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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 67 BAND

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CAPE TOWN

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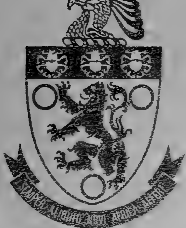

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(*continued inside back cover*)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **67** Band
March **1975** Maart
Part **1** Deel

TWO NEW SPECIES OF CAMPANULARIAN HYDROIDS FROM SOUTH AFRICA

By

C. GOW

&

N. A. H. MILLARD

Cape Town Kaapstad

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TWO NEW SPECIES OF CAMPANULARIAN HYDROIDS FROM SOUTH AFRICA

By

C. Gow

Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg

&

N. A. H. Millard

South African Museum, Cape Town

(With 2 figures)

[*MS accepted 22 July 1974*]

ABSTRACT

Two new hydroid species of the family Campanulariidae are described from False Bay, South Africa, namely *Campanularia pecten* and *Campanularia roberti*. Both are unusual in the form of the gonotheca which is shaped like a bivalve shell.

CONTENTS

INTRODUCTION

These two small species were discovered by the first author during the preparation of a project for an honours degree at the University of Cape Town in 1968. Both colonies were fertile and were retained alive in the laboratory until the release of the products of the gonothecae. Microscopic examinations were made of fresh material and permanent stained mounts, a useful technique being to slip an empty hydrotheca onto a fine insect pin and rotate it into different positions.

DESCRIPTION OF MATERIAL

Campanularia pecten sp. nov.

Fig. 1

Holotype: St James, False Bay, on the sea-grass *Caulerpa filiformis* (Suhr.), just below L.W.S. Collected 29 March 1968. Catalogue number: SAM H1659.

Description

Hydrorhiza creeping and reticular, giving rise to solitary hydrothecae and gonothecae. Hydrothecal pedicel smooth, constricted at base, with a single

Ann. S. Afr. Mus. **67** (1), 1975; 1–6, 2 figs.

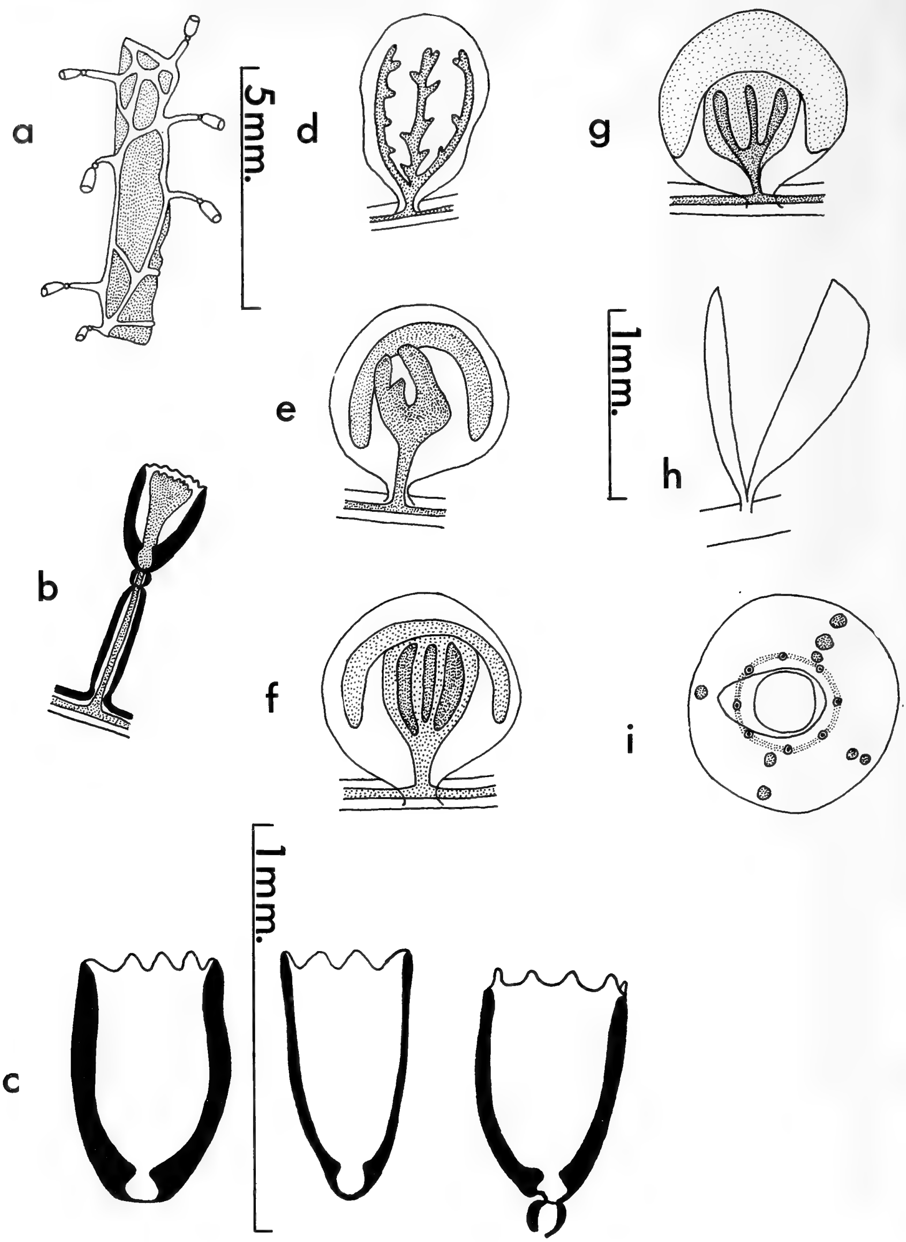

Fig. 1. *Campanularia pecten* sp. nov.

a, colony on *Caulerpa*; b, hydrotheca and pedicel; c, hydrothecae, the centre one in end-on view; d–g, gonophores in various stages of development; h, empty gonotheca, side view; i, medusoid, showing from the centre outwards: opening to subumbrellar cavity, exumbrellar aperture, ring of statocysts, gonads on radial canals.

terminal spherule and with thickened perisarc. Irregular nodes sometimes present due to regeneration.

Hydrotheca deep-campanulate, slightly compressed, with toothed margin. Marginal teeth generally nine in number, rarely ten, usually narrower than the bays between them, with bluntly rounded apices. Perisarc generally strongly thickened on two opposite sides imparting a bilateral symmetry and an oval cross-section. An annular perisarcal thickening present near base demarcating a spherical basal chamber.

Gonotheca borne directly on hydrorhiza on a short, smooth pedicel, scallop-shaped, rounded in broad view, opening around the circumference like a bivalve shell and with one valve considerably flatter than the other, sometimes with concentric ridges on the outer surface of the deeper valve. Gonophore (only male present) eumedusoid, with four radial canals with the gonads distributed along their length, with eight statocysts, without hypostome or marginal tentacles, with a short free-living existence.

Measurements (mm)

Pedicel, length	0,52–1,74
maximum diameter	0,10–0,20
Hydrotheca, depth	0,51–0,69
diameter at mouth (broad view)	0,24–0,41
diameter at mouth (narrow view)	0,30–0,33
Gonotheca, length including pedicel	0,93–1,09
maximum diameter	0,68–1,20

Remarks

In the early stages of development the gonotheca is oval in broad view, becoming circular later. At this early stage the four branching radial canals are clearly visible, but they become obscured later by the developing gonads. Three eumedusae were released from the gonothecae in the laboratory and were retained alive for 24 hours, during which period they reached a diameter of 0,9–1,0 mm. They performed periodical spasms of contraction. The gonads at this stage consisted of a number of small spherical aggregations along the radial canals and were presumably partly spent. The exumbrellar surface of the medusoid appeared to be pierced by an asymmetrical elliptical aperture.

Campanularia roberti[*] sp. nov.

Fig. 2

Holotype: Partridge Point, False Bay, on the weed *Sargassum longifolium* (Turn.) attached to *Ecklonia maxima* (Osbeck). Collected 24 March 1968. Catalogue number: SAM H1660.

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[*] Named after Robert W. Day, who collected the material.

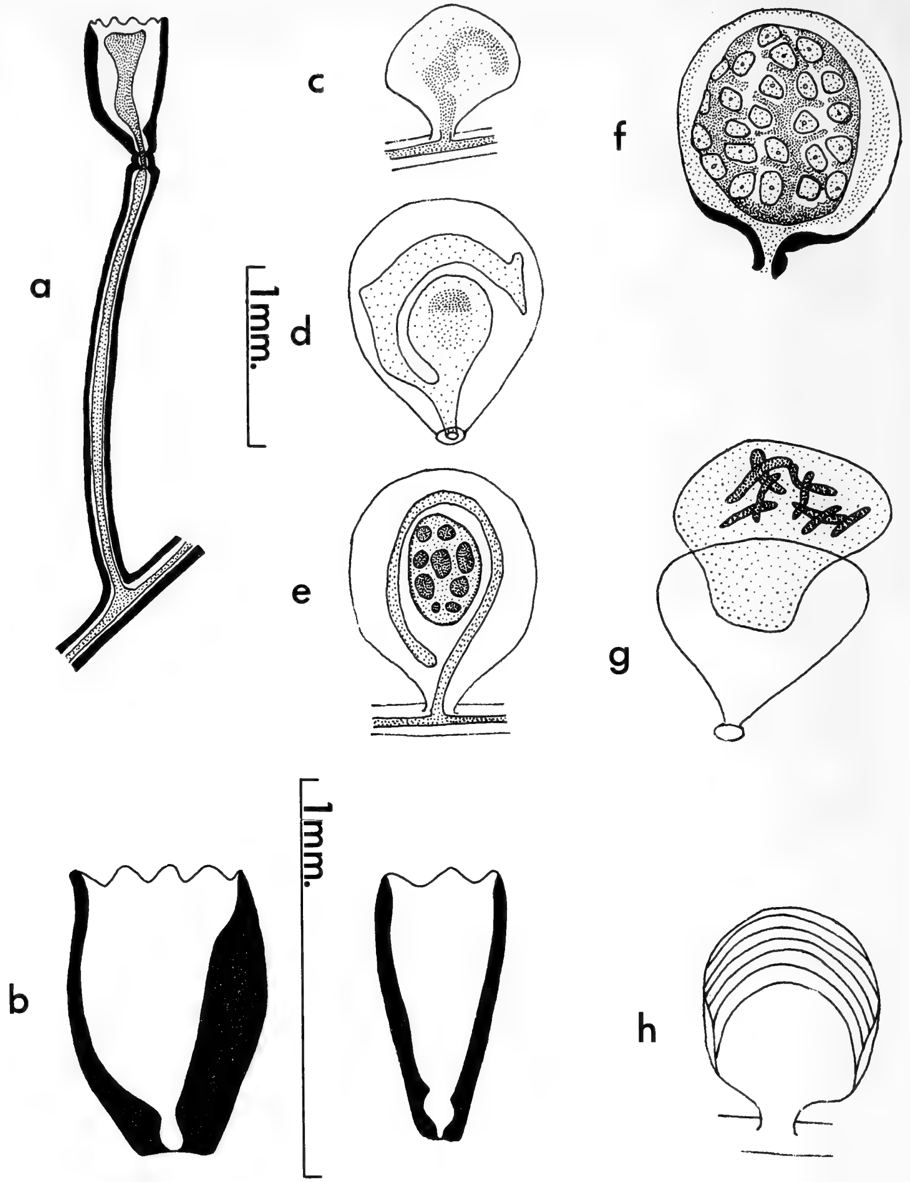

Fig. 2. *Campanularia roberti* sp. nov.

a, hydrotheca and pedicel; b, hydrothecae, left in broad view, right in end-on view; c–f, gonophores in various stages of development, f showing the branching radial canals; g, mature gonotheca with gonophore containing planulae squeezed out of opening; h, upper view of gonotheca showing concentric ridges.

Description

Hydrorhiza creeping and reticular, giving rise to solitary hydrothecae and gonothecae. Hydrothecal pedicel smooth, with a single terminal spherule, with thickened perisarc. Regeneration nodes present in some.

Hydrotheca deep-campanulate, slightly compressed, with toothed margin. Marginal teeth generally nine in number, rarely ten, triangular with bluntly rounded apices. Perisarc generally strongly thickened on two opposite sides and more so on one side than the other, imparting an oval cross-section and an asymmetrical appearance when viewed from the broad side. An annular perisarcal thickening present near base demarcating a spherical basal chamber.

Gonotheca borne directly on hydrorhiza on a short, smooth pedicel, scallop-shaped, rounded in broad view, opening around the circumference like a bivalve shell, recumbent and held with the flat lower surface against the weed; upper valve curved above, thicker than lower valve, with distinct concentric ridges when mature. Gonophore (only female present) in the form of a fixed sporosac, with four branching radial canals but no other medusoid structures, containing over 30 large eggs between the diverticuli of the radial canals. Eggs fertilized and developing into planulae within the gonotheca.

Measurements (*mm*)

Pedicel length	0,40–2,66
maximum diameter	0,13–0,24
Hydrotheca, depth	0,64–0,88
diameter at mouth (broad view)	0,38–0,55
diameter at mouth (narrow view)	0,30–0,46
Gonotheca, length including pedicel	0,75–1,50
maximum diameter	0,69–1,28

DISCUSSION

These two species are clearly closely related. Both belong to the hydranth genus *Orthopyxis* L. Agassiz, 1862, and *Campanularia pecten* belongs to the medusa genus *Agastra* Hartlaub, 1897. These two genera are now commonly included in *Campanularia* Lamarck, 1816 (Naumov 1960; Vervoort 1972; Millard & Bouillon 1974).

It is possible that *C. pecten* is the male and *C. roberti* the female of a single species, for it is not unknown among the hydroids for sexual dimorphism to occur and for the gonophore of one sex to reach a less advanced stage of development than the other. However, there are certain differences in the trophosome which distinguish the two and which support the retention of two species at least until further material is forthcoming. Thus, the hydrotheca of *C. roberti* is characteristically asymmetrical, with thicker perisarc on one side than the other, whereas *C. pecten* has the perisarc symmetrically thickened at the two narrow ends. Further, the hydrothecae of *C. roberti* are slightly larger than those of *C. pecten*, although there is an overlap between them. Finally the marginal thecal teeth of *C. roberti* are in general slightly wider than those of *C. pecten*.

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Vervoort, W. 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty Geological Observatory.—*Zool. Verh. Leiden* **120**: 1–247.

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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, 1945: 37.
Leda plicifera A. Adams, 1956: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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'. . . in *C. namacolus* (Fig. 10) . . .'

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e.g. Du Toit but A. L. du Toit
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e.g. Therocephalia, but therocephalian

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Reference to the author should be expressed in the third person

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VOLUME 67 PART 2 JUNE 1975 ISSN 0303-2515

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(*continued inside back cover*)

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Volume **67** Band
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A NEW DICYNODONT REPTILE FROM THE *TAPINOCEPHALUS* ZONE (KAROO SYSTEM, BEAUFORT SERIES) OF SOUTH AFRICA, WITH EVIDENCE OF THE JAW ADDUCTOR MUSCULATURE

By

MICHAEL A. CLUVER

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By

MICHAEL A. CLUVER
South African Museum, Cape Town

(With 7 figures)

[*MS accepted 15 August 1974*]

ABSTRACT

A new dicynodont, *Chelydontops altidentalis*, from the farm Die Cypher, Beaufort West, South Africa, is described from an incomplete skull and jaw in the South African Museum. Important characteristics of the new form are the wide intertemporal region, the vaulted anterior part of the secondary palate, the well-developed rows of teeth on the palate and dentary, and a low but distinct coronoid process of the lower jaw. Upper and lower tooth rows are bounded laterally by bony platforms, whose function is discussed in terms of jaw musculature and mastication. The coronoid process on the lower jaw indicates that the medial external adductor muscle of the lower jaw inserted on the rear of the dentary, as in the advanced pelycosaur *Dimetrodon*. It is postulated that the dorsal surface of the dentary, lateral to the tooth row, and the platform on the maxilla, lateral to the palatal tooth row, indicate the presence in life of a reptilian cheek, such as recently proposed for certain ornithischian dinosaurs. Similar but relatively larger palatal and dentary platforms are found in the chronologically younger *Endothiodon* (including *Esoterodon*, *Emydochampsa* and *Endogomphodon* as junior synonyms) and *Pachytegos*, and it is proposed that the subfamily Endothiodontinae be enlarged to include *Chelydontops* and *Prodicynodon*. In terms of jaw function, these genera appear to be distinct from other dicynodont groups.

CONTENTS

INTRODUCTION

In his treatment of the South African *Tapinocephalus* zone Dicynodontia, Boonstra (1948) briefly mentioned an unprepared skull (SAM–11558) which he considered might eventually prove to be a new endothiodont. The specimen, from the farm Die Cypher, Beaufort West, has recently been fully prepared and clearly represents a new type of dicynodont, with *Endothiodon* and possibly *Prodicynodon* its closest allies. A second specimen, a skull and jaw (SAM–12259) from Beukesplaas, Fraserburg, is generally similar to the Die Cypher

Ann. S. Afr. Mus. **67** (2), 1975: 7–23, 7 figs.

skull, but differs in some respects; lateral crushing of this specimen has made a close comparison with SAM–11558 difficult, and it has been used chiefly to provide supplementary information in areas lacking in the type.

The dicynodonts of the *Tapinocephalus* zone were last reviewed by Boonstra (1948) and Toerien (1953), but in the light of new classificatory criteria (Hotton & Cluver, in preparation), the group is once more under investigation by the present author. The specimens described and discussed below are, however, systematically sufficiently far removed from their contemporaries to warrant a separate, independent account.

SYSTEMATICS

As yet no satisfactory dicynodont classification exists. However, the following scheme, modified from Haughton & Brink (1954) and Romer (1966), may serve to indicate the systematic position of the form under consideration.

Class : Reptilia
Order : Therapsida
Suborder : Anomodontia
Infraorder : Dicynodontia
Family : Endothiodontidae
Subfamily : Endothiodontinae

Chelydontops gen. nov.

Diagnosis

Skull with wide intertemporal region and broadly exposed parietals. Pineal opening large and situated on high boss. Maxilla rising high in snout, septomaxilla entirely within nostril. Caniniform process rudimentary, vestigial caniniform tooth may be present. No anterior palatal ridges, anterior premaxillary part of palate deeply vaulted. Palatine large, meeting premaxilla. Posterior, palatal portion of maxilla raised to form prominent ledge, with medial crest bearing nine robust teeth. Choanal vault wide and deeply recessed, vomers forming narrow anterior septum. Long interpterygoidal vacuity. Medial edge of dentary bearing row of ten teeth. Dentary extended posterodorsally as a clear coronoid process.

Chelydontops altidentalis gen. et sp. nov.

Diagnosis: As for genus.

Type: Snout, occiput, partial lower jaw and cervical vertebrae in South African Museum, Cape Town (Cat. No. 11558).

Locality: Die Cypher, Beaufort West, Cape Province.

Horizon: *Tapinocephalus* zone, Beaufort Series.

Collector: L. D. Boonstra.

DESCRIPTION OF THE MATERIAL

Type specimen (SAM–11558)

Skull

The skull is represented by the major portion of the snout and the occipital segment up to the anterior border of the pineal foramen (Figs 1, 2, 3A). In the skull roof the frontals, postorbital bars and zygomatic arches are lacking, while in the ventral midline there is a gap in the pterygoid-basisphenoid central stem at the level of the internal carotid artery foramina. There is thus no contact between the front and rear halves of the skull, but as both portions agree completely in size, in colour and in texture of bone and matrix, and were (apparently) in close association when collected, there seems no reason to doubt that they represent parts of a single individual.

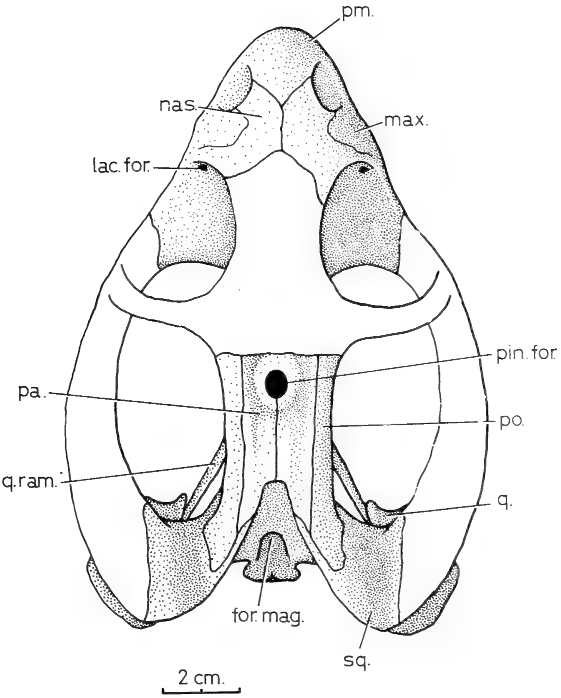

Fig. 1. *Chelydontops altidentalis* gen. et sp. nov. Skull reconstructed in dorsal view, missing areas shown in outline. One-half natural size.

In the snout the premaxilla is smoothly curved and slopes far back between the nasals. Behind the nostril the maxilla extends up to meet the nasal, and the septomaxilla is confined to within the nostril. The nasals form low bosses above the nostrils. Although neither side of the palatal rim is completely preserved, it is evident that no distinct caniniform process was present. On both sides the base of a small marginal tooth is visible.

The lacrimal is a large bone in the antero-ventral corner of the orbit; a short anterior process extends forwards on to the side of the snout to meet the nasal in front and the maxilla below (Fig. 3A). The snout is not preserved above this level, and the relationships of the frontals and pre-frontals could not be determined. However, the base of the zygomatic arch can be seen clearly in section on both sides. A large maxillary antrum is enclosed between the jugal and lacrimal, and these two bones are in turn supported anteriorly and ventrally by the maxilla and ectopterygoid. As in most dicynodonts, a large opening between the inner edges of the lacrimals, jugals and palatines leads forward from the orbital region into the bony nasal chamber.

The palate is marked by several distinctive features (Figs 2, 4). The palatal rim is low and carries a weakly developed tooth in its rear, maxillary part. There are no anterior palatal ridges on the premaxilla, but medially this bone carries a prominent posterior ridge which meets the forked anterior edge of the vomer. The anterior part of the palate and palatal rim is incomplete, but it can nevertheless be seen that the premaxilla is deeply recessed in the anterior midline so that, when complete, the secondary palate would have featured a

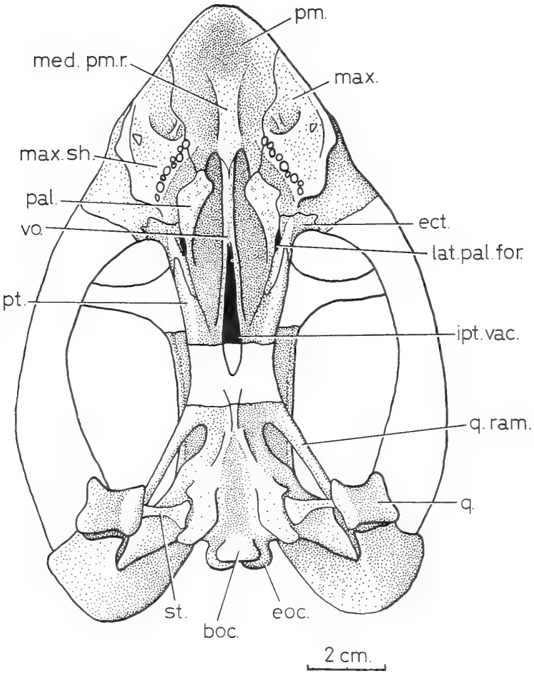

Fig. 2. *Chelydontops altidentalis* gen. et sp. nov. Skull reconstructed in ventral view, missing areas shown in outline. One-half natural size.

high and narrow anterior vault. Much of the secondary palate is made up by the premaxilla which, extending back to meet the anterior tip of the palatine, excludes the maxilla from the choana. In palatal view, both premaxilla and palatine are raised above the level of the adjoining maxilla, while laterally there is a raised platform-like area on the maxilla medial to the posterior part of the palatal rim (Fig. 2, max. sh.). This maxillary shelf, together with the palatal rim, extends backwards to terminate posteriorly as a sharply defined crest below the base of the zygomatic arch. The medial edge of the raised area bears an irregular row of nine teeth, of which a few are newly erupted. The fully developed teeth are relatively powerful, and the row extends back 17 mm from the premaxilla–maxilla suture (where the base of the leading tooth is at least partly surrounded by premaxilla) to the posterior limit of the maxillary shelf.

The palatal portion of the palatine is large and raised above the surface of the surrounding premaxilla and maxilla. Posteriorly it lies high in the side wall of the choana, medial to the ectopterygoid. This latter bone is strongly

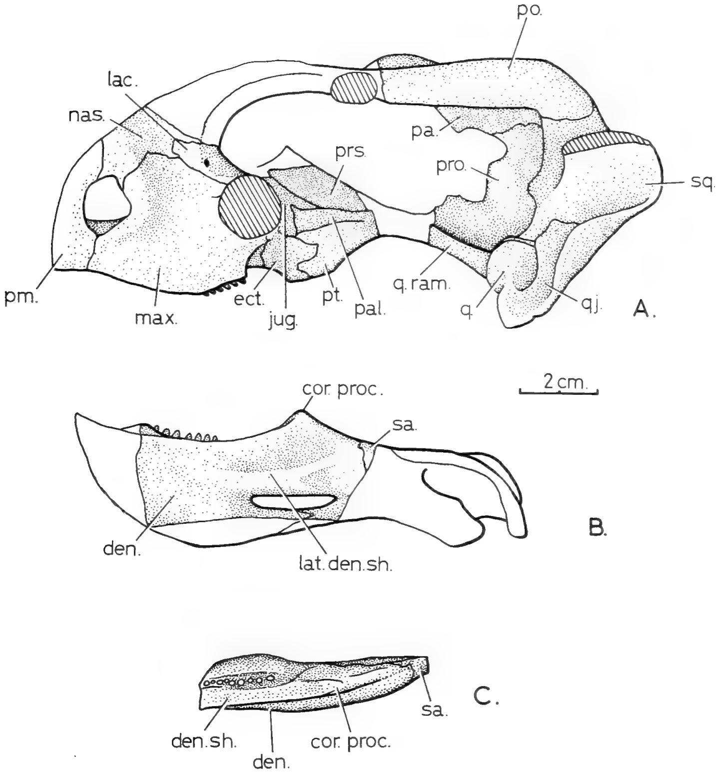

Fig. 3. *Chelydontops altidentalis* gen. et. sp. nov. A. Skull reconstructed in lateral view, missing areas shown in outline. B. Lower jaw fragment in lateral view and (C) in dorsal view. All one-half natural size.

developed, and consists of a lateral sheet, which lies beneath the base of the zygomatic arch, and a posterior portion, which helps form part of the lateral wall of the choana and appears to clasp the anterior edge of the pterygoid. This section of the choanal side wall, composed of palatine, ectopterygoid and pterygoid, is deep and the choana, seen as a whole, is a very wide and deeply vaulted structure.

Behind its junction with the premaxilla, the vomer divides the internal nares as a high, median septum, but postero-dorsally it bifurcates to enclose the anterior part of the large (but incompletely preserved) interpterygoidal vacuity.

In the occipital section the intertemporal part of the skull roof is preserved up to the anterior margin of the pineal foramen. The postorbitals are well separated by the parietals (Fig. 1) and lie mainly along the lateral margins of the temporal roof. The broadly exposed parietals form a prominent boss around the pineal foramen. The occiput is high, with the tripartite condyle set at a relatively low level. A pair of deep basioccipital tubera, separated by a median cleft, is present, and on the left side a slender stapes is partially preserved. The squamosal, supporting the quadratojugal and quadrate ventrally, is of the usual triradiate, dicynodont type.

Fig. 4. Stereophotograph of palate of *Chelydontops altidentalis* gen. et sp. nov.

Lower jaw

The middle portion (Fig. 3B, C) of each dentary is preserved and on the left side the articular is in natural articulation with the quadrate. In each jaw ten well-developed teeth are present, lying in an irregular row on the inside of the dorsal edge of the dentary. A row of posterior serrations can be seen in several of these teeth. Lateral to the tooth row the dorsal dentary surface is a flat shelf (Fig. 3C, den. sh.), gently concave in lateral view. At the level of the anterior dentary teeth, the inside edge of the dorsal dentary shelf is raised to form the beginning of a high crest, which would have continued on to the missing symphyseal region. Posteriorly the shelf extends past the end of the tooth row and terminates on the anterior face of a small coronoid process, unique in dicynodonts. From the tip of this coronoid process the dentary slopes back and down to meet the surangular.

A fairly distinct lateral dentary shelf (Fig. 3B, lat. den. sh.), for insertion of the lateral portion of the external adductor muscle, is present and overlies a long and narrow mandibular fenestra. The articular of the left side, in contact with the quadrate, appears to be of the normal dicynodont pattern.

SAM–12259

Lateral compression in this specimen has obscured some details of the intertemporal region and palate, but there are strong resemblances with the type specimen in the nature of the palatal rim, the maxillary part of the secondary palate and the dentary.

The palatal rim is complete, and only a very modest caniniform process is present. Somewhat behind the process is a marginal tooth, at the level of the anterior choanal embayments. Medial to this the maxillary is thickened to form a distinct platform, similar to that of the type specimen, and carries a number of robust teeth along its inner border. Two large teeth and one smaller one are present on the right-hand side, while on the left side there are three or possibly four teeth; crushing and dislodging of the teeth of both upper and lower jaws on this side has made an exact assessment of the tooth number difficult.

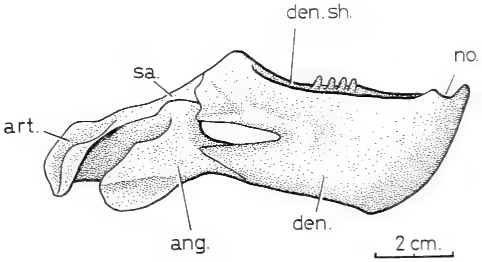

Fig. 5. *Chelydontops* ?sp. SAM–12259. Mandible in lateral view. One-half natural size.

As in the type, the palatal rim and maxillary platform lateral to the teeth are extended back to a clearly marked termination below the base of the zygomatic arch.

As far as can be seen, the anterior part of the palate slopes up fairly steeply in front of the median premaxillary ridge, but lateral compression has made the extent of this vaulting uncertain. More posteriorly, the pterygoids and ectopterygoids of each side form a deep side wall to the choana, but the shape of the vomer and the exact forward extent of the palatine is not clear.

The lower jaw (Fig. 5) is well preserved, and closely resembles what remains of the type jaw. On the dorsal surface of the dentary there is a long, wide and shallow trough, bounded by a distinct coronoid process posteriorly and by sharp edges medially and laterally. The medial edge carries a row of four teeth, which show a series of fine posterior serrations. In front of these teeth the medial edge of the dentary is continued forwards for a short way as a sharp crest, which merges anteriorly with the dorsal surface of symphysis. At the symphysis the dorsal surfaces of the two jaw rami are separated by a median cleft, but the front of the jaw is a fairly high and sharp blade, notched on each side (Fig. 5, no.).

JAW MUSCULATURE AND FUNCTION IN *CHELYDONTOPS*

JAW MUSCULATURE

Crompton & Hotton (1967) have reconstructed the jaw musculature of the dicynodonts *Emydops* and *Lystrosaurus*, and have analysed the probable range of jaw movements during mastication. A few modifications of their interpretations have been suggested by Cluver (1971, 1974), these pertaining chiefly to the crushing role played by the dentary during the final stages of the mastication cycle, and to the insertion areas on the lower jaw of the jaw adductor muscle fibres. Recently Barghusen (1968, 1972, 1973) has published a series of important papers dealing with the adductor musculature and jaw mechanics in both primitive and advanced synapsids, and many of his findings are relevant to considerations of dicynodont jaw musculature.

Areas of origin of jaw adductor muscles

In dicynodonts the highly modified temporal region provides two large areas of origin for the external adductor musculature. An inner division, the medial external adductor muscle, arose from the lateral, posterior and medial borders of the temporal fossa, these areas being formed by the squamosal and postorbital (Fig. 6B). The outer surface of the postorbital, forming the dorsal, inner border of the temporal fenestra, merges smoothly with the upper surface of the squamosal, where this bone forms the posterior border of the fenestra. This surface is continued laterally and forward on to the inside of the zygomatic arch, and in this way an extensive area of origin is formed.

Laterally to the temporal fossa the squamosal extends back and outwards as a characteristic external plate below the rear of the zygomatic arch. The anterior surface of this smoothly moulded sheet is continued dorsally on to the lateral face of the zygomatic arch, and includes the anterior face of the quadratojugal ventrally. This substantial area served for the origin of the lateral external adductor muscle (Fig. 6C), and among therapsids is found only in dicynodonts.

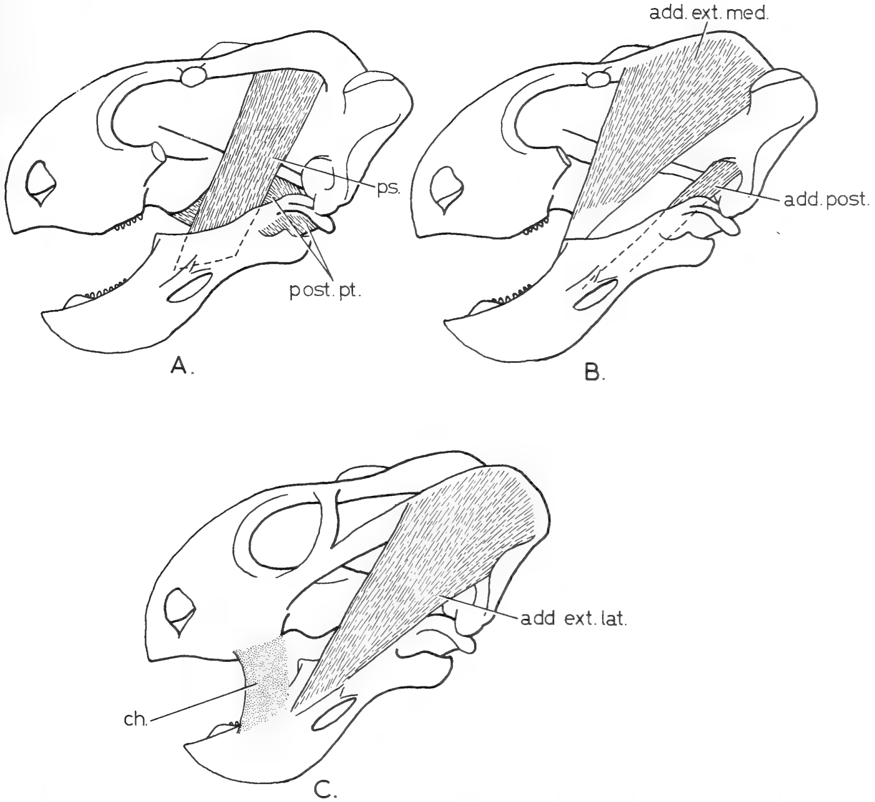

Fig. 6. *Chelydontops altidentalis.* Skull reconstructed in lateral view to show (A) pseudotemporalis and posterior pterygoideus muscles, (B) medial external adductor and posterior adductor muscles and (C) lateral external adductor muscle and cheek.

The degree of development of the intertemporal part of the skull roof varies considerably in dicynodonts. In a genus such as *Daptocephalus* the parietals are greatly reduced on the skull roof and the postorbitals approach each other closely (Ewer 1961), while in cistecephalids (Keyser 1973; Cluver 1974) the parietals are broad elements and the postorbitals and temporal fenestrae are widely separated. However, a constant feature in all dicynodonts is a clearly demarcated recess beneath the lateral edge of the inter-temporal skull roof, bounded medially by a ventral flange of the parietal and, more anteriorly, by the expanded dorsal part of the epipterygoid. This recess is similar in position to the 'medial depression' described by Barghusen (1973: 829) in the undersurface of the skull roof of the advanced pelycosaur *Dimetrodon*. Barghusen considered the depression to be the site of origin of the pseudotemporalis muscle of the internal jaw adductor group (Fig. 6A, ps.), which presumably also attached to the epipterygoid and parietal.

In addition, the area of origin of a posterior adductor muscle, also part of the internal jaw adductor musculature, can be inferred. In recent reptiles this muscle arises from the medial part of the quadrate bone, and Barghusen (1973: 831) reconstructs it in *Dimetrodon* as arising from 'the lateral face of the well-developed anterior process of the quadrate which contacts the pterygoid bone'. In a dicynodont such as *Chelydontops* the portion of the quadrate above the condyle is a high and broad sheet lying up against the squamosal and the posterior end of the quadrate ramus of the pterygoid, and is well situated to serve as a site of origin of a muscle, such as the posterior adductor, running to the inside of the lower jaw (Fig. 6B, add. post.).

In dicynodonts, the posterior pterygoideus muscle (*sensu* Barghusen 1973) of the internal adductor group very likely arose from the ventro-lateral edge of the pterygoid, where this forms the lateral boundary of the choana, and from the pterygoid's quadrate ramus (Fig. 6A, post. pt.). Such a posterior pterygoideus muscle would include both the anterior and posterior pterygoideus muscles of Crompton & Hotton (1967) and Cluver (1971).

Areas of insertion of jaw adductor muscles

The adductor musculature's attachment areas on the lower jaw are more clearly indicated in *Chelydontops* than in other dicynodonts. It seems most likely that the lateral dentary shelf, present in varying degrees of prominence above the mandibular fenestra in all dicynodonts (Crompton & Hotton 1967; Cluver 1970, 1971, 1974) marks the site of insertion of the lateral external adductor muscle (Fig. 6C). Such a purely lateral insertion area corresponds well with the lateral position of the area of origin of this muscle in dicynodonts. The insertion area of the medial external adductor muscle in *Chelydontops* is of special significance. The low but distinct coronoid process on the rear end of the dentary is strong evidence of a tendinous attachment, and it seems very likely that the large medial division of the external adductor muscle (Fig. 6B) inserted on to the lower jaw via a 'bodenaponeurosis', such as reconstructed by Barghusen (1973) in *Dimetrodon*, on the basis of comparisons with recent reptiles. This is in contrast with Crompton & Hotton's (1967) restoration, according to which the medial external adductor muscle inserts into a deep groove in the dorsal edge of the dentary behind the symphyseal region.

The pseudotemporalis muscle appears to have had a fleshy attachment on the inside of the lower jaw above the adductor (Meckelian) fossa. In *Chelydontops* the surangular and rear part of the dentary are smoothly excavated above this fossa and, in fact, it is likely that it was to accommodate a changed orientation of the pseudotemporalis muscle that the dorsal part of the lower jaw is bowed laterally in cistecephalids (Cluver 1974).

The adductor posterior muscle, arising from the anteromedial face of the quadrate, has a clear insertion site in and around the adductor fossa, while the pterygoideus posterior muscle (Fig. 6A) extended to the lower edge of the jaw and inserted on the lateral face of the angular, at least partly beneath the reflected lamina (Crompton & Hotton 1967; Cluver 1971; Barghusen 1973). A posterior slip of this muscle probably inserted on the inner surface of the retroarticular process.

With one exception, the jaw adductor musculature thus reconstructed in *Chelydontops* is essentially comparable with that restored in *Dimetrodon* by Barghusen (1968, 1973) and is readily derivable from a reptilian model. The exception is the lateral division of the external adductor muscle, this representing a basic dicynodont innovation. Moreover, it seems probable that the insertion of the medial external adductor in *Chelydontops* is typical in its position (although exaggerated in form) since the rear end of the dentary was the most anterior area of insertion of the external adductor muscle in primitive synapsids (Barghusen 1973).

In *Chelydontops* the slightly excavated dorsal surface of the dentary behind the symphysis may be compared with the deep dorsal dentary groove seen in some other dicynodonts (Crompton & Hotton 1967; Cluver 1970, 1971) but, lying as it does in front of the coronoid process and directly lateral to the tooth row, it seems unlikely that it served as an area of muscle attachment. In *Chelydontops* this part of the dentary should more properly be considered in conjunction with the raised area of maxilla lateral to the row of palatal teeth. As shown below, it is unlikely that more than the most medial part of this platform was directly involved in any chewing activity and, in effect, there is a space between the upper and lower tooth rows and the side of the snout. This structural arrangement is perhaps best explained in terms of the development of a reptilian cheek, such as reconstructed by Galton (1973) in certain ornithischian dinosaurs which show evidence of similar platforms lateral to the tooth row. In *Chelydontops*, evidence suggesting the presence of a cheek consists of the crest running back from the weak caniniform process to the rear of the maxillary platform. This crest can be interpreted as marking the dorsal line of attachment of the cheek, while its ventral attachment was most likely along the sharp lateral edge of the dorsal dentary platform. A cheek of this sort would have occupied more or less the same position as the 'Mundplatt' reconstructed by Crompton & Hotton (1967) in *Emydops*. In fact, modification of the reptilian 'Mundplatt' offers a simple derivation for the cheek reconstructed in *Chelydontops* (Fig. 6C).

The actual structure of the cheek reconstructed for *Chelydontops* is uncertain, but the possibility that it was muscular does exist. Galton (1973) suggests that musculature in his reconstructed ornithischian cheek might easily have been derived from either the reptilian levator angularis oris muscle, or the pars superficialis of the reptilian external adductor jaw musculature—a similar derivation is possible in *Chelydontops.* Crompton & Hotton (1967) reconstructed a levator oris muscle arising from the infraorbital bar in *Emydops* and inserting on the 'Mundplatt'. As shown by Galton (1973) it is not necessary to draw an analogy with mammals to postulate the presence of a muscular cheek in reptiles. When a mammalian type muscular cheek, innervated by the facial nerve, arose is uncertain; if such an event occurred in therapsids, it may have been a late development in the most progressive of therapsid lines, i.e. the cynodonts.

JAW FUNCTION

Cheek function in a reptile such as *Chelydontops* should be considered in conjunction with the probable range of jaw movements during the masticatory cycle. As shown by Crompton & Hotton (1967), the power stroke during dicynodont mastication occurred during retraction of the lower jaw, and this would certainly have been true in *Chelydontops.* While some slicing would very likely have occurred between the lateral sides of the lower jaw beak and the palatal rim, the batteries of powerful mandibular and palatal teeth suggest that considerable slicing and cutting between these teeth took place towards the end of the stroke. Both upper and lower tooth rows (best preserved in the type specimen) are obliquely orientated, with the anterior teeth of each row lying medial to the posterior teeth. Upper and lower tooth rows are practically the same distance apart, and it is apparent that strictly orthal retraction would cease when the mandibular tooth rows meet the palatal tooth rows in face-to-face contact. This arrangement would prevent the mandibular teeth from immediately reaching the inflated palatal portions of the palatines, so obviously involved in the mastication process in other dicynodonts (Crompton & Hotton 1967; Cluver 1971).

A sideways displacement of the mandible on the quadrates, to permit the upper and lower tooth rows to slide past each other, would result in a complex series of tooth-to-tooth and tooth-to-beak contacts coming into play, during which only one palatine at a time would be involved. However, movement of this type would be possible only if the articulation between the quadrate and lower jaw lacked the tightly interlocking articular facets seen in most dicynodonts (Cluver 1974). Since, as far as can be seen, this is not the case in *Chelydontops,* an alternative possibility involving two separate phases of masticatory activity may be considered. Thus, apart from a shearing phase during which the lower jaw is drawn back from a protracted position until the mandibular teeth meet the palatal tooth rows, a purely up-and-down biting action, involving both tooth rows and the palatines, could have taken place with the lower jaw in an almost fully retracted position.

With only incomplete material available, the range of lower jaw movements during mastication must remain uncertain, but it seems clear that the upper and lower tooth rows played an important part in the process. Retention of, and control over, partly chewed plant matter, which would tend to move to the side of the mouth, could become a critical factor, and the need for a cutaneous or muscular sheet in the corner of the mouth might very likely arise. A non-contractile cheek would serve merely to retain masticated food until this could be drawn back into the oral cavity by the tongue. A muscular cheek would be capable of actively assisting in mastication by returning partly-chewed material to the teeth. It is noteworthy that only in forms where the palatal and mandibular teeth are strongly developed, such as *Chelydontops* and *Endothiodon*, is a lateral maxillary shelf formed; to this extent, jaw function sets these genera apart from other dicynodonts.

AFFINITIES OF *CHELYDONTOPS*

In several of its characters *Chelydontops* closely resembles members of the sub-family Endothiodontinae, which, according to Cox (1964), includes the genera *Endothiodon* (with *Esoterodon*, *Emydochampsa* and *Endogomphodon* as junior synonyms) and *Pachytegos*, the latter from the Ruhuhu Valley of Tanzania. Resemblances between *Chelydontops* and *Endothiodon* involve features of the palate and mandible. Thus, the anterior part of the secondary palate in *Endothiodon* is deeply vaulted as in *Chelydontops*, and there is no true caniniform process. A ventral process of the anterior, premaxillary part of the palatal rim, characteristic of *Endothiodon*, is seen also in SAM–12259—this portion of the palatal rim is incomplete in the *Chelydontops* type specimen. Prominent features in both the palate and mandible of *Endothiodon* are the wide and shallow troughs lying lateral to the upper and lower tooth rows. In the palate (Fig. 7A) this is especially marked, and the shelf of each side is bounded by a distinct crest which is extended back and outwards below the zygomatic arch as in *Chelydontops*. Cox (1964) mentions this feature, which may be regarded as an expanded equivalent of the maxillary platform of *Chelydontops* and indication of a fairly extensive cheek. The palatal part of the premaxilla in *Endothiodon* also extends far back, but does not meet the palatine as it does in *Chelydontops*. A point of importance is the rooting in *Endothiodon* of the first two palatal teeth in the rear of the premaxilla. Unfortunately it was not possible to determine with certainty whether the first tooth in *Chelydontops* is placed in the premaxilla in the same way, but it is clear that at least part of the base of this tooth is surrounded by the premaxilla.

Although these are for the most part important resemblances, *Chelydontops* differs sharply from *Endothiodon* in the retention of a broad intertemporal region, with widely exposed parietals, and also in the apparently smoothly rounded snout, without the longitudinal ridges so characteristic of the dorsal surface of the *Endothiodon* snout.

Besides *Endothiodon*, *Chelydontops* shares several features with the poorly-known genus *Prodicynodon* (Broom 1912). The type specimen of *Prodicynodon*

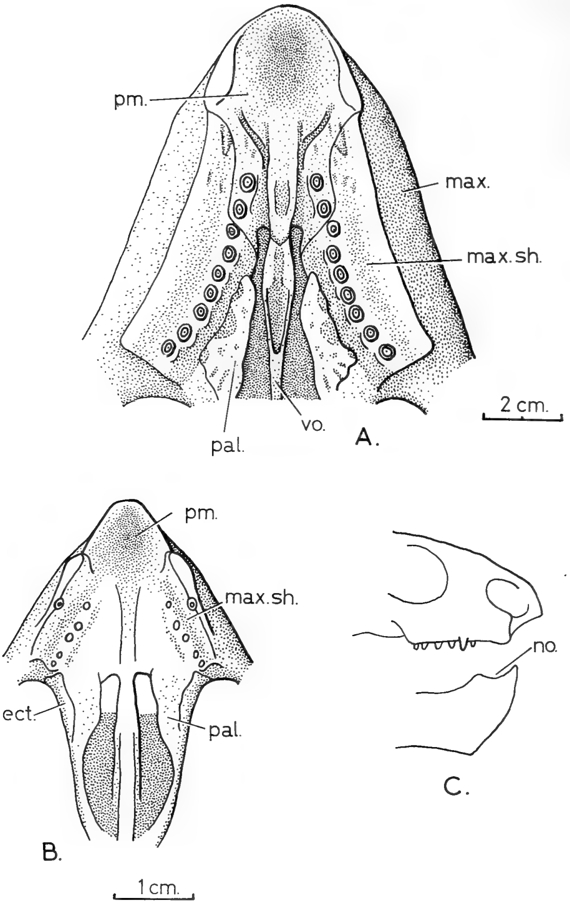

Fig. 7. *Endothiodon uniseries* BMNH–49414. Palatal reconstruction of type specimen. B. *Prodicynodon beaufortensis* AMNH–5509. Palatal reconstruction of type specimen. Both one-half natural size.

pearstonensis (AM–2551) is too crushed and incomplete to allow adequate comparisons to be made, but recent preparation of the type specimen of *P. beaufortensis* (AMNH–5509) shows that in addition to the pointed anterior beak of the lower jaw, typical of *Endothiodon* (Cox 1964), this form has a row of *Endothiodon*-like teeth bounded laterally by a wide, shallow trough (Fig. 7B). A small marginal tooth lies on the palatal rim, in the same position as in *Chelydontops*, and a caniniform process is absent. However, a weak ventral process at the maxilla–premaxilla meeting on the palatal rim resembles that of *Endothiodon* and *Chelydontops*. In the palate the premaxilla is vaulted in the endothiodontinid manner to receive the anterior tip of the lower beak, while a notch behind this anterior tip is reminiscent of the condition in SAM–12259.

Cox (1964) recognizes two genera in the subfamily Endothiodontinae, these being *Endothiodon* itself, from the Endothiodon zone (*Cistecephalus* zone of Kitching 1970) and *Pachytegos* from the Ruhuhu Beds of Tanzania. It now seems necessary to include *Chelydontops* and *Prodicynodon* in this subfamily. *Prodicynodon pearstonensis* is from Pearston, and *Prodicynodon beaufortensis* is from Kuilspoort, Beaufort West; both are probably from *Endothiodon* zone (Kitching's *Cistecephalus* zone) strata. *Chelydontops,* from the *Tapinocephalus* zone of Beaufort West, represents the earliest known member of this distinctive group of dicynodonts.

SUMMARY

The skull and mandible of *Chelydontops altidentalis* from the *Tapinocephalus* zone of the Beaufort Series show strong affinities with *Endothiodon* and *Prodicynodon,* and, together with *Pachytegos* of Tanzania, these three genera should be included in the subfamily Endothiodontinae. While several conservative characters and its low stratigraphic occurrence make *Chelydontops* a primitive (but not necessarily ancestral) member of the subfamily, a functional reconstruction of the skull helps interpret the characteristic skull structure of the group as a whole. A clear coronoid process on the dentary allows a reconstruction of the external jaw adductor muscles to be made with fair confidence, while a shelf lateral to each upper tooth row is taken as indication of the former presence of a reptilian cheek, such as has been recently proposed for ornithischian dinosaurs. There is a possibility that fibres from either the levator angularis oris or adductor externus lateralis muscles had invaded the primarily non-contractile cheek, which was very likely derived from a reptilian 'Mundplatt'.

With the identification of *Chelydontops altidentalis,* the *Endothiodon* grade of dicynodont development can be traced farther back into the Permian than before, and since the functional innovations seen in *Chelydontops* are continued and improved upon in the later genera, this grade can now be more closely defined and better understood.

ACKNOWLEDGEMENTS

I am indebted to Drs A. J. Charig and Eugene S. Gaffney of the Departments of Vertebrate Palaeontology of, respectively, the British Museum (Natural History), London, and the American Museum of Natural History, New York, for permission to study and prepare specimens in their charge, and to Mr Gilbert Stucker of the American Museum of Natural History for the preparation of the type skull of *Prodicynodon beaufortensis.* A study grant from the South African Council for Scientific and Industrial Research and the Trustees of the South African Museum enabled me to visit the above institutions during 1972/73.

For the loan of the type specimen of *Prodicynodon pearstonensis* I am indebted to the authorities of the Albany Museum, Grahamstown. The preparation and photography of the type specimen of *Chelydontops altidentalis* and the related specimen SAM–12259 were undertaken by, respectively, Imogen M. Chesselet and Neville J. Eden, of the Department of Palaeontology, South African Museum.

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ABBREVIATIONS

add. ext. lat.	lateral division of external adductor muscle
add. ext. med.	medial division of external adductor muscle
add. post.	posterior adductor muscle
ang.	angular
art.	articular
boc.	basioccipital

ch. . . .	cheek
cor. proc. . .	coronoid process
den. . . .	dentary
den. sh. . .	dentary shelf
ect. . . .	ectopterygoid
eoc. . . .	exoccipital
for. mag. . .	foramen magnum
ipt. vac. . .	interpterygoidal vacuity
jug. . . .	jugal
lac. . . .	lacrimal
lac. for. . .	lacrimal foramen
lat. den. sh. .	lateral dentary shelf
lat. pal. for. .	lateral palatal foramen
max. . .	maxilla
max. sh. . .	maxillary shelf
med. pm. r. .	median premaxillary ridge
nas. . . .	nasal
no. . . .	notch
pa. . . .	parietal
pal. . . .	palatine
pin. for. . .	pineal foramen
pm. . . .	premaxilla
po. . . .	postorbital
post. pt. . .	posterior pterygoideus muscle
ps. . . .	pseudotemporalis muscle
pt. . . .	pterygoid
q. . . .	quadrate
qj. . . .	quadratojugal
q. ram. . .	quadrate ramus of pterygoid
sa. . . .	surangular
sq. . . .	squamosal
st. . . .	stapes
vo. . . .	vomer
AM . .	Albany Museum, Grahamstown
AMNH . .	American Museum of Natural History, New York
BMNH . .	British Museum (Natural History), London
SAM . .	South African Museum, Cape Town

6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., etc.

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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 (figs 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:
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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

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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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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(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.

MICHAEL A. CLUVER

A NEW DICYNODONT REPTILE FROM THE *TAPINOCEPHALUS* ZONE (KAROO SYSTEM, BEAUFORT SERIES) OF SOUTH AFRICA, WITH EVIDENCE OF THE JAW ADDUCTOR MUSCULATURE

VOLUME 67 PART 3 JUNE 1975 ISSN 0303-2515

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CAPE TOWN

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(c) *Table of contents* giving hierarchy of headings and subheadings
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(continued inside back cover)

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TAXONOMIC STATUS OF THE PYGOCEPHALOMORPHIC CRUSTACEA FROM THE DWYKA 'WHITE BAND' (PERMO-CARBONIFEROUS) OF SOUTH AFRICA

By
BRIAN KENSLEY

Cape Town Kaapstad

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By

BRIAN KENSLEY

South African Museum, Cape Town

(With 4 figures)

[*MS accepted 14 October 1974*]

ABSTRACT

The taxonomic status of *Notocaris tapscotti* Broom, a pygocephalomorphic crustacean from the Dwyka 'White Band' of South Africa is discussed, a reconstruction of the external morphology suggested and new collecting localities recorded.

CONTENTS

INTRODUCTION

Since 1923, when Woods gave a brief description of a peracaridean crustacean from Kimberley under the generic name *Pygocephalus*, some confusion has arisen regarding the status of this organism. Additional localities of this crustacean have since been found, this new material allowing the description of the fossil to be supplemented. The purpose of this paper is to record these localities and to attempt to resolve the taxonomic confusion.

The following works refer to Dwyka pygocephalomorphic crustaceans from South Africa:

Rogers & Du Toit (1909: 193) mention the presence of crustacean fossils 'probably *Anthrapalaemon*' in the Upper Dwyka shales, while Haughton (1919) records *Anthrapalaemon* from the Dwyka White Band at Orange River Station.

Woods (1923) recorded a *Pygocephalus* from the Dwyka White Band at Kimberley, but did not provide a specific name.

Broom (1931) re-examined Woods' material and gave the species the name *Notocaris tapscotti* n. gen. et sp.

Du Toit (1954) and Haughton (1969) merely repeat the previous records of *Notocaris* and *Anthrapalaemon*.

Fabre (1967) described *Pygaspis ginsburgi* from material collected at Laingsburg, Cape, also from the Dwyka White Band.

Ann. S. Afr. Mus. **67** (3), 1975: 25–33, 4 figs.

Secretan (1967) in a discussion of lines of evolution in the Archaeostraca, deals with *Pygaspis ginsburgi*, its tagmatization and segmentation.

Brooks (1969) synonymized *Pygaspis* Beurlen (type species *P. brasiliensis*) and *Liocaris* Beurlen with *Paulocaris* Clarke. Brooks incorrectly ascribed the specific name *tapscotti* to Woods. Pinto (1971), however, re-examined the South American species of *Pygaspis*, *Liocaris*, and *Paulocaris*, and concluded that the three genera should be maintained. He also tentatively suggested that *Pygaspis* (Beurlen 1934) was a synonym of *Notocaris* (Broom 1931). Savage (1971) described trails from the Dwyka of Natal and related them to syncaridan and peracaridan crustaceans, although not actually correlating the trails with any Pygocephalomorpha.

McLachlan & Anderson (1973) review and contribute to the evidence for marine conditions during Dwyka times in South Africa, but note that by the time of the deposition of the White Band (Upper Carboniferous or Lower Permian), with its associated crustaceans, palaeoniscid fish, and the small aquatic reptile *Mesosaurus*, conditions were probably non-marine. (This conclusion has by no means been fully proven.)

In their list of Dwyka invertebrate fossils (1973: 54) McLachlan & Anderson conclude that the names *Anthrapalaemon*, *Pygaspis ginsburgi* and *Notocaris tapscotti* probably refer to the same crustacean.

SYSTEMATICS

Superclass CRUSTACEA

Class MALACOSTRACA

Subclass EUMALACOSTRACA

Superorder EOCARIDA

Order PYGOCEPHALOMORPHA

Family **Pygaspidae**

Genus *Notocaris* Broom, 1931

Generic diagnosis

Carapace lacking mid-dorsal carina, cervical groove, and tubercles, but possessing 1–3 antero-lateral spines, as well as a suprabranchial suture. Abdomen reflexed, somewhat reduced.

Discussion

Pinto (1971) notes that it is necessary to compare '*Pygaspis*' and *Notocaris*, as these may well be synonymous. Comparison of *Pygaspis brasiliensis* and *Notocaris tapscotti* shows that several differences exist in the nature of the carapaces. In the former species the carapace is covered with tiny tubercles, especially well developed at the cervical sulcus and dorsal carina. There are no antero-lateral spines, but five or six spaced lateral spines, while a bifurcate cervical sulcus curves posteriorly in the medio-dorsal region, forming a smooth carina which stretches almost to the posterior margin. In *Notocaris* there is a well-developed antero-lateral spine (not always preserved or visible in many specimens) as well as one or two lateral spines. The carapace, however, bears no sign of tubercles, a cervical groove, or median carina, but signs of a longitudinal suprabranchial suture can be detected on a few specimens.

Whether these characters are of generic or infrageneric significance amongst the pygocephalomorphic crustaceans requires investigation, as indeed does the whole generic complex within this group. Presence or absence of carapace grooves, carinae, and spines amongst living crustaceans, e.g. the Caridean decapods, is of definite value in generic separation. If this applies in the present case, the South American *Pygaspis* and the South African *Notocaris* must be maintained as valid genera.

Notocaris tapscotti Broom

(Figs 1–4)

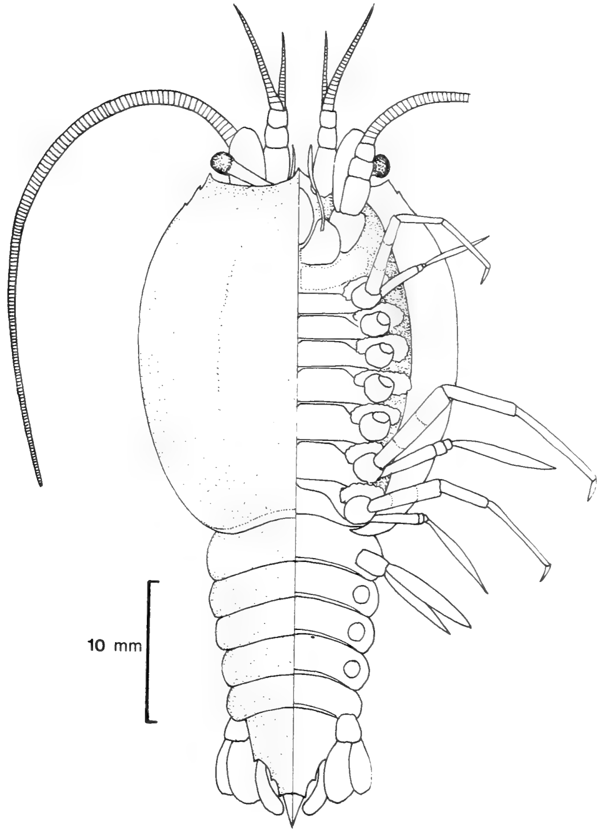


Fig. 1. Dorsal/ventral reconstruction of *Notocaris tapscotti*.

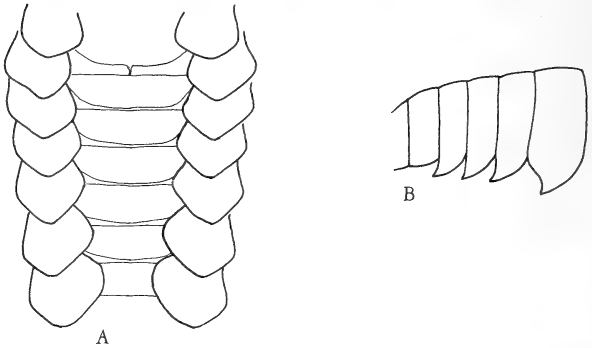


Fig. 2. A. Reconstruction of ventral view of female thorax, showing oostegites. B. Pleon in lateral view.

Description

Exoskeleton very thin. Carapace almost circular (when compressed), apparently attached to the body only in the anterior region. No sign of a medio-dorsal carina. Rostrum short, triangular. Antero-lateral corner of carapace bearing one small acute spine; occasionally a second or even a third tiny spine may be seen posterior to the antero-lateral spine. Anterior margin of carapace slightly concave. A faint longitudinal suprabranchial suture, stretching from the region of the anterior margin to the posterior margin may be seen on the carapace of some specimens. Posterior margin of carapace dorsally concave. Abdomen usually under thorax, consisting of five segments plus telson. (A reduced first segment, hidden by the posterior part of the thorax and carapace may be present.) Pleura of abdominal segments apically acute, apices directed posteriorly.

Antennule with 3-segmented peduncle, basal segment equal in length to two distal segments together, peduncle extending beyond antennal scaphocerite. Inner flagellum slightly shorter than outer, latter only slightly longer than peduncle.

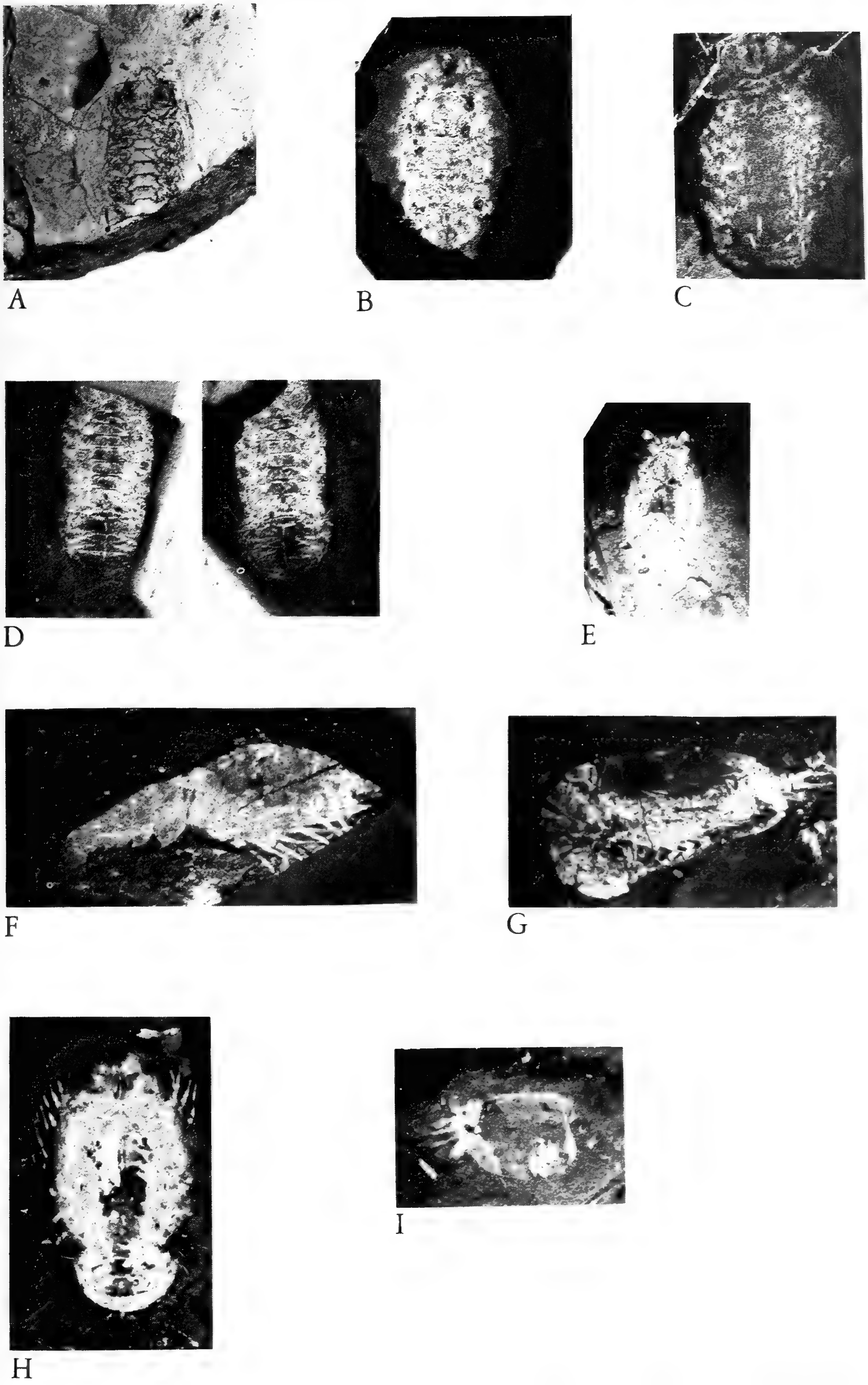
Antennal scaphocerite elongate-oval, reaching to end of second segment of antennular peduncle. Single flagellum reaching posteriorly to level of posterior carapace margin.

Eyestalks slender, situated dorsal to the antennae.

Epistome ventral, elongate-oval, separating the mandibles. Position and structure of the mouthparts uncertain. An elongate slender mandibular palp

Fig. 3. *Notocaris tapscotti.* (All figures natural size.) A–D. Laingsburg. E. Ratelklip, Calvinia. F–I. Kimberley.

A. Specimen showing ventral sternites and eyestalks. B–D. The Laingsburg specimens preserved in dark grey shale, appear to have a 'smear' of white material surrounding and obscuring the fossil and its impressions. E. Specimen showing eyestalks. F–G. Specimens in lateral view. Note pleonal pleura, peraeopodal exopodites, and antennae. H. Specimen showing typically enrolled pleon. I. Carapace in lateral view. Note also antennal scaphocerites.



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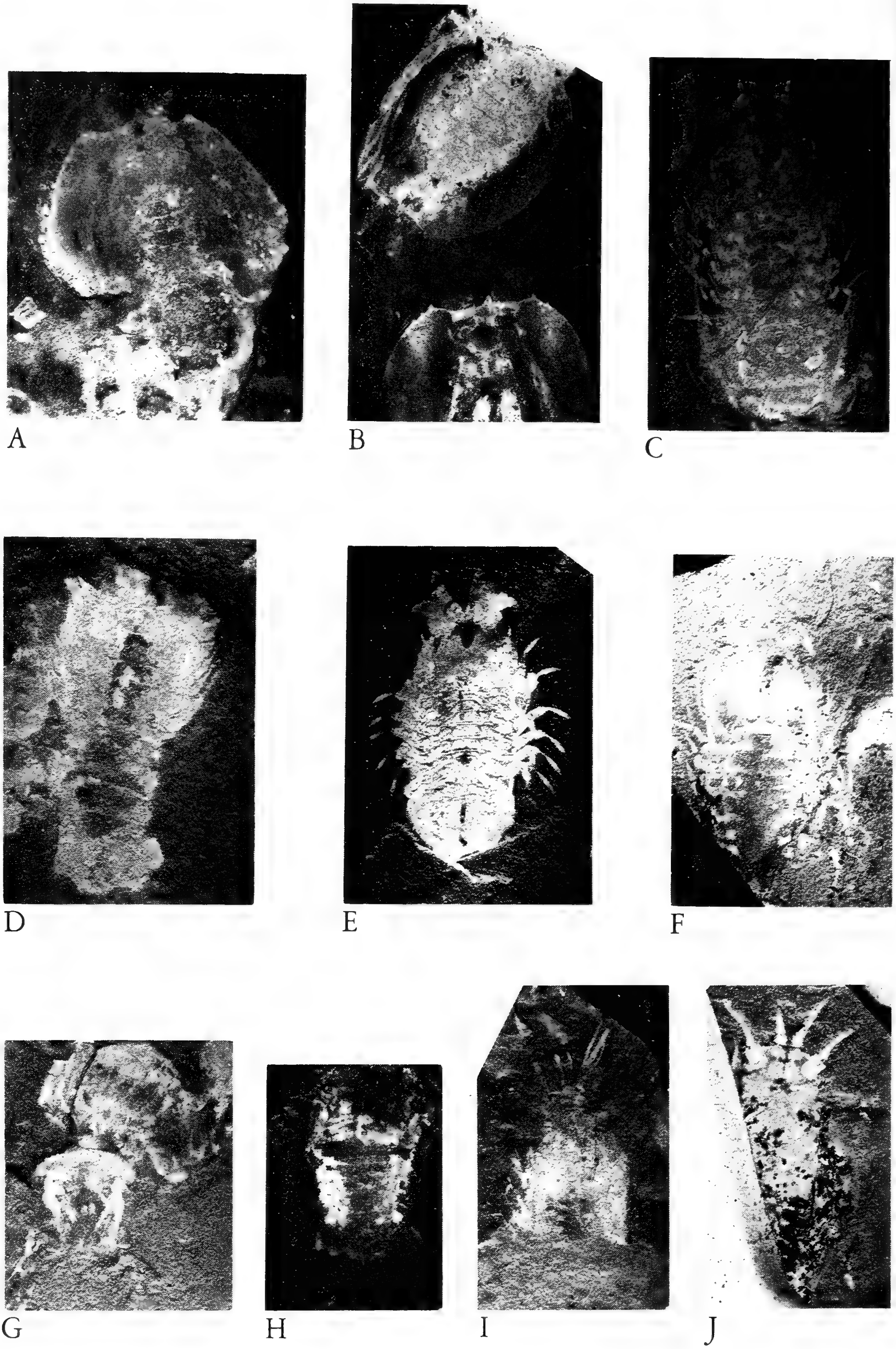

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present, the distal portion protruding beyond the anterior carapace margin, medial to the antennular peduncles.

Seven posterior appendages essentially similar, biramous. Exopod consisting of an elongate basal segment, two short distal segments, plus plume-like flagellum. Endopod longer than exopod, consisting of short dactyl, slender propodus one-third longer than carpus, three or four proximal segments indistinct. In female, seven pairs of overlapping roughly circular oostegites, those of opposite sides not meeting, the brood pouch thus remaining open. Seven series of gills present around the bases of the peraeopods, exact structure indistinct.

Pleopods seldom seen, biramous, consisting of short protopod and two plume-like rami.

Uropods consisting of short basal segment plus two broad rami; outer ramus shorter and narrower than inner.

Telson triangular, bearing three lateral spines plus an articulating median spine extending beyond furcal lobes. Latter flattened, strongly curved. There is still some uncertainty about the exact proportions of the uropodal rami.

MATERIAL AND LOCALITIES

		Carapace length range (including rostrum)
Kimberley, Cape	28.45S, 24.46E	7–27 mm
Laingsburg, Cape	33.12S, 20.51E	14–19 mm
Loeriesfontein, Cape	30.59S, 19.29E	13–28 mm
Ratelklip, district Calvinia, Cape	32.02S, 19.48E	13 mm
Orange River Station district Hopetown, Cape	29.38S, 24.15E	(material not seen)

Discussion

The presence of two closely-related genera, viz. *Notocaris* and *Pygaspis*, each represented by a single very similar species from the same stratum (i.e. the White Band) of the Dwyka of the Great Karoo Basin (McLachlan & Anderson 1973) demands close scrutiny. Fabre (1967), in discussing the affinities of his new species, *P. ginsburgi*, concludes that it is closely related to the South American *P. brasiliensis*. Regarding *Notocaris*, Fabre mentions having examined some material of *N. tapscotti* in the Albany Museum, Grahamstown, but did not see any of the Kimberley material. He notes similarities in size, appendages, and

Fig. 4. *Notocaris tapscotti* (All figures natural size.) A–J. Loeriesfontein.
A. Carapace showing short triangular rostrum and acute anterolateral angles. B. Carapace showing rostrum, antero-lateral spines, and supra-branchial suture. C. Note antennal peduncle structure. D. Specimen with extended pleon, in dorsal view. E. Note peraeopodal exopodite structure. F. Note antennal structure. G. Detached pleon above; possibly a single pleonal segment with its attached pleopods below. H. Extended pleon. Note telsonic and uropodal structure. I–J. Note antennal and antennular structure.

general structure but without closer examination of *Notocaris* material, prefers to place his material in the genus *Pygaspis*.

Examination of type material of *Notocaris tapscotti* from Kimberley, the type material of *Pygaspis ginsburgi* from Laingsburg, as well as additional material from Loeriesfontein, Calvinia and Laingsburg, Cape, makes it obvious that only one species is involved here. Fabre observes that Woods mentions enrolled individuals (individus enroulés) and that this could not clearly be seen in the Laingsburg specimens. In fact, Woods meant the flexure of the abdomen, and from Fabre's figures 2 and 3, it is obvious that his material also showed this flexure, although the ventral view (fig. 3) is somewhat confusing regarding the uropod and telsonic structure. No differences regarding general form, or structure of the appendages, can be detected, which would suggest that not more than one species is involved amongst the material from Kimberley, Laingsburg, and Loeriesfontein. As Broom's name has precedence, all the known pygocephalomorphic crustaceans from the abovementioned localities must therefore bear the name *Notocaris tapscotti*, while *Pygaspis ginsburgi* becomes a synonym of this earlier name.

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WOODS, H. 1923. Note on *Pygocephalus* from the Upper Dwyka shales of Kimberley.—*Trans. geol. Soc. S. Afr.* **25**: 41–42.

6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., 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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'
'. . . 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

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'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.

BRIAN KENSLEY

TAXONOMIC STATUS OF THE PYGOCEPHALOMORPHIC CRUSTACEA FROM THE DWYKA 'WHITE BAND' (PERMO-CARBONIFEROUS) OF SOUTH AFRICA

VOLUME 67 PART 4 JULY 1975 ISSN 0303-2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes 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.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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MARINE ISOPODA FROM THE CONTINENTAL SHELF OF SOUTH AFRICA

By

BRIAN KENSLEY

Cape Town Kaapstad

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By

Brian Kensley

South African Museum, Cape Town

(With 27 figures and 3 tables)

[*MS accepted 15 October 1974*]

ABSTRACT

A collection of marine isopods taken from the continental shelf on the Agulhas Bank in the regions of Still Bay, False Bay, Saldanha Bay, and the southern west coast, is dealt with. Descriptions and figures of two new genera, viz. *Agulanthura* and *Austroarcturus*, as well as fourteen new species are provided.

CONTENTS

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INTRODUCTION

As part of a survey of the fauna of the continental shelf of South Africa, the Zoology Department of the University of Cape Town carried out a bottom transect in a line off the coast from Still Bay, Cape. This line extended over the relatively shallow platform of the Agulhas Bank in a south-easterly direction. The samples were taken from the university vessel, the *T. B. Davie*, in June 1972 and May 1973. The bottom fauna was sampled from depths of 15 to 350 metres by means of trawls, dredges, and grabs. The isopods collected were submitted to the South African Museum for identification, together with some samples from False Bay, Cape, Saldanha Bay, Cape, and the southern west coast, thought to have a bearing on the material from the Agulhas Bank.

Fifty-four species, of which fourteen are new, are described in this study; also two new genera.

A discussion of zoogeography, ecology, and distributional patterns for the area will be carried out by members of the Zoology Department, once all the animal groups (most of which have proved to be extremely interesting) have been identified.

The bulk of the collection of isopods is housed in the Zoology Department

Ann. S. Afr. Mus. **67** (4), 1975: 35–89, 27 figs, 3 tables.

of the University of Cape Town, while all type material is in the collection of the South African Museum.

In the accompanying figures, all dimensions are in millimetres.

SPECIES LIST

The material dealt with in this paper comes from the following localities:

False Bay (FAL) approximately 34°S., 18°E.
Lambert's Bay (LBT) 32.04S., 18.20E.
South coast dredge material (SCD)
Still Bay (SST) approximately 35°S., 22°E.
Saldanha Bay (SB) 33.01S., 17.58E.
Southern west coast (WCD)

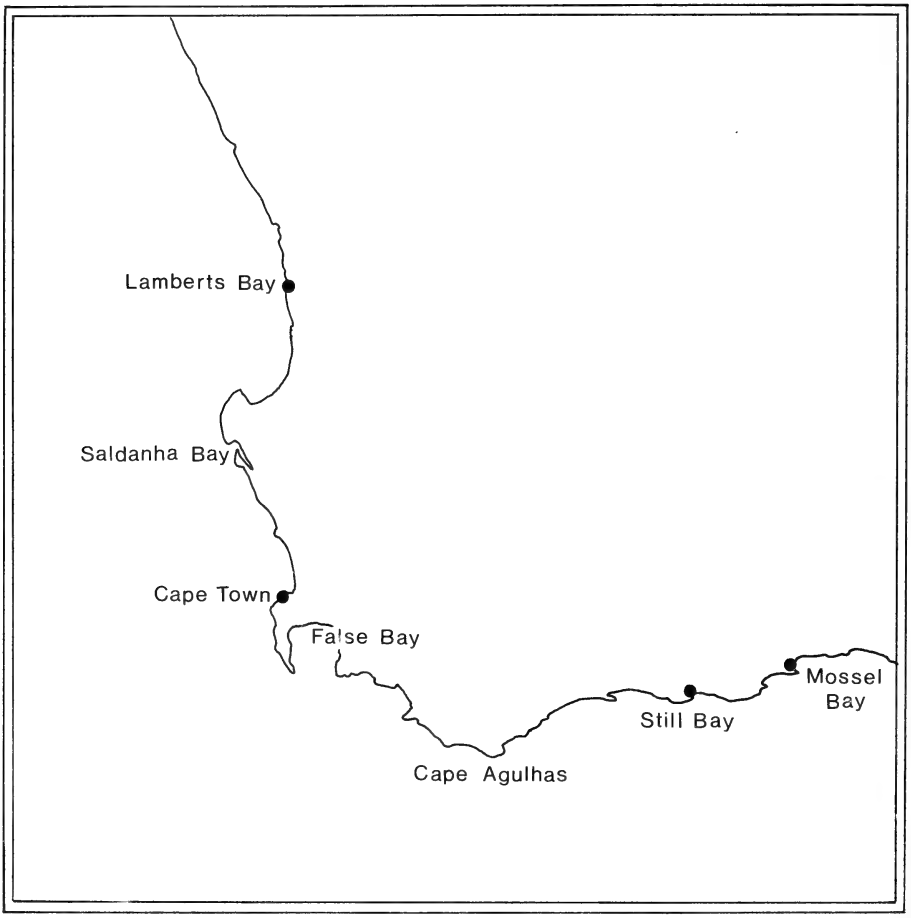

Fig. 1. Coastline of the south-western Cape, showing collecting localities.

	Cat. No.	*Depth (M)*	*Substrate*
Suborder VALVIFERA			
Family **Arcturidae**			
Antarcturus kladophorus Stebbing	SST.11.D	200	Coarse khaki sand and rock
Arcturella brevipes Barnard	SST.47.Q	30	Coarse sand and shell
	SST.109.Q	30	Rock
Arcturella corniger (Stebbing)	SST.11.C	200	Coarse khaki sand and rock
	SST.96.R	120	Rock and shell
Arcturella lobulata Barnard	SST.96.W	120	Rock and shell
Arcturina hexagonalis Barnard	FAL.487.D	62	Green sand and shell
	FAL.496.O	42	Rock
	FAL.506.I	68	Yellow sand
	FAL.510.U	68	Yellow sand
	FAL.654.T	75	Khaki sand and shell
	FAL.657.E	75	Khaki sand, shell and gravel
	FAL.658.T	87	Fine khaki sand and shell
	FAL.674.X	66	Khaki shell and sand
	FAL.686.X	61	Fine khaki sand
	FAL.702.R	44	Khaki sand
	FAL.706.S	87	Khaki sand
	FAL.798.E	87	Green mud, shell and sand
	FAL.840.H	49	Sand and rock
	SST.101.E	80	Coarse sand and shell
Arcturina scutula sp. nov.	FAL.654.S	75	Khaki sand and shell
	FAL.658.U	87	Fine khaki sand
	FAL.670.B	66	Coarse khaki sand and shell
Arcturina triangularis Barnard	SST.61.U	15	Sand and fine shell
Astacilla bacillus Barnard	SST.11.C	200	Coarse khaki sand and rock
	SST.27.U	80	Coarse sand and shell
Austroarcturus africanus sp. nov.	FAL.335.D	51	Coarse shell and sand
	FAL.428.P	41	Shell
	FAL.442.E	39	Sand
	FAL.589.E	—	—
	SB.187.J	13	Coarse sand and shell
	SB.270.H	15	Green mud, shell
	SB.304.U	20	Coarse shell
	SCD.243.N	49	Sand, mud, rock
	SCD.293.W	84	Coarse sand and shell
	SCD.337.P	42	Mud
	SCD.339.P	42	Mud
	WCD.206.R	50	Shell
	WCD.211.K	79	Shell, sand, green mud
Austroarcturus foveolatus sp. nov.	FAL.760.N	71	Coarse green sand
	SCD.204.E	183	Khaki sand
	SCD.235.C	183	Khaki sand
	SCD.272.O	182	Khaki sand and shell
	SCD.326.E	172	Dark mud
	SST.1.Y	200	Coarse khaki sand
	SST.11.J	200	Coarse khaki sand and rock
Holidotea unicornis Barnard	SST.101.G	80	Coarse sand and shell
Microarcturus laevis sp. nov.	FAL.423.D	48	Khaki sand and shell
	FAL.803.K	75	Coarse sand and shell
Microarcturus ornatus sp. nov.	SST.10.H	200	Coarse khaki sand and rock
	SCD.217.R		
Microarcturus quadriconus sp. nov.	SST.101.H	80	Coarse sand and shell

	Cat. No.	*Depth (M)*	*Substrate*
Microarcturus similis (Barnard)	SST.40.J	50	Green mud
	SST.46.C	50	—
	SST.106.A	50	Green mud
Neastacilla tranquilla sp. nov.	SST.11.F	200	Coarse khaki sand and rock
Pleuroprion chuni (zur Strassen)	SST.11.E	200	Coarse khaki sand and rock
Family **Idoteidae**			
Synidotea hirtipes (Milne Edwards)	SST.46.B	50	—
	SST.91.V	200	Rock
	SST.102.N	80	Coarse sand and shell
	SST.106.B	50	Green mud
Synidotea setifer Barnard	SST.101.F	80	Coarse sand and shell
Suborder ANTHURIDEA			
Family **Anthuridae**			
Agulanthura serenasinus sp. nov.	FAL.487.E	62	Green sand and shell
	FAL.496.L	42	Rock
	FAL.654.N–R	75	Khaki sand, shell
	FAL.685.B–D	29	White shell and sand
	FAL.666.X–Y	26	Sand, shell and gravel
	FAL.763.R–S	56	Fine green sand
	SCD.188.P	97	Green mud
	SCD.329.R	22	Fine sand and shell
	SST.67.S	20	Sand and coral fragments
	SST.74.G	—	—
Apanthura africana Barnard	SST.5.L	200	Coarse khaki sand
	SST.17.E	200	Coarse khaki sand and rock
	SST.31.V	80	Coarse khaki sand and shell
	SST.76.U	15	Coarse sand
	SST.92.B	200	Rock and sand
Exanthura sp.	SST.1.X	200	Rock and coarse khaki sand
Exanthura filiformis (Lucas)	SST.17.D	200	Coarse khaki sand and rock
	SST.21.R	120	Sand and rock
	SST.101.J	80	Coarse sand and shell
Haliophasma cf coronicauda Barnard	SST.37.K	80	Coarse sand and shell
	SST.101.C	80	Coarse sand and shell
Haliophasma foveolata Barnard	SST.8.C	200	Coarse khaki sand
	SST.19.K	120	Coarse sand and shell
Holoroanthura capensis sp. nov.	LBT.72.K	400	Sand and clay
	WCD.64.P	128	Green mud
	WCD.109.A	172	Fine dark green mud
	WCD.111.J	141	Dark green mud
	WCD.114.U	183	Dark green mud
Katanthura laevitelson sp. nov.	SST.47.K	30	Coarse sand and shell
Leptanthura agulhasensis sp. nov.	FAL.673.J–L	66	Shell, khaki sand, and gravel
	SCD.204.B	183	Khaki sand
	SCD.343.Q	121	Sand and shell
	SST.27.S	80	Coarse khaki sand and shell
	SST.31.U	80	Coarse khaki sand and shell
	WCD.77.G	320	Green sand and mud
Leptanthura laevigata (Stimpson)	SST.65.M	15	Sand and fine coral fragments
	SST.70.Z	20	Sand
	SST.92.A	200	Rock and sand
	SST.101.K	80	Coarse sand and shell
	SST.114.A	15	Sand

	Cat. No.	*Depth (M)*	*Substrate*
Leptanthura urospinosa sp. nov.	FAL.442.K	39	Sand
	FAL.654.N–R	75	Khaki sand and shell
	FAL.666.X–Y	26	Sand, shell and gravel
	FAL.838.Z	5	Sand and rock
	SCD.310.B	50	Coarse sand
	SST.1.W	200	Coarse khaki sand
	SST.19.L	120	Coarse sand and shell
Paranthura punctata (Stimpson)	SST.17.F	200	Coarse khaki sand and rock
	SST.21.Q	120	Sand and rock
	SST.37.M	80	Coarse sand and shell
	SST.96.S	120	Rock and sand
Suborder FLABELLIFERA			
Family **Cirolanidae**			
Cirolana borealis Lilljeborg	SST.57.A	30	Coarse sand and shell
	SST.114.B	15	Sand
Cirolana cingulata Barnard	SST.47.R	30	Coarse sand and shell
Cirolana hirtipes Milne Edwards	SST.27.T	80	Coarse sand and shell
Cirolana imposita Barnard	SST.87.H	350	Rock
	SST.11.L	200	Coarse khaki sand and rock
	SST.91.W	200	Rock
	SST.96.V	120	Rock and sand
Cirolana obtusispina sp. nov.	SST.19.N	120	Coarse sand and shell
	SST.21.U	120	Sand and rock
Cirolana pilula Barnard	SST.68.Y	20	Sand and fine coral fragments
	SST.76.J	15	Coarse sand
	SST.77.W	10	Coarse sand
	SST.114.C	15	Sand
Cirolana virilis Barnard	SST.54.N	30	Coarse sand and shell
	SST.101.D	80	Coarse sand and shell
Family **Sphaeromatidae**			
Cymodoce alia sp. nov.	SST.17.A	200	Coarse khaki sand and rock
	SST.21.S	120	Sand and rock
Cymodoce cf. *umbonata* Barnard	SST.21.T	120	Sand and rock
Cymodoce velutina sp. nov.	SST.20.Z	120	Coarse sand and shell
	FAL.700.R–T	—	—
Cymodocella sp.	SST.21.W	120	Sand and rock
Dynamenella sp.	SST.54.P	30	Coarse sand and shell
Family **Aegidae**			
Aega antillensis Schioedte & Meinert	SST.84.A	200	Coarse sand
Aega monilis Barnard	SST.84.B	200	Coarse sand
Family **Corallanidae**			
Lanocira gardineri Stebbing	SST.21.V	120	Sand and rock
	SST.109.P	30	Rock
Lanocira sp.	SST.91.Y	200	Sand and rock
Suborder GNATHIIDEA			
Family **Gnathiidae**			
Gnathia africana Barnard	SST.11.H	200	Coarse khaki sand and rock
Gnathia cryptopais Barnard	SST.10.K	200	Coarse khaki sand and rock
Gnathia spongicola Barnard	SST.11.H	200	Coarse khaki sand and rock
Gnathia sp.	SST.10.J	—	—

	Cat. No.	Depth (M)	Substrate
Suborder ASELLOTA			
Family **Munnidae**			
Munna sp.	SST.21.X	120	Sand and rock
Family **Stenetriidae**			
Stenetrium crassimanus Barnard	SST.96.T	120	Rock and sand
Stenetrium dagama Barnard	SST.91.X	200	Rock
	SST.92.C	200	Rock
	SST.11.K	200	Coarse khaki sand and rock
Stenetrium sp.	SST.8.B	200	Coarse khaki sand
	SST.37.N	80	Coarse sand and shell

SYSTEMATIC DISCUSSION

Suborder VALVIFERA

Family **Arcturidae**

Barnard (1920: 381) summarized the differences between four families of the Valvifera. The characters used by Barnard to redefine the family Pseudidotheidae Ohlin (1901) were partly based on his new genus *Holidotea*. With the present material, and especially the two species of the new genus *Austroarcturus*, as well as four species of *Microarcturus* available, a more critical examination of *Holidotea* shows that it is not a member of the Pseudidotheidae but is rather a member of the family Arcturidae. Reasons for the change follow the descriptions of the species of the new genus *Austroarcturus*.

Holidotea unicornis Barnard

Figs 2a–j

Holidotea unicornis Barnard, 1920: 382; 1940: 493. Nordenstam, 1933: 113. Nierstrasz, 1941: 262.

Remarks

It was thought useful to include figures of some of the appendages of this species not given in Barnard's description, as these are relevant to the discussion of the family position of the species.

Austroarcturus gen. nov.

Body dorso-ventrally flattened. Eyes dorsal. Lateral margins of head entire. Peraeonal segment I fused with head, yet distinguishable. Pleon consisting of two distinct segments plus pleo-telson. Penis single, apically bifid. Peraeopod I shorter than following peraeopods, strongly setose. Peraeopods II to IV sparsely setose, more slender than peraeopods V to VII. Exopod of male pleopod 1 modified; stylet present on endopod of male pleopod 2. Inner ramus of uropod minute.

Type species of the genus: *Austroarcturus foveolatus* sp. nov.

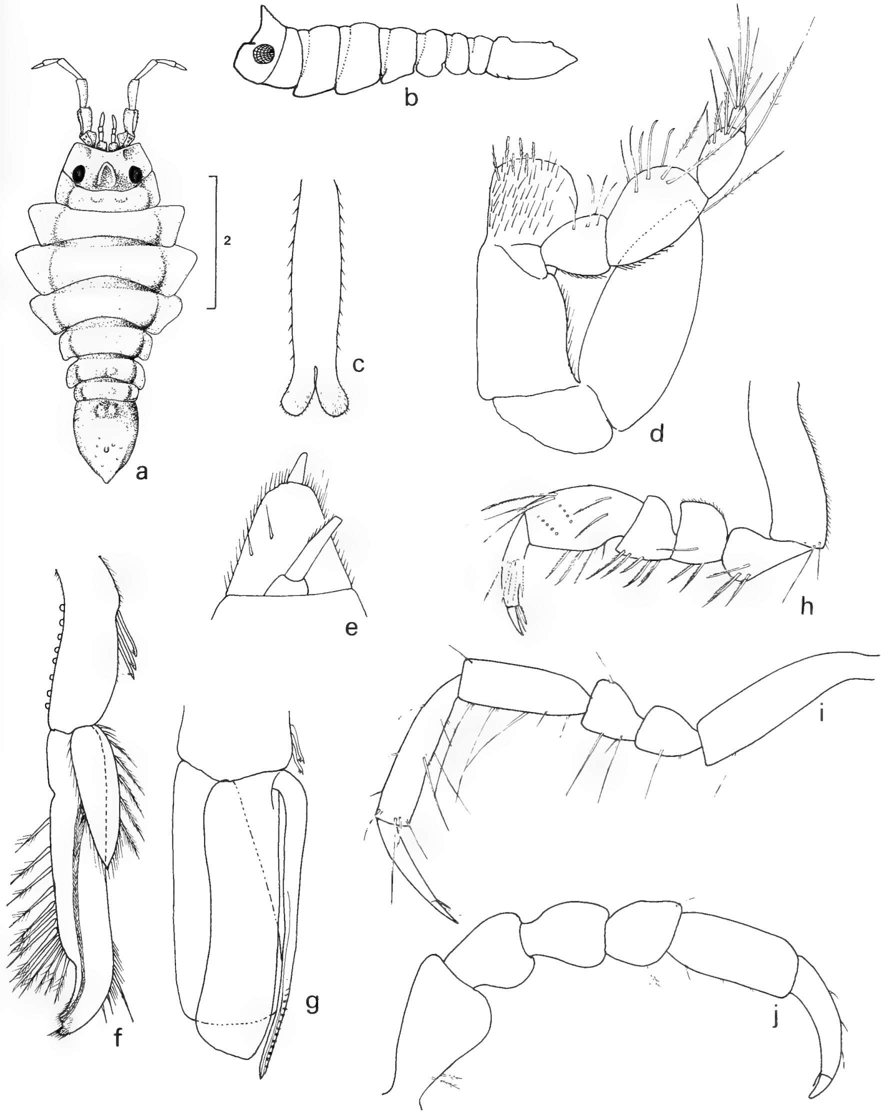

Fig. 2. *Holidotea unicornis* Barnard.

a. ♂, dorsal view; b. ♂, lateral view; c. penis; d. maxilliped; e. apex of uropod; f. pleopod 1 ♂; g. pleopod 2 ♂; h. peraeopod I; i. peraeopod III; j. peraeopod VI.

Austroarcturus foveolatus sp. nov.

Figs 3a–n

Description of ♀

Body dorso-ventrally flattened. Dorsal surface finely pitted. Peraeonal segment I fused with head yet distinguishable. Body widest at peraeonal segments II and III, segments IV to VII becoming gradually narrower. Pleon consisting of two free segments plus pleo-telson. Latter with distinct indentation proximo-laterally. Head bearing mid-dorsal sloping crest between eyes, continued on posterior portions of segments II to IV, strongest on segments II and IV.

Antennule about one-third length of antenna, peduncle 3-segmented, flagellum a single segment bearing several aesthetascs.

Antennal peduncle 5-segmented, 2nd segment triquetral, with prominent lateral flange; two proximal segments subequal; 4th and 5th segments slender. elongate; flagellum of two segments, tipped with strong spine.

Mandible bearing tridentate incisor process; lacinia mobilis tridentate with three penicils at its base, molar process large, bearing numerous short bristles.

1st maxilla biramous, outer ramus tipped with about 10 spines, inner ramus bearing three stout plumose setae.

2nd maxilla, outer ramus bilobed, outer lobe with three serrate spines, inner with two, inner ramus bearing six plumose setae and four simple setae.

Maxilliped with 5-segmented palp, endite distally slightly convex, bearing numerous bristles plus about seven fringed setae.

Peraeopod I shorter than rest, basal segment equal in length to merus, ischium, carpus, and half of propodus. Merus with broad dorsal flange; propodus broadly oval in shape; dactylus stout, somewhat hook-like; two distal segments bearing numerous fringed setae, those on propodus arranged in rows.

Peraeopods II to IV slender, with elongate propodi, carpi, and bases; dactyli slender, curved.

Peraeopods V to VII stout, shorter than earlier peraeopods except peraeopod I, propodus equal in length to carpus and merus together.

Uropods articulating with pleon at about midpoint of outer margin, basally rounded, distally lanceolate, bearing two rami, outer ramus tiny, inner ramus reduced to papilla bearing single serrate spine.

Description of ♂

Head and peraeon appendages as in female. Rounded crest on head and dorsal crests of peraeonal segments III and IV relatively stronger than in female. Penis elongate, single, distally bifid, rounded, bearing numerous fine bristles.

Pleopod 1, propodus shorter than rami, bearing row of short blunt spines on outer margin, four hooks on inner margin; outer ramus equal in length to

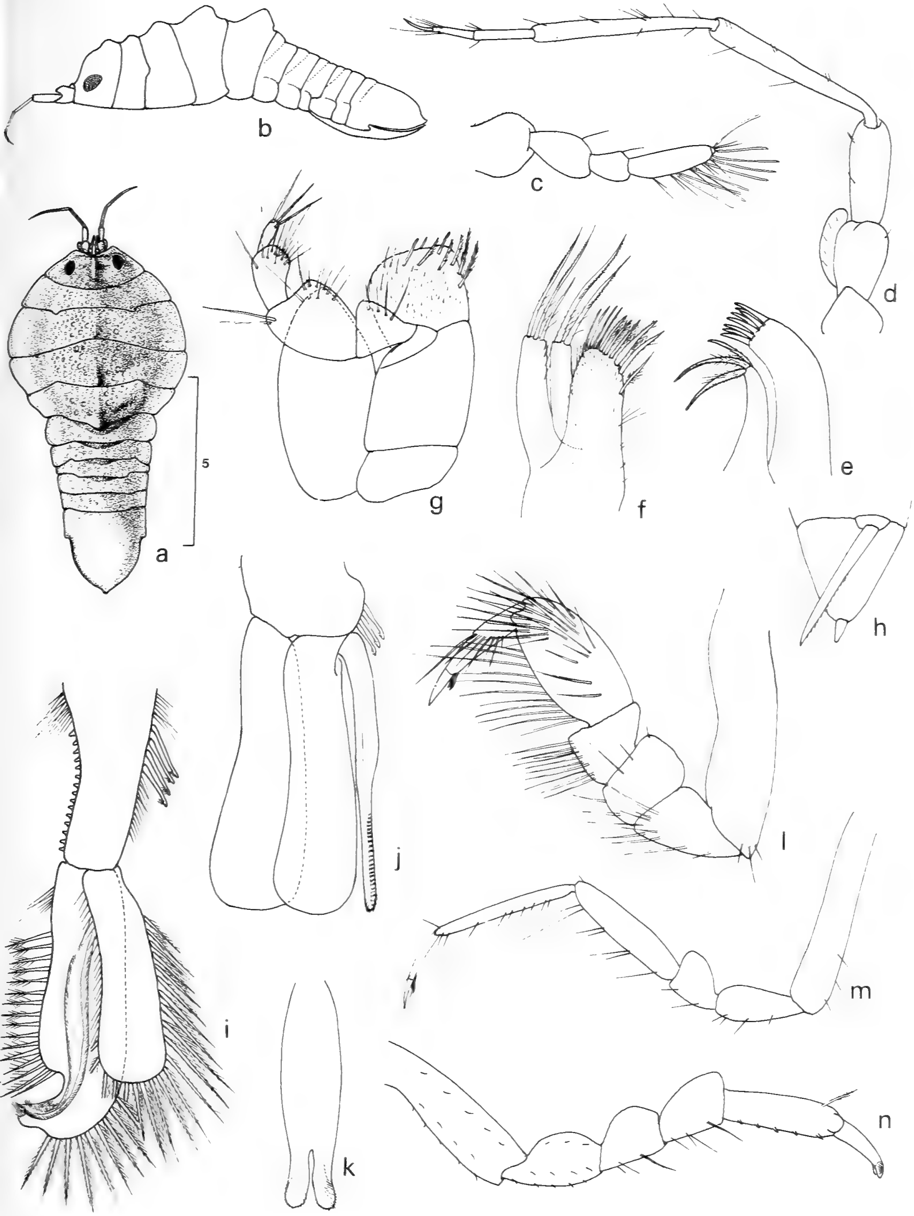

Fig. 3. *Austroarcturus foveolatus* sp. nov.

a. ♀, dorsal view; b. ♀, lateral view; c. antennule; d. antenna; e. 1st maxilla; f. 2nd maxilla; g. maxilliped; h. apex of uropod; i. pleopod 1 ♂; j. pleopod 2 ♂; k. penis; l. peraeopod I; m. peraeopod II; n. peraeopod VII.

propodus, fringed with plumose setae; inner ramus apically modified, curved towards median line, with convoluted tip.

Pleopod 2 bearing elongate stylet on base of inner ramus; stylet with several rows of fine bristles.

Material

			♀	♂
Holotype	SAM–A13540	SST.1.Y	9,0	—
Allotype	SAM–A13540	SST.11.J	—	7,0
Paratypes	SAM–A13541	SCD.272.C	7,4 4,9	4,5
		SCD.204.D	4,9	—
		SCD.217.R	3,2	

Single juvenile specimens from SCD.235.C, SCD.326.F, FAL.760.N.

Austroarcturus africanus sp. nov.

Figs 4a–k

Description of ♀

Body dorso-ventrally flattened, integument smooth. Peraeonal segment I fused with head yet distinguishable. Body widest at peraeonal segment II; peraeonal segment IV not as wide as III or V. Segments V and VI equal in width, segment VII shorter and narrower than preceding segments. Pleon consisting of two free segments plus pleo-telson. Latter with proximo-lateral lobes, strongly convex, distally bluntly rounded. Head evenly rounded, convex. No dorsal crests or ridges.

Antennule about one-quarter length of antenna, peduncle 3-segmented, flagellum of a single segment bearing several aesthetascs.

Antennal peduncle 5-segmented, segments 2 to 5 subequal in length, 2nd triquetral with prominent flattened lateral flange; flagellum of two segments.

Mouthparts as in *Austroarcturus foveolatus*.

Peraeopods II to IV more slender than peraeopods V to VII, with scattered setae and numerous fine setules on ventral surface. Peraeopods V to VII stout, also bearing numerous setae and setules.

Outer ramus of uropod tiny, with terminal fringed spine, inner ramus reduced to a papilla bearing a single fringed spine.

Description of ♂

Similar to female, but epimeres of peraeonal segments V and VI more rounded, and more obviously extending laterally beyond segment IV. Penis elongate, single, distally bifid for about one-third of length, lobes distally rounded, bearing setules.

Pleopod 1 propodus basally wider than distally, bearing about 18 short blunt spines on outer margin, four elongate hooks on inner. Outer ramus elongate-rectangular, fringed with plumose setae. Inner ramus distally modified,

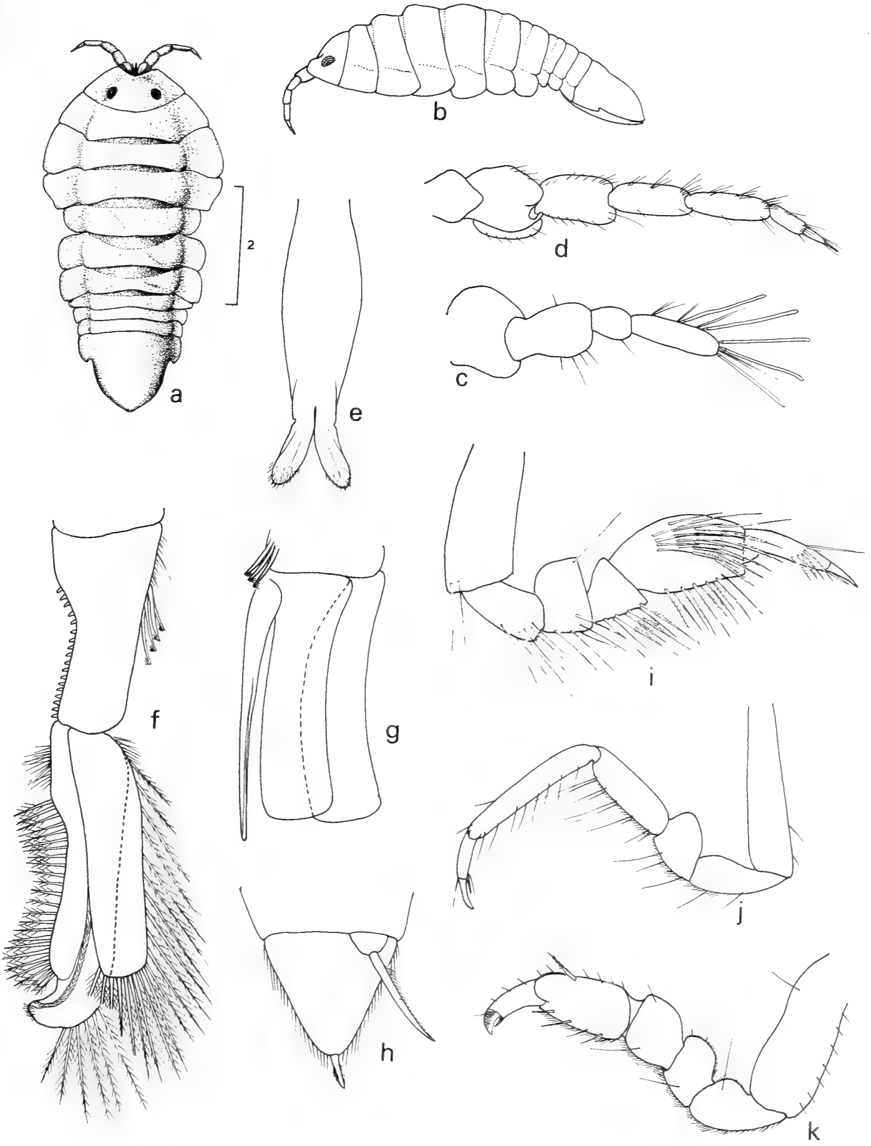

Fig. 4. *Austroarcturus africanus* sp. nov.

a. ♂, dorsal view; b. ♂, lateral view; c. antennule; d. antenna; e. penis; f. pleopod 1 ♂; g. pleopod 2 ♂; h. apex of uropod; i. peraeopod I; j. peraeopod II; k. peraeopod VII.

bearing row of about 25 stiff plumose setae on outer margin, distally curved and rounded.

Pleopod 2 bearing slender elongate stylet on base of inner ramus, extending slightly beyond tips of rami.

Material

			♀	♂
Holotype	SAM–A13542	FAL.442.E	—	5,4
Allotype	SAM–A13542	FAL.442.E	6,0 ovig.	—
Paratypes	SAM–A13543	FAL.428.P	7,0 ovig. 5,9 ovig.	6,5

Numerous males (3,9–6,2 mm) and females (4,9–7,0 mm) from the following stations: FAL.589.E., FAL.335.D., SST.102.M., SCD.337.P., SCD.339.P., SCD.243.N., SCD.293.W., SB.304.U., SB.187.J., SB.270.H., WCD.206.R., WCD.211.K.

Remarks

The present species is obviously closely related to the foregoing *Austroarcturus foveolatus*, but differs in several definite and constant features. In *A. foveolatus* peraeonal segments V to VII and the pleo-telson taper gently and evenly posteriorly; in *A. africanus* the epimeres of segments V and VI extend laterally well beyond those of segments IV and VII. The proximo-lateral lobes at the base of the pleo-telson are more strongly developed in *A. africanus*, and consequently the notch formed distally at the fusion to the pleo-telson is wider. The integument of this latter species is not so obviously granular and pitted as in *A. foveolatus*, and when seen in profile, *A. africanus* lacks the high median crest of *A. foveolatus*. In the appendages (excluding the mouthparts) there are subtle differences but the most striking are in the antennae. In *A. foveolatus* the 4th and 5th peduncle segments are very elongate and slender, each being equal in length to the three basal segments together. *A. africanus* does not have elongate segments in the antennal peduncle.

It is the author's opinion that *Holidotea* should be placed in the Arcturidae because the species is more or less intermediate between species of *Austroarcturus* and *Microarcturus* of that family. The reasons are as follows:

A similar differentiation of the peraeopods is apparent in species of the threegenera.

The mouthparts and uropodal rami are similar.

The outer ramus of pleopod 1 in the male, although showing slight differences, follows the same basic plan in all three genera.

The 2nd pleopods in the males are similar, as are the penes. From this list, the three genera would seem to be quite closely related.

Barnard (1920) separated the Pseudidotheidae from the Arcturidae (Astacillidae in his table) by the following features:

1. Body flattened in Pseudidotheidae, cylindrical in Arcturidae.
2. Peraeonal segment IV never elongate in Pseudidotheidae, often elongate in the Arcturidae.

3. Peraeopod I prehensile in the Pseudidotheidae, slender and setiferous in the Arcturidae.
4. Peraeopods II to IV stout (moderately) in Pseudidotheidae, slender and setiferous in the Arcturidae.

Comparison of species of the three genera make it obvious that these criteria can be given little strength in the separation of the two families.

Several members of the Arcturidae possess a body to some degree dorso-ventrally depressed, especially species of *Arcturella* and *Microarcturus.* This flattening is especially noticeable in the females.

Several species of the arcturids do not possess elongate 4th peraeonal segments, e.g. *Arcturella* and *Microarcturus.*

From the species here discussed, and from the figures supplied, it can be seen that the 1st peraeopods are very similar in structure, as are peraeopods II to IV, and V to VII. Ohlin (1901), in his description of the family Pseudidotheidae based on *Pseudidothea bonnieri,* notes that peraeopods II to VII are nearly the same in structure and size. His figure of *P. bonnieri* shows a very idoteid-like isopod, quite unlike *Holidotea unicornis.* It would seem that *Holidotea unicornis* is more closely related to species of the arcturids than to species of the Pseudidotheids. It is proposed that *Holidotea* thus be placed in the Arcturidae. The criteria used to separate species of the three genera, *Holidotea, Austroarcturus,* and *Microarcturus,* are summarized in Table 1.

Table 1

	Holidotea Barnard	*Austroarcturus* Kensley	*Microarcturus* Nordenstam
Lateral margins of head	Entire	Entire	Incised
Eyes	Dorsal	Dorsal	Dorso-lateral
Peraeonal segment I	Distinguishable, fused to head	Distinguishable, fused to head	Indistinct, completely fused to head
Pleon	No distinct segments anterior to pleo-telson	2 distinct segments anterior to pleo-telson	2–3 distinct segments anterior to pleo-telson
Inner ramus of pleopod 1 ♂	Less than half length of outer ramus, distally acute	More than half length of outer ramus, distally truncate-rounded	More than half length of outer ramus, distally truncate-rounded

Microarcturus similis (Barnard)

Figs 5a–b

Antarcturus similis Barnard, 1925: 395; 1940: 508.
Microarcturus similis: Nordenstam, 1933: 128.

Material

SST.106.A–C	1♂
SST.40.J	1♂
SST.46.C	1♀

Remarks

For comparison with the new species described below, a male and female of this species are figured in dorsal view.

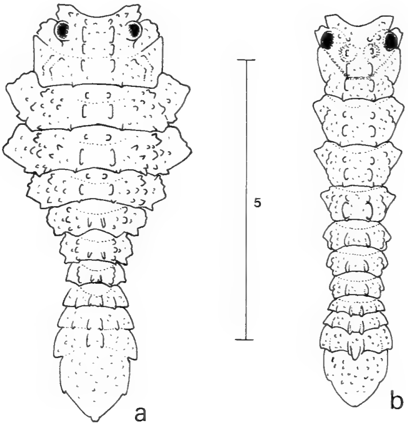

Fig. 5. *Microarcturus similis* (Barnard).
a. ♀, dorsal view; b. ♂, dorsal view.

Microarcturus laevis sp. nov.

Figs 6a–l

Description of ♀

Integument smooth. Body dorso-ventrally flattened, head and peraeonal segment I fused, but with lateral margins free. Body widest at peraeonal segments II and III; peraeonal segments V to VII and pleo-telson narrow, all of similar width. Pleon consisting of two free segments, with third segment indicated on pleo-telson. Head bearing two large dorso-lateral eyes separated by convex semicircular portion, antero-lateral corners slightly produced. Epistome produced into blunt tapering process, tip just visible in dorsal view. All epimeres distinct, those of peraeonal segments II and III evenly convex in dorsal view. Peraeonal segments all dorsally convex, segment III bearing two broadly convex submedian dorsal bulges. Rounded boss at base of pleo-telson.

Antennule slightly less than one-third length of antenna, consisting of 3-segmented peduncle and one flagellar segment. Basal segment broad, bearing fine setae, flagellum equal in length to distal two peduncle segments.

Antennal peduncle 4-segmented, 3rd segment longest, flagellum 2-segmented, tipped with single spine.

Mandible with strongly chitinised quadridentate incisor process, lacinia mobilis tridentate with three penicils at its base, large broad molar process covered with fine bristles.

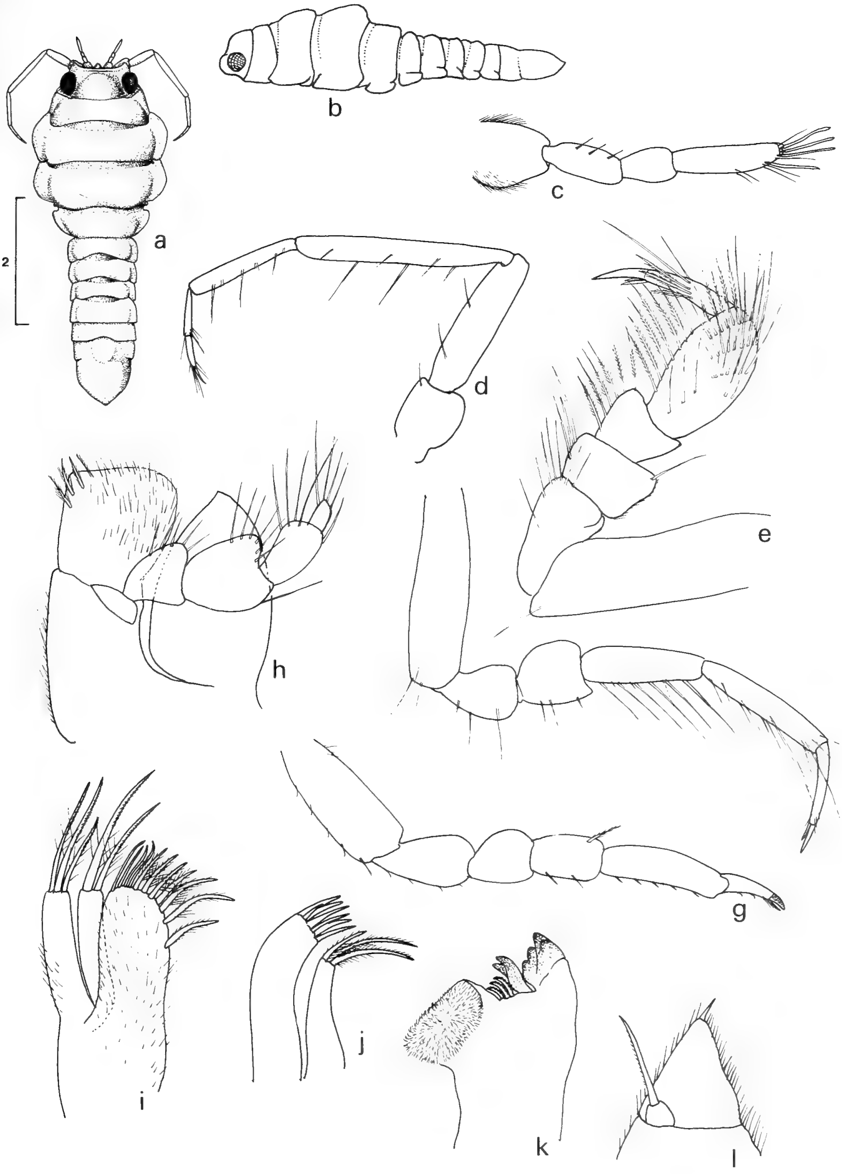

Fig. 6. *Microarcturus laevis* sp. nov.

a. ♀, dorsal view; b. ♀, lateral view; c. antennule; d. antenna; e. peraeopod I; f. peraeopod II; g. peraeopod VII; h. maxilliped; i. 2nd maxilla; j. 1st maxilla; k. mandible; l. apex of uropod.

Inner ramus of 1st maxilla bearing three long plumose setae, outer ramus tipped with about 10 spines.

Inner ramus of 2nd maxilla bearing seven plumose setae and four slender spines distally; inner lobe of outer ramus with two distal serrate spines, outer lobe with three.

Maxilliped palp 5-segmented, 3rd segment broadest; endite broad, bearing numerous simple setae plus several short fringed setae on inner distal angle.

Peraeopod I shorter than following peraeopods; basis equal in length to ischium, merus, and carpus together; propodus bearing three rows of setae on outer distal face; dactylus armed with serrate setae.

Peraeopods II to IV slender, dactyli, propodi, and carpi elongate, unguis of dactylus blunt, striated.

Uropods proximally evenly rounded; outer ramus minute, inner ramus tiny, reduced to papilla bearing a single serrate spine.

Material

Holotype	SAM–A12544	1 ovigerous ♀	6,4 mm	FAL.803.K
Paratype	SAM–A13545	1 ovigerous ♀	5,2 mm	FAL.423.D

Microarcturus ornatus sp. nov.

Figs 7a–o

Description of ♀

Body with large tubercles, widest at peraeonal segment III. Head with antero-lateral corners acute; broad transverse furrow separates rounded posterior ridge from rest of head. Eyes large, lateral. Peraeonal segment I with epimeres ventrally directed, tridentate. Epimeres of peraeonal segments II to IV expanded laterally. Peraeonal segments with two medio-lateral tubercles, largest on segments I to IV. Pleon consisting of one indistinct and two distinct segments plus pleo-telson. Latter terminally acute, with strong lateral teeth, and bearing scattered tubercles. Antennule reaching to midpoint of 2nd antennal peduncle segment. Peduncle 3-segmented, basal segment broadest, 3rd segment one-quarter length of flagellum.

Antennal peduncle 4-segmented, basal segment about half length of 2nd segment, with antero-lateral corner acute, 2nd segment with distal spine, 3rd and 4th segments slender, subequal in length, flagellum 2-segmented with slender terminal spine.

Mandible with tridentate incisor process; lacinia mobilis tridentate with three penicils at base, and broad setose molar process with four slender setae at its base.

1st maxilla with three setae on inner ramus, several spines on outer ramus.

2nd maxilla inner ramus bearing five simple spines and five stout setae, outer lobe of outer ramus bearing three elongate spines, inner lobe with two fringed setae.

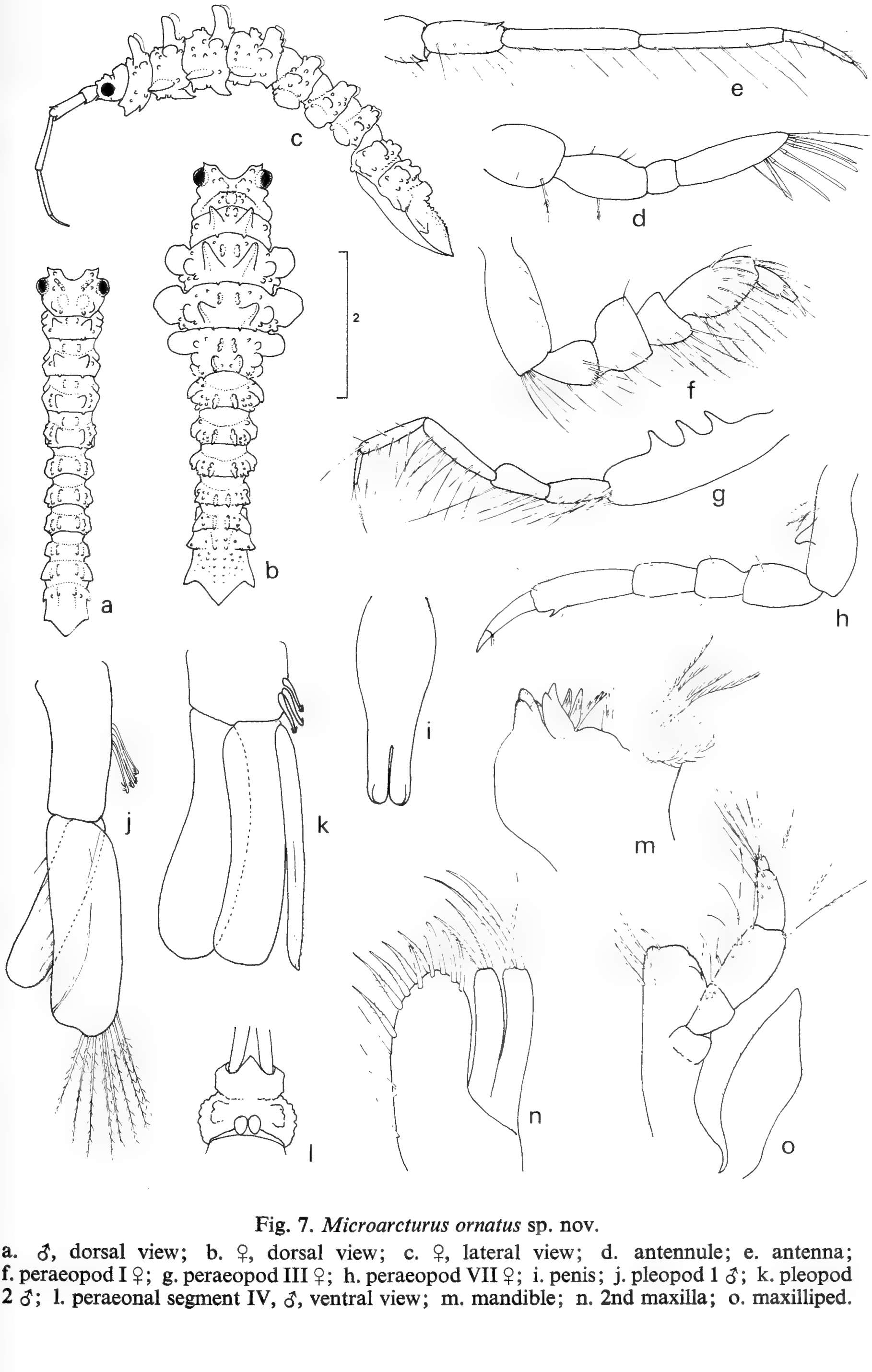

Fig. 7. *Microarcturus ornatus* sp. nov.

a. ♂, dorsal view; b. ♀, dorsal view; c. ♀, lateral view; d. antennule; e. antenna; f. peraeopod I ♀; g. peraeopod III ♀; h. peraeopod VII ♀; i. penis; j. pleopod 1 ♂; k. pleopod 2 ♂; l. peraeonal segment IV, ♂, ventral view; m. mandible; n. 2nd maxilla; o. maxilliped.

Maxilliped palp 5-segmented, endite relatively narrow, with three setae at inner distal angle.

Peraeopod I shorter than following peraeopods; propodus twice length of dactylus, basis equal in length to ischium and merus together.

Peraeopods II to IV increasing in length posteriorly, five distal segments relatively slender, bearing elongate setae; basis stout, bearing two strong spinose processes on dorsal margin in peraeopods II and III, three processes on peraeopod IV; terminal segment with strong serrate spine apically.

Peraeopods V to VII with all segments robust, propodus bearing small disto-ventral spine, basis with strong spinose process at about midpoint of outer face.

Description of ♂

Body elongate, parallel-sided, hardly depressed, bearing numerous tubercles. Peraeonal segments I to IV with more prominent submedian dorsal tubercles. Peraeonal segment IV bearing ventrally a triangular process between bases of peraeopods, plus two submedian oval flattened processes distally. Peraeopods II to IV lacking processes on bases.

Pleopod 1 with outer ramus broader and longer than inner, bearing oblique curved groove on anterior face, ending on a rounded distal prominence. Stylet on inner ramus of pleopod 2 sabre-like. Penis basally broad, distally bifid, rami not diverging.

Material

Holotype	SAM–A13546	SST.10.H	♀ ovig.	6,4 mm
Allotype	SAM–A13546	SST.10.H	♂	5,0 mm
Paratypes	SAM–A13547	SST.10.H	2 ♂♂	5,0 mm 4,1 mm

Microarcturus quadriconus sp. nov.

Figs 8a–i

Description of ♀

Peraeon segments II and III broadest. Head and peraeonal segment I fused, with shallow furrow indicating line of fusion. Anterior margin of head concave, eyes dorso-lateral, two large submedian conical tubercles in line with eyes, each flanked by a tiny anterior and posterior tubercle. Submedian tubercles of peraeonal segment I tiny, two lateral rounded tubercles slightly larger. Peraeonal segments II to IV each with four large conical tubercles. Peraeonal segments V to VII each with two tubercles. Pleon having two segments anterior to pleo-telson, latter with large rounded boss mid-dorsally at base. Pleo-telson pentagonal, distally acute. Antennular peduncle 4-segmented, basal segment equal in length to 2nd and 3rd segments together; flagellum 2-segmented.

Mouthparts typical of the genus.

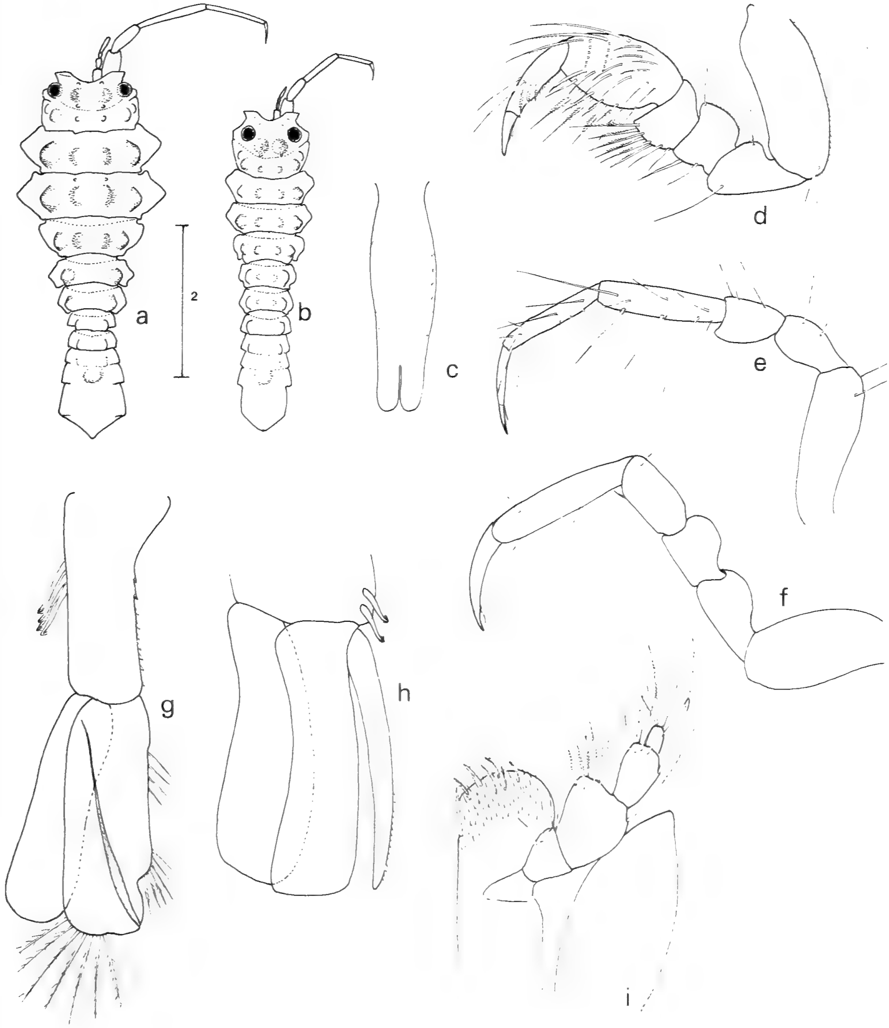

Fig. 8. *Microarcturus quadriconus* sp. nov.
a. ♀, dorsal view; b. ♂, dorsal view; c. penis; d. peraeopod I; e. peraeopod II; f. peraeopod VII; g. pleopod 1 ♂; h. pleopod 2 ♂; i. maxilliped.

Peraeopod I shorter than following peraeopods, three distal segments bearing numerous serrate spines.

Peraeopods II to IV more slender than following ones, bearing few scattered elongate setae.

Peraeopods V to VII somewhat shorter than preceding ones, distal segments stouter.

Uropod with outer ramus tiny, inner ramus reduced to papilla with single serrate spine.

Description of ♂

Body elongate, peraeonal segments II and III only slightly wider than rest of body. Sculpture as in female.

Pleopod 1 rami subequal in length, outer ramus with oblique groove running almost entire length, ending at slight bulge at outer distal angle.

Pleopod 2 inner ramus distally truncate, equal in length to stylet, latter sabre-shaped. Penis single, distally bifid, distal rounded lobes not diverging. Pleo-telson not as obviously pentagonal as in female.

Material

Holotype	SAM–A13548	SST.101.C–K	♀ ovig.	5,2 mm
Allotype	SAM–A13548		♂	4,0 mm
Paratypes	SAM–A13549		♀ ovig.	5,6 mm
				4,8 mm
		SCD.217.R	♀ ovig.	4,9 mm

Remarks

The genus *Microarcturus* was defined by Nordenstam (1933: 128). The following characters which set it apart from species of *Arcturus*, are present in the foregoing three species, as well as in *M. similis*:

> Lateral margins of head incised; eyes dorso-lateral; peraeonal segment I fused with head, often indistinct; pleon possessing two free segments plus one indicated on the pleo-telson; antennae shorter than body; antennal flagellum 2-segmented (2–4-segmented); pleo-telson never longer than last four peraeonal segments together.

M. ornatus resembles *M. rugosus* Nordenstam in the spination of the peraeopods II to IV, but lacks the numerous elongate acute tubercles and spinose epimeres of the Antarctic species. Apart from this similarity, the three species described here are rather distinctive, and most closely resemble *M. similis*. Table 2 summarizes the main differences between the four species.

Table 2

	M. similis	*M. ornatus*	*M. quadriconus*	*M. laevis*
Epimeres of peraeonal segments II & III ♀	Angular	Rounded	Angular	Rounded
Dorsal integument	Granular-tuberculate	Granular-tuberculate	Non-granular tuberculate	Smooth
Bases of peraeopods II to IV ♀	Non-spinose	Spinose	Non-spinose	Non-spinose
Pleo-telson	Rounded boss at base present or absent	No rounded boss at base	Rounded boss at base	Rounded boss present at base

Genus *Arcturina* Koehler, 1911

Barnard (1957) mentions the error in Koehler's description of the male of *Arcturina rhomboidalis,* where the figured second pleopod is labelled and referred to as the first pleopod. Barnard's material of *A. hexagonalis* consisted of a female and an immature male. Many males are now available, thus pleopod 2 of mature males can be recorded. *Arcturina rhomboidalis* and the three species included here are compared in table 3.

Arcturina hexagonalis Barnard

Figs 9a–k

Arcturina hexagonalis Barnard, 1925: 400; 1957: 6.

Description of ♂

Body slender, geniculate. Peraeonal segment I fused with head but distinguishable. Peraeonal segments I to III subequal in length, IVth segment subcylindrical, bearing two submedian somewhat indistinct bands of pile-like short hairs. Peraeonal segment V slightly longer than following segments. Pleon consisting of three fused segments plus pleo-telson. Fused segments subequal, short, each bearing two dorsal clumps of fine hairs. Antennae, antennules, and mouthparts as in female.

Peraeopod I within lateral wall of buccal cavity. Peraeopods II to IV directed anteriorly; peraeopods V to VII stout, considerably longer than anterior peraeopods.

Penial rami fused for half of length, tips hardly expanded.

Exopod of pleopod 1 with indentation on outer margin, bearing numerous fine simple setae plus three stout plumose setae. Exopod slightly longer than endopod.

Pleopod 2 bearing slender stylet on inner margin of endopod; apex of stylet with one short and two elongate spines extending well beyond endopod apex.

Previous records

Off Cape St Blaize, 75 metres.

Material

45 ♂♂, 33 ♀♀, False Bay.

Arcturina triangularis Barnard

Figs 10a–h

Arcturina triangularis Barnard, 1957: 4, fig. 3.

Description of ♂

Body slender, peraeonal segment I distinguishable, fused with head. Ventro-lateral margin of head slightly scalloped. Peraeonal segment IV equal in

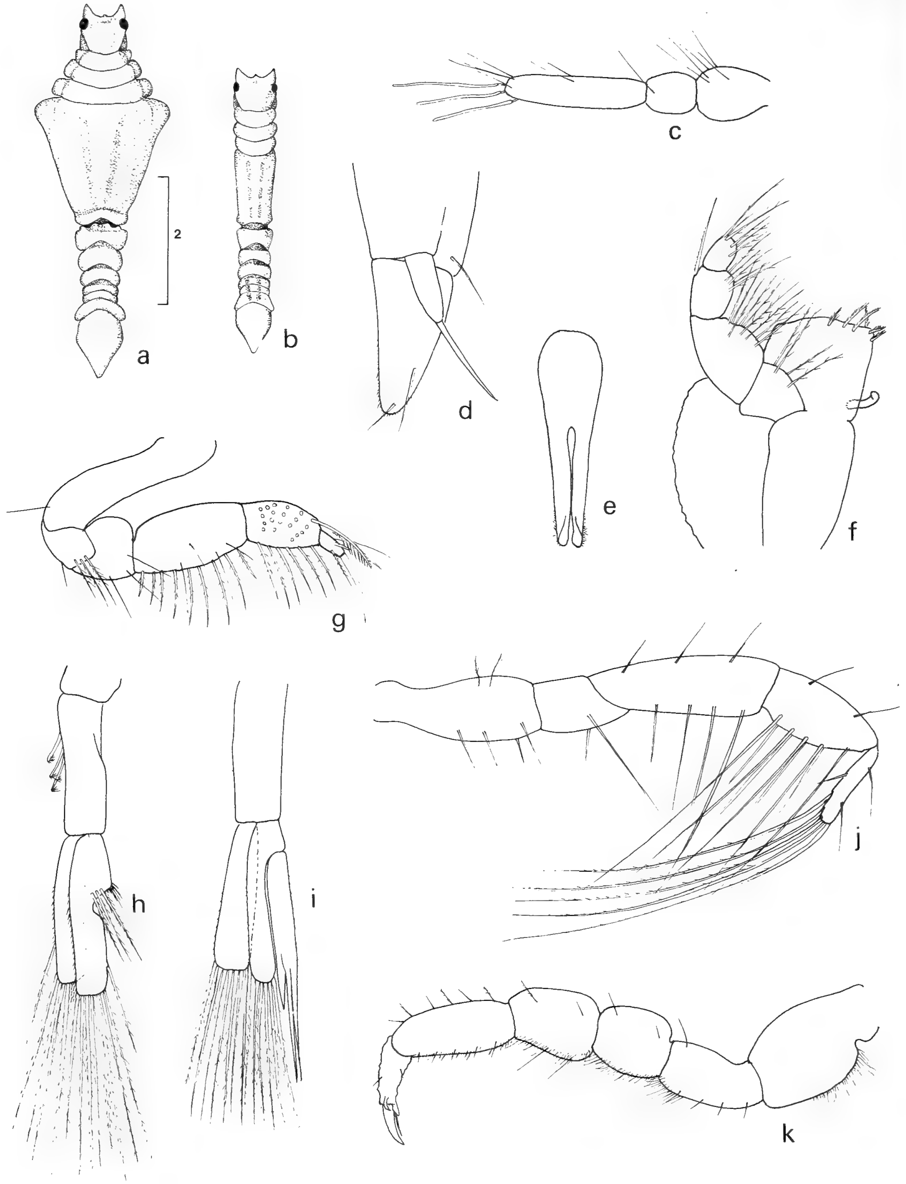

Fig. 9. *Arcturina hexagonalis* Barnard.

a. ♀, dorsal view; b. ♂, dorsal view; c. antennule; d. apex of uropod; e. penis; f. maxilla; g. peraeopod I; h. pleopod 1 ♂; i. pleopod 2 ♂; j. peraeopod III; k. peraeopod VI.

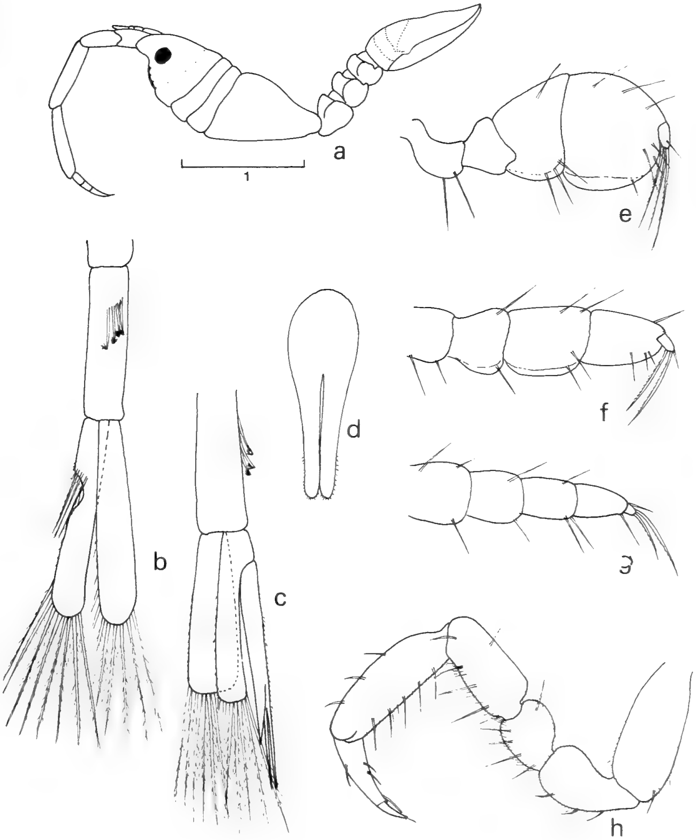

Fig. 10. *Arcturina triangularis* Barnard.
a. lateral view; b. pleopod 1 ♂; c. pleopod 2 ♂; d. penis; e. peraeopod II ♂; f. peraeopod III ♂; g. peraeopod IV ♂; h. peraeopod VI ♂.

length to head plus anterior three peraeonal segments. Ventral margin of peraeonal segment IV very slightly convex. Head and anterior four peraeonal segments bearing two submedian dorsal ridges which diverge posteriorly. Submedian ridges again visible on peraeonal segments VI and VII and on anterior portion of pleon. Peraeonal segments V to VII having strong lateral ridge. Mouthparts as in female. Peraeopod I hidden by lateral border of buccal cavity. Peraeopod II with reduced dactylus; propodus and carpus inflated and broad. Peraeopods III and IV more slender. Peraeopods V to VII stout, heavily setose. Pleopod 1 with exopod having indentation at proximal third, with three stout plumose setae, and numerous fine hairs. Pleopod 2 endopod bearing slender stylet on inner margin; stylet apically bearing one short and two long slender spines.

Previous records

Mossel Bay, Cape, 9 metres.

Material

8 ♂♂, 11 ♀♀. SST.61.U.

Arcturina scutula sp. nov.

Figs 11a–i, 12a–n

Description of ♀

Head and anterior four peraeonal segments together forming a lozenge-shaped structure. Head with well-developed antero-lateral lobes. Peraeonal segment I fused with head yet distinguishable. Two submedian dorsal ridges extend from anterior margin of head to posterior margin of peraeonal segment IV. Peraeonal segments V to VII bearing strong lateral ridges, Vth segment slightly larger than following segments. Pleon consisting of three indistinct segments fused to pentagonal pleo-telson.

Antennule 4-segmented, basal segment broad, 2nd and 3rd segments together equal in length to flagellum; latter bearing single terminal aesthetasc.

Antenna having 5-segmented peduncle and 3-segmented flagellum; first three peduncle segments together equal in length to 4th segment, latter equal to 5th.

Mandible consisting of tridentate strongly chitinised incisor process, smaller tridentate lacinia mobilis and two penicils at its base, and molar process bearing many close-set short bristles.

1st maxilla biramous, outer ramus tipped with about seven or eight simple spines, inner ramus bearing three terminal plumose setae.

2nd maxilla biramous, inner ramus tipped with six simple spines, outer ramus bilobed, each lobe bearing two elongate plumose setae.

Maxilliped with single coupling hook on inner margin of endite, few scattered fringed setae near upper margin; palp 5-segmented, 3rd segment longest, broadly oval, terminal segment about one-third length of penultimate segment.

Peraeopod I within lateral border of buccal cavity, propodus bearing numerous elongate serrate spines; dactylus bearing two setae and single strong curved spine.

Peraeopods II and III subequal in length, dactylus reduced, bearing three serrate spines, propodus broad.

Peraeopod IV slightly shorter than III, dactylus reduced, bearing two serrate spines, propodus more elongate than in previous peraeopods.

Peraeopods II to IV with well-developed oostegites, that of the IVth largest.

Peraeopods V to VII becoming successively slightly smaller.

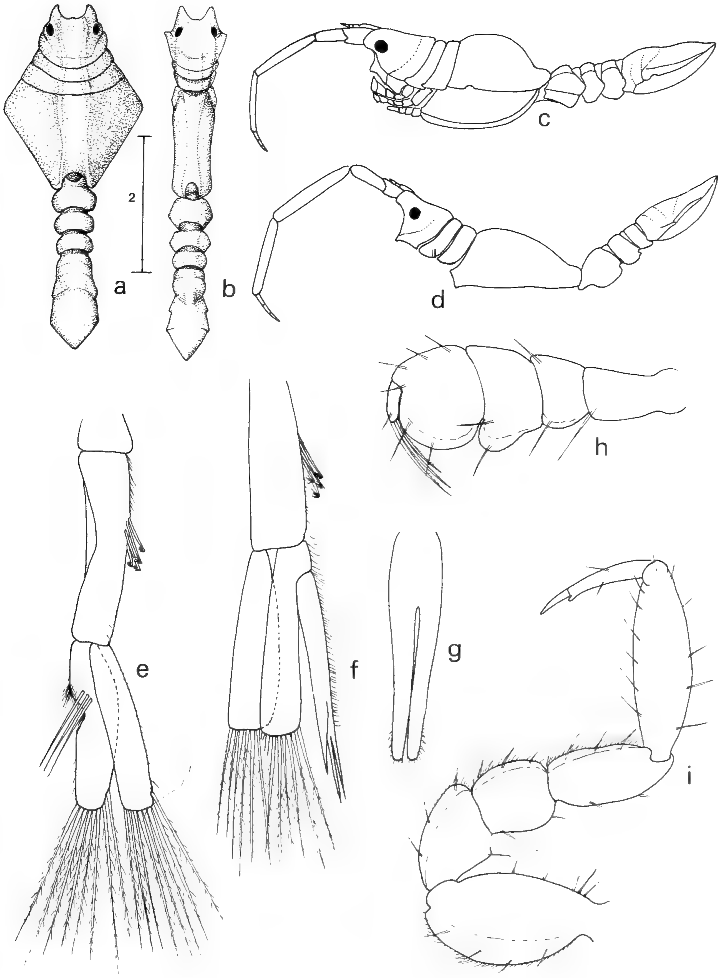

Fig. 11. *Arcturina scutula* sp. nov.

a. ♀, dorsal view; b. ♂, dorsal view; c. ♀, lateral view; d. ♂, lateral view; e. pleopod 1 ♂; f. pleopod 2 ♂; g. penis; h. peraeopod II ♂; i. peraeopod VI.

Uropods anteriorly rounded, distally tapering, bearing strong longitudinal carina near median margin, outer ramus small, inner ramus about half length and one-quarter breadth of outer, tipped with single simple seta.

Description of ♂

Body slender. Head and anterior three peraeonal segments together somewhat shorter than peraeonal segment IV. Head plus anterior four peraeonal segments longer than peraeonal segments V to VII plus pleo-telson. Head with

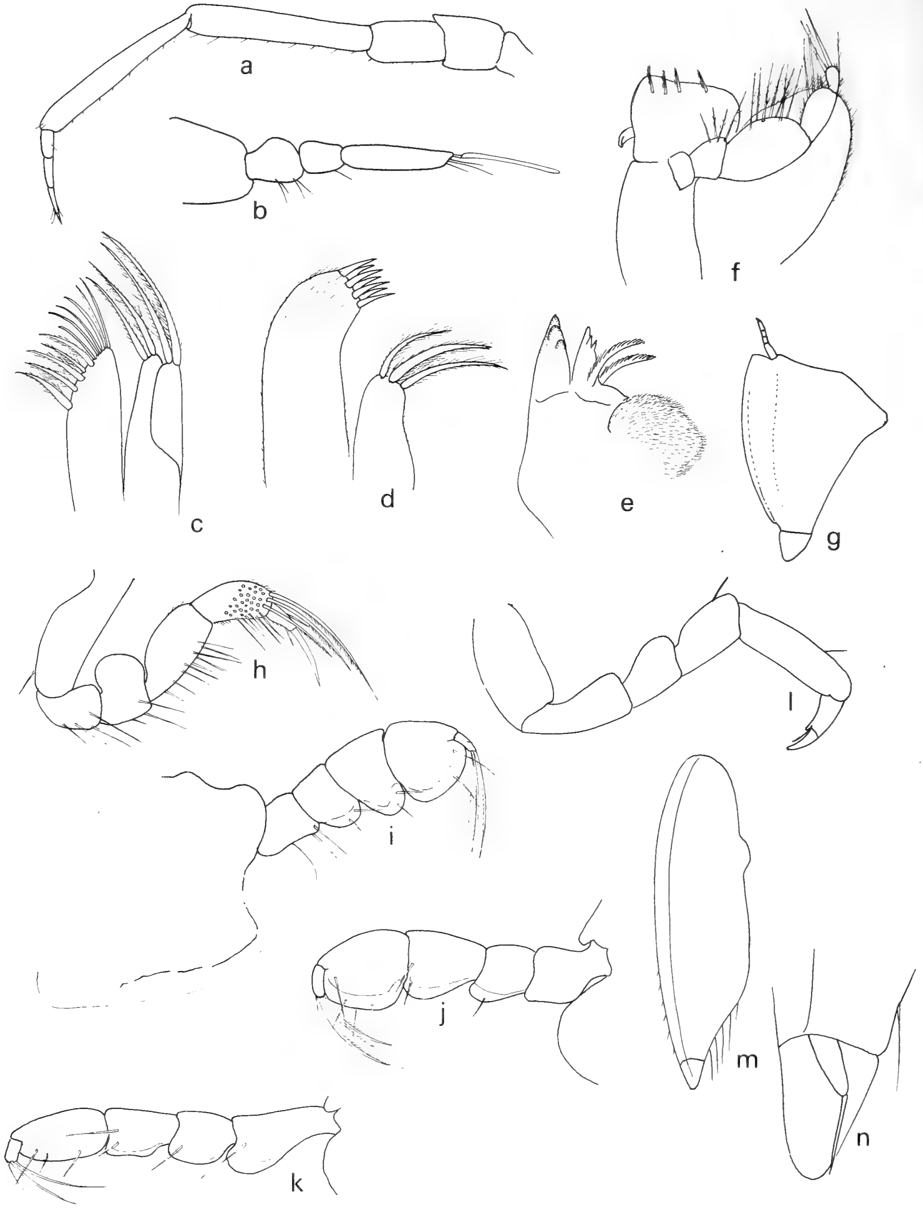

Fig. 12. *Arcturina scutula* sp. nov.

a. antenna; b. antennule; c. 2nd maxilla; d. 1st maxilla; e. mandible; f. maxilliped; g. oostegite of peraeonal segment IV; h. peraeopod I ♀; i. peraeopod II ♀; j. peraeopod III ♀; k. peraeopod IV ♀; l. peraeopod V ♀; m. uropod; n. apex of uropod.

well-developed antero-lateral lobes. Peraeonal segment I forming acute lateral projection at level of eyes. Two indistinct submedian ridges on Ist to IIIrd peraeonal segments. Peraeonal segment IV with two strong submedian ridges dorsally, slightly arched in lateral view, bearing an antero-ventral rectangular projection.

Antennae, antennules, mouthparts, and anterior four pairs of peraeopods similar to female. Peraeopods V to VII decreasing slightly in size posteriorly, basis with membranous ventral flange; propodus about equal in length to carpus plus merus; all segments bearing simple setae.

Penis consisting of two slender elongate rami fused basally for about one-quarter of their length.

Pleopod 1 endopod elongate, apically truncate, exopod with indentation on outer margin flanked by three stout setae.

Pleopod 2 endopod bearing slender stylet on inner margin; stylet distally consisting of one short and two elongate and more slender spines, reaching beyond apex of endopod.

Material

Holotype	SAM–A13537	False Bay	♂	4,5 mm
Allotype	SAM–A13537	False Bay	♀	3,5 mm
Paratypes	SAM–A13538	False Bay	4 ♂♂	4,3–5,1 mm
Paratypes	SAM–A13539	False Bay	3 ♀♀	3,5–3,8 mm

Numerous males and females from False Bay; also 4 ♂♂, 5 ♀♀, Algoa Bay.

Remarks

Three species of *Arcturina* have been described, viz. *A. rhomboidalis* Koehler, from Morocco and Mauritania, *A. hexagonalis* Barnard from Cape St Blaize, and *A. triangularis* Barnard, from Mossel Bay. Table 3 summarizes the differences between these three species and the new species *A. scutula.*

Table 3

♂	*A. rhomboidalis*	*A. hexagonalis*	*A. triangularis*	*A. scutula*
Dorsal ridges	More or less parallel extending on to anterior segments and head	Only on peraeonal segment IV	More or less parallel extending on to head and anterior segments	More or less parallel extending on to head and anterior segments
Peraeonal segment IV	Dorsally straight in lateral view	Dorsally straight in lateral view	Slightly arched dorsally in lateral view	Slightly arched dorsally in lateral view
	No antero-ventral projection	No antero-ventral projection	No antero-ventral projection	Truncate antero-ventral projection
	Greatest height ¼ length	Greatest height ⅓ length	Greatest height ⅔ length	Greatest height ½ length
Total length	6–7 mm	Average for 10 specimens: 4,0 mm	Average for 3 specimens: 3,7 mm	Average for 10 specimens: 3,7 mm

Table 3 (*continued*)

♀	*A. rhomboidalis*	*A. hexagonalis*	*A. triangularis*	*A. scutula*
Total length	4 mm	Average for 10 specimens: 5,5 mm	Average for 7 specimens: 3,6 mm	Average for 10 specimens: 3,7 mm
Dorsal ridges	Separate, parallel, extending on to head	Anteriorly divergent absent from head and anterior 3 segments	Extending on to head converging on 3rd and anterior of 4th segment	Separate, more or less parallel, extending on to head
Peraeonal segment IV	Dorsally slightly curved; lozenge-shaped (with anterior 3 segments in dorsal view)	Straight in lateral view; widest anteriorly, anterior segments rounded	Smoothly curved in lateral view; lozenge-shaped, margins of anterior segments not as rounded as in *hexagonalis*	Strongly convex in lateral view; lozenge-shaped, margins of anterior segments not rounded
Antennule	2nd & 3rd segments serrate	No serrate segments	No serrate segments	No serrate segments
Uropods	Non-carinate	Non-carinate	Carinate	Strongly carinate

Neastacilla tranquilla sp. nov.

Figs 13a–d

Description of ♀

Head with ventral margins somewhat expanded; antero-dorsal corner also expanded anterior to dorso-lateral eye; two low rounded submedian dorsal bulges present. Peraeonal segment I fused with head, line of fusion marked by a narrow groove, and with lateral suture visible between head and Ist segment. Peraeonal segments I to III subequal, IVth segment about 3½ times length of three anterior segments together, tapering posteriorly in dorsal view. Peraeonal segment V slightly longer than following segments, segments V to VII each with three small lateral tubercles. Pleon consisting of three fused segments plus pleotelson, latter tapering to acute tip, sides slightly concave. Antennular flagellum of a single segment, equal in length to two distal peduncular segments together.

Antennal peduncle 5-segmented, 4th segment longest; flagellum 3-segmented, bearing about eight ventral spines. Three pairs of oostegites present.

Material

Holotype	SAM–A13615	SST.11.F.	♀ ovig.	6,3 mm
Paratype	SAM–A13616	SST.11.F.	♀ ovig.	6,3 mm

Remarks

Nordenstam (1933) defined the genus *Neastacilla* and mentioned some of the differences from *Astacilla*. The present material agrees with *Neastacilla* in

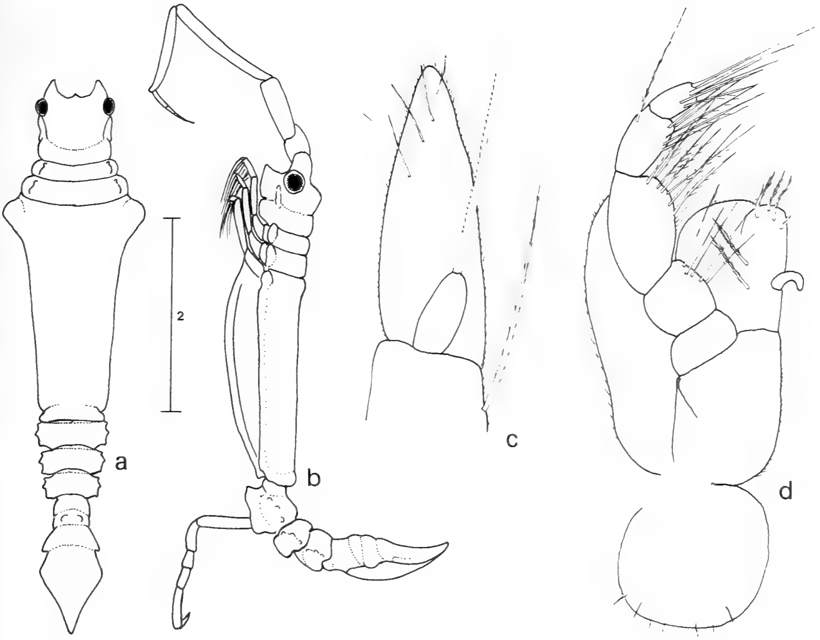

Fig. 13. *Neastacilla tranquilla* sp. nov.

a. ♀, dorsal view; b. ♀, lateral view; c. apex of uropod; d. maxilliped.

having peraeonal segment I fused with the head (the fusion marked by a shallow groove), the pleon consisting of three fused segments plus pleo-telson, and the inner ramus of the uropod bearing a long apical seta. The material does, however, show characteristics of species of *Astacilla*. These include the presence of a short lateral suture between the head and peraeonal segment I, and the lateral portions of the head and peraeonal segment I somewhat expanded. Peraeopod I however, does possess an unexpanded unguis on the dactylus. It would seem that Nordenstam's remark (1933: 119) concerning the superfluity of *Neastacilla* in view of species intermediate between *Astacilla* and *Neastacilla* may well be accurate.

N. tranquilla differs from the often recorded *N. bacillus* in several features, especially in the shape of the eyes, in being a relatively less slender species, and in possessing a 'shoulder' on the antero-lateral corners of peraeonal segment IV These shoulders are lacking in *N. bacillus*.

N. mediterranea, the other species recorded from South Africa, has a granulate integument and a spinose head, while *N. tranquilla* is quite smooth and non-spinose.

Suborder ANTHURIDEA

Family **Anthuridae**

Leptanthura agulhasensis sp. nov.

Figs 14a–k, 15a–d

Description of ♀

Head about half length of peraeonal segment I. Peraeonal segments I to VI subequal, segment VII two-thirds length of VIth. Pleonal segments free and distinct, pleon longer than peraeonal segment VII. Dorso-lateral keels only obvious on anterior peraeonal segments when seen in lateral view. Eyes absent.

Antennular peduncle 3-segmented, distal segment bearing several setae; flagellum very short, 4(5)-segmented.

Antennal peduncle 5-segmented, flagellum 4-segmented.

Mouthparts modified for piercing and sucking.

Mandible typical of the genus, elongate-acute; palp 3-segmented, broad middle segment three times length of basal segment, terminal segment short and narrow, bearing two terminal serrate spines.

Maxilla slender, elongate, distally serrate on inner margin, bearing three barbs on outer membranous margin.

Maxilliped elongate, basal segment at least four times longer than broad; followed by two (?three) distal segments bearing setae.

Peraeopod I with palm of propodus straight, with no thumb at base, with a row of seven short stout fringed setae flanked by simple elongate setae; carpus triangular, with three distal fringed setae, 2nd and 3rd segments subequal in length, 2nd segment wider.

Peraeopods II and III similar to I but becoming progressively more elongate.

Peraeopods IV to VII with dactyli slightly shorter than propodi, bearing 10–12 short setae on ventral margin; ventral margin of propodus with three spines; carpus triangular, small, underriding propodus, with two spines.

Exopod of pleopod 1 broadly oval, endopod half width of exopod, both rami fringed with elongate plumose setae.

Uropod exopod lanceolate, shorter than basis; latter with strong dorsal ridge, triangular in cross-section; endopod tapering to narrowly rounded apex extending beyond telsonic apex.

Telson with proximal two-thirds parallel-sided, distal third tapering to acute apex bearing a few fine setae. Single statocyst pore opening dorsally near base. Four pairs of oostegites present.

Description of ♂

Peraeopod I differs from female in having numerous setae on the palm, and in lacking a row of short fringed setae. Propodus with short blunt proximal projection.

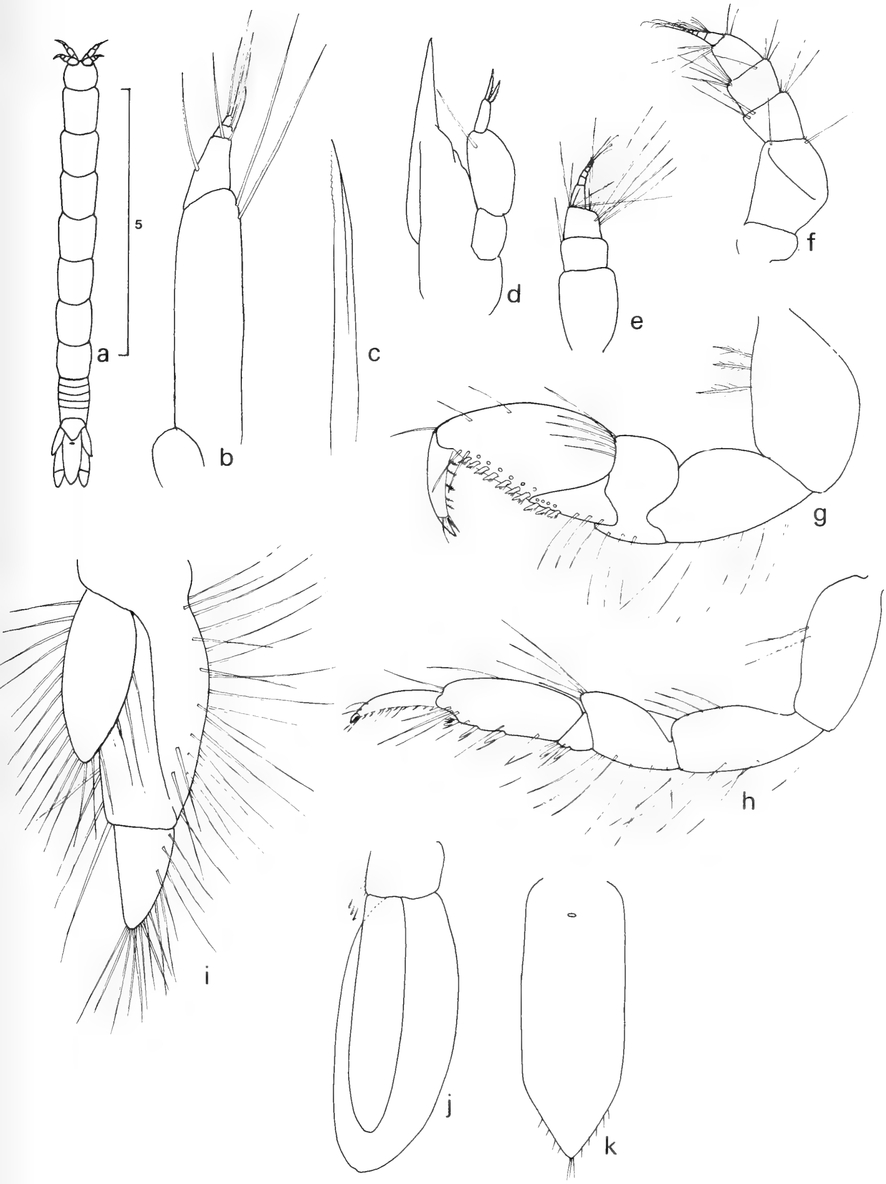

Fig. 14. *Leptanthura agulhasensis* sp. nov. ♀.
a. ♀, dorsal view; b. maxilliped; c. maxilla; d. mandible; e. antennule; f. antenna; g. peraeopod I; h. peraeopod VII; i. uropod; j. pleopod 1; k. telson.

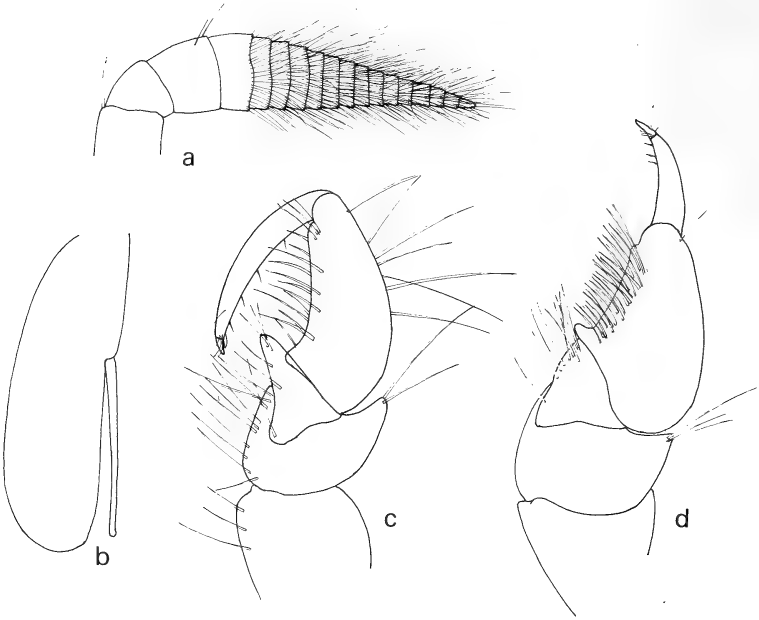

Fig. 15. *Leptanthura agulhasensis* sp. nov. ♂.
a. antenna; b. pleopod 2; c. peraeopod II; d. peraeopod I.

Peraeopod II more slender than peraeopod I, palm of propodus concave; blunt proximal projection of propodus outflanked by more elongate projection of carpus.

Antenna with brush-like flagellum of about 12 segments.

Pleopod 2 endopod with stylus not quite reaching apex of rami, apically rounded.

Material

Holotype	SAM–A13550	FAL.673.J–L	♂	9,0 mm
Allotype	SAM–A13551	SST.27.S	♀	8,0 mm
Paratypes	SAM–A13617	FAL.673.J–L	♂♂	9,1 mm 9,0 mm
Paratypes	SAM–A13618	SCD.343.Q	♀♀	7,9 mm 6,5 mm
		SCD.204.B	♀	6,8 mm
		WCD.77.G	♀	7,9 mm
		SST.31.U	♀	8,0 mm

Remarks

The present species would seem to be most closely related to *L. tenuis* (Sars) recorded from the North Atlantic. The two species agree in the structure of the antennae, antennules, mouthparts, telson, and pleopods. In the structure of the peraeopods, however, the two species do differ. The palm of peraeopod I (as figured by Sars 1897, pl. 20; and Schultz 1969, fig. 129) of *L. tenuis* is concave, with a marked thumb, whereas the present species has a straight palm and no thumb. Peraeopods IV to VII differ in spination and setation. The uropods are also different. The present species has a marked dorsal ridge on the basis which is triangular in cross-section. This feature is not present in *L. tenuis*. The uropod exopod of the latter species is broader and proportionally longer than in *L. agulhasensis*.

Leptanthura urospinosa sp. nov.

Figs 16a–k

Description of ♀

Head about half length of peraeonal segment I. Peraeonal segments I to VI subequal in length. Peraeonal segment VII two-thirds length of VIth. Pleon equal in length to peraeonal segment VII. Pleonal segments free and distinct, 5th segment longer than preceding segments, 6th semicircular. Eyes absent.

Antennular peduncle 3-segmented, distal segment bearing several setae, flagellum 6-segmented.

Antennal peduncle 5-segmented, second segment longest, flagellum 3-segmented. Mouthparts modified for piercing and sucking.

Mandibular palp 3-segmented, median segment about twice longer than broad, distal segment bearing two serrate spines.

Maxilla slender, inner margin serrate, outer membranous margin bearing three separate barbs.

Maxilliped slender, elongate, basal segment extended distally on inner margin followed by two setae-bearing segments.

Peraeopod I with palm of propodus straight, bearing six stout serrate setae plus several simple setae; carpus triangular, bearing three stout sensory setae.

Peraeopod VII with propodus carrying four sensory setae on ventral margin; carpus underriding propodus, triangular, carrying two sensory setae; unguis of dactylus very short and blunt.

Pleopod 1 exopod broadly oval, operculate.

Uropod exopod broadly leaf-shaped, inner margin proximally with a right-angled bend marked by short spine, inner margin dentate, slightly longer than basis, not reaching telsonic apex; basis with strong dorsal ridge, triangular in cross-section; endopod triangular, extending beyond telsonic apex.

Telson tapering gently, but distal quarter tapering more acutely; single statocyst situated near base.

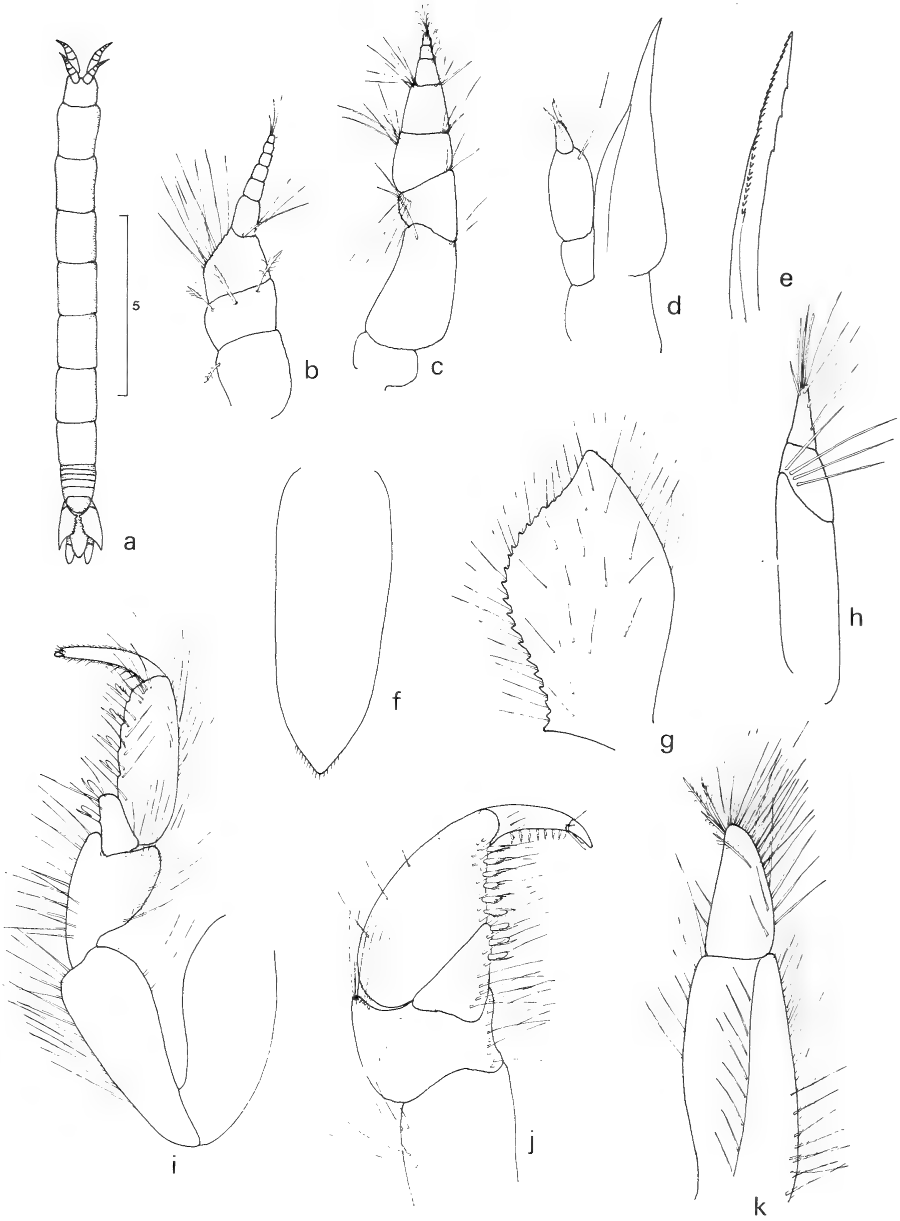

Fig. 16. *Leptanthura urospinosa* sp. nov.

a. ♀, dorsal view; b. antennule; c. antenna; d. mandible; e. maxilla; f. telson; g. uropodal exopod; h. maxilliped; i. peraeopod VII; j. peraeopod I; k. uropodal basis and endopod.

Material

Holotype	SAM–A13619	FAL.666.X–Y	♀	10,5 mm
Paratype	SAM–A13620	FAL.838.Z	♀	13,3 mm
		FAL.654.N–R	♀ ovig.	8,8 mm
			♀	9,6 mm
		FAL.442.K	3 ♀♀	8,5 mm
				6,4 mm
				6,0 mm
		SST.1.W	♀	5,4 mm
		SST.19.L	♀	8,0 mm
		SCD.310.B	♀	5,2 mm

Remarks

In several respects, *L. urospinosa* resembles the foregoing species, *L. agulhasensis.* These similarities include the mandible, maxilla, antennae, peraeopods I to VII, and the telson. The major difference is to be seen in the uropod exopods. In *L. agulhasensis* the exopod is a short lanceolate structure, while in *L. urospinosa,* this is a broadly oval structure, dentate on the inner margin, with the exopod of each side almost touching basally. The maxilliped of *L. agulhasensis* appears to have at least one segment more than in *L. urospinosa,* while the antennular flagellum of the latter species consists of six segments, of four to five segments in the former. The shape of the uropod exopod (except for its dentate inner margin) is similar to that of *L. tenuis.*

Katanthura laevitelson sp. nov.

Figs 17a–k

Description of ♀

Head and first six peraeonal segments of equal length, peraeonal segment VII very short; segments IV to VI with shallow transverse furrow anteriorly. Pleon slightly shorter than peraeonal segment VI. Pleonal segments distinct. Dorsal surface of pleon and peraeon bearing irregular brown reticulate pattern. Frontal margin of head with tiny rostral point; large well-developed oval eyes on antero-lateral corner.

Antennule shorter than antenna, basal segment twice length of 2nd segment, flagellum of 11 segments.

Antennal peduncle 5-segmented, 2nd segment widest and longest, flagellum of 20 segments.

Mouthparts adapted for piercing and sucking.

Mandibular palp 3-segmented, basal segment short, 2nd segment equal in length but narrower than 3rd, bearing single simple setae; 3rd segment bearing a single elongate fringed seta distally, plus row of 17 or 18 spines on outer margin. Mandible with piercing portion tapering, with single strong spine-like process, ensheathed by an apparently membranous structure.

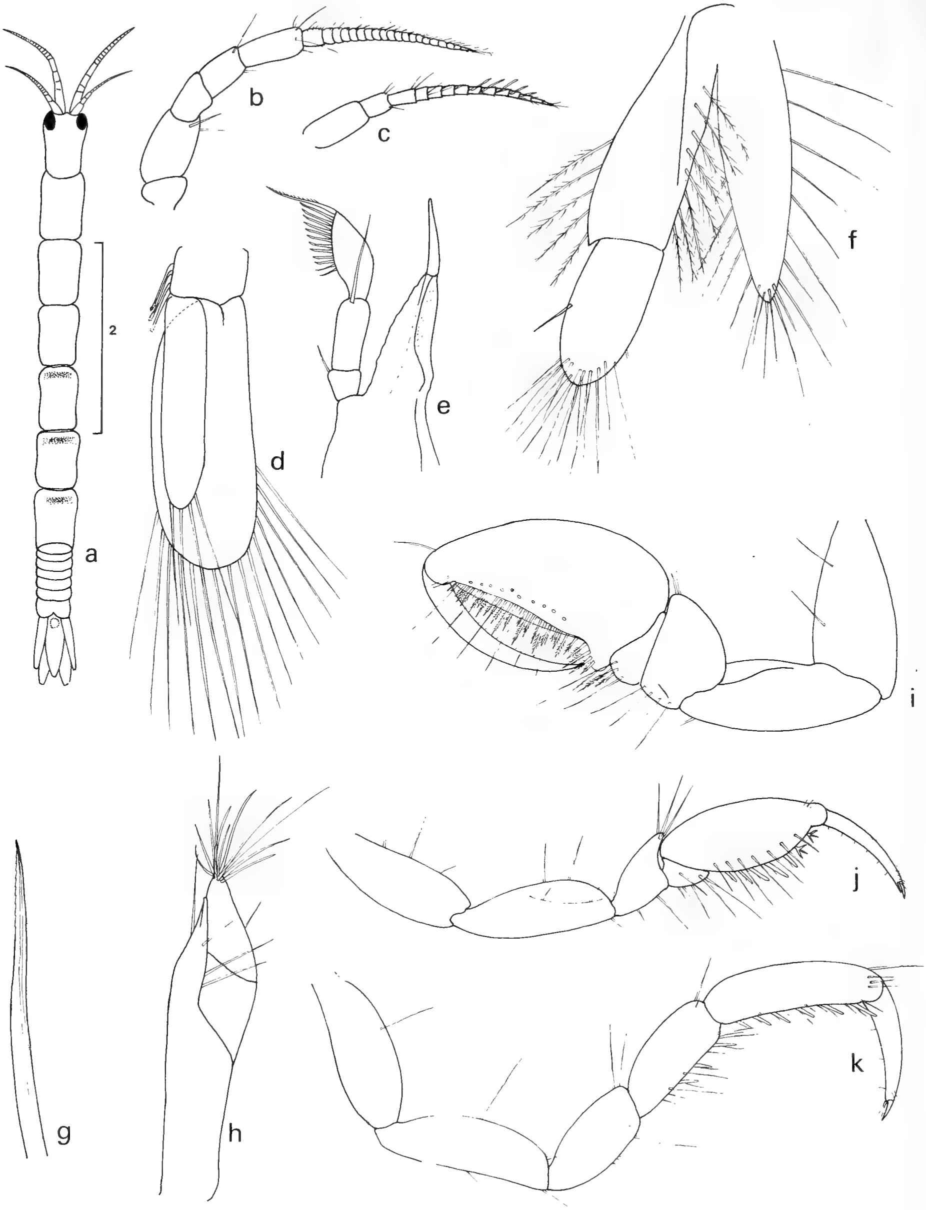

Fig. 17. *Katanthura laevitelson* sp. nov.

a. ♀, dorsal view; b. antenna; c. antennule; d. pleopod 1; e. mandible; f. uropod; g. maxilla; h. maxilliped; i. peraeopod I; j. peraeopod II; k. peraeopod VI.

Maxilla slender, harpoon-like, distally serrated on one margin, and with fine groove running length of the appendage, widening proximally.

Maxilliped of three segments; proximal segment slightly longer than two distal segments, with slender lobe-like extension on medio-distal angle; terminal segment tapering to narrowly-rounded apex with cluster of about 13 slender setae.

Peraeopod I strong, subchelate, dactylus strongly curved, with no obvious unguis; propodus proximally broader than distally, palm only slightly curved, with row of more or less alternating long and short fringed spines, and scattered long setae; palm flanked by single row of fringed spines; base of palm with rounded lobe. Carpus short, triangular, merus with broadly rounded dorsal area; ischium and basis subequal, more elongate.

Peraeopod II with propodus not as strong or as wide as in peraeopod I; dactylus curved, with short unguis; propodus with row of seven spines on inner margin, two distal spines tripartite, proximal five spines having sensory tip.

Peraeopod III similar to II.

Peraeopods IV to VI with dactylus having distinct small unguis, propodus with five or six stout spines on inner margin, carpus with three spines on ventral margin. Peraeopod VII absent.

Pleopod 1 not operculiform, outer ramus elongate, distally broadly rounded, about three times width of inner ramus, with several distal plumose setae; inner ramus narrow, not curved.

Pleopod 2 with outer ramus only slightly longer than inner.

Uropod with exopod longer than basis, slender lanceolate, apically narrowly rounded, with numerous setae; endopod twice longer than wide, apically rounded with numerous setae, extending beyond telsonic apex.

Telson elongate, tapering gently to point, bearing distal setae, large median proximal statocyst, but no sculpture.

Material

Holotype	SAM–A13552	SST.47.K	♀	6,4 mm

Remarks

The genus *Katanthura* was defined by Nierstrasz (1941) for *K. barnardi* from the Solar Straits. It has the following characteristics, recorded by Barnard (1925):

> Mouthparts modified for piercing and sucking.
> No statocyst in telson.
> Carpus of peraeopods IV to VI not underriding propodus.
> Maxilliped 4-segmented.
> Peraeonal segment VII very short, lacking peraeopods.

The male is not known. Nierstrasz based his description on a single female, as is done in the present case. The specimen described here is so well preserved and so markedly different from the female of *K. barnardi* that it is described as a new species.

The differences between the two species of *Katanthura* are given in the following table.

	K. barnardi	*K. laevitelson*
Mandibular palp	Terminal segment with 2 rows of spines, no elongate spine	One row of spines, one elongate spine
Maxilla	Possessing free lancets	No free lancets
Antennule	Flagellum of 14 segments	Flagellum of 11 segments
Antenna	Flagellum of 22 segments	Flagellum of 20 segments
Peraeopod VI	Propodus with 3 (?) spines	Propodus with 6 ventral spines
Pleopod 1	Endopod distally curved	Endopod not curved
Telson	Bearing 6 weak ridges	Unsculptured
Statocyst	Absent	Present
Total length	14 mm	6,4 mm
Uropod	Relatively slender	Not as slender as *K. barnardi*

Agulanthura gen. nov.

Diagnosis

Mouthparts normal, not modified for piercing and sucking. Maxilliped 5-segmented. Third segment of mandibular palp shorter than 1st or 2nd. Eyes present. Unguis of peraeopod I long. Peraeopod II smaller than I. Carpus of peraeopods IV to VII not underriding propodus, but distally expanded, distal margin straight. Pleopod 1 operculiform. Pleonal sutures indistinct in male and female. Stylet on pleopod 2 of male slender, acute. Exopod of uropod folding over telson. Latter lanceolate, dorsally convex, with two statocysts at base.

Type species of the genus: *Agulanthura serenasinus.*

Agulanthura serenasinus sp. nov.

Figs 18a–o

Description of ♂

Body elongate, head half length of peraeonal segment I. Peraeonal segments subequal in length, each segment about twice as long as wide. Pleonal segments indistinct, apparently fused, except segment 6 which is free. Segmental part of pleon equal in length to telson.

Antennule shorter than antenna, three basal peduncular segments short, flagellum consisting of 10 segments each bearing numerous short setae.

Antennal peduncle with basal segment longest, slightly longer than 2nd and 3rd segments together, 4th segment slightly longer than 3rd; flagellum with six segments each with disto-ventral tuft of about 10 setae.

Mandibular palp 3-segmented, basal and 2nd segments equal in length, each with single distal fringed seta, terminal segment shortest, with five distal spines; incisor process bearing bluntly rounded irregular teeth.

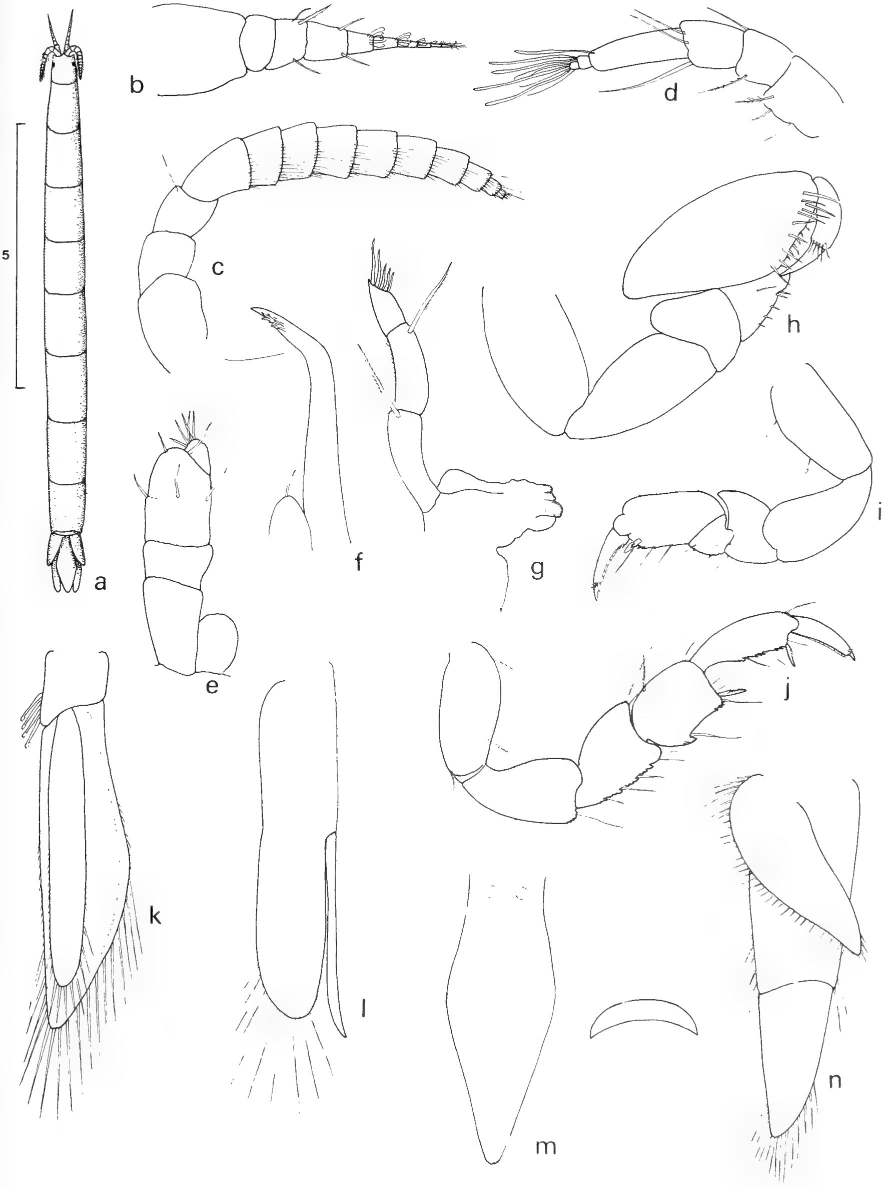

Fig. 18. *Agulanthura serenasinus* sp. nov.

a. ♂, dorsal view; b. antennule; c. antenna ♂; d. antenna ♀; e. maxilliped; f. maxilla; g. mandible; h. peraeopod I; i. peraeopod II; j. peraeopod VII; k. pleopod 1 ♂; l. pleopod 2 ♂; m. telson, with cross-section; n. uropod.

Maxilla slender, distally curved, tapering to point, with four or five subterminal spines.

Maxilliped 5-segmented, terminal segment set obliquely on penultimate segment, bearing five distal setae; 2nd segment three times length of 3rd, latter half length of 4th segment.

Peracopod I longer and stouter than II, unguis almost same length as rest of dactylus, gently curved; propodus three times longer than wide, palm sinuous, flanked by irregular row of 15 spine-like setae; carpus triangular, with seven or eight setae; ischium and basis subequal in length.

Peraeopod II dactylus with very short unguis, slightly curved, with ventral groove flanked by membranous flange; propodus twice as long as wide, disto-ventral corner with two short spines, plus short spine bearing accessory spinules; carpus small, triangular.

Peraeopods IV to VII with dactylus slightly shorter than propodus, gently curved, ventrally serrate, unguis very short; propodus twice width of dactylus, bearing several short spines disto-ventrally, plus strong blunt spine bearing accessory spinules; carpus almost square, distal margin not underriding propodus but straight, disto-ventral corner serrate, bearing strong blunt spine; ventral margin bipartite, proximal portion defined by few serrations and very short spines; merus equal in length to carpus, ventral margin with three equally-spaced groups of serrations.

Pleopod 1 outer ramus operculiform, median margin straight, outer margin evenly convex, bearing elongate distal plumose setae; inner ramus lying ventral to outer ramus, half width of outer, and slightly shorter.

Pleopod 2 rami subequal in length, tipped with plumose setae, stylet slender, elongate, apically acute.

Telson lanceolate, widest at midpoint, tapering to narrowly-rounded apex with proximo-lateral ridge covered by closely adpressed exopod of uropod.

Uropod endopod slightly shorter than telson, tapering evenly to narrowly rounded apex; basis medially hollowed to accommodate telson; exopod narrowly leaf-shaped, curved dorsally over, and adpressed to telson; margin fringed with plumose setae.

Description of ♀

Antennule longer than antenna, basal segment equal in length to following three segments, median face hollowed to accommodate antenna, flagellum of six segments, each with distal cluster of setae.

Antenna with three basal peduncle segments subequal, stout, 4th segment more elongate, flagellum reduced, consisting of only two tiny segments.

All appendages with exception of pleopod 2 as in male.

Material

Holotype	SAM–A13553	FAL.487.F	♂	11,0 mm
Allotype	SAM–A13554	FAL.685.B–D	♀	14,5 mm

Paratype	SAM–A13621	SCD.329.R	♀	13,0 mm
Paratype	SAM–A13622	SB.310.S	♀	14,0 mm
Paratypes	SAM–A13623	SST.74.G	3 ♀♀	12,9 mm 7,1 mm 6,9 mm
			♂	11,0 mm

Single female specimens from SST.67.S, SCD.188.P, FAL.763.R–S, FAL.496.L, FAL.685.B–D, FAL.666.X–Y, FAL.654.N–R, 6,0 mm–12,3 mm.

Remarks

Agulanthura serenasinus has several features in common with species of *Haliophasma*. These include the unsegmented pleon, the 5-segmented maxilliped, operculiform pleopod 1; also, the carpi of the posterior peraeopods do not underride the propodi. Several other features in combination, however, seem to indicate the separation of the present species into a new genus. These features include the feebly developed eyes, the uropod exopod which is closely adpressed to the telson, the proximo-laterally ridged telson, the long unguis of the dactylus of peraeopod I, the square-ended carpus of peraeopod VII, and the uninterrupted body profile of the animal.

Holoroanthura capensis sp. nov.

Figs 19a–l, 20a–c

Description of ♀

Head shorter than peraeonal segment I, having slight rostral point. Eyes absent. Peraeonal segments I to IV gradually increasing in length, segments V and VI subequal, segment VII slightly shorter. Pleonal segments distinct, together equal to VIth peraeonal segment in length. Dorso-lateral ridges distinct only on anterior two peraeonal segments.

Antennule slightly shorter than antenna, consisting of three peduncle segments, and 4-segmented flagellum tipped with two aesthetascs.

Antennal peduncle 4-segmented, flagellum 7-segmented.

Mandible with incisor portion consisting of upper chitinised portion of three teeth, and five weakly chitinised teeth, separated from a blunt tooth by a row of tiny denticles; palp 3-segmented, terminal segment short, bearing three distal spines, middle segment twice length of basal segment. Maxilla moderately stout, distally curved with one strong and four or five smaller spines.

Maxilliped slender, 1st free segment three to three and a half times longer than wide, with digitiform extension at medio-distal angle; 2nd and 3rd segments subequal, 4th segment half length of 3rd, terminal segment tiny.

Peraeopod I no different in size from peraeopod II, unguis one-third length of dactylus; palm of propodus bearing three setae; carpus triangular, ventro-distal extension forming thumb, but not as marked as in following two pairs of peraeopods.

Peraeopods II and III with thumb-like projection of carpus well developed,

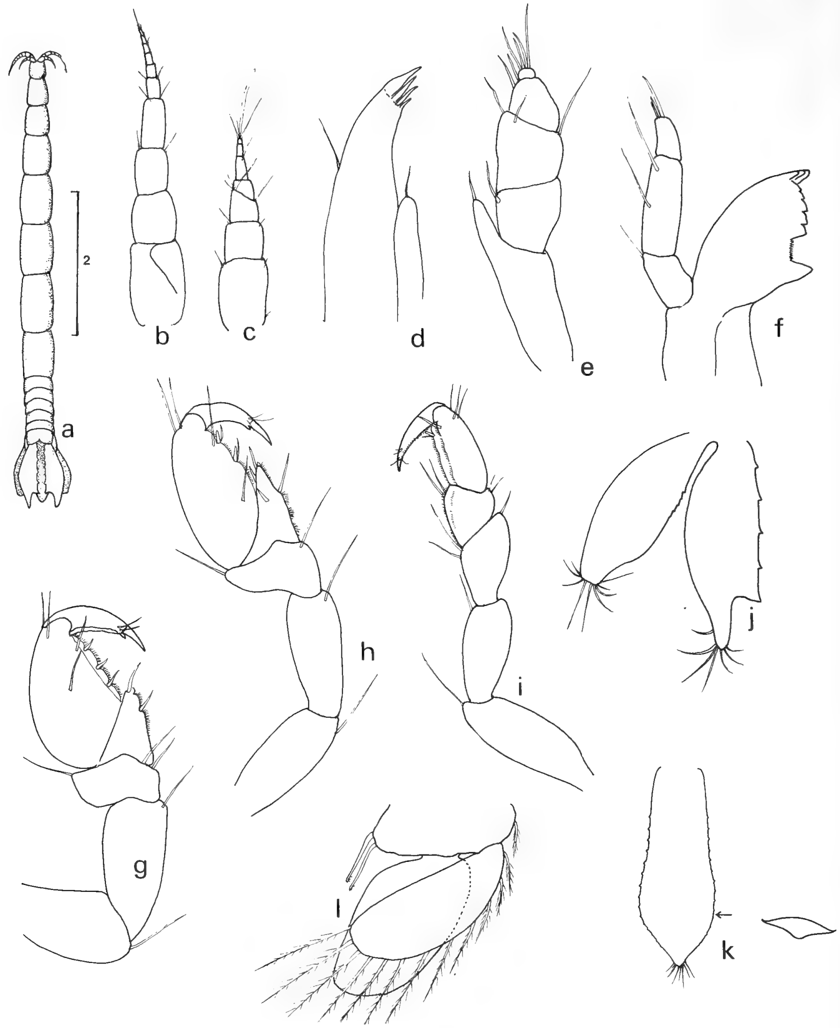

Fig. 19. *Holoroanthura capensis* sp. nov.

a. ♀, dorsal view; b. antenna; c. antennule; d. maxilla; e. maxilliped; f. mandible; g. peraeopod I; h. peraeopod II; i. peraeopod VII; j. uropod; k. telson, with cross-section at level of arrow; l. pleopod 1.

bearing two setae and short terminal blunt spine; palm of propodus armed with two spines.

Peraeopods IV to VII with carpus triangular, underriding propodus; three distal segments bearing ventral fringe of very fine setules.

Pleopod 1 not operculiform, similar to following pleopods, rami subequal in length, fringed with long plumose setae.

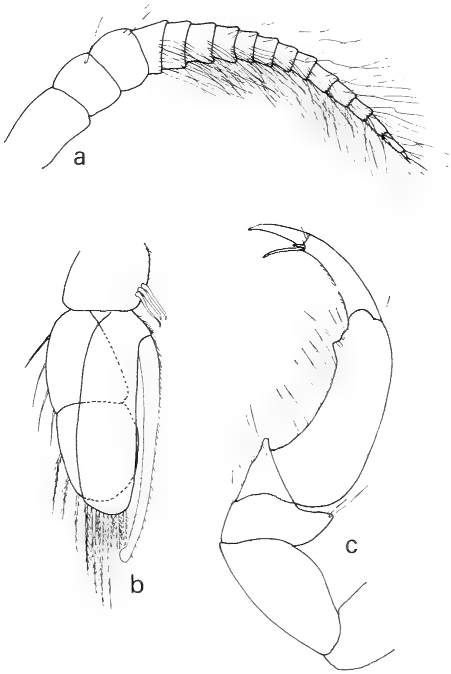

Fig. 20. *Holoroanthura capensis* sp. nov. ♂.
a. antenna; b. pleopod 2; c. peraeopod I.

Uropods and telson indurated, slightly splayed. Endopod of uropod almost twice length of basis, apically truncate, bearing few denticles proximally; outer margin of exopod sinuous, ending in narrowly rounded lobe, inner margin straight, bearing four to six denticles, ending in strong triangular tooth well separated from distal narrow lobe.

Telson margins serrate, distally lanceolate, with strong medio-ventral rounded ridge.

Description of ♂

Antenna consisting of three peduncular segments, basal one longest, plus flagellum of 13 to 14 segments bearing numerous fine setae.

Peraeopod I unguis one-third length of dactylus, latter curved; propodus with concave palm, bearing about 10 setae; carpus triangular, distally forming tiny thumb.

Pleopod 2 with slender slightly curved stylet on inner margin of endopod, extending well beyond endopod apex, apically blunt, rounded.

Material

Holotype	SAM–A13555	WCD.64.P	♂	3,8 mm
Allotype	SAM–A13624	LBT.72.K	♀	6,1 mm
Paratypes	SAM–A13625	WCD.109.A	♂	3,1 mm
			5 ♀♀	4,2–5,0 mm
		WCD.64.P	♀	4,0 mm
		WCD.111.J	♀	4,0 mm
		WCD.114.U	4 ♀♀	3,5–4,9 mm

Remarks

The present material agrees well with the generic definition of *Holoroanthura* Menzies & Frankenberg (1966: 41) which is characterized by the lack of eyes, the possession of normal biting mouthparts, a short unguis on peraeopod I of the female, the carpus of peraeopods IV to VII underriding the propodus, the maxilliped 5-segmented, and all pleonal segments distinct.

The type species of the genus, *H. irpex*, is represented by a single female recorded off Georgia, U.S.A. *H. capensis* differs in several respects from the American species. In the latter the telson is sharply pointed and not indurated, the spines on the exopods of the uropods elongate, and the inner margin of the endopod of the uropod as well as the telson margins are entire. In *H. capensis* the telson is broadly lanceolate (not sharply tapering) and indurated, the spines on the inner margin of the exopod of the uropod tiny, the inner margin of the uropod endopod and the telson margins finely denticulate. The basal maxilliped segment in *H. capensis* is more obviously lobed than in the American species.

Suborder FLABELLIFERA

Family **Cirolanidae**

Cirolana borealis Lilljeborg

Figs 21a–g

Cirolana borealis: Sars, 1897: 70. Hansen, 1905: 342. Richardson, 1905: 101. Schultz, 1969: 182. Riedl, 1970: 345.

Material

SAM–A13556	SST.57.A–B	♀	6,3 mm
SAM–A13557	SST.114.A–G	♀	damaged

Previous records

Atlantic coast of North America, eastern North Atlantic, Mediterranean.

Remarks

The present material agrees well with the above-mentioned descriptions. A very few differences with the northern species do exist. Unfortunately, no male

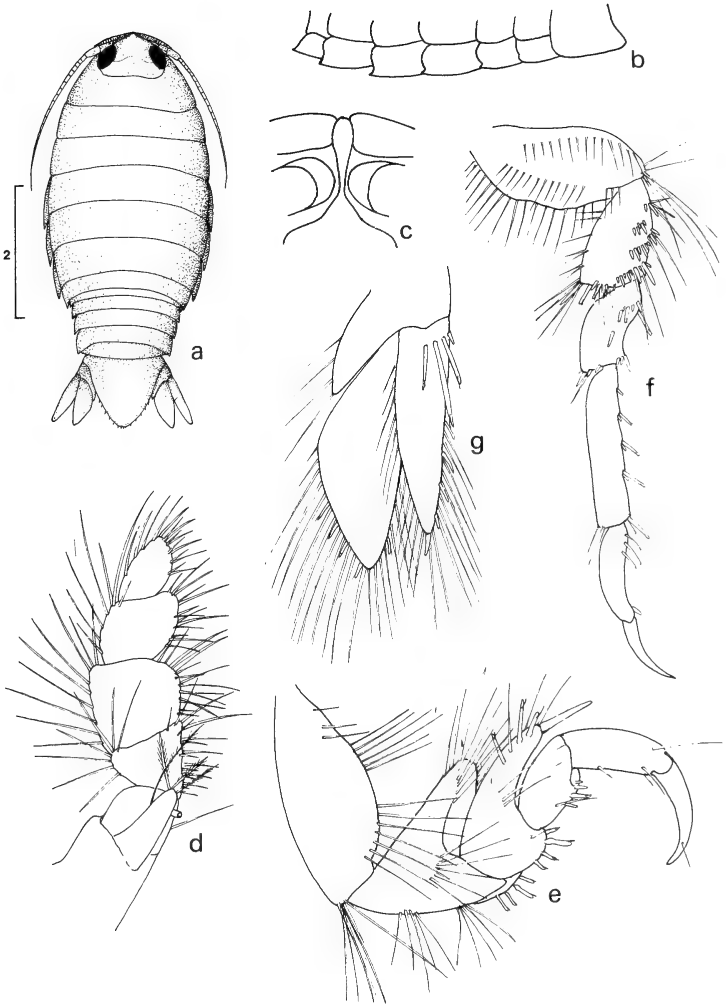

Fig. 21. *Cirolana borealis* Lilljeborg.

a. ♀, dorsal view; b. peraeonal epimeres; c. epistome; d. maxilliped; e. peraeopod I; f. peraeopod VI; g. uropod.

is available for comparison of pleopod structure. In the present material the epimeres are postero-ventrally acute and also have a tiny notch subterminally especially on epimeres III to VI. The northern species seems to lack this tiny notch. This feature may, however, be due to the immaturity of the specimens, as the species apparently matures sexually at about 12 mm length.

Cirolana obtusispina sp. nov.

Figs 22a–i, 23a–f

Description of ♂

Body two and a half times longer than wide, smooth, widest at peraeonal segment III. Head with impressed line joining posterior margins of eyes. Each peraeonal segment with transverse impressed line in posterior third. Pleo-telson triangular, tapering to subacute apex, with two submedian dorsal rounded longitudinal ridges, strongest proximally, becoming obscure distally. Epimeres II to IV rounded to quadrate. Epimeres V to VII becoming progressively more acute and elongate. Epimere of pleon segment 4 overlapping 5th. Epistome longer than wide, distally rounded, with slight lateral 'shoulders'. Antennule shorter than antenna, basal segment with ventral groove to accommodate basal segment of antenna; 3rd peduncular segment twice length of 2nd, flagellum 9–10-segmented. Antennal peduncle 5-segmented, two distal segments largest, flagellum of about 12 segments.

Mandibles with 3-segmented palp, terminal segment bearing 12–14 curved simple spines, middle segment with 12–14 serrate spines, molar process produced, with row of teeth on upper margin; incisor process with three strong chitinised teeth, and secondary cluster of six smaller spine-like teeth.

1st maxilla with outer ramus bearing 10 slightly curved spines, some of which are denticulate; inner ramus with three stout plumose setae.

2nd maxilla outer ramus bilobed, each lobe digitiform, bearing several plumose setae; inner ramus broadly rounded, bearing several plumose setae.

Maxilliped with 5-segmented palp, 3rd segment broad, 4th segment somewhat lobed on inner margin; endite about half width of basal lobe, tapering slightly distally, bearing four plumose setae, single very short blunt spine, and single coupling hook.

Peraeopod I dactylus with distinct unguis; propodus armed with three spines on ventral margin; carpus triangular, merus bearing five blunt knob-like modified spines, and three acute spines on ventral margin.

Peraeopod VII with propodus, carpus, merus, and ischium each bearing several simple and serrate spines on distal margin, plus pair of spines at midpoint of ventral margin.

Penial processes moderately elongate, digitiform.

Pleopod 1 with roughly rectangular basis bearing five coupling hooks; endopod one-third width of exopod, latter oval-round.

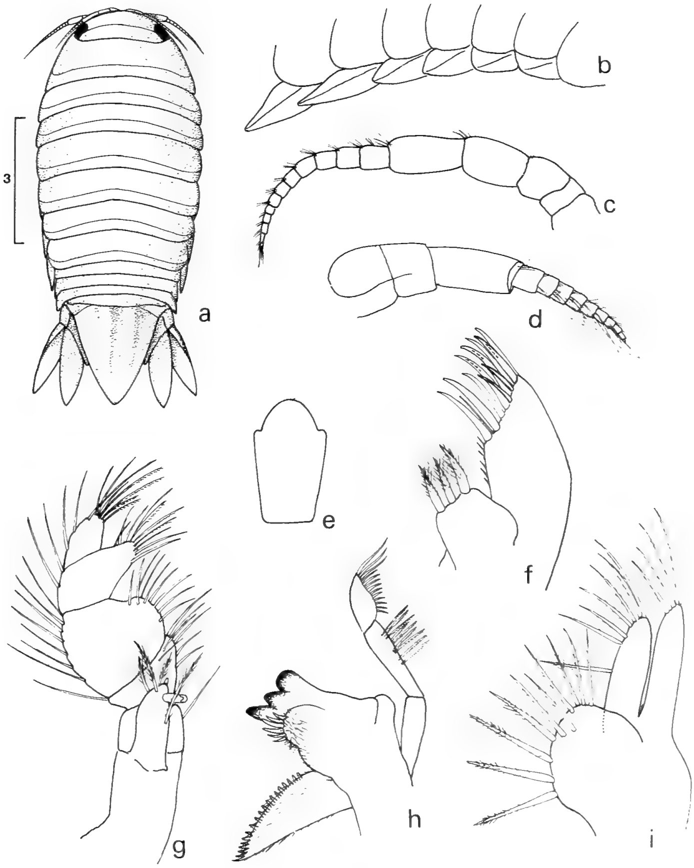

Fig. 22. *Cirolana obtusispina* sp. nov.
a. ♀, dorsal view; b. peraeonal epimeres; c. antenna; d. antennule; e. epistome; f. 1st maxilla; g. maxilliped; g. mandible; i. 2nd maxilla.

Pleopod 2 endopod bearing sabre-shaped stylet on inner margin, extending well beyond end of rami.

Uropod base produced on inner margin of inner ramus, latter with numerous setae and few spines; outer ramus lanceolate, shorter than inner, bearing several setae and two short spines on inner margin.

Material

Holotype	SAM–A13558	SST.19.N	♂	8,0 mm
Paratypes	SAM–A13559	SST.21.U	2 ♀♀	5,2 mm 5,0 mm

Remarks

The present species is distinct as regards several features. These include the lack of dorsal sculpture, the 2-ridged pleo-telson, the form of the epistome, and the knob-like spines of the meri of peraeopods I to III. *Cirolana theleceps* Barnard, 1940 possesses a pleo-telson bearing two longitudinal ridges, but its denticulate distal margin, and also the shape and character of the uropods immediately distinguishes this species from *C. obtusispina.*

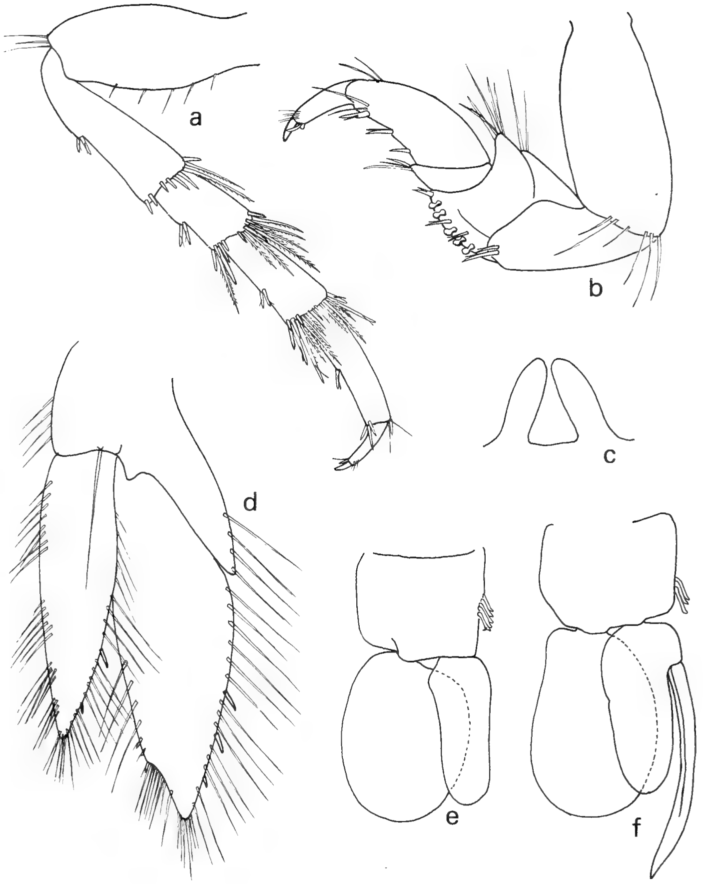

Fig. 23. *Cirolana obtusispina* sp. nov.
a. peraeopod VII; b. peraeopod I; c. penial processes; d. uropod; e. pleopod 1 ♂; f. pleopod 2 ♂.

Family **Sphaeromatidae**

Cymodoce alia sp. nov.

Figs 24a–h, 25a–h

Description of ♂

Body about two and a half times longer than broad, dorsally strongly convex. Peraeonal segment I broader than II, ventrally expanded with anterior lobe running ventral to eye, dorsally with broad transverse groove just behind head, plus row of small granules near posterior margin, and two larger submedian granules. Peraeonal segments II to IV with narrow epimeres, each with tiny granules near posterior margin, and two larger submedian granules. Epimeres of segments V to VII broader than preceding segments; peraeonal segment VII overlapping anterior pleon dorsally, finely granular, hind margin with two prominent tubercles on each side. First three pleon segments granular, overlapped by VIIth peraeonal segment. Pleon segment 4 with two large conical submedian tubercles and smaller lateral tubercle. Pleo-telson with two large conical submedian tubercles, apex notched, trilobed, median lobe smaller and lower than lateral lobes.

Antennule with basal segment strongly chitinised, large, external face granular; 2nd segment one-quarter length of first, also strongly chitinised; 3rd segment slender, slightly longer than 2nd; flagellum of 11–12 segments.

Antennal peduncle of five segments, two distal segments longest; flagellum of 11–12 segments; base hidden by basal segment of antennule. Basal segments of antennule flanking and closely adpressed to epistome.

Mandible with incisor process strongly chitinised, cutting edge evenly rounded; molar process also chitinised; six spines between incisor process and lacinia mobilis; palp 4-segmented.

1st maxilla outer ramus with 10 curved spines, inner ramus with four fringed setae.

2nd maxilla with both lobes of exopod tipped with about eight curved serrated spines; endopod bearing 11–12 fringed setae.

Maxilliped palp with 2nd, 3rd, and 4th segments lobed, lobes tipped with setae.

Peraeopod I dactylus with short spine at base of strong unguis, propodus two and a half times longer than wide, with four spines on ventral margin, spines all apically trifid; carpus triangular, also bearing four trifid spines; merus with one short and five long spines.

Peraeopod VII more slender and somewhat longer than first three pairs of peraeopods; propodus twice length of dactylus, with four simple spines on ventral margin; ventral margins of propodus, carpus, and merus with thick pile of short setules.

Pleopod 1 with triangular endopod, shorter than exopod.

Pleopod 2 with endopod bearing elongate slender stylet.

Pleopod 3 exopod 2-segmented, endopod broad, median margin straight.

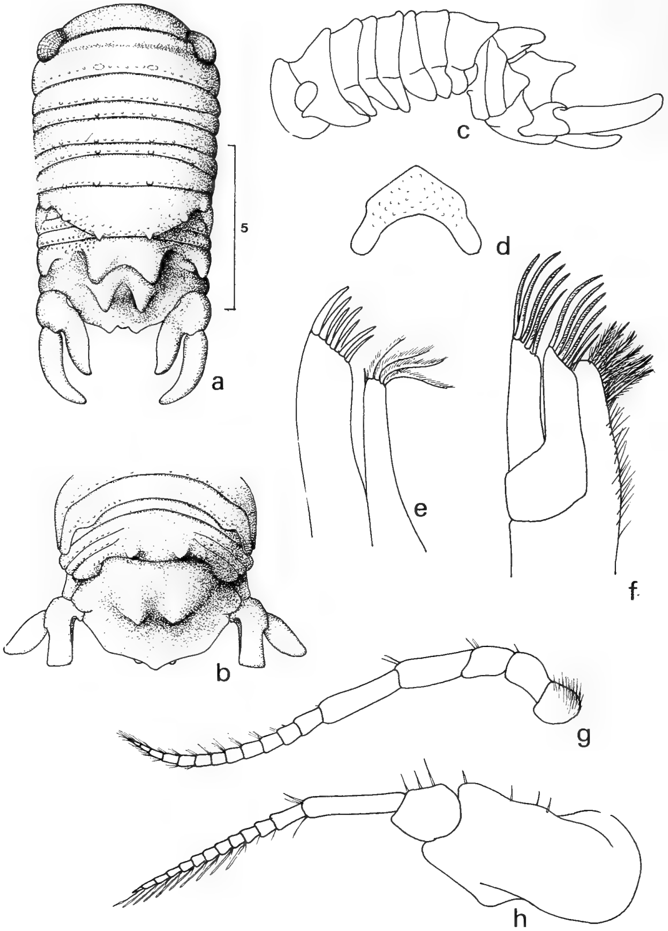

Fig. 24. *Cymodoce alia* sp. nov.

a. ♂, dorsal view; b. posterior peraeon and pleon ♀; c. ♂, lateral view; d. epistome; e. 1st maxilla; f. 2nd maxilla; g. antenna; h. antennule.

Pleopod 4 endopod with transverse pleats, apex with tiny lobe.

Pleopod 5 exopod bearing five spinule-bearing cushions, endopod bilobed, bearing transverse pleats.

Uropod with inner ramus fused to base, leaf-shaped, oval in cross-section, outer ramus longer than inner, curved towards midline, basally oval in cross-section, distally circular in cross-section, both rami bearing short setules.

Description of ♀

Not as granular as male, conical submedian process on 4th pleon segment and pleo-telson not as large as in male. Telsonic apex notched, trilobed, but

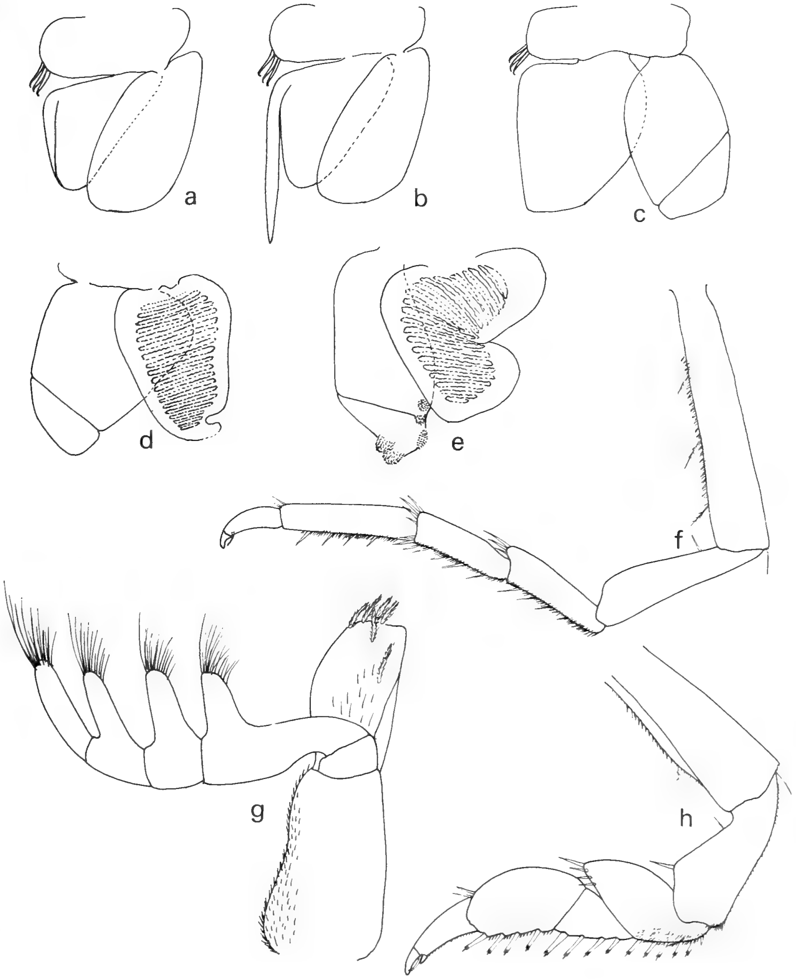

Fig. 25. *Cymodoce alia* sp. nov.
a. pleopod 1 ♂; b. pleopod 2 ♂; c. pleopod 3; d. pleopod 4; e. pleopod 5; f. peraeopod VII; g. maxilliped; h. peraeopod I.

curved ventrally. In dorsal view, median lobe longer than lateral lobes, latter just visible. Inner uropodal ramus distally quadrate, flattened, as long as outer ramus, latter leaf-shaped. Peraeonal segment VII not extending over pleon.

Material

Holotype	SAM–A13560	SST.21.S	♂	9,0 mm
Allotype	SAM–A13560	SST.21.S	♀ ovig.	8,5 mm
Paratypes	SAM–A13561	SST.21.S	♀	8,5 mm
		SST.17.A–B	♀ juv.	

Remarks

The following features are used to place the present material in the genus *Cymodoce*; hemibranchiate pleopods, pleo-telsonic apex notched in both sexes. maxillipedal segments lobed, both uropodal rami well-developed, no medial process on pleo-telson, mouthparts sexually dimorphic.

The present species most closely resembles *Cymodoce amplifrons* Stebbing of the numerous South African representatives of this genus, in possessing a strong pair of conical processes on both the last pleon segment and on the pleo-telson. The nature of the uropods and the trilobed medial lobe of the pleo-telson in the male of Stebbing's species, distinguish it from the present species.

Cymodoce velutina **sp. nov.**

Figs 26a–k, 27a–e

Description of ♂

Body about twice longer than wide, dorsally strongly convex. Most of dorsal surface of head, peraeon, pleon, and pleo-telson covered with tiny delicate membranous scale-like structures, with stout apically bifid seta arising from base of each. Pleo-telson smoothly convex, apex notched, trilobed, median lobe slightly longer than lateral lobes.

Antennular peduncle 3-segmented, basal segment strongly chitinised, flagellum 11–12-segmented.

Antennal peduncle 5-segmented, distal segment longest; flagellum 10-segmented. Mandible with strongly-chitinised incisor process having straight edge, tridentate lacinia mobilis; molar process broad, bristle-covered; palp 3-segmented.

1st maxilla outer ramus with about 10 curved spines, inner ramus with four apical fringed setae.

2nd maxilla with both lobes of exopod tipped with curved serrate spines, endopod bearing about six fringed setae.

Maxilliped palp with 2nd, 3rd, and 4th segments lobed, lobes tipped with setae. Peraeopod I shorter than following peraeopods, dactylus with short spine at base of strong unguis, propodus, carpus, and merus each carrying four fringed spines, ischium with numerous fine setae on ventral margin. Following peraeopods similar to I, but with meri and bases somewhat longer.

Penial processes slender, elongate, apically slightly broadened.

Pleopod 1 endopod about half width of exopod.

Pleopod 2 with stylet on endopod extending beyond apex of ramus, slender, apically slightly hooked.

Uropod with inner ramus apically truncate, outer ramus about half length of inner, leaf-shaped.

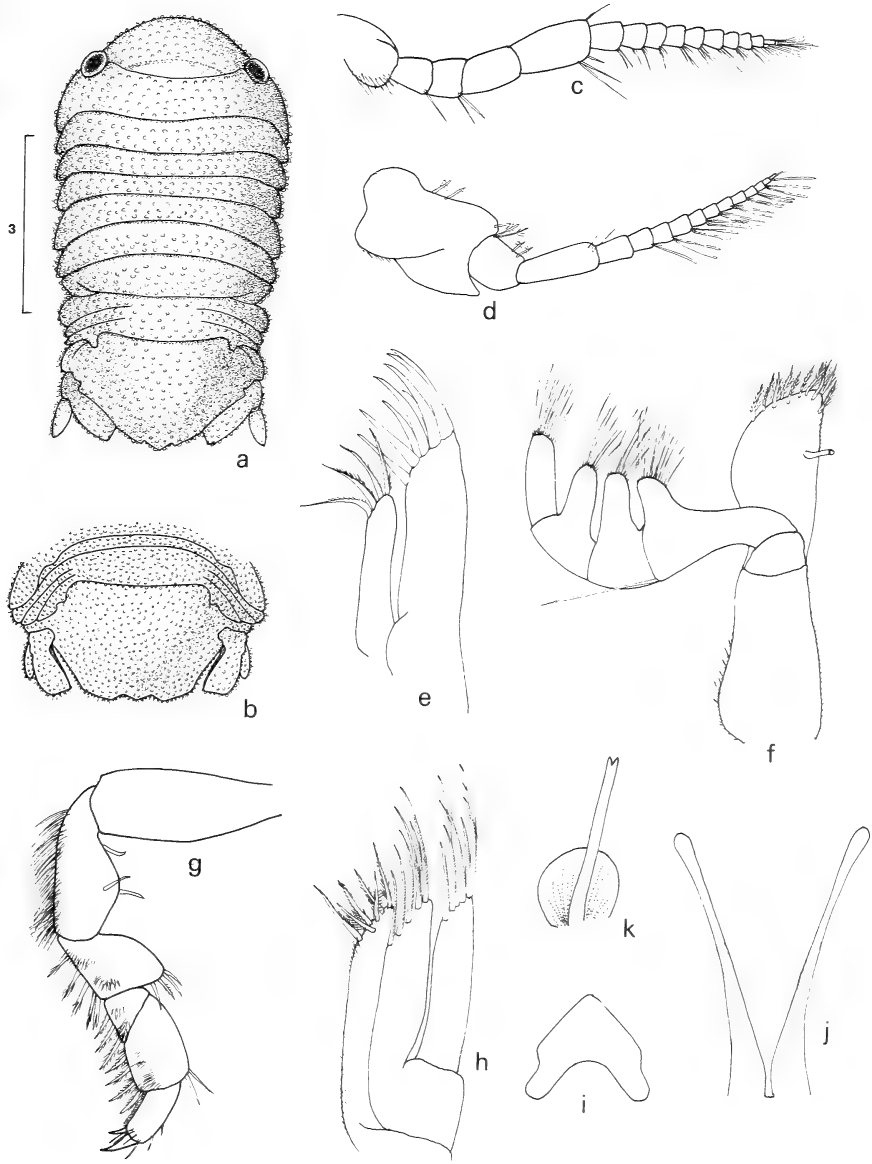

Fig. 26. *Cymodoce velutina* sp. nov.

a. ♂, dorsal view; b. ♀, pleo-telson dorsal view; c. antenna; d. antennule; e. 1st maxilla; f. maxilliped; g. peraeopod I; h. 2nd maxilla; i. epistome; j. penial processes; k. one scale and seta.

Description of ♀

Very similar to male, pleo-telson slightly broader, apex trilobed, lobes subequal.

Material

Holotype	SAM–A13629	FAL.700.R–T	♂	5,9 mm
Allotype	SAM–A13562	SST.20.Z	♀ ovig.	8,0 mm
Paratypes	SAM–A13630	FAL.700.R–T	3 ♂♂	6,0–6,9 mm

Remarks

The unmistakable body covering of this species is not found in any of the other southern African species of *Cymodoce*, nor in any of the exotic species. The unsculptured pleo-telson with trilobed apex is also distinctive.

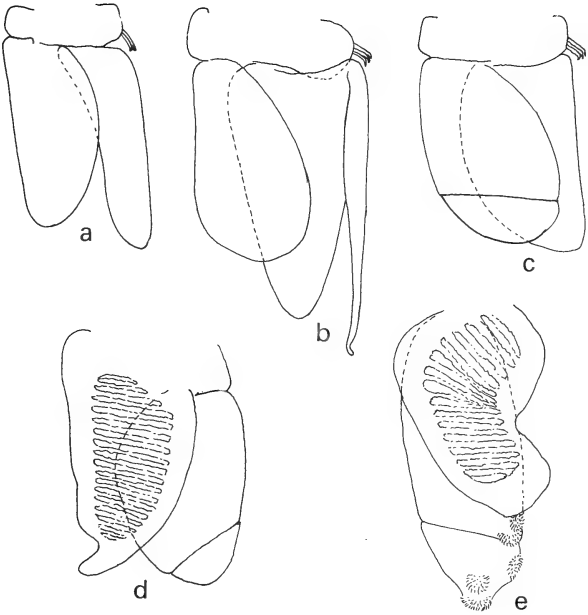

Fig. 27. *Cymodoce velutina* sp. nov. ♂.
a. pleopod 1; b. pleopod 2; c. pleopod 3; d. pleopod 4; e. pleopod 5.

ACKNOWLEDGEMENTS

I am grateful to Professor J. H. Day of the Department of Zoology of the University of Cape Town, for making the present collection available to the South African Museum for description.

My thanks are due to Dr J. Field of the Department of Zoology, for preliminary identifications of some of the isopods, and to Dr N. Christie of the Department of Zoology for the specimen of *Holoroanthura* from Lambert's Bay.

My sincere thanks are due to Dr George A. Schultz of Hampton, New Jersey, for reading the manuscript, and for his many helpful comments and criticisms.

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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 (figs 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:
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SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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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.

BRIAN KENSLEY

MARINE ISOPODA FROM THE CONTINENTAL SHELF OF SOUTH AFRICA

VOLUME 67 PART 5 AUGUST 1975 ISSN 0303–2515

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

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THE AMPHIPODA OF SOUTHERN AFRICA
PART 5
THE GAMMARIDEA AND CAPRELLIDEA OF THE CAPE PROVINCE WEST OF CAPE AGULHAS

By

C. L. GRIFFITHS

Cape Town Kaapstad

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THE GAMMARIDEA AND CAPRELLIDEA OF THE CAPE PROVINCE WEST OF CAPE AGULHAS

By

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(With 21 figures)

[*MS accepted 18 December 1974*]

ABSTRACT

A systematic account of the marine gammaridean and caprellid Amphipoda of the Cape Province of South Africa west of Cape Agulhas (20°E) is provided. The analysis is based on collections totalling over 70 000 specimens in the possession of the University of Cape Town and of the South African Museum, as well as records from the existing literature.

Two hundred and thirty-two species are recognized from the area. These include fourteen species which are recorded for the first time from southern Africa, as well as the following eleven species which are described as new to science: *Panoploea stegosaura, Maera emarginata, Maera komma, Maera thrixa, Melita mucronata, Listriella saldanha, Socarnes septimus, Perioculodes pallidus, Heterophoxus cephalodens, Heterophoxus opus* and *Podocerus pyurae.*

In addition the following changes in taxonomy are proposed:

A new family—the Temnophliidae—is erected for *Temnophlias* K. H. Barnard, 1940. *Ceradocus aviceps* K. H. Barnard, 1940 is removed to *Quadrivisio. Tryphosella africana* K. H. Barnard, 1955 is synonymized with *Hippomedon longimanus. Tryphosella normalis* K. H. Barnard, 1955 is removed to *Hippomedon* and *H. rotundipleura* Ledoyer, 1973 synonymized with it. *Microlysias indica* K. H. Barnard, 1937 is synonymized with *M. xenoceras. Uristes induratus* K. H. Barnard, 1925, is removed to *Procyphocaris* where *P. primata* J. L. Barnard, 1961 falls into synonymy with it. *Podocerus cristatus* of K. H. Barnard (1916) and Griffiths (1973, 1974*a*, *c*) is referred to *P. inconspicuus. Allorchestes inquirendus* is synonymized with *Hyale grandicornis, Talorchestia inaequalipes* with *Orchestia gammarella* and *Caprella falsa* with *C. penantis.*

CONTENTS

INTRODUCTION

The following account forms the fifth and last part of a series surveying the known gammaridean and caprellid Amphipoda of various geographical zones within southern Africa (defined as Africa south of 20°S). Previous sections

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have dealt with Moçambique (Griffiths 1973), South West Africa (Griffiths 1974*a*), Natal (Griffiths 1974*b*) and the Cape Province east of Cape Agulhas (Griffiths 1974*c*), while the present portion deals with the remaining area between Cape Agulhas and the South West African border.

Oceanographic conditions along the Atlantic coast from Cape Point to South West Africa are primarily influenced by the Benguela Current. The cold waters of this current originate in the sub-antarctic, but before reaching the African coast they have been covered by a thick layer of warmer, less dense South Atlantic water, 200–500 m thick. However, along the coastal margin the dominant south or south-easterly winds of summer frequently blow the warm oceanic water offshore, allowing cold Benguela water to upwell to the surface. Thus although surface temperatures a few kilometres offshore average 15–17°C the narrow band of inshore upwelled water may be as cold as 8°C (normally 10–14°C). As wind stress varies so the width of the upwelled zone waxes and wanes, indeed during periods of north-westerly winds the warmer Atlantic water extends to the shoreline.

Conditions in the area between Cape Agulhas and Cape Point are even more variable than those experienced along the west coast, since warm Agulhas Current and cold Benguela Current waters mix in this region. The limits of the warm and cold waters are controlled largely by wind conditions and are consequently highly variable. During periods of south-easterly winds, particularly in summer, warm Agulhas water may extend into False Bay, and as an offshore tongue of water, right around Cape Point. Where this water reaches the shore the temperature may rise above 20°C, but this rise is not universal since local upwelling cells are produced along the west coasts of projecting shore features, creating much colder conditions. Conversely north-westerly winds of winter force warmer surface waters offshore and allow cold Benguela water to round Cape Point and upwell along the east coasts of peninsulas. As a result of this upwelling system the fauna of peninsulas along this stretch of coast tends to contain more cold-water forms while in sheltered bays more warm-water forms are to be found.

These unusual physical conditions and the proximity to the marine research centres of Cape Town have combined to attract a great deal of research effort to the south-western Cape coast. The marine benthos of the area has been extensively sampled, with the exception of the region north of Lambert's Bay, which remains virtually untouched. The University of Cape Town alone has collected more than 2 000 benthic samples between Lambert's Bay and Cape Agulhas, particular attention having been given to the Saldanha Bay complex and to False Bay, each of which accounts for over 500 samples. In addition, other South African institutions and international expeditions have made smaller benthic collections in the area. Extensive intertidal collections also exist, notably those of K. H. Barnard (presently housed at the South African Museum) and of the University of Cape Town. These collections largely originate from the Cape Peninsula but include samples from numerous localities between Cape Agulhas and Port Nolloth. Compared with the Indian Ocean coast, the Atlantic coast of the Cape Province is poor in estuaries but those which do exist have been comparatively well studied, allowing fruitful comparison with the more numerous estuaries of other regions.

THE COLLECTING STATIONS

The scope of the collections from the area considered here is so great that it has become impracticable to list individual stations, as has been the format in previous parts of this series. Instead a generalized discussion of the various collecting areas is given and the distributions of individual species are provided in the more compact form outlined in the systematic section.

Collections from estuaries

(*a*) *Klein River Estuary, Hermanus*

A full description of the Klein River Estuary and of its fauna is provided by Scott, Harrison & Macnae (1952). The estuary extends from Walker Bay for a distance of about 12 km to the village of Stanford. Initially the river is canal-like before opening up into a shallow lagoon about 0,75 km wide. The lagoon consists mostly of muddy shallows through which deeper channels meander, but near the mouth the bottom becomes sandy with rocky outcrops along the shore. The lagoon is closed for most of the year but during the winter rains it fills steadily until a passage is artificially cut through the sandbar at the mouth to prevent flooding. The mouth remains open during the spring, when the lagoon is tidal, and then gradually closes, remaining so until the next year's rains.

On sandy shores around the lagoon numerous *Talorchestia australis* are to be found, whereas this species is replaced by *Orchestia ancheidos* under stones and in gravel areas. Amongst the weeds of the lagoon *Melita zeylanica* is abundant, as is *Corophium triaenonyx*. The tubicolous *Grandidierella lutosa*, a species found only in this vicinity, is common on the mudflats, although *Corophium triaenonyx* is present here too. *Orchestia rectipalma* occurs under stones on gravel bottoms as well as amongst weeds. In the upper reaches of the estuary *Quadrivisio aviceps* has its only known habitat.

(*b*) *Milnerton River system*

This system, which consists of a river, the Diep River, which flows into a shallow lake, Riet Vlei, and from there through the Milnerton Estuary to the sea, has been fully described by Millard & Scott (1954). At the time of this study the system was relatively undisturbed, but Riet Vlei is at present being developed into a marina. In its original state the system experienced a consistent fresh-water flow during winter, but in summer a sandbar closed the mouth while Diep River and Riet Vlei dried out, causing the estuary to become hypersaline.

Under these rigorous conditions of fluctuating salinity the fauna of the

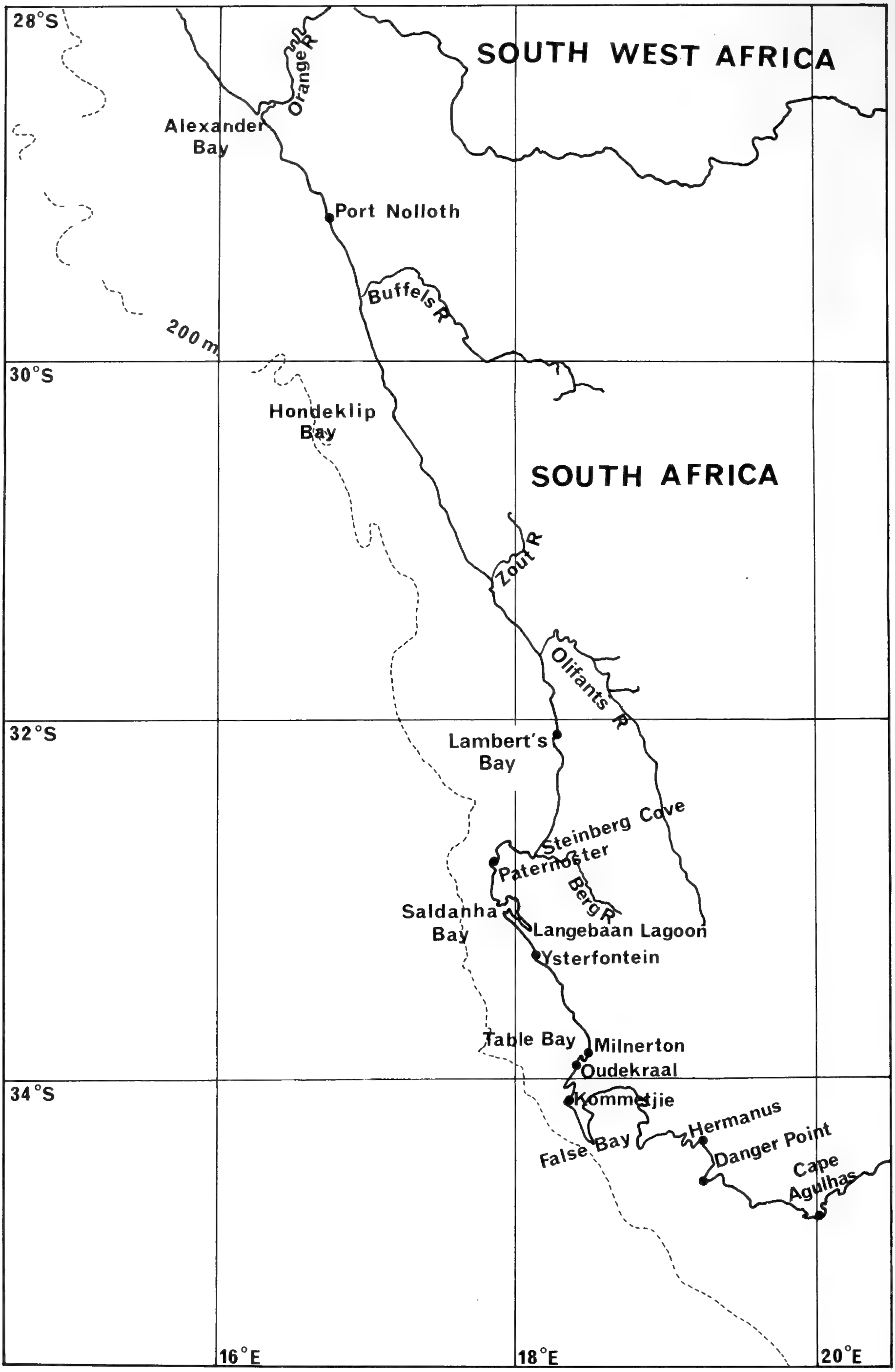

Fig. 1. The Atlantic coast of the Cape Province showing main collecting areas.

system was relatively impoverished. The amphipod fauna consisted of only two species, *Afrochiltonia capensis* and *Melita zeylanica.* Both these well-known euryhaline forms were found amongst weeds and polychaete tubes in the lower reaches of the estuary, where they were most abundant in early summer.

(*c*) *Berg River Estuary*

The Berg River Estuary was the subject of a brief collecting expedition by the University of Cape Town in September 1949. The estuary is about 60 m wide and 6 km long with a maximum depth of about 10 m, and enters the sea at the head of St Helena Bay. *Talorchestia quadrispinosa* is common on the sandbanks around the mouth, while the waters of the estuary harbour the typical estuarine species *Afrochiltonia capensis, Melita zeylanica, Orchestia rectipalma* and *Orchestia ancheidos.*

(*d*) *Olifants River Estuary*

The Olifants River Estuary consists of a fairly straight stretch of water about 200 m wide and 2–5 m deep flowing through a deep valley surrounded by arid scrubland. The flood plain consists of a muddy saltmarsh partially cut off by a shallow blind arm which represents a previous river mouth. The present mouth is fringed by sandbanks to the south, while the north bank is rocky. The river bed is mostly soft mud which becomes progressively more sandy towards the mouth.

Eight amphipod species have been collected from the estuary. Five of these are typical marine forms and were found only around the mouth, while the remaining three species were common further upstream. These euryhaline species are *Afrochiltonia capensis, Melita zeylanica* and *Orchestia rectipalma.*

Collections from the marine environment

(*a*) *Shore collections*

During early studies by the University of Cape Town on the constitution of the rocky intertidal fauna around the South African coast, collections were made at a number of west coast localities. These stations were more or less evenly spaced between Cape Agulhas and Buffels River, there being eleven stations between these two points. More recently numerous other shore collections have been made, particularly around the Cape Peninsula.

Sandy beaches in these areas may harbour enormous populations of either *Talorchestia quadrispinosa* or *Talorchestia capensis* along the drift line and above, while at lower levels *Bathyporeia* sp. and *Urothoe elegans* are to be found burrowing in the sand. The fauna of rocky areas is considerably more complex but is dominated by *Hyale* spp., principally *H. grandicornis* and *H. saldanha.* At lower levels *Ceradocus rubromaculatus* and *Lysianassa ceratina* are common under rocks, while *Aora kergueleni, Amaryllis macrophthalma, Paramoera* *capensis* and *Caprella* spp. occur in great numbers amongst algae and bryozoa. The unusual *Temnophlias capensis* is to be found crawling over rock surfaces while many other species are locally abundant.

(*b*) *Langebaan Lagoon*

A full description of Langebaan Lagoon and of its fauna is given by Day (1959). The lagoon is about 3 km wide and extends for about 15 km south of its origin on the southern shore of Saldanha Bay. The whole area is completely protected from the sea by a narrow finger of land projecting parallel to the shore and by two small islands at the mouth of the lagoon. Tidal flow is considerably restricted and retarded, particularly at the head of the lagoon. The water is generally clear and the bottom mainly sand. The consistency of the sand varies greatly, being fine and clean at the mouth of the lagoon, whereas in the body of the lagoon the beach slopes fairly steeply to mean sea-level and then flattens out into a wide, waterlogged bed of fine, often muddy sand. These sandflats are riddled with *Callianassa* holes and abound in patches of the loose alga *Gracilaria* and of *Zostera*. At the high-water mark saltmarsh vegetation occurs, this zone becoming extremely wide at the head of the lagoon. Salinity in the lagoon is generally as high or slightly higher than experienced in the open sea, while solar radiation also tends to raise the temperature somewhat.

The amphipod fauna of Langebaan Lagoon is rich and varied, some 65 species having been recorded there. The rocky islands at the mouth of the lagoon and isolated rocky patches elsewhere support large populations of *Elasmopus affinis*, *Paramoera capensis*, *Cymadusa filosa* and *Hyale* and *Caprella* spp. living amongst the rich algal cover. *Ceradocus rubromaculatus* is common under rocks, while *Polycheria atolli* is frequently recovered from sponges and compound ascidians. Along the beaches *Talorchestia* spp. are fairly common at the driftline, while the rich fauna of the *Zostera* and *Gracilaria* beds is dominated by *Cymadusa filosa* and *Lysianassa ceratina*. At lower tidal levels the mudflats are inhabited by the tubicolous *Ampelisca palmata* and burrowing *Urothoe* spp. as well as *Lysianassa ceratina*. *Bathyporeia* sp. becomes common at lower water springs. The sand-bottomed channels which cut through the sandflats yield a variety of species of which *Lysianassa ceratina* and *Paramoera capensis* are the most abundant. Both these species, as well as *Ampelisca palmata* and *Perioculodes longimanus*, also occur in the plankton at night.

(*c*) *Saldanha Bay*

Lying about 120 km north of Cape Town, Saldanha Bay consists of an almost semicircular bay about 8 km across, from the southern end of which stretches Langebaan Lagoon (above). The main bay is moderately protected from wave action by rocky headlands, between which lie three small islands. The eastern shore of the bay is formed of a long sandy beach interrupted by a few isolated rocky points. The bottom of the bay consists almost entirely of sands of various textures, these tending to be coarse and shelly in areas of turbulence, particularly around the islands, and finer elsewhere. Extensive harbour development is at present taking place in the area and this can be expected to result in major changes in the physical conditions and fauna in the bay.

The fauna of Saldanha Bay has been extensively sampled and 72 amphipod species have been recorded there. Along the driftline of sandy beaches *Talorchestia australis* is common, while rocky points along the shore are populated by numerous *Ceradocus rubromaculatus*, *Aora kergueleni*, and *Hyale* spp. *Caprella* spp. are also common on algae and hydroids and *Polycheria atolli* is frequently found burrowing into compound ascidians and sponges. Amongst the benthos of the bay *Lysianassa ceratina* and *Paramoera capensis* are the most frequently encountered species, while *Ampelisca anomala* dominates areas of shelly sand. Where the sand is fine and clean *Ampelisca brevicornis* is abundant with a number of other species also common, particularly *Urothoe grimaldi*, *Orchomene plicata*, *Bathyporeia* sp., *Perioculodes longimanus* and *Megaluropus namaquaeensis*. Local concentrations of *Photis* spp. and of *Siphonoecetes dellavallei* are associated with solid objects on the bottom.

(*d*) *False Bay*

A description of False Bay and its biology is given by Day (1970). The bay is roughly square with a side of some 35 km. Its eastern and western shores are generally precipitous, although sandy beaches do occur along the Cape Peninsula to the west, notably Simonstown and Fish Hoek. The northern shore of the bay is flat and low-lying, forming wide sandy beaches from which the bottom shelves gently towards the mouth, where it reaches a maximum depth of about 90 m. The substrate of the bay consists largely of sand; this may be fine and clean, or coarse and mixed with shell in the shallower areas, but over most of the bay it is fine and khaki-coloured, merging into green mud in deeper water near the mouth. Numerous rocky patches are to be found throughout but are particularly numerous to the east.

Hydrological conditions in the area are of particular interest since the bay is subject to both Atlantic and Indian Ocean regimes. Under the influence of north-westerly winds in winter, surface water is blown south and cold Benguela water enters the bay around Cape Point, causing the temperature to drop to 13–14°C at the surface and as low as 10°C in the deeper parts. With the spring south-easterly winds Agulhas water drifts into the bay, striking the western shore and drifting clockwise from there. At this stage surface temperatures average 17–18°C but may rise to 20°C by the end of summer when blue Agulhas water dominates the bay. At this stage a distinct thermocline is usually found at about 20 m.

As a result of its unusual hydrological regime and its proximity to Cape Town, False Bay has been the subject of a good deal of research. The Zoology Department of the University of Cape Town has collected some 500 benthic and numerous intertidal samples from the bay and recorded over 140 amphipod species from these.

The amphipod fauna of False Bay is both rich and complex, the species composition varying widely with depth and substrate composition. The clean sands of the surf zone are dominated by burrowing forms, particularly *Perioculodes longimanus* and *Urothoe grimaldi* in the shallower areas, and *Urothoe pulchella* and *Mandibulophoxus stimpsoni* slightly deeper. The fine hard-packed sands beyond the surf zone are predominantly occupied by tubicolous filter-feeders, notably *Ampelisca anomala*, *A. palmata* and *A. brevicornis*, although both *Photis uncinata* and *Aora gibbula* are locally common. The deepest areas of the bay are composed of green muds and here *Hippomedon normalis*, a scavenging species, is the most common amphipod, although *Ampelisca brevicornis* also extends into this zone.

The fauna of rocky areas is very diverse with numerous *Amaryllis macrophthalma*. Other lysianassids such as *Lysianassa variegata* and *Orchomene plicata* are also common. *Ampithoe ramondi* is well represented, as are *Caprella* spp. *Paramoera capensis* is the most common species in the bay and is found both in rocky and sandy areas as well as at night in the plankton.

(*e*) *Lambert's Bay*

The University of Cape Town has recently undertaken a study of benthic distribution in the Lambert's Bay area. Sampling has taken the form of a transect running from high-water springs to a depth of 800 m. The substrate from 0 to 60 m consists of fine or medium well-sorted sands, while between 80 and 100 m there is an area of muddy sand characterized by the presence of the large tubicolous polychaete, *Diopatra monroi*. Below this zone lies a further area of fine silty sand which extends to the limit of the transect line at 800 m.

The amphipod fauna can be considered as falling into a number of faunistic zones. The first of these is the driftline fauna, the only amphipod represented here being *Talorchestia quadrispinosa*. The lower intertidal levels and surf zone (to 5 m depth) are characterized by a dominance of burrowing forms such as *Perioculodes longimanus*, *Bathyporeia* sp., *Urothoe grimaldi* and especially the deep-burrowing *Cunicus profundus*. The area between 5 and 40 m has a rich amphipod fauna with *Paramoera capensis* the most common species. Burrowing forms, particularly *Bathyporeia* sp. and *Perioculodes longimanus*, are still common, while tubicolous forms, notably *Ampelisca brachyceras* and *Photis longidactylus*, become important. *Cunicus profundus* is replaced by other haustoriids, notably *Urothoe grimaldi* and *Urothoe pulchella*. The muddy sands of the *Diopatra* zone between 80 and 100 m have a similar fauna, particularly abundant in *Paramoera capensis*, *Megaluropus namaquaeensis* and *Bathyporeia* sp., however *Ampelisca brachyceras* is replaced by *Ampelisca anomala*. *Ampelisca anomala* continues as the dominant ampeliscid to 120 m, where it is replaced by the larger *A. brevicornis*. Stations deeper than 120 m are also marked by the appearance of such deep-water forms as *Paraphoxus oculatus*, *Eriopisella capensis* and *Hippomedon onconotus*.

(*f*) *Other benthic samples*

In addition to the discrete collections discussed above numerous other collections exist, particularly in the possession of the University of Cape Town. These include material originating from commercial trawlers; donated by the Division of Sea Fisheries and collected by the university's research vessels R.V. *Gilchrist* and *Thomas B. Davie*. The area covered is primarily that between Cape Point and Lambert's Bay. Very few of the samples are from further north or from depths of more than 200 m and many species undoubtedly await discovery in these regions.

Since the collections were not planned with any predefined concepts of faunistic analysis in mind, their interpretation is complicated by the interaction of variables of location, season, depth, substrate and collecting gear. Although over 100 species are represented, some are notable in their scarcity. For example, *Mandibulophoxus stimpsoni*, so abundant in False Bay and eastward, is rare along the west coast, as is *Photis uncinata*, which is replaced by the similar *P. longidactylus*. Sandy and muddy areas are normally dominated by burrowers (*Perioculodes*, *Urothoe*, *Bathyporeia*) and tubicolous forms (*Byblis*, *Photis* and especially *Ampelisca*), although *Paramoera*, *Lysianassa* and *Hippomedon* are also common. Relatively few samples originate from rocky areas, but these include numerous *Lysianassa*, *Paramoera*, *Chevalia*, *Maera* and *Leucothoe* as well as various caprellids.

SYSTEMATICS

The taxonomy of Gammaridea follows the system outlined by J. L. Barnard (1969) and subsequently revised by J. L. Barnard (1970*a*, 1972*b*, 1973). The revision of the family Gammaridae proposed by Bousfield (1973) is still contentious (Holsinger 1974) and has thus been disregarded here. Familial taxa within the Caprellidea are those proposed by McCain (1970).

The system of listing individual records for each species, as employed in earlier portions of this series, has proved too cumbersome to encompass the 2 000 stations and 70 000 specimens reported on here. A more concise system has thus been devised in which the ranges of species are indicated by the latitude/longitude squares in which they have been recorded. These are followed by letters denoting the depth of the various records (E = estuarine, I = intertidal, T = 0–29 m, O = 30–99 m, D = 100–499 m, VD = 500–1 000 m). The latitude/longitude square 34°S/18°E includes both the cold Atlantic and warmer False Bay coasts of the Cape Peninsula, and in order to distinguish between these the letters FB are appended to records from False Bay. Thus a range indicated as 32/18/I, S to 34/18/FB/I, T indicates that the species in question is found intertidally and at depths of less than 30 m between 32°S/18°E and 34°S/18°E (False Bay).

In the account which follows the arrangement of families, genera and species is alphabetic. Limbs of the pereon are referred to as gnathopods 1 and 2, followed by pereiopods 1–5 and the segments of these limbs are referred to as articles 1–7, article 1 being the coxal plate (whether this is present or absent). The analysis is restricted to species occurring between the driftline and 1 000 m depth, with estuarine species being included. Holotypes of all new species and representative material of all other species have been placed in the South African Museum, Cape Town.

Suborder GAMMARIDEA

Family **Acanthonotozomatidae**

Iphimedia capicola K. H. Barnard, 1932

Iphimedia capicola K. H. Barnard, 1932: 118, fig. 66.

Records: 34/18/FB/T, O to 32/18/T, O, moderately common.

Distribution: Endemic, Port Elizabeth to Lambert's Bay.

Panoploea excisa K. H. Barnard, 1932

Panoploea excisa K. H. Barnard, 1932: 129, fig. 73.

Records: 33/17/T, a single record.

Diagnosis: Rostrum acute, not strongly deflexed; pereon segments 1–6 smooth, 7 with a small pair of dorsal denticles; pleon segments 1–3 each with a pair of dorsolateral procumbent teeth; gnathopod 1 chelate, gnathopod 2 subchelate; article 2 of pereiopod 5 posteriorly serrate, postero-distally excised to leave a large semicircular concavity; telson oblong, apically truncated, slightly emarginate.

Distribution: Endemic, the above record is the only one to date.

Panoploea stegosaura sp. nov.

Fig. 2

Description of male (4 mm): Head slightly shorter than enlarged pereon segment 1, rostrum downturned, extending to tip of article 1 of antenna 1, eyes round, rust brown; articles 1 and 2 of antenna 1 medio-distally produced into an acute tooth, article 3 slender (flagellum broken), accessory flagellum absent; flagellum of antenna 2 broken; upper lip slightly incised apically; mandible without molar, consisting simply of a subacute process, palp 3-articulate (Fig. 2B); lower lip (Fig. 2C) with inner lobes, their apices obscurely incised; palp of maxilla 1 (Fig. 2D) bi-articulate, not extending to apex of outer plate, outer plate bearing 14 strong serrate spines, inner plate with two short apical setae; plates of maxilla 2 subequal; palp of maxilliped (Fig. 2E) 3-articulate, article 2 medially produced to apex of article 3, both articles terminally setose,

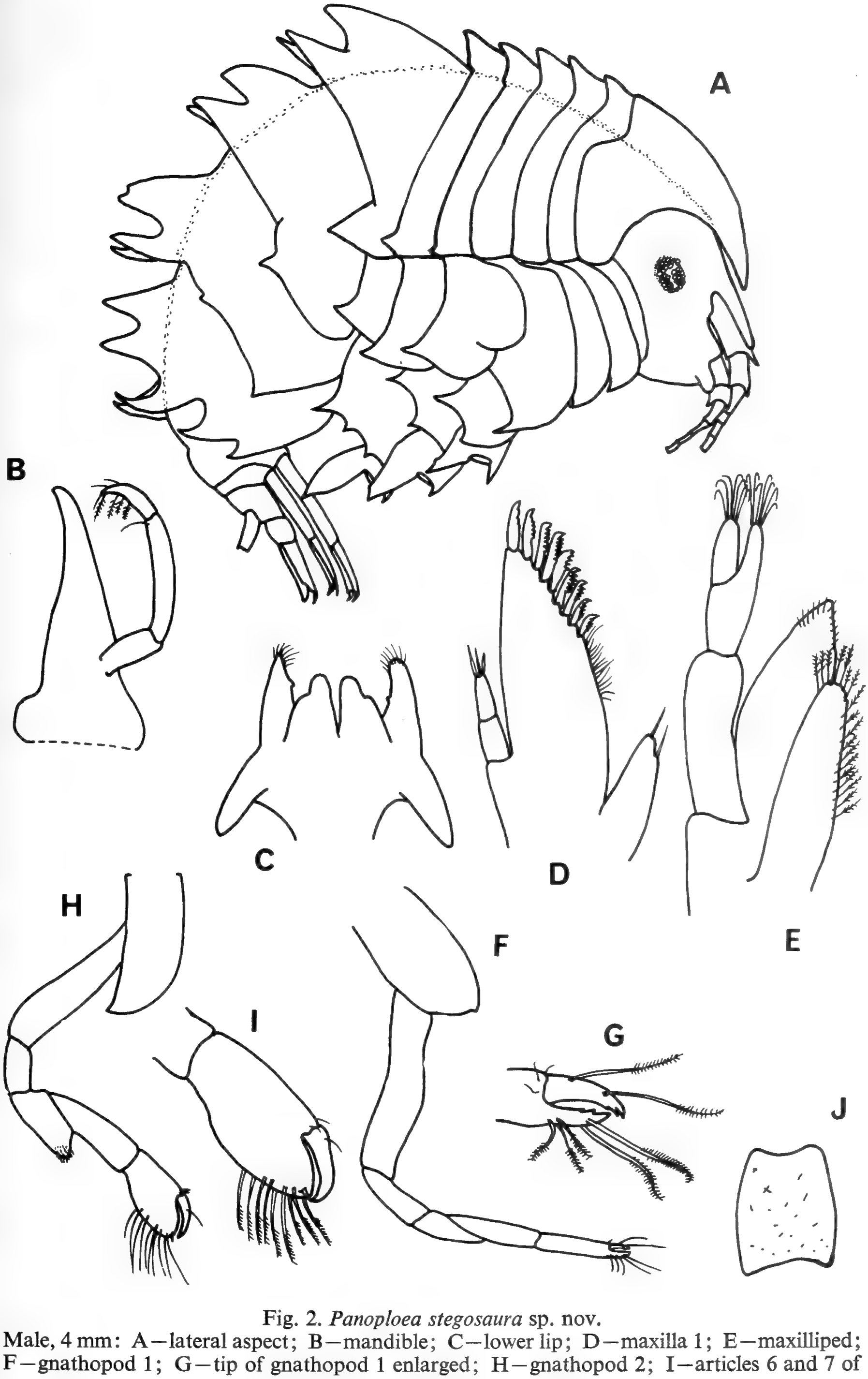

Fig. 2. *Panoploea stegosaura* sp. nov.
Male, 4 mm: A—lateral aspect; B—mandible; C—lower lip; D—maxilla 1; E—maxilliped; F—gnathopod 1; G—tip of gnathopod 1 enlarged; H—gnathopod 2; I—articles 6 and 7 of gnathopod 2 enlarged; J—telson.

outer plate bearing short marginal setae, inner plate with 18 short marginal plumose setae.

Pereon segments all medio-dorsally keeled, 1 produced anteriorly over head, 7 with a posterior pair of sub-dorsal teeth; anterior coxae acuminate, 4 posteriorly excavate, 5–7 posterodistally produced into acute teeth; gnathopod 1 minutely chelate (Fig. 2F–G), articles 5 and 6 subequal, 6 and 7 distally bearing a few long plumose setae; gnathopod 2 weakly chelate (Fig. 2H–I), palm defined by a small spine, posterior margin with a row of pectinate setae; pereiopods 1 and 2 slender, article 4 antero-distally lobed (articles 5–7 missing); posterior margin of article 2 of pereiopods 3 and 4 with a strong medial tooth, pereiopod 5 with four teeth on posterior margin of article 2; article 4 of pereiopods 3–5 slightly produced antero-distally, strongly lobed postero-distally (articles 5–7 missing).

Pleon segments 1 and 2 each with an anterior medio-dorsal tooth and a posterior pair of upright sub-dorsal processes; pleon segment 3 with two triangular medio-dorsal teeth and a pair of reverted sub-dorsal processes posteriorly; first pleonal epimeron postero-distally rounded but with an acute process at centre of posterior margin, second pleonal epimeron similar but postero-distally acute; third pleonal epimeron with stronger posterior and postero-distal teeth; uropods 1 and 3 extending equally, slightly exceeding apex of uropod 2, rami lanceolate, outer ramus of uropods 2 and 3 slightly the longer; telson apically truncated, broadly excavate (Fig. 2J).

Holotype: SAM–A13228, male, 4 mm, unique.

Type-locality: 34°14′S/18°29′E, 15 February 1965, depth 40 m, substrate coarse khaki sand.

Relationships: The highly developed dorsal armature of this species and the unusual manner in which pereon segment 1 is produced anteriorly over the head distinguish it from other members of the genus, none of which show carinae on all pereon segments.

Family **Ampeliscidae**

Ampelisca acris Griffiths, 1974

Ampelisca excavata (*non* K. H. Barnard, 1925): K. H. Barnard, 1955: 82, fig. 40A.
Ampelisca acris Griffiths, 1974*c*: 268, fig. 3.

Records: 34/18/FB/T, O, 34/18/O, a few records.

Distribution: Endemic, Port Elizabeth to Cape Peninsula.

Ampelisca anisuropa (Stebbing, 1908)

Byblis anisuropus Stebbing, 1908*b*: 12, pl. 10.
Ampelisca anisuropa: Griffiths, 1974*b*: 220.

Records: 32/16/D to 34/18/D and 34/18/FB/T, O, quite common.

Distribution: Endemic, Natal to Lambert's Bay.

Ampelisca anomala Sars, 1882

Ampelisca anomala: Sars, 1895: 178, pl. 62 (fig. 2).

Records: 31/18/O, D and 32/16/VD to 34/18/T, O, D and 34/18/FB/T, O, locally abundant.

Distribution: Scandinavia, southern Africa.

Ampelisca brachyceras Walker, 1904

Ampelisca brachyceras Walker, 1904: 252, pl. 2 (fig. 13).

Records: 32/18/T to 34/18/FB/T, O, many records.

Distribution: Ceylon, southern Africa.

Ampelisca brevicornis (Costa, 1853)

Ampelisca brevicornis: Reid, 1951: 204–210, figs 9–15. Kaim Malka, 1969: 928–932, pls 1–6.

Records: 32/18/T, O, 32/17/D, 32/16/D to 34/18/FB/T, O, numerous records.

Distribution: Cosmopolitan.

Ampelisca chiltoni Stebbing, 1888

Ampelisca chiltoni: J. L. Barnard, 1961: 61, fig. 31.

Records: 32/16/D, 34/18/I and 34/18/FB/T, O, a few records.

Distribution: Australia, New Zealand, southern Africa.

Ampelisca diadema (Costa, 1853)

Ampelisca diadema: Chevreux & Fage, 1925: 82, fig. 74.

Records: 32/18/T, O, 32/17/D, 32/16/D to 34/18/FB/T, O, locally common.

Distribution: Cosmopolitan.

Ampelisca excavata K. H. Barnard, 1925

Ampelisca excavata K. H. Barnard, 1925: 336, pl. 34 (figs 5–7). Gray & J. L. Barnard, 1970: 67–83, figs 1–5, pl. 1.

(*non*) *Ampelisca excavata:* K. H. Barnard, 1955: 82 (= *A. acris*, above).

Records: 34/18/FB/I, T, uncommon.

Diagnosis: Antennae subequal, about 40% body length; three pairs of eyes with obscure corneal lenses; article 5 of pereiopods 3 and 4 not greatly lobed distally; article 2 of pereiopod 5 posteriorly produced to tip of article 5, posterior margin distally excavate, apex bifurcate, article 3 half length of 4, neither article lobed; third pleonal epimeron postero-distally rounded; inner ramus of uropod 3 apically bifid; pereon segment 7 bearing two hard dorsal ridges enclosing an elongate furrow.

Distribution: Endemic to False Bay and vicinity; apparently limited to cirripede burrows in encrusting algae, usually on the shells of large gastropods.

Ampelisca fusca Stebbing, 1888

Ampelisca fusca Stebbing, 1888: 1052, pl. 105.

Records: 31/16/D to 34/18/O, D and 34/18/FB/T, O, more common at the deeper stations.

Distribution: Endemic, Moçambique to South West Africa.

Ampelisca palmata K. H. Barnard, 1916

Ampelisca palmata K. H. Barnard, 1916: 136, pl. 28 (figs 30–31).

Records: 33/17/T, O to 34/18/FB/T, O, abundant in sandy and muddy substrates.

Distribution: Senegal to Moçambique.

Ampelisca spinimana Chevreux, 1887

Ampelisca spinimana: Chevreux & Fage, 1925: 81, fig. 73.

Records: 32/18/T, O to 34/18/FB/T, O, fairly common in sandy areas.

Distribution: Europe, West and southern Africa.

Byblis gaimardi (Kröyer, 1846)

Byblis gaimardi: Mills, 1971: 367–370, figs 6A, 7.

Records: 34/18/D, a single record.

Distribution: Probably cosmopolitan.

Triodos insignis K. H. Barnard, 1916

Triodos insignis K. H. Barnard, 1916: 140, pl. 26 (figs 8–10).

Records: 34/18/D, several records.

Distribution: Endemic, Natal to Cape Peninsula.

Remarks: These records mark the rediscovery of this genus and species, previously known solely from Barnard's original two specimens collected off Natal in 1900.

Family **Amphilochidae**

Amphilochus neapolitanus Della Valle, 1893

Amphilochus neapolitanus: J. L. Barnard, 1962*b*: 126, fig. 3.

Records: 34/18/FB/O, a single record.

Distribution: Cosmopolitan in tropical and temperate seas.

Cyproidea ornata Haswell, 1880

Cyproidea ornata: J. L. Barnard, 1972*a*: 21, figs 4–5.

Records: 33/18/T to 34/18/FB/T, O, a few records.

Distribution: Indo-Pacific, extending to South West Africa.

Gitanopsis pusilla K. H. Barnard, 1916

Gitanopsis pusilla K. H. Barnard, 1916: 144.

Records: 33/18/I, T and 33/17/O to 34/18/FB/I, T, O, fairly common.

Distribution: South Atlantic, southern Indian Ocean.

Hoplopleon australis (K. H. Barnard, 1916)

Peltocoxa australis K. H. Barnard, 1916: 146, pl. 26 (fig. 13).

Records: 33/18/I, a single record.

Diagnosis: Coxae 1 and 2 concealed by greatly enlarged coxae 3 and 4; gnathopods 1 and 2 subchelate, article 6 ovate, palm oblique, convex, defined by a small spine and studded with numerous small denticles, dactyl subequal to palm, inner margin bearing a comb-like row of strong upstanding teeth; article 2 of pereiopod 3 linear, that of pereiopods 4 and 5 expanded; pleon segment 4 elongate with a high medio-dorsal crest along its whole length; outer ramus of uropods 1 and 2 the shorter.

Distribution: Endemic, known only from the above record.

Hoplopleon medusarum K. H. Barnard, 1932

Hoplopleon medusarum K. H. Barnard, 1932: 105, fig. 54.
(*non*) *Hoplopleon medusarum:* Penrith & Kensley, 1970: 230 (= *Cyproidea ornata*).

Records: 32/18/T to 34/18/FB/O, a few records.

Distribution: Endemic; Mossel Bay to Lambert's Bay.

Remarks: The distribution given by Griffiths (1974*a*) was based on the erroneous records of Penrith & Kensley; this species has not in fact been found farther north than Lambert's Bay.

Family **Ampithoidae**

Ampithoe africana K. H. Barnard, 1925

Ampithoe africana K. H. Barnard, 1925: 361.

Records: 34/18/FB/T, a single record.

Distribution: Endemic, Natal to False Bay.

Ampithoe falsa K. H. Barnard, 1932

Ampithoe brevipes: K. H. Barnard, 1916: 255, pl. 28 (fig. 34).
Ampithoe falsa: Ruffo, 1969: 57, figs 18–20.

Records: 33/18/T, 34/18/FB/I, a few records.

Distribution: Indian Ocean, South Africa.

Ampithoe ramondi (Audouin, 1826)

Ampithoe vaillanti K. H. Barnard, 1916: 253.
Ampithoe ramondi: J. L. Barnard, 1970*b*: 50, figs 18–19.

Records: 29/16/I to 34/18/FB/I, T, fairly common.

Distribution: Circumtropical.

Cymadusa filosa Savigny, 1818

Grubia australis K. H. Barnard, 1916: 258.
Cymadusa australis: K. H. Barnard, 1940: 480.
Cymadusa filosa: J. L. Barnard, 1955: 29, fig. 15.

Records: 29/17/I to 34/18/FB/I, abundant in Langebaan Lagoon, otherwise uncommon.

Distribution: Cosmopolitan in tropical and temperate seas.

Macropisthopus stebbingi K. H. Barnard, 1916

Macropisthopus stebbingi K. H. Barnard, 1916: 260, pl. 28 (figs 15–17).

Records: 34/18/I, 34/18/FB/I, T, a few records.

Distribution: Endemic, Port Elizabeth to Table Bay.

Family **Argissidae**

Argissa hamatipes Norman, 1869

Argissa Stebbingi: Chevreux & Fage, 1925: 90, figs 81–82.
Argissa hamatipes: Nagata, 1965: 154, fig. 7. Bousfield, 1973: 121, pl. 20 (fig. 2).

Records: 34/18/FB/O, a few records.

Diagnosis: Accessory flagellum bi-articulate; coxae 1–3 successively smaller, coxa 4 larger than 1; gnathopods 1 and 2 simple; pereiopods 1 and 2 not glandular; urosome segments 2 and 3 slightly carinate; telson deeply cleft.

Distribution: Cosmopolitan.

Remarks: It is now generally accepted that *A. stebbingi* is synonymous with *A. hamatipes* (Nagata 1965; J. L. Barnard 1967). The eyes of this species are highly variable, ranging from absent to well developed with cuticular lenses. The specimens recorded here, which are the first from this family to be found in southern Africa, show well-developed eyes each bearing four cuticular lenses.

Family **Cheluridae**

Chelura terebrans Philippi, 1839

Chelura terebrans: Bousfield, 1973: 207, pl. 69 (fig. 1).

Records: 33/18/T, a single record.

Distribution: Cosmopolitan, wood-boring.

Family **Colomastigidae**

Colomastix pusilla Grube, 1864

Colomastix pusilla: J. L. Barnard, 1971: 55, fig. 24.

Records: 34/18/T, O, D, 34/18/FB/T, a few records.

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Corophiidae**

Aora anomala Schellenberg, 1926

Aora typica forma *anomala* Schellenberg, 1926*a*: 372, fig. 59.

Records: 34/18/FB/T, O, a few records.

Diagnosis: Coxa 1 ♂ not enlarged; article 2 of gnathopod 1 ♂ anteriorly smooth, articles 2 and 3 not antero-distally lobed, article 4 distally produced into a long process which extends beyond tip of article 5, article 5 postero-distally produced into an acute tooth, 6 half as large as 5, palm very short, defined by a small spine, dactyl serrate; article 6 of gnathopod 2 half length of article 5, palm convex; uropod 1 with strong interramal spine.

Distribution: Southern Atlantic.

Remarks: Both this species and the two following species have been raised to specific rank by J. L. Barnard (1972*b*).

Aora gibbula K. H. Barnard, 1932

Aora typica forma *gibbula* K. H. Barnard, 1932: 220, fig. 135.

Records: 34/18/FB/T, O, numerous records.

Diagnosis: Coxa 1 ♂ greatly enlarged, concealing most of head; gnathopod 1 ♂ greatly elongate, article 2 produced near its origin into a marginally crenulate anterior lobe, articles 2 and 3 not antero-distally lobed, 4 distally produced into a long process extending almost to apex of article 5, article 5 postero-distally rounded, 6 half as large as 5, palm obscure, dactyl weakly serrate; article 6 of gnathopod 2 half as long as 5, palm excavate; uropod 1 with strong interramal spine.

Distribution: Endemic, known only from False Bay.

Aora kergueleni Stebbing, 1888

Aora kergueleni Stebbing, 1888: 1073, pl. 109A, D.
Aora typica (*non* Kröyer, 1845): K. H. Barnard, 1916, 236; 1940: 478 (*partim*). Griffiths, 1973: 278; 1974*a*: 179; 1974*b*: 255; 1974*c*: 277.

Records: 29/16/I to 34/18/FB/I, T, O, abundant.

Diagnosis: Coxa 1 ♂ not enlarged; article 2 of gnathopod 1 ♂ anteriorly smooth, articles 2 and 3 not antero-distally lobed, article 4 distally produced into an elongate process extending to apex of article 5, 5 postero-distally rounded, 6 almost as large as 5, palm short, defined by a spine, dactyl elongate, serrate; articles 5 and 6 of gnathopod 2 subequal, palm linear; uropod 1 with strong interramal spine.

Distribution: Kerguelen Island, southern Africa.

Aorcho delgadus J. L. Barnard, 1961

Aorcho delgadus J. L. Barnard, 1961: 114, fig. 80.

Records: 34/18/D, a few records.

Diagnosis: Article 3 of peduncle of antenna 1 as long as article 1, accessory flagellum 2–4 articulate; gnathopods subequal; coxae short, hardly serially touching, pereiopods 1 and 2 glandular; uropods 1 and 2 with large terminal peduncular spines; rami of uropod 3 subequal, longer than peduncle, outer ramus with terminal fascicle of setae, inner with small terminal spine; telson entire, subcircular.

Distribution: Tasman Sea, South Africa.

Remarks: The above records are the first of this species from southern Africa. The material differs from that of J. L. Barnard (1961) in that the accessory flagellum of the only specimen possessing a first antenna is 2-articulate, whereas Barnard described it as 4-articulate.

Cheiriphotis megacheles (Giles, 1885)

Cheiriphotis megacheles: Walker, 1904: 284, pl. 6 (fig. 42). K. H. Barnard, 1937: 167, fig. 14A.
?*Cheiriphotis durbanensis* K. H. Barnard, 1916: 247. Ruffo, 1969: 55.
Cheiriphotis walkeri Stebbing, 1918: 68, pl. 13.
?*Cheiriphotis megacheles* forme *durbanensis:* Ledoyer, 1973: 65, pl. 14A.

Records: 33/17/T, O, D to 34/18/FB/T, O, fairly common.

Distribution: Indo-Pacific.

Remarks: The taxonomic status of this species has historically been somewhat confused and I do not wish to compound that confusion here by making definite decisions on synonymy. However, material from southern Africa can be regarded as falling into two distinct forms. The first, 'megacheles' form, common in the Cape Province, has the palm of gnathopod 2 ♂ transverse and multidentate. This form corresponds to Walker's *C. megacheles* and Stebbing's *C. walkeri* as well as K. H. Barnard's (1937) figure 14B. The second form, found in Natal and Moçambique, corresponds with that figured by K. H. Barnard (1937) figure 14A and described by Ledoyer (1973) and can be regarded as the 'durbanensis' form. Here the palm of gnathopod 2 ♂ is oblique and bears three large teeth, that nearest the finger-hinge being apically notched.

J. L. Barnard (1962*a*) figures a third form (subsequently assigned to *C. delloyei* by Ruffo) and suggests that the various forms of gnathopod 2 represent growth stages. However, mixed populations of the two southern

African forms have not yet been found. Moreover, the 'durbanensis' form, the presumed juvenile, is often larger than the 'megacheles' form and juvenile 'megacheles' specimens show no tendency to resemble the 'durbanensis' form. This would suggest that the two morphs represent distinct population groups and should be given at least sub-specific status.

Chevalia aviculae Walker, 1904

Chevalia aviculae: J. L. Barnard, 1971: 88, fig. 42.

Records: 32/18/O to 34/18/T, O, D and 34/18/FB/T, O, numerous records.

Distribution: Cosmopolitan in tropical and temperate seas.

Corophium acherusicum Costa, 1857

Corophium acherusicum: J. L. Barnard, 1971: 59, figs 17, 26. Bousfield, 1973: 201, pl. 62 (fig. 2).

Records: 33/18/T, 34/18/FB/T, a few records.

Distribution: Cosmopolitan in tropical and temperate seas.

Corophium triaenonyx Stebbing, 1904

Corophium triaenonyx Stebbing, 1904: 25, pl. 6A.

Records: 34/18/FB/T, 34/19/E, a few records.

Distribution: Widespread tropical and subtropical, particularly in brack waters.

Gammaropsis afra Stebbing, 1888

Eurystheus afer: K. H. Barnard, 1916: 249, pl. 28 (fig. 11).
Gammaropsis afra: J. L. Barnard, 1961: 113, fig. 79; 1970*b*: 170, fig. 108.

Records: 31/18/O, 32/16/D, 34/18/FB/O, 35/18/D, a few records.

Distribution: Circumtropical.

Gammaropsis atlantica Stebbing, 1888

Eurystheus atlanticus: Stebbing, 1910*a*: 461.
Gammaropsis atlantica: J. L. Barnard, 1970*b*: 174, figs 111–113.

Records: 33/18/T to 34/18/FB/T, O and 34/18/O, D, abundant.

Distribution: Circumtropical.

Gammaropsis holmesi (Stebbing, 1908)

Eurystheus holmesi Stebbing, 1908*b*: 85, pl. 14A. K. H. Barnard, 1955: 95, fig. 48A–D.
Eurystheus semidentatus K. H. Barnard, 1916: 250, pl. 28 (figs 13, 14).
Gammaropsis holmesi: Griffiths, 1974*b*: 244.

Records: 34/18/T, O, 34/18/FB/I, T, O, fairly common.

Distribution: Endemic, Natal to Cape Peninsula.

Gammaropsis longicarpus (Reid, 1951)

Fig. 3

Eurystheus longicarpus Reid, 1951: 259, fig. 50.

Records: 34/18/FB/T, O, a few records.

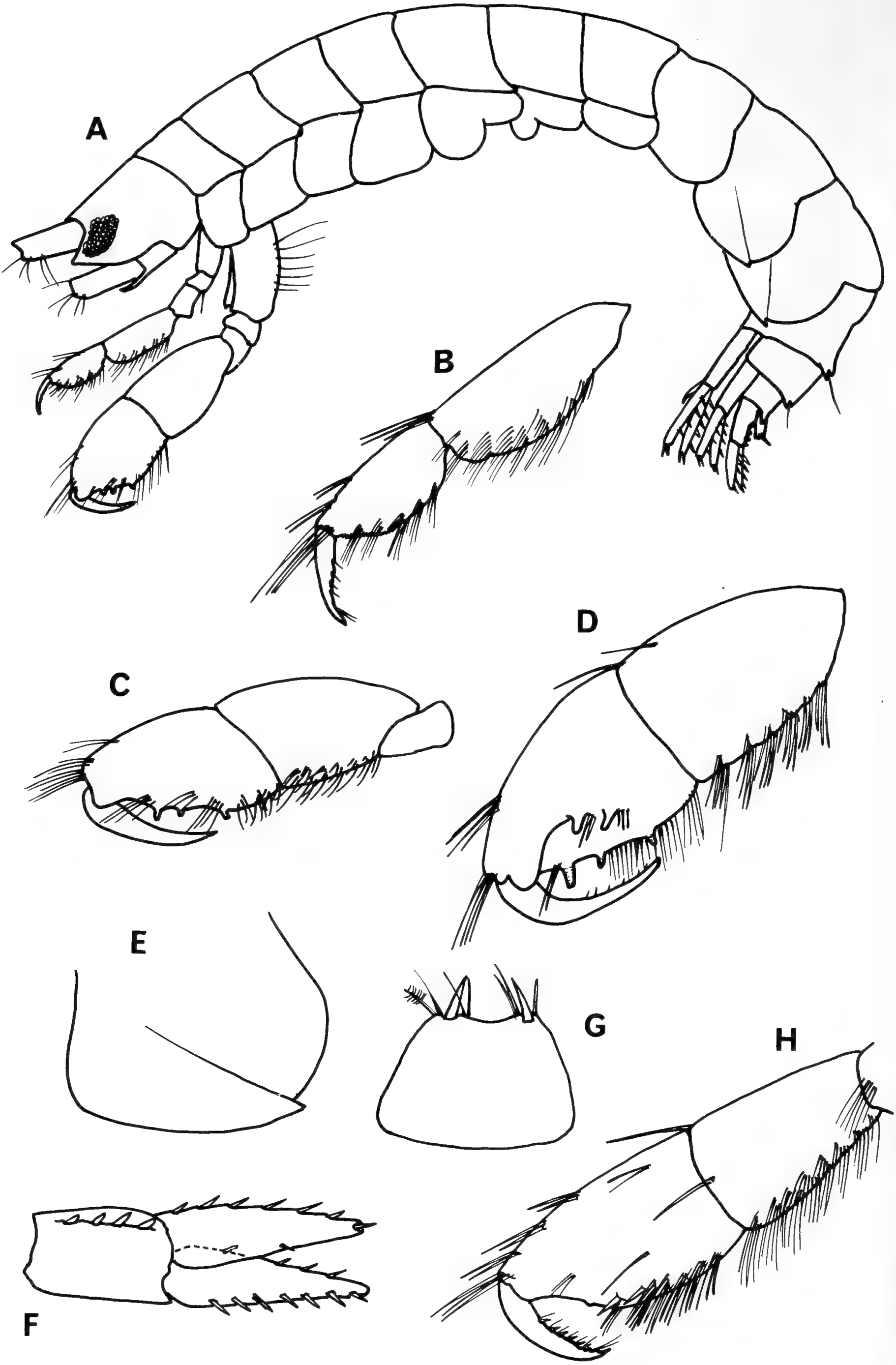

Fig. 3. *Gammaropsis longicarpus* (Reid, 1951)
Male, 7 mm: A—lateral aspect; B—gnathopod 1; C—gnathopod 2 (outer aspect); D—gnathopod 2 (inner aspect); E—third pleonal epimeron; F—uropod 3; G—telson. Female, 6 mm: H—gnathopod 2.

Diagnosis: Eyes quadrate; coxa 1 not strongly produced forwards; articles 5 and 6 of gnathopod 2 ♂ subequal, article 6 of terminal male with two peg-like teeth on medial margin and three such teeth along palmar margin (subadult with palmar teeth but lacking medial teeth); third pleonal epimeron with an oblique ridge running to a small postero-distal tooth, hind margin strongly convex; urosome segments 1 and 2 each with a pair of small subdorsal teeth; uropod 3 slightly exceeding 1 and 2, rami subequal to peduncle.

Distribution: West and southern Africa.

Remarks: Adult males from the present material are larger and show more highly developed second gnathopods than those described by Reid (1951). However, subadults from False Bay agree closely with Reid's brief description and on this basis I have associated the two.

Gammaropsis palmoides (K. H. Barnard, 1932)

Eurystheus palmoides K. H. Barnard, 1932: 231, fig. 144; 1955: 96, fig. 48e–g.

Records: 34/18/FB/T, O, numerous records.

Diagnosis: Eyes round, optic lobes short, rounded; article 6 of gnathopod 2 ♂ much longer than 5, palm oblique, occupying almost entire posterior margin of hand, defined by an acute tooth and bearing a large medial tooth and two small distal teeth, dactyl equal to palm, closing within it; pleon segments dorsally smooth; third pleonal epimeron minutely produced postero-distally; uropod 3 very short, not extending to apex of uropod 2.

Distribution: Endemic to False Bay.

Gammaropsis scissimanus (K. H. Barnard, 1925)

Fig. 4

Eurystheus scissimanus K. H. Barnard, 1925: 361, pl. 34 (fig. 15).

Records: 33/17/O, 34/18/D, 34/18/FB/O, a few records.

Diagnosis: Eyes oval; ocular lobes of head acute; article 6 of gnathopod 2 ♂ considerably larger than 5, palm transverse, shorter than hind margin, defined by a small tooth and with a deep semicircular concavity distally, remainder of palm minutely crenulate; pleon segments dorsally smooth; third pleonal epimeron postero-distally rounded-quadrate; uropod 3 moderately elongate, reaching apex of uropod 2.

Distribution: Endemic, False Bay to Saldanha Bay.

Remarks: This species has not been adequately figured before so I have provided full figures here. Antenna 1 was previously unknown and has an 11-articulate flagellum with a 5-articulate accessory flagellum. This confirms the correct placement of *G. scissimanus* in *Gammaropsis* rather than *Podoceropsis* (in which the accessory flagellum is 0–2 articulate).

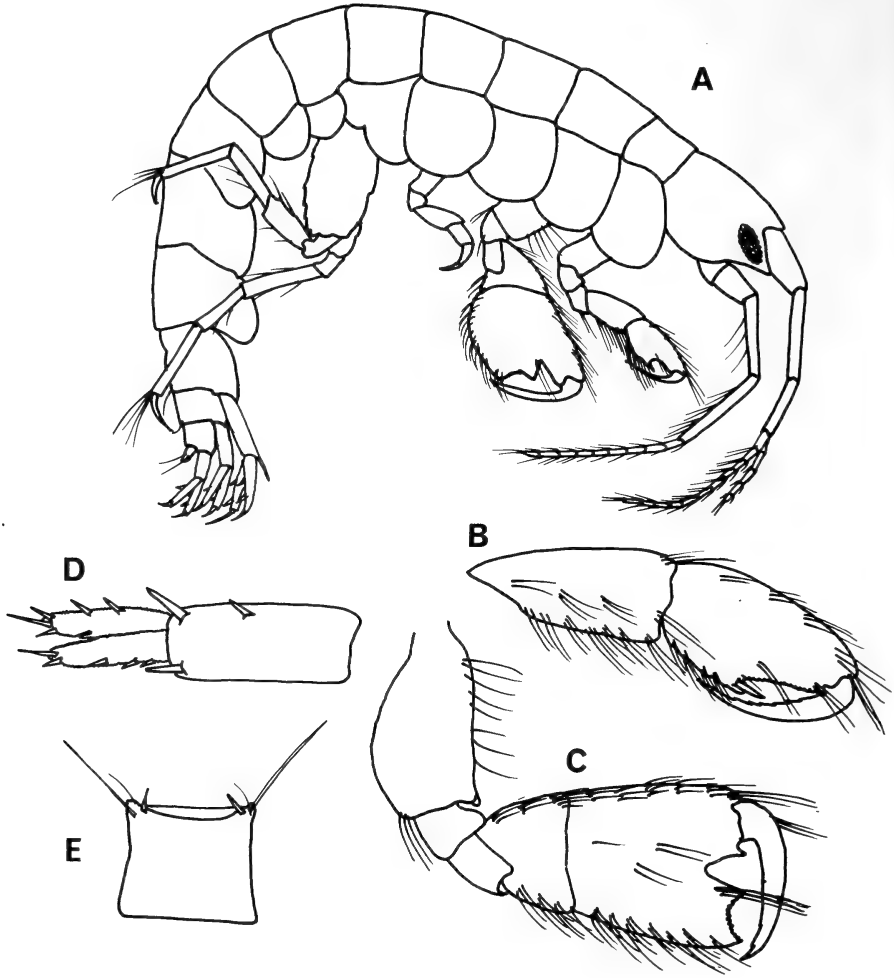

Fig. 4. *Gammaropsis scissimanus* (K. H. Barnard, 1925)
Male, 4 mm: A—lateral aspect; B—gnathopod 1; C—gnathopod 2; D—uropod 3; E—telson.

Grandidierella lignorum K. H. Barnard, 1935

Grandidierella lignorum K. H. Barnard, 1935: 300, fig. 14.

Records: 34/19/E, a single record.

Distribution: Endemic, Cape Agulhas to Natal, estuarine.

Grandidierella lutosa K. H. Barnard, 1952

Grandidierella lutosa K. H. Barnard, 1952: 280, fig. 3.

Records: 34/19/E, two records.

Diagnosis: Pereon segments without medio-ventral processes; coxae 1 and 2 quadrate, not acutely pointed; article 2 of gnathopod 1 ♂ widening distally, article 5 enlarged, two strong teeth on distal margin, article 6 curved, palm transverse, dactyl hardly exceeding palm; gnathopod 2 ♂ subchelate, much smaller than gnathopod 1.

Distribution: Endemic to estuaries near Hermanus.

Lemboides acanthiger K. H. Barnard, 1916

Lemboides acanthiger **K. H. Barnard, 1916: 239, pl. 28 (figs 7–8).**

Records: 34/18/FB/O, a single record.

Distribution: Endemic, Natal to False Bay.

Lemboides afer Stebbing, 1895

Lemboides afer: **K. H. Barnard, 1932: 222, fig. 137.**

Records: 33/18/T, 34/18/FB/T, O, fairly common.

Distribution: Endemic, False Bay to South West Africa.

Lemboides crenatipalma K. H. Barnard, 1916

Lemboides crenatipalma **K. H. Barnard, 1916: 240, pl. 28 (figs 9–10).**

Records: 32/18/T, 33/18/T, 33/17/O, a few records.

Distribution: Endemic, Saldanha Bay to South West Africa.

Lembos hirsutipes Stebbing, 1895

Lembos hirsutipes **Stebbing, 1895: 207, pl. 8, 9B. Karaman, 1972: 101, figs 1–2.**

Records: 32/18/T to 34/18/FB/T, O, a few records.

Diagnosis: Pereon segments ventrally smooth; article 2 of gnathopod 1 ♂ strongly setose posteriorly, palm slightly oblique, a small tooth near finger hinge separated from long defining tooth by a deep cleft; article 2 of gnathopod 2 ♂ not antero-distally produced, article 5 longer than 6; article 4 of pereiopods 1 and 2 ♂ strongly setose.

Distribution: South Africa to tropical West Africa.

Lembos hypacanthus K. H. Barnard, 1916

Lembos hypacanthus **K. H. Barnard, 1916: 237, pl. 28 (figs 5–6).**

Records: 33/18/T, 34/18/I, 34/18/FB/I, a few records.

Diagnosis: Pereon segments 3–7 in ♂ each bearing a strong medio-ventral spinose process; article 2 of gnathopod 1 ♂ weakly setose, palm slightly oblique, defined by a single spine and bearing a minute tooth near finger hinge and a larger spiniform one near defining angle; article 2 of gnathopod 2 ♂ with antero-distal apex produced as a recurved hook, article 6 as long as, but narrower than, 5; article 4 of pereiopods 1 and 2 ♂ not strongly setose.

Distribution: Endemic, Natal to South West Africa.

Lembos leptocheirus Walker, 1909

Lembos leptocheirus: Walker, 1909: 338, pl. 43 (fig. 7). Schellenberg, 1926*a*: 373.

Records: 33/17/T, 33/18/T, 34/18/FB/T, a few records.

Diagnosis: Pereon segments ventrally smooth; article 2 of gnathopod 2 ♂ naked, palm slightly oblique, convex distally and with a semicircular concavity next to defining tooth; article 2 of gnathopod 2 ♂ not produced antero-distally, article 6 much longer than 5; article 4 of pereiopods 1 and 2 ♂ sparsely setose.

Photis dolichommata Stebbing, 1910

Photis dolichommata Stebbing, 1910*b*: 609, pl. 55B.

Records: 34/18/FB/T, O, a few records.

Distribution: Australia, South Africa.

Photis longidactylus Griffiths, 1974

Photis longidactylus Griffiths, 1974*a*: 193, fig. 6.

Records: 32/18/T, O to 34/18/FB/T, O, numerous records.

Distribution: Endemic, False Bay to South West Africa.

Photis longimanus Walker, 1904

Photis longimanus: Rabindranath, 1971*b*: 71, figs 3–4.
(*non*) *Photis longimanus:* K. H. Barnard, 1916: 224 (= *P. kapapa*).

Records: 32/18/T to 34/18/FB/T, O, common, especially in Saldanha Bay and False Bay.

Distribution: India, Ceylon, southern Africa.

Remarks: The material from Durban Bay attributed to this species by K. H. Barnard (1916) and subsequently reported by Griffiths (1974*b*) in fact represents *P. kapapa* J. L. Barnard. This species is distinguished from *P. longimanus* by the shape of articles 2 and 6 of the ♂ second gnathopod and the presence of stridulation ridges on the anterior coxae.

Photis uncinata K. H. Barnard, 1932

Photis longicaudata: K. H. Barnard, 1916: 243, pl. 28 (fig. 26).
Photis uncinata K. H. Barnard, 1932: 223, fig. 138.

Records: 33/17/T, O to 34/18/FB/T, O, abundant, particularly in False Bay.

Distribution: Endemic to South Africa.

Podoceropsis sophiae Boeck, 1861

Podoceropsis sophiae: Chevreux & Fage, 1925: 316, fig. 324. Reid, 1951: 264, fig. 53. Karaman, 1972: 121, figs 9–11.

Records: 34/18/FB/O, two records.

Diagnosis: Accessory flagellum absent; palm of gnathopod 1 ♂ undefined, dactyl almost as long as hand, its inner margin serrate; article 5 of gnathopod 2 ♂ very short, bearing a narrow posterior lobe, article 6 with medial surface strongly setose, palm oblique, subequal to hind margin, strongly concave proximally, a large lobe near finger hinge distally divided into two teeth, dactyl sinuous near base, closing within palm; article 2 of pereiopod 3 posteriorly produced into a distinctive rectangular projection.

Distribution: Atlantic.

Remarks: This is the first record of this species from southern Africa.

Pseudomegamphopus jassopsis (K. H. Barnard, 1951)

Lembos jassopsis K. H. Barnard 1951, 706, fig. 6.
Pseudomegamphopus jassopsis: Myers 1974: 195, figs 1–4

Records: 32/18/T, 33/17/T, 33/18/T, a few records.

Diagnosis: Article 5 of gnathopod 1 narrow, triangular, article 6 enormous, palm oblique, defined by a huge lobe which becomes fleshy and triangular in terminal male, dactyl bearing long setae on posterior margin; outer ramus of uropod 3 shorter and broader than inner, bearing a small article 2 terminating in two long setae.

Distribution: Endemic, the above records (most of which are from Saldanha Bay) are the only ones to date.

Remarks: This species has been removed from *Lembos* to *Pseudomegamphopus* by Myers 1974, who also supplies a detailed redescription of the species. *Pseudomegamophopus* may be distinguished from *Lembos* by the deeply recessed head and elongate article 3 of antenna 1.

Siphonoecetes dellavallei Stebbing, 1893

Siphonoecetes dellavallei: Chevreux & Fage, 1925: 361, fig. 369.

Records: 33/18/T, 33/17/T, O to 34/18/FB/T, O and 34/19/E, common, particularly in False Bay and Saldanha Bay.

Distribution: Mediterranean, southern Africa.

Unciolella foveolata K. H. Barnard, 1955

Uniolella foveolata K. H. Barnard, 1955: 97, fig. 49.

Records: 34/18/FB/O, 32/16/D, a few records.

Diagnosis: Integument coarsely pitted; accessory flagellum 4–5 articulate; pereon segments without ventral spines; gnathopods subequal, subchelate, medial surfaces of articles 5 and 6 of gnathopod 2 strongly setose; uropods 1 and 2 hardly extending beyond tip of uropod 3, uropod 3 uniramous, ramus with apical tuft of plumose setae.

Distribution: Endemic, False Bay to Lambert's Bay.

Unciolella spinosa Griffiths, 1974

Unciolella spinosa Griffiths, 1974*b*: 229, fig. 3.

Records: 33/17/T, O, D to 34/18/FB/T, O, a few records.

Distribution: Endemic, Natal to Saldanha Bay.

Remarks: The discovery of further specimens of this form has shown that, as is the case in other Corophiidae (e.g. *Grandidierella bonnieroides*), the medioventral spines of the ♂ pereon may be present or absent within the same species. This feature should thus not be relied upon during identification. In the present instance *U. spinosa* is best distinguished from *U. foveolata* on the basis of its elongate first and second uropods, which exceed uropod 3 by about half their length.

Family **Dexaminidae**

Atylus granulosus (Walker, 1904)

Atylus granulosus: Ledoyer, 1967: 127, fig. 8.

Records: 32/18/T, O to 34/18/FB/T, O, numerous records.

Distribution: Indian Ocean.

Atylus guttatus (Costa, 1851)

Nototropis guttatus: Chevreux & Fage, 1925: 194, figs 201–203.

Records: 32/18/T, O to 34/18/FB/T, fairly common, especially in Saldanha Bay.

Distribution: Eastern Atlantic, extending around south coast of South Africa.

Atylus homochir Haswell, 1885

Atylus homochir: Stebbing, 1888: 908–913, pl. 74. J. L. Barnard, 1974: 12, figs 7–9.

Records: 33/17/O, a single record.

Distribution: Australia, South Africa.

Atylus swammerdami (Milne-Edwards, 1830)

Atylus swammerdami: Bousfield, 1973: 131.

Records: 32/18/T, a few records.

Distribution: Atlantic, extending along south coast of South Africa.

Dexamine spiniventris (Costa, 1853)

Dexamine spiniventris: Chevreux & Fage, 1925: 262, figs 271–273.

Records: 33/18/T, a single record.

Diagnosis: Accessory flagellum absent; mandible without palp; maxillipedal palp 3-articulate; article 2 of pereiopods 3–5 successively wider, article 4 shorter than 5 plus 6; pleon segments 2–3 (sometimes 1–3) each with a medio-dorsal tooth and a pair of lateral teeth; third pleonal epimeron acutely produced postero-distally; urosomite 1 with an acute medio-dorsal carina; urosomites 2 and 3 coalesced; telson 60% cleft, reaching almost to apex of uropod 3.

Distribution: Mediterranean, Atlantic.

Guernea rhomba Griffiths, 1974

Guernea laevis (*non* Chevreux, 1887): K. H. Barnard, 1916: 213.
Guernea rhomba Griffiths, 1974*a*: 183, fig. 3.

Records: 34/18/I, a single record.

Distribution: Endemic, Cape Town to South West Africa.

Paradexamine pacifica (Thomson, 1879)

Paradexamine pacifica: J. L. Barnard, 1972*b*: 60.

Records: 34/18/FB/T, a single record.

Diagnosis: Article 5 of gnathopods 1–2 about 1,3 times length of article 6, palms pectinate; pleon segment 1 dorsally smooth, pleon segments 2 and 3 each with a medio-dorsal tooth and a pair of lateral teeth; third pleonal epimeron postero-distally acutely produced; urosomite 1 with a sharp medio-dorsal tooth and a pair of subdorsal spines; urosomites 2 and 3 fused, bearing two subdorsal spines on each side; apices of telson cut into 8–10 serrations.

Distribution: Indo-Pacific.

Polycheria atolli Walker, 1905

Polycheria antarctica: Chilton, 1912: 502. K. H. Barnard, 1916: 211.
Polycheria atolli: Ledoyer, 1972*a*: 205, pl. 27.

Records: 32/18/T to 34/18/FB/T, O, numerous records.

Distribution: Southern oceans, extending to tropical Indian Ocean.

Family **Eusiridae**

Calliopiella michaelseni Schellenberg, 1925

Calliopiella michaelseni: K. H. Barnard, 1940: 451, fig. 24. Griffiths, 1974*a*: 180.

Records: 33/17/I, T to 34/19/I, common under the shells of *Patella* spp.

Distribution: Endemic, Cape Agulhas to South West Africa.

Cleonardopsis carinata K. H. Barnard, 1916

Cleonardopsis carinata K. H. Barnard, 1916: 176, pl. 27 (figs 7–9).

Records: 35/18/VD, a single record.

Diagnosis: Accessory flagellum uni-articulate; gnathopods subchelate, article 5 almost as long as 6, lobed posteriorly, palm very oblique, undefined; pereon segments 6 and 7 and pleon segments 1 and 2 with medio-dorsal carinae ending in acute teeth; pleon segment 3 with medio-dorsal carina posteriorly extended with a hooked process; telson unarmed, 30% cleft.

Distribution: Endemic to deep waters around Cape Peninsula.

Eusiroides monoculoides (Haswell, 1880)

Eusiroides monoculoides: J. L. Barnard, 1964: 221, fig. 1.

Records: 32/18/T to 34/18/FB/T, O, fairly common.

Distribution: Circumtropical.

Paramoera bidentata K. H. Barnard, 1932

Paramoera bidentata K. H. Barnard, 1932: 211, figs 118m, 129.

Records: 32/18/I to 34/18/FB/I and 34/18/T, a few records.

Distribution: Endemic, Still Bay to Lüderitz.

Paramoera capensis (Dana, 1853)

Paramoera capensis: K. H. Barnard, 1916: 183–186.
Paramoera schizurus Stebbing, 1918: 66, pl. 10.

Records: 29/16/I to 34/18/FB/T, O and 34/19/I, E, the most abundant species found in this area at depths of less than 100 m.

Distribution: Southern oceans.

Rhachotropis grimaldi (Chevreux, 1887)

Rhachotropis grimaldii: Stebbing, 1888: 1641. K. H. Barnard, 1916: 179.

Records: 32/17/D, 34/18/D, VD, a few records.

Distribution: Atlantic, extending to Natal.

Rhachotropis kergueleni Stebbing, 1888

Rhachotropis kergueleni Stebbing, 1888: 955, pl. 85.

Records: 34/18/VD, a single record.

Diagnosis: Pereon dorsally smooth; pleon segments 1 and 2 each with an acute-tipped medio-dorsal carina and a pair of acutely tipped subdorsal ridges; pleon segment 3 with a single carina, 4 with a single carina terminating in a large tooth; pleonal epimera 1 and 2 postero-distally rounded, 3 postero-distally serrate; hind margin of article 2 of pereiopods 3–5 serrate, postero-distal corner acute, slightly produced.

Distribution: Kerguelen Island, South Africa.

Rhachotropis paeneglaber K. H. Barnard, 1916

Rhachotropis paeneglaber K. H. Barnard, 1916: 181, pl. 27 (fig. 10).

Records: 34/18/D, VD, two records.

Diagnosis: Pereon dorsally smooth; pleon segment 1 with an obscure median keel, 2 with three keels each terminating in an acute tooth, 3 with three distally untoothed keels; pleon segment 4 with median keel ending acutely, subdorsal keels not extending as far as posterior margin of segment; pleonal epimera 1 and 2 postero-distally rounded, 3 postero-distally serrate; hind margin of article 2 of pereiopods 3 and 4 smooth, that of pereiopod 5 faintly serrate, postero-distal corner rounded.

Distribution: Endemic, the above records are the only ones to date.

Rhachotropis palporum Stebbing, 1908

Rhachotropis palporum Stebbing, 1908*a*: 194, pl. 28.

Records: 34/18/D–VD, a single record.

Diagnosis: Pereon dorsally smooth; pleon segments 1–3 each with three keels, all ending in elongate acute teeth; pleon segment 4 with a minute medio-dorsal tooth; pleonal epimera 1 and 2 with a single acute tooth at centre of posterior margin, postero-distally rounded, third pleonal epimeron similar but postero-distally acutely produced; article 2 of pereiopods 3–5 with a large blunt process arising from centre of posterior margin, otherwise smooth.

Distribution: North and South Atlantic.

Family **Gammaridae**

Ceradocus rubromaculatus (Stimpson, 1855)

Ceradocus rubromaculatus: J. L. Barnard, 1972*a*: 220, fig. 129.

Records: 29/16/I to 34/18/FB/I, T, O, and 35/18/D, abundant, particularly intertidally and in shallow rocky areas.

Distribution: Indo-Pacific, extending to South West Africa.

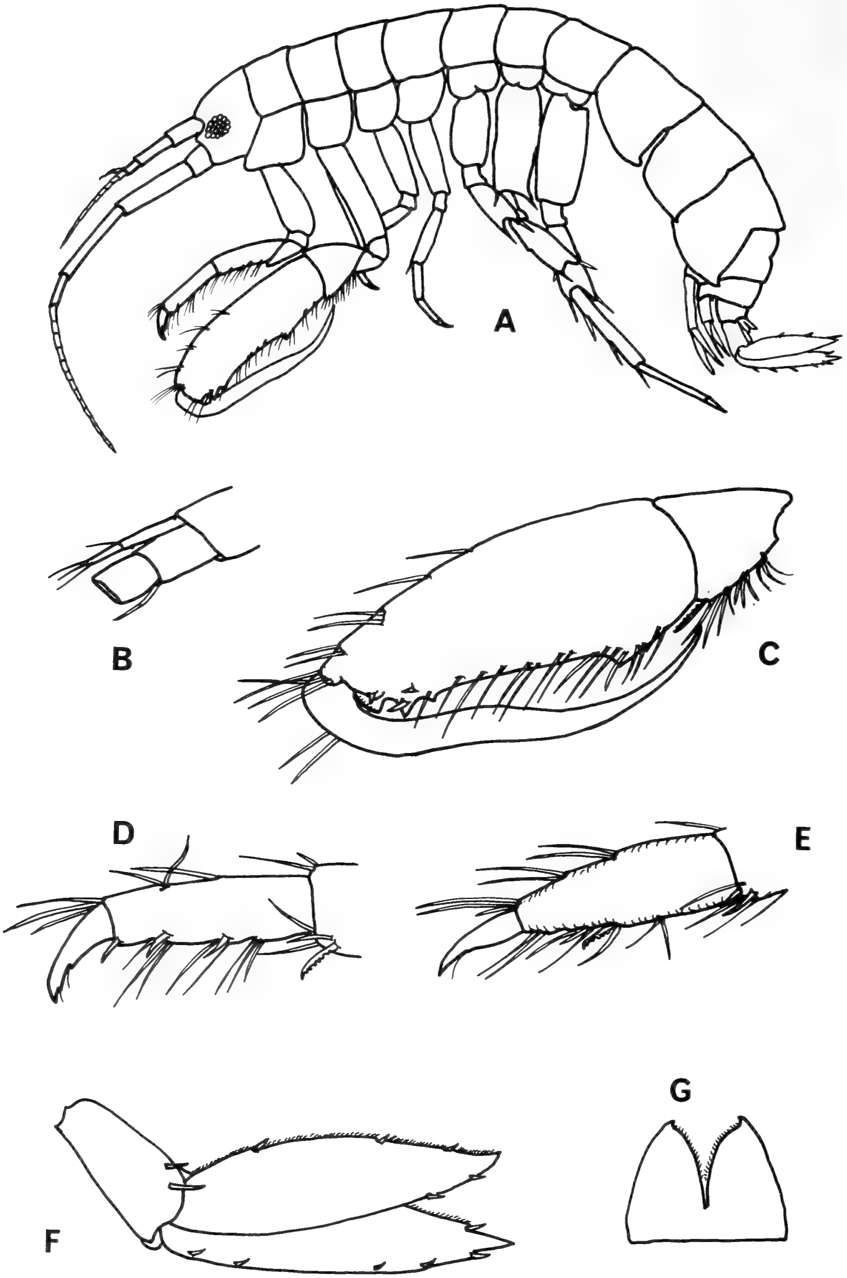

Fig. 5. *Cheirocratus inermis* Ledoyer, 1968
Male, 4 mm: A—lateral aspect; B—accessory flagellum; C—articles 5–7 of gnathopod 2. Female, 3,5 mm: D—articles 6 and 7 of gnathopod 1; E—articles 6 and 7 of gnathopod 2; F—uropod 3; G—telson.

Cheirocratus inermis Ledoyer, 1968

Fig. 5

Cheirocratus inermis Ledoyer, 1968: 36, pl. 12.

Records: 34/18/FB/O, a few records.

Diagnosis: Antenna 1 shorter than peduncle of antenna 2, accessory flagellum 2-articulate; body dorsally smooth; gnathopod 1 simple; gnathopod 2 ♀ simple; gnathopod 2 ♂ strongly subchelate, article 6 elongate, palm occupying almost whole hind margin of hand, distally cut into three teeth, dactyl sinuous, exceeding length of hand; uropod 3 greatly exceeding 1 and 2, rami equal, the inner uni-articulate; telson cleft nearly to base.

Distribution: Madagascar, South Africa.

Remarks: This is the first record of a male of this species and only the second time the species has been found. The female agrees closely with Ledoyer's original description, while the male shows powerful second gnathopods, a feature unusual for this genus. *C. inermis* is the only member of the genus *Cheirocratus* in which the pereon is dorsally smooth.

Elasmopus affinis Della Valle, 1893

Elasmopus affinis: Sars, 1895: 521, pl. 183.

Records: 33/17/T, 33/18/I, T, fairly common.

Distribution: Mediterranean, Atlantic, southern Indian Ocean.

Elasmopus japonicus Stephensen, 1932

Elasmopus japonicus: Sivaprakasam, 1968: 278, figs 3–5.

Records: 34/18/FB/I, a few records.

Distribution: Indo-Pacific, extending to South West Africa.

Elasmopus pectenicrus Bate, 1862

Elasmopus pectenicrus: J. L. Barnard, 1970*b*: 125, figs 73–74.

Records: 34/18/FB/I, a single record.

Distribution: Cosmopolitan in tropical and temperate seas.

Eriopisa epistomata Griffiths, 1974

Eriopisa epistomata Griffiths, 1974*a*: 186, fig. 4.

Records: 34/18/FB/O, a single record.

Distribution: Endemic, Port Elizabeth to South West Africa.

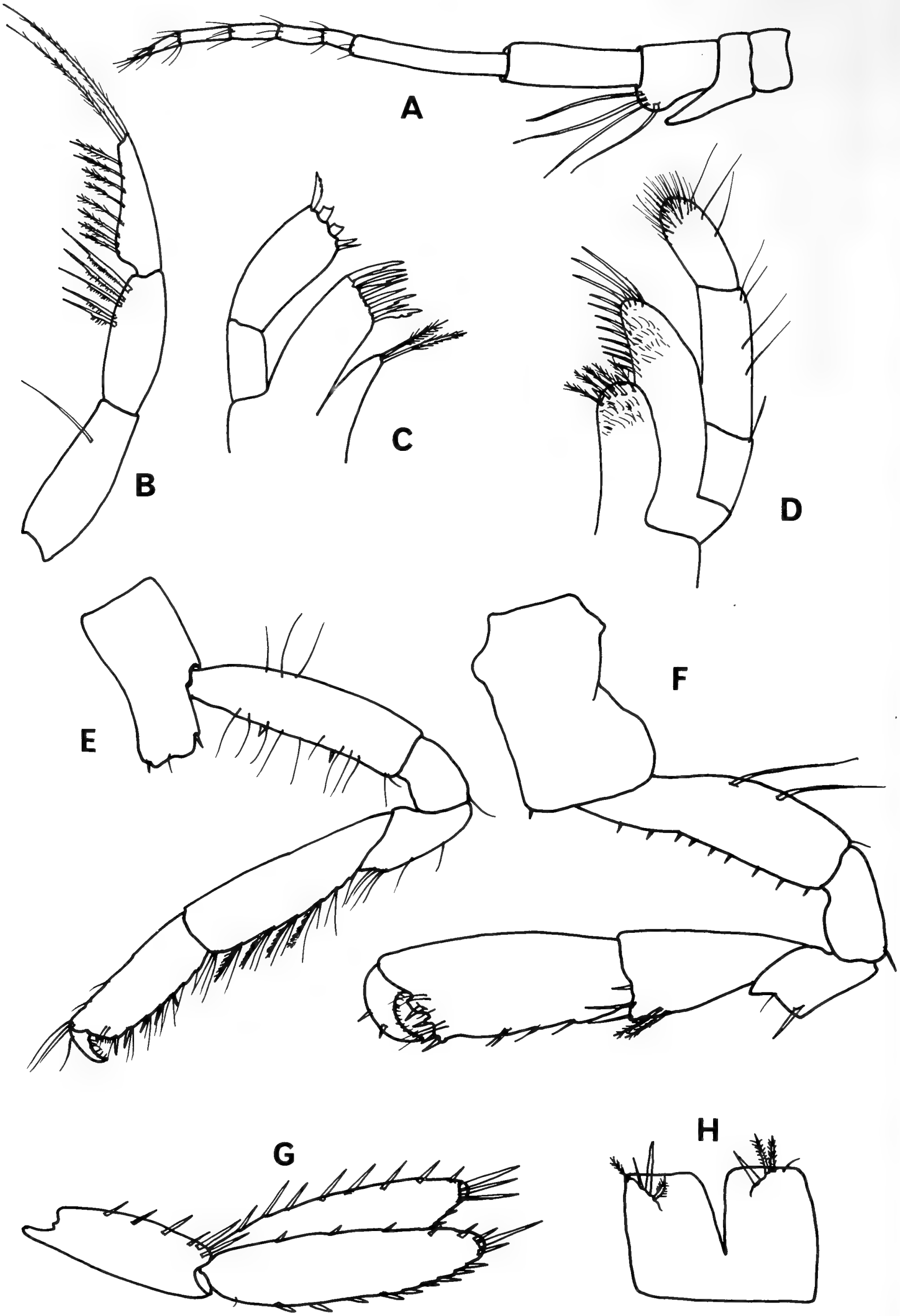

Fig. 6. *Jerbarnia mecochira* Croker, 1971
Male, 6 mm: A—antenna 2; B—mandibular palp; C—maxilla 1; D—maxilliped; E—gnathopod 1; F—gnathopod 2; G—uropod 3; H—telson.

Eriopisella capensis (K. H. Barnard, 1916)

Eriopisa capensis K. H. Barnard, 1916: 187, pl. 27 (figs 16–19).

Records: 32/17/D, 32/16/D to 34/18/D, a few records.

Distribution: Endemic to south and west coasts of South Africa.

Jerbarnia mecochira Croker, 1971

Fig. 6

Jerbarnia mecochira Croker, 1971: 382–386, figs 1–2.

Records: 34/18/FB/T, O, a few records.

Diagnosis: Accessory flagellum multi-articulate; article 3 of antenna 2 with a posterior setose lobe; maxillipedal palp 3-articulate; gnathopod 2 extremely long, article 3 elongate; coxae 5–7 and pleonal epimera 1–3 each with a spine at postero-distal corner; pleon segments 1–3 dorsally cut into five teeth, a seta in each concavity; pleon segments 4 and 5 with two posterior teeth, 6 with two dorsal spines; uropod 3 greatly exceeding 1 and 2, outer ramus minutely bi-articulate or not; telson quadrate, 50% cleft.

Distribution: Eniwetok Atoll, South Africa.

Remarks: As shown by figure 6 the present material conforms closely to that described by Croker from the Pacific. The specimen figured is considerably larger than Croker's (6 mm as against 4,5 mm) but is apparently less mature, having a relatively shorter article 3 of gnathopod 2 and less highly developed coxae.

Maera boecki (Haswell, 1879)

Elasmopus boeckii: K. H. Barnard, 1916: 199, pl. 27 (figs 13–14).
Maera boeckii: K. H. Barnard, 1940: 460.

Records: 34/18/FB/T, O, a few records.

Distribution: Australia, South Africa.

Maera bruzeli Stebbing, 1888

Fig. 7

Maera bruzelii Stebbing, 1888: 1014, pl. 97.
Maera mastersi (*non* Haswell, 1880): Griffiths, 1974*c*: 290.

Records: 33/17/O, 34/18/D, 34/18/FB/T, O, 34/19/?, a few records.

Distribution: Endemic, Port Elizabeth to Saldanha Bay.

Remarks: This species was originally described only from the female and when samples containing only males were recovered by Griffiths (1974*c*) these were erroneously identified as *M. mastersi*. However, the present samples contain both males and females and clearly show the two to represent the same species. The

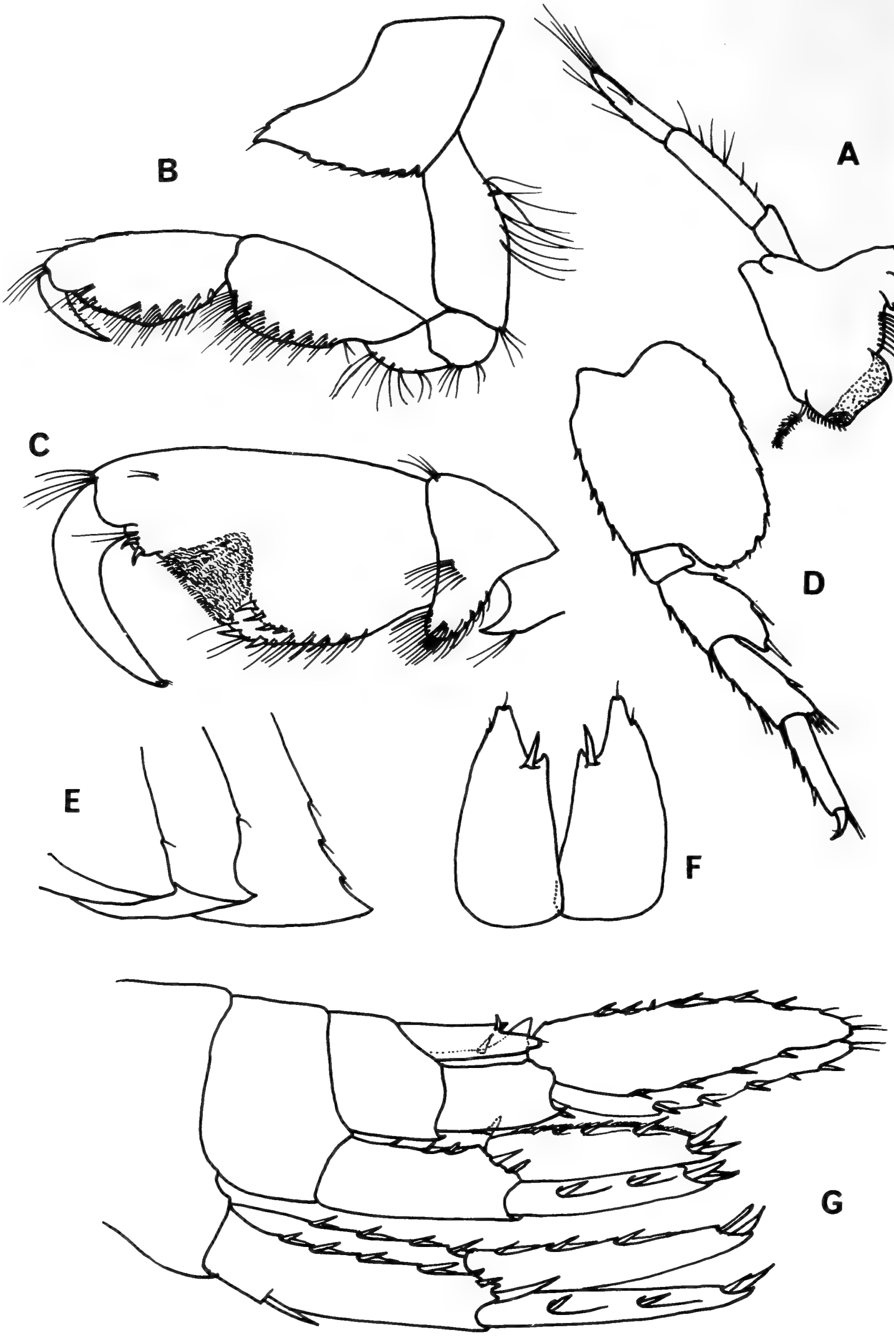

Fig. 7. *Maera bruzeli* Stebbing, 1888
Male, 14 mm: A—mandible; B—gnathopod 1; C—articles 5–7 of gnathopod 2 (inner aspect); D—pereiopod 5; E—pleonal epimera; F—telson; G—urosome.

male *M. bruzeli* is distinguished by the unusual second gnathopod, in which the inner surface of the palm is covered by a dense pad of short tightly-packed setae (Fig. 7C).

(The record of *M. mastersi* from Moçambique by K. H. Barnard (1916), is of the true *mastersi*.)

Maera emarginata sp. nov.

Fig. 8

Description of male (5 mm): Head as long as first two pereon segments, lacking lateral cephalic notch, eyes absent; antenna 1 as long as pereon, articles 1 and 2 subequal, much longer than 3, flagellum subequal to peduncle, 16-articulate, accessory flagellum (Fig. 8B) of two long articles and one short one; antenna 2 much shorter than 1, gland cone conspicuous, flagellum 7-articulate; mandible (Fig. 8C) with tridentate incisor, lacinia mobilis of four strong teeth, spine row of four spines, molar powerful, palp 3-articulate, article 2 the longest; lower lip without inner lobes; lobes of maxillae 1 and 2 setose only terminally; palp of maxilliped 4-articulate.

Gnathopod 1 considerably smaller than 2, articles 5 and 6 subequal, densely setose posteriorly, palm oblique, subequal to hind margin, but not clearly defined from it, palmar margin finely pectinate with submarginal rows of small spines; gnathopod 2 strongly subchelate, article 6 considerably larger than 5, palm oblique, subequal to hind margin, defined by two spines and bearing three equally spaced teeth (Fig. 8D), dactyl subequal to palm; pereiopods 1 and 2 slender, 2 somewhat the shorter; (pereiopods 3 and 4 missing); pereiopod 5 elongate, extending to apex of uropods 1 and 2, article 2 not greatly expanded posteriorly, posterior margin cut into seven moderate serrations, articles 4 and 5 with strong posterior spines.

Pleonal epimera 1 and 2 smoothly rounded, 3 with a slight postero-distal tooth; none of pleon segments dorsally dentate or carinate; uropod 1 (Fig. 8E) slightly exceeding 2, peduncle with a strong proximal spine and a large distal spine on medial surface, outer ramus 70% length of inner, both strongly spinose apically; peduncle of uropod 2 (Fig. 8F) with five dorsal spines, outer ramus slightly the shorter, bearing four dorsal and three apical spines, inner ramus with a row of ten upright dorsal spines and five apical spines; uropod 3 (Fig. 8G) greatly exceeding 1 and 2, rami subequal, outer ramus with one large and two small dorsal spines, also three apical spines, inner ramus with four ventral fascicles of spines and four spines apically; telson (Fig. 8H) not more than 25% cleft, a single blunt spine within a shallow notch at apex of each lobe.

Holotype: SAM–A13473, male, 5 mm.

Type-locality: 34°17′S/18°29′E, 15 February 1965, depth 27 m, substrate shelly sand.

Relationships: The telson of *M. emarginata* sp. nov. is highly unusual in that it

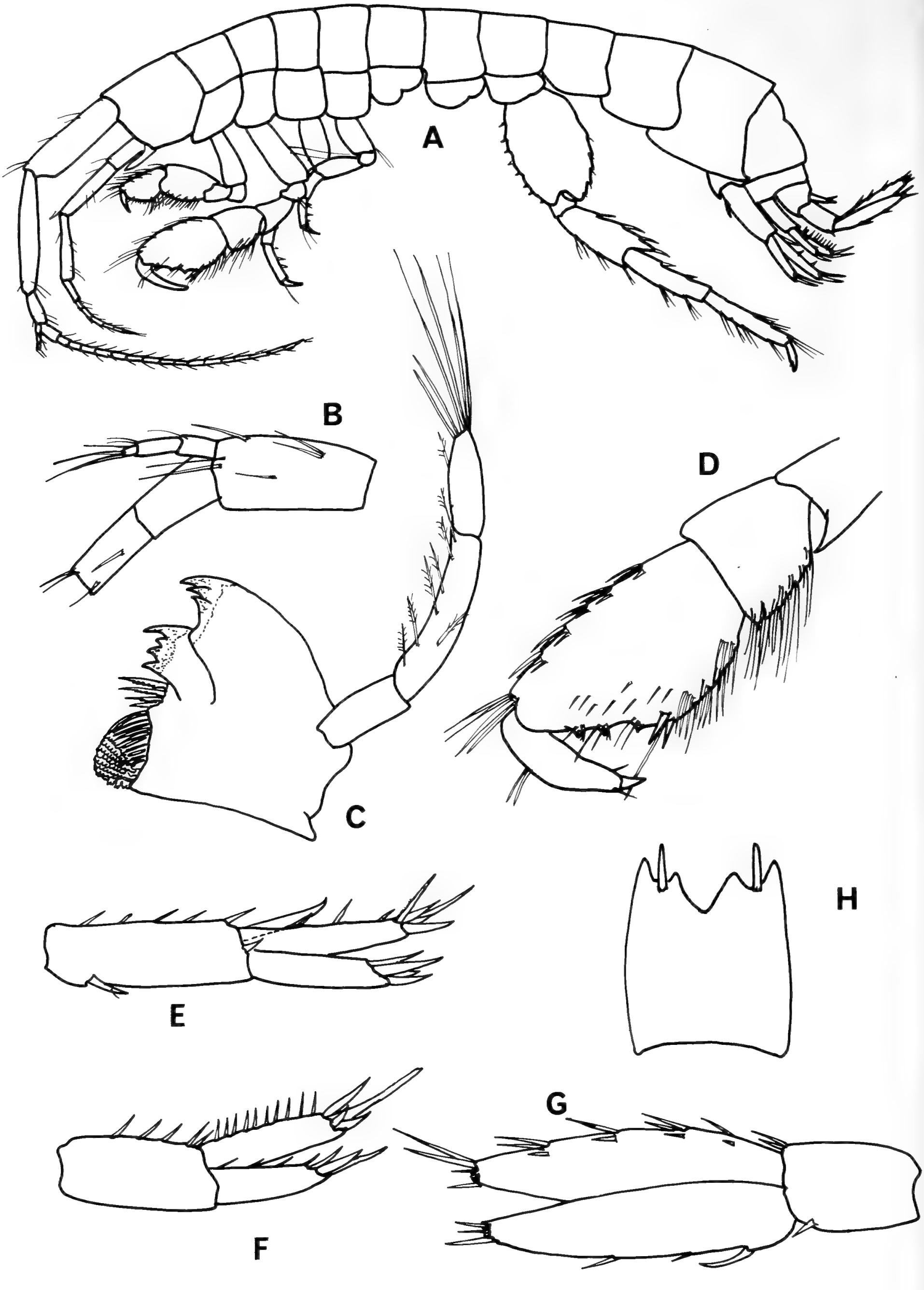

Fig. 8. *Maera emarginata* sp. nov.
Male, 5 mm: A—lateral aspect; B—accessory flagellum; C—mandible; D—articles 5–7 of gnathopod 2; E, F, G—uropods 1, 2, 3; H—telson.

is hardly cleft, most other species having telsons at least 50% cleft. *M. eugeniae* Schellenberg also has an incompletely cleft telson but here the apices are strongly divergent. Moreover, in *M. euginiae* the palm of gnathopod 2 ♂ is undefined.

Material: Three specimens from the type locality.

Maera grossimana (Montagu, 1808)

Maera grossimana: Chevreux & Fage, 1925: 239, figs 248, 250. Karaman & Ruffo, 1971: 114, figs 1–3.

Records: 33/17/T, two records.

Distribution: Mediterranean, Atlantic.

Maera hamigera (Haswell, 1880)

Maera hamigera: J. L. Barnard, 1965: 507, fig. 16. Karaman & Ruffo, 1971: 152, figs 21–23.

Records: 32/17/D, 33/18/I, T to 34/18/FB/I, T and 34/19/I, a few records.

Distribution: Indo-Pacific, extending around west coast of South Africa.

Remarks: The form of gnathopod 2 ♂ in this species is highly variable. Males in the present collection show a series of regular teeth along the distal portion of the palm, as figured by K. H. Barnard (1916), while females agree closely with the form figured by Karaman & Ruffo (1971).

Maera hirondellei Chevreux, 1910

Maera hirondellei: K. H. Barnard, 1916: 194. Chevreux & Fage, 1925: 241, fig. 252. Karaman & Ruffo, 1971: 122, figs 4–7.

Records: 33/18/I, 33/17/D, two records.

Distribution: Mediterranean, Atlantic.

Remarks: This species can be distinguished from *M. grossimana* by virtue of its elongate third uropod, which exceeds the apex of uropod 2 by about half the length of its rami.

Maera inaequipes (Costa, 1851)

Maera inaequipes: Karaman & Ruffo, 1971: 143, figs 17–20.

Records: 29/16/I to 34/18/FB/T, O and 34/18/D, abundant.

Distribution: Cosmopolitan in tropical and temperate seas.

Maera komma sp. nov.

Fig. 9

Description of male (7 mm): Head without cheek notch, eyes large (half height of head), composed of 20–30 separate ocelli; antenna 1 as long as pereon plus pleon, article 2 longer than 1, 3 short, flagellum 26-articulate, accessory flagellum of three elongate articles; antenna 2 extending 25% along flagellum of antenna 1, flagellum 12-articulate; mandible (Fig. 9A) with large strongly triturative molar, article 2 of palp slightly longer than 3.

Coxa 1 (Fig. 9B) strongly produced forwards, lower margin with one anterior tooth and two posterior teeth, remaining coxae quadrate; articles 5 and 6 of gnathopod 1 subequal, palm (Fig. 9C) oblique, defined by a single small spine, palmar margin finely pectinate throughout, dactyl subequal to palm; gnathopod 2 (Fig. 9D) strongly subchelate, article 2 anteriorly smooth, 3 not lobed, 5 strongly setose posteriorly, 6 elongate, widest at its base, posterior margin strongly setose proximally, concave distally, palm not defined, dactyl half length of hand, strongly curved so that when closed an oval gap remains between finger and palm; pereiopods 1 and 2 slender; article 2 of pereiopods 3–5 elongate-oval, posteriorly serrate, distal articles linear.

First pleonal epimeron very small, postero-distally quadrate; second pleonal epimeron much larger than first, postero-distally slightly produced; third pleonal epimeron postero-distally slightly produced, posterior margin with four small serrations, lower margin with five anterior spines; uropods 1 and 2 extending equally, slightly exceeding apex of peduncle of uropod 3; uropod 1 (Fig. 9G) with four pairs of dorsal spines and a strong spine on medial distal margin, inner ramus dorsally smooth, outer with three dorsal spines; outer ramus of uropod 2 marginally shorter than inner; uropod 3 (Fig. 9H) large, rami broad, laminar, margins finely pectinate, weakly spinose; telson (Fig. 9I) 80% cleft, each lobe dorsally bearing two proximal setae and a subterminal seta in a small notch plus a minute terminal seta.

Female: Similar to the male except for shorter third uropods and smaller gnathopod 2 (Fig. 9J) which has an oblique palm defined by four strong spines and minutely pectinate distally.

Holotype: SAM–A13477, male, 7 mm.

Type-locality: 34°05′S/17°45′E, 8 February 1963, depth 142 m, substrate dark green mud.

Relationships: M. komma sp. nov. lies close to *M. thrixa* sp. nov. (below) and *M. knudseni* Reid, 1951. However, it may be distinguished from these species by the shape of the palm and dactyl of gnathopod 2 ♂ and, in the case of *M. thrixa,* by the absence of an anterior keel on article 2 of gnathopod 2.

Material: 32/17/D, 34/18/D, two records.

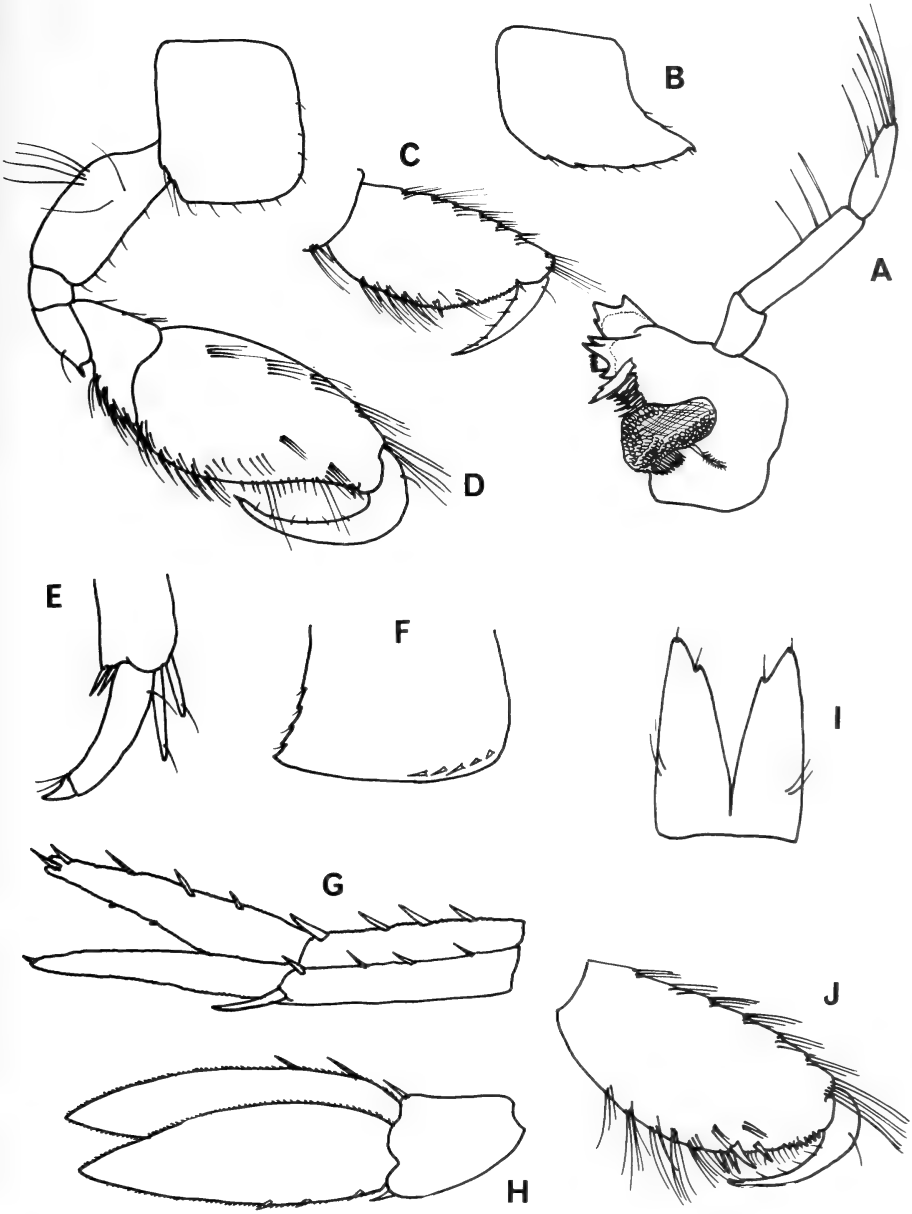

Fig. 9. *Maera komma* sp. nov.
Male, 7 mm: A—mandible; B—coxa 1; C—articles 6 and 7 of gnathopod 1; D—gnathopod 2; E—dactyl of pereiopod 5; F—third pleonal epimeron; G, H—uropods 1, 3; I—telson. Female, 7 mm: J—articles 6 and 7 of gnathopod 2.

Maera thrixa sp. nov.

Fig. 10

Description of male (9 mm): Head slightly exceeding length of first pereon segment, with a small cheek notch, eyes small, round, black; antenna 1 as long as pereon, article 1 slightly shorter than 2, 3 very short, flagellum 30-articulate, accessory flagellum 4-articulate; antenna 2 reaching 30% along flagellum of antenna 1, article 4 considerably longer than 5, flagellum 11-articulate; mandible with strong triturative molar, article 1 of palp not produced distally (Fig. 10C), articles 2 and 3 subequal.

Coxa 1 not strongly produced forwards, lower margin faintly serrate, remaining coxae sub-quadrate; gnathopod 1 (Fig. 10A) with articles 5 and 6 subequal, palm oblique, defined by two small spines, minutely pectinate throughout, dactyl smooth, subequal to palm; gnathopod 2 (Fig. 10B) powerfully subchelate, anterior margin of article 2 distally produced into a triangular keel, article 3 with an anterior pellucid lobe, article 5 strongly setose posteriorly, article 6 elongate, anterior margin setose, palm not distinct from hind margin, setose, dactyl closely appressed to palm, half length of hand; pereiopods 1 and 2 slender; pereiopod 3 short, extending only to tip of article 4 of pereiopod 4; article 2 of pereiopods 4 and 5 elongate-oval, posteriorly serrate, none of distal articles strongly expanded.

First and second pleonal epimera with oblique ridge running to minutely produced postero-distal corner; third pleonal epimeron (Fig. 10E) acutely produced postero-distally, posterior margin with two faint serrations, lower margin not serrate, anteriorly bearing five small spines; urosomites dorsally smooth; uropods 1 and 2 extending to tip of peduncle of uropod 3, rami subequal, weakly spinose dorsally and apically; uropod 3 large, rami elongate-oval (Fig. 10F), weakly spinose; telson (Fig. 10G) longer than peduncle of uropod 3, 80% cleft, each lobe with two dorsal setae, a sub-apical spine in a small notch and two minute apical setae.

Female: Similar to male except for smaller second gnathopod (Fig. 10H) which has smooth article 2 and oblique palm lined with strong spines.

Holotype: SAM–A13230, male, 9 mm.

Type-locality: 34°18′S/18°48′E, 18 February 1965, depth 51 m, substrate coarse shelly sand and rock.

Relationships: This species falls into a group typified by *M. knudseni* Reid and *M. othonis* (Milne-Edwards). The anterior keel on article 2 of gnathopod 2 is not, however, found in other members of the group. This keel appears in specimens of about 7 mm and in fully adult males (9–12 mm) becomes extremely prominent, reaching a maximum width about 1,5 times that of the body of article 2 of gnathopod 2.

Material: 34/18/FB/T, O, several records.

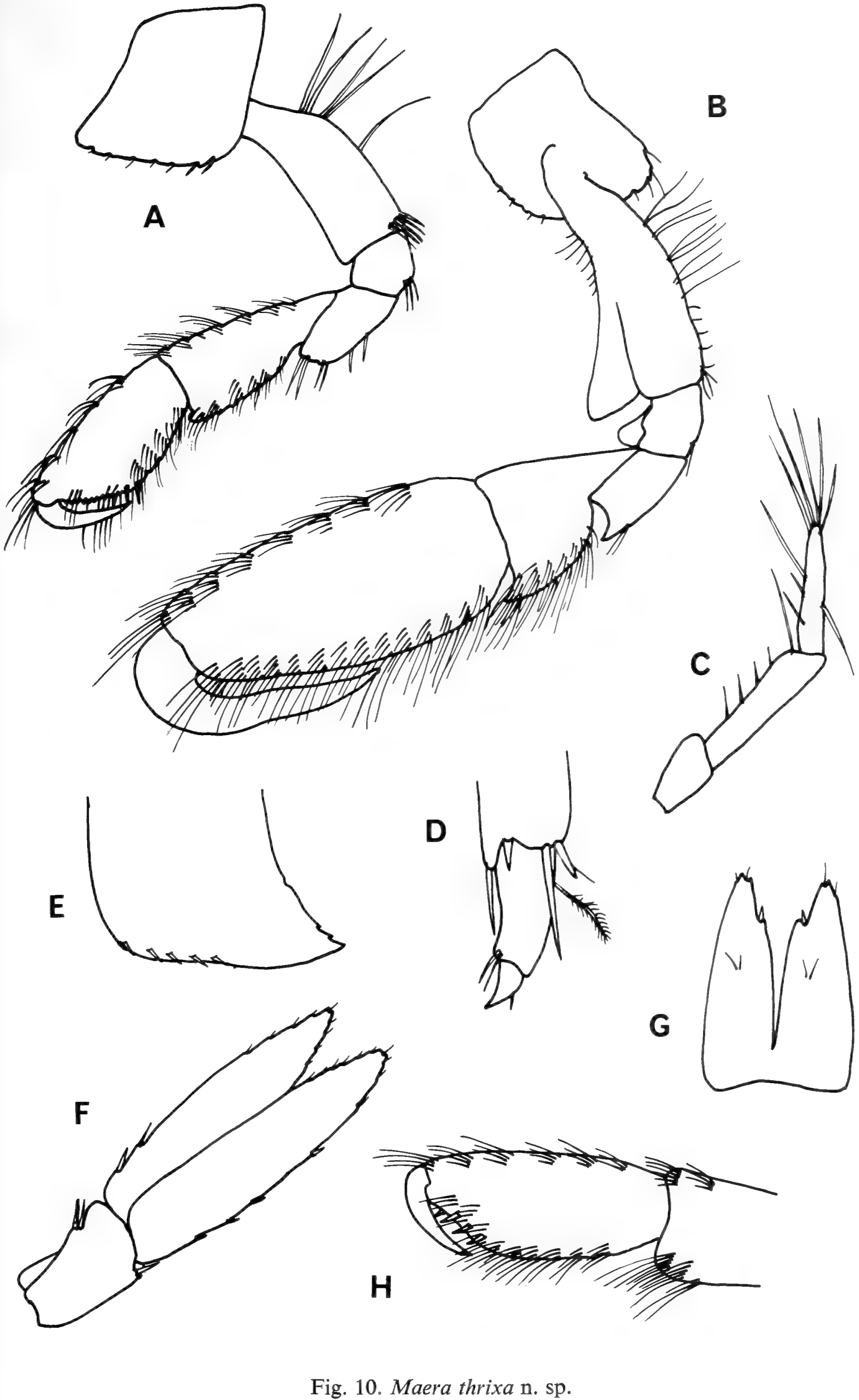

Fig. 10. *Maera thrixa* n. sp.
Male, 9 mm: A—gnathopod 1; B—gnathopod 2; C—mandibular palp; D—dactyl of pereiopod 5; E—third pleonal epimeron; F—uropod 3; G—telson. Female, 10 mm: H—articles 6 and 7 of gnathopod 2.

Maera vagans K. H. Barnard, 1940

Elasmopus laevis K. H. Barnard, 1916: 200, pl. 27 (fig. 15).

Maera vagans K. H. Barnard, 1940: 459.

Records: 31/17/I to 34/18/FB/T, O, fairly common.

Distribution: Endemic, False Bay to Lüderitz.

Megaluropus agilis Hoek, 1889

Phylloropus capensis K. H. Barnard, 1932: 146, figs 84–85.
Megaluropus agilis: Pillai, 1957: 50, fig. 10.

Records: 33/18/I, T, 34/18/FB/T, O, a few records.

Distribution: Europe, India, South Africa.

Megaluropus namaquaeensis Schellenberg, 1953

Megaluropus namaquaeensis Schellenberg, 1953: 117, fig. 5.

Records: 32/18/T, O to 34/18/FB/T, O, abundant.

Distribution: Endemic, Natal to South West Africa.

Melita machaera K. H. Barnard, 1955

Melita machaera K. H. Barnard, 1955: 90–92, fig. 45.

Records: 33/18/I, T, 34/18/FB/T, O, a few records.

Distribution: Endemic, Plettenberg Bay to Saldanha Bay.

Melita mucronata sp. nov.

Fig. 11

Description of female (4,5 mm): Head equal to first two pereon segments, eyes round, brown (as preserved in 70% alconol); antenna 1 almost as long as body, article 1 slightly shorter than 2, 3 short, flagellum of 29 elongate articles, accessory flagellum of three long articles and one short article; antenna 2 shorter than 1, peduncle longer than that of antenna 1, flagellum 11-articulate; mandible (Fig. 11B) with incisor of three strong teeth, lacinia mobilis bifurcate, spine row of nine spines, molar quadrate, articles 2 and 3 of palp subequal, much longer than 1; inner plate of maxilla 2 strongly setose medially.

Coxae 1–4 quadrate, subequal, postero-distal corners minutely toothed; gnathopod 1 with articles 5 and 6 subequal, palm oblique, dactyl equal to palm; gnathopod 2 (Fig. 11C) larger than 1, article 4 postero-distally acutely produced, 5 slightly shorter than 6, palm oblique, defined by a single spine, dactyl slightly longer than palm, inner margin faintly crenulate; pereiopods 1 and 2 slender, dactyl with strong anterior accessory cusp; (pereiopods 3–5 missing).

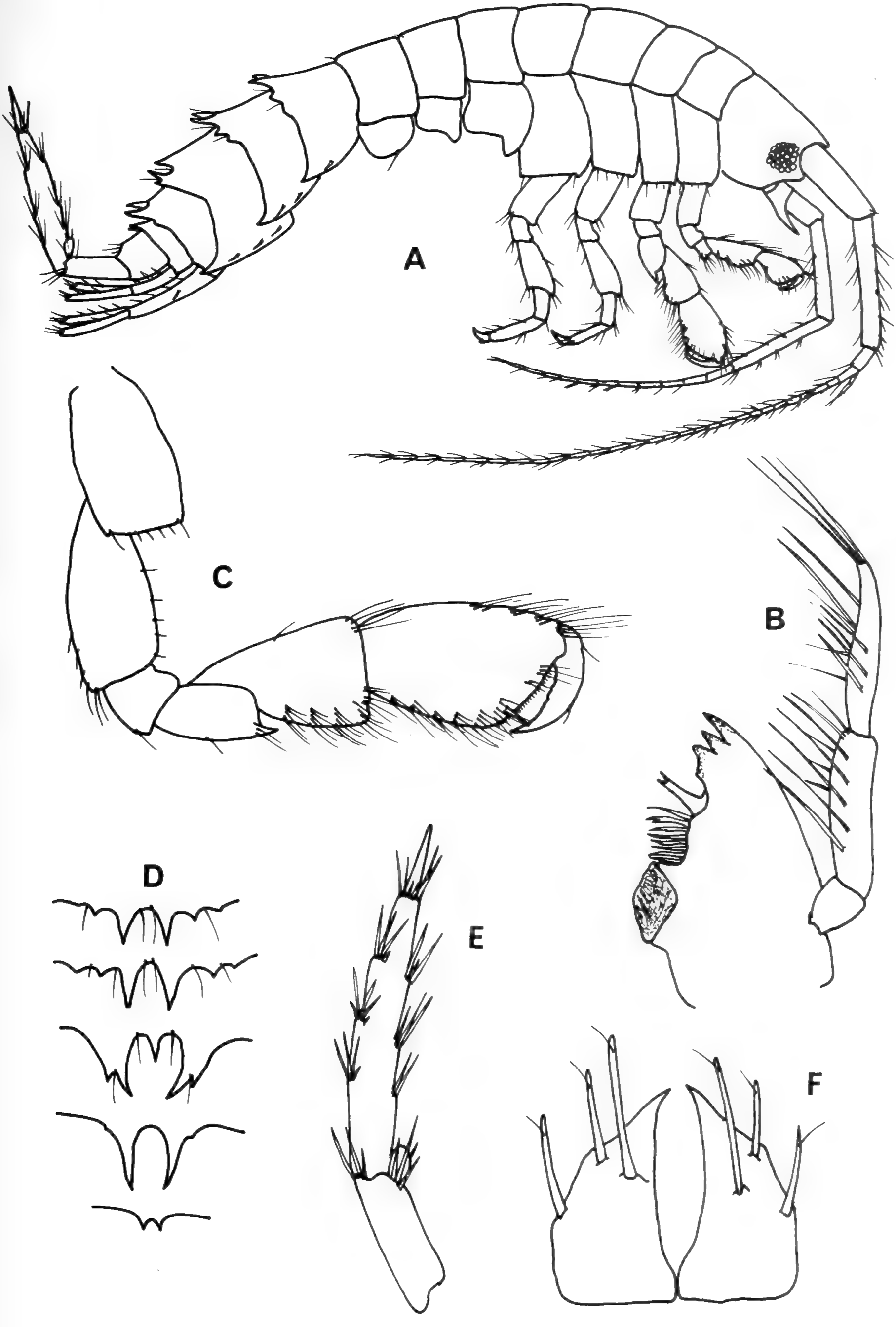

Fig. 11. *Melita mucronata* sp. nov.
Female, 4,5 mm: A—lateral aspect; B—mandible; C—gnathopod 2; D—dorsal margins of pleon segments 1–5; E—uropod 3; F—telson.

Pleonal tooth formula 4 : 6 : 5 : 2 : 2 (Fig. 11D) with a suggestion of a third pair of teeth on pleon segment 1; pleonal epimera 1–3 acutely produced postero-distally, distal margins with 1, 2 and 3 spines respectively; uropods 1 and 2 extending equally, peduncles and rami dorsally spinose, apices of rami truncated, surrounded by rings of slender spines; uropod 3 (Fig. 11E) greatly exceeding 1 and 2, inner ramus about 10% length of outer, bearing a single apical spine, outer ramus with small spiniform article 2, article 1 with three lateral fascicles of spines on each side and a terminal fascicle of spines surrounding base of article 2; telson (Fig. 11F) cleft to base, each lobe with a medio dorsal and two lateral strong spines, apices of lobes acute.

Holotype: SAM–A13233, female, 4,5 mm, unique.

Type-locality: 34°21′S/18°41′E, 22 February 1965, depth 85 m, substrate fine green mud.

Relationships: The pleonal tooth formula of this species is diagnostic. Similar formulae are those of *M. dentata* (Kröyer) and *M. gladiosa* Bate, which have a central tooth on pleon segments 4 and 5, and *M. pallida* Sars which lacks a central tooth on pleon segment 3.

Melita orgasmos K. H. Barnard, 1940

Melita orgasmos K. H. Barnard, 1940: 454. Sivaprakasam, 1966: 114, fig. 12k–m.

Records: 29/16/I to 34/19/I, a few records, mostly intertidal.

Distribution: India, southern Africa.

Melita subchelata (Schellenberg, 1925)

Melita fresnelii var. *subchelata* Schellenberg, 1925: 153. K. H. Barnard, 1932: 211, fig. 130.

Records: 32/18/T, 33/17/T, O, a few records.

Distribution: Endemic, Saldanha Bay to South West Africa.

Melita zeylanica Stebbing, 1904

Melita zeylanica: J. L. Barnard, 1972*a*: 235, figs 139–141.

Records: 33/18/I and 31/18/E to 34/19/E, common in estuaries and areas of lowered salinity.

Distribution: Indo-Pacific, a brack-water species.

Parelasmopus suluensis (Dana, 1853)

Parelasmopus suluensis: Stebbing, 1888: 1029, pl. 100. Ledoyer, 1972*a*: 233, pls 48–49. Griffiths, 1974*c*: 292.

Records: 34/18/FB/T, a single record.

Distribution: Indo-Pacific.

Quadrivisio aviceps (K. H. Barnard, 1940)

Ceradocus aviceps K. H. Barnard, 1940: 456, fig. 25.

Records: 34/19/E, a few records.

Diagnosis: None of pereon or pleon segments dorsally dentate; gnathopod 2 ♂ with article 6 elongate-oval, distally scabrous, dactyl very short and strongly hooked, closing inwards against inner surface of hand; pleonal epimera 1–3 weakly crenulate posteriorly, minutely produced postero-distally; rami of uropod 3 elongate-oval, apically rounded, setose ventrally and distally; telson cleft to base, apices notched with a single spine within notch.

Distribution: Endemic to estuaries in the Hermanus district.

Remarks: A re-examination of the existing material of this species has shown article 1 of the mandibular palp to be distally rounded and article 3 to be almost as long as 2. These characters are inconsistent with the definition of *Ceradocus* and *C. aviceps* should be removed from that genus to *Quadrivisio* Stebbing, 1907. Members of this genus resemble '*C*'. *aviceps* closely in the foliaceous condition of the rami of uropod 3 and in their estuarine habits. As originally defined *Quadrivisio* showed two pairs of eyes, but this has been shown to be a variable character (Schoemaker 1933), the eyes in fact developing from oval to dumbbell-shaped and then separating into two portions. In the present species the eyes are distinctly bilobed although the two halves are still connected even in the largest known specimens.

Q. aviceps differs from other species of *Quadrivisio* in the unusual condition of gnathopod 2 ♂, in which the stunted dactyl closes medially against the inner surface of the hand, rather than longitudinally against the palmar margin.

Family **Haustoriidae**

Bathyporeia sp.

Bathyporeia gracilis (*non* Sars, 1891): K. H. Barnard, 1951: 704.
Bathyporeia sp.: Vader, 1970: 161.

Records: 32/18/T, O to 34/18/FB/I, T, O, numerous records.

Distribution: Endemic, eastern Cape Province to South West Africa.

Remarks: These specimens were sent to Dr Wim Vader, who is to describe a new species from them.

Cunicus profundus Griffiths, 1974

Cunicus profundus Griffiths, 1974*c*: 293–297, figs 8–9.

Records: 32/18/T, 34/18/D, 34/18/FB/O, abundant locally.

Distribution: Endemic, Port Elizabeth to Lambert's Bay.

Remarks: This species appears to be an extremely efficient burrower. Although rarely collected by conventional methods it has been recovered in considerable numbers by a diver-operated suction-sampler which extracts sand samples of 60 cm depth and more.

Urothoe coxalis Griffiths, 1974

Urothoe coxalis Griffiths, 1974*b*: 239, fig. 5.

Records: 32/17/O, a single record.

Distribution: Endemic, Natal to Saldanha Bay.

Remarks: U. coxalis is closely related to *U. cuspis* Imbach (1967), a description of which I have only recently been able to obtain. The two species may be distinguished by the presence of an antero-distal cusp on coxa 2 of *U. cuspis* and the elongate posteriorly-directed process of coxa 4 of *U. coxalis.*

Urothoe elegans Bate, 1857

Urothoe elegans: Chevreux & Fage, 1925: 101, fig. 95.

Records: 32/17/D, 33/18/I, T to 34/18/FB/I, T, O, numerous records.

Distribution: Atlantic, Indian Ocean.

Urothoe grimaldi Chevreux, 1895

Urothoe grimaldii: Chevreux & Fage, 1925: 99, fig. 93. K. H. Barnard, 1955: 84, fig. 41B.

Records: 32/18/T, O, 32/17/D to 34/18/FB/T, O, one of the most abundant species found in sandy sediments.

Distribution: Mediterranean, Atlantic, Indian Ocean.

Urothoe pinnata K. H. Barnard, 1955

Urothoe pinnata K. H. Barnard, 1955: 86, fig. 42.

Records: 34/18/FB/T, O, fairly common.

Distribution: Endemic, Natal to False Bay.

Urothoe pulchella (Costa, 1853)

Urothoe pulchella: Chevreux & Fage, 1925: 99, fig. 92. K. H. Barnard, 1955: 83, fig. 41A.

Records: 32/18/T, 32/17/D to 34/18/FB/T, O, numerous records.

Distribution: Mediterranean, Atlantic, South Africa.

Urothoe tumorosa Griffiths, 1974

Urothoe tumorosa Griffiths, 1974*b*: 241, fig. 6.

Records: 34/18/FB/T, O, a few records.

Distribution: Endemic, Natal to False Bay.

Family **Ischyroceridae**

Cerapus tubularis Say, 1818

Cerapus tubularis: J. L. Barnard, 1962*a*: 61, figs 27–28. Bousfield, 1973: 197, pl. 60 (fig. 1).

Records: 33/18/O, 34/18/FB/T, O, a few records.

Distribution: Cosmopolitan in tropical and temperate seas.

Ericthonius brasiliensis (Dana, 1853)

Ericthonius brasiliensis: J. L. Barnard, 1971: 61, fig. 17E. Bousfield, 1973: 195, pl. 59 (fig. 2).

Records: 31/18/E, 32/18/T to 34/18/FB/T, O, numerous records.

Distribution: Cosmopolitan in tropical and temperate seas.

Isaeopsis tenax K. H. Barnard, 1916

Isaeopsis tenax K. H. Barnard, 1916: 267, pl. 28 (figs 19–21).

Records: 33/18/I, 34/18/I, two records.

Diagnosis: Accessory flagellum of a single elongate article; coxae serially touching, 1 about 75% length of 2, 6 half as long as 5; articles 5 and 6 of gnathopod 1 subequal; gnathopod 2 ♂, palm lacking defining tooth (resembling that of *Ischyrocerus anguipes*); pereiopods prehensile, article 2 widened.

Distribution: Endemic, known only from the above records.

Ischyrocerus anguipes Kröyer, 1835

Ischyrocerus anguipes: Bousfield, 1973: 192, pl. 58 (fig. 1).

Records: 33/18/T, O to 34/18/FB/I, T, O, fairly common.

Distribution: Cosmopolitan in tropical and temperate seas.

Ischyrocerus carinatus K. H. Barnard, 1916

Ischyrocerus carinatus K. H. Barnard, 1916: 266, pl. 28 (fig. 18).

Records: 33/18/I, 34/18/FB/I, T, a few records.

Distribution: Endemic, False Bay to South West Africa.

Ischyrocerus ctenophorus Schellenberg, 1953

Fig. 12

Ischyrocerus ctenophorus Schellenberg, 1953: 121, fig. 7.

Records: 34/18/FB/I, a single record.

Distribution: Endemic, False Bay to Lüderitz.

Remarks: The above record is the first of a male of this species and only the second of a female. The female is identical with that figured by Schellenberg. Gnathopod 1 of the male is similar to that of the female while gnathopod 2 (Fig. 12D) is much larger and of typical *Ischyrocerus* type. *I. ctenophorus* is distinguished from other members of the genus by the large dorsal teeth on the outer ramus of uropod 3 (Fig. 12H) and by the comb-like rows of setae along the lateral margins of the dactyls of gnathopods 1 and 2 in both sexes.

Ischyrocerus gorgoniae K. H. Barnard, 1940

Ischyrocerus gorgoniae K. H. Barnard, 1940: 481, fig. 35.

Records: 34/18/FB/T, a few records.

Diagnosis: Pereon segments 1–6 each medio-dorsally carinate; article 2 of gnathopod 2 ♂ long and slender, margins entire, article 6 elongate-oval, palm straight with a narrow elongate tooth near hinge, dactyl laterally compressed; inner ramus of uropod 3 slightly the shorter, bearing a small apical spine, outer ramus with a large apical spine and two large dorsal teeth.

Distribution: Endemic, known only from the above records.

Jassa falcata Montagu, 1808

Jassa falcata: Sexton & Reid, 1951: 30–47, pls 4–30. Bousfield, 1973: 190, pl. 58 (fig. 2).

Records: 32/18/T, O, D to 34/18/FB/I, T, numerous records.

Distribution: Cosmopolitan.

Parajassa chikoa Griffiths, 1974

Parajassa chikoa Griffiths, 1974*c*: 300, fig. 11.

Records: 34/18/FB/O, a few records.

Distribution: Endemic, Cape St. Francis to False Bay.

Ventojassa frequens (Chilton, 1883)

Jassa frequens: Schellenberg, 1953: 119, fig. 6. Griffiths, 1974*a*: 196.
Ventojassa frequens: J. L. Barnard, 1972*b*: 135, figs 74–75.

Records: 34/18/FB/T, O, two records.

Distribution: New Zealand, southern Africa.

Remarks: The genus *Ventojassa*, as created by J. L. Barnard (1972*b*), differs

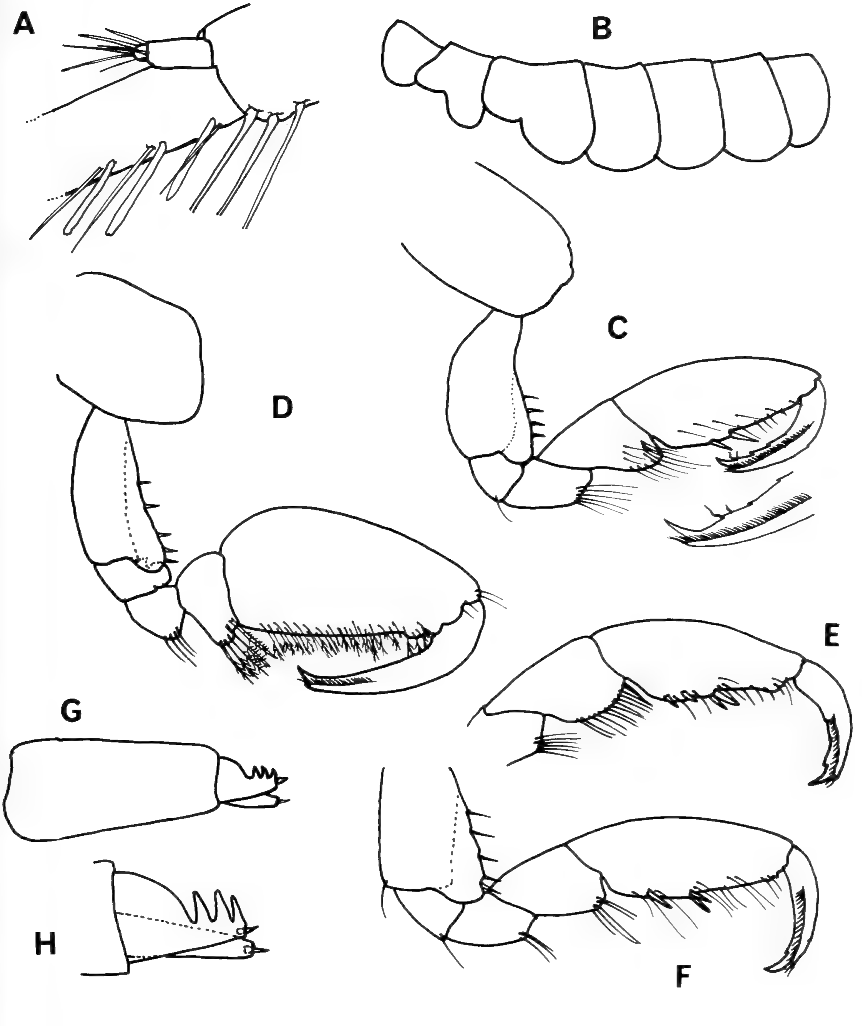

Fig. 12. *Ischyrocerus ctenophorus* Schellenberg, 1953
Male, 4 mm: A—accessory flagellum; B—coxae 1–7; C—gnathopod 1 with tip of dactyl enlarged; D—gnathopod 2. Female, 3,5 mm: E, F—gnathopods 1, 2; G—uropod 3; H—rami of uropod 3 enlarged.

from *Jassa* in the form of uropod 3, the dorsal ornamentation of the outer ramus consisting of one or more wire-like setae, rather than the one to three sharp reverted cusps typical of *Jassa.*

Family **Leucothoidae**

Leucothoe ctenochir K. H. Barnard, 1925

Leucothoe ctenochir K. H. Barnard, 1925: 342, pl. 34 (fig. 8).

Records: 34/18/T, 34/18/FB/T, O, a few records.

Distribution: Endemic, Durban to Cape Peninsula.

Leucothoe dentitelson Chevreux, 1925

Leucothoe dentitelson Chevreux, 1925: 297, figs 7–8. Reid, 1951: 227, fig. 25.

Records: 33/18/T, two records.

Diagnosis: Antennae short, extending only to pereon segment 2; article 7 of gnathopod 1 about 20% length of article 6; gnathopod 2 quite different in the two sexes, that of ♂ large, article 5 apically serrate, palm oblique, nodulose proximally, distally bearing four fairly large flat-topped teeth; gnathopod 2 ♀ smaller, article 5 apically crenulate, 6 antero-distally produced over base of dactyl, process acute, setose, palm slightly oblique, finely nodulose, defining angle almost rectangular, dactyl very stout; second pleonal epimeron acutely produced; third pleonal epimeron with a notch above a postero-distal tooth, posterior margin sinuous.

Distribution: Senegal, west coast of South Africa.

Remarks: This species has not previously been recorded from southern Africa.

Leucothoe dolichoceras K. H. Barnard, 1916

Leucothoe dolichoceras K. H. Barnard, 1916: 157, pl. 26 (fig. 14); 1925: 343.

Records: 33/17/T, O, 33/18/FB/T, O, a few records.

Distribution: Endemic, Natal to Saldanha Bay.

Leucothoe richiardi Lessona, 1865

Leucothoe richiardi: Sivaprakasam, 1967: 385, fig. 2.

Records: 32/18/T, 32/17/D to 34/18/FB/I, T, O, numerous records.

Distribution: Mediterranean, India, South Africa.

Leucothoe spinicarpa (Abildgaard, 1789)

Leucothoe spinicarpa: Sivaprakasam, 1967: 384, fig. 1.

Records: 33/18/T to 34/18/FB/T, O and 35/18/D, a few records.

Distribution: Cosmopolitan.

Family **Liljeborgiidae**

Liljeborgia dubia (Haswell, 1880)

Eusirus dubius Haswell, 1880: 331, pl. 30 (fig. 3).

Records: 33/17/O, 34/18/FB/T, O, a few records.

Distribution: Indo-Pacific.

Liljeborgia epistomata K. H. Barnard, 1932

Liljeborgia epistomata K. H. Barnard, 1932: 114, fig. 83; 1955: 89, fig. 44.

Records: 31/18/O, 32/17/D to 34/18/FB/T, O, numerous records.

Distribution: Endemic, Natal to Lambert's Bay.

Liljeborgia kinahani (Bate, 1862)

Liljeborgia kinahani: Chevreux & Fage, 1925: 157, fig. 157.

Records: 34/18/D, 34/18/FB/T, O, a few records.

Distribution: North Atlantic, South Africa.

Liljeborgia palmata Griffiths, 1974

Liljeborgia palmata Griffiths 1974*c*: 304, fig. 12.

Records: 32/17/D, 32/16/D to 34/18/D, a few records.

Distribution: Endemic, Still Bay to Lambert's Bay.

Liljeborgia proxima Chevreux, 1908

Liljeborgia proxima Chevreux, 1908: 475, figs 4–5.

Records: 34/18/FB/T, a single record.

Diagnosis: Palm of gnathopod 2 ♂ smoothly convex; pleon segments 1, 2 and 4 each bearing a single medio-dorsal tooth, segments 3 and 5 dorsally smooth.

Distribution: Atlantic coast of Africa.

Listriella lindae Griffiths, 1974

Listriella lindae Griffiths, 1974*a*: 197, fig. 7.

Records: 32/18/O, a single record.

Distribution: Endemic, Lambert's Bay to South West Africa.

Listriella saldanha sp. nov.

Fig. 13

Description of male (8 mm): Head as long as 1,5 pereon segments, eyes round, black; antenna 1 half as long as 2, flagellum 9-articulate, accessory flagellum (Fig. 13B) 3-articulate; antenna 2 extending to pereon segment 5, flagellum 8-articulate; mandible (Fig. 13C) with incisor cut into five strong teeth, lacinia mobilis of five teeth, spine row of nine spines, molar represented by five setae,

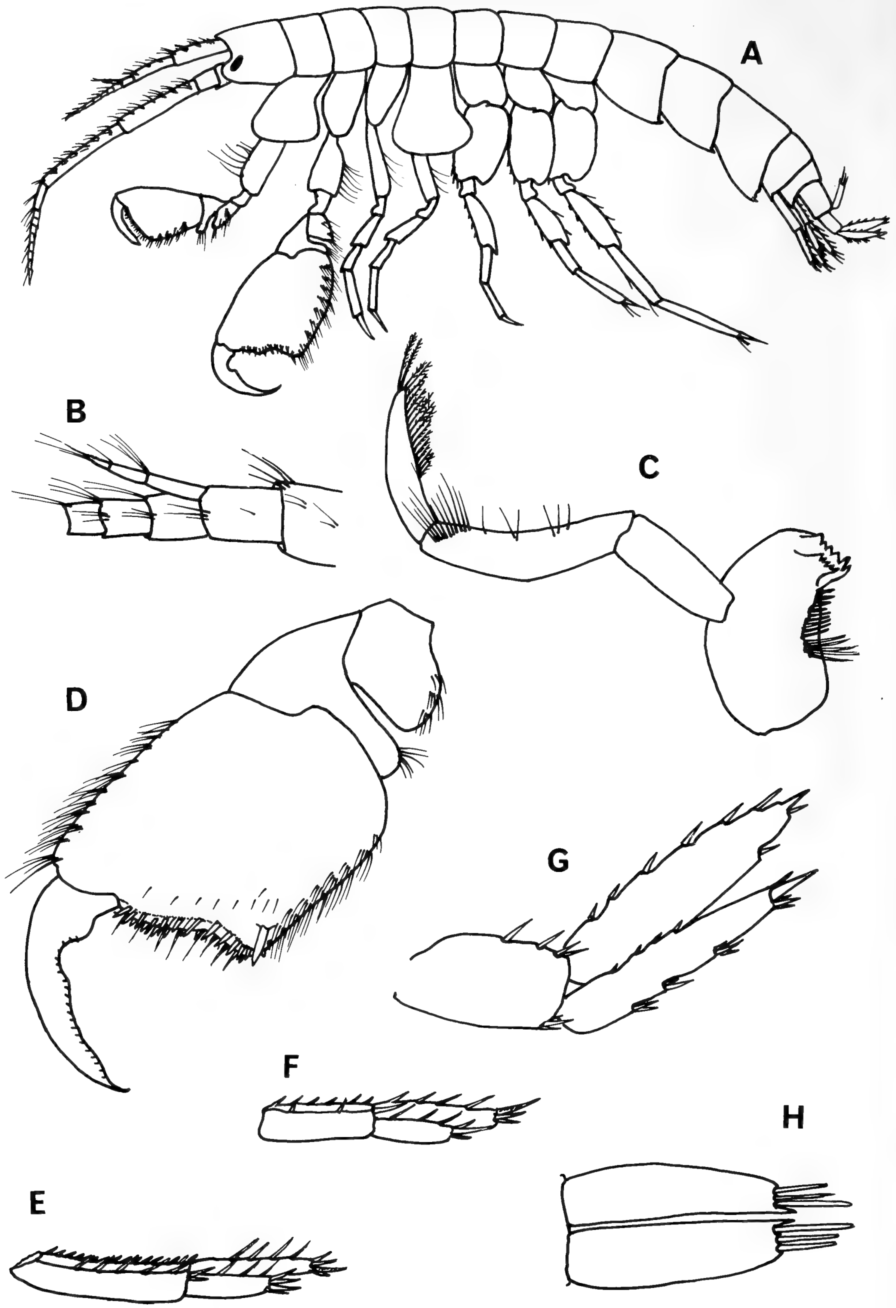

Fig. 13. *Listriella saldanha* sp. nov.
Male, 8 mm: A—lateral aspect; B—accessory flagellum; C—mandible; D—articles 4–7 of gnathopod 2; E, F, G—uropods 1, 2, 3; H—telson.

palp 3-articulate, article 3 lined with plumose setae; inner plate of maxilla 1 terminating in a single seta, outer plate bearing about eight pectinate spines, palp bi-articulate, with two terminal spines and a double row of setae along distal margin.

Coxae 1–4 without distal teeth, 1 slightly produced forwards; gnathopod 1 subchelate, considerably smaller than 2, palm slightly oblique, evenly convex, lined by alternating setae and spines; gnathopod 2 (Fig. 13D) powerful, palm sinuous, almost transverse, defined by a large spine and with a row of short spines on either side of its setose margin, dactyl indistinctly serrate throughout, excavate near its base; pereiopods 1 and 2 slender, pereiopods 3–5 successively longer.

Pleonal epimera 1–3 each postero-distally produced into a small tooth, posterior margins entire; urosome segments dorsally smooth; uropods 1 and 2 (Fig. 13E–F) extending equally; peduncle of uropod 1 with a medio-dorsal row of about 20 close-packed spines, outer margin with about six more widely spaced spines, outer ramus slightly the shorter, both rami dorsally and apically spinose, longest terminal spine of each ramus striated; uropod 3 (Fig. 13G) reaching well beyond apices of 1 and 2, outer ramus with a minute second article; telson (Fig. 13H) cleft to base, each lobe truncated distally with a medio-distal tooth and three strong terminal setae.

Female: The accessory flagellum of the only ♀ recorded to date is 4-articulate, as opposed to 3-articulate in the ♂. The palm of gnathopod 2 ♀ is transverse but not sinuous as in the ♂, also the telsonic apices each bear four rather than three setae.

Holotype: SAM–A13227, male, 8 mm.

Type-locality: 33°01′S/17°58′E, 2 May 1972, depth 12 m, substrate sand.

Relationships: All representatives of this genus with the exception of the three southern African species, *L. lindae* Griffiths, *L. sinuosa* Griffiths and *L. saldanha* sp. nov. have bi-articulate accessory flagellae. *L. saldanha* can be distinguished from the other two local species by virtue of the transverse palm of the second gnathopod and the shape of the third pleonal epimeron.

Material: 33/18/T, 34/18/FB/O, a few records.

Family **Lysianassidae**

Acidostoma obesum (Bate, 1862)

Acidostoma obesum: K. H. Barnard, 1925: 322. Chevreux & Fage, 1925: 32, fig. 9.

Records: 33/17/D, a single record.

Diagnosis: Antenna 1 ♂ very stout; mouthparts forming a conical bundle; mandibular palp attached proximal to the weak molar; gnathopod 1 simple; gnathopod 2 lacking dactyl; pereiopods 3–5 very stout, articles 4 and 5 as wide as long; uropod 3 very short, extending only to middle of rami of uropod 2; telson 50% cleft.

Distribution: North and South Atlantic.

Amaryllis macrophthalma Haswell, 1880

Amaryllis macrophthalma: J. L. Barnard, 1972*a*: 262–269, figs 156–158.

Records: 29/16/I, 32/18/T, 32/17/O, D to 34/18/FB/I, T, O and 34/19/I, one of the most abundant species in the area.

Distribution: Southern hemisphere.

Aristias symbiotica K. H. Barnard, 1916

Aristias symbiotica K. H. Barnard, 1916: 122.

Records: 32/18/I, T, 32/17/D to 34/18/I, D, 34/18/FB/T, O, fairly common.

Distribution: Endemic, Moçambique to South West Africa.

Cyphocaris anonyx Boeck, 1871

Cyphocaris anonyx: Schellenberg 1926*b*: 210, figs 2b, 5a–b, pl. 5 (fig. 2).

Records: 34/16/VD, a single record.

Diagnosis: Pereon segment 1 overhanging head, not produced into a 'horn'; article 2 of pereiopod 3 postero-distally produced to tip of article 5, both margins of process strongly serrate.

Distribution: Cosmopolitan, bathypelagic.

Cyphocaris challengeri Stebbing, 1888

Cyphocaris challengeri Stebbing, 1888: 661, pl. 17.

Records: 34/16/VD, a single record.

Distribution: Cosmopolitan, bathypelagic.

Cyphocaris richardi Chevreux, 1905

Cyphocaris richardi: J. L. Barnard, 1954: 53, pls 2–3.

Records: 33/15/VD, 34/16/VD, two records.

Diagnosis: Pereon segment 1 of adult overhanging head and anteriorly produced into an elongate, forward-projecting 'horn'; article 2 of pereiopod 3 not greatly produced postero-distally, posterior margin with about 10 strong serrations.

Distribution: Cosmopolitan, bathypelagic.

Euonyx biscayensis Chevreux, 1908

Euonyx biscayensis: K. H. Barnard, 1916: 110. J. L. Barnard, 1961: 34, fig. 4.

Records: 35/18/VD, a single record.

Diagnosis: Article 1 of antenna 1 slender, linear; eyes weak or absent; gnathopod 1 distinctly chelate, chela about 40% length of hand; article 6 of gnathopod 2 half as long as 5; third pleonal epimeron quadrate; dorsal surface of pleon segment 4 with basal depression and rounded distal hump.

Distribution: Mediterranean, eastern Atlantic, East Africa.

Euonyx conicurus K. H. Barnard, 1955

Euonyx conicurus K. H. Barnard, 1955: 80, fig. 38.

Records: 34/18/FB/T, a few records.

Distribution: Endemic, Port Elizabeth to False Bay.

Eurythenes obesus (Chevreux, 1905)

Katius obesus: K. H. Barnard, 1932: 56–58, fig. 21, pl. 1 (fig. 1).
Eurythenes gryllus: K. H. Barnard, 1940: 440.
Eurythenes obesus: J. L. Barnard, 1961: 38, fig. 8.

Records: 33–34/15–16/VD, a single record.

Diagnosis: Coxa 1 much smaller than 2 and partially concealed by it; gnathopod 1 subchelate, article 6 twice as long as 5; gnathopod 2 subchelate, article 6 half as long as 5; article 2 of pereiopod 3 very small, 20% or less of length of limb; dactyl of pereiopods 3–5 large, over 50% length of article 6.

Distribution: Cosmopolitan in tropical and temperate seas.

Hippomedon longimanus (Stebbing, 1888) *new synonymy*

Platamon longimanus Stebbing, 1888: 643, pl. 13.
Hippomedon longimanus: K. H. Barnard, 1916: 125.
Tryphosa africana K. H. Barnard, 1955: 81.
Tryphosella africana: Griffiths, 1974*c*: 315.

Records: 32/18/T, O, 32/17/D to 34/18/FB/T, O, one of the most abundant species in this area.

Distribution: Atlantic, South African east coast.

Remarks: In the past both K. H. Barnard and I have designated specimens to either *Hippomedon longimanus* or *Tryphosella* (=*Tryphosa*) *africana* on the basis of the length of the postero-distal tooth of the third pleonal epimeron. However, as more material has become available, this situation has become untenable, since a continuous range of variation in the size of this process has been found to occur. Other than this feature, the description of *Tryphosa africana* in Barnard (1955) applies equally well to *Hippomedon longimanus*. Unfortunately Barnard failed to allocate a holotype of *Tryphosa africana*, but he based his brief description on specimens in my possession and which are apparently identical with those of *Hippomedon longimanus* from the same area.

The composite species formed by the amalgamation of the above forms is definitely a *Hippomedon* rather than a *Tryphosella* since the mandibular molar is ridged and unsetulose, the dactyl of gnathopod 1 simple, the inner ramus of uropod 2 unconstricted and the branchiae complete with accessory lobes.

Hippomedon normalis (K. H. Barnard, 1955) *new synonymy*

Tryphosa normalis K. H. Barnard, 1955: 80, fig. 39.
Tryphosella normalis: Griffiths, 1974*a*: 201; 1974*b*: 249; 1974*c*: 315.
Hippomedon rotundipleura Ledoyer, 1973: 75, pl. 19.

Records: 33/18/I, T, O, to 34/18/FB/T, O, numerous records.

Distribution: Madagascar, South Africa.

Remarks: Barnard's incorrect placement of '*Tryphosa africana*' (above) has prompted a re-examination of the taxonomic status of his other '*Tryphosa*'—*T. normalis*. This species also appears to be a *Hippomedon* for the same reasons as given for '*Tryphosa africana*'.

A survey of the literature of *Hippomedon* has shown that the same species described by Barnard as *Tryphosa normalis* has subsequently been redescribed as a *Hippomedon*—*H. rotundipleura*—by Ledoyer (1973). His figures (which are of a ♀, not a ♂) agree closely with females in my possession (gnathopods 1 and 2 are transposed in Ledoyer's figures), the only notable difference being that my specimens have an accessory flagellum of five articles and a few fine setae along the dorsal margins of the rami uropod 3. Male specimens differ from females in the length of antenna 1, which is usually as long as the body, and in the more strongly setose margins of the rami of uropod 3.

Hippomedon onconotus (Stebbing, 1908)

Tryphosa onconotus Stebbing, 1908*b*: 65, pl. 35.
Hippomedon onconotus: J. L. Barnard, 1962*c*: 29.

Records: 32/17/D, 32/16/D to 34/18/FB/T, O, 35/18/VD, numerous records.

Distribution: Endemic, Natal to Lambert's Bay.

Lepidepecreum clypeatum Chevreux, 1888

Fig. 14

Lepidepecreum clypeatum: Chevreux, 1900: 28, pl. 4 (fig. 2). Chevreux & Fage, 1925: 63, fig. 52.

Records: 34/18/FB/O, a single record.

Diagnosis: Articles 1 and 2 of antenna 1 dorsally carinate and produced (Fig. 14A), accessory flagellum absent; eyes lacking; article 2 of pereiopod 5 greatly elongate (Fig. 14G), postero-distally produced to tip of article 5; pereon segments dorsally smooth; pleon segment 3 postero-dorsally raised into an acute tooth, segment 4 with a triangular dorsal carina; third pleonal epimeron with an oblique ridge running to acutely produced postero-distal corner.

Distribution: North Atlantic, South Africa.

Remarks: The above record is the first of a male of this species and the first of *L. clypeatum* from the Southern hemisphere. As can be seen from the figure the material agrees closely with the females described and figured by Chevreux (1900) and Chevreux & Fage (1925) except for such obviously sexually dimorphic characters as antenna 2 and uropod 3.

Lepidepecreum clypodentatum J. L. Barnard, 1962

Lepidepecreum clypodentatum J. L. Barnard, 1962*c*: 27, figs 9–10.

Records: 33/17/D, a single record.

Diagnosis: Article 1 of antenna 1 dorsally carinate and produced, accessory

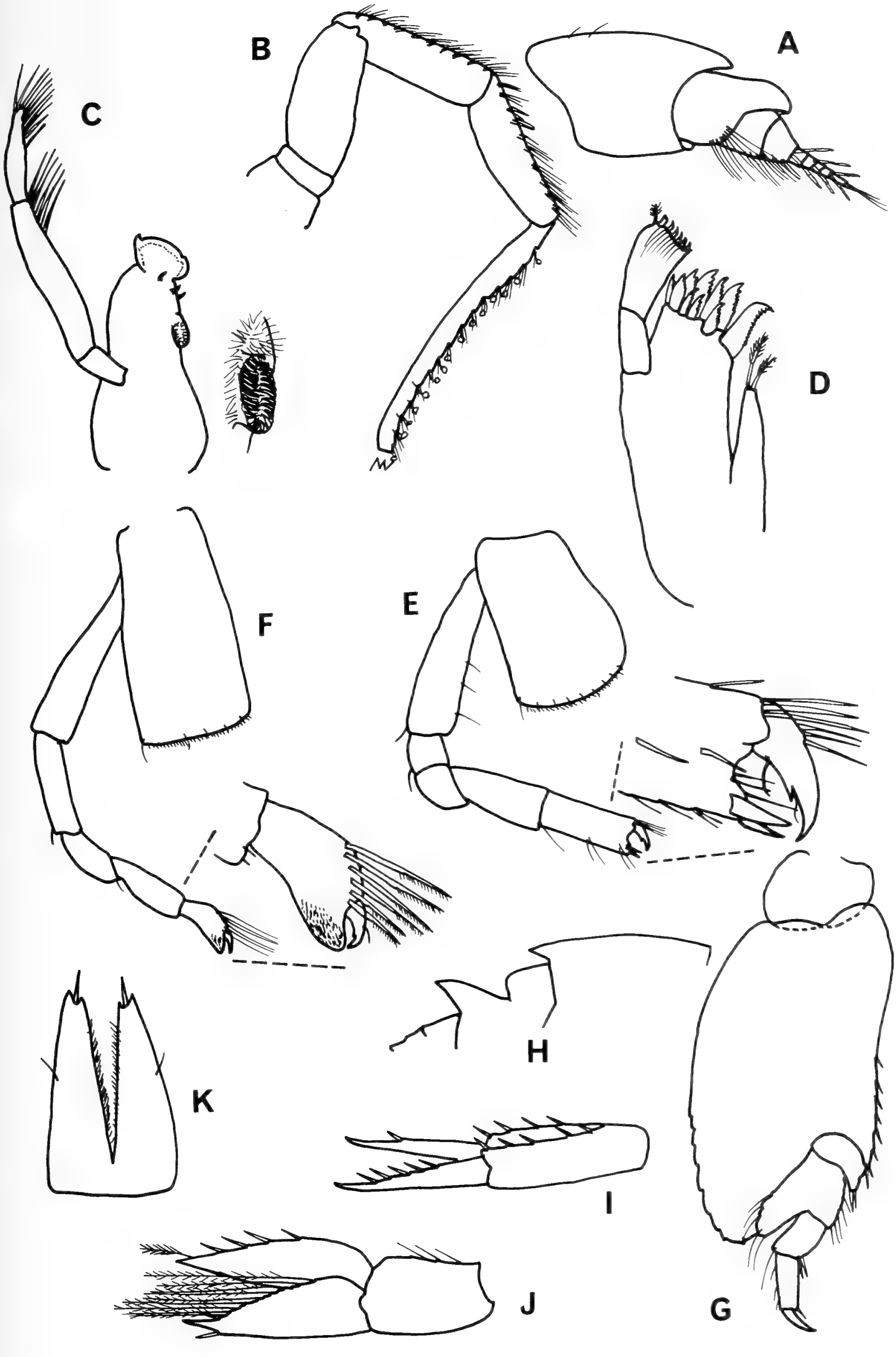

Fig. 14. *Lepidepecreum clypeatum* Chevreux, 1888
Male, 5 mm: A—antenna 1; B—antenna 2; C—mandible with molar enlarged; D—maxilla 1; E—gnathopod 1 with palm enlarged; F—gnathopod 2 with articles 6 and 7 enlarged; G—pereiopod 5; H—profile of pleon segments 3–5; I, J—uropods 1, 3; K—telson.

flagellum of two or three minute articles; eyes absent; article 2 of pereiopod 5 greatly elongate, postero-distally produced to tip of article 5; pereon segments dorsally ridged; pleon segments 1–3 each postero-dorsally produced into an acute tooth, segment 4 with an erect hook-like dorsal process; third pleonal epimeron postero-distally quadrate, without oblique ridge.

Distribution: West coast of South Africa.

Remarks: The above record is the first of a female of this species and the only record other than that of J. L. Barnard (1962*c*). The single specimen differs from Barnard's male only in regard to sexual characters of antenna 1 and uropod 3.

Lepidepecreum twalae Griffiths, 1974

Lepidepecreum twalae Griffiths, 1974*c*: 310, fig. 14.

Records: 32/17/D, a single record.

Distribution: Endemic, Mossel Bay to Lambert's Bay.

Lysianassa ceratina (Walker, 1889)

Lysianassa cubensis: K. H. Barnard, 1916: 120.
Lysianassa ceratina: Chevreux & Fage, 1925: 42, fig. 23.

Records: 29/16/I, 32/18/I, T, O to 34/18/FB/I, T, O, where it is one of the most abundant shallow-water species.

Distribution: Atlantic, Indian Ocean, Mediterranean.

Lysianassa variegata (Stimpson, 1855)

Lysianassa variegata: Stebbing, 1888: 682, pl. 23.

Records: 32/18/O, D to 34/18/FB/T, O, abundant.

Distribution: Africa south of the equator.

Microlysias

The genus *Microlysias* was originally instituted by Stebbing (1918) for his *M. xenoceras* from Durban Bay. Although his description was fully figured he failed to illustrate structure of the epistome and upper lip. K. H. Barnard (1937) subsequently erected a second species, *M. indica*, said to differ from *M. xenoceras* in the shape of the epistome and upper lip. However, Barnard, who did not have access to Stebbing's types, based his concept of the mouth parts of *M. xenoceras* on specimens he himself collected and identified (reported K. H. Barnard 1940), Griffiths (1973) later identified and figured further specimens of '*M. indica*', using Barnard's (1937) figures as a basis for identification.

A recent examination of Barnard's (1940) '*M. xenoceras*' from Plettenberg Bay by the author has revealed that they in fact represent *Orchomene plicata* and not *Microlysias*. As a result of this error the fabric of Barnard's argument for the creation of *M. indica* collapses, since its erection was based on comparison with *Orchomene* mistaken to be *M. xenoceras*. It thus appears that all existing records of *M. indica* are referable to *M. xenoceras*, the profile of the epistome and upper lip of which is figured as *M. indica* by Barnard (1937). *Microlysias* is best distinguished from *Orchomene* by the structure of antenna 2 ♂, both genera having branchiae pleated on both sides and article 4 of pereiopods 3–5 expanded.

Orchomene plicata (Schellenberg, 1925)

Orchomenopsis chilensis Schellenberg, 1925: 119, fig. 3. K. H. Barnard, 1925: 330.
Microlysias xenoceras (*non* Stebbing, 1918): K. H. Barnard, 1940: 441.
Orchomenella plicata: K. H. Barnard, 1940: 440.

Records: 29/16/I, 32/18/T, O to 34/18/FB/I, T, O, abundant.

Distribution: Cosmopolitan.

Remarks: For discussion of synonymy see *Microlysias* above.

Phoxostoma algoense K. H. Barnard, 1925

Phoxostoma algoense K. H. Barnard, 1925: 323, pl. 34 (fig. 2).

Records: 33/18/T. 34/18/FB/O, a few records.

Distribution: Endemic, Algoa Bay to Table Bay.

Procyphocaris induratus (K. H. Barnard, 1925) *new synonymy*

Uristes induratus K. H. Barnard, 1925: 333, pl. 34 (fig. 3).
Procyphocaris primata J. L. Barnard, 1961: 49, fig. 18.

Remarks: This species does not strictly fall into the scope of the present paper, since it is restricted to depths exceeding 1 000 m. However, I have included it here since its taxonomy is in need of revision.

In his original description of '*Uristes*' *induratus* K. H. Barnard (1925) failed to appreciate the taxonomic significance of the reduced first and second coxae, an error brought to light by J. L. Barnard (1962*c*) who rejected the species from a revised list of *Uristes* species. J. L. Barnard had, however, inadvertently already redescribed the same species as the type of a new genus (*Procyphocaris primata* J. L. Barnard, 1961). K. H. Barnard's type specimen agrees almost exactly with J. L. Barnard's figures, the only differences being in the posterior margin of article 2 of pereiopod 3, which is smooth in the South African specimen and bears three weak serrations in the Australian one. (K. H. Barnard's statement that the flagellum of antenna 2 is bi-articulate is incorrect, there are nine segments in an unbroken flagellum.)

The holotype of the resultant species, correctly known as *Procyphocaris induratus*, is South African Museum number SAM–A4545.

Schisturella adversicola (K. H. Barnard, 1925)

Lakota adversicola K. H. Barnard, 1925: 327.
Chironesimus adversicola: Schellenberg, 1926*a*: 219, fig. 13. J. L. Barnard, 1962*c*: 22, fig. 2.
Schisturella adversicola: J. L. Barnard, 1967: 71.

Records: 35/18/VD, a single record.

Diagnosis: Eyes absent, coxa 1 reduced, partially concealed by 2; gnathopod 1 subchelate, palm almost transverse; third pleonal epimeron postero-distally acutely produced; inner ramus of uropod 2 strongly constricted medially; outer ramus of uropod 3 bi-articulate; telson about 50% cleft.

Distribution: Endemic to deep waters off the Cape Peninsula.

Socarnes septimus sp. nov.

Fig. 15

Description of male (2,5 mm): Head hardly longer than pereon segment 1, lateral lobes strongly produced, apically subacute, eyes (Fig. 15A) composed of about 30 separate red ocelli, antenna 1 about as long as head plus two pereon segments, peduncle very stout, article 1 greatly exceeding 2 plus 3 (Fig. 15B), flagellum 5-articulate, bearing aesthetascs, accessory flagellum 3-articulate; antenna 2 (Fig. 15C) only about 1,5 times length of 1, article 5 of peduncle half as long as 4, flagellum 6-articulate; upper lip produced lobately beyond epistome; mandible (Fig. 15D) with weakly toothed incisor, spine row of two small spines, molar large, not strongly ridged, palp 3-articulate, article 2 naked, more than twice length of 1, article 3 with two terminal setae; maxilla 1 (Fig. 15E) with bi-articulate palp, palp article 2 distally serrate, bearing only a single minute apical seta, outer plate with seven strong serrate spines; maxilliped (Fig. 15F), outer plate with seven medial nodules, palp 4-articulate, greatly exceeding outer plate.

Pereon segments with a few scattered dorsal setules; coxae 1–4 considerably longer than their body segments, 1 not concealed by 2, 4 excavate posteriorly; gnathopod 1 (Fig. 15G) simple, articles 5 and 6 subequal, 6 medially constricted, dactyl with accessory tooth; gnathopod 2 (Fig. 15H) chelate, article 6 about 60% length of 5; article 2 of pereiopods 3–5 subcircular, posterior margin crenulate with minute setae, anterior margin lined with strong spines, article 4 almost as wide as long, lobed posteriorly, 5–7 slender.

Pleonal epimera 1 and 3 postero-distally rounded, 2 produced into a minute tooth; uropod 1 slightly exceeding 2 and 3, peduncle with a single dorsal spine, outer ramus 70% length of inner, bearing two dorsal spines and one apical spine, inner ramus with one dorsal and one apical spine; peduncle of uropod 2 (Fig. 15I) latero-dorsally keeled, outer ramus with a single dorsal spine, inner ramus with two dorsal spines; uropod 3 (Fig. 15J) with outer margin of peduncle dorsally keeled, outer ramus with small article 2, inner ramus smooth, telson twice as long as broad, 60% cleft, lobes divergent (Fig. 15K), each terminating in two small setae, one plumose.

Female: Similar to male, ovigerous at 2 mm, usually carries only a single enormous ovum.

Holotype: SAM–A13466, male, 2,5 mm.

Type-locality: 34°12′S/18°37′E, 15 May 1961, depth 48 m, substrate khaki sand and shell.

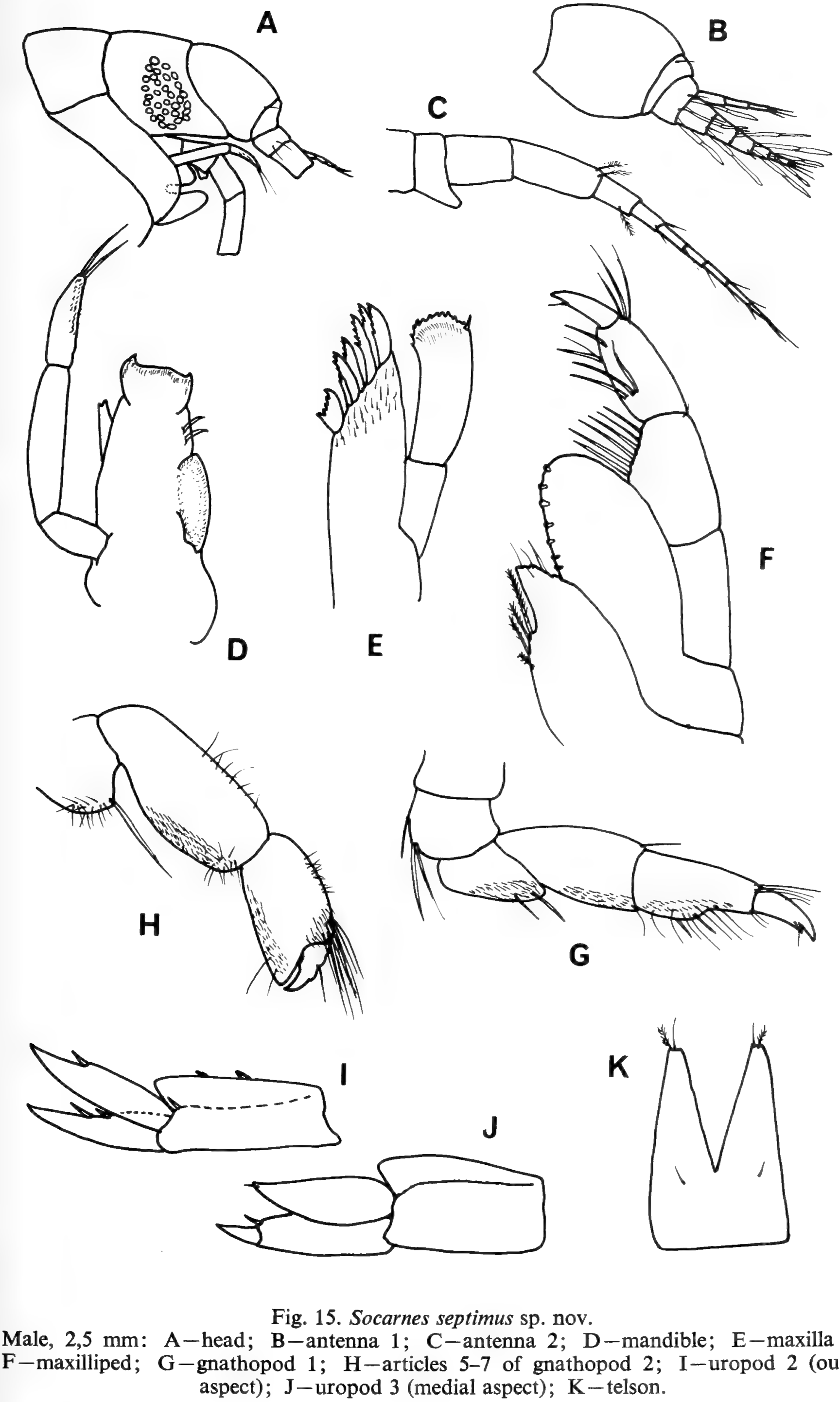

Fig. 15. *Socarnes septimus* sp. nov.
Male, 2,5 mm: A—head; B—antenna 1; C—antenna 2; D—mandible; E—maxilla 1; F—maxilliped; G—gnathopod 1; H—articles 5–7 of gnathopod 2; I—uropod 2 (outer aspect); J—uropod 3 (medial aspect); K—telson.

Relationships: The minute size of this species alone distinguishes it from most other members of the genus. In addition the rounded third pleonal epimeron differs from those of *Socarnes unidentatus* Schellenberg and *S. bidentata* (Bate). *S. dissimulantia* Imbach lacks eyes, while other members of the genus have considerably more slender and longer first antenna than *S. septimus* sp. nov.

Material: 34/18/FB/T, O, fairly common.

Socarnopsis crenulata Chevreux, 1910

Socarnopsis crenulata: K. H. Barnard, 1916: 124. Chevreux & Fage, 1925: 49, figs 31–32.

Records: 33/17/O, 34/18/FB/O, a few records.

Distribution: Mediterranean, Atlantic, South Africa.

Stomacontion capense K. H. Barnard, 1916

Stomacontion capense K. H. Barnard, 1916: 109, pl. 28 (figs 27–28); 1937: 140, fig. 1.

Records: 32/17/D, 34/18/FB/O, two records.

Diagnosis: Head almost entirely obscured by triangular coxa 1; gnathopod 1 slender, simple, dactyl minute; dactyl of gnathopod 2 inserted at middle of distal margin of article 6; article 2 of pereiopod 5 greatly lobed posteriorly, lobe extending to tip of article 5 and postero-distally rectangular; pleon segment 4 with rounded dorsal protuberance; uropod 3 without rami or rami vestigial.

Distribution: Endemic, False Bay to Lambert's Bay.

Stomacontion prionoplax Monod, 1937

Stomacontion prionoplax Monod, 1937: 6, figs 1–6. Griffiths, 1974*c*: 313, fig. 15.

Records: 34/18/FB/O, a single record.

Distribution: Suez Canal, South Africa.

Trischizostoma paucispinosum K. H. Barnard, 1916

Trischizostoma paucispinosum K. H. Barnard, 1916: 107, pl. 26 (fig. 1).

Records: 34/18/D, two records.

Diagnosis: Rostrum inconspicuous; coxa 1 almost completely concealed by 2; gnathopod 1 powerful, article 6 truncated oval, palm subequal to hind margin, sparsely spinose, dactyl smooth, slightly exceeding palm, articles 4 and 5 of pereiopods 3–5 slender; telson 50% cleft.

Distribution: Endemic to deep waters off the Cape Peninsula.

Trischizostoma remipes Stebbing, 1908

Trischizostoma remipes Stebbing, 1908*b*: 61, pl. 34. K. H. Barnard, 1925: 321.

Records: 30/16/D to 34/18/FB/O, fairly common.

Distribution: Endemic, Natal to Hondeklip Bay.

Trischizostoma serratum K. H. Barnard, 1925

Trischizostoma serratum K. H. Barnard, 1925: 320, pl. 34 (fig. 1).

Records: 34/18/FB/T.

Distribution: Endemic, Natal to False Bay.

Uristes sulcus Griffiths, 1974

Uristes sulcus Griffiths, 1974*c*: 315; fig. 16.

Records: 34/18/FB/O, a few records.

Distribution: Endemic, Plettenberg Bay to False Bay.

Family **Ochlesidae**

Ochlesis lenticulosus K. H. Barnard, 1940

Ochlesis lenticulosus K. H. Barnard, 1940: 447, fig. 23.

Records: 34/18/FB/T, O, a few records.

Distribution: Endemic, Natal to False Bay.

Family **Oedicerotidae**

Halicreion ovalitelson K. H. Barnard, 1916

Halicreion ovalitelson K. H. Barnard, 1916: 165, pl. 27 (fig. 4).

Records: 34/18/VD, a single record.

Diagnosis: Rostrum extending to apex of article 1 of antenna 1; eyes absent; article 5 of gnathopods 1 and 2 produced posteriorly into a lobe guarding posterior margin of article 6; uropod 2 extending only to tip of peduncle of uropod 3; telson elongate-oval; entire.

Distribution: Endemic, the above record is the only one to date.

Monoculodopsis longimana Ledoyer, 1973

Monoculodopsis longimana Ledoyer, 1973: 79, figs 22–24.

Records: 32/18/T, O to 34/18/FB/T, O, numerous records.

Diagnosis: Primary cutting edge of mandible projecting, toothed, molar represented by a small hump bearing a few spines; inner lobes of lower lip separate; gnathopods dissimilar, both wide posterior lobe of article 5 fully guarding posterior margin of article 6; article 6 of gnathopod 1 broad, expanding distally, palm as long as hind margin, evenly convex, defined by a single spine; article 6 of gnathopod 2 four times as long as broad, palm oblique, convex, defined by a small spine; uropod 2 reaching apex of uropod 3; telson apically emarginate.

Distribution: Madagascar, South Africa.

Remarks: This species has not previously been recorded from South Africa. The above specimens differ from these of Ledoyer (1973) only in that the mandibular molar is represented by four spines rather than two (gnathopods 1 and 2 are transposed in Ledoyer's figure 22).

Oediceroides cinderella Stebbing, 1888

Oediceroides cinderella Stebbing, 1888: 850, pls 62–63.

Records: 32/18/T, 32/16/D, two records.

Diagnosis: Eyes present; rostrum not strongly deflexed, tapering evenly to an acute point just beyond tip of article 1 of antenna 1; gnathopods similar, article 5 about half length of 6, produced posteriorly as a rounded lobe projecting at right angles, not protecting posterior margin of article 6, palm oblique, convex.

Distribution: Falkland Islands, west coast of South Africa.

Perioculodes longimanus (Bate & Westwood, 1868)

Perioculodes longimanus: Chevreux & Fage, 1925: 162, figs 163–164. Ledoyer, 1972*b*: 775–781, figs 2–3.

Records: 32/18/T, O, 32/17/D to 34/18/FB/T, O, abundant.

Distribution: Mediterranean, Atlantic, Indian Ocean.

Perioculodes pallidus sp. nov.

Fig. 16

Description of female (2,5 mm): Head about as long as two pereon segments, rostrum extending to apex of article 1 of antenna 1, eyes absent; antenna 1 about 30% length of pereon, articles 1–3 subequal, flagellum 4-articulate; accessory flagellum absent; antenna 2 marginally longer than 1, flagellum 4-articulate; mandible (Fig. 16B) with incisor not strongly toothed, molar represented by a spinose hump, palp 3-articulate, article 2 the longest, article 3 with three strong terminal setae; lower lip without inner lobes; maxilla 1 (Fig. 16C) with bi-articulate palp terminally bearing six setae, outer plate with seven strong apical spines; inner plate of maxilla 2 with four setae, outer plate with six (Fig. 16D); inner plate of maxilliped with two long apical setae, outer plate reaching to centre of article 2 of 4-articulate palp.

Coxae 1–4 successively larger, 4 with a strong seta at postero-distal corner; gnathopods subchelate, similar, article 5 posteriorly guarding article 6; article 6 of gnathopod 1 (Fig. 16F) shorter and stouter than that of gnathopod 2 (Fig. 16G), palm defined by a small spine and with submarginal rows of minute setae, dactyl slightly exceeding palm, constricted just before apex, pereiopods 1 and 2 strongly setose, dactyl small (Fig. 16H), surrounded by setae; pereiopod 3 much smaller than 4, article 2 as wide as long, 5 with two strong anterior spines; article 2 of pereiopod 4 (Fig. 16I) strongly lobed posteriorly, anteriorly and

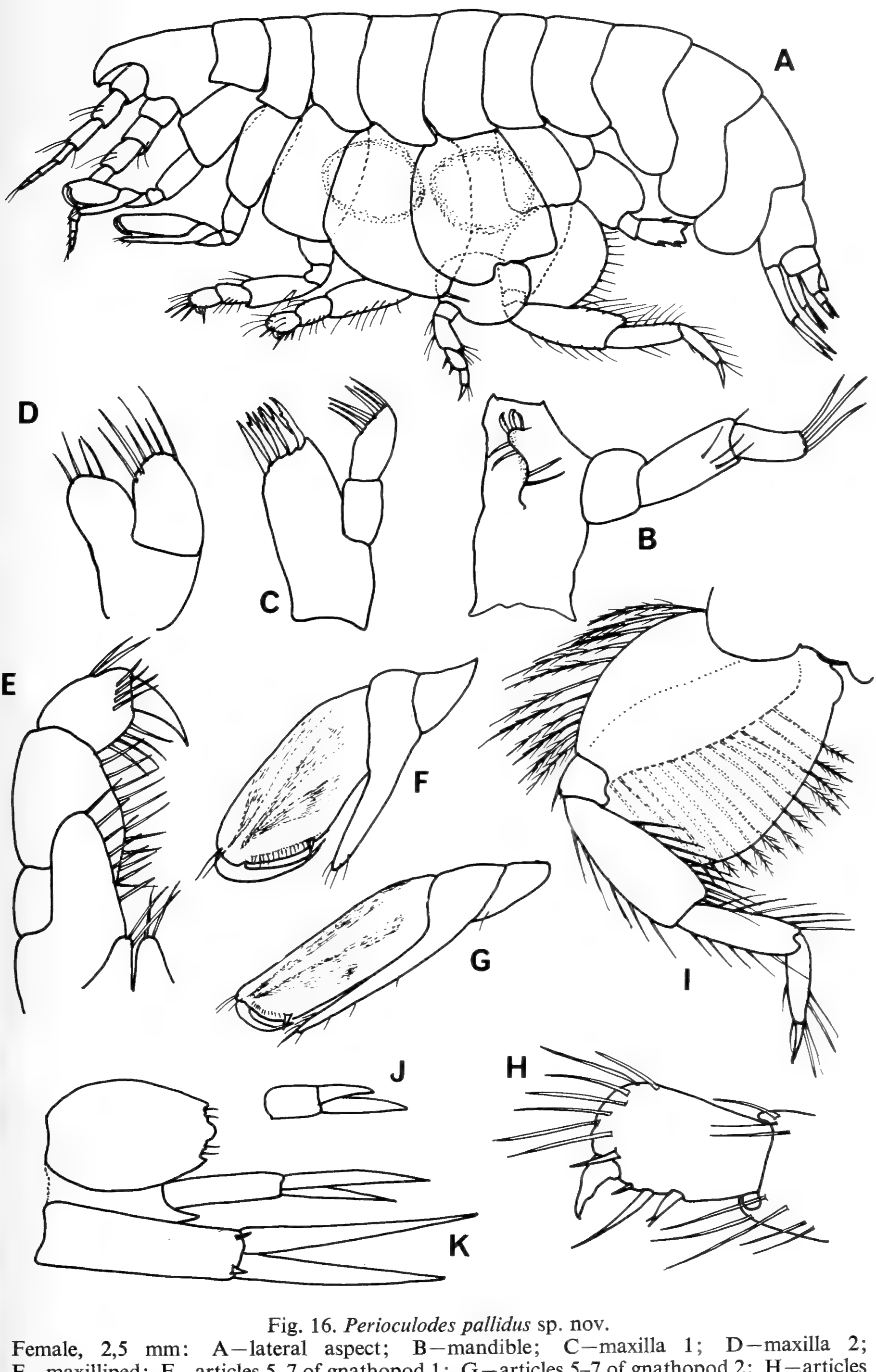

Fig. 16. *Perioculodes pallidus* sp. nov.
Female, 2,5 mm: A—lateral aspect; B—mandible; C—maxilla 1; D—maxilla 2; E—maxilliped; F—articles 5–7 of gnathopod 1; G—articles 5–7 of gnathopod 2; H—articles 6 and 7 of pereiopod 1; I—pereiopod 4; J—uropod 3. Male, 2,5 mm: K—uropods 2 and 3 and telson.

medially strongly setose, articles 4–6 strongly setose on both margins; articles 5–7 of pereiopod 5 missing but articles 2–4 much smaller than those of pereiopod 4.

Pleonal epimera 1–3 smoothly rounded; uropod 1 extending beyond 2 and 3, rami smooth, lanceolate; uropod 2 slightly exceeding 3, peduncle with two small distal spines, rami smooth; uropod 3 very short, outer ramus 60% length of inner, both smooth (Fig. 16J); telson entire, with two small apical concavities, each containing two setae, on either side of a small medial bump.

Male: Flagellum of antenna 1 hirsute; flagellum of antenna 2 7-articulate, palm of gnathopod 2 transverse; article 2 of pereiopods 3 and 4 not as strongly lobed as in ♀; uropod 3 considerably longer (Fig. 16K) than that of ♀.

Holotype: SAM–A13232, ovigerous female, 2,5 mm.

Type-locality: 34°13′S/18°31′E, 22 May 1961, depth 39 m, substrate sand.

Relationships: Perioculodes pallidus sp. nov. differs from other members of the genus by reason of its large coxae, reduced third (and fifth?) pereiopods, short antennae in both sexes and naked uropods.

Remarks: The most notable feature of the holotype is the small size of the proximal articles of pereiopod 5, indicating a probable total length considerably less than that of pereiopod 4. This would be in conflict with the normal condition in the genus, or indeed the family Oedicerotidae, which characteristically has pereiopod 5 larger than 4. However, pereiopod 5 was found only on one side of one of the individuals collected, being lost in all other cases—a characteristic often associated with great length. Thus, until the condition of pereiopod 5 is verified by undamaged specimens, I have placed this species in the genus *Perioculodes* on the basis of other characters, particularly the structure of the gnathopods which in the ♀ are practically identical with those of *P. aequimanus* (Kossmann). Should the reduced condition of pereiopod 5 be confirmed by further material this would be strong evidence for the creation of a new genus.

Material: 34/18/O, two records.

Synchelidium tenuimanus Norman, 1871

Synchelidium tenuimanus: Oldevig, 1933: 131, fig. 2.

Records: 34/18/FB/D, 34/18/D, a few records.

Diagnosis: Rostrum strong, reaching almost to apex of article 1 of antenna 1; eyes of moderate size; gnathopod 2 extremely slender and elongate, the chela occupying only about 15% of its length.

Distribution: Atlantic, South Africa.

Westwoodilla manta Griffiths, 1974

Westwoodilla manta Griffiths, 1974*c*: 318, fig. 17.

Records: 31/18/O, D to 34/18/FB/D, fairly common.

Distribution: Endemic, Plettenberg Bay to Lambert's Bay.

Family **Paramphithoidae**

Epimeria longispinosa K. H. Barnard, 1916

Epimeria longispinosa K. H. Barnard, 1916: 172, pl. 27 (fig. 6).

Records: 34/18/D–VD, a single record.

Diagnosis: Pereon dorsally smooth; coxae 1–3 acutely pointed below, 4 crescent-shaped, much longer than 3, 5 postero-distally produced into a narrow spiniform process which extends to end of pleon segment 1; pleon segments 1–4 feebly carinate, carinae on segments 2–4 posteriorly toothed; pleonal epimera quadrate, without accessory teeth.

Distribution: Endemic, the above record is the only one to date.

Epimeria semiarmata K. H. Barnard, 1916

Epimeria semiarmata K. H. Barnard, 1916: 171, pl. 27 (fig. 3).

Records: 34/18/D, a single record.

Diagnosis: Pereon segments dorsally smooth; coxae 1–3 acutely pointed below, 4 somewhat longer than 3, 5 pentagonal, not postero-distally produced; pleon segments 1 and 2 dorsally smooth, 3 with a faint carina ending in a minute tooth, 4 depressed basally, distally humped; pleonal epimera 2 and 3 slightly produced postero-distally, lacking accessory teeth.

Distribution: Endemic to deep waters off the Cape Peninsula.

Family **Pardaliscidae**

Halice anacantha K. H. Barnard, 1925

Halice anacantha K. H. Barnard, 1925: 347, pl. 34 (fig. 12)
Pardisynopia anacantha: J. L. Barnard, 1969: 400. Griffiths, 1974*c*: 320.
Halice anacantha: Karaman 1974: 13.

Records: 32/17/D, 34/18/D, a few records.

Distribution: Endemic, Plettenberg Bay to Lambert's Bay.

Remarks: In revising the family Pardaliscidae Karaman (1974) has amalgamated *Pardisynopia* with *Halice* on the basis that component species can no longer be separated into discreet groups, but provide a full range of variability between the two previous generic definitions.

Family **Phoxocephalidae**

Heterophoxus cephalodens sp. nov.

Fig. 17

Description of female (3,5 mm): Head (Fig. 17A) as long as first three pereon segments, rostrum medio-dorsally keeled, lateral margins with small cornified ridges, apex acute, reaching beyond apex of article 3 of antenna 1, lower corner of head produced into a strong acute tooth, eyes small, composed of 4–5 individual ocelli; antenna 1 (Fig. 17B) with 7-articulate flagellum, accessory flagellum 6-articulate; antenna 2 (Fig. 17C) with basal ensiform process, flagellum 7-articulate; mandibular incisor strongly toothed, spine row of seven spines, molar represented by a small process bearing two serrate spines, palp elongate, article 2 with three distal setae, article 3 as long as 2, falciform, bearing nine apical setae; maxilla 1 with bi-articulate palp exceeding outer plate; article 4 of maxillipedal palp (Fig. 17D) with two small marginal setae and one long terminal seta.

Gnathopods 1 and 2 subequal, subchelate, palm oblique, defined by a distinct step; pereiopods 1 and 2 normal; coxae 1–4 distally setose, coxa 4 excavate posteriorly; article 2 of pereiopod 3 (Fig. 17E) slender, hardly wider than article 3, articles 4–6 lined on both margins with plumose setae, article 7 spiniform; pereiopod 4 larger than 3 or 5; pereiopod 5 (Fig. 17F) with article 2 postero-distally produced to tip of article 4, posterior margin cut into about seven teeth, a minute seta in each notch; antero-distal corner of article 2 with four long plumose setae, articles 3 and 4 each with two plumose setae anteriorly.

First pleonal epimeron (Fig. 17G) minutely produced postero-distally, second with five distal setae, postero-distal corner subacute; third pleonal epimeron with an oblique row of setae leading to a small seta-bearing notch above rounded postero-distal corner; uropods 1–3 extending about equally; uropod 1 (Fig. 17H) with outer ramus spiniform, 60% length of inner, inner ramus with six dorsal and two apical spines; uropod 2 (Fig. 17I) with outer margin of peduncle dorsally keeled, bearing six dorsal spines, rami equal, outer with eight dorsal and two terminal spines, inner with three dorsal and two terminal spines; peduncle of uropod 3 (Fig. 17J) ventrally spinose, outer ramus with second article 25% length of first and terminating in two plumose setae, inner ramus as long as article 1 of outer; telson (Fig. 17K) short, extending only to tip of peduncle of uropod 3, 80% cleft, each lobe bearing two small brush setae and a minute subapical spine.

Holotype: SAM–A13468, ovigerous female, 3,5 mm.

Type-locality: 34°19′S/18°29′E, 13 July 1967, depth 51 m, substrate khaki sand.

Relationship: The reduced spiniform outer ramus of uropod 2 distinguishes this species from other members of the genus. The produced post-antennal corner of the head is unusual, being shared only by *H. opus* sp. nov. (below).

Material: 34/18/FB/O, 32/18/T, D, VD, a few records.

Heterophoxus opus sp. nov.

Fig. 18

Description of female (4 mm): Head as long as first two pereon segments, rostrum dorsally smooth, apically rounded, extending to apex of article 3 of antenna 1, post-antennal corner of head acutely produced (Fig. 18A), eyes

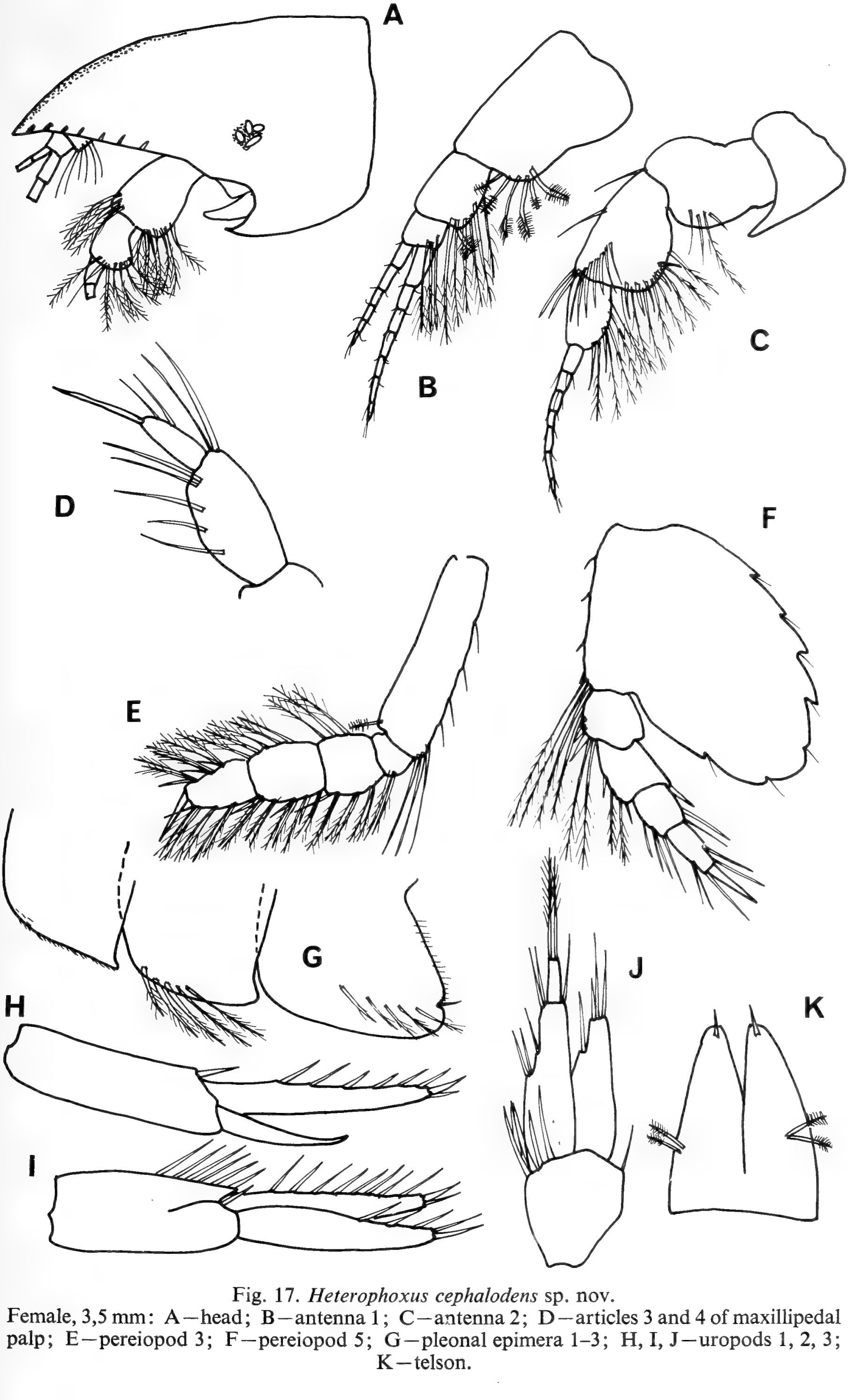

Fig. 17. *Heterophoxus cephalodens* sp. nov.
Female, 3,5 mm: A—head; B—antenna 1; C—antenna 2; D—articles 3 and 4 of maxillipedal palp; E—pereiopod 3; F—pereiopod 5; G—pleonal epimera 1–3; H, I, J—uropods 1, 2, 3; K—telson.

composed of about eight individual ocelli; article 1 of antenna 1 (Fig. 18B) with four posterior brush setae, articles 2 and 3 much smaller than 1, flagellum 6-articulate, accessory flagellum 4-articulate; antenna 2 (Fig. 18C) with ensiform process, flagellum 7-articulate; mandibular incisor with distinct teeth, spine row of eight spines, molar represented by a process bearing two serrate spines, article 2 of palp naked, article 3 with three terminal setae; maxilla 1 (Fig. 18D) with bi-articulate palp terminating in seven spines, outer plate with eleven apical spines, inner plate with three simple setae and one brush seta; article 4 of maxillipedal palp (Fig. 18E) with two small lateral setae and one strong terminal seta.

Gnathopods subchelate, palm oblique, defined by a small lobe, gnathopod 2 slightly the larger; pereiopods 1 and 2 normal; coxae 1–4 ventrally setose; pereiopod 3 (Fig. 18F) with article 2 hardly wider than 3, articles 4–6 setose, 4 and 5 with a long postero-distal plumosa seta; pereiopod 4 longer than 3 or 5, dactyl elongate, spiniform; pereiopod 5 (Fig. 18G) with article 2 greatly expanded posteriorly, distally produced to middle of article 4, posterior margin with 11 minute serrations each bearing a setule, antero-distal corner of article 2 with a single plumose seta, articles 3 and 4 without plumose setae.

First pleonal epimeron with two distal plumose setae, postero-distally quadrate, second pleonal epimeron with four distal setae, postero-distally quadrate; third pleonal epimeron (Fig. 18H) with two distal spines, postero-distally rounded with two minute setulose notches on posterior margin; uropod 1 slightly exceeding 2, peduncle with four dorsal spines, rami subequal (Fig. 18I), outer with three dorsal spines, inner dorsally smooth; uropod 2 (Fig. 18J) with six dorsal and one terminal peduncular spines, rami subequal, outer with four dorsal spines, inner dorsally smooth; uropod 3 (Fig. 18K) with peduncle apically spinose, outer ramus with article 2 50% length of 1, bearing a long apical spine, inner ramus 80% length of outer, naked; telson (Fig. 18L) short, 80% cleft, each lobe with a dorsal brush seta, and small apical spine.

Holotype: SAM–A13469, female, 3,5 mm.

Type-locality: 34°18′S/18°29′E, 13 July 1967, depth 51 m, substrate khaki sand.

Relationships: Because of its eyes this species falls into the genus *Heterophoxus*, although the third uropods are more closely allied to those of *Harpinia*, which is an eyeless genus as presently defined. However, recent findings indicate that the presence or absence of eyes is a dubious generic character, since species possessing both oculate and anoculate forms have recently been described. If eyes were to be disregarded as generic characters a considerable revision of the group would be required, a task I am not in a position to carry out. I have thus allocated this species to *Heterophoxus* provisionally so as to at least maintain the *status quo*.

Heterophoxus opus sp. nov. may be distinguished from *H. cephalodens* sp. nov. by the rami of uropod 1, which are subequal, and from other species in the genus by the produced post-antennal corner of the head.

Material: 34/18/FB/O, two records.

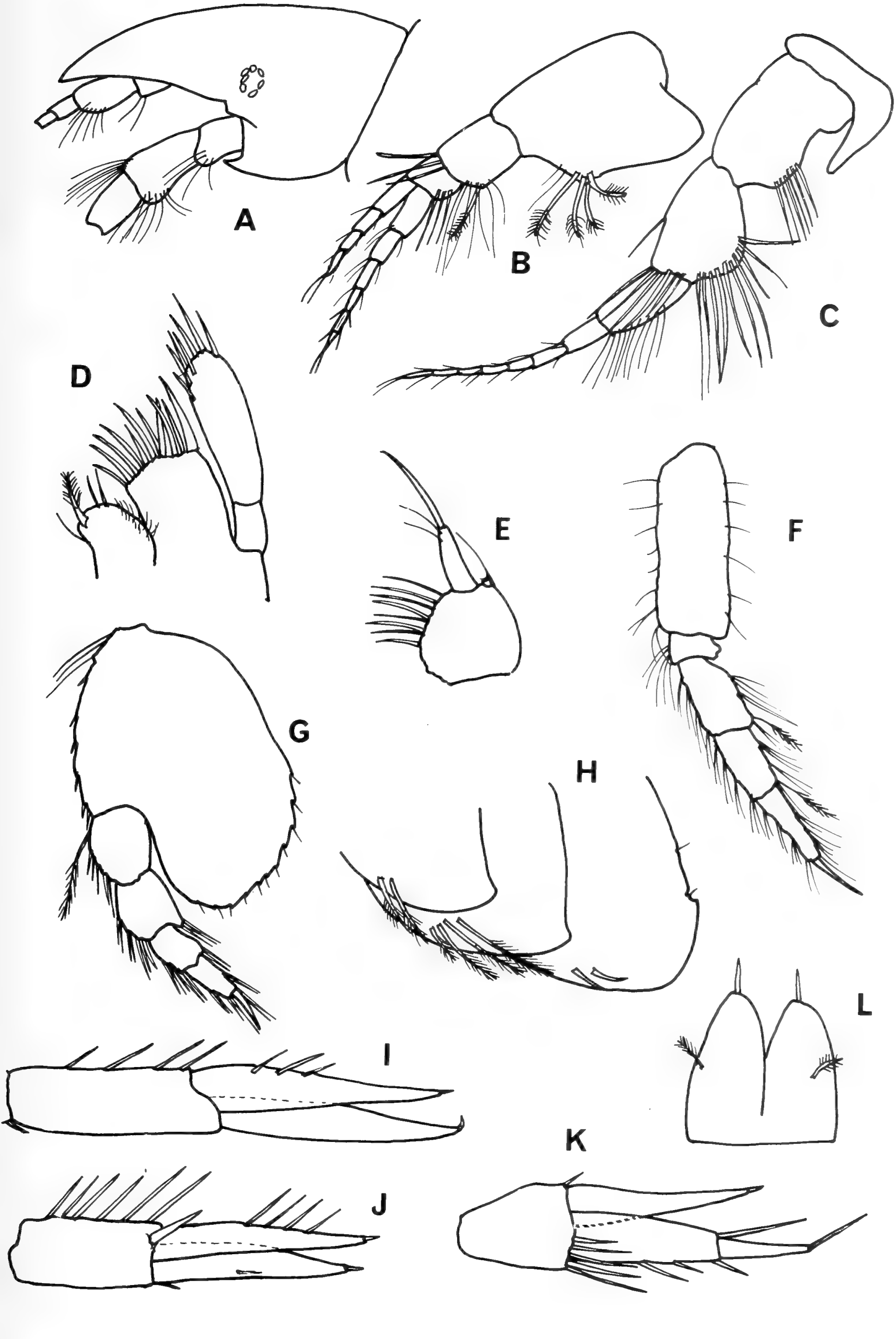

Fig. 18. *Heterophoxus opus* sp. nov.
Female, 4 mm: A—head; B—antenna 1; C—antenna 2; D—maxilla 1; E—articles 3 and 4 of maxillipedal palp; F—pereiopod 3; G—pereiopod 5; H—pleonal epimera 1–3; I, J, K—uropods 1, 2, 3; L—telson.

Mandibulophoxus stimpsoni (Stebbing, 1908)

Pontharpinia stimpsoni Stebbing, 1908*b*: 75, pl. 11.
Mandibulophoxus stimpsoni: J. L. Barnard, 1957: 436, figs 3–4.

Records: 32/18/T, 34/18/FB/T, O, D, abundant in False Bay but uncommon elsewhere.

Distribution: West and South Africa.

Paraphoxus oculatus Sars, 1891

Paraphoxus oculatus: J. L. Barnard, 1960: 240–243, pls 27–28.

Records: 32/17/D, 32/16/D, VD to 34/18/FB/T, O, 34/18/D, numerous records.

Distribution: Circumboreal.

Platyischnopus herdmani Walker, 1904

Platyischnopus capensis K. H. Barnard, 1925: 338, pl. 34 (figs 13–14).
Platyischnopus herdmani: Rabindranath, 1971*a*: 521, figs 1–2.

Records: 32/18/T to 34/18/FB/T, O, numerous records.

Distribution: India, South Africa.

Pseudharpinia excavata (Chevreux, 1887)

Harpinia excavata: K. H. Barnard, 1925: 340. J. L. Barnard, 1962*c*: 47, figs 37–38.

Records: 32/17/D to 34/18/FB/O, 34/18/D, a few records.

Diagnosis: Head with small post-antennal tooth, eyes absent; article 2 of pereiopod 5 with several antero-distal setae, posterior margin with 10 small serrations; third pleonal epimeron with small postero-distal tooth.

Distribution: Atlantic, Pacific.

Family **Podoceridae**

Laetmatophilus purus Stebbing, 1888

Laetmatophilus purus Stebbing, 1888: 1198, pl. 132.

Records: 32/18/O, 32/16/D to 34/18/FB/T, O, 34/18/D, numerous records.

Distribution: Endemic, Moçambique to South West Africa.

Laetmatophilus tridens K. H. Barnard, 1916

Laetmatophilus tridens K. H. Barnard, 1916: 275, pl. 28 (fig. 22).

Records: 33/18/I, 34/18/FB/T, O, a few records.

Distribution: Endemic, Moçambique to Saldanha Bay.

Podocerus africanus K. H. Barnard, 1916

Podocerus africanus K. H. Barnard, 1916: 278, pl. 28 (figs 24–25); 1937: 176, fig. 19.

Records: 33/17/T, 34/18/T, 34/18/FB/I, T, O, a few records.

Distribution: Arabia, Natal to South West Africa.

Podocerus inconspicuus (Stebbing, 1888) *new synonymy*

Podocerus palinuri K. H. Barnard, 1916: 277, pl. 28 (fig. 23).
Podocerus cristatus (*non* Thompson, 1879): K. H. Barnard, 1916: 276. Griffiths, 1973: 298; 1974*a*: 202; 1974*c*: 323.

Records: 29/16/I, 31/16/D to 34/18/FB/T, O, 34/18/O, D, numerous records.

Distribution: Indian Ocean, west coast of South Africa.

Remarks: K. H. Barnard (1916, 1940) and Griffiths (1973, 1974*a*, *c*) have previously recognized two South African species—*Podocerus inconspicuus* (= *palinuri*) and '*P. cristatus*'—distinguishing them on the basis of degree of dorsal carination. As more material has been collected, however, it has become obvious that the two forms represent the extremes of a continuous range of variation. All previous records of these two forms have thus been combined under the name *P. inconspicuus*. This form is probably not synonymous with the original *P. cristatus* of Thompson, which lacks a defining tooth on the palm of gnathopod 2 ♂, a feature present in all southern African specimens. *P. inconspicuus* has now been recorded in every condition from totally lacking dorsal carinae (Stebbing 1888), through various intergrades (e.g. Pirlot 1938) to fully carinate (Barnard 1916—as *P. palinuri*).

P. inconspicuus should be rediagnosed as follows: Body showing variable carination, carinae at first developing on pereon segments 6 and 7 and progressing forwards until in adult specimens the head has a low rounded keel and all pereon segments show distinct carinae, these being largest on pereon segments 5–7 and on pleon segments 1 and 2, small subdorsal processes may also develop on the posterior pereon segments; palm of gnathopod 1 ♂ oblique, dactyl serrate; palm of gnathopod 2 ♂ defined by a small lobe and with two strong distal teeth; palm of gnathopod 1 ♀ transverse, minutely serrate; palm of gnathopod 2 ♀ defined by a small lobe and with two small distal teeth; uropods moderately spinose; telson with 6–8 dorsal spine setae.

P. inconspicuus may be distinguished from *P. hystrix* Stebbing and *P. danae* Stebbing by the presence of a defining lobe on the palm of gnathopod 2 and the absence of a strong upstanding head process.

Podocerus multispinis K. H. Barnard, 1925

Podocerus multispinis K. H. Barnard, 1925: 367, pl. 34 (fig. 18).

Records: 33/17/O, 34/18/O, 34/18/FB/O, a few records.

Distribution: Endemic, Natal to Saldanha Bay.

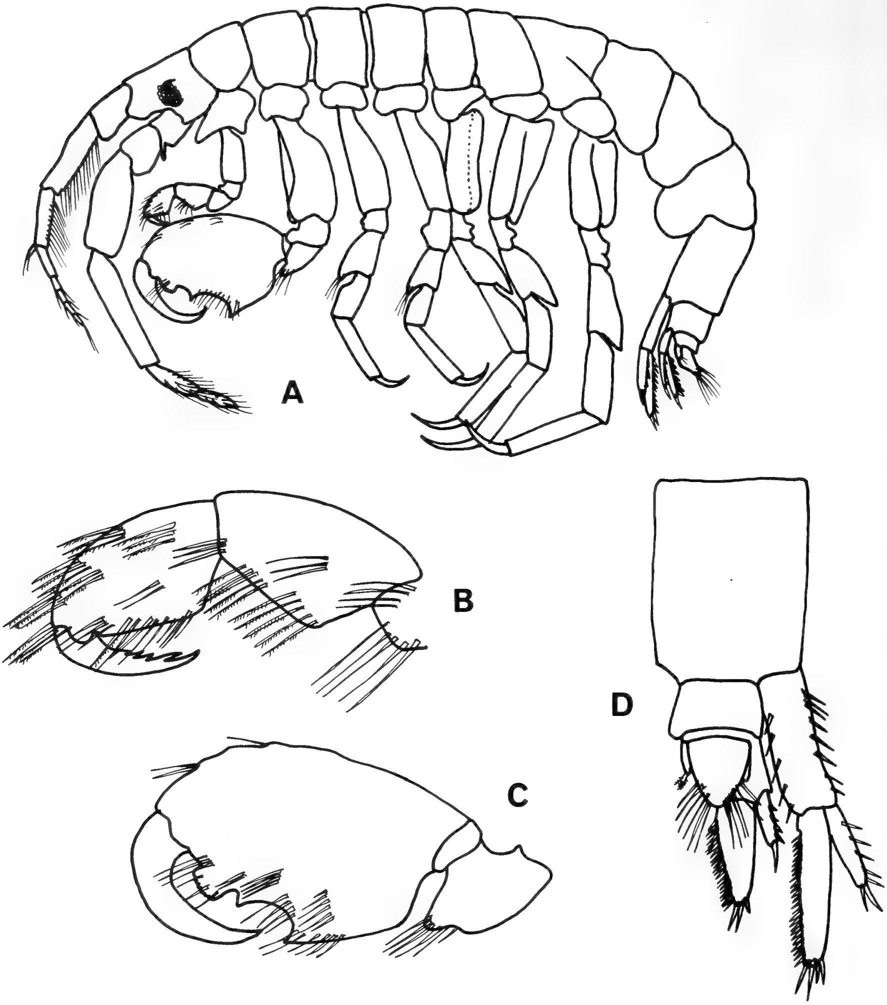

Fig. 19. *Podocerus pyurae* sp. nov.
Male, 7 mm: A—lateral aspect; B—articles 5–7 of gnathopod 1; C—articles 4–7 of gnathopod 2; D—urosome (dorsal aspect).

Podocerus pyurae sp. nov.

Fig. 19

Description of male (7 mm): Body without dorsal carinae, tubercles or spines; head slightly longer than first pereon segment, eyes round, red, not reaching margin of head; antenna 1 shorter than peduncle of 2, articles 1 and 3 of peduncle subequal, slightly shorter than 2, flagellum 5-articulate, accessory flagellum of a single article; antenna 2 considerably stouter than 1, article 5 longer than 4, flagellum of two large articles and one small article.

Coxa 1 antero-distally produced forwards, following coxae subquadrate; gnathopod 1 (Fig. 19B) subchelate, articles 5 and 6 subequal, palm oblique, undefined, dactyl cut into several strong teeth; gnathopod 2 powerfully subchelate (Fig. 19C), article 2 anteriorly keeled, not strongly lobed distally, article 4 not strongly produced distally, hind margin of article 6 almost as long as palm, palm oblique, defined by a strong tooth and with a smaller triangular tooth distally and then a strong rectangular castellate process near finger-hinge, dactyl strongly curved, subequal to palm; pereiopods 1–2 considerably shorter than 3–5, article 2 four times as long as wide, 4 somewhat produced antero-distally, 6 longer than 5, dactyl large; article 2 of pereiopods 3–5 posteriorly keeled, keel external on pereiopod 3, medial on pereiopods 4 and 5, article 4 somewhat produced postero-distally.

Pleonal epimera 1–3 postero-distally rounded; uropod 1 (Fig. 19D) much longer than 2, peduncle with two dorsal rows of slender spines, outer ramus 60% length of inner and considerably narrow than it, with five dorsal and two terminal spines, inner ramus with a comb-like row of close-set slender spines dorsally and four larger spines apically; uropod 2 similar to 1 but considerably shorter and with fewer spines; uropod 3 consisting of a small lobe with two minute terminal setae; telson with about six distal setae on each margin.

Female: Indistinguishable from the male except for the presence of brood plates.

Holotype: SAM–A13480, male, 7 mm.

Type-locality: Branchial cavity of ascidian (*Pyura stolonifera*) collected intertidally at Kalk Bay, on the shores of False Bay, by Miss R. J. Imrie, 10 December 1973.

Relationships: This species has close affinities with *P. hanapepe* J. L. Barnard, *P. mangarevae* Chevreux and *P. zeylanica* Walker but differs from all these species in possessing comb-like rows of spines on the dorsal surfaces of the inner rami of uropods 1 and 2.

Material: Seven specimens from the type-locality.

Family **Sebidae**

Seba saundersi Stebbing, 1875

Fig. 20

Paravalettia chelata K. H. Barnard, 1916: 112, pl. 26 (figs 2–3).
Seba saundersii: K. H. Barnard, 1957: 7, fig. 4.

Records: 33/18/I, 34/18/FB/O, a few records.

Diagnosis: Gnathopod 1 developing from chelate and lacking in palmer teeth, through subchelate with palm transverse and moderately toothed to subchelate with palm oblique and strongly toothed; article 5 of gnathopod 2 shorter than 6; article 2 of pereiopods 4 and 5 subcircular, article 4 weakly expanded in juveniles, greatly expanded and strongly produced postero-distally in adults; pleonal epimera postero-distally with a small tooth.

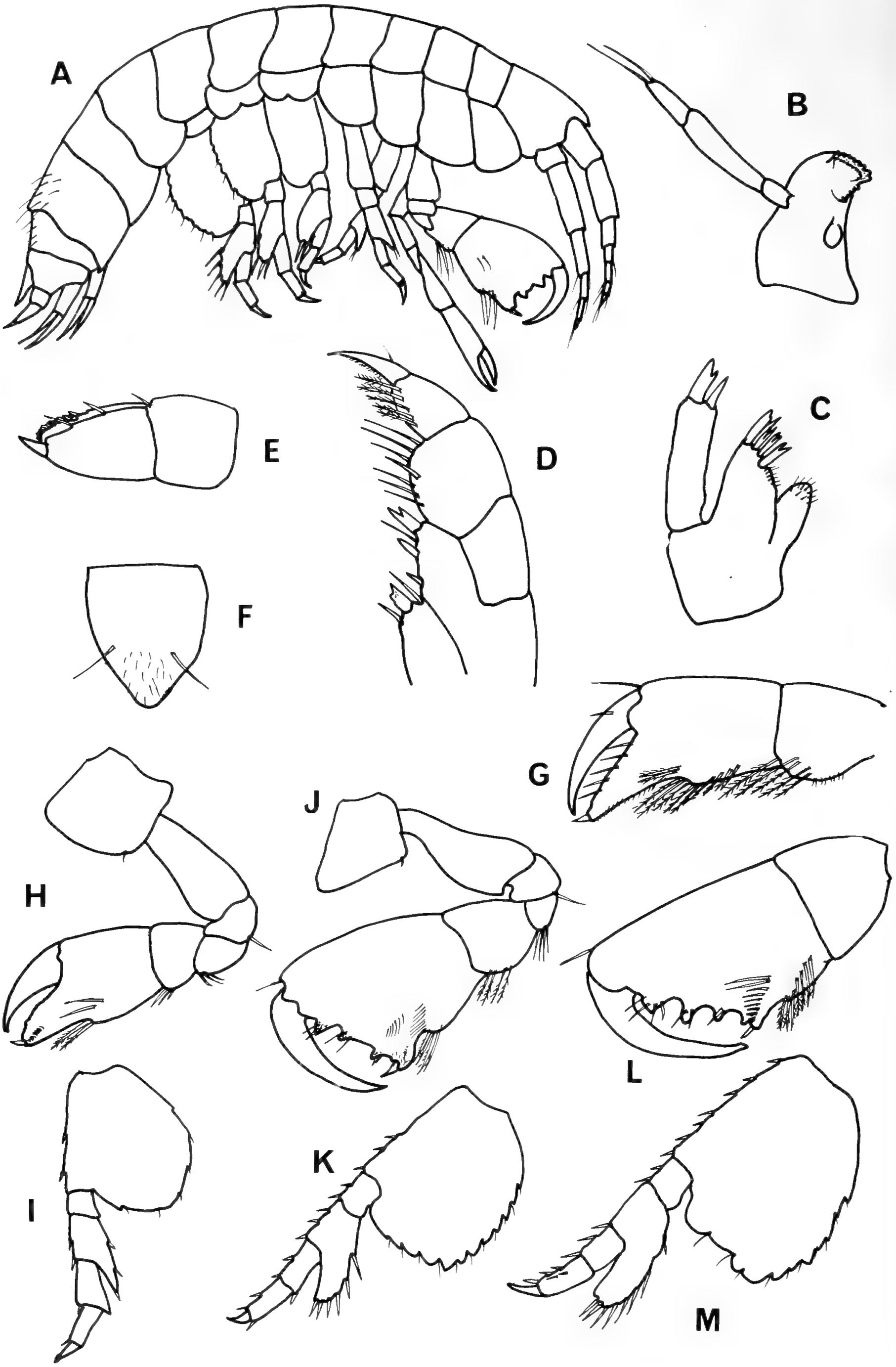

Fig. 20. *Seba saundersi* Stebbing, 1888
Male, 2,5 mm: A—lateral aspect; B—mandible; C—maxilla 1; D—maxilliped; E—uropod 3; F—telson. Female, 2 mm: G—gnathopod 1. Male, 1,4 mm: H—gnathopod 1; I—pereiopod 5. Male, 2,4 mm: J—gnathopod 1; K—pereiopod 5. Male, 3,0 mm: L—gnathopod 1; M—pereiopod 5.

Distribution: Southern Atlantic.

Remarks: The current material includes a sample of 24 individuals from a single station and this opportunity has been utilized to provide figures of growth stages (Fig. 20). The variability of the structure of gnathopod 1 and of pereiopod 5 is remarkable and, as these characters are often used for identification, it seems likely that when developmental stages of other species are known a revision of the genus will become necessary.

Family **Stegocephalidae**

Stegocephaloides attingens K. H. Barnard, 1916

Stegocephaloides attingens K. H. Barnard, 1916: 131, pl. 26 (fig. 5). J. L. Barnard, 1961: 60, fig. 29.

Records: 34/18/VD, two records.

Diagnosis: First pereon segment tumid; eyes absent; coxae very large, forming a continuous shield; coxa 4 with inferior margin very short, evenly curved; article 2 of pereiopod 5 apically acute, reaching to apex of article 5, hind margin weakly serrate; third pleonal epimeron postero-distally subquadrate.

Distribution: Angola to Cape Point.

Stegocephaloides australis K. H. Barnard, 1916

Stegocephaloides australis K. H. Barnard, 1916: 129, pl. 28 (fig. 29).

Records: 32/18/O to 34/18/FB/O, 34/18/D, VD, a few records.

Distribution: Endemic, Plettenberg Bay to Lambert's Bay.

Family **Stenothoidae**

Proboloides rotunda (Stebbing, 1917)

Metopa rotundus Stebbing, 1917: 39, pl. 7A.
Proboloides rotunda: K. H. Barnard, 1940: 444.

Records: 33/17/O, 34/18/D, 34/18/FB/O, fairly common.

Distribution: Endemic, Natal to Saldanha Bay.

Stenothoe adhaerans Stebbing, 1888

Stenothoe adhaerans Stebbing, 1888: 748, pl. 39.

Records: 32/18/T, 33/17/O, 34/18/?, a few records.

Diagnosis: Antennae subequal, half body length; palm of gnathopod 1 defined by five spines, pectinate throughout, dactyl pectinate; gnathopod 2 ♂ fairly large, palm occupying 70% length of hand, defined by two spines and irregularly dentate throughout with one larger tooth near finger-hinge; article 4 of pereiopods 3–5 considerably expanded, postero-distally produced almost to tip of article 5; uropod 3 uniramous, article 2 of ramus straight.

Distribution: Endemic, Cape Agulhas to Lambert's Bay.

Remarks: This species was previously known only from the female.

Stenothoe valida Dana, 1853

Stenothoe valida: J. L. Barnard, 1970*b*: 250, fig. 165.

Records: 32/18/T, 33/17/O, a few records.

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Synopiidae**

Tiron australis Stebbing, 1908

Tiron australis Stebbing, 1908*b*: 79, pl. 38.

Records: 34/18/FB/T, O, 34/19/O, a few records.

Distribution: Endemic, Natal to False Bay.

Superfamily TALITROIDEA

Family **Ceinidae**

Afrochiltonia capensis K. H. Barnard, 1916

Chiltonia capensis K. H. Barnard, 1916: 224, pl. 27 (figs 38–40).
Afrochiltonia capensis: K. H. Barnard, 1955: 93.

Records: 34/18/FB/E to 31/18/E, a few records.

Distribution: Endemic, Kosi Bay to Olifants River, a brack-water species.

Family **Talitridae**

Hyale diastoma K. H. Barnard, 1916

Hyale diastoma K. H. Barnard, 1916: 232, pl. 28 (fig. 8).

Records: 33/18/I, 34/18/FB/I, a few records.

Distribution: False Bay to South West Africa.

Hyale grandicornis (Kröyer, 1845) *new synonymy*

Allorchestes inquirendus K. H. Barnard, 1940: 477, fig. 34b–c. Griffiths, 1974*a*: 202; 1974*c*: 328.
Hyale grandicornis: Hurley, 1957: 904, figs 1–29.

Records: 26/16/I to 34/19/I, numerous records.

Distribution: Cosmopolitan in tropical and temperate seas.

Remarks: Allorchestes inquirendus was erected by K. H. Barnard (1940) solely on the basis of the lobe on article 5 of gnathopod 2 ♂, a feature supposedly absent in the otherwise identical *Hyale grandicornis.* The transitory or variable nature of such processes has, however, been known for some time, thus Hurley (1957) writes: 'Although this diagnostic character is unmistakable in the adult ♂ of *Allorchestes* the generic distinction is slurred over by the development of a similar process in the juveniles of *Hyale*; a process which does not always disappear in the adult males . . . being well exemplified by *Hyale grandicornis*.' Reid (1951) has noted similar changes in *H. perieri* and a continuous range of variation is found amongst *H. grandicornis* from South Africa. *Allorchestes inquirendus* is thus an invalid species and falls to *Hyale grandicornis*.

Hyale hirtipalma (Dana, 1852)

Hyale hirtipalma: K. H. Barnard, 1916: 234. Hurley, 1957: 922, figs 118–146.
Hyale macrodactyla (*non* Stebbing, 1899): K. H. Barnard, 1916: 235.

Records: 29/16/I to 34/18/FB/I, a few records.

Distribution: Pacific, South Atlantic.

Hyale maroubrae Stebbing, 1899

Hyale maroubrae: Hurley, 1957: 913, figs 51–71.

Records: 33/18/I, 34/18/FB/I, a few records.

Distribution: Widespread in Southern hemisphere.

Hyale plumulosa (Stimpson, 1853)

Hyale plumulosa: Bousfield, 1973: 155, pl. 44 (fig. 2).

Records: 34/19/I, a single record.

Diagnosis: Article 1 of antenna 1 not postero-distally lobed; article 5 of antenna 2 and flagellum covered with a dense growth of fine plumose setae; coxae 1–4 with posterior triangular processes; palm of gnathopod 1 transverse; palm of gnathopod 2 ♂ oblique, evenly convex, subequal to hind margin; article 2 of pereiopods 1–5 weakly crenulate posteriorly; uropod 1 with long spine on inner distal margin of peduncle.

Distribution: Atlantic and Pacific coasts of North America, South Africa.

Remarks: The above specimens, the first of this species recorded from Africa, agree perfectly with the description given by Bousfield (1973).

Hyale saldanha Chilton, 1912

Hyale saldanha Chilton, 1912: 509, pl. 2 (figs 24–29).

Records: 29/16/I to 34/19/I, numerous records.

Distribution: Endemic, East London to South West Africa.

Orchestia ancheidos (K. H. Barnard, 1916)

Talorchestia ancheidos K. H. Barnard, 1916: 221, pl. 27 (figs 35–36); 1940: 470, fig. 31. Ruffo, 1947: 121, figs 3–5.
Orchestia ancheidos: Ruffo, 1958: 43, figs 3–4.

Records: 32/18/E to 34/19/E, a few records.

Distribution: Madagascar, southern and West Africa, usually in brack waters.

Orchestia dassenensis (K. H. Barnard, 1916)

Parorchestia dassenensis K. H. Barnard, 1916: 227, pl. 28 (figs 1–2).

Records: 33/18/I, 34/19/I, a few records.

Diagnosis: Antenna 1 almost as long as 2, antenna 2 slender; articles 4–6 of gnathopod 1 ♂ each with a posterior pellucid lobe; articles 2 and 3 of gnathopod 2 ♂ anteriorly lobed, article 6 oval, palm oblique, moderately spinose, a small notch near finger-hinge and another near defining angle, dactyl slightly exceeding palm, inner margin sinuous, tip averted; articles 4 and 5 of pereiopod 5 linear; third pleonal epimeron quadrate with a minute postero-distal tooth; outer ramus of uropod 1 smooth.

Distribution: Endemic, Cape Agulhas to Saldanha Bay.

Orchestia gammarella (Pallas, 1766) *new synonymy*

Orchestia gammarella: Chevreux & Fage, 1925: 274, fig. 284. Bousfield, 1973: 159, pl. 45 (fig. 1)
Talorchestia inaequalipes K. H. Barnard, 1951: 705, fig. 5a–b. Griffiths, 1974*c*: 330.

Records: 33/18/I, a few records.

Diagnosis: Articles 4 and 5 of antenna 2 ♂ not expanded; palm of gnathopod 2 ♂ evenly convex, smooth, subequal to hind margin, dactyl evenly convex, tip not averted, slightly exceeding palm; articles 4 and 5 of pereiopod 5 of adult ♂ strongly expanded, giving limb an oar-like appearance; outer ramus of uropod 1 dorsally spinose.

Distribution: North Atlantic, South Africa.

Remarks: A re-examination of Barnard's types of *Talorchestia inaequalipes* has shown gnathopod 1 ♀ to be distinctly subchelate. This species thus should be transferred to *Orchestia* where it appears to be synonymous with *Orchestia gammarella*.

Orchestia platensis Kröyer, 1845

Orchestia platensis: Bousfield, 1973: 160, pl. 46 (fig. 2).

Records: 34/19/I, two records.

Diagnosis: Articles 4 and 5 of antenna 2 ♂ greatly inflated; palm of gnathopod 2 ♂ convex, oblique, subequal to hind margin, a sharp notch near defining angle followed by a small hump which is prolonged as a ridge running along medial margin of hand, dactyl slightly exceeding palm, tip not averted; articles 4 and 5 of pereiopod 5 ♂ strongly inflated but cylindrical (not oar-like as in *O. gammarella*); outer ramus of uropod 3 smooth.

Distribution: Cosmopolitan in tropical and temperate seas.

Remarks: This species has not previously been recorded from South Africa.

Orchestia rectipalma K. H. Barnard, 1940

Orchestia rectipalma K. H. Barnard, 1940: 473, fig. 32.

Records: 31/18/E to 34/19/E, a few records.

Distribution: Endemic, Natal to South West Africa, a brack-water species.

Talorchestia australis K. H. Barnard, 1916

Talorchestia australis K. H. Barnard, 1916: 220, pl. 27 (figs 33–34); 1940: 470, fig. 30.

Records: 34/19/I, E to 33/18/I, a few records.

Distribution: Endemic, Moçambique to South West Africa.

Talorchestia capensis (Dana, 1853)

Talorchestia capensis: K. H. Barnard, 1916: 216; 1940: 470, fig. 28.

Records: 29/16/I to 34/19/I, a few records.

Distribution: Mediterranean, Atlantic, South Africa.

Talorchestia quadrispinosa K. H. Barnard, 1916

Orchestoidea fischerii (*non* Milne-Edwards, 1826): Stebbing, 1910*a*: 459.
Talorchestia quadrispinosa K. H. Barnard, 1916: 217, pl. 27 (figs 29–32); 1940: 470, fig. 29.

Records: 29/16/I to 34/18/FB/I, the most abundant sandy beach species in this area.

Distribution: Endemic, False Bay to South West Africa.

Family **Temnophliidae** fam. nov.

Diagnosis: Talitroidea with body dorsally depressed, pereon segments produced laterally as pleurae; coxae reduced; mandibular molar nontriturative; maxilla 1 without palp; palp of maxilliped bi-articulate; uropods 1 and 2 uniramous, uropod 3 without rami; telson entire.

Type-genus: Temnophlias K. H. Barnard, 1916.

Remarks: It has long been recognized that the genus *Temnophlias* should be removed from the Phliantidae, into which it was originally placed, since its body shape and reduced mouthparts and uropods are inconsistent with the norm for that family (J. L. Barnard 1969, 1972*b*). J. L. Barnard (1972*b*) has suggested the possibility of placing *Temnophlias* in the Eophliantidae; however my feeling is that the depressed body form and entire telson of *Temnophlias* preclude this possibility and that the genus warrants its own family—the Temnophliidae. The removal of *Temnophlias* enables the diagnosis of Phliantidae to be tightened to read as follows:

Family Phliantidae: Talitroidea with body greatly depressed; pereon segments not laterally extended as pleurae; coxae not reduced; mandibular molar nontriturative; maxilla 1 with or without palp; palp of maxilliped 3 or 4-articulate; uropod 1 biramous, uropod 2 biramous (except *Pereionotus*), uropod 3 uniramous or rami absent; telson entire.

Temnophliidae would thus be distinguished from Phliantidae by the presence of pleurae on the pereon, the reduced maxillipedal palp and uniramous first uropod.

Temnophlias capensis K. H. Barnard, 1916

Fig. 21

Temnophlias capensis K. H. Barnard, 1916: 158, pl. 26 (figs 25–35).

Records: 29/16/I to 34/19/I, fairly common intertidally and in shallow waters.

Distribution: Endemic, Still Bay to South West Africa.

Remarks: This species has been refigured here (Fig. 21) in order to provide a suitable reference for the new family Temnophliidae. Although the lateral margins of the pereon segments are distinctly discontinuous it should be noted that this is not as marked as would appear from K. H. Barnard's (1916) figures. The distinction in body shape between *T. capensis* and *T. hystrix* is not in fact very great—the latter merely having developed strong dorsal carinae and lateral processes on the pereonites and coxae.

Temnophlias hystrix K. H. Barnard, 1954

Temnophlias hystrix K. H. Barnard, 1954: 130, fig. 8.

Records: 30/17/I to 34/18/I, a few records.

Diagnosis: Head with tridentate dorsal process; pereon segments each with a pair of lateral processes, 1 with two medio-dorsal processes, 2–7 with a single medio-dorsal process; coxae 1–4 bifid, 5–7 trifid; pereiopods all chelate in both sexes.

Distribution: Endemic, False Bay to Cape Hangklip, usually intertidal.

Suborder CAPRELLIDEA

Family **Aeginellidae**

Eupariambus fallax K. H. Barnard, 1957

Eupariambus fallax K. H. Barnard, 1957: 9, fig. 6.

Records: 32/17/O, D to 34/18/FB/O, 34/18/D, numerous records.

Distribution: Endemic, Still Bay to Lambert's Bay.

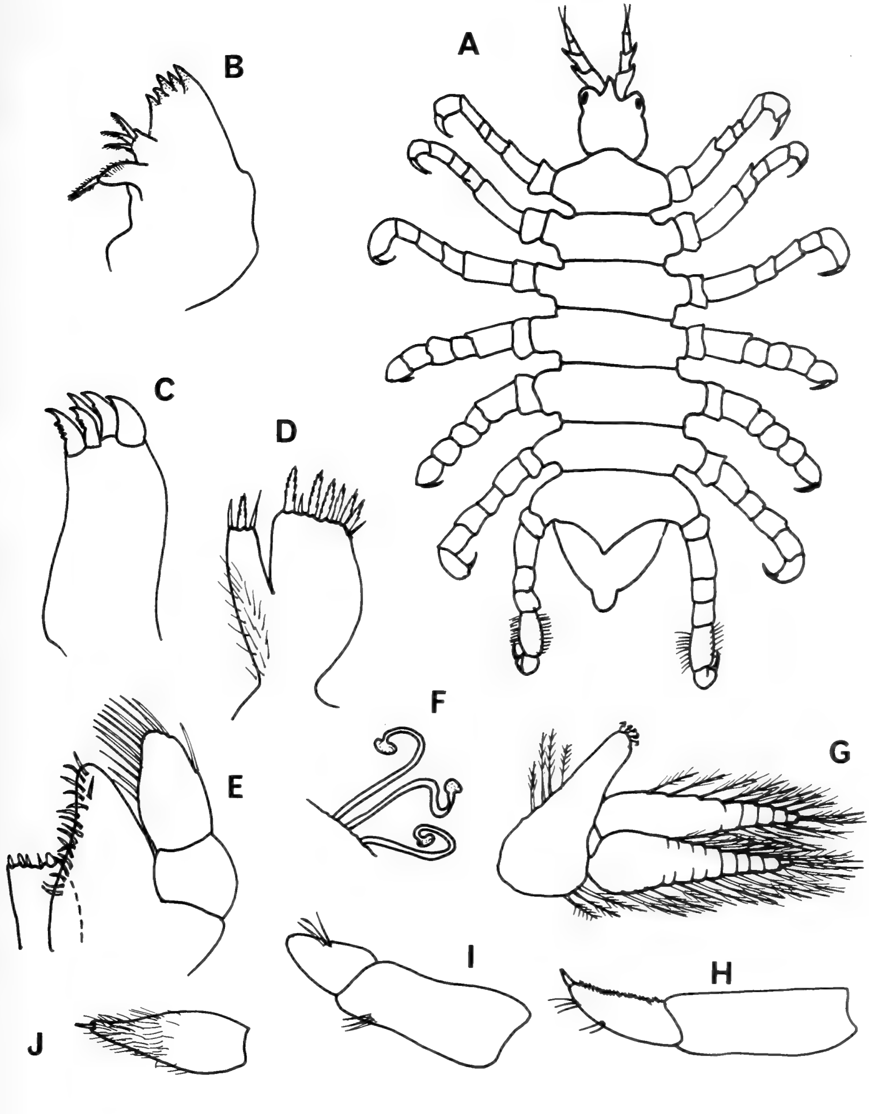

Fig. 21. *Temnophlias capensis* K. H. Barnard, 1916
Female, 7 mm: A—dorsal aspect; B—mandible; C—maxilla 1; D—maxilla 2; E—maxilliped; F—setae of brood lamellae; G—pleopod 3; H, I, J—uropods 1, 2, 3.

Orthoprotella mayeri K. H. Barnard, 1916

Orthoprotella mayeri: K. H. Barnard, 1916: 284; 1925: 372.

Records: 34/18/D, a single record.

Distribution: Indo-Pacific.

Paradeutella serrata Mayer, 1903

Paradeutella serrata Mayer, 1903: 47, pl. 2 (fig. 6), pl. 6 (figs 68–69).

Records: 34/18/FB/I, a single record.

Diagnosis: Head with dorsal spiniform process; pereon segments 1 and 2 also with large medio-dorsal processes, remaining segments with small medio-dorsal humps; antenna 2 about as long as peduncle of 1; article 2 of gnathopod 2 longer than pereon segment 2, bearing an acute distal process, palm poorly defined with three small teeth near finger-hinge, dactyl simple; pereiopods 1 and 2 minute, uniarticulate; pereiopods 3–5 fully developed; abdomen of ♂ with two pairs of small lobes.

Distribution: Endemic, known only from the above record.

Pseudaeginella tristanensis (Stebbing, 1888)

Pseudaeginella tristanensis: Stephensen, 1949: 52, fig. 23.

Records: 33/18/T, a single record.

Distribution: Tristan da Cunha, South Africa.

Pseudoprotella phasma (Montagu, 1804)

Pseudoprotella phasma: Chevreux & Fage, 1925: 437, fig. 423.

Records: 29/14/D, a single record.

Diagnosis: Head with strong rostral projection; pereon segment 1 with a medio-dorsal process posteriorly, 2 with a pair of processes medially and another posteriorly (large specimens with further spinose processes on pereon segments 3 and 4); lateral spinose processes above insertions of gnathopod 2 and gills; pereiopods 1 and 2 of a single minute segment; pereiopods 3–5 fully developed; abdomen of ♂ with two pairs of uniarticulate appendages.

Distribution: Mediterranean, eastern Atlantic.

Family **Caprellidae**

Caprella cicur Mayer, 1903

Caprella cicur Mayer, 1903: 75, 97, pl. 4 (figs 5–7), pl. 8 (figs 3–5).

Records: 32/18/T to 34/18/FB/I, T, O, numerous records.

Distribution: Endemic, Natal to Lambert's Bay.

Caprella danilevski Czerniavski, 1868

Caprella danilevskii: McCain, 1969: 22–25, figs 10–11.

Records: 32/18/T, 33/18/I, 34/18/FB/I, a few records.

Distribution: Widespread, pantropical.

Caprella equilibra Say, 1818

Caprella equilibra: McCain, 1968: 25–30, figs 12–13.

Records: 32/18/T, O to 34/18/FB/T, O, numerous records.

Distribution: Cosmopolitan.

Caprella natalensis Mayer, 1903

Caprella acutifrons var. *natalensis* Mayer, 1903: 81, pl. 3 (figs 22–23).
Caprella natalensis: Laubitz, 1972: 47, pl. 9 (figs F–G), pl. 10 (figs F–K).

Records: 33/18/I, 34/18/T, two records.

Distribution: Pacific North America, Tristan da Cunha, South Africa.

Caprella laevipes Mayer, 1903

Caprella laevipes Mayer, 1903: 108, pl. 5 (fig. 2), pl. 8 (figs 14–16).

Records: 32/18/T to 34/18/FB/T, O, a few records.

Distribution: Endemic, Natal to Lambert's Bay.

Caprella penantis Leach, 1814 *new synonymy*

Caprella falsa Mayer, 1903: 101, pl. 4 (fig. 15).
Caprella penantis: McCain, 1968: 33–40, figs 15–16. Laubitz, 1972: 41, pl. 9 (figs A–E), pl. 10 (figs A–E).

Records: 32/18/T to 34/18/FB/I, T, O, numerous records.

Distribution: Cosmopolitan in tropical and temperate seas.

Remarks: The maintenance of *C. falsa*, created by Mayer (1903) solely on the basis of the inflated article 2 of antenna 1, appears unjustified, since similar variations in the stoutness of antenna 1 are found within other species (e.g. *C. cicur* of Mayer, 1903: pl. 4, figs 6–7).

Caprella scaura Templeton, 1836

Caprella scaura: McCain, 1968: 40–44, figs 17–18.

Records: 29/16/I, 32/18/T to 34/18/T, quite common.

Distribution: Cosmopolitan.

Hemiaegina minuta Mayer, 1890

Hemiaegina minuta: McCain, 1968: 61–64, figs 29–30.

Records: 34/18/FB/T, a single record.

Distribution: Cosmopolitan in tropical and temperate seas.

Family **Cyamidae**

Cyamus balaenopterae K. H. Barnard, 1931

Cyamus balaenopterae: K. H. Barnard, 1932: 309, fig. 171.

Records: Ectoparasitic on Blue and Fin Whales, Saldanha Bay whaling station.

Distribution: Widespread on Fin and Blue Whales.

Cyamus boopis Lutken, 1873

Paracyamus boöpis: K. H. Barnard, 1932: 312.
Cyamus boopis: Margolis, 1955: 124, figs 7–12.

Records: Ectoparasitic on Humpback Whales, Saldanha Bay whaling station.

Distribution: Widespread on Humpback Whales.

Cyamus erraticus Roussel de Vauzème, 1834

Paracyamus erraticus: K. H. Barnard, 1932: 310, fig. 172.
Cyamus erraticus: Margolis, 1955: 132, figs 1–6.

Records: Ectoparasitic on Right Whales, Cape Town and Saldanha Bay whaling stations.

Distribution: Widespread on Right Whales.

Cyamus gracilis Roussel de Vauzème, 1834

Paracyamus gracilis: K. H. Barnard, 1932: 312, fig. 173.

Records: False Bay, ectoparasitic on Right Whale.

Diagnosis: Palp of maxilliped present in juveniles, lost in adult; body parallel sided; head fused to pereon segment 1; pereon segment 2 laterally rounded, branchiae on segments 3 and 4 single, as long as segments 3–5 together, accessory lobes in ♂ double on both segments (in ♀ absent); pereon segments of ♂ without ventral processes, ♀ with a single pair of processes on pereon segment 5.

Distribution: Southern oceans, ectoparasitic on Right Whales.

Cyamus ovalis Roussel de Vauzème, 1834

Cyamus ovalis: K. H. Barnard, 1932: 307, fig. 170.

Records: Cape Town, False Bay, Saldanha Bay, ectoparasitic on Right Whales.

Diagnosis: Maxillipedal palp present in juvenile and adult; body broadly oval; pereon segment 1 distinguished from head by an oblique groove; pereon segment 2 produced postero-distally into a hooked process which engages an anterior process of pereon segment 3; branchiae on segments 3 and 4 each consisting of two equal lobes as long as segments 2–6 together, accessory lobes in ♂ single on segment 3, double on segment 4; ♂ pereon with one pair of ventral processes on each of segments 6 and 7, ♀ with a pair of blunt processes on segment 5 and a pair of tubercles on each of segments 6 and 7.

Distribution: Widespread on Right Whale and North Pacific Whale.

Isocyamus delphini (Guérin-Méneville, 1836)

Isocyamus delphini: K. H. Barnard, 1932: 313–314. Stephensen, 1942: 454–455.

Records: 'From dolphin'—exact location unknown.

Diagnosis: Body ovate, head completely fused to pereon segment 1; gills on pereon segments 3 and 4 short and stout, accessory gills in ♂ single, almost as long as gill, an outward-directed process projecting from base of each gill; ♂ pereon with a pair of ventral tubercles on each of segments 5–7, ♀ with a pair of inward-directed processes on segment 5 and a pair of tubercles on each of segments 6 and 7.

Distribution: Widespread on dolphins, Pilot Dolphins and False Killer Whales.

Remarks: This species has not previously been recorded from southern Africa.

Neocyamus physeteris (Pouchet, 1888)

Paracyamus physeteris: Stephensen, 1942: 453.
Neocyamus physeteris: Margolis, 1955: 131, figs 21–23.

Records: SAM–A12307—station data unknown.

Diagnosis: Body slender with pereon segments 3 and 4 half as wide as 5 and 6; gills short, each divided into about 12 filiform appendages, accessory gills absent.

Distribution: Widespread on Sperm Whales and rarely Ocean Dolphin.

Remarks: This is the first record of this species from southern Africa.

Family **Phtisicidae**

Caprellina longicollis (Nicolet, 1849)

Caprellina longicollis: McCain, 1969: 289, fig. 2.

Records: 29/16/I to 34/18/I, T, 34/18/FB/I, T, fairly common.

Distribution: Mediterranean, southern oceans.

Caprellina spiniger K. H. Barnard, 1916

Caprellina spiniger K. H. Barnard, 1916: 282, pl. 28 (fig. 35).

Records: 33/18/I, 34/18/FB/I, a few records.

Distribution: Endemic, Mossel Bay to South West Africa.

Phtisica marina Slabber, 1769

Phtisica marina: Chevreux & Fage, 1925: 434, fig. 422. McCain, 1968: 91–97, fig. 46.

Records: 32/18/T, 32/17/D to 34/17/D, 34/18/FB/O, numerous records.

Distribution: Mediterranean, Atlantic, southern Africa.

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6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., 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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

C. L. GRIFFITHS

THE AMPHIPODA OF SOUTHERN AFRICA

PART 5

THE GAMMARIDEA AND CAPRELLIDEA OF THE CAPE PROVINCE WEST OF CAPE AGULHAS

VOLUME 67 PART 6 OCTOBER 1975 ISSN 0303-2515

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PLEISTOCENE MOLLUSCS FROM THE WEST AND SOUTH COASTS OF THE CAPE PROVINCE, SOUTH AFRICA

By

R. N. Kilburn

Natal Museum, Pietermaritzburg

&

A. J. Tankard

South African Museum, Cape Town

(With 22 figures)

[*MS accepted 6 January 1975*]

ABSTRACT

Nineteen species of Pleistocene to Recent littoral molluscs are discussed, belonging to the families Trochidae, Stomatiidae, Potamididae, Cerithiidae, Calyptraeidae, Buccinidae, Terebridae, Acteonidae, Nuculanidae, Ungulinidae, Lucinidae, Veneridae, Petricolidae, Donacidae and Tellinidae. New species and subspecies are described for the genera *Cerithidea* (*Cerithidea*), *Crepidula capensis* (subsp. nov.), *Triumphis*, *Duplicaria*, *Pupa* (*Strigopupa*), *Petricola* (*Claudiconcha*), *Donax*, *Gastrana*. New synonyms, new combinations, new records, and cases of revised status are discussed. These include *Cantharidus suarezensis suarezensis* (Fischer, 1878), *C. s. fultoni* (Sowerby, 1889), *Pseudostomatella orbiculata* (A. Adams, 1850), *Cerithium scabridum rufonodulosum* E. A. Smith, 1901, *Nuculana* (*Lembulus*) *bicuspidata* (Gould, 1845), *Felania diaphana* (Gmelin, 1791), *Loripes* (*Microloripes*) *liratula* (Sowerby, 1889), *Venerupis dura* (Gmelin, 1791), *Macoma* (*Heteromacoma*) *tricostata* (Römer, 1872), *Leporimetis* (*Leporimetis*) *hanleyi* (Dunker, 1853).

CONTENTS

INTRODUCTION

Numerous exposures of Pleistocene marine sediments are preserved on the wave-cut platforms adjacent to the present South African coast, and in estuaries and lagoons. Radio-carbon measurements show that these deposits are beyond the range of the ^{14}C dating technique (Tankard, in press). Generally the Pleistocene faunas of the South African coastlands are poorly known. More than 160 species of invertebrate fossils have so far been identified in this project.

The west and south coasts of the Cape Province have been tectonically

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unstable in the Tertiary and possibly through the Early and Middle Pleistocene. Between Cape Town and St Helena Bay (Fig. 1) Neogene marine sediments are found at lower elevations than their chronostratigraphic equivalents on the Cape south coast, or the South West African coast. Furthermore, between Cape Town and St Helena Bay the highest observed Pleistocene beach deposits are at 10 m a.s.l. (above mean sea level) (Tankard, in press). Carrington & Kensley (1969) record a series of transgressive complexes up to 90 m a.s.l. on the Namaqualand coast, while Davies (1971) has identified Pleistocene raised beaches at 60 m a.s.l. on the south coast. We envisage that intermittent sagging took place in the area between the Olifants River and the Cape Peninsula throughout most of the Cenozoic.

In the Saldanha–Langebaan area there are several exposures of Early Pleistocene shelly sands. Just north of Langebaan (1,5 km) in a shallow quarry at 9,5 m a.s.l. there is a shelly deposit overlying Tertiary limestone. The fauna is characterized by *Fissurella robusta* Sowerby, *Cerithidea* sp. nov., *Triumphis* sp. nov., *Purpura praecingulata* (Haughton), *Petricola* sp. nov., and large *Perna perna* (Linnaeus) (= *Mytilus tomlini* Haughton). Similar deposits are exposed on either side of the Hoedjiespunt peninsula where they lie either directly on a quartz porphyry platform or on Miocene phosphorite. Behind the Sea Harvest factory on the Hoedjiespunt peninsula the littoral deposit includes wave-generated beach boulders. Here the horizon is exposed up to 8 m a.s.l. and is composed largely of *Patella* spp., although *Fissurella robusta*, *Petricola* sp. nov., and large *Perna perna* (Linnaeus) are common. These deposits are assigned to the Early Pleistocene, rather than the Late Pleistocene, because the mollusc fauna is more primitive than any of the Late Pleistocene sites so far examined, and does not contain any of the warm-water fauna that characterizes deposits from other Late Pleistocene embayments and estuaries and is poorly preserved when compared with these younger deposits.

Generally the mollusc fauna from the Early Pleistocene sites at Saldanha and Langebaan is near-shore in character. At the Langebaan site the barnacle *Balanus amphitrite* Darwin encrusts the Tertiary limestone. *B. amphitrite* is today an inhabitant of the lower intertidal to infratidal zones. This would imply that the strand line should really be recorded at about 10 m a.s.l.

The mollusc fauna, particularly *Fissurella robusta*, *Triumphis* sp. nov. *Purpura praecingulata*, large *Perna perna*, and *Petricola* sp. nov. suggests correlation with Haughton's (1932) Zone-D of the Namaqualand coast, and the 45–50 m transgression complex of Carrington & Kensley (1969). If this correlation is correct the 10 m shoreline in the Langebaan–Saldanha area would be of Early Pleistocene age.

In contrast, extensive Late Pleistocene beach deposits occur up to 7,0 m a.s.l. on the west coast (e.g. Velddrif) and 7,2 m a.s.l. on the south coast (e.g. Coega River mouth). The mollusc faunas that characterize these beach deposits have a distinctly modern aspect and are identical with the present and adjacent open-coast faunas. But preserved in Pleistocene estuarine and lagoonal deposits are

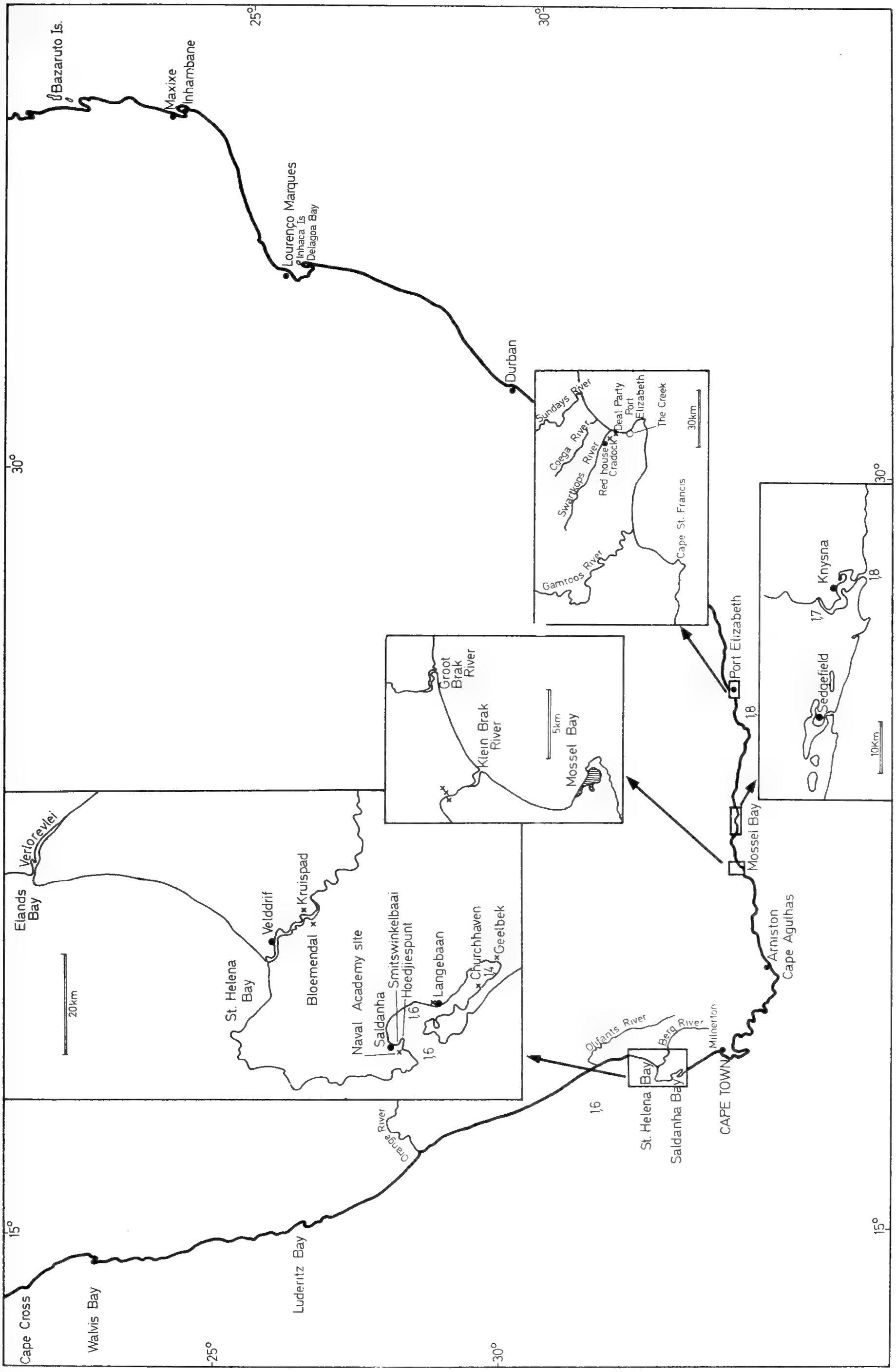

Fig. 1. Locality map. Numerals along the coastline and in estuaries refer to present tidal range in metres.

thermally anomalous fossil mollusc faunas. The intertidal molluscs and ostracods all suggest a 6,5 m strandline.

The most characteristic feature of the fossil molluscs from the lagoonal and estuarine facies is that they constitute mixed cool-water/warm-water assemblages. This mixed assemblage of taxa with mutually exclusive modern geographic ranges is characterized by populations of warm-water molluscs that existed in the last interglacial far south of their known present day geographic range end-points. The cool-water element is similar to that of present day open-coast faunas. The occurrence of the warm-water molluscs in the sheltered environments is probably the result of a brief extension of their southerly range during a relatively warmer part of the marine climatic cycle. Only in the sheltered environments of the estuaries, far removed from the effect of cold oceanic circulation, were the warm-water taxa able to establish reproductive populations. Higher water temperatures than at present found in these sheltered environments was probably the result of increased solar radiation (Tankard 1975). We believe that this warm period coincides with the well documented period of higher palaeotemperature at 120 000 B.P., the substage 5e of Shackleton (1969) and Shackleton & Opdyke (1973).

In the present paper the taxonomy of a number of problematical molluscs, encountered during studies on Pleistocene deposits, are discussed. While some have proved to be referable to species still extant elsewhere, several are clearly undescribed species.

Throughout this study height above sea level (a.s.l.) is referred to mean sea level. Tidal ranges are shown in Figure 1. In the following text Natal Museum has been abbreviated to N.M. and South African Museum to S.A.M. Where possible, the elevation of sample localities is listed.

SYSTEMATIC DESCRIPTIONS

Class GASTROPODA

Family **Trochidae**

Cantharidus (*Jujubinus*) *suarezensis* (Fischer, 1878)

In analysing the systematics of this species, five names must be considered:

(1) *Trochus suarezensis* Fischer, 1878. This trochid appears to have remained unknown to English workers, even though Dautzenberg (1929) implied it to be a common Malagasy species. This is evidently the result of an error in Pilsbry's 1889 translation of Fischer's description, to which Dr Harald Rehder has kindly drawn our attention. The word 'geminatis' ('twinned') of the original description was evidently misread as 'gemmatis', which was rendered as 'slightly granose' in Pilsbry's text, and 'distinctly granose' in his comments. As a consequence the number of spiral lirae was also incorrectly cited, the duplication of these producing a total of twelve in the type, instead of only seven.

(2) *Trochus fultoni* Sowerby, 1889. Although this name appears in Sowerby's

text, in the caption to his original plate he used the name *Trochus stenomphalus.* Tomlin (1931: 419), acting as first reviser, selected *T. fultoni* as senior synonym. This name was based on supposedly recent shells from Port Elizabeth. However, like a number of other species described from there (e.g. *Monilea ponsonbyi* (Sowerby, 1888), *Loripes liratula* (Sowerby, 1889) and *Cerithium scabridum rufonodulosum* E. A. Smith, 1901), it does not appear to live in that region, and the type material may be presumed to have been derived from a raised beach. To this day specimens of most of these species, including '*T.*' *fultoni*, are often washed up on the shore on either side of the mouth of the Swartkops River, which is here designated as the restricted type locality for '*T.*' *fultoni.*

(3) *Calliostoma farquhari* Sowerby, 1892. While this was described as coming from Port Elizabeth, a note has been left by H. C. Burnup to the effect that John Farquhar had personally informed him that his shells were in reality collected in Durban Bay. Thus the three Durban examples from the Ponsonby collection in the British Museum, mentioned by Tomlin (1931), are possibly syntypes. Similar shells, in more or less fresh condition, are common in Durban Bay, although no living specimens have as yet come to the authors' attention.

(4) *Calliostoma bisculptum* E. A. Smith, 1906. Described from a single specimen from Durban.

(5) *Calliostoma mosselense* Tomlin, 1926. Described from Quaternary deposits on the Klein Brak River.

Sowerby (1889) did comment on the resemblance of his *Trochus fultoni* to *T. suarezensis*, but no direct comparison has hitherto been made. The interrelationships of the other taxa were discussed by Tomlin (1931) and Barnard (1963*a*). The former synonymized *T. farquhari* with *T. fultoni*, but provisionally accepted *Calliostoma bisculptum* as a valid species. Barnard treated *Calliostoma bisculptum*, *Calliostoma farquhari* and *Calliostoma mosselense* all as synonyms of *Cantharidus fultoni*. However, examination of large series from various localities indicates that two morphologically distinguishable populations, isolated, as far as can be determined, both temporally and geographically, can be distinguished. These should be given subspecific rank. One population (*fultoni*) is restricted to Pleistocene deposits of the southern Cape shoreline, the other is Recent, occurring living from Natal to Tanzania and Madagascar. Specimens from the Malagasy Republic (*suarezensis*), lent to us by Dr H. Rehder, agree well in all characters (including dentition) with material from Durban and Moçambique (*farquhari* and *bisculptum*), and are clearly conspecific; *Trochus suarezensis* is thus the earliest *nomen* applicable to this taxon.

Macnae & Kalk (1969: 127) and apparently Spry (1968: 6) have utilized the name '*Calliostoma interrupta* (Wood)' for examples of *Cantharidus suarezensis. Cantharidus* (*Jujubinus*) *interruptus* (Wood, 1828), judging by Western Australian specimens in the N.M., is indeed superficially similar, but has a completely different colour pattern, is markedly narrower, and has more feebly pliculate interstices.

Barnard's figure (1963*a*: fig. 14i) of the radula of the present species is

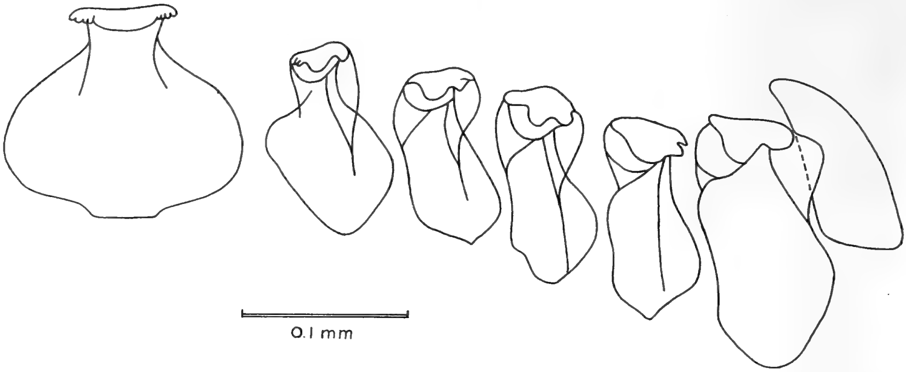

Fig. 2. Rachidian and lateral plates of *Cantharidus suarezensis suarezensis* (Fischer, 1878), with intermediate plate of preceding row drawn *in situ*.

inaccurate, and the rachidian and lateral teeth are here refigured (Fig. 2). In general the dentition closely resembles that of *C.* (*J.*) *strigosus* (Gmelin, 1791), as figured by Fischer-Piette & Gailliard (1959: 59, fig. 1). As in many trochids there is a degenerate, non-cuspidate plate between the laterals and marginals. While it seems to be conventional to follow Troschel (1879) in regarding this as an inner marginal tooth, it should be noted that this plate not infrequently bears traces of an alate side lamella, which is a characteristic of the lateral series of teeth, not the marginals. In *C. suarezensis* and others this intermediate plate seems to act as a buttress for the cutting head of the outermost lateral in the succeeding row.

We are here relegating *Jujubinus* Monterosato, 1884, to subgeneric rank under *Cantharidus* Montfort, 1810. Although maintained as a full genus by some recent authors, *Jujubinus* appears to differ only in its more angular body whorl and narrower spire angle.

Cantharidus suarezensis suarezensis (Fischer, 1878)

Fig. 3

Trochus suarezensis Fischer, 1878: 63; 1879: 378, pl. 115 (figs 2–2a).
Cantharidus suarezensis: Pilsbry, 1889: 130, pl. 45 (fig. 55). Dautzenberg, 1929: 332.
Calliostoma farquhari Sowerby, 1892: 43, pl. 2 (fig. 42). Syn. nov.
Calliostoma bisculptum E. A. Smith, 1906: 54, pl. 8 (fig. 4). Syn. nov.
Cantharidus fultoni (*partim*)*:* Barnard, 1963*a*: 281, figs 14i, 19.
Calliostoma interrupta (*non* Wood, 1828): Spry, 1968: 6. Macnae & Kalk, 1969: 127.

Diagnosis

Distinguished by the thin, flat-topped spiral lirae, frequently arranged in pairs, particularly medially; these lirae generally number 11–16 on the penultimate whorl, more rarely as few as 6 (fide Barnard 1963*a*). Intervals with delicate, oblique axial plicules, which barely cross the intervening spirals.

Colour variable, often light green with articulated darker green dots on the lirae, which may, by confluence, form oblique dark green lines or flames; in others the ground colour is greenish-yellow or greenish-white with dark grey or olive-brown axial flames; these often bifurcate at the basal periphery, which may bear red marks; the intervals between the spiral lirae are characteristically orange-red, although an occasional interval may lack this colour.

Dimensions

Holotype: 18 × 13 mm. B/Ht 0,72.
Durban Bay: 11,9 × 8,8 mm; 11,0 × 7,8 mm; 10,9 × 8,2 mm. B/Ht range 0,68–1,19.
Inhaca Island: 17,8 × 12,7 mm; 17,6 × 13,5 mm; 17,3 × 13,0 mm. B/Ht range 0,63–1,07.
Malagasy: 11,7 × 9,5 mm; 11,5 × 8,8 mm; 11,5 × 8,6 mm. B/Ht range 0,74–0,81.

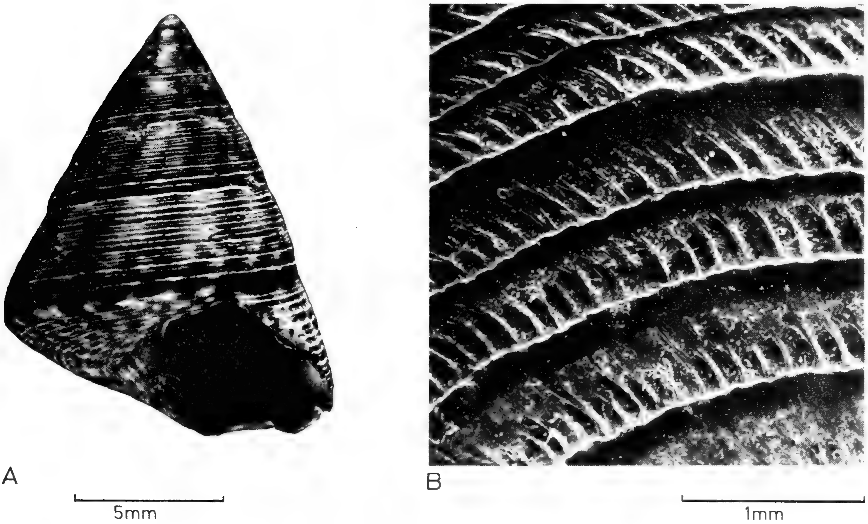

Fig. 3. *Cantharidus suarezensis suarezensis* (Fischer, 1878). B. Scanning electron photomicrograph showing sculpture on the base. (Inhaca Island.)

Distribution records

Natal: Durban Bay (N.M. *et auct.*). Moçambique: Inhaca Island and Delagoa Bay (N.M. and S.A.M.); Maxixe and Inhambane (S.A.M.); Bazaruto and Benguera Islands and off Inhagondo region (N.M.); Moçambique Island (Barnard and N.M.); Porto Amelia (N.M.). Tanzania: Dar-es-Salaam (N.M.). Malagasy Republic: Nossi Bé (S.A.M.); Tulear and 13°23′S, 48°13′E (United States National Museum); numerous other localities (Dautzenberg 1929).

Barnard's (1963*a*) Isipingo record is doubtful as there are no suitable modern habitats nor raised beach deposits at that locality; and the specimen dredged off Cape Morgan at 47 fathoms cannot be positively identified in the South African Museum collection.

Habitat

On the sheltered mudflats on the west side of Inhaca Island and elsewhere in Moçambique *C. s. suarezensis* lives in abundance on the leaves of the marine angiosperm *Cymodocea ciliata* (Forsk.) Ehrenb. ex Aschers., which forms extensive beds along the infratidal fringe. Dautzenberg also records the species as living 'dans les Cymodocées' in the Malagasy Republic.

Cantharidus suarezensis fultoni (Sowerby, 1889)

(Revised status)

Fig. 4

Trochus (*Calliostoma*) *fultoni* Sowerby, 1889: 153; 1892: 43, pl. 2 (fig. 43).
Trochus stenomphalus Sowerby, 1889: pl. 3 (fig. 7).
Calliostoma mosselense Tomlin, 1926: 81.
Cantharidus fultoni (*partim*): Barnard, 1963*a*: 281.

Diagnosis

Superficially smooth, but under magnification with fine declivous spiral lirae, never as strong as in the nominate subspecies, sometimes almost obsolete, although always distinct in juveniles; these lirae are also always well developed on the base. Oblique growth lines present, occasionally strong enough in places

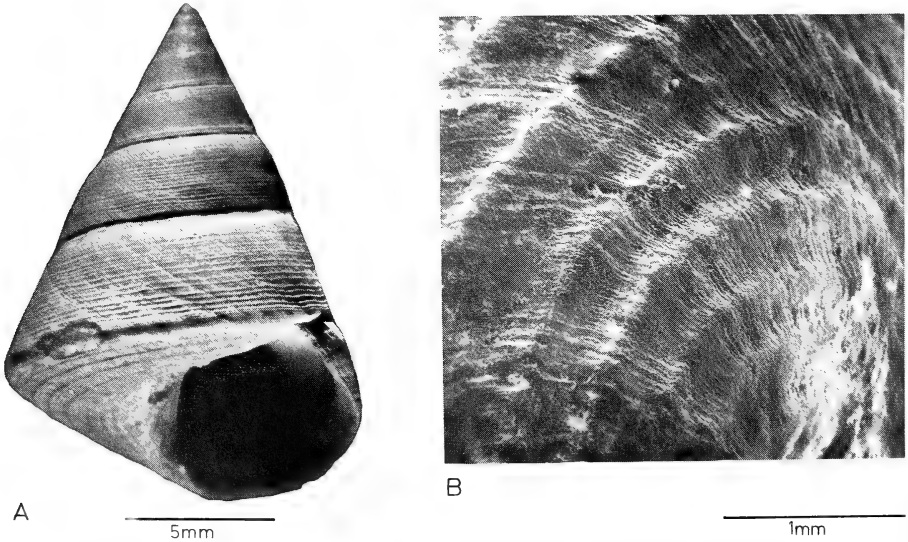

Fig. 4. *Cantharidus suarezensis fultoni* (Sowerby, 1889). B. Scanning electron photomicrograph showing sculpture on the base. (Swartkops River mouth.)

to form fine plicules, which, however, always override the spiral sculpture, instead of forming interstitial plicules such as characterize *C. s. suarezensis*. Colour buff with oblique reddish or yellowish brown axial lines or spiral rows of dots.

Dimensions

Swartkops River: 17,0 × 12,7 mm; 16,9 × 13,1 mm; 16,7 × 12,0 mm. B/Ht range 0,72–0,94.
Klein Brak River: 12,1 × 8,9 mm; 11,8 × 8,3 mm; 11,3 × 7,8 mm. B/Ht range 0,65–1,00.
Sedgefield: 10,8 × 7,5 mm; 9,5 × 7,3 mm; 9,0 × 7,6 mm. B/Ht range 0,69–0,85.

Distribution records

Type locality: Port Elizabeth, here restricted to the Swartkops River beds. The known range of the subspecies is from Algoa Bay (Coega) to the Klein Brak River, in beds of the 7 m level, and 4–5 m level. Swartkops River mouth (N.M., S.A.M.); Redhouse (N.M.); Coega River mouth (N.M., S.A.M.); Knysna 4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M.); Groot Brak River (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.); Mossel Bay (N.M.).

Remarks

The diagnostic characters that serve to separate *C. s. suarezensis* and *C. s. fultoni* have already been cited. In Figures 5A and 5B height is compared with the ratio breadth/height for these two subspecies. It must be stressed, however, that sampling was non-random; specimens were selected to present an even distribution of size. As these graphs show, separation of the two subspecies on shell dimension is not possible. The marked differences even within a single subspecies may possibly be the result of habitat. For instance, as stated, the Inhaca Island sub-population of *C. s. suarezensis* lives on the broad bladed 'sea grass' *Cymodocea ciliata* (Forsk.). In Durban Bay *Cymodocea* is replaced by *Zostera*, which is the probable habitat of the local *C. s. suarezensis* population. By comparison with *Cymodocea*, *Zostera* is thin-leafed and much less robust. Arguably, *Zostera* could not support broad specimens such as live on *Cymodocea*. Figure 5 shows that the same difference in dimensions exists within *C. s. fultoni*, but unfortunately the fossil record provides no indication as to which marine angiosperms inhabited the Late Pleistocene estuaries and lagoons.

The differences in dimensions within each subspecies could equally be due to the tendency for the development of local demes. Pelagic larval stages are absent in European *Cantharidus* spp. and if this is applicable also to *C. suarezensis*, it would contribute towards the isolation of sub-populations. For example, there could be little gene exchange between the living Inhaca and Durban Bay sub-populations, and between the Late Pleistocene Swartkops River and Klein Brak River ones.

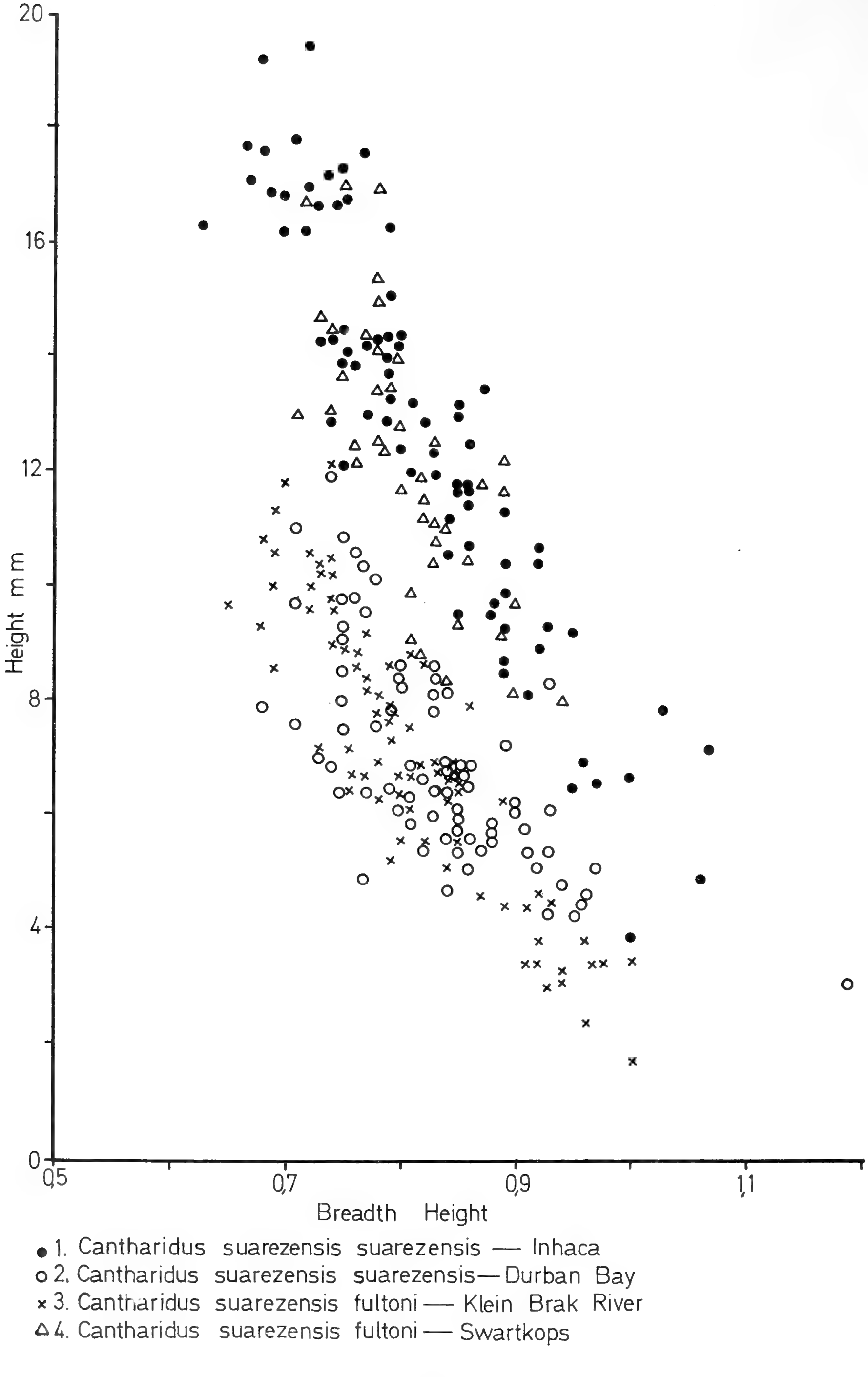

Fig. 5A

Fig. 5. Comparison of height with breadth/height for *Cantharidus suarezensis suarezensis* and *C. s. fultoni.* A. Scatter diagram. B. Calculated best-fit lines through the individual scatter diagram populations.

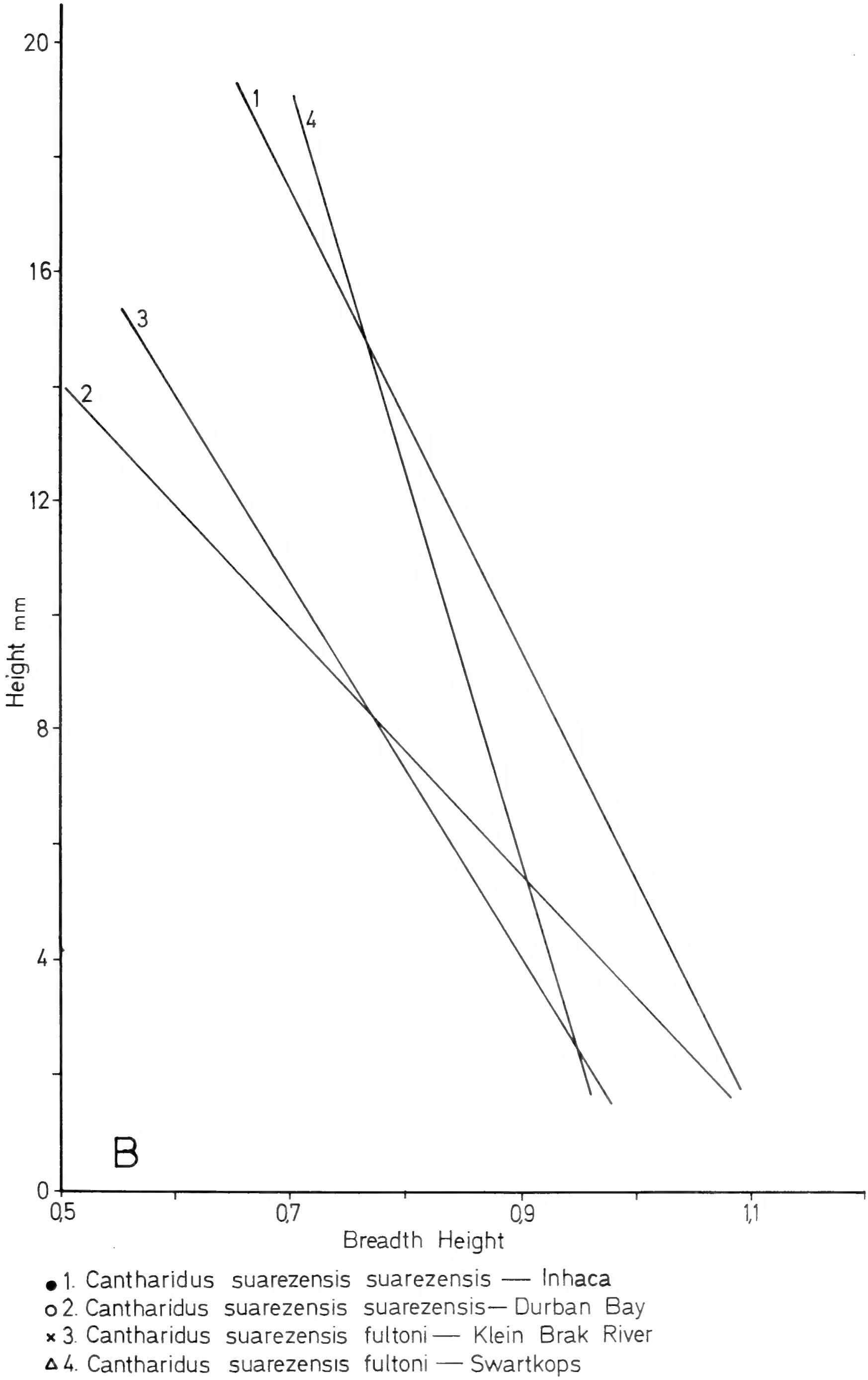
20
16
12
8
4
0
Height mm
0,5
0,7
0,9
1,1
Breadth Height
1
2
3
4
B
● 1. Cantharidus suarezensis suarezensis — Inhaca
○ 2. Cantharidus suarezensis suarezensis— Durban Bay
× 3. Cantharidus suarezensis fultoni — Klein Brak River
△ 4. Cantharidus suarezensis fultoni — Swartkops

Fig. 5B

Family **Stomatiidae**

Pseudostomatella orbiculata (A. Adams, 1850)

Fig. 6

Stomatella orbiculata A. Adams, 1850: 31; 1854: 837, pl. 174 (figs 23–24). Sowerby, 1874: pl. 4 (fig. 23). Tomlin, 1923: 50.
Stomatella sp: Barnard, 1963*a*: 245, fig. 12a.

Distribution records

Knysna, 4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.).

Remarks

Specimens from Pleistocene raised beaches (S.A.M.) in the Mossel Bay–Algoa Bay area agree well with Recent specimens (N.M.) from Moçambique Island, Bazaruto and Santa Carolina Islands (Moçambique) and from Dar-es-Salaam. The species was recorded from Algoa Bay by Tomlin (1923), but this example was almost certainly washed out of a raised beach, as there is no other record of Recent specimens from South African waters. There are in fact numerous specimens from the Swartkops beds in the S.A.M. collection. The type locality was Moçambique and it has been recorded from as far north as Ceylon (Robertson 1969).

Barnard (1963*a*) described Pleistocene specimens of *P. orbiculata* in detail.

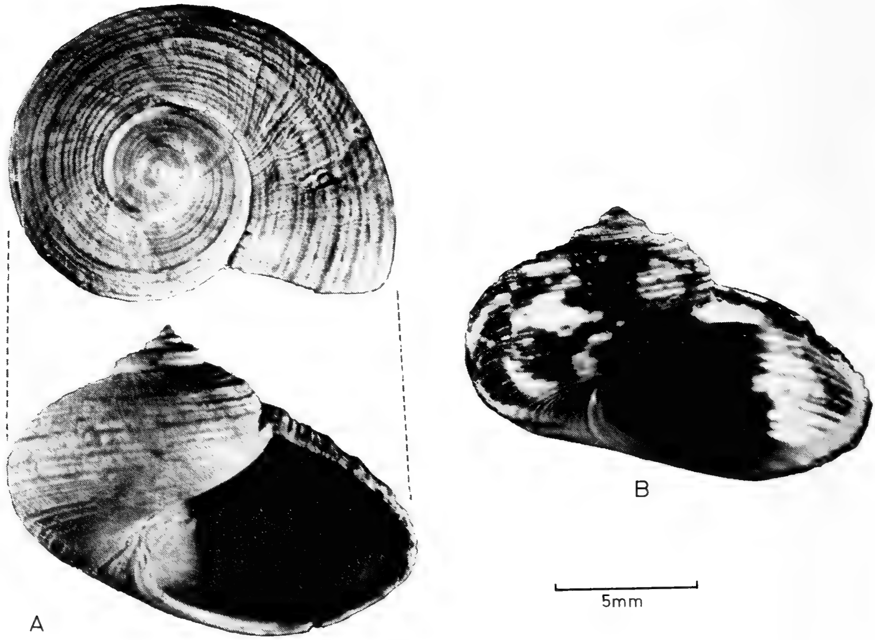

Fig. 6. *Pseudostomatella orbiculata* (A. Adams, 1850). A. Fossil (Knysna). B. Living (Dar es Salaam).

Family **Potamididae**

Cerithidea (Cerithidea) bifurcata sp. nov.

Fig. 7

?*Cerithium cf. guinaicum* (*non* Philippi): Haughton, 1932: 45.

Type material

Holotype: SAM–K4496.
Paratypes 1 and 2: NM–A 80/T 1821.
Paratype 3: SAM–K4563.

Diagnosis

Apex decollate, later part of spire cyrtoconic, sutures narrowly canaliculate; sculpture of fine axial riblets and well-developed subsutural crenules, crossed by fine spiral lirae.

Description

Adult acuminately pupoid, with flaring aperture and decollate apex; whorls gently convex, periphery situated at base of each whorl; sutures very narrow but canaliculate. Aperture rounded quadrate, angular posteriorly, with a small parietal denticle in the angle, labium evenly curved, margin of columella callus free, but not erect; labrum evenly rounded, gently opisthocline; siphonal canal short, very oblique, truncate, and deeply channelled. Axial sculpture consists of fine, close, opisthocyrt riblets, about 35–41 in number on penultimate whorl, rather weak towards back of lip, developing below the suture into strong crenule-like nodules, 17–20 on the penultimate whorl. Spiral sculpture is present anterior to these nodules, consisting of three narrow and sometimes very shallow grooves on the penultimate whorl; their intervals are flattened, rarely forming nodules at the intersections with axial ribs; spiral grooves are more closely spaced on base of body whorl. One specimen retains traces of brown coloration in the spiral grooves.

Adults (two 'complete' examples available) retain 5½ whorls; no perfect juveniles have been seen, but the only two immature specimens examined show 7 and 8½ whorls respectively (their apices seem to be broken, however). The exact stage at which decollation occurs cannot at present be estimated.

Dimensions

Holotype: adult, 20,6 × 10,1 mm.
Paratype 1: adult, 21,6 × 10,7 mm.
Paratype 2: juvenile, 25,8 × 10,8 mm (labrum broken).
Paratype 3: juvenile, 19,9 × 7,7 mm.

Distribution records

Early Pleistocene beach deposits at 9,5 m a.s.l., 1,5 km north-east of Langebaan in quarry (type locality).

Remarks

The naturally decollate apex distinguishes *C. bifurcata* from most members of the genus *Cerithidea* Swainson, 1840, certainly from all Recent Atlantic species. The closest ally to *C. bifurcata* appears to be *C. decollata* (Linnaeus, 1758), a Recent Indo-Pacific species common in mangrove swamps in Natal, but living among salt marsh vegetation in estuaries as far west as the Gamtoos River (approx. 25°05′E). *C. decollata* differs in possessing regular suture-to-suture axial ribs, a shallower siphonal canal, a definite posterior apertural angle, and non-channelled sutures.

The pupoid shape and subsutural crenules of *Cerithidea bifurcata* may have led to Tomlin (in Haughton 1932) misidentifying it as the Recent tropical Atlantic *Cerithium guinaicum* Philippi, 1849; in complete specimens shape and sculptural details are very dissimilar.

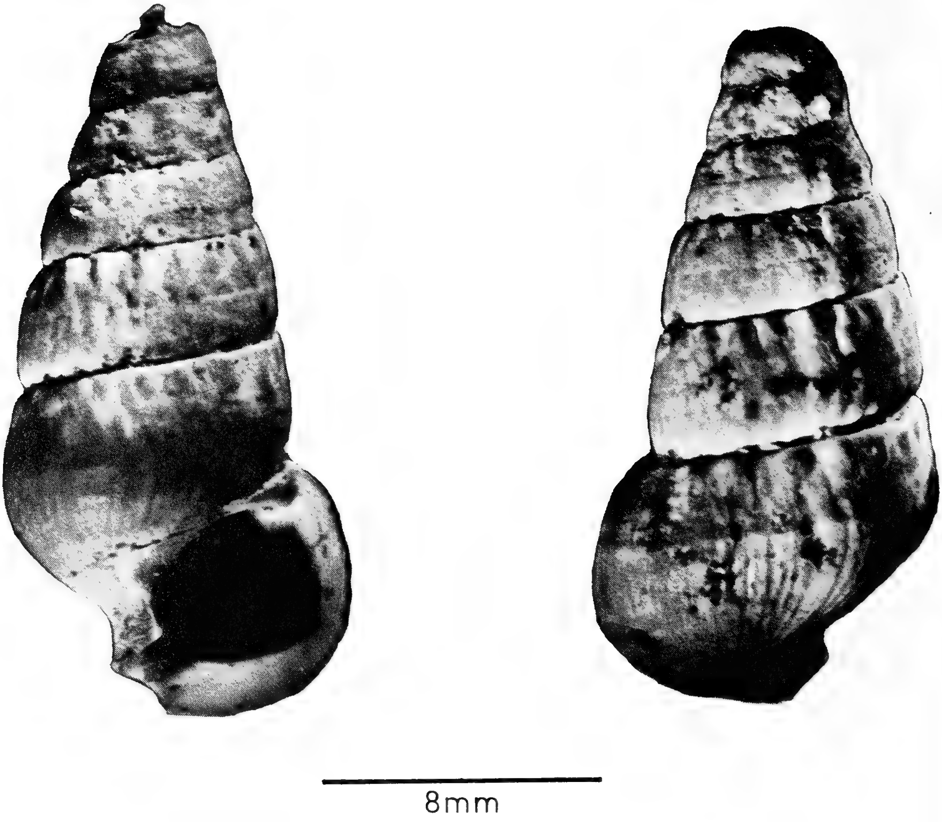

Fig. 7. *Cerithidea* (*Cerithidea*) *bifurcata* sp. nov. Holotype. (Quarry 1,5 km north of Langebaan.)

Family **Cerithiidae**

Cerithium scabridum rufonodulosum E. A. Smith, 1901
(Revised status)

Fig. 8

Cerithium mediterraneum (*non* Deshayes): Sowerby, 1892: 35. Turton, 1932: 125.
Cerithium rufonodulosum E. A. Smith, 1901: 108, pl. 1 (fig. 8). Barnard, 1963: 131.
Cerithium vulgatum (*non* Bruguière): Bartsch, 1915: 116. Turton, 1932: 125.

Distribution records

4–5 m and 7 m levels: Coega River mouth (S.A.M.); Redhouse (S.A.M.); Knysna, 4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M.); Groot Brak River (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.); Arniston (S.A.M.).

Remarks

As in the case of several other Cape Pleistocene molluscs, *C. rufonodulosum* from Port Elizabeth was described as a Recent species. These specimens were no doubt washed out of raised beaches along the banks of the Swartkops River. The Port Alfred specimens recorded as *C. vulgatum* and *C. mediterraneum* were also presumably derived from local deposits. *Cerithium rufonodulosum* closely resembles Sowerby's figure of his *C. nigropunctatum* (1855: 860, pl. 180, fig. 97) from an unknown habitat, as was indicated by Smith. Unfortunately the original description of *C. nigropunctatum* contains insufficient detail, and from Smith's phraseology it would appear that the types are lost. Reeve (1865*a*) omitted the

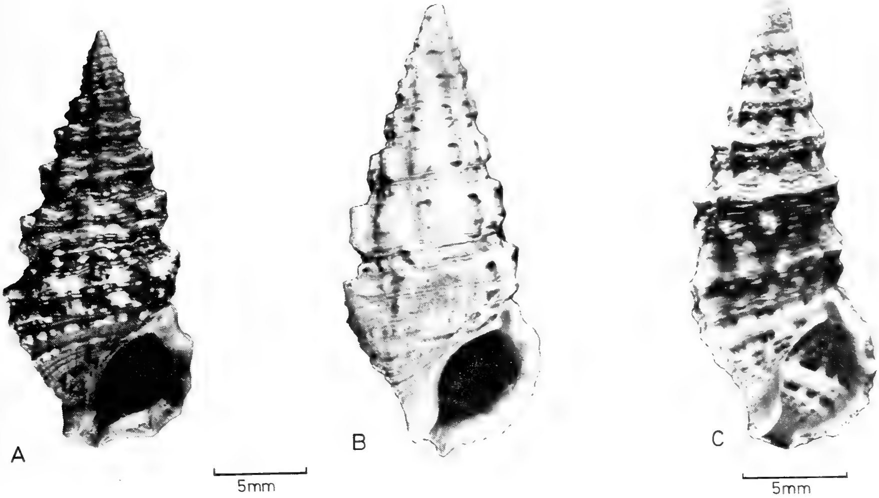

Fig. 8. A. *Cerithium scabridum rufonodulosum* E. A. Smith, 1901 (Algoa Bay). B. *C. s. rufonodulosum* E. A. Smith, 1901 (Sedgefield). C. *C. s. scabridum* Philippi, 1848 (Muscat, Gulf of Oman).

species, and Kobelt (1898: 242, pl. 42, fig. 10) merely copied Sowerby's description and figure. *C. nigropunctatum* must therefore be rejected as a *nomen dubium*, at least until the type (if extant) is located. The possibility does exist, nevertheless, that it may indeed be based on a discoloured specimen of the present species.

Of Recent species *C. rufonodulosum* appears to be allied only to *Cerithium scabridum* Philippi, 1848. This species is recorded from the Red Sea, Persian Gulf and India, south to the Mascarene Islands and Quirimba Island (12,4°S, 40,7°E), but has not yet been reported from farther south. The morphological differences between *C. scabridum* and *C. rufonodulosum* are very small and we believe that the relationship should be regarded as a subspecific one. Comparison with specimens of *C. s. scabridum* from the Gulf of Oman (N.M.: F. Luther) shows it to differ from *C. s. rufonodulosum* only in having less prominent tubercles. While fresh examples of *C. s. scabridum* are pale greyish, sometimes zoned with orange-brown, and with rows of articulated black and white marks crossing the rows of tubercles, an old, dead specimen is light brownish-buff with dark brownish-orange tubercles, exactly as in most South African *C. s. rufonodulosum* (some examples are tinged violet), suggesting that the coloration to be seen in specimens of the latter is secondary.

A syntype of *C. s. rufonodulosum* (NM–1041/T512) measures 22,5 × 8,7 mm. It is here designated as lectotype; although the labrum is broken it is otherwise in good condition.

Family **Calyptraeidae**

Crepidula capensis praerugulosa subsp. nov.

Fig. 9

Crepidula rugulosa Dunker, 1846 (*partim*). Barnard, 1963: 72, fig. 9f.

Type material

Holotype: SAM–K4564.
Paratypes 1–8: NM–9229/1825.
Paratypes 9–11: SAM–K4580.

Diagnosis

A Pleistocene chronosubspecies of *Crepidula capensis* Quoy & Gaimard, 1835, differing in its marginal apex and larger size, and in the absence of rugose sculpture.

Description

Outline curved-pyriform, breadth variable, apex spirally coiled, situated on postero-lateral margin, protoconch frequently retained in moderately large specimens; outer surface with regular, well-marked growth lines. Septum as in *Crepidula capensis*, i.e. margin sigmoid, shallowly concave on right, with a prominent lobe to the left of the midline, and a deep, narrow sinus on the left side.

Dimensions

Holotype: 27,1 × 21,7 mm.
Paratypes: 27,7 × 18,2 mm;
35,6 × 31,0 mm.

Distribution records

Late Pleistocene: found extensively in exposures of 7 m beach adjacent to present open coast between Elands Bay and Saldanha Bay; Kruispad, 4,6 m a.s.l. (S.A.M.); Velddrif West, 4–7 m a.s.l. (S.A.M.) (type locality); Milnerton lagoon (S.A.M.).

Remarks

Although many species of *Crepidula* are notoriously variable in shell shape, the numerous specimens of *C. c. praerugulosa* show its characters to be relatively constant, save for some variation in proportions as discussed below. While it is always distinguishable from *C. capensis* Quoy & Gaimard, 1835 (syn. *C. rugulosa* Dunker, 1846, cf. Kilburn, 1974), the form of the septum and general shape of *C. c. praerugulosa* agree very closely with that species. *C. capensis* does not occur in the same deposits, and it seems advisable to rank *C. c. praerugulosa* as a chronosubspecies rather than as a full species.

The regularly curved ventral margin of *C. c. praerugulosa* suggests that it lived attached to mussel shells, a common habitat of *Crepidula porcellana* Lamarck, 1801. *C. c. capensis* appears to live entirely on the undersides of rocks. Indeed the wide range of proportions found in *C. c. praerugulosa* (breadth ranging between 0,66 and 0,87 of length) somewhat parallels that of *C. porcellana*. In the latter species the broader form generally occurs in individuals attached to the wider, flatter, posterior part of the bivalve surface, while the narrower form generally lives on the strongly curved anterior or umbonal part. Possibly the same may have applied to *C. c. praerugulosa*. One paratype even shows a series

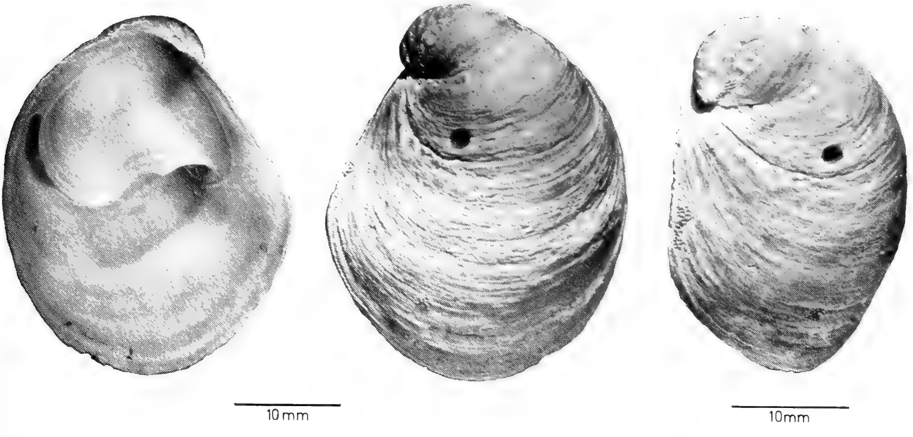

Fig. 9. *Crepidula capensis praerugulosa* subsp. nov. Holotype. (Velddrif West.)

of xenomorphic ridges, strongly suggesting attachment to the ribbed mussel *Aulacomya ater* (Molina, 1782).

In addition to the type series of *C. c. praerugulosa*, a set of eight specimens from an older deposit 1,5 km north of Langebaan (9,5 m a.s.l.) has been examined. These are in a very poor state of preservation, but are morphologically most interesting. Not only is the apex in these specimens more terminal than in typical *C. c. praerugulosa*, and the shells on the average more compressed, but the left side of the septum appears to be less lobate. This might be construed as indicating an origin from a *porcellana*-type ancestor. Much more and better material is needed, however.

Family **Buccinidae**

Triumphis dilemma sp. nov.

Fig. 10

Type material

Holotype: SAM–K4565.
Paratype 1: NM–A1217/T1827.

Diagnosis

Anal canal well developed; shell covered by thin spiral lirae with feeble axial folds on the spire.

Description

Ovate-fusiform, aperture nearly twice length of spire, whorls moderately convex, aperture constricted, labrum thickened, expanded, anal canal trough-like, rendering the lip shouldered; labrum with ten internal ridges, terminating in denticles of which the anterior two are partially fused; labium with a

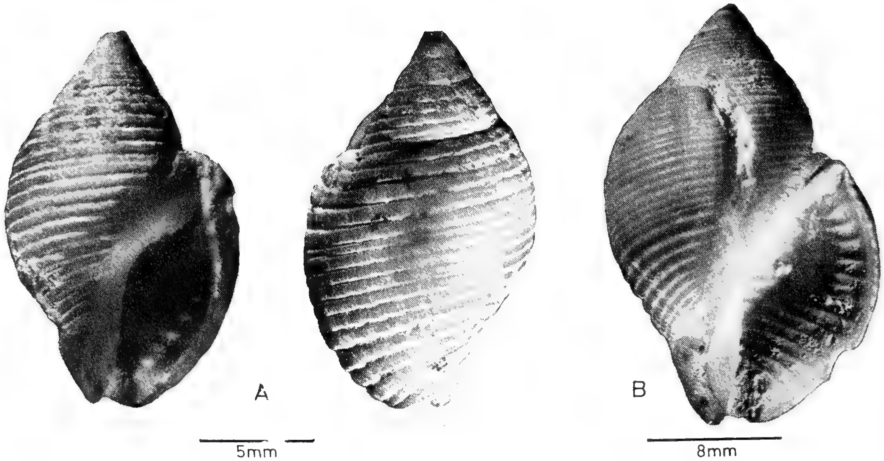

Fig. 10. *Triumphis dilemma* sp. nov. A. Holotype. B. Paratype 2. (Quarry 1,5 km north of Langebaan.)

moderately wide, flattened callus, which is continuous with that of the labrum; paries with one or two denticles, columella with three basally; fasciole weak. Sculptured by tabulate spiral cords, with sharply incised intervals; cords 5–6 in number on penultimate whorl, 17–18 on body whorl, median ones on last whorl mostly shallowly bisected; intervals between cords with fine axial plicules; spire with obscure traces of axial folding. Apex worn, four teleoconch whorls remaining.

Dimensions

Holotype: 16,3 × 10,4 mm.
Paratype 1: 14,8 × 9,3 mm.
Paratype 2: 24,9 × 16,0 mm.

Distribution records

Early Pleistocene at Langebaan, 9,5 m beach (type locality).

Remarks

Although the thickened labrum and fully-developed apertural characters suggest that the type specimens are adult, two larger specimens from the same deposit are probably conspecific. The latter are, however, in poor condition (one being fragmentary), and there are no intermediate specimens to connect the two extremes. They are therefore excluded from the type material. Although similar in general shape, proportions and sculpture, these larger individuals show reduced development of the anal canal, less constricted apertures and reduced lip denticles. Thus the labrum is lirate internally, without denticles, the columella pustules are weak, and the paries bears only one low tubercle. On the body whorls of these two specimens there are 25–34 spiral ridges. The more complete specimen (four teleoconch whorls remaining, apex worn) measures 25 × 16,3 mm.

The affinities of *Triumphis dilemma* are not clear. In some respects it resembles species of the genus *Cantharus* Röding, 1798, but in apertural characters is closer to *Triumphis* Gray, 1857. It differs from the Recent Panamic *T. distorta* (Wood, 1838) in shape, in the presence of sculpture over the whole surface, and in the less developed anal canal.

Family **Terebridae**

Duplicaria otiosa sp. nov.

Fig. 11

Type material

Holotype: NM-8185/T1832.
Paratype: SAM-K4567.

Diagnosis

Small (15,0 mm), with 11 strong, rounded axial ribs with sloping sides, shallowly cut by a subsutural groove, demarcating a series of oblong subsutural nodules; no other spiral sculpture.

Description

Acuminate, 7 teleoconch whorls; whorls strongly convex; spire about twice length of aperture; siphonal fasciole strongly twisted and carinate, columella thinly calloused, aperture elongately ovate-rhombic. Subsutural groove situated one-third of whorl length from upper suture, shallow, incising axial ribs, but barely cutting interstices; only visible from the 4th whorl onwards. Axial ribs extending from suture to suture, feebly opisthocyrt, rounded with gently sloping sides, narrower than intervals, strongly developed throughout, 11–12 in number on first teleoconch whorl, 11 on penultimate whorl; posterior part of each rib (cingulum), where cut off by the sulcus, is axially oblong, not noduliform. No sign of spiral striae, but growth lines conspicuous. Protoconch worn, bluntly conical, of about $2\frac{1}{4}$ whorls.

Dimensions

Holotype: 14,5 × 4,5 mm.
Paratype: 16,4 × 4,6 mm, labrum broken.

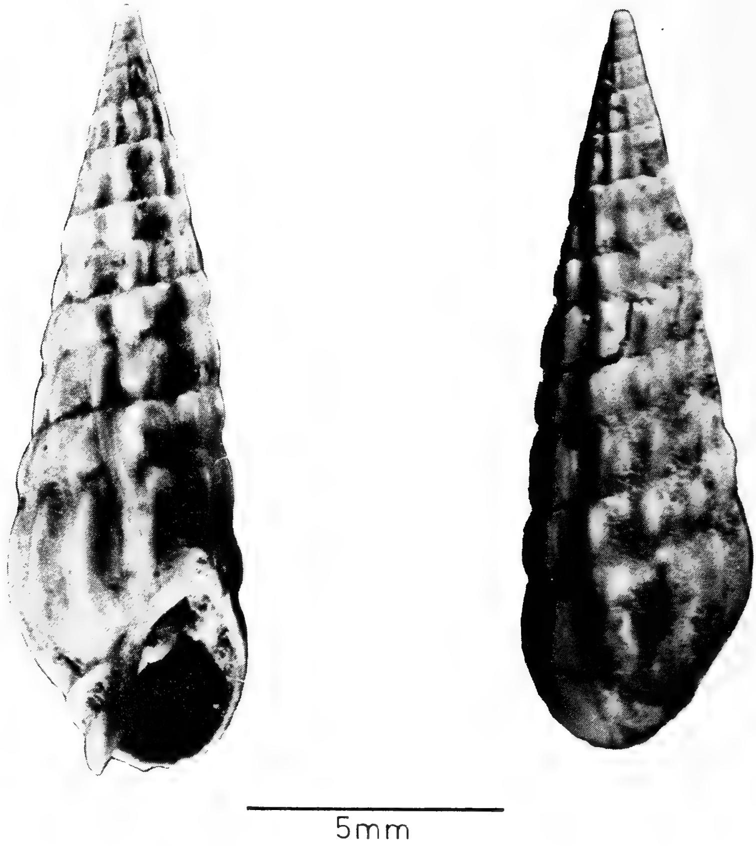

Fig. 11. *Duplicaria otiosa* sp. nov. Holotype. (Coega salt works.)

Distribution records

Pit at Coega salt works, 4,5 m a.s.l. (type locality).

Remarks

Closely allied to *Strioterebrum* (*Partecosta*) *wilkinsi* Dance & Eames, 1966, from the Recent Hammar Formation of Iraq. *Duplicaria wilkinsi* differs in its more nodular subsutural band, in the development of the subsutural groove on the early whorls and in its convex whorl profile. Cernohorsky (1969: 221) lists *D. wilkinsi* as a synonym of the unfigured *Terebra fuscobasis* E. A. Smith, 1877. However, Melvill & Standen (1917: 208) noted the presence of spiral microstriae in the latter, these being apparently absent in both *Duplicaria wilkinsi* and *D. otiosa*.

Of species recorded from South Africa *D. otiosa* resembles only *D. evoluta* (Deshayes, 1859) from Natal and the Indo-Pacific; this is a much larger species (30–40 mm), with a bigger protoconch and a finely punctate subsutural groove, with the axial ribs shouldered where they border the latter.

The radula of *D. otiosa* will never be known, and we are referring it to the genus *Duplicaria* Dall, 1908, on account of its general resemblance to Recent species such as *D. evoluta* and *D. fictilis* (Hinds, 1845).

Family **Actaeonidae**

Pupa* (*Strigopupa*) *daviesi sp. nov.

Fig. 12

Actaeon (*Solidula*) *suturalis* (*non* A. Adams): Sowerby, 1892: 52.
?*Actaeon pudica* (*non* A. Adams): Turton, 1932: 2.
Solidula sulcata (*non* Gmelin, 1791): Barnard, 1962: 192 (*partim*); 1963*a*: 316.
?*Solidula suturalis:* Barnard, 1963*a*: 316.

Type material

Holotype: SAM–K4568.
Paratypes: NM–A1218/T1828;
NM–A1219/T1827;
NM–8186/T1824.

Diagnosis

Narrowly pupoid, lip flattened, left side of base obliquely truncate, columella with a single bifid fold, no parietal tubercle, sculpture of low, tabulate spiral ridges; axial colour lines visible under ultraviolet light.

Description

Narrowly pupiform, with acute, cyrtoconical spire, sutures moderately deep but not channelled, whorls gently convex; profile of labrum somewhat flattened in middle, basally initially sharply rounded, becoming obliquely truncate on left side, which lies in plane of curvature of left side of body whorl profile. Columella with a single strong fold, shallowly bisected by a groove, paries fairly straight above, strongly curved below, basal parietal tubercle absent. Surface sculptured by low, flat-topped spiral ridges separated by narrow grooves; first teleoconch whorl with three spiral cords, increasing to 7–11 on the fourth whorl; in the middle of the body whorl these ridges tend to be bisected by median grooves, and on the base split into thinner and more widely spaced lirae. Growth lines regular and rather coarse, crossing spiral cords and forming fine plicules in the intervals, rendering these superficially foveolate.

Shell always bleached, but under U.V. illumination pigments fluoresce to produce a negative pattern of numerous thin, wavy axial lines, the posterior ends of which tend to fuse below the suture.

Dimensions

Holotype: 14,6 × 6,8 mm.
Paratypes: 21,6 × 10,0 mm;
20,8 × 9,4 mm;
20,8 × 9,3 mm.

Distribution records

Coega salt works, 4–7 m a.s.l. (N.M.); Redhouse, 7 m a.s.l.; The Creek, 5,7 m a.s.l.; Knysna, 4,6 m a.s.l. (S.A.M.) (type locality); Sedgefield, 5 m a.s.l. (S.A.M.); Klein Brak River, 3,3 m a.s.l. (N.M., S.A.M.). See Davies (1972) for site information.

Remarks

Pupa daviesi was initially reported from South Africa as the Philippine *Pupa suturalis* (A. Adams, 1855), as indicated by N.M. material originally from the Crawford collection, on specimens from which Sowerby based his 1892 record. Some of these were subsequently sent by Henry Burnup to E. A. Smith as *P.* '?*suturalis*', and were returned as *P.* '*solidula* var.'. J. R. le B. Tomlin, who saw the same material, disagreed with both identifications, but did not suggest an alternative. We agree that neither *P. suturalis* nor *P. solidula* is at all similar to the present species. Adams (1855: 61) in his original description of *P. suturalis* stressed the conspicuously channelled suture, this being shallow in *P. daviesi*. *P. solidula* (Linnaeus, 1758) is a large (20–30 mm), globose species with very different columella folds and a rounded base. *P. daviesi* was probably the species that was recorded from Port Alfred beach drift as *Acteon pudica* (A. Adams, 1855) by W. H. Turton. Judging by Reeve's figure (1865*a*: pl. 3 fig 13) this is a true *Acteon* (with simple columella pleat); otherwise it does resemble *Pupa daviesi* in form and sculpture, but has a wider aperture and a rounded base.

P. daviesi is referable to the subgenus *Strigopupa* Habe, 1958, which includes only a few species, all characterized by their obliquely truncate base and strigate colour pattern. Other species referable here are *P. strigosus* (Gould, 1859), *P. affinis* (A. Adams, 1855) and *P. fumata* (Reeve, 1865). *P. strigosus* from Japan appears to have a far more prominent double columella fold than any of the others; it shows a well-developed parietal denticle, and has the groove separating this from the columella fold markedly reduced; spiral sulci are fewer than in *P. daviesi*. *P. affinis* (of which *P. fumata* should be regarded as a synonym) is even closer to *P. daviesi*, differing only in possessing a parietal tubercle and a more strongly bisected columella fold; although generally slightly narrower than *P. daviesi*, there is some overlap in this respect. *P. affinis* at the present day lives as far south as Durban Bay (it is the species misidentified by Barnard (1963*a*: 316) as *Solidula sulcata* (Gmelin, 1791)). In all probability *Pupa daviesi* originated as an isolated deme of the *P. affinis* population, but in view of the structural differences we believe that it should be given full species status. This species has been named in honour of Professor O. Davies, collector of much of the Natal Museum Pleistocene material used in this study.

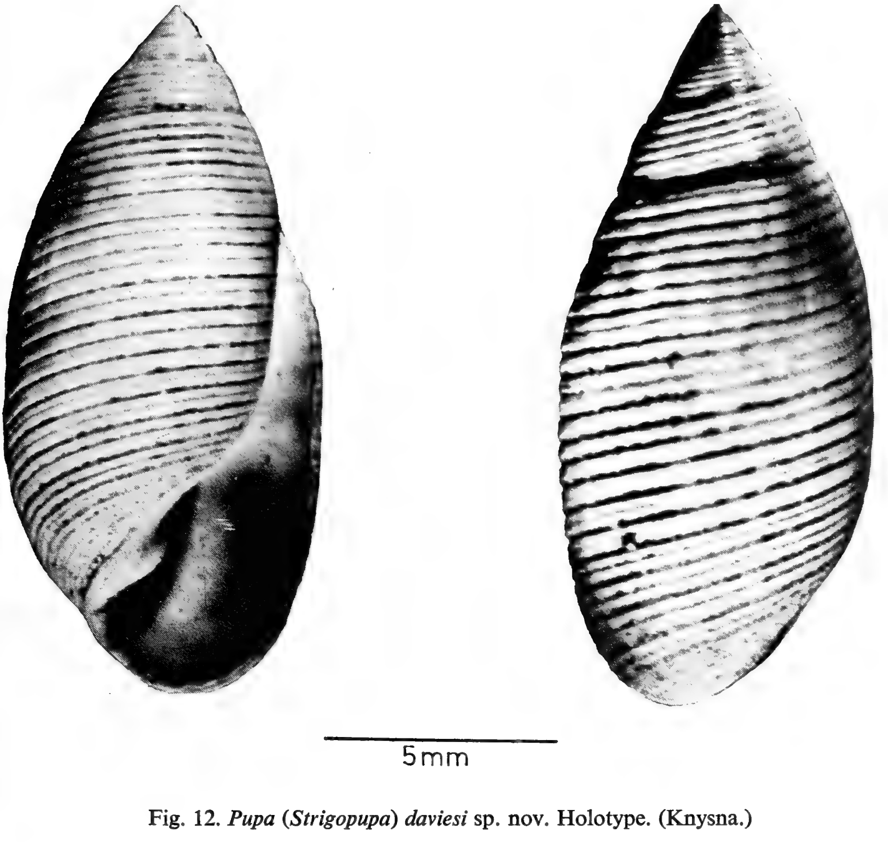

Fig. 12. *Pupa* (*Strigopupa*) *daviesi* sp. nov. Holotype. (Knysna.)

Class BIVALVIA

Family **Nuculanidae**

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

Fig. 13

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.
Nucula largillierti Philippi, 1851: 87.
Leda plicifera A. Adams, 1856: 50.
Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110 (further references).

Description

Cape Pleistocene material: nuculaniform, rostrum conspicuous but short, very truncate; shell thin; umbo anterior to midline, antero-dorsal and anterior margins well rounded, ventral margin gently convex, postero-dorsal margin long

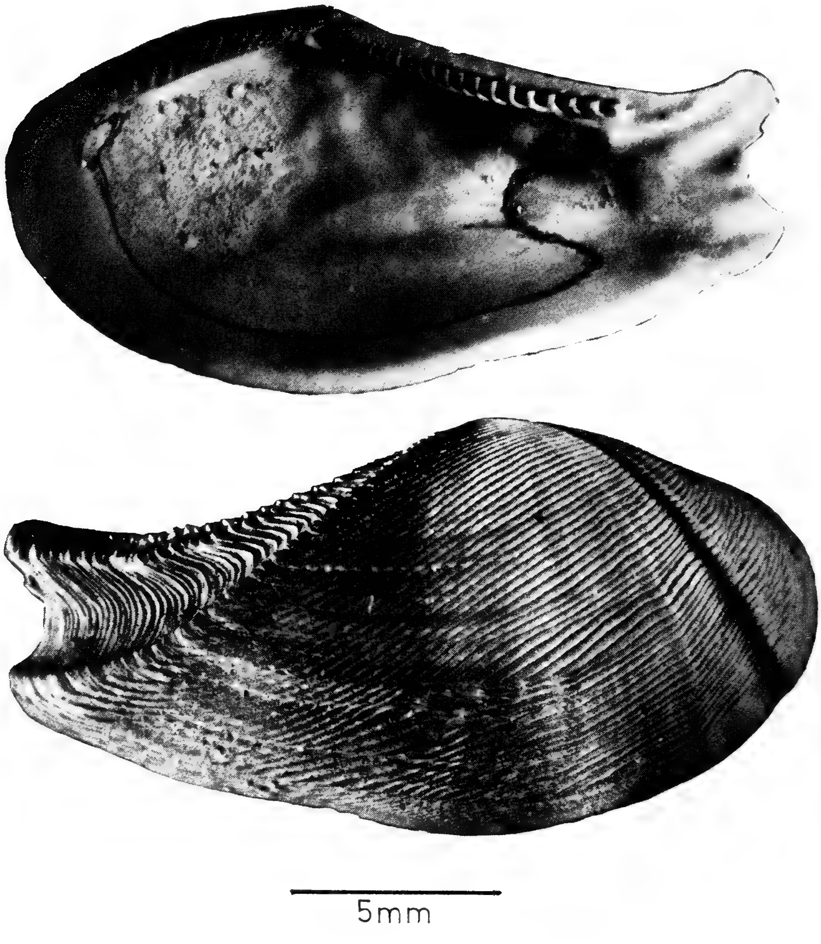

Fig. 13. *Nuculana* (*Lembulus*) *bicuspidata* (Gould, 1845). (Kruispad, Velddrif.)

and slightly concave. Surface sculpture of regular, oblique, sharply incised ribs, becoming concentric anteriorly, growth lines faint. Posterior end with a prominent broad sulcus, bordered in front by a sharp umbonal ridge, and behind by a broader dorsal ridge, rendering posterior margin bicuspidate; this sulcus is crossed by lunulate, comarginal ridges, which form small squamose denticles along the crest of the umbonal ridge, and two similar rows on the dorsal ridge, separated by a shallow furrow. Anterior end bearing a low, narrow umbonal ridge, bordered behind by a shallow concavity, rendering the margin sinuous at this point; surface anterior to the ridge sometimes with 1 or 2 feeble radial lirae. Resilifer small, triangular; hinge teeth chevron shaped, at shell length of 18 mm with 25 teeth posteriorly, 21 anteriorly. Lunule concave, lanceolate, extending to posterior end, bearing growth lines only. Muscle scars and pallial line very weakly impressed, pallial sinus short, ascending, not confluent with pallial line.

Dimensions

17,1 × 9,5 mm, 17,1 × 9,4 mm, 16,6 × 9,3 mm.

Distribution records

Redhouse (S.A.M.); Kruispad, 5,1 m a.s.l. (S.A.M.); Milnerton (S.A.M.).

Remarks

Pleistocene material agrees well with published figures and with a Recent N.M. specimen from Senegal. The species at the present day ranges from Mauritania to Angola (Nicklès 1950). A closely allied species, *N. gruveli* Nicklès, 1952, from the Quaternary of Gabon, differs in having a weaker posterior sulcus, a more central umbo, and in being less truncate posteriorly.

The only two comparable species known from South Africa are *N. lamellata* Sowerby, 1904, and *N. gemmulata* Sowerby, 1904, both Recent species from moderately deep water off Natal/Zululand. In these two the posterior sulcus is traversed by a median ridge or ridges, and there is no anterior umbonal ridge.

Family **Ungulinidae**

Felania diaphana (Gmelin, 1791)

Fig. 14

Venus diaphana Gmelin, 1791: 3292.
Lucina adansoni Reeve, 1850 (*non* Orbigny): pl. 9 (fig. 51).
Lucina senegalensis Reeve, 1850: appendix.
Felania diaphana: Recluz, 1851: 71. Chavan, 1962: 5.
Felania rosea Recluz, 1851: 72, pl. 2 (figs 10–12).
Diplotodon [*sic*] cf. *senegalensis:* Smith in Rogers, 1906: 294.
Diplodonta (*Felania*) *diaphana:* Lamy, 1920: 371 (references). Fischer-Piette, 1942: 317, pl. 14 (fig. 7) (holotype). Nicklès, 1950: 188, fig. 351.
?*Diplodonta* (*Felania*) *agulhasensis* Thiele & Jaeckel, 1931 (*partim*): 219. Barnard, 1964: 468.
Diplodonta cf. *senegalensis:* Van Hoepen, 1940: 191. Barnard, 1962: 185; 1964: 463.
Ungulina alba (*non* Rang): Fischer-Piette in Davies, 1972: 254.

Distribution records

Cenozoic: Swartkops River (S.A.M.); Coega salt works, 7,1 m a.s.l; Redhouse, 7,2 m a.s.l.; Cradock, 13,5 m a.s.l.; Deal Party, 5,1 m a.s.l.; Knysna,

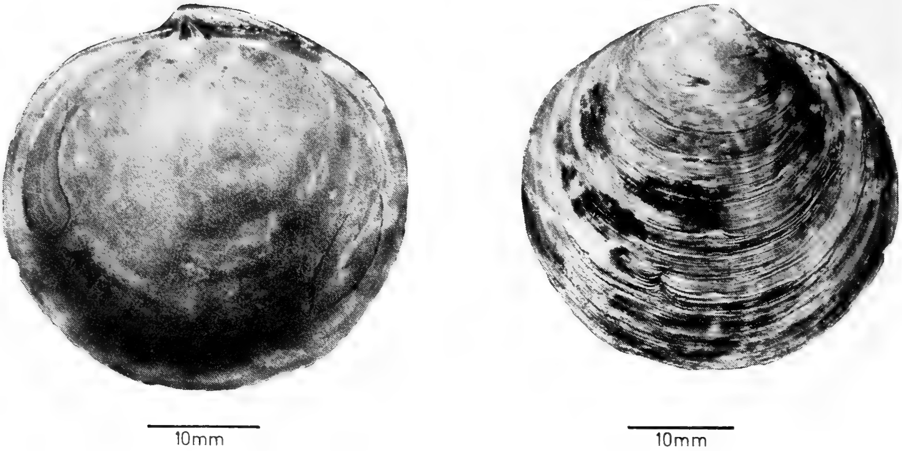

Fig. 14. *Felania diaphana* (Gmelin, 1791). (Mossel Bay.)

4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.); Mossel Bay (N.M.); Cape Cross Bay, S.W.A. (N.M.). See Davies (1972) for site descriptions.

Remarks

This Recent West African species is fairly common in raised Pleistocene beaches along the south Cape coast. Such specimens agree closely with figures of *Felania diaphana*, and with valves from the Cuanza River mouth, 75 km south of Luanda, Angola (N.M.: B. R. Stuckenberg). A rather fresh right valve from Cape Cross Bay, South West Africa (N.M.: O. Davies) may indicate the Recent occurrence of the species within South African limits. However, Thiele & Jaeckel's record (1931: 219) of the species (as *Diplodonta* (*Felania*) *rosea*) from deep water on the Agulhas Bank requires confirmation. The species at present is known to range from Mauritania to Angola (Nicklès 1950).

Family **Lucinidae**

Loripes (*Microloripes*) *liratula* (Sowerby, 1889)

Fig. 15

Lucina (*Divaricella*) *liratula* Sowerby, 1889: 155, pl. 3 (fig. 5); 1892: 61, pl. 2 (fig. 63).
Lucina liratula: Haughton, 1932: 35.
Lucina contempta (*non* Cossman): Turton, 1932: 235, pl. 62 (fig. 1641).
Divaricella liratula: Barnard, 1964: 479.

Description

Subcircular, moderately compressed; sculptured by growth lines and fine acentric lirae, which are rather irregular, but tend to be somewhat oblique across the middle, distinctly undulating at each end. Lunule small, ovate, concave, wider in right valve than left. Resilifer deep, internal, oblique. Hinge plate narrow; right valve with a strong, elevated anterior lateral tooth, a ridge-like posterior lateral, partly overlying distal end of resilifer, and a single oblique cardinal; left valve with anterior and posterior ridge-like laterals and a cuneiform anterior cardinal with a low posterior cardinal ridge adjacent to it. Anterior adductor scar flexuous. Internal margin crenulate.

Dimensions

17 × 17 mm, 16,2 × 16,5 mm, 15,2 × 15,4 mm.

Distribution records

Swartkops River (S.A.M.); Cradock, 13,5 m a.s.l.; Coega salt works, 7,1 m a.s.l. (S.A.M.); Knysna, 4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M., N.M.); Groot Brak River (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.); Verlorevlei, 4 m a.s.l. (S.A.M.); Kruispad, 5,1 m a.s.l. (S.A.M.); Bloemendal (S.A.M.); Geelbek, 4,5 m a.s.l. (S.A.M.); Churchhaven, 1,5 m and 4,3 m a.s.l. (S.A.M.).

Remarks

The present species was described as a *Divaricella*, but its oblique internal ligament shows it to be a *Loripes*. We follow Chavan (1937) in treating *Microloripes* as a subgenus of *Loripes*, in preference to his 1969 system under which it is transferred to the genus *Parvilucina*. In *Parvilucina* the ligament is sunken, but not internal, and lies parallel to the dorsal margin.

Descriptions and figures strongly suggest that *Loripes liratula* is a synonym of the Recent West African *Loripes* (*Microloripes*) *contrarius* (Dunker, 1846). However, as no comparative material is available, we are forced to retain Sowerby's name *pro tem*. Although described and recorded as a Recent species, *L. liratula* appears to be extinct in South Africa, beach specimens being derived from Pleistocene deposits.

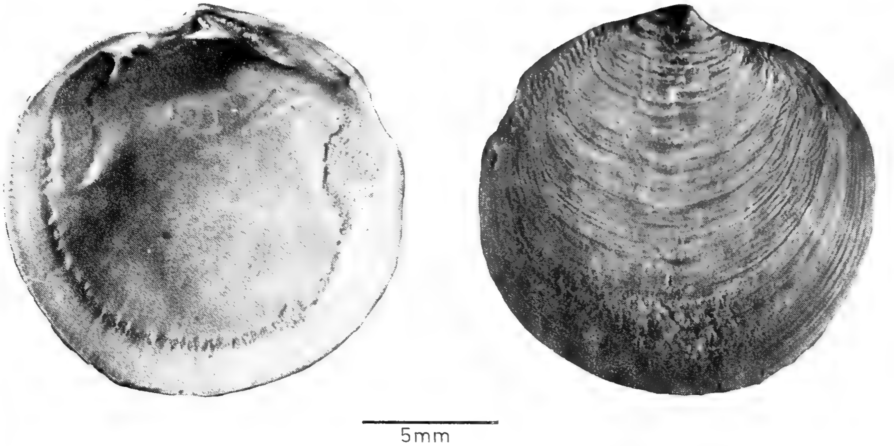

Fig. 15. *Loripes* (*Microloripes*) *liratula* (Sowerby, 1889). (Kruispad, Velddrif.)

Family **Veneridae**

Pitar (*Lamelliconcha*) *madecassina* (Fischer-Piette & Delmas, 1967)

Cytherea manillae (*non* Sowerby, 1851): Sowerby, 1897: 24.
Pitaria manillae Barnard, 1964: 503. Boshoff, 1965: 164, pl. 10 (fig. 2).
Dosinia (*Sinodia*) *madecassina* Fischer-Piette & Delmas, 1967: 12, pl. 3 (figs 17–19).
Pitar (*Lamelliconcha*) *madecassina:* Fischer-Piette, 1968: 789, pl. 1 (figs 3–4).

Distribution records

Cenozoic: Cradock, at head of Papkuils estuary, 15,2 m a.s.l. (N.M.).

Remarks

Fischer-Piette (1968) compared *Pitar madecassina* with *P. manillae,* and recorded the former from various localities in Moçambique and Natal. He did not, however, suggest that this was the species that had previously been reported from South Africa as *P. manillae. P. madecassina* ranges from the type locality, Madagascar, south to Pondoland (Mzamba, N.M.; Port St Johns, S.A.M.). Although articulated specimens are rarely washed up on the shore, the species lives in abundance at depths of 12–50 fathoms off Natal.

Barnard (1962: 185; 1964: 503) erred in regarding '*Chamelea*' *schwarzi* Newton, 1913 (syn. '*C.*' *rogersi* Newton, 1913, first reviser Barnard, 1962) as being based on worn *P. madecassina.* This late Cenozoic species differs conspicuously from *P. madecassina* in its compressed valves, oblong-ovate shape, moderately curved umbo and weak umbonal ridge; also the anterior and median cardinals of the left valve only intersect at the very dorsal margin. *P. madecassina* is tumid, ovate-trigonal, posteriorly subrostrate with a strong umbonal ridge, umbo strongly prosogyrate, left anterior and median cardinals intersecting some distance below the dorsal margin. '*Chamelea*' *krigei* Newton, 1913, is even more different in form and dentition.

Venerupis dura (Gmelin, 1791)

Fig. 16

Venus dura Gmelin, 1791: 3292.
Tapes dura var. *simili* [*sic*] (? *non similis* Deshayes, 1853): Schwartz, 1910: 116.
Venerupis (*Polititapes*) *dura:* Nicklès, 1950: 203, fig. 387.
Macrocallista lilacina (*non* Lamarck, 1818): Barnard, 1964: 505.
Venerupis dura: Fischer-Piette & Métivier, 1971: 11 (references and synonymy).
Venerupis rufiscensis Fischer-Piette & Métivier, 1971: 13, pl. 3 (figs 2–7). Syn. nov.

Distribution records

Cenozoic: Redhouse (S.A.M.); Knysna, 4,6 m a.s.l. (S.A.M.); Geelbek (S.A.M.); Kruispad, 5,1 m a.s.l. (S.A.M.); Verlorevlei, 4 m a.s.l. (S.A.M.).

Remarks

Venerupis dura is a West African species, living as far south as Luanda (Angola), but also abounding in Late Pleistocene sediments of the south-western and southern Cape. This extinct deme differs morphologically from the Recent

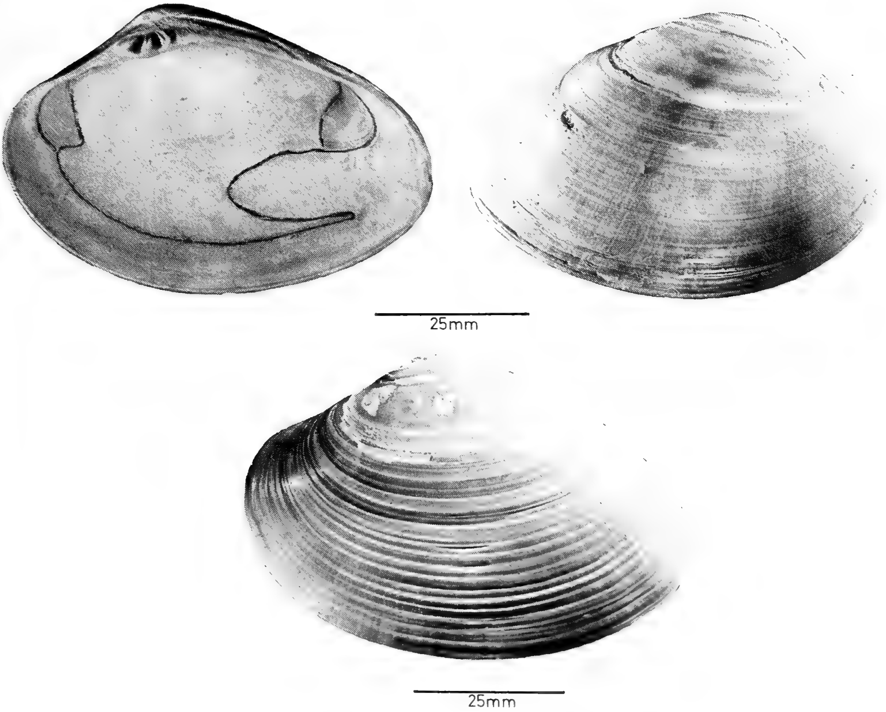

Fig. 16. *Venerupis dura* (Gmelin, 1791). (Kruispad, Velddrif.)

form in its weak to almost obsolete concentric sculpture; while in most specimens shallowly incised concentric grooves are present, in some examples coarse growth lines are the only external surface feature. In addition the pallial sinus is usually somewhat narrower and sharper than in Recent Angolan *V. dura.* Mr C. P. Nuttall, who kindly examined specimens from Verlorevlei, has suggested (*in litt.* 26 August 1971) that these may be comparable with '*Callistotapes vetulus* (Basterot) var. *plioglabroides* Sacco from the Pliocene (Astian) of Piedmont', Italy.

The S.A.M. specimens recorded by Barnard as *Macrocallista lilacina* (Lamarck, 1818) [= *Callista spuma* (Röding, 1798)] are referable to *Venerupis dura.*

We believe *Venerupis rufiscensis* to be based merely on coarsely-ribbed examples of *V. dura.* The range of supposed differences between the two is no greater than that found in the present material. Two Recent Angolan shells (N.M. coll.) even appear to combine the ridge number of *V. dura* with the ridge profile of *V. rufiscensis.*

We are following Fischer-Piette & Métivier (1971) in referring this species to *Venerupis* Lamarck, 1818. However, despite the gradually ascending pallial sinus, its true affinities (as suggested by shape, sculpture, colour and hinge structure) probably lie not with *Venerupis* but with *Paphia* Röding, 1798. Differences between *Paphia*, *Venerupis* and *Tapes* Von Mühlfelt, 1811, are, however, small and possibly artificial. The species at present ranges from southern Morocco to Angola (Nicklès 1950).

Family **Petricolidae**

Petricola* (*Claudiconcha*) *prava sp. nov.

Fig. 17

Type material

Holotype:	SAM–K4569.
Paratypes 1–3:	1 right, 2 left valves, NM–A79/T1820.
Paratype 4:	right valve, SAM–K4570.
Paratype 5:	right valve, SAM–K4571.

Diagnosis

Shell relatively large (40–50 mm), inequivalve, always deformed and irregular; sculptured by fine radial lirae, often only visible posteriorly, and coarse, irregular, non-lamellar growth lines; pallial sinus very deep.

Description

Shape very irregular and always more or less deformed, often somewhat rostrate posteriorly with the ventral margin concave; valves thick and very convex; umbo orthogyrate, strongly curved, varying in position from submedian to less than one-third of distance from anterior end. Sculpture of fine radial lirae, often only visible posteriorly, and coarse, irregular growth lines, sometimes elevated posteriorly, but not lamellar.

Right hinge with two peg-like cardinal teeth, of which the posterior one may be shallowly bisected by a groove. Left hinge with three cardinals of which the anterior is reduced to a small denticle, the central is peg-like, triangular in cross-section, and medially concave below (but not bifid), and the posterior one is an oblique lamella partly fused to the nymph. Nymphs are very large, sometimes massive, more or less projecting and spathulate, separated from valve margin by a deep groove. Pallial sinus free, apically rounded, very deep, extending well below midline.

Dimensions

Holotype: left valve, 49,9 × 37,2 mm;
right valve, 52,0 × 37,4 mm;
breadth of valves together (inflation), 31,3 mm (posterior end chipped).
Paratypes: single left valve, 51,0 × 36,5 mm;
single right valve, 49,3 × 39,9 mm.

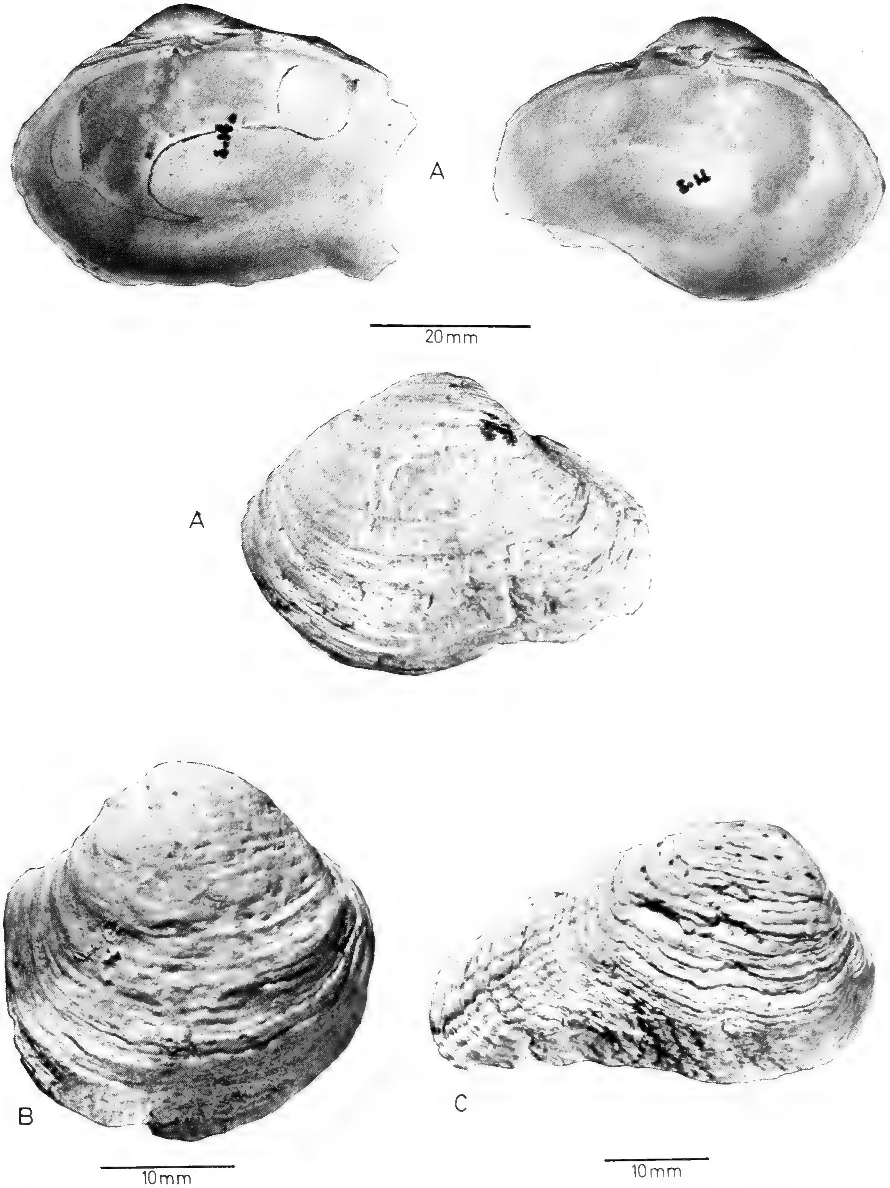

Fig. 17. *Petricola* (*Claudiconcha*) *prava* sp. nov. A. Holotype. B. Paratype 4. A (lower), B, C show variation in shell form. (Quarry 1,5 km north of Langebaan.)

Distribution records

Smitswinkelbaai (Saldanha), behind Sea Harvest factory, 6,5–8 m a.s.l.; quarry 1,5 km north of Langebaan, 9,5 m a.s.l. (type locality). Early Pleistocene.

Remarks

The markedly inequivalve shell of *Petricola prava* shows it to be referable to the subgenus *Claudiconcha* Fischer, 1887. Of described members of the taxon, *Petricola japonica* Dunker, 1882, from Japan, *P. quadrasi* (Hidalgo, 1886) from the Philippines and Indonesia, *P. cumingi* Deshayes, 1853, from South Australia, and *P. chinensis* Deshayes, 1853, from China and the Philippines, differ in possessing strong concentric sculpture without radials. On the other hand, while *P. monstrosa* (Gmelin, 1791) from Nicobar and the Ryukyu Islands, and *P. madreporica* (Jousseaume, 1895) from the Red Sea, do show dominant radial lirae as in *P. prava*, in these the lirae are stronger and more uniformly developed, and shell size is markedly smaller. The closest species is probably *P. robusta* Sowerby, 1834, from tropical west America, which is usually regarded as a *Rupellaria*, but has the unequal valves of *Claudiconcha*; this differs from *Petricola prava* in its somewhat weaker radials and much shallower pallial sinus.

The distinctly inequivalve shell and large size distinguish *P. prava* from the three Recent South African species, *Petricola* (*Rupellaria*) *bicolor* Sowerby, 1854, *P.* (*Petricola*) *ponsonbyi* Sowerby, 1892, and *P.* (*P.*) *divergens* (Gmelin, 1791). The latter two also differ in their divaricate sculpture. *P. bicolor* is the most similar, as not only are some individuals very slightly inequivalve, but a rock-boring morph which occurs in South West Africa is frequently deformed in much the same manner as *P. prava*. However, the stronger radial sculpture and shallower pallial sinus of *P. bicolor*, together with the characters cited above, are diagnostic.

Family **Donacidae**

Donax sanctuarium sp. nov.

Fig. 18

Type material

Holotype: right valve, SAM–K4572.
Paratypes: 1 right, 1 left valve, NM–A1216/T1826;
2 right, 2 left valves, SAM–K4573.

Diagnosis

Moderately large (40–60 mm); oblong-trigonal, posteriorly truncate, umbonal ridge feeble; smooth, posterior end with concentric ridges, and a series of interstitial radials just behind the umbonal ridge; inner margin smooth. Nymphs very prominent, lateral teeth present, except for the right anterior one, which may be absent.

Description

Oblong-trigonal, length 2,1 × height, umbo approximately one-third distance from posterior end; antero-dorsal margin straight, anterior end well-

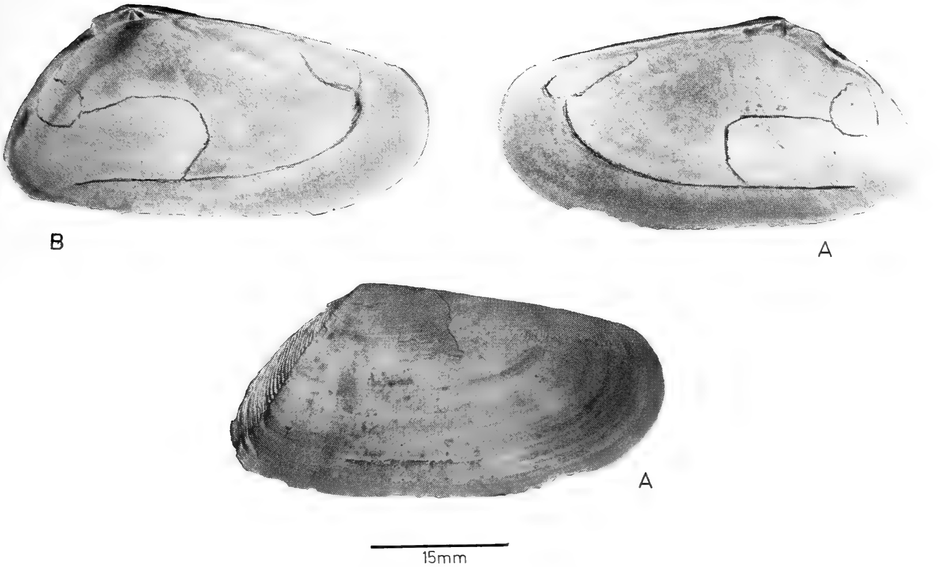

Fig. 18. *Donax sanctuarium* sp. nov. A. Holotype. B. Paratype. (Churchhaven.)

rounded, postero-dorsal margin convex, declivous, posterior end sharply rounded, ventral margin gently and evenly curved, ends narrowly gaping, posterior end with a very slight umbonal ridge, but no distinct angle, posterior face moderately truncate. Greater part of shell smooth, except for growth lines, posterior face corrugated by fine, wavy, concentric ridges, with a narrow area adjacent to the umbonal ridge also traversed by interstitial radial riblets; inner ventral margin of valves smooth. Hinge of left valve with two narrow, subequal, divergent cardinals, a low ridge-like anterior lateral tooth situated close to the cardinals, and a rather remote and stronger ridge-like posterior lateral. Hinge of right valve with a somewhat trigonal posterior cardinal, somewhat variable in shape, but always bisected by a shallow groove, occasionally weakly bifurcate; anterior cardinal long, oblique and ridge-like, anterior lateral feeble or absent, posterior lateral strong and elongate, bordered dorsally by a trough. Nymph prominent, variable, but usually large and projecting conspicuously beyond dorsal margin. Pallial sinus extending to midline, lower margin fused with pallial line, not markedly ascending, shape variable, but usually straight dorsally, roundly truncate anteriorly.

Dimensions

Holotype: 46,4 × 22,9 mm.
Paratypes: 59,5 × 28,2 mm;
52,4 × 24,7 mm.

Distribution records

Churchhaven, 1,5 m a.s.l. (N.M., S.A.M.) (type locality).

Remarks

Donax sanctuarium appears to be quite distinct from any other member of the genus. It may perhaps be compared with *D.* (*Capsella*) *variegata* (Gmelin, 1791), from the Mediterranean, which, however, is rounded and smooth posteriorly, and has a weaker nymph. *D. haughtoni* Carrington & Kensley, 1969, from the Late Cenozoic of Namaqualand, is a larger, deeper and more ovate species, with a more central umbo and a smooth posterior face. *D. oweni* Hanley, 1843, from West Africa is smaller (25 mm) and has a very curved ventral margin.

D. sanctuarium (whose specific name is a literal translation of the type locality Churchhaven) does not agree with any of the described subgeneric units (cf. Keen 1969) of the genus *Donax*. As the current system of classification is most unsatisfactory, we have not erected a new taxon for its reception.

Family **Tellinidae**

Gastrana fibrosa sp. nov.

Fig. 19

Type material

Holotype: right and left valves (articulated shell), SAM–K4574.
Paratypes: 1 articulated shell, 1 right valve, 2 left valves, NM–A1220/T1830;
2 right valves, 2 left valves, SAM–K4581.

Diagnosis

Large (60–70 mm), very solid, posterior end produced but not rostrate; sculptured medially by radial threads, more or less replaced at each end by lamellose concentric threads. Hinge plate massive, left anterior cardinal projecting and spathulate, not bifid.

Description

Shell very solid, moderately compressed, with a narrow gape at each end. Umbo situated two-fifths of total length from anterior end; anterior end broadly rounded, posterior end somewhat tapering, with a very slight umbonal ridge; between the umbonal ridge and the postero-dorsal margin there is a faint indication of a ridge, visible more as an alteration in the direction of the concentric sculpture than as a prominence; postero-dorsal margin straight or slightly convex, ventral margin evenly convex or with a suggestion of a sinuosity posteriorly.

Sculpture tripartite, with regular thread-like concentric lamellae posteriorly, another weaker series anteriorly, and the median half or two-thirds bearing fine, uneven, radial threads, crossed by growth lines which may render them almost cancellate; in odd individuals the concentric threads may cross the whole surface, although becoming irregular medially.

Hinge complex massive, two cardinal teeth in each valve, no laterals. Right

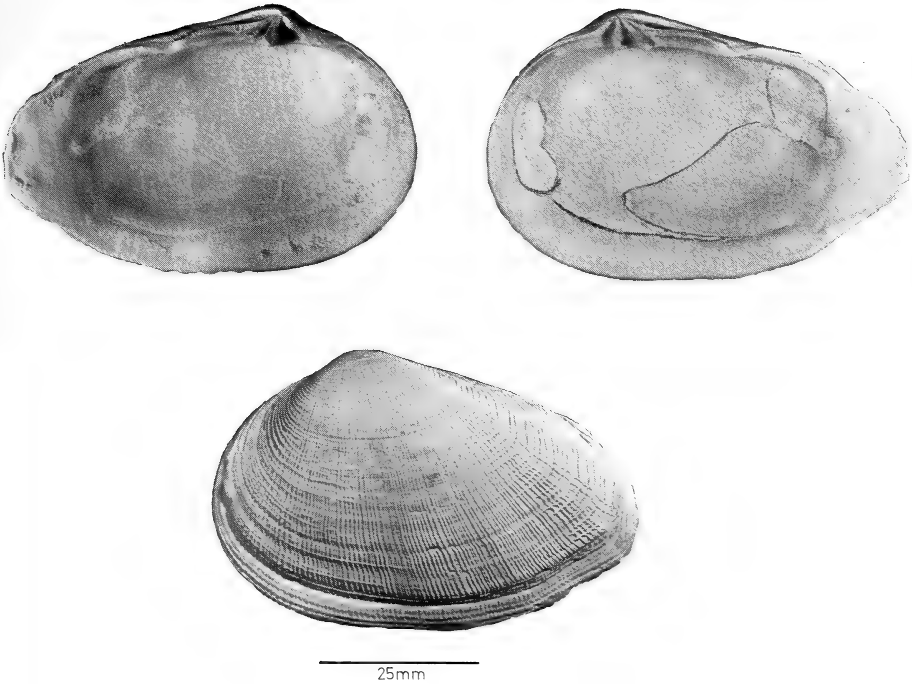

Fig. 19. *Gastrana fibrosa* sp. nov. Holotype. (Naval Academy, Saldanha.)

anterior cardinal almost perpendicular to hinge axis and diverging from posterior cardinal at an angle of 40–45°; both teeth are simple and ridge-like, not, or very slightly, bisected, posterior cardinal longer than anterior one. Left anterior cardinal large and spathulate, projecting conspicuously from hinge plate, tip rounded and simple, with only a trace of a median groove; posterior cardinal a rather low, triangular ridge. Nymphs well developed. Adductor muscle scars and pallial line well impressed, pallial sinus deep, largely confluent with pallial line, end rounded to subacute.

Dimensions

Holotype: 66,5 × 43,5 mm;
total breadth 25,3 mm.
Paratypes: 72,4 × 46,6 mm;
68,8 × 46,0 mm.

Distribution records

Naval Academy, Saldanha (1,7 m a.s.l.) (type locality) and Churchhaven (1,5 m a.s.l.).

Remarks

Gastrana fibrosa is very closely allied to the poorly known *G. multangula* (Gmelin, 1791) (syn. *Tellina polygona* Röding, 1798, *non* Gmelin, 1791) from

Gambia, and may prove to be only a subspecies of that. Judging by Römer's description and figures (1872: 272, pl. 51 figs 5–7), *G. multangula* differs in possessing a subcentral umbo, very fine interstitial radial lirae, continuous concentric threads which traverse the middle, and a stronger umbonal ridge. Unfortunately details of the shape of the left anterior cardinal are unknown, Römer referring to this merely as 'subfisso', which barely applies to *G. fibrosa.* It should be noted, too, that while Römer's figure of *G. multangula* shows a wholly free pallial sinus, his text contradicts this.

G. fibrosa closely approaches *G. rostrata* Carrington & Kensley, 1969, from the Lower Pleistocene of Namaqualand in size and sculpture, but differs in its non-rostrate posterior end and straight or convex dorsal margin, this being concave in *G. rostrata*; hinge details also differ, notably the characteristic left anterior cardinal, which in *G. rostrata* is short and distinctly bisected, rendering the tip almost bifid.

G. fibrosa differs widely from the remaining two comparable species of *Gastrana*, *G. matadoa* (Gmelin, 1791) (syn. *Tellina abildgaardiana* Spengler, 1798) from South and West Africa, and *G. fragilis* (Linnaeus, 1758) from the Mediterranean, both of which are of Recent occurrence. It differs in its much larger size, greater solidity, in outline, non-bifid left anterior cardinal, and different sculpture, the radial element being well developed and the concentric one irregular or restricted to the ends; in *G. matadoa* and *G. fragilis* the concentric lamellae are well developed over the whole surface, and radial sculpture is reduced to very fine interstitial striae.

Tellina (Eurytellina) madagascariensis Gmelin, 1791

Fig. 20

Tellina madagascariensis Gmelin, 1791: 3237. Römer, 1871: 64, pl. 17 (figs 4–7). Dautzenberg. 1912: 102. Nicklès, 1950: 224, fig. 435. Paes da Franca, 1960: 36.
Tellina rosea (*non* Spengler, 1798): Haughton, 1932: 37.
Tellina (Eurytellina) madagascariensis: Boss, 1969: 122, pl. 10 (fig. 3).

Description

Elongate-elliptical, compressed, umbo peaked, slightly anterior to middle, posterior end strongly flexed to right, narrowly gaping; right valve less convex than left; anterior margin broadly rounded, postero-dorsal margin declivous, shallowly concave behind umbo, then straight or slightly convex, posterior end narrowly rounded or feebly truncate, ventral margin evenly curved. External surface with fine growth striae and very faint, scratch-like radial striae; right valve with a low, blunt umbonal ridge, corresponding to a shallow depression in the left valve. Right anterior cardinal tooth simple, posterior one bifid as is the left anterior cardinal; right posterior cardinal thin, ridge-like and simple. Anterior lateral teeth close to cardinals, posterior ones distant, situated at end of nymph; in right valve anterior lateral is strong, posterior one feeble; both left laterals are weak. Nymphs well developed, each with a ridge on its inner surface.

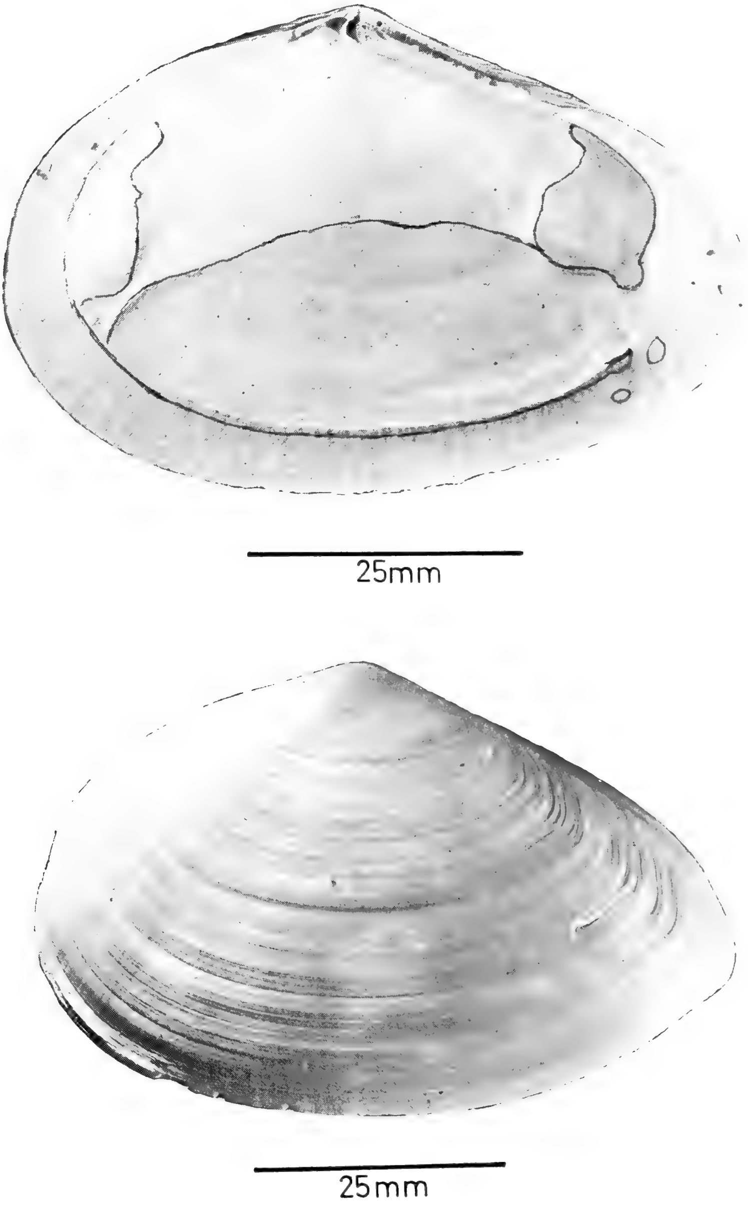

Fig. 20. *Tellina* (*Eurytellina*) *madagascariensis* Gmelin, 1791. (Churchhaven.)

Adductor muscle scars well impressed; two faint cruciform scars just below posterior end of pallial line. Pallial sinus not ascending, lower margin wholly confluent with pallial line, extending almost to anterior adductor.

Dimensions

69,5 × 41,3 × 17,3 mm, 66,8 × 44 × 19 mm.

Distribution records

Redhouse (S.A.M.); Deal Party, 12–23,8 m (N.M.); Cradock, 45,7 m (N.M.); Klein Brak River (Boss 1969); Churchhaven, 1,5 m a.s.l. (S.A.M.); Geelbek (S.A.M.); Verlorevlei, 4 m a.s.l. (S.A.M.); Cape Cross, S.W.A. (S.A.M.).

Boss (1969) showed that previous Recent records of *Tellina madagascariensis* from South Africa were based on *Tellina alfredensis* Bartsch, 1915. He did, however, record the true West African *T. madagascariensis* from a raised beach at the 'Klein' (i.e. Klein Brak) River mouth. During the Pleistocene this species was in fact abundant along much of the south and west coast of the Cape, and in South West Africa. After its extinction along the South African coast, no doubt due to climatic change, *T. madagascariensis* was replaced by the endemic *T. alfredensis*.

Tellina madagascariensis occurs living today from Baia dos Tigres (17°S) to Sao Thome (0°) (Boss 1969).

Macoma (*Heteromacoma*) *tricostata* (Römer, 1872)

Fig. 21

Tellina tricostata Römer, 1872: 235, pl. 49 (figs 10–12).

Description

Both valves rather inflated, right valve slightly deeper than left; outline ovate-trigonal, umbones high, usually situated two-fifths of length from anterior end, but sometimes nearly median; posterior end moderately rostrate, tapering rapidly, end roundly truncate; postero-dorsal margin straight and evenly declivous, rest of margin evenly rounded. Shell slightly flexed to right posteriorly, right valve with a very weak umbonal ridge, followed by 1–2 very feeble ridges, left one with a depressed umbonal ray, followed by a weak ridge near the dorsal margin; surface otherwise sculptured by growth lines only. Pallial sinus very deep, almost reaching anterior adductor scar, non-ascending, lower margin completely fused with pallial line, upper margin feebly bilobate; sinus larger in right valve than in left. Hinge of each valve with two cardinal teeth, of which the posterior ones form thin, feeble ridges, the anterior ones being erect and more peg-like, simple in the right, apically bifurcate in the left. Nymphs large, thick, bordered by deep ligamental furrows.

Dimensions

53,6 × 43,1 × 23,0 mm; 46 × 36,3 × 18,7 mm; 47,2 × 38,3 × 19 mm; 41,3 × 35,0 mm.

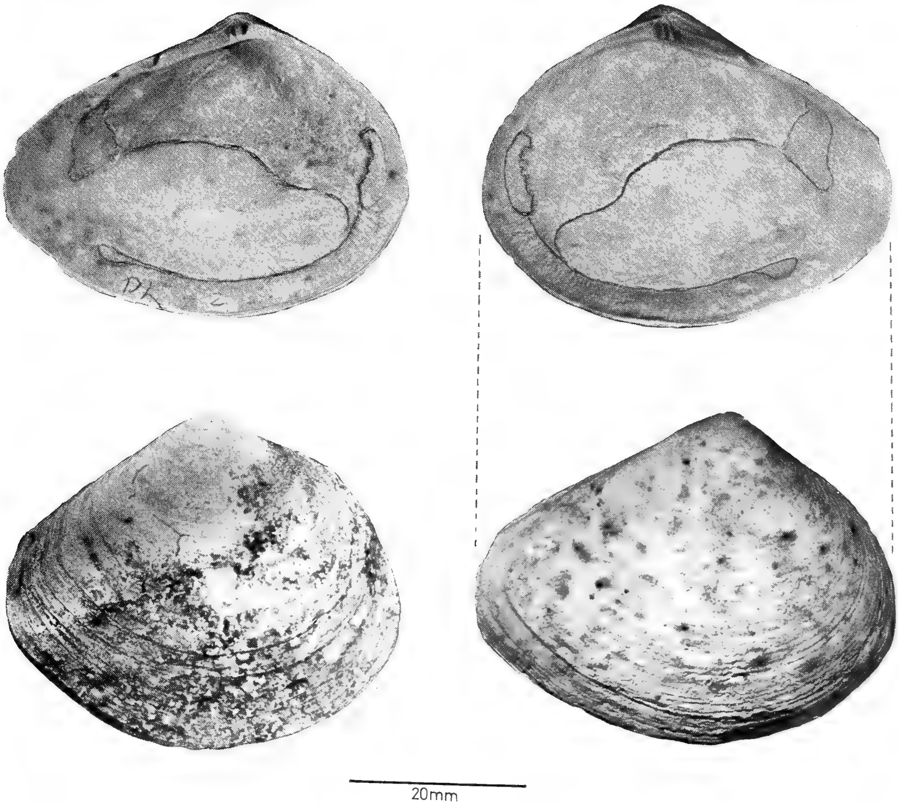

Fig. 21. *Macoma* (*Heteromacoma*) *tricostata* (Römer, 1872). Note variation in form. (Verlorevlei.)

Distribution records

Verlorevlei, 4 m a.s.l. (S.A.M.).

Remarks

Specimens from Verlorevlei agree well with Recent valves from Angola, except in being thicker. While these specimens resemble Nicklès's figure (1950: fig. 432) of the exterior of *Tellina nymphalis* Lamarck, 1818, they disagree with Römer's excellent figures (1872: pl. 45, figs 1–4) of the same species. These show a non-rostrate shell with more extensive, rounded pallial sinus. On the other hand these specimens agree closely with Römer's *T. tricostata* from Gabon. There is, however, some variation in shape in the present material, and one specimen somewhat approaches Römer's concept of *T. nymphalis* in its moderately reduced posterior end. Not only does the relationship between the two require investigation, but re-examination of the holotype of *T. nymphalis* is desirable in order to confirm Römer's interpretation. For the present it is advisable to use the name *tricostata*, which undoubtedly applies to the present material.

The only comparable South African *Macoma* is *M.* (*Macoma*) *litoralis* (Krauss, 1848), a smaller, more compressed species with a lower umbo, stronger hinge-teeth and inconspicuous nymphs.

Leporimetis (*Leporimetis*) *hanleyi* (Dunker, 1853)

Fig. 22

Tellina hanleyi Dunker, 1853: 53, pl. 10 (figs 4–6). Römer, 1871: pl. 14 (figs 7–9); 1872: 214.
Apolymetis orbicularis (*partim non* Sowerby); Barnard, 1964: 549.
Apolymetis papyracea (*non* Gmelin, 1791); Kilburn in Davies, 1972: 252.

Description

Ovate, with peaked umbones situated slightly posterior to middle; shell flexed to the right and narrowly gaping posteriorly; antero-dorsal margin gently convex, anterior end strongly rounded, postero-dorsal margin straight or slightly

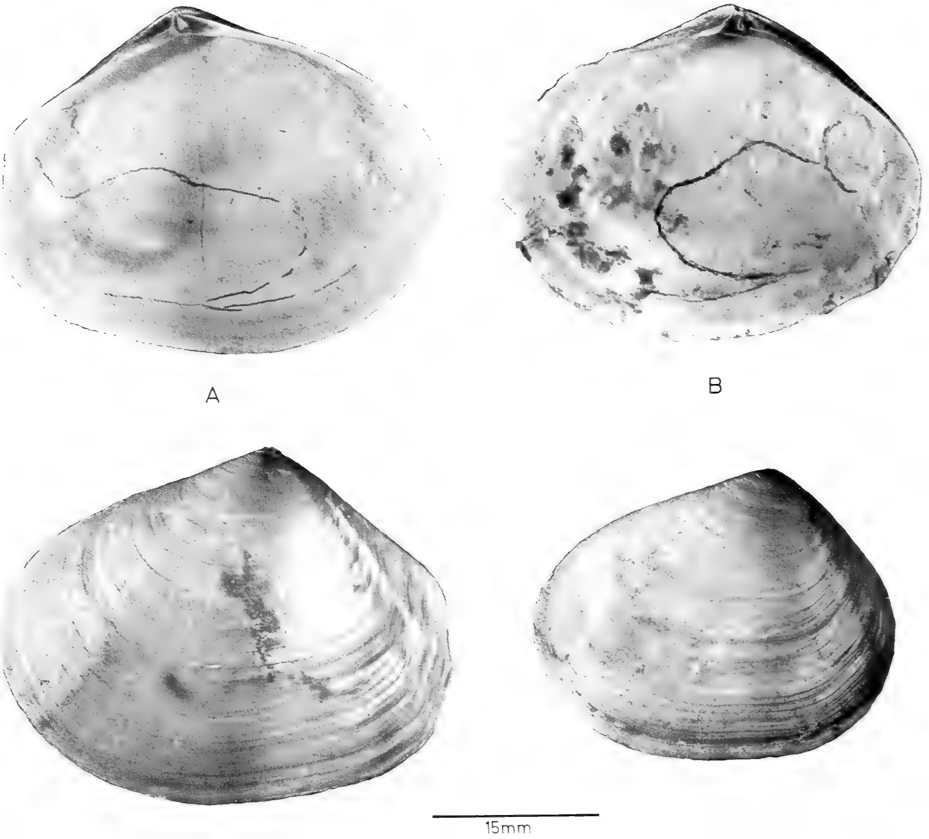

Fig. 22. *Leporimetis* (*Leporimetis*) *hanleyi* (Dunker, 1853). (A. Knysna. B. Redhouse.)

convex, fairly steeply descending, posterior margin truncate to broadly rounded, often showing a weak double sinuosity; ventral margin evenly curved, not sinuated. Sculptured by fine growth lines, becoming coarse posteriorly; umbonal ridge very feeble, often not visible in right valve, in left valve bordered behind by a shallow trough, followed by a second feeble ridge. Hinge in each valve with two ridge-like cardinals, of which the anterior ones are the stronger. Nymphs well developed, moderately impressed into hinge-plate. Pallial sinus deep, extending almost to anterior adductor scar, lower margin largely free from pallial line, upper margin shallowly concave, end rounded to moderately truncate.

Dimensions

41,8 × 31,8 mm, 44,7 × 35,0 mm, 39,0 × 30,5 × 14,4 mm (complete example).

Distribution records

Cenozoic: Redhouse, 7,2 m a.s.l. (N.M.); Knysna, 4,6 m a.s.l. (S.A.M.); Sedgefield, 5 m a.s.l. (S.A.M.); Klein Brak River, 3,3 m a.s.l. (S.A.M.).

Remarks

Pleistocene specimens agree well with Römer's detailed description and figures of *Tellina hanleyi* from Luanda (the original description is not available to us). While South African examples are rarely as rounded posteriorly as in these figures there is much variation in this respect, and one example from Redhouse is decidedly curved behind. The species does not appear to have been discussed by recent authors.

The only comparable species is the Recent West African *Leporimetis* (*Florimetis*) *papyracea* (Gmelin, 1791), which differs in its more elevated, subcentral umbones, markedly more inflated valves, and distinct umbonal ridge, median flexure and postero-ventral sinuosity. Although French workers commonly utilize the name '*lacunosa* Schröter, 1788' for *L. papyracea*, that *nomen* was proposed in a non-binomial work, and was not validated until 1817 (by Dillwyn).

The fossil material recorded by Barnard (1964) as *Apolymetis orbicularis* is actually *Leporimetis hanleyi*. The Recent *Leporimetis* (*Florimetis*) *orbicularis* (Sowerby, 1889) from the False Bay–Port Alfred area is a strongly inflated, suborbicular species with a well-developed umbonal ridge, and there are also differences in details of the cardinal complex.

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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 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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R. N. KILBURN & A. J. TANKARD

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THE MORPHOLOGY AND RELATIONSHIPS OF A CROCODILIAN, *ORTHOSUCHUS STORMBERGI*, FROM THE UPPER TRIASSIC OF LESOTHO

By

DIANE S. NASH

Cape Town Kaapstad

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By

DIANE S. NASH

*Birkbeck College, University of London**

(With 44 figures and 4 tables)

[*MS. accepted 13 January 1975*]

ABSTRACT

The skull, lower jaws and most of the postcranium of the type of *Orthosuchus stormbergi* Nash, 1968 were collected in 1963, by an expedition of the South African Museum, from the Upper Triassic Red Beds Formation of Lesotho. The skull and jaws of a smaller specimen, collected from the same horizon but a separate locality, are considered to be congeneric.

The cranial table is flattened, and of typical crocodilian form and sculpturing. There is a deep otic recess, and pronounced otic notch which lies open posteriorly. The quadrate and quadratojugal are strongly inclined, and the quadrate sutures with the parietal and squamosal within the superior temporal fossa. A short bony secondary palate is developed, and the pterygoids bear prominent flanges characteristic of crocodilians.

The anterior dorsal ribs are flanged on both the leading and rear margins. The coracoid, radiale and ulnare are elongated. The acetabulum is open, and the pubis excluded from the acetabular margin. The ankle joint is crocodilian in type, and a paired row of dorsal scutes, which are imbricated and sculptured, is developed over the trunk and tail.

Orthosuchus is closely related to *Notochampsa*, *Erythrochampsa* and *Protosuchus*, and probably also to *Stegomosuchus* and *Pedeticosaurus*. It is also related to *Hemiprotosuchus* though possibly less closely.

The thecodontian heritage of *Orthosuchus* can be seen in the presence of an antorbital fenestra, small basipterygoid process, and in that the quadrate has a posterior contact with the squamosal. The lower jaw includes a prearticular, and a retroarticular process is not developed.

The musculature of *Orthosuchus* probably differed little from that of living crocodiles. As in the modern group, the hind-limb and tail musculature were probably powerful, while there was a general reduction in the lower arm and hand musculature associated with great mobility of the wrist joint, and use of the elongated carpus as an extra limb segment.

The presence of a soft secondary palate, which in life extended well back to the base of the skull, suggests that *Orthosuchus* spent much of its time in water. The laterally orientated nostrils and orbits, and the relatively longer proximal limb elements, indicate that *Orthosuchus* was less well adapted to this environment than are living crocodiles.

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INTRODUCTION

In April 1963 an expedition of the South African Museum, led by Professor A. W. Crompton (now Director of the Museum of Comparative Zoology at Harvard University) collected reptilian material from the Upper Triassic Red Beds Formation of the Stormberg Series of southern Africa. It soon became clear that among this material was a nearly entire skeleton of a new type of crocodilian. Pending further preparation and more detailed study, a preliminary description was published (Nash 1968) in which the type was named *Orthosuchus stormbergi.*

A second smaller skull had also been collected from the same horizon, but from a separate locality. An analysis of this second specimen demonstrates that this material is congeneric.

This paper is mainly concerned with the detailed description of the skull and postcranial skeleton of *Orthosuchus*. The probable arrangement of the musculature of head and limbs is given, and some observations are made as to its mode of life. The position of *Orthosuchus* in relationship to both thecodontians and crocodilians is discussed.

Fig. 1. *Orthosuchus stormbergi* type skeleton (K409). Dorsal view of the skull and postcranium.

Fig. 2. *Orthosuchus stormbergi* type skeleton (K409). Ventral view of the skull and postcranium.

HISTORICAL REVIEW

Although a number of forms of Triassic age have recently been associated with the Crocodilia, there are still only a limited number which bear a direct relationship to this group. *Notochampsa* was the first of these to be described (Broom 1904). On the basis of two specimens from the same locality (Barkly East, Cape Province, South Africa) but different horizons, Broom proposed two species within this genus which he included within the crocodilian suborder Mesosuchia. *Notochampsa istedana* was collected from the Cave Sandstone of the Stormberg Series, and the second, *Notochampsa longipes*, from near the top of the underlying Red Beds. It is now generally considered that the Cave Sandstone does not represent a separate formation, but is merely a facies of the Red Beds.

Having further developed the material of *Notochampsa istedana*, Haughton (1924) redescribed the type, and questioned its crocodilian relationship. Haughton came to the conclusion that there were close resemblances between *Notochampsa istedana* and *Pedeticosaurus leviseuri* Van Hoepen, 1915 and provisionally placed the two genera in the same family, the Notochampsidae. He considered them advanced pseudosuchians having affinities with the Crocodilia.

At this time, Haughton also reconsidered the specimen described by Broom as *Notochampsa longipes*. In his opinion Broom had attached too much significance to the resemblances between the dorsal scutes of the two forms *Notochampsa istedana* and *longipes*. Haughton considered the two types quite distinct, and erected a new genus, *Erythrochampsa*, for *Notochampsa longipes*, placing this type in the Crocodilia.

Von Huene (1925) disagreed with Haughton's and Broom's interpretations and placed both *Notochampsa* and *Erythrochampsa* in the Pseudosuchia. In his view, the Pseudosuchia contained forms all of which indicate a link between this group and the crocodilians. He postulated an evolutionary sequence with the following pseudosuchians leading to the Crocodilia: *Erpetosuchus*, *Aëtosaurus*, *Stegomosuchus*, *Sphenosuchus*, and *Pedeticosaurus*. Presumably, *Notochampsa* and *Erythrochampsa* form the final link in this series.

Broom (1927) reassessed the material of *Sphenosuchus* and returned to the question of the taxonomic position of *Notochampsa* and *Erythrochampsa*. He was now quite satisfied that their generic separation was valid, but included both within the Crocodilia. Furthermore, he questioned the evolutionary sequence proposed by Von Huene. He considered *Erpetosuchus* and *Aëtosaurus* too specialized; he believed *Pedeticosaurus* to be bipedal and not related to crocodilian ancestry, and *Sphenosuchus* to be closely allied to *Pedeticosaurus*. He was of the opinion that *Stegomosuchus* might well occupy a position close to crocodilian ancestry, though the type was too imperfectly known to be sure. Broom was of the opinion that a group of pseudosuchians of a form similar to *Euparkeria* left dry ground and inhabited the marshes, developing the comparatively feeble long limbs and flattened skulls characteristic of the crocodiles.

There is now an excellent redescription of *Euparkeria* from the Lower Triassic beds of Aliwal North, South Africa, by Ewer (1965). Ewer considered *Euparkeria* as the probable direct ancestor to advanced forms like *Ornithosuchus* and *Hesperosuchus*.

In 1930 and 1931 the first North American specimens of an ancestral crocodile of Upper Triassic or basal Jurassic age were collected from the Dinosaur Canyon Sandstone of Cameron, Arizona. Barnum Brown published a preliminary notice in 1933 in which he named the type *Archaeosuchus richardsoni* and established a new family, the Archaeosuchidae. Unfortunately, the name *Archaeosuchus* was already preoccupied (*Archaeosuchus cairncrossi* Broom, 1905, a titanosuchian), and in 1934 Brown renamed this important reptile *Protosuchus richardsoni*, changing the family name to Protosuchidae.

In a revision of the classification and evolution of the Crocodilia, Mook (1934) proposed a new suborder, the Protosuchia, to contain the single genus *Protosuchus richardsoni*. No mention was made of either *Notochampsa* or *Erythrochampsa*. Mook considered that *Protosuchus* should be placed very near the line of direct ancestry of the mesosuchian crocodiles.

Subsequently Colbert & Mook (1951) redescribed *Protosuchus*, this time relating it to both *Notochampsa* and *Erythrochampsa*. They remained firmly convinced of the crocodilian nature of *Protosuchus*, but considered that the relationships of *Notochampsa* were less certain. Consequently they suggested that the family Protosuchidae be retained in preference to Notochampsidae. In their opinion, *Pedeticosaurus* was less definitely crocodilian than either *Erythrochampsa* or *Notochampsa* and should be placed among the pseudosuchians.

Other forms for which crocodilian affinity has at some time been suggested include *Platyognathus hsui* Young, 1944, from the Dark Red Beds of the Lower Lufeng Series, Yunnan Province, China. Additional material was described by Simmons in 1965. Following Young, Simmons placed *Platyognathus* in a new family of Pseudosuchia, the Platyognathidae. He believed *Platyognathus* to be a specialized form, not on the direct line of descent toward *Notochampsa* and *Erythrochampsa*. However Romer (1972*b*) was of the opinion that this species did not merit the erection of a separate family, and included *Platyognathus* within the Protosuchia.

Microchampsa scutata, also from the Lower Lufeng Series, is generally considered a protosuchian though of an essentially new type (Young 1951; Simmons 1965).

A preliminary notice of another crocodilian, probably of Upper Triassic age, from a fissure in the Carboniferous Limestone of Glamorgan, Wales, was given by Kermack (1956). A complete description of this type is still awaited.

More recently (Bonaparte 1969, 1971) *Hemiprotosuchus leali* has been described as a crocodilian closely related to *Protosuchus*. *Hemiprotosuchus* is from the upper beds of the Los Colorados Formation, La Rioja Province, Argentina.

In 1959 Reig described the skull of *Proterochampsa barrionuevoi* from the late Middle or basal Upper Triassic Ischigualasto beds of San Juan Province, Argentina. Sill reassessed this material in 1967, and agreed with Reig that it represented an early crocodilian. Sill suggested that whereas both *Notochampsa* and *Proterochampsa* strongly resemble one another, neither genus is very close to *Protosuchus*. It therefore appeared to Sill that there were two lines of crocodilian evolution during the Triassic. *Proterochampsa* could be regarded as representing an earlier and more typical line of crocodilians, and *Protosuchus* as representing an aberrant and more terrestrial group. In Sill's view, *Chasmatosaurus* probably most nearly represents the group of thecodontians from which the Crocodilia arose.

Sill proposed a new suborder, the Archaeosuchia, an unfortunate choice in view of Brown's earlier experience. This was to contain two families, the new Proterochampsidae, for the single genus *Proterochampsa*, and, provisionally, the Notochampsidae, to contain *Notochampsa* and *Erythrochampsa*. He suggested a separate suborder Protosuchia, to contain the Protosuchidae, with the sole genus *Protosuchus*, and questionably the Sphenosuchidae, with *Sphenosuchus*, *Pedeticosaurus* and *Platyognathus*.

Sill's interpretation of *Proterochampsa* was strongly criticized by Walker (1968). In his opinion the advanced crocodilian characters described by Sill are actually phytosaurian in nature. Walker's reinterpretation of the skull of *Protosuchus* indicates its close relationship to *Notochampsa* and reaffirms the position of *Protosuchus* as an ancestral crocodile.

In Walker's view *Stegomosuchus longipes* is sufficiently well known to establish its close relationship to *Protosuchus*. He has proposed grouping these forms together with *Erythrochampsa* and *Orthosuchus* in one family, the

Stegomosuchidae. Walker suggested *Cerritosaurus* Price, 1946, from the Santa Maria Formation of Brazil, as a probable ancestor, pointing out that since *Cerritosaurus* shows resemblances to *Chasmatosaurus*, both phytosaurs and crocodiles appear to converge back on *Chasmatosaurus*.

More recently Romer (1971, 1972*a*) has demonstrated a close relationship between *Cerritosaurus* and *Proterochampsa*, and two newly discovered thecodontians, *Chanaresuchus bonapartei* and *Gualosuchus reigi*. Romer regards these four types as forming a close family, the Proterochampsidae, which represents a sterile offshoot of the primitive proterosuchian stock.

Walker (1970) has suggested a major regrouping of crocodiles and closely allied forms within a proposed order Crocodylomorpha. The Stegomosuchidae is placed as the sole family in the infraorder Protosuchia of the suborder Crocodylia, which also includes the taxa Mesosuchia and Eusuchia, now ranking as infraorders. A suborder Paracrocodylia is proposed to include the infraorders Pedeticosauria, Baurusuchia and Hallopoda. The Pedeticosauria includes only the Upper Triassic family Pedeticosauridae with the genera *Pedeticosaurus*, *Sphenosuchus*, *Saltoposuchus*, *Platyognathus* and *Hesperosuchus*.

In view of this, Romer (1972*b*) has advocated retaining the Protosuchia as a suborder, but to include both ancestral forms and those others that are trending toward the crocodiles from the typical thecodontian pattern. *Protosuchus*, *Notochampsa*, *Erythrochampsa*, *Orthosuchus*, *Stegomosuchus* and questionably *Platyognathus* and *Microchampsa* are placed in the family Protosuchidae, while *Sphenosuchus*, *Hemiprotosuchus* and questionably *Pedeticosaurus* are grouped in the Sphenosuchidae.

On the other hand, Bonaparte (1971) considers that the Crocodilia as a group are too distinct for the inclusion of *Sphenosuchus*, and has suggested that the allies of *Sphenosuchus* are found in *Pseudhesperosuchus* Bonaparte, 1969 and *Hesperosuchus*. These three forms he groups in the Sphenosuchidae within the suborder Pseudosuchia.

TAXONOMIC POSITION, DIAGNOSIS AND MATERIALS UNDER CONSIDERATION

TAXONOMIC POSITION

Orthosuchus has retained from thecodontian ancestors a number of primitive features, notably the antorbital fenestra and prearticular. However, many other characters present in *Orthosuchus* are diagnostic of the Crocodilia. These are as follows:

(1) Sculpturing of the external surfaces of the bones of the skull and lower jaw.
(2) Forwardly sloping quadrate and development of an extensive otic notch.
(3) Midline fusion of the parietals.
(4) Some degree of secondary palate formation.
(5) Firm fusion of the pterygoid and quadrate with the braincase; the pterygoid bears a flange with a guide facet on its external margin for the lower jaw.

(6) Elongated coracoid, radiale and ulnare.
(7) The acetabulum is open; the pubis is excluded from the acetabulum by a forward process of the ischium.
(8) Femur without marked fourth trochanter; no development of greater trochanter.
(9) Ankle joint of crurotarsal pattern with well developed tuber on the calcaneum.
(10) External surfaces of the dorsal scutes are sculptured.

Orthosuchus is closely related to *Protosuchus, Notochampsa* and *Erythrochampsa,* and indeed probably also to *Pedeticosaurus, Stegomosuchus* and *Hemiprotosuchus.* All these forms may reasonably be included within the same family. *Pedeticosaurus* and *Stegomosuchus* are both insufficiently known to establish the family on either type. Furthermore, although the relationships of *Notochampsa* are no longer in any doubt, it seems more reasonable to retain the family Protosuchidae because of its previous general acceptance.

Protosuchia	Mook	1934
Protosuchidae	Brown	1934
Pedeticosaurus	Van Hoepen	1915
Notochampsa	Broom	1904
Stegomosuchus	Von Huene	1922
Erythrochampsa	Haughton	1924
Protosuchus	Brown	1934
Orthosuchus	Nash	1968
Hemiprotosuchus	Bonaparte	1969

Type

Orthosuchus stormbergi Nash, 1968, SAM–K409. An articulated skeleton, nearly complete.

Horizon

Upper Red Beds Formation of the Stormberg Series, Upper Triassic.

Locality

Orange River Valley in the Qacha's Nek Province, Lesotho (formerly Basutoland).

GENERIC AND SPECIFIC DIAGNOSIS

Skull bones ornamented; extensive slender preorbital region; skull table flattened; external nares separate and terminal; temporal fenestrae approximately equal in size; upper temporal fenestra large and posteriorly situated on the skull table; intertemporal area narrow, antorbital fenestra opening into a sinuous groove posteriorly; tooth count 7–8/15–18; pronounced lateral notch lies on the premaxilla/maxilla suture; two supraorbital bones on each side; frontal enters the superior temporal fenestra; midline fusion of parietals; a deep otic notch formed by the forwardly sloping quadrate and quadratojugal and overhung by the postorbital and squamosal which together form a wide upper temporal arch; quadrate fenestrated and with a posterior articulation with the squamosal; secondary palate formed from the premaxillae and maxillae, primary palate vaulted; pterygoid and quadrate fused to the braincase, the pterygoid bearing a prominent flange with external facet to guide the lower jaw on closure; lateral and median eustachian openings lying anteriorly in the basisphenoid; small basipterygoid process present. External mandibular fenestra large; prearticular well developed; the surangular forming a horizontal flange; no pronounced retroarticular process. Vertebrae amphicoelous; dorsal ribs with both an anterior and posterior flange. The coracoid elongated, the proximal expansion greater than the distal. Humerus not greatly expanded proximally, deltopectoral crest prominent; radiale and ulnare elongated, radiale longer than the metacarpals; a pisiform and two distal carpal elements present; manus small. Iliac blade forming a pointed preacetabular process; the ischium with a forward process that excludes the pubis from the acetabulum; the astragalus and calcaneum large, the calcaneum bearing a prominent tuber; four elongated metatarsals, the fifth reduced in length. A complete dorsal cuirass of paired ornamented scutes, gastralia present.

MATERIALS UNDER CONSIDERATION

SAM–K409, the type, listed above.

SAM–K4639, skull and lower jaws in articulation. This specimen was excavated from an elevation of 2 115 metres on the slopes of Majubanek Mountain facing the Kromme Spruit River. It is from the same stratigraphic level as the type specimen.

Preservation and preparation

The general condition of the type specimen, K409, is excellent though there is some distortion of parts attributable to post-mortem damage. Further, the skull fractured during excavation, and the trunk was broken in two places. The right femur was also broken. Major breaks were restored in the field. The material was X-rayed before preparation was undertaken.

All preparation has been carried out by mechanical means, and this proved a lengthy process. The vibro-tool was used extensively, but much of the work was done with the use of a pin-vice. A few areas of bone had been eroded before preservation, and these parts were restored with N.H.P. self-hardening Model Plastic.

The preserved parts of specimen K409 include the skull and both rami of the lower jaw, twenty-one presacral (three or possibly four mid-dorsals are lacking), two sacral and eight caudal vertebrae, two cervical ribs, eleven dorsal ribs and rib fragments, both scapulae, the right coracoid and part of the left coracoid; the left fore-limb, carpus and manus, the proximal carpal elements and distal portions of the right radius and ulna; the entire pelvis; both hind-limbs, the tarsus and incomplete left pes, and the right astragalus and calcaneum;

a double row of dorsal scutes covering the trunk and anterior caudal region; several gastralia.

The second specimen, K4639, is a smaller skull and articulated lower jaws partially embedded in matrix. The bone is very delicate. The block is split into two halves to expose the lateral surface of the skull. It was possible to prepare the posterior region of the skull, but anteriorly it had been crushed during preservation and work was not found to be profitable in this area.

DESCRIPTION OF *ORTHOSUCHUS*

THE SKULL

The skull of the type specimen is entire and fully prepared. It is in an excellent state of preservation, although there has been slight post mortem crushing and some consequent distortion of the cranial region. The smaller specimen, K4639, lacks the extreme tip of the snout and occiput.

External features

The skull is flattened along its length. The cranial table is broad and narrows to a slender snout with a slightly bulbous tip. The entire external skull surface is sculptured in the form of an irregular pattern of shallow pits.

The antorbital fenestra is oval in shape. It opens posteriorly into a sinuous groove which runs obliquely down towards the lateral orbital margin. The orbit is large, and is directed outward and forward. Laterally, paired supraorbitals together form a complete functional dorsal roof to the orbit. These elements are triangular in shape, the anterior supraorbital being the larger of the two. Sclerotic bones are not present. The temporal fenestrae are of approximately equal size, and they approximate the size of the orbit.

Dermal roofing elements (Fig. 3)

Premaxilla

The premaxilla meets the tip of the nasal anteriorly on the snout, and together these elements form a curved suture which passes back from the posterior border of the external naris. The posterior margin of the premaxilla lies within a deep backwardly directed notch on either side of the snout.

The premaxilla curves round to the palatal surface of the skull where it makes a small contribution to the formation of a secondary palate. At the tip of the snout, the premaxillae meet in the midline. Behind this, each borders a premaxillary foramen which lies obliquely orientated to the long axis of the skull. The medial edge of the foramen is made by the maxilla. In life the premaxillary foramina would have been closed by membrane, as in living crocodiles. The premaxilla also extends inwards as a rounded area of bone behind the premaxillary foramen, where it is sutured with the maxilla.

Each premaxilla carries four (previously described as six) discrete alveoli. Two entire teeth are known, most of the remainder of the alveoli hold broken teeth. The teeth are conical and recurved, and the crowns bear longitudinal striations. Internal to the alveolar border the premaxilla is perforated by vascular and nervous foramina.

Nasal

The nasal is a large element forming most of the dorsal surface of the rostrum. There is a distinct suture between the nasals in the midline. The tip of the snout has been superficially weathered away, but the bony bar which separates the nares must have been formed by the nasal, much as in the modern alligator, *Alligator mississippiensis.*

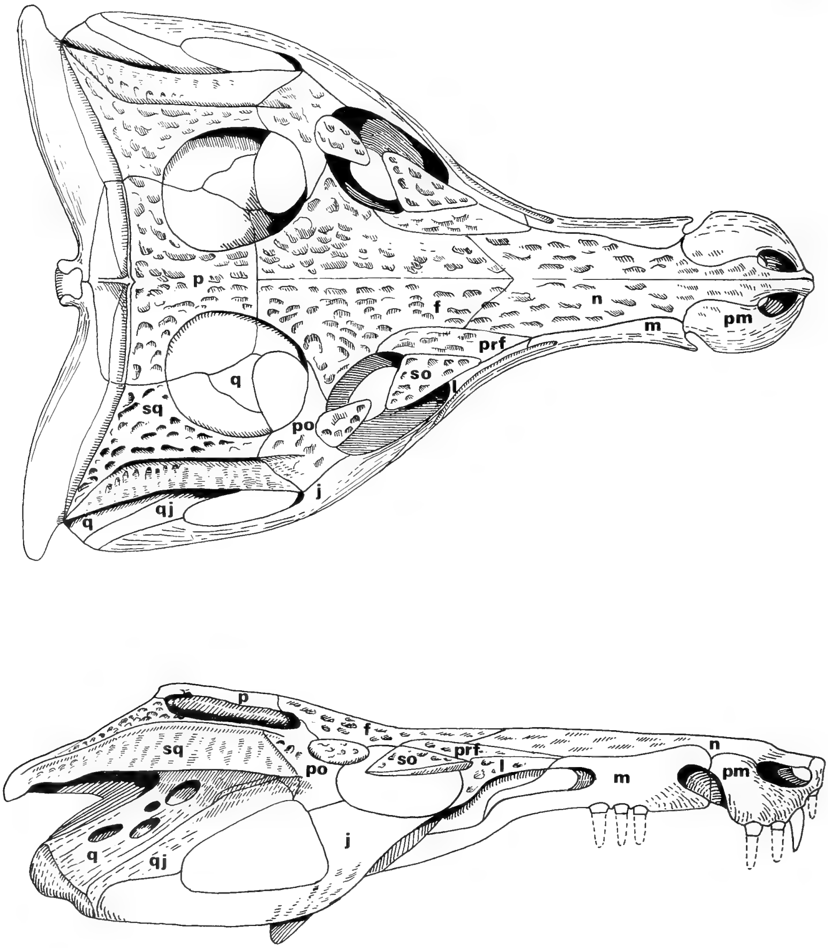

Fig. 3. *Orthosuchus stormbergi.* Reconstruction of the skull (natural size). A. Dorsal view. B. Lateral view.

The nasal unites laterally with the premaxilla and, behind the lateral notch, with the maxilla to the level of the antorbital fenestra. Posteriorly the nasal forms a wedge of bone which meets the prefrontal laterally, and the frontal medially.

Frontal

The area previously shown as the prefrontal (Nash 1968) is no longer regarded as a discrete element, but as part of the frontal. The frontal is a paired element, as it generally is in mesosuchians, e.g. *Alligatorellus* and *Goniopholis*. This is unlike the condition in the eusuchians, where both the frontals and parietals are fused in the midline.

In *Orthosuchus* an anterior process of the frontal interposes between the nasals in the midline. Laterally each frontal forms a curved suture with the prefrontal. The frontal broadens considerably and extends postero-laterally to form an oblique suture with the postorbital. A medial process extends posteriorly to meet the parietal within the margin of the superior temporal fenestra. A part of the orbital margin is formed by the frontal, as is the anterior margin of the superior temporal fenestra. The laterosphenoid makes broad sutural contact with the posterior medial process of the frontal on its ventral surface.

Parietal

This forms the greater part of a narrow temporal bar separating the two superior temporal fenestrae. In specimen K4639, a median suture is discernible, a juvenile condition, but in K409 the left and right parietals have fused together to form a single element. There is no trace of a pineal foramen.

Only the anterior third of the superior temporal fossa* is open from below for the passage of the m. adductor mandibulae externus profundus (= temporalis adductor). Laterally the quadrate and squamosal form part of the floor of the fossa, while medially the remainder is formed by the parietal. The parietal also forms the major part of the posterior wall of the fenestra, and meets the squamosal in an interdigitating suture.

The posterior edge of the parietal is concave and is bent down to form the superior edge of the occiput where it meets the supraoccipital ventrally. A small foramen, visible on the left side, probably in life provided passage for the temporal artery which ran through a canal into the superior temporal fossa. Part of the roof of this canal is formed by the parietal and part by the squamosal, while the floor is made by the supraoccipital and exoccipital.

Maxilla

Anteriorly the maxilla forms a knife-like edge which projects forwards and conceals part of the lateral notch. Behind this it forms the lateral wall of the rostrum and the anterior and lateral margins of the antorbital fenestra.

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* The terms 'temporal fenestra' and 'temporal fossa' are not synonymous. The former is used for the opening in the side of the skull; the latter refers to the space within the skull medial to (for instance) a superior temporal fenestra.

Unfortunately, the type is damaged on both sides at the anterior margin of the orbits and a suture between the maxilla and jugal cannot be seen with any certainty. However, it seems likely that the maxilla was excluded from the border of the orbit by the lachrymal and jugal. By inference, the maxilla probably excludes the jugal ventrally from the lateral margin of the post-palatine vacuity.

On the palatal surface, and at the level of the mandibular notch, the maxillae extend towards one another, meeting in the midline to form a short secondary palate. An anterior process from each maxilla runs forward between the premaxillae and the premaxillary foramina. Paired, elongate choanae open at the level of the first maxillary tooth, and extend back to the palato-maxillary suture. The alveolar wall of the maxilla borders the choana and carries three or four alveoli.

Jugal

An anterior process of the jugal forms the lateral margin of the orbit. This process also extends inwards along its length so that it forms a shelf of bone bordering the orbital region on the palatal surface of the skull. Although sutures cannot be discerned, the jugal probably forms a short suture with the lachrymal and, more posteriorly, with the maxilla on the palatal surface. Behind this, the jugal meets the ectopterygoid in a straight suture.

An ascending process of the jugal meets the postorbital to form a superficial postorbital bar. Although the postorbital bar is preserved on both sides of the skull in K409, it is traversed by numerous cracks, and no clear suturing between the jugal and postorbital is evident. The internal surface of the bar can be seen on the right side of K4639, but again there is no suture visible along its length. On balance, it seems likely that the jugal and postorbital together form an overlapping suture, as is the case in modern crocodiles. In this way the jugal reaches up to around the halfway point on the external surface of the bar, while the internal surface is formed by the postorbital.

A narrow, posterior process of the jugal forms the lateral margin of the inferior temporal fenestra. Posteriorly it forms an oblique suture with the quadratojugal.

Lachrymal

The element previously described as the lachrymal (Nash 1968) is now interpreted as consisting of both lachrymal and prefrontal. On the left side of the type the lachrymal is damaged at its extremities, and very little is preserved on the right.

The lachrymal is triangular in shape, and is sutured medially with the prefrontal. Its lateral border forms the medial wall of the antorbital fenestra and groove. The lachrymal meets the maxilla both in front of the antorbital fenestra and behind, where it forms the anterior margin of the orbit. This margin is thickened, and penetrated by a foramen which in life provided passage for the lachrymal duct.

Prefrontal

The prefrontal is bounded by the lachrymal laterally, and by the nasal and frontal medially. It forms the antero-medial margin of the orbit. Two processes of the prefrontal extend down from the internal orbital margin. The outer process lies along the internal edge of the posterior margin of the lachrymal; it is relatively short and tapers off halfway along the preorbital bar. Its extreme tip is broken so that it is impossible to be sure how far it extended, but it is doubtful that it reached the maxilla. In modern crocodiles a comparable process is found, small and never reaching the maxilla. The inner descending process passes medially and somewhat posteriorly, but again in *Orthosuchus* it is incomplete. This process corresponds to that which articulates with the pterygoid and palatine bones in living crocodiles. By inference it seems likely that in *Orthosuchus* this process met its fellow in the midline and may also have met the pterygoid ventrally.

Postorbital

This bone lies between the orbit and the temporal fenestrae and forms the anterior corner of the cranial table. Medially the postorbital unites with the postero-lateral process of the frontal in an oblique suture, while laterally it extends to form the postorbital bar with the jugal. Posteriorly the postorbital extends back a short distance between the superior and inferior temporal fenestrae to make oblique sutural contact with the squamosal. This suture lies in much the same position as it does in living crocodiles. The postorbital forms little of the lateral margin of the superior temporal fenestra, and does not contribute to its floor. Neither does it contribute to the dorsal margin of the inferior temporal fenestra.

Squamosal

This is a very large bone which forms the major area of the lateral and posterior margins of the cranial table. In K409 the borders of the superior temporal fenestra are thickened and heavily sculptured. However, in K4639 there is no such obvious thickening, a feature that again might be due to an age difference.

In the type specimen a longitudinally running groove delimits a thickened inner border of the upper temporal arch from a thinner flange which slopes down and overhangs a large, forwardly directed otic recess. In living crocodiles a groove in this position marks the junction between scales covering the skull and those covering the upper ear flap. It therefore seems probable that in life the ear of *Orthosuchus* was similarly protected by ear flaps.

In living crocodiles the ear flaps are open anteriorly when the top of the animal's head is out of water, and closed when it submerges. This action does not completely exclude water from the otic recess, but presumably it protects the tympanic membrane from mechanical injury when the animal is submerged (Shute & Bellairs 1955).

In *Orthosuchus* the otic recess is closed anteriorly by the squamosal, which extends down beneath the squamosal flange to unite with the quadratojugal below. In this way, a narrow process of the squamosal interposes between the postorbital and quadratojugal. Posteriorly the flange extends back as a tapering process, the extremity of which is carried back significantly beyond the level of the single basioccipital condyle. Posteriorly the squamosal contributes to the occiput, meeting the exoccipital ventrally and the parietal medially. Its occipital surface is not sculptured (Fig. 6).

Within the floor of the superior temporal fossa, the squamosal is sutured obliquely to the palatal wing of the quadrate, and more posteriorly forms a straight suture with the parietal. In this way the squamosal forms the external portion of the floored area of the superior temporal fossa. Anteriorly a small area of the squamosal is visible on the palatal surface, the squamosal at this point being bent very sharply back on itself. However, this is probably the result of dorso-ventral compression during preservation; this region would have been more gently rounded in life.

Quadratojugal

The anterior third of the floor of the otic recess is formed by this element, which lies with its longitudinal axis oblique to the long axis of the skull. In this way, the quadratojugal forms the posterior margin of the inferior temporal fenestra and makes an acute angle with the lower temporal arch. It is a thin, unsculptured and rather fragile element.

The quadratojugal extends back as a wedge of bone between the quadrate and the jugal. It forms an oblique suture with the quadrate, and an overlapping suture with the jugal. Anteriorly the quadratojugal meets the squamosal in a horizontal suture which runs across the internal surface of the upper temporal arch. Internally the quadratojugal is sutured to the palatal extension of the squamosal. Medially it cannot be ascertained whether the quadratojugal meets the postorbital.

Quadrate (Fig. 4)

This forms the greater part of the floor of the otic recess, and, like the quadratojugal, it is unsculptured and lies in a strongly inclined position. Its upper end meets the ventral surface of the squamosal along the lateral margin of the superior temporal fenestra to form the otic recess.

The lateral surface of the quadrate is markedly fenestrated, and dorsal contact with the squamosal is made by slender bars of bone. In recent crocodilians the tympanic cavity is linked to air passages within the quadrate and supraoccipital, and by an elaborate system of cavities and tubes to the throat.

The posterior quadrate contact in *Orthosuchus* forms a somewhat expanded head, socketed immediately beneath the rear end of the squamosal in typical archosaurian fashion. The posterior margin of the quadrate within the otic recess is curved, forming a distinct otic notch. This, together with the overhanging tip of the squamosal and paroccipital process, forms the bony housing for the tympanic membrane (Fig. 4). The posterior quadrate contact is lost in recent crocodiles, and indeed is also absent in teleosaurs such as *Pelagosaurus.*

In living crocodiles the squamosal, together with the opisthotic, extends down to gain contact with the rear margin of the quadrate, so closing the notch posteriorly. This can be seen in crocodilians of Upper Cretaceous age such as *Leidyosuchus.* The closure of the otic notch in these forms has meant that the tympanic membrane now adheres to bone all along its periphery.

Although the exoccipital in *Orthosuchus* is incomplete, it clearly overlaps the major portion of the posterior margin of the quadrate. These two bones are closely apposed, and the exoccipital blocks the major part of the primitive area of the cranioquadrate passage.

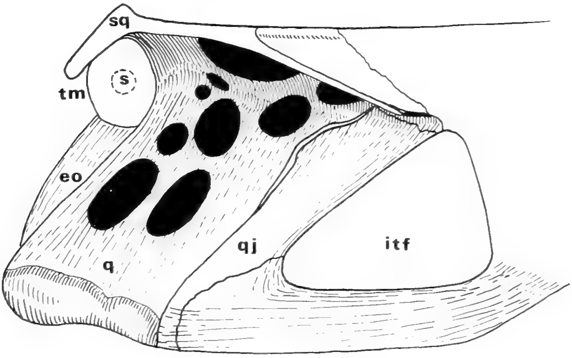

Fig. 4. *Orthosuchus stormbergi.* Reconstruction of the right quadrate of the skull, seen in postero-lateral view. The lateral flange of the squamosal has been removed to show the otic notch and suggested position of the tympanum (× 1½).

The palatal process of the quadrate passes forward and curves around the anterior margin of the floored part of the superior temporal fossa. In this way the quadrate forms a saddle-shaped area wedged in between parietal and squamosal dorsally within the superior temporal fossa. Internally, the palatal wing, as seen on the right side of the type specimen, meets the laterosphenoid in a short suture which runs vertically down from the superior temporal fossa. A semi-lunar foramen lies on this suture, and this no doubt gave passage to the three divisions of the trigeminal nerve. Below the foramen, the quadrate is sutured to the pterygoid, the suture continuing its vertical passage down to the basicranium. The quadrato-pterygoid suture then runs back for a short distance parallel to the midline before running obliquely out to the medial edge of the condylar surface. The articular surface for the lower jaw consists of two condyles separated by a shallow groove. The internal condyle is the larger of the two.

The quadrate is certainly firmly fused to the pterygoid and doubtless to the prootic also. Unfortunately, very little of the medial end of the quadrate can be made out, and it is in a poor state of preservation.

Pterygoid (Fig. 5)

The pterygoid is an extensive element. It probably reaches forward to the choanae, and extends far back to the occiput. It forms a narrow plate of bone on the floor of the basicranium where the pterygoids meet in the midline. Posteriorly the pterygoids diverge to form a narrow wing on each side which passes back to unite with the exoccipital. Medially the pterygoid wing overlaps the basisphenoid, forming a curved suture. Laterally the pterygoid is sutured to the palatal wing of the quadrate.

The quadrate ramus of the pterygoid extends vertically over the anterior wall of the braincase, as in all crocodiles. Dorsally this ramus unites with the laterosphenoid at the level of the foramen for the trigeminal nerve. Below the quadrate ramus, the pterygoid extends in a latero-posterior direction as a prominent pterygoid flange which forms an overlapping suture with the ectopterygoid. The outer edge of the flange is made by the ectopterygoid ventrally and by the pterygoid dorsally, much as in *Gavialis*. The pterygoid flange lies farther forward in *Orthosuchus*, and although it is somewhat inclined ventrally it does not descend as steeply as it does in living crocodiles. Each flange bears a facet which guides the lower jaw on closure.

The rear edge of the pterygoid flange of *Orthosuchus* is considerably thickened to form a horizontal ridge. Medially the ridge divides to run in both directions along the basicranium parallel to the midline. In addition, the pterygoids form a continuous median ridge which runs forwards from the pterygoid-basisphenoid suture to become confluent with the vomerine septum.

Immediately in front of the pterygoid flange, a triangular-shaped plate of bone extends forwards on each side to the level of the antorbital fenestra. The exact contribution of pterygoid and palatine to this area is problematical since the bone is poorly preserved. It seems likely that the pterygo-palatine suture runs transversely just in front of the pterygoid flange, the pterygoid extending forwards in the midline to meet the vomer. However, there is no possibility of verifying the presence or absence of this suture.

Ectopterygoid

This element meets the lateral edge of the pterygoid flange and then extends laterally as a flat bar of bone. Externally it meets the jugal, and may well also unite with an internal extension of the postorbital. It is unlikely that the ectopterygoid has any sutural contact with the maxilla as it has in modern crocodiles. The anterior margin of the ectopterygoid forms the major part of the posterior border of the post-palatine fenestra. Its posterior margin forms the outer half of the anterior border of the pterygoid fossa.

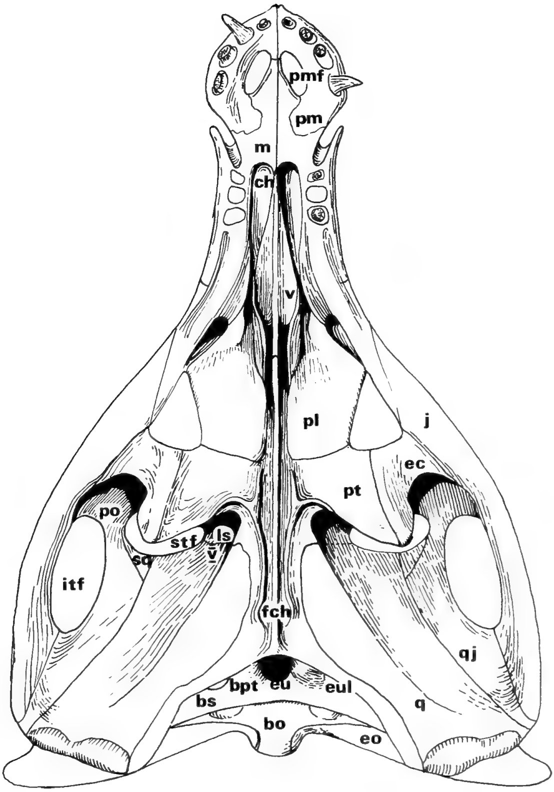

Fig. 5. *Orthosuchus stormbergi.* Reconstruction of the palate (natural size).

Palate (Fig. 5)

The type specimen of *Orthosuchus* is unique among the protosuchians in that the palate is well preserved. Although sutures are not entirely clear, there is little doubt as to the extent of the various elements. Elongate choanae open behind a short secondary palate made by the premaxillae and maxillae. The choanae correspond to what Huxley (1877) called 'the primitive posterior nares of the Crocodilia'. In modern crocodiles these lie between the septum formed by the vomers and the anterior processes of the pterygoids centrally, the palatines behind and the maxillae in front and at the sides, and this is exactly the case in *Orthosuchus*.

In *Orthosuchus* the median septum formed by the vomers is continuous with a median pterygoid septum which runs to the rear of the skull. Laterally, each vomer forms a deep channel which opens on to the pterygoid. In this way the bony secondary palate opens into a pair of narial tubes formed by the vomers anteriorly and the pterygoids posteriorly. *Orthosuchus* differs from living crocodiles in that these tubes are not floored by bone, though there can be little doubt that they were covered by membrane in life. Hence the functional choana opened on the rear margin of the pterygoid in much the same position as in recent crocodiles.

The shape of the palatine is also suggestive of its incipient inclusion in the formation of the secondary palate. Anteriorly the palatine forms an oblique suture with the maxilla, posterior to the alveolar border. Behind this the palatine twists along its length and its lateral border appears to be in the process of rotating ventro-medially to attain the tubular shape that characterizes this element in living crocodiles.

Occiput and braincase (Fig. 6)

The occiput of the type specimen is distorted because of the dorso-ventral compression that has occurred in this region, and it would have been more nearly vertical in the natural state. Telescoping of the right quadrate, together with reduction in height of the foramen magnum, indicates the degree of compression that has occurred.

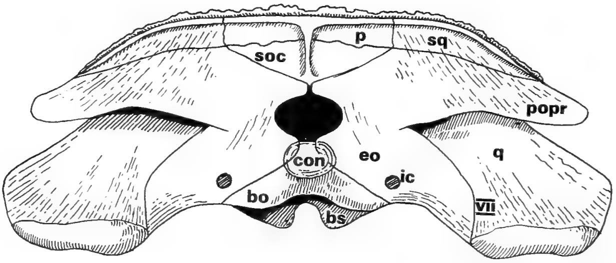

Fig. 6. *Orthosuchus stormbergi*. Reconstruction of the occiput (natural size).

Supraoccipital

This is an unpaired, triangular-shaped element which bears a median vertical ridge. It meets the parietals above in a horizontally running suture, and the exoccipitals below in an oblique suture. There is no evidence of a dermo-supraoccipital bone.

Exoccipital

The exoccipital forms the superior margin and lateral boundary of the foramen magnum, and also a small part of the occipital condyle, as in modern crocodiles. On either side, the exoccipital fuses with the large paroccipital wing of the opisthotic and divides laterally into two processes, as it does in the teleosaur *Pelagosaurus*. The more extensive upper wing is sutured dorsally to the squamosal, and the lower wing overlaps the posterior margin of the quadrate. The main trunk of the facial nerve, the ceratohyal, the orbitotemporal artery and the lateral head vein would then have passed back from the middle ear region, probably along the grooved exoccipital-quadrate suture. In living crocodiles this groove is no longer open, but is transformed into a narrow canal by the much broader fusion of the quadrate with the upper paroccipital wing.

Ventrally the exoccipital unites with the basioccipital medially, and more laterally with the pterygoid. Although the exoccipital has suffered some damage, there appears to be evidence of a small foramen lying dorsal to the exoccipital-pterygoid suture. This probably provided passage for the internal carotid artery and may also have transmitted the vagus and hypoglossal nerves. In living crocodilians twin foramina lie to either side of the foramen magnum. The inner carries the hypoglossal nerve, while the glossopharyngeal, vagus and accessory nerves and vein pass through the larger vagus foramen. Antero-ventrally to this lies a foramen through which the internal carotid enters the middle ear.

Basioccipital

Although the major part of the occipital condyle is formed by the basioccipital, this element forms only a small median part of the ventral border of the foramen magnum. The remainder of the margin is made by the exoccipital. The condyle is clearly delimited and is oval in shape. Laterally the basioccipital meets the exoccipital, and although this suture is difficult to discern, it must run downwards and outwards to the lower boundary of the rear margin of the skull. The basioccipital continues forwards on the ventral surface of the skull for only a very short distance before uniting with the basisphenoid in a curved suture. In this region there is a small basal tuber on either side for the ventral neck muscles.

Basisphenoid

The basisphenoid is seen as a half-moon-shaped element interposed between the basioccipital and the pterygoids, although very probably it extends far forwards above the pterygoids. Small basipterygoid processes lie behind the basisphenoid-pterygoid suture. A very deep pit is located in the midline and paired slit-like foramina can be seen lateral to each basipterygoid process. These foramina lie within the basisphenoid, although the anterior margin of each is formed by the pterygoid. There can be little doubt that they are the openings of the eustachian system, although no connection between median and lateral pits can be discerned. Within the median pit a narrow channel runs forwards above the pterygoid, and a larger channel runs back into the body of the basisphenoid.

Living crocodiles have both lateral and a large median eustachian opening, but they lie between the basisphenoid and basioccipital. They lead upward by a complex system of tubes to the ear, and downward by three membranous tubes to the throat, eventually forming one tube which opens almost at the level of the choanae.

Laterosphenoid

As seen on the right side of the type specimen, the laterosphenoid has the same form and relationship to other elements as found in living crocodilians.

Antero-dorsally the laterosphenoid articulates with the internal surface of the frontal, and also extends laterally and probably just touches the postorbital. Postero-dorsally the laterosphenoid unites with the internal surface of the parietal. The laterosphenoid-quadrate suture runs perpendicularly down to the foramen which transmitted the trigeminal nerve. Ventrally the laterosphenoid meets the quadrate ramus of the pterygoid.

Otic region

Nothing can be said of either the prootic or epiotic, since these elements are concealed by the quadrate, parietal and supraoccipital. The opisthotic forms the large, horizontally directed paroccipital process to which the exoccipital is fused. Medially it fuses with the supraoccipital and dorsally it is sutured to the squamosal. Internal to the quadrate, fragments of bone can be seen and very probably the otic elements were crushed during preservation due to compression of the skull in this region. The stapes is also unknown.

THE LOWER JAW (Fig. 7)

Both mandibular rami of the type specimen are well preserved although slightly distorted. The middle area of the right has been restored, and the articular region is firmly attached to the condylar surface of the quadrate. The articular region of the left ramus is incompletely preserved. In K4639, the rear halves of both rami are visible although the posterior margin is incomplete in both cases.

Dentary

This is the largest of the lower jaw elements and externally forms the lower half of the mandible. It is sculptured in the form of numerous small, shallow pits which grade into slit-like markings, more sparsely arranged, farther back. A

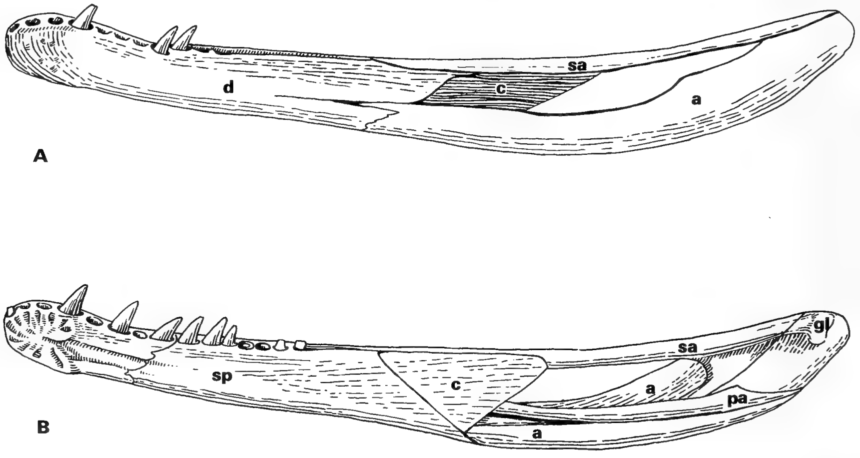

Fig. 7. *Orthosuchus stormbergi*. Reconstruction of the lower jaw (natural size). A. Lateral view. B. Medial view.

careful comparison of the alveolar border of both rami suggests that there were probably 15 dentary teeth, though up to 18 could have been present. The teeth, like those of the upper jaw, are conical, longitudinally striated and somewhat recurved. There is no differentiation of tooth shape and there appear to be no marked differences in tooth size, apart from those reflecting the pattern of tooth replacement.

The mandibular symphysis is short and stout, and is complete at the level of the fourth mandibular tooth. Extending back from the middle of the symphysis is a longitudinally running groove, the Meckelian canal. This carried the mandibular artery, vein and nerves, and was almost certainly covered by the splenial in life. This latter element may have entered the symphysis; on both rami the anterior border of the splenial is incomplete. Posteriorly the dentary extends to the anterior margin of a large, elongate external fenestra which lies between the dentary, angular and surangular.

Splenial

This element lies wholly on the anterior inner surface of the mandible, uniting with the dentary above and below. The exact position of its posterior margin is uncertain, as suture lines are difficult to distinguish in this region. Probably the splenial extended back to the mid-region of the ramus, where it united with the coronoid and, below this, to a smaller extent with the angular.

Coronoid

The single coronoid element forms the anterior margin of an extensive adductor fossa, and occupies much the same position as it does in recent crocodiles. Posteriorly the coronoid has a rounded edge which overlaps the surangular. The suture between these elements then runs forwards just below the dorsal margin of the ramus on its internal surface.

Surangular

The surangular extends over the external mandibular fenestra as a narrow flange, and in this respect the element differs from that of living crocodiles. Externally the posterior region of the surangular forms an overlapping suture with the angular. Internally it borders the adductor fossa dorsally, and behind this a descending process meets the prearticular ventrally. Posteriorly the surangular is overlapped medially by the articular.

Angular

This is a large postero-ventral element which forms the ventral border of the external mandibular fenestra. The angular wraps round the rear margin of the mandible, and is sutured internally to the articular. A retroarticular process is not developed. On the inner surface, the upper margin of the angular is bordered by the prearticular. These two elements diverge anteriorly to form a slit-like foramen, of which the anterior boundary is formed by the coronoid. This corresponds to the Meckelian foramen which, in living crocodilians, lies between the angular and splenial.

Prearticular

This element is not normally found in crocodilians, but it occurs in early mesosuchians such as *Pelagosaurus* and *Metriorhynchus.* In *Orthosuchus* it is a slender, elongate element which forms the ventral margin of the adductor fossa. Anteriorly it is overlapped by the coronoid, and may have extended forward medially to this element to contribute to the inner wall of the Meckelian canal. The foramen which transmits the chorda tympani branch of the facial nerve, and which is almost universally present on the inner surface of the prearticular, cannot be discerned. However, there is a groove running along its inner surface. Posteriorly the prearticular lies over the anterior edge of the articular.

Articular

On the right side this element is fused by matrix to the condylar surface of the quadrate, while only fragments of the left articular are preserved. The glenoid fossa cannot be seen, although from the contour of the articular area it appears to consist of a large internal and smaller external articular surfaces.

THE VERTEBRAL COLUMN AND RIBS

General features

The presacral series is complete but for a gap which corresponds to three mid-dorsal vertebrae, giving a presacral count of 24. Of these, probably eight may be regarded as cervicals. Two sacral vertebrae are in articulation with the most anterior caudal vertebra. Seven other caudal vertebrae are known, of which only one is in a reasonable state of preservation.

The vertebral column shows regional differentiation both in the progressive

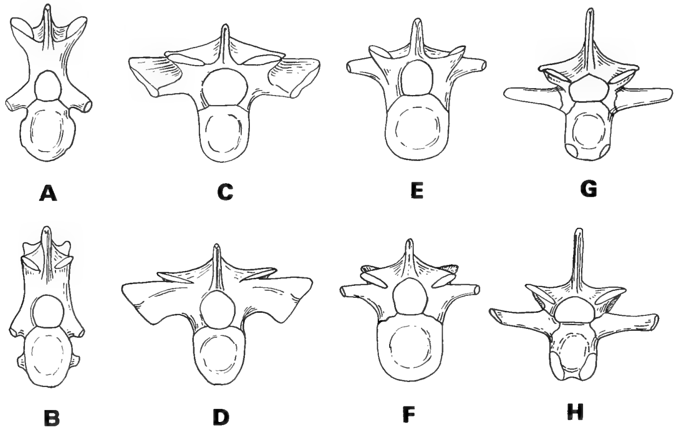

Fig. 8. *Orthosuchus stormbergi.* Anterior (upper row), and posterior (lower row) views of vertebrae (natural size). A. Cervical six. B. Cervical five. C & D. Dorsal seventeen. E & F. Dorsal twenty-four. G & H. Caudal four.

changes that occur in the rib articulation facets, and in the overall dimensions of the vertebrae. The centra of the anterior cervicals are short, and a progressive increase in length occurs through to the lumbar region, as shown in Table 1.

The vertebrae are spool-shaped and, unlike the procoelous vertebrae of eusuchians, in *Orthosuchus* they are all amphicoelous. In the majority of the vertebrae a clear sutural union of the neural arch on the centrum is visible. The neural spines are not high in any region of the column, but are tallest in the cervical region and decrease slightly through to the lumbar region. The articular surfaces of the zygapophyses are more or less vertical on the cervicals, but in the mid-dorsals they change to a more nearly horizontal direction. Posterior to this they again become more nearly vertical in orientation (Fig. 8).

Table 1

Measurements of the vertebrae in mm

Length of centrum (L). Height of centrum posteriorly (H). Width across posterior end of centrum (W). Height of neural spine (NH). Maximum height of vertebra (VH).

Vertebra No.	L	H	W	NH	VH
Cervical					
Atlas . .	—	—	—	—	15,5
Axis . . .	7,7	7,9	5,5	8,0	17,0
3 . . .	6,4	8,5	6,0	—	—
4 . . .	6,6	8,5	6,0	8,0	21,0
5 . . .	6,8	7,7	6,0	8,0	21,0
6 . . .	6,8	—	—	6,0	20,0
7 . . .	6,8	7,6	6,0	6,0	19,0
8 . . .	6,8	—	6,5	6,0	18,0
Dorsal					
9 . . .	7,4	6,5	6,5	6,0	18,0
10 . . .	8,4	—	—	6,0	18,0
11 . . .	8,4	—	—	6,0	18,0
12 . . .	8,8	7,3	6,5	6,0	18,0
13 . . .	8,8	7,3	6,0	6,0	18,0
14 . . .	—	—	—	—	—
15 . . .	—	—	—	—	—
16 . . .	—	—	—	—	—
17 . . .	10,0	7,0	6,5	6,0	18,0
18 . . .	10,0	7,5	6,5	6,0	18,0
19 . . .	10,5	7,5	6,5	6,0	18,0
20 . . .	10,5	7,5	6,0	6,0	18,0
21 . . .	10,0	8,0	6,7	5,0	19,0
22 . . .	9,6	8,5	—	5,0	19,5
23 . . .	9,6	8,5	7,0	5,0	20,0
24 . . .	9,6	8,5	8,7	5,0	18,5
Sacral					
1 . . .	10,0	8,5	7,5	7,0	18,0
2 . . .	10,0	8,0	7,0	7,0	18,0
Caudal					
1 . . .	8,0	7,0	6,2	—	19,0
2 . . .	7,7	7,0	6,4	—	—
3 . . .	7,7	7,5	6,0	9,0	20,0
4 . . .	7,7	—	6,0	9,0	20,0
Mid-caudal . (isolated vertebra)	9,0	5,5	4,5	—	—

Atlas and axis (Fig. 9)

The intercentrum of the atlas is well developed, and in cross-section forms a dumb-bell shape. A single-headed rib is in articulation with the intercentrum postero-laterally, while dorso-laterally the intercentrum supports the stout base of the pedicel of the neural half-arch on each side. Dorsally a narrow gap separates the two neural half-arches. Presumably this gap was filled by cartilage and overlapped by a pro-atlas in life, as in recent forms. Posteriorly the dorsal portion of the neural arch is drawn back to form an almost horizontal postzygapophysis which overlaps the axis. The prezygapophysis of the axis with which it articulates is not visible, but is probably quite small.

The centrum of the atlas, the odontoid process, can be seen lying between the pedicel bases of the neural half-arches of the atlas. The anterior face of this process articulates with the occipital condyle, as in living crocodiles. The postero-lateral margin of the odontoid process together with the adjacent edge of the axis centrum bears an articular facet for the second rib. This rib is closely apposed to the first, and is also single-headed.

The axis centrum is very stout, and posteriorly is pulled down to form a hypapophysis. The neural spine is long and low, and is pointed anteriorly where it projects between the atlas neural half-arches.

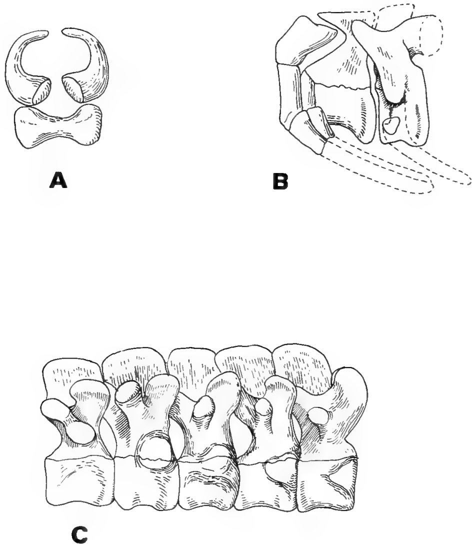

Fig. 9. *Orthosuchus stormbergi.* Vertebrae (natural size). A. Atlas seen in anterior view. B. Atlas, axis and third cervical seen from the left side. C. Anterior presacrals, vertebrae eight to twelve inclusive, seen from the right side.

Cervical vertebrae 3 to 8

The most anterior vertebrae are strongly keeled and the centrum of each bears both an anterior and a posterior hypapophysis. The keeling becomes progressively less marked through to the posterior cervicals, and is absent on vertebra eight. In modern crocodiles this keeling is extended to the anterior dorsal vertebrae, and all bear a hypapophysis.

Laterally each centrum bears a prominent parapophysis for the articulation of the capitulum. Each parapophysis is broad anteriorly and tapers to the mid-region of the centrum. On the third vertebra, the parapophysis lies near to the ventral surface, but through the succeeding vertebrae it gradually alters its position so that on vertebra eight it is borne near to the neurocentral suture.

The neural arch has a pronounced diapophysis on each side for the tuberculum. The position and shape of the diapophysis also changes progressively along the length of the cervical vertebrae. On the third the diapophysis is a thickened ridge along the anterior half of the neurocentral suture. Through the cervical series this becomes progressively raised on a transverse process.

Dorsal vertebrae (Fig. 9)

The progressive changes of the positions of the articular facets for the ribs which occur along the cervical series continue through the anterior dorsal vertebrae. The parapophysis continues to move dorsally up the anterior margin of the centrum, coming to lie beneath the diapophysis on vertebra twelve. Coupled with this movement, the parapophysis also becomes larger and more round in shape. The diapophysis does not alter its position from that seen on the eighth cervical, though both the transverse process and the diapophysis become progressively broader through to the twelfth vertebra.

Behind this the parapophysis continues to migrate upward, coming to lie on the same level, although still separate from the diapophysis on vertebra twenty-two. Both the facets and the transverse processes then diminish in size towards the pelvis so that on the last presacral the transverse process is quite slender and short and the two facets fused. In modern crocodiles these facets are confluent and the dorsal ribs single-headed on the eighteenth vertebra. In this way the transverse processes become narrower earlier on in the series.

Sacral vertebrae (Fig. 10)

The centra of the sacrals are long, slightly exceeding the length of the posterior dorsals. The transverse process of the first sacral vertebra is stout and short, as is the first sacral rib. In addition to its articulation with the transverse process, the rib also unites with the centra of both the last presacral and first sacral vertebrae. An identical condition is found in living crocodilians. The transverse process of the second sacral vertebra faces somewhat posteriorly. Distally it articulates with a very broad rib, which, as in modern crocodiles, also articulates with the posterior portion of the lateral surface of the centrum.

The sacral ribs form a very strong support for the ilium. The articular areas are triangular in shape in both cases, though that between the second sacral rib and the ilium is the more extensive. Only a very small median portion of the ilium is free.

Caudal vertebrae

Only eight caudal vertebrae are known. One of these is in articulation with the sacral series, and three others are from the proximal region of the tail. The remainder have small, elongate centra and must be mid-caudal vertebrae. Probably the tail was long, of the order of 30 to 40 vertebrae.

The neural spines of the anterior caudals are taller than elsewhere in the column, and are directed slightly backwards. The zygapophyses slope so that their facets meet more or less vertically. The first chevrons probably lie between the third and fourth caudal vertebrae. The fourth bears a nearly entire caudal rib, although elsewhere these are broken above their bases.

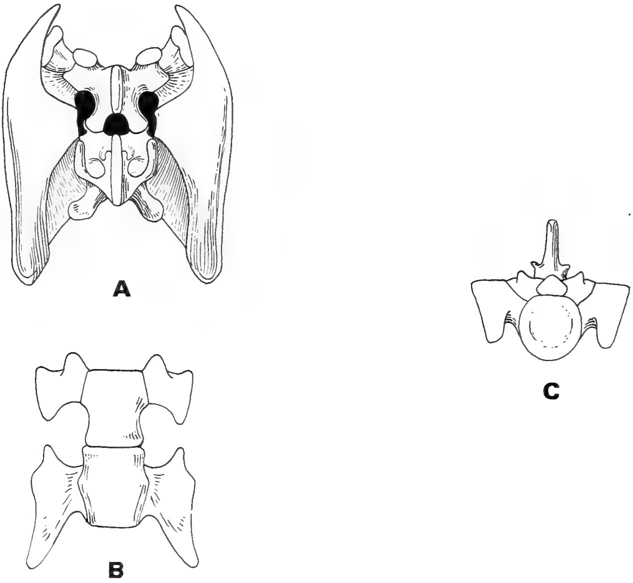

Fig. 10. *Orthosuchus stormbergi.* Sacrum, corrected for distortion (natural size). A. Dorsal view with sacral ribs and internal surfaces of the ilia. B. Ventral view with sacral ribs. C. First sacral vertebra seen in anterior view.

Ribs (Fig. 11)

The proximal ends of the atlantal and second rib are present on both sides. They are slender and single-headed. The first has a large articular facet for union with the intercentrum of the atlas, and the second rib has a smaller facet for union partly with the odontoid and partly with the centrum of the axis. This differs from modern crocodiles where the axial rib is double-headed, the second facet lying on the odontoid.

Only one other cervical rib is complete, the fifth, and this is indistinguishable in type from that of living crocodiles. It is double-headed and has a short shaft which runs parallel to the long axis of the vertebral column. The capitular and tubercular processes rise at right angles to the shaft of the rib and diverge as they pass upward to the centrum of the vertebra.

The shaft of the eighth cervical rib is transitional in type between that of the cervicals and anterior dorsals. It more closely resembles that of the latter though it is much more slender.

Behind this, on the left side, dorsal ribs nine to fourteen inclusive are preserved *in situ.* Three right dorsal ribs were also associated with the material. All the dorsal ribs are double-headed and their shafts long and strongly curved. The articular facets for the union of rib with vertebra move further apart passing from the sixth cervical back to vertebra nine, and are at their widest on this vertebra. Posterior to this they come closer together. Further, in each case, the tubercular process lies above and anterior to the capitulum, the two being separated by a shallow groove. In the ninth rib, the tubercular process is the larger of the two, but from the twelfth this is altered and the rib articulates principally by the capitular process.

Ribs nine to fourteen are expanded to form prominent antero-ventral and postero-dorsal flanges. Because of this, the mid-dorsal ribs particularly are very flat and broad proximally, and narrow abruptly to a cylindrical shaft.

The antero-ventral flange rises immediately behind the head of the rib much as in living crocodiles. In recent genera, the flange is limited to the first two to four dorsal ribs, the number being greater in older individuals. The postero-dorsal flange is more gently rounded in shape and is developed slightly lower down the shaft of the rib. Presumably this flange is homologous with the cartilaginous 'uncinate' process which is developed in this position in living crocodiles. This process is normally carried on the third to fifth dorsal ribs, and may occasionally ossify slightly. Both anterior and posterior flanges serve for muscle attachment. In *Orthosuchus* the postero-dorsal flange of one rib overlaps the antero-ventral flange of the succeeding rib.

Posteriorly only the proximal part of ribs in articulation on the left side of vertebrae eighteen and nineteen are known. These ribs are double-headed, but, unlike that of the anterior dorsals, the capitular and tubercular processes lie on the same level. The capitular process is the larger of the two. Each rib is strongly curved backwards, and is broad and flat immediately behind its head. The rib rapidly contracts to a cylindrical shaft and there is no evidence of either an anterior or a posterior flange. Probably at least the last two presacral vertebrae did not bear ribs.

Overlying vertebrae nineteen and twenty on the right side is an accumulation of the remains of several fine gastralia.

THE LIMB GIRDLES AND LIMBS

Pectoral girdle (Fig. 12)

The shoulder girdle shows a remarkable approach towards that seen in recent crocodiles. It consists of scapula and coracoid only. Both scapulae are preserved entire, although the right has been somewhat flattened during preservation. Of the coracoids, the right is fractured and its distal margin incomplete, while only the proximal end of the left coracoid is present.

The scapula is a tall element, with its superior end considerably expanded

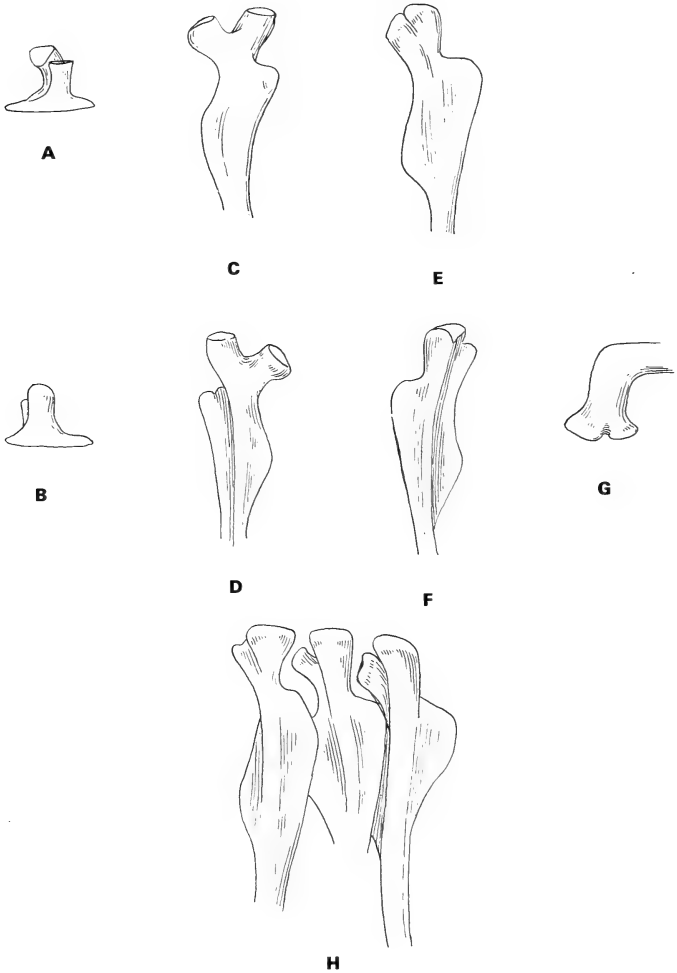

Fig. 11. *Orthosuchus stormbergi*. Lateral (upper row), and medial (middle and lower rows) views of ribs (natural size). A & B. Right fifth cervical. C & D. Right first dorsal. E & F. Right mid-dorsal. G. Left tenth dorsal. H. Left mid-dorsals showing overlapping of the rib flanges.

and drawn out posteriorly. It narrows to a stout shaft which curves sharply inwards to form a more conservatively expanded inferior region. Characteristically, the posterior margin of this bears a large rough facet which forms the upper half of the glenoid surface. Another triangular-shaped facet for the coracoid lies along the lower edge, its broadest part lying posteriorly and below the glenoid facet. The anterior margin of the lower region of the scapula is overhung by a ridge, just as in recent forms. Below this ridge, the concave surface afforded attachment for a large muscle, the scapulo-humeralis posterior.

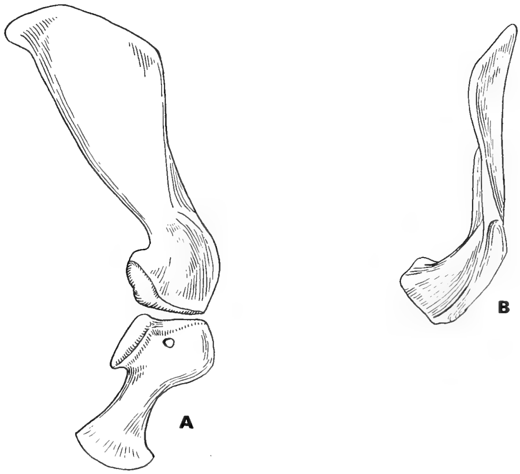

Fig. 12. *Orthosuchus stormbergi.* Pectoral girdle (natural size). A. Lateral view of right side. B. Anterior view of left scapula.

The coracoid is half as long as the scapula. Its upper region is expanded to match the lower end of the scapula, while the posterior margin is thickened to form the lower half of the glenoid. In front of this lies a prominent coracoid foramen. Distally the coracoid flares out to form a blade-like inferior end. The long axis of the coracoid, like that of the scapula, lies obliquely orientated so that in life the bone would have been directed inwards.

The sternum and interclavicle are unknown, and were presumably cartilaginous in life.

Fore-limb (Figs 13–14)

The fore-limb is completely known from the left side and, in addition, part of the lower right fore-limb is present.

In general shape the humerus is remarkably similar to that of living crocodiles. The shaft is well developed and slender. It is twisted along its length, so that with the proximal expansion lying antero-medially, the distal expansion faces antero-laterally. In living crocodiles the proximal and distal expansions lie more or less in the same plane.

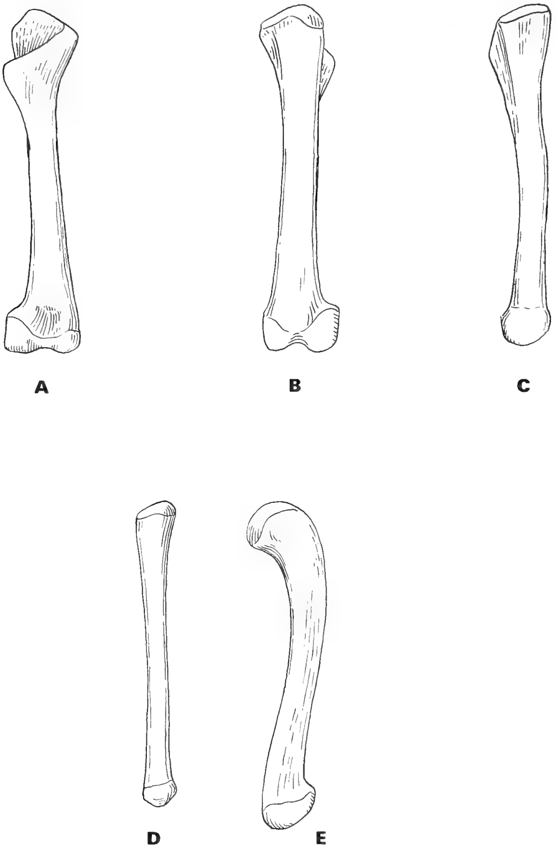

Fig. 13. *Orthosuchus stormbergi.* Fore-limb (natural size). A–C. Left humerus. A. Anterior. B. Posterior. C. Lateral views. D. Lateral view of the radius. E. Lateral view of the ulna.

In both *Orthosuchus* and in living crocodiles, the proximal expansion is of moderate size, although in recent forms it extends farther medially. The articular surface lies along the upper posterior edge and is oval in shape. The deltopectoral crest originates on the lateral edge of the proximal expansion and curves obliquely down across the anterior face of the shaft. This crest is more strongly developed in *Orthosuchus* than it is in living crocodiles, and encloses a deeper concavity on the anterior surface of the humerus. Distally the bone is thickened into two condyles. The capitellum is marginally the larger of the two, and is separated from the trochlea by a shallow groove. There is little projection of ectepicondyle or entepicondyle, and distal foramina are lacking.

The radius is a slender bone. Proximally it is thickened where it touches and partly obscures the proximal expansion of the ulna. The ulna extends beyond

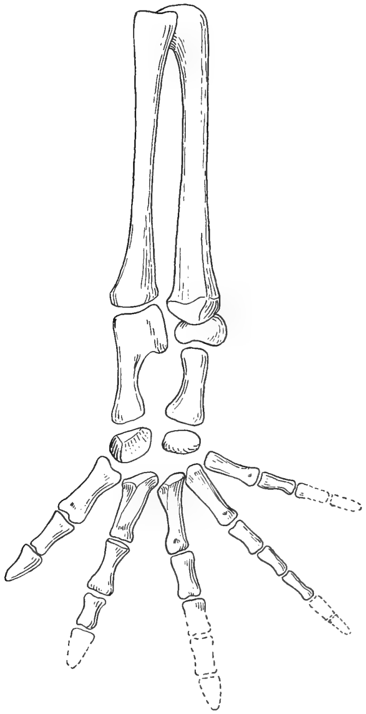

Fig. 14. *Orthosuchus stormbergi.* Lower fore-limb (natural size). Anterior view of the left radius, ulna, carpus and manus.

the limit of the radius, but it does not form an olecranon. The facet for the humerus is terminal. The articular surface of the ulna faces both forward and upward.

Distally the radius is expanded medio-laterally and forms an oval articular surface for the radiale. The ulna is also expanded distally, but in the antero-posterior direction. The ulna articulates distally with the pisiform and ulnare, and meets the radiale internally.

As in modern crocodiles, the radius is the shortest of the long bones while the ulna is the next shortest. However, the proximal part of the fore-limb is only marginally longer than the distal, the length of the radius being 88 % that of the humerus. As is typical of archosaurs, the ulna is stronger than the radius and would have carried the major part of the weight borne by the fore-limb.

The carpus shows the same remarkable degree of specialization found in modern crocodiles, for the radiale and ulnare are elongated and so add an extra segment to the fore-foot. Of the two, the radiale is the longer and stouter element. Proximally the radiale is greatly enlarged to a triangular head which articulates with both radius and ulna. Consequently the weight of the body could be transmitted from both the ulna and radius through the radiale to the middle and inner digits. The pisiform is a large, flat, kidney-shaped bone which interposes posteriorly between the ulna and ulnare.

The distal row of carpals consists of two elements and these are not elongated. The larger of the two is somewhat angular and lies distal to the radiale. This presumably represents a fusion of distal one and a centrale. The second is more elliptical in shape, and is formed by fusion of distals three and four. In modern forms, generally, only one distal carpal is ossified though two other cartilaginous elements may be present.

Despite the fragile nature of the manus, five digits are known. However, only the first of these is complete, although very little is missing from the second, fourth and fifth. About half of the third digit is lacking. Clearly, the first digit is both the shortest and the stoutest, and the fifth the weakest. Further, the second and fourth digits are longer than the first, and digit three was probably the longest.

Each metacarpal is expanded proximally. The first has a shallow articular surface for the medial distal carpal, which also meets flat articular surfaces on metacarpals two and three. The proximal articular surfaces on the fourth and fifth metacarpals are in articulation with the lateral distal carpal. The metacarpals overlap one another proximally from medial to lateral sides. Each metacarpal is also expanded distally and forms a convex articular surface.

Similarly, the phalanges form articular surfaces that are concave proximally, and convex distally. The first digit bears two phalanges, the terminal phalanx being a claw. The second digit has two phalanges and the proximal part of a third. Probably this terminal phalanx is a claw, though it is impossible to be sure. Of the third digit, only the proximal phalanx and part of the next are known. The fourth and fifth digits are very weak, and because of this the number of phalanges present in each case cannot be determined with any certainty. Probably three phalanges of the fourth, and two of the fifth, are known. The phalangeal formula was probably 2, 3, 4, ?5, 3.

Pelvic girdle (Fig. 15)

The pelvis is complete, although some fragments of bone are missing. The left pubis was removed to make it possible to clean all the vertebrae. It originally occupied a position that could have been little changed from the one held in life. The right pubis is still *in situ*, but it is displaced from the pelvis. The ilium on that side is somewhat compressed dorso-ventrally.

The pelvic girdle is remarkably crocodilian in form in that the pubis is excluded from the acetabulum by the ischium. The acetabulum is large and deep, and is perforated ventrally. Dorsally a very prominent ridge, the supra-acetabular buttress, overhangs the acetabulum. In life the femur would have exerted its thrust against this.

Above the buttress, the blade of the ilium is narrow and is produced

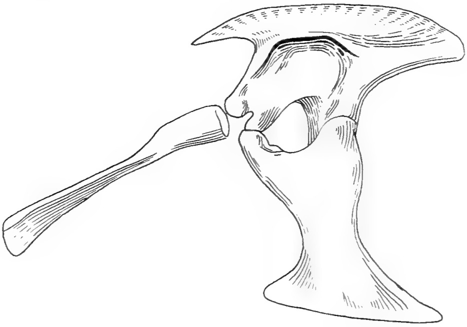

Fig. 15 *Orthosuchus Stormbergi.* Pelvic girdle (natural size). Lateral view of left side.

anteriorly to form a long, pointed process. This process is reduced in living crocodiles. Posteriorly the ilium forms a more robust post-acetabular process, much as in living crocodiles. The outer surface of the blade of the ilium, both above the supra-acetabular buttress and on the post-acetabular process, is covered by a series of fine striations. In life, the major extensor of the leg musculature, the m. ilio-tibialis and the smaller extensor, the m. ilio-fibularis, would have originated here, as would the powerful abductor, the m. ilio-femoralis.

Ventrally the ilium forms two stout processes which between them form the roof and walls of the acetabular opening. The most anterior of these bears two rounded facets, the upper of which articulates with the pubis; the lower meets the pubic process of the ischium. The posterior process bordering the acetabulum also meets the ischium.

Internally, the visible surface of the ilium is smooth, although apart from a very short median region, the whole of the internal acetabular and post-acetabular surfaces are supported by a very firm union with the two sacral ribs (Fig. 10).

The long axis of the ischium passes obliquely back in the dorso-ventral plane. The main sutural contact with the ilium is posterior, and in this region the ischium is thickened to form a broad margin to the postero-ventral edge of the acetabulum. The ischium also sends forward a narrow pubic process which curves round the ventral and ventro-lateral margin of the acetabulum. It bears a rounded surface on its leading edge for articulation with the pubis, and above this for the ilium.

Below this the ischium forms a short, narrow shaft. On both sides the ischia are fractured at this point, reflecting the distortion of the pelvis. Distally the ischium is expanded, particularly posteriorly, and its lower margin is striated. The ischia meet ventrally in the midline.

The pubis is a remarkably rod-like element, flattened on its lateral surface. It is nearly as long as the ilium and is longer than the ischium. Proximally the head is slightly expanded and bears a large articular surface for the ilium. Below this lies a smaller surface for articulation with the pubic process of the ischium. In modern crocodilians contact with the ilium has been lost and the pubis articulates only with the ischium.

Behind the articular surface there is a shallow depression laterally on the head of the pubis. This area represents the pubic rim, which is well developed in early reptiles, and is seen in forms like *Howesia.* Below this there is torsion in the pubic shaft so that proximal and distal expansions are at right angles to each other. The distal expansion is not great, though it is almost twice the size of the proximal expansion. Clearly the pubes were not fused distally to form a pubic plate, but it is probable they met distally in cartilage, as they do in modern crocodiles.

Hind-limb (Figs 16–17)

Unfortunately, both femora are broken. The break in the right femur was restored in the field, and very little of this bone can be missing. Assuming the estimated femur length to be correct, then it is still the longest of the long bones, the humerus being 79% of the length of the femur.

In form the femur is very similar to that of a modern crocodile. It has a long, curved, somewhat flattened shaft with both proximal and distal ends expanded. These expansions lie more or less obliquely to one another. There is no constriction between the head and the shaft of the femur. The head has a pronounced articular surface which is convexly rounded and oval in shape. As in living crocodiles, the articular surface is developed on the upper edge of the head, but in *Orthosuchus* it extends farther medially.

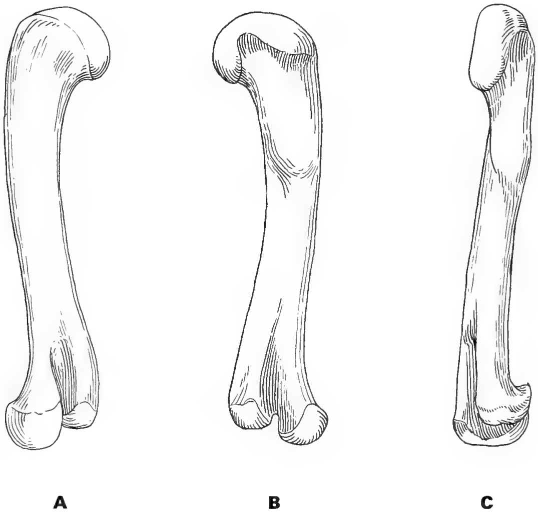

Fig. 16. *Orthosuchus stormbergi.* Reconstruction of the right femur (natural size). A. Anterior. B. Posterior. C. Medial views.

Proximally on the posterior face of the femur a shallow depression is present. This area represents the intertrochanteric fossa. Adjacent to this the lateral margin of the bone is thickened and possibly represents the remnants of the internal trochanteric crest. This area carries the insertion of the m. pubo-ischio-femoralis externus. There is no development of the greater trochanter and the ilio-femoralis musculature inserted farther down the shaft.

A thickening of bone towards the medial edge on the posterior surface of the shaft represents the fourth trochanter, to which was attached the coccygeo-femoral = caudifemoral musculature. The ratio of the distance from the proximal end of the femur to the centre of the fourth trochanter, over the distance from the distal end to the centre of the fourth trochanter in *Orthosuchus* is 0,46. In a large specimen of *Crocodylus acutus* it is 0,55, but in two small specimens of *Alligator mississippiensis* the ratio is the same as that for *Orthosuchus*. The distal condyles of the femur of *Orthosuchus* are well developed, the lateral being the larger of the two.

The left tibia and fibula are entire, and are in articulation with the tarsus and proximal pes. The proximal part of the right tibia, together with an impression of the fibula, is in articulation with the femur. The distal parts of these bones are in articulation with the astragalus and calcaneum.

The tibia is the stouter of the two bones and is particularly well developed for articulation with the femur. It is expanded posteriorly to form a large articular surface for the medial condyle of the femur, and also extends laterally to contribute to the articular surface for the lateral condyle. The fibula is modestly expanded posteriorly to complete this surface. Both articular surfaces are concave. The shaft of both the tibia and fibula is circular in cross-section in the mid-region, but lower down the inner surface becomes gently concave on the tibia and flat on the fibula.

Distally the tibia is again more developed than the fibula. Laterally the tibia is about equal in length to the fibula, but it extends farther down medially to form a large area for articulation with the astragalus. The distal articular surface of the tibia is rounded medially and has a flat, sloping lateral surface. This follows a similar contour on the upper face of the astragalus. The fibula articulates with the astragalus medially in a more or less vertical plane, and with the calcaneum ventrally where its articular surface is slightly concave.

The tibia and fibula are marginally shorter than the femur, the length of the tibia being 94% that of the femur. The fore-limb is distinctly shorter than the hind when only the long bones are considered. However when the length of the radiale is taken into account, the fore-limb is 91% the length of the hind.

The astragalus and calcaneum of *Orthosuchus* are identical in shape with these bones in living crocodiles. The astragalus is a very large element which occupies both the medial and mid-region of the tarsus. It is somewhat flattened in the mid-region, although on its medial border it is thickened and forms an oval convexity anteriorly. The calcaneum is a small, rectangular element anteriorly, but posteriorly it forms a very prominent tuber. On its posterior face

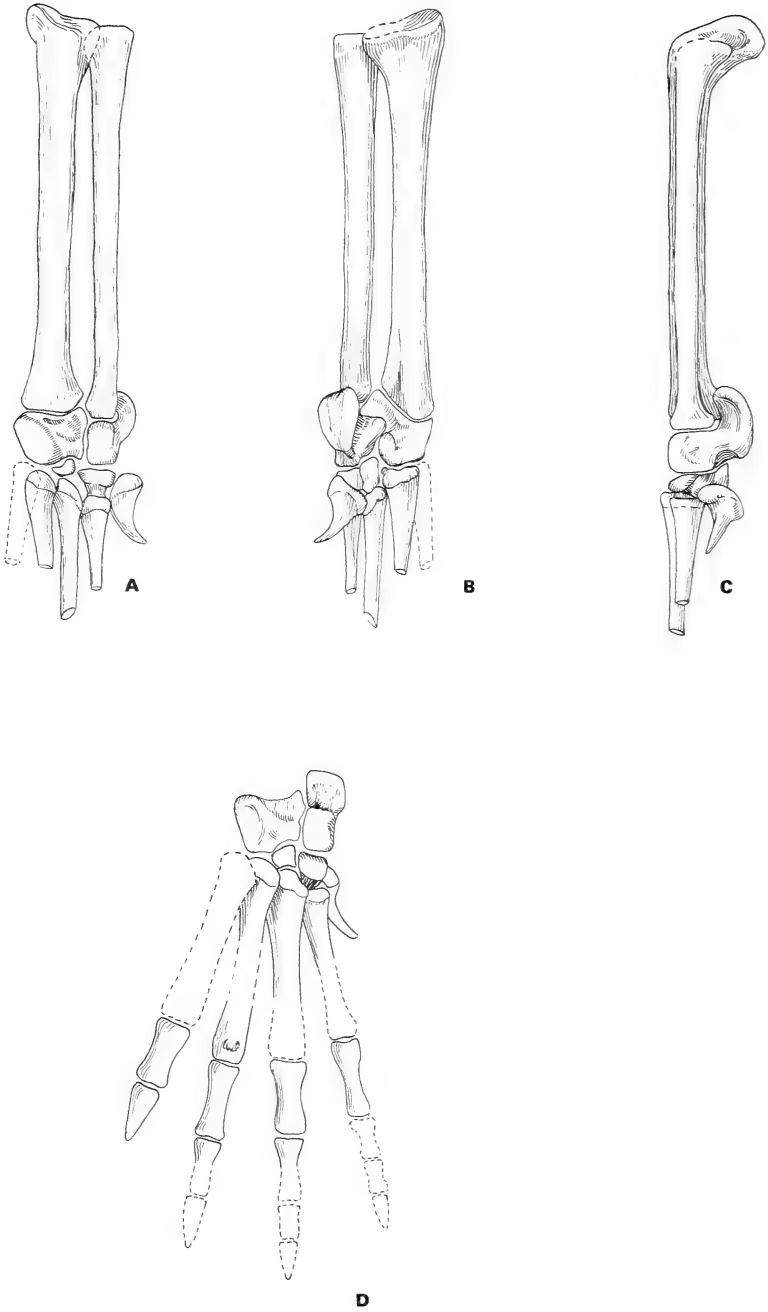

Fig. 17. *Orthosuchus stormbergi.* Lower hind-limb (natural size). A–C. Left tibia and fibula, tarsus and metatarsus, as preserved. A. Anterior. B. Posterior. C. Lateral views. D. Reconstruction of left tarsus and pes.

the tuber is grooved vertically for the passage of the gastrocnemius tendons. The calcaneum also extends obliquely up over the posterior surface of the astragalus.

The astragalus articulates on its upper surface both with the expanded distal end of the tibia and with the medial surface of the fibula, the major articulation here being between the astragalus and tibia. The astragalus also articulates with the calcaneum. Superficially this articulation would seem to be identical with that found in modern crocodiles and probably, as in these forms, a small ball and socket articulation exists between these two bones. Movement between them is therefore in the vertical plane and the joint is a crurotarsal one, with the astragalus functioning with the crus, and the calcaneum with the pes. In contrast to the articulation between tibia and astragalus, that between the fibula and calcaneum is a freely movable one.

The astragalus articulates distally with the innermost of two distal tarsals and metatarsal two. It clearly also met metatarsal one, though this is known only from an impression. The calcaneum articulates distally with the lateral distal tarsal. The tarsalia of *Orthosuchus* occupy the same position in the tarsus as is found in living crocodiles.

The medial tarsal is the smaller of the two, and meets metatarsals two and three distally. Presumably it represents tarsal three. The larger lateral tarsal extends posteriorly and is probably tarsal four. Posteriorly it meets metatarsal five, anteriorly it meets metatarsal four and just touches metatarsal three.

The metatarsals overlap one another proximally from medial to lateral surfaces. The third seems to be the stoutest. The fifth is reduced to a hook-like element which quite clearly lacks phalanges and is held behind the third and fourth metatarsals. All the elongate metatarsals are incomplete, although the distal end of one was found in association with a few phalanges of the left pes overlying the mid-dorsal ribs. This is most likely part of metatarsal two, and the digits are preserved in inverted sequence in relation to their metatarsals. The distal end of the metatarsal is grooved on its dorsal surface near to the articular region. Of this second digit, one phalanx and part of a second are known. A phalanx and claw of digit one is present, although metatarsal one is known only from an impression. One phalanx from each of digits three and four are known. The proximal articular surface of each of these is concave, and its distal end rounded.

BODY ARMOUR (Fig. 18)

Dorsally the body is covered by a double row of large rectangular scutes. Neither ventral nor lateral scutes are present, nor is there any evidence which suggests that the body was protected ventrally in this way. Virtually nothing remains of the scutes of the caudal region.

The number of scute pairs corresponds to the number of vertebrae present. In addition, a very small scute is present at the extreme anterior end of the trunk, and this could correspond to the pro-atlas. The scutes increase in length,

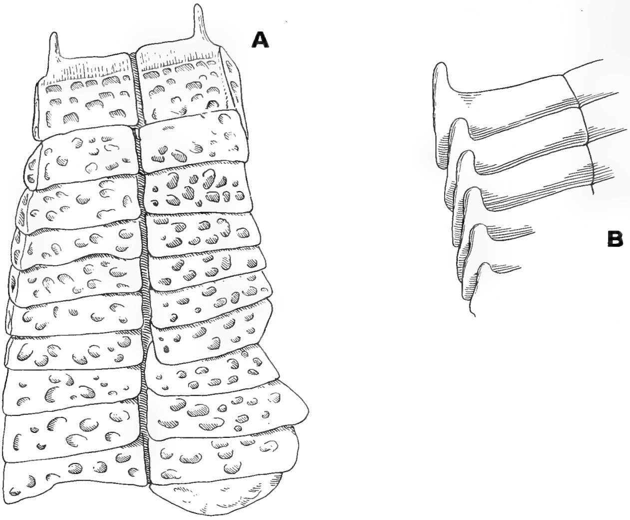

Fig. 18. *Orthosuchus stormbergi.* Dorsal scutes (natural size). A. Dorsal view of anterior scutes, the most anterior pair are figured entire. B. Ventral view of cervical scutes.

passing back along the length of the body in an identical manner to that which occurs in the vertebrae. Hence, the scutes are shortest antero-posteriorly in the cervical, and longest in the sacral region. A broadening of the scutes also occurs back to the anterior dorsal series. Behind this they decrease in width. In the sacral region their exposed dorsal surfaces are rectangular in shape.

The posterior edge of each scute overlies and conceals the anterior edge of the following scute. Approximately one-third of the length of each scute is concealed in this way. Where this border is visible it is seen to be smooth, while the exposed surface of each scute is sculptured by a system of deep pits which form a pattern similar to that on the skull. The extreme outer edge of each scute bends sharply down to form a narrow lateral part. In this way, a sharp ridge borders the lateral margin of each scute dorsally. In the cervical and dorsal regions the outer anterior edge of each scute extends forwards as a blunt, peg-like process which lies below the preceding scute.

MYOLOGY OF *ORTHOSUCHUS*

Although the restoration of musculature in an extinct reptile must always involve an element of uncertainty, it seems likely that in *Orthosuchus* the muscle arrangement could not have been very different from that found in living crocodiles. The nomenclature used throughout follows that of Romer (1956), and where this differs from that used by other workers in this field, their nomenclature has been cited in parentheses.

Table 2

Measurements of the skull and postcranium in mm

	K4639	K409
Length of skull, front of snout to parietal/supraoccipital suture	54,0	90,0
Preorbital length, front of snout to anterior margin of orbit	25,0	46,0
Maximum breadth of skull across external borders of quadratojugals	38,0	70,7
Breadth of cranial table at mid-level of superior temporal fenestrae	33,0	55,0
Breadth of intertemporal region at mid-level of superior temporal fenestrae between their inner borders	6,0	6,0
Breadth of interorbital region at mid-level between inner borders of orbits	11,0	16,0
Breadth of posterior region of the snout immediately anterior to orbits	*ca* 4,5	26,0
Breadth of anterior region of snout across premaxillae	10,0	17,4
Maximum length of superior temporal fenestra	10,0	19,0
Maximum length of inferior temporal fenestra	—	21,0
Maximum height of inferior temporal fenestra	—	12,0
Maximum length of orbit	13,0	17,0
Maximum length of antorbital fenestra	—	13,0
Distance between tip of snout and anterior border of choana	—	21,6
Length of lower jaw	—	*ca* 110,0
Length of mandibular symphysis	—	9,0
Length of external mandibular fenestra	—	34,0
Maximum height of scapula	—	46,0
Maximum height of coracoid	—	23,0
Maximum length, antero-posteriorly, of superior scapula	—	*ca* 22,0
Maximum length, antero-posteriorly, of inferior coracoid blade	—	11,2
Length of humerus	—	45,0
Length of radius	—	39,5
Length of ulna	—	43,1
Length of radiale	—	16,3
Length of ulnare	—	10,0
Length of metacarpal 1	—	9,0
Length of metacarpal 2	—	9,8
Length of metacarpal 3	—	10,5
Length of metacarpal 4	—	9,0
Length of metacarpal 5	—	7,3
Length of digit 1	—	20,5
Maximum length of iliac blade	—	36,8
Height of ilium above acetabular fenestra	—	12,5
Maximum height of acetabulum	—	15,3
Length of pubis	—	33,5
Breadth of distal pubis	—	9,0
Height of ischium	—	22,0
Length of ventral ischial margin	—	24,0
Length of femur	—	*ca* 57,0
Distance between proximal femur and centre of fourth trochanter	—	18,0
Length of tibia	—	53,5
Length of fibula	—	51,0
Length of metatarsal 5	—	9,5

MUSCULATURE OF THE HEAD (Fig. 19)

A general account of the facial musculature of crocodilians given by Von Wettstein (1937) was found helpful in this analysis. In addition, Anderson (1936) based the reconstruction of the jaw musculature of the phytosaur *Machaeroprosopus* on that of modern reptiles, particularly *Alligator* and

Spenodon. Colbert (1946) also applied the myology of the head of living crocodiles to that of the crocodilian *Sebecus.*

It is generally agreed that in Crocodilia the m. adductor mandibulae separates into the external, posterior and internal portions as tabulated below, though Edgeworth (1935) failed to identify a posterior (= medial of Edgeworth) portion.

Jaw muscles of the Crocodilia based on the nomenclature of Lakjer (1926) *and Anderson* (1936)

Innervated by the trigeminal

Adductor mandibulae externus	superficialis medialis profundus
Adductor mandibulae posterior	
Adductor mandibulae internus	pseudotemporalis pterygoideus dorsalis = pterygoideus D of Lakjer pterygoideus ventralis intramandibularis

Innervated by the facial
Depressor mandibulae

The m. adductor mandibulae externus was probably divisible into three muscle sheets in *Orthosuchus* as in living crocodiles. In modern genera the m. mandibulae externus superficialis arises along the outer edge of the quadrate between the jaw articulation and the postorbital, and inserts on the dorsal surface of the surangular. There is no reason to suppose that this muscle had a different arrangement in *Orthosuchus.* However, this muscle presumably inserted mainly on the horizontal flange of the surangular of *Orthosuchus.* It is also likely that the m. adductor mandibulae externus medialis occupied a similar position in *Orthosuchus* to that seen in *Alligator.* It probably arose partly from the ventral surface of the postorbital and partly from the pterygoid face of the quadrate deep to the superficial sheet of the m. adductor mandibulae externus. The m. adductor mandibulae externus medialis would also have inserted on the dorsal surface of the surangular underneath the superficial sheet.

Deeper again and running below the m. adductor mandibulae externus medialis lies the m. adductor mandibulae externus profundus. This is the only muscle to penetrate the superior temporal fenestra. Without doubt the major origin of this muscle in *Orthosuchus*, as in *Alligator*, must have been from the parietal, squamosal and quadrate within the superior temporal fossa, though other slips may have attached more ventrally to the quadrate and postorbital. Similarly the major insertion of this muscle in *Orthosuchus* must have been into the membrane lying over the adductor fossa.

In *Orthosuchus* both the temporal fenestrae and the adductor fossa are very large relative to the length of the skull. Indeed they are larger in *Orthosuchus* than they are in all the living crocodiles, including *Gavialis*. The large floored area of the superior temporal fossa indicates that the m. adductor mandibulae externus profundus had a much larger insertion area in *Orthosuchus* than it has in living crocodiles. Further the large size of the inferior temporal fenestra and adductor fossa suggest that this muscle required a larger area in which to bulge. It therefore seems probable that the m. adductor mandibulae externus profundus was larger and more powerfully developed in *Orthosuchus* than it is in living forms.

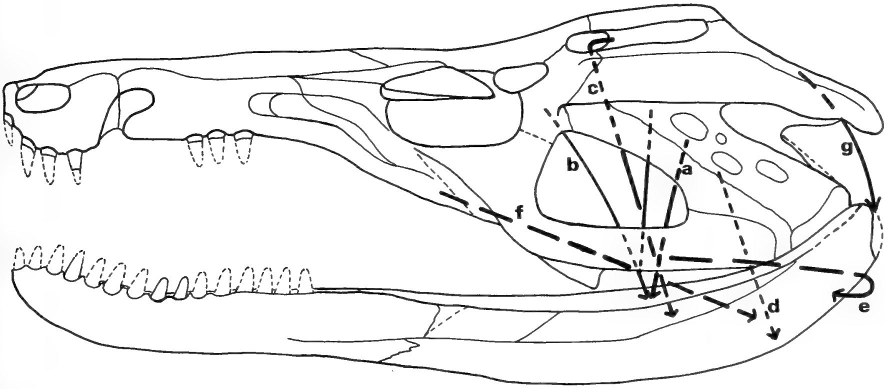

Fig. 19. ***Orthosuchus stormbergi***. Diagrammatic reconstruction of the inferred general location of the jaw muscles.

Abbreviations: a: m. adductor mandibulae externus superficialis; b: m. adductor mandibulae externus medialis; c: m. adductor mandibulae externus profundus; d: m. adductor mandibulae posterior; e: m. pterygoideus ventralis; f: m. pterygoideus dorsalis; g: m. depressor mandibulae.

The second part of the adductor, the m. adductor mandibulae posterior, no doubt also occupied a similar position in *Orthosuchus* to that seen in living crocodiles. It must have been a short, stout muscle which attached to the pterygoid face of the quadrate, and then ran slightly obliquely down to the lower jaw. In living crocodiles this muscle inserts on the lower surface of the angular along the posterior part of the external mandibular fenestra, and on the inner wall of the angular medial to this fenestra. Since the angular does not extend medially in *Orthosuchus* as it does in living genera, it seems likely that this muscle inserted in part on the prearticular.

In *Alligator* the m. adductor mandibulae posterior is divided at its insertion by the m. pseudotemporalis. Probably a similar arrangement existed in *Orthosuchus*. This muscle would have originated on the postorbital.

The second part of the m. adductor mandibulae internus, the m. pterygoideus, is extremely large in living crocodiles. There can be little doubt that in

Orthosuchus it arose mainly from the posterior edge of the pterygoid flange. It probably also attached to the ectopterygoid, and to the basisphenoid and adjacent medial portion of the pterygoid, as it does in living crocodiles.

In eusuchians a ventral slip of the m. pterygoideus wraps round the lower jaw and inserts on the retroarticular process, below and behind the glenoid. Since this process is absent in *Orthosuchus* a comparable muscle must have had a more anterior insertion principally in front of the glenoid. The ventro-lateral surface of the posterior region of the angular of *Orthosuchus* indicates an area of muscle attachment in life. This is suggested as the insertion area of the m. pterygoideus ventralis. In this position the muscle would have acted more or less at right angles to the lower jaw when this was widely open, and would have been efficient in closing the jaws. The migration of the m. pterygoideus ventralis on to the retroarticular process in later crocodiles has reduced its efficiency in closing the jaw. However, as Ewer (1965) has pointed out, a muscle in this position stabilizes the articulation.

In living crocodiles it is the powerfully developed anterior extension of the pterygoideus, the m. pterygoideus dorsalis (= the pterygoideus D of Lakjer), that serves to close the lower jaw. This muscle originates along the length of the inner surface of the snout. Anteriorly it extends well in front of the orbit, and attaches to the dorsal surface of the maxilla, palatine and pterygoid. It inserts on the medial surface of the angular, below and in front of the glenoid.

In view of the large pterygoid flange present in *Orthosuchus* it is probable that some development of the m. pterygoideus dorsalis had occurred. However it could not have been as extensive in *Orthosuchus* as it is in eusuchians. Probably it originated from the dorsal surfaces of both the pterygoid and palatine, but it could not have extended any farther forward than the anterior margin of the orbit in view of the limited development of the bony secondary palate. Posteriorly it probably attached to the membrane over the very large adductor fossa, and may have inserted on the prearticular.

The evidence suggests that the m. pterygoideus ventralis and the m. pterygoideus dorsalis were not as well developed in *Orthosuchus* as they are in living crocodiles. Nevertheless this muscle must have been considerable, as shown by the large size of the pterygoid flange. Further, the positioning of this muscle suggests that it was fully effective in closing the jaws. On the other hand, the large size of the superior temporal fenestra clearly indicates that the m. adductor mandibulae externus profundus was also extensive, as it is in *Gavialis*, so increasing the efficiency of snapping shut the jaws.

Dollo (1884) related the development of this musculature to the size of the antorbital fenestra. He concluded that where the m. adductor mandibulae externus was more important than the m. pterygoideus dorsalis, the antorbital fenestra was reduced. Conversely this fenestra was enlarged where the m. pterygoideus dorsalis was well developed. Gregory & Adams (1915) and later workers supported this idea. Walker (1961) expressed the opinion that in *Ornithosuchus* the m. pterygoideus dorsalis originated in large part from a membrane stretched across the depressed area on the snout surrounding the antorbital fenestra, and probably also from the depressed area itself.

Certainly the small size of the antorbital fenestra may be correlated to the greater importance of the m. adductor mandibulae externus profundus in *Orthosuchus*. On the other hand, Ewer (1965) has pointed out that in all later crocodiles it is the m. pterygoideus dorsalis that is the more extensive of the two muscles, yet the antorbital fenestra has been lost. This would not have occurred had the fenestra been the main area of origin of the muscle. There seems little doubt that in *Orthosuchus* the antorbital fenestra was unrelated to the jaw musculature. It probably housed a gland in life.

According to Lakjer (1926) and Anderson (1936), the m. intramandibularis is differentiated from the m. adductor mandibulae in living crocodiles. This muscle arises from the membrane lying over the adductor fossa, and then passes over the coronoid through the Meckelian fossa and along the primordial canal to insert on Meckel's cartilage. In Anderson's view, since the m. adductor mandibulae externus profundus and the m. pterygoideus dorsalis have slips which attach to the m. intramandibularis, the anterior insertion of this muscle increases the efficiency of the other muscles. It is possible that a similar muscle was present in *Orthosuchus*, although presumably it passed over the prearticular before entering the jaw.

In view of the insignificant development of the retroarticular process in *Orthosuchus*, it seems probable that the m. depressor mandibulae was not strongly developed. No doubt it had a similar arrangement to that seen in living crocodiles, and arose on the occipital surface of the parietal, squamosal and exoccipital, and inserted on the posterior margin of the articular. In living crocodiles where the retroarticular process is prominent, the m. depressor mandibulae is correspondingly strongly developed. Adams (1919) suggests that since crocodiles generally lie with their heads on the ground, this muscle serves to lift the cranium rather than lower the bottom jaw. It may be that this muscle was less well developed in *Orthosuchus*, and that the skull did not reach the massive size attained by many of the living species.

MUSCULATURE OF THE SHOULDER AND FORE-LIMB (Figs 20–21)

Fürbringer (1876, 1900) described in detail the musculature of the shoulder and upper arm of various reptiles, and this work was followed by Von Wettstein (1937) in his account of the Crocodilia. Gregory & Camp (1918) also reviewed the identification of the shoulder muscles. This account follows the terms used by these workers.

Axial muscles associated with the pectoral girdle

The pectoral girdle of *Orthosuchus* differs from that of living crocodiles in that while the scapula is long, relative to the size of the humerus, the coracoid is shorter. Presumably, therefore, attachment areas of certain muscles would have differed from those occurring in living crocodiles. On the other hand a clavicle is lacking in *Orthosuchus*, as it is in living crocodiles, and it seems likely that specializations in the axial musculature which are associated with this bone's absence in modern genera had already taken place in *Orthosuchus*.

In *Orthosuchus* the m. capito-dorso-clavicularis (= trapezius of Fürbringer) probably arose from the parietal and squamosal, and merged posteriorly into the m. latissimus dorsi, as it does in recent crocodiles. The m. sterno-mastoideus consists of two parts in crocodiles. The muscle arises on the skull, but is divided by the atlantal rib before it inserts on the sternum. Presumably this muscle was similarly modified in *Orthosuchus*, since a well-developed atlantal rib is present.

Although it is not found in other living reptiles, the m. rhomboideus is developed in the Crocodilia. It arises from the fascia above the eighth and ninth cranial nerves, and inserts on the anterior two-thirds of the dorsal inner surface of the supra-scapula. Since this muscle is also well developed in birds, it seems probable that it was present in ancestral archosaurs. In *Orthosuchus* the large size of the scapula suggests that the rhomboideus muscle may have inserted principally on this element rather than on the supra-scapula. Similarly, it seems probable that the deeper m. levator scapulae superficialis inserted on the upper anterior external margin of the scapula in *Orthosuchus*. The surface of this margin shows fine striations which possibly indicate muscle attachment areas. The muscle presumably took origin on the cervical vertebrae.

In living crocodiles the m. serratus superficialis arises on the last cervical and first three dorsal ribs, behind the pectoral girdle and below the m. latissimus dorsi. There is fundamentally no difference between these ribs in *Orthosuchus* and those of living crocodiles. However, whereas in living species the 'uncinate' processes are normally cartilaginous, in *Orthosuchus* they are fully ossified. This muscle most likely inserted on the posterior margin of the scapula. Similarly, the deep-lying m. serratus profundus presumably arose from the transverse process of the cervical vertebrae, and inserted on the inner and upper surface of the scapula. The m. omohyoid must also have inserted on to this surface of the scapula.

Dorsal muscles of the fore-limb

The m. latissimus dorsi is weakly developed in modern crocodiles and shows some differentiation into two parts. In *Orthosuchus* it would have taken origin from the external surfaces of the dorsal ribs and inserted on the head of the humerus near its posterior margin. Almost certainly the m. subcoraco-scapularis (= subscapularis) inserted near to this muscle, and arose from the rear edge of the scapula. Similarly, it is likely that the m. teres major was present in *Orthosuchus*. According to Fürbringer, although this muscle is absent in *Sphenodon*, and occurs in only a few lacertilians (Agamidae), it is developed in living crocodilians. In *Orthosuchus* the upper, backwardly projecting margin of the scapula probably acted as the area of attachment for this muscle, which extended beneath the m. latissimus dorsi to insert on the lateral surface of the humerus.

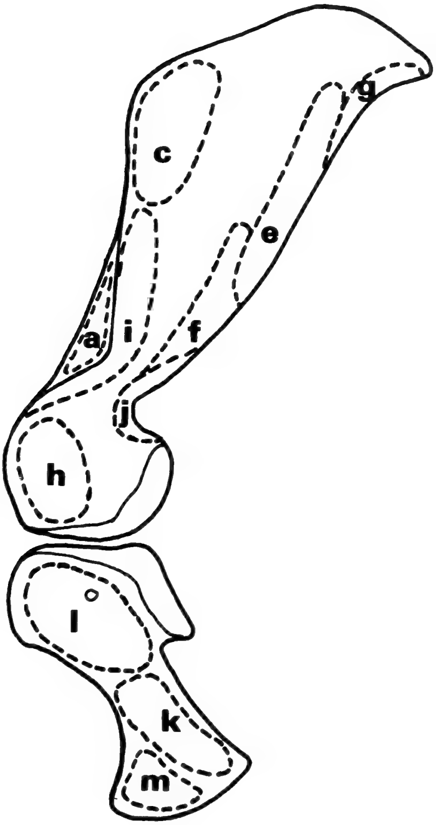

Fig. 20. *Orthosuchus stormbergi.* Lateral surface of the pectoral girdle showing inferred general areas of muscle attachments.

Abbreviations: a: m. trapezius; b: m. rhomboideus; c: m. levator scapulae superficialis; d: m. latissimus dorsi; e: m. serratus superficialis; f: m. subscapularis; g: m. teres major; h: m. scapulo-humeralis posterior; i: m. dorsalis scapulae and m. deltoides clavicularis; j: m. triceps; k: m. coracobrachialis brevis; l: m. supracoracoideus; m: m. biceps brachii.

In living crocodiles the m. scapulo-humeralis anterior is lacking, though the posterior division is well developed. A similar arrangement almost certainly existed in *Orthosuchus,* since there is a well-marked depression ventrally on the external surface of the scapula, near to its anterior border. A similar area on the scapula of living crocodiles marks the origin of this muscle. The m. scapulo-humeralis posterior (= scapulo-humeralis profundus of Fürbringer) would have inserted on the lateral surface of the humerus. In *Orthosuchus* this area of the humerus is marked by fine striations.

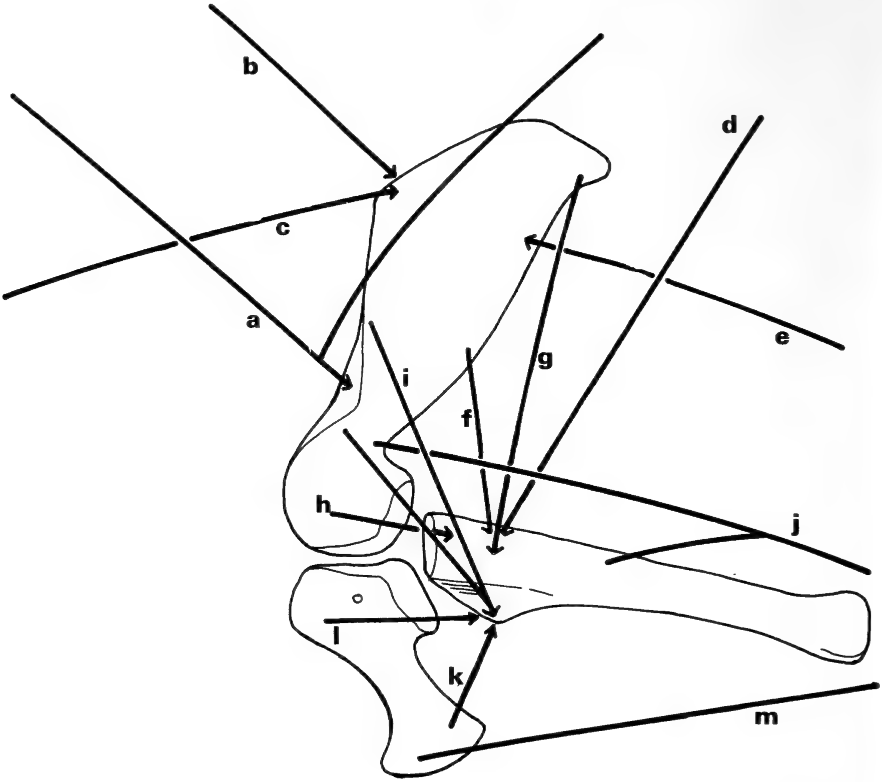

Fig. 21. *Orthosuchus stormbergi.* Diagrammatic reconstruction of the inferred main lines of action of the muscles of the fore-limb. Abbreviations as in Figure 20.

The deltoid muscle in reptiles is typically a broad but thin sheet which arises in two parts: one, the m. dorsalis scapulae (= deltoides scapularis superior of Fürbringer), arises from the upper part of the scapula, and the second, the m. deltoides clavicularis (= cleido-humeralis), from the clavicle and interclavicle. Since the clavicle has been lost in crocodiles, the m. deltoides clavicularis has shifted its origin to the scapula. A similar arrangement must have existed in *Orthosuchus*, and both parts of the deltoid would have inserted on the outer surface of the deltopectoral crest. Fine striations indicate this area as one of muscle attachment in life.

Despite the absence of an olecranon process in living crocodilians, the major dorsal muscle of the arm, the m. triceps, still forms a massive muscle body. In view of this, and since the proximal end of the ulna is expanded in crocodilian fashion, there is no reason to suppose that the m. triceps was not well developed in *Orthosuchus*. It is also likely that the areas of attachment of this muscle on to the pectoral girdle and humerus were fragmented into five centres of origin, as they are in living crocodiles. In these forms the muscle consists of two layers, the deeper of which arises from the upper, posterior and medial surfaces of the humerus, and the outer having its origins on the pectoral girdle. In *Orthosuchus* the scapula is grooved above the glenoid facet, and very probably this area denotes in part the origin of the m. triceps. The insertion of this muscle must have been by a common tendon on to the head of the ulna.

Ventral muscles of the fore-limb

The m. pectoralis in *Orthosuchus* no doubt formed a well-developed superficial muscle layer, originating on the interclavicle and ribs and inserting on the apex of the deltopectoral crest.

In living crocodiles the longus division of the m. coracobrachialis is absent and a similar arrangement was probably present in *Orthosuchus*, since distally the humerus resembles that of extant forms. Probably the m. coracobrachialis brevis would have arisen on the postero-ventral margin of the coracoid. However, this area of attachment must have been relatively smaller than that found in living crocodiles, since distally the coracoid is neither as elongate nor as expanded in *Orthosuchus* as it is in the eusuchians. This muscle would have inserted in the concavity antero-medial to the deltopectoral crest, as it does in living species. Again, its area of insertion must have been more limited in *Orthosuchus* than in modern crocodiles, judging by the more robust nature of the deltopectoral crest.

According to Von Wettstein, the m. supracoracoideus in living crocodiles has partially shifted its origin on to the inner face of the coracoid and lower edge of the scapula because of the considerable development of the m. coracobrachialis. It is possible that in *Orthosuchus*, where the m. coracobrachialis was more feebly developed, the area of origin of the m. supracoracoideus was confined to an area above that of the m. coracobrachialis. The m. supracoracoideus would then have inserted on the deltopectoral crest lateral to the point of attachment for the m. pectoralis.

The outer surface of the coracoid of *Orthosuchus* must also have given origin to the m. biceps brachii, which would have inserted on to the proximal part of the radius and ulna. The m. brachialis inferior was probably well developed, and in life would have attached to the anterior margin of the humerus, and inserted on the proximal end of the ulna.

Muscles of the lower arm

The following account is based on the work of Von Wettstein, who followed Ribbing (1907), and of Haines (1939), who made a comparative study of the extensor muscles of the forearm.

In view of the marked similarity between the lower arm elements of *Orthosuchus* and that of living crocodiles, there seems every reason to suppose that the musculature of this region in *Orthosuchus* would have resembled that of eusuchians. In this group in general there is a reduction in the lower arm and hand musculature.

Typically, the long extensors of the forearm attach to the ectepicondyle of the humerus. This projection is only slightly more developed in *Orthosuchus* than it is in living crocodiles, where it is minimal. Very likely, therefore, the m. extensor digitorum communis (= humerodorsalis of Haines) was as reduced in *Orthosuchus* as it is in modern forms. In living crocodiles this muscle no longer inserts on to all the digits, but chiefly on to metacarpal two, with extensions to four and the radiale.

There can be little doubt that in *Orthosuchus* the m. supinator (= extensor antibrachii radialis of Ribbing) also arose from the ectepicondyle in two parts, as in both living crocodiles and lizards, with the m. extensores carpi radiales attaching to the radius. Similarly, the m. anconeus (= extensor antibrachii ulnaris of Ribbing) was probably well developed and also took origin on the ectepicondyle. On the other hand, the m. extensor carpi ulnaris may well have been somewhat limited in extent. In living crocodiles this muscle is confined to the ulna, and does not extend to the pisiform.

The m. abductor pollicis longus (= abductor digiti 1 of Ribbing = supinator manus of Haines) was no doubt extensively developed in *Orthosuchus*. It probably originated on the radius as well as on the ulna, and inserted on to the radiale as it does in living crocodiles. The m. extensores digitorum breves would have extended on to the digits. In Haines's view these specializations in musculature are associated with a great mobility of the wrist joint and the use of the elongated carpus as an extra limb segment.

Typically, the flexor muscles of the lower arm are more powerful than the extensors, since the main propulsive effort is a backward push of the distal part of the limb. The long flexors arise from the entepicondyle of the humerus which, although of limited development in crocodiles, is a little more pronounced and rugose in *Orthosuchus* than it is in later forms.

In living crocodiles, the m. flexor digitorum profundus (= flexor accessorius of Ribbing) is well developed, while the m. flexor palmaris superficialis (= flexor primordialis communis of Ribbing) is less extensive. This latter muscle is united with the m. flexores breves superficiales. Possibly a similar arrangement existed in *Orthosuchus*. Certainly in life this medial muscle mass would have inserted on a palmar aponeurosis and effected flexion of the toes.

In living genera the m. pronator teres (= flexor antibrachii radialis of Ribbing) is joined together with the m. supinator, but neither the m. flexor carpi radialis nor the m. epitrochleoanconeus (= antibrachii ulnaris of Ribbing) is present. Whether or not reduction of musculature had proceeded this far in *Orthosuchus* is difficult to determine. These muscles are present in lizards and *Sphenodon*, but in these forms the entepicondylar process is well developed. On balance, it seems likely that in *Orthosuchus* these muscles were at best only feebly developed.

Deep in the forearm, the m. pronator profundus, connecting radius and ulna, probably had a similar arrangement to that seen in living crocodiles, passing between the m. flexor digitorum profundus and the m. pronator teres.

As in recent genera, the m. abductor digiti V was most likely well developed, taking origin on the palmar aponeurosis and inserting on the metacarpals and phalanges of the fifth digit.

MUSCULATURE OF THE PELVIS AND HIND-LIMB (Figs 22–24)

The probable arrangement of the muscles of the pelvis and upper leg of *Orthosuchus* is based on that found in *Alligator* (Romer 1923).

Axial muscles associated with the pelvis

The dorsal axial muscles in *Orthosuchus* would have run antero-posteriorly above the lumbar and caudal transverse processes and attached to the dorsal surfaces of the sacral vertebrae and internal surfaces of the ilium.

Similarly, the ventral axial musculature must have consisted of a series of muscle sheets covering the flanks of the body. In *Alligator* the three lateral members of this series all take origin from the lumbo-dorsal fascia. This fascia arises from the surface of the dorsal musculature and from the tips of the transverse processes of the lumbar vertebrae, and attaches posteriorly to the anterior edge of the blade of the ilium. In *Orthosuchus* this area of the ilium is extended forward to form a prominent anterior process, and may have provided a stronger base of attachment for the fascia.

Presumably these lateral muscles, the m. obliquus abdominis externus, the m. obliquus abdominis internus and the m. transversus abdominis, had a similar arrangement in *Orthosuchus*. The m. obliquus abdominis externus inserts on the anterior margin of the acetabulum, the last abdominal rib and on an aponeurosis over the main part of the m. rectus abdominis. The m. obliquus abdominis internus inserts on the posterior ribs and gastralia, and the m. transversus abdominis inserts on the m. rectus abdominis. The m. rectus abdominis no doubt ran posteriorly in the ventral midline to attach principally to the gastralia and abdominal ribs, though a part of it may have inserted on the posterior edge of the pubis and on the m. ilio-ischio-caudalis, as it does in *Alligator*.

In *Orthosuchus* the posterior process of the iliac blade extends well back. Similarly, the postero-ventral edge of the ischium is produced far posteriorly. This indicates increased attachment areas for the m. ilio-ischio-caudalis. In life this muscle would have occupied the ventral half of the tail on either side between the transverse processes and the midline ventrally. It is, therefore, fairly certain that the tail was a highly muscular organ.

Troxell (1925) has pointed out that the decrease in size of the vertebrae in both directions from the pelvis in living crocodilians is of advantage to the animal in swimming, where the tail is the propelling organ. A similar change in size of the vertebrae occurs in *Orthosuchus*. Presumably the tail could act as a propulsive organ in swimming, and no doubt also assisted in movement over land. However, the nature of the articular surfaces of the centra indicates that the degree of angular movement between successive vertebrae could not have been as great as that in living crocodiles, where the vertebrae are procoelous.

Dorsal muscles of the hind-limb

Above the acetabulum, and along the upper part of the posterior process, the ilium bears a number of distinct striae which suggest an area of muscle attachment. The most dorsal of these would probably have been the m. ilio-tibialis. This constitutes one part of the major dorsal muscle of the thigh, the m. quadriceps femoris. In *Alligator*, the m. ilio-tibialis has three distinct heads, but it is impossible to determine whether a similar arrangement existed in *Orthosuchus*, or whether its origin was still undivided.

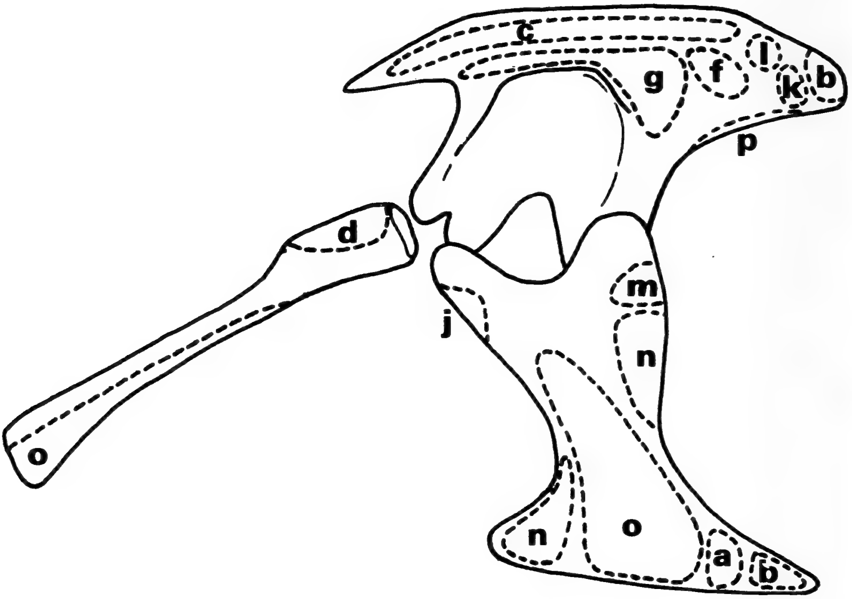

Fig. 22. *Orthosuchus stormbergi.* Lateral surface of the pelvic girdle showing inferred general areas of muscle attachments.

Abbreviations: a: m. rectus abdominis; b. m. ilio-ischio-caudalis; c: m. ilio-tibialis; d: m. ambiens; e: m. femoro-tibialis; f: m. ilio-fibularis; g: m. ilio-femoralis; h: m. ischio-trochantericus; i: m. pubo-ischio-femoralis-internus; j: m. pubo-ischio-tibialis; k: m. flexor, tibialis internus parts 1 and 2; l: m. flexor tibialis externus; m: m. flexor tibialis internus part 3; n: m. adductor femoris; o: m. pubo-ischio-femoralis externus; p: m. caudi-femoralis (= coccygeo-femoralis brevis); q: m. caudi-femoralis (= coccygeo-femoralis longus).

The m. ambiens in *Alligator* has two areas of origin. The smaller part arises on the proximal medial surface of the pubis, but the major origin is on the junction of the external surface of the pubis and the cartilage which lies in front of the acetabulum. The upper edge of the proximal end of the pubis of *Orthosuchus* is marked by a shallow depression. Very probably this denotes the area of origin of the major part of the m. ambiens. Since the proximal end of the pubis lies in a more dorsal position, the m. ambiens must have had a higher area of origin in *Orthosuchus* than it does in living crocodilians. In *Alligator* both elements of the m. ambiens unite with the m. ilio-tibialis. In addition, the larger element forms a tendon which passes through the extensor tendon of the m. ilio-tibialis across the knee to the lateral surface of the leg, where it joins the external head of the m. gastrocnemius. A similar tendon had probably been developed in *Orthosuchus*.

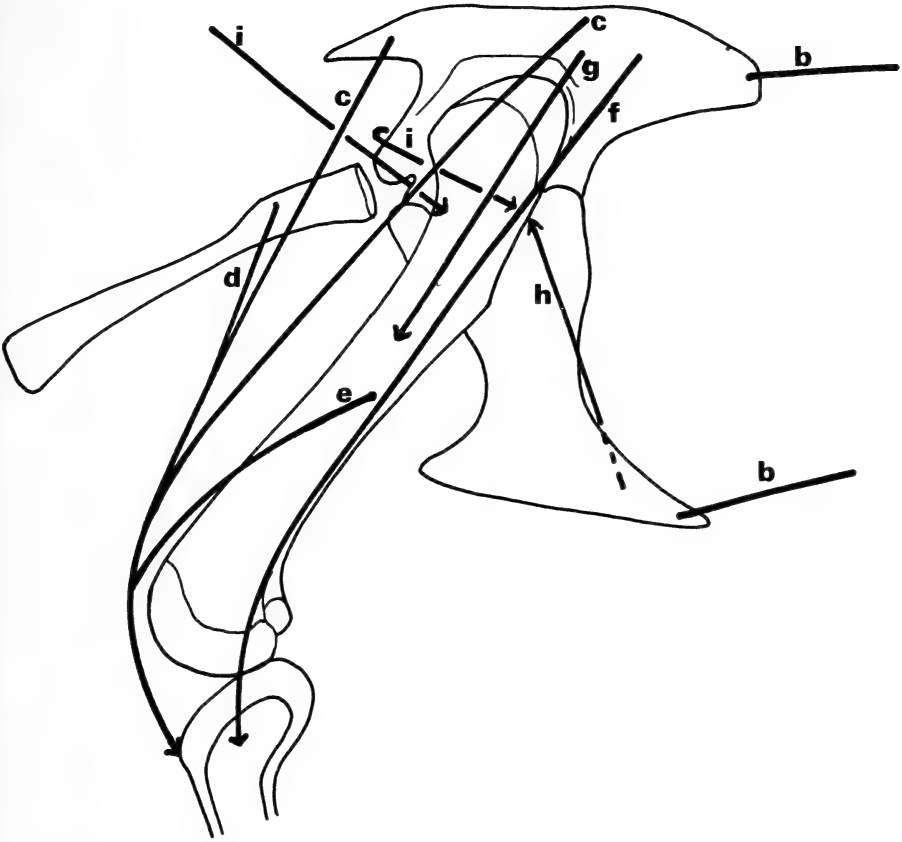

Fig. 23. ***Orthosuchus stormbergi***. Diagrammatic reconstruction of the inferred main lines of action of the dorsal muscles of the thigh. Abbreviations as in Figure 22.

The anterior (= dorsal of Romer) and medial (= anterior of Romer) surfaces of the greater part of the shaft of the femur no doubt provided an attachment area for the origin of the m. femoro-tibialis, the third component of the m. quadriceps femoris. In *Alligator* this muscle has a second, more lateral (= posterior of Romer) origin, but it is impossible to determine whether this was also the case in *Orthosuchus*. Its insertion would have been on to the weakly developed cnemial crest of the tibia. Nevertheless it seems that in *Orthosuchus*, as in living crocodiles, the m. quadriceps femoris was a powerful extensor of the thigh. Presumably the m. ilio-fibularis, a smaller extensor, ran parallel to it from just below the m. ilio-tibialis, and inserted into the head of the fibula. It may also have connected to the external head of the m. gastrocnemius as it does in *Alligator*.

The blade of the ilium above the acetabulum is deeper in *Orthosuchus* than it is in *Alligator*. This expansion no doubt reflects an increased area of origin for the m. ilio-femoralis, which arises below the m. ilio-tibialis. In life this muscle would have inserted on the lateral border of the femur for the greater part of the length of the shaft, and would have been a very powerful abductor.

In *Alligator* a small muscle, the m. ischio-trochantericus, runs from the posterior part of the inner surface of the ischium and inserts at the outer anterior edge of the femur, near to its head. There is no reason to suppose that a similar muscle did not exist in *Orthosuchus*.

The m. pubo-ischio-femoralis internus primitively originates on the medial surface of the pubis. However, Romer (1923) has shown that in *Alligator* this muscle is present in two parts and has more dorsal origins. The similarity of the pelvis in *Orthosuchus* suggests that this change had already occurred. One part of the muscle probably originated from the ventral surfaces of the posterior dorsal vertebrae, and possibly also attached to the inner surface of the anterior process of the blade of the ilium. This muscle would have inserted on the anterior surface of the proximal part of the femur. The evidence of strong muscle attachment in this area is shown by fine striations marking the bone at this point. The second part of the m. pubo-ischio-femoralis internus probably originated from the internal surfaces of the ventral margin of the ilium and dorsal margin of the ischium. It may also have attached to the ventral portions of the sacral ribs, as it does in *Alligator*. This muscle would then have extended anteriorly to insert on the femur, postero-medially to the insertion of its counterpart. A shallow depression on the femur of *Orthosuchus* at this point supports this conclusion. In life the m. pubo-ischio-femoralis internus would have been a powerful muscle drawing the femur inward, upward and forward.

Ventral muscles of the hind-limb

In view of the marked development of the dorsal musculature in *Orthosuchus*, it is clear that a corresponding development in ventral musculature must have existed, as it does in *Alligator*. In the latter, the superficial layer of muscles flexing the knee consists of six muscles which unite into two groups at their insertion on the tibia.

Romer has demonstrated that in *Alligator* the external group of muscles is composed of the m. pubo-ischio-tibialis and two parts of the m. flexor tibialis internus. In lizards the m. pubo-ischio-tibialis arises along the entire ventral margin of the girdle, but in crocodiles it is confined to a small area on the lower margin of the anterior process of the proximal ischium. Since this process is more

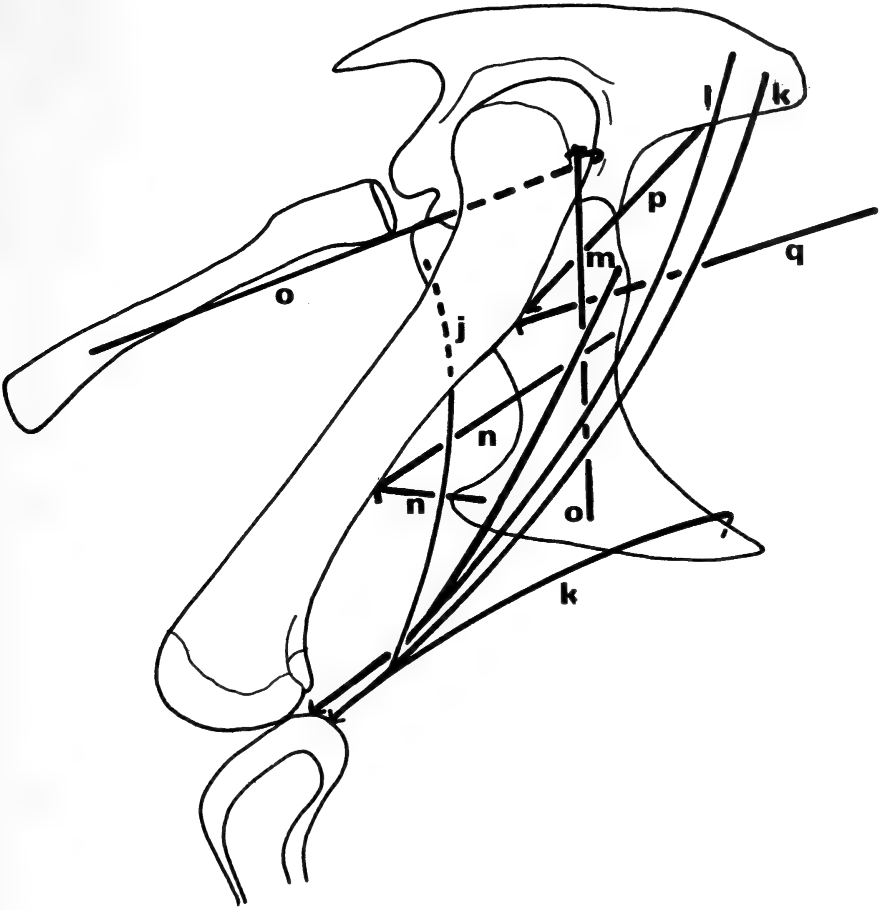

Fig. 24. *Orthosuchus stormbergi*. Diagrammatic reconstruction of the inferred main lines of action of the ventral muscles of the thigh. Abbreviations as in Figure 22.

strongly developed in *Orthosuchus* than it is in living crocodiles, it may be that the muscle too was more extensive. The m. flexor tibialis internus probably originated both on the medial surface of the ischium at its postero-ventral angle and from the posterior angle of the iliac blade. As in *Alligator*, these muscles would have inserted by a common tendon on to the medial surface of the tibia, internal to other flexors of the lower leg.

The second, internal group of muscles in *Alligator* consists of the m. flexor tibialis externus and two further parts of the m. flexor tibialis internus. In *Orthosuchus* the m. flexor tibialis externus almost certainly arose behind the m. ilio-tibialis on the posterior postacetabular iliac process. The m. flexor tibialis internus commonly arises from the ilio-ischiadic ligament, and presumably also did so in *Orthosuchus*. However, there may have been a second point of origin from the posterior margin of the proximal ischium, as occurs in *Alligator*. In both *Orthosuchus* and *Alligator* the ischium forms a marked prominence at this point. The m. flexor tibialis externus, together with the m. flexor tibialis internus, would have inserted medially on the head of the tibia. In addition, a second tendon may have passed down to unite with the m. gastrocnemius near the foot, as it does in living crocodiles.

Since the m. pubo-tibialis has been lost in both living crocodiles and birds, it seems reasonable to assume that this muscle was also absent in *Orthosuchus*.

A m. adductor femoris probably arose both below the m. flexor tibialis internus on the posterior margin of the ischium, and also from the anteroventral angle of the blade of the ischium. This muscle would have inserted on the posterior (= ventral of Romer) surface of the femur.

The deepest muscle of the ventral musculature, the m. pubo-ischiofemoralis externus, is a powerful muscle which no doubt had much the same arrangement in *Orthosuchus* as it has in *Alligator*. In the latter, one part arises from the main area of the blade of the ischium between the two adductors, a second from the ventro-lateral surface of the pubis, and a third from the dorsomedial surface of the pubis and adjacent gastralia. These parts unite and insert on the postero-lateral margin of the femur close to its head. The femur of *Orthosuchus* bears a marked rugosity at this point, and there can be little doubt that this represents the insertion area of this muscle.

Muscles connecting the femur to the tail, which made possible a backward and downward pull on the femur, were also well developed in *Orthosuchus*. The m. coccygeo-femoralis brevis (= caudifemoralis of Gadow) almost certainly arose from the last sacral and first caudal vertebrae, and attached to the ventral surface of the posterior process of the ilium. In *Orthosuchus* this process is stouter than it is in *Alligator*, and possibly the iliac slip of the muscle was more important than the caudal. This muscle would have inserted on the femur above the fourth trochanter.

Since the fourth trochanter is relatively less well developed in *Orthosuchus* than it is in *Alligator*, a weaker m. coccygeo-femoralis longus (= caudi femoralis of Gadow) than that of recent types is indicated. This muscle would have originated on the ventral surfaces of the caudal vertebrae and inserted both on the fourth trochanter and on to the fibula.

The muscles of the lower hind-limb

A comprehensive account of the musculature of the lower hind-limb of living crocodiles was given by Von Wettstein (1937), who followed the work of Gadow (1882).

Since the form of the lower hind-limb of *Orthosuchus* is closely comparable to that of living crocodiles, there seems little doubt that its musculature also followed a similar pattern. The common extensor of the digits, the m. extensor digitorum communis, would have originated on the lateral femoral condyle and inserted on to the bases of the metatarsals. In *Alligator* this muscle unites with the m. tibialis anterior, which arises on the proximal part of the tibia, and there is a common insertion on to the four long metatarsals. This differs from the pattern found in lizards, where the two muscles remain separate. Presumably in *Orthosuchus* these muscles had an arrangement similar to that found in *Alligator*.

In crocodiles, unlike *Sphenodon*, the m. extensor peroneus brevis (anterior) and the m. extensor peroneus longus (posterior) are separate. The m. peroneus brevis arises on the fibula and inserts on the dorsal and lateral surfaces of metatarsal five, and on the dorso-lateral surface of the calcaneum. The calcaneum of *Orthosuchus* shows a shallow depression at this point, and the fifth metatarsal bears a rugosity. It therefore seems likely that in *Orthosuchus* the m. peroneus brevis had a similar relationship and, as in living genera, a comparable function of dorsiflexing the foot and elevating its lateral border. In *Alligator* the m. peroneus longus arises on the lateral condyle of the femur and inserts on to the calcaneal tuber, so that it functions to flex the lower limb. Since the tuber is strongly developed in *Orthosuchus*, there can be little doubt that this muscle had an arrangement and function comparable to that in living crocodiles.

Similarly, the m. abductor and extensor hallucis was probably as well developed in *Orthosuchus* as it is in *Alligator*. It would have originated on the distal end of the fibula and from the calcaneum, and then crossed the dorsal surface of the foot to insert on the first metatarsal.

The main flexor of the lower limb, the m. gastrocnemius, is superficial in position and has two areas of origin. In *Orthosuchus* one part would have attached to the lateral condyle of the femur, and the second to the tibia, as in *Alligator*. Further, since the calcaneum of *Orthosuchus* is strikingly similar to that of living crocodiles, there can be little doubt that this muscle had a similar insertion. One part of the m. gastrocnemius would have run from the femur to the calcaneal tuber, partly inserting on its upper surface and forming a stout tendon which ran down the vertical groove to insert on the plantar aponeurosis. The second part of the m. gastrocnemius must have inserted entirely on the tuber. In life this muscle effected flexion of the foot during the propulsive effort.

The arrangement of the m. flexor digitorum longus (= flexor primordialis communis of Von Wettstein) in crocodiles is similar to that found in other reptiles. In *Orthosuchus* it very probably had several heads of origin, principally from the lateral condyle of the femur and proximal fibula. These would have united and run medially to the calcaneal tuber to the plantar aponeurosis, finally forming tendons inserting on the distal phalanges.

In living crocodiles the m. popliteus (= tibialis posticus of Gadow) is a powerful muscle which arises from the fibula and tibia, and distally forms a tendon which passes over a groove on the astragalus to insert on to the bases of metatarsals one and two. There is no reason to suppose that a similar arrangement did not exist in *Orthosuchus*. Presumably, too, the m. pronator profundus arose on the proximal part of the tibia and inserted on to the fibula. In living crocodiles, according to Von Wettstein, the distal part of this muscle, the m. interosseus, is absent.

AGE VARIATIONS IN THE SKULLS OF RECENT CROCODILIA AND AN ANALYSIS OF THE DIFFERENCES BETWEEN THE SKULLS OF THE TYPE, K409, AND K4639

The overall skull plan in K4639 compares well with that seen in the type, K409. The skull elements of the smaller specimen also have the same relationship to one another that they have in the type. On the other hand, certain differences are also apparent. Skull dimensions are dissimilar, and in K4639 the superior temporal fenestra is oval in shape and smaller than the orbit, whereas in K409 it is more or less circular and approximates the size of the orbit.

In view of the small size and low degree of ossification of the skull elements, there can be little doubt that K4639 is a juvenile form. The lack of fusion between the parietals and lack of a squamosal ridge in this specimen could also be attributed to the juvenile condition. In K409 the parietals are fused, and there is a ridge marking the position held by ear flaps in life.

The question then is whether the differences in skull proportions can be attributed to a difference in age between individuals of a single species, or whether they are specific differences. It cannot, unfortunately, be assumed that K409 is of breeding size, though clearly it would be helpful if this point could be established.

With this in mind, some attempt to analyse the differences, and to compare these with similar dimensions in the protosuchian, *Protosuchus*, and in eusuchians, was undertaken. Mook (1921*a*) studied a series of skulls of *Crocodylus acutus* (= *Crocodilus americanus*), *Alligator mississippiensis* and *Caiman crocodilus* (= *C. sclerops*), and noticed a number of characters which could be attributed to differences in age. To supplement this a series of nine skulls of *Crocodylus porosus*, from the collection at the British Museum (Natural History), have been examined by the author.

Breadth of skulls compared with length (Fig. 25)

Mook concluded from his data that in *Crocodylus acutus* and *Caiman crocodilus* there is a marked, though irregular, broadening of the skull with age. In *Alligator mississippiensis* there is only a slight change from young to old, a slight narrowing being noticeable in older specimens.

When breadth (ordinates) and length of skulls (abscissae) are plotted against one another a somewhat curved line is obtained. If both are converted into log. form, the lines are still curved, but if log. (length) is plotted against log. (breadth–10) the lines become, for practical purposes, straight.

Regression coefficients (b) for $\log_{10}$(breadth–10) on $\log_{10}$(length) were

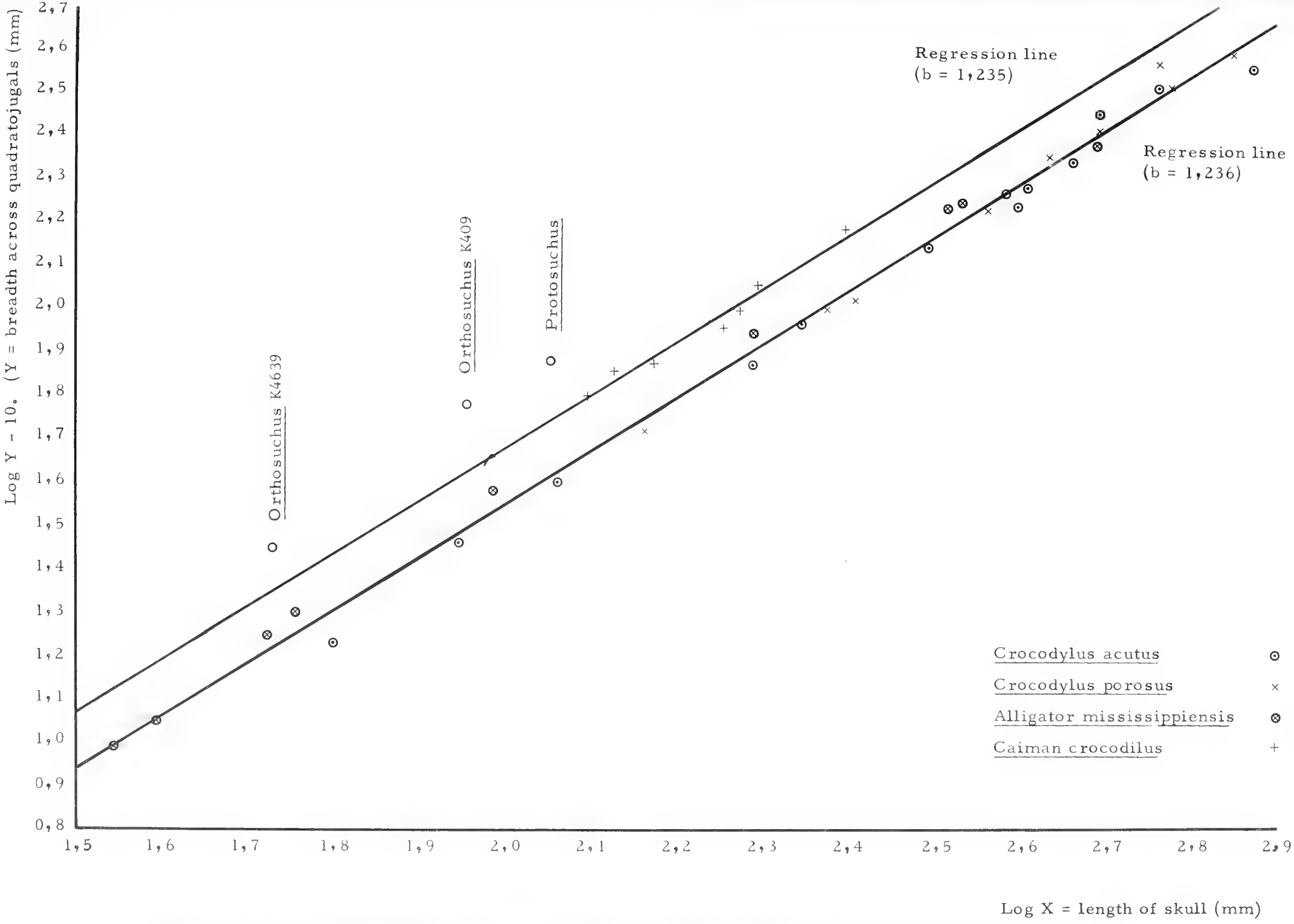

Fig. 25. Graph showing relationship between breadth and length of skull in eusuchians and protosuchians.

calculated separately for the four living species, and the following values obtained:

Caiman crocodilus b = 1,235
Alligator mississippiensis b = 1,236
Crocodylus acutus b = 1,271
Crocodylus porosus b = 1,332

The graph shows that the last three of these form a rather close group, with *Caiman* standing well outside. In the close group, the regression coefficients of *Crocodylus porosus* and of *Alligator* are the most distinct, but a *t* test shows that the difference between these coefficients is not significant (t = 1,950 with 14 d.f.).

While the position of the line for *Alligator* is perhaps marginally above the other two, it seems convenient for present purposes to combine the points for these three species and calculate one regression line. This is given by: $y = 1{,}236x - 0{,}9207$.

From this it can be shown that the ratio of breadth/length of skull has a minimum value (0,45) for animals of skull length 115 mm. In smaller and in larger animals the breadth of the skull is relatively greater.

Although the slope of the regression line for *Caiman crocodilus* (b = 1,235) is not distinct from the slope of the line (b = 1,236) for the other three combined, the regression line for *Caiman* lies clearly separated above that for the other three groups (t = 11,265 with 34 d.f.). Thus *Caiman crocodilus* is demonstrated as a species with a relatively broader skull.

Compared with this, there is no doubt that *Orthosuchus* (K409 and K4639) and *Protosuchus* have broader skulls than living species. The values for K409 and K4639 fall together reasonably well, and the value for *Protosuchus* is in close conformity with these.

Relative size of the cranial table (Figs 26–27)

Mook (1921*a*) established that the cranial table is relatively broader in young individuals than in older ones. He related the cranial table to the breadth of the skull across the quadratojugals. The ratios of breadth of cranial table/breadth of skull in *Orthosuchus* are:

K409 = 0,78
K4639 = 0,87

These ratios compare favourably with those Mook obtained for *Alligator* and suggest that a similar growth pattern occurred in *Orthosuchus.*

It can also be seen from the data that within a species the relationship approximates to a direct proportionality between breadth of cranial table and length of skull.

The estimated ratios (from the graphs) are approximately:

Crocodylus porosus = 0,26 (Fig. 26)
Crocodylus acutus = 0,27
Alligator mississippiensis = 0,28 (Fig. 27)
Caiman crocodilus = 0,35

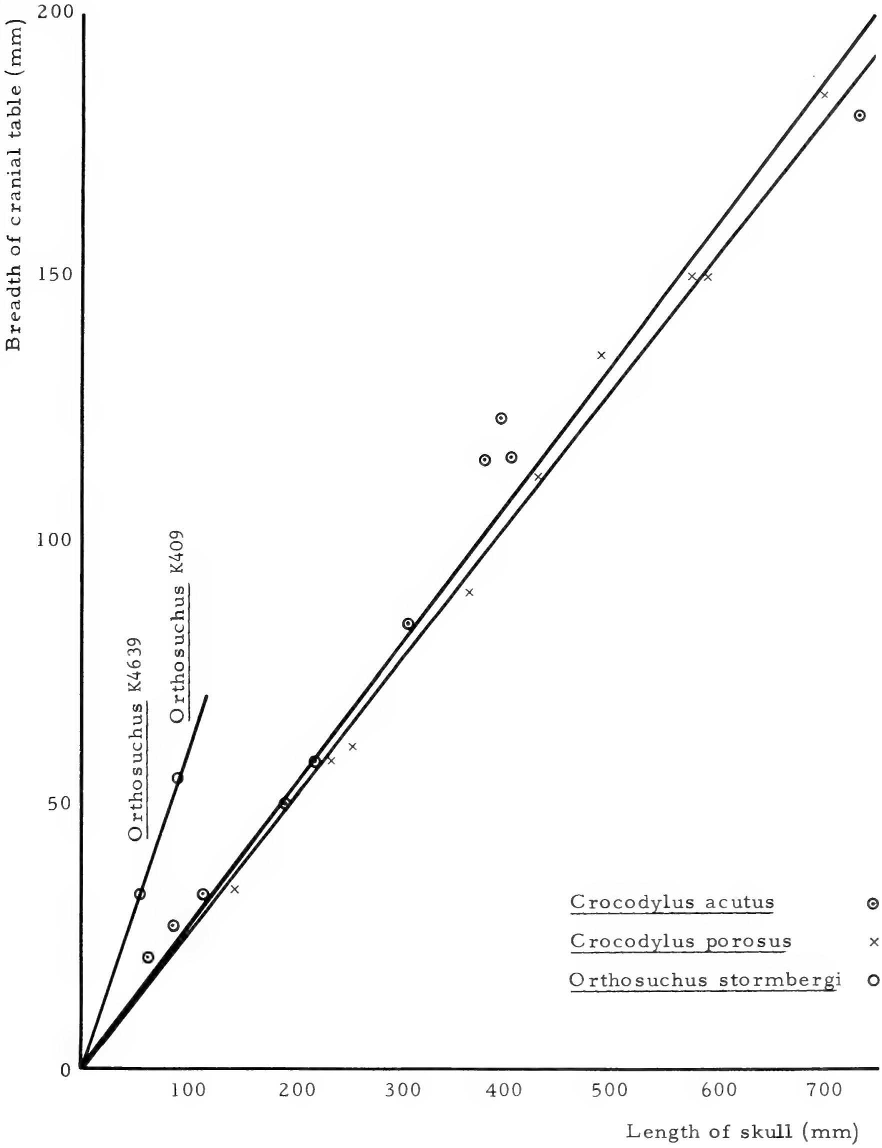

Fig. 26. Graph showing relationship between breadth of cranial table and length of skull in *Crocodylus acutus*, *C. porosus* and *Orthosuchus stormbergi*.

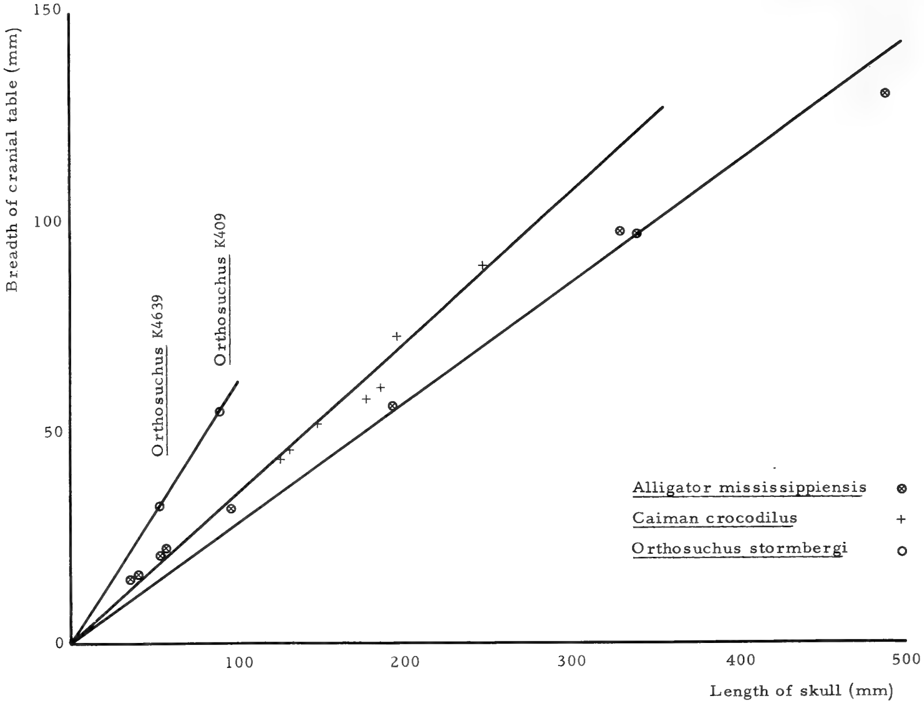

Fig. 27. Graph showing relationship between breadth of cranial table and length of skull in *Alligator mississippiensis*, *Caiman crocodilus* and *Orthosuchus stormbergi.*

Against these *Orthosuchus* shows a much higher ratio: 0,62 for both K409 and K4639.

These figures clearly separate *Orthosuchus* from the eusuchians and also show a close relationship between K409 and K4639.

Relation of preorbital to postorbital length (Fig. 28)

Mook's work on modern species showed a progressive increase in the length of the facial region as compared with the cranial region during growth. The degree to which this occurs depends on the form of the adult.

The ratios of postorbital over preorbital length for *Orthosuchus* are:

K409 = 0,96
K4639 = 1,16

These values compare favourably with those Mook obtained for brevirostrate forms, in particular that of *Caiman*. On the other hand *Protosuchus* is shown

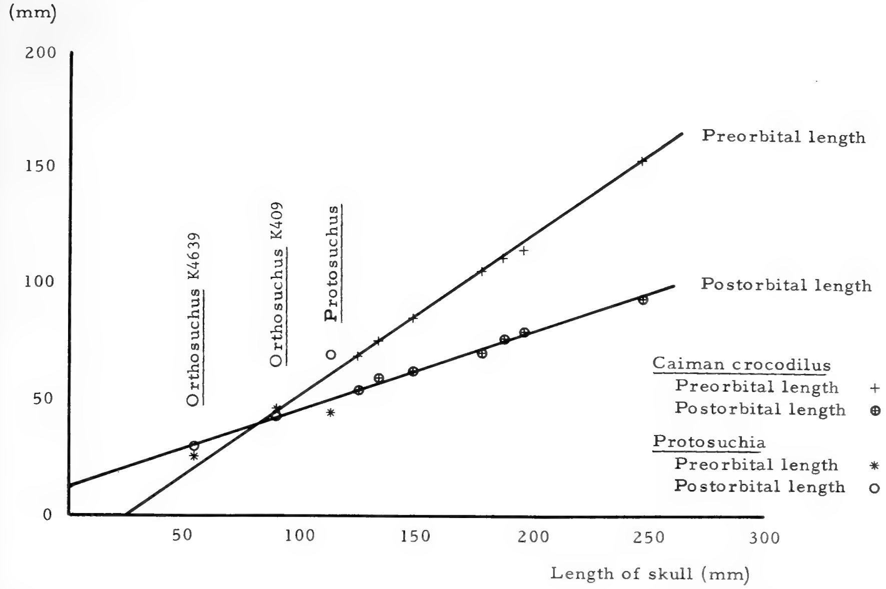

Fig. 28. Graph showing relationship between preorbital and postorbital length in *Caiman crocodilus*, *Orthosuchus* and *Protosuchus*.

to have a surprisingly short preorbital region, even assuming that Colbert & Mook (1951) made no allowance for the damaged tip. *Protosuchus* could perhaps be regarded as a juvenile of a species very much larger than *Orthosuchus*. However, both types seem to be young animals.

Relative size of the orbits (Fig. 29)

Mook noticed that the orbits of young crocodilians are relatively much larger than in full-grown animals, and expressed this as a ratio of length of orbit/length of skull. Further, he pointed out that there is a progressive increase in the relative breadth of the interorbital plate.

When the values for *Orthosuchus* K409 and K4639 are seen against those for *Crocodylus acutus* they again fall together reasonably well. In other words, the relatively longer orbits and the narrower interorbital plate of K4639, as compared with K409, could be attributed to a size (i.e. age) difference.

Although the values for *Orthosuchus* correspond closely to those for *Crocodylus acutus*, compared to both *Alligator* and *Caiman* the orbits of *Orthosuchus* are short relative to skull length. On the other hand, the interorbital region is broader in *Orthosuchus* than it is in any of these living species of a comparable size.

Relative proportions and position of the superior temporal fenestrae

Mook suggested that as a general rule, in the very young stages the superior temporal fenestrae are small and slit-like, that in later stages they

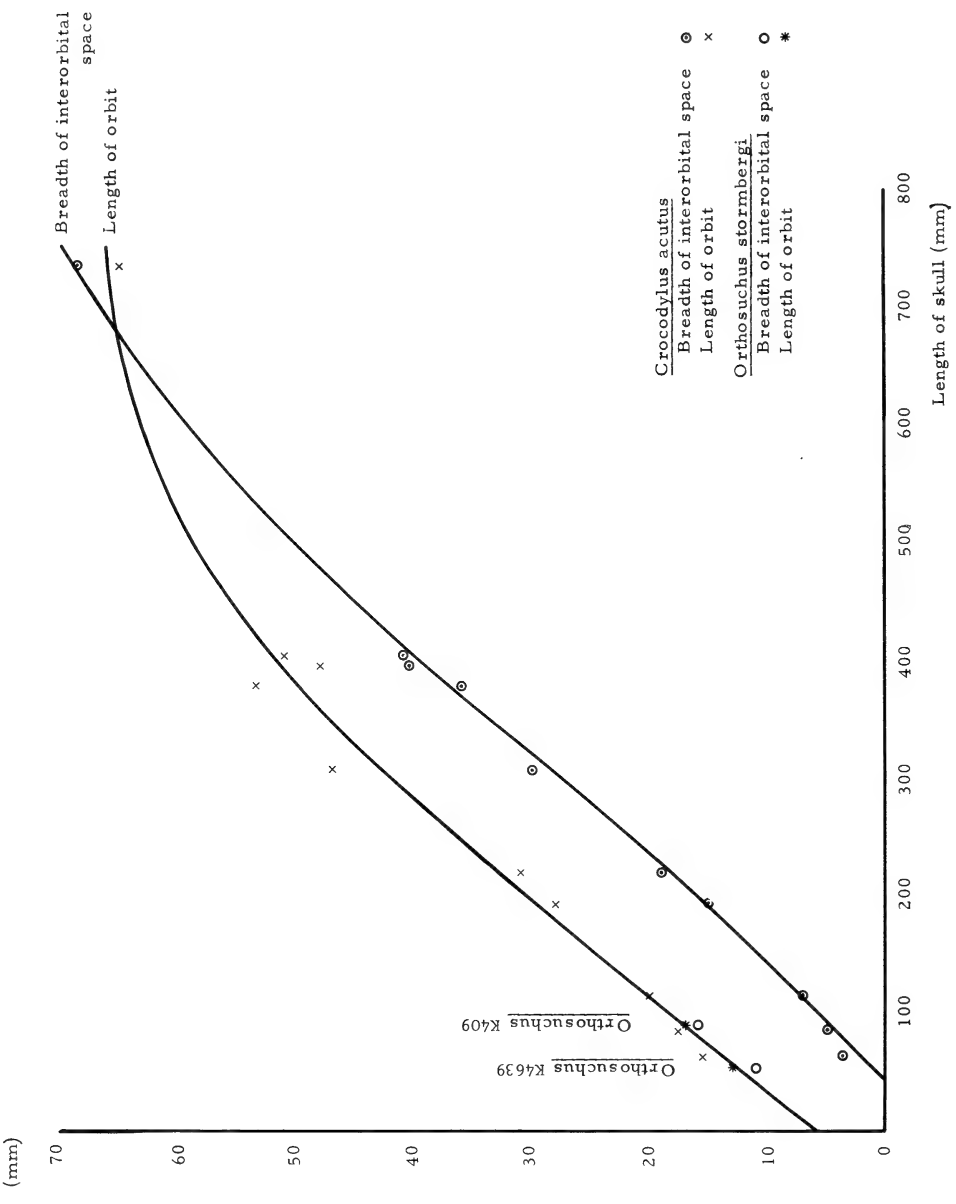

Fig. 29. Graph showing relationship between length of orbit and breadth of interorbital space n *Crocodylus acutus* and *Orthosuchus stormbergi*.

become rounder, and in old animals they usually become small and nearly circular. That the size and shape of the fenestrae are definitely size (i.e. age) related characters for the majority of species seems unquestionable. However, the precise pattern of development varies from species to species.

Mook notes that in young specimens of *Caiman crocodilus* the fenestrae are relatively large, and that in older ones they are smaller and may even eventually close at the surface. Skulls of *Crocodylus porosus* (British Museum (Natural History)) indicate that in this species the fenestrae are, in the early stages, elongate in the longitudinal direction, but when the skull reaches 300 to 400 mm in length they become round, only to elongate in the same longitudinal direction in larger specimens (Table 3).

To some extent the very elongate shape of the superior temporal fenestrae in K4639 may be due to lateral compression of the skull during preservation. However, even without this consideration it is still possible that this is a juvenile character in *Orthosuchus*, the fenestrae becoming broader and assuming a more or less circular shape in later stages. It is, of course, impossible to say whether they would have remained large, as they do in *Gavialis*, or whether they would eventually have become smaller, relative to skull size, as in other living crocodiles.

Mook also noticed that in crocodiles other than *Caiman* the superior temporal fenestrae appear to migrate inwards during growth, due to failure of growth of the intertemporal region. Hence in young specimens the centres of the superior temporal fenestrae are immediately posterior to the centres of the orbits, while in older individuals the centres of the fenestrae are posterior to the inner part of the orbits. Again, the series of skulls of *Crocodylus porosus* suggests that growth between the superior temporal fenestrae is minimal compared with increase in length and breadth of the skull, in the early stages. However, there is some evidence of a reversal of this position in skulls over 450 to 500 mm in length.

In *Orthosuchus*, despite the fact that K409 is almost twice as long as K4639, the width of the intertemporal region is the same for the two skulls (i.e. 6 mm).

On balance therefore, there seem to be no strong reasons indicating the separation of K409 and K4639. In view of the similarity of skull plan and relationship of individual elements, it seems more likely that the differences are attributable to size (i.e. age) variation. Whether K409 is juvenile, or of breeding size, is indeterminable. Much of the evidence seems to indicate that it is a young animal.

MODE OF LIFE

Orthosuchus was rather lizard-like in body proportions. The type specimen measures about two-thirds of a metre in length, and although this may well have been a young animal, other known Triassic protosuchians are all more or less the same size. The slender jaws and feeble dentition are clearly not those of a voracious predator, and on land it would have had a number of formidable competitors.

Table 3
Skull proportions in *Orthosuchus*, and *Crocodylus porosus* in mm

	Orthosuchus		*Crocodylus porosus*								
	SAM–K4639	K409	B.M.(N.H.) No. b.b.b.	1932 7.19.1.	1929 2.22.5	86.5.20.3	67.4.2.188	89.5.13.13	65.8.22.1	1902 12.19.1	47.3.5.33
Length of skull, front of snout to parietal/supra-occipital suture	54,0	90,0	145,0	235,0	255,0	365,0	430,0	490,0	575,0	590,0	700,0
Breadth of skull across external margin of quadratojugals	38,0	70,7	62,0	110,0	115,0	180,0	234,0	270,0	380,0	335,0	400,0
Breadth of cranial table at mid-level of superior temporal fenestrae	33,0	55,0	34,0	58,0	61,0	90,0	112,0	135,0	150,0	150,0	185,0
Intertemporal width	6,0	6,0	8,0	10,0	10,0	14,0	17,0	18,0	18,0	25,0	30,0
Length of superior temporal fenestra	10,0	19,0	12,0	20,0	17,0	20,0	30,0	30,0	45,0	50,0	55,0
Breadth of superior temporal fenestra	5,0	17,0	8,0	18,0	18,0	22,0	27,0	35,0	40,0	35,0	35,0
Breadth of skull/length of skull	0,70	0,79	0,43	0,47	0,45	0,49	0,54	0,55	0,66	0,57	0,57
Breadth of cranial table/breadth of skull	0,87	0,78	0,55	0,53	0,53	0,50	0,48	0,50	0,40	0,45	0,46
Breadth of superior temporal fenestra/length of superior temporal fenestra	0,50	0,89	0,67	0,90	1,06	1,1	0,90	1,17	0,89	0,70	0,64
Intertemporal width/breadth of skull	0,18	0,08	0,13	0,09	0,09	0,08	0,07	0,07	0,05	0,07	0,08

The Triassic was a time of dramatic faunal changes, with the earlier types, which were predominantly therapsids, being gradually replaced, mainly by archosaurs. Unquestionably, the dominant forms of the Upper Triassic lay among the saurischian dinosaurs. These were prosauropods of generally large size, and included both herbivorous forms like *Thecodontosaurus* and *Plateosaurus*, and carnivores like *Melanorosaurus*. It is now quite clear that the earliest known ornithischians also occurred at this time, as shown by *Fabrosaurus*, *Heterodontosaurus* and *Lycorhinus*. Thecodontians also occur in the earlier Triassic of South Africa, and *Sphenosuchus* is known from the Red Beds.

Although the mammal-like reptiles were reduced to a few genera, advanced ictidosaurs, *Tritylodon* in particular, are characteristic of the Upper Triassic. The earliest known mammal, *Erythrotherium*, is also known from these beds of South Africa. Elsewhere in the late Triassic procolophonids are present, labyrinthodont amphibians are found in Australia, and rhynchosaurs in Nova Scotia, Scotland and India.

At the end of the Triassic the large pseudosuchians and many of the prosauropods disappeared. However, the crocodiles flourished through the Jurassic, at least in a chiefly aquatic environment, as evidenced by large teleosaurs like *Mystriosaurus* and *Steneosaurus*, and highly specialized marine forms like *Metriorhynchus*.

Coupled with the change in fauna there was, at least in South Africa (Haughton 1924), a progressive increase in aridity from the Lower through to the Upper Triassic. Yet, however tempting it may be to suppose that *Orthosuchus* was essentially terrestrial in habit, there are undeniable indications that it spent much of its time in water, as do living crocodiles.

This is most clearly shown by the form of the palate. Although *Orthosuchus* has only a short secondary palate, the form of the vomers and palatines and ridging on the pterygoids leave little doubt that a functional secondary palate extended well back to the base of the skull, as in living crocodiles. The palate of *Orthosuchus* differs only in that it was floored by soft tissue rather than by bone. Hence in *Orthosuchus* the functional choanae opened well back, and conceivably a valve apparatus was present which sealed off the glottis when the mouth was open. *Orthosuchus* was probably able to remain submerged, leaving only the external nares open above water to act as a snorkling device.

Ear flaps may also have evolved to prevent flooding of the otic region. Shute & Bellairs (1955) have shown that modern crocodiles close the ear-flaps when they submerge, though this action does not necessarily prevent water from entering the recess. It is difficult to see why ear flaps would have been developed for a terrestrial habit, when their closure in modern species reduces conduction of aerial sound to the ear by 10 to 12 db over most of a frequency range of 100 to 6 000 cycles (Wever & Vernon 1957).

Amongst living crocodiles the overall skull shape of *Orthosuchus* is paralleled most closely by that of the Indian gharial, *Gavialis gangeticus*. In both forms the snout is very slender and set off sharply from the skull table, though in *Gavialis* the snout is very much more elongate than it is in *Orthosuchus*. *Gavialis* feeds primarily on small fish. An individual will creep towards a shoal of fish, and then remain motionless whilst snapping sideways at the prey. The skull shape of *Orthosuchus* is possibly an adaptation for this kind of aquatic predation.

Most probably *Orthosuchus* spent much of its time in lakes or swamps, and this mode of life would have afforded certain advantages. Food in the form of small fishes and aquatic invertebrates would have been plentiful and more easily obtainable than a comparable diet on land, while the water would have provided an admirable escape route from terrestrial predators.

Ewer (1965) came to the conclusion that the antorbital fenestra in *Euparkeria* housed a gland, suggesting that this might have been a salt gland. The nature of the fenestra in *Orthosuchus* also strongly indicates that in life it housed a gland, whose secretion would have passed through a duct occupying the groove leading to the lower orbital margin.

However, whereas thecodontians like *Euparkeria* typically have a large antorbital fenestra, it decreases in relative size through *Orthosuchus* to early aquatic mesosuchians like *Teleosaurus*, is nearly always absent in highly specialized marine forms like *Metriorhynchus* and *Geosaurus* and is lost in living crocodiles. Presumably therefore the gland was more important in terrestrial than in marine forms.

In contrast, a salt-secreting gland is predominantly important in marine animals. Salt secretion by marine turtles is particularly well known, and occurs from one of the orbital glands. Among other reptiles salt secretion is known to occur from the nasal gland in lizards. Although some terrestrial forms, such as the tropical lizard, *Iguana iguana*, and the American desert lizard, *Dipsosaurus dorsalis*, secrete significant quantities of salt, they do not do so in the large amounts found in their marine relatives (Schmidt-Nielsen 1963). Birds also possess a salt-secreting nasal gland, which is normally located in the orbit. Again, in terrestrial forms it is very small, but is large in marine species. Indeed, to some extent its size varies with exposure to salt loads.

Unfortunately, almost no work has been carried out in this field on crocodiles. Schmidt-Nielsen (1960) found that a single specimen of the estuarine crocodile, *Crocodylus porosus*, did not respond to osmotic loads. This is the most thoroughly aquatic and frequently marine species of all living crocodiles.

In living crocodiles a well-developed nasal gland lies anterior to the preconcha, with its duct running anteriorly. Both a lachrymal and a large Harderian gland lie within the orbit. The antorbital gland of *Orthosuchus* was possibly an additional orbital gland, and the patches of glandular tissue which occur on the conjunctiva of the lower lid in *Crocodylus porosus* may represent the vestige of this gland.

Taking fore- and hind-limb lengths as humerus + radius + radiale, and femur + tibia respectively, the length of the fore-limb approximates that of the hind-limb in both *Orthosuchus* and contemporary crocodilians (table 4). Two large specimens of *Crocodylus niloticus* showed a fore-limb 83% and 88% the

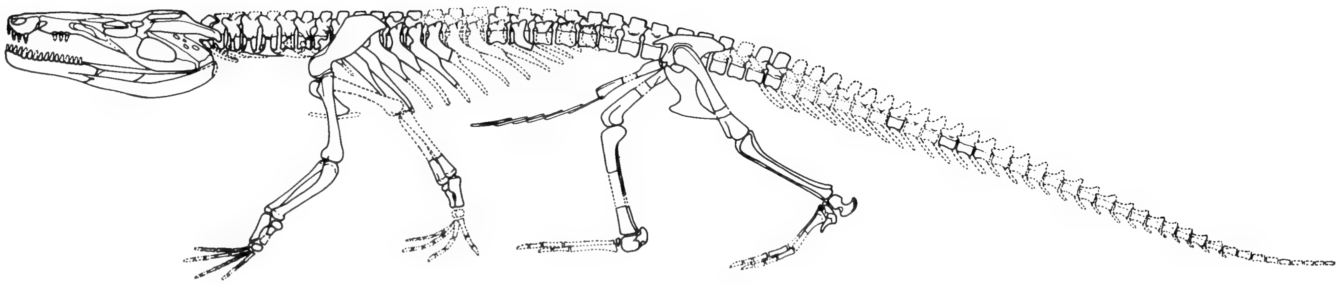

Fig. 30. *Orthosuchus stormbergi*. Restoration of the skeleton in standing pose (tail based on proportions found in living crocodiles) ($\frac{1}{4}$ natural size).

length of the hind. A smaller individual of *C. acutus* had a ratio of 98%, while in a juvenile of *Alligator mississippiensis* the ratio was 91%. Although both femora of *Orthosuchus* are now broken, the suggested measurement of 57 mm can only be a little short, if at all, of the true length. Using this measurement, the fore-limb is then 91% the length of the hind. *Orthosuchus* falls well within the range for living crocodilians and was quadrupedal (Fig. 30).

Ewer (1965) noted the significance of trunk length in determining the type of locomotion. Trunk length is taken as the distance along the vertebral column from a point directly over the pectoral glenoid to one over the acetabulum. The longer the trunk, relative to the length of the hind-limb, the more quadrupedal the type.

Of four large specimens of *Crocodylus* studied, it was found that in *C. niloticus* the hind-limb was 44% and 52% the length of the trunk, in *C. acutus* it was 49%, and in *C. porosus* 50%. In a juvenile *Alligator* the trunk is shorter relative to the length of the hind-limb, as is also the case in *Orthosuchus*, a value of 61% being obtained in both types. Ewer found a value of 40% and 50% in *Varanus* and *Sphenodon* respectively, and 70% in the fast-running quadrupedal *Agama*.

There can be little doubt that *Orthosuchus* could rest on its belly with the femur held horizontally as is the practice of modern reptiles. On the other hand, the structural features of the femur and pelvis indicate that the femur was pulled into a more nearly vertical position when the animal was moving. Living crocodiles when walking unhurriedly over land, and when hauling out of water, do so with the limbs held vertically; a movement described by Cott (1961) as the high walk. A comparison of the femur of *Orthosuchus* with that of living crocodiles shows remarkable similarity in form between the two types. However, in *Orthosuchus* the articular surface of the femoral head is more medially directed, suggesting that the femur was usually held in a vertical position. The deep acetabulum and pronounced supra-acetabular buttress would have been advantageous with the femur held in this position. The musculature essential for this type of movement was well developed.

The crurotarsal ankle joint of *Orthosuchus* is admirably suited to the action of a vertically orientated femur. By virtue of the longer length of the tibia posteriorly, it is possible for the pes to be forwardly directed while the crus passes backwards. The presence of a calcaneal tuber clearly gives greater leverage to movement of the foot. *Orthosuchus* would therefore have moved in a plantigrade manner, much as living crocodiles do when walking over land.

Although the pectoral musculature was apparently well developed, in certain respects the humerus of *Orthosuchus* is more primitive in form than that of living crocodiles. The pronounced medially directed deltopectoral crest seems to obviate any possibility of the humerus being held vertically. In this position it would foul the coracoid, on protraction at least. The humerus also shows greater twisting through its axis, so that the distal articular surface, and the lower fore-limb, must have been more laterally directed than it is in living crocodiles. On the other hand, the elongation of the radiale and ulnare appears to be a means of both lengthening the fore-limb, and providing a more flexible wrist movement, so making quadrupedal locomotion more efficient.

On rare occasions juvenile crocodiles move by galloping. Cott (1961) likens this movement to the bounding of a squirrel. In view of the more primitive posture held by the fore-limb of *Orthosuchus* it seems unlikely that the animal could have moved in this way. The lengthening of the coracoid in living crocodiles has presumably increased the length of the adductor muscles of the fore-limb, and also their efficiency.

Similarly, the tail in living crocodiles is probably used more efficiently as a propulsive organ when swimming than it was in *Orthosuchus*. The vertebrae of *Orthosuchus* are amphicoelous, whereas in eusuchians they are procoelous except for the centrum of the first caudal, which is biconvex. Further, the caudifemoral musculature was probably less well developed, as seen by the small size of the fourth trochanter. Presumably therefore the tail was less mobile than it is in living crocodiles, where it can be swung through a full circle of 360 degrees.

RELATIONSHIP OF *ORTHOSUCHUS* TO THECODONTIANS

Orthosuchus demonstrates many characters which are indicative of a thecodontian heritage. The snout is slender, as is typical of thecodontians like *Cerritosaurus* (Price 1946), and the maxilla is excluded from the boundary of paired, laterally orientated external nares. The teeth are thecodont, conical and undifferentiated.

An antorbital fenestra, bounded by the maxilla antero-ventrally and by the lachrymal postero-dorsally, is present in *Orthosuchus* as in thecodontians. Similarly, both temporal openings are well developed. The posterior margin of the inferior temporal fenestra is angular.

There is no tabular or supratemporal in *Orthosuchus*, and a postparietal is also absent. This element is known in a few thecodontians such as *Euparkeria* (Ewer 1965), but is lost in later forms. A parietal foramen is absent, as it is in the majority of thecodontians. A very tiny parietal foramen is present in certain early types such as *Chasmatosaurus* (Brink 1955) and *Erythrosuchus* (Broom 1905).

An otic notch is present in *Orthosuchus*. Although this is not developed in early thecodontians like *Chasmatosaurus* (Broili & Schröder 1934), it is generally present in later forms. In these types, as in *Orthosuchus*, the notch is open posteriorly.

In *Orthosuchus* the head of the quadrate rests in a socket of the squamosal adjacent to the paroccipital process. This is characteristic of thecodontians such as *Stagonolepis*. Similarly, a small basipterygoid process of the basisphenoid is present in *Orthosuchus*. In thecodontians such as *Chasmatosaurus* and *Euparkeria* these joints are highly developed and mobile. Case (1922) describes prominent basipterygoid processes in *Desmatosuchus spurensis* and Walker (1961) notes their presence in *Stagonolepis*, and (1964) in *Ornithosuchus*. Short basipterygoid processes allowing for some possibility of movement are also seen in phytosaurs such as *Machaeroprosopus* (Camp 1930).

In that the pterygoid is firmly applied both to the quadrate and to the basipterygoid process, it seems unlikely that the basal articulation of *Orthosuchus* was movable. Similarly, movement between the squamosal and the superior edge of the quadrate and quadratojugal seems unlikely, and the supraoccipital and parietal are firmly united. The skull of *Orthosuchus* should not therefore be regarded as kinetic, though it cannot be far removed from an ancestor with this type of skull.

In both *Desmatosuchus* and *Stagonolepis* a simple pit lies between prominent basipterygoid processes in exactly the same position as in *Orthosuchus*. It therefore seems probable that the median eustachian system of the Crocodilia does not correspond to the spiracular gill slit, but is a secondary formation developed as an intucking of the basisphenoid.

The lower jaw of *Orthosuchus* is slender with a very large external mandibular fenestra. This is characteristic of thecodontians, with the exception of primitive forms such as *Chasmatosaurus* and *Erythrosuchus*. The internal adductor fossa is also large.

Thecodontians show a range in the count of presacral vertebrae. *Euparkeria* has 22, while both *Vjuskovia* (Von Huene 1960) and *Stagonolepis* have 25. In *Orthosuchus* the number is probably 24. There are seven cervicals in *Euparkeria*, while the probable number in *Orthosuchus* is eight. The centra are amphicoelous in each case.

Behind the axis, the cervical vertebrae of both *Orthosuchus* and thecodontians like *Euparkeria* and *Ornithosuchus* show strong ventral keeling, and hypapophyses are not developed. The dorsal vertebrae, however, are not keeled.

The areas of attachment for the cervical ribs of *Orthosuchus* are distinctive and show the same progressive change in rib articulations that occurs in archosaurs generally. The parapophysis of the anterior cervical vertebra lies antero-ventrally on the centrum. Above this the diapophysis lies anteriorly, low down on the neural arch. Back through the cervicals the parapophysis moves up the centrum, while the diapophysis rises and moves posteriorly so that at the end of the series it is borne on a transverse process.

The migration of the parapophysis continues through to the dorsals, where early on it comes to lie wholly above the neurocentral suture. In *Euparkeria* it reaches this position on vertebra fourteen (i.e. dorsal six), in the phytosaur *Machaeroprosopus* on vertebra twelve (i.e. dorsal five) and in *Stagonolepis* on vertebra ten (i.e. dorsal one). In *Orthosuchus* this occurs on vertebra twelve (i.e. dorsal four). The diapophysis does not change its position further back in the series, though the parapophysis continues to move upwards until the two facets come to lie at the same level on the posterior dorsals. They become confluent on the last presacral. This can be seen in *Chasmatosaurus* and *Ornithosuchus*, and also occurs in *Orthosuchus*. In many thecodontians, such as

Euparkeria and *Chasmatosaurus*, the transverse processes become shorter from the mid-dorsal vertebrae back to the sacrals, as they do in *Orthosuchus*. In others, such as *Stagonolepis* and *Parringtonia* (Von Huene 1939), they remain the same size.

The sacral vertebrae of *Orthosuchus* are very similar to those of many thecodontians. *Orthosuchus* has retained the primitive count of two sacrals, as found in various thecodontians, including *Erythrosuchus*, *Aëtosaurus* (Walker 1961) and *Ticinosuchus* (Krebs 1963*a*). In other thecodontians, however, the number of sacrals has been increased. In *Ornithosuchus* there are three, and in *Schleromochlus* (Woodward 1907) there are four.

Atlantal and axial ribs are poorly known in thecodontians, but in some types at least, as in *Euparkeria* and *Chasmatosaurus*, they are single-headed, as in *Orthosuchus*. Other cervical ribs of *Orthosuchus* have a shape which is typical of both thecodontians and crocodilians. That is, the blade of the rib is directed antero-posteriorly with two heads rising vertically from a point along the length of the shaft. The length of the shaft is variable. It is long and slender relative to the length of the cervical vertebra in *Chasmatosaurus*, but it is short in *Orthosuchus*, as it is in the unrelated phytosaurs.

In both thecodontians and crocodilians the cervical ribs grade into the quite different form of dorsal rib. Coupled with the change which occurs in the position of the rib facets, the capitulum becomes terminal on the rib shaft, and the tubercle gradually approaches this. In *Orthosuchus* the two processes remain distinct throughout the major part of the dorsal series. A similar condition occurs in *Euparkeria*.

The scapula of *Orthosuchus* is similar to that of *Stagonolepis* and *Euparkeria* in that it is a tall, narrow element expanded at both its upper and lower ends. In many of the less specialized lepidosaurs like *Sphenodon* the scapula is relatively short and broad.

The humerus is long and slender in *Orthosuchus* as in thecodontians generally, as shown by *Hesperosuchus* (Colbert 1952) and *Ornithosuchus*. It further resembles that of thecodontians like *Euparkeria* and differs from lepidosaurs in that distally the two condyles are well apart, and the ectepicondylar and entepicondylar expansions are slight.

In *Orthosuchus* as in all archosaurs, the ulna is stouter than the radius. Further, there is no development of an olecranon process, and the head of the ulna is expanded for weight support. In thecodontians generally there is little or no development of an olecranon, though Walker (1961) notes its presence in *Stagonolepis*.

The ilium of *Orthosuchus* is, in general form, persistently primitive. As in *Erythrosuchus* and *Machaeroprosopus* it has a low iliac blade with a well-developed posterior extension. There is also a pronounced supra-acetabular buttress overhanging the acetabulum.

In the presence of a fourth trochanter and absence of a greater trochanter, the femur of *Orthosuchus* closely resembles that of thecodontians. Ewer describes the fourth trochanter of *Euparkeria* as lying well down the shaft, but in both *Orthosuchus* and *Stagonolepis* it arises about one-third of the way down.

The ankle joint of *Orthosuchus* is of crurotarsal type, a feature which has been considered of diagnostic significance for the Crocodilia. Yet, as Krebs (1963*b*) has shown, the crurotarsal ankle joint is common to all but a few pseudosuchians of Lower and Middle Triassic age. *Euparkeria* has the crurotarsal type of ankle joint, though it lacks the elaborate articulation between the astragalus and calcaneum that is found in crocodiles. The ankle joints of *Aëtosaurus* and *Typothorax* are also crurotarsal (Walker 1961). In these forms, as in *Orthosuchus*, two distal tarsals are present. A pronounced tuber is present on the posterior face of the calcaneum of *Orthosuchus*, and this too occurs in some thecodontians, such as *Saltoposuchus* (Von Huene 1921) and *Aëtosaurus*.

Thecodontians in general show some reduction of the fifth digit. In *Euparkeria* the fifth metatarsal is somewhat hooked in shape, and bears three shortened phalanges. In *Aëtosaurus* the fifth digit is more or less similar to this but bears four phalanges. In *Orthosuchus* this metatarsal is further reduced and phalanges are lacking. The pseudosuchian *Schleromochlus* apparently shows a condition identical to that seen in *Orthosuchus*.

Orthosuchus was protected dorsally throughout its length by a paired row of bony plates. Many thecodontians show a similar development of armour. *Ornithosuchus* has, as far as is known, only dorsal armour, the scutes being arranged in a paired, longitudinal series. *Ticinosuchus* and *Euparkeria* have both dorsal and lateral scutes, while *Stagonolepis* was protected at least in part on its ventral surface as well. *Ornithosuchus* and *Stagonolepis* also show the same bending down of the outer portions of the scutes at right angles to the dorsal portions, as seen in *Orthosuchus*. Furthermore, the characteristic peg and socket articulations between adjacent scutes in *Orthosuchus* also occurs in both *Stagonolepis* and *Ornithosuchus*.

Gastralia are present in *Orthosuchus*, as they are in thecodontians such as *Euparkeria*, *Ticinosuchus*, *Stagonolepis*, *Schleromochlus* and *Rutiodon* (McGregor 1906).

RELATIONSHIP OF *ORTHOSUCHUS* TO CROCODILIANS

There are few unquestionable crocodilians of Upper Triassic age. *Protosuchus richardsoni* from Arizona is the best known of these. The type described by Colbert & Mook (1951) is a nearly complete, articulated skeleton. Seven other partial skeletons were also collected from the same locality and stratigraphic level.

Two partial skeletons of *Notochampsa istedana* are known. The type described by Broom (1904) from the Cape Province is an impression of the nasal and temporal regions of the skull, a good pectoral girdle and fore-limb, part of the hind-limb and dorsal armour. The other specimen, British Museum (Natural History) No. R8503, as yet undescribed, is from Lesotho and consists

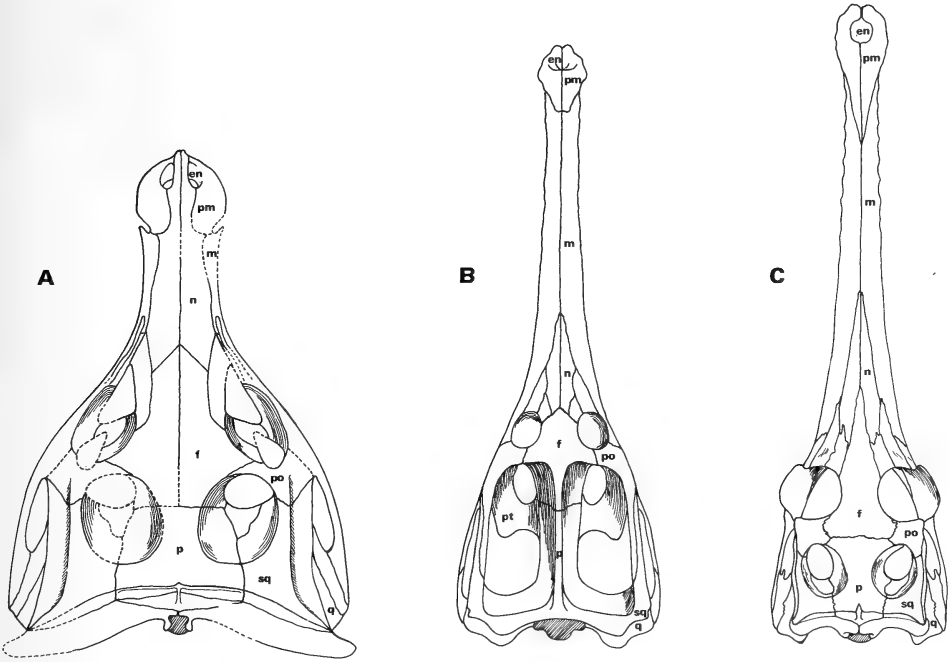

Fig. 31. Dorsal views of the skulls of A. *Orthosuchus stormbergi* ($\frac{2}{3}$ natural size). B. *Steneosaurus durobrivensis,* after Andrews (1913*a*) ($\frac{1}{12}$ natural size). C. *Gavialis gangeticus* (juvenile).

of the left temporal region of the skull and part of a jaw ramus, a few vertebrae, some isolated limb elements and armour.

Erythrochampsa longipes is rather poorly known only from part of the postcranium and armour. The type specimen is from the Cape Province, and was described by Broom (1904). Further material from the Orange Free State was assigned to this genus by Broili & Schröder (1936).

In general form the skull of *Orthosuchus* is very similar to those of *Protosuchus* and *Notochampsa.* In all these forms the cranial table is broad and flat, and is of characteristic crocodilian shape. The snout is slender and clearly marked off from the rest of the skull, a pattern which is seen in many mesosuchians, notably teleosaurs, metriorhynchids and pholidosaurs, and one which is retained in certain eusuchians, principally *Gavialis* (Fig. 31). Further, the bones are sculptured in true crocodilian fashion in all these forms.

It seems likely that the external nares of *Orthosuchus* are similar to those of *Notochampsa.* Haughton (1924) felt that there was sufficient evidence in the nasal region to prove that they were paired and somewhat lateral. The tip of the snout of *Protosuchus* is not known, but in *Steneosaurus* (Andrews 1913*a*) the external nares are confluent. Ventrally the premaxilla of *Steneosaurus* is not extensive and differs little from that of *Orthosuchus.*

In both *Orthosuchus* and *Protosuchus* there is a short region of the snout which does not bear teeth. In *Protosuchus* this is described as being comparable to the notch region in later crocodiles, though in *Orthosuchus* a prominent notch also occurs. Behind this there are in *Orthosuchus* three or four maxillary teeth, in *Notochampsa* between six and nine, and in *Protosuchus* about eleven. Von Huene (1925) described the teeth of *Notochampsa* as not compressed and without edges, and this description is equally applicable to *Orthosuchus* and *Protosuchus*.

The orbits of *Orthosuchus* and *Protosuchus* are directed outward and forward rather than predominantly upward as in more advanced forms. There is now no doubt that Colbert & Mook (1951) interpreted the orbital region of *Protosuchus* incorrectly. They considered the orbital region to be wide, but clearly in both *Orthosuchus* and *Protosuchus* this region is relatively narrow and is bordered on either side by two supraorbital elements. Unfortunately, the orbital region of *Notochampsa* is not preserved, though in the more recent material, British Museum (Natural History) No. R8503, the anterior margin of the left postorbital bears a facet for a supraorbital element. This surely indicates that the orbit was outwardly directed as in *Orthosuchus*.

The postorbital-jugal bar in *Orthosuchus* and *Protosuchus* is superficial in position, as it is in teleosaurs. The superior part becomes sunken in metriorhynchids, pholidosaurs and notosuchids, and it is wholly displaced internally in goniopholids and atoposaurs, and in all eusuchians.

Much has been written regarding the position of the orbits of crocodiles in relation to an aquatic mode of life. It seems that the change in orientation from the more lateral position found in early crocodiles to the dorsal inclination of living forms should be attributed to the movement of the jugal upwards from an essentially horizontal position in *Orthosuchus* into a nearly vertical one. This is coupled with the inward movement of the postorbital bar. Supraorbital elements lie over the roof of the orbit in the eyelid in both modern crocodiles and *Orthosuchus*.

Despite the position of the orbits in *Orthosuchus*, there are clear indications in the form of the palate and overall shape of the skull, that the trend towards a semi-aquatic mode of life was already well established. In view of the remarkable similarity in form between the North American and southern African protosuchians, it seems that *Protosuchus* too was rather more aquatic in habit than has previously been supposed.

Differences between the protosuchians lie in the shape of the superior temporal fenestrae. *Notochampsa* is characterized by the moderately sized, almost pear-shaped superior temporal fenestra, which lies with its broadest end anteriorly. In *Protosuchus* this fenestra is circular in shape, and is smaller than the orbit, and in this respect shows an inherent thecodontian condition. In *Orthosuchus* the superior temporal fenestra is also circular, but equals the size of the orbit. This indicates a progression toward the condition shown by early mesosuchians such as *Teleosaurus* (Andrews 1913*a*) where the fenestra is greatly enlarged at the expense of the parietal and squamosal.

Kalin (1955) suggests that the enlargement of the superior temporal fenestra seen especially in long snouted groups, such as the gharial, is correlated with the form of the musculature. In those longirostrate forms adapted for fish eating there is a need for a well-developed m. adductor mandibulae externus, which arises within the superior temporal fossa. On the other hand, in brevirostrate crocodiles, where prey is held in the water to drown it, or where large animals are torn apart, it is the m. pterygoideus which is strongly developed.

Since *Orthosuchus* would appear to be more progressive than *Protosuchus* with regard to the size of the superior temporal fenestra, it is surprising that an antorbital fenestra is present in *Orthosuchus* and lacking in *Protosuchus.* Unfortunately this question remains unresolved for *Notochampsa*. Haughton (1924) omits to mention this point at all. According to Von Huene (1925) an antorbital fenestra is present in *Notochampsa*, though Broom (1927) considered it absent. In fact, the material is too incomplete for a proper determination to be made.

Among mesosuchians an antorbital fenestra is seen in teleosaurs like *Steneosaurus* and *Pelagosaurus* (Eudes-Deslongchamps 1864) and also occurs in notosuchids such as *Notosuchus* and *Araripesuchus* (De Gasparini 1971). It has previously been supposed that this represents a secondary formation, but the presence of an antorbital fenestra in *Orthosuchus* demonstrates that this is not the case. In all types the opening lies between the maxilla and lachrymal.

In *Orthosuchus* the frontal contributes to the anterior border of the superior temporal fenestra, as it does in all mesosuchians with the exception of a few notosuchids like *Notosuchus.* In view of this it seems most unlikely that the frontal is excluded from the fenestra in *Protosuchus*, as Colbert & Mook (1951) suggest. They indicate a short suture running from the medial border of the superior temporal fenestra on each side, and it seems likely that this represents the fronto-parietal suture. In eusuchians this suture is located further forward, so that the parietal articulates with the postorbital.

In both *Orthosuchus* and *Notochampsa* British Museum (Natural History) No. R8503 a deep otic recess is made between the overhanging squamosal and sloping quadrate. In each case the squamosal bears a longitudinal groove, indicating that in life the recess was concealed by ear-flaps.

As is also characteristic for the Crocodilia, in both these forms the quadrate contributes to the floored-in area of the superior temporal fossa. The relationships of the quadrates of *Notochampsa* and *Orthosuchus* are, in fact identical. In both the otic notch is shallow and the quadrate has a posterior articulation with the squamosal. Mesosuchians differ in that the notch is deepened by the loss of the posterior articulation, as seen in *Pelagosaurus*. In eusuchians the squamosal extends down to close the notch posteriorly (Fig. 32).

Notochampsa also has a highly fenestrated quadrate, though it differs from that of *Orthosuchus* in its overall pattern. A well-developed rhomboidal sinus lying behind the prootic-opisthotic suture, between the braincase and

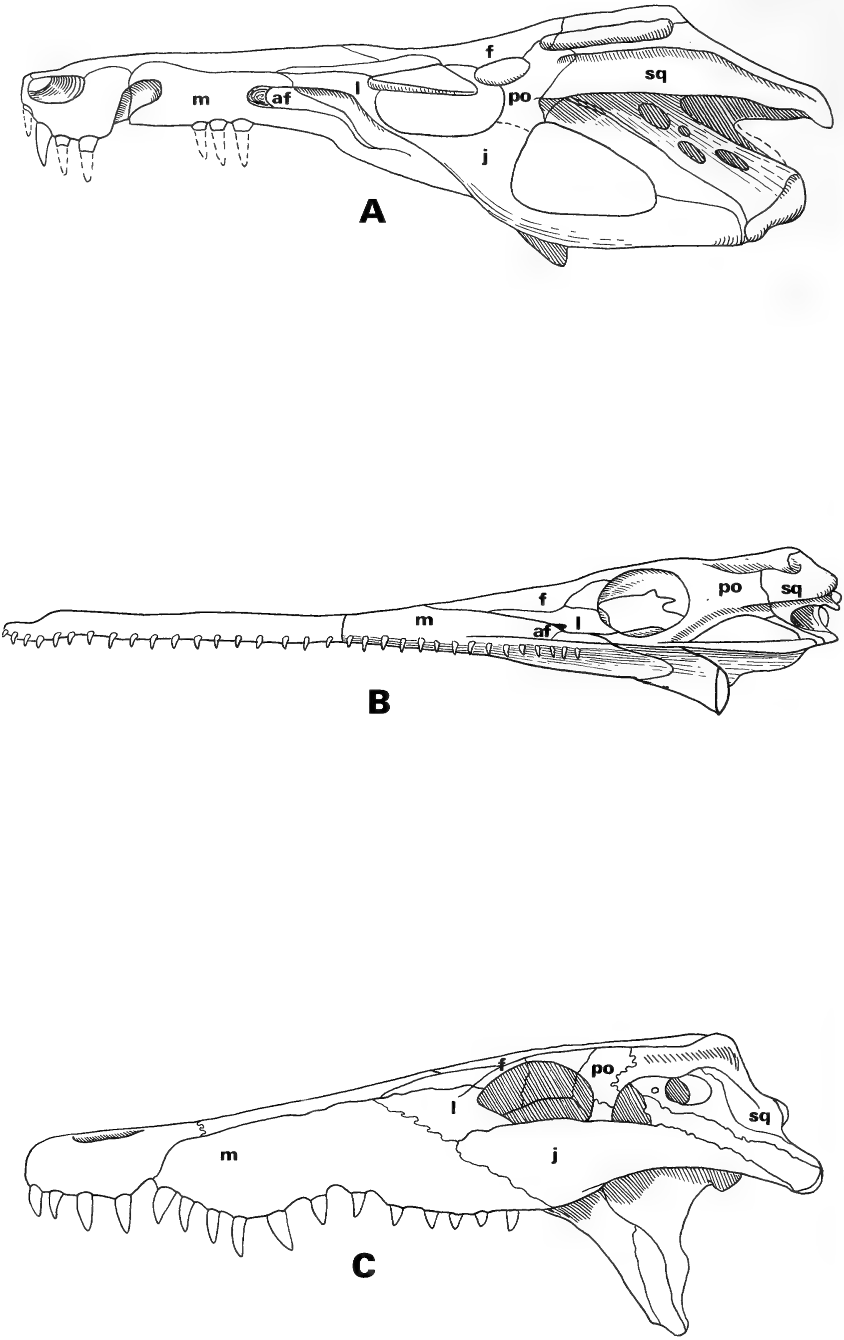

Fig. 32. Lateral views of the skulls of A. *Orthosuchus stormbergi* (natural size). B. *Pelagosaurus typus*, after Eudes-Deslongchamps (1864) (⅓ natural size). C. *Crocodylus*, after Romer (1956).

exoccipital, is present in *Notochampsa.* This clearly indicates an early stage in the enlargement of the tympanic cavity in crocodiles. The rhomboidal sinus probably opened into the throat through lateral eustachian foramina. These can be seen in *Orthosuchus.*

In living crocodiles the tympanic cavities are further enlarged and linked together by large air spaces within the supraoccipital. Each cavity is also connected to air passages within the quadrate and articular as well as to a rhomboidal sinus. This is linked to the throat by a lateral eustachian tube which passes up between the basisphenoid-basioccipital suture. In addition, a third eustachian tube passes up in the midline and divides above into an anterior and a posterior canal. Each of these forks into horizontally running canals which also terminate in the rhomboidal sinus.

This complex system of eustachian tubes is partially developed in *Pelagosaurus* and *Steneosaurus*, where the anterior branch of the median eustachian tube, with its horizontal branches, is found. Unfortunately, in *Orthosuchus* it is impossible to determine whether the comparable anterior canal also leads to a rhomboidal sinus on either side.

A very large horizontal canal connects the median and lateral eustachian foramina on each side in *Pelagosaurus* and *Steneosaurus.* These surely represent the canals of the posterior branch of the median eustachian system. These canals are not developed in *Orthosuchus.* On the other hand, in both *Orthosuchus* and *Steneosaurus* an additional canal leads backwards from the median opening and, in *Steneosaurus*, runs into the body of the basioccipital and Andrews (1913*a*) was of the opinion that this canal was vascular in function.

In mesosuchians the lateral eustachian tubes are membranous, as is the median tube, and each lateral foramen opens above directly to a rhomboidal sinus. Presumably the enclosure of these tubes by bone occurred as a result of growth of the basioccipital and basisphenoid. This, coupled with the more limited extension of the pterygoid posteriorly, must account for the apparent change in position of the eustachian foramina from the pterygoid-basisphenoid suture, as in *Orthosuchus*, to that between the basisphenoid and basioccipital, as in later crocodiles.

This complex eustachian system in crocodiles probably functions as a series of resonance chambers to improve auditory capacity. Wever & Vernon (1957) have demonstrated that because the two middle ear cavities are interconnected, the application of sounds to one ear stimulates the other ear almost equally well.

The pterygoid of *Steneosaurus* is essentially similar in form to that of *Orthosuchus* (Fig. 33). In both types it has a posterior process which extends back along the side of the basis cranii as far as the basisphenoid-basioccipital suture and makes contact with the exoccipital so that the quadrate does not meet the basisphenoid as it does in modern forms. In *Pelagosaurus* this process of the pterygoid does not extend as far back, and in modern forms only a vestige remains.

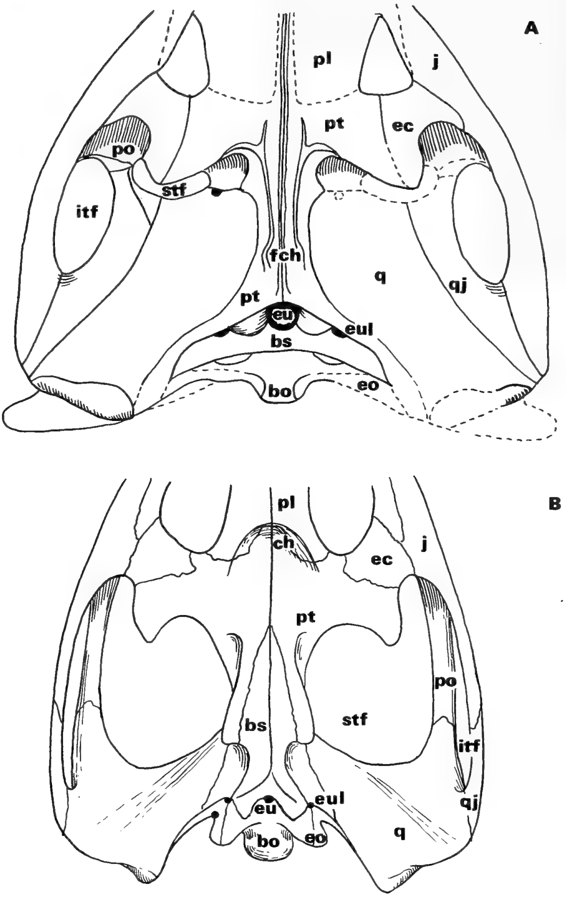

Fig. 33. Basicranial region of the skulls of A. *Orthosuchus stormbergi* (natural size). B. *Steneosaurus durobrivensis*, after Andrews (1913*a*) ($\frac{1}{6}$ natural size).

In *Orthosuchus*, as in *Steneosaurus* and *Pelagosaurus*, the flange of the pterygoid does not project below the level of the alveolar border to the same extent as seen in recent crocodiles. This downward movement of the flange in living crocodiles has involved a change in orientation of the ectopterygoid, so that it lies essentially in a vertical position. In *Orthosuchus* and *Steneosaurus* it is more or less horizontal.

Mesosuchians, again, differ from *Orthosuchus* in that the palatine forms part of the wall and floor of the secondary palate. This is brought about by fusion of the palatines ventrally in the midline, and has also resulted in the enlargement of the postpalatine fenestra on each side. In forms like *Pelagosaurus* and *Pholidosaurus* (Andrews 1913*b*) the choanae are large and confluent, and the anterior border is formed by the palatine and the pterygoid forms the roof.

In recent crocodiles the pterygoids also contribute to the secondary palate and are hollowed out behind the palatines and between the pterygoid flanges so that the narial tubes are continued posteriorly. The ridges on the body of the pterygoids of *Orthosuchus* mark the position of the choanae in eusuchians (Fig. 34). A transitional stage between these is seen in the mesosuchian *Theriosuchus* (Joffe 1967) where the internal nares lie in a depression which is walled laterally by the pterygoids and roofed by the palatines.

The prefrontal of *Orthosuchus* forms an internal process which extends down towards the palate. In living crocodiles this process unites with that from the other side in the midline, and also with the palatine and pterygoid. A similar process occurs in *Pelagosaurus* British Museum (Natural History) No. 32599 and also in *Steneosaurus* and *Metriorhynchus*, though it is incomplete in each case. Andrews (1913*a*) was of the opinion that in the latter types these processes did meet in the midline and also met the palatine ventrally.

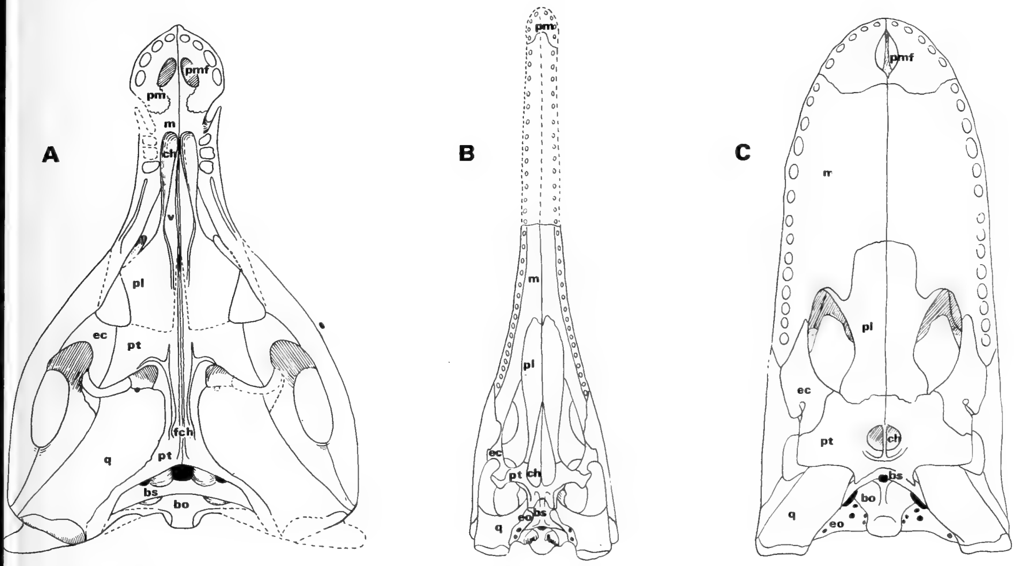

Fig. 34. The palate of the skulls of A. *Orthosuchus stormbergi* ($\frac{2}{3}$ natural size). B. *Pelagosaurus typus*, after Eudes-Deslongchamps (1864) ($\frac{2}{9}$ natural size). C. *Alligator mississippiensis*, after Kalin (1955) ($\frac{2}{5}$ natural size).

The symphysial region of the lower jaw of *Protosuchus* is unknown, but in *Notochampsa* (Haughton 1924) and *Orthosuchus* it is short. In *Protosuchus* and many thecodontians the rear end of the lower jaw lacks the marked prolongation of the angular and articular bones that characterizes mesosuchians and eusuchians, and this is probably also the case in *Orthosuchus*.

Orthosuchus is the first Triassic crocodile known to possess a prearticular (the internal surface of the lower jaw is unknown in *Protosuchus*) and, indeed, this element is known in only two other crocodilians. It is well developed in *Pelagosaurus*, of Lower Jurassic age, but in the Upper Jurassic form *Metriorhynchus* it is quite short. It is absent as a separate element in Crocodilia from more recent strata. In contemporary crocodilians, where the prearticular fuses with the articular during development (De Beer 1937) the region normally occupied by the prearticular is filled by a medial process of the angular. The gradual elimination of the prearticular through the Crocodilia is shown in Figure 35.

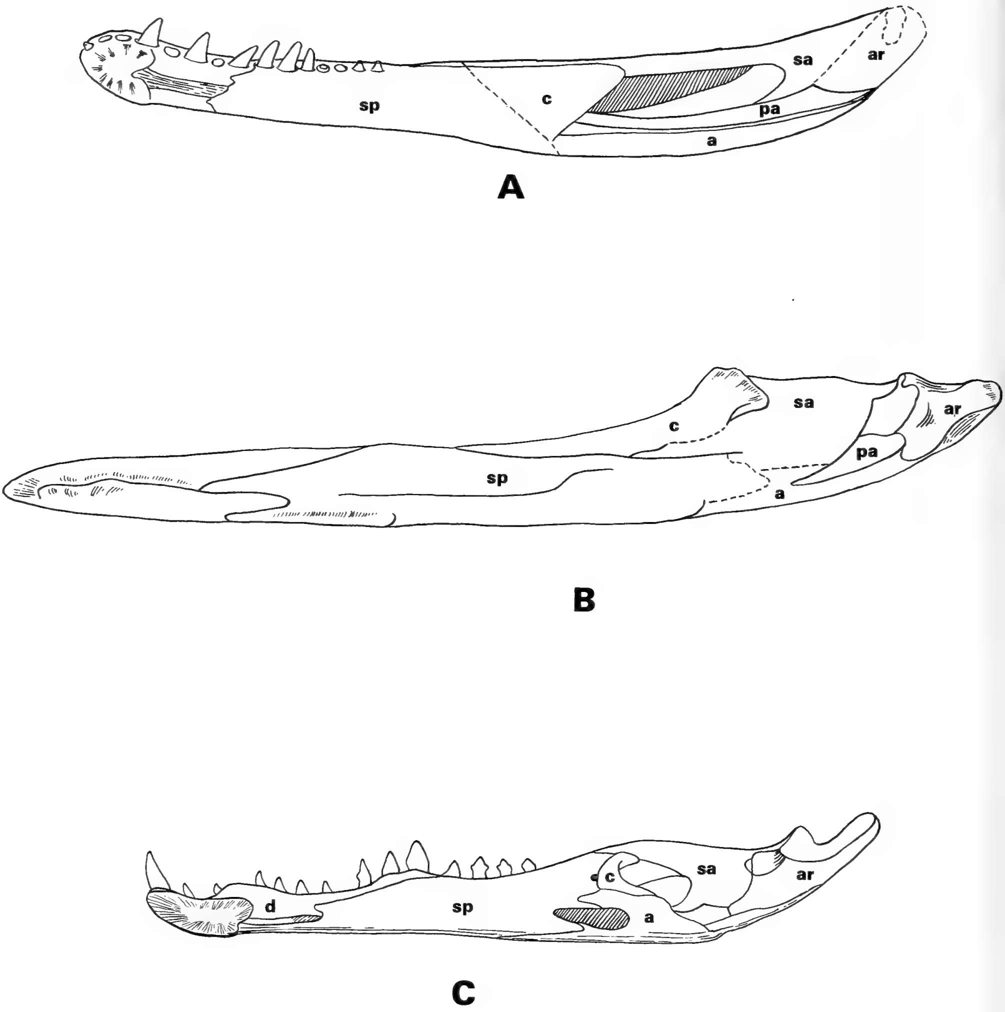

Fig. 35. Medial view of the lower jaws of A. *Orthosuchus stormbergi* (natural size). B. *Metriorhynchus cultridens*, after Andrews (1913*a*) ($\frac{1}{6}$ natural size). C. *Crocodylus vulgaris*, after Kalin (1955) ($\frac{1}{5}$ natural size).

Although the entire vertebral column of *Protosuchus* is known, it is obscured dorsally, and to a lesser extent ventrally, by scutes. Colbert & Mook (1951) estimated a presacral count of 24 vertebrae, as is suggested for *Orthosuchus*. All early crocodilians possess thecodontian spool-shaped, amphicoelous vertebrae, and this condition was retained generally among mesosuchians. The anterior vertebrae are keeled in *Orthosuchus*, but in the marine Jurassic crocodiles this keeling is lost. In living crocodiles keeling has been extended to include the anterior dorsals.

A similar change in position of the rib facets through the cervical series back down the column occurs in both *Protosuchus* and *Orthosuchus*. In *Protosuchus* the parapophysis lies at the base of the transverse process above the neurocentral suture on vertebra twelve, and in this respect shows an identical condition to that seen in *Orthosuchus*. Further, in both types the two rib facets remain distinct up to the last presacral vertebra, a condition retained in forms like *Steneosaurus*.

Protosuchus and *Orthosuchus* also share the primitive count of two sacral vertebrae. In both forms, and in later crocodiles, the extremities of the sacrum are large because each sacral rib articulates both with the centrum and with the transverse process.

The cervical ribs of *Protosuchus* and *Erythrochampsa* (Broili & Schröder 1936) closely resemble those of *Orthosuchus*, but are also indistinguishable from those of many thecodontians as seen in *Ticinosuchus*.

The dorsal ribs of *Protosuchus* are of particular interest, and are identical to those of *Orthosuchus*. In both types the shaft is flanked by an antero-ventral and a postero-dorsal flange. In the thecodontians *Euparkeria* and *Ticinosuchus*, they are not flanged in this way, while in teleosaurs only anterior flanges are developed in the first two or three dorsal ribs.

The scapulae of *Orthosuchus*, *Protosuchus* and *Notochampsa* are strikingly similar in shape. They are crocodilian in form in that the upper end is expanded, particularly posteriorly, and is very much larger in size than the lower end. This expansion is not found in teleosaurs (Fig. 36), but this no doubt is an aquatic adaptation. However, the coracoids of these forms are closely similar in shape, and are elongate elements expanded both proximally and distally. This represents an advanced stage over that seen in typical thecodontians where the coracoid is rather an insignificant element, subcircular in shape.

In addition, these early crocodilians differ from, and are more specialized than, thecodontians in that they lack a clavicle. Von Huene (1925) did suggest that a clavicle is present in *Notochampsa*, though Broom (1927) expressed the opposite view and believed the element in question to be a scute. Broom appears to have been correct in this.

In 1924 Haughton expressed doubts concerning the crocodilian form of the humerus of *Notochampsa*. He was of the opinion that it is more thecodontian in form, much like that of *Stagonolepis*. However, the description does not support this view, and the recent find of *Notochampsa* includes two humeri which are

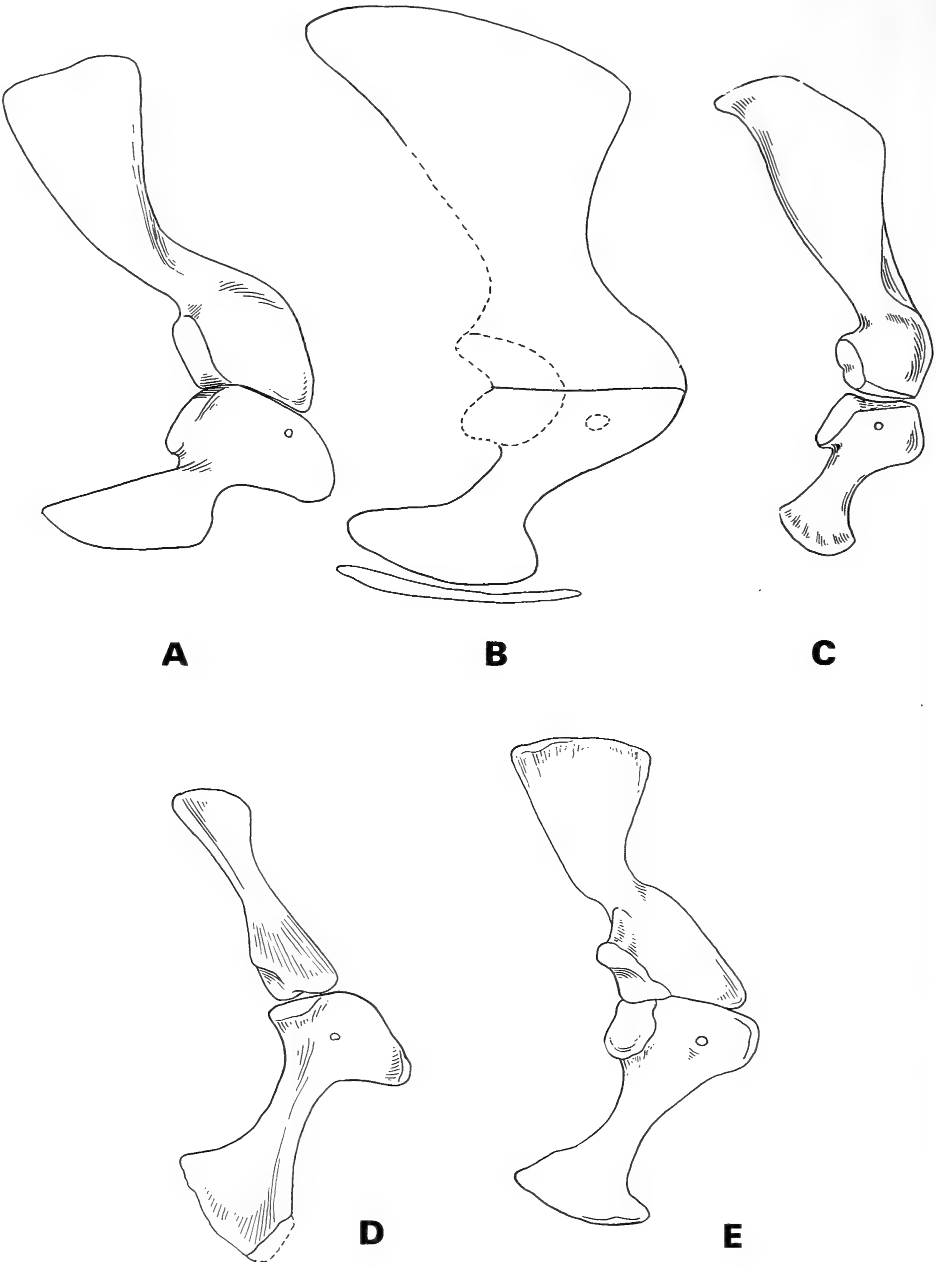

Fig. 36. Lateral views of the pectoral girdles of A. *Prctosuchus richardsoni*, after Colbert & Mook (1951) (natural size). B. *Notochampsa istedana*, after Broom (1927) (natural size). C. *Orthosuchus stormbergi* (natural size). D. *Steneosaurus durobrivensis*, after Andrews (1913*a*) ($\frac{1}{3}$ natural size). E. *Crocodylus acutus* (= *C. americanus*) (reversed), after Mook (1921*b*) ($\frac{1}{5}$ natural size).

very similar to those of *Orthosuchus* and *Protosuchus*. In these forms, as in living crocodiles, the humerus bears a deltopectoral crest which rises to an apex about one-third of the way down a long slender shaft.

A very striking crocodilian character can be seen in the form of the carpus. Broom (1927) commented on the metacarpal-like nature of the radiale and ulnare in *Notochampsa*, and an identical condition is present in both *Protosuchus* and *Orthosuchus*. In the latter form the ulnare is only just shorter than the longest metacarpal (the third), and the radiale is more than one and a half times its length. Hence, as in modern crocodiles, the carpus is elongated to add an extra segment to the fore-limb.

Protosuchus further resembles *Orthosuchus* in that a large pisiform element is preserved in the carpus. However, in *Orthosuchus* two distal carpals are present, whereas in *Protosuchus* and *Notochampsa* there is only one (Fig. 37). In these forms the distal carpal lies in articulation with the ulnare.

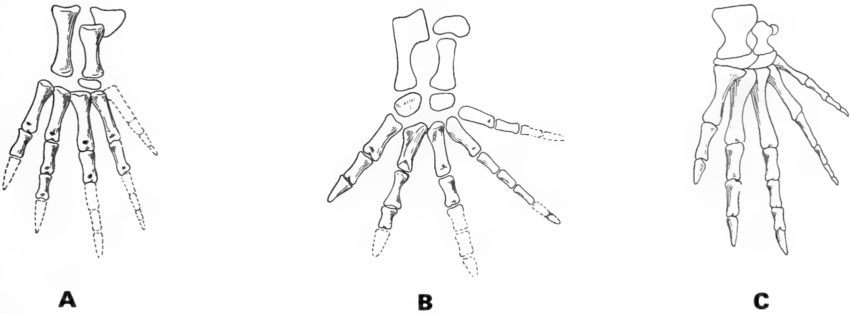

Fig. 37. Carpus and manus of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (⅔ natural size). B. *Orthosuchus stormbergi* (⅔ natural size). C. *Crocodylus*, after Romer (1956).

The pelvis in *Orthosuchus* is closely similar to that of *Protosuchus*. In both the acetabulum is perforated ventrally, a feature separating these forms quite clearly from all thecodontians where the acetabulum is imperforate. The ischia are also very alike and resemble that of *Erythrochampsa*. The most significant feature here is the development of the anterior process to exclude the pubis from the acetabulum. Unfortunately, on neither side of the body is the pubis of *Erythrochampsa* complete, although Broom was of the opinion that the pubis does not enter the acetabulum.

In all three forms the iliac blade is produced anteriorly to form a bluntly-pointed process. This was reduced in teleosaurs, and only a vestige remains in eusuchians (Fig. 38). In *Orthosuchus*, anterior to the acetabulum, the ilium is notched. The inner of the two processes meets the ischium, and the outer, together with the ischium, articulates with the pubis. A similar condition probably exists in *Protosuchus*. In *Steneosaurus* the head of the pubis occupies a more ventral position, and in living crocodiles the pubis articulates only with the ischium.

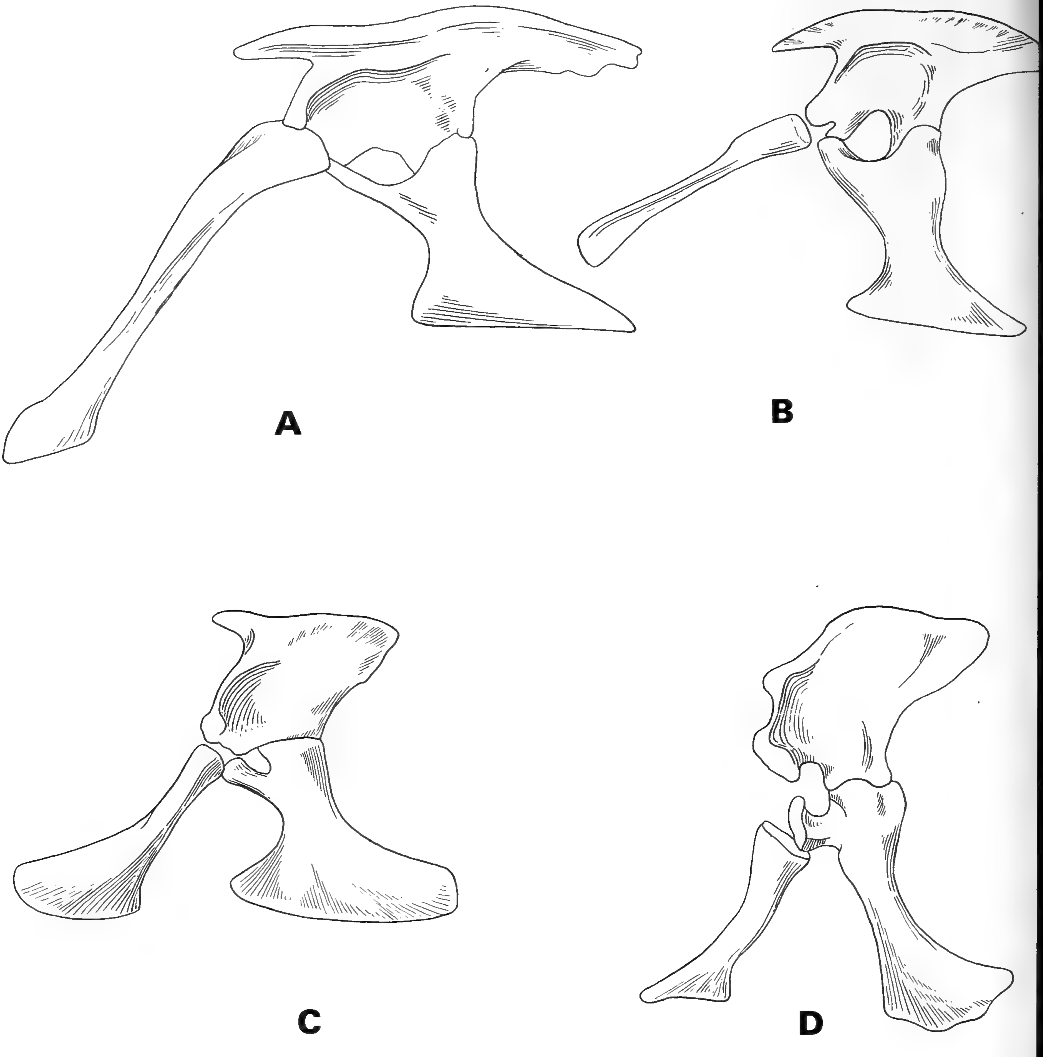

Fig. 38. Lateral views of the pelvic girdles of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (natural size). B. *Orthosuchus stormbergi* (natural size). C. *Steneosaurus leedsi*, after Andrews (1913*a*) ($\frac{1}{4}$ natural size). D. *Alligator*, after Romer (1956).

The femur of *Orthosuchus* is remarkably similar to that of *Protosuchus*, and in fact differs little from that of living crocodiles. The tibia lacks a distinct cnemial crest in each case. Similarly, there is little difference between the tarsus of *Orthosuchus* and that of *Protosuchus*. In both types the calcaneum bears a tuber which is more prominently developed than it is in living crocodiles and which is grooved on its posterior surface. However, whereas in *Orthosuchus* there are two distal tarsals, in *Protosuchus* only one is known.

The structure of the tarsus of *Erythrochampsa* is difficult to determine. According to Haughton (1924) it consists of two proximal and two distal elements. The calcaneum bears a small posterior tuber. Broom (1927) described the same tarsus as similar to that of the Upper Jurassic mesosuchian *Alligatorellus*. Lortet (1892) had incorrectly described three distal tarsals in this type, but Broom figured the tarsus of *Erythrochampsa* as consisting of astragalus and calcaneum only. At most, only two elements can be identified in the type, as shown by Broom, though it is questionable as to what these are.

The metatarsus of *Orthosuchus* is composed of four elongated metatarsals with the fifth reduced to a hook and held behind the other four. *Protosuchus* shows a similar condition. Broom (1904) described four digits in *Erythrochampsa*, but in 1927 figured four elongated elements and a short, hook-shaped fifth. Von Huene (1925) figured the same specimen showing four elongated and a slightly shortened fifth metatarsal in articulation with two phalanges.

At my request, Dr M. A. Cluver (South African Museum) examined the type specimen and came to the conclusion that both Broom and Von Huene had misinterpreted the specimen. Broom gave the correct number of unreduced metatarsals (four), but did not indicate that the fourth is incomplete. Von Huene miscounted and regarded the broken fourth metatarsal as a fifth member and figured it in articulation with phalanges. Although the material is difficult to interpret, there is a piece of bone underlying the proximal end of the fourth metatarsal which does not seem to be part of the distal end of the tibia or fibula. This could well be a reduced fifth metatarsal. On balance it seems likely that the metatarsus of *Erythrochampsa* is identical to that of both *Orthosuchus* and *Protosuchus* (Fig. 39). In view of this, it is unfortunate that Kalin (1955) chose to reproduce Von Huene's incorrect figure.

Protosuchian armour may be distinguished from thecodontian armour by a combination of characters. The dorsal scutes are arranged in two rows, with the anterior margin of each overlapped by the preceding scute. The articular surface of each dorsal scute is smooth, and behind this the exposed surface is strongly pitted. Further, the lateral portion of each scute is strongly bent downward and the bend is strengthened by a dorsal ridge.

Many mesosuchians such as *Alligatorellus* show an identical development of dorsal armour. In others like *Crocodileimus* (Lortet 1892), although the scutes covering the neck and lumbar region are paired, the mid-dorsals are arranged in four rows. In living genera as many as ten scutes may be present in a row.

The most anterior scutes of the dorsal armour of *Orthosuchus* and *Notochampsa* carry a peg-like process which extends forward from the anterior margin of the dorsal ridge, and fits into a groove on the ventral surface of the preceding scute. This feature is inherited from thecodontians, and is one which was passed on to at least some of the mesosuchians, like *Steneosaurus*, *Pholidosaurus* and *Goniopholis*.

Although ventral armour of the type specimen of *Notochampsa* is not known, five ventral scutes form part of the material of specimen British Museum

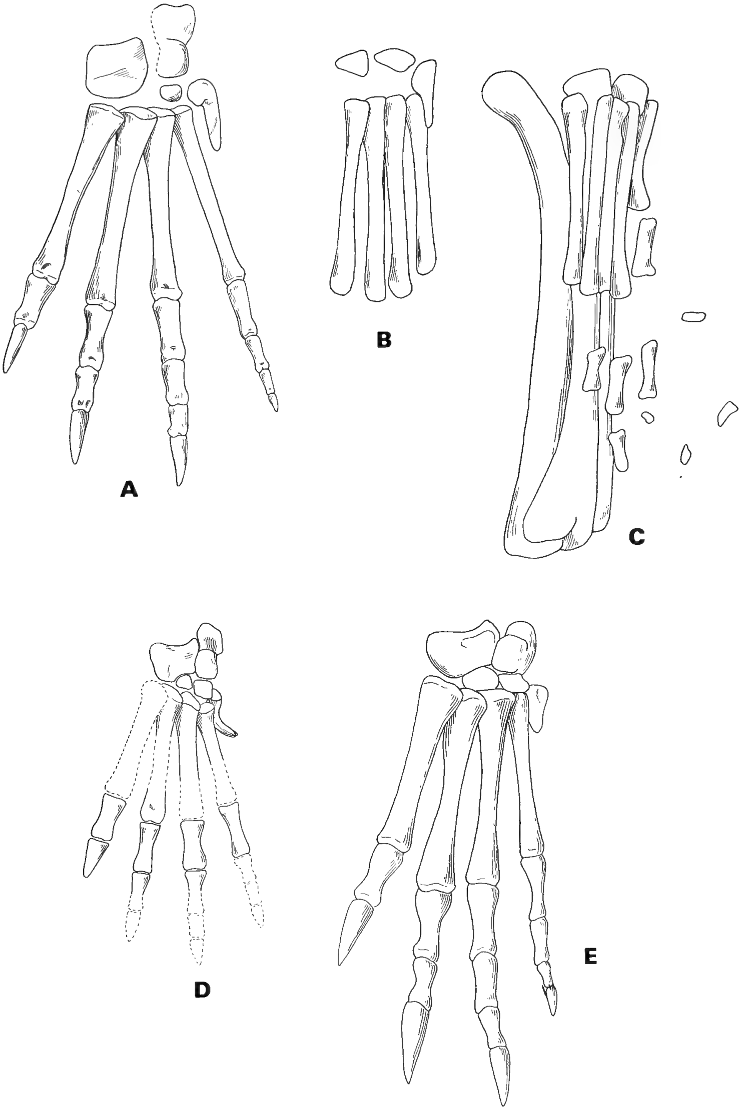

Fig. 39. Tarsus and pes of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (⅔ natural size). B. *Erythrochampsa longipes*, after Broom (1927). C. *Erythrochampsa longipes* (reversed), after Von Huene (1925). D. *Orthosuchus stormbergi* (⅔ natural size). E. *Crocodylus*, after Romer (1956).

(Natural History) No. R8503. *Protosuchus* and *Erythrochampsa* were also protected by dorsal and ventral, but not lateral scutes, except over the tail. Probably *Orthosuchus*, too, was covered in this way, though its ventral armour is as yet unknown. The teleosaur *Mystriosaurus* has a similar covering of ventral armour, and it is also found in *Crocodileimus* and *Pholidosaurus*, although here the scutes are polygonal in shape. Ventral armour is not known in atoposaurs, and is generally absent in living crocodiles.

Ventrally and at the level of the distal portion of the pubis, both *Orthosuchus* and *Protosuchus* show an accumulation of gastralia. In life these were probably more numerous and extended farther forwards. Gastralia are known in some mesosuchians, like *Atoposaurus* and *Alligatorellus*, and are present in eusuchians.

LIMB AND LIMB GIRDLE PROPORTIONS IN CROCODILIA AND THECODONTIA

Relationship between lengths of scapula and humerus (Fig. 40)

The relationship between length of scapula and length of humerus for the seven available pairs of measurements on contemporary animals may conveniently be shown by plotting $\log_{10}$ humerus length (x axis) against $\log_{10}$ of scapula (y axis). They may be represented by the regression line $y = 1{,}167x - 0{,}522$. If Y and X are the actual lengths of scapula and humerus respectively, the equation becomes $Y = 0{,}301X^{1{,}17}$.

The regression coefficient 1,167 is significantly different from 1,0 ($t = 4{,}674$ with 5 d.f.). This shows that the scapulae of these contemporary crocodilians increases in length at a proportionally greater rate than the humerus, i.e. the ratio between the two is greater in the larger animals.

In Figure 40 are included points for selected fossil crocodilians and thecodontians, though of these the thecodontians *Vjushkovia* and *Euparkeria*, and the protosuchians *Orthosuchus* and *Protosuchus*, form a group of very ancient animals which may reasonably be separated from the mesosuchians, whether land or marine forms.

The regression coefficient for the above four is given by $b = 1{,}170$. This is patently not significantly different from the above value 1,167. The separation of these two regression lines is however significant at the 1% level ($t = 3{,}780$ with 7 d.f.). That is, these four animals form a group separate from the contemporary crocodilians. The equation for the above four is: $y_1 = 1{,}170x_1 - 0{,}3107$ so that the initial dimensions are related by: $Y_1 = 0{,}489X_1^{1{,}17}$.

Comparing this with the previous equation it is seen that in these forms the ratio of scapula length to humerus length is about 1,6 times as great, for any particular value of scapula length. These higher ratios are in fact very apparent in Table 4, and clearly apply to *Orthosuchus*. The very high value of the ratio for *Vjushkovia* is not out of place, and can be attributed to the fact that it is a member of this ancient group, and is a very large animal.

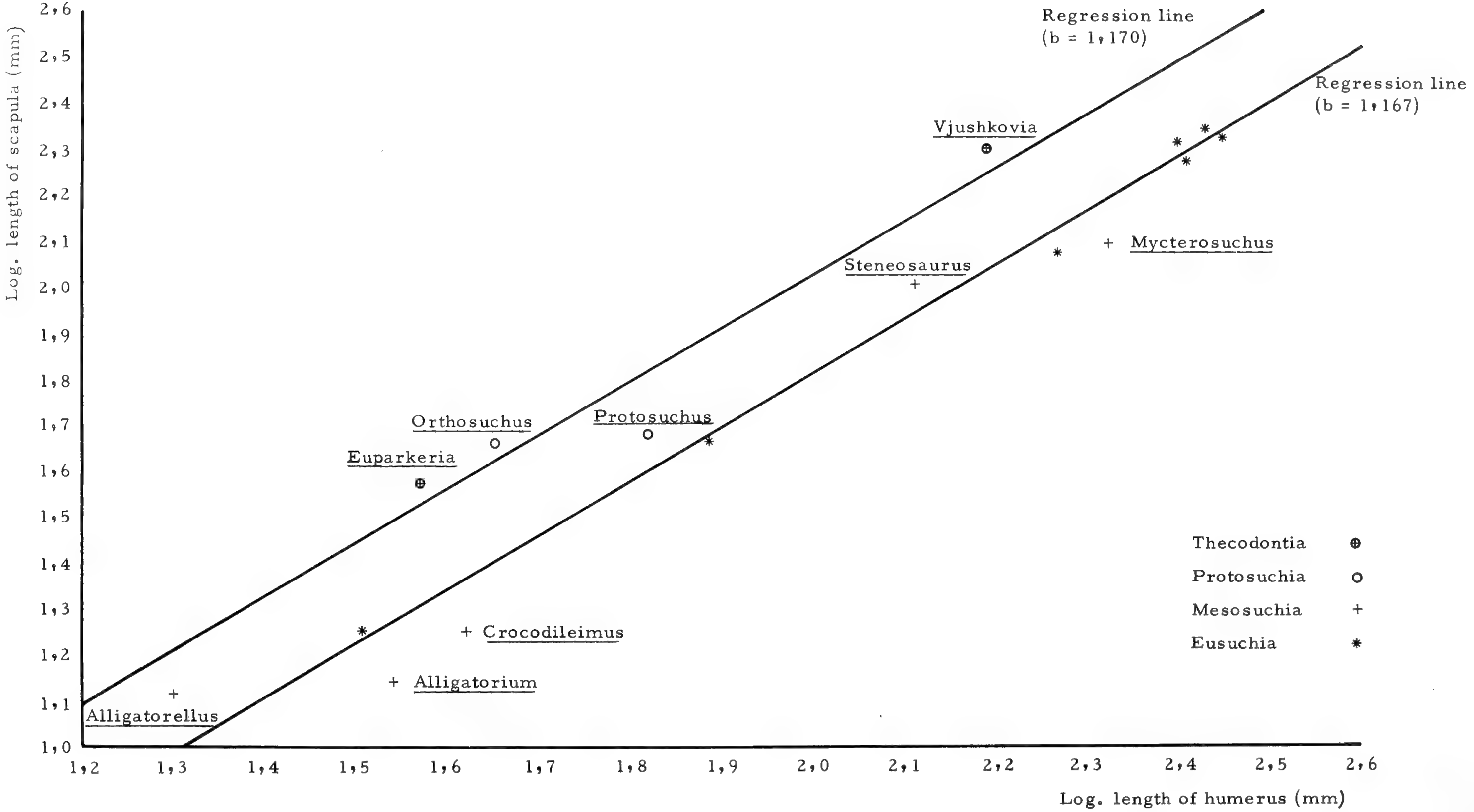

Fig. 40. Graph showing the relationship between lengths of scapula and humerus (shown in log. form) for selected living and fossil crocodilians and thecodontians.

Table 4
Comparison of proportions in selected thecodontians and crocodilians

	Thecodontia			Protosuchia		Mesosuchia						Eusuchia							
	Chasmatosaurus yuani Data from Young (1936)	*Vjushkovia triplicostata* Von Huene (1960)	*Euparkeria capensis* SAM–5867 Ewer (1965)	*Orthosuchus stormbergi* SAM–K409	*Protosuchus richardsoni* A.M.N.H. No. 3024 Colbert & Mook (1951)	*Steneosaurus leedsi* B.M.N.H. No. R3806 Andrews (1913*a*)	*Mycterosuchus nasutus* B.M.N.H. No. R2617 Andrews (1913*a*)	*Alligatorellus beaumonti* Lortet (1892)	*Alligatorium meyeri* Lortet (1892)	*Crocodileimus robustus* Lortet (1892)	*Theriosuchus pusillus* B.M.N.H. No. 48216	*Alligator mississippiensis* (juvenile)	*Alligator mississippiensis* Zool. Mus. ZH. Ex. 13180 Krebs (1963*a*)	*Crocodylus porosus* (juv.) A.M.N.H. No. 69125 Colbert & Mook (1951)	*Crocodylus porosus* B.M.N.H. No. 1902. 12.19.1	*Crocodylus niloticus* B.M.N.H. No. 1969. 1565	*Crocodylus niloticus* B.M.N.H. No. 111.11.1.89a	*Crocodylus acutus* B.M.N.H. gallery specimen	*Crocodylus acutus* A.M.N.H. No. 7139 Mook (1921*b*)
Scapula/humerus (%) . . .	—	121,2	98,9	102,2	72,7	78,5	63,9	65,0	40,0	42,9	—	55,9	—	59,7	75,0	74,5	82,0	64,9	82,1
Coracoid/scapula	—	59,0	—	50,0	52,1	98,0	111,1	46,2	100,0	88,9	—	100,0	—	91,3	90,5	100,0	92,7	100,0	90,5
Radius/humerus	—	81,8	84,1	87,8	78,8	51,5	54,5	82,5	80,0	66,7	78,9	69,9	65,0	59,7	57,1	52,9	57,2	59,5	55,6
Radiale/radius	23,7	—	—	41,3	26,9	—	—	30,3	33,9	37,5	—	24,4	—	21,7	—	27,4	28,0	29,1	—
Tibia/femur	—	88,0	85,7	93,9	83,0	50,7	50,0	95,8	85,1	70,9	88,9	82,2	77,3	74,4	68,1	60,9	65,7	71,8	69,8
Humerus/femur	—	66,0	67,7	78,9	66,0	43,0	52,8	83,3	73,7	76,4	70,4	88,2	89,6	89,5	87,5	79,7	84,2	94,9	82,5
Humerus + radius + radiale/ femur + tibia . . .	—	—	—	91,2	72,1	—	—	88,3	82,9	85,6	—	90,5	—	86,7	—	82,9	88,0	97,6	—
Femur + tibia/length of trunk	—	—	—	65,0	—	—	—	—	—	—	—	61,0	—	—	50,0	52,0	44,0	49,0	—

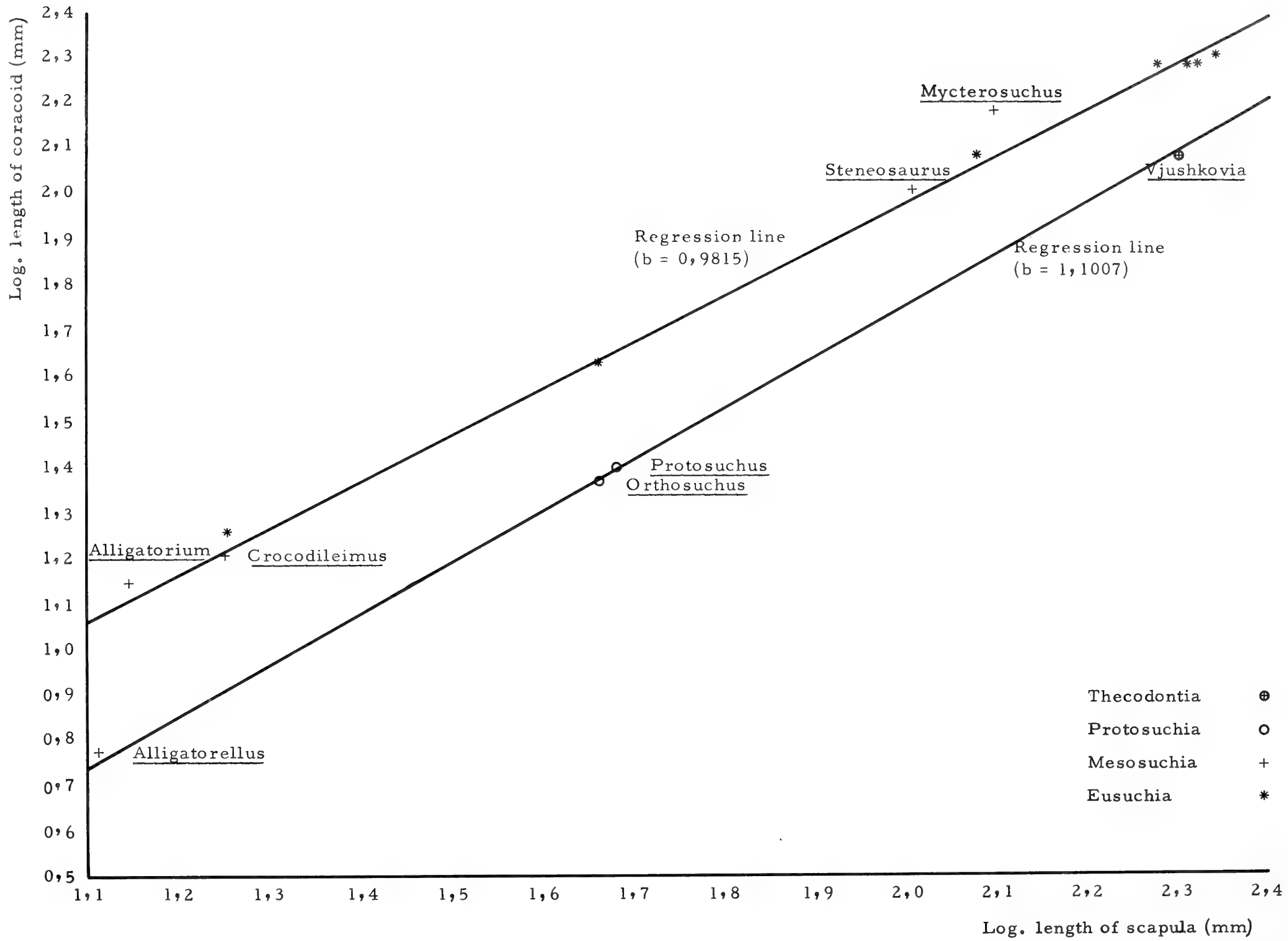

Fig. 41. Graph showing the relationship between length of coracoid and scapula (shown in log. form) for selected living and fossil crocodilians and thecodontians.

The mesosuchians on this graph show rather more scatter than the eusuchians, but no different trends. The regression slope, and the relationship with size which it shows, appear to be applicable to all of these forms.

Relationship between lengths of scapula and coracoid (Fig. 41)

It can be seen from Table 4 that in the thecodontian *Vjushkovia,* and the protosuchians *Orthosuchus* and *Protosuchus,* the coracoid is approximately half as long as the scapula, whereas in the modern crocodilians these elements are more or less equal in length. The relationships may be shown when $\log_{10}$ scapula is plotted against $\log_{10}$ coracoid. This has been done for all contemporary and fossil forms.

Two regression lines are of interest. The regression of log coracoid (y) on log scapula (x) for the seven contemporary forms is given by: $y = 0{,}9815x + 0{,}0150$. The regression for *Vjushkovia, Orthosuchus* and *Protosuchus* however is given by: $y_1 = 1{,}1007x_1 - 0{,}4605$.

The difference between the coefficients 0,9815 and 1,1007 in the above equations is significant at the 5% level.

It now becomes interesting to note that *Steneosaurus, Alligatorium* and *Crocodileimus* lie closely on the first line, while *Alligatorellus* lies virtually on the second. *Mycterosuchus* is remarkable in that the scapula is actually shorter than the coracoid, but this is surely due to aquatic adaptation.

It is also surprising to find that *Vjushkovia* falls into a group with the protosuchians, since in thecodontians the coracoid is normally less elongate relative to the scapula than it is in crocodilians. In forms like *Euparkeria* and *Stagonolepis,* for example, the coracoid is considerably wider than it is high.

Relationship between lengths of humerus and radius (Fig. 42)

The relationship between lengths of radius (Y) and of humerus (X) in fossil and contemporary forms is again best seen in a plot of $y = \log Y$ against $x = \log X$. All available values have been plotted.

Two regression lines are given, one for the thecodontians *Vjushkovia* and *Euparkeria,* together with the protosuchians *Orthosuchus* and *Protosuchus* (upper line, $b = 1{,}007$), and the other for the eight contemporary crocodilians (lower line, $b = 0{,}9028$).

The lower line has a regression coefficient significantly smaller than 1,0 ($t = 3{,}721$, significant at the 1% level). The regression coefficients of the two lines, however, are not significantly different ($t = 1{,}811$). The spatial separation of the two lines though is significant at the 1% level. Thus the difference between these two groups of animals is well established on this evidence.

The radius/humerus ratios in *Orthosuchus* and *Protosuchus* and in the thecodontians *Vjushkovia* and *Euparkeria* are all very similar and very much higher than in the living genera. This high ratio was retained, or very nearly, by certain of the small mesosuchians *Alligatorellus, Alligatorium* and *Theriosuchus.* However, in *Crocodileimus,* a mesosuchian of similar age and size, the radius is

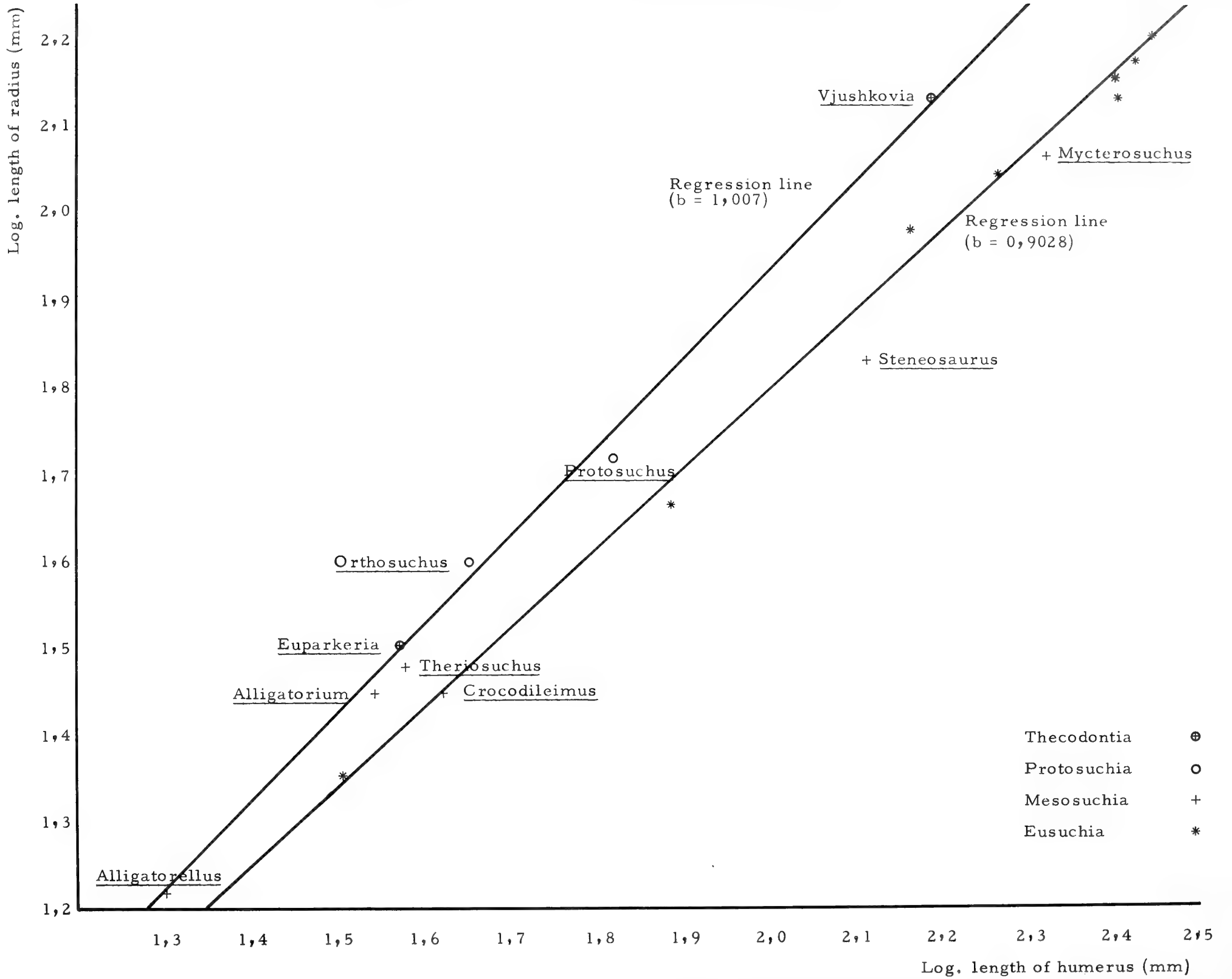

Fig. 42. Graph showing the relationship between lengths of radius and humerus (shown in log. form) for selected living and fossil crocodilians and thecodontians.

shorter relative to the length of the humerus. This animal agrees well, in respect of radius/humerus ratio, with living genera. In these the ratio, in each case, is less than 0,70, the ratio becoming smaller in older (i.e. larger) animals. In the more fully aquatic mesosuchians like *Steneosaurus*, the ratio is rather similar to that in contemporary crocodiles.

Relationship between lengths of radius and radiale

Data is available here for the thecodontian *Chasmatosaurus*, the protosuchians *Orthosuchus* and *Protosuchus*, the mesosuchians *Alligatorellus*, *Alligatorium* and *Crocodileimus*, and for five contemporary crocodiles. In each of these the radiale is an elongate bone, averaging in the eleven examples about 29,5 % of the length of the radius. In *Orthosuchus* it is 41,3 % of the length of the radius. This is significantly longer, relative to the radius, than in the other ten animals above (significant at the 5 % level).

Relationship between lengths of femur and tibia (Fig. 43)

This relationship is again brought out in a plot of $\log_{10}$ tibial length against $\log_{10}$ length of femur. On this evidence there is no reason for separating the mesosuchians from the contemporary crocodiles, though the thecodontians and protosuchians could at first sight be supposed somewhat different, as could the more fully aquatic forms.

The regression coefficient for the mesosuchians and modern forms taken together is $b = 0{,}8822$. The difference between this value and 1,0 is significant at the 0,1 % level. The relationship between length of femur (X) and length of tibia (Y) for these specimens is represented by: $Y = 1{,}31X^{0{,}88}$.

This equation shows that the relative length of tibia to length of femur decreases significantly as the size of the animal increases. In other words, the tibia elongates more slowly than the femur.

The thecodontians *Vjushkovia* and *Euparkeria*, and the protosuchians *Orthosuchus* and *Protosuchus*, lie rather above this line, and *Steneosaurus* and *Mycterosuchus* below it.

The regression coefficient for the thecodontians and protosuchians is $b = 1{,}0125$ and is not significantly different from $b = 0{,}8822$ above ($t = 2{,}038$ with 12 d.f.). A test for the separation of the two lines, however, gives $t = 3{,}768$ with 12 d.f., significant at the 1 % level, hence showing the thecodontians and protosuchians to have significantly higher tibia/femur ratios at corresponding animal sizes than the mesosuchians and eusuchians.

The tibia is therefore long relative to the length of the femur in *Orthosuchus* and *Protosuchus*, as in the thecodontians *Euparkeria* and *Vjushkovia*. In eusuchians, the femur grows at a faster rate than the tibia during development from juvenile to mature stage, so that the tibia/femur ratio decreases with age (i.e. size). The more fully aquatic *Steneosaurus* and *Mycterosuchus* have very low tibia/femur ratios, *ca* 0,50, values which are low even though the large sizes of these forms are taken into account. In *Metriorhynchus* this value is further reduced to about 0,40, and this again is clearly a result of aquatic adaptation.

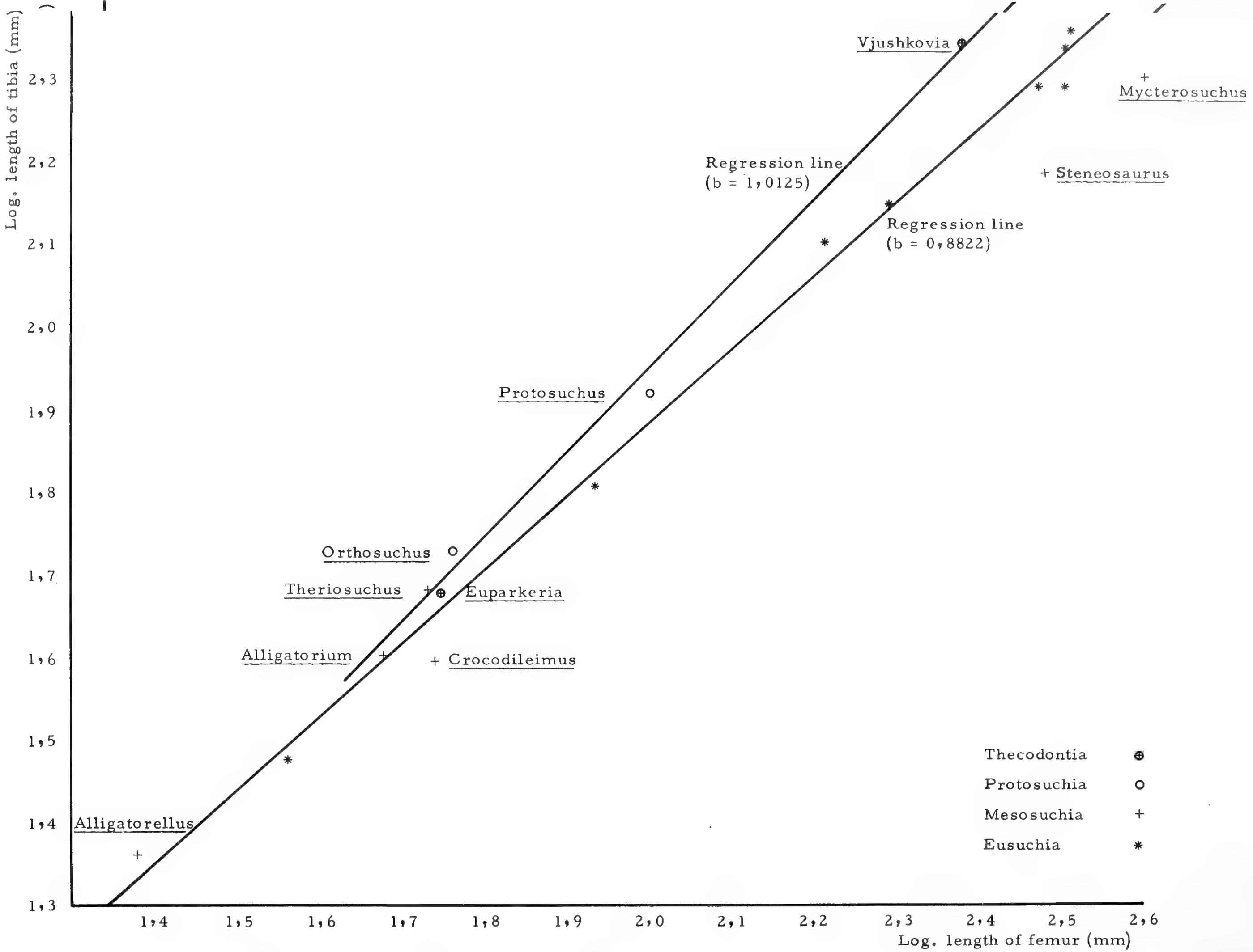

Fig. 43. Graph showing relationship between lengths of tibia and femur (shown in log. form) for selected living and fossil crocodilians, and thecodontians.

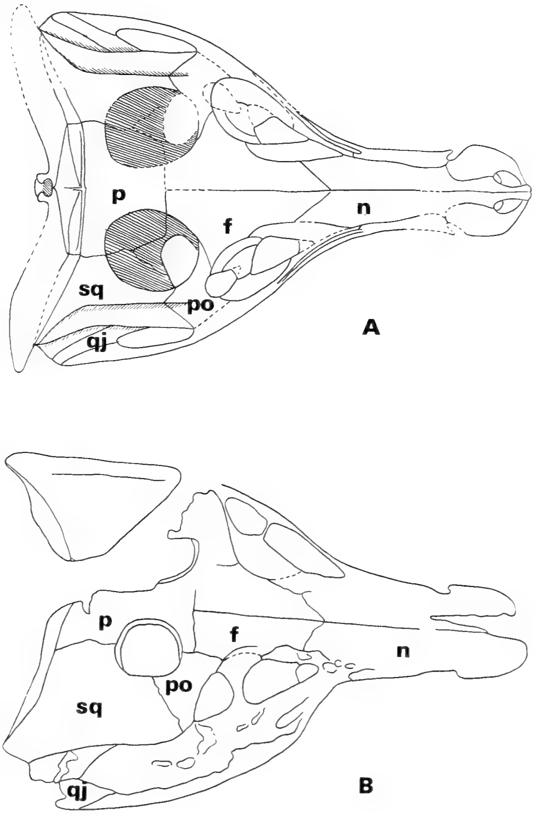

Fig. 44. Dorsal views of the skulls of A. *Orthosuchus stormbergi* (⅔ natural size). B. *Protosuchus richardsoni*, after Walker (1970) (⅔ natural size).

RELATIONSHIP OF THE PROTOSUCHIANS TO FORMS OF QUESTIONABLE CROCODILIAN AFFINITY

In 1967 Sill suggested *Proterochampsa barrionuevoi*, of late Middle Triassic age from South America, as the most ancient of known crocodilians. Sill believed that *Proterochampsa* is closely related to *Notochampsa*, and that *Protosuchus* is representative of a more aberrant line of crocodilian heritage.

According to Sill, in both *Notochampsa* and *Proterochampsa* the skull is relatively long compared to width, is flat, and the orbits lie in the horizontal plane. There is, however, no reason at all for supposing that the orbits of *Notochampsa* are dorsally orientated as Sill claimed. On the contrary, it seems much more likely that they face laterally as in *Orthosuchus*. Again, Sill relied heavily on Haughton's description (1924) of the auditory region of *Notochampsa*, and claimed that a further resemblance to *Proterochampsa* could be found in the

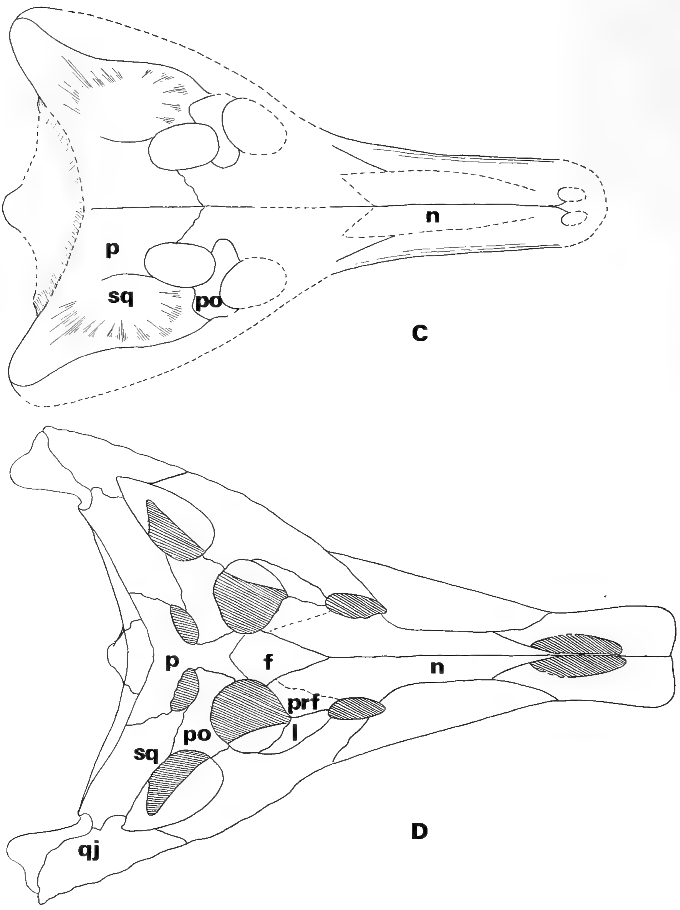

Fig 44 *continued* C. *Notochampsa istedana*, after Broom (1927) ($\frac{2}{3}$ natural size). D. *Proterochampsa barrionuevoi*, after Sill (1967) ($\frac{2}{9}$ natural size).

presence of an auditory canal on the posterior face of the skull. However, this description of the type specimen of *Notochampsa* cannot be correct; the skull of specimen British Museum (Natural History) No. R8503 shows a deep otic recess, and pronounced otic notch.

The resemblances between *Notochampsa* and *Proterochampsa* are clearly not impressive, whereas the similarity between the skulls of *Orthosuchus*, *Protosuchus* and *Notochampsa* is striking (Fig. 44). Sill (1968 personal communication) now agrees that he cannot substantiate his earlier claims, though he doubts the phytosaurian affinity of *Proterochampsa* postulated by Walker (1968). In Walker's view (1970) the position of the choanae alone is sufficient to exclude *Proterochampsa* as a crocodilian ancestor.

The vertebral column of *Proterochampsa* is known only from the thirteen most anterior vertebrae. Rather surprisingly, the parapophysis retains a low position on the centrum throughout this series. Presumably it changes position farther back along the column, and so may parallel the condition found in some primitive thecodontians like *Chasmatosaurus* and *Erythrosuchus* where the parapophysis does not begin to rise until the eleventh vertebra (Hughes 1963). Indeed, Romer (1971, 1972*a*) has now demonstrated a close relationship between *Proterochampsa*, *Cerritosaurus*, *Gualosuchus* and *Chanaresuchus*. He has argued convincingly that they are a sterile group, representing a modest advance over the Proterosuchia, which in Middle Triassic times occupied a position in the ecology similar to that of the phytosaurs of the late Triassic and the crocodilians of the later Mesozoic.

Stegomosuchus longipes, from the Upper Triassic of the Connecticut Valley, is poorly known because of the form of its preservation. As Walker (1970) has commented, resemblances to protosuchians are seen in the broad, flattened cranial table, in the longitudinal groove which runs along its margin, and in the presence of two supraorbital elements on each side. The skull roof is pitted as in protosuchians. Postcranially, crocodilian affinity is shown by the broad, triangular apex of the scapula, the presence of a calcaneal tuber and four elongated metatarsals of the hind-foot, and the similarity of the dorsal armour. This evidence, though slender, suggests that *Stegomosuchus* may reasonably be regarded as a protosuchian.

Microchampsa scutata from the Upper Triassic of the Yunnan, China, is known only from part of the postcranium. In view of this, Simmons (1965) was hesitant to establish its systematic position but suggested that *Microchampsa* might represent a new type of crocodilian. He described the vertebral structure as most crocodilian, but it is difficult to see what is meant by this, since the pattern found in protosuchians is also common to thecodontians. Further, the neural spines of the posterior dorsal vertebrae of *Microchampsa* are terminally expanded to accommodate the median row of dorsal scutes, and this is certainly not the case in any of the protosuchians. Spine tables are developed on the posterior cervical and anterior dorsal vertebrae of *Euparkeria*, and on the posterior dorsal vertebrae of *Stagonolepis*.

The ribs of *Microchampsa* are also quite different from those of *Protosuchus* and *Orthosuchus*. In *Microchampsa* they are short and entirely devoid of the double flanges so characteristic of protosuchians. Furthermore, in *Microchampsa* the lumbar ribs are fused to lateral scutes; an impossible condition in protosuchians which lack scutes in this region. The armour, moreover, is not of the type found in protosuchians. In *Microchampsa* there is but a single median row of dorsal scutes, not pitted or ornamented in any way. This row is flanked by a row of dorso-lateral scutes on each side. These are simply pitted and have rugosities. These features, taken together, make a good case for excluding *Microchampsa* from the Crocodilia, and regarding it, for the present, as a pseudosuchian.

The archosaur material from the Upper Triassic of South Wales, at present being studied by Kermack, includes several partly associated skeletons. The skull has an antorbital fenestra, and the carpus is crocodilian in type in that the radiale and ulnare are elongated. With regard to the number of distal carpals present, the specimens from Wales resemble *Protosuchus* and differ from *Orthosuchus*. It is however surprising to find the pelvis and hind-limb more primitive in type than that of both *Orthosuchus* and *Protosuchus*. In Kermack's opinion (1956), the pubis contributes to the formation of the acetabulum, and is perforated by an obturator foramen. It is possible that in *Protosuchus* the pubis contributes marginally to the acetabulum, but in neither *Protosuchus* nor *Orthosuchus* is it perforated. On the other hand the acetabulum is open, and the ischium similar in each case.

Kermack described the metatarsus of his material as having a fifth digit with two reduced phalanges, and likened it to the metatarsus of *Erythrochampsa*. However he relied upon Von Huene's interpretation of *Erythrochampsa* which is now shown to be incorrect. In view of the crocodilian nature of the pelvis, and also of the carpus, there is little doubt that the Welsh form is a primitive crocodilian, differing in a number of respects from the South African and North American forms.

Hemiprotosuchus leali, from the Upper Triassic of Argentina, is represented by a skull and jaws, and several postcranial elements. Bonaparte (1971) believes it to be a protosuchian, and has closely compared *Hemiprotosuchus* with *Protosuchus*.

Hemiprotosuchus is of moderate size, much the same as other known protosuchians. The cranial table has a characteristic crocodilian configuration, though the sculpturing is in the form of rugosities rather than pitting. The interorbital area is slender, as it is in *Orthosuchus*, but the orbit and preorbital region is higher than in other protosuchians. The nares are terminal, as in *Orthosuchus*, and the superior temporal fenestra is elongate, as in *Notochampsa*. An antorbital fenestra is present, as in *Orthosuchus*, and leads to the ventral edge of the orbit.

As is characteristic of crocodilians, the quadratojugal and quadrate are sutured to the postorbital and squamosal in the anterior dorsal region of the inferior temporal fenestra. Further, the squamosal overhangs the otic region which is open posteriorly as in protosuchians. A short, bony secondary palate is developed, and the pterygoid and basisphenoid show the same relationship as found in *Orthosuchus*. The lower jaw is persistently primitive, as in *Orthosuchus* in that a prearticular is present, but a retroarticular process is lacking. However, whereas the jaw in *Hemiprotosuchus* is deep, in *Orthosuchus* it is quite slender.

The characters of the skull indicate that *Hemiprotosuchus* should be regarded as a protosuchian, and the associated postcranial elements confirm this diagnosis. The coracoid is elongated postero-ventrally, the astragalus and calcaneum are crocodilian in type, and the scutes covering the trunk are paired and imbricated. Unfortunately it is not possible to determine whether the scutes are sculptured.

Walker (1970) has suggested that a number of other Upper Triassic genera of disputed affinities are also closely related to, though distinct from, the 'true' crocodiles. These are *Pedeticosaurus* from the Cave Sandstone of South Africa, *Sphenosuchus* from the underlying Red Beds, *Hesperosuchus* from the Chinle Formation of Arizona, *Saltoposuchus* from the Stubensandstein of Germany and *Platyognathus* from the Dark Red Beds of the Lower Lufeng Series, Yunnan, China.

Bonaparte (1971) has since demonstrated that the skull of *Pseudhesperosuchus jachaleri* is closely similar to that of *Sphenosuchus acutus*. He is of the opinion that rather more significance should be placed on differences between the skulls of sphenosuchians and protosuchians, notably the absence in sphenosuchians of the typical crocodilian cranial table, and the pseudosuchian nature of the basicranium, suspensory region and palate. Hence, although sphenosuchians are transitional between thecodontians and crocodilians, in Bonaparte's view they show a series of characters which relate them most closely to thecodontians.

Bonaparte has further suggested that *Pseudhesperosuchus* is closely linked to *Hesperosuchus agilis*. Evidence for this is based mainly on the form of the coracoid and humerus. Bonaparte and Walker are both of the opinion that the 'problematical' element figured by Colbert (1952) is a coracoid, and there can be little dispute about this identification. However, according to Colbert, this element consists of two bones sutured together, the suture being interrupted by a large foramen. In my opinion this element resembles a therapsid coracoid rather than that of an archosaur. Colbert had, in addition, identified the proximal portion of the left coracoid of *Hesperosuchus*.

Should the 'problematical' element prove to be the coracoid of a different animal, and not that of *Hesperosuchus*, then the latter shows no crocodilian characteristics. In *Sphenosuchus* the coracoid is elongate, and in *Pseudhesperosuchus* the coracoid, radiale and ulnare are all elongated, but the presence of certain diverse crocodilian features in these types does not in itself confirm crocodilian affinity.

Pedeticosaurus leviseuri (Van Hoepen 1915) is preserved mainly as an impression of the right side of the skull and limbs. The skull, as far as can be seen, differs little from that of known protosuchians. The scapula, humerus, radius and ulna appear to be similar in general outline to these elements in *Orthosuchus*, though the coracoid is unknown. Walker has suggested that the element previously identified by Van Hoepen as a metacarpal is an elongated radiale associated with the first metacarpal and two phalanges. This could indicate crocodilian affinity, but since no other bones of the carpus and manus are present, this cannot be confirmed. Although the evidence is slight, on balance it seems that *Pedeticosaurus* lies closer to protosuchians than to forms like *Sphenosuchus*.

Saltoposuchus is at present too inadequately known for a meaningful comparison to be made.

Platyognathus hsui represents an unusual type in that the teeth are irregularly polygonal, and finely denticulate. The jaw also differs from that of protosuchians in that it is short and terminally expansive. The development of a rudimentary secondary palate in this type was regarded by Simmons (1965) as a crocodilian characteristic, but this type of development has also been noted in such diverse forms as *Sphenosuchus*, *Erpetosuchus* and phytosaurs. It does not compare with the form of the palate in *Orthosuchus*.

Simmons (1965) described the vertebral column of *Platyognathus* as being protosuchian, but with procoelous centra. The latter is clearly a very remarkable character in a form of Upper Triassic age, and is found in neither thecodontians nor protosuchians. The vertebrae also differ from those of protosuchians in the development of spine tables. Further, the dorsal ribs show the unusual condition of being flanged on the sternal segment. The dorsal scutes are paired and overlapping, but bear rugosities as well as pits. Indeed, the only crocodilian character present is seen in the elongate form of the coracoid. This is clearly insufficient reason to link *Platyognathus* with the Protosuchia, and its affinities more probably lie with the Pseudosuchia.

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ABBREVIATIONS

a	angular	m	maxilla
af	antorbital fenestra	n	nasal
ar	articular	p	parietal
bo	basioccipital	pa	prearticular
bpt	basipterygoid process	pl	palatine
bs	basisphenoid	pm	premaxilla
c	coronoid	pmf	premaxillary foramen
ch	choana	po	postorbital
con	condyle	popr	paroccipital process
d	dentary	prf	prefrontal
ec	ectopterygoid (transverse)	pt	pterygoid
en	external naris	q	quadrate
eo	exoccipital	qj	quadratojugal
eu	median opening of eustachian tubes	s	stapes
eul	lateral eustachian pit	sa	surangular
f	frontal	so	supraorbital
fch	position of functional choana	soc	supraoccipital
ic	foramen for internal carotid	sp	splenial
gl	jaw articulation (glenoid fossa)	sq	squamosal
itf	inferior temporal fenestra	stf	superior temporal fenestra
j	jugal	tm	tympanic membrane
l	lachrymal	v	vomer
ls	laterosphenoid		

A.M.N.H.	American Museum of Natural History, New York
B.M.N.H.	British Museum (Natural History), London
S.A.M.	South African Museum, Cape Town
Zool. Mus.	Zoologisches Museum, Berlin

Foramina for cranial nerves in roman numerals

6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., 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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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'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.

DIANE S. NASH

THE MORPHOLOGY AND RELATIONSHIPS OF A CROCODILIAN, *ORTHOSUCHUS STORMBERGI*, FROM THE UPPER TRIASSIC OF LESOTHO

VOLUME 67 PART 8 OCTOBER 1975 ISSN 0303–2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes 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.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
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ARCHAEOCYATHA PROVENANT DE BLOCS ERRATIQUES DES TILLITES DE DWYKA (AFRIQUE DU SUD)

Par
FRANÇOISE DEBRENNE

Cape Town Kaapstad

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ARCHAEOCYATHA PROVENANT DE BLOCS ERRATIQUES DES TILLITES DE DWYKA (AFRIQUE DU SUD)

Par

FRANÇOISE DEBRENNE

Institut de Paléontologie

Museum National d'Histoire Naturelle, Paris

(Avec 11 figures et 1 tableau)

[*MS accepté 20 Janvier 1975*]

RÉSUMÉ

L'étude paléontologique des Archéocyathes contenus dans les blocs glaciaires des tillites de Dwyka montre une grande similitude avec la faune d'Antarctique. Il se confirme que l'origine des blocs est à rechercher dans cette région. L'affinité de la faune avec l'Australie, d'autre part, renforce l'hypothèse de l'unité d'un continent austral dès le Cambrien inférieur. Sont décrits: Pseudosyringocnemididae fam. nov., *Flexanulus oosthuizeni* gen. et sp. nov., *Statanulocyathus oosthuizeni* gen. et sp. nov., *Andalusicyathus cooperi* sp. nov.

ABSTRACT

ARCHAEOCYATHA FROM GLACIAL ERRATICS FROM THE DWYKA TILLITES (SOUTH AFRICA)

Palaeontological studies of the Archaeocyatha embedded in the erratic cobbles of the tillites from the Dwyka sub-group give evidence of great similarity with the Antarctic faunas. They show that the origin of these cobbles has to be looked for in Antarctica. On the other hand, the affinities with the Australian faunas give support to the hypothesis of the unity of the southern continents since the Lower Cambrian. Pseudosyringocnemididae fam. nov., *Flexanulus oosthuizeni* gen. and sp. nov., *Statanulocyathus oosthuizeni* gen. and sp. nov. and *Andalusicyathus cooperi* sp. nov. are described.

TABLE DES MATIERES

Ann. S. Afr. Mus. **67** (8), 1975: 331–361, 11 figs, 1 table

INTRODUCTION

L'ensemble du matériel, comportant les Archéocyathes provenant de blocs erratiques des tillites de Dwyka, à Zwartskraal a été découvert et récolté par M. R. Oosthuizen entre 1966 et 1968. Bien que ces enclaves contenant des Archéocyathes soient extrêmement rares, on peut les suivre à travers la tillite depuis sa base meuble, à travers la partie centrale plus dure jusqu'au sommet plus meuble de nouveau. R. Oosthuizen a découvert quelques exemplaires in situ dont quelques-uns sont inclus dans la gangue. M. M. Cooper a pris l'initiative de me confier l'étude du matériel confié par M. Oosthuizen au South African Museum. Je les remercie très vivement et souligne le grand intérêt scientifique de cette découverte, la première en Afrique du Sud.

DESCRIPTION PALÉONTOLOGIQUE DU MATÉRIEL

Famille **Robustocyathidae** Debrenne, 1964

Genre *Stapicyathus* Debrenne, 1964

1964—*Archaeocyathellus* (*Stapicyathus*) Ford.—Debrenne: 127.
1970—*Stapicyathus* Debrenne.—Debrenne: 43.
1972—*Stapicyathus* Debrenne.—Hill: E 66.

Espèce-type: Archaeocyathus stapipora Taylor, 1910: 118.

Diagnose

Calices à 2 murailles poreuses et cloisons radiales imperforées, sauf une rangée de pores qui se combine avec l'unique rangée verticale de pores que la muraille interne possède en face de chaque cloison. La muraille externe est simple et régulièrement poreuse.

Discussion

In Debrenne 1974*b*.

Répartition

URSS, Extrême-Orient, Australie, Antarctique.

Stapicyathus incisus (Hill), 1965

Fig. 1a

1920—*Thalamocyathus tubavallum* Taylor.—Gordon: 168, pl. 1 (fig. 15).
1965—*Robustocyathus incisus* Hill: 68–69, pl. 3 (figs 2–5).
1974*b*—*Stapicyathus incisus* (Hill).—Debrenne: 121, pl. 25 (fig. 3).

Holotype: British Museum (Natural History) S 8398.

Matériel étudié: 4 exemplaires, SAM–K4495 B.

Description

Espèce conique, atteignant de 5 à 6 mm de diamètre, avec un intervallum de 1,2 mm et des cloisons distantes de 0,6 à 0,7 mm. Le coefficient pariétal

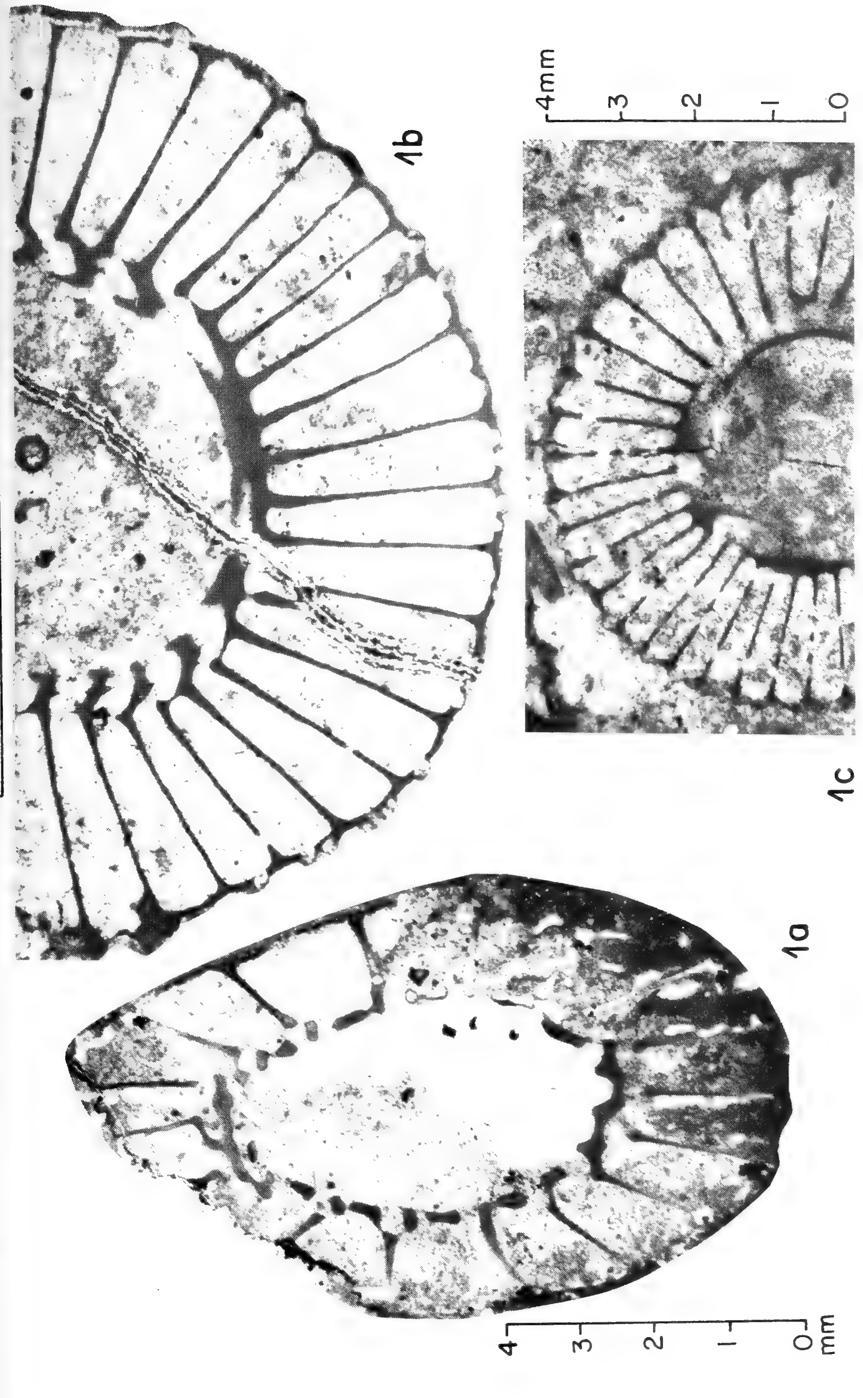


Fig. 1a. *Stapicyathus incisus* (Hill), SAM-K4495 B-15b. Coupe transversale oblique, × 10.
Fig. 1b. *Thalamocyathus tectus* Debrenne, SAM-K4495 A-10. Détail d'une coupe transversale, × 20.
Fig. 1c. *Thalamocyathus tectus* Debrenne, SAM-K4495 B-17b. Coupe transversale, × 10.

est de 3, les chambres interseptales de 1/2. La muraille externe, mal conservée, a 4 à 5 rangées de pores par intersept (diamètre environ 0,05 mm—linteaux et épaisseur 0,10 mm). Le pore de la muraille interne est large (0,27 mm) séparé par des linteaux importants (0,20–0,25 mm) d'épaisseur 0,20 mm.

Affinités

Correspond en tous points aux mesures et coefficients des formes d'Ajax Mine, de Weddel Sea et de Wichaway Nunatak.

Famille **Cyclocyathellidae** Zhuravleva, 1959

Thalamocyathus tectus Debrenne, 1973

Fig. 1b–c

1920—*Thalamocyathus trachealis* (Taylor) pars.—Gordon: pl 2 (figs 24–25).
1936—*Bronchocyathus trachealis* (Taylor) pars.—R. & J. Bedford: 25, pl. 26 (figs 100–102).
1955—*Thalamocyathus trachealis* (Taylor) pars.—Hill: 94–96, pl. 7 (fig. 2a–e).
1955—?*Thalamocyathus* sp.—Hill: 94–96, pl. 7 (figs 7a–b—8a–b).
1973—*Thalamocyathus tectus* Debrenne: 11, figs 5B, 6–8, pl. 1 (figs 5–7), pl. 4 (fig. 2).

Holotype: Princeton University 86722 (165).

Matériel étudié: 6 calices, SAM-K4495.

Description

Calices coniques à cloisons droites qui perdent leur porosité quand les individus atteignent 7 mm de diamètre. Le coefficient pariétal est élevé (7), les chambres interseptales ont un rapport des côtés de 1/4,8. La muraille externe porte des tumuli peu nombreux (2 par intersept dans les calices jeunes, souvent un seul ensuite). Leur paroi est mince (0,05 mm); ils forment des monticules assez élevés (0,06 mm au-dessus de la muraille) qui couvrent une ouverture de 0,10 mm. Ces monticules peuvent être interprétés comme pores-diaphragmes turgescents (Debrenne 1973: 6, 11, fig. 5A–B). La muraille interne est annulaire avec une forme en auge, concave vers le haut; au milieu et sous cette gouttière se développe une carène plus ou moins bien marquée. La largeur de l'anneau est de 0,27 mm, la distance entre 2 anneaux, 0,16 mm. L'épaisseur moyenne de la paroi est 0,06 mm. A la base, on peut observer des anneaux incomplets, ce qui permet de rapprocher les stades jeunes du genre *Sanarkocyathus* Zhuravleva.

Il n'y a pas de planchers pectinés visibles.

Affinités

La distinction entre les tumuli (type *Kijacyathus* Zhuravleva ou *Annulocyathella* Vologdin) et les pores diaphragmes turgescents a été exposée antérieurement (Debrenne 1973: 6, 11). Il est actuellement difficile de se prononcer sur la valeur systématique de ces saillies hémisphériques (vacuoles—bubbles dans Hill 1955: 95). Actuellement une espèce, *tectus*, rattachée au moins provisoirement au gentre *Thalamocyathus* a été établie (Debrenne 1973: 11). Elle présente une muraille externe avec capsules hémisphériques. Son coefficient pariétal est plus faible que celui de *trachealis* (Debrenne 1973: 11).

Certaines formes décrites en Antarctique par Gordon et Hill et dans la composition de l'espèce *trachealis* avaient déjà été incluses dans *tectus* (Debrenne 1973). Les échantillons d'Afrique du Sud, par leurs caractéristiques anatomiques et leurs coefficients font également partie de l'espèce.

?Famille **Kijacyathidae** Zhuravleva, 1964

Genre ***Flexanulus*** gen. nov.

Diagnose

Calices à 2 murailles et cloisons radiales peu perforées. La muraille externe est formée d'un ensemble de tubes allongés, courbés avec ouvertures dans le plan vertical. Au point de rebroussement un crochet recourbé vers le bas se développe, fermant partiellement le tube immédiatement inférieur (Fig. 2). Les cloisons s'appuient sur les parois latérales des tubes et forment avec elles des parties squelettiques épaissies. La muraille interne est annulaire; les anneaux sont en S très allongés se recouvrant l'un l'autre.

Espèce-type: Flexanulus oosthuizeni sp. nov.

Affinités

Genre proche d'*Annulocyathus* Vologdin et de *Kijacyathus* Zhuravleva, il en diffère par la forme particulière des tubes externes et des anneaux internes.

Flexanulus oosthuizeni sp. nov.

Figs 2–3a–b

Holotype: SAM–K4495 B–12a.

Matériel étudié: 4 calices.

Description

Calices coniques de petite taille (5,4 mm) traversés de cloisons peu perforées, délimitant des chambres interseptales de rapport 1/5. Le coefficient pariétal est de 5,7. Les canaux de la muraille externe, 2 par intersept, se développent en s'appuyant sur les cloisons à l'intérieur de l'intervallum; leur diamètre est de 0,20 mm, l'épaisseur de leur paroi 0,01 mm et leur longueur 0,21 mm. Ils sont formés d'une partie intervallaire en tube oblique vers l'extérieur et le haut, puis se redressent brusquement presqu'à angle droit au niveau des ouvertures externes. A ce point se développe un crochet recourbé vers le bas, symétrique de la partie redressée par rapport à la paroi du tube (Fig. 3a–b). La muraille interne est formée d'anneaux en S très allongés et imbriqués: l'ouverture entre les anneaux est de 0,16 mm, la hauteur des anneaux 1,15 mm, l'épaisseur de leur paroi 0,04 mm. Les cloisons sont droites, peu poreuses, épaisses de 0,04 mm.

Affinités

Une seule espèce connue actuellement.

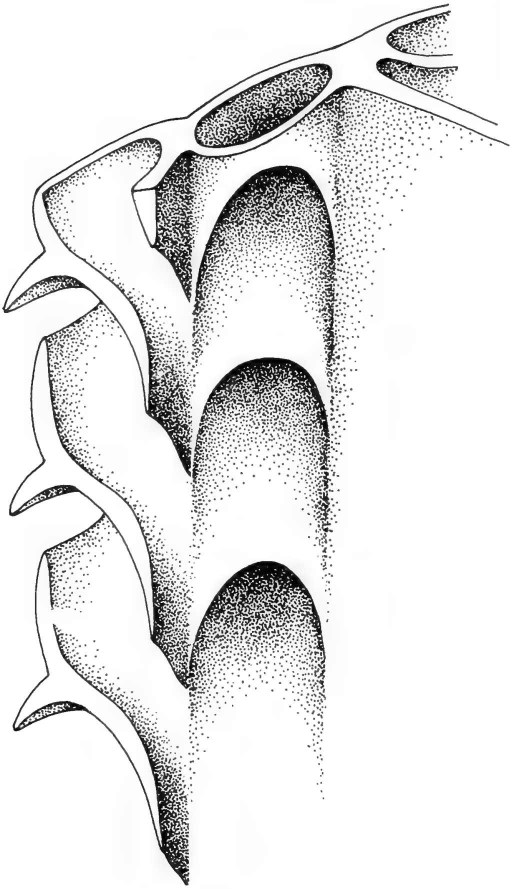


Fig. 2. Reconstitution des tubes de la muraille externe de *Flexanulus* gen. nov.

Famille **Erbocyathidae** Vologdin & Zhuravleva, 1956

?*Ladaecyathus* sp.

Fig. 4a

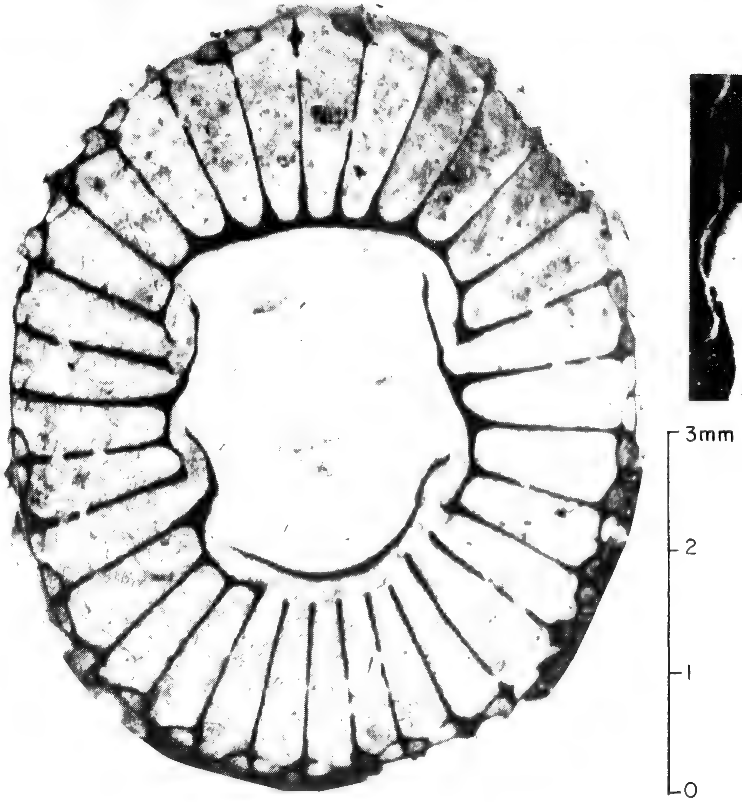
1 exemplaire, SAM–K4495 A–9.

Description

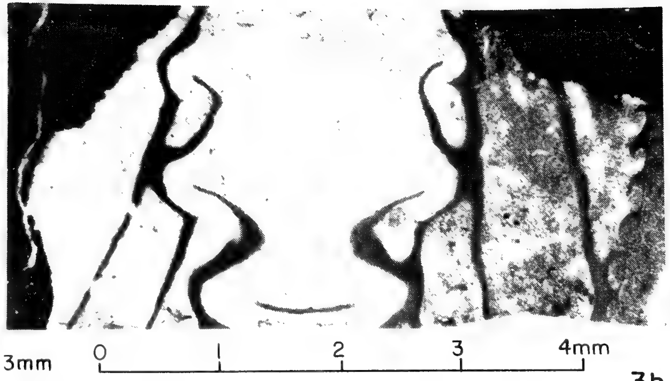
Fragment d'un petit calice dont les murailles externe et interne paraissent recouvertes d'une seconde enveloppe microporeuse. Les cloisons sont épaisses onduleuses et parfois bifurquées.

Dimensions

Diamètre: 6,5 mm; intervallum: 1,65 mm; distance entre les cloisons variable: en moyenne 0,6 mm; muraille externe principale, diamètre des pores:

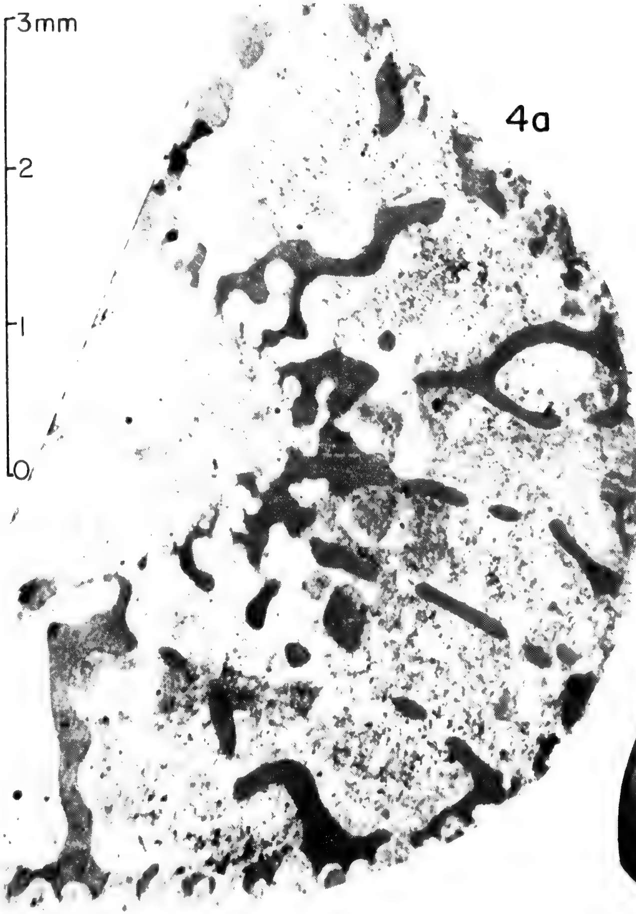


3a



3b

Fig. 3a. *Flexanulus oosthuizeni* gen. et sp. nov., SAM–K4495 B–12a. Coupe transversale, × 15.
Fig. 3b. *Flexanulus oosthuizeni* gen. et sp. nov., SAM–K4495 B–12a. Coupe longitudinale, × 15.



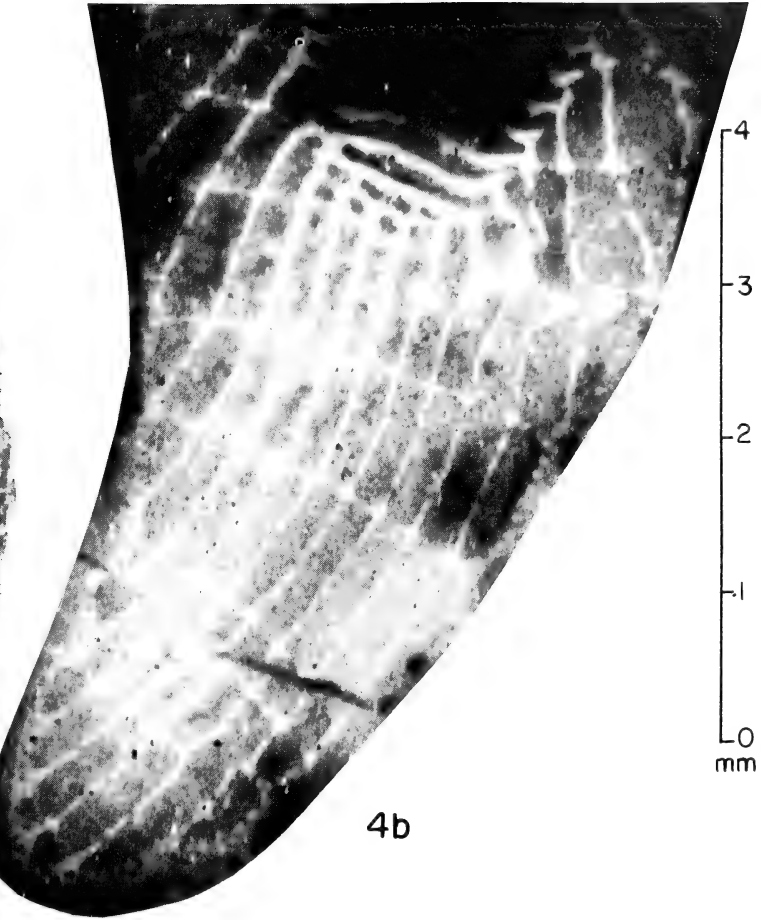


Fig. 4a. ?*Ladaecyathus* sp., SAM–K4495 A–9. Coupe transversale oblique, × 20.
Fig. 4b. *Thalamopectinus arterialis* Debrenne, SAM–K4495 B–13. Coupe longitudinale (calcaire attaqué à l'acide), × 20.

0,16 mm, linteaux: 0,05 mm, épaisseur: 0,10 mm; muraille interne, diamètre: 0,16 mm, linteaux: 0,08 mm, épaisseur: 0,21 mm, épaisseur des cloisons: 0,09 mm, pores: 0,10 mm.

Discussion

Les espèces rapportées par Hill (1955) à *Ladaecyathus* Zhuravleva, 1960, sont représentées par des fragments d'exemplaires de grande taille (60 mm pour *L. pratti* Hill, 35 mm pour *fortiseptatus* Hill). Il est difficile de rattacher le fragment découvert ici à l'une ou l'autre espèce. D'autre part l'attribution au genre *Ladaecyathus* de ces fragments aussi bien ceux décrits par Hill, que celui dont il est question ici, est douteuse. La façon dont se construisent les doubles murailles et la relative irrégularité des cloisons font penser plutôt à *Metaldetes ramulosus* (R. & J. Bedford)—Debrenne 1974*a*: 226–227, fig. 24.

Famille **Bronchocyathidae** R. & J. Bedford, 1936

Thalamopectinus arterialis Debrenne, 1972

Fig. 4b

1936—*Bronchocyathus trachealis* (Taylor).—R. & J. Bedford: 25, pl. 25 (fig. 99C–D).
1955—*Thalamocyathus trachealis* (Taylor).—Hill: 96, pl. 7 (fig. 3).
1973—*Thalamopectinus arterialis* Debrenne: 8.

Matériel étudié: SAM–K4495 B–13.

Description

Calice cylindrique à cloisons radiales peu ou pas perforées et planchers pectinés assez régulièrement répartis, distants d'un millimètre en moyenne. Le diamètre atteint 5 mm avec un intervallum de 0,75 mm; l'écartement des cloisons est de 0,15 mm, soit un coefficient intervallaire de 0,15 et un rapport de 1/5 pour les chambres interseptales. La muraille externe a une porosité simple, elle est formée d'une lame perforée régulièrement de pores arrondis disposés en quinconce, 3 rangées par intersept (diamètre: 0,06 mm, linteaux: 0,02 mm). La muraille interne est annulaire avec une section en auge soulignée vers le bas par une petite carène; les anneaux sont distants de 0,1 mm, l'épaisseur de la paroi est variable (de 0,1 à 0,2 mm) suivant l'endroit de la mesure. La largeur totale de l'anneau est de 0,25 mm.

Affinités

Une étude récente sur la valeur systématique qui devait être accordée aux planchers pectinés (Debrenne *et al.* 1973) a établi qu'il était nécessaire de classer en des genres distincts les formes avec et les formes sans planchers pectinés. Le genre *Thalamocyathus* Gordon est réservé aux formes à cloisons peu poreuses, le genre *Thalamopectinus* Debrenne aux formes à cloisons peu poreuses et planchers pectinés.

L'espèce découverte en Afrique du Sud est en tout point comparable à celle figurée par Hill (1955, pl 7 fig. 3) (British Museum (Natural History) 58416); bien qu'elle ne signale pas de planchers pectinés cette structure a été observée sur la lame et apparaît même sur la figuration citée.

Un exemplaire de la collection Bedford (Princeton University 248) est très voisin de celui étudié ici; il semble donc que les formes d'Antarctique et d'Afrique du Sud entrent dans les limites de l'espèce *arterialis* Debrenne qui aurait donc existé dans les trois régions.

Famille **Anaptyctocyathidae** Debrenne, 1969

Gentre *Erugatocyathus* Debrenne, 1969

Espèce-type: Coscinocyathus papillatus R. & W. R. Bedford, 1934: 3, fig. 12.

Diagnose

Coscinocyathe avec muraille externe à double porosité et muraille interne protégée par des crochets très recourbés recouvrant le pore de base.

Discussion

La seconde enveloppe microporeuse n'est pas indépendante de la muraille principale. Elle est de type *Erbocyathus* (Debrenne 1973: 18) et non *Tomocyathus*.

Erugatocyathus scutatus (Hill), 1965

Fig. 5a–b

1965—*Torgaschinocyathus scutatus* Hill: 104–105, pl. 8 (figs 1–4).

Holotype: British Museum (Natural History) S 8434.

Matériel étudié: 12 calices.

Description

Calices coniques ne dépassant pas 12 mm de diamètre. Un exemplaire montre que l'animal débute par un stade à 2 murailles et intervallum vide sauf quelques lames de tissu vésiculeux. A 2 mm de diamètre se forment les premiers planchers poreux qui précèdent l'apparition des cloisons. La muraille externe est d'abord compacte et épaissie par du stéréoplasme. La double porosité est acquise très tôt, au niveau des premiers planchers, lorsque le stéréoplasme disparaît. Les individus les plus nombreux ont un diamètre de 5 à 7 mm avec un intervallum de 1 à 1,5 mm. Les cloisons radiales sont assez espacées, formant des chambres interseptales dont le rapport des côtés varie de 1/1,25 à 1/2, tandis que le coefficient pariétal s'établit entre 3 et 3,7.

La porosité de la muraille externe est souvent dificile à observer, la fossilisation étant souvent grossière, et les structures souvent masquées par des algues qui s'accolent aux calices. Cependant certains endroits plus favorables montrent la double enveloppe. Les pores principaux ont un diamètre de 0,15 mm, des linteaux de 0,10 mm; l'épaisseur totale de la muraille est de 0,10 mm. La muraille

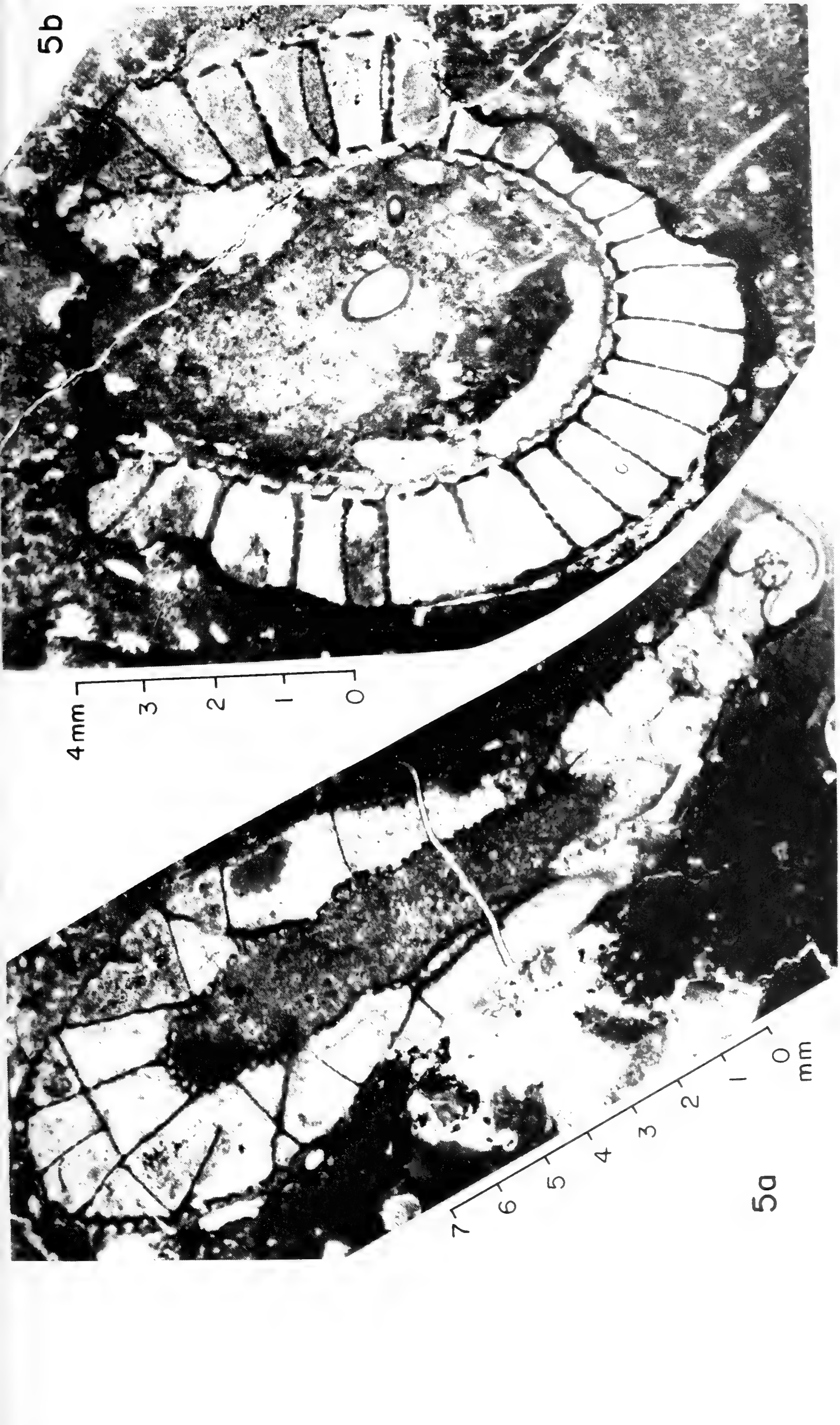


Fig. 5a. *Erugatocyathus scutatus* (Hill), SAM–K4495 B–3a, Coupe longitudinale, × 7,5.
Fig. 5b. *Erugatocyathus scutatus* (Hill), SAM–K4495 B–7. Coupe transversale, × 10.

interne comporte 2, plus rarement 3 rangées de pores en quinconce par intersept. Le développement des crochets courbés vers le haut et complétés par des épines vers le bas est variable: complets et bien marqués dans les faibles diamètres, ils diminuent d'importance et ont presque disparu dans le calice de 12 mm.

Les cloisons sont très poreuses: 5 à 8 pores en rangées régulières (diamètre 0,05 mm, linteaux: 0,16 mm, épaisseur: 0,04 mm). Les planchers ont des pores de même diamètre, mais plus denses (8 par intersept, diamètre: 0,05 mm, linteaux: 0,04 mm).

Affinités

L'observation personnelle des collections du British Museum (Natural History) S 8433–S 8434 (lames) nous a permis d'observer la présence d'une double muraille externe, souvent masquée par des algues et décrite par Hill (1965) comme 'thin projecting collar'. Les plaques recourbées au-dessus des pores de la muraille interne sont tout à fait semblables à celles du type de *Erugatocyathus* Debrenne. Les mesures et coefficients de *E. scutatus* (Hill) correspondent à ceux des échantillons étudiés ici qui doivent donc être rapportés à cette espèce.

E. scutatus (Hill) diffère de *E. papillatus* (R. & W. R. Bedford) par une plus grande minceur des éléments squelettiques, une plus faible porosité des cloisons et des chambres interseptales différentes (1/2,5 contre 1/5).

?*Erugatocyathus* sp.

Fig. 6a

Un exemplaire: SAM–K4495 B–17a.

Description

Un calice de 5 mm de diamètre, ayant un coefficient pariétal de 3,6 et des chambres interseptales de 1/2,7 de côté présente un seul pore recouvert d'une papille par intersept à la muraille interne.

Discussion

La présence d'un seul pore, caractère généralement considéré comme important pour la systématique, éloigne cet exemplaire des *E. scutatus* types. Cependant en l'absence de sections supplémentaires dans cet exemplaire, il n'est pas possible de savoir si la figure observée traduit un trait constant ou seulement un accident sporadique.

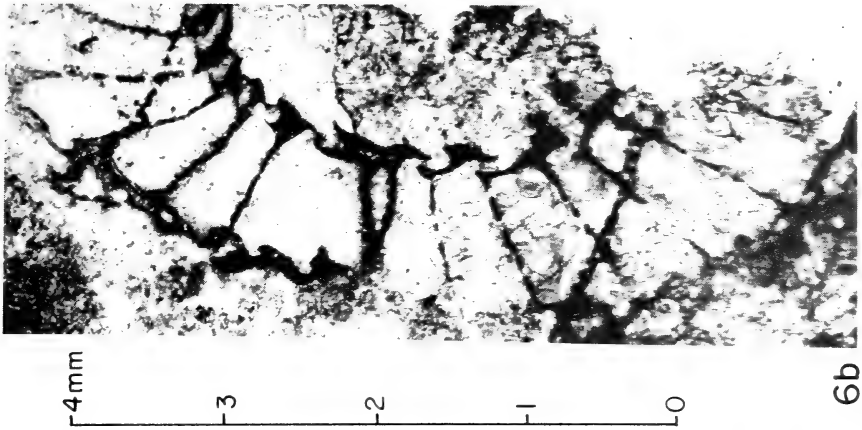
Famille **Porocoscinidae** Debrenne 1964

Genre ***Statanulocyathus*** gen. nov.

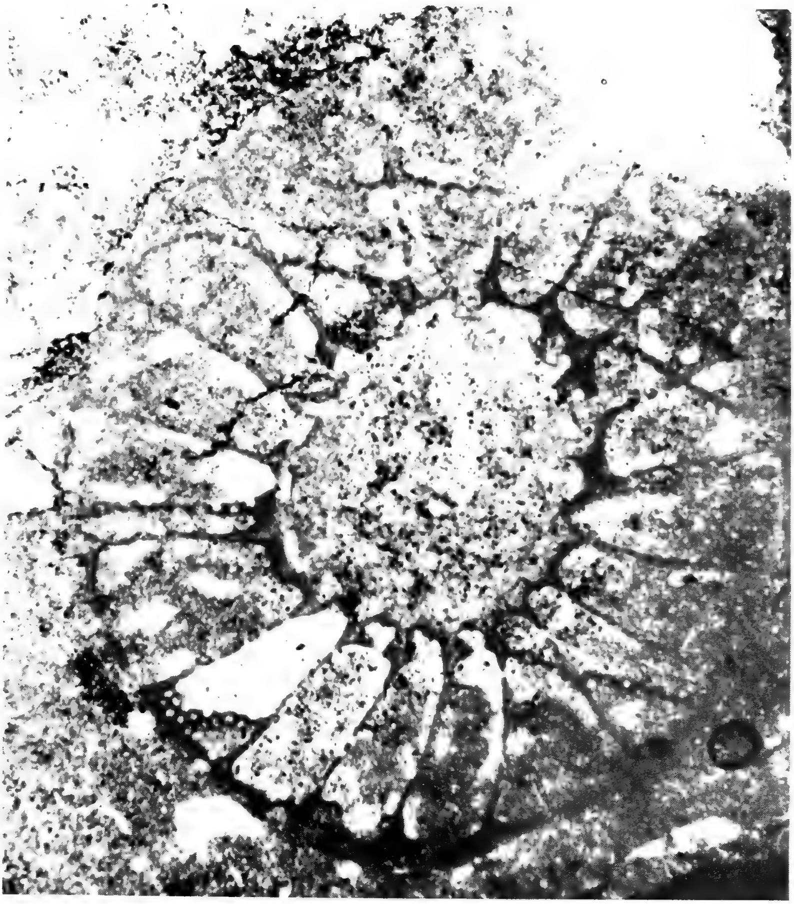
Espèce-type du genre: Statanulocyathus oosthuizeni sp. nov.

Diagnose

Calices à 2 murailles, cloisons et planchers poreux. La muraille externe a des pores recouverts de bractées; la muraille interne est principalement cons-



6b



6a

Fig. 6a. *Erugatocyathus* sp., SAM-K4495 B-17a. Coupe transversale, × 20.
Fig. 6b. ?*Didymocyathus* sp., SAM-K4495 A-13a.

tituée par des pores recouverts par des bractées, un par intersept; ces bractées se soudent périodiquement pour former un anneau complet, au niveau de chaque plancher.

Les cloisons et les planchers sont normalement poreux.

Discussion

Il est probable que nous ayions affaire à des faux anneaux formés par la fusion et le développement plus important des bractées qui soulignent les pores internes. Ce caractère a précédemment été décrit dans différents genres (*Cadniacyathus* R. & J. Bedford, *Tennericyathus* Rozanov, *Denaecyathus* Zhuravleva). L'auteur (Debrenne, 1974*b*) ne considère pas que ces formations soient de vrais anneaux. La forme découverte et décrite ici montre que ces fusions en anneaux peuvent être périodiques et que la muraille principale reste une muraille à canaux et bractées. C'est pourquoi ce nouveau genre est inclus dans la famille Porocoscinidae Debrenne et non pas Sigmocoscinidae R. & J. Bedford.

Statanulocyathus oosthuizeni sp. nov.

Fig. 7a–b

Holotype: SAM–K4495 A–7.

Matériel étudié: 1 exemplaire.

Description

Petits calices de 5 mm de diamètre, avec un intervallum de 1 mm de large, traversé de cloisons distantes entre elles de 0,21 mm et de planchers plus irréguliers répartis (de 0,54 mm à 1 mm). Le coefficient pariétal est de 12. La muraille externe a 2 rangées de pores par intersept, d'ouverture 0,12 mm, recouverts de bractées recourbées formant des cupules de 0,04 mm de hauteur au-dessus de la muraille dont l'épaisseur totale atteint 0,08 mm. La muraille interne comporte une rangée de pores par intersept, aplatis dans le sens de la hauteur et alignés horizontalement, ils sont soulignés de bractées. L'ensemble se présente comme un court tuyau en V, d'ouverture 0,12 mm et de largeur 0,16 mm; l'épaisseur du squelette de ces éléments ne dépasse pas 0,03 mm. Au niveau de chaque plancher se construit une formation annulaire large et épaisse (0,26 mm) recourbée vers le haut.

Il semble que les systèmes poreux des cloisons et des planchers soient les mêmes (pores: 0,03 mm, linteaux: 0,07 mm).

Famille **Sigmocyathidae** Krasnopeeva, 1955

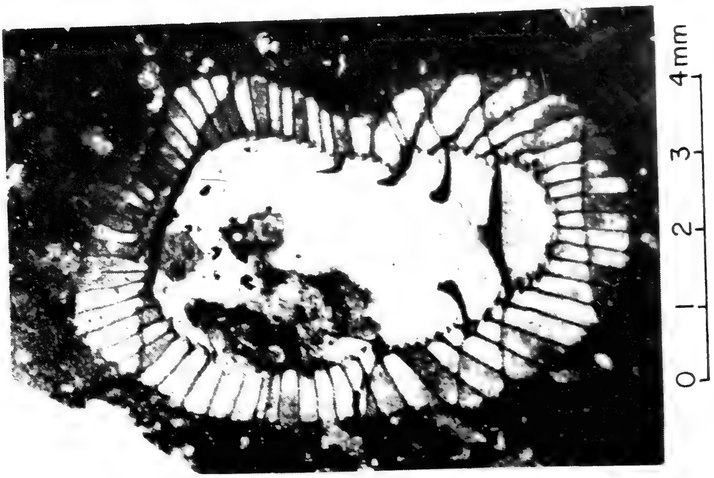
Genre *Didymocyathus* Debrenne & Rozanov, 1972

Espèce-type: Didymocyathus hillae Debrenne & Rozanov, 1972.

Diagnose

Calices à 2 murailles annulaires, cloisons et planchers poreux.

7a



7b

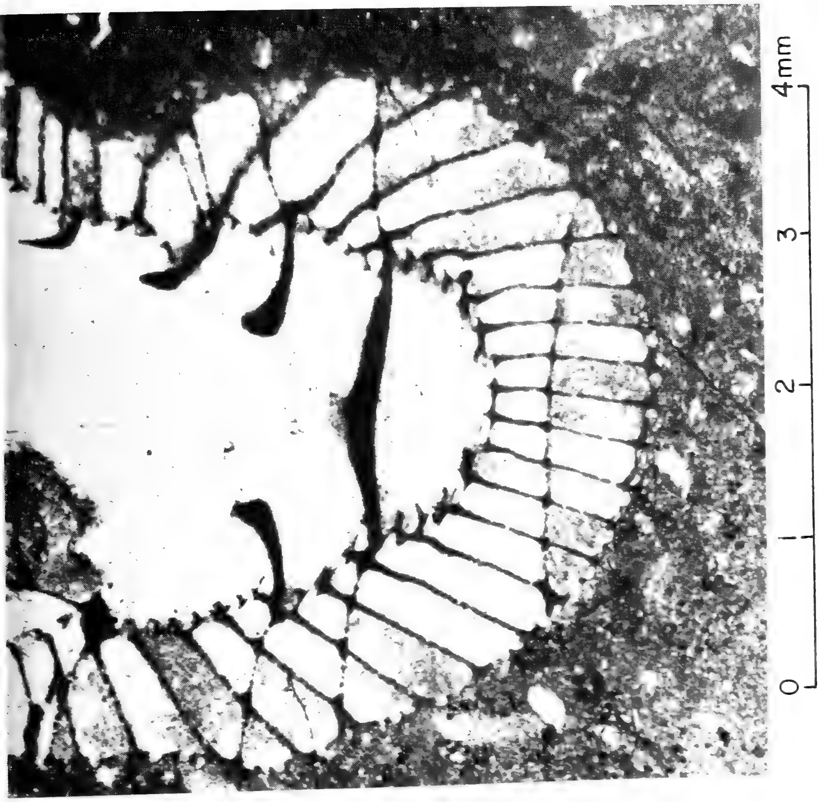


Fig. 7a. *Statanulocyathus oosthuizeni* gen. et sp. nov., SAM-K4495 A-7. Coupe transversale oblique, × 10.
Fig. 7b. *Statanulocyathus oosthuizeni* gen. et sp. nov., SAM-K4495 A-7. Détail des murailles.

Affinités

Diffère de *Sigmocyathus* par la porosité des murailles.

Répartition

Jusqu'à maintenant seulement Ajax Mine (Australie).
Afrique du Sud?

?*Didymocyathus* sp.

Fig. 6b

Un exemplaire: SAM–K4495 A–13a.

Description

Fragment d'une coupe transversale oblique permettant d'observer l'amorce des anneaux des murailles, les cloisons et les planchers poreux.

Diamètre: 10 mm environ, intervallum: 1,5 mm, coefficient intervallaire: 0,15, interseptum: 0,65 mm, chambres interseptales: 1/2,3.

La largeur des murailles est de 0,4 mm, l'ouverture entre les anneaux de 0,01 mm, l'épaisseur de l'anneau varie, elle s'amincit vers la terminaison libre. Les cloisons sont perforées de 6 rangées de pores, 4 pores des planchers apparaissent dans la largeur de l'intersept.

Discussion

La petitesse et la rareté du matériel ne nous a pas permis de mettre indubitablement en évidence la présence d'anneaux externes, tels qu'ils sont suggérés par la coupe observée. Cependant les structures visibles sont très nettement en faveur de cette hypothèse. Les formes de *Didymocyathus* connues à ce jour sont de grande taille (jusqu'à 62 mm); les calices jeunes ou plus petits ne sont pas connus ce qui ne permet pas d'identifier la forme d'Afrique du Sud aux espèces d'Australie.

Famille **Archaeopharetridae** Debrenne, 1970

Genre *Archaeopharetra* R. & W. R. Bedford, 1936

Espèce-type: Archaeopharetra typica R. & W. R. Bedford, 1936.

Diagnose

Petits calices à muraille externe imperforée, muraille interne assez tardivement différenciée. L'intervallum comporte des éléments squelettiques irrégulièrement disposés et du tissu vésiculeux en lames horizontales.

Affinités

Proche de *Bicyathus* Vologdin qui pourrait être un synonyme récent d'*Archaeopharetra* Bedford.

Archaeopharetra cf. *typica* R. & W. R. Bedford, 1936

Fig. 8a

1936—*Archaeopharetra typica* R. & W. R. Bedford: 17, pl. 17 (fig. 75).
1937—*Archaeopharetra typica* R. & W. R. Bedford.—R. & J. Bedford: 30–31, pl. 29 (fig. 120A–B).
1970—*Archaeopharetra typica* R. & W. R. Bedford.—Debrenne: 29.
1974*a*—*Archaeopharetra typica* R. & W. R. Bedford.—Debrenne: 195–196, fig. 3a–b.

Holotype: South Australian Museum P 969.

Matériel étudié: un exemplaire.

Description

Petit calice (4 mm) à cavité centrale étroite (0,5 mm). L'épaisseur de la muraille externe (0,15 mm) et celle des barres intervallaires (0,10 mm) sont inférieures à celle de l'espèce australienne.

Famille **Chouberticyathidae** Debrenne, 1974

Genre *Chouberticyathus* Debrenne, 1964

Espèce-type: Chouberticyathus clatratus Debrenne, 1964: 208, pl. 32 (figs 1–7).

Diagnose

Calices à muraille externe compacte, striée horizontalement, muraille interne simplement poreuse. L'intervallum est traversé de barres cylindriques horizontales disposées le plus souvent radialement et reliées par des barres obliques horizontales ou verticales. Tissu vésiculeux parfois présent.

Répartition

Maroc, Espagne, Australie.

Chouberticyathus cf. *fragilis* (R. & W. R. Bedford), 1936

Fig. 8b

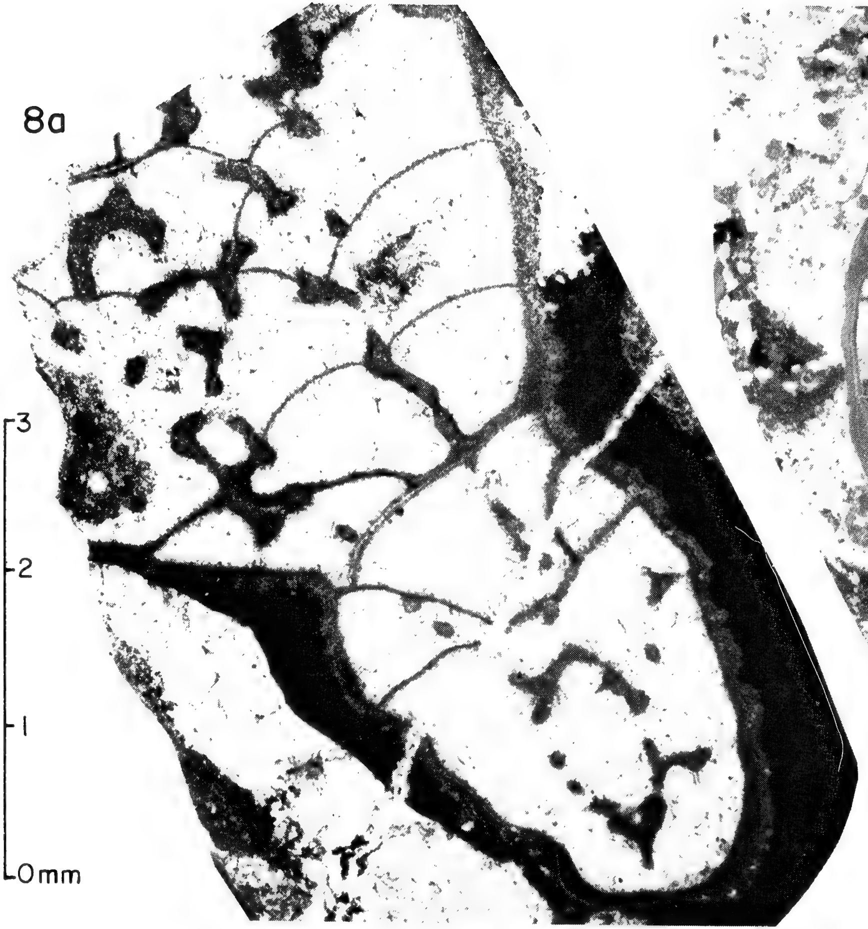
1936—*Dictyocyathus fragilis* R. & W. R. Bedford: 13, pl. 11 (fig. 57).
1964—*Chouberticyathus fragilis* (R. & W. R. Bedford).—Debrenne: 208.
1974*a*—?*Chouberticyathus fragilis* (R. & W. R. Bedford).—Debrenne: 192–193, fig. 2.

Holotype: South Australian Museum P. 945 (59).

Matériel étudié: 4 calices.

Description

Petits calices de 4 mm de diamètre, avec intervallum de 0,7–0,8 mm traversé de barres cylindriques horizontales radiales. La muraille externe compacte est épaisse et présente une structure feuilletée (0,20 mm). La muraille interne est grossièrement poreuse (diamètre 0,3 mm).



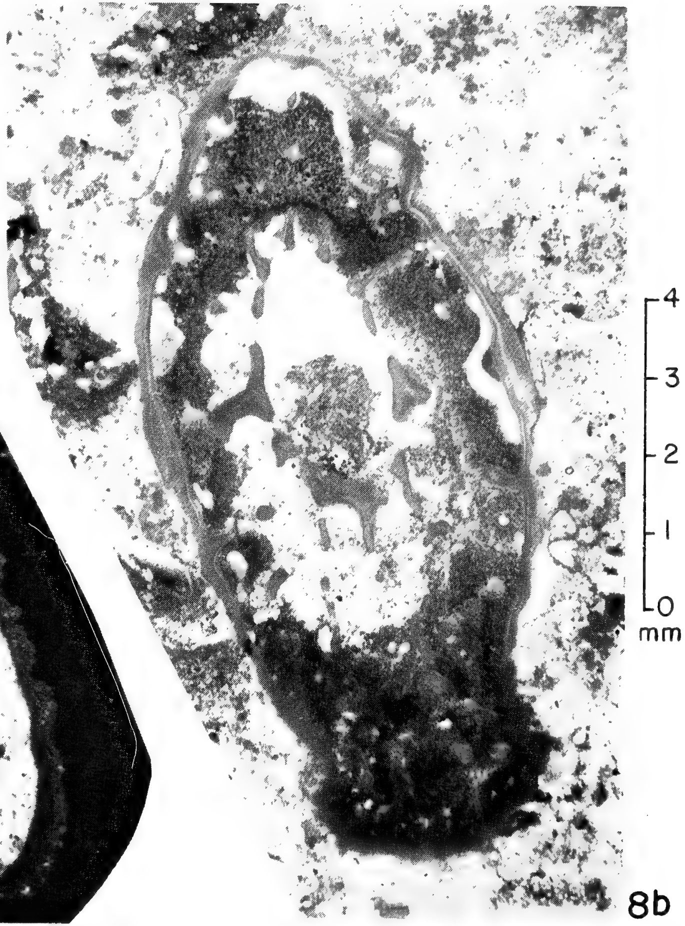


Fig. 8a. *Archaeopharetra* cf. *typica* R. & W. R. Bedford, SAM–K4495 B–15a. Coupe longitudinale oblique, × 20.
Fig. 8b. *Chouberticyathus* cf. *fragilis* R. & W. R. Bedford, SAM–K4495 A–6L. Coupe longitudinale oblique, × 10.

Discussion

Par la taille et la répartition des éléments squelettiques cette forme se rapproche de l'espèce australienne *C. fragilis* (R. & W. R. Bedford). L'attribution générique dans les 2 cas est faite avec réserve, la rareté et la petitesse du matériel ne permettant pas de mettre en évidence les relations des structures intervallaires.

Répartition

Australie du Sud, Afrique du Sud.

Famille **Protopharetridae** Vologdin, 1957

Genre *Protopharetra* Bornemann, 1884

Espèce-type: (Simon 1939) *Protopharetra polymorpha* Bornemann, 1884 (1887, pl. 5 (fig. 4)).

Diagnose

Calices souvent ramifiés, parfois solitaires. Muraille externe souvent imperforée ou, dans les grandes formes, constituée par l'ouverture du réseau intervallaire recouvert d'un pellis sans pores visibles. La muraille interne est une simple ouverture du réseau intertaenial. L'intervallum est rempli de plaquettes branchues reliées entre elles par leurs branches ou par des tigelles en position de synapticules. Elles peuvent s'orienter d'une façon privilégiée en pseudocloisons, surtout vers la muraille interne. Le tissu vésiculeux est abondant.

Répartition

Mondiale.

Protopharetra densa Bornemann, 1887

Fig. 9a

1887—*Protopharetra densa* Bornemann: 48, pl. 8 (figs 6c–7b–8).
1887—*Protopharetra polymorpha* Bornemann: pl. 5 (fig. 5).
1940*a*—*Protopharetra laqueata* Vologdin: 40–42, fig. 7.
?1959—*Syringocnema colevilensis* Greggs: 72–73, pl. 13 (figs 5–6).
1967—*Protopharetra densa* Bornemann.—Zhuravleva *et al.*: 90–91, pl. 39 (figs 5–6).

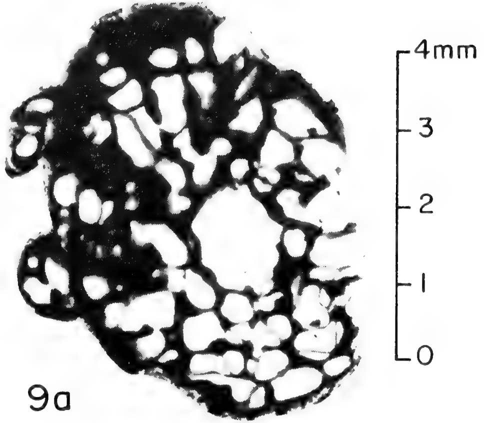
Holotype: lectotype Bornemann, 1887, pl. 8 (fig. 8).

Matériel étudié: 1 échantillon, SAM-K4495 A-3.

Description

Petits calices de 4 mm de diamètre à cavité centrale étroite (1 mm) mais libre d'éléments squelettiques et de tissu vésiculeux.

La muraille externe est compacte et porte de courts bourgeonnements. L'intervallum est rempli de plaquettes fortement liées en taeniae denses (distantes radialement de 0,3 à 0,4 mm) épaisses de 0,15 mm. La muraille interne a une ouverture par espace intertaenial de 0,2 mm.



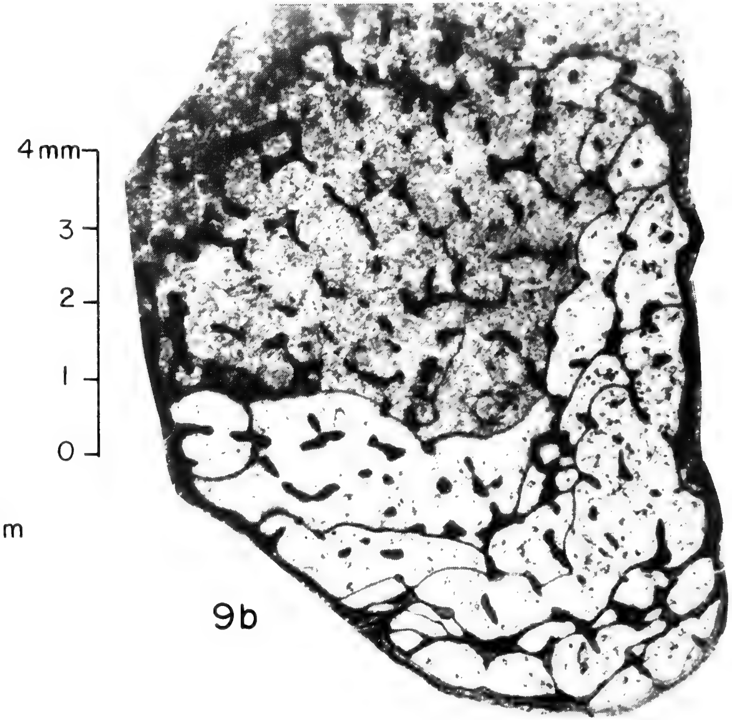


Fig. 9a. *Protopharetra densa* Bornemann, SAM-K4495 A-3T. Coupe transversale, × 10.
Fig. 9b. *Protopharetra grandicaveata* Vologdin, SAM-K4495 A-12a^1. Coupe oblique, × 10.
Fig. 9c. ?*Protopharetra pauciseptata* (Gordon), SAM-K4495 B-2. Fragment de coupe transversale.

Affinités

Très proche par la taille et les coefficients de la forme type.

Répartition

Sardaigne; URSS: Mongolie, Tuva, Altaï Sajan; Maroc; ?USA.

Protopharetra grandicaveata Vologdin, 1940

Fig. 9b

1940*b*—*Protopharetra grandicaveata* Vologdin: 42, pl. 3 (figs 1–2).
1960—*Protopharetra grandicaveata* Vologdin.—Zhuravleva *et al.*: 139, pl. 10 (figs 7–8).
1964—*Protopharetra grandicaveata* Vologdin.—Repina *et al.*: 239, pl. 26 (figs 5–6).
1964—*Protopharetra* aff. *grandicaveata* Vologdin.—Debrenne: 216, pl. 32 (figs 8–9).

Holotype non précisé.

Matériel étudié: 5 échantillons, SAM–K4495 A–12a–a^1, B–5aT, A–1, B–15a.

Description

Calices solitaires de forme conique irrégulière de 6 à 8 mm de diamètre; la cavité centrale est peu importante (1,5 mm maximum) souvent traversée de lames de tissu vésiculeux. La muraille externe est compacte, épaisse de 0,1 mm, sans pores visibles. L'intervallum, assez large, est rempli de plaquettes rares, grossièrement orientées verticalement et radialement avec quelques liaisons tangentielles. Leur épaisseur est du même ordre que celle de la muraille externe (0,08 mm—0,1 mm). La distance moyenne entre les plaquettes est de 0,4–0,5 mm. La muraille interne est simple, avec des ouvertures de 0,25 mm de diamètre. Le tissu vésiculeux est abondant et traverse l'intervallum et la cavité centrale.

Affinités

Tout à fait semblable aux formes de *Protopharetra* à rares éléments intervallaires groupées dans l'espèce *grandicaveata* Vologdin.

Répartition

URSS: Salair, Sajan oriental, Tuva, Kuzneck-Alatau; Maroc; Afrique du Sud.

?*Protopharetra pauciseptata* (Gordon), 1920

Fig. 9c

1920—*Archaeocyathus pauciseptatus* Gordon: 687, pl. 6 (figs 63–64).

Holotype: King's College S 148.

Matériel étudié: 1 exemplaire.

Description

Petits calices à taeniae presque droits vers la muraille interne et dissociés vers la muraille externe. Le diamètre atteint 5 mm avec un intervallum de 1,2 mm. La muraille externe, mal conservée par places, paraît compacte. La distance entre les pseudo-cloisons est de 0,4 mm. La muraille interne est simple, à un seul pore par espace intertaenial (diamètre 0,4 mm).

Le tissu vésiculeux est peu abondant ici.

Affinités

Il est difficile de déterminer cet unique calice. La présence de taeniae radiales presque complètes éloigne cette forme des *Protopharetra* typiques; le faible développement du tissu vésiculeux est la seule différence marquante avec l'exemplaire décrit par Gordon, que l'on doit également rapporter avec doute au genre *Protopharetra*. Sur des formes de si petite taille il est difficile d'être parfaitement affirmatif quant à leur position systématique.

Répartition

Antarctique (Weddel Sea); Afrique du Sud.

?Famille **Flindersicyathidae** R. & J. Bedford, 1939

Genre *Andalusicyathus* Perejon MS

1939—*Archaeocyathellus* (*Archaeofungia*) Simon: 76.
1964—*Spirocyathella* Vologdin.—Debrenne: 137.

Espèce-type: Archaeocyathellus (*Archaeofungia*) *andalusicus* Simon, 1939, Cordoue, Las Ermitas (Espagne.)

Diagnose (d'après Perejon, Manuscrit)

'Calices solitaires ou coloniaux de forme cylindrique ou légèrement conique, avec expansion basale pour la fixation.

Muraille externe simple avec 3 rangées longitudinales de pores par intersept, pouvant présenter de légères ondulations longitudinales. Intervallum avec septes (ou pseudo-septes) à larges pores généralement allongés dans le sens longitudinal et réunis par des synapticules qui se situent au voisinage de la muraille externe qui semblerait avoir un pore par intersept.

Il existe du tissu vésiculeux localisé dans des zones plus restreintes et qui détermine une modification de la fossilisation des éléments squelettiques et l'apparition d'un pellis.'

L'auteur considère en outre que les espèces (*Spirocyathus*) *latus* Vologdin et (*Spirocyathus*) *extremus* Vologdin tombent en synonymie avec *andalusicus* Simon.

Répartition

URSS: Sanachtygkol; Espagne: Las Ermitas; Afrique du Sud.

Andalusicyathus cooperi sp. nov.

Fig. 10

Holotype: SAM–K4495 A–5.

Description

Calices à large cavité centrale et intervallum construit par des pseudo-cloisons largement perforées reliées par des synapticules et quelques lames de

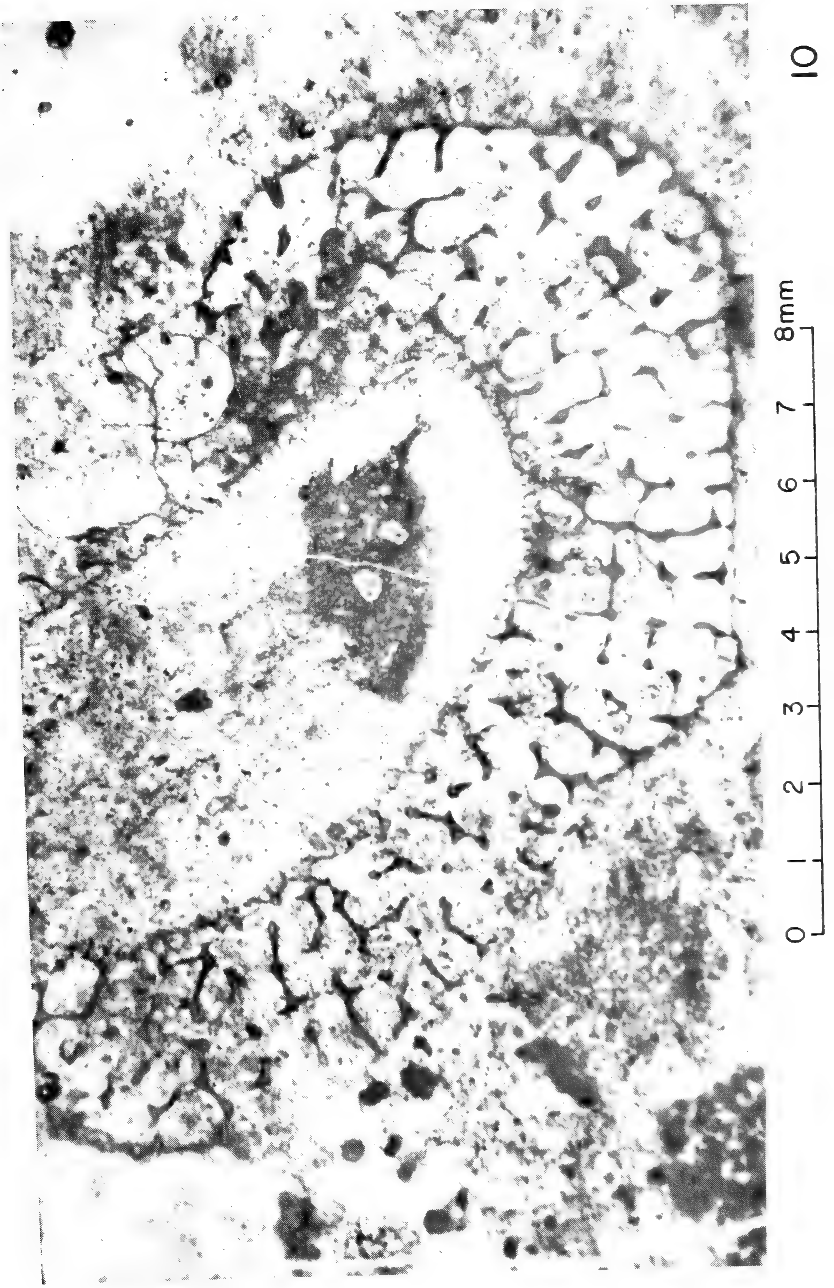


Fig. 10. *Andalusicyathus cooperi* sp. nov., SAM-K4495 A-5. Coupe transversale oblique, × 10.

tissu vésiculeux. Le diamètre est de 10 à 11 mm, l'intervallum de 2,5 mm. La muraille externe est perforée de 2 pores par espace intertaenial (diamètre; 0,10 mm, linteaux: 0,10 mm) souvent recouverte vers l'extérieur d'une membrane de même nature que le tissu vésiculeux. La muraille interne est indépendante du réseau intervallaire et comporte 2 pores en quinconce entre 2 pseudo-septes (diamètre; 0,21 mm, linteaux: 0,05 mm) pouvant porter de courtes épines. L'espace entre 2 pseudo-septes est de 0,5 mm., l'épaisseur des plaquettes de 0,08 mm.

Affinités

Cloisons moins rapprochées et cavité centrale plus large que dans *andulusicus* et tissu vésiculeux plus abondant.

Ordre des SYRINGOCNEMIDIDA

Définition: Intervallum à loculi prismatiques radiaux poreux.

Discussion

La définition de tubes poreux intervallaires, de section polygonale et de disposition radiaire, n'a jusqu'ici pas été donnée avec une précision suffisante et bien souvent, on a confondu sous ce terme des constructions de types différents.

En effet, l'interprétation de cloisons ondulées reliées par des synapticules aplaties (type *Pycnoidocyathus decipiens*) comme des tubes quadratiques a souvent été proposée. Ces 'tubes' diffèrent essentiellement de ceux des Syringocnemidida par leur forme (section quadratique), leur porosité (un pore par côté), leur orientation (oblique vers l'extérieur et le haut, très rarement subhorizontale). Enfin, et c'est l'argument majeur, ces tubes évoluent plus ou moins rapidement au fur et à mesure de la croissance de l'individu en pseudo-cloisons radiales planes (type *Pycnoidocyathus synapticulosus*). L'évolution des tubes prismatiques des Syringocnemidida en pseudo-cloisons radiales n'est jamais observée.

C'est pourquoi il faut reprendre avec soin l'étude de la composition de cet ordre:

Le genre *Syringsella* Krasnopeeva, 1961 est problement un synonyme récent d'*Archaeofungia* Taylor, 1910, sous réserve de l'examen de la porosité des cloisons.
Le genre *Batenevia* Krasnopeeva, 1961 est proche de *Flindersicoscinus* Debrenne, 1970 dont il diffère par l'acquisition d'une muraille externe à double porosité.
Le genre *Tubocyathus* Vologdin, 1940 est à rapprocher des Pycnoidocyathidae. Malheureusement sa position systématique à l'intérieur du groupe ne peut être précisée actuellement, la constitution des murailles n'étant pas connue en détail. D'après la figuration il y aurait peut-être une enveloppe microporeuse externe et interne.

Beticocyathus Simon, 1939, genre par ailleurs caduc car les murailles ne sont pas conservées, n'est pas non plus une forme à loculi prismatiques, mais à taenia, pseudo-cloisons ondulées et synapticules.

Syringocyathus Vologdin, 1940 a fait l'objet d'une étude particulière par I. T. Zhuravleva (1960: 42–46) qui considère ce genre comme appartenant aux Regulares; l'intervallum comporte des cloisons radiales régulièrement perforées reliées non par des synapticules simples, mais par des plaquettes de liaison perforées, délimitant des loges verticales incomplètes.

Par contre doivent être maintenus dans l'ordre des Syringocnemidida les familles et genres suivants:

Famille des Syringocoscinidae Vologdin & Jasmir, 1969
muraille externe simple } *Syringocoscinus* Vologdin-Jasmir
muraille interne simple }

Famille des Pseudosyringocnemididae fam. nov.
muraille externe ? simple ou 1 tumulus } *Pseudosyringocnema*
muraille interne: ? un canal oblique } Handfield, 1971
1 pore par côté du tube intervallaire

Famille des Fragilicyathidae fam. nov.
muraille externe à canaux horizontaux } *Fragilicyathus* Beljaeva, 1969
muraille interne à canaux coudés }
tubes à plusieurs pores par côté

Famille des Syringocnemididae Taylor (Debrenne emend.)
muraille externe à crible multiperforé } *Syringocnema* Taylor
muraille interne: un canal coudé }

Famille **Pseudosyringocnemididae** fam. nov.

Genre *Pseudosyringocnema* Handfield, 1971

Espèce-type: Pseudosyringocnema uniporus Handfield, 1971: 76, pl. 15 (figs 3a–c, 4–5).

Diagnose originale

'The cups may be solitary or colonial with the intervallum containing hexagonal tubules. The tubules sides have only a single row of pores. The inner wall has oblique 'S' shaped pores tubes, 2 or 3 per tubule in vertical arrangement.'

Discussion

L'examen des figurations plate 15, figures 3a, 3c suggère le fait que les tubules intervallaires se recourbent vers le bas, comme c'est le cas dans toutes les formes à tubes hexagonaux, et se rétrécissent jusqu'à se raccorder à un seul canal interne et non 2 ou 3; cette hypothèse est confirmée par la section oblique figure 3a oú le raccord de chaque tube intervallaire se fait avec un canal correspondant de la muraille interne.

La diagnose proposée doit être ainsi modifiée: calices dont l'intervallum est constitué de tubules dont les côtés sont perforés d'une seule rangée de pores. Muraille externe mal définie, probablement un pore au sommet d'un tumulus. Muraille interne un canal par tubule, dirigé vers le centre et le haut de la cavité centrale.

Affinités

Diffère de *Syringocnema* par la porosité des tubes intervallaires. Se rapproche de certaines espèces de *Pycnoidocyathus* mais ne forme jamais de pseudo-cloisons radiales.

Pseudosyringocnema cf. *gracilis* Gordon, 1920

Fig. 11a

1920—*Syringocnema gracilis* Gordon: 699, pl. 4 (fig. 43).
1965—*Syringocnema gracilis* Gordon. Hill: 136, pl. 11 (figs 17–18).

Holotype: King's College, Londres; syntypes S 108—S 112—S 115—S 118—S 120—S 121.

Matériel étudié: 4 calices.

Description

Petits calices de 6 à 7 mm de diamètre avec un intervallum de 2 mm de large. Les tubes hexagonaux sont perforés d'une rangée de pores de 0,2 mm de diamètre. Les alvéoles ont une ouverture de 0,5 mm dans leur partie médiane. Les tubes se rétrécissent et se raccordent aux pores de la muraille interne dont le diamètre est de 0,2 mm. Les tubes sont fermés extérieurement par une muraille bombée au sommet de laquelle se trouve probablement un pore, mais cette ouverture n'a pas été observée.

Discussion

La forme décrite ici diffère de l'espèce-type et des échantillons rapportés à l'espèce par Hill (1965) par un intervallum plus large pour un même diamètre (2 mm contre 1,5 mm) mais les autres éléments squelettiques ont des mesures comparables, notamment les tubes intervallaires.

?*Pseudosyringocnema* cf. *uniserialis* (Hill), 1965

Fig. 11b–c

1965—*Flindersicyathus uniserialis* Hill: 123, pl. 11 (figs 1–2).

Holotype: British Museum (Natural History) S 8441.

Matériel étudié: 3 fragments.

Description

Fragment d'un calice conique assez haut (12 mm) avec un intervallum relativement étroit (2,5 mm pour un diamètre de 5 mm). La muraille externe n'est pas conservée. Les alvéoles de l'intervallum ont un diamètre de 0,4 mm

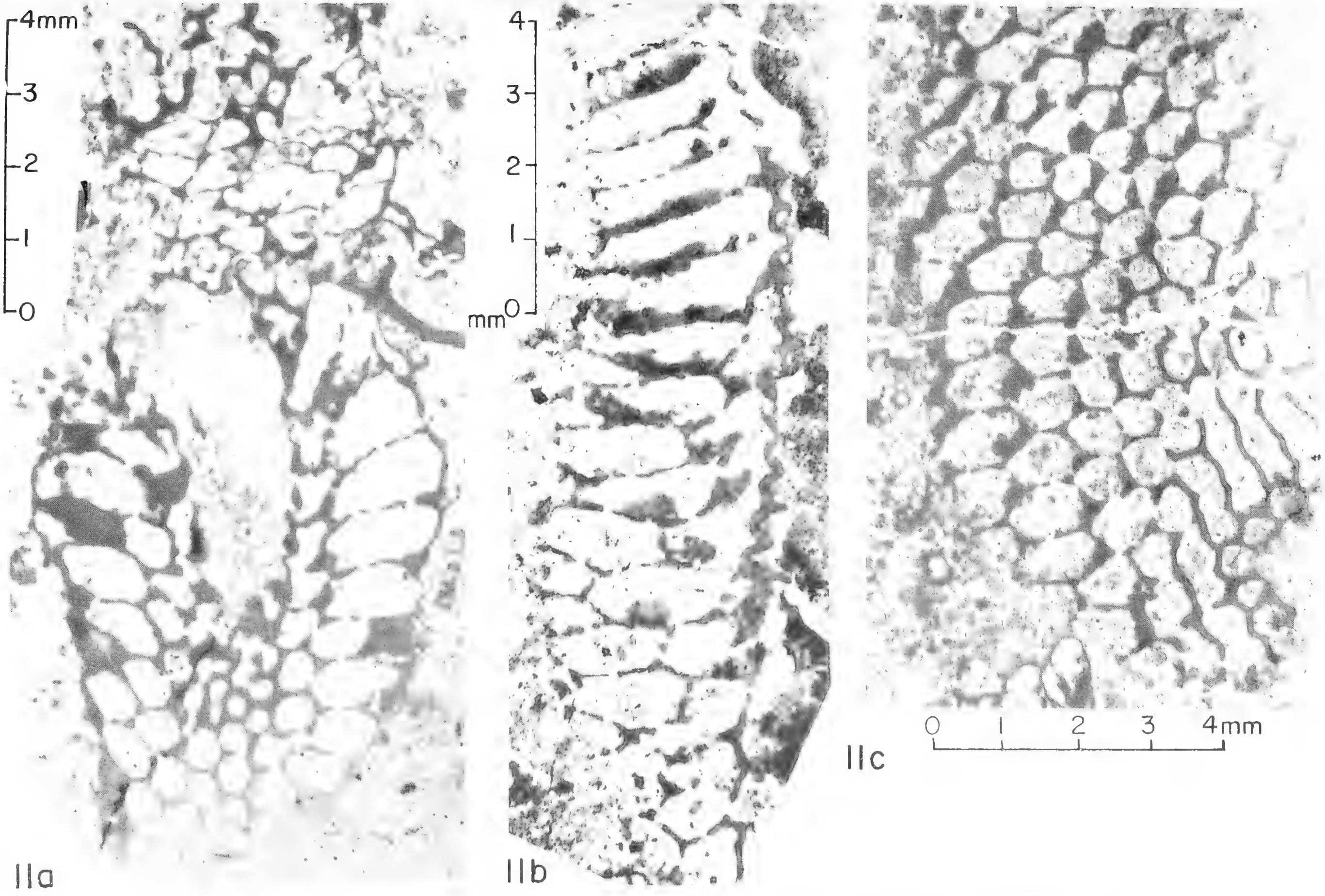


Fig. 11a. *Pseudosyringocnema* cf. *gracilis* (Gordon), SAM-K4495 A-5. Coupe transversale, × 10.
Fig. 11b. *Pseudosyringocnema* cf. *uniserialis* (Hill), SAM-K4495 A-13a¹. Coupe longitudinale, × 10.
Fig. 11c. *Pseudosyringocnema* cf. *uniserialis* (Hill), SAM-K4495 A-13a. Coupe à travers l'intervallum, × 10

L'épaisseur des parois est de 0,07 mm percée de pores d'un diamètre de 0,15 mm. La muraille interne a un court tube d'ouverture 0,20 mm.

Discussion

L'appartenance de l'espèce *uniserialis* au genre *Flindersicyathus* comme le démontre Hill (1965: 123–124) repose sur la forme quadratique et non hexagonale des tubes intervallaires. Structure difficile à mettre en évidence. La forme étudiée actuellement bien que légèrement plus petite, peut être comparée à *uniserialis* Hill; elle paraît avoir des loculi hexagonaux et non quadratiques. Mais le matériel est trop rare et trop fragmentaire pour que l'on puisse décider de trancher ici le délicat problème des formes à loculi prismatiques dans l'intervallum.

CONCLUSIONS

Les résultats de l'étude paléontologique sont reportés dans le Tableau 1.

Sur les 18 espèces décrites 10 sont communes avec l'Antarctique, 8 avec l'Australie et 5 avec les deux.

Ce tableau appelle un certain nombre de précisions:

(1) les espèces les plus fréquentes sont *Erugatocyathus scutatus* (Hill), *Pseudosyringocnema* cf. *gracilis* (Gordon), *Pseudosyringocnema* cf. *uniserialis* (Hill), espèces connues dans l'Antarctique—et *Thalamocyathus tectus*, connue en Antarctique et en Australie.

(2) Les espèces des genres *Protopharetra* et *Archaeopharetra* sont cosmopolites et ne peuvent apporter d'arguments décisifs dans ce cas.

(3) La présence de formes à planchers pectinés (*Thalamopectinus* Debrenne) est très importante; si l'on suit l'hypothèse émise récemment (Debrenne *et al* 1973: 33, fig. 4) selon laquelle les planchers pectinés seraient liés aux climats équatoriaux, les blocs erratiques de Dwyka viendraient de la zone équatoriale Australo-Antarctique.

(4) La découverte d'espèces et même de deux genres nouveaux peut s'expliquer, non par l'endémicité de ces taxons, mais par le caractère sporadique et incomplet des récoltes faites en Antarctique (dragage, moraines, prises en place limitées en nombre) et par la rareté actuelle des localités étudiées en Australie, dont la faune d'Archéocyathes connue est, en fait, restreinte à la région d'Ajax Mine. Il est probable que ces nouvelles formes, rares (1 ou 2 exemplaires découverts ici) pourront être mises en évidence plus tard dans les régions antarctiques et australiennes. On peut affirmer, grâce à la similitude des espèces que les blocs erratiques des tillites de Dwyka proviennent de la région antarctique.

L'hypothèse d'un continent austral, futur Gondwanaland, en bordure duquel se développaient les Archéocyathes, peut trouver ici une justification supplémentaire.

Tableau 1

	Australie	*Antarctique*	*Afrique du Sud*	*Autres localités*
Stapicyathus incisus (Hill) . .	+	+	+	
Thalamocyathus tectus Debrenne	+	+	+	
Flexanulus oosthuizeni sp. nov. .	○	○	+	
?*Ladaecyathus*	+	+	+	
Thalamopectinus arterialis Debrenne	+	+	+	?URSS
Erugatocyathus scutatus (Hill) .	○	+	+	
?*Erugatocyathus* sp.	?	?	+	
Statanulocyathus oosthuizeni sp. nov.	○	○	+	
?*Didymocyathus* sp.	+	○	+	
Archaeopharetra cf. *typica* (Born.)	+	○	+	?URSS
Chouberticyathus cf. *fragilis* (Bed.)	+	○	+	
Protopharetra polymorpha Bornemann	+	+	+	mondiale
Protopharetra densa Bornemann .	○	?	+	Sardaigne, Maroc, URSS, ?USA
Protopharetra grandicaveata Vologdin.	○	○	+	URSS, Maroc
?*Protopharetra pauciseptata* Gordon	○	+	+	
Andalusicyathus cooperi sp. nov. .	○	○	+	
Pseudosyringocnema cf. *gracilis* (Gordon)	○	+	+	
Pseudosyringocnema cf. *uniserialis* (Hill)	○	+	+	

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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 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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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.:

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(continued inside back cover)

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A NEW SPECIES OF *MEIOSQUILLA* (CRUSTACEA, STOMATOPODA) FROM SOUTH AFRICA

By

RAYMOND B. MANNING

Cape Town Kaapstad

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A NEW SPECIES OF *MEIOSQUILLA* (CRUSTACEA, STOMATOPODA) FROM SOUTH AFRICA

By

RAYMOND B. MANNING

Smithsonian Institution, Washington, D.C., U.S.A.

(With 1 figure)

[*MS accepted 4 March 1975*]

ABSTRACT

Meiosquilla barnardi sp. nov. from Natal, South Africa, is described and a key to Mediterranean and African species of *Meiosquilla* is provided.

CONTENTS

INTRODUCTION

The new species of *Meiosquilla* reported below was first recorded from South Africa by Barnard (1950) who identified the single specimen available to him with the Mediterranean *Squilla desmarestii* Risso. I followed Barnard in identifying additional material from off Durban with Risso's species (Manning 1969), then known as *Meiosquilla desmarestii*. Subsequently, in studying material of other species of *Meiosquilla* from West Africa, which resulted in the description of two new species (Manning 1974), I came to the conclusion that the South African *Meiosquilla* represented a new species which is described below.

DESCRIPTION

Meiosquilla barnardi sp. nov.

Fig. 1

Squilla desmarestii Barnard, 1950: 842, fig. 1a.
Meiosquilla desmarestii Manning, 1969: 13.

Holotype

1 ♂, total length 30 mm; Cape Natal, South Africa; SAM–A1328.

Paratypes

1 ♂, total length 26 mm; 1 juvenile, total length 15 mm; 1 fragment, carapace length 6,4 mm; off Durban, Natal; 29.37,5S, 31.33E; 175–200 metres, sand, mud; 8 September 1964; University of Cape Town.

1 ♀, total length 27 mm; data same; USNM 125361.

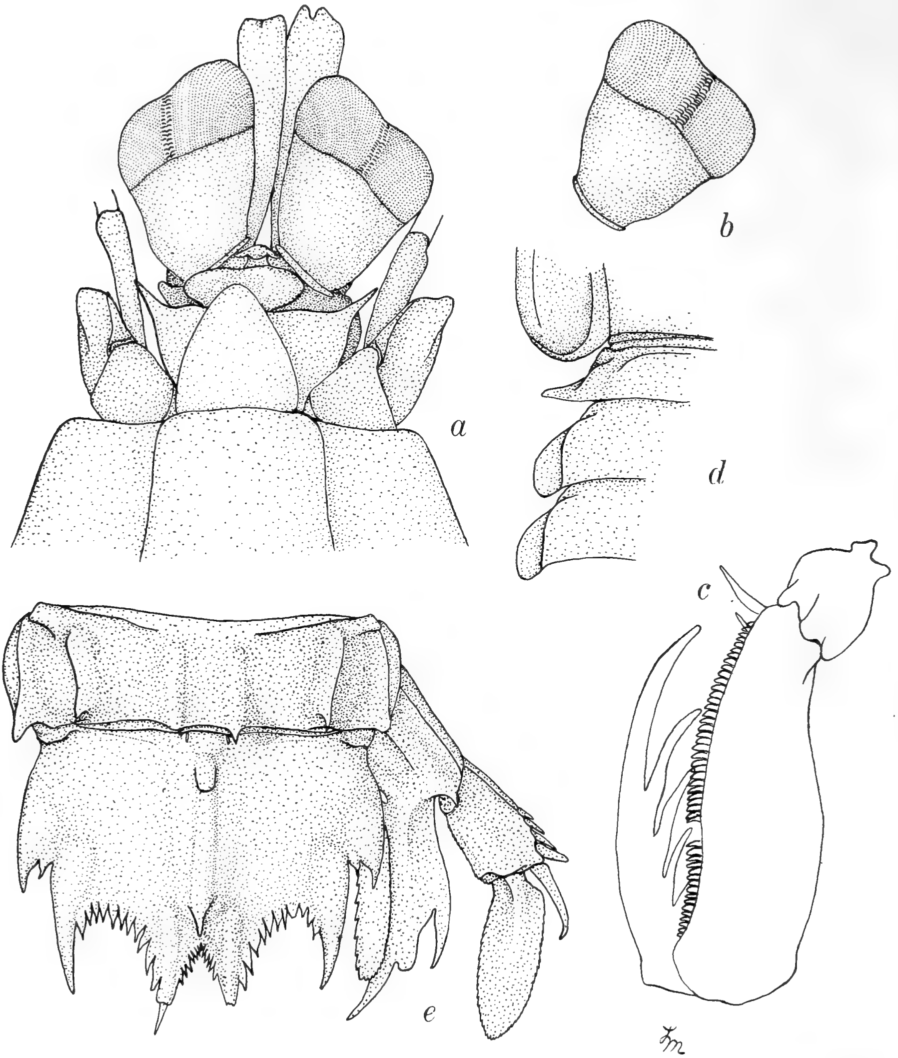

Fig. 1. *Meiosquilla barnardi* sp. nov. Female paratype, TL 27 mm: *a*, anterior portion of body; *b*, eye. Male holotype, TL 30 mm: *c*, outline of raptorial claw; *d*, lateral processes of fifth, sixth, and seventh thoracic somites; *e*, sixth abdominal somite, telson, and uropod. (Setae omitted in all figures.)

Description

Eye large, triangular, cornea bilobed, set almost transversely on stalk. Ocular scales subtruncate. Anterior margin of ophthalmic somite rounded. Antennal protopod subequal to or slightly longer than carapace. Rostral plate cordiform, length and width subequal, apex rounded. Carapace smooth, lacking spines or carinae except for short reflected marginals and laterals on posterior fourth. Dactylus of raptorial claw with 5 teeth. Propodus of claw shorter than carapace, greatest depth near midlength, not markedly tapering distally. Dorsal ridge of carpus of claw undivided, terminating in rounded lobe. Mandibular palp absent; 4 epipods present. Exposed thoracic somites lacking submedian carinae, intermediates present on sixth to eighth somites. Lateral process of fifth thoracic somite a slender, oblique, laterally-projecting lobe, rounded laterally; sharp ventral spine present under each lateral process. Lateral processes of sixth and seventh thoracic somites broadly rounded. Ventral keel of eighth thoracic somite slender, erect, apex rounded. Abdomen lacking submedian carinae on anterior 5 somites, abdominal carinae spined as follows: submedian 6, intermediate 5–6, lateral 5–6, marginal 4–5. Telson with 3 pairs of marginal teeth, bases inflated in male holotype, prelateral lobes absent; submedian teeth with movable apices; carinae of submedian teeth short; denticles sharp, 6–8, 10–11, 1; ventral surface of telson with short postanal keel. Uropodal exopod broad, distal segment longer than proximal; proximal segment with 5 movable spines on outer margin, distalmost not extending past midlength of distal segment. Basal prolongation of uropod with inner margin crenulate, not armed with spinules, inner spine with low, rounded lobe on outer margin.

Colour

Completely faded in all specimens examined.

Size

Males, total length 26–30 mm; only known female, total length 27 mm; juvenile, total length 15 mm. Other measurements of male holotype, total length 30 mm; in mm: carapace length *ca* 7 (damaged); cornea width (damaged); length antennular peduncle 7,6; length, width rostral plate, 2,4; 2,4; raptorial claw propodus length, depth 6,6; 2,0.

Discussion

Meiosquilla barnardi is the fifth species of the genus to be recorded from localities outside of the Americas. It resembles the Mediterranean and West African species and differs from the American species of the genus in having 5 rather than 4 teeth on the dactylus of the raptorial claw (the number 4 used by me (1969: 4) for *M. barnardi* in a key to South African species was a *lapsus*). It differs from *M. pallida* (Giesbrecht) and *M. calypso* Manning and resembles *M. africana* Manning and *M. desmarestii* (Risso) in having a short antennular peduncle; in *M. calypso* and *M. pallida* the antennular peduncle is longer than the carapace and rostral plate combined. It differs from *M. africana* in lacking erect spinules on the inner margin of the basal prolongation of the uropod. It agrees with *M. africana* and differs from *M. desmarestii* in having a broad propodus on the raptorial claw. The propodus in both *M. africana* and *M. barnardi* does not markedly taper distally whereas the propodus in *M. calypso M. desmarestii*, and *M. pallida* is broadest near its midlength and markedly tapers distally.

Meiosquilla barnardi appears to mature at a smaller size than *M. desmarestii.*

The holotype of the new species shows marked swellings at the bases of the teeth of the telson, a secondary sexual characteristic that does not become apparent in specimens of *M. desmarestii* smaller than 50 mm in total length.

It is a pleasure to dedicate this species to Dr K. H. Barnard whose work on South African decapod and stomatopod crustaceans contributed so much to our knowledge of these animals.

The 5 species of *Meiosquilla* occurring in African waters are very similar morphologically and very difficult to distinguish without comparative material. The following key may help to separate them.

KEY TO MEDITERRANEAN AND AFRICAN SPECIES OF *MEIOSQUILLA*

1. Antennular peduncle as long as carapace and rostral plate combined 2
   Antennular peduncle shorter than or subequal to carapace in length 3
2. Lateral process of fifth thoracic somite parallel to body line, flattened dorsoventrally. Uropod with 5–6 movable spines on outer margin. (Propodus of claw with greatest depth at midlength) . . . . *M. pallida* (Giesbrecht)
   Lateral process of fifth thoracic somite obliquely flattened, appearing as slender lobe in dorsal view. Uropod with 8 spines on outer margin. (Propodus of claw with greatest depth at midlength) . . . . *M. calypso* Manning
3. Basal prolongation of uropod with 9–17 erect spinules on inner margin. (Propodus of claw with greatest depth distally) . . . . *M. africana* Manning
   Basal prolongation of uropod at most crenulate, unarmed on inner margin . . . 4
4. Propodus of claw slender, tapering distally, greatest depth at midlength *M. desmarestii* (Risso)
   Propodus of claw broad, not markedly tapering beyond midlength . *M. barnardi* sp. nov.

ACKNOWLEDGEMENTS

I thank Dr B. F. Kensley, South African Museum, for allowing me to study the specimen originally reported by Barnard (1950). The illustrations were prepared by my wife Lilly. My studies on stomatopods from the Indian Ocean have been supported by the Smithsonian Institution through its Research Awards Program.

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Manning, R. B. 1974. Stomatopod Crustacea. Campagne de la Calypso dans le Golfe de Guinée et aux Iles Principe, Sao Tome et Annobon (1956), et Campagne aux Iles du Cap Vert (1959) (suite).—*Annls Inst. océanogr., Monaco* **50** (1): 1–22.

6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., 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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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'. . . in *C. namacolus* (Fig. 10) . . .'

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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.

RAYMOND B. MANNING

A NEW SPECIES OF *MEIOSQUILLA* (CRUSTACEA, STOMATOPODA) FROM SOUTH AFRICA

VOLUME 67 PART 10 OCTOBER 1975 ISSN 0303-2515

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

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques.—*J. Conch., Paris* **88**: 100–140.

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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.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **67** Band
October **1975** Oktober
Part **10** Deel

FIVE SPECIES OF *JAEROPSIS* FROM THE SOUTHERN INDIAN OCEAN (CRUSTACEA, ISOPODA, ASELLOTA)

By

BRIAN KENSLEY

Cape Town Kaapstad

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By

Brian Kensley

South African Museum, Cape Town

(With 10 figures)

[*MS accepted 10 March 1975*]

ABSTRACT

Five species of *Jaeropsis* are figured and diagnosed. These include *J. waltervadi*, a new species from Walter's Shoal, and *J. beuroisi*, a new species from St Paul and Amsterdam Islands, as well as *J. paulensis* Vanhöffen from St Paul and Amsterdam Islands, and *J. curvicornis* (Nicolet) from Marion Island. The common intertidal South African species, which was previously misidentified, is given a new name, i.e. *J. stebbingi*.

CONTENTS

INTRODUCTION

Material of the genus *Jaeropsis* from the following sources necessitated this short report:

Two specimens from Walter's Shoal (33.13S, 43.51E) collected by the R/V *Anton Bruun* during the International Indian Ocean Expedition in 1964.

One specimen from Marion Island (46.53S, 37.52E) collected by the third South African Biological Expedition to the island in 1972–3.

Numerous specimens of two species from St Paul Island (38.44S, 77.30E) and Amsterdam Island (37.55S, 77.40E) collected by the French Expedition to these islands in 1970–2.

In addition, the species commonly found intertidally around both the west and east coasts of South Africa was found to be misidentified, and has been included in this report.

In the accompanying figures, dimensions are in millimetres.

DESCRIPTION OF MATERIAL

Family **Jaeropsidae**

Genus *Jaeropsis* Koehler

Jaeropsis waltervadi sp. n.

Figs 1–2

Diagnosis

Cephalon dorsally broadly convex, with frontal plate anteriorly slightly concave, lateral margins smooth. Lateral margins of pleotelson bearing 7 small

Ann. S. Afr. Mus. **67** (10), 1975: 367–380, 10 figs.

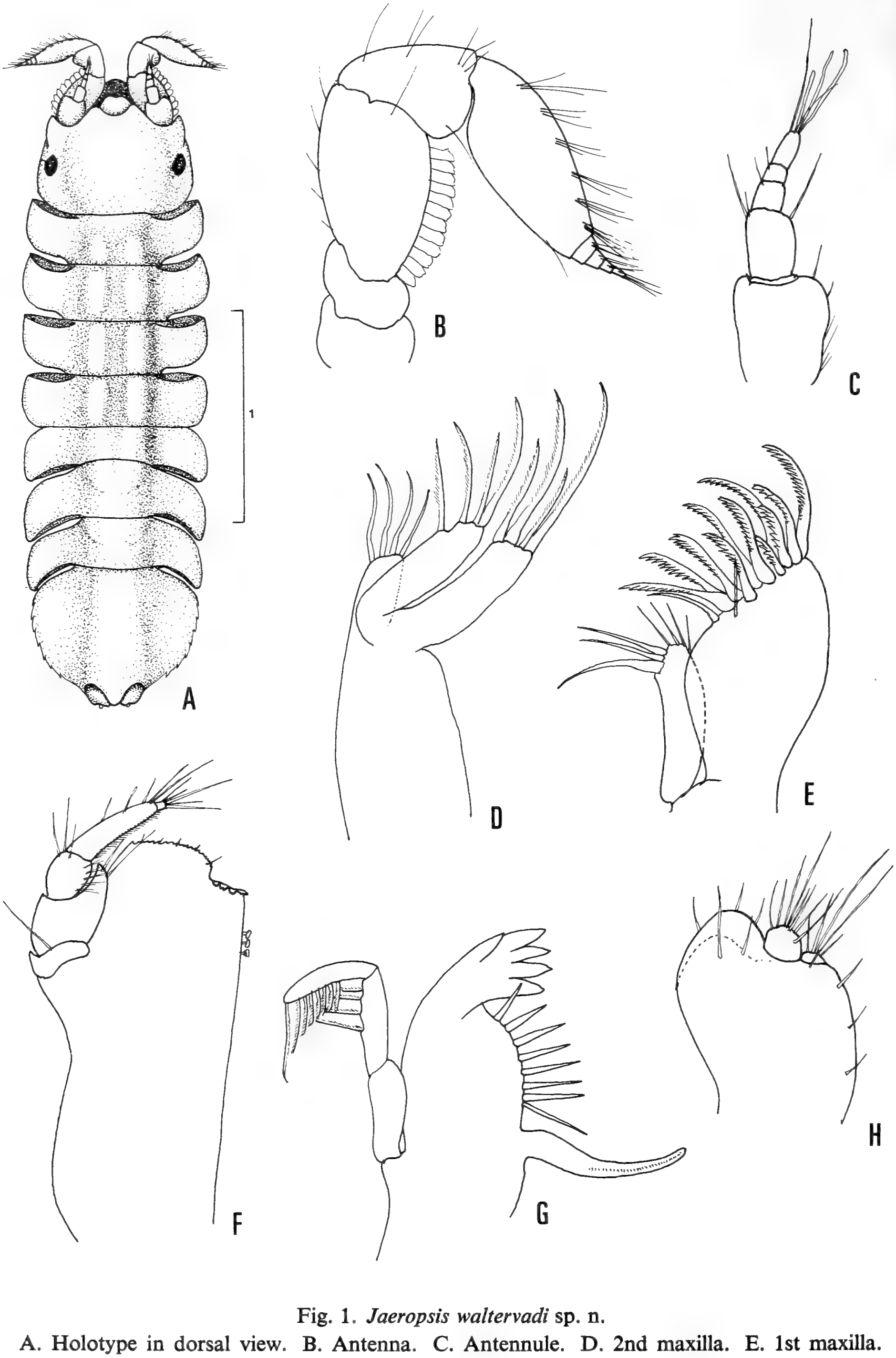

Fig. 1. *Jaeropsis waltervadi* sp. n.
A. Holotype in dorsal view. B. Antenna. C. Antennule. D. 2nd maxilla. E. 1st maxilla. F. Maxilliped. G. Mandible. H. Uropod.

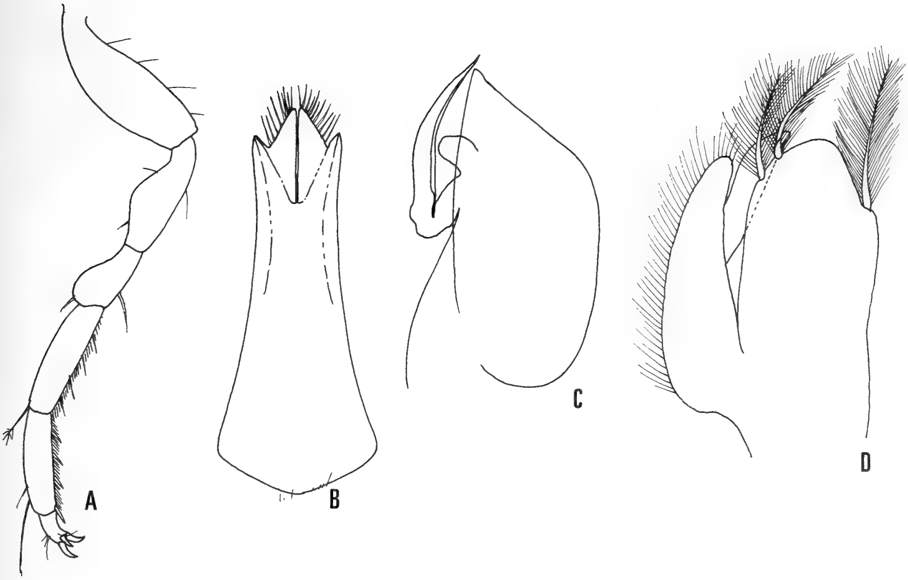

Fig. 2. *Jaeropsis waltervadi* sp. n.
A. VIIth peraeopod. B. 1st pleopod, ♂. C. 2nd pleopod, ♂. D. 3rd pleopod, ♂.

denticulations. Uropodal basis about as long as broad, inner distal angle rounded, unarmed, hardly extending beyond narrowly rounded pleotelsonic apex. Body with broadly rounded median raised area on pleotelson and Vth to VIIth pereional segments, becoming a double, more defined ridge on perieonal segments I to IV.

Material

Holotype SAM–A13646 ♂ 2,9 mm Walter's Shoal, 38–46 metres depth.
Paratype SAM–A13646 ♂ 2,4 mm Walter's Shoal, 38–46 metres depth.

Remarks

The median dorsal ridge, unarmed uropodal basis, and shape of the frontal plate of this species make it distinct from any previously described species of *Jaeropsis*.

Jaeropsis curvicornis (Nicolet)

Figs 3–4

Jaeropsis curvicornis (Nicolet), Menzies & Schultz, 1967: 174, figs 27–28 (complete synonymy).
non J. curvicornis: Barnard, 1914: 224; 1940: 494.

Diagnosis

Cephalon with frontal plate bearing small median point, lateral margins smooth. Lateral margins of pleotelson with single incision and stout seta. Uropodal basis longer than wide, with small hook on inner distal angle,

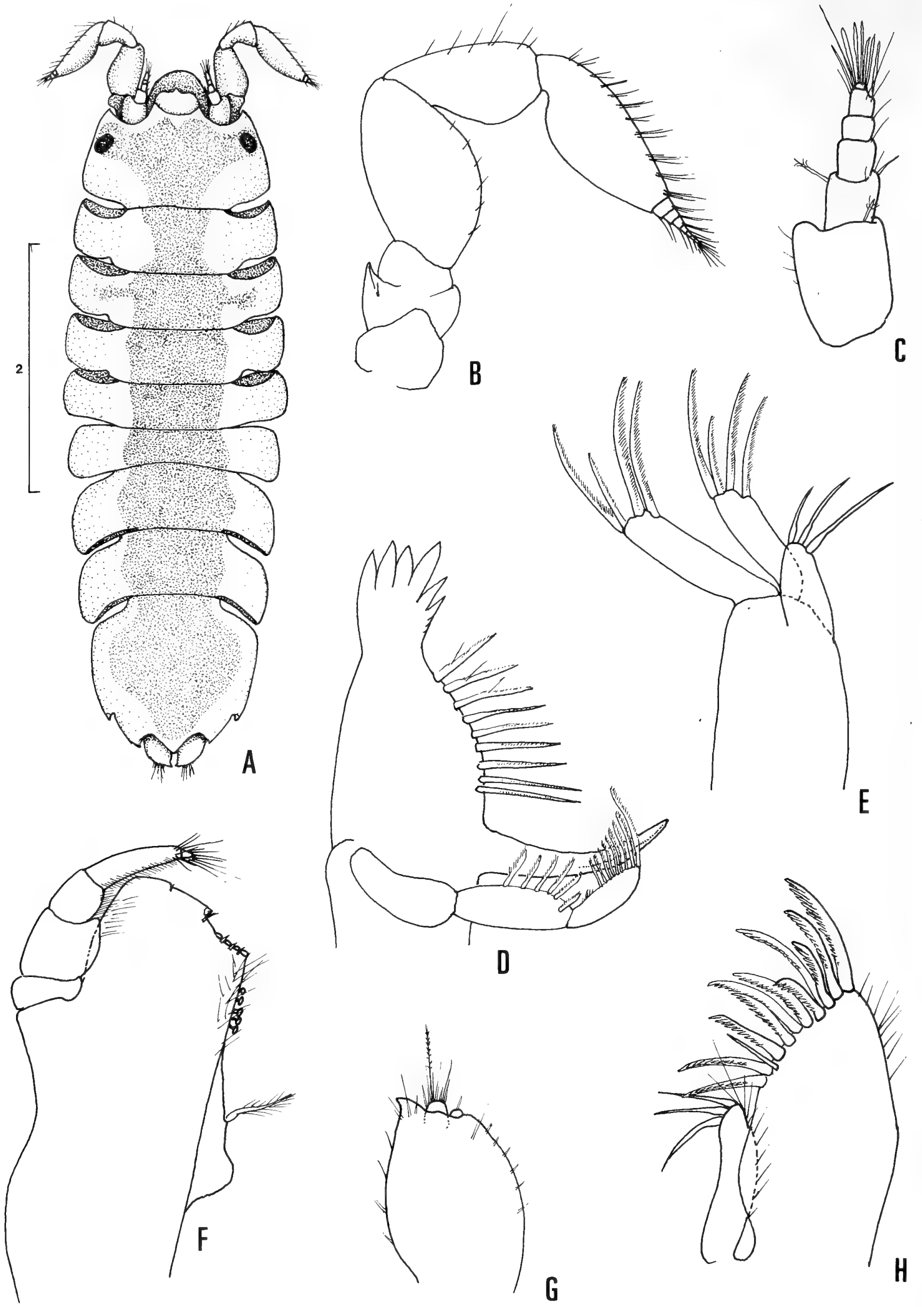

Fig. 3. *Jaeropsis curvicornis* (Nicolet)
A. ♂ in dorsal view. B. Antenna. C. Antennule. D. Mandible. E. 2nd maxilla. F. Maxilliped. G. Uropod. H. 1st maxilla.

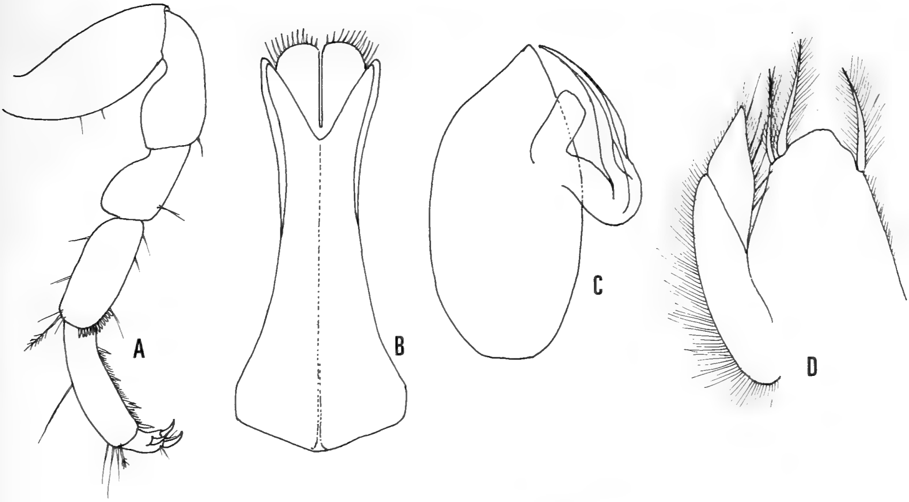

Fig. 4. *Jaeropsis curvicornis* (Nicolet)
A. VIIth peraeopod. B. 1st pleopod, ♂. C. 2nd pleopod, ♂. D. 3rd pleopod, ♂.

extending well beyond pleotelsonic apex. Body bearing broad band of red-brown pigment dorsally, expanded on cephalon to include eyes, also somewhat expanded on pleotelson.

Material

SAM–A13647 ♂ 5,0 mm Marion Island.

Distribution

Patagonia, Falkland Islands, Macquarie Island, Chile, Magellan Straits, Fuegian Archipelago.

Remarks

The colour pattern of the present specimen agrees well with that given by Richardson (1909) for *J. patagoniensis* (= *J. curvicornis*). Slight differences in the mouthparts are apparent between the present specimen and the description given by Menzies & Schultz (1967). The Marion Island specimen has nine serrated spines on the mandible (13 in the Antarctic specimens) and five fringed setae on the middle segment of the mandibular palp (as opposed to eight). For the rest, the specimen agrees well with the figures in the abovementioned descriptions.

Jaeropsis paulensis Vanhöffen

Figs 5–6

Jaeropsis paulensis Vanhöffen, 1914: 531, fig. 59a–1. Barnard, 1965: 201, fig. 2b.

Diagnosis

Cephalon with frontal plate rounded, medially entire, lateral margins entire. Lateral margins of pleotelson entire, fringed with alternating long and short

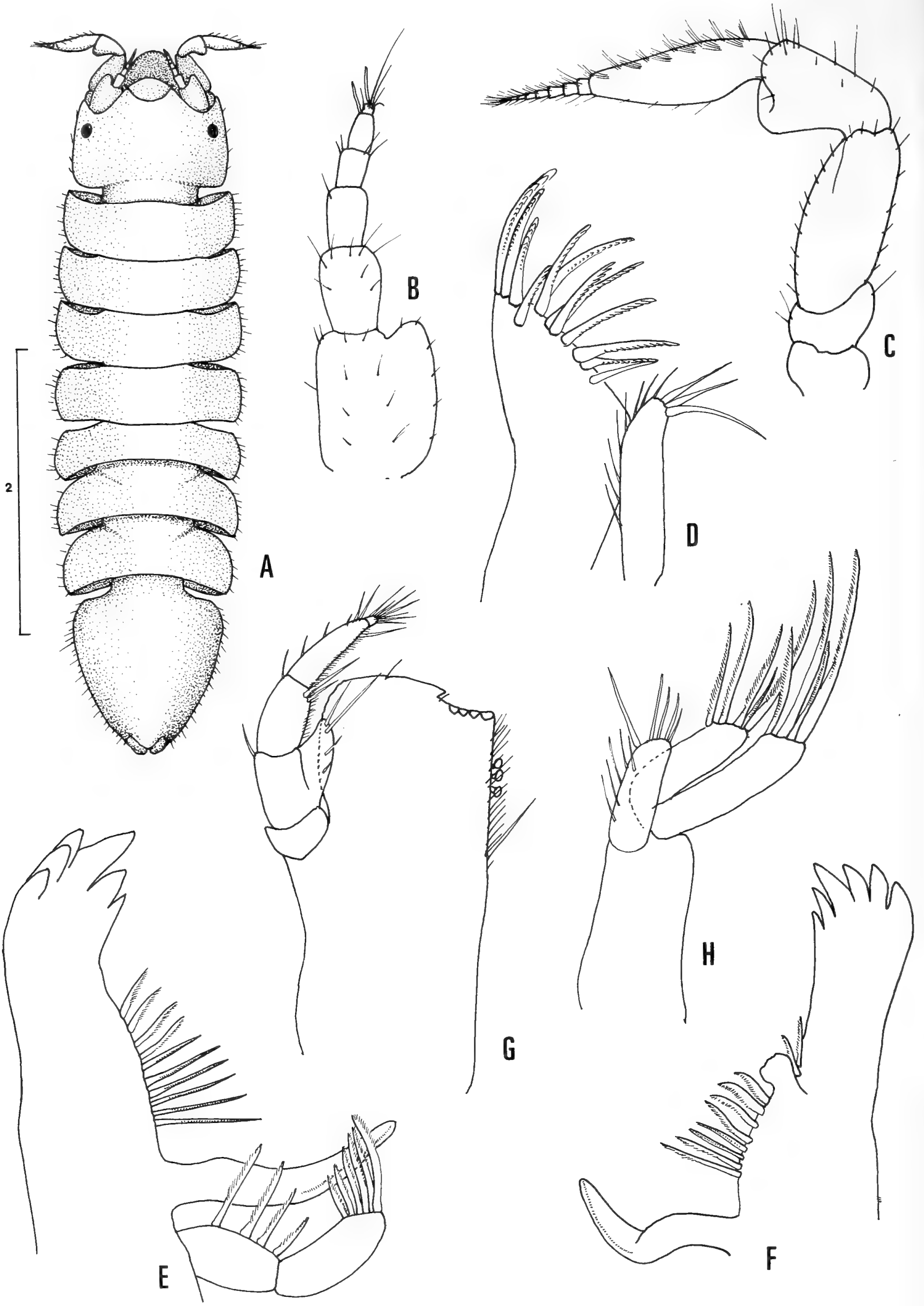

Fig. 5. *Jaeropsis paulensis* Vanhöffen

A. ♂ in dorsal view. B. Antennule. C. Antenna. D. 1st maxilla. E. Mandible. F. Mandible. G. Maxilliped. H. 2nd maxilla.

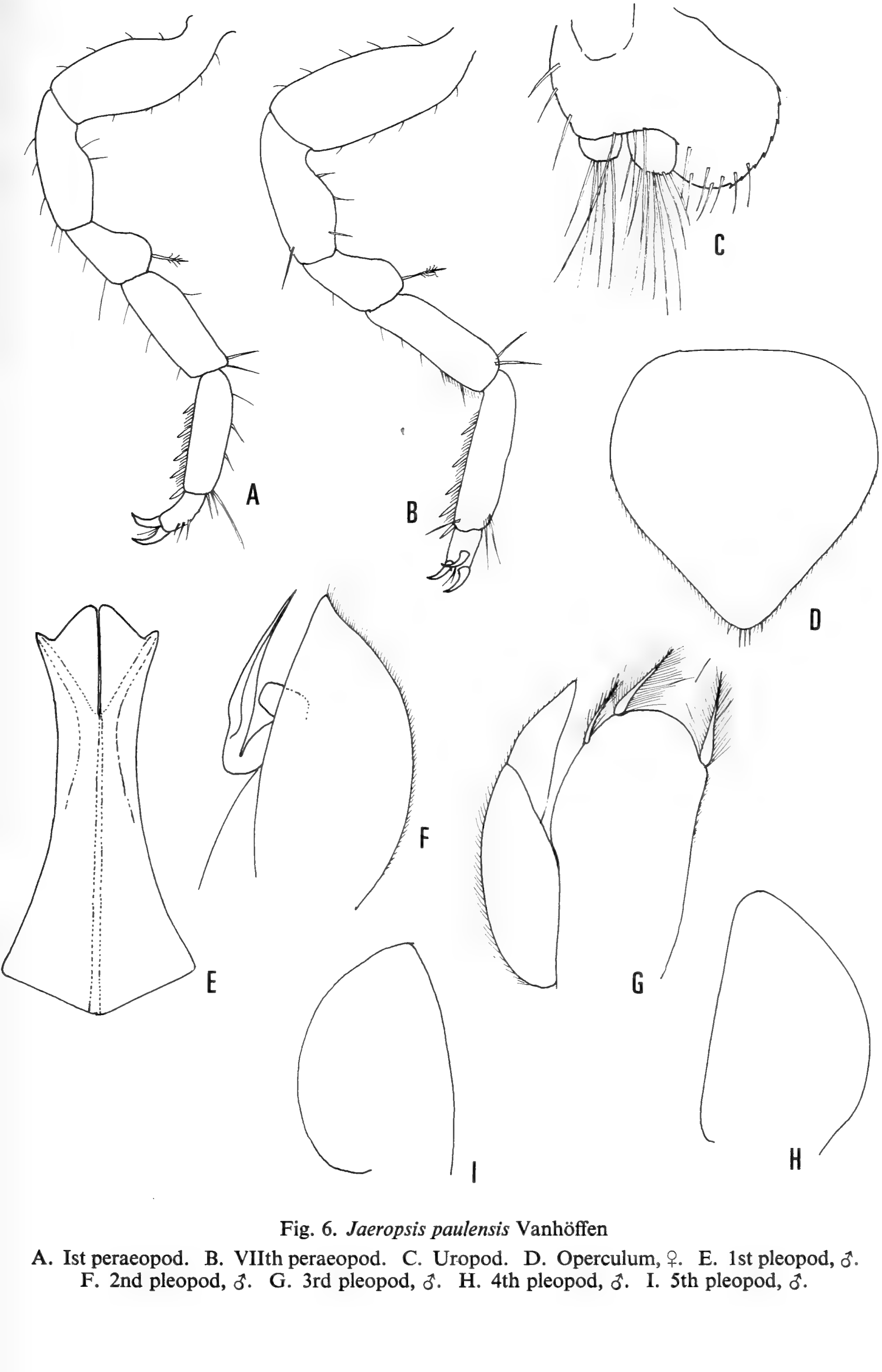

Fig. 6. *Jaeropsis paulensis* Vanhöffen

A. Ist peraeopod. B. VIIth peraeopod. C. Uropod. D. Operculum, ♀. E. 1st pleopod, ♂. F. 2nd pleopod, ♂. G. 3rd pleopod, ♂. H. 4th pleopod, ♂. I. 5th pleopod, ♂.

setae. Uropodal basis with broadly rounded lobe medially, unarmed, mediodistal margin serrulate.

Material

SAM–A12285, Gough Island, 2 ♀♀ 1 ♂.

St Paul Island
Station No.
8a. 1 ovig. ♀, 5 ♀♀, 14 ♂♂
8b. 2 ovig. ♀♀, 1 ♀, 3 ♂♂
8c. 2 ovig. ♀♀, 3 ♀♀, 9 ♂♂
93. 4 ovig. ♀♀, 2 ♀♀, 7 ♂♂

Amsterdam Island
Station No.
a4. 8 ovig. ♀♀, 9 ♂♂
a8. 2 ♀♀
a9. 1 ♂
b3. ovig. ♀♀, 6 ♀♀, 3 ♂♂
14. 1 ovig. ♂, 2 ♀♀, 2 ♂♂
27/3/1970/b. 1 ♂

Remarks

Barnard (1965) remarks that Vanhöffen figures the maxillipedal palp displaced, and with the second segment unlobed. Figure 5G above shows that in fact this segment is lobed on the inner margin.

Jaeropsis beuroisi sp. n.

Figs 7–8

Diagnosis

Cephalon with frontal plate obtusely angled, lateral margins with four or five spinules, more noticeable in smaller specimens, often lacking in adults. Lateral margins of pleotelson in male with one or two small serrations, in female with five or six serrations. Uropodal basis longer than wide, with medial lobe extending furthest distally, tipped with tiny hook; uropods extending beyond pleotelsonic apex.

Material

Holotype ♂ 6,0 mm St Paul st.90.

Allotype ♀ 4,2 mm St Paul st.20.

Paratypes 12 ovig. ♀♀, 5 ♀♀, 22 ♂♂. St Paul 22a.

Paratypes 3 ovig. ♀♀, 5 ♀♀, 5 ♂♂. Amsterdam Island st.28.

St Paul Island
Station No.
3. 2 ♀♀, 1 ♂
7b. 10 ovig. ♀♀, 13 ♀♀, 13 ♂♂
18. 4 ovig. ♀♀, 3 ♀♀, 5 ♂♂
20. 1 ovig. ♀, 1 ♀, 1 ♂
22c. 9 ovig. ♀♀, 4 ♀♀, 12 ♂♂
77a. 1 ovig. ♀, 1 ♀, 4 ♂♂
90. 20 ♀♀, 18 ♂♂

Amsterdam Island
Station No.
39. 1 ovig. ♀, 1 ♀
41a. 1 ♀, 1 ♂
41b. 1 ♂
44. 1 ♀
64a. 1 ovig. ♀, 1 ♂
74. 4 ♂♂
94. 2 ♂♂

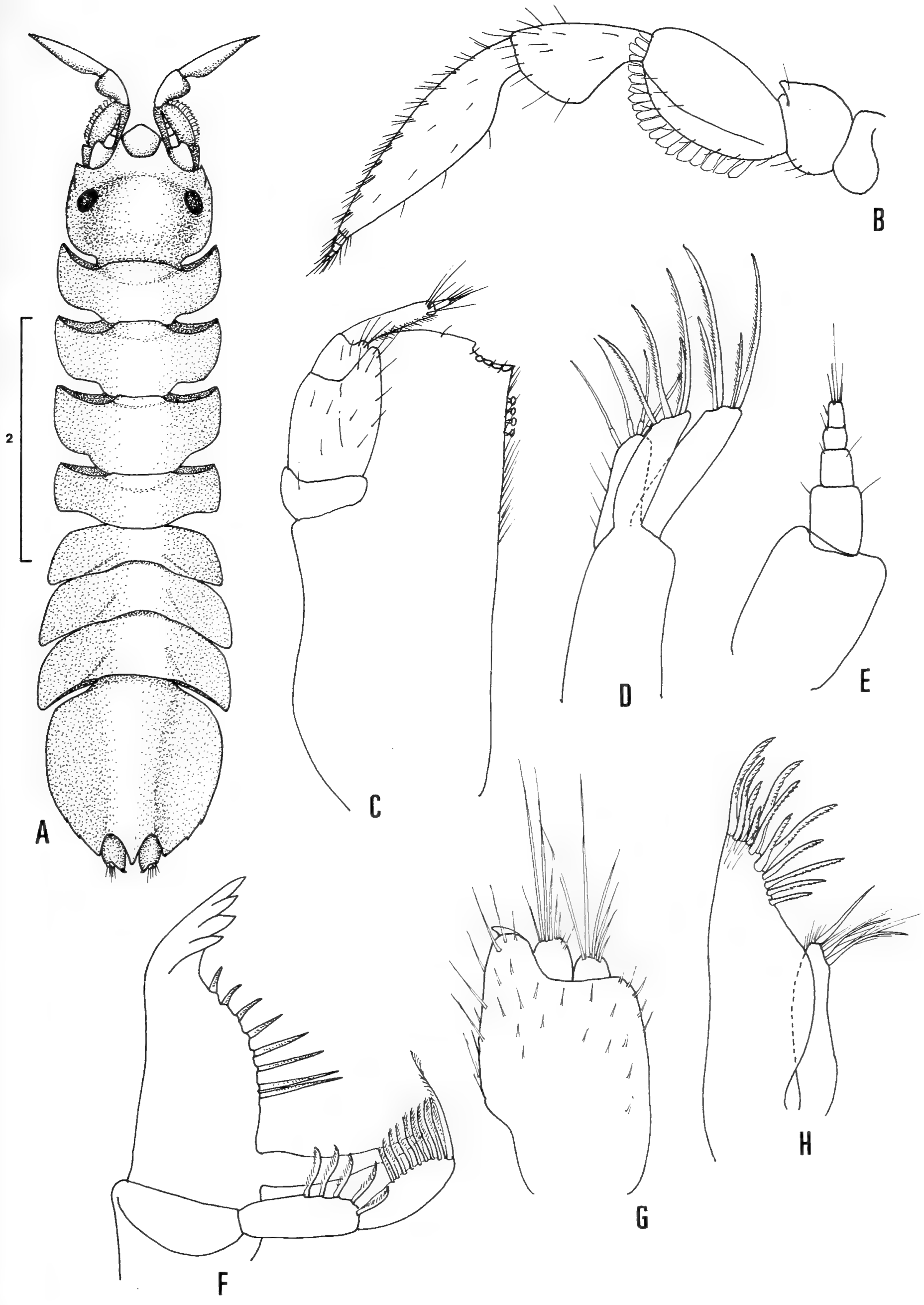

Fig. 7. *Jaeropsis beuroisi* sp. n.

A. Holotype in dorsal view. B. Antenna. C. Maxilliped. D. 2nd maxilla. E. Antennule. F. Mandible. G. Uropod. H. 1st maxilla.

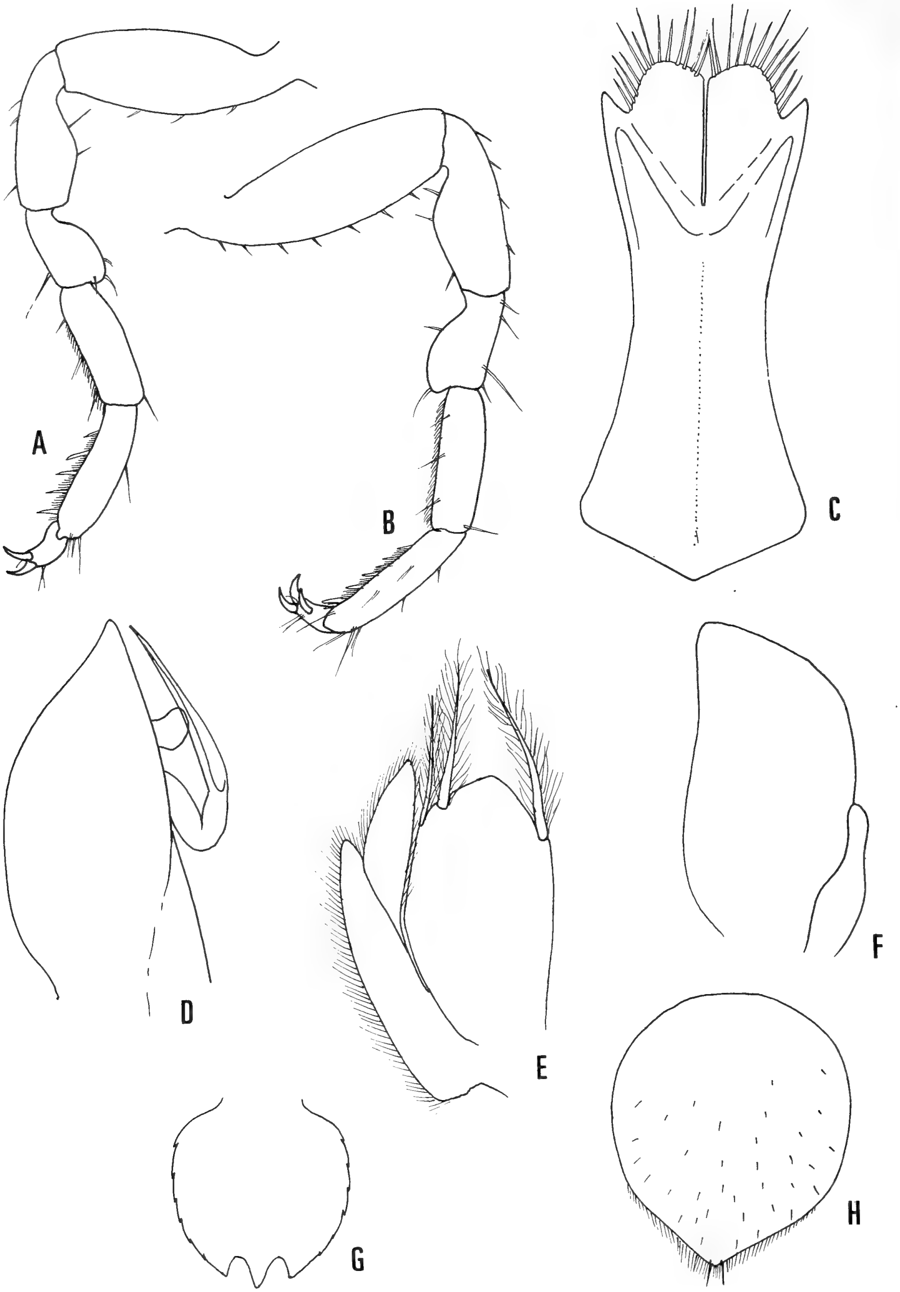

Fig. 8. *Jaeropsis beuroisi* sp. n.

A. Ist peraeopod. B. VIIth peraeopod. C. 1st pleopod, ♂. D. 2nd pleopod, ♂. E. 3rd pleopod, ♂. F. 4th pleopod, ♂. G. Pleotelson. H. Operculum, ♀.

St Paul Island
Station No.
B7. 1 ♀
B19. 1 ♀, 1 ♂
D6. 1 ovig. ♀, 2 ♀♀, 5 ♂♂
29/12/1970. 1 juv.
29/1/1971. 1 ♀

Amsterdam Island
Station No.
119. 2 ovig. ♀♀, 8 ♀♀, 11 ♂♂
142b. 2 ovig. ♀♀, 3 ♀♀, 2 ♂♂
147. 1 ♀, 1 ♂
173. 4 ovig. ♀♀, 6 ♀♀, 6 ♂♂
D12. 1 ovig. ♀, 1 ♀, 2 ♂♂

Remarks

Jaeropsis beuroisi resembles *J. intermedius* (Nicolet) recorded from Argentina to southern Chile, the Falkland Islands, and Antarctica, in the structure of the uropods, antennae (especially the fringed antennae), but differs in the degree of spination of the cephalic and pleotelsonic margins. The frontal plate in *J. intermedius* is more acute than in the present species. Several differences in the setation and spination of the mouthparts are also apparent.

There is some resemblance to *J. marionis* Beddard (1886*a*, 1886*b*), but the figures of this species are probably somewhat misleading. As the species was described from a single male, the specific definition needs to be supplemented.

The species is named for Dr J. Beurois of Marseilles, who collected most of the material.

Jaeropsis stebbingi sp. n.

Figs 9–10

Jaeropsis curvicornis non Nicolet, Barnard, 1914: 224, pl. 20c; 1940: 434, 494; 1965: 202, fig. 2c. Menzies & Schultz, 1967: 174. Stebbing, 1905: 51, pl. 11 (fig. C).

Diagnosis

Cephalon with frontal plate rounded, medially entire, lateral margins entire. Lateral margins of pleotelson usually with four very fine serrations on each side, often difficult to detect. Uropodal basis with broadly rounded medial lobe tipped with short hook, hardly interrupting pleotelsonic marginal outline; medio-distal margin serrulate. Cephalon bearing broad curved dark pigment band.

Material

Holotype SAM–A13649, ♂ 5 mm. Mouille Point, Table Bay.
Allotype SAM–A13648, ovig. ♀ 3,6 mm. Lüderitz, South West Africa.
SAM–A12738 2 ovig. ♀♀, 2 ♀♀, 1 ♂ Lüderitz, intertidal.
SAM–A12405 1 ♂ Lüderitz.
SAM–A12406 1 ♂ Lüderitz.
SAM–A12588 a ♀ Lüderitz.
SAM–A10381 1 ovig. ♀, 1 ♂ Lambert's Bay.
SAM–A2617 }
SAM–A2695 } 5 ovig. ♀♀, 7 ♀♀, 6 ♂♂ Mouille Point, Table Bay.
SAM–A2687 1 ovig. ♀ St James, False Bay.

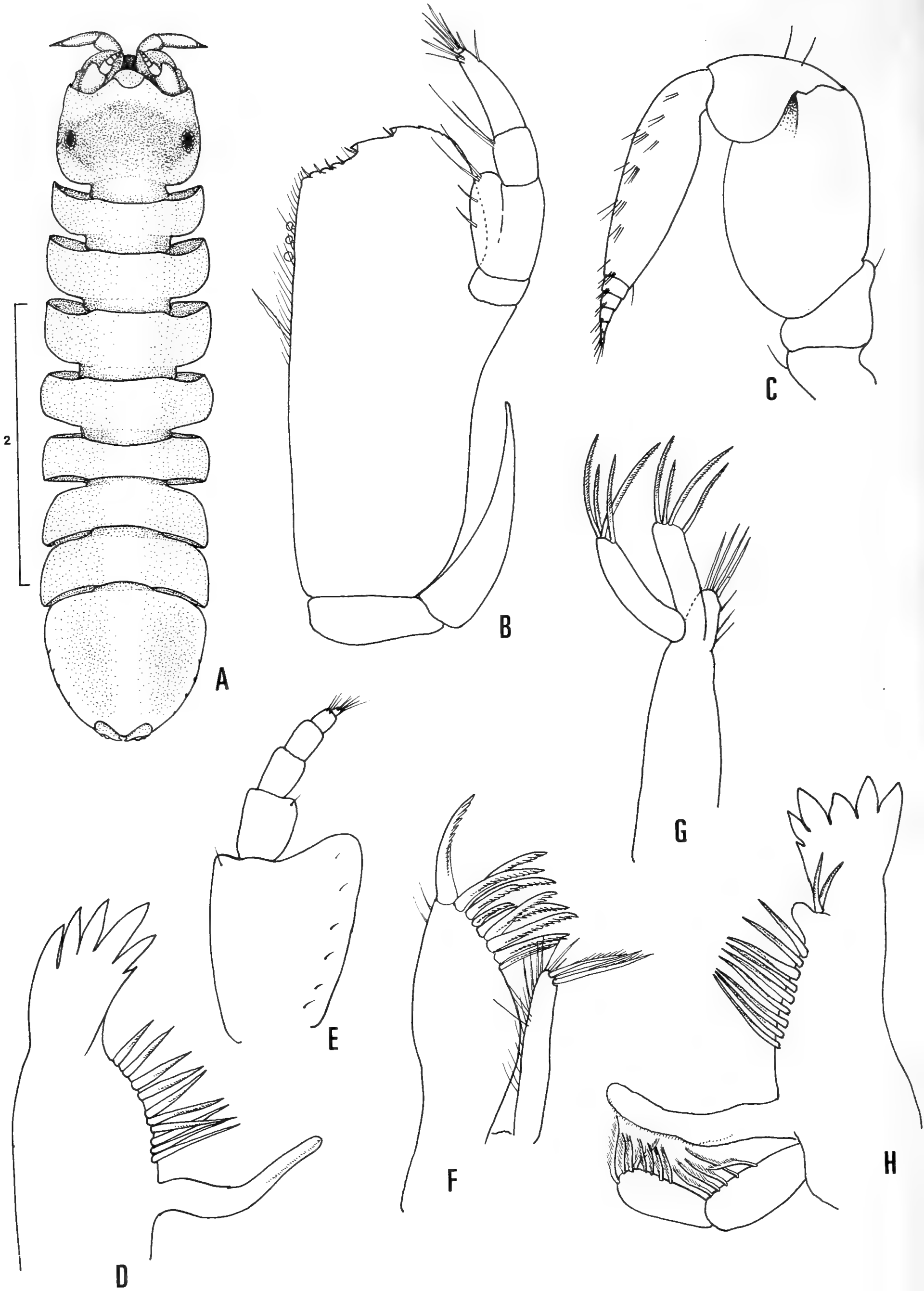

Fig. 9. *Jaeropsis stebbingi* sp. n.
A. Holotype in dorsal view. B. Maxilliped. C. Antenna. D. Mandible. E. Antennule. F. 1st maxilla. G. 2nd maxilla. H. Mandible.

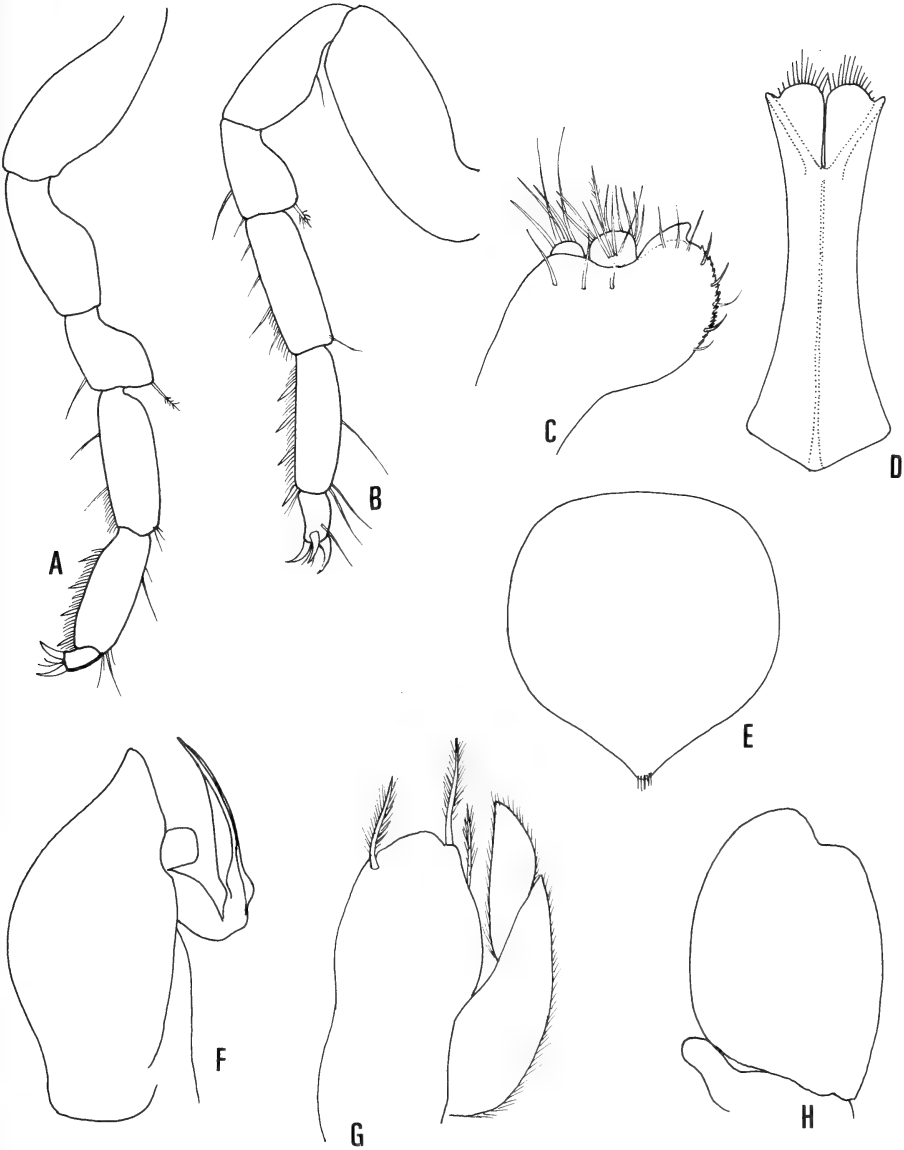

Fig. 10. *Jaeropsis stebbingi* sp. n.
A. Ist peraeopod. B. VIIth peraeopod. C. Uropod. D. 1st pleopod, ♂. E. Operculum, ♀. F. 2nd pleopod, ♂. G. 3rd pleopod, ♂. H. 4th pleopod, ♂.

Remarks

As noted by Barnard (1965) and Menzies & Schultz (1967), the *Jaeropsis curvicornis* described by Stebbing (1905) from Ceylon and later recorded from South Africa was probably not the same as *J. curvicornis* described by Nicolet (1849) from Chile. From the excellent figures provided by Menzies & Schultz (1967) of *J. curvicornis* (Nicolet), from the Antarctic, it is immediately apparent that the South African species is not the same as the Antarctic–Subantarctic species. The most obvious differences are to be seen in the uropods (curved and hooked in *J. stebbingi*, straight and elongate in *J. curvicornis*), the rostral plate (evenly convex in *J. stebbingi*, truncate with small median tooth in *J. curvicornis*) and in the lateral margins of the pleotelson (serrate in *J. stebbingi*, with a single strong incision in *J. curvicornis*).

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

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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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

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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.

BRIAN KENSLEY

FIVE SPECIES OF *JAEROPSIS* FROM THE SOUTHERN INDIAN OCEAN (CRUSTACEA, ISOPODA, ASELLOTA)

VOLUME 67 PART 11 OCTOBER 1975 ISSN 0303-2515

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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. Etudes sur les échanges respiratoires des littorines.—*Archs Zool. exp. gén.* 74: 627–634.
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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.
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(continued inside back cover)

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A PRELIMINARY CATALOGUE OF IDENTIFIABLE FOSSIL FISH MATERIAL FROM SOUTHERN AFRICA

By

R. A. JUBB & B. G. GARDINER

Cape Town Kaapstad

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&

B. G. Gardiner

Queen Elizabeth College, University of London

(With 38 figures)

[*MS. accepted 26 March 1975*]

ABSTRACT

Records comprising systematics, type and other material and localities of fossil fish material from the Witteberg, Dwyka, Ecca and Stormberg Series, from Tertiary marine deposits and from obscure horizons of southern Africa, are listed.

CONTENTS

INTRODUCTION

The rich fossil beds of the Beaufort Series, South Africa, containing reptilian and amphibian remains, first discovered by Andrew Geddes Bain in the fifties of the last century, attracted a great deal of attention from both professional and amateur palaeontologists. From that time onwards until early this century a large quantity of fossil material, including fishes, was collected, much of which was sent overseas. Fortunately, as far as fossil fishes are concerned, most of the type material not housed in museums in the Republic of South Africa is to be found in collections in the United Kingdom. Reference to type material in the British Museum and other institutions in the United Kingdom, so necessary for the preparation of this catalogue and identification

Ann. S. Afr. Mus. **67 (11), 1975: 381–440, 38 figs.**

of new material, was thus greatly facilitated by the collaboration of a leading authority on fossil fishes, Dr B. G. Gardiner of Queen Elizabeth College, London University.

From published data the fossil fish record in this part of Africa goes back to the Lower Carboniferous. The occurrence of fragmentary fish remains in the Upper Witteberg Series was known for some time but it was only in the years 1962 to 1963 (Theron 1962; Marais 1963) that the extent of the fossil bed, which proved to be a strike of some 400 kilometres, was known. In describing this Upper Witteberg fish fauna Gardiner (1969) recognized eleven new species representing eight families, and Jubb (1965) described one new species.

To date the Dwyka Series (Upper Carboniferous) and the Ecca Series (Lower Permian) have produced only a few fossil fish species. During Beaufort times (Upper Permian to Lower Triassic) fishes appear to have flourished and twenty-eight species representing twelve families were described (Broom 1909*a*, 1913*a–c*; Brough 1931, 1934; Haughton 1934; Woodward 1889). This period was followed by a decline in the number of species known, there being only three from the Cave Sandstone of the Stormberg Series. These are *Semionotus capensis* Woodward, specimens of which have been found in large numbers in the Ficksburg and Senekal districts (Jubb 1973), a single specimen of *Daedalichthys formosa* (Broom), recorded by Haughton (1924) from Siberia, Wodehouse District, and a single specimen of *Endemichthys likhoeli* Forey & Gardiner, recorded from Mount Likhoeli, western Lesotho (Forey & Gardiner 1973).

Referring to *Endemichthys likhoeli*, Forey & Gardiner (1973) draw attention to the fact that although the Lower Triassic of South Africa has yielded an array of early dictyopygids (Brough 1931, 1936) not one of those advanced dictyopygids so characteristic of the Upper Triassic of North America (Schaeffer 1967) has so far been recorded from the African continent. The geographical distribution of the dictyopygids appears to be a discontinuous one with the Lower Triassic forms coming mainly from South Africa, the Middle Triassic ones from Australia, and the Upper Triassic forms from North America. It is thus surprising to find a seemingly advanced dictyopygid in the rather unfossiliferous Cave Sandstone of Lesotho.

The Cave Sandstone of the Stormberg Series marks the end, in southern Africa, of the fish fossil record. Apart from sharks' teeth from marine deposits of Cainozoic times (Mountain 1962; Davies 1965) no fossil fishes have been found in Cretaceous, Tertiary or Quaternary deposits. However, in Africa north of the equator, particularly in the Sahara region (Greenwood 1974) (Fig. 1), fossil fishes representing extant families and genera have been found at numerous sites. In Australia all available evidence indicates that the chief genera of extant freshwater fishes of Australia were present in the continent during much, if not all of Cainozoic times and for the most part they continue to flourish (Hills 1958).

In southern Africa fossil fish material is housed in the major museums, the

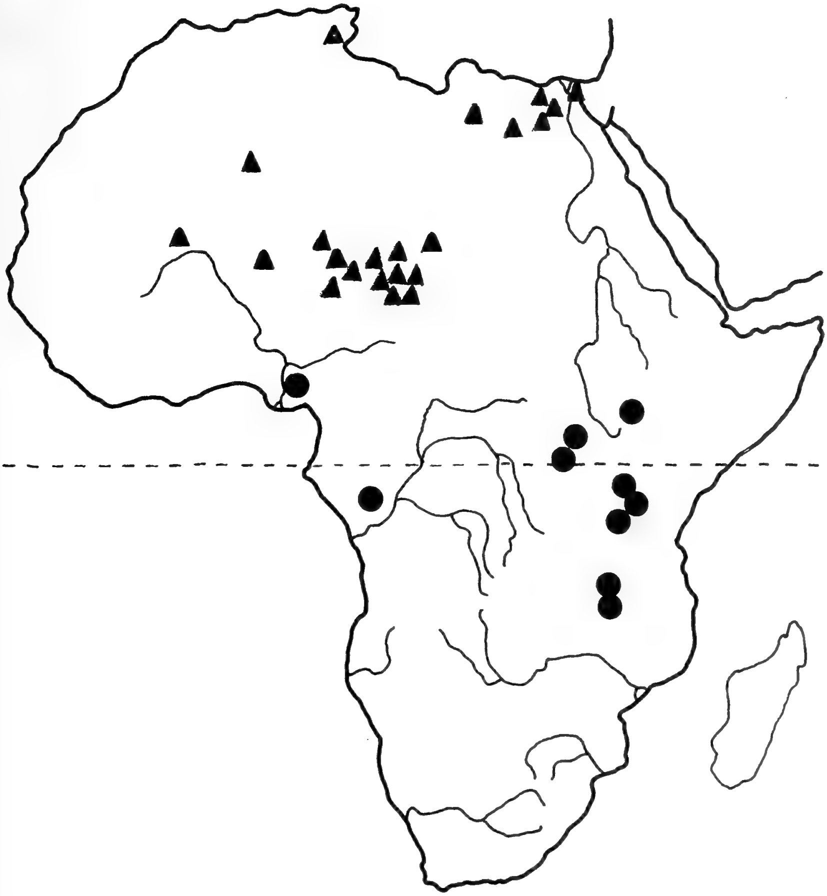

Fig. 1. Simplified map showing sites where fossil fish remains, representing extant genera of African freshwater fishes, have been found. (After Greenwood 1974.)

△ Mainly Miocene (Algeria and Egypt) to Upper Pleistocene (Sahara).

○ Mainly Lower Pleistocene to Holocene.

The following genera are represented at scattered sites: *Protopterus, Polypterus, Hyperopisus, Hydrocynus, Alestes, Labeo, Barbus, Clarotes, Bagrus, Auchenoglanis, Chrysichthys, Synodontis, Clarias, Heterobranchus, Lates, Tilapia, Chrysophris.*

Geological Survey Department, Pretoria, the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, and the Rubidge Collection, Wellwood Farm, Graaff-Reinet. In connection with various studies most of the old and recent material has been studied either by Gardiner or by Jubb, and overseas material studied by Gardiner and Hutchinson (1973). All the major museums in the Republic of South Africa and Rhodesia were visited by Jubb and type specimens and other catalogued material photographed using Kodachrome II 35 mm film. This particular film was chosen for colour transparencies because of its excellent colour detail and lack of grain. For taxonomic revision and confirmation of identifications these colour transparencies were forwarded to Gardiner for comparison with type and other material in collections in the United Kingdom. As many of the older descriptions were based on fragmentary samples, mere scales or poorly preserved material, as well as unsatisfactory locality records, exchange of photographic slides by air proved far more satisfactory than the exchange of weighty samples by sea when revising old material, or identifying more recent discoveries. For guidance on geological horizons from which certain fossil fishes may have come particular tribute must be paid to Dr J. W. Kitching and Mesdames H. M. Anderson and J. M. Anderson of the Bernard Price Institute for Palaeontological Research.

BRIEF SUMMARY OF FOSSIL FISH RECORDS

WITTEBERG SERIES

Family **Rhadinichthyidae** Romer, 1945
    Genus *Mentzichthys* Jubb, 1965
        M. walshi Jubb, 1965
        M. jubbi Gardiner, 1969
        M. maraisi Gardiner, 1969
        M. theroni Gardiner, 1969

Family **Holuridae** Moy-Thomas, 1939
    Genus *Australichthys*, Gardiner, 1969
        A. longidorsalis Gardiner, 1969

Family **Atherstoniidae** Gardiner, 1967
    Genus *Aestuarichthys* Gardiner, 1969
        A. fulcratus Gardiner, 1969

Family **Willomorichthyidae** Gardiner, 1969
    Genus *Willomorichthys* Gardiner, 1969
        W. striatulus Gardiner, 1969

Family **Canobiidae** Aldinger, 1937
    Genus *Sundayichthys* Gardiner, 1969
        S. elegantulus Gardiner, 1969

Family **Dwykiidae** Gardiner, 1969
    Genus *Dwykia* Gardiner, 1969
        D. analensis Gardiner, 1969

Family **Amphicentridae** Moy-Thomas, 1939
    Genus *Adroichthys* Gardiner, 1969
        A. tuberculatus Gardiner, 1969

Family **Platysomidae** Young, 1866
  Genus *Soetendalichthys* Gardiner, 1969
    S. cromptoni Gardiner, 1969

Family **Acanthodidae** Agassiz, 1833
  Genus *Acanthodes* Agassiz, 1833
    Acanthodes sp. Gardiner, 1973

DWYKA SERIES

Family **Elonichthyidae** Aldinger, 1937
  Genus *Namaichthys* Gürich, 1923
    N. schroederi Gürich, 1923

Family **Cosmoptychiidae** Gardiner, 1963
  Genus *Watsonichthys* Aldinger, 1937
    W. lotzi (Gürich, 1923)

Family **Palaeoniscidae** Aldinger, 1937
  Genus *Palaeoniscum* Agassiz, 1833
    P. capensis Broom, 1913

Note

The type specimen of *Palaeoniscum capensis*, SAM–1061, is stated to come from the Hantam Mountains, 19 km west of Calvinia, Upper Dwyka. The original record, crossed out in the register, says Waterval Farm, Prince Albert District, Cape Province. Under the same name are two specimens SAM–1062 and SAM–1066 with squamation quite different from that of the type specimen, SAM–1061. These two specimens are recorded as coming from the White Band, Upper Dwyka Shales, Toren, Hantam Mountains, near Calvinia. They are not *P. capensis* and have been provisionally assigned to *Watsonichthys lotzi.*

Recorded by Gürich (1923) are fragments from the Upper Dwyka Shales, Ganikobis, South West Africa, representing *Elonichthys* (?) and *Rhadinichthys* (?) species, but no additional material available.

Recorded by Anderson (1972, 1974) are probable fish trails from interglacial sediments in the Dwyka Series, near Vryheid, Natal.

Recorded by Dr V. von Brunn, Natal University, Pietermaritzburg (*in litt.* 1974) are fish trails from the Dwyka on the farm Rooipoort 565, south-east of Vryheid.

ECCA SERIES

Family **Elonichthyidae** Aldinger, 1937
  Genus *Namaichthys* Gürich, 1923
    N. digitata (Woodward, 1891)
    [*N. molyneuxi* (Woodward, 1903) = *N. digitata*]

Family **Coelacanthidae** Agassiz, 1843
  Genus *Coelacanthus* Agassiz, 1844
    C. dendrites Gardiner, 1973

BEAUFORT SERIES

Lower Beaufort

Tapinocephalus Zone

Endothiodon Zone

Daptocephalus Zone

Family **Palaeoniscidae** Vogt, 1852
  Genus *Pteronisculus* White, 1933
    Pteronisculus sp.

Family **Atherstoniidae** Gardiner, 1967
  Genus *Atherstonia* Woodward, 1889
    A. scutata Woodward, 1889
    [(?) *A. sculptus* (Egerton, 1856) = *A. scutata* Woodward, 1889]
    [(?) *A. bainii* (Egerton, 1856) = *A. scutata* Woodward, 1889]
    A. minor Woodward, 1889
    A. seeleyi Woodward, 1889
    A. cairncrossi Broom, 1913 = *A. scutata* Woodward, 1889

Family **Elonichthyidae** Aldinger, 1937
  Genus *Elonichthys* Giebel, 1848
    E. whaitsi Broom, 1913

Note

There is a remarkable resemblance between *E. whaitsi* from Droogvoets Farm, Fraserburg District, and *E. browni* (Broom) from Bekker's Kraal fossil fish bed, *Cynognathus* Zone.

Middle Beaufort

Lystrosaurus Zone

Family **Platysomiidae** Young, 1866
  Genus *Caruichthys* Broom, 1913
    C. ornatus Broom, 1913

Upper Beaufort

Procolophon Zone

Cynognathus Zone

Family **Hybontidae** Owen, 1846
  Genus *Hybodus* Agassiz, 1837
    H. africanus Broom, 1909

Family **Ceratodontidae** Gill, 1872
  Genus *Ceratodus* Agassiz, 1838
    C. capensis Woodward, 1889
    C. ornatus Broom, 1909
    C. kannemeyeri Seeley, 1897

Family **Coelacanthidae** Agassiz, 1843
  Genus *Coelacanthus* Agassiz, 1844
    C. africanus Broom, 1905

Family **Elonichthyidae** Aldinger, 1937
  Genus *Elonichthys* Giebel, 1848
    E. browni (Broom), 1909 (Originally described as *Oxygnathus browni*)

Family **Dicellopygidae** Romer, 1945
  Genus *Dicellopygae* Brough, 1931
    D. draperi (Woodward, 1893)
    [*D. tenuis* (Broom, 1909) = *D. draperi* (Woodward)]
    [*D. macrodentatus* Brough, 1931 = *D. draperi* (Woodward)]
    D. lissocephalus Brough, 1931

Family **Redfieldiidae** Berg, 1940
  Genus *Daedalichthys* Brough, 1931
    D. formosa (Broom, 1909)
    [*D. higginsi* Brough, 1931 = *D. formosa* (Broom)]
  Genus *Helichthys* Broom, 1909
    H. browni Broom, 1909
    [*H. stegopygae* Brough, 1931 = *H. browni* (Broom)]
    [*H. obesus* Brough, 1931 = *H. browni* (Broom)]
    H. elegans Brough, 1931
    H. ctenipteryx Brough, 1931
    H. grandipennis Brough, 1931

Family **Colobodontidae** Stensiö, 1916
  Genus *Meidiichthys* Brough, 1931
    M. browni (Broom, 1909) (Originally described as *Pholidophorus browni*)

Family **Brookvaliidae** Berg, 1940
  Genus *Ischnolepis* Haughton, 1934
    I. bancrofti Haughton, 1934
  Genus *Atopocephala* Brough, 1934
    A. watsoni Brough, 1934

Family **Cleithrolepididae** Wade, 1935
  Genus *Cleithrolepidina* Berg, 1940
    C. extoni (Woodward, 1888)
    C. minor (Broom, 1909)

Family **Hydropessidae** Hutchinson, 1973
  Genus *Hydropessum* Broom, 1909
    H. kannemeyeri Broom, 1909

STORMBERG SERIES

Molteno Beds

Family **Semionotidae** Agassiz, 1832
    Genus *Semionotus* Agassiz, 1832
        S. cf. *capensis* Woodward, 1888

Red Beds

Cave Sandstone

Family **Semionotidae** Agassiz, 1832
    Genus *Semionotus* Agassiz, 1832
        S. capensis Woodward, 1888

Family **Dictyopygidae** Hay, 1889
    Genus *Endemichthys* Forey & Gardiner, 1973
        E. likhoeli Forey & Gardiner, 1973

TERTIARY MARINE DEPOSITS

Family **Lamnidae**
    Genus *Carcharodon* Müller & Henle, 1838
        C. megalodon Agassiz, 1843
        C. angustidens Agassiz, 1843
        C. sulcidens Agassiz, 1843
        C. carcharias (Linnaeus, 1758)
    Genus *Oxyrhina* Agassiz, 1838
        O. desori Agassiz, 1843
        O. crassa Agassiz, 1843 = *Isurus benedictus* Davies, 1964

Family **Carchariidae**
    Genus *Carcharius* Rafinesque, 1810
        C. taurus Rafinesque, 1810
    Genus *Odontaspis* Agassiz, 1838
        O. macrota (Agassiz, 1843)
        O. elegans (Agassiz, 1843)

Family **Galeorhinidae**
    Genus *Galeocerdo* Müller & Henle, 1837
        G. cuvier (Le Seuer, 1818)
    Genus *Hemipristis* Agassiz, 1843
        H. serra Agassiz, 1843

FOSSIL FISH MATERIAL FROM THE WITTEBERG SERIES

Fragmentary fish remains in the Upper Witteberg Series (Lower Dwyka Shales) have been known for some time (Haughton *et al.* 1953: 19; Du Toit 1954: 27). More recently Theron (1962: 263) collected nodules containing fossil fish from the Dwyka River to Willowmore but more particularly in the Prince

Albert and the Strydomsvlei–Soetendals Vlei areas. In 1963 Mr G. Walsh, an official of the Sundays River Irrigation Board, discovered a deposit of fossil fish in the mountain just south of Lake Mentz and close to the entrance of Karoopoort (Jubb 1965). Material from Lake Mentz was sent to Gardiner by the Geological Survey Department, Pretoria, as well as by the Albany Museum, Grahamstown (Gardiner 1969).

In the Soetendals Vlei area the so-called 'passage beds' are approximately 500 metres thick and the fish-bearing nodules occur some 200–214 metres from the top of these (Theron 1962: 264). The 'passage beds' were formerly regarded as Lower Dwyka Shales, but are now considered to represent the Upper Witteberg Series. The nodules are found scattered in a zone some 9 metres thick and consist of a black, fine-grained, carbonaceous mudstone somewhat flinty in character. Within the nodules the fish are only moderately well preserved and occur either singly or up to five or more in a single nodule.

The Lake Mentz fossils come from the northern slope of the Suurberg Range on Schiet Hoogte farm about 4,5 km south-west of the lake. The fossiliferous outcrops are situated 549 metres west of the Sundays River at the point where it enters the main Suurberg Gorge (Marais 1963: 192, fig. 1). The Upper Witteberg stage in this area is some 405 metres thick and the fossiliferous band occurs 225 metres above the base in the Upper Shale zone, or some 183 metres from the top and therefore in the same stratigraphical position as the fish nodules in the Soetendals Vlei area. The fish are confined to a narrow band of sandy marl about 125 mm in thickness where they are completely flattened and occur in vast concentrations, indicating rapid extermination and subsequent burial.

Fragmentary fish remains have also been collected by Mr J. Loock, Department of Geology, University of the Orange Free State, at Floriskraal Dam south of Laingsburg, and also by the Geological Survey Department in the region of the Dwyka River, the above sites being the same horizon as that of Soetendals Vlei. Thus these Upper Witteberg fish have been along a strike of some 400 km.

Family **Rhadinichthyidae** Romer, 1945

Genus *Mentzichthys* Jubb

1965—*Mentzichthys* Jubb: 270.

Mentzichthys walshi Jubb

1965—*Mentzichthys walshi* Jubb: 267–272, figs 1–2, pl. 6A–B.
1969—*Mentzichthys walshi* Jubb. Gardiner: 426.

Locality

Upper Witteberg Series, Lake Mentz. Described in detail by Marais (1963: 191–202).

Holotype

Almost complete fish in the Albany Museum, Grahamstown, AM 4562.

Other material

Parts of fishes representing this species on slabs AM 4563, AM 4564 and AM 4565 in the Albany Museum. Specimens SAM–K1169 and SAM–K1170 are in the South African Museum, Cape Town.

Mentzichthys jubbi Gardiner

Fig. 2

1963—Species 'A', Marais: pl. 3A–D.
1969—*Mentzichthys jubbi* Gardiner: 426–429, figs 1–3.

Locality

Upper Witteberg Series, Lake Mentz.

Holotype

Almost complete fish in Geological Survey Department, Pretoria. No number available.

Other material

Another specimen on same block as holotype in Geological Survey Department, one block with two specimens in Albany Museum, Grahamstown, AM 4562.

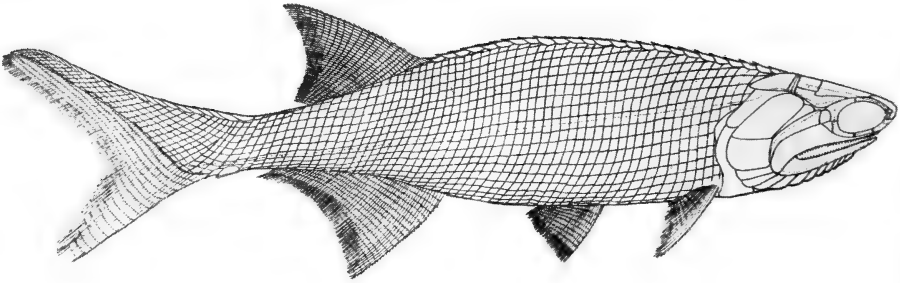

Fig. 2. *Mentzichthys jubbi* Gardiner, total length approximately 38 cm. Restoration by Gardiner.

Mentzichthys maraisi Gardiner

1969—*Mentzichthys maraisi* Gardiner: 430, pl. 2.

Locality

Upper Witteberg Series, Lake Mentz.

Holotype

Almost complete fish with caudal missing in Geological Survey Department, Pretoria. No number available.

Other material

One large block with two moderately complete specimens, one block with a single specimen, and some fragments, all in Geological Survey Department, Pretoria.

Mentzichthys theroni Gardiner

1969—*Mentzichthys theroni* Gardiner: 431.

Locality

Upper Witteberg Series, Soetendals Vlei.

Holotype

Almost complete fish with caudal missing in South African Museum, Cape Town, SAM–13570.

Other material

Block containing three incomplete specimens from Soetendals Vlei in South African Museum. An almost complete specimen from Lake Mentz in the collection of the Geological Survey Department, Pretoria.

Family **Holuridae** Moy-Thomas, 1939

Genus *Australichthys* Gardiner

1969—*Australichthys* Gardiner: 432.

Australichthys longidorsalis Gardiner

1969—*Australichthys longidorsalis* Gardiner: 432, figs 4–6.

Locality

Upper Witteberg Series, Lake Mentz.

Holotype

Tolerably complete fish wanting caudal and paired fins, Geological Survey Department, Pretoria. No number available.

Other material

A well-preserved skull from the same site, Albany Museum, Grahamstown, AM 4596A.

Family **Atherstoniidae** Gardiner, 1967

Genus *Aestuarichthys* Gardiner

1969—*Aestuarichthys* Gardiner: 434.

Aestuarichthys fulcratus Gardiner

Fig. 3

1969—*Aestuarichthys fulcratus* Gardiner: 434, figs 7–9.

Locality

Upper Witteberg Series, Soetendals Vlei.

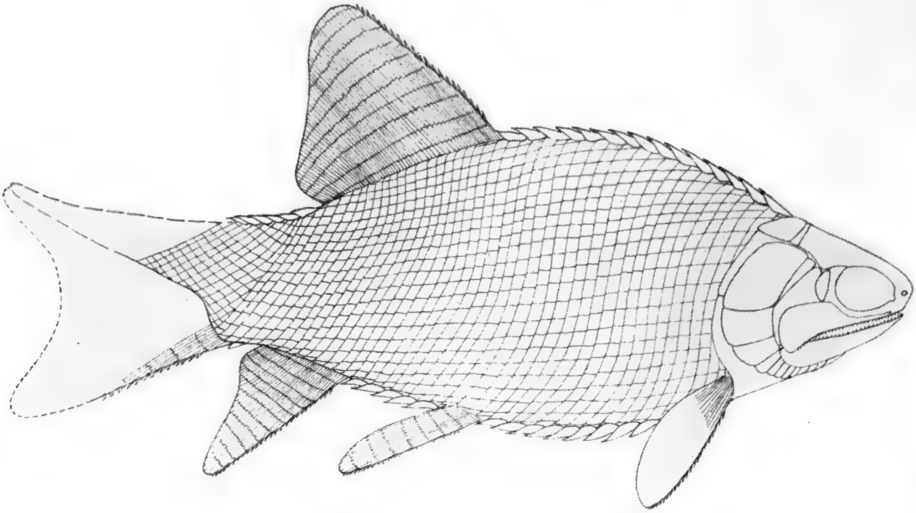

Fig. 3. *Aestuarichthys fulcratus* Gardiner, total length approximately 10,5 cm. Restoration by Gardiner.

Holotype

Poorly preserved fish wanting caudal and pectoral fins, South African Museum, Cape Town, SAM–13562.

Other material

One tolerably complete fish from Soetendals Vlei in the South African Museum, and two tolerably complete specimens from Lake Mentz in the Albany Museum, Grahamstown, AM 4596D.

Family **Willomorichthyidae** Gardiner, 1969

Genus *Willomorichthys* Gardiner

1969—*Willomorichthys* Gardiner: 438.

Willomorichthys striatulus Gardiner

Fig. 4

1969—*Willomorichthys striatulus* Gardiner: 438, figs 10–12.

Locality

Upper Witteberg Series, Soetendals Vlei.

Holotype

A rather distorted fish with caudal missing, South African Museum, Cape Town, SAM–13541.

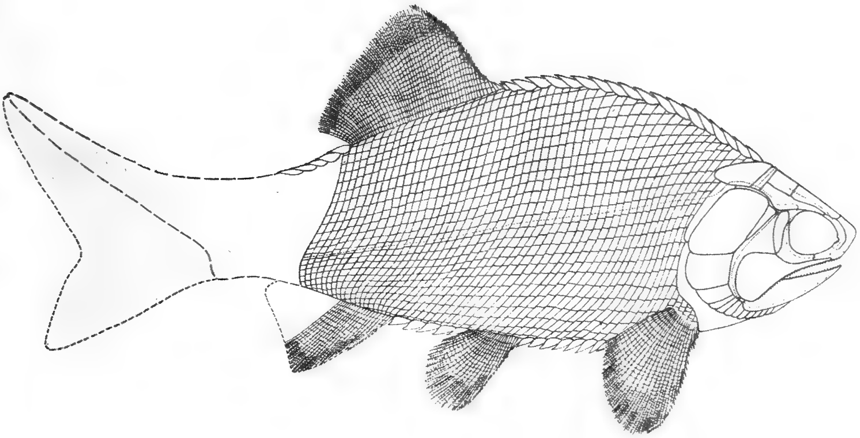

Fig. 4. *Willomorichthys striatulus* Gardiner, total length approximately 25 cm. Restoration by Gardiner.

Other material

Three tolerably complete specimens in the South African Museum from Soetendals Vlei. One specimen consisting of head and anterior third of body in the Albany Museum, Grahamstown, AM 4596B, from Lake Mentz, and AM 4597 from the same site.

Family **Canobiidae** Aldinger, 1937

Genus *Sundayichthys* Gardiner

1969—*Sundayichthys* Gardiner: 442.

Sundayichthys elegantulus Gardiner

Fig. 5

1969—*Sundayichthys elegantulus* Gardiner: 443, fig. 13.

Locality

Upper Witteberg Series, Lake Mentz.

Holotype

Fish with caudal missing, Geological Survey Department, Pretoria. No number available.

Other material

One specimen consisting of anterior third of fish from Soetensdal Vlei in the South African Museum, and portion of fish in the Albany Museum, Grahamstown, AM 4596C, from Lake Mentz.

Family **Dwykiidae** Gardiner, 1969

Genus *Dwykia* Gardiner

1969—*Dwykia* Gardiner: 443.

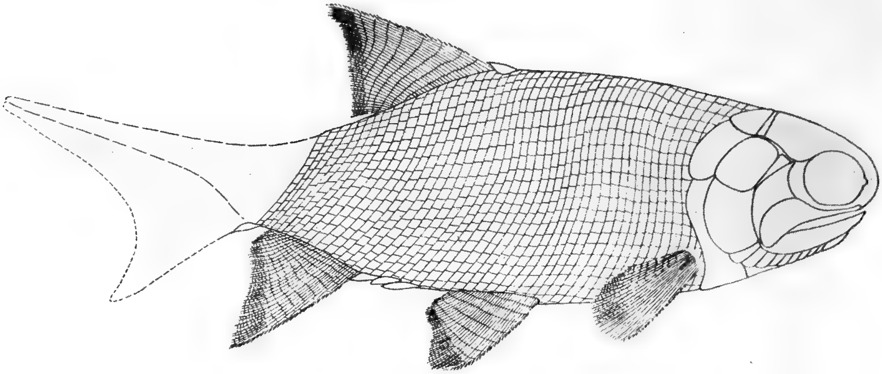

Fig. 5. *Sundayichthys elegantulus* Gardiner, total length approximately 10 cm. Restoration by Gardiner.

Dwykia analensis Gardiner

1969—*Dwykia analensis* Gardiner: 443, pl. 1.

Locality

Lower Dwyka Shales, Soetendals Vlei.

Holotype

Posterior half of fish, wanting dorsal and pelvic fins, in the South African Museum, Cape Town, SAM–13561.

Family **Amphicentridae** Moy-Thomas, 1939

Genus *Adroichthys* Gardiner

1969—*Adroichthys* Gardiner: 445.

Adroichthys tuberculatus Gardiner

Fig. 6

1969—*Adroichthys tuberculatus* Gardiner: 445, figs 14–16.

Locality

Upper Witteberg Series, Soetendals Vlei.

Holotype

An incomplete fish, wanting fins and caudal, in the South African Museum, Cape Town, SAM–13597.

Other material

Five tolerably complete specimens in counterpart, three isolated skulls and one small specimen in the South African Museum, all from Soetendals Vlei. One juvenile specimen in the Albany Museum, Grahamstown, from Lake Mentz, AM 4570.

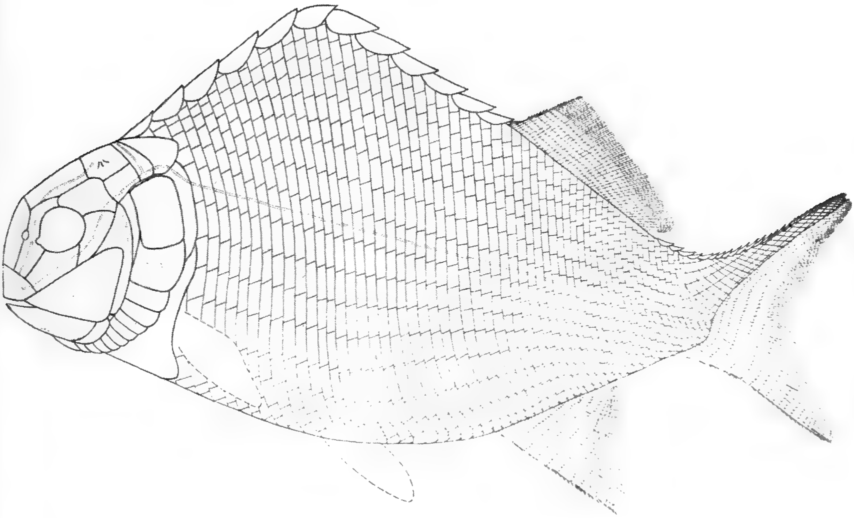

Fig. 6. *Adroichthys tuberculatus* Gardiner, total length approximately 40 cm. Restoration by Gardiner.

Family **Platysomidae** Young, 1866

Genus *Soetendalichthys* Gardiner

1969—*Soetendalichthys* Gardiner: 447.

Soetendalichthys cromptoni Gardiner

1969—*Soetendalichthys cromptoni* Gardiner: 449, figs 17–18.

Locality

Upper Witteberg Series, Soetendals Vlei.

Holotype

Incomplete fish, wanting caudal and front of head, in the South African Museum, Cape Town, SAM–13560.

Other material

Two incomplete specimens from Soetendals Vlei in the South African Museum.

Family **Acanthodidae** Agassiz

Fig. 7A–B

1932—Acanthodidae. Zittel: 55, fig. 76.
1937—Acanthodidae. Watson: 49, pls 5–14.
1963—Acanthodii. Greenwood: 302.
1963—Acanthoëssidae. Jordan: 591.
1973—*Acanthodes* sp. Gardiner: 33, figs 2–3.

Acanthodian remains occur in strata from the Upper Silurian to the Lower Permian; complete or well-preserved remains are comparatively rare. These

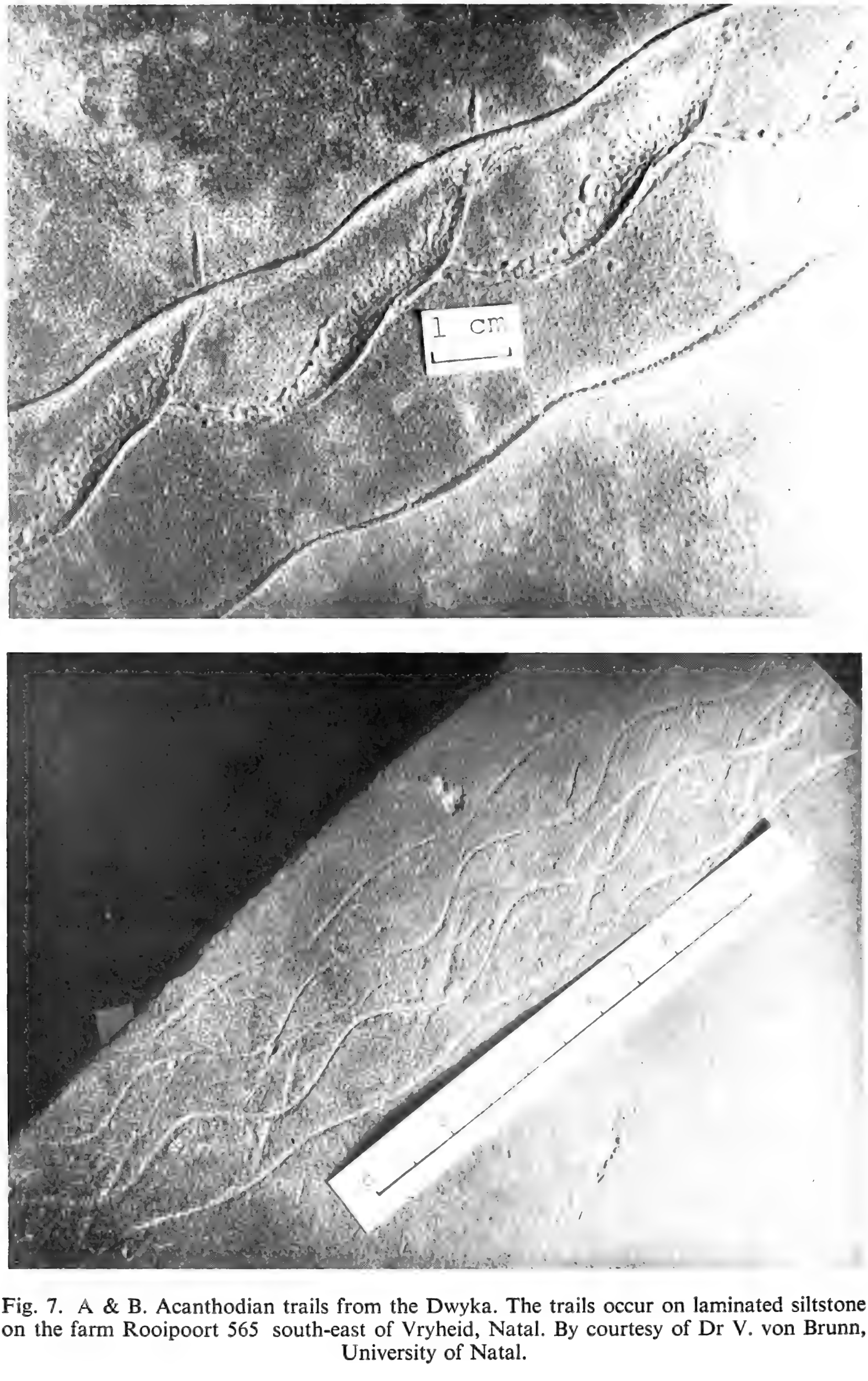

Fig. 7. A & B. Acanthodian trails from the Dwyka. The trails occur on laminated siltstone on the farm Rooipoort 565 south-east of Vryheid, Natal. By courtesy of Dr V. von Brunn, University of Natal.

small Palaeozoic fishes, 75 mm to 150 mm in length, have fins of an unusual type. Both paired and unpaired fins have a strong spine at the anterior edge and in some species there are additional spines situated ventrally between the pectoral and ventral spines. In many examples only spines are visible in fossil material. The first recorded acanthodian spine from Africa (Gardiner 1973) came from Upper Witteberg Shales 9,6 km south–south-east of Laingsburg, Cape Province. There are, however, examples of characteristic trails, attributed to the movement of acanthodian fishes over mud (Haughton 1927) to be found in Dwyka and Ecca deposits. These have been studied by Dr V. von Brunn, Natal University, Pietermaritzburg, and Miss Ann Anderson (1972) of the Bernard Price Institute for Palaeontological Research, Johannesburg. Miss Anderson continued her research on preserved animal trails and has presented her findings as a Ph.D. thesis.

FOSSIL FISH MATERIAL FROM THE DWYKA SERIES

Family **Elonichthyidae** Aldinger, 1937

Genus *Namaichthys* Gürich, 1923

1923—*Namaichthys* Gürich: 55.
1962—*Namaichthys* Gürich. Gardiner: 10.

Namaichthys schroederi Gürich, 1923

1923—*Namaichthys schroederi* Gürich: 55, figs 14–16, pl. 2.
1954—*Namaichthys schroederi* Gürich. Du Toit: 280.
1962—*Namaichthys schroederi* Gürich. Gardiner: 10, figs 1–3, pl. 6.
1973—*Namaichthys schroederi* Gürich. McLachlan & Anderson: 37, table 4.

Locality

Ganikobis, 16 km west of Tses Station, Berseba Reserve, South West Africa. Shale beds, bottom of Upper Dwyka Shales.

Holotype

The type material described by Gürich (1923) was housed in the Preussische Geologische Landesanstalt zu Berlin, now known as Sammlung des Zentralen Geologischen Dienstes der Staatlichen Geologischen Kommission der D.D.R., Berlin. As a result of World War II many of the specimens housed in this museum were lost.

Neotype

Geological Survey Department, Pretoria, Republic of South Africa, No. 7099 and counterpart, head and anterior part of body. From Ganikobis South West Africa.

Other material

Fragments of specimens in the British Museum (Natural History), London, from Ganikobis. Bernard Price Institute for Palaeontological Research, Johannesburg: specimens P.1–P.6 from Zwartbas, Warmbad Basin, South West

Africa; specimens P.11–P.23, P.29–P.42. Alexander McGregor Memorial Museum, Kimberley: specimens 4902 and 5008 from base of Upper Dwyka Shales near Kimberley (McLachlan & Anderson 1973 table 4).

Family **Cosmoptychiidae** Gardiner

1963—Family Cosmoptychiidae Gardiner: 259.

Genus *Watsonichthys* Aldinger, 1937

1937—Genus *Watsonichthys* Aldinger: 254, fig. 72.
1963—Genus *Watsonichthys* Aldinger. Gardiner: 260.

Watsonichthys lotzi (Gürich, 1923)

1923—*Acrolepis lotzi* Gürich: 34, figs 2, 4–9, pl. 1.
1937—*Acrolepis lotzi* Gürich. Aldinger: 260.
1954—*Acrolepis lotzi* Gürich. Du Toit: 280 (name only).
1962—*Watsonichthys lotzi* (Gürich). Gardiner: 16.
1963—*Watsonichthys lotzi* (Gürich). Gardiner: 260.
1973—*Watsonichthys lotzi* (Gürich). McLachlan & Anderson: 37, table 4.

Locality

Upper Dwyka Shales, Ganikobis, near Tses, South West Africa.

Holotype

Incomplete fish, showing underside of head and one third of the body. This specimen was in the Sammlung des Zentralen Geologischen Dienstes der Staatlichen Geologischen Kommission der D.D.R., Berlin, but may have been lost, together with Gürich's type material of *Namaichthys schroederi*, during World War II (Gardiner 1962: 16).

Other material

Specimens in the South African Museum: SAM–1062 and SAM–1066, collected by Mr A. C. Bain, February 1907, White Band, Upper Dwyka Shales, Toren, Hantam Mountains, near Calvinia. Recorded previously as *Palaeoniscus capensis* Broom but now provisionally assigned to *Watsonichthys lotzi*. Specimen SAM–1066, the largest available, is of the caudal section of a fish including the anal fin. The anal has about 50 rays and is distinctly fringe-like posteriorly. The caudal fin is heterocercal, inequilobate and deeply cleft. Enlarged fulcral scales are visible; scales on the sides ornamented with ridges which run longitudinally along the length of the scale and end in 4 to 7 serrations or teeth posteriorly, the number of serrations depending on the position of the scale.

There are also fragmented impressions of scales and portions of fishes from, the White Band, Upper Dwyka Shales, from near Loeriesfontein, in the South African Museum, registered number SAM–K1162. Except for one specimen containing numerous scales, these add little to our knowledge of this species. These scale impressions are excellent, some showing as many as 8–9 ridges, some joining posteriorly to end in 5–6 serrations. The fragmented caudal sections are identical with the caudal section of SAM–1066.

Family **Palaeoniscidae** Vogt, 1852

Genus *Palaeoniscum* Agassiz, 1833

1833—*Palaeoniscum* Agassiz: 5, 66.
1891—*Palaeoniscus* (*Palaeoniscum*) Blainville. Woodward: 476.
1967—*Palaeoniscus* Agassiz. Gardiner: 198.

Palaeoniscum capensis Broom, 1913

1913*a*—*Palaeoniscus capensis* Broom: 1, pl. 2(2).
1923—*Palaeoniscus capensis* Broom. Gürich: 28, 32.
1926—*Palaeoniscus capensis* Broom. Deecke: 122.
1937—*Palaeoniscus capensis* Broom. Aldinger: 96.
1954—*Palaeoniscus capensis* Broom. Du Toit: 279.
1962—*Palaeoniscus capensis* Broom. Gardiner: 16.
1973—*Palaeoniscus capensis* Broom. McLachlan & Anderson: 37, table 4.

Locality

Hantam Mountains, 19 km west of Calvinia, Upper Dwyka. The original record, crossed out in the register, states Waterval Farm, Prince Albert District, Cape Province.

Holotype

Caudal section of a fish in the South African Museum, SAM–1061.

Other material

Specimens SAM–1062 and SAM–1066 appear in previous literature as representing the same species, *P. capensis*. They are recorded as coming from the Hantam Mountains but they are not *P. capensis* and have been transferred to *Watsonichthys lotzi* provisionally. See note under *Watsonichthys lotzi*.

FOSSIL FISH MATERIAL FROM THE ECCA SERIES

Family **Elonichthyidae** Aldinger, 1937

Namaichthys digitata (Woodward)

Fig. 8

1891—*Acrolepis* (*?*) *digitata* Woodward: 508, pl. 15 (fig. 4).
1903—*Acrolepis molyneuxi* Woodward: 285, pl. 20.
1909—*Acrolepis digitata* Woodward. Rogers & Du Toit: 209 (name only).
1910—*Acrolepis* sp. Woodward: 229, pl. 9 (figs 2–4).
1913*b*— *?Acrolepis addamsi* Broom: 400, pl. 20. (See note below.)
1913*c*—*Acrolepis* (*?*) *digitata* Woodward. Broom: 391.
1923—*Acrolepis digitata* Woodward. Gürich: 32, 51.
1923—*Acrolepis molyneuxi* Woodward. Gürich: 32, 51.
1926—*Acrolepis* (*?*) *digitata* Woodward. Deeke: 105 (name only).
1937—*Acrolepis* (*?*) *digitata* Woodward. Aldinger: 258.
1947—*Acrolepis molyneuxi* Woodward. Macgregor: 50 (additional site).
1954—*Acrolepis molyneuxi* Woodward. Du Toit: 323 (name only).
1962—*Acrolepis* (*?*) *digitata* Woodward. Gardiner: 15 (emended diagnosis).
1962—*Acrolepis molyneuxi* Woodward. Gardiner: 15 (emended diagnosis).
1973— *?Acrolepis addamsi* Broom. McLachlan & Anderson: 56, table 4.

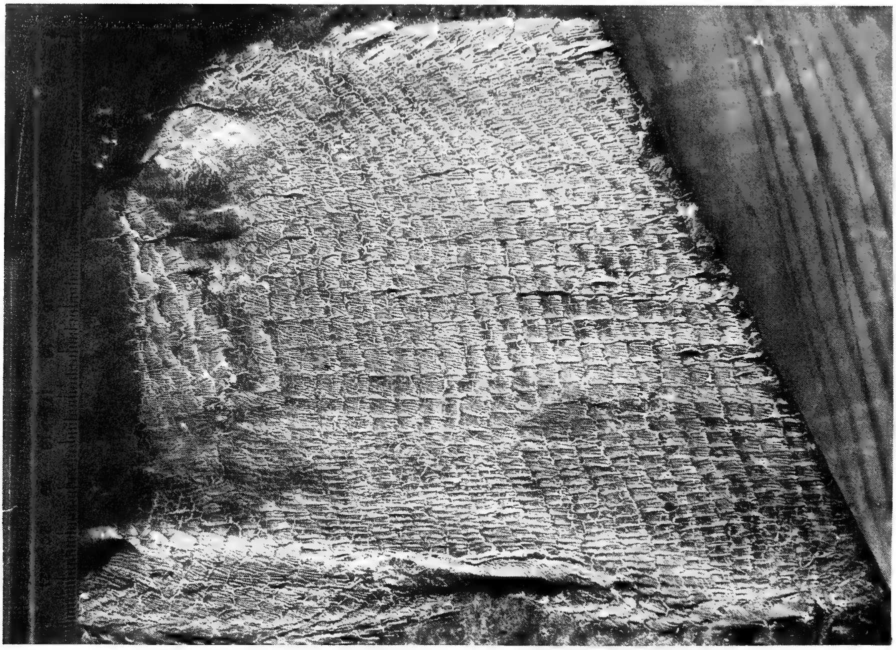

Fig. 8. *Namaichthys digitata* (Woodward). Photograph of Albany Museum specimen AM 263, the cast of which was used by Woodward as a paratype.

Locality

Acrolepis (?) *digitata:* Woodward's type, a group of scales, is recorded as coming from Graaff-Reinet. Woodward's paratype, Albany Museum specimen AM 263, is recorded by Broom (1913*c*) as coming from Coombs River, near Grahamstown, but this is also not strictly correct, see note below.

Acrolepis molyneuxi: Sengwe Coalfield, Rhodesia, Upper Ecca Shales.

(?) *Acrolepis addamsi* Broom, 1913, from the Premier Mine, Wesselton, Kimberley, 41-metre level, approximately of Dwyka age.

Holotype

Acrolepis (?) *digitata;* group of scales, in the British Museum (Natural History), London, No. 47080.

Paratype

In the British Museum (Natural History) a cast of Albany Museum, Grahamstown, specimen AM 263, cast BM(NH) P.6300. Broom (1913*c*) records AM 263 (Fig. 8) as coming from Koomes (Coombs) River, 24 km east of Grahamstown, but an older record states 'Fish River'. As it appeared that the slab had been washed down the Fish River, and may have been discovered at the confluence of the Coombs and Fish Rivers, it was sent to Dr J. W. Kitching for examination. Kitching reported (*in litt.* 1969): 'I have examined the slab with the fossil fish on it and have no doubt in my mind that it is a piece of slaty shale

Fig. 8A. Scales of *Namaichthys cf. digitata* (Woodward) approximately 5 mm × 5 mm showing 'downwardly directed denticulations'. Specimen F.36 collected Libertas Farm, annex Fountains Farm, Pearston, C.P. by J. W. Kitching, Bernard Price Institute, Johannesburg.

derived from the Ecca Beds. The slab is badly water-worn and must have been carried by water for some distance. It compares very favourably with the Ecca shales in Natal which also yielded fish scales.' In his 'Note on palaeoniscid fish-scales from the Ecca shales, near Ladysmith' Woodward (1910) remarked on the resemblance of these scales to those of *Acrolepis* (*?*) *digitata* and *Acrolepis molyneuxi*.

Other material

In the South African Museum: SAM–985, Sengwe Coalfield, Rhodesia; SAM–K4637, farm Zwartskraal, Prince Albert District, from the lowest part of the Upper Ecca. Specimens from the same site in the Albany Museum, AM 4774. In the British Museum (Natural History) a group of scales assigned to *Acrolepis molyneuxi*, P.9840.

In the National Museum, Bulawayo, Rhodesia, specimen 5913, a large fish, lacking detail, some 36 cm in length. Specimens QG 14, fragments, in the Queen Victoria Museum, Salisbury. Some of these latter have well-preserved *Glossopteris* impressions as well.

Family **Coelacanthidae** Agassiz, 1843

Genus *Coelacanthus* Agassiz, 1843

Coelacanthus dendrites Gardiner

1973—*Coelacanthus dendrites* Gardiner: 33, fig. 1.

Locality

Coal Measures of Somkele, KwaZulu (northern Natal), South Africa.

Holotype

In the British Museum (Natural History) specimen P.10510.

Other material

Identical scales occur in the Madumabisa Shales, Chimwar Ranch, Gwacei Valley, Rhodesia, British Museum (Natural History) specimens P.27563–5. Like the Coal Measures of Somkele the Madumabisa Shales are considered to be Lower Beaufort.

Similar scales have also been recorded from nodules well below the White Band in the lower parts of the Dwyka sediments at Klipneus in the Warmbad basin, South West Africa.

FOSSIL FISH MATERIAL FROM THE BEAUFORT SERIES

Family **Atherstoniidae** Gardiner, 1967

1967—Atherstoniidae Gardiner: 176, 198.

Genus *Atherstonia* Woodward, 1889

1889*a*—*Atherstonia* Woodward: 242.
1928—*Broometta* Chabakov: 1291.

Atherstonia scutata Woodward, 1889

Fig. 9

1856—(?) *Palaeoniscus sculptus* Egerton: 227, pl. 28 (figs 28–30, 32, 35–36, 39–42).
1856—(?) *Palaeoniscus bainii* Egerton: 227, pl. 28 (figs 26–27, 31, 33–34, 37–38).
1876—(?) *Hypterus bainii* Owen: 9.
1889*a*—*Atherstonia scutata* Woodward: 242, figs 1–3.
1891—(?) *Palaeoniscus sculptus* Egerton. Woodward: 485.
    (?) *Palaeoniscus bainii* Egerton. Woodward: 485.
    Atherstonia scutata Woodward. Woodward: 514.
1913*a*—*Atherstonia cairncrossi* Broom: 3, pl. 1 (fig. 2).
1913*c*—*Amblypterus capensis* Broom: 392, pl. 28.
1923—*Atherstonia scutata* Woodward. Gürich: 32, 53, figs 12, 13a–b.
    (?) *Palaeoniscus bainii* Egerton. Gürich: 32.
    (?) *Palaeoniscus sculptus* Egerton. Gürich: 32.
1926—(?) *Palaeoniscus sculptus* Egerton. Deeke: 122.
    (?) *Palaeoniscus bainii* Egerton. Deeke: 122.
1928—*Broometta cairncrossi* Chabakov: 1281.
1937—(?) *Palaeoniscus sculptus* Egerton. Aldinger: 96.
    (?) *Palaeoniscus bainii* Egerton. Aldinger: 96.
1946—(?) *Palaeoniscus sculptus* Egerton. Bond: 128, pl. 10.
1962—(?) *Namaichthys sculptus* (Egerton). Gardiner: 14.

Locality

The type specimen of *Atherstonia scutata* Woodward is one of four specimens which came from Colesberg, and which was sent to the British Museum (Natural History) by Dr W. Guyborn Atherstone of Grahamstown. The fossil site lies within the *Daptocephalus* Zone (Kitching 1972) of the Beaufort Series.

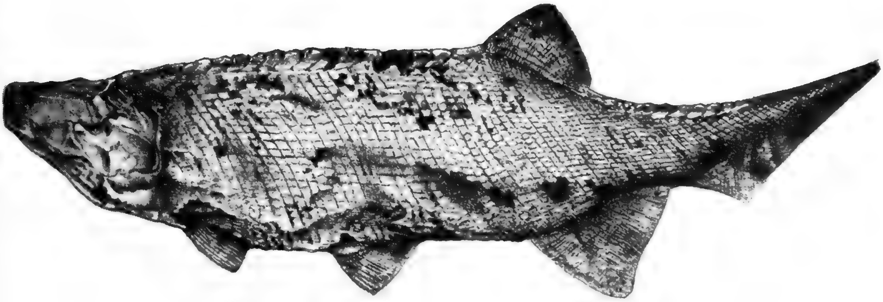

Fig. 9. *Atherstonia scutata* Woodward. Illustration of type specimen P.4735 in the British Museum (Natural History). Total length approximately 25 cm.

Holotype

An almost complete specimen BM(NH) P.4735 in the British Museum (Natural History), London.

Other material

Specimens AM 260, AM 261 and AM 262 in the Albany Museum, Grahamstown, which came from the type locality, Colesberg.

The type specimen of *Amblypterus capensis* Broom, 1913, which came from a quarry near Alice, Cape Province. The counterpart of this fish fossil is in the British Museum (Natural History), P.46007, labelled originally as *Hypterus bainii* Owen, but identified as *Atherstonia scutata* by Woodward.

Note

The species *Palaeoniscus sculptus* and *Palaeoniscus bainii* described by Egerton (1856) were described from scanty and poorly preserved scales collected on Styl Krantz (Steilekrans) Farm near New Bethesda, north of Graaff-Reinet. The syntypes are in the British Museum (Natural History), P.12192, P.12193 and P.12194. Both the material and the description are unsatisfactory for identification purposes. The species *Hypterus bainii* Owen, 1876, was not described, only the name was submitted (BM(NH) P.46007).

The Albany Museum has fragments of fish from Styl Krantz, mostly scales, recorded AM 4149, some of which have been examined by Gardiner. These scales can be referred to *Atherstonia scutata*. Kitching has informed Jubb (*in litt*. 1973) that he has collected at Styl Krantz and, apart from fish scales, has found no other fish material. The horizon where fish scales were found can be referred to the *Daptocephalus* Zone (Kitching 1972).

Atherstonia seeleyi Woodward, 1893

Figs 10, 12–13

1893—*Atherstonia seeleyi* Woodward: 393, pl. 17 (figs 3–3a).

Locality

Farm Klip Fontein, south-west of Fraserburg, Nieuwveldt Range, Cape Colony. *Daptocephalus* Zone, Lower Beaufort.

Syntype

Fragment of a fish with distinctive scales, in the British Museum (Natural History) P.8613 (Fig. 10).

Other material

A number of fine specimens, V 55–V 64 in the Victoria West Museum, V 63 and V 64 being almost complete, from Blourug 16 km east of Victoria West (Figs 12–13).

Atherstonia minor Woodward, 1893

Fig. 11, 14

1893—*Atnerstonia minor* Woodward: 395, pl. 17 (figs 2–2a).

Locality

Farm Klip Fontein, south-west of Fraserburg, Nieuwveldt Range, Cape Colony. *Daptocephalus* Zone, Lower Beaufort.

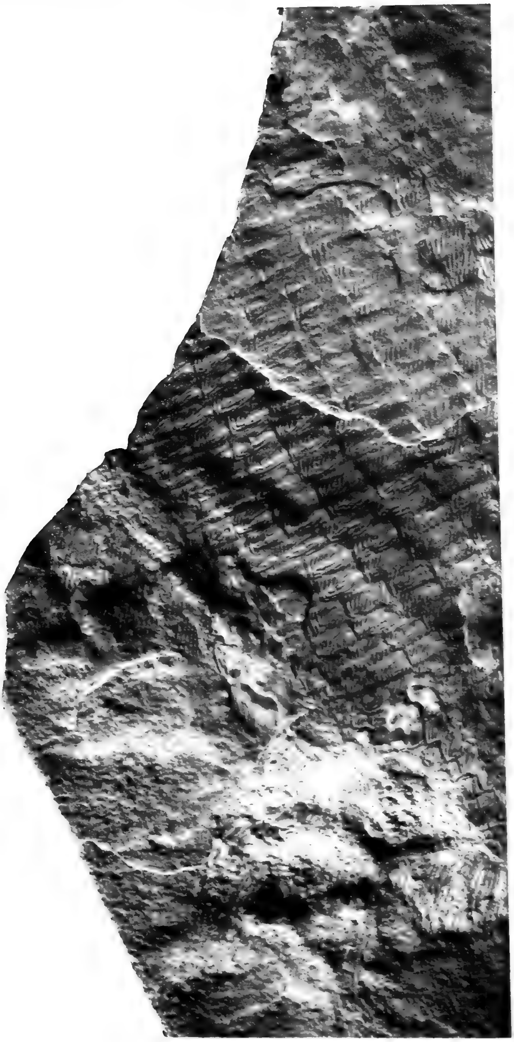

Fig. 10. Holotype of *Atherstonia seeleyi* Woodward, British Museum (Natural History) P.8613. × 2. By courtesy British Museum (Nat. Hist.), London.

Syntype

Scales only; middle portion of small fish with distinctive scales, in the British Museum (Natural History) P.8614 (Fig. 11).

Other material

Almost complete specimen in the Albany Museum, AM 4290, from Plaatjiesfontein near Dwaal, Hanover District. Also fragments from Blouhoogte, New Bethesda District.

Both the above sites are considered to be in the *Daptocephalus* Zone (Kitching 1972: 309–311; Kitching *in litt.* 1973).

Family **Elonichthyidae** Aldinger, 1937

Genus *Elonichthys* Giebel, 1848

1848—*Elonichthys* Giebel: 249.
1937—*Elonichthys* Giebel. Aldinger: 16.
1967—*Elonichthys* Giebel. Gardiner: 197.

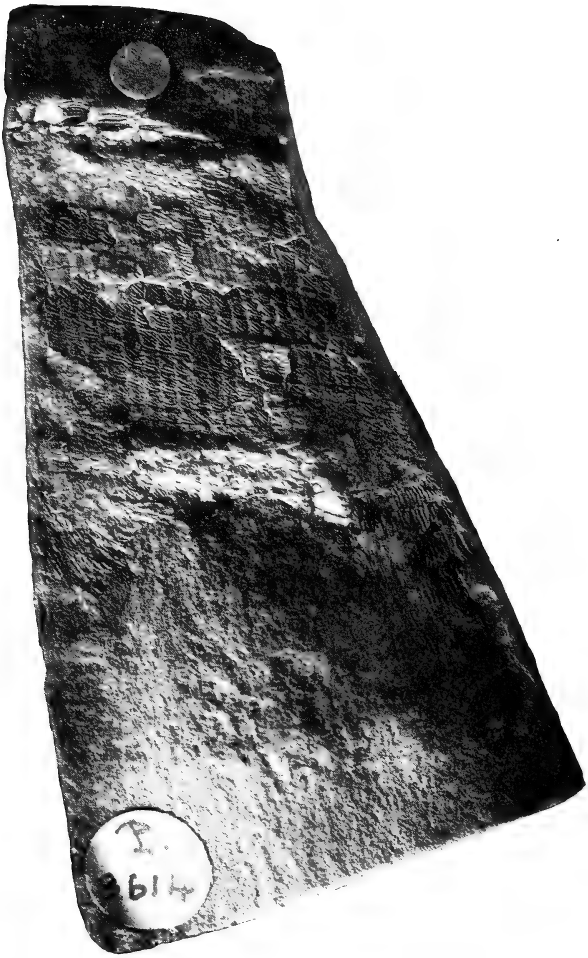

Fig. 11. Holotype of *Atherstonia minor* Woodward. British Museum (Natural History) P.8614. × 2. By courtesy British Museum (Nat. Hist.), London.

Fig. 12. *Atherstonia seeleyi* Woodward. Specimen V.63, Victoria West Museum. Total length approximately 19 cm. By courtesy of the Victoria West Museum.

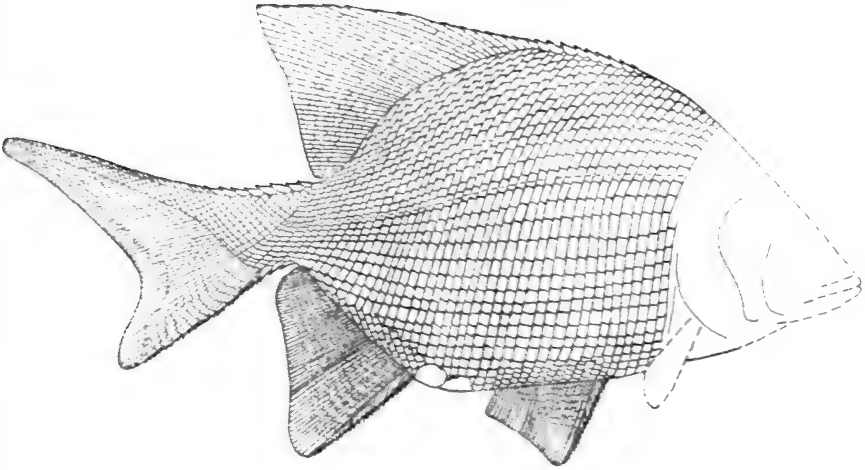

Fig. 12A. Reconstruction of *Atherstonia seeleyi* Woodward by M. A. Cooper from material in the Victoria West Museum. Total length approximately 17 cm.

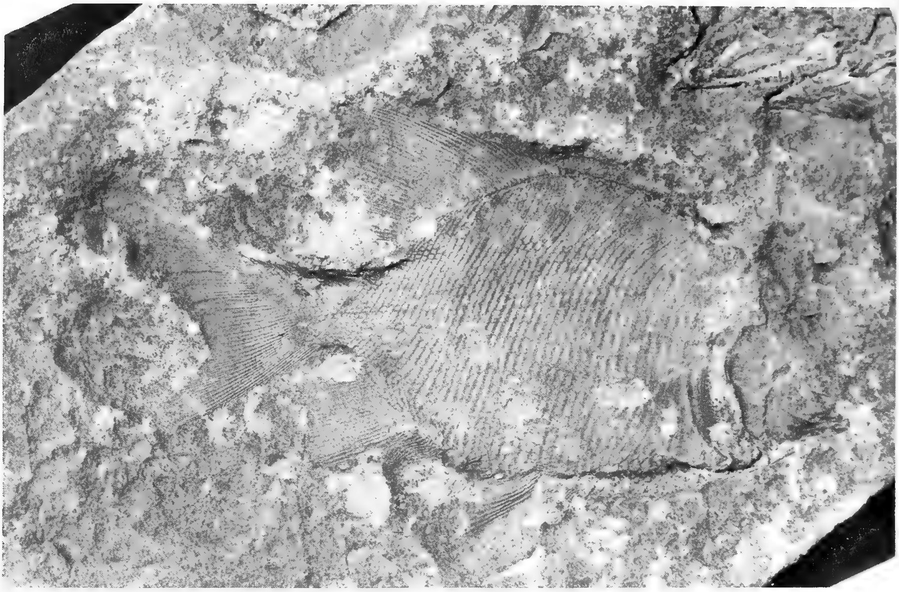

Fig. 13. *Atherstonia seeleyi* Woodward. Specimen V.64, Victoria West Museum. Total length approximately 17 cm. By courtesy of the Victoria West Museum.

Elonichthys whaitsi Broom, 1913

1913*a*—*Elonichthys whaitsi* Broom: 2, pl. 2 (fig. 2).
1923—*Elonichthys whaitsi* Broom. Gürich: 32.
1926—*Elonichthys whaitsi* Broom. Deeke: 111.
1962—*Elonichthys whaitsi* Broom. Gardiner: 17.

Locality

Droogvoets Farm, Fraserburg District, Lower Beaufort Series, *Cistecephalus* Zone.

Holotype

Almost complete fish, well preserved, in the South African Museum, SAM–2358.

Other material

None.

Note

There is a remarkable resemblance between *Elonichthys whaitsi* and *Elonichthys browni* (Broom) from Bekker's Kraal, Rouxville District, Orange Free State, a species from the *Cynognathus* Zone, Upper Beaufort Series.

Fig. 14. *Atherstonia minor* Woodward. Specimen AM 4290 in the Albany Museum. Total length approximately 12 cm.

Family **Platysomidae** Young, 1866

Genus *Caruichthys* Broom

1913*a*—*Caruichthys* Broom: 4.
1967—*Caruichthys* Broom. Gardiner: 197.

Caruichthys ornatus Broom

1913*a*—*Caruichthys ornatus* Broom: 4, pl. 1 (fig. 1).

Locality

Lystrosaurus Zone of the Beaufort Series. Described as coming from the Doorn River, Cradock District.

Holotype

Part of a fish, poorly preserved, with the caudal section missing, in the South African Museum, SAM–748.

Other material

None.

Note

In a letter from Mr J. van Rensburg, Secretary, Cradock Divisional Council, C/2, dated 9 October 1974, he states: 'As far as I can establish the farm Doorn River where a fish fossil was discovered by a Mr J. S. du Plessis in 1905 is farm No 232/2. It adjoins the farm Lorraine and is about twenty-seven miles from Cradock on the road to Graaff-Reinet.'

Family **Hybontidae** Owen, 1846

Genus *Hybodus* Agassiz

1837—*Hybodus* Agassiz: vol. 3: 41.
1932—*Hybodus* Agassiz. Zittel: 68, figs 94–95.

Hybodus africanus Broom

Fig. 15

1909*a*—*Hybodus africanus* Broom: 252, pl. 12 (fig. 1).

Locality

Lower *Cynognathus* Zone of the Beaufort Series at Bekker's Kraal, Rouxville, Orange Free State.

Holotype

Almost complete fish in the South African Museum, SAM–1082.

Other material

Fragments SAM–1084, SAM–1183, SAM–1185, SAM–1186, SAM–2776, SAM–6020, SAM–6039.

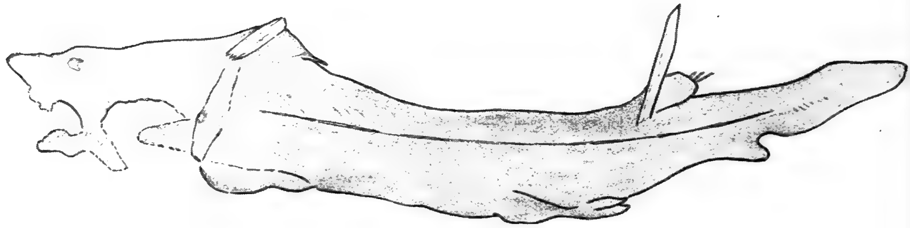

Fig. 15. *Hybodus africanus* Broom. Total length approximately 21 cm. Reconstruction by Broom.

Family **Ceratodontidae** Gill, 1872

Genus *Ceratodus* Agassiz, 1837

1837—*Ceratodus* Agassiz: vol. 3: 129.
1891—*Ceratodus* Agassiz. Woodward: pt 2: 264.
1932—*Ceratodus* Agassiz. Zittel: 104, figs 164–165.

Ceratodus capensis Woodward, 1889

1889—*Ceratodus capensis* Woodward: 243, pl. 14 (fig. 4).
1891—*Ceratodus capensis* Woodward. Woodward: 269.
1909*a*—*Ceratodus capensis* Woodward. Broom: 253.

Locality

Recorded as coming from Smithfield, Orange Free State, but no doubt part of the fish fauna of Bekker's Kraal, Lower *Cynognathus* Zone.

Holotype

Dental plate wanting one or perhaps two anterior denticles in the British Museum (Natural History), specimen P.4807.

Ceratodus kannemeyeri Seeley, 1897

1897—*Ceratodus kannemeyeri* Seeley: 543.
1909*a*—*Ceratodus kannemeyeri* Seeley. Broom: 253.

Locality

Given as Kraai Fontein, Indwe District, above the coal seams, and thus probably within the Molteno Beds.

Holotype

No record.

Ceratodus ornatus Broom, 1909

1909*a*—*Ceratodus ornatus* Broom: 253, pl. 12 (fig. 4).

Locality

Found at Vaalbank near Burghersdorp, *Cynognathus* Zone of the Beaufort Series.

Holotype

Dental plate, specimen SAM–3601 in the South African Museum.

Family **Coelacanthidae** Agassiz, 1843

Coelacanthus africanus Broom

1905—*Coelacanthus africanus* Broom: 338.
1909*a*—*Coelacanthus africanus* Broom. Broom: 253, pl. 12 (fig. 3).
1931—*Coelacanthus africanus* Broom. Brough: 238, pl. 1 (fig. 1).

Locality

Bekker's Kraal Farm, Rouxville District, *Cynognathus* Zone, Upper Beaufort Series.

Holotype

In the South African Museum SAM–6027, Bekker's Kraal, Rouxville. Caudal section of a fish.

Other material

In the South African Museum SAM–6028, from same locality as SAM–6027. Small section of a fish.

Family **Elonichthyidae** Aldinger, 1937

Genus *Elonichthys* Giebel, 1848

1848—*Elonichthys* Giebel: 249.
1937—*Elonichthys* Giebel. Aldinger: 16.
1967—*Elonichthys* Giebel. Gardiner: 197.

Elonichthys browni (Broom, 1909)

1909*a*—*Oxygnathus browni* Broom: 259, pl. 13 (fig. 8).
1931—*Oxygnathus browni* Broom. Brough: 236.
1932—*Oxygnathus browni* Broom. Zittel: vol. 2: 120.

Locality

Bekker's Kraal Farm, Rouxville District, Orange Free State. *Cynognathus* Zone, Upper Beaufort Series.

Holotype

Nearly complete fish with *Cleithrolepidina* and other species on the same slab in the South African Museum, SAM–5978.

Other material

South African Museum, SAM–001, no locality, is probably the same species. Attention is drawn to the similarity between this species and *Elonichthys whaitsi* Broom from Droogvoets Farm, Fraserburg, *Cistecephalus* Zone.

Family **Dicellopygidae** Romer, 1945

Genus *Dicellopygae* Brough, 1931

1931—*Dicellopygae* Brough: 238.
1945—*Dicellopygae* Brough. Romer: 579.
1967—*Dicellopygae* Brough. Gardiner: 198.

Dicellopygae draperi (Woodward, 1893)

Figs. 16–17

1893—*Dictyopygae* (*?*) *draperi* Woodward: 393, pl. 17 (fig. 1).
1909*a*—*Helichthys draperi* (Woodward). Broom: 257, pl. 13 (fig. 6).
1909*a*—*Helichthys tenuis* Broom: 258.
1909*b*—*Helichthys draperi* (Woodward). Broom: 286.
1931—*Dicellopygae macrodentatus* Brough: 239, fig. 1.
1931—*Helichthys draperi* (Woodward). Brough: 247.
1931—*Dictyopygae* (*?*) *draperi* (Woodward). Brough: 247.

Locality

Stated by Woodward (1893) to be Rouxville, Orange Free State, Stormberg Series, Upper Karoo. This undoubtedly refers to Bekker's Kraal, Rouxville District, *Cynognathus* Zone, Upper Beaufort Series.

Holotype

A complete fish except for the caudal fin. Housed in the National Museum, Bloemfontein, specimen QR 1507. This specimen was housed in the Natal Museum, Pietermaritzburg, for a while with the registered number NM 20.

Other material

Specimen SAM–6022, South African Museum, described and figured by Broom (1909*a*), which came from Bekker's Kraal, Rouxville District, *Cynognathus* Zone, Upper Beaufort Series; SAM–2762, which came from the same site.

The Natal Museum, Pietermaritzburg, has two incomplete specimens, registered number NM 21, which were described by Woodward (1893) as representing an 'Unidentified Palaeoniscid Fish'. The locality recorded is

Fig. 16. *Dicellopygae draperi* (Woodward). Specimen SAM–6022 in the South African Museum. Total length approximately 13 cm.

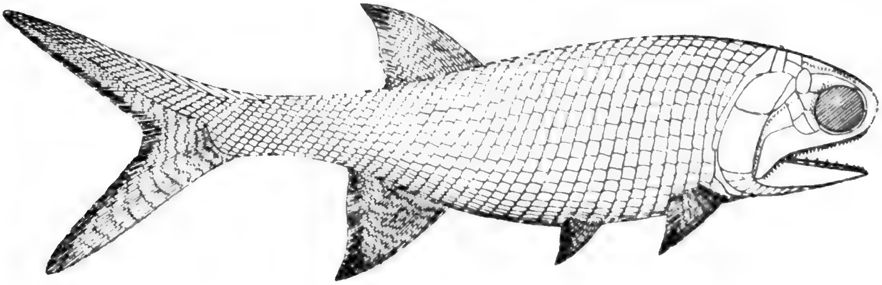

Fig. 17. *Dicellopygae draperi* (Woodward). Reconstruction of *Dicellopygae macrodentatus* Brough, by Brough. Total length approximately 11,5 cm.

'Molteno Beds, 150 feet above main coal seam, Sutherlands Quarry, Biggarsberg'. These specimens have been examined and identified as representing *Dicellopygae draperi*. As Biggarsberg lies well within the Ecca Series this matter was referred to Mr M. H. P. Rilett, the geologist who was responsible for mapping the Biggarsberg area. Mr Rilett has confirmed (*in litt.* 1973) that the recorded locality is in doubt.

Identical to NM 21 above is fossil fish 1201D in the Port Elizabeth Museum (Jubb 1973). This fossil is recorded as coming from near a coal mine, Stormberg, Cape Province. This specimen, like QR 1507 above, was sent to Gardiner who identified it as *Dicellopygae draperi*. Here again the recorded locality requires careful investigation.

Dicellopygae lissocephalus Brough, 1931

1931—*Dicellopygae lissocephalus* Brough: 242, fig. 2.

Locality

Lower *Cynognathus* Zone, Lower Beaufort Series, Bekker's Kraal, Rouxville District, Orange Free State.

Holotype

In the Watson Collection, London University, P.13.

Note

Poor preservation does not enable definite diagnosis but it is highly probable that *D. lissocephalus* is a synonym of *D. draperi* (Woodward, 1893).

Family **Redfieldiidae** Berg, 1940

Genus *Daedalichthys* Brough, 1931

1931—*Daedalichthys* Brough: 245.
1973—*Daedalichthys* Brough. Hutchinson: 271.

Daedalichthys formosa (Broom, 1909)

Fig. 18

1909*a*—*Dictyopyge formosa* Broom: 262.
1931—*Daedalichthys higginsi* Brough: 245, fig. 3, pl. 1 (fig. 4).
1934—*Daedalichthys higginsi* Brough: 559, fig. 1, pl. 1 (fig. 1).
1973—*Daedalichthys higginsi* Brough. Hutchinson: 273, figs 19–20.

Locality

Lower *Cynognathus* Zone of the Beaufort Series at Bekker's Kraal, Rouxville, Orange Free State.

Holotype

Almost complete fish in the South African Museum, SAM–2761.

Holotype of *Daedalichthys higginsi* Brough, University Museum of Zoology, Cambridge, GN 301.

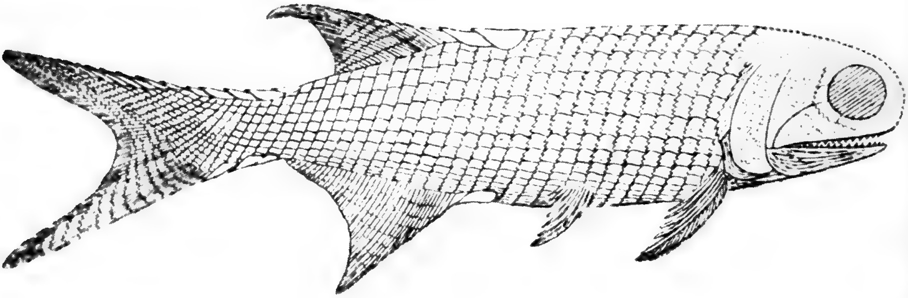

Fig. 18. *Daedalichthys formosa* (Broom). Reconstruction of *Daedalichthys higginsi* Brough, by Brough. Total length approximately 10,5 cm.

Other material

British Museum (Natural History): P.17532, P.17533, P.17538.

Genus *Helichthys* Broom, 1909

1909*a*—*Helichthys* Broom: 254.
1931—*Helichthys* Broom. Brough: 246.
1932—*Helichthys* Broom. Zittel: 123.
1967—*Helichthys* Broom. Gardiner: 200.
1973—*Helichthys* Broom. Hutchinson: 274.

Helichthys browni Broom, 1909

Fig. 19

1909*a*—*Helichthys browni* Broom: 254, pl. 12 (fig. 7).
1931—*Helichthys stegopygae* Brough: 252, fig. 6.
1931—*Helichthys obesus* Brough: 254, fig. 7.

Locality

Lower *Cynognathus* Zone, of the Beaufort Series at Bekker's Kraal, Rouxville, Orange Free State.

Holotype

Almost complete fish with caudal fin missing, in the South African Museum, specimen SAM–2767.

Other material

South African Museum: specimens SAM–1086, SAM–1182, SAM–5980, SAM–6021.

Holotype of *Helichthys stegopygae* Brough, P 12D in the D. M. S. Watson Collection, University College, London. Holotype of *Helichthys obesus* Brough, P 12B and P 12C in the D. M. S. Watson Collection, University College, London.

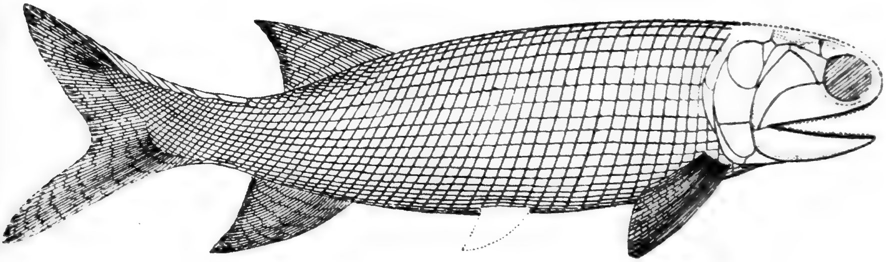

Fig. 19. *Helichthys browni* Broom. Reconstruction of *Helichthys stegopygae* Brough, by Brough. Total length approximately 10,5 cm.

Helichthys elegans Brough, 1931

Fig. 20

1931—*Helichthys elegans* Brough: 248, figs 4–5, pl. 2 (figs 1–2).
1973—*Helichthys elegans* Brough. Hutchinson: 275, figs 21–22.

Locality

Lower *Cynognathus* Zone of the Beaufort Series, Bekker's Kraal, Rouxville District, Orange Free State.

Holotype

Represented by three nearly complete specimens in the D. M. S. Watson Collection, housed in the University Museum of Zoology, Cambridge, P 13A, P 13B, P 19A.

Other material

Specimen GN 316, in the University Museum of Zoology, Cambridge, England.

Helicthys ctenipteryx Brough, 1931

1931—*Helicthys ctenipteryx* Brough: 256, fig. 8.

Locality

Lower *Cynognathus* Zone of the Beaufort Series, Bekker's Kraal, Rouxville, Orange Free State.

Holotype

An imperfect specimen lacking caudal fin, dorsal fin and posterior part of body, P 12A in the D. M. S. Watson Collection, University College, London.

Other material

Counterpart of above, P 11A.

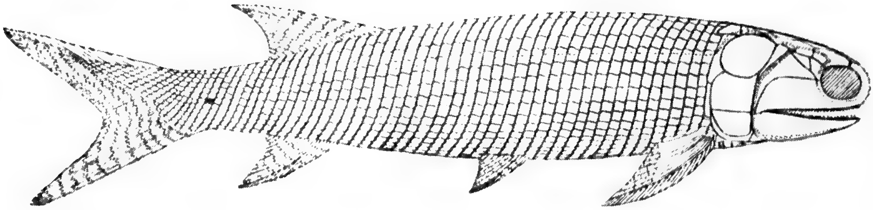

Fig. 20. *Helichthys elegans* Brough. Reconstruction by Brough. Total length about 10,5 cm.

Helichthys grandipennis Brough, 1931

Fig. 21

1931—*Helichthys grandipennis* Brough: 259, fig. 10.

Locality

Lower *Cynognathus* Zone of the Beaufort Series, Bekker's Kraal, Rouxville, Orange Free State.

Holotype

Almost complete specimen, lacking tail and part of head, in the D. M. S. Watson Collection, University College, London, P 14 and P 24.

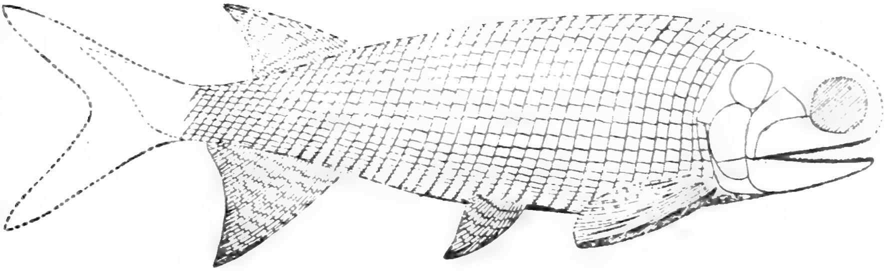

Fig. 21. *Helichthys grandipennis* Brough. Reconstruction by Brough. Total length about 11 cm

Family **Colobodontidae** Stensiö, 1916

Genus *Meidiichthys* Brough, 1931

1931—*Meidiichthys* Brough: 261.
1973—*Meidiichthys* Brough. Hutchinson: 292.

Meidiichthys browni (Broom, 1909)

Fig. 22

1909*a*—*Pholidophorus browni* Broom: 267, pl. 13 (fig. 10).
1931—*Meidiichthys browni* (Broom). Brough: 262, figs 11–12, pl. 4 (fig. 1).
1973—*Meidiichthys browni* (Broom). Hutchinson: 293, figs 32–33.

Locality

Lower *Cynognathus* Zone of Beaufort Series at Bekker's Kraal, Rouxville, Orange Free State.

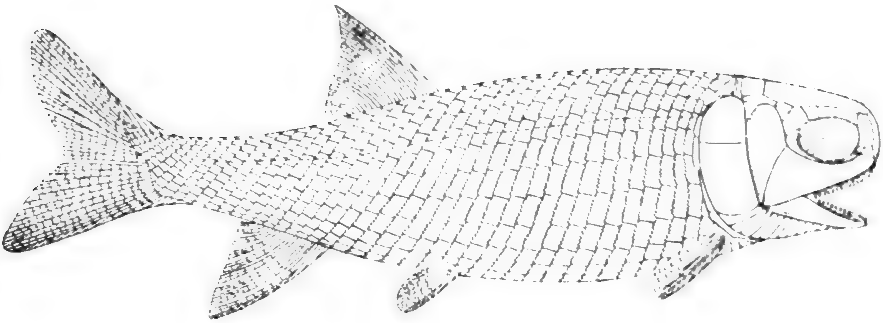

Fig. 22. *Meidiichthys browni* (Broom). Reconstruction by Brough. Total length approximately 10 cm.

Holotype

In the South African Museum, specimen SAM–6030.

Other material

South African Museum: SAM–6034. British Museum (Natural History): P.16074, P.16075. University Museum of Zoology, Cambridge: GN 304–305, GN 311–314, GN 317, GN 348, GN 355.

Family **Brookvaliidae** Berg, 1940

Genus *Atopocephala* Brough

1934—*Atopocephala* Brough: 564.
1973—*Atopocephala* Brough. Hutchinson: 249.

Atopocephala watsoni Brough

1934—*Atopocephala watsoni* Brough: 564, figs 2–3, pl. 1.
1973—*Atopocephala watsoni* Brough. Hutchinson: 250, fig. 7.

Locality

Lower *Cynognathus* Zone, Beaufort Series, Bekker's Kraal, Rouxville, Orange Free State.

Holotype

A specimen with counterpart, the only specimen known to date, P.16079–80, British Museum (Natural History), London.

Family **Dictyopygidae** Hay, 1889

Genus *Ischnolepis* Haughton

1934—*Ischnolepis* Haughton: 97.
1973—*Ischnolepis Haughton.* Hutchinson: 239.

Ischnolepis bancrofti Haughton

Figs 23–24

1934—*Ischnolepis bancrofti* Haughton: 97, figs 1–2, pl. 29.
1973—*Ischnolepis bancrofti* Haughton. Hutchinson: 240, figs 1–6.

Locality

Madumabisa shales, 132 km from Kabwe (Broken Hill), Lunsempfwa Valley, Zambia. Upper Beaufort Series (Hutchinson 1973: 237).

Holotype

Two almost complete fish on slab SAM–9338 together with counterpart SAM–9339 in the South African Museum.

Other material

Material in the British Museum (Natural History) consists of two blocks, part and counterpart, P.27577–8, and several fragments recorded P.27579; all contain specimens of *Ischnolepis* together with an unidentified palaeoniscoid. From the same locality there are in the South African Museum specimens SAM–9340, SAM–9350, SAM–9352 and SAM–9353 which contain fragments of possibly two species of unidentified palaeoniscoid fishes.

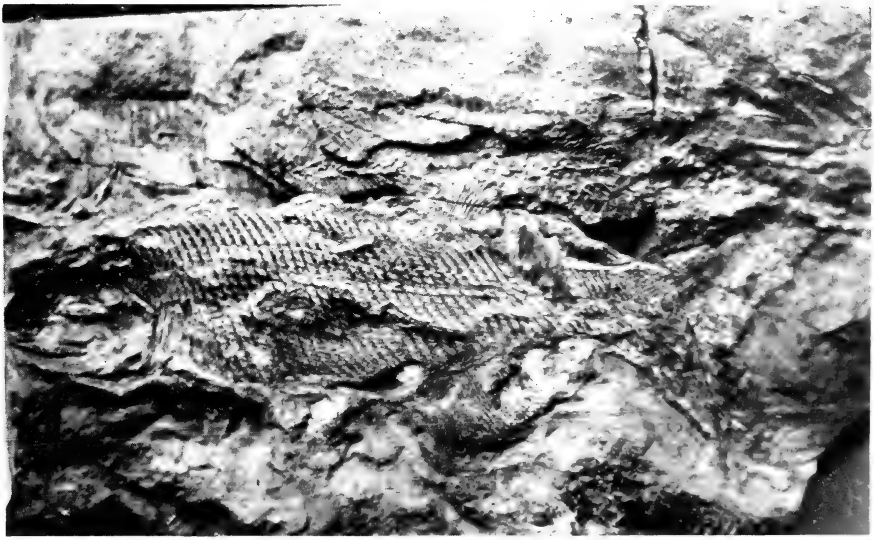

Fig. 23. *Ichnolepis bancrofti* Haughton. Photograph of SAM–9338 in South African Museum.

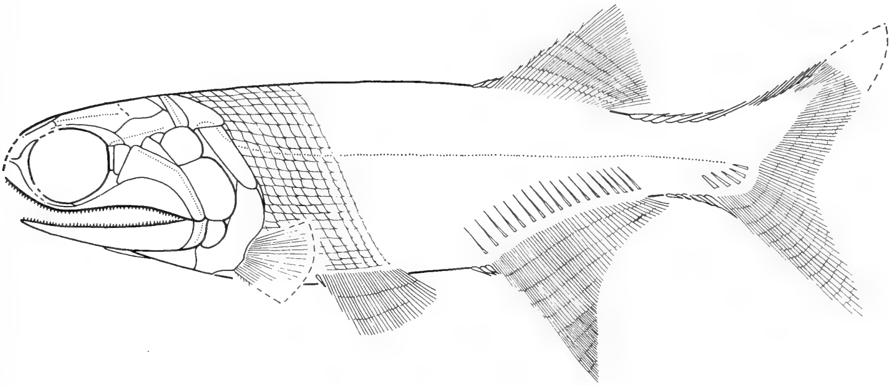

Fig. 24. *Ichnolepis bancrofti* Haughton. Reconstruction by Hutchinson. Total length approximately 7 cm.

Family **Cleithrolepididae** Wade, 1935

Genus *Cleithrolepidina* Berg, 1940

1940—*Cleithrolepidina* Berg: 405.
1973—*Cleithrolepidina* Berg. Hutchinson: 302.

Cleithrolepidina extoni (Woodward)

Figs 25–26

1888—*Cleithrolepis extoni* Woodward: 141, pl. 6 (figs 6–7).
1895—*Cleithrolepis extoni* Woodward. Woodward: 156.
1909*a*—*Cleithrolepis extoni* Woodward. Broom: 264.
1973—*Cleithrolepidina extoni* (Woodward). Hutchinson: 305, figs 40–42.

Locality

Lower *Cynognathus* Zone, Beaufort Series at Bekker's Kraal, Rouxville, Orange Free State.

Holotype

In the British Museum (Natural History) specimen P.5455.

Other material

British Museum (Natural History): specimens P.5455a, P.16043 with counterpart P.16044, P.16045, P.16105 with counterpart P.16106. South

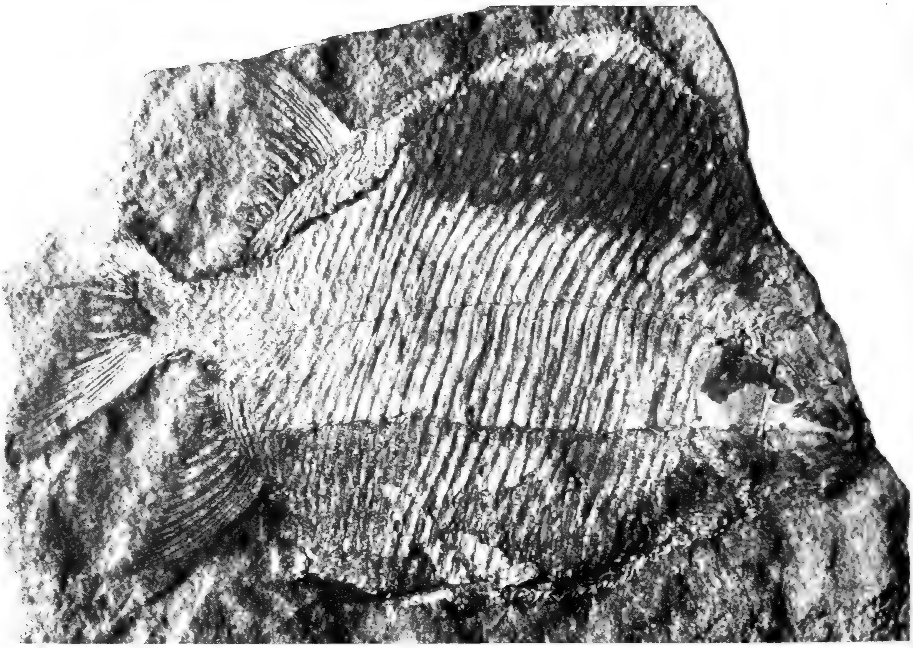

Fig. 25. *Cleithrolepidina extoni* (Woodward). Specimen SAM–1335, counterpart SAM–1085 in the South African Museum. Total length approximately 10 cm.

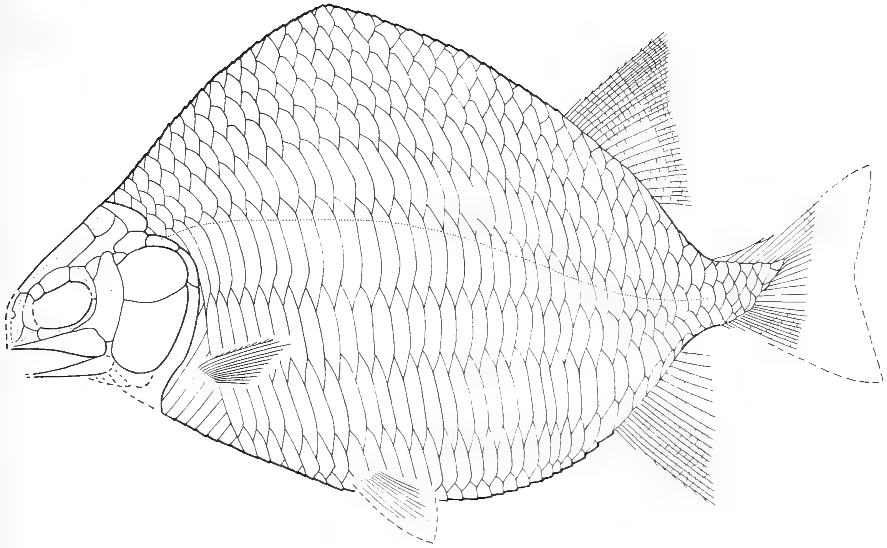

Fig. 26. *Cleithrolepidina extoni* (Woodward). Reconstruction by Hutchinson. Total length 10 cm.

African Museum: specimens SAM–1059 (Caledon River), SAM–1085, SAM–1335 and SAM–5981.

Cleithrolepidina minor (Broom)

Fig. 27

1909*a*—*Cleithrolepis minor* Broom: 266, pl. 13 (fig. 9).
1931—*Cleithrolepis minor* Broom. Brough: 267, fig. 13.
1940—*Cleithrolepidina minor* (Broom). Berg: 405.
1973—*Cleithrolepidina minor* (Broom). Hutchinson: 303, figs 38–39.

Locality

Lower *Cynognathus* Zone, Beaufort Series, at Bekker's Kraal, Rouxville, Orange Free State.

Holotype

In the South African Museum, SAM–6037.

Other material

British Museum (Natural History): P.12594, P.16048–51, P.16067–8 and counterpart P.16069. University Museum of Zoology, Cambridge: GN 194, GN 293, GN 328, GN 330 and counterpart GN 331. South African Museum: SAM–1081, SAM–1084, SAM–5963, SAM–5983, SAM–5985, SAM–5987 and SAM–5988 all from Bekker's Kraal, Rouxville; SAM–2763 from the Caledon River, Orange Free State.

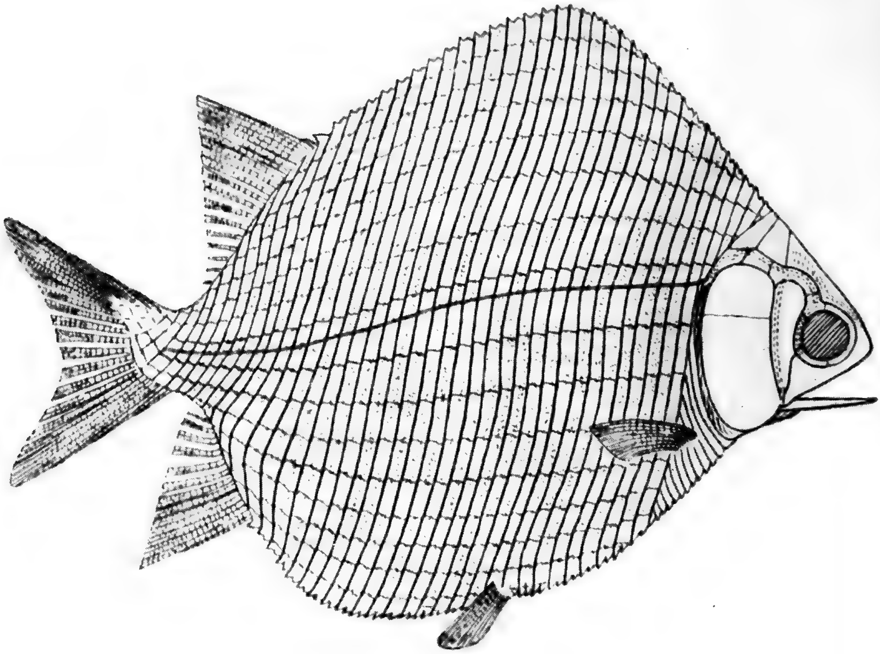

Fig. 27. *Cleithrolepidina minor* (Broom). Reconstruction by Brough. Total length approximately 5,3 cm.

Family **Hydropessidae** Hutchinson, 1973

Genus *Hydropessum* Broom, 1909

1909*a*—*Hydropessum* Broom: 266, pl. 12 (fig. 5).
1967—*Hydropessum* Broom. Gardiner: 200.
1973—*Hydropessum* Broom. Hutchinson: 316, figs 45–47.

Hydropessum kannemeyeri Broom, 1909

Fig. 28

1909*a*—*Hydropessum kannemeyeri* Broom: 266, pl. 12 (fig. 5).
1931—*Hydropessum kannemeyeri* Broom. Brough: 236.
1973—*Hydropessum kannemeyeri* Broom. Hutchinson: 316, figs 45–47.

Locality

Lower *Cynognathus* Zone of the Beaufort Series, Bekker's Kraal, Rouxville District, Orange Free State.

Holotype

South African Museum specimen SAM–1334.

Other material

British Museum (Natural History): P.16042, P.16180, P.16181. University Museum of Zoology, Cambridge: No. 358. See Figure 28 for reconstruction by Hutchinson.

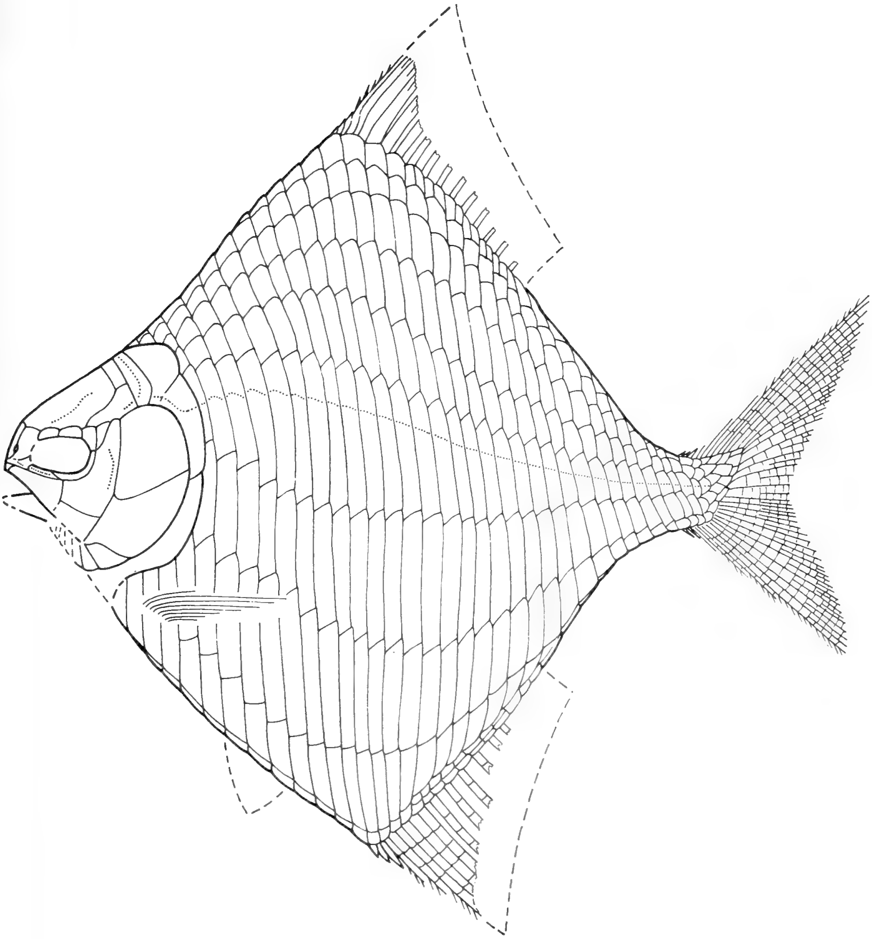

Fig. 28. *Hydropessum kannemeyeri* Broom. Reconstruction by Hutchinson. Total length approximately 9 cm.

FOSSIL FISH MATERIAL FROM THE STORMBERG SERIES

Family **Dictyopygidae** Hay, 1889

Genus *Endemichthys* Forey & Gardiner, 1973

Endemichthys likhoeli Forey & Gardiner

1973—*Endemichthys likhoeli* Forey & Gardiner: 29, fig. 1.

Locality

Specimen found lying on a Cave Sandstone plateau at the base of the north-eastern tip of Mount Likhoeli, 5 km south by south-east of Mafeteng, Mafeteng District, Lesotho.

Holotype

University College, London, catalogue number UC 10 000. Posterior section of a fish showing dorsal and anal fins.

Other material

None.

Family **Semionotidae** Agassiz, 1832

Genus *Semionotus* Agassiz, 1832

1832—*Semionotus* Agassiz: 140.
1895—*Semionotus* Agassiz. Woodward: 55.
1960—*Semionotus* Agassiz. Gardiner: 355.

Semionotus capensis Woodward, 1888

Figs 29–30

1888—*Semionotus capensis* Woodward: 138, pl. 6 (figs 1–5).
1895—*Semionotus capensis* Woodward. Woodward: 58.
1909*a*—*Semionotus capensis* Woodward. Broom: 262.
1915—*Semionotus capensis* Woodward. Hennig: 49, pl. 3.
1924—*Semionotus capensis* Woodward. Haughton: 388.
1960—*Semionotus capensis* Woodward. Gardiner: 355, fig. 71.
1973—*Semionotus capensis* Woodward. Jubb: 17, figs 1–5.

Locality

Base of Cave Sandstone, Stormberg Series, Ficksburg, Orange Free State.

Holotype

Four nearly complete fishes on one block, British Museum (Natural History) P.4089.

Other material

Abundant material in state and provincial museums, some particularly good specimens being:

South African Museum: SAM–K436, Clocolan, O.F.S.; SAM–1065, Ficksburg, O.F.S.
National Museum, Bloemfontein: C 286, Senekal, O.F.S.; C 292, Senekal, O.F.S.; C 2606, Ficksburg, O.F.S.; C 2821, Ficksburg, O.F.S.; C 2827, Ficksburg, O.F.S.; C 2842, Witteberge, north-west of Fouriesburg, O.F.S.
Natal Museum, Pietermaritzburg: NM 741, NM 821, Ficksburg, O.F.S.
McGregor Memorial Museum, Kimberley: No. 428, Ficksburg, O.F.S.
Transvaal Museum, Pretoria: No. 2829, two slabs from Ficksburg; No. 2830, one small block from Rouxville, O.F.S.
Albany Museum, Grahamstown: No. 477, two slabs from National Museum, Bloemfontein, recorded as coming from Senekal, O.F.S.

As described by Jubb (1973) there are some interesting specimens, B.P.I. Nos 355, 750 and 752, from the Molteno Stage of the Stormberg Series, in the Bernard Price Institute for Palaeontological Research, which have been assigned provisionally to this species.

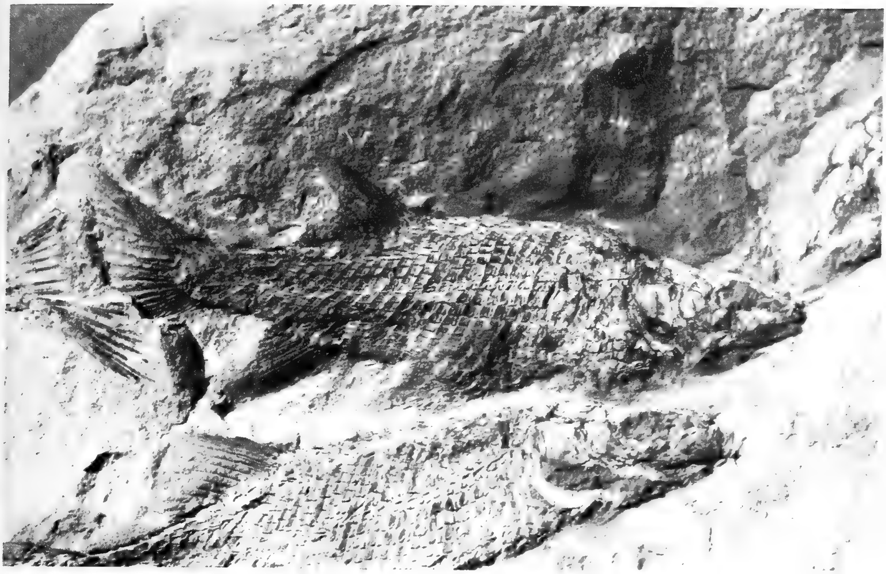

Fig. 29. *Semionotus capensis* Woodward. Specimen No. 428 in the McGregor Memorial Museum, Kimberley. Total length of upper fish 12 cm.

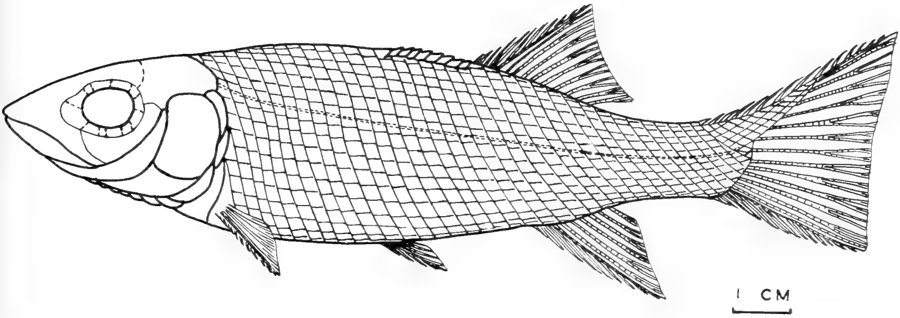

Fig. 29A. Reconstruction of *Semionotus capensis* Smith Woodward. Details taken from several specimens.

SPECIES WHOSE HORIZON IS OBSCURE

Family **Holuridae** Moy-Thomas, 1939

Genus *Disichthys* Broom, 1913

1913*b*—*Disichthys* Broom: 400.
1967—*Disichthys* Broom. Gardiner: 197.

Disichthys kimberleyensis Broom, 1913

1913*b*—*Disichthys kimberleyensis* Broom: 400, pl. 21 (figs 1–2).

Locality

From De Beers Wesselton Diamond Mine, Kimberley. Horizon obscure.

Holotype

A poorly preserved specimen, almost complete fish, McGregor Memorial Museum, Kimberley, No. 535.

Other material

Portion of a fish, poorly preserved, with the same number in the McGregor Memorial Museum, Kimberley.

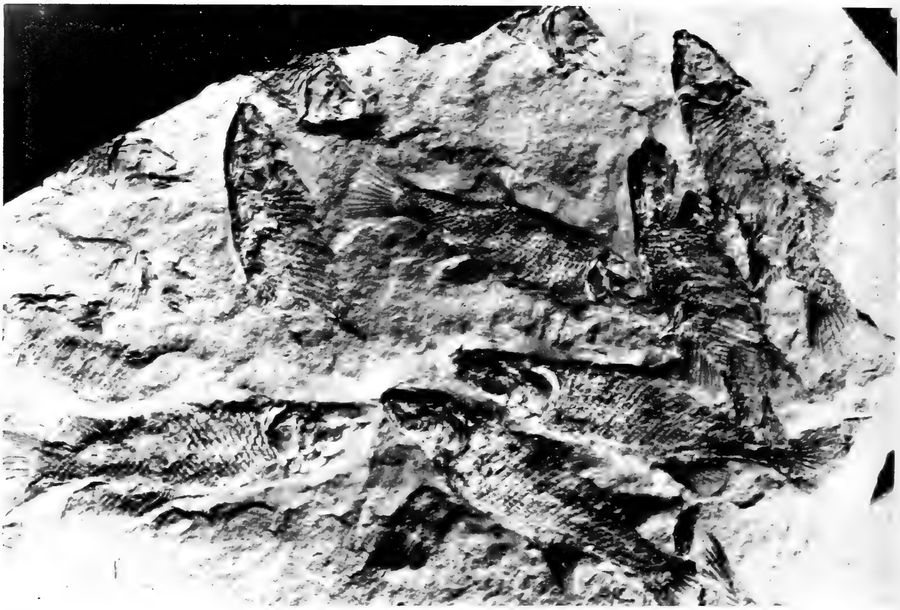

Fig. 30. *Semionotus capensis* Woodward. Specimen No. 428 in the McGregor Memorial Museum, showing concentration of fishes.

Family **Holuridae** Moy-Thomas, 1939

Genus *Peleichthys* Broom, 1913

1913*b*—*Peleichthys* Broom: 401.
1967—*Peleichthys* Broom. Gardiner: 197.

Peleichthys kimberleyensis Broom, 1913

1913*b*—*Peleichthys kimberleyensis* Broom: 401, pl. 22 (fig. 1).

Locality

De Beers Mine, Kimberley. Horizon obscure.

Holotype

Almost complete fish, poorly preserved, in the McGregor Memorial Museum, Kimberley, No. 536.

Other material

None.

FOSSIL FISH MATERIAL FROM TERTIARY MARINE DEPOSITS

ELASMOBRANCHII

The elasmobranchs listed are those which appear in current literature.

Family **Lamnidae**

Genus *Carcharodon* Müller & Henle, 1838

1838—*Carcharodon* Müller & Henle: 70.
1932—*Carcharodon* Müller & Henle. Zittel: 78, fig. 120.

Carcharodon megalodon Agassiz, 1843

Figs 31–32

1843—*Carcharodon megalodon* Agassiz: 247, pl. 29.
1889*b*—*Carcharodon megalodon* Agassiz. Woodward: pt 1: 417.
1932—*Carcharodon megalodon* Agassiz. Zittel: 78, fig. 120.
1954—*Carcharodon megalodon* Agassiz. Du Toit: 434.
1962—*Carcharodon megalodon* Agassiz. Mountain: 9.
1964—*Carcharodon megalodon* Agassiz. Davies: 47, fig. 23.
1973—*Carcharodon megalodon* Agassiz. Case: 36, figs 135–137.

Locality

Eocene and Phosphate Beds: Alabama and South Carolina, U.S.A. Miocene: France, Spain, Portugal, Malta, Sicily, Corsica, Germany, Austria and Maryland, U.S.A. Pliocene: Italy, Belgium and south-east England. Various Tertiary deposits: Arabian Desert, Central and South America, South Australia, New Zealand and South Africa.

Type specimens

Various detached teeth in the museums of Paris, Carlsruhe and Strassburg (Woodward 1889*b*).

Other material

Teeth from early Miocene: Uloa, Zululand. Mid to Upper Eocene: Bogenfels, South West Africa; Alexandria Beds in South Africa, especially Birbury Farm, Bathurst District, Albany Museum AM 903, AM 1905–1906, AM 2912, AM 2915, AM 2917–2918, AM 2920, AM 2924, AM 4255.

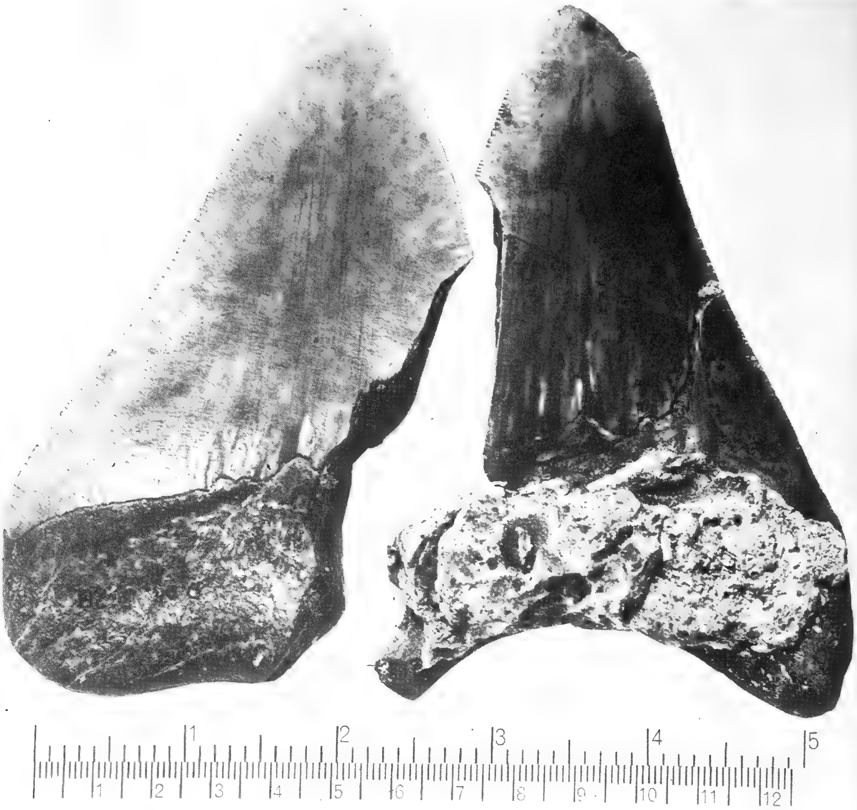

Fig. 31. Teeth of *Carcharodon megalodon* Agassiz from Uloa, Zululand. By courtesy of the Oceanographic Research Institute, Durban.

Carcharodon angustidens Agassiz, 1843

Fig. 33

1843—*Carcharodon angustidens* Agassiz: 255, pl. 28 (figs 20–25), pl. 30 (fig. 3).
1889*b*—*Carcharodon angustidens* Agassiz. Woodward: 412.
1954—*Carcharodon auriculatus* (Blainville). Du Toit: 434.
1962—*Carcharodon angustidens* Agassiz. Mountain: 9.
1973—*Carcharodon angustidens* Agassiz. Case: 35, figs 134, 138–139.

Locality

Middle and Upper Eocene: South-east England, northern France, Belgium, Bavaria, South Carolina and Alabama, U.S.A. Miocene: Western France, Belgium, north Germany, Italy, Sicily and Maryland, U.S.A. Pliocene: Antwerp, Belgium. Lower and Middle Tertiary: Egypt, Arabia, Australia, New Zealand and Alexandria Beds of South Africa.

Holotype

No record.

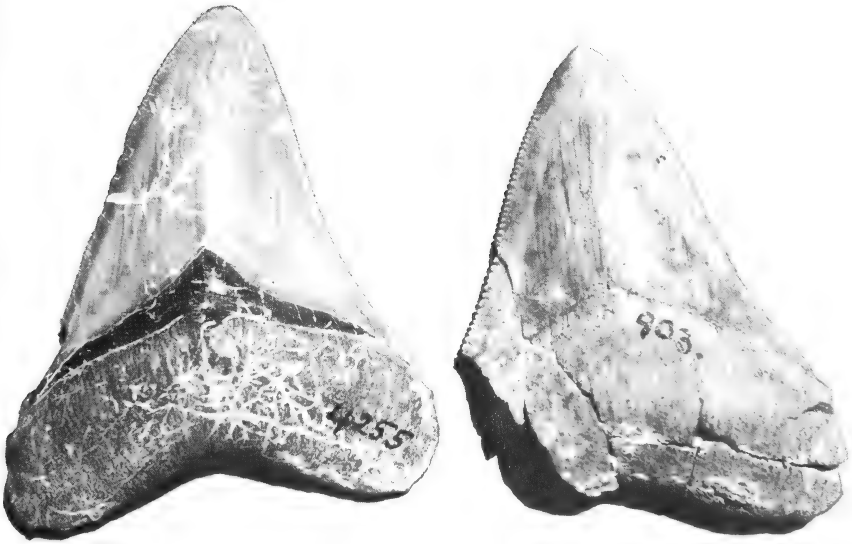

Fig. 32. Teeth of *Carcharodon megalodon* Agassiz from Birbury Farm, Bathurst District, south-east Cape. Albany Museum specimens AM 4255 and AM 903, the length of the former 70 mm.

Fig. 33. Teeth of *Carcharodon angustidens* Agassiz from Birbury Farm, Bathurst District, south-east Cape. Albany Museum specimens AM 1902 and AM 902, the former being 65 mm in length.

Other material

See Woodward (1889*b*: 411–415). In South Africa known from Birbury Farm, Bathurst District. Albany Museum specimens AM 902, AM 1898, AM 1902, AM 2913–2914, AM 4029.

Carcharodon sulcidens Agassiz, 1843

Fig. 34

1843—*Carcharodon sulcidens* Agassiz: 254, pl. 30*a* (figs 3–7).
1889*b*—*Carcharodon sulcidens* Agassiz. Woodward: 420.
1964—*Carcharodon sulcidens* Agassiz. Davies: 12, fig. 9.
1965—*Carcharodon sulcidens* Agassiz. Davies: 48, fig. 24.
1973—*Carcharodon sulcidens* Agassiz. Case: 35, fig. 134.

Locality

Pliocene: Italy, Sicily and England. Miocene and Eocene: South Carolina, U.S.A. Tertiary: Chili and South Africa, Uloa and Sapolwana Beds (Miocene), northern Zululand.

Holotype

Detached teeth, Palaeontological Museum, Munich (Münster Collection).

Other material

See Woodward (1889*b*: 420–421). Detached teeth in the Oceanographic Research Institute, Durban (Fig. 34).

Carcharodon carcharias (Linnaeus, 1758)

Fig. 35

1925—*Carcharodon carcharias* (Linnaeus). Barnard: 33, pl. 1 (fig. 7).
1932—*Carcharodon rondeleti* Müller & Henle. Zittel: 78.
1961—*Carcharodon carcharias* (Linnaeus). Smith: 49, pl. 1 (fig. 26).
1964—*Carcharodon carcharias* (Linnaeus). Davies: 9.
1973—*Carcharodon carcharias* (Linnaeus). Case: 44, figs 178–180.

This is a widely distributed species which dates back to the Miocene. Although specimens were not recorded by Davies (1964), material has since been collected at Sapolwana, Zululand. Two teeth from the collection in the Oceanographic Research Institute, Durban, are illustrated in Figure 35.

Genus *Oxyrhina* Agassiz, 1838

1838—*Oxyrhina* Agassiz: vol. 3: 86.
1889*b*—*Oxyrhina* Agassiz. Woodward: 376 (1).
1932—*Oxyrhina* Agassiz. Zittel: 77.

Oxyrhina desori Agassiz, 1843

1843—*Oxyrhina desori* Agassiz: vol. 3: 282, pl. 37 (figs 8–13).
1889*b*—*Oxyrhina desori* Agassiz. Woodward: 382.
1932—*Oxyrhina desori* Agassiz. Zittel: 77.
1962—*Oxyrhina desori* Agassiz. Mountain: 9.
1973—*Oxyrhina desori* Agassiz. Case: 36, fig. 151.

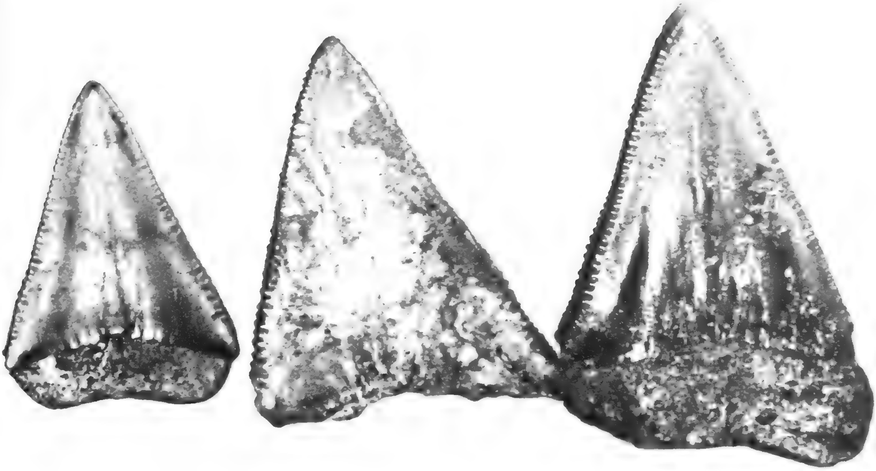

Fig. 34. Teeth of *Carcharodon sulcidens* Agassiz from Uloa, Zululand. By courtesy of the Oceanographic Research Institute, Durban. Largest tooth 60 mm in length.

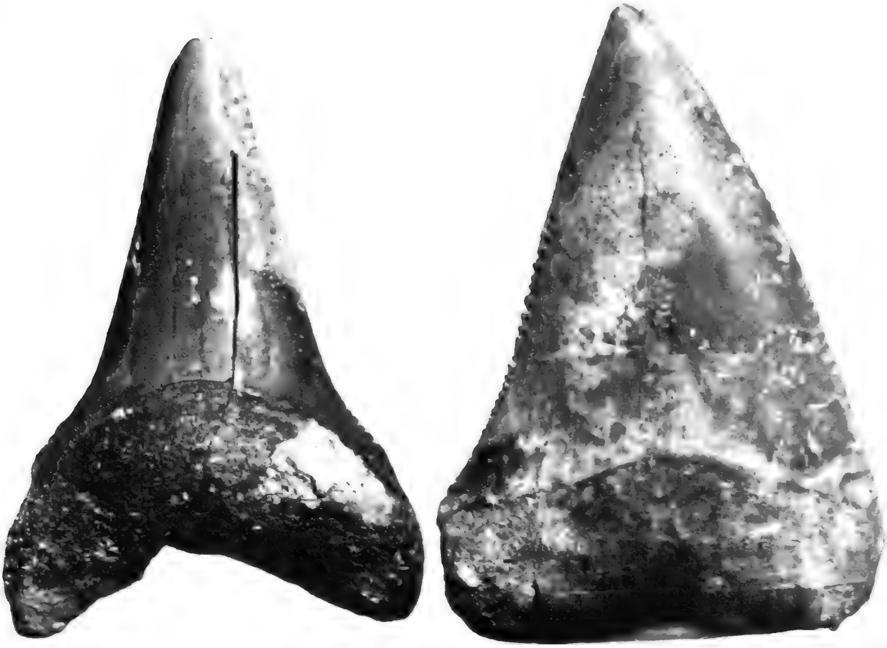

Fig. 35. Teeth of *Carcharodon carcharias* (Linnaeus) from Uloa, Zululand. By courtesy of the Oceanographic Research Institute, Durban. Larger tooth 52 mm in length.

Locality

Upper Eocene: Prussia, Italy, Alabama and South Carolina, U.S.A. Miocene: France, Belgium, Switzerland, Germany, Malta, Italy, Sicily and Corsica. Pliocene: Belgium and Italy. Alexandria Beds, South Africa.

Holotype

Detached teeth.

Other material

See Woodward (1889*b*: 383). Albany Museum material identified by Dr E. I. White of the British Museum (Natural History) cannot be traced.

Oxyrhina crassa Agassiz, 1843

Fig. 36

1843—*Oxyrhina crassa* Agassiz: vol. 3: 283, pl. 37 (fig. 16).
1871—*Oxyrhina benedeni* Le Hon: 6.
1889*b*—*Oxyrhina crassa* Agassiz. Woodward: 389.
1964—*Isurus benedictus* = (*Oxyrhina benedeni*) Davies: 12, fig. 11.
1965—*Isurus benedictus* = (*Oxyrhina benedeni*) Davies: 48, fig. 25.
1973—*Oxyrhina* (*benedeni*) *crassa* Agassiz. Case: 36, fig. 149.

Locality

Eocene: South Carolina and Alabama, U.S.A. Eocene or Miocene: Valley of the Rhine. Miocene: Sicily. Pliocene: Italy and Belgium.

Holotype

Detached tooth—no other record.

Other material

See Woodward (1889*b*: 390). Davies (1964), Oceanographic Research Institute, Durban, records one tooth from the Lower Miocene, Uloa, Zululand.

Family **Carchariidae**

Genus *Carcharias* Rafinesque, 1810

1810—*Carcharias* Rafinesque: 10.
1961—*Carcharias* Rafinesque. Smith: 48.
1963—*Carcharias* Rafinesque. Jordan: 77, 599.

Carcharias taurus Rafinesque, 1810

Fig. 37, 38C

1810—*Carcharias taurus* Rafinesque: 10.
1961—*Carcharias taurus* Rafinesque. Smith: 25, pl. 1 (fig. 25).
1964—*Carcharias taurus* Rafinesque. Davies: 11, fig. 10C.
1965—*Carcharias taurus* Rafinesque. Davies: 48, fig. 26C.
1973—*Carcharias taurus* Rafinesque. Case: 44, fig. 184.

Locality

Upper Cretaceous to present day, widely distributed.

Fig. 36. Tooth of *Oxyrhina crassa* Agassiz (*Oxyrhina benedeni* Le Hon) from Uloa, Zululand. By courtesy of the Oceanographic Research Institute. Total length 50 mm.

Holotype

Muséum National d'Histoire Naturelle, Paris.

Other material

Detached teeth from Miocene fossil beds, Sapolwana, South Africa, and recent material in the Oceanographic Research Institute, Durban. Detached teeth from Birbury Farm, Bathurst District in Albany Museum AM 4773A (Fig. 37).

Note

In some literature the genus *Carcharias* Rafinesque has been replaced by *Odontaspis* Agassiz, 1838.

Genus *Odontaspis* Agassiz, 1838

1838—*Odontaspis* Agassiz: vol. 3: 87.
1889*b*—*Odontaspis* Agassiz. Woodward: 360.
1932—*Odontaspis* Agassiz. Zittel: 76.

Fig. 37. Tooth of *Carcharias taurus* Rafinesque from Birbury Farm, Bathurst District, south-east Cape. Total length 35 mm. See also Figure 38C showing teeth of *C. taurus* from Sapolwana, Zululand.

Odontaspis macrota (Agassiz, 1843)

1843—*Otodus macrotus* Agassiz: vol. 3: 273, pl. 32 (figs 29–31).
1889*b*—*Lamna macrota* (Agassiz). Woodward: 402.
1932—*Odontaspis macrota* (Agassiz). Zittel: 76.
1962—*Odontaspis macrota* (Agassiz). Mountain: 9.
1973—*Odontaspis macrota* (Agassiz). Case: 32, fig. 119.

Locality

Lower Eocene: South-east England and South Carolina, U.S.A. Middle Eocene: London and Hampshire Basins, and northern France. Upper Eocene: Southern Germany. Lower Miocene: Belgium and West Germany, Oamaru and Waipara Systems, New Zealand. Alexandria Beds, South Africa.

Holotype

Detached teeth, Muséum National d'Histoire Naturelle, Paris.

Other material

See Woodward (1889*b*: 402–403). Albany Museum AM 4773B, Birbury Farm, Bathurst District.

Note

Quoting Woodward (1889*b*: 360): 'Teeth of all but the few hindermost series with a high, narrow, compressed coronal eminence, flanked by one or two pairs of small pointed denticles; the fourth tooth from the symphysis upon each side of the upper jaw very small; the teeth of the most anterior pair in the lower jaw small and relatively very slender.'

Odontaspis elegans (Agassiz, 1843)

1843—*Odontaspis elegans* (Agassiz): vol. 3: 289, pl. 35 (figs 1–5), pl. 37 (fig. 59).
1889*b*—*Odontaspis elegans* (Agassiz). Woodward: 361.
1932—*Odontaspis elegans* (Agassiz). Zittel: 76.
1962—*Odontaspis elegans* (Agassiz). Mountain: 9.
1973—*Odontaspis elegans* (Agassiz). Case: 32, fig. 118.

Locality

Eocene: south-east England, France, Belgium and Germany, also Alabama and South Carolina, U.S.A. Lower Miocene: Belgium and Corsica, also Oamaru and Waireka Series, New Zealand.

Holotype

Detached teeth, no other record.

Other material

See Woodward (1889*b*: 363–366). Albany Museum specimen AM 4118 identified by Dr E. I. White, British Museum (Natural History), with reservation.

Family **Galeorhinidae**

Genus *Galeocerdo* Müller & Henle, 1837

1837—*Galeocerdo* Müller & Henle: 308.
1889—*Galeocerdo* Müller & Henle. Woodward: 443.
1932—*Galeocerdo* Müller & Henle. Zittel: 79, fig. 121.
1961—*Galeocerdo* Müller & Henle. Smith: 43.

Galeocerdo cuvier (Le Seuer, 1818)

Fig. 38A

1818—*Galeocerdo cuvier* (Le Seuer): vol. 1: 222–235
1961—*Galeocerdo cuvier* (Le Seuer). Smith: 44, pl. 1 (fig. 14).
1964—*Galeocerdo cuvier* (Le Seuer). Davies: 11, fig. 10A.
1965—*Galeocerdo cuvier* (Le Seuer). Davies: 48, fig. 26A.
1973—*Galeocerdo cuvier* (Le Seuer). Case: 44, fig. 187.

Locality

From Eocene marine beds to present day where found in all warm seas.

Holotype

Muséum National d'Histoire Naturelle, Paris.

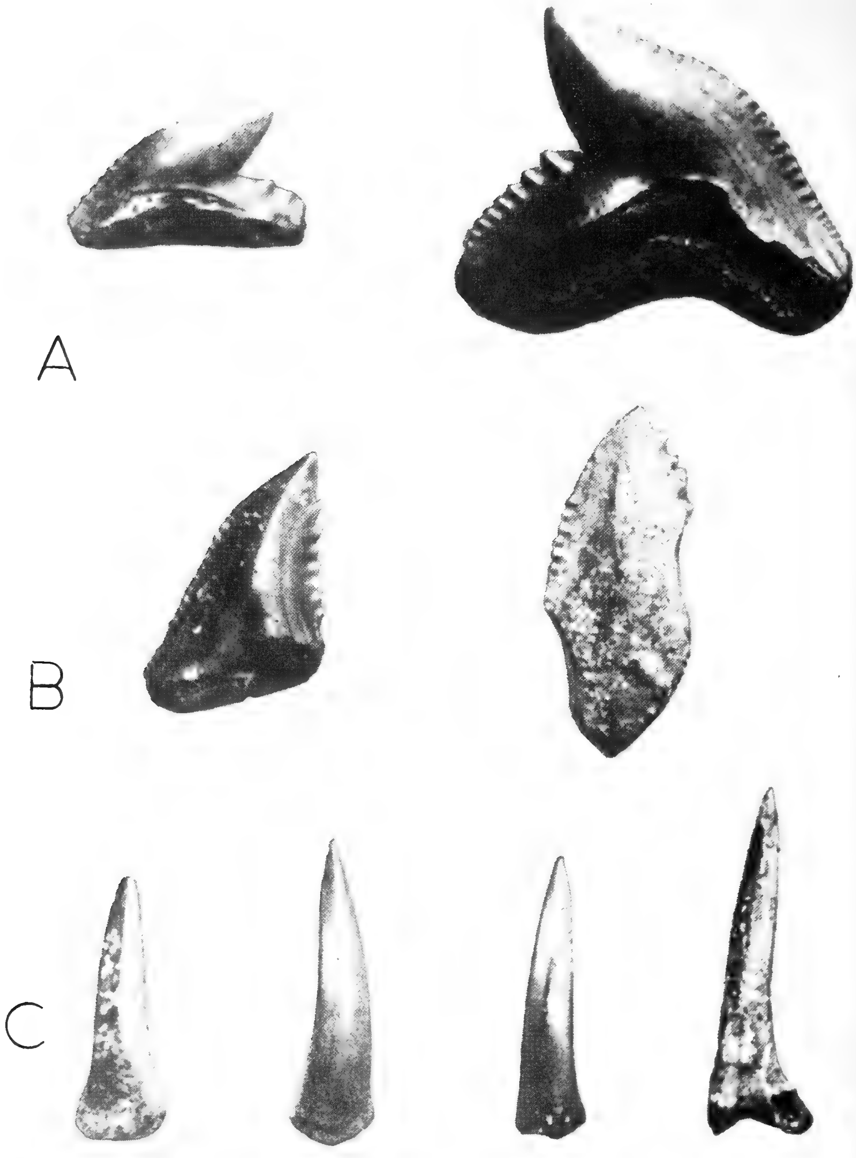

Fig. 38. A. Teeth of *Galeocerdo cuvier* (Le Sueur) from Uloa, Zululand. Larger tooth 25 mm. B. Teeth of *Hemipristis serra* Agassiz from Uloa, Zululand. Larger tooth 25 mm. C. Teeth of *Carcharias taurus* Rafinesque from Uloa, Zululand. Largest tooth 25 mm. By courtesy of the Oceanographic Research Institute, Durban.

Other material

Detached teeth from Miocene deposits, Sapolwana, Zululand, South Africa, as well as recent material housed in the Oceanographic Research Institute, Durban.

Genus *Hemipristis* Agassiz, 1843

1843—*Hemipristis* Agassiz: 237.
1889*b*—*Hemipristis* Agassiz. Woodward: 448.
1932—*Hemipristis* Agassiz. Zittel: 79.

Hemipristis serra Agassiz, 1843

Fig. 38B

1843—*Hemipristis serra* Agassiz: vol. 3: 237, pl. 27 (figs 18–30).
1889*b*—*Hemipristis serra* Agassiz. Woodward: 449.
1964—*Hemipristis serra* Agassiz. Davies: 11, fig. 10B.
1965—*Hemipristis serra* Agassiz. Davies: 48, fig. 26B.
1973—*Hemipristis serra* Agassiz. Case: 36, fig. 146.

Locality

Eocene: South Carolina, U.S.A. Miocene: Germany, Austria, Italy, Sicily, Malta, Corsica, Switzerland, France, Maryland and Virginia, U.S.A. Pliocene: Tuscany. Miocene beds: Uloa, Zululand, South Africa.

Holotype

Detached teeth, Muséum National d'Histoire Naturelle, Paris.

Other material

See Woodward (1889*b*: 450–451). Detached teeth in the Oceanographic Research Institute, Durban.

ACKNOWLEDGEMENTS

In August 1974 Dr A. J. D. Meiring of Alice presented fossil fish material to the Albany Museum. This came from a quarry (Lower Beaufort) near the town. On one slab and counterpart, together with a specimen of *Atherstonia scutata*, there is the anterior portion of a large palaeoniscid. From photographs and description sent to him Gardiner has provisionally identified this fossil as representing an undescribed species of the genus *Pteronisculus* White, 1933, of the Triassic of Madagascar.

Current research by Mr J. Loock of the University of the Orange Free State, and Dr J. N. Theron of the Geological Survey Department, also involves undescribed fish fossil material. Theron's specimens from the Bokkeveld Beds date back to the Devonian. Both these workers are collaborating with Gardiner.

Miss Ann Anderson, Mrs Seidi Anderson, Dr J. W. Kitching and Dr I. R. McLachlan of the Bernard Price Institute for Palaeontological Research have been unstinting in their supply of material and data. Illustrations of sharks' teeth from Uloa, Zululand, were kindly supplied by the Director of the Oceanographic Research Institute, Durban.

During his tour of the state and provincial museums to examine fish fossil material Jubb was provided with every assistance by the respective directors and staff members concerned. This co-operation is gratefully acknowledged, as well as that of the Curator and staff of the Bulawayo Museum, Rhodesia.

This project, proposed by Dr T. H. Barry, Director of the South African Museum, and made possible by the collaboration of Dr B. R. Gardiner of the Queen Elizabeth College, London, is part of a research programme sponsored by the South African Council for Scientific and Industrial Research, Pretoria. By courtesy of the Director, Mr C. F. Jacot Guillarmod, this catalogue was prepared at the Albany Museum, Grahamstown.

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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 (figs 8a–b).
Nucula largillierti Philippi, 1861: 87
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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R. A. JUBB & B. G. GARDINER

A PRELIMINARY CATALOGUE OF IDENTIFIABLE FOSSIL FISH MATERIAL FROM SOUTHERN AFRICA

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(continued inside back cover)

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By

B. G. GARDINER & R. A. JUBB

Cape Town Kaapstad

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(With 1 figure)

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ABSTRACT

Pteronisculus meiringi sp. nov. from Alice, Cape Province, is described. This is the first record of this species from South Africa and extends the range of the genus from the Lower Trias into the Upper Permian.

CONTENTS

INTRODUCTION

In 1974 Professor A. J. D. Meiring, recently retired from the Department of Zoology, University of Fort Hare, Alice, presented some fish fossil material to the Albany Museum. This material had been discovered by him amongst rock taken from a quarry situated on the immediate outskirts of Alice in an outcrop of the Lower Beaufort Series. As both before and after this discovery the quarry had been used extensively for crushed stone required for road-making, the search for additional material at this particular site was abandoned.

As far back as 1876 Owen recorded, without formal description, a fossil fish under the name *Hypterus bainii* from Alice. This fossil was presented to the British Museum (Natural History), London, by the Trustees of the Albany Museum. Under the registered number P.46007 it was included by Woodward with the material used for his description of *Atherstonia scutata* in 1889. The counterpart of P.46007 is in the Albany Museum with the registered number AM 264, the site recorded being a quarry near Alice. In 1913 Broom described

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AM 264 as a new species *Amblypterus capensis* but this confusion has been resolved. By comparing AM 264 with other material it is agreed that it is a specimen of *Atherstonia scutata.*

Meiring's material has been examined and found to represent two species, several specimens of *Atherstonia scutata,* a species first described from the *Daptocephalus* zone of the Lower Beaufort Series near Colesberg, and a new species identified by the senior author as belonging to the genus *Pteronisculus* White, 1933, which is described below.

SYSTEMATIC DESCRIPTION

Order PALAEONISCIFORMES

Family **Palaeoniscidae** Aldinger, 1937

Diagnosis

See Aldinger 1937: 229.

Genus *Pteronisculus* White, 1933

1921—*Glaucolepis* Stensiö: 200.

Diagnosis

See Nielsen 1942: 265.

Type species

Pteronisculus cicatrosus White, 1933.

Remarks

The genus was erected by White (1933: 118) to include the two species *P. cicatrosus* White and *P. macropterus* White from the Lower Trias of Madagascar. Later Nielsen (1936: 1942) showed that *Pteronisculus* was synonymous with the genus *Glaucolepis* of Stensiö (1921), but failed to note that the name *Glaucolepis* was preoccupied.

Other species included within this genus are: *P. arambourgi* Lehman (1952: 39) and *P. broughi* Lehman (1952: 39) also from the Lower Trias of Madagascar; *P. gyrolepidoides* (Stensiö, 1921: 200) from the Lower Trias of Spitsbergen; *P. artica* (Stensiö, 1932: 119), *P. stensioi* (Nielsen, 1942: 271), *P. magna* (Nielsen, 1942: 272), *P. gunnari* (Nielsen, 1942: 273), and *P. aldingeri* (Nielsen, 1942: 274) all from the Lower Trias of East Greenland.

It has been suggested by Aldinger (1937: 96) that *Palaeoniscum crassus* Woodward (1908: 9) from the late Middle or early Upper Trias of New South Wales, Australia bears a closer resemblance to *Pteronisculus* than to *Palaeoniscum.* However, all the fins are small and quite unlike those of *Pteronisculus,* while the enlarged ridge scales in front of the dorsal fin is a primitive feature and should not be taken to indicate a relationship to *Pteronisculus* as suggested by Aldinger. It is thought that Woodward's fish will probably prove to be a redfieldid.

DESCRIPTION

Pteronisculus meiringi sp. nov.

Fig. 1

Diagnosis

A large, slender species with an estimated length of 40 cm. Dermal bones of head ornamented with tubercles and striae. The suspensorium is oblique. Pectoral fin large, expanded in the horizontal plane and with a well-developed scaly lobe; there are some 20 to 22 stout lepidotrichia unsegmented in their proximal third. In each of the anterior 10 transverse scale rows there are a number of flank scales higher than broad, remaining trunk scales rhombic.

Fig. 1. Type specimen of *Pteronisculus meiringi* sp.n.
Lower Beaufort Series, Alice, Cape Province.

Immediately behind the cleithrum there are approximately 20 scales in each transverse row. Scales ornamented with stout, diagonal ridges of ganoine which end in delicate serrations posteriorly.

Holotype

Specimen AM 4770A in the Albany Museum, Grahamstown; anterior one-third of fish with snout missing, from the Lower Beaufort Series of Alice, Cape Province.

Other material

Specimen AM 4770B, counterpart of holotype AM 4770A, in the Department of Zoology, University of Fort Hare, Alice.

Specimen AM 4772 in the Albany Museum; part of the caudal fin.

Remarks

This species is named in honour of Professor A. J. D. Meiring of the Fort Hare University for Bantu.

CONCLUSIONS

This is a large fish only approached in size by *P. magna* (Nielsen) and from which it may easily be separated by the relatively small number of its pectoral fin rays (*P. magna* has 45 to 50).

Until the discovery of this new species from South Africa all known members of the genus *Pteronisculus* came from the Lower Trias. If the horizon of the type locality of *P. meiringi* at Alice is Lower Beaufort then the range of this genus has been pushed back into Upper Permian.

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6. SYSTEMATIC papers must conform with 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. n., sp. n., comb. n., syn. n., 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 (figs 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 (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

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

B. G. GARDINER & R. A. JUBB

A NEW PALAEONISCID FROM THE LOWER BEAUFORT SERIES OF SOUTH AFRICA