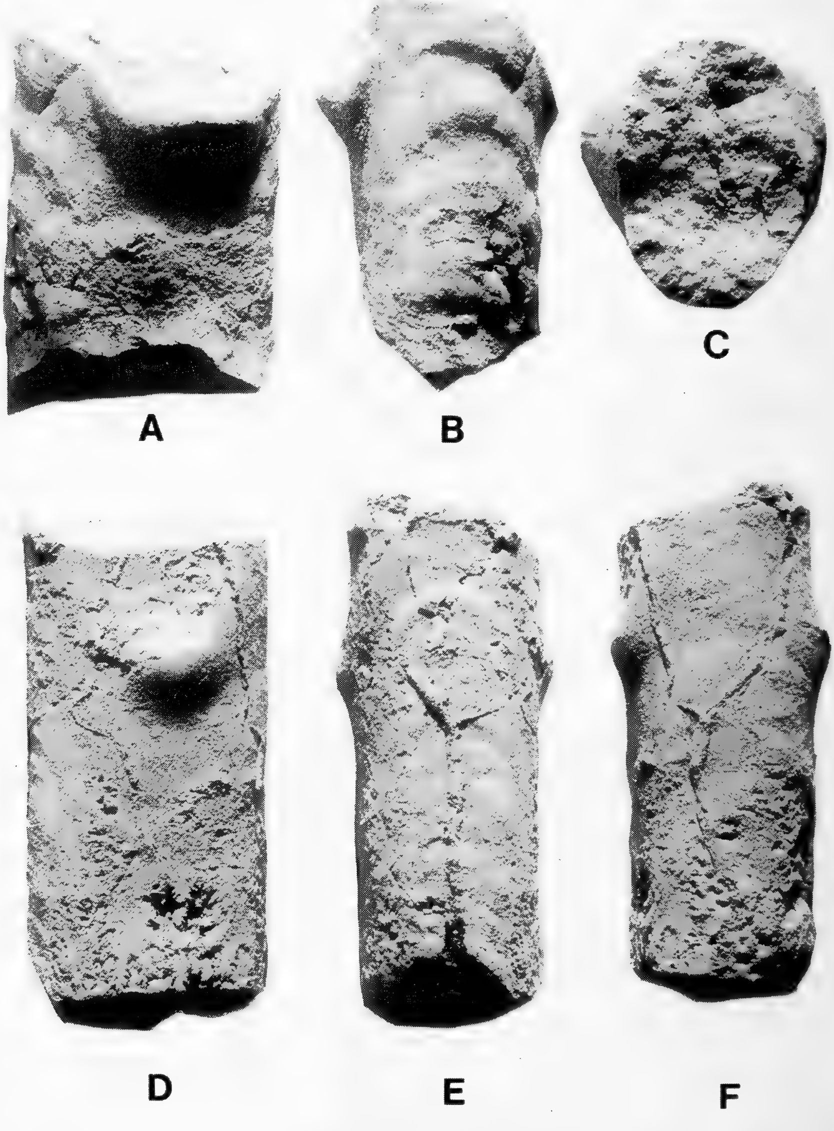

Fig. 95. *Baculites vanhoepeni* Venzo, 1936. A–C. SAM-PCZ7635. D–F. SAS A2034. Both from locality 110, Zululand, St Lucia Formation, Campanian II–?III. Both × 1.

Fig. 96 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. A. SAM-PCZ7640. B. NMB D1302b. C–E. NMB D1302a. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

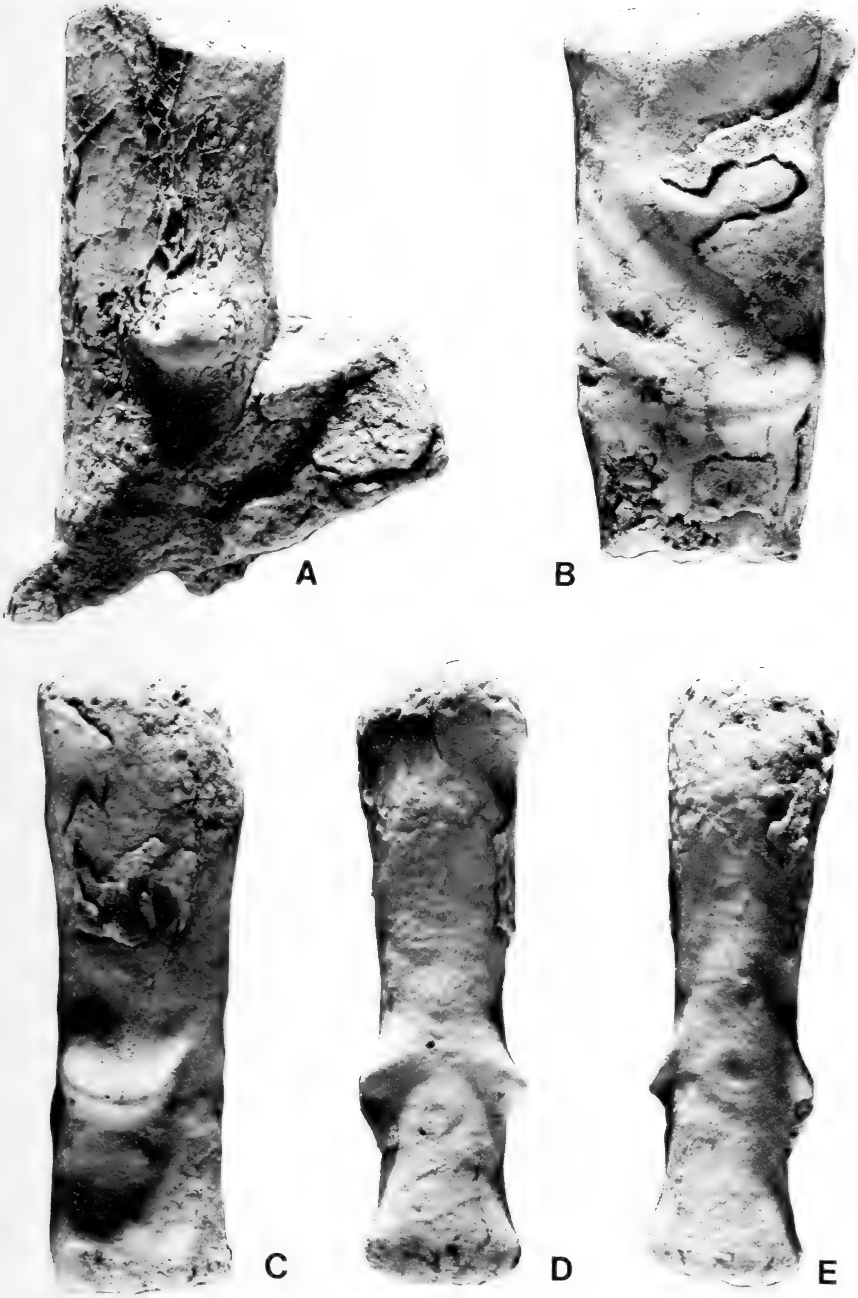

Fig. 96

The dorsal projection of the bullae is striking. Viewed dorsally, their outline is pointed, mammiform and, together with the dorsal ribbing, forms an open-ended, inverted V. The whorl section varies from ovoid at the smaller end to elliptical at the larger.

The essential features of this species are the widely spaced, dorsolateral auricular bullae. In the adult stage, they are distinctly auricular in lateral view and conical mammiform in dorsal view. (Figs 96D, 99C). These are generally widely spaced, about one per twice the whorl height, but in some specimens, especially on the body chamber, they may be more closely spaced—up to three per whorl height (e.g. SAS A477—Fig. 94D), or even more widely spaced (e.g. PCZ9404, Fig. 102C), but this is exceptional.

There is some variation in the shape of the bullae. At the one extreme they are reduced to thin riblets on the flanks, e.g. Fig. 111A–C; at the other they are low and rounded to bullate, rather than transversely elongated, e.g. SAS A2034 (Fig. 95D–F), PCZ7640 (Fig. 96A), and Figures 110A–C, 112A–C, D, E–F. Specimens from locality 109A (Fig. 114A–C) have more widely spaced, smaller and rounded tubercles. We suspect that these are slightly older than typical forms at locality 109 and 110. These could also possibly be referred to as ?early forms of *B. vanhoepeni*, or, given more material, possibly be separated specifically.

The presence of riblets on the ventral half of the flanks and accompanying corrugation on the venter is an extremely variable feature and of no apparent taxonomic value. In some examples, e.g. PCZ8764 (Fig. 91A–C), PCZ7717 (Fig. 91D–F), PCZ1860h (Fig. 101D), PCZ1911 (Fig. 101F), these are quite distinct, but in the majority of specimens they are absent or very faint. The majority of specimens with ventral ribbing are small, but as shown in Figure 91, other specimens of similar size totally lack these ventral ribs. In short, ventral ribbing appears to be a variable character, sometimes, but not always associated with early stages of growth, and taxonomically of no significance in *B. vanhoepeni*.

The aperture is preserved in several specimens, e.g. Z1911 (Fig. 92D), Z1863e (Fig. 92G–H), Z2077 and consists of a short, rounded dorsal rostrum, a prominent lateral sinus and a longer ventral rostrum. Distribution of maximum whorl height (Fig. 113) suggests that *B. vanhoepeni* is dimorphic, but that some overlap in size occurs between macro- and microconchs. In one specimen, SAM–PCZ7091 (Fig. 91M–O) part of the body chamber is distinctly flared. This is very similar to a specimen of *B. obtusus* figured by Birkelund (1965, pl. 9 (fig. 3a–c)).

Fig. 97 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. A. SAS Z1860a. B. SAS A2029b. C. SAM–PCZ7655. D. SAS Z1860b. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

Fig. 98 (*see overleaf*). *Baculites vanhoepeni* Venzo, 1936. A. SAS Z1190. B. SAS Z1860c. Both from locality 110, Zululand, St Lucia Formation, Campanian II–?III. Both × 1.

Fig. 99 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. A. SAS Z1911. Specimen with typical adult lateral ornament. D. SAS A2029a. E. SAM–PCZ12020. F. NMB D1302a. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

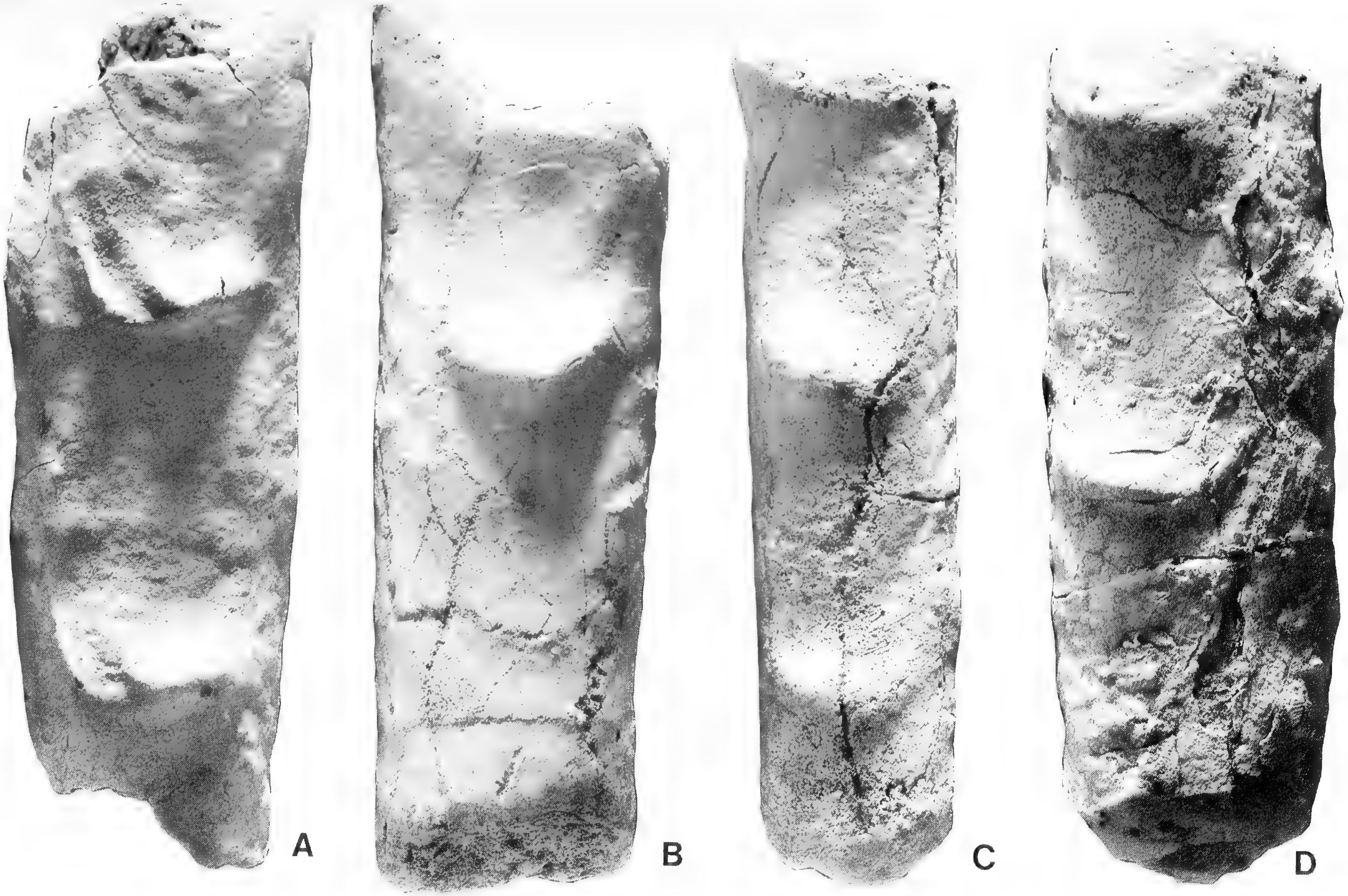

Fig. 97

Fig. 98

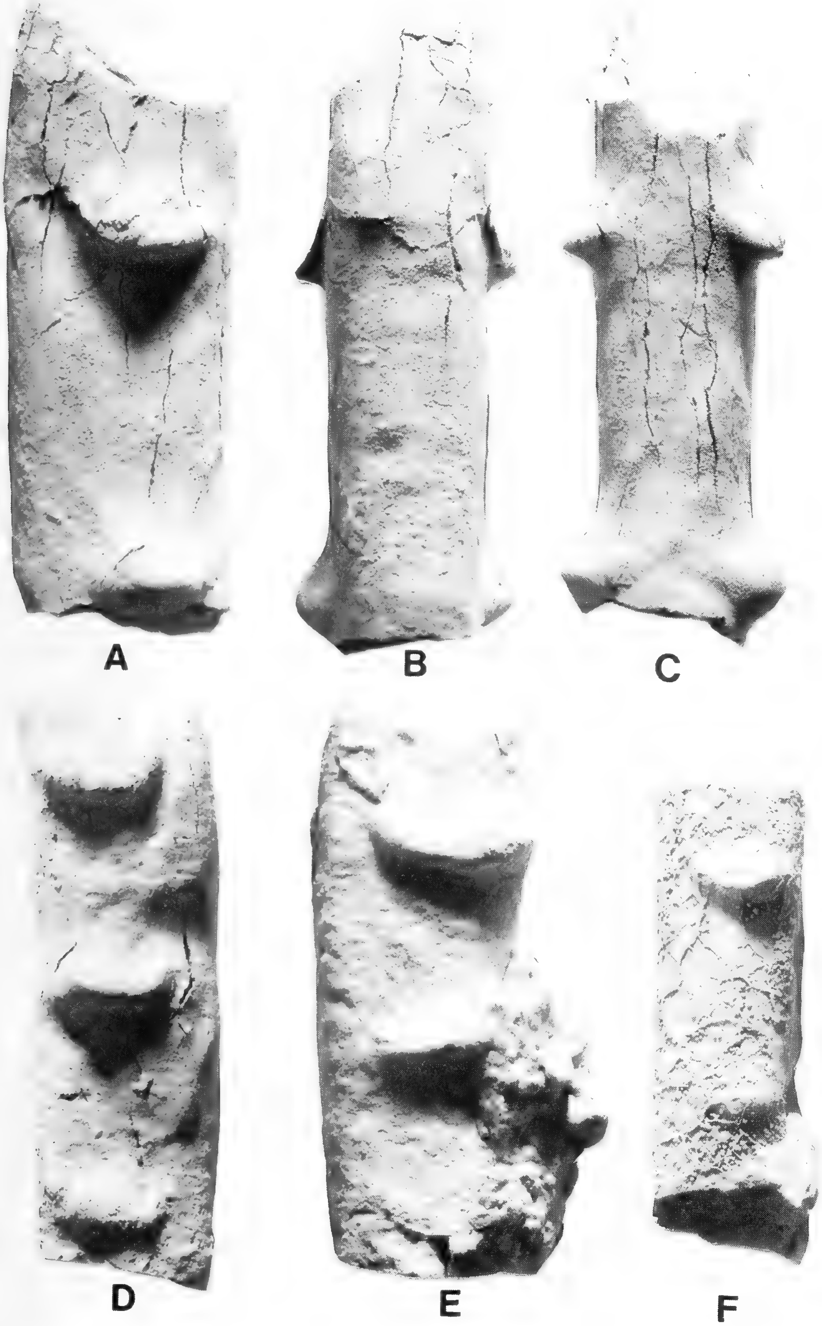

Fig. 99

The suture line of *B. vanhoepeni* (Figs 104–108) is slightly more complex than that of the majority of the Lower and Middle Campanian baculitid species from Madagascar (Figs 61–62, 85) and quite variable. The lateral lobe (L) tends to become constricted. In some, e.g. Z1923 (Fig. 108A), the suture is highly incised and dendritic, with narrow-stemmed saddles and a prominent, asymmetrically trifid, constricted lateral lobe, whereas in others (e.g. SAM–PCZ7706—Fig. 104A) it is relatively simple with quadrate saddles and lobes with open (unconstricted) lobes.

Discussion

This species was originally described as *B. vagina* var. *van Hoepeni* by Venzo (1936: 116 [58], pl. 10 [6] (figs 11–12)). Venzo incorrectly included the Pondoland specimens described and figured by Van Hoepen (1921: 18, pl. 3 (figs 7–8)) as *B. sulcatus* in the synonymy of this species. *Baculites vagina* is a typical Maastrichtian *Eubaculites*, and totally different from the present species, bituberculate, with a tabulate venter (see e.g. Klinger & Kennedy 1993). *Baculites sulcatus*, as here interpreted, is an older species, occurring in the Lower Campanian of Pondoland, and typically lacks the strong lateral ornament of *B. vanhoepeni*.

Baculites vanhoepeni is easily identified by the distinct, auricular dorsolateral ornament, especially in the adult stage, and, most conspicuously, by its large size, which distinguishes it from all the older Lower and other Middle Campanian baculitid species of Zululand and Madagascar.

Juvenile stages of *B. vanhoepeni* are rare, probably for taphonomic and/or diagenetic reasons. Available specimens (Fig. 109H) are indistinguishable from similarly sized specimens of *B. increscens* (Fig. 79I–J) or *B. sulcatus* (Fig. 73I). This suggests a phylogenetic lineage starting with *B. capensis*, via *B. sulcatus* and *B. increscens* or similar forms, to *B. vanhoepeni*. The adult stages, however, are clearly different—both in terms of ornament and maximum adult size.

As mentioned above, there is some variation in lateral ornament. Typical specimens have widely spaced, auricular bullae but, in some, the bullae are reduced to thin lateral riblets (Fig. 111A–D), or the bullae are more closely spaced and sharp crested (Fig. 94D), whereas in some the bullae are large and rounded and mammiform (Figs 95D–F, 96A). Some of these morphologies are already present in some of the Lower and Middle Campanian baculitids of Madagascar described by Collignon (1969, 1970).

Fig. 100 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. A–B. SAS Z1860d. C–E. SAM–PCZ7645. Both from locality 110, Zululand, St Lucia Formation, Campanian II–?III. Both × 1.

Fig. 101 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. A. SAM–PCZ7786. B. SAM–PCZ7690. C. SAS A2036a. D. SAS Z1860h. E. SAS A2036. F. SAS Z1911. G. SAS Z1923. H. SAS Z1860f. All from locality 110, Zululand, St Lucia Formation, Campanian II–?III. All × 1.

Fig. 102 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. A–B. SAS Z1860b. C. SAM–PCZ9404. Both from locality 110, Zululand, St Lucia Formation, Campanian II–?III. Both × 1.

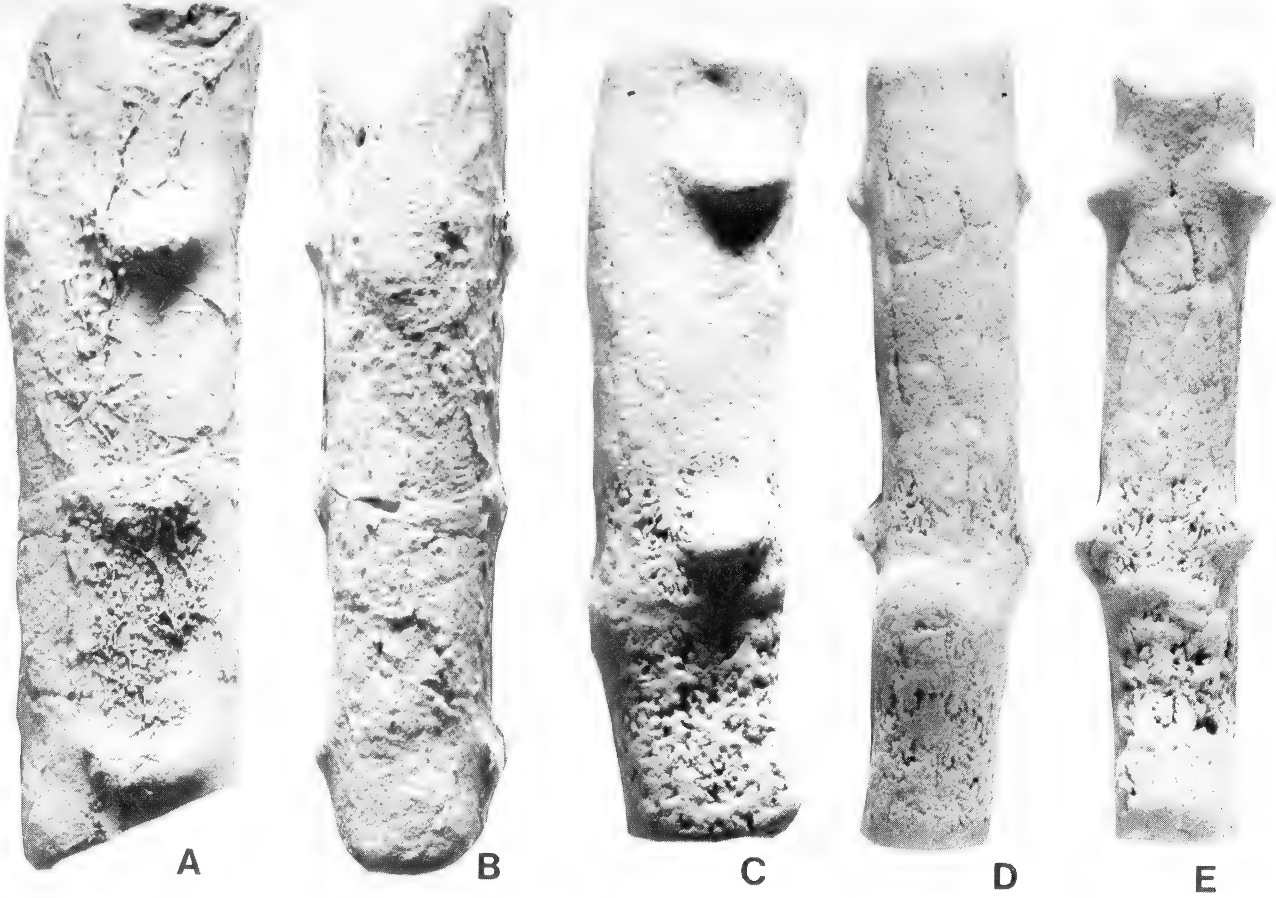

Fig. 100

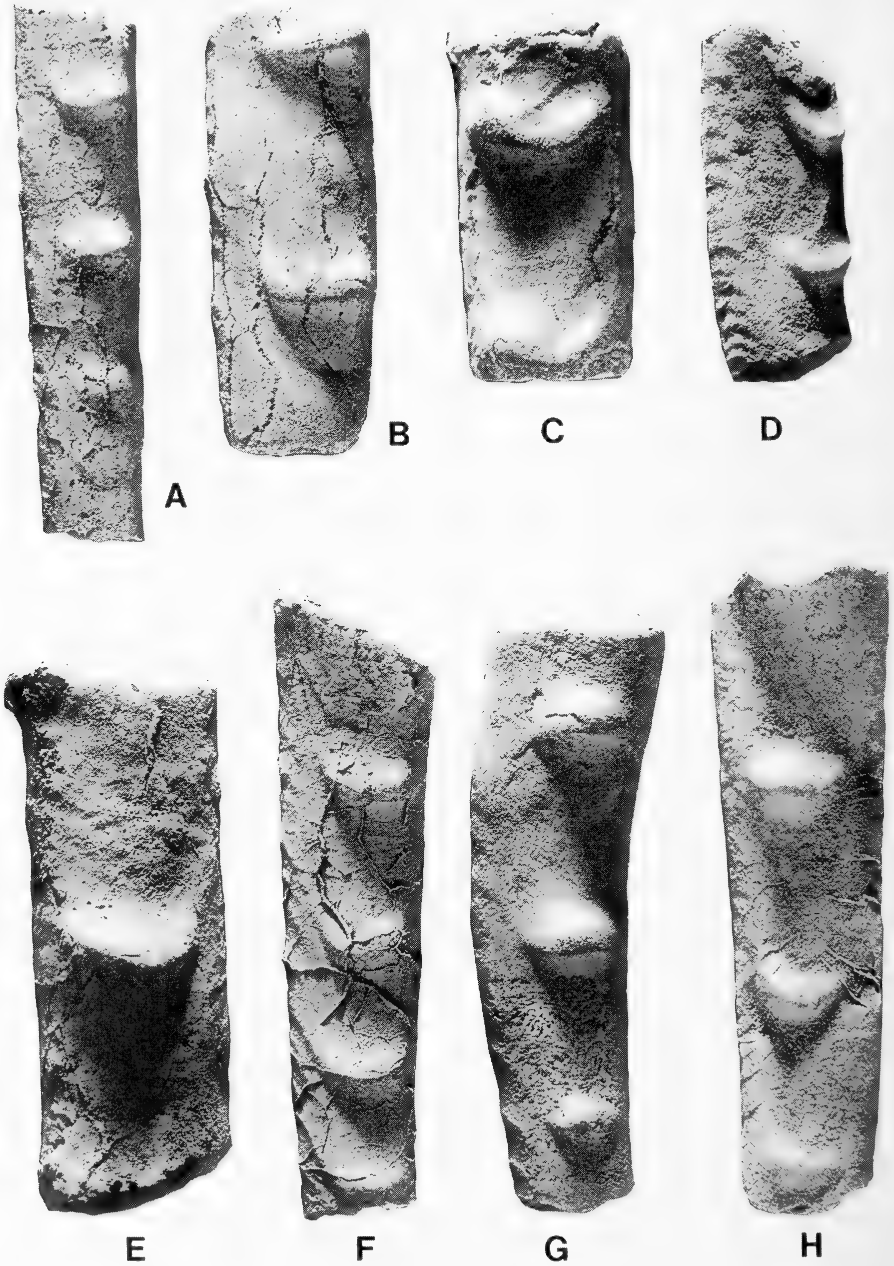

Fig. 101

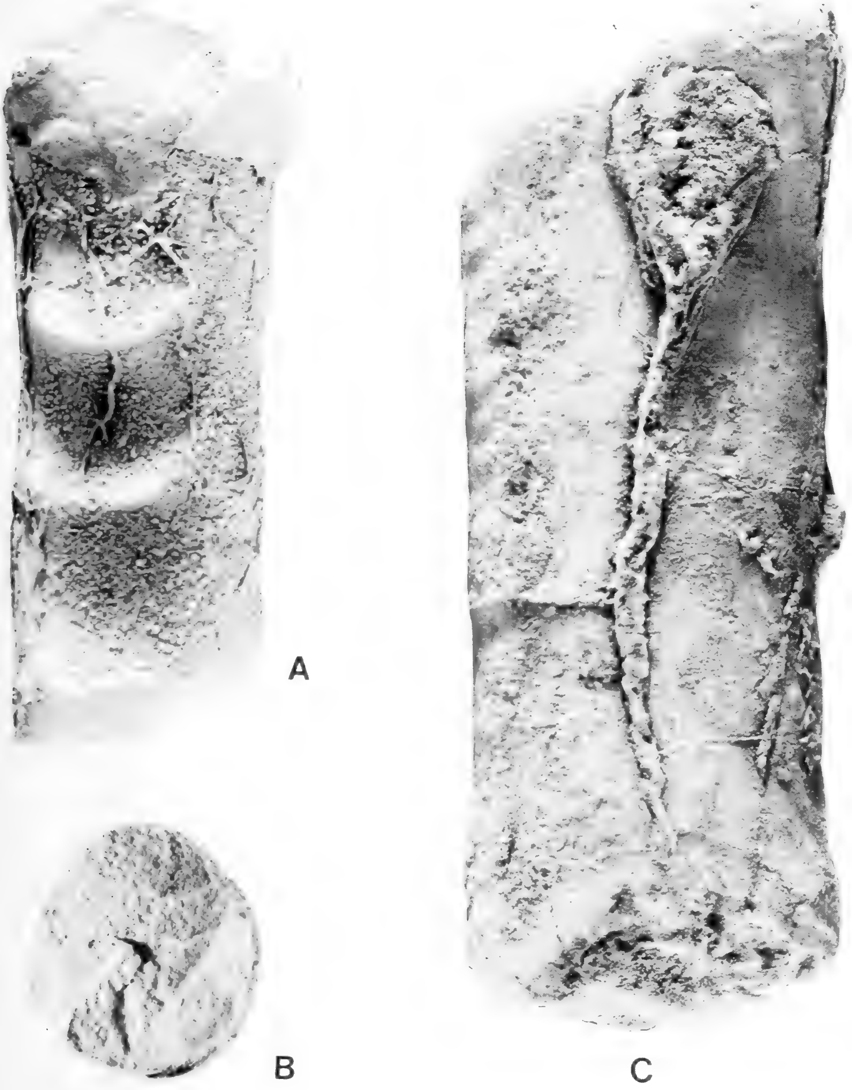

Fig. 102

Fig. 103. *Baculites vanhoepeni* Venzo, 1936. NMB D1320b. One of the largest specimens of this species from locality 110, Zululand, St Lucia Formation, Campanian II–?III. × 1.

Large, mammiform nodes already occur in Lower Campanian *B. sparsinodosus* (Fig. 60) and are well developed in *B. mamillatus* (Fig. 84A–C) in the Middle Campanian. Thin, rib-like ornament, albeit very closely spaced, occurs in *B. coagmentatus* (Fig. 88) and *B. leopoliensis* Collignon *non* Nowak (= *Baculites collignoni* nom. nov.) (Fig. 86) in the Middle Campanian of Madagascar.

We initially thought (Klinger & Kennedy 1977: 74) that *B. tanakae* Matsumoto & Obata (1963: 51, pl. 13 (fig. 4), pl. 16 (figs 1–5), pl. 17 (figs 1–5), pl. 18 (figs 1, 3–4), pl. 19 (figs 1, 4), text-figs 97–113, 115) was a synonym of *B. vanhoepeni*, but now rather regard it as being closer to *B. capensis* than to *B. vanhoepeni* as discussed above (p. 109), and probably a senior synonym of *B. menabensis* Collignon.

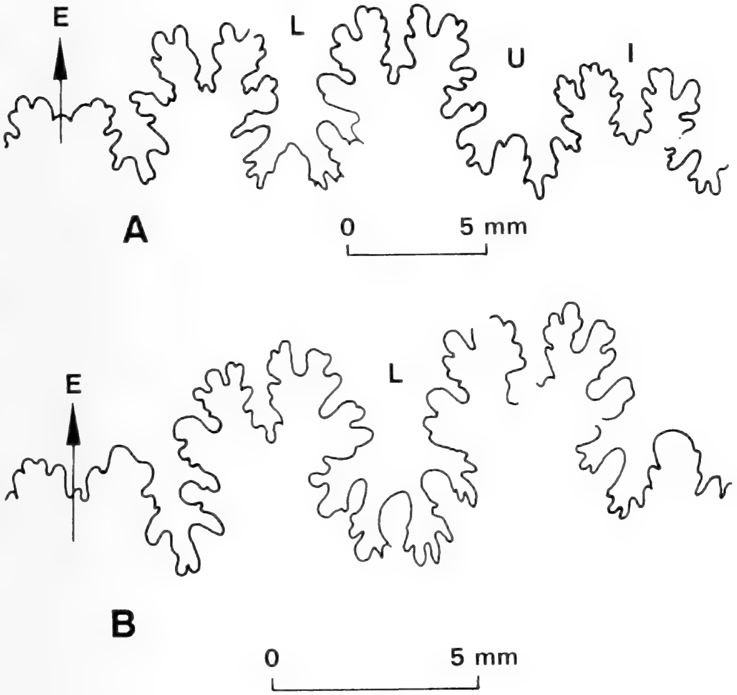

Fig. 104. *Baculites vanhoepeni* Venzo, 1936.
Suture lines. A–B. SAM-PCZ7706.
Scale bar for size.

Baculites taylorensis Adkins (1929: 204, pl. 5 (figs 9–11)), recently revised by Kennedy & Cobban (1993*a*: 93, figs 10.1–10.9, 10.11–10.12, 10.16, 10.18–10.19; 11.1–11.2; 1993*d*: 143, pl. 6 (figs 1–9), pl. 7 (figs 1–6, 10–13), text-fig. 8b, d), from the Middle Campanian Taylor Formation of Texas and the Annona Chalk in Arkansas, is indistinguishable from *B. vanhoepeni* on the basis of the original descriptions and figures of Adkins. The specimens figured by

Kennedy & Cobban, however, all seem to be consistently more weakly ornamented than *B. vanhoepeni* and more like *B. sparsinodosus*.

Matsumoto & Obata (1963: 55) also noted the parallelism between the lineages of *B. capensis–B. tanakae* in the Indo-Pacific region, and *B. codyensis* (as *B. asper*)–*B. taylorensis* in the Gulf–Atlantic region. In both lineages, which cover more or less the same time interval, there is a progressive increase in size, and coarsening and wider spacing of ornament.

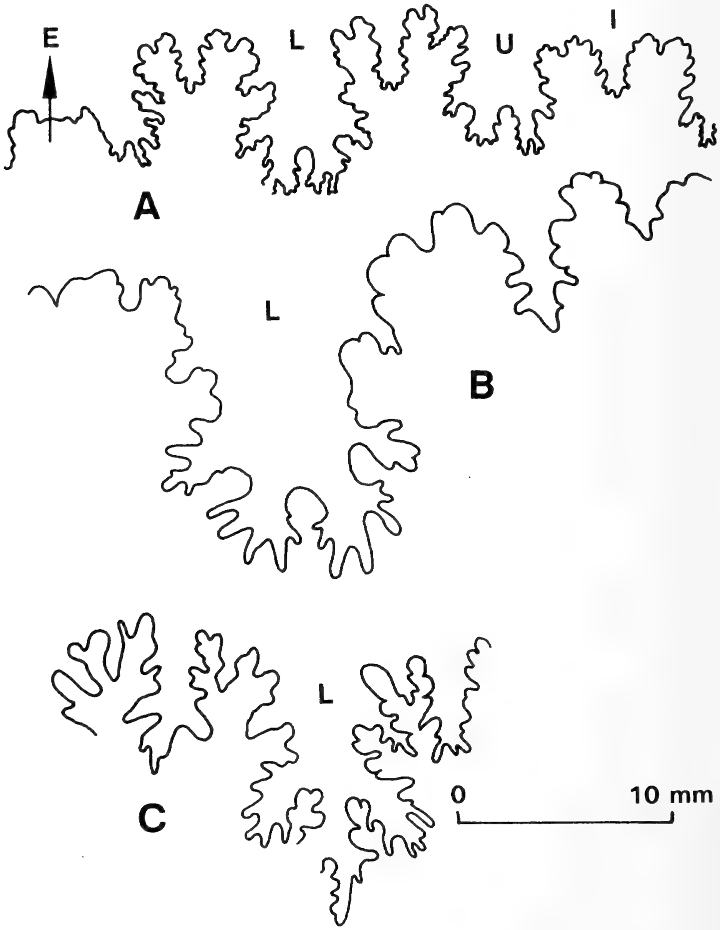

Fig. 105. *Baculites vanhoepeni* Venzo, 1936. Suture lines.
A–B. NMBD1302. C. SAM-PCZ7640.
Scale bar for size.

Baculites sp. (in Stephenson 1941: 407, pl. 76 (figs 7–8)) has similar lateral ornament, but the dorsum seems more flattened—as in *B. nibelae* sp. nov. According to Matsumoto (1959: 126), the former may be a representative of *B. lomaensis* Anderson (1958: 191, pl. 48 (figs 5–6)). The latter, however, apparently occurs in the Lower Maastrichtian of California.

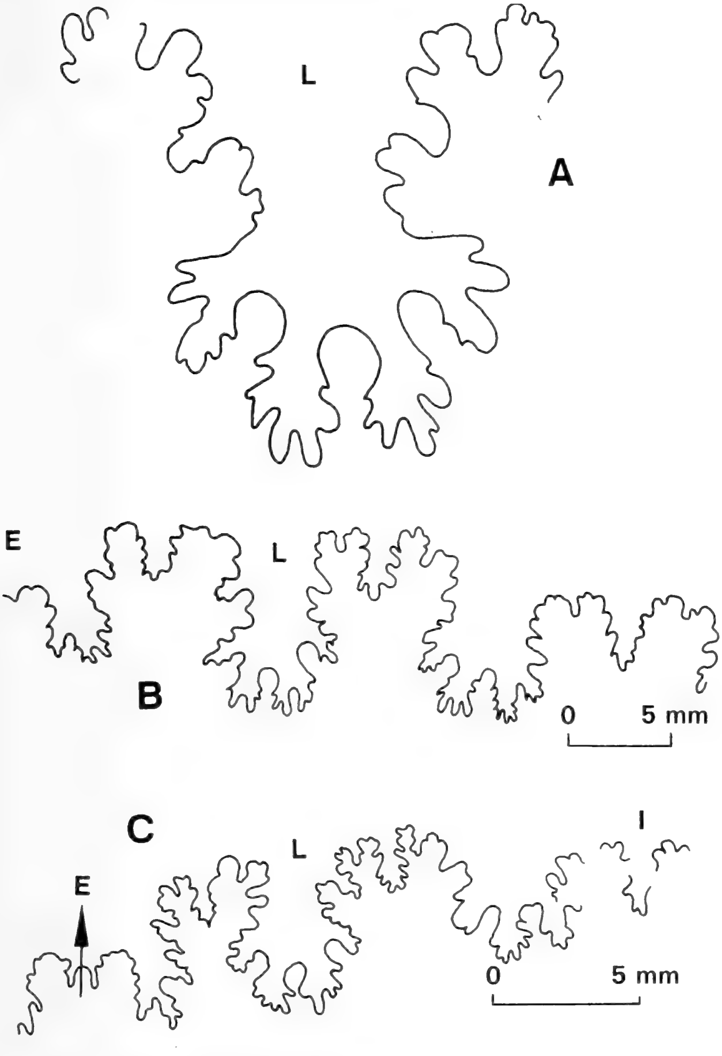

Fig. 106. *Baculites vanhoepeni* Venzo, 1936. Suture lines.
A–B. NMBD1302. C. SASZ1191.
Scale bar for size of B and C.

A similar convergent lineage occurs in the Middle Campanian of the U.S. Western Interior, consisting of *B. obtusus*–*B. maclearni*–*B. asperiformis*. The latter part of this lineage, *B. asperiformis*, is remarkably similar to *B. vanhoepeni*; compare e.g. *B. asperiformis* in Cobban (1962, pl. 106 (figs 10–11)) and Figure 91. The lateral ornament is identical, as is the occurrence of ventral ribbing. The sutures are also similar, although some specimens of *B. vanhoepeni* may have a more complex, dendritic suture. However, the early part of this lineage, *B. obtusus*, has closely spaced dorsolateral crescentic ribs and a strongly corrugated venter—quite unlike any of the Indo-Pacific material. *Baculites vanhoepeni* can perhaps be considered analogous to *B. obtusus*, but there are sufficient differences to separate them.

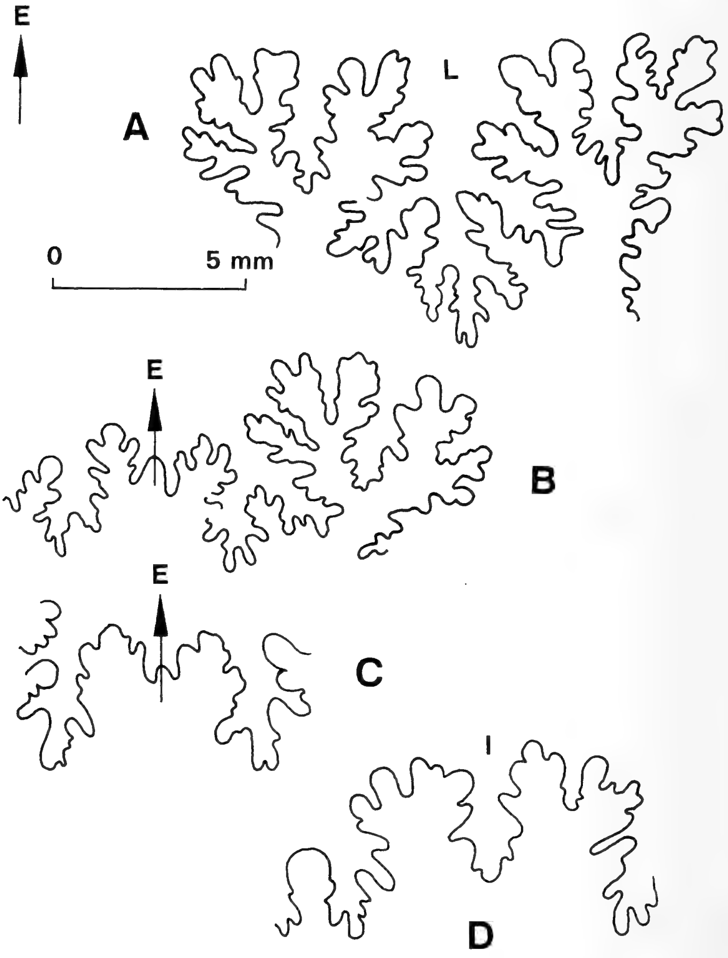

Fig. 107. *Baculites vanhoepeni* Venzo, 1936. Suture lines. A–D. SAS Z1923. Specimen with complex suture line and constricted lateral lobe (L). See also Fig. 108. Scale bar for size.

As far as the ornament is concerned, small specimens of *B. vanhoepeni* show a remarkable similarity to *Boehmoceras arculus* from the U.S. Gulf Coast described by Kennedy & Cobban (1991*b*), already referred to above (p. 121). Apart from the lack of the distinct curvature, specimens of *B. vanhoepeni*, e.g. Figure 91A–O are indistinguishable from *B. arculus* in Kennedy & Cobban (e.g. 1991*b*: fig. 9.11–52). Some specimens of *B. vanhoepeni*, e.g. PCZ8764 (Fig. 91A–C), do show slight curvature, but nowhere as pronounced as in

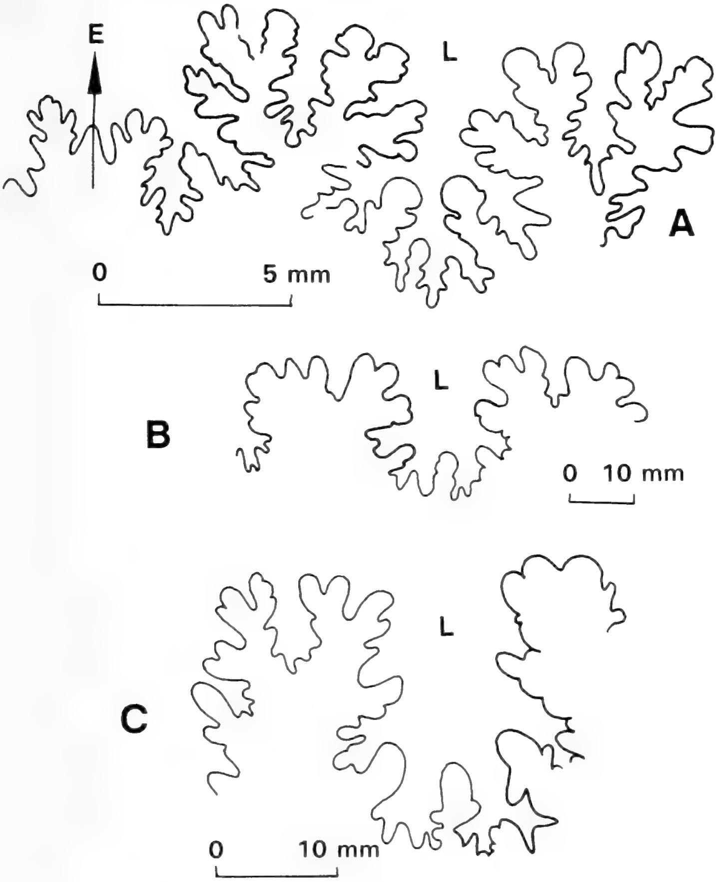

Fig. 108. *Baculites vanhoepeni* Venzo, 1936. Suture lines. A. SAS Z1923. Extremely complex, dendritic suture compared to other specimens. B. SAS A2029. C. SAS A2034. Scale bar for size.

Boehmoceras arculus. Apart from the curvature, *B. arculus* is an older species, occurring in the Upper Santonian, whereas *B. vanhoepeni* is definitely younger, occurring in the Middle to Upper Campanian of Zululand.

It thus appears that three, apparently unrelated baculitid lineages in the Indo-Pacific, the Gulf Atlantic and the U.S. Western Interior, respectively, gave rise in the Middle Campanian to remarkably similar forms with prominent, widely spaced arcuate bullae, viz. *B. vanhoepeni*, *B. taylorensis* and *B. asperiformis*. Another lineage gave rise to similar ornament in *Boehmoceras* in the Upper Santonian. This is a remarkable example of both isochronous and heterochronous homoeomorphy. It also illustrates the difficulties in trying to identify baculites on isolated specimens on the basis of ornament alone. A fuller discussion on these aspects of baculitid evolution is covered in Klinger & Kennedy (in press).

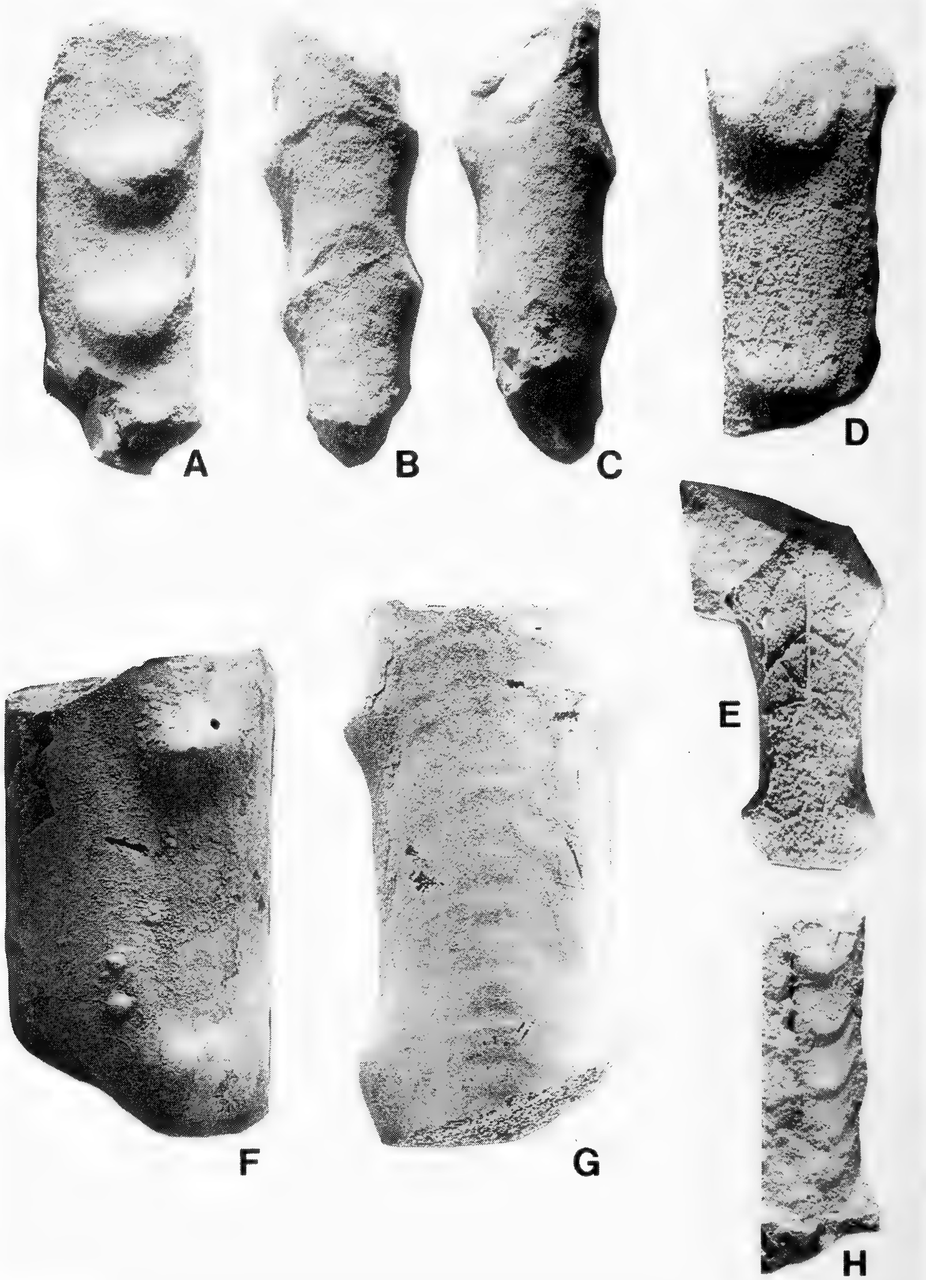

Fig. 109. *Baculites vanhoepeni* Venzo, 1936. A–C. SAS Z1868. D–E. SAM–PCZ7705. H. SAM–PCZ7714, all from locality 110, Zululand, St Lucia Formation, Campanian II–?III. F–G. From the collections of the Geology Department, University of Natal, from locality 4, Durban, Mzamba Formation, Campanian II. All × 1.

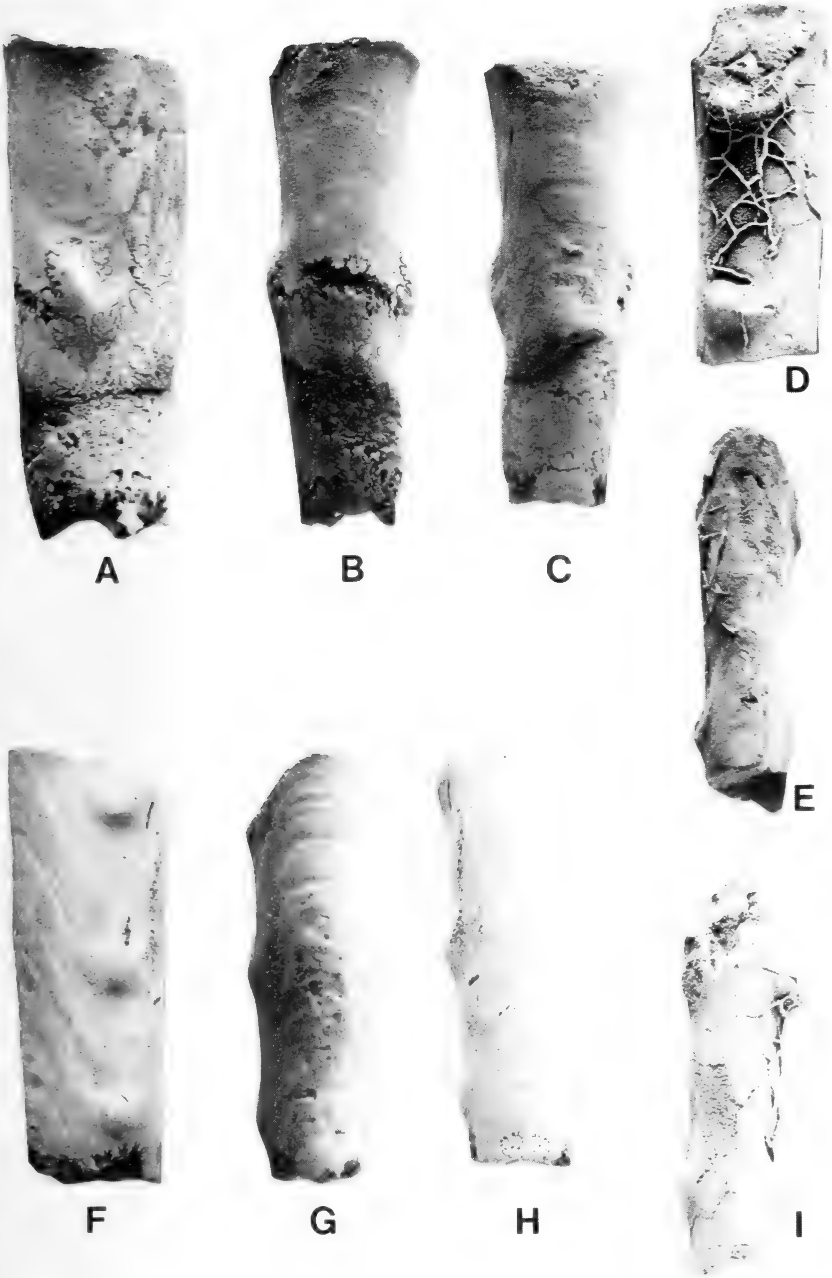

Fig. 110. *Baculites vanhoepeni* Venzo, 1936. A–I. Three unregistered specimens in the collections of the Geology Department, University of Natal, from locality 4, Durban, Mzamba Formation, Campanian II. All × 1.

Kennedy (1986*b*: 110, pl. 17 (figs 7–9, 13–15, 21–23), pl. 18 (figs 18–22), pl. 23 (figs 1, 7), text-fig. 8A, C) informally described a baculitid from the Upper Campanian of France as *Baculites* sp. 1. *Baculites vanhoepeni* was regarded as being closest to this informally named baculitid. In addition, Holzapfel's (1888: 64, pl. 4 (figs 5–6)) and Müller & Wollemann's (1906: 4, pl. 2 (figs 2–5)) *Baculites incurvatus* were regarded as belonging to this species. As discussed above, *B. incurvatus* is a Coniacian–Santonian species, and the German records from the Lower Campanian are obvious misidentifications. They seem closer to the Madagascan *B. menabensis*, which in turn is probably a synonym of *B. tanakae*.

Some of the larger French specimens figured by Kennedy (e.g. 1986*b*, pl. 18 (figs 18–22)) have ornament comparable to that of *B. vanhoepeni*, but more material is necessary for definite comparisons.

Occurrence

Baculites vanhoepeni typically occurs with a Middle Campanian texanitid fauna of *Australiella* and *Delawarella*, but we suspect that it ranges into the Upper Campanian by its association with *Hoplitoplacenticeras howarthi*, both at locality 110 in Zululand (Klinger & Kennedy 1989), and at Somtseu, Durban (Kennedy & Klinger 1973).

Baculites nibelae sp. nov.

Figs 116–120

? 1970 *Baculites* cf. *taylorensis* Adkins; Collignon, p. 13, pl. 612 (fig. 2285).
? 1970 *Baculites* sp. (nov.?) cf. *aquilaensis* Reeside; Collignon, p. 81, pl. 639 (fig. 2358).

Type

Holotype is SAM-PCZ9148b from locality 111, cliff section just east of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian III.

Material

Paratypes are SAM-PCZ7570, 7578, 7625, 7629, 7644, 7698a–e, 7702, 7850, 9155, 9163 and 9166, all from locality 109C; SAM-PCZ7569 from locality 109A, SAM-PCZ7631a, 7699, 7630, 7632, 7700 and 7701, from locality 109D, all on the western shores of the Nibela Peninsula, Zululand, St Lucia Formation, Campanian III; and SAM-PCZ9146, 9147, 9148a–e, 9149a–f, 9150a–g and 9151–9154, all from locality 111, St Lucia Formation, Campanian III.

Fig. 111 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. Two unregistered specimens in the collections of the Geology Department, University of Natal, from locality 4, Durban, Mzamba Formation, Campanian II. Note similarity of A–C to *Baculites collignoni* nom. nov. (see Fig. 96). All × 1.

Fig. 112 *(see overleaf)*. *Baculites vanhoepeni* Venzo, 1936. Three unregistered specimens in the collections of the Geology Department, University of Natal, from locality 4, Durban, Mzamba Formation, Campanian II. Note similarity to *Baculites mamillatus* (see Fig. 84A–C). All × 1.

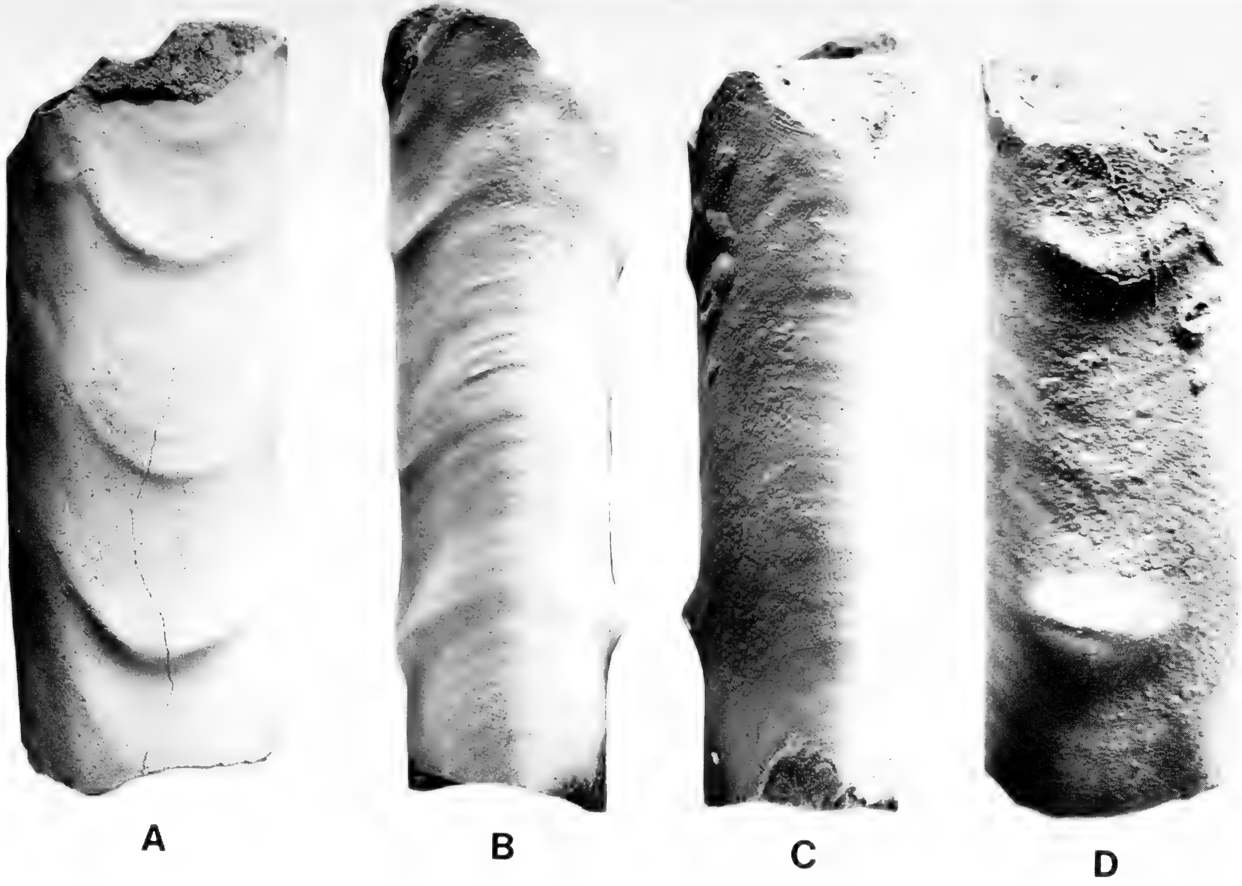

Fig. 111

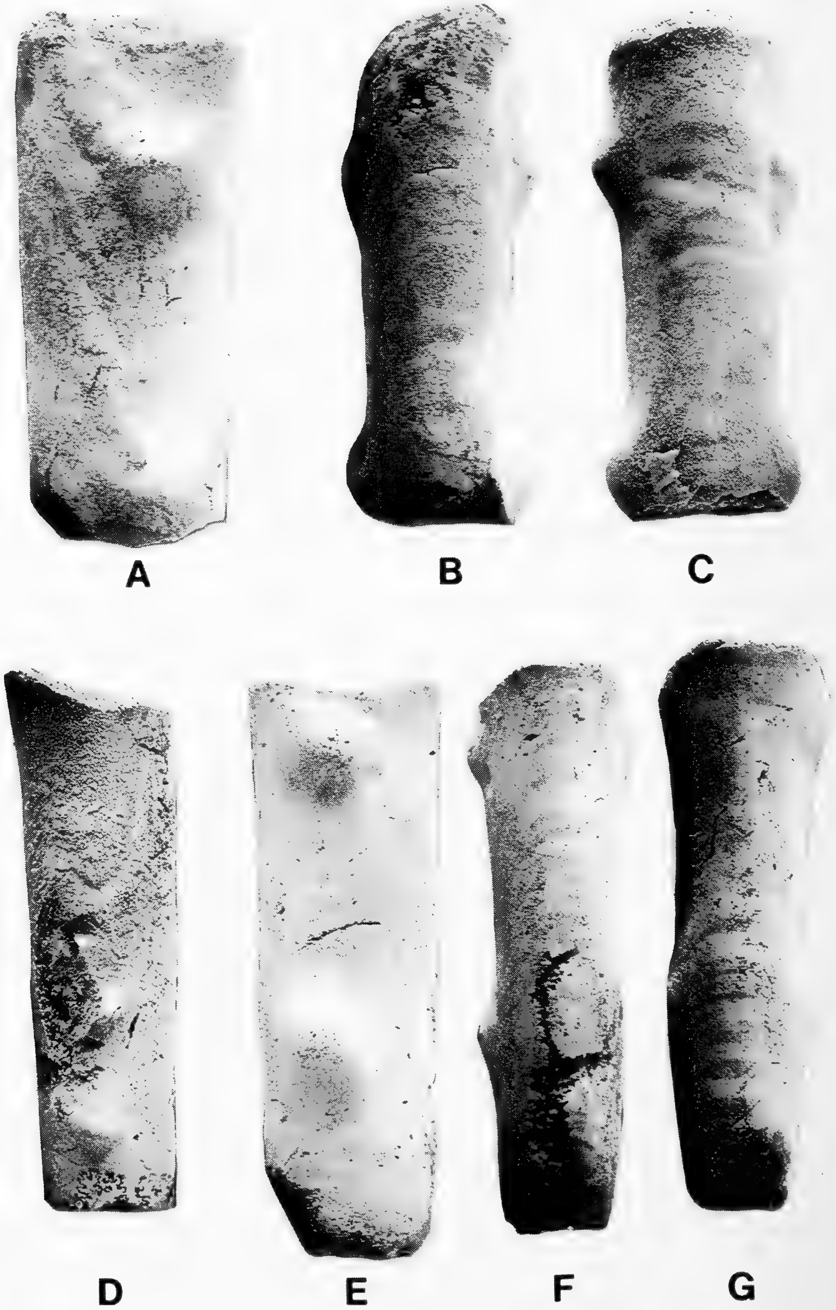

Fig. 112

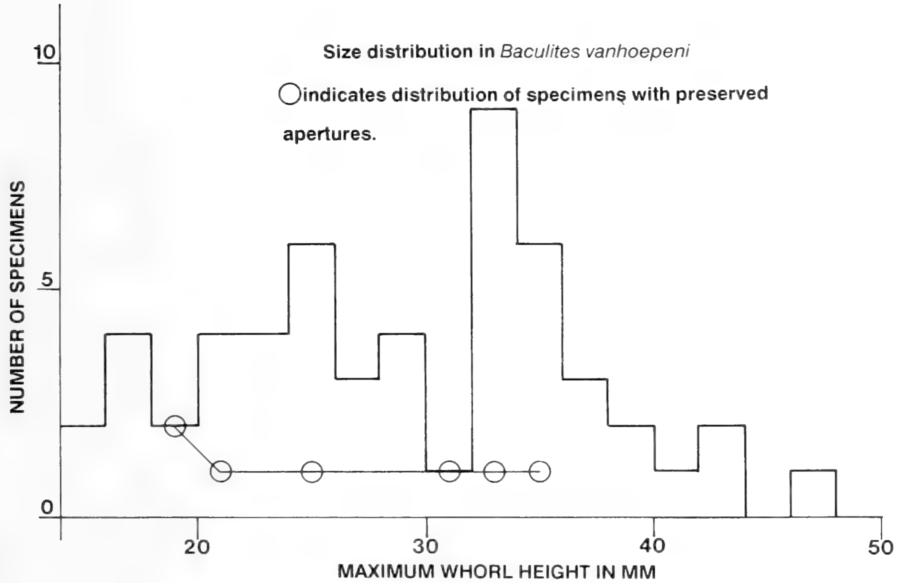

Fig. 113. Histogram illustrating maximum size distribution in *Baculites vanhoepeni* Venzo, 1936. Open circles indicate specimens with the aperture preserved.

Dimensions

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Ri*
PCZ7578	26.0	34.0	0.76	—	—	—	—	—	—
PCZ9148b	22.0	29.0	0.76	18.0	26.0	0.70	96	3.1	2½
PCZ7698a	21.0	29.0	0.72	—	—	—	—	—	—
PCZ7699	21.0	29.0	0.72	—	—	—	—	—	—
PCZ9148a	20.0	27.0	0.74	17.0	22.0	0.77	70	7.1	—
PCZ9153	20.0	30.0	0.67	19.0	28.0	0.68	68	7.1	2½
PCZ9149b	18.0	23.0	0.78	16.0	23.0	0.7	52	—	2½
PCZ9149d	18.0	25.0	0.72	—	—	—	—	—	—
PCZ7631	17.5	24.0	0.73	—	—	—	—	—	—
PCZ9149a	—	15.0	—	—	12.0	—	54	5.6	2½
PCZ9148e	10.0	14.0	0.71	9.0	13.0	0.61	60	1.7	2½

Diagnosis

Baculitid with subtrigonal whorl section and arcuate lateral ornament.

Description

The maximum observed whorl height is 34 mm. In typical forms the whorl section is subtrigonal with a distinctly flattened dorsum and flanks converging to a rounded venter (Fig. 118B–G). In juvenile specimens the whorl section is distinctly ovoid to tear-shaped with the venter much narrower than the dorsum.

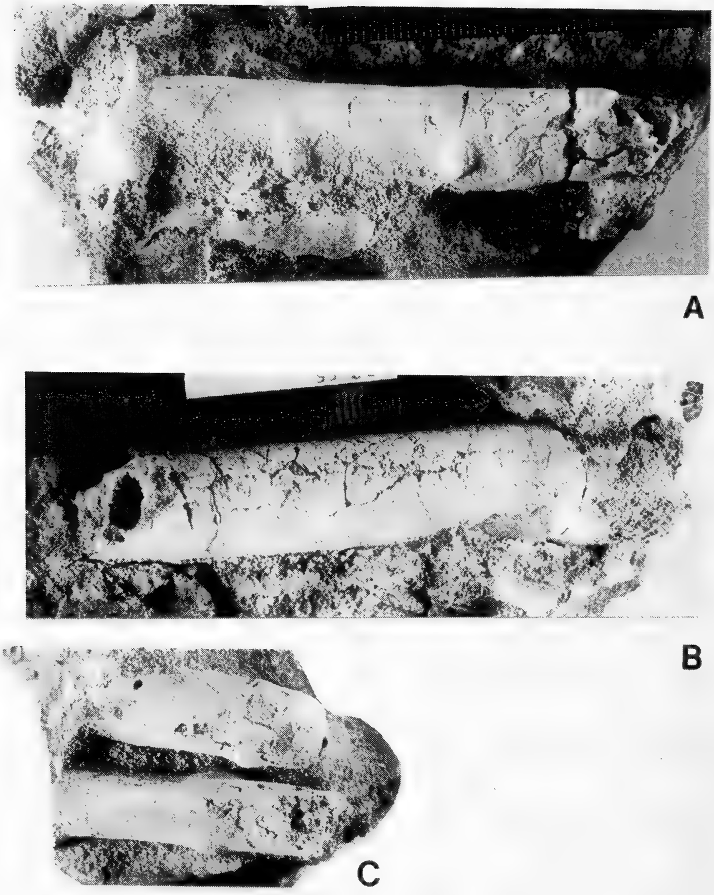

Fig. 114. *Baculites vanhoepeni* Venzo, 1936. ?Early forms. A–B. SAM–PCZ9255. C. SAM–PCZ9252. Both from locality 109A, Zululand, St Lucia Formation, Campanian II. All × 1.

Fig. 115 *(see facing page)*. *Baculites vanhoepeni* Venzo, 1936. A–C. Typical form, SAM–PCZ9284 from locality 110. D–F. SAM–PCZ9131, ?early form, from locality 109A. Both × 1.

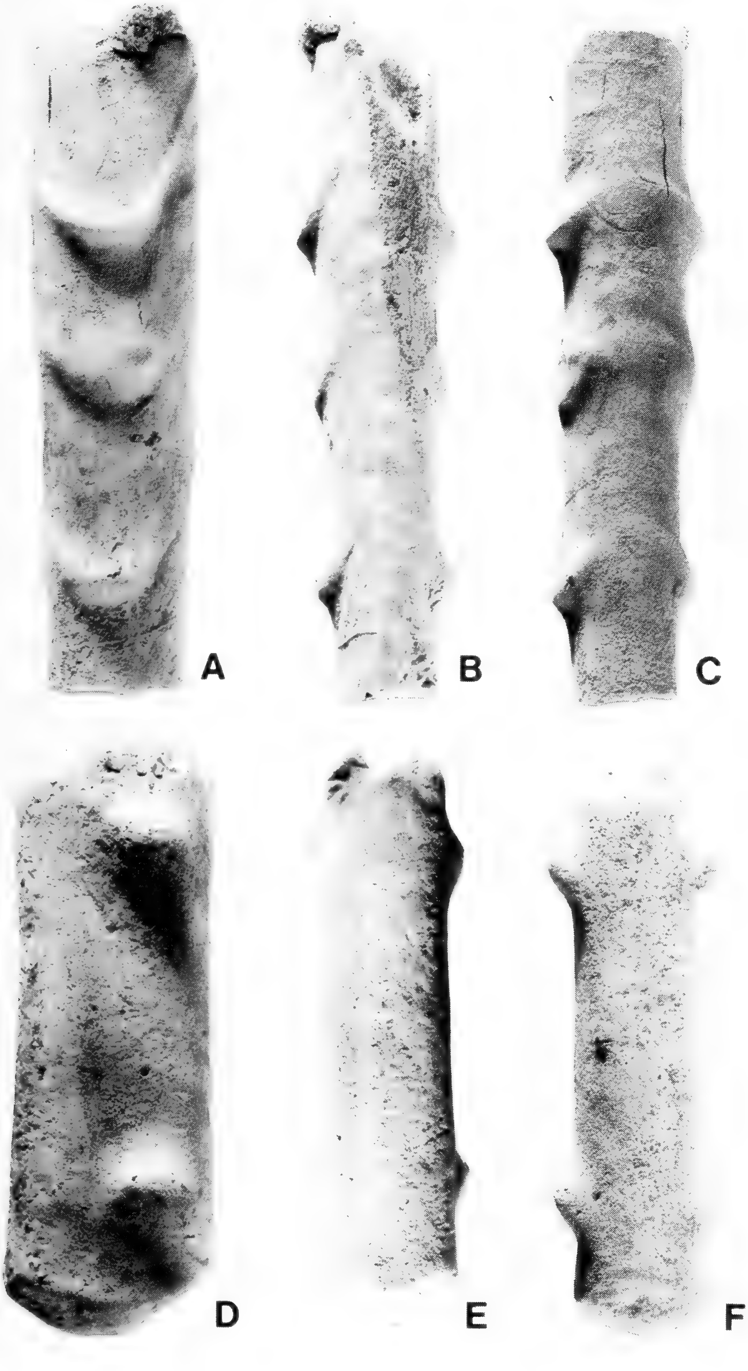

Fig. 115

Fig. 116. *Baculites nibelae* sp. nov. The holotype, SAM-PCZ9148, from locality 111, St Lucia Formation, Campanian III. × 1.

Fig. 117 *(see facing page)*. A-D, F-I. *Baculites nibelae* sp. nov. A. SAM-PCZ9148a. B. SAM-PCZ9149a. C-D. SAM-PCZ9150e. Specimen with part of aperture preserved. F-H. SAM-PCZ9153. I. SAM-PCZ7631. All from locality 111, St Lucia Formation, Campanian III. E. *Baculites duharti* Hünicken, 1975. SAM-PCZ9873c, from concretion at base of cliff at locality 110, Zululand, St Lucia Formation, Campanian II. All × 1.

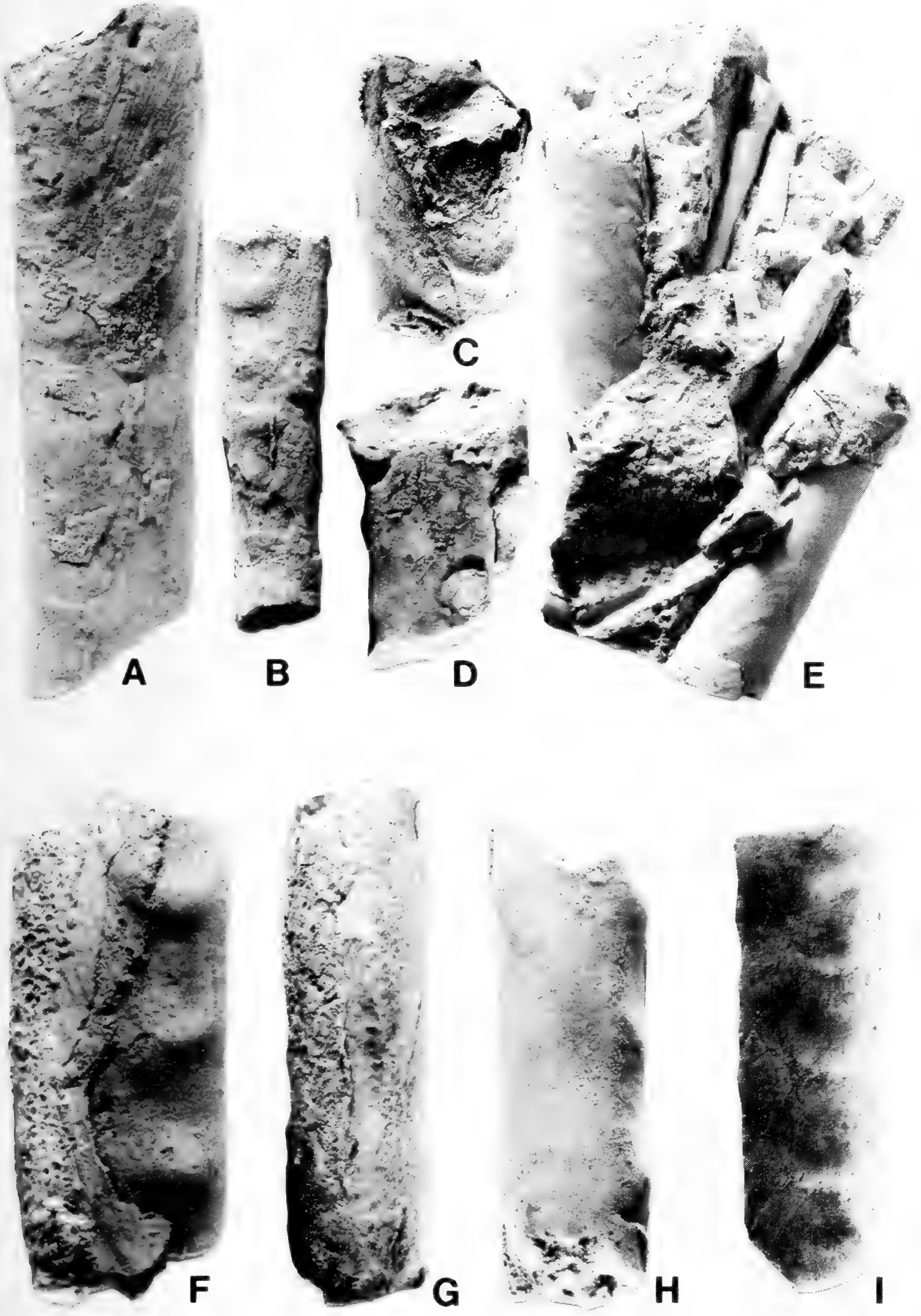

Fig. 117

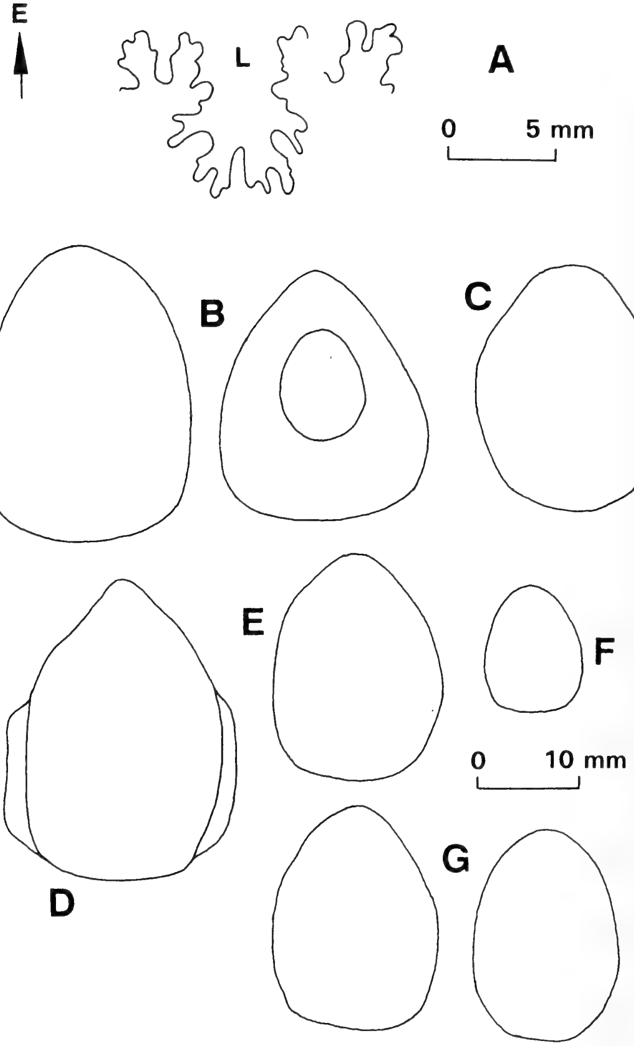

Fig. 118. *Baculites nibelae* sp. nov. Partial suture line and whorl sections. A. SAM-PCZ7630. B. SAM-PCZ7631. C. SAM-PCZ7701. D. SAM-PCZ7644. E. SAM-PCZ7630. F. SAM-PCZ7631. G. SAM-PCZ7698. Venter in whorl section facing upward. Scale bar for size.

Fig. 119 *(see facing page)*. *Baculites nibelae* sp. nov. A. SAM-PCZ7702. B–D. SAM-PCZ7361a. E–F, I. SAM-PCZ7578. G. SAM-PCZ7698. H. SAM-PCZ9153. All from locality 109, Zululand, St Lucia Formation, Campanian III. All × 1.

Fig. 120 *(see overleaf)*. *Baculites nibelae* sp. nov. A. SAM-PCZ7630. B–D. SAM-PCZ12021. E. SAM-PCZ9149. F. SAM-PCZ7698. G. SAM-PCZ9148e. All from locality 109, Zululand, St Lucia Formation, Campanian III. All × 1.

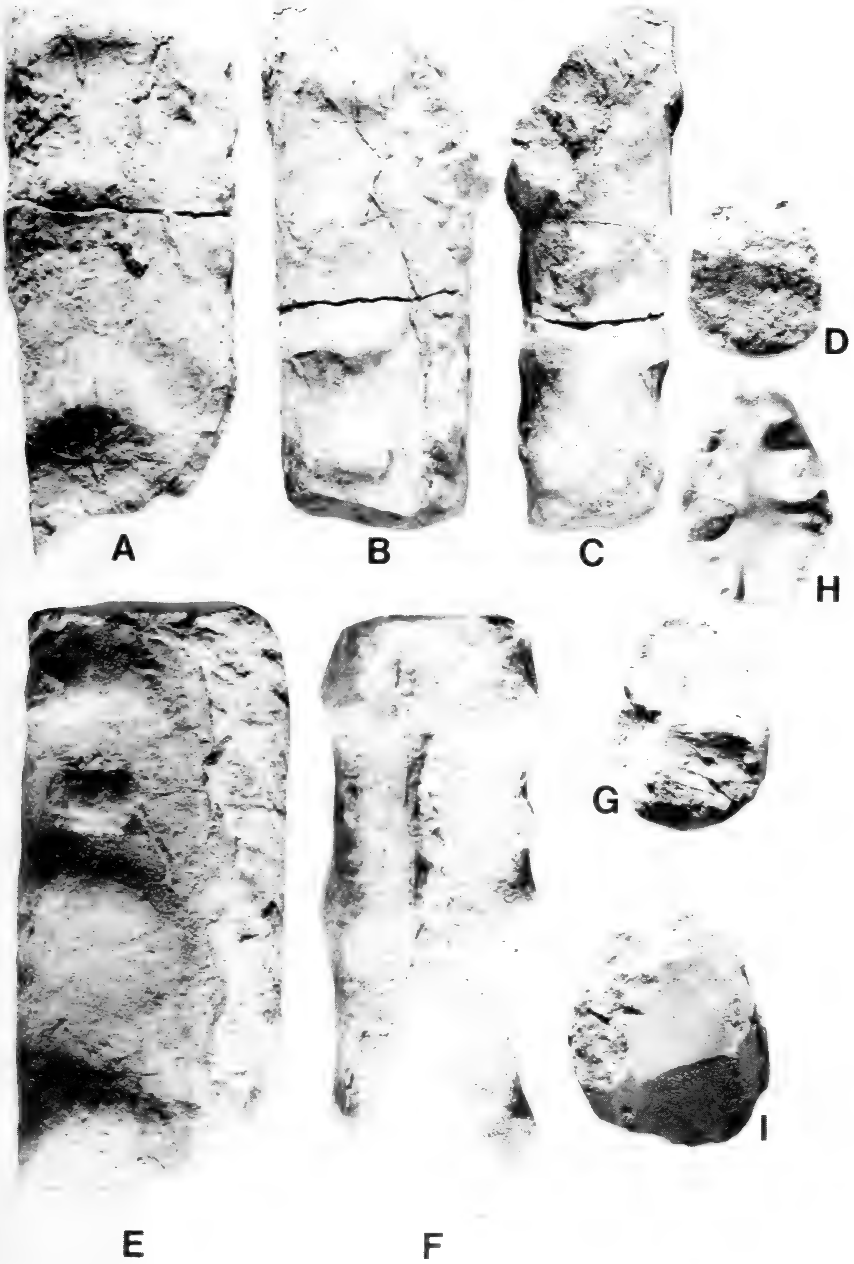

Fig. 119

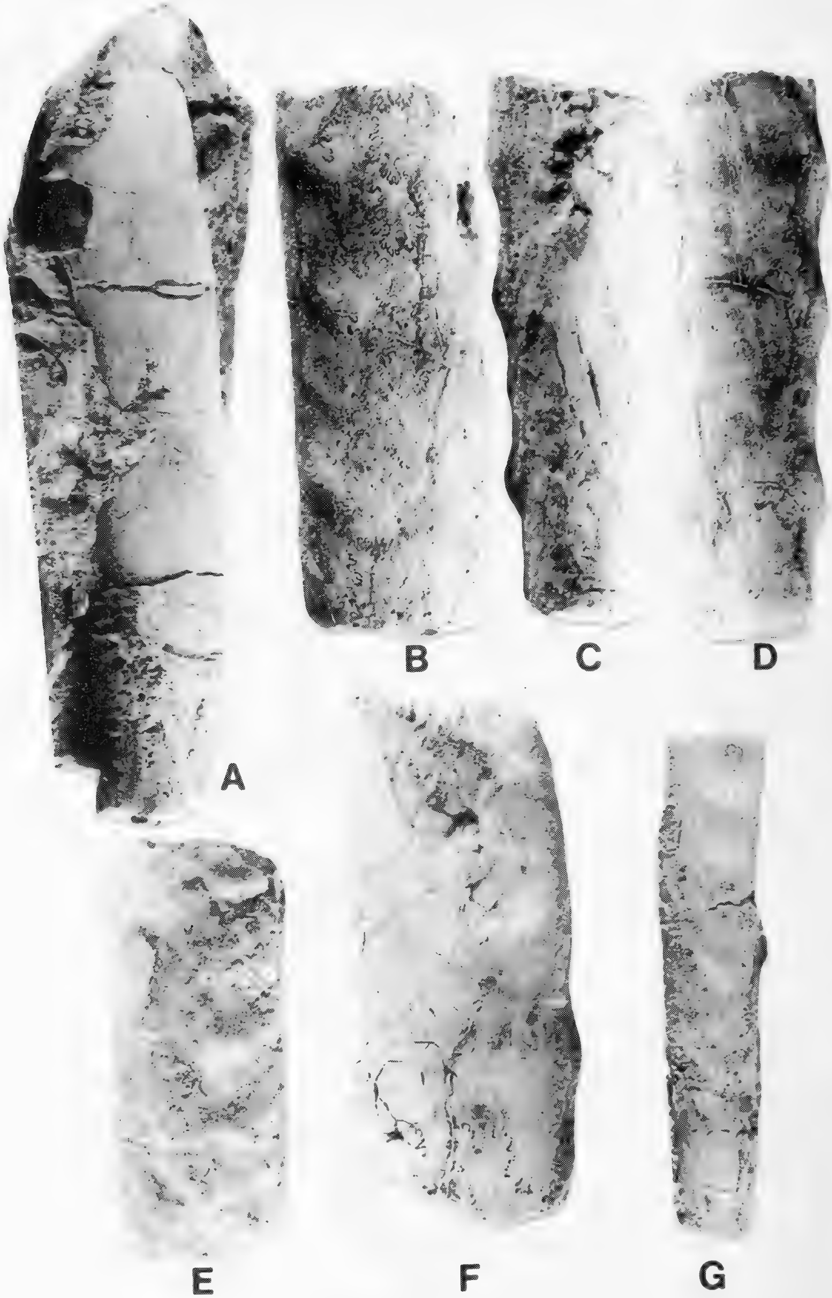

Fig. 120

Lateral ornament consists of crescentic ribs of variable strength, which cover the dorsal two thirds of the flanks—occurring at a frequency of 2–3 per whorl height. In some, e.g. PCZ7630 (Fig. 120A) and PCZ7701, the flanks are virtually smooth; in others, e.g. PCZ7702 (Fig. 119A), the ribs are quite prominent. In the latter, the costal whorl section is conspicuously trigonal to cuneate. In some specimens the venter appears to be slightly undulating.

The aperture is preserved in PCZ9150e (Fig. 117C–D). The dorsal rostrum is short, and the ventral rostrum only a little longer, and distinctly spoon-shaped.

The suture is only partially exposed in a few specimens, e.g. PCZ9150h and PCZ7630 (Fig. 118A). It shows narrow lateral saddles and a splayed lateral lobe (L).

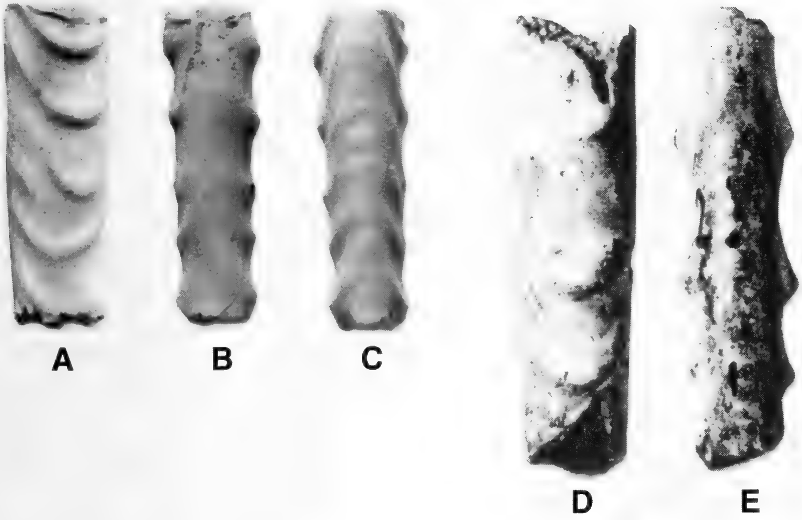

Fig. 121. A–C. *Baculites* sp. (?nov.) cf. *B. aquilaensis* Reeside. Plaster cast of GD12358, the original of Collignon (1970, pl. 639 (fig. 2358)), from the Upper Campanian, zone of *Hoplitoplacenticeras marroti* of gisement 227–2, Mokotibe (Antsalova), Madagascar. D–E. *Baculites bassei* Besairie, 1930. Copy of the lectotype illustrated in Besairie (1930, pl. 22 (fig. 8–8a)), from the Upper Campanian or Lower Maastrichtian, of north of Trangahy, Madagascar. Both × 1.

Discussion

The subtrigonal whorl section clearly distinguishes *B. nibelae* from *B. vanhoepeni*, the latter having a typically elliptical whorl section. The shape of the lateral ribs in both species is similar but those of *B. vanhoepeni* are much more robust, and the latter species grows to a much larger size than *B. nibelae*. The occurrence of *B. nibelae* at locality 111, east of 110, suggests that it is younger than *B. vanhoepeni*, but still in the Campanian.

The subtrigonal whorl section of *B. nibelae* places this species close to the group of baculitids described by Collignon (1970) from the lower part of the Middle Campanian of Madagascar. The closest match is probably *B. rectangulatus* Collignon (1970: 12, pl. 611 (figs 2279–2281)) (herein Fig. 87), but the whorl section of *B. nibelae* is more prominently triangular and, in typical forms, it has stronger lateral ornament.

The specimen described by Collignon (1970: 13, pl. 612 (fig. 2285)) from the upper part of the Middle Campanian of Madagascar as *Baculites* cf. *taylorensis* is probably the same as *B. nibelae*. *Baculites* sp. (nov.?) cf. *B. aquilaensis* in Collignon (1970: 81, pl. 639 (fig. 2358)) (Fig. 121A–C) from the Upper Campanian of Madagascar has stronger ornament than any of our *B. nibelae*, but the whorl section suggests that it is closely allied. *Baculites bassei* Besairie (1930: 222, pl. 22 (fig. 8, 8a)) (herein Fig. 121D–E), from the Upper Campanian or Lower Maastrichtian of north of Trangahy (Maintirano) in Madagascar, is known from a single specimen only. It is also very similar to *B. nibelae*. Given more and precisely located material from Madagascar, *B. bassei* may prove to be a senior synonym of *B. nibelae*.

The Campanian baculitid from Andimaka described by Collignon (1938) as *B. aspero-anceps* (Collignon 1938: 89, pl. 6 (fig. 7)), also has a trigonal whorl section similar to that of *B. nibelae*, and may belong to this species.

In terms of lateral ornament and to a lesser extent, the whorl section, *B. nibelae* is similar to *B. subanceps* Haughton (Figs 130, 131A–H) (see also Howarth 1965: 368, pl. 5 (fig. 3), pl. 6 (figs 6–7), pl. 7 (fig. 1), text-figs 4, 13–15). In the latter species, however, the venter tends to become flat and, in some specimens, even forms an incipient tabulate ventral keel as in typical *Eubaculites*.

The whorl section and ornament of *B. nibelae* are very similar to those of *Eubaculites labyrinthicus* (Morton), recorded from the Lower Maastrichtian of Madagascar by Collignon (1971: 18, pl. 646 (fig. 2395)) (as *Eubaculites otacodensis* Stol.). As yet undescribed baculitids from the Upper Campanian of Israel, with even more angular trigonal whorl section and prominent lateral ribbing, are even closer to *E. labyrinthicus*. *Baculites lomaensis* Anderson (1958: 191, pl. 48 (figs 5, 5a–6)) (see also Matsumoto 1959: 126, pl. 34 (figs 1a–c, 2a–c), text-figs 35–38, 39–41), from the Lower Maastrichtian of California, has a similar trigonal whorl section, but apparently weaker dorsolateral bullae. We doubt if *B. nibelae*, *B. lomaensis* and the Israeli baculitids are ancestral to *E. labyrinthicus*, but the style of ornament and whorl section are remarkably similar.

The evolution of baculitids with a trigonal whorl section, as in *E. labyrinthicus*, appears to be a wide-spread feature near the Campanian–Maastrichtian boundary, as already noticed by Lewy (1986: 5) (see also Klinger & Kennedy in press).

Fig. 122 *(see facing page)*. *Baculites duharti* Hünicken, 1975. A–D. SAM-7683 from locality 109H, Zululand, St Lucia Formation, Campanian II. E–G. SAM-PCZ9873a from locality 110, Zululand, St Lucia Formation, Campanian II.
A, E–G × 1; B–D × 0.75.

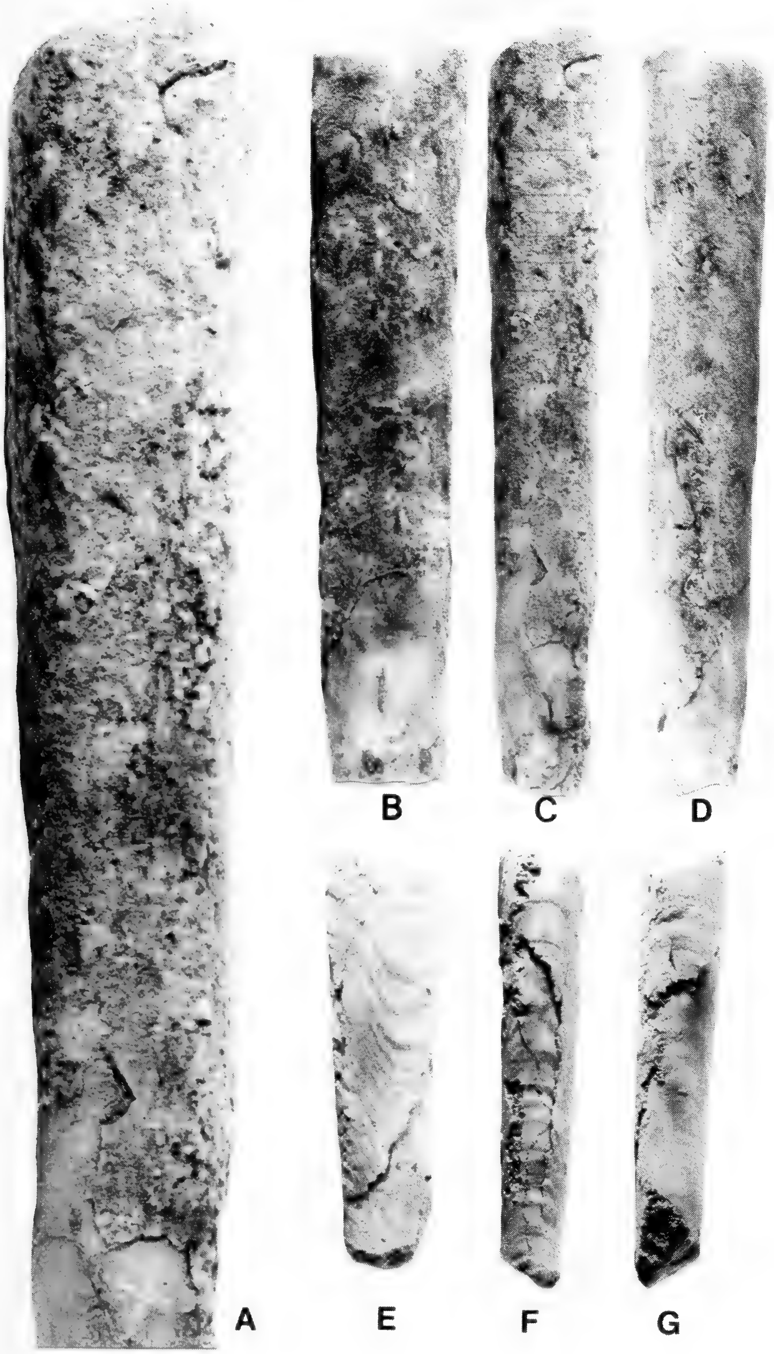

Fig. 122

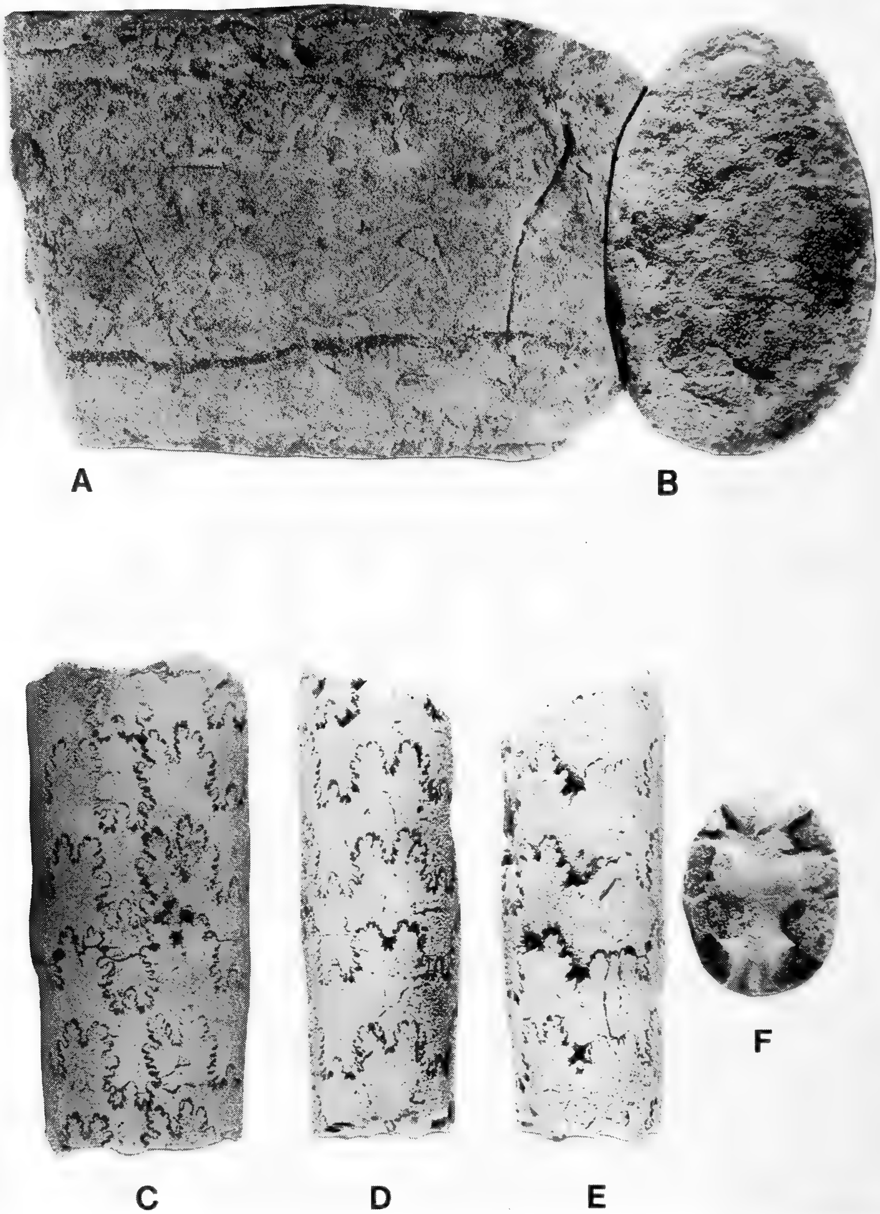

Fig. 123. *Baculites duharti* Hünicken, 1975. A–B. SAM-PCZ7703a. C–F. SAM-PCZ7685, both from locality 109G, Zululand, St Lucia Formation, Campanian II. Both × 1.

Fig. 124 *(see facing page)*. *Baculites duharti* Hünicken, 1975. Concretion, SAM-PCZ9873, from base of cliff at locality 110, Zululand, St Lucia Formation, Campanian II. All × 1.

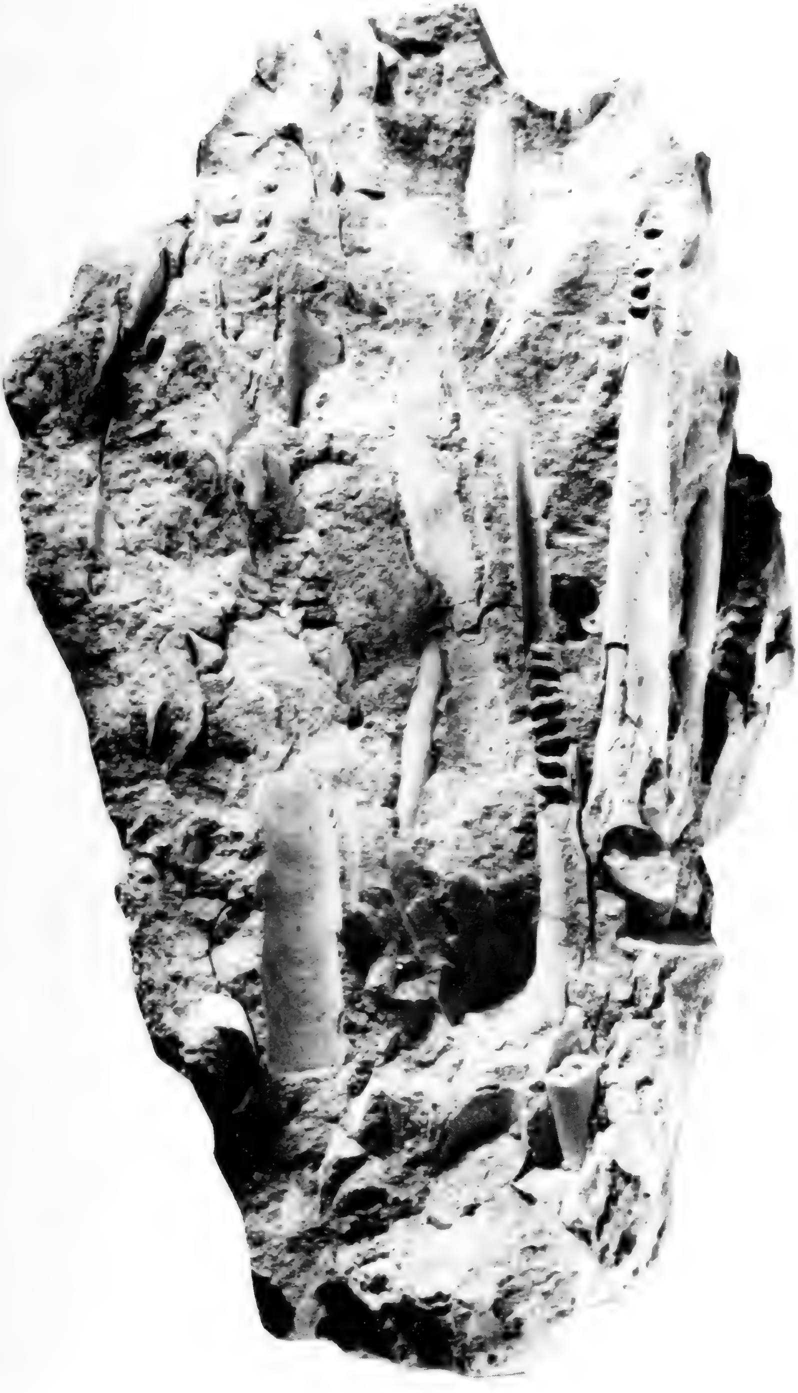

Fig. 124

Occurrence

Campanian III of Zululand.

Baculites duharti Hünicken, 1975

Figs 122–127

1975 *Baculites duharti* Hünicken, *in* Hünicken *et al.* 1975, p. 116, pl. 1 (figs 1–4), pl. 2 (figs 1–2), pl. 3 (figs 5–8), text-figs 2a–d, 3a–c, 4–5.

1980 *Baculites duharti* Hünicken; Hünicken, Charrier & Lahsen, p. 224, pl. 1 (figs 1a–b, 2), pl. 2 (figs 1a–c, 2, 3a–b, 4–5, 6a–b), text-figs 3–9.

Type

Holotype is the specimen figured by Hünicken (in Hünicken *et al.* 1975, pl. 1 (figs 1–4), text-figs 2c–d, 4a) from the Middle and/or Upper Campanian of Member 'e' of the Cerro Matero Formation, at Rio Sur, Tierra del Fuego, Chile, CPC D1127.

Material

More than 100 specimens from a single concretion, SAM–PCZ9873, 9873a–v, found at the base of the section at locality 110, Nibela Peninsula, Zululand, St Lucia Formation, Campanian III; SAM–PCZ7683, 7685, and 7703, from locality 109G; and SAM–PCZ7689 from locality 109H, Nibela Peninsula, Zululand (Fig. 90), St Lucia Formation, Campanian II.

Dimensions

Spec.	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*
PCZ9873a	12.0	17.0	0.71	8.6	12.0	0.72	48	10.4
PCZ7689	22.0	31.0	0.71	21.0	28.0	0.75	64	4.69
PCZ7685	22.0	29.0	0.76	20.0	26.0	0.77	57	5.26
PCZ7683	34.0	43.0	0.79	23.5	31.0	0.76	200	6.0
PCZ7703	35.0	58.0	0.60	—	—	—	—	—

Description

A large concretion from the base of the section at locality 110 is crammed with more than 100 specimens of a smooth baculitid (Figs 124–126), differing markedly from the heavily ornamented *B. vanhoepeni* from the higher parts of the section. Four other smooth baculitids from the south-western part of the Nibela Peninsula at localities 109G and 109H (Figs 122A–D, 123A–F) are much larger than those from locality 110, but we assume they belong to the same species—being of more or less the same age.

Fig. 125 *(see faing page)*. *Baculites duharti* Hünicken, 1975. Concretion, SAM–PCZ9873, from the base of cliff at locality 110, Zululand, St Lucia Formation, Campanian II. Note slight wavy venter on top right. × 1.

Fig. 125

Fig. 126. *Baculites duharti* Hünicken, 1975. Concretion, SAM-PCZ9873, from base of cliff at locality 110, Zululand, St Lucia Formation, Campanian II. Note wavy venter at top left. × 1.

The whorl section (Figs 123B, F, 127) is distinctly elliptical, to ovoid, with the venter only very little narrower than the dorsum. Lateral ornament consists of very fine striae only, but in some specimens, e.g. PCZ9873a (Fig. 122E–G), low, fold-like ribs develop over the ventral half of the flanks. In some of the larger specimens, where the shell is preserved (Figs 125, 126), the venter is ornamented with scale-like undulations.

A slight constriction is visible on the venter of SAM–PCZ7685 (Fig. 123C–F). The species grows to a large size—the maximum whorl height measured is 60 mm (Fig. 123A–B). The suture is finely incised with open saddles and lobes (Fig. 127A–C).

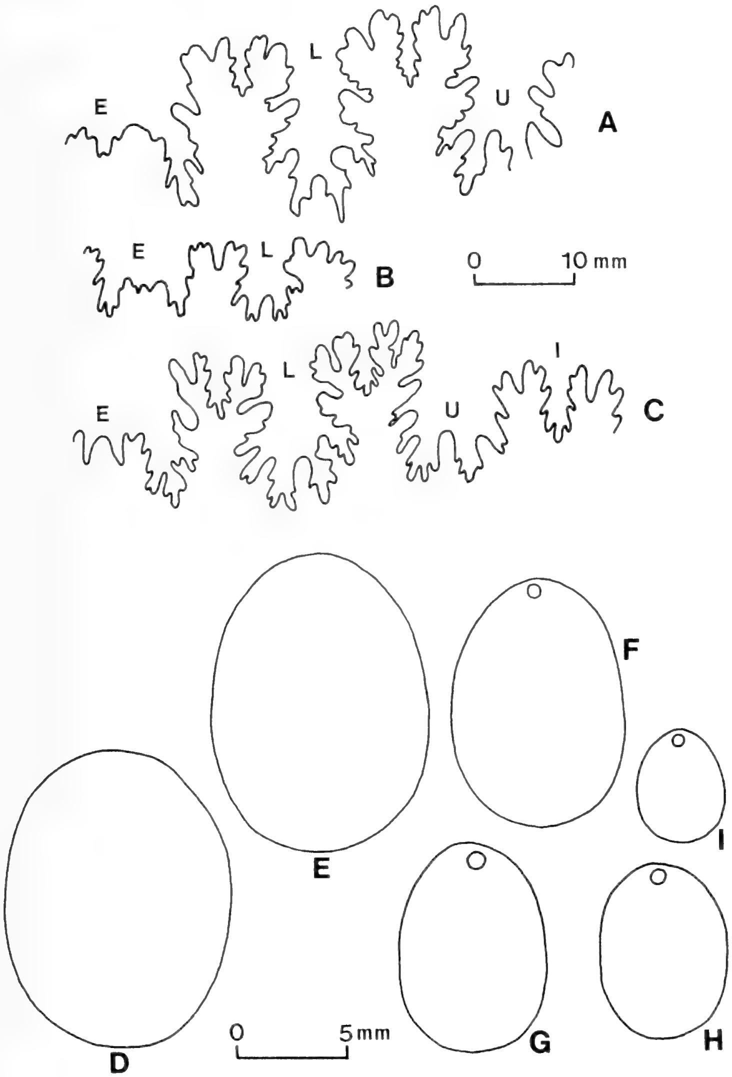

Fig. 127. *Baculites duharti* Hünicken, 1975. Suture lines and whorl sections. Venter facing upwards. Scale bar for size.

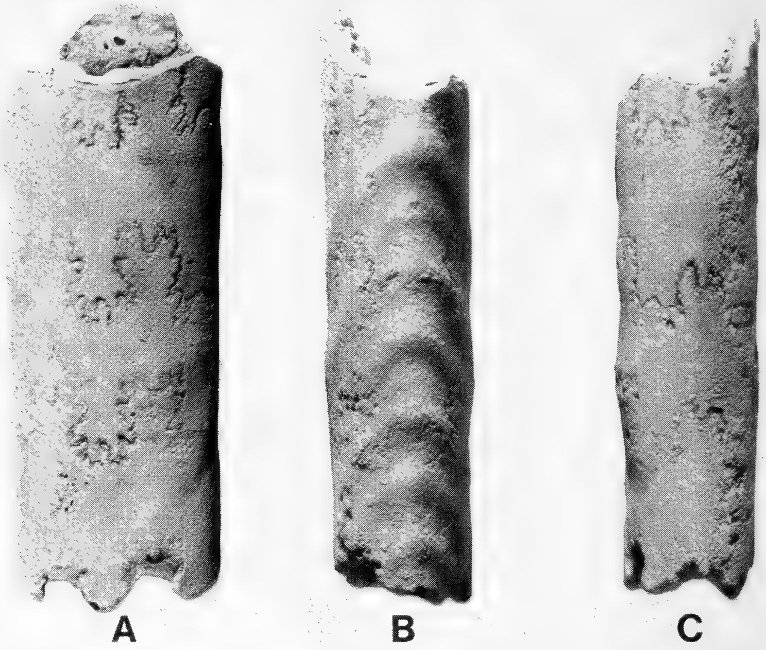

Fig. 128. *Baculites ambatryensis* Collignon, 1971. Plaster cast of the holotype, GD12392, the original of Collignon (1971, pl. 645 (fig. 2392)) from the Lower Maastrichtian of gisement 400, Cote d'Ambatry (Betioky), Madagascar. All × 1.

Discussion

The elliptical whorl section and relatively simple suture show that this baculitid belongs to the group of *B. vanhoepeni*. However, the total absence of lateral ornament in more than a hundred specimens clearly shows that this is indeed a consistently smooth baculitid species and not merely a smooth variant of *B. vanhoepeni*.

As discussed above, identifying or separating smooth *Baculites* species is very difficult unless the whorl section and sutures are very distinctive, or if the exact age is known.

The closest match we could find both in morphology and age is *B. duharti* first described from Tierra del Fuego by Hünicken (in Hünicken *et al.* 1975: 116, pl. 1 (figs 1–4), pl. 2 (figs 1–2), pl. 3 (figs 5–8), text-figs 2a–d, 3a–c), 4–5) and imprecisely dated as Campanian–Maastrichtian. Later, Hünicken *et al.* (1980: 224, pl. 1 (figs 1a–b, 2), pl. 2 (figs 1a–c, 2, 3a–b, 4–5, 6a–b),

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Fig. 129 *(see facing page)*. *Baculites asperoanceps* Lasswitz, 1904. Plaster cast of the lectotype, nr 3045 s (k), MGUWr, from Austin, Texas, in the collections of the Henryk Teisseyre Geological Museum of the Institute of Geological Sciences of the University of Wroclaw. × 1.

Fig. 129

text-figs 3–9) described additional material, also from Tierra del Fuego, but more precisely dated as Middle to Late Campanian. The drawings of the suture lines by Hünicken *et al.* (1980, text-figs 3–9) show a suture more complex and phylloid than ours, but photographs of the sutures (e.g. their pl. 2 (figs 3–6)) are much simpler and comparable to the Zululand material. From a palaeobiogeographical point of view, the record of *B. duharti* from Zululand also is acceptable.

Baculites duharti differs from the older *B. bailyi* mainly in being much larger and having a predominantly elliptical, rather than ovoid, whorl section. We do not think that *B. duharti* is derived from the *B. bailyi* lineage; instead we regard it as a smooth offshoot of the *B. capensis–B. vanhoepeni* lineage.

Baculites duharti clearly differs from *B. rectus* in having a much simpler suture.

The only Middle Campanian Madagascan baculitid species with which *B. duharti* could possibly be compared, is *B. ankilizatensis* (Collignon 1970: 13, pl. 612 (figs 2282–2284)) (herein Fig. 89), especially as far as maximum size is concerned. However, some specimens of *B. ankilizatensis* show distinct, albeit low, lateral ornament.

Some specimens of *B. subanceps* in the collections of the South African Museum, e.g. SAM–6829a (Figs 130D–F) are indistinguishable from *B. duharti*, but this species includes forms with distinct lateral ornament, and the whorl section is quite distinctive in some specimens, tending to form a tabulate ventral keel.

Our material also resembles *Baculites* smooth species of Cobban (1962: 714, pl. 108 (figs 1–4), text-figs 1i–j) from the Middle Campanian of eastern Wyoming. This species was renamed *B. cobbani* by Khakimov (in Atabekian & Khakimov 1976: 98, pl. 11 (figs 2–7)) for material from the Lower Campanian of Central Asia.

The largest of our specimens (Fig. 123A–B) is superficially similar to *B. knorrianus* Desmarest, 1817 (recently reviewed by Kennedy & Summesberger 1987: 32, pl. 4 (figs 4–6), pl. 5 (figs 1–14), text-fig. 2; Birkelund 1993: 52, pl. 13 (figs 12–14) and Kennedy 1993: 109, pl. 5 (figs 13–22), pl. 6 (figs 11–13, 18–23), text-fig. 5a–c). However, *B. knorrianus* is restricted to the Lower Maastrichtian, and has a far more compressed whorl section and a more complex suture line.

Fig. 130 *(see facing page)*. *Baculites subanceps* Haughton, 1925. A–C. SAM–6824, the lectotype. D–F. SAM–6829a. G. SAM–6829b. All from the Upper Campanian–Lower Maastrichtian of Carimba, Angola.

Fig. 131 *(see overleaf)*. A–H. *Baculites subanceps* Haughton, 1925. A–C. SAM–6829c. D–G. SAM–6829d. H. SAM–6829e. All from the Upper Campanian–Lower Maastrichtian of Carimba, Angola.
I–M. *Baculites anceps* Lamarck, 1822. I–K. SAM–6145b. L. SAM–6145c. M. SAM–6748, from the ?Lower Maastrichtian east of Capolo. N–R. *Baculites* sp. from the uppermost Turonian or basal Coniacian at Mossamedes, Angola. The oldest tuberculate baculite. Unregistered specimens from Cooper collection, SAM.
A–C, G, I–R × 1; D–F × 0.5.

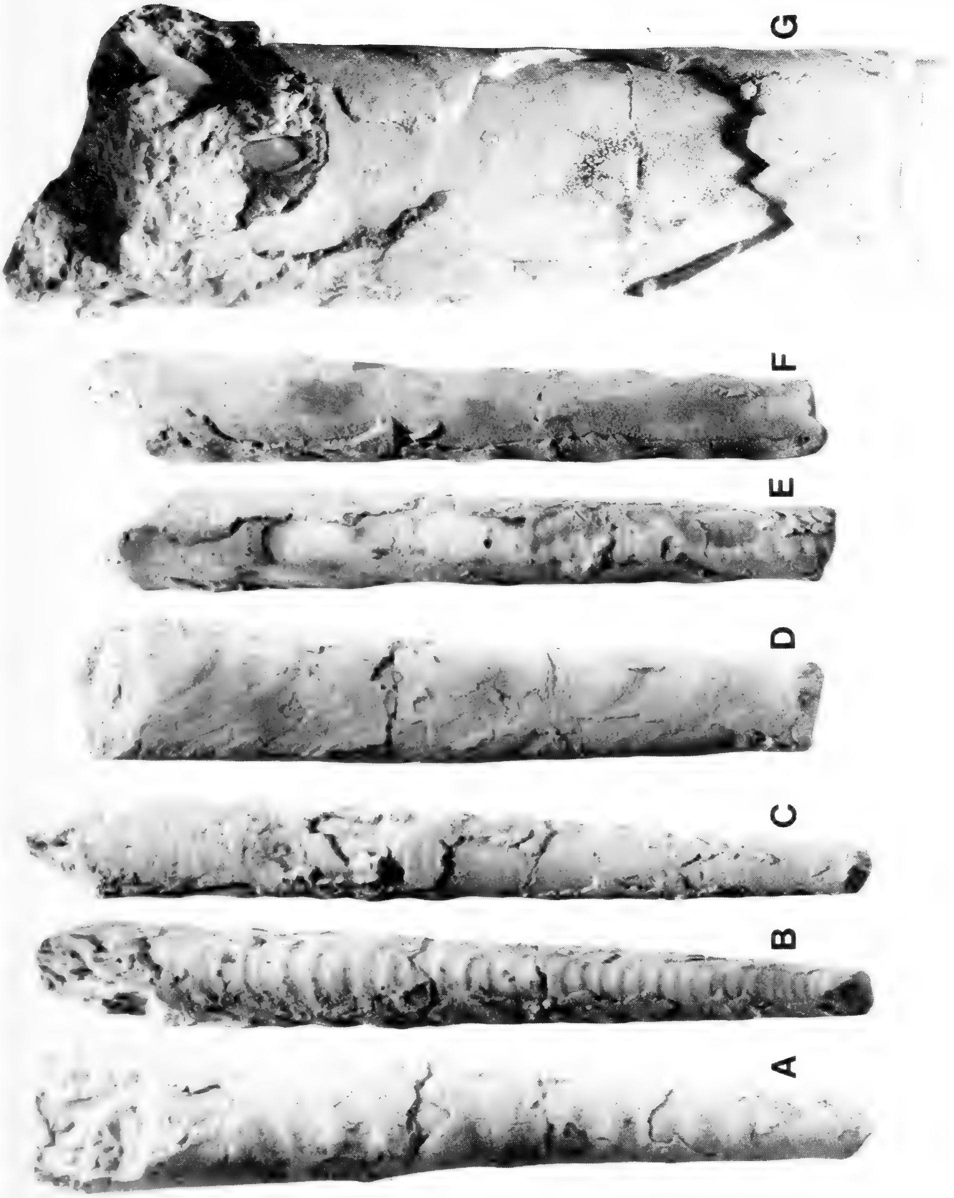

Fig. 130

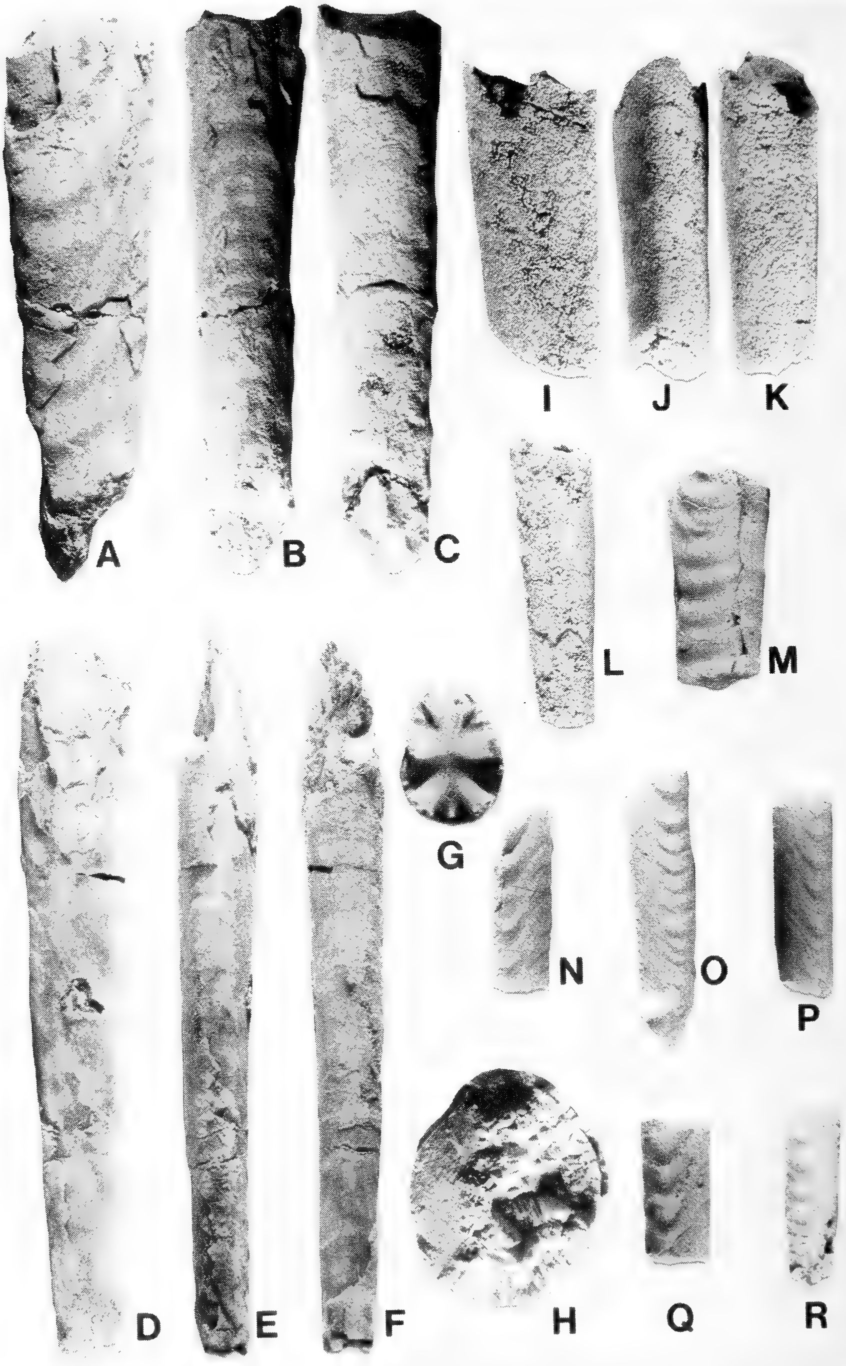

Fig. 131

Baculites ambatryensis Collignon (1971: 14, pl. 645 (fig. 2392)) (herein Fig. 128) from the Lower Maastrichtian of Madagascar is also superficially similar, but has a more compressed whorl section at comparable diameters (Wb : Wh 19.5 : 29), and coarse corrugations over the venter.

Baculites eliasi Cobban (1958: 663, pl. 91 (figs 1–11), text-figs 1f–g, i–j) from the Lower Maastrichtian of the U.S. Western Interior also has a more complex suture with a constricted lateral lobe (L).

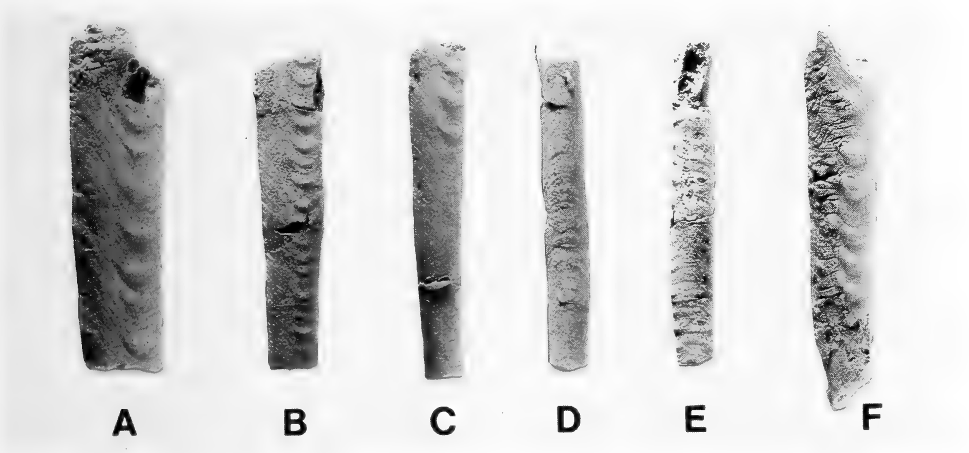

Fig. 132. *Baculites* sp. from the uppermost Turonian or basal Coniacian at Mossamedes, Angola. The oldest tuberculate baculite. Cooper Collection, S.A. Museum. A. SAM-1742. B–D. SAM-1743. E. SAM-1733. F. SAM-1745. All × 1.

Baculites fuchsi Redtenbacher (1873: 134, pl. 30 (fig. 15)) is difficult to interpret (see above, p. 47) but it is older, Santonian, being associated with *B. incurvatus*.

Baculites inornatus Meek (1862: 316) (see especially Matsumoto 1959: 155, pl. 38 (fig. 1a–c), pl. 43 (fig. 5a–c), text-figs 72a–b, 73a–d, 74–79; Ward 1978: 1151, pl. 1 (figs 1–2), text-fig. 5) is a predominantly smooth species from the Lower Campanian of California, British Columbia and Hokkaido. Records of *B. inornatus* from the Coniacian of Venezuela by Renz (1982: 105, pl. 34 (figs 3–4, 5a–b, 6), text-fig. 80) are obvious misidentifications. The suture of *B. inornatus* is complex, with phylloid folioles, clearly differing from our material.

Baculites kotanii Matsumoto *et al.* (1980: 408, figs 1–2) from the Upper Campanian of Shikoku, Japan, is nearly smooth, with only faint subcostae on the flanks. Again, the suture appears to be more complex with narrower saddles and lobes than the Zululand material.

Baculites vertebralis Lamarck, 1801, is a compressed, smooth species from the Upper Maastrichtian of Europe and North Africa, and resembles our largest specimen. Age difference apart, it also has a far more complex suture line (see e.g. Kennedy 1986*a*, text-fig. 7D–E).

Occurrence

Middle and/or Upper Campanian of Tierra del Fuego, and Campanian III of Zululand.

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APPENDIX

List of material and dimensions of *Baculites bailyi*, *Baculites capensis*, and *Baculites vanhoepeni*.

Baculites bailyi

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*
PCP6769	4.8	6.4	0.75	3.6	5.2	0.69	21	5.7
PCZ8390i	4.8	6.5	0.74	4.0	5.5	0.73	20.5	4.9
PCP6766	6.0	8.0	0.75	5.0	6.5	0.77	17	8.8
D108	6.2	8.9	0.7	—	—	—	—	—
PCZ8390j	6.7	9.0	0.74	—	—	—	—	—
PCZ8366a	6.8	9.5	0.72	5.5	7.0	0.79	30	8.3
PCZ8390a	7.0	9.3	0.75	4.8	6.6	0.73	38	7.1
PCZ8344	7.0	9.0	0.78	4.4	6.0	0.73	60	5.0
PCZ8355	7.0	9.0	0.78	5.4	7.4	0.73	20	8.0
PCZ8352	7.2	9.7	0.74	5.5	7.8	0.71	28	6.8
PCZ8354	7.4	9.5	0.78	6.6	8.6	0.76	21	4.3
SAM–4822	7.6	8.7	0.87	6.6	6.6	1.0	42	2.6
PCZ8367	8.0	10.8	0.74	8.0	10.0	0.8	35	2.3
PCZ8360	8.0	10.6	0.76	6.3	8.9	0.71	34	5.0
PCZ8016	8.6	11.4	0.75	7.8	10.6	0.74	20	4.0
PCZ8359	9.0	14.0	0.64	8.0	12.0	0.67	39	5.1
PCZ8375	9.2	12.6	0.73	—	—	—	—	—
PCZ8374	9.2	12.1	0.76	8.6	11.2	0.77	28	3.2
PCZ8020	10.0	14.0	0.71	9.0	12.7	0.71	28	4.6
PCZ8370	10.3	13.6	0.76	—	—	—	—	—
PCZ8387	10.8	13.2	0.82	9.3	11.6	0.80	43	3.7
PCZ8373	11.0	15.0	0.73	—	—	—	—	—

Baculites bailyi (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*
PCZ8349	11.6	15.0	0.77	—	—	—	—	—
PCZ8347	11.7	14.2	0.82	10.6	13.4	0.79	25	3.2
PCZ9940	12.0	15.0	0.8	12.3	15.0	0.82	42	0
PCZ8369	12.5	16.3	0.77	9.7	13.8	0.70	64	3.9
PCZ8346	13.0	17.0	0.76	11.0	14.0	0.79	44	6.8
PCZ8371	13.0	16.0	0.81	11.6	15.3	0.76	40	1.7
PCZ8345	13.0	17.0	0.76	11.3	14.8	0.76	51	4.3
PCZ8366b	15.5	20.5	0.76	—	—	—	—	—
PCZ9952	15.6	21.0	0.74	14.4	20.7	0.70	44	0.9
PCZ9945	17.0	21.0	0.81	—	—	—	—	—

Baculites capensis

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
D1124/8	4.4	7.0	0.63	3.3	5.5	0.6	20	7.5	2
H200/15	6.0	9.0	0.67	5.0	7.0	0.71	25	8.0	2
H149/19	6.2	8.0	0.77	4.5	6.4	0.70	24	6.67	3
D1124/7	6.7	9.5	0.70	5.3	7.0	0.76	24	10.4	—
H200/61	7.0	9.0	0.78	5.4	7.4	0.73	25	6.4	3
H200/29	7.0	9.0	0.78	6.0	8.0	0.75	22	4.5	4

Baculites capensis (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
H200/47	7.0	10.0	0.7	6.0	8.4	0.71	23	6.96	3
D1124/4	7.0	10.0	0.7	5.0	7.0	0.71	47	6.38	3
H200/59	7.2	10.4	0.69	7.0	9.0	0.78	20	7.0	3–4
H203/48	7.3	10.6	0.69	7.0	9.0	0.78	15	10.7	3
H201/13a	7.4	10.0	0.74	5.7	7.7	0.74	20	11.5	2
H200/70	7.4	9.0	0.82	6.0	7.0	0.86	27	7.4	2.5
H200/62	7.4	9.6	0.77	5.4	7.2	0.75	29	8.28	3
H203/1	7.5	11.6	0.65	6.5	8.0	0.81	34	10.6	2.5
D1124/2	7.5	10.8	0.69	5.5	8.0	0.68	36	7.78	3–4
H201/17	8.0	11.0	0.73	6.6	8.7	0.76	30	7.67	2
H200/51	8.0	10.3	0.78	6.3	8.6	0.73	34	5.0	2.5
H200/25	8.0	12.0	0.67	8.0	12.0	0.67	28	0	2.5–3
D1028/21	8.0	10.0	0.8	7.0	9.0	0.78	21	4.76	2
D1124/4	8.0	13.0	0.61	7.7	10.0	0.77	28	10.7	2
PCZ8351b	8.4	11.3	0.74	7.6	10.0	0.76	28	4.56	—
H201/25	9.0	13.0	0.69	8.0	12.0	0.67	28	3.57	2
H200/39	9.0	13.0	0.69	8.0	11.4	0.70	34	4.7	2.5–3
H200/57	9.0	12.0	0.75	7.7	10.8	0.73	22	5.45	2.5
PCZ8034	9.0	13.0	0.69	8.4	10.6	0.79	27	8.89	2
H1B/12	9.0	12.0	0.75	7.7	10.5	0.73	37	4.05	2.5
H148/3a	9.0	13.0	0.69	7.0	9.6	0.73	47	7.23	3
H200/44	9.3	13.0	0.72	7.0	10.0	0.7	30	10.0	2.5
H149/16	9.3	14.4	0.65	8.6	13.0	0.66	33	4.24	2
D1028/4	9.5	13.0	0.73	8.0	12.0	0.67	38	2.63	2
PCP8054	9.5	13.0	0.73	—	—	—	—	—	2.5
H200/56	9.6	13.4	0.72	—	—	—	—	—	—

Baculites capensis (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
D1124/5	9.6	13.0	0.74	9.2	12.0	0.77	28	3.57	2
H202/11	9.8	12.5	0.78	9.0	12.0	0.75	29	1.72	2–2.5
H202/7a	10.0	14.8	0.68	10.0	13.0	0.77	39	4.6	2.5
SAM–4823	10.0	14.0	0.71	8.7	13.0	0.66	23	4.3	2
D66	10.0	14.5	0.69	7.4	13.0	0.57	35	4.3	1.5–2
PCP8241	10.0	13.0	0.77	9.0	12.4	0.73	20	3.0	0
PCP8662	10.0	13.8	0.77	9.0	12.4	0.73	21	6.7	2.5–3
PCP8663	10.0	14.0	0.71	8.0	12.0	0.67	30	6.7	2
PCP8664	10.0	13.3	0.75	8.6	13.0	0.66	28	1.07	2
H205/12	10.0	14.0	0.71	10.0	14.0	0.70	24	0	3.5
H203/46	10.0	13.5	0.74	10.0	13.0	0.77	23	2.2	—
H201/23	10.0	13.7	0.73	9.0	12.7	0.71	25	4.0	2
H201/19	10.0	14.0	0.71	9.0	13.0	0.69	25	4.0	2
H200/53	10.0	12.0	0.83	8.8	12.0	0.73	19	0	4
H200/101	10.0	14.0	0.71	7.6	13.2	0.58	25	3.2	3
H200/40	10.0	14.0	0.71	9.0	13.0	0.69	21	4.76	2.5
D1028	10.0	15.0	0.67	9.0	14.0	0.64	35	2.86	3
KK72a	10.0	14.0	0.71	8.0	13.0	0.61	37	2.70	1
PCZ8039	10.0	13.0	0.76	—	—	—	—	—	—
H1B/23	10.0	13.5	0.74	7.5	12.0	0.62	42	3.57	—
D1124/1	10.0	15.0	0.67	9.0	14.0	0.64	33	3.03	2
D1124/3	10.0	14.0	0.71	9.6	12.4	0.77	26	6.15	2.5
H200/99	10.5	14.3	0.73	—	—	—	—	—	—
H203/6	11.0	15.0	0.73	9.5	14.5	0.65	32	1.56	2.5–3
H202/7	10.6	13.6	0.78	9.2	11.4	0.81	29	7.59	3
H200/55	11.0	15.0	0.73	10.0	14.0	0.71	31	3.2	2

Baculites capensis (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
H200/16	11.0	14.0	0.79	—	—	—	—	—	—
H200/102	11.0	17.0	0.65	9.8	14.5	0.68	27	9.26	3
D1028/16	11.0	15.0	0.73	9.0	13.0	0.69	36	5.56	2
S541	11.0	15.0	0.73	9.5	14.0	0.68	43	2.32	2
PCZ8036	11.0	15.0	0.77	—	—	—	—	—	—
H1B/24	11.0	15.0	0.73	8.8	13.0	0.68	39	5.12	3
H1B/13	11.0	15.0	0.73	10.0	14.0	0.71	28	3.57	3
Z632e	11.0	15.0	0.73	10.0	14.0	0.71	25	4.0	2
H148/3b	11.0	15.4	0.71	10.0	13.4	0.75	50	4.0	—
D1028/10	11.6	17.0	0.68	—	—	—	—	—	—
H200/09	11.7	15.0	0.78	11.0	14.7	0.75	35	0.86	3–3.5
H204/1	12.0-	16.0	0.75	12.0	15.0	0.8	24	4.2	2.5
H201/10	12.0	16.0	0.75	11.0	15.0	0.73	35	2.86	2
H201/7	12.0	17.0	0.71	11.0	16.5	0.67	35	1.43	2
H200/13	12.0	18.0	0.67	12.0	17.5	0.69	31	1.61	2–2.5
H200/36	12.0	15.0	0.8	11.0	15.0	0.73	28	0	2.5
H201/12b	12.0	16.0	0.75	—	—	—	—	—	—
D1028/12	12.0	16.0	0.75	10.0	13.0	0.77	55	5.45	2
D1028/a	12.0	16.0	0.75	10.0	14.0	0.71	44	4.54	2
A361	12.0	17.0	0.71	12.0	16.0	0.75	55	1.82	3
PCZ8032	12.0	17.0	0.71	11.0	15.0	0.73	29	6.90	1
D1028/18	12.0	16.0	0.75	—	—	—	—	—	—
D1052	12.0	15.0	0.8	9.0	12.0	0.75	50	6.0	—
D1124a	12.0	17.0	0.71	11.5	16.3	0.71	37	1.89	2
H25/6	12.0	17.0	0.71	10.0	14.0	0.71	33	9.09	2.5
A606	12.5	15.0	0.83	11.0	14.0	0.79	33	3.03	1.5–2

Baculites capensis (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
H203/4	12.5	15.6	0.80	—	—	—	—	—	—
H201/12a	12.6	18.0	0.70	11.0	15.0	0.73	40	7.5	2.5
PCP8052	12.7	18.0	0.70	—	—	—	—	—	—
H201/9	13.0	17.0	0.76	11.0	15.5	0.71	35	4.29	2
H205/18	13.0	18.0	0.72	—	—	—	—	—	—
H202/5	13.0	16.6	0.79	—	—	—	—	—	—
H201/26	13.0	18.0	0.72	—	—	—	—	—	—
H201/21	13.0	18.0	0.72	—	—	—	—	—	—
PCZ8004	13.0	16.0	0.81	11.0	14.8	0.74	38	3.16	2
H200/14	13.0	17.0	0.77	12.0	16.0	0.75	26	3.84	2
Z1795d	13.0	18.0	0.72	9.0	13.0	0.69	80	6.25	2
Z1795g	13.0	17.0	0.77	11.0	15.0	0.73	46	4.3	2
H1B/6	13.0	17.5	0.74	11.0	15.0	0.73	47	3.19	2.5
H204/3	13.3	18.0	0.74	11.0	16.0	0.69	26	7.7	2
H149/2	13.5	18.2	0.74	13.0	16.0	0.81	72	3.06	2
PCZ8385	14.0	18.0	0.78	12.0	16.5	0.72	44	3.4	—
H201/24	14.0	19.0	0.74	—	—	—	—	—	—
H201/20	14.0	19.0	0.74	—	—	—	—	—	—
H200/79	14.0	18.0	0.78	12.0	17.0	0.71	39	2.56	2
D1028/3	14.0	20.0	0.7	13.0	17.0	0.77	55	5.45	2
Z1795c	14.0	19.0	0.74	11.0	18.0	0.61	60	1.67	2
Z632c	14.0	16.0	0.87	11.0	15.0	0.73	37	2.70	2
H1B/4a	14.0	19.0	0.74	13.0	17.0	0.77	?	—	2
H1B/4b	14.5	19.2	0.75	13.0	17.0	0.76	54	4.07	—
PCZ8035	14.5	18.0	0.81	13.0	16.4	0.79	30	5.33	2
PCZ8027	15.0	18.0	0.83	12.0	16.0	0.75	64	3.12	—

Baculites capensis (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
H201/15	15.0	19.0	0.79	13.0	16.0	0.81	31	9.68	2
H201/11	15.0	20.0	0.75	14.0	19.0	0.74	43	2.32	2
PCZ8033	15.0	19.0	0.79	11.0	16.0	0.69	69	4.34	2
KK72b	15.0	21.0	0.71	13.3	17.4	0.76	54	6.67	0
Z1795f	15.0	21.0	0.71	13.0	18.0	0.72	53	5.66	2
D1052c	15.0	19.0	0.78	12.0	15.4	0.78	49	7.3	3
H201/13b	15.5	20.0	0.78	14.0	18.0	0.78	54	3.70	2
D1124	15.7	22.8	0.69	14.0	19.0	0.74	34	11.8	0
H205/20	16.5	21.0	0.79	14.0	19.0	0.74	27	7.4	0
D1052/1	16.5	22.7	0.73	13.7	19.6	0.70	87	3.56	—
A353	16.6	22.4	0.74	14.0	18.7	0.75	58	6.38	2
Z1795	17.0	23.0	0.74	13.0	18.0	0.72	90	5.56	2.5
SAM–4825	18.0	23.6	0.76	17.0	20.0	0.85	80	4.5	1.5–2
H200/84	18.0	23.5	0.77	15.0	21.0	0.71	95	1.58	—
PCZ8038	18.0	22.0	0.82	—	—	—	—	—	—
Z632a	18.5	26.0	0.71	15.0	20.0	0.75	80	7.5	2–2.5
Z632b	19.0	26.0	0.73	17.0	24.0	0.71	40	5.0	2.5
H201/43	19.0	28.0	0.68	—	—	—	—	—	—
D1052b	19.0	27.0	0.70	—	—	—	—	—	—
D1028/22	20.0	26.0	0.77	19.0	26.0	0.73	76	0	2
36/3234	20.0	27.0	0.74	—	—	—	—	—	—
H201/38	21.0	26.0	0.80	—	—	—	—	—	—
PCZ7218	21.0	27.0	0.78	—	—	—	—	—	—

Baculites vanhoepeni

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
D1467	11.0	20.6	0.53	10.7	17.3	0.62	55	6.0	0.5
PCZ7706	11.5	15.3	0.75	7.0	12.6	0.56	64	4.2	0.75
PCZ7717	12.0	15.8	0.76	10.5	13.3	0.79	33	7.6	0.9
PCZ7707	12.7	17.0	0.75	10.6	15.0	0.71	46	4.3	0.7
87a	13.3	17.6	0.76	9.6	12.8	0.75	88	5.5	1
87b	14.0	20.0	0.7	—	18.0	—	47	4.3	1
PCZ7716	15.0	21.0	0.71	—	—	—	—	—	—
PCZ7705	15.0	19.2	0.78	13.7	18.0	0.76	28	4.3	0
A2029a	15.0	25.0	0.6	14.6	23.5	0.62	55	2.7	1
Z1190a	15.0	20.0	0.75	11.0	15.0	0.73	63	7.9	0.8
PCZ7690	15.6	21.7	0.72	13.6	20.0	0.68	36	4.7	0.6
PCZ7692	17.0	24.0	0.71	—	—	—	—	1	
PCZ8636	17.0	24.0	0.71	20.0	24.0	0.83	48	0	0.7
A2036	18.0	25.0	0.72	18.0	24.0	0.75	50	2.0	—
A2036a	18.0	24.0	0.75	16.4	22.0	0.74	31	6.5	0.8
PCZ7640	18.0	28.0	0.64	—	—	—	—	—	1
PCZ8637	18.6	25.5	0.73	—	—	—	—	—	—
PCZ7645	19.0	27.2	0.7	17.5	24.6	0.71	54	4.8	0.5
A2031	21.0	27.0	0.78	17.0	24.0	0.71	57	5.3	2
A2032	21.0	28.0	0.75	—	—	—	—	—	—
PCZ7655	21.0	28.0	0.75	20.0	26.0	0.77	85	2.3	0.6
D1302a	21.0	26.0	0.81	17.0	22.0	0.77	55	7.3	1
PCZ7677	23.0	32.0	0.72	—	—	—	—	—	—
PCZ7407a	24.0	30.0	0.8	—	—	—	—	—	—
PCZ8631	24.0	32.0	0.75	22.0	28.0	0.79	83	4.8	1
109a	25.0	32.0	0.78	23.0	29.0	0.80	82	3.7	1
PCZ8635	25.0	35.0	0.71	25.0	34.0	0.73	65	1.5	1

Baculites vanhoepeni (cont.)

Specimen	*MxWb*	*MxWh*	*Wb/Wh*	*MnWb*	*MnWh*	*Wb/Wh*	*D*	*Ti*	*Tu/Wb*
Z1860	25.0	32.0	0.78	22.0	29.0	0.76	78	3.8	1
PCZ7635	25.0	35.0	0.71	—	—	—	—	—	—
A2034	25.0	33.0	0.76	24.0	32.0	0.75	55	1.8	1
A477	26.0	32.0	0.81	26.0	31.0	0.84	38	2.6	3
A2039	26.0	35.0	0.74	—	—	—	—	—	—
109b	27.0	35.0	0.77	—	—	—	—	—	—
Z1860	27.0	37.0	0.73	27.0	33.0	0.82	75	5.3	0.8
D1302b	27.0	32.0	0.84	24.0	26.0	0.97	45	13.3	2
Z1860b	27.0	35.0	0.77	26.0	36.0	0.72	51	1.9	2
Z1190b	28.0	35.0	0.8	25.0	34.0	0.73	87	1.2	0.5
PCZ8630	28.0	36.0	0.78	—	—	—	—	—	—
PCZ7417	28.0	36.0	0.78	28.0	34.0	0.82	58	3.4	1
PCZ7406	28.0	32.0	0.87	24.0	30.0	0.80	55	3.6	—
PCZ8638	31.0	42.0	0.74	—	—	—	—	—	—
A2029b	31.0	40.0	0.77	27.0	35.0	0.77	80	6.2	1
PCZ7411	32.0	43.0	0.74	—	—	—	—	—	—
Z1860d	32.0	38.0	0.84	—	—	—	—	—	—
PCZ7407b	37.0	46.0	0.80	—	—	—	—	—	—

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

HERBERT CHRISTIAN KLINGER
&
WILLIAM JAMES KENNEDY

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA. THE AMMONITE FAMILY BACULITIDAE GILL, 1871 (EXCLUDING THE GENUS *EUBACULITES*)

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ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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2. LAYOUT should be as follows:
   (a) *Centred masthead to consist of*: title: informative but concise, without abbreviations and not including the names of new genera or species; Author's(s') name(s); address(es) of author(s) (institution where work was carried out); number of illustrations and tables
   (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
   (c) *Table of contents* giving hierarchy of headings and subheadings
   (d) *Introduction*
   (e) *Subject matter* of the paper, divided into sections to correspond with those given in table of contents
   (f) *Summary* (if paper is lengthy)
   (g) *Acknowledgments*
   (h) *References*
   (i) *Abbreviations*, where these are numerous.

3. MANUSCRIPT should be typed, double spaced with adequate margins. Four copies should be provided. First lines of paragraphs should be indented. Tables and a list of figure captions should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are centred small capitals; second subheadings are shouldered small capitals; third subheadings are shouldered italics; fourth subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations. Footnotes should be avoided unless they are short and essential. All generic and specific names should be underlined or italicized.

4. ILLUSTRATIONS should be reducible to a size not exceeding 12.5 × 18.5 cm (19.5 cm including caption); the reduction or enlargement required should be indicated in pencil on the reverse of the figure; originals larger than 36 × 48 cm should not be submitted; photographs should be rectangular in shape and final size. The size of illustrated objects may be indicated by a metric scale on the figure (if appropriate), or the enlargement or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

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5. REFERENCES cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (ibid., idem, loc. cit., op. cit. are not acceptable):

(a) Author's name and year of publication given in text, e.g.:

'Smith (1969) described . . .'
'Smith (1969: 36, fig. 16) described . . .'
'As described (Smith 1969*a*, 1969*b*; Jones 1971)'
'As described (Haughton & Broom 1927) . . .'
'As described (Haughton *et al.* 1927) . . .'

Note: no comma separating name and year; pagination indicated by colon, not p. (except in synonymies, see example 2); names of joint authors connected by ampersand; *et al.* in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc., to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.
For journal articles give title of article, title of journal in italics (according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number in parentheses (if pagination discontinuous), pagination (first and last pages of article).

Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88**: 100–140.

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KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2**: 309–320.

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THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

ANNALS OF THE SOUTH AFRICAN MUSEUM
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A LOWER CRETACEOUS PLIOSAUROID FROM SOUTH AFRICA

By

ARTHUR R. I. CRUICKSHANK

Cape Town Kaapstad

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A LOWER CRETACEOUS PLIOSAUROID
FROM SOUTH AFRICA

By

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(With 6 figures and 1 table)

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ABSTRACT

A revised account is given of the skull and partial skeleton of a small plesiosaur from the Lower Cretaceous (Upper Valanginian) Sundays River Formation of the Algoa Basin, South Africa. The specimen was originally described as *Plesiosaurus capensis* by C. W. Andrews in 1911, nominally as a 'small-headed' form of plesiosaurian, but is in fact a member of the 'large-headed', predaceous Pliosauroidea. Its apparent closest relative is the English 'Wealden' (Barremian) species, *Leptocleidus superstes* Andrews, 1922. Both specimens seem to be very similar to, but smaller than, the Liassic genus *Rhomaleosaurus*. The Sundays River Formation is of shallow marine to estuarine–lagoonal provenance. A brief review is included of other, particularly Southern Hemisphere, occurrences of marginal and non-marine Plesiosauria.

CONTENTS

INTRODUCTION

The value of well-curated fossil collections is nowhere better displayed than in the specimen redescribed here. Very nearly one hundred years ago, Rogers & Schwarz (1901: 8–9) reported the recovery of the remains of a plesiosaurian

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[illegible]

reptile. It had been discovered by Schwarz in a cliff at the locality Picnic Bush, in the Zwartkops River Valley, south of Uitenhage. In the terminology of the day it was therefore ascribed to the Sundays River Beds of the Uitenhage Series. An age of Upper Valanginian to Lower Hauterivian was assumed, corresponding to the upper part of the 'Wealden' succession of England (Andrews 1911), but see below for further discussion. So far as is known this remains the only record of a plesiosaurian from southern Africa, although their remains are relatively common in Australia and New Zealand (Welles & Gregg 1971; Molnar 1982, 1984). The well-preserved, semi-articulated nature of this specimen encourages the hope that more may yet be found in the late Mesozoic rocks of Eastern Cape Province and KwaZulu-Natal.

Andrews (1911) assigned the specimen to a new species, *Plesiosaurus capensis*, and therefore by inference, to the small-headed superfamily Plesiosauroidea (Brown 1981). Several years later Andrews (1922) described a very similar specimen from the English Wealden (Berwick Brick Pit, Sussex) under the name of *Leptocleidus superstes*, and drew attention to close similarity of the Algoa Basin specimen to his new species, although the skull of *L. superstes* was lacking most of its structure anterior to the orbits. Strömer (1935) thought the South African specimen to be sufficiently different to warrant a distinct genus to itself, and created the genus *Peyerus* for it. However, Persson (1963) pointed out that Andrews original comparisons were sufficient to place *P. capensis* into the genus *Leptocleidus*, and that therefore Strömer's genus was effectively a subjective junior synonym for *Leptocleidus*. This course will be followed in this paper. The specimen is therefore *Leptocleidus capensis* (Andrews, 1911).

The specimen is of particular interest from several points of view. Firstly, it is a member of the superfamily Pliosauroidea, family Pliosauridae (Brown 1981)—aquatic animals showing extreme adaptations towards a predatory way of life, with skulls about half the length of the neck and large, conical, striated teeth adapted for piercing and tearing. It does not belong with the Plesiosauroidea, the contrasting group within the Plesiosauria, which show adaptations towards feeding on small or soft-bodied prey, and which possess heads very much less than half the length of the neck and slim elongate teeth. Secondly, the general structure of the skull of *Leptocleidus* is very close to that of the Liassic (Lower Jurassic) genus *Rhomaleosaurus* (Taylor 1992*a*, 1992*b*; Cruickshank 1994*a*). Thirdly, the palaeoenvironment of the sediments in which the specimen was found indicates close inshore, perhaps lagoonal, conditions (McLachlan & McMillan 1976; McMillan in press). A brief literature survey shows that several plesiosaurs, particularly those from southern continents, have originated from non-marine sediments, and hence a totally marine association of these predaceous aquatic reptiles is not necessarily to be expected (Bartholomai 1966; Molnar 1982, 1984; Rich *et al.* 1991). This paper will address these points, firstly by redescribing the specimen in the aftermath of further preparation, and by reviewing some occurrences of similar fossils.

Material referred to in the text is lodged in the following institutions: Palaeontology Department, Natural History Museum, Cromwell Road, London (BMNH); and Palaeontology Collections, Earth Sciences Division, South African Museum, Cape Town (SAM).

MATERIAL AND METHODS

LOCALITY AND GEOLOGICAL HORIZON

The specimen is recorded as having been discovered on the face of the cliff overlooking the farm Redhouse, in the Zwartkops (Swartkops) River Valley, from between the two upper mudstone beds, in a nodular clay limestone (Rogers & Schwarz 1901: 8–9; Rogers & Du Toit 1909). The locality is approximately 33°49'S 25°33'E (South African Topocadastral Series, sheet 3325). The specimen originally comprised 'portions of the shoulder girdle and some fifteen vertebrae, embedded in a nodule with the accompanying jaws (and ?skull), teeth, cervical vertebrae, hind limb bones and bones of the fore-arm and paddle loosely embedded in the dark grey clay' (Rogers & Schwarz 1901: 8–9).

The sediments are those of the Sundays River Formation, a lagoonal to shallow marine succession (McLachlan & McMillan 1976; McMillan in press), which forms the upper component of the Uitenhage Group of the Eastern Cape South Coastal Belt. The age of the Sundays River Formation has been variously reported as ranging from the 'Lower Greensand' to Liassic, but the general consensus of opinion holds that it is of Upper Valanginian–Lower Hauterivian age (Lower Cretaceous) (McLachlan & McMillan 1976: 205–206). This is confirmed by a recent analysis of the foraminiferans (McMillan in press), which shows that the Picnic Bush locality lies at the top of his new Biozone Bb, and is placed by him in the Uppermost Valanginian. From an associated palaeoecological study, McMillan shows that Biozone Bb equates with his Transgressive Zone. The entire Valanginian sequence of the Sundays River Formation is characterized, to a greater or lesser extent, by the presence of freshwater foraminiferans . The probability is that Biozone Bb was laid down under estuarine or marginal marine conditions. *Leptocleidus capensis* possibly lived, and was certainly preserved, in an inshore environment.

PRESERVATION

The remains of the shoulder girdle, forearm and teeth are no longer in the collections of the South African Museum. Nine posterior cervical and sixteen dorsal vertebrae run in an unbroken sequence but, at what appears to be the cervical–pectoral junction, there is a marked break in their line. Andrews (1911) recorded that the left side of the skull was obscured by the neural spines of six (?anterior) dorsal vertebrae—but which six is no longer clear, as they have all been cleared from the skull and may be among the several fragments that accompany the specimen.

The break in the line of the vertebrae may indicate that the animal was essentially complete when its carcass came to rest on the bottom, only the head becoming detached and coming to lie alongside the vertebral column. One paddle must have been close by, as it donated a phalange to lie within the left temporal arcade, and a carpal(?) to lie inside the left orbit. The presence of hind limbs (two femoral shafts, two fibulae and a tibia) reinforces the idea that the skeleton was nearly complete at the time of burial, and had suffered minimal damage through scavenging and current action. A situation not unlike that reported by Taylor (1992*a*) for *Rhomaleosaurus zetlandicus* is a strong possibility for this specimen.

The skull has been symmetrically squashed dorso-ventrally, but mainly over the parietal region. The snout seems undistorted, but a pair of symmetrically placed depressions (dep) on either side of the mid-nasal ridge (dmc) might also be taphonomic damage, although not shown as such in the reconstructions (Figs 1, 2). As a result of the distortion of the parietal crest, the sidewall of the braincase is no longer easily interpreted (Fig. 2).

In summary, what is currently preserved of the specimen is as follows: an almost complete skull, portions of both jaws rami, but not the symphysis, 22 cervical and 16 dorsal vertebrae, two fibulae, one tibia, the remains of two femora, several carpals/tarsals and the bulk of a paddle.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA

Subclass SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLIOSAUROIDEA (Grey, 1825) Welles, 1943

Family **Pliosauridae** Seeley, 1874

Genus *Leptocleidus* Andrews, 1922

Type species. Leptocleidus superstes Andrews, 1922: 285–298, pls 14–15, based on specimen BMNH R4824, from the Berwick Brick Pit, near Lewes, Sussex, United Kingdom, Upper Weald Clay (= Barremian), Lower Cretaceous.

Remarks

The classification of the Plesiosauria is at present in a state of flux. Hitherto, a clear-cut division of the order into two superfamilies, the Pliosauroidea and Plesiosauroidea, seemed to offer a stable solution to their classification (Brown 1981). However, recent descriptions of plesiosaurians from the Rhaeto–Liassic of England indicate that this simple relationship can no longer be held (Brown 1993; Storrs & Taylor 1993; Cruickshank 1994*a*, 1994*b*; Brown & Cruickshank 1995). In many of the characters of the skull, the genus *Leptocleidus* is very close to *Rhomaleosaurus* from the Liassic of Europe, but as the critical region of the lower jaw symphysis is not known with certainty in *Leptocleidus*, its final position must remain undecided for the present (see Table 1).

Leptocleidus capensis (Andrews, 1911)

1911	*Plesiosaurus capensis* Andrews, p. 309.
1922	*Leptocleidus capensis* Andrews, p. 291.
1935	*Peyerus capensis* Strömer, p. 44.
1963	*Leptocleidus capensis* Persson, p. 19.

Material

SAM–K5822, from Picnic Bush site, Swartkops River Valley, Cape Province, overlooking Redhouse Farm, 33°49'S 25°33'E, Sundays River Formation (= Uppermost Valanginian).

Diagnosis

Pliosauroid plesiosaur very similar to, but smaller than, *Rhomaleosaurus*, having a subtriangular skull outline, possessing a dorsomedian foramen on the midnasal ridge of the premaxillae, dorsomedian troughs on the articulars and prearticulars, expanded lateral rami of the pterygoids, strong descending postorbital flanges, a snout bearing a rosette of procumbent teeth; teeth conical, circular in section with striae and weak carinae. It differs from *Rhomaleosaurus* in having a relatively shorter snout, fewer teeth in both upper and lower jaws, and a recurved crest on the forward-facing part of the vertex.

Remarks

Strömer (1935) created the genus *Peyerus* to accommodate *Plesiosaurus capensis*, but Andrews (1922) had already strongly suggested that *P. capensis* and *Leptocleidus superstes* were congeneric. This route was followed by Persson (1963), who formally incorporated *P. capensis* into the genus *Leptocleidus*. The genus *Peyerus* therefore becomes a subjective junior synonym for *Leptocleidus*. Persson (1963: 19) also made the point that *L. capensis* was '. . . a Rhomaleosauroidean genus', pointing out that the skull was well preserved, was comparatively large, and had a distinct constriction at the maxillo–premaxillary suture.

DESCRIPTION OF SPECIMEN

Skull (Figs 1–3)

The skull is that of an adult, the sutures being very difficult to distinguish in places and none of the bones show any sign of disarticulation (Cruickshank 1994*b*). This interpretation is reinforced by an examination of the vertebrae, where the neural arches are seen to be firmly fused to their centra, an accepted indication of adulthood (Brown 1981).

The skull is about 310 mm long on the dorsal midline, and 172 mm across the quadrates, giving a length : width ratio of 1.7 : 1. It appears little damaged, but some bone is missing from the lower rim of the right orbit (orb) and adjacent palate, and most of the right cheek-bar is reconstructed in plaster-of-Paris. The now fragile occiput has been strengthened by a layer of plaster-of-Paris, which has obscured its details. However, most of the 'fixed points' can be determined to give the outline as illustrated in the figures.

The bones of the left side and anterior of the palate are clear, although several of the sutures on the skull roof are not at all easily seen. In particular, it is not certain if there is a lacrimal in this species, and the outline of the frontals (fr) and postfrontals (pof), where they meet, has had to be interpreted. Andrews (1911, fig. 1) reconstructed the palate from information contained on the

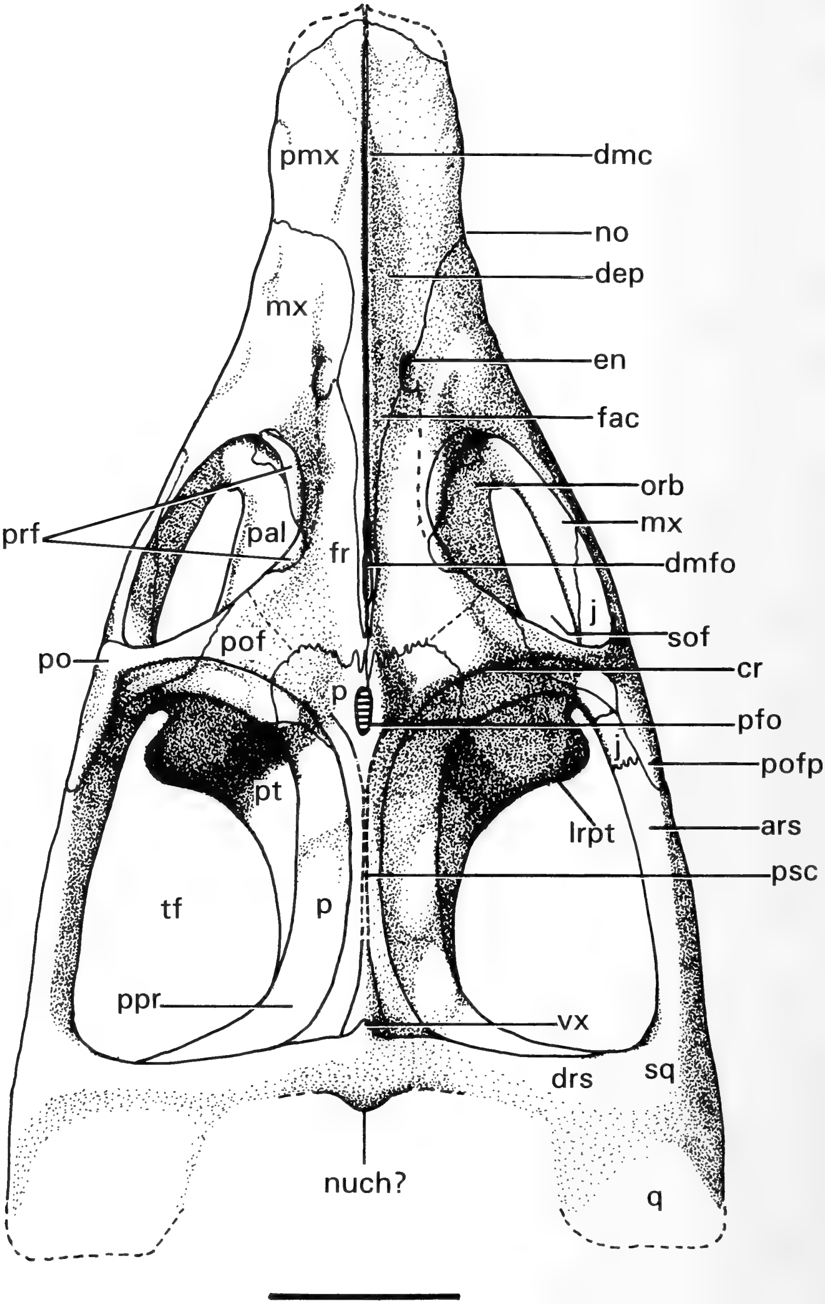

Fig. 1. Skull of *Leptocleidus capensis* (Andrews, 1911) in dorsal view. For abbreviations to this and other figures see p. 225. Scale bar = 50 mm.

damaged right side, and indicated that the ectopterygoid (ec) was an anteroposteriorly elongated bone. However, using the clear outlines of the bones now exposed on the left side of the palate, it is clear that the ectopterygoid is a leaf-like bone applied to the ventral surface of the lateral ramus of the pterygoid (lrpt), and elongated from side-to-side, with a connecting process linking it to the jugal (j).

The internal nares (in) are very similar to those of *Rhomaleosaurus*, having steeply-walled posterior limits, connected to a shallow channel (ch), which runs towards the diastema (dia) at the maxilla–premaxillary suture. Unlike *Rhomaleosaurus* and other pliosauroids, there do not seem to be any auxiliary foramina or channels associated with the narial system in this animal. The internal nares are positioned anterior to the external nares (en), and seem to have been part of an underwater olfactory system as described by Cruickshank *et al.* (1991) and Taylor & Cruickshank (1993).

A difference from the palates of species of *Rhomaleosaurus* is the proportion and placing of the parasphenoid (ps). In pliosauroids recently described (Taylor 1992*b*; Cruickshank 1994*a*), the parasphenoid is a relatively wide plate that spans the midline of the posterior interpterygoid vacuity (piv), and which effectively covers the bulk of the basioccipital and basisphenoid (bo, bs), with the exception of a small rim of basioccipital on the posterior limit of the palate, and the occipital condyle. In *Leptocleidus*, the parasphenoid is a narrow rod running back from a wedge inserted between the posterior portions of the anterior rami of the pterygoids, exposing the basicranium. In this specimen it is not possible to distinguish the suture between the basi- and parasphenoids, nor that between the basisphenoid and basioccipital in the region of the posterior interpterygoid vacuity. A similar structure of the rear of the palate is known in *Liopleurodon* and the plesiosauroid plesiosaurs (Andrews 1910–1913). The significance of this variation is not known at present.

The lateral ramus of the pterygoid descends below the line of the cheek bar, but is not at all robust, and does not have the 'boss' that is so strongly developed in *Rhomaleosaurus*. The postorbital bar (pob) has a very marked descending flange, very similar to that in *Rhomaleosaurus*, composed of elements of the parietals (p), postorbitals (po) and postfrontals (pof). However, the structure of this flange differs in two respects from that of *Rhomaleosaurus*. The postorbital itself has a very much reduced exposure on the descending flange, when compared with *Rhomaleosaurus* species (Taylor 1992*a*; Cruickshank 1994*b*), an area taken over by the postfrontal in *L. capensis*, but in turn the postorbital has a well-developed 'footplate' (pofp) running backwards over the junction of the jugal (j) and squamosal (sq). The descending flange also seems to be much deeper than in *Rhomaleosaurus*, closely approaching the dorsal surface of the palatal bones.

The articular surfaces of the quadrates (q) are missing, but the breaks seem to have been made only just above the joint surfaces, where the line of the medial surfaces of the quadrates start to turn outwards, as is indicated in the reconstructions (Figs 1–3).

Some post-mortem damage to the parietal crest (psc) has caused the line of the crest to be depressed, which has also damaged the side-walls of the braincase. However, impressions of the jaw adductor muscles seem to be apparent on

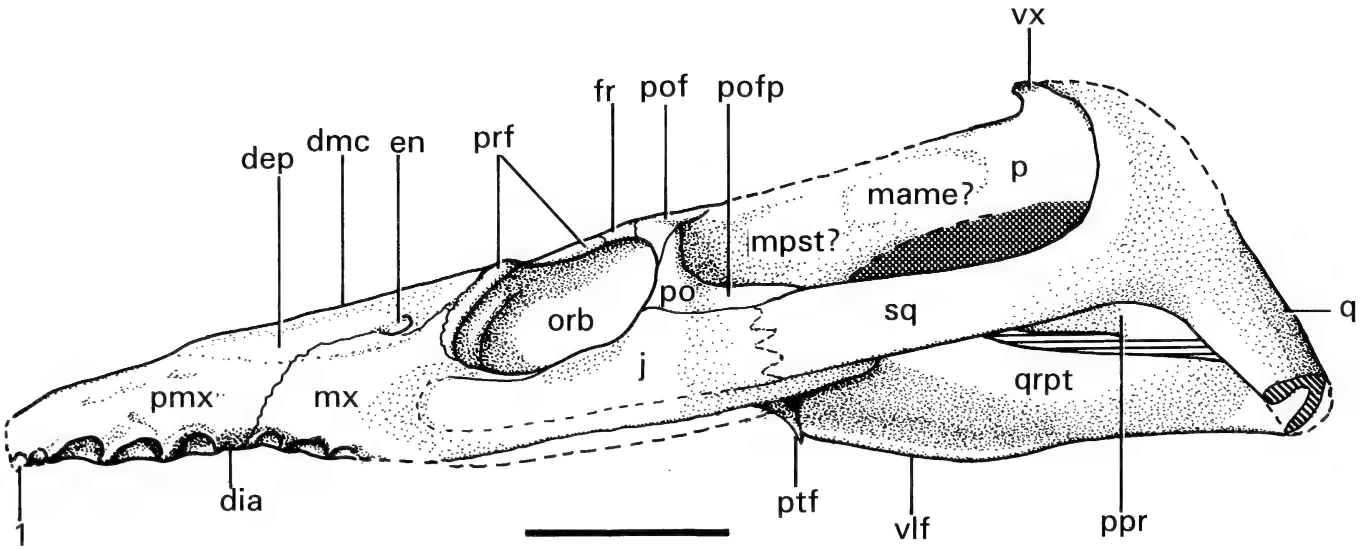

Fig. 2. Skull of *Leptocleidus capensis* (Andrews, 1911) in side view. Scale bar = 50 mm.

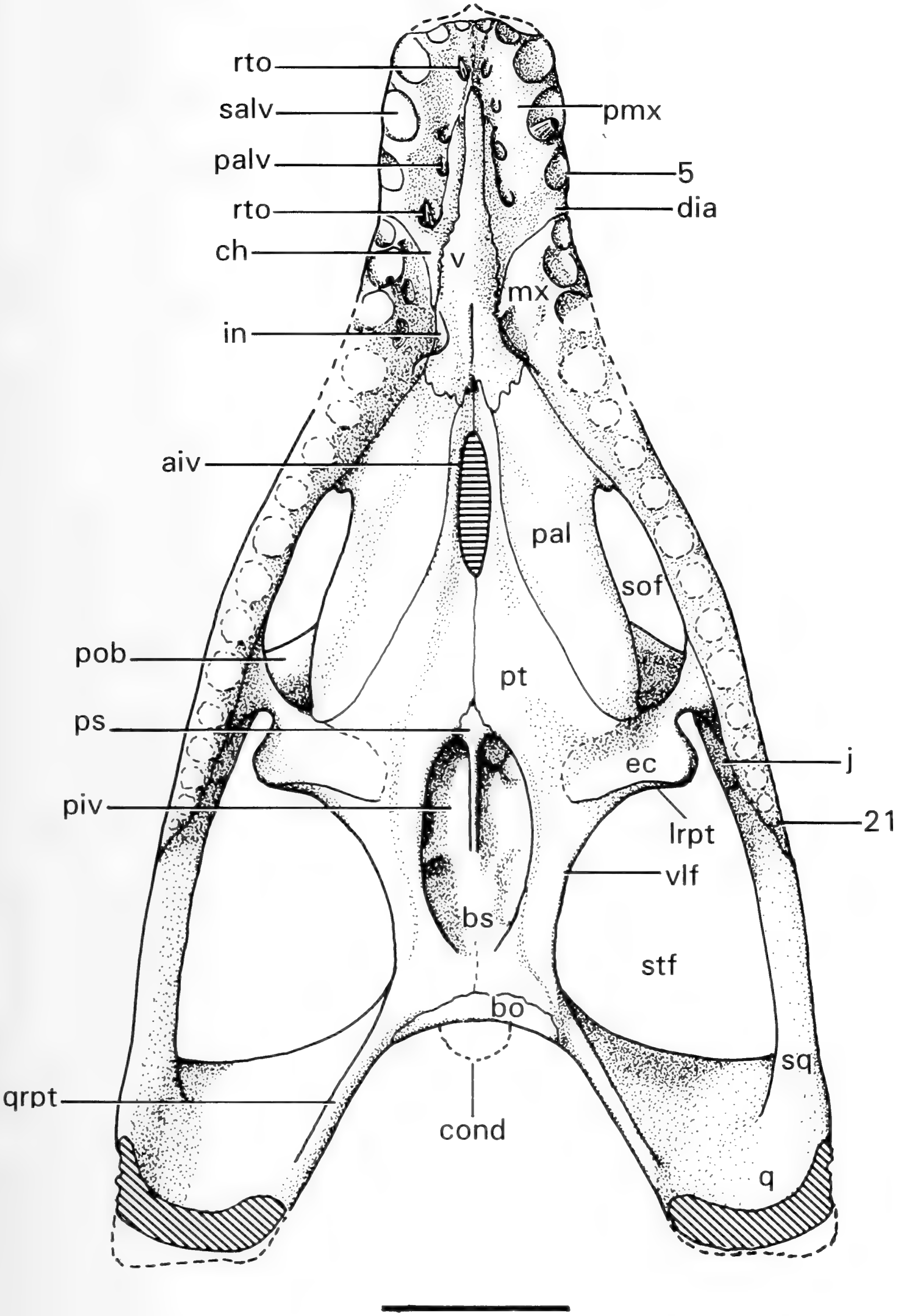

Fig. 3. Skull of *Leptocleidus capensis* (Andrews, 1911) in palatal view. Scale bar = 50 mm.

the surface of the parietals (mpst?, mame?) in very much the same situation as interpreted by Taylor (1992*b*) for *Rhomaleosaurus zetlandicus*. The midline of the vertex (vx) of the occiput has been drawn out to form a 'cock's-comb'-like process, which is also seen in *L. superstes*. Preparation damage from the time of discovery or the original descriptions has eroded the ventral rim of the posterior processes of the maxillae (mx), so that the tooth sockets are indistinct.

Mandible (Figs 4, 5)

There are five pieces of the lower jaw. The left ramus is represented by a length of dentary (d), and associated bones (c, sp), with 16 tooth positions preserved, and the posterior portion of the ramus from about the coronoid eminence (ce) to the retroarticular process (rap), with five tooth positions

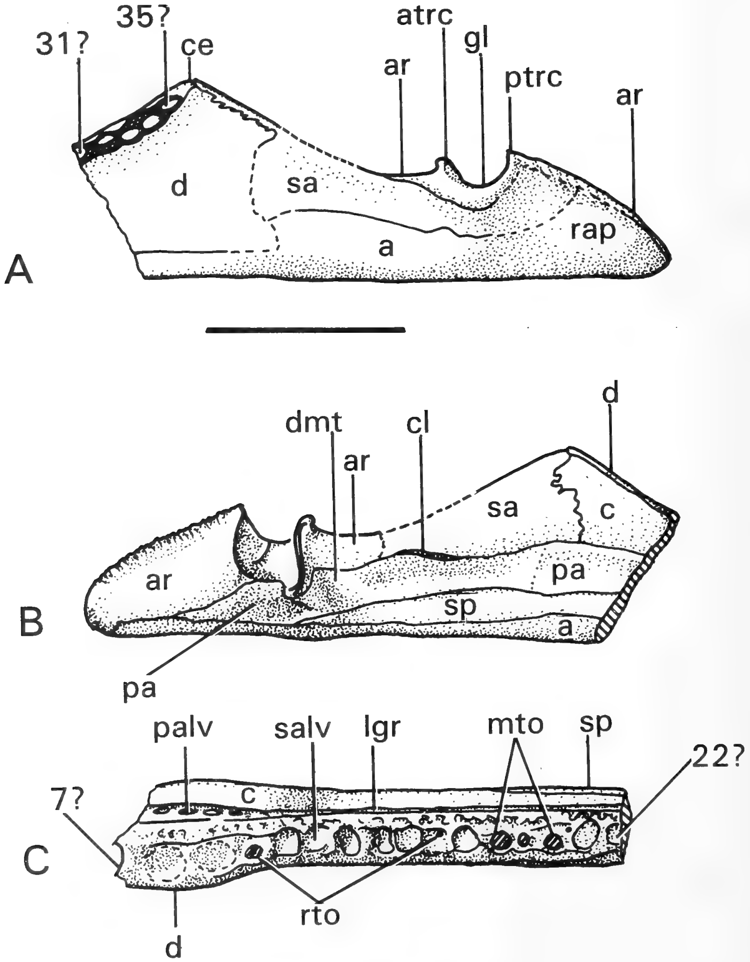

Fig. 4. *Leptocleidus capensis* (Andrews, 1911). A. Posterior portion of left ramus of lower jaw, outer view. B. Posterior portion of left ramus of lower jaw, inner view. C. Mid-region of lower jaw, dorsal view. Scale bar = 50 mm.

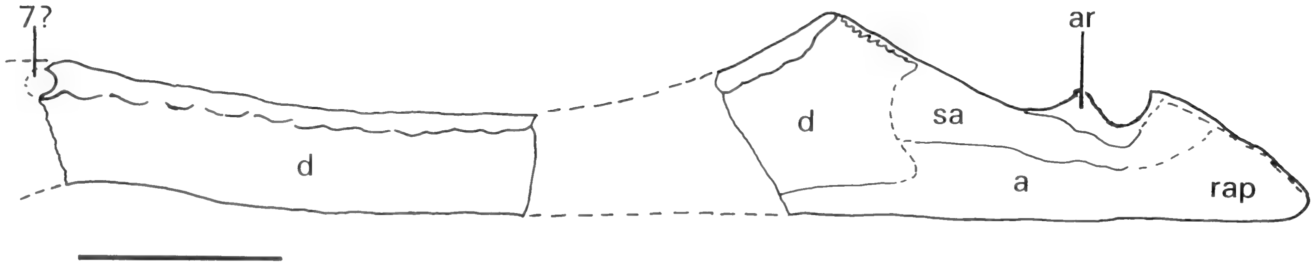

Fig. 5. Semi-diagramatic reconstruction of left lower jaw of *Leptocleidus capensis* (Andrews, 1911) to show missing portions. Scale bar = 50 mm.

preserved. The right ramus is represented by three portions: a short piece from just behind the symphysis (i.e. a mirror image of the very anterior of the anterior part of the other ramus); a badly broken piece from the mid-dentary region; and the very end of the ramus from just in front of the glenoid (gl) to the retroarticular process. Only the left jaw remnants are figured.

It is important to try to estimate how much of the front of the jaw is missing, as significant taxonomic decisions are made on the nature of the jaw symphysis (Tarlo 1960; Brown 1981). Also, it is of interest to try to calculate the amount missing from the ramus between the two portions, as this would help in arriving at a tooth-count for this species.

Neither of the anterior-most portions of the jaw have any indication of a symphyseal facet, but they both show the characteristic swelling that occurs in *Rhomaleosaurus* for at least two tooth positions behind the symphysis. Therefore, if the relationship with *Rhomaleosaurus* is appropriate and a symphyseal tooth-count of five is to be expected, then the first preserved tooth position cannot be more anterior than the sixth. In *Rhomaleosaurus*, the symphysis slopes backward ventrally and covers about one more tooth position after the fifth. Behind this the outer edges of the jaw rami are still parallel, to at least the seventh position, where the teeth start to reduce in diameter (Taylor 1992*b*, fig. 6; Cruickshank 1994*a*, figs 7, 9). Assuming the swelling to cover only one tooth position behind the symphysis would make the first preserved position the sixth, with an expectation of there being evidence for the remnants of the symphysis preserved on the lower edge of the jaw fragment; this is not evident. In order to be cautious, and assuming that the spatulate swelling of the anterior of the jaw covered more than seven positions, the first preserved tooth position is marked as the seventh.

Placing the jaw fragment in what appears to be a natural resting position against the upper jaw allows the swelling on the lower jaw to fit just behind the diastema (dia), leaving a distance sufficient to accommodate about five or six teeth to the front. Placing the glenoid against the (broken) end of the quadrate on the left side leaves a gap of about 75 mm on the lower edge of the jaw, into which about eight teeth could fit. Assuming that these approximations are nearly correct in their values, gives a tooth count of (6) + 16 + (8) + 5 = 35 for the lower jaw, a value within the known range for pliosauroids (Taylor 1992*a*).

The remainder of the jaw fits the general pliosauroid pattern, with, on the inner surface, a large coronoid (c) and substantial prearticular (pa) on each side. The splenial (sp) wedges between the prearticular and angular (a), and the prearticular runs under the medial flange of the articular (ar), to a point well behind the glenoid (Taylor 1992*b*; Cruickshank 1994*a*, 1994*b*).

No part of the Meckelian fossa is preserved, but a cleft (cl) between the prearticular and surangular (sa) marks the position of insertion of a portion of the jaw adductors (Taylor 1992*b*). A well-defined dorsomedian trough (dmt) is seen on the anterior faces of the articular and prearticular, as in *Rhomaleosaurus*, and which is believed to be characteristic of that genus (Taylor 1992*a*; Cruickshank 1994*a*) and its close relatives.

The mandible is a slender box-beam, with a low coronoid eminence lying fairly far back relative to the temporal fossa, just under the dorsally expanded vertex. A component of the external mandibular adductor muscles may have originated in this pocket under the vertex and inserted in the cleft just in front of the glenoid. Such a muscle would act at its most efficient when the jaw was some way open, and enhance the speed at which it closed—a useful attribute in a generalized predator. This proposed muscle would be an addition to the main mass of the external mandibular adductor (mame?).

Dentition (Fig. 6)

In the upper jaw there is room for about 16 teeth in each maxilla, and five in each premaxilla, giving a total of 21 for the upper dentition. As calculated above, there seem to be about 35 teeth in each ramus of the lower jaw. These counts are within the known range for pliosauroids (Brown 1981; Taylor 1992*a*).

In the upper jaw, the first five teeth on each side commence with a very small tooth, which appears to have protruded almost horizontally, followed by four of increasing size, but also procumbent. In the upper jaw there is a diastema, at the maxilla–premaxilla junction, which is followed by a smaller tooth, behind which they enlarge again over two or three positions. However, damage to the maxillae behind this point has removed much information, and only what can be seen is indicated on the reconstruction—a run of substantial teeth extending to the limit of each maxilla. Little can be said of the mandibular dentition; the mesial part of the symphyseal region (in common with *Rhomaleosaurus*) shows several large tooth positions, followed by a marked decrease in size from about the postulated tenth position, to the end of the dentary. As judged from the visible replacement teeth (rto), each tooth is a substantial, slightly recurved cone, with strong striae on the lingual surfaces, and weak mesio-distal carinae. None of the teeth referred to by Andrews (1911) has survived, but he illustrated (pl. 18 (fig. 4)) a small (= ?posterior) tooth with a very much greater curvature to its tip. The implication is that the anterior teeth are simple cones, such as are found in *Rhomaleosaurus*, but that the posterior teeth were acting to help prey be swallowed, as is common in many modern reptiles,

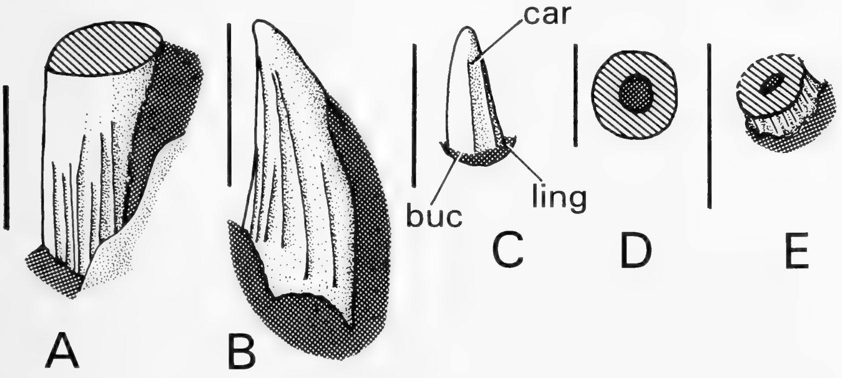

Fig. 6. Camera lucida drawings of selected teeth of *Leptocleidus capensis* (Andrews, 1911). A. Base of third left premaxillary replacement tooth. B. Apex of eighth right dentary replacement tooth. C. Apex of first right premaxillary replacement tooth. D. Cross-section of tenth right mature dentary tooth. E. ?Tenth left dentary mature tooth. Scale bars (all to left of figure) = 5 mm.

and which condition has been described in the Upper Jurassic pliosauroid, *Pliosaurus brachyspondylus* (Taylor & Cruickshank 1993).

The form of the teeth corresponds closely to Massare's (1987) 'generalist' predator type, being adapted to apprehending active, struggling prey (Taylor 1992*b*), or being capable of dismembering large carcasses by gripping strongly, and wrenching out mouthfuls by 'twist-feeding' (Taylor 1987), each mouthful being swallowed whole.

Postcranial skeleton

Andrews (1911) described the postcranial elements very well, and no further attempt will be made here to amplify his comments, except to note some items regarding the vertebrae.

A total of 38 vertebrae have been identified during this study, one more than originally described, but which can be accounted for by taking into account half centra on the ends of the preserved sequences. They comprise 22 cervicals and 16 dorsals (which is where the count differs from that of Andrews). Eleven of the cervicals occur in four dissociated groups, and two single, damaged vertebrae. Nine posterior cervicals are articulated with the 16 dorsals. All vertebrae show their neural arches firmly fused to their centra and are, therefore, from an adult animal (Brown 1981). All the centra are as long as they are wide, an unusual state for a Cretaceous pliosauroid (Brown 1981).

Leptocleidus capensis had at least 22 cervicals but, as neither atlas nor axis are represented here, the count must rise to a minimum of 24. The known range of cervicals for *Rhomaleosaurus* is 28–32, and hence a value within that range is possible for *Leptocleidus capensis*. This is unusual to say the least, as it is assumed that within the Pliosauroidea, by the Cretaceous, the cervical count has diminished to about 13 highly compressed vertebrae (Brown 1981). It is impossible to see whether the rib-heads are single or double.

The smallest (anterior) cervical vertebrae have zygapophyses orientated almost horizontally. The larger, posterior, cervicals and the dorsals have their zygapophyses orientated at about 50° to the horizontal. Within the limits allowed by connective tissues and similar constraints, this might indicate that the posterior of the neck was less mobile, horizontally, than was the anterior (Evans, MS 1993). A certain amount of vertical movement, both above and below the horizontal is presumed, but controlled largely by relative interference by the neural spines with one another.

DISCUSSION

Leptocleidus is very similar to *Rhomaleosaurus* (Taylor 1992*a*, 1992*b*; Cruickshank 1994*a*; Table 1 herein). Twenty-six characters can be evaluated under the headings of (a) gross similarities, (b) gross differences, (c) size-related differences, (d) those characters of uncertain validity and (e) characters not known or which are unpreserved in *Leptocleidus*.

(a) Head shape, the expanded lateral ramus of the pterygoid, the snout with rosette of intermeshing teeth, and the general tooth shape and character are all probably plesiomorphic and therefore not significant. What may prove to be

TABLE 1

Comparisons of *Rhomaleosaurus* and *Leptocleidus*. Similarities: head subtriangular; dorsomedian foramen between facial processes*; dorsomedian trough on anterior face of articular and prearticular*; expanded lateral ramus of pterygoid; strong descending flange on postorbital bar*; snout with rosette of intermeshing teeth; teeth conical, circular in section; teeth with weak caninae.

Rhomaleosaurus	*Leptocleidus*
GROSS DIFFERENCES	
Lower Jurassic age	Lower Cretaceous age
Skull profile smooth	Vertex with dorsal notch
Boss on lateral ramus of pterygoid	No boss
Postorbital = postfrontal on postorbital bar	Postorbital smaller than postfrontal
Wide exposure of parasphenoid on palate	Narrow parasphenoid
Postorbital lacks ventral footplate	Postorbital with footplate
Teeth uniform shape	Posterior teeth slightly recurved
Teeth striated all round	Buccal surface of teeth smooth
Accessory grooves on anterior of palate	No accessory grooves on palate
SIZE-RELATED DIFFERENCES	
Skull length-to-width ratio—2 : 1	1.7 : 1
Tooth count in upper jaw—30	21
A DIFFERENCE OF UNCERTAIN VALIDITY	
Lacrimal present	Lacrimal absent
UNPRESERVED OR NOT KNOWN FOR *LEPTOCLEIDUS*	
Moderately large; > 5 m	Overall length of 2 m, based on skull length 310 mm
Head 15 per cent of overall length*	
5 teeth in lower jaw symphysis	< 7 teeth in symphysis*
Symphysis spatulate/elongate	Symphysis shape not known
Neck 28–32 vertebrae	Neck at least 24 vertebrae
Presacral vertebrae 58	Presacral count not known
Neck 25 per cent overall length	Neck length not known

*—possible autapomorphies for rhomaleosaurids

autapomorphies for *Rhomaleosaurus* and its close allies are the possession of dorsomedian foramina between the facial processes of the premaxillae and dorsomedian troughs on the anterior faces of the articulars and prearticulars, allied with strong descending flanges on the postorbital bars.

(b) The eight gross differences noted between the two genera might all be considered the result of the time difference between the two; six of these are concerned with the reaction of the skull to feeding stresses (Taylor 1992*b*). In

Leptocleidus, the extension of the vertex is seen as allowing a slip of the external adductor muscles (mame) to grow slightly longer, and hence add to the speed of closure of the jaw. The lack of a boss on the lateral ramus of the pterygoid, and reduction of the pterygoid flange, indicates that the gullet was being opened up to enhance the speed of ingestion of food (cf. *Pliosaurus*—Taylor & Cruickshank 1993). The weakening of the skull in this region against lateral forces, as a result of that process, has been partially compensated for by the deepening of the ventral flange on the postorbital bar, and the change in proportions of the postorbital and postfrontal bones. This is associated with the development of the footplate on the postorbital, where it overlaps the jugal and squamosal; the maxilla is already known to have overlapped the jugal--squamosal junction by the Lower Jurassic (Cruickshank 1994*a*). As far as the teeth are concerned, there is a tendency for them to lose their ornament on the outer (buccal) surfaces, and to adopt a triangular section (Tarlo 1960). In addition the smaller, posterior teeth tend to become recurved, or hooked, to aid passing prey down the throat. *Leptocleidus* has teeth with unornamented buccal surfaces, and has slightly recurved small (?posterior) teeth, but they retain a circular section. In these ways it is advanced over *Rhomaleosaurus*, but only slightly. The lack of accessory grooves on the anterior palate—the significance of which is unknown—is a difference from *Rhomaleosaurus* (Cruickshank *et al.* 1991) and the reduced exposure of the parasphenoid on the palate is similar to the condition in the Plesiosauroidea, and may be a size-related factor.

(c) Other size-related factors are the skull length-to-width ratios and the number of teeth in the upper jaw. It is believed that the smaller animal would naturally have a relatively 'wider' skull than the larger, and with less space, the upper jaw at least would have fewer teeth.

(d) A character of unknown validity is the lack of an observed lacrimal in *Leptocleidus*, bearing in mind its occurrence even in late Jurassic forms (Taylor 1992*b*; Taylor & Cruickshank 1993; Cruickshank 1994*a*).

(e) Characters that cannot be commented on with certainty are those which are missing or which cannot be calculated, such as the relative size of the head in *Leptocleidus*, the number of teeth in its lower jaw symphysis, its count of neck vertebrae, the total number of presacrals and the relative length of its neck. However, circumstantial evidence can be brought to bear to indicate that all these characters are most likely to be 'rhomaleosaurid' in character.

Another point of significance is that *Leptocleidus capensis* was recovered from sediments with freshwater foraminifers—probably lagoonal or close inshore in character (McMillan in press). The animal was about the size of a seal, and may have lived very much in the same way, hunting fish and other modest-sized prey in the inshore zone of a shallow sea.

Other localities which have yielded 'non-marine' plesiosaurs include Berwick Brick Pit, Sussex, England, Wealden (= Barremian) (*L. superstes*—Andrews 1922), near Mount Morgan Copper Mine, Queensland, Australia, Lower Jurassic (*Leptocleidus* cf. *L. superstes*—Bartholomai 1966; Molnar 1982), south-eastern Australia, Lower Cretaceous (isolated teeth and ribs—Rich *et al.* 1989), Coober Pedy, South Australia, Lower Cretaceous (*Leptocleidus* cf. *L. superstes*—Ritchie 1991), Nanning, Kwangsi, China, Lower Cretaceous

(*Sinopliosaurus fusinensis*—Hou *et al.* 1975) and *Bishopliosaurus* also from the Chinese Lower Jurassic. The Antarctic record includes elasmosaurids and cryptoclidids from Late Cretaceous nearshore marine and coastal-deltaic sediments (Chatterjee & Small 1989).

The probability is that some pliosauroids, perhaps the smaller species at least, were exploiting the inshore habitat (Hudson 1966) and this would explain the apparent anomaly of a conventionally marine group having such a strong freshwater character. One can speculate that the (less advanced) representatives of the original pliosauroid stock were forced under competition to seek refuge in a relatively protected environment in the inshore shallows, whereas their replacements worked their way into the resulting vacant niches. One other area of mystery in the plesiosaurs is the lack of juveniles in the fossil record. Perhaps these inshore records reflect the result of unsuccessful egg-laying forays up rivers or on to sandbars?

SUMMARY & CONCLUSIONS

The skull of the pliosauroid plesiosaur *Plesiosaurus capensis* Andrews, 1911, from the uppermost Valanginian (Lower Cretaceous) Algoa Basin, South Africa, is figured and redescribed.

Plesiosaurus capensis shares many of its characters with *Leptocleidus superstes* Andrews, 1922, from the Barremian of the Weald Basin, England, and therefore can be ascribed to the latter genus, as suggested by Persson (1963). The name therefore becomes *Leptocleidus capensis* (Andrews, 1911).

Both these forms seems similar to undescribed Lower Cretaceous pliosauroids from Australia. *Leptocleidus* is close to and may be derived from the Lower Jurassic *Rhomaleosaurus* Seeley, 1874.

All three Lower Cretaceous forms come from lagoonal, or very shallow, close inshore, marine facies.

A brief review of the literature shows that several plesiosaurian finds are from freshwater facies in both Jurassic and Cretaceous age sediments.

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ABBREVIATIONS

(USED IN TEXT AND FIGURE CAPTIONS)

a	angular
aiv	anterior interpterygoid vacuity
ar	articular
ars	anterior ramus of the squamosal
atrc	anterior transverse crest of the glenoid fossa
bo	basioccipital
bs	basisphenoid
buc	buccal surface of tooth
c	coronoid
car	carina of tooth
ce	coronoid eminence
ch	channel
cl	cleft
cond	occipital condyle
cr	crest
d	dentary
dep	depression
dia	diastema
dmc	dorsomedian crest
dmfo	dorsomedian foramen
dmt	dorsomedian trough
drs	dorsal ramus of the squamosal
ec	ectopterygoid
en	external naris
fac	facial process of the premaxilla
fr	frontal
gl	glenoid fossa
in	internal naris
j	jugal
lgr	longitudinal groove on dentary
ling	lingual surface of tooth
lrpt	lateral ramus of pterygoid
mame?	m. adductor mandibulae externus
mpst?	m. pseudotemporalis
mto	mature tooth
no	notch
nuch?	origin of nuchul ligament
orb	orbit
p	parietal
pra	prearticular
pal	palatine
palv	primary alveolus
pfo	parietal foramen
piv	posterior interpterygoid vacuity
pmx	premaxilla
po	postorbital
pob	postorbital bar
pof	postfrontal
pofp	footplate to postorbital
ppr	paroccipital process
prf	prefrontal
ps	parasphenoid
psc	parasagittal crest

pt	pterygoid	salv	secondary alveolus
ptf	pterygoid flange	sof	suborbital fenestra
ptrc	posterior transverse crest to glenoid	sp	splenial
		sq	squamosal
q	quadrate	stf	subtemporal fenestra
qrpt	quadrate ramus of the pterygoid	tf	temporal fenestra
rap	retroarticular process	v	vomer
rto	replacement tooth	vx	vertex
sa	surangular	1–35	tooth positions

Mechanical stipple—matrix; horizontal lines—openings in skull; diagonal lines—broken or eroded bone.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

ARTHUR R. I. CRUICKSHANK

A LOWER CRETACEOUS PLIOSAUROID FROM SOUTH AFRICA

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ANNALS
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   - (e) *Subject matter* of the paper, divided into sections to correspond with those given in table of contents
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Major headings of the paper are centred capitals; first subheadings are centred small capitals; second subheadings are shouldered small capitals; third subheadings are shouldered italics; fourth subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations. Footnotes should be avoided unless they are short and essential. All generic and specific names should be underlined or italicized.

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Examples (note capitalization and punctuation)

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ON THE AFFINITIES OF *MADAGASCARITES ANDIMAKENSIS* COLLIGNON, 1966, AND ALLIED UPPER CRETACEOUS HETEROMORPH AMMONITES

By

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&
W. J. KENNEDY

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(With 17 figures)

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ABSTRACT

Coiling in the Santonian heteromorph ammonite genus *Madagascarites* Collignon, 1966 (type species *M. andimakensis* Collignon, 1966), was originally compared to that of *Nipponites* Yabe, 1904. This is shown to be incorrect. *Hyphantoceras ingens* Collignon, 1966, is regarded as a synonym of *M. andimakensis*. Material from the Turonian of Japan ascribed to the genus *Madagascarites* clearly does not belong to this genus and is referred to *Ryuella* gen. nov., with *Madagascarites ryu* Matsumoto & Muramoto, 1967, as type species. *Heteroceras amapondense* van Hoepen, 1921, which was also tentatively referred to *Madagascarites*, is here referred to *Eubostrychoceras (Amapondella)* subgen. nov. of which it is the type species.

CONTENTS

SYSTEMATIC DESCRIPTIONS AND DISCUSSIONS

We (Klinger & Kennedy in prep.) are at present revising the Upper Cretaceous heteromorph ammonites from Zululand described by Klinger (1976) on the basis of additional and new material. Our views on the systematics and phylogeny of these heteromorphs will be discussed fully in this revision. For the present we restrict ourselves to the affinities of the poorly known genus *Madagascarites* Collignon, 1966, and allied forms.

The genus *Madagascarites* Collignon, 1966, with type species *Madagascarites andimakensis* Collignon, 1966 (p. 26, pl. 465 (figs 1897–1898)) from the Middle Santonian of Madagascar was introduced (Collignon 1966: 26) as follows: 'MADAGASCARITES ANDIMAKENSIS nov. gen. nov. sp. G.T. Il s'agit d'une Ammonite à déroulement aussi désordonné que celui de *Nipponites* . . . mais en différant par l'ornamentation, puisque *Nipponites* n'a pas des côtes tuberculées.

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Ici, les côtes serrées, annulaires, minces et tranchantes, sont groupées par 5–7 environ, et sont encadrées de côtes à boucles à 4 tubercules, comme chez *Hyphantoceras ingens* nov. sp. Mais les côtes à boucles commencement dès le début et ne sont pas limitées à la chambre d'habitation. Le mode de déroulement est aussi bien différent et permet, à mon sens, de séparer ces divers échantillons, celui d'Antsoha se rattachent naturellement à *Hyphantoceras*, au moins pour le moment, car des séries d'exemplaires de toutes tailles pourraient peut-être permettre de les rattacher les uns aux autres dans le genre *Madagascarites* qui serait alors caractérisé aussi bien par son ornamentation que par son mode particulier de déroulement.'

Fig. 1. *Madagascarites andimakensis* Collignon, 1966. The holotype, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 734, Sud Ambiky (Belo sur Tsiribihina), Madagascar. This specimen cannot, at present, be traced in the collections of the Université de Bourgogne in Dijon. × 1.

According to Collignon's diagnosis, *Madagascarites* thus has (irregular) coiling as in *Nipponites*, but ornament throughout as on the body chamber of *Hyphantoceras ingens*.

Apart from the holotype, Collignon (1966: 26, pl. 465 (fig. 1898)) figured a second specimen consisting of part of a helical whorl and the succeeding, ascending body chamber.

Several questions have to be addressed:

1. The relationship between *Madagascarites* and *Nipponites*.
2. The relationship between *Madagascarites andimakensis* and *Hyphantoceras ingens*.
3. Affinities with *Hyphantoceras*.
4. The identity of *Madagascarites ryu* Matsumoto & Muramoto, 1967.
5. The affinities of *Hyphantoceras (Madagascarites?) amapondense* (van Hoepen).

Fig. 2. *Madagascarites andimakensis* Collignon, 1966. The holotype, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 734, Sud Ambiky (Belo sur Tsiribihina), Madagascar. This specimen cannot, at present, be traced in the collections of the Université de Bourgogne in Dijon. × 1.

The holotype of *Madagascarites andimakensis* has two early whorls, which are situated at an angle to each other (Figs 1–4). Having examined the holotype, Klinger (1976: 71) suggested that this may be due to post-mortem fracture of the shell; the totally crushed, ascending body chamber may confirm this. These early whorls suggest helical coiling, either contiguous or slightly separated, and are succeeded by a final helical whorl and an ascending body chamber that reaches at least to the top of the early whorls—a mode of coiling analogous to that of the Upper Campanian genus *Anaklinoceras* Stephenson, 1941.

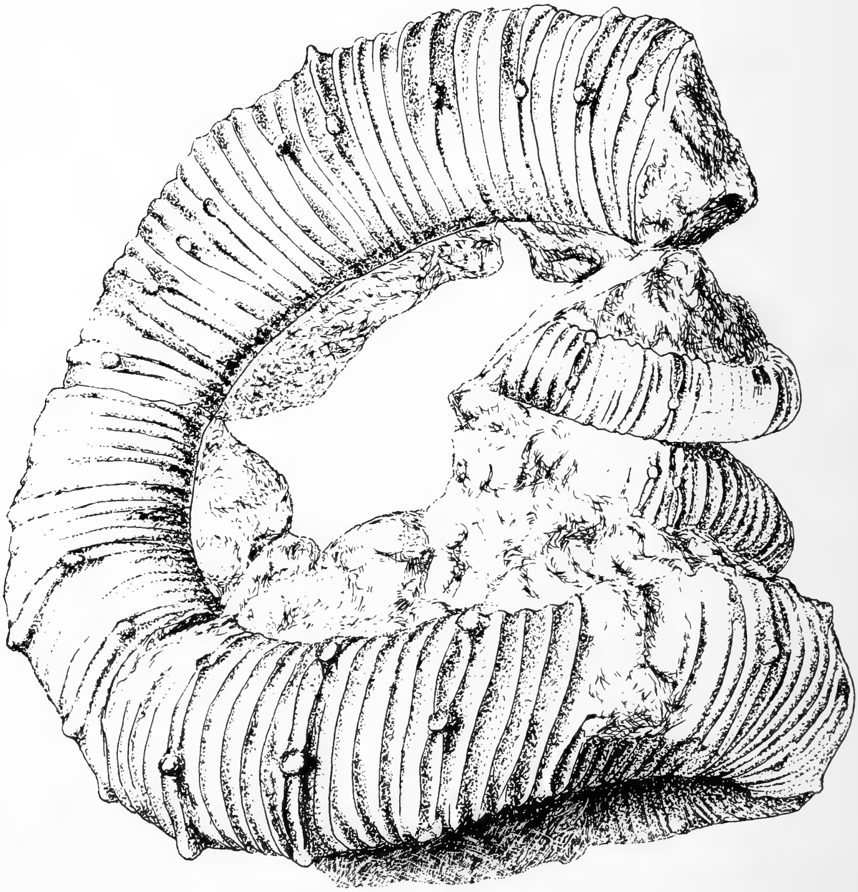

Fig. 3. *Madagascarites andimakensis* Collignon, 1966.
Line drawing based on Figure 1. × 1.

Unfortunately, the holotype of *M. andimakensis* cannot, at present, be located in the Collignon collection at Dijon (J.-H. Delance—pers. comm. 31 August 1994). When last seen and photographed by Klinger in 1973, it was displayed in General Collignon's study. We suspect that it may have been misplaced during the transfer of the Collignon collection to Dijon. However, another specimen (757), with a label in Collignon's handwriting and which identifies it as *Madagascarites andimakensis* (Figs 5–6A), is present amongst the undescribed material at Dijon. This specimen is much smaller than the holotype and lacks the early whorls. The last part of the phragmocone is poorly preserved and tubercles, if present, are either very weak or absent. Tubercles are only prominent on the ascending part of the body chamber.

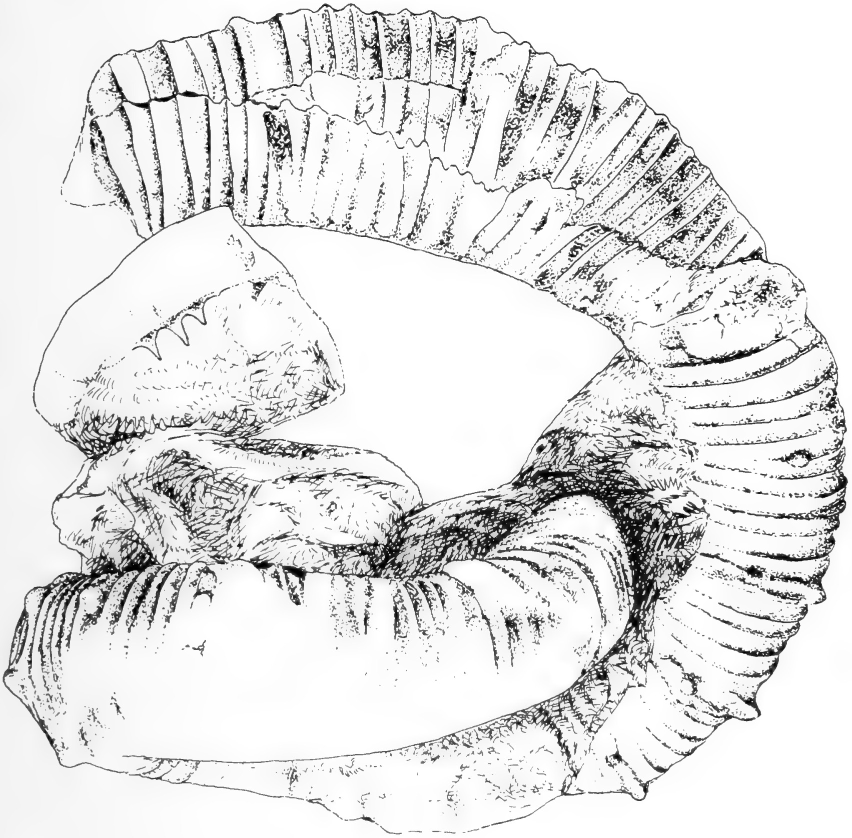

Fig. 4. *Madagascarites andimakensis* Collignon, 1966.
Line drawing based on Figure 2. × 1.

1. As discussed above, the preserved early whorls of the holotype of *Madagascarites andimakensis* suggest a helical mode of coiling in the early, but not earliest, part of the phragmocone, and ends in a final helical whorl, followed by an ascending body chamber, which may embrace the helical phragmocone. Coiling in well-preserved *Nipponites* is very distinctive, consisting of a series of U-shaped sections, comparable to the sutures on a tennis ball, and ends in a looped or U-shaped body chamber, suspended below the phragmocone (Okamoto 1989; herein Fig. 7). The genus is thus far only known from the Middle Turonian to Lower Coniacian with records from Japan, Saghalien, Kamchatka and Oregon (see Matsumoto 1977). Similarities between the coiling of *Madagascarites* and *Nipponites*, as suggested by Collignon (1966: 26), cannot be sustained.

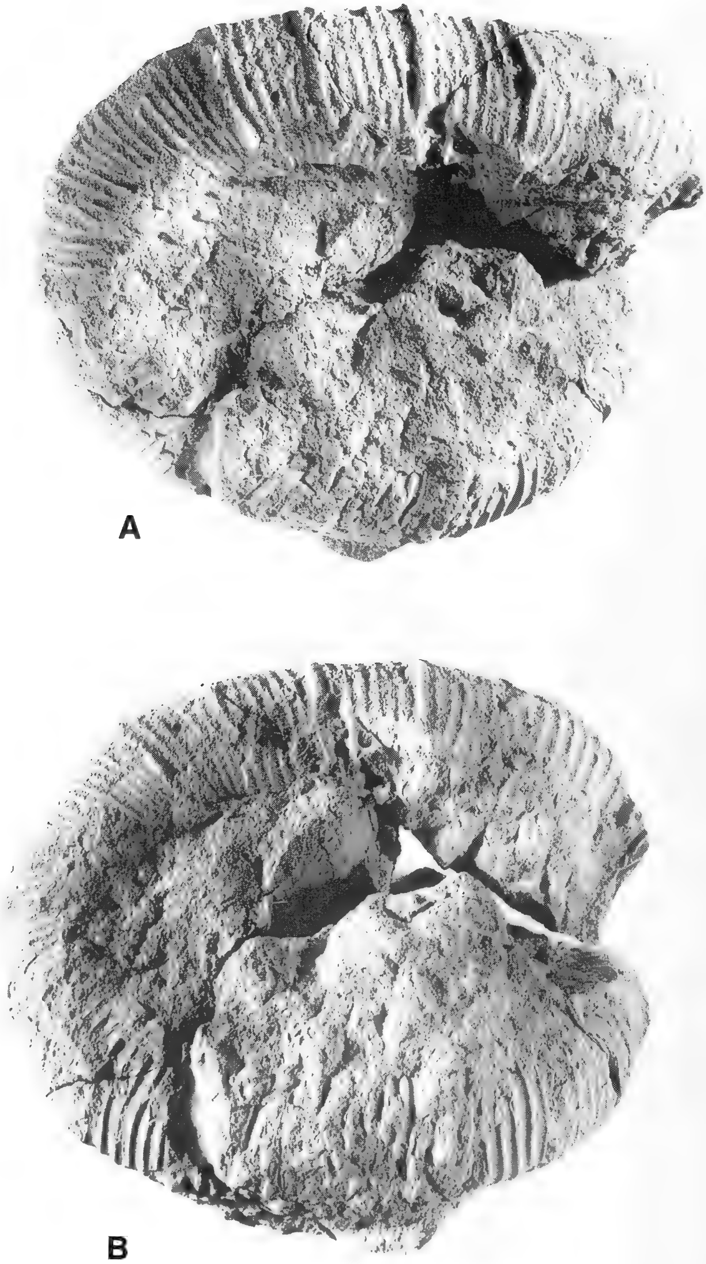

Fig. 5. *Madagascarites andimakensis* Collignon, 1966. Undescribed specimen from the Middle Santonian, zone of *Texanites hourqi* at gisement 757, km 8500 Coupe S. Beantaly, Souromarinaro (Belo sur Tsiribihina), Madagascar. A. View from top, looking down on ascending part of body chamber. B. Lateral view, with ascending part of body chamber pointing upwards. Both × 1.

2. *Madagascarites andimakensis* and *Hyphantoceras ingens* have identical body chamber ornament. This consists of several simple, non-tuberculate ribs separating looped ribs with four rows of tubercles. According to Collignon (1966: 26), these looped, quadrituberculate ribs already occur on the early whorls of *M. andimakensis* but only appear on the body chamber of *H. ingens*.

Both species are dated as Middle Santonian, but the types are from different localities. However, we have a specimen (SAM–GMC737, Fig. 6B–C) identified as *H. ingens* by General Collignon from the same locality as the figured paratype of *M. andimakensis*. *Hyphantoceras ingens* and *M. andimakensis* are thus, in part at least, coeval. The early whorls of *H. ingens* are not known, but the last part of the body chamber of the holotype (Fig. 8) and specimen SAM–GMC737 (Fig. 6B–C) show signs of an upward curvature, suggesting a final mode of coiling similar to that of *M. andimakensis*.

The holotype of *H. ingens* (Fig. 8) is nearly twice the size of that of the holotype of *M. andimakensis* (Figs 1–4). SAM–GMC737 (Fig. 6B–C) shows indications of the onset of upward coiling of the body chamber at a diameter similar to that of the holotype of *M. andimakensis*. On the other hand, the third specimen of *M. andimakensis* (Figs 5, 6A) is only about one-half the size of the holotype.

These observations suggest that the holotype of *H. ingens* is merely a large form of *Madagascarites andimakensis*. In addition, the third, and smallest specimen of *M. andimakensis* appears to lack tubercles on the phragmocone—a feature originally thought to be characteristic of *Hyphantoceras ingens*.

We believe *H. ingens* and *Madagascarites andimakensis* to be synonyms, as suggested earlier (Klinger & Kennedy 1977: 79) and, as first revising authors, select the name *andimakensis* for the species. Thus interpreted, *M. andimakensis* shows a wide range in adult size, some specimens being twice as large as others, presumably a reflection of dimorphism. In addition, the ontogenetic stage at which ornament changes (from uniform simple ribbing to simple ribs separating periodic quadrituberculate major ribs) is quite variable.

3. *Hyphantoceras*, as interpreted in terms of the type species *Hyphantoceras reussianum* (d'Orbigny, 1850) (see Kaplan & Schmid 1988; Metzdorf 1993, for full reviews) (Figs 9, 16D), has flared quadrituberculate ribs throughout and we would prefer to retain this name for those ornamented forms with helical coiling, a low apical angle, and a retroversal body chamber.

Madagascarites can probably be derived from *Hyphantoceras* on the basis of the common presence of flared quadrituberculate ribs. An origin could be less probably sought in *Schlueterella* of the group of *S. compressus* Klinger,

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Fig. 6 *(see overleaf)*. A. *Madagascarites andimakensis* Collignon, 1966. Undescribed specimen from the Middle Santonian of gisement 757 at km 8 500 Coupe S. Beantaly, Souromarinara (Belo sur Tsiribihina), Madagascar. Lateral view, showing last part of helical phragmocone whorl and ascending part of body chamber at top. B–C. Undescribed specimen of *Hyphantoceras ingens* SAM–GMC733, ex Collignon collection, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 733, Coupe d'Ambikity, Andimaka (Belo sur Tsiribihina), Madagascar, the same locality as the paratype of *M. andimakensis* Collignon (1966, pl. 465 (fig. 1898)). All × 1.

Fig. 7 *(see overleaf)*. *Nipponites mirabilis* (Yabe). Cast of specimen figured by Matsumoto (1977, pl. 56 (fig. 1)), GK H5846 from locality T1022p, Saku-gakko-no-sawa, Saku area, Hokkaido. × 1.

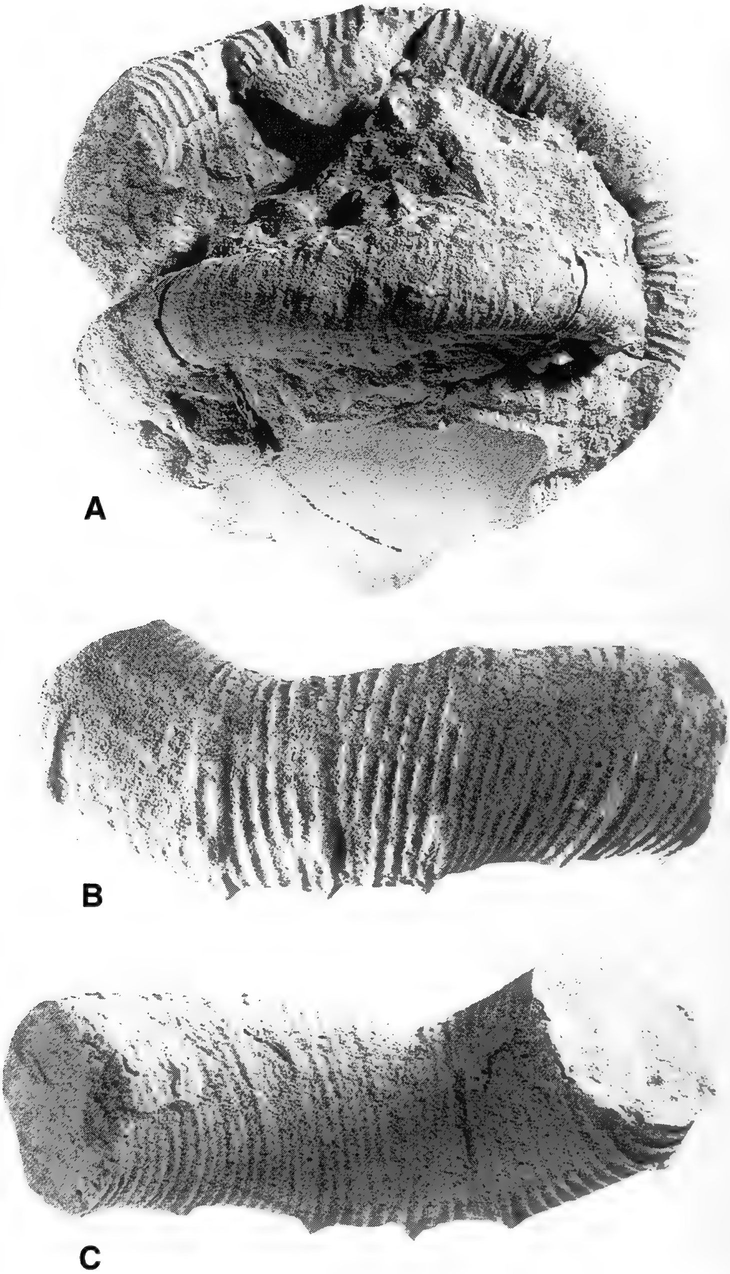

Fig. 6

Fig. 7

Fig. 8. The holotype of '*Hyphantoceras ingens*' Collignon, 1966, from the Middle Santonian, zone of *Texanites hourcqi* at gisement 230, Ansoha (Antsalova), Madagascar. × 0.85.

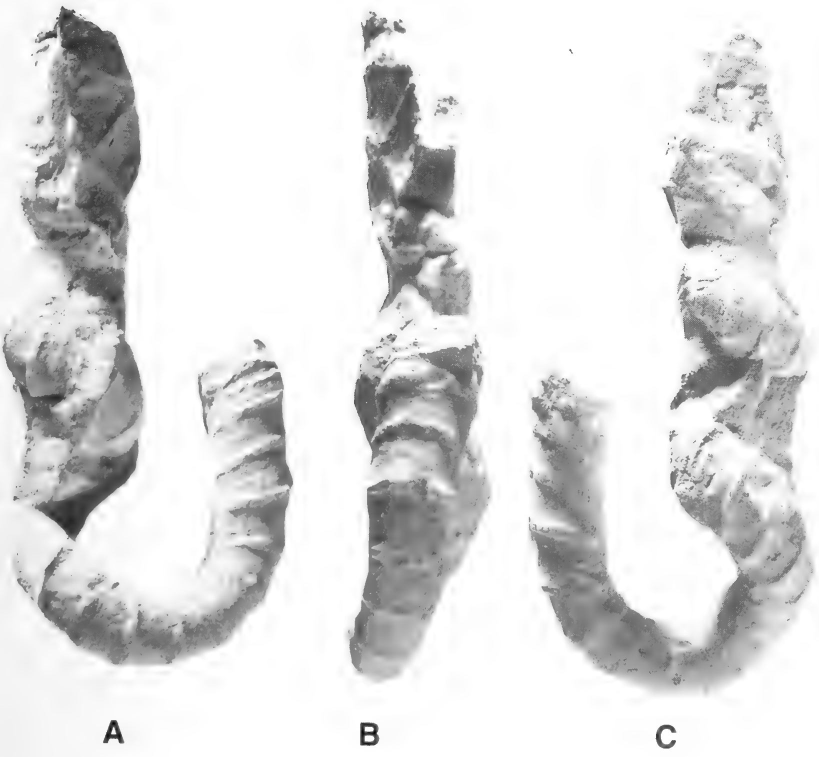

Fig. 9. *Hyphantoceras reussianum* (d'Orbigny, 1850). Cast of the original of Schlüter (1876, pl. 32 (fig. 18)). Unregistered specimen in the collections of the Geological and Palaeontological Institute, Göttingen, Germany. × 1.

1976, of the Lower Santonian. The quadrituberculate ornament of the latter (see especially Immel *et al.* 1982: 25, pl. 9 (fig. 3), pl. 10 (figs 1–4), pl. 11 (fig. 3)) is remarkably similar to that of *M. andimakensis*, although the modes of coiling are quite different.

4. Matsumoto & Muramoto (1967: 362, pl. 19 (fig. 3), pl. 22 (fig. 1), pl. 23 (figs 1–4)) described *Madagascarites ryu* from the uppermost Turonian of Hokkaido. The species (Figs 10–11) has coiling as in *Nipponites bacchus* Matsumoto & Muramoto, 1967, with the major part of the shell consisting of U-shaped sections, terminating in a hook-shaped body chamber suspended below the early part of the shell. Tanabe *et al.* (1981) showed details of coiling in *M. ryu*, especially of the early growth of the shell, which include an initial straight shaft (Fig. 11). But instead of simple ribbing as in *Nipponites*, *M. ryu* has quadrituberculate major ribs and finer intermediary ribs (Figs 10–11). It is, in fact, a *Nipponites* with *Hyphantoceras*-like ornamentation, and not a representative of *Madagascarites*. We presume that *Madagascarites ryu* arose from

Hyphantoceras in a manner analogous to that of *Nipponites* from *Eubostrychoceras japonicum* (Yabe, 1904), as suggested by Okamoto (1989: 133). Apart from differences in coiling, there is a considerable time gap between Late Turonian *Madagascarites ryu* and Middle Santonian *M. andimakensis*. We regard them as heterochronous homoeomorphs in terms of ornament (but not coiling) and do not consider them to be congeneric.

We here propose the genus ***Ryuella*** gen. nov. for this Japanese species, with type species *Madagascarites ryu* Matsumoto & Muramoto, 1967. The diagnosis is as follows: coiling in major part of phragmocone as in *Nipponites*, consisting

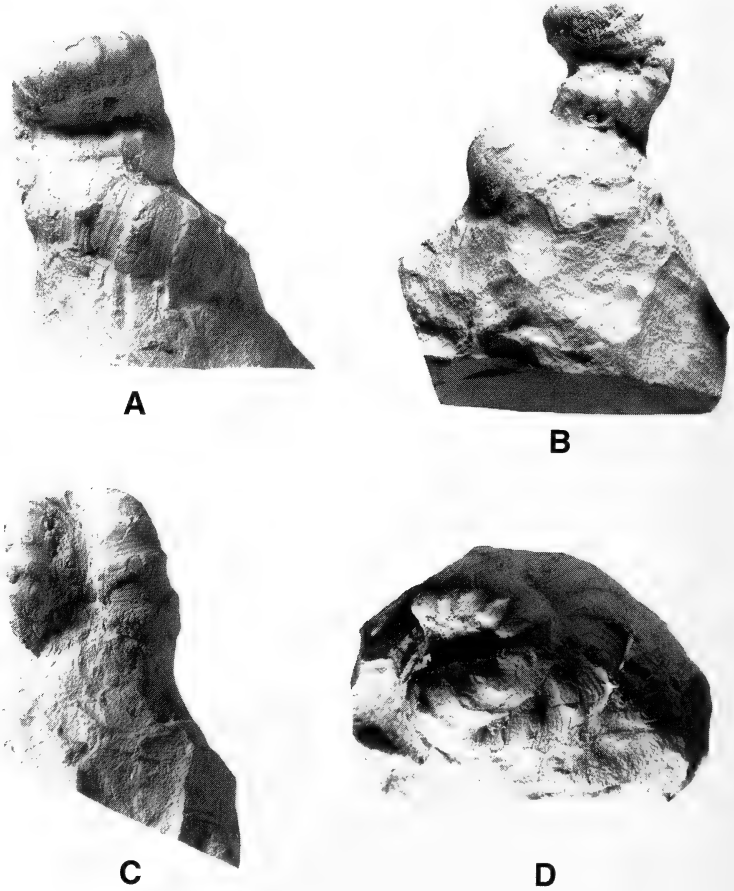

Fig. 10. *Ryuella ryu* (Matsumoto & Muramoto, 1967). Plaster cast of a paratype figured by Matsumoto & Muramoto (1967, pl. 23 (fig. 1a–c)), Muramoto collection 9100B, from the uppermost Turonian, zone of *Reesidites minimus* at Ikushumbets, Hokkaido. × 1.

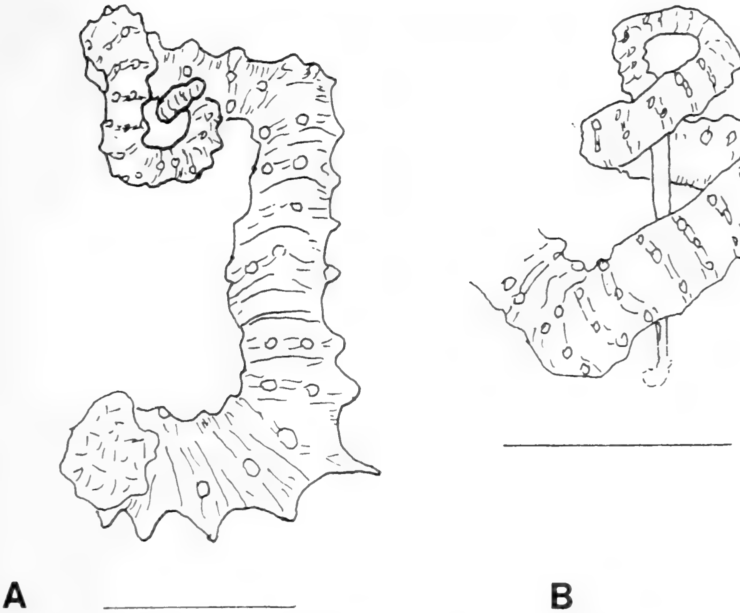

Fig. 11. *Ryuella ryu* (Matsumoto & Muramoto, 1967). A. Sketch of phragmocone showing typical *Nipponites*-like coiling. Scale = 10 mm. B. Sketch of early stage of ontogeny. Scale = 5 mm. Both after Tanabe *et al.* 1982, text-fig. 4.

Fig. 12 *(see overleaf)*. *Eubostrychoceras (Amapondella) amapondense* (van Hoepen, 1921). A–C. SAM-4820, the specimen described and figured by Woods (1906: 340, pl. 44 (fig. 3a–c)) as *Hamites (Anisoceras)*. E–F. Cast of the holotype, Transvaal Museum collections, both from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, probably uppermost Santonian or basal Campanian. D. Specimen labelled *Hyphantoceras* ex Collignon collection from the Santonian of gisement 147–148, Mitraiky, north of Manimbilo, Madagascar. All × 1.

Fig. 13 *(see overleaf)*. A–C. *Eubostrychoceras (Amapondella) amapondense* (van Hoepen, 1921). SAM-PCZ7328 from locality 105, Zululand, St Lucia Formation, Campanian I. All × 1.

Fig. 14 *(see overleaf)*. A. *Eubostrychoceras (Amapondella) amapondense* (van Hoepen, 1921). Catalogue and locality data as in Figure 13. B–C. *Eubostrychoceras (E.) auriculatum* (Collignon, 1965). SAM-GMC335 from the lower Coniacian at gisement 335, Beantaly (Belo sur Tsiribihina), Madagascar. All × 1.

Fig. 15 *(see overleaf)*. A–E. *Eubostrychoceras (Amapondella) amapondense* (van Hoepen, 1921). A–B. SAM-PCZ12881 (ex H126E/1) from Bed E, locality 105, Zululand, St Lucia Formation, Campanian I. C–D. SAM-PCZ12882 (ex Cape of Good Hope Geological Commission collection) from an unspecified horizon at the type locality of the Mzamba Formation at the Mzamba River Estuary, probably uppermost Santonian or basal Campanian. E. '*Allocrioceras*' sp. SAS-Z2071. Latex peel showing hamitid early irregular whorls and part of body chamber with bituberculate flared ribs. From an unknown horizon at locality 105. All × 1.

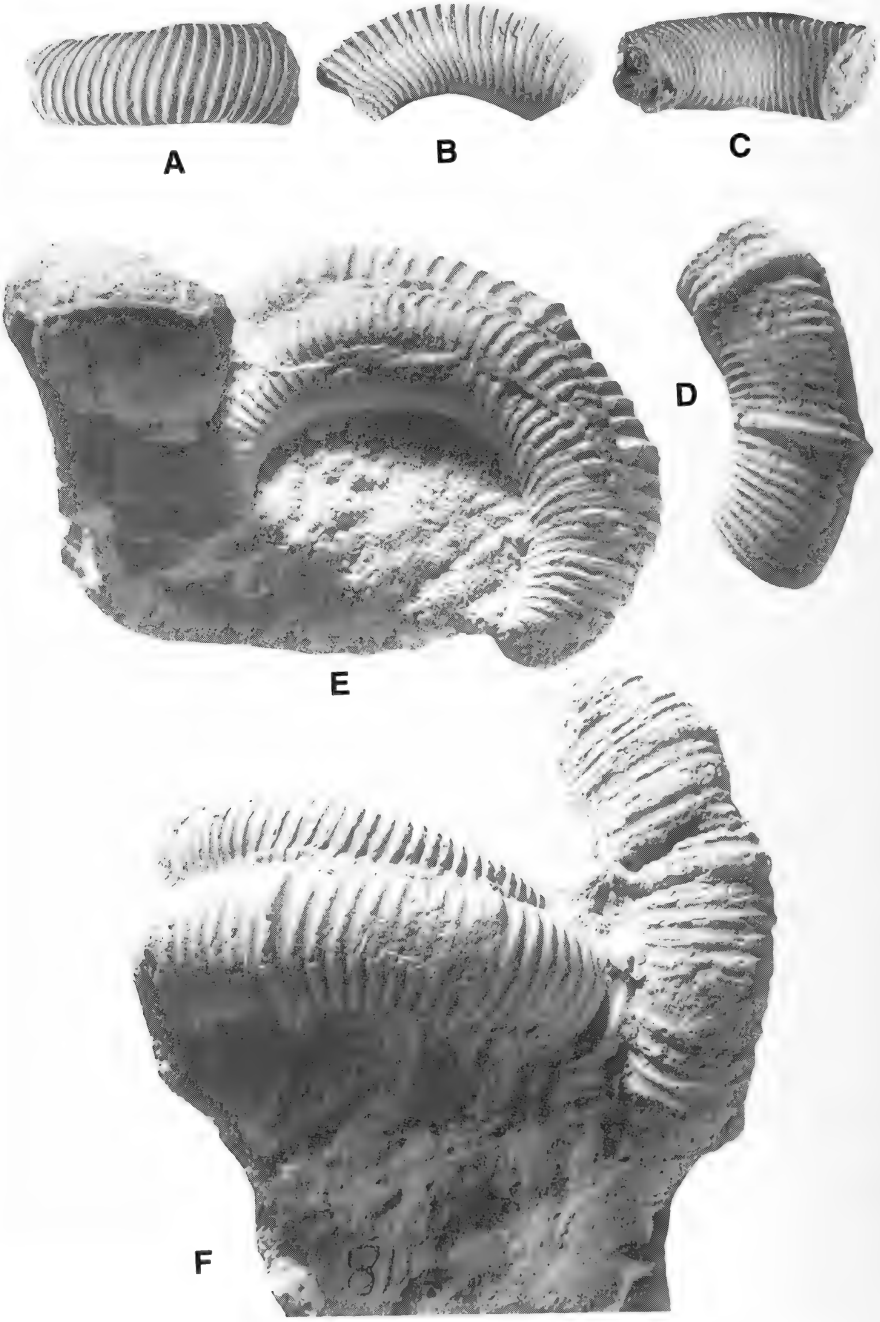

Fig. 12

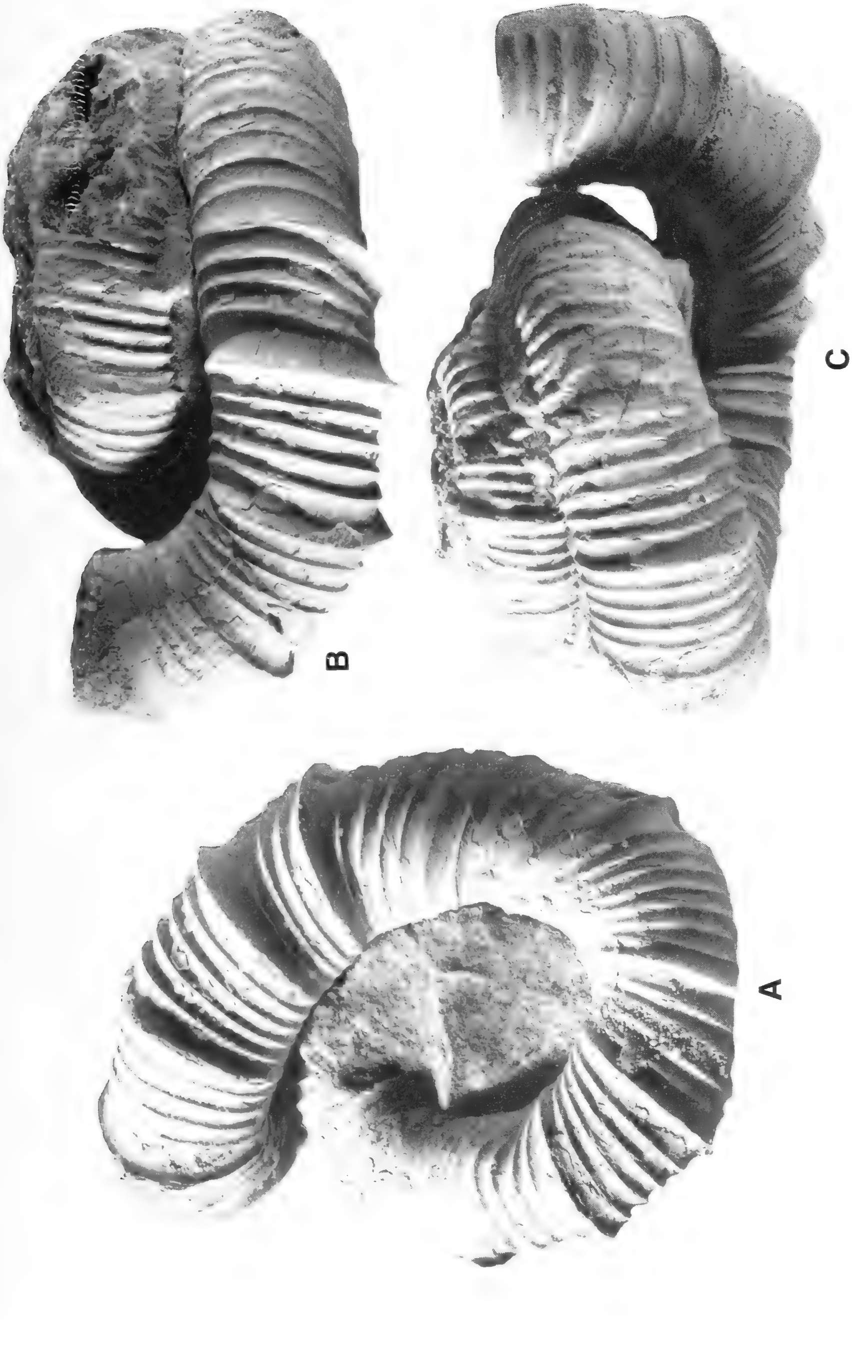

Fig. 13

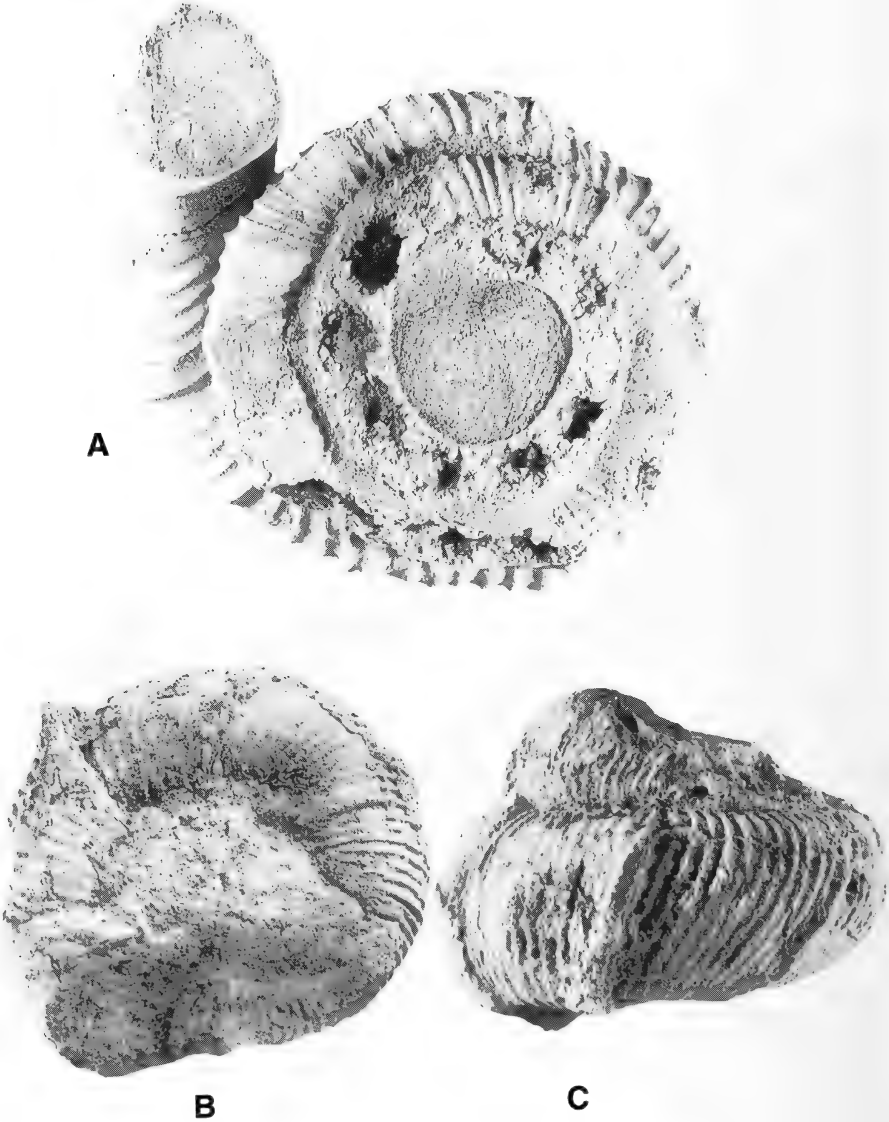

Fig. 14

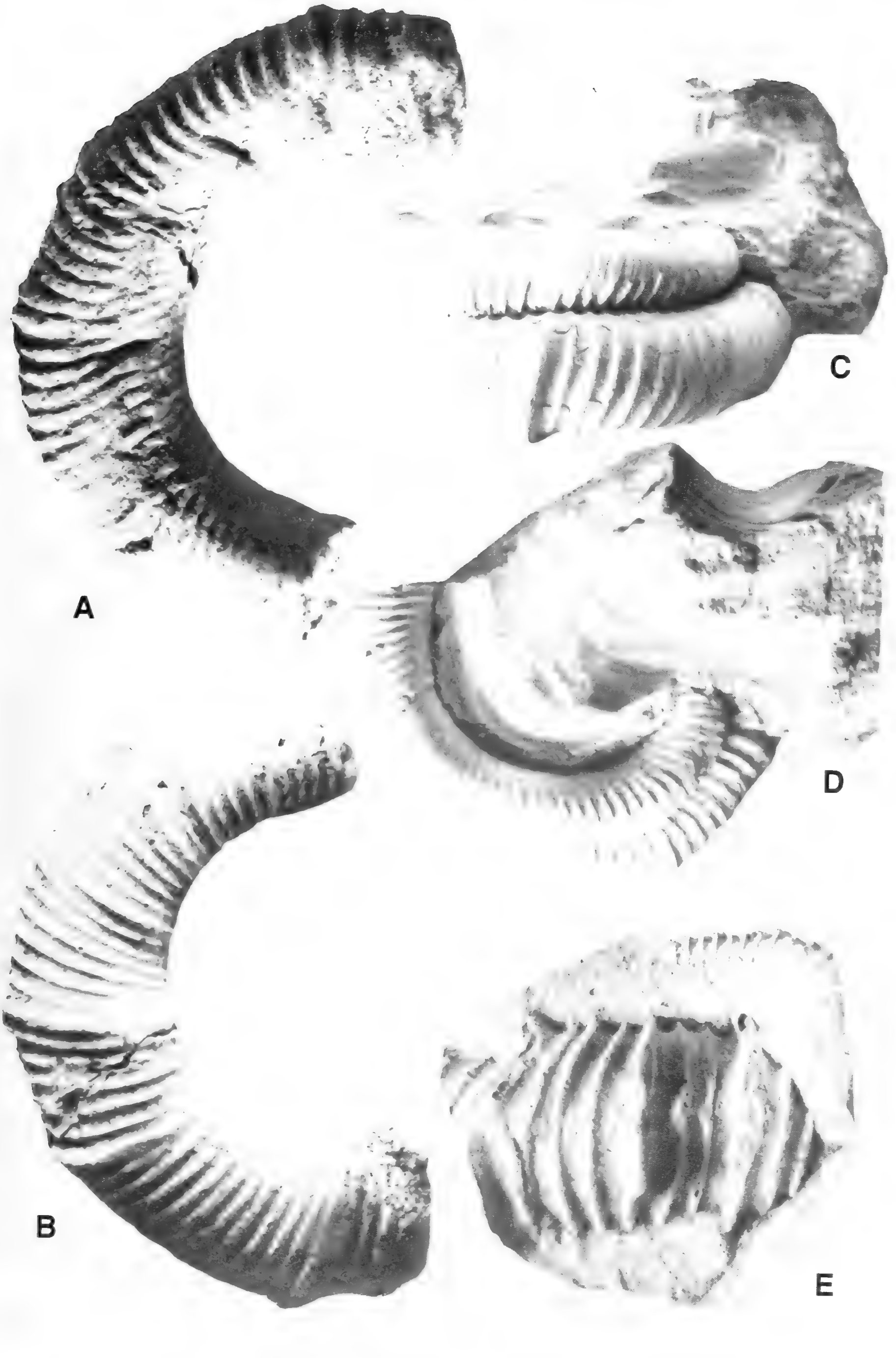

Fig. 15

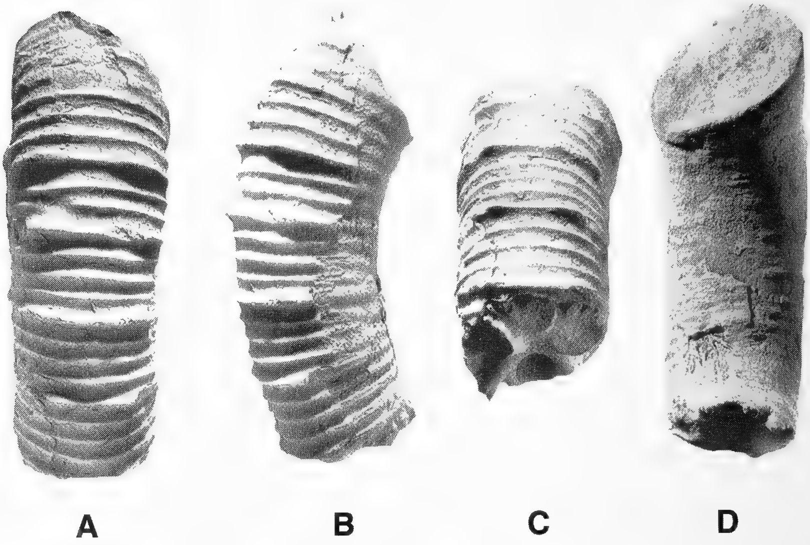

Fig. 16. '*Allocrioceras*' sp., SAM-Z2071 from locality 105, Zululand, St Lucia Formation, uppermost Santonian or basal Campanian. Note the distinct bituberculate flared ribs. × 1.

of an initial straight shaft, followed by a helical whorl and a series of closely connected U-shaped sections, ending in a retroversal body chamber hook. Ornament as in *Hyphantoceras* with major quadrituberculate ribs and intermediary, fine, non-tuberculate ribs. The genus is thus far only known from the Upper Turonian of Hokkaido.

It differs from *Nipponites* by the *Hyphantoceras*-like ornament, and from the latter genus by its distinctive coiling.

5. Klinger (1976: 71, pl. 32 (fig. 5a–b), pl. 33 (figs 2–3), text-fig. 10d–e) identified Van Hoepen's (1921: 17, pl. 4 (figs 1–2)) *Heteroceras amapondense* from the uppermost Santonian and basal Campanian of Pondoland and Zululand as *Hyphantoceras (Madagascarites?) amapondense*. The lower Campanian Madagascan species described as *Anaklinoceras? stephensoni* by Collignon (1969: 50, pl. 532 (fig. 2096)) was regarded as a synonym of the former. Klinger's reasons for this identification were that the ascending body chamber of *H. amapondense* was reminiscent of that of *Madagascarites*, whereas the ornamentation of the late growth stage with periodic flared ribs, was reminiscent of *Hyphantoceras*. This tentative generic and subgeneric designation was followed by Summesberger (1979, 1980), Lewy (1983), Klinger (1985), Immel (1987), Kennedy & Cobban (1991) and Wright (1996).

Comparison with the type species of *Hyphantoceras* and *Madagascarites* shows that *Heteroceras amapondense* belongs to neither genus. It lacks the quadrituberculate ornament of both; instead, it has *Hamites*- or *Eubostrychoceras*-like ornament on the early whorls, with periodic flared ribs appearing at later growth stages. Klinger (1976: 72) stated that well-preserved *H. amapondense* had flared ribs with two rows of fine tubercles and that the early whorls showed irregular coiling (e.g. Klinger 1976, pl. 33 (figs 2–3)) (herein Fig. 15E). Newly collected specimens of *H. amapondense* show that this is not so. Coiling in the early stages of *H. amapondense* is helical (see Lewy 1983, figs 4–6), and the flared ribs never bear tubercles. Fragments with tuberculate, flared ribs and irregular early whorls that occur with *H. amapondense* were regarded as late Upper Santonian or basal Campanian representatives

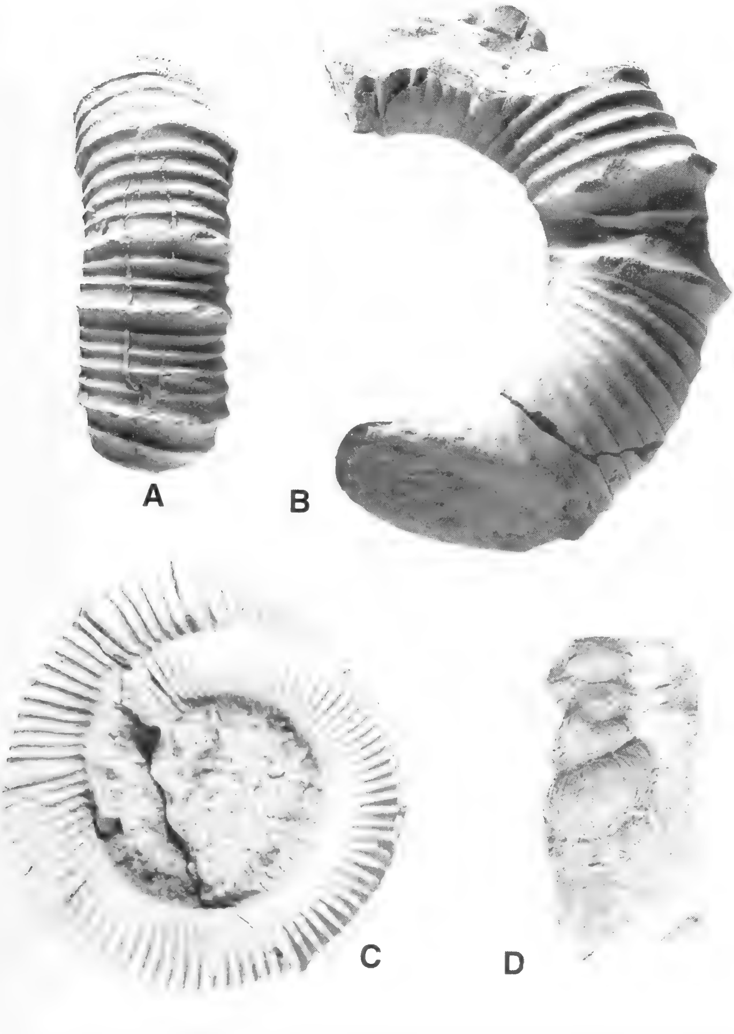

Fig. 17. A–C. *Eubostrychoceras (Amapondella) amapondense* (van Hoepen, 1921). A. Specimen labelled '*Hyphantoceras*', SAM-GMC252, ex Collignon collection from gisement 252, Coupe de Bevaho (Belo sur Tsiribihina), Lower Campanian, Zone of *Anapachydiscus wittekindi* and *Eulophoceras jacobi*. B. SAS-Z1455 from locality 105, Zululand, St Lucia Formation, uppermost Santonian or basal Campanian. C. SAM-PCP6890 from bed 7 at locality 1, the type section of the Mzamba Formation, Santonian III. D. SAM-PCZ12883 *Hyphantoceras reussianum* (d'Orbigny, 1850) from the abandoned limestone quarry Annelise near Bad Rothenfelde, northern Germany. All × 1.

of *Allocrioceras* by Cooper (1994: 362). Whether these are indeed *Allocrioceras* or Santonian–Campanian homoeomorphs is impossible to tell at this time. Some fragments (Fig. 15E) consist of hamitid early whorls and planispiral later whorls as in some *Didymoceras*, e.g. *Didymoceras binodosum* (Kennedy & Cobban (see Cobban & Kennedy in press). The early whorls of *H. amapondense* differ in no significant respects from those of *Eubostrychoceras* species, and we interpret it as a late subgenus of the latter characterized by the development of flared ribs and a distinctive coiling of the body chamber at maturity.

We here propose the subgenus ***Amapondella***, with type species *Heteroceras amapondense* van Hoepen, 1921. The diagnosis is as follows: major part of phragmocone coiled in a low helix with the whorls touching or slightly impressed; the body chamber curves upwards and embraces the flanks and apex of the helix. Early ornament consists of uniform ribbing only; later ornament has intercalated, flared ribs and occasional constrictions. The stage at which the flared ribbing starts appearing is quite variable; in some it may appear on the very early parts of the helix. Variation in size is probably due to dimorphism. It is known from the Upper Santonian of south-west France, Israel, Austria, Mississippi, Upper Santonian and Lower Campanian Pondoland and Zululand, offshore south coast of Natal, and Lower Campanian of Madagascar. *Eubostrychoceras auriculatum* (Collignon, 1965) (Fig. 14B–C) is possibly a related form in that it acquires flared ribs on the body chamber, but it has an acute apical angle and lacks the ascending body chamber of *Amapondella amapondensis*.

ACKNOWLEDGEMENTS

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

KLINGER, H. C.
&
KENNEDY, W. J.

ON THE AFFINITIES OF *MADAGASCARITES ANDIMAKENSIS* COLLIGNON, 1966, AND ALLIED UPPER CRETACEOUS HETEROMORPH AMMONITES

VOLUME 105 PART 4 MARCH 1998 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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1\. MATERIAL should be original and not published elsewhere, in whole or in part.

2\. LAYOUT should be as follows:

(a) *Centred masthead to consist of*
  Title: informative but concise, without abbreviations and not including the names of new genera or species
  Author's(s') name(s)
  Address(es) of author(s) (institution where work was carried out)
  Number of illustrations (figures, enumerated maps and tables, in this order)
(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
(f) *Summary*, if paper is lengthy
(g) *Acknowledgements*
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(i) *Abbreviations*, where these are numerous.

3\. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 3 cm margins all round. First lines of paragraphs should be indented. Tables and a list of captions for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4\. ILLUSTRATIONS should be reducible to a size not exceeding 12 × 18 cm (19 cm including caption); the reduction or enlargement required should be indicated (and preferably uniform); originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the caption; if the latter, then the final reduction or enlargement should be taken into consideration.

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Note: no comma separating name and year
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  names of joint authors connected by ampersand
  et al. in text for more than two joint authors, but names of all authors given in list of references.

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Examples (note capitalization and punctuation)

Bullough, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
Fischer, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88** (3): 100–140.
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(continued inside back cover)

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FOUR NEW SPECIES OF POLYCHAETA FROM SUBANTARCTIC MARION ISLAND

By

MARGO L. BRANCH

Cape Town Kaapstad

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FOUR NEW SPECIES OF POLYCHAETA FROM SUBANTARCTIC MARION ISLAND

By

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(With 5 figures)

[*MS accepted 17 August 1995*]*

ABSTRACT

Four new species of Polychaeta are described from Subantarctic Marion Island. *Orbiniella dayi* sp. nov. (family Orbiniidae) occurs from mid-tide levels to depths of 15 m and is separated from *Orbiniella minuta* Day, 1954, from Tristan da Cunha, by its larger size and the presence of a small post-setal lobe to the parapodia. *Scolelepis marionis* sp. nov. (family Spionidae) was buried up to 0.5 m in sandy substrata in shallow subtidal depths. It is closely related to *Scolelepis lamellicincta* Blake & Kudenov, 1978, from Australia, but can be distinguished by its notosetae, which are all capillaries, and neurosetae of bifid hooded hooks that occur from setigers 42–46 and posteriorly. *Malmgreniella fimbria* sp. nov. (family Polynoidae) is tentatively placed in the genus *Malmgreniella*, but the presence of a sixteenth pair of elytra distinguishes the species and requires an expansion of the definition of the genus. *Malmgreniella fimbria* was dredged from a depth of 410–644 m between Marion and Prince Edward islands. *Lanice marionensis* sp. nov. (family Terebellidae) was previously referred to as *Lanice flabellum*. *Lanice marionensis* sp. nov. occurs at depths of 5–475 m on soft sediments.

CONTENTS

INTRODUCTION

The polychaete fauna of Subantarctic Marion and Prince Edward islands (MPE) (46°54'S 37°45'E) has been sampled by a number of expeditions. The benthos of these isolated volcanic islands was first sampled by the H.M.S. *Challenger* expedition in 1873 and McIntosh (1885) reported on the 11 polychaete species collected. Further collections were made by dredging from *Discovery II* in 1935 (Monro 1936). Day (1971) reported on 25 species and De Villiers (1976) conducted a thorough study of the intertidal community, finding 21 species of polychaetes. The French ship *Marion Dufresne* sampled

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* The original manuscript was submitted in February 1994. Although the names of the new species were used in another paper by Branch (1994), the present paper provides the formal descriptions of the new taxa.

the offshore benthos during its MD/08 expedition in 1976 and listed 77 species from Marion, Prince Edward and Crozet islands (Gillet 1991). During 1982–89, the University of Cape Town undertook an extensive dredging programme (Branch *et al.* 1993) and, in 1988, a quantitative SCUBA diving survey to a depth of 15 m at three sites (Beckley & Branch 1992). D. Glassom examined the intertidal beach fauna in 1989 (unpublished data).

The author has analysed these recent collections and provided illustrated keys to the 90 species of polychaetes now recognized from Marion and Prince Edward islands, as well as data on species abundance and distribution (Branch 1994). The collections described included three polychaete forms that could not be assigned to any known species and are therefore described here as new species. A fourth species, previously referred to as *Lanice flabellum*, is also described as new. *Lanice flabellum* was originally described from empty tubes and its exact type locality is unknown. As a result the present specimens cannot, with certainty, be attributed to that species.

SYSTEMATICS

Order ORBINIIDA

Family **Orbiniidae** Hartman, 1942

Orbiniella Day, 1954

Orbiniella dayi sp. nov.

Fig. 1

Orbiniella minuta Day, 1971: 386 (*non* Day, 1954). Beckley & Branch, 1992: 558.

Material examined

Holotype. SAM–A21273: specimen 5 mm long × 0.4 mm wide, 35 segments, from Bullard's Bay, Marion Island at 5 m depth, collected by SCUBA diving by L. Beckley on 10 April 1988.

Paratypes. SAM–A21393: 2 specimens, 3 mm and 5 mm long, from the same sample as the holotype.

Other material. SAM–A21364: from Transvaal Cove, Marion Island under rocks at mid-tide level, collected by N. Fuller, January 1965 (Day 1971). SAM–A21272: 3 specimens from Cabbage Point, Marion Island, collected with SCUBA at 5 m depth by G. M. Branch.

Several hundred specimens from Transvaal Cove, Bullard's Bay and Trypot Point, collected by SCUBA at 5, 10 and 15 m depths by L. Beckley in April 1988 (unsorted collection).

Etymology

Named *dayi* after Professor J. H. Day from the University of Cape Town, who was well known for his significant contributions to marine biology in southern Africa and particularly for his work on polychaetes.

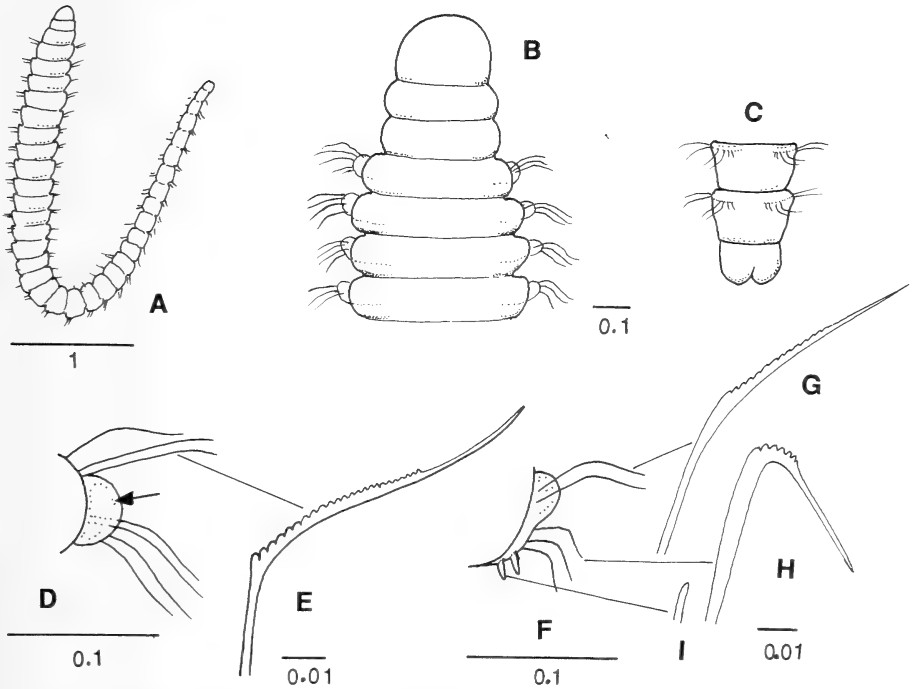

Fig. 1. *Orbiniella dayi* sp. nov., holotype, 5 mm. A. Entire worm. B. Head and anterior six segments. C. Posterior end, ventral view. D. Anterior parapodium, post-setal lobe arrowed. E. Notoseta. F. Posterior parapodium. G. Notoseta. H. Capillary neuroseta. I. Neurosetal hook. Scales in mm.

Description (of holotype)

Body length 5 mm, width 0.4 mm, 35 segments, separated by deep intersegmental constrictions. White in alcohol. Prostomium bluntly triangular with rounded tip and no eyes or appendages. Proboscis not extrusible. First two segments asetigerous. Following setigerous segments separated from one another by deep intersegmental constrictions. Gills absent. Parapodia form lateral ridges near the anterior margin of each segment with a small foliose post-setal lobe, largest at the origin of the notosetae (Fig. 1D). Anterior 10 segments shorter and broader than the posterior segments, which are slightly biannular. Four or five notosetae project from the upper margin of the anterior parapodia, which is elongated to form a small posterior lobe. Notosetae crenulate capillaries with distinct teeth and long curved tapering tips. Notosetae of posterior segments similar but shorter. Neurosetae arise from the lower edge of the parapodial ridge. Anterior neurosetae similar to the notosetae but posterior neurosetae are of two types, one or two inferior simple acicular setae, which are short, stout and blunt-tipped, and two or three crenulate setae, which become progressively shortened posteriorly. Pygidium simple with a small terminal slit. Not gravid.

Remarks

Orbiniella minuta Day, 1954, from Tristan da Cunha, is smaller and the parapodia are reduced to a simple parapodial ridge, whereas *O. dayi* sp. nov. has distinct parapodial lobes posterior to the notosetae. *Orbiniella aciculata* Blake, 1985, from the Galapagos rift at 2 730 m depth, has prominent acicular spines in both the noto- and neuropodia. *Orbiniella nuda* Hobson, 1974, from off British Columbia, has several acicular spines and capillaries in the neuropodia and lacks the small post-parapodial lobe of *O. dayi*. *Orbiniella uniformis* Hartman, 1967, from Anverse Island, Antarctic Peninsula, was described as being exceedingly plain and unadorned; it is of similar size to *O. dayi* with similar setae, but the segments are uniannulated throughout and there are no post-setal lobes to the parapodia.

Distribution

Subantarctic Marion Island, intertidal to 15 m depth. A quantitative SCUBA survey by Beckley at depths of 5, 10 and 15 m on rocky substrata at Transvaal Cove, Bullard's Bay and Trypot Point produced a total of several hundred specimens of *Orbiniella dayi* at all three stations and depths, with up to 75 specimens.m^{-2} at 5 m depth at Bullard's Bay (Beckley & Branch 1992).

Order SPIONIDA

Family **Spionidae** Grube, 1850

Scolelepis Blainville, 1828

Type species. *Lumbricus squamatus* Müller, 1806, by monotypy.

Remark

Blainville's (1828) diagnosis of this genus has been revised and emended by various authors (e.g. Pettibone 1963: 91; Blake & Kudinov 1978: 175).

Scolelepis marionis sp. nov.

Fig. 2

Material

Holotype. SAM–A21254: incomplete specimen, 43 mm long × 6 mm wide, 73 segments, from sandy shore at Ship's Cove, Marion Island, buried to depth of 0.5 m in shallow sub-tidal depths; collected by D. Glassom in April 1989.

Paratypes. SAM–A21392: 6 incomplete specimens, anterior regions only; 70 setigers, 45 mm × 6 mm; 63 setigers, 35 mm × 5 mm; 33 setigers, 33 mm × 7 mm; 35 setigers, 25 mm × 6 mm; 14 setigers, 10 mm × 5 mm; 11 setigers, 7 mm × 3 mm width; from the same sample as the holotype.

Etymology

Named *marionis* after the French navigator, Marion Dufresne, who discovered Marion Island, the type locality.

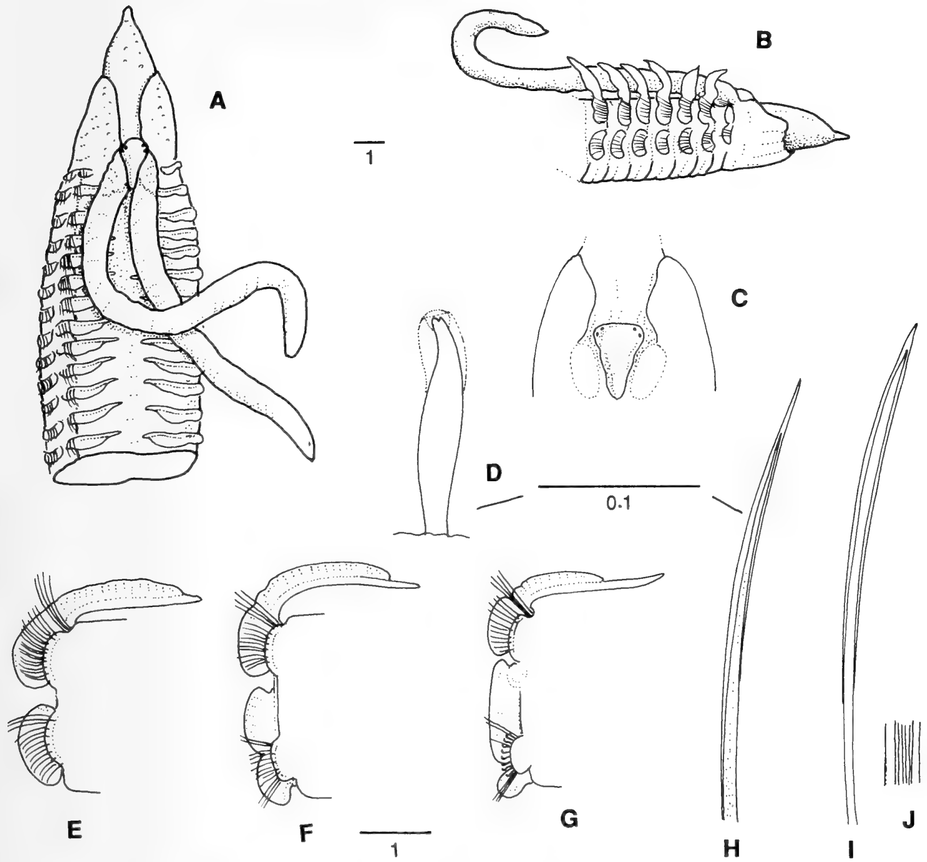

Fig. 2. *Scolelepis marionis* sp. nov., holotype, 43 mm. A. Anterior end, dorsal view. B. Anterior end, lateral view. C. Dorsal view of head caruncle with palps removed. D. Neurosetal hook from posterior setiger. E. Setiger 10. F. Setiger 33. G. Setiger 50. H. Capillary neuroseta. I. Notoseta. J. Detail of notoseta. Scales in mm.

Description (of holotype)

Body very regular, firm, vermiform, rectangular in cross section, incomplete anterior region, length 45 mm, width 5–6 mm, 73 segments. Body regions not marked except by shape of parapodia. Red-brown in alcohol. Prostomium projects anteriorly to narrow point and extends posteriorly as narrow, attached lobe (caruncle) between the palps. Caruncle bears two pairs of small eyes laterally and obscured by anterior base of palps. Proboscis unarmed, with a ventral cushion. Peristomium well developed with lateral wings partially overlapping the prostomium. A pair of large grooved palps arise dorsally from the posterior margin of the peristomium, extending back to the seventeenth segment with a lateral membrane at the base.

Setiger 1 reduced with a leaf-like dorsal lamella and rounded ventral lamella. Dorsal gills from setiger 2. Dorsal lamellae from setiger 2, swollen, foliose, folded over the dorsal body, branchia fused along the outer margin of each lamella for whole length, except near the tip where the free lamella is narrow and pointed. Post-setal neuropodial lamellae in the anterior region form a single rounded lobe, swollen and foliose. Neuropodial lamellae increase in size posteriorly and become notched at about segment 30, and after segment 41 are bilobed with a long, narrow inter-ramal lamella and a small, rounded ventral lamella. There are low, swollen presetal ridges. Notosetae all capillaries in the anterior setigers, about 40 in two to three groups. From setiger 60 the numbers diminish to about 20–30, in two groups, those in the dorsal group are longest, 0.6 mm, ventral setae to 0.5 mm. Anterior neurosetae similar to notosetae, about 40. From setiger 42 three hooded hooks appear in the neuropodia and increase to about 9–11 by setiger 70. Hooded hooks bilobed with a smooth, circular, funnel opening to the hood. It is still uncertain if there are hooded hooks also in the far posterior notopodia. Pygidium unknown.

Remarks

Scolelepis marionis sp. nov. is closely related to *S. lamellicincta* Blake & Kudenov, 1978, from Australia. The structure of their parapodia is very similar, especially with the presence of long inter-ramal lamellae in the middle and posterior segments. This feature separates these two species from all the other species (see Audouin & Milne Edwards 1833; Mesnil 1896; Day 1967; Blake & Kudenov 1978; Blake 1983). The two species are distinguished by their setae: *S. marionis* has bifid hooded hooks from setiger 42–46 increasing from 3 to 11 per ramus, and the notosetae are all capillaries. *Scolelepis lamellicincta* has unidentate hooded hooks from setiger 25–38 with only 5–6 to a ramus, and has hooded hooks in notopodia from setigers 75–80. The posterior lobe, or caruncle, of the prostomium in *S. marionis* is a flat and slender triangle about 1 mm thick, whereas that of *S. lamellicincta* is a blunt lobe that projects from the surface. *Scolelepis eltaninae* Blake, 1983, from the Antarctic Ocean, has triangular inter-ramal lamellae and an occipital tentacle.

Order PHYLLODOCIDA

Family **Polynoidae** Malmgren, 1867

Subfamily Harmothoinae Willey, 1902

Malmgreniella Hartman, 1967

Type species. *Malmgreniella dicirra* Hartman, 1967: 37, pl. 11A–D, by monotypy.

Remark

Hartman's (1967) diagnosis of this genus was emended by Pettibone (1993: 9–10).

Malmgreniella fimbria sp. nov.

Fig. 3

Material

Holotype. SAM–A21346: body 50 mm long, 20 mm wide for 46 segments, from Marion Island, dredged from Station 44, 46°40.58'S 37°50.20'E, 410–644 m depth, on rocky substrata, collected by D. Gianakouras on 3 September 1988.

Etymology

From the Latin *fimbria* (fringe)—an allusion to the ventral cirrus that carries a dense fringe of hairs.

Description (of holotype)

Body entire, length 50 mm, width 20 mm, 46 segments. Dorsum smooth and convex, ventrum with a deep neural groove, otherwise smooth. Elytrae 16 pairs on segments 2, 4, 5 and 7 then alternate segments until 23, 26, 29, 32 and 33, and last 13 segments with dorsal cirri only. Elytrae subreniform, soft, fleshy and almost smooth apart from a few microtubercles on the posterior region. Elytrae do not overlap in the mid-dorsum and are not easily shed.

Prostomium bilobed, wider than long with an anterior 'V'-shaped notch and anterior lobes produced into cephalic peaks. Two pairs of eyes, anterior pair large and anterolaterally placed, posterior pair small, close to posterior margin. Ceratophore of median antenna large, in anterior notch, style missing. Ceratophores of single pair of lateral antennae inserted anteriorly, below cephalic peaks of prostomium, styles short, broad, tapering. Palps large, stout, tapering, three times length of prostomium. Tentaculophores on segment 1, lateral to prostomium with a pair of dorsal and ventral slender tentacular cirri, four times length of prostomium. Antennae and tentacles covered with fine fleshy papillae.

Segment 2, with first pair of elytrophores and small elytrae, biramous parapodia with long narrow ventral cirrus and a short cirrophore. Remaining parapodia also biramous but with unusual short, fleshy, curved ventral cirri covered with a dense mat of long hairs and a short cirrophore; cirrus broad at the base but with a narrow attenuated tip. Dorsal cirri have a thick, short cirrophore and a long fleshy, hairy style, and alternate with elytrae. Notopodia small with a projection on the lower side. Neuropodia larger with subconical presetal lobes with digitiform tip and short rounded post-setal lobes. Notosetae form dorsally radiating bundles in first eight parapodia, absent from most of the middle parapodia, and present as small bundles in the 13 posteriormost parapodia; slightly stouter than neurosetae, with simple tips and a few fine lateral teeth. Neurosetae in two groups, upper and lower, all setae long-shafted with an expanded terminal third, bifid tips, a very narrow secondary tooth and setal surface finely serrated.

Remarks

This species exhibits some characters associated with the genera *Malmgreniella* Hartman, 1967, *Lepidofimbria* Hartman, 1967, *Subadyte* Pettibone,

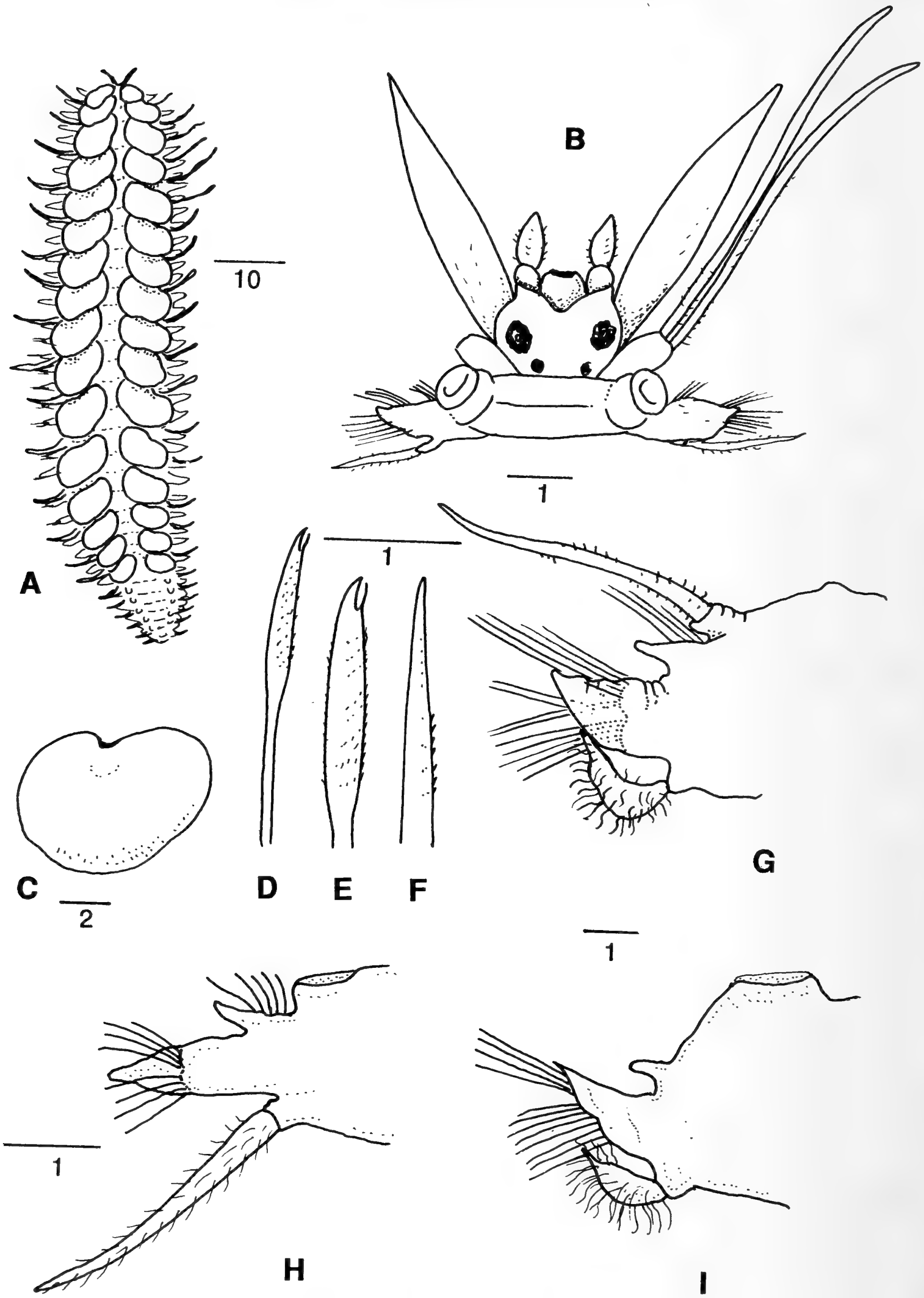

Fig. 3. *Malmgreniella fimbria* sp. nov., holotype, 50 mm. A. Entire worm. B. Head. C. Elytra. D. Neuroseta. E. Detail of neuroseta. F. Notoseta. G. Parapodium 6. H. Elytral parapodium 2. I. Elytral parapodium 17. Scales in mm.

1969, *Scalisetosus* McIntosh, 1885, *Austrolaenilla* Bergström, 1916, and *Leucia* Sars, 1863. The genus *Malmgreniella* Hartman, 1967, was emended by Pettibone (1993) to include *Malmgrenia* and, in the revised diagnosis, the lateral antennae may be inserted subterminally, subventrally or ventrally. The genus *Malmgreniella* was regarded by Fauchald (1977) as belonging to the subfamily Lepidonotinae Willey, 1902, but Pettibone (1993) considered it a member of the subfamily Harmothoinae Willey, 1902.

Species of *Malmgreniella* have 15 pairs of elytrae that are delicate and almost smooth with microtubercles. They differ from species of *Harmothoe*, in which the 15 pairs of elytrae are tough and ornamented. Species of *Malmgreniella* have up to 46 segments, the prostomium is bilobed, usually without distinct cephalic peaks, notosetae are similar in width to neurosetae, which are bifid, or unidentate, or both. The major difference between the present species and previously described species of *Malmgreniella* is that the former have 16 pairs of elytrae, the sixteenth pair occurring on segment 33, the prostomium also has cephalic peaks, the anterior pair of eyes are large, and the ventral cirri are fleshy and fimbriate.

The large eyes and fimbriate ventral cirri of the present species are characters shared with *Lepidofimbria occulata*, the only member of the genus *Lepidofimbria* Hartman, 1967. It has three ventral papillae on the body segments and no elytrae were described. However, the prostomium does not have cephalic peaks and the ceratophores of the antennae are continuations of the prostomium (characteristic of the subfamily Lepidonotinae). The parapodia are also different with reduced notopodia, no notosetae and smooth neurosetae with a smooth unidentate tip. *Lepidofimbria occulata* was collected at abyssal depths in the Weddell Sea and described from a disconnected anterior end and six anteromedian segments.

When considering the feature of 16 pairs of elytrae, five genera of the subfamily Harmothoinae, each with 16 pairs of elytrae and ventral insertion of the lateral antennae, were compared with the present species.

In the genus *Subadyte* Pettibone, 1969, the notosetae and neurosetae have semilunar pockets of spines, which were not evident in the present material.

In the genus *Scalisetosus* McIntosh, 1885, the notosetae are much coarser than the neurosetae; neurosetae are slender and distally entire; and the notopodia as well as the neuropodia have long presetal lobes, not features of the present species.

The monotypic genus *Leucia* Malmgren, 1867 (type species *L. nivea* (Sars, 1863)), is short bodied; the prostomium has peaks; the elytrae possess large spiny tubercles; the notosetae are coarser than the neurosetae and serrated; and the neurosetae are long and slender with unidentate tips and serrated edge—characters that distinguish this genus from the present specimen.

In the genus *Austrolaenilla* Bergström, 1916, there are 15–16 pairs of elytrae; 40–43 segments; ventral cirri are digitate and the ventrum is usually smooth, notosetae thicker than neurosetae with transverse rows of teeth; neurosetae with unidentate or bidentate tips with the distal end penicillate (brush-like). The present material differed with 45 segments, the ventral cirrus curled, fleshy and broad, and the neurosetae with bifid tips, not distally penicillate.

However, *M. fimbria* does have characters in common with *Antinoella antarctica fulgens* (Fauvel, 1936) from Western Antarctica, in which the neurosetae are less plumose in their distal ends than in *A. antarctica antarctica*.

Malmgreniella fimbria has been tentatively placed in the genus *Malmgreniella* on the strength of the similarity in the basic structure of the parapodia, the short antennae, the smooth elytrae and neurosetae with bifid tips, with a slender secondary tooth. The definition of the genus needs to be expanded to give the number of elytrae as 15–16 pairs.

Malmgreniella fimbria can be distinguished from other species of *Malmgreniella* by the presence of 16 pairs of elytrae, fimbriate ventral cirri and the large anterior eyes.

Order TEREBELLIDA

Family **Terebellidae** Grube, 1851

Subfamily Amphitritinae Malmgren, 1866

Lanice Malmgren, 1866

Type species. *Nereis conchilega* Pallas, 1766: 31, pl. 9 (figs 14–22), by monotypy.

Remark

Malmgren's diagnosis (1866) of the genus was revised and emended by Hutchings & Glasby (1988: 17–18).

Lanice marionensis sp. nov.

Figs 4–5

non *Terebella flabellum* Baird, 1865: 157, pl. 5 (figs 1–2).
Lanice flabellum (Baird) Gillet, 1991: 368.
Lanice conchilega (*non* Pallas, 1776) Branch *et al.*, 1993: 29–30.

Material examined

Holotype. SAM–A21205: incomplete specimen 40 mm long × 6 mm wide, removed from tube, dredged from volcanic ash and rock substrata at 58–85 m depths, Marion Island, 46°58.6'S 37°45'E, collected by D. Gianakouras, University of Cape Town survey.

Paratypes. SAM–A21209: two incomplete specimens in tubes dredged from rocky substrata, Marion Island, 46°41.20'S 37°49'E, UCT survey. SAM–A20326: one complete specimen 60 mm long × 3 mm wide, 17 thoracic setigers, 104 abdominal setigers; eight incomplete specimens, Marion Island 46°49.8'S 37°52.2'E; Charcot dredge, collected by P. Gillet, *Marion Dufresne* benthos expedition, 1976. SAM–A21207: two complete specimens 50 mm long × 3 mm wide and 50 mm × 4 mm; 11 incomplete worms 28–42 mm long, Marion Island, 46°35'S 37°56'E, dredged from 48–50 m depth, UCT survey.

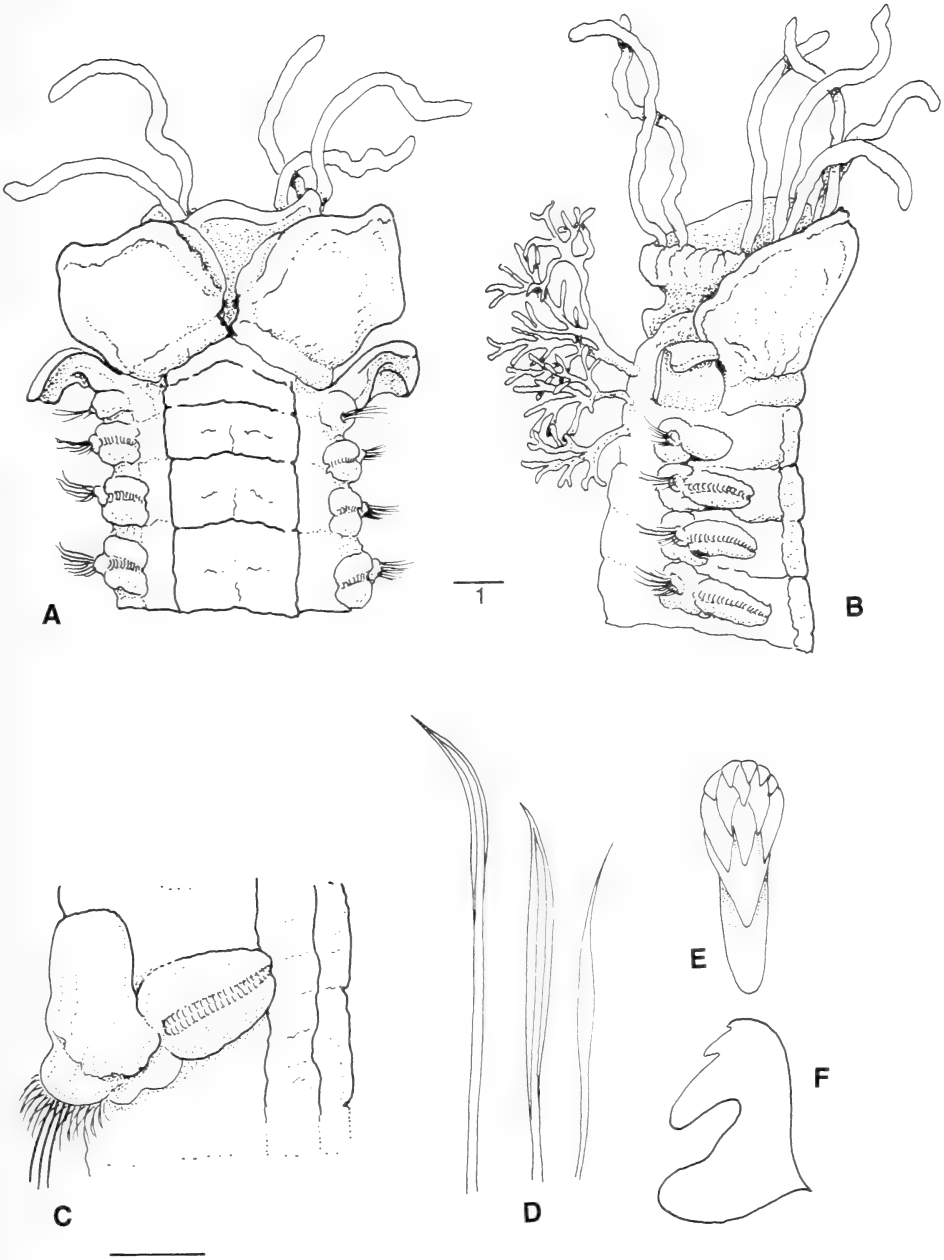

Fig. 4. *Lanice marionensis* sp. nov., holotype, 40 mm. A. Head, ventral view. B. Head, lateral view. C. Parapodium 14. D. Thoracic notosetae segment 14. E. Neuroseta, front view, segment 30. F. Neuroseta, side view, segment 30. Scales in mm.

Other material. SAM–A21204, SAM–A21206, SAM–A21207, SAM–A21208, SAM–A21210 to SAM–21220 (as *Lanice conchilega*—see Branch *et al.* 1993). From Marion Island in depths of 5–475 m, predominantly on soft substrata, UCT survey.

Etymology

Named *marionensis* after Marion Island, the type locality.

Description (of holotype)

Cartilaginous tube, covered with shell fragments and coarse sand. A characteristic fringe of chitinous filaments extends from the ventral side of the tube aperture and forms a fan with a narrow base. There is a smooth semicircular flap over the dorsal side of the aperture. Body with a swollen thorax, 6 mm wide and slender abdomen 3 mm wide, length over 40 mm, terminal portion missing. Brown in alcohol. Prostomium compact with numerous grooved buccal tentacles and a broad projecting ventral lip. Buccal segment with large, broad ventrolateral lobes that are thick and fleshy and meet at the ventral base. Segment 2 lacks lateral lobes. Segment 3 with smaller, laterally displaced, rectangular lateral lobes that extend forward over segment 2 and curl back at the tip. Gills three pairs on segments 2–4 with short trunks, and many dichotomous branches. Gills unequal, the first pair on segment 2 being larger.

Notopodia from segment 4, continue for 17 segments. Notosetae consist of winged capillaries in groups of about 20. Neuropodia from segment 5 (setiger 2), occur on all following thoracic and abdominal segments present.

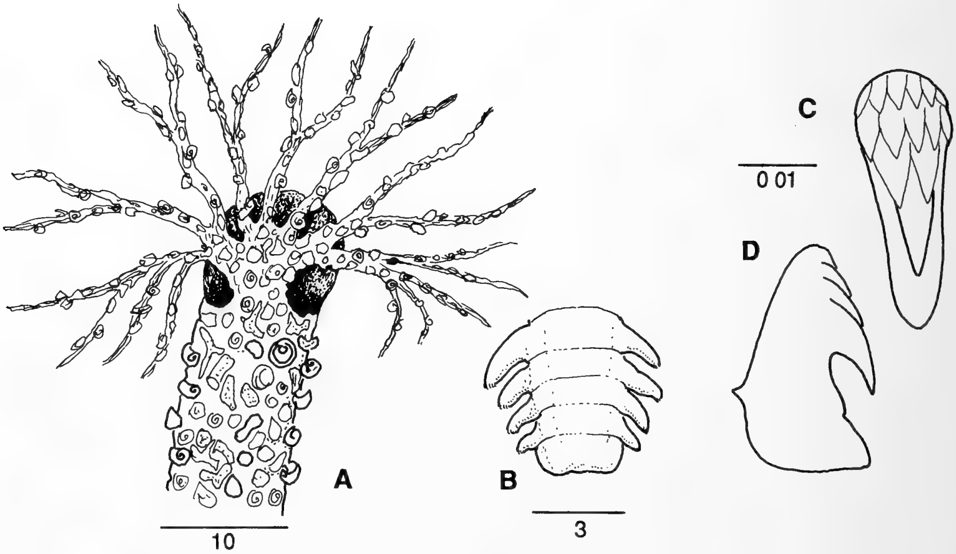

Fig. 5. *Lanice marionensis* sp. nov. A. Holotype, 40 mm. Tube anterior end. B–D. Paratype, 60 mm. B. Posterior abdomen segments 100–104. C. Neuroseta, front view, segment 100. D. Neuroseta, side view, segment 100. Scales in mm.

Uncini initially arranged in single rows, but from seventh uncinigerous thoracic segment to the last thoracic segment uncini arranged in double rows back to back (2 × 20–35 per neuropodium). Uncini avicular with a large fang surmounted by 3–4 rows of smaller teeth arranged with dental formula MF 3 : 2 : 1 : 5 at thoracic segment 7. The thoracic neuropodial ridges are raised and glandular but do not extend to the ventral glandular pads. About 20 ventral glandular pads form a continuous glandular area anteriorly, which tapers to a glandular streak. Abdominal uncini borne in single row on long pinnules.

Nephridial pore on setigers 3–6 just posterior to the notopodia.

Variation

Some of the larger paratypes had very swollen lateral lobes. The specimen SAM–A21209 was projecting from the tube showing the orientation of the ventral fanned extension to the tube in relation to the animal. The most complete specimen was paratype SAM–A20326 with 17 thoracic setigers and 104 abdominal setigers. The segments became progressively narrower and shorter to the simple last joint with short paddle-like neuropodia bearing 24 uncini at setigers 25–30 and 12 uncini by setigers 80–90. The uncini were similar in shape throughout although the posterior abdominal uncini had a dental formula of MF 2–3 : 4–8 : 4–8. This was not chosen as the holotype as the head appendages were not as complete.

Large numbers of *L. marionensis* were collected from the soft substrata between Marion and Prince Edward islands, consisting of sand, mud and gravel. Sizes up to about 60 mm with 25–35 mm being common, although most of them were posteriorly incomplete.

Remarks

The original description of *Lanice flabellum* (Baird, 1865) was based on tubes only and the exact type locality is unknown. It is considered to be an indeterminate name (Hartman 1959; Hutchings pers. comm.). *Lanice flabellum* from Australia (Baird 1865) and from East Africa (Ehlers 1908) have similar tubes but need to be re-examined. Specimens from the Antarctic labelled *L. flabellum* present in the British Museum (Natural History) collections may also prove to be *L. marionensis* (see Hutchings & Glasby 1988: 18).

As there are no type specimens, only tubes, of *L. conchilega* (Pallas, 1766), Hutchings & Glasby (1988) described a specimen of *L. conchilega* from the type locality, Netherlands, as having a narrow rectangular lobe on segment three with a dorsolateral flag-like extension. Hutchings & Glasby (1988) distinguished the smaller Australian *L. bidewa*, which has tubes with smooth margins, from *L. conchilega*, which has frayed margins.

Day (1967) described *L. conchilega* from South Africa. Day's specimen, SAM–A20350, from South Africa, was examined and compared with *L. marionensis*. The tube was also covered with sand and shell fragments but differed from that of *L. marionensis* in that it was flattened and expanded at the opening with fringe extensions on both the dorsal and ventral edge of the margin, whereas in *L. marionensis* the fan-like fringe extended only on the ventral edge of the opening. In SAM–A20350, the ventrolateral flaps on the buccal segment were longer and more triangular, whereas the flap on segment 3 was broader than in *L. marionensis*. The thoracic neuropodia were much wider with 2 rows of 40–50 uncini in raised glandular patches that extended almost to the ventral pad. The uncini also had fewer teeth. Day's (1967) specimens referred to *Lanice conchilega* may also be a new species and need to be redescribed, but this is beyond the scope of this paper.

Lanice bidewa Hutchings & Glasby, 1988, from Australia and New Zealand can be distinguished from *L. marionensis* by its small size (up to about 20 mm) and it is colourless when preserved. All pairs of gills are equal in size. The opening of the tube has smooth margins.

Lanice sinata Hutchings & Glasby (1990), an intertidal species from Western Australia, is distinguished by the presence of a deep pocket-shaped sinus formed by a dorsal ridge on segment 4.

Distribution

Subantarctic Marion and Prince Edward islands, 5–475 m depth. Highest densities occur in the area between the two islands on soft substrata, with an average of 50 individuals in each dredge sample and many empty tubes. ?Antarctica, ?East Africa.

ACKNOWLEDGEMENTS

I would like to thank Di Gianakouras, Dave Glassom, Prof. George Branch and Dr Lynnath Beckley for the opportunity to work on material collected by them during the University of Cape Town expeditions. Specimens were also supplied by Dr P. Gillet from the 1976 survey of the *Marion Dufresne*. Prof. Charles Griffiths is thanked for valuable guidance with the description of the new species. Dr Pat Hutchings gave advice regarding the uncertainties relating to *L. flabellum*. I am very grateful to the staff of the Marine Biology unit and Library at the South African Museum for their patience and help. Funding was supplied by the South African Steering Committee for Antarctic Research (SASCAR) and the Department of Environment Affairs.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
comma separates author's name and year
semicolon separates more than one reference by the same author
full stop separates references by different authors
figures of plates are enclosed in parentheses to distinguish them from text-figures
dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51′S 25°39′E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .': '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

MARGO L. BRANCH

FOUR NEW SPECIES OF POLYCHAETA FROM SUBANTARCTIC MARION ISLAND

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ANNALS
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(b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
(c) *Table of contents* giving hierarchy of headings and subheadings
(d) *Introduction*
(e) *Subject matter* of the paper, divided into sections to correspond with those given in table of contents
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'Smith (1969: 36, fig. 16) described . . .'
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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88**: 100–140.

FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungreise im westlichen und zentralen Süd Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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PHYLOGENETIC IMPLICATIONS OF THE EXISTENCE OF TWO MODERN GENERA OF BATHYERGIDAE (MAMMALIA, RODENTIA) IN THE PLIOCENE SITE OF LANGEBAANWEG (SOUTH AFRICA)

By

CHRISTIANE DENYS

Cape Town Kaapstad

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(With 7 figures and 4 tables)

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ABSTRACT

The oldest known *Bathyergus* and *Cryptomys* are found together in the Langebaanweg 'E' Quarry site of the Varswater Formation in Cape Province (South Africa). They are represented by two previously unrecorded species: *Bathyergus hendeyi* sp. nov. and *Cryptomys broomi* sp. nov. These species are characterized by primitive characteristics and may represent ancestors of the extant species. Their affinities with modern Bathyergidae, especially *Georychus capensis* and the fossil *Gypsorychus*, are discussed in the light of new chromosomal and electrophoretic data. The fossils provide some calibrations and arguments to the molecular hypotheses.

CONTENTS

INTRODUCTION

Bathyergidae are hystricognathous rodents characterized by a digging mode of life and are endemic to the African continent. Until recently, their systematic position has remained very controversial. However, Maier & Schrenk (1987), in an ontogenetic study of the development of the masseteric muzzle, demonstrated their position among hystricomorphous rodents. This has confirmed the previous work of Lavocat (1973) on Miocene fossils.

Modern South African Bathyergidae are represented by three endemic genera that were separated into two subfamilies by Roberts (1951) on the basis of morphometric characteristics. These are the subfamily Bathyerginae, which includes the genus *Bathyergus*, and the subfamily Georychinae, which includes

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the genera *Georychus* and *Cryptomys*. This division of the family was partly supported by Nevo *et al.* (1987), who concluded that there was need of urgent revision of the taxonomic status of these rodents.

In their general discussion of the genetic distance extrapolated from allozyme differentiation between the genera, Nevo *et al.* (1987) proposed two different hypotheses concerning the phylogenetic relationships and the origins of cladogenesis among these genera (Fig. 1). Both clusters agree in giving a divergence age between *Bathyergus janetta* and *B. suillus* and between *Cryptomus h. natalensis* and *C. h. hottentotus* of around 2.5 Ma, but there are still problems relating to earlier divergences of some taxa (Fig. 1). The difficulty arises from the intermediate position of *Georychus*. In the first cluster, *Georychus* is considered as the sister-genus of *Cryptomys*, being closer to *C. damarensis* than to *Bathyergus*. This leads to the first hypothesis of a differentiation of *Bathyergus* (Bathyerginae) at 12 Ma, and a cladogenesis of *Cryptomys* and *Georychus* (Georychinae) at about 5 Ma (Fig. 1A). In the second hypothesis, Nevo *et al.* (1987) suggested that *Georychus* is the sister-genus of *Bathyergus*, and is farther away from *Cryptomys*. The latter hypothesis is in contradiction to Roberts's (1951) classification and implies that the divergence between *Bathyergus* and *Georychus* occurred around 8 Ma, and that *Cryptomys* appeared more recently at around 4.5 Ma (Fig. 1B). The study of mitochondrial DNA variation among bathyergid rodents also shows closer affinities between *Bathyergus* and *Georychus* than between *Bathyergus* and *Cryptomys* (Honeycutt *et al.* 1987).

These two hypotheses suggest that around 4–5 Ma there was probably a major phase of differentiation among the three modern South African genera. According to the first hypothesis, there is a differentiation among the three modern South African genera. The first hypothesis suggests a differentiation of *C. damarensis* and *Georychus* at this date; and the second hypothesis suggests an early differentiation between *C. damarensis* and other species of *Cryptomys*. If either of these hypotheses is true, it should be possible to find some trace of the purported events in the fossil record.

The bathyergid fossil record is poor but the family is well known in East and South Africa from lower Miocene times (about 20 Ma). The family is represented in South Africa by three extinct genera whose affinities have been discussed by Lavocat (1973). *Bathyergoides* is known from 20 to 14 Ma and represents a primitive form not related to the modern genera. *Proheliophobius* is found at the same time and, according to Lavocat (1973), could represent a good ancestor to *Heliophobius*, *Georychus* and *Cryptomys*. The most recent genera, *Paracryptomys* and *Richardus* (14 to 12 Ma), could be the direct ancestors of *Cryptomys* and *Heterocephalus* (Lavocat 1973, 1989). There is no record of bathyergids in the upper Miocene times due to a general gap in the fossil record of tropical Africa.

The lower Pliocene sites are, in general, poorly documented for rodents both in East and South Africa, except for the Langebaanweg site (Cape Province, South Africa) in the Varswater Formation. This site is famous for having yielded numerous, well-preserved fossil vertebrates, which include thousands of rodents. Langebaanweg is estimated at around 5–4.5 Ma (see discussion in Hendey 1981), and it has yielded an important assemblage of Bathyergidae. The excavations have shown at least two different and important strata (Hendey

1981): the Quartzose Sand Member (QSM) at the base of the formation, and the Pelletal Phosphorite Member (PPM), which includes beds 3AS and 3AN. Both levels date from the Pliocene, and have different faunas, although Hendey (1981) has suggested that a very short time period occurred between the deposition of the two members.

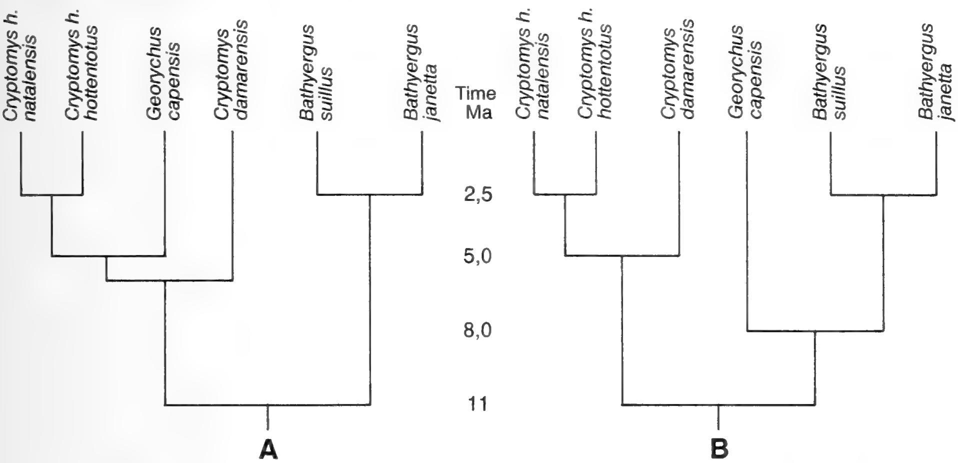


Fig. 1. Summary of the two phylogenetic hypotheses proposed by Nevo *et al.* (1987) from chromosomal and electrophoretic data on modern Bathyergidae from South Africa. The main differences between the hypotheses concern the affinities of *Georychus capensis* and its age of divergence. A. *Georychus* is closest to *Cryptomys* and has recently diverged (about 5 Ma). B. *Georychus* is closer to *Bathyergus* and was differentiated earlier (about 8 Ma).

In a preliminary study of the rodent material from 'E' Quarry at Langebaanweg, Pocock (1976) reported two bathyergids—*Bathyergus* sp. and *Cryptomys* sp. This author examined only one level (QSM), and the material was simply listed and not described or further identified. Re-examination of specimens at the South African Museum from the QSM and description of supplementary material from the PPM have shown that Bathyergidae are the most abundant rodents of the 'E' Quarry site at Langebaanweg. They are very well represented in the QSM and also in the PPM members, reaching 80 per cent of the total rodents in the PPM 3AN member. The morphological study of these fossils and their comparison with modern equivalents should provide some indication of the relationships among modern genera, as well as those of the Miocene, and should provide further evidence on the relationships of *Georychus*.

A systematic study of the Langebaanweg Bathyergidae has been undertaken in order to test the two evolutionary hypotheses of Nevo *et al.* (1987), and to try to determine the polarity of the characters. Comparisons between fossil and modern forms have been made through examination of the collections of the Transvaal Museum (TM), the Bernard Price Institute at the University of the Witwatersrand, Johannesburg (BPI), the South African Museum (SAM), the Natural History Museum of Paris (MNHN), the Natural History Museum, London (BMNH), and the Los Angeles County Museum (LACM).

SYSTEMATIC STUDY

Family **Bathyergidae** Waterhouse, 1841

Genus *Bathyergus* Illiger, 1811

The dune molerat (*Bathyergus*) is represented in south-western Africa by two distinct extant species: *B. suillus* Schreber, 1782 (the Cape dune molerat) and *B. janetta* Thomas & Schwann, 1904 (the Namaqua dune molerat) (Meester *et al.* 1986). This distinction, based initially on the morphology, has been confirmed by chromosomal studies (Nevo *et al.* 1985) (*B. suillus* being characterized by 2N = 56 and *B. janetta* by 2N = 54). A local population containing smaller-sized individuals, *B. suillus intermedius* Roberts, 1926, from Klaver, Cape Province, has also been taken into consideration.

Few representatives of the genus *Bathyergus* have been recorded from the southern African Pliocene fossil record, and the species of *Bathyergus* from Langebaanweg is, at present, the earliest one. The family Bathyergidae is well represented in the Miocene times but by different genera whose affinities remain uncertain (Lavocat 1973). In the most recent Plio–Pleistocene cave deposits at Taung (North-West Province) and Makapansgat (Northern Province), a large bathyergid of unknown affinities, *Gypsorychus* Broom, 1934, has been described. An undescribed skull of *Bathyergus* has also been recorded at the Upper Pleistocene site of Elandsfontein (De Graaff 1981—1–0.3 Ma).

Bathyergus hendeyi sp. nov.

Figs 2, 3A–D, 4–6

Bathyergus hendeyi sp. nov. is a large bathyergid that is the most abundant of the Langebaanweg rodent assemblages. It is characterized by the existence of 2–4 cheek-teeth, depending on the age of the individual. As in modern species of *Bathyergus*, the upper incisors have a median groove separating them in two at their tip, and the lower incisors are ungrooved. The upper incisors do not extend behind the tooth row as in *Georychus* and, according to Meester *et al.* (1986), the angular portion of the mandible is produced to well behind the occipital condyles, as in modern *Bathyergus* species.

Etymology

The species is named in honour of Dr Q. B. Hendey, who devoted his time to the Langebaanweg excavations and studied many large mammals from this site.

Material

Holotype. SAM–PQL20402 in the South African Museum (Cape Town). Anterior skull fragment with left and right DP^4–M^3, from the Quartzose Sand Member (QSM) of the Varswater Formation in 'E' Quarry, Langebaanweg (Figs 2C–E, 3A, 3C).

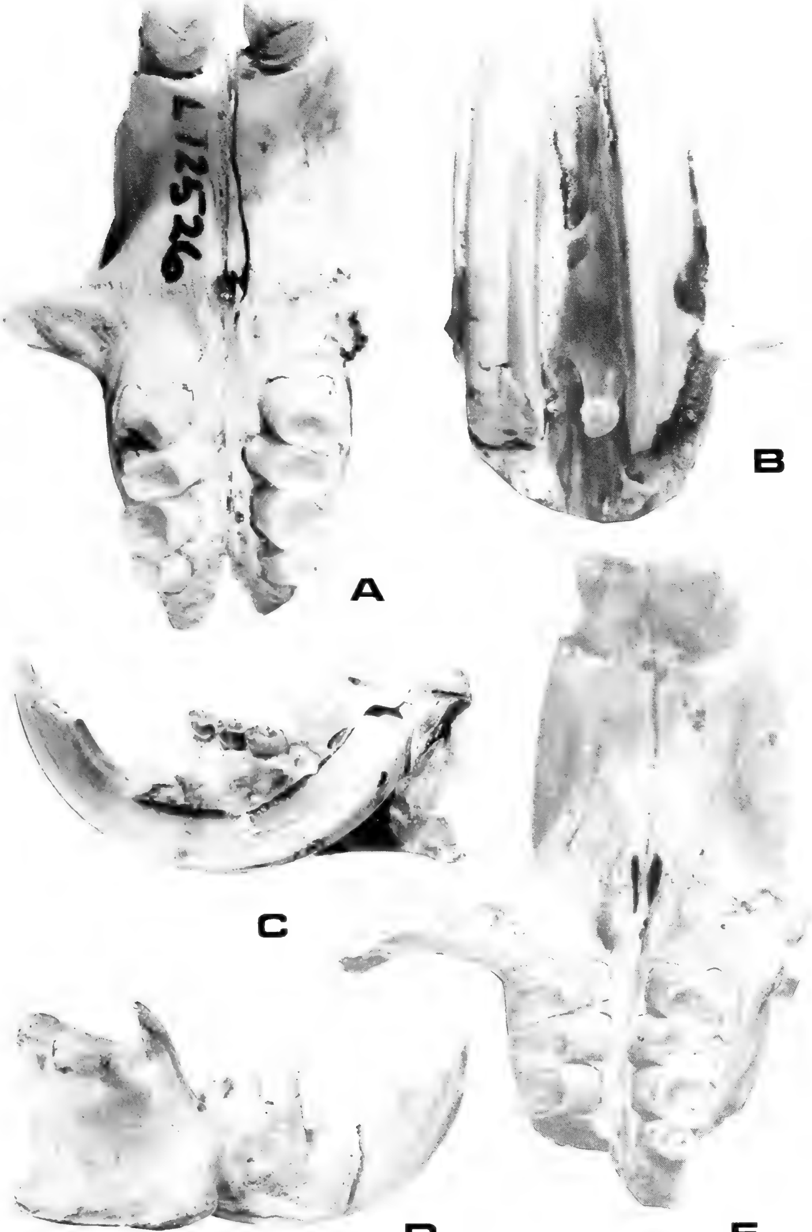


Fig. 2. *Bathyergus hendeyi* sp. nov. A–B. Skull, SAM-PQL12526 from Langebaanweg PPM 3AS member. A. Ventral view of anterior skull fragment (× 2.6). B. Dorsal view (× 1.5). C–E. Skull and mandible, SAM-PQL20402, holotype, from Langebaanweg QSM member. C. Internal view of right mandible (× 2.8). D. External view of mandible (× 2.8). E. Ventral view of anterior skull fragment with upper dental rows (× 1.5).

Skull fragments

QSM: SAM-PQL28388, anterior skull fragment with left and right DP^4–M^3.

PPM 3AN: SAM-PQL63443, anterior skull fragment with left DP^4–M^3.

PPM 3AS: SAM-PQL12526 (Fig. 2A, B), anterior skull fragment with left and right DP^4–M^3.

Mandible fragments

QSM: 11 right and 9 left mandible fragments with DP_4–M_3; 49 right and 72 left mandible fragments with DP_4–M_2; 27 right and 34 left mandible fragments with DP_4–M_1; 7 right and 6 left mandible fragments with DP_4; 2 right and 2 left mandible fragments with M_{13}; 4 right and 4 left mandible fragments with M_{23}; 6 right and 2 left mandible fragments with M_1; 4 right and 4 left mandible fragments with M_2; 1 left mandible fragment with M_3; 15 right and 14 left mandible fragments with M_{12}; 8 right and 18 left mandible fragments without teeth.

PPM 3AN: 7 right and 3 left mandible fragments with DP_4–M_3; 43 right and 27 left mandible fragments with DP_4–M_2; 22 right and 12 left mandible fragments with DP_4–M_1; 6 right and 5 left mandible fragments with DP_4; 2 right and 1 left mandible fragments with M_{13}; 24 right and 44 left mandible fragments with M_1; 19 right and 21 left mandible fragments with M_2; 46 right and 45 left mandible fragments with M_{12}; 108 right and 69 left mandible fragments without teeth.

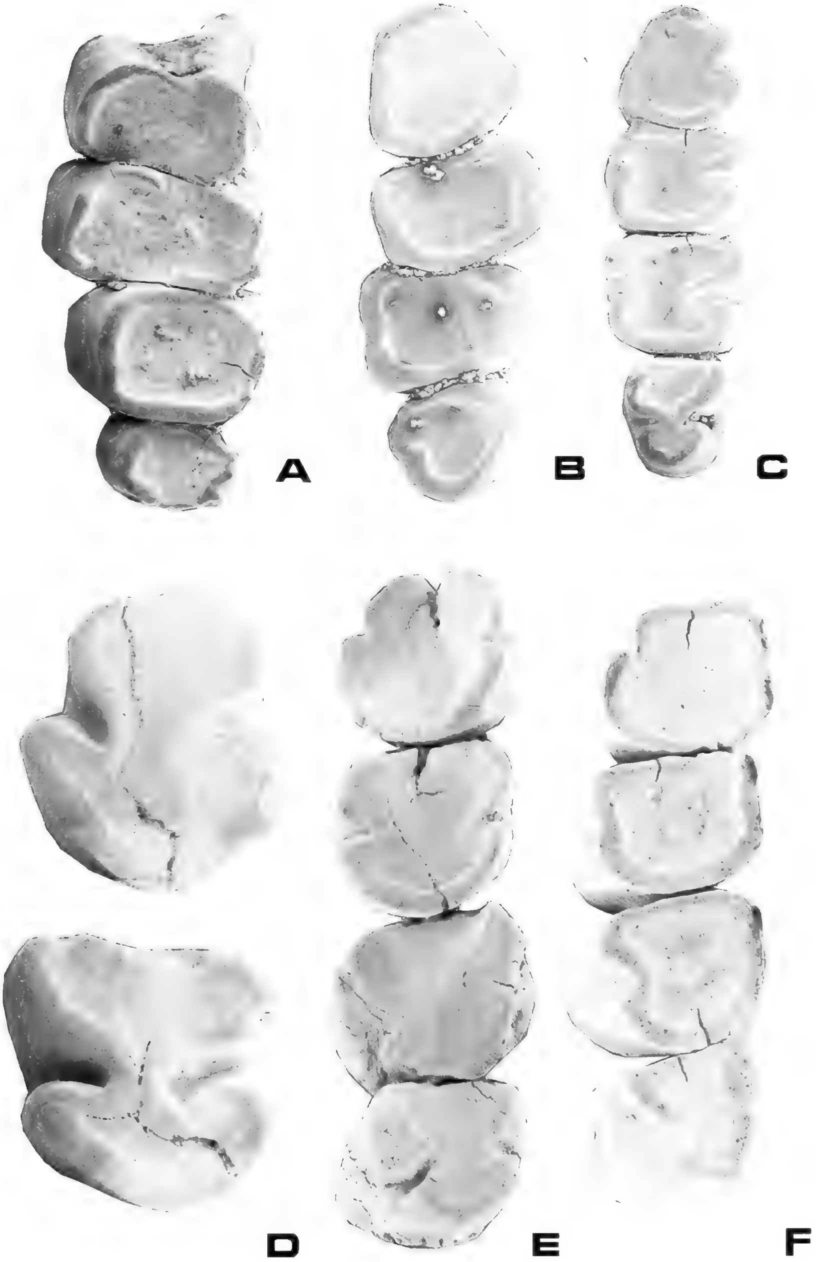
PPM 3AS: 4 right and 4 left mandible fragments with DP_4–M_3; 17 right and 14 left mandible fragments with DP_4–M_2; 9 right and 8 left mandible fragments with DP_4–M_1; 2 right mandible fragments with DP_4; 3 right and 1 left mandible fragments with M_{13}; 1 left mandible fragment with M_{23}; 2 right and 2 left mandible fragments with M_1; 6 right and 4 left mandible fragments with M_2; 4 right and 3 left mandible fragments with M_{12}; 6 right and 12 left mandible fragments without teeth.

Upper tooth rows

QSM: 8 right and 4 left maxillary fragments with DP^4–M^3; 5 right and 4 left maxillary fragments with DP^4–M^2; 1 right and 7 left maxillary fragments with DP^4–M^1; 3 right and 5 left maxillary fragments with DP^4; 1 left maxillary fragment with M^{13}; 3 left maxillary fragments with M^{23}; 1 right maxillary fragment with M^1; 1 right and 4 left maxillary fragments with M^{12}.

Fig. 3 (*see facing page*). Teeth of specimens of Bathyergidae from Langebaanweg. A–D. *Bathyergus hendeyi* sp. nov. from QSM member. A. SAM-PQL20402, holotype. Left upper molar row with DP^4–M^3 (× 7.4). B. SAM-PQL13060/B, right mandible with DP_4–M_3 (× 7.4). C. SAM-PQL20402, holotype. Right mandible with DP_4–M_3 (× 7). D. SAM-PQL50230, isolated left DP_4 (up) and M_1 (down) (× 16).

E–F. *Cryptomys broomi* sp. nov. from QSM member. E. SAM-PQL25101, left dental row with DP_4–M_3 (× 14). F. SAM-PQL24012, holotype, left dental row, with DP_4–M_3 (× 13).


A
B
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PPM 3AN: 1 left maxillary fragment with DP^4–M^3; 4 right and 2 left maxillary fragments with DP^4–M^2; 1 right and 1 left maxillary fragments with DP^4–M^1; 1 left maxillary fragment with M^{23}; 1 right and 1 left maxillary fragments with M^1; 1 left maxillary fragment with M^{12}; 1 left and 1 right maxillary fragments with M^2; 2 right and 2 left maxillary fragments without teeth.

PPM 3AS: 5 right and 1 left maxillary fragments with DP^4–M^3; 2 right and 2 left maxillary fragments with DP^4–M^2; 1 right and 3 left maxillary fragments with DP^4; 4 right and 2 left maxillary fragments with M^{23}; 1 left maxillary fragment with M^1; 1 right and 1 left maxillary fragments with M^{12}; 1 left maxillary fragment without teeth.

Diagnosis

Medium-sized *Bathyergus* with a relatively large infraorbital foramen and a wide angle between the zygomatic arch and the dental row; anterior part of skull high; low-crowned molars. Upper incisors reaching the level of M^{12} instead of DP^4–M^1 on modern *Bathyergus*; DP_4 rounded, not elongated.

Differentiated from *B. suillus* by the smaller size of skull and molars, especially of the DP_4, less rectilinear nasals, lower crowns, and narrower upper incisors. Differentiated from *B. janetta* by the slightly larger size of the skull and slightly smaller molars, lower crowns and wider upper incisors.

Description

Measurements are given in Tables 1 and 2.

Skull. Only anterior parts of skulls were found at Langebaanweg. The frontal region is high in lateral view and the upper incisors reach the level of the M^{12}. The nasals are enlarged posteriorly, whereas the muzzle is wide. The infraorbital foramen is wide and the zygomatic arch departure makes a right angle with the dental row (Fig. 2A, B, E).

Mandible. This species is characterized by a very important hystricognathous angle of the mandible and the close proximity of the symphysial joint to the DP^4. There is a relatively large space between the distal part of the dental row and the beginning of the coronoid process (Fig. 2C, D).

Teeth. Molars are described here but, as in all bathyergids, there is a large variation in the size and shape of the teeth that is age dependent (Taylor *et al.* 1985; Denys 1988) (Fig. 4).

Upper molars. The DP^4 is a square tooth comprising two lobes, each separated by an internal and an external sinus. These sinuses are only slightly invaginated towards the centre of the tooth; the labial invagination is deeper than the lingual one. In most cases these sinuses are invisible and the tooth appears round. The M^1 is more compressed antero-posteriorly than the DP^4 and has a rectangular shape. No internal or external sinuses are seen. The M^2 tooth is rounded and shows very slight sinuses. The DP^4, M^1 and M^2 are nearly equivalent in size, whereas the M^3 is the smallest tooth of the dental row and shows some variation in shape. It is sometimes round and unilobated; in other cases it is more elongated with a small posterior lobe; there is a trace of a small external sinus (Fig. 3A).

TABLE 1

Dental measurements (in mm) of *Bathyergus hendeyi* sp. nov. from Langebaanweg. Abbreviations: QSM—Quartzose Sand Member; 3AN and 3AS—Pelletal Phosphorite Member levels 3AN and 3AS, respectively; n—number of individuals; S.D.—standard deviation.

		QSM		3AN		3AS	
Tooth		Length	Width	Length	Width	Length	Width
DP^4	n	9		5		2	
	Minimum	1.83	2.68	1.96	2.5	1.83	3.08
	Maximum	2.17	3.5	2.13	3.29	2.15	3.1
	Mean	1.92	2.99	2.03	2.88	—	—
	S.D.	0.09	0.27	0.14	0.31	—	—
M^1	n	11		5		2	
	Minimum	1.29	2.42	1.79	2.42	1.93	3.42
	Maximum	1.92	4	2.17	3.25	1.96	3.5
	Mean	1.42	3.12	2.02	2.94	—	—
	S.D.	0.23	0.46	0.06	0.34	—	—
M^2	n	10		3		4	
	Minimum	2.04	2.41	2.08	2.33	2	2.88
	Maximum	2.5	3.33	2.38	2.92	2.67	3.42
	Mean	2.22	2.95	2.24	2.72	2.46	3.07
	S.D.	0.18	0.29	0.15	0.25	0.31	0.25
M^3	n	9		3		3	
	Minimum	1.67	1.92	1.83	1.96	1.67	2.08
	Maximum	1.9	2.71	2.08	2.5	1.92	2.33
	Mean	1.86	2.2	1.93	2.2	1.75	2.19
	S.D.	0.36	0.27	0.13	0.28	0.13	0.13
DP$_4$	n	22		21		10	
	Minimum	2.15	1.89	2.21	2.25	2.21	2.29
	Maximum	2.96	2.73	2.88	3.33	2.88	3
	Mean	2.44	2.31	2.62	2.69	2.62	2.57
	S.D.	0.18	0.18	0.18	0.27	0.21	0.21
M$_1$	n	22		25		11	
	Minimum	1.85	2	2	2	1.92	2.75
	Maximum	2.38	2.82	2.58	3.25	2.58	3.17
	Mean	2.12	2.43	2.32	2.64	2.32	2.99
	S.D.	0.15	0.21	0.15	0.35	0.23	0.15
M$_2$	n	15		22		11	
	Minimum	2	2.04	2.08	2.13	2.08	2.42
	Maximum	2.58	2.85	2.83	3.42	2.67	3.38
	Mean	2.27	2.51	2.49	2.8	2.42	2.9
	S.D.	0.15	0.29	0.19	0.39	0.2	0.35
M$_3$	n	3		7		7	
	Minimum	1.75	1.77	1.96	2.17	2.13	2.08
	Maximum	2	2.15	2.75	2.5	2.58	2.58
	Mean	1.76	1.9	2.33	2.27	2.31	2.3
	S.D.	0.4	0.13	0.18	0.27	0.18	0.16

Lower molars. The DP_4 is a rectangular tooth slightly enlarged distally. This premolar shows a great variation of morphology related to the wear stages. The youngest specimens show a small anterior median sinus and the DP_4 is divided into two lobes by an external oblique sinus and a very small internal sinus. On the lingual distal part, some more mature individuals show an enamel fold that isolates a small island (Fig. 2). This island is, on other specimens, related to the second lobe of the tooth making an intermediate loph reminiscent of some phiomorphs. The latter structure is only seen in a few examples. Another variation occurs in some specimens, where the lingual sinus is very deep and the enamel island is linked to the second lobe.

The M_1 is more squared than the DP_4. The anterior lobe is equal to the posterior one. The external and internal sinuses are almost the same size and are transverse. The anterior wall is rectilinear, whereas the posterior one is very convex. The M_2 is larger than the M_1. The external sinus is slightly more developed than the internal. Both sinuses almost meet in the central part of the tooth. The anterior and posterior walls are convex. The anterior part of the tooth is wider than the posterior one. The M_3 is composed of one or two lobes—with a higher proportion being bilobated. The anterior lobe is the widest, and the second lobe is round and separated from the first by the internal and external sinuses that join in the centre part of the tooth (Fig. 3B–F).

Comparison of Bathyergus hendeyi *with modern and fossil Bathyergidae*

Comparison with modern Bathyergus *species*

The two modern species of *Bathyergus* are distinguished essentially by their size, *B. janetta* being smaller than *B. suillus* s.l. They also show a different arrangement of the back of the skull and the tympanic bullae (De Graaff 1985). The population of *B. suillus intermedius* from Klaver (Cape Province) is characterized by a slightly smaller size (Roberts 1926) than *B. suillus*, but is larger than *B. hendeyi* sp. nov.

The comparison of skulls and mandibular characteristics of *B. hendeyi* sp. nov. with the modern species shows some differences. The angulation of the zygomatic arch is more open in *B. hendeyi* sp. nov. The infraorbital foramina are larger in the fossil species. The upper incisors reach the level of the DP^4–M^1 in modern specimens, whereas they reach the level of the M^{12} in the Langebaanweg form. The skulls from Langebaanweg are higher in their anterior part than in modern *Bathyergus* species, in which the muzzle is very low. In dorsal view, the nasals of *B. hendeyi* show an anterior expansion similar to those of *B. janetta*, whereas in *B. suillus* s.l. the nasals are more rectilinear.

The mandible of the modern *Bathyergus* species differs from those of *Georychus* and *Cryptomys* in showing a large space behind the tooth row between the M_3 and the beginning of the coronoid process. The foramen situated in this space is round and deep. The latter characteristics are also found in *B. hendeyi*.

Bathyergus hendeyi sp. nov. has low-crowned molars in which the roots are always visible, whereas in *B. suillus* the roots are fused and unrecognizable. In molars of *B. janetta* traces of roots can be seen. In the modern species of *Bathyergus*, the four jugal teeth have, in general, the same proportions, whereas

TABLE 2

Measurements (in mm) of mandibular and dental parameters of *Bathyergus hendeyi* sp. nov. and those of modern species. Some measurements of the dental rows are taken directly from Roberts (1951); in the case of *B. suillus intermedius* all measurements are from this source, except for a single specimen from the Transvaal Museum. Abbreviations: QSM—Quartzose Sand Member; 3AN and 3AS—Pelletal Phosphorite Member levels 3AN and 3AS; n—number of individuals; S.D.—standard deviation; WINC—width of the upper incisor; H-DP_4—height of the external part of the mandible just below the alveola of the DP_4; DP^4-M^3—length of upper jugal teeth row; DP_4-M_3—length of lower jugal teeth row.

		Bathyergus hendeyi			*Bathyergus suillus suillus*	*Bathyergus suillus intermedius*	*Bathyergus janetta*
		QSM	3AN	3AS			
WINC	n	4	0	1	8	1	3
	Minimum	3.25	—	2.6	3.3	3.37	2.6
	Maximum	3.65	—	—	4.7	—	2.92
	Mean	3.43	—	—	3.93	—	2.73
	S.D.	0.17	—	—	0.5	—	0.17
H-DP_4	n	23	9	9	8	1	3
	Minimum	8	9.6	9.9	14	16.1	11.5
	Maximum	13	15	13.7	18	—	12
	Mean	10.9	12.5	13	16.2	—	11.7
	S.D.	0.18	0.17	0.07	0.13	—	0.03
DP^4-M^3	n	8	1	1	22	7	7
	Minimum	7.5	8.3	7.7	10.5	8.3	7.5
	Maximum	8.2	—	—	12	10	10
	Mean	8	—	—	11.2	9.3	8.4
	S.D.	0.5	—	—	0.6	0.6	0.76
DP_4-M_3	n	21	7	6	8	1	3
	Minimum	8.2	8.75	8.15	10.5	10	8.5
	Maximum	10.3	10.6	10.6	13.2	—	9.55
	Mean	9.1	9.6	9.9	12.1	—	9.1
	S.D.	0.5	0.6	0.4	0.9	—	0.5

in *B. hendeyi*, the M^3 and the DP_4 are the smallest teeth (Table 1). The mean lengths of the upper and lower dental rows and the height of the mandible under the DP_4 (Table 2) are smaller in *B. hendeyi* than in *B. suillus*, and show similar variation in size to that recorded in *B. janetta* (Figs 5, 6). The t-tests gave highly significant results for the comparisons between *B. hendeyi* and the two subspecies of *B. suillus*— *B. suillus suillus* and *B. suillus intermedius*, and non-significant results between *B. hendeyi* and *B. janetta*. However, the size variation in modern specimens of *B. janetta* is not well known. The width of the upper incisor of *B. hendeyi* is intermediate between those of *B. suillus* and *B. janetta*.

The molars of modern and fossil *Bathyergus* species are not very different, except for the length of the DP$_4$ (Fig. 6). This tooth is more elongated in the two modern species than in *B. hendeyi*, but there is a great variation in size and shape of the molars during the life of these molerats.

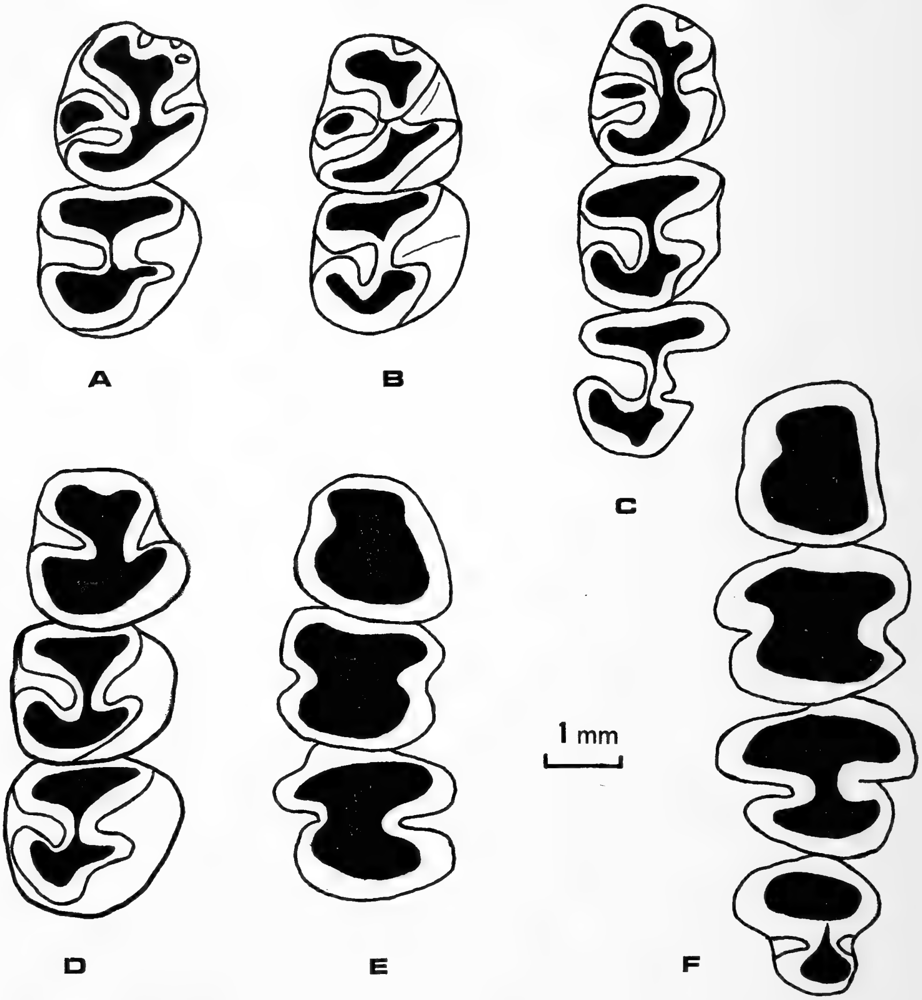

Fig. 4. *Bathyergus hendeyi* sp. nov. Morphological variation during wear in molars. A. Stage 1: right mandible (two molars) with DP$_4$–M$_1$; the DP$_4$ shows two internal sinuses and a single external one. B. Stage 1: right mandible with DP$_4$–M$_1$ the internal sinuses isolate an enamel island. C. Stage 2: on teeth more worn than in stage 1, the germ of M$_2$ shows two lobes separated by a narrow longitudinal crest. D. Stage 3: only one internal sinus and one external one; no trace remains of the enamel island and the M$_2$ is well developed. E. Stage 4: the teeth are worn and the internal sinus is small, whereas the external one has disappeared on the DP$_4$. On M$_{12}$ the sinuses are less marked than in the previous stage. F. Stage 5: there is the development of a small M$_3$ made of two lobes separated by a longitudinal crest; two sinuses divide the tooth in two parts, the posterior one being the narrowest. Scale bar = 1 mm.

Comparison with the fossil Gypsorychus

The upper teeth of *Gypsorychus darti* Broom, 1934, and *G. minor* Broom, 1948, differ considerably from those of *B. hendeyi* sp. nov., and are also very different from all known modern Bathyergidae. They are high crowned and have a greater width than length. The molars are unfolded, except the upper M^3, which consists of two lobes (Broom 1937). In *Gypsorychus* the M^3 is the longest tooth in the dental row, whereas in *B. hendeyi* and most other southern African Bathyrgidae (except *Georychus*) the M^3 is the smallest. According to Broom (1948), the skull of *Gypsorychus* is as large as that of *Bathyergus* and he concluded that the affinities of *Gypsorychus* lay with *Cryptomys*. Present observations confirm that *Gypsoychus* does not share common characteristics with *B. hendeyi* or *Cryptomys*.

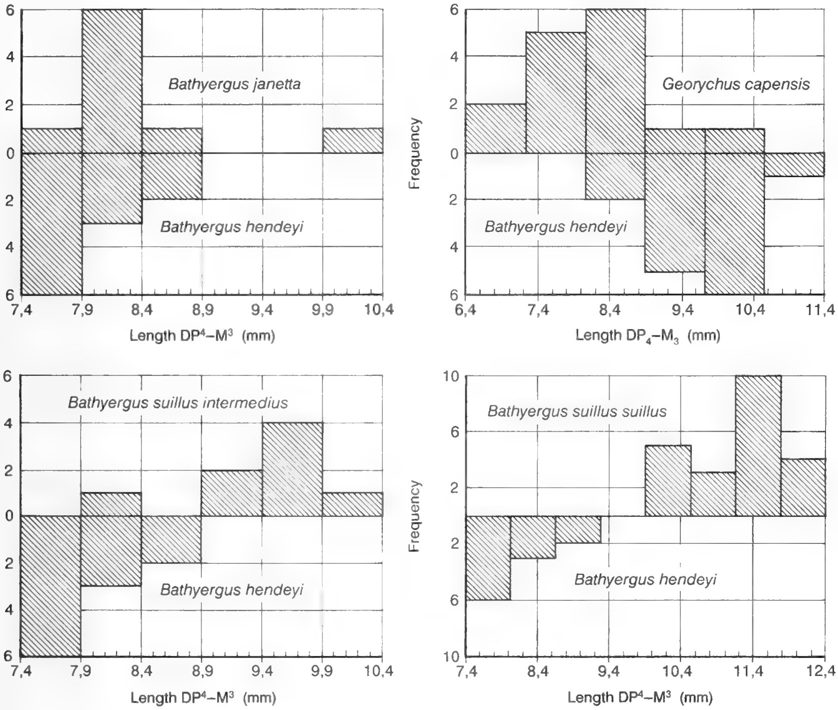

Fig. 5. Comparisons of *Bathyergus hendeyi* sp. nov. with modern species of *Bathyergus* and *Georychus capensis*. Frequency histograms of DP^4–M^3. Axes: abscissa = length in mm; ordinate = frequencies.

Discussion

Whereas no morphological differences are seen between the molars of *Bathyergus hendeyi* sp. nov. found in QSM and PPM levels, there are indications of size differences (Table 1). The *B. hendeyi* specimens from the QSM level are slightly smaller in size and more frequently show traces of supplementary sinuses on the DP_4 than their homologues of the PPM level. This

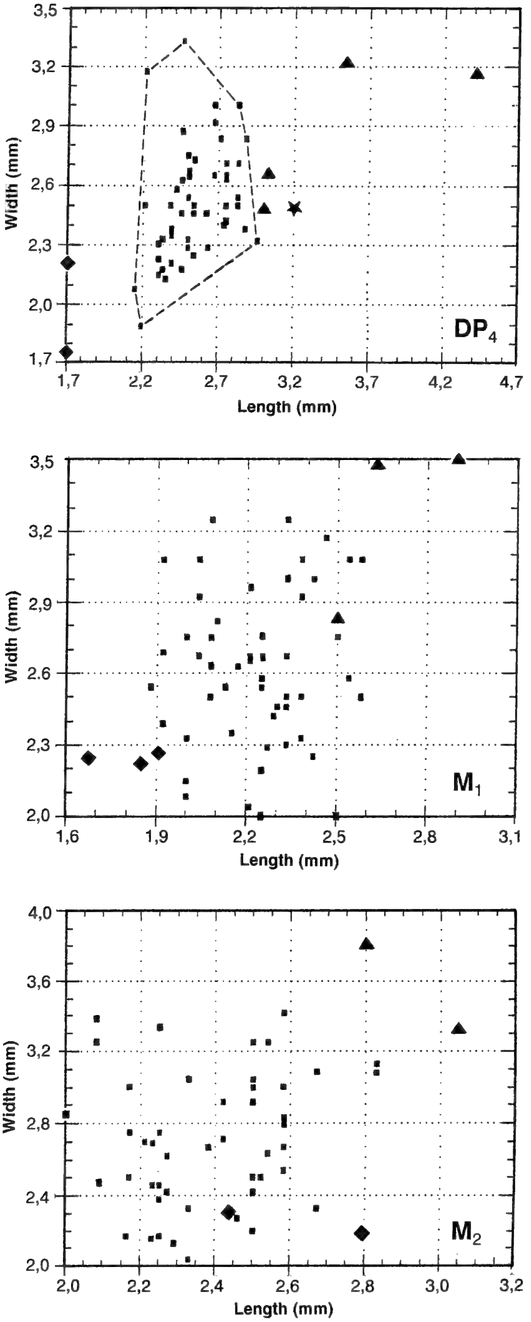

Fig. 6. Scatterplot of the DP$_4$, M$_1$ and M$_2$ molars of modern and fossil species of *Bathyergus* and comparison with *Georychus capensis*. Symbols: ■—*B. hendeyi* sp. nov. from Langebaanweg, ✶—*B. janetta*; ▲—*B. suillus*; ◆—*G. capensis*. Measurements in mm. Axes: abscissa—length; ordinate—width.

could indicate a tendency towards an increase in general size and simplification of the molars with time in the *Bathyergus* lineages.

Bathyergus hendeyi sp. nov. may represent a common ancestor to *B. suillus* and *B. janetta*. Among the species of the genus *Bathyergus*, evolutionary tendencies could be expressed by the increase of the size of skulls and teeth, diminution in the height of the skull, simplification and elongation of the DP_4, and increased hypsodonty.

Bathyergus janetta shares with *B. hendeyi* enlarged nasals and almost identical length of upper and lower dental rows, which could indicate relatively close affinities. However, these characteristics may also be primitive for the genus. In the absence of intermediate fossils, the relationships between modern and fossil species remain unclear.

At 5–4 Ma, *Bathyergus* is well differentiated from other bathyergids, which supports its position in a separate subfamily following Roberts (1951) and suggests a rather early differentiation (around 12 Ma) of the genus, as suggested by molecular trees (Nevo *et al.* 1987) (Fig. 1). However, *Bathyergus* cannot be related directly to a Miocene ancestor due to the gap in the fossil record between 12 and 5 Ma. Moreover, in his study of lower Miocene bathyergids, Lavocat (1973) did not suggest any ancestor to *Bathyergus* among fossil genera and the origins, as well as the age of its divergence, remains unknown.

On the contrary, the suggested age of 2.5 Ma, as determined by the molecular hypotheses, for the divergence between *B. janetta* and *B. suillus* from ancestral *B. hendeyi* is highly probable according to the dental morphology of the fossil examined here.

Genus *Cryptomys* Gray, 1864

One extant species of *Cryptomys* is found in the south-western Cape region—*C. hottentotus* Lesson, 1826 (the common molerat). Within this species Honacki *et al.* (1982) recognized a further five subspecies in *C. hottentotus* s.l. These are *C. h. bocagei*, *C. h. damarensis*, *C. h. darlingi*, *C. h. holosericus*, and *C. h. natalensis*. Recent examination of the karyotypes of the South African bathyergids has shown (Nevo *et al.* 1985) that *Cryptomys*, traditionally considered as monospecific, could comprise at least three distinct forms. These are *C. hottentotus hottentotus* (2N = 54), *C. hottentotus natalensis* (2N = 54) and *C. h. damarensis* (2N = 74 and 78). The study of mtDNA, allozyme and chromosomal variation among the three subspecies of *C. hottentotus* suggested that *C. h. damarensis* should be raised to specific rank (Honeycutt *et al.* 1987). According to Roberts (1951), *C. damarensis* is distinguished by a perforation at the front edge of the orbit (antorbital foramen) that is smaller and not as oblong (being only a little higher than wider) than in *C. hottentotus*. The subspecific status of *C. hottentotus hottentotus* and *C. hottentotus natalensis* is retained at present, despite some genetic differences. In the absence of morphological revision and good external criteria, the term *C. hottentotus sensu lato* (s.l.) will be employed in this paper to designate modern representatives of *C. hottentotus*. Woods (1993) included the subspecies *darlingi*, *holosericus* and *natalensis* in *C. hottentotus*.

Fossil *Cryptomys* are relatively abundant in the Plio–Pleistocene Transvaal caves. Broom (1937) described *C. robertsi* from the Plio–Pleistocene bone breccia at Krugersdorp, near Pretoria (Gauteng Province). Pocock (1987) reported the coexistence of two species at Kromdraai and Sterkfontein: *Cryptomys* cf. *C. hottentotus natalensis* and a larger species, *C. robertsi* Broom, 1937. Pocock (1987) also recorded *Cryptomys* cf. *C. hottentotus* in all sites at Makapansgat, these specimens being smaller than *Cryptomys* cf. *C. h. natalensis* from Sterkfontein. These forms have not yet been described in detail.

Cryptomys broomi sp. nov.

Figs 3E–F, 7

In addition to the numerous remains of *Bathyergus* found at Langebaanweg, a small bathyergid with ungrooved molars and four cheek-teeth has been found. Represented only by a small number of mandibles associated with the teeth, this bathyergid shows a very large diastema and few markedly hystricognathous characteristics of modern *Cryptomys* species, as well as the absence of sinuses on the molars. The existence of an M_2 of nearly identical size to the M_1 differentiates this small bathyergid from Langebaanweg from *Georychus*, and the constant number of 4 cheek-teeth permits separation of the fossil from the modern genus *Heliophobius* that has 2 to 6 cheek-teeth.

Etymology

This species is named in honour of Dr Broom who first paid attention to the rodents of South African Plio–Pleistocene caves.

Material

Holotype. SAM–PQL24012 in the South African Museum (Cape Town). Mandible with DP_4–M_3 from the Quartzose Sand Member (QSM) of the Varswater Formation in East Stream Elephant site of 'E' Quarry at Langebaanweg (Fig. 3F).

Other material

QSM: 1 left mandible fragment with DP_4–M_3; 3 left mandible fragments with DP_4–M_2; 1 right mandible fragment with DP_4–M_2; 1 left and 1 right maxillary fragments with DP^4; 2 right mandible fragments with M_1; 1 left mandible fragment with M_1; 2 right mandible fragments with M_{12}; 1 left and 1 right mandible fragments without molars.

PPM: 1 left mandible fragment with M_{23}; 1 right mandible with M_{23}; 1 left mandible fragment with M_{13}; 1 right mandible fragment with DP_4–M_2; 1 right mandible fragment with M_{12}; 1 right mandible fragment with DP_4–M_1; 3 right and 3 left mandibles with M_1; 3 mandible fragments without molars.

Diagnosis

Cryptomys with low-crowned molars, showing traces of cusps, and similar in size to the molars of *C. damarensis*, *C. hottentotus* s.l. and *C. robertsi*.

Differentiated from *C. hottentotus* s.l. by a narrower angle of the mandible (90°), by a more robust mandible, and by lower crowns. Differentiated from *C. robertsi* by lower crowns and more visible traces of cusps. Differentiated from *C. damarensis* by the slightly larger molars, especially the DP_4, and by lower crowns.

Description of the molars

Measurements are given in Tables 3 and 4.

DP_4 is small, rather rounded and not elongate, with shallow internal and external sinuses. There is a frontal, median, anterior sinus. When the tooth is worn the internal sinus disappears. This premolar has two roots, one anterior to the other (Fig. 3E, F).

M_1 is more squared and slightly larger than DP_4, with an external sinus more developed than on DP_4. The internal sinus is marked but no more deep than on DP_4. On worn teeth, the internal sinus disappears first, followed by the external sinus (Fig. 3E, F).

On M_2, the external sinus is more developed than on the M_1 and almost reaches the centre of the occlusal surface, dividing the molar into two lobes. The first lobe is wider than the posterior one. The internal sinus may be either less developed than on the M_1 or absent (Fig. 3E, F).

M_3 comprises two lobes, well separated by the deep external sinus, and is more elongate than M_1. The second lobe is narrower than the first. There are three roots, two anterior and one posterior (Fig. 3E, F).

TABLE 3

Dental measurements (in mm) of *Cryptomys broomi* sp. nov. (n—number of individuals; S.D.—standard deviation; min.—minimum value; max.—maximum value).

Tooth		Length				Width			
	n	Min.	Max.	Mean	S.D.	Min.	Max.	Mean	S.D.
DP_4	3	1.5	1.58	1.54	0.04	1.75	1.83	1.79	0.04
M_1	6	1.29	1.79	1.43	0.18	1.66	2.17	1.88	0.17
M_2	4	1.4	1.75	1.62	0.15	1.75	2.00	1.85	0.12
M_3	2	1.3	1.66	—	—	1.05	1.75	—	—

Comparison of Cryptomus broomi *with modern and fossil Bathyergidae*

Comparison between modern and fossil Cryptomys

Cryptomys and other bathyergids are well known for the extreme variability in size and shape of their jugal teeth during growth (Taylor *et al.* 1985; Denys 1988) and for having teeth that do not erupt simultaneously. This renders comparison very difficult, because *Cryptomys broomi* sp. nov. is represented by only a few specimens. Comparison of molar dimensions shows that *C. broomi* has variation similar to that found in modern *C. hottentotus* s.l. and *C. robertsi* from Kromdraai B and Sterkfontein sites. The small Langebaanweg *Cryptomys* sample shows as much variability as in all other modern and fossil representatives of the genus (Tables 3, 4). Comparison of the length of DP_4 of four species of *Cryptomys* (Fig. 7) shows that *C. broomi* is slightly larger than *C. damarensis*. The length of the lower dental row is very similar to that of the specimens of *C. hottentotus* s.l. and *C. damarensis* (Table 4). The t-tests gave non-significant differences between *C. hottentotus*, *C. damarensis* and *C. broomi* at the 95 and 99 per cent levels.

From a morphological point of view, the most striking trait of *C. broomi* sp. nov. is the low-crowned teeth. Roots of teeth are seen in all *C. broomi* specimens, whereas they remain invisible in *C. robertsi* and all modern *Cryptomys*, which have higher crowns.

Some juvenile specimens from Langebaanweg retain more clearly a trace of cusps on their molars, especially the lower M_3 of the type specimen. The M_3 is very wide anteriorly compared to other species of *Cryptomys*. Modern and fossil *Cryptomys* share the same shape and disposition of the mandible with a long and transverse symphysial joint and a small diastema; however, this character is highly variable. The incisors of *C. broomi* sp. nov. are less straightened and the wear facets more oblique than in *C. hottentotus* s.l. and *C. damarensis*.

Comparison of Cryptomus broomi *with modern* Georychus capensis

Georychus capensis has a more robust mandible than *C. broomi* sp. nov. and larger teeth that retain traces of the crests until an advanced stage of wear. There is no trace of the roots in *G. capensis* and the jugal teeth are relatively high crowned. In *G. capensis*, the molars increase in size from the M_1 to the M_3, the M_3 being the largest tooth, whereas in *C. broomi* sp. nov. and other *Cryptomys* species the M_3 is the smallest molar (Fig. 7).

Discussion

In the absence of a more detailed morphometric study of the different modern *Cryptomys* species, any attempt to relate *C. broomi* sp. nov. to one or other species of the genus remains difficult. The size of the Langebaanweg fossil places it very close to *C. robertsi* from Plio–Pleistocene sites of Gauteng and North-West Province. *Cryptomys broomi* shows a plesiomorphic character in being less high crowned. However, the phylogenetic relationships between *C. broomi* and the modern *Cryptomys* cannot yet be established, particularly the relationship between *C. broomi* and *C. damarensis*.

The presence of a primitive *Cryptomys* at Langebaanweg, aged about 5–4 Ma, can be discussed in the light of the molecular hypotheses of Nevo *et al.* (1987), summarized in Figure 1. The morphological characteristics of *C. broomi* sp. nov. appear primitive and could be interpreted in the following two ways. In a first hypothesis, from its dental morphology, *C. broomi* is the common ancestor of *C. hottentotus* s.l. and of *C. damarensis*, and their divergence occurred after 5–4 Ma. (This differs slightly from the two hypotheses of Nevo *et al.* (1987), which—in both cases—suggested an earlier divergence age of *C. damarensis* at 6–5 Ma (Fig. 1A, B)). In the second

TABLE 4

Comparison of DP$_4$–M$_3$ length in four species of *Cryptomys* and in *Georychus capensis*.

		Cryptomys broomi sp. nov.	*Cryptomys robertsi*	*Cryptomys damarensis*	*Cryptomys hottentotus*	*Georychus capensis*
DP$_4$–M$_3$	n	4	1	6	16	17
	Mean	6.4	—	6.2	5.7	8
	Minimum	5.9	5.7	5.5	4.7	6.4
	Maximum	6.6	—	7	6.8	10
	S.D.	0.3	—	0.6	0.6	0.9

hypothesis, *C. broomi* is more closely related to *C. hottentotus* s.l. and was differentiated separately from *C. damarensis*. In the latter case, *C. damarensis* represents another lineage differentiated before or after other *Cryptomys*. However, *C. damarensis* is too close to *C. broomi* to suppose a very early or late differentiation of *C. damarensis*, and the age of 5–6 Ma given by molecular data for its differentiation is acceptable. So far as is known, no fossil of *C. damarensis* has yet been found to support either the dental or molecular hypothesis.

The relationships of *C. broomi* sp. nov. with *G. capensis* must also be discussed here. The comparison of the dental morphology of the two species shows that *Georychus capensis* is very different from *C. broomi* and also from *C. damarensis*, which suggests an earlier differentiation than 5 Ma, contrary to the first suggestion provided by the molecular data of Nevo *et al.* (1987) (Fig. 1A) and supports the second hypothesis of a very early divergence for *Georychus* (Fig. 1B). This corresponds with the results of the mitochondrial DNA data of Honeycutt *et al.* (1987). The absence of *Georychus* from Langebaanweg could be due to ecological or taphonomic reasons rather than phylogenetic ones.

CONCLUSIONS

The description of two distinct and modern Bathyergidae at Langebaanweg has some phylogenetic implications and permits more precise interpretation of parts of the molecular trees that have been proposed. In addition, the study provides calibrations and morphological arguments in support of one or other of the hypotheses proposed by Nevo *et al.* (1987).

Firstly, the fact that the two bathyergid genera of Langebaanweg are modern ones, supports Nevo *et al.*'s (1987) hypotheses that the differentiation between *Cryptomys* and *Bathyergus* occurred before 5–4 Ma. However, the lack of a fossil record in upper Miocene times precludes a precise determination of the age of their divergence at the generic level.

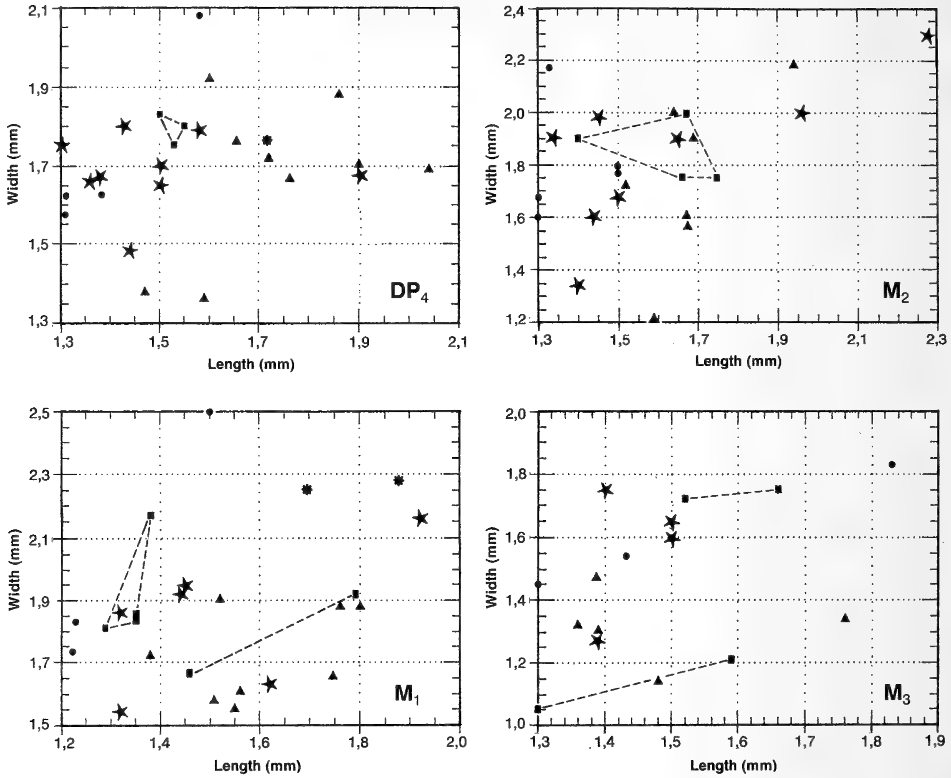

Fig. 7. Scatterplot of DP$_4$ and M$_1$ measurements in modern and fossil species of *Cryptomys*. Symbols: ✱—*G. capensis*; ■—*C. broomi* sp. nov. from Langebaanweg; ●—*C. damarensis*; ▲—*C. hottentotus* s.l.; ✶—*C. robertsi*. Measurements in mm; abscissa—length; ordinate—width.

At the specific level, the fossil record is better documented and the study of dental morphology supports the molecular hypotheses. The small size of *Bathyergus hendeyi* sp. nov. from Langebaanweg and its many primitive characteristics make it a good ancestor to either *B. suillus* or *B. janetta*. This supports Nevo *et al.*'s (1987) age of 2.5 Ma for the divergence of the two modern species. Indeed, examination of the *Bathyergus* skull from the Elandsfontein site (1–0.3 Ma) (Pleistocene) shows that it is clearly *B. suillus*. Moreover, the study of different South African rodent lineages has shown that the time period around 2.5 Ma corresponds to different speciation events (Denys 1990).

The *Cryptomys broomi* sp. nov. from Langebaanweg is, according to present knowledge, the oldest known representative of the genus *Cryptomys*. It has some primitive characteristics and seems to be relatively closely related to either *C. hottentotus* s.l. or *C. damarensis*. *Cryptomys broomi* could be the ancestor of modern *C. hottentotus* s.l. and could be closely related to the fossil *C. robertsi* (whose specific attribution needs careful revision). *Cryptomys damarensis* is also very closely related to *C. broomi*. In the absence of fossils of *C. damarensis*, it is difficult to determine if this species arose from a lineage other than the *C. broomi—C. robertsi* one or to assess the precise age of its specific divergence.

The study of the oldest *Cryptomys* and *Bathyergus* representatives of the lower Pliocene site of Langebaanweg provides some information on relationships of the South African bathyergids. Despite the lack of intermediate fossils, it is clear that *Cryptomys* and *Georychus* are distinct. On evidence from dental and skull morphology, *Georychus* appears to be relatively distant from *Bathyergus*. The hypothesis of a rather early differentiation of *Georychus* is supported by dental anatomy, as well as the molecular data of Nevo *et al.* (1987) (see Fig. 1B) and of Honeycutt *et al.* (1987). The examination of the Miocene bathyergids shows that, according to Lavocat (1973), the best ancestor of the modern *Georychus-Heliophobius* group could be *Proheliophobius*. The revision of the numerous species of Miocene Bathyergidae from East and South Africa should provide further information concerning the origin of the first *Bathyergus*. The relationships of the Pliocene genus *Gypsorychus* remain to be studied, and it is clear that the family Bathyergidae shows a more complex history and evolutionary scenario than the systematics of modern Bathyergidae has led us to understand.

ACKNOWLEDGEMENTS

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Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

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CHRISTIANE DENYS

PHYLOGENETIC IMPLICATIONS OF THE EXISTENCE OF TWO MODERN GENERA OF BATHYERGIDAE (MAMMALIA, RODENTIA) IN THE PLIOCENE SITE OF LANGEBAANWEG (SOUTH AFRICA)

VOLUME 105 PART 6 NOVEMBER 1998 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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ANNALS OF THE SOUTH AFRICAN MUSEUM
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BACULITES ALAVENSIS SANTAMARIA ZABALA, 1996 (CEPHALOPODA, AMMONOIDEA), FROM THE UPPER CAMPANIAN OF NORTHERN SPAIN

By

HERBERT CHRISTIAN KLINGER
&
THOMAS KÜCHLER

Cape Town Kaapstad

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(With 5 figures)

[*MS accepted 1 October 1998*]

ABSTRACT

Several specimens of the poorly known *Baculites alavensis* Santamaria Zabala, 1996, are described from the Upper Campanian of Ecay, northern Spain. These fully display the typical ornament of the species. Affinities with *B. leopoliensis* Nowak, 1908, *B. alonsoi* Santamaria Zabala, 1996, *Trachybaculites columna* Morton, 1834, *B. vanhoepeni* Venzo, 1936, and *B. sulcatus* Baily, 1855, are discussed.

CONTENTS

INTRODUCTION

Baculites alavensis is here described on the basis of numerous specimens collected by one of us (T.K.) in Spain to illustrate the intraspecific variation of the species, as well as to compare it with baculitid species of similar morphologies.

Ann. S. Afr. Mus. **105** (6), 1998: 287–296, 5 figs.

LOCATION OF SPECIMENS

All the Spanish specimens are housed in the private collection of T. Küchler, Berlin, Germany; other figured specimens are housed in the collections of the South African Museum, Cape Town.

SYSTEMATIC PALAEONTOLOGY

Class CEPHALOPODA Cuvier, 1797

Order AMMONOIDEA Zittel, 1884

Suborder ANCYLOCERATINA Wiedmann, 1966

Family **Baculitidae** Gill, 1871

Genus *Baculites Lamarck*, 1799

Baculites alavensis Santamaria Zabala, 1996

Figs 1, 2A–F, 3, 4, 5I–L

? 1986*a*	*Baculites* sp. 5. Kennedy, p. 113, pl. 18 (figs 2–3).
? 1986*b*	*Baculites leopoliensis* Nowak; Kennedy, p. 1013, pl. 2 (figs 1–2, 11–12), pl. 3 (figs 22–24).
1996	*Baculites alavensis* Santamaria Zabala, p. 14, pl. 3 (figs 7–9).

Type

Holotype by original designation is the specimen figured by Santamaria Zabala (1996, pl. 3 (fig. 8)) from the Upper Campanian of Ullibarri-Jauregui in the province of Alava, northern Spain.

Material

EC1–100+26 m/1–3, 7–8; EC1–102/3–4; EC1–104/a–b; EC1–106/a–e; EC1–106/1–7; EC1–107/a–b, EC1–108/a–d, all from the Upper Campanian of Ecay, Navarra, northern Spain.

Description

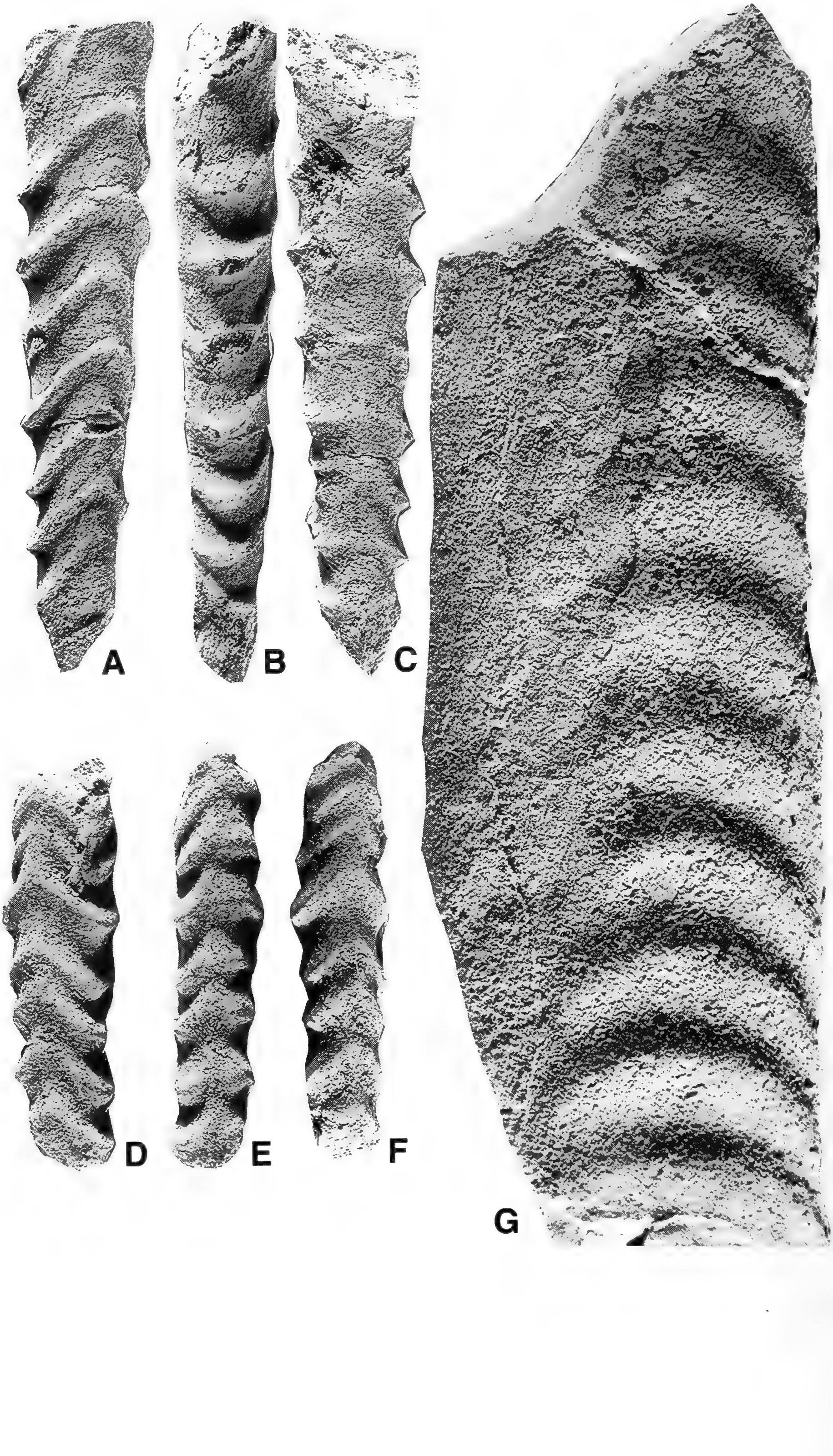
All the specimens appear to be composite moulds, preserved in grey siltstone; all are crushed to varying degrees and none shows the suture lines.

Most of the specimens have a compressed, ovoid whorl section, but we suspect that this is mainly due to secondary deformation. A few specimens, e.g. Figure 5I–J, show a near-circular whorl section.

The most striking feature of this species is the strong lateral, ventral and, in some cases, also dorsal ribbing. These ribs arise near the dorsum, curve back near the upper quarter of the dorsum, and then curve forwards over the ventral part of the flanks. In some specimens, e.g. Figure 4B–D, the ribs are markedly thickened at the point where the curvature of the ribs changes. In most

Fig. 1. *Baculites alavensis* Santamaria Zabala, 1996. EC1–108a from the Upper Campanian of Ecay. × 1.

specimens, the ribs pass over the venter without diminishing in strength and with a sharp apertural curvature. Bifurcating or intercalatory ribs near the venter are extremely rare. Ribbing over the dorsum is generally much weaker than on the flanks or on the venter (e.g. Fig. 2A–C), but in some specimens (e.g. Fig. 2D–F) ribbing on the dorsum is nearly, or as strong as, on the rest of the shell. Rib density is generally two-and-a-half to three ribs per whorl height, but it may be as low as two (Fig. 3G–I). Some of our specimens appear to be completely devoid of ribbing (e.g. Fig. 4A). We suspect that these are merely rare, smooth variants of *B. alavensis* rather than a different species. Part of the aperture is preserved in one specimen (Fig. 3A–C).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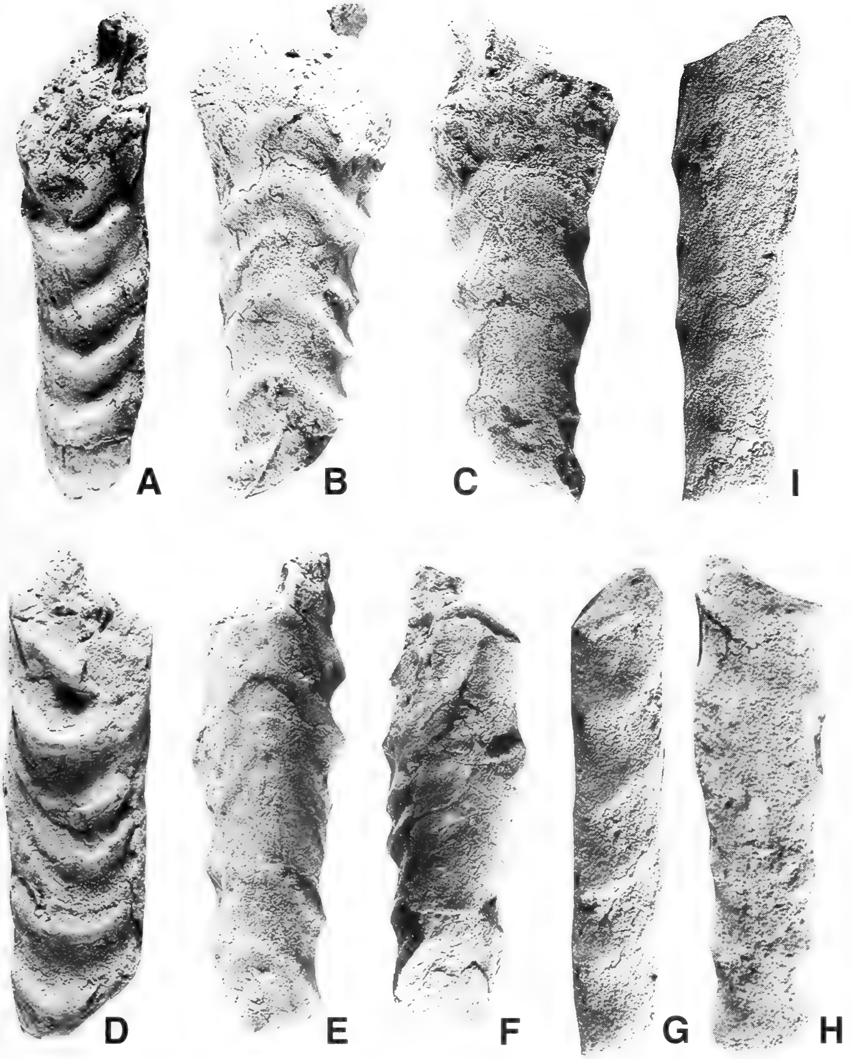


Fig. 3. *Baculites alavensis* Santamaria Zabala, 1996. A–C. EC1–107. D–F. EC1–106/e. G–I. EC1–106/d. All from the Upper Campanian of Ecay. All × 1.

Fig. 2 *(see facing page)*. A–F. *Baculites alavensis* Santamaria Zabala, 1996. A–C. EC1–100+26 m/7. D–F. EC1–100+26 m. Both from the Upper Campanian of Ecay. G. *Baculites leopoliensis* Nowak, 1908 (SAM-PCPo12917) from the Lower Maastrichtian (?Upper Campanian) of Piotrawin, Poland. All × 1.

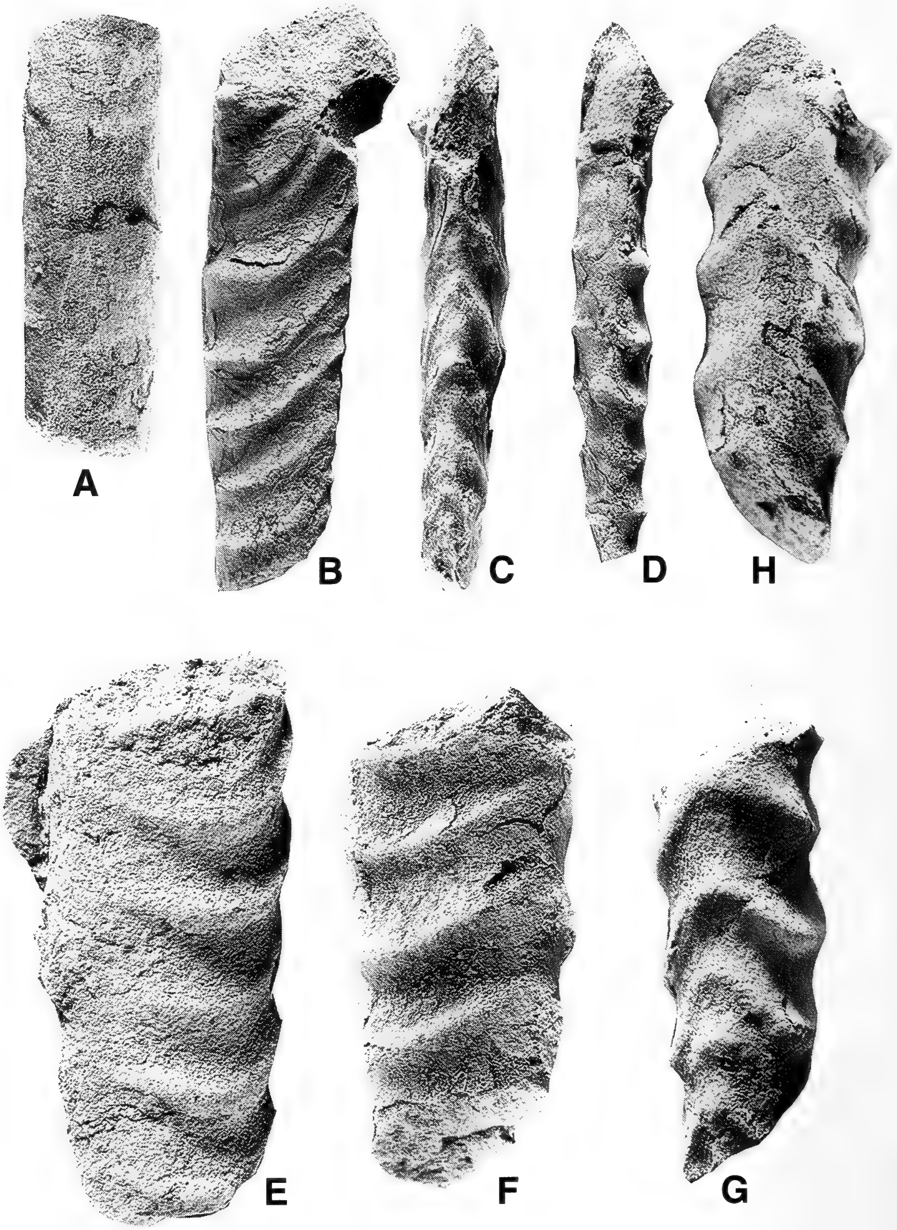


Fig. 4. *Baculites alavensis* Santamaria Zabala, 1996. A. EC1–102/4. B–D. Ec1–106/a. E. Ec1–106/b. F–H. Ec1–106/c. All from the Upper Campanian of Ecay. B, D × 1; A, E–H × 2.

Discussion

The strong lateral and ventral, and in some cases dorsal ribbing, easily distinguishes this species from all other European Campanian baculites.

Our material adds to the range of variation of *B. alavensis* described by Santamaria Zabala (1996: 14, pl. 3 (figs 7–9)). The holotype (pl. 3 (fig. 8)) and one of the paratypes (pl. 3 (fig. 9)) clearly show the strong circumperipheral ribbing as found in some of our specimens.

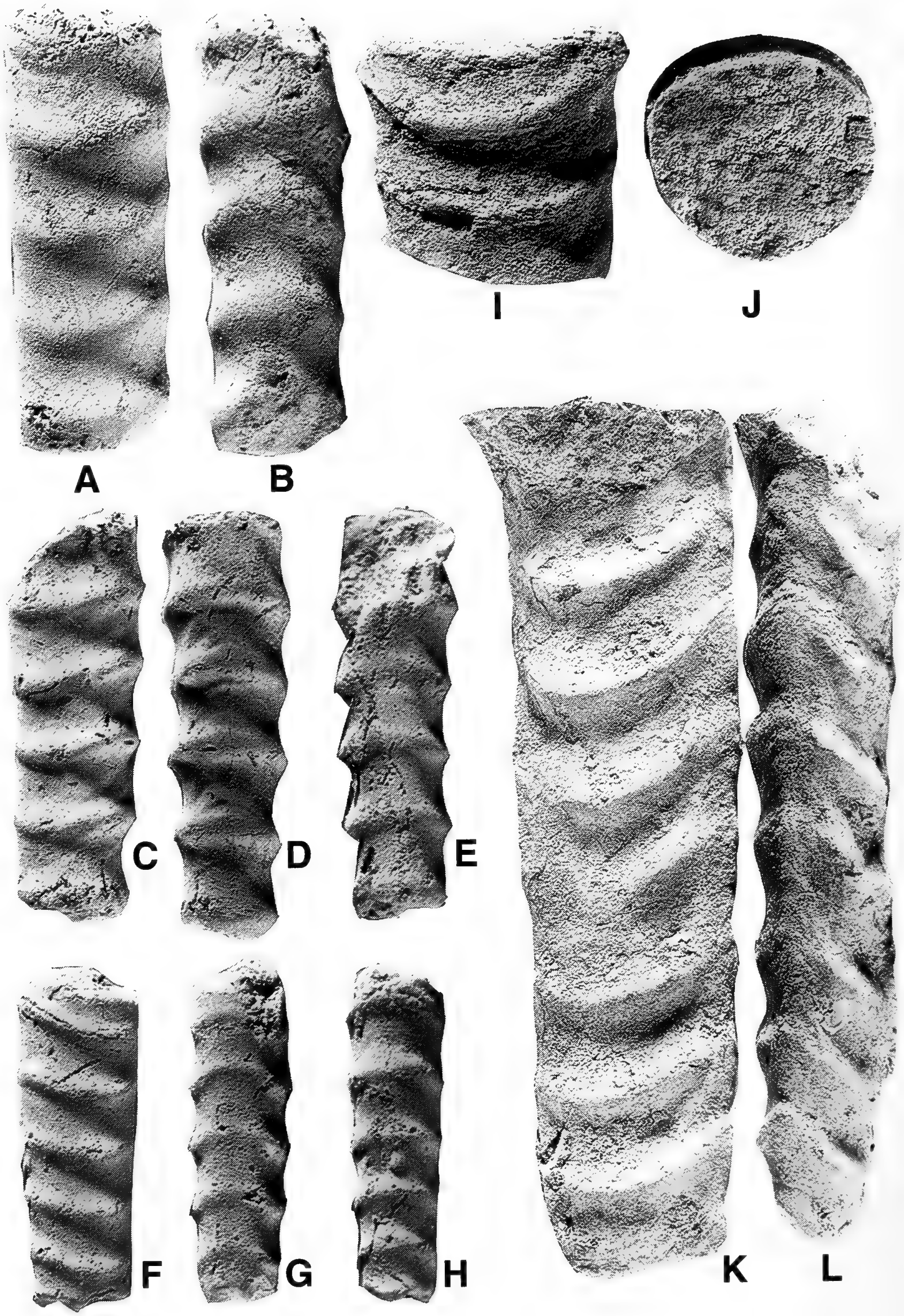
We suspect that the material described as *B. leopoliensis* by Kennedy in Kennedy *et al.* (1986, pl. 2 (figs 1–2, 11–12), pl. 13 (figs 22–24)), does not belong to that species but rather to *B. alavensis*. Ornament in *B. leopoliensis* normally consists of crescentic ribs on the flanks that project over the venter, often with intercalatories. Some specimens, however, lack the lateral ribs and are completely smooth. None of the Polish examples of *B. leopoliensis*, as figured by Nowak (1908, pl. 14 (figs 1–11)) and material in Klinger's (SAM) collection, Figure 2G, however, have as strong ribbing as that of *B. alavensis*; nor have we seen any with strong dorsal ribbing. Even though most of our material and that of Santamaria Zabala is diagenetically deformed, some specimens show a virtually circular whorl section. That of *B. leopoliensis* is distinctly compressed. The age of *B. leopoliensis* is uncertain. Following Nowak (1908), the species was traditionally regarded as being of Maastrichtian age (see e.g. Kennedy 1986*a*, 1986*b*). However, according to Hancock & Kennedy (1993: 165), they found *B. leopoliensis* only in the Upper Campanian zone of *Nostoceras (N.) hyatti* in various sections in Poland. Klinger (Machalski 1996), however, found *B. leopoliensis* (Fig. 2G) associated with *Diplomoceras cylindraceum* at Piotrawin in Poland, which suggests that the stratigraphic range of *B. leopoliensis* may extend into the Maastrichtian, or, alternatively, that *D. cylindraceum* may already occur in the Upper Campanian.

The generally stronger ribbing, which in cases may be circumperipheral, and the more inflated whorl section are sufficient to distinguish *B. alavensis* from *B. leopoliensis*.

Baculites alonsoi Santamaria Zabala (1996: 13, pl. 3 (figs 3–6)) is more weakly ornamented than typical *B. alavensis* and ribbing is restricted to the dorsal part of the flanks. Morphologically it is intermediate between *B. leopoliensis* and *B. alavensis*.

The specimen described by Kennedy (1986*a*: 113, pl. 18 (figs 2–3)) as *Baculites* sp. 5 from the Upper Campanian of Courgeac (Charente) Acquitaine is probably *B. alavensis*. What is of interest, is that Kennedy compared the species to *Baculites columna* Morton (1834: 44, pl. 19 (fig. 8)) (Fig. 5A–H), the type species of the Maastrichtian genus *Trachybaculites* Cobban & Kennedy, 1995. That species, however, typically has straight, circumperipheral ribbing rather than crescentic as in *B. alavensis*. *Trachybaculites* has simplified sutures (see e.g. Cobban & Kennedy 1995, fig. 17.25–17.26). Unfortunately, none of our specimens shows the suture, so it is not possible to determine if *B. alavensis* could possibly be an early Upper Campanian representative of *Trachybaculites*.

Amongst the Indo-Pacific species, only *B. sulcatus* Baily, 1855, and juvenile *B. vanhoepeni* Venzo, 1936, have ornament similar to that of *B. alavensis*. Both species were recently reviewed by Klinger & Kennedy (1997). *Baculites*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vanhoepeni has closely spaced crescentic lateral ribs in the juvenile stage (see Klinger & Kennedy 1997, fig. 79m), but in the adult stage the ornament consists of very characteristic auricular, widely spaced ribs that are confined to the flanks (see e.g. Klinger & Kennedy 1997, fig. 93). Ornament in the Lower Campanian *B. sulcatus* is extremely variable, ranging from nearly smooth to strong, circumperipheral ribs. Some strongly ornamented forms of *B. sulcatus* (Klinger & Kennedy 1997, fig. 64e–g, m–l) are indistinguishable from *B. alavensis*, but in the majority of specimens ornament is more of the *B. capensis–B. vanhoepeni* type.

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Financial assistance to Klinger by the FRD (South Africa) is gratefully acknowledged. Prof. R. Marcinowski kindly invited Klinger to visit Poland in 1996, and I. Walaszcyck and M. Machalski showed him the section at Piotravin. Prof. E. Mancini (Alabama) provided the specimens of *Trachybaculites columna* for comparison. Samantha Black and Ingrid Klinger photographed the material.

Fig. 5. A–H. *Trachybaculites columna* (Morton, 1834). A–B. SAM-PCA112918. C–E. SAM-PCA112919. F–H. SAM-PCA112920. All from the Upper Maastrichtian Prairie Bluff Chalk at roadside at railway track, south side of Linden, Marengo County, Alabama. I–L. *Baculites alavensis* Santamaria Zabala, 1996. I–J. Unregistered. K–L. Ec1-107. Both from the Upper Campanian of Ecay.
A–H × 2; J–L × 1.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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HERBERT CHRISTIAN KLINGER
&
THOMAS KÜCHLER

BACULITES ALAVENSIS SANTAMARIA ZABALA, 1996 (CEPHALOPODA AMMONOIDEA) FROM THE UPPER CAMPANIAN OF NORTHERN SPAIN

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HERMIT CRABS OF THE GENUS *PAGURUS* FABRICIUS (CRUSTACEA, DECAPODA, PAGURIDAE) FROM SOUTH-EASTERN SOUTH AFRICA

By

PATSY A. MCLAUGHLIN
&
JACQUES FOREST

Cape Town Kaapstad

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(With 7 figures)

[*MS accepted 22 April 1998*]

ABSTRACT

Specimens of the hermit crab genus *Pagurus*, primarily from the *Meiring Naude* cruises of 1982–1986, have prompted a review of south-eastern South African species assigned to the genus. *Pagurus barnardi* Forest has been re-examined, based on the type material, i.e., Barnard's '*Incertae sedis*'. This species has proved to be synonymous with *Pagurus liochele* (Barnard). The presence of *Pagurus cuanensis* Bell in the Western Indian Ocean has been verified and is formally acknowledged as the senior subjective synonym of *Pagurus placens* (Stebbing).

Pagurus spinulentus as interpreted initially by Stebbing and later by Barnard, not *Pagurus spinulentus* (Henderson), has been found to be conspecific with *Pagurus prideaux* Leach; however, Henderson's *P. spinulentus* has proved to bear considerable similarities with *P. cavicarpus* (Paul'son) reported here for the first time west of the Red Sea. The range of *Pagurus liochele* is extended to off Whale Rock, Transkei. A new species resembling the West African species, *Pagurus souriei* (Forest) and *Pagurus gordonae* (Forest), is described from KwaZulu-Natal. A key to the regional species of *Pagurus* is presented. Stebbing's *Pagurus deprofundis* has been redescribed from the holotype. This species has recently been transferred to the genus *Propagurus* McLaughlin & de Saint Laurent.

CONTENTS

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INTRODUCTION

Since the early accounts of South African species of *Pagurus* Fabricius, 1775 (reported as *Eupagurus* Brandt, 1851), by Stebbing (1910, 1920, 1924) and Odhner (1923), there have been elements of uncertainty about the true identities of the local species of the genus, particularly those occurring in the littoral and deeper waters off the south-eastern coast. For example, Barnard (1950) reported the occurrence of eight species of *Pagurus* (as *Eupagurus*) and one '*Incertae sedis*' in South African waters, of which four were present off the southern Indian Ocean coast. Although Barnard concurred with Odhner (1923) that Balss' (1912) *Pagurus pollicaris* var. *alcocki* (Balss, 1911) deserved full specific rank, he omitted Odhner's (1923) *Pagurus variabilis* (= *P. mbizi* (Forest, 1955); not *P. variabilis* (A. Milne Edwards & Bouvier, 1892)), *P. triangularis* (Chevreux & Bouvier, 1892), and *P. cuanensis* Bell, 1845 (as *Eupagurus cuanensis* Thompson), from his key to the South African species for 'lack of comparative material and literature'. Barnard (1950) was 'inclined to suspect' that Odhner's (1923) *P. cuanensis* really represented *Pagurus placens* (Stebbing, 1924).

Forest (1955) addressed some of the questionable identifications and/or descriptions of Stebbing (1920, 1924), Odhner (1923), and Barnard (1950) in his monograph of the pagurids from the west coast of Africa. Specifically, Forest (1955) compared specimens of the South African taxon attributed first by Stebbing (1910) to *Eupagurus tristanensis* Henderson, 1888, and subsequently by Stebbing (1920) and Barnard (1950) to *Pagurus spinulentus* (Henderson, 1888), with the holotype of the latter, and concluded that Stebbing's (1920) and Barnard's (1950) taxon was not conspecific with either of Henderson's taxa. However, Forest (1955: 106) noted the marked resemblance between the South African taxon and *Pagurus prideaux* Leach, 1815 (as *Eupagurus prideauxi*), and emphasized the need for detailed examinations of more specimens from south-eastern South Africa.

Forest (1955) also noted that *Eupagurus zebra* Henderson, 1893, reported from South Africa by Balss (1912), Stebbing (1920) and Barnard (1950), probably represented a species of *Pylopaguropsis* Alcock, 1905. Henderson's (1893) taxon was formally transferred to *Pylopaguropsis* by McLaughlin & Haig (1989); however, these authors were unable to locate Stebbing's (1920) specimens. Based on Stebbing's reference to '. . . slenderness of the second and third peraeopods . . .', McLaughlin & Haig (1989) considered Stebbing's (1920) taxon '*incertae sedis*'. The presence of *Pylopaguropsis zebra* in south-eastern Africa has since been confirmed (e.g., McLaughlin 1997*b* (printer's spelling error as *Pylopagurosis*)).

Both of Stebbing's (1924) species, *Pagurus placens* and *P. deprofundis* (Stebbing), were based on single specimens; however, two additional specimens, presumably of *P. placens*, collected later near the type locality, permitted Barnard (1950) to redescribe the species, and to make one of those specimens available for Forest's (1955) subsequent examination. Forest (1955: 106) found considerable agreement between this specimen and *Pagurus cuanensis* (reported as *Eupagurus cuanensis* Thompson), but indicated that if certain differences in ornamentation of the chelipeds were found in additional South African specimens, *Pagurus placens* might be considered a geographical variety of *Pagurus cuanensis*. None the less, Forest (1955: 114) included Stebbing's taxon in his synonymy of *P. cuanensis*. Forest also pointed out the need for a more thorough description of *P. deprofundis*, still represented only by the holotype. Although Forest (1966) did not include *P. placens* in his synonymy of *P. cuanensis*, he reported that *P. cuanensis* had a very extended distribution from Norway to South Africa 'oú il a été signalé sous le nom d'*Eupagurus placens* Stebbing' (Forest 1955: 116). Kensley (1981) listed the South African distribution of *P. cuanensis* as False Bay to Port Elizabeth, and that of *P. placens* as False Bay to Knysna. Ingle (1993), without comment, cited *Pagurus placens* as a synonym of *P. cuanensis*, and was followed in this action by Sandberg & McLaughlin (1998), although none of these authors examined Stebbing's (1924) species.

The type specimens of Barnard's (1947) *Pylopagurus liochele* were re-examined by McLaughlin (1988). The absence of paired first pleopods in the female of this species caused McLaughlin (1998) to reassign Barnard's (1947) species to *Pagurus*. Forest (1966), in discussing the similarities of a group of closely allied western African *Pagurus* species, proposed the name *Pagurus barnardi* for Barnard's (1950) '*Incertae sedis*' specimens. Therefore, depending upon the accuracy of Forest's (1955), Ingle's (1993) and Sandberg & McLaughlin's (1998) synonymy of *P. placens* with *P. cuanensis*, the number of *Pagurus* species occurring in south-eastern South Africa could be expected to number five or six, despite the questionable identity of Stebbing's (1920) and Barnard's (1950) *P. spinulentus*.

Kensley (1981) defined southern Africa as the area extending from Moçâmedes on the west coast to Mozambique on the east coast. However, for the pagurid fauna, at least, the northern limit along the Atlantic coast lies between Lüderitz and Walvis Bay, which corresponds with Barnard's (1974) geographical limit for the Mollusca. With the exclusion of Angola, Odhner's (1923) species, other than *P. cuanensis*, have not been considered in this report, nor has *Pagurus dartevellei* (Forest, 1958*b*), collected by Kensley & Penrith (1973) from Moçâmedes.

We have recently had the opportunity to examine a small, but very important, collection of pagurids housed at the University of Transkei, Umtata, which has provided the data necessary to address the true identities of the *Pagurus* species of south-eastern South Africa. This collection contains specimens of all but one of the species of *Pagurus* discussed herein, including *P. cuanensis*, *P. liochele*, and *P. spinulentus* sensu Stebbing (1920) and Barnard (1950). A species closely allied to *P. souriei* (Forest, 1952) and *P. gordonae* (Forest, 1956) is described as *Pagurus emmersoni* sp. nov. *Pagurus cavicarpus* (Paul'son, 1875) is represented in samples collected off KwaZulu–Natal. One immature male specimen can, for the present, only be described as *Pagurus* sp.; however, it does not appear to be conspecific with any other known regional species. Until very recently (McLaughlin & de Saint Laurent 1998), *Pagurus deprofundis* was known only from its holotype, which is redescribed herein. These authors reassigned it to their newly established genus *Propagurus* McLaughlin & de Saint Laurent, 1998. Seven *Pagurus* species would have been documented for south-eastern South Africa had *P. barnardi* not proved to be synonymous with *P. liochele*. Diagnoses, redescriptions, or full descriptions and illustrations are provided for all of these taxa, together with a key to the regional species of *Pagurus*.

MATERIALS AND METHODS

Collections and museums. Much of the University of Transkei material used in this study represents part of the pagurid fauna collected during cruises of the R.V. *Meiring Naude*, 1982–1986. It has been supplemented by Stebbing's type specimen of *Pagurus deprofundis* from The Natural History Museum, London (NHM), three of Barnard's (1950) '*Incertae sedis*' specimens (= syntypes of *P. barnardi*) from the South African Museum, Cape Town (SAM), and specimens from the University of Cape Town Ecological Survey, now in the collections of the South African Museum and Muséum national d'Histoire naturelle, Paris (MNHN). Specimens of *Pagurus spinulentus* sensu Stebbing and Barnard from the South African Museum and the Muséum national d'Histoire naturelle have been compared with the type specimens of *Pagurus tristanensis* and *P. spinulentus* from The Natural History Museum, and with specimens of *Pagurus prideaux* from the Zoological Museum Amsterdam (ZMA), and one from the authors' personal reference collection (PMcL).

Thorough searches of the collections of both The Natural History Museum and the South African Museum failed to locate the type specimen of *Pagurus placens*; however, the two 'typical' specimens from the South African Museum that were compared by Barnard (1950) and Forest (1955) have been re-examined. Odhner's *P. cuanensis* has been borrowed from the Swedish Museum of Natural History (SMNH). The identity of specimens resembling *Pagurus cavicarpus* (Paul'son, 1875) has been confirmed by comparison with a specimen of this species from the Red Sea borrowed from the National Natuurhistorisch Museum, Leiden, The Netherlands (RMNH), and with NHM specimens from the *John Murray Expedition* identified by Thompson (1943) as *Pagurus carpoforaminatus* (Alcock, 1905), a junior synonym of the former according to Lewinsohn (1969). Comparative material of *P. cuanensis* has come from the Muséum national d'Histoire naturelle and PMcL's reference collection. All borrowed specimens have been returned to their museums of origin; the type material of *Pagurus emmersoni* sp. nov. has been deposited in the South African Museum and Muséum national d'Histoire naturelle. Representative specimens of the other species from the *Meiring Naude* cruises have been deposited in the collections of the Muséum national d'Histoire naturelle, National Museum of Natural History, Smithsonian Institution (USNM), National Natuurhistorisch Museum, South African Museum, The Natural History Museum, and PMcL's personal collection.

Illustrations. Drawings were made using a Wild M–5 dissection microscope with *camera lucida* attachment.

Measurements. One measurement, shield length, given in parentheses, and measured from the tip of the rostrum, or midpoint of the rounded rostral lobe, to the midpoint of the posterior margin of the shield, provides an indication of specimen size.

Terminology. Terminology used in the diagnoses and descriptions generally follows that of McLaughlin (1974), with the exception of the fourth pereopod (after McLaughlin 1997*a*) and telson (after McLaughlin & Forest 1997).

DESCRIPTIONS

Family **Paguridae** Latreille, 1802

Genus *Pagurus* Fabricius, 1775

Cancer Linnaeus, 1758: 625 (in part).
Pagurus Fabricius, 1775: 410 (in part).
Eupagurus Brandt, 1851: 105 (in part).
Bernhardus Dana, 1851: 267 (in part).
non *Pagurus* Berthold, 1827: 255 (*nomen nudum*).
non *Pagurus* Fabricius sensu Dana, 1851: 267 (= *Dardanus* Paul'son, 1875).

Type species. *Cancer bernhardus* Linnaeus, 1758 (as defined by lectotype selection by Forest & Holthuis 1955: 312; specimen figured by Swammerdam 1737, pl. 2 (fig. 1)). Gender masculine.

Diagnosis

Eleven pairs of biserial gills (cf. McLaughlin & de Saint Laurent 1998). Rostrum variable. Ocular acicles simple, bifid or multifid. Ischium of third maxilliped with crista dentata well developed and one or more accessory teeth. Sternite of third maxillipeds unarmed or armed. Chelipeds generally very unequal, right usually appreciably larger. Dactyls of ambulatory legs commonly with spinose ventral margins. Sternite of third pereopods with variably shaped anterior lobe. Fourth pereopods usually semichelate, with one to several rows of scales in propodal rasp. Fifth pereopods usually chelate, occasionally semichelate. Sternite of fifth pereopods variable.

Coxae of fifth pereopods generally symmetrical in both sexes. Males with paired gonopores; no well-developed sexual tubes; no paired pleopods, usually with 3 or 4 unpaired left pleopods, rarely without unpaired pleopods. Females usually with paired gonopores; no paired pleopods, usually 4 unpaired left pleopods, rarely only 3. Abdomen usually spirally twisted, rarely straight. Uropods most commonly asymmetrical, occasionally symmetrical. Telson typically with mediolateral indentation, indistinctly delineating anterior and posterior regions; posterior region frequently separated into distinct lobes by well-developed median cleft, with terminal margins rounded, straight or oblique.

Pagurus cavicarpus (Paul'son, 1875)

Fig. 1A–C, E–I, K

Eupagurus cavicarpus Paul'son, 1875: 91, pl. 12 (fig. 3–3a); 1961: 97, pl. 12 (fig. 3–3a). Nobili, 1906: 123. Riddell, 1911: 261. Ramadan, 1936: 4 (list).

Eupagurus carpoforaminatus var. *nephromma* Alcock, 1905: 131, ?not pl. 11 (fig. 4–4a) (see remarks).

Eupagurus carpoforaminatus: Thompson, 1943: 425 (in part) (see remarks).
Pagurus cavicarpus: Gordan, 1956: 327 (lit). Lewinsohn, 1969: 61 (in part), fig. 10.
non *Eupagurus carpoforaminatus* var. *nephromma*: Terao, 1913: 370 (= *Pagurus megalops* (Stimpson, 1858)).

Material

Pagurus cavicarpus. RMNH, 1 ♂ (4.7 mm); Red Sea. Aqaba, Jordan, collected by H. Schumacher. USNM 276077, 1 ♂, 1 ♀ (3.0, 2.2 mm); vicinity of Kosi River mouth, *Meiring Naude* Stn ZA2, 26°56'S 32°54.7'E, 50 m, 6 June 1987. RMNH, 1 ♂, 1 ovigerous ♀ (2.4, 2.9 mm); vicinity of Kosi River mouth, *Meiring Naude* Stn ZA2, 26°56'S 32°54.7'E, 50 m, 6 June 1987. PMcL, 1 ♂ (3.2 mm); off Kosi River mouth, *Meiring Naude* Stn ZA3, 26°54.8'S 32°54.6'E, 6 June 1987. NHM 1997.726–727, 1 ♂, 1 ♀ (3.3, 2.5 mm); off Kosi River mouth, *Meiring Naude* Stn ZA5, 26°54.7'S 32°55'E, 45 m, 6 June 1987. SAM–A43223, 2 ♂, 1 ♀ (2.4–3.7 mm); off Kosi River mouth, *Meiring Naude* Stn ZA23, 26°54.1'S 32°54.8'E, 50 m, 8 June 1987. PMcL, 1 ovigerous ♀ (3.2 mm); off Boteler Point, *Meiring Naude* Stn ZB3, 27°12'S 32°54.2'E, 50 m, 6 June 1987. MNHN Pg5518, 1 ♂ (2.9 mm); *Meiring Naude* Stn ZG1, 27°26.2'S 32°44.2'E, 55–60 m, 3 June 1987. SAM–A43406, 1 ♂ (4.7 mm), off KwaZulu-Natal, Stn NAD 87W, 29°10'S 31°37'E, 43 m, 29 July 1964. SAM–A43404, 1 ♂ (6.6 mm), off KwaZulu-Natal, Stn NAD 8N, 29°53.6'S 31°04.6'E, 38 m, 16 May 1958. SAM–A43405, 2 ♂ (3.3, 3.3 mm), off KwaZulu-Natal, Stn NA 18V, 29°58'S 31°02'E, 49 m, 12 August 1958.

Pagurus carpoforaminatus sensu Thompson, 1943. NHM 1952.6.17.72–78, 3 ♂, 2 ovigerous ♀ (3.2–4.1 mm); South Arabian coast, John Murray Expedition, H.E.M.S. *Mabahiss* Stn 45, 18°03'300N 57°02'300E, 38 m, 29 October 1933. NHM 1952.6.17.72–78, 1 ♂ (4.4 mm); Stn 53, 19°22'360N 57°53'000E, 13.5 m, 2 November 1933.

Diagnosis

Shield slightly broader than long. Rostrum usually broadly rounded, not produced beyond level of lateral projections. Ocular peduncles broadest at bases of corneas; approximately equal to length of antennal peduncles, but reaching only to approximately mid-length of antennular peduncles; corneas somewhat dilated; ocular acicles triangular. Antennal peduncles with anterolateral distal angles of second segments extending to distal half of fourth peduncular segment, but not reaching distal margin; acicle reaching to or beyond mid-length of ultimate peduncular segment, but usually not reaching distal margins of corneas.

Chelipeds with numerous distinctly plumose setae, but not masking armature and not appreciably more dense on ventral surfaces and margins of meri. Right cheliped moderately slender; dactyl with row of spines on dorsomesial margin; palm with row of teardrop-shaped spines on dorsomesial margin, medianly elevated dorsal surface similarly armed and set off by longitudinal grooves mesially and laterally; carpus with row of spines on dorsomesial margin, dorsal surface with several rows of spines, ventral surface usually, but not always, with distinct foramen centrally near distal margin. Left cheliped appreciably shorter than right; palm with single or double row of spines on dorsolateral

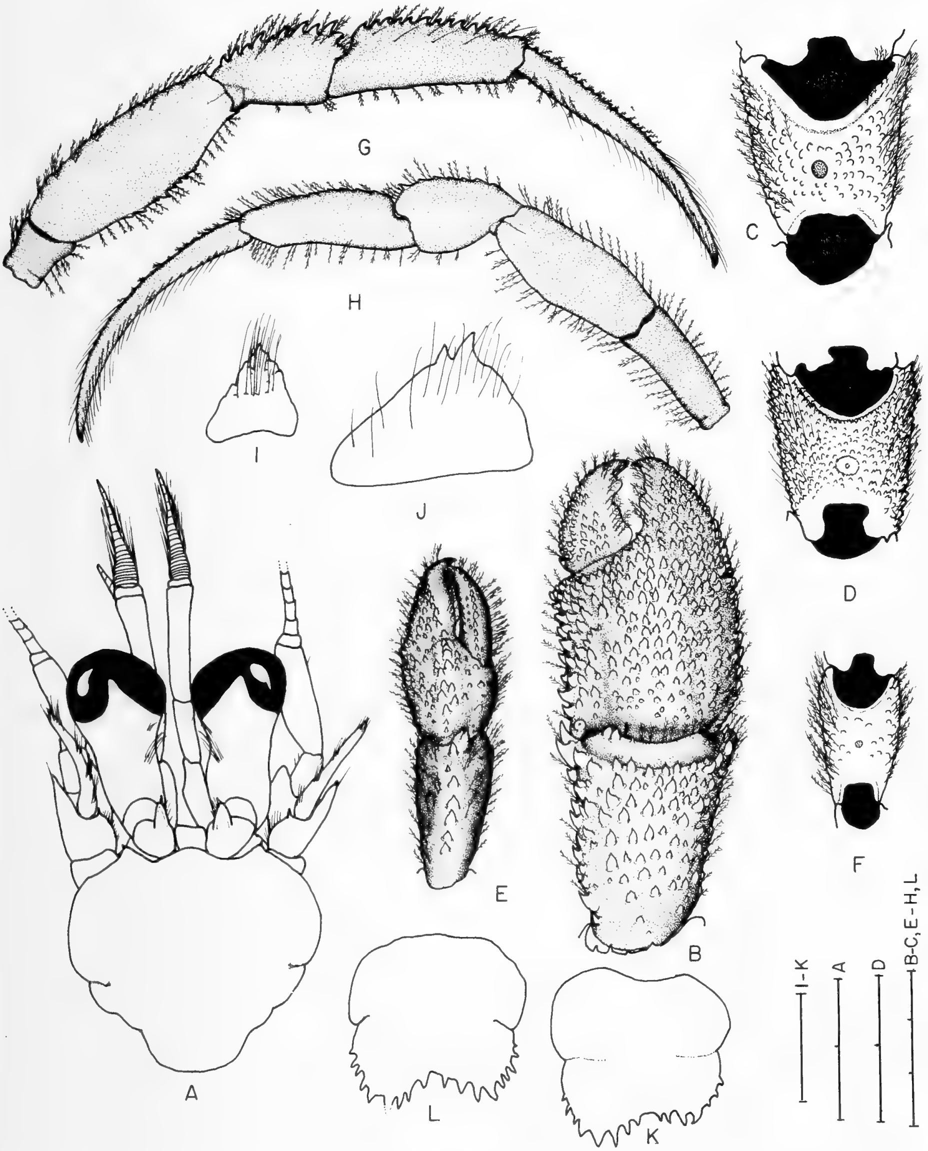

Fig. 1. A–C, E–I, K. *Pagurus cavicarpus* (Paul'son, 1875), ♂ (3.2 mm) from *Meiring Naude* Stn Z3 (PMcL). D, J, L. *Pagurus spinulentus* (Henderson, 1888), holotype ♀ (8.7 mm) from *Challenger* Stn Tables Island (NHM 88.33). A. Shield and cephalic appendages. B. Chela and carpus of right cheliped (dorsal view). C–D. Carpus of right cheliped (ventral view.). E. Chela and carpus of left cheliped (dorsal view). F. Carpus of left cheliped (ventral view). G. Right second pereopod (lateral view). H. Left third pereopod (lateral view). I–J. Anterior lobe of sternite of third pereopods. K–L. Telson. Scales I–K, 1.0 mm; A, 2.0 mm; B–C, E–H, L, 3.0 mm; D, 10 mm.

margin and additional double or triple row on elevated dorsal midline; carpus with row of strong spines dorsally, ventral surface usually, but not always, with distinct foramen or circular depression. Ambulatory legs with dactyls appreciably longer than propodi; dorsal margins of propodi and carpi each with row of spines; meri of second pair with spinose dorsal and ventral margins.

Males with 4 unpaired uniramous or unequally biramous left pleopods. Telson with faint, partial transverse suture indicating division into anterior and posterior portions; terminal margins of posterior lobes each with row of strong corneous-tipped spines extending on to lateral margins.

Redescription

Shield (Fig. 1A) usually slightly broader than long; anterior margin concave between rostral lobe and lateral projections; lateral margins each distinctly notched to produce small raised lobe; posterior margin roundly truncate. Rostrum obsolete or broadly rounded, not produced beyond level of strongly developed lateral projections. Lateral projections triangular, with small marginal or submarginal spine.

Ocular peduncles 0.80 to as long as shield; moderately slender basally, but broad at bases of slightly to considerably dilated corneas, 1 or 2 distinct tufts of setae dorsomesially. Ocular acicles triangular, moderately slender, terminating subacutely and with prominent submarginal spine; separated basally by 0.50–0.75 basal width of one acicle.

Antennular peduncles over-reaching distal margins of corneas by 0.50–0.95 length of ultimate segment. Ultimate and penultimate segments glabrous or with only 1 or 2 short setae. Basal segment with prominently produced distolateral subacute lobe; small spine on distolateral margin of statocyst lobe.

Antennal peduncles over-reaching distal margins of corneas very slightly to nearly 0.18 length of ultimate segment. Fifth and fourth segments each with few scattered setae. Third segment with small spine on ventrodistal margin, at least partially obscured by long setae. Second segment with dorsolateral distal angle produced, reaching mid-length of fourth segment, terminating with simple or very small bifid spine, mesial margin unarmed or with 2 or 3 spinules; dorsomesial distal angle with strong spine. First segment with dorsolateral distal margin unarmed or with small spinule, ventrolateral margin produced into very prominent spine. Antennal acicle reaching approximately to mid-length of ultimate peduncular segment; with terminal spine partially obscured by tuft of setae; mesial surface with few tufts of setae.

Ischium of third maxilliped with 1 accessory tooth on moderately short crista dentata. Sternite of third maxillipeds with spine on either side of midline.

Right cheliped appreciably larger than left, chela often more slender than in illustrated male (Fig. 1B); dactyl overlapped by fixed finger, but separated by slight hiatus; cutting edges of both with calcareous teeth. Dactyl slightly shorter, equal to, or slightly longer than palm; dorsal surface flattened, with covering of rather closely-spaced, low, somewhat teardrop-shaped spines at least from midline mesially and including dorsomesial margin, sometimes extending to tip; dorsomesial margin also with numerous short plumose setae; mesial face not distinctly delimited; ventral surface with few low tubercles and 1 or 2 rows of short plumose setae. Palm approximately equaling length of carpus; dorsomesial margin slightly elevated, with 2 or 3 rows of regular and teardrop-shaped spines, extending somewhat on to mesial face, medially elevated dorsal surface armed with numerous teardrop-shaped spines and set off by distinct longitudinal groove mesially and fainter longitudinal groove laterally; dorsolateral margin not delimited, but rounded lateral surface armed with irregular rows of short, thick, tuberculate or teardrop-shaped spines extending nearly to tip of fixed finger; dorsal surface of fixed finger covered, but not densely, with tuberculate spines; ventral surface of fixed finger with short tufts of plumose setae. Carpus (Fig. 1B–C) approximately same length as merus; dorsodistal margin with few to several small to moderately strong spines or spinose tubercles; dorsomesial margin with almost double row of prominent spines, frequently separated by generally smooth longitudinal strip from remainder of spinose dorsal surface; dorsolateral margin not delimited, lateral face with similar tuberculate or teardrop-shaped spines and tufts of plumose setae; mesial face with few teardrop-shaped spines and scattered short plumose setae; ventral surface with flattened but still somewhat teardrop-shaped tubercles and usually, but not always, with distinct median foramen; ventromesial and ventrolateral margins spinose and setose. Merus with several small spines on dorsodistal margin, dorsal margin with short transverse spinulose ridges and plumose setae; lateral face with some transverse spinulose ridges and plumose setae, mesial face with plumose setae; ventromesial margin with nearly double row of small scale-like blunt or subacute spines, ventral surface with few similar spines, sometimes partially obscured by plumose setae; ventrolateral margin with scale-like blunt spines becoming more acute distally. Ischium with row of very small subacute spines or tubercles on ventromesial margin; ventrolateral distal angle with small but prominent acute spine.

Left cheliped (Fig. 1E) reaching only slightly beyond mid-length of palm of right cheliped; dactyl strongly overlapped by fixed finger. Dorsomesial margin of dactyl with tufts of plumose setae, dorsal surface with row of spinules reaching nearly to tip; cutting edge with row of corneous teeth concealed by tufts of plumose setae. Palm half or slightly less than half length of carpus; dorsal surface with broad strongly elevated median ridge not extending on to fixed finger, dorsal midline with double to triple row of acute or subacute, teardrop-shaped spines proximally, becoming single row distally and extending on to fixed finger but not reaching tip; dorsal surfaces laterad and mesiad of raised median ridge each with small spines, much more numerous laterally, dorsolateral margin with generally double row of regular or teardrop-shaped small spines, not extending to tip of fixed finger and accompanied by tufts of plumose setae; dorsal surface of fixed finger somewhat flattened and with numerous teardrop-shaped small spines, cutting edge with row of small calcareous teeth, generally concealed by tufts of plumose setae; ventral surfaces of dactyl, fixed finger and palm with tufts of plumose setae. Carpus (Fig. 1E–F) slightly shorter than merus, subtriangular; dorsal surface with row of acute spines laterally; lateral and mesial surfaces with low protuberances and tufts of plumose setae; ventral surface with numerous flattened, scale-like tubercles and usually, but not always with, median foramen or circular depression. Merus with 2 or 3 spines on dorsodistal margin, dorsal surface with few short transverse ridges and tufts of plumose setae; mesial face with scattered plumose setae, ventromesial margin crenulate or with row of subacute spines; ventral surface with numerous blunt tuberculate spines, partially obscured by tufts of plumose setae; ventrolateral margin with row of low tuberculate spines proximally, becoming stronger and more acute distally, lateral face with low flattened scale-like tubercles ventrally, distolateral margin with row of very small spines. Ischium with row of small spinules or spinulose tubercles on ventromesial margin; ventrolateral distal angle with acute spine.

Second and third pereopods (Fig. 1G–H) of right side slightly longer than left, but neither over-reaching tip of right cheliped. Dactyls slender, curved, 1.50–2.0 length of propodi; dorsal surfaces spinulose, spinules of second pereopods stronger and extending to distal third of segment, all dactyls with short plumose setae proximally and long simple setae distally; lateral faces each with row of long stiff simple setae near ventral margin proximally and curving upward to mid-width at base of claw; mesial faces each with faint longitudinal sulcus proximally, row of tufts of stiff simple setae ventrally and extending on to ventral margin in distal third or fourth; ventral margins lacking row of corneous spinules. Propodi 1.25–1.35 length of carpi; dorsal margins of second each with row of strong spines and frequently additional smaller spines on lateral face dorsally accompanied by tufts of short plumose setae; mesial faces with few spinules dorsally; ventral margins of second each with row of spinules; propodi of third each with row of smaller spines or spinulose protuberances and tufts of short plumose setae, mesial and lateral faces unarmed, ventral surfaces with tufts of plumose setae and occasionally 1 or 2 spinules distally. Carpi each with row of acute spines on dorsal surface, smaller on third, accompanied by tufts of plumose setae; ventral surfaces with few tufts of plumose setae. Meri each with short transverse ridges and tufts of plumose setae dorsally; ventrolateral and ventromesial margins of second pereopods each with row of small spines and 1 acute spine at ventrolateral distal angle; ventral margins of third pereopods unarmed or with minute protuberances and tufts of plumose setae. Fourth pereopods semichelate; segments all with numerous tufts of long plumose setae; propodal rasps each consisting of 3 or 4 rows of quite small corneous scales. Fifth pereopods semichelate, with dactyl considerably overreaching produced area of propodus when extended. Sternite of third pereopods with triangular anterior lobe (Fig. 1I) slightly skewed to left, surface with several low protuberances and usually terminal spine, partially obscured by long setae.

Males with paired gonopores, each partially masked by tuft of long stiff setae; 4 uniramous, or markedly asymmetrical biramous unpaired left pleopods. Females with 4 unpaired pleopods, first three biramous, last uniramous. Telson (Fig. 1K) with faint, partial transverse suture indicating division into posterior and anterior portions; posterior lobes asymmetrical, median cleft obsolete or absent, lobes separated simply by unarmed median space; left posterior lobe with row of strong corneous or corneous-tipped spines extending on to lateral margin to at least mid-length; right posterior lobe similarly armed but spines tending to be smaller and often not extending as far on lateral margin.

Colour

In preservative: ivory white (Alcock 1905).

Habitat

Collected at depths from 38 to 1 507 m.

Distribution

Northern KwaZulu–Natal, South Africa; Gulf of Aqaba, Red Sea; South Arabian coast, and Indian Ocean between Maldives and Cape Comorin.

Remarks

In his description of *P. cavicarpus*, Paul'son (1875, 1961) reported that the chelipeds resembled those of '*Eu. Monticulosus*', a name that neither Dr Rafael Lemaitre of the National Museum of Natural History (pers. comm.) nor we have been able to apply to any known taxon. That Paul'son simply misspelled *Pagurus meticulosus* Roux, 1828–30 (= *Pagurus excavatus* (Herbst, 1791)), is certainly a possibility, although the chelipeds of the two taxa would not be considered similar by today's standards. The description that Paul'son gave of *P. cavicarpus* was relatively thorough, including spinose chelipeds and the notation of a foramen on the ventral surface of each carpus of the chelipeds; the Red Sea was cited as the type locality. Although his specimens have not been available for re-examination, it has been possible to compare the *Meiring Naude* specimens with a specimen of *P. cavicarpus* subsequently collected in the Red Sea. This specimen agrees quite well with those from South Africa, although the spines of the chelae of the former are generally more slender and acute, and the setation of chelipeds and ambulatory legs is denser.

Alcock (1905) described *Pagurus carpoforaminatus* from the west and east coasts of India and Sri Lanka (as Ceylon), together with a deep-water variety, *P. carpoforaminatus* var. *nephromma*, from an *Investigator* station between the Maldives and Cape Comorin. Both taxa were distinguished, in part, by the presence of a foramen on the ventral surface of the carpus of the right cheliped, and frequently also of the left. These foramina were specified as being a 'pin hole' in *P. carpoforaminatus* and larger in *P. c.* var. *nephromma*. *Pagurus carpoforaminatus* was described as having chelipeds similar to those of *P. prideaux*, and the 'nude' ambulatory legs considerably longer than the right cheliped. In contrast, *P. carpoforaminatus* var. *nephromma*, according to Alcock (1905), had the dorsal surface of the chela covered with coarse spines; the ambulatory legs were only slightly longer than the right cheliped. Alcock reportedly figured *P. c.* var. *nephromma*; however, his figures (Alcock 1905, pl. 11 (fig. 4, 4a)) certainly appear to be of *P. carpoforaminatus*, not of *P. c.* var. *nephromma*.

Terao (1913) reported on two specimens of *Pagurus megalops* (as *Eupagurus*) that had a ventral carpal pin-hole foramen on each cheliped. He expressed the opinion that these specimens, although referable to *P.megalops*, also agreed with Alcock's (1905) description of *Pagurus carpoforaminatus* var. *nephromma* (as *Eupagurus*). Terao placed Alcock's variety in synonymy with *P. megalops* and stated that if his assumption was correct, Alcock's nominal variety (*Pagurus carpoforaminatus*) should be called *Eupagurus megalops* var. *carpoforaminatus*. Terao appears to have been correct in believing that Stimpson (1858) overlooked the foramen when he described *P. megalops*. The male specimen

(5.8 mm) from Minahe, Wahayama, Japan, that we have personally examined does have a carpal foramen on the right cheliped, although none is present on the left. However, *P. megalops* unquestionably is not the senior synonym of *P. carpoforaminatus nephromma*. The presence of a carpal foramen is not mentioned by Miyake (1978) in his diagnosis of *P. megalops*, although he did cite Terao's (1913) specimens from Nagasaki in his synonymy.

Lewinsohn (1969) included in the synonymy of *P. cavicarpus*, *Pagurus carpoforaminatus* (Alcock, 1905), together with the reports of the latter species by Southwell (1906, 1910) and Thompson (1943), stating the two species were undoubtedly identical. From his discussion, it is clear that Lewinsohn (1969) compared the descriptions of Paul'son (1875) and Alcock (1905). However, the distinct differences in these descriptions appear to have been overshadowed in his mind by the presence of a foramen on the ventral surface of the carpus of each cheliped in both taxa. He made no comment about its presence in *P. c. nephromma*. Lewinsohn (1969) certainly was correct in his surmise that Alcock (1905) was not aware of Paul'son's species, as the latter author's work was not translated from Russian until 1961. Had it been, Alcock (1905) very well might have recognized the similarities between his *P. carpoforaminatus* var. *nephromma* and *P. cavicarpus*, which include spinose chelipeds and setose ambulatory legs.

Neither Alcock's (1905) type specimens nor Southwell's specimens have been re-examined; however, we have been able to examine all of the specimens collected during the John Murray Expedition that Thompson (1943) reported. Specimens agreeing with Alcock's (1905) description of *P. carpoforaminatus* were exclusively present at station 72 (Gulf of Oman), whereas five of the specimens from station 45 and the single specimen from station 53 agree with Alcock's description of *P. carpoforaminatus* var. *nephromma*. The two taxa are not conspecific, but it is the specimens from station 72 that correspond to Alcock's (1905, pl. 11 (fig. 4–4a)) figures. As indicated earlier, it appears that Alcock incorrectly attributed these figures to *P. carpoforaminatus* var. *nephromma*. Comparison of Thompson's (1943) specimens with those from the Red Sea and eastern South Africa show conclusively that it is *P. carpoforaminatus nephromma* that is synonymous with *P. cavicarpus*. *Pagurus carpoforaminatus* is a distinct species, easily differentiated by the characters described by Alcock (1905).

Southwell (1906) reported *P. carpoforaminatus* from Sri Lanka (as Ceylon) but, as he gave no information on his specimens, it is impossible to determine if his material was actually *P. carpoforaminatus*. Sarojini & Nagabhushanam (1972) reported this species from Lawson's Bay, Waltair, but their diagnosis and description are simply paraphrased from Alcock's (1905) original description. Their illustrations (Sarojini & Nagabhushanam 1972, text-fig. 5 (4a–c)) are too diagrammatic to permit evaluation; however, the collection locality of their specimens suggests that they probably accurately reported *P. carpoforaminatus*.

Stebbing (1920) and Barnard (1950) both reported *Pagurus spinulentus* from South African waters; however, Forest (1955) compared one of the South African specimens with the type of *P. spinulentus* and found them to represent distinct species. In the course of this study, we re-examined the type of *P. spinulentus* and found it to be extremely close to *P. cavicarpus* in general configuration, including the suggestion of a carpal foramen or indication of one (Fig. 1C–D, F), and similarities in the structure of the anterior lobe of the sternite of the third pereopod (cf. Fig. 1I, J) and telson (cf. Fig. 1K, L). Henderson's (1888) species is known only from the holotype collected off Tablas Island in the Philippines, and his figure (Henderson 1888, pl. 7 (fig. 3)) does not adequately depict the strength of the armature of the chelipeds. Henderson made no mention of the suggestion of a moderately large median foramen on the ventral surface of the carpus of the right cheliped, which, as illustrated, is quite similar to that seen in *P. cavicarpus*; however, in *P. spinulentus* this area is not depressed, nor is an actual opening present. No foramen is present on the carpus of the left cheliped in Henderson's specimen. *Pagurus spinulentus* differs from *P. cavicarpus* in the following characters: (1) the dorsolateral distal angles of the second segments of the antennal peduncles reach to the distal margins of the fourth peduncular segments; (2) the mesial faces of the dactyl and palm of the right cheliped are clearly defined and strongly spinose; (3) the dorsal surface of the carpus of the left cheliped has a nearly double median row of spines and numerous accessory spines; (4) the ventrodistal margins of the meri of the chelipeds each carries a dense fringe of pinnate setae; (5) the setae of the chelipeds and ambulatory legs are a mixture of simple and pinnate setae.

Although most of the specimens identified as *P. spinulentus* by Stebbing and Barnard proved to be *P. prideaux*, among Barnard's identified material from off KwaZulu-Natal, we found four specimens attributable to *P. cavicarpus*.

Pagurus cuanensis Bell, 1845

Fig. 2A–L

Pagurus Bernhardus: Risso, 1816: 55; 1827: 37. Hope, 1851: 12. Non *Pagurus bernhardus* (Linnaeus, 1758).

Pagurus Cuanensis Thompson, 1844: 267 (*nomen nudum*).

Pagurus cuanensis Bell, 1845: 178, unnumbered fig. Kensley, 1981: 33 (distribution list). Ingle, 1985: 760, figs 1, 7, 17, 45, 56, 62; 1993: 129, figs 101–104 and synonymy. Sandberg & McLaughlin, 1998: 58, fig. 17.

Pagurus spinimanus Lucas, 1846: 29, pl. 3 (fig. 3). Forest, 1958*a*: 99.

Eupagurus spinimanus: Stimpson, 1858: 236. Forest, 1956: 364; 1958*a*: 99.

Eupagurus cuanensis: Stimpson, 1858: 237. Chevreux & Bouvier, 1892: 97, pl. 2 (figs 16–17). A. Milne-Edwards & Bouvier, 1900: 227, pl. 28 (figs 19–20). Selbie, 1921: 26, pl. 2 (figs 16–17). Odhner, 1923: 10, 25. Bouvier, 1940: 132, fig. 88. Forest, 1955: 114, text-fig. 24, pl. 5 (fig. 6); 1966: 154. Rossignol, 1962: 127.

Eupagurus Lucasi Heller, 1863: 163, pl. 5 (fig. 10).

Spiropagurus forbesii: Sars, 1890: 161. Non *Pagurus forbesii* Bell, 1845.

Eupagurus placens Stebbing, 1924: 241, pl. 4. Barnard, 1950: 462, fig. 85e.

Pagurus placens: Kensley, 1981: 33 (distribution list).

Material

Pagurus cuanensis. PMcL, 1 ♂, 1 ovigerous ♀ (2.4, 3.8 mm); Denmark–Sweden, Kattagat Strait, collected by O. Schmitt. PMcL, 1 ♂, 1 ♀ (5.8, 6.2 mm); Bay of Naples, collected by F. Gherardi, July 1989. SMNH 16150, 1 ♂, 1 ovigerous ♀ (3.3, 3.5 mm); Port Alexander, Angola, 73 m, collected by Skoog, 11 August 1912. MNHN Pg5500, 1 ♂ (4.0 mm); Vema Seamount, South

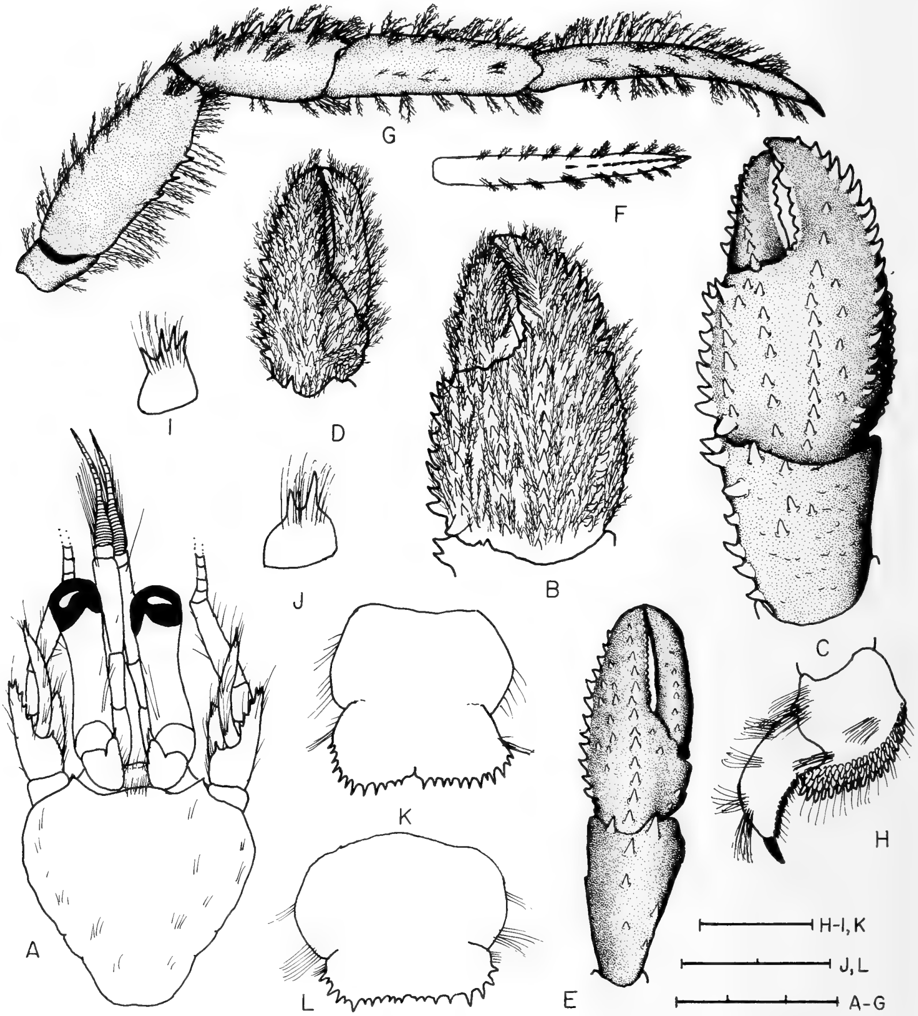

Fig. 2. A–J. *Pagurus cuanensis* Bell, 1845, ovigerous ♀ (4.4 mm) from *Meiring Naude* Stn XX113 (NHM 1997.724-725. K. Female (8.0 mm) from False Bay (SAM–A1538). L. Male (6.8 mm) from Cape St Blaize (SAM–A1539). A. Shield and cephalic appendages. B. Chela of right cheliped. C. Chela and carpus of right cheliped with setae omitted. D. Chela of left cheliped. E. Chela and carpus of left cheliped with setae omitted. F. Right second pereopod (lateral view). G. Dactyl of right second pereopod (ventral view). H. Dactyl and propodus of left fourth pereopod (lateral view). I–J. Anterior lobe of sternite of third pereopods. K–L. Telson. Scales H–I, K, 1.0 mm; J, L, 2.0 mm; A–G. 3.0 mm.

Africa, Stn VEM 4.4, 31°38'S 08°02'E, approximately 40 m, 14 November 1964. MNHN Pg5507, 1 ♂ (3.0 mm); Vema Seamount, South Africa, Stn VEM 20D, 31°38'S 08°02'E, approximately 40 m, 16 November 1964. MNHN Pg5508, 1 ♂, 1 ♀ (4.8, 6.0 mm); near Mossel Bay, 110 m, January 1954. USNM 276077, 2 ♂, 1 ♀ (2.4–3.1 mm); *Meiring Naude* Stn XX?, 30°13.8'S 30°54.2'E, 70 m, 8 July 1986. NHM 1997.724–725, 1 ♂, 1 ovigerous ♀ (2.1, 4.4 mm); *Meiring Naude* Stn XX113, 29°50.2'S 31°12.3'E, 95 m, 9 July 1986. PMcL, 1 ♂ (2.7 mm); *Meiring Naude* Stn XX114, 29°56.2'S 31°10.2'E, 88 m, 9 July 1986. SAM–A43224, 1 ovigerous ♀ (2.0 mm); *Meiring Naude* Stn XX115, 29°50.05'S, 31°14.2'E, 130 m, 9 July 1986.

Eupagurus placens. SAM–A1538, 1 ♀ (8.0 mm); False Bay, 55 m. SAM–A1539, 1 ♂ (6.8 mm); Cape St. Blaize, 100 m.

Diagnosis

Shield (Fig. 2A) as broad or slightly broader than long. Rostrum obsolete or occasionally slightly rounded; lateral projections produced, with small marginal or submarginal spine. Ocular peduncles moderately long and slender, 0.75–0.85 length of shield; corneas slightly dilated. Ocular acicles roundly or ovately triangular, with strong submarginal spine. Antennular peduncles slightly over-reaching distal margins of corneas; antennal peduncles usually not over-reaching corneas. Second segment of antennal peduncle with dorsolateral distal angle produced, elongate, terminating in simple or bifid spine, mesial margin with 1 to 6 spines. Antennal acicle reaching to or beyond mid-length of ultimate peduncular segment.

Right cheliped with dorsal surfaces of chela (Fig. 2B) and, to lesser extent, carpus covered with tufts of plumose setae, usually at least partially concealing armature. Dactyl with row of spines on dorsomesial margin and additional row in dorsal mid-line. Palm (Fig. 2C) with row of spines on dorsomesial margin, dorsal surface with 3 or 4 irregular rows of moderate to strong spines, median row usually strongest and most prominent; dorsolateral margin rounded, but with row of smaller spines proximally, increasing in size and extending nearly to tip of fixed finger; dorsal surface of fixed finger with only 2 or 3 small spines. Carpus (Fig. 2C) with row of strong spines on dorsomesial margin, 2–4 slender spines on dorsodistal margin; dorsal surface with median row of spines (large specimens) or 2 or 3 spines (smaller specimens) and several short transverse sometimes setose and sometimes spinulose ridges, extending on to lateral face.

Left cheliped with dorsal surfaces of chela (Fig. 2D) and carpus covered with tufts of setae usually concealing armature. Hiatus between dactyl and fixed finger becoming more pronounced with increased animal size. Palm (Fig. 2E) with medial row of moderate to strong spines on dorsal surface. Carpus (Fig. 2E) with 3 or 4 strong spines on or adjacent to dorsolateral margin.

Ambulatory legs somewhat dissimilar. Segments of both pairs of pereopods with numerous tufts of plumose setae, but dactyl and propodus of left third noticeably more setose. Dactyls of both second and third pereopods each with row of 10–17 very small, closely-spaced corneous spines (Fig. 2F) on distal 0.50–0.65 of ventral margin. Carpus and propodus of second right (Fig. 2G) each with row of spines on dorsal surface; carpus of second left with 1 dorsodistal and frequently 1–4 more proximal spines on dorsal surface, dorsal surface of propodus unarmed or with few minute spinulose protuberances; meri each with row of spines on ventral margin. Third pereopods with propodi and carpi unarmed or similar in armature to second left; meri unarmed. Fourth pereopods with 3 or 4 rows of corneous scales in propodal rasp (Fig. 2H). Anterior lobe of sternite of third pereopods (Fig. 2I–J) triangular to subquadrate, with 2–4 blunt or acute projections or spines and tufts of setae.

Males with unpaired left pleopods on abdominal somites 2–5. Telson (Fig. 2K–L) with short narrow median cleft; terminal and lateral margins of posterior lobes with moderately strong sometimes corneous-tipped spines, often irregularly interspersed with smaller spines.

Colour (in preservative)

Ocular peduncles yellowish, with two rather darker rings, one anterior and one posterior, some white spots posterior to proximal ring. Basal segment of antennular peduncles reddish; two distal segments translucent, with whitish spots; flagellum colourless. Basal segments of the antennae dark reddish brown, fourth and fifth segments clear, striated longitudinally with red; flagella red, with white rings; antennal acicle light colour, striated longitudinally with red. Meri of chelipeds reddish, sprinkled with whitish spots and with some dark vinaceous colour on dorsal margin; carpi reddish, more accented than meri, with proximal transverse dark red spot; palms reddish, covered completely with long, earth-coloured setae. Meri of second and third pereopods reddish with whitish spots and some darker red on dorsal margins; carpi reddish, with one large dark red longitudinal spot and some small whitish spots covering much of lateral face; propodi similar, dactyls with two longitudinal whitish stripes. (After Sandberg & McLaughlin 1998.)

Habitat

Sometimes associated with sponge-covered shells, rarely with compound ascidians. Reported from depths of 15–91 m in the North Atlantic, and 0–250 m in the Mediterranean (Ingle 1993; Sandberg & McLaughlin 1998). In South Africa, 40 m at Vema Seamount, 55–100 m at False Bay and Cape St. Blaize, 110 m near Mossel Bay, and 70–130 m off Durban and KwaZulu–Natal.

Distribution

North Atlantic from the coasts of Norway and Sweden to the Atlantic coast of France; Mediterranean; Central and South Atlantic from Spain to île Principe and São Tomé (Forest 1966); Southern Africa from Angola to KwaZulu–Natal.

Remarks

One of us (Forest 1955, 1961, 1966) had previously reported on the very southern extension of the range of *P. cuanensis* and, after examining a specimen recorded by Barnard (1950) as *P. placens*, could find only minor differences between that specimen and *P. cuanensis*. Together with Odhner's (1923) report of this species from Port Alexander, Angola, and Vema Seamount and Mossel Bay specimens in the collection of the Muséum national d'Histoire naturelle, the presence of *P. cuanensis* in south-eastern South Africa seemed certain, and its synonymy with *P. placens* probable. Specimens from the *Meiring Naude* cruises confirm the distribution of this species as far north as KwaZulu–Natal in eastern South Africa.

Despite the inaccuracies and poor quality of Stebbing's (1924) description and illustrations of *P. placens*, we re-emphasize the characters that almost certainly confirm its conspecificity with *P. cuanensis*, particularly in the shape, proportions and ornamentation of the chelae. For example, virtually identical strong spines are found on the mesial margins of the right chelae in both taxa, as well as two primary longitudinal rows of spines on the dorsal surfaces. The dactyls of the left chelae both are arched, more elongate than the palms, and separated from the fixed fingers by a prominent hiatus. Additionally, the ambulatory legs of both species have curved dactyls fringed with setae and are longer than the propodi. We have re-examined both of Barnard's (1950) specimens attributed to *P. placens* and there is no question that they represent *P. cuanensis*. Given the close proximity of Barnard's collection sites to the type locality of *P. placens*, and the similarities observed, we must conclude that *P. placens* is a junior subjective synonym of *P. cuanensis*. (Also see remarks under *Pagurus* sp.)

Barnard's (1950) specimens are larger than any of the specimens collected off KwaZulu-Natal and differ from the latter in having more slender right chelae, a complete median row of spines on the dorsal surface of the carpus of the right cheliped, a more prominent hiatus between the dactyl and fixed finger of the left cheliped, and stronger corneous-tipped spines laterally on the terminal margins of the telsons. However, these differences are well within the range of variation reported for *P. cuanensis* (cf. Ingle 1993). All of the South African specimens generally have fewer spines on the dorsal surfaces and these are arranged in more regular rows, than are seen in some specimens from the North Atlantic and Mediterranean. The dactyls of the ambulatory legs also are longer in the South African specimens.

Pagurus emmersoni sp. nov.

Fig. 3A–F

Material

Holotype. SAM–A43426, 1 ♂ (9.7 mm), Tugela River mouth, December 1968.

Paratypes. SAM–A43222, ovigerous ♀ (2.7 mm); KwaZulu–Natal, reef 5 km south of Tongaat Beach, 12–15 m, 5 April 1987. MNHN Pg5834 (formerly SAM- A19138), 1 ♂ (6.6 mm), off Danger Point, Cape, 34°39'13.60S 19°19'1.80E, 34 m, 11 April 1984.

Diagnosis

Shield as or nearly as long as broad. Rostrum obtusely triangular, produced beyond level of lateral projections. Ocular peduncles approximately 0.60–0.80 shield length; cornea not dilated; ocular acicles rounded mesially, terminating subacutely and with small submarginal spine. Antennular peduncles overreaching distal margins of corneas by approximately 0.20 length of ultimate segment. Antennal peduncles variable in length; antennal acicles reaching to bases of corneas or considerably beyond. Third maxilliped with one accessory tooth on crista dentata.

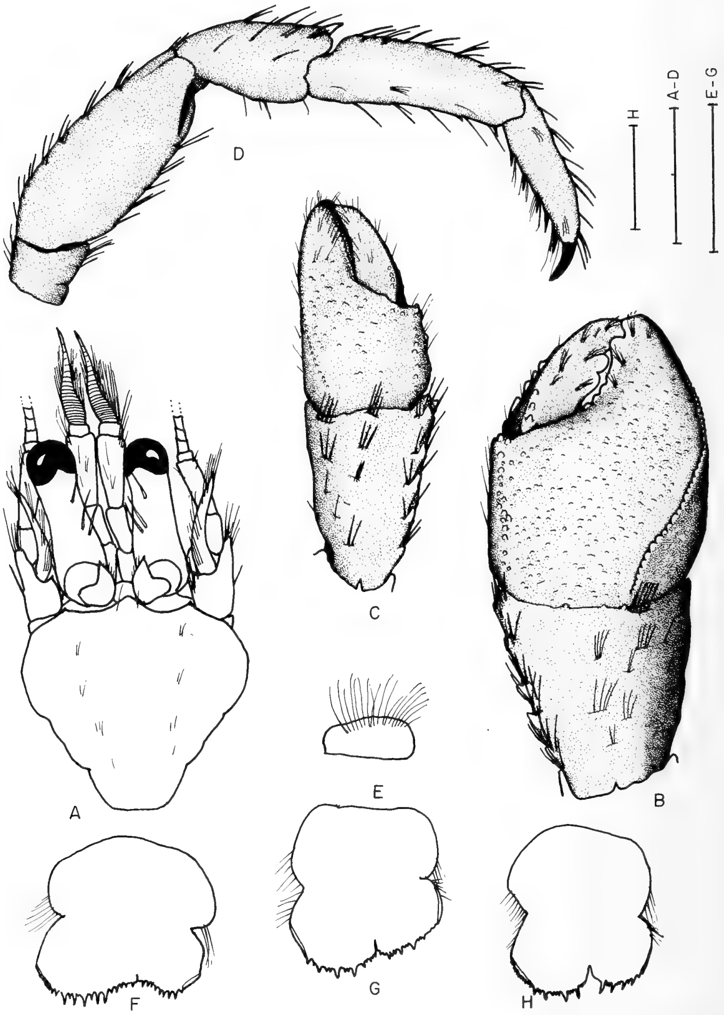

Fig. 3. A–F. *Pagurus emmersoni* sp. nov., ovigerous ♀ (2.7 mm) from reef south of Tongaat Beach. G. *Pagurus souriei* (Forest, 1952) ♀ (2.7 mm) from Gorée (PMcL). H. *Pagurus gordonae* (Forest, 1956), ♂ (3.7 mm) from Tamara (I. de Los), Guinea (PMcL). A. Shield and cephalic appendages. B. Chela and carpus of right cheliped. C. Chela and carpus of left cheliped. D. Right second pereopod (lateral view). E. Anterior lobe of sternite of third pereopods. F–H. Telson. Scales E–F, H, 1.0 mm; A–D, 2.0 mm.

Right cheliped stout, chela somewhat operculate; dorsomesial margin of dactyl with row of rounded tubercles not reaching to tip. Dorsomesial and dorsolateral margins of palm each with row of tubercles, scale-like on dorsolateral margin, dorsal surface with scattered tubercles or granules. Carpus with row of tuberculate spines on dorsomesial margin. Ventromesial margins of carpus and merus not developing wing-like projections.

Left cheliped with small tubercles in dorsal midline of dactyl, dorsomesial margin unarmed or not delimited. Dorsomesial and dorsolateral margins of palm each with row of tubercles. Carpus with row of spines on dorsomesial margin.

Ambulatory legs with left pair slightly shorter than right. Dactyls with 5–8 strong corneous spines on ventral margins. Carpi each with dorsodistal spine. Meri unarmed or with spinule at ventrolateral distal angle of second right. Fourth pereopods semichelate; propodal rasp consisting of single row of scales. Sternite of third pereopods with roundly subrectangular anterior lobe.

Telson with posterior lobes separated by shallow median cleft; terminal margins each with row of small to moderately large spines; lateral margins with solid or serrated plate.

Description

Shield (Fig. 3A) as or nearly as long as broad, and slightly shorter to slightly longer than posterior carapace; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin truncate; dorsal surface with sparse tufts of setae. Rostrum obtusely triangular, terminally subacute, reaching beyond level of lateral projections. Lateral projections obtusely triangular, each with marginal or submarginal spinule.

Ocular peduncles approximately 0.60–0.80 length of shield, moderately swollen distally in small paratype, dorsal and mesial surfaces with few stiff setae; corneas not noticeably dilated. Ocular acicles with rounded mesial margins, terminating subacutely, and with small submarginal spinule; separated basally by approximately 0.65 basal width of one acicle.

Antennular peduncles, when fully extended, over-reaching distal margins of corneas by 0.20–0.40 length of ultimate segment. All three segments with few fine setae.

Antennal peduncles not quite reaching distal margins of corneas in small paratype, but considerably longer in holotype. Fifth and fourth segments with few scattered short setae. Third segment with spinule at ventrodistal angle practically obscured by tuft of stiff setae. Second segment with dorsolateral distal angle produced, terminating bluntly and with several stiff setae; dorsomesial distal angle with small spine. First segment with spinule on ventrolateral margin. Antennal acicles long and slender, reaching at least to bases of corneas, with terminal spine and row of stiff setae on mesial face. Antennal flagellum, with 1 or 2 short (1–2 article length) setae every several articles. Third maxillipeds with strong accessory tooth on crista dentata.

Right cheliped (Fig. 3B) stout, with somewhat operculate chela; stronger but not appreciably longer than left. Dactyl approximately same length as palm and slightly overlapped by fixed finger; cutting edge with 3 or 4 strong calcareous teeth, terminating in small corneous claw; dorsomesial margin with row of low rounded tubercles not extending to tip, dorsal surface generally flat or somewhat elevated in midline, with three to incomplete row of small tubercles, and with few tufts of setae; ventral surface with tufts of short stiff setae. Palm with dorsal surface slightly convex and with scattered very small granules or minute tubercles, becoming larger and forming longitudinal row on fixed finger mesially; dorsomesial margin with irregular row of quite small tubercles, dorsolateral margin with row of closely-spaced scale-like tubercles, decreasing in size on fixed finger but not reaching to tip; mesial, lateral and ventral surfaces with sparse tufts of short setae. Carpus with relatively flat dorsal surface, dorsomesial margin with row of tuberculate spines, extending on to distomesial margin dorsally and partially obscured by sparse tufts of stiff setae; dorsodistal margin with few spinulose tubercles; dorsolateral margin not distinctly delimited, but with few short transverse rows of stiff setae; mesial, lateral and ventral surfaces each with scattered stiff setae, ventromesial margin not produced into wing-like projection. Merus with dorsodistal spine; surfaces all with few sparse tufts of stiff setae; ventromesial margin not developing wing-like projection.

Left cheliped (Fig. 3C) more slender than right, reaching beyond distal margin of palm of right; similarly but more weakly armed. Dactyl with row of small tubercles in dorsal midline proximally, becoming obsolete distally; dorsomesial margin unarmed; dorsal, mesial and ventral surfaces each with few sparse tufts of short setae; cutting edge with row of corneous teeth, terminating in small corneous claw. Palm slightly more than half length of carpus; with row of single or double small subacute spines or tubercles on dorsomesial margin, dorsal surface slightly convex, weakly tuberculate, with small cluster of tubercles near base of dactyl, dorsolateral margin slightly raised and with row of small tubercles, not extending to tip of fixed finger; mesial face sometimes with few spinulose tubercles dorsally, scattered setae ventrally; lateral and ventral surfaces with tufts of stiff setae; cutting edge of fixed finger with row of very small calcareous teeth. Carpus with row of subacute spines on dorsomesial margin, dorsal surface with short transverse ridges and tufts of stiff setae laterally; dorsodistal margin, mesial, lateral and ventral surfaces all with sparse tufts of long stiff setae and occasional blunt tubercles. Merus with dorsodistal spine; surfaces with sparse tufts of long stiff setae; ventrolateral distal angle with small spine or row of low tubercles continuing on to ventral margin. Ischium with long stiff setae dorsally and ventrally.

Ambulatory legs (Fig. 3D) of right side approximately equal to length of right cheliped, left slightly shorter; generally similar, each with sparse tufts of stiff setae, particularly dorsally and ventrally. Dactyls slightly shorter than propodi, ventral margins each with 5 or 6 (second) or 6 to 8 (third) strong corneous spines. Propodi each with 1 or 2 prominent corneous spines at ventrodistal margin and 1–3 smaller spines on ventral margin in distal half. Carpi each with dorsodistal spine. Meri unarmed except for small spine or spinule at ventrolateral distal angle of second pair. Fourth pereopod semichelate; propodal rasp consisting of single row of corneous scales. Sternite of third pereopods with roundly subrectangular anterior lobe (Fig. 3E).

Anterior ventral region of abdomen with doubly protruded membranous lobes, left appreciably larger. Male with 3 unequally biramous left pleopods. Female with 4 unpaired left pleopods; second to fourth with both rami well-developed; fifth with rudimentary endopod. Telson (Fig. 3F) with transverse notch indicating division into anterior and posterior regions; somewhat asymmetrical posterior lobes separated by shallow median cleft; terminal margins each with row of small to moderately large spines, anterior portions of lateral margins with solid or serrated plate.

Colour (in preservative)

Background colour of calcified regions white with faint tint of orange, and streaks of darker red. Anterior region of shield light red-orange. Ocular peduncles with faint band of red-orange basally. Chelae red-orange, most intense on dorsal surfaces, with distal halves of dactyls and fixed fingers white; carpi and meri whitish, with faint red longitudinal lines on carpi and transverse lines on meri. Ambulatory legs each with one submedian mottled red-orange ring on merus, one similar median ring on propodus; dactyls each with one proximal and one subdistal ring of same tint; carpi each whitish, with three or four faint red longitudinal lines.

Etymology

This species is named for Professor Winston (Winks) Emmerson, University of Transkei, who provided much of the material for this study.

Habitat

Subtidal reef; 12–15 m.

Type locality

Tugela River mouth, KwaZulu-Natal.

Distribution

KwaZulu-Natal and southern Cape coasts, South Africa.

Remarks

Pagurus emmersoni is clearly assignable to the *anachoretus* group of *Pagurus*, named for its first member, *Pagurus anachoretus* Risso, 1827, from the Mediterranean, and including *P. souriei*, *P. gordonae*, *P. laurentae* Forest, 1978, and *P. anachoretoides* Forest, 1966, from the tropical eastern Atlantic, and the South African *P. barnardi* (= *P. liochele*) (Forest 1978). Forest & Ngoc-Ho (1992) added *P. kulkarnii* Sankolli, 1961, from the Arabian Sea. With the discovery of *P. emmersoni* and the formal inclusion of *P. hedleyi* (Grant & McCulloch, 1906) from Queensland, Australia, the Arafura Sea, and Hong Kong (new locality record), the *anachoretus* group now contains nine species.

Although the group was well defined by Forest & Ngoc-Ho (1992: 224), one supplemental character should be added, i.e., the propodal rasp of the fourth pereopod that consists of a single row of squamiform scales. Characteristic of the group is the shape of the right cheliped. The dorsal surface of the palm is always more or less rounded, and the mesial and lateral margins are more or less convex and symmetrical, but a very distinct gradient is seen in the elongation of the palm. Despite the fact that intraspecific variation in the ratio of breadth to length is observed in adults of each species, the mean values still provide a specific character. Another character, the strong wing-like projection of the ventromesial margin of the carpus and merus of the right cheliped, especially well-developed in the large males, appears to correlate with species having enlarged palms. Living colour is also a specific characteristic for species of the *anachoretus* group, and permits confident identification in the field. Most often the colour patterns consist of patches and/or longitudinal stripes of pigment, continuous or not, covering part or all of the segments of the chelipeds and ambulatory legs.

The above-mentioned species of *Pagurus* seem to form a homogeneous group whose members are distinguished from one another, at least in part, by the gradual differences in the form of the chelipeds. With the exception of this cheliped form, four other species from the tropical western Atlantic fit the definition of the *P. anachoretus* group: *P. triangularis*, *P. fimbriatus* Forest, 1966, *P. alcocki*, and *P. dartevellei* (cf. Forest & Ngoc-Ho 1992). Their cheliped differences most probably reflect adaptations to their particular modes of life. The latter two species in particular exhibit profound modifications of the chelipeds in that both chelae are especially adapted to form an operculum.

Apart from *P. anachoretus* and *P. hedleyi*, which have relatively broad distributions, the other species are more strictly localized. Although some are reported from the same geographic regions, they usually inhabit different bathymetric levels. *Pagurus gordonae* and *P. laurentae*, whose distributions overlap from Gambia to Ghana are one example. Whereas *P. gordonae* is found in the intertidal zone, *P. laurentae* lives in depths between 30 and 40 metres.

After comparing *P. emmersoni* with *P. alcocki*, *P. gordonae*, *P. hedleyi*, *P. kulkarnii*, *P. liochele*, and *P. souriei*, there is no doubt that the new species is most closely allied with *P. liochele*, *P. gordonae*, and *P. souriei*. In fact, *P. emmersoni*, while clearly a distinct species, appears to be intermediate between *P. souriei* and *P. gordonae*, sharing certain morphological and colour characters with one or both. Specifically, the rostrum of *P. emmersoni* is subacute, as in *P. gordonae*, rather than obtuse and rounded as in *P. souriei*. The antennular and antennal peduncles both considerably over-reach the distal margins of the corneas in *P. gordonae*, whereas they are equal or only very slightly longer in *P. souriei*. In *P. emmersoni*, the antennular peduncles over-reach the distal margins of the corneas by approximately 0.20 the length of the ultimate segments, whereas the antennal peduncles do not reach the distal corneal margin. Although the shape of the chelipeds is very similar in all three species, the dactyl of the right cheliped has a longitudinal unarmed ridge in the dorsal mid-line of *P. souriei*, a row of small spines extending nearly to the tip in *P. gordonae*, but only three small proximal tubercles in *P. emmersoni*. The ventromesial margins of the meri of the right chelipeds of both *P. gordonae* and *P. souriei* are armed with several small spines that are lacking in *P. emmersoni*. The palm of the left cheliped has a weakly granular or tuberculate dorsal surface in both *P. gordonae* and *P. emmersoni*, but a median longitudinal row of spines in *P. souriei*. The ambulatory dactyls of *P. emmersoni* are intermediate between the very short, stout dactyls of *P. gordonae* and the longer, more slender dactyls of *P. souriei*. The telson of *P. emmersoni*, although distinguishable, is more similar to the telson of *P. souriei* (Fig. 3G) than that of *P. gordonae* (Fig. 3H).

The colour patterns of *P. emmersoni* combine those of the two West African species. Whereas the entire chelipeds of *P. souriei* are intense red-orange, only the palms of the chelae of *P. emmersoni* show this coloration; the distal portions of the fingers are whitish. The carpi of *P. emmersoni*, like those of *P. gordonae*, are whitish with only longitudinal lines of red; however, the meri of *P. emmersoni* are marked by transverse lines of reddish colour, whereas those of *P. gordonae* carry irregular patches of colour. In contrast, the banding patterns of the ambulatory legs agree completely with those of *P. souriei*, whereas *P. gordonae* has longitudinal stripes on the lateral faces of the carpi and similar stripes on the proximal portions of the meri and propodi.

Pagurus emmersoni differs from both of the West African species in: (1) the dorsolateral projections of the second peduncular segments in *P. emmersoni* terminate bluntly or in a tiny spinule, whereas in both *P. gordonae* and *P. souriei* these projections terminate in one or two spinules; (2) both *P. gordonae* and *P. souriei* have a long row of spines on the dorsomesial margin or the dactyl of the right cheliped, but this margin is armed with only rounded tubercles in *P. emmersoni*.

Pagurus emmersoni is known only from a few specimens; however, the carpus of the right cheliped, even in the very large male holotype, does not exhibit the development of a wing-like projection such as is seen in males of *P. gordonae*. This development of wing-like projections on the merus and carpus of the right cheliped is correlated with size rather than sex in *P. liochele* and *P. kulkarnii*, but even in small specimens of the former species (< 2.5 mm shield length) some development is apparent.

Pagurus liochele (Barnard, 1947)

Fig. 4A–J

Pylopagurus liochele Barnard, 1947: 376; 1950: 455, fig. 84a–f. Kensley, 1974: 66; 1981: 33.
Incertae sedis: Barnard, 1950: 456.
Eupagurus sp.: Forest, 1956: 363.
Pagurus barnardi Forest, 1966: 153; 1978: 531. Forest & Ngoc-Ho, 1992: 224.
?*Phimochirus liochele*: McLaughlin, 1981*a*: 5 (by implication); 1981*b*: 354.
Pagurus liochele: McLaughlin, 1988: 6, figs 1–2.

Material

Syntypes of Pagurus liochele. SAM–A4038, 1 ♂ (7.0 mm); 5.5 mi SE Cape Seal, 68 m. SAM–A1543, 1 ♀ (3.3 mm); Bird Island Passage, Algoa Bay, 18 m.

Syntypes of *Pagurus barnardi* (Forest, 1966). SAM–A8228, 1 ♀ (4.3 mm); False Bay, littoral. SAM–A10963, 1 ♂ (3.7 mm); Simonstown, littoral. SAM–A8496, 1 ovigerous ♀ (2.8 mm); Port Elizabeth, littoral.

Other material examined. MNHN Pg5509, 1 ♀ (2.1 mm); False Bay, Stn FB757, 34°07.5'S 18°31'E, 27–28 m, rock, 22 February 1947. MNHN Pg5510, 1 ♂, 1 ♀ (3.5, 4.2 mm), 1 ovigerous ♀ (3.3 mm); Stn FB792, 34°10.2'S 18°26.2'E, 14 m, shelly sand, 27 August 1951. MNHN Pg5511, 2 ♂ (3.1, 3,8 mm), 1 ♀ (2.6 mm), 3 ovigerous ♀ (3.0–4.2 mm); Stn FAL87, south of Kogel Bay, 14–17 m, 19 August 1952. MNHN Pg5512, 1 ovigerous ♀ (5.2 mm); Stn FAL188, 34°12.8'S 18°36.5'E, 46 m, 10 September 1953, shelly sand. MNHN Pg5513, 2 ♂ (4.3, 7.9 mm), 2 ♀ (5.3, 5.7 mm); near Mossel Bay, 110 m, January 1954. MNHN Pg5514, 1 ♂ (3.8 mm); Stn LIZ7

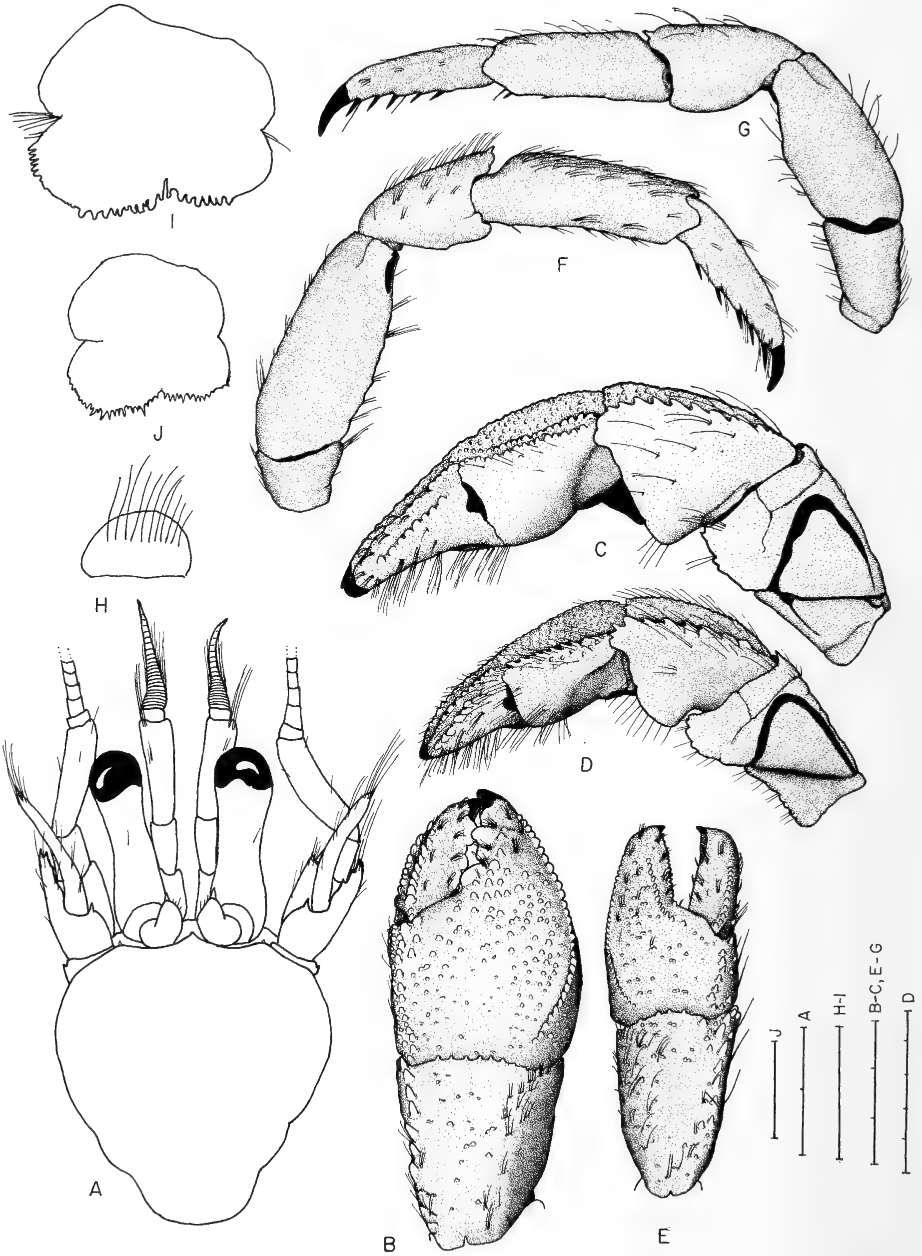

Fig. 4. A–C, E–I. *Pagurus liochele* (Barnard, 1947), syntype of *Pagurus barnardi* Forest, 1966, ♂ (4.3 mm) from False Bay (SAM–A10963. D, J. Male (5.2 mm) from *Meiring Naude* Stn N13 (NHM 1997.729). A. Shield and cephalic appendages. B. Chela and carpus of right cheliped (dorsal view). C–D. Right cheliped (mesial view). E. Chela and carpus of left cheliped. F. Right second pereopod (lateral view). G. Left third pereopod (lateral view). H. Anterior lobe of sternite of third pereopods. I–J. Telson. Scales H–J, 1.0 mm; A, 2.0 mm; and B–C, E–G, 3.0 mm; D, 5.0 mm.

Algoa Bay, 33°58.1'S 25°38.9'E, 9 m, stones and rock, 6 April 1954. MNHN Pg5515, 1 ovigerous ♀ (4.8 mm); Stn FAL270, Roman Rock, 14–17 m, rock, 18 September 1954. MNHN Pg5516, 1 ovigerous ♀ (3.1 mm); Stn FAL279, Roman Rock, 12–14 m, rock, 23 September 1954. MNHN Pg5517, 1 ♂ (3.9 mm); Stn FAL285, Roman Rock, 12–14 m, rock, 23 September 1954. SAM–A43421, 1 ♂, 1 ♀ (6.2, 7.5 mm); Stn FAL332T, 34°15'S 18°36'E, 51 m, 31 January 1959. SAM–A43391, 1 ovigerous ♀ (3.9 mm); Stn FAL755, north of Seal Island, 4 m, 16 February 1965. SAM–A43429, 1 ♀ (2.2 mm); Stn DBN264S, east Centre Bank of Congella River Channel, intertidal, 25 April 1952. USNM 276078, 1 ♂ (4.1 mm); *Meiring Naude* Stn M1, 31°56.9'S 29°13.5'E, 20–26 m, 16 July 1982. NHM 1997.729, 1 ♂ (5.2 mm); *Meiring Naude* Stn N13, 32°04'S 29°05.7'E, 25–30 m, 19 July 1982.

Diagnosis

Shield (Fig. 4A) longer than broad. Rostrum triangular, produced to or slightly beyond level of obtusely triangular or broadly rounded lateral projections. Ocular peduncles 0.50–0.65 length of shield, slightly swollen basally; corneas slightly dilated; ocular acicles roundly triangular, terminating subacutely and with small submarginal spine. Antennular peduncles over-reaching ocular peduncles by 0.50–0.65 length of ultimate segment. Antennal peduncles over-reaching ocular peduncles by approximately half length of fifth segment, and slightly shorter than antennular peduncles. Second segment with dorsolateral distal angle strongly produced, reaching to mid-length of fourth peduncular segment, terminating in strong spine, mesial margin with 1–5 additional spines; dorsomesial distal angle with acute spine. Antennal acicles arcuate, reaching to proximal 0.35–0.50 of ultimate peduncular segment, with small terminal spine; mesial margin with row of rather stiff setae.

Right cheliped (Fig. 4B–D) with somewhat operculate chela; stronger but not appreciably longer than left. Dactyl approximately same length as palm; dorsomesial margin with row of strong, closely-spaced blunt or spinulose tubercles, dorsal surface slightly laterad of midline with longitudinal row of distinct, very closely-spaced tubercles, often neither row extending to tip of dactyl, remainder of dorsal surface generally flattened; ventral surface usually with numerous tufts of setae. Palm with row of blunt spines or tubercles on dorsomesial margin, dorsal surface only faintly convex, usually with scattered low simple or bifid tubercles, but pitted in male syntype, stronger row of tubercles adjacent to cutting edge of fixed finger, often not extending to tip; dorsolateral margin with row of closely-spaced tubercles, slightly stronger on fixed finger but not extending to tip; ventral surface with numerous tufts of setae distally and on fixed finger. Carpus deep, ventromesial margin developing into wing-like projection in larger specimens (shield length > 5.0 mm); dorsomesial margin with row of moderately strong blunt or acute spines, dorsodistal margin with few short, blunt or subacute spines; dorsolateral margin often not distinctly delimited, but surface with single to multiple rows of denticles, low tubercles or transverse ridges and tufts of setae, dorsal surface minutely spinulose to tuberculate. Merus with 1 or 2 acute spines on dorsodistal margin; ventromesial margin weakly scalloped or with low spinulose tubercles, developing into strong wing-like protuberance with increasing size; ventrolateral margin smooth.

Left cheliped (Fig. 4E) generally similar to right. Dactyl approximately 1.3–2.0 length of palm, dorsomesial margin with row of closely-spaced tubercles not extending to tip, dorsal surface often with 1 tubercle proximally; mesial face with 1 or 2 rather prominent tubercles near proximal margin. Palm with row of subacute spines on dorsomesial margin and frequently adjacent second row, dorsal surface slightly convex, unarmed (male syntype) or somewhat tuberculate, dorsolateral margin slightly raised and with row of small tubercles, usually not extending to tip of fixed finger. Carpus with row of subacute spines on dorsomesial margin, dorsal surface usually weakly tuberculate in mesial half and with short transverse ridges and tufts of stiff setae laterally, dorsodistal margin with 2 to several small spines. Merus with 1–3 spines on dorsodistal margin; ventromesial and ventrolateral margins each with row, or only few, very small blunt spinules or tubercles.

Ambulatory legs (Fig. 4F–G) short and stout. Dactyls approximately 0.75 length propodi; 0.25–0.35 as deep (lateral view) as long; tufts of setae dorsally, mesially and laterally; ventral margins each with row of 5 to 8 strong corneous spines. Propodi approximately equal to carpi; dorsal surfaces each with transverse rows of setae; ventral margins each with 2 to several corneous spines or spinules. Carpi each with small spine at dorsodistal margin, dorsal surfaces with low sometimes spinulose protuberances and tufts of setae, or occasionally 2 to short row of small spines in large males, row of tufts of setae on lateral faces dorsally. Meri with setae dorsally and ventrally, ventral margins unarmed or with low protuberances or spinules, particularly on second pereopods. Sternite of third pereopods with roundly subrectangular anterior lobe (Fig. 4H). Sternite of fifth pereopods with widely separated lobes, each with moderately long setae.

Males with 3 unpaired left pleopods; females with 4. Telson (Fig. 4I–J) with lateral incision indicating anterior and posterior portions; posterior lobes slightly asymmetrical, separated by very small median cleft; terminal margins each with row of calcareous teeth and sometimes second smaller adjacent row on telson surface, at least on left lobe; spines sometimes extending on to lateral margins.

Colour

Ocular peduncles sienna at base, distal half cobalt, with narrow dark sienna ring immediately adjacent to black cornea; meral segment of right and left chelipeds with a cobalt band bordered with sienna, and distal margin dark sienna; granules on dorsal surfaces of palms white on a pale sienna ground, sienna longitudinal stripes on dactyls and fixed fingers; proximal halves of meral segments of second and third pereopods sienna, distal halves pale, longitudinal sienna stripes on carpi and dactyls and dorsally on proximal halves of propodi, distal halves of propodi yellowish, passing into cobalt apically. (After Barnard 1950: 457 for '*Incertae sedis*' specimens.)

Distribution

Orange River mouth to Transkei, South Africa; littoral to 110 m.

Habitat

Mud and fine sand, sometimes associated with sponges and gorgonians.

Remarks

When Barnard (1947) described *Pylopagurus liochele*, he apparently assumed, because of the generally operculate right chela, that the female would have possessed paired first pleopods modified as gonopods had its abdomen not been lost. Barnard (1950) redescribed and illustrated the species, but made no mention of the ventral wing-like projections of the mesial faces of the carpus and merus of the right cheliped. After reviewing the type material and additional specimens subsequently collected and finding no paired female gonopods, McLaughlin (1988) transferred Barnard's (1947) taxon to *Pagurus*.

In Barnard's (1950) account, he briefly described as '*Incertae sedis*', four specimens collected littorally from False Bay, Simonstown, Jeffreys Bay and Port Elizabeth, and these were subsequently given the name *Pagurus barnardi* sp. nov. by Forest (1966). Barnard (1950) remarked that the specimens might have been identified as *Pylopagurus ungulatus* Balss, 1912, had it not been for the absence of paired first abdominal pleopods in his single female specimen. He considered *Pagurus* (as *Eupagurus*) the only other available genus; however, Barnard (1950) was of the mistaken belief that males of *Pagurus* all had four unpaired pleopods. His three males had only three left pleopods. In reality, *Pagurus* males have three or four unpaired pleopods, or in the case of *P. prideaux*, no unpaired pleopods. Barnard also misinterpreted the positions of the three male pleopods in his taxon, reporting their occurrence on the second, third and fifth abdominal somites. Actually, the males that we examined have typical unpaired left pleopods on the third, fourth and fifth abdominal somites. Barnard's description indicated the considerable similarities with *P. liochele* that he observed.

Although Barnard (1950) listed the four specimens as '*Incertae sedis*', the specimens are not so labelled. Of the three specimens available for examination, the male from Simonstown and the ovigerous female from Port Elizabeth are labelled only as '*Eupagurus* sp.' In the vial of the latter is also the label '*Eupagurus* sp. Forest, 1953'. This specimen is in poor condition; the cephalic appendages of the right side are missing as are the two right and third left pereopods, and most calcification has been lost. The male from False Bay is labelled '*Eupagurus* or *Pylopagurus*', and clearly reflects Barnard's ambivalence. This male, the largest, does not show any lengthening of the ventromesial face of the carpus of the right cheliped; however, there is slight development of the ventromesial face of the merus. Two specimens, clearly identifiable as *P. liochele* were present in the Transkei collection. The smaller of the two males exhibits carpal and meral development similar to that of this male of *P. barnardi*, whereas the larger specimen has the ventromesial projections very well-developed (Fig. 4D). The residual colour patterns of these specimens agree with the patterns described for *P. barnardi*. The Transkei specimens have been carefully compared with the syntypes of *P. barnardi*, and no characters have been found upon which the two taxa can be distinguished. Therefore, *P. barnardi* must be considered a subjective junior synonym of *P. liochele*. McLaughlin (1988) reported that variation in the armature of the chelipeds and ambulatory legs appeared to be, at least in part, a function of size, but made no direct mention of development of the carpal and meral projections. These too appear to be size related.

In the absence of colour, *P. liochele* and *P. emmersoni* are superficially quite similar species with overlapping patterns of distribution. The wing-like expansions of the ventromesial faces of the right cheliped of *P. liochele* will immediately distinguish this species from *P. emmersoni*.

Additionally, the dactyls of the ambulatory legs are thinner and the setation of the appendages more abundant in *P. liochele*. However, setal density also appears to be influenced by animal size. Smaller specimens generally have more numerous tufts of long setae than are seen in larger individuals.

Pagurus prideaux Leach, 1815

Fig. 5A–F

Pagurus prideaux Leach, 1815, pl. 26 (figs 5–6). Holthuis, 1977: 60. Ates & Schakenbos, 1985: 36, colour photo. Ingle, 1985: 760, figs 6, 12, 16, 22, 50, 61, 67; 1993: 148, figs 121–124 and detailed synonymy.

Pagurus solitarius Risso, 1827: 40; 1844: 94. Roux, 1828–1830, unnumbered text pages, pl. 36.

?*Pagurus Crenatus*: Hope, 1851: 13.

Eupagurus prideauxii: Heller, 1863: 161, pl. 5 (figs 1–8).

Eupagurus tristanensis: Stebbing, 1910: 356. Non *Eupagurus tristanensis* Henderson, 1888.

Eupagurus prideauxi: Pesta, 1918: 239, fig. 73. Nobre, 1931: 218, figs 120–121b. Zariquiey Alvarez, 1946: 121, pl. 6 (fig. b).

Eupagurus spinulentus: Stebbing, 1920: 260. Barnard, 1950: 460, fig. 85a–d. Non *Eupagurus spinulentus* Henderson, 1888.

Pagurus prideauxi: Forest, 1958*a*: 99. Zariquiey Alvarez, 1968: 250, figs 89h, 90e, p, 91f, n.

Pagurus cf. *prideauxi*: Lewinsohn, 1969: 68.

Material

ZMA, 1 ♀ (3.9 mm); Terse Zee, Netherlands, 11 June 1972. PMcL, 1 ♂, 1 ♀ (7.6, 11.4 mm); near Cabo Creus and Golfo de Rosa, Spain, 100 m, collected by L. B. Holthuis, 28 July 1961.

As *Pagurus spinulentus*. SAM–A8223, 1 ovigerous ♀ (3.7 mm); Mossel Bay, South Africa. SAM–A1498, 1 ♂, 1 ovigerous ♀ (4.1, 5.7 mm); Umvoti River, N x W 0.5 W 4.25 mi, 49 m. SAM–A1504, 1 ♂, 1 ovigerous ♀ (5.2, 6.8 mm); Umvoti River, N x W 0.5 W 4.25 mi, 49 m. SAM–A8224, 1 ♂ (3.7 mm); Umhloti River, NW 0.5W 15.5 mi, 183 m. SAM–A1548, 1 ovigerous ♀ (4.3 mm); Tongaat River, NW x N 0.25N 5.5 mi, 66 m. SAM–A1497, 1 ♂ (2.5 mm); Scottsburgh Lighthouse NW x N 8 mi, 168 m. SAM–A43407, 3 ♂, 1♀, 3 ovigerous ♀ (2.2–5.2 mm), off KwaZulu-Natal, Stn NAD 87W, 29°10'S 31°37'E, 43 m, 29 July 1964. SAM–A43408, 12 ♂, 7 ovigerous ♀ (4.9–8.4 mm), off KwaZulu-Natal, Stn NAD 8N, 29°53.6'S 31°04.6'E, 38 m, 16 May 1958.

Pagurus prideaux. USNM 276079, 2 ♂, 1 ♀, 3 ovigerous ♀ (3.8–5.9 mm); *Meiring Naude* Stn XX91, 30°12.9'S 30°52.5'E, 50 m, 8 July 1986. PMcL, 1 ♀ (6.2 mm); *Meiring Naude* Stn XX96, 30°15'S 30°54.3'E, 100 m, 8 July 1986. NHM 1997.729, 1 ovigerous ♀ (5.6 mm); *Meiring Naude* Stn XX104, 30°07.2'S 30°58.2'E, 50 m, 8 July 1986. SAM–A43225, 1 ♂ (3.9 mm);

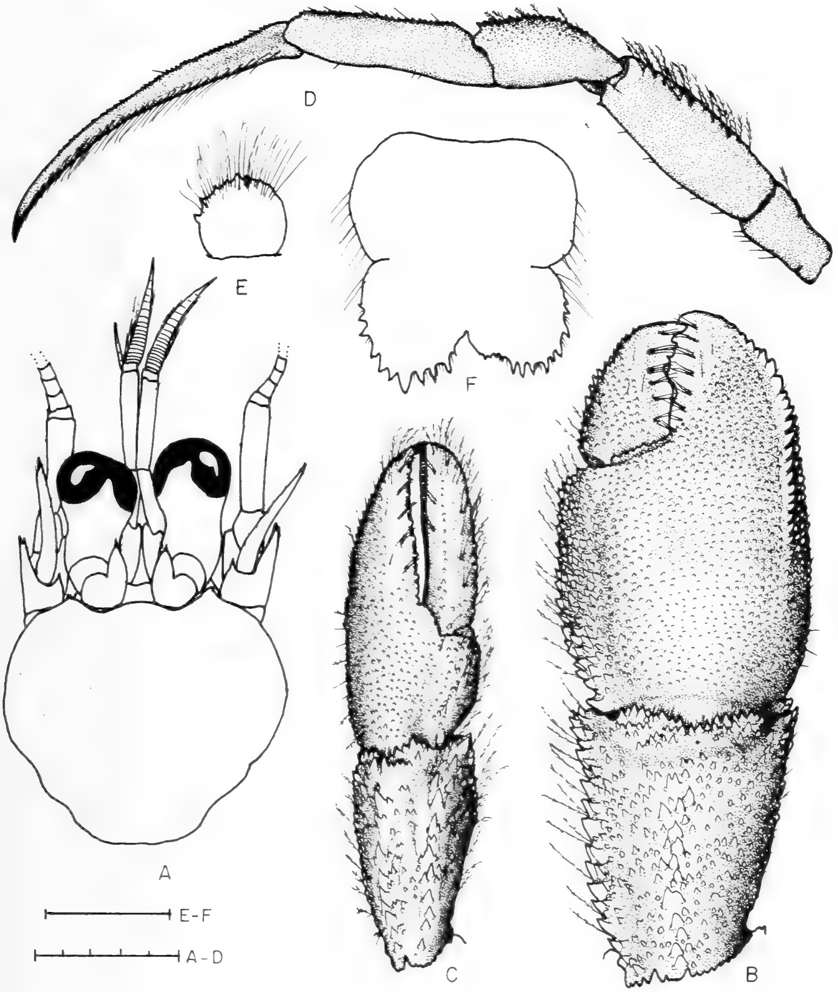

Fig. 5. *Pagurus prideaux* Leach, 1815, ovigerous ♀ (5.9 mm) from *Meiring Naude* Stn XX91 (USNM 276079). A. Shield and cephalic appendages. B. Chela and carpus of right cheliped. C. Chela and carpus of left cheliped. D. Left third pereopod (lateral view). E. Anterior lobe of sternite of third pereopods. F. Telson. Scales E, F, 1.0 mm; A–D, 5.0 mm.

Meiring Naude Stn XX114, 29°56.2'S 31°10.2'E, 88 m, 9 July 1986. RMNH, 1 ♂ (4.0 mm); *Meiring Naude* Stn XX115, 29°50'S 31°14.2'E, 130 m, 9 July 1986.

Diagnosis

Shield (Fig. 5A) broader than long. Rostrum usually broadly rounded, occasionally obtusely triangular. Ocular peduncles short, stout; corneas strongly dilated; ocular acicles subovate, moderately slender, with moderate to strong submarginal spine. Antennular peduncles over-reaching ocular peduncles by nearly entire length of ultimate segment. Antennal peduncles equalling or over-reaching ocular peduncles by up to 0.25 length of ultimate segment; antennal acicle slender, unarmed, reaching from slightly beyond base to distal margin of cornea, occasionally over-reaching cornea.

Right cheliped (Fig. 5B) with chela often much longer than carpus. Palm with single or double row of small spines or tubercles, occasionally only granules, on dorsomesial margin; convex dorsal surface granular or minutely spinulose, with short spinose median elevation at proximal margin; dorsolateral margin with somewhat elevated row of small spines or tubercles extending to or nearly to tip of fixed finger. Carpus with irregular single or double row of moderate to strong tubercles or spines on dorsomesial margin and smaller row in dorsal midline, convex dorsal surface covered with numerous small spines or tubercles; dorsodistal margin often broadly v-shaped and armed with single or double row of small spines; dorsolateral margin indistinctly delimited by row of spines, strongest proximally.

Left cheliped with propodal–carpal articulation rotated 15–30° counterclockwise from perpendicular. Dactyl with row of small spines on dorsomesial margin. Palm (Fig. 5C) weakly elevated in dorsal midline and with short single or double row of small spines proximally, dorsal surface of palm and fixed finger granular; dorsomesial and dorsolateral margins each with irregular single or double row of small spines. Carpus with row of simple to multifid spines on dorsolateral margin and irregular single or double row of slightly smaller spines on dorsomesial margin.

Ambulatory legs (Fig. 5D) with elongate slender dactyls strongly twisted; dorsal surfaces each with row of tiny spinules, mesial faces each with longitudinal sulcus and row of long setae extending to claw, lateral faces each with longitudinal sulcus in proximal half and row of setae extending to claw; ventral margins each with row of closely-spaced, very small corneous spinules. Dorsal surfaces of carpi and propodi each with row of spines, strongest on second; lateral faces spinulose at least in dorsal halves. Anterior lobe of sternite of third pereopods (Fig. 5E) broadly subtriangular to subquadrate, usually with several small spines or spinulose protuberances.

Males without paired or unpaired pleopods. Females with four unpaired biramous left pleopods (2–5). Telson (Fig. 5F) with posterior lobes separated by broad shallow median cleft, terminal and lateral margins with row of irregularly-sized spines.

Colour (in preservative)

Ocular peduncles very pale yellow, with more reddish or salmon pink band next to cornea, or with small clearer area; corneas dark greenish gray. Antennular peduncles very pale yellow, with light reddish traces. Antennae of similar tone, but colour of reddish spots on the peduncles more accentuated; flagella yellowish. Right cheliped rose coloured, darker salmon on dorsal surfaces of merus and carpus; propodus salmon, with violet hue in posterior part of upper face, but extending entire and on each side of longitudinal keel, but granules always rose coloured on all the segments; dactyls lighter, coloured like pumpkin; claw whitish rose. Left cheliped similar, but much more accentuated in hue and in extent of violet on propodus, and showing also a reddish spot on propodus and dactyl. Second and third pereopods with meri pale salmon, some paler areas, reddish spots and darker transverse band near margin; carpi similar but usually with somewhat darker colour tone, spines whitish; propodi with transverse clear band in centre, reddish proximally and distally, white centrally on longitudinal keel; also transverse white stripe and some reddish spots; dactyls pale coloured, with numerous spots or specks throughout. (After Sandberg & McLaughlin 1998.)

Habitat

Commonly found in symbiotic relationship with the 'cloak anemone' *Adamsia carciniopados* (Otto) formerly known as *Adamsia palliata* (Bohadsch); 20–400 m. In the South African specimens, Barnard (1950) reported that all shells that had been preserved with the crabs had a single anemone encircling the shell aperture. This was similarly the case in the specimens from the *Meiring Naude*.

Distribution

Eastern Atlantic from Norway to Cape Verde; Mediterranean Sea; South Africa; and Red Sea.

Remarks

As previously noted, Stebbing (1910) initially identified a single specimen (SAM–A1497) as *Pagurus tristanensis*, but changed this and subsequently assigned it to *Pagurus spinulentus* (as *Eupagurus*). Neither Henderson's (1888) descriptions nor figures of either species are sufficiently diagnostic to permit confident identifications without references to the type specimens themselves. The illustrations of the right chelipeds of both species (Henderson 1888, pl. 5 (figs 3, 5a)) are relatively similar and do bear considerable superficial similarity to *P. prideaux*; however, it would appear that neither Stebbing (1910, 1920) nor Barnard (1950) examined their specimens closely enough to notice the complete absence of pleopods in the males. Henderson (1888) made no mention of the sex of his single specimen of *P. tristanensis*, which is a male, and immediately distinguished from *P. prideaux* by the presence of three unpaired left pleopods, as well as the better-developed, obtusely triangular rostrum and chelipeds armed with rows of strong spines. Henderson's single specimen of *P. spinulentus* is a female and the spines present on the dorsal surfaces of the chelae are not apparent in his figure. The dorsal surfaces of the chelae of *P. prideaux* are covered with granules or spinules, thus making recognition of the two species elementary. The very close relationship of *P. spinulentus* to *P. cavicarpus*, a species recognized for the first time in south-eastern South African waters, has been discussed under the latter taxon.

Pagurus prideaux is the second species common to the north-eastern Atlantic fauna to be found in south-eastern South Africa. In contrast to *P. cuanensis*, whose distribution appears continuous from Norway to the Atlantic coast of South Africa and into the south-western Indian Ocean, the most southernly record of *P. prideaux* in the eastern Atlantic is Cape Verde. It was questionably reported from the Red Sea by Lewinsohn (1969). Its presence in the south-western Indian Ocean and southernmost portion of South Africa provides credence to its occurrence in the Red Sea. Future surveys of the deeper waters off eastern Africa may provide additional information on the southernly migration of *P. prideaux* in the western Indian Ocean.

Pagurus sp.

Fig. 6A–H

Material

SAM–A43226, 1 ♂ (1.6 mm); KwaZulu-Natal (off Park Rynie), *Meiring Naude* Stn X6, 30°23.2'S 30°50.8'E, 140 m, 19 August 1981.

Description

Shield (Fig. 6A) slightly broader than long; anterior margin between rostrum and lateral projections concave; anterolateral margin sloping; posterior margin truncate. Rostrum broadly rounded, not produced beyond level of lateral projections. Lateral projections triangular, each with small submarginal spine. Dorsal surface of shield with sparse tufts of stiff setae posterior to anterior margin at level of lateral projections, ocular acicles and rostrum. Third maxilliped with accessory tooth on crista dentata; merus and carpus each with strong or blunted dorsodistal spine.

Ocular peduncles approximately 0.80 shield length; short and moderately stout, dorsomesial surface with 1 or 2 tufts of setae and tuft of thick setae at base of slightly dilated corneas. Ocular acicles narrowly triangular, dorsal surface somewhat concave, with strong inwardly directed submarginal spine; separated basally by more than basal width of one acicle.

Antennular peduncles slightly over-reaching distal margins of corneas. Ultimate segment with 1 or 2 setae near dorsolateral distal angle and few scattered surface setae. Penultimate segment with few scattered setae. Basal segment unarmed.

Antennal peduncles reaching to or not quite to distal margins of corneas, and reaching approximately to distal half of ultimate segments of antennular peduncles. Fifth and fourth segments with scattered setae. Third segment with small spine at ventrodistal margin. Second segment with dorsolateral distal angle produced strongly, reaching at least distal half of fourth peduncular segment, with strong terminal spine, mesial margin unarmed, lateral margin unarmed or with small spine distally; dorsomesial distal angle with strong spine. First segment with spine on dorsolateral margin distally; ventrolateral margin with 1 spine. Antennal acicle arcuate, reaching distal 0.33–0.50 of ultimate peduncular segment, with terminal spine and few tufts of long setae on mesial face. Antennal flagellum short, approximately 2.5 times length of peduncle, with 1 or 2 short (< 1 article length) setae every 1 or 2 articles.

Right cheliped (Fig. 6B) much shorter than ambulatory legs. Dactyl approximately as long as palm; cutting edge with row of corneous teeth in distal fourth, three large, calcareous teeth proximally; terminating in corneous claw; slender hiatus between dactyl and fixed finger; dorsal surface convex, with scattered long setae and 3 small spines proximally; dorsomesial margin with 1 spine

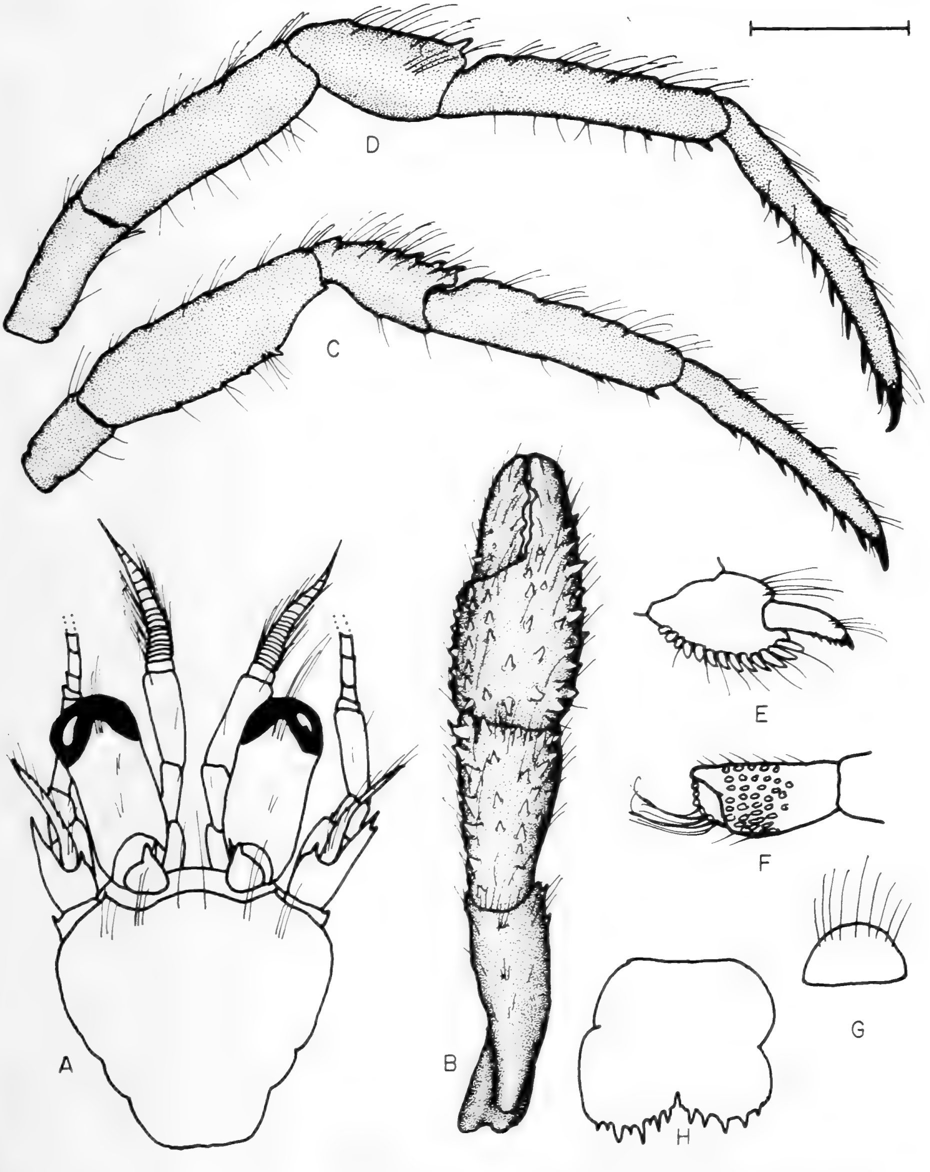

Fig. 6. A–H. *Pagurus* sp., ♂ (1.6 mm) from *Meiring Naude* Stn X6 (SAM–A43226). A. Shield and cephalic appendages. B. Right cheliped. C. Right second pereopod (lateral view). D. Right third pereopod (lateral view). E. Dactyl and propodus of right fourth pereopod. F. Dactyl and propodus of left fifth pereopod. G. Anterior lobe of sternite of third pereopods. H. Telson. Scales G–H, 0.50 mm; A–F, 1.0 mm.

proximally; mesial and ventral surfaces with tufts of long setae. Palm moderately slender; approximately 0.75 length of carpus; dorsomesial margin rounded, with double row of small spines and spinulose tubercles; dorsal surface somewhat convex, with 2 irregular rows of spines, accompanied by scattered long stiff setae; dorsolateral margin with row of small spines and adjacent row of larger spines proximally, becoming single row distally and extending to proximal half of fixed finger; ventral surface with scattered long setae; fixed finger with scattered setae on dorsal and ventral surfaces, cutting edge with row of low, broad calcareous teeth. Carpus approximately as long as merus; dorsomesial margin with irregular row of strong spines, dorsal surface and dorsodistal margin each with few spines; dorsolateral margin rounded but with row of small spines becoming irregular double row distally; lateral face with few small spines dorsally in distal half, 1 tiny spinule at ventrolateral distal angle; mesial face with scattered long setae. Merus with unarmed dorsodistal margin, dorsal and mesial surfaces and ventromesial margin all with sparse long setae; ventrolateral margin with 2 spines in distal third. Ischium unarmed. Left cheliped missing.

Ambulatory legs (Fig. 6C–D) (left third missing) with dactyl of third right slightly longer than second pair; dactyls moderately long and slender, approximately equal to length of propodi (second) or 1.2 longer (third right); in dorsal view straight; in lateral view straight (second) or slightly curved (third); dorsal surfaces with transverse low protuberances and long setae; lateral and mesial surfaces with few moderately long setae; ventral margins each with row of strong corneous spines (7 on second, 8 on third). Propodi of second pereopods shorter than third; dorsal surfaces each with transverse low ridges or protuberances and long setae; lateral and mesial faces with setae; ventral margins each with 2 or 3 corneous spinules. Carpi of second right with row of 6 spines, second left with row of 5 spines and numerous setae on dorsal surfaces; dorsal surface of third right with 1 spinulose protuberance proximally and dorsodistal spine; lateral faces all with sparse long setae. Meri all with transverse setose ridges dorsally; second pair each with small spine at ventrolateral distal angle, ventral margin of right second with row of 4 spinules, distal-most strongest, left with single distal spinule and row of widely-spaced protuberances; third right pereopod unarmed. Ischia unarmed. Fourth pereopods (Fig. 6E) weakly semichelate; propodal rasp consisting of 1 row of large corneous scales. Fifth pereopods (Fig. 6F) chelate. Sternite of third pereopods with submarginal row of setae on subsemicircular anterior lobe (Fig. 6G). Sternite of fifth pereopods with 2 closely-spaced subovate lobes.

Immature male with gonopores not open. Left third pleopod short, biramous, with subequal rami; fourth and fifth better developed, uniramous. Uropods very asymmetrical. Telson (Fig. 6H) with small transverse incision indicative of transverse suture separating anterior and posterior regions; nearly symmetrical posterior lobes separated by small median cleft; terminal margins each with row of moderately strong spines, interspersed on left lobe with smaller spines.

Colour

Unknown.

Habitat

Collected at depth 140 m.

Distribution

Known only from KwaZulu–Natal, South Africa.

Remarks

This quite small juvenile male specimen with a spinose right cheliped clearly is not referable to *P. cuanensis* or *P. cavicarpus*. We initially were inclined to think that this specimen might represent Stebbing's (1924) (but not Barnard's (1950)) *P. placens*, as Stebbing (1924) noted in his description of *'P.' deprofundis* that it agreed with *P. placens* in having numerous rows of 'teeth or sharpened tubercles' on the chelae and carpi of the chelipeds, and in the development of the fourth pereopods.

As previously mentioned, the holotype and unique specimen of *P. placens* has not been located, and interpretation of *P. placens* has been difficult, as Stebbing's (1924: 242, pl. 4) description and illustrations are both inadequate and inaccurate. He described the rostral region as 'obscurely produced between the ophthalmic scales', but illustrated a well-developed tridentate rostrum reaching nearly to the mid-length of the ocular acicles. The rostrum of the KwaZulu–Natal specimen is, as Stebbing described, rounded and not produced.

Although his figure (Stebbing 1924, pl. 4 (car)) shows a simple spinose termination of the ocular acicles. Stebbing described them as 'wide apart, bilobed, not denticulate, but the larger inner lobe produced into an acute apex'. The ocular acicles of the KwaZulu–Natal specimen (Fig. 6A) are widely separated, terminate subacutely (equivalent to Stebbing's outer lobe), and each has a strong, submarginal, inwardly directed spine (equivalent to Stebbing's inner lobe) reaching well beyond the tip of the acicle.

The fourth pereopod of *P. placens* illustrated by Stebbing (1924, pl. 4 (prp4)) appears to have been drawn in mesial view, with no propodal rasp visible, but Stebbing described it as being like that of *'P.' deprofundis*, which he illustrated (Stebbing 1924, pl. 5 (prp4)) as having a rasp consisting of a single row of corneous scales. Although Stebbing actually was incorrect in ascribing a single row of scales to the propodal rasp of *'P.' deprofundis*, his illustration is in agreement with the rasp of the KwaZulu–Natal specimen.

However, there the similarities begin to falter. Although Stebbing gave no indication of heavy setation, other than to mention long setae adjacent to the cutting edges of the dactyl and fixed finger of the right chela that concealed the hiatus between the two, his figures of both chelae depict long setae, similar to that seen in *P. cuanensis*. The KwaZulu–Natal specimen has a scattering of long, finer and less abundant setae.

Perhaps more importantly, the shield and cephalic appendages of the KwaZulu–Natal specimen differ from the holotype of *P. placens* in the reported armature of the anterior part of the shield, length of the antennal flagellum, and the armature of the dorsolateral distal lobe of the second segment of the antennal peduncle, which Stebbing (1924: 242, pl. 5, figs (car, a.c.)) referred to as the outer branch of the antennal acicle. Stebbing described the anterior carapace behind each ocular acicle (scale) as being 'produced backward [as] a faint ridge of the carapace, its front margin forming a small denticle on the outer side of each scale'. His figure (pl. 2 (car)) shows only a series of three lines on the left and one on the right side of the shield posterior to the ocular acicles; the lateral projections of the shield do each have a small spinule. In the KwaZulu–Natal specimen there are only two or three long setae in these positions posterior to the ocular acicles, but the lateral projections each have a distinct spinule. The antennal flagellum of *P. placens* was described as 'devoid of setae and more than four times as long as the peduncle' (Stebbing 1924: 242). The antennal flagellum of the KwaZulu–Natal specimen is approximately 2.5 times the length of the peduncle and has one or two very short setae every two or three articles. The produced dorsolateral distal angle of the second antennal segment is well-developed in both the illustrated holotype and in the KwaZulu–Natal specimen; however, in the KwaZulu–Natal specimen the process of the left side is unarmed, and that of the right has a spine on the lateral margin. Stebbing described this process as denticulate and illustrated a row of spines on the mesial margin such as is also seen in *P. cuanensis*. Perhaps the most distinctive difference between *P. placens,* as Stebbing described it, and the KwaZulu–Natal specimen, is in the armament of the dactyl of the right chela. The holotype reportedly has a row of spines on the dorsomesial margin. There is only a single spine on this margin in the KwaZulu–Natal specimen.

The KwaZulu–Natal specimen also shows some similarities to *P. tristanensis* in having short stout ocular peduncles, rounded rostrum, moderately slender, spinose right cheliped and propodal rasp of the fourth pereopod with a single row of scales. However, despite its similarly small size (shield length 2.12 mm, carapace length 3.62 mm), the holotype of *P. tristanensis* (NHM 1888.33) is a male with well-developed gonopores. It differs from the KwaZulu–Natal specimen in the armature of the dorsolateral distal angle of the second segment of the antennal peduncle, spine configuration of the right cheliped, segmental ratios and armature of the ambulatory legs, configuration of the anterior lobe of the sternite of the third pereopods, and armature of the telson.

Until additional and more mature specimens become available, the KwaZulu–Natal specimen must simply be referred to as *Pagurus* sp.

KEY TO THE REGIONAL SPECIES OF *PAGURUS*

1A. Dorsal surface of palms of chelipeds armed with spines 2
1B. Dorsal surface of palms of chelipeds unarmed or armed only with granules or small tubercles 4

2A. Right second pereopod with dorsal row of spines on propodus 3
2B. Right second pereopod without dorsal row of spines on propodus .... *Pagurus* sp. (Fig. 6)

3A. Ocular peduncles short, stout. Dorsal surface of palm of right chela with small tubercles or spines, strongest mesially and laterally; carpi of chelipeds each, or at least right, usually with prominent foramen on ventral surface .... *Pagurus cavicarpus* (Paul'son, 1875) (Fig. 1A–C, E–I, K)

3B. Ocular peduncles moderately long and slender. Dorsal surface of palm of right chela with rows of spines, strongest in midline; carpi of chelipeds each, or at least right, without prominent foramen on ventral surface .... *Pagurus cuanensis* Bell, 1845 (Fig. 2)

4A. Dactyls of ambulatory legs shorter to only slightly longer than propodi .. 5
4B. Dactyls of ambulatory legs at least 1.5 length of propodi .... *Pagurus prideaux* Leach, 1815 (Fig. 5)

5A. Ventromesial face of merus and carpus of right cheliped developed as wing-like projection in both sexes .... *Pagurus liochele* (Barnard, 1947) (Fig. 4)
5B. Ventromesial face of merus and carpus of right cheliped not developed as wing-like projection in either sex .... ***Pagurus emmersoni*** sp. nov. (Fig. 3A–F)

Propagurus McLaughlin & de Saint Laurent, 1998

Pagurus Fabricius, 1775: 410 (in part).
Propagurus McLaughlin & de Saint Laurent, 1998: 159.

Type species. *Pagurus gaudichaudii* H. Milne Edwards, 1836: 269. Gender masculine.

Diagnosis

Thirteen pairs of symmetrical or asymmetrical quadriserial gills (cf. McLaughlin & de Saint Laurent 1998); moderately well-developed or rudimentary pleurobranch above pereopod 2, rudimentary pleurobranch above pereopod 3, well-developed pleurobranch above pereopod 4. Antennal peduncles with supernumerary segmentation; dorsolateral distal angle of second segment well-developed, with spinose mesial margin. Maxillule with external lobe of endopod varying from rudimentary to well-developed, arched, but not strongly recurved. Ischium of third maxilliped with well-developed crista dentata and strong accessory tooth. Fourth pereopods with propodal rasp consisting of 3 or 4 rows of corneous scales. Sternite of fifth pereopods broadly and ovately subrectangular lobes, each with transverse tuft of long setae. Tergite of sixth abdominal somite strongly calcified, with deep submedian transverse furrow dividing tergite into subquadrate anterior and subrectangular posterior lobes. Telson with submedian transverse indentation providing indication of division into anterior and posterior portions; asymmetrical posterior lobes separated by median cleft.

Males with paired gonopores, each with adjacent tuft of stiff setae; no sexual tubes; no paired pleopods, usually 3 stout unpaired left pleopods (3–5) (very rarely 4, pleopods 2–5), each with somewhat foliaceous elongate endopod and rudimentary exopod. Females with paired gonopores; no paired pleopods, 4 stout unpaired left pleopods, second with subequal rami, both short, paddle-shaped, third and fourth each with elongate somewhat foliaceous endopod and short somewhat paddle or blade-shaped exopod; fifth as in male.

Remarks

During the course of this investigation, one of us (JF) recognized the morphological similarities of Stebbing's (1924) *Pagurus deprofundis* and the South American *Pagurus gaudichaudii* H. Milne Edwards, 1836. Earlier, Forest & de Saint Laurent (1968) had noted the unusual gill structure of *P. gaudichaudii*, which resembled that of some undescribed Indo-Pacific species. For those species McLaughlin & de Saint Laurent (1998) recently proposed the genus *Propagurus*. One of those species proved to be conspecific with Stebbing's (1924) taxon.

Propagurus deprofundis (Stebbing, 1924)

Fig. 7A–K

Eupagurus deprofundis Stebbing, 1924: 243, pl. 70. Barnard, 1950: 164. Forest, 1955: 107.
Pagurus deprofundus: Kensley, 1981: 33 (list) (misspelling).
Propagurus deprofundis: McLaughlin & de Saint Laurent, 1998: 170, figs 2D, E, 4B, 7B, 8A–D, 9, 11C, D.

Material

Holotype. NHM 1928.12.1.245, 1 ♀ (9.3 mm); 13 miles north-west of Cape Morgan, South Africa, 457–585 m.

Diagnosis

Shield varying from slightly longer than broad to distinctly broader than long. Rostrum commonly triangular, usually produced beyond level of lateral projections; usually with prominent terminal spine. Ocular peduncles slightly less to slightly more than half shield length; moderately stout; corneas slightly dilated; ocular acicles ovately or acutely triangular, dorsal surfaces somewhat concave; with strong submarginal spine. Fully extended antennular peduncles over-reach distal margins of corneas by 0.20 length of ultimate segments to 0.25 length of penultimate segments. Antennal peduncles over-reach distal margins of corneas by 0.10–0.75 length of ultimate segments; antennal acicle reaching at least to mid-length of ultimate peduncular segment, usually considerably beyond, with strong terminal spine.

Right cheliped considerably stronger than left, but not always appreciably longer; sometimes with hiatus between dactyl and fixed finger. Dactyl often with few acute tubercles proximally on convex dorsal surface; dorsomesial margin with single or double row of small teeth. Palm varying from moderately slender to moderately broad, with irregular double row of spines on dorsomesial margin, convex dorsal surface sparsely covered with short setae and with 6 somewhat irregular rows of spines, usually accompanied by long stiff setae; dorsolateral margin not distinctly delimited proximally, but with irregular row of teeth becoming marginal and extending nearly to tip of fixed finger. Carpus with irregular row of strong spines on dorsomesial margin accompanied by adjacent slightly irregular row of spines on dorsal surface, separated by broad nearly naked longitudinal band from median row of shorter spines. Merus with 0–3 spines on dorsodistal margin; ventrolateral margin with row of acute or subacute teeth; ventral surface often with few small and occasionally 2 large tubercles.

Left cheliped frequently with hiatus between dactyl and fixed finger; also often with few tubercles proximally on rounded dorsal surface of dactyl. Palm with median single or double row of acute tubercles on convex dorsal surface, becoming less regular on proximal half of fixed finger; dorsomesial face usually with central row of tubercles and nearly double row of slightly smaller tubercles near margin; dorsolateral face with several irregular rows of small closely-spaced blunt or acute tubercles or denticles, appreciably stronger dorsally, but not extending to tip of fixed finger. Carpus with 1 or 2 spines on dorsodistal margin, dorsomesial margin with irregular row of moderate to strong spines. Merus with 1–3 spines at dorsodistal margin; ventromesial margin with row of spines proximally and frequently also small spine distally; ventrolateral margin with row of spines sometimes becoming double row proximally.

Ambulatory legs over-reaching left cheliped by at least 0.75 length of dactyls. Dactyls and propodi of left and right morphologically similar, but left with greater setation on lateral faces. Dactyls 1.10–1.85 length of propodi; dorsal surfaces with transverse low protuberances and long stiff setae; lateral surfaces each with faint longitudinal sulcus; ventral margins each with row of 8–21 strong corneous spines. Propodi each with transverse low ridges and long stiff setae on dorsal and lateral surfaces; mesial faces of second pereopods (each with longitudinal keel in ventral third), extending from near distal margin to proximal half or third. Carpi of second pereopods with row of 3–8 spines and transverse setose ridges on dorsal surfaces; dorsal surfaces of third each with 0–5 smaller spines and transverse setose ridges in addition to strong dorsodistal spine. Meri with ventral margins of second each with ventral row of spines, ventral margins of third unarmed or rarely with denticle on ventrolateral margin and stronger denticle on ventromesial margin distally. Sternite of third pereopods with submarginal row of setae on subsemicircular to roundly subrectangular anterior lobe.

Males with 3, rarely 4 unpaired left pleopods. Mature females usually with dense setae on coxae of fifth pereopods. Telson with asymmetrical posterior lobes separated by slender median cleft; terminal margins often considerably produced laterally, each with row of small calcareous teeth becoming stronger toward outer angles, largest teeth, particularly on left, somewhat hooked.

Redescription of holotype

Shield (Fig. 7A) slightly longer than broad; anterior margin between rostrum and lateral projections concave; anterolateral margin terraced; posterior margin roundly truncate. Rostrum well-developed, triangular, produced beyond level of lateral projections, with prominent terminal spinule. Lateral projections obtusely triangular, each with strong submarginal spine. Dorsal surface of shield with row of tufts of stiff setae on either side of midline and additional tufts posterior to anterior margin and rostrum. Ten pairs of well-developed asymmetrical intermediate arthrobranchs (Fig. 7B–C), moderately well-developed pleurobranch above second pereopod, rudimentary pleurobranch above third pereopod, pleurobranch above fourth pereopod normally developed.

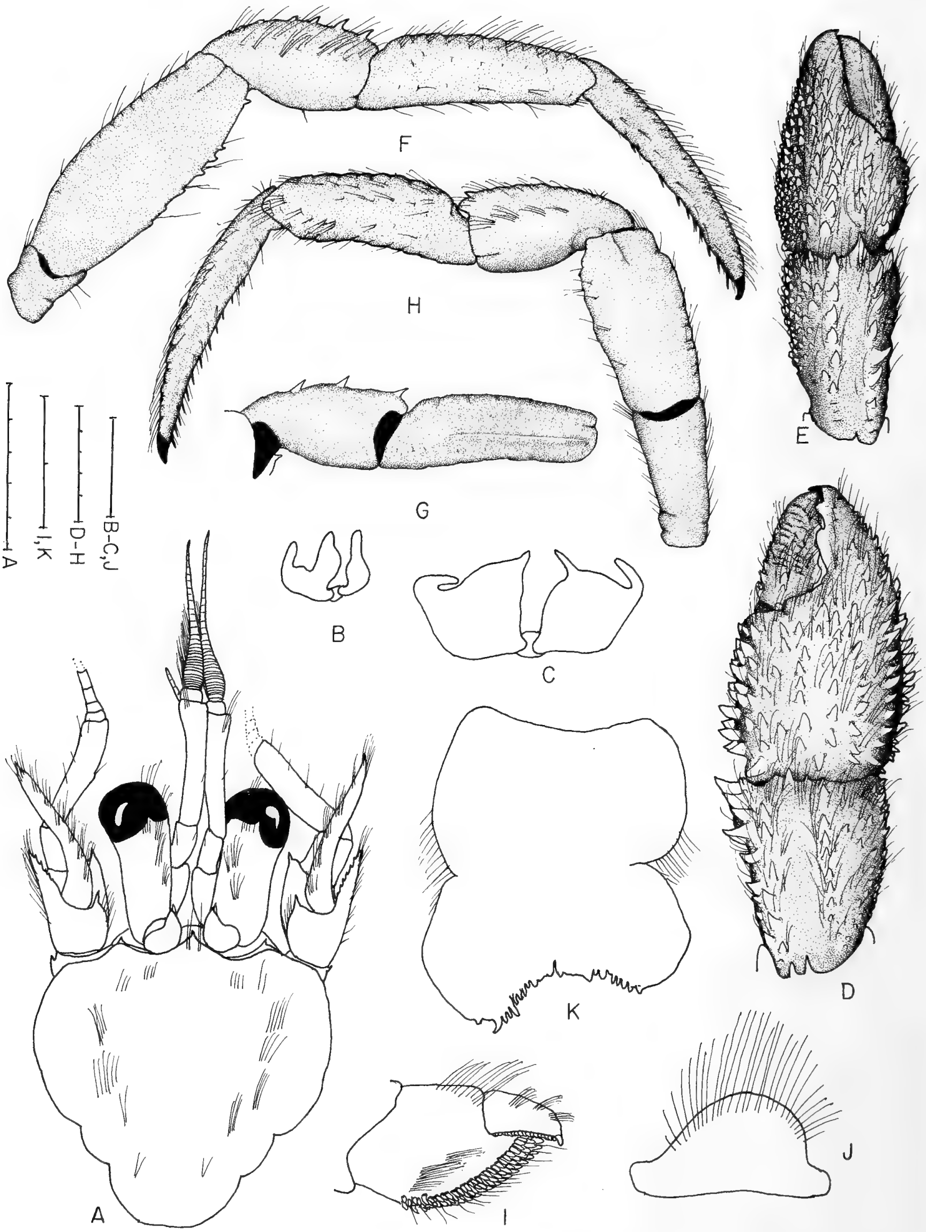

Fig. 7. A–K. *Propagurus deprofundis* (Stebbing, 1924), holotype ♀ (9.3 mm) from off Cape Morgan (NHM 1928.12.1.245). A. Shield and cephalic appendages. B. Arthrobranch lamella from gill of third maxilliped. C. Arthrobranch lamella from gill of fourth pereopod. D. Chela and carpus of right cheliped (setal density not precise). E. Chela and carpus of left cheliped (setal density not precise). F. Right second pereopod (lateral view). G. Propodus and carpus of left second pereopod (mesial view). H. Third left pereopod (lateral view). I. Dactyl and propodus of right fourth pereopod. J. Anterior lobe of sternite of third pereopods. K. Telson. Scales B–C, 0.50 mm; J, 1.0 mm; A, D–H, 5.0 mm.

Third maxilliped with very strong accessory tooth on crista dentata; merus with strong dorsodistal spine and small spine medially on ventral margin; carpus with small dorsodistal spine.

Ocular peduncles slightly more than half shield length; moderately short and stout, broader at base of cornea than proximally, dorsomesial surface with row of tufts of setae; corneas slightly dilated. Ocular acicles acutely triangular, dorsal surfaces somewhat concave, each with strong submarginal spine; separated basally by slightly less than basal width of one acicle.

Antennular peduncles over-reach distal margins of corneas by nearly entire length of ultimate segments. Ultimate segment with tuft of setae near dorsolateral distal angle, and few scattered surface setae. Penultimate segment with few scattered setae. Basal segment with very strong spine on lateral surface in distal half.

Antennal peduncles over-reach distal margins of corneas by nearly half length of ultimate segments, and reach approximately to distal half of ultimate segments of antennular peduncles. Fifth and fourth segments with scattered setae. Third segment with very strong spine at ventrodistal margin. Second segment with dorsolateral distal angle produced strongly, reaching distal half of fourth peduncular segment, with simple or bifid terminal spine, mesial margin with 7 or 8 small spines, lateral margin with tufts of long setae; dorsomesial distal angle with very strong spine. First segment with spine on distolateral margin dorsally; ventrolateral margin with 2 or 3 small spines. Antennal acicle arcuate, reaching distal half of ultimate peduncular segment, with strong terminal spine and numerous tufts of long stiff setae on mesial face. Antennal flagellum with 1 or 2 setae of moderate length (4 or 5 article length) every 5 or 6 articles proximally and more widely spaced distally.

Detached right cheliped (Fig. 7D) considerably stronger than left. Dactyl approximately as long as palm (although appearing slightly shorter in illustration); cutting edge with row of corneous teeth in distal third, 3 large, broad calcareous teeth proximally; terminating in strong corneous claw; small hiatus between dactyl and fixed finger; dorsal surface convex, marked by transverse rows of tufts of stiff setae and 2 small spines proximally; dorsomesial margin with double row of small spines proximally, becoming single row in distal 0.65 and accompanied by long setae; ventral surface with 3 longitudinal rows of long setae. Palm moderately slender; slightly shorter than carpus; dorsomesial margin with irregular double row of spines, some minutely corneous-tipped; dorsal surface convex, with 6 somewhat irregular rows of spines, and accompanied by scattered long stiff setae; dorsolateral margin not distinctly delimited, but with irregular row of spines extending on to tuberculate lateral face, ventral surface with low simple or multifid tubercles and scattered long stiff setae; fixed finger with 5 spines on dorsal surface and distinct row of short spines on dorsolateral margin, cutting edge with short row of corneous teeth distally and 2 large broad calcareous teeth proximally, lateral face with spinose tubercles proximally, tufts of short setae distally and on ventral surface. Carpus slightly shorter than merus; dorsomesial margin with irregular row of strong spines accompanied by adjacent slightly irregular row of spines on dorsal surface, separated by broad nearly naked longitudinal strip from median row of shorter spines, few scattered spines laterally; dorsolateral margin rounded but with row of small spines becoming double row distally; lateral face with forwardly directed spines and spinules; mesial face with scattered low protuberances and long setae; ventral surface with row of spines mesially and laterally. Merus with 2 spines on dorsodistal margin, dorsal margin with short transverse ridges; mesial face with perpendicular ridge distally presumably with setae now missing, scattered protuberances proximally; ventromesial margin with row of spines, strongest proximally; lateral face with transverse ridges more spinulose in ventral half, ventrolateral margin with row of subacute spines; ventral surface with few small spines. Ischium with row of widely-spaced, very small blunt tubercles on ventromesial margin.

Left cheliped (Fig. 7E) moderately long and slender. Dactyl with few spinules proximally on rounded dorsal surface, mesial face with 2 spinules proximally and transverse ridges accompanied by long setae. Palm approximately 0.75 length of carpus; dorsal surface convex, midline with double row of spines becoming less regular on proximal half of fixed finger and replaced by short transverse setose ridges distally; dorsomesial face with central row of spines and nearly double row of slightly smaller spines extending on to mesial face distally as low spinulose tubercles; dorsolateral face with several irregular rows of small tubercles, appreciably more spinose dorsally, but not extending to tip of fixed finger; ventrolateral margin delineated only proximally by row of very small, closely-spaced blunt spinules. Carpus approximately same length as merus; dorsodistal margin with 1 very strong spine and second spine directly beneath; dorsomesial margin with irregular row of strong spines, dorsal surface unarmed, slightly depressed, rounded dorsolateral margin with row of spines; lateral surface with semi-perpendicular rows of small tuberculate spines decreasing in size proximally, ventrolateral margin with row of small subacute spines; mesial surface with short transverse ridges, presumably accompanied by long setae; ventral surface with 2 blunt spines distally and tufts of long setae. Merus with 1 small spine at dorsodistal margin, dorsal margin and mesial face each with transverse ridges presumably accompanied by setae, becoming multispinose ventrally on mesial face; ventromesial margin with row of subacute spines proximally and small acute spine distally; lateral face with short transverse ridges becoming flattened multifid tubercles ventrally, ventrolateral margin with row of prominent spines becoming double row proximally. Ischium with row of small spinules on ventromesial margin and tiny spinule on ventrolateral margin.

Ambulatory legs (Fig. 7F–H) over-reaching left cheliped by at least 0.75 length of dactyls. Dactyls of left and right similar; moderately long and stout, 1.10–1.35 length of propodi; in dorsal view slightly twisted; in lateral view straight (second) or slightly curved (third); dorsal surfaces with transverse low protuberances and long stiff setae (many broken); lateral surfaces each with very faint longitudinal sulcus and row of long or moderately long setae; mesial faces each with transverse ridges and setae dorsally; ventral margins each with row of strong corneous spines (8 or 9 on second, 12 or 13 on third). Propodi of third pereopods slightly shorter than second; dorsal and lateral surfaces each with transverse low ridges and long stiff setae; mesial faces of second pereopods (Fig. 7G) each with longitudinal keel in ventral third, extending from near distal margin to proximal third. Carpi of second right with row of 5 spines, second left with row of 3 spines and transverse setose ridges on dorsal surfaces; dorsal surfaces of third each with only transverse setose ridges and dorsodistal spine; lateral faces all with short transverse ridges and long setae. Meri all with transverse setose ridges dorsally, ventral margins of second pereopods each with ventromesial row of spines, more numerous and stronger on left, ventrolateral distal angles each with spine; ventral margin of third right unarmed, third left with tiny spinule on ventrolateral margin and stronger spinule on ventromesial margin distally. Ischia each with row of very small spinules on ventromesial margins. Fourth pereopods (Fig. 7I) semichelate; propodal rasp consisting of 3 rows of small corneous scales. Sternite of third pereopods with submarginal row of setae on large subsemicircular anterior lobe (Fig. 7J). Sternite of fifth pereopods damaged, but still with dense setae.

Female with paired gonopores; no paired pleopods; 4 unpaired left pleopods (2–5), with rami of second nearly equal, third and fourth with exopod approximately half length of endopod, fifth with exopod markedly reduced. Uropods very asymmetrical. Telson (Fig. 7K) with deep mediolateral incision indicative of transverse suture separating anterior and posterior regions; asymmetrical posterior lobes separated by slender median cleft; terminal margins each with row of small calcareous spines becoming stronger toward outer angles, largest spines of left somewhat hooked.

Colour

Unknown for holotype. Other specimens in preservative: Shield mottled white and orange. Ocular peduncles orange; ocular acicles orange basally, white distally. Antennular peduncles whitish with orange flagella. Antennal peduncles faintly orange, darkest on proximal segments. Chelipeds with orange tint, darkest on dactyls. Ambulatory legs each with orange band proximally and distally on meri; carpi, propodi and dactyls all faintly orange, darkest on distal halves of dactyls. (After McLaughlin & de Saint Laurent 1998.)

Habitat

Holotype collected from depth of 457–585 m. Elsewhere specimens found in variety of gastropod shells, sometimes with attached anemone; 200–915 m.

Distribution

In South African waters, known only from type locality north-west of Cape Morgan; however, now recognized from southern Australia eastward to New Zealand; Philippines and Hawaiian islands.

Remarks

Stebbing's (1924) description of *P. deprofundis* (as *Eupagurus*) is not only brief, but very inaccurate; his illustrations are equally unsatisfactory. He remarked that the telson had a 'curiously produced lobe with calcified rim at the right extremity' and the right uropod was larger than the left. Clearly, as may be seen in Figure 7K, the telson is normally developed. Apparently Stebbing was looking at the telson with one of the two posterior lobes folded under. The abdomen of the holotype does twist strongly and it must have been this torsion that gave Stebbing the impression that he was looking at a larger right uropod. The specimen has normally asymmetrical uropods, the left is appreciably larger. The one remaining antennal flagellum is long, as Stebbing reported, but does not have the long setae depicted in his plate 5 (a.i.). It is probable that the flagellum was laying across one of the setose appendages and he attributed this setation to the flagellum. Stebbing did not actually describe the propodal rasp of the fourth pereopod, other than to say that it was like that of *Pagurus placens*; however, he illustrated a rasp with a single row of corneous scales (Stebbing 1924, pl. 5 (prp4)). We have re-examined the appendage and found that it has three rows of small corneous scales (Fig. 7I), rather than the single row of large scales he depicted.

Certain important morphological attributes of *Propagurus deprofundis* were overlooked by Stebbing, i.e., the gill number and structure, and the presence of a longitudinal keel on the mesial face of the propodus of each second pereopod. As indicated in the generic diagnosis, species of *Propagurus* have 13 pairs of symmetrical or asymmetrical trichobranchiate or intermediate gills (as defined by Lemaitre 1989). The degree of asymmetry observed in the holotype is greater than reported by McLaughlin & de Saint Laurent (1998) in specimens from Australia. The distinctive propodal keel (Fig. 7G) may actually represent a primitive stridulatory mechanism, used in conjunction with the tubercles on opposing lateral surfaces of the chelae.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 ***Nucula (Leda) bicuspidata*** Gould, p. 37.
1856 ***Leda plicifera*** A. Adams, p. 50.
1859 ***Laeda bicuspidata*** (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 ***Nucula largillierti*** Philippi, p. 87.
1871 ***Laeda bicuspidata*** (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 ***Leda bicuspidata*** (Gould): Nicklès, p. 163, fig. 301.
1955 ***Leda bicuspidata*** (Gould): Nicklès, p. 110.
1964 ***Leda bicuspidata*** (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

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PATSY A. MCLAUGHLIN
&
JACQUES FOREST

HERMIT CRABS OF THE GENUS *PAGURUS* FABRICIUS (CRUSTACEA, DECAPODA, PAGURIDAE FROM SOUTH-EASTERN SOUTH AFRICA

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OF THE SOUTH AFRICAN MUSEUM

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   (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88**: 100–140.

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THE TERRESTRIAL AMPHIPODS (CRUSTACEA, AMPHIPODA) OF SOUTH AFRICA

By

CHARLES L. GRIFFITHS

Cape Town Kaapstad

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THE TERRESTRIAL AMPHIPODS (CRUSTACEA: AMPHIPODA) OF SOUTH AFRICA

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(With 7 figures)

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ABSTRACT

A re-examination of all available terrestrial amphipod material from South Africa has resulted in the recognition of seven valid species. Four of these, *Talitriator calva*, *T. cylindripes*, *T. eastwoodae* and *T. setosa* were previously *formae* of *Talitriator* (formerly *Talitroides*) *eastwoodae* that have been raised to species rank elsewhere, but without being adequately diagnosed or figured. A fifth such species, *Talitriator macronyx*, is considered invalid and is here synonymized with *T. setosa*. *Talitriator africana*, which was first described over a century ago but has subsequently been considered either a synonym of *T. eastwoodae* or a *species inquirenda*, is re-erected. The remaining two taxa, *Talitroides alluaudi* and *T. topitotum* are introduced forms, both of which have been widely dispersed around the world, but are here recorded for the first time from South Africa. A brief diagnosis, illustrations and distribution data are provided for each of the species, and a key to the terrestrial amphipod fauna of the region is presented.

CONTENTS

INTRODUCTION

Amphipods are a primarily aquatic group, and only one family, the Talitridae, has successfully invaded the terrestrial environment. The talitrids have in fact colonized a broader variety of habitats than any other amphipod family and span both coastal marine and freshwater environments, in addition to terrestrial ones. In the past some confusion has surrounded the use of the term 'terrestrial' as applied to talitrid amphipods and this has prompted the adoption of a more specific terminology by Bousfield (1984) and Friend & Richardson

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(1986). These authors recognize four ecological groupings, as follows: (a) sandhoppers—burrowing forms found in the intertidal and supralittoral zones of sandy beaches; (b) beachfleas—non-burrowing species associated with algae on rocky shores or coastal marine habitats; (c) palustrid talitrids—which are semi-aquatic in salt marshes, mangroves and estuarine habitats; and (d) landhoppers—which occur mostly in forest litter and live independent of water bodies. It is only this last, truly terrestrial group that is considered here, the remaining groups having been included in a review of the southern African marine Amphipoda by Griffiths (1976).

Landhoppers are largely nocturnal, cryptic residents of the forest floor in the Southern Hemisphere and tropics, where they feed on angiosperm leaves and detritus. A few have colonized specialized habitats above ground, or live in moist grasslands and caves, and at least one has taken to burrowing in the soil (Friend & Richardson 1986). Most species are local endemics, although a few so-called 'tramp' species have been widely dispersed by man (Bousfield 1984).

The taxonomic history of the South African terrestrial amphipod fauna is a long and confusing one. The first species recorded from the region was *Talorchestia? africana*, described by Bate (1862) from a single female collected in Port Natal (= Durban). Although Stebbing (1910) included this species in his *Catalogue of South African Crustacea*, Methuen (1913) made no mention of Bate's paper when describing a second terrestrial species, *Talitriator eastwoodae*, from the Northern Transvaal. This was possibly because Methuen was under the mistaken impression that his species was aquatic, rather than terrestrial, in its habits. Barnard (1916) expanded on Methuen's description of *Talitriator eastwoodae*, recognized that it is in fact a terrestrial form, and allocated additional material to the species from various sites around South Africa. Shortly thereafter Stebbing (1917) synonymized Methuen's species with Bate's under the earlier name *Talitriator africanus* (Bate).

In a later paper, Barnard (1940) accepted Schellenberg's (1934) recommendation that *Talitriator* should fall into synonymy with *Talitroides*, but rejected Stebbing's synonymy of *Talitroides eastwoodae* with *T. africanus*—largely on the basis of differences in the degree of expansion of article 5 of gnathopod 1, which is distinctly lobed in *eastwoodae*, but distinctly linear in Bate's figure of *africanus*. He also recognized, but only very briefly characterized, five distinct *formae* of *Talitroides eastwoodae*, these being based largely on the relative lengths of antenna 1 and 2, the form of gnathopod 1, and the structure of the pleopods. Finally, Bousfield (1984) elevated each of Barnard's *formae* to full specific status within the genus *Talitriator*, but without providing any additional descriptions or figures. The departure point from which this study develops is thus one in which the recognized terrestrial amphipod fauna of the region consists of five species of *Talitriator*, of which only one, *T. eastwoodae*, has ever been adequately described or illustrated. One additional form, *T. africana*, is of dubious status and is presently a *species inquirenda*.

The principal aims of this paper are to clarify the taxonomic status of each of the terrestrial amphipods previously reported from South Africa, to identify any new or unrecorded forms, to establish the distribution patterns of the species, and to provide diagnoses and illustrations of the key features of each. This information is also used to produce a key to the regional fauna.

MATERIALS AND METHODS

A written appeal for terrestrial amphipod material was sent to all natural history museums in South Africa and a similar notice circulated via e-mail to members of the Zoological Society of southern Africa. The principal collections eventually examined were those of the South African Museum, the Transvaal Museum and the Natal Museum—these being the main institutions in the region that maintain wet invertebrate collections. Additional material was collected by the author, or contributed by individual researchers who responded to the appeal for specimens. These additional collections have been deposited in the South African Museum, Cape Town. Drawings were done with the aid of a camera lucida attached to a Wild stereo microscope and a Nikon compound microscope.

TAXONOMY

KEY TO THE TERRESTRIAL AMPHIPODS OF SOUTH AFRICA

1A. Pleopod 3 greatly reduced, less than half as long as pleopods 1 and 2 and either lacking rami, or with the single (inner) ramus reduced to a one-segmented vestige (*Talitroides*) 2

1B. Pleopod 3 not greatly reduced, more than half as long as pleopods 1 and 2 and distinctly biramous (*Talitriator*) 3

2A. Pleopod 3 a minute unsegmented vestige; antenna 2 about 25 per cent body length, flagellum equal to peduncle (Fig. 1A, E); adult body length not exceeding 7 mm .... *Talitroides alluaudi*

2B. Pleopod 3 a short, slender peduncle with a single, one-segmented inner ramus; antenna 2 about half body length, flagellum 1.5 times length of peduncle (Fig. 1G, K); adult body length up to 13 mm .... *Talitroides topitotum*

3A. Antenna 1 extending beyond mid-point of article 5 of antenna 2; pleopods long and slender (Figs 2, 5); distribution mostly east of 26°E (*c.* Port Elizabeth) 4

3B. Antenna 1 not extending as far as mid-point of article 5 of antenna 2; pleopods short and stout (Figs 3, 4, 6); distribution mostly west of 26°E (*c.* Port Elizabeth) 5

4A. Article 6 of gnathopod 1 with distinct palm; outer margins of peduncles of pleopods setose throughout; rami of pleopods 1 and 2 equal; coxal gills of pereopods 3–5 with branched, three-digitate posterior processes (Fig. 5) .. .. *Talitriator eastwoodae*

4B. Article 6 of gnathopod 1 tapering, without palm; outer margins of peduncles of pleopods normally setose only distally; rami of pleopods unequal, outer 80 per cent length of inner; coxal gills of pereopods 3–5 with simple posterior lobes (Fig. 2) .... *Talitriator africana*

5A. Article 5 of gnathopod 1 not lobed posteriorly; article 6 tapering distally, without distinct palm, antenna 2 about half body length, pereopod 7 extending well beyond tip of uropods (Fig. 4) .... *Talitriator cylindripes*

5B. Article 5 of gnathopod 1 distinctly lobed posteriorly, article 6 rectangular, with distinct palm, antennae usually one-third or less body length, pereopod 7 not extending well beyond tip of uropods (Figs 3, 6) 6

6A. Pleopod 1 shorter than 2 or 3, peduncles of pleopods 2 and 3 (and sometimes 1) setose along outer margins, rami subequal in length (Fig. 6) .... *Talitriator setosa*

6B. Pleopod 1 longer than 2 or 3, peduncles of pleopods not setose, rami globular in appearance, the inner in each case considerably the shorter, 50–70 per cent length of outer (Fig. 3) .... *Talitriator calva*

Talitroides Willem, 1898

This genus currently comprises just two species, *Talitroides alluaudi* and *T. topitotum*. Both are unusual amongst terrestrial amphipods in that they have been widely dispersed by man, undoubtably along with soil and leaf mould carried with exotic plants. Indeed their dispersal has been so widespread that it has become difficult to determine where the species originated. In Hawaii *Talitroides* spp. have largely displaced native species and may pose a threat to their future survival (Friend & Lam 1985), but as yet neither species has been recorded outside of urban areas in South Africa.

Both *Talitroides* species are easily distinguished from *Talitriator* spp. (below) by the reduced form of their pleopod 3.

Talitroides alluaudi (Chevreux, 1896)

Fig. 1A–F

Talitrus Alluaudi Chevreux, 1896: 112, figs 1–4. Chevreux & Fage, 1925, figs 280–281.
Talitroides alluaudi: Morino & Ortal, 1993: 332–338, figs 1–2. Stock & Biernbaum, 1994: 809.

Distribution

Recorded only from compost heaps in the nursery of the University of Cape Town and suburban gardens in the nearby suburb of Claremont.

Diagnosis

At a maximum length of only 5–6 mm *T. alluaudi* is smaller than any other South African landhopper. The species is best recognized by its minute, unsegmented pleopod 3 and the greatly reduced, 1–3 articulate inner rami of pleopods 1–2. Both antennae and pereopod 7 are also unusually short, antenna 1 being only 25 per cent of body length (as compared to 50 per cent in *T. topitotum*).

Remarks

Talitroides alluaudi was originally described from material collected in Paris (where it was certainly introduced), and from the Seychelles. Present distribution records include the Seychelles, Madagascar, Australia, various Atlantic

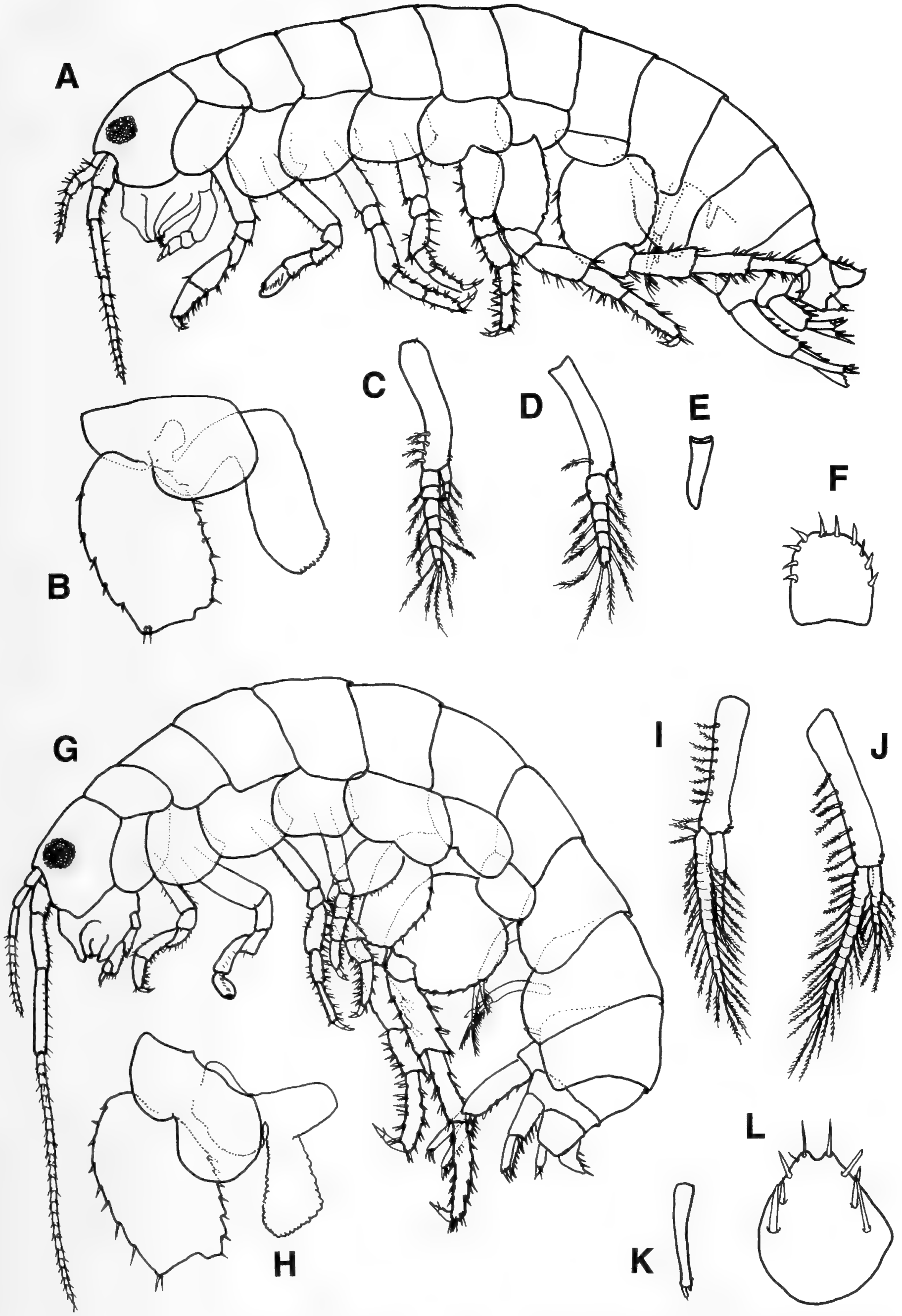

Fig. 1. A–F. *Talitroides alluaudi* (Chevreux, 1896), male, 5 mm, UCT gardens. A. Lateral aspect. B. Base of pereopod 6 showing gill. C–E. Pleopods 1, 2, 3. F. Telson. G–L. *Talitroides topitotum* (Burt, 1934), male, 11 mm, Pinelands, Cape Town. G. Lateral view. H. Base of pereopod 6 showing gill. I–K. Pleopods 1, 2, 3. L. Telson.

and Pacific islands, the USA, and most European countries (Friend & Richardson 1986), as well as Israel (Morina & Ortal 1993) and now South Africa. The present material agrees closely with the detailed description given in Morino & Ortal (1993).

Talitroides topitotum (Burt, 1934)

Fig. 1G–L

Talitrus (Talitropsis) topitotum Burt, 1934: 184–190, pls 12–13, text-fig. 1.
Talitrus sylvaticus (*non* Haswell, 1880): Shoemaker, 1936: 60–64, figs 1–2.
Talitroides topitotum: Friend & Lam, 1985: 27–33, figs 1–2.

Distribution

Recorded only from a suburban garden in Pinelands, Cape Town, and the gardens of the University of Pretoria.

Diagnosis

Most easily distinguished from *T. alluaudi* (above) by the much larger size of up to 13 mm body length, the longer antenna 2, which is about 45 per cent of body length, and the more elongate pleopod 3, which retains minute single-segmented vestigial rami.

Remarks

Like *T. alluaudi*, *T. topitotum* is a 'tramp' species, which has been widely dispersed by man. The species was originally described by Burt (1934) from specimens found under a packing case in a garage in Ceylon (Sri-Lanka). Subsequent records include Southern India, Australia, various Indian, Pacific and Atlantic ocean islands, Brazil, the USA, and glasshouses in Europe (Friend & Richardson 1986). This is the first record from Africa. The distribution is now so widespread that it is difficult to determine where the species originated.

The present material corresponds closely to the descriptions given by Shoemaker (1936), who incorrectly identified his material as *Talitrus sylvaticus*, and by Friend & Lam (1985). Although Shoemaker reported the species as occasionally reaching pest densities in Californian gardens, introduced landhoppers are not normally considered as problem animals, since they are decomposers of dead organic material and do not feed on the living tissues of plants.

Talitriator Methuen, 1913

As currently defined this genus is endemic to southern Africa and the only species are those detailed below. The author has received unconfirmed reports of terrestrial amphipods occurring north into Zimbabwe, but has to date not been able to obtain specimens to confirm the identity of the species concerned.

Talitriator africana (Bate, 1862)

Fig. 2

Talorchestia? Africana Bate, 1862: 15–16, pl. 2 (fig. 6). Stebbing, 1910: 459.
Talitriator africanus: Stebbing, 1917: 330–331 (*partim*).
Talitroides eastwoodae forma *typica*: Barnard, 1940: 465–467 (*partim*).

Distribution

Widespread from Port Elizabeth along a broad coastal strip northwards and eastwards to northern KwaZulu-Natal and then inland through Swaziland into Mpumalanga (formerly Eastern Transvaal) (Fig. 7).

Diagnosis

Antenna 1 relatively elongate, reaching almost to tip of article 5 of antenna 2; antenna 2 about one-third body length. Article 5 of gnathopod 1 moderately lobed posteriorly, length about twice width; article 6 elongate, tapering distally, without a distinct palm; article 6 of gnathopod 2 broadly rounded distally. Pereopods relatively short, tip of pereopod 7 barely extending to end of body. Pleopods slender and elongate; pleopod 2 slightly longer (105 per cent) than 1, pleopod 3 65 per cent length of 1; peduncles slender, 4–6 times longer than wide, outer margins typically setose only along distal half (rarely setose along whole margin); inner rami of pleopods 1 and 2 equal to peduncle; outer rami 80 per cent length of inner; pleopod 3 with outer ramus 75 per cent and inner ramus 60 per cent length of peduncle. Telson usually with four strong lateral and one terminal spine on each lobe (lateral spines reduced to one or absent in some Eastern Cape and Mpumalanga specimens). Coxal gills relatively simple, that of gnathopod 2 smooth-edged, with a long upward-lobed anterior process, of pereopods 3 and 4 smaller and postero-ventrally produced into a pointed lobe, of pereopod 5 the smallest and a simple twisted lobe, of pereopod 6 much larger, with an oval basal lobe and larger flat plate.

Remarks

Bate's original (1862) description of this species from Port Natal (Durban) is the first record of a terrestrial amphipod from South Africa. However, neither Methuen (1913), in his description of *T. eastwoodae*, nor Barnard (1916), referred to Bate's species, although it had been listed by Stebbing (1910). Stebbing (1917) subsequently synonymized the two forms—*africana* taking precedence. Barnard (1940) pointed out inconsistencies between the descriptions of *T. africana* and *T. eastwoodae*—principally as regards the shape of article 5 of gnathopod 1, but—unable to examine material from the type locality—nevertheless retained their synonymy under the name *T. eastwoodae* forma *typica*.

Based on examination of a wide range of material, including the co-types of *T. eastwoodae* held by the South African Museum, it is now clear that two distinct species are represented. These are Methuen's *T. eastwoodae*, which is the dominant talitrid in the inland regions of KwaZulu-Natal and the former Transvaal, and Bate's *T. africana*, which is formally re-erected here and is the

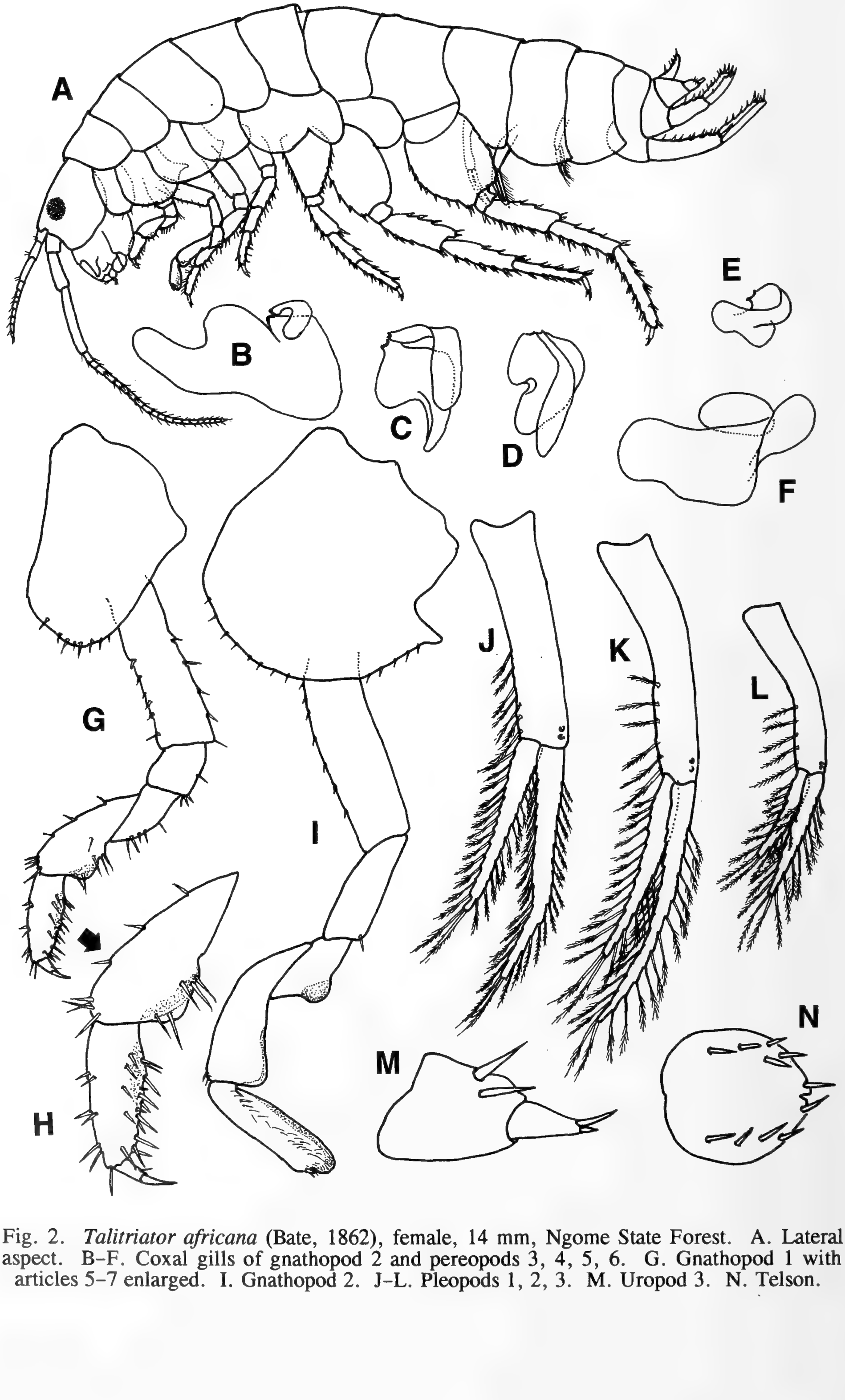

Fig. 2. *Talitriator africana* (Bate, 1862), female, 14 mm, Ngome State Forest. A. Lateral aspect. B–F. Coxal gills of gnathopod 2 and pereopods 3, 4, 5, 6. G. Gnathopod 1 with articles 5–7 enlarged. I. Gnathopod 2. J–L. Pleopods 1, 2, 3. M. Uropod 3. N. Telson.

most common terrestrial amphipod in the coastal areas of KwaZulu-Natal and the Eastern Cape. *Talitriator africana* is most easily distinguished from *T. eastwoodae* by the absence of a palm on article 6 of gnathopod 1 and the unequal rami of pleopods 1–3.

The species shows some local variation, notably in the setation of the peduncles of the pleopods, which is generally restricted to the distal half, but rarely extends over the full length. In some samples towards the fringes of the distribution range the lateral spines on the telson are also absent or reduced to one.

Talitriator calva (Barnard, 1940)

Fig. 3

Talitroides eastwoodae forma *calva* Barnard, 1940: 468.
Talitriator calva: Bousfield, 1984: 206, 209.

Distribution

From Cape Town eastwards along a coastal belt to Grahamstown in the Eastern Cape Province (Fig. 7).

Diagnosis

Antenna 1 short, article 1 of peduncle wider than long, flagellum not extending more than half way along article 5 of antenna 2. Antenna 2 typically only about one-third body length (longer to the east). Article 5 of gnathopod 1 lobed posteriorly, twice as long as wide, article 6 widest at base and tapering distally, with distinct palm. Pleopods progressively decreasing in length, the second 90 per cent and the third 80 per cent as long as the first. Peduncles of pleopods not setose, rami unjointed, but incisions marking the limits of the segments deep, such that the rami appear as a series of subglobose segments; inner ramus of each pair considerably the shorter, that of pleopod 1 70 per cent, of pleopod 2 60 per cent and of pleopod 3 50 per cent length of outer ramus. Coxal gill on gnathopod 2 a simple forward-directed lobe, of pereopods 3–5 a folded oval plate and of pereopod 6 a complex structure of several elongate lobes. Telson usually with a single apical spine, but one or two lateral spines present in some Eastern Cape samples.

Remarks

In his brief description, Barnard (1940) implied, by his comparison with *T. setosa*, that the rami of the pleopods in this form are subequal. This is not the case, although the differences in the relative lengths of the rami in specimens to the east of the range are less marked than depicted here. The absence of setae on the peduncles of all the pleopods and their globular, unsegmented rami are characteristic of the species. Samples from the Eastern Cape have longer antenna 2 (up to 25 flagellar segments) and pereopods and have one or two lateral spines on the telson.

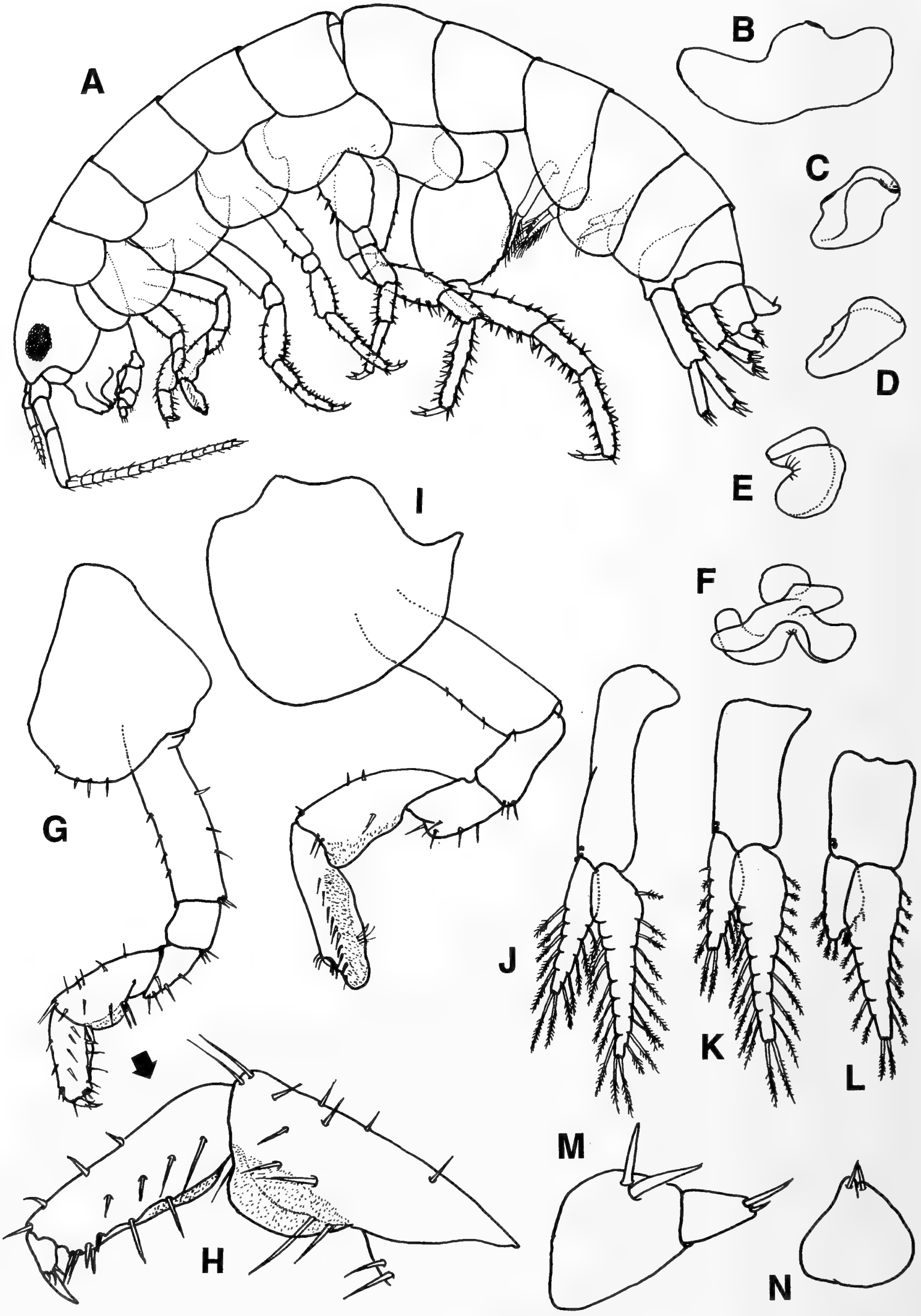

Fig. 3. *Talitriator calva* (Barnard, 1940), male, 9 mm, Onrustriver. A. Lateral aspect. B–F. Coxal gills of gnathopod 2 and pereopods 3, 4, 5, 6. G. Gnathopod 1 with articles 5–7 enlarged. I. Gnathopod 2. J–L. Pleopods 1, 2, 3. M. Uropod 3. N. Telson.

Talitriator cylindripes (Barnard, 1940)

Fig. 4

Talitroides eastwoodae forma *cylindripes* Barnard, 1940: 467, fig. 27e–h.
Talitriator cylindripes: Bousfield, 1984: 207, 209.
Talitriator insularis Stock & Biernbaum, 1994: 800–808, figs 2–6.

Distribution

From Table Mountain and the Cape Peninsula eastwards to Hermanus and north to Picketberg (Fig. 7).

Diagnosis

Antenna 1 short, reaching less than half way along article 5 of antenna 2; antenna 2 relatively elongate, about half as long as body and with flagellum of up to 28 segments. Article 5 of gnathopod 1 parallel-sided, not lobed posteriorly, length 3 times width; article 6 evenly tapering, palm very poorly developed. Article 6 of gnathopod 2 produced into a long, slightly upturned, rugose lobe. Pereopods elongate, the sixth and seventh reaching well beyond tips of uropods. Coxa 4 with a characteristic long, down-turned posterior tooth. Coxal gill of gnathopod 2 with large, forward-projecting lobe, of pereopods 3–5 smaller and bilobed, of pereopod 6 large and complex with crenulate margin posteriorly. Pleopods relatively short and stout, peduncles setose only along distal margin, peduncle of pleopod 1 expanded distally, rami swollen proximally and unequal, the inner two-thirds as long as the outer. Pleopods 2 and 3 progressively shorter, 70 per cent and 60 per cent length of pleopod 1 respectively, inner rami half as long as outer, not visibly segmented. Each lobe of telson with 2–3 dorsal and a single apical spine.

Remarks

Although originally described as a form of *T. eastwoodae*, this taxon clearly merits specific status, as recommended by Bousfield (1984). Characteristic features include the linear article 5 and long tapering article 6 of gnathopod 1, long upturned tip to article 6 of gnathopod 2 and unique form of the pleopods.

Talitriator insularis, as described from Ascension and Saint Helena islands by Stock & Biernbaum (1994), is clearly synonymous with *T. cylindripes*. Stock & Biernbaum indeed suspected that their species had been introduced from South Africa, but were misled into describing it as new by the poor quality of the original illustrations in Barnard (1940), which exaggerate the length and slenderness of articles 5 and 6 of gnathopod 1 in *T. cylindripes*.

Talitriator eastwoodae Methuen, 1913

Fig. 5

Talitriator eastwoodae Methuen, 1913: 109–112, pl. 10–22. Barnard, 1916: 223–224 (*partim*). Bousfield, 1984: 206, 209.
Talitroides eastwoodae forma *typica* Barnard, 1940: 465–467 (*partim*), fig. 27a–d.

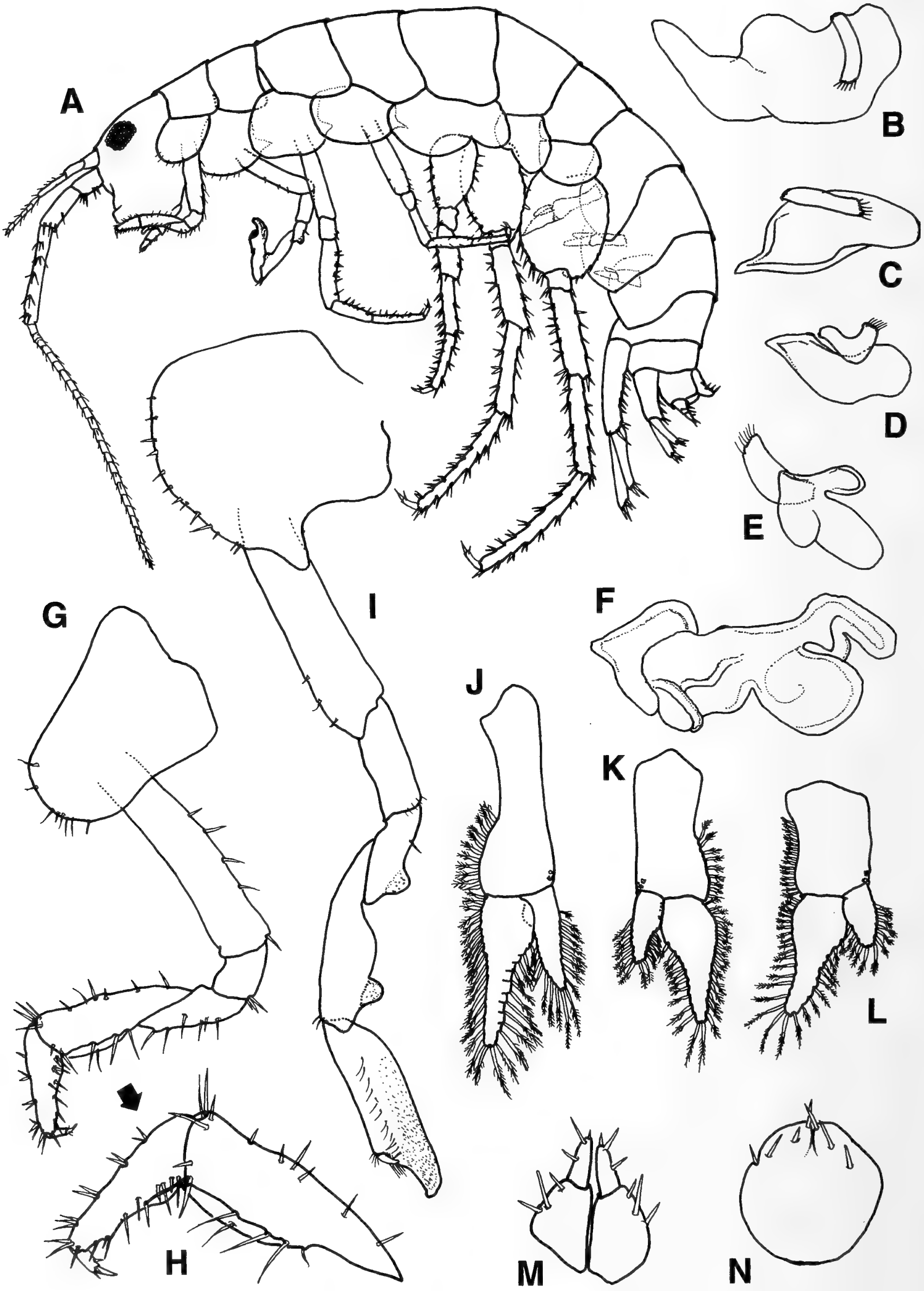

Fig. 4. *Talitriator cylindripes* (Barnard, 1940), male, 12 mm, Constantia, Cape Town. A. Lateral view. B–F. Coxal gills of gnathopod 2 and pereopods 3, 4, 5, 6. G. Gnathopod 1 with articles 5–7 enlarged. I. Gnathopod 2. J–L. Pleopods 1, 2, 3. M. Uropod 3. N. Telson.

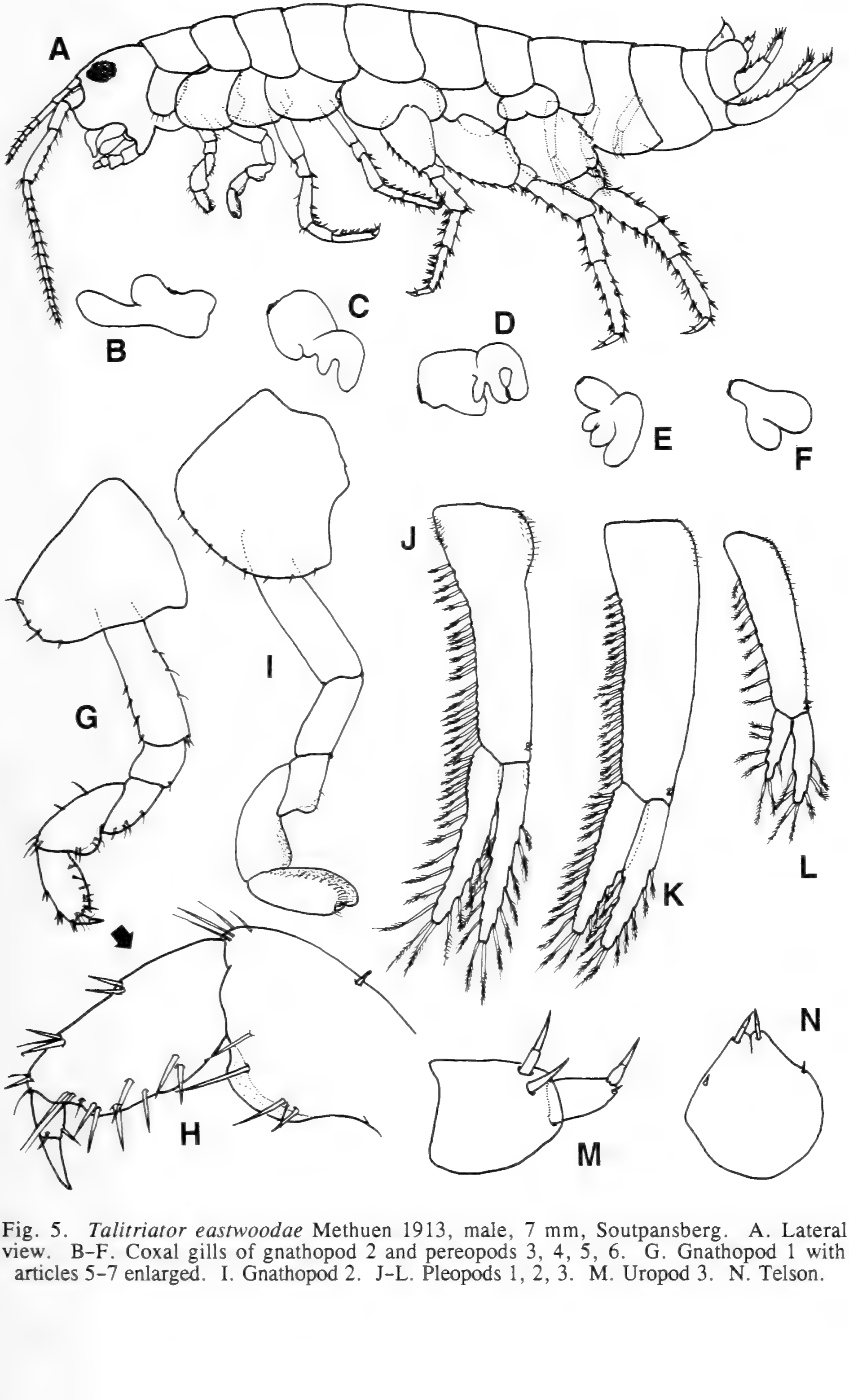

Fig. 5. *Talitriator eastwoodae* Methuen 1913, male, 7 mm, Soutpansberg. A. Lateral view. B–F. Coxal gills of gnathopod 2 and pereopods 3, 4, 5, 6. G. Gnathopod 1 with articles 5–7 enlarged. I. Gnathopod 2. J–L. Pleopods 1, 2, 3. M. Uropod 3. N. Telson.

Distribution

In a broad band from southern KwaZulu-Natal northwards into Northern Province, but well inland from the coast (Fig. 7).

Diagnosis

Antenna 1 relatively elongate, extending almost to tip of article 5 of antenna 2; antenna 2 about one-third body length. Article 5 of gnathopod 2 distinctly and broadly lobed posteriorly, length twice width, article 6 relatively short, with distinct palm. Pleopods relatively elongate, their peduncles slender, linear and at least four times as long as broad, outer margins setose throughout. Pleopods 1 and 2 equal in length, pleopod 3 only 65 per cent as long. Rami of pleopods 1 and 2 equal, but outer ramus of pleopod 3 only 70 per cent length of inner. Each lobe of telson with a single lateral and one strong terminal spine. Coxal gills of pereopods 3–5 each with a three-digitate posterior lobe.

Remarks

This species was accurately described by Methuen (1913), but Barnard (1916) subsequently (and incorrectly) referred all other landhopper material from South Africa to this species. In 1940, he subdivided this material into a series of recognized forms, allocating all specimens collected east of 26°E to his forma *typica*. These forms were raised to species rank by Bousfield (1984). In the present analysis, two species are recognized from the material formerly allocated to *T. eastwoodae* forma *typica*—Methuen's original *Talitriator eastwoodae* and Bate's long-obscure *T. africana*, which is re-erected for specimens mainly from the KwaZulu-Natal region.

Talitriator eastwoodae can be distinguished from all species found in the western regions of South Africa by its longer antenna 1 and pleopods, and from *T. africana* by having a palm on gnathopod 1, setae along the entire outer margins of the pleopod peduncles, equal rami on pleopods 1 and 2 and complex digitate coxal gills on pereopods 3–5. Some specimens have lateral spines on the telson that are considerably stronger than shown in the illustration.

Talitriator setosa (Barnard, 1940)

Fig. 6

Talitroides eastwoodae forma *setosa* Barnard, 1940: 467.
Talitroides eastwoodae forma *macronyx* Barnard, 1940: 468, fig. 27 i, j.
Talitriator setosa: Bousfield, 1984: 206, 209.
Talitriator macronyx: Bousfield, 1984: 206, 209.

Distribution

In high-lying areas from Table Mountain northwards into the Cederberg and eastwards to the Langeberg Mountains near Heidelberg (Fig. 7).

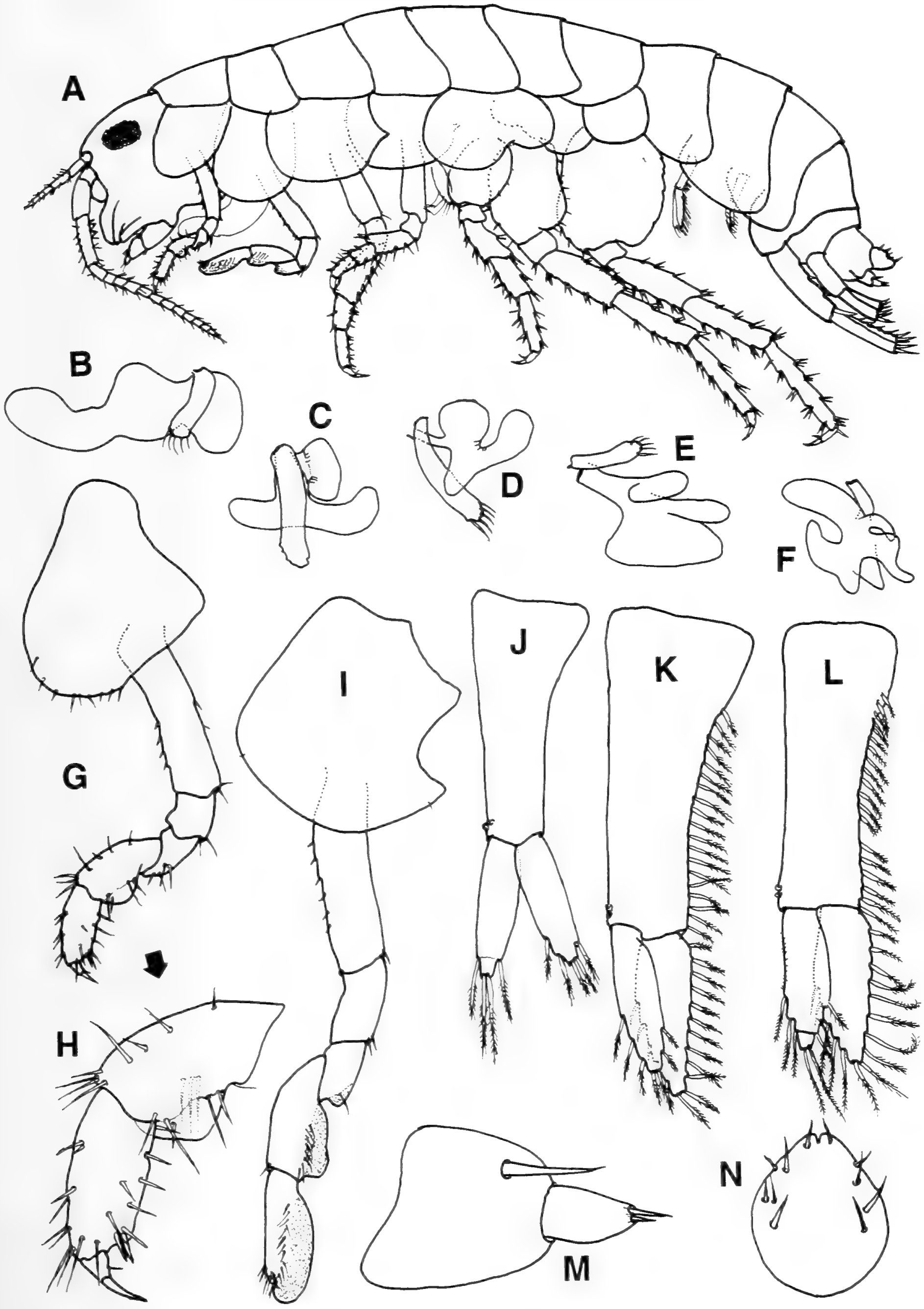

Fig. 6. *Talitriator setosa* (Barnard, 1940), female, 8 mm, Constantiaberg, Cape Peninsula. A. Lateral view. B–F. Coxal gills of gnathopod 2 and pereopods 3, 4, 5, 6. G. Gnathopod 1 with articles 5–7 enlarged. I. Gnathopod 2. J–L. Pleopods 1, 2, 3. M. Uropod 3. N. Telson.

Diagnosis

Antennae short, article 1 of antenna 1 wider than long, tip of flagellum reaching less than half way along article 5 of antenna 2; antenna 2 short, only about 25 per cent body length. Article 5 of gnathopod 1 lobed posteriorly, length about twice width, article 6 with distinct palm. Pleopods with elongate peduncles and shorter, subequal rami. Pleopod 1 75 per cent length of 2 or 3, peduncle setose along outer margin or not, rami half length of peduncle. Peduncles of pleopods 2 and 3 with close-set plumose setae along whole outer margin, rami equal and 65 per cent length of peduncle. Coxal gill of gnathopod 2 an elongate forward-projecting lobe, of pereopods 3–5 variously branched lobes on narrow stalks, and of pereopod 6 a complex, branched structure. Each lobe of telson with 4–5 dorsal and one terminal spine.

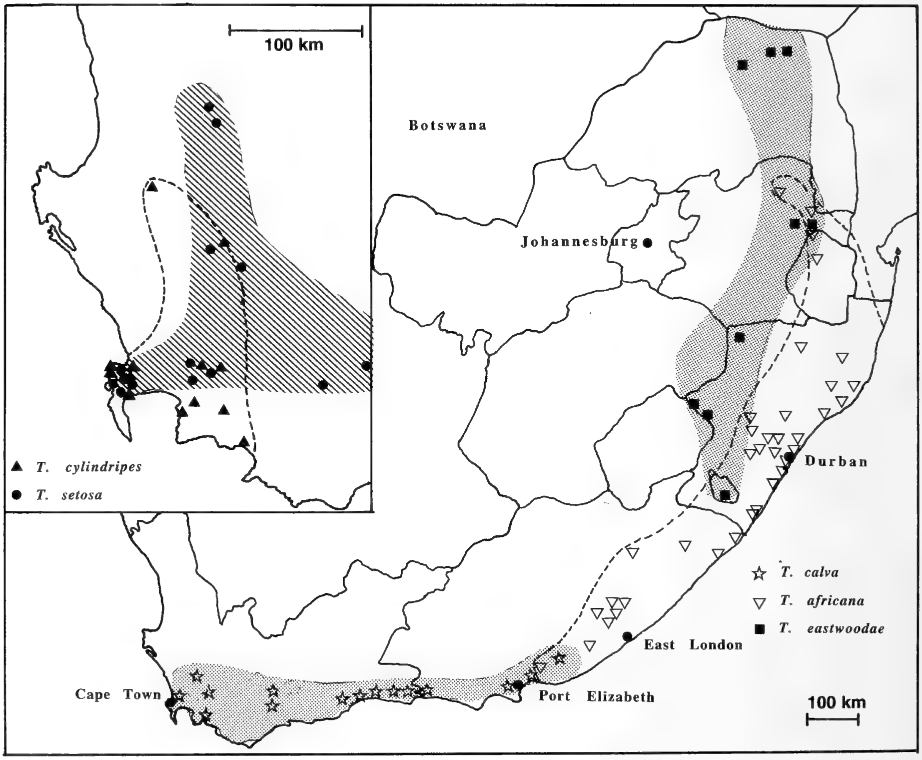

Fig. 7. Map of South Africa showing distributional records and ranges of the known species of *Talitriator*.

Remarks

In his brief description, Barnard (1940) described the pleopods of this form as having close-set plumose setae along the whole of the sinuous outer margin of the peduncle, although he found some specimens in which only the distal third of the peduncles was setose. The present material is inconsistent in this character, at least as regards pleopod 1, where the setae range from absent to lining most of the outer margin of the peduncle. The peduncles of pleopods 2 and 3 are uniformly setose throughout.

The unusual shortened pleopod 1 readily identifies this species. It is often found together with *T. cylindripes*, from which it can be distinguished in the field by its much shorter antenna and pereopods. Live specimens collected by the author were bright orange in life, although this faded quickly in alcohol.

Talitriator macronyx is hereby synonymized with *T. setosa*. On the basis of Barnard's extremely brief diagnosis, he distinguished his forma *macronyx* from forma *setosa* essentially on two counts—the unlobed form of article 5 and elongate, strongly spined article 6 of gnathopod 1 and the unusually long ingues on both gnathopods and pereopods. I found his diagram of gnathopod 1 to be exaggerated in this regard and the actual specimens to show a broadened article 5 and shorter article 6 of gnathopod 1, very similar to that depicted for *T. setosa* in Figure 6. Similarly the spinule on the dactyl of gnathopod 1 and the elongate ungues are not significantly more pronounced or elongate than those of *T. setosa*. The fact that *T. macronyx* was recorded only from a single sample that falls well within the range of *T. setosa* also suggests that it simply represents an extreme form of *T. setosa*.

ACKNOWLEDGEMENTS

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 *Nucula (Leda) bicuspidata* Gould, p. 37.
1856 *Leda plicifera* A. Adams, p. 50.
1859 *Laeda bicuspidata* (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 *Nucula largillierti* Philippi, p. 87.
1871 *Laeda bicuspidata* (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 *Leda bicuspidata* (Gould): Nicklès, p. 163, fig. 301.
1955 *Leda bicuspidata* (Gould): Nicklès, p. 110.
1964 *Leda bicuspidata* (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

CHARLES L. GRIFFITHS

THE TERRESTRIAL AMPHIPODS (CRUSTACEA, AMPHIPODA) OF SOUTH AFRICA

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ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

FISCHER, P. H. 1948. Données sur la résistance et de la vitalité des mollusques. *Journal de conchyliologie* **88**: 100–140.

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DEEP-SEA HOLOTHUROIDS TAKEN BY THE R.V. *AFRICANA II* IN 1959, FROM OFF THE WEST COAST OF THE CAPE PENINSULA, SOUTH AFRICA

By

AHMED S. THANDAR

Cape Town Kaapstad

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(With 16 figures and 2 tables)

[*MS accepted 11 June 1998*]

ABSTRACT

Some 106 specimens of deep-sea holothuroids taken by the R.V. *Africana II* cruises off the west coast of the Cape Peninsula, South Africa, in 1959 by the then Division of Sea Fisheries, are diagnosed and/or described.

The material is distributed over 10 families, 13 genera, 15 nominal and two indeterminate species, and includes three recently described species (Thandar 1998), a new species, *Molpadia millardae*, and nine new records for the southern African region, south of the tropic of Capricorn. Previous records of *Echinocucumis typica* sensu Clark, 1923 (*non* Sars, 1859), and *Sphaerothuria talismani* (partim) sensu Deichmann, 1930 (*non* E. Perrier, 1886), are based on misidentifications of *Ypsilothuria bitentaculata* (Ludwig, 1893).

CONTENTS

Ann. S. Afr. Mus. **105** (9), 1999: 363–409, 16 figs, 2 tables.

INTRODUCTION

Numerous specimens plus some fragments of deep-sea holothuroids taken during the months of August and December 1959, by the then Division of Sea Fisheries' R.V. *Africana II* routine cruises off the west coast of the Cape Peninsula, South Africa, have until now remained undescribed. The material was deposited in the South African Museum (SAM). Subsequently, most of the material was sent to the late Dr Cherbonnier of the Museum National d'Histoire Naturelle, Paris (MNHN) for identification and reporting. Duplicates of the samples and some other remaining material was loaned to the author for inclusion in his monograph of the southern African Holothuroidea that was being prepared for a doctoral thesis. The thesis was completed some time ago (see Thandar 1984) but the results of the R.V. *Africana II* collections were not published, awaiting a report of the material at the MNHN. Since no report was forthcoming and after the retirement of Dr Cherbonnier, the writer asked the SAM to request a return of the specimens from France. This was acceded to and on their arrival the specimens were forwarded to the writer.

All the R.V. *Africana II* material was collected with a 15-foot beam trawl from nine deep-sea localities off the west coast of the Cape Peninsula between latitudes 33°26'S and 34°42'S and longitudes 16°15'E and 17°21'E, in water depths ranging from 2 269 to 3 257 m. All material studied is deposited in the SAM, under SAM–A catalogue numbers. The R.V. *Africana II* stations, the species taken from each station and other pertinent data are listed below. Full station lists and other data for the period 1 April 1959 to 31 March 1960 can be found in the Division of Sea Fisheries Annual Report (Anon. 1963: 204–213).

R.V. *AFRICANA II* STATIONS, SPECIES AND OTHER DATA

A 190, west of Dassen Island, 33°26'S 16°33'E, 26 August 1959, 2 268–2 377 m.

SAM–A22149, *Ypsilothuria bitentaculata* (Ludwig), 13 specimens.
SAM–A27715, *Elpidia gracilis* Belyaev, 1 specimen and 2 fragments.

A 191, west of Dassen Island, 33°36'S 16°15'E, 26 August 1959, 2 780–2 871 m.

SAM–A22165, *Laetmogone perplexa* Thandar, 1998 (holotype), 1 specimen.
SAM–A27716, *Benthodytes lingua* R. Perrier, 1 specimen.
SAM–A27717, *Benthodytes valdiviae* Hansen, 2 specimens.
SAM–A22175, *Benthodytes ?typica* Théel, 1 specimen.

A 193, west of Cape Town, 33°50'S 17°21'E, 26 August 1959, 2 268 m.

SAM–A22147, *Scotoplanes globosa* Théel, 4 specimens.

A 315, west of Cape Point, 34°37'S 17°03'E, 8 December 1959, 2 890–2 963 m.

SAM–A27718, *Echinocucumis hispida* (Barrett), 1 specimen.
SAM–A22150, *Ypsilothuria bitentaculata* (Ludwig), 7 specimens.
SAM–A22169, *Molpadia millardae* sp. nov., 1 specimen (paratype).

A 316, south-west of Cape Point, 34°42'S 16°54'E, 8 December 1959, 3 155–3 255 m.

SAM–A22146, *Paracucumaria capense* Thandar, 1998, 2 specimens.
SAM–A27719, *Psolidium vitreum* Ohshima, 1 specimen.
SAM–A22155, *Psolidothuria octodactyla* Thandar, 1998, 1 specimen.
SAM–A22145, *Psolidothuria octodactyla* Thandar, 1998, 1 specimen.
SAM–A22130, *Echinocucumis hispida* (Barrett), 3 specimens.
SAM–A22142, *Echinocucumis hispida* (Barrett), 1 specimen.
SAM–A22143, *Echinocucumis hispida* (Barrett), 3 specimens plus fragments.
SAM–A22158, *Orphnurgus protectus* (Sluiter), 1 specimen.
SAM–A22156, *Meseres atlanticus* (R. Perrier), 2 specimens.
SAM–A22172, *Peniagone* sp. indet., 1 specimen.

A 317, west of Saldanha Bay, 33°15'S 16°30'E, ?8/9 December 1959, 2 708–3 038 m.

SAM–A22151 *Ypsilothuria bitentaculata* (Ludwig), 1 specimen.

A 318, west of Cape Peninsula, 33°52'S 16°51'E, 9 December 1959, 2 524–2 780 m.

SAM–A22166, *Paracucumaria capense* Thandar, 1998, 1 specimen.
SAM–A27722, *Paracucumaria capense* Thandar, 1998, 3 specimens.
SAM–A22164, *Psolidothuria octodactyla* Thandar, 1998, 1 specimen (holotype).
SAM–A27710, *Psolidothuria octodactyla* Thandar, 1998, 2 specimens (paratypes).
SAM–A27590, *Psolidothuria octodactyla* Thandar, 1998, 3 specimens.
SAM–A27720, *Echinocucumis hispida* (Barrett), 1 specimen.
SAM–A27721, *Echinocucumis hispida* (Barrett), 4 specimens.
SAM–A22167, *Echinocucumis hispida* (Barrett), 2 specimens.
SAM–A22132, *Ypsilothuria bitentaculata* (Ludwig), 6 specimens.
SAM–A22144, *Ypsilothuria bitentaculata* (Ludwig), 2 specimens.
SAM–A22168, *Molpadia millardae* sp. nov., 2 specimens.

A 319, west of Cape Town, 34°05'S 16°58'E, 9 December 1959, 2 688–2 725 m.

SAM–A27723, *Echinocucumis hispida* (Barrett), fragment.
SAM–A22139, *Ypsilothuria bitentaculata* (Ludwig), 10 specimens plus fragment.
SAM–A22140, *Gephyrothuria alcocki* Koehler & Vaney, 2 specimens.
SAM–A22174, *Molpadia millardae* sp. nov., 1 specimen.
SAM–A22141, *Molpadia* sp. indet., 2 specimens.

A 322, south-west of Cape Point, 34°36'S 17°00'E, 10 December 1959, 2 743 m.

SAM–A22148, *Ypsilothuria bitentaculata* (Ludwig), 12 specimens.
SAM–A22163, *Molpadia millardae* sp. nov., 1 specimen (holotype).
SAM–A27711, *Molpadia millardae* sp. nov., 3 specimens (paratypes).

METHODS

The specimens were studied according to conventional methods outlined by Fisher (1907), Deichmann (1948), and Rowe & Doty (1977). The spicules were removed in antiformin (see Mahoney 1966), washed in two changes of distilled water, and illustrated with a *camera lucida*.

For scanning electron microscopy the spicules were transferred, through two changes of absolute alcohol, on to a specimen stub to which they normally stick once the alcohol evaporates. They were then sputter-coated with gold at 30–40 mAmp for 5 minutes and photographed using the Philips SEM 500.

Although all the available data for the new species described herein are repeated in the text under 'Material examined', for the remaining species only the locality data are given in the text and then by reference to latitude/longitude degree squares as was previously done by the writer (Thandar 1984, 1991), following Day's (1967) method for the polychaetes. The letters WCP denote Western Cape Province and vd, very deep (> 500 m).

SYSTEMATIC ACCOUNT

Order DENDROCHIROTIDA Grube, 1840

Family **Psolidae** R. Perrier, 1902

Psolidium vitreum Ohshima, 1915

Figs 1, 16B

Psolidium vitreum Ohshima, 1915: 281, pl. 11 (fig. 32).
Psolus sp. Théel, 1886: 15 (*syn. nov.*).

Diagnosis (after Ohshima 1915: 281)

Body form elliptical, mouth and anus on conical prominences. Colour white, glassy. Ventral pedicels in zigzag row on each ambulacrum on margin of sole, few also in odd ambulacrum. Dorsal pedicels minute. Sole deposits round to oval, often overlapping, faintly knobbed plates, up to 0.40 mm in diameter, with large, regularly arranged holes (up to 36), partially or completely occluded in larger specimens, size of plates and number of holes increasing with age. Dorsal scales thin, smooth, rounded, imbricating, 1.0–1.5 mm in diameter, some with holes for dorsal pedicels. Ventral pedicels with end-plates and other curved, elongated plates with two series of holes; dorsal pedicels with reduced end-plates and supporting rods. Plates of tentacles similar to those of pedicels but broader, with more holes.

Previous southern African record

None.

Material examined

SAM–A27719, WCP (34/16/vd), 1 specimen.

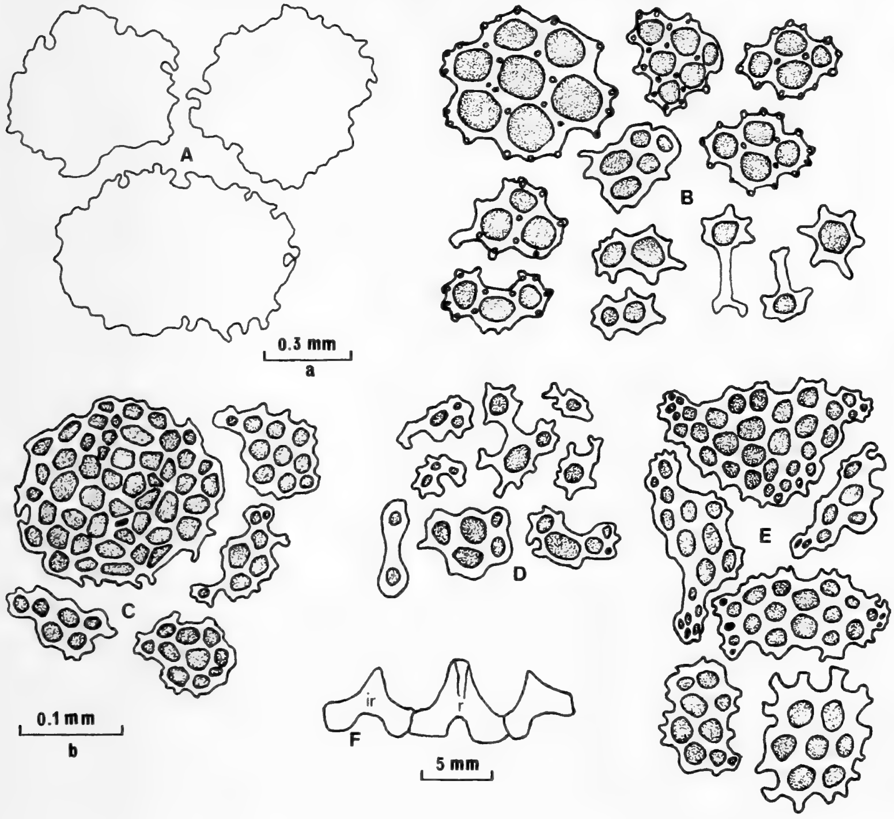

Fig. 1. *Psolidium vitreum* Ohshima. Spicules and calcareous ring. A. Scales from dorsal wall. B. Deposits from sole. C. End plate and other perforated plates from ventral podia. D. Plates and rods from dorsal podia. E. Tentacle plates. F. One radial and two interradial plates of calcareous ring. A—scale a; B–E—scale b.

Description

Form cylindrical, dorsal surface arched, ventral flattened, damaged. Length 10 mm, width in mid-body 3 mm. Colour white, in alcohol. Anterior and posterior ends turned up, mouth and anus dorsal, oral and anal cones not conspicuous; anus surrounded by five calcareous plates, each flanked by anal papillae. Tentacles 10, eight large and bushy, ventralmost two very much reduced. Sole displaced anteriorly, oval, 3.5 mm in length, bordered by a rim of well-developed pedicels in a single zigzag row in each ventrolateral ambulacrum, none detected in damaged odd ambulacrum; total number of ventral pedicels 18. Dorsal pedicels minute, scarce.

Alimentary canal lost; polian vesicle and stone canal not seen. Calcareous ring (Fig. 1F) simple, radial and interradial plates with pointed anterior projections, interradial plates about two-thirds the size of radial plates, latter with anterior depression for insertion of retractor muscle; posterior surface of radial plates deeply notched, that of interradial plates concave. Gonad immature. Respiratory trees as paired, simple tubes, each branched dichotomously once.

Dorsal scales (Figs 1A, 16B), circular but imbricating, up to 1 mm in diameter, made up of more than one layer of calcareous material. Sole deposits (Fig. 1B) as rods and usually faintly knobbed, perforated plates, 0.095–0.15 mm long (mean 0.12 mm); holes large, 1–7 in number, knobs along margin of plates and on surface; usually only a few of the smaller plates smooth. Ventral pedicels with well-developed end-plates and other smooth perforated plates (up to 0.14 mm long), of various shapes and irregular margins (Fig. 1C). Dorsal pedicels with reduced end-plates and other smooth irregular plates with one or more holes, often curved and basket-like (Fig. 1D). Tentacles with plates similar to those of ventral pedicels, but larger, up to 0.25 mm in length, and with more numerous holes (Fig. 1E).

Remarks

Ohshima (1915) compared his species from the North West Pacific with *Psolidium dorsipes* Ludwig from the South East Pacific, pointing out several differences between the two. He further commented that *Psolus incertus* Théel from Kerguelen Island and *Psolus* sp.—a defective specimen described by Théel (1886) from the Gulf of Mexico—are also close to *P. vitreum*. Whereas *Psolus incertus* clearly belongs in the genus *Psolus*, the presence of dorsal pedicels ('flexible cylindrical appendages' of Théel 1886: 16) in *Psolus* sp., clearly places it in the genus *Psolidium*. From the brief description given by Théel, it appears that, apart from the arrangement of ventral pedicels in double rows and the absence of pedicels in the odd ambulacrum, there appear to be no other differences between *Psolus vitreum* and the specimen collected by S.S. *Blake*, to which it is here referred. The southern African specimen similarly differs from the type of the species only in the absence of pedicels in the odd ambulacrum (perhaps an age variation). One other species, namely *P. disjunctum* Sluiter from the tropical West Pacific, is also similar to *P. vitreum* but its dorsal pedicels are stated to be in double rows and ventral in three rows.

Distribution

Known from Japan, the Gulf of Mexico, and south-west coast of Africa, 184–3 255 m.

Family **Cucumariidae** Ludwig, 1894

Paracucumaria capense Thandar, 1998

Fig. 15B

Trachythyone ?parva Thandar, 1991 (*non* Ludwig): 134, figs 11, 15.
Paracucumaria capense Thandar, 1998: 83, figs 2c–e, 3a–e.

Diagnosis (from Thandar 1998)

Small, somewhat U-shaped species, up to 36 mm in length along ventral surface. Colour, in alcohol, uniformly white. Pedicels restricted to ambulacra in double rows, sometimes a few also scattered in interambulacra of dorsal surface. Tentacles 8–10, of more or less equal size. Radial plates of calcareous ring blunt, without incisions but with concave posterior margins. Body wall spicules a superficial layer of baskets, usually confined to anal region, rarely occurring elsewhere, and an inner layer of large, irregular, smooth to faintly nodular, imbricating plates with up to 12 large holes. Pedicels with mostly perforated, sometimes knobbed, irregular rods and plates, end-plates reduced. Tentacle deposits similar but larger. Introvert with perforated plates of varying shapes, margins jagged or knobbed, surface finely knobbed.

Remarks

This species was identified as *Trachythyone ?parva* by Thandar (1991) but, after examination of the additional specimens received from the MNHN, it became obvious that the material does not represent a *Trachythyone* but a new species of *Paracucumaria*, recently described by Thandar (1998) and compared with other nominal species of the genus.

Order DACTYLOCHIROTIDA Pawson & Fell, 1965

Family **Vaneyellidae** Pawson & Fell, 1965

Psolidothuria octodactyla Thandar, 1998
Fig. 15A

Psolidothuria octodactyla Thandar, 1998: 80, figs 1a–f, 2a, b.

Diagnosis (from Thandar 1998)

Small, U-shaped dactylochirotid holothuroids with mouth and anus at opposite ends. Tentacles eight, unequal in size, finger-like but finely branched. Calcareous ring simple, consisting of eight, more or less similar plates without posterior prolongations. Thecal plates simple, imbricating, occasionally faintly nodular; holes few (up to 20), large, spires absent.

Remarks

This species was recently described by Thandar (1998), who also amended the diagnosis of the family Vaneyellidae and erected the new genus *Psolidothuria* to accommodate the new southern African form; hence only the diagnosis is repeated here. It appears that the new genus bridges the gap between the families Vaneyellidae and Ypsilothuriidae within the dactylochirotid holothuroids.

Family **Ypsilothuriidae** Heding, 1942

This family, when proposed by Heding (1942), included only the genera *Echinocucumis* and *Ypsilothuria*. However, Panning (1949) referred several other genera to it; subsequently Pawson (1965) restricted the Ypsilothuriidae to include only three genera, namely *Echinocucumis* Sars, *Ypsilothuria* E. Perrier and *Ypsilocucumis* Panning. Of these, only the former two are represented in southern Africa and present in the collection here studied.

Genus *Echinocucumis* Sars, 1859

This genus includes ypsilothuriids with thecal plates made up of only a single layer of calcareous material. Currently only four species—the cosmopolitan type species *Echinocucumis hispida* (Barrett, 1856), the Western Indian Ocean *E. paratypica* Ludwig & Heding, 1935, and the Eastern Atlantic *E. tenera* Cherbonnier, 1958, and *E. multipodia* Cherbonnier, 1964, are included in the genus. The latter two species possess bifurcate processes to the calcareous ring and hence may not strictly belong in *Echinocucumis*.

Echinocucumis hispida (Barrett, 1856)

Figs 2, 14A–C

Eupyrgus hispidus Barrett, 1856: 46, pl. 4 (figs a–b).

Echinocucumis typica Sars, 1861: 102, pl. 10 (figs 11–20), pl. 11 (figs 1–17). Théel, 1886: 9, fig. 3.

Cucumaria typica Ludwig, 1901: 149.

non *Echinocucumis typica* Clark, 1923: 418 (= *Ypsilothuria bitentaculata* (Ludwig)).

Echinocucumis hispida Mortensen, 1927: 404, figs 242 (i), 243. Deichmann, 1930: 150, pl. 18 (fig. 9). Ludwig & Heding, 1935: 167. Heding, 1942: 29, figs 31, 32. Panning, 1949: 454. Pawson, 1965: 8, fig. 2.

Diagnosis (from Pawson 1965)

Tentacles 10, unequal in size. Body U-shaped, mouth and anus placed at ends of non-retractile tubes. Pedicels scarce, slender, thread-like, restricted to ambulacra. Body covered by large (*c*. 1 mm in diameter) scales with an excentric spire, placed near margin; scales with numerous regular holes and either single-layered or with a coarse reticulum spreading out from the base of spire and partially covering primary disc.

Previous southern African record

None.

Material examined

SAM–A22130, A22142, A22143, A22167, A27718, A27720, A27721, A27723; WCP (33/16/vd to 34/17/vd), 15 specimens plus fragments.

Description

Specimens typically U-shaped (Fig. 2A), largest 40 mm along greater curvature. Tentacles 10 (Fig. 2G)—in dissected specimens one on each side very long, four slightly smaller and four very small, two largest branched at base. Each respiratory tree (Fig. 2I) with two main trunks, one whitish, the other brownish, each trunk with short extensions (?caeca) and, in addition, short thread-like processes at base.

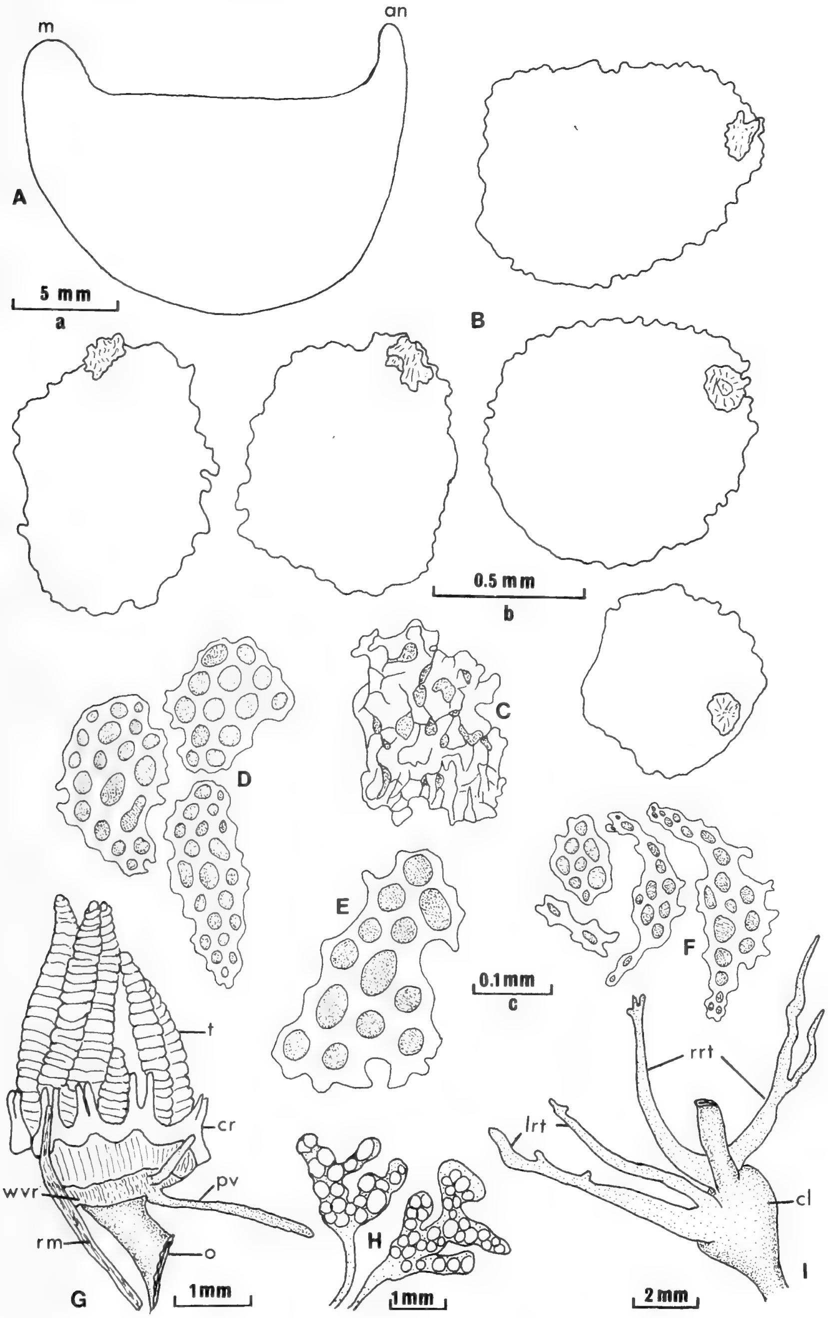

Fig. 2. *Echinocucumis hispida* (Barrett). Structure and spicules. A. Entire animal. B. Spired plates from body wall. C. Spire (from side). D. Smooth plates from oral siphon. E. Smooth plate from anal siphon. F. Tentacle plates. G. Calcareous ring and associated organs. H. Gonadal tubules of female. I. Cloaca with respiratory trees. A–scale a; B—scale b; C–F—scale c.

Thecal plates (Figs 2B, 14B) 0.60–0.90 mm, with a coarse reticulum spreading out from base of spire to partially cover primary disc. Spires (Fig. 2B, C) 0.165–0.270 mm, placed near margin, gradually lost towards oral and anal ends. Plates of anal siphon thick, holes large (Fig. 2E); those of oral siphon thin, holes small (Fig. 2D). Tentacles with plates and rods (Fig. 2F).

Remarks

Although the form of the specimens, the number of tentacles and the marginal spires suggest that the present material belongs in *Echinocucumis*, the base of the spire spreads out as a coarse reticulum partially covering the primary plate so that it appears as if part of each thecal plate is made up of more than one layer of calcareous material. Since a coarse reticulated network has also been described by Deichmann (1930) for *Ypsilocucumis asperrima* (Théel), one may be inclined to consider the present material as being identical with that species. The tentacle deposits also resemble those illustrated by Deichmann. However, judging from Théel's (1886) description of the holotype, it is certain that the thecal plates of *Y. asperrima* are clearly multilayered. In fact, Heding (1942: 27) commented that 'Deichmann did not distinguish clearly between the different forms of *Ypsilothuria* and *Echinocucumis*'.

The thecal plates of the present specimens in fact resemble those of *Ypsilothuria talismani talismani* E. Perrier, illustrated by Heding (1942: 28, fig. 27 (3)), more than any other ypsilothuriid. However, Heding stated that *Ypsilothuria* always has 8 tentacles and 8 plates to the calcareous ring. *Echinocucumis*, on the other hand, has 10 tentacles with 10 plates to the calcareous ring. If the number of tentacles is not of any great phylogenetic significance, as suggested by Deichmann (1930) (she noted that the two ventral tentacles may be aborted), then there appears to be some overlap of characters between the southern African *E. hispida* and *Y. talismani talismani*. As a point of interest, the spires in the southern African material are more excentric than those illustrated by Pawson (1965) for the New Zealand form.

According to both Sars (1861) and Heding (1942), the four dorsal tentacles always have two digits each, whereas the two large lateral ones are branched. In the present material, however, only the two largest tentacles have a few branches at their base. Nevertheless, unbranched tentacles have been described for the species by Deichmann (1930), who worked on Scandinavian material, and by Pawson (1965), who studied the New Zealand form.

The respiratory trees, unlike those described for the species by both Deichmann (1930) and Pawson (1965), are well developed, with separate origins, each supplied with two main stems and some supplementary branches. This observation is in agreement with that of Heding (1942).

The bathymetric range of *E. hispida*, according to Heding (1942), is 50–1 300 m. He stated that deeper records are those of *Y. talismani* and not *E. hispida*. However, Pawson's material from the eastern side of New Zealand came from a depth of 1 530 m. If the southern African material represents a true *E. hispida* then a depth of 2 525–3 257 m is the deepest yet recorded for the species. The structural differences between the southern African form and the typical *E. hispida* may be ascribed to both geographic and depth variations. At least, at infraspecific level, distinction can be drawn between the North Atlantic, southern African, New Zealand and West Indian (forma *atypica* Deichmann, 1930) forms of the species, each possibly representing a subspecies.

Clark's (1923) specimens of *E. typica*, recorded from Cape Point, are herein re-identified as *Ypsilothuria bitentaculata* (see remarks under *Y. bitentaculata*).

Local distribution

Known only from off south-western Cape Province, 2 525–3 257 m.

General distribution

Cosmopolitan, 50–3 257 m.

Genus *Ypsilothuria* E. Perrier, 1886

Heding (1942) recognized only two species in this genus, namely *Ypsilothuria talismani* E. Perrier and *Y. bitentaculata* (Ludwig). According to him, *Y. talismani* has two Atlantic varieties (subspecies) whereas *Y. bitentaculata* has one Atlantic and two Indo-Pacific varieties (subspecies).

Ypsilothuria bitentaculata (Ludwig, 1893)

Figs 3, 14D–F

Sphaerothuria bitentaculata Ludwig, 1893: 112; 1894: 141, pl. 12 (figs 16–17), pl. 14 (figs 5–14). Deichmann, 1930: 152, pl. 19 (figs 4–5). Ludwig & Heding, 1935: 196, figs 55–57.

Ypsilothuria bitentaculata Koehler & Vaney, 1905: 87. Heding, 1942: 28, pl. 2 (figs 1–10), text-figs 25 (1–4, 9–10), 26 (4–7), 27 (2, 5), 30. Panning, 1949: 455. Pawson, 1965: 6, fig. 1 (2–5).

Echinocucumis typica Clark, 1923: 418 (non *Echinocucumis typica* Sars, 1859 = *E. hispida* Barrett, 1856).

Sphaerothuria talismani Deichmann, 1930: 154, pl. 19 (fig. 3) (*partim*) (non *Sphaerothuria talismani* (E. Perrier) = *Ypsilothuria talismani* E. Perrier).

Diagnosis

Globular to spherical ypsilothuriids with plates of body wall forming a rigid test almost as hard as a young echinoid; thecal plates with uneven margins and composed of several layers of calcareous material; holes reaching periphery of plates; spires never marginal in position.

Previous southern African record

WCP (34/18/vd) as *Echinocucumis typica* by Clark (1923), 1 647–1 830 m.

Material examined

SAM–A22132, A22139, A22144, A22148, A22149, A22150, A22151; WCP (33/16/vd to 34/17/vd), 51 specimens plus fragments.

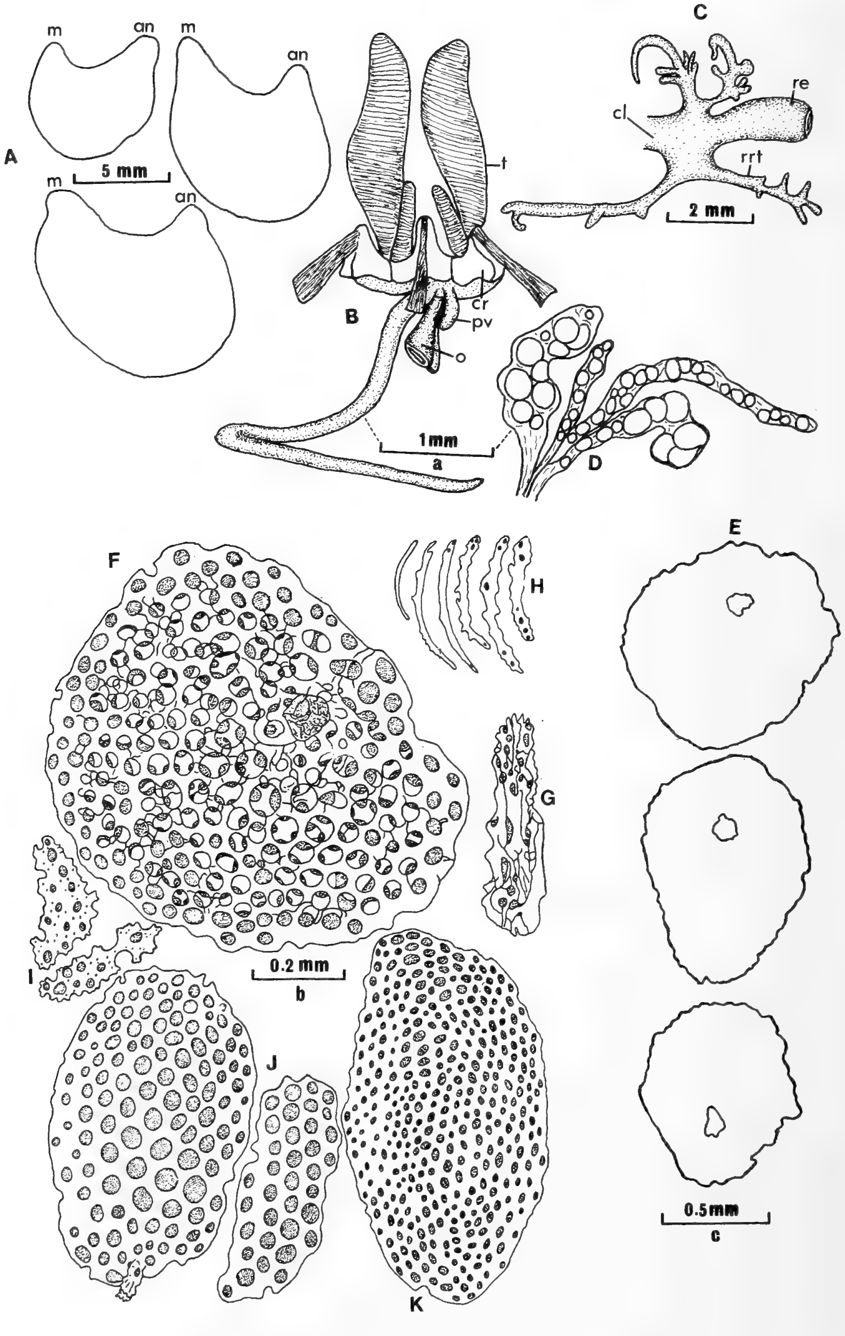

Fig. 3. *Ypsilothuria bitentaculata* (Ludwig). Structure and spicules. A. Entire animals. B. Calcareous ring and associated organs. C. Respiratory trees. D. Gonadal tubules of female. E. Spired plates of body wall. F. Detail of one spired plate. G. Spire (from side). H. Tentacle rods. I. Introvert plates. J. Plates from oral siphon. K. Plate from anal siphon. B, D—scale a; F–K—scale b; E—scale c.

Description

Specimens globular to spherical (Fig. 3A), largest 25 mm along greater curvature. Tentacles 7–8, unbranched (Fig. 3B), lateral two largest; of remaining tentacles, two dorsal and 3–4 ventral in position. Respiratory trees each with two main trunks, each trunk with sac-like extensions (caeca) (Fig. 3C).

Thecal plates (Figs 3E, F, 14D, E) 0.71–1.27 mm, multi-layered, spire up to 0.5 mm high (Fig. 3G), slightly excentric (Fig. 3E). Plates of oral siphon single-layered, with or without a spire (Fig. 3J); the latter, if present, marginal. Plates of anal siphon also single-layered with small, concentrically arranged holes (Fig. 3K). Tentacle rods curved, margins spinose (Fig. 3H). Introvert plates with minute nodules and jagged edges (Fig. 3I).

Remarks

Of the two species included in this genus there is no doubt that the present specimens belong to *Y. bitentaculata*. This is borne out by the shape and texture of the specimens, the form of the calcareous ring, and the structure of the thecal plates. According to Heding (1942), *Y. bitentaculata* is as rigid as a little echinoid, whereas *Y. talismani* is soft; the latter species is much smaller, reaching a length of 15 mm, whereas *Y. bitentaculata* reaches a length of 20 mm. Heding also stated that *Y. bitentaculata* always occurs at abyssal depths (true for the southern African material), whereas *Y. talismani* occurs in shallow waters.

The specimens agree well with Heding's (1942) description of *Y. bitentaculata attenuata* except that they reach a size of 25 mm, the thecal plates (0.7–1.3 mm) are smaller than those recorded for the variety (1.2–1.8 mm), and the tentacle spicules resemble those of *Y. talismani talismani* illustrated by Heding rather than those of his *Y. bitentaculata attenuata*. Perhaps not all these differences are significant as the size of the animal may vary depending on the method of measuring, and the tentacle deposits may differ from the base of a tentacle to the tip. The present specimens are not referable to the Indo-Pacific *Y. bitentaculata bitentaculata* since Heding stated that the size of the plates in this form exceeds 1.8 mm.

Clark (1923) recorded two spherical forms collected by the R.V. *Pieter Faure* from Cape Town in 1916 as *Echinocucumis typica* (= *E. hispida*). Deichmann (1930), who re-examined one of Clark's specimens, referred it to *Sphaerothuria* (= *Ypsilothuria*) *talismani*, although she described the body as spherical, a shape typical for *Y. bitentaculata*. According to Heding, *Y. talismani* is oblong–spherical with a thin soft body wall similar to *E. hispida*. A dry specimen in the SAM type collection, labelled as *E. typica*, is possibly one of the specimens examined by Clark. Judging from its size, shape and external structure it is indistinguishable from *Y. bitentaculata* described herein. Hence *E. typica* Clark, 1923 (*non* Sars, 1861) and *S. talismani* (*partim*) Deichmann, 1930 (*non* E. Perrier, 1886), are here re-identified as *Y. bitentaculata*.

Local distribution

Known only from off south-western Cape Province, 1 647–2 965 m.

General distribution

Possibly cosmopolitan, 375–3 231 m.

Habitat

Green mud.

Order ASPIDOCHIROTIDA Grube, 1840

Family **Synallactidae** Ludwig, 1874

Meseres atlanticus (R. Perrier, 1902)

Figs 4, 16A

Pseudostichopus atlanticus R. Perrier, 1902: 333, pl. 17 (figs 15–20). Mortensen, 1927: 387 (*passim*). Deichmann, 1930: 87.
Molpadiodemas atlanticus: Heding, 1940: 357.
Meseres atlanticus O'Loughlin, 1998: 493, 497.

Diagnosis

Large, sac-like, often flattened synallactid up to 170–180 mm long with no encrusting foreign bodies on skin, the latter smooth, naked. Anus in an inconspicuous furrow; mouth surrounded by 15–20 tentacles. Appendages minute, hair-like. Colour brown to grey to white. Large, round solid deposits with warty or spiny surface in skin; branching rods and reticulate plates in skin around mouth. Tentacle deposits prominent, including curved rods, often thickened in middle.

Material examined

SAM–A22156, WCP (34/16/vd), 2 specimens.

Description

Form cylindrical, U-shaped, anterior end extending beyond level of anus. Dorsal surface conspicuously arched. Length of larger specimen 80 mm, diameter of mid-body 15 mm. Dorsal and ventral surfaces not clearly demarcated. No adhering foreign bodies, except for a few *Globigerina* on ventral surface. Colour uniformly grey.

Mouth anterior; 15 tentacles in one specimen, 20 in the other. Tentacles distinctly peltate with a short stem and a large disc with few lateral projections. No collar or brim at anterior end. Anus situated in a furrow, indistinct due to the contraction of the posterior end of body.

Appendages minute, sparse, inconspicuous, few scattered dorsally, longer and in double rows ventrally, giving the mid-ventral ambulacrum a villus-like appearance. All appendages inconspicuous, hence body appears naked like that of a molpadiid.

Body wall thin, translucent, bearing externally a pleated appearance—the pleats traversing the body in all directions.

Calcareous deposits present in body wall, peristome, tentacles, papillae and gonadal tubules; absent from anal region. Body-wall spicules discoidal, mulberry-like plates, up to 0.2 mm in diameter (Fig. 4C), similar to that illustrated by Perrier (1902, pl. 17 (fig. 20)). Such plates unusual, unlike anything seen in other holothuroids. Peristomial deposits (Fig. 4D) branching rods, branching resulting in complex reticulate structures almost impossible to remove whole; such plates and rods resemble those of the type illustrated by Perrier (1902, pl. 17 (figs 17–19)). Papillae deposits, few, appearing as simple smooth rods, without perforations (Fig. 4E). Tentacle deposits prominent, curved rods of a variety of forms, with or without perforations (Figs 4A, 16A),

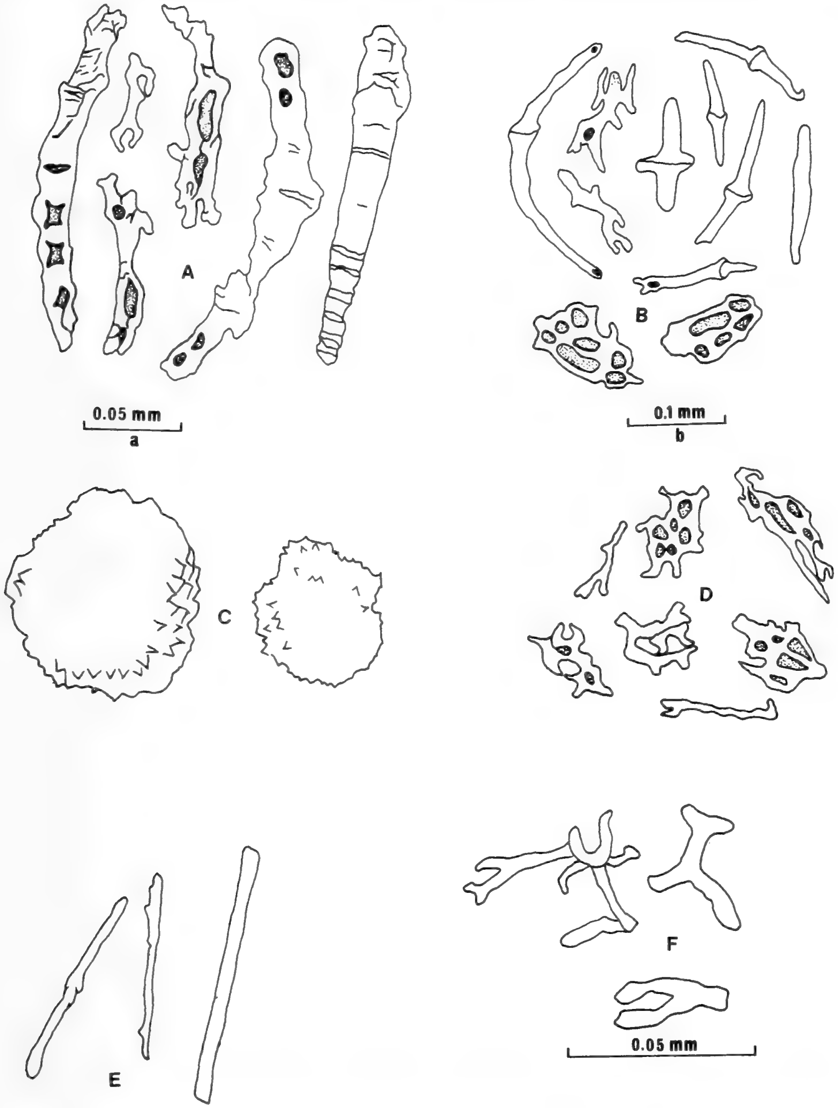

Fig. 4. *Meseres atlanticus* (R. Perrier). Spicules. A. Large rods from tentacle. B. Small rods from tentacle. C. Mulberry-like plates from body wall. D. Deposits from peristomial membrane. E. Rods from papillae. F. Rods from gonad. A—scale a; B–E—scale b.

the latter often with a swollen middle (Fig. 4B); some rods developed as perforated plates similar to those of the peristome. Minute simple smooth rods in the gonadal tubules (Fig. 4F).

Remarks

The two specimens come closer to *Pseudostichopus atlanticus* Perrier, 1902, than to any other species of the genus, agreeing with it in body form, the almost naked appearance of the skin, the presence of peculiar mulberry-shaped spicules

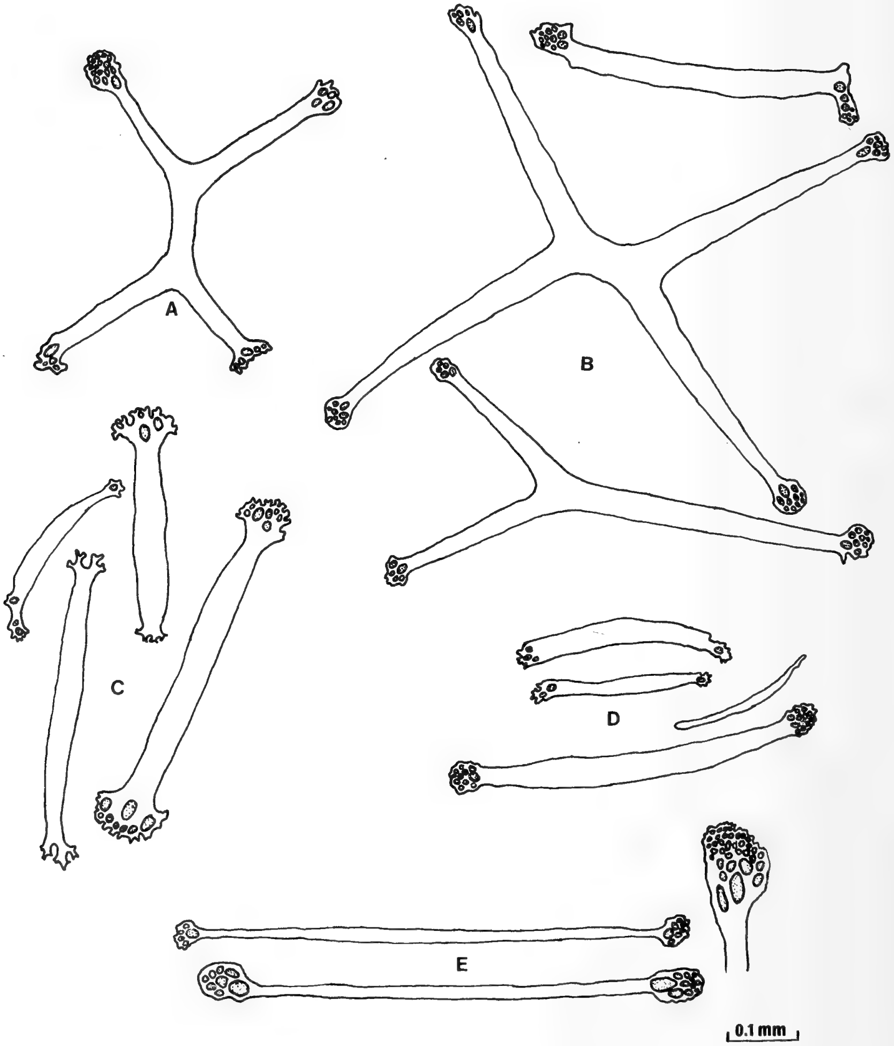

Fig. 5. *Orphnurgus protectus* (Sluiter). Spicules. A. Cross from anterodorsal body wall. B. Rods and crosses from ventral body wall. C. Tentacle deposits. D. Pedicel deposits. E. Papillae deposits.

in the skin, and the form of deposits in the tentacles and peristome. However, it differs in size (Perrier's specimens measured 170–180 mm in length), coloration, and the presence of some tentacle rods with a central thickening. Such differences are perhaps geographic variations as Perrier's specimens came from between the Azores and France, at a depth of 3 614 m. Deichmann (1930) recorded a single 95 mm specimen of this species from off Bequia in the West Indies, at a depth of 2 920 m. According to her, *P. villosus* Hérouard (*non* Théel), described in 1923 from Morocco, is also perhaps identical with Perrier's species.

Heding (1935) erected the genus *Molpadiodemas* for a similar species, *M. acaudum*, taken by the Danish Ingolf Expedition from the North Atlantic. He referred the genus to the family Gephyrothuriidae in the order Gephyrothurioidea (erected by him in 1931), close to the order Molpadioidea. However, Heding (1940), in his account of the holothuroids collected by the German Deep-Sea Expedition, abandoned the order Gephyrothurioidea and transferred the family Gephyrothuriidae back to the order Aspidochirotida, in which it was classified when erected by Koehler & Vaney (1905). To the genus *Molpadiodemas*, Heding (1940) further referred *Pseudostichopus atlanticus* Perrier, 1902, *P. occultatus* von Marenzeller, 1893, and *P. villosus* Théel, 1886. In 1942, Heding reaffirmed his earlier (1935) decision and commented that he had no doubt about the validity of the genus *Molpadiodemas* but hesitated to support his inclusion of the three other species he assigned to it in 1940.

Thandar (1992), in his comment on the status of the genus *Pseudostichopus*, suggested that it be removed from the family Gephyrothuriidae and transferred again to the Synallactidae in the order Aspidochirotida.

Rowe (*in* Rowe & Gates 1995), in error followed Heding's (1940) views on the Gephyrothuriidae. This was, however, corrected by O'Loughlin (1998) who restricted Gephyrothuriidae to the genera *Gephyrothuria* and *Hadalothuria*, and classified the family in the order Molpadiida; the remaining genera of the Gephyrothuriidae he transferred back to the Synallactidae. He further relegated *Molpadiodemas* to the synonymy of *Meseres* and accepted the validity of *P. atlanticus* as a distinct species of *Meseres*, in the combination *M. atlanticus* (R. Perrier, 1902).

Order ELASIPODIDA Hansen, 1975

Family **Deimatidae** Ekman, 1926

Orphnurgus protectus (Sluiter, 1901)

Figs 5, 16C–E

Scotodeima protectum Sluiter, 1901*a*: 20–21; 1901*b*: 61–62, pl. 2 (fig. 7), pl. 9 (fig. 4).
Orphnurgus protectus Hansen, 1975: 47.

Diagnosis (from Hansen 1975)

Tentacles 15, discs with irregular ramifications on the margin. Ventrolateral tube feet 24 pairs, midventral tube feet few and rudimentary. Dorsal papillae

22 pairs, in irregular double rows. Ventrolateral papillae 21 pairs. Spatulated crosses of body wall measuring 0.7 mm across. Spatulated rods densely packed in the slender and rigid papillae.

Material examined

SAM–A22158, WCP (34/16/vd), 2 fragments.

Description

Both fragments in poor state of preservation. Anterior fragment 48 mm long, 21 mm in width in broadest part of body; posterior fragment 37 mm long and 20 mm wide. Not possible to determine whether both fragments belong together and if they do whether they represent a complete specimen. Body wall thin, brittle as a result of numerous spicules. Colour dirty greyish white.

Mouth anterior, ventral. Tentacles 15, of unequal size—five large, five medium and five small, irregularly arranged with large ones anterior, medium on right side and small on left; all tentacles with contracted ramifications and no marginal knobs. Circum-oral papillae absent. Ventrolateral pedicels maximum of four pairs on anterior fragment; seven on right and five on left side of posterior fragment; however, left side of latter damaged, hence some pedicels possibly lost.

If both fragments represent a single specimen, it appears that there were no more than 11 pairs of pedicels. All pedicels short, stout, in two zigzag rows. Mid-ventral pedicels not observed.

Dorsal papillae—five pairs on anterior fragment and approximately five pairs on posterior fragment. Papillae thin, long, with a maximum length of 8 mm, decreasing slightly in size posteriorly.

Ventrolateral papillae—only three pairs detected with any degree of certainty, on anterior fragment; difficult to count on posterior fragment.

Due to the poor state of preservation of both the fragments, the numbers here given for both pedicels and papillae are approximate. All papillae rigid with spicules.

Internal anatomy little preserved; interior packed with *Globigerina*.

Spicules of body wall comprise spatulated crosses, tripartite deposits and rods; crosses (Figs 5A, B, 16C) up to 1.3 mm in length. Rods and tripartite deposits (Fig. 5B) only present in ventral body wall. Spatulated rods confined to pedicels (Figs 5D, 16D) and papillae (Fig. 5E), in the former up to 0.9 mm in length, in the latter up to 2.35 mm long. Tentacle deposits as more or less straight rods with expanded, spinulated and perforated ends, sometimes bifurcate (Figs 5C, 16E).

Remarks

This species resembles *Oneirophanta setigera* (Ludwig) with which it shares most of the characters, differing from it in the presence of tentacles with ramified processes and without marginal knobs on discs. According to Hansen (1975), the crosses of *O. setigera* measure up to 3 mm across whereas those of the single specimen of *Orphnurgus protectus* are only 0.7 mm across. The size of the crosses of the southern African material hence appears intermediate between the two. Dr Gebruk, to whom my description and drawings were sent, concurs with my identification (pers. comm.) but is sceptical about the presence of rods in the ventral integument.

Distribution

Celebes Strait and west coast of South Africa, 1 301–3 255 m.

Family **Laetmogonidae** Ekman, 1926

Genus *Laetmogone* Théel, 1879

Hansen (1975) included four genera in the family but of these only the genus *Laetmogone* occurs in southern Africa, with only *L. fimbriata* (Sluiter, 1901) hitherto recorded. This species is not present in the collection at hand. Its record is that of Hansen (1975), based on 10 specimens (12–35 mm long) taken by the Galathea Expedition, off Durban. However, a single specimen in the present collection is new and has recently been described as *L. perplexa* (Thandar, 1998). In the number, form and distribution of pedicels and papillae and the maximum size (0.18 mm) of the wheels, the new species differs considerably from *L. fimbriata*, and can readily be distinguished with the aid of the key that follows. Since the new species is described elsewhere only the diagnosis is given below.

Key to the southern African species of *Laetmogone*

1A. Papillae conspicuous, white; pedicels crowded, slender from base to tip; large wheels usually (95 per cent) with 9 spokes .... *Laetmogone fimbriata* (Sluiter, 1901)

1B. Papillae inconspicuous, dark violet; pedicels not crowded, short, truncate, retractile into pockets; large wheels usually (72 per cent) with 10–12 spokes .... *Laetmogone perplexa* Thandar, 1998

Laetmogone perplexa Thandar, 1998

Fig. 15C, D

Laetmogone perplexa Thandar, 1998: 84, figs 2f–i, 4a–c.

Diagnosis (from Thandar 1998)

A large subcylindrical species, holotype 220 mm long. Colour uniform dark violet. Tentacles 15, slightly lobed. Pedicels 20 on each side, short, truncate, retractile into pockets, the latter situated on an indistinct brim, which also encircles mouth. Papillae minute (1 mm), retractile, about 25 on each side. Body wall spicules restricted to anterior and posterior ends; rods of varying shapes, 0.40–0.55 mm long; wheels not sharply differentiated into two types, diameter varying from 0.05 mm to 0.18 mm with mostly (72 per cent) four central rays and 10–12 spokes.

Family **Psychropotidae** Théel, 1882

This elasipodid family includes the genera *Benthodytes, Psychropotes* and *Psycheotrephes*, all erected by Théel (1882) and characterized by the presence of spicules, midventral pedicels, and a brim of fused pedicels surrounding the body. Only the former two genera are known from southern Africa, of which only *Benthodytes* is represented in the collection at hand.

Genus *Benthodytes* Théel, 1882

Benthodytes is characterized by soft retractile tentacles, circum-oral or post-oral papillae and the absence of an unpaired dorsal appendage. It includes eight species, of which *B. sanguinolenta*, *B. lingua*, *B. plana* and *B. typica* have hitherto been recorded from southern Africa. The R.V. *Africana II* material includes only *B. lingua*, two specimens herein referred to *B. valdiviae*, and a single incomplete specimen perhaps representing *B. typica*. A key to all five southern African species is provided.

Key to the southern African species of *Benthodytes*

1A. Spicules cross-shaped; dorsal papillae usually well developed 2
1B. Spicules rod-shaped or absent; dorsal papillae minute 4

2A. Brim narrow, often completely enclosed in body wall, body somewhat cylindrical .... *Benthodytes lingua* R. Perrier, 1896
2B. Brim broad, its margin forming the edge of the rather flattened body 3

3A. Anterior and posterior ends of body rounded; tentacular crown placed a considerable distance from anterior edge of body .... *Benthodytes plana* Hansen, 1975
3B. Anterior and posterior ends of body somewhat tapered; tentacular crown adjoining anterior edge of body .... *Benthodytes valdiviae* Hansen, 1975

4A. Dorsal papillae numerous arranged in two bands; tentacles 18; post-oral papillae present .... *Benthodytes sanguinolenta* Théel, 1882
4B. Dorsal papillae few, arranged in two single rows; tentacles 15–20; circum-oral papillae present .... *Benthodytes typica* Théel, 1882

Benthodytes lingua R. Perrier, 1896

Fig. 6

Benthodytes lingua R. Perrier, 1896: 902; 1902: 456, pl. 12 (figs 1–2), pl. 21 (figs 1–9). Deichmann, 1930: 124. Hansen, 1975: 80, pl. 9 (figs 3–5), pl. 12 (figs 2–3), text-fig. 29.
Benthodytes janthina Grieg, 1921: 11 (*non* von Marenzeller).
Pannychia glutinosa Hérouard, 1902: 32, pl. 4 (fig. 17).

Diagnosis (from Hansen 1975)

Body usually rounded in cross section. Skin usually thick and gelatinous. Tentacles 12–15, usually 12. Brim narrow, completely retractile. Ventral sole usually feebly delimited from remaining part of body. Dorsal papillae in single rows, up to 12 pairs, filiform or slightly conical. Dorsal deposits large crosses with bipartite apophyses, the two arms of which are outwardly curved and gradually tapered. Ventral deposits rudimentary or absent.

Previous southern African record

Locality unknown (Hansen 1975).

Material examined

SAM–A27716, WCP (33/16/vd), 1 specimen.

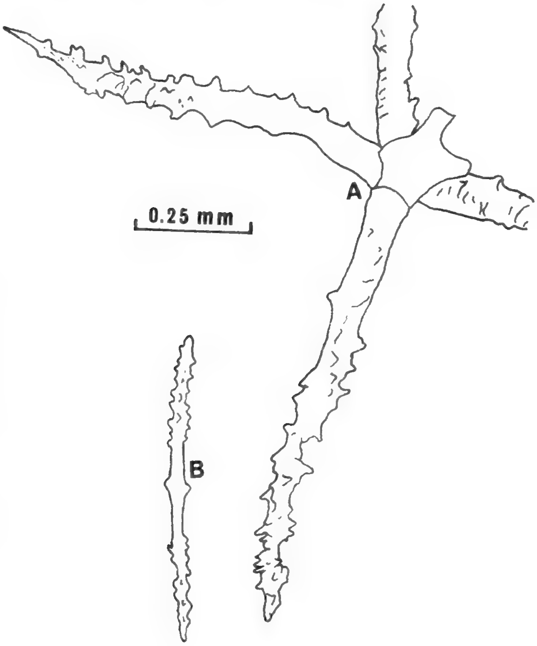

Fig. 6. *Benthodytes lingua* R. Perrier. Spicules. A. Cross-shaped rod with bipartite apophysis from dorsal body wall. B. Rod from anal region.

Description

Length 250 mm. Pedicels, dorsal papillae and brim not recognizable. Circum-oral papillae well developed. Each longitudinal muscle consisting of 4–7 strands, united at point of origin and insertion.

Spicules common only anteriorly and posteriorly—dominant type large crosses with bipartite apophyses (Fig. 6A), but latter rarely preserved, arms spinous (0.75–1.0 mm, usually 0.75 mm), spines increasing in density distally. Other spicules include crosses without apophyses, tripartite rods and spinous rods (Fig. 6B); arms of crosses 0.35 mm long, spinous rods up to 0.6 mm long. Tentacles with rods, tripartite spicules and crosses, spinose at ends. Gonad with crosses and tripartite spicules without apophyses but with distally spinose arms.

Remarks

The only previous record of this species from southern Africa is that of Hansen (1975) based on seven specimens from an unknown locality. According to Hansen, the apophyses in this species are bipartite from the base but this could not be conclusively demonstrated in the few spicules in which the apophyses were intact. However, the size of the R.V. *Africana II* specimen, its cylindrical shape, thick gelatinous body wall, the type of tentacle discs, and the size and robustness of the deposits, all agree with Hansen's description of *B. lingua*. The closest relative of this species is the Eastern Pacific *B. incerta* from which it differs in its form, thick skin, well-developed circum-oral papillae and the absence of the characteristic crosses of the type illustrated by Hansen (1975: 79, fig. 28).

Local distribution

Off south-western Cape, 2 780–2 871 m.

General distribution

North and South Atlantic, 860–3 192 m.

Benthodytes valdiviae Hansen, 1975

Fig. 7

Benthodytes valdiviae Hansen, 1975: 82, figs 30–31.
Benthodytes lingua Heding, 1940: 368 (*non* R. Perrier).
Benthodytes janthina Heding, 1940: 368 (*non* von Marenzeller).

Diagnosis (from Hansen 1975)

Body flattened, somewhat tapered at both ends. Tentacle crowns adjoining anterior edge of body. Tentacles 12–15, usually 15. Brim broad, but retractile. Dorsal papillae 5–10 pairs, slender from base to tip. Deposits, dorsally large crosses with bipartite apophyses; ventrally absent, or reduced to small rods.

Previous southern African record

None.

Material examined

SAM–A27717, WCP (33/16/vd), 2 specimens.

Description

Specimens flattened, larger 42 mm long. Colour light violet to dirty grey. Tentacles dark purple, 15 in the larger and 12 in the smaller specimen. Tentacle crowns adjoining anterior edge of body. Circum-oral papillae, dorsal papillae and mid-ventral pedicels not seen. Brim broad, pedicels of brim more or less completely fused, except anteriorly, but lateral canals often visible.

Dorsal spicules crosses (with apophyses), tripartite deposits and rods. Crosses of two types: one type large, similar to that described for *B. lingua*, with arms up to 0.8 mm long; other type (Fig. 7A, C, D) slender, with 4–5 smooth to slightly thorny arms, 0.35–0.60 mm long, with distally bipartite apophysis, feebly spinose at ends. Ventral spicules similar to dorsal, including crosses, tripartite spicules and spinose to smooth rods (Fig. 7B).

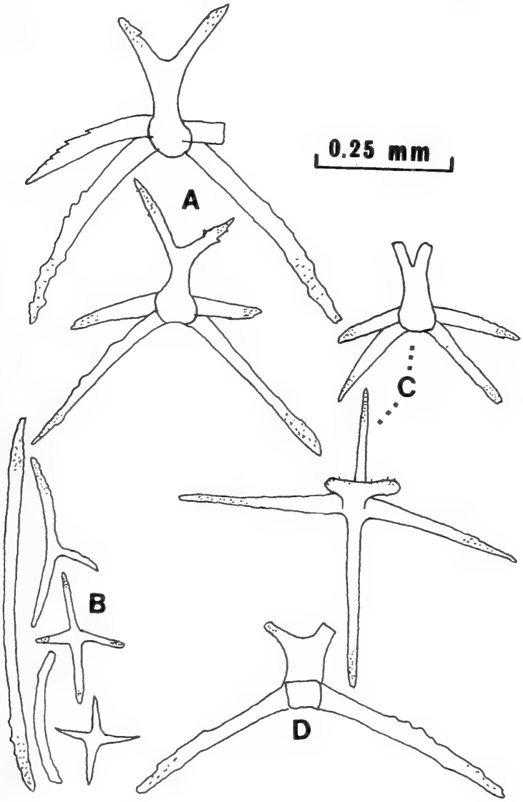

Fig. 7. *Benthodytes valdiviae* Hansen. Spicules. A. Cross-shaped rods with bipartite apophysis from dorsal body wall. B. Rods, crosses and tripartite deposit from ventral body wall. C. Cross-shaped rods from ventral body wall of second specimen. D. Same from dorsal body wall. All drawn to same scale.

Remarks

Although the specimens are here referred to *B. valdiviae*, their flattened nature, free anterior pedicels and five-armed spicules suggest that they may belong to *B. plana*. However, since *B. valdiviae* differs from *B. plana* only in the shape of the body, the more anterior position of the tentacles and a greater robustness of the deposits (Hansen 1975), the present material is referred to it.

A point of some interest is that whereas *B. plana* appears to be an Indian Ocean species, currently known only from the east coast of southern Africa and from between Seychelles and Sri Lanka, *B. valdiviae* is probably Eastern Atlantic in distribution, formerly known from Canary Islands and now possibly off the Cape Peninsula, South Africa.

In the presence of two types of crosses with apophysis, it is quite unlike any other species except *B. incerta*. The latter species, however, is semicircular in cross section with a warty skin and peculiar crosses of the type illustrated by Hansen (1975: 79, fig. 28).

Local distribution

Off south-western Cape, 2 780–2 871 m.

General distribution

East Atlantic.

Benthodytes ?typica Théel, 1882

Fig. 8

Benthodytes typica Théel, 1882: 103, pl. 27 (fig. 7), pl. 35 (fig. 4), pl. 38 (fig. 5), pl. 44 (fig. 8); 1886: 2. Grieg, 1921: 10, pl. 3 (figs 6–7). Hérouard, 1923: 101, pl. 6 (fig. 4), text-fig. 8. Deichmann, 1930: 123.
Benthodytes papillifera Théel, 1882: 102, pl. 34 (fig. 14).
Benthodytes glutinosa R. Perrier, 1896: 902; 1902: 462–465, pl. 13 (fig. 5), pl. 20 (fig. 31). Koehler & Vaney, 1905: 72–74, pl. 12 (fig. 10). Grieg, 1921: 10, pl. 3 (figs 1, 2).
Benthodytes janthina Hérouard, 1923: 103.

Diagnosis (from Hansen 1975)

Tentacles 15–20, discs irregularly incised at the margin, and retractile into the stalks. Circum-oral papillae present. Brim well developed, the dark pigmented canals of the enclosed tube feet often clearly visible both from the dorsal and ventral side. Dorsal papillae minute and few, placed in a single row along the anterior part of the dorsal radii. Skin soft and usually covered in mucous. Deposits absent or rod-shaped.

Previous southern African records

Eastern Cape Province (33/32/vd), KwaZulu-Natal (29/33/vd), and Mozambique (14/45/vd).

Material examined

SAM–A22175, WCP (33/16/vd), 1 specimen.

Description

Specimen damaged, internal organs lost. Length 35 mm. Colour off-white. Tentacles 18, with marginal knobs on discs. Circum-oral papillae numerous. Other external structures not visible. Longitudinal muscles paired. Spicules of

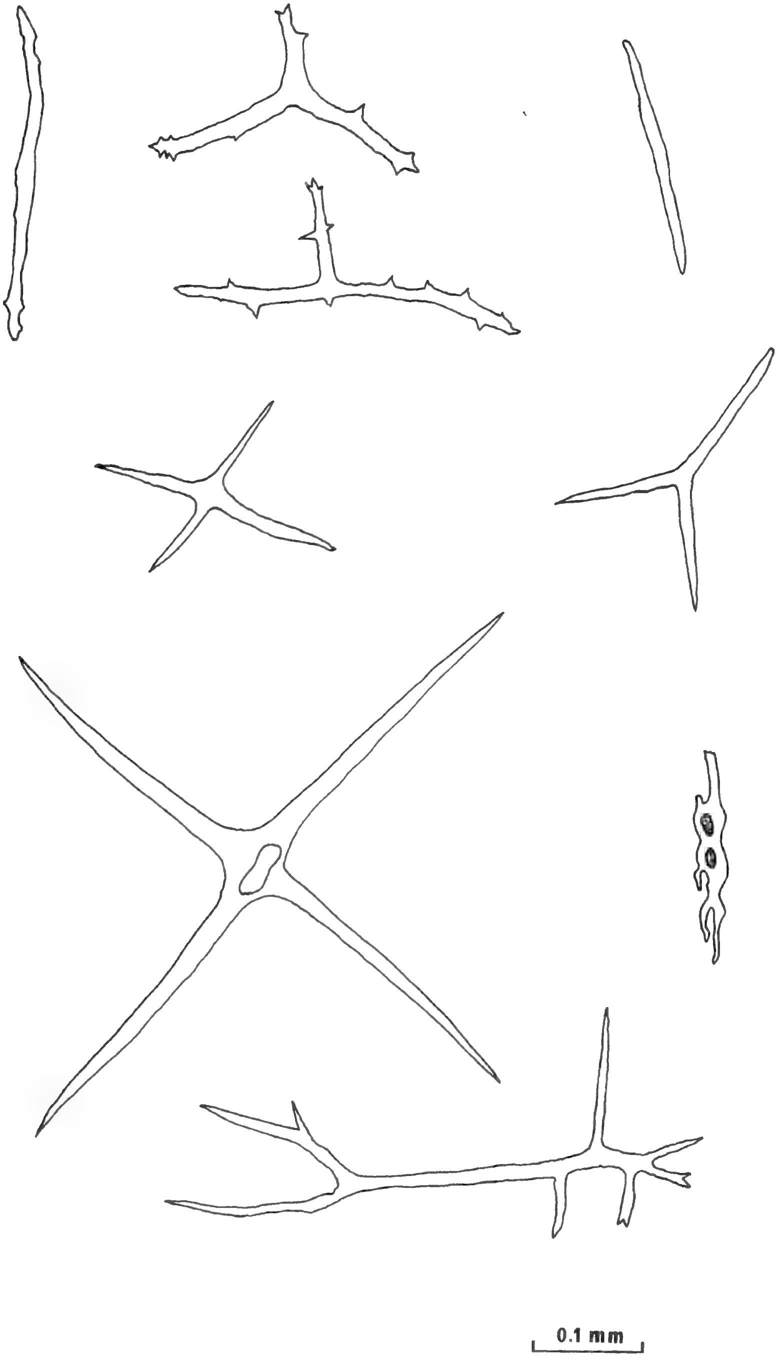

Fig. 8. *Benthodytes ?typica* (Théel). Rods from body wall.

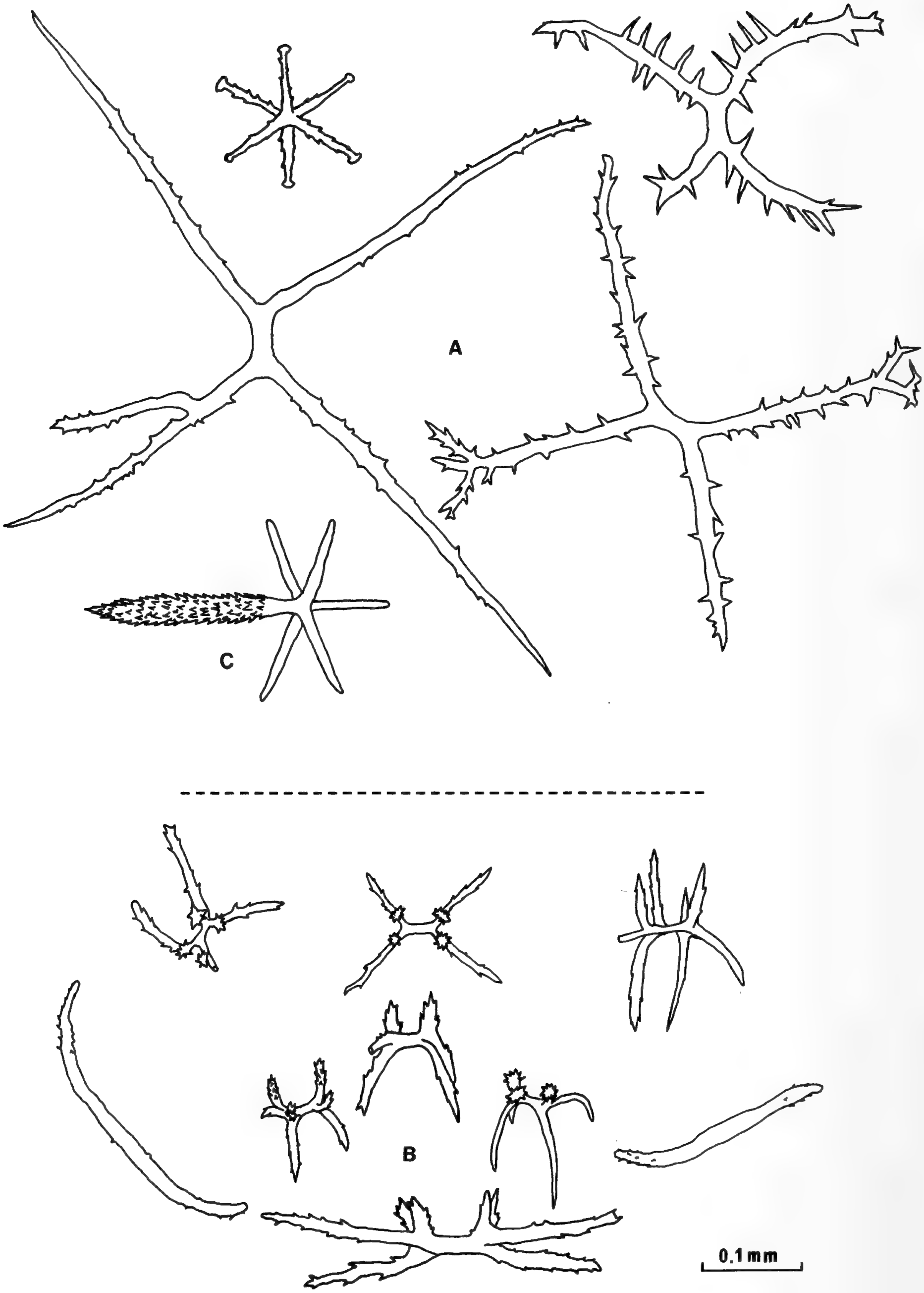

Fig. 9. *Peniagone* sp. indet. Deposits from body and podia. A. Crosses without apophyses. B. Rods and crosses with apophyses. C. Smooth cross with densely setose apophysis. All drawn to same scale.

body wall (Fig. 8) only rods and tripartite deposits, the former terminally spinulated, the latter either smooth or spinose. A single cross-shaped spicule with broken apophysis also observed, but this could be of foreign origin. Rods up to 0.35 mm long, longest arm of tripartite deposits up to 0.20 mm.

Remarks

The identity of this single incomplete specimen is in doubt due to the fragmentary nature and scarcity of the deposits. The specimen was initially thought to represent *B. sanguinolenta*, since this species was recorded by Clark (1923) from Cape Point. The description of the specimen and drawings of its spicules were sent to Dr Gebruk, who has since confirmed (pers. comm.) that it cannot represent *B. sanguinolenta*, which is always purple to violet in colour with spicules that are rather difficult to locate. According to him, the specimen may represent *B. typica*, since rods are the dominant type of spicules. Dr Gebruk further commented that the 'Presence of tripartite elements is not of significant value in this genus'. The presence of circum-oral papillae also supports the identity of this specimen. Additional cross-shaped deposits with apophysis, here suspected to be of foreign origin, could not be detected; they may prove that the specimen is referable to another species.

Distribution

Cosmopolitan, 1 873–4 700 m.

Family **Elpidiidae** Théel, 1879

This family comprises small elasipodid holothuroids with few tentacles (10–12), pedicels and papillae. Hansen (1975), who critically analysed the family, rejected the ideas expressed by Hérouard (1923) and Ekman (1926) that the genera represent two evolutionary lines. He reduced the number of genera from 13 to 10. Only the genera *Peniagone*, *Elpidia* and *Scotoplanes*, each represented by a single species, are here recorded from southern Africa for the first time.

Peniagone sp. indet.

Figs 9, 16F

Previous record

None.

Material examined

SAM–A22172, WCP (34/16/vd), 1 specimen (mutilated).

Description

Specimen badly mutilated, no external or internal characters preserved. Colour dirty yellowish-grey in alcohol. Deposits typical of genus, comprising mostly primary crosses with bent arms and apophyses and, in addition, large spinous crosses without apophyses and curved spinous rods. Spinous crosses without apophyses (Figs 9A, 16F) are the commonest deposits and may represent pedicel spicules. Rare variations of these may be 3–6-armed with one or more arms branched at tips, length of stem 0.03–0.40 mm, length of arms 0.05–0.35 mm. Curved spinous rods scarce, 0.24–0.30 mm in length. Spinous 4-armed crosses with 2–4 apophyses (Fig. 9B) not common; length of stem 0.02–0.30 mm, apophysis length 0.05–0.27 mm, longest arm 0.06–0.16 mm; most apophyses short and arms usually strongly curved inwards. There may also be present smooth crosses with 1–4 apophyses, often much longer than the arms of the rods; when single apophysis present, this is densely setose (Fig. 9C). In addition, there are numerous other smooth crosses, with up to 0.8 mm long arms, and rods up to 2 mm in length, of possibly foreign (?sponge) origin.

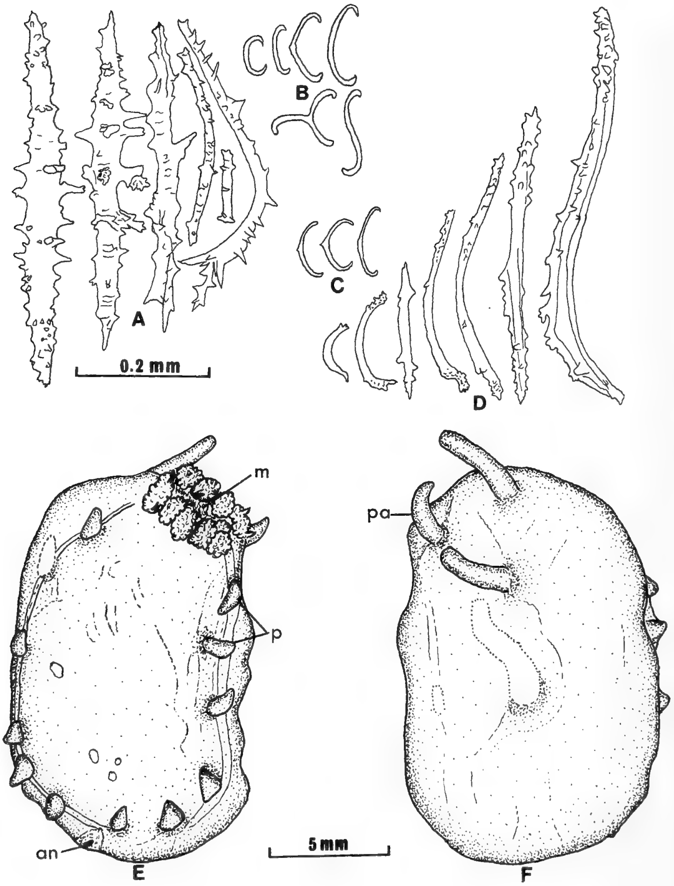

Fig. 10. *Scotoplanes globosa* Théel. Entire specimen and spicules. A. Rods from body wall. B. C-, S- and Y-shaped deposits from body wall. C. C-shaped deposits from tentacles. D. Rods from tentacles. E. Ventral view of entire specimen. F. Dorsal view. All spicules drawn to same scale.

Remarks

Hansen's (1975) key to the species within the genus is based on several external characters that are lost in this mutilated specimen. However, my description of the material and drawings of spicules were sent to Dr Gebruk, who concurs that the specimen at hand definitely represents a *Peniagone* because of the 4-armed spicules with bent arms and apophyses. According to him, the colour of the specimen and the type and sizes of the crosses, indicate that the specimen is perhaps referable to *P. azorica* von Marenzeller from the North East Atlantic, and related to the Antarctic *P. purpurea* (Théel), *P. incerta* (Théel), *P. affinis* Théel and *P. willemoesi* (Théel). In fact, the writer was first inclined to consider the species as identical to the latter species or to *P. horrifer* Théel also from the Antarctic.

Genus *Scotoplanes* Théel, 1882

This genus includes only the type species *S. globosa* Théel and *S. clarki* Hansen, distinguished primarily by the presence of smooth skin with sturdy papillae in the former and warty skin with slender papillae in the latter. In southern Africa only the type species occurs, here reported for the first time.

Scotoplanes albida Théel, 1882, collected by the 'Challenger' from off the south-western Cape coast at 347 m is, according to Hansen (1975), probably referable to *Ellipinion* Hérouard, 1923.

Scotoplanes globosa (Théel, 1879)

Figs 10, 15F

Elpidia globosa Théel, 1879: 14, figs 17–19.
Elpidia murrayi Théel, 1879: 16, figs 23–25.
Scotoplanes globosa Théel, 1882: 29, pl. 4, pl. 5 (fig. 3), pl. 34 (figs 8–9), pl. 36 (figs 5–6), pl. 44 (fig. 12). Hansen, 1975: 167, pl. 9 (fig. 9), text-figs 83, 95 (4).
Scotoplanes murrayi Théel, 1882: 34, pl. 3 (figs 3–4), pl. 34 (fig. 2), pl. 44 (fig. 4).
Scotoplanes theeli Ohshima, 1915: 242; 1916–1919, 3 figs.

Diagnosis (from Hansen 1975)

Skin smooth. Dorsal papillae rather sturdy.

Previous southern African record

None.

Material examined

SAM–A22147, WCP (33/17/vd), 4 specimens.

Description

Largest specimen (Fig. 10E, F) 15 mm long. Colour grey. Pedicels 5–6 pairs, situated in distinct ventrolateral grooves. Only 2–3 papillae identifiable on right side, only anterior ones well preserved on left side.

Rods (Figs 10A, 15F) either slender with a few spines or robust with strongly developed, often ramified spines; slender rods up to 0.02 mm thick and about 0.40 mm long; stout rods up to 0.05 mm thick and 0.55 mm long; C-, S- and Y-shaped bodies (Figs 10B, 15F) 0.05–0.12 mm in length, delicate in smallest specimen. Tentacles with spinous rods (Fig. 10D) and C-shaped bodies (Fig. 10C).

Remarks

The present specimens are identical to Théel's species. Because of their poor state of preservation, no significance can be attached to the distribution of papillae. The rods, however, are similar to those of Hansen's material from the deepest Kermadec stations (5 850–6 770 m). Such rods can attain a maximum length of 1 mm as shown both by Théel (1882) and Hansen (1975).

Local distribution

Known only from off Cape Point, 2 268 m.

General distribution

Almost cosmopolitan but not yet known from the North Atlantic, 2 100–6 770 m.

Habitat

Diatom ooze, grey mud.

Genus *Elpidia* Théel, 1876

This genus is well characterized by its rod-shaped spicules with two pairs of obliquely placed horizontal arms and two vertical apophyses. The genus was formerly regarded as monotypic, but due to the work of mostly Hansen (1956, 1975) and Belyaev (1971, 1975), the genus currently contains 13 nominal and three unnamed species. Some scanty material collected off the south-west coast of southern Africa is here referred to *E. gracilis* Belyaev, 1975.

Elpidia gracilis (Belyaev, 1975)

Figs 11, 15E

Elpidia gracilis Belyaev, 1975: 266. Gebruk, 1993: 235.

Diagnosis (after Belyaev (1975) and Gebruk (1993); modified herein)

Body length up to 25 mm. Dorsal papillae three pairs, up to 9 mm long, decreasing posteriorly. Tube feet four pairs. Deposits varying from 0.65–1.20 mm, sometimes serrate. Diameter of axis 0.03–0.04 mm. Length of arms 35 per cent of shaft length. Apophyses straight and acicular, 10–78 per cent length of deposits. Tentacle deposits curved with reduced or absent arms and apophyses, 0.13–0.90 mm in length.

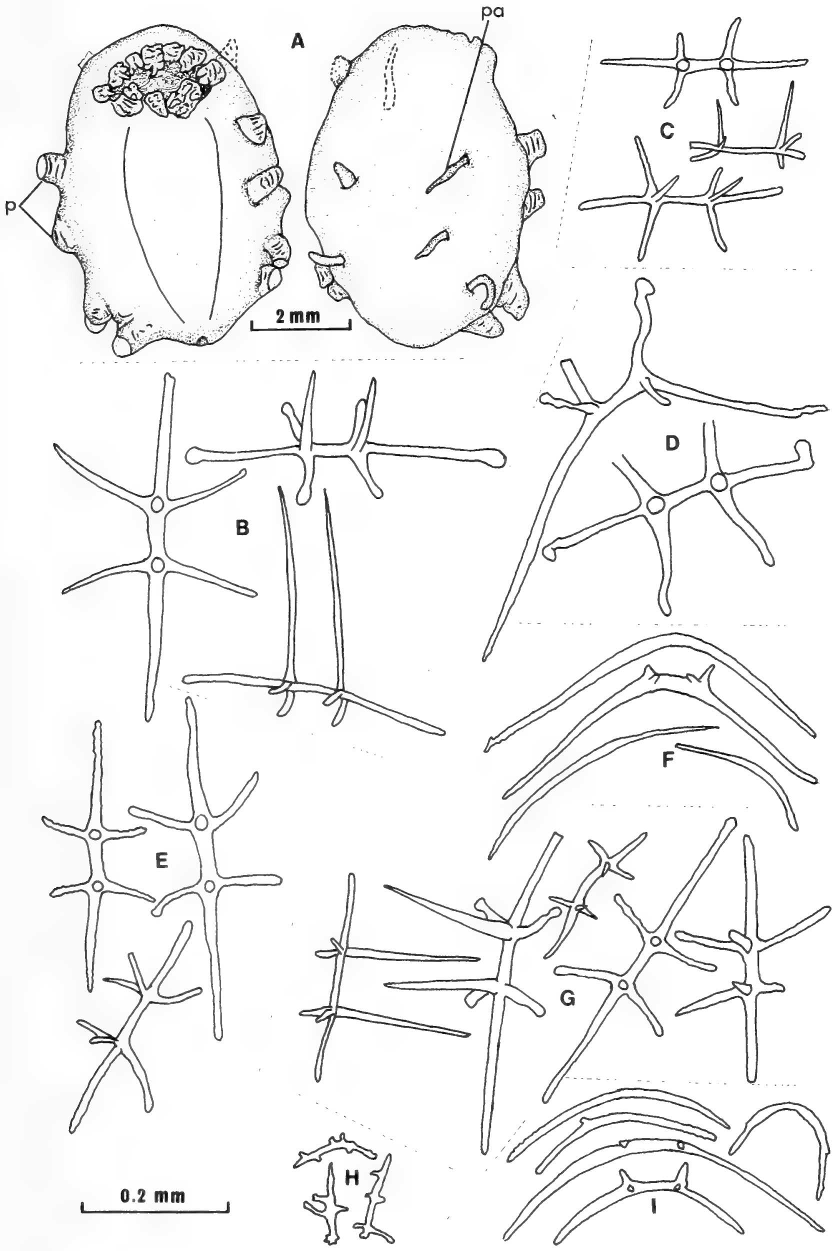

Fig. 11. *Elpidia gracilis* Belyaev. Structure and spicules. A. Ventral and dorsal views of complete specimen. B. Normal spicules of dorsal body wall. C. Devleoping spicules of dorsal body wall. D. Abnormal spicules of dorsal body wall. E. Normal spicules of ventral body wall. F. Tentacle spicules. G. Normal spicules from fragmented specimen. H. Branched rods from same. I. Tentacle spicules. All spicules drawn to same scale.

Material examined

SAM–A27715, WCP (33/16/vd), 1 specimen plus 2 fragments.

Description

Complete specimen (Fig. 11A) whitish in alcohol; length 7 mm, width 5 mm. Skin thin, delicate, ruptured at several points, apophyses of spicules projecting from skin all round. Mouth ventral, tentacles 10, short (*c.* 1 mm), truncate, with slender retractile processes; diameter of oral disc *c.* 30 per cent of body length. Anus terminal. Pedicels about 4 pairs—two short projections, one on each side of oral disc, may represent fifth pair of pedicels or are probably torn fragments of body wall. Papillae dorsal, only five counted with certainty, first definite pair between first definite pair of pedicels, second pair between second and third pair of pedicels, single posterior papillae on right side between third and fourth pairs of pedicels; longest papilla *c.* 1 mm long. An unpaired papilla-like structure at anterior end of left side may represent a sixth papilla or a torn piece of body wall.

Dorsal and ventral spicules (Figs 11B–E, 15E) slender and elongate, axis and arms smooth or slightly serrate with rounded extremities. Spicules 0.16–0.65 mm long, longest dorsal spicule 0.65 mm (Fig. 11B), longest ventral spicule (Fig. 11E) 0.50 mm; maximum diameter of axis of dorsal spicules 0.03 mm, of ventral spicules 0.02 mm. Arms up to 31 per cent length of spicule; extremities of some spicules bent off plane (Fig. 11D).

Apophyses straight, acicular, of dorsal spicules 0.050–0.285 mm long or 18–78 per cent length of spicules, of ventral spicules 0.045–0.070 mm long or 12–21 per cent length of spicules. Some spicules abnormal with strongly curved axis and arms of unequal length (Fig. 11D). Tentacle spicules (Fig. 11F) 0.20–0.45 mm, slightly or strongly curved with both arms and apophyses reduced and/or absent.

Fragments

Tentacles as in complete specimen. Body wall spicules (Fig. 11G) 0.175–0.520 mm long; diameter of axis 0.02 mm. Arms up to 32 per cent length of spicules. Apophyses 0.018–0.205 mm long or 10–62 per cent length of spicules. Irregularly branched rods (Fig. 11H), 0.11–0.13 mm in length also present. Tentacle spicules (Fig. 11I) as in complete specimen, 0.130–0.445 mm long.

Remarks

Of the two fragments, the posterior was contained in the same vial as the complete specimen, whereas the anterior fragment was included with a synaptid in another vial that contained four labels, as follows: everted part of holothurian; sac-like holothurian; SAM, A189C, 25 August 1959; and SAM, A190N, 26 August 1959. It is certain that the second and last labels belong together and refer to the elpidiid since the station number and date of collection are the same as those of the complete specimen and the remaining fragment. The two fragments most probably belonged to a single specimen.

The southern African material is here referred to *E. gracilis* Belyaev because of short papillae, smooth as well as serrate extremities of spicules and

Table 1. Comparison of characters of the type specimens of *Elpidia gracilis* with the southern African form.

Character	Type	South African
Length	6.4–25 mm	7 mm
Width	14 mm	5 mm
Pedicels	4 pairs	4–(?5) pairs
Papillae	3 pairs, in anterior half of body or throughout body length	?3 pairs; in posterior half of body
Papillae length	up to 9 mm (adults), 1.5 mm (juvenile)	up to 1 mm (? juvenile)
Oral disc	20–30% body length	30% body length
Spicules		
Longest dorsal spicule	1.2 mm	0.65 mm
Longest ventral spicule	0.8 mm	0.5 mm
Maximum diameter of axis	dorsal: 0.04 mm ventral: 0.03 mm	dorsal: 0.03 mm ventral: 0.02 mm
Arms	length 35% of shaft; smooth, occasionally serrate at extremity	length 37% of shaft; smooth or serrate at extremity
Apophyses	0.15–0.20 mm (20–70% length of spicules)	0.020–0.285 mm (10–78% length of spicules)
Tentacle spicules	length 0.8–0.9 mm arms short, or absent, apophyses well developed	length 0.13–0.45 mm, arms and apophyses reduced or absent

arms, length of arms relative to the axis, and the form and maximum size of the apophyses. However, there are slight differences, initially considered to be geographic variations worthy of subspecific ranking (Thandar 1984). These differences (summarized in Table 1) include the presence of papillae in the posterior rather than the anterior half of the body, the short maximum size of the spicules, the slightly narrower diameter of the central axis of the spicules and the shorter and less-developed tentacle deposits. According to Dr Gebruk (pers. comm.) these differences fall within the range of variation of the species and do not support the establishment of geographical subspecies. Hence the original diagnosis of the species is here modified to include not only the southern African form but also a single well-preserved specimen described recently by Gebruk (1993).

The soft thin nature of the skin and the extremely slender spicules with well-developed acicular apophyses are reminiscent of *E. theeli* Hansen, *E. minutissima* Belyaev, *E. chilensis* Belyaev and *E. adenensis* Belyaev. However, whereas both *E. theeli* and *E. minutissima* have spicules up to 0.60 and 0.80 mm in length respectively, the diameter of the central axis is 0.02 mm with the apophyses 20–50 per cent the length of the spicules in *E. theeli* and only 25–35 per cent in *E. minutissima* (Hansen 1975). Further, *E. theeli* has

5–7 pairs of long (12 mm) papillae. *Elpidia adenensis* is characterized by smooth spicules up to 1.25 mm long, with the diameter of axis as 0.02 mm and the apophyses only 7–15 per cent the length of the spicules. Like *E. gracilis*, *E. chilensis* also has smooth to serrate spicules but its apophyses are only 10–14 per cent the length of the spicules and there are only two pairs of papillae.

Elpidia gracilis has only previously been recorded from South Orkney Islands and trench at 5 450–6 145 m. According to Dr Gebruk (pers. comm.), the species also occurs in the North Atlantic.

Local distribution

South-western Cape Province, 2 268–2 377 m.

General distribution

South Orkney Island and trench, and the Atlantic Ocean.

Order MOLPADIIDA Haeckel, 1896

Family **Gephyrothuriidae** Koehler & Vaney, 1905

Gephyrothuria alcocki Koehler & Vaney, 1905

Fig. 12

Gephyrothuria alcocki Koehler & Vaney, 1905: 78, pl. 5 (figs 6–8).
Himasthlephora glauca Clark, 1907: 40, 184, pl. 13 (figs 1–4).
Gephyrothuria europeensis Hérouard, 1923: 30, pl. 9 (figs 10a, b).
Gephyrothuria glauca Deichmann, 1930: 202.

Diagnosis (modified from O'Loughlin 1998: 495)

Tentacles 15, each with 2–3 pairs of digits, mouth terminal, anterior, anal furrow present with anal canal extension. Papillae long, up to five pairs, with ampullae. Papulae present, some drawn out into papillae-like extensions, at least posteriorly. Calcareous ring with three dorsal interradials. Gonadal tubes with up to four sac-like branches. Males with prominent mid-dorsal genital papillae at anterior end. Spicules absent.

Material examined

SAM–A22140, WCP (34/16/vd), 2 specimens.

Previous southern African record

None.

Description

Specimen SAM–A22140a. Body form cylindrical, barrel-shaped (Fig. 12A). Mouth and anus terminal. Length 23 mm, height in mid-body 8 mm. Mouth open, bordered by 15 tentacles, each with 2–4 lobes. Anterior end constricted and slightly turned up. Skin thin, translucent, ribbed. Calcareous ring clearly visible through body wall. Dorsal papillae—only five identified with any degree of certainty. A papilla-like structure on skin covering the calcareous ring may represent genital papilla. Of the five dorsal papillae, three situated anteriorly, and two in the middle of the body. A papilla-like structure behind the three anterior papillae may represent a sixth papilla. Largest papillae about 3 mm. Anal papillae distinct. Porous skin in region of anus and mouth may be evidence of retracted podia. Ribs on surface of body can be confused with papillae adhering on to body surface. Colour uniformly grey, including tentacles and papillae.

Calcareous ring well developed, radial and interradial plates well calcified and weakly fused (Fig. 12B). External appearance of ring suggests 15 plates but dissection revealed only 10 plates—five radials, each with paired anterior projections and five interradials, each with a single anterior projection; radials, in addition, with paired anterior depressions for tentacle attachment. All plates roughly rhomboidal in shape and posteriorly concave.

Polian vesicle single, elongate. Stone canal not seen. Gonad in two tufts of 5–6 terminally bifurcate tubes per tuft. Both respiratory trees short, right one more so, each with few lobes. Longitudinal muscles unpaired, clearly visible through translucent body wall. Gut filled with *Globigerina*.

Spicules absent in body wall, appendages and tentacles.

Specimen SAM–A22140b. Length 22 mm, breadth in mid-body 6 mm. Colour grey speckled with a black substance of possibly foreign origin. Mouth and anus terminal, the former slightly turned up due to the constricted anterior

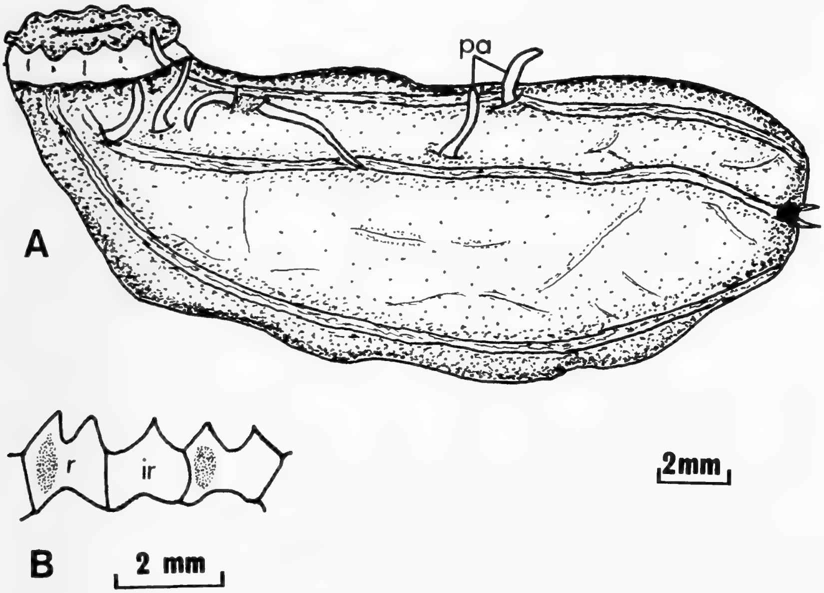

Fig. 12. *Gephyrothuria alcocki* Clark. A. Entire specimen. B. Two radial and one interradial plates of calcareous ring.

Table 2. Comparison of principal characters of the holotypes of *Gephyrothuria* with the southern African form.

Character	*Gephyrothuria alcocki* Koehler & Vaney (type)	*Gephyrothuria glauca* (Clark) (type)	South African form
Length	50 mm	± 20 mm	23 mm
Width	17–18 mm	8 mm	8 mm
Colour	rose	grey	grey
Tentacle lobes	2	4	2–4
Papillae	3–5 prs (5–6 mm long)	4–6 prs (5–6 mm long)	3–4 prs (3 mm long)
Pedicel-like outgrowths	absent	present	present
Genital papillae	?	prominent	prominent (in one spec.)
Polian vesicle	single, 4 mm	?	single
Stone canal	free	?	?
Gonadal tubules	branched	unbranched	branched
Distribution	Atlantic	Indo-Pacific	South Africa

end. Body form cylindrical, barrel-shaped. Mouth bordered by 15 tentacles, each with 2–4 digits. Anal papillae distinct. Dorsal papillae four pairs, longest about 2 mm in length. Pedicel-like structures crowded posteriorly, sparse anteriorly. Genital papillae absent. Calcareous ring as in specimen A22140a, each radial plate with a pore for radial nerve. Spicules absent.

Remarks

Because of the presence of a tail-like process, Clark (1907) described his material as a new species and assigned it to the genus *Himasthlephora* erected for this purpose. He, however, suspected that this process could be an ejected part of the gut. Hence Hérouard (1923) declared *Himasthlephora* a junior subjective synonym of *Gephyrothuria*, a genus erected by Koehler & Vaney (1905) for their *G. alcocki*; in this he was supported by Deichmann (1930). Hérouard (1923), in addition, described *G. europeensis* which, according to Deichmann (1930), is clearly conspecific with *G. glauca*. Thandar (1992), citing Rowe (pers. comm.), considered that *G. alcocki* and *G. glauca* may be conspecific. O'Loughlin (1998) synonymized *G. glauca* with *G. alcocki* after examining material from different localities. He retained the genus in the family Gephyrothuriidae and the order Molpadiida, together with the genus *Hadalothuria*.

The southern African material, although scant, is well preserved. In its size, coloration, number of tentacle-lobes, presence of pedicel-like outgrowths and the genital papilla (in at least one specimen) appears to be identical with Clark's form. However, both specimens lack an extension to the anal canal. Differences between the southern African material and both Koehler & Vaney's (1905) and Clark's (1907) specimens are summarized in Table 2.

This is the first record of this species from the southern Atlantic Ocean.

Distribution

Atlantic Ocean, 1 316–3 678 mm.

Family **Molpadiidae** Müller, 1850

Genus *Molpadia* Risso, 1826

This more or less cosmopolitan genus is represented in southern Africa by *Molpadia millardae*, here described as new to science, and *M. capensis* Heding, 1935. Two specimens of an indeterminate species in the present collection are also referred to this genus.

Key to the southern African nominal species of *Molpadia*

1A. Calcareous ring without significant sculpturings, radial plates with or usually without posterior bifurcations; body wall spicules exclusively tables .... ***Molpadia millardae*** sp. nov.

1B. Calcareous ring deeply sculptured, radial plates with posterior bifurcations; body wall spicules fusiform rods, plates and tables .... *Molpadia capensis* Heding, 1935

Molpadia millardae sp. nov.

Figs 13, 15G

Diagnosis

Total length up to 29 mm; tail up to one-third body length, often shorter. Colour dirty grey, anterior end (oral disc) and tail whitish to grey. Tentacles 15 with usually 3 digits, including unpaired one which is the largest. Calcareous ring without significant sculpturings, radial plates often with a long, posterior prolongation. Longitudinal muscles paired. Phosphatic deposits absent. Spicules exclusively tables with a solid spire derived from three pillars fused for most of their length. Body wall tables with usually 3–6, sometimes more (up to 12) perforations, average diameter 0.15 mm; tail tables rod-like, average length 0.30 mm, with up to 12 holes, often fewer.

Etymology

The species is named after Dr Naomi Millard, formerly of the South African Museum, for making the R.V. *Africana II* and other material available to me.

Material examined

Holotype. SAM–A22163, off south-western Cape Province, R.V. *Africana II* Stn A322, 34°36'S 17°00'E, 2745 m, 10 December 1959.

Paratypes. SAM–A27711, same data as holotype, 3 specimens; SAM–A22168, Stn A318, 33°52'S 16°51'E, 2525–2782 m, 8 December 1959 2 specimens; SAM–A22169, Stn A315, 34°37'S 17°03'E, 2891–2965 m, 8 December 1959, 1 specimen; A22174, Stn A319, 34°05'S 16°58'E, 2690–2727 m, 8 December 1959, 1 specimen.

Description

Holotype. Specimen small, total length 22 mm (including tail), diameter of body 11 mm, tail roughly one-third body length. Colour of body dirty grey, anterior end (oral disc) and tail whitish to grey. Radii with five longitudinal lines demarcating positions of longitudinal muscles. Tentacles retracted, digits not visible. Mouth terminal, circular, in centre of oral disc. Body wall thin, somewhat translucent and gritty to the touch; oral disc and skin around mouth rigid due to well-formed calcareous ring.

Internal organs poorly preserved, interior filled with sand and *Globigerina*. Calcareous ring well developed (Fig. 13E), radial and interradial plates not fused and without significant external sculpturing; anterior margin of ring scalloped, each radial plate notched anteriorly once and slightly prolonged posteriorly to form a rudimentary process; interradial plates each with two anterior notches. Longitudinal muscles distinctly paired.

Body wall spicules exclusively tables (Fig. 13F, G) with small discs (average diameter 0.14 mm) with 3–6, usually 3, large holes, additional holes alternating with three primary ones; spire high (0.09–0.15 mm), composed of three pillars solidly fused at apex. Tail spicules (Fig. 13H) tables with elongate, rod-like or fusiform discs (average length 0.27 mm) with up to 12, but usually

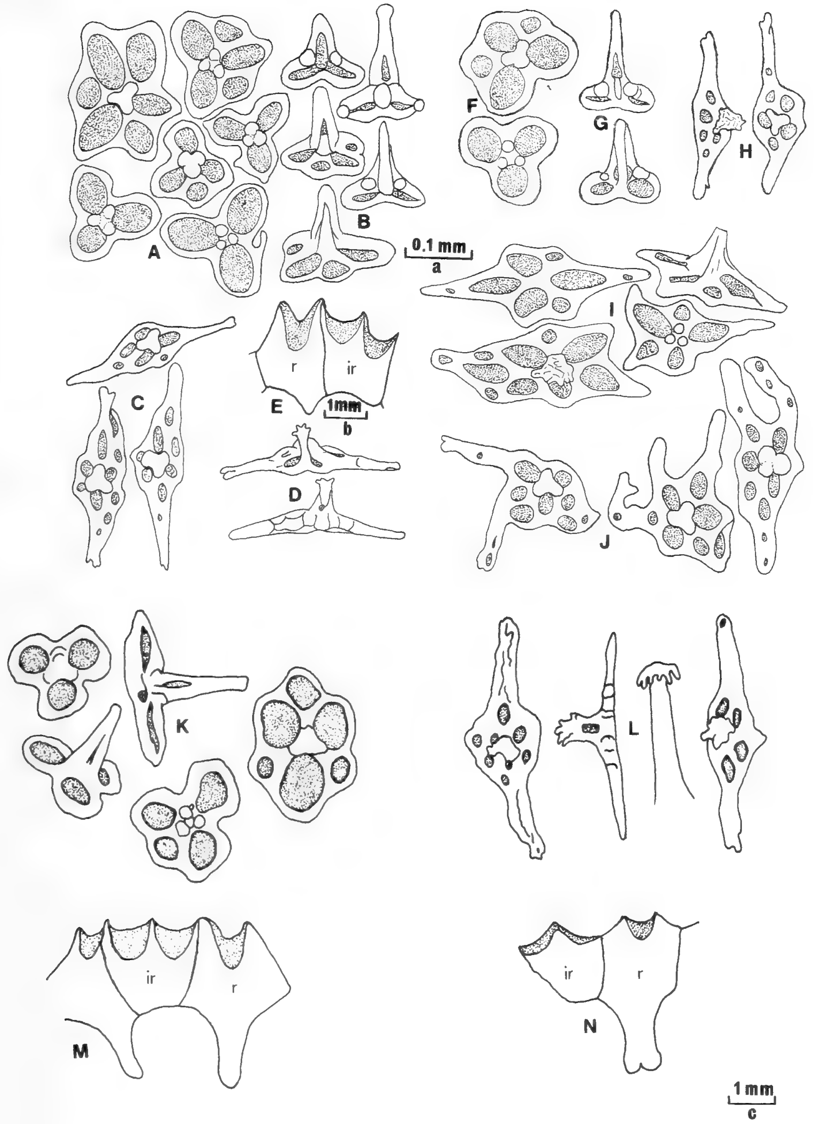

Fig. 13. *Molpadia millardae* sp. nov. Spicules. A. Tables from body wall of paratype SAM–A27711. B. Same from side. C. Tables from tail of paratype SAM–A27711. D. Same from side. E. Part of calcareous ring of holotype, SAM–A22163. F. Tables from body wall of holotype. G. Same from side. H. Tables from tail of holotype. I. Tables from anterior body wall of holotype. J. Tables from base of tail of holotype. K. Spicules from body wall of paratype SAM–A22168. L. Spicules from tail of same. M. Part of calcareous ring of same. N. Part of calcareous ring of paratype SAM–A27711. All spicules drawn to scale a; E—scale b; M, N—scale c.

less than 10 holes; spire low with three discrete pillars or pillars solidly fused together, terminating in few blunt teeth.

Table discs of anterior body wall large, somewhat irregular, slightly elongate (up to 0.33 mm), with usually more than six holes (Fig. 13I). Table discs from base of tail equally long and irregular but with pseudopodia-shaped extensions, usually pierced by several small holes (Fig. 13J). Phosphatic deposits absent.

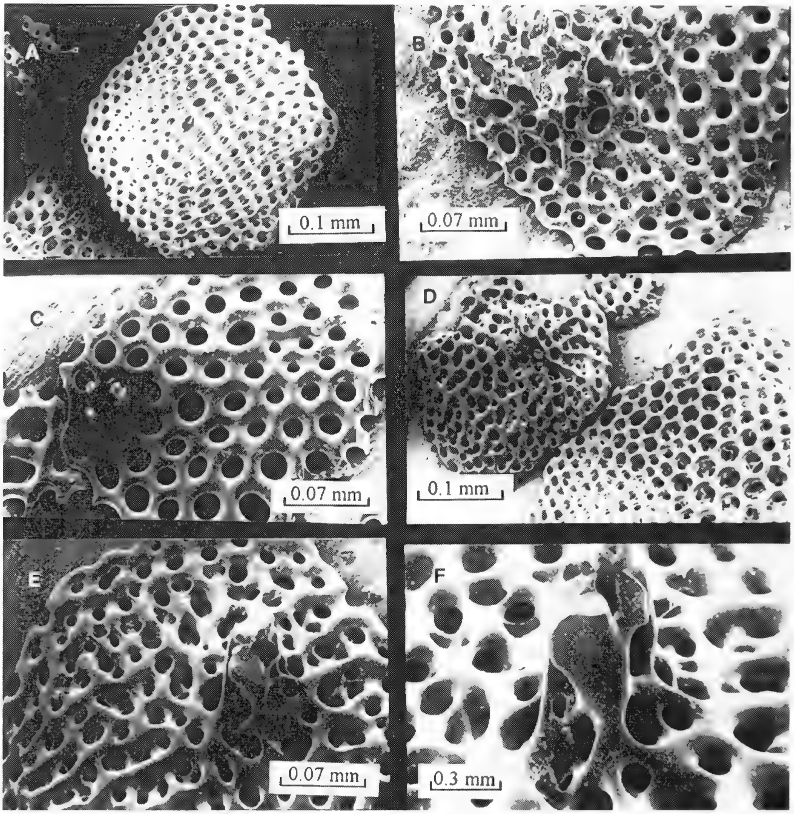

Fig. 14. SEM micrographs of spicules of R.V. *Africana II* holothuroids. A. Thecal plate (undersurface) of *Echinocucumis hispida*. B. Part of same (upper surface) to show spire. C. Another plate of *E. hispida* (under surface). D. Thecal plate of *Ypsilothuria bitentaculata*. E. Same enlarged to show spire. F. Spire enlarged.

Paratype, SAM–A27711. Total length of largest specimen 21.5 mm; diameter of body 10 mm, tail about one-quarter body length. Radial plates of calcareous ring of dissected specimen with long, terminally bifurcate, posterior prolongations (Fig. 13N). Longitudinal muscles paired. Body wall tables (Fig. 13A, B) sometimes scarce, discs with up to 12 perforations, often fewer; tail tables (Fig. 13C) common, with elongate discs, with up to 10, sometimes occluded holes.

Paratype, SAM–A22168. Both specimens poorly preserved and damaged. Total length of larger specimen 20 mm, tail about one-third body length. Radial plates of calcareous ring with long posterior process, not terminally bifurcate (Fig. 13M). Longitudinal muscles paired. Body wall tables with discs up to 0.25 mm and 3–6 holes (Fig. 13K). Tail table discs (Fig. 13L) up to 0.35 mm in length, with up to eight holes. Some table spires very long, of three pillars, totally fused together and with terminal cluster of several downwardly directed spines (Fig. 13L). Smaller specimen damaged, about 13 mm in total length.

Paratype, SAM–A22169. Largest specimen in collection—total length 29 mm, diameter of body 12 mm, tail length 5 mm. Tentacles 15, each with about three digits, unpaired digit the largest. Radial plates of calcareous ring each with a long posterior process, not terminally bifurcate. Longitudinal muscles paired. Gonad filled with large eggs. Body wall tables with disc up to 0.25 mm in length, with 4–8 perforations. Tail tables up to 0.35 mm in length with about five central perforations and a low, sometimes arched spire.

Paratype, SAM–A22174. Total length 27 mm, tail about half body length. Body wall tables not common, discs up to 0.15 mm in length with usually 3–6, usually 3, perforations. Tail table discs long, up to 0.4 mm in length, with up to six large central holes.

Remarks

The new species has close similarities with the Antarctic *Molpadia abyssicola* Pawson, 1977. On first examination, the South African material was referred to this species, albeit with some hesitation (see Thandar 1984). On examination of more material, there appears to be sufficient grounds to regard the southern African material as a new species. It differs from *M. abyssicola* in its size, coloration, smaller tail tables, and the very significant paired nature of the longitudinal muscles. Pawson's species is stated to reach a total length of 105 mm, and is purple or white in colour, with tail tables having an average length of 0.36 mm with up to 20 holes, and undivided longitudinal muscles. In contrast, the largest (mature, female) specimen of *M. millardae* reaches a total length of only 29 mm, all specimens are greyish in colour, the tail tables have a average length of 0.30 mm with only up to 12 holes. There is, however, no doubt that both species are closely related.

It may also be argued that both are geographical variants of the same species, but the above differences speak against this conclusion. Since an adult female measures only 29 mm in total length it does not seem likely that the new species grows to any appreciable size.

The calcareous ring illustrated for the holotype may be abnormal with its arrested posterior processes to the radial plates since at least three paratype dissected show distinct processes to the radial plates. This is in direct contrast to *M. abyssicola* in which Pawson concluded that the ring with long processes to the radial plates in the holotype was abnormal as no such processes were evident in his dissected paratypes.

In the small size of the tables, the present specimens approach also *M. blakei* Théel but, judging from both Deichmann's (1930) and Pawson's (1977) illustrations of the spicules of this species (the latter from the holotype),

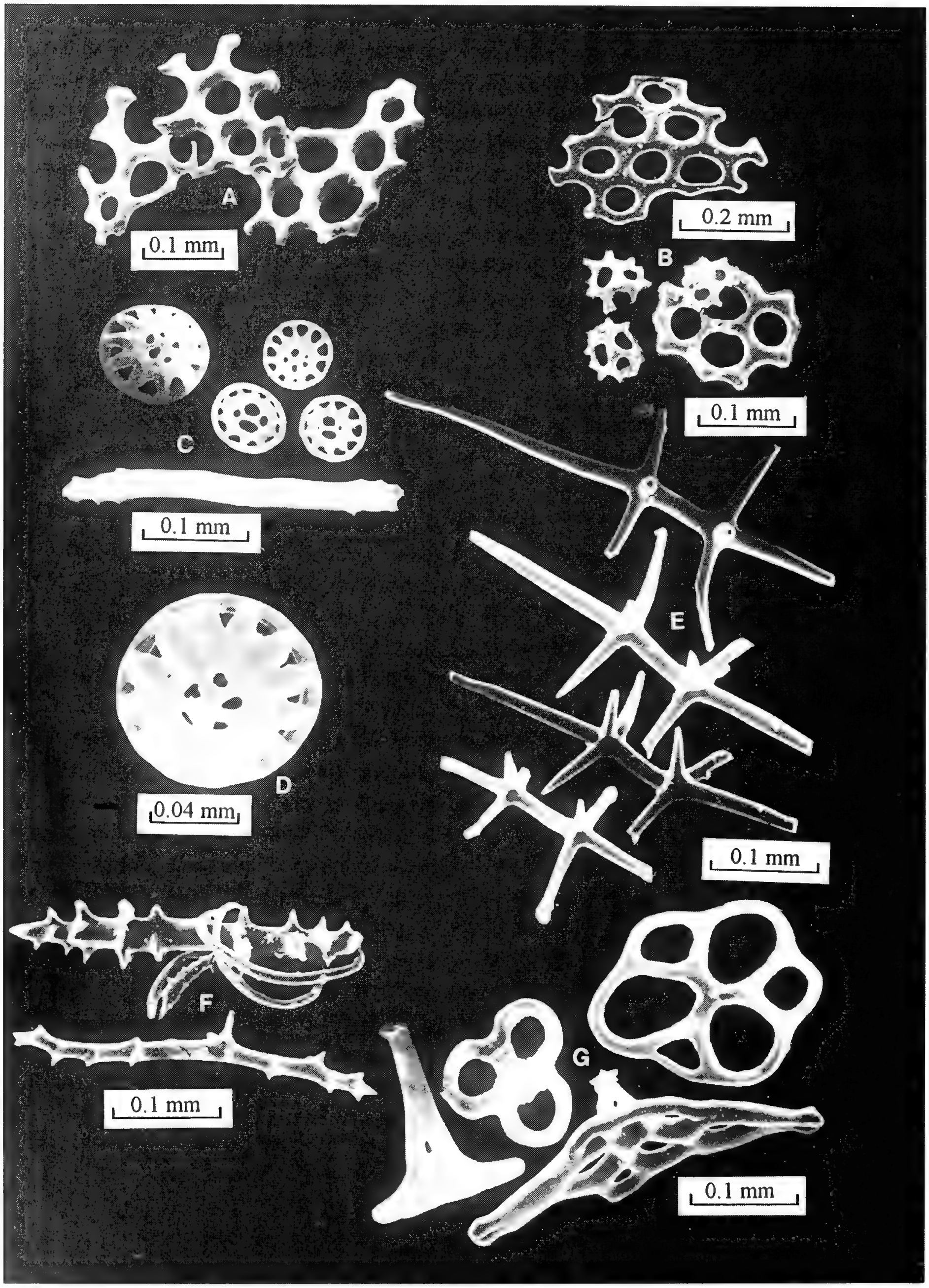

Fig. 15. SEM micrographs of spicules of R.V. *Africana II* holothuroids. A. *Psolidothuria octodactyla*, holotype. B. *Paracucumaria capense*, holotype. C. *Laetmogone perplexa*, holotype. D. Single wheel of same (enlarged). E. *Elpidia gracilis*. F. *Scotoplanes globosa*. G. *Molpadia millardae* sp. nov., holotype.

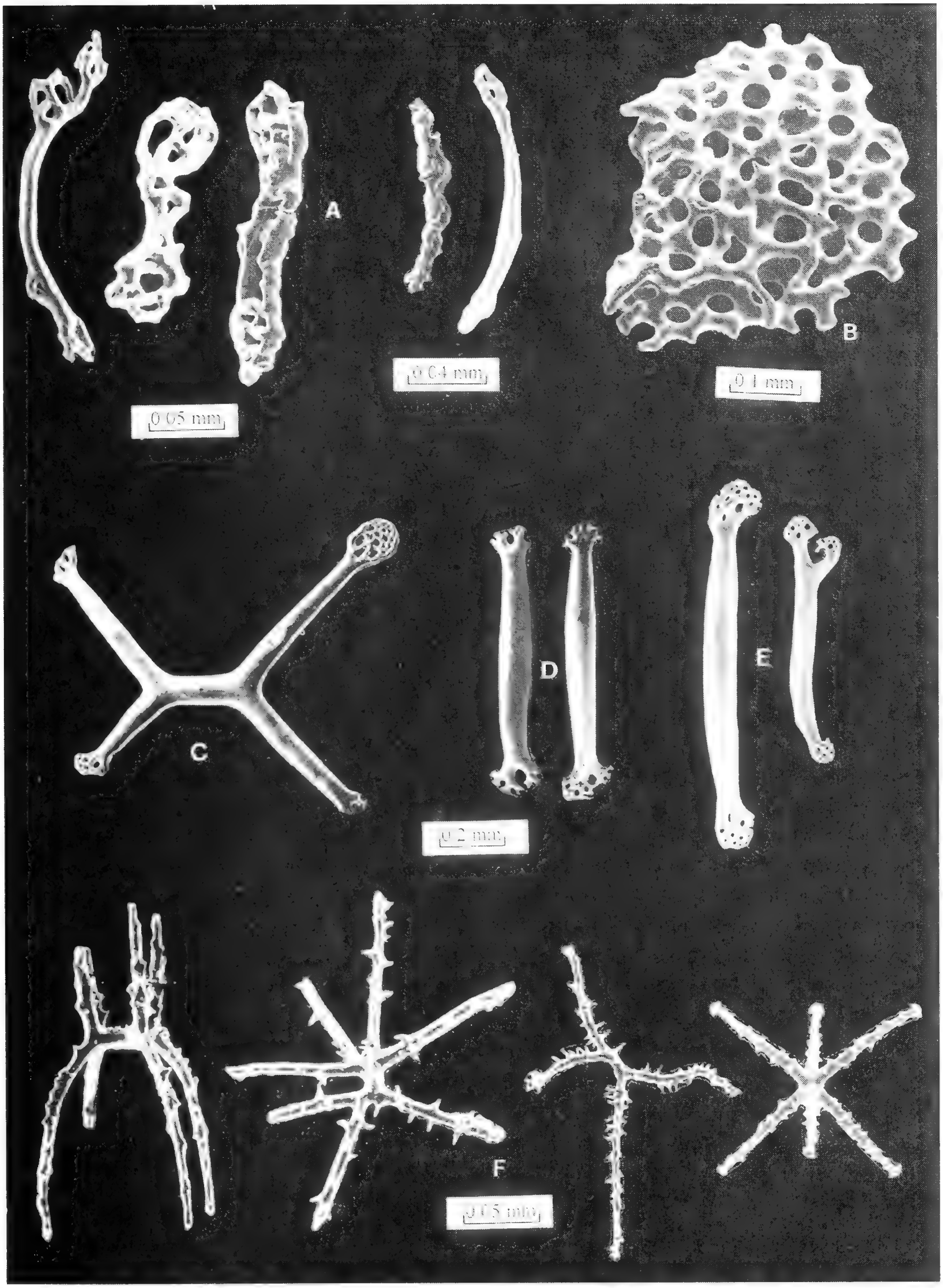

Fig. 16. SEM micrographs of spicules of R.V. *Africana II* holothuroids. A. Tentacle spicules of *Meseres atlanticus*. B. Complex plate from *Psolidium vitreum*. C–E. *Orphnurgus protectus*. C. Cross from body wall. D. Pedicel deposits. E. Tentacle deposits. F. Crosses from *Peniagone* sp. indet.

the spires of the body wall tables are extremely long with downwardly directed teeth. Only one such table was observed in one of the paratypes of the new species here described. *Molpadia millardae* also comes quite close to *M. granulata* (Ludwig) (= *M. bathybia* Clark), but Pawson (1977), who synonymized these species, stated that *M. granulata* has body wall tables with six or more (up to 20) perforations. In addition, *Molpadia granulata* reaches a length of 110 mm, is brownish-yellow in colour and has larger table discs in both the body and the tail.

Pawson's (1977) supposition that those molpadiids without phosphatic deposits always have undivided radial muscles must be discounted unless larger specimens of the new species are found with phosphatic deposits.

This is a second record of a molpadiid from southern Africa. The first is that of Heding (1935) who presented a rather incomplete description of his *M. (Paramolpadia) capensis*, collected by the Ingolf Expedition from the Western Cape Province.

Distribution

South-western Cape Province, South Africa, 2 525–2 965 m.

Molpadia sp. indet.

Material examined

SAM–A22141, WCP (34/16/vd), 2 specimens.

Description

Form and colour as in *M. millardae*; tail absent (?lost). Length 16 mm and 23 mm.

Calcareous ring small, radial plates about twice as wide as interradial plates, notched at both ends, posterior processes absent. Each interradial plate with a blunt, triangular, anterior projection and an indented posterior margin. Longitudinal muscles unpaired. Spicules absent (?dissolved).

Remarks

Since the specimens lack a tail and spicules, it is not possible to determine their specific identity. Although their general appearance (except for the smooth skin) and coloration are identical to *M. millardae*, the form of the calcareous ring and muscles suggest that they belong to another species.

Distribution

Off Cape Point, 2 688–2 725 m.

ACKNOWLEDGEMENTS

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ABBREVIATIONS

an—anus
cl—cloaca
cr—calcareous ring
ir—interradial plate
lrt—left respiratory tree
m—mouth
o—oesophagus
p—pedicel/tube foot
pa—papilla
pv—polian vesicle
r—radial plate
re—rectum
rm—retractor muscle
rrt—right respiratory tree
t—tentacle
wvr—water vascular ring

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc. The name of the taxon should be followed, without intervening punctuation, by the author's name (not abbreviated) and the year of publication; a comma must separate author's name and year. The author's name and date must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be either according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order (see example 1), or according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry (see example 2). The author should adopt one style or the other throughout a paper.

Family **Nuculanidae**
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Example 1

Nucula (Leda) bicuspidata Gould, 1845: 37.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata (Gould) Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871, pl. 2 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata (Gould): Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example: comma separates author's name and year; semicolon separates more than one reference by the same author; full stop separates references by different authors; figures of plates are enclosed in parentheses to distinguish them from text-figures; dash, not comma, separates consecutive numbers.

Example 2

1845 ***Nucula (Leda) bicuspidata*** Gould, p. 37.
1856 ***Leda plicifera*** A. Adams, p. 50.
1859 ***Laeda bicuspidata*** (Gould) Hanley, p. 118, pl. 228 (fig. 73).
1861 ***Nucula largillierti*** Philippi, p. 87.
1871 ***Laeda bicuspidata*** (Gould): Sowerby, pl. 2 (fig. 8a–b).
1950 ***Leda bicuspidata*** (Gould): Nicklès, p. 163, fig. 301.
1955 ***Leda bicuspidata*** (Gould): Nicklès, p. 110.
1964 ***Leda bicuspidata*** (Gould): Barnard, p. 234, figs 8–9.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated allotype (if applicable) and/or paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype. SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text, e.g. '. . . the Figure depicting *C. namacolus* . . .', or '. . . in *C. namacolus* (Fig. 10) . . .'
(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names: e.g. Du Toit, but A. L. du Toit; Von Huene, but F. von Huene
(c) Scientific names, but not their vernacular derivatives e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary. Reference to the author should preferably be expressed in the third person. **Roman numerals** should be converted to arabic, except when forming part of the title of a book or article, e.g. 'Revision of the Crustacea. Part VIII. Amphipoda.'. A **specific name** must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter (except at the beginning of a sentence or paragraph), provided the same generic name is used consecutively. The name of **new genus or species** should not be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of *Biological Abstracts*.

8. GENERAL. Once referees' reports have been received by the editor, these will be discussed by the editorial committee. If the paper is considered acceptable after minor or major revision, the reports will be forwarded to the author who must then thoroughly revise in accordance with the referees' suggestions. Final acceptance of the revised manuscript will be considered by the editorial committee. In the case of major revision being necessary, the committee reserves the right to consult one or more referees regarding the revised manuscript.

AHMED S. THANDAR

DEEP-SEA HOLOTHUROIDS TAKEN BY THE R.V. *AFRICANA II* IN 1959, FROM OFF THE WEST COAST OF THE CAPE PENINSULA, SOUTH AFRICA