ANNALS OF THE
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ANNALE VAN DIE
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VOLUME 90

BAND 90

ANNALS OF THE SOUTH AFRICAN MUSEUM
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VOLUME 90 BAND

LIST OF CONTENTS

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INSTRUCTIONS TO AUTHORS

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

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   (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
   (f) *Summary*, if paper is lengthy
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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.

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   'As described (Haughton & Broom 1927) . . .'
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   et al. in text for more than two joint authors, but names of all authors given in list of references.

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   For books give title in italics, edition, volume number, place of publication, publisher.
   For journal article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals.* 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, 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 le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
   FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
   KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
   KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
   THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

REVISION OF THE FAMILY PHILOSCIIDAE (CRUSTACEA, ISOPODA, ONISCOIDEA) FROM SOUTH AFRICA

By

STEFANO TAITI
&
FRANCO FERRARA

Cape Town   Kaapstad

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(CRUSTACEA, ISOPODA, ONISCOIDEA) FROM SOUTH AFRICA

By

Stefano Taiti

&

Franco Ferrara

Centro di Studio per la Faunistica ed Ecologia Tropicali del Consiglio Nazionale delle Ricerche, Florence

(With 25 figures and 1 table)

ABSTRACT

This revision includes a list of 13 species representing 6 genera and the description of one new genus *Barnardoscia*, and 5 new species, *Nahia louwi*, *Natalscia thomsoni*, *N. rotundata*, *N. appletoni*, and *Barnardoscia maculata*. All the previously known genera and species are redefined. Also given are keys to the South African genera and species and a synopsis of all the Afrotropical genera of Philosciidae, as well as the distribution of the South African philosciid fauna and its affinities.

CONTENTS

INTRODUCTION

Taiti & Ferrara (1980) tentatively revised the family Philosciidae from the Afrotropical region, defining all the known genera (though some of them in a provisional way, due to the lack of material) according to modern criteria, and describing or redescribing several species.

1

Unfortunately neither the South African endemic genera (*Nahia* Budde-Lund, 1908, and *Benthanops* Barnard, 1932) nor the species had been examined directly, thus the generic diagnoses and species list were based on the available literature.

S. Taiti was recently given the opportunity of collecting several philosciids during his stay in South Africa on a fellowship provided by the Department of National Education of the Republic of South Africa. Materials preserved in the South African Museum, Cape Town, and Natal Museum, Pietermaritzburg, and some types in the British Museum (Natural History) were also studied or revised.

Abbreviations used throughout the text:

b   distance of the nodulus lateralis from the posterior margin of the pereon segment

b/c   ratio between b and c

BM   British Museum (Natural History)

c   length of the pereon tergite

d   distance of the nodulus lateralis from the lateral margin of the pereon segment

d/c   ratio between d and c

juv.   juvenile(s)

MZUF   Museo Zoologico dell'Università, Florence

NM   Natal Museum, Pietermaritzburg

NRS   Naturhistoriska Riksmuseet, Stockholm

ovig.   ovigerous

SAM   South African Museum, Cape Town.

KEY TO THE SOUTH AFRICAN GENERA OF PHILOSCIIDAE

1. Frontal line present (Fig. 1C)... *Aphiloscia*
– Frontal line missing 2
2. Eye with a single large ommatidium (Fig. 5A) .... *Benthanops*
– Eye with several ommatidia 3
3. Insertion of uropod exo- and endopodites at the same level (Fig. 6B); d/c co-ordinates of noduli laterales with maxima on pereon segments 2 and 4 (Fig. 6A)
                                                                        Afrophiloscia
– Insertion of endopodites more or less proximal to those of exopodites (Figs 8E, 12C, 20D); d/c co-ordinates without a maximum on pereon segment 2 (Figs 8A, 12A, 20A) 4
4. d/c co-ordinates without evident maxima (Fig. 8A) .... *Nahia*
– d/c co-ordinates with maxima on pereon segments 1 and 4 (Figs 12A, 20A) 5
5. Two noduli laterales on pereon segment 7; endite of maxilliped without a penicil (Fig. 12B) .... *Natalscia*
– Four noduli laterales on pereon segment 7; endite of maxilliped bearing a penicil (Fig. 20B) .... *Barnardoscia*

Genus *Aphiloscia* Budde-Lund, 1908

Diagnosis

Sulcus marginalis and gland pores present. Two series of noduli laterales on each side of pereon segments (Fig. 1B). Frontal and supra-antennal lines present (Fig. 1C). Pleon epimera very produced. Molar penicil of mandible consisting of a single unbranched seta; outer branch of maxilla 1 with 4 + 6 (5 cleft) teeth; endite of maxilliped without a penicil (Fig. 2B). Pleopod exopodites with respiratory areas (Fig. 2F, H). Uropod protopodite with a triangular depression on outer margin; insertion of endopodite proximal to that of exopodite (Fig. 2C).

Type species

Philoscia guttulata Gerstaecker, 1873, from Tanzania.

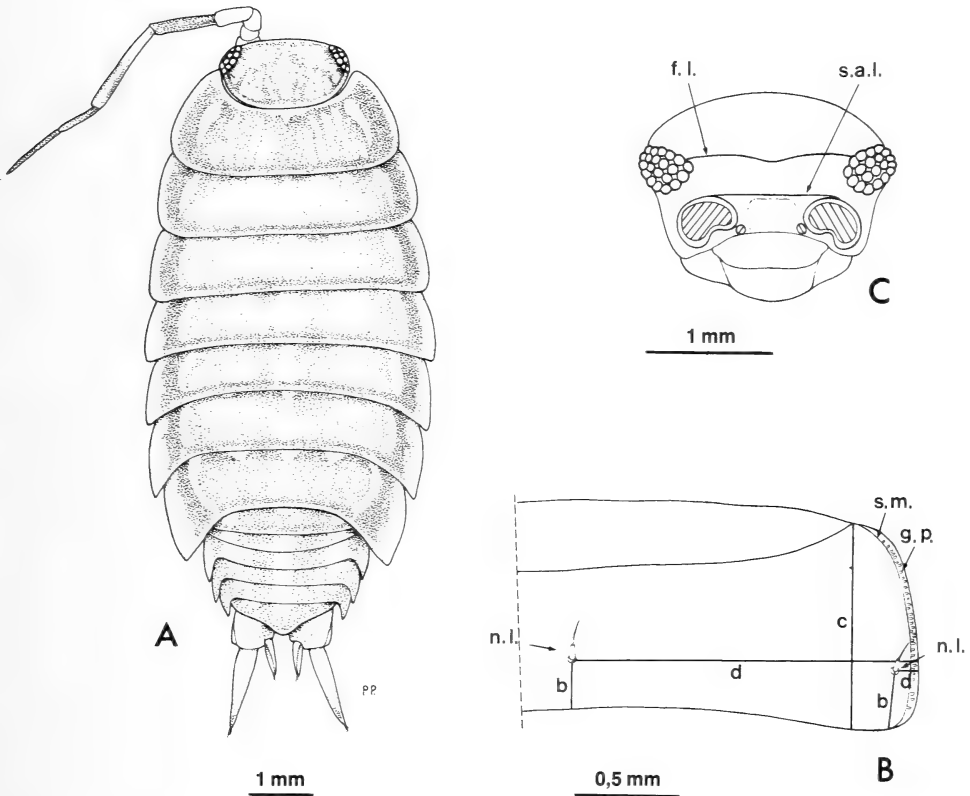Fig. 1. *Aphiloscia vilis* (Budde-Lund, 1885). A. Adult female. B. Right half of pereon segment 4: b—distance of the nodulus lateralis (n.l.) from the posterior margin of the segment, c—length of the pereon tergite, d—distance of the nodulus lateralis from the lateral margin of the pereon segment, g.p.—gland pore, s.m.—sulcus marginalis. C. Frontal view of cephalon: f.l.—frontal line, s.a.l.—supra-antennal line.

Remarks

Aphiloscia is distinguished by the presence of two series of noduli laterales on each side of pereon segments, a frontal line, very produced pleon epimera, and respiratory areas in the pleopod exopodites.

Besides *A. guttulata* and *A. vilis*, the genus includes the following species: *A. annulicornis* (Budde-Lund, 1885) widely distributed throughout Madagascar and surrounding islands; *A. maculicornis* (Budde-Lund, 1898) from Uganda, Tanzania, Zambia; *A. sordida* Arcangeli, 1950, *A. congolensis congolensis* Arcangeli, 1950, *A. congolensis damasi* Arcangeli, 1950, all from Zaïre; *A. montana* Taiti & Ferrara, 1980, from Zimbabwe; *A. trifasciata* Taiti & Ferrara, 1980, from Kenya; and *A. digitata* Taiti & Ferrara, 1980, from Tanzania, Malawi, and Mozambique.

<div align="center">

Aphiloscia vilis (Budde-Lund, 1885)

Figs 1–2

</div>

Philoscia vilis Budde-Lund, 1885: 210. Dollfus, 1895*b*: 351. Barnard, 1937: 164. Brian, 1953: 9.
Philoscia (Aphiloscia) vilis: Budde-Lund, 1908: 292. Barnard, 1932: 239, figs 16g, i, l—n, u, 17a, 18d, 19c. Barnard, 1960*a*: 47. Appleton, 1974: 51. Lawrence, 1977: 175.
Aphiloscia vilis: Stebbing, 1910: 443. Arcangeli, 1950: 66. ?Barnard, 1956: 436. Barnard, 1960*b*: 505, 508. Ferrara & Taiti, 1979: 112. Taiti & Ferrara, 1980: 58.
Philoscia dilectum Collinge, 1917: 579, pl. 42 (figs 21–31). Collinge, 1920: 478. Collinge, 1945: 345. Brian, 1953: 9.

Material

Barnard Collection. Transvaal: 5 ♀♀, Louis Trichardt, Hanglip forest, 4 500 ft alt., leg. R. F. Lawrence, February 1960, NM–6493; 4 ♀♀, Louis Trichardt, Hanglip forest, 3 000 ft alt., leg. R. F. Lawrence, February 1960, NM–6497; 1 ♂, 3 ♀♀, Entabeni forest, Louis Trichardt, leg. R. F. Lawrence, February 1960, NM–6501; 2 ♀♀, Barberton, leg. R. F. Lawrence, March 1960, NM–6518; 1 ♂, 1 ♀, 6 juv., Louis Trichardt, Hanglip, leg. R. F. Lawrence, February 1960, NM–6519.

New material. Transvaal: 1 ♀, Gladdespruit, near Nelspruit, leg. C. C. Appleton, 18 July 1969, No. 2L, SAM–A16843; 4 ♂♂, 16 ♀♀, same data, October 1969–October 1971, No. 165G–H, SAM–A16844; 2 ♀♀, same data, No. 169S, SAM–A16845; 1 ♀, same data, No. 129H, SAM–A16846; 1 ♂, 4 ♀♀, same data, No. 177Q, SAM–A13162; 1 ♀, same data, No. 165Z, SAM–A16847. Natal: 16 ♂♂, 26 ♀♀, Pietermaritzburg, leg. S. Taiti, 19 April 1980, MZUF–995; 3 ♂♂ Gillits, leg. S. Taiti and K. C. Thomson, 26 April 1980, MZUF–996; 3 ♀♀, Durban, leg. G. Cosnett, 28 March 1980, MZUF–997; 34 ♂♂, 32 ♀♀, Umdloti, leg. S. Taiti and K. C. Thomson, 26 April 1980, MZUF–998. Zululand: 3 ♂♂, 12 ♀♀, near Lake Sibaya Research Station, coastal dune forest, leg. C. C. Appleton, date ?, No. 18L, SAM–A16848; 1 ♂, 4 ♀♀, same data, 10 October 1973, No. 76E, SAM–A16849; 4 ♂♂, 2 ♀♀, same data, 18 December 1973, No. 13E, SAM–A16850; 6 ♂♂, 4 ♀♀, same data, 29 July 1973, No. 49L, SAM–A16851;
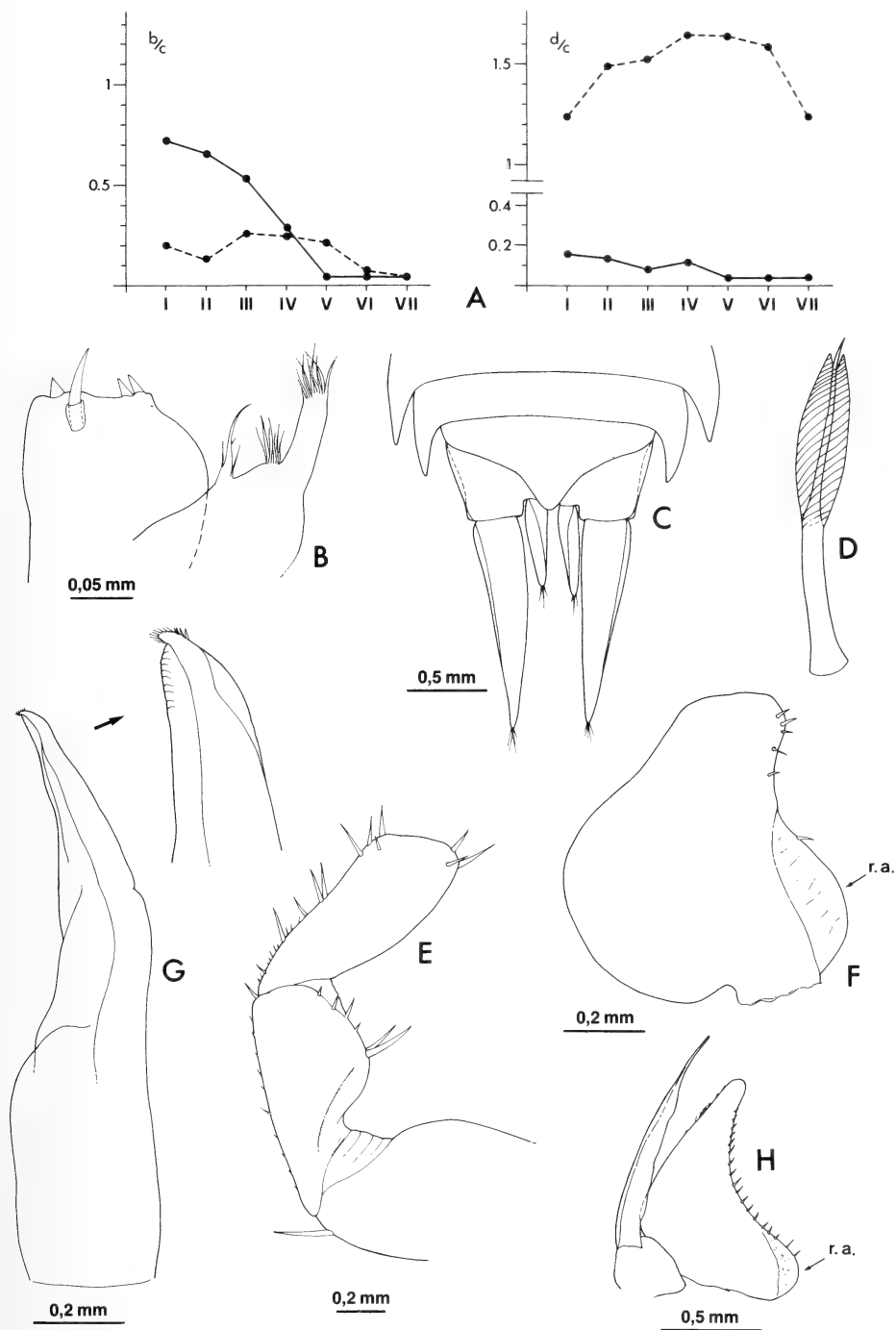
Fig. 2. *Aphiloscia vilis* (Budde-Lund, 1885). A. b/c and d/c co-ordinates. B. Apex of maxilliped. C. Telson and uropods. D. Spine of pereopod 1 carpus (♂). E. Pereopod 7 ischium and merus (♂). F. Pleopod 1 exopodite (♂): r.a.—respiratory area. G. Pleopod 1 endopodite (♂). H. Pleopod 2 (♂).

1 ♂, 2 ♀♀, same data, date?, No. 18D, SAM–A16852; 2 ♂♂, Lake Sibaya
Research Station grounds, leg. C. C. Appleton, 18 September 1973, No. 63C,
SAM–A16853; 2 ♀♀, Lake Sibaya Research Station, garden, leg. C. C.
Appleton, 7 January 1973, No. 8L, SAM–A16854.

Description

9 mm long (according to Barnard, $11 \times 4{,}5$ mm). Colour extremely vari-
able, usually plumbeous with lighter mottling; pale spot at the base of pereon
epimera; epimera dark with external margin orange; joints 1–3 and basal half of
joint 5 of antenna orange; basis of pereopods with a dark spot; uropods orange.
Eye with twenty-five to thirty ommatidia. Each pereon segment with numerous
gland pores (about thirty) per side, arranged along the whole sulcus marginalis.
Noduli laterales with b/c and d/c co-ordinates as in Figure 2A. Telson (Fig. 2C)
with concave sides, dorsally impressed, narrowly rounded apex. Antenna: ratio
of flagellum joints 4 : 3 : 3.

Male

Pereopods 1–4 merus and carpus with brushes of trifid spines (Fig. 2D).
Pereopod 7 ischium with a narrow and shallow depression on the rostral surface
(Fig. 2E). Pleopod 1 exopodite with subquadrate posterior lobe (Fig. 2F);
endopodite with apex slightly bent outward and equipped with fine setae
(Fig. 2G). Pleopod 2 as in Figure 2H.

Remarks

A. vilis is very close to A. montana Taiti & Ferrara, 1980, from Mt.
Selinda (Zimbabwe). It is distinguished in the male (cf. Taiti & Ferrara 1980,
figs 7–11) by the less enlarged pereopod 7 ischium which is not excavated at the
base; the shorter posterior lobe of pleopod 1 exopodite; the presence of setae
on pleopod 1 endopodite apex; the pleopod 2 endopodite that is only slightly
longer than exopodite.

The exact locality of the type material is unknown. Budde-Lund
(1885: 210) quotes 'Caput Bonae Spei' but, as pointed out by Barnard
(1932: 240) the specimen was collected by the botanist Drege, who travelled
both in the Cape and in Natal. Most probably the record refers to the latter
region, where A. vilis is widely distributed. It is definitely not found in the
Cape Peninsula.

This species occurs throughout southern Mozambique, Zimbabwe, eastern
Transvaal, Zululand, and Natal, and is also known in East London (Cape
Province) and Mafa (Ovamboland). In our opinion the latter record needs
further confirmation as this is the only occasion that A. vilis has been found
outside south-eastern Africa.

Genus *Benthanops* Barnard, 1932

Diagnosis

A few gland pores are present on the anterior part of the pereon segments. One series of noduli laterales on each side of pereon segments 1–6; two noduli laterales on each side of pereon segment 7; d/c co-ordinates with a maximum on segment 4. Eye with a single large ommatidium. Frontal line absent; supra-antennal line present. Pleon epimera reduced, with very small posterior points visible in dorsal view. Molar penicil of mandible consisting of a tuft of plumose setae each arising separately (Fig. 3B); outer branch of maxilla 1 with 4 + 5 serrate teeth (Fig. 3C); endite of maxilliped without a penicil (Fig. 3D). Pereopods without dactylar seta. Pleopod exopodites without respiratory areas. Uropod protopodite grooved on outer margin; insertion of endo- and exopodite almost at the same level.

Type species

Philoscia (Benthanops) fulva Barnard, 1932, from South Africa.

Remarks

Benthanops is very close to the South American genera *Benthana* Budde-Lund, 1908, *Benthanoscia* Lemos de Castro, 1958*a*, and *Benthanoides* Lemos de Castro, 1958*b*, from which it is distinguished by the presence of a single ommatidium and the different shape of the molar penicil of mandible. Even greater affinities exist between this and *Ctenoscia* Verhoeff, 1928, from which *Benthanops* differs in the number and position of the noduli laterales (cf. Fig. 3A, and E) as well as the shape of the molar penicil.

The genus includes only the type-species.

Benthanops fulva Barnard, 1932
Figs 3A–D, 4, 5A

Philoscia (Benthanops) fulva Barnard, 1932: 247, figs 16c, f, r, 18e, 19f, 20. Brian, 1953: 9.
Benthanops fulva: Ferrara & Taiti, 1979: 112. Taiti & Ferrara, 1980: 87.

Material

Barnard Collection. Cape Province: 1 ♀, Caledon, leg. K. H. Barnard, March 1908, SAM–A5894; 1 ♂, 17 ♀♀, Noordhoek forest, leg. K. H. Barnard, 19 January 1928, SAM–A7329; 6 ♀♀, Kalk Bay Mt., leg. K. H. Barnard, January 1929, SAM–A7880; 2 ♂♂, 1 ♀, Noordhoek forest, leg. K. H. Barnard, 16 June 1929, SAM–A7881; 5 ♂♂, 45 ♀♀, Table Mt., leg. K. H. Barnard, September 1919, SAM–A7883; 1 ♀, Kleinmond, leg. K. H. Barnard, 1927, SAM–A7946; 2 ♀♀, Hout Bay, leg. ?, 9 August 1931, SAM–A10364.

New material. Cape Province: many ♂♂ and ♀♀, Cape of Good Hope Nature Reserve, leg. S. Taiti, 10 April 1980, MZUF–999; 34 ♂♂, 35 ♀♀,
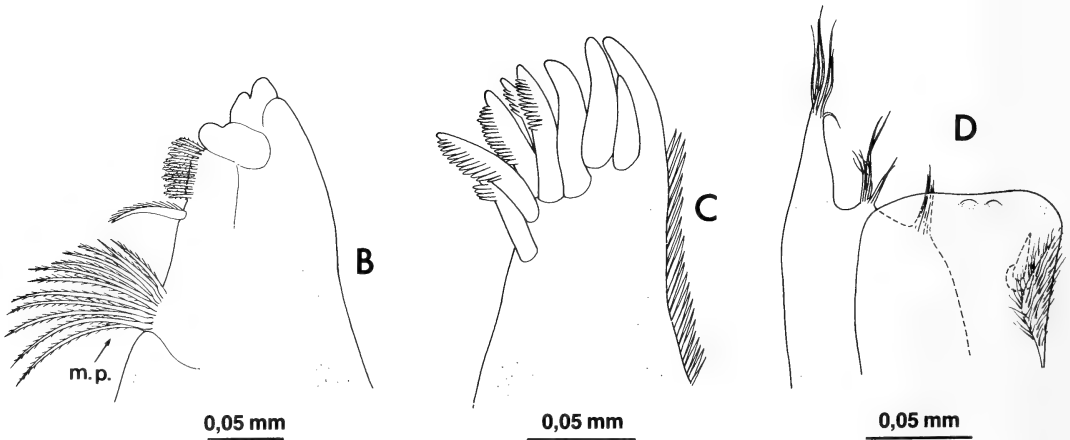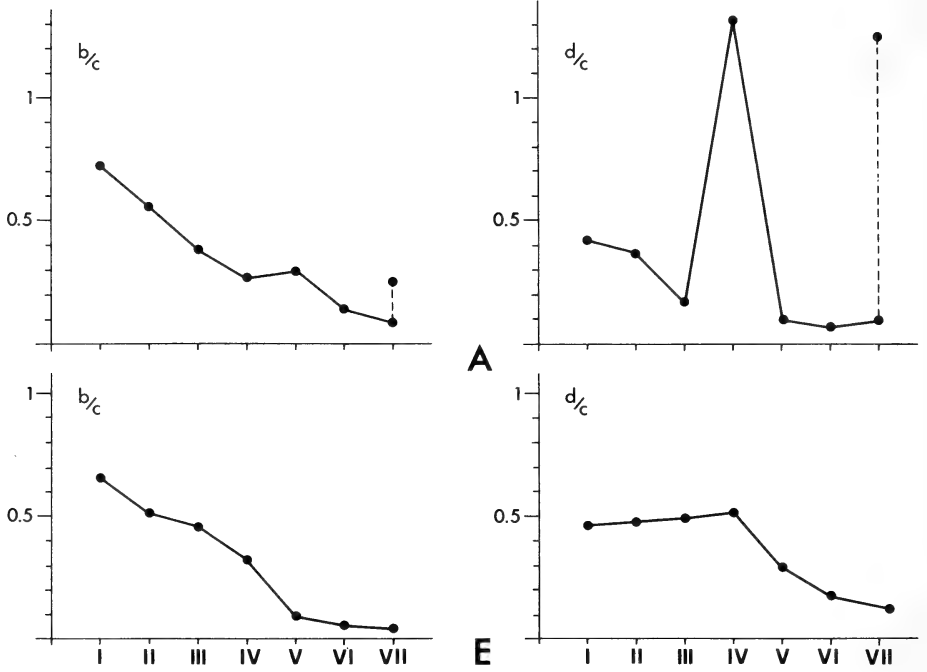
Fig. 3. A–D. *Benthanops fulva* Barnard, 1932. A. b/c and d/c co-ordinates. B. Apex of mandible: m.p.—molar penicil. C. Outer branch of maxilla 1. D. Apex of maxilliped. E. *Ctenoscia minima* (Dollfus, 1892). b/c and d/c co-ordinates.
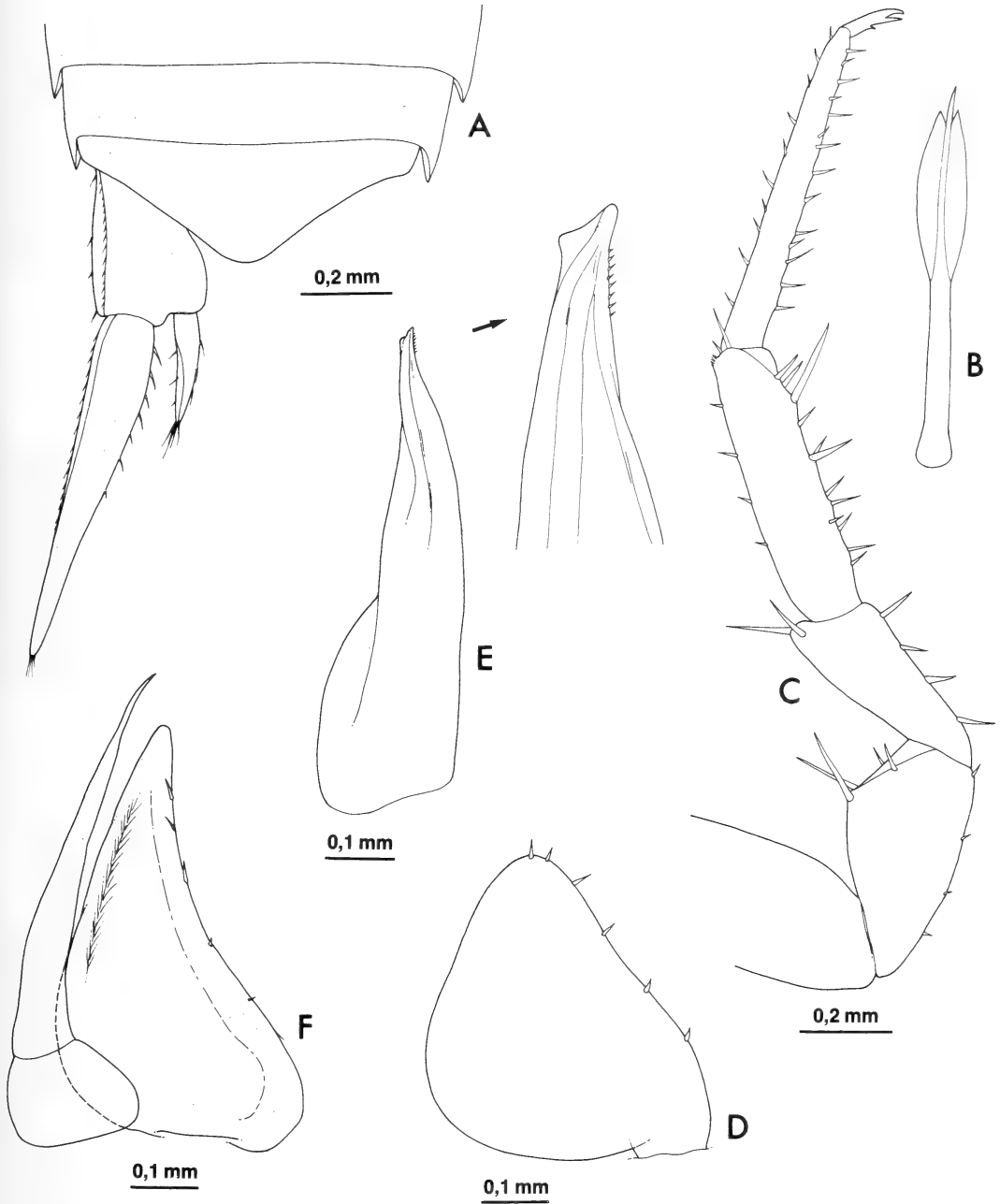
Fig. 4. *Benthanops fulva* Barnard, 1932. Telson and left uropod. B. Spine of pereopod 1 carpus (♂). C. Pereopod 7 (♂). D. Pleopod 1 exopodite (♂). E. Pleopod 1 endopodite (♂). F. Pleopod 2 (♂).
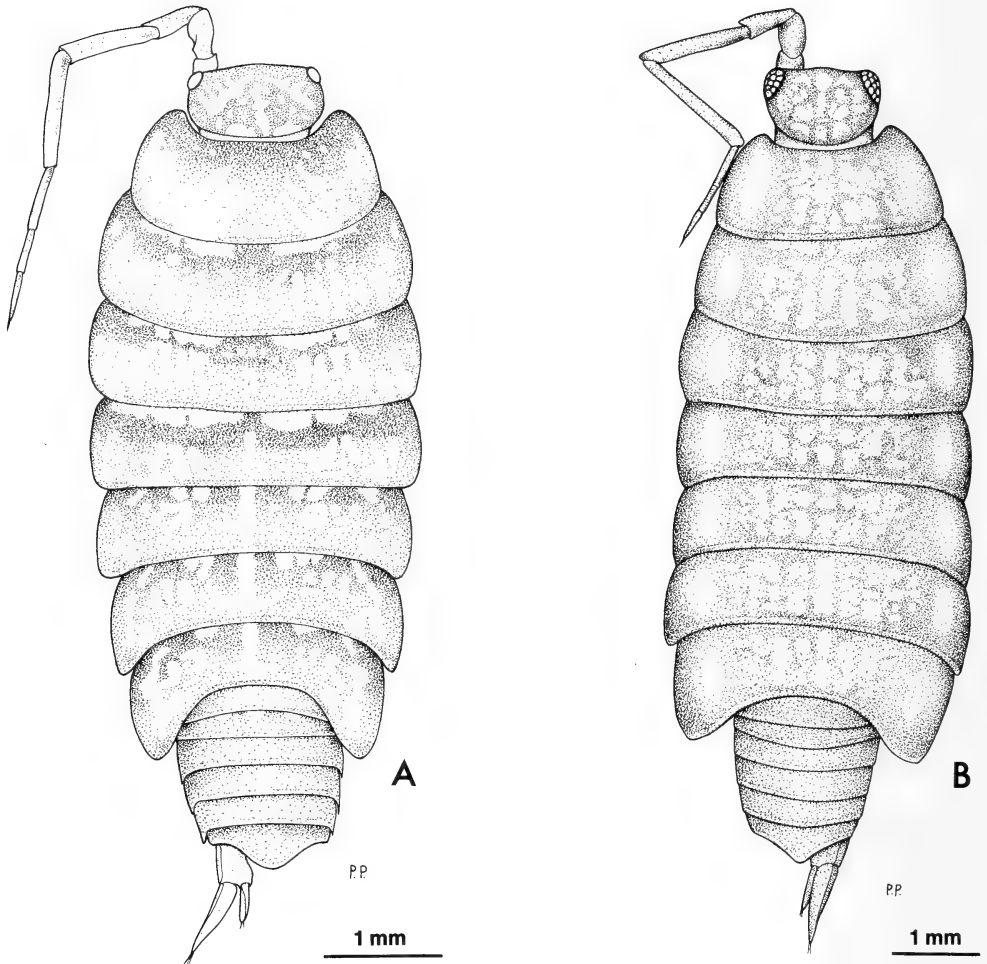
Fig. 5. A. *Benthanops fulva* Barnard, 1932. Adult female. B. *Afrophiloscia ocellata* (Barnard, 1960). Adult female.

Table Mt., Skeleton Gorge, leg. S. Taiti, 13 April 1980, MZUF–1000; 1 ♂, 3 ♀♀, Betty's Bay, leg. J. Hoy, 23 April 1980, MZUF–1001.

Description

♂ 4,5 mm long; ♀ 7 mm long. Yellowish brown, with more or less evident transversal brown stripes at the anterior margins of segments. Noduli laterales with b/c and d/c co-ordinates as in Figure 3A. Telson (Fig. 4A) with feebly concave sides, rounded apex. Antenna: ratio of flagellum joints 5 : 4 : 4. Uropod exopodite very long (about three times longer than endopodite).

Male

Pereopod 1–2 merus and carpus with very sparse brushes of spines (Fig. 4B). Pereopod 7 without specializations (Fig. 4C). Pleopod 1 exopodite (Fig. 4D) with outer margin feebly concave, rounded apex; endopodite (Fig. 4E) equipped with some short spines on the medial surface and triangular lobe on the external surface. Pleopod 2 as in Figure 4F.

Remarks

Benthanops fulva differs from all the other South African (and Afrotropical) philosciids by the presence of a single ommatidium.

Barnard (1932: 249) states that this species occurs on mountains but not at low levels. In the Cape Peninsula it is abundant in bushes close to the sea. It is common between Cape Town and Caledon (Cape Province).

Genus *Afrophiloscia* Taiti & Ferrara, 1980

Diagnosis

Sulcus marginalis and gland pores absent; one series of noduli laterales on each side of pereon segments; d/c co-ordinates with maxima on pereon segments 2 and 4. Frontal line absent; supra-antennal line present. Pleon epimera reduced, adpressed. Molar penicil of mandible consisting of a single unbranched seta; outer branch of maxilla 1 with 4 + 6 (5 cleft) teeth; endite of maxilliped without a penicil. Pleopod exopodites without respiratory areas. Uropod protopodite grooved on outer margin; insertion of endo- and exopodite at the same level.

Type species

Afrophiloscia kinolensis Taiti & Ferrara, 1980, from Tanzania.

Remarks

This genus, recently instituted and discussed (Taiti & Ferrara 1980), differs from the other South African genera of Philosciidae by maxima on pereon segments 2 and 4 of the noduli laterales d/c co-ordinates; the setose apex and typical indentation on the medial margin of the maxilliped endite (see Fig. 6D) and insertion of the uropod exo- and endopodites at the same level.

Afrophiloscia, besides *A. kinolensis* and *A. ocellata*, includes the following species: *A. uncinata* (Ferrara, 1974) and *A. brevicauda* Taiti & Ferrara, 1980, from Tanzania; *A. africana* (Schmoelzer, 1974), *A. rotundata* Taiti & Ferrara, 1980, and *A. kenyensis* Taiti & Ferrara, 1980, all from Kenya.

Afrophiloscia ocellata (Barnard, 1960)
Figs. 5B–6

Philoscia (Setaphora) ocellata Barnard, 1960a: 48. Lawrence, 1977: 175.
Setaphora ocellata: Ferrara & Taiti, 1979: 119. Taiti & Ferrara, 1980: 83.

Material

Barnard Collection. Transvaal: 2 ♂♂, 3 ♀♀ (types), Magoebaskloof, 4 000 ft alt., leg. R. F. Lawrence, March 1960, NM–6512; 2 ♀♀, Mariepskop, 6 000 ft alt., leg. R. F. Lawrence, March 1960, NM–6504; 1 ♀, 1 juv., Graskop, leg. R. F. Lawrence, March 1960, NM–6508; 3 ♀♀, Malta forest, Selati Estate, leg. R. F. Lawrence, NM–6516.

New material. Transvaal: 1 ♀, Gladdespruit, near Nelspruit, leg. C. C. Appleton, October 1969–October 1971, No. 174T, SAM–A16855.

Description

9,5 mm long (according to Barnard 7 × 2,5–2,75 mm). Brown with pale irroration on head and pereon; pleon almost a uniform brown; large oval pale spot at the base of pereon epimera. Eyes with about sixteen ommatidia. Noduli laterales with b/c and d/c co-ordinates as in Figure 6A. Pleon epimera adpressed with very short posterior points, not visible in dorsal view. Telson (Fig. 6B–C) with slightly concave sides, narrowly rounded or subacute apex. Antenna with ratio of flagellum joints 5 : 3 : 3. Endite of maxilliped (Fig. 6D) as in the other species of *Afrophiloscia.*

Male

Pereopods 1–2 are missing in the males observed. Pereopod 7 without any evident specialization (Fig. 6E). Pleopod 1 exopodite (Fig. 6F) with triangular posterior point bent outwards; endopodite (Fig. 6G–H) with an oval lobe equipped with fine setae. Pleopod 2 exopodite much shorter than endopodite (Fig. 6I).

Remarks

Re-examination of the type material showed that these specimens belong to the genus *Afrophiloscia* Taiti & Ferrara, 1980. *A. ocellata* differs from *A. africana* and *A. uncinata* by the lack of specializations (hooks) on pereopod 7 merus ♂; and from those and from all the other species of *Afrophiloscia* by the swollen setose apex of pleopod 1 endopodite ♂. The distinctive coloration is a useful trait in identifying this species.

Afrophiloscia ocellata occurs throughout the eastern Transvaal. Its presence in South Africa considerably enlarges the range of the genus *Afrophiloscia* previously known only in Kenya and Tanzania.
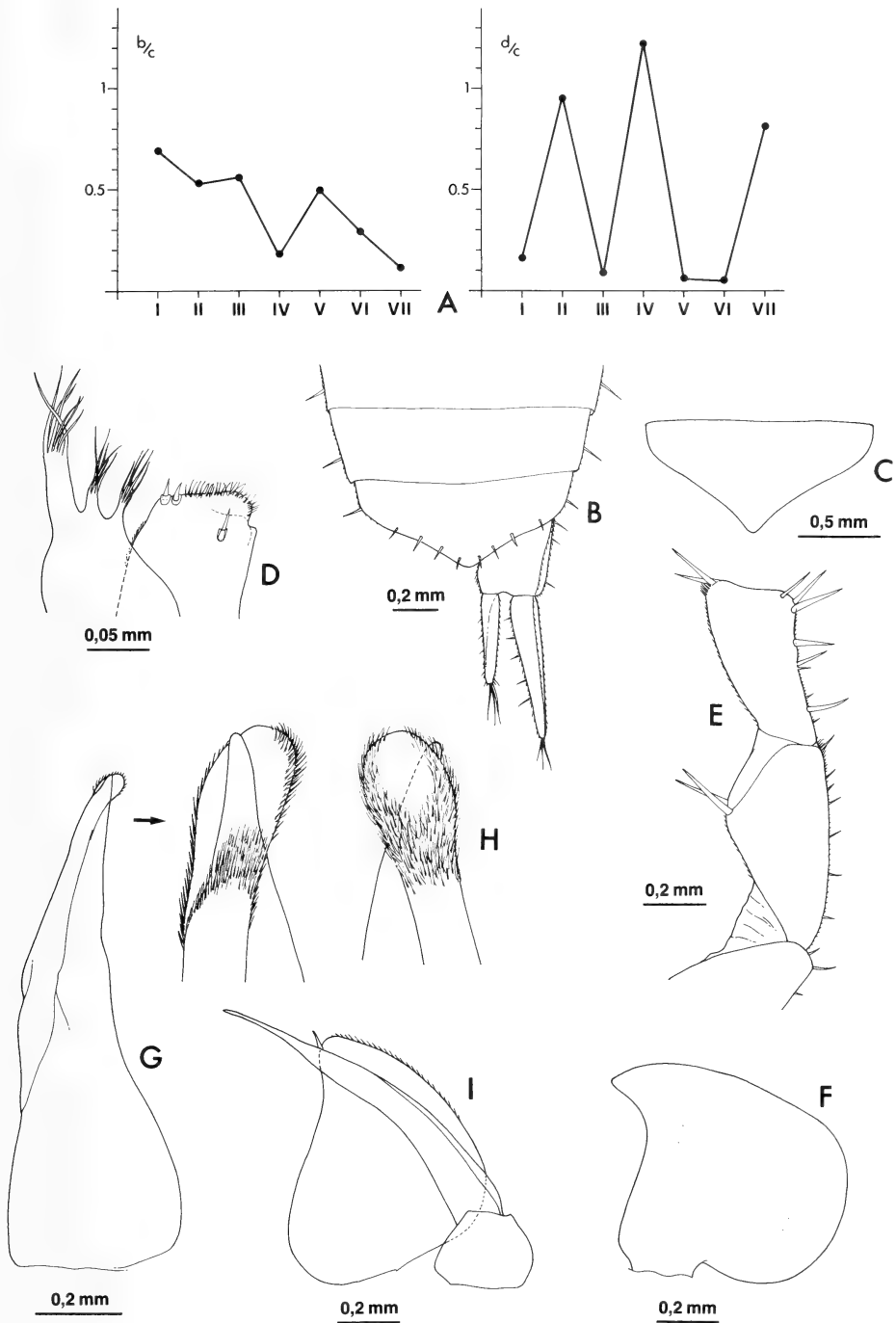
Fig. 6. *Afrophiloscia ocellata* (Barnard, 1960). A. b/c and d/c co-ordinates. B. Telson and right uropod. C. Telson of a female specimen from Graskop. D. Apex of maxilliped. E. Pereopod 7 ischium and merus (♂). F. Pleopod 1 exopodite (♂). G. Pleopod 1 endopodite (♂). H. Apex of pleopod 1 endopodite (♂), ventral view. I. Pleopod 2 (♂).

Genus *Nahia* Budde-Lund, 1908

Diagnosis

Sulcus marginalis and gland pores present. One series of noduli laterales on each side of pereon segments; their d/c co-ordinates lacking evident maxima (Figs 8A, 10A). Frontal line absent and supra-antennal line present. Pleon epimera reduced. Molar penicil of mandible consisting of a single unbranched seta (Fig. 8B); outer branch of maxilla 1 with 4 + 6 (5 cleft) teeth (Fig. 8C); endite of maxilliped without a penicil (Fig. 8D). Pereopods with a flagellar dactylar seta. Pleopod exopodites without respiratory areas. Uropod protopodite grooved on outer margin; insertion of endopodite slightly proximal to that of exopodite.

Type species

Philoscia hirsuta Budde-Lund, 1906, from South Africa.

Remarks

An incomplete diagnosis of *Nahia* was given by Taiti & Ferrara (1980: 87), based on the diagnoses by Budde-Lund (1906) and Barnard (1932), as well as on the description and figures of *Philoscia warreni* (= *Nahia hirsuta* according to Barnard 1932) by Collinge (1917).

The study of several specimens of *Nahia* (*N. hirsuta* and *N. louwi* n.sp.) resulted in a complete diagnosis of the genus and in the demonstration that—as will be discussed below—*P. warreni* is not a junior synonym of *Nahia hirsuta* as proposed by Barnard (1932).

Nahia differs from all the afrotropical genera in the absence of peaks in the d/c curve. This trait, which places it in the *Plymophiloscia* group, gives it affinity to the genus *Bilawrencia* Vandel, 1973*b*, from which it differs in the absence of a penicil on the maxilliped and in the simple, rather than dichotomized, molar penicil of the mandible. *Nahia* is also very close to the genus *Australophiloscia* Vandel, 1973*a*, from which it differs essentially in the position of the noduli laterales.

The genus *Nahia* includes only two species, both from South Africa.

<div align="center">KEY TO THE SPECIES OF <i>NAHIA</i></div>

1. Pereopod 7 ♂: merus with a setose protrusion at the base (Fig. 8H). Pleopod 1 ♂: exopodite with outer margin truncated and distally deeply excised (Fig. 9A); endopodite with spines and a crest-shaped lobe close to the apex (Fig. 9B–C)
<div align="right"><i>N. hirsuta</i> (Budde-Lund)</div>

\- Pereopod 7 ♂: merus without setose protrusion at the base (Fig. 10C). Pleopod 1 ♂: exopodite with outer margin not truncated and not excised (Fig. 10D); endopodite with goblet-shaped apex (Fig. 10E) .... *N. louwi* sp. nov.

Nahia hirsuta (Budde-Lund, 1906)
Figs 7–9

Philoscia hirsuta Budde-Lund, 1906: 89, pl. 3 (figs 42–52). Barnard, 1937: 164. Barnard, 1949: 403.
Philoscia (Nahia) hirsuta: Budde-Lund, 1908: 290. Budde-Lund, 1909: 64. Barnard, 1932: 245, figs 16j–k, p, v, 18c, 19f, *partim.* Brian, 1953: 9.
Nahia hirsuta: Stebbing, 1910: 442. Ferrara & Taiti, 1979: 115. Taiti & Ferrara, 1980: 88.
Anchiphiloscia karongae: Stebbing, 1922: 6.

Material

Barnard Collection. Cape Province: 12 ♂♂, 34 ♀♀, Zeekoevlei, Cape Flats, leg. K. H. Barnard, 29 October 1929, SAM–A7397; 14 ♂♂, 16 ♀♀, Keurbooms River, leg. K. H. Barnard, January 1931, SAM–A7858; 3 ♂♂, 4 ♀♀, same data, October 1930–January 1931, SAM–A7856; 1 ♂, 9 ♀♀, same data, January 1931, SAM–A7842; 2 ♂♂, 6 ♀♀, Noordhoekvlei, leg. K. H. Barnard, 24 January 1928, SAM–A7332; 1 ♂, 3 ♀♀, Houw Hoek, leg. K. H. Barnard, 1931, SAM–A8021; 2 ♀♀, Doorn River, leg. S. H. Haughton and C. W. Thorne, 1931, SAM–A7957; 8 ♂♂, 14 ♀♀, Forebay, leg. K. H. Barnard, January 1931, SAM–A7869; 3 ♂♂, 3 ♀♀, Wilderness, leg. S. H. Haughton and C. W. Thorne, 1931, SAM–A7950; 2 ♀♀, Knysna, leg. R. F. Lawrence, 1929, SAM–A7390.

New material. Cape Province: 4 ♂♂, 3 ♀♀, Queenstown, leg. V. B. Whitehead, 21 June 1975, SAM–A16856; 1 ♂, Die Bosch, Bredasdorp, leg. B. F. Kensley, 1969, SAM–A16857; 1 ♀, near Calitzdorp, 7 November 1971, SAM–A16858; 27 ♀♀, Zoutpansklipheuwel on Olifants River, 3 January 1975, SAM–A16859; 18 ♂♂, 37 ♀♀, Cape of Good Hope Nature Reserve, leg. S. Taiti, 10 April 1980, MZUF–1002; 8 ♂♂, 41 ♀♀, Rondeberg, 65 km N of Cape Town, leg. S. Taiti, 20 March 1980, MZUF–1003; 1 ♂, Table Mt., Skeleton Gorge, leg. S. Taiti, 13 April 1980, MZUF–1004.

Description

♂ 6,5 mm long; ♀ ovig. 8 mm long. Slate-grey mottled with lighter spots, a narrow white and a wide black stripe at the base of pereon epimera; joints 2–5 of peduncle of antenna with a white ring at the base. Eye with about twenty-two ommatidia. Back equipped with numerous upright setae. Each pereon segment with ten to fifteen gland pores per side arranged along the whole sulcus marginalis. Noduli laterales with b/c and d/c co-ordinates as in Figure 8A. Telson (Fig. 8E–F) short, with straight or slightly concave sides, rounded apex. Antenna: ratio of flagellum joints 4 : 3 : 4.

Male

Pereopods 1–3 merus and carpus with brushes of spines as in Figure 8G. Pereopod 7 ischium with a deep concavity; merus with an evident setose protrusion at the base (Fig. 8H). Pleopod 1 exopodite with outer margin truncated and distally deeply excised (Fig. 9A); endopodite with apex equipped with spines and a crest-shaped lobe (Fig. 9B–C). Pleopod 2 as in Figure 9D.

1 mm
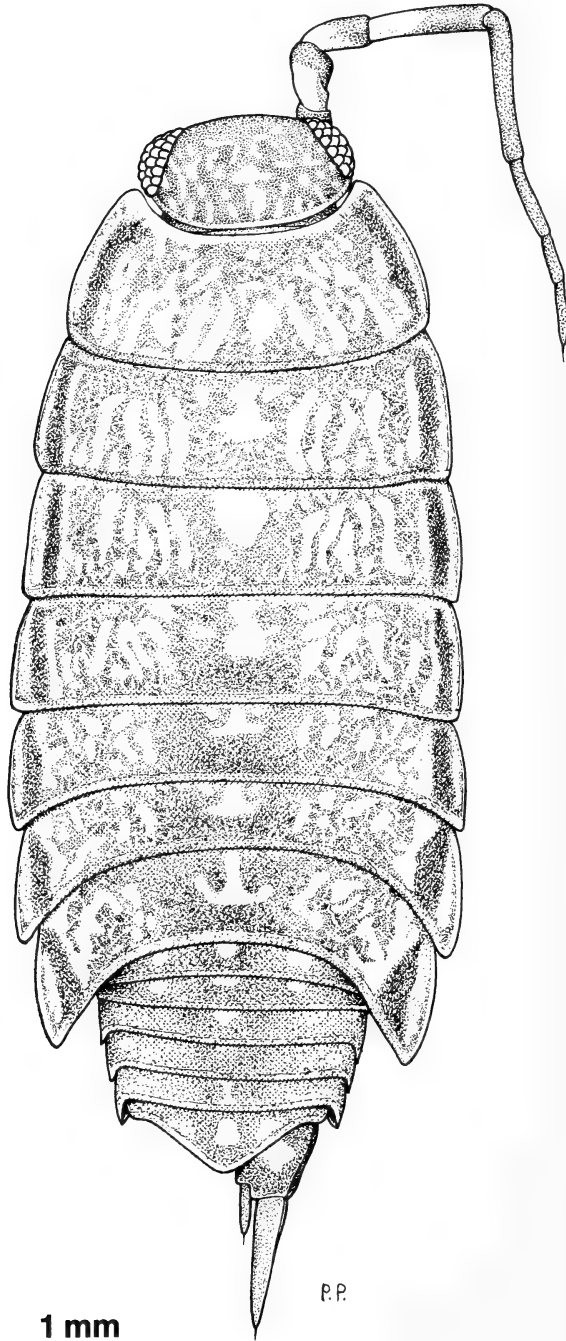
Fig. 7. *Nahia hirsuta* (Budde-Lund, 1906). Adult female.
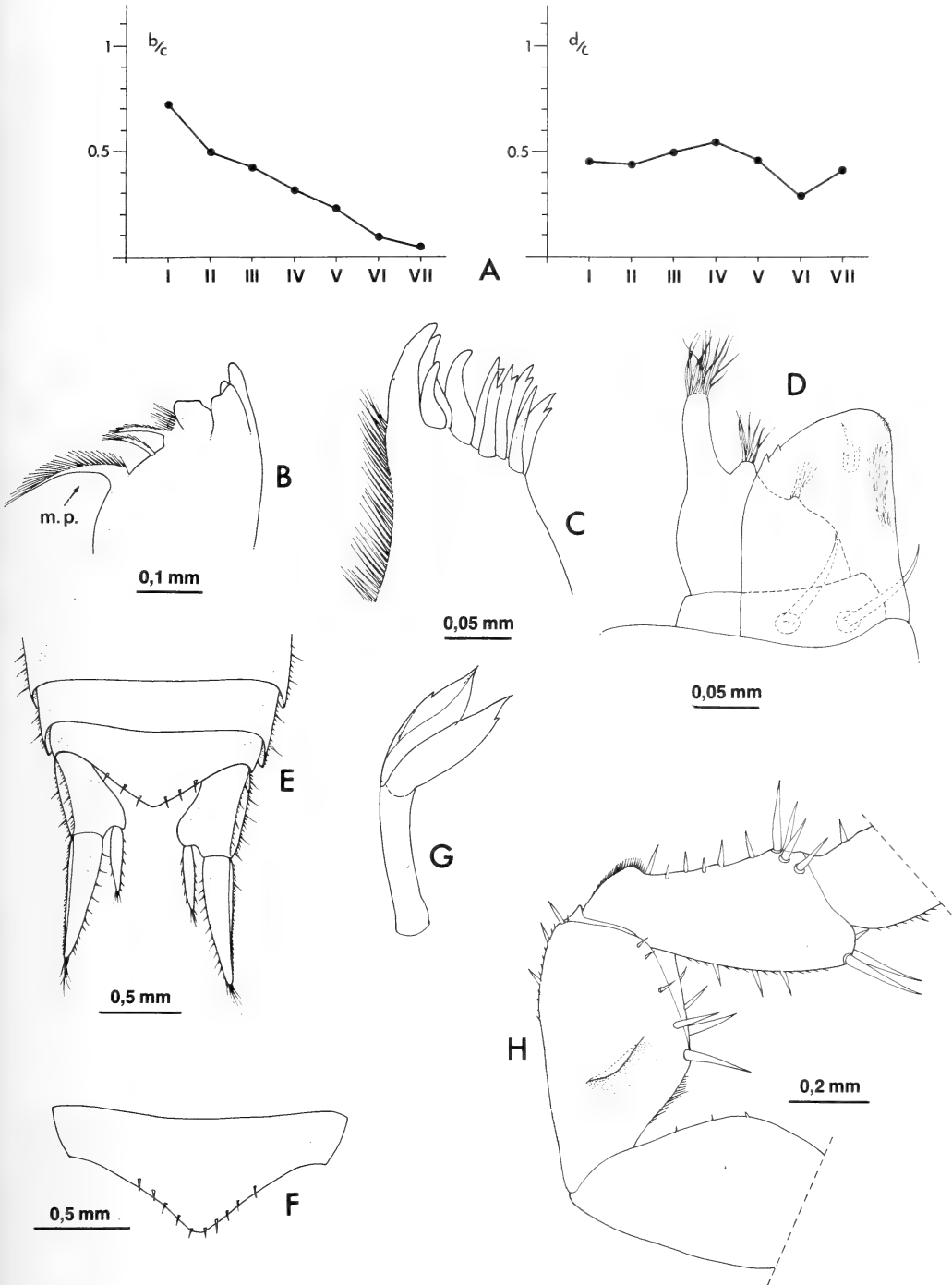
Fig. 8. *Nahia hirsuta* (Budde-Lund, 1906). A. b/c and d/c co-ordinates. B. Apex of mandible: m.p.—molar penicil. C. Outer branch of maxilla 1. D. Apex of maxilliped. E. Telson and uropods. F. Telson of another specimen. G. Spine of pereopod 1 carpus (δ). H. Pereopod 7 ischium and merus (δ).

0,1 mm

0,05 mm

0,2 mm

0,1 mm
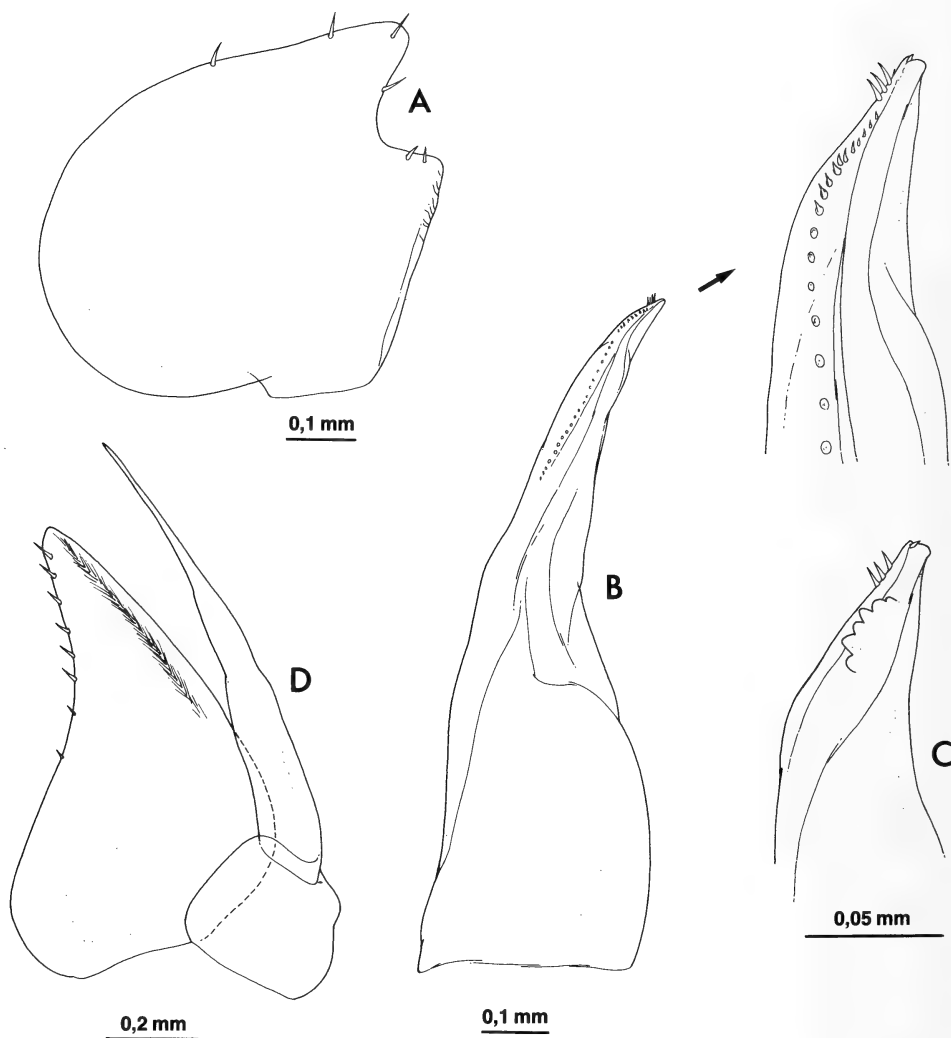
Fig. 9. *Nahia hirsuta* (Budde-Lund, 1906). A. Pleopod 1 exopodite (♂). B. Pleopod 1 endopodite (♂). C. Apex of pleopod 1 endopodite (♂), ventral view. D. Pleopod 2 (♂).

Remarks

A study of part of Barnard's collection showed that he had identified two different species as *Nahia hirsuta*. The specimens from Addo Bush (Barnard 1932: 246) belong, in fact, to a new species of *Nahia* (see below). Consequently only the verified material can be considered as correctly assigned, while all the other records must be considered as *sub judice*.

Furthermore, as *Philoscia warreni* Collinge, 1917, from Natal is not a synonym of *N. hirsuta*, as affirmed by Barnard (1932: 247), all his records from

this region must be considered as doubtful. In our opinion this species occurs only in the southern part of Cape Province.

It is likely that *Chaetophiloscia elongata* from Cape Town (Dollfus 1895*b*: 350) refers to *N. hirsuta*, as its colour pattern and general body shape are very similar to this species.

Nahia louwi sp. nov.
Fig. 10

Philoscia (Nahia) hirsuta: Barnard, 1932: 245, *partim* (the specimens from Addo Bush).

Material

Barnard Collection. Cape Province: 1 ♂, Addo Bush, leg. J. Drury, July 1919, holotype SAM–A16860; 9 ♂♂, 13 ♀♀, same data, paratypes SAM–A6067.

Description

♂ 7,5 mm long; ♀ 8 mm long. Colour faded by long conservation. Eye with about twenty-two ommatidia. Back with numerous upright setae. Number and disposition of gland pores as in *N. hirsuta*. Noduli laterales with b/c and d/c co-ordinates as in Figure 10A. Telson (Fig. 10B) with concave sides, rounded apex. Antenna: ratio of flagellum joints 5 : 4 : 4.

Male

Pereopods 1–3 merus and carpus with sparse brushes of spines as in *N. hirsuta*. Pereopod 7 ischium very similar to that of the preceding species, merus lacking the setose protuberance (Fig. 10C). Pleopod 1 exopodite with outer margin not excised (Fig. 10D); endopodite with goblet-shaped apex, equipped with many setae (Fig. 10E). Pleopod 2 as in *N. hirsuta*.

Etymology

The species is named for Prof. G. N. Louw, Head of the Department of Zoology of the University of Cape Town.

Remarks

These specimens were identified as *Nahia hirsuta* by Barnard. The new species, even if closely related to *N. hirsuta*, is readily distinguished in the male by the lack of a meral protrusion on pereopod 7, the non-truncated and non-excised outer margin of pleopod 1 exopodite, and goblet-shaped apex of pleopod 1 endopodite.

Genus *Natalscia* Verhoeff, 1942

Diagnosis

Sulcus marginalis and gland pores present; one series of noduli laterales on each side of pereon segments; d/c co-ordinates with a maximum on pereon
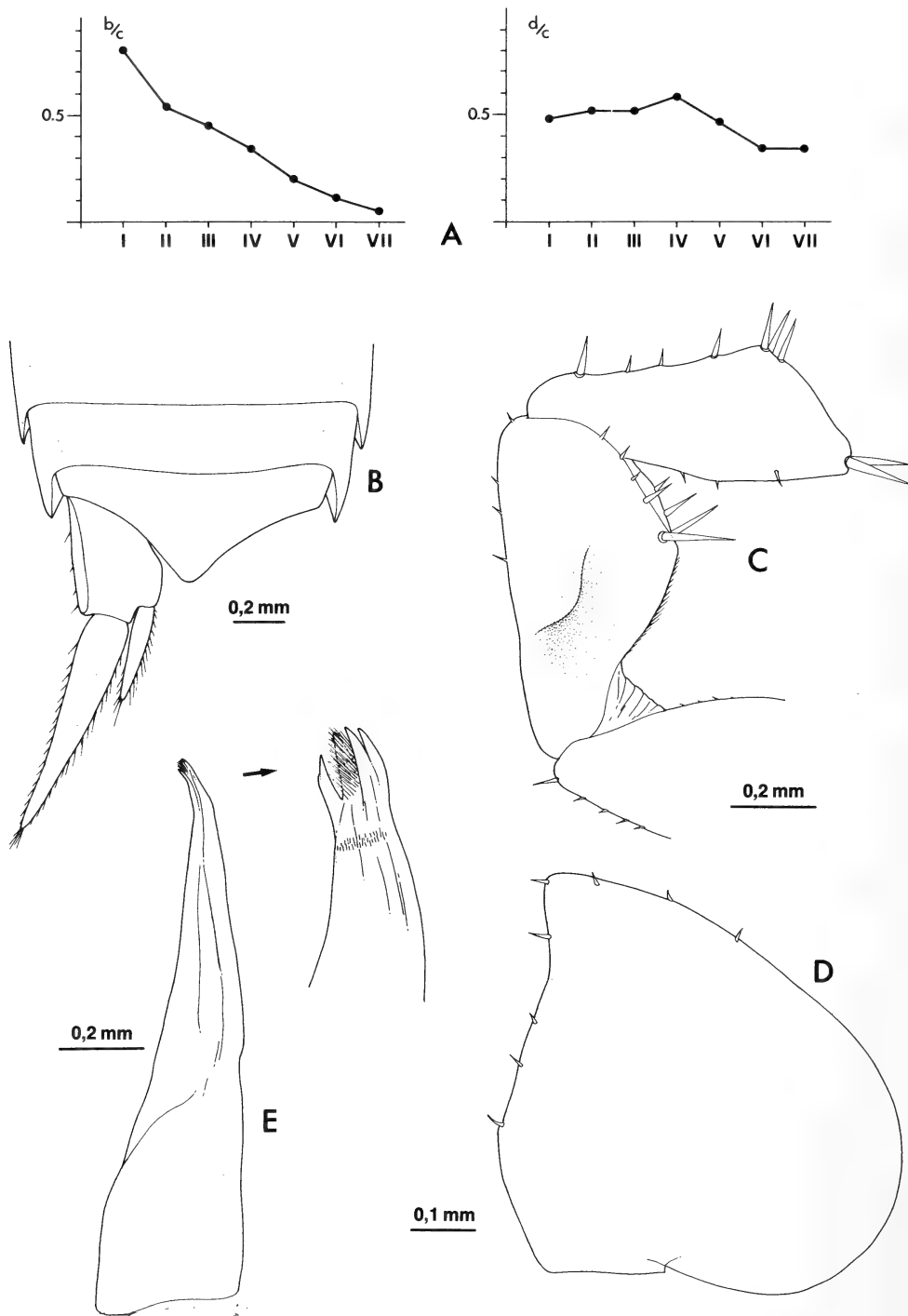
Fig. 10. *Nahia louwi* sp. nov. A. b/c and d/c co-ordinates. B. Telson and left uropod. C. Pereopod 7 ischium and merus (♂). D. Pleopod 1 exopodite (♂). E. Pleopod 1 endo-podite (♂).

segment 4 and a lower one on segment 1 (Figs 12A, 14A, 15A, 16A, 17A). Frontal line absent, supra-antennal line present. Pleon epimera reduced, with small posterior points visible in dorsal view. Molar penicil of mandible consisting of a single unbranched seta; outer ramus of maxilla 1 with $4 + 6$ (5 cleft) teeth; endite of maxilliped with tiny setae at the apex and without penicil (Fig. 12B). A long flagellar dactylar seta is present. Pleopod exopodites without respiratory areas. Uropod protopodite grooved on outer margin; insertion of endopodite proximal to that of exopodite.

Type species

Philoscia warreni Collinge, 1917 = *Philoscia mina* Budde-Lund, 1885, from South Africa.

Remarks

Natalscia was established by Verhoeff (1942: 64) for *Philoscia warreni* Collinge, 1917. As Barnard (1932: 247) considered this to be a synonym of *Nahia hirsuta* (Budde-Lund, 1906), the genus *Natalscia* also became synonymous with *Nahia*. Instead, a study of Collinge's material showed that *P. warreni* and *N. hirsuta* belong to distinct genera, and thus *Natalscia* is to be considered as a valid genus. However, Verhoeff's diagnosis—based exclusively on Collinge's description and figures (often erroneous)—is incomplete and incorrect in at least two points: the frontal line is absent (present according to Verhoeff), and the outer branch of maxilla 1 has ten instead of eight teeth. Thus it proved necessary to redefine the genus *Natalscia*.

It is very close to the new genus *Barnardoscia* from which it differs by the presence of two, rather than four, noduli laterales on pereon segment 7 and the lack of a penicil on the maxilliped. It differs from *Nahia* in the different position of the noduli laterales (compare Figs 8A and 12A for b/c and d/c co-ordinates), and from *Setaphora* Budde-Lund, 1908, in the position of the noduli laterales (compare Fig. 12A with Fig. 83 in Taiti & Ferrara 1980), the lack of a maxillipedal penicil, and the different level of insertion of the uropod endo- and exopodites.

A comparison of the type material showed that *P. warreni* is a junior synonym of *P. mina* Budde-Lund, 1885.

The genus *Natalscia* includes five species, all from South Africa. A sixth form (*Natalscia* sp.) is known from Transvaal.

<div align="center">KEY TO THE SPECIES OF NATALSCIA</div>

1. Telson semicircular (Fig. 16B) . . . . *N. rotundata* sp. nov.
–   Telson triangular (Figs 12C, 14B, 15B, 17B)   2
2. Pereopods 1–2 carpus and merus ♂ without brushes of spines . . . . .   *N. mina* (Budde-Lund)
–   Pereopods 1–2 carpus and merus ♂ with brushes of spines (Figs 15C, 17C)   3
3. Pleopod 1 ♂: exopodite with an evident triangular protrusion on outer margin (Fig. 15E); endopodite with an elongate hyaline lobe at the apex (Fig. 15G)
<div align="right">N. thomsoni sp. nov.</div>
–   Pleopod 1 ♂: exopodite without triangular protrusion on outer margin (Figs 14E, 17E); endopodite without terminal hyaline lobe   4

4. Pleopod 1 ♂: endopodite with styliform apical part, apex equipped with tiny setae
   (Fig. 17F) .... *N. appletoni* sp. nov.
– Pleopod 1 ♂: endopodite without styliform apical part, apex without setae (Fig. 14F)
   .... *N. cingulata* (Barnard)

Natalscia mina (Budde-Lund, 1885)
Figs 11–13

Philoscia mina Budde-Lund, 1885: 219. Dollfus, 1895*b*: 351. Stebbing, 1910: 443. Barnard,
   1937: 164. Barnard, 1949: 402.
Philoscia warreni Collinge, 1917: 578, pl. 42 (figs 10–20). Collinge, 1920: 477, pl. 27 (fig. 6).
   Collinge, 1945: 346.
Philoscia (Setaphora) mina: Barnard, 1932: 242, figs 18b, 19e. Brian, 1953: 9.
Natalscia warreni: Verhoeff, 1942: 64.
Philoscia Warreni: Brian, 1953: 9.
Setaphora mina: Ferrara & Taiti, 1979: 119. Taiti & Ferrara, 1980: 83.
nec Philoscia (Setaphora) mina: Barnard, 1960a: 47.

Material

   Budde-Lund Collection. 2 ♂♂, 1 ♀, Cape, leg. J. F. Drege, BM–1921:
10: 18: 1899–1901 (syntypes).
   Collinge Collection. 3 ♂♂, 9 ♀♀, Umbilo Bush, near Durban, Natal,
leg. E. Warren, BM–1919: 4: 26: 469–478 (*P. warreni*; paratypes).
   New material. Natal: 4 ♂♂, 1 ♀, Pietermaritzburg, leg. S. Taiti, 19 April
1980, MZUF–1005; 2 ♂♂, Gillits, leg. S. Taiti, 26 April 1980, MZUF–1006;
1 ♂, 2 ♀♀, Umhlanga Rocks, coastal forest, leg. S. Taiti and K. C. Thomson,
26 April 1980, MZUF–1007; 17 ♂♂, 30 ♀♀, mouth of Mdloti River, man-
grove forest, leg. S. Taiti and K. C. Thomson, 26 April 1980, MZUF–1008;
25 ♂♂, 34 ♀♀, Umdloti, leg. S. Taiti and K. C. Thomson, 26 April 1980,
MZUF–1009.
   Transkei: ? 1 ♂, ? 8 ♀♀, Umgazana, near Port St. Johns, leg. B. F.
Kensley, 18 August 1974, SAM–A16861.

Description

   11 × 4,5 mm long (according to Barnard the maximum dimensions are
13 × 5 mm). Brown colour, more or less suffused with yellowish; a white oval
spot at the base of pereon epimera and medial dark spot on the posterior part
of pereon segments; pleon with a light stripe in the mid-line (Fig. 11); appen-
dages pigmented. Though the light and dark spots are always visible, very pale
specimens (due to isolated chromatophores) are rather common. Eye with
about twenty-two ommatidia. Each pereon segment with ten to twenty gland
pores per side. Noduli laterales with b/c and d/c co-ordinates as in Figure 12A.
Telson (Fig. 12C) with subacute apex. Antenna: ratio of flagellum joints
5 : 3 : 3. Pereopod with a flagellar dactylar seta (Fig. 12D).

Male

Anterior pereopods without brushes of spines. Pereopod 7 ischium with a
strong spine on sternal margin (Fig. 12E). Pleopod 1 exopodite with a long
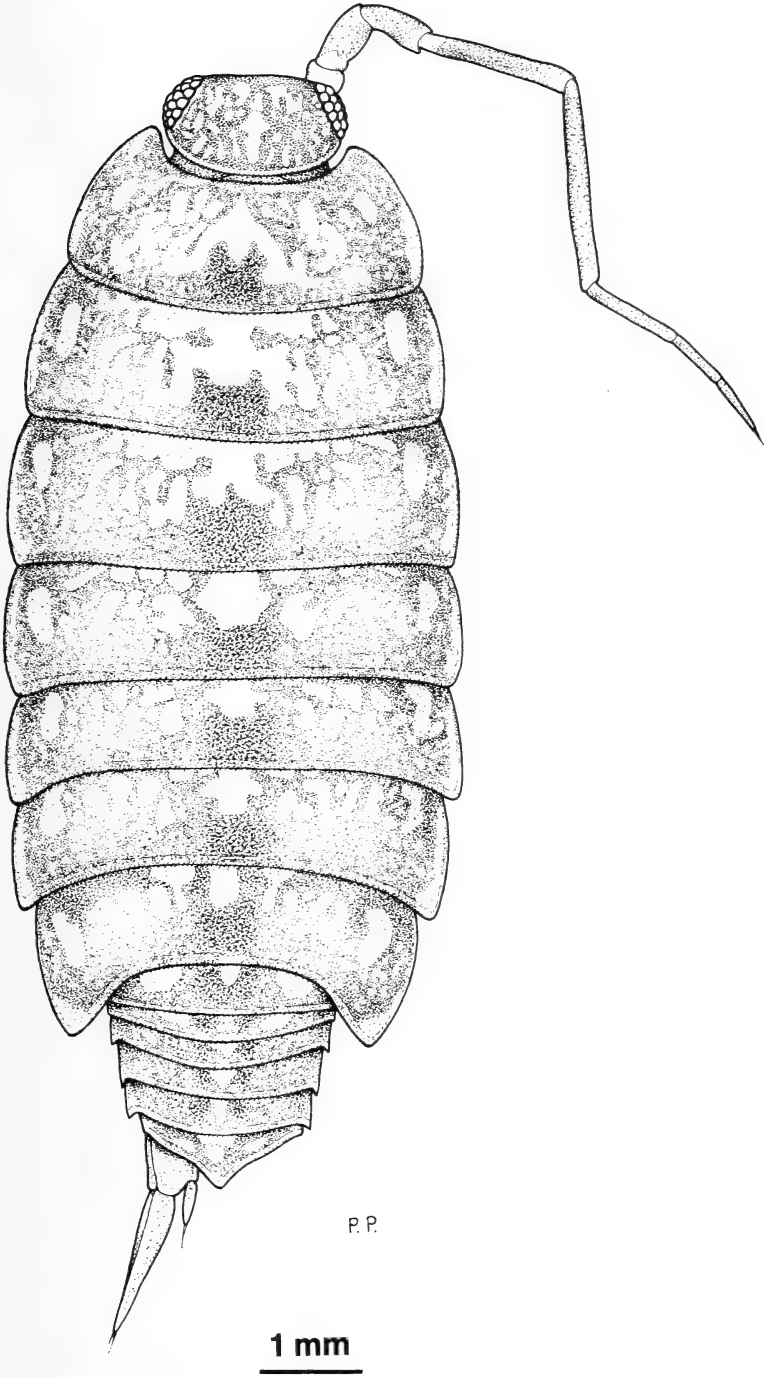
P. P.

1 mm

Fig. 11. *Natalscia mina* (Budde-Lund, 1885). Adult female.
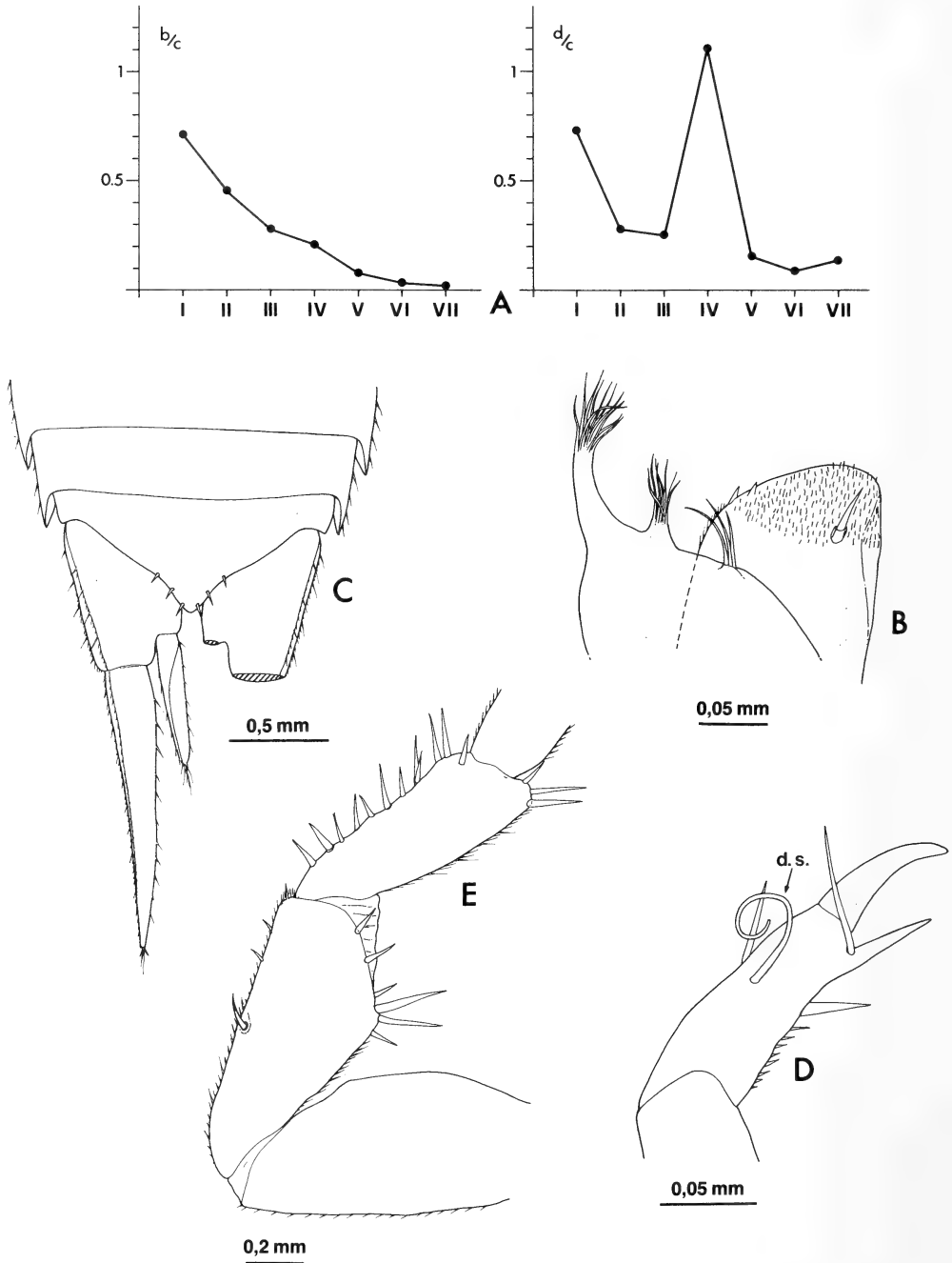
Fig. 12. *Natalscia mina* (Budde-Lund, 1885). A. b/c and d/c co-ordinates. B. Apex of maxilliped. C. Telson and uropods. D. Pereopod 1 dactylus: d.s.—dactylar seta. E. Pereopod 7 ischium and merus (♂).
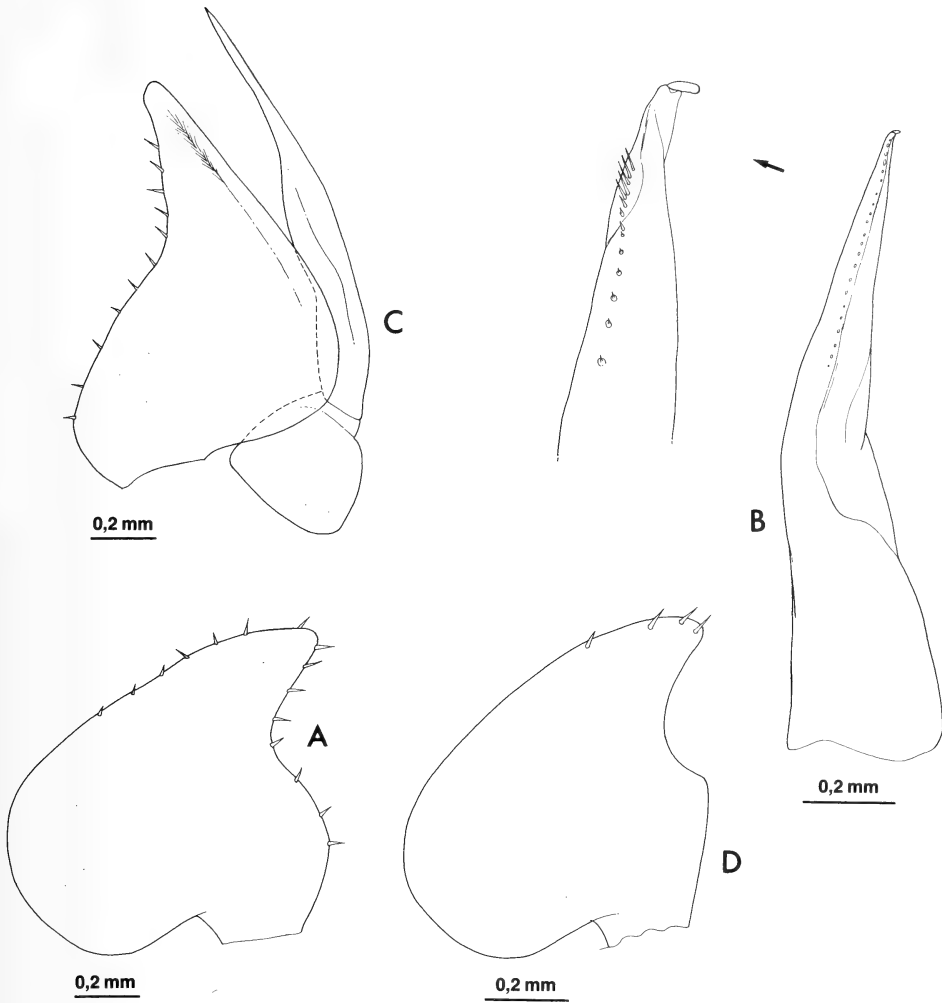
Fig. 13. *Natalscia mina* (Budde-Lund, 1885). A. Pleopod 1 exopodite (♂). B. Pleopod 1 endopodite (♂). C. Pleopod 2 (♂). D. Pleopod 1 exopodite in the male from Umgazana.

triangular point bent outward, outer margin sinuose (Fig. 13A); endopodite with a row of spines and a narrow hyaline lobe at the apex (Fig. 13B). Pleopod 2 as in Figure 13C.

Remarks

As mentioned above, a comparison of type material of *Philoscia warreni* and *P. mina* showed these to be the same species. The original material of *P. mina* collected by Drege is labelled 'Cape' but, as pointed out by Barnard (1932: 244), these specimens probably come from Natal.

As with *Nahia hirsuta*, the uncertainties and errors in identification by the early authors make it impossible to define the exact distribution of *Natalscia mina*. It is definitely common in southern Natal.

The male from Umgazana has the outer margin of pleopod 1 exopodite truncated instead of rounded (Fig. 13D), while all the other characters coincide with the typical *N. mina*. This could be a specific difference but the authors cannot reach a firm conclusion due to the insufficient material.

Natalscia cingulata (Barnard, 1932)
Fig. 14

Philoscia (Setaphora) cingulata Barnard, 1932: 244, figs 16o, 17b, 18b, 19b, Brian, 1953: 9.
Philoscia cingulata: Barnard, 1949: 403.
Setaphora cingulata: Ferrara & Taiti, 1979: 118. Taiti & Ferrara, 1980: 83.

Material

Barnard Collection. Natal: 1 ♂, 9 ♀♀, Port Shepstone, leg. K. H. Barnard, 1912, BM–1933:1:25:87–92 (syntypes).

New material. Transkei: ? 10 ♀♀, Port St. Johns, leg. B. F. Kensley, 14 August 1974, SAM–A16862.

Description

♂ 6 mm long; ♀ ovig. 7 mm long. Colour as described by Barnard: 'Pale yellowish, with broad greyish bands across front of head between eyes, and across the peraeon and pleon segments, on the latter usually interrupted in the middle line; antennae pale greyish, legs pale without gray marks.' Eye with eighteen to twenty ommatidia. Each pereon segment with about ten gland pores per side arranged along the whole sulcus marginalis. Noduli laterales with b/c and d/c co-ordinates as in Figure 14A. Telson with pointed apex (Fig. 14B). Antenna: ratio of flagellum joints 6 : 5 : 5. Dactylar seta of pereopods flagelliform, slightly enlarged at apex (Fig. 14C). Uropod as in Figure 14D.

Male

Pereopods 1–2 carpus and merus with a brush of spines as in *N. thomsoni*. Pereopods 3–7 are missing in the only male. Pleopod 1 exopodite with short triangular posterior point (Fig. 14E); endopodite dorsally with a row of long spines close to the apex (Fig. 14F). Pleopod 2 endopodite much longer than exopodite (Fig. 14G).

Remarks

The examination of the type material showed that this species belongs to the genus *Natalscia*. *N. cingulata* closely resembles *N. mina* from which it differs by the smaller size, presence of a brush of spines on the anterior pereopods and the shorter posterior point of pleopod 1 exopodite ♂. The colour pattern is also a distinguishing character.
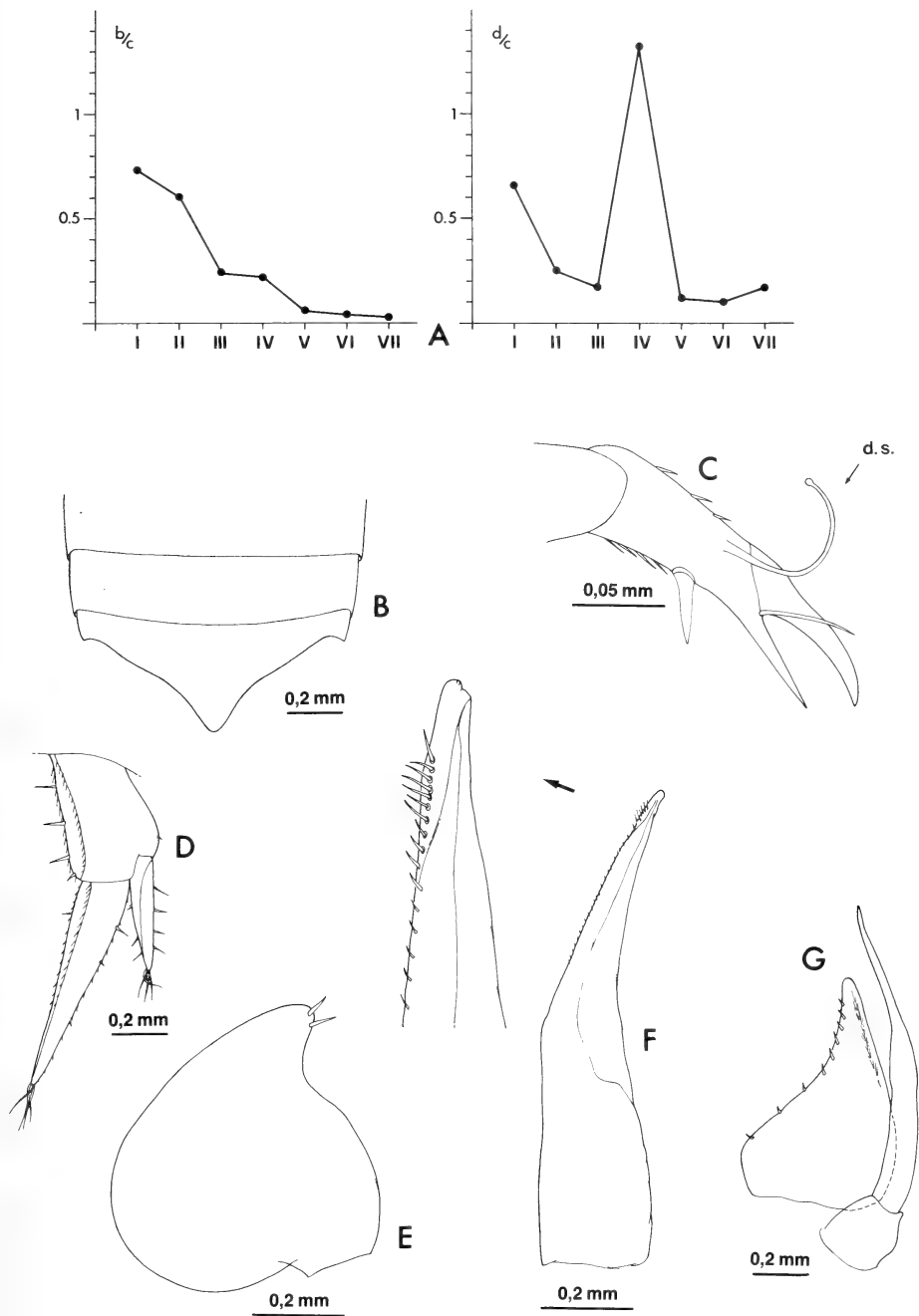
Fig. 14. *Natalscia cingulata* (Barnard, 1932). A. b/c and d/c co-ordinates. B. Telson. C. Pereopod 1 dactylus: d.s.—dactylar seta. D. Left uropod. E. Pleopod 1 exopodite (♂). F. Pleopod 1 endopodite (♂). G. Pleopod 2 (♂).

The specimens from Port St. Johns are tentatively ascribed to this species, due to the lack of males.

N. cingulata is recorded from Howick and Port Shepstone.

Natalscia thomsoni sp. nov.
Fig. 15

Material

Natal: 1 ♂, Claridge, near Pietermaritzburg, leg. S. Taiti and K. C. Thomson, 27 April 1980, holotype SAM–A16863; 2 ♂♂, 2 ♀♀, same data, paratypes SAM–A16864; 33 ♂♂, 28 ♀♀, same data, paratypes MZUF–1010; 1 ♀, Town Bush, leg. S. Taiti and J. H. Londt, 22 April 1980, paratype MZUF–1011; 2 ♂♂, 2 ♀♀, Karkloof, leg. S. Taiti and J. H. Londt, 24 April 1980, paratypes MZUF–1012.

Description

♂ 8 mm long; ♀ 9 mm long. Colour extremely variable: whitish with isolated, more or less clustered chromatophores; or yellowish with three longitudinal black stripes: a median one from cephalon to pleon segment 3 and two at the base of pereon epimera; the lateral stripes have a row of white spots in the middle; pleon segments 4–5 and telson black; antennae with a white ring at the base of joints 4 and 5; pereopods, pleopods and uropods slightly pigmented. Eye with about twenty-five ommatidia. Each pereon segment with about fifteen gland pores per side arranged along the whole sulcus marginalis. Co-ordinates of noduli laterales as in Figure 15A. Telson (Fig. 15B) with almost straight sides. Antenna: ratio of flagellum joints 8 : 6 : 5. Pereopods with a dactylar seta as in Figure 15D.

Male

Pereopods 1–2 merus and carpus with thick brushes of spines (Fig. 15C). Pereopod 3 merus and carpus with sparse brushes. Pereopod 7 (Fig. 15D) ischium with concave sternal surface equipped with short spines, closer together distally; merus with the same spines at the base. Pleopod 1 exopodite (Fig. 11E) with posterior point bent outwards and with one spine at apex; outer margin distally concave with a small triangular protrusion, missing in juveniles (Fig. 11F); endopodite with an elongated hyaline lobe at apex (Fig. 11G). Pleopod 2 as in Figure 11H.

Etymology

The new species is named for Mr K. C. Thomson, Pietermaritzburg, for his invaluable help in collecting material.

Remarks

N. thomsoni differs from *N. mina* by the presence of thick brushes of spines on pereopods 1–2 ♂ carpus and merus and the distinctly concave sternal
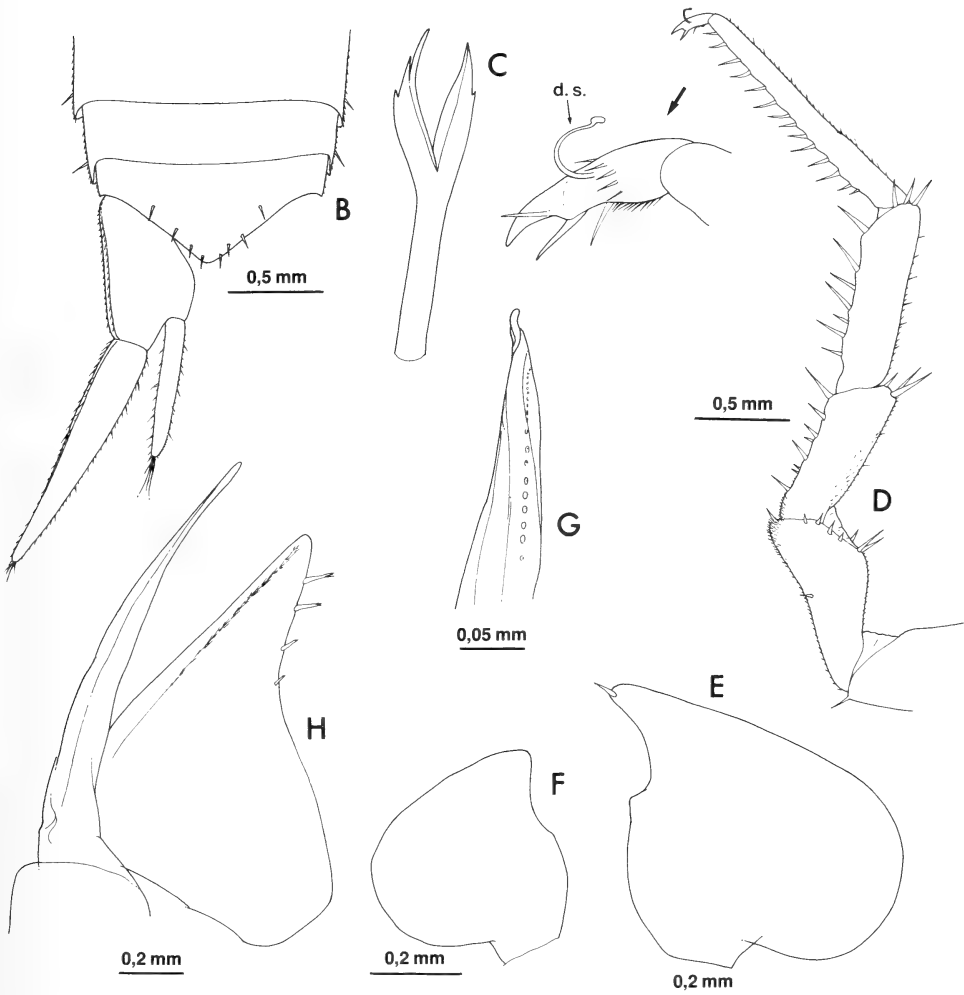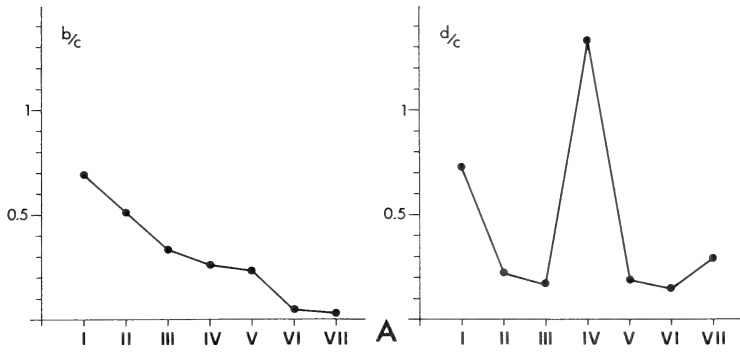
Fig. 15. *Natalscia thomsoni* sp. nov. A. b/c and d/c co-ordinates. B. Telson and left uropod. C. Spine of pereopod 1 carpus (♂). D. Pereopod 7 (♂): d.s.—dactylar seta. E. Pleopod 1 exopodite (♂). F. Pleopod 1 exopodite (♂) juvenile. G. Apex of pleopod 1 endopodite (♂). H. Pleopod 2 (♂).

margin of pereopod 7 ischium which is straight in *N. mina*; from *N. cingulata* which lacks both a hyaline lobe on the pleopod 1 ♂ endopodite apex and a triangular protrusion on the outer margin of pleopod 1 ♂ exopodite; from *N. appletoni* sp. nov. by the shape of pereopod 7 ♂ ischium (cf. Figs 15D and 17D) and pleopod 1 ♂ (cf. Figs 15E, G and 17E–F); from *N. rotundata* sp. nov. which has a semicircular rather than a triangular telson.

Natalscia rotundata sp. nov.
Fig. 16

Material

Natal: 1 ♂, Umdloti, leg. S. Taiti and K. C. Thomson, 26 April 1980, holotype SAM–A16865; 1 ♂, 1 ♀, same data, paratypes SAM–A16866; 3 ♂♂, 6 ♀♀, same data, paratypes MZUF–1013.

Description

♂ 5,5 mm long; ♀ 6 mm long. Yellowish colour mottled with brown; antenna with joints 1–3 of peduncle reddish; pereopods and pleopods slightly pigmented. Eye with sixteen to eighteen ommatidia. Back equipped with upright setae, closer together on pleon; each pereon segment with five to ten gland pores per side arranged along the whole sulcus marginalis; b/c and d/c co-ordinates of noduli laterales as in Figure 16A. Telson semicircular (Fig. 16B). Antenna: ratio of flagellum joints 10 : 7 : 8. Dactylar seta (Fig. 16C) as in *N. thomsoni*.

Male

Pereopods 1–2 merus and carpus with sparse brushes of spines similar to *N. thomsoni*. Pereopod 7 (Fig. 16C) ischium with sternal margin swollen in the middle. Pleopod 1 exopodite (Fig. 16D) with acute posterior point; endopodite with some spines close to apex (Fig. 16E). Pleopod 2 as in Figure 16F.

Etymology

The specific name refers to the rounded telson, a character which immediately separates *N. rotundata* from all the other species of *Natalscia*.

Natalscia appletoni sp. nov.
Fig. 17

Material

Zululand: 1 ♂, Lake Sibaya Research Station, garden, leg. C. C. Appleton, 7 January 1973, No. 8L, holotype SAM–A16867; 6 ♂♂, 3 ♀♀, same data, paratypes SAM–A16868; 7 ♂♂, 13 ♀♀, near Lake Sibaya Research Station, coastal dune forest, leg. C. C. Appleton, 18 December 1973, No. 13E, paratypes SAM–A16869; 1 ♀, same data, 29 July 1973, No. 49L, paratype
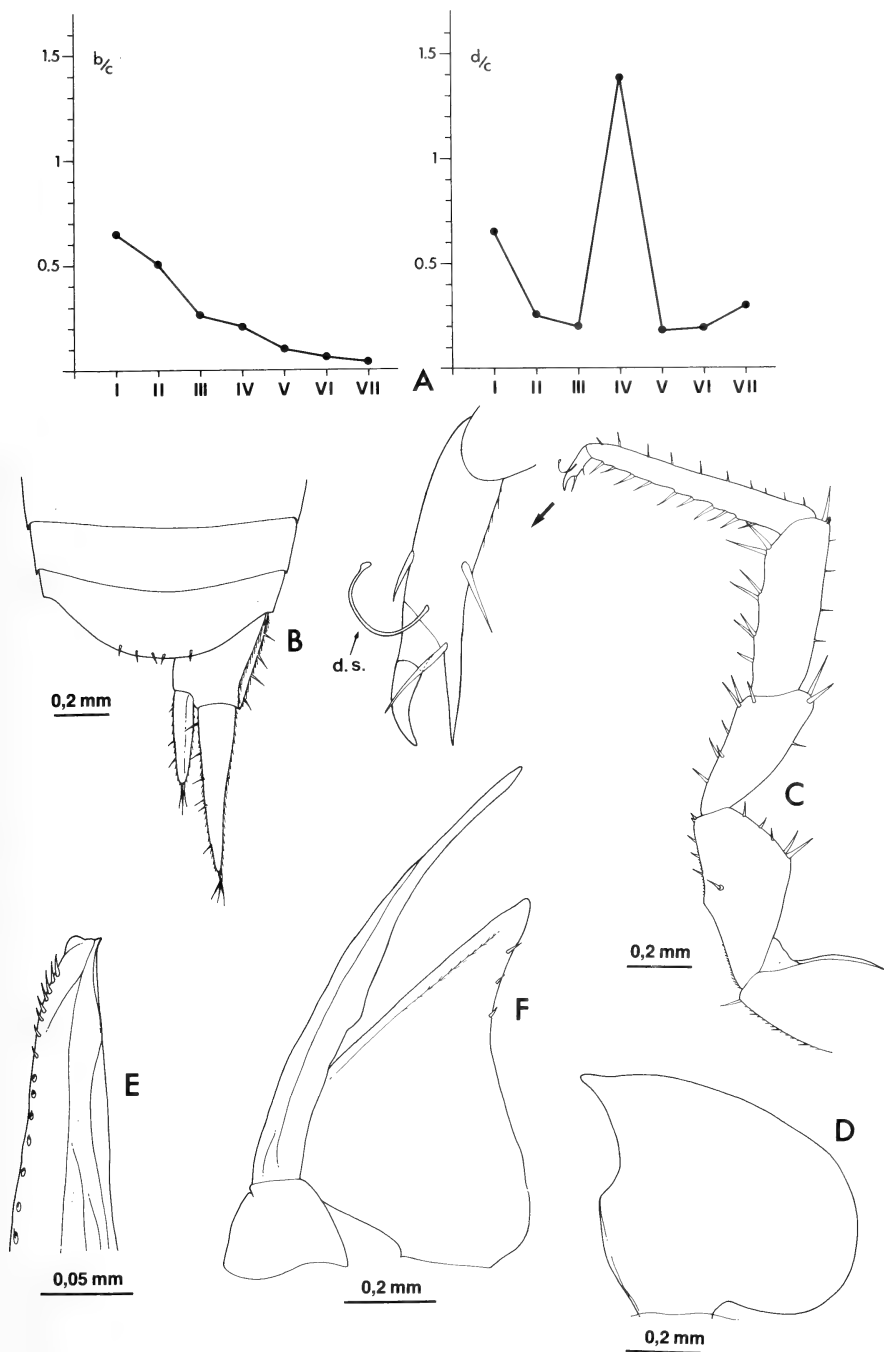
Fig. 16. *Natalscia rotundata* sp. nov. A. b/c and d/c co-ordinates. B. Telson and right uropod. C. Pereopod 7 (♂): d.s.—dactylar seta. D. Pleopod 1 exopodite (♂). E. Apex of pleopod 1 endopodite (♂). F. Pleopod 2 (♂).
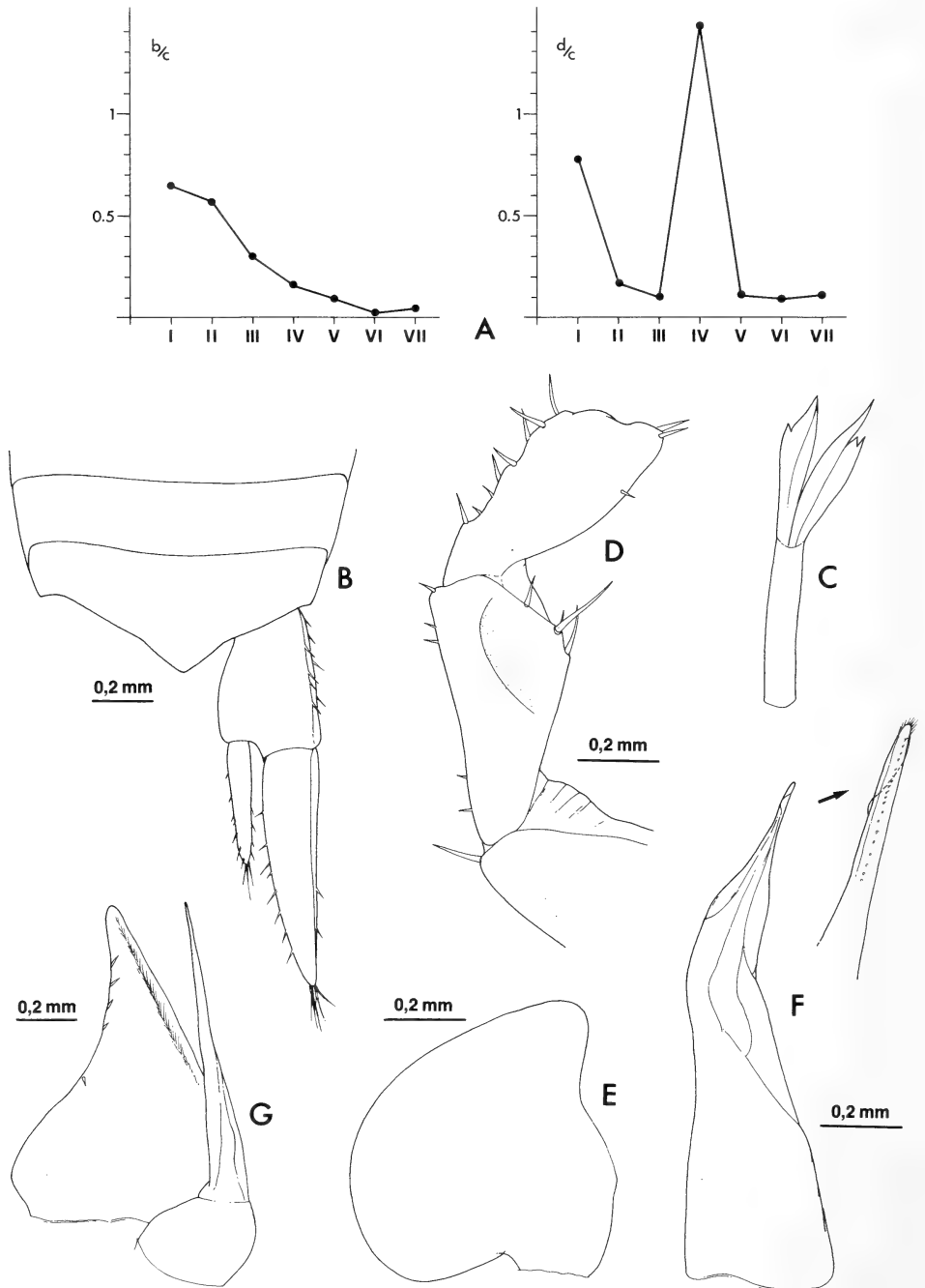
Fig. 17. *Natalscia appletoni* sp. nov. A. b/c and d/c co-ordinates. B. Telson and right uropod. C. Spine of pereopod 1 carpus (♂). D. Pereopod 7 ischium and merus (♂). E. Pleopod 1 exopodite (♂). F. Pleopod 1 endopodite (♂). G. Pleopod 2 (♂).

SAM–A16870; 3 ♂♂, 21 ♀♀, same data, date ?, No. 18D, paratypes SAM–A16871; 6 ♀♀, same data, date ?, No. 18L, paratypes SAM–A16872; 1 ♀, same data, 10 October 1973, No. 76E, paratypes SAM–A16873; 2 ♀♀, same data, date ?, No. 62F, paratypes SAM–A16874; 2 ♀♀, same data, date ?, No. 71Q, paratypes SAM–A16875.

Description

6 mm long. Pale brown colour; antenna with joints 1–3 and proximal part of 5 yellowish; pereopods and pleopods pigmented. Eye with twenty to twenty-two ommatidia. Each pereon segment with about ten gland pores per side arranged along the whole sulcus marginalis; b/c and d/c co-ordinates of noduli laterales as in Figure 17A. Telson (Fig. 17B) with apex at an obtuse angle. Antenna with subequal flagellum joints. Dactylar seta of pereopods as in *N. rotundata*.

Male

Pereopods 1–2 carpus with brushes of spines as in Figure 17C. Pereopod 7 ischium with sternal margin almost straight and a semicircular depression on rostral surface (Fig. 17D). Pleopod 1 exopodite (Fig. 17E) with rounded posterior point, outer margin feebly concave; endopodite (Fig. 17F) with a long styliform distal part, apex equipped with tiny setae. Pleopod 2 as in Figure 17G.

Etymology

This species is named for Dr C. C. Appleton, Congella, who collected these specimens.

Remarks

N. appletoni differs from all the other species of *Natalscia* by the presence of a semicircular depression on pereopod 7 ♂ ischium; the largely rounded posterior point of pleopod 1 ♂ exopodite and the styliform pleopod 1 ♂ endopodite apex.

<p align="center">*Natalscia* sp.
Fig. 18</p>

Philoscia (Setaphora) mina: Barnard, 1960a: 47. Lawrence, 1977: 175.

Material

Barnard Collection. Transvaal: 1 ♂, 3 ♀♀, Graskop, leg. R. F. Lawrence, March 1960, NM–6509; 3 ♀♀, Marieskop, ± 6 000 ft, leg. R. F. Lawrence, March 1960, NM–6505.
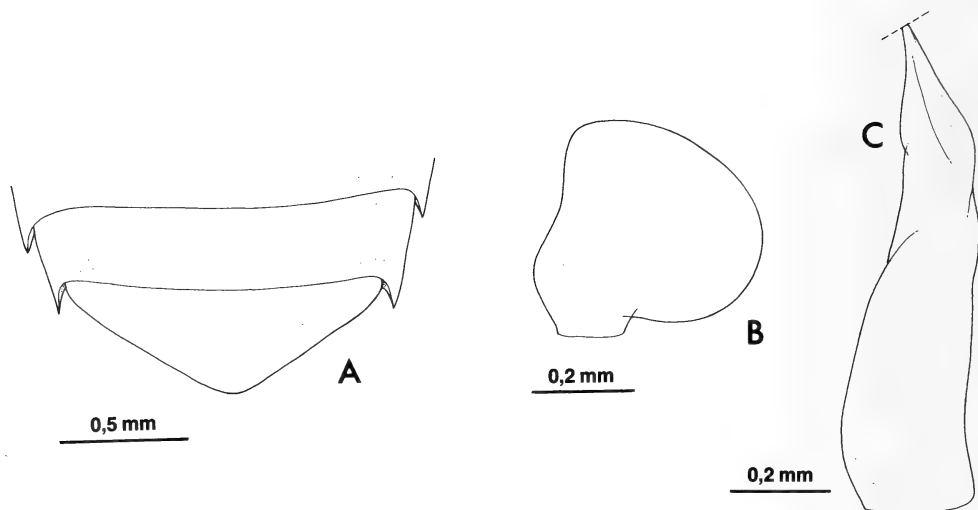
Fig. 18. *Natalscia* sp. A. Telson. B. Pleopod 1 exopodite (♂). C. Pleopod 1 endopodite (♂).

Remarks

Barnard (1960a) identified these specimens as *Philoscia (Setaphora) mina*. A check of his material showed that these belong to the genus *Natalscia* but are not conspecific with *N. mina*. In fact, the shape of the telson (Fig. 18A) and general shape of pleopod 1 ♂ endopodite (Fig. 18C) differ notably from those of *N. mina*. The only male available (5 mm long) is probably a juvenile, as suggested by the shape of pleopod 1 exopodite (Fig. 18B), and has the apices of pleopod 1 endopodites damaged. Thus a distinctive description is not possible.

In discussing this material, Barnard (1960a: 48) stated that he also saw 'specimens from Inhaca Island (Delagoa Bay) which appeared conspecific'. It is not clear whether he referred to the typical *N. mina* or to the specimens from Transvaal. The re-examination of the material from Inhaca Island (Mozambique) is necessary for a correct identification.

Genus *Barnardoscia* nov.

Diagnosis

Sulcus marginalis and gland pores present; one series of noduli laterales on each side of pereon segments 1–6; two noduli laterales on each side of pereon segment 7; d/c co-ordinates with a maximum on pereon segment 4 and a lower one on segment 1 (Figs 20A and 22A). Frontal line absent; supra-antennal line present. Pereon segments 5–7 with acute posterior angles (Fig. 20C). Pleon epimera reduced but with long posterior points. Molar penicil of mandible consisting of a single unbranched seta; outer branch of maxilla 1 with 4 + 6 (5 cleft) teeth; endite of maxilliped with a small penicil (Fig. 20B). Pereopods

with a flagellar dactylar seta. Pleopod exopodites without respiratory areas. Uropod protopodite grooved on outer margin; insertion of endopodite proximal to that of exopodite.

Type species

Philoscia (Setaphora) demarcata Barnard, 1932, from South Africa.

Etymology

The genus is named for Dr K. H. Barnard to whom we are indebted for many important papers on South African terrestrial Isopoda.

Remarks

The re-examination of the type material of *Philoscia (Setaphora) demarcata* showed that this species belongs to a new genus, *Barnardoscia*, akin to *Natalscia* from which it is distinguished by the presence of four noduli laterales on the pereon segment 7 and the presence of a penicil on maxilliped.

Barnardoscia includes two species, both from South Africa.

KEY TO THE SPECIES OF *BARNARDOSCIA*

1. Pereopod 7 ♂: ischium with a depression on the middle of the rostral surface (Fig. 20G). Pleopod 1 ♂: exopodite with posterior point equipped with one or two apical spines (Fig. 21A–C) . . . . *B. demarcata* (Barnard)
– Pereopod 7 ♂: ischium with a depression close to the base of the rostral surface (Fig. 22C). Pleopod 1 ♂: exopodite without posterior point and spines (Fig. 22D) *B. maculata* sp. nov.

Barnardoscia demarcata (Barnard, 1932)

Figs 19–21

Philoscia (Setaphora) demarcata Barnard, 1932: 244, figs 16q, 17c, 18a, 19b.
Philoscia demarcata: Barnard, 1937: 164. Barnard, 1949: 402. Brian, 1953: 9.
Setaphora demarcata: Ferrara & Taiti, 1979: 118. Taiti & Ferrara, 1980: 83.

Material

Barnard Collection. Natal: 4 ♂♂, 3 ♀♀, (in fragments), Pietermaritzburg, leg. K. H. Barnard, 1917, BM–1933:1:25:93–97 (syntypes).

New material. Natal: 17 ♂♂, 42 ♀♀, Claridge, Pietermaritzburg, leg. S. Taiti, 27 April 1980, MZUF–1014; 5 ♂♂, 25 ♀♀, Cedara, near Pietermaritzburg, leg. S. Taiti, 20 April 1980, MZUF–1015; 23 ♂♂, 34 ♀♀, Karkloof, near Howick, leg. S. Taiti and J. H. Londt, 24 April 1980, MZUF–1016; 1 ♂, 3 ♀♀, Town Bush, near Pietermaritzburg, leg. S. Taiti and J. H. Londt, 22 April 1980; MZUF–1017; 1 ♂, 1 ♀, Lundys Hill, about 70 km W of Pietermaritzburg, leg. S. Taiti and K. C. Thomson, 25 April 1980, MZUF– 1018; 1 ♂, Bulwer, leg. S. Taiti and K. C. Thomson, 25 April 1980, MZUF–1019.

Description

♂ 7,5 mm long; ♀ 9 mm long. Dark brown with light mottling. Eye with about twenty large ommatidia. Each pereon segment with seventeen to twenty
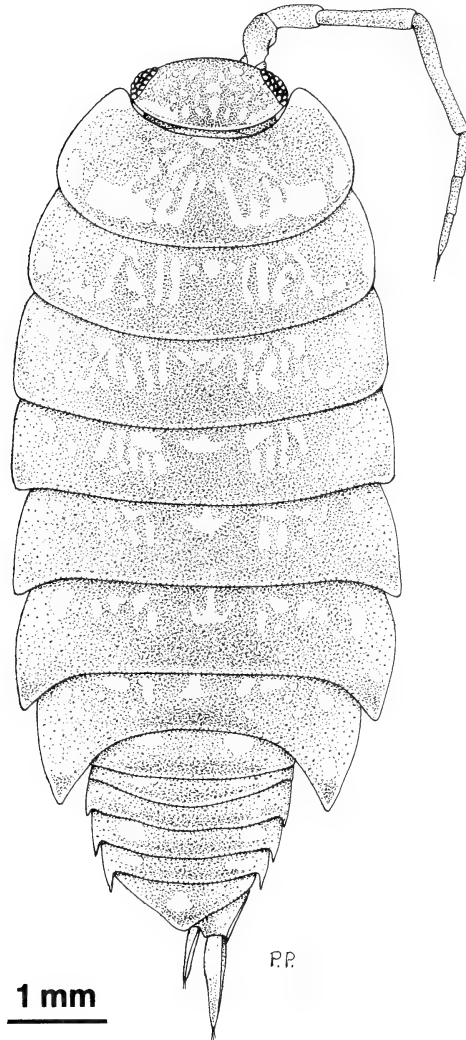
Fig. 19. *Barnardoscia demarcata* (Barnard, 1932). Adult female.

gland pores per side; b/c and d/c co-ordinates of noduli laterales as in Figure 20A. Pereon segments 2–4 demarcated in some female specimens. Telson (Fig. 20D) with concave sides, narrowly rounded apex. Flagellum joints of antenna subequal.

Male

Cephalon with a bulbous profrons (compare Fig. 20E, ♀, and Fig. 20F, ♂). Pereopods 1–3 merus and carpus with sparse brushes of spines similar to those of *Natalscia thomsoni*. Pereopod 7 ischium (Fig. 20G) with a large
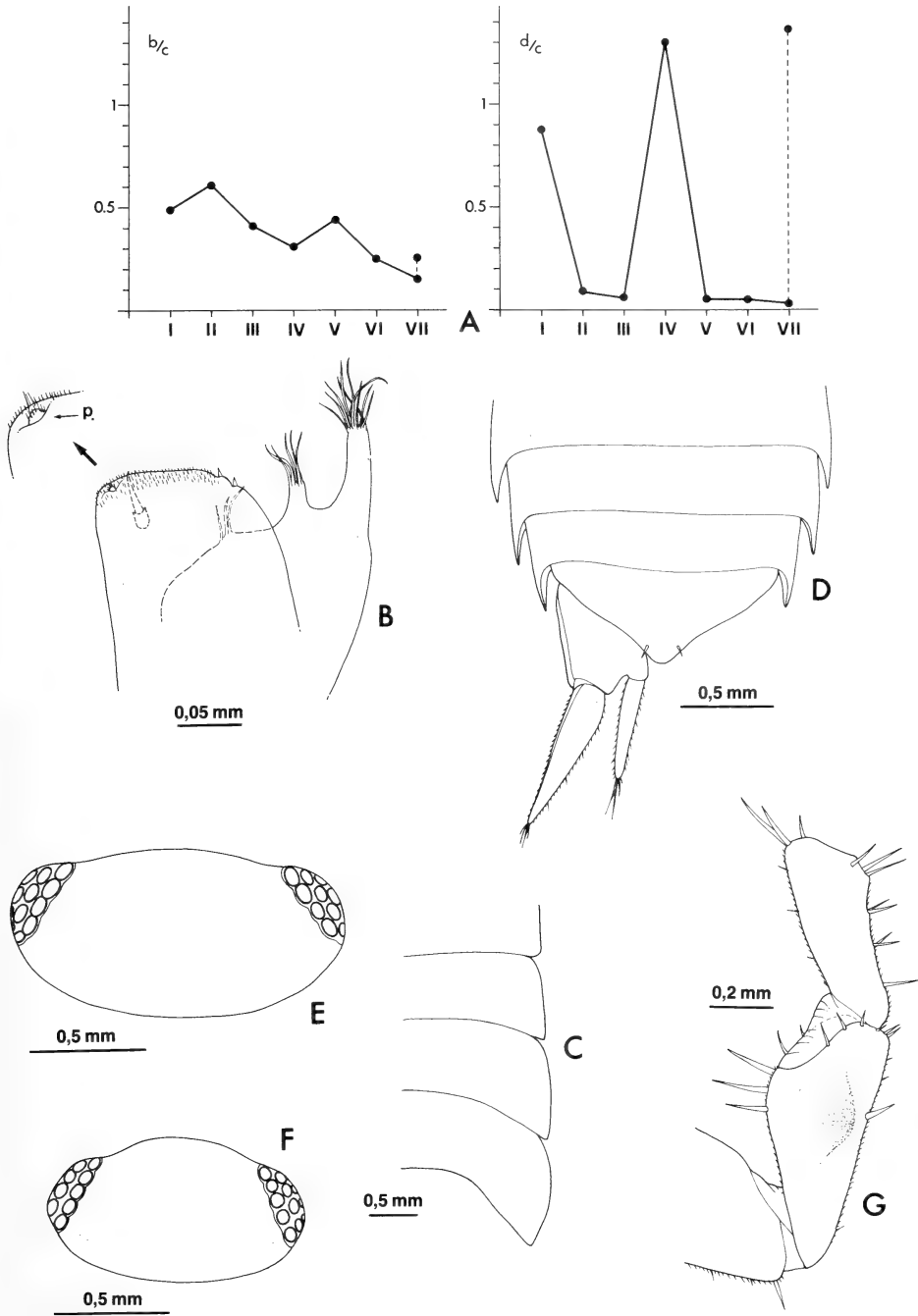
Fig. 20. *Barnardoscia demarcata* (Barnard, 1932). A. b/c and d/c co-ordinates. B. Apex of maxilliped: p.—penicil. C. Pereon epimera 4–7, right. D. Telson and left uropod. E. Cephalon from above (♀). F. Cephalon from above (♂). G. Pereopod 7 ischium and merus (♂).
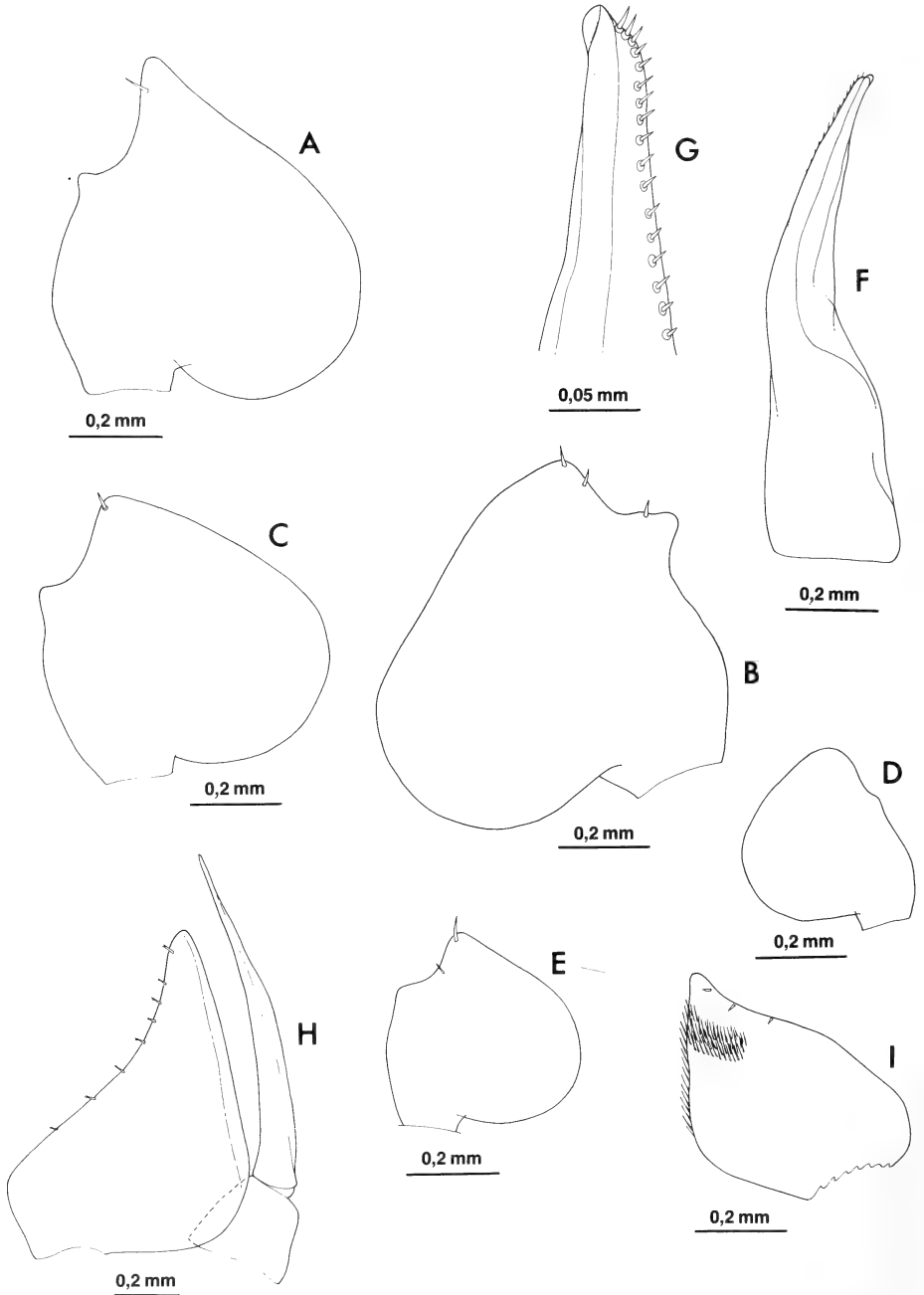
Fig. 21. *Barnardoscia demarcata* (Barnard, 1932). A. Pleopod 1 exopodite (♂). B. Pleopod 1 exopodite (♂) in another specimen. C. Pleopod 1 exopodite (♂) in one syntype from Pietermaritzburg. D. Pleopod 1 exopodite (♂), juvenile 4 mm long. E. Pleopod 1 exopodite (♂), juvenile 4,7 mm long. F. Pleopod 1 endopodite (♂). G. Apex of pleopod 1 endopodite (♂). H. Pleopod 2 (♂). I. Pleopod 5 exopodite (♂).

depression on the middle of the rostral surface. Pleopod 1: exopodite varies in shape (Fig. 21A–C). In some specimens the posterior, rather than the external, point, is the most developed (Fig. 21A), while in other specimens the posterior point is more rounded and less pronounced, and the external point is the most developed (Fig. 21B). During the course of development (Fig. 21D–E) the external point progressively increases in size with respect to the posterior point.

Apex of pleopod 1 endopodite (Fig. 21F–G) with spines and a small triangular lobe. Pleopod 2 as in Figure 21H. Pleopod 5 exopodite with straight medial edge (Fig. 21I).

Remarks

The suture at the base of the pereon epimera 2–4 ♀ is a sporadic trait, as it is in every other species of terrestrial isopod presenting this character.

The external point of the pleopod 1 exopodite ♂ develops progressively with the growth of the specimen. This appendage also varies greatly in shape in fully adult males (see Fig. 21A–C) of the same lot.

Barnardoscia maculata sp. nov.
Fig. 22

Material

Natal: 1 ♂, near Bulwer, leg. S. Taiti, 25 April 1980, holotype SAM–A16876; 2 ♂♂, 2 ♀♀, same data, paratypes SAM–A16877; 7 ♂♂, 12 ♀♀, 20 juv., same data, paratypes MZUF–1020.

Description

♂ 7 mm long; ♀ 7,5 mm long. Iron-grey with lighter mottling, a white stripe at the base and a pale spot in the middle of pereon epimera. Eye with about twenty-five small ommatidia. Each pereon segment with ten to twelve gland pores per side, arranged along the whole length; b/c and d/c co-ordinates of noduli laterales as in Figure 22A. None of the females with pereon epimera 2–4 demarcated. Telson with almost straight sides, rounded apex (Fig. 22B). Antenna with flagellum joints subequal.

Male

Cephalon as in *B. demarcata*. Pereopods 1–2 carpus and merus with sparse spines of the same type as in *Natalscia thomsoni*. Pereopod 7 ischium with a depression close to the base on the rostral surface (Fig. 22C). Pleopod 1 exopodite (Fig. 22D–E) typically without posterior point and apical spine; endopodite (Fig. 22F) similar to that of *B. demarcata*. Pleopod 5 exopodite with oblique medial edge (Fig. 22G).

Etymology

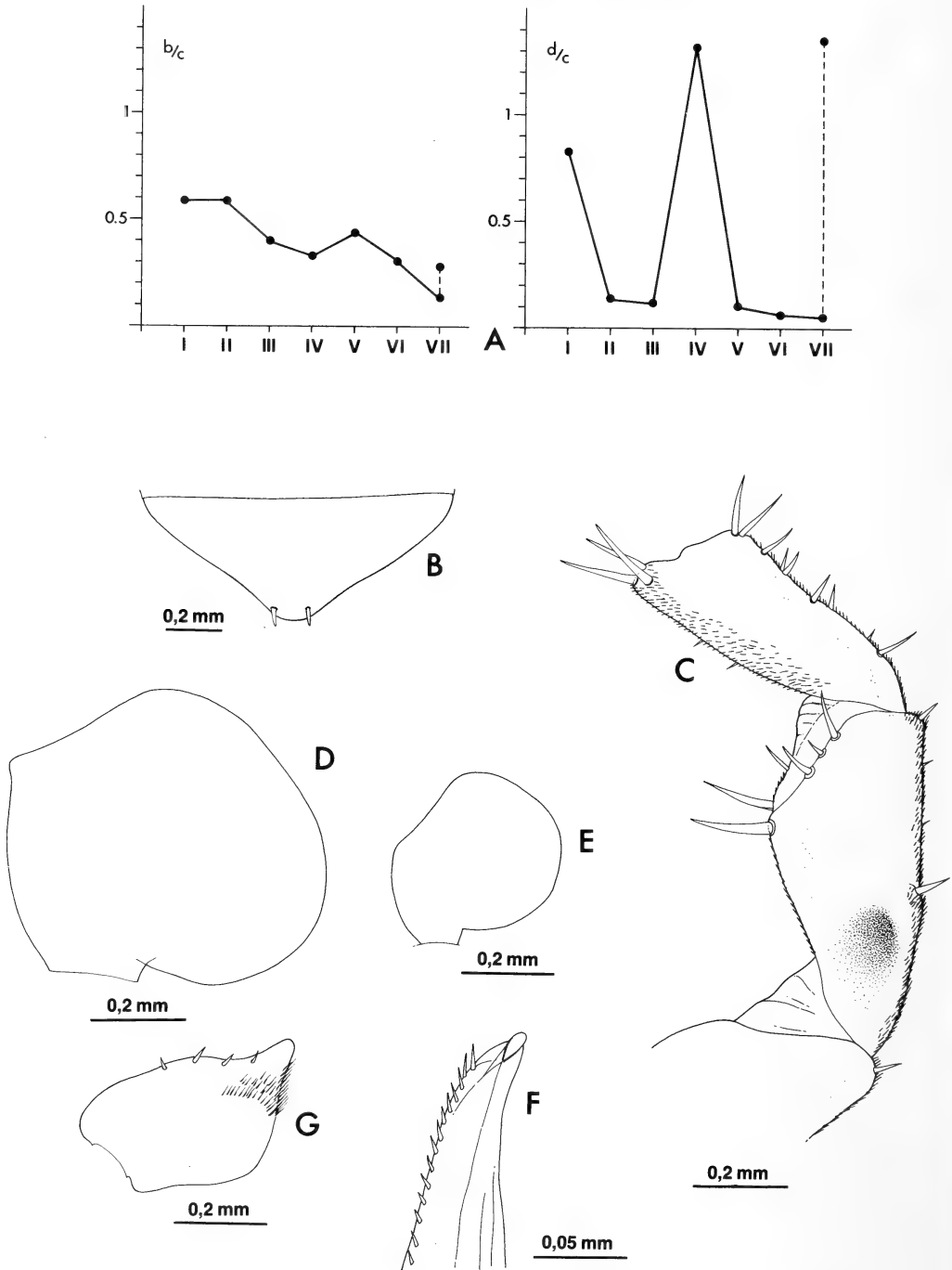The specific name refers to the characteristic coloration of this species.

Fig. 22. *Barnardoscia maculata* sp. nov. A. b/c and d/c co-ordinates. B. Telson. C. Pereopod 7 ischium and merus (♂). D. Pleopod 1 exopodite (♂). E. Pleopod 1 exopodite (♂), juvenile 4,2 mm long. F. Apex of pleopod 1 endopodite (♂). G. Pleopod 5 exopodite (♂).

Remarks

The new species is very close to *B. demarcata* from which it differs by the (i) different colour pattern, (ii) smaller and more numerous ommatidia, (iii) fewer number of gland pores, and (iv) male modifications: pereopod 7 ischium with a smaller depression much closer to the base, pleopod 1 exopodite with truncated apex, shape of pleopod 5 exopodite.

SYSTEMATIC DISCUSSION

To date the following species were known in South Africa:

Aphiloscia vilis (Budde-Lund, 1885)
Benthanops fulva Barnard, 1932
Nahia hirsuta (Budde-Lund, 1906)
Setaphora mina (Budde-Lund, 1885)
Setaphora cingulata Barnard, 1932
Setaphora demarcata Barnard, 1932
Setaphora ocellata Barnard, 1960
Chaetophiloscia elongata (Dollfus, 1884)
Philoscia muscorum (Scopoli, 1763)

All the species listed were re-examined, with the exception of the last two which are of Mediterranean origin and whose presence in South Africa—if confirmed—is due to importation by man. In the authors' opinion the *Chaetophiloscia elongata* quoted by Dollfus (1895) corresponds to *Nahia hirsuta*, while the records of *Philoscia muscorum* from Natal, 'Hilton Road and Mid-Illovo' (Collinge 1920), are definitely a misidentification (see also Verhoeff 1942).

Five new species have also been described. Of even greater interest is the fact that it was possible to assign each species to the correct genus, each of which was redefined according to modern criteria.

As a result, *Benthanops* Barnard, 1932, and *Ctenoscia* Verhoeff, 1928, which appeared to be identical according to the early descriptions, proved to be distinct even if extremely close genera.

The study of most of Barnard's material allowed the authors to redefine the genus *Nahia* Budde-Lund, 1908, clarify the identifying traits of the only species known to date, *N. hirsuta*, and describe a new one, *N. louwi*.

The task of correctly collocating the four species assigned by Barnard (1932, 1960a) to *Setaphora* Budde-Lund, 1908, was complicated above all by the uncertain diagnosis of this genus. It was established by Budde-Lund (1908) for *Philoscia suarezi* Dollfus, 1895, from Diego-Suarez in Madagascar. Budde-Lund reportedly found this species not only in Madagascar but on several islands of the west Indian Ocean, and later (1910) in east Africa (Kibonoto, Meru and Kibosho). In 1913, Budde-Lund published a list of species belonging to the genus *Setaphora*, including two new species from the Seychelles: *S. ovata* and *S. pallidemaculata*. Herold (1931) redefined the genus

and described some species from the Sunda islands without, however, adding any truly unequivocable traits. The same can be said for the diagnosis presented by Barnard (1932). While Taiti & Ferrara (1980) and Ferrara & Taiti (in press) presented a diagnosis of this genus based on the study of the syntypes of *S. ovata* and *S. pallidemaculata*, they affirmed that only the study of the type species *S. suarezi* could provide an exact diagnosis.

As the problem of identifying the genus *Setaphora* reappeared with the South African material, it was decided to check the specimens of *Philoscia suarezi* on which Budde-Lund (1908) had based the new genus. The study of this material (BM No. 1921:10:18:2351–2358) did little clarify the problem as the specimens contained in the tube (i) come from two different collections (Voeltzkow and Alluaud) and two different localities (Nossi Bè and Diego-Suarez) (Ellis & Lincoln 1975: 92), (ii) are in poor condition and unable to withstand much handling, (iii) belong to two distinct species, one of which probably corresponds to the *Philoscia suarezi* described by Dollfus and the other to the *Philoscia suarezi* intended by Budde-Lund, and (iv) allow no conclusions on the genus (or genera?) to which they belong. Furthermore, the Danish author had established *Setaphora* on specimens—which he identified as *P. suarezi*—from other islands of the western Indian Ocean (Réunion, Comoro, Fundu) as well, but which probably belong to other species. It is indicative that the east African specimens identified by Budde-Lund (1910) as *S. suarezi* (NRS Is. 5826: Meru) not only do not correspond to the description of *P. suarezi* by Dollfus (1895a) but are not conspecific with the British Museum specimens. In fact, they belong to *Afrophiloscia uncinata* (Ferrara, 1974).

Until further information is available, the authors consider their diagnosis of *Setaphora* (Taiti & Ferrara 1980; Ferrara & Taiti in press) as valid. The four species assigned by Barnard to the genus belong to three distinct genera, none of which fits the proposed diagnosis of *Setaphora*. In fact, *Setaphora ocellata* belongs to the genus *Afrophiloscia* Taiti & Ferrara, 1980, *S. demarcata* is the type species of the new genus *Barnardoscia*, which also includes *B. maculata* sp. nov., while *S. mina* and *S. cingulata* belong to the genus *Natalscia* Verhoeff, 1942, together with the new species *N. thomsoni*, *N. rotundata*, and *N. appletoni*.

ZOOGEOGRAPHIC DISCUSSION

At present the list of South African Philosciidae—excluding *Chaetophiloscia elongata* and *Philoscia muscorum* for the above-mentioned reasons—is as follows:

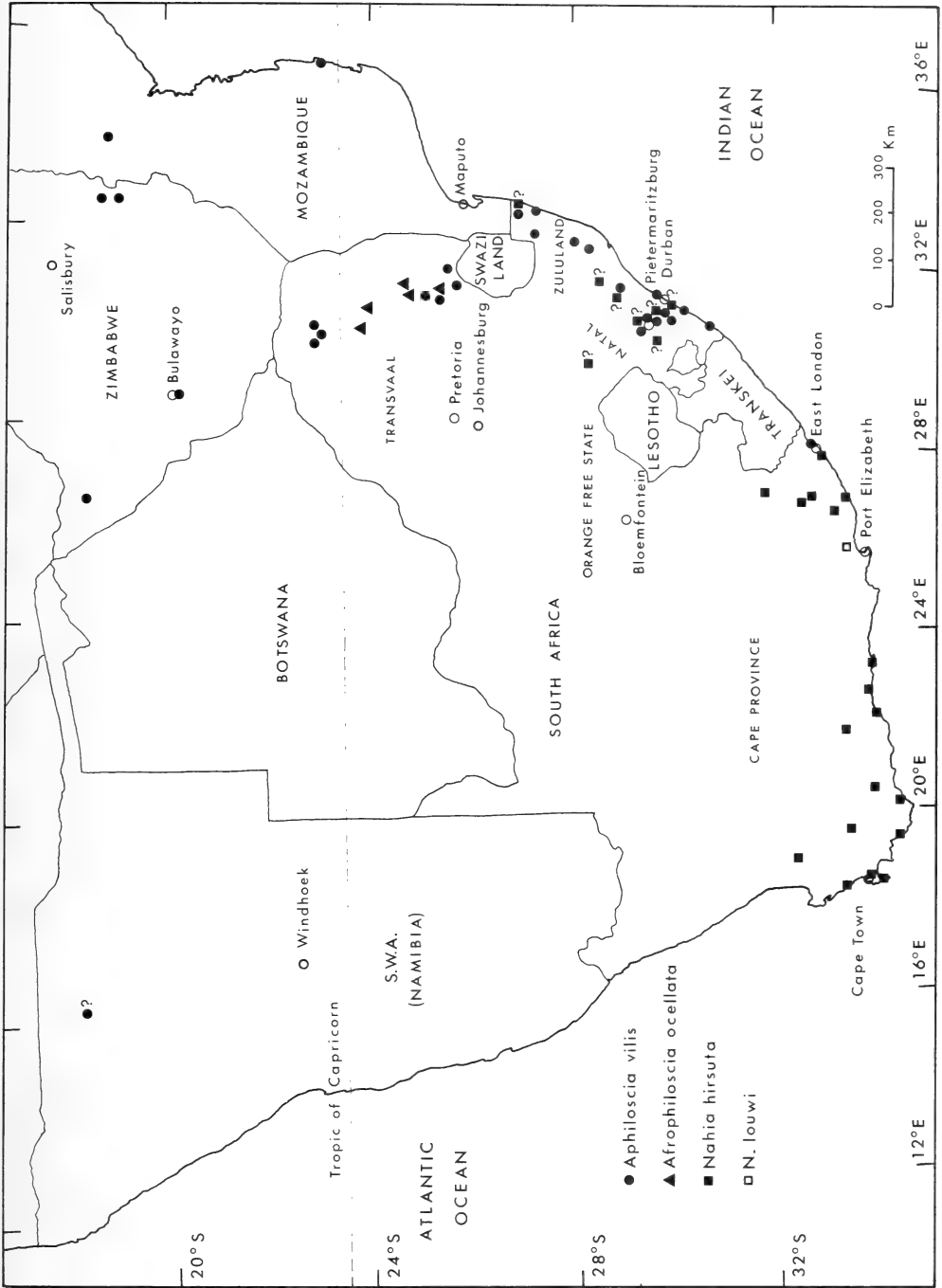|	
Aphiloscia vilis (Budde-Lund, 1885)	Mozambique, Zimbabwe, Transvaal, Natal, Zululand, Cape Province, ?Ovamboland
Benthanops fulva Barnard, 1932	Cape Province

Fig. 23. Map of southern Africa showing distribution records of *Aphiloscia vilis*, *Afrophiloscia ocellata* and *Nahia* species. The question marks indicate doubtful or unconfirmed records.

Afrophiloscia ocellata Barnard, 1960)	Transvaal
Nahia hirsuta (Budde-Lund, 1906)	?Natal, ?Zululand, Cape Province
Nahia louwi sp. nov.	Cape Province
Natalscia mina (Budde-Lund, 1885)	Natal, ?Transkei, ?Cape Province
Natalscia cingulata (Barnard, 1932)	Natal, ?Transkei
Natalscia thomsoni sp. nov.	Natal
Natalscia rotundata sp. nov.	Natal
Natalscia appletoni sp. nov.	Zululand
Natalscia sp.	Transvaal
Barnardoscia demarcata (Barnard, 1932)	Natal
Barnardoscia maculata sp. nov.	Natal

The recorded distribution of each species is shown in Figures 23–25. The records of *Aphiloscia vilis* from Ovamboland, *Nahia hirsuta* from Natal and Zululand, and *Natalscia mina* from Cape Province are doubtful due to the uncertainties and errors in identification by the early authors. Because of the insufficient material the records of *Natalscia mina* and *N. cingulata* from Transkei need confirmation. Thus far, only *Aphiloscia vilis* has been found outside South Africa as well.

The distribution of South African philosciids is of particular interest: of the six known genera, four (*Benthanops*, *Nahia*, *Natalscia*, and *Barnardoscia*) are exclusive to this region. *Benthanops*, however, shows many affinities to the
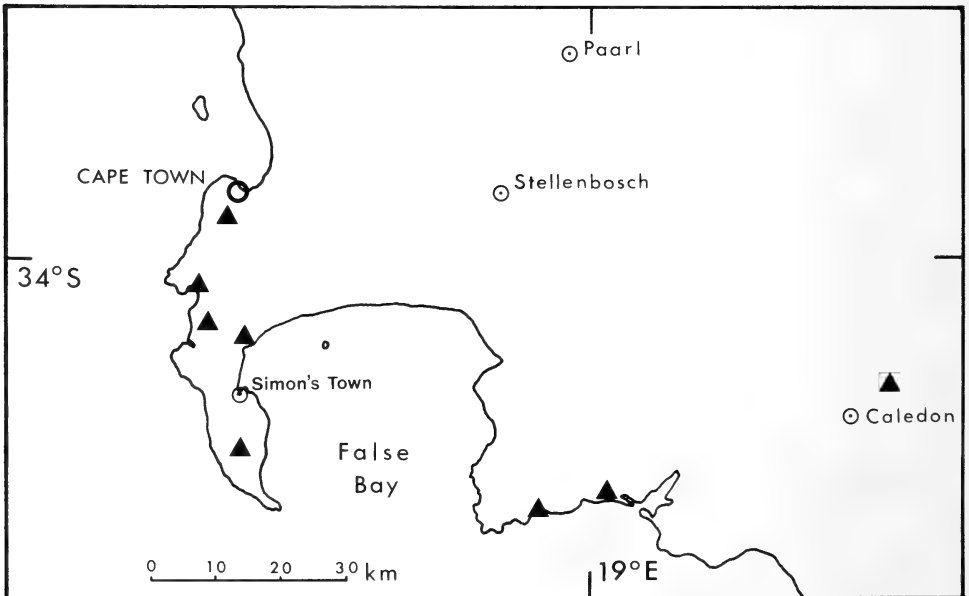

Fig. 24. Map of the south-western Cape Province showing distribution records of *Benthanops fulva*.
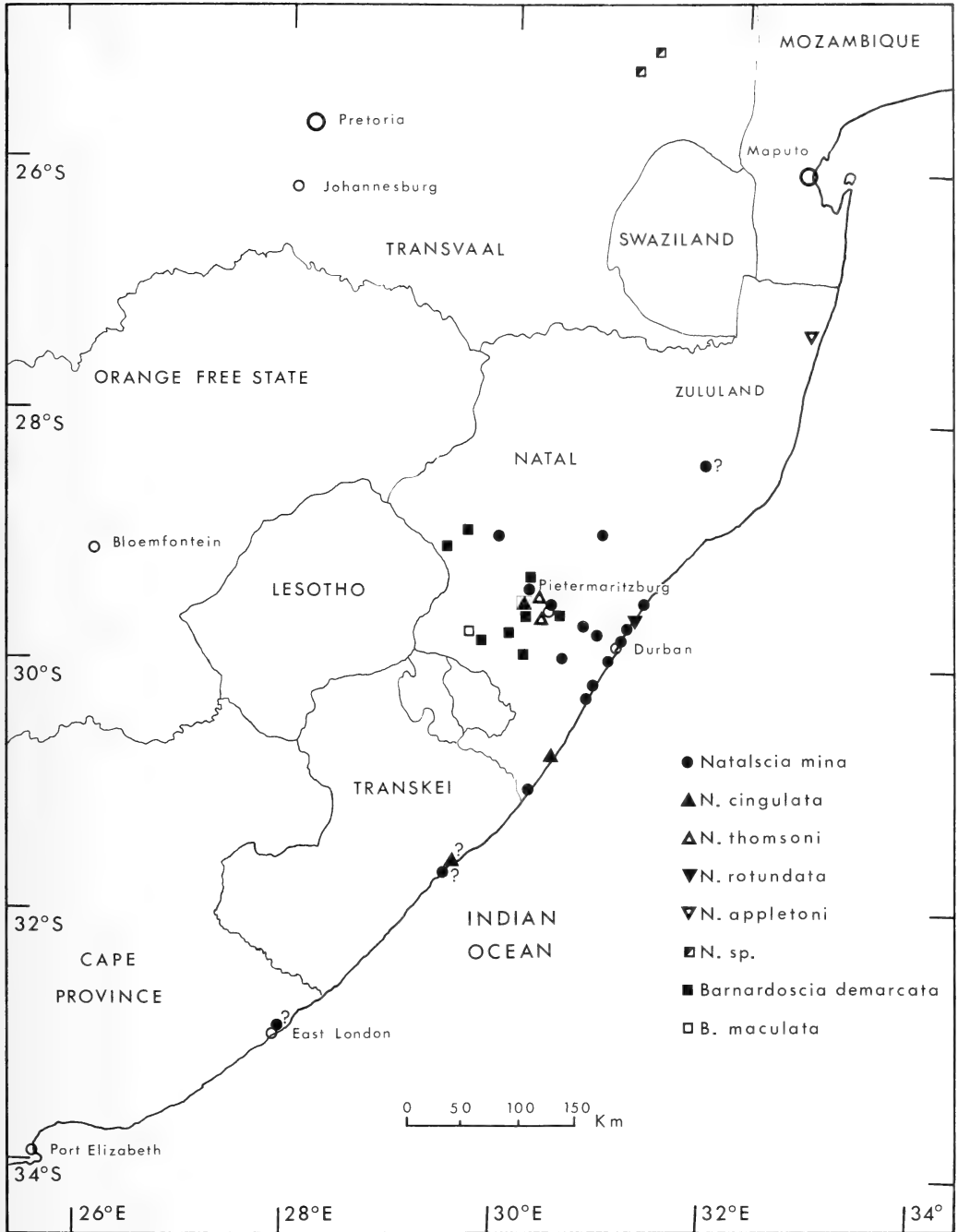
Fig. 25. Map of eastern South Africa showing distribution records of *Natalscia* and *Barnardoscia* species. The question marks indicate doubtful or unconfirmed records.

South American *Benthana* Budde-Lund, 1908, and allied genera and to the palearctic genus *Ctenoscia*, while *Nahia* belongs to the *Plymophiloscia* group (Vandel 1973*a*, 1973*b*) which occurs throughout the Orient and Australia. Of this group, only *Bilawrencia occidentalis* Ferrara & Taiti, in press, from Seychelles is known in Africa and surrounding islands. *Natalscia* and *Barnardoscia* are very close to each other and appear to be isolated from all the other African philosciids. *Aphiloscia* and *Afrophiloscia* are the only genera found in other African countries. The former is distributed throughout central and east Africa, Madagascar and other islands of the western Indian Ocean, while the latter occurs in Kenya and Tanzania. The fact that both genera are found only in the eastern part of South Africa is proof of the faunistic continuity of this area with east Africa.

TABLE 1

Synopsis of the Afrotropical genera of Philosciidae.

	gland pores	2 noduli laterales/ segment	4 noduli laterales on segment 7	4 noduli laterales/ segment	d/c maxima	frontal line	supra-antennal line	pleon epimera	molar penicil of mandible	teeth of maxilla 1	penicil of maxilliped	respiratory areas	insertion of uropod exo-endopodite
Aphiloscia	+			+		+	+	p	s	c	−	+	≠
Buddelundiscus	?	?	?	?	?	+	+	p	?	c	−	+	≠
Massaiscia	+	?	?	?	?	+	+?	p	?	c	−	−	≠
Komatia	?	?	?	?	?	+	+	p	s	c	−?	?	=
Perinetia	?	?	?	?	?	+	+?	r	s	s(1)	?	−	?
Pleopodoscia	?	?	?	?	?	+	+	r	d	c	−	−	≠
Didima (3)	+			+		−	+	r	d	c(2)	−	−	=
Renelloscia	+	+			II, IV	−	+	r	s	c	+	−	=
Sechelloscia	−	+			II, IV	−	+	r	s	s	+	−	=
Afrophiloscia	−	+			II, IV	−	+	r	s	c	−	−	=
Setaphora	+	+			IV	−	+	r	s	c	+	−	=
Barnardoscia (3)	+		+		I, IV	−	+	r	s	c	+	−	≠
Natalscia (3)	+	+			I, IV	−	+	r	s	c	−	−	≠
Uluguroscia	+	+			IV	−	+	r	s	c	−	−	=
Bilawrencia	−	+			−	−	+	r	d	c	+	−	≠
Helenoscia (3)	−	+			?	−	+	r	d	c	+	−	≠
Nahia (3)	+	+			−	−	+	r	s	c	−	−	≠
Benthanops (3) (4)	+		+		IV	−	+	r	d(5)	se	−	−	=
Congophiloscia	+		+		II, IV	−	−	r	d	c	+	+	≠
Gabunoscia	+		+		II, IV	−	−	r	d	c	−	−	≠
Togoscia	+		+		II, IV	−	−	r	d	c	+	−	=
Vandelophiloscia	−		+		(II), IV	−	−	r	d	s	−	−	≠
Zebrascia	−		+		II, IV	−	−	r	s	c	+	−	=
Arcangeloscia	+		+		IV	−	−	r	d	c	+	−	≠

+, present; −, absent; =, at the same level; ≠, spaced; c, cleft; d, dichotomized; p, produced; r, reduced; s, simple; se, serrate.
(1) 3 + 2 teeth; (2) 2 additional plumose teeth; (3) a dactylar seta is present; (4) a single large ommatidium; (5) a tuft of plumose setae each arising separately.

SYNOPSIS OF THE AFROTROPICAL GENERA OF PHILOSCIIDAE

In a previous paper on African philosciids (Taiti & Ferrara 1980), the diagnosis of four genera was either incomplete (*Benthanops*, *Nahia*) or non-existent (*Natalscia*, *Barnardoscia*) due to the lack of material, and thus it was thought useful to present a new synopsis of the known afrotropical genera (Table 1).

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.

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.:

<div style="text-align:center">

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A
</div>

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 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.
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.

STEFANO TAITI
&
FRANCO FERRARA

REVISION OF THE FAMILY PHILOSCIIDAE (CRUSTACEA, ISOPODA, ONISCOIDEA) FROM SOUTH AFRICA

ANNALS

OF THE SOUTH AFRICAN
MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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*
   (h) *References*
   (i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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 legend); the reduction or enlargement required should be indicated; 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 legend; if the latter, then the final reduction or enlargement should be taken into consideration.

   All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

   The number of the figure should be lightly marked in pencil on the back of each illustration.

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) describes . . .'
    'Smith (1969: 36, fig. 16) describes . . .'
    'As described (Smith 1969a, 1969b; 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.
           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 (1969a, 1969b) and not Smith (1969, 1969a).

   For books give title in italics, edition, volume number, place of publication, publisher.
   For journal article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals.* 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, 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. *J. Conch., Paris* **88**: 100–140.
   FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
   KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
   KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
   THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

PATTERNS OF UNGULATE MORTALITY AND UNGULATE MORTALITY PROFILES FROM LANGEBAANWEG (EARLY PLIOCENE) AND ELANDSFONTEIN (MIDDLE PLEISTOCENE), SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

RICHARD G. KLEIN

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(With 16 figures and 4 tables)

ABSTRACT

An ungulate species in which females usually have one young (or less) per year will have a catastrophic (= survivorship = 'lx') age profile with a down-staircase shape in which successively older age classes contain progressively fewer individuals. The corresponding attritional (= mortality = 'dx') profile will tend to be U-shaped, with a large peak in the youngest age class and a second smaller peak beyond 40–50 per cent of potential individual lifespan, or L-shaped, with a large peak in the youngest age class and no obvious peaks thereafter. A species in which females regularly produce more than one young per year will have catastrophic and attritional profiles that both exhibit the down-staircase form. In samples of fossil ungulates, reasonably accurate age (mortality) profiles may be calculated from dental crown heights, using quadratic formulae that assume that the rate of dental wear slows with age. Without sound contextual information, available from Langebaanweg (early Pliocene) but not from Elandsfontein (Middle Pleistocene), age profiles may be difficult to interpret, even when their form (catastrophic v. attritional) is clear. Establishing whether bones accumulated seasonally or not and determining the sex ratio in fossil ungulate samples is far more difficult than establishing age profiles. In conjunction with contextual information, age profiles in fossil samples may be used to infer basic biological facts in a species, such as the common rate of reproduction. The major impediment to broader application of age (mortality) profile analysis in palaeontology and archaeology is the rarity of suitably large samples.

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INTRODUCTION

The purpose of this paper is twofold: first, to review those aspects of ungulate mortality that are of special interest to palaeontologists and second, to construct and interpret ungulate mortality profiles from the fossil sites of Langebaanweg (early Pliocene) and Elandsfontein (mid-Pleistocene) in the south-western Cape Province of South Africa. Both are key sites for understanding Late Cenozoic mammalian evolution in Africa, and much of their importance derives from the fact that they have provided unusually large samples of well-preserved bones. These samples are useful not only for understanding the origins and meaning of the Langebaanweg and Elandsfontein fossil accumulations but also for illustrating the potential and the limitations of mortality profile analysis based on fossil ungulate remains.

Mortality profile analysis is essentially an aspect of the field of population dynamics whose central tool is generally the 'life table' as discussed, for example, by Deevey (1947). The emphasis here, however, will not be on 'life tables' but on mortality profile shape as a means of determining cause of death in fossil samples. The discussion here builds on and expands concepts and insights provided by many other investigators, particularly Deevey (1947) and Spinage (1972a) with respect to mortality patterns in general, and Kurtén (1953) and Voorhies (1969) with respect to mortality patterns in fossil mammals.

SOME GENERAL PRINCIPLES OF POPULATION DYNAMICS IN LARGE MAMMALS

A convenient way of illustrating some basic principles of large mammal population dynamics is to formulate a hypothetical population such as the one whose age structure is presented in the column labelled 'lx' in Table 1. Maximum individual longevity in this population is 9 years. Each year 500 new individuals are born.

If we require that the overall population size remain constant from year to year, the 500 births will have to be balanced by 500 deaths. If we further require that the age structure remain unchanged, the 500 deaths will have to be strictly apportioned among the various age classes. More specifically, the number of deaths in each age class will have to equal the number of individuals that survive to that age class minus the number that survive to the next age class. The resulting death tallies are listed in the 'dx' column of Table 1, and the relationship between corresponding 'lx' and 'dx' values is illustrated graphically in Figure 1. Although the requirements of a constant population size and constant age structure may appear arbitrary, natural populations adapting to stable environments probably do tend to both a constant size and a constant age structure.

The 'dx' entries in Table 1 are measures of absolute mortality in successive age classes. Dividing each 'dx' entry by its corresponding 'lx' entry provides a

TABLE 1

The age structure of a hypothetical population of large mammals in which females give birth once a year, total births are 500 per year, and potential individual longevity is 9 years.

Age (x) (years)	Number of live individuals (lx)	Number of dead individuals (dx)	Rate of mortality % (qx)
0–1	500	250	50
1–2	250	25	10
2–3	225	22	10
3–4	203	20	10
4–5	183	37	20
5–6	146	44	30
6–7	102	41	40
7–8	61	37	60
8–9	24	24	100
9–10	0	0	

Fig. 1. Left. Blank bars: the age structure of a hypothetical population of large mammals in which females give birth once a year, total births are 500 per year, and potential individual longevity is 9 years. Hatched bars: the number of individuals of each age who must die each year if the population size and age structure are to remain unchanged.
Right: A separate display of the hatched bars, reflecting the age profile of those individuals who die each year in the hypothetical population.

measure of relative mortality or what is commonly called 'the rate of mortality'. Rates of mortality for successive age classes are listed in the 'qx' column of Table 1. In population biology, 'lx', 'dx', and 'qx' are conventional notations for tallies of live individuals, dead individuals, and rates of mortality respectively. When these notations are used, age is designated by 'x'.

As a rule, individual large mammals achieve sexual maturity at an age that is roughly 10 per cent of maximum potential longevity. In our hypothetical

population this would mean that essentially all individuals over 1 year of age would be sexually mature. The total of such individuals (from the 'lx' column of Table 1) is 1 194. Assuming that half of these individuals (597) are female and females can produce only one offspring per year, then 84 per cent of the females ($\frac{500}{597}$) would have to give birth every year to maintain a constant population.

It is interesting to determine what would happen to the hypothetical population if the key constraints were removed. Suppose, for example, that we wanted to force the population into decline. The most direct way would be to increase mortality in the youngest sexually mature age classes. This is because there are only 597 females to produce 500 young every year. Even a slight rise in mortality in the youngest sexually mature age classes would drive the total number of sexually mature females below 500, not only immediately reducing the size of the population but also reducing the number of new births in the coming year. An increase in mortality in the youngest sexually mature females can be particularly disastrous under natural circumstances, since not all sexually mature females in natural populations will actually be capable of breeding. Some will certainly be barren, particularly in the oldest age classes. Often, older individuals also tend to be infirm, so that they suffer higher rates of mortality, a circumstance which has been assumed for our hypothetical population.

If, instead of decline, we wanted to promote population growth, the most direct way would be to reduce mortality in the first age class, since even a small percentage decrease would significantly increase the number of individuals that reach sexual maturity. There would be a cumulative effect, since this would also increase the number of births in the following year. However, even though Table 1 shows that current first-year mortality is 50 per cent, which seems quite high, a reduction in rate may be very difficult to achieve. This is because the very young in many species are extremely vulnerable to death by predation, disease, accidents, starvation, etc. First-year mortality rates in the vicinity of 50 per cent are, in fact, common in many naturally occurring populations of large mammals.

So far we have assumed that each female is capable of producing only one young per year. It is instructive to see what happens if the number of potential young is increased to two per year. A constant population size can now be maintained with only half as many females as before. If, in fact, population size is to remain unchanged, mortality rates must rise in the youngest age classes to reduce the number of sexually mature individuals. Table 2 provides 'lx', 'dx', and 'qx' values for a hypothetical population similar to our original one in constant overall size, but characterized by 1 000 births per year from 500 females. The relationship between corresponding 'lx' and 'dx' values in Table 2 is illustrated graphically in Figure 2.

To summarize, populations of large mammals that are constant in size and age structure will exhibit age profiles in which successively older age classes

TABLE 2
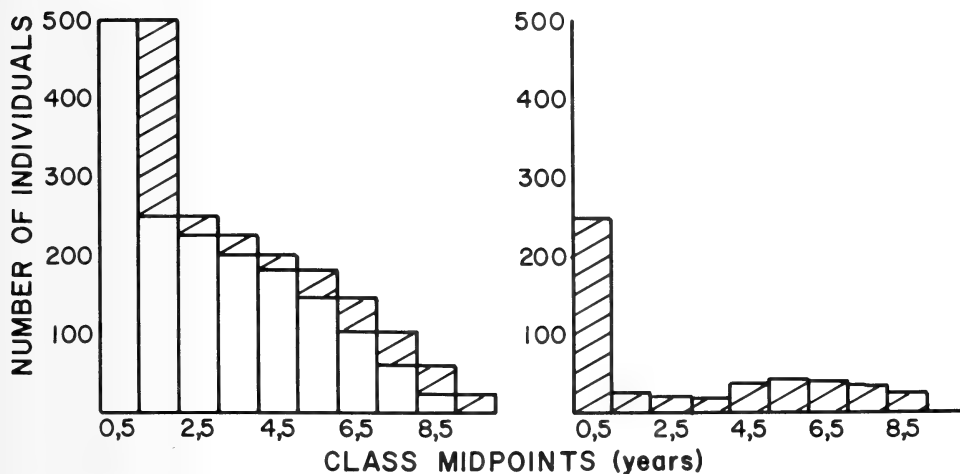
The age structure of a hypothetical population of large mammals in which females give birth twice a year, total births are 1 000 per year, and potential individual longevity is 9 years.

Age (x) (years)	Number of live individuals (lx)	Number of dead individuals (dx)	Rate of mortality % (qx)
0–1	1 000	700	70
1–2	300	150	50
2–3	150	75	50
3–4	75	30	40
4–5	45	9	20
5–6	36	7	20
6–7	29	6	20
7–8	23	12	50
8–9	11	11	100
9–10	0	0	
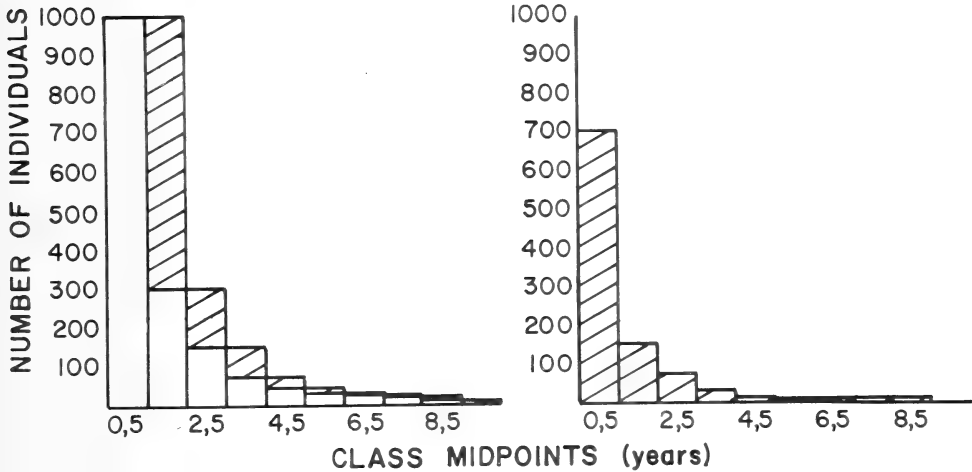
Fig. 2. Left. Blank bars: the age structure of a hypothetical population of large mammals in which females give birth twice a year, total births are 1 000 per year, and potential individual longevity is 9 years. Hatched bars: the number of individuals of each age who must die each year if the population size and age structure are to remain unchanged.
Right. A separate display of the hatched bars, reflecting the age profiles of those individuals who die each year in the hypothetical population.

contain progressively fewer individuals (Figs 1 and 2, left). If the females in the population can have only one young per year, the age profile of those individuals who die each year will generally be U-shaped (Fig. 1, right), reflecting the fact that the rates of mortality are generally highest in the very young and in the old. If, as may be the case in some natural populations, the rate of mortality does not rise sharply in older age classes, the age profile of those individuals who die each year may be L-shaped, with no obvious peaks

after the one in the youngest age class (see below). Whatever the case, however, the age profiles characterizing the live and dead segments of the population in any given year will be formally quite distinct (Fig. 1, left v. Fig. 1, right.)

If the females in the population produce more than one young per year, the age profile of those individuals who die each year will be quite similar in shape to the age profile of those who remain alive, reflecting the fact that rates of mortality remain high into middle life. The main point is that, unlike populations in which females produce only one young per year, the age profiles characterizing the live and dead segments of the population will be difficult, if not impossible, to distinguish on form alone (Fig. 2, left v. Fig. 2, right).

AGE STRUCTURE AND MORTALITY IN EXTANT
POPULATIONS OF LARGE MAMMALS

Characteristic age structures and mortality patterns have been established for remarkably few populations of large mammals One major reason is that many populations are fluctuating rapidly in size or rapidly declining, often as a result of human activity. There is no way of determining the typical age structure and mortality pattern of a population whose overall size is changing rapidly. Another problem is that, even for stable populations, it is difficult to collect reliable data. Three basic methods exist (Deevey 1947). First, survivorship to successive age classes may be recorded in a cohort of individuals born at more or less the same time; second, a census may be conducted of all those individuals alive at any one time; and third, individuals that die within a restricted time may be aged and tallied. In the conventional terminology of population biology, the first two methods produce 'lx' data, while the third produces 'dx' data. In theory, all three methods will provide the same age structure and mortality pattern for a population with a fixed size and age structure.

In practice, the first method—tallying the numbers of individuals from a single birth cohort that survive to successive ages—is all but impossible to apply to free-ranging populations of large mammals. It will also not yield results quickly, since individual large mammals have relatively long potential lifespans.

The second method—live censusing—is more practical, but it requires either that an entire population be studied or that there be some way of obtaining a reasonably large, unbiased sample. It further requires a method for ageing live individuals reliably, often only by observing them from a distance. The third method—tallying deaths—is, in fact, usually the most practical, since it may be based on skeletal material, which is relatively easy to sample and age.

Some representative mortality ('dx') profiles obtained by the death-tally method are presented here in Figure 3. All the profiles have been cast so that the number of age classes in each is approximately equal, while the second age class generally contains the youngest sexually mature individuals. Each profile
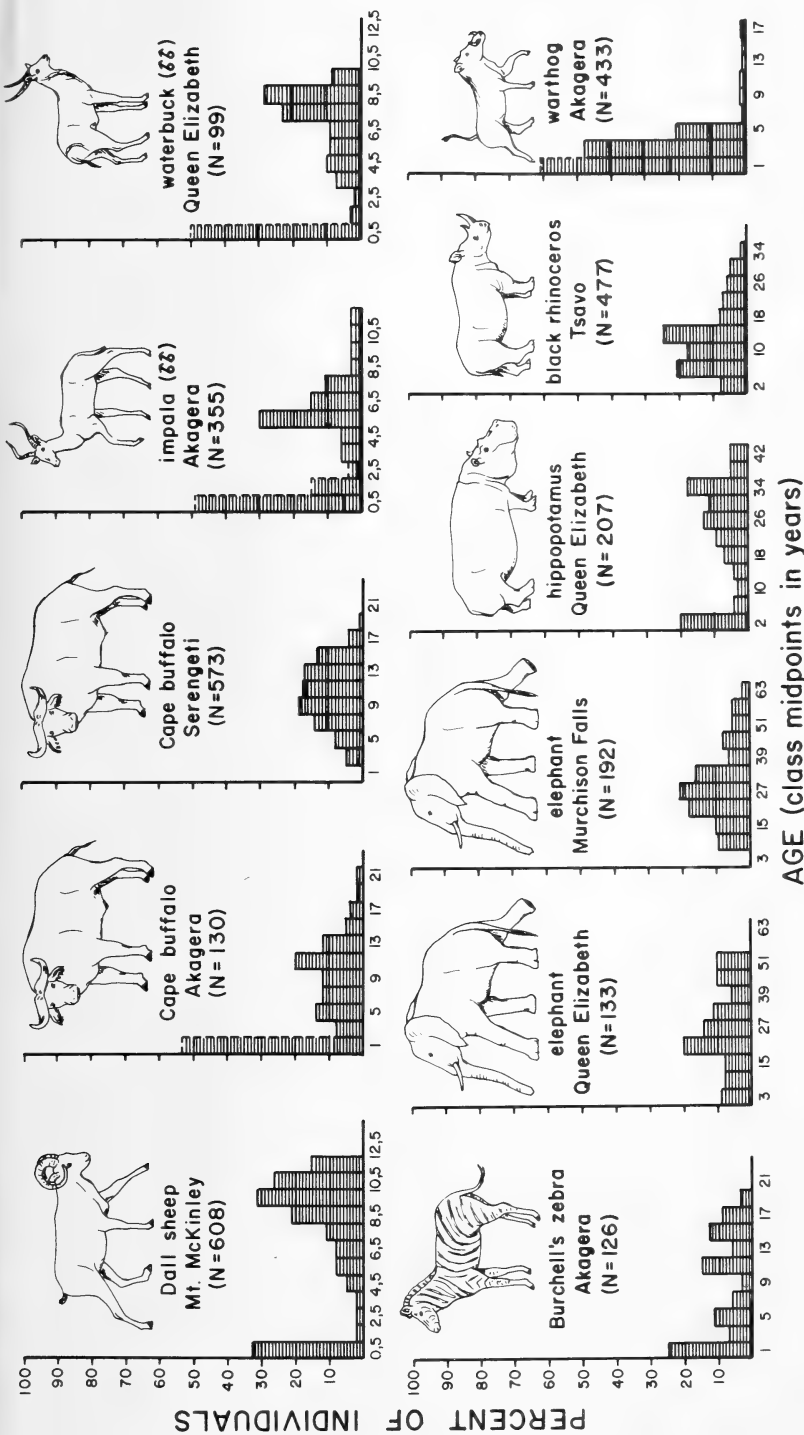
MORTALITY ('d$_x$') PROFILES IN SOME POPULATIONS OF FREE-RANGING LARGE MAMMALS.

Fig. 3. Representative mortality profiles in populations of free-ranging large mammals. The profiles have been cast so that the number of age classes is approximately the same in each. All the profiles are based on systematically collected skulls or jaws from populations that were at least roughly stable in size and age composition during the period when mortality took place. In all the profiles, very young individuals (in the first age class) are underrepresented because their skeletal remains are more likely to disintegrate before recovery. Dotted bars in the profiles for the Cape buffalo, impala, and wart-hog from Akagera National Park indicate the original analyst's attempt to use observations on live populations to 'correct' the underrepresentations of very young individuals.

Sources: Dall sheep (*Ovis dalli*) in Mount McKinley National Park (Murie 1944); Cape buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), Burchell's zebra (*Equus burchelli*), and wart-hog (*Phacochoerus aethiopicus*) in Akagera National Park (Spinage 1972a); waterbuck (*Kobus ellipsiprymnus*) in Queen Elizabeth Park (Spinage 1970); Cape buffalo in the Serengeti National Park (Sinclair 1977); elephant (*Loxodonta africana*) in Queen Elizabeth and Murchison Falls Parks (Laws 1966); hippopotamus (*Hippopotamus amphibius*) in Queen Elizabeth Park (Laws 1968); and black rhinoceros (*Diceros bicornis*) in Tsavo National Park (Goddard 1970).

is based on systematically collected skulls or jaws from individuals that died of 'natural' causes such as predation, accidents, and endemic diseases. Age was established by counting the annual rings on horns (Dall sheep) or by estimation from dental eruption and wear (remaining species). The base populations differ in the extent to which they were stable in overall size and age structure during the period when mortality took place, but all approximated stability sufficiently for present purposes.

Very young individuals (in the first age class) are underrepresented in all the profiles, because their skulls are more fragile than those of older individuals. The extent of underrepresentation probably varies from profile to profile depending upon local preservational conditions and on differences among species in skull architecture. Dotted bars in Figure 3 indicate the original analyst's attempts to 'correct' for underrepresentation of the very young in the mortality profiles of buffalo (at Akagera), impala, waterbuck, and wart-hog.

Keeping in mind the universal, though not necessarily equal, underrepresentation of very young individuals, the profiles of all the species but wart-hog are broadly similar in form, suggesting that in each case very young individuals and older adults suffer substantially higher rates of mortality than do younger (young sexually mature) adults. The pattern is very similar to the 'dx' (mortality) pattern in the hypothetical population of Figure 1 (right), in which females were assumed to have no more than one young per year.

In all the species but wart-hog, females also have no more than one young per year, and it was with these real species in mind that the hypothetical population was devised. The 'real' profiles suggest that species in which females bear one young (or less) per year are, in fact, often characterized by especially high rates of mortality among the very young and the old. It is possible, however, that the definition of 'old' may vary from population to population. Figure 3 suggests that in Dall sheep, waterbuck, and hippopotamus a substantial increase in the rate of mortality occurs in adults that are at 60–70 per cent of potential lifespan, while in the other species it tends to occur among somewhat younger adults at about 40–50 per cent of potential lifespan. Many more observations will be necessary to determine if this difference and other apparent differences among the profiles are real, perhaps due to differences in environment or species biology, or whether they are spurious, perhaps due to chance ('sampling error'), to differences in the extent to which the various populations were truly stable, or to differences in the extent to which individuals in different species can be accurately aged from skeletal remains. Since mortality patterns may differ somewhat between males and females in the same population (e.g. Spinage 1970 on waterbuck, or Sinclair 1977 on buffalo), it is further possible that some of the differences among profiles in Figure 3 reflect differences in the sex composition of the samples.

The wart-hog mortality profile is radically different from all the others in that it indicates very high mortality rates not only for very young individuals but also for young (sexually mature) adults. As the original analyst (Spinage

1972*a*) points out, the distinctive pattern of the wart-hog profile almost certainly reflects the fact that, unlike females in the other species, wart-hog females regularly produce more than one young per year (the common pattern is for a litter of 2 to 7). The wart-hog profile is, in fact, very similar in shape to the 'dx' (mortality) profile of the hypothetical population in Figure 2 (right) in which females were assumed to produce more than one young per year.

Though often less reliable than death-tally profiles such as those in Figure 3, live censuses of large mammal populations support the generalizations that the death-tally profiles suggest. A representative 'census' based on non-selective shooting and observations of live female Himalayan thar (*Hemitragus jemlahicus*) in New Zealand (Caughley 1966) is presented in Figure 4 (left). The population was probably roughly stable in size and age structure when the 'census' was taken. Female thar generally have no more than one young per year, and the inferred mortality ('dx') profile is obviously broadly similar to that of the species in Figure 3 in which females also have one young (or less) per year.
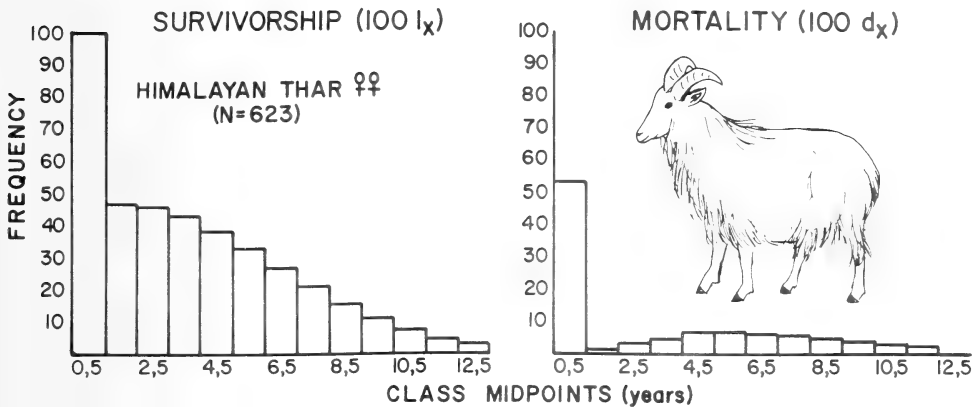

Fig. 4. Survivorship ('lx') and mortality ('dx') profiles in a population of female Himalayan thar (*Hemitragus jemlahicus*) in New Zealand, as reported by Caughley (1966). The survivorship profile is based on random shooting and live counts, while the mortality profile was inferred from the survivorship count. The mortality profile exhibits a tendency for the rate of mortality to rise fairly sharply in individuals at 40–50 per cent of potential lifespan.

In sum, the available data on extant large ungulate populations suggest that ones in which females have one young (or less) per year will tend to exhibit a mortality pattern in which the rate of mortality is much higher in very young individuals and in older adults than in younger ones. Depending upon the population, 'older' adults may be ones at an age between 40–50 per cent and 60–70 per cent of potential lifespan. The live ('lx') age structure of such a population will be similar to that of the hypothetical population of Figure 1 (left), with a shape similar to a down staircase in which a very steep first step is followed by a series of much less steep but steadily steepening ones. The

mortality ('dx') profile of the population will tend to be U-shaped as in Figure 1 (right).

The limited data presented here on large mammals that have more than one young per year may be supplemented by data on fast-breeding small mammals (references in Spinage 1972a) to support the conclusion drawn here that high mortality rates will persist into young adult classes in such populations. The live age structure of the population will be similar to that of a down staircase in which the initial three or four very steep steps are followed by a series of barely perceptible ones. The corresponding mortality profile will recall a very similar staircase, though the very last, barely perceptible, steps will tend to ascend rather than descend (Fig. 2, right). Since the difference in shape between the corresponding live ('lx' or survivorship) and death ('dx' or mortality) profiles is so subtle, a very large sample will be necessary to show which profile is represented by an age structure drawn from material whose context did not allow an a priori determination. The significance of this point will become clear below.

AGE STRUCTURE AND MORTALITY IN SOME FOSSIL POPULATIONS OF LARGE MAMMALS

There is a sense in which the age profile of a fossil population is always a mortality or 'dx' profile, since the individuals involved are all dead. However, it will only resemble the 'dx' profile of an extant population if the fossil individuals died as a result of accidents, predation, endemic disease, and other routine attritional factors that ordinarily have their greatest impact on the very young and the old. If, instead, the fossil individuals died as the result of a great flood, volcanic eruption, epidemic disease, or other catastrophic event that affected individuals of all ages to the same extent, the mortality profile of the fossil population will directly reflect its original live age structure. In other words, it will, in fact, be a survivorship or 'lx' profile. In practice then, the age profile of a fossil population may reflect either mortality ('dx') or survivorship ('lx') as they are commonly defined.

The observations on extant populations presented in the last section suggest that shape alone may be sufficient to determine whether a large mammal mortality profile reflects catastrophic ('lx') or attritional ('dx') mortality, at least in species where females commonly have one young or less per year. In such species a 'catastrophic' (= survivorship = 'lx') profile will tend to be shaped like a down staircase, with the first and near-last steps being the steepest. An 'attritional' (= true mortality = 'dx') profile will tend to be U-shaped, with a large peak or mode in the youngest age class, followed by a marked dip, and then a second, smaller peak in individuals at 40–50 per cent to 60–70 per cent of potential longevity.

In many instances, it is, of course, possible to infer mode of death (catastrophic or attritional) independently of profile shape. For example, cata-

strophic death by drowning is a likely explanation for a fossil example derived from ancient fluvial deposits packed with bones belonging mainly to only one or two species. Catastrophic death is probably also implied in most cases where an age distribution is clearly discontinuous, that is, composed of discrete age classes, each separated from the next by an age gap into which no individuals fall. This could happen only if birth and death were both seasonally restricted events, and a priori, seasonally restricted death (perhaps by flood or brush fire) is more likely to be catastrophic than attritional. This is particularly true if the dead animals accumulated in a deposit over a period of several years, so that their deaths had to occur in the same season each year.

Since it is often possible to infer mode of death (catastrophic or attritional) in a fossil sample by criteria other than age profile shape, age profiles in fossil samples may be used to help establish the general characteristics of survivorship and mortality in large mammals. In this regard they may even prove more suitable than many samples from extant populations, since they are often larger (or can be enlarged quickly with relatively little effort) and they frequently derive from a substantial period of time during which short-term fluctuations in population size and age structure will tend to have cancelled each other out. This means that a fossil sample is more likely to produce an age profile that is truly typical of the population.

Unquestionably the most famous studies of age structure and mortality in fossil populations of large mammals are those by Kurtén (1953) and Voorhies (1969) on samples from late Miocene fluvial deposits in north China and Nebraska respectively. Voorhies carefully excavated his sample himself, while Kurtén analysed material collected by others under conditions that were probably much less well controlled. There is no reason to suppose, however, that collecting seriously biased the age profiles of any of the species that Kurtén studied.

Voorhies's sample was heavily dominated by the extinct pronghorn antelope *Merycodus furcatus*, with the three-toed horse *Protohippus* cf. *perditus* a distant second, and other species still less common. Kurtén's samples came from several localities, at each of which one species tended to dominate heavily, though not necessarily the same species at each locality. In their analyses of dental eruption and wear in the principal species in their samples, both Kurtén and Voorhies found that individuals fell into discrete age modes or clusters, each cluster probably representing a cohort of individuals born at more or less the same time and killed more or less simultaneously. Together with the sedimentary context, this indicates that mortality in the various species studied by Kurtén and Voorhies was 'catastrophic' rather than 'attritional'.

The catastrophic ('lx') profiles of *M. furcatus* and *P.* cf. *perditus* from Nebraska and of the ovibovine bovids *Plesiaddax depereti* and *Urmiatherium intermedium* and the gazelle *Gazella dorcadoides* from north China are displayed on the left-hand side of Figure 5 here. In *M. furcatus* the youngest individuals represented were already old enough at death for their jaws to be

about as durable as those of adults. As a consequence, there is no reason to suppose serious underrepresentation of very young *M. furcatus* in the age profile. In the other four species, however, the jaws of individuals in the youngest (first) age class, and in the ovibovines also in the second age class, were relatively fragile, and such individuals are probably seriously underrepresented in the age profiles. The dotted bars in Figure 5 represent the present writer's attempt to correct for this underrepresentation in the gazelle and ovibovine profiles by assuming roughly 50 per cent first-year mortality in all three species and roughly 10 per cent second-year mortality in the ovibovines. In all five species involved, females probably had no more than one young a year. Keeping in mind that very young individuals are seriously underrepresented in four of the profiles, they are all very similar in form to those of extant species with the same reproductive potential.

The 'dx' profiles that are inferable from the 'lx' ones are shown on the right-hand side of Figure 5. They are also broadly similar to the 'dx' profiles of the extant species, though in general they do not exhibit a clear second peak among older individuals. The absence of a clear second peak may reflect chance ('sampling error') or it may indicate that in some populations of large mammals the rate of mortality does not rise sharply among older adults, leading to an L-shaped (v. U-shaped) shaped mortality profile. The possibility that 'dx' profiles may be L-shaped is not widely recognized but must clearly be borne in mind when interpreting mortality profiles such as those from Langebaanweg and Elandsfontein considered below.

AGE PROFILES PRODUCED BY PREDATION ON SOME POPULATIONS OF LARGE MAMMALS

Figure 6 presents age profiles of Burchell's zebra and Cape buffalo killed by lions on the Serengeti Plain (Schaller 1972), of chamois (*Rupicapra rupicapra*) shot by recent hunters in the Alps (Kurtén 1953 using data from Bourlière 1951), and of pronghorn antelope (*Antilocapra americana*) killed by the late prehistoric occupants of the Eden–Farson site, Wyoming (Nimmo 1971; Frison 1978a). In each case, individual age was established from dental eruption and wear. Very young zebra, buffalo, and chamois are all seriously underrepresented in Figure 6. Lions consume very young zebra and buffalo too quickly and completely for observers to estimate accurately the number of very young killed, while the hunters who shot the chamois were not interested in very young animals because they make poor trophies. If it had been possible to record all kills of zebra and buffalo, very young individuals would certainly be the best represented age class in the kill profiles. Similarly, very young animals would have been the most common individuals in a completely random shot sample of chamois. Only in the pronghorn kill sample, derived by careful excavation of well-preserved bone, are very young animals probably present in more or less their proper proportion.
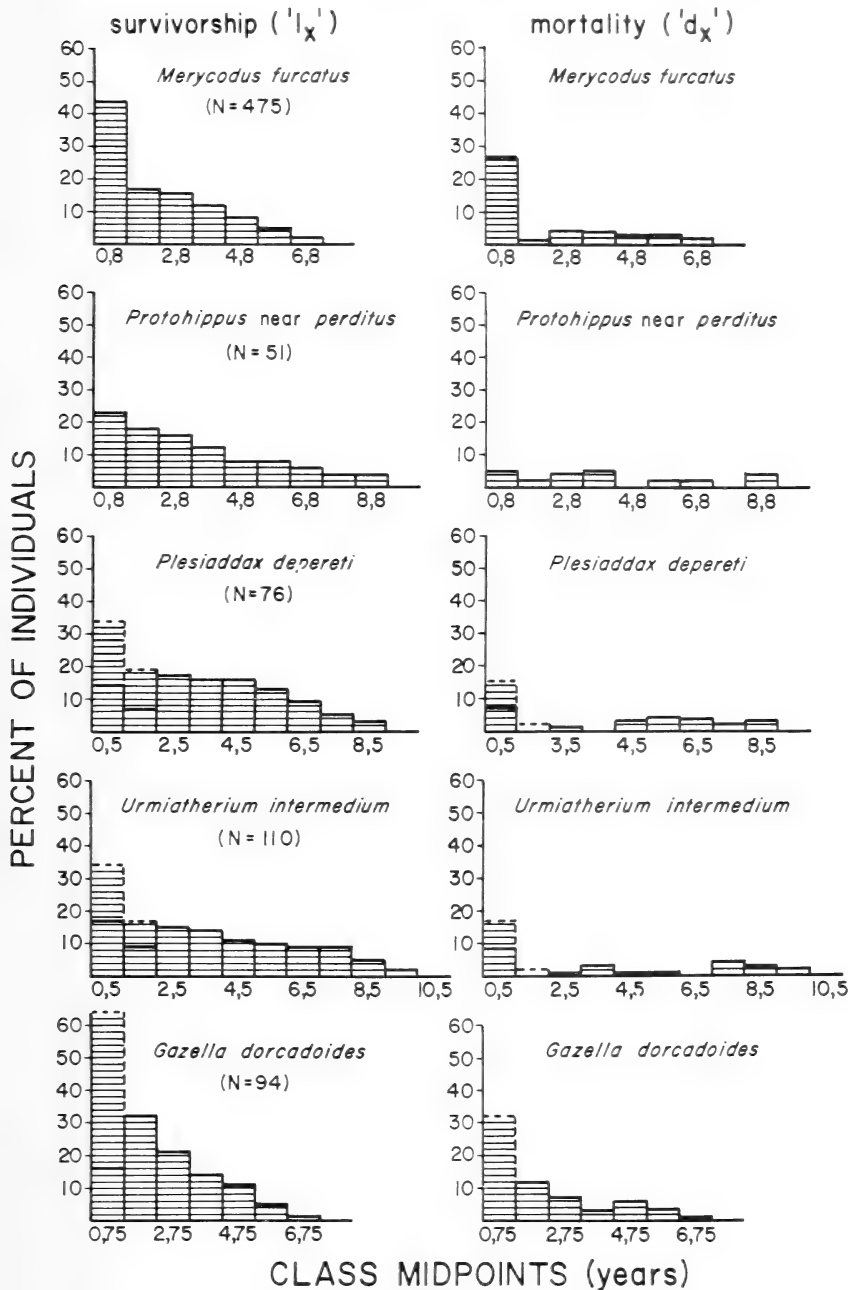
Fig. 5. Catastrophic (= survivorship = 'lx') profiles (left) and attritional (death = 'dx') profiles (right) in *Merycodus furcatus* and *Protohippus* near *perditus* from late Miocene deposits at Verdigre Quarry, Nebraska (Voorhies 1969), and in *Plesiaddax depereti*, *Urmiatherium interme-dium*, and *Gazella dorcadoides* from various late Miocene localities in north China (Kurtén 1953). The dotted bars represent the present author's attempts to 'correct' for the underrepre-sentation of young individuals in the profiles of the north Chinese species. In general, the 'death' (= 'dx') profiles in this Figure contrast with those in Figures 3 and 4 in lacking a clear second peak among older adults. This may be due to chance, or it may indicate that such a peak is not a necessary feature of attritional mortality in large mammals.
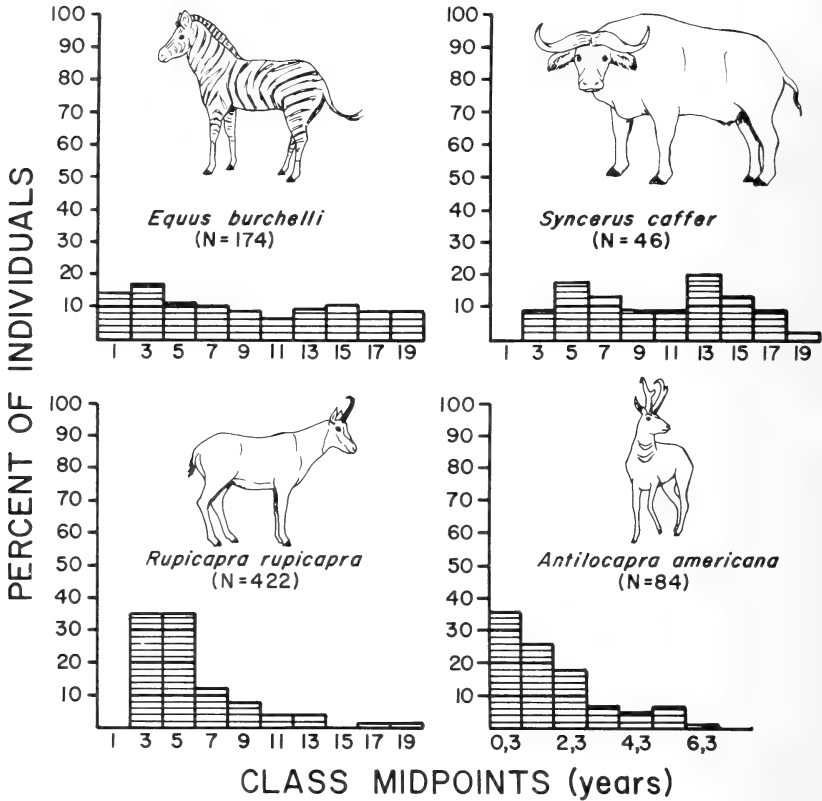
Fig. 6. Age profiles resulting from predation by lions on Burchell's zebra and Cape buffalo (Serengeti Plain) (Schaller 1972); from unrestrained, non-selective shooting of chamois in the Alps (Kurtén 1953 using data from Bourlière 1951); and from prehistoric American Indian hunting of pronghorn antelope (Eden–Farson site, Wyoming) (Nimmo 1971). The numbers of very young zebra and buffalo killed by lions cannot be accurately estimated, but very young individuals would certainly dominate the kill profiles if accurate counts could be made. The hunters who shot the chamois essentially ignored very young individuals because they do not make good trophies. Only in the pronghorn profile are very young animals probably represented in more or less their proper (true) proportion.

The zebra data have been reorganized from the original presentation, with individuals in what were sometimes broader age classes distributed evenly among the two-year age classes used here. All other data are as presented in the original sources.

In all four species, females generally bear no more than one young per year, which means that the profiles in Figure 6 are best compared with those in Figure 1, representing catastrophic (= 'lx' = survivorship) and attritional (= 'dx' = mortality) profiles of a hypothetical population with the same basic reproductive potential. Taking into account the severe underrepresentation of very young individuals in the zebra, buffalo, and chamois profiles, and assuming that attritional profiles need not display a sharp rise in the rate of mortality

among older individuals, the zebra and buffalo profiles are essentially attritional, while the chamois and pronghorn ones are clearly catastrophic.

The reason that the buffalo profile has an attritional shape is because the physical condition, large size, and social organization of young adult buffalo make them largely immune to lion predation. When lions hunt buffalo they are forced to concentrate on the very young and the old. It is probable that similar features of size, condition, and social organization also make young adult zebra less vulnerable to lion predation, though the difference in shape between the zebra and buffalo profiles in Figure 6 suggests the possibility that lions find it easier to kill young adult zebra than young adult buffalo. Whatever the case, lions apparently kill zebra and buffalo of various ages in broadly the same proportions as they would die anyway. Such a pattern of predation is perhaps to be expected in a situation where predator and prey populations have long coexisted, since the prey populations could sustain it indefinitely.

In contrast to the attritional shapes of the zebra and buffalo profiles, the catastrophic shape of the chamois profile reflects the activity of a predator (men with rifles) that was not forced to concentrate on any particular age class. In further contrast to predation on the zebra and buffalo, predation on the chamois could not have continued indefinitely. This is because the elimination of so many reproductively active young adults would depress the birthrate, leading to a decline in numbers and perhaps even extinction. In fact, historic observations indicate that hunting did seriously reduce the chamois population on which the profile in Figure 6 is based.

The method by which the pronghorn were hunted must be inferred, since it could not be directly observed. Given aboriginal American hunting technology, the method most likely to produce a catastrophic profile would be the communal drive, which was, in fact, observed ethnohistorically among Indians hunting pronghorn (Frison 1978a). As in the case of the chamois, a method netting so many young (sexually mature) adults would lead to a significant decline in overall pronghorn population size, if it were relentlessly employed. Historically, drives did apparently eliminate local pronghorn populations, which then took several years to recuperate through immigration from neighbouring regions. The point to be made is that hunting methods resulting in catastrophic kills must be restrained, voluntarily or otherwise, if they are not to reduce prey and thus ultimately predator numbers.

In sum, the examples presented here show that predation may produce either attritional ('dx') or catastrophic ('lx') mortality profiles in prey, depending upon the characteristics of prey and predator. An attritional profile, indicating that the predator was largely restricted to very young and old individuals, is perhaps to be expected in any situation where predator and prey have long coexisted. Catastrophic prey profiles, indicating that the predator possessed a capture method to which individuals of all ages were about equally vulnerable, will generally reflect unstable predator–prey relationships, probably mainly ones in which recent people were the predators. If methods leading to

catastrophic kills are not restrained, they can be counter-productive, since they will eventually cause prey populations to decline or even disappear.

ESTIMATING THE AGE OF A FOSSIL UNGULATE AT DEATH

In general, the most useful skeletal elements for estimating the age of individual ungulates at death are the teeth. In many species the age of a recently dead (or still living) individual may be estimated by counting the number of 'annuli' in the cementum covering dental roots (see Morris 1972 or Spinage 1973 for overviews). The cementum annulus method is generally not useful for estimating the age at death of fossil individuals, however, because fossil cementum often does not retain the annulus structure, at least in a way that can be detected with standard preparation techniques (Spiess 1979). Additionally, specimen preparation is destructive, rendering teeth all but useless for further study.

With fossil teeth, the only truly practical method of estimating individual age is to evaluate the state of eruption and wear. This can be done subjectively by comparing fossil dentitions to ones from known-age individuals, if a species is still extant, or objectively by measuring a dental dimension that clearly changes with age. In some fossil samples, such as those studied by Kurtén (1953) and Voorhies (1969), the seasonally restricted birth and death of the species involved allows subjective arrangement of the dentitions into a series of discrete eruption and wear classes. These reflect discrete age clusters, each separated from the last by approximately one year. Assuming that the youngest age class is made up of individuals in the first year of life, it is then possible to assign approximate (modal) ages to each of the successive eruption and wear classes.

In general the subjective method of age determination has the disadvantage that different investigators may estimate different ages from the same fossil dentition and also that it usually requires complete demi-mandibles or maxillae. In many, perhaps most, fossil samples, many individuals are represented only by isolated teeth. The objective method, based on measurement, has the advantage that it produces easily replicable results. Perhaps even more important, it can also be readily applied to isolated teeth, as long as their former position in the mouth can be determined. In sum, for fossil material, the measurement method of estimating individual age from teeth is almost certainly the best. At least with regard to high-crowned ungulates, the most obvious dental dimension to measure is crown height.

The mathematical relationship between advancing age and decreasing crown height has not been thoroughly established for any high-crowned ungulate species. The principal reason is the rarity of large samples of known-age dentitions, particularly ones from a wide variety of age classes. In the absence of a sound body of empirical observations the estimation of age from crown height requires some 'theoretical' assumptions on the nature and rate of crown attrition. In work to this point, the author has made the following assumptions:

1. That reduction in crown height is roughly constant through the life of a tooth, that is, that the relationship between decreasing crown height and advancing age is approximately linear.

2. That for a deciduous tooth, the chronological age of complete crown reduction—when the crown is all but worn away—is the age when the tooth is replaced by its permanent counterpart. For a permanent tooth, the chronological age of complete crown reduction is the age past which no individuals survive in the wild, sometimes known as 'potential ecological longevity'. For most species, the dental eruption and replacement schedule and potential ecological longevity may be obtained directly from wildlife biology publications or indirectly by inference from publications on closely related species of similar size.

3. That the amount of crown height lost per unit time on a deciduous tooth equals the initial unworn crown height divided by the time interval between age of eruption (usually birth) and age of replacement by a permanent tooth. The amount of crown height lost per unit time on a permanent tooth equals the initial unworn crown height divided by the time interval between age of eruption and age of potential ecological longevity. Initial unworn crown height may usually be estimated from unworn or lightly worn teeth occurring in any sample that is large enough to warrant mortality profile construction. In the author's experience, individual variability in unworn crown heights within a local population of a species tends to be very limited, so that the mean of a fossil sample is an adequate estimate, even if it is based on very few specimens.

Klein *et al.* (1981) showed that these assumptions lead to the following age-prediction formulae:

for a deciduous tooth:
AGE = AGEs—(AGEs/CHo) (CROWN HEIGHT)

for a permanent tooth:
AGE = AGEpel—((AGEpel—AGEe)/CHo) (CROWN HEIGHT)

where AGEs is the age at which a deciduous tooth is shed, AGEe is the age at which a permanent tooth erupts, AGEpel is the age past which no individuals appear to survive in the wild ('potential ecological longevity'), and CHo is initial (unworn) crown height.

Among the various assumptions perhaps the most questionable one is that the rate of crown attrition is constant throughout the life of a tooth. Various studies have suggested that wear is more rapid early in the life of a tooth than later on (see, for example, Grimsdell 1973 on extant Cape buffalo, or Kurtén 1953 and Voorhies 1969 on the fossil ungulate species whose age profiles are presented in Figure 5). Spinage (1971, 1972b, 1973) has pointed out that known changes in occlusal topography—roughest at the very beginning, smoothest near the end—imply that attrition will slow with age. Only in mid-life, when the topography tends to remain relatively constant, will attrition occur at a more or less constant rate. In order to accommodate a variable rate of wear of the kind

the changes in occlusal topography suggest, Spinage has proposed age estimation formulae that have the following form, when they are expressed using the terms above:

for a deciduous tooth:
AGE = AGEs ((CROWN HEIGHT—CHo)/CHo)^2
for a permanent tooth:
AGE = (AGEpel—AGEe) ((CROWN HEIGHT—CHo)/CHo)^2 + AGEe

In a study involving a relatively large sample (N = 170) of known-age wapiti (*Cervus elaphus canadensis*), Klein *et al.* (in press) found that Spinage's formulae do, in fact, provide more accurate age estimates from crown height than do the formulae based on a constant wear rate. Perhaps even more important, Spinage's formulae tend to underestimate true age about as often as they overestimate it, while the linear formulae mostly overestimate it. In the language of statistics Spinage's formulae are much less biased estimators. The important point is that they are more likely to produce a truly accurate age profile from a sample of crown heights, since overestimated ages would tend to be balanced out by underestimated ones.

The principal disadvantage of Spinage's formulae is that they are more cumbersome to calculate than those based on a constant wear rate. However, this is not a serious problem if a programable calculator or computer is available. An additional problem is that changes in the values assigned to the constants AGEs, AGEe, AGEpel, and CHo in Spinage's formulae have a greater effect on estimated ages than do comparable changes in the linear formulae. This means that the values of the constants must be selected as carefully as possible when Spinage's formulae are applied.

Whichever formulae are used, it is advisable to group the ages estimated from crown heights into classes that are at least as broad as the average error in age estimation. In virtually all instances, a class interval based on 10 per cent of potential ecological longevity will probably suffice. An important characteristic of such an interval is that age profiles based on it will be immediately comparable even among species with very different potential longevities.

In the case of species such as wapiti in which potential lifespan (AGEpel) is long relative to initial (unworn) crown height (CHo), both the linear and Spinage's formulae will produce quite similar age profiles, when the class interval is 10 per cent of potential lifespan, especially if the permanent tooth used to estimate age is one whose crown height is still measurably greater than '0' when potential longevity is approached. In most species, the tooth that meets this requirement best is the third molar (M3). In very hypsodont species such as equids in which potential lifespan is much shorter relative to initial (unworn) crown height, the linear formulae and Spinage's formulae may produce quite different age profiles, regardless of what tooth is used (Fig. 7). In the case of such species it is imperative that Spinage's formulae be used or the age profiles that result may be quite misleading.
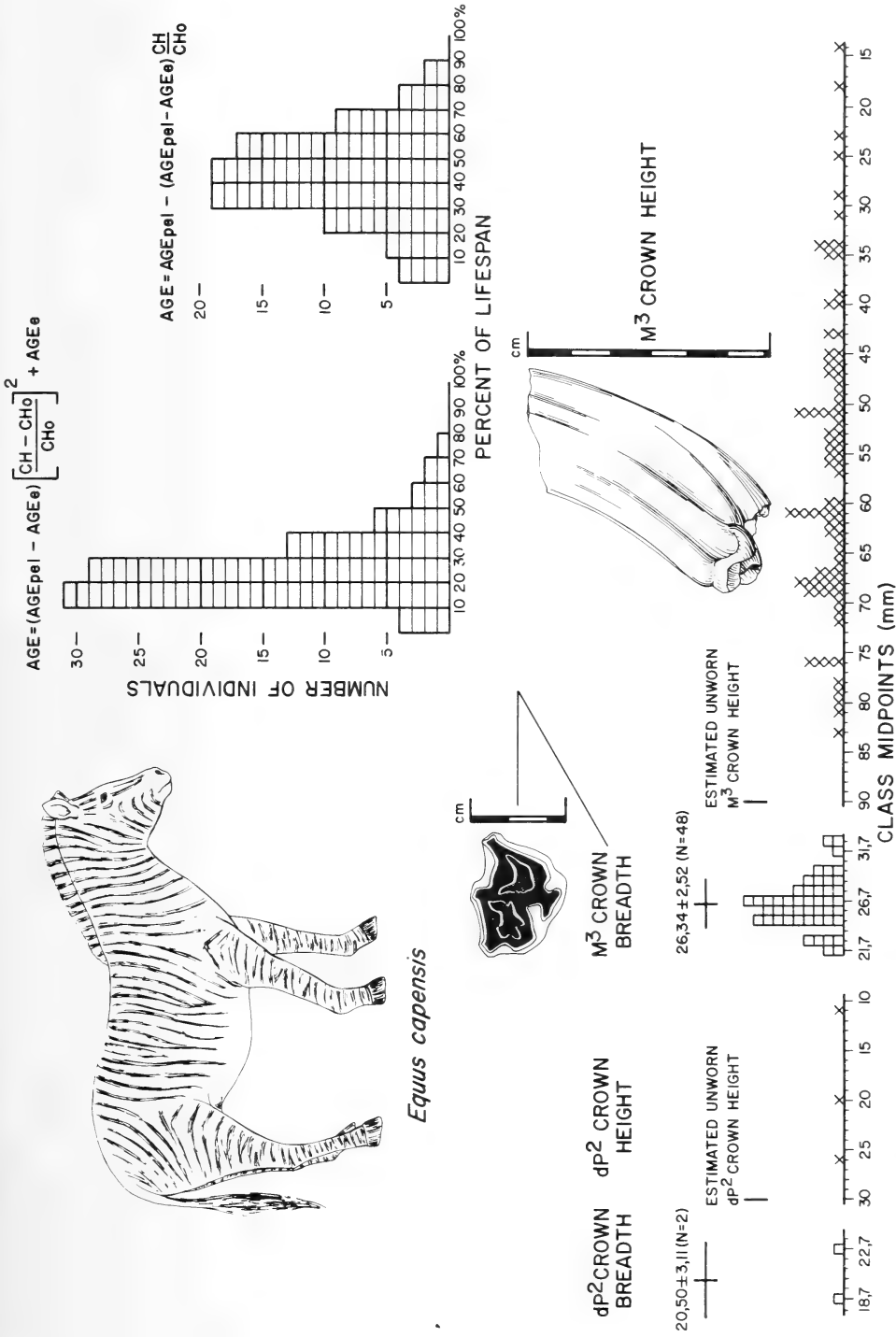
Fig. 7. Below: dP2 and M3 crown breadths and crown heights of *Equus capensis* from Elandsfontein. Above: Mortality (age) profiles derived from the crown heights using the quadratic formula suggested by Spinage (1972b) and a linear formula suggested by Klein *et al.* (1981). The different formulae will almost always produce very different profiles for a species such as *Equus capensis* in which the ratio of initial (unworn) crown height (CHo) to potential longevity (AGEpel) is high. For reasons discussed in the text, the profile provided by the quadratic equation is almost certainly the more accurate one.

All the age profiles presented below were calculated using Spinage's formulae. For the sake of consistency, some age profiles that were presented in a previous paper where the linear formulae were used (Klein 1981a), have been recalculated, even though their essential form remains the same, since the species involved were low-crowned relative to potential lifespan. All calculations were performed on an IBM Personal Computer.

THE LANGEBAANWEG FOSSIL SITE

Langebaanweg (32°58'S 18°9'E) is located approximately 110 km north-north-west of Cape Town (Fig. 8). Fossils were first reported from Langebaanweg in 1958 (Singer & Hooijer 1958; Singer 1961). In 1969 Q. B. Hendey of the South African Museum initiated a research programme at the site, which has led to a vast accumulation of vertebrate fossils belonging to more than 150
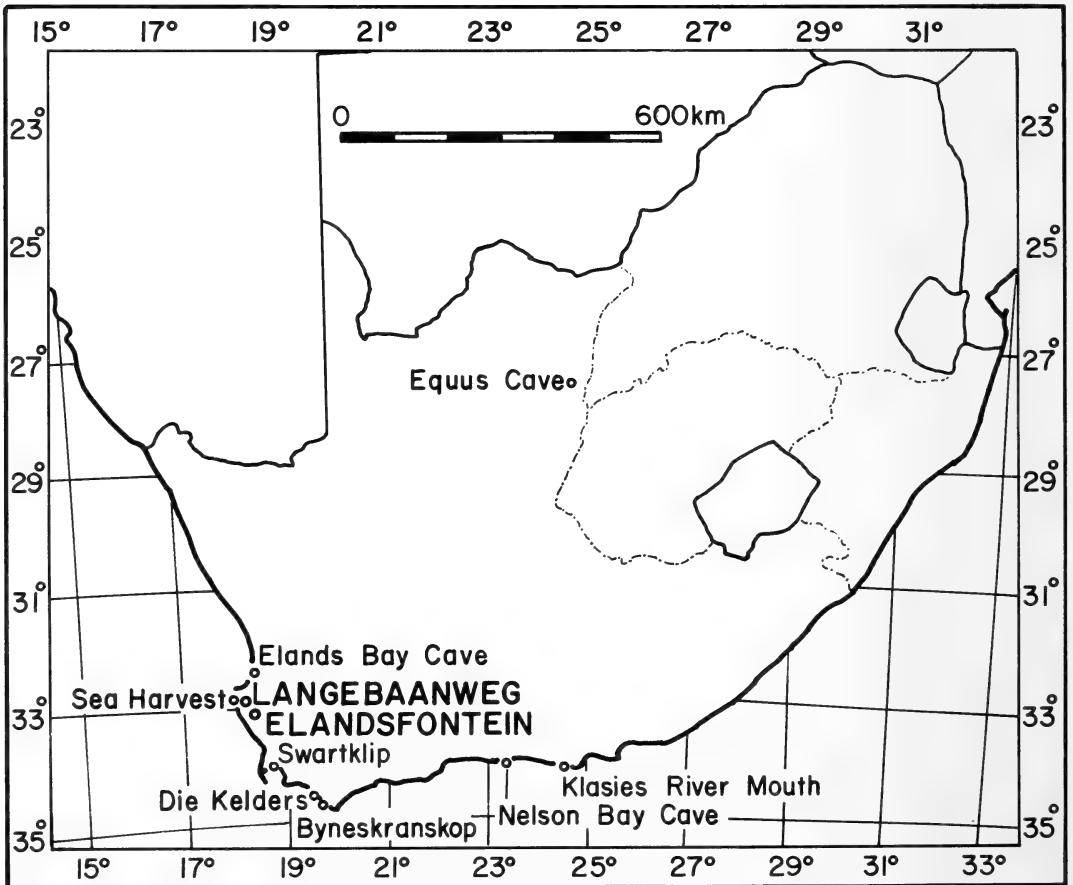
Map showing the approximate locations of sites mentioned in the text.

Fig. 8. The approximate locations of the sites mentioned in the text.

species, primarily mammals and birds. Publications on the site include numerous taxonomic and phylogenetic studies by Hendey and others, and overviews focusing on geologic context and palaeoecology (Hendey 1981a, 1981b, with references).

The overwhelming majority of Langebaanweg fossils, including all those considered here, come from the Quartzose Sand Member (QSM) (older) and Pelletal Phosphorite Member (PPM) (younger) of the Varswater Formation, as exposed in Langebaanweg 'E' Quarry. There are no materials suitable for chronometric dating, but Hendey's analysis of the Langebaanweg stratigraphic succession in relation to global sea-level and climatic events, together with the vertebrate taxa represented, indicate that the QSM and PPM both accumulated approximately 5 million years ago, or during the early Pliocene as this term is presently defined.

The QSM consists primarily of fine-grained, white quartz sands laid down on the estuarine floodplain of a river that probably entered the sea just to the south-west of 'E' Quarry. The PPM consists of relatively coarse well-sorted sands laid down primarily in the channel of the same river as its bed moved progressively northward. Within the PPM there are two distinct, especially fossiliferous channel fills, known as bed 3aS (further south) and bed 3aN (further north) respectively.

Essentially the same mammalian taxa occur in both the QSM and the PPM, but their mode of occurrence and their relative abundance differ dramatically between the two units. In the QSM partial, semi-articulated skeletons are common and abraded bones are rare. In the PPM partial, semi-articulated skeletons are rare and abraded bones are common. In the QSM several species are more or less equally represented, with no single species dominating overwhelmingly. In the PPM alcelaphine antelopes (*Damalacra acalla* and *D. neanica*) and giraffids (*Giraffa* sp. and especially *Sivatherium hendeyi*) are superabundant compared to all other species, the alcelaphines dominating particularly in bed 3aS and the giraffids in bed 3aN.

In an earlier paper Klein (1981a) showed that various species in the QSM are characterized by attritional mortality profiles, while the superabundant giraffids of bed 3aN are characterized by catastrophic profiles. Together with the sedimentary context and mode of fossil occurrence, the mortality profiles clearly suggest that individuals represented in the QSM died mainly of attritional factors such as predation, accidents and endemic disease. Subsequently, their skeletons were disarticulated and partially removed or destroyed by scavengers and other biological agents, but the bones probably lie very near the points of death. In contrast, the superabundant giraffids of bed 3aN probably died mainly by drowning during high floods, perhaps some distance from where the bones occur today, judging by the lack of articulated skeletons and the frequency of abrasion. In this paper the mortality profile analysis is extended to other QSM and PPM species, especially the alcelaphines of PPM beds 3aS and 3aN.

THE ELANDSFONTEIN FOSSIL SITE

Elandsfontein (= 'Saldanha' = 'Hopefield') (33°05'S 18°15'E) is located approximately 100 km north-north-west of Cape Town and roughly 10 km from Langebaanweg (Fig. 8). Covering an area of approximately 1,5 × 3 km, the site consists of a series of large barchan dunes separated by 'bays' in which deflation has exposed numerous mammalian fossils and occasional artefacts. Singer (1957) initiated scientific research, consisting mainly of surface collecting, at the site in 1951. Limited excavations were conducted in the early 1960s, most notably at the 'Cutting 10 Acheulean Site' (Singer & Wymer 1968; Klein 1978a). Except for occasional one-day status checks by staff of the South African Museum or the University of Stellenbosch, the site has been largely neglected since 1966. In 1981 G. and D. M. Avery of the South African Museum reinitiated scientific research at the site.

Most of the fossils found at Elandsfontein occur in or on a nodular calcareous duricrust that Butzer (1973) interprets as a subsoil manifestation of a former land-surface. It is possible that more than one such duricrust, and thus more than one former land-surface, are represented. Some fossils are also associated with a stratigraphically higher ferruginous duricrust, related to a somewhat more recent palaeo-surface. Finally, a small proportion of the fossils (including all those from the 'Bone Circle' of Inskeep & Hendey 1966) have been found in loose sands above the ferruginous duricrust. Butzer believes the Elandsfontein geologic sequence reflects climatic oscillations between wetter and drier during a large portion of the Middle and Upper Pleistocene.

The Elandsfontein fauna comprises one or two species of tortoise (Chelonia), a small number of bird species (most prominently ostrich, *Struthio camelus*), and more than fifty species of mammals (Hendey 1974), including 'Saldanha Man' represented by a skull cap and a mandible fragment found on the surface in 1953 (Drennan 1953, 1955; Singer 1954, 1958; Rightmire 1976). Unfortunately, most of the bones that are presently available for study were collected from the surface without any record of their position within the site or of their fossil associations, so it is impossible now to relate them to each other or to the geology. Still, on taxonomic grounds, it is clear that there are at least two faunal stratigraphic units represented, a Middle Pleistocene one and an Upper Pleistocene one (Hendey 1974; Klein 1978a). Mid-Pleistocene fossils, probably including the 'Saldanha Skull', predominate heavily.

The Middle Pleistocene fossils were probably all associated with the calcareous duricrusts, while the Upper Pleistocene ones probably came from the ferruginous crust or from the overlying loose sands. In keeping with the possibility of multiple calcareous crusts, the taxonomic composition of the Middle Pleistocene fauna suggests it may be a composite of faunas spanning a large portion of the Middle Pleistocene, as this is now commonly defined (from the beginning of the Brunhes Normal Palaeomagnetic Epoch, approximately 700 000 years ago, to the beginning of the Last Interglacial, approximately 130 000 years ago).

Although the contexts of most of the Elandsfontein bones presently available for study were not recorded, it is probable that they occurred in basically the same contexts as the numerous bones that have been exposed by deflation at the site since 1966, when compilation of the collection essentially ceased. At the site today clusters of bones clearly gnawed by porcupines are common (as are porcupine-gnawed specimens in the collected sample). Perhaps equally frequent are semi-articulated portions of skeletons, particularly crania, vertebrae, ribs, and distal extremities of a giant buffalo (*Pelorovis* sp.), which is perhaps the most abundant mammalian species at the site. In both the already collected and presently exposed samples, stone artefacts are relatively rare, as are bones unquestionably cut or bashed by artefacts. Hyena coprolites, and bones exhibiting damage from carnivore teeth are probably more common. The overall impression is that the site is a complex aggregation of occurrences—porcupine burrows, 'natural' deaths, hyena burrows, and occasional hominid camps or kills—all now resting on the same deflation surfaces. Animals were probably drawn to the locality by the availability of perennial surface water throughout much, if not all, of the Middle and Upper Pleistocene.

The ungulate mortality profiles presented in this paper represent the first attempt to determine whether the available Elandsfontein collections can be made to provide palaeoecological information, in spite of the less-than-ideal way in which they were compiled and the obvious complexity of the site.

THE LANGEBAANWEG AND ELANDSFONTEIN UNGULATE SAMPLES AND AGE PROFILES

Table 3 lists the Langebaanweg and Elandsfontein ungulate taxa whose mortality profiles are considered here. In order to be included, a taxon had to be represented by a minimum of ten individuals that could be aged from teeth. Table 3 also presents the dental eruption and wear parameters (AGEe, AGEs, and AGEpel) that were used to calculate individual ages from crown heights. The initial (unworn) crown heights (CHo) used are presented in Table 4.

A complication in the Langebaanweg samples is that teeth cannot always be identified to species. Thus, while it is clear that two species of *Damalacra* are represented by horn-cores (Gentry 1980), the species cannot be readily separated even on complete dentitions. Similarly, although most of the teeth assigned to *Giraffa* sp. probably come from a single species, some probably derive from a dentally very similar species of palaeotragine, which is represented at Langebaanweg by occasional limb bones and ossicones (Hendey 1981a). Finally, although most of the *Nyanzachoerus* teeth probably come from a single species (*N.* cf. *pattersoni*), some (in the PPM) probably come from a dentally very similar second species (*N.* cf. *jaegeri*) (Hendey 1981a).

The choice was then either to exclude the *Damalacra*, *Giraffa* and *Nyanzachoerus* samples from consideration or to analyse them as if only one species were represented in each case. The second alternative was chosen, since it

TABLE 3

The ages of dental eruption (AGEe), shedding (AGEs), and potential ecological longevity (AGEpel) used to calculate age from crown height in the Langebaanweg and Elandsfontein ungulate samples considered in this paper. For extinct species, ages were inferred from published ages for closely related extant species. Where extinct species differed in size from their extant counterparts, the ages for the extinct species were adjusted by a factor reflecting the size difference. All quoted ages are in years.

Sources on pertinent ages in the extant species are: black rhinoceros (*Diceros bicornis*)—Goddard (1970); Burchell's zebra (*Equus burchelli*)—Klingel (1965), Klingel & Klingel (1966), Smuts (1974); mountain zebra (*Equus zebra*)—Joubert (1972); giraffe (*Giraffa camelopardalis*)—Hall-Martin (1976); bush-pig (*Potamochoerus porcus*)—Sowls & Phelps (1968); Cape buffalo (*Syncerus caffer*)—Grimsdell (1973), Sinclair (1977); greater kudu (*Tragelaphus strepsiceros*)—Simpson (1966); Lichtenstein's hartebeest (*Alcelaphus lichtensteini*)—Mitchell (1965); tsessebe (*Damaliscus lunatus*)—Huntley (1973); black wildebeest (*Connochaetes gnou*)—Von Richter (1971, 1974); eland (*Taurotragus oryx*)—Kerr & Roth (1970); and Cape grysbok (*Raphicerus melanotis*)—Manson (1974), and personal observation. Mentis (1972) was consulted for estimates of potential ecological longevity in all relevant extant species.

LANGEBAANWEG

	dP$\overline{4}$		P$\overline{4}$		
	AGEe	AGEs	AGEe	AGEpel	Source
Ceratotherium praecox	0	6	6	35	Inference from dentally very similar black rhinoceros.

	dP$\overline{2}$		P$\overline{2}$		
	AGEe	AGEs	AGEe	AGEpel	
Hipparion cf. *baardi*	0	3	3	20	Assumption that *H.* cf. *baardi* parameters would be roughly 10 % smaller than those for Burchell's zebra and mountain zebra.

	dP4		M3		
	AGEe	AGEs	AGEe	AGEpel	
Giraffa sp.	0	4,5	3,5	28	Inference from dentally very similar modern giraffe.
Sivatherium hendeyi	0	6	4,67	37,24	Assumption that *S. hendeyi* parameters would be roughly 33 % larger than those of modern giraffe.
Mesembriportax acrae	0	2,5	2	18	Inference from extant bovids of similar size, such as greater kudu, Lichtenstein's hartebeest, and black wildebeest.
Simatherium demissum	0	3,0	2,5	20	Assumption that *S. demissum* parameters would be roughly 25 % smaller than those of Cape buffalo.
Damalacra spp.	0	2,5	2	18	Inference from extant bovids of similar size, such as greater kudu, Lichtenstein's hartebeest, tsessebe, and black wildebeest.
Nyanzachoerus sp(p).	0	2,5	2	18	Assumption that *Nyanzachoerus* parameters would be roughly 20 % greater than those for bush-pig.

ELANDSFONTEIN

	dP$\overline{2}$		M$\overline{3}$		
	AGEe	AGEs	AGEe	AGEpel	Source
Equus capensis	0	3,6	3,6	26,4	Assumption that *E. capensis* parameters would be roughly 20% larger than those for Burchell's zebra and mountain zebra.

	dP4		M3		
	AGEe	AGEs	AGEe	AGEpel	
Pelorovis sp.	0	4,35	3,28	26,4	Assumption that *Pelorovis* parameters would be roughly 10% greater than those for Cape buffalo.
Taurotragus oryx	0	3,6	2,5	20	Data on modern eland.
Hippotragus gigas	0	4	3	24	Assumption that *H. gigas* parameters would be similar to those of Cape buffalo.

	dP4		M1		
	AGEe	AGEs	AGEe	AGEpel	
Raphicerus sp.	0	1,25	0,25	6	Inference from closely related Cape grysbok.

seemed unlikely that mixed samples would produce interpretable age profiles unless one member of a pair heavily dominated a sample or both members were, in fact, characterized by the same profile shape to begin with.

In order to obtain a complete age (mortality) profile for each taxon, it was necessary to make crown height measurements on a deciduous tooth and on a permanent one that erupted before the deciduous tooth was shed. For each taxon, the choice of an appropriate deciduous-permanent pair was determined by:

 (i) the abundance of various teeth (probably dictated mainly by relative durability; for example, in most species, mandibular teeth are more durable than maxillary ones, and molars are more durable than premolars);

 (ii) the extent to which it was possible to determine the former place in the mouth of an isolated tooth (for example, in most species, isolated M1's are difficult to tell from M2's from the same jaw, while isolated M3's are immediately recognizable);

(iii) the ease of measurement (particularly important in the case of a species represented by a number of teeth still mounted in jaws; in such an instance the base of the crown of a late-erupted tooth (e.g. M3) will often be masked by jaw-bone, and crown height can be measured only on a tooth (e.g. M1) that entered occlusion considerably earlier).

The crown heights and age profiles (calculated by the linear formulae) for Langebaanweg *Sivatherium hendeyi* (bed 3aN), *Giraffa* sp. (and palaeotragine) (bed 3aN), *Ceratotherium praecox* (QSM), *Mesembriportax acrae* (QSM and bed 3aN), and *Simatherium demissum* (bed 3aN) were presented in an earlier paper (Klein 1981*a*). The age profiles alone, recalculated using the quadratic

TABLE 4

The initial (unworn) crown heights (in mm) used to calculate the age profiles of the Langebaan-
weg and Elandsfontein ungulate species considered in this paper.

	$\overline{\text{dP4}}$	$\overline{\text{P4}}$
Ceratotherium praecox	45,0	65,1
	$\overline{\text{dP2}}$	$\overline{\text{P2}}$
Hipparion cf. *baardi*	25,0	60,0
	$\overline{\text{dP2}}$	$\overline{\text{M3}}$
Equus capensis	30,0	90,0
	d$\underline{\text{P4}}$	$\underline{\text{M1}}$
Raphicerus sp.	5,4	10,6
	d$\underline{\text{P4}}$	$\underline{\text{M3}}$
Giraffa sp.	16,3	27,8
Sivatherium hendeyi	23,4	45,1
Nyanzachoerus sp(p).	—*	45,1
Damalacra spp.	15,0	39,6
Mesembriportax acrae	10,0	33,0
Simatherium demissum	16,3	36,0
Pelorovis sp.	22,7	71,5
Hippotragus gigas	23,9	54,7
Taurotragus oryx	19,0	44,8

* No specimens

formulae, are presented here in Figure 15. The crown heights and age profiles (calculated by the quadratric formulae) for Langebaanweg *Damalacra* spp. (beds 3aS and 3aN), *Nyanzachoerus* sp(p). (QSM and PPM) and *Hipparion* cf. *baardi* (QSM and PPM), and for Elandsfontein *Equus capensis*, *Hippotragus gigas*, *Taurotragus oryx*, *Raphicerus* sp., and *Pelorovis* sp. are presented here in Figure 7 and Figures 9–13. Figure 14 presents a recasting of the Langebaanweg *C. praecox* crown heights and age profile, based on a somewhat larger sample than in the earlier paper (and with the age profile calculated by the quadratic formulae).

The various Figures also illustrate the crown height dimension that was measured in each case. In general, this dimension was the minimum distance between the occlusal surface of a tooth and the line separating the enamel of the crown from the dentine of the roots, measured on the buccal surface of mandibular teeth and on the lingual surface of maxillary ones. On multilobed (or multilophed) teeth the measurement was made on the first (anteriormost) lobe (or loph), except in samples specifically noted in the Figures, where it was necessary to measure the second lobe because the first one was so often damaged or missing.

Finally, the Figures present and illustrate crown breadth measurements for each taxon. These were analysed for excessive variability and for deviations from statistical normality that may indicate the underlying samples were mixed or heterogeneous. In no instance was a significant departure from normality detectable. This is a particularly important finding in the case of these dental samples—especially the large one of *Damalacra* from Langebaanweg—that probably or certainly derive from two closely related species. If the crown

Fig. 9. dP4 and M3 crown breadths and crown heights of *Taurotragus oryx* and *Hippotragus gigas* from Elandsfontein, and the age (mortality) profiles calculated from the crown heights.
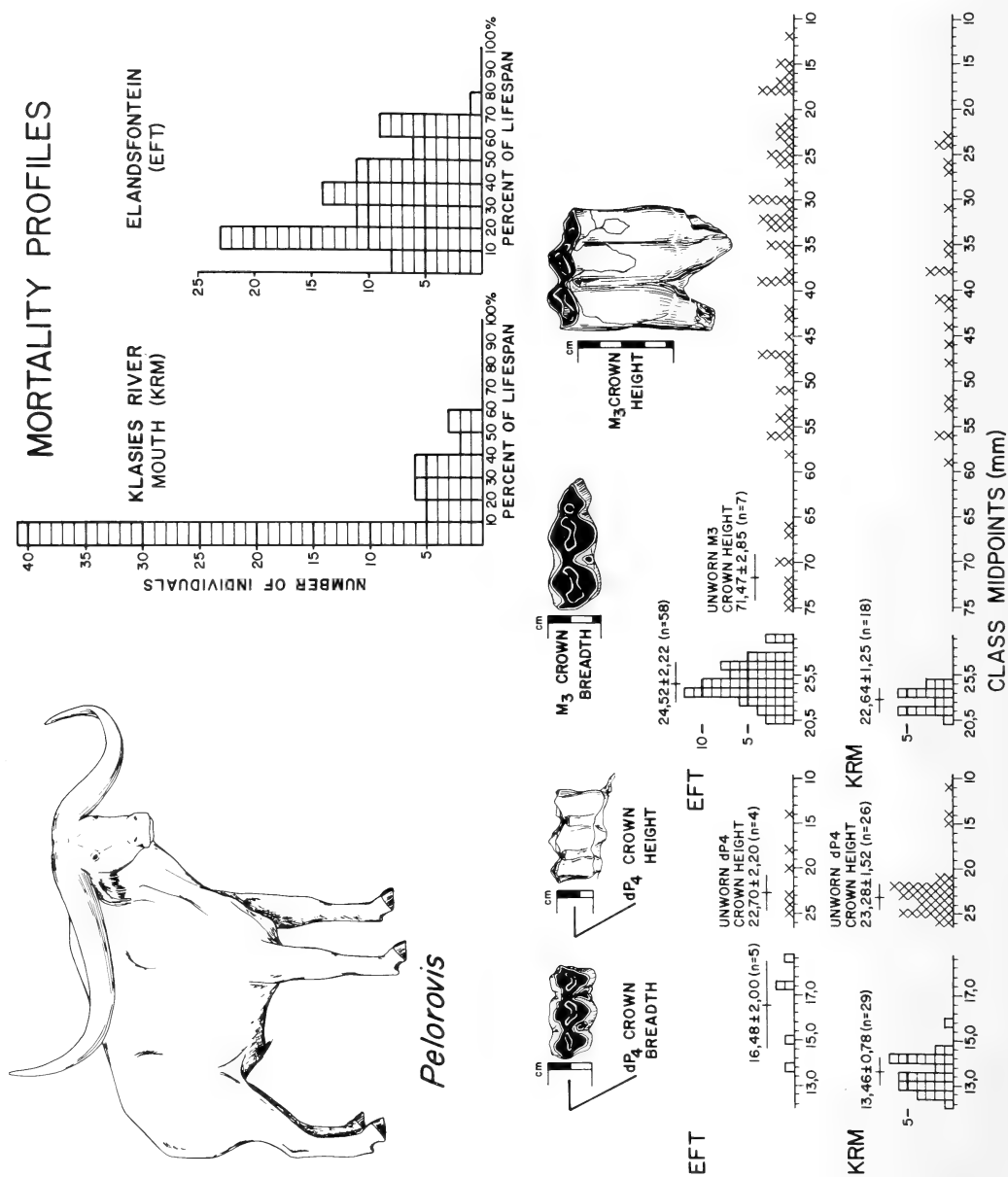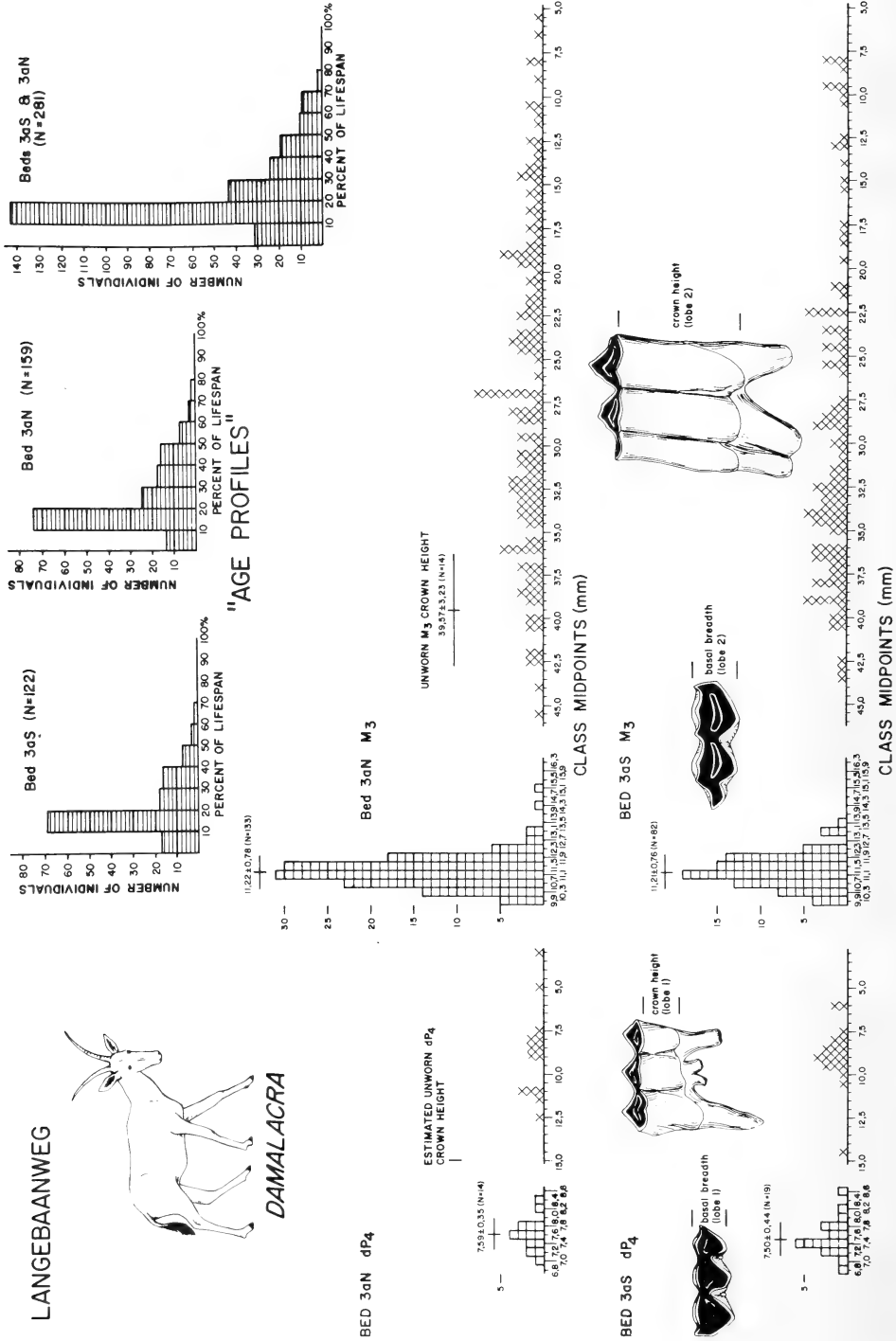
Fig. 10. dP4 and M3 crown breadths and crown heights of *Pelorovis* from Elandsfontein and Klasies River Mouth Cave 1, and the age (mortality) profiles calculated from the crown heights. The much greater abundance of very young individuals (in the first 10% of lifespan) in the Klasies River profile suggests that the Klasies River Stone Age people actively hunted *Pelorovis*, for reasons discussed in the text.
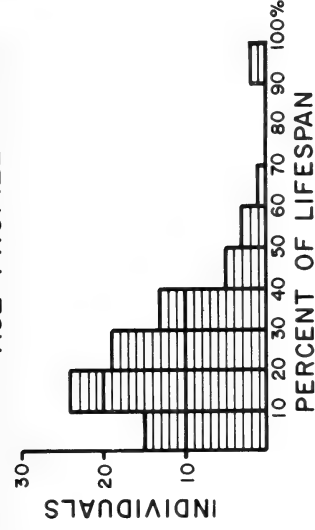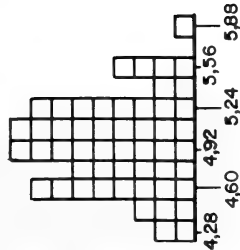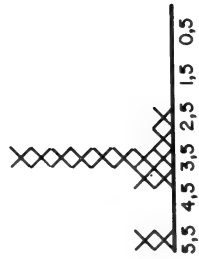
Fig. 11. dP4 and M1 crown breadths and crown heights of *Raphicerus* sp. from Elandsfontein, and the age (mortality) profile calculated from the crown heights.
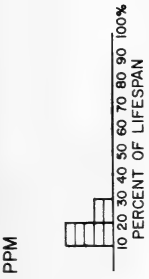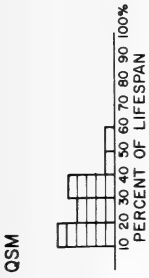
Fig. 12. dP4 and M3 crown breadths and crown heights of *Damalacra* spp. from Beds 3aS and 3aN at Langebaanweg, and the age (mortality) profiles calculated from the crown heights.
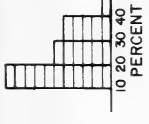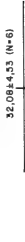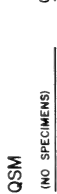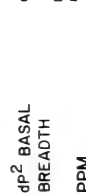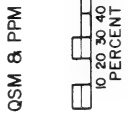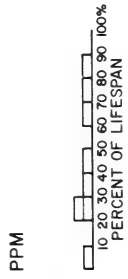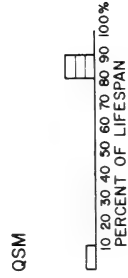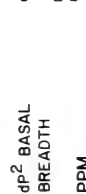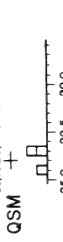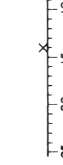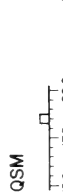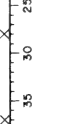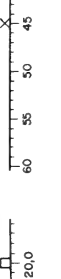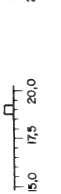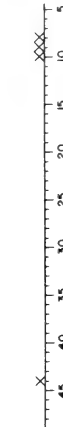
Fig. 13. Above: dP4 and M3 crown breadths and crown heights of *Nyanzachoerus* from Langebaanweg, and the age (mortality) profiles calculated from the crown heights. Below: dP2 and P2 crown breadths and crown heights of *Hipparion* from Langebaanweg, and the age (mortality) profiles calculated from the crown heights.

METACARPAL III

cm

minimum
breadth

54,49±2,96 (n=70)

'Sex Profile'

10 —

specimens

5 —

48,5 | 50,5 | 52,5 | 54,5 | 56,5 | 58,5 | 60,5 |
   49,5 51,5 53,5 55,5 57,5 59,5 61,5
        class midpoints (mm)

'AGE PROFILE'

25

NUMBER OF INDIVIDUALS

20

15

10

5

10 20 30 40 50 60 70 80 90 100%
        PERCENT OF LIFESPAN

cm

basal breadth

P4

cm

crown
height

70,42±3.05 (n=47)

10 —

specimens

5 —

65   70   75
  class midpoints (mm)

estimated unworn
crown height
|

65   60   55   50   45   40 — 35   30   25   20   15
                        class midpoints (mm)

cm

basal breadth

dP4

cm

crown
height

Ceratotherium praecox

57,74±2,96 (n=13)

5 —

specimens

55   60   65
  class midpoints (mm)

estimated unworn
crown height
|

45   40   35   30   25   20   15
        class midpoints (mm)

LANGEBAANWEG

Fig. 14. Below: dP$\overline{4}$ and P$\overline{4}$ crown heights and crown breadths of *Ceratotherium praecox* from Langebaanweg. Above right: the age (mortality) profile calculated from the crown heights. Above left: the distribution of measurements of the minimum mediolateral diameter ('minimum breadth') of the third metacarpal of *Ceratotherium praecox* from Langebaanweg. The two modes probably represent the sexes, as discussed in the text.

breadth distribution had departed significantly from normality, then the use of a single set of constants to calculate ages from crown heights in the mixed samples would be open to serious question.

All crown heights and breadths were measured to the nearest tenth of a millimetre with a single pair of Helios dial-reading calipers.

INTERPRETATION OF THE LANGEBAANWEG AND ELANDSFONTEIN AGE PROFILES

Figure 15 presents the Langebaanweg and Elandsfontein age profiles in directly comparable summary form. With the exception of females in *Nyanza-choerus* (Langebaanweg) and *Raphicerus* (Elandsfontein), females in all the taxa involved probably had no more than one young per year, based on observations of their living representatives or of their closest living relatives. With the exceptions of *Nyanzachoerus* and *Raphicerus* then, all the taxa were probably characterized by catastrophic ('lx') and attritional ('dx') profiles that were very different in form. More specifically, each species would have a catastrophic profile in which successively older age classes contained progressively fewer individuals. It would have an attritional age profile that was either U-shaped, with a large mode in the youngest class and a second smaller one in an age class beyond 40 per cent of potential lifespan, or possibly L-shaped, with a large mode in the youngest age class and no obvious modes thereafter.

From Figure 15, it is apparent that the relevant profiles do separate fairly clearly between the expected attritional and catastrophic types. Thus, the profiles for Langebaanweg *Ceratotherium praecox* (QSM), *Mesembriportax acrae* (QSM), *Simatherium demissum* (bed 3aN), and *Hipparion* cf. *baardi* (QSM and PPM composite) are all basically attritional, while those for Langebaanweg *Sivatherium hendeyi* (bed 3aN), *Giraffa* sp. (bed 3aN), and *Damalacra* spp. (beds 3aS and 3aN), and for Elandsfontein *Equus capensis*, *Hippotragus gigas*, and *Taurotragus oryx* are all basically catastrophic.

A problem arises with respect to the profiles of Langebaanweg *Mesembriportax acrae* (PPM 3aN) and Elandsfontein *Pelorovis* sp., which could be interpreted as either catastrophic or L-shaped attritional. Since the *Pelorovis* profile is based on a relatively large sample and since its form contrasts with the clearly catastrophic form of the profile for *Equus capensis*, based on a sample of similar size, it seems most likely that the *Pelorovis* profile is attritional or perhaps mixed attritional-catastrophic. There is also a problem with regard to the Langebaanweg *Hipparion* cf. *baardi* profile, which contains enough individuals for consideration only when material from two very different sedimentary units is lumped. Although its form appears clearly attritional, it will be ignored in what follows.

The profiles that appear to be clearly attritional are not completely identical to each other, nor are those that appear to be clearly catastrophic. Some of the differences are probably due to chance ('sampling error'), particu-
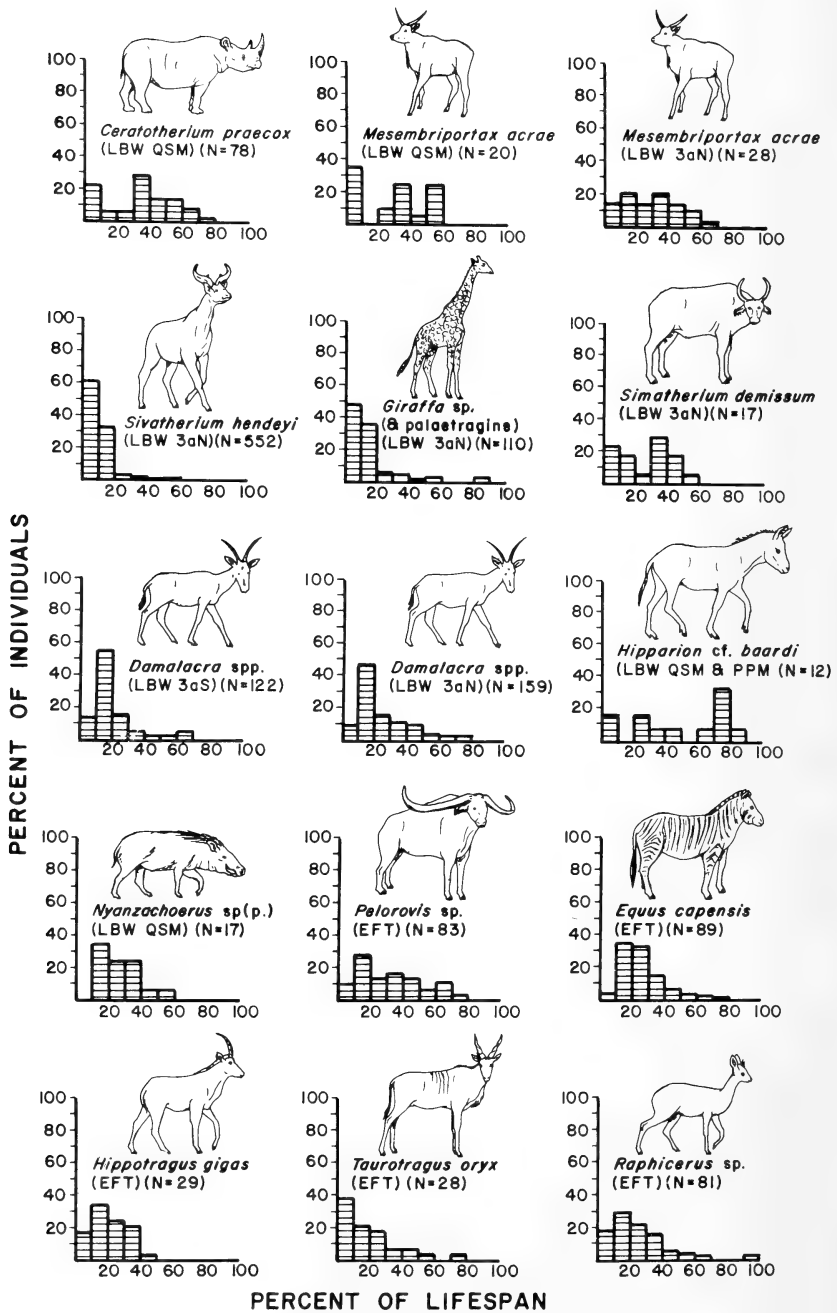
Fig. 15. Age (mortality) profiles of all the Langebaanweg and Elandsfontein ungulate species discussed in the text.

larly likely to affect some of the smaller samples. Other differences are probably due to errors in the constants used in the age estimation formulae. Such errors are almost certainly too small to affect overall profile shape, but could well affect the precise content of particular age classes.

Neither chance nor the constants used in the formulae, however, can explain the fact that all the profiles except the ones for *Sivatherium hendeyi* and *Giraffa* sp. (and palaeotragine) contain many fewer very young individuals (in the first 10% of lifespan) than would be expected in either a catastrophic or an attritional age profile. At both Langebaanweg and Elandsfontein bone preservation is good to excellent, so that selective post-depositional destruction of very young (relatively fragile) jaws and teeth is probably not the reason for their frequent underrepresentation. Much more likely is pre-depositional destruction or removal, primarily by scavengers.

It was pointed out above that selective destruction or removal of the bones of very young individuals almost certainly accounts for their underrepresentation in mortality profiles based on jaws collected recently by wildlife biologists. The smaller the species, the greater the underrepresentation, which probably accounts for the fact that very young individuals are so poorly represented in *Damalacra* spp. as against their abundance in the giraffids, though in both cases, the basic mortality pattern is catastrophic. In order to avoid confrontations with other scavengers attracted to catastrophic death sites, individual scavengers probably often carried off the carcasses of very young *Damalacra*, but had to feed in place on the much larger (and relatively less fragile) carcasses of very young giraffids.

The catastrophic age profiles for *Sivatherium*, *Giraffa*, and *Damalacra* from the Langebaanweg PPM (beds 3aS and 3aN) suggest that death occurred by drowning during peak or flash flooding. This suggests in turn that *Damalacra* and the giraffids are so much more abundant than other species in the PPM channel fills because their feeding habits tied them to the ancient river even during those periods (?seasons) when increased precipitation meant that surface water and green vegetation were widespread. For the giraffids, the river margins might have been fatally attractive because the trees or high bush on which they fed were restricted to this environment. For *Damalacra* spp. the attraction might have been floodplain meadows or the ecotone between riverine forest and fringing grassland, habitats clearly favoured today by their close living relative the tsessebe (*Damaliscus lunatus*) (Smithers 1971; Child *et al.* 1972).

Hendey (1981*a*) has suggested that between the deposition of bed 3aS (earlier) and bed 3aN (later), grassland increased at the expense of bush and forest in the ancient Langebaanweg environment. By 3aN times bush and forest might have been all but absent away from the river margins. This could account for the remarkable increase in giraffids compared to *Damalacra* in the bed 3aN (compared to 3aS) channel fill. The nutritional stress that habitat reduction induced in the bed 3aN sivatheres may explain the hypoplasia that is sometimes obvious in their dental enamel (Hendey 1981*a*).

The attritional profiles of *Ceratotherium praecox* and *Mesembriportax acrae* from the Langebaanweg QSM suggest that death occurred mainly as a result of predation, disease, starvation and other attritional factors, in keeping with a mode of bone occurrence and sedimentary context that imply subaerial death very near the places where the bones lie. The attritional profiles of *Simatherium demissum* and possibly of *Mesembriportax acrae* from the Langebaanweg PPM channel fills are more difficult to understand. Given the rarity of these species in the PPM, it is possible their bones were either swept by the river from the adjacent floodplain or reworked from deposits of a more ancient floodplain on which attritional mortality was the rule. It is further possible that the ambiguous, neither clearly catastrophic nor clearly attritional, shape of the PPM 3aN *M. acrae* profile reflects a mixture of catastrophic mortality by drowning and attritional mortality on the adjacent floodplain.

The probably attritional shape of the *Pelorovis* age profile from Elandsfontein is in keeping with the fact that this species is commonly represented by semi-articulated skeletons scattered across the ancient land-surface(s) now exposed by deflation at the site. It is not difficult to imagine that *Pelorovis* deaths were due mainly to attritional factors at or near the ancient waterholes that probably led to concentrations of animals at Elandsfontein.

Whatever the precise causes of *Pelorovis* mortality at Elandsfontein, the rarity of very young individuals is interesting in so far as these are well represented in an attritional profile of *Pelorovis* from the Middle Stone Age (early Upper Pleistocene) archaeological site of Klasies River Mouth (Klein 1978*b*) (Fig. 10 here). Since the rarity of very young *Pelorovis* at Elandsfontein probably reflects pre-depositional destruction or removal by carnivores and scavengers, their abundance in an archaeological site implies either that people were able to locate the carcasses of very young individuals before other predators or that they actively hunted the very young. A priori, the second alternative seems more likely.

With the *Pelorovis* profile in mind, it is puzzling that the other relatively abundant large ungulates at the site—*Equus capensis*, *Hippotragus gigas*, and *Taurotragus oryx*—are characterized by catastrophic rather than attritional profiles. In the case of *H. gigas* and *T. oryx* it is possible that larger samples would turn what now appear to be catastrophic profiles into L-shaped attritional ones, but the *Equus capensis* sample is clearly too large to suppose that even a substantial increase in size would transform what is an almost classic catastrophic profile into an attritional one.

At Elandsfontein today, the bones of *Equus capensis* (and of most other species) appear to occur differently than do *Pelorovis* bones, with fewer instances of semi-articulated skeletons. This may reflect the fact that *E. capensis* (and most other species) lacked the massive skulls and vertebral columns of *Pelorovis* sp., so that semi-articulated *E. capensis* skeletons are both less likely to occur and less likely to be noticed, or it may mean that the *E. capensis* bones are coming mainly from deflated porcupine or carnivore lairs.

An indeterminate, albeit smaller, proportion of the *Pelorovis* bones may also come from such lairs, adding a pseudo-catastrophic overlay to an otherwise essentially attritional profile. Skeletal element counts from the fossil carnivore (probable hyena) lairs at Swartklip and elsewhere in southern Africa show size or weight sorting of large ungulate bones that may bias age profiles based only on teeth towards the catastrophic side (Klein 1975, and unpublished).

As a final alternative, it is possible that the *E. capensis* bones derive mainly from predation by a creature that had the ability to kill individuals of all ages in roughly their live proportions. Further speculation on this would be fruitless, and perhaps the major point to be made is that the interpretative potential of mortality profile analysis is obviously dependent upon the availability of good contextual information.

With respect to the *Nyanzachoerus* profile (Langebaanweg QSM) and the *Raphicerus* profile (Elandsfontein), sample profile shape alone is inadequate for determining whether death was largely attritional or catastrophic. This is because female *Nyanzachoerus* probably had litters of two or more, as have extant African suids (Mentis 1972). Extant *Raphicerus* females generally bear just one young at a time, but are fully capable of producing two surviving young per year (Mentis 1972). Given this reproductive potential, high rates of mortality in the fossil populations of *Nyanzachoerus* and *Raphicerus* could well have continued into young adult age classes, leading to catastrophic and attritional profiles that would both have the down-staircase form of catastrophic mortality in a species where females have a much lower reproductive rate.

Figure 15 shows that the *Nyanzachoerus* and *Raphicerus* profiles both exhibit down-staircase shapes. Since the *Nyanzachoerus* material was drawn from a sedimentary unit (Langebaanweg QSM) in which context and the mortality profiles of other species imply that attritional mortality was the rule, it seems most likely that the *Nyanzachoerus* profile, in fact, reflects attritional mortality in a species that regularly bore two young or more at a time.

It is more difficult to argue that attritional mortality is probably reflected in the Elandsfontein *Raphicerus* profile, because it is unclear from modern observations whether female *Raphicerus* do commonly produce two young per year. The problem is that *Raphicerus* spp. (grysbok and steenbok) are solitary, secretive, and inconspicuous, in short, difficult to observe systematically. It is pertinent, however, that *Raphicerus* mortality profiles from a wide variety of southern African sites, including both archaeological ones (Die Kelders, Nelson Bay, Klasies River Mouth, and others) and carnivore (probable hyena) ones (Swartklip, Sea Harvest, and others), all display the same down-staircase shape as the Elandsfontein profile (Klein 1981*b*) (Fig. 16 here). None of the profiles displays the classic U- or L-shape that would reflect attritional mortality in a species characterized by a birth rate of one young (or less) per female per year.

The essential similarity in form of the *Raphicerus* profiles from such a wide variety of contexts, where both attritional and catastrophic mortality are probably represented, strongly suggests that *Raphicerus* populations are,
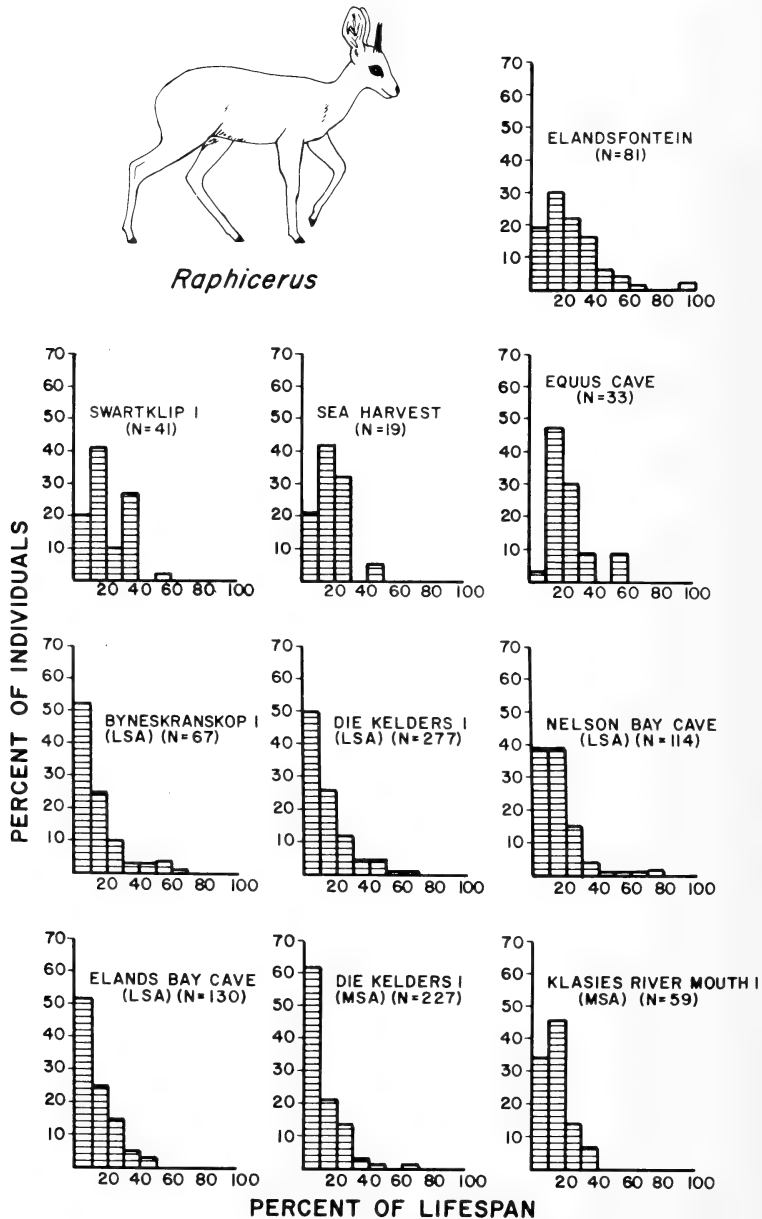
Fig. 16. Age (mortality) profiles of *Raphicerus* from Elandsfontein and from the fossil carnivore (probable hyena) lairs at Swartklip, Sea Harvest, and Equus Cave, the Middle Stone Age levels of Die Kelders Cave 1 and Klasies River Mouth Cave 1, and the Late Stone Age levels of Byneskranskop Cave 1, Nelson Bay Cave, Elands Bay Cave, and Die Kelders Cave 1. Very young individuals are probably underrepresented in several of the profiles because of the relative fragility of their jaws and teeth. Keeping this fact in mind, the profiles all display a general tendency for successively older age classes to contain progressively fewer individuals. Since some (?most) of the profiles are probably attritional, while others may be catastrophic, the implication is that *Raphicerus* females commonly bear more than one young per year, as discussed in the text.

indeed, ones in which catastrophic and attritional profiles do not contrast notably in form. This would be the case only if female *Raphicerus* regularly produce two young per year. The *Raphicerus* example points up the fact that age profiles based on fossil samples may be used to draw basic biological inferences—in this case, the common rate of reproduction—that may be difficult to determine from observations of live populations.

SEASON OF BONE ACCUMULATION AT LANGEBAANWEG AND ELANDSFONTEIN

It was pointed out above that individuals from a fossil population in which both birth and death were seasonally restricted events would fall into discrete age classes or clusters, each separated from the next by an age gap in which no individuals occur. Kurtén (1953) was probably the first to point out that crown heights of a tooth drawn from a population with a discontinuous age distribution may also form clusters or modes, each cluster representing a group of individuals born at about the same time. In his study of the same north Chinese ungulates discussed above (age profiles in Figure 5), he believed he could detect crown height modes reflecting seasonal birth or death, the latter probably by flooding (drowning).

In his study of the extinct pronghorn antelope, *Merycodus furcatus*, Voorhies (1969) also found crown height multimodality. It is more convincing than in Kurtén's samples, since Voorhies's sample was so much larger. Variably convincing crown height multimodality, taken as evidence for seasonal birth and death, has also been reported for *Bison* spp. from several archaeological sites in the western United States (Frison 1978*b*, with references).

Both the crown height distributions and the distributions of estimated individual ages (ungrouped) of all the ungulate samples reported here were examined for multimodality that would reflect seasonal birth and death. The possibility of finding such multimodality seemed particularly good for the giraffids and *Damalacra* spp. from the Langebaanweg PPM channel fills, both because the flooding that was the probable cause of death might well have been seasonal and because the dental samples involved are quite large. However, a convincing pattern of multimodality was not found.

For the giraffids, the problem may be that, like their close living relative, *Giraffa camelopardalis* (Mentis 1972; Foster & Dagg 1972), they bore their young more or less throughout the year, without clear seasonal peaks. Additionally, giraffid teeth are low crowned relative to potential individual lifespan, so that crown height modes, even if they existed, would be very close together and difficult to detect, except in truly enormous samples. In this context it is pertinent that Klein *et al.* (1981) failed to find convincing crown height multimodality in a large sample of wapiti with a similarly low crown height to lifespan ratio, though seasonal birth and death in the wapiti population was historically documented.

It is also possible that *Damalacra* spp. were not seasonal breeders, though their closest living relatives, various alcelaphine antelopes, generally are (Mentis 1972). Furthermore, individuals of *Damalacra* spp. had much higher crowns and shorter potential lifespans than the giraffids. Perhaps the reason the *Damalacra* samples fail to exhibit clear multimodality is that they comprise two species, each with a somewhat different birth season or perhaps somewhat different initial crown heights and eruption schedules.

In sum, it remains possible that bones did accumulate in the Langebaanweg PPM channel fills seasonally, but it will take either larger samples, or more homogeneous ones, or both to show this from crown heights.

SEX RATIOS IN THE FOSSIL SAMPLES

Although ungulate species usually exhibit sexual dimorphism in bone morphology or size, or both, there are serious practical obstacles to estimating the sex ratio in most fossil samples. The principal problem is that the skeletal parts that reflect sex the best are generally not very durable, and they are often less durable in one sex than in the other. In bovids, for example, the skeletal part from which sex can be most readily determined is the frontlet or part of the skull that bears the horns. In most species female frontlets either lack horns or exhibit ones that are quite different in size or shape from male horns. The problem is that frontlets are among the least durable parts of the skeleton, and the pre- and post-depositional destructive pressures that have affected most fossil samples remove frontlets selectively. Thus in most samples they are too rare for the reliable estimation of a sex ratio. Additionally, male frontlets tend to be more robust than female ones, so that even when the number of frontlets is large enough to estimate a sex ratio, there is a likely bias in favour of males.

In the present context the relative fragility of frontlets, particularly female ones, almost certainly accounts for the fact that frontlets are much less common than other bovid skeletal elements (particularly jaws and teeth) at both Langebaanweg and Elandsfontein, while male frontlets clearly predominate.

In equids the skeletal parts from which sex can be most readily determined are the anterior portions of the jaws, which usually bear large canines in males and very small ('vestigial') canines or none in females. Unfortunately, the relevant parts of equid jaws are not very durable, while in females they are even less durable due to the lack of large canines. Again, in the fossil equid samples considered here, the relevant parts of the jaws are relatively rare and male specimens dominate heavily.

An alternative and, in general, less biased way to estimate the sex ratio derives from the fact that in most species, probably including all those considered here, bones of males are larger on average than their homologues in females (Boessneck & Von den Driesch 1978, with references). The search for size bimodality reflecting sex must generally be limited to bones on which the epiphyses are fused, or modes reflecting the sexes may be confounded with

ones reflecting different age groups. In any case, bones on which the epiphyses are unfused tend to be rare in many fossil samples, probably because of their relative fragility. In general, among bones with fused epiphyses, the most fruitful ones to scrutinize for size bimodality are those that bear weight, since they will probably reflect larger male size most strongly.

With regard to the samples considered here, three—those of *Ceratotherium praecox* from Langebaanweg and of *Equus capensis* and *Pelorovis* sp. from Elandsfontein—contain a sufficient number of mature, weight-bearing bones to undertake a search for size bimodality. In each case the most suitable bones in terms of sample size and the likelihood of showing a sex difference were the central metapodials (III or III/IV). (The numbers of central metacarpals and metatarsals were respectively 80 and 65 for *C. praecox*, 76 and 87 for *E. capensis*, and 127 and 96 for *Pelorovis* sp.) In so far as bone completeness permitted, a total of six measurements was made on each metapodial (maximum total length, maximum proximal mediolateral diameter, maximum proximal anteroposterior diameter, maximum distal mediolateral diameter, maximum distal anteroposterior diameter, and minimum mediolateral shaft diameter).

The measurements on both the metacarpals and metatarsals in each sample were examined for size bimodality, using the histogram-creating capability of IDA (Interactive Data Analysis—Ling & Roberts 1982), as implemented on the University of Chicago's Amdahl 470 computer. The advantage of using IDA is not only the speed with which it produces histograms from measurements but its ability to produce a histogram based on any desired class breadth or distribution midpoint. Sometimes a narrower class breadth, chosen second, will reveal bimodality that a broader one, chosen first, had masked.

No histogram of *Equus capensis* metacarpal or metatarsal measurements displayed convincing bimodality, while the only *Pelorovis* histogram to display any was that for total length of the metacarpal, and even in this case the bimodality was relatively weak. The problem is probably not that the sexes in *E. capensis* or *Pelorovis* sp. were the same in average size but rather that the difference in average size would show up clearly only in much larger metapodial samples.

The results for *Ceratotherium praecox* were more gratifying, in that a plot of the minimum mediolateral shaft diameter of metacarpal III showed clear and convincing bimodality, as reproduced here in Figure 14. Assuming the individuals represented by the lower mode of the plot are females and those represented by the higher mode are males, the plot suggests that male and female *C. praecox* are about equally represented. This compares with apparent parity in the adult sex ratios of the closest living relatives of *C. praecox*, the white rhinoceros (*C. simum*), and the black rhinoceros (*Diceros bicornis*) (Mentis 1972). The implication is that the pattern of attritional mortality reflected in the *C. praecox* age structure did not differ significantly between the sexes, as it apparently does not in the living relatives of *C. praecox*.

In sum, a reliable sex ratio is much more difficult to establish than a reliable age profile from fossil material. An additional complication, which should be noted here, is that even given a reliable sex ratio from a fossil sample, interpretation may prove difficult. This is because modern observations indicate that the sex ratio in ungulates varies considerably, both among species and among populations of the same species.

CONCLUSIONS

The principal conclusions of this paper may be listed as follows:

1. An ungulate species in which females regularly produce one young (or less) per year will have a catastrophic (= 'lx') age profile with a down-staircase shape in which successively older age classes contain progressively fewer individuals. The corresponding attritional (= 'dx') profile will tend to be U- shaped, with a large peak in the youngest age class and a second smaller peak beyond 40–50 per cent of potential individual lifespan, or L-shaped, with a large peak in the youngest age class and no obvious peaks thereafter.

2. An ungulate species in which females regularly produce more than one young per year will have catastrophic and attritional mortality profiles that both exhibit the down-staircase form. In such species, a difference in form between the profiles will occur mainly at the 'tail' of old individuals, which will tend to exhibit a small rise (or peak) in attritional profiles but not in catastrophic ones. Detecting such a rise and demonstrating its statistical reality will probably require samples larger than the ones palaeontologists or archaeologists can usually obtain.

3. Very young ungulates will generally be underrepresented (in contrast to their live abundance) in mortality profiles obtained from skeletal remains, whether these are recent or fossil. The reason is that the bones of very young individuals are more fragile than those of older ones. In fossil sites where bone preservation is good, so that post-depositional destruction was probably minimal, the underrepresentation of very young individuals is most likely due to pre-depositional destruction or removal by carnivores and scavengers. It follows that sites in which very young individuals are abundant must either be ones at which carnivores and scavengers were absent, or ones to which they took bones but did not consume them. In the case of a hominid (archaeological) site where bones of very young individuals are abundant, the implication is either that the people were able to locate the carcasses of very young individuals before other predators, or that they actively hunted the very young individuals. A priori, the second alternative seems more likely.

4. Predation on ungulates may produce either attritional or catastrophic mortality profiles. Attritional mortality profiles will tend to characterize long-standing predator–prey relationships. It is probable that only recent man regularly produces catastrophic prey profiles. Predation that leads to catastrophic profiles must be restrained, voluntarily, or otherwise, if it is not to reduce or extinguish prey populations.

5. The interpretation of mortality profiles derived from fossil samples is dependent upon the availability of sound contextual information. Thus, the conclusion that the giraffid and *Damalacra* individuals in the Langebaanweg channel fills died by drowning during flash or peak floods is based both on the mortality profiles that characterize the samples and on the sedimentary facies in which they occur. The lack of contextual information for most of the bones collected at Elandsfontein makes it difficult, if not impossible, to interpret the Elandsfontein mortality profiles meaningfully.

6. Mortality profiles based on fossil samples may be useful for establishing basic biological facts about certain species that are difficult to establish by observation of live populations. Thus the fact that mortality profiles of *Raphicerus* from a wide variety of sites always exhibit the same down-staircase form, in spite of the fact that mortality at some (?most) of the sites was probably attritional, implies that *Raphicerus* females commonly bear more than one young per year. More generally, many fossil samples are probably derived from populations in which short-term fluctuations in overall size and age structure have balanced each other out, so that the survivorship and mortality patterns that the samples exhibit are the long-term ones that biologists seek in order to gauge the ecological status or health of living populations.

7. In theory, the crown height distributions of a fossil population that was characterized by seasonally restricted birth and death will exhibit patterned multimodality reflecting the discontinuity of the underlying age distribution. In practice, the discovery of convincing multimodality will require much larger samples than most palaeontologists or archaeologists generally obtain, preferably from species in which dental crowns were very high relative to potential individual lifespan.

8. In fossil samples, sex ratios are generally more difficult to establish and more difficult to interpret than age profiles. Measurements on weight-bearing bones that are likely to reflect size differences provide the most widely applicable means of estimating the sex ratio in fossil ungulate samples.

9. Although ageing animals from skeletal remains can be problematic, for many high-crowned ungulate species ageing from teeth using quadratic formulae such as those employed in this paper will probably provide age profiles that are reasonably accurate. The wider application of mortality profile analysis in palaeontology and archaeology is not limited by problems of ageing but by the frequent lack of sufficiently large samples.

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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.:

<div align="center">

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A
</div>

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 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.

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.

RICHARD G. KLEIN

PATTERNS OF UNGULATE MORTALITY AND UNGULATE MORTALITY PROFILES FROM LANGEBAANWEG (EARLY PLIOCENE) AND ELANDSFONTEIN (MIDDLE PLEISTOCENE), SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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*
    (h) *References*
    (i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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 legend); the reduction or enlargement required should be indicated; 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 legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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) describes . . .'
    'Smith (1969: 36, fig. 16) describes . . .'
    '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.
          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 article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, 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 le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
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KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269–270.

REVISION OF THE
SOUTHERN AFRICAN ANTHURIDEA
(CRUSTACEA, ISOPODA)

By

BRIAN KENSLEY

REVISION OF THE SOUTHERN AFRICAN ANTHURIDEA
(CRUSTACEA, ISOPODA)

By

Brian Kensley

Smithsonian Institution, Washington, D.C.

(With 64 figures)

ABSTRACT

The South African anthuridean isopod fauna, which includes thirty-seven species in sixteen genera and two families, is reviewed. Full synonymies, diagnoses, and all available material examined have been included for each species. The following new species have been described: *Haliophasma austroafricana*, *Malacanthura schotteae*, *M. transkei*, and *Mesanthura dimorpha*.

The following nomenclatural changes have been made: *Natalanthura foveolata* is placed in the genus *Apanthuroides*; *Haliophasma caecus* in *Centranthura*; *Exanthura filiformis* (*sensu* Barnard), and *E. macrura* in *Haliophasma*; *Horoloanthura capensis* in *Kupellonura*; *Haliophasma coronicauda*, *H. foveolata*, *H. hermani*, *H. ornata*, *H. pseudocarinata*, and *Agulanthura serenasinus* in *Malacanthura*; *Anthelura remipes* in *Quantanthura*; and *Zulanthura laevitelson* in *Accalathura*.

The distribution patterns of the southern African anthurideans are compared with those of other geographical areas.

CONTENTS

INTRODUCTION

Between 1925, when Barnard summarized the knowledge of anthuridean isopod systematics, and the early 1970s, no major study of the group has appeared. At present, however, there are several workers concentrating on the group, which is consequently approaching some degree of generic stability. Because of Barnard's interest in the anthurideans and because of much subsequent collecting, the southern African area is now represented by thirty-seven species, more than any other region in the world. It was thus felt that a systematic review of the southern African anthurideans would be useful, especially in updating generic and specific diagnoses.

For this study, the entire holdings of the South African Museum and the University of Cape Town's Department of Zoology have been examined, as well as some material in the British Museum of Natural History, the Smithsonian Institution, the Muséum National d'Histoire Naturelle, Paris, and the Zoological Museum, Copenhagen. Also included is material from the 1978 and 1979 *Meiring Naude* cruises of the South African Museum.

Full synonymies are provided for each species. Full descriptions of new or poorly-known species are given; for species already well documented, only a diagnosis containing the species' most distinctive features is given. The material examined has been divided into two sections, viz. type material and other material. For a few species the whereabouts of the types are unknown. Those described by Stimpson from the United States North Pacific Exploring Expedition, collected in False Bay, Cape, are presumed to have been lost in the Chicago fire of 1871 (see Rathbun 1907). Localities, along with depth records where known, are given for all material.

Keys to families, genera, and species have been constructed for ease of use, and do not necessarily use phylogenetically significant features.

In the *Material* sections, distinction is made between ovigerous and non-ovigerous females, mature males (bearing whorls of filiform aesthetascs on the antennular flagella), submales (representing a stage in the protogynous development from female to male, and recognized by the lack of antennular aesthetascs), juveniles, and mancas (the latter having not yet developed the seventh pair of pereopods).

For most of the species, a figure of the entire animal (usually a mature female) is provided, plus line figures of the most significant features. In addition, scanning electron micrographs have been used to illustrate some details. Occasionally, a feature may be illustrated both by line drawings and SEMs. In such cases, the SEMs are regarded as essential for interpretation of fine surface detail, as well as for three-dimensional configuration and orientation. It is felt that an abundance of figures, especially SEMs, will give a better understanding of functional morphology of the group, and cast light on aspects of adaptive radiation and phylogeny.

The present treatment of the southern African Anthuridea is certainly not the final word, as the author has examined material that has not been included.

For example, an undescribed species of *Mesanthura* from Lüderitz (represented by a single specimen), and several immature or damaged specimens from the continental shelf off the east coast have been omitted. Only with more specimens can this material be adequately described. Reinterpretation of some genera and species (e.g. *Apanthura* and *Leptanthura*) will almost certainly become necessary.

The following abbreviations are used throughout the paper:

BMNH   British Museum (Natural History)
SAM   South African Museum
SIO   Scripps Institution of Oceanography
USNM   United States National Museum of Natural History, Smithsonian Institution
ZMC   Zoological Museum, Copenhagen
juv.(s) juvenile(s)
ovig.   ovigerous
TL   total length

All locality references to False Bay refer to False Bay, Cape, and not False Bay, Natal. In the sections *Other material*, all localities are given from west to east.

SYSTEMATIC DISCUSSION

KEY TO THE FAMILIES OF THE ANTHURIDEA

1. Mouthparts adapted for biting and cutting, i.e. mandible possessing (usually) molar and incisor, maxilla with several distal spines.................................... Anthuridae
– Mouthparts adapted for piercing and sucking, i.e. mandible lancet-like, lacking molar and incisor, maxilla styliform .... Paranthuridae

KEY TO THE SOUTH AFRICAN GENERA OF THE FAMILY ANTHURIDAE

1. Pleonites 1–6 free 2
– At least pleonites 1–5 fused 4
2. Pleonites 1–6 free-elongate
   Exopod of pleopod 1 non-operculiform.. 3
– At least pleonites 1–5 free, short
   Exopod of pleopod 1 operculiform....................................... *Panathura*
3. Telson dorsoventrally flattened
   Maxilliped of 5 segments .... *Kupellonura*
– Telson spiniform, terete
   Maxilliped of 7 segments .... *Neohyssura*
4. Maxilliped of 6 segments .... *Quantanthura*
– Maxilliped of fewer than 6 segments 5
5. Maxilliped of 5 segments 6
– Maxilliped of fewer than 5 segments 9
6. Persistent brown-black dorsal pigment pattern present...................... *Mesanthura*
– Persistent pigment pattern absent... 7
7. Pereopods 1–3 subsimilar, barely subchelate
   Molar of mandible absent on one side .... *Apanthuroides*

– Pereopod 1 subchelate, markedly larger than following pereopods
  Molar of mandible normal, present on both sides 8
8. Pereopods 4–7 with triangular carpus.................................... *Apanthura*
– Pereopods 4–7 with rectangular carpus .... *Malacanthura*
9. Maxilliped of 4 segments 10
– Maxilliped of 3 segments .... *Centranthura*
10. Pereopods 4–7 with triangular carpus.................................... *Cyathura*
– Pereopods 4–7 with rectangular carpus .... *Haliophasma*

Family **Anthuridae**
Apanthura Stebbing, 1900

Diagnosis

Antennular flagellum of two to four articles; antennal flagellum of two to four articles. Mandible with three-segmented palp; incisor, lamina dentata, and molar present. Maxilliped five-segmented, endite present or absent. Pereopod 1 subchelate, propodus expanded. Pereopods 4–7 with triangular carpus underriding propodus. Pleopod 1 exopod operculiform. Pleonites 1–5 fused, pleonite 6 free. Telson with two basal statocysts.

Type species

Apanthura sandalensis Stebbing, 1900.

KEY TO THE SOUTH AFRICAN SPECIES OF *APANTHURA*

1. Uropodal exopod strongly notched .... *dubia*
– Uropodal exopod margin entire, convex or sinuous 2
2. Eyes present; telson with distal raised lozenge-shaped area .... *africana*
– Eyes absent; telson with faint mid-dorsal ridge .... *insignifica*

Apanthura africana Barnard, 1914
Figs 1–2

Apanthura africana Barnard, 1914: 340a, pl. 28C; 1925a: 142; 1940: 490, 498. Nierstrasz,
    1941: 241. Day, Field & Penrith, 1970: 47. Kensley, 1975a: 38; 1978a: 46, fig. 20G–I.
Apanthura cf. *sandalensis:* Penrith & Kensley, 1970: 226.

Diagnosis

Integument lacking sculpture. Pereonites 4–6 each with mid-dorsal pit. Pleonites 1–5 fused, dorsal lines of fusion complete between pleonites 1–4, incomplete between pleonites 4 and 5; pleonite 6 free, with mid-dorsal notch in posterior margin. Telson slightly raised, lozenge-shaped in distal half; distally rounded. Pereopod 1 propodus expanded; palmar margin setose, with low rounded lobe at midpoint. Uropodal exopod with outer margin slightly sinuous distally.

Type material

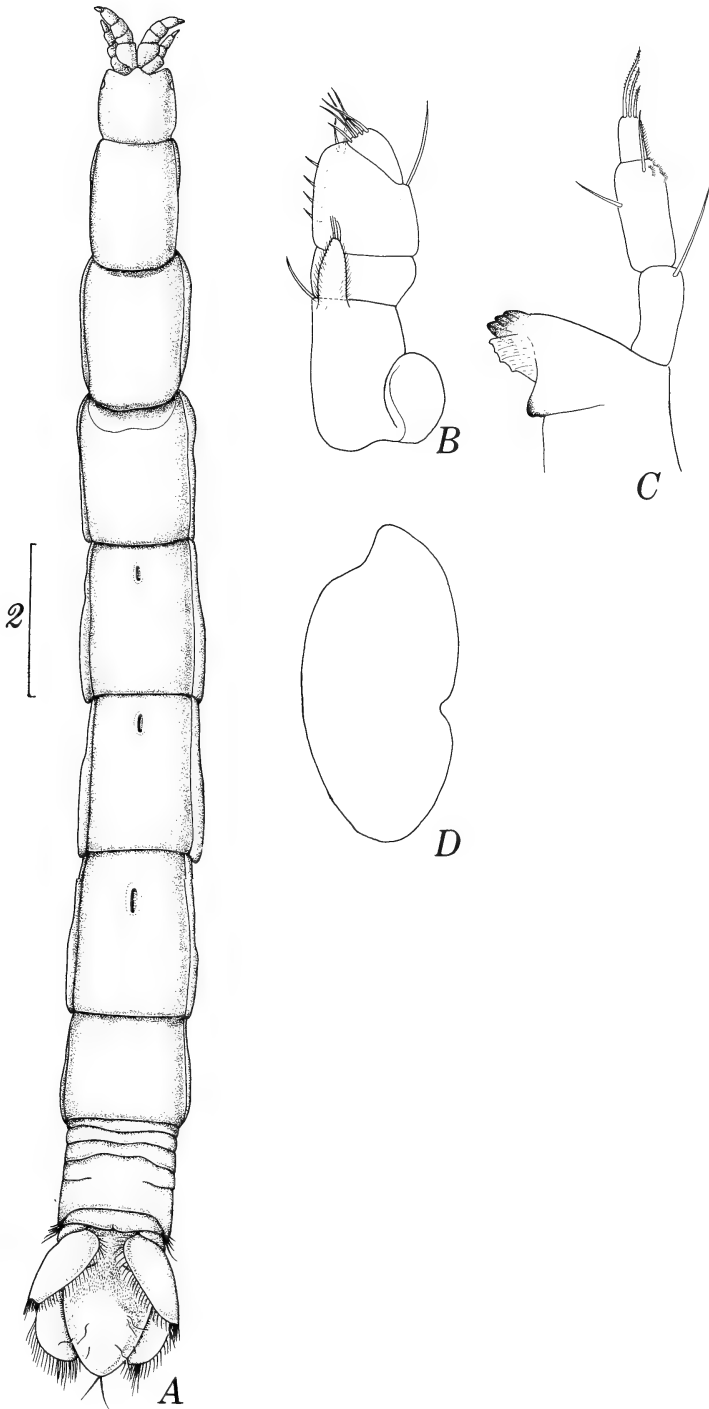Holotype, non-ovig. ♀, SAM–A63, 17,0 mm, off Saldanha Bay, 160 m.

Fig. 1. *Apanthura africana*. A. ♀, dorsal view. B. Maxilliped. C. Mandible. D. Uropodal exopod. Scale in mm.

Other material

SAM–A12615, 2 non-ovig. ♀, Lüderitz, intertidal. SAM–A12630, 1 juv., Lüderitz, intertidal. SAM–A12739, 3 juvs, Lüderitz, intertidal. SAM–A5961, 1 ♀, off Saldanha Bay, 174 m. SAM–A14040, 1 non-ovig. ♀, off Saldanha Bay, 16 m. SAM–A14046, 1 sub♂, off Saldanha Bay, 146 m. SAM–A14047, 1 non-ovig. ♀, off Saldanha Bay, 148 m. SAM–A14048, 1 sub♂, 1 non-ovig. ♀, off Saldanha Bay, 79 m. SAM–A14052, 1 sub♂, 27 non-ovig. ♀, 13 juvs, off Saldanha Bay, 11 m. SAM–A14053, 4 juvs, off Saldanha Bay, 91 m. SAM–A14054, 1 non-ovig. ♀, off Saldanha Bay, 172 m. SAM–A14055, 6 non-ovig. ♀, 12 juvs, off Saldanha Bay, 146 m. SAM–A14056, 1 sub♂, 4 non-ovig. ♀, 4 juvs, off Saldanha Bay, 142 m. SAM–A14057, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14067, 2 ♂, 4 non-ovig. ♀, 13 juvs, off Saldanha Bay, 146 m. SAM–A14113, 1 non-ovig. ♀, off Saldanha Bay, 13 m. SAM–A14118, 3 non-ovig. ♀, 2 juvs, off Saldanha Bay, 15 m. SAM–A14325, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14326, 1 ♂, off Saldanha Bay. SAM–A14327, 1 sub♂, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14348, 1 non-ovig. ♀, off Saldanha Bay, 148 m. SAM–A14060, 1 juv., False Bay, 35 m. SAM–A14043, 2 non-ovig. ♀, 1 juv., off Still Bay, 200 m. SAM–A14051, 1 non-ovig. ♀, off Jeffreys Bay, 32 m. SAM–A14063, 1 non-ovig. ♀, off Jeffreys Bay, 25 m.

Distribution

Lüderitz to Jeffreys Bay, intertidal to 200 m.

Apanthura dubia Barnard, 1914
Figs 3–4

Apanthura dubia Barnard, 1914; 342a, pl. 28D; 1955: 5.
Apanthura sandalensis non Stebbing, Barnard, 1925a: 141; 1940: 490, 498. Nierstrasz, 1941: 241 (*partim*). Day, Field, & Penrith, 1970: 47. Kensley, 1978a: 46, fig. 20J–K; 1980: 12, fig. 7.

Diagnosis

Pleonites 1–5 fused, three complete fusion line-grooves between pleonites 1–4, incomplete line between pleonites 4 and 5. Telson widest at midlength, with low rounded proximal mid-dorsal ridge, becoming obsolete distally. Antennular flagellum of two articles. Antennal flagellum of single article. Maxilliped five-segmented, with small triangular endite. Pereopod 1 in male and female with corneous proximal tooth on propodal palm; carpus triangular, with distal corneous tooth, more marked in male. Uropodal exopod with deep distal notch.

Type material

Syntypes, SAM–8826, 2 non-ovig. ♀, 10,0 mm (both damaged), St. James, False Bay, intertidal.
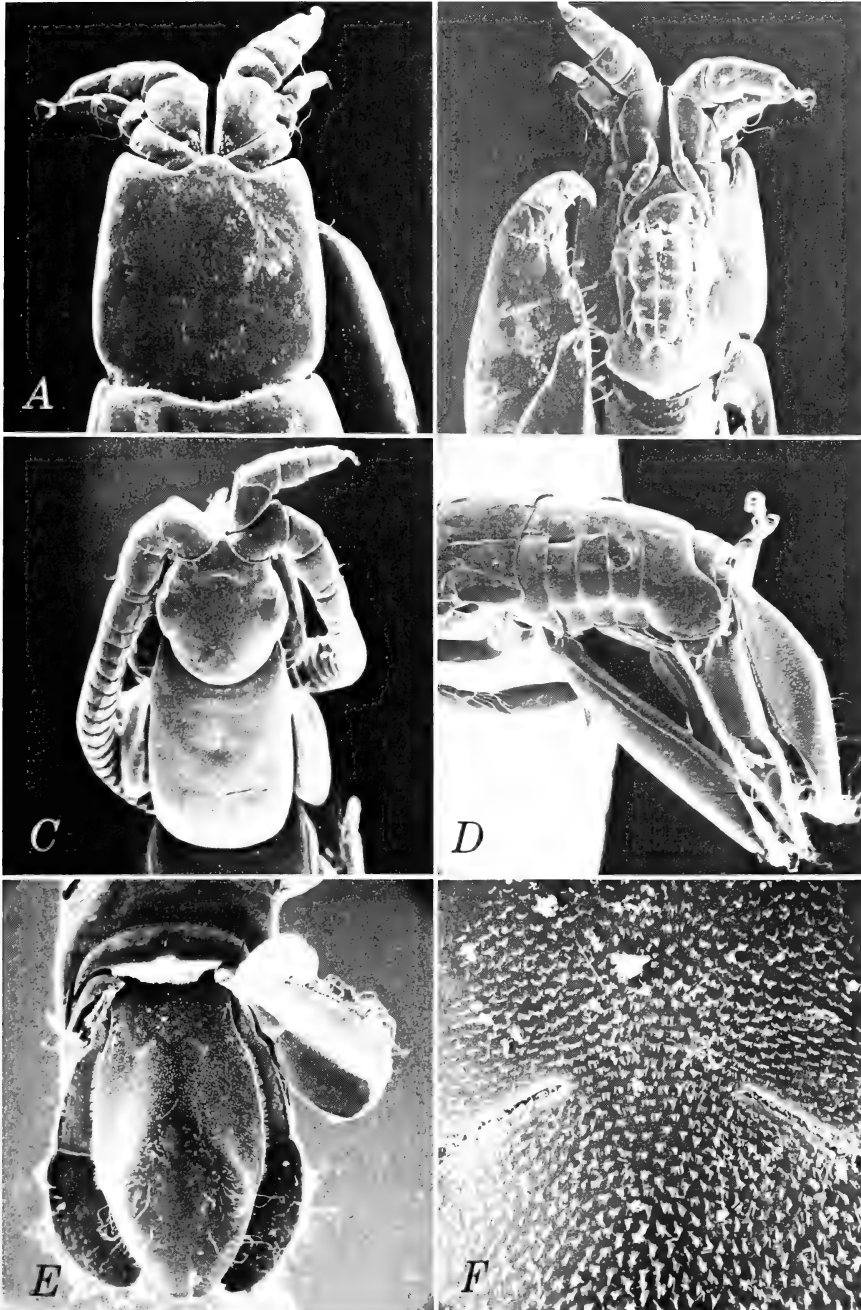
Fig. 2. *Apanthura africana*. A. ♀ cephalon, dorsal view. B. ♀ cephalon, ventral view. C. Sub♂ cephalon. D. Pleon and telson. E. Telson, dorsal view. F. Statocyst apertures.
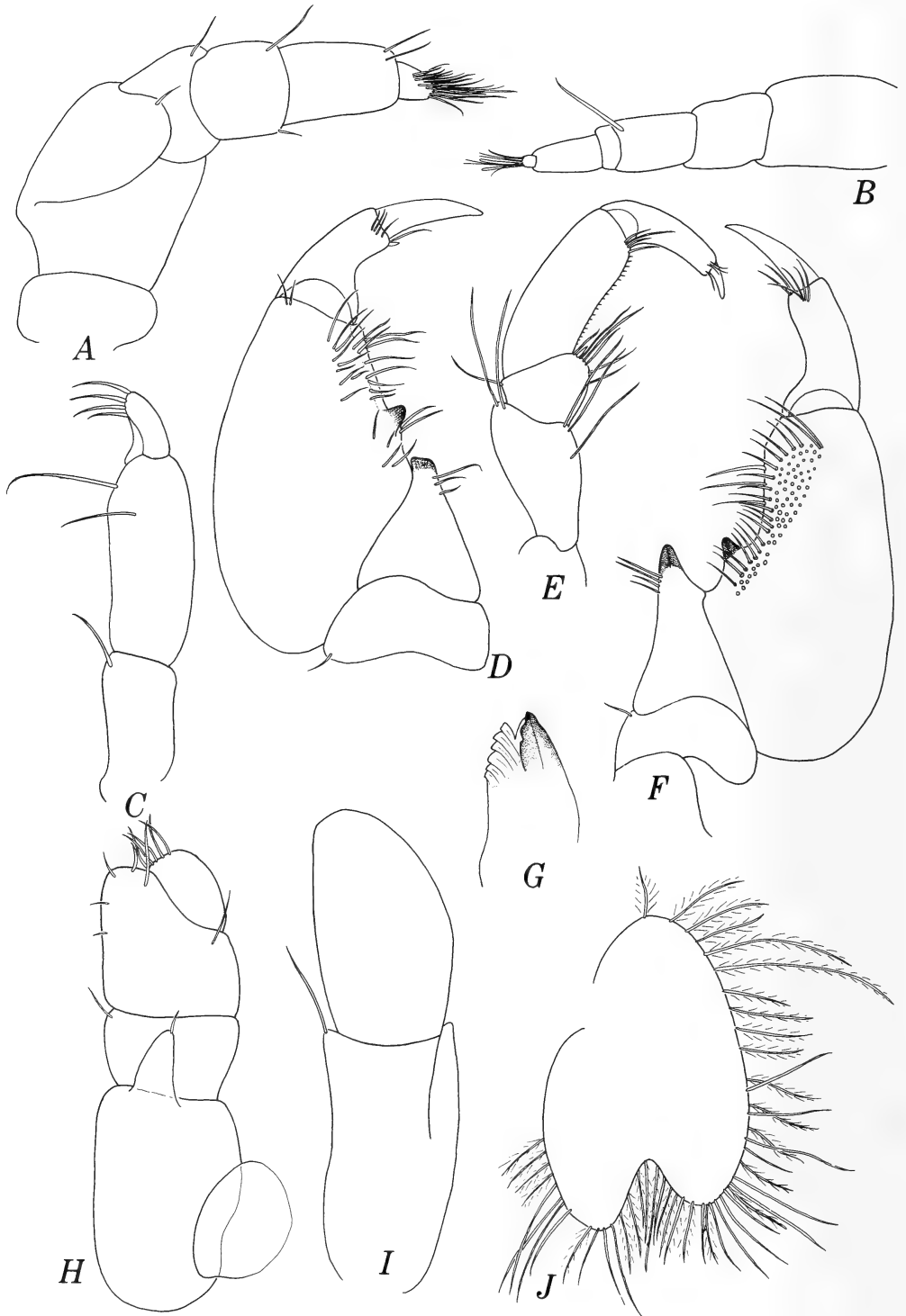
Fig. 3. *Apanthura dubia*. A. Antenna. B. Antennule. C. Mandibular palp. D. Pereopod 1 ♀. E. Pereopod 7. F. Pereopod 1 ♂. G. Mandibular incisor and lamina dentata. H. Maxilliped. I. Uropodal peduncle and endopod. J. Uropodal exopod.

Other material

SAM–A17494, 1 non-ovig. ♀, 11,0 mm, Saldanha Bay. SAM–A14069, 2 non-ovig. ♀, Agulhas Bank, 36–54 m. SAM–A14353, 1 non-ovig. ♀, 11,0 mm, Agulhas Bank, 27 m. SAM–A14401, 1 non-ovig. ♀, 8,0 mm, Agulhas Bank, 27 m. SAM–A14068, 1 ♂, off Still Bay, 200 m. SAM–A14070, 5 non-ovig. ♀, 1 ♂, off Still Bay, 200 m. SAM–A17495, 1 non-ovig. ♀, off Mossel Bay. SAM–A14072, 2 non-ovig. ♀, off Jeffreys Bay. SAM–A17496, 3 juvs, off Transkei, 150–200 m.

Distribution
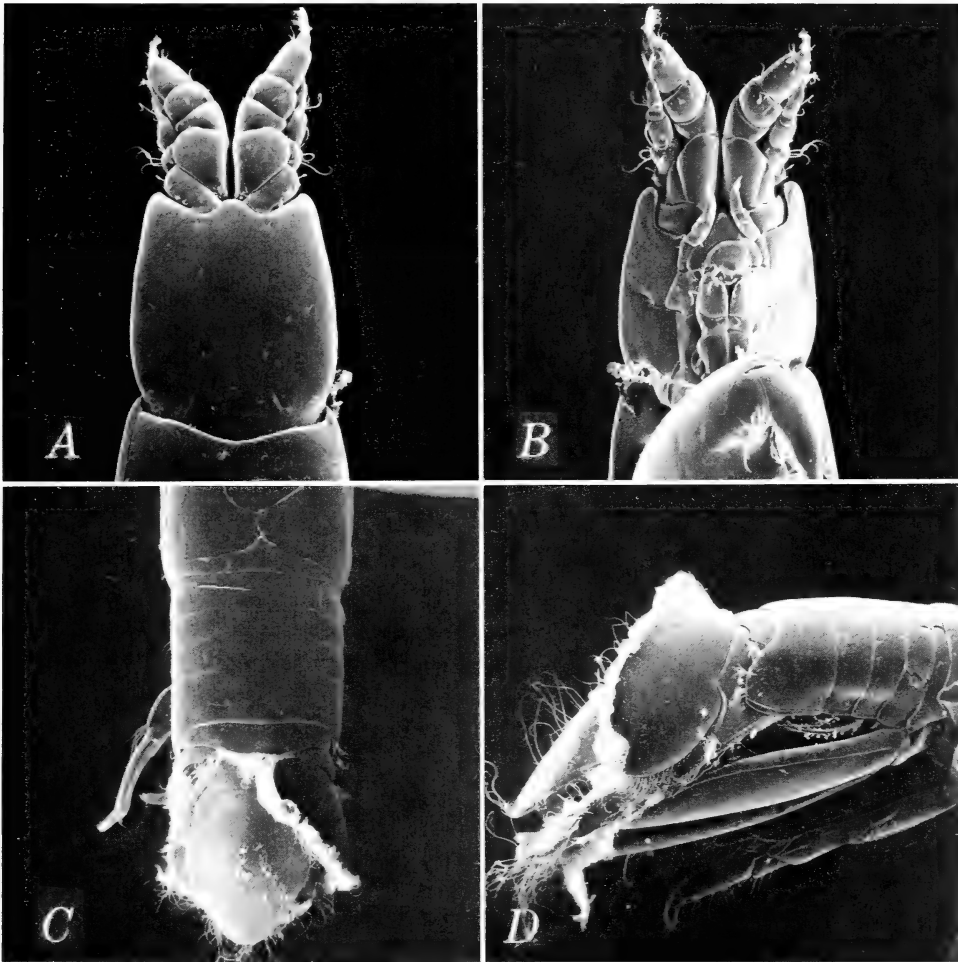
Saldanha Bay to Transkei, intertidal to 200 m.

Fig. 4. *Apanthura dubia*. A. ♀ cephalon, dorsal view. B. ♀ cephalon, ventral view. C. Pleon and telson, dorsal view. D. Pleon and telson, lateral view.

Remarks

Apanthura dubia has for many years masqueraded under the name of *A. sandalensis* Stebbing, following Barnard's synonymizing his own species. *Apanthura sandalensis* Stebbing (1900), from the Loyalty Islands, south-western Pacific Ocean, however, does not have a triangular process on the carpus or propodal palm of pereopod 1. (Barnard, 1925a, does mention that a co-type in the British Museum (Natural History) has a palmar tooth as in *A. dubia*, which casts doubt on the identity of the specimen.) The telson of *A. dubia* is distally narrower, the antennal flagellum has fewer articles, and the uropodal exopod is broader than in *A. sandalensis*.

Barnard's (1935) *A. sandalensis* from Travancore, Kerala, India, and Pillai's (1966) *A. sandalensis* from Kerala, India, probably belong to neither of these species. Pillai's species shows a uropodal endopod too slender, a more setose telson, and antennae having too many flagellar articles.

Chilton (1924) recorded *A. sandalensis* from Chilka Lake, India, but the very slender antenna and antennule, the former with a three-articulate flagellum, makes this identification doubtful. Larwood (1940, fig. 7) recorded *A. sandalensis* (which he too synonymized with *A. dubia*) from Alexandria, Mediterranean Sea, but the sinus of the uropodal exopod is not as deep as in *A. dubia*, while the uropodal endopod is less elongate. Larwood's material thus probably does not belong to either species.

Apanthura insignifica Kensley, 1978

Figs 5–6

Apanthura insignifica Kensley, 1978b: 2, figs 1–2.

Diagnosis

Eyes weakly pigmented. Telson elliptical-oval, with weak mid-dorsal longitudinal ridge, distal margin broadly rounded. Uropodal exopod oval, margin entire.

Type material

Holotype, SAM–A15646, 1 non-ovig. ♀, 5,9 mm, off Natal, 690 m. Paratypes, SAM–A15647, 1 non-ovig. ♀, 4,5 mm. 1 sub♂, 5,6 mm, off Natal, 850 m. Paratype, SAM–A15646, 1 non-ovig. ♀, 5,2 mm, off Natal, 690 m. Paratypes, USNM 170542, 2 non-ovig. ♀, 5,4–5,6 mm, off Natal, 850 m.

Other material

SAM–A17497, 1 non-ovig. ♀, 4,5 mm, off East London, 630 m. SAM–A17499, 2 non-ovig. ♀, 4,3 mm, 4 juvs, south of East London, 90 m. SAM–A17500, 1 ♂, 6,3 mm, off Natal, 850 m. SAM–A17498, 1 ♂, 5,0 mm, 1 non-ovig. ♀, 4,6 mm, off Zululand, 550 m.
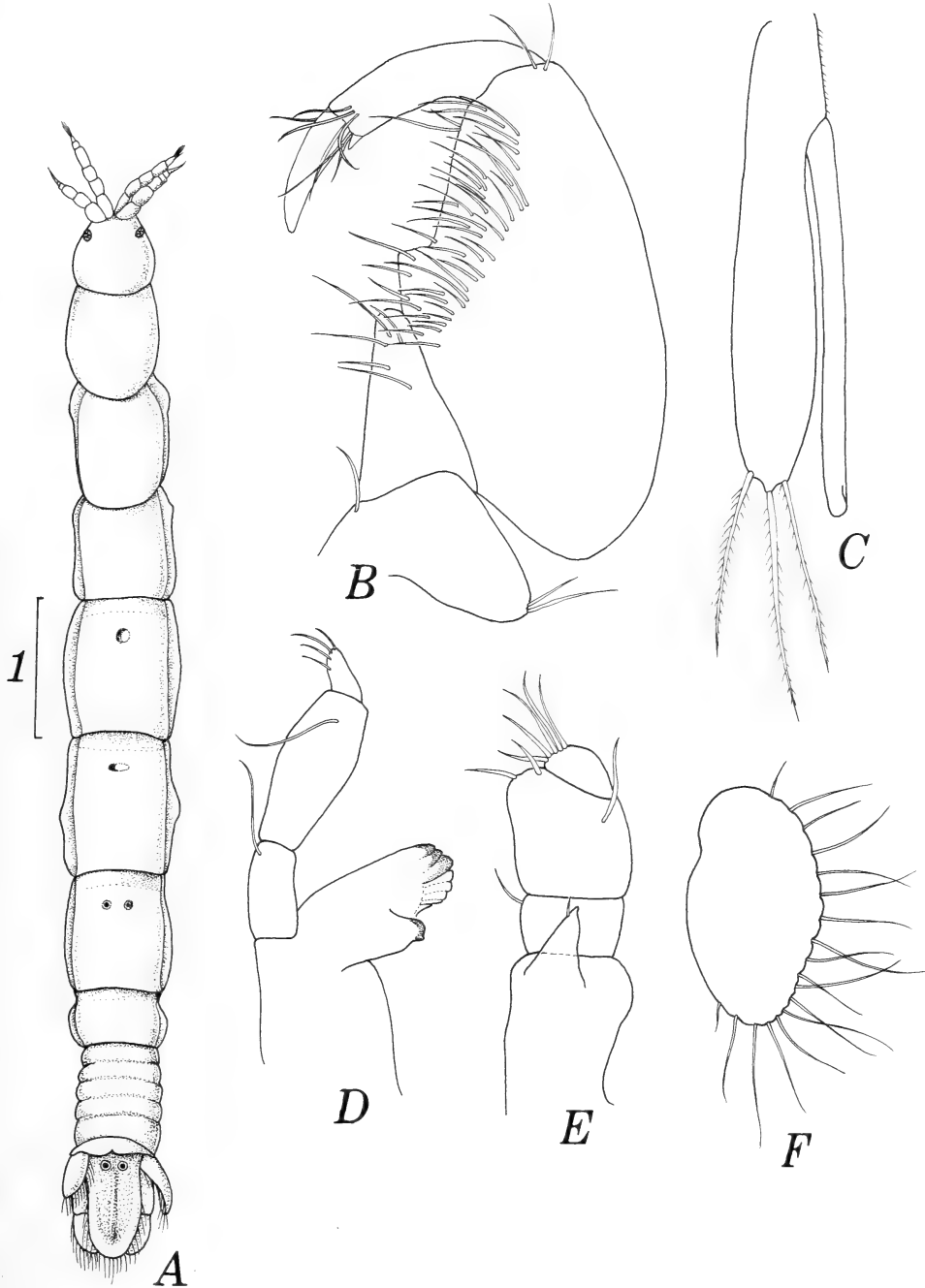
Fig. 5. *Apanthura insignifica*. A. ♀ dorsal view. B. Pereopod 1 ♀. C. Pleopod 2 endopod ♂. D. Mandible. E. Maxilliped. F. Uropodal exopod. Scale in mm.
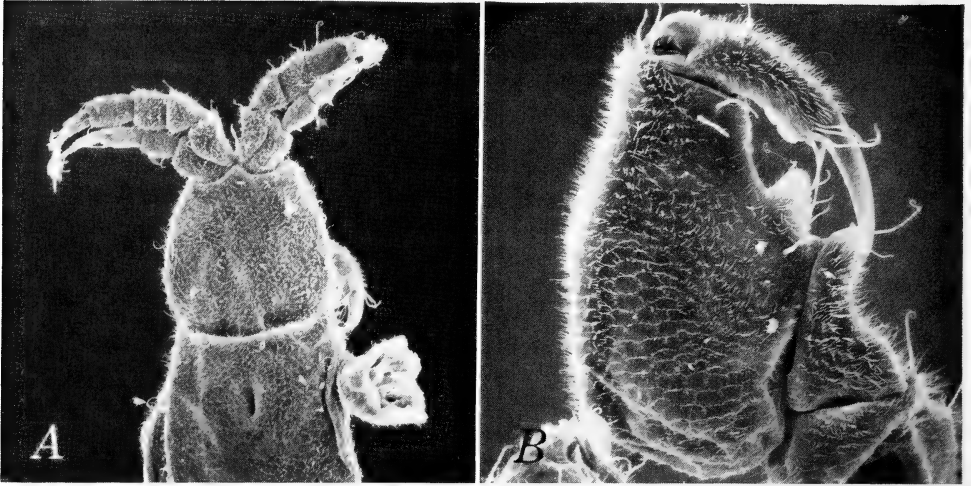
Fig. 6. *Apanthura insignifica*. A. ♀ cephalon, dorsal view. B. Pereopod 1 ♀.

Distribution

South of East London to Zululand, 90–850 m.

Apanthuroides Menzies & Glynn, 1968

Natalanthura Kensley, 1978*b*: 5.

Diagnosis

Eyes present. Mandibular palp three-segmented; molar slender and spike-like on one side, absent on other. Maxilliped five-segmented, endite present. Pereopods 1–3 subsimilar, barely subchelate. Pereopods 4–7 with rectangular carpus. Pleopod 1 exopod and endopod together forming operculum. Pleonites 1–5 fused; pleonite 6 fused with telson. Telson with basal statocysts. Integument pitted.

Type species

Apanthuroides millae Menzies & Glynn, 1968.

Remarks

Re-examination of the types of *Apanthuroides millae* from Puerto Rico, and fresh material from Belize, Central America, has shown that the pleonal segmentation, and especially the unusual mandibular structure, is identical to that of *Natalanthura*.

Apanthuroides foveolata (Kensley, 1978)

Figs 7–8

Natalanthura foveolata Kensley, 1978*a*: 6, figs 3–4; 1980: 3, 32. Wägele 1981: 88–90.
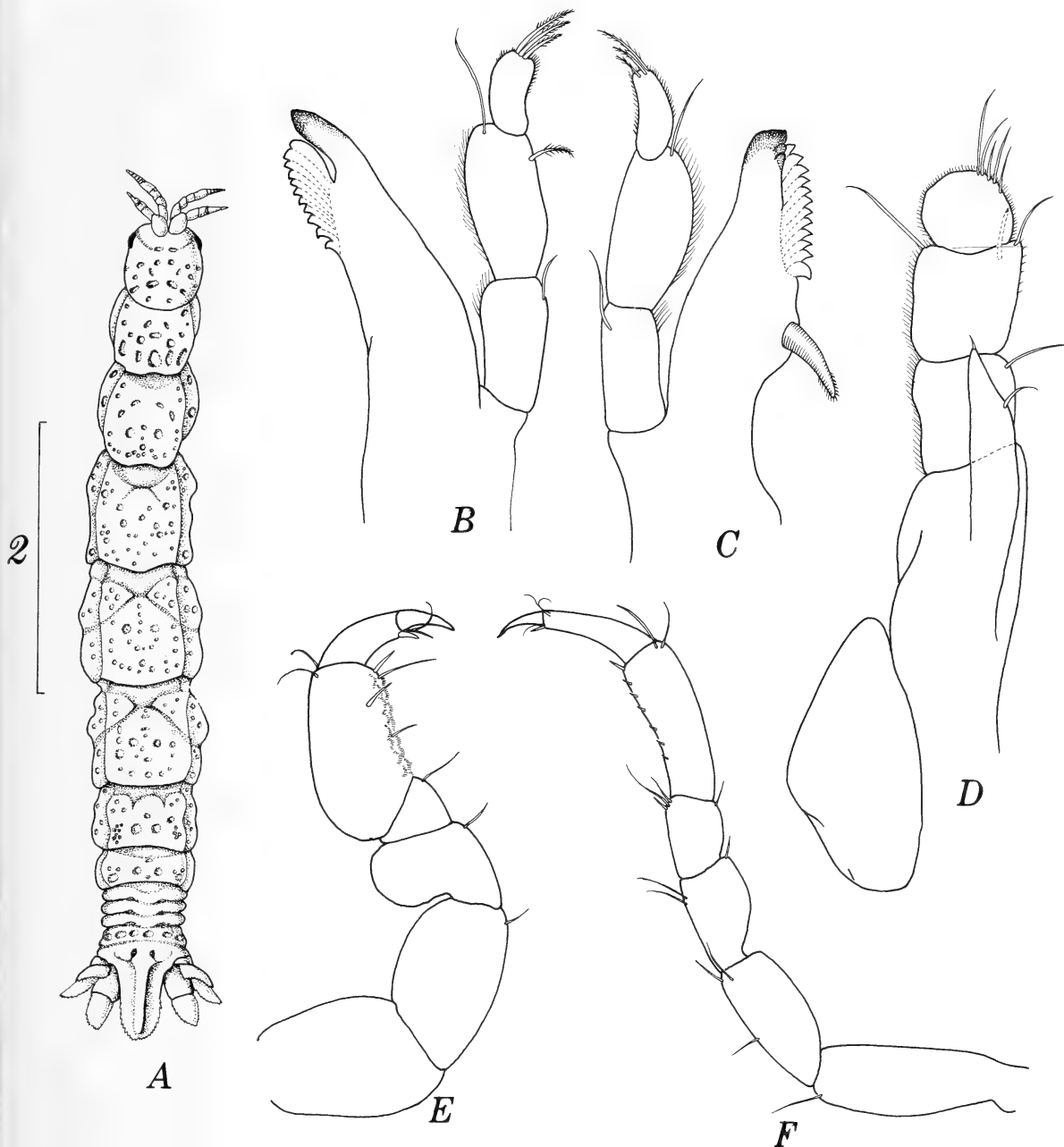*Natalanthura natalensis* Kensley, 1979: 823, (*laps. cal.*)

Fig. 7. *Apanthuroides foveolata*. A. ♀ dorsal view. B. Right mandible. C. Left mandible. D. Maxilliped. E. Pereopod 1. F. Pereopod 7. Scale in mm.
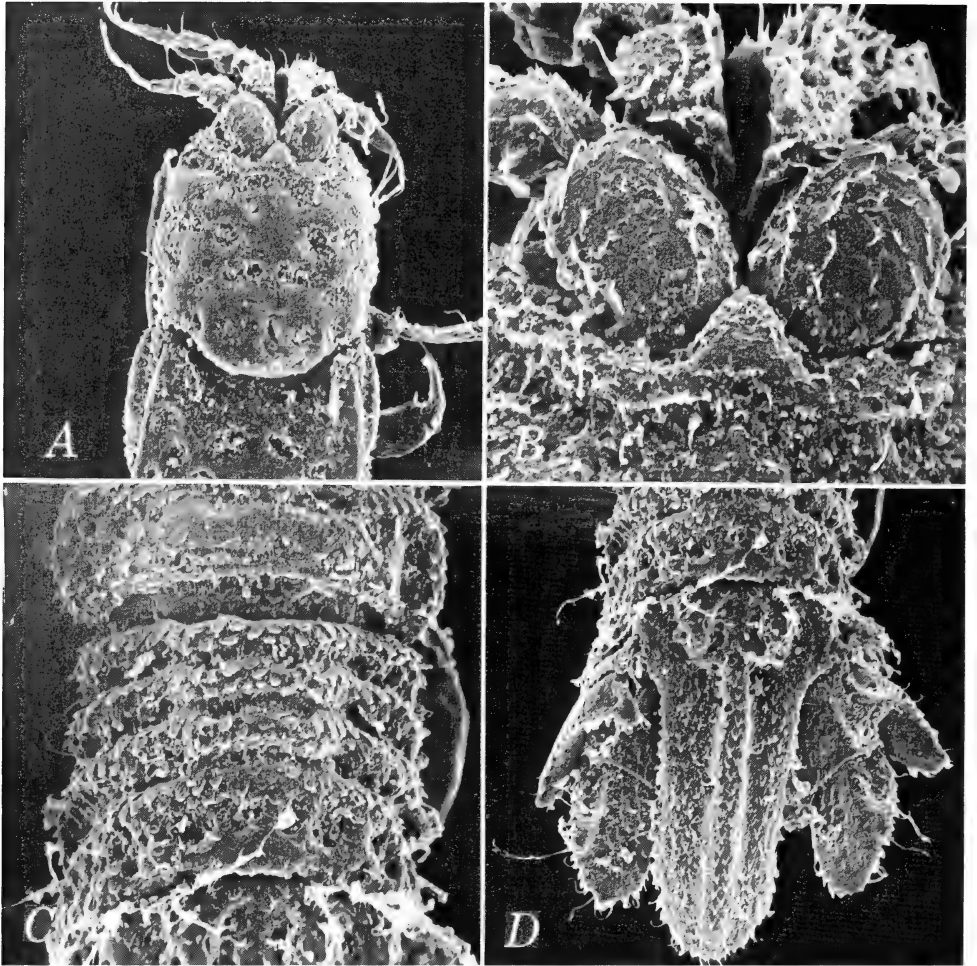
Fig. 8. *Apanthuroides foveolata*. A. ♀ cephalon. B. Rostrum and antennal bases. C. Pleon in dorsal view. D. Telson and uropods.

Diagnosis

Telson with strong mid-dorsal longitudinal ridge. Telsonic and uropodal margins serrate. Antennular flagellum of three articles; antennal flagellum of six articles. Eyes feebly pigmented.

Type material

Holotype, SAM–A15648, 1 non-ovig. ♀, 5,8 mm, off Zululand, 550 m. Paratypes, SAM–A15648, 2 non-ovig. ♀, 3,5–5,4 mm, off Zululand, 550 m. Paratype, SAM–A15649, 1 juv., 3,4 mm, off Natal, 690 m. Paratype,

SAM–A15650, 1 ovig. ♀, 6,9 mm, off Natal, 850 m. Paratypes, USNM 170543, 3 non-ovig. ♀, 4,3–4,6 mm, off Zululand, 550 m.

Other material

SAM–A17501, 1 non-ovig. ♀, off Transkei, 630 m. SAM–A17502, 1 ovig. ♀, 3 non-ovig. ♀, 1 sub♂, 1 juv., off Transkei, 710–775 m. SAM–A17503, 1 juv., off Transkei, 560–620 m.

Distribution

Zululand to Transkei, 550–850 m.

Centranthura Wägele, 1981

Centranthura Wägele, 1981: 113.
Haliophasma: Kensley, 1975b, *partim.*

Diagnosis

Eyes absent. Antennular flagellum of three articles; antennal flagellum of two articles. Maxilliped three-segmented; endite absent. Pereopod 1 sub-chelate, propodus expanded. Pereopods 4–7 with narrow rectangular carpus. Pleonites 1–5 fused, pleonite 6 free. Telson with two basal statocysts.

Type species

Haliophasma caecus Kensley, 1975b.

Centranthura caeca (Kensley, 1975)

Figs 9–10

Haliophasma caecus Kensley, 1975b: 209, figs 1–2; 1978a: 49, fig. 21 E.
Centranthura caecus: Wägele, 1981: 113.

Diagnosis

Pereonites 4–6 with mid-dorsal pit. Telson widest at midlength, with low rounded proximal ridge, distally narrowed, distal margin broadly rounded. Antennule with three-articulate flagellum; antenna with two-articulate flagellum. Pereopod 1 subchelate, propodus expanded, propodal palm sinuous in female, with peg-like tooth in male. Pereopods 4–7 with narrow rectangular carpus not underriding propodus. Uropodal exopod oval, outer margin sinuous, apex acute.

Type material

Holotype, SAM–A13626, 1 ♂, 18,2 mm, Lambert's Bay. Allotype, SAM–A13626 1 non-ovig. ♀, 16,0 mm, Lambert's Bay. Paratypes, SAM–A13627, 1 ♂, 21,0 mm, 5 non-ovig. ♀, 12,5–17,5 mm, Langebaan Lagoon.
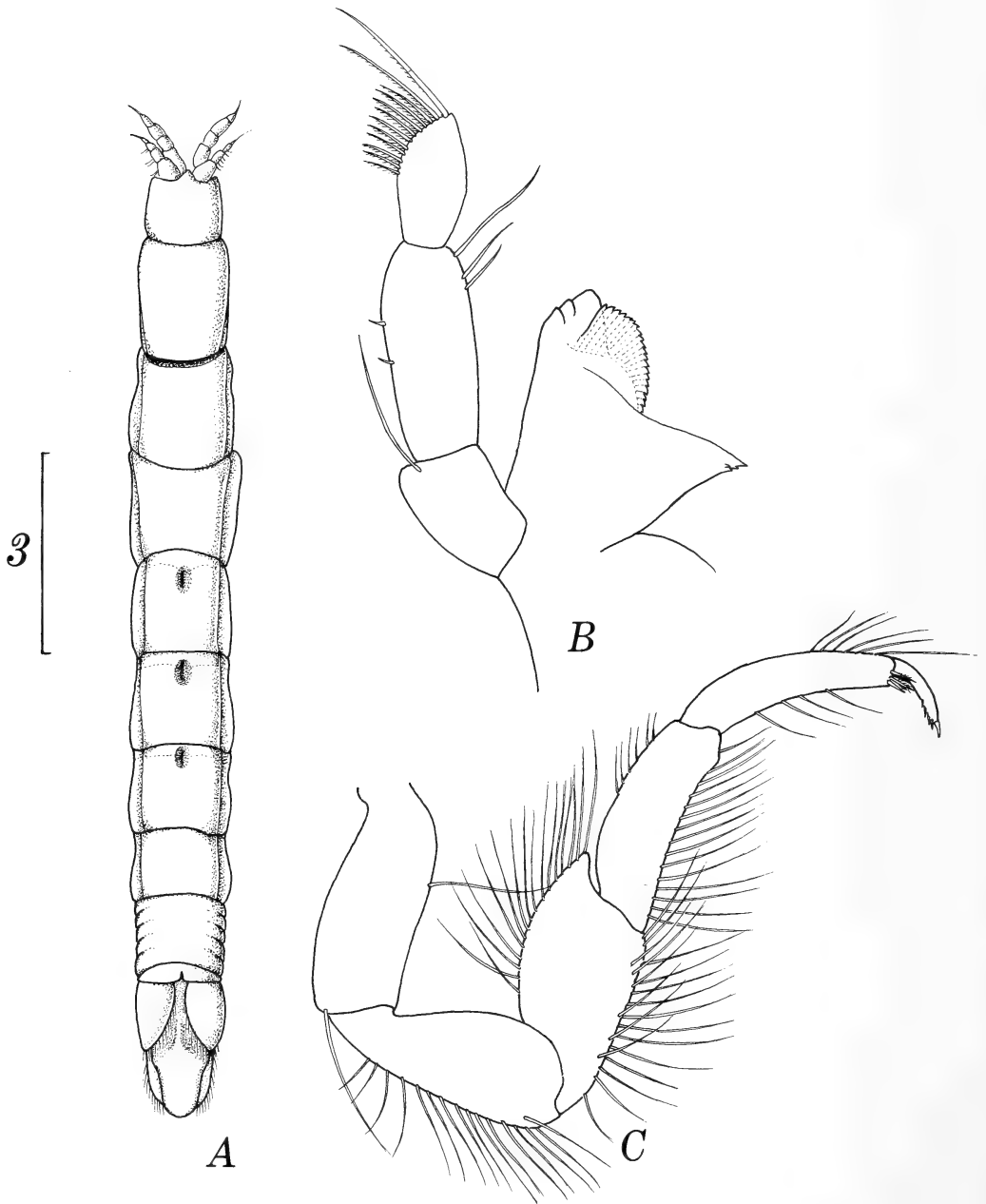
Fig. 9. *Centranthura caeca*. A. ♀ dorsal view. B. Mandible. C. Pereopod 7. Scale in mm.

Other material

SAM–A14419, 15 non-ovig. ♀, 17 juvs, Lambert's Bay. SAM–A14064, 1 juv., off Saldanha Bay, 51 m. SAM–A14106, 1 non-ovig. ♀, 12 juvs, off Saldanha Bay, 22 m. SAM–A14107, 1 ♂, off Saldanha Bay, 172 m. SAM–A14108, 2 non-ovig. ♀, Saldanha Bay, 31 m. SAM–A14109, 1 non-ovig. ♀, off Saldanha Bay, 18 m. SAM–A14110, 3 non-ovig. ♀, off Saldanha Bay, 62 m. SAM–A14114, 2 non-ovig. ♀, off Saldanha Bay, 62 m. SAM–A14116, 2 ♂, 7 non-ovig. ♀, 1 juv., off Saldanha Bay, 51 m. SAM–A14122, 1 ♂, 3 juvs, off Saldanha Bay, 15 m. SAM–A14123, 1 non-ovig. ♀, off Saldanha Bay, 54 m. SAM–A14407, 1 non-ovig. ♀, Saldanha Bay, 27 m. SAM–A14408, 4 non-ovig. ♀, 4 juvs, off Saldanha Bay, 68 m. SAM–A14409, 1 non-ovig. ♀, 2 juvs, Saldanha Bay, 9 m. SAM–A14413, 1 non-ovig. ♀, off Saldanha Bay, 32 m. SAM–A14417, 4 non-ovig. ♀, 16 juvs, Saldanha Bay, 31 m. SAM–A14421, 9 non-ovig. ♀, off Saldanha Bay, 27 m. SAM–A14422, 1 non-ovig. ♀, Saldanha Bay, 5 m. SAM–A14847, 1 juv., off Saldanha Bay, 68 m. SAM–A17469, 2 non-ovig. ♀, 3 juvs, off Saldanha Bay. SAM–A17470, 1 non-ovig. ♀, 1 juv., off Saldanha Bay. SAM–A17471, 1 non-ovig. ♀, off Saldanha Bay. SAM–A17472, 7 non-ovig. ♀, 4 juvs, off Saldanha Bay. SAM–A17473, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14410, 3 non-ovig. ♀, 2 juvs, Langebaan Lagoon. SAM–A14412, 11 non-ovig. ♀, Langebaan Lagoon. SAM–A14414, 2 ♂, 3 non-ovig. ♀, Langebaan Lagoon. SAM–A14423, 1 ♂, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14424, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14425, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14426, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14428, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14429, 4 non-ovig. ♀, Langebaan Lagoon. SAM–A14430, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14431, 1 ♂, 2 non-ovig. ♀, Langebaan Lagoon. SAM–A14432, 1 non-ovig. ♀, Langebaan Lagoon. SAM–A14427, 1 ♂, 1 non-ovig. ♀, 1 juv., Langebaan Lagoon. SAM–A14112, 1 ♂, False Bay, 9 m. SAM–A14121, 1 non-ovig. ♀, False Bay, 7–9 m. SAM–A14126, 1 non-ovig. ♀, False Bay, 68 m. SAM–A14406, 1 juv., False Bay, 31 m. SAM–A14415, 1 sub♂, False Bay, 31 m. SAM–A14416, 1 non-ovig. ♀, False Bay, 31 m. SAM–A14411, 1 ♂, Agulhas Bank, 44 m. SAM–A14041, 1 non-ovig. ♀, Still Bay, 80 m. SAM–A14420, 1 non-ovig. ♀, Mossel Bay.

Distribution

Lambert's Bay to Mossel Bay, 5–68 m.

Remarks

Wägele (1981) placed *Haliophasma caecus* into the new genus *Centranthura* for the following reasons: the 'primitive' antennule bearing four aesthetascs, the telson which is neither significantly elongate nor dorsally strongly keeled, and the antenna, which has a shorter flagellum than most
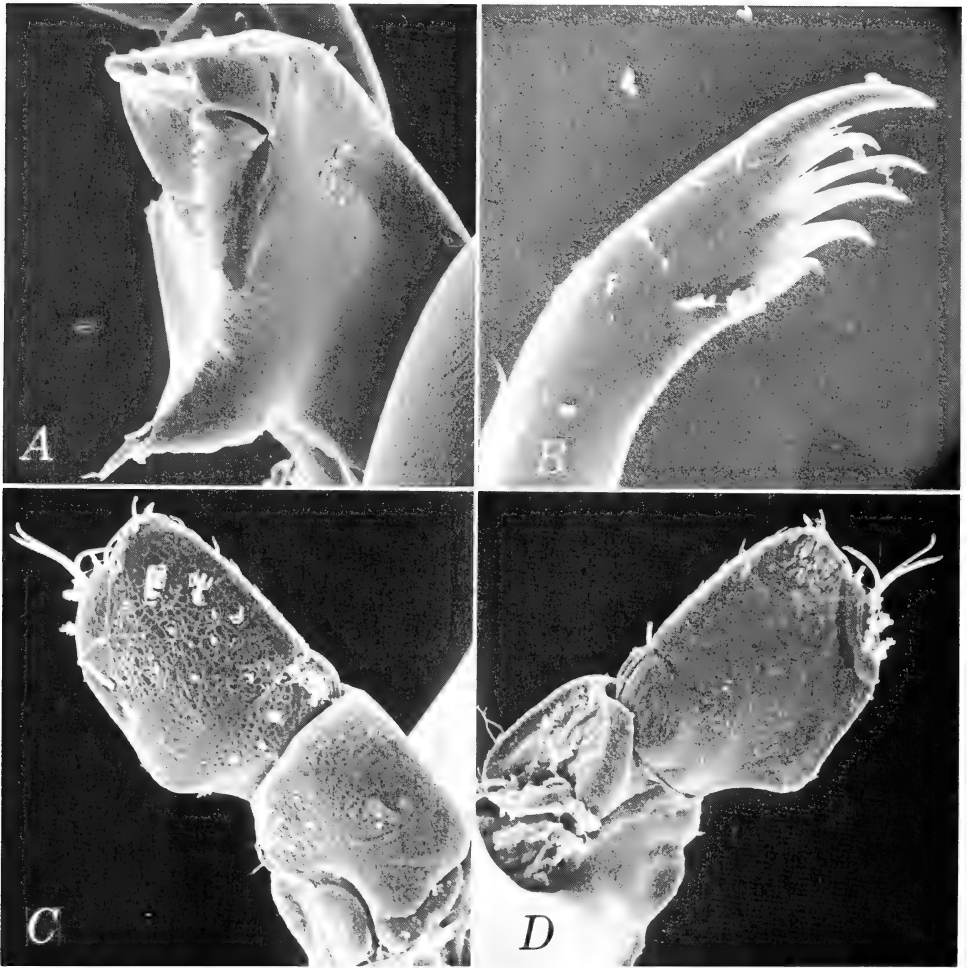
Fig. 10. *Centranthura caeca*. A. Mandible. B. Maxilla. C. Maxilliped, external surface.
D. Maxilliped, internal surface.

species of *Haliophasma*. It is now felt that *H. caecus* should, indeed, be in a separate genus, but not for the reasons given by Wägele.

In the original description, Kensley (1975*b*) indicated that the maxilliped was three- or four-segmented, and that the terminal segment was not distinct. In the scanning electron micrograph (Fig. 10) a distinct groove is visible, delimiting an obliquely-inserted fourth segment bearing five setae. In a cleared and mounted specimen, however, this groove is seen to be not a true suture, but a superficial fold perhaps indicating a line of fusion. The first maxillipedal palp segment was indicated (1975*b*, fig. 1g) as having an indistinct groove in its

proximal third. In the scanning electron micrograph this groove is seen on the external face of the segment, but barely indicated on the internal face, once again indicating a line of fusion. The cleared and mounted specimen again shows this not to be a true suture. The maxilliped is therefore regarded as being three-segmented, as in *Anthura*, *Exallanthura*, *Pendanthura*, *Ptilanthura*, *Venezanthura*, and *Xenanthura*.

Centranthura differs from these genera in the following respects: it does not have the six free elongate pleonites of *Xenanthura*; it lacks the very shortened pleon and maxillipedal endite of *Pendanthura*; it does not have a single-segmented mandibular palp as seen in *Ptilanthura* and *Exallanthura*; it lacks the maxillipedal endite and two-segmented mandibular palp of *Venezanthura*. Wägele (1981) separates *Centranthura* from *Anthura* on the basis of the five distal maxillipedal setae being inserted in a shallow distal indentation, rather than laterally as in *Anthura*. Further differences include the multidentate lamina dentata and the spiculate molar of *C. caeca*, and the reduced antennal flagellum.

Centranthura caeca perhaps represents a form in the evolution of reduction of the maxillipedal segments from five (as in *Malacanthura*) and four (as in *Haliophasma*). This reduction is probably correlated with a specialized mode of feeding as part of the infauna of fine-sediment embayments. The marginally setose and broad segments of pereopods 2–7 are probably also correlated with this habitat choice.

Cyathura Norman & Stebbing, 1886

Diagnosis

Eyes present or absent. Mandibular palp 3-segmented. Maxilliped 4-segmented; endite absent. Pereopod 1 subchelate, propodus expanded; pereopods 2–3 ambulatory; pereopods 4–7 with triangular carpus underriding propodus. Pleopod 1 exopod operculiform. Pleonites 1–5 fused, pleonite 6 free or fused to telson. Telson with two basal statocysts.

Type species

Anthura carinata Krøyer, 1847.

Cyathura estuaria Barnard, 1914

Figs 11–12

Cyathura estuaria Barnard, 1914: 334a, pl. 27D; 1955: 5. Miller & Burbanck, 1961: 62, 65. Burbanck & Burbanck, 1972: 274. Kensley, 1978a: 47, fig. 21A–B.
Cyathura carinata non Krøyer, Barnard, 1940: 490. Day, Millard, & Harrison, 1952: 408. Day, Millard, & Broekhuysen, 1954: 152. Millard & Harrison, 1954: 176. Day, 1959: 532; 1969: 78, fig. (unnumbered). Boltt, 1969: 253, 255, 259, 261.
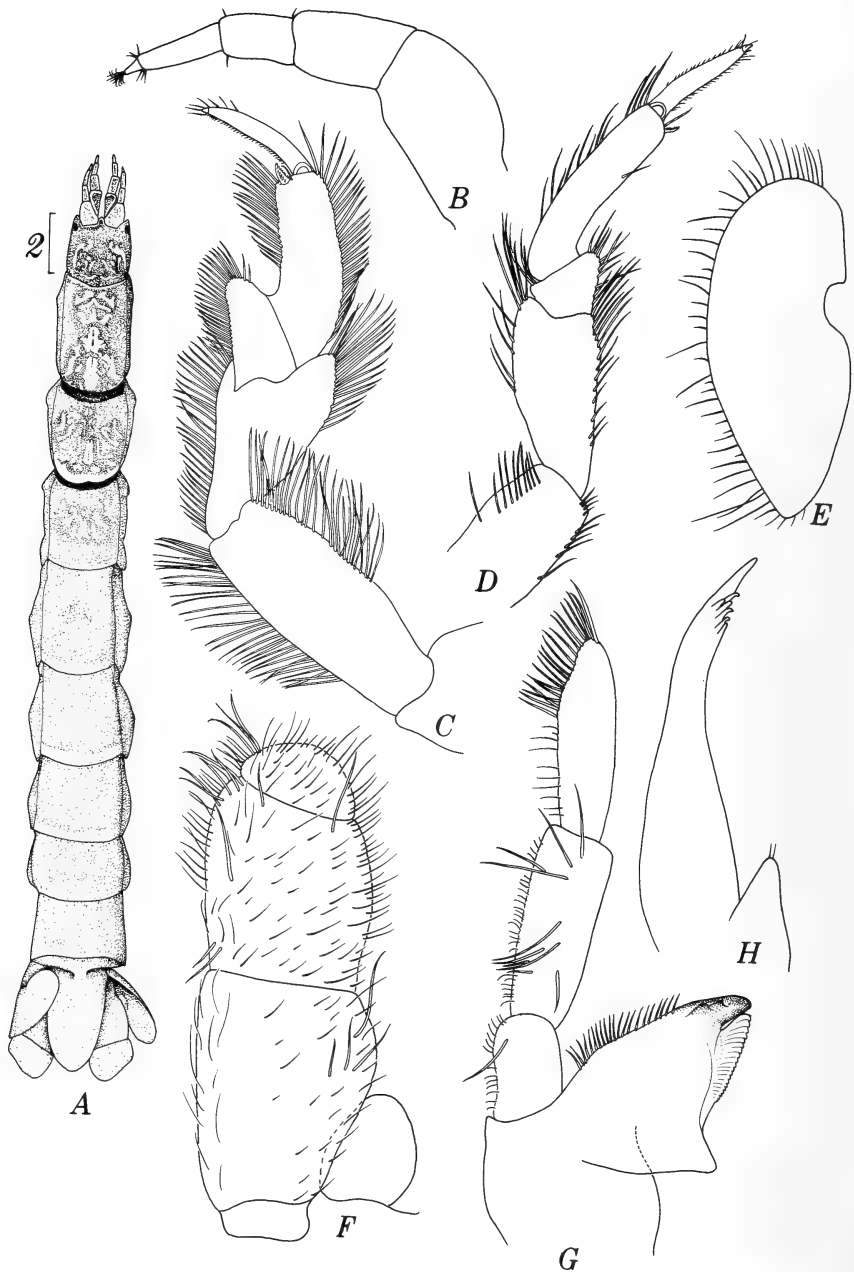*Cyathura* sp., Day, 1967: figs 3–4.

Fig. 11. *Cyathura estuaria*. A ♀ dorsal view. B. Antennule. C. Pereopod 2. D. Pereopod 7. E. Uropodal exopod. F. Maxilliped. G. Mandible. H. Maxilla. Scale in mm.

Diagnosis

Integument moderately setose. Telson parallel-sided for three-quarters of length, distally rounded, fused mediodorsally with pleonite 6. Copulatory stylet of pleopod 2 endopod in male not extending beyond ramus. Pereopod 1 female with rounded tooth on propodal palm; carpus distally produced, rounded.

Type material

Syntype, SAM–A68, 1 non-ovig. ♀, 27,5 mm, Buffalo River estuary. Syntypes, SAM–A2269, 14 juvs, 3,2–8,0 mm, Zwartkops River estuary. Syntypes, SAM–A14073, 3 juvs, 7,0 mm. Zwartkops River estuary.
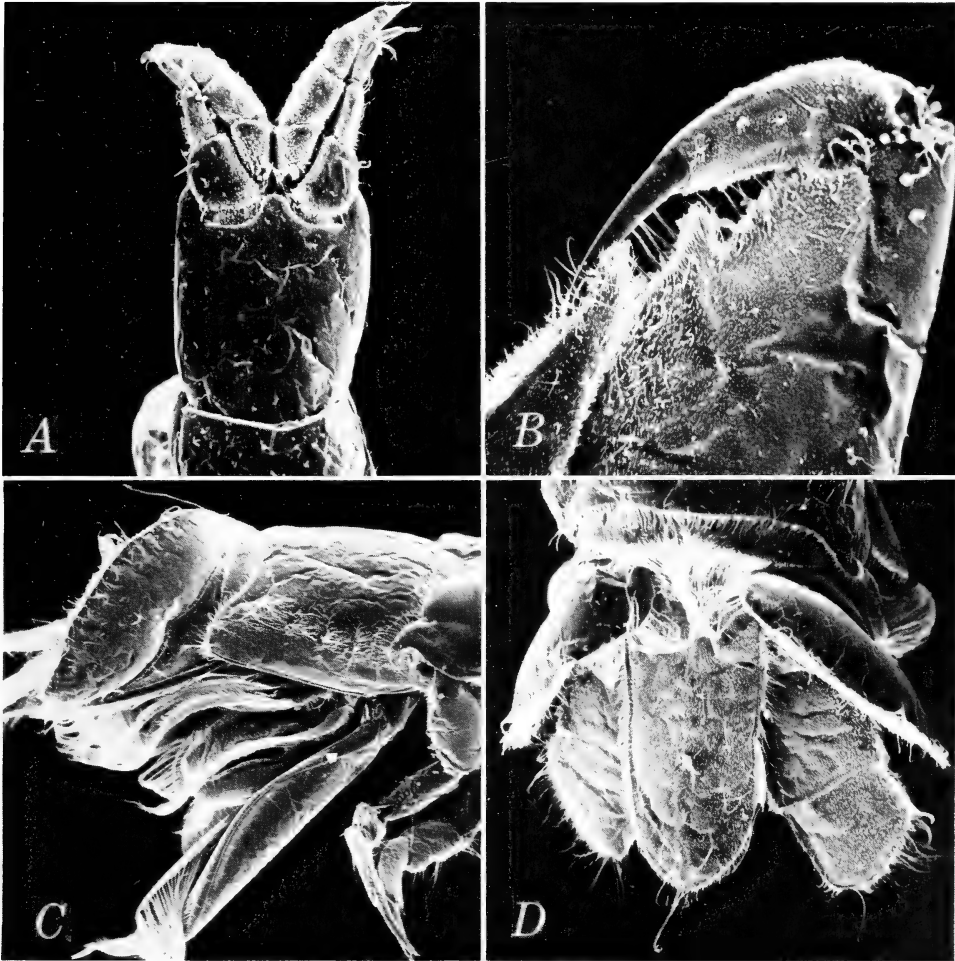

Fig. 12. *Cyathura estuaria.* A. ♀ cephalon. B. Pereopod 1, dactylus and propodus. C. Pleon, lateral view. D. Telson and uropods, dorsal view.

Other material

SAM–A6289, 1 juv., St. Lucia estuary. University College of Zululand, 1 non-ovig. ♀, 20,1 mm, Lake Msingazi, Zululand.

Distribution

Langebaan Lagoon; east coast estuaries and lakes from Zwartkops River, Port Elizabeth, to Zululand.

Remarks

The species has been taken from estuarine muds in salinities ranging from 0 to 35‰.

Haliophasma Haswell, 1881

Exanthura Barnard, 1914: 336a.

Diagnosis

Integument usually indurate, often with scattered small pits. Pereonites 4–6 each with single mid-dorsal pit. Pleonites 1–5 fused, pleonite 6 free, or rarely more or less fused with telson. Telson often sculptured, indurate, with pair of basal statocysts. Antennular flagellum of two to six articles. Antennal flagellum of four to seven articles. Mandibular palp three-segmented. Maxilliped four -segmented, rarely with very reduced endite. Pereopod 1 propodus expanded. Pereopods 2–3 ambulatory, propodi not expanded. Pereopods 4–7 with rectangular carpi, not underriding propodi. Pleopod 1 exopod operculiform, often indurate.

Type species

Haliophasma purpureum Haswell, 1881.

Remarks

Since the diagnosis of *Haliophasma* provided by Poore (1975), it has become obvious that several of the South African species formerly in this genus really belong to *Malacanthura* with its characteristically five-segmented maxilliped. Only *H. tricarinatum* remains of the seven southern African species previously placed in *Haliophasma*.

The genus *Exanthura* Barnard, 1914, was created for *E. macrura* Barnard, *E. filiformis* (Lucas) being added later. On the basis of *E. macrura* however, there is little justification for separating this genus from *Haliophasma*. The maxilliped of *E. macrura* does carry a tiny endite, not seen in *Haliophasma* s.s., while the basal antennular segment bears a strong recurved spiniform process that becomes obsolete in mature specimens. This antennular feature is regarded as being only of specific value.

The position of *E. filiformis* (Lucas) is uncertain, as the type has not been located. The description and figures given by Larwood (1940) for *E. filiformis*
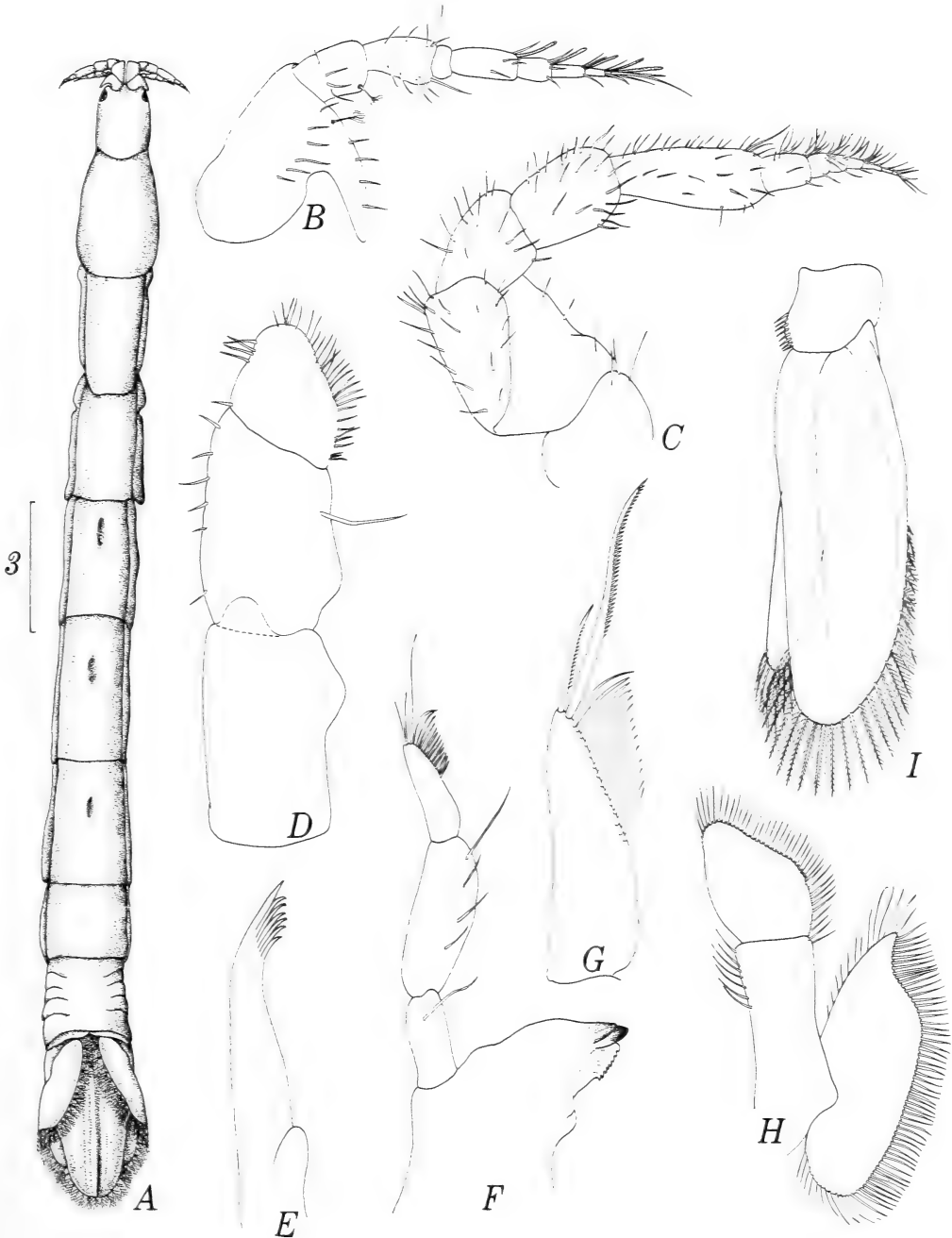
Fig. 13. *Haliophasma austroafricana*. A. ♀ dorsal view. B. Antennule. C. Antenna.
D. Maxilliped. E. Maxilla. F. Mandible. G. Distal mandibular palp segment. H. Uropod.
I. Pleopod 1. Scale in mm.

from the Mediterranean, however, show a five-segmented maxilliped. As the South African and Mediterranean material previously assigned to this species obviously do not belong to the same species, a new name is provided for the former.

<div style="text-align:center">KEY TO THE SOUTH AFRICAN SPECIES OF HALIOPHASMA</div>

1. Telson dorsally smooth, distally truncate .... *macrurum*
– Telson dorsally ridged, distally rounded 2
2. Telson with single mid-dorsal ridge .... *austroafricanum*
– Telson with 3 dorsal ridges .... *tricarinatum*

<div style="text-align:center">

Haliophasma austroafricanum sp. nov.

Figs 13–15
</div>

Exanthura filiformis (*non* Lucas): Barnard, 1920: 340; 1925*b*: 388; 1925*a*: 131, pl. 4, fig. 22; 1940: 490, 497; 1959: 715, fig. 1. Nierstrasz, 1941: 239 (*partim*). Day, Field & Penrith, 1970: 47. Kensley, 1975*a*: 38; 1978*a*: 47, fig. 21C. Wägele, 1981: 114.

Diagnosis

Body slender, parallel-sided; pereonites 4–6 each with strong mid-dorsal pit. Basal segment of antennule with strong conical, posteriorly-directed tooth-like process. Telson with strong mid-dorsal carina. Mature female unknown.

Description

Non-ovigerous female. Integument moderately indurate; numerous short setae arising from shallow 'dimples' scattered over entire integument. Body proportions: $C < 1 = 2 > 3 < 4 < 5 > 6 > 7 = P$. Cephalon with strong triangular rostrum slightly overreaching anterolateral corners. Large dorsolateral eyes. Pereonites 4–6 each with strong mid-dorsal elongate-oval pit. Pleonites 1–5 fused, fusion lines marked by dorsolateral grooves; pleonite 6 free, very short, with mid-dorsal notch in posterior margin. Telson with lateral margins subparallel, faintly sinuous; distal margin truncate-rounded, densely setose; strong longitudinal mid-dorsal carina present.

Basal antennular peduncle segment longer and broader than two following segments, with strong tapering posteriorly-directed tooth-like process; flagellum of six articles, four distal articles each with single aesthetasc. Antenna bearing numerous short setae, second peduncle segment longer than segment 3; segments 3 and 4 subequal, segment 5 one-third longer than 4; flagellum of seven setose articles. Mandibular palp segment 2 longest, segment 3 with fourteen simple distal spines and one short and one elongate serrate spine; incisor of two cusps; lamina dentata of nine serrations; molar reduced, rounded. Maxilla with one strong and six more slender distal spines. Maxilliped four-segmented, distal segment rounded, setose, set obliquely on segment 3; endite absent, segments 2 and 3 subequal in length. Pereopod 1 subchelate, expanded; unguis strong, more than half length of rest of dactylus; propodal
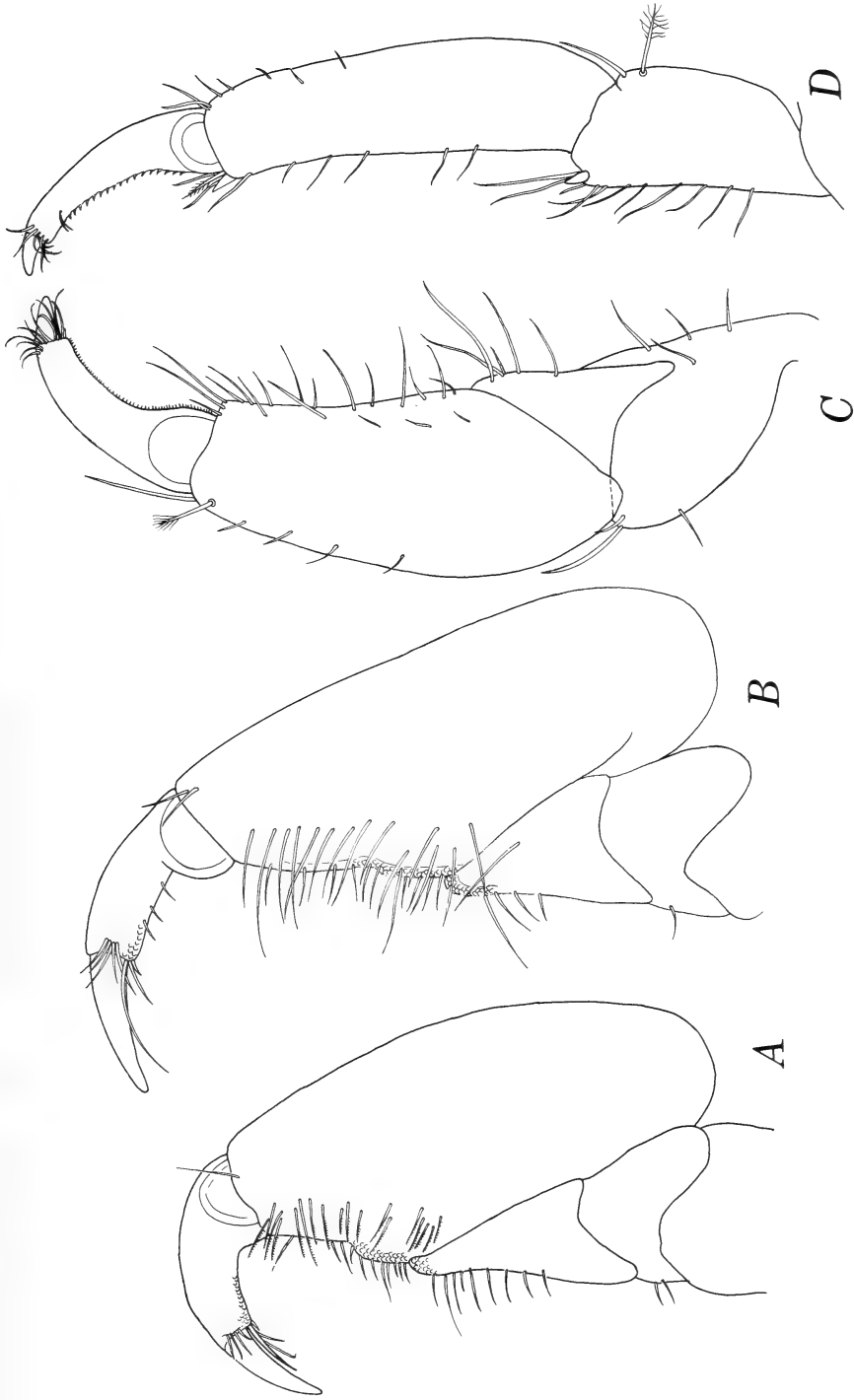
Fig. 14. *Haliophasma austroafricanum*. A. Pereopod 1 ♀. B. Pereopod 1 ♂. C. Pereopod 2. D. Pereopod 7.

palm with low rounded scale-bearing lobe in proximal half, few simple marginal setae; inner surface near palm with several fringed spines; carpus triangular, short. Pereopods 4–7 with unguis about one-fifth length of dactylus; propodus elongate-rectangular, with short spine at posterodistal angle; carpus rectangular, with short spine at posterodistal angle. Pleopod 1 exopod operculiform, distal margin densely fringed with plumose setae, outer surface with groove close to lateral margin, shorter ridge set back from medial margin; endopod tapering, not reaching exopod apex; basis with seven or eight coupling hooks, Uropodal exopod reaching beyond base of endopod, margin finely denticulate, densely setose, distally acute, lateral margin with strong distal sinuousity; endopod not reaching telsonic apex, margins finely denticulate, strongly setose, tapering distally, apically rounded.

Male. Antennular flagellum of twenty aesthetasc-bearing articles. Pereopod 1 propodus with dense band of simple setae on inner surface near palm. Pleopod 2 endopod with copulatory stylet reaching distal margin of ramus, distally spooned.

Type material

Holotype, SAM–A14078, non-ovig. ♀, 26,5 mm, 33°50′S 25°47′E (near Port Elizabeth), 36 m. Paratype, SAM–A5965, non-ovig. ♀, 21,5 mm, off Cape Infanta, 86 m. Paratype, SAM–A4012, non-ovig. ♀, 22,5 mm, off Cape Peninsula, 460 m.

Other material

SAM–A14079, 1 juv., False Bay, 68 m. SAM–A14081, 1 juv., False Bay, 75 m. SAM–A14086, 1 juv., False Bay, 33 m. SAM–A14088, 3 juvs, False Bay, 42 m. SAM–A14089, 1 sub♂, False Bay, 87 m. SAM–A14090, 1 juv., False Bay, 73 m. SAM–A14095, 1 juv., False Bay, 36 m. SAM–A14096, 1 juv., False Bay, 31 m. SAM–A14098, 1 juv., False Bay, 18 m. SAM–A14102, 1 juv., False Bay. SAM–A14075, 1 non-ovig. ♀, Agulhas Bank, 45 m. SAM–A14077, 1 non-ovig. ♀, Agulhas Bank, 44 m. SAM–A14085, 1 juv., Agulhas Bank, 200 m. SAM–A14091, 1 juv., Agulhas Bank, 42 m. SAM–A14092, 1 juv., Agulhas Bank, 183 m. SAM–A17504, 2 juvs, off Natal–Transkei, 80 m. SAM–A17505, 1 juv., off Natal–Transkei, 90 m. SAM–A17506, 1 juv., off Natal–Transkei, 560–620 m. SAM–A17507, 1 juv., off Natal–Transkei, 150–200 m. SAM–A17508, 1 juv., off Natal–Transkei, 550 m.

Distribution

Saldanha Bay to Natal, 19–620 m.

Etymology

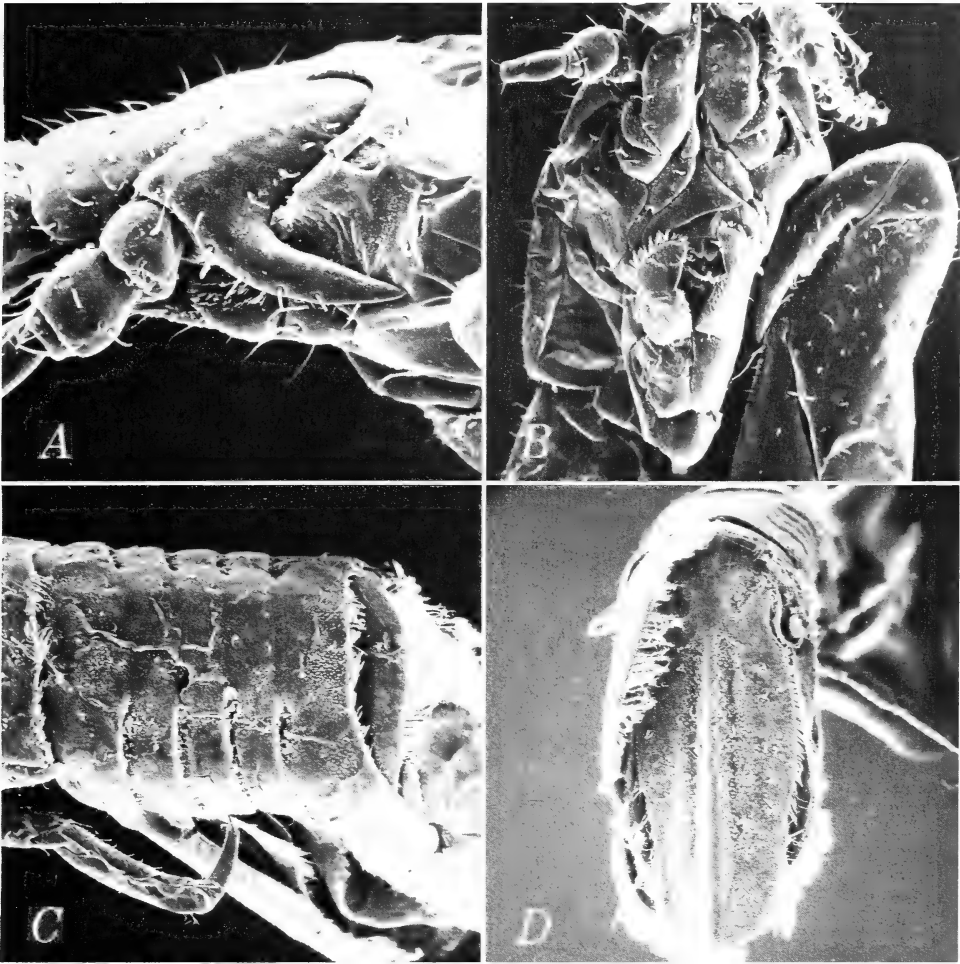The specific name refers to South Africa, where the species appears to be endemic.

Fig. 15. *Haliophasma austroafricanum*. A. Antennular base. B. Cephalon, ventral view. C. Pleon. D. Telson.

Haliophasma macrurum (Barnard, 1914)
Figs 16–18

Exanthura macrura Barnard, 1914: 337a, pl. 28A; 1925a: 131, fig. 7; 1940: 490, 497; 1955: 5. Penrith & Kensley, 1970: 227. Kensley, 1978a: 47, fig. 21D. Wägele, 1981: 114.
Exanthura macruron (*sic*): Nierstrasz, 1941: 239.

Diagnosis

Body widening posteriorly, pereonites 4–6 each with strong mid-dorsal pit. Telson widening posteriorly, distal margin truncate. Uropods and telson together forming cup-shaped protective 'operculum', margins densely setose.
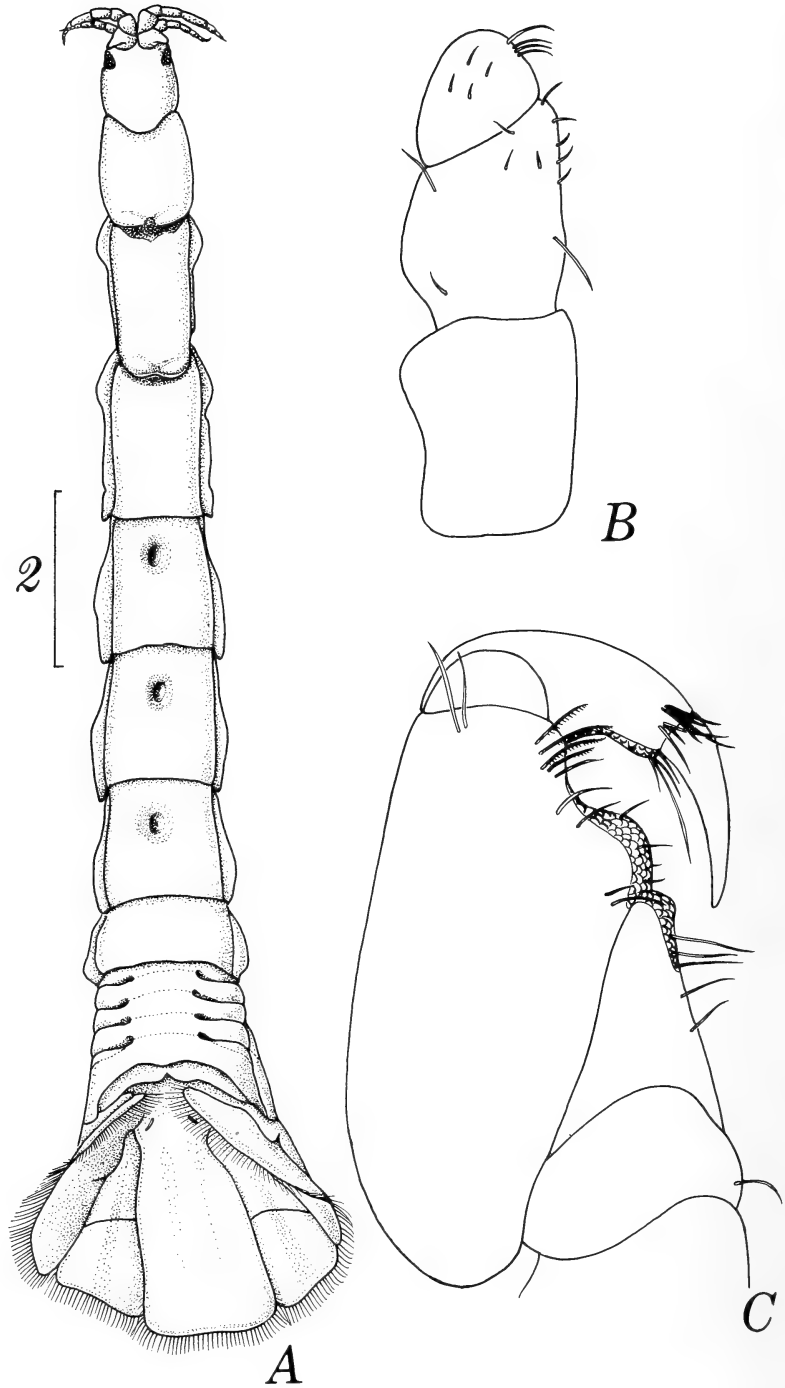
Fig. 16. *Haliophasma macrurum*. A. ♀ dorsal view. B. Maxilliped. C. Pereopod 1. Scale in mm.

Antennule with basal segment bearing conical, posteriorly-directed tooth-like process. Male unknown.

Type material

Holotype, SAM–A2667, non-ovig. ♀, ± 22 mm TL (telson sectioned by Barnard), Sea Point, Table Bay.

Other material

SAM–A12740, 2 juvs, 1 non-ovig. ♀, 28,0 mm, Lüderitz, intertidal. SAM–A14105, 1 juv., 15,2 mm, Strandfontein, Cape, intertidal. SAM–A14104,
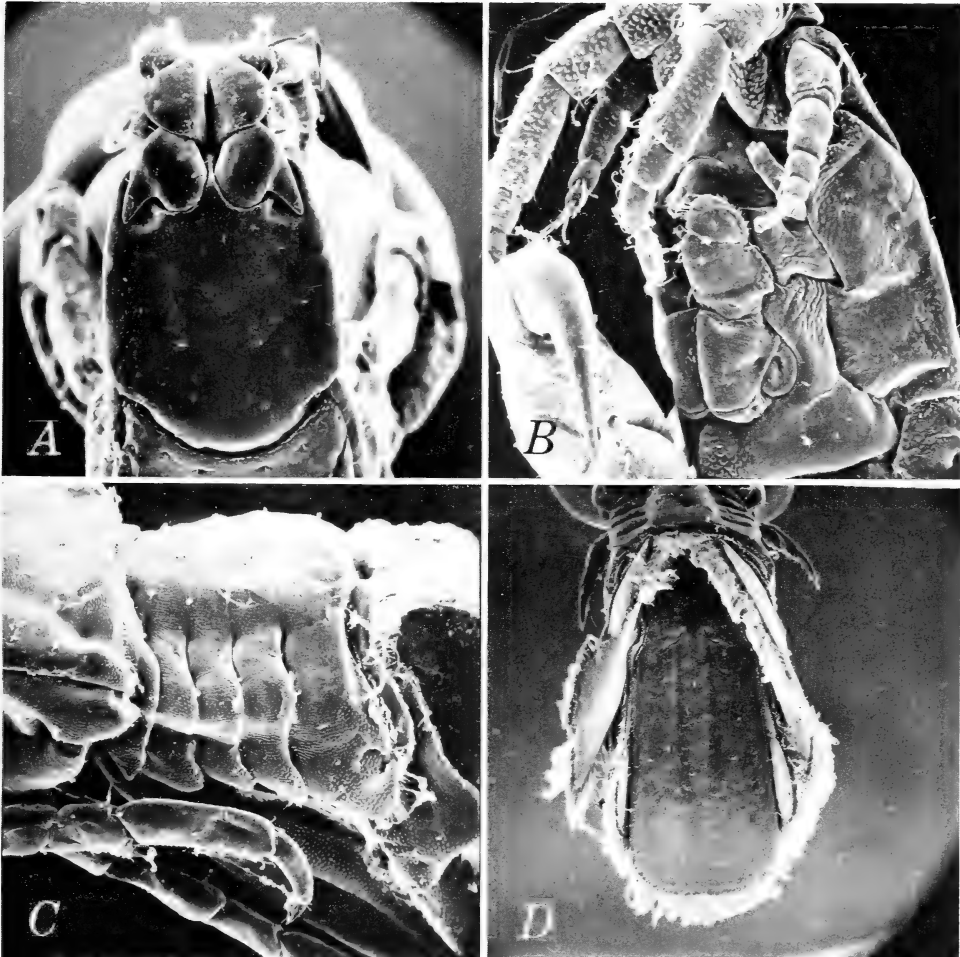

Fig. 17. *Haliophasma macrurum*. A. ♀ cephalon, dorsal view. B. Cephalon, lateral view. C. Pleon. D. Telson.

Fig. 18. *Haliophasma macrurum*. A. Pereopod 7. B. Pleopod 1 exopod. C. Statocyst apertures. D. Rounded bosses at base of pleopod 1.

1 juv., 17,0 mm, Kommetjie, Cape. SAM–A14103, 1 juv., 12,0 mm, locality unknown.

Distribution

Lüderitz to False Bay.

Remarks

Haliophasma macrurum has been found on several occasions in the tubes of the intertidal reef-building polychaete worm *Gunnerea capensis*, on which it probably preys. The cup-shaped and sclerotized tail fan neatly closes the tube mouth, affording the isopod protection while it feeds.
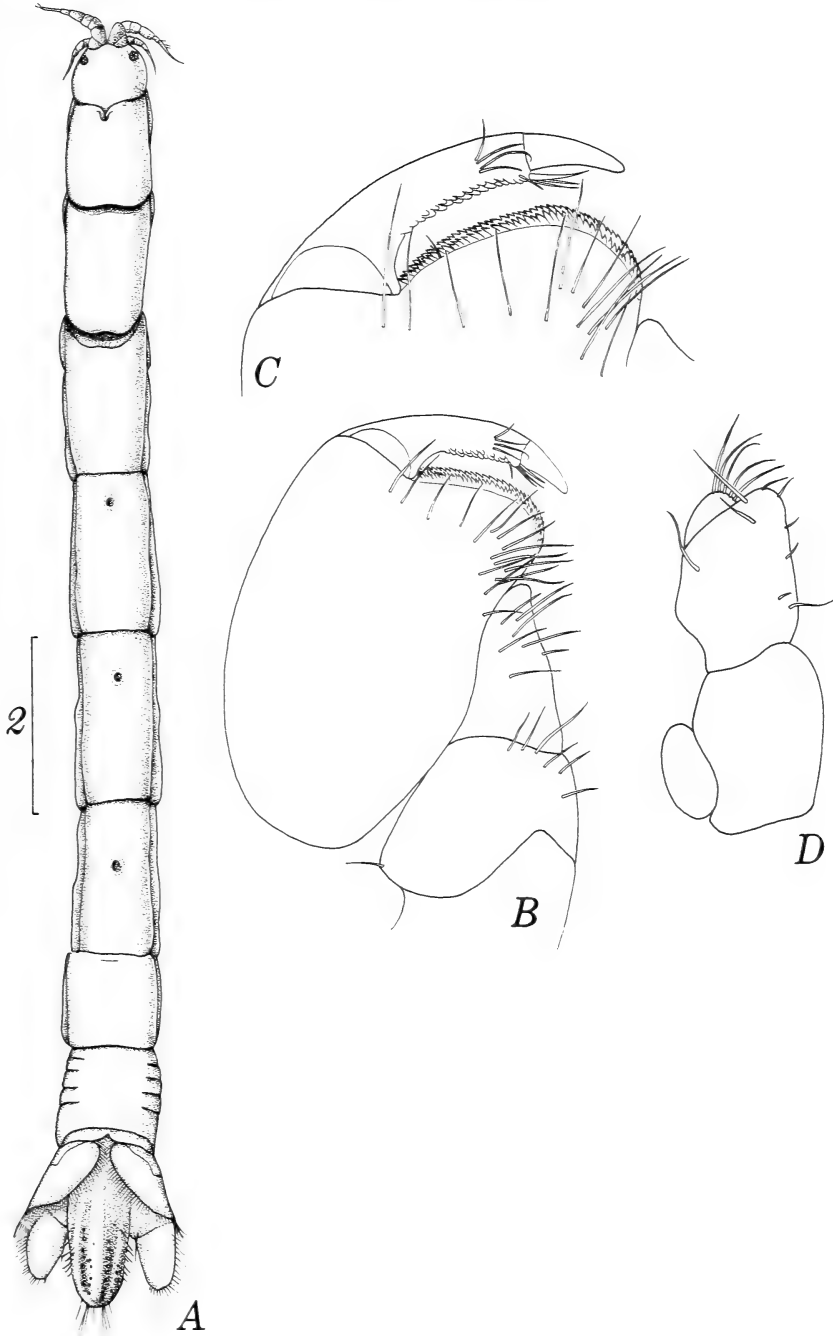
Fig. 19. *Haliophasma tricarinatum*. A. ♀ dorsal view. B. Pereopod 1 ♀. C. Dactylus and propodal palm of pereopod 1 ♀. D. Maxilliped. Scale in mm.

Haliophasma tricarinatum Barnard, 1925
Figs 19–20

Haliophasma tricarinata Barnard, 1925a: 132, pl. 4 (fig. 2); 1925b: 385; 1940: 490, 498; 1955: 50. Day, Field & Penrith, 1970: 47. Kensley, 1978a: 50, fig. 22D.
Haliophasma tricarinatum: Nierstrasz, 1941: 239. Poore, 1975: 532.

Diagnosis

Body slender. Pereonites 4–6 each with mid-dorsal pit. Telson with three dorsal rounded longitudinal ridges, with scattered pits between; strong longitudinal midventral keel; posterior margin broadly rounded. Basal antennular segment with outer margin rounded. Pereopod 1 propodal palm a broadly rounded lobe with rows of fine acute scales along margin. Male unknown.

Type material

Holotype, SAM–A5968, non-ovig. ♀, 14,0 mm, Agulhas Bank, 80 m.

Other material

SAM–A14188, 1 juv., off Saldanha Bay, 70 m. SAM–A14076, 1 juv., False Bay, 53 m. SAM–A14083, 1 juv., False Bay, 80 m. SAM–A14084, 1 juv., False Bay, 39 m. SAM–A14186, 1 non-ovig. ♀, False Bay. SAM–A14191, 1 juv., False Bay. SAM–A14192, 1 juv., False Bay, 48 m. SAM–A14093, 1 juv., Agulhas Bank, 183 m. SAM–A14101, 1 juv., Agulhas Bank, 73 m. SAM–A14190, 1 non-ovig. ♀, Agulhas Bank, 84 m. SAM–A5967, 1 non-ovig. ♀, off Cape St. Blaize, 84 m. SAM–A17509, 1 juv., off East London, 90 m.

Distribution

Saldanha Bay to south of East London, 48–183 m.

Kupellonura Barnard, 1925a

Diagnosis

Eyes small or absent. Mandibular palp three-segmented; molar relatively short. Maxilliped seven-segmented; endite well developed. Pereopods 1–3 subsimilar, subchelate; pereopods 4–7 with triangular carpus underriding propodus. Pleonites 1–6 elongate, free. Pleopod 1 similar to following pleopods, not operculiform.

Type species

Kupellonura mediterranea Barnard, 1925a.

Kupellonura capensis (Kensley, 1975a)
Fig. 21

Holoroanthura (sic) capensis Kensley, 1975a: 75, figs 19–20.
Horoloanthura capensis: Kensley, 1978a: 50, fig. 22 E–G.
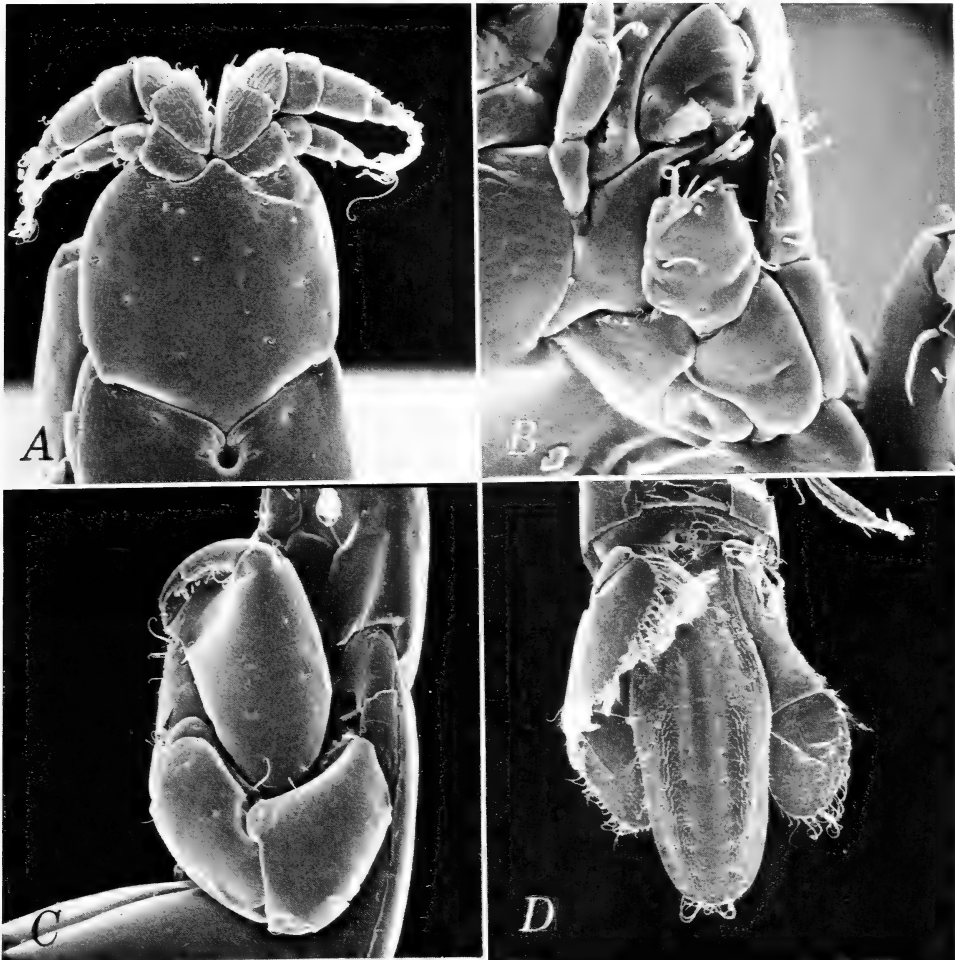*Kensleyanthura capensis:* Wägele, 1981: 106.

Fig. 20. *Haliophasma tricarinatum*. A. ♀ cephalon, dorsal view. B. Mouthparts.
C. Pereopod 1. D. Telson.

Diagnosis

Eyes absent. Telson somewhat broadened in posterior half, then tapering to narrowly rounded apex; margin denticulate. Uropodal exopod folding over telson, with narrow distal extension; medial margin dentate.

Type material

Holotype, SAM–A13555, 1 ♂, 3,8 mm, off Lambert's Bay, 128 m. Allotype, SAM–A13624, 1 non-ovig. ♀, 6,1 mm, off Lambert's Bay, 400 m. Paratypes, SAM–A13625, 1 sub♂, 3,1 mm, 5 non-ovig. ♀, 4,2–5,0 mm, off Lambert's Bay, 172 m.

Other material

SAM–A14193, 1 non-ovig. ♀, off Saldanha Bay, 141 m. SAM–A14194, 2 non-ovig. ♀, off Saldanha Bay, 183 m. SAM–A14195, 4 non-ovig. ♀, off Saldanha Bay, 183 m. SAM–A14196, 1 non-ovig. ♀, off Lambert's Bay, 128 m. SAM–A14197, 1 non-ovig. ♀, Agulhas Bank, 183 m.

Distribution

Lambert's Bay to Agulhas Bank, 128–400 m.

Remarks

Horoloanthura irpex Menzies and Frankenberg, the type species of *Horoloanthura*, was incorrectly described and figured as having six free elongate pleonites and a five-segmented maxilliped lacking an endite. In fact, pleonite 6 is fused to the spiculate telson, and the maxilliped is seven-segmented, with a well-developed endite. Wägele (1981) correctly states that *H. irpex* should be in the genus *Neohyssura*. Thus *H. capensis*, which is not a *Neohyssura*, must be accommodated elsewhere. Wägele (1981) erected the new genus *Kensleyanthura* for *H. capensis*. Unfortunately, Kensley's description was inaccurate in the configuration of the maxilliped, which is seven-segmented with an endite. In fact, *H. capensis* agrees closely with *Kupellonura mediterranea* Barnard, and *K. serritelson* Wägele, 1981, in all features of the mouthparts, antennules, pleon, telson, and uropods.

Kupellonura capensis differs from *K. serritelson* in having a digitiform lobe on the uropodal exopod, and in having the uropodal endopod margins entire (the outer margin is serrulate in the Bermudan species). The telson of *K. capensis* is widest at about the distal third and is apically narrowly rounded. The telson of *K. serritelson* is widest at the midlength and distally broadly rounded.

Kupellonura mediterranea, of which the type from the Copenhagen Museum has been examined, has a telson similar in shape to *K. capensis* but with entire margins, except for a shallow subterminal notch on each side, and a uropodal exopod as in *K. serritelson*.

Malacanthura Barnard, 1925

Agulanthura Kensley, 1975a: 72.
Haliophasma: Barnard, 1925a: 131; 1940: 382; 1955: 50 (*partim*). Kensley, 1975a: 72. (*partim*).

Diagnosis

Eyes present. Antennular flagellum of three to six articles. Antennal flagellum of four to seven articles. Mandible with three-segmented palp; incisor, lamina dentata, and molar present. Maxilliped five-segmented, endite small to rudimentary, or absent. Pereopod 1 subchelate, propodus expanded. Pereopods 2–3 smaller than pereopod 1, ambulatory. Pereopods 4–7 with rectangular carpus not underriding propodus. Pleopod 1 exopod operculiform.
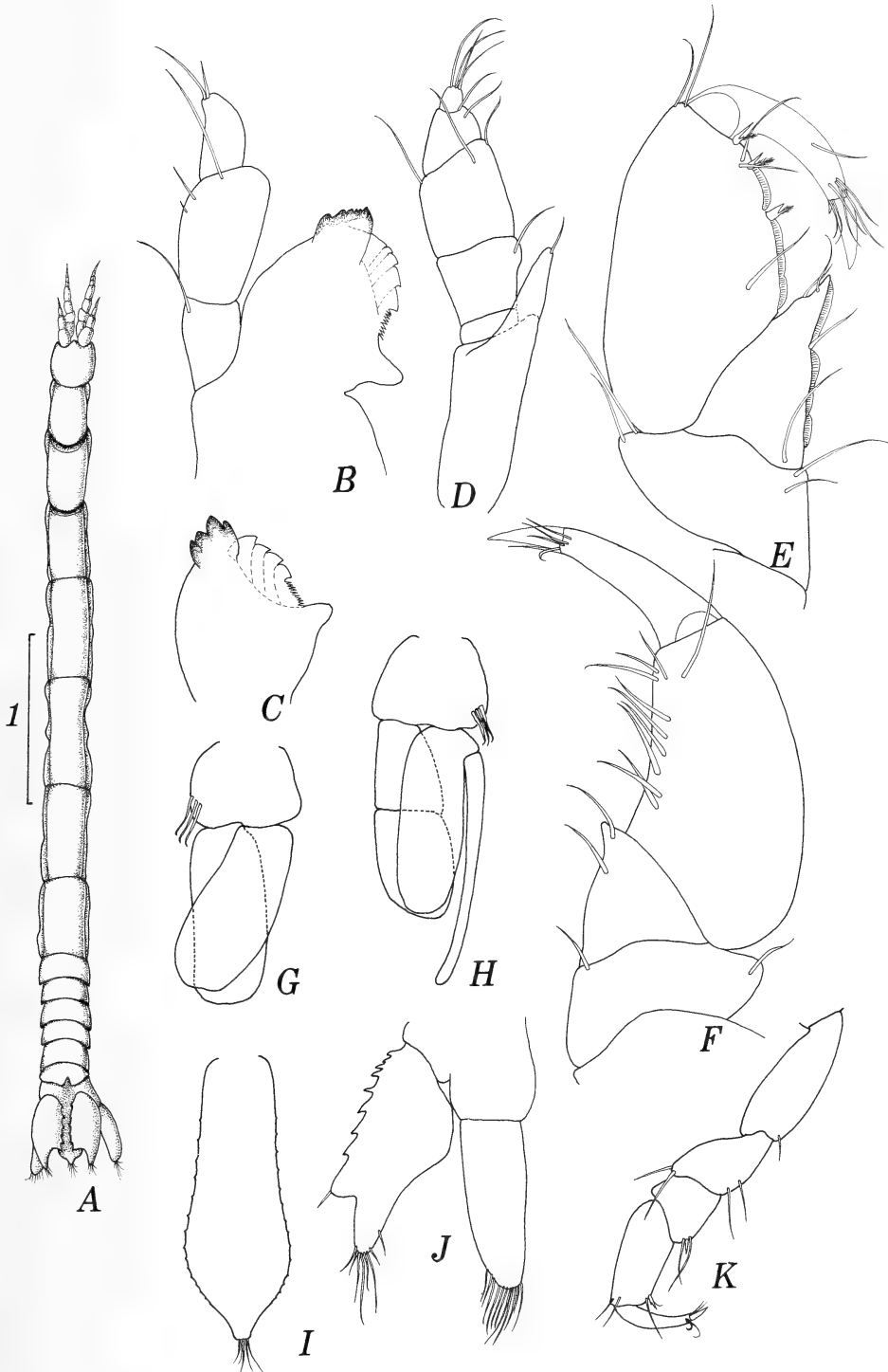
Fig. 21. *Kupellonura capensis*. A. ♀ dorsal view. B. Right mandible. C. Left mandibular incisor, lamina dentata, and molar. D. Maxilliped. E. Pereopod 1. F. Pereopod 2. G. Pleopod 1. H. Pleopod 2 ♂. I. Telson. J. Uropod. K. Pereopod 7. Scale in mm.

Pleonites 1–5 fused, pleonite 6 free. Telson with two basal statocysts. Pleon in male frequently more elongate than in female.

Remarks.

With Poore's 1975 redefinition of *Haliophasma*, it has become obvious that several of Barnard's species of *Haliophasma* belong to *Malacanthura* as now defined. Similarly, Kensley's *Agulanthura*, viewed in the light of the above redefinitions, is now regarded as a specialized *Malacanthura*.

Type species

Apanthura linguicauda Barnard, 1920.

KEY TO THE SOUTH AFRICAN SPECIES OF *MALACANTHURA*

1. Integument with numerous small pits 2
– Integument lacking numerous small pits 4
2. Telson unpitted, with single mid-dorsal ridge 3
– Telson pitted, obscurely tri-ridged .... *foveolata*
3. Uropodal exopod distally strongly notched .... *schotteae*
– Uropodal exopod oval-lanceolate, unnotched .... *transkei*
4. Telson unsculptured 5
– Telson with mid-dorsal and/or lateral ridges 6
5. Telson dorsally convex; uropodal exopod closely adpressed to telson .... *serenasinus*
– Telson dorsally flat; uropodal exopod freestanding, not adpressed to telson .... *linguicauda*
6. Telson dorsally concave, with very strong mid-dorsal ridge .... *hermani*
– Telson dorsally flat or convex 7
7. Telson with faint lateral ridges, lacking mid-dorsal ridge .... *ornata*
– Telson with faint lateral and mid-dorsal ridges 8
8. Telson almost as wide as long .... *pseudocarinata*
– Telson almost twice as long as wide .... *coronicauda*

Malacanthura coronicauda (Barnard, 1925)
Figs 22–23

Haliophasma coronicauda Barnard, 1925a: 132; 1925b: 386; 1940: 490, 498; 1955: 50.
   Nierstrasz, 1941: 239. Day, Field & Penrith, 1970: 47. Poore, 1975: 532. Kensley,
   1975a: 38; 1978a: 49, fig. 21F. Christie, 1976: 155.

Diagnosis

Telson with mid-dorsal raised area, faintly tri-ridged. Pereopod 1 propodal palm with arcuate proximal lobe, numerous simple setae along inner palmar margin.

Description

Non-ovigerous female. Integument moderately indurate, dorsally smooth, lacking pits. Proportions: $C < 1 = 2 = 3 > 4 < 5 > 6 > 7$. Cephalon with low rostrum, rounded anterolateral corners, large dorsolateral eyes. Pleonites 1–5 fused, no indication of lines of fusion in dorsal view; posterior margin of pleonite 5 with slight mid-dorsal point; pleonite 6 free, with mid-dorsal notch in posterior margin. Telson with 2 basal statocysts, widest at midlength, distally
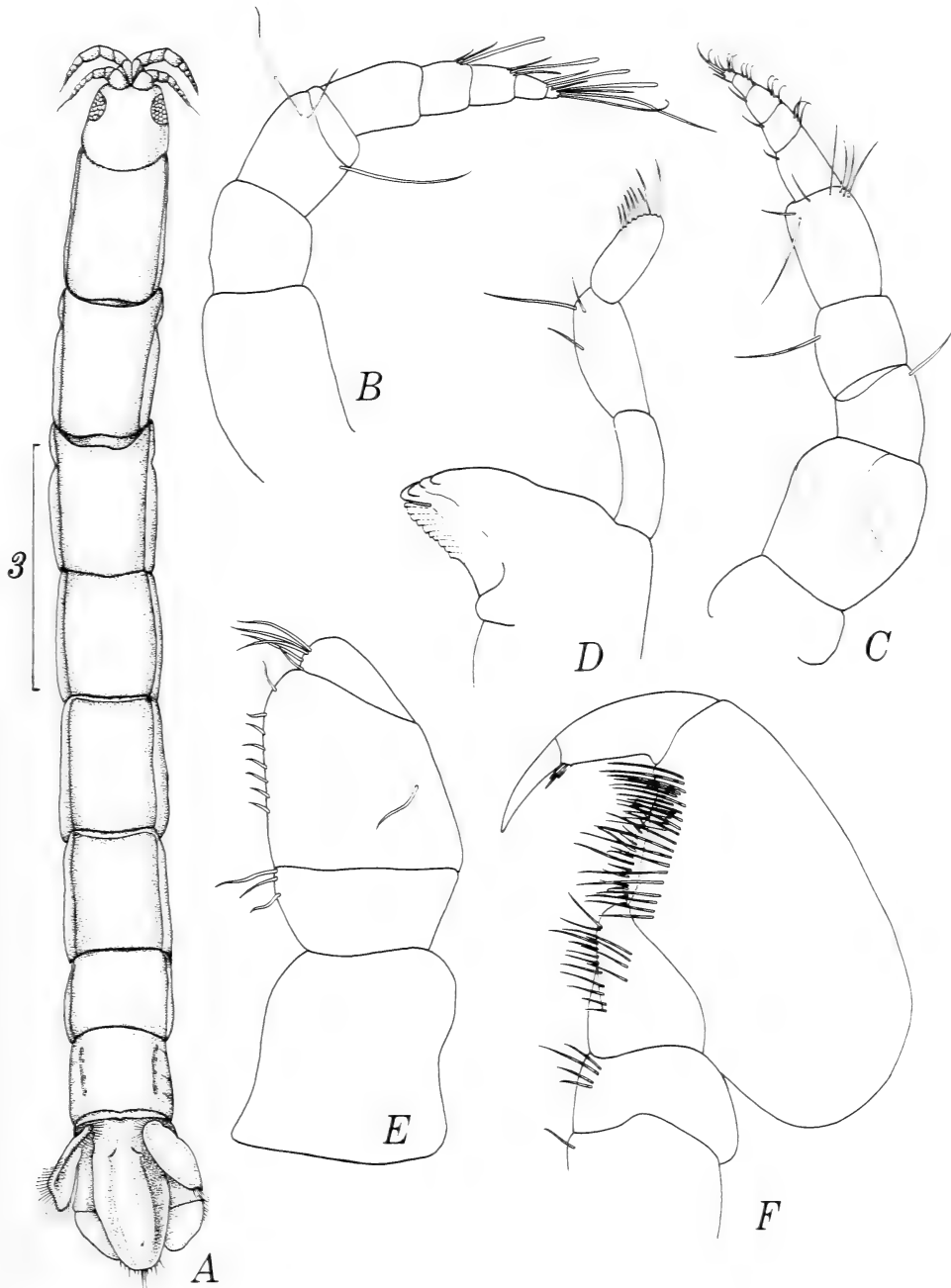
Fig. 22. *Malacanthura coronicauda*. A. ♀ dorsal view. B. Antennule. C. Antenna. D. Mandible. E. Maxilliped. F. Pereopod 1. Scale in mm.

broadly rounded with very low rounded mid-dorsal longitudinal ridge, and stronger lateral ridges.

Basal antennular segment equal to two distal segments together; flagellum of five articles. Antenna with segment 5 slightly longer than 4; flagellum of six articles. Mandibular palp three-segmented; molar low, rounded. Maxilliped five-segmented, terminal segment short, set obliquely on penultimate segment; latter with row of short medial setae; endite lacking. Pereopod 1 unguis more than half length of remainder of dactylus; propodus expanded, palm with low convex lobe proximally bearing setae, inner palmar margin with numerous simple setae. Pereopods 2–3 ambulatory; pereopods 4–7 with rectangular carpi; propodi, carpi, and meri with elongate setae on posterior margins. Pleopod 1 exopod operculiform, bearing numerous plumose setae distally, with strong groove on outer surface close to median line. Uropodal exopod just reaching distal margin of basis, apically narrowly rounded, with distinct sinuosity distally; endopod triangular, distally rounded.

Type material

Syntypes, SAM–A5962, 2 non-ovig. ♀, 16,0 mm, off Saldanha Bay, 174 m.

Other material

SAM–A14131, 1 juv., off Saldanha Bay, 82 m. SAM–A14135, 1 juv., off Saldanha Bay, 84 m. SAM–A14141, 1 ♂, off Saldanha Bay 141 m. SAM–A14144, 1 ♂, off Saldanha Bay, 146 m. SAM–A14146, 1 ♂, 2 non-ovig. ♀, off Saldanha Bay, 146 m. SAM–A14169, 1 non-ovig. ♀, off Saldanha Bay, 79 m. SAM–A14171, 1 non-ovig. ♀, off Saldanha Bay, 148 m. SAM–A14177, 1 ♂, off Saldanha Bay, 148 m. SAM–A14119, 1 non-ovig. ♀, False Bay, 26 m. SAM–A14125, 1 juv., False Bay, 81 m. SAM–A14127, 1 ♂, False Bay, 87 m. SAM–A14129, 2 non-ovig. ♀, False Bay, 80 m. SAM–A14130, 1 sub♂, 1 non-ovig. ♀, False Bay. SAM–A14132, 1 non-ovig. ♀, False Bay, 102 m. SAM–A14134, 1 ♂, 1 non-ovig. ♀, False Bay. SAM–A14136, 1 ♂, 3 non-ovig. ♀, False Bay, 82 m. SAM–A14137, 2 non-ovig. ♀, False Bay 71 m. SAM–A14138, 1 ♂, False Bay. SAM–A14140, 1 non-ovig. ♀, False Bay. SAM–A14142, 1 ♂, 1 non-ovig. ♀, False Bay SAM–A14143, 4 non-ovig. ♀, 1 juv., False Bay, SAM–A14145, 2 ♂, False Bay. SAM–A14147, 1 ♂, False Bay. SAM–A14149, 4 non-ovig. ♀, 2 juvs, False Bay. SAM–A14150, 2 ♂, 4 non-ovig. ♀, False Bay. SAM–A14151, 1 juv., False Bay. SAM–A14152, 1 non-ovig. ♀, False Bay. SAM–A14167, 3 non-ovig. ♀, 1 juv., False Bay, 53 m. SAM–A14168, 1 non-ovig. ♀, 1 juv., False Bay. SAM–A14170, 5 non-ovig. ♀, False Bay. SAM–A14172, 1 juv., False Bay, 53 m. SAM–A14173, 1 ♂, False Bay. SAM–A14174, 3 non-ovig. ♀, False Bay, 85 m. SAM–A14178, 2 non-ovig. ♀, False Bay, 87 m. SAM–A14179, 1 non-ovig. ♀, False Bay, 73 m. SAM–A14111, 1 non-ovig. ♀, Still Bay, 80 m. SAM–A14124, 1 non-ovig. ♀, Still Bay, 80 m. SAM–A14153, 1 ♂, 2 juvs, Agulhas Bank, 97 m. ZMC 51.68,
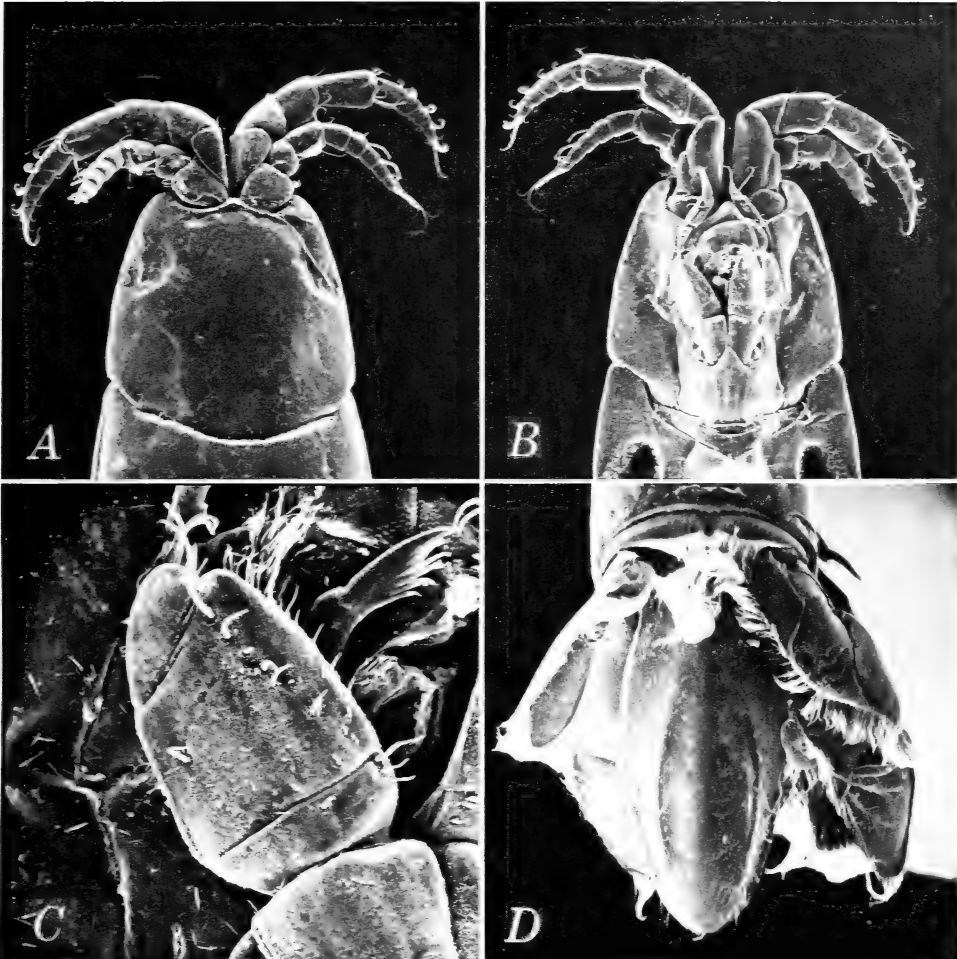
Fig. 23. *Malacanthura coronicauda*. A. ♀ cephalon, dorsal view. B. ♀ cephalon, ventral view. C. Maxilliped. D. Telson and uropods.

Th. Mortensen Expedition, 1 ♂, False Bay. ZMC, *Galathea* Expedition, station 165, 1 ♂, 1 juv., False Bay.

Distribution

Saldanha Bay to Agulhas Bank, 26–174 m.

Malacanthura foveolata (Barnard, 1940)
Figs 24–25

Haliophasma foveolata Barnard, 1940: 384, 490, 498, fig. 2; 1955: 50, fig. 24 a–c. Day, Field & Penrith, 1970: 47. Poore, 1975: 532. Kensley, 1975a: 38; 1978a: 49. Wägele, 1981: 86.
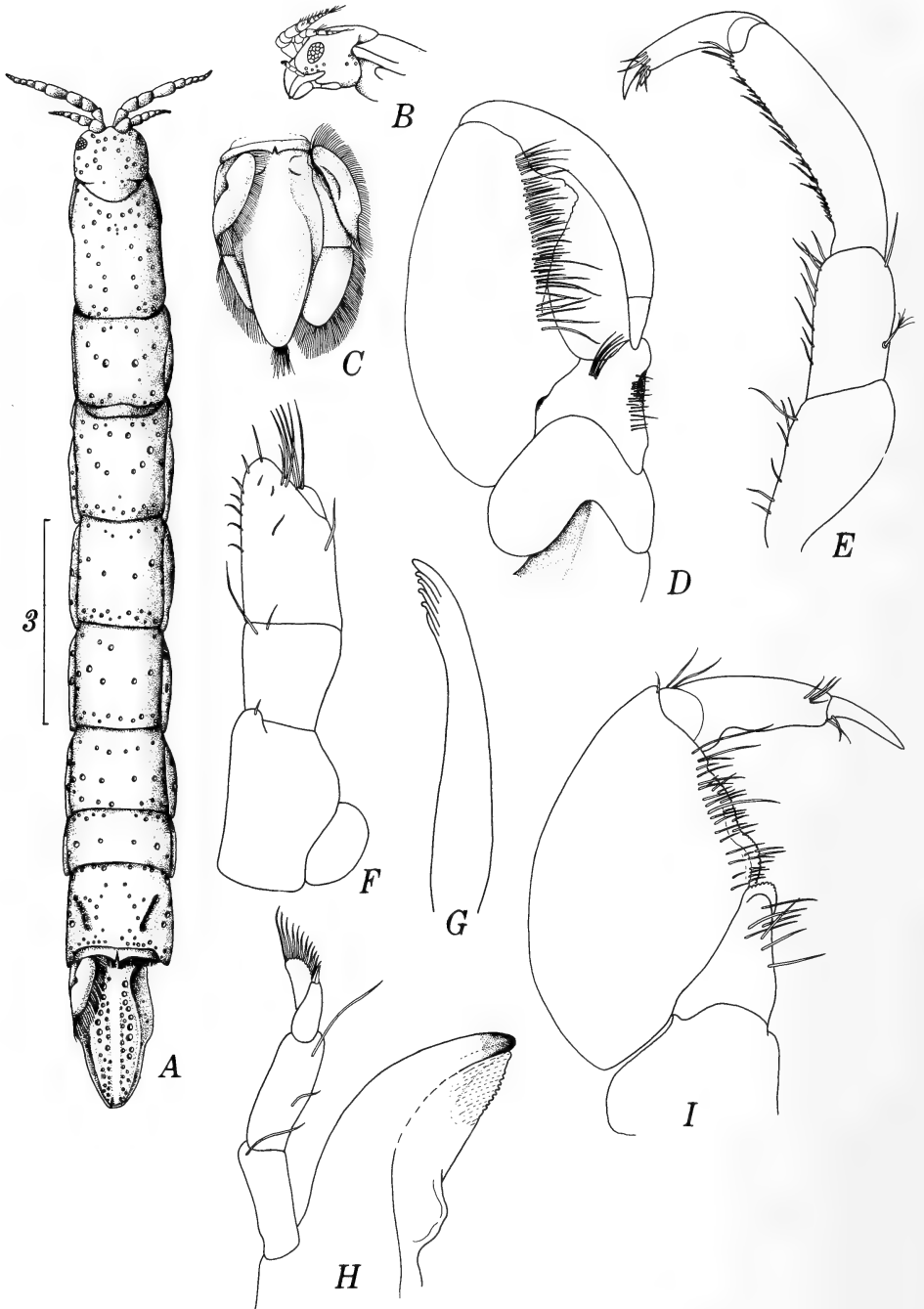
Fig. 24. *Malacanthura foveolata*. A. ♀ dorsal view. B. Cephalon, lateral view. C. ♂ telson. D. Pereopod 1 ♂. E. Pereopod 7. F. Maxilliped. G. Maxilla. H. Mandible. I. Pereopod 1 ♀. Scale in mm.

Diagnosis

Body strongly indurate, with numerous small scattered pits. Telson in female constricted at midlength, with rounded mid-dorsal longitudinal and lower lateral ridges, several pits between ridges. Telson in male similar in outline to female, but ridges less marked, pits lacking. Pereopod 1 in female with propodal palm somewhat sinuous, setose; in male, propodal palm deeply concave, with distal broadly triangular process; band of simple setae on inner surface near palmar margin.

Type material

Holotype, SAM–A8280, 1 non-ovig. ♀, 12,1 mm, Port Elizabeth, intertidal.

Other material

SAM–A14158, 8 juvs, Saldanha Bay, 5 m. SAM–A14162, 1 non-ovig. ♀, Saldanha Bay, 24 m. SAM–A14180, 1 ♂, Saldanha Bay, 35 m. SAM–A14322, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14397, 2 non-ovig. ♀, off Saldanha Bay, 79 m. SAM–A14849, 1 sub♂, Langebaan Lagoon. SAM–A14155, 1 ♂, False Bay. SAM–A14159, 1 non-ovig. ♀, False Bay, 31 m. SAM–A14160, 1 non-ovig. ♀, False Bay, 73 m. SAM–A14161, 3 juvs, False Bay. SAM–A14163, 1 non-ovig. ♀, False Bay, 5 m. SAM–A14164, 1 sub♂, False Bay, 40 m. SAM–A14165, 1 non-ovig. ♀, False Bay. SAM–A14166, 1 non-ovig. ♀, False Bay, 22 m. SAM–A14846, 1 non-ovig. ♀, False Bay. SAM–A14950, 1 non-ovig. ♀, False Bay. SAM–A14156, 1 non-ovig. ♀, Agulhas Bank, 27 m. SAM–A14157, 1 non-ovig. ♀, off Still Bay, 120 m.
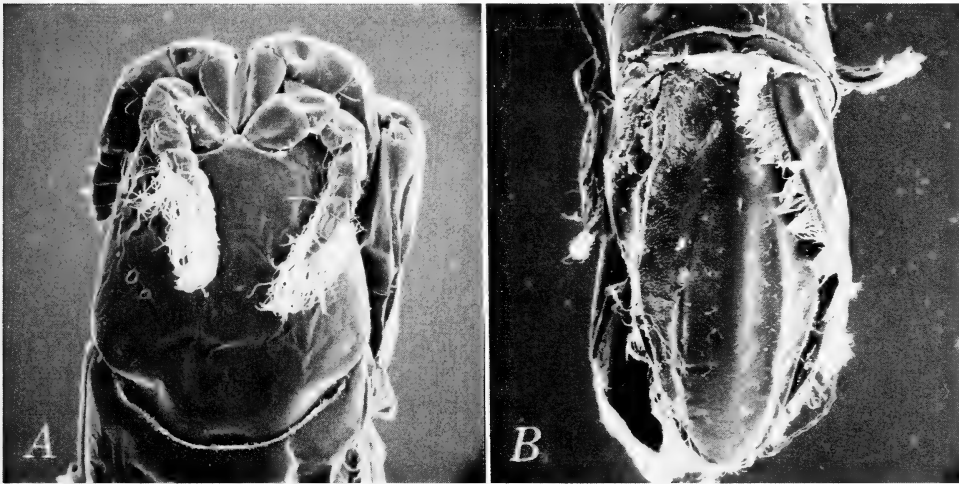

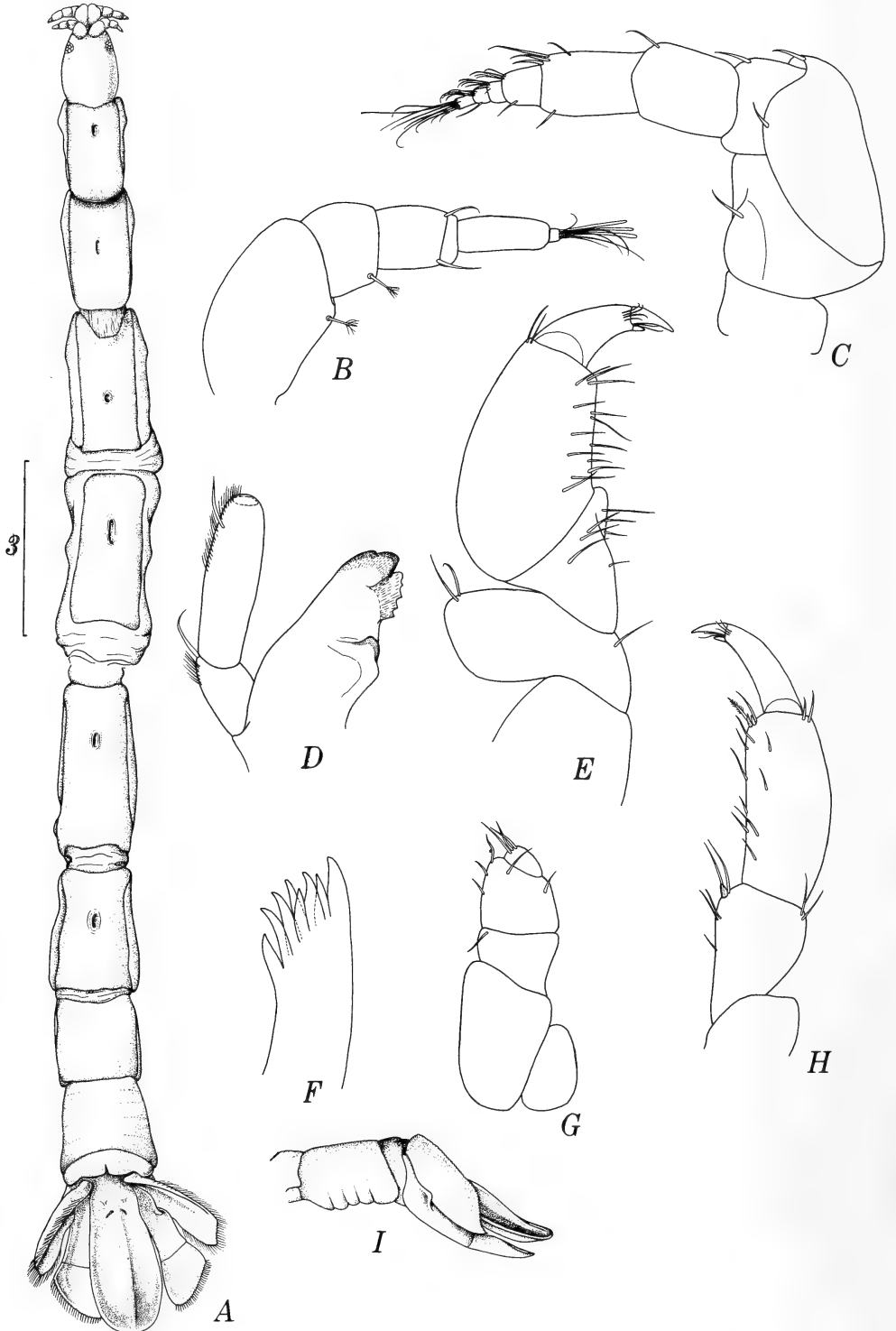Fig. 25. *Malacanthura foveolata*. A. Cephalon ♂ dorsal view. B. Telson ♂.

Fig. 26. *Malacanthura hermani*. A. ♀ dorsal view. B. Antennule. C. Antenna.
D. Mandible (distal palp segment missing). E. Pereopod 1. F. Maxilla. G. Maxilliped.
H. Pereopod 7. I. Pleon lateral view. Scale in mm.

Distribution

Saldanha Bay to Port Elizabeth, intertidal to 120 m.

Remarks

There is a marked loss of integumental pits as specimens increase in size, especially in the transition from female to submale to male.

Malacanthura hermani (Barnard, 1940)
Fig. 26

Haliophasma hermani Barnard, 1940: 383, 490, 498, fig. 1; 1955: 50. Poore, 1975: 532.
     Kensley, 1978a: 49, fig. 22A.

Diagnosis

Mid-dorsal pits on pereonites 1–6. Telson distally broadly rounded, dorsally concave, with strong mid-dorsal longitudinal carina, and strong midventral carina. Pereopod 1 propodal palm almost straight, sparsely setose. Posterior margins of uropodal rami finely denticulate. Male unknown.

Type material

Holotype, SAM–A8076, non-ovig. ♀, 20,0 mm, Hermanus, Cape.

Distribution

Known from type locality only.

Remarks

The single known specimen was taken from a cavity in the base of an *Allopora* sp. coral.

Malacanthura linguicauda (Barnard, 1920)
Fig. 27

Anthura linguicauda Barnard, 1920: 338.
Malacanthura linguicauda: Barnard, 1925a: 133 (*partim*); 1940: 497 (*partim*). Nierstrasz,
     1941: 240 (*partim*). Kensley, 1978a: 52, fig. 23A.
Non Malacanthura linguicauda: Barnard, 1925b: 388.

Diagnosis

Integument hardly indurate. Pereonites 4–6 each with mid-dorsal elongate pit. Pleonites 1–5 fused, lines of fusion indicated by faint lateral grooves; pleonite 6 free. Telson oval in outline, distally rounded, dorsally very gently convex. Maxilliped with short endite. Uropodal exopod with sinuous outer distal margin.

Description

Male. Integument hardly indurate. Proportions: $C < 1 = 2 > 3 < 4 = 6 > 7$. Cephalon with large dorsolateral eyes. Anterior margin of pereonites 2 and 3 with rectangular depression for articulation. Slit-like mid-dorsal pit present on
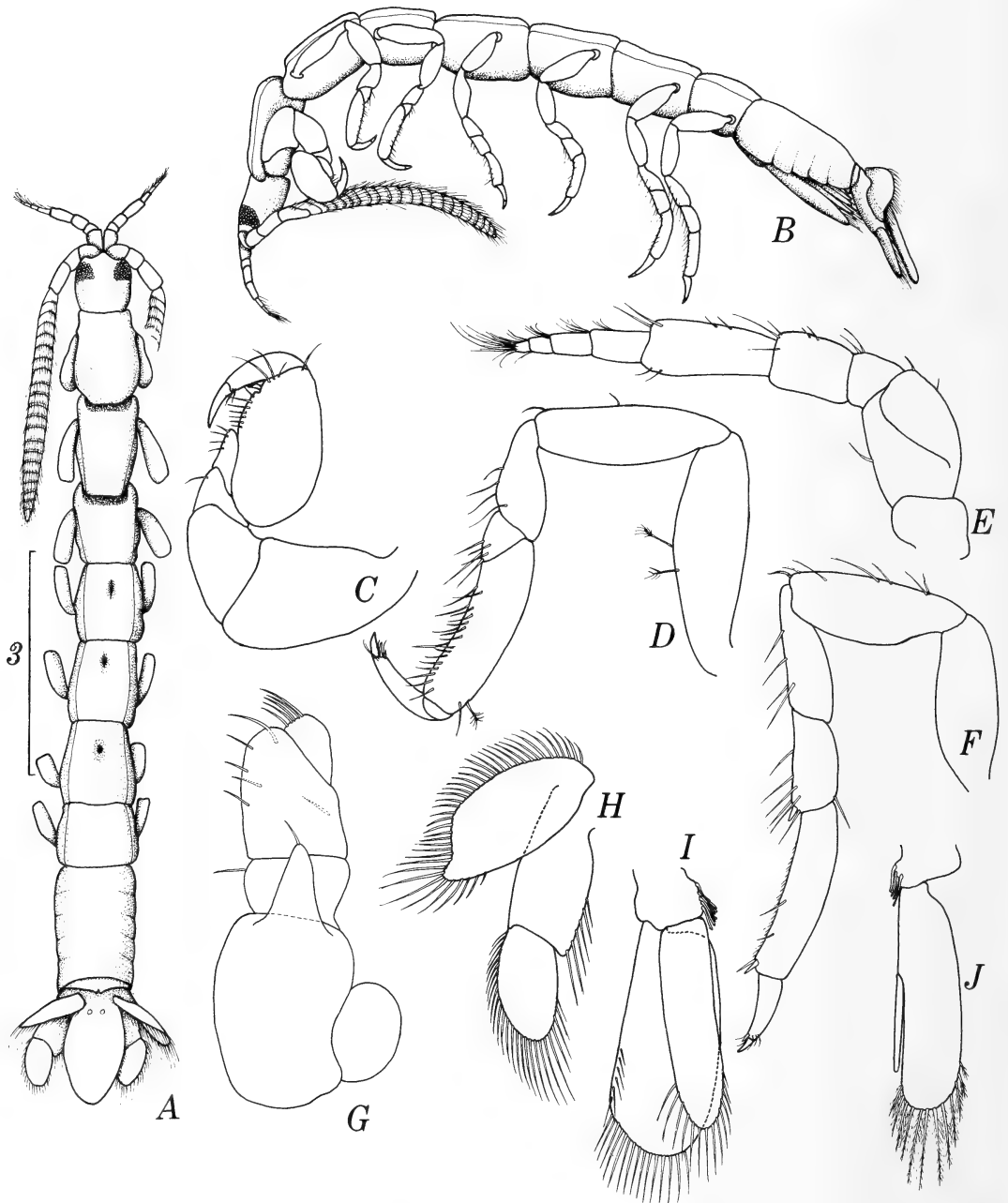
Fig. 27. *Malacanthura linguicauda*. A. ♂ dorsal view. B. ♂ lateral view. C. Pereopod 1 ♂. D. Pereopod 2. E. Antenna. F. Pereopod 7. G. Maxilliped. H. Uropod. I. Pleopod 1. J. Pleopod 2 ♂ endopod. Scale in mm.

pereonites 4–6. Pleonites 1–5 fused, pleonites indicated ventrolaterally by short slits; pleonite 6 free, with small mid-dorsal notch in posterior margin. Telson elongate-oval, posteriorly rounded, dorsally gently convex, with two proximal statocysts.

Antennular peduncle three-segmented, basal segment broadest; flagellum of twenty to twenty-two articles bearing whorls of aesthetascs, reaching back to pereonite 3. Antennal peduncle five-segmented, segment 2 broadest, grooved to accommodate antennule; flagellum of four articles. Maxilliped five-segmented, terminal segment set obliquely on segment 4, with five setae on medial margin; segment 4 with few setae on medial margin; endite on inner surface reaching base of segment 4, triangular, with single distal seta. Pereopod 1 unguis one-third length of rest of dactylus; dactylus with small posterior lobe on inner margin; propodal palm convex, with distal notch and row of six to eight setae. Pereopod 2 unguis one-fourth length of rest of dactylus, with two small basal spines; propodus elongate-rectangular, with several setae on posterior margin; carpus short, triangular. Pereopods 4–7 with posterodistal spine on carpus and propodus; carpus half length of, and not underriding propodus. Pleopod 1 exopod operculiform; endopod half width and three-fourths length of exopod; basis with eight retinaculae. Pleopod 2 endopod with simple rod-like copulatory stylet on medial margin not reaching distal end of ramus; basis with four retinaculae. Uropodal exopod reaching to distal margin of basis, outer margin distally sinuous, bearing numerous plumose setae; endopod oval, bearing numerous plumose setae.

Type material

Holotype, SAM–A4172, ♂, 11,0 mm, off Umhlangakulu River, Natal, 100 m.

Distribution

Off Natal, 100 m.

Remarks

The specimen recorded by Barnard (1925b: 388) from off the Cape Peninsula, bears four short proximal lobes on the inner margin of the dactylus of pereopod 1, as well as a strong posteriorly-directed spine-like process on the basal antennular segment. Neither of these features is present in the holotype of *M. linguicauda*. As this specimen is a submale, and shows these differences, it cannot be considered the same species.

The holotype was dissected, probably by Barnard, and the mandible and maxilla have not been located.

Malacanthura ornata (Barnard, 1957)

Fig. 28

Haliophasma ornatum Barnard, 1957: 3, fig. 2. Poore, 1975: 531. Kensley, 1978a: 50, fig. 22B.
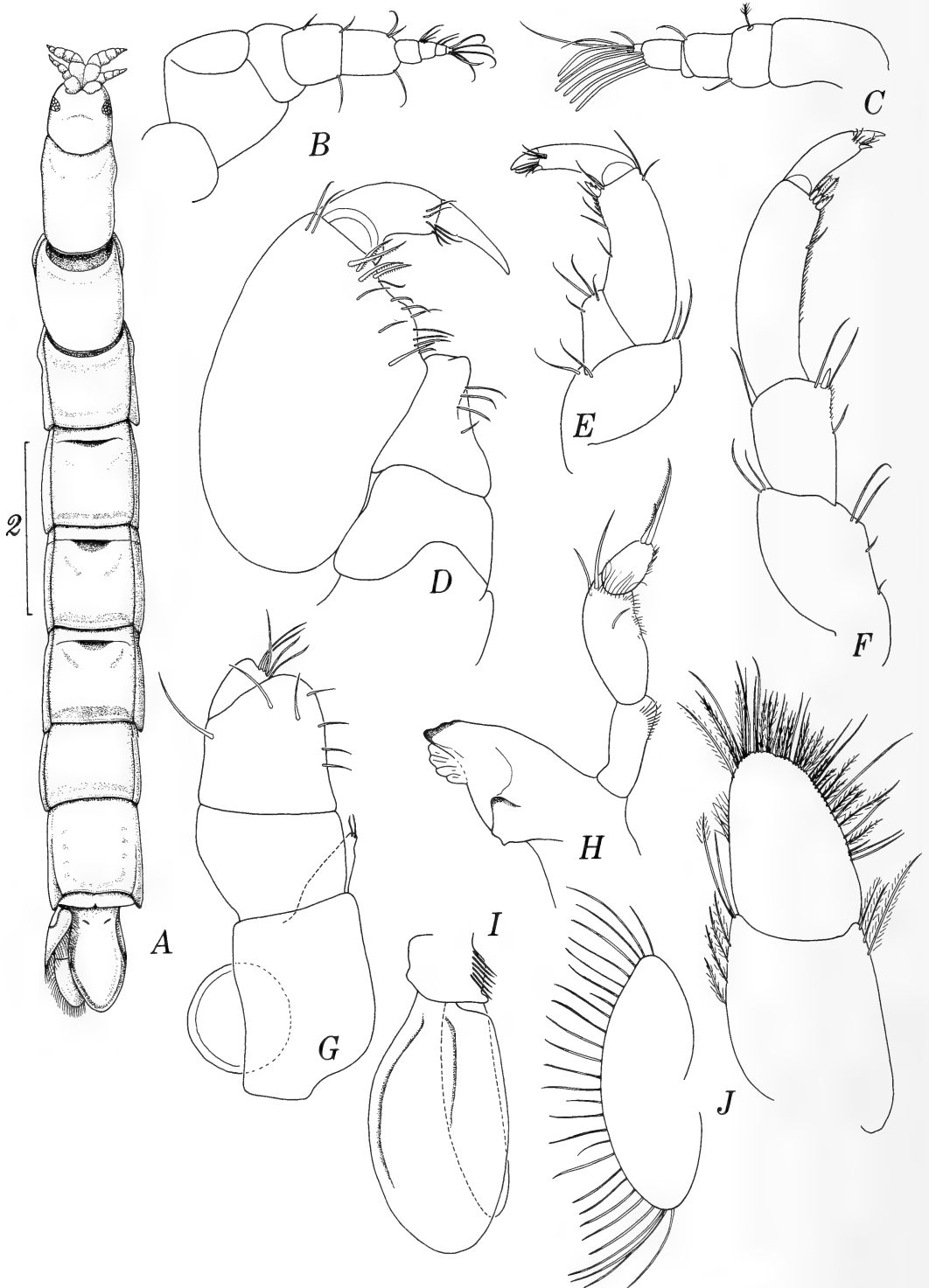
Fig. 28. *Malacanthura ornata*. A. ♀ dorsal view. B. Antenna. C. Antennule.
D. Pereopod 1. E. Pereopod 2. F. Pereopod 7. G. Maxilliped. H. Mandible. I. Pleopod 1.
J. Uropod. Scale in mm.

Diagnosis

Body lacking sculpture. Telson dorsally gently convex, lacking mid-dorsal ridge, with slight lateral flange, distally broadly rounded. Pereopod 1, unguis only a little shorter than rest of dactylus; propodus broadly expanded, palm with low proximal convexity, bearing few setae and spines. Maxilliped with small bisetose endite. Male unknown.

Type material

Holotype, SAM–A10599, non-ovig. ♀ (with eggs in body cavity), 10,0 mm, Mouille Point, Table Bay, intertidal.

Other material

SAM–A14181, 1 non-ovig. ♀, 9,5 mm, off Cape Point.

Distribution

Table Bay, west coast of Cape Peninsula, intertidal.

<div align="center">

Malacanthura pseudocarinata (Barnard, 1940)

Fig. 29

</div>

Haliophasma pseudocarinata Barnard, 1940: 385, 490, 498, fig. 3a–c; 1955: 5, 50. Day, Field & Penrith, 1970: 47. Poore, 1975: 531. Kensley, 1978a: 50, fig. 22C.

Diagnosis

Integument indurate, with small pits only noticeable on cephalon, pleon, and first pleopods. Pleonite 6 fused with telson dorsally, fusion line visible. Telson broad, with strong lateral ridge and barely noticeable mid-dorsal longitudinal ridge. Pereopod 1 propodal palm faintly sinuous, denticulate; row of finely fringed setae on inner propodal surface near palm in female. Male unknown.

Type material

Holotype, SAM–A8281, non-ovig. ♀, 17,0 mm, Port Elizabeth, intertidal.

Other material

SAM–A14323, 1 juv., 9,1 mm, off Saldanha Bay. SAM–A14184, 1 juv., 9,6 mm, False Bay. SAM–A14154, 1 juv., 6,0 mm, Port Elizabeth. SAM–A14182, 1 non-ovig. ♀, 19,2 mm, locality unknown.

Distribution

Saldanha Bay to Port Elizabeth, intertidal to 4 m.

Remarks

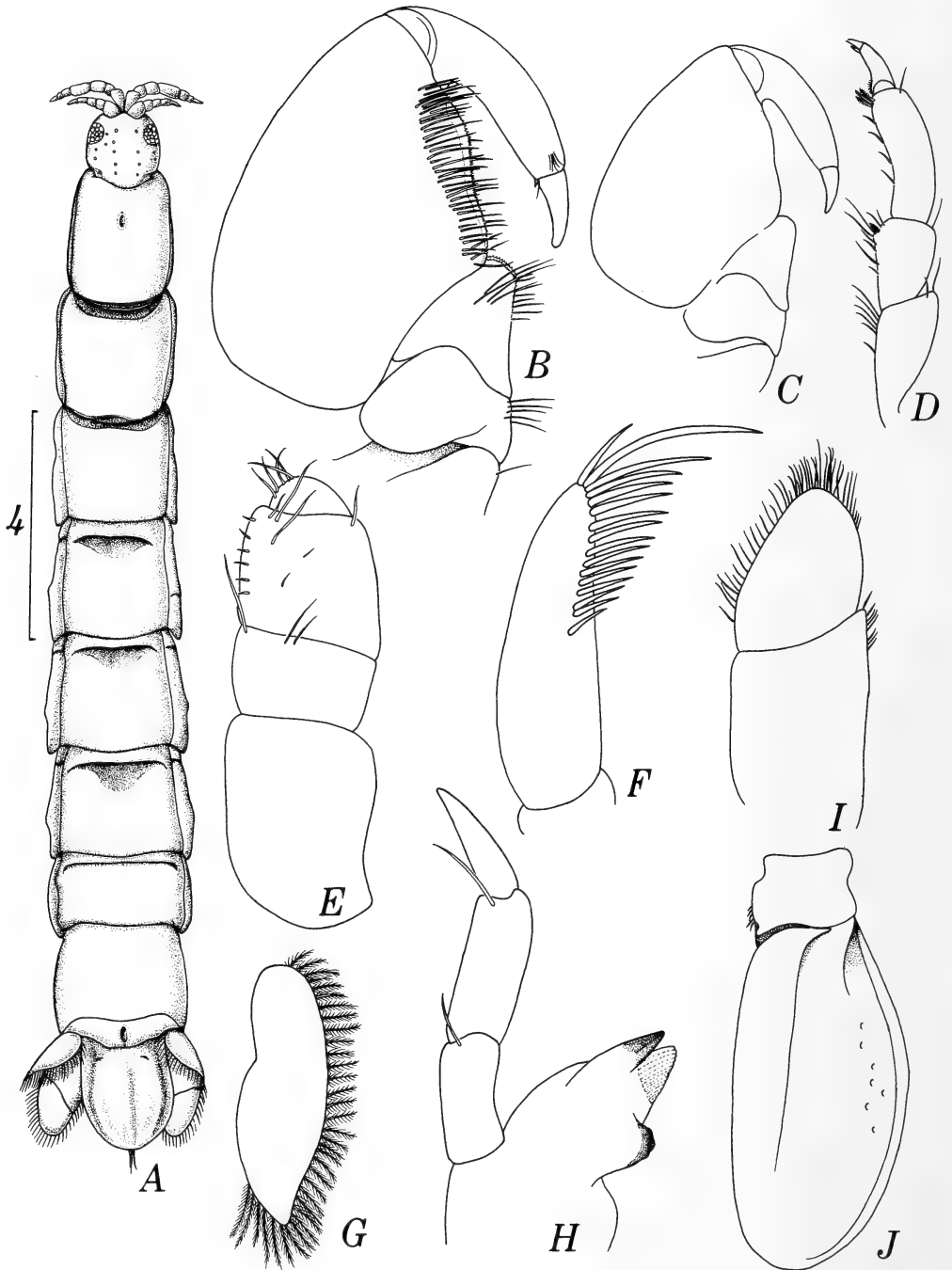The single specimen from off Saldanha Bay has numerous rhizocephalan parasites attached to the ventral pereon.

Fig. 29. *Malacanthura pseudocarinata*. A. ♀ dorsal view. B. Pereopod 1 inner view. C. Pereopod 1 outer view. D. Pereopod 7. E. Maxilliped. F. Distal mandibular palp segment. G. Uropodal exopod. H. Mandible. I. Uropodal basis and endopod. J. Pleopod 1 exopod. Scale in mm.
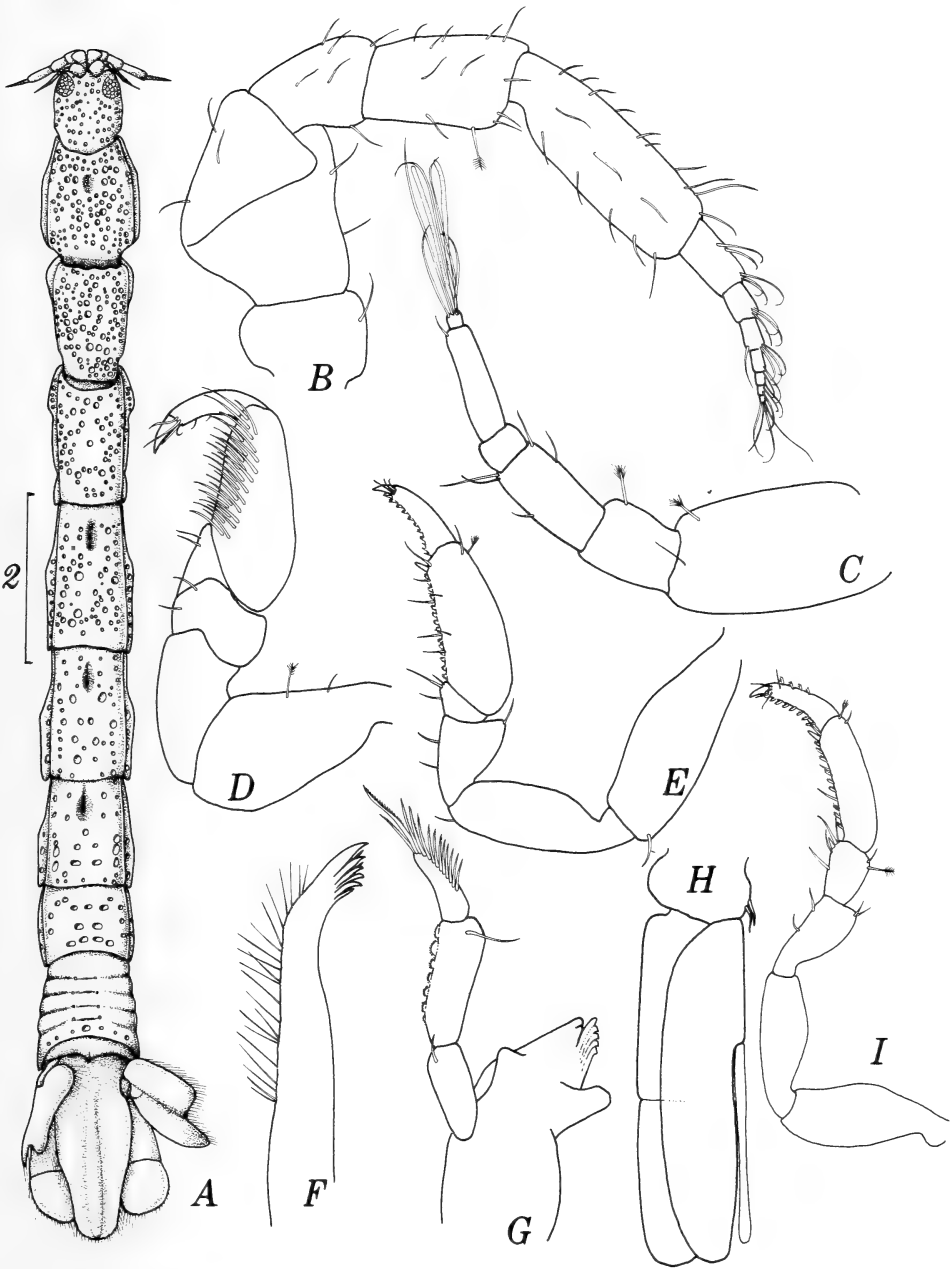
Fig. 30. *Malacanthura schotteae*. A. ♀ dorsal view. B. Antenna. C. Antennule. D. Pereopod 1 ♂. E. Pereopod 2. F. Maxilla. G. Mandible. H. Pleopod 2 ♂. I. Pereopod 7. Scale in mm.

Malacanthura schotteae sp. nov.
Figs 30–31

Diagnosis

Integument indurate, bearing numerous pits. Pereopod 1 propodus greatly expanded proximally in female; dactylus with rounded scaled lobe at base of unguis in female, absent in male. Telson narrow, widest at proximal third, with strong rounded mid-dorsal longitudinal ridge; posterior margin broadly rounded. Uropodal exopod with strong notch in outer margin.

Description

Non-ovigerous female. Integument indurate, with numerous small pits, each containing single sensory seta; pits less numerous on posterior pereonites. Proportions: $C < 1 = 2 = 3 < 4 > 5 > 6 > 7$. Cephalon with large eyes; well-developed rounded rostrum. Pereonites 4–6 with large mid-dorsal slit-like pit. Pleonites 1–5 fused, fusion indicated laterally by shallow grooves; pleonite 6 free, with mid-dorsal slit in posterior margin. Telson narrowed in posterior half, posterior margin broadly rounded, with strong rounded longitudinal mid-dorsal ridge; cuticular scales becoming more developed in posterior half; margin with many finely fringed setae.

Antennule with three-segmented peduncle; flagellum of three articles, article 2 longer than 1 and 3 together; distal article bearing two aesthetascs. Antennal peduncle segment 2 strongly grooved; segment 5 longest; flagellum of seven setose articles. Mandibular palp three-segmented, distal segment bearing twelve fringed spines, subterminal spine longest; incisor of two cusps; lamina dentata with five serrations; molar rounded. Maxilla with eight distal spines. Maxilliped five-segmented, distal segment semicircular, fringed with setae. Pereopod 1 strongly subchelate; unguis almost half length of rest of dactylus; latter with rounded lobe on inner margin bearing fringed scales at base of unguis; propodus expanded, elongate, pitted, with proximal rounded lobe of palm bearing fringed scales. Pereopod 2 much less robust than pereopod 1. Pereopods 5–7 with carpus roughly rectangular. Pleopod 1 exopod operculiform, outer surface pitted and bearing longitudinal groove; fringed with elongate plumose setae.

Male. Body indurate, relatively more slender than female; telson not as markedly narrowed posteriorly as in female. Eyes relatively larger than in female. Antennule elongate, reaching posteriorly to end of pereonite 1, with numerous whorls of filiform aesthetascs. Pereopod 1 not robust, dactylus and propodus lacking scaled rounded lobe as in female; propodal inner surface with numerous minutely fringed setae. Pleopod 2 endopod with slender rod-like copulatory stylet not quite reaching distal end of ramus.

Type material

Holotype, SAM–A17525, non-ovig. ♀, 12,5 mm, south of East London, 90 m. Allotype, SAM–A17526, 1 ♂, 8,4 mm, south of East London, 90 m.
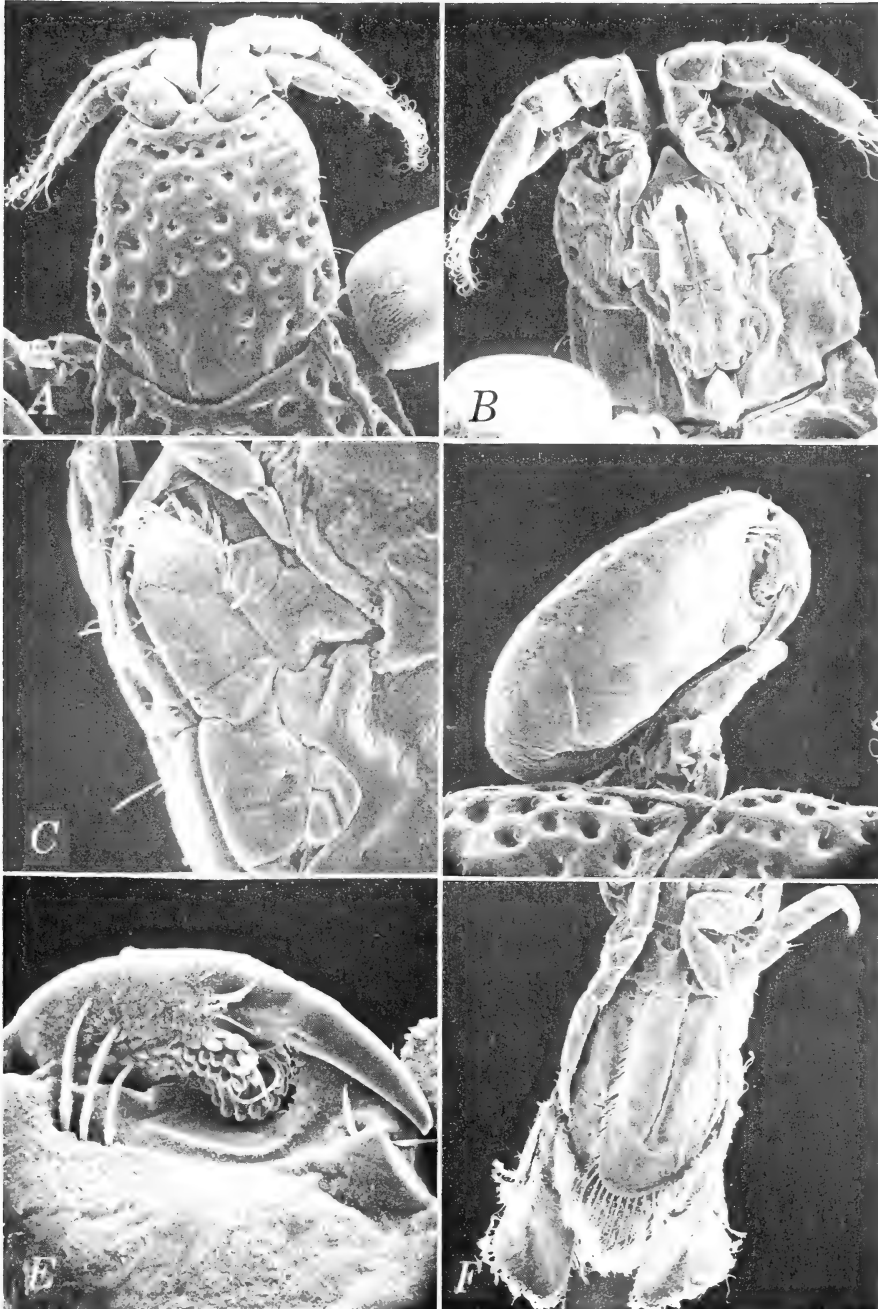
Fig. 31. *Malacanthura schotteae*. A. Cephalon ♀ dorsal view. B. Cephalon ♀ ventral view. C. Maxilliped. D. Pereopod 1. E. Dactylus pereopod 1. F. Ventral pleon.

Paratype, SAM–A17527, 1 non-ovig. ♀, 6,5 mm, 10 juvs, south of East London, 90 m. Paratype, USNM 189055, 1 non-ovig. ♀, 7,6 mm, south of East London, 90 m. Paratype, SAM–A17528, 1 non-ovig. ♀, 8,3 mm, off Transkei, 150–200 m. Paratype, USNM 189056, 1 non-ovig. ♀, 9,0 mm, off Transkei, 150–200 m.

Other material

SAM–A14094, 1 non-ovig. ♀, 10,8 mm, off Still Bay, 80 m. SAM–A14080, 1 non-ovig. ♀, 11,5 mm, off Still Bay, 120 m. SAM–A14099, 1 juv., off Still Bay, 120 m. SAM–A17259, 1 non-ovig. ♀, off Transkei, 710–775 m.

Distribution

Still Bay to Transkei, 80–775 m.

Etymology

The species is named for Marilyn Schotte, of the Department of Invertebrate Zoology, Smithsonian Institution, in appreciation of the many illustrations she executed for this paper.

Remarks

Of the seven earlier-described species of *Malacanthura*, only *M. foveolata* has an integument as densely pitted as in the two new species described here. The telson of *M. foveolata*, however, is obscurely tri-ridged, with pits between the ridges, while *M. schotteae* and *M. transkei* have a single mid-dorsal ridge and no pits on the telson.

Malacanthura schotteae has a strongly notched uropodal exopod, a posteriorly constricted telson, and scaled lobes on the dactylus and propodal palm, while *M. transkei* has an unnotched oval-lanceolate uropodal exopod, evenly convex telsonic margins, and lacks propodal and dactylar lobes in pereopod 1. *Malacanthura transkei* also has mid-dorsal depressions on pereonites 2 and 3, not seen in *M. schotteae*.

Malacanthura serenasinus (Kensley, 1975)

Figs 32–33

Agulanthura serenasinus Kensley, 1975a: 72, fig. 18; 1978: 46, fig. 20B–E.

Diagnosis

Body profile smooth; uropodal exopods closely adpressed to telson; latter with gentle ventral curvature in posterior half, lanceolate, dorsally convex, posterior margin narrowly rounded. Eyes small, weakly pigmented. Antennular
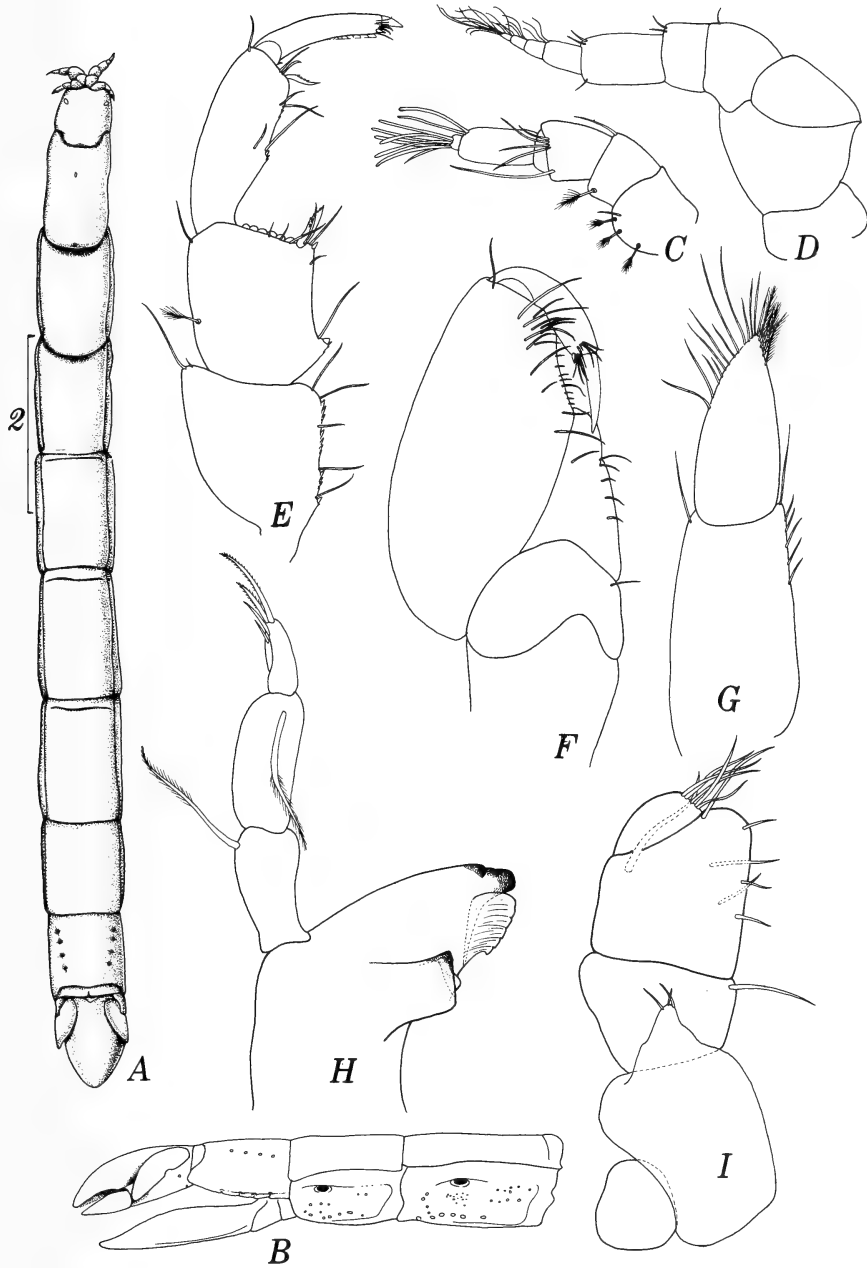
Fig. 32. *Malacanthura serenasinus*. A. ♀ dorsal view. B. Pereonites 6 and 7, and pleon lateral view. C. Antennule. D. Antenna. E. Pereopod 7. F. Pereopod 1. G. Uropodal basis and endopod. H. Mandible. I. Maxilliped. Scale in mm.

flagellum in female with two articles. Antennal flagellum of four articles. Pereopod 1 propodus expanded, palm slightly concave in female, slightly convex in male. Pereopods 4–7 with carpi and meri expanded, rectangular. Maxilliped five-segmented with small endite.

Type material

Holotype, SAM–A13553, 1 ♂, 11,0 mm, False Bay, 62 m. Allotype, SAM–A13554, 1 non-ovig. ♀, 14,5 mm, False Bay, 29 m. Paratype, SAM–A13621, 1 non-ovig. ♀, 13,0 mm, Agulhas Bank, 22 m. Paratype, SAM–A13622, 1 non-ovig. ♀, 14,0 mm, Saldanha Bay, 5 m. Paratypes, SAM–A13623, 1 ♂, 11,0 mm, 3 non-ovig. ♀, 6,9–12,9 mm, off Still Bay, 20 m.

Other material

SAM–A17790, 6 non-ovig. ♀, off Saldanha Bay, 79 m. SAM–A14029, 1 juv., False Bay, 56 m. SAM–A14030, 1 non-ovig. ♀, False Bay, 29 m. SAM–A14031, 1 non-ovig. ♀, False Bay, 26 m. SAM–A14032, 1 non-ovig. ♀, False Bay, 61 m. SAM–A14033, 1 non-ovig. ♀, False Bay, 42 m. SAM–A14034, 1 ♂, False Bay, 66 m. SAM–A14035, 1 non-ovig. ♀, False Bay, 75 m. SAM–A14036, 1 juv., False Bay, 48 m. SAM–A14037, 1 non-ovig. ♀, Agulhas Bank, 125 m. SAM–A14038, 1 non-ovig. ♀, Agulhas Bank, 97 m. SAM–A14062, 1 non-ovig. ♀, Agulhas Bank, 36 m. SAM–A14039, 5 non-ovig. ♀, off Still Bay, 15 m.

Distribution

Saldanha Bay to Still Bay, 5–125 m.

Remarks

When originally described as the type species of *Agulanthura*, the species was placed in a new genus on the basis of the smooth body profile, the lack of pereonal pits, and the expanded carpi and meri of the posterior pereopods. With rediagnosis of the genera *Haliophasma* and *Malacanthura* this species is now regarded as a specialized fossorial *Malacanthura*. The five-segmented maxilliped with weak endite, the antennular and antennal structure in the female, and the presence of small ventrolateral pits on the posterior pereonites support this placement.

The smooth body profile, the reduced and weakly pigmented eyes, the uropodal exopods closely adpressed to the telson, and the expanded carpi and meri of the posterior pereopods could all be adaptations for a fossorial mode of life. Almost all the specimens recorded above were taken from fairly fine sediments by grab, another indication of the burrowing habit.

In the original description (Kensley 1975a: 72), the appendages figured were those of a male. With examination of a female, it would seem that with the change from female to male the mandible undergoes some reduction and loss of function.
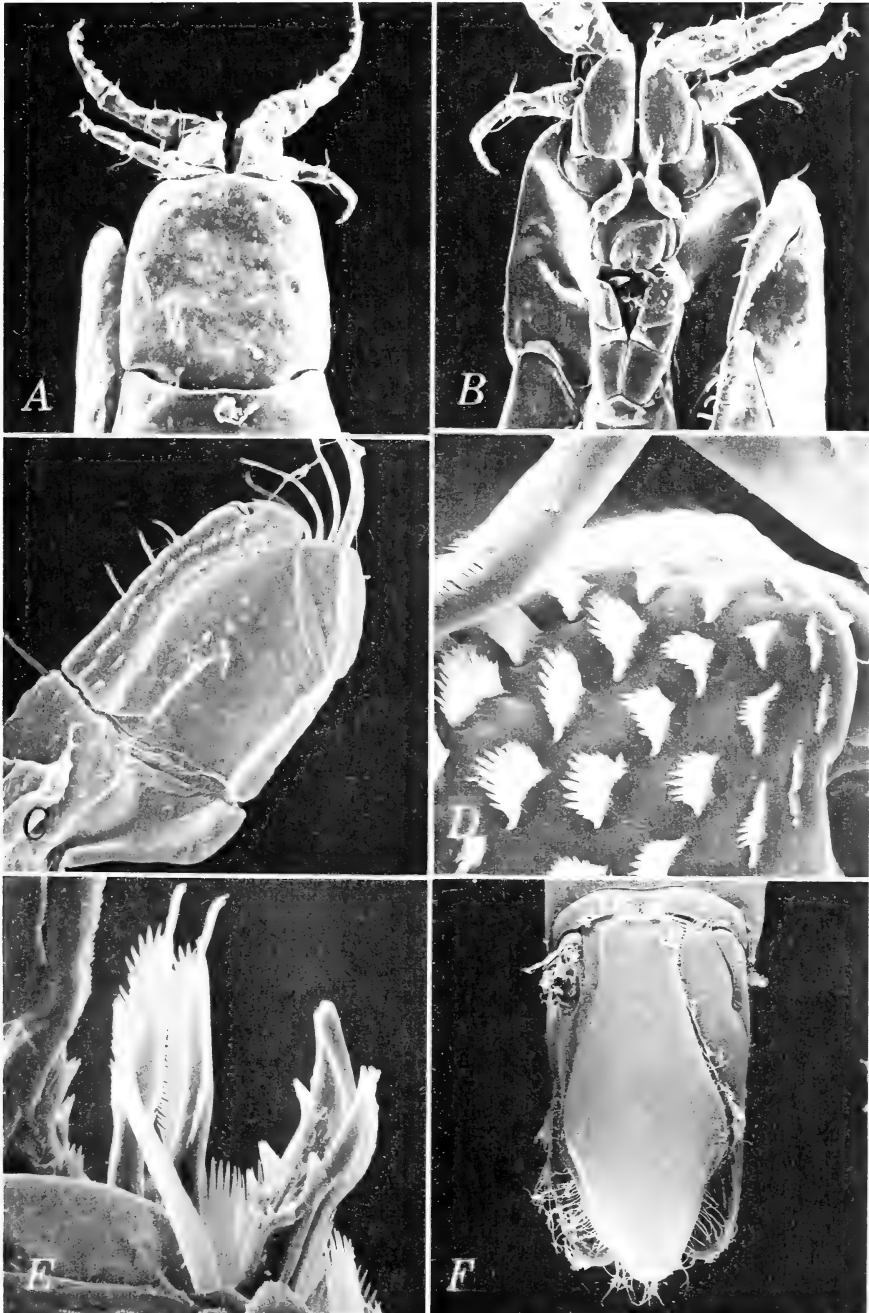
Fig. 33. *Malacanthura serenasinus*. A. ♀ cephalon dorsal view. B. ♀ cephalon ventral view. C. Maxilliped inner view. D. Integumental scales on pereopod 1 propodus. E. Ventrodistal spines on pereopod 2 propodus. F. Telson dorsal view.

Malacanthura transkei sp. nov.
Figs 34–35

Diagnosis

Integument indurate, heavily pitted, Pereopod 1 propodus expanded. Telson narrow, extending beyond uropodal endopod, widest at about midpoint, posterior margin broadly rounded, finely denticulate; strong rounded mid-dorsal longitudinal ridge present.

Description

Female. Integument indurate, heavily pitted dorsally and ventrally. Proportions: $C < 1 < 2 > 3 < 4 = 5 > 6 > 7$. Cephalon with rounded rostrum extending as far as anterolateral lobes; shallow groove present between anterior margin and well-developed eyes. Pereonite 1 with bilobed posterior margin; pereonite 2 with shallow mid-dorsal area ending posteriorly in shallow circular depression; pereonites 3–5 with mid-dorsal elongate pit in shallow depression. Pleonites 1–5 fused, fusion lines indicated by dorsolateral grooves. Pleonite 6 free, posterior margin with short mid-dorsal notch. Telson widest at about midpoint, lateral margins gently convex, posterior margin broadly rounded, denticulate.

Basal antennular segment somewhat shorter than segments 2 and 3 together; flagellum three-articulate, second article more than twice length of first or third; distal article bearing three aesthetascs. Antenna with numerous setae on all segments; peduncle segment two strongly grooved; segment 5 longest; flagellum five-articulate. Mandibular palp three-segmented, terminal segment with seven fringed spines; incisor of three cusps; lamina dentata with four teeth; molar conical. Maxilla with six distal spines. Maxilliped five-segmented, distal segment oval, set obliquely on segment 4, with numerous fine setules; endite absent. Pereopod 1 unguis more than half length of dactylus; propodus expanded proximally, palm gently concave, with five submarginal spines; carpus triangular, distal rounded lobe bearing spine-scales, Pereopod 2 unguis half length of dactylus, with strong auxiliary spine at base; propodus rectangular, with strong sensory spine at posterodistal corner, posterior margin bearing fringed scales; carpus triangular, with strong posterodistal spine. Pleopod 1 exopod operculiform, subequal in length and about three times width of endopod. Uropodal exopod elongate-oval, outer margin dentate, setose, distally acute; endopod broadly oval, margin setose, finely dentate.

Male. Antennule with ten-articulate flagellum. Pereopod 1 propodal palm straight, with dense band of fringed spines on inner surface. Pleopod 2 endopod with slender distally expanded copulatory stylet reaching slightly beyond ramus. Pleon, telson, and uropods relatively more elongate than in female.
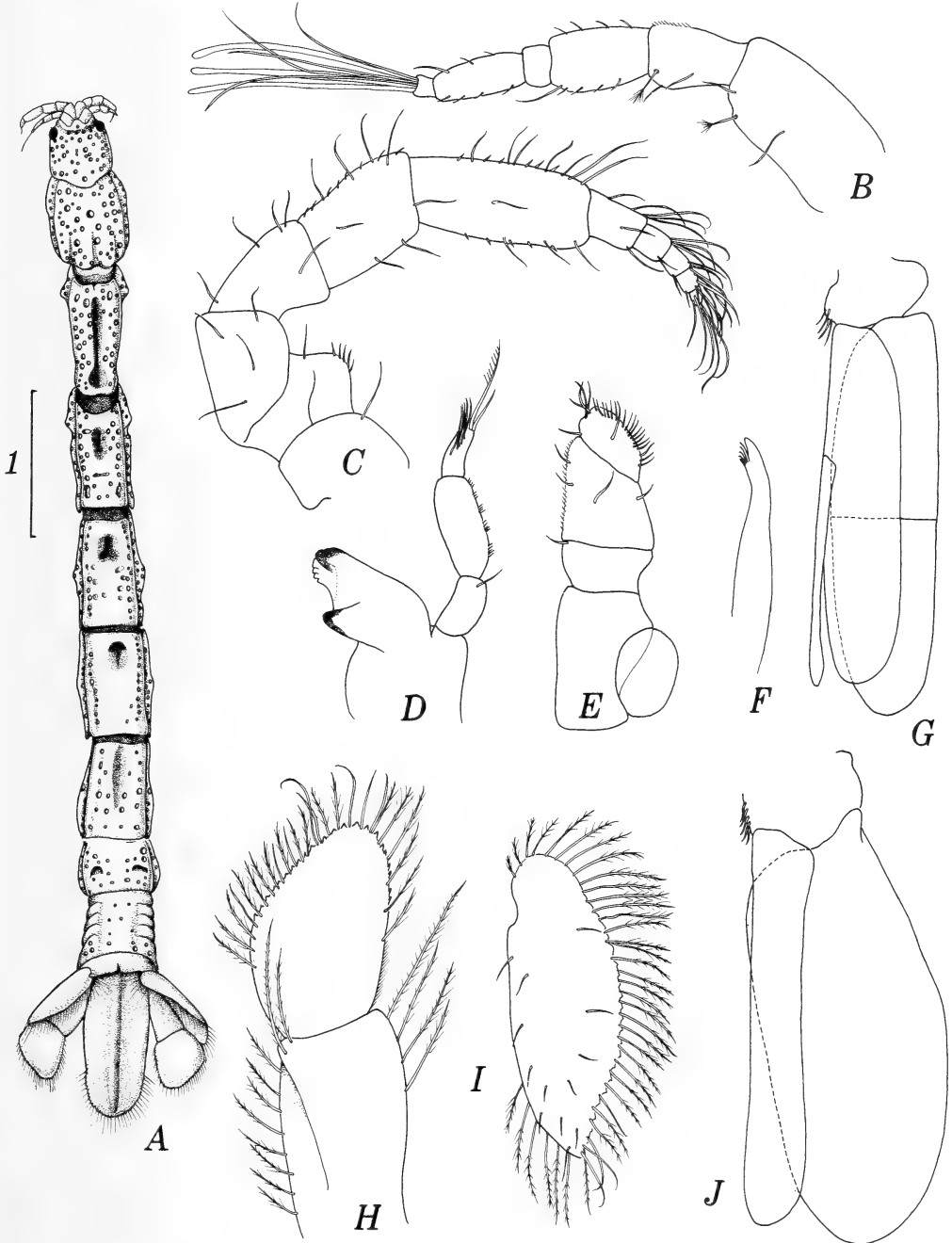
Fig. 34. *Malacanthura transkei*. A. ♀ dorsal view. B. Antennule. C. Antenna.
D. Mandible. E. Maxilliped. F. Maxilla. G. Pleopod 2 ♂. H. Uropodal endopod and
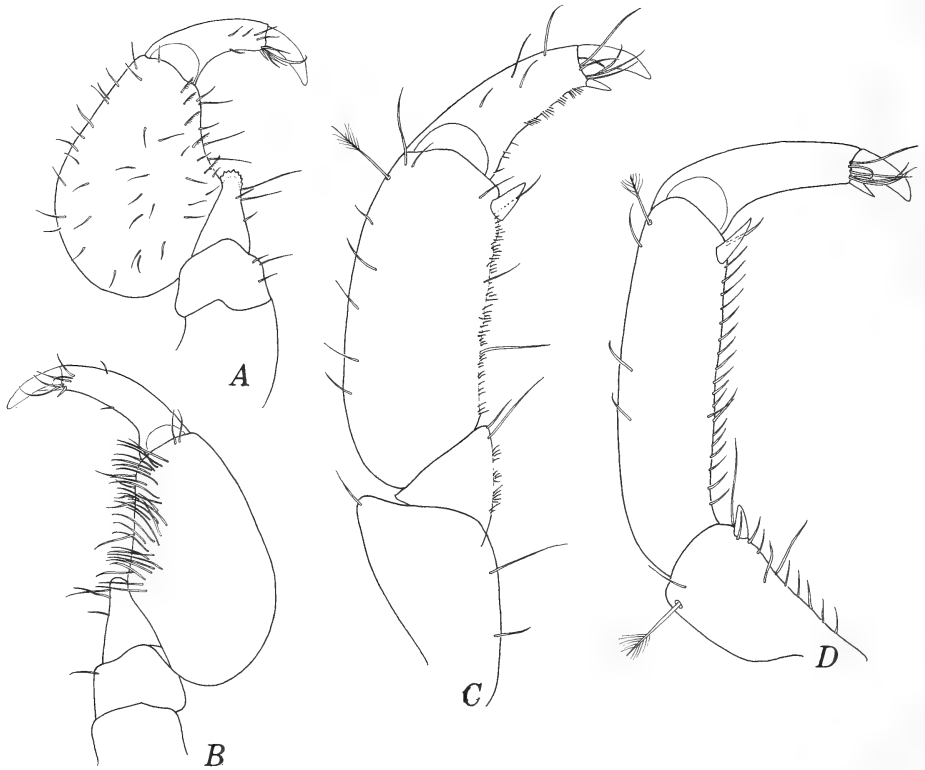basis. I. Uropodal exopod. J. Pleopod 1. Scale in mm.

Fig. 35. *Malacanthura transkei*. A. Pereopod 1 ♀. B. Pereopod 1 ♂. C. Pereopod 2.
D. Pereopod 7.

Type material

Holotype, SAM–A17531, 1 ♂, 7,5 mm, off Transkei, 710–775 m.
Allotype, SAM–A17532, 1 non-ovig. ♀, 7,5 mm, off Transkei, 710–775 m.
Paratype, SAM–A17533, 1 non-ovig. ♀, 6,1 mm, off Transkei, 710–775 m.
Paratype, USNM 184667, 1 non-ovig. ♀, 6,3 mm, off Transkei, 710–775 m.

Etymology

The specific name derives from the area of the coastline of southern
Africa, off which the species was collected.

Remarks

See discussion at end of *M. schotteae* discussion.

Mesanthura Barnard, 1914

Diagnosis

Eyes present. Antennular flagellum of two articles; antennal flagellum of three articles. Mandibular palp three-segmented. Maxilliped five-segmented, endite rudimentary or absent. Pereopod 1 expanded, subchelate, sometimes highly modified in male. Pereopods 2–3 ambulatory; pereopods 4–7 with triangular carpus underriding propodus. Pleopod 1 exopod operculiform. Pleonites 1–5 fused, 6 free. Telson with two basal statocysts. Dorsal integument with chromatophores in species-specific pattern.

Type species

Anthura catenula Stimpson, 1855.

KEY TO THE SOUTH AFRICAN SPECIES OF *MESANTHURA*

1. Dorsal pigment in solid triangle on cephalon, posterior bars on pereonites 4–7 .. *dimorpha*
– Dorsal pigment in open rings or rectangles on cephalon and all pereonites .... *catenula*

Mesanthura catenula (Stimpson, 1855)
Figs 36–37

Anthura catenula Stimpson, 1855: 393. Beddard, 1886: 143. Stebbing, 1910: 420.
Mesanthura catenula: Barnard, 1914: 343a, pl. 29A; 1925a: 143, fig. 9a; 1940: 490; 1955: 5.
    Nierstrasz, 1941: 242. Day, Field & Penrith, 1970: 47. Kensley, 1978a: 52, fig. 23B–C;
    1978b: 1.

Diagnosis

Pigment pattern: hollow rectangular patches on cephalon and pereonites 1–7; broad transverse band on pleon; dense oval patches on uropodal exopod, endopod, and telson. Pereopod 1 propodus expanded, palm sinuous, with hyaline margin. Uropodal exopod with distinct distal notch.

Type material

Stimpson's type from Simon's Bay in False Bay was apparently lost, perhaps in the Chicago fire of 1871.

Other material

SAM–A2719, 1 juv., Mouille Point, Table Bay, intertidal. SAM–8825, 1 non-ovig. ♀, 3 juvs, St. James, False Bay. SAM–A250, 2 non-ovig. ♀, 10,5–11,8 mm, Kalk Bay in False Bay, intertidal. SAM–A2106, 1 non-ovig. ♀, St. James, False Bay. SAM–A3302, 1 juv., 8,0 mm, Buffels Bay in False Bay. SAM–A14350, 1 ovig. ♀, 14,0 mm, False Bay, 4 m. SAM–A4171, 1 ovig. ♀, 18,4 mm, East London, intertidal. SAM–A14352, 2 non-ovig. ♀, 14,5 mm, locality unknown.

Distribution

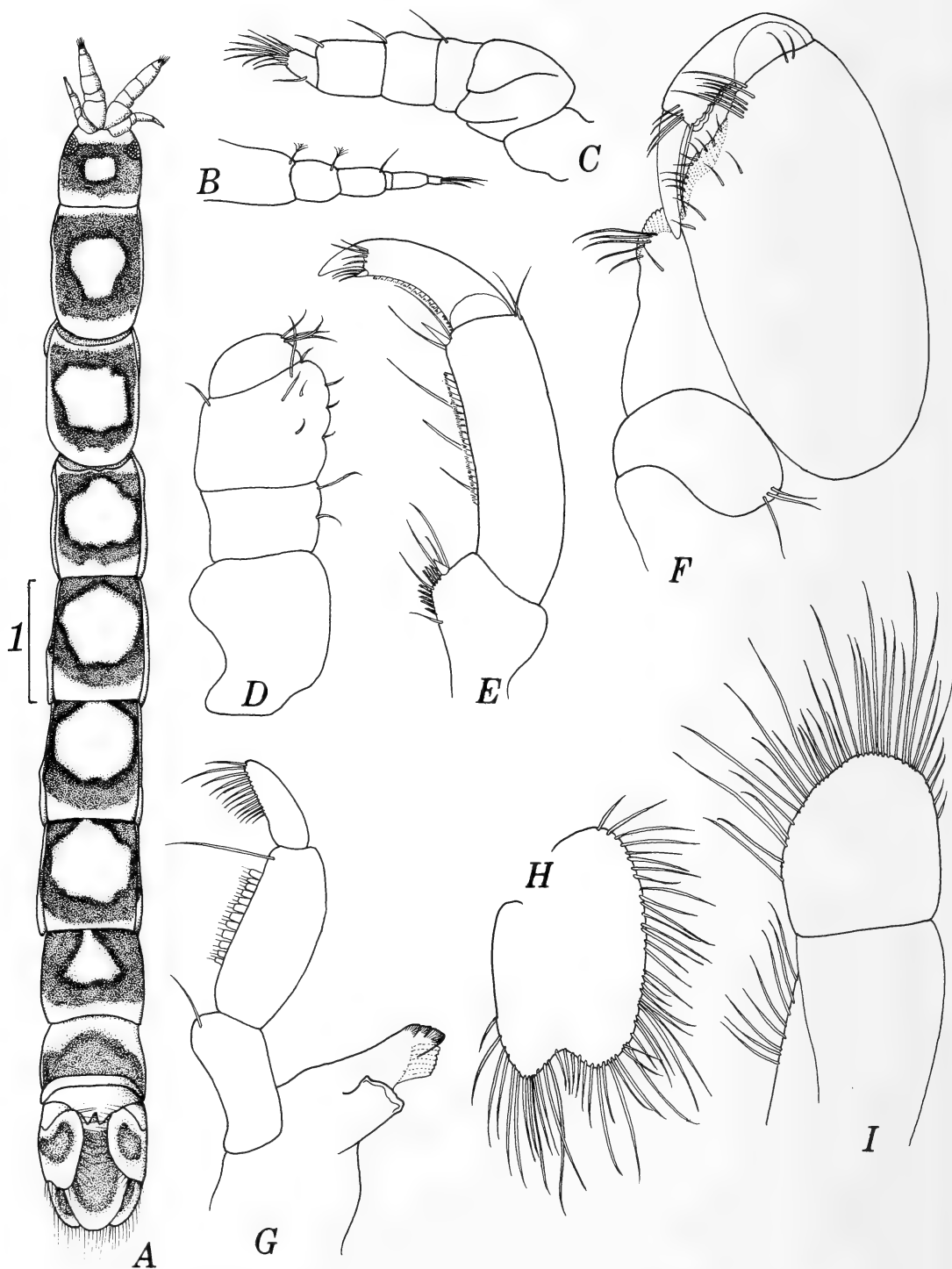Table Bay to East London, intertidal to 4 m.

Fig. 36. *Mesanthura catenula*. A. ♀ dorsal view. B. Antennule. C. Antenna. D. Maxilliped. E. Pereopod 7. F. Pereopod 1. G. Mandible. H. Uropodal exopod. I. Uropodal basis and endopod. Scale in mm.
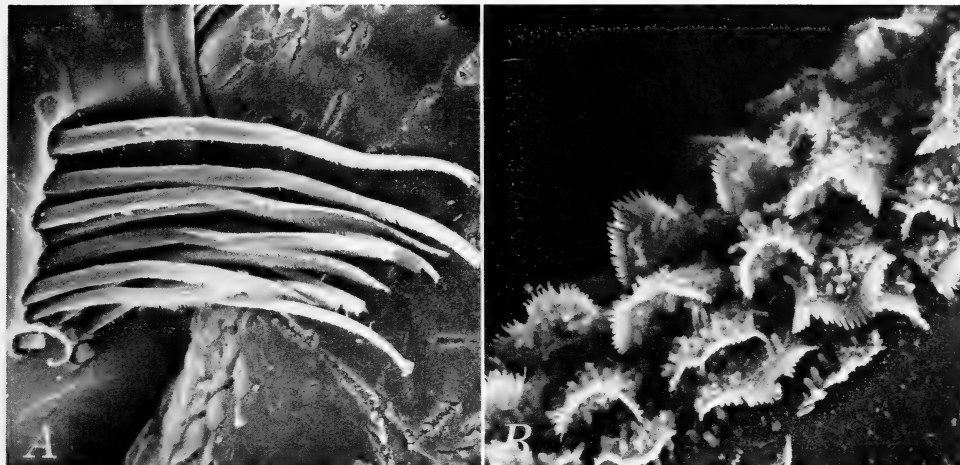
Fig. 37. *Mesanthura catenula.* A. Spine cluster at dactylar-propodal articulation of pereopod 1.
B. Pereopod 2 propodal scales.

Remarks

In some of the specimens listed above, which were collected in the early part of this century, the colour pattern has faded, but in material collected since 1932 the pigment persists. Some variation in the pattern has been noted e.g., occasionally there is a simple broad bar across the cephalon posterior to the eyes, while pereonite 1 sometimes has a solid patch of pigment. In spite of these variations the overall pattern makes the species unmistakable, and it may easily be separated from *M. dimorpha* by the structure of pereopod 1 in the male and female.

Mesanthura dimorpha sp. nov.
Figs 38–39

Diagnosis

Pigment pattern: triangle on cephalon; ring on pereonites 1–3; posterior bar on pereonites 4–7; bar on pleonite 6; oval on telson. Cephalon in male with midventral lamellar process. Pereopod 1 in female, propodal palm with low tooth at midpoint, carpus distally acute; pereopod 1 in male, propodal palm concave, carpus distally strongly produced into bilobed process.

Description

Female. Integument moderately indurate. Body proportions: $C < 1 = 2 = 3 < 4 = 5 > 6 > 7$. Cephalon with low rostral point; eyes dorsolateral. Fused pleonites 1–5 subequal in length to pereonite 7; pleonite 6 free, with tiny mid-dorsal notch in posterior margin. Telson posteriorly evenly
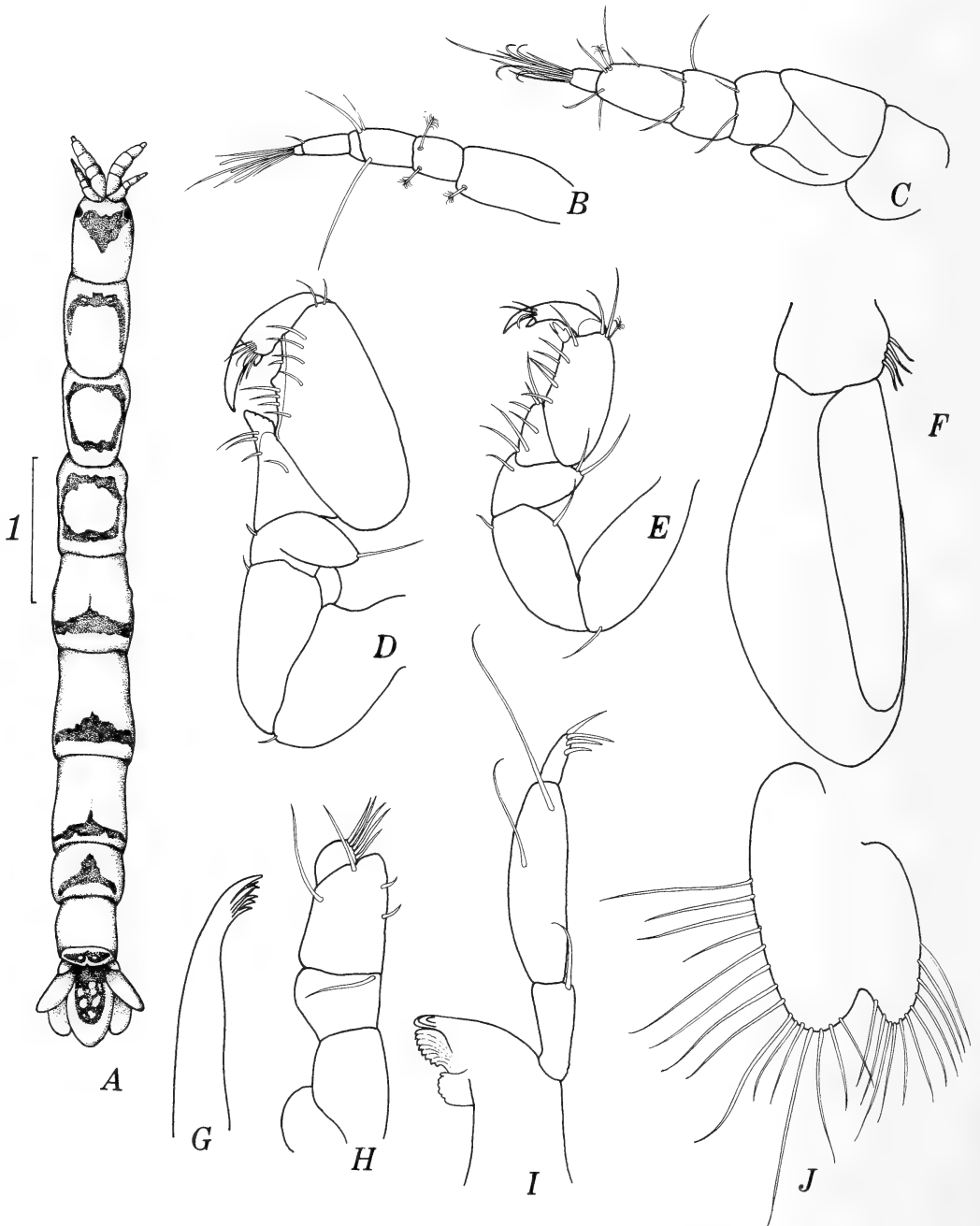
Fig. 38. *Mesanthura dimorpha*. A. ♀ dorsal view. B. Antennule. C. Antenna.
D. Pereopod 1 ♀. E. Pereopod 2 ♀. F. Pleopod 1. G. Maxilla. H. Maxilliped.
I. Mandible. J. Uropodal exopod. Scale in mm.

rounded, central pigmented part dorsally gently convex. Antennule with basal peduncular segment equal in length to, but broader than two distal segments; flagellum of two articles. Antennal peduncle with second segment grooved to accommodate antennule; flagellum of one article. Mandibular palp three-segmented, segment 2 twice length of basal segment, with two simple distal setae; terminal segment with four distal spines; incisor of three cusps; lamina dentata of eight serrations. Maxilla with seven distal spines. Maxilliped five-segmented, lacking endite; subterminal segment with two short setae on median margin; terminal segment with five setae on median margin. Pereopod 1 subchelate, expanded; unguis about one-third length of dactylus; propodal palm with blunt tooth at midpoint; carpus triangular, with corneous triangular extension distally. Pereopods 2–3 ambulatory, with strong sensory spine at posterodistal corner of propodus. Pereopods 4–7 with short roughly triangular carpus. Pleopod 1 exopod operculiform; endopod less than half width and shorter than exopod; basis with four retinaculae. Uropodal exopod with deep notch in distal margin; endopod not reaching telsonic apex.

Male. Antennule with multiarticulate flagellum bearing filiform aesthetascs. Midventral keel of cephalon expanded into slightly hollowed platelike process. Pereopod 1 strongly indurate; unguis almost half length of dactylus; propodus with concave palm bearing distal keeled tooth; inner surface with single row of spines and strong proximal tooth; carpus triangular, distally produced well beyond propodal base into narrowly rounded bilobed process. Pereopods 2–3 with dactylus meeting distal extension of triangular carpus. Pleopod 2 endopod with simple rod-like copulatory stylet not reaching apex of ramus.

Colour pattern

Similar in male and female. Cephalon with triangular patch of pigment with base between eyes. Pereonite 1 with narrow hoop of pigment in anterior half. Pereonites 2–3 with hollow rectangle of pigment. Pereonites 4–7 with transverse band of pigment near posterior margin. Pleonite 6 with transverse band. Telson with oval reticulation of pigment.

Type material

Holotype, SAM–A17534, ♂, 6,3 mm. Allotype, non-ovig. ♀, 5,9 mm. Paratypes, 2 non-ovig. ♀, 4,8–5,4 mm, 2 juvs, off East London, 90 m. Paratype, SAM–A14347, ♂, 9,0 mm, off Natal. Paratype, SAM–A14354, ♂, 7,5 mm, off Port Elizabeth, 84 m. Paratypes, USNM 184666, ♂, 6,0 mm, 1 non-ovig. ♀, 5,0 mm, off East London, 90 m.

Distribution
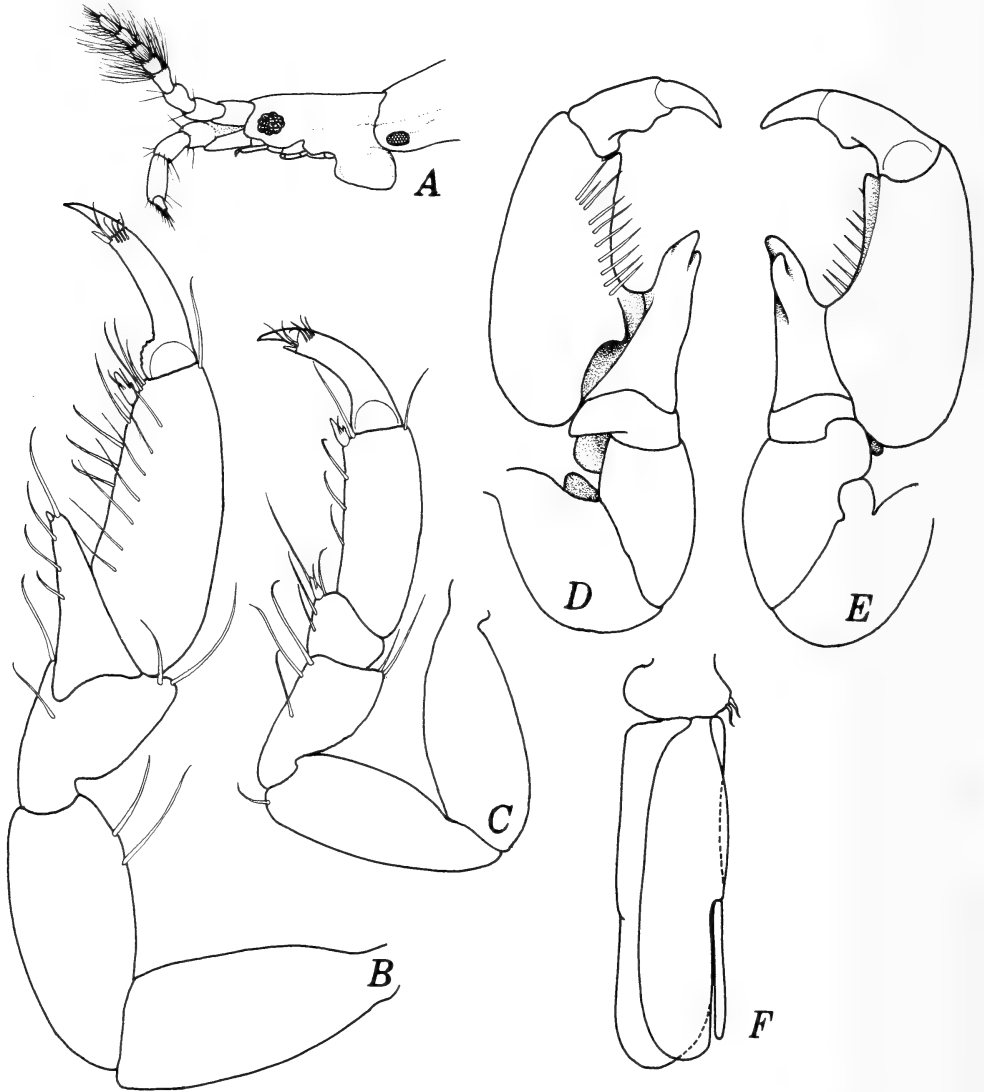
Natal to Port Elizabeth, 84–90 m.

Fig. 39. *Mesanthura dimorpha*. A. Cephalon ♂ lateral view. B. Pereopod 2 ♂.
C. Pereopod 7 ♂. D. Pereopod 1 ♂ inner surface. E. Pereopod 1 ♂ outer surface.
F. Pleopod 2 ♂.

Etymology

The specific name derives from the dimorphic nature of the first pereonite
and first pereopods.

Remarks

Of the described species of *Mesanthura*, the present species resembles only *M. ocellata* Barnard, 1925*a*, from Thailand, especially in having rings of pigment on the anterior pereonites. Barnard's species, however, also has rings on the posterior pereonites. Examination of Barnard's type material reveals further differences. The proportions of the mandibular palp segments, the pereopods 1 of the female, and the uropods all show differences from the present species.

Neohyssura Amar, 1952

Diagnosis

Eyes present or absent. Antennular flagellum of three to five articles; antennal flagellum of seven articles. Mandibular palp three-segmented. Maxilliped seven-segmented; endite present. Pereopods 1–3 similar, sub-chelate; pereopods 4–7 with triangular carpus underriding propodus. Pleonites 1–5 free, 6 fused with telson. Pleopod 1 non-operculiform. Telson indurate, spiniform.

Type species

Hyssura spinicauda Walker, 1901.

Neohyssura skolops Kensley, 1978
Figs 40–41

Neohyssura skolops Kensley, 1978*b*: 9, figs 5–6.

Diagnosis

Telson terete, spike-like. Uropodal exopod dentate on mesial margin. Maxilliped with thin-walled endite. Eyes present.

Type material

Holotype, SAM–A15651, 1 non-ovig. ♀, 5,8 mm, off Natal, 850 m.

Other material

SAM–A17535, 2 juvs, 3,1 mm, off East London, 90 m.

Distribution

East London to Natal, 90–850 m.

Panathura Barnard, 1925*a*

Diagnosis

Eyes present. Antennular flagellum of two to five articles; antennal flagellum of two to three articles. Mandible with three-segmented palp.
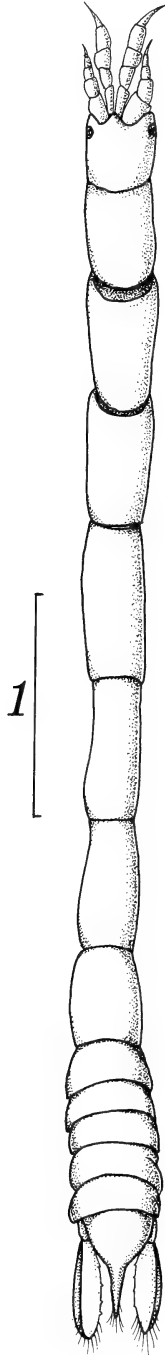
Fig. 40. *Neohyssura skolops*.
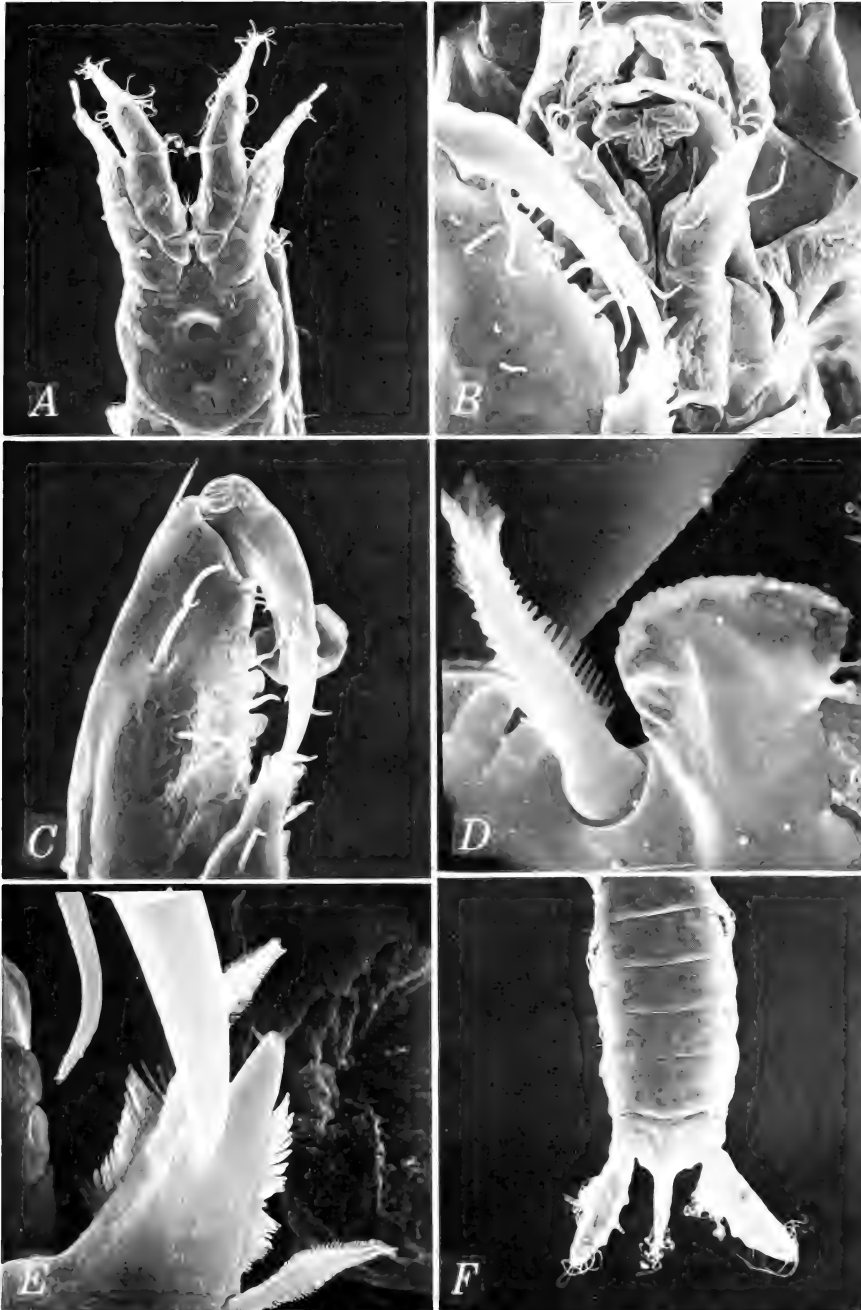♀ dorsal view. Scale in mm.

Fig. 41. *Neohyssura skolops*. A. ♀ cephalon dorsal view. B. Mouthparts and pereopod 1 palm. C. Pereopod 1 propodus and dactylus. D. Pereopod 1 propodal palm spine and lobe. E. Pereopod 1 apex of carpus. F. Pleon and telson.

Maxilliped six- (seven) segmented; endite well developed, distally rounded or acute. Pereopods 1–3 subchelate, subsimilar. Pereopods 4–7 with triangular carpus underriding propodus. Pleopod 1 exopod operculiform. Pleonites 1–6 free, short. Telson lacking statocysts.

Type species

Apanthura serricauda Barnard, 1920.

KEY TO THE SOUTH AFRICAN SPECIES OF *PANATHURA*

1. Pereopod 1 propodal palm with strong triangular proximal tooth; telson distally narrowly rounded .... *amstelodami*
– Pereopod 1 propodal palm with several low rounded teeth; telson distally broadly and evenly rounded .... *serricauda*

Panathura amstelodami Kensley, 1976
Fig. 42

Panathura amstelodami Kensley, 1976: 277, figs 4–5; 1977: 239; 1978*a*: 54, fig. 23D; 1980: 32.
Expanathura amstelodami: Wägele, 1981: 121.

Diagnosis

Telson and uropods not indurate; telson posteriorly tapering to broadly rounded apex, margins finely serrate. Maxillipedal endite distally narrowed. Lamina dentata of mandible with finely denticulate part; molar reduced. Pereopod 1 propodal palm with single strong proximal tooth, followed by two smaller teeth.

Type material

Holotype, Muséum National d'Histoire Naturelle, Paris, IS.1002, 1 ♂, 5,0 mm, Amsterdam Island. Paratypes, M.N.H.N., Paris, IS.1003, 2 non-ovig. ♀, 3,2–3,8 mm, Amsterdam Island, upper infralittoral to 80 m. Paratypes, SAM–A14994, 2 ♂, 3,0–3,2 mm, 1 non-ovig. ♀, 4,4 mm, Amsterdam Island.

Other material

SAM–A14356, 1 ovig. ♀, 4,9 mm, off Natal. SAM–A17536, 1 ♂, 3,1 mm. 1 ovig. ♀, 2,9 mm, 1 non-ovig. ♀, 3,0 mm, Walter's Shoal, 33°13'S 45°51'E, 38–46 m. USNM 171731, 11 ♂, 6 ovig. ♀, 31 non-ovig. ♀, south of Beira, Mozambique, 62 m. USNM 171732, 1 ovig. ♀, 4 non-ovig ♀, 1 juv., south coast of Madagascar, 46 m. USNM 171733, 1 ♂, 3 ovig. ♀, 8 non-ovig. ♀, 6 juvs, south coast of Madagascar, 38 m.

Distribution

St. Paul and Amsterdam Islands, southern Indian Ocean; Walter's Shoal, south-western Indian Ocean; Natal to Mozambique and Madagascar, upper infratidal to 80 m.
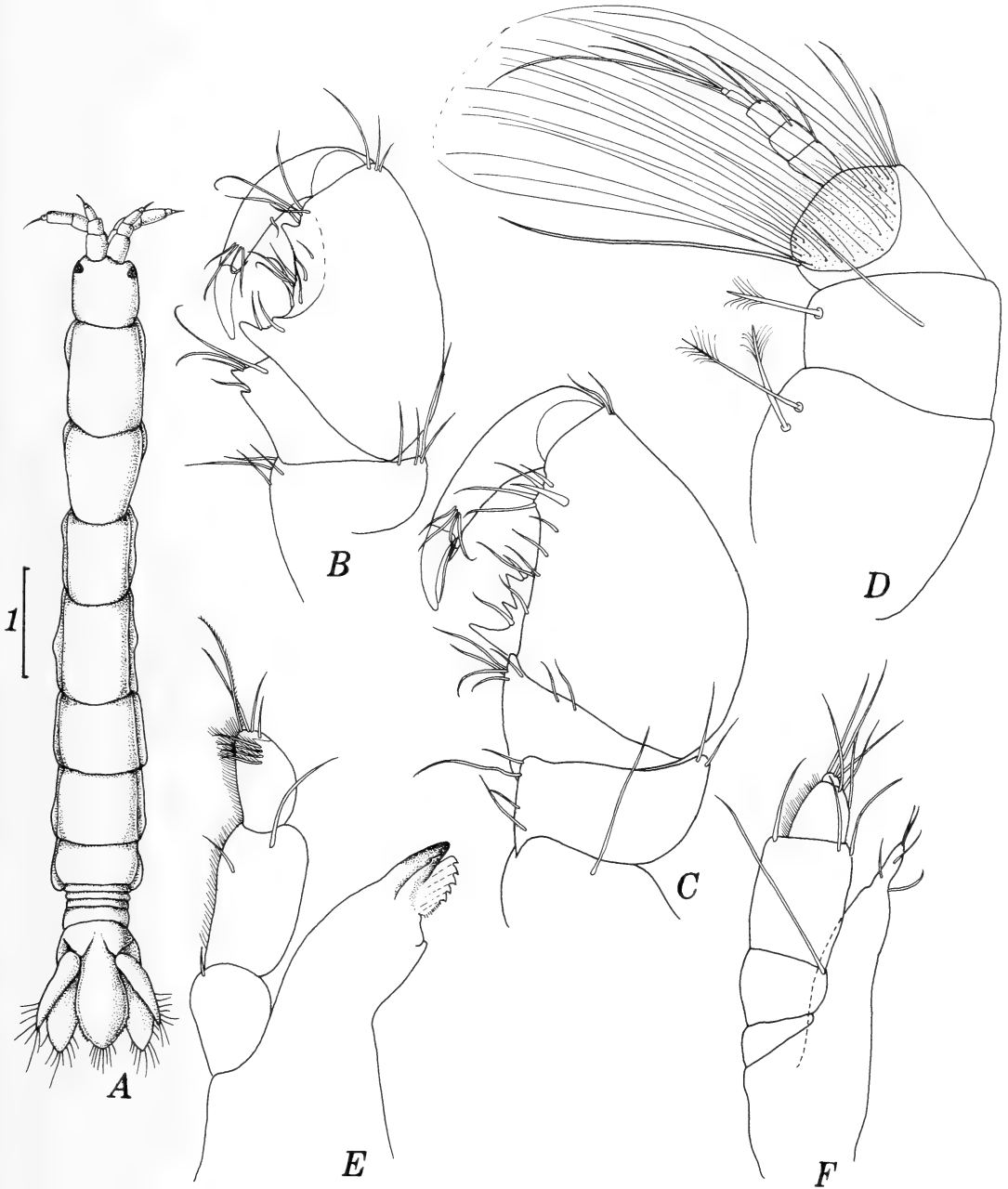
Fig. 42. *Panathura amstelodami*. A. ♀ dorsal view. B. Pereopod 1. C. Pereopod 2.
D. Antennule ♂. E. Mandible. F. Maxilliped. Scale in mm.

Panathura serricauda (Barnard, 1920)
Figs 43–44

Apanthura serricauda Barnard, 1920: 339, pl. 15 (figs 11–12).
Panathura serricauda: Barnard, 1925*a*: 143; 1940: 490; 1955: 5. Nierstrasz, 1941: 241. Penrith
    & Kensley, 1970: 228, Day, Field & Penrith, 1970: 47. Kensley, 1976: 264, fig. 6;
    1978*a*: 54, fig. 23E–G. Wägele, 1981: 118.
Panathura serricaudata (*sic*): Day, 1969: 78.

Diagnosis

Uropods and telson indurate. Telson distally evenly rounded, margins
serrate. Maxillipedal endite distally obtuse. Pereopod 1 propodal palm bearing
several blunt, almost rectangular teeth.

Type material

Syntypes, SAM–A2620, 1 non-ovig. ♀, damaged, Mouille Point, Table
Bay, intertidal. Syntypes, SAM–A2698, 2 non-ovig. ♀, Mouille Point, Table
Bay, intertidal. Syntypes, SAM–A2692, 1 non-ovig. ♀, St. James, False Bay,
intertidal.

Other material

SAM–A12741, 2 ovig. ♀, 4,5 mm, 1 non-ovig. ♀, 4,5 mm, 1 juv.,
Lüderitz, intertidal. SAM–A14355, 1 ovig. ♀, 5,0 mm, 1 non-ovig. ♀, 3,9 mm,
Langebaan Lagoon. SAM–A14359, 3 ovig. ♀, 4,0–5,0 mm, 3 juvs, 15
non-ovig. ♀, Schaapen Island, Langebaan. SAM–A14358, 2 non-ovig. ♀,
False Bay, 42 m. SAM–A14357, 1 non-ovig. ♀, Agulhas Bank, 49 m.
SAM–A17550, 7 ovig. ♀, 3,0–4,0 mm, 9 non-ovig. ♀, 2,5–3,2 mm, south of
East London, 90 m. SAM–A15511, 2 non-ovig. ♀, St. Paul Island.

Distribution

Lüderitz to East London, intertidal to 90 m; St. Paul Island, southern
Indian Ocean.

Remarks

Panathura serricauda is most frequently collected from the holdfasts of the
kelp *Ecklonia maxima*.

Quantanthura Menzies & George, 1972

Diagnosis

Eyes present or absent. Antennular flagellum of five to seven articles;
antennal flagellum of four to nine articles. Mandibular palp three-segmented.
Maxilliped six-segmented; endite well developed. Pereopod 1 subchelate,
propodus expanded; pereopods 2–3 smaller than pereopod 1; pereopods 4–7
with rectangular carpus. Pleopod 1 exopod operculiform. Pleonites 1–5 fused,
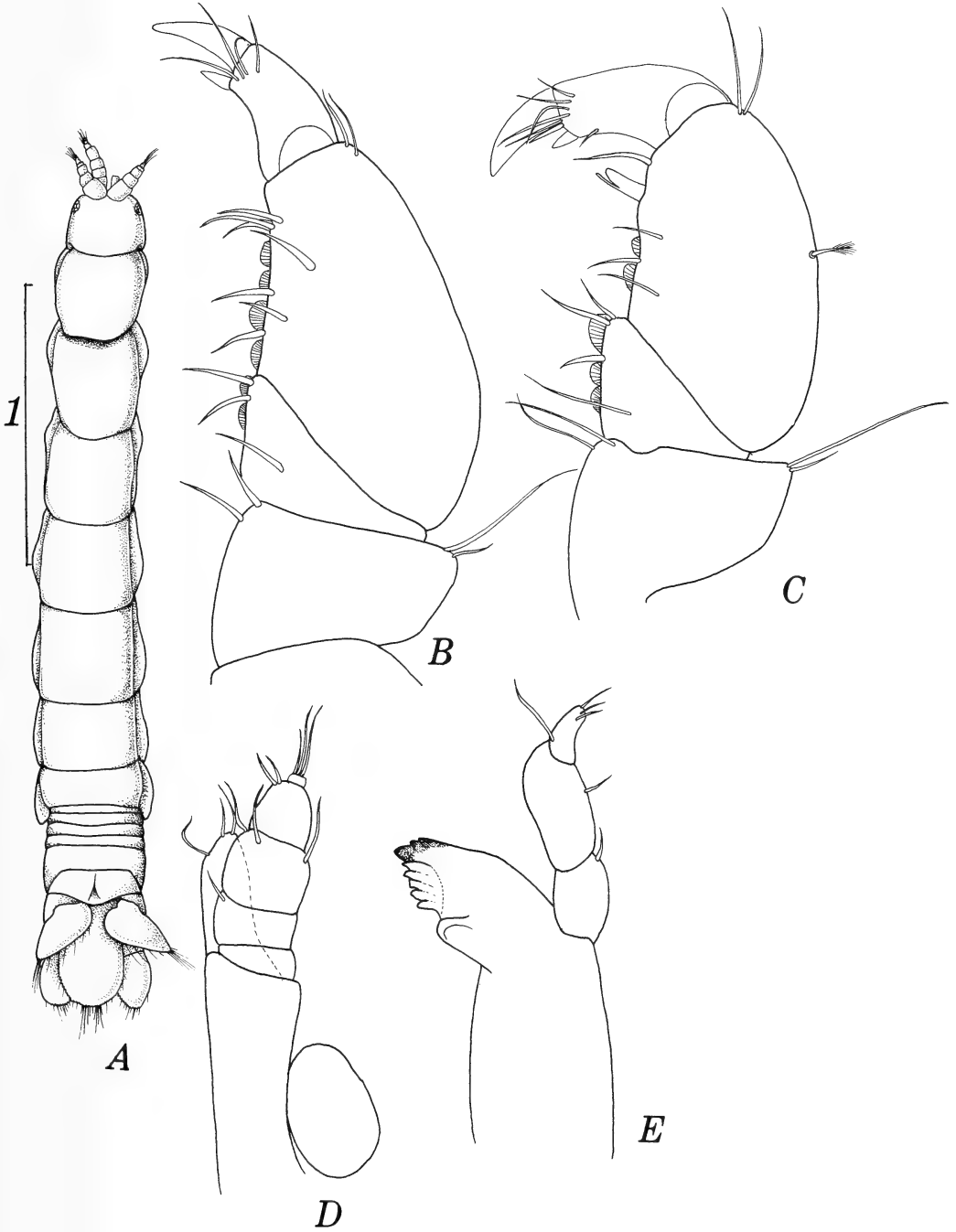pleonite 6 free. Telson with two basal statocysts.

Fig. 43. *Panathura serricauda*. A. ♀ dorsal view. B. Pereopod 1. C. Pereopod 2.
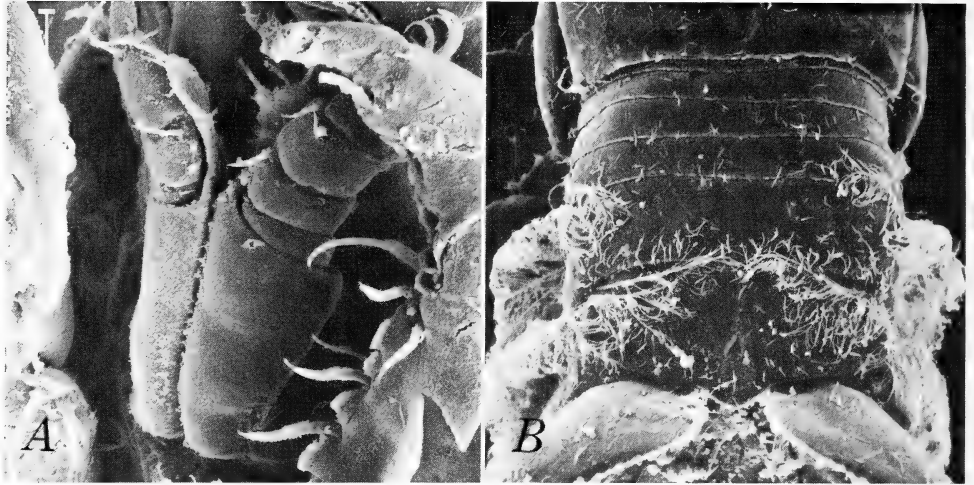D. Maxilliped. E. Mandible. Scale in mm.

Fig. 44. *Panathura serricauda*. A. Maxilliped. B. Pleon dorsal view.

Type species

Quantanthura globitelson Menzies & George, 1972.

Quantanthura remipes (Barnard, 1914)
Figs 45–46

Anthelura remipes Barnard, 1914: 338a, pl. 28B; 1925a: 135; 1940: 490. Nierstrasz, 1941: 240.
    Kensley, 1977: 239; 1978a: 46, fig. 20F.
Non Anthelura remipes Kensley, 1978b: 1.

Diagnosis

Eyes absent. Antennular flagellum of five articles. Antennal flagellum of four to five articles, reduced. Maxilliped with broad, distally rounded endite. Pereopod 1 propodus expanded, palm convex, with groove on inner surface. Telson elliptical, posteriorly narrowly rounded, dorsally convex. Uropodal exopod ovoid, outer margin sinuous.

Type material

Holotype, SAM–A58, 1 non-ovig. ♀, 28,1 mm, (damaged), off Cape Peninsula, 312 m.

Other material

SAM–A14402, 1 non-ovig. ♀, 10,2 mm, Agulhas Bank, 78 m. SAM–A14993, 1 non-ovig. ♀, 15,9 mm, Lambert's Bay.

Distribution

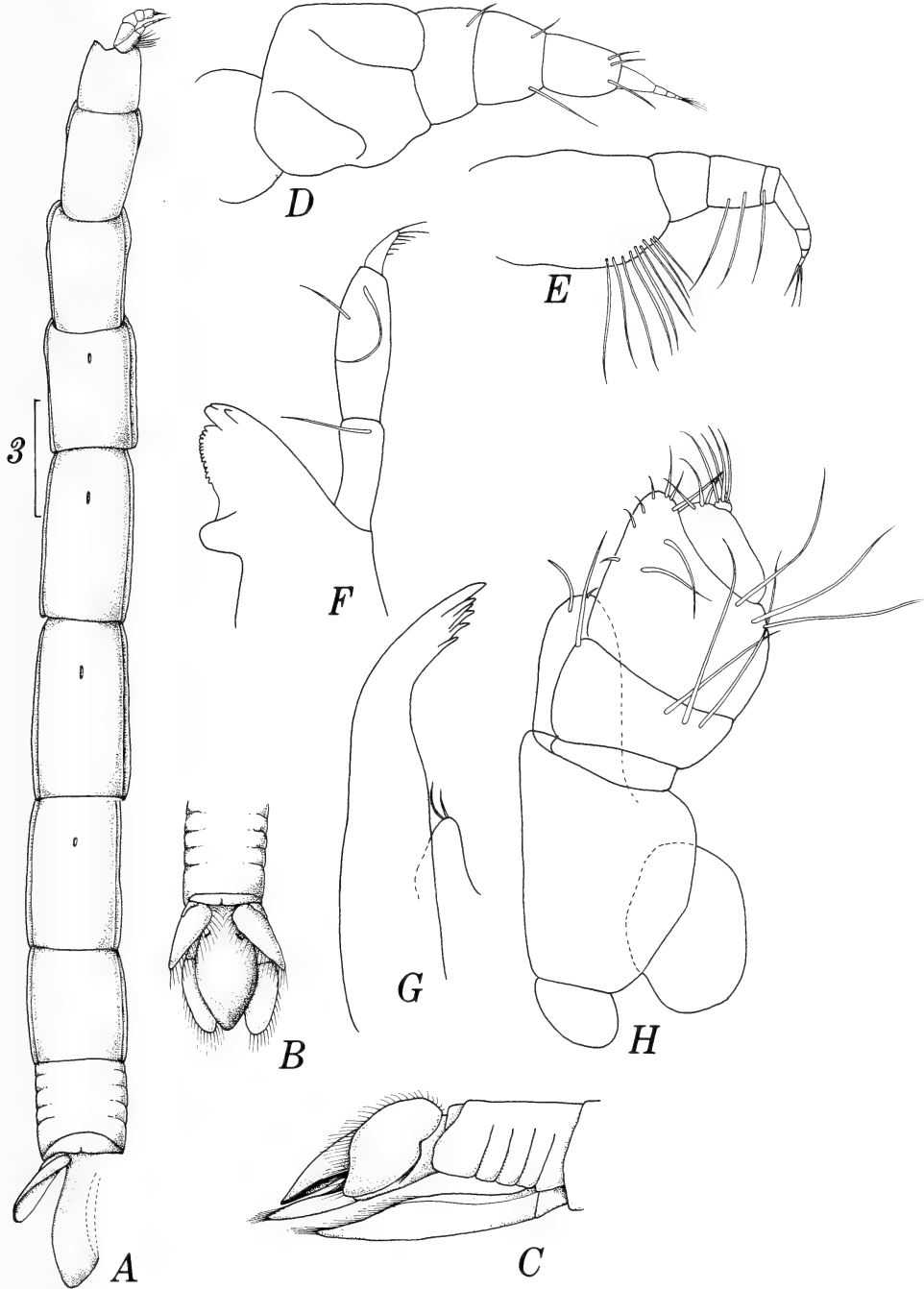Lambert's Bay to Agulhas Bank, 78–312 m.

Fig. 45. *Quantanthura remipes*. A. Holotype ♀ dorsal view. B. Pleon ♀ dorsal view. C. Pleon lateral view. D. Antenna. E. Antennule. F. Mandible. G. Maxilla. H. Maxilliped. Scale in mm.
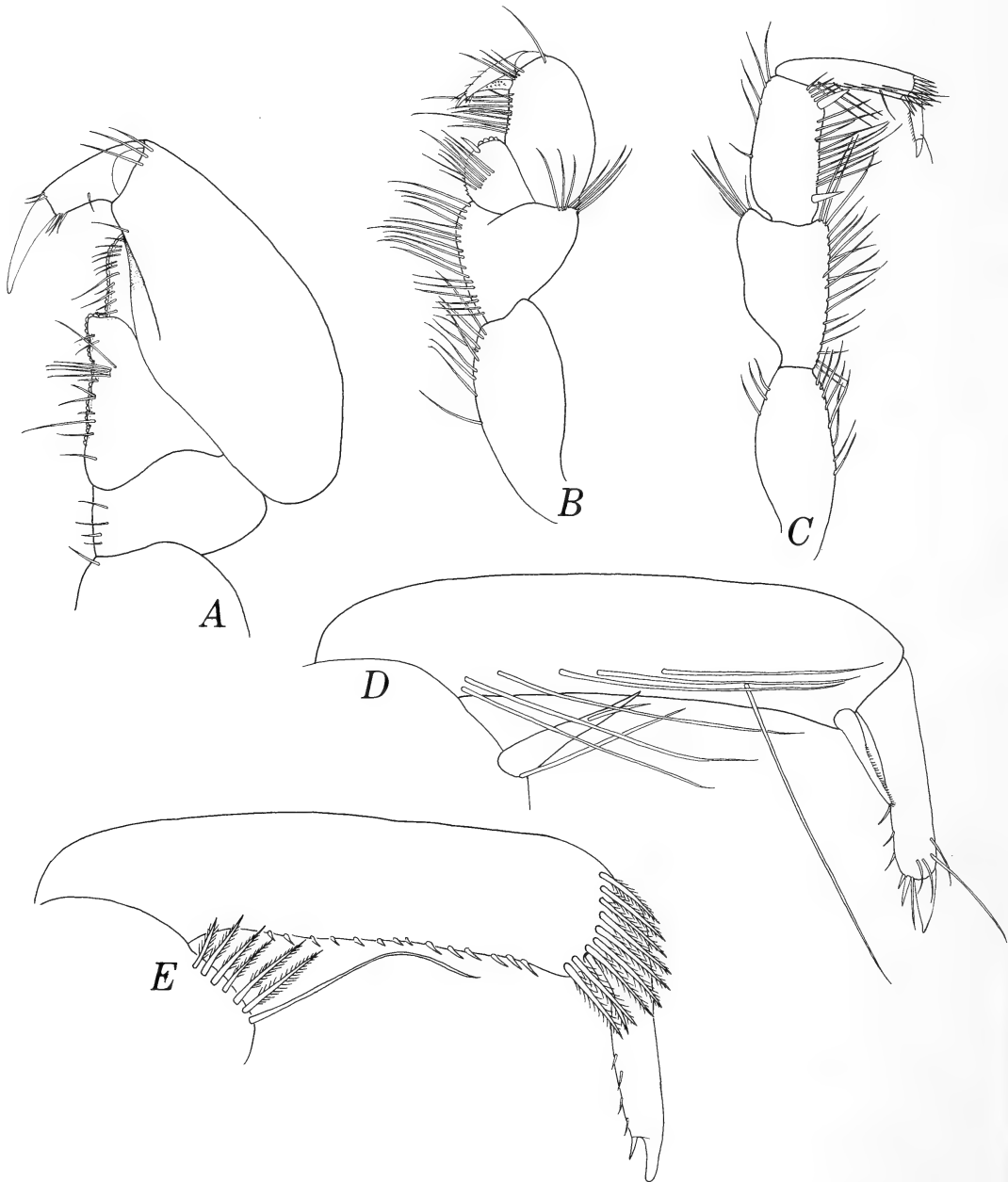
Fig. 46. *Quantanthura remipes*.   A. Pereopod 1.   B. Pereopod 2.   C. Pereopod 7.
D. Pereopod 7 dactylus and propodus outer surface.   E. Pereopod 7 dactylus and propodus
inner view.

Remarks

Since the revision of the diagnosis of *Anthelura* (Kensley 1978*d*: 787) and *Quantanthura* (Kensley and Koening, 1979: 953), there can be little doubt that the present species is a member of the latter genus.

KEY TO SOUTH AFRICAN GENERA OF THE FAMILY PARANTHURIDAE

1. Antennular and antennal flagella of more than 10 articles.................. *Accalathura*
– Antennular and antennal flagella with fewer than 10 articles 2
2. Pereopod 7 absent .... *Colanthura*
– Pereopod 7 present.. 3
3. Uropodal exopod reduced, endopod and basis fused .... *Pseudanthura*
– Uropodal exopod not reduced, endopod free 4
4. Eyes absent; pereopod 7 with triangular carpus .... *Leptanthura*
– Eyes present; pereopod 7 with rectangular carpus .... *Paranthura*

Family **Paranthuridae**
Accalathura Barnard, 1925*a*

Diagnosis

Eyes present. Flagella of antennule and antenna multiarticulate. Mandibular palp three-segmented. Maxillipedal endite reaching almost to end of palp; latter of two segments. Pereopod 1 subchelate, propodus expanded; pereopods 2–3 ambulatory; pereopods 4–7 with rectangular carpus. Telson with or without statocyst.

Type species

Calathura crenulata Richardson, 1905.

Accalathura indica (Nierstrasz, 1941)
Fig. 47

Metanthura indica Nierstrasz, 1941: 247, figs 15–24.
Accalathura indica: Kensley, 1977: 250, fig. 8; 1978*a*: 44, fig. 20A. Poore, 1980: 59.

Diagnosis

Antennular and antennal flagella of about twenty-eight and thirty-five articles respectively. Eyes well developed. Pleonite 6 longest, bilobed. Telson elongate-lanceolate, with single basal statocyst. Uropodal exopod elongate-oval.

Type material

Whereabouts unknown.

Other material

SAM–A15348, 1 ovig. ♀, off Mozambique, 100 m. SAM–A17577, 1 ovig. ♀, off Natal, 90 m. SAM–A17578, 1 ♂, off Sodwana Reef, Zululand, 17 m.
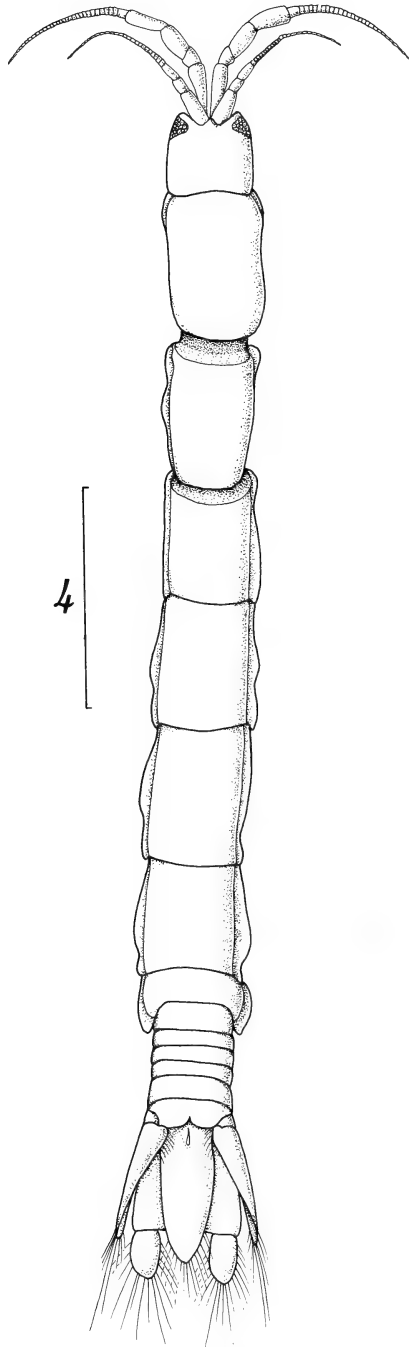
Fig. 47. *Accalathura indica*. ♀ dorsal view.
Scale in mm.

Distribution

Natal, Mozambique, to Java Sea, 17–100 m.

Accalathura laevitelson (Kensley, 1975)

Fig. 48

Katanthura laevitelson Kensley, 1975a: 69, fig. 17; 1978a: 50, fig. 22H–I.
Zulanthura laevitelson: Poore, 1980: 65.

Diagnosis

Eyes present. Pleonites 1–6 free. Maxilliped with strong endite, palp two-segmented. Pereopods 2–3 smaller than pereopod 1; pereopods 4–6 with rectangular carpus not underriding propodus. Single telsonic statocyst present.

Type material

Holotype, SAM–A13552, 1 manca, 6,4 mm, off Still Bay, 30 m.

Distribution

Off Still Bay, 30 m.

Remarks

G. Poore (1981 pers. comm.) has examined this specimen, and is convinced that it is a manca of an *Accalathura* species, almost certainly not *A. indica*. Because the single specimen is immature, a key to the two species of southern African *Accalathura* is not included.

Colanthura Richardson, 1902

Diagnosis

Eyes present or absent. Mandibular palp absent. Antennular and antennal flagella with few short articles. Maxilliped lacking endite or palp segments. Pereopod 1 subchelate, propodus expanded; pereopods 4–6 with rectangular carpi. Pereonite 7 very short, lacking pereopod. Pleonites 1–6 short, free. Pleopod 1 exopod operculiform. Telson lacking statocyst.

Type species

Colanthura tenuis Richardson, 1902.

Colanthura uncinata Kensley, 1978

Figs 49–50

Colanthura uncinata Kensley, 1978b: 12, figs 7–8.
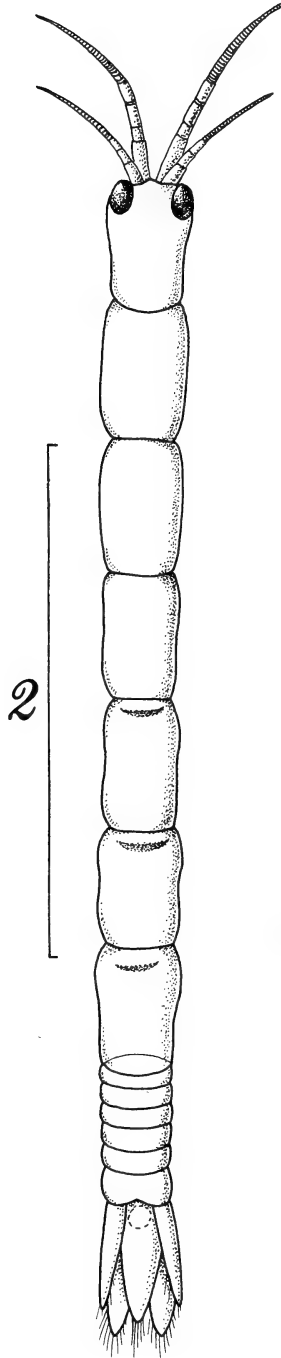
Fig. 48. *Accalathura laevitelson*. Holotype dorsal view. Scale in mm.

Diagnosis

Telson posteriorly evenly rounded, with low mid-dorsal rounded ridge. Pleopod 2 of male, apex of copulatory stylet with single recurved hook. Pereopod 1 male with fourteen fringed spines on inner propodal surface; female with six spines. Uropodal exopod narrowly oval, endopod more broadly oval.

Fig. 49. *Colanthura uncinata*. A. ♂ dorsal view. B. Antennule ♂. C. Antennule ♀. D. Antenna. E. Maxilliped. F. Pereopod 1 ♂. G. Uropodal exopod. H. Uropodal basis and endopod. Scale in mm.

Type material

Holotype, SAM–A15652, 1 ♂, 3,9 mm. Allotype, SAM–A15652, 1 ovig. ♀, 4,5 mm, off Natal, 28°31'S 32°34'E, 680 m. Paratypes, SAM–A15653, 2 ♂, 3,4 mm, 1 ovig. ♀, 4,0 mm, off Natal, 27°59'S 32°40'E, 550 m. Paratypes, USNM 170544, 2 ♂, 3,9 mm, 1 ovig. ♀, 4,5 mm, off Natal, 28°31'S 32°34'E, 680 m.
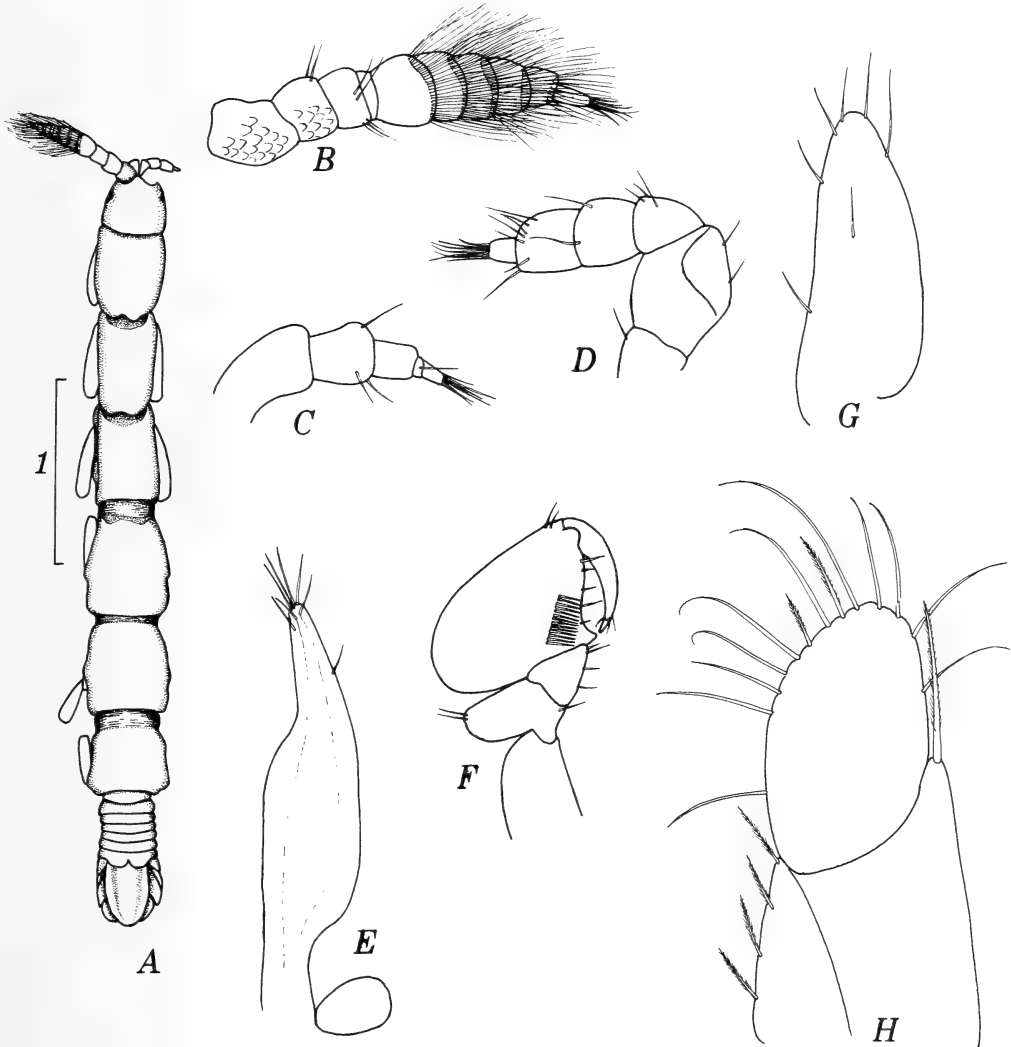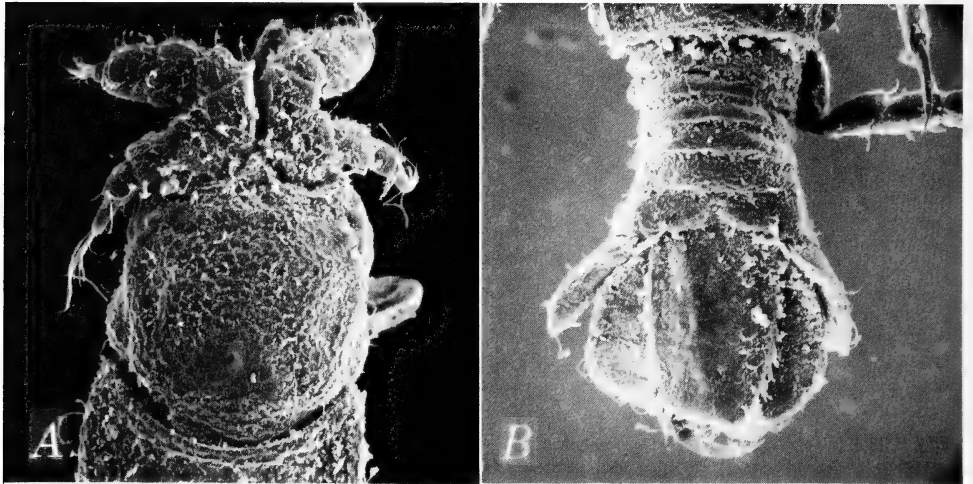

Fig. 50. *Colanthura uncinata*. A. Cephalon dorsal view. B. Pleon dorsal view.

Other material

SAM–A17581, 1 ♂, off Transkei, 32°28'S 28°58'E, 710–775 m. SAM–A17582, 1 ♂, 2 ovig. ♀, off Transkei, 31°59'S 29°22'E, 150–200 m. SAM–A17579, 1 ♂, 2 sub♂, 2 non-ovig. ♀, 4 ovig. ♀, off Natal, 27°59'S 32°40'E, 550 m. SAM–A17580, 6 ♂, 3 sub♂, 5 ovig. ♀, 4 juvs, off Natal, 28°31'S 32°34'E, 680 m.

Distribution

Northern Natal to Transkei, 150–775 m.

Leptanthura Sars, 1899

Diagnosis

Eyes absent. Flagella of antennule and antenna reduced. Mandibular palp three-segmented. Maxillipedal endite rudimentary or absent; palp of one to three articles, with one to two terminal spines only. Pereopod 1 subchelate; pereopods 2–3 similar to but smaller than pereopod 1; pereopods 4–7 with

triangular carpus lacking free anterior margin. Pleonites free. Pleopod 1 exopod operculiform. Uropodal exopod often broadly oval. Telson with single statocyst.

Type species

Anthura tenuis Sars, 1873.

KEY TO THE SOUTH AFRICAN SPECIES OF *LEPTANTHURA*

1. Uropodal exopod margin serrate .... *urospinosa*
 – Uropodal exopod margin entire 2
2. Telson posteriorly broadly rounded 3
 – Telson posteriorly tapered, apically acute .... *agulhasensis*
3. Uropodal exopod with strong notch in distal margin .... *laevigata*
 – Uropodal exopod unnotched 4
4. Uropodal endopod triangular; midventral processes absent from pereon .... *minuta*
 – Uropodal endopod narrow; midventral processes present on some pereonites ... *natalensis*

Leptanthura agulhasensis Kensley, 1975

Fig. 51

Leptanthura agulhasensis Kensley, 1975a: 64, figs 14–15; 1978a: 52, fig. 22M. Poore, 1978: 141, 144.

Diagnosis

Telson parallel-sided, posterior third tapering to acute apex; dorsal surface with few scattered fringed scales. Uropodal exopod narrow, lanceolate, not reaching endopod. Maxilliped five-segmented, three distal segments tiny.

Type material

Holotype, SAM–A13550, 1 ♂, 9,0 mm, False Bay, 66 m. Allotype, SAM–A13551, 1 non-ovig. ♀, 8,0 mm, off Still Bay, 80 m. Paratypes, SAM–A13617, 2 ♂, 9,0–9,1 mm, False Bay, 66 m. Paratypes, SAM–A13618, 2 non-ovig. ♀, 6,5–7,9 mm, Agulhas Bank, 183 m. SAM–A17583, 2 ovig. ♀, 1 non-ovig. ♀, south of East London, 90 m.

Other material

SAM–A14198, 1 ovig. ♀, off Saldanha Bay, 320 m. SAM–A14328, 1 non-ovig. ♀, off Saldanha Bay. SAM–A14343, 1 ovig. ♀, 1 non-ovig. ♀, False Bay, 75 m. SAM–A14344, 2 non-ovig. ♀, False Bay, 26 m. SAM–A14346, 3 non-ovig. ♀, False Bay, 39 m. SAM–A14345, 1 non-ovig. ♀, Agulhas Bank, 50 m. SAM–A14199, 1 non-ovig. ♀, Still Bay, 183 m. SAM–A17584, 1 ovig. ♀, Still Bay, 80 m. SAM–A14933, 1 ♂, 1 ovig. ♀, locality unknown.

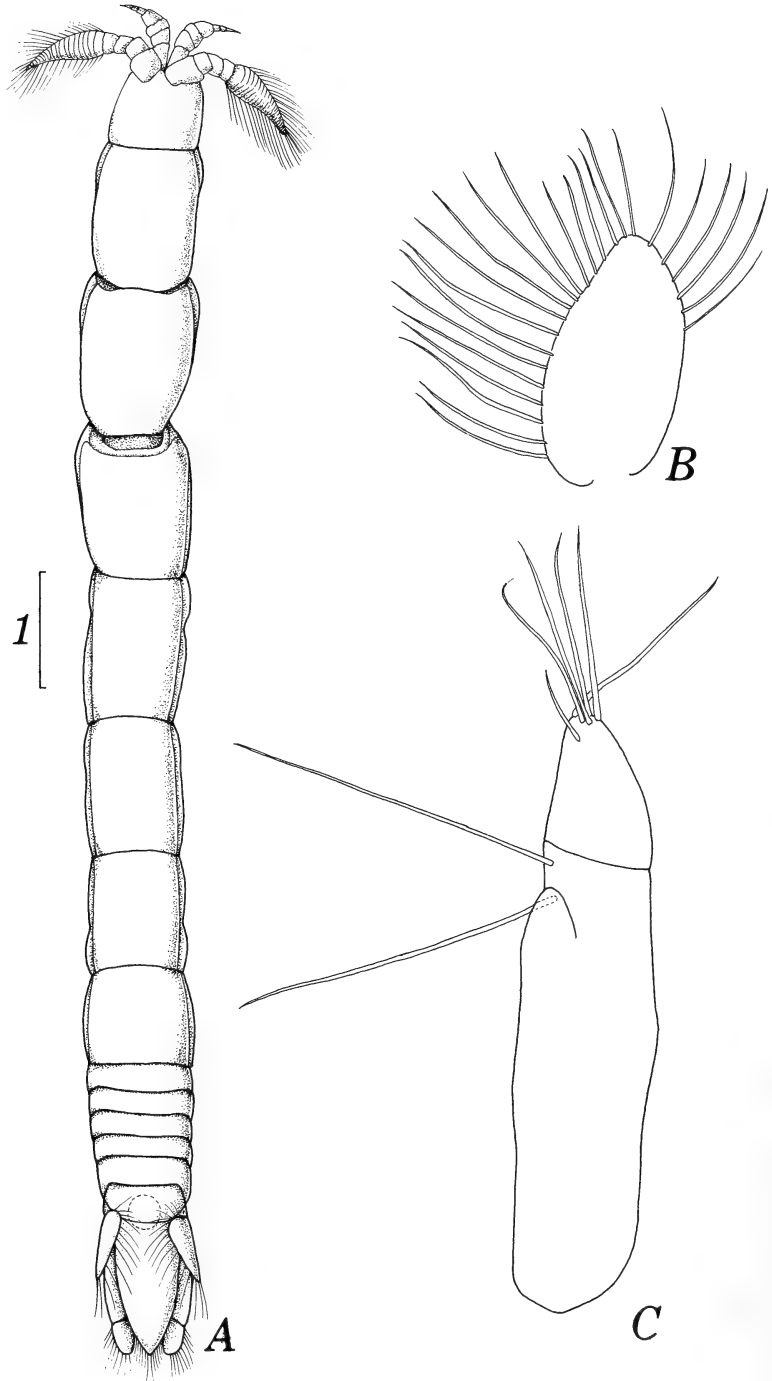## Distribution

Saldanha Bay to East London, 26–320 m.

Fig. 51. *Leptanthura agulhasensis*. A. ♂ dorsal view. B. Uropodal exopod.
C. Maxilliped. Scale in mm.

Leptanthura laevigata (Stimpson, 1855)

Figs 52–53

Anthura laevigata Stimpson, 1855: 393.
Leptanthura faurei Barnard, 1914: 345a, pl. 29B.
Leptanthura laevigata: Vanhöffen, 1914: 492, fig. 30. Barnard, 1925a: 151. Kensley, 1975a: 38;
    1978a: 52, fig. 22N; 1980: 2. Poore, 1978: 138; 1980: 62.

Diagnosis

Telson posteriorly evenly rounded; dorsal surface covered with numerous regular imbricate scales. Uropodal exopod almost circular, with strong notch in distal margin.

Type material

Whereabouts unknown, Type locality: Simon's Bay in False Bay, '12 fathoms'.

Other material

SAM–A14208, 1 ♂, 1 non-ovig. ♀, off Orange River mouth, 170 m. SAM–A14298, 1 non-ovig. ♀, off Orange River mouth. SAM–A14234, 1 non-ovig. ♀, Saldanha Bay. SAM–A14273, 1 ♂, Saldanha Bay, 88 m. SAM–A14284, 1 non-ovig. ♀, Saldanha Bay. SAM–A14329, 3 juvs, off Saldanha Bay. SAM–A14331, 2 ♂, Saldanha Bay. SAM–A14333, 1 non-ovig. ♀, 2 juvs, Saldanha Bay. SAM–A14335, 1 ♂, 5 juvs, Saldanha Bay. SAM–A14336, 1 non-ovig. ♀, 2 juvs, Saldanha Bay. SAM–A14337, 1 sub♂, 2 juvs, Saldanha Bay. SAM–A14231, 1 ovig. ♀, 1 non-ovig. ♀, Langebaan. SAM–A14839, 1 juv., Langebaan. SAM–A14246, 1♂, off Cape Peninsula. SAM–A14205, 1 ♂, 4 non-ovig. ♀, 1 juv., False Bay, 57 m. SAM–A14206, 1 non-ovig. ♀, False Bay, 66 m. SAM–A14207, 1 non-ovig. ♀, False Bay, 54 m. SAM–A14209, 1 ♂, False Bay, 26–29 m. SAM–A14210, 2 non-ovig. ♀, 1 juv., False Bay, 22 m. SAM–A14211, 3 ♂, 1 sub♂, 1 ovig. ♀, 4 non-ovig. ♀, 7 juvs, False Bay 75 m. SAM–A14212, 3 non-ovig. ♀, 1 juv., False Bay, 66 m. SAM–A14213, 1 non-ovig. ♀, False Bay, 29 m. SAM–A14214, 1 non-ovig. ♀, False Bay, 36 m. SAM–A14215, 2 ♂, 1 non-ovig. ♀, False Bay, 87 m. SAM–A14216, 1 ♂, 4 non-ovig. ♀, False Bay 40 m. SAM–A14217, 2 non-ovig. ♀, 1 juv., False Bay, 17 m. SAM–A14219, 2 ♂, 1 non-ovig. ♀, False Bay, 42 m. SAM–A14221, 2 ♂, 2 ovig. ♀, 2 non-ovig. ♀, 2 juvs, False Bay, 87 m. SAM–A14222, 5 ♂, 2 sub♂, 3 ovig. ♀, 14 non-ovig. ♀, 25 juvs, False Bay, 61 m. SAM–A14224, 2 non-ovig. ♀, False Bay 33 m. SAM–A14225, 3 non-ovig. ♀, False Bay, 26 m. SAM–A14226, 1 ♂, 1 ovig. ♀, 6 non-ovig. ♀, 2 juvs, False Bay, 66 m. SAM–A14227, 1 juv., False Bay, 44 m. SAM–A14288, 1 juv., False Bay, 26 m. SAM–A14233, 1 ♂, 2 non-ovig. ♀, 6 juvs, False Bay. SAM–A14235, 1 non-ovig. ♀, False Bay, 48 m. SAM–A14237, 1 sub♂, False Bay. SAM–A14239, 1 non-ovig. ♀, False Bay, 13 m. SAM–A14240, 1♂, 1 sub♂, 1 non-ovig. ♀, 1 juv., False Bay. SAM–A14241, 1 non-ovig. ♀, False
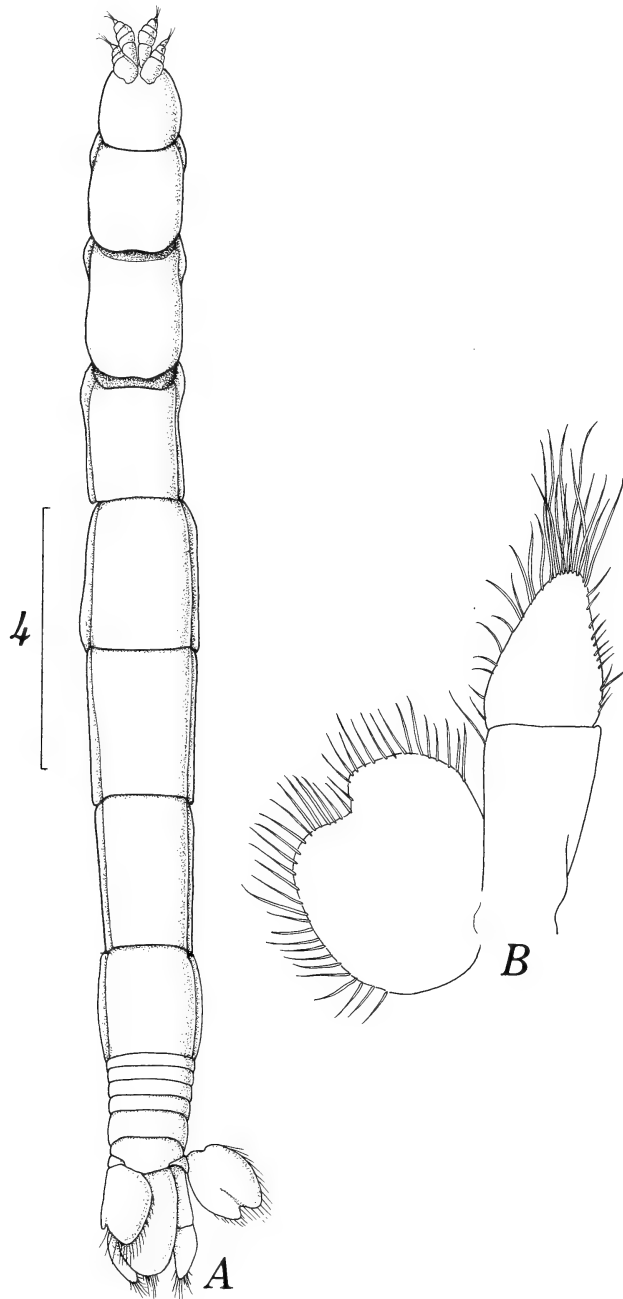
Fig. 52. *Leptanthura laevigata*. A. ♀ dorsal view. B. Uropod.
Scale in mm.
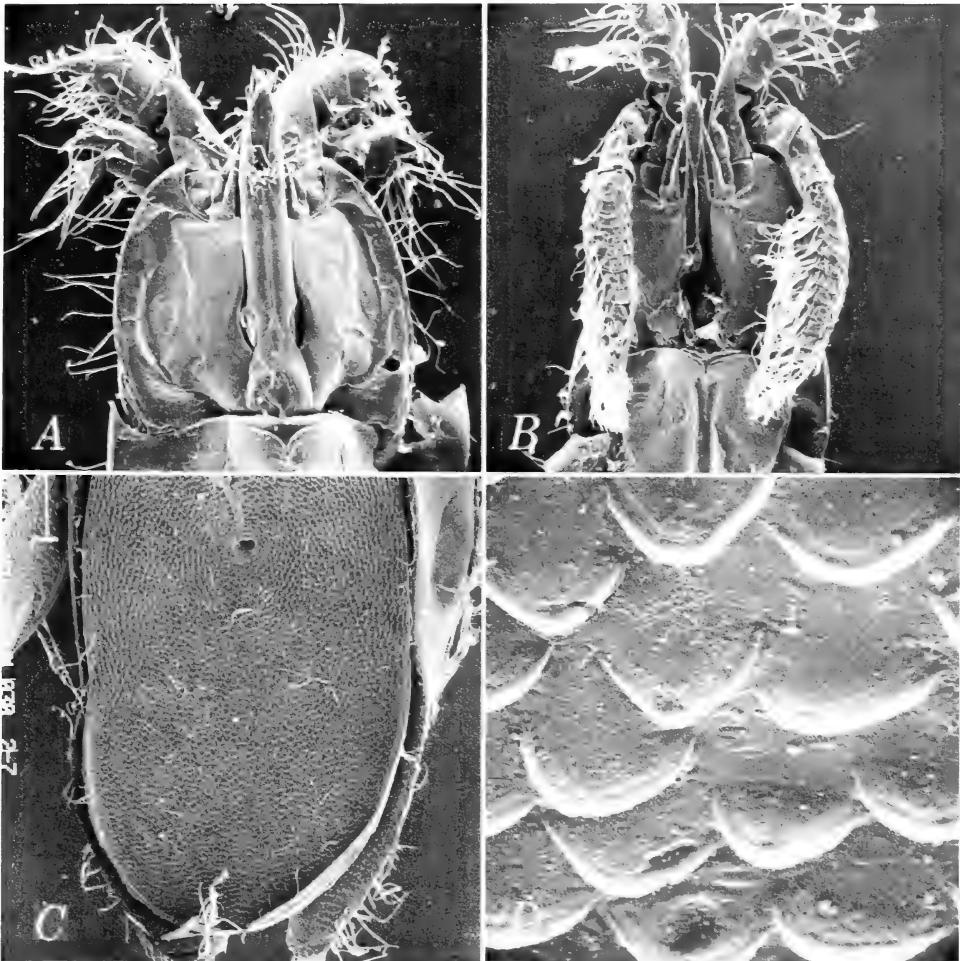
Fig. 53. *Leptanthura laevigata*. A. Cephalon ♀ ventral view. B. Cephalon ♂ ventral view. C. Telson. D. Telsonic scales enlarged.

Bay, 53 m. SAM–A14242, 2 non-ovig. ♀, False Bay, 27 m. SAM–A14243, 1 non-ovig. ♀, False Bay, 48 m. SAM–A14244, 3 non-ovig. ♀, 1 juv., False Bay, 42 m. SAM–A14245, 1 non-ovig. ♀, False Bay, 50 m. SAM–A14253, 1 ovig. ♀, False Bay, 68 m. SAM–A14254, 1 ovig. ♀, False Bay, 64 m. SAM–A14255, 1 juv., False Bay, 44 m. SAM–A14256, 1 non-ovig. ♀, False Bay. SAM–A14257, 1 non-ovig. ♀, False Bay. SAM–A14259, 1 juv., False Bay. SAM–A14260, 2 non-ovig. ♀, False Bay, 42 m. SAM–A14261, 2 ovig. ♀, 3 non-ovig. ♀, False Bay, 81 m. SAM–A14262, 2 ♂, 2 ovig. ♀, 4 non-ovig. ♀, False Bay. SAM–A14268, 1 ovig. ♀, 1 non-ovig. ♀, False Bay, 50 m.

SAM–A14269, 1 juv., False Bay. SAM–A14271, 1 sub♂, 1 ovig. ♀, False Bay. SAM–A14272, 1 ♂, 1 non-ovig. ♀, 4 juvs, False Bay. SAM–A14277, 1 ♂, 1 ovig. ♀, 4 non-ovig. ♀, False Bay, 82 m. SAM–A14279, 1 non-ovig. ♀, False Bay, 79 m. SAM–A14280, 1 ♂, False Bay, 40 m. SAM–A14283, 2 juvs, False Bay, 23 m. SAM–A14287, 2 ovig. ♀, 6 non-ovig. ♀, False Bay, 58 m. SAM–A14289, 2 non-ovig. ♀, 1 juv., False Bay, 82 m. SAM–A14290, 1 non-ovig. ♀, False Bay, 36 m. SAM–A14291, 1 sub♂, 2 ovig. ♀, 1 non-ovig. ♀, False Bay, 59 m. SAM–A14292, 1 ♂, 3 juvs, False Bay, 80 m. SAM–A14293, 3 non-ovig. ♀, False Bay, 58 m. SAM–A14295, 11 juvs, False Bay, 5 m. SAM–A14297, 1 ♂, 1 non-ovig. ♀, False Bay, 59 m. SAM–A14299, 1 ♂, 5 non-ovig. ♀, 6 juvs, False Bay, 39 m. SAM–A14300, 1 ovig. ♀, 1 non-ovig. ♀, 2 juvs, False Bay, 53 m. SAM–A14301, 1 ovig. ♀, 1 juv., False Bay, 82 m. SAM–A14302, 1 ♂, 2 non-ovig. ♀, False Bay, 53 m. SAM–A14303, 1 non-ovig. ♀, False Bay, 16 m. SAM–A14304, 1 ♂, 1 sub♂, False Bay, 44 m. SAM–A14305, 1 juv., False Bay. SAM–A14306, 1 ovig. ♀, 4 juvs, False Bay, 19 m. SAM–A14307, 1 ♂, 1 sub♂, 2 ovig. ♀, 3 non-ovig. ♀, False Bay, 82 m. SAM–A14308, 1 non-ovig. ♀, 5 juvs, False Bay, 18 m. SAM–A14309, 1 ♂, False Bay, 38 m. SAM–A14312, 2 ♂, 4 non-ovig. ♀, 2 juvs, False Bay, 87 m. SAM–A14314, 1 ♂, 3 juvs, False Bay, 56 m. SAM–A14313, 1 non-ovig. ♀. 1 juv., False Bay, 59 m. SAM–A14315, 4 non-ovig. ♀, False Bay, 38 m. SAM–A14317, 3 non-ovig. ♀, 2 juvs, False Bay, 23 m. SAM–A14318, 2 ovig. ♀, 2 non-ovig. ♀, False Bay, 58 m. SAM–A14320, 2 ♂, 1 non-ovig. ♀, 4 juvs, False Bay, 58 m. SAM–A14321, 1 ♂, 1 non-ovig. ♀, False Bay, 40 m. SAM–A14330, 1 ♂, 1 sub♂, 2 non-ovig. ♀, 3 juvs, False Bay, 40 m. SAM–A14332, 1 juv., False Bay, 38 m. SAM–A14338, 1 ♂, 2 ovig. ♀, 5 non-ovig. ♀, 1 juv., False Bay. SAM–A14340, 1 non-ovig. ♀, False Bay, 26 m. SAM–A14836, 3 juvs, False Bay. SAM–A14838, 2 ♂, 4 ovig. ♀, 6 non-ovig. ♀, 3 juvs, False Bay, 40 m. SAM–A14218, 1 ovig. ♀, 1 non-ovig. ♀, Agulhas Bank, 44 m. SAM–A14229, 1 ovig. ♀, 2 non-ovig. ♀, 1 juv., Agulhas Bank, 75 m. SAM–A14236, 2 juvs, Agulhas Bank, 84 m. SAM–A14247, 1 non-ovig. ♀, Agulhas Bank, 100 m. SAM–A14248, 1 juv., Agulhas Bank, 27 m. SAM–A14249, 1 non-ovig. ♀, Agulhas Bank, 26 m. SAM–A14251, 1 juv., Agulhas Bank, 172 m. SAM–A14252, 1 non-ovig. ♀, Agulhas Bank, 183 m. SAM–A14263, 1 ♂, 1 non-ovig. ♀, Agulhas Bank, 124 m. SAM–A14264, 1 sub♂, Agulhas Bank, 93 m. SAM–A14265, 1 non-ovig. ♀, Agulhas Bank, 97 m. SAM–A14267, 1 non-ovig. ♀, Agulhas Bank, 84 m. SAM–A14270, 1 non-ovig. ♀, Agulhas Bank, 108 m. SAM–A14274, 1 ovig. ♀, 2 non-ovig. ♀, Agulhas Bank, 106 m. SAM–A14275, 6 juvs, Agulhas Bank, 107 m. SAM–A14276, 4 non-ovig. ♀, Agulhas Bank, 183 m. SAM–A14278, 1 ovig. ♀, Agulhas Bank, 46 m. SAM–A14282, 2 non-ovig. ♀, 1 juv., Agulhas Bank, 125 m. SAM–A14288, 1 non-ovig. ♀, Agulhas Bank, 11 m. SAM–A14294 1 ♂, 1 non-ovig. ♀, 1 juv., Agulhas Bank, 44 m. SAM–A14296, 1 ovig. ♀, Agulhas Bank, 300 m. SAM–A14310, 1 non-ovig. ♀, Agulhas Bank, 44 m. SAM–A14316, 1 ovig. ♀,

1 non-ovig. ♀, Agulhas Bank, 44 m. SAM–A14837, 2 non-ovig. ♀, Mossel Bay. SAM–A14230, 1 non-ovig. ♀, off Knysna. SAM–A14200, 1 ♂, 12 non-ovig. ♀, 15 juvs, Still Bay, 20 m. SAM–A14201, 2 non-ovig. ♀, Still Bay, 80 m. SAM–A14202, 1 non-ovig. ♀, 1 juv., Still Bay, 15 m. SAM–A14203, 3 non-ovig. ♀, Still Bay, 15 m. SAM–A14204, 1 juv., Still Bay, 200 m. SAM–A14286, 3 juvs, off Port Elizabeth. SAM–A57, 2 ♂, 2 non-ovig. ♀, off East London, 86 m. SAM–A62, 1 ovig. ♀, off Keiskamma Point, 66 m. SAM–A64, 1 ovig. ♀, off Cape St. Francis, 50 m. SAM–A2745, 3 non-ovig. ♀, off East London, 104 m. SAM–A4169, 1 juv., off Cape Seal, 160 m. SAM–A5959, 2 ovig. ♀, 2 non-ovig. ♀, off Duminy Point, 174 m. SAM–A5960, 1 ovig. ♀, off Cape St. Blaize, 84 m.

Distribution

Orange River mouth to Agulhas Bank; Durban to Mozambique Channel, 42–1 360 m.

Remarks

The material recorded by Kensley (1980) from Madagascar, Mauritius, and Sumatra, although superficially similar to *L. laevigata* in uropodal and telsonic shape, tends to be ovigerous at a smaller size and lacks imbricate scales on the telson. These differences would indicate that at least one other species is involved in the western Indian Ocean.

Leptanthura minuta Kensley, 1978
Fig. 54

Leptanthura minuta Kensley, 1978*b*: 16, figs 9–10.

Diagnosis

Adult male and female less than 5,0 mm total length. Integument not indurate. Telson elliptical, posteriorly broadly rounded. Uropodal exopod broadly oval, margin crenate.

Type material

Holotype, SAM–A15654, 1 ♂, 4,6 mm. Allotype, 1 ovig. ♀, 4,5 mm. Paratypes, 1 ♂, 1 ovig. ♀, 1 non-ovig. ♀, off Natal, 27°59′S 32°40′E, 550 m. Paratypes, USNM 170545, 1 ♂, 1 ovig. ♀, 1 non-ovig. ♀, off Natal, 27°59′S 32°40′E, 550 m.

Other material

SAM–A15655, 1 ovig. ♀, off Natal, 27°31′S 32°50′E, 750 m. SAM–A15656, 2 ♂, 1 non-ovig. ♀, off Natal, 30°53′S 30°31′E, 850 m.
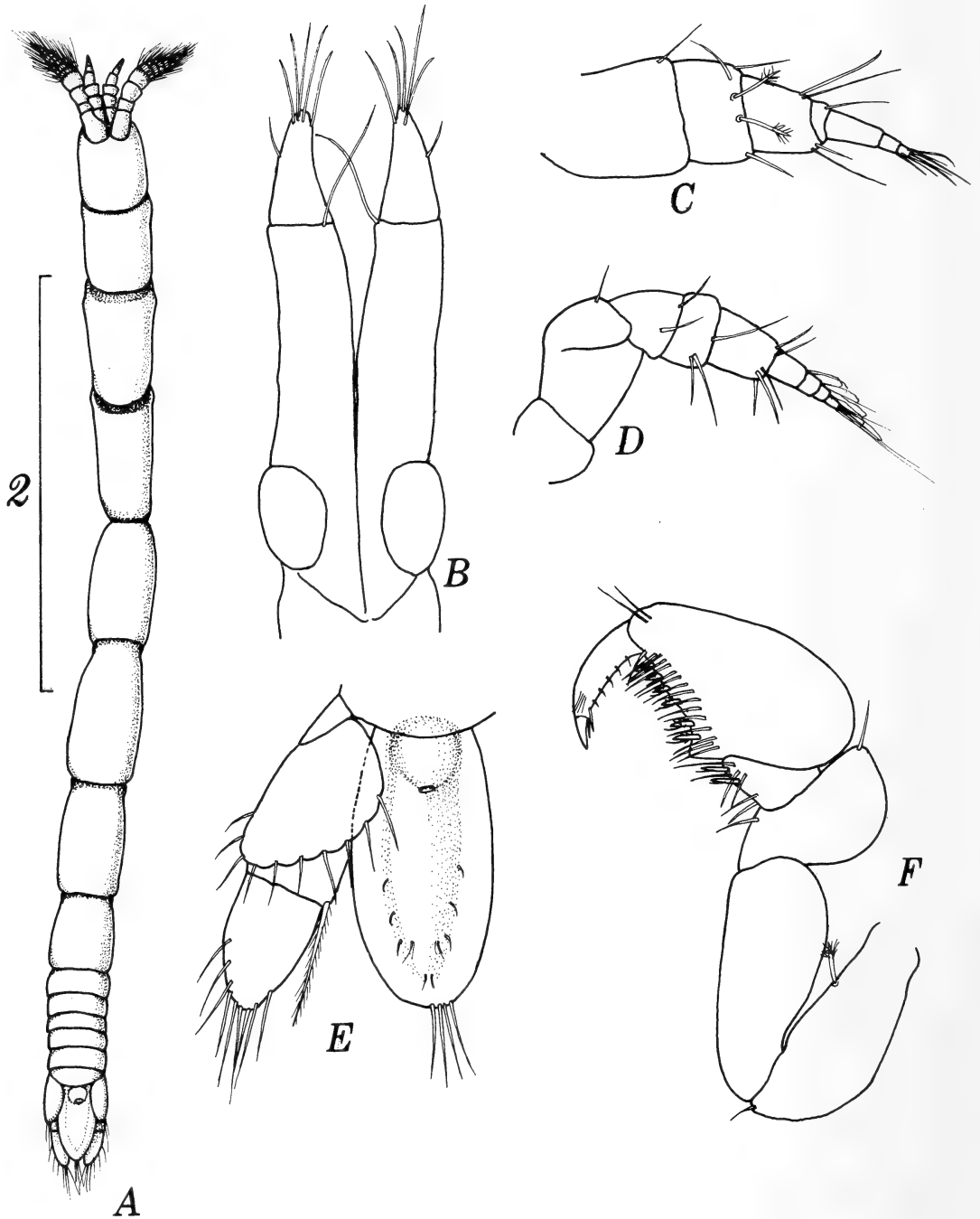
Distribution

Off Natal, 550–850 m.

Fig. 54. *Leptanthura minuta*. A. ♂ dorsal view. B. Maxilliped. C. Antennule ♀.
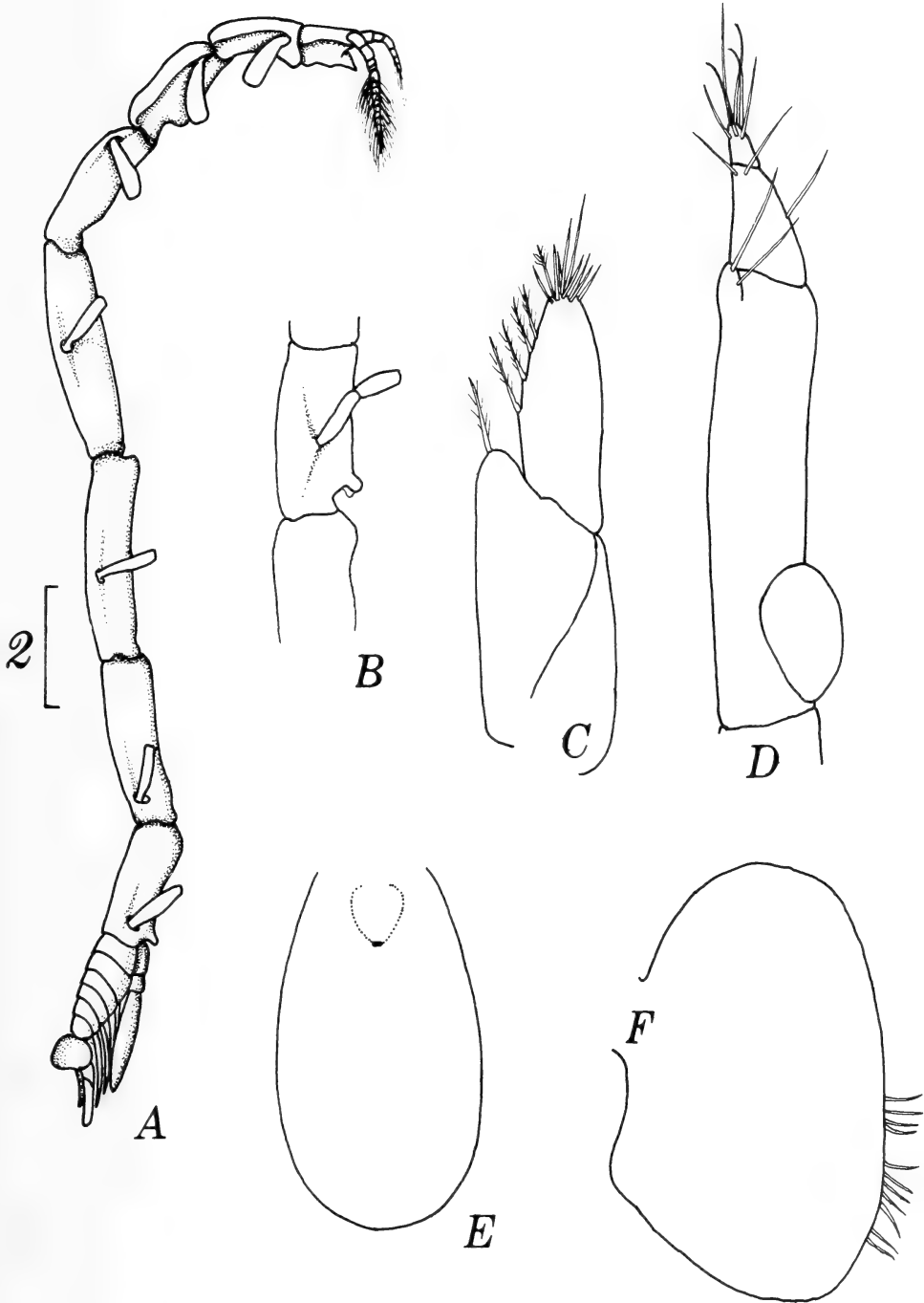D. Antenna. E. Telson and uropod. F. Pereopod 1 ♂. Scale in mm.

Fig. 55. *Leptanthura natalensis*. A. ♂ lateral view. B. Pereonite 5 ♂ lateral view. C. Uropodal endopod and basis. D. Maxilliped. E. Telson. F. Uropodal exopod. Scale in mm.

Leptanthura natalensis Kensley, 1978

Figs 55–56

Leptanthura natalensis Kensley, 1978b: 20, figs 11–12.

Diagnosis

Integument moderately indurate. Telson posteriorly evenly rounded. Uropodal exopod broadly oval-subcircular. Short posteroventral lobes present on some pereonites.

Type material

Holotype, SAM–A15657, 1 ♂, 20,6 mm, off Natal, 27°09′S 32°58′E, 800 m. Paratypes, SAM–A15658, 2 ♂, 6,7–6,8 mm, 1 juv., off Natal, 26°51′S 33°12′E, 720 m. Paratypes, SAM–A15659, 2 ♂, 6,7–7,5 mm, off Natal, 27°10′S 32°58′E, 820 m. Paratypes, USNM 170546, 1 ♂, 8,0 mm, 1 non-ovig. ♀, 5,7 mm, off Natal, 30°17′S 31°10′E, 820 m.

Other material

SAM–A15660, 1 ♂, 1 juv., off Natal, 30°33′S 30°48′E, 690 m. SAM–A15661, 7 non-ovig. ♀, off Natal, 30°53′S 30°31′E, 850 m.

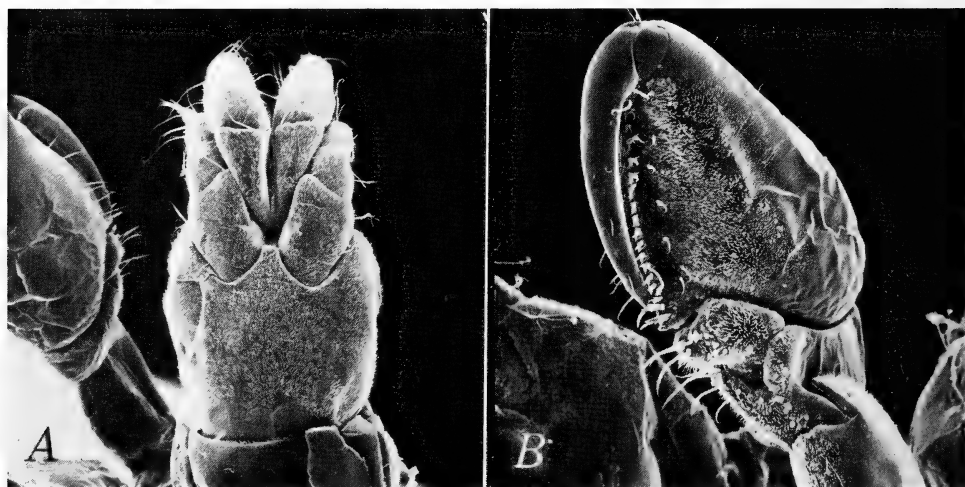### Distribution

Off Natal, 690–850 m.

Fig. 56. *Leptanthura natalensis*. A. Cephalon ♂ dorsal view. B. Pereopod 1 inner surface.

Leptanthura urospinosa Kensley, 1975

Fig. 57

Leptanthura urospinosa Kensley, 1975*a*: 67, fig. 16; 1978*a*: 52, fig. 22K–L. Poore, 1980: 62.

Diagnosis

Telson parallel-sided, posterior third tapering to acute apex. Uropodal exopod broadly oval, with dentate medial margin. Maxilliped four-segmented.

Type material

Holotype, SAM–A13619, 1 non-ovig. ♀, 10,5 mm, False Bay, 26 m. Paratype, SAM–A13620, 1 non-ovig. ♀, 13,3 mm, False Bay, 5 m.

Other material

SAM–A17611, 1 ovig. ♀, 8,8 mm, 1 non-ovig. ♀, 9,6 mm, False Bay, 75 m. SAM–A17612, 3 non-ovig. ♀, 6,0–8,5 mm, False Bay, 39 m. SAM–A14341, 1 non-ovig. ♀, 8,0 mm, off Still Bay, 120 m. SAM–A14342, 1 non-ovig. ♀, 5,4 mm, off Still Bay, 200 m. SAM–A17613, 1 non-ovig. ♀, 5,2 mm, Agulhas Bank, 50 m.

Distribution

False Bay to Still Bay, 5–200 m.

Paranthura Bate & Westwood, 1868

Diagnosis

Eyes present. Pleonites more or less distinct. Antennular flagellum shorter than peduncle. Antennal flagellum of one or more articles, short, flattened. Mandibular palp three-segmented. Maxillipedal endite small to obsolete; palp of one or two articles. Pereopod 1 propodus expanded, subchelate; pereopods 2–3 smaller than 1; pereopods 4–7 with rectangular carpi, anterior margins subequal to posterior margins. Pleopod 1 exopod operculiform. Telson lacking statocyst.

Type species

Paranthura costana Bate & Westwood, 1868.

Remarks

Paranthura is probably the most speciose genus of the Paranthuridae, with many of the species being superficially very similar. Species reported to have wide geographical distributions should be viewed with suspicion; close examination and attention to fine details of tail-fan structure especially will probably reveal several restricted species masquerading under long-established names.
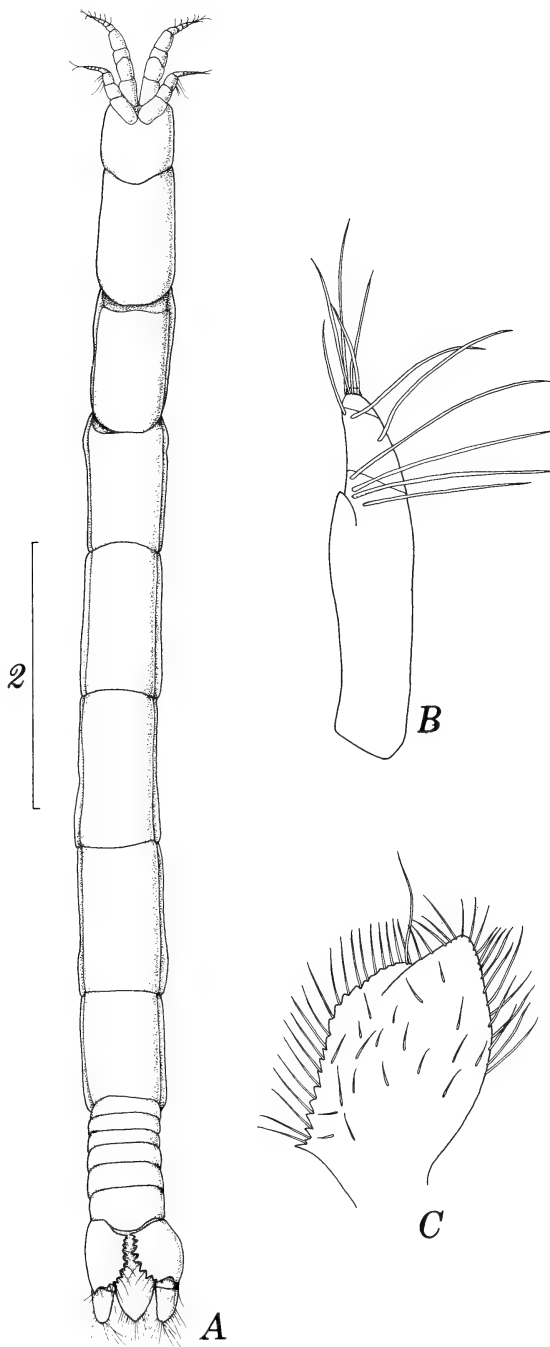
Fig. 57. *Leptanthura urospinosa*. A. ♀ dorsal view.
B. Maxilliped. C. Uropodal exopod. Scale in mm.

Paranthura latipes Barnard, 1955

Fig. 58

Paranthura latipes Barnard, 1955: 51, fig. 24d–f. Kensley, 1978a: 54, fig. 23H–I. Poore, 1980: 63.

Diagnosis

Telson ovate-lanceolate, bearing elongate finely plumose setae. Uropodal exopod ovate, bearing plumose setae. Pereopod 1 with basal tooth on propodal palm 'not prominent' (Barnard 1955: 51). Ischia and bases of pereopods 4–7 broad, subcircular.

Type material

Holotype, ♂, 7,5 mm, Maxixe, Inhambane Bay, Mozambique, intertidal. This specimen was not received by the South African Museum, and is apparently lost.

Distribution

Inhambane, Mozambique; intertidal.

Remarks

This species has not been recorded since the original description.

Paranthura punctata (Stimpson, 1855)

Figs 59–60

Anthura punctata Stimpson, 1855: 393. Stebbing, 1910: 419.
Paranthura punctata: Hilgendorf, 1878: 847. Barnard, 1914: 348a, pl. 29C; 1920: 343; 1925a: 154; 1940: 490. Nierstrasz, 1941: 252. Thomson, 1951: 2. Hurley, 1961: 283. Grindley & Kensley, 1966: 8. Kensley, 1975a: 39; 1978a: 55, fig. 23J; 1978b: 2. Chapman & Lewis, 1976: 162, fig. 105. Poore, 1980: 64.

Diagnosis

Antennular flagellum of four articles; antennal flagellum of one article. Mandibular palp segment 3 with comb of fourteen to sixteen fringed spines. Maxilliped with rudimentary endite, palp of single setose segment. Pereopod 1 propodus expanded. Pleon shortened, pleonites free; pleonite 6 strongly incised. Telson lanceolate, posteriorly rounded. Uropodal exopod narrowly oval-lanceolate.

Type material

Whereabouts unknown. Type locality: False Bay, '20 fathoms'.
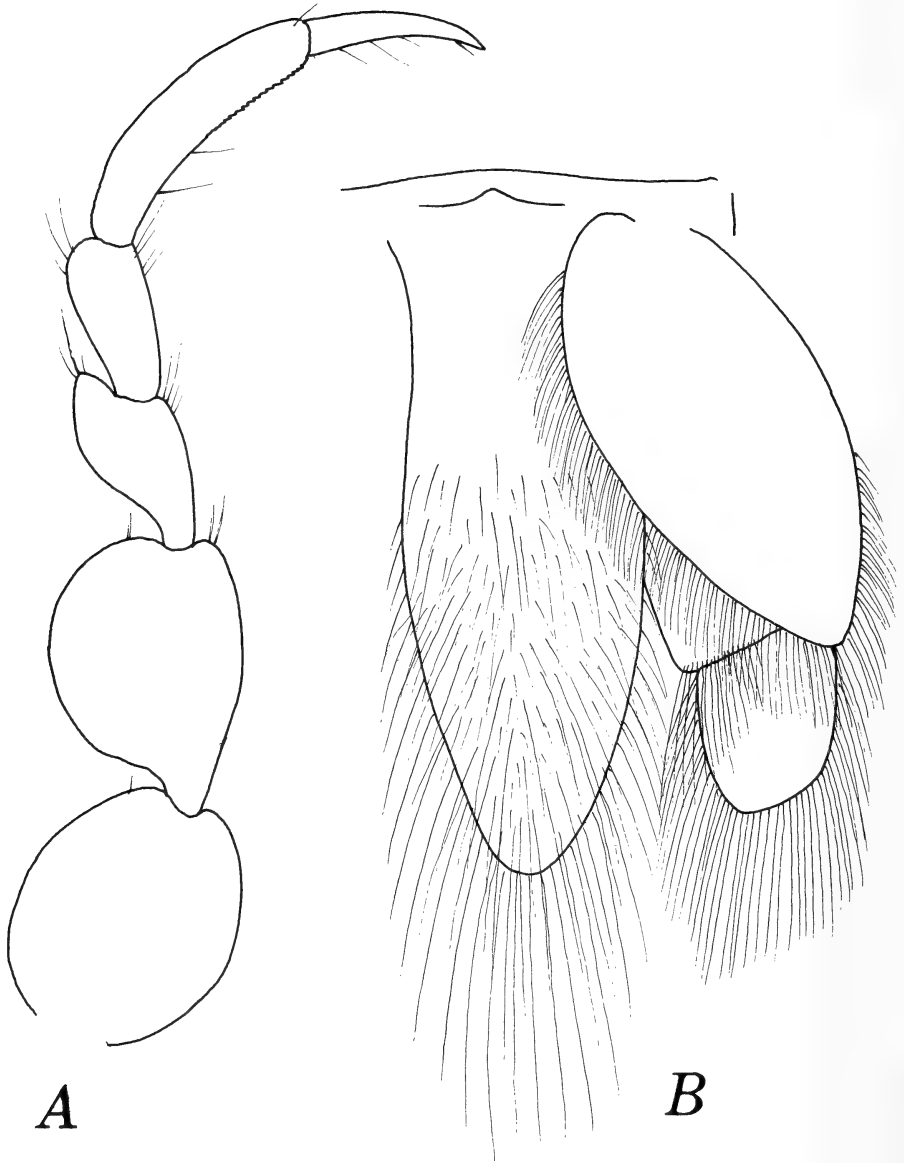
Fig. 58. *Paranthura latipes*. A. Pereopod 5. B. Uropod and telson (from Barnard 1955).
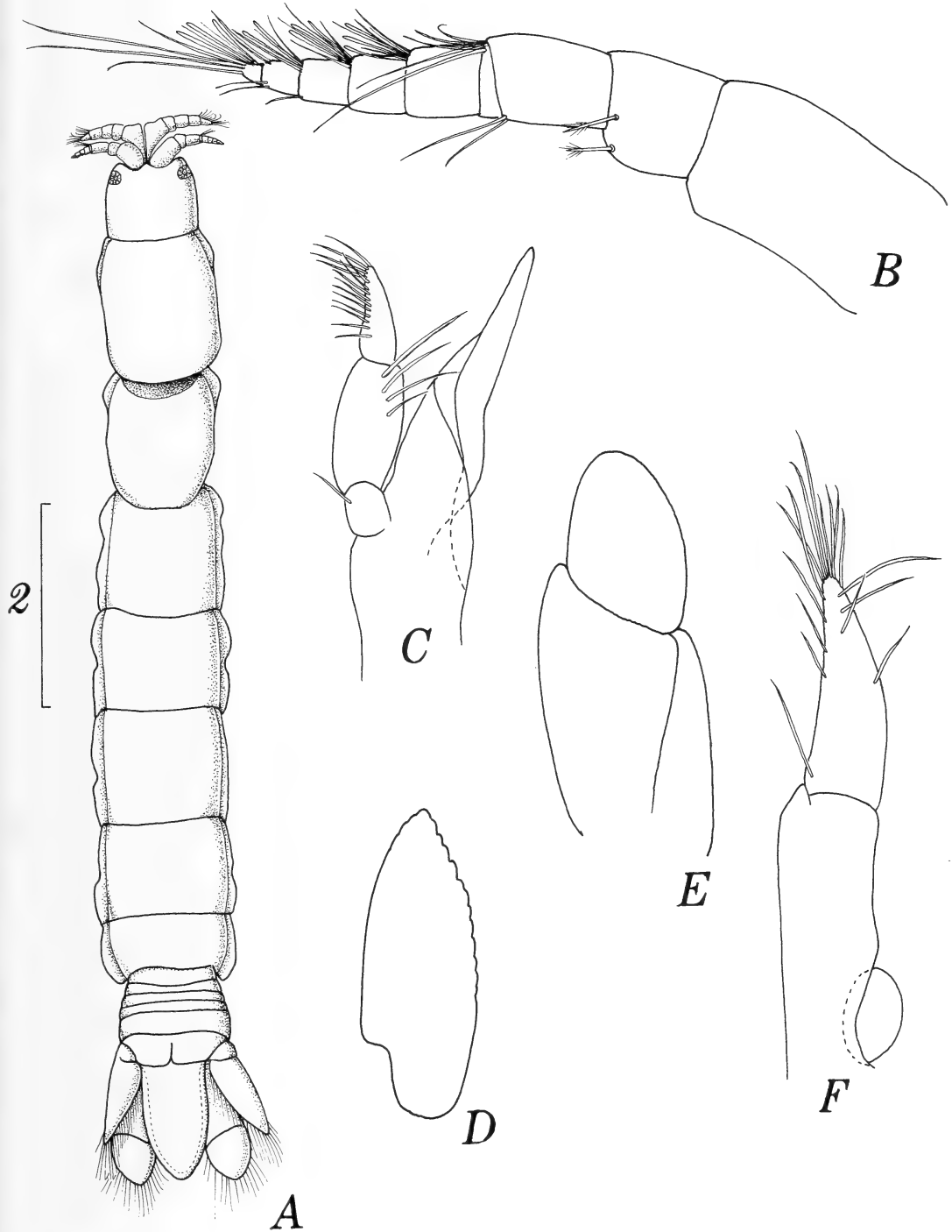
Fig. 59. *Paranthura punctata*. A. ♀ dorsal view. B. Antennule. C. Mandible. D. Uropodal exopod. E. Uropodal basis and endopod. F. Maxilliped. Scale in mm.

Other material

SAM–A12256, 1 non-ovig. ♀, 1 juv., off Orange River mouth. SAM–A14371, 1 non-ovig. ♀, off Saldanha Bay, 50–54 m. SAM–A2612, 2 non-ovig. ♀, 1 juv., Mouille Point, Table Bay. SAM–A14361, 1 non-ovig. ♀, False Bay, 44 m. SAM–A14363, 1 non-ovig. ♀, False Bay, 39 m. SAM–A14364, 8 ovig. ♀, 3 non-ovig. ♀, 14 juvs, False Bay, 42 m. SAM–A14366, 1 non-ovig. ♀, False Bay, 42 m. SAM–A14368, 1 non-ovig, ♀, False Bay, 13 m. SAM–A14369, 1 non-ovig. ♀, False Bay. SAM–A14377, 5 non-ovig. ♀, False Bay, 17 m. SAM–A14382, 1 non-ovig. ♀, 1 juv., False Bay, 40 m.

Fig. 60. *Paranthura punctata*. A. Cephalon ♀ dorsal view. B. Cephalon ♀ ventral view. C. Antennal flagellum. D. Apex of oral cone, with projecting tips of maxillae.

SAM–A14383, 1 non-ovig. ♀, False Bay, 42 m. SAM–A14384, 1 non-ovig. ♀, False Bay, 27 m. SAM–A14386, 1 ovig. ♀, 1 non-ovig. ♀, False Bay, 66 m. SAM–A14387, 2 ovig. ♀, 2 juvs, False Bay. SAM–A14388, 1 non-ovig. ♀, False Bay, 35 m. SAM–A14389, 1 juv., False Bay, 51 m. SAM–A14391, 1 juv., False Bay, 7 m. SAM–A14392, 1 non-ovig. ♀, 2 juvs, False Bay, 18 m. SAM–A14394, 2 ovig. ♀, False Bay, 19 m. SAM–A14372, 2 juv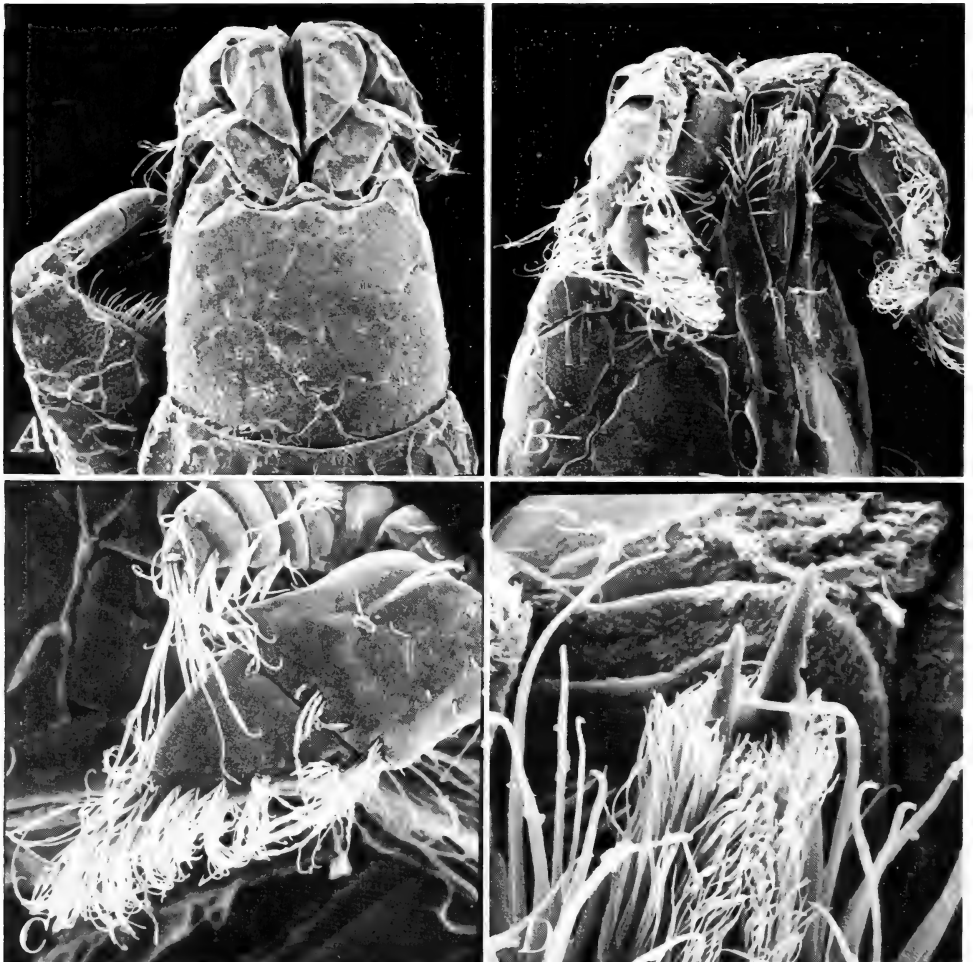s, Still Bay, 80 m. SAM–A14396, 1 non-ovig. ♀, Still Bay, 120 m. SAM–A14365, 1 juv., Agulhas Bank, 183 m. SAM–A14367, 1 non-ovig. ♀, Agulhas Bank, 10 m. SAM–A14370, 1 juv., Agulhas Bank, 11–18 m. SAM–A14374, 1 ovig. ♀, 1 juv., Agulhas Bank, 121 m. SAM–A14375, 1 non-ovig. ♀, Agulhas Bank, 110 m. SAM–A14379, 1 ovig. ♀, 2 juvs, Agulhas Bank, 84 m. SAM–A14380, 1 juv., Agulhas Bank, 84 m. SAM–A14390, 1 ovig. ♀, Agulhas Bank, 84 m. SAM–A14393, 1 non-ovig. ♀, Agulhas Bank, 88 m. SAM–A2555, 1 non-ovig. ♀, off Umhlangakulu River, Natal, 100 m.

Distribution

Orange River mouth to Natal, 7–200 m.

Remarks

The specimens recorded from Australia (Thomson 1951) and New Zealand (Hurley 1961; Chapman & Lewis 1976) need to be re-examined, as few anthurideans have been found to have such wide distributions.

Barnard (1920) recorded a specimen of *P. punctata* being taken from a *Leuconia* sp. sponge.

Pseudanthura Richardson, 1911

Diagnosis

Eyes absent. Pereonite 7 considerably shorter than preceding segments. Pleonites and telson fused, anterior five pleonites indicated by shallow grooves, pleonite 6 indistinguishable from telson. Statocyst absent. Maxilliped four-segmented, endite present. Pereopod 1 subchelate, propodus expanded; pereopods 2–3 ambulatory; pereopods 4–7 with rectangular carpi, not underriding propodi. Pleopod 1 exopod operculiform, indurate; endopod reduced. Uropodal exopod reduced to short triangular structure; endopod and basis tending towards fusion. Brood pouch in female of four oostegites.

Type species

Pseudanthura lateralis Richardson, 1911.

KEY TO THE SOUTH AFRICAN SPECIES OF *PSEUDANTHURA*

1. Pleopod 1 endopod one-fourth length of exopod. Faint articulation between uropodal basis
and endopod . . . . *tenuis*
 – Pleopod 1 endopod one-third length of exopod. No articulation between uropodal basis and
endopod . . . . *lateralis*

Pseudanthura lateralis Richardson, 1911

Figs 61–62

Pseudanthura lateralis Richardson, 1911: 7. Barnard, 1920: 343, pl. 15 (figs 13–16); 1925a: 157,
figs 1s, 3e, 5d; 1940: 490, 497. Nierstrasz, 1941: 252. Menzies, 1962: 191, fig. 70. Kensley,
1978a: 55, fig. 23K–L; 1978c: 229, figs 5–6; 1982: 42, figs 40–42. Poore, 1980: 64.

Diagnosis

Pleopod 1 endopod one-third length of exopod, triangular. No articulation
between uropodal basis and endopod; exopod short, triangular.

Type material

Holotype, whereabouts unknown. Paratype, USNM 42171, 17,5 mm, off
Dakar, west Africa, 930–3 200 m.

Other material

SAM–A3832, 1 ♂, 15,5 mm, 1 non-ovig. ♀, 15,6 mm, 1 ovig. ♀
(damaged) ± 16,0 mm, off Cape Point, 1 800–2 000 m. SIO station WHOI 191,
1 ♂, 16,0 mm, 2 non-ovig. ♀, off South West Africa (Namibia), 23°04′S
12°31′E, 1553 m. USNM 185042, 2 ♂, 15,4–20,4 mm, 7 non-ovig. ♀, 10 juvs,
off South West Africa (Namibia), 23°01′S 12°19′E, 2136 m.

Distribution

West Africa to Cape Point, South Africa, 930–3 200 m.

Pseudanthura tenuis Kensley, 1978

Figs 63–64

Pseudanthura tenuis Kensley, 1978a: 224, figs 1–2; 1978b: 23, fig. 13. Poore, 1980: 64.

Diagnosis

Pleopod 1 endopod one-fourth length of exopod, triangular. Faint
articulation between uropodal basis and endopod; exopod short, triangular.
Telsonic margins straight. Male unknown.

Type material

Holotype, 1 non-ovig. ♀, SAM–A15664, 25,3 mm. Paratypes, 3 non-ovig.
♀, SAM–A15664, 6,0 17,1 23,4 mm, off Natal, 28°31′S 32°34′E, 680 m.
Paratype, 1 non-ovig. ♀, SAM–A15665, 9,9 mm, off Natal, 26°51′S 33°12′E,
720 m. Paratypes, 2 non-ovig. ♀, USNM 170272, 6,0 18,9 mm, off Natal,
28°31′S 32°34′E, 680 m.

Other material

SAM–A17614, 1 juv., off Natal, 26°51′S 33°12′E, 720 m. SAM–A17615, 2
non-ovig. ♀, 14,0 18,5 mm, 3 juvs, off Natal, 30°53′S 30°31′E, 850 m.
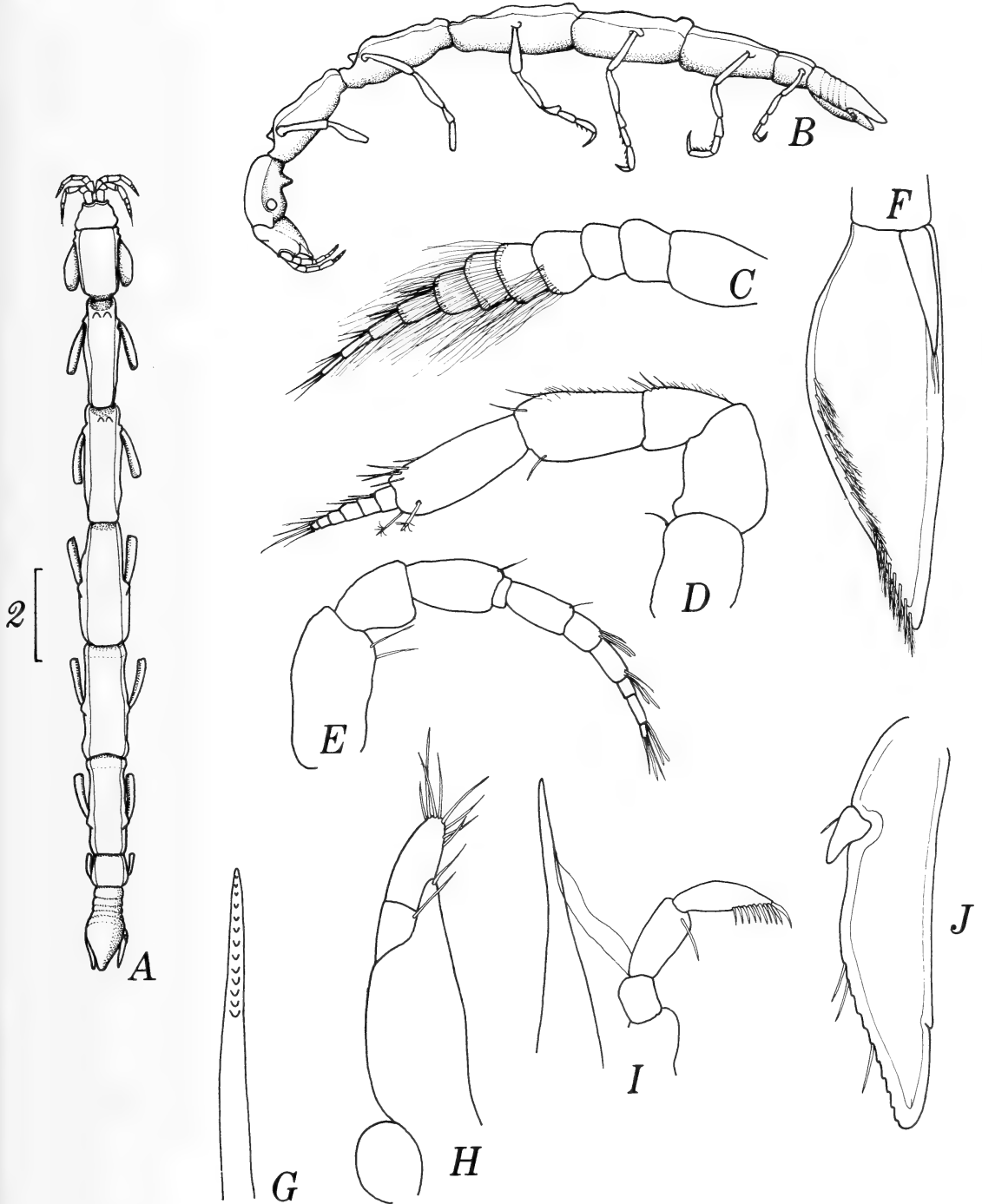
Fig. 61. *Pseudanthura lateralis*. A. ♀ dorsal view. B. ♀ lateral view. C. Antennule ♂.
D. Antenna. E. Antennule ♀. F. Pleopod 1. G. Maxilla. H. Maxilliped. I. Mandible.
J. Uropod. Scale in mm.
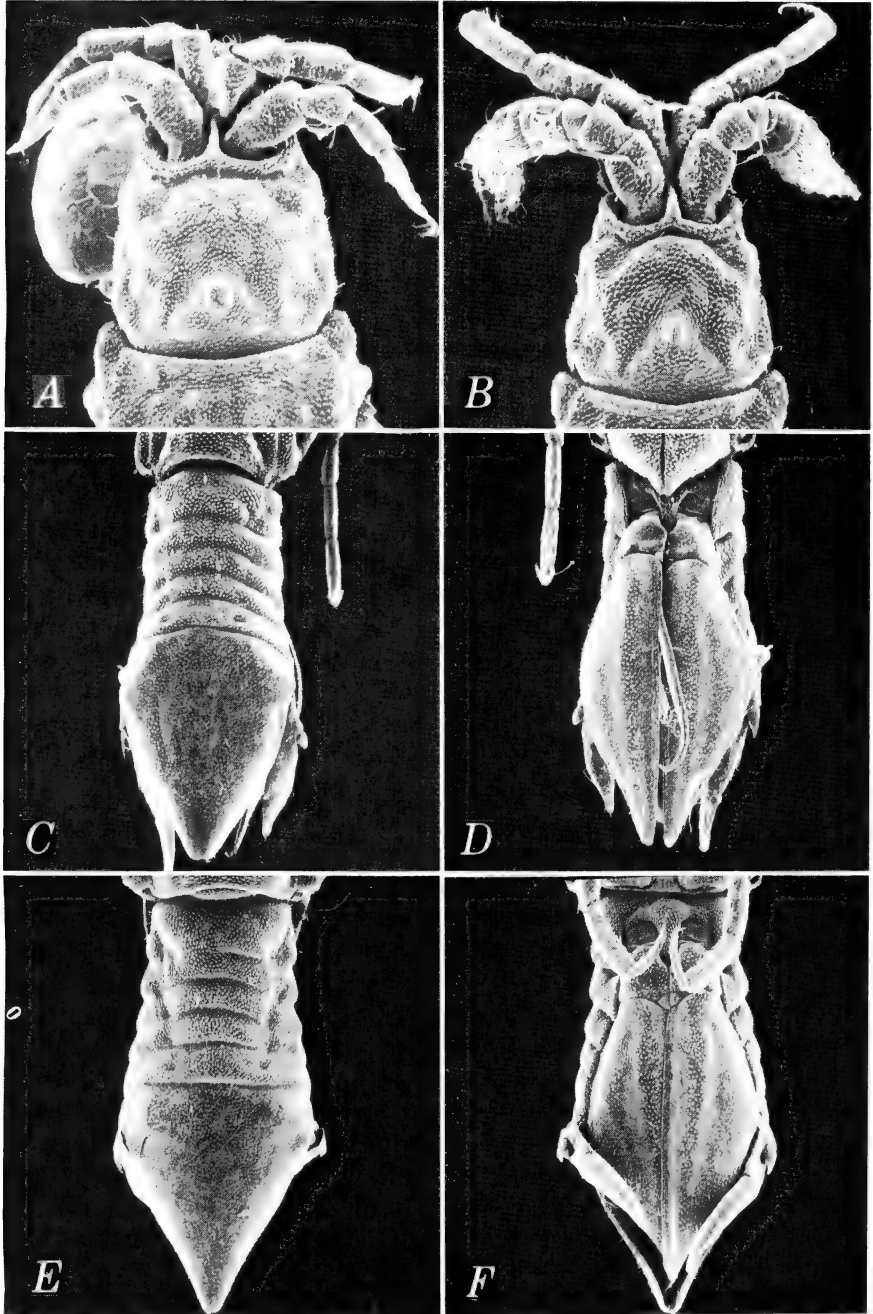
Fig. 62. *Pseudanthura lateralis*. A. ♀ cephalon dorsal view. B. ♂ cephalon dorsal view. C. ♀ pleon dorsal view. D. ♂ pleon ventral view; note copulatory stylet. E. ♀ pleon dorsal view. F. ♂ pleon ventral view.
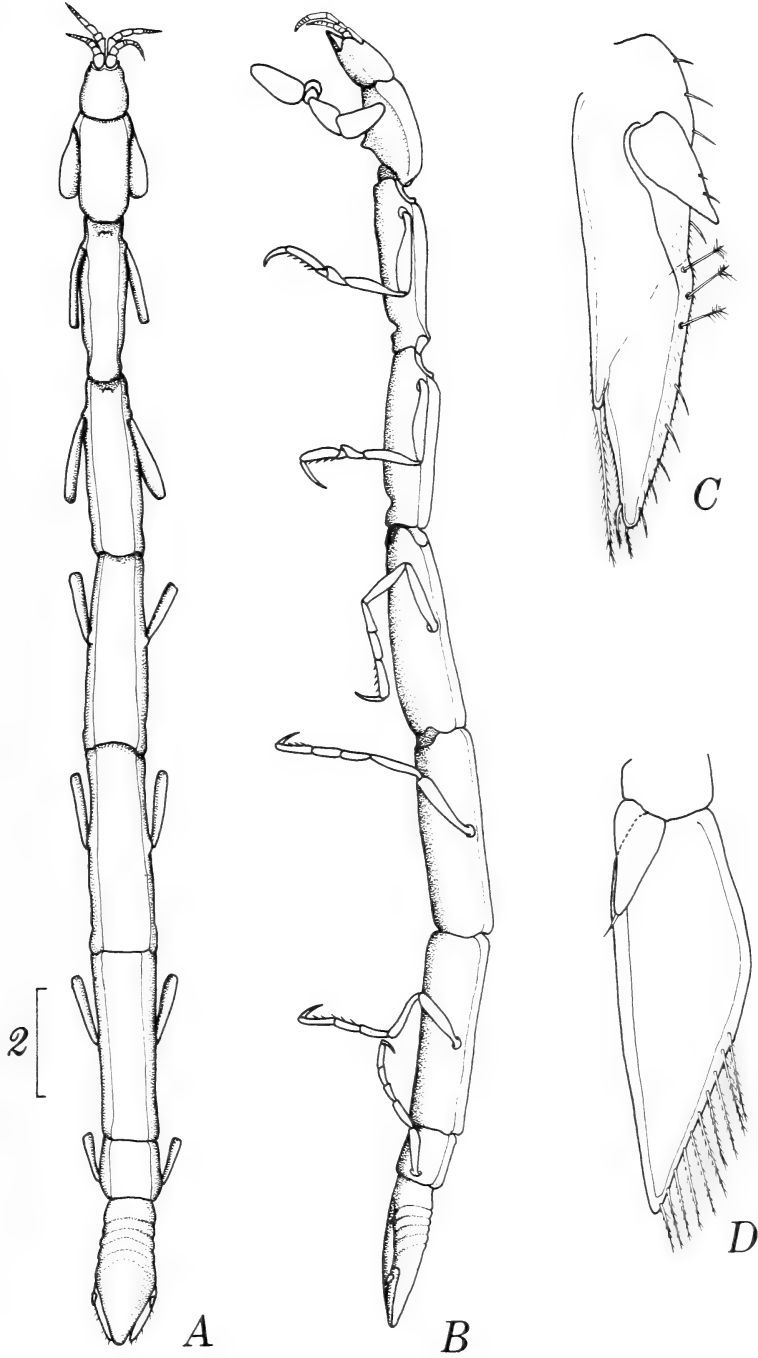
Fig. 63. *Pseudanthura tenuis*. A. ♀ dorsal view. B. ♀ lateral view. C. Uropod. D. Pleopod 1. Scale in mm.

SAM–A17616, 2 non-ovig. ♀, 14,2 mm (damaged) off Transkei, 32°14′S 29°10′E, 560–620 m.

Distribution

Northern Natal to Transkei, 560–850 m.

Fig. 64. *Pseudanthura tenuis.* A. ♀ cephalon dorsal view. B. ♀ cephalon ventral view. C. Pleon dorsal view. D. Pleon lateral view, uropod *in situ.*

ZOOGEOGRAPHICAL COMMENTS

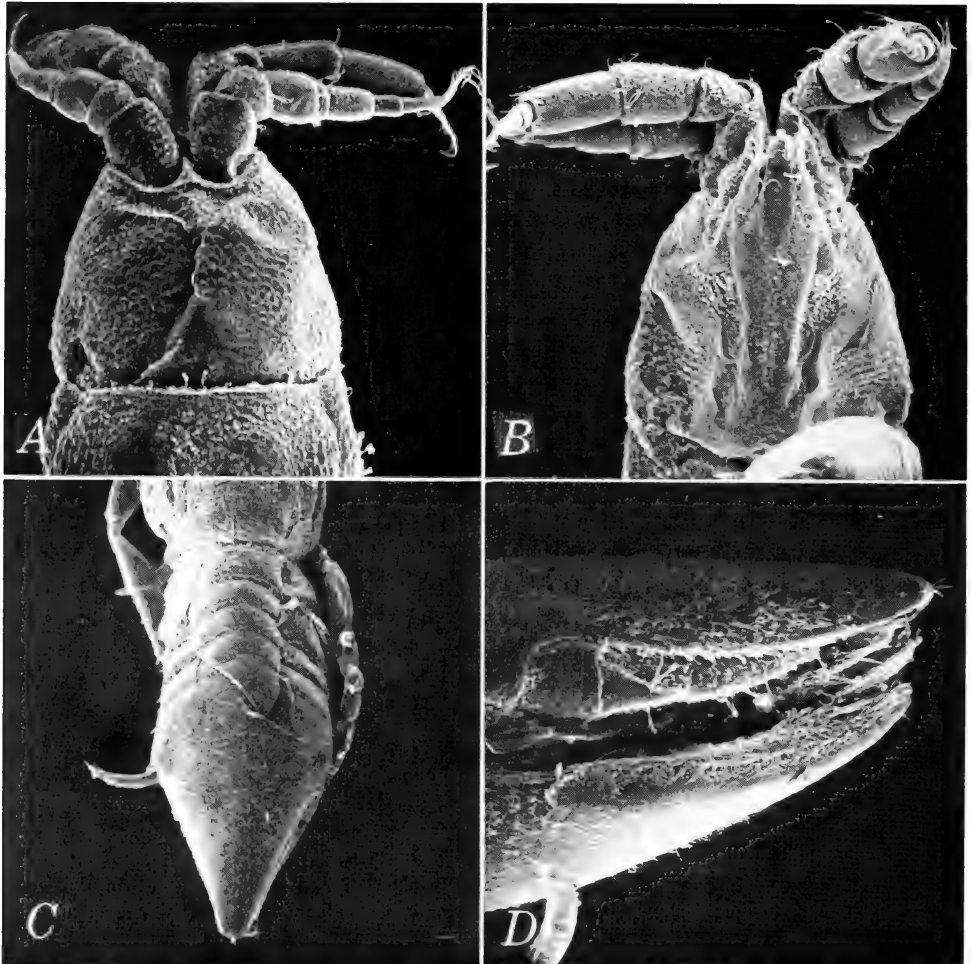In the following brief discussion, the genera and species of both the Anthuridae and Paranthuridae are dealt with as a unit. The southern African region is defined as being from the intertidal to the outer edge of the continental shelf, between the

mouth of the Kunene River on the west coast to Vilanculos in Mozambique on the east coast.

Of the 37 species here dealt with, 15 have been recorded from deeper than 200 m, while 5 of these range from considerably less than, to well beyond 200 m. Of these 15 deepwater species, only *Pseudanthura lateralis*, originally described from West Africa, has been recorded outside the region under discussion. When dealing with species occurring in deep water, little regarding geographic distribution may be deduced, such deep areas being seldom well sampled. Certainly, discussion of endemism in this context is futile. In fact, several species of deep-water Atlantic anthurideans have much wider geographical distribution than most shallow-water species (Kensley 1982).

The shallow-water forms display a distributional pattern also seen in other areas (e.g. southern Australia and the Caribbean), in which the anthurideans have received any attention, viz. very high specific, and very low generic endemism. Of the sixteen genera, only *Centranthura* (a recently created monotypic genus) is limited to the southern African region. Almost all the remaining genera have been recorded from tropical to cold-temperate regions of most of the world's oceans. Of the twenty-two shallow-water species, only *Accalathura indica* (occurring widely in the Indian Ocean) and *Panathura amstelodami* (known from the St. Paul and Amsterdam islands, northern Mozambique, and Madagascar) are not endemics.

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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.:

<div align="center">

Family **Nuculanidae**

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A
</div>

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: Nickles, 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 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.
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.

BRIAN KENSLEY

REVISION OF THE
SOUTHERN AFRICAN ANTHURIDEA
(CRUSTACEA, ISOPODA)

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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*
   (h) *References*
   (i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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 legend); the reduction or enlargement required should be indicated; 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 legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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) describes . . .'
    'Smith (1969: 36, fig. 16) describes . . .'
    '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.
          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 article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals.* 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, 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 le vitalité des mollusques. *J. Conch., Paris* 88: 100–140.
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MORPHOLOGICAL AND BIOLOGICAL NOTES ON SIX SOUTH AFRICAN BLOW-FLIES (DIPTERA, CALLIPHORIDAE) AND THEIR IMMATURE STAGES

By

A. J. PRINS

MORPHOLOGICAL AND BIOLOGICAL NOTES ON SIX SOUTH AFRICAN BLOW-FLIES (DIPTERA, CALLIPHORIDAE) AND THEIR IMMATURE STAGES

By

A. J. Prins

South African Museum, Cape Town

(With 5 figures)

ABSTRACT

Short biological notes and illustrations are given on *Lucilia sericata* (Meigen), *Chrysomya albiceps* (Wiedemann) and *C. chloropyga* (Wiedemann). Larvae and pupae of *Calliphora croceipalpis* Jaennicke, *Chrysomya regalis* Robineau-Desvoidy, and *C. megacephala* (Fabricius) are described and illustrated with notes on their biology and association with decaying organic matter. A key for the identification of the larvae is provided.

CONTENTS

INTRODUCTION

The blow-flies commonly known as bluebottles and greenbottles are mostly carrion breeders and, apart from the newly introduced oriental latrine fly, *Chrysomya megacephala* (Fabricius), the large bluebottle, *C. regalis* Robineau-Desvoidy, and the cadaver fly, *Calliphora croceipalpis* Jaennicke, are usually the first flies to appear at more or less fresh carcasses and cadavers in the south-western parts of the Cape Province. Both the last-named species have been involved in the past in myiasis in man, *C. regalis* in traumatic myiasis and *C. croceipalpis* in wound and enteric myiasis (Porter 1924; Zumpt 1956).

According to observations made during surveys along the coastal areas from Mossel Bay to Port Nolloth, *C. regalis* infests mainly large animals such as eland and gnu, whereas *C. croceipalpis* was seen to infest bird carcasses and some of the smaller mammals such as rats and dassies; occasionally, however, its larvae were recovered from larger animals such as gnu, but very few adults

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were reared in these cases due to competition by *C. albiceps* (Wiedemann), *C. chloropyga* (Wiedemann), and *C. megacephala*. Both these species infest human cadavers, *C. croceipalpis* apparently mostly during the winter and early spring, and *C. regalis* mostly during the warmer autumn months.

Chrysomya megacephala may also be regarded as a first-wave fly at decaying carcasses; however, it still seems to be restricted to the Cape Town–Yzerfontein and Durban areas as it has not been observed elsewhere. It is commonly found at the Cape Town docks, breeding in ships' holds carrying fish-meal, and this is probably also one of the ways in which it was introduced into this country; the larvae are often found during the late autumn crawling along the railway lines where they breed in dead rats and pigeons.

The green-tailed blow-fly, *Chrysomya chloropyga* (Wiedemann), and the green blow-fly, *Lucilia sericata* (Meigen), are widely distributed in South Africa and are often associated with the above-mentioned species as first- and second-wave flies respectively. Both these flies are facultative parasites and are responsible for sheep myiasis, the first one being subordinate to the second. The final instar larvae of a third species, the banded blow-fly, *Chrysomya albiceps* (Wiedemann), are mostly predaceous on the larvae of the others and they usually develop in carcasses in an advanced state of decomposition.

It is interesting to note that adult blow-flies obtain their carbohydrate requirements from nectar and honeydew, and therefore play an important part in the pollination of flowers such as *Stapelia* (Ryke 1969). Specimens of *Calliphora croceipalpis*, *Chrysomya chloropyga*, and *Sarcophaga* spp. coloured red on the head and thorax by pollen of the plant *Ferraria crispa* (Iridaceae) were often observed in the sandy areas along the west coast. These flies apparently also serve as pollinators of this plant.

In order to study the different instars, the eggs or larvae were placed on rotting flesh in glass jars covered with gauze cloth and containing a layer of about 75 mm of clean, damp sand. Drawings were made with a camera lucida from specimens preserved in 80 per cent alcohol.

Lucilia sericata (Meigen)

Fig. 1A

Adult and larval instars were described by Zumpt (1956, 1965). This brilliant green, shiny blow-fly is apparently attracted by a different set of odours than is the cadaver fly *(Calliphora croceipalpis)* and in most of the cases that were examined it appeared as a second-wave fly. In a few instances, however, particularly in gutted animals, it occurred as a first-wave invader together with one of the flesh flies *(Sarcophaga* sp.). It is one of the most common blow-flies on the islands along the west coast and often breeds in decaying kelp on the beach together with the kelp fly, *Coelopa africana* Malloch.
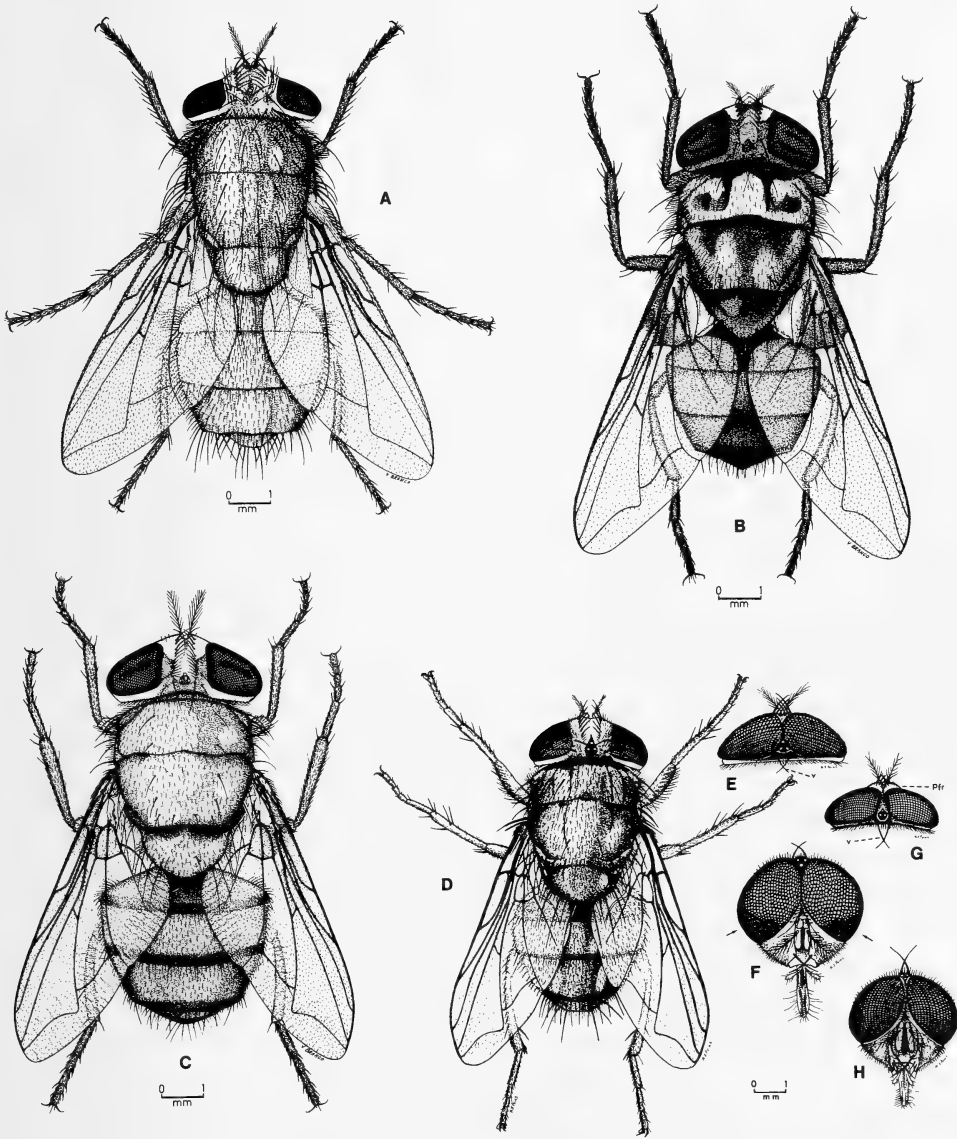
Fig. 1. A. *Lucilia sericata*, female. B. *Chrysomya chloropyga*, female. C. *C. albiceps*, female. D. *C. megacephala*, female. E. *C. megacephala*, head of male from above. F. *C. megacephala*, head of male from the front. G. *C. chloropyga*, head of male from above. H. *C. chloropyga*, head of male from the front.

Eggs collected on human corpses measure, 1,2–1,36 × 0,32–0,36 mm, and closely resemble those of *Chrysomya megacephala* (Fig. 3M), being creamy white, smooth and shiny, and almost without any visible reticulation. The ledges are narrow, as close together as in *C. megacephala*, and extend for nearly seven-eighths of the length of the egg. In most cases the eggs hatched 14 hours after oviposition.

In one test in the laboratory at a room temperature of 25–28 °C, the first instar occupied 14–15 hours and the second 14–17 hours, the larvae reaching a length of 3,4–4 mm 13–16 hours after hatching. The third instar lasted 143–150 hours and the pupal stage about 120 hours, the total larval lifespan in this case was nearly 170–180 hours. In another instance, however, the first and second instars occupied almost 48 hours at 26 °C and the third instar 140–160 hours. The total larval lifespan was 187–204 hours and the pupal stage 192 hours.

Chrysomya albiceps (Wiedemann)
Fig. 1C

Adult and larval instars were described by Zumpt (1956, 1965). The fly varies from 5 to 10 mm in length and is metallic green with a black transverse band across the posterior border of each abdominal segment. It is very widely distributed and as a sheep myiasis producer it is a secondary fly; as far as is known, it has not been recorded on human beings. It has been observed on a wide range of carcasses and cadavers and is usually the last blow-fly to be attracted before the skin-and-hide beetles appear.

Eggs collected on decaying seal carcasses along the west coast vary from 1,4 to 1,5 mm by 0,30 to 0,34 mm, and are very similar to those of *Lucilia sericata* but are duller and with a more pronounced reticulation. All eggs examined hatched 21 hours after oviposition (at temperatures of 25–28 °C).

In the laboratory the first instar lasted 15–20 hours at room temperatures of 25–28 °C, and reached a length of 3 mm about 12 hours after hatching. The second instar occupied 26–30 hours after which they were 6–7 mm long. The third instar varied from 153 hours to 158 hours, the total larval lifespan being 199 hours to 204 hours. The pupal period was 96 hours.

Chrysomya chloropyga (Wiedemann)
Fig. 1B, G–H

Adult and larval instars were described by Zumpt (1956, 1965). A metallic greenish-blue fly with the posterior part of the abdomen greenish yellow, and easily recognized by the ⌐ ⌐ marks on the presutural area of the mesonotum, which are absent in the very similar *C. megacephala*. The eyes of the males without distinct separation of upper and lower facets (Fig. 1H).

The eggs collected on a dead cow measure about 1,6 mm × 0,36 mm and are very similar to those of *C. megacephala*, being also shiny white with an indistinct reticulation.

In two laboratory tests the first instars lasted 20–22 hours at a room temperature of 22–25 °C, after which they measured about 3,5 mm in length. They increased in size reaching 7,9–8,7 mm about 48 hours after hatching; this second instar occupied at least 25–27 hours. The third instar larvae matured after 114–177 hours, the total larval lifespan being 162–230 hours, depending on food availability, temperature and humidity; the mature larvae reached a length of 16–17 mm. The pupal stage lasted from 188 to 204 hours.

In the case of third instar larvae (12–13 mm long), which were removed 85 hours after hatching from their original food source, cessation of feeding was observed and pupation occurred about 38 hours after removal. The total larval lifespan was 85–86 hours. The pupal stage lasted 144–168 hours, the flies emerging being of normal size, but the time necessary to straighten their wings and to assume their normal colour was much longer than in the other tests where the larvae were left undisturbed to mature on their original food supply.

Calliphora croceipalpis Jaennicke

Adult (Fig. 2A–C)

For a detailed description of the adult see Zumpt (1956, 1965). Head and thorax blackish blue to steel blue, almost dull; abdomen more greenish blue and almost shiny and with whitish pollinosity forming large patterns; dark iridescent transverse band present on posterior border of each abdominal segment. Tuft of strong setae present on each side of first visible abdominal segment, just before its posterior border. Four short distinct vittae present on anterior half of presutural area of mesonotum, indistinct over rest of mesonotum. Reddish colour of basal parts of third antennal segments and orange colour of palpi very characteristic. In the males, frontal stripe narrowed by eyes and there are only two vertical bristles, outer verticals (present in female) being absent. Normal length 9–12 mm.

Widely distributed throughout the Subsaharan region, except probably the western parts of Africa. It is common in South Africa and also occurs on some of the islands along the west coast such as Dassen Island.

Larva

First Instar

Similar to mature larva, but spinose girdles on segments 7 and 8 and on posterior side of 11 much less distinct. Cephalopharyngeal skeleton (Fig. 2J) different from that of second and third instars; basal piece widely and deeply emarginate behind; dorsal and ventral cornuae narrow and connected by narrow central piece; anterior dorsal bridge very narrow and widely separating the two dorsal cornuae; parastomal sclerite absent. Mouth-hooks rather weak, and connected to median piece as shown in Figure 2J. Anterior spiracles very indistinct and branches absent. Posterior spiracles (Fig. 2P) with partly developed peritremal ring, orifices ovate and touching ventrally. Just before moulting larvae reach a length of 3,3–4,0 mm.
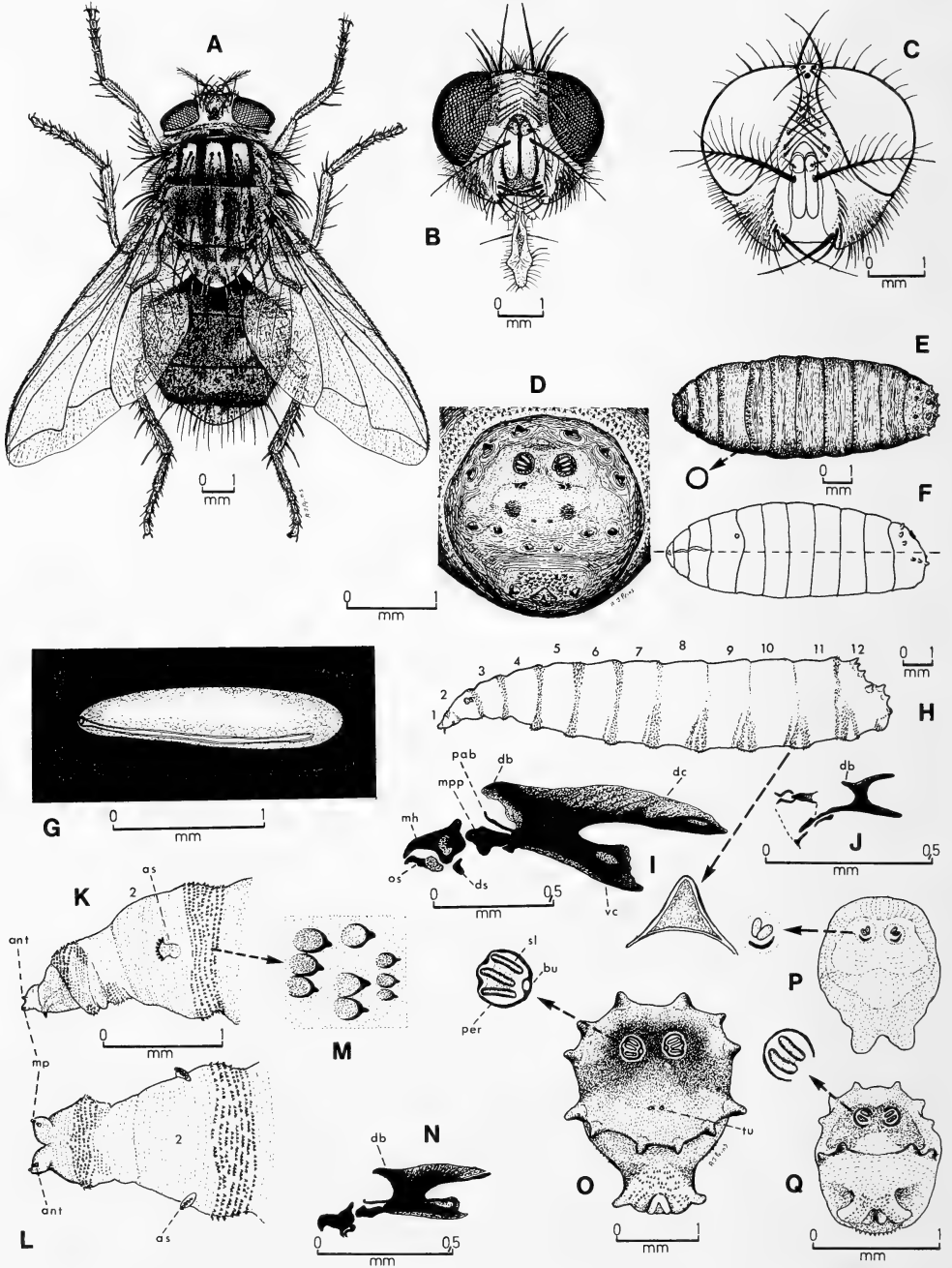
Fig. 2. *Calliphora croceipalpis*. A. Adult female. B. Head, frontal view of female. C. Head, frontal view of male. D. Caudal aspect of puparium. E. Puparium, dorsal view. F. Puparium, left lateral view. G. Egg. H. Third stage larva, left lateral view. I. Cephalopharyngeal skeleton of third instar larva. J. Cephalopharyngeal skeleton of first instar larva. K. First two segments of third instar larva, left lateral view. L. First two segments of third instar larva, dorsal view. M. Spines highly magnified. N. Cephalopharyngeal skeleton of second instar larva. O. Caudal aspect of third instar larva. P. Caudal aspect of first instar larva. Q. Caudal aspect of second instar larva.

Second Instar

Very similar to final instar, including number of branches on anterior spiracles and spinose girdles on body segments. However, cephalopharyngeal skeleton (Fig. 2N) much more heavily sclerotized than in first instar and rather similar to that of third instar larva, except for absence of oral sclerite. Mouth-hooks are more robust and dorsal projections longer and more acute than those of first instar. Parastomal bars or sclerites slender, almost horizontal in specimens seen, and directed upward at extreme apex. Posterior spiracles (Fig. 2Q) much larger and each one with two ovate orifices and an open peritremal ring. Larvae vary from 4,6 to 8 mm in length before moulting occurs.

Third Instar (Fig. 2H–I, K–M, O)

Length 16,5–18 mm when full-grown and creamy white to reddish white, depending on food. Segments 2–8 with complete anterior spinose girdles (sometimes also on segment 9); segments 9–11 with spinose girdles on ventral and lateral sides only; posterior girdles also on ventral side of segments 6–11, that on 11 complete; lateral spines not very distinct in some specimens; segment 12 with anterior ventral girdle and some spines surrounding anus. Spines typically with rounded apical dents, those on more posterior segments with rather broader dents, while larger spines on ventral parts of segments 8–12 are more or less triangular. Head deeply emarginate in front, forming oval lobe on each side, which bears small but rather conspicuous antennae and maxillary palpi. First spinose girdle with dorsal and ventral spines well developed, those placed laterally rather inconspicuous.

Cephalopharyngeal skeleton (Fig. 2I) with ventral cornuae of basal piece shorter than dorsal ones, each with light area with less sclerotization; dorsal ones with lightly sclerotized dorsal area and also with small oval, less sclerotized area near posterior border. When viewed from above the two cornuae fairly parallel or slightly diverging posteriorly. Anterior dorsal bridge complete, somewhat truncate in front and apparently without anterior and posterior projecting lobes. Parastomal bars slender and directed slightly upward particularly at apex. Median piece with complete arched ventral bridge and almost H-shaped when viewed from below. Mouth-hooks fairly wide apart, upper surface in lateral view fairly straight and forming a rounded projection posteriorly. Dental sclerites present; accessory oral sclerite wider than in *C. vicina* (see Zumpt 1965), its basal lobes broad and lightly sclerotized. When seen from below it forms a Y-shaped structure, its basal lobes connected to mouth-hooks, forming posterior arms.

Last abdominal segment (Fig. 2O) with twelve conspicuous fleshy tubercles as well as two smaller inconspicuous tubercles located in posterior cavity some distance above the two median ventral tubercles. Each yellowish posterior spiracle consists of three elongate, brownish oval slits surrounded by closed black peritremal ring with button on inner margin; distance between

spiracles is about same as diameter of a spiracle. Anterior spiracles with eight to nine branches.

Puparium (Fig. 2D–F)

Smooth, dull or slightly shiny, finely and transversely striate; posterior face finely rugulose. Light red when freshly formed, becoming brownish red after day or so. Somewhat constricted just behind anterior spiracular openings, which are small and circular. Respiratory horns absent. Anterior lateral ridges stretch over second and third segment. Twelve small, but conspicuous tubercles surround posterior spiracular plates (Fig. 2D). Posterior spiracles with three distinct elongate slits. Just below each spiracle there is a darker patch and below this patch an almost circular to oval dark spot, slightly smaller than spiracles and absent or inconspicuous in some specimens; between these two patches are two tiny tubercles. Also short black tubercle on each side of anal opening; latter about same size or slightly larger than spiracles. Posterior face convex; spiracles flush with surface and fairly high above longitudinal axis. Normally puparia measure about 9–10 mm.

Biology

This blow-fly was observed around Cape Town almost throughout the year, but was found to be more active during the winter months and early spring. It attacks carcasses of both birds and mammals and, as already stated, is usually the first fly to be attracted to human cadavers. In the laboratory eggs were deposited on the surface of fresh meat, but the flies refused to lay eggs on fairly decayed meat.

Eggs (Fig. 2G) vary from $1,7 \times 0,44$ mm to $1,8 \times 0,44$ mm and are white in colour, almost matt, with the surface finely reticulate; the lateral ledges or flanges are narrow and close together, extending for almost the whole length of the egg, the median area between the flanges is narrow. In most cases the eggs hatched within 21–23 hours after oviposition at a room temperature ranging from 18 to 23 °C during August to September. When the temperature was raised to 26 or 28 °C, some of the eggs hatched within 18 hours and in one case three eggs hatched after 15 hours.

The amount of food available and the temperature play an important part in the development of the larvae. However, the available information indicates that the duration of the first stage larva is 23–24 hours, after which the first moult occurs. Just before each moult the spiracles of the next stage become visible through the integument so that it is fairly easy to establish the time of the next moult.

The lifespan of the second instar larva is 37–40 hours at a room temperature of 18–23 °C. The third instar, which may occur about 60 hours after hatching, feeds voraciously for 5–6 days, after which it enters the soil to rest for another 2–5 days before pupation occurs. In most cases the total lifespan of third instar larva was about 8,5 days. The total lifespan of the larvae from egg

to pupa may vary from about 8 days during October to December to about 13 days during July to August, depending on the prevailing humidity and temperature; in tests during August with a room temperature of 18 °C the lifespan of the larvae was 10,75 days (258 hours).

Puparia are formed in the soil without the formation of cocoons and the flies appear after about 14 days from October to December and after 20 days from July to September. The whole cycle from egg to adult is about 25 days during September to November, to about 33 days during July to August.

As only two cases have been reported in the past in which this oviparous species had been identified as causing dermal and intestinal myiasis in man (Porter 1924), it would seem to be only an occasional facultative parasite, probably because it is easily disturbed and because of its habit of alighting and flying around under such circumstances rather than settling down.

Chrysomya regalis Robineau-Desvoidy

Adult (Fig. 3A–C)

This was previously described by Smit (1929) and the genitalia of the male by Zumpt (1956). Colour bright bluish, presutural area of mesonotum somewhat lighter in colour than rest of body, its extreme anterior margin black and with two paramedian longitudinal lines of lighter colour. First visible segment of abdomen blackish, other abdominal segments each with posterior black transverse band; median area of each segment with white pollinosity, showing up as paler areas in incident light. Eyes in life bright red. Parafrontalia and genae yellowish due to presence of fine pubescence and longer fine yellowish hairs, which are blackish round ocellar triangle. Frontal stripe, antennae and palpi somewhat reddish. Vibrissae consisting of only two long black setae.

Females with outer and inner verticals and with no separation between upper and lower facets of eyes. In males only inner verticals present and eyes contiguous in middle; large upper facets of eyes clearly separated from lower smaller facets, as in *C. megacephala*. Easily distinguished from latter species by white anterior thoracic spiracles (blackish brown in *C. megacephala*) and by dark costal margin of wing. Length 9,9–11,5 mm.

Widely distributed over Subsaharan region and also present in Arabia, certain parts of India and the Madagascar region. Although present in most areas surveyed, it is not common.

Larva

Third Instar (Figs 3F, H–K, 4C, 5A)

Length 14–18 mm, similarly coloured to that of *C. croceipalpis*, with complete anterior spinose girdles on segments 2–11, segment 12 with ventral band only and some spines around anus. Anterolateral swelling present on segments 5–10; these adjoin spinose girdles and bear some spines. Head
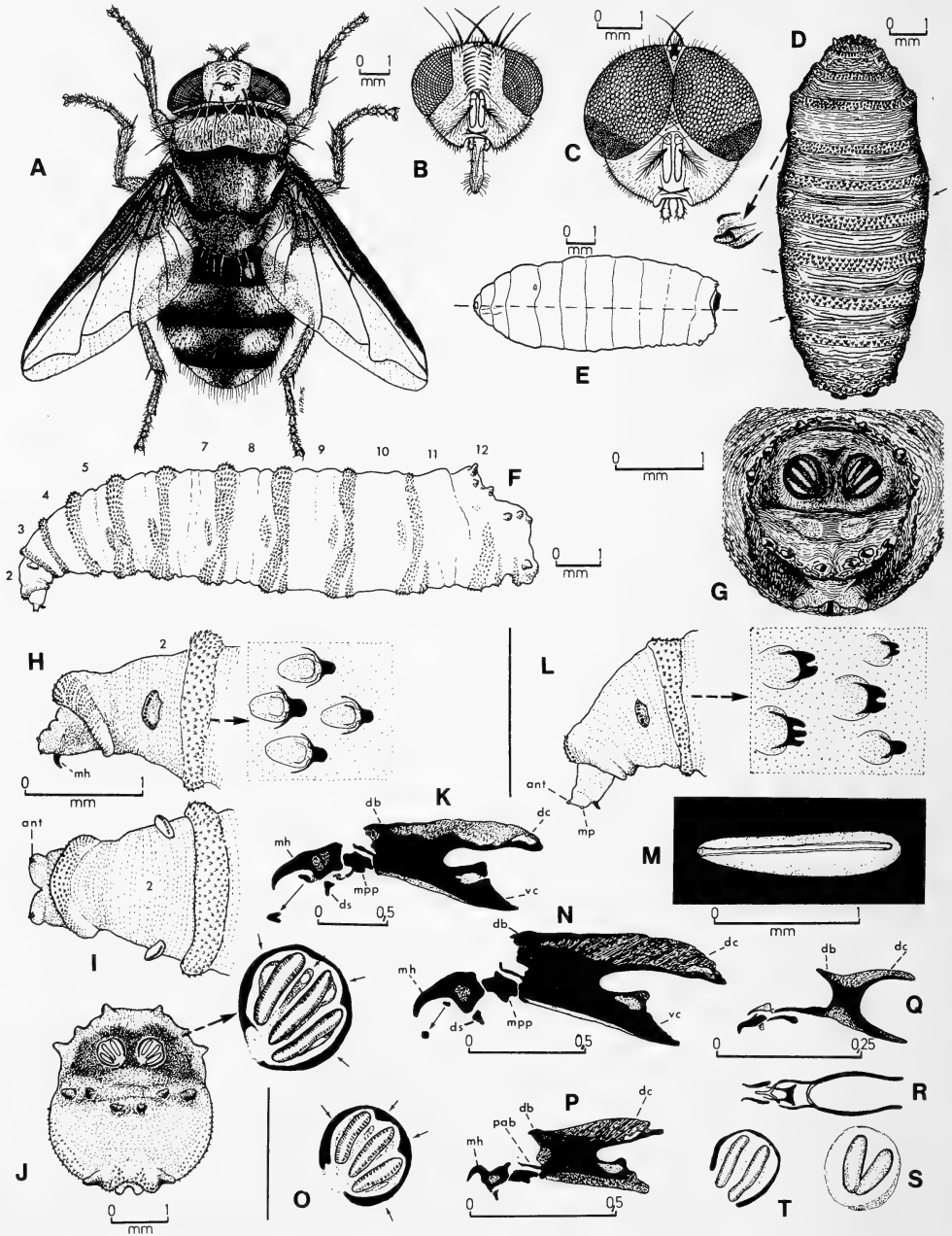
Fig. 3. A–K. *Chrysomya regalis*. A. Female. B. Head of female from front. C. Head of male from front. D. Puparium, dorsal view. E. Puparium, left lateral view. F. Larva, left lateral view. G. Posterior view of puparium. H. First two segments of third instar larva, left lateral view. I. First two segments of third instar larva, dorsal view. J. Posterior view of third instar larva. K. Cephalopharyngeal skeleton of third instar larva. L–T. *Chrysomya megacephala*. L. First two segments of third instar larva, left lateral view. M. Egg. N. Cephalopharyngeal skeleton of third instar larva. O. Right posterior spiracle of third instar larva. P. Cephalopharyngeal skeleton of second instar larva. Q. Cephalopharyngeal skeleton of first instar larva. R. Cephalopharyngeal skeleton of first instar larva, dorsal view. S. Right posterior spiracle of first instar larva. T. Right posterior spiracle of second instar larva.

Fig. 4. A. Mature larva of *Chrysomya chloropyga*. B. Mature larva of *C. megacephala*. C. Mature larva of *C. regalis*. D. Mouth-hook of *C. chloropyga*, left lateral view. E. Cephalopharyngeal skeleton of *Lucilia sericata*.

divided into two lobes, each bearing short antenna and maxillary palp. First spinose girdle almost surrounding second segment, spines on its lateral and ventral side small and inconspicuous. All spines on all segments much thicker than in *C. croceipalpis* and almost spoon-shaped. Antennae and maxillary palpi clearly visible.

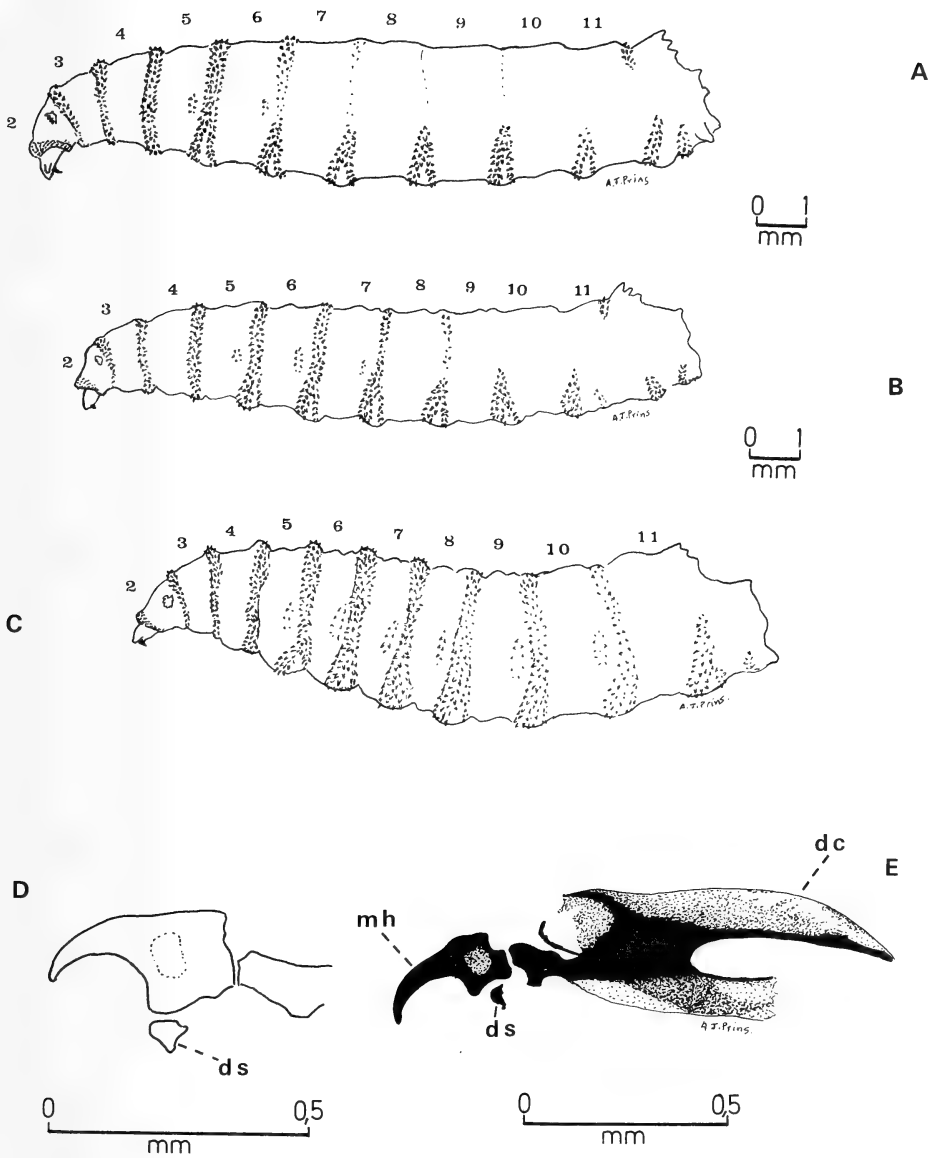Posterior spiracles large and yellowish, distance between them slightly less than half the diameter of spiracle, each with open thin black peritremal ring and with three elongate brownish oval slits; each slit with a projection with less sclerotized central area and also with sclerotized elongate sclerite between two inner slits, with circular opening dorsally. These projections, rather characteristic of this species, also present in *C. megacephala*, but spiracles are smaller and projections therefore less noticeable; apparently absent in *C. chloropyga* and *C. albiceps*. Anterior spiracles with eleven to fifteen short branches, the spiracles short and wider than in *C. croceipalpis*.

Cephalopharyngeal skeleton (Fig. 3K) with ventral cornuae almost as long as dorsal ones; anterior dorsal bridge complete, somewhat rounded when seen from above and without any projections; cornuae slightly diverging towards back and forming a narrow V. Parastomal bars slender, fairly straight, somewhat wider in front than behind and somewhat inclined anteriorly, also extended slightly upwards at extreme apex in some specimens (e.g. *C. croceipalpis*).

Median piece with complete, arched ventral bridge, rather similar to that of *C. croceipalpis*. Mouth-hooks without any posterior projections or with short projections, shorter than in *C. croceipalpis*; dorsal surface fairly straight in lateral view, in some specimens slightly raised in middle. Small V-shaped dental sclerite present laterally and only V-shaped basal part of accessory oral sclerite present. Last body segment (Fig. 3J) rather similar to that of *C. croceipalpis*, but two small tubercles present in latter could not be traced.

Puparium (Fig. 3D–E, G)

Smooth, dull, fairly coarsely and transversely striate, striations forming oval rugulose patterns laterally, posterior face also rugulose in certain areas. Colour light reddish when newly formed, but later becoming dark blackish brown. Very small respiratory horns present and puparium somewhat constricted just behind these horns. Anterior lateral ridges not very conspicuous, extending over second and third segments and located on or just below longitudinal axis. Anterior spiracles somewhat fan-shaped and yellow. Spinose bands present on almost all segments, those on segment 9 inconspicuous and narrower than those on others. Posterior face (Fig. 3G) rather truncate, spiracles large, somewhat protruding and enclosed in black peritremal ring, slits yellowish brown to almost orange. Twelve tubercles surrounding spiracular plates not very distinct. Oval shallow depression present below each spiracle, latter situated above longitudinal axis. Anal opening similar to that of *C. croceipalpis* and with short projections on each side. Puparium measures 8,9–10 mm long.

Biology

According to Ullyett (1950) *Chrysomya chloropyga*, *C. albiceps*, and *Lucilia* have a distinct advantage over *C. regalis* in interspecific competition for food, as the total growth period of the latter species is longer than any of the above-mentioned species. He also states that *C. regalis* is the least well adapted to withstand the adverse conditions engendered by larval overcrowding. Because of its larger size and considerably longer period of growth, combined with the essentially limited nature of available carrion in the field, it is not well favoured for the production of large populations of adults, as is possible in the case of *Lucilia*. This statement does not seem to be altogether true, as in three carcasses of large mammals examined during the present investigation (particularly that of an eland) very large populations of this fly were produced, with a fairly low rate of mortality, and in all the samples taken (some of which comprised up to 8 000 larvae) dwarfing was not observed; although a fairly large number of eggs was produced by *C. albiceps*, none survived. Apart from this, *C. regalis* is a first-wave blow-fly and, by the time the *C. albiceps* adults were attracted, large numbers of *C. regalis* larvae had already hatched, and due to their vigorousness they managed to compete for survival both intra- and interspecifically. *C. regalis* may, however, be subordinate to *C. chloropyga*, also a first-wave blow-fly and, as in the case of the latter, appears to be attracted to fairly fresh meat, but has not been found during these surveys in association with other blow-flies except *C. albiceps*.

The larval lifespan in all cases examined was about 11 days during late summer (compare with *C. chloropyga*, in which it was 6–9 days (summer) and *C. croceipalpis*, with a larval span of 8–9 days (summer)). The pupal stage lasts about 9 days during summer and about 14 days during spring (*C. chloropyga* 5–8 days and *C. croceipalpis* about 14 days (early summer) to 20 days (late winter)).

This blow-fly seems to be restricted to the autumn months as most of the infestations occurred during March and April, the fly being almost absent during the summer months, which is in agreement with the findings of Smit (1931). The puparia are usually formed under the carcass or in the soil without the formation of cocoons.

Chrysomya megacephala (Fabricius)

Adult (Fig. 1D–F)

Various stages previously described by Zumpt (1965) and Prins (1979). Colour metallic greenish; easily separated from our other South African species (*albiceps*, *chloropyga* and *regalis*) by the blackish-brown anterior thoracic spiracles (white in the other species). In females there is no separation between facets of the upper and lower halves of eyes but in males lower, smaller facets are clearly separated from larger ones in upper half of eyes (Fig. 1F). Otherwise very similar to *C. regalis*, but lacking dark costal area of the wings. Length 8,9–10 mm.

Widely distributed in Oriental, Madagascan, Australasian and Palaearctic regions; recently also found in Brazil, Senegal, and the west coast and Durban areas of South Africa.

Larva

First Instar (Fig. 3Q–S)

Very similar to last-stage larva except for size and shape of posterior spiracles (Fig. 3S), which have two elongate slits touching each other ventrally. Peritreme somewhat stronger developed on ventrolateral side and rather similar to that of *Calliphora croceipalpis*. Cephalopharyngeal skeleton (Fig. 3Q–R) also similar to that of first instar of *C. croceipalpis*; however, mouth-hooks broader in lateral view and with definite short dorsal projections. Central piece connecting the two cornuae broader than in *C. croceipalpis*; the sclerite when seen from above not so pointed in front as in that species.

Second Instar (Fig. 3P, T)

Very similar to mature larva, except for absence of anterior lateral swellings, which are present on segments 5–8 in mature larvae. Anterior spiracles with eight to nine small branches. Posterior spiracles (Fig. 3T) similar to those of *C. croceipalpis* but smaller, slits oval and elongate. Cephalopharyngeal skeleton (Fig. 3P) with basal piece similar to that of third instar larva; anterior dorsal bridge complete and with short posterior projections; mouth-hooks in lateral view narrower than those of *C. croceipalpis* and directed slightly upwards; posteriorly a small, almost acute projection also present. Ventral bridge of middle piece more arcuate and therefore more clearly visible laterally than in *C. croceipalpis*. Small dental sclerite present on each side.

Third Instar (Figs 3L, O, 4B, 5B, E)

Very similar to that of *C. regalis*, measuring 13,5–15 mm in length. Anterior spinose girdles present on all segments, those on segments 2–8 complete, that on segment 9 interrupted laterally. Segment 10 without dorsal spines; segment 11 with posterior girdle; segment 12 with ventral band and some spines around anus. Segments 5–8 with anterior lateral spinose swellings similar to those of *C. regalis*. First spinose girdle on second segment with dorsal spines strongly developed, lateral ones small and inconspicuous; ventral ones somewhat better developed. Head divided as in *C. regalis*. Antennae fairly conspicuous. Posterior face of abdomen hollowed out as in latter species, the fleshy tubercles surrounding spiracular plates and those on each side of anus also as in that species. Spines on body integument mostly bi- or tridentate, including some smaller ones, others spoon-shaped as in *C. regalis*.

Anterior spiracles with 8–10 short branches (Zumpt (1965) gives the number as 11–13); posterior yellowish brown spiracles (Fig. 3O) similar to those of *C. regalis* but smaller, projections not so conspicuous as in that species and distance between spiracles about half or slightly more than half diameter of spiracle.
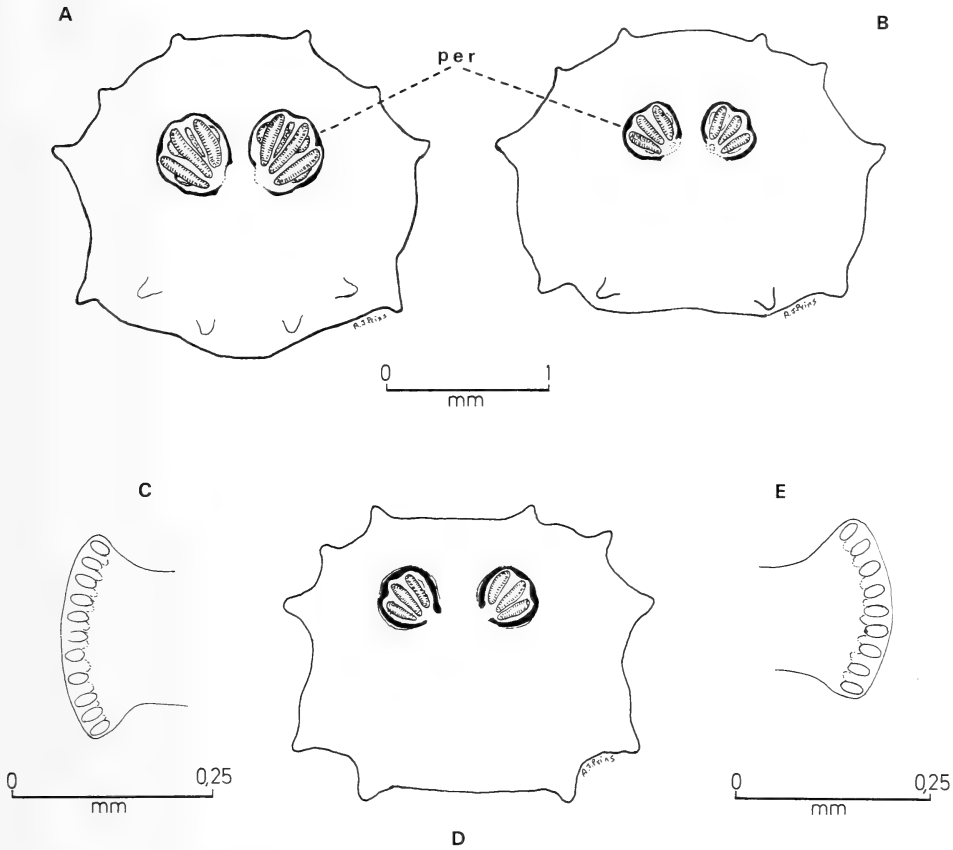
Fig. 5. A. Posterior view of mature larva of *Chrysomya regalis*. B. Posterior view of mature larva of *C. megacephala*. C. Left anterior spiracle of mature larva of *C. chloropyga*. D. Posterior view of mature larva of *C. chloropyga*. E. Right anterior spiracle of mature larva of *C. megacephala*.

Cephalopharyngeal skeleton (Fig. 3N) similar to that of *C. regalis*, but basal part of oral sclerite smaller and not V-shaped in most specimens seen; dorsal outline of mouth-hooks in lateral view more convex, the concave posterior area smaller. Anterior dorsal bridge complete and with short posterior projection on each side, almost rounded in front in some specimens.

Puparium

Colour reddish brown to mahogany brown, with anterior spiracle fan-shaped and yellow. Rather similar to that of *C. regalis*. but oval, rugulose areas absent on sides. Ridge around the spiracular plates formed by surrounding tubercles not so conspicuous as in latter species and spiracles much smaller, their diameter being about one-fifth diameter of posterior area surrounded by tubercles (in *C. regalis* diameter of spiracles is about one-fourth diameter of

posterior area). As in the latter, two oval depressions are present below spiracles, which may be confluent in some specimens. Respiratory horns very small as in *C. regalis* and in most specimens examined anterior part of puparium is somewhat broader and shorter when seen from above than in latter species.

Biology

Adult flies were observed mostly during the late summer and early autumn and were attracted to both mammal and bird carcasses as well as to human excrement. The eggs (Fig. 3M) are very similar to those of *C. croceipalpis* but are smaller, measuring about 1,38 × 0,33 mm, and fairly shiny, with the reticulation very superficial and visible only under certain light conditions. As in *C. croceipalpis*, the ledges are narrow, close together and extend for almost the whole length of the egg. The incubation period is short, only about 14 hours at 26 °C.

In breeding tests in the laboratory the duration of the first larval instar was about 23 hours, during which period they reached a length of 3–4 mm; the second instars lasted about 21 hours at 26 °C. When the second moult occurs they are usually about 6 mm long and by this time the spiracles of the last instar are clearly visible through the integument. After reaching the third instar (about 44 hours after hatching), they feed for 60–72 hours and then burrow into the soil to pupate. The total larval lifespan at 26 °C was 140–148 hours in the laboratory. According to Wijesundara (1957) the life cycle from egg to adult takes 204 hours in Sri Lanka; in Cape Town it varied from 276 to 306 hours, the pupal stage lasting 136–144 hours.

KEY FOR IDENTIFICATION OF LARVAE

The following key will assist in the identification of the full-grown larvae of the six common blow-flies described above.

1. Larvae with fleshy processes on most segments . . . . *Chrysomya albiceps*
— Larvae without fleshy processes on most segments.
2. Posterior spiracles with closed peritremal ring (Fig. 2O) 5
— Posterior spiracles with open peritremal ring.
3. Posterior spiracles large in relation to posterior face (Fig. 5A), the projections between slits, particularly the one between the inner two slits, distinct. Dorsal spines of girdles on at least anterior half of body broadly rounded, not cleft (Fig. 3H). Segments 2–11 with complete spinose girdles (Fig. 4C). Mouth-hooks with small accessory oral sclerite present . . . . *Chrysomya regalis*
— Posterior spiracles smaller in relation to posterior face (Fig. 5B, D), the projections between slits, particularly the one between the inner two slits, indistinct. Most of dorsal spines of girdles on at least anterior half of body bi- or tridentate (Fig. 3L). Segments 2–9 with complete spinose girdles 4
4. Segments 2–7 and sometimes 8 with obviously complete spinose girdles (Fig. 4A). Mouth-hooks devoid of accessory oral sclerite (Fig. 4D), and anterior spiracles with 10–12 branches (Fig. 5C) . . . . *Chrysomya chloropyga*
— Segments 2–8 and sometimes 9 with obviously complete spinose girdles (Fig. 4B). Mouth-hooks with small accessory oral sclerite (Fig. 3N), and anterior spiracles with 8–10 short branches (Fig. 5E) . . . . *Chrysomya megacephala*
5. Mouth-hooks with accessory oral sclerite (Fig. 2I) . . . . *Calliphora croceipalpis*
— Mouth-hooks without accessory oral sclerite (Fig. 4E) . . . . *Lucilia sericata*

ACKNOWLEDGEMENTS

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ABBREVIATIONS

ant	antenna	mpp	middle piece or
as	anterior spiracle		hypostomal sclerite
bu	button	os	accessory oral sclerite
db	anterior dorsal bridge	pab	parastomal bar
dc	dorsal cornua	per	peritremal ring
ds	dental sclerite	sl	slit
mh	mouth-hook	tu	tubercle
mp	maxillary palp	vc	ventral cornua

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.:

<div align="center">

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A
</div>

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: Nickles, 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 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.
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.

A. J. PRINS

MORPHOLOGICAL AND BIOLOGICAL NOTES ON SIX SOUTH AFRICAN BLOW-FLIES (DIPTERA, CALLIPHORIDAE) AND THEIR IMMATURE STAGES

ANNALS

OF THE SOUTH AFRICAN MUSEUM

INSTRUCTIONS TO AUTHORS

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*
    (h) *References*
    (i) *Abbreviations*, where these are numerous

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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 legend); the reduction or enlargement required should be indicated; 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 legend; if the latter, then the final reduction or enlargement should be taken into consideration.

    All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

    The number of the figure should be lightly marked in pencil on the back of each illustration.

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) describes . . .'
    'Smith (1969: 36, fig. 16) describes . . .'
    '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.
        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 article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, 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 le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
    FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
    KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
    KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
    THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In*: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

REVISION OF *ANCYLOCERAS BIPUNCTATUM*
SCHLÜTER, 1872
(CEPHALOPODA, AMMONOIDEA) AND
DISCUSSION OF THE VALIDITY, PHYLOGENY
AND LIMITS OF THE GENUS
NEANCYLOCERAS SPATH, 1926

By

HERBERT CHRISTIAN KLINGER

REVISION OF *ANCYLOCERAS BIPUNCTATUM* SCHLÜTER, 1872 (CEPHALOPODA, AMMONOIDEA) AND DISCUSSION OF THE VALIDITY, PHYLOGENY AND LIMITS OF THE GENUS *NEANCYLOCERAS* SPATH, 1926

By

HERBERT CHRISTIAN KLINGER

South African Museum, Cape Town

(With 10 figures)

ABSTRACT

The syntypes and topotype material of *Ancyloceras bipunctatum* Schlüter, 1872, the type species of the genus *Neancyloceras* Spath, 1926, are described and illustrated photographically. Schlüter's figures are misleading, being partially based on idealized reconstructions. Even if the effects of post-depositional deformation are taken into consideration, it appears that coiling in *Ancyloceras bipunctatum* as here interpreted may vary from open ancyloceratid to aspinoceratid or crioceratitid. *Neancyloceras* does not merit separation from *Exiteloceras* Hyatt, 1894, nor do *Axonoceras* Stephenson, 1941, or *Exicrioceras* Anderson, 1958. Affinities of *Exiteloceras* with *Neocrioceras* Spath, 1921, and *Pseudoxybeloceras* Wright & Matsumoto, 1954, are discussed and a possible common origin in the Turonian is postulated. Species previously referred to *Neancyloceras* are reviewed.

CONTENTS

INTRODUCTION

Two or, possibly, all three of Schlüter's figured syntypes of *Ancyloceras bipunctatum* (Schlüter 1872: 98, pl. 29 (figs 1–3)) (Fig. 1 (1–3 herein)) as well as a number of other possible syntypes and topotype material were located in the collections of the Geologisch-Paläontologisches Institut und Museum der Georg-August Universität, Göttingen. Examination of Schlüter's original and topotype material allows better definition of the species and discussion of the validity, origin, phylogeny, and limits of the genus *Neancyloceras* Spath, 1926, of which it is the type species.
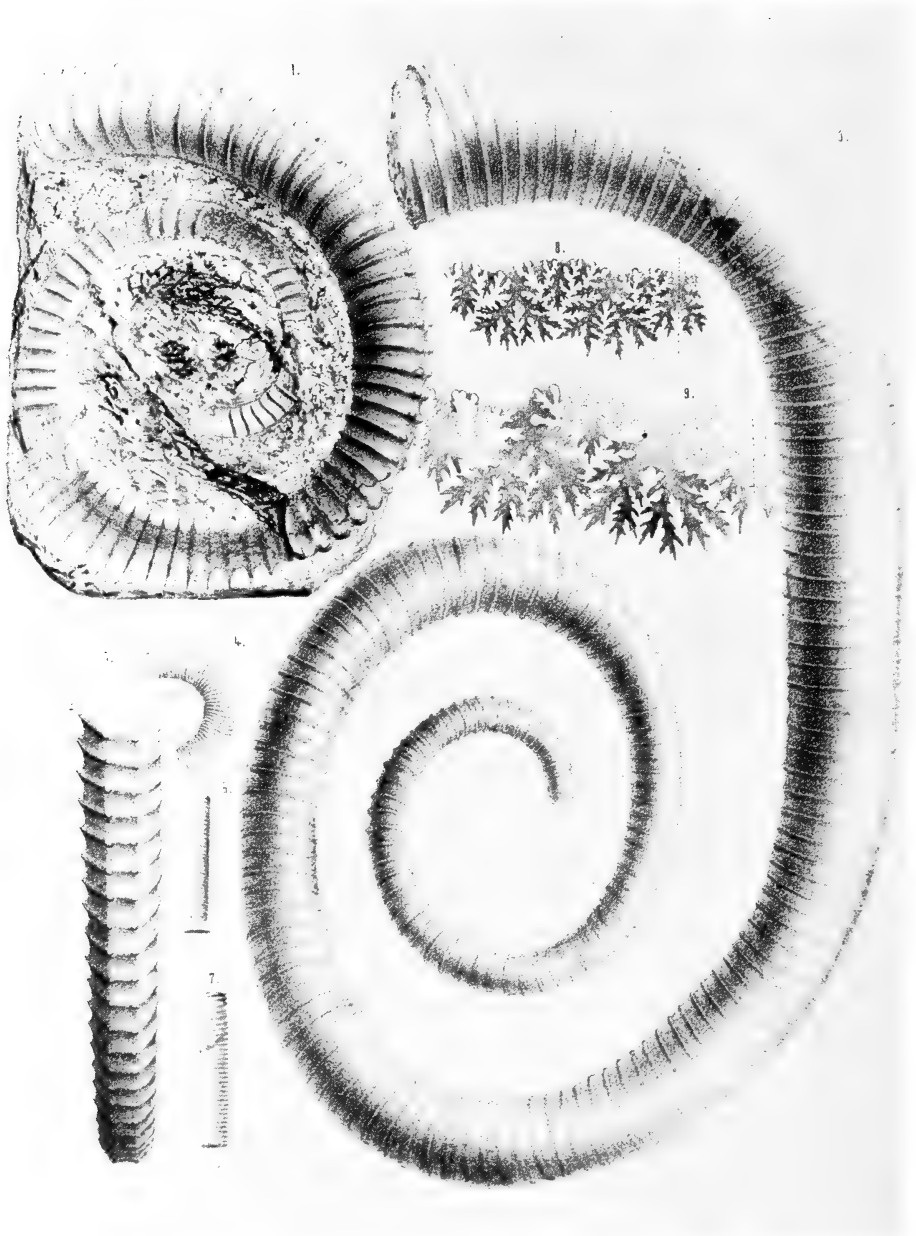
219

Fig. 1. Copy of Schlüter's (1872) original plate 29. × 0,67.

SYSTEMATIC DESCRIPTION

Ancyloceras bipunctatum Schlüter, 1872

Figs 1 (1–3), 2–8 A–E, 9

Ancyloceras bipunctatum Schlüter, 1872: 98, pl. 29 (figs 1–3) (erroneously spelt *bipunctum* in explanation to plate figures).
Ancyloceras bipunctatum Schlüter: Wegner, 1905: 210. Nalivaiko, 1936: 35, pl. 16 (fig. 39). Michailov, 1951: 88, pl. 16 (figs 66–71). Pasternak, 1954: 157, text-fig. p. 158.
Neancyloceras bipunctatum (Schlüter): Naidin, 1959: 182, pl. 3 (fig. 6). Hancock, 1961: 30. Giers, 1964: 283. Blank *et al*. 1974: 169.

Type

The lectotype, herein designated, is the specimen figured by Schlüter (1872, pl. 29 (fig. 1)) from the Campanian of Ahlten, near Hanover, West Germany, housed in the collections of the Geologisch-Paläontologisches Institut und Museum der Georg-August Universität, Göttingen, GPIG Orig. 65–10.

Material

The paralectotype figured by Schlüter (1872, pl. 29 (fig. 3)) (catalogue number GPIG Orig. pending), a specimen tentatively identifiable with the third figured specimen in Schlüter (1872, pl. 29 (fig. 2)) (GPIG Orig. 65–11), and forty-six other specimens, all from the same locality and in the same collections, were available for study. Schlüter's descriptions were based on five specimens in the collections at Göttingen, and on a sketch of one of the specimens in the collection of Mr Witte of Hanover. The latter collection was subsequently presented to the above-mentioned Institute in Göttingen (see Schlüter 1876: 181 footnote) and incorporated in their collections. Apart from the lectotype and paralectotype(s), it is impossible to determine from the labelling which specimens were Schlüter's original syntypes, and which belonged to the Witte collection.

Descriptions

Lectotype GPIG Orig. 65–10 (Fig. 2A)

Schlüter's illustration of the lectotype is reversed and much restored. Only half of the outer whorl and less than a quarter of the inner whorls are actually preserved as internal moulds. The rest of the specimen is indicated only by brown (?limonitic) stained impressions. The double row of ventral tubercles in the actual specimen is by no means as pronounced as in the lithograph, nor are both rows as clearly exposed as the figures suggest. The strongly flared ribbing (as indicated on the lower half of Schlüter's figure) is also idealized. The last part of the whorl seems to detach itself from the open spiral. The last septum is in the last half of this whorl.

Fig. 2. *Exiteloceras bipunctatum* (Schlüter, 1872).
A. The lectotype, figured in reverse by Schlüter (1872, pl. 29 (fig. 1)) GPIG Orig. 65–10.
B. A large, slightly curved body chamber fragment with differentiated ribbing. GPIG–8.
Both specimens from the Upper Campanian of Ahlten, West Germany. × 1.

Paralectotype GPIG Orig. pending (Figs 3, 4A)

According to Schlüter (1872, pl. 29 (fig. 3)) the figure of the paralectotype was based on a sketch of a complete specimen in the possession of Mr Witte of Hannover. Part of the shaft and open hook in the figure can be identified with a crushed specimen (GPIG Orig. pending). The loosely coiled inner whorls of the sketch on which the lithograph was based are very similar to those of GPIG–2 (Fig. 5A), but this specimen does not belong to the same individual as GPIG Orig. pending, nor do any of the other available specimens. It must be assumed either that the initial inner whorls of paralectotype GPIG Orig. pending are lost, or that Witte's sketch from which Schlüter's lithograph was constructed was, in fact, a synthetograph based on GPIG Orig. pending and GPIG–2 or another specimen similar to it such as GPIG–3 (Fig. 6). Whatever the case may be, Schlüter's illustration of the shaft and hook is misleading. Ribbing is not uniform throughout as the illustration suggests, but stronger ribs separated by a variable number of normal ribs are present. These major ribs are bituberculate, like the normal ribs. At the adapical end of the shaft the major ribs are separated by about eight normal ribs, but towards the hook the major ribs become more prominent, their tuberculation less distinct, and intermediaries decrease to as little as two. Traces of the last septa are visible near the lower end of the straight shaft.

?Paralectotype GPIG Orig. 65–11

A slightly crushed specimen, GPIG Orig. 65–11 (Fig. 5B–D) is of the same size as the third specimen figured by Schlüter (1872 pl. 29 (fig. 2)), but due to lack of documentation the author is unable to confirm whether or not this is indeed the figured specimen in its unrestored form. None of the available specimens shows the perfect bilateral symmetry as seen in Schlüter's figures, suggesting that asymmetrical whorl section and ornament were the norm rather than the exception, as will be discussed further.

Topotype material

Two specimens, GPIG–2 (Fig. 5A) and GPIG–3 (Fig. 6) show the early, irregular crioceratitid coiling as seen in the lectotype. GPIG–3 is the most complete and has a somewhat irregular mode of coiling. Three-quarters of the outer whorl is occupied by body chamber. The last part of the body chamber appears to uncoil slightly and then recoil again. Only the last rib is thickened. GPIG–2 (Fig. 5A) has a virtually circular inner whorl as found in the lectotype, but a body chamber that uncoils and then recoils similar to that of GPIG–3. Here only the last half whorl is body chamber, and thickened ribs do not occur.

All the specimens are deformed to some extent; however, it does appear that the whorl section and ornament are asymmetrical in the majority, with tuberculation displaced towards one side. This suggests that the inner phragmocone whorls were coiled in a low, perhaps irregular or elliptical helix rather than in one plane. At the smallest whorl diameter preserved (6 mm), the

Fig. 3. *Exiteloceras bipunctatum* (Schlüter, 1872).
The paralectotype, GPIG Orig. pending upon which
Schlüter's (1872, pl. 29 (fig. 3)) reconstruction was partially
and incorrectly based. From the Upper Campanian of
Ahlten, West Germany. × 0,77.

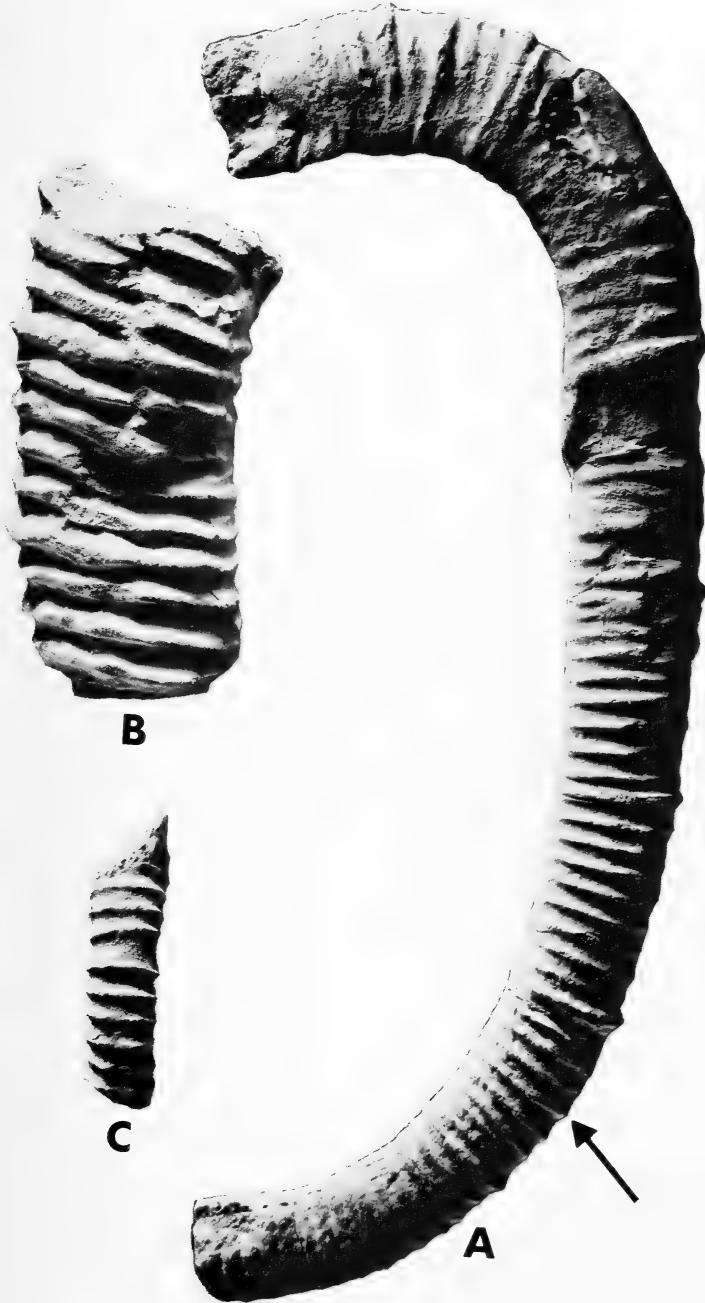Fig. 4. *Exiteloceras bipunctatum* (Schlüter, 1872).
A. The paralectotype, GPIG Orig. pending upon which Schlüter's (1872, pl. 29 (fig. 3)) reconstruction was partially and incorrectly based. B. Topotype specimen GPIG–5; a straight body chamber fragment. C. Topotype specimen GPIG–12 showing shallow, wide constriction.
All specimens from the Upper Campanian of Ahlten, West Germany. A × 0,77; B–C × 1.
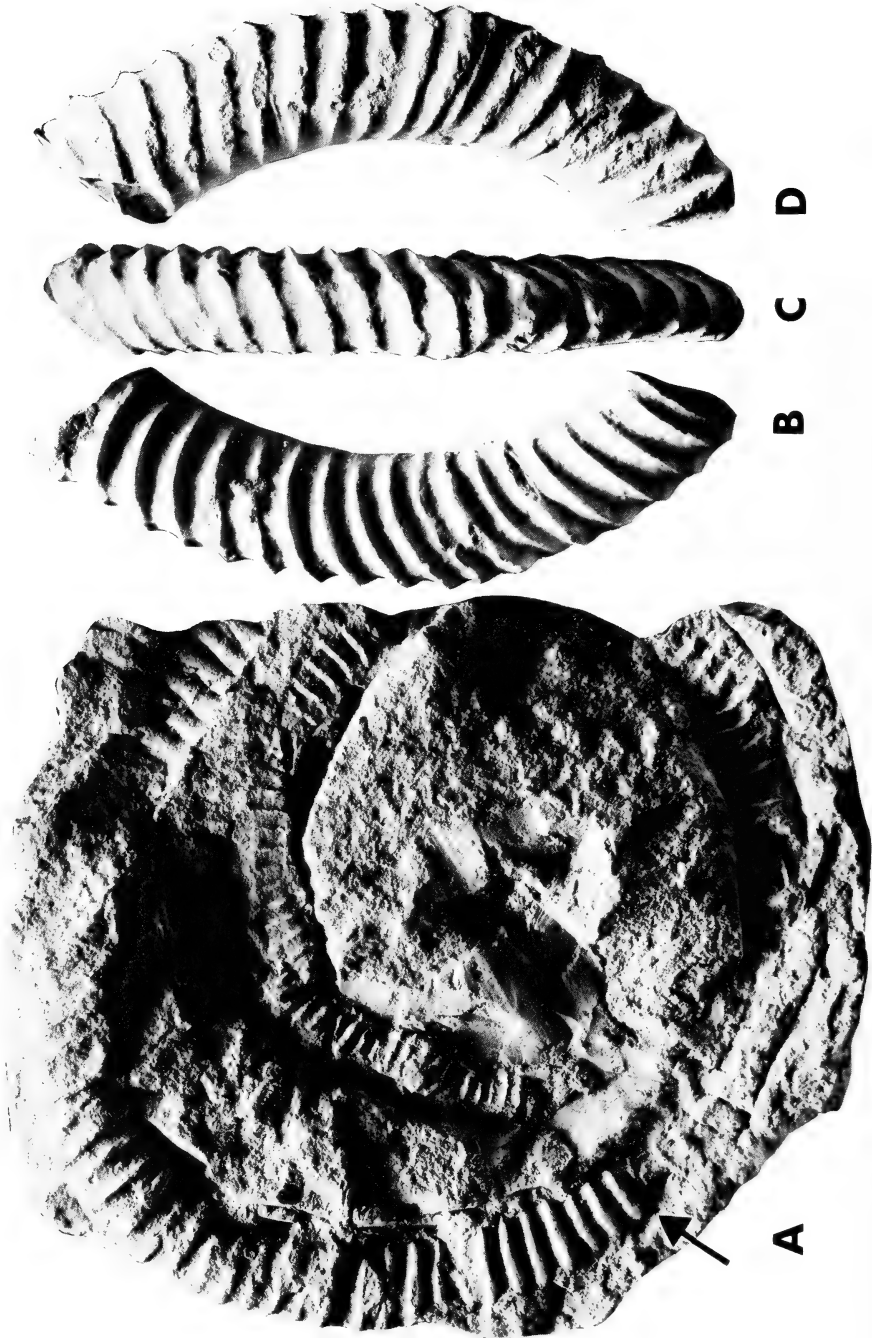
Fig. 5. *Exiteloceras bipunctatum* (Schlüter, 1872).

A. Topotype specimen GPIG–2. Arrow points to last visible septum. B–D. Possible paralectotype GPIG Orig. 65–11 (see Schlüter 1872, pl. 29 (fig. 2)).

Both specimens from the Upper Campanian of Ahlten, West Germany. × 1.

Fig. 6. *Exiteloceras bipunctatum* (Schlüter, 1872). Topotype specimen GPIG–3. Arrow points to last visible septum. From Ahlten, West Germany. × 1.
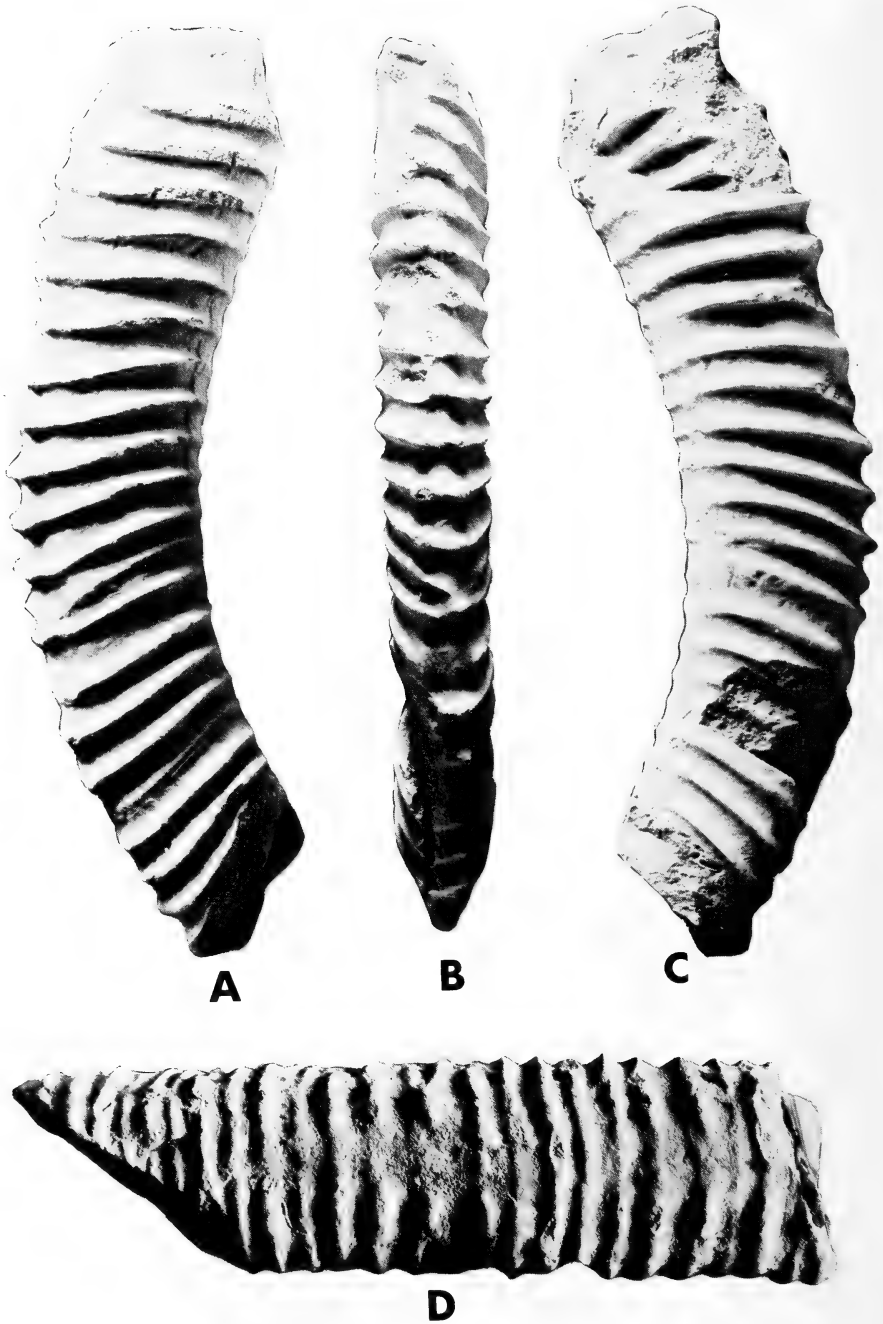
Fig. 7. *Exiteloceras bipunctatum* (Schlüter, 1872).
A–C. Topotype specimen GPIG–9. D. Straight body chamber fragment GPIG–10.
Both specimens from the Upper Campanian of Ahlten, West Germany. × 1.

whorls are still coiled, and do not show straight or otherwise aberrant early coiling. GPIG–16 (Fig. 8D–E) shows labeceratid coiling but this is probably due to post-mortem deformation.

On the phragmocone, rib density is generally between four and five per maximum whorl diameter, but may be as high as eight. Some specimens, e.g. GPIG–12 (Fig. 4C) and GPIG–13 (Fig. 9B), show slight irregularities in ribbing which may be interpreted as shallow constrictions. The sharp-crested, slightly rursiradiate, bituberculate and even ribbing is characteristic of the major part of the shell. Stronger ribs appear only on the last part of the phragmocone and on the body chamber in some specimens.

Straight and curved body chamber fragments can be identified. GPIG–5 (Fig. 4B), GPIG–10 (Fig. 7D), GPIG–11 (Fig. 9D), and GPIG–17 (Fig. 9A) are straight or slightly curved body chamber fragments identifiable with the open ancyloceratid paralectotype, GPIG pending (Figs 3, 4A). GPIG–11 (Fig. 9D) is of interest in not having major ribs. GPIG–8 (Fig. 2B) and GPIG–9 (Fig. 7A–C) are large, curved body chamber fragments; the former has distinct differentiated ribbing. GPIG–17 (Fig. 9A) is a body chamber fragment much larger than any of the other specimens.

Indistinct traces of trifid lobes are present on the lower ends of the paralectotype GPIG pending and GPIG–3.

DEFINITION OF THE SPECIES

As can be seen from the description of the original and topotype material, there is considerable variation in the coiling, ornament, and size of *Ancyloceras bipunctatum*. Even if the effects of the post-mortem deformation are taken into consideration, coiling of the body chamber ranges from distinctly open ancylo-ceratid to possibly aspinoceratid or crioceratitid. Unmistakable ancyloceratid forms include the paralectotype GPIG pending (Figs 3, 4A), and parts of straight shafts such as GPIG–5 (Fig. 4B), GPIG–7 (Fig. 9C), GPIG–10 (Fig. 7D), and GPIG–11 (Fig. 9D). The last septum in the paralectotype GPIG pending is located in the lower end of the straight shaft. In the lectotype GPIG–Orig. 65–10 (Fig. 2A) half of the outer whorl is body chamber, whereas in GPIG–3 (Fig. 6) three-quarters of the outer whorl is body chamber. This, together with the presence of such large body chamber fragments as GPIG–8 (Fig. 2B) and GPIG–9 (Fig. 7A–C), suggests crioceratitid or aspinoceratid coiling for some specimens rather than distinct open ancyloceratid coiling as suggested by Schlüter's reconstructed figure.

The relationship between these different modes of coiling is obscure. It is partially due to post-mortem deformation, but may also be a manifestation of dimorphism or, less probably, extreme intraspecific variation due to the fact that the material is from more than one stratigraphic horizon. Schlüter (1876: 248 and footnote) had already expressed doubts on whether or not the material from Ahlten all belonged to one zone.
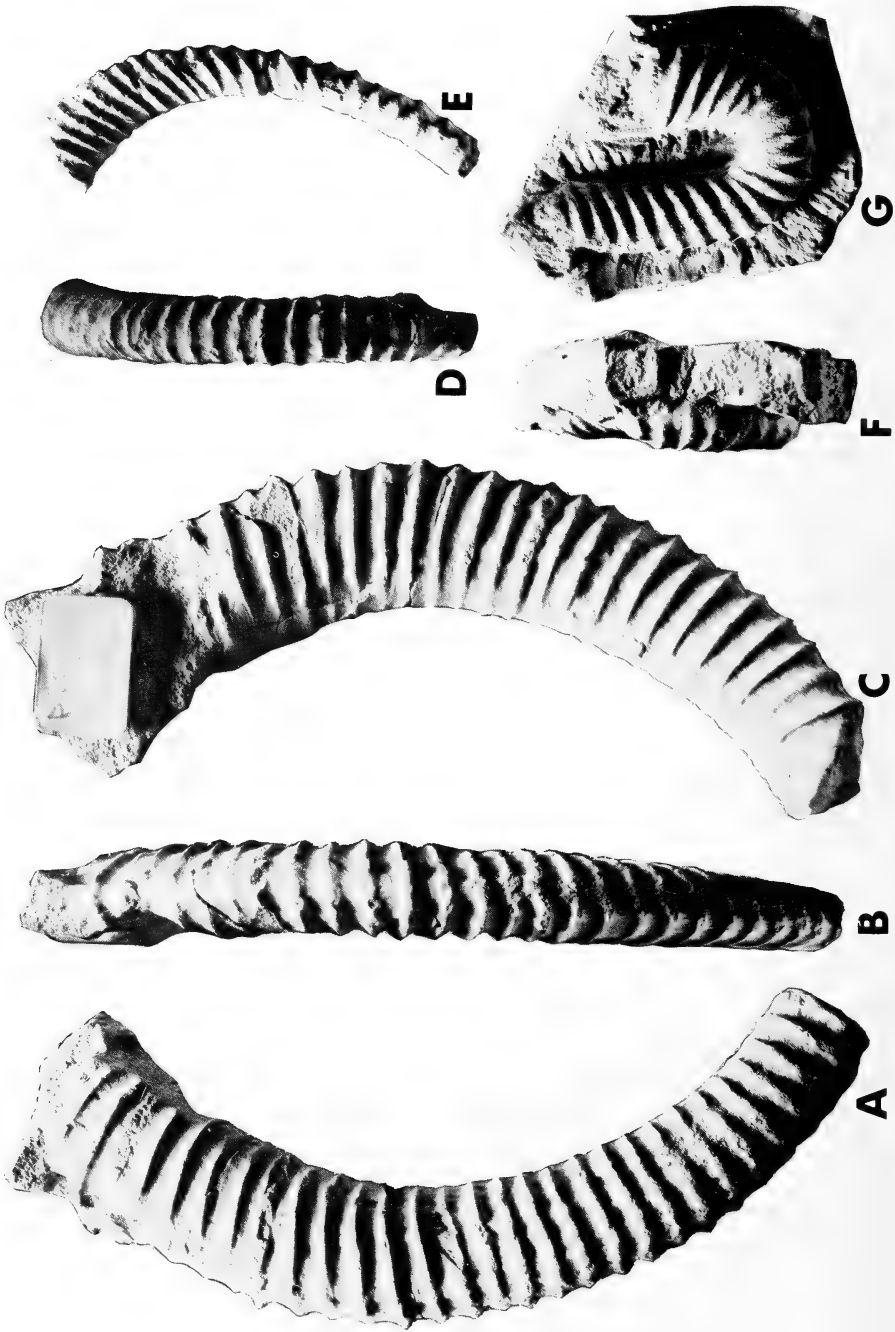
Fig. 8. A–C. *Exiteloceras bipunctatum* (Schlüter, 1872). Typical phragmocone fragment. GPIG-14. D–E. *Exiteloceras bipunctatum* (Schlüter, 1872). GPIG-16, specimen with labeceratid coiling due to deformation. F–G. *Pseudoxybeloceras (Parasolenoceras) interruptus* (Schlüter, 1872). The holotype by monotypy GPIG Orig. 65–13. All specimens from the Upper Campanian of Ahlten, West Germany. × 1.

Fig. 9. *Exiteloceras bipunctatum* (Schlüter, 1872).
A. Gigantic body chamber fragment GPIG–17. B. Body chamber fragment with differentiated ribbing and shallow constriction. GPIG–13. C. Slightly curved body chamber fragment GPIG–7. D. Straight body chamber fragment GPIG–11.
All from the Upper Campanian of Ahlten, West Germany. × 1.

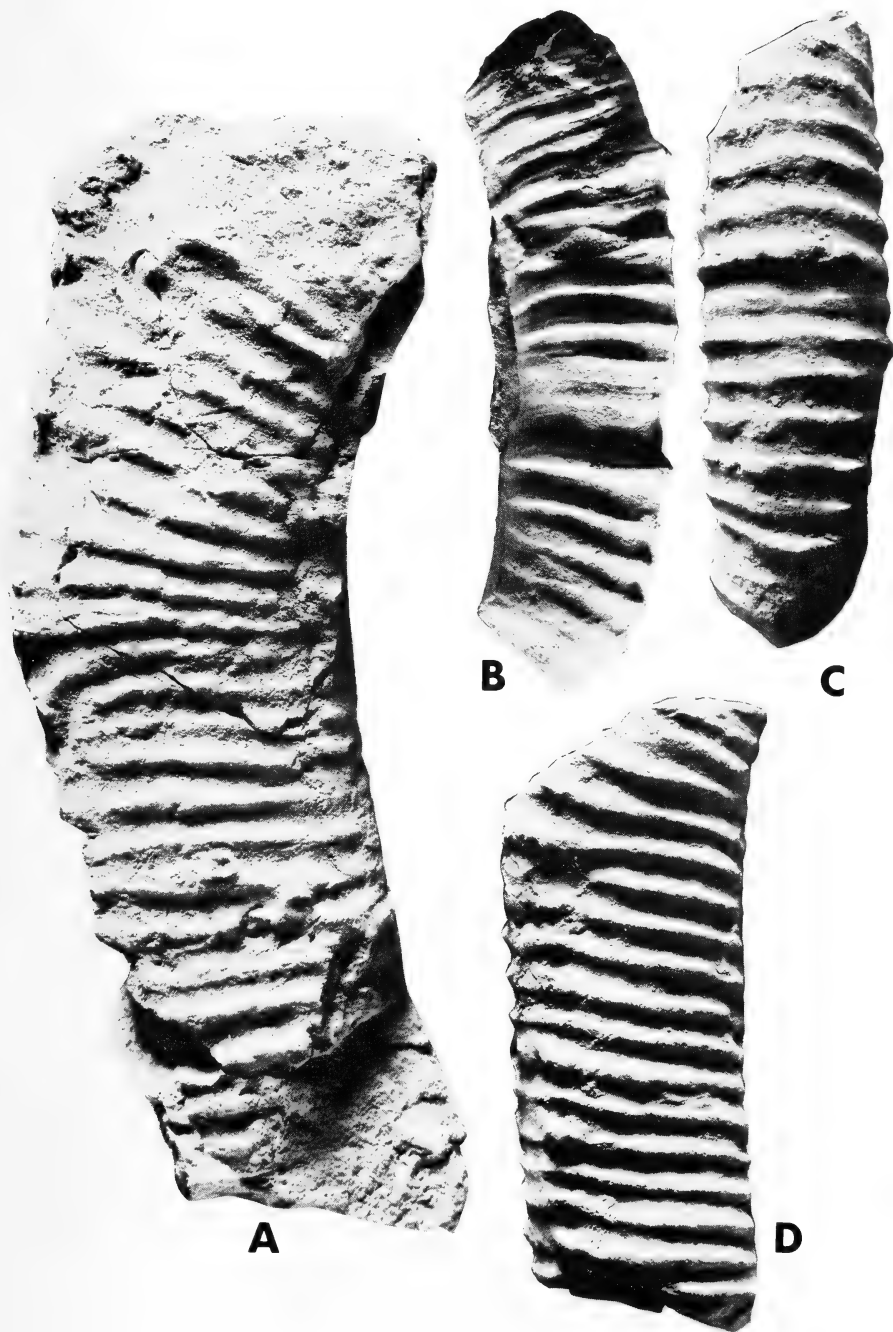On the basis of the material available, it is not possible to give a definitive answer to these questions, and all the specimens are included in the same species. Specimens figured by Michailov (1951: 88, pl. 16 (figs 66–71)) as *Ancyloceras bipunctatum* also suggest an open, crioceratitid or aspinoceratid mode of coiling in some specimens, although a straight fragment was also figured.

From the descriptions above, *Ancyloceras bipunctatum* may be defined as probably being dimorphic. The shell probably has an initial, loosely coiled, shallow helix with similar ribbing, and tubercles displaced slightly to one side. Wide, shallow constrictions may occur. This is followed in smaller specimens by an open, ancyloceratid shaft and hook, and in the larger specimens by irregular, crioceratitid or aspinoceratid coils. Major ribs occur variably on the last part of the phragmocone and on the body chamber.

GENERIC STATUS

Spath (1926: 80) erected the genus *Neancyloceras* merely by citing *Ancyloceras bipunctatum* Schlüter, 1872, as type species and added that 'this stock of the *mucronata* zone is obviously distinct from *Oxybeloceras* Hyatt, with which the writer (loc. cit. Zululand, 1921, p. 254) had formerly united it'. Later, Spath (1953: 16) added that '*Oxybeloceras* and *Neancyloceras* are distinguished by their regular and very sharp costation' and (Spath 1953: 17) '*Ancyloceras* (?) *pseudoarmatum* Schlüter . . . is probably a somewhat homoeomorphous development of *Neancyloceras*'.

Wright (1957: L227) interpreted *Neancyloceras* as differing 'from open-whorled species of *Glyptoxoceras* in less regular coiling and bituberculate periphery'. Comparisons with *Glyptoxoceras* as suggested by Wright are superficial, as no true glyptoxoceratid is bituberculate, and coiling is by no means as regular as is claimed. Comparisons with *Neoglyptoxoceras* Collignon can be ignored on the same grounds.

Interpreted in terms of the type species as here defined, *Neancyloceras* bears closer affinity to the Upper Cretaceous genera *Exiteloceras* Hyatt, 1894, *Axonoceras* Stephenson, 1941, and *Exicrioceras* Anderson, 1958. Differences between these taxa are slight and it is doubtful if they even merit generic separation. All generally have simple bituberculate ribbing.

Axonoceras Stephenson, 1941, (type species *Axonoceras multicostatum* Stephenson, 1941) is best known from Texas (Stephenson 1941), ?California (Anderson 1958), Angola (Haas 1943), and Madagascar (Collignon 1971). All specimens are small—less than 50 mm in diameter. *Axonoceras* is identified mainly by the irregular coiling of the inner whorls, that is, uncoiling and recoiling, resulting in a polygonal outline and irregular spaces between successive whorls. Stephenson (1941: 422) initially regarded the genus as having planispiral coils, but Haas (1943: 9) found that the Angolan species *A. angolanum* Haas was coiled helically. Most ribs in *Axonoceras* are bitubercu-

late, but non-tuberculate intermediaries do occur in the Texan species. In addition, Collignon (1971: 13) reported the occurrence of occasional stronger ribs in *A. multicostatum ellipticum* Collignon. Apart from the uncoiling and the recoiling of the inner whorls, the general shell shape of *Axonoceras* seems to be that of a low helix or loosely coiled spiral. Straight shafts and recurved hooks are unknown.

Scott & Cobban (1965) provided a reconstruction of the type species of *Exiteloceras, E. jennyi*. Gill & Cobban (1966: A32) and Scott & Cobban (1970: D73) defined the species as 'an aberrant ammonite that has juvenile whorls as straight limbs connected by semicircular bends, and later whorls loosely coiled in a plane without contact between adjacent whorls. Ornamentation consists of moderately coarse ribs, each of which terminates in a node at the margin of the venter'.

The irregularly coiled inner whorls of *Axonoceras* are compatible with the straight early limbs of *Exiteloceras*. Ornament and coiling in later whorls in both genera are similar, and it seems a reasonable procedure to regard *Axonoceras* as a junior synonym of *Exiteloceras*, as tentatively suggested by Wiedmann (1962: 198), and advocated by Matsumoto (1967: 340), Lewy (1969: 123), and Klinger (1976: 76).

Lewy (1969) described two new species of *Exiteloceras* from the Late Campanian of Israel, *E. unciforme* and *E. eteqense*. The first shows scaphitoid coiling (uncoiling or recoiling) of the body chamber, and the latter irregular tuberculation on the venter, analogous to that found in *Neocrioceras* s.s. Spath, 1921. (Matsumoto & Morozumi (1980: 18), however, regard *E. eteqense* and other species described by Lewy as possibly representing a new genus allied to *Neocrioceras (Schlueterella)* Wiedmann, 1962.) Wiedmann (1962: 206) also referred an uncoiled body chamber fragment from the Upper Campanian of Spain to *Exiteloceras*.

Thus interpreted, *Exiteloceras* cannot satisfactorily be separated from *Neancyloceras* as represented by the type species *Ancyloceras bipunctatum*. Furthermore the irregular crioceratitid or aspinoceratid coiling in some *Ancylocerus bipunctatum* is similar to that found in *Exicrioceras* Anderson, 1958, type species *Exicrioceras ortigalitense* Anderson, 1958. The scaphitoid coiling of the body chamber of *Exiteloceras unciforme* Lewy easily connects the ancyloceratid coiling of some *Ancyloceras bipunctatum* with the closer, crioceratitid coiling of typical *Exiteloceras*. The only real difference between *Neancyloceras* and *Exiteloceras* as interpreted above seems to be the differentiation of ribbing near or on the body chamber, but it is doubtful whether this merits separation, even at subgeneric level. If they were to be separated on this basis, *Axonoceras multicostatum ellipticum* Collignon with differentiated ribbing on the inner whorls would also have to be separated, thereby just increasing the list of heteromorph taxa based on insignificant differences.

Given that there appears to be no real difference between *Exiteloceras*, *Axonoceras*, *Exicrioceras*, and *Neancyloceras*, it is probably best to refer them all to the oldest available name, *Exiteloceras*.

Unfortunately detailed stratigraphic data are lacking, but it would be interesting to see the relationship between the ancyloceratid ('*Neancyloceras*' pars), ellipsoceratid ('*Exicrioceras*'), scaphitoid (*Exiteloceras unciforme*) and closer-coiled crioceratitid forms (e.g. *Exiteloceras jennyi*). Is there a trend towards recoiling, as observed in numerous heteromorph groups (see e.g. Wiedmann 1969) or is this merely part of intraspecific or generic variation or dimorphism?

ORIGIN AND PHYLOGENY

Matsumoto (1967: 339–40) considered it possible to derive *Exiteloceras* and *Axonoceras* from *Nostoceras* through widening of the apical angle of the helix. Indeed, forms such as '*Bostrychoceras polyplocum* Roemer ? var. *doneziana* Michailov' (Michailov 1951: 53, pl. 4 (figs 23–24)), which are coiled in a loose helix and with bituberculate ornament, are remarkably similar to the phragmo-cone whorls of *Exiteloceras bipunctatum*. Similarly, the early straight whorls of forms such as *Didymoceras* cf. *D. nebrascense* (Lewy 1969: 116, pl. 1 (fig. 2)) are comparable to the early whorls of *Exiteloceras jennyi*.

As far as coiling and ornament are concerned, there are a number of features in common between *Exiteloceras*, *Neocrioceras*, and *Pseudoxybelo-ceras* that appear to be too related to be considered as merely homoeomorphic development (as tentatively suggested by Spath 1953: 17), and the author would rather derive these taxa from a common ancestor than from the contem-poraneous nostoceratid forms as advocated by Matsumoto (1967).

Neocrioceras Spath, 1921, as interpreted by Wiedmann (1962: 205) com-prises two subgenera, *Neocrioceras* s.s., type species *Crioceras spinigerum* Jimbo, 1894, with crioceratitid coiling, simple ribbing and irregular tubercula-tion over the venter; and *N. (Schlueterella)*, type species *Ancyloceras pseudo-armatum* Schlüter, 1872. *N. (Schlueterella)* is a rather heterogenous group, but includes ancyloceratid to polyptychoceratid forms in which the tubercles are situated either on stronger or on looped ribs. Generally *Neocrioceras* s. l. can be separated from *Exiteloceras* by the presence of four rows of tubercles in the former but only two in the latter, but, as will be seen in *Pseudoxybeloceras*, the presence or absence of lateral tubercles may be of low systematic value. Points of similarity between *Exiteloceras* and *Neocrioceras* are: early helical coils occur in some *Exiteloceras* and in some *Neocrioceras*, e.g. *Neocriceras* cf. *spinigerum* (Spath 1921: 52, pl. 7 (fig. 6)); ancyloceratid coiling occurs in some *Exiteloceras bipunctatum* as well as *N. (Schlueterella) pseudoarmatum* (Schlüter), although admittedly the latter already tends towards polyptychoceratid coiling; and irregular ornament occurs in both *Exiteloceras eteqense* Lewy and *N. (Neocrio-ceras) spinigerum* (Jimbo).

Closer resemblance is to be found in the genus *Pseudoxybeloceras* Wright & Matsumoto, 1954, as interpreted by Klinger (1976: 75), Matsumoto & Morozumi (1980), and (in essence) Ward & Mallory (1977), which includes

Christophoceras Collignon, 1969 (type species *Christophoceras ramboulai* Collignon, 1969) and *Parasolenoceras* Collignon, 1969 (type species *Parasolenoceras splendens* Collignon, 1969) as subgenera. The early whorls of *Pseudoxybeloceras* are unknown; thus far only J-shaped fragments have been found, but there is a distinct trend towards polyptychoceratid coiling in the later stages. *Pseudoxybeloceras* s.s. is quadrituberculate on every rib in the adult stage, but Matsumoto (1977: 346) has recently shown that the early stages of *Pseudoxybeloceras (P.) quadrinodosum* (Jimbo) lack the lateral tubercles, and that ornament in this respect is similar to that of *Exiteloceras. Pseudoxybeloceras (Parasolenoceras)* is apparently bituberculate throughout, like the juvenile stages of *Pseudoxybeloceras (Pseudoxybeloceras) quadrinodosum*, but already has distinct polyptychoceratid coiling in the early stages of growth. *Pseudoxybeloceras (Christophoceras)* has similar coiling and bituberculate ornament on the phragmocone, but develops major ribs on the body chamber and acquires lateral tubercles on these. The bituberculate ornament in *P. (Parasolenoceras)* and *P. (Christophoceras)* is analogous to that found in *Exiteloceras* in general, whereas differentiation of ornament on the body chamber of *P. (Christophoceras)* is similar to that of *Exiteloceras bipunctatum*.

The essential ingredients for the 'Bauplan' of these predominantly Santonian-Campanian genera *Exiteloceras*, *Neocrioceras*, and *Pseudoxybeloceras* were already present in the Turonian.

Parts of the early whorls of *Exiteloceras bipunctatum* are indistinguishable from the predominantly Turonian genus *Allocrioceras* Spath, 1926. Spath (1926: 81) had already noticed this, but regarded it as 'only superficial resemblance'. *Allocrioceras* consists mainly of helically coiled forms with undifferentiated, bituberculate ribbing. Differentiated ribbing does, however, occur in forms such as *Allocrioceras cuvieri* (Schlüter, 1872) and *A. turoniense* (Schlüter, 1872). *Ancyloceras paderbornense* Schlüter (1872: 97, pl. 30 (figs 1–2)) already has distinct *Neocrioceras (Schlueterella)* ornament. *Hamites multinodosus* Schlüter (1872: 106, pl. 32 (figs 1–2)) is part of a straight body chamber fragment, and shows ornament similar to that of *Christophoceras*.

Ward & Mallory (1977, test-fig. 2) show a lineage starting with *Neocrioceras* and *Pseudoxybeloceras* in the Turonian, trending towards more polyptychoceratid coiling through '*Cyphoceras*' Ward & Mallory, 1977 (= *P. (Christophoceras)* and *P. (Parasolenoceras)*) to *Solenoceras* in the Maastrichtian. *Exiteloceras* first appears in the Upper Campanian, and it seems unlikely that its origins can be traced directly to *Neocrioceras* or *Pseudoxybeloceras* of the Turonian–Coniacian. Matsumoto (1959: 162) originally regarded *Exiteloceras* and *Pseudoxybeloceras* as having evolved in parallel or sister relationship from a 'plastic genus *Hyphantoceras*'.

Exiteloceras was probably derived from *Pseudoxybeloceras* s.s. in parallel with *P. (Christophoceras)* and *P. (Parasolenoceras)* in the Campanian (Fig. 10). In the latter two subgenera the trend is towards acquisition of polyptychoceratid coiling and reduction of the helical stage, whereas *Exiteloceras* retains the
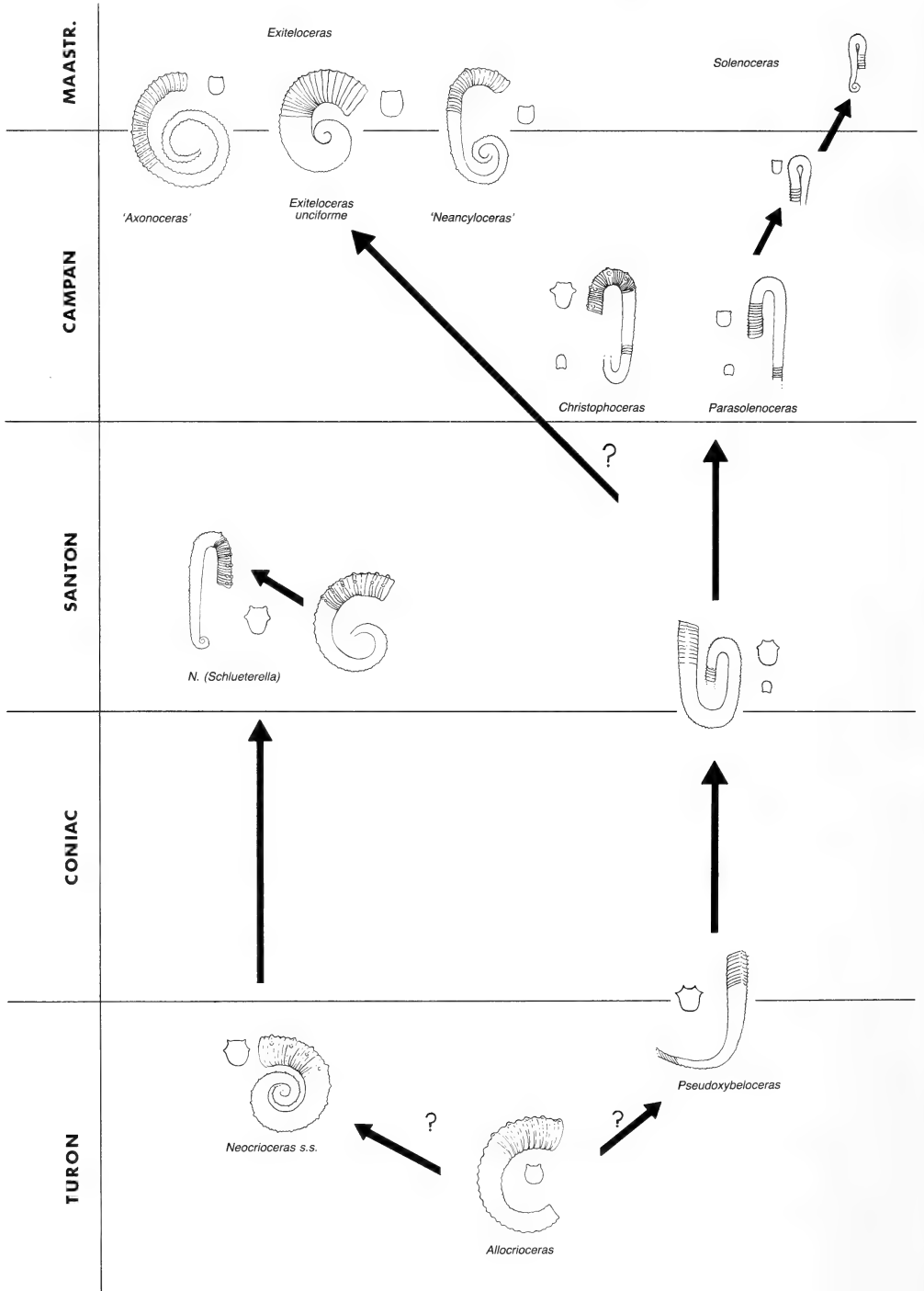
Fig. 10. Inferred phylogenetic relationship of *Exiteloceras*. Part of the diagram after Ward & Mallory (1977, text-fig. 2).

helical or crioceratitid stage to greater diameters and may possibly have solved hydrodynamic requirements by trending towards planispiral coiling.

LIMITS

Several species that have been referred to '*Neancyloceras*' probably do not belong there (see e.g. Naidin 1959; Wiedmann 1962; Blank *et al.* 1974), e.g. *Hamites wernickei* Wolleman, 1902, *Ancyloceras retrorsum* Schlüter, 1872, *Hamites interruptus* Schlüter, 1872, and *Hamites phaleratus* Griepenkerl, 1889.

Ancyloceras retrorsum lacks ventral tubercles throughout and is apparently a large glyptoxoceratid, as examination of Schlüter's types has shown, a view supported by Atabekian & Khakimov (1976: 61) and Blank *et al.* (1974: 168).

Hamites interruptus is thus far known only from small recurved fragments. The holotype (Fig. 8F–G) is still septate at the larger end, thus indicating that it is not a body chamber hook. The possibility cannot be excluded that this represents the early whorls of a form similar to *Exiteloceras jennyi*, but because of the polyptychoceratid coiling it is probably best placed in *Pseudoxybeloceras (Parasolenoceras)*. Blank *et al.* (1974: 167) place it in *Solenoceras*.

Hamites wernickei is difficult to interpret. The small specimen with two shafts in contact, figured by Wolleman (1902, pl. 4 (fig. 5)) under that name, was previously regarded (Klinger 1976: 73) as better placed in *Solenoceras*. Should that specimen be conspecific with the larger hooks figured under that name by Wolleman (1902, pl. 4 (fig. 4), pl. 5 (figs 1–2)) or Pervinquière (1907: 86, pl. 3 (fig. 33)), the species may also be referred to *Pseudoxybeloceras (Parasolenoceras)*.

Collignon (1971: 11, pl. 644 (fig. 2380)) described a small straight fragment from the Maastrichtian of Madagascar as *Neancyloceras ambindense*. In that specimen only every third rib is tuberculate. Collignon's generic allocation seems correct.

Blank *et al.* (1974: 169) refer *Hamites phaleratus* to *Neancyloceras*, but the figures of Griepenkerl (1889, pl. 11 (fig. 3), pl. 12 (figs 3–4)) suggest coiling to be polyptychoceratid, which would place it closer to *Pseudoxybeloceras (Parasolenoceras)* than to *Exiteloceras*.

Spath (1953: 49) mentions *Neancyloceras* from Angola, but this material has never been described, and the generic allocation cannot be verified.

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.

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
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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 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
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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.

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.

HERBERT CHRISTIAN KLINGER

REVISION OF *ANCYLOCERAS BIPUNCTATUM* SCHLÜTER, 1872 (CEPHALOPODA, AMMONOIDEA) AND DISCUSSION OF THE VALIDITY, PHYLOGENY AND LIMITS OF THE GENUS *NEANCYLOCERAS* SPATH, 1926

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.

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       Number of illustrations (figures, enumerated maps and tables, in this order)
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    (f) *Summary*, if paper is lengthy
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends 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.

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

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All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

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    FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.
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CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA THE AMMONITE SUBFAMILY BARROISICERATINAE BASSE, 1947

By

WILLIAM JAMES KENNEDY,

CLAUD WILLIAM WRIGHT

&

HERBERT CHRISTIAN KLINGER

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE SUBFAMILY BARROISICERATINAE BASSE, 1947

By

William James Kennedy,

Claud William Wright

Geological Collections, University Museum, Oxford

&

Herbert Christian Klinger

South African Museum, Cape Town

(With 51 figures)

ABSTRACT

Representatives of the subfamily Barroisiceratinae are locally common in the Coniacian of Zululand. The following are described: *Reesideoceras lornae* (van Hoepen, 1968), *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), to which all previously named South African *F. (Forresteria)* and many other species are referred, *F. (F.) madagascariensis* (Collignon, 1965), *F. (F.)* cf. *hobsoni* (Reeside, 1932), *Yabeiceras orientale* Tokunaga & Shimizu, 1926, *Y.* cf. *orientale*, *Y. transiens* sp. nov., *Y. ankinatsyense* Collignon, 1965, *Y. costatum* Collignon, 1965, *Y. manasoaense* Collignon, 1965, *Y.* aff. *manasoaense*, *Y. crassiornatum* sp. nov., *Y. cobbani* sp. nov. and *Yabeiceras* sp. indet.

Itwebeoceras van Hoepen, 1968, is shown to be a synonym of *Reesidites* Wright & Matsumoto, 1954; *Zumpangoceras* Basse, 1947, *Collignonella* van Hoepen, 1957, *Basseoceras* van Hoepen, 1968, *Eedenoceras* van Hoepen, 1968, and *Neokanabiceras* Collignon, 1965, are synonyms of *Forresteria (Forresteria)*, and it is suggested that *Harleites* Reeside, 1932, is a senior synonym of *Reesideoceras* Basse, 1947.

CONTENTS

INTRODUCTION

The Barroisiceratinae are a small subfamily of the Collignoniceratidae derived from late Collignoniceratinae, perhaps via *Subprionocyclus* Shimizu. They vary from compressed and involute to evolute and inflated, and either

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have strong to weak ribs arising singly or in groups from bullae, or not. Ventrolateral and siphonal clavi are generally developed at some stage during ontogeny, the latter sometimes fusing into a keel. A lateral tubercle develops in some taxa and several lose virtually all ornament on the body whorl, which may be either tabular or compressed with fastigiate or tabulate venter. The sutures are generally simple with short, moderately incised saddles.

Within several genera large and small species with modified body chambers occur and are in some cases afforded subgeneric status. This may represent an as yet poorly perceived dimorphism: the evidence is still inconclusive.

The group as a whole differs from the ancestral Collignoniceratinae in having only one rather than two rows of ventrolateral nodes. On this basis *Reesidites* Wright & Matsumoto, 1954, belongs to this subfamily, which thus ranges from Upper Turonian through the Coniacian. The subfamily has a wide geographic distribution, and most members are taken as stratigraphic indicators of the Coniacian. As is clear from recent discussions by Hancock & Kennedy (1981) and Matsumoto (in Matsumoto *et al.* 1981: 63) amongst others, the true stratigraphic distribution of species and genera is still unsettled. The present firmly dated records from Zululand are thus of more than local significance. Added to this, the local abundance of one genus, *Forresteria* Reeside, 1932, allows a discussion of ontogenetic development and intraspecific variation that clarifies several taxonomic problems.

LOCATION OF SPECIMENS

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

BMNH   British Museum (Natural History)
SAM   South African Museum, Cape Town
SAS   South African Geological Survey, Pretoria
USNM   National Museum of Natural History, Washington, D.C.

FIELD LOCALITIES

Details of localities mentioned in the text are given by Kennedy & Klinger (1975); fuller descriptions of sections are deposited in the Palaeontology Department of the British Museum (Natural History), London; Geological Survey, Pretoria; and the South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions are given in millimetres:

D = diameter,   Wb = whorl breadth,   Wh = whorl height,   U = umbilical diameter; *c* and *ic* refer to costal and intercostal measurements respectively.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), reviewed by Kullman & Wiedmann (1970) is followed here:

I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family **Collignoniceratidae** Wright & Wright, 1951
Subfamily Barroisiceratinae Basse, 1947

Genus *Reesidites* Wright & Matsumoto, 1954
(= *Itwebeoceras* van Hoepen, 1968)

Type species

Barroisiceras minimum Hayasaka & Fukada (1951: 325 (ex Yabe 1925, *nom. nud*)), from the Upper Turonian of Japan, by the original designation of Wright & Matsumoto (1954: 130).

Diagnosis

Involute, compressed, flat-sided sinuous ribs arise in groups of two or three from variably developed umbilical bullae. Shorter intercalated ribs are inserted on the middle to outer flank and all ribs bear strong ventrolateral clavi from which they project forward to prominent siphonal clavi. Ribs broaden and flatten with increasing age.

Suture with markedly asymmetric E/L in the type species at least.

Discussion

Reesidites has been discussed at length by Wright & Matsumoto (1954: 130), Obata (1965), and Matsumoto (1965: 61). There seems little doubt that *Reesidites minimus* and *R. elegans* Matsumoto & Inoma (1971: 139, pl. 23 (figs 1–3), text-figs 5–7) are derived from an involute collignoniceratid, probably *Subprionocyclus* (see e.g. Reyment 1975). The ornament of the two genera differs only in the presence of both inner *and* outer ventrolateral tubercles in the latter. The suture of *Subprionocyclus* (e.g. Matsumoto 1965, text-figs 28–30) already shows the asymmetry of E/L, that is so distinctively developed in *Reesidites*.

The ornament of *Reesidites minimus* differs little from that of *Barroisiceras haberfellneri* (von Hauer) (compare Fig. 1A and Fig. 1B–D), being a little more flexuous in *Reesidites* and projected strongly forward on the ventrolateral shoulder rather than straight. The sutures differ more obviously; in *B. haberfellneri* there is no comparable asymmetry (see Fig. 2). However, the type specimen of *Itwebeoceras lornae* van Hoepen, 1968, described below, has the ornament of *Reesidites* without sutural asymmetry. Taken together these obser-
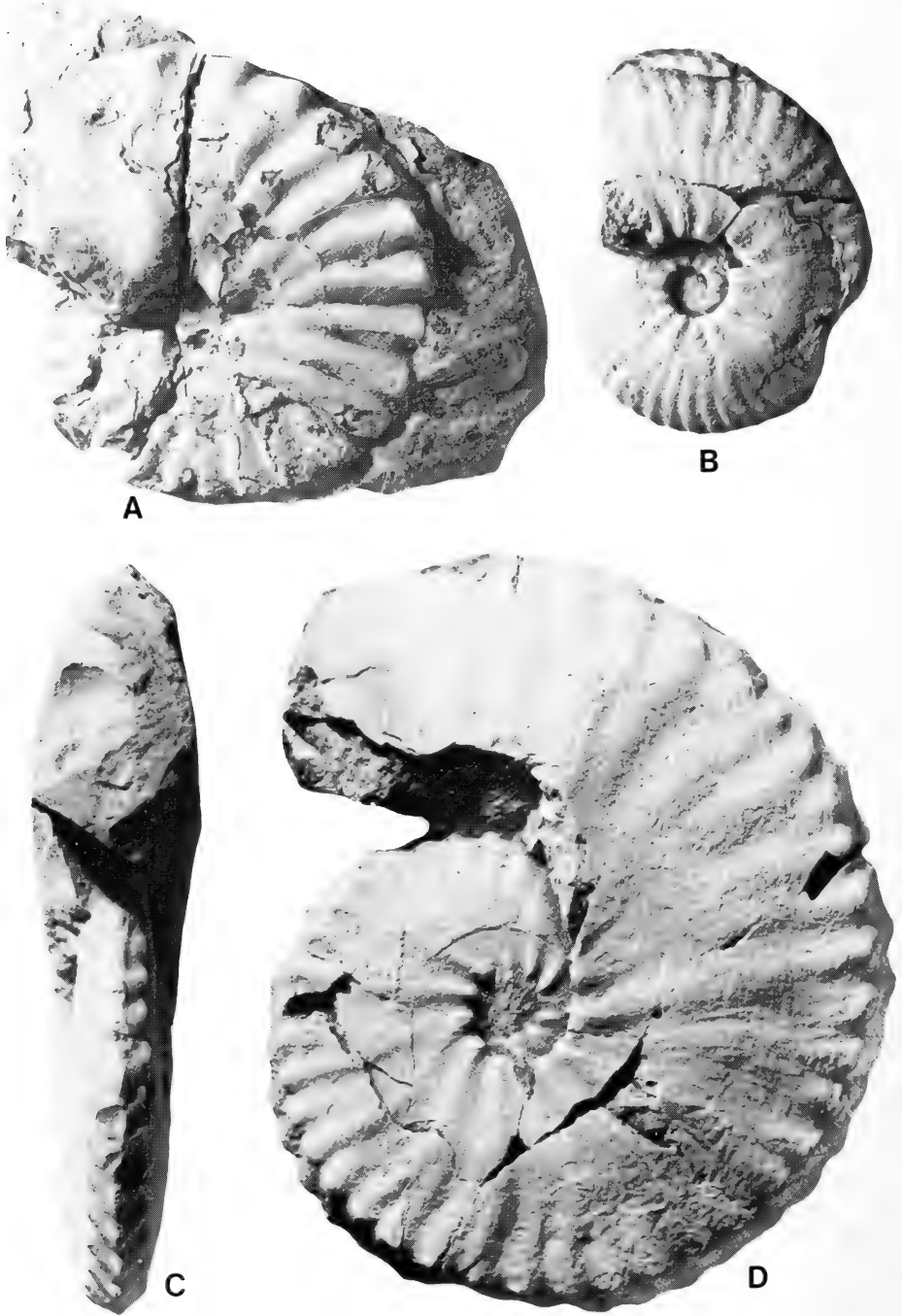
Fig. 1. A. *Barroisiceras haberfellneri* (von Hauer, 1866). Geological Survey of Austria Collections 3764, from the Gosau Beds of Gams near Hieflau Austria. (Original of Von Hauer 1866: 30, pl. 1 (figs 1–2).) ×1. B–D. *Reesidites minimus* (Hayasaka & Fukada, 1951). B. University of Kyushu Collections H4089G bis, from the Upper Turonian of the Ikushumbets, Hokkaido. ×1. C–D. Holotype, Hokkaido University Collections, from the Upper Turonian of the Ikushumbets. ×1.
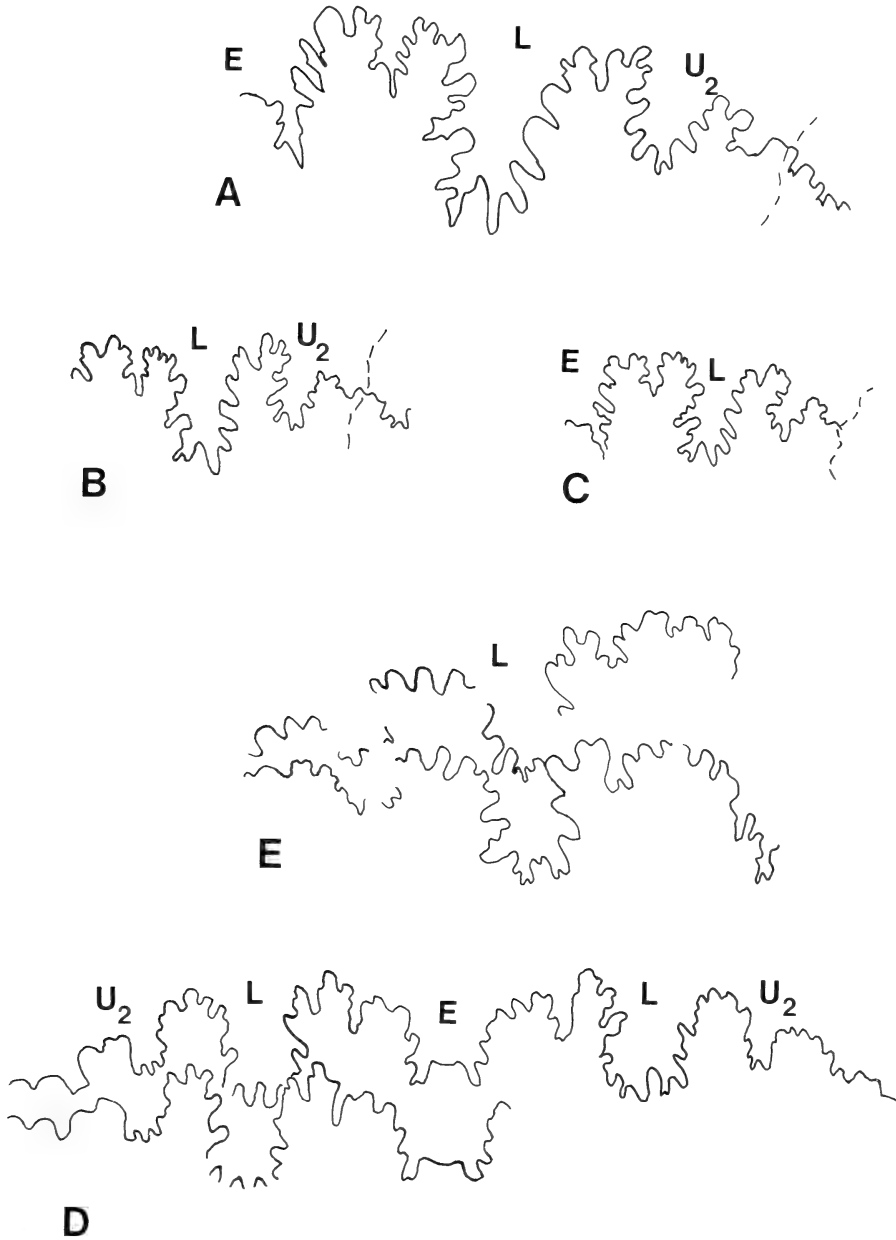
Fig. 2. A–C. *Reesidites lornae* (van Hoepen, 1968). Sutures of the holotype SAS Z1128. D. *Barroisiceras haberfellneri paeon* (Redtenbacher, 1873). Sutures of a specimen in the Geological Survey of Austria Collections 3481, from Ofenwald near Ströbl-Weissenbach, Austria. (Original of Redtenbacher 1873: 103, pl. 23 (fig. 3c–e).) E. *Reesidites minimus* (Hayasaka & Fukada, 1951). Sutures of the holotype. (After Matsumoto 1965: 65, text-fig. 36.) All ×2.
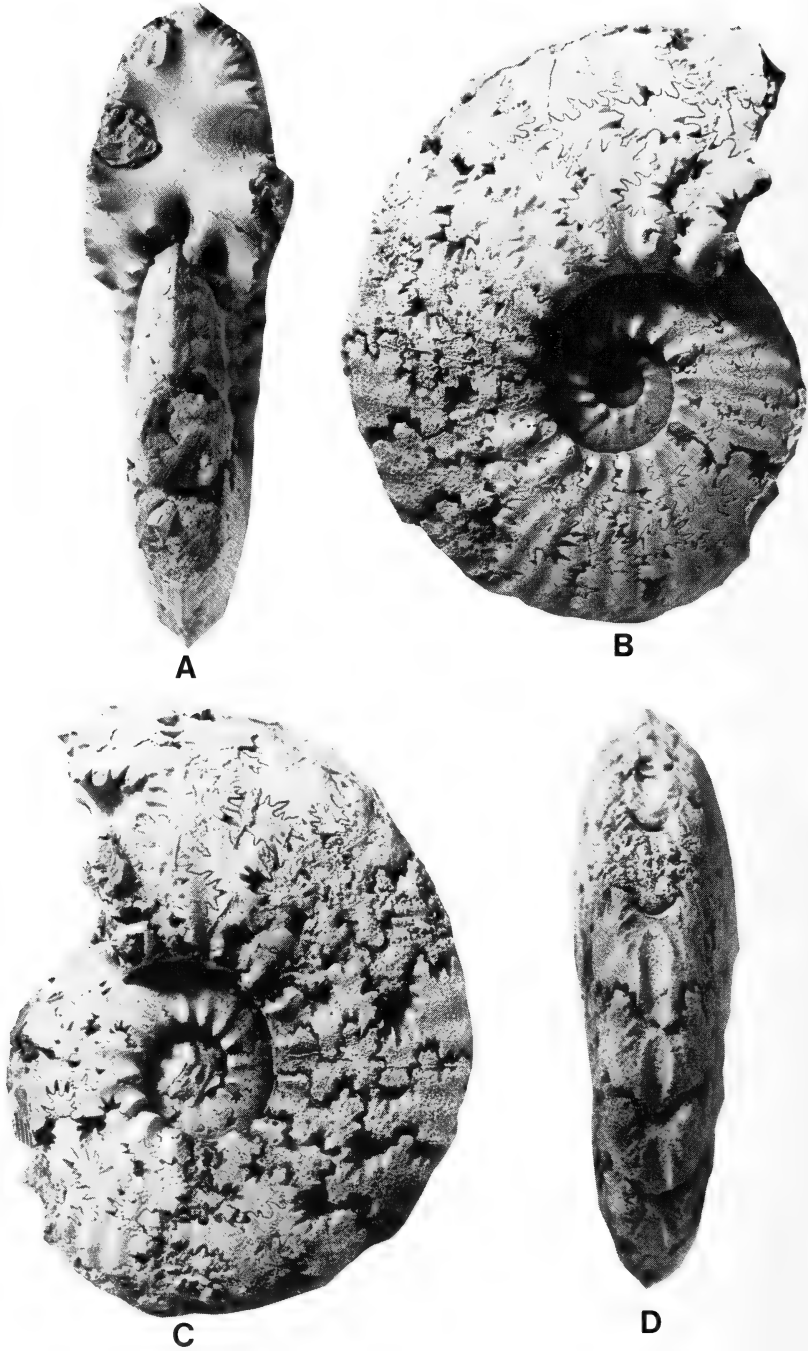
Fig. 3. *Reesidites lornae* (van Hoepen, 1968). Holotype SAS Z1128. ×1.

vations suggest that *Reesidites* may best be treated as a subgenus or even strict synonym of *Barroisiceras*. However, until the type material of *B. haberfellneri* is redescribed and its stratigraphic position clarified, *Reesidites* and *Barroisiceras* are here maintained as separate taxa.

Itwebeoceras van Hoepen, 1968 (type species *Itwebeoceras lornae* van Hoepen, 1968), from the ?Upper Coniacian of Zululand, has the same ornament as *Reesidites*, differing only in detail from that of *R. minimus*. It does not show the same asymmetry of E/L but is here regarded as a synonym. *Buenoceras* Etayo-Serna (1979: 101; type species *B. loboi* Etayo-Serna (1979: 101, pl. 14 (fig. 2), text-figs 9R, U)) from the Coniacian of Colombia is based on a fragment only and may also be a synonym.

Occurrence

Upper Turonian of Japan and Armenia; Coniacian of Colombia, Venezuela, and Zululand.

<div align="center">

Reesidites lornae (van Hoepen, 1968)

Figs 2A–C, 3–4.
</div>

Itwebeoceras lornae van Hoepen: 1968a: 184, pl. 4.

Holotype

By monotypy, SAS Z1128, from the St. Lucia Formation, (Coniacian ?IV), locality 13 of Van Hoepen (1968a, 1968b) = locality 73 of Kennedy & Klinger (1975).

Dimensions

D	Wb	Wh	Wb : Wh	U
c. 74,5(100)	21,0(—)	31,5(—)		22,7(—)
46,5(100)	14,1(30,3)	20,0(43,0)	0,71	13,2(28,3)
36,6(100)	11,1(30,3)	16,0(43,7)	0,69	10,0(27,3)

Description

The holotype is a wholly septate internal mould, somewhat corroded on the ventral region of the outer whorl; the estimated maximum diameter is approximately 75 mm.

The smallest diameter at which the specimen can be examined is 17 mm (Fig. 4). At this size the coiling is rather involute, half the previous whorl being covered. The whorl section is compressed (whorl breadth to height ratio is 0,8), with the greatest breadth at the umbilical bullae. The flanks are flattened and convergent, the ventrolateral shoulders narrowly rounded, and the venter fastigiate. There are twelve prominent umbilical bullae per whorl; these give rise to pairs of low, broad prorsiradiate ribs strengthened into an oblique ventrolateral clavus from which they sweep forward across the ventrolateral shoulder, declining as they do so. There is an initially entire siphonal keel

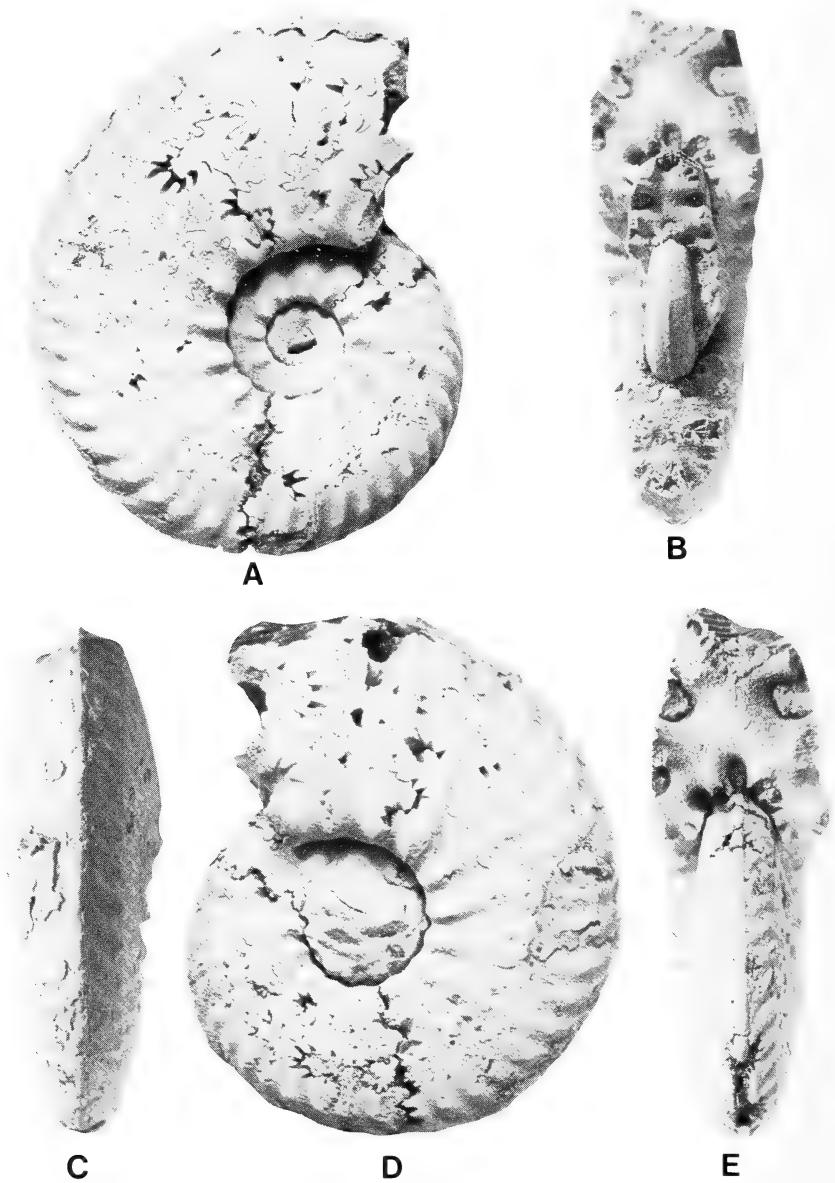Fig. 4. *Reesidites lornae* (van Hoepen, 1968). Holotype SAS Z1128. ×2.

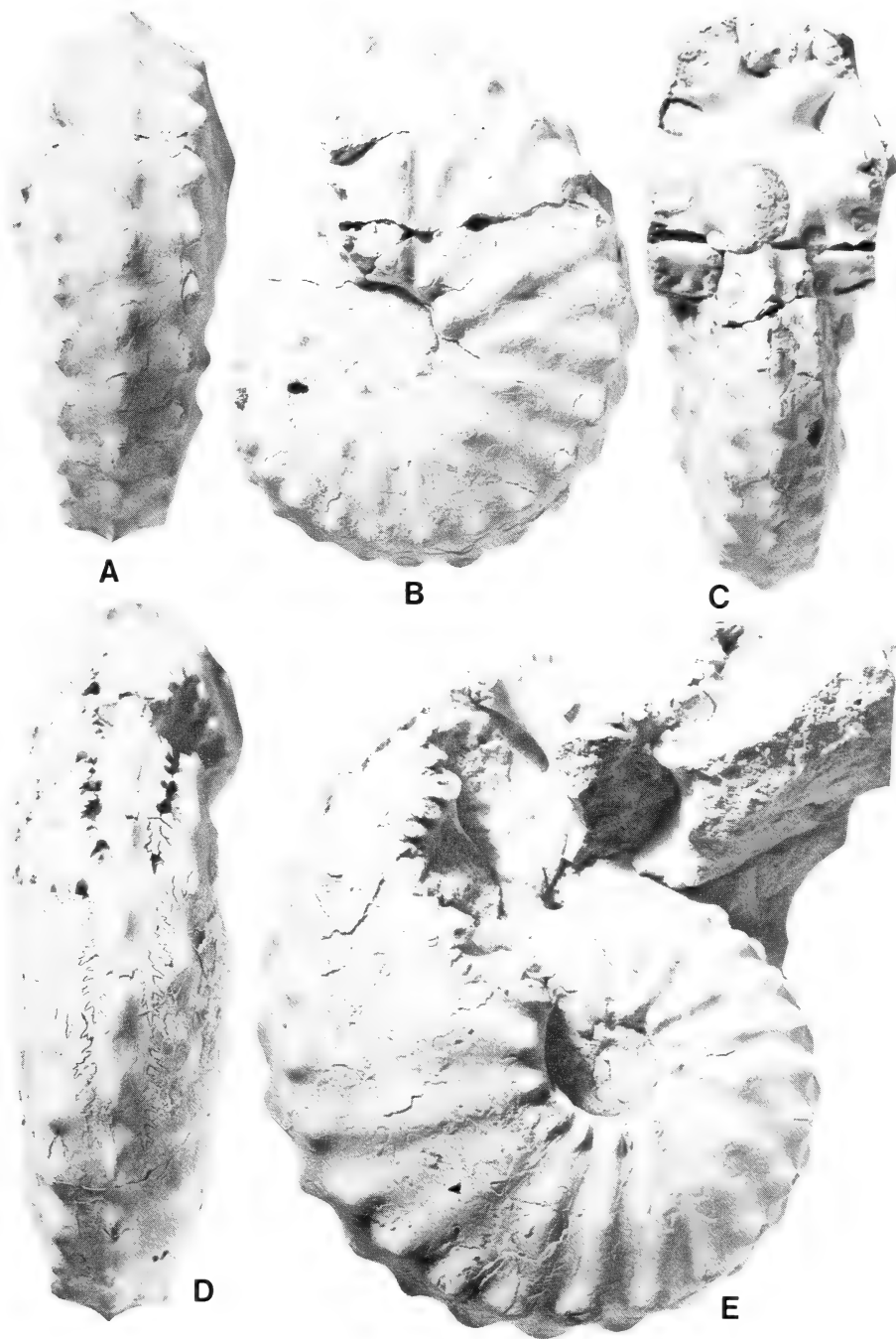Fig. 5. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–C. A paratype of '*Basseoceras krameri*' van Hoepen, 1968, SAS Z1437. D–E. Another paratype, SAS Z978. All ×1.

Fig. 6. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Basseoceras krameri*' van Hoepen, 1968, SAS Z935.

flanked by faint, shallow grooves, which subsequently develops low crenulations, each of which corresponds to a rib. As size increases, ribbing and tuberculation becomes increasingly differentiated. At a diameter of 36 mm the coiling has become a little more evolute (umbilicus is 27,3% of diameter) and higher-whorled (whorl breadth to height ratio of 0,69). There are fifteen medium-sized umbilical bullae per whorl. These give rise to pairs of low, relatively broad, flexuous prorsiradiate ribs that sweep forward across the inner flank, are feebly convex across the mid-flank and feebly concave across the outer flank. Occasional intercalated ribs are inserted around mid-flank and all the ribs develop a small, conical ventrolateral tubercle. These give rise to broad prorsiradiate extensions of the ribs that sweep forward to link with elongate siphonal clavi borne on the siphonal keel. There are thirty-eight ribs per whorl at this diameter, corresponding to a slightly smaller number of ventral clavi.

This style of ornament extends to the greatest diameter preserved where there are seventeen to eighteen umbilical bullae per whorl and a total of forty-two ribs.

The suture line is shown in Fig. 2A–C. Elements are relatively simple and little subdivided, with a broad, slightly asymmetric bifid E/L, narrower bifid L, narrow, slightly asymmetric L/U_2, small U, and broad, simple U_2/U_3.

Discussion

Reesidites lornae resembles *R. minimus* (see Matsumoto 1965: 63, pl. 14 (fig. 1), pl. 15 (figs 1–3), text-figs 34–39) but differs in being more evolute, with stronger bullae, broader whorls, narrower, better differentiated ribs, and an essentially symmetrical rather than asymmetric E/L. *R. elegans* Matsumoto & Inoma (1971: 139, pl. 23 (figs 1–3), text-figs 5–7) is much more delicately and flexuously ribbed, with more secondary ribs. *R. subtuberculatus* (Gerhardt) (1897: 156, pl. 3 (fig. 12)) has far fewer ribs, lacks bullae, and has a broader venter without obvious ribs but rather with striae between ventrolateral and siphonal clavi.

There is a striking similarity between *R. lornae* and '*Schlönbachia (Gauthiericeras)*' *crioceratiformis* Lüthy (1918: 43, pl. 3 (fig. 2)) from the Coniacian of Peru. The outer whorl of the wholly septate holotype of this species uncoils, perhaps due to pathological disturbance of growth, and further material is needed before placing *lornae* in synonymy with *crioceratiformis*.

Occurrence

St. Lucia Formation of Zululand. Precise age unknown but certainly Coniacian and possibly Coniacian IV.

Genus *Forresteria* Reeside, 1932

Type species

Barroisiceras (Forresteria) forresteri Reeside (1932: 17, pl. 5 (figs 2–7)), by the subsequent designation of Wright (1957: L432) = *Acanthoceras (Prionotro-*
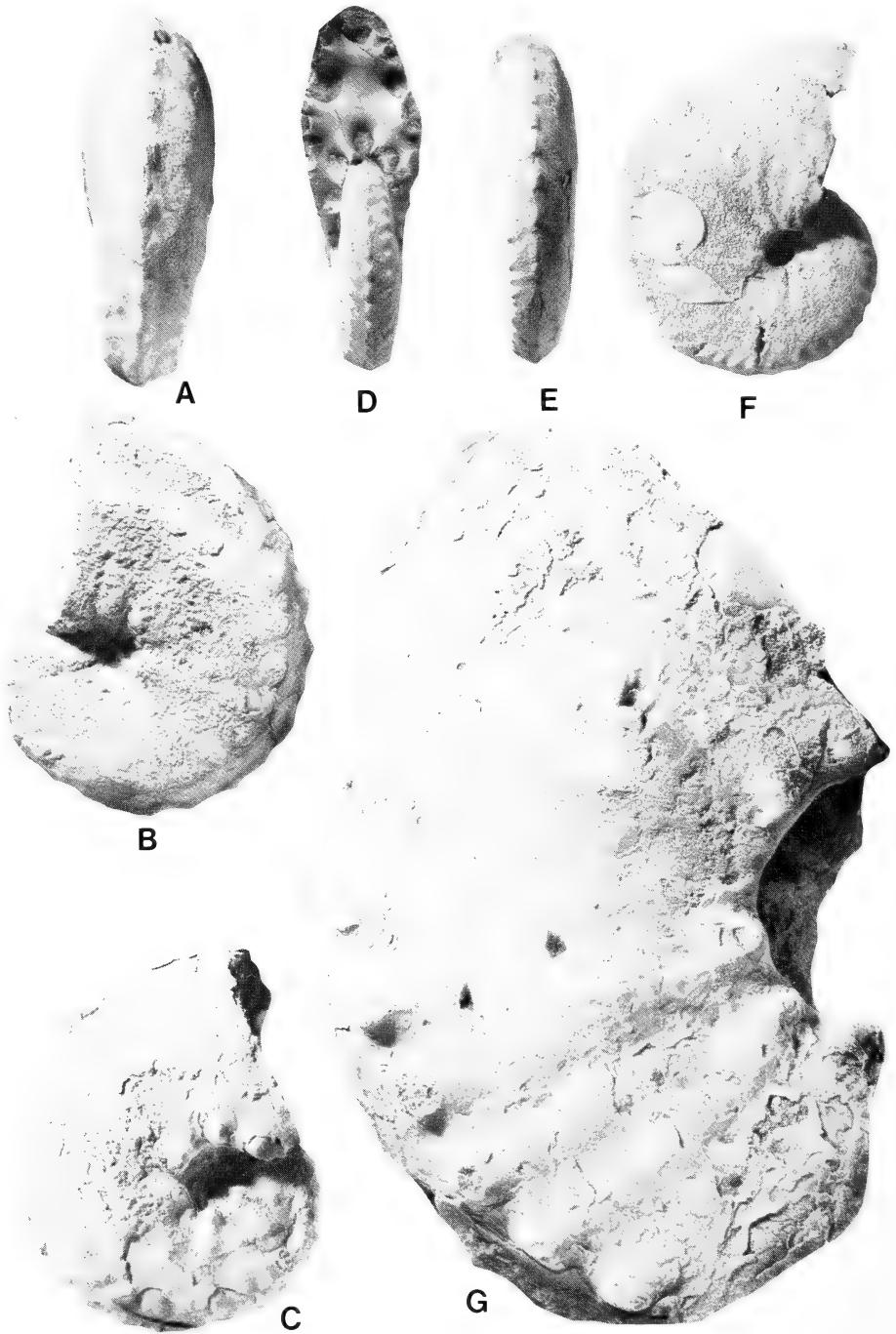
Fig. 7. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Slender variants. A–C. SAM–D1187G. D–F. '*Barroisiceras (Harleites) castellense*' Reeside, 1932. The holotype USNM 73758 from the Mancos Shale, some 61 m (200 ft) above the top of the Ferron Sandstone in Sevier County, Utah. G. SAS Z913, large septate fragment. All ×1.

pis) alluaudi Boule, Lemoine & Thévenin (1907: 32, pl. 8 (figs 6–7), text-fig. 17).

Diagnosis

Both small species (adult at 80–100 mm) and large ones (adult at 250 mm) are known. Coiling varies from involute to moderately evolute, the whorls from compressed to depressed. Early whorls bear weak umbilical bullae, strong to weak lateral tubercles or spines linked by primary ribs, the latter giving rise to pairs of weak to strong secondary ribs which, with intercalatories, are linked to variably developed ventrolateral and siphonal clavi. Ornament may be lost at small diameters, with a smooth or feebly ornamented lanceolate or tabulate venter on the body whorl, or persist, with the tubercles declining only at maturity. The suture is simple with a broad E, narrow E/L and L, with large U_2 in many species.

Occurrence

Coniacian of France, Austria, Czechoslovakia, Israel, west Africa, Zululand, Madagascar, Japan, Colombia, Mexico, and the United States (Utah and Wyoming).

Subgenus *Forresteria (Forresteria)* Reeside, 1932

(= ?*Zumpangoceras* Basse, 1947: 144; *Collignonella* van Hoepen, 1957: 350 (*pro Collignoniceras* van Hoepen, 1955: 361), *non* Breistroffer, 1947: unpaged; *Basseoceras* van Hoepen, 1968*b*: 162 (*non* Collignon, 1965: 73); *Eedenoceras* van Hoepen, 1968*b*: 171; *Neokanabiceras* Collignon, 1965: 42).

Diagnosis

Variable, early whorls as in *Forresteria sensu lato*. In compressed variants the umbilical and lateral tubercles are lost at an early growth stage ('*Basseoceras*' van Hoepen) leaving feeble flank ribs, ventral and siphonal clavi, and a high angular whorl section that persists to over 200 mm. These grade into massively whorled hypernodose individuals with persistent ribs and tubercles. The lateral and ventrolateral tubercles fuse in some species, in others they survive separate to the beginning of the body chamber; thereafter tubercles decline and ribs dominate ornament.

Discussion

The type species of *Forresteria (Forresteria)* was based on a single juvenile specimen (see Fig. 14E–H) from the Mancos Shale of Sevier County, Utah, some 61 m (200 ft) above the top of the Ferron Sandstone. Reeside (1932: 17) remarked that it 'seems very close indeed to the form from the Senonian of Diego-Suarez, Madagascar, described by Boule, Lemoine and Thévenin as *Acanthoceras (Prionotropis) alluaudi*, which seems to the writer to be a species
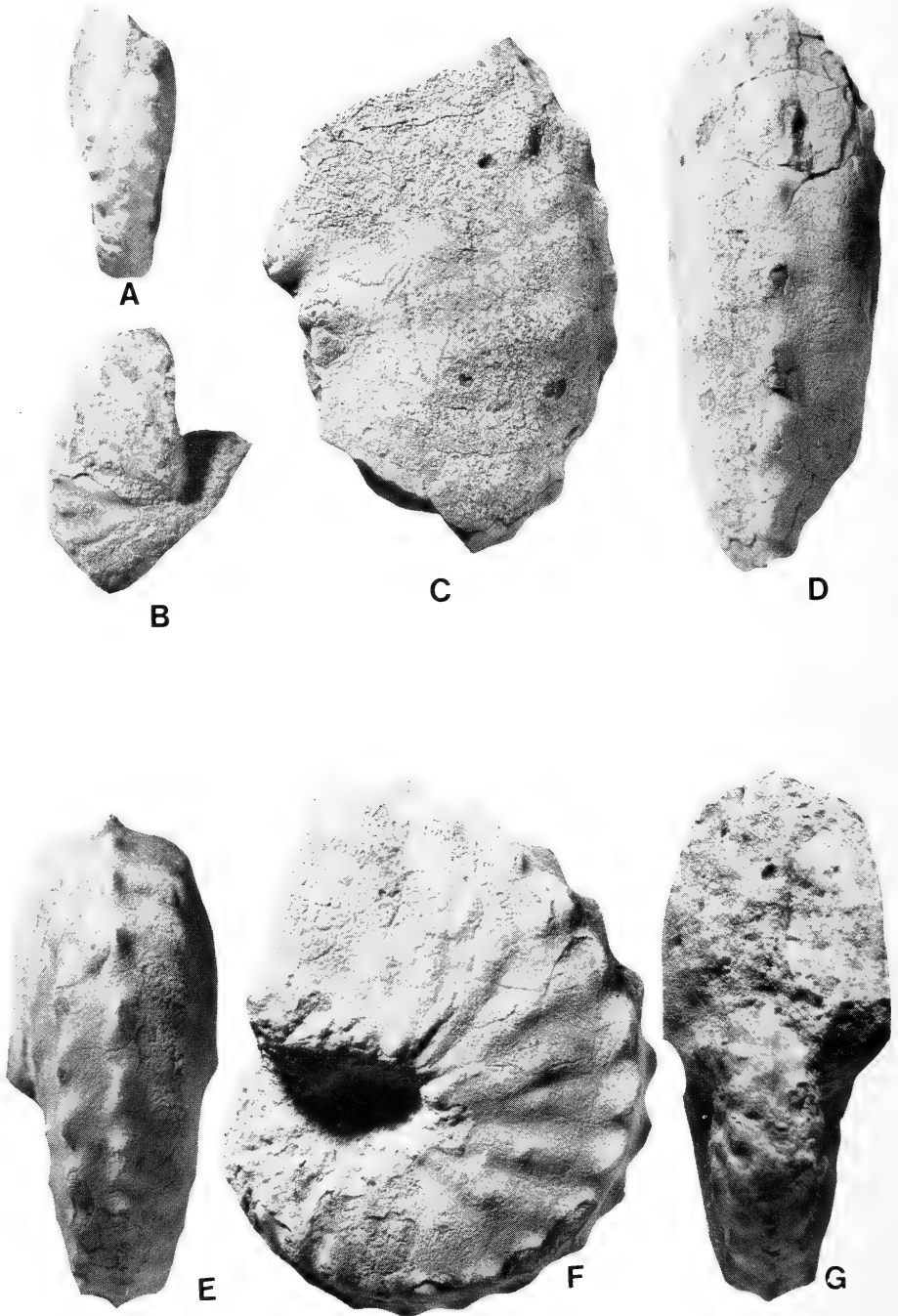
Fig. 8. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAM–D1187H. C–D. SAM–D1187F. E–G. SAM–D1187G. All ×1.

of *Barroisiceras*. *B. forresteri* differs chiefly in its fewer ribs and nodes'. It is believed that the types of *F. (F.) forresteri* and *F. (F.) alluaudi* are so similar that they cannot be separated specifically, as discussed below.

Subsequent accounts of *Forresteria (Forresteria)* have been hampered by the small number of specimens generally available and as a result numerous species, subgenera, and genera have been introduced for a range of ammonites that the large Zululand collections described here suggest belong to no more than a single species.

Initial discussion is restricted to the type material only. The holotype of *F. (F.) forresteri* occurred with a compressed ammonite of similar size and ornament, described by Reeside (1932: 16, pl. 4 (figs 4–8)) as *Barroisiceras (Alstadenites) sevierense* (the holotype, and only specimen described, is illustrated here, Fig. 14A–D), and an even more compressed, involute and feebly ornamented species, also represented by only one specimen and described by Reeside as *Barroisiceras (Harleites) castellense* Reeside (1932: 19, pl. 6 (figs 1–5) (see Fig. 7D–F herein). These three species, referred to three subgenera, in fact represent no more than variable juveniles of a single species, as W. A. Cobban has demonstrated to the authors on the basis of his unpublished new collections. Furthermore, the new American material shows that *Barroisiceras (Forresteria) stantoni* Reeside (1932: 17, pl. 7 (figs 1–7)) is yet a further variant of the same species (Figs 15A–B, 35C–E).

This same variablity of nuclei is confirmed by the South African material described here. Not only do no two nuclei match, but the same range from compressed '*castellense*' forms (e.g. Fig. 7A–C) through feebly ribbed (e.g. Fig. 11A–B) to depressed spinose juveniles (e.g. Fig. 11C–N) can be demonstrated.

Medium sized and large individuals preserve this same wide variation, and the type material of *Basseoceras* van Hoepen, 1968*b* (type species *Basseoceras krameri* van Hoepen, 1968*b*: 164, pl. 7, (fig 2b–g), *non Basseoceras* Collignon, 1965) corresponds to the slender variant with feeble ornament, while *Collignonella* van Hoepen, 1957 (= *Collignoniceras* van Hoepen, 1955, type species *Collignoniceras hammersleyi* van Hoepen, 1955: 361, figs 7–9, *non* Breistroffer 1947) is no more than a large adult of the coarsely ornamented, stout-whorled form (Figs 16A–C, 17A–C).

Size apart, there are no significant or diagnostic differences between this adult and the holotype and only described specimen of *Eedenoceras* van Hoepen, 1968*b* (type species *Eedenoceras multicostatum*, van Hoepen 1968*b*: 171, pl. 12, text-fig. 4b) (re-illustrated here as Figs 12A–B, 13E); it is also a synonym of *Forresteria (Forresteria)*.

Although specifically separable from *F. (F.) alluaudi*, the type species of *Neokanabiceras* Collignon, 1965, *N. madagascariense* Collignon (1965: 42, pl. 432 (figs 1784–1786), including var. *ankinatsyense* (fig. 1787)), is a perfectly good *Forresteria (Forresteria)* as is apparent from Wiedmann's recent re-illustration of the type material (in Herm, Kauffman & Wiedmann 1979: 44, pl. 7A–B, text-figs 7D, 8). There are small umbilical bullae linked by primary ribs
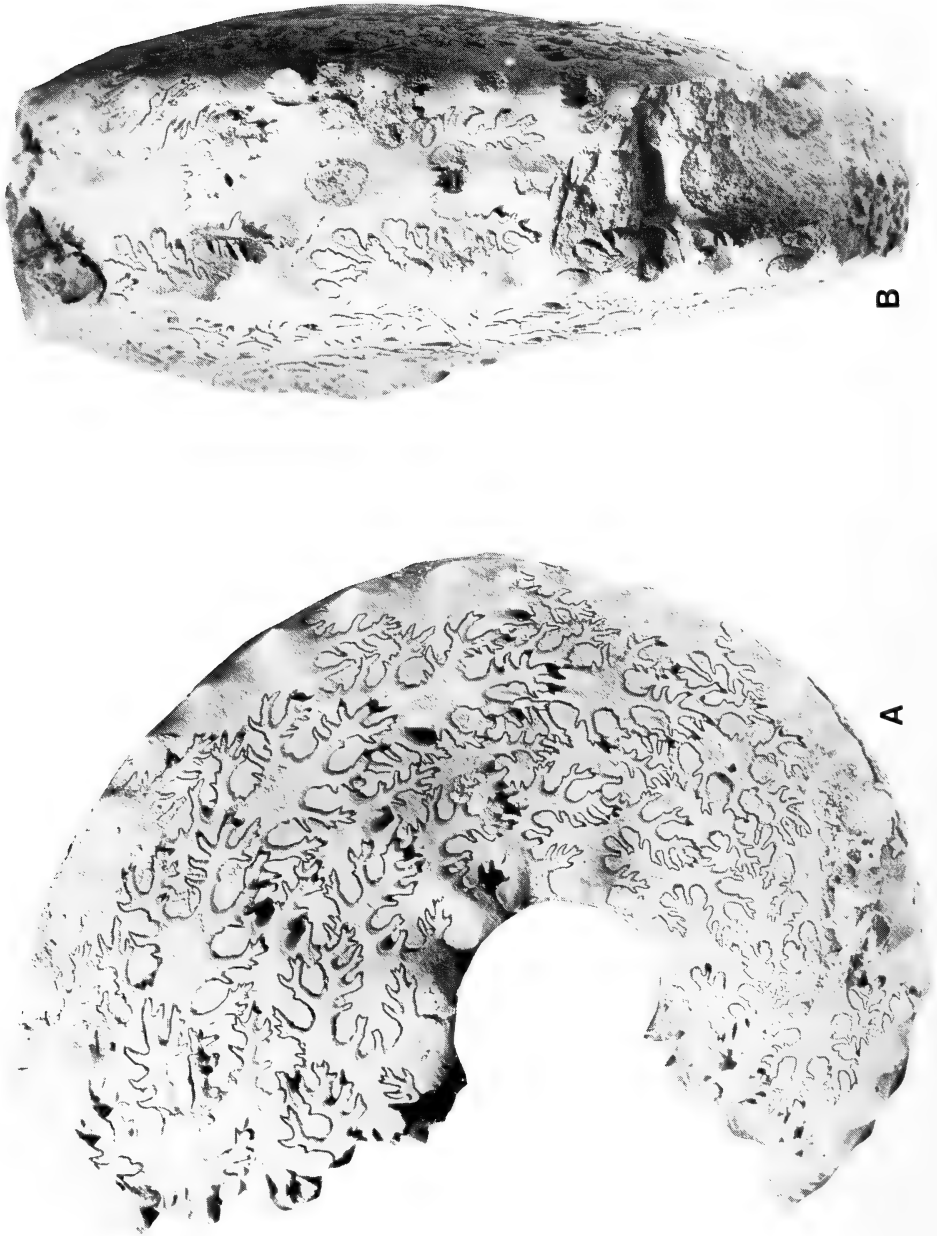
Fig. 9A–B. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). BMNH C8333. ×0,7.

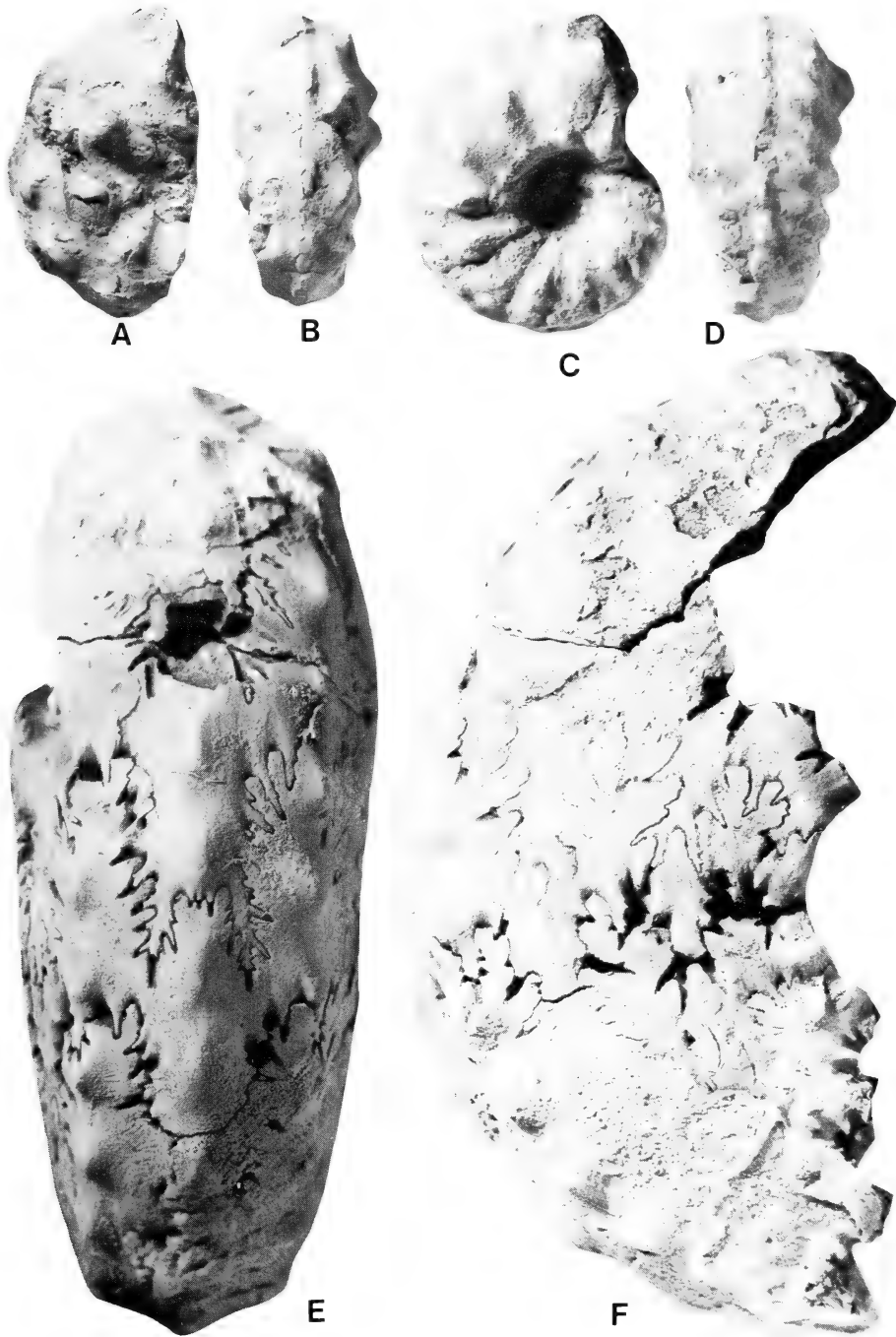Fig. 10. A–B, E–F. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAM–D1187L. E–F. SAM–Z167. C–D. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965). SAM–D1187I. All ×1.
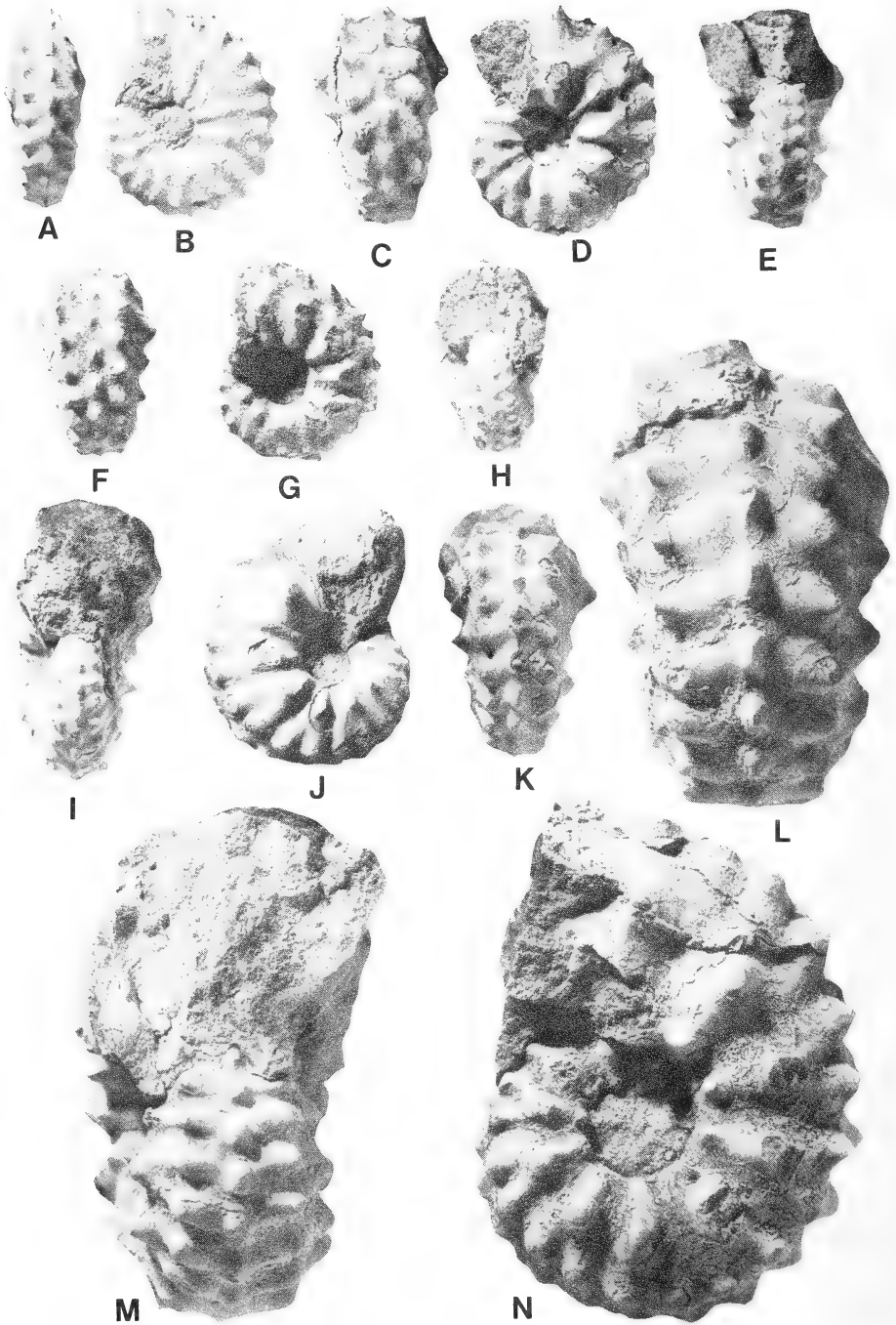
Fig. 11. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z2195. C–E. SAS Z1453A. F–H. SAS Z1453B. I–K. SAS Z1438B. L–N. SAS Z946. All ×1.

to massive lateral nodes that give rise to pairs of ribs linking to ventral clavi, exactly as in *Forresteria*; the only difference appears to be that the siphonal clavi are raised on a low siphonal keel. Several specimens of *F. (F.) alluaudi* that have been examined show this feature developed weakly at some stage in ontogeny (e.g. Fig. 13A–B): it is regarded here as no more than a specific difference.

Zumpangoceras Basse, 1947 (type species *Zumpangoceras burckhardti* Basse, 1947: 144) was based on the ammonites described by Burckhardt (1919: 99–108) as *Barroisiceras*, and later illustrated by him (1921, pl. 22 (fig. 16), pl. 23 (figs 1–2), pls 24–25). Basse originally thought this to be a subgenus of *Barroisiceras* and noted the very fine ornament—especially the well-preserved growth striae—and the presence of a lateral tubercle. Etayo-Serna (1979: 99) has designated the original of Burckhardt (1921, pl. 23 (fig. 1)) lectotype of the species. This is a large fragment with lateral (+ ?umbilical) tubercles and more numerous ventral and siphonal clavi linked by ribs and dense growth striae. It appears to be a fragment of a typical *Forresteria (Forresteria)*, so that *Zumpangoceras* also falls into synonymy.

Harleites Reeside, 1932, type species by original designation *Barroisiceras haberfellneri* var. *harlei* de Grossouvre (1894: 56, pl. 2 (figs 2, 7–8)), is based on specimens from the basal Coniacian of the Dordogne, France, now preserved in the collections of the Sorbonne, Paris. This was originally described as a subgenus of *Barroisiceras*, but Basse (1947) noted the presence of a tiny umbilical and inner lateral tubercle on the inner whorls of some of the type material which, taken with the more numerous but feeble ventrolateral and siphonal clavi, led her to treat it as a subgenus of *Forresteria*, a view followed by Wright (1957). Both these authors regarded *Alstadenites* Reeside, 1932 (type species, herein designated, *Ammonites alstadenensis* Schlüter, 1876: 151, pl. 40 (figs 13–16); lectotype, herein designated, the original of Schlüter's pl. 40 (figs 13–16)) as a synonym, a view followed here (indeed, the type species are probably synonymous).

Matsumoto (1969: 327) has, however, afforded *Harleites* full generic status (following Parnes 1964: 21) on the basis of the more involute shell and weak lateral ornament with finer, more numerous and more persistent ventrolateral and siphonal tubercles.

As discussed above, the compressed variants of *Forresteria (Forresteria) alluaudi* in both North America and Zululand are *Harleites*-like in morphology; however, what is the position of the type species?

Re-examination of De Grossouvre's material shows that the large, almost smooth holotype of *H. harlei* (e.g. De Grossouvre 1894, pl. 2 (fig. 2)) shows no trace of tubercles on the earliest part of the outer whorl (in part, perhaps, due to abrasion), but weak umbilical bullae appear on the body chamber (the specimen is septate to a diameter of approximately 60 mm). The same is true of the smaller paratype (De Grossouvre 1894, pl. 2 (fig. 8)), but there are specimens such as that figured in De Grossouvre's pl. 2 (fig. 7) that have an

Fig. 12. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of 'Eedenoceras multicostatum' van Hoepen, 1968, SAS Z972. C–D. SAS Z591. E–F. SAS Z591. A–B ×0,75; C–F ×1.
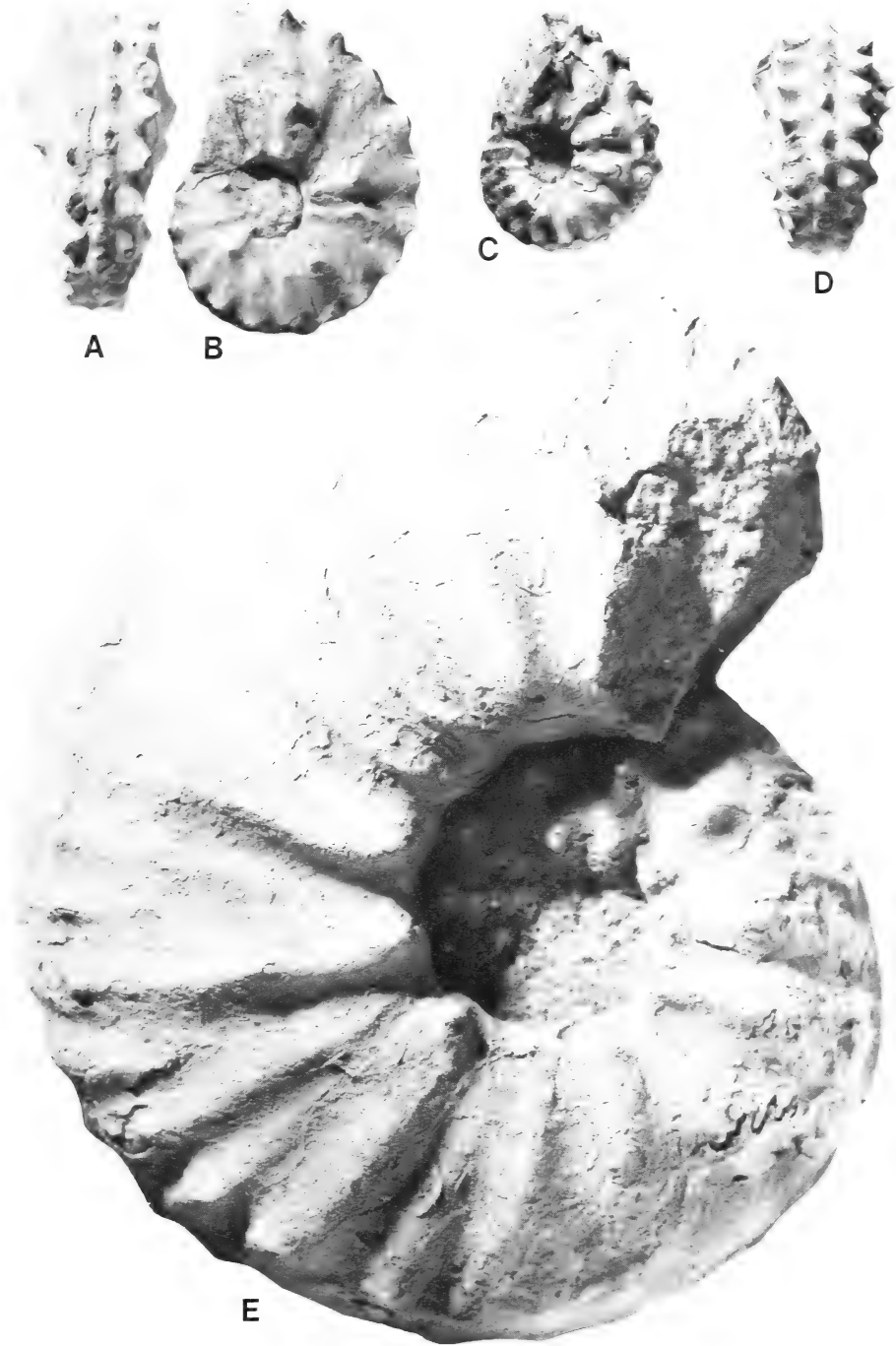
Fig. 13. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z987. C–D. SAS Z1438G. E. Holotype of '*Eedenoceras multicostatum*' van Hoepen, 1968, SAS Z972. All ×1.

Fig. 14. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–D. Holotype of '*Barroisiceras (Alstadenites) sevierense*' Reeside, 1932, USNM 73756, from the Mancos Shale, some 61 m (200 ft) above the Ferron Sandstone, Sevier County, Utah. E–H. Holotype of '*Barroisiceras (Forresteria) forresteri*' Reeside, 1932, from the same locality and horizon as the original of Figure 14A–D. All ×2.

early stage (up to 25 mm) with tiny umbilical and stronger lateral tubercles before the smooth *harlei* stage. These connect via specimens such as De Grossouvre's var. *alstadenensis* (1894, pl. 2 (fig. 4)) to the variable but strongly ribbed and tuberculate phragmocones of typical *Ammonites petrocoriensis* Coquand (1859: 995) (= *Reesideoceras gallicum* Basse, 1947: 133), the type species of *Reesideoceras* Basse, 1947. The largest French *Harleites* described retain a sharp fastigiate venter with distinct ventral and siphonal clavi to the beginning of the adult body chamber, with renascent umbilical bullae, as noted above. Unfortunately the venter of the holotype of *harlei* is damaged so that the mature venter is not recognizable. According to the figure of Schlüter (1876, pl. 40 (fig. 14)), the lectotype of *H. alstadenensis* shows persistent ventrolateral clavi with a broadly arched flattened venter. In the largest known *Reesideoceras petrocoriensis* (De Grossouvre 1894, pl. 1 (fig. 2)) the siphonal clavi are lost at the beginning of the body chamber and the ventral clavi are raised above a flattened venter, with all tubercles lost on the last quarter whorl.

It is concluded that the types of *Harleites harlei* lie in the same relationship to the type of *Reesideoceras petrocoriense* and other comparably ribbed specimens, as does the holotype of *Harleites castellense* to the holotype of *Forresteria forresteri* (= *alluaudi*) in the United States, or *Basseoceras krameri* to *Forresteria alluaudi* in South Africa. *Reesideoceras* is thus a synonym of *Harleites*, the type species of the latter being *Ammonites petrocoriensis* Coquand, 1859 = *Ammonites alstadenensis* Schlüter, 1876, = *Barroisiceras haberfellneri* de Grossouvre, 1894 (*non* von Hauer) (including varieties *harlei* and *alstadenensis* but not *desmoulinsi* de Grossouvre) = *Reesideoceras gallicum* Basse, 1947.

Harleites (= *Reesideoceras*) is regarded as a subgenus of *Forresteria*, distinguished from *F. (Forresteria)* on the basis of smaller adult size, fusion of mediolateral and umbilical tubercles, and early loss of siphonal clavi leaving a flat or concave venter on the body chamber, on the latter parts of which the ventral clavi may also disappear.

We are not sure how many of the *Harleites* species described by previous authors are referable to the subgenus as interpreted here; Japanese and Madagascan examples may well be no more than compressed and feebly ornamented variants of *F. (Forresteria)*.

Because *F. (Forresteria)* and *F. (Harleites)* have very different geographical distributions the present authors do not believe them to be macro- and microconchs.

Forresteria (Muramotoa) Matsumoto, 1969, type species by original designation *F. (M.) yezoensis* Matsumoto (1969: 317, pl. 42 (figs 1–2), text-figs 8–9) is based on three specimens only from the Coniacian of Hokkaido, Japan. The inner whorls are identical in style and proportions to those of *F. (Forresteria)*, but the ornament is rapidly lost at maturity, leaving a body chamber smooth but for a faintly serrated siphonal ridge. The holotype of the type species is
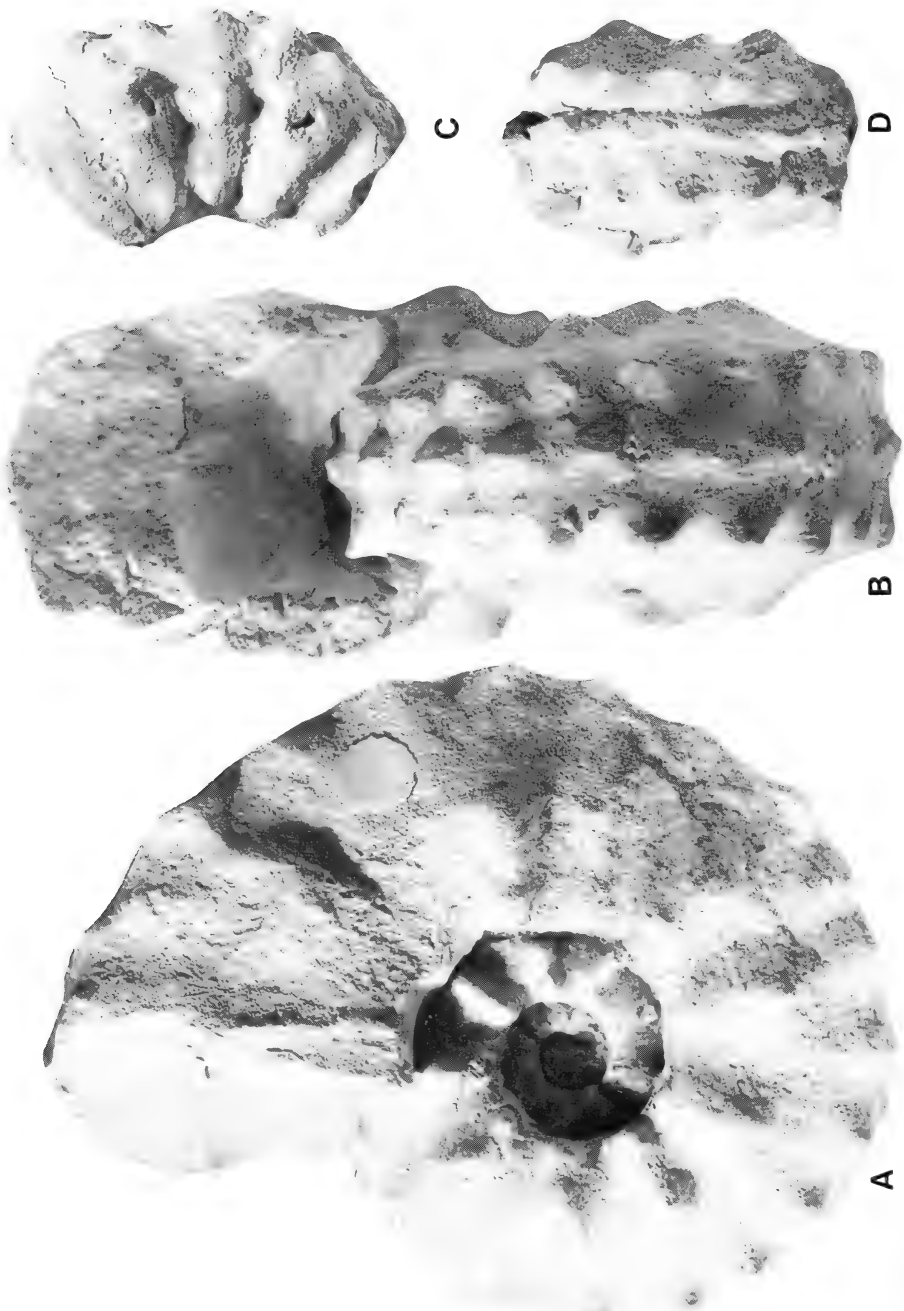
Fig. 15. A–B. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Barroisiceras (Forresteria) stantoni*' Reeside, 1932, USNM 73761, from the Frontier Formation, south-east of Lander, Wyoming. C–D. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965), SAS Z1187F. All ×1.
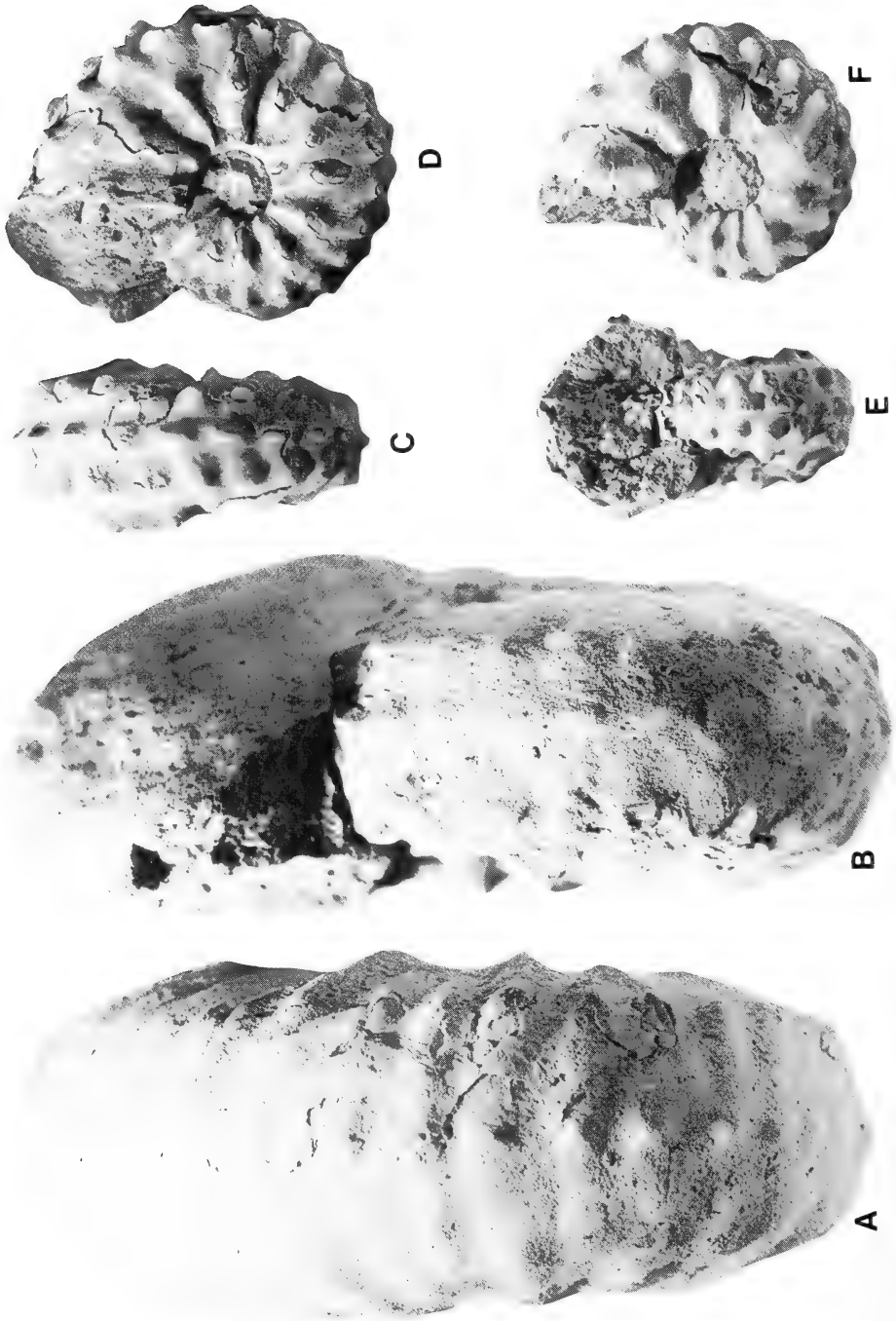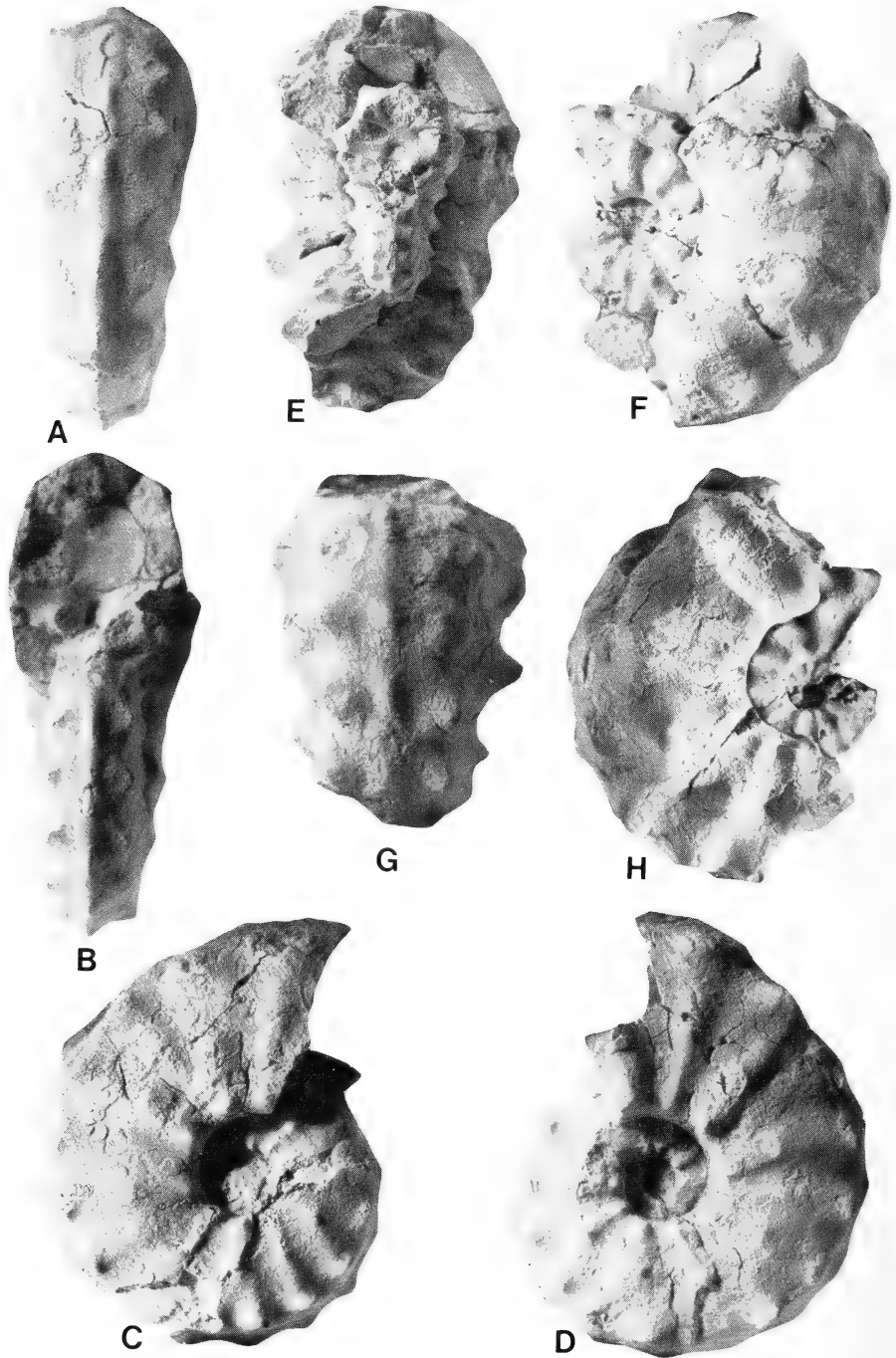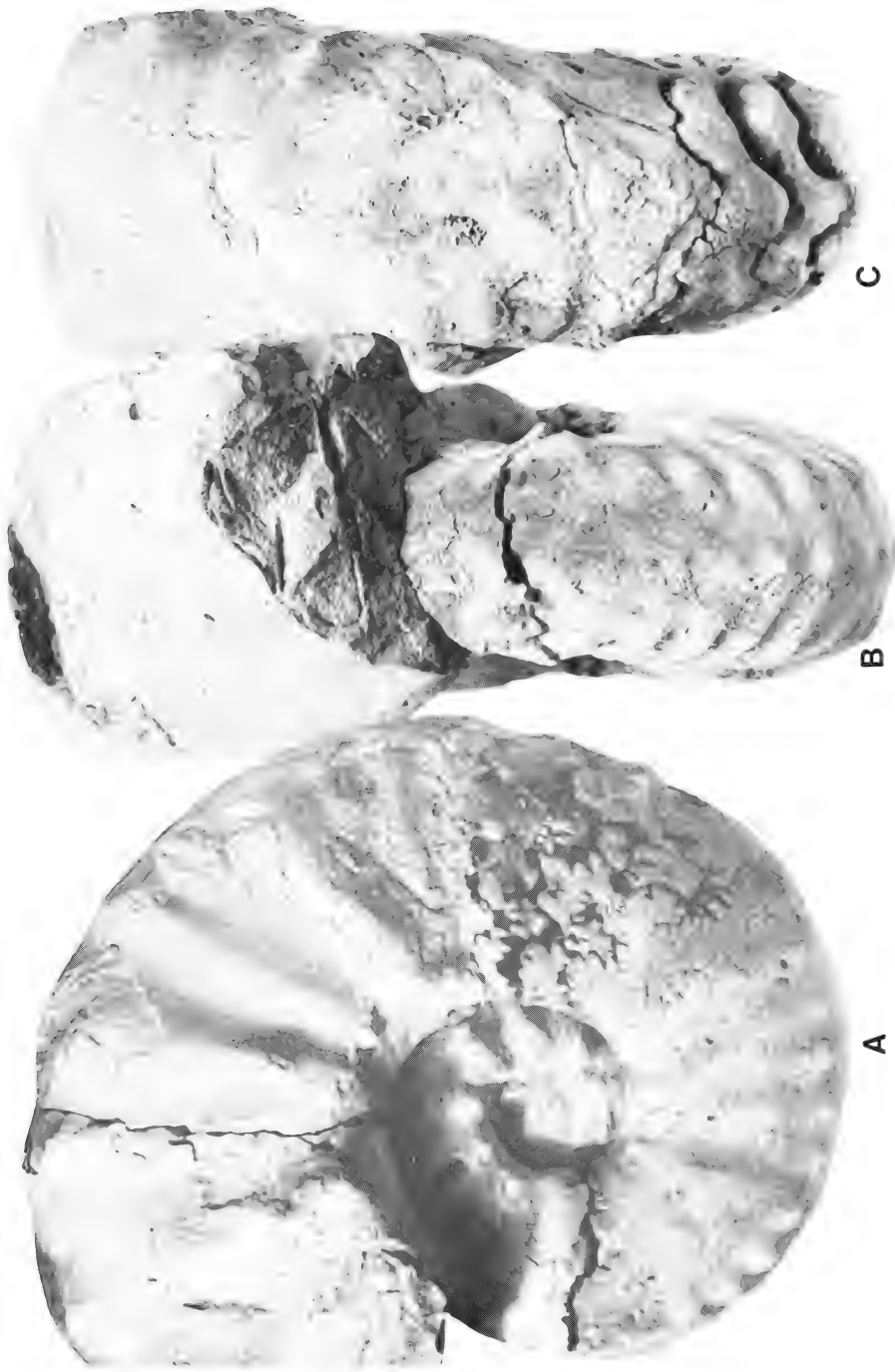
Fig. 16. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Collignoniceras hammersleyi*' van Hoepen, 1955, SAS Z16. ×0.5.

Fig. 17. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of the holotype of '*Collignoniceras hammersleyi*' van Hoepen, 1955, SAS Z16. ×1.

only 75 mm in diameter and the second Japanese species, *F. (M.) muramotoi* Matsumoto (1969: 320, pl. 43 (fig. 1), text-fig. 11), is equally diminutive.

If adult, *Forresteria (M.) yezoensis* and *F. (M.) muramotoi* may represent a specialized micromorph offshoot of *F. (Forresteria)*. That no such specimens are known outside Japan again suggests them to be micromorph, rather than microconch.

We cannot agree with Matsumoto (1969) that *Basseoceras* van Hoepen, 1968 (*non* Collignon, 1965) is a synonym of *Muramotoa*. The type species *Basseoceras krameri* retains ventrolateral and siphonal clavi to a large size and is simply a feebly ribbed, tuberculate compressed and involute variant of *F. (F.) alluaudi*.

Forresteria (Forresteria) is easily distinguished from genera such as *Barroisiceras* de Grossouvre, 1894 (and subgenera), *Pseudobarroisiceras* Shimizu, 1932, and *Niceforoceras* Basse, 1948, on the basis of the presence of strong lateral tubercles.

Solgerites Reeside, 1932 (= *Piveteauoceras* Basse, 1947) may have lateral tubercles, but the body chamber becomes rounded with persistent siphonal clavi in some, or strong ventrolateral nodes. It could represent a derivative of *F. (Forresteria)* of the *hobsoni* group but, not having good material for study, the position of the genus is unclear to the present authors.

Occurrence

Forresteria (Forresteria) is known from the Coniacian of Israel, west Africa, Zululand, Madagascar, Japan, Mexico, Colombia, and the United States (Utah, Colorado and Wyoming).

Forresteria (Forresteria) alluaudi (Boule, Lemoine & Thévenin, 1907)

Figs 5–9, 10A–B, E–F, 11–14, 15A–B, 16–31, 33–34, 35C–E, 40D–E

Acanthoceras (Prionotropis) alluaudi Boule, Lemoine & Thévenin, 1907: 12, pl. 1 (figs 6–7), text-fig. 17.
Prionotropis alluaudi Boule, Lemoine & Thévenin, 1907: Lisson, 1908: 17, pl. 17. Brüggen, 1910: 772. Basse, 1935: 90. Hourcq, 1936: 6.
Barroisiceras (Forresteria) alluaudi (Boule, Lemoine & Thévenin): Reeside, 1932: 12, 14. Benavides-Cáceres, 1956: 478, pl. 61 (fig. 1).
Barroisiceras (Alstadenites) sevierense Reeside, 1932: 16, pl. 4 (figs 4–8).
Barroisiceras (Forresteria) forresteri Reeside, 1932: 17, pl. 5 (figs 2–7).
Barroisiceras (Forresteria) stantoni Reeside, 1932: 17, pl. 7 (figs 1–7), pl. 8 (figs 1–3), pl. 9 (fig. 1).
Barroisiceras (Harleites) castellense Reeside, 1932: 19, pl. 6 (figs 1–5).
Mortoniceras vinassai Venzo, 1935: 88, pl. 7 (fig. 12).
Forresteria alluaudi blt. [*sic*]: Basse, 1947: 128, pl. 8 (fig. 3), pl. 9, (fig. 2).
Forresteria sevierense Reeside: Basse, 1947: 131.
Harleites (?) *castellensis* Reeside: Basse, 1947: 140.
Collignoniceras hammersleyi van Hoepen, 1955: 361, figs 7–9.
Collignoniceras peregrinator van Hoepen, 1955: 364, figs 10–11.
Forresteria (Forresteria) alluaudi Boule, Lemoine & Thévenin: Wright, 1957: L432, fig. 551 (2).
? *Forresteria* cf. *alluaudi* (BLT) [*sic*]: Parnes, 1964: 23, pl. 2 (figs 7–8).
Forresteria alluaudi B.L.Th [*sic*]: Collignon, 1965: 76, pl. 448 (fig. 1828).

Forresteria razafiniparyi Collignon, 1965: 78, pl. 449 (figs 1829–1831).
Forresteria costata Collignon, 1965: 80, pl. 450 (figs 1833–1834).
Basseoceras krameri van Hoepen, 1968: 164, pl. 7, text-fig. 2b–g.
Forresteria hammersleyi (van Hoepen, 1955): van Hoepen, 1968: 166, pl. 8.
Forresteria vandenbergi van Hoepen, 1968: 167, pl. 9, text-fig. 3a–b.
Forresteria itwebae van Hoepen, 1968: 169, pl. 10, text-fig. 3c.
Forresteria reymenti van Hoepen, 1968: 169, pl. 9, text-figs 3d–e, 4a.
Eedenoceras multicostatum van Hoepen, 1968: 171, pl. 12, text-fig. 4b.
Forresteria (Forresteria) alluaudi (Boule, Lemoine & Thévenin, 1907): Matsumoto, 1969: 308, pl. 40 (figs 1–4), text-figs 5–7. González-Arreole, 1977: 171, text-fig. 2f–h.
Forresteria (Forresteria) armata Matsumoto, 1969: 313, pl. 41 (fig. 1), text-fig. 8.
? Zumpangoceras ospinai Etayo-Serna, 1979: 99, pl. 14 (fig. 8), text-fig. 9O–P.

Types

The smaller of the two specimens from Madagascar figured by Boule, Lemoine & Thévenin (1907, pl. 1 (fig. 7), text-fig. 17), is here designated lectotype of the species.

Material

More than a hundred specimens in the SAM, SAS, and BMNH collections, from the St. Lucia Formation, Coniacian II of localities 10, 13, 92, 93, and 145, including the holotypes of *Collignoniceras hammersleyi* van Hoepen, 1955, *C. peregrinator* van Hoepen, 1955, the holotype and syntypes of *Basseoceras krameri* van Hoepen, 1968b, the holotype of *Forresteria vandenbergi* van Hoepen, 1968b, *F. itwebae* van Hoepen, 1968b, *F. reymenti* van Hoepen, 1968b, and *Eedenoceras multicostatum* van Hoepen, 1968b.

Dimensions

		D	Wb	Wh	Wb : Wh	U	ut[1]	vt[2]
SAS Z935, holotype of								
B. krameri	*c*	107,5(100)	41,2(26,1)	54,9(51,1)	0,75	17,8(16,6)		
SAS Z167	*c*	89,3(100)	37,5(42,0)	43,7(48,9)	0,86	19,5(21,8)	?15	23–24
SAS Z1429	*c*	81,2(100)	35,5(43,7)	37,8(46,6)	0,94	17,9(22,0)	12	24–25
SAS Z1437	*c*	74,2(100)	30,7(41,5)	34,6(46,6)	0,89	13,8(18,6)	12	25
	ic	74,2(100)	29,3(39,4)	32,2(43,4)	0,91			
SAS Z978	*c*	93,5(100)	— (—)	45,0(48,1)	—	18,9(20,0)	13/14	26/27
SAS Z987	*c*	43,0(100)	20,8(48,4)	20,2(47,0)	1,03	9,6(22,3)	9	19
	ic		18,0(41,9)	18,5(43,0)	0,97			
SAS Z591		45,4(100)	21,6(47,6)	21,0(47,6)	1,0	10,6(23,3)	13	?23
			18,2(40,1)	19,8(43,6)	0,92			
SAS 1773	*c*	51,3(100)	— (—)	23,0(44,8)	—	13,5(26,3)	—	—
	ic		— (—)	22,3(43,5)	—			
SAS Z1583, larger								
specimen	*c*	44,0(100)	24,0(54,5)	20,6(46,8)	1,16	10,9(24,8)	12	—
	ic		21,4(48,6)	17,9(46,7)	1,20			
SAS Z513	*c*	51,5(100)	33,2(64,5)	23,5(45,6)	1,41	15,3(29,7)	12/13	21/22
	ic		27,7(53,8)	20,2(39,2)	1,37			
SAS Z514	*c*	59,7(100)	36,3(60,8)	26,5(44,4)	1,37	18,3(32,6)	13	—
	ic		31,4(52,6)	23,0(38,5)	1,36			
SAS Z7124	*c*	92,0(100)	51,0(55,4)	42,5(46,2)	1,2	24,5(26,6)	—	—
	ic		41,5(45,1)	40,3(43,8)				
SAS Z1687	*c*	103,0(100)	66,7(64,7)	50,0(48,5)	1,33	31,5(30,6)	9	22
	ic		54,0(52,4)	— (—)				
SAS Z922 holotype of								
F. reymenti	*c*	110,0(100)	— (—)	52,5(47,7)		27,5(25,0)	10	24
	ic		— (—)	50,0(45,5)				
	c	87,3(100)	60,5(69,3)	46,3(53,0)	1,31	23,0(26,3)	—	—
	ic		50,0(57,3)	42,0(48,1)	1,19			

ut^1=umbilical tubercles; vt^2=ventral tubercles

		D	Wb	Wh	Wb : Wh	U	ut^1	vt^2
SAS Z923	c	109,0(100)	39,5(36,2)	50,3(46,1)	0,79	27,5(25,2)	14	26/27
	ic		38,0(34,9)	49,3(45,2)	0,77			
	c	83,5(100)	39,5(47,3)	38,5(46,1)	1,03	19,6(23,4)	—	—
	ic		36,3(43,5)	36,3(43,5)	1,00			
	c	— (—)	30,8(—)	27,5(—)	1,12			
	ic		26,5(—)	25,3(—)	1,05			
SAM–D1187N	c	99,0(100)	41,0(41,4)	43,3(43,7)	0,95	28,0(28,3)	9/10	—
	ic		39,2(39,6)	40,5(40,9)	0,97			
SAS Z972 holotype of								
E. multicostatum	c	140,0(—)	— (—)	64,5(46,0)		36,5(26,1)	13	—
	ic		— (—)	61,5(43,9)				
SAS Z16 holotype of								
F. hammersleyi	c	106,5(100)	60,0(56,3)	52,3(49,1)	1,15	28,5(26,8)	11	24
	ic		56,0(52,6)	48,5(45,5)	1,15			
SAS Z16	c	150,0(100)	76,5(51,0)	— (—)	—	39,0(26,0)	12	28
	ic		70,5(47,0)	— (—)	—			
	c	230,0(—)	106,0(46,0)	102,3(44,3)	1,04	65,0(28,2)	13/14	32/33
	ic		96,0(41,7)	100,0(43,5)	0,96			

ut^1 = umbilical tubercles; vt^2 = ventral tubercles

Description

Previous accounts of *Forresteria (Forresteria) alluaudi* and other species have been based on small numbers of specimens, and a number of species are based on single specimens. Over a hundred specimens were available, all from a narrow stratigraphic interval and, in a number of cases, associated specimens from single lines of concretions. These show that *F. (F.) alluaudi* is variable in the extreme, and that there is widespread co-variance between depth and relative diameter of umbilicus, whorl height, and strength and rate of disappearance of ornament. On the basis of this material the authors place in synonymy all the previously named South African *Forresteria*, all those described from Madagascar (except *F. (F.) madagascariensis* previously referred to *Neokanabiceras*), plus a number of other Japanese and North American forms.

The compressed, involute, feebly ornamented members of the species are represented by specimens formerly referred to as *Basseoceras krameri* van Hoepen. All specimens studied here are wholly septate juveniles. The smallest specimen seen is SAS Z2195 (Fig. 11A–B), which retains some body chamber and has about twelve primary ribs per whorl, corresponding to twenty-two ventral clavi. The whorl section is compressed with a breadth to height ratio of 0,72, the greatest breadth being at the mid-lateral tubercle. This is linked to SAS Z249, which still retains a full complement of ribs and tubercles at a diameter of 61,2 mm.

SAS Z1429 is somewhat stouter, with a breadth to height ratio of 0,87 at a diameter of 82 mm. There are thirteen to fourteen umbilical bullae at this diameter, and twenty-four ventral and siphonal clavi. The flank ornament is beginning to decline, with the lateral tubercle represented by a slight strengthening of the ribs only from about 55 mm onwards.

The holotype of *Basseoceras krameri*, SAS Z935 (Fig. 6), retains the lateral tubercle and feeble ribs at the smallest diameter visible, being only a little more compressed than Z1429. It is wholly septate and so worn that the
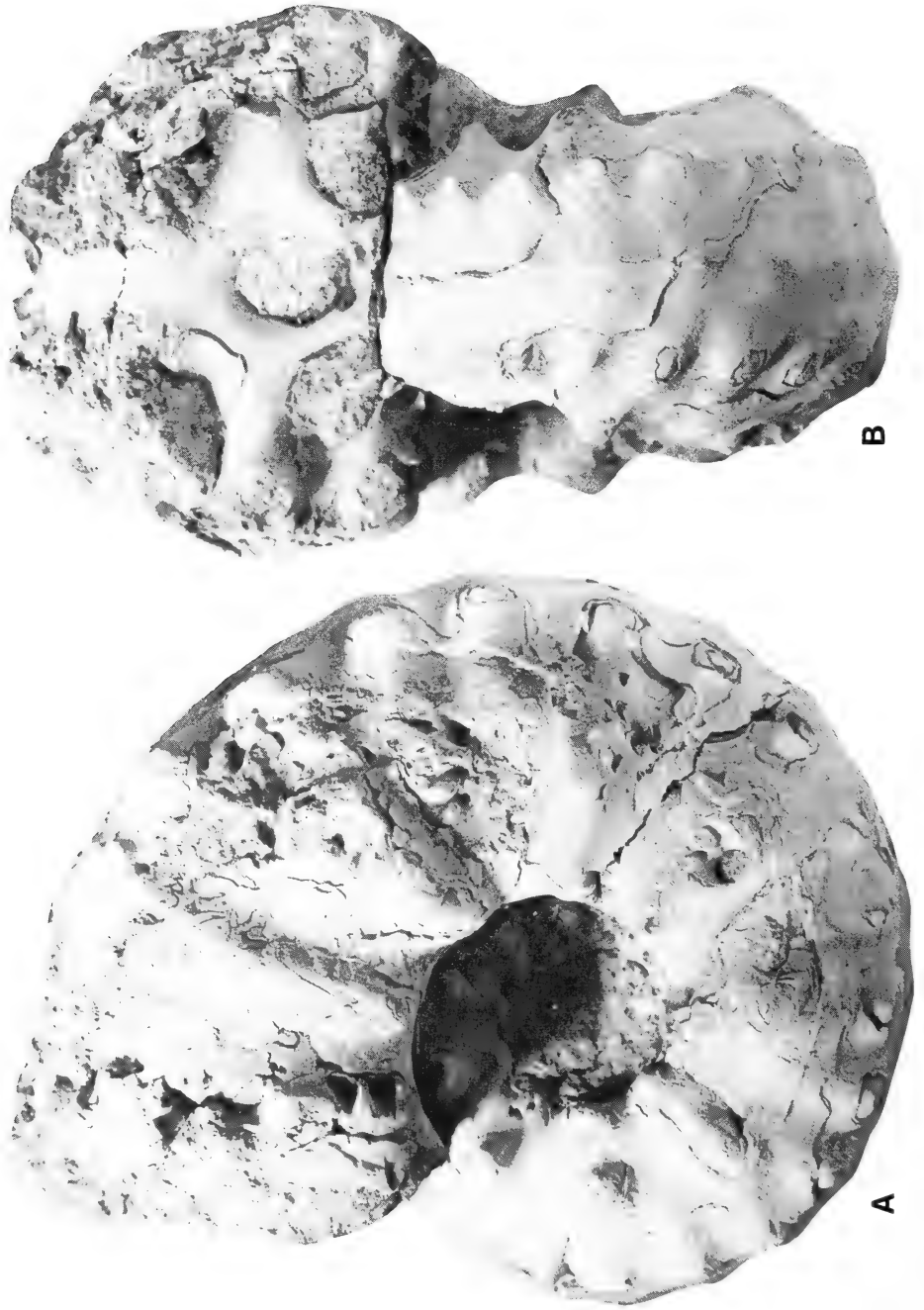
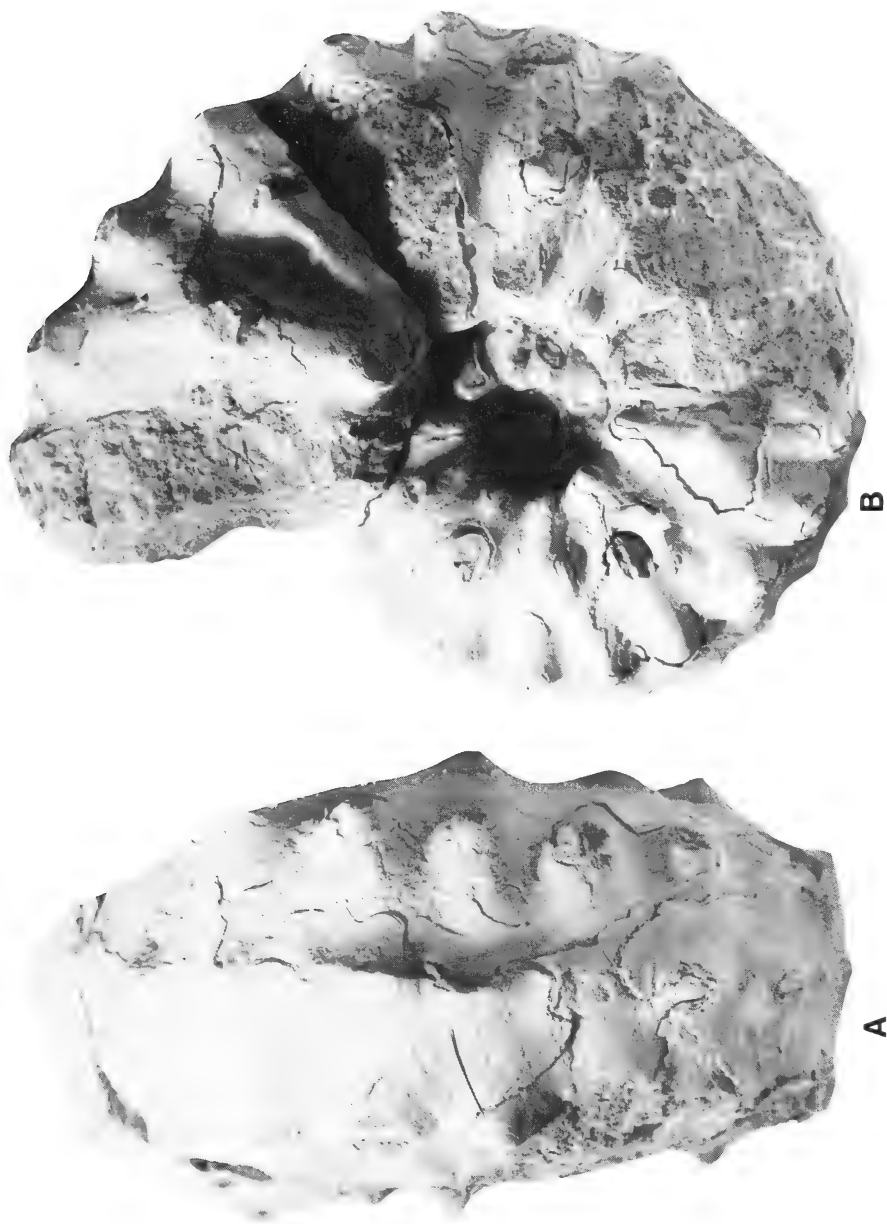Fig. 18. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of stout variant, SAS Z1687. ×1.

Fig. 19. *Forresteria (Forresteria) allaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of 'Forresteria reymenti' van Hoepen, 1968, SAS Z922. ×1.

Fig. 20. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria armata*' Matsumoto, 1969, from the Ikushumbets area of Hokkaido, Kyūshū University Collections H 5621. ×1.

ornament is artificially subdued. Umbilical bullae, ribs, and ventral and siphonal clavi are retained throughout, however, and lateral tubercles might well have originally survived to a larger diameter than at present. This is certainly the case in SAS Z913, a very large, wholly septate fragment with a whorl height of 65 mm that still retains low, broad ribs and subdued mid-laterals (Figure 7G).

Amongst other individuals that are relatively compressed is the figured (Van Hoepen 1968*b*, pl. 6) paratype of *Basseoceras krameri*, SAS Z1437 (Fig. 5A–C), which is strongly ribbed with distinct tubercles to a diameter of 75 mm (costal whorl breadth to height ratio 0,87; intercostal 0,79). SAS Z978 is a rather more evolute specimen, with U = 21 per cent as opposed to 16,6 per cent in the holotype. It is especially well preserved (Fig. 5D–E), retaining aragonitic shell, and is wholly septate. The lateral tubercles are distinct to a diameter of about 60 mm but decline thereafter. SAS Z949 is similar, with stronger decoration to the inner whorls but a similar decline beyond 60–65 mm diameter.

The authors have many small specimens of up to about 50–60 mm diameter that show a progressive increase in strength of ornament with increasing whorl inflation, e.g. SAS Z591 (Fig. 12C–D).

Similar transitions at a somewhat greater diameter—up to 120 mm—link SAS Z976 (Fig. 26), Z969 (Fig. 27), and Z922 (Fig. 19, the holotype of *Forresteria reymenti*).

Within this range of ornament and size fall the types of *Forresteria alluaudi* (Boule, Lemoine & Thévenin), *F. forresteri* (Reeside), *F. razafiniparyi* Collignon and *F. costata* Collignon, all of which can be matched in this series.

There are also specimens that show sparse ribbing—SAS Z1782 (Fig. 21) and the holotype of *F. peregrinator* (van Hoepen) (Fig. 25A–B). Although at first sight appearing distinct, they are simply a further variant of the species and these small individuals match the inner whorls of the large specimens described as *F. vandenbergi* van Hoepen (Fig. 23A–B) and *F. itwebae* van Hoepen (Figs 31, 40D–E). *F. armata* Matsumoto (Fig. 20) is an individual of this type, and also probably a synonym.

With increasing diameter, changes in ornament suggesting the approach of maturity are shown by a number of specimens. SAS Z979 (Fig. 29) and SAS Z923 (Fig. 28) have inner whorls only moderately inflated, ribbed, and tuberculated up to a diameter of about 65 mm, whereafter the whorls become more evolute, lateral tubercles decline, and ribs crowd. This to a degree follows the changes seen in feebly ribbed *Basseoceras krameri* variants. The more inflated holotype of *Eedenoceras multicostatum* van Hoepen (Figs 12A–B, 13E) shows typical strong, inflated inner whorls to a diameter of about 70–80 mm; thereafter the lateral tubercles decline and one or two shorter intercalated ribs become prominent on the last half whorl. This is essentially what is shown by SAS Z923 but with more intercalatories. This is regarded as individual body chamber variation in a small adult.

Contrasting with these specimens that appear adult at 120–160 mm are specimens that remain septate to beyond this diameter; this applies to feebly
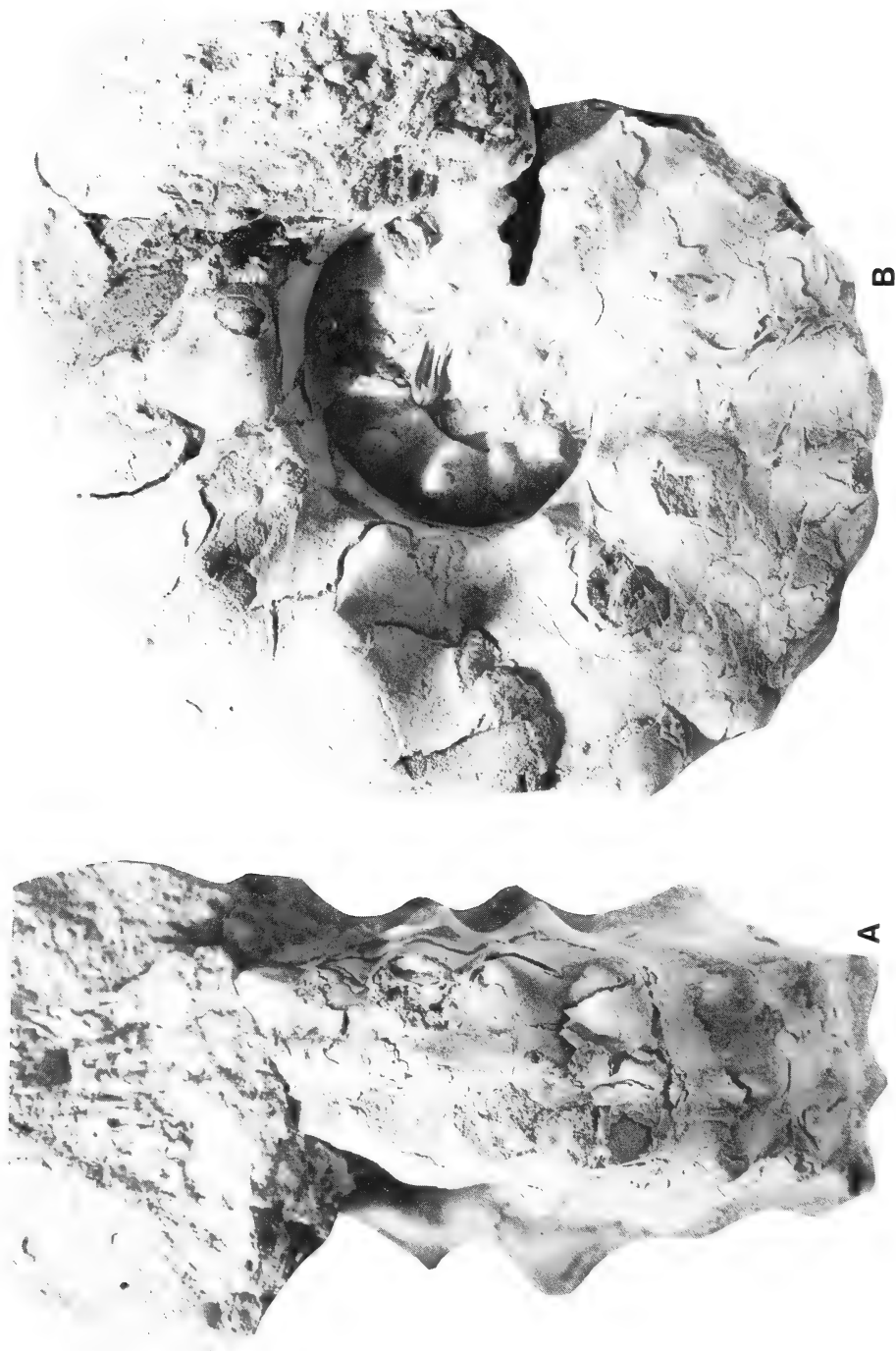
Fig. 21. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z1782. × 1.

ornamented specimens, e.g. SAS Z913, rather compressed and sparsely ribbed individuals, e.g. the type of *Forresteria vandenbergi*, and more inflated and strongly decorated individuals such as SAS Z1981. The most complete of these large adults is the holotype of *F. hammersleyi* (van Hoepen) (Figs 16–17). This shows intercalated ribs, singly or in pairs, as in the smaller adult holotype of '*Eedenoceras*' *multicostatum*, but with traces of the lateral tubercle to the end of the clearly adult body chamber at almost 230 mm diameter.

The sutures are variable, depending on whorl section and position relative to ribs and tubercles, as shown in Figures 33–34.

Discussion

The description given above indicates that all the species originally described from Zululand (*Basseoceras krameri* van Hoepen, *Forresteria hammersleyi*, (van Hoepen), *F. peregrinator* (van Hoepen), *F. vinassai* (Venzo), *F. vandenbergi* van Hoepen, *F. itwebae* van Hoepen, *F. reymenti* van Hoepen, *Eedenoceras multicostatum* van Hoepen, and the Madagascan *Forresteria razafiniparyi* Collignon, *F. costata* Collignon, and *F. alluaudi* (Boule, Lemoine and Thévenin)) can be matched in the present collection and that they are to be treated as no more than variants of a single, apparently dimorphic species, for which the name *F. (F.) alluaudi* has priority. It has been recognized that the North American *F. forresteri* Reeside (1932: 17, pl. 5 (figs 2–7)) (Fig. 14E–H) was also a synonym of *F. (F.) alluaudi*, and this is confirmed by the Zululand material. *F. forresteri* co-occurs with *Barroisiceras (Harleites) castellense* Reeside (1932: 19, pl. 6 (figs 1–5)) (Fig. 7D–F herein) which is a very compressed variant of this species.

Forresteria stantoni Reeside (1932: 17, pl. 7 (figs 1–7); pl. 8 (figs 1–3), pl. 9 (fig. 1)) (Fig. 35C–E herein) is no more than a variant of *F. alluaudi* as is *Barroisiceras (Alstadenites) sevierense* Reeside (1932: 16, pl. 4 (figs 4–8)) (Fig. 14A–D herein). In contrast, *Forresteria hobsoni* Reeside (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)) (Fig. 35A–B herein) is a quite distinct species, discussed further below. It is more evolute and slender-whorled, and shows a development of sparse ventrolateral horns developed by fusion of lateral and ventrolateral tubercles, amongst other differences. *Neokanabiceras madagascariensis* Collignon (1965: 42, pl. 432 (figs 1784–1787)) is regarded here as a distinct species of *Forresteria* only, rather than meriting generic separation. It differs from the variable *F. alluaudi* in being more slowly expanding and in the development of very strong horns from the lateral tubercle with increasing diameter. The horns bear rounded ribs that link them to pairs of rather small transverse or oblique ventrolateral tubercles. The siphonal clavi are borne on a low ridge. It is thus closer to *F. hobsoni*.

Forresteria nwalii (Reyment) (= *Barroisiceras nwalii* Reyment, in Offodile & Reyment 1976: 61, fig. 14a–b), from the Coniacian of Nigeria, the holotype and only known specimen, refigured here as Figure 39, is also a distinct species allied to *F. madagascariensis*. It differs very obviously from

Fig. 22. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z1456. × 1.
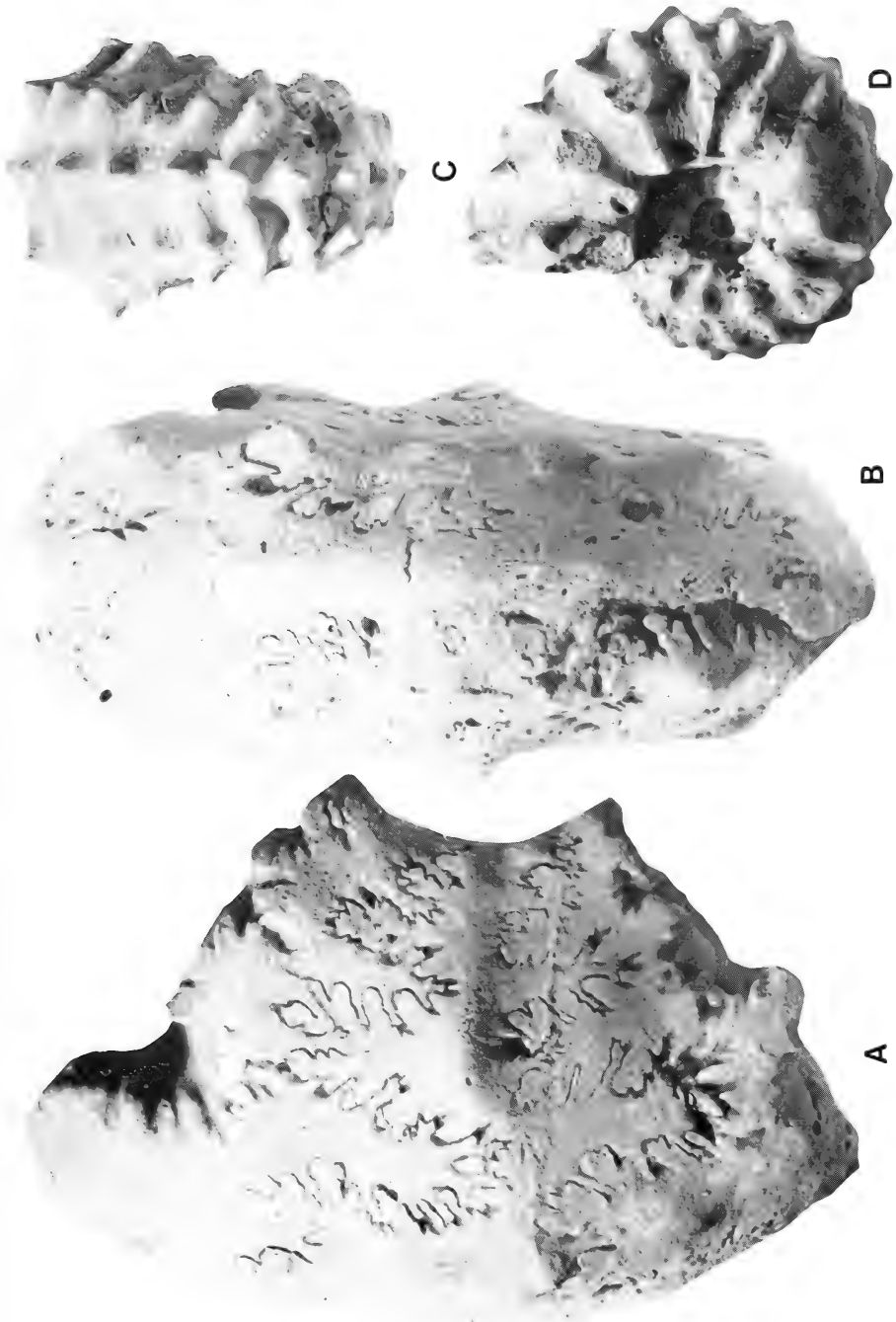
Fig. 23. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of '*Forresteria vandenbergi*' van Hoepen, 1968. SAS Z70. ×0,75. C–D. SAS Z513. ×1.
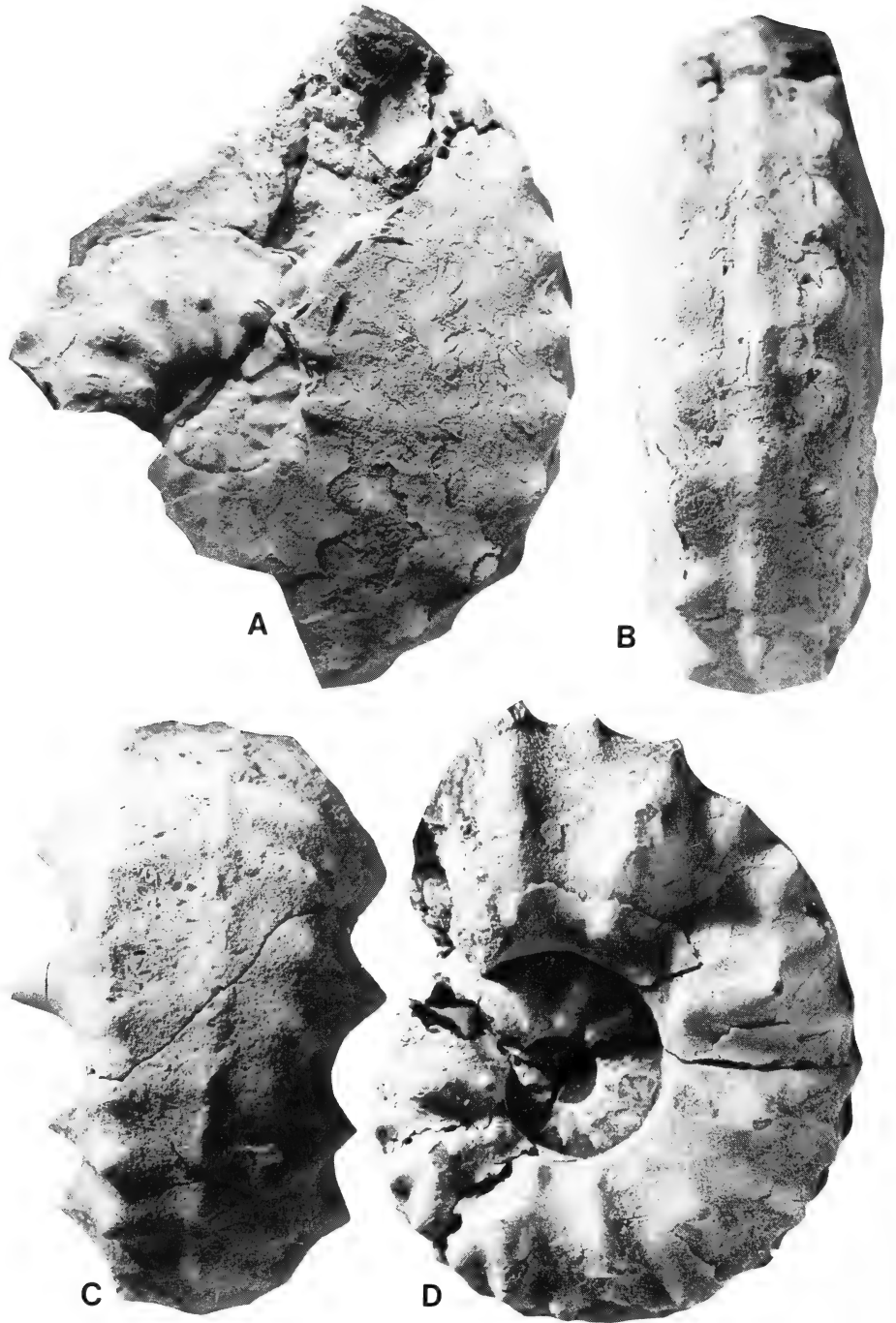
Fig. 24. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z949. C–D. SAS H196/2. All ×1.

F. (F.) alluaudi in developing massive pinched lateral horns that bear looped ribs connecting to ventral clavi and lacks an umbilical bulla (whether the lateral horn develops from the fusion of an umbilical bulla and lateral tubercle on the inner whorls or represents merely the outward migration and accentuation of the umbilical bulla above is not clear, due to artificial carving of ribs on the inner whorl of the type specimen). *F. serrata* Reyment (1955: 69, pl. 15 fig. 3a–b)), from the Coniacian Awgu-Ndeaboh Shales near Enugu, Nigeria, is known from the holotype only, a juvenile 36,5 mm in diameter. The flanks are flattened and subparallel, with a rounded fastigiate venter. Weak umbilical bullae give rise to narrow primary ribs that develop into a bullate tubercle on the ventrolateral shoulder, where they are joined by one or two non-tuberculate intercalatories. The ribs terminate in a blunt ventrolateral bulla separated by a smooth zone from a row of weak siphonal clavi. This ornament is very different from that of most *F. (Forresteria)* species, and is transitional towards *Yabeiceras*.

Reyment (1958: 68, pl. 6 (fig. 1)) referred *Reesideoceras camerounense* Basse, 1947 (= *Barroisiceras haberfellneri* von Hauer var. *alstadenensis* (Schlüter) de Grossouvre of Solger, 1904: 170, pl. 5 (fig. 6), text-figs 56–57) to *Forresteria (Forresteria)*. It appears rather to be a *F. (Reesideoceras)*. The *Forresteria* cf. *allaudi* [*sic*] of Parnes (1964: 23, pl. 2 (figs 7–8)) may belong here or to *F. (F.) peruanum* (Brüggen) (see below); it is crushed. *F. (F.) peruana* (= *Gauthiericeras margae* var. *peruanum* Brüggen, 1910: 720, pl. 27 (fig. 3) = *F. (F.) bassae* Benavides-Cácéres (1956: 477, pl. 58 (fig. 5)) from the Coniacian of South America appears to be a distinctive compressed species, perhaps closer to *F. (F.) hobsoni*. The best representation of this species is by Lüthy (1918: 41, pl. 1 (fig. 2a–b)). It does not find a match in the material here referred to *F. (F.) alluaudi*.

Zumpangoceras ospinai Etayo-Serna (1979: 90, pl. 74 (fig. 8), text-figs 9O, 9P) from Colombia may be a synonym of *F. (F.) alluaudi* but is figured in side view only. *F. (F.) armata* Matsumoto (1969: 313, pl. 41, (fig. 1), text-fig 8) is a clear synonym, as discussed above.

Occurrence

This species characterizes the Coniacian in many areas of the world and is known from Zululand, Madagascar, Japan, Mexico, the United States Western Interior, ? Colombia, Peru, and perhaps Israel. In South Africa it is restricted to Coniacian II of Kennedy & Klinger (1975).

Forresteria (Forresteria) cf. *hobsoni* (Reeside, 1932)

Fig. 32

Compare

Barroisiceras (Forresteria) hobsoni Reeside, 1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2).
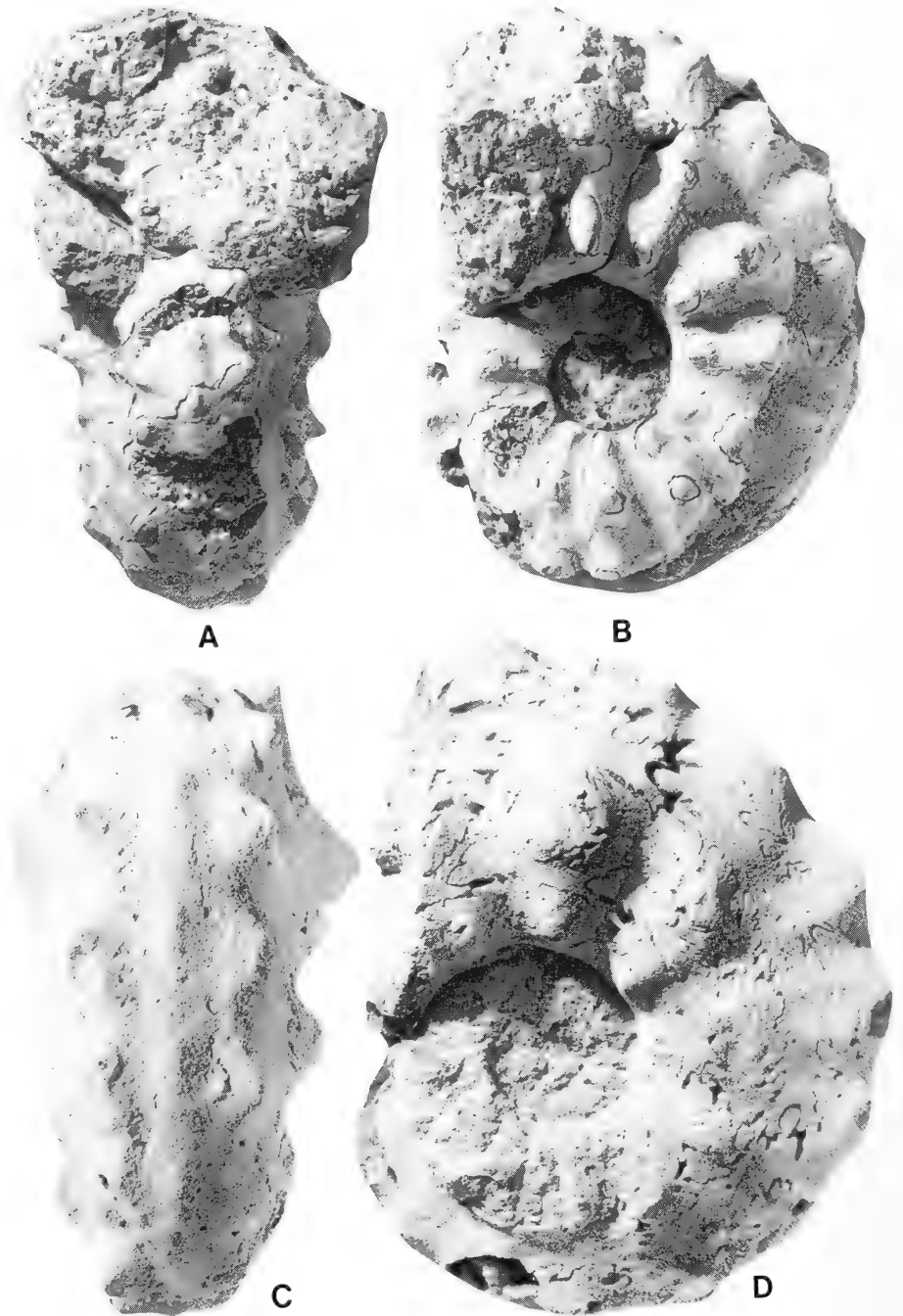
Fig. 25. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of '*Collignoniceras peregrinator*' van Hoepen, 1968, SAS Z18. C–D. SAS Z714. All ×1.

Material

SAM–D1187J, from locality 145 at Morrisvale, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

D	Wb	Wh	Wb : Wh	U
182,0(100)	—(—)	69,5(38,2)	—	65,0(35,7)

Description

This specimen is a worn internal mould retaining traces of recrystallized shell. Approximately two-thirds of the outer whorl is body chamber.

The coiling is very evolute, the umbilicus comprises 35,7 per cent of the diameter and only 20 per cent of the previous whorl is covered. The umbilicus is shallow, the umbilical wall low and vertical. The whorl section is compressed, with an estimated whorl breadth to height ratio of 0,85–0,90, the greatest breadth being at the lateral tubercle in costal section and close to the umbilical shoulder in intercostal section.

There are seventeen primary ribs on the outer whorl. On the first half, which is the best preserved, the low vertical umbilical wall terminates in an abruptly rounded umbilical shoulder bearing small and variably developed umbilical bullae.

From these arise broad and somewhat weak, straight prorsiradiate ribs that extend to mid-flank, where they bear midlateral tubercles that vary irregularly from weak to massive. These give rise to a pair of straight ribs that connect with small obliquely placed ventrolateral clavi from which low, broad ribs sweep forward in a broad chevron, the apex of which is a strong, elongate siphonal clavus.

Similar ornament is locally preserved on the very worn body chamber, where the irregular development of lateral tubercles is especially noticeable.

Where the inner whorls are visible the ribs seem to be relatively stronger and coarser with respect to the tuberculation than on the outer whorls.

The sutures are too worn for useful description.

Remarks

This specimen has closely similar proportions to, and shows the same style of ribbing and tuberculation as, the unique holotype of *Forresteria (Forresteria) hobsoni* (Reeside) (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)) (Fig. 35A–B herein). The latter is more evolute, however, with an outward sloping umbilical wall. To what degree this and other minor differences reflect the different preservations (distorted chalk composite internal mould in *F. (F.) hobsoni*, worn sandstone mould in the African specimen) cannot be ascertained with such limited material, as a result of which the present specimen is identified as *F. (F.)* cf. *hobsoni*. This specimen shows the same style of ornament as the more numerous *F. (F.) madagascariensis* with which it occurs, especially in
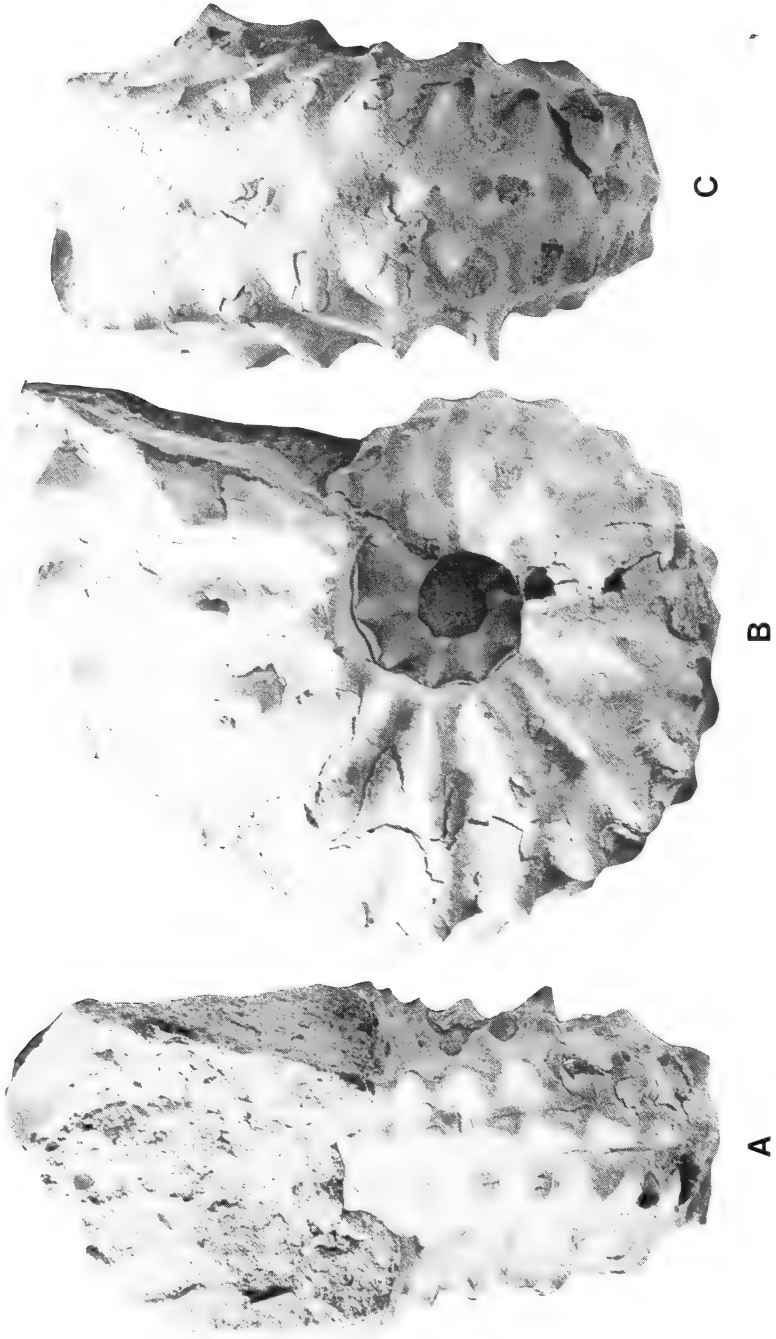
Fig. 26. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria hammersleyi*' van Hoepen, 1968, SAS Z976. ×1.

Fig. 27. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z969. ×1.
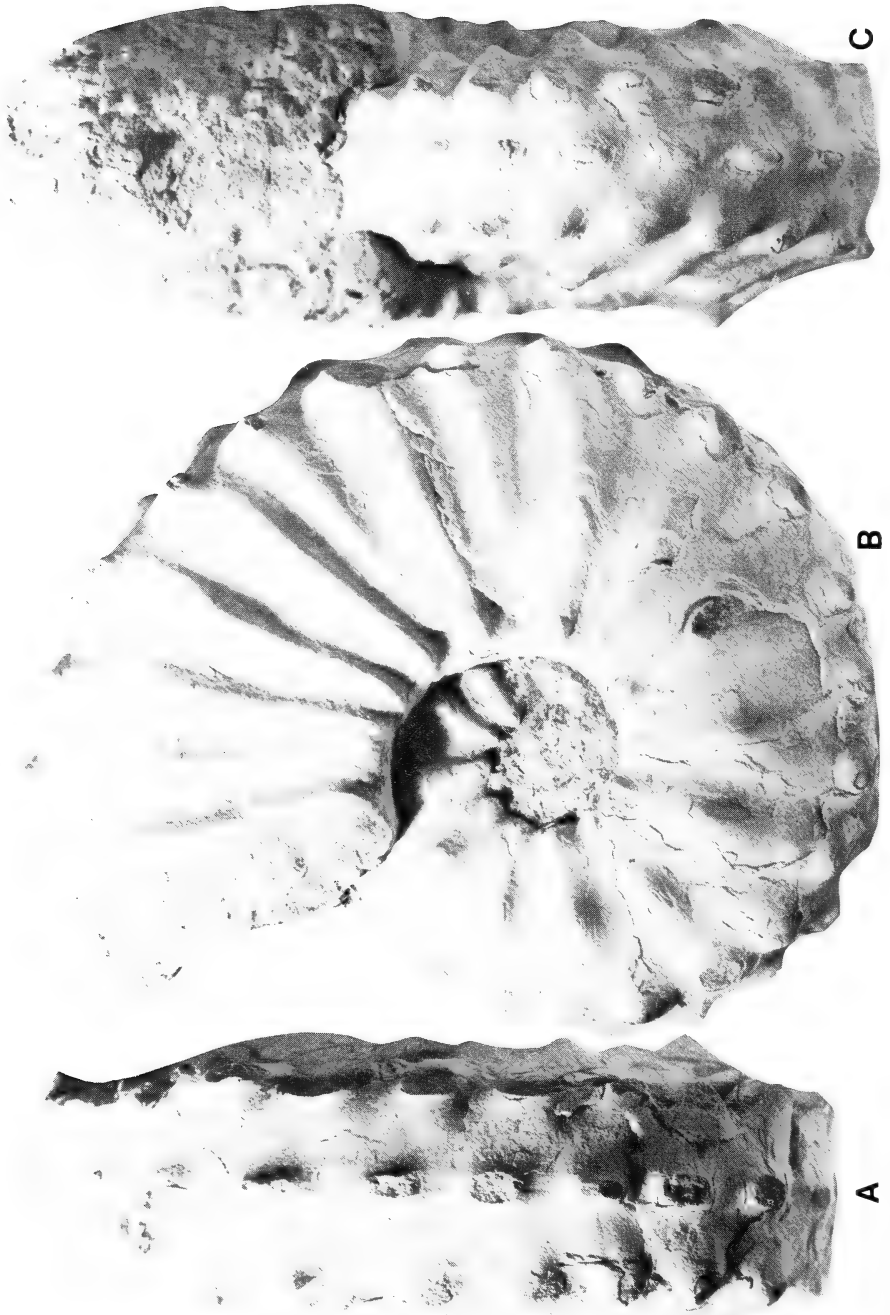
Fig. 28. *Forresteria (Forresteria) allaudi* (Boule, Lemoine & Thévenin, 1907). Adult ?microconch with body chamber, SAS Z923. ×1.

terms of variable lateral tuberculation and ventrolateral ribbing and tubercula-
tion. It may, indeed, be no more than the compressed and relatively weakly
ornamented end of the variation range in the species, but it is not possible to
tell on the basis of the available material; if true, the specific name *hobsoni* has
priority over *madagascariensis*.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Forresteria (Forresteria) madagascariensis (Collignon, 1965)
Figs 10C–D, 15 C–D, 36–38

Neokanabiceras madagascariense Collignon, 1965: 42, pl. 432 (figs 1784–1786, 1787 (var.
    ankinatsyensis)). Wiedmann in Herm, Kauffman & Wiedmann, 1979: 44, pl. 7 (figs A–B);
    text-fig. 7D.
Neokanabiceras apambiense Collignon, 1965: 44, pl. 432 (fig. 1788).

Holotype

The original of Collignon (1965: 42, pl. 432 (fig. 1784)) from the middle
Coniacian Zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of
Ankinatsy (Belo sur Tsiribihina), Madagascar.

Material

SAM–D1187A–I and SAS Z1084A, from 'Pisana', on the Msindusi River,
presumably equivalent to locality 145 of Kennedy & Klinger (1975), St. Lucia
Formation, Coniacian II.

Dimensions

		D	Wb	Wh	Wb : Wh	U
SAM–D1187H	c	43,2(100)	24,3(56,3)	17,8(41,2)	1,37	12,7(29,4)
	ic		20,5(47,5)	15,8(36,6)	1,30	
SAM–D1187I	c	43,9(100)	27,7(63,0)	18,9(43,0)	1,47	11,8(26,9)
SAM–D1187D	c	93,0(100)	50,5(54,3)	36,0(38,7)	1,40	32,3(34,7)
	ic		39,3(42,3)	34,2(36,8)	1,15	
at D =	c	78,5(100)	46,2(58,9)	30,0(38,2)	1,54	28,3(36,1)
	ic		35,8(45,6)	27,8(35,4)	1,29	
SAM–D1187C	c	105,5(100)	—(—)	41,7(39,5)	—	36,1(34,2)
		128,0(100)	68,8(53,8)	50,0(39,0)	1,38	41,2(32,2)
			54,5(42,6)	46,8(36,6)	1,16	

Description

All the available specimens are internal moulds retaining traces of shell.
The largest, SAM–D1187A, is still septate at a diameter of 130 mm.
    The earliest visible stages are shown by SAM–D1187I (Fig. 10C–D). The
coiling is evolute, with a deep umbilicus (26–34 % of diameter). The whorl
section is depressed, coronate (whorl breadth to height ratio is 1,3 to 1,4 in
intercostal, and 1,37 to 1,47 in costal section) the maximum breadth at the
massive lateral tubercles in costal section and low on the flank in intercostal

Fig. 29. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z979. ×1.

Fig. 30. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A pathological body chamber, SAS Z977. ×1.

Fig. 31. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of 'Forresteria itwebae' van Hoepen, 1968, SAS Z250. ×1.

section. Twelve or thirteen strong, broad, rounded ribs arise at the umbilical seam. They develop umbilical bullae of variable strength and pass slightly prorsiradiate across the flanks to massive conical mid-lateral tubercles. These give rise to a pair of straight or feebly concave ribs that link to strong oblique ventral clavi twice as numerous as the lateral tubercles. These in turn give rise to weaker, broad prorsiradiate ribs that form a chevron over the venter with a strong siphonal clavus at the apex of the 'V'.

Even at this diameter there is great variation in the relative strengths of tubercles and ribs, the former dominating in SAM–D1187G, the latter in SAM–D1187I.

Two slightly larger fragments, SAM–D1187E and F, show essentially similar ornament at estimated diameters of 70 mm; SAM–D1187E (Fig. 36A–B) shows the beginning of differentiation in strength of the lateral tubercles, every fourth one of which is much stronger than the others, while SAM–D1187F has shell preserved on sharp, high siphonal clavi (Fig. 15C–D).

SAM–D1187D shows the ornamentation at a diameter of 93 mm. There are twelve to thirteen strong ribs per whorl, bearing weak to strong umbilical bullae that link to variable strong to massive lateral tubercles. These give rise to pairs of strong ribs linking to strong ventral clavi from which weaker, broad ribs form a chevron linking to the strong, sharp siphonal clavi.

SAM–D1187D (Fig. 36C–D) is a comparable specimen with approximately 110 mm diameter. The style of ornament on the first half of the outer whorl is similar, if less hypernodose, while on the outer whorl ribbing is relatively better developed with respect to the tubercles. Both these specimens and SAM–D1187B, a rather poorly preserved individual, also show occasional primary ribs without umbilical bullae or lateral tubercles. The largest specimen, SAM–D1187A (Fig. 37A–B), maintains the same style of ornament described above, with thirteen strong, tuberculate primary ribs per whorl.

The suture line is incompletely exposed on SAM–D1187C only. E/L is elongate, rectangular, little incised, and asymmetrically bifid, L is narrow and deep.

Discussion

The specimens referred to this species vary greatly in proportions and relative development of ribs and tubercles, but are linked by coronate form, sparse primary ribs, massive, if variable lateral tubercles, paired outer flank ribs, and ventral and siphonal clavi. They match closely with the types of *Neokanabiceras madagascariense* Collignon (1965: 42, pl. 432 (figs 1784–1786)) and encompass the predominantly ribbed var. *ankinatsyensis* Collignon (1965: 43, pl. 432 (fig. 1878)). The authors have little doubt that, given a somewhat larger collection, *Neokanabiceras apambiense* Collignon (1965: 43, pl. 432 (fig. 1788)) would prove to be no more than a very depressed variant of this species.
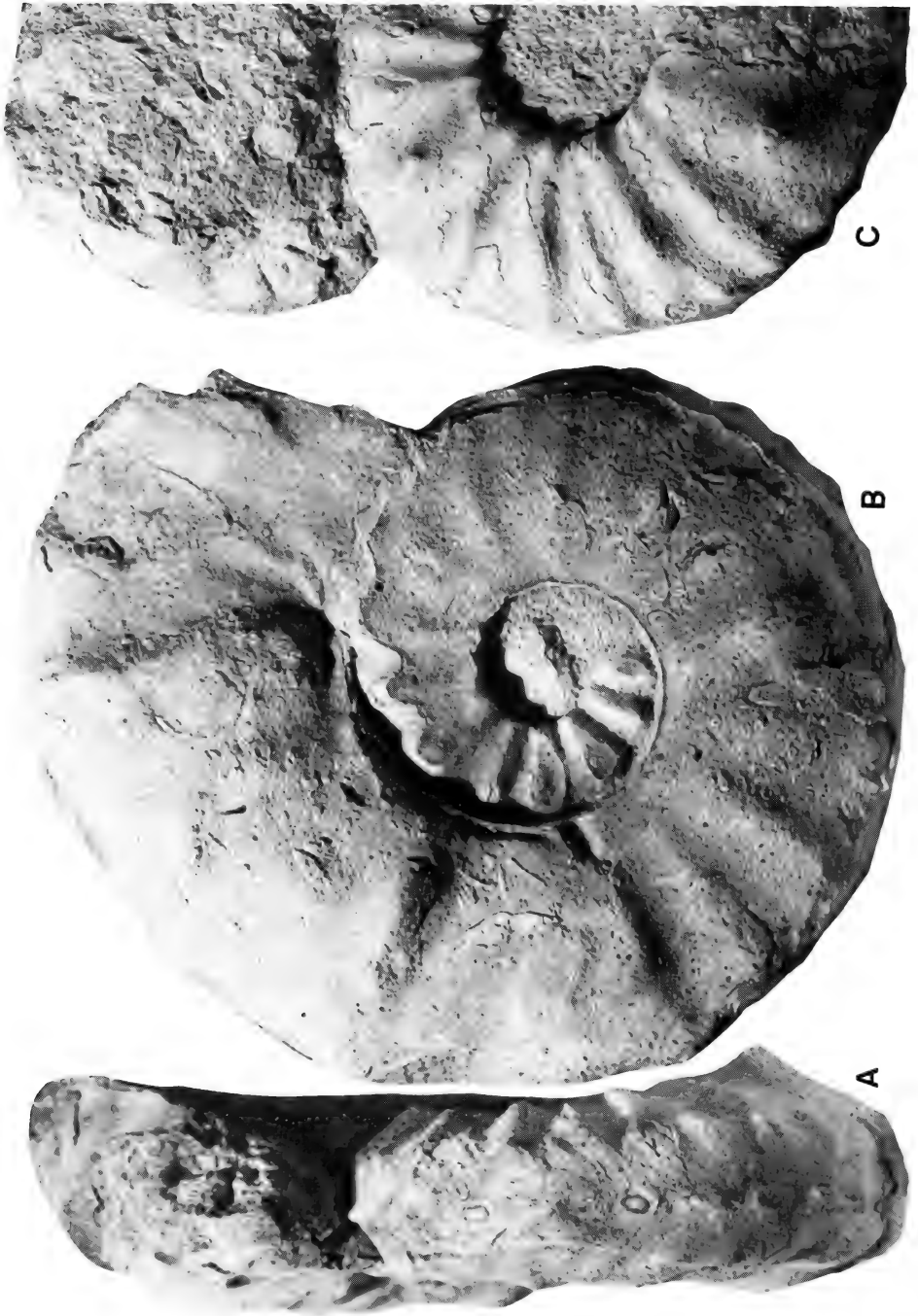
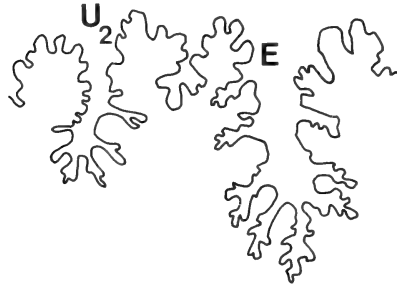Fig. 32. *Forresteria (Forresteria)* cf. *hobsoni* (Reeside, 1932). SAM–D1187. ×0,78.

Fig. 33. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). External suture of an inflated specimen, SAS Z1438. ×2.
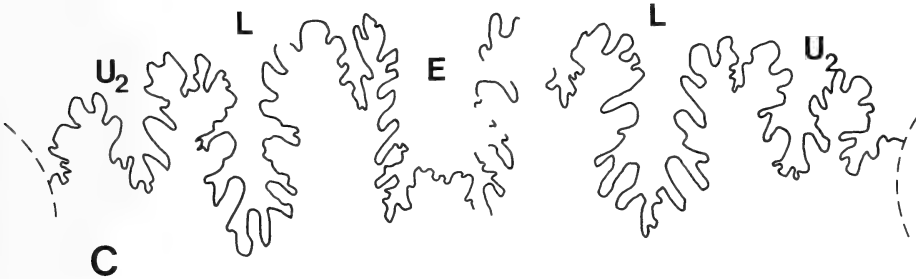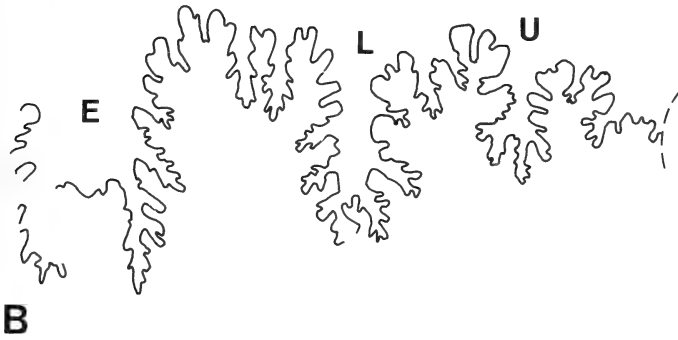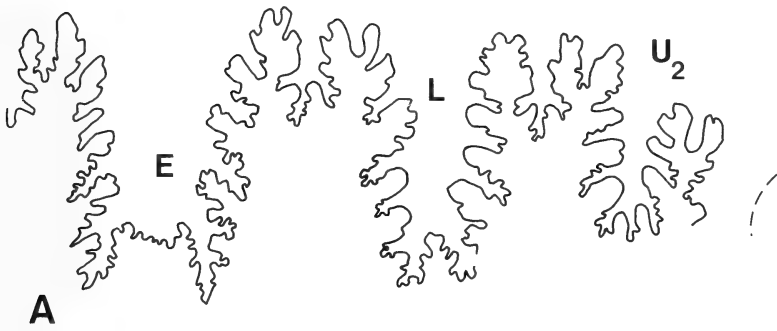

Fig. 34. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Showing external sutures. A. A compressed specimen, SAS Z1429. B. A compressed specimen, SAS Z978. C. A pathological specimen, SAS Z1523. All ×2.

Fig. 35. A–B. *Forresteria (Forresteria) hobsoni* (Reeside, 1932). The holotype from the Timpas Limestone near Carlile Springs, Colorado, USNM 73762. ×0,67. C–E. *Forresteria (Forresteria) alluaudi* (Boule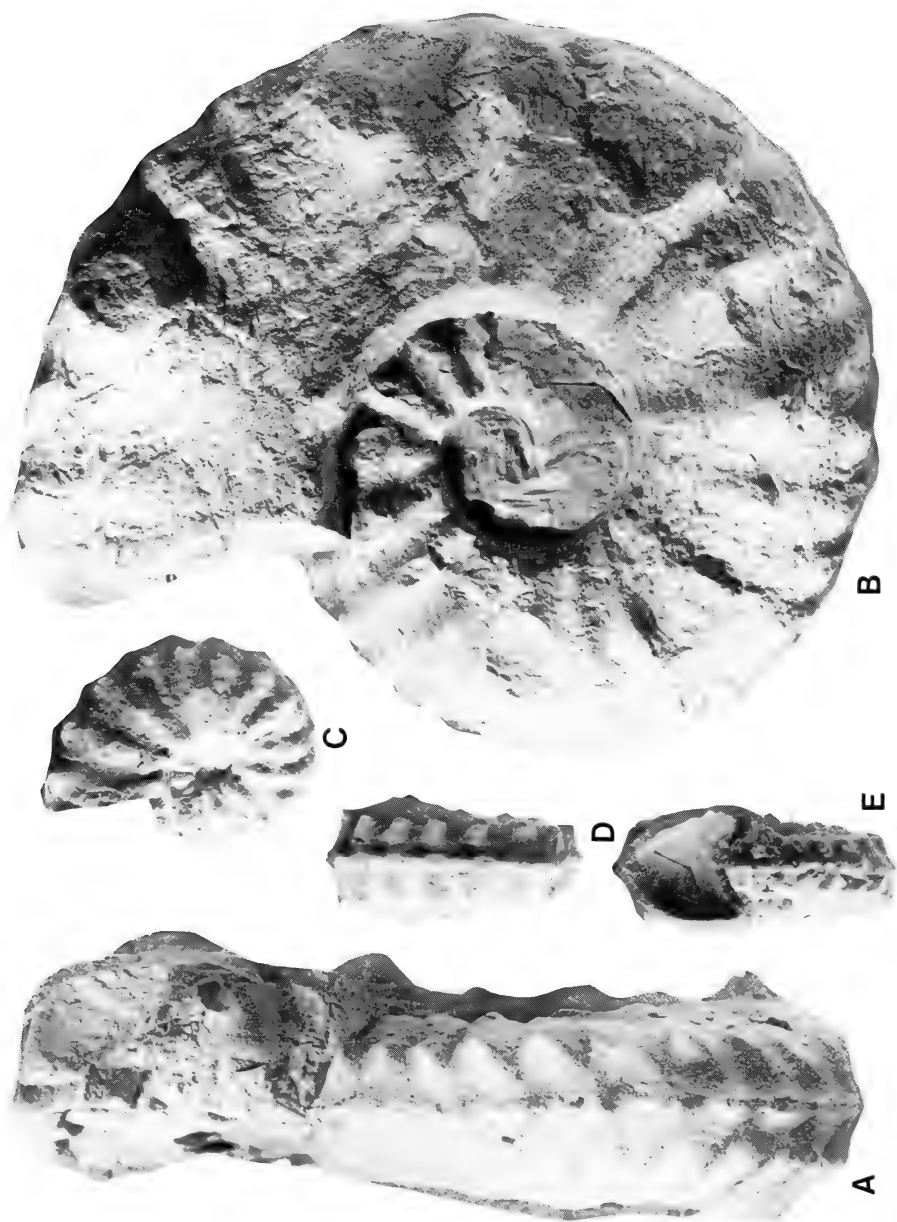, Lemoine & Thévenin, 1907). A paratype of '*Barroisiceras (Forresteria) stantoni*' Reeside (1932, pl. 7 (figs 3–7)). ×1.

There is close resemblance to *Forresteria (Forresteria) hobsoni* Reeside (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)), a species originally described from the Coniacian of the United States Western Interior and refigured here as Figure 35A–B. A single specimen compared with this species occurs with the collection of *F. (F.) madagascariensis*, but differs in being compressed rather than depressed and with more primary ribs per whorl. It does, however, show a similar strong and variably developed lateral tubercle that gives rise to pairs of ribs linking to ventral clavi that in turn link to a ventral chevron and row of siphonal clavi. This specimen may be simply a compressed variant of a population that encompasses both *F. (F.) madagascariensis* and *F. (F.) hobsoni* (the latter name having priority), but as the type of *F. (F.) hobsoni* is the only known specimen from the United States, this cannot be certain, and they are maintained separate.

There are also similarities to *Yabeiceras transiens* sp. nov. (Fig. 46A–C), described and discussed below, which points to the close affinities of *Yabeiceras* and *Forresteria*.

When compared to the variable *Forresteria (Forresteria) alluaudi* described above, the most obvious differences are to be found in the combination of massive lateral tubercles and strong ribs, plus the presence of a ridge support- ing the siphonal clavi.

There is a closer similarity to *Forresteria (Forresteria) nwalii* (Reyment, 1976) (in Offodile & Reyment 1976: 61, fig. 14A–B), the holotype of which is re-illustrated here as Figure 39A–B. There are a similar number of strong primary ribs in both species with a weaker umbilical than lateral tubercle, the latter variably and massively developed. In *F. (F.) nwalii*, however, it is pinched and narrow, the pairs of ribs linking to the ventral clavi are stronger and not uncommonly accompanied by one or two weaker additional ribs looping between lateral and ventral tubercles. In the Nigerian form, which has an altogether clumsier ornament, the ventral clavi are relatively larger, ventral ribs stronger, and chevron angle larger.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand; Coniacian of Madagascar.

<div align="center">Genus Yabeiceras Tokunaga & Shimizu, 1926
(= Eboroceras Basse, 1946)</div>

Type species

Yabeiceras orientale Tokunaga & Shimizu (1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1)) from the Coniacian of Japan, by the original designation of Tokunaga and Shimizu (1926: 20).

Diagnosis

Very evolute. Inner whorls depressed, coronate, with lateral tubercles, oblique ventrolateral tubercles twice as numerous as the lateral, and a rounded

siphonal ridge with low clavi. These persist into middle growth in some species. In others the tubercles decline and are replaced by ribs; the venter has a rounded siphonal ridge flanked by variably developed grooves, the outer edges of which may be slightly raised. Ornament persists in some species, in others the outer whorl is smooth or has a ventral keel and sulci only. Smooth body chambers develop at disparate sizes, suggesting a size dimorphism.

Suture with rather narrow, deeply incised elements.

Discussion

The inner whorls of *Yabeiceras* are so similar to those of *Forresteria (Forresteria)* that close affinity cannot be doubted; it is a member of the subfamily Barroisiceratinae (compare Figs 11A–K, 41A–D) as Matsumoto *et al.* (1964) and Matsumoto (1969) have shown. *Yabeiceras transiens* sp. nov., described below (p. 303), shows an intermediate morphology even in middle growth (Fig. 46). *Forresteria (Harleites)* appears at the base of the Coniacian (Hancock & Kennedy 1981; Kennedy, Wright & Hancock 1982) and the line of descent is taken here to be *F. (Harleites) → F. (Forresteria) → Yabeiceras*.

Eboroceras Basse (1946: 73), type species *Eboroceras magnumbilicatum* Basse (1946: 73, pl. 2 (fig. 2), text-fig. 2), is a clear synonym. *Yabeiceras* is a very rare genus in terms of numbers and, as is commonly the case, many species have been described that differ only in details:

1. *Yabeiceras orientale* Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7). Shimizu, 1926: 547. Matsumoto *et al.* 1964: 323, pl. 48 (figs 1–2), text-figs 1–3. Matsumoto, 1969: 324, pl. 44 (figs 1–2), pl. 45 (fig. 1), text-figs 12–13. The unique holotype from the upper reaches of the Sakurazawa in Oriki, Japan, was destroyed in World War II. Two specimens are known from the Futaba area of north-eastern Japan (Matsumoto *et al.* 1964) and two more are described by Matsumoto (1969).

2. *Yabeiceras kotoi* Tokunaga & Shimizu, 1926: 202, pl. 22 (fig. 8), pl. 28 (fig. 16). This was based on a single specimen from the same horizon and locality as the holotype of *Y. orientale*, and was also destroyed by fire.

3. *Yabeiceras himuroi* Tokunaga & Shimizu, 1926: 203, pl. 22 (fig. 9), pl. 27 (fig. 2). This was based on a single fragment with the same origin and fate as the previous species. It is best treated as a *nomen dubium*.

4. *Yabeiceras magnumbilicatum* (Basse, 1946): Basse, 1946: 73, pl. 2, (fig. 2), text-fig. 2. Collignon, 1965: 82, pl. 451 (fig. 1835): 84, pl. 452 (fig. 1837). This species was described on the basis of the holotype only. Two other specimens are described by Collignon. All are from Madagascar.

5. *Yabeiceras bituberculatum* Collignon, 1965: 82, pl. 451 (fig. 1836): 84, pl. 452 (fig. 1838). Two specimens only have been illustrated, from the *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* Zone of Ampozaloaka, Madagascar.

6. *Yabeiceras manasoaense* Collignon, 1965: 84, pl. 452 (fig. 1839). Matsumoto, 1971: 144, pl. 24 (fig. 2), text-fig. 9. Klinger *et al.*, 1976: 162, figs 1–4. The holotype is from the same horizon as the previous species at Manasoa (Betioky), Madagascar. Two others, from Japan and the South African offshore Alphard Group, have also been described.

7. *Yabeiceras menabense* Collignon, 1965: 86, pl. 453 (fig. 1840). The holotype is the only described specimen and is from the *Peroniceras dravidicum* Zone of Ankinatsy-Souroumaraina (Belo sur Tsiribihina), Madagascar.

8. *Yabeiceras costatum* Collignon, 1965: 87, pl. 454 (fig. 1841). The holotype is the only described specimen and is from the same horizon and locality as the previous species.

9. *Yabeiceras ankinatsyense* Collignon, 1965: 87, pl. 454 (fig. 1842). Only the holotype was described and is from the same horizon and locality as the previous species.

It will be seen that there are only 17 described specimens of *Yabeiceras*, 8 from Japan, referred to 4 species, 8 from Madagascar, referred to 5 species, and 1 from the South African offshore Alphard Group.

The present collection of fourteen specimens from Zululand nearly doubles the described material of this genus. Unfortunately it complicates rather than clarifies the taxonomy; because there are so few specimens, the authors cannot assess the limits of intraspecific variability nor gauge the effect of suspected yet unconfirmed dimorphism. In contrast to the genus *Forresteria*, where the extent of intraspecific variation could satisfactorily be demonstrated, a conservative morphological taxonomy is therefore followed below, with many species that may prove to be no more than fragments of one or a few variable species.

Occurrence

Coniacian of Japan, Madagascar, Zululand, and the South African offshore Alphard Group.

Yabeiceras orientale Tokunaga & Shimizu, 1926

Figs 41, 42G–I, 45

Yabeiceras orientale Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1). Shimizu, 1926: 547. Matsumoto *et al.*, 1964: 323, pl. 48 (figs 1–2), text-figs 1a–d, 2a–e, 3. Matsumoto 1969: 324, pl. 44 (figs 1–2), pl. 45 (fig. 1), text-figs 12–13.

Holotype

The original of Tokunaga & Shimizu (1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1a–c)), from the Coniacian Futaba Formation of the upper reaches of the Sakurazawa in the Oriki, north-eastern Japan, destroyed in World War II.

Material

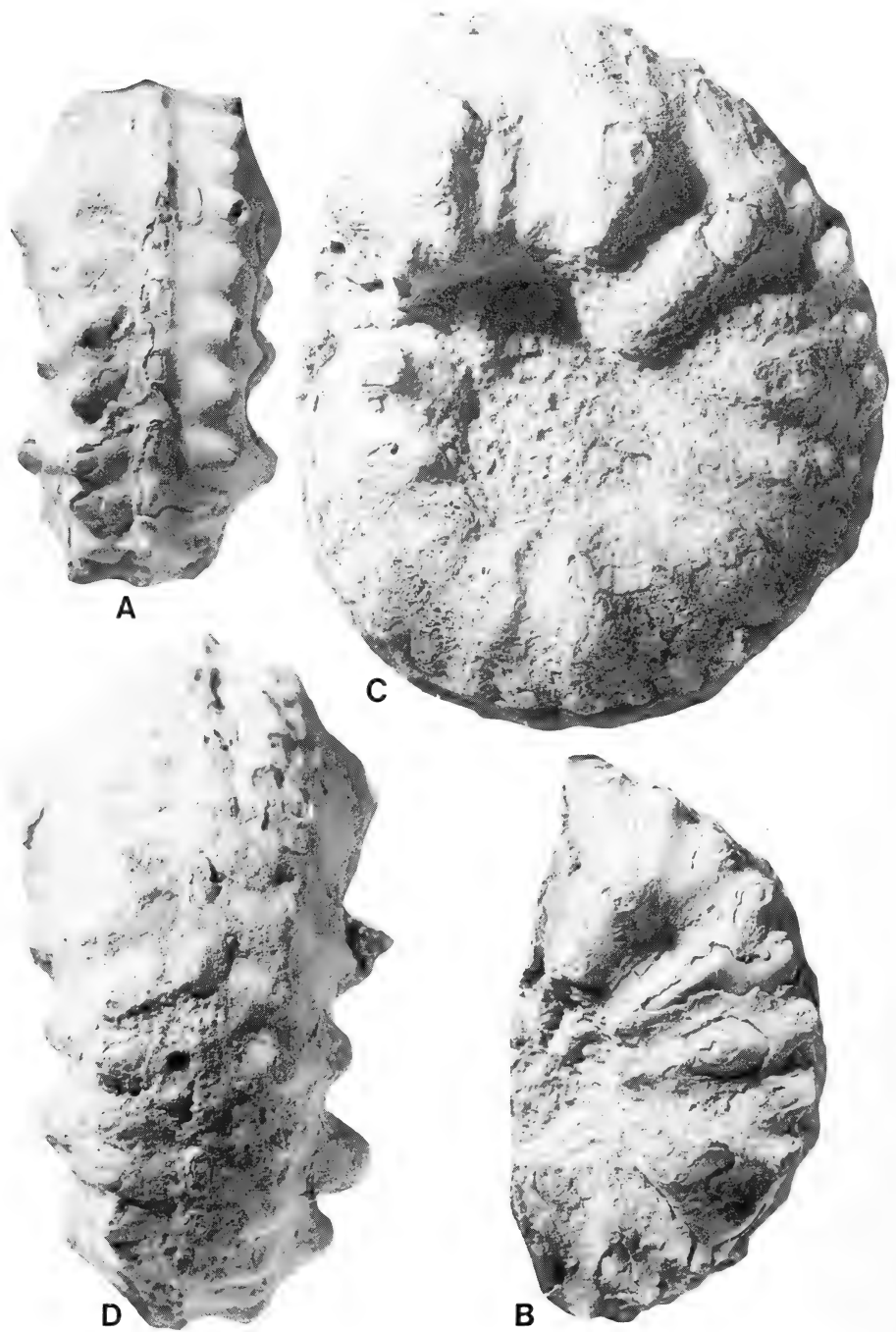SAS H196/1, from the west bank of the Hluhluwe River, Zululand, 32°19′30″E 28°5′30″S, St. Lucia Formation, Coniacian II.

Fig. 36. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965). A–B. SAM–D1187E.
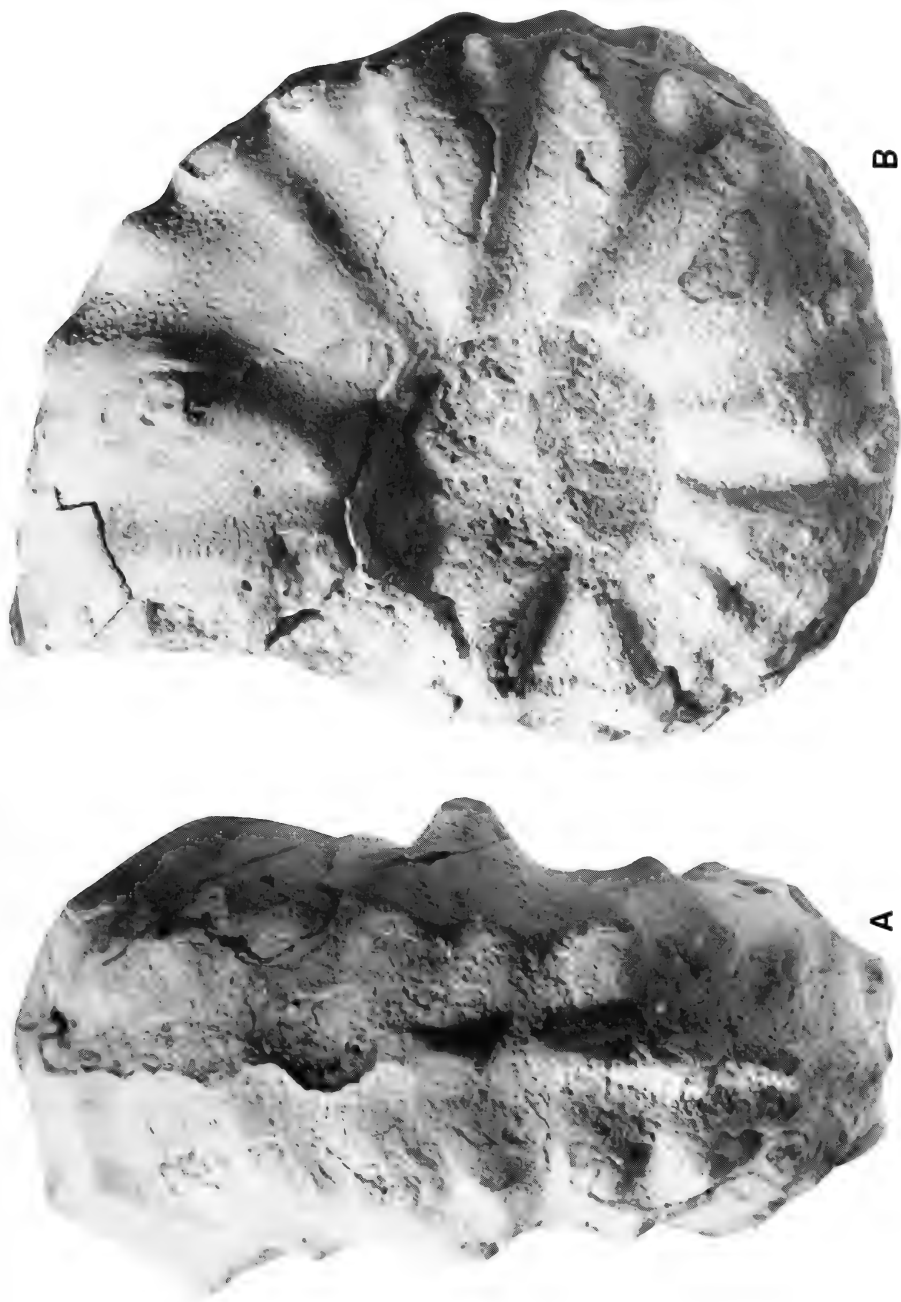C–D. SAM–D1187D. All ×1.

Fig. 37. *Forresteria (Forresteria) madagascariensis* (Collignon 1965). SAM-D1187A. ×1.

Fig. 38. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965) SAM–D1187C. ×1.

Dimensions

	D	Wb	Wh	Wb : Wh	U
c	64,0(100)	26,5(41,4)	18,5(28,9)	1,43	29,3(45,8)
ic	64,0(100)	23,8(37,2)	18,5(28,9)	1,29	29,3(45,8)

Description

The earliest stage visible is at a diameter of 20 mm (Fig. 41C–D). The coiling is evolute with a deep umbilicus, the whorl section depressed, with the greatest breadth low on the flank intercostally and at the lateral tubercle costally. There are thirteen to fourteen strong primary ribs per whorl, arising on the umbilical shoulder. They develop into strong bullate to conical umbilico-lateral tubercles that increase rapidly in strength as size increases. At the smallest diameter visible these tubercles give rise to pairs of strong prorsiradi-ate ribs that terminate in oblique ventral clavi. A shallow depression separates these from a corresponding number of siphonal clavi. This same style of ornament continues to 20 mm but the ribs become broader and lower. Beyond this the whorl section becomes very depressed, the tubercles conical and progressively stronger to a diameter of about 50 mm, at the same time migrating outwards from the umbilicus (Fig. 42G–I). The ribs progressively decline and are effaced on the outer flank, the ventral grooves are weak, and a line of low, weak siphonal clavi is still visible.

The coiling is very evolute on the outer whorl, less than 25 per cent of the previous whorl being covered. The whorl section is depressed and reniform, with an intercostal whorl breadth to height ratio of 1,29 and a costal ratio of 1,43, the greatest breadth being close to the umbilical shoulder.

The flanks are reduced and the venter is very broad and rounded. The umbilicus is of moderate width, comprising 45 per cent of the diameter, with a low, rounded, outward-sloping wall indented to accommodate the tubercles of the preceding whorl.

Ornament consists of eighteen strong, broad primary ribs arising at the umbilical wall and developing into strong umbilicolateral tubercles. These are initially conical but become progressively bullate as size increases. Single ribs or pairs of low, rounded, concave, prorsiradiate ribs arise from these tubercles, sweep forward over the ventrolateral shoulders and become increasingly weakened as size increases, terminating in weak, obliquely placed ventral clavi. These are separated by a feeble, broad groove from a spiral siphonal swelling that bears low, rounded clavi corresponding to the ventrolaterals.

The suture line is well exposed (Fig. 45).

Discussion

This interesting specimen shows the ontogenetic development from a di-ameter similar to that of specimens of *Yabeiceras orientale* described by Matsumoto *et al.* (1964), to which it is essentially identical. The change in tuberculation round the outer whorl is comparable to that in *Y. orientale*,
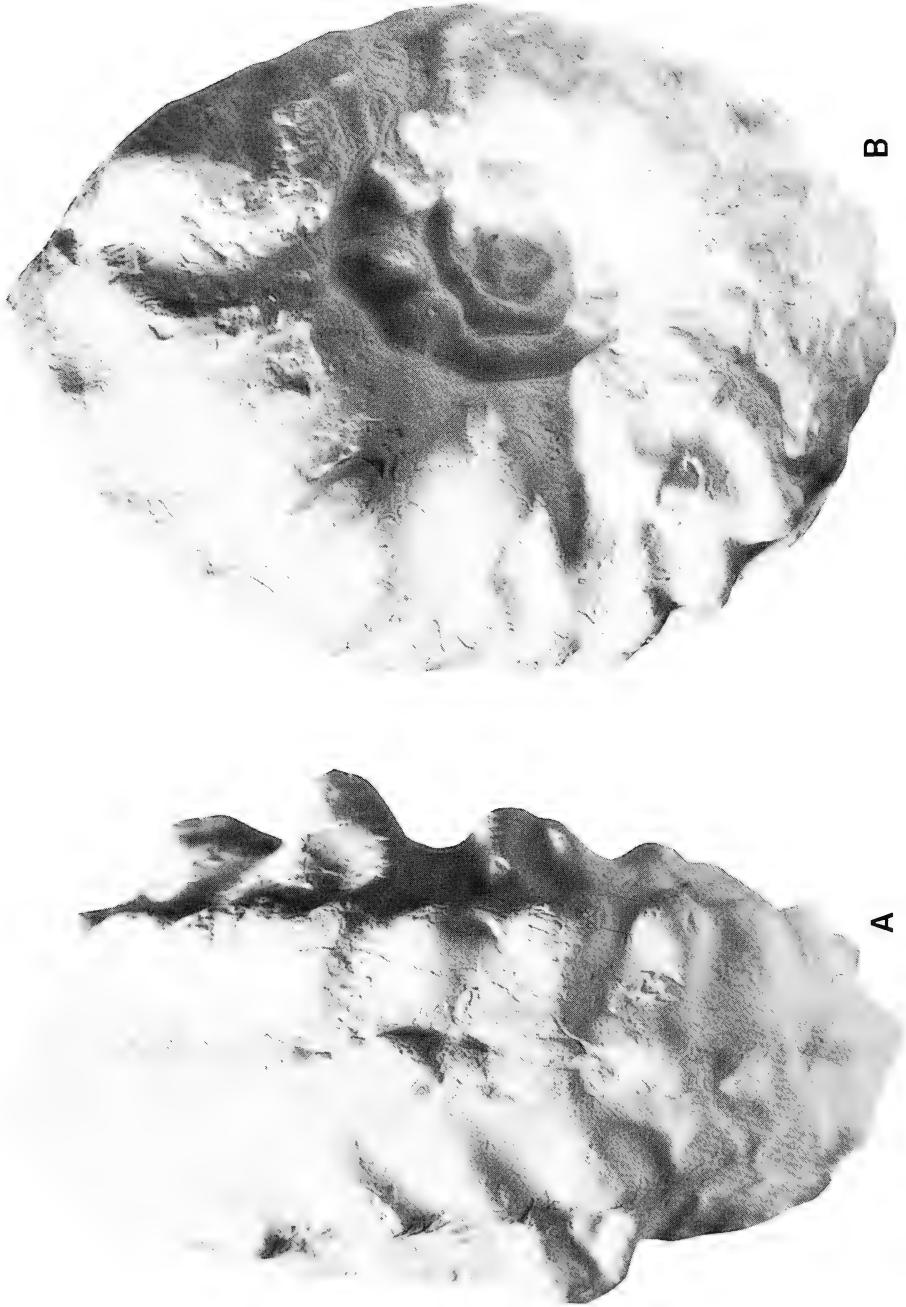
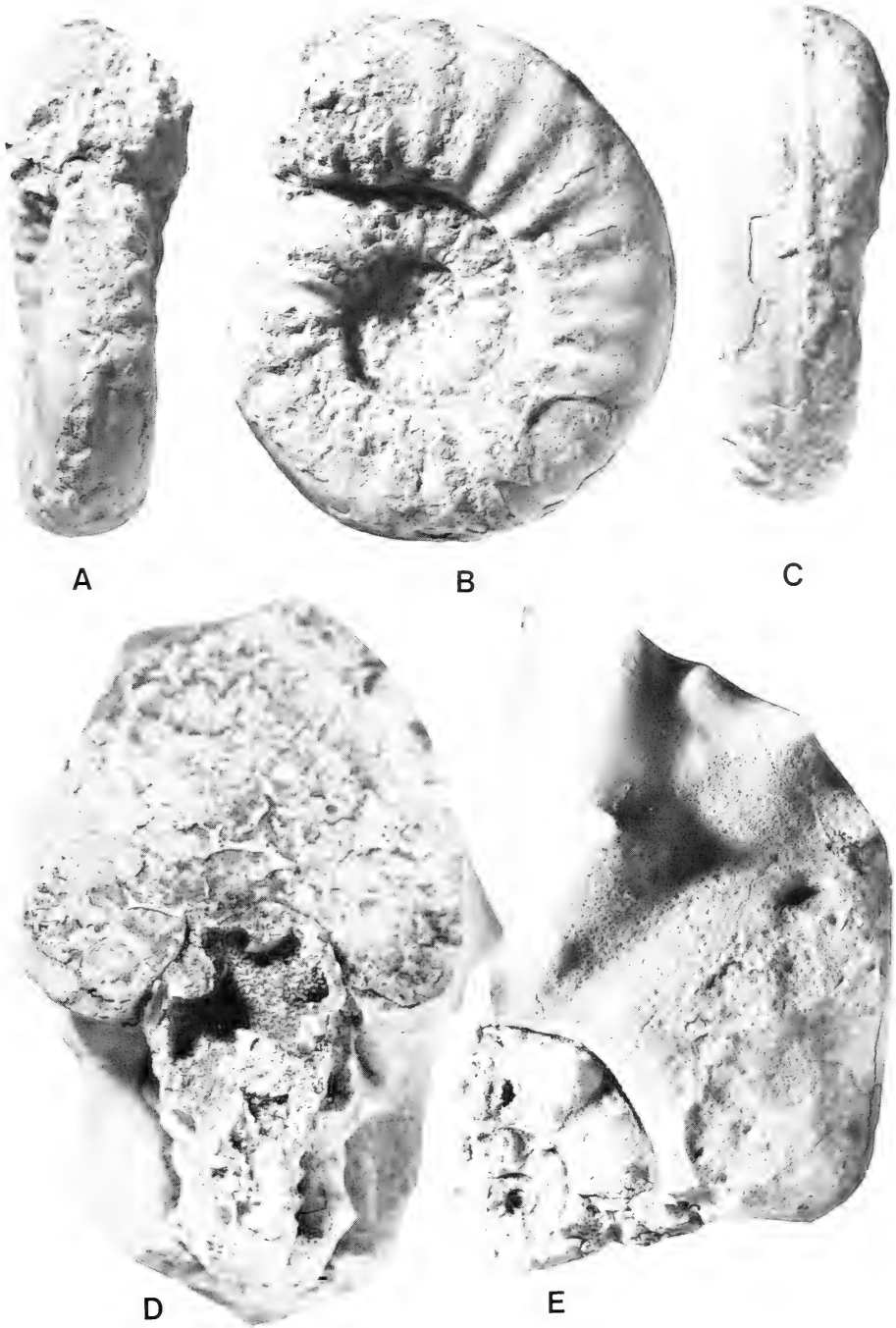Fig. 39. *Forresteria (Forresteria) nwalii* (Reyment, 1976). The holotype from Nkalagu, Anambra State, Nigeria. ×1.

Fig. 40. A–C. *Yabeiceras costatum* Collignon, 1965. SAM–D1188C. D–E. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of the holotype of '*Forresteria itwebae*' van Hoepen, 1968, SAS Z250. All ×1.
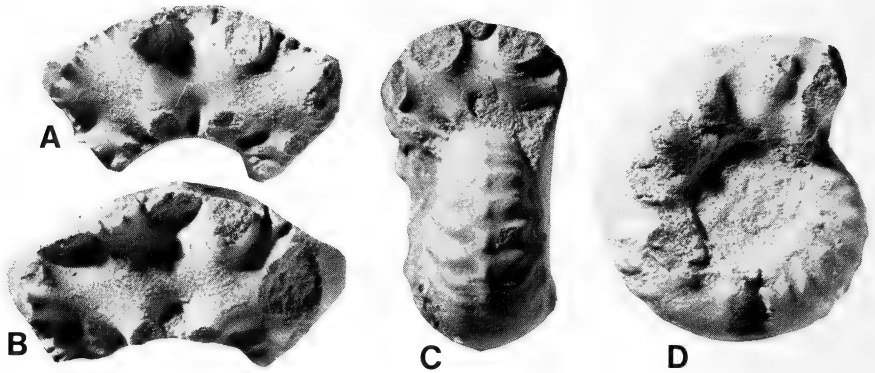
Fig. 41. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. Inner whorls of SAS H196/1. ×2.

although occurring at a slightly different diameter. It is too small to show the change from depressed tuberculate whorls to high, compressed, smooth whorls of adult *Y. orientale* (e.g. Figs 43–44), but in spite of this the authors believe it to represent the same species.

Occurrence

The species is known from the Futaba area of north-eastern Japan and from Hokkaido. The present specimen is from the St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras cf. *orientale* Tokunaga & Shimizu, 1926

Fig. 42A–C

Compare

Yabeiceras orientale Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1).

Material

SAM–D1188F, from locality 145 in the Morrisvale area to the north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Discussion

This poorly preserved juvenile has sixteen primary ribs with rather strong umbilicolateral tubercles. It most closely recalls *Y. orientale*, discussed above.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras transiens sp. nov.

Fig. 46

Holotype

SAM–D1188A, by monotypy, from locality 145 in the Morrisvale area to the north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Refers to the transitional features of the species between *Forresteria* and *Yabeiceras*.

Dimensions

c	83,9(100)	40,5(48,3)	32,0(38,1)	1,27	30,3(36,1)
ic		35,0(41,7)	31,8(37,9)	1,1	
	68,5(100)	32,9(48,0)	25,4(37,1)	1,30	24,4(35,6)
		29,5(43,1)	25,0(36,5)	1,18	

Description

The holotype and only known specimen is a well-preserved, wholly septate mould retaining traces of recrystallized shell. Coiling is moderately evolute with approximately 40 per cent of the previous whorl being covered. The whorl section is depressed; at the beginning of the outermost whorl the whorl breadth to height ratio is 1,65, the costal section polygonal, and the intercostal section a depressed oval. At the greatest preserved diameter the whorl breadth to height ratio is 1,27 costally and 1,1 intercostally, the greatest breadth being at the lateral tubercle on the ribs and close to the umbilical shoulder intercostally. The umbilicus comprises 36,1 per cent of the diameter, is relatively deep with a flattened, vertical umbilical wall and abruptly rounded umbilical shoulder. There are eighteen primary ribs on the outer whorl. These bear well-developed umbilical bullae of variable strength. They are prorsiradiate and straight or slightly concave, strong and bar-like to mid-flank where they bear a lateral tubercle. This is strong and spinate at the smallest diameter visible but declines around the outer whorl, becoming bullate. Each lateral tubercle gives rise to a pair of somewhat weaker, broader, rounded ribs that bear strong, obliquely placed ventrolateral clavi, an estimated total of thirty to thirty-three per whorl. These project forward over the venter where they are interrupted by a broad shallow groove on either side of a rounded siphonal keel. This bears distinct siphonal clavi at the smallest diameter visible, corresponding in number to, but displaced adaperturally of, the ventrolateral clavi. These decline around the outer whorl giving a low, undulose keel at the greatest diameter preserved.

The suture line is incompletely exposed. E/L is broad and bifid with moderate incision; L deep, narrow and bifid; L/U$_2$ smaller and symmetrically bifid.
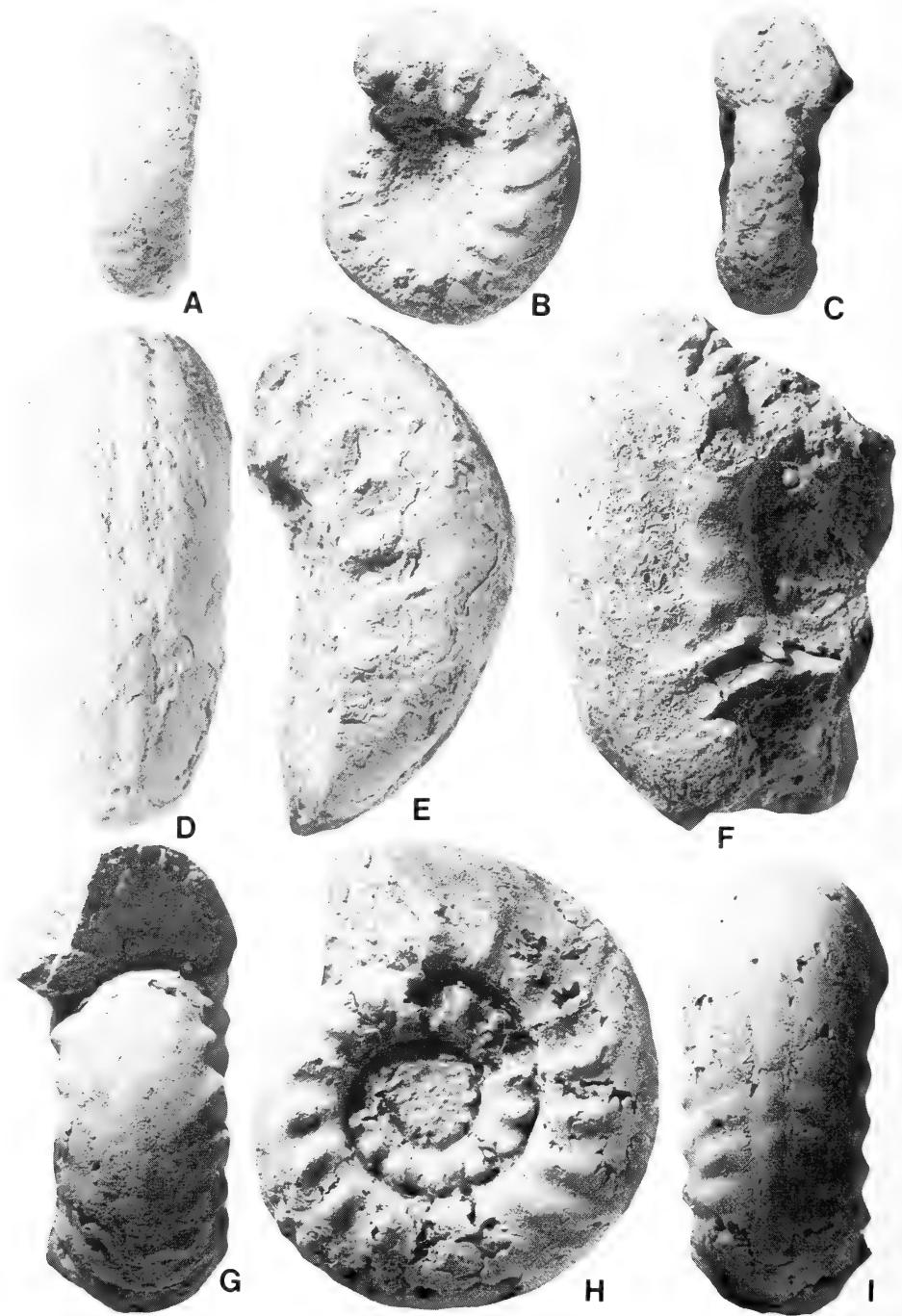
Fig. 42. A–C. *Yabeiceras* cf. *orientale* Tokunaga & Shimizu, 1926, SAM–D1188F. D–E. *Yabeiceras costatum* Collignon, 1965, SAM–D1188E. F. *Yabeiceras* sp. indet., SAM– D1182. G–I. *Yabeiceras orientale* Tokunaga & Shimizu, 1926, SAS H196/1. All ×1.
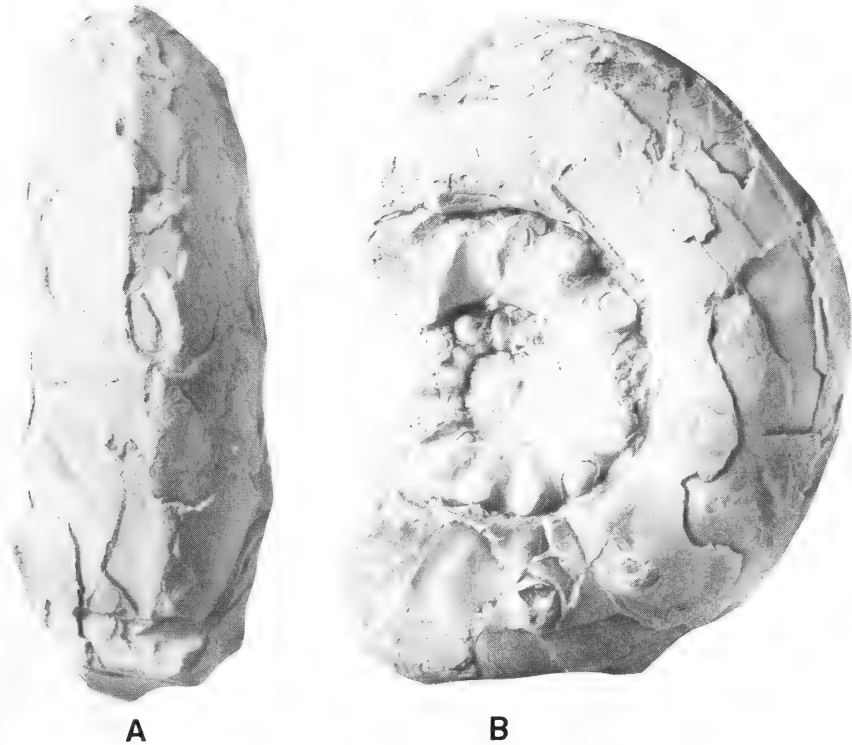
A   **B**

Fig. 43. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. From the upper reaches of the Ikushumbets, Hokkaido, Japan, Kyūshū University Collections H5624. ×1.

Discussion

As suggested by the name, this new species combines features of both *Yabeiceras* and *Forresteria*, having inner whorls with strong ribs and tubercles like the latter and a carinate-bisulcate venter like *Yabeiceras* that retains traces of siphonal clavi to a much greater diameter than any other species referred to the genus.

The only described species with which it is likely to be confused is *Yabeiceras bituberculatum* Collignon (1965: 82, pl. 341 (fig. 1836), pl. 342 (fig. 1838)). They differ in that the ribs are relatively stronger and more numerous in the new species and bear umbilical bullae throughout, while ribbing and tuberculation are retained to a diameter where *Y. bituberculatum* has already developed a smooth, constricted body chamber. Among *Forresteria (Forresteria)* species, the closest resemblance is to *F. (F.) madagascariensis* with which it occurs (see above). All the specimens of this species are stronger ribbed with massive, variable lateral tubercles, stronger ventrolateral and siphonal clavi and no obvious ventral sulci. In the *F. (Forresteria)*-like inner and smoothing outer
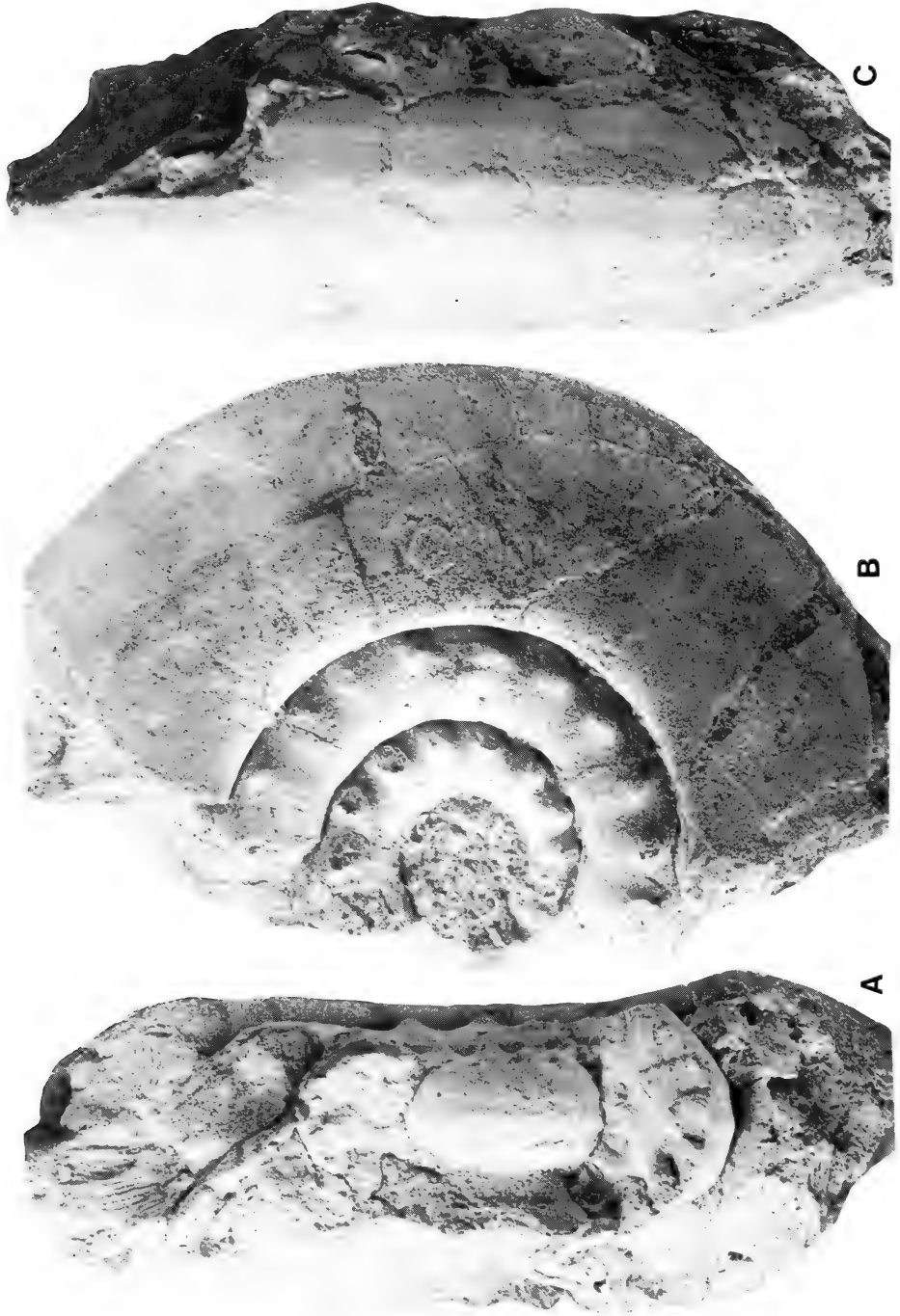
Fig. 44. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. Tohoku University Collections IGPS 35342, from the Bibai, Ishikari Province, Hokkaido, Japan. ×1.
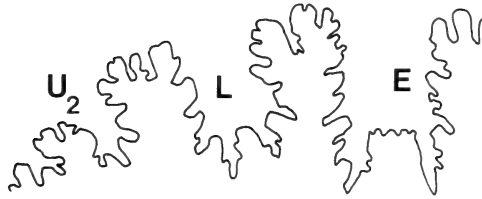
Fig. 45. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. External suture of SAS H196/1. ×2.

whorls there is a resemblance to *F. (Muramotoa)*, but all described species are more involute and high-whorled and show a rapid loss of ornament.

It may be that *Yabeiceras transiens* is a micromorph and perhaps a microconch of some other barroisiceratid, for, as has been noted above, both micro- and macromorph taxa occur throughout the family (see p. 242).

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras ankinatsyense Collignon, 1965

Fig. 50C–D

Yabeiceras ankinatsyense Collignon, 1965: 87, pl. 454 (fig. 1842).

Holotype

The original of Collignon (1965: 87, pl. 454 (fig. 1842)), from the *Peroniceras dravidicum* Zone of Ankinatsy (Belo sur Tsiribihina), Madagascar.

Material

SAS H196/3, from the west bank of the Hluhluwe River, 32°19′30″E 28°5′30″S Zululand, St. Lucia Formation, Coniacian II.

Dimensions

	D	Wb	Wh	Wb : Wh	U
SAS H196/3	34,2(100)	15,5(45,3)	12,8(37,4)	1,2	8,2(24,0)
Holotype (after Collignon)	70,0(100)	24,0(34)	24,0(34)	1,0	27,0(39)

Description

This specimen is only 34,2 mm in diameter, moderately evolute with a rather small umbilicus comprising 24 per cent of the diameter. The whorl section is a depressed oval in intercostal section, with the greatest width low on the flanks and at the umbilical bullae in costal section. The umbilical wall is subvertical, undercut, and of moderate elevation, the umbilical shoulder abruptly rounded, the inner flanks moderately inflated, the outer flattened, with a broadly rounded, flattened venter.
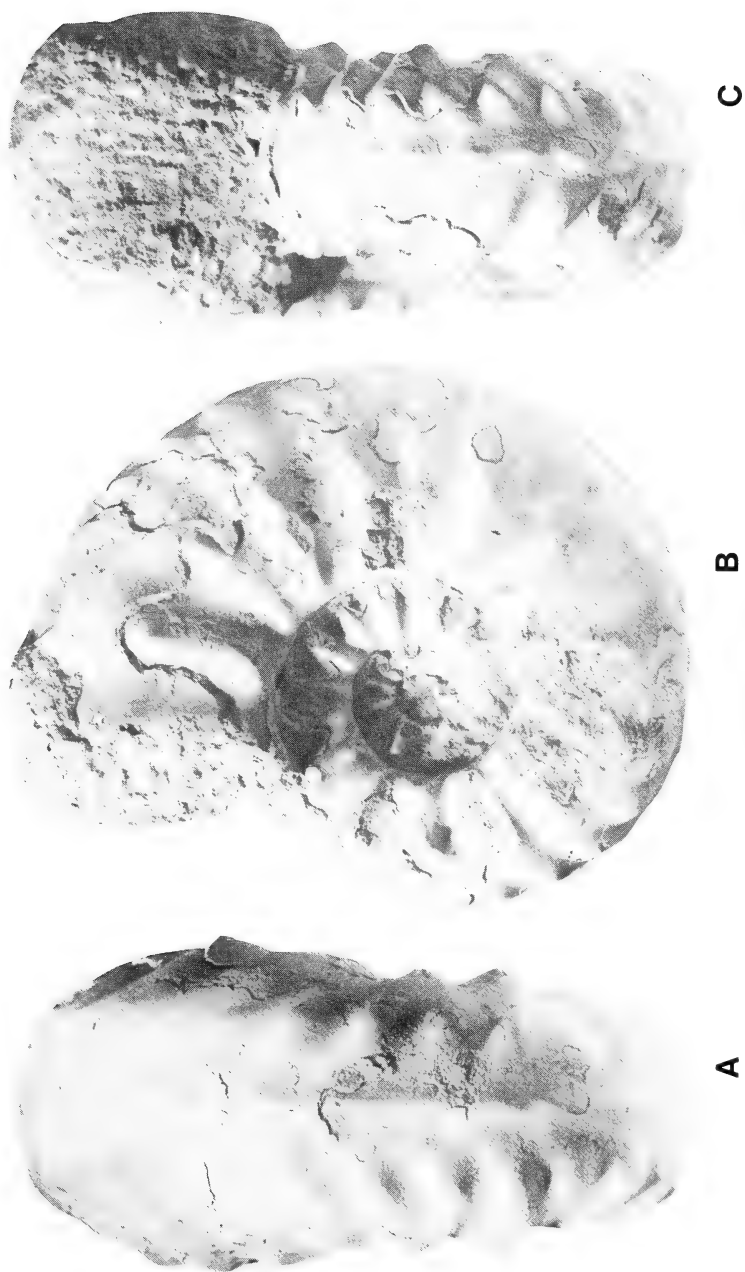
Fig. 46. *Yabeiceras transiens* sp. nov. Holotype, SAM–D1188A. ×1.

There are sixteen strong, narrow ribs per whorl. These arise as mere striae at the umbilical seam but strengthen at the umbilical shoulder, developing feebly defined bullae. They are strong, rounded and narrow on the inner half of the flanks, straight and prorsiradiate, and bear a strong, sharp, bullate lateral tubercle. The lateral tubercles usually give rise to pairs of weak, concave secondaries that are accompanied by a few intercalated secondaries to give a total of thirty ribs per whorl on the outer parts of the flanks. These sweep forward across the ventrolateral shoulder where they terminate in low, swollen, oblique ventrolateral clavi. There is a low, broad, rounded undulose siphonal ridge flanked by shallow grooves, developing ill-defined siphonal clavi corresponding in position and number to the ventrolateral clavi.

The sutures are not exposed.

Discussion

Few *Yabeiceras* species are known at this diameter but all those that are show the umbilicolateral, ventrolateral, and siphonal tuberculation of the present specimen to various degrees. *Y. orientale* Tokunaga & Shimizu is more depressed with strong lateral tubercles. Strength of tubercles also distinguishes *Y. magnumbilicatum, manasoaense, menabense, transiens*, and *bituberculatum* at this size as far as can be seen from the inner whorls of the much larger type specimens, while there are also differences in number of ribs. The costal whorl sections of *Y. bituberculatum* and *Y. transiens* are markedly polygonal and easily distinguished. The inner whorls of the holotype of *Y. costatum* are much more coarsely and closely ribbed with stronger flank tubercles. The inner whorls of *Y. ankinatsyense* thus provide the closest comparisons—rib density and strength are similar, as far as is visible—but the umbilicus at the admittedly greater diameter (70 compared to 34,5 mm) is much wider (39% compared to 24%) and the whorls are as wide as high rather than depressed. These differences may well be entirely due to the disparate sizes of our specimen and the holotype.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

<center>*Yabeiceras costatum* Collignon, 1965</center>

<center>Figs 40A–C, 42D–E</center>

Yabeiceras costatum Collignon, 1965: 87, pl. 454 (fig. 1841).

Material

SAM–D1180C and E, both from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

	D	Wb	Wh	Wb : Wh	U
SAM–D1188C	68,0(100)	25,5(37,5)	21,5(31,6)	1,19	29,2(43,0)
Holotype (after					
Collignon 1965)	74,0(100)	29,0(39)	24,0(32)	1,20	36,0(49,0)

Description

SAM–D1180C is a well-preserved specimen, largely septate, and retaining recrystallized shell. The coiling is very evolute, with a broad umbilicus comprising 43 per cent of the diameter. The umbilical wall is relatively low, rounded, and undercut. The whorl section is depressed (whorl breadth to height ratio is 1,19) with the greatest breadth at the lateral tubercles, where present, or at mid-flank. The flanks are flattened and converge to a broadly rounded venter.

There are twenty-five to twenty-six primary ribs per whorl. These arise at the umbilical seam, pass backward across the umbilical wall and strengthen into an umbilical bulla of variable, generally weak development at the umbilical shoulder. The ribs are straight, broad, rounded, and prorsiradiate, strengthen across the inner flank and bear a well-defined pointed midlateral tubercle up to a diameter of 45 mm, beyond which it progressively declines. The ribs weaken across the outer flank; on the first half of the outer whorl, to a diameter of around 55 m, they strengthen as they sweep slightly forward across the ventro-lateral shoulder, giving the appearance of an ill-defined oblique, rounded ventral clavus that terminates against a shallow, broad ventral groove flanking the siphonal keel. Beyond 55 mm diameter the ribs weaken markedly over the ventrolateral shoulder.

The siphonal keel is rounded, obscurely undulose at the smallest diameter visible, becoming continuous over the last half whorl.

SAM–D1188E, a partially septate specimen with an estimated original diameter of 75 mm, shows the continuing disappearance of the midlateral tubercle and weakening of the ribs over the ventrolateral shoulder.

The sutures are not exposed.

Discussion

Style of ornament, in particular the predominance of ribbing and early decline of the midlateral tubercle, link this specimen with the holotype of *Y. costatum* Collignon (1965: 87, pl. 454 (fig. 1841)); it differs only in having a slightly narrower umbilicus (43 % compared to 49).

Y. costatum most closely resembles *Y. ankinatsyense* Collignon (1965: 87, pl. 354 (fig. 1842)) from the same horizon at Ankinatsy (Belo sur Tsiribihina), which has slightly different proportions (D = 70 (100); Wb = 24(34,0); Wh = 24(34); U = 27(39,0)), in particular a whorl section as wide as high and a narrower umbilicus (39 % of diameter). There are few ribs—fifteen to sixteen per whorl, concave and, according to Collignon, lacking tubercles. The holotype is the only known specimen.

Y. menabense Collignon (1965: 86, pl. 453 (fig. 1840)) and *Y. manasoaense* Collignon (1965: 84, pl. 452 (fig. 1839)) are easily distinguished by their massive whorls and the development of large umbilicolateral tubercles at diameters comparable to our specimens.

The holotype of *Y. bituberculatum* Collignon (1965: 82, pl. 451 (fig. 136a–c)) again has massive umbilical tubercles; the smaller paratype referred to the species (Collignon 1965: 84, pl. 452 (fig. 1836)) has a polygonal whorl, with massive lateral and prominent ventral tubercles, the latter twice as numerous as the former.

Y. magnumbilicatum (Basse) (1946: 73, pl. 2 (fig. 2a–b) text-fig. 2) has strong, sparse umbilical and lateral tubercles, and loses all ornament on the body chamber.

Of *Yabeiceras* described from Japan, *Y. orientale* Tokunaga & Shimizu, 1926, has fewer, stronger lateral tubercles that give rise to pairs of secondaries with ventral clavi in middle growth and a smooth body chamber.

Y. kotoi Tokunaga and Shimizu (1926: 302, pl. 22 (fig. 8), pl. 26 (fig. 15)), the types of which were destroyed in World War II, has not been discussed by subsequent Japanese workers. According to the original account it is compressed (whorl breadth to height ratio is 0,83 at a diameter of 80 mm).

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras manasoaense Collignon, 1965

Figs 47, 51A–C

Yabeiceras manasoaense Collignon, 1965: 84, pl. 452 (fig. 1839). Matsumoto 1971: 144, pl. 24 (fig. 2), text-fig. 9. Klinger, Kennedy & Siesser, 1976: 162, figs 1–4.

Holotype

The original of Collignon (1965: 84, pl. 452 (fig. 1839)) from the zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of Manasoa, Madagascar.

Material

BMNH C81465 and C81472, both from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

	D	Wb	Wh	Wb:Wh	U
BMNH C81472 *c*	65,9(100)	35 (53,1)	19,7(29,9)	1,78	31,6(48,0)
ic		31,8(48,3)	19,7(29,9)	1,61	
BMNH C81465 *c*	114,5(100)	42,0(36,7)	33,3(29,1)	1,26	54,0(47,2)
ic		40,8(35,6)	33,3(29,1)	1,23	
c	89,8(100)	39,3(43,8)	26,1(29,1)	1,50	41,6(46,3)
ic		35,7(39,8)	26,1(29,1)	1,37	

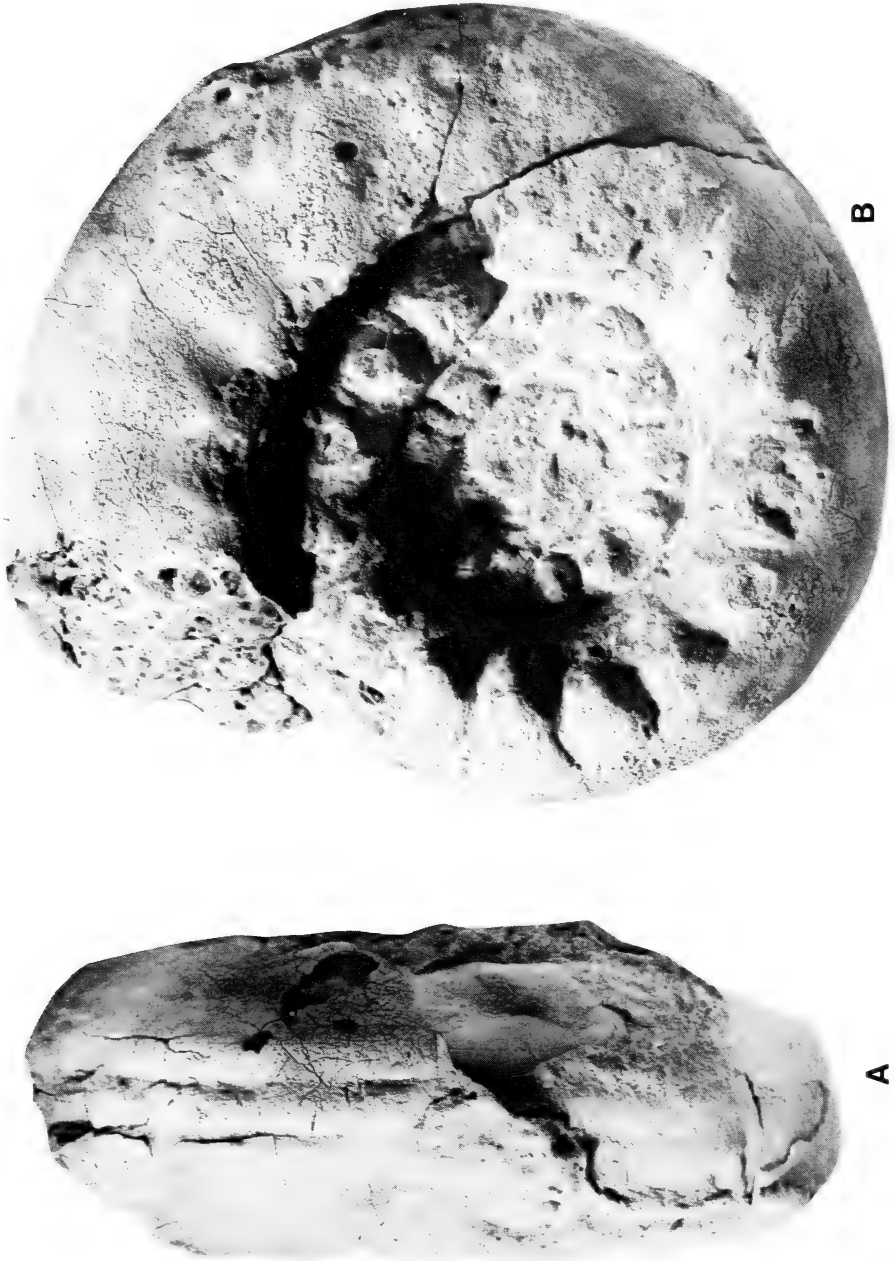Fig. 47. *Yabeiceras manasoaense* Collignon, 1965. BMNH C81465. ×1.

Description

The two specimens both retain recrystallized shell; the smaller shows details of early development previously unknown in the species. Coiling is evolute (the umbilicus comprises 48 % of the diameter) with the strong tubercles exposed within the umbilicus. The whorl section is depressed (breadth to height ratio is 1,61 intercostally, 1,78 at the tubercles), with the greatest breadth low on the flank between the ribs and at the strong tubercles, the cross-section reniform, with a broadly rounded venter and almost no flanks. The umbilicus is broad (48 % of the diameter), relatively deep, with a rounded wall.

There are seventeen massive conical to bullate umbilicolateral tubercles per whorl. At the smallest diameters visible these tubercles give rise to groups of two or three low, broad, straight prorsiradiate ribs that sweep forward across the ventrolateral shoulders and venter, terminating at the edge of the broad, shallow ventral grooves on either side of the low, broad, rounded siphonal ridge. The termination of the ribs is thickened but never develops into a tubercle; as size increases the ribs broaden and weaken, leaving the venter essentially smooth or with only faint undulations.

In the larger specimen the strong umbilical tubercles decline abruptly on the body chamber from a diameter of 95 mm onwards, beyond which ornament consists of distant, low, broad, concave flank ribs that decline and disappear over the venter. At the same time the whorl section becomes less depressed costally and intercostally, and the coiling becomes slightly eccentric.

The sutures are not exposed.

Discussion

The combination of massive, coronate, tuberculate inner whorls with a decline to a ribbed and smoothing adult whorl match well with the Madagascan holotype and the larger specimen from Japan described by Matsumoto (in Matsumoto & Inoma 1971: 144, pl. 24 (fig. 2), text-fig. 9). When compared with other species the massive tubercles of early-middle growth immediately distinguish this species from comparably sized *Yabeiceras magnumbilicatum*, *Y. costatum*, and *Y. ankinatsyense*. The tubercles of *Y. menabense* are spatulate rather than conical. In *Y. bituberculatum* the umbilicolateral tubercles are smaller, ribbing stronger, and ventrolateral tubercles better developed. *Y. transiens* sp. nov. has a polygonal whorl section, ribbing strongly developed, and umbilical, lateral, and ventrolateral tubercles. *Y. orientale* is less depressed and has relatively weaker tubercles and stronger ribs.

Occurrence

The types are from the Zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of Manasoa (Betioky), Madagascar; the present specimens are from the St. Lucia Formation, Coniacian II, of Zululand, and it is also recorded from the Alphard Group off the southern Cape coast. It is also known from Japan, occurring in Teshio Province, Hokkaido.
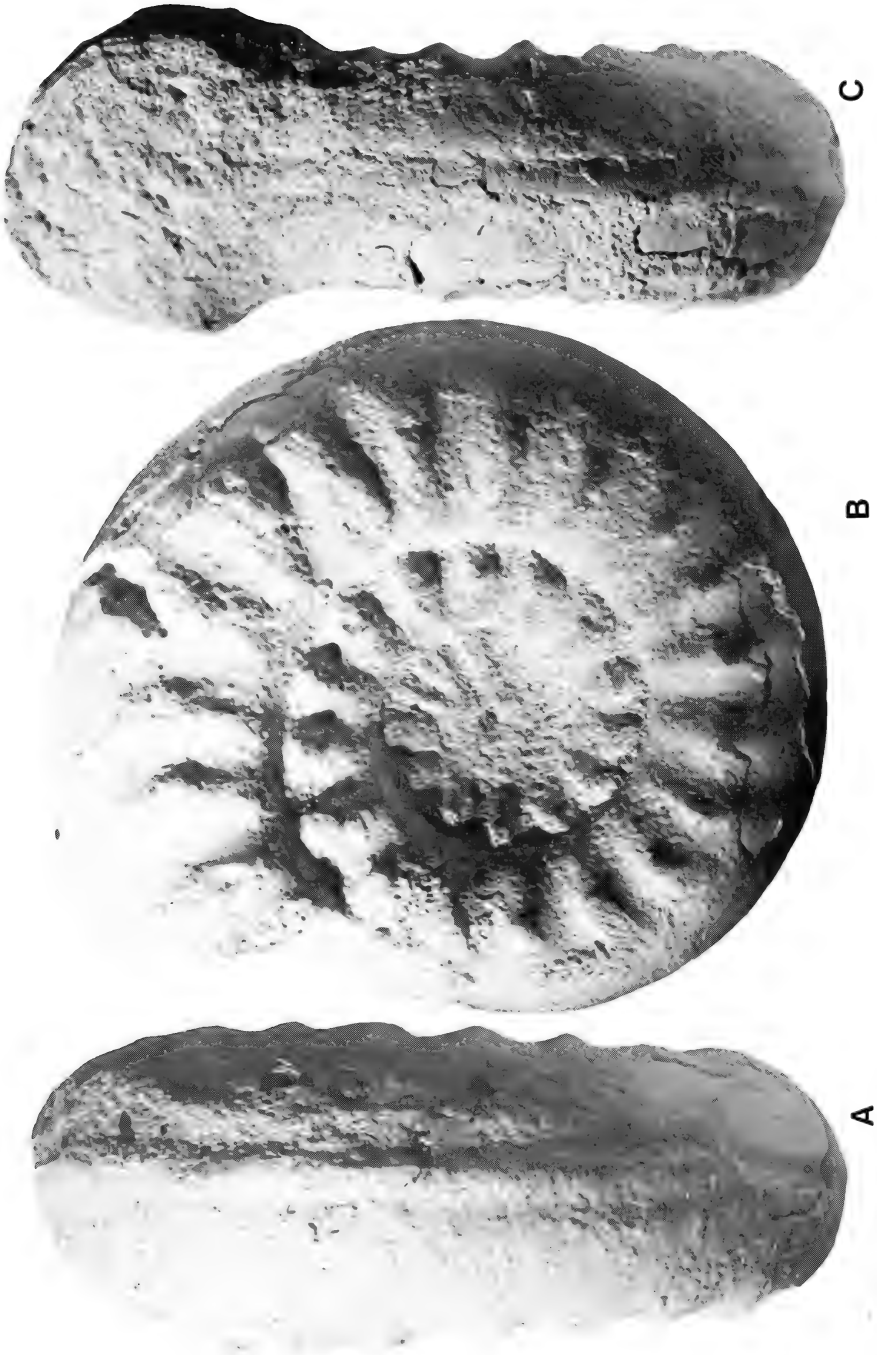
Fig. 48. *Yabeiceras* aff. *manasoaense* Collignon, 1965. SAM–D1188B. ×1.

Yabeiceras aff. *manasoaense* Collignon, 1965

Figs 48–49

Compare

Yabeiceras manasoaense Collignon, 1965: 84, pl. 452 (fig. 1839).

Material

SAM–D1188B–C from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

		D	Wb	Wh	Wb : Wh	U
SAM–D1188B	c	101,9(100)	37,8(37)	30,3(29,7)	1,25	49,8(48,9)
	ic		34,5(33,9)	30,3(29,7)	1,14	
		82,0(100)	32,5(39,6)	24,6(30)	1,32	37,8(46,1)
			29,0(35,4)	24,6(30)	1,18	
SAM–D1188C		97,4(100)	—(—)	27,5(28,2)	—	45,5(46,6)
	c	90,0(100)	35,6(39,6)	26,0(28,9)	1,37	41,0(45,6)
	ic		32,3(35,9)	26,0(28,9)	1,24	

Description

These two specimens are both wholly septate and retain recrystallized shell.

The coiling is very evolute, approximately 25 per cent of the previous whorl being covered. The umbilicus is broad (up to 49,8% of the diameter), shallow, with a low, rounded, outward sloping wall. The whorl section is depressed (costal breadth to height range 1,37–1,25; intercostal 1,24–1,14), with the greatest intercostal breadth low on the flank, the greatest costal breadth at the lateral tubercles.

Low, broad primary ribs, fifteen to sixteen per whorl at the smallest diameters visible (approximately 60 mm in SAM–D1188B and 50 mm in SAM– D1188C), arise at the umbilical seam and bear strong conical umbilico-lateral tubercles housed in notches in the umbilical wall of the succeeding whorl. As size increases this tubercle migrates outward to a lower lateral position. The ventrolateral and ventral region is visible only from a diameter of 60 mm; in SAM–D1188C the tubercles are seen to give rise to single ribs or, more rarely, pairs of ribs, which terminate in a blunt, low, oblique ventrolateral clavus.

The outer whorl bears twenty primary ribs arising at the umbilical seam and bearing a strong conical lateral tubercle at the beginning of the whorl. This declines progressively, leaving only strong inner flank ribs in SAM–D1188B at a diameter of 100 mm, and a small, somewhat bullate midlateral tubercle in SAM–D1188C at the same diameter. In both specimens this tubercle gives rise to a broad, prorsiradiate concave rib that declines and effaces over the ventrolateral shoulder, leaving a smooth or gently undulose zone on either side

Fig. 49. *Yabeiceras* aff. *manasoaense* Collignon, 1965. SAM–D1188C. ×1.

of the strong, rounded siphonal keel and shallow flanking ridges, the outer sides of which are raised into weaker ridges.

The sutures are not exposed.

Discussion

Rounded rather than polygonal whorl section, absence of umbilical tubercles, loss of ventral tuberculation and entire, rather than nodate, siphonal keel readily distinguish this species from *Yabeiceras transiens* sp. nov., described above.

Y. crassiornatum sp. nov., described below, is more coarsely ribbed and tuberculate and retains its ribs and ventral tubercles to a much larger diameter. *Y. orientale* has rather similar inner whorls, as far as comparison is possible, but at a diameter of 80–90 mm loses all ornament and becomes compressed, whereas the present species retains its ornament. This loss of ornament and acquisition of smooth outer whorls at a relatively small size also allows our specimens to be distinguished from *Y. magnumbilicatum* (Basse), which also has rather fewer primary ribs per whorl in the early stages (thirteen in the specimen figured by Collignon 1965, pl. 451 (fig. 1835)).

Y. bituberculatum has altogether distinct, smooth adult whorls at a relatively small size, and utterly distinctive inner whorls. *Y. menabense* differs in its curious spatulate tubercles on the inner whorls and loss of ribbing at a size where these are retained by our specimens.

Y. ankinatsyense is more delicately ornamented with the ribs dominant over tubercles at the same size, as in *Y. costatum*.

The closest comparisons thus appear to be with *Y. manasoaense* Collignon; this, however, has much coarser lateral tubercles and a more depressed whorl section. In the holotype (Collignon 1965: 84, pl. 452 (fig. 1839)), coarse tubercles, fourteen to fifteen per whorl, persist to a diameter where the present specimens already show a decline and predominance of ribs or feebly tuberculate ribs that number 20 per whorl.

The larger specimen figured by Matsumoto (1971, pl. 24 (fig. 2)) has eighteen tubercles per whorl at a diameter of 100 mm and retains blunt ribs, thus more closely resembling our specimens. When compared with the two specimens from the same locality that have been referred to *Y. manasoaense* above, the coarser, more massive tubercles and whorls and distinctively different ontogenetic changes around the last whorl are again distinctive.

With so few specimens, we cannot tell if these differences are within the range of intraspecific variation of the species *Y. manasoaense* or whether a distinctive form is present. They are therefore referred to as *Yabeiceras* aff. *manasoaense*, acknowledging both the similarities to and differences from the Madagascan holotype and other material.

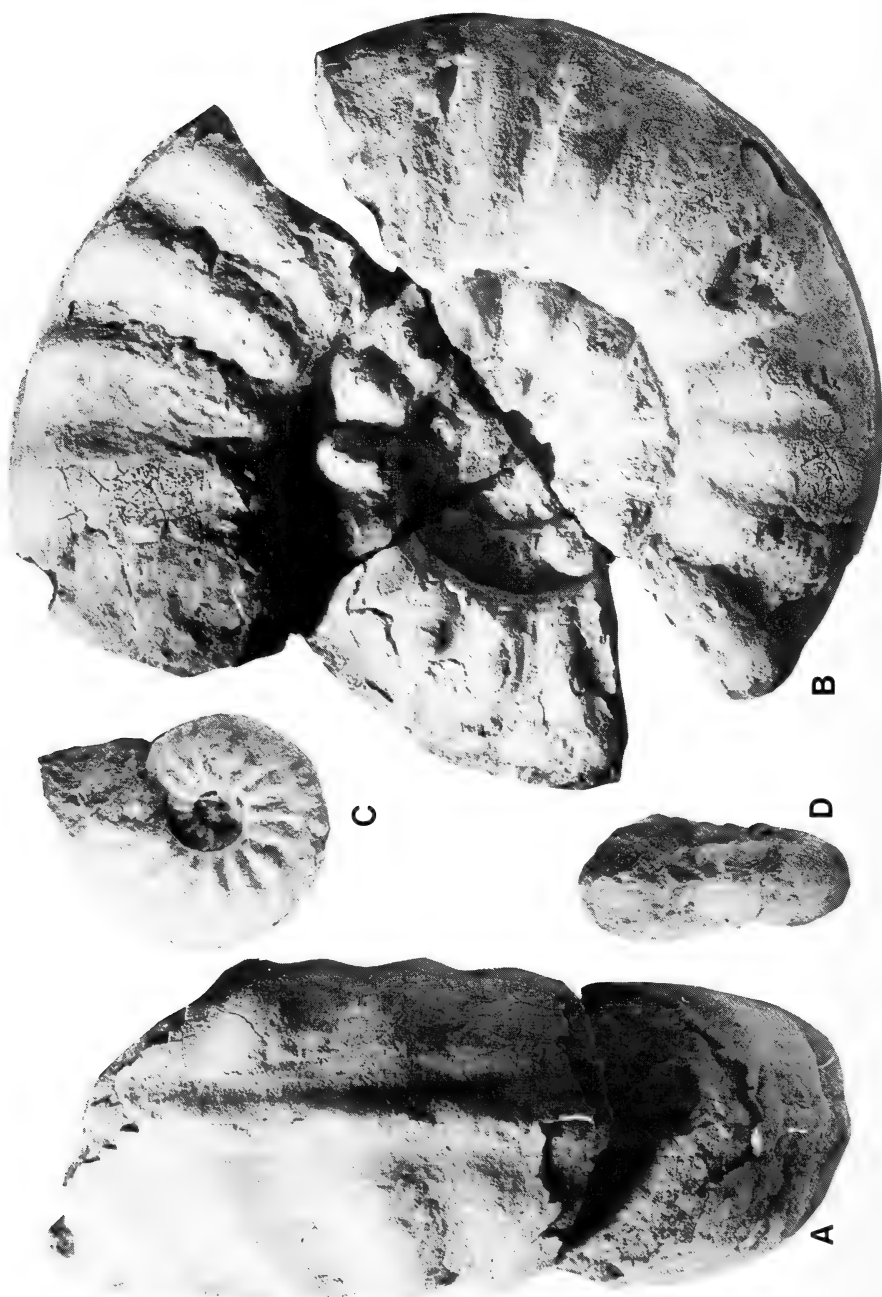*Occurrence*

St. Lucia Formation, Coniacian II, of Zululand.

Fig. 50. A–B. *Yabeiceras crassiornatum* sp. nov. BMNH C81561. C–D. *Yabeiceras ankinatsyense* Collignon, 1965. SAS H196/3. All ×1.

Yabeiceras crassiornatum sp. nov.

Fig. 50A–B

Holotype

BMNH C81501, from locality 145 in the Morrisvale area, north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Refers to the coarse ornament.

Dimensions

	D	Wb	Wh	Wb : Wh	U
c	137,00(100)	52,5(38,3)	44,0(32,1)	1,19	61,7(45,0)
ic		50,5(36,9)	44,0(32,1)	1,15	

Description

The coiling is very evolute, serpenticone, with a broad, rather shallow umbilicus that comprises 45 per cent of the diameter. The whorls are slightly depressed (whorl breadth to height ratio is 1,19 costally and 1,15 intercostally), the greatest breadth being well below midflank. The inner flanks are strongly rounded, the outer flanks flattened, converging to the broad venter. The inner whorls bear fifteen strong, broad, coarse primary ribs per whorl. These bear strong clavate tubercles that migrate progressively outward from an umbilico-lateral to lower lateral position. At the smallest diameter visible, the beginning of the outer whorl, these tubercles give rise to broad, coarse, single ribs that terminate in blunt ventrolateral tubercles. There is a strong, broad, rounded siphonal keel flanked by broad, shallow grooves.

Traced around the outer whorl, the ribs remain coarse, distant and strong, totalling 18 or 19 per whorl. The lateral tubercles, initially strong, decline over the last third of a whorl and disappear, leaving only concave ribs on the flank. In contrast the ventral tubercles strengthen and persist as obliquely placed clavi on either side of the persistent coarse keel and shallow flanking grooves.

The sutures are not exposed.

Discussion

The persistence of coarse ribs and coarse ventral clavi to a very large diameter combined with the strong lateral tubercles in middle growth distinguishes this specimen from all other described forms; it is consequently afforded specific status.

Occurrence

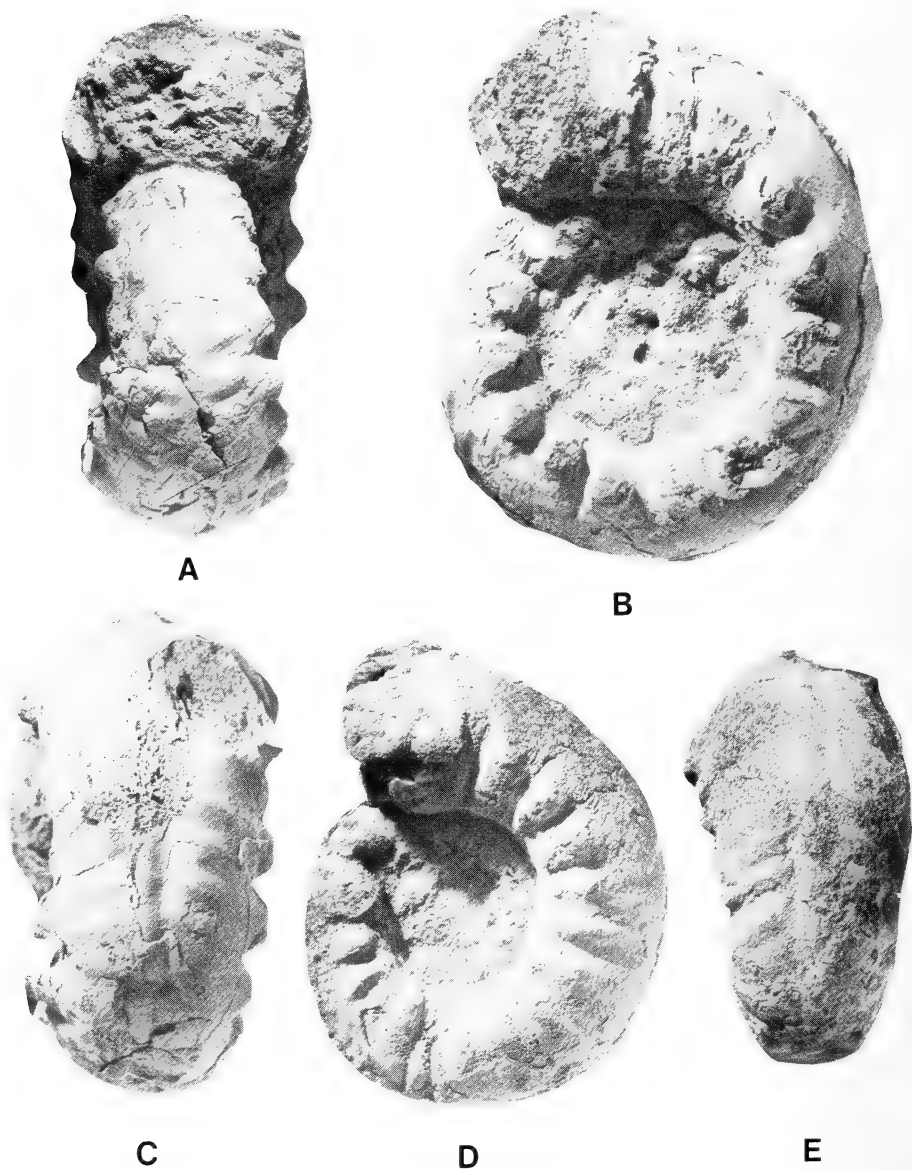St. Lucia Formation, Coniacian II, of Zululand.

Fig. 51. A–C. *Yabeiceras manasoaense* Collignon, 1965. BMNH C81472. D–E. *Yabeiceras cobbani* sp. nov. BMNH C81542. All ×1.

Yabeiceras cobbani sp. nov.

Fig. 51D–E

Holotype

BMNH C81542, by monotypy, from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Named for Dr W. A. Cobban of the United States Geological Survey, Denver.

Material

Only the holotype.

Description

The single specimen is distorted, but retains recrystallized shell and has a maximum preserved diameter of 60 mm. The coiling is evolute, the umbilicus deep, and comprises an estimated 35–40 per cent of the diameter. The whorl section is depressed reniform in intercostal section with the greatest breadth low on the flanks. In costal section the greatest breadth is at the lateral tubercle; the estimated whorl breadth to height ratio is 1,7. There are an estimated eighteen primary ribs per whorl. These arise from umbilical tubercles of variable strength at the smallest diameter visible and migrate to a low lateral position around the outer whorl. They give rise to pairs of broad, coarse, concave prorsiradiate ribs that terminate in coarse, obliquely placed ventro-lateral clavi. These are separated by a smooth, shallow groove from a broad, rounded siphonal keel that bears blunt clavi corresponding approximately to the ventral clavi. Interspaces between ribs are periodically deepened into constrictions, strong across the flanks but absent over the venter. There are four or five of these on the outer whorl.

Discussion

None of the described *Yabeiceras* species combines a coarse ornament of umbilicolateral, ventrolateral, and siphonal tubercles in the manner shown by this specimen and none develops constrictions.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras sp. indet.

Fig. 42F

Material

SAM–D1182, from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Description

This fragment shows an inner whorl with medium-sized conical lateral tubercles. The outer whorl has a whorl breadth to height ratio of 1,15 with rounded flanks and a broadly rounded venter. The flanks bear closely spaced concave flank ribs that die out across the ventrolateral shoulders. There is a strong, rounded ventral keel flanked by broad grooves, in turn flanked by slight lateral keels.

Discussion

The fragment has typically tuberculate inner whorls, as seen in many specimens of *Yabeiceras*, combined with a ribbed phase recalling *Y. costatum* at small diameters (e.g. Fig. 40A–C). It is, however, specifically indeterminate.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

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.

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.:

<div align="center">

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A
</div>

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 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.
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.
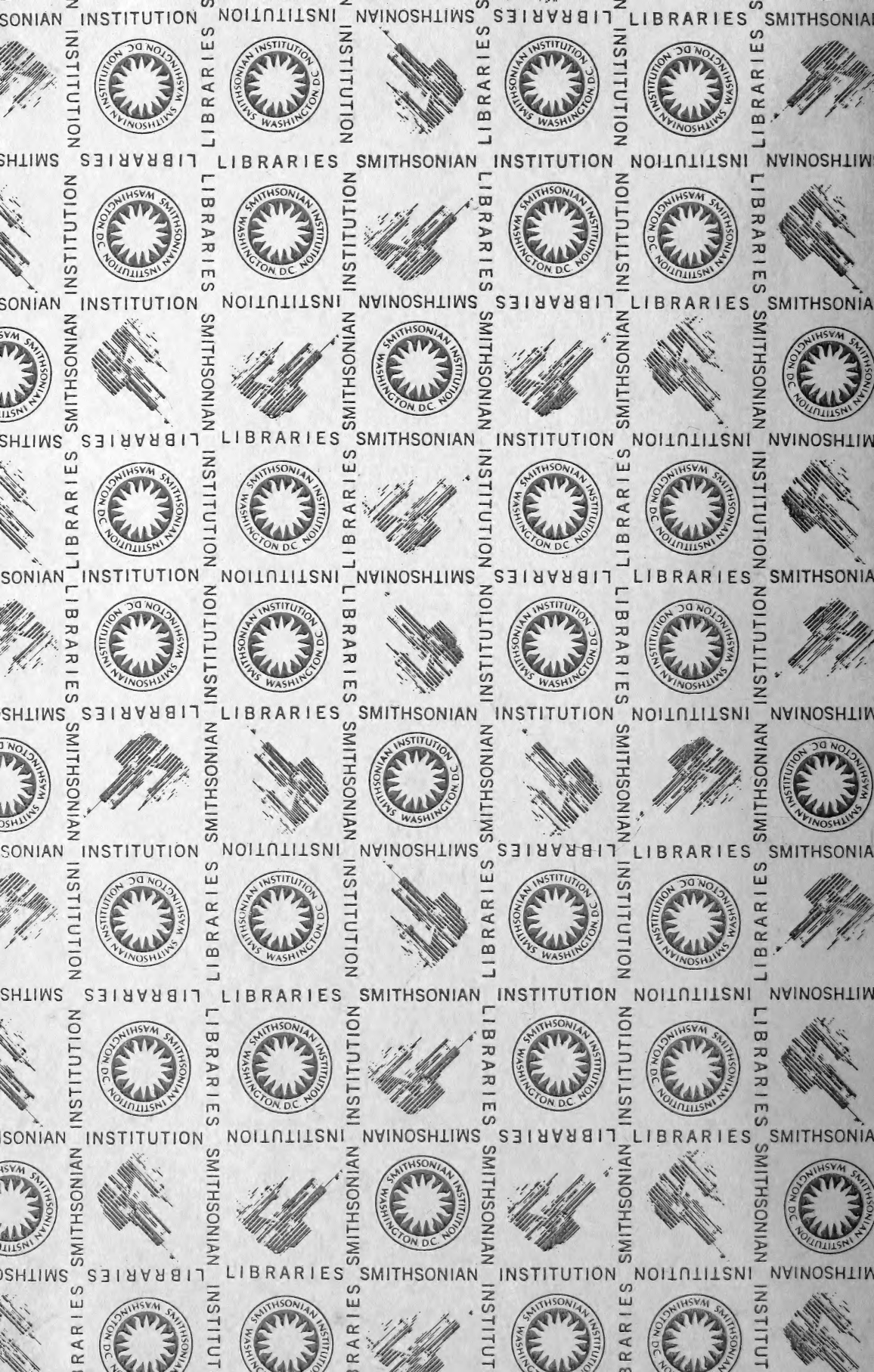
WILLIAM JAMES KENNEDY,
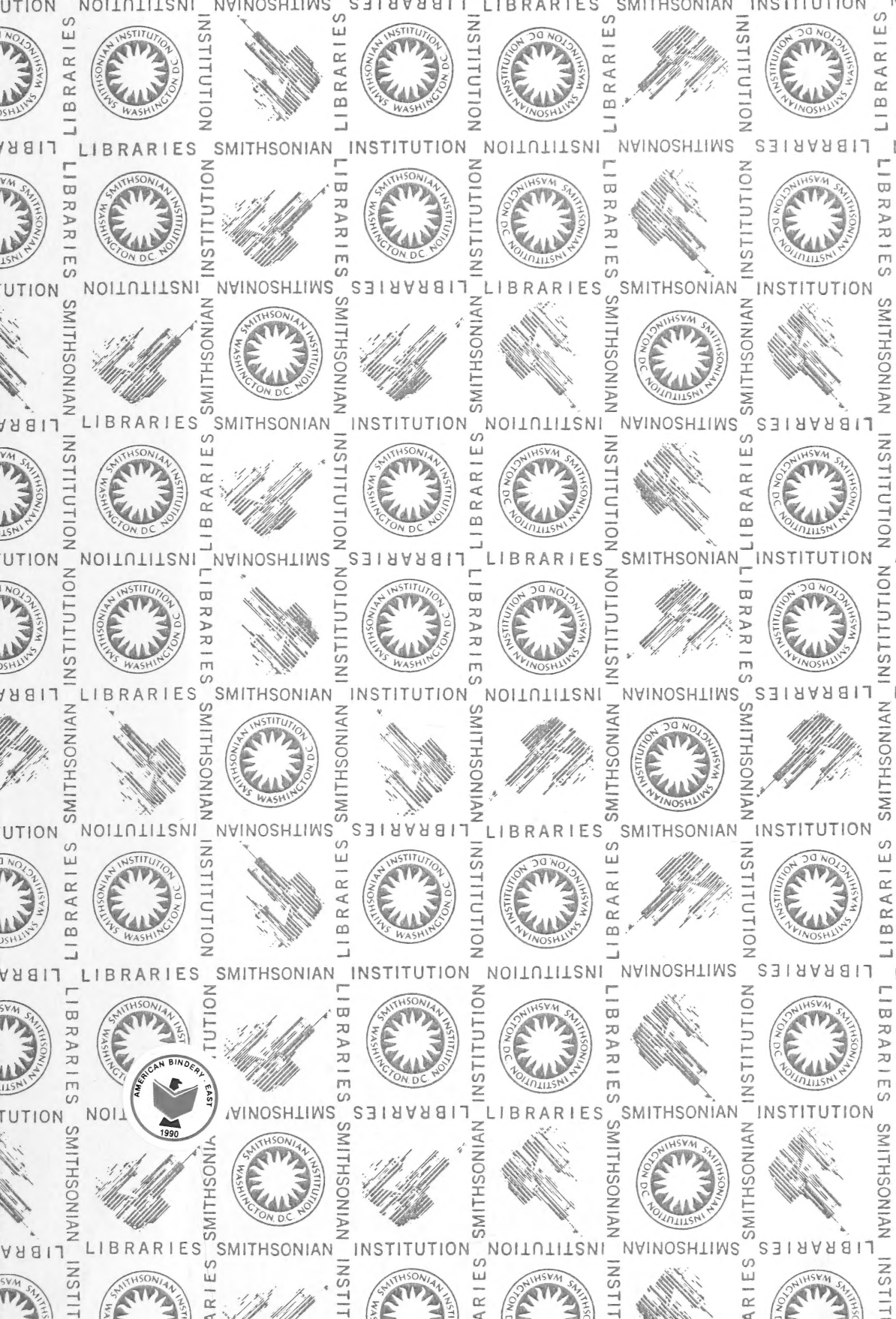CLAUD WILLIAM WRIGHT
&
HERBERT CHRISTIAN KLINGER

CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA THE AMMONITE SUBFAMILY BARROISICERATINAE BASSE, 1947