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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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PRELIMINARY REPORT ON THE MIOCENE VERTEBRATES FROM ARRISDRIFT, SOUTH WEST AFRICA

By

Q. B. HENDEY

Cape Town Kaapstad

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PRELIMINARY REPORT ON THE MIOCENE VERTEBRATES FROM ARRISDRIFT, SOUTH WEST AFRICA

By

Q. B. Hendey

South African Museum, Cape Town

(With 13 figures and 11 tables)

[*MS. accepted 14 March 1978*]

ABSTRACT

At least 28 vertebrate species, of which 22 are mammals, are recorded from the early middle Miocene (*c.* 16 m.y. old) fossil occurrence at Arrisdrift on the Orange River in South West Africa. The material postdates Miocene vertebrates previously recorded from the Namib desert. The mammals include at least 3 new species (a hyracoid, a palaeomerycid and an ochotonid), while there are at least 8 genera represented which have not hitherto been known in southern Africa. *Austrolagomys simpsoni* Hopwood, 1929, is referred to *Kenyalagomys* Whitworth, 1954, and *Prohyrax* is placed in the Pliohyracinae, a group which apparently had its origins in southern Africa.

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INTRODUCTION

Until recently the only substantial information on southern African Miocene terrestrial vertebrates came from several small fossil assemblages collected in the southern Namib desert (Stromer 1926; Hopwood 1929; Hamilton & Van Couvering 1977). The described material is limited in both quality and quantity. The discovery of a new Miocene vertebrate locality in terrace deposits at Arrisdrift on the Orange River further south in the same region (Fig. 1) has proved an important addition to the local Miocene fossil record (*South African Journal of Science* 1976; Corvinus & Hendey 1978). The number of fossils already collected at Arrisdrift exceeds the combined total from the other Namib desert occurrences, although the quality of the specimens is not necessarily superior. The presence on the subcontinent of several taxa has been revealed for the first time. These include the deinothere, *Prodeinotherium hobleyi* (Harris 1977).

The fossils were discovered in a prospect pit (Pit 2 of Drill-line AD 8) in deposits being investigated by the Consolidated Diamond Mines of South

Ann. S. Afr. Mus. **76** (1), 1978: 1–41, 13 figs, 11 tables.

West Africa (Pty) Ltd. Further fossiliferous deposit has since been exposed by extending the original pit, but the limits of the occurrence have not been established.

The material already prepared includes remains of at least 28 vertebrate species, of which 22 are mammals (Table 1). Most have yet to be positively identified and studies have so far been confined largely to cranial material, which is much less common than postcranial bones. The condition of specimens varies considerably, some being well preserved and reasonably complete, but most having suffered post-mortem damage. The fossils occur in a poorly sorted

TABLE 1

The vertebrates from Pit 2/AD 8 at Arrisdrift, South West Africa.

OSTEICHTHYES	gen. et sp(p). indet.
AMPHIBIA	gen. et sp. indet.
REPTILIA	
Squamata	gen. et sp. indet.
Crocodilia	*? Crocodylus niloticus*
Chelonia	gen. et sp(p). indet.
AVES	gen. et spp. indet.
MAMMALIA	
Insectivora	
Macroscelididae	*Myohyrax* cf. *oswaldi*
Carnivora	
Amphicyonidae	*Amphicyon* cf. *steinheimensis*
Amphicyonidae or Ursidae	gen. et sp. indet.
?Ursidae	?Hemicyoninae gen. & sp. indet.
?Felidae	*? Metailurus* sp.
Mustelidae	*? Ischyrictis* sp.
indet.	gen. & sp. indet.
Hyracoidea	
Procaviidae	*Prohyrax* n. sp.
Proboscidea	
Gomphotheriidae	gen. et sp. indet.
Deinotheriidae	*Prodeinotherium hobleyi*
Perissodactyla	
Rhinocerotidae	*Dicerorhinus* sp.
Artiodactyla	
Suidae	gen. et sp. indet. *Lopholistriodon moruoroti*
Tragulidae	*Dorcatherium* cf. *pigotti*
Palaeomerycidae	*Climacoceras* sp. nov.
Bovidae	gen. et sp. indet.
Pecora	gen. et sp. indet.
Lagomorpha	
Ochotonidae	*Kenyalagomys* sp. nov.
Rodentia	
?Bathyergidae	*? Bathyergoides* sp.
Thryonomyidae	*Paraphiomys pigotti*
indet.	gen. et spp. indet.

fluvial gravel and their imperfections are due mainly to their having been transported by water in a high-energy environment. Only one instance is recorded of skeletal elements occurring in articulation and, in addition to disarticulation and fragmentation, many specimens are abraded and distorted. Incrustations of gypsum have etched and even destroyed parts of some specimens. Since the deposit incorporating the fossils is consolidated, power tools were required during their excavation and this has caused further damage to specimens. In spite of its shortcomings, the Arrisdrift fossil assemblage is perhaps the most important one of Miocene age yet discovered in southern Africa.

The purpose of the present report is to place on record some details of the nature and number of specimens belonging to the various taxa already recognized. With the exception of the deinothere teeth, none of the material has been thoroughly studied, although such studies will be undertaken by various authorities in the future. The geological investigation of the deposits in the vicinity of Arrisdrift is being undertaken by employees of the mining company prospecting the area.

The specimens discussed in this report are housed in the Department of Cenozoic Palaeontology at the South African Museum, Cape Town. The full catalogue numbers begin SAM–PQ–, which identify the institution and department concerned, but this lettering is omitted in the text and only the site prefix (AD) and serial numbers of individual specimens are given. The full site reference is Arrisdrift, Pit 2/AD 8.

OTHER MIOCENE VERTEBRATE OCCURRENCES IN THE NAMIB DESERT

The first Miocene vertebrates from the southern Namib desert were discovered during the First World War and were described in a series of papers by Stromer (1922, 1923, 1924, 1926). This material came from three localities, namely, Elisabethfeld, 38 km south of Lüderitz; a borehole near Plant 4 of the Kolonial Bergbau Gesellschaft, 20 km south of Lüderitz (= Elisabeth Bay Pan, see Greenman 1966); and Langental near Bogenfels, 80 km south of Lüderitz (Fig. 1).

Subsequently Hopwood (1929) described another small assemblage of specimens from the same region, but his material lacks precise locality data and was recorded as being from 'south of Lüderitz Bay'.

Little additional material was collected in the region in the decades which followed. The South African Museum has an undescribed ruminant mandible fragment (SAM–PQ–G 8356) from Bogenfels, which may be a synonym of Stromer's Langental locality. Some fragmentary material was collected by Greenman (1966) from Fiskus and Grillental in the Elisabethfeld area. This material is also in the South African Museum, but includes little that is diagnostic.

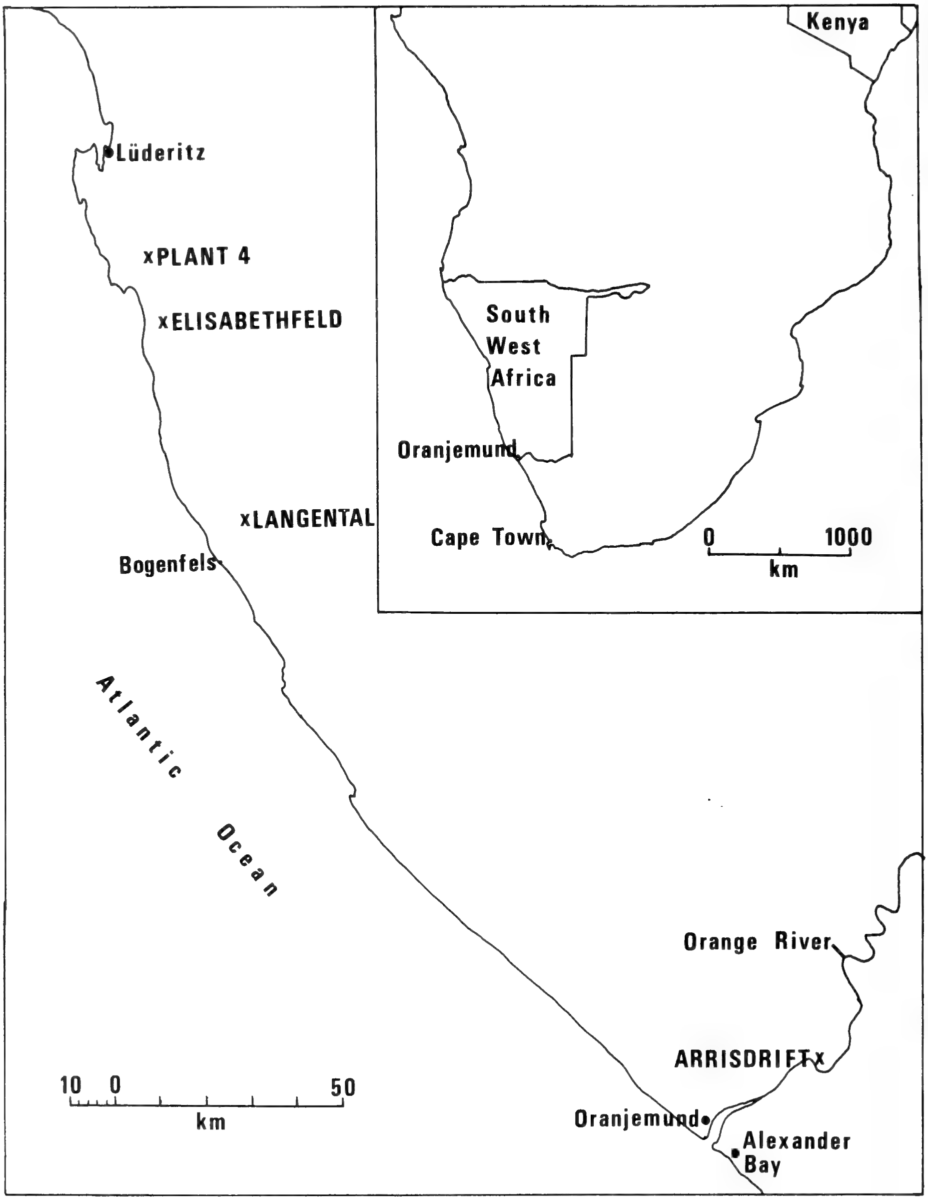

Fig. 1. Location of Arrisdrift and other South West African Miocene fossil occurrences.

Hamilton & Van Couvering (1977) recently revisited the area and collected more material from the various localities. They have reviewed and supplemented the original faunal lists and compared and contrasted a revised list with others from early Miocene occurrences elsewhere in Africa.

The Namib fossils are generally regarded as early Miocene ('Burdigalian') in age, their source is usually recorded as 'Namib desert' or 'South West Africa', and they are treated as if they were a single assemblage. The described material is here listed as four separate assemblages (Table 2). Since each is limited in size and each includes unidentified or incompletely identified taxa, the bases for comparing them to each other, and to assemblages elsewhere, are limited. The comments which follow are confined largely to the implications of individual taxa in respect of the age of the assemblages. Other references to this material are included in the discussions on the Arrisdrift fossils.

There is one species from Elisabethfeld, *Metapterodon kaiseri*, which Savage (1965) believed to be represented in east Africa by specimens from Karungu and Rusinga, which are between 18 and 20 m.y. old. Savage also recognized a second species of *Metapterodon* from Rusinga, namely, *M. zadoki*. Van Valen (1967: 252) found 'that the two east African species distinguished by Savage are much more similar to each other than are the east and Southwest African forms of "*M. kaiseri*"'. He concluded that the east African species are more advanced than *M. kaiseri* and synonymized *Metapterodon* with *Pterodon*. Although this material is problematical, Van Valen's opinion suggests that the Elisabethfeld species may predate its east African counterparts. Its age might therefore be greater than 20 m.y., that is, 'Aquitanian' rather than 'Burdigalian' in terms of the European mammal age nomenclature (Van Couvering 1972).

Another of the Elisabethfeld species, *Myohyrax doederleini*, was regarded as a synonym of the east African *M. oswaldi* (Whitworth 1954; Patterson 1965), a species which has a recorded age range of 18 to 22 m.y. (see Whitworth 1954; Walker 1969; Van Couvering 1972). An 'Aquitanian' to 'Burdigalian' age is therefore indicated. Since a *Myohyrax* resembling *M. oswaldi* is now also recorded from Arrisdrift, this species may have survived beyond the 'Burdigalian' (see below), and appears to be of little use for relative dating purposes.

The Elisabethfeld *Propalaeoryx austroafricanus* is a primitive ruminant which is likely to be broadly contemporaneous with the Rusinga *P. nyanzae* (Whitworth 1958; Hamilton 1973), but the available material of these species is too scanty to determine possible differences of temporal significance.

The only other identified species from Elisabethfeld are *Parapedetes namaquensis* and *Austrolagomys inexpectatus*. They are not known elsewhere, although there are related genera, *Megapedetes* and *Kenyalagomys*, recorded from the early Miocene of east Africa, again from the 18 to 22 m.y. period.

According to MacInnes (1957) *Megapedetes* is less specialised than *Parapedetes*, but he did not regard this as indicating an age difference, ascribing it instead to different evolutionary trends on two contemporary lineages. This interpretation raises the question of whether assemblages such as those from Elisabethfeld can be dated in a relative sense by comparing them with east African assemblages. If MacInnes's interpretation of the pedetids is correct, then it follows that seemingly primitive taxa such as *Pterodon kaiseri* may

TABLE 2. Miocene mammals from the Lüderitz/Bogenfels area of the Namib desert.

ELISABETHFELD[1]	PLANT 4 BOREHOLE[1]	LANGENTAL[1]	SOUTH OF LÜDERITZ[2]	REVISED IDENTIFICATIONS AND ADDITIONS[3]
Myohyrax doederleini	—	—	*Myohyrax doederleini*	*Myohyrax oswaldi*
—	*Myohyrax oswaldi*	—	—	*Myohyrax oswaldi*
—	—	—	*Myohyrax osborni*	*Protypotheroides beetzi*
—	—	*Protypotheroides beetzi*	—	*Protypotheroides beetzi*
Metapterodon kaiseri	—	—	—	*Pterodon kaiseri*
Creodonta/Carnivora indet.	—	—	—	Creodonta/Carnivora indet.
—	—	*Prohyrax tertiarius*	—	*Prohyrax tertiarius*
—	—	—	—	*Gomphotherium* sp.
—	—	Rhinocerotidae indet.	—	*Brachypotherium heinzelini*
Artiodactyla indet.	Artiodactyla indet.	—	—	Artiodactyla indet.
—	—	*Diamantohyus africanus*	—	*Xenochoerus africanus*
—	—	? *Propalaeochoerus* sp.	—	? *Propalaeochoerus* sp.
—	—	—	—	*Brachyodus africanus*
—	—	—	Tragulidae indet.	*Dorcatherium* sp.
—	—	—	Tragulidae indet.	Pecora indet.
—	? cf. *Strogulognathus* sp.	cf. *Strogulognathus* sp.	—	*Propalaeoryx austroafricanus*
Propalaeoryx austroafricanus	—	—	—	*Propalaeoryx austroafricanus*
Austrolagomys inexpectatus	—	—	—	*Austrolagomys inexpectatus*
—	—	—	*Austrolagomys simpsoni*	*Kenyalagomys simpsoni*
Parapedetes namaquensis	—	—	—	*Parapedetes namaquensis*
—	*Bathyergoides neotertiarius*	*Bathyergoides neotertiarius*	—	*Bathyergoides neotertiarius*
—	*Neosciuromys africanus*	*Neosciuromys africanus*	—	*Paraphiomys pigotti*
—	*Phiomyoides humilis*	—	—	*Phiomyoides humilis*
—	cf. *Phiomys andrewsi*	—	—	—
—	—	*Diamantomys luederitzi*	—	*Diamantomys luederitzi*
—	—	*Pomonomys dubius*	—	*Pomonomys dubius*
—	—	—	*Apodecter stromeri*	*Paraphiomys stromeri*
—	—	—	*Phthinylla fracta*	*Paraphiomys pigotti*
—	—	—	—	*Paracryptomys mackennae*
—	Rodentia indet.	Rodentia indet.	Rodentia indet.	Rodentia indet.

[1] Stromer (1926) [2] Hopwood (1929) [3] Hamilton & Van Couvering (1977); this report.

simply be conservative southern counterparts of 'advanced' east African species.

This problem arises again with the ochotonids. There are clear differences between *Austrolagomys* and *Kenyalagomys* (MacInnes 1953), which may be interpreted as indicating that the former is the more primitive (Cooke 1972). In this instance the fact that the ochotonid represented at Arrisdrift (which evidently does postdate both the Elisabethfeld and the east African 'Rusinga-type' faunas) is a *Kenyalagomys*, may be an indication that *Austrolagomys* really is a primitive and early form.

To sum up, there is some evidence to suggest that the Elisabethfeld fauna represents a southern African equivalent of that of the European Aquitanian. This conclusion is, however, tentative and should be re-examined if more material becomes available and/or when the zoogeographic relationships of east and southern African early Miocene faunas are better understood.

The Langental fauna includes five species which are known from the early Miocene of east Africa. They are *Bathyergoides neotertiarius*, *Paraphiomys pigotti*, *Diamantomys luederitzi* (Lavocat 1973), *Xenochoerus africanus* (Wilkinson 1976) and *Brachypotherium heinzelini* (Heissig 1971). In addition, *Prohyrax tertiarius* is a primitive species and apparently consistent with an early Miocene date (see p. 33). This hyrax is regarded as one of the more certain indications that there was some endemism in southern African faunas during the earlier part of the Miocene and that the complication in comparing east and southern African taxa mentioned above does have some substance.

The other identified taxa from Langental, *Protypotheroides beetzi* and *Pomonomys dubius*, are apparently known only from the Namib desert and, since they may be southern endemics, they may not be useful for relative dating purposes.

The available evidence indicates that the Langental fauna dates from the early Miocene and that it may be a 'Burdigalian' rather than 'Aquitanian' equivalent.

The Plant 4 borehole and Langental faunas have three species in common, namely, *Myohyrax oswaldi*, *Bathyergoides neotertiarius* and *Paraphiomys pigotti*. This suggests that the former may also be of early Miocene age. On the other hand, all three taxa are, or may be represented at Arrisdrift as well (see below), so a slightly younger age (early middle Miocene) is also possible.

The material described by Hopwood (1929) includes three species known from the east African early Miocene. They are *Paraphiomys pigotti*, *P. stromeri* and *Myohyrax oswaldi*. In addition, this assemblage includes an ochotonid which is apparently closely related to the east African *Kenyalagomys minor* (see p. 31). Hopwood's material also includes the large myohyracine, *Protypotheroides beetzi*, which is represented at Langental. Once again an early Miocene age is indicated. In view of the earlier comments on ochotonids, the presence of *Kenyalagomys* in Hopwood's assemblage may mean that this assemblage, or part of it, postdates that from Elisabethfeld.

In spite of the uncertainties relating to the four assemblages, there is no justification for the recent practice of treating the faunas as a unit. Even if it could be established that they are exact contemporaries, it is as well to accord them individual status. Since the Arrisdrift fauna is younger than some or all of those from the Lüderitz–Bogenfels area, there is certainly no justification for adding it to the Namib Miocene mixture, and for this reason alone it will now be inconvenient and inappropriate to refer to '*the* Miocene fauna' from this region.

THE FOSSIL VERTEBRATES FROM ARRISDRIFT

Class Osteichthyes

One or more species of fish are represented by a few isolated vertebrae (e.g. AD 668, AD 672) and fin spines (e.g. AD 759, AD 779). The latter apparently belong to catfish (Clariidae).

Class Amphibia

A single postcranial bone (AD 811) belongs to a frog or toad.

Class Reptilia

ORDER SQUAMATA

There are two snake vertebrae (AD 707, AD 1110) in the assemblage.

ORDER CROCODILIA

? *Crocodylus niloticus* Laurenti, 1768

The most commonly represented lower vertebrate is a crocodile, probably *Crocodylus niloticus*, of which many isolated teeth (e.g. AD 71, AD 310) and scutes (e.g. AD 335, AD 341) are preserved. Postcranial bones and skull fragments are less common. The best specimens include two incomplete dentaries (AD 344, AD 999). Crocodiles are not uncommon as fossils in east Africa and elsewhere but have not previously been recorded from Tertiary occurrences in southern Africa and are rare in Quarternary deposits.

ORDER CHELONIA

A few isolated scutes (e.g. AD 73, AD 832) belong to one or more species of tortoise.

Class Aves

Birds are represented by a few isolated and incomplete postcranial bones (e.g. AD 725, AD 841) belonging to more than one species.

CLASS MAMMALIA

ORDER INSECTIVORA

Family **Macroscelididae**

Myohyrax cf. *oswaldi* Andrews, 1914

A *Myohyrax* is the most commonly occurring small mammal in the assemblage and is represented by many isolated teeth and mandible fragments (e.g. AD 125, AD 1104) (Fig. 2). Most of the mammalian postcranial bones have yet to be classified and this material probably includes specimens belonging to *Myohyrax.*

Stromer (1926) recorded three myohyracines from the Namib, namely, *M. oswaldi*, *M. doederleini* and *Protypotheroides beetzi*, while Hopwood (1929) subsequently named an additional species, *M. osborni*, from the same region. In the most recent review of this material, Patterson (1965) recognized only *M. oswaldi* (including *M. doederleini*) and *P. beetzi* (including *M. osborni*). In doing so he followed Whitworth (1954), except that Whitworth did not regard *Protypotheroides* as a valid genus.

The Arrisdrift *Myohyrax* is apparently indistinguishable from *M. oswaldi*, but the identification is qualified since the teeth are a little smaller than those

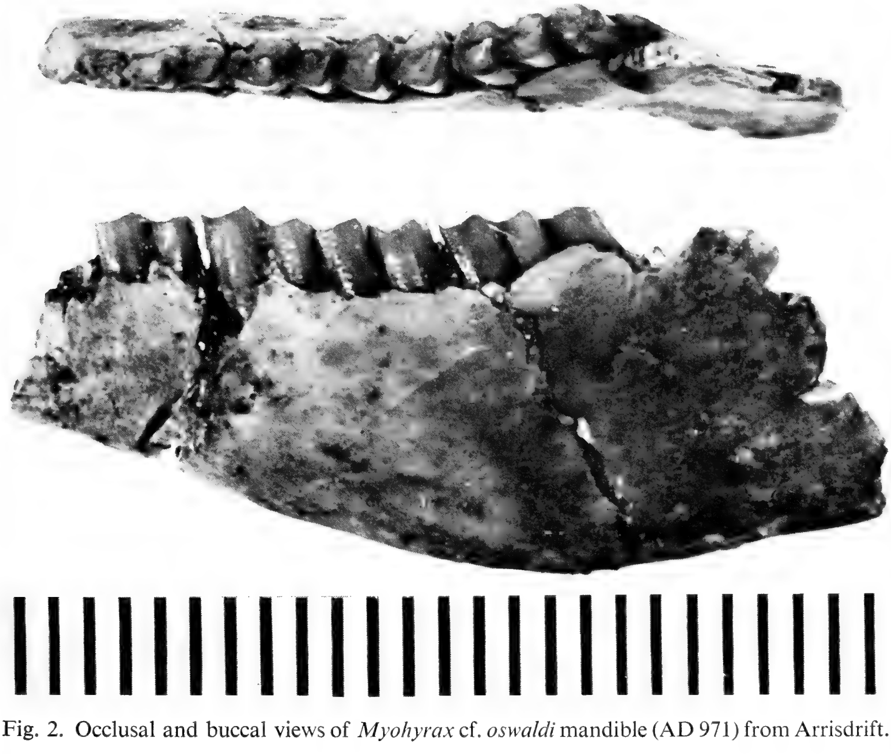

Fig. 2. Occlusal and buccal views of *Myohyrax* cf. *oswaldi* mandible (AD 971) from Arrisdrift.

of typical east African *M. oswaldi*. This was one of the features which Stromer (1926) claimed characterized *M. doederleini*. Whitworth (1954) found that *M. doederleini* fell within the size variation observed in east African *M. oswaldi*, but since Arrisdrift provides a second sample of specimens from the Namib in which the teeth are comparatively small, there may be a taxonomically significant mean difference between the *Myohyrax* from the two regions. In addition, since examination of the Arrisdrift *Myohyrax* during the present study was cursory, the material may differ from typical *M. oswaldi* in characters other than size.

The Arrisdrift *Myohyrax* is evidently younger than any previously recorded myohyracine (see p. 32), and this is another factor to be taken into account when the material is studied in detail.

ORDER CARNIVORA

Although poorly represented, the only identifiable carnivores from Arrisdrift are Carnivora rather than Creodonta. It is, however, possible that certain non-diagnostic specimens such as isolated canines and postcranial bones do belong to creodonts, a group whose presence is to be expected in view of the apparent age of the Arrisdrift assemblage (see p. 35).

Family **Amphicyonidae**

Amphicyon cf. *steinheimensis* Fraas, 1885

An incomplete left mandible (AD 133) belongs to an amphicyonid (Fig. 3, Table 3). There are also several postcranial bones which may belong to this

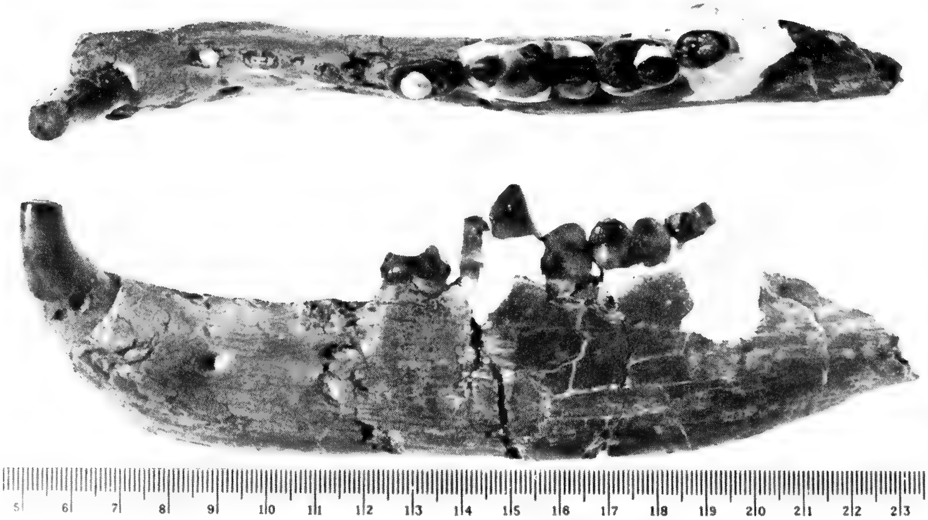

Fig. 3. Occlusal and buccal views of *Amphicyon* cf. *steinheimensis* mandible (AD 133) from Arrisdrift.

TABLE 3

Dimensions of the lower teeth and mandibles of the unidentified large carnivore (AD 1520), *Amphicyon* (AD 133), Hemicyoninae indet. (AD 611) and *? Ischyrictis* (AD 614) from Arrisdrift.

	$\overline{C}$		P_1		P_2		P_3		P_4		M_1		M_2		M_3	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b
AD 1520	—	—	—	—	—	—	*c.* 20,0*	—	21,7	14,2	36,0	19,5	*c.* 26,0	21,1	*c.* 16,0*	—
AD 133	16,2	10,4	5,5*	—	7,2*	—	*c.* 9,0*	—	14,6	7,6	27,1	12,2	16,5	11,7	10,8	8,2
AD 611	—	—	*c.* 3,0*	—	8,5*	—	13,6*	—	17,5*	—	—	—	—	—	—	—
AD 614	*c.* 8,1	5.5	2,7*	—	5,7	3,0	6,5	3,4	9,0	4,3	14,6	6,3	*c.* 3,5*	—	—	—

* Alveolus

	AD 1520	AD 133	AD 611	AD 614
Depth of mandible below P_3	60,2	32,5	45,0	14,9
Breadth of mandible below P_3	30,3	13,5	18,5	7,6
Depth of mandible below M_1	62,6	38,0	54,5	*c.* 15,5
Breadth of mandible below M_1	29,0	*c.* 16,0	21,5	9,3

species, but they were excluded from consideration.

The amphicyonids, which are sometimes regarded as a subfamily within the Canidae (e.g. Kuss 1965), or as a separate family (e.g. Hunt 1972), were a successful, diverse and widespread group in the Old World and North America during the Oligocene and Miocene. They are not well known in Africa and prior to the Arrisdrift discovery had not been recorded in southern Africa. The taxonomy of the group is complex and, in spite of recent revisions, the identification of specimens such as AD 133 is difficult.

AD 133 lacks the ascending ramus, the incisors and P_1 to P_3. Of the remaining teeth only the M_3 is largely intact, although the salient features of the $\overline{C}$ and P_4 to M_2 are preserved. This specimen indicates that the species was an unspecialized, slender-jawed *Amphicyon* of moderate size. The P_1 to P_3, of which only the roots or alveoli remain, are reduced in size and more or less evenly spaced between the C and P_4. The P_1 was single-rooted, P_2 had two roots which has coalesced at the alveolar margin, while P_3 was also double-rooted. The P_4, which has lost the principal cusp, has an anterior accessory cusp, a larger posterior accessory cusp and a tiny cusp on the posterior cingulum. The M_1 is a high-crowned tooth with a prominent protoconid and stout metaconid. The talonid is sectorial, it lacks the entoconid and makes up about one-third of the length of the tooth. The M_2 has a double-cusped trigonid and single-cusped talonid. The M_3 has little relief on the occlusal surface and, like M_1 and M_2, is relatively narrow.

AD 133 resembles specimens belonging to the middle Miocene *A. steinheimensis* from Europe (see Kuss 1965), and is tentatively identified with this species. It may, however, belong to a previously unrecorded African species of *Amphicyon*. The only amphicyonids recorded from east Africa are two early Miocene species, *Hecubides euryodon* and *H. macrodon* (Savage 1965). The Arrisdrift species differs from *H. eurydon* in several respects, including its larger size. It cannot be compared with *H. macrodon*, which is known only from an isolated M^1.

Superfamily **Canoidea** (*senso* Savage 1977)

Amphicyonidae or Hemicyoninae gen. et sp. indet.

A largely intact, but somewhat abraded right mandible with well worn P_4 to M_2 (AD 1520) belongs to a very large canoid (Fig. 4). This specimen compares in size with the mandible of the largest terrestrial carnivore previously recorded from southern Africa, namely, the early Pliocene *Agriotherium africanum* from Langebaanweg, Cape Province (Hendey 1972, 1977).

In some respects AD 1520 resembles the European middle to late Miocene amphicyonid, *Amphicyon major*. For example, the mandibles of the two species are of similar overall size, while the preserved teeth of AD 1520 are morphologically similar to the corresponding teeth of *A. major*. Like all amphicyonids, AD 1520 lacks a premasseteric fossa. Its teeth are closest in size to those of

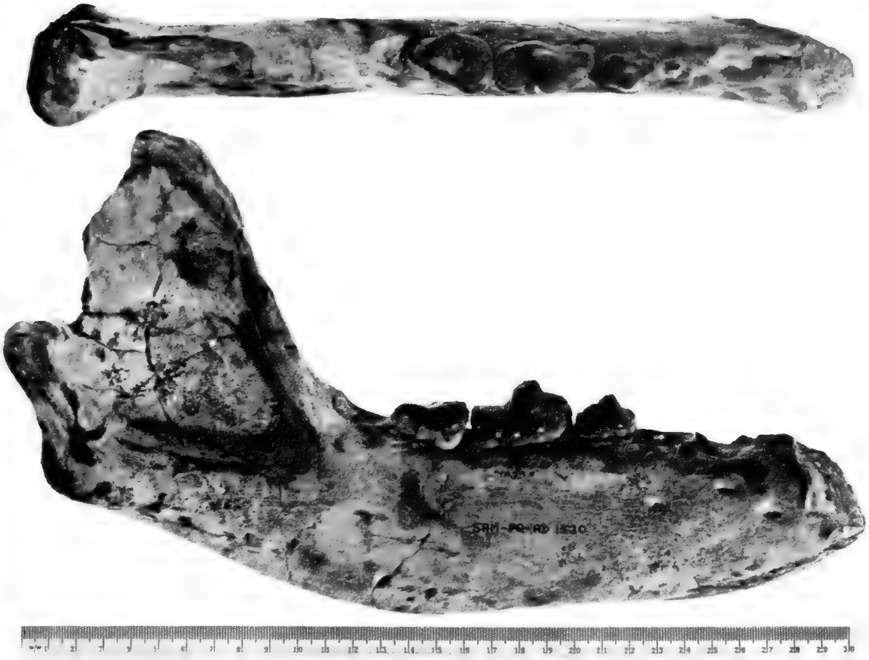

Fig. 4. Occlusal and buccal views of large canoid mandible (AD 1520) from Arrisdrift.

later varieties of *A. major* (see Kuss 1965; Table 3, this report). They do, however, differ in being relatively broad, a feature which applies particularly in the case of P_4. Although lost, the P_2 and P_3 of AD 1520 were evidently also relatively large and, together with P_4, formed a closed series.

The large size of the premolars distinguishes the Arrisdrift species from previously recorded *A. major* and, indeed, from all other Miocene amphicyonids. Apparently only in certain Oligocene species are the premolars relatively large and in the form of a closed series (see Springhorn 1977). If AD 1520 is indeed related to *A. major*, it must be more primitive than recorded representatives of this taxon even though it is 'advanced' in terms of overall size. The origins of *A. major* are obscure (Kuss 1965) and it may well have arrived in Europe as an immigrant from Africa. The Arrisdrift species may represent the stock from which *A. major* was derived.

There is, however, a second alternative which must be considered. The Hemicyoninae, a group of Miocene ursids which share many characters with amphicyonids, also include a very large species whose origins are obscure. This is *Dinocyon thenardi* of the later middle Miocene of Europe (Hürzeler 1944). The hemicyonines also have reduced premolars, although the reduction is not necessarily as marked as in contemporary amphicyonids. They presumably evolved from forms in which the premolars were relatively large and in this respect the Arrisdrift species may be seen as an appropriate ancestor for *D. thenardi*. The lower molars of the former are a little smaller than those of the Grive St Alban *D. thenardi*, and in this respect as well the Arrisdrift species is the less specialized (i.e. more primitive).

AD 1520 does, however, differ from *D. thenardi*, and other hemicyonines, in lacking a premasseteric fossa. This would not necessarily exclude it from an ancestral role, but it does suggest an amphicyonid, rather than hemicyonine connection.

A third alternative is that the Arrisdrift species represents the stock from which both *A. major* and *D. thenardi* were derived. It has been suggested that *Amphicyon* and *Dinocyon* are closely related (e.g. Matthew 1924), although more recent interpretations of canoid inter-relationships indicate that similarities between these taxa are due to parallel evolution. Nevertheless, the fact that neither *A. major* nor *D. thenardi* have known immediate ancestors does raise the possibility that they may have had one in common.

Finally, AD 1520 may belong to a species related to the early Miocene *Afrocyon burolleti* from Gebel Zelten in Libya (Arambourg 1961). The holotype of this species is a mandible fragment with P_4 to M_3, which is similar in overall size to AD 1520, but which differs in having smaller P_4 to M_2 and a double-rooted M_3. If the two forms are indeed related, then *A. burolleti* is clearly the more primitive and the Arrisdrift species could still be ancestral to the European *A. major* and/or *D. thenardi*.

In view of the uncertainties about the relationships of AD 1520, it would be fruitless at this stage to consider the taxonomic implications of the various alternatives mentioned above. Although unidentified, AD 1520 is still significant in revealing the presence of a type of carnivore not hitherto known from the Miocene of southern Africa and in suggesting that the phylogeny of similar taxa elsewhere may require reinterpretation.

? Family **Ursidae**

? Hemicyoninae gen. et sp. indet.

A mandible fragment (AD 611) belongs to a carnivore intermediate in size between the *Amphicyon* cf. *steinheimensis* and the large canoid discussed above (Table 3). Only the anterior part of the mandibular corpus is preserved, and of the teeth only the roots or alveoli of P_1 to P_4 and a small part of the crown of M_1 are preserved. It is readily distinguished from the *Amphicyon* cf. *steinheimensis* by its larger size and in having a deep mandibular corpus. In the latter respect it resembles the large canoid, but the overall size difference is more than would be expected in intra-specific variation.

Although AD 611 has yet to be positively identified, it matches in size and other observable respects corresponding parts of the *Hemicyon californicus* holotype from the Miocene of North America (Frick 1926: 34, fig. 12B). It is larger than specimens of European *Hemicyon* and *Harpaleocyon* described by

Hürzeler (1944), but since hemicyonines and other ursids exhibit appreciable sexual dimorphism (see Colbert 1939), size differences are not necessarily a reliable criterion for distinguishing species. Even if it could be established that AD 611 represents a hemicyonine, it is unlikely that the species concerned could be identified.

Hemicyonines have not previously been recorded from Africa, but elsewhere they occur in association with some of the characteristically Miocene taxa which have been found at Arrisdrift. The size of AD 611 suggests a middle Miocene rather than earlier age.

? Family **Felidae**

? *Metailurus* sp.

An isolated upper canine (AD 616) apparently belongs to a large felid of the group which includes the extinct genera *Metailurus* and *Dinofelis*. The specimen is 16 mm long, 12,6 mm wide and has a crown height of 44 mm.

The species concerned was larger than the only *Metailurus* hitherto recorded in Africa, namely, *M. africanus* from the east African early Miocene (Savage 1965). AD 616 compares in size with the $\underline{C}$ of *M. major* from the late Miocene of China (Zdansky 1924), but differs in being slightly shorter and broader. It also resembles the $\underline{C}$ of the early Pliocene *Dinofelis* aff. *diastemata* from Langebaanweg (Hendey 1974), particularly the specimen SAM–PQ–L 20685. Once again the only difference is that AD 616 is a little shorter and broader. This difference suggests that the Arrisdrift species was less advanced than the other two species.

Since carnivore canines are not necessarily diagnostic, AD 616 is only tentatively identified and is referred to *Metailurus*, a Miocene genus, rather than *Dinofelis*, a Plio/Pleistocene genus, in view of the age of the Arrisdrift assemblage.

Family **Mustelidae**

? *Ischyrictis* sp.

An incomplete left mandible (AD 614) belongs to a small carnivore with a high-crowned canine, relatively narrow and high-crowned premolars and carnassial, and a reduced M_2 (Fig. 5, Table 3). The M_1 has a small metaconid, while the talonid is short and lacks the entoconid. The small M_2 and sectorial M_1 talonid suggests that the relationships of AD 614 may lie with the primitive gulonine *Ischyrictis* and it is identified accordingly. This genus has not previously been recorded in Africa, but is known from the Miocene of Europe and Asia Minor (see Crusafont-Pairo 1972; Schmidt-Kittler 1976).

The high-crowned teeth and relatively narrow premolars of AD 614 would be primitive characters in an *Ischyrictis*, and the Arrisdrift species may prove to be an appropriate ancestor for the early Vindobonian *I. zibethoides* of Europe.

Fig. 5. Occlusal and lingual views of *? Ischyrictis* mandible (AD 614) from Arrisdrift.

Two other mandible fragments (AD 128, AD 756) apparently belong to the same species as AD 614.

Other Carnivora

At least one species in addition to those already mentioned is included in the Arrisdrift carnivore assemblage. An isolated canine (AD 127) belongs to a species smaller than the *? Ischyrictis*. The 'Carnivora gen. et sp. indet.' in the accompanying faunal list (Table 1) refers to this specimen.

Also unidentified are two mandible fragments (AD 139, AD 773), three canines (AD 55, AD 122, AD 214), an I^3 (AD 619) and several postcranial bones, most of which are incomplete. These specimens may include some belonging to species in addition to those listed.

ORDER HYRACOIDEA

Family **Procaviidae**

Prohyrax sp. nov.

By far the most commonly represented vertebrate in the Arrisdrift assemblage is a hyrax belonging to a group sometimes given subfamily rank, the Pliohyracinae (Whitworth 1954). This was the most widespread of the hyrax groups and is known from localities in Eurasia as well as Africa. Most of the recorded species were extremely large in comparison to living hyracoids and some specimens have been mistakenly identified as rhinoceroses and chalicotheres. Later representatives were apparently aquatic or amphibious animals (see Osborn 1899; Vekua 1972).

As here understood, the Pliohyracinae include the following genera:

Prohyrax—relatively small; early to middle Miocene of South West Africa (Stromer 1923, 1926; this report)

Parapliohyrax—large; middle to late Miocene of east and north Africa (Lavocat 1961; Bishop & Pickford 1975)

Pliohyrax—very large; late Miocene and Pliocene of Europe and China (Forsyth-Major 1899; Osborn 1899; Viret 1949; Viret & Thenius 1952; Tung & Huang 1974)

Kvabebihyrax—very large; late Miocene of the Soviet Union (Gabunia & Vekua 1966)

Postschizotherium—very large; late Miocene and Pliocene of China (Von Koenigswald 1966; Tung & Huang 1974)

The relationships of *Prohyrax tertiarius* from Langental have hitherto been obscure since it has been known only from fragmentary material, the holotype being a maxillary fragment with P^3 to M^2 and part of M^3 (Stromer 1926: Pl. 41, fig. 33). Only limited comparisons with the abundant Arrisdrift material are therefore possible, but there can be little doubt that the two forms are closely related. They are probably not conspecific since the Arrisdrift material belongs to a larger species, but they are here taken to be congeneric. Since the Arrisdrift species is undoubtedly a pliohyracine, *Prohyrax* is accordingly included in this subfamily.

The Arrisdrift species shares some characters with other pliohyracines but it is not conspecific with any of them, the most obvious difference being its smaller size. It is apparently closest to the east and north African *Parapliohyrax* and differs appreciably from the three Eurasian genera, which are the youngest and most highly specialized members of the group.

The Arrisdrift hyrax is here interpreted as a new species of the genus *Prohyrax*, probably directly descended from the Langental *P. tertiarius* and a likely ancestor of the later pliohyracines from further north in Africa and from Eurasia.

Although the species will be dealt with in detail elsewhere, some observations on it are included here since it is such an important element in the Arrisdrift assemblage.

More than forty individual animals of all ontogenetic ages are represented, mainly by mandible and maxilla fragments, although isolated teeth and post-cranial bones are not uncommon. The best specimen is a nearly complete skull (AD 363) which lacks only the mandible, right I^2, left M^1, and parts of the right M^3 and right zygomatic arch (Fig. 6, Table 4). The skull is slightly distorted

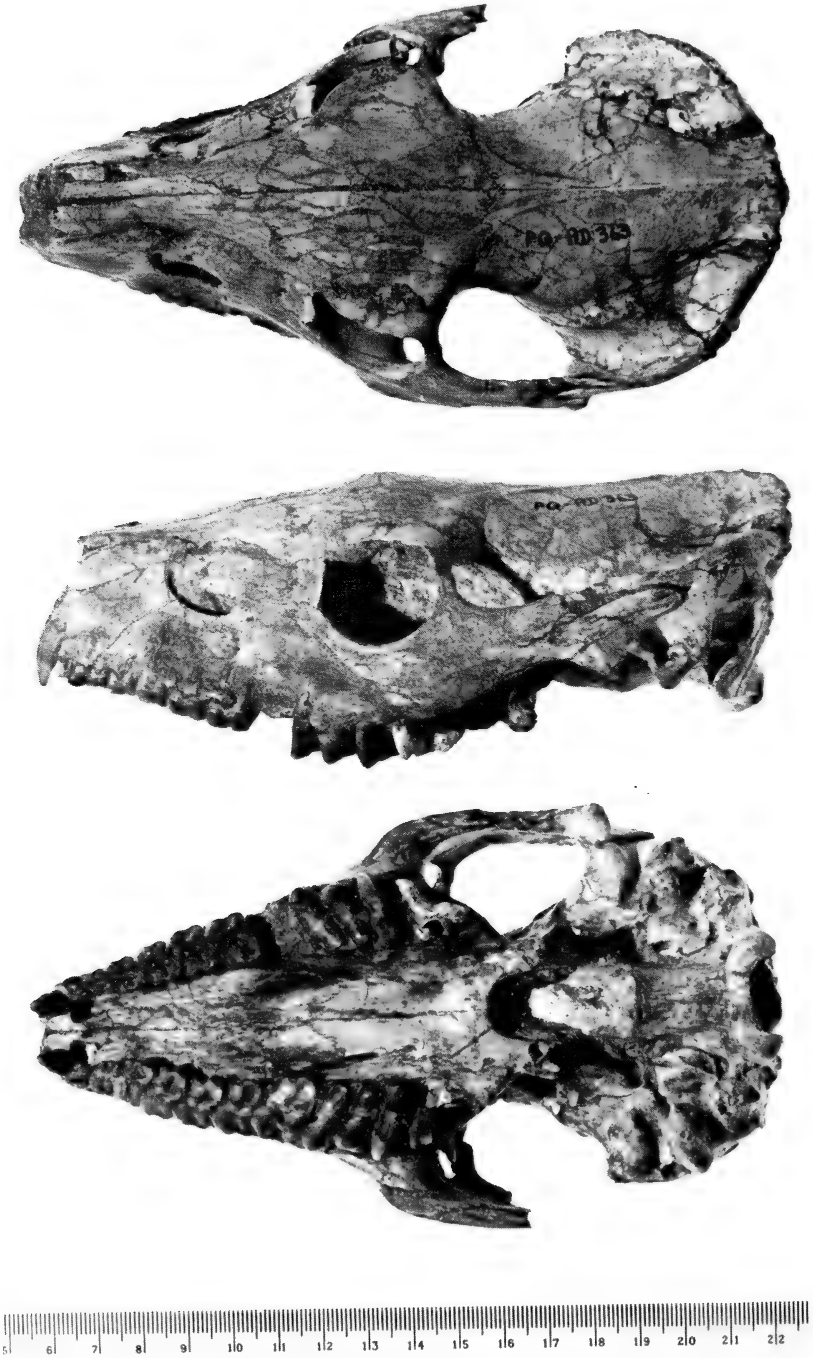

Fig. 6. Dorsal, lateral and ventral views of *Prohyrax* skull (AD 363) from Arrisdrift.

TABLE 4

Dimensions of the *Prohyrax* skull (AD363) from Arrisdrift.

Overall length	160,8
Condylobasal length	152,0
Palate length along midline	97,7
Anterior margin of orbit to anterior margin of I^1	68,0
I^1 to M^3 length	96,9
P^1 to P^4 length	32,9
M^1 to M^3 length	*c.* 47,5
M^3 length	24,7
M^3 breadth	17,3
Interorbital width	36,7
Postorbital width	37,1
Zygomatic width	91,0
Mastoid width	73,8
Palate width at M^3	26,3
Horizontal diameter of orbit	24,3
Vertical diameter of orbit	21,0
Ventral margin of orbit to M^3 alveolar margin	18,7

in places, particularly the posterior part of the braincase. Distinctive features, some of which are characteristic of other pliohyracines, include closed orbits, naso-maxillary fossae which lead ventrally and posteriorly into antorbital foramina situated immediately above the infraorbital foramina, a dental formula of 3.1.4.3 with the I^2 to M^3 series closed, a premolariform $\underline{C}$ and an elongated M^3 with an additional (third) lobe situated posteriorly. The preceding comments on the upper teeth also apply to the lowers. The mandibles lack the fossae and fenestrae found in some other Tertiary hyracoids.

Apart from its smaller size, the Arrisdrift species is most readily distinguished from later pliohyracines by its less elevated orbits and narrower skull.

ORDER PROBOSCIDEA

Family **Gomphotheriidae**

Gen. et sp. indet.

Four largely intact molars and a premolar (e.g. AD 252, AD 257) belong to at least three individuals of an unidentified gomphothere (Fig. 7). They resemble, and may be conspecific with, specimens from Maboko in Kenya which date back about 16 m.y.

This material was originally identified by MacInnes (1942) as *Trilophodon angustidens kisumuensis.* Arambourg (1945) believed that two taxa were represented and named a new genus and species, *Protanancus macinnesi*, to accommodate some specimens. Subsequently Tobien (1973) suggested that the Maboko material belongs to a *Platybelodon* (*P. kisumuensis*), while Maglio (1974) referred it to *Gomphotherium* cf. *angustidens.* Recently Tassy (1977) identified it with *Choerolophodon* (*C. kisumuensis*).

This diversity of opinion is an indication of the difficulties which exist in identifying fragmentary proboscidean remains, and it was decided to withhold

Fig. 7. Occlusal view of Gomphotheriidae third molar (AD 257) from Arrisdrift.

even a tentative identification of the Arrisdrift species. It is, however, unlikely to be a *Platybelodon* since none of the numerous tusk fragments from Arrisdrift are of the *Platybelodon* type.

Even though the material is unclassified, it is important since the molars are more advanced than those of early Miocene gomphotheres elsewhere and they are one of the elements in the assemblage which suggest a late 'Burdigalian' or post-'Burdigalian' age for the fauna.

Family **Deinotheriidae**

Prodeinotherium hobleyi (Andrews, 1911)

The Arrisdrift deinothere is represented by three cheekteeth which have been described by Harris (1977).

Other Proboscidean Material

In addition to the cheekteeth already mentioned, there are many tusk fragments and a few postcranial bones which evidently belong to either the gomphothere or the deinothere. They have yet to be studied.

ORDER PERISSODACTYLA

Family **Rhinocerotidae**

Dicerorhinus sp.

At least three individuals of a rhinoceros are represented by several isolated cheekteeth (e.g. AD 635, AD 827) and postcranial bones (e.g. AD 251, AD 601), the latter being mainly elements of the pes.

The metatarsals which are known are relatively long compared with those of the living *Diceros bicornis* and *Ceratotherium simum*, which suggests that

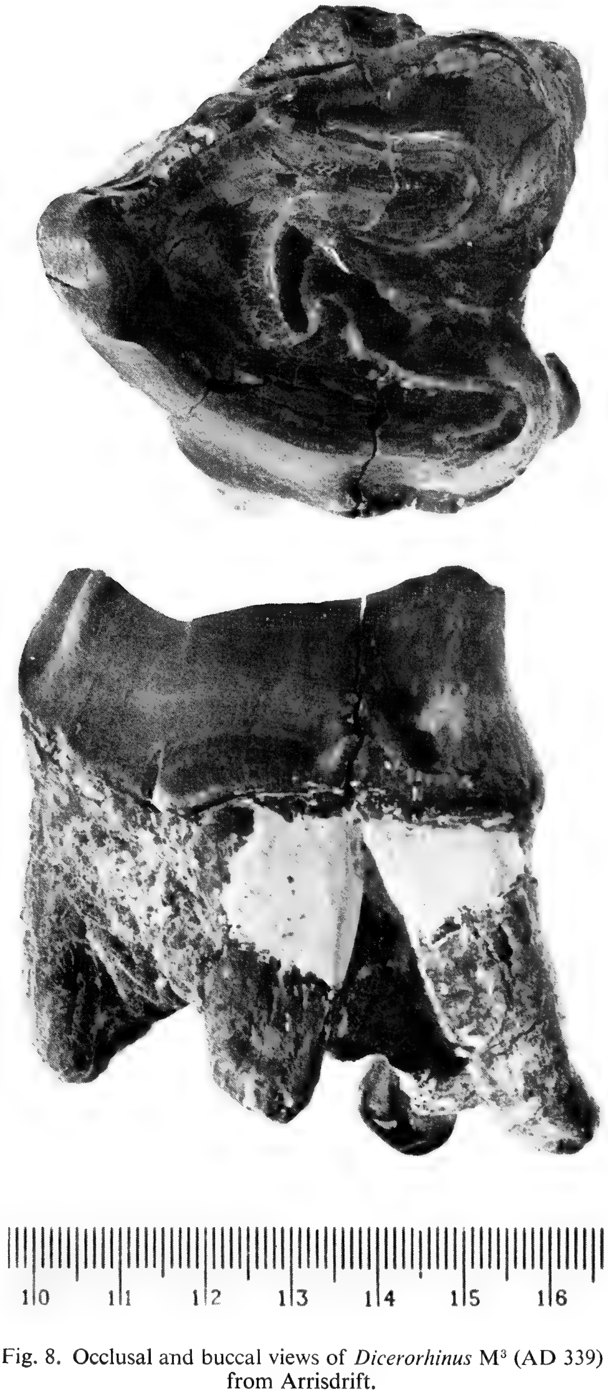

Fig. 8. Occlusal and buccal views of *Dicerorhinus* M^3 (AD 339) from Arrisdrift.

the species concerned was either an *Aceratherium* or a *Dicerorhinus* (see Hooijer 1966) (Table 5). The cheekteeth of African Miocene representatives of these genera may be difficult or impossible to distinguish (Hooijer 1966, 1968*a*), but two M^3's from Arrisdrift (AD 339, AD 1103) resemble those of *Dicerorhinus* rather than *Aceratherium* in having metacone bulges and unconstricted protocones (Fig. 8). These characteristics, together with the elongated metatarsals, distinguish the Arrisdrift species from other recorded African Miocene rhinoceroses, namely, *Paradiceros*, *Brachypotherium* and *Chilotheridium* (Hooijer 1966, 1968*b*, 1971).

Several Miocene species of *Dicerorhinus* have been recorded in Eurasia and Africa (Hooijer 1966), including *D. leakeyi* from the east African early Miocene. The teeth of the Arrisdrift species are larger than those of *D. leakeyi* and in this respect resemble the European middle Miocene *D. schleiermacheri* from Eppelsheim (Table 6). The Arrisdrift metatarsals are longer than those of *D. leakeyi*, which are themselves 'remarkable for their length' (Hooijer 1966: 178), and although the metatarsals of *D. schleiermacheri* are not known, Hooijer believed that they probably 'exceeded those of *D. leakeyi* in length'. Once again a similarity between the Arrisdrift and Eppelsheim species is indicated.

The Arrisdrift species may also be more advanced than *D. leakeyi* in having a less prominent metacone bulge, but there is doubt as to how much significance should be attached to variations in this feature (Hooijer 1966: 128).

The available rhinoceros material from Arrisdrift is probably inadequate for identifying the species concerned, but it does suggest one which was not conspecific with the early Miocene *D. leakeyi* and which was perhaps closer to the middle Miocene *D. schleiermacheri* in an evolutionary sense.

TABLE 5

Dimensions of *Dicerorhinus* metatarsals from Arrisdrift.

	AD251 Mt II	AD249 Mt III	AD253 Mt IV
Median length	177	190	170
Proximal width	33	61	43
Proximal antero-posterior diameter	48	—	—
Middle width	30	50	—
Middle antero-posterior diameter	25	26	—
Ratio middle width/length	0,17	0,26	—

All measurements approximte owing to condition of specimens.

TABLE 6

Dimensions of *Dicerorhinus* M^3's from Arrisdrift.

	AD339	AD1103
Antero-posterior diameter	55,0	54,3
Transverse diameter	61,0	54,1
Length of outer surface	65,9	66,3

ORDER ARTIODACTYLA

Family **Suidae**

Gen. et sp. indet.

A mandible fragment with two cheekteeth (AD 631) belongs to a small suid whose identity has yet to be determined.

Family **Suidae**

Lopholistriodon moruoroti Wilkinson, 1976

Several specimens belong to a small listriodont pig. They include a maxilla fragment with P^4 to M^3 (AD 136) and two isolated M_3's (AD 135, AD 636) (Fig. 9, Table 7).

TABLE 7

Dimensions of *Lopholistriodon moruoroti* teeth from Arrisdrift.

	P^4		M^1		M^2		M^3		M_3	
	l	b	l	b	l	b	l	b	l	b
AD 136 . .	6,5	8,3	9,0	9,2	10,3	10,4	11,4	10,1	—	—
AD 135 . .	—	—	—	—	—	—	—	—	14,0	7,9
AD 636 . .	—	—	—	—	—	—	—	—	12,4	8,1

In an unpublished thesis, Wilkinson (1972) described and named a new species of pig, *Xenochoerus ? moruoroti*, from Moruorot Hill in Kenya. He subsequently referred it to the genus *Lopholistriodon* Pickford & Wilkinson, 1975 (Wilkinson 1976). The teeth of the Arrisdrift listriodont are virtually indistinguishable from those of the Moruorot *L. moruoroti* and it is identified accordingly.

According to Pickford & Wilkinson (1975) this species is present at Moruorot (17 m.y.), Maboko (16 m.y.) and Muruyur (13 m.y.), so its presence at Arrisdrift is taken as a further indication that this fauna is late 'Burdigalian' or post-'Burdigalian' in age.

Family **Tragulidae**

Dorcatherium cf. *pigotti* Whitworth, 1958

Two mandible fragments (AD 104, AD 262) and a few postcranial bones belong to a small tragulid. The teeth are morphologically indistinguishable from those of *Dorcatherium* and, of the African species of this genus, they are closest in size to those of *D. pigotti* of the east African early Miocene (Whitworth 1958) (Table 8).

TABLE 8

Dimensions of *Dorcatherium* teeth from Arrisdrift.

	P_2		P_3		M_1		M_2	
	l	b	l	b	l	b	l	b
AD104	6,9	2,4	7,9	3,0	—	—	—	—
AD262	—	—	—	—	8,5	5,5	9,1	6,2

Fig. 9. Occlusal and buccal views of *Lopholistriodon moruoroti* maxilla (AD 136) from Arrisdrift.

The Arrisdrift specimens are only tentatively identified with this species since the grounds for distinguishing poorly represented fossil tragulids are limited. There is little variation in tooth morphology and there has been a tendency to name distinct species in Europe, Asia and Africa on the basis of size differences. It is by no means certain that similarly sized species on the different continents represent different species.

Family **Palaeomerycidae** (*senso* Hamilton 1973)

Climacoceras sp. nov.

The Arrisdrift ruminant assemblage includes several fragments of antler-like frontal appendages (ossicones) (e.g. AD 130, AD 132) (Fig. 10). The beams of the 'antlers' are straight, transversely compressed, and have small knobs situated at irregular intervals both anteriorly and posteriorly. They evidently also carried some small tines, several detached specimens having been discovered (e.g. AD 129, AD 785). The tines are circular in cross-section and slightly curved. AD 648 indicates that there was bifurcation and greater flattening of the 'antlers' distally. AD 483 apparently represents the proximal part of an 'antler' and since it lacks a burr, the 'antlers' were evidently not deciduous. They were, therefore, not true antlers of the kind which characterize the Cervidae.

Fig. 10. Lateral view of *Climacoceras* 'antler' fragments from Arrisdrift: AD 648 (+AD 763)—distal end showing bifurcation (left); AD 130—beam fragment showing knobs (centre); AD 129—tine (right).

The complete 'antlers' must have resembled those of *Climacoceras africanus* from Maboko (MacInnes 1936). *Climacoceras* is also present at Fort Ternan (Gentry 1970). The Arrisdrift specimens are distinguished from east African specimens by their larger size, the difference being of the order of 20 per cent according to A. W. Gentry (pers. comm.). The beam circumference of specimens from Maboko varies from 54 to 92 mm (MacInnes 1936), while the corresponding figures for Arrisdrift specimens are 85 to 110 mm. The longest of the Maboko tines recorded by MacInnes measures 48 mm, whereas two of the Arrisdrift specimens (AD 129, AD 1177) are about 60 mm long and both are incomplete.

The larger size of the Arrisdrift specimens is taken to indicate that they belong to a hitherto unrecorded species of *Climacoceras*, although the morphological similarity to specimens from Maboko suggests that the Arrisdrift species was in a comparable evolutionary state to *C. africanus*.

Many mandible and maxilla fragments, isolated teeth and postcranial bones probably belong to this species. It is, however, not certain that all the material provisionally assigned to the *Climacoceras* belongs only to this species. A comparison between two of the more complete mandibles (AD 261, AD 612; Fig. 11, Table 9) revealed differences which may be taxonomically significant. For example, AD 612 has slightly larger teeth, an appreciably deeper mandibular corpus, larger basal pillars on the molars and a less expanded P_4 metaconid. In addition, the lingual surface of the M_3 third lobe is directly connected to the second and is flanked by a small, more or less circular enamel island which evidently corresponds to the central cavities of the first and second lobes. By contrast, the M_3 third lobe of AD 261 is transversely compressed dorsally and is connected lingually to the second lobe by a deeply indented loop in the enamel. It also lacks a 'central cavity'.

TABLE 9

Dimensions of lower teeth and mandibles AD 261 and AD 612, tentatively assigned to *Climacoceras* from Arrisdrift.

	P_3		P_4		M_1		M_2		M_3	
	l	b	l	b	l	b	l	b	l	b
AD 261	—	—	14,0	7,6	15,3	9,7	*c.* 17,5	12,5	24,0	9,5
AD 612	*c.* 15,5	*c.* 7,5	16,5	8,5	*c.* 17,0	—	21,3	*c.* 11,6	26,3	10,7

	AD 261	AD 612
Depth of mandible below P_4	25,0	29,0
Breadth of mandible below P_4	12,1	14,5
Depth of mandible below M_3	28,5	37,7
Breadth of mandible below M_3	13,0	15,8

Sorting the remaining mandible fragments on the basis of these criteria was not entirely satisfactory owing to the poor condition of some specimens and because in some instances 'characteristics' of one type occurred in conjunction with 'characteristics' of the second. Nevertheless, AD 259, AD 263, AD 269 and AD 270 are apparently of the AD 612 type and represent at least 4 individuals, while AD 271, AD 272, AD 346, AD 356 and AD 621 appear to be of the AD 261 type and represent 6 individuals.

The two sets of specimens are otherwise similar and amongst the shared characteristics are a giraffoid-like orientation of the diastema region relative to the cheektooth row, low-crowned cheekteeth, absence of P_1 and simple, crescentic central cavities on the lower molars, the posterior one opening lingually in early wear. Although several symphyseal teeth are known, they do not include bilobed giraffoid-like canines.

The less numerous maxillae and upper teeth have not been closely examined. Gentry (pers. comm.) has found that although the large ruminant teeth and

Fig. 11. Occlusal and buccal views of *? Climacoceras* mandibles, AD 261 (above) and AD 612 (below), from Arrisdrift.

dentitions from Arrisdrift share several characters with the early Miocene *Propalaeoryx* from Elisabethfeld and the Fort Ternan *Climacoceras*, they are in some respects intermediate between the two. For example, the Elisabethfeld *Propalaeoryx* is more primitive in retaining P_1. On the other hand, at least some of the Arrisdrift M_3's (the AD 612 type) have 'central cavities' on the third lobes, whereas the Fort Ternan *Climacoceras* M_3's lack this feature. In addition, the Arrisdrift teeth are probably less high-crowned than those of the Fort Ternan *Climacoceras*, while the metastylids are developed to a degree intermediate between the Elisabethfeld and Fort Ternan species.

Since the Maboko *Climacoceras* predates the Fort Ternan species and is younger than the Elisabethfeld *Propalaeoryx*, a temporal link with the Arrisdrift species is suggested. Unfortunately the only described teeth assigned to the Maboko *Climacoceras* are three lower molars (MacInnes 1936), so the basis for comparisons with Arrisdrift specimens is limited. The Maboko teeth are, however, similar to the AD 261 type in size and some morphological characters, including reduced or absent basal pillars and dorsally compressed third lobe of M_3.

There are several complete specimens amongst the postcranial bones tentatively assigned to the *Climacoceras*. They include a tibia (AD 1100), several radii (e.g. AD 494, AD 562) and metapodials (e.g. AD 198, AD 199), as well as elements of the manus and pes. The long bones are slender and elongated compared with those of living bovids and cervids of similar overall size (e.g. *Damaliscus dorcas*, *Cervus unicolor*). The housing of the extensor tendon of the distal metatarsals shows the bovid and giraffid rather than the cervid condition (see Whitworth 1958: 23).

Family **Bovidae**

Gen. et sp. indet.

Several mandible fragments (e.g. AD 103, AD 106) and postcranial bones belong to a small ruminant (Fig. 12, Table 10). Morphologically the teeth are perhaps closest to those of the somewhat larger *Walangania africanus* (= *Palaeomeryx africanus* + *Walangania gracilis* (see Hamilton 1973)) of the east African early Miocene. *W. africanus* was once thought to be a bovid, but

TABLE 10

Dimensions of the lower cheekteeth and mandibles of the Bovidae indet. from Arrisdrift.

	P_3		P_4		M_1		M_2		M_3	
	l	b	l	b	l	b	l	b	l	b
AD 105 . .	7,8	4,2	8,3	4,8	—	—	9,4	6,7	13,0	6,5
AD 106 . .	—	—	8,1	4,5	9,1	6,3	9,7	6,6	—	—

	AD 105	AD 106
Depth of mandible below P_4	*c.* 12,4	14,3
Breadth of mandible below P_4	6,3	6,1
Depth of mandible below M_3	15,5	18,7
Breadth of mandible below M_3	7,6	7,9

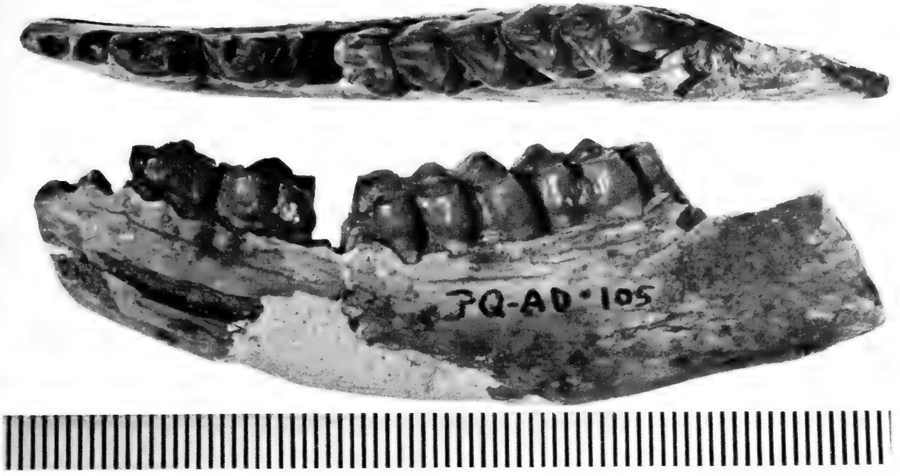

Fig. 12. Occlusal and buccal views of Bovidae mandible (AD 105) from Arrisdrift.

Gentry (pers. comm.) now believes it could be congeneric with the primitive ruminant *Dremotherium* from the European late Oligocene to early Miocene.

Gentry (pers. comm.) reports on the Arrisdrift material as follows: 'The smaller metastylids of the lower molars are more advanced towards bovids than those of *Walangania.* Similarly, the weaker anterior ribs and the better developed closure of the central cavities. The Maboko bovid fragment with M_2 (see Whitworth 1958: 25, fig. 10a–c) appears to agree with the Arrisdrift species except in not being smaller than *Walangania*: its metastylid is weak, the anterior rib is not localized, and the central cavities are more enclosed within the tooth.'

He concludes that the Arrisdrift species 'is a bovid, although finding a horn core is needed to be conclusive'.

Other Ruminants

The possibility of a second taxon being represented amongst the material assigned to the *Climacoceras* has already been mentioned.

In addition, there are several ruminant postcranial bones which are too small to belong to the *Climacoceras*, but far too large to belong to the bovid. They include a distal humerus (AD 39), proximal metacarpals (AD 764, AD 964) and a first phalanx (AD 895). The 'Pecora gen. & sp. indet.' on the accompaying faunal list (Table 1) refers to this material

ORDER LAGOMORPHA

Family **Ochotonidae**

Kenyalagomys sp. nov.

A mandible fragment with M_1 and M_2 (AD 813) (Fig. 13) and an isolated P^3 (AD 1185) belong to a small ochotonid which resembles species previously

Fig. 13. Occlusal and buccal views of *Kenyalagomys* mandible (AD 813) from Arrisdrift.

recorded from early Miocene deposits in the Namib desert and east Africa.

The first African Miocene ochotonid to be described was *Austrolagomys inexpectatus* from Elisabethfeld (Stromer 1924, 1926). Hopwood (1929) recorded a second species from the same region, namely *A. simpsoni*. Subsequently MacInnes (1963) identified a second genus, *Kenyalagomys*, on the basis of material from east Africa and named two species, *K. rusingae* and *K. minor*.

MacInnes made no reference to Hopwood's species, but amongst the characters used to distinguish *Kenyalagomys* from *Austrolagomys* (MacInnes 1953: 20–21) are two of the three characters which distinguish *A. simpsoni* from *A. inexpectatus* (Hopwood 1929: 2). They are a deep external fold on P_3 and a marked median angulation (rib) on the posterior walls of the anterior lobes of P_4 to M_2. It follows that if the generic distinction is justified, and it is here assumed that it is, then *A. simpsoni* must be referred instead to *Kenyalagomys*.

Judged on the basis of size, neither of the east African species is a synonym of *K. simpsoni*. *K. rusingae* is larger and, although *K. minor* is similar in overall size, it differs in having a smaller P_3 and larger molars.

Another species of *Kenyalagomys*, *K. mellalensis*, was recently recorded from the middle Miocene (*c.* 14 m.y.) of Beni Mellal in Morocco (Janvier & De Muizen 1976).

The molars of the Arrisdrift mandible (AD 813) are almost identical in size to the corresponding teeth of the *K. simpsoni* holotype, but the posterior walls of the anterior lobes lack the prominent ribs which characterize *Kenyalagomys*. There is, however, a faint indication of such ribs and the teeth of AD 813 are closer to the condition in *Kenyalagomys* than that in *Austrolagomys*, where the posterior walls are smoothly curved.

The Arrisdrift P^3 (AD 1185), which measures 1,6 by 3,2 mm, is similar in size to that of *K. minor*, it is smaller than that of *K. rusingae* and longer, but narrower than that of *K. mellalensis*. It also resembles *K. minor* in having the postero-external corner pointed rather than rounded as in both *A. inexpectatus* and *K. rusingae*. *K. mellalensis* is in an intermediate position in this respect. AD 1185 differs from *K. minor* in having the posterior border more or less straight rather than convex and in this respect resembles *K. rusingae* and *K. mellalensis*. Visible on the occlusal surface is a deeply indented enamel fold which resembles corresponding features in the east and north African species of *Kenyalagomys*, but which is absent in *Austrolagomys*.

The Arrisdrift ochotonid is here regarded as a previously unrecorded species of *Kenyalagomys*, whose closest relatives are *K. minor* and *K. simpsoni*. If there is a phyletic relationship between the latter two species and the one from Arrisdrift, then the reduced median ribs of the anterior lobes of the lower molars of AD 813 may be interpreted as being either in an incipient or in a vestigial state. The latter alternative is more likely in view of the probable younger age of the Arrisdrift species relative to the Rusinga *K. minor* and its apparent contemporary from the Namib, *K. simpsoni*. Since *K. mellalensis* is more likely to be related to *K. rusingae* than the smaller African ochotonids, its evolutionary state relative to that of the Arrisdrift species is not determinable.

To sum up, the Arrisdrift ochotonid is apparently a new species of *Kenyalagomys* which is more advanced than the smaller species already recorded from the early Miocene of Africa.

ORDER RODENTIA

? Family **Bathyergidae**

? Bathyergoides sp.

Two incomplete lower incisors (AD 141, AD 1024) belong to a large rodent, possibly a bathyergid. They are tentatively attributed to *Bathyergoides*, a genus recorded from the early Miocene of the Namib (Stromer 1926) and east Africa (Lavocat 1973).

Family **Thryonomyidae**

Paraphiomys pigotti Andrews, 1914

Two incomplete mandibles (AD 629, AD 1049) belong to a rodent which appears indistinguishable from that described by Stromer (1922, 1926) as *Neosciuromys africanus.* This taxon has since been recognized as a junior synonym of *Paraphiomys pigotti* by Lavocat (1973). *P. pigotti* is one of the more commonly occurring rodents in deposits of early Miocene age in both east Africa and the Namib desert. The Arrisdrift *P. pigotti* evidently postdates all previous records of this species (see below).

Other Rodents

The Arrisdrift assemblage includes many isolated rodent incisors and, judged on the basis of size, they represent at least two species in addition to those mentioned above.

AGE OF THE OCCURRENCE

The fauna from Pit 2/AD 8 at Arrisdrift undoubtedly dates from the Miocene and it has been suggested elsewhere (*South African Journal of Science* 1976; Corvinus & Hendey 1978) that it falls within the age limits of 12 to 18 m.y. The present study has tended to confirm the older limit, but it has also suggested that the 12 m.y. limit is too young.

At present the fauna can be dated only in a relative sense by comparing individual taxa with more securely dated ones elsewhere. The non-mammalian vertebrates cannot yet be used in this way and the comments which follow are confined to the mammals.

On the basis of previous records only two of the twenty-two mammalian species suggest an early Miocene date for the fauna. They are *Myohyrax* cf. *oswaldi* and *Paraphiomys pigotti*, which in east Africa are recorded from deposits ranging in age from 18 to 22 m.y. Since little has been published on the midde Miocene small mammals of east Africa, it cannot yet be assumed that these taxa did become extinct there 18 m.y. ago. In addition, since there is some evidence of differences in the patterns of mammalian evolution in east and southern Africa during the earlier part of the Miocene (see below), it is possible that taxa such as *M. oswaldi* and *P. pigotti* survived longer in southern Africa.

Two other species, the large canoid and *? Ischyrictis* sp., may also be indicative of an early Miocene date, but in both instances doubts about identification render them unreliable for relative dating purposes.

Five of the twenty-two species suggest a middle Miocene date, that is, late 'Burdigalian' at the earliest, but more probably 'Vindobonian' or even

'Maremmian' (*senso* Berggren & Van Couvering 1974). They are *Amphicyon* cf. *steinheimensis*, Gomphotheiidae indet., *Dicerorhinus* sp., *Lopholistriodon moruoroti* and *Climacoceras* sp. nov. In addition, there are another three species which are, or probably are, more advanced than previously recorded African 'Burdigalian' species and would be consistent with a middle Miocene date. They are *Prohyrax* sp. nov., Bovidae indet. and *Kenyalagomys* sp. nov. These eight species are regarded as the most significant for dating purposes.

Four of the twenty-two species would be consistent with any age from 'Burdigalian' to 'Vallesian'. They are ?Hemicyoninae indet., *? Metailurus* sp., *Prodeinotherium hobleyi* and *Dorcatherium* cf. *pigotti.*

The remaining six species provide no evidence of age. They are the unidentified carnivore, suid, pecoran and rodents.

Negative evidence also gives some indication of the probable age of the fauna. For example, the absence of equids suggests it is pre-'Vallesian' (see Hooijer 1975), while the absence of positively identifiable bovids and palaeotragines suggests that it predates the 14 m.y. old Fort Ternan fauna (see Gentry 1970; Churcher 1970).

There is, in fact, no secure evidence that the Arrisdrift fauna is as young as that from Fort Ternan, while there is good evidence that it postdates the 'Rusinga-like' faunas of east Africa. Consequently, the likely age limits may be reduced to between 14 and 18 m.y., with the median estimate being about 16 m.y. This is the age of the Maboko fauna and, although it has yet to be fully described, it includes at least six species which are conspecific with, or closely related to species from Arrisdrift (Table 11). They are *Choerolophodon kisumuensis*, *Prodeinotherium hobleyi*, *Lopholistriodon moruoroti*, *Dorcatherium pigotti*, *Climacoceras africanus* and the unidentified bovid. This suggests that the two faunas are, indeed, of the same order of age. On the other hand, the deinothere and tragulid are of little use as precise age indicators, while the two faunas do differ in certain respects. Primates and creodonts are absent or

TABLE 11

The mammals from Maboko, Kenya, and their counterparts from Arrisdrift, South West Africa.

MABOKO*	ARRISDRIFT
Primates	—
Paracynohyaeonodon leakeyi	Various Carnivora
Megalohyrax championi	*Prohyrax* sp. nov.
Choerolophodon kisumuensis	Gomphotheriidae indet.
Prodeinotherium hobleyi	*Prodeinotherium hobleyi*
Aceratherium acutirostratum	*Dicerorhinus* sp.
Lopholistriodon moruoroti	*Lopholistriodon moruoroti*
Brachyodus aequitorialis	—
Dorcatherium spp., including *D. pigotti*	*D.* cf. *pigotti*
Climacoceras africanus	*Climacoceras* sp. nov.
Bovidae indet.	Bovidae indet.

* Bishop (1967); Hooijer (1968*a*); Pickford & Wilkinson (1975); Tassy (1977); Van Valen (1967); Whitworth (1958).

apparently absent, at Arrisdrift and the hyracoids from the two occurrences are at least generically distinct. These differences will be discussed again later, but they indicate that either the two faunas were not exactly contemporaneous, or that there were regional differences between contemporary east and southern African faunas at that time.

The final word on the age of the Arrisdrift fauna has yet to come, but available evidence suggests that it is early middle Miocene, with an inferred date of about 16 m.y. before present.

PALAEOENVIRONMENT

The Arrisdrift fauna dates from a zoogeographically important period. Andrews & Van Couvering (1975: 85–87) have discussed the 'abrupt changes' which occurred in the faunas of east Africa between 14 and 18 m.y. ago and ascribe them to the development of a land bridge between Africa and Eurasia and the consequent immigration of new taxa. According to Berggren & Van Couvering (1974) the land bridge in question resulted from the closure of the eastern Tethys between 18 and 20 m.y. ago. Faunal changes must also have been experienced in southern Africa during this period, although it cannot be assumed that they were coincident with, or that they were an exact parallel of those in east Africa. There is, in fact, some evidence that the situation in southern Africa did differ from that in east Africa.

Andrews & Van Couvering (1975) pointed out that during the early Miocene the dominant hyracoids in east Africa were geniohyids and that they were replaced in the middle Miocene (post-Fort Ternan) by procaviids. In the Namib region the only recorded hyrax is the procaviid *Prohyrax*, which was contemporary with geniohyids in east Africa (up to and including Maboko). It follows that the procaviids are likely to have had southern Africa as their centre of origin and that they moved into east Africa at a time when this region was also receiving Eurasian immigrants. Even if there are changes in the classification of the hyracoid taxa concerned, the substance of the preceding theory remains the same since the east and southern African forms clearly belong to different lineages, and it is the southern African one (a pliohyracine) which had descendants in east Africa (and elsewhere) in post-early Miocene times.

Also relevant here is MacInnes's (1957) opinion that the southern African *Parapedetes* and east African *Megapedetes* were contemporary representatives of different lineages since it, too, suggests that there was some independent evolution of related taxa in the two regions. Other of the Namib rodents, as well as the ochotonid *Austrolagomys*, may also have been southern endemics.

In comparing faunas, it may be unwise to emphasize the absence of certain taxa since this may be due to sampling deficiencies or even incorrect identification of specimens. While the apparent absence of, for example, primates at Arrisdrift might be due to such factors, if their absence is real then it must be palaeoenvironmentally significant. The absence or great rarity of primates at another southern African late Tertiary locality, namely, Langebaanweg, has already been mentioned elsewhere (Hendey 1976: 234), while this group is also not recorded from the other Miocene localities in the Namib.

By contrast, Andrews & Van Couvering (1975: 86) noted that during the early Miocene of east Africa 'there was a notable proliferation of hominoid primates, seven species in all; and there were at least five species of prosimians'. Primates became much less common in east Africa during the middle Miocene, although during the 14 to 18 m.y. transition period monkeys were 'common at Maboko', whereas 'there is little evidence for their presence in the Early Miocene environments' (Andrews & Van Couvering 1975: 93). The primates are thus one group which reflect the 'abrupt changes' referred to earlier, but in this instance the change is not manifested in the southern African record.

The apparent absence of primates in southern Africa during the earlier part of the Miocene is made even more remarkable by the fact that this group features in the 'Burdigalian' faunal interchange between east Africa and southern Eurasia. Thus, while a northward movement of primates from east Africa is documented, there is no record of a corresponding movement to the south.

To sum up, there is some evidence which suggests that early in the Miocene faunal interchange between east and southern Africa was inhibited and that at least some related taxa evolved independently of one another in the two regions. This indicates the existence of an environmental barrier between the two regions and it is most likely to have been comprised of the extensive river system of central Africa, together with the Rift Valley lakes (see Kortlandt 1972). Even in their present form the Congo and Zambezi river systems, especially in the region of the Congo/Zambezi divide, make up a broad and almost continuous area of channels and marshes between east and south-west Africa. Tectonic disturbances in central Africa during the mid-Tertiary may well have complicated the headwater drainage patterns of these rivers and so have created an even more effective barrier to limit the crossing of at least certain mammals.

Another possible barrier may have been that of an intervening arid and semi-arid region. A more extended form of the present Kalahari desert would have effectively separated east and south-west Africa from one another. This alternative is perhaps less likely since the present aridity of the south-western parts of Africa was apparently initiated only in the very late Tertiary (A. J. Tankard & J. Rogers, unpublished manuscript). Prior to this the climate and vegetation of Africa may have been of a more uniform nature.

The preceding observations suggest that in assessing the character and composition of southern African Miocene faunas, allowance must be made for deviations from the better documented east African pattern because geography is a complicating factor, the full implications of which have yet to be established.

In this connection the apparent absence of creodonts at Arrisdrift may also be significant. Creodonts predominate in the carnivore faunas of the 18 to 22 m.y. period in east Africa and the only identified carnivore from contemporary occurrences in the Namib is also a member of this group. Similarly the only recorded carnivore from Maboko is a creodont, while at Fort Ternan creodonts are common if not predominant. In other words, creodonts were an important element in the 'Aquitanian' to 'Vindobonian' faunas of east Africa. Consequently, it is to be expected that they would not only be present at Arrisdrift but would be more commonly represented than fissiped carnivores.

Since carnivores are less restricted by environmental factors than herbivores, the dispersal of immigrant taxa may well have been rapid in spite of barriers which impeded the movement of, for example, primates. Should it be established that creodonts are, indeed, rare or absent at Arrisdrift, the situation could be explained in only one of two ways.

Firstly, southern Africa was an important centre of fissiped evolution and they superseded creodonts in this region before the same happened in east Africa. This possibility can be dismissed in view of what is known of fissiped origins and evolution (Savage 1977) and since it would require complete isolation of southern Africa from east Africa during the early Miocene.

The second possibility is that Arrisdrift is younger than was indicated previously and dates from a period when the creodonts had been largely or completely replaced by fissipeds. The carnivores would then be the only obvious 'advanced' element in the Arrisdrift fauna, while those taxa which suggest a *c.* 16 m.y. date would be 'primitive' forms which survived longer in the Namib region than in east Africa. This interpretation would require, for example, that early bovids and giraffids such as those found at Fort Ternan had been prevented from spreading southwards by the hypothetical zoogeographic barrier, whereas immigrant fissipeds had already surmounted it and become established in southern Africa by the time that the Arrisdrift fossils were being deposited.

Perhaps the only firm conclusion to be drawn from the preceding discussion is that the present state of knowledge of southern African Miocene faunas leaves much to be desired.

Some information on the nature of the environment in the immediate vicinity of Arrisdrift at the time that the fossiliferous deposits were laid down is suggested by both the fossils and the deposits themselves.

There is no doubt that the fossils accumulated in a river channel, the vertebrate remains simply being an additional element in the coarse sediment fraction of a fluvial gravel. The fact that a *Prohyrax* skull and other delicate fossils were recovered from the deposits indicates that they at least could not have been transported far in what was evidently a turbulent channel. Even those specimens which are abraded are not seriously damaged. Thus, most of the fossils must represent the remains of animals which lived in the immediate vicinity or a little further upstream.

The only invertebrate in the fossil assemblage, a serpulid polychaete (cf. *Mercierella* sp.), is a typically estuarine form (B. Kensley, pers. comm.) and its presence suggests that at the time of deposition the coastline, which is at present about 30 km away, was much closer. This, together with the fact that the fossiliferous deposits are about 50 m above sea-level, suggests that deposition took place during a period of relatively high sea-level. There is evidence for a world-wide marine transgression during the Miocene, between 10 and 20 m.y. ago (Flemming & Roberts 1973) and presumably at least part of the Arrisdrift terrace sequence can be correlated with this event. Arrisdrift is situated in a hilly area on the last meander of the Orange River before it reaches the flat and low-lying coastal section of its valley, which is likely to have been inundated during the transgression. The mouth of the river was, therefore, probably only a few kilometres west of Arrisdrift.

The area around Arrisdrift is now very arid, with Alexander Bay at the mouth of the Orange River having a mean annual rainfall of less than 50 mm (Dept. of Transport 1965). The Orange River is, however, a large perennial river and is flanked by a narrow belt of bushes and trees, although the vegetation becomes ephemeral a short distance away. There is little or no soil cover in the area and aeolian sands and bedrock exposures are ubiquitous. Although the climate is ameliorated by the proximity of the cold Atlantic Ocean, it is nevertheless an inhospitable area capable of supporting only sparse populations of a relatively small number of mammalian species (see Shortridge 1934).

The environment at the time that the fossils were deposited must have been very different. Although poorly preserved plant remains occur in the Pit 2/AD 8 deposits, no direct information on the nature of the vegetation is yet available. The large mammals, particularly the two proboscideans, suggest a densely vegetated and probably wooded environment. Harris (1975) has suggested that both *Prodeinotherium* and gomphotheres preferred such a habitat. The low-crowned teeth of the rhinoceros suggest that it, too, was a browser, while the long limbs and low-crowned teeth of the *Climacoceras* indicate that it was not adapted to grazing. Both are likely to have been woodland species.

The smaller herbivores are probably indicative of a dense undergrowth at least in the immediate vicinity of the river. Living tragulids are forest-dwelling browsers and their Miocene ancestors, including the Arrisdrift *Dorcatherium*, probably had a similar habitat preference. The same is likely to apply to the bovid and two suids since they resemble the *Dorcatherium* in both size and hypsodonty, while the *Prohyrax* probably occupied a similar habitat, but with somewhat different vegetable-food preferences.

Since later pliohyracines were aquatic or amphibious animals, early forms such as the Arrisdrift *Prohyrax* may already have developed a preference for life in water-side situations. The fact that it is the most commonly occurring vertebrate in the assemblage supports the theory that it was a riparian species since remains of such animals are more likely to be incorporated in fluvial deposits than those of other terrestrial species. In this connection it is probably significant that the other commonly occurring vertebrate at Arrisdrift is a crocodile, which undoubtedly is a riparian species.

The picture which emerges is of a forested riverine setting, probably with dense undergrowth adjacent to the river and with the sea no more than a few kilometres away. An essentially similar environment was suggested for those areas further north in the Namib where the early Miocene vertebrates were discovered (Stromer 1926; Hopwood 1929). In the case of these occurrences the contrast to the modern environment is even more striking since there are no rivers in the area today. There is, however, ample evidence of their presence during the Miocene.

The Arrisdrift fossils, together with the older ones from the Lüderitz–Bogenfels area, provide some of the evidence which supports the theory that the present Namib desert is relatively young (A. J. Tankard & J. Rogers, unpublished manuscript). Whether or not a desert existed in the area in pre-Miocene times is still a matter of dispute, but the earlier part of the Miocene was evidently a period of relatively high rainfall and more luxuriant vegetation.

Andrews & Van Couvering (1975) believed that during this period a belt of lowland forest stretched across equatorial Africa and was flanked on either side by woodlands. The evidence from Arrisdrift and the other occurrences suggests that these woodlands extended at least as far south as the Orange River.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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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 (fig. 8a–b).
Nucula largillierti Philippi, 1861: 87.
Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:
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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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

Q. B. HENDEY

PRELIMINARY REPORT ON THE MIOCENE VERTEBRATES FROM ARRISDRIFT, SOUTH WEST AFRICA

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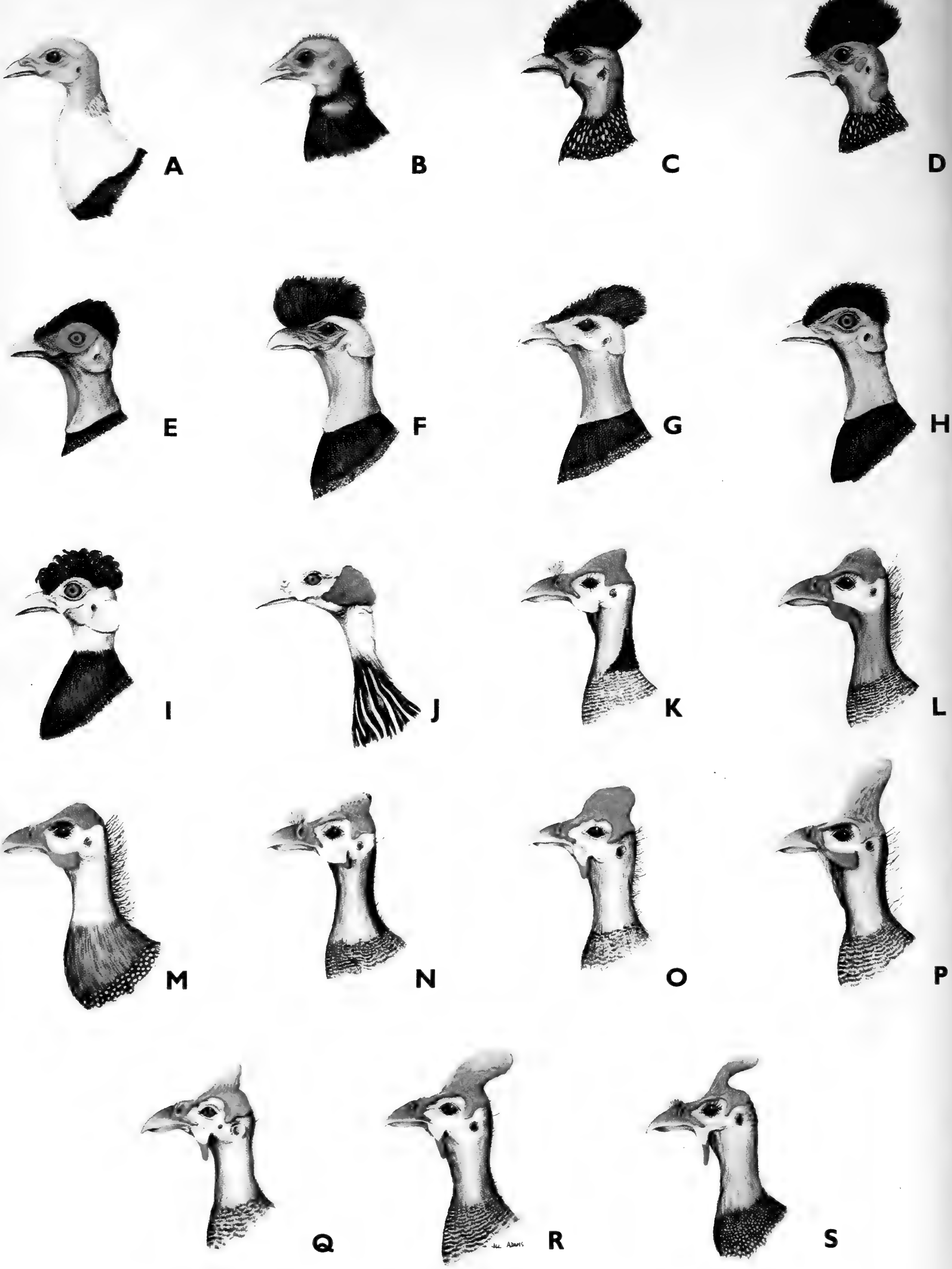

Fig. 1. Guineafowl taxa recognized in this study.

A. *A. meleagrides.* B. *A. niger.* C. *Guttera plumifera plumifera.* D. *G. p. schubotzi.* E. *G. pucherani pucherani.* F. *G. p. verreauxi.* G. *G. p. sclateri.* H. *G. p. barbata.* I. *G. p. edouardi.* J. *Acryllium vulturinum.* K. *Numida meleagris meleagris.* L. *N. m. sabyi.* M. *N. m. galeata.* N. *N. m. somaliensis.* O. *N. m. marungensis.* P. *N. m. reichenowi.* Q. *N. m. mitrata.* R. *N. m. coronata.* S. *N. m. damarensis.*

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THE EVOLUTION OF GUINEA-FOWL (GALLIFORMES, PHASIANIDAE, NUMIDINAE) TAXONOMY, PHYLOGENY, SPECIATION AND BIOGEOGRAPHY

By

T. M. CROWE

Cape Town Kaapstad

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THE EVOLUTION OF GUINEA-FOWL (GALLIFORMES, PHASIANIDAE, NUMIDINAE) TAXONOMY, PHYLOGENY, SPECIATION AND BIOGEOGRAPHY

By

T. M. Crowe

FitzPatrick Institute, University of Cape Town

(With 53 figures, 11 tables and 2 appendices)

[*MS. accepted 15 March 1978*

ABSTRACT

Patterns of qualitative and quantitative character variation in 1 833 museum specimens encompassing all taxa attributed to the Numidinae are analysed to produce an hypothetical taxonomy and phylogeny for the subfamily. Quantitatively and ecologically defined genus, species and subspecies concepts are applied in erecting the taxonomy. A cladistic approach, based in postulated primitive-derived character sequences, is used in developing the phylogeny. 4 genera, 6 species and 16 subspecies are recognized. Cladistic events are linked to likely causal geological and palaeoecological events to determine a possible evolutionary chronology. Genera are thought to have arisen as a consequence of Miocene and Pliocene radiations; species and subspecies as a result of Pleistocene divergence. An hypothetical map of African avifaunal zones, based on evolutionary patterns found in guinea-fowl, is offered. Comparisons of this map with other African avifaunal maps and with distribution maps of selected francolin taxa suggest that biogeographic patterns found in guinea-fowl reflect broad patterns found in many African birds. An hypothesis as to the causes of relatively high species richness in francolins is offered.

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INTRODUCTION

There are many reasons why an understanding of the evolution of guinea-fowl (Numidinae; Sibley & Ahlquist 1972) should provide an insight into patterns of avian evolution and biogeography in Africa.

1. The Numidinae are endemic to Africa, and presumably evolved and/or radiated there from a francolin-like ancestor (Ghigi 1936; Cracraft 1973; Olson 1974).

2. At least one guinea-fowl species has become adapted to life in each major terrestrial African biome outside of desert, Mediterranean vegetation and montane forest (Crowe & Snow 1978).

3. Guinea-fowl are sedentary birds (Chapin 1932*a*; Priest 1933; Archer & Godman 1937; Elgood *et al.* 1973), and thus should be more susceptible to local selection pressures than would be more mobile species (Ehrlich & Raven 1969).

4. The distributions of some guinea-fowl taxa do not correlate well with present-day vegetation and topography (Chapin 1932*a*). Such anomalous distributions of plants and animals can be used to infer environmental conditions and the distributions of African biomes during the Tertiary and Quaternary (Chapin 1932*a*; Moreau 1963, 1966; Roberts 1975; Hamilton 1974; Axelrod & Raven 1978).

5. The genetic basis of morphological variation in several guinea-fowl species is relatively well understood (Ghigi 1936).

6. Perhaps most importantly, guinea-fowl species are relatively well represented in museum collections and, accordingly, lend themselves to quantitative analysis, which is desirable in formulating precise evolutionary and biogeographic hypotheses (Mayr *et al.* 1953; F. Vuilleumier 1975).

Thus, guinea-fowl provide a simple, characteristically African system from which evolutionary and biogeographic hypotheses may be derived. The aims of the present study are to:

1. re-examine and revise, if necessary, the rather confused taxonomy within the subfamily (Table 1), using a repeatable, relatively objective quantitative methodology;
2. produce a parsimonious phylogeny based on the analysis of shared derived character states;
3. develop models of speciation, which are consistent with the phylogeny developed herein and the likely past geological and climatic history of Africa;

4. suggest tentative avifaunal subregions, provinces and districts for Africa, based on analysis of the distributions of recognized guinea-fowl taxa.

The possible familial status of the subfamily (Wetmore 1960), the adaptiveness of inter- and intra-specific morphological variation in guinea-fowl, and the predictive value of evolutionary and biogeographic models based on patterns found in guinea-fowl, will be discussed briefly, if at all, herein. These topics will be dealt with in greater detail in future papers.

METHODS

MATERIAL AND CHARACTERS

The author examined 1 833 museum specimens, including all taxa attributed to the subfamily in Table 1. All characters investigated (Appendices 1 and 2, Figs 2–4) appear to have a genetic basis (Ghigi 1936), and have been discussed in previous studies (e.g. Beddard 1898; Bannerman 1930; Chapin 1932*a*; Ghigi 1936; Archer & Godman 1937; Jackson 1938; Boetticher 1954; Mackworth-Praed & Grant 1952, 1962, 1970). Therefore, they need not be described again in detail. Characters were chosen to reflect as much of the phenotype as possible, while eliminating the necessity of close comparisons of specimens from different collections. Due to logistical constraints (e.g. small sample sizes of each sex, time allotted for examination of specimens, and variation in the detail of collectors' notes and care in specimen preparation) some of the quantitative characters listed in Appendix 1 were assessed relatively subjectively, and data for both sexes were lumped. This introduces a certain amount of imprecision into the analysis. But, subjective assessments were made against a set of reference specimens, photographs or drawings encompassing the range of observed variation. Also, the previous studies mentioned above have stated that sexual dimorphism is absent, or relatively minor in comparison with geographical variation in guinea-fowl. Moreover, it was felt that the advantages accruing from considering a large number of characters for many specimens outweighed any sampling bias due to imprecise measurement and sexual dimorphism.

TAXONOMIC PHILOSOPHY

The taxonomic philosophy adhered to in the present study follows that outlined by Mayr *et al.* (1953). A species is a group of actually or potentially interbreeding individuals which has diverged sufficiently in allopatry to have become reproductively isolated from other such groups. A genus is a monophyletic taxon which is decidedly qualitatively distinct, and is adapted to a particular mode of life, i.e. a generic 'niche'.

The subspecies is much more difficult to define. Table 1 shows that much of the 'taxonomic variation' in guinea-fowl systematics is at the subspecies level. Some systematists (e.g. Wilson & Brown 1953; Moreau 1957; Selander 1971; Gould & Johnston 1972) state that the category is useless, and even

TABLE 1

A history of the taxonomy of guinea-fowl.[1]

Taxa			Chapin (1932*a* and *in litt.*)	Peters (1934)	Ghigi (1936)	Boetticher (1954)	Mackworth-Praed & Grant (1952; 1962; 1970)	White (1965)	Crowe (this study)
Phasidus	*niger*		×	×	×	×	×		
Agelastes	*niger*							×	×
	meleagrides		×	×	×	×	×	×	×
Acryllium	*vulturinum*		×	×	×	×	×	×	×
Guttera	*plumifera*	*plumifera*	×	×	×	×	×	×	×
		schubotzi	×	×	×	×	×	×	×
	pucherani[4]		×	×			×	×	
	edouardi[4]	*edouardi*	×	×	×	×	×	×	×
		suahelica		×	×	×			
		schoutedeni	×	×	×	×	×	×	
		seth-smithi	×	×	×	×	×	×	
		verreauxi[2]	×	×	×	×	×	×	×
		sclateri	×	×	×	×	×	×	×
		chapini	×	×		×	×	×	
		granti	×		×			×	
		barbata		×	×	×	×	×	×
		lividicollis			×	×			
		kathleenae[3]	×				×	×	
		symonsi					×		
		pucherani			×	×			×
Numida	*meleagris*	*meleagris*	×	×	×	×	×	×	×

	intermedia	×	×	×	×	×	×	
	toruensis	×	×	×	×	×	×	
	neumanni			×				
	omoensis			×				
	ansorgei			×				
	inermis							
	sabyi	×	×	×	×			×
	galeata	×	×	×	×	×	×	×
	marchei	×	×	×	×	×		
	strasseni	×	×	×	×	×	×	
	mitrata	×	×	×	×	×	×	×
	reichenowi	×	×	×	×	×		×
	marungensis	×	×	×	×	×	×	×
	callewaerti	×	×	×	×	×	×	
	maxima	×	×	×	×			
	uhehensis			×	×			
	rikwae			×	×			
	frommi			×				
	coronata	×	×	×	×		×	×
	limpopoensis		×		×			
	transvaalensis				×			
	papillosa	×	×	×	×	×	×	
	damarensis	×	×	×	×	×	×	×
	blancoui[3]				×			
reichenowi							×	

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[1] Unless otherwise specified, nomenclature follows Peters (1934).

[2] *G. e. verreauxi* = *G. e. pallasi*, see White (1965).

[3] See White (1965).

[4] Since these two taxa are considered to be conspecific in the present study, following the principle of priority the specific name recognized is *G. pucherani*.

TABLE 1

A history of the taxonomy of guinea-fowl.[1]

Taxa			Chapin (1932*a* and *in litt.*)	Peters (1934)	Ghigi (1936)	Boetticher (1954)	Mackworth-Praed & Grant (1952; 1962; 1970)	White (1965)	Crowe (this study)
Phasidus	*niger*		×	×	×	×	×		
Agelastes	*niger*							×	×
	meleagrides		×	×	×	×	×	×	×
Acryllium	*vulturinum*		×	×	×	×	×	×	×
Guttera	*plumifera*	*plumifera*	×	×	×	×	×	×	×
		schubotzi	×	×	×	×	×	×	×
	pucherani[4]		×	×			×	×	
	edouardi[4]	*edouardi*	×	×	×	×	×	×	×
		suahelica		×	×	×			
		schoutedeni	×	×	×	×	×	×	
		seth-smithi	×	×	×	×	×	×	
		verreauxi[2]	×	×	×	×	×	×	×
		sclateri	×	×	×	×	×	×	×
		chapini	×	×		×	×	×	
		granti	×		×			×	
		barbata		×	×	×	×	×	×
		lividicollis			×	×			
		kathleenae[3]	×				×	×	
		symonsi					×		
		pucherani			×	×			×
Numida	*meleagris*	*meleagris*	×	×	×	×	×	×	×
		major	×	×	×	×	×	×	
		macroceras	×	×	×	×	×	×	
		somaliensis	×	×	×	×	×	×	×
		intermedia	×	×	×	×	×	×	
		toruensis	×	×	×	×	×	×	
		neumanni			×				
		omoensis			×				
		ansorgei			×				
		inermis							
		sabyi	×	×	×	×			×
		galeata	×	×	×	×	×	×	×
		marchei	×	×	×	×	×		
		strasseni	×	×	×	×	×	×	
		mitrata	×	×	×	×	×	×	×
		reichenowi	×	×	×	×	×		×
		marungensis	×	×	×	×	×	×	×
		callewaerti	×	×	×	×	×	×	
		maxima	×	×	×	×			
		uhehensis			×	×			
		rikwae			×	×			
		frommi			×				
		coronata	×	×	×	×		×	×
		limpopoensis		×		×			
		transvaalensis				×			
		papillosa	×	×	×	×	×	×	
		damarensis	×	×	×	×	×	×	×
		blancoui[3]				×			
	reichenowi							×	

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[1] Unless otherwise specified, nomenclature follows Peters (1934).

[2] *G. e. verreauxi* = *G. e. pallasi*, see White (1965).

[3] See White (1965).

[4] Since these two taxa are considered to be conspecific in the present study, following the principle of priority the specific name recognized is *G. pucherani*.

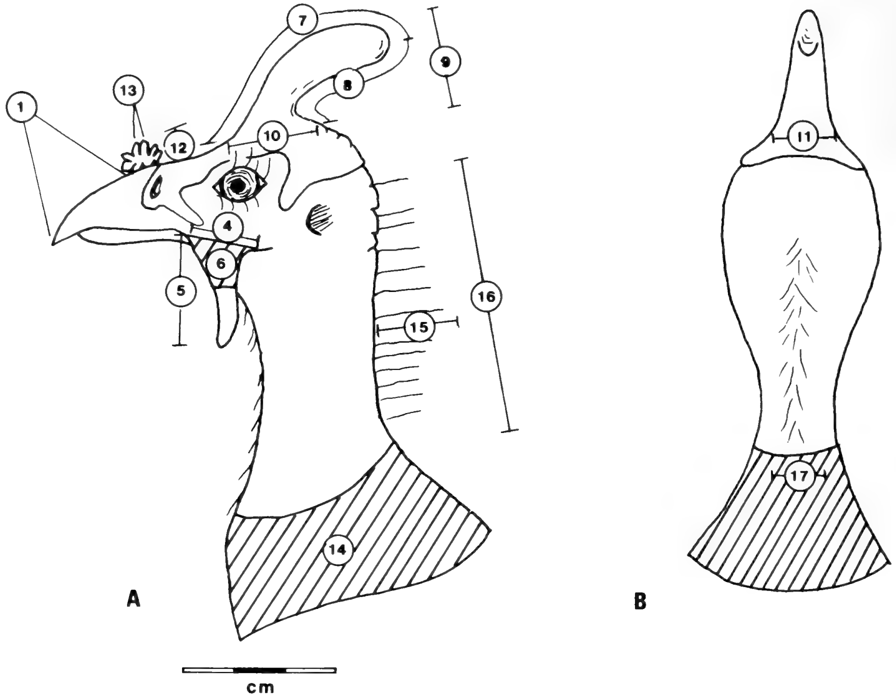

Fig. 2. Quantitative characters 1, 4–17. A. Lateral view of head, neck and collar of *Numida meleagris*. B. Dorsal view of the same.

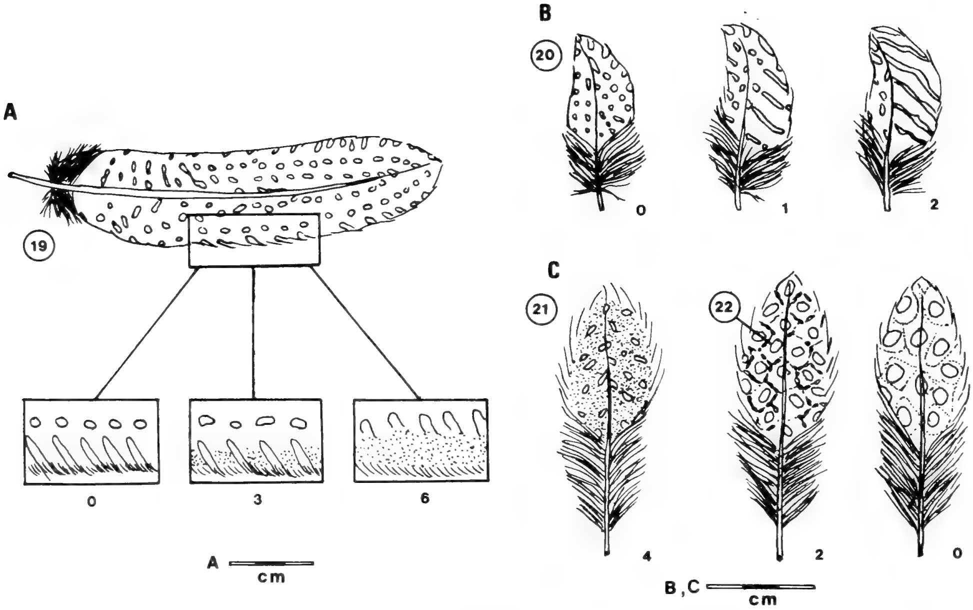

Fig. 3. Quantitative characters 19–22. A. Secondary remex from *Numida meleagris*. B. Wing covert from *N. meleagris*. C. Mid-dorsal feather of the same.

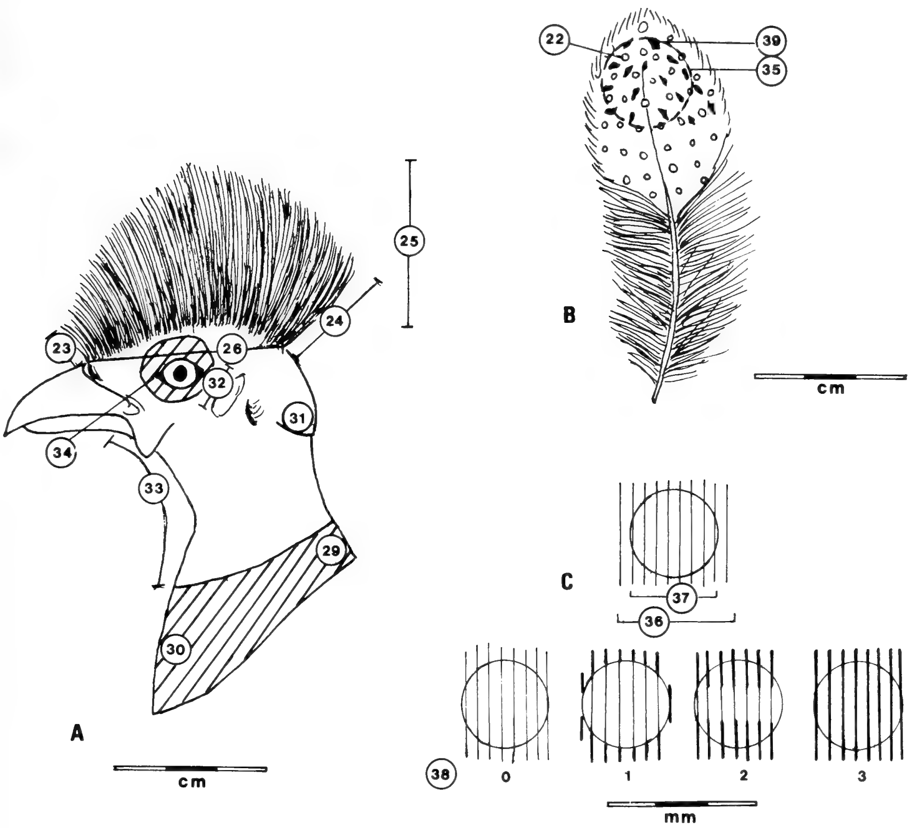

Fig. 4. Quantitative characters 22–26, 29–39. A. Lateral view of head, neck and collar of *Guttera plumifera*. B. Mid-dorsal feather of *G. pucherani edouardi*. C. Spots on mid-dorsal feathers of *Guttera* spp.

detrimental to the understanding of geographic variation and intra-specific evolution. These critics maintain that:

1. characters used to delineate subspecies usually have patterns of geographic variation which are discordant with each other and with the distribution attributed to the taxon;
2. indistinguishable phenotypes occur in geographically isolated areas, presumably due to parallel evolution under similar selective regimes;
3. no objective degree of difference can be offered to distinguish subspecies from slightly differentiated local populations.

In an attempt to satisfy these legitimate criticisms, Ford (1974) offers the taxo-evolutionary subspecies concept, the concept adhered to in the present study. This concept limits the awarding of subspecies status to geographic aggregates of populations which appear to have undergone genetic and phenotypic divergence in allopatry. Past allopatric divergence may be inferred for presently parapatric taxa if their distributions can be derived from concordant character variation, and if they are separated by a zone of secondary intergradation (Ford 1974).

TAXONOMIC METHODOLOGY

Since both the recognition of taxa and their assignment to taxonomic categories (with the possible exception of the species) are ultimately subjective processes (Mayr *et al.* 1953; Selander 1971; Ford 1974), it is of utmost importance to outline the methodology underlying taxonomic decisions.

With the foregoing taxonomic philosophy in mind, the procedure used to determine genera involved four steps:

1. a sorting of specimens into groups which consisted of members of both sexes, and which possessed unique combinations of qualitative characters;
2. a cluster analysis of these groups according to the number of shared qualitative character states;
3. presentation of the clustering similarity matrix in the form of a phenogram;
4. interpretation of the matrix and the phenogram, according to the taxonomic philosophy outlined above, to determine genera.

Once genera were identified, each was analysed separately to determine species and subspecies. Two multivariate statistical computer programmes were used in tandem in these analyses. The first programme, BMDP2M (Dixon 1975), was used to cluster specimens into operational taxonomic units (OTUs, Sneath & Sokal 1973). In BMDP2M, the clustering algorithm first amalgamates the two specimens which are most similar. The amalgamated specimens are then treated as one case in future comparisons. This clustering algorithm continues until all specimens are grouped into one large cluster. The similarity measure used is the Euclidean distance, and the clustering method is the weighted average pair group method (Sneath & Sokal 1973). The printed output of BMDP2M includes a phenogram which illustrates the results of the cluster analysis in a hierarchical manner. OTUs were identified from examination of these phenograms. In a phenogram, OTU status was awarded to any specimen cluster which contained members of both sexes from several geographically contiguous localities, and which was morphologically more distinct (i.e. linked up with other such groups at a lower similarity) than was a group of specimens from a single, relatively well-sampled locality within the range of an undisputed taxon listed in Table 1.

OTUs were compared using stepwise multiple discriminant analysis programme BMDP7M (Dixon 1975). This programme calculates a series of linear classification functions in a stepwise manner, such that within-OTU variance is minimized and between-OTU variance maximized. At each step in the analysis, the character not yet entered into the functions that best separates OTUs is included. This procedure continues until all significant ($P < 0{,}05$) characters are included in the functions. The printed output of BMDP7M includes a probabilistic statement as to the OTU membership of each specimen. In the final step, BMDP7M computes canonical discriminant functions between OTUs, and plots the first two so as to give an optimal two-dimensional picture of the separation of the OTUs. This plot consists of a multivariate centroid for each OTU, surrounded by a cloud of individual points corresponding to specimens in that OTU. In this study, an OTU, or group of OTUs, was awarded species rank if none of the component specimens were intermediate between two OTUs (i.e. were assigned a probability greater than 0,05 of belonging to another OTU).

Once species were identified, character variation within each species consisting of several OTUs was analysed to determine if any component OTUs merited subspecies status. The taxonomic procedure used in these analyses involved four steps:

1. division of the species range into uniform areas;
2. computation of mean values and coefficients of variation (COV, Sokal & Rohlf 1969) for each character for each area;
3. contour mapping of mean values for each character, and of the total COV for all characters for each area;
4. interpretation of the contour maps to determine OTUs whose distributions could be derived from concordant character variation, and whose boundaries were circumscribed by a zone of secondary intergradation.

Subspecies rank was awarded to any OTUs whose distributions could be derived from concordant variation in at least three characters, and which enclosed an area of relatively low total COV bounded by an area(s) of high total COV. Areas with relatively low variability (i.e. low total COV) were taken to be probable 'core regions' for their associated subspecies. Areas with relatively high variability (i.e. high total COV) were taken to be regions of secondary intergradation.

The smallest uniform area that produced sample sizes that were statistically adequate was that enclosed by a block four degrees on a side. Contour mapping was done with the assistance of a computer, using contouring programme GPCP (CALCOMP 1971). This programme fits an approximate contour surface to the data using least squares polynomial analysis.

PHYLOGENETIC PHILOSOPHY

A cladistic approach (Marx & Rabb 1970; Cracraft 1972) was used to infer phylogenetic relationships between guinea-fowl genera and species. Cladistic analysis involves discernment and use of derived character states. Derived states are those which are unique or relatively restricted to the taxa under study, or which could be adaptive in a social or ecological context (Marx & Rabb 1970). Shared primitive character states, i.e. those commonly inherited from distant ancestors, cannot be used to unite more recently evolved taxa (Cracraft 1972). Other than its consistent, relatively objective methodology, the major advantage of a cladistic analysis is that a proposed phylogeny can be refuted on clearly specified grounds. A proposed phylogeny must be modified or abandoned if: derived characters used to produce it are shown to be primitive; another interpretation of the same or different combination of derived character states yields a more parsimonious phylogeny, i.e. requiring fewer convergences; a fossil form is found which possesses a character suite incompatible with the proposed phylogeny; or if it is grossly at variance with known biogeographic events (Cracraft 1972; F. Vuilleumier 1975).

PHYLOGENETIC METHODOLOGY

Since the presumed ancestor of the guinea-fowl is a francolin-like phasianid (Ghigi 1936), any character state common among extant francolins or guineafowl-phasianid hybrids was taken to be primitive. Ghigi (1936), Mackworth-Praed & Grant (1952, 1962, 1970) and Hall (1963) were used as sources of information on francolins. Ghigi (1936), Bourke (1967) and R. Chapin (*in litt.*) were the sources of information on the phenotypes of hybrids. Any character state unique to, or relatively common among, guinea-fowl species was taken to be derived.

Once hypothetical primitive-derived sequences of character states were determined, a parsimonious phylogeny was produced following methods outlined by Cracraft (1972).

SPECIATION

There is now widespread agreement among evolutionary biologists and biogeographers that speciation, extinction and drastic distributional shifts in plants and animals have been common and world-wide during the Tertiary and Quaternary (Moreau 1966; B. Vuilleumier 1971; Axelrod & Raven 1978). As mentioned in the introduction, past geological and climatic events have almost certainly helped to shape patterns of speciation and biogeography in Africa. Several authors (Chapin 1932*a*; Cooke 1962; Howell & Bourlière 1963; Moreau 1966; Carcasson 1964; Butzer 1967; Hamilton 1974; Axelrod & Raven 1978) have given maps of Africa depicting the hypothetical distribution of vegetation during relatively wetter and/or drier conditions in the past. Livingstone (1975), Hamilton (1974) and Axelrod & Raven (1978) have provided some temporal estimates for climatic and geological events which may have caused these conditions. As a preface to this study, the various hypothetical vegetation maps were compared, and compromise 'wet' and 'dry' maps (Figs 5–6) were drawn which incorporated salient features of each. An hypothetical pattern and chronology for speciation in guinea-fowl were developed by relating the phylogeny derived herein to present-day (Fig. 7) and hypothetical past 'wet' and 'dry' vegetation maps in the light of temporal estimates given by authors mentioned above.

BIOGEOGRAPHY

Once the taxonomy and phylogeny of a group are defined, biogeographic hypotheses based on patterns found in that group may be formulated. Since

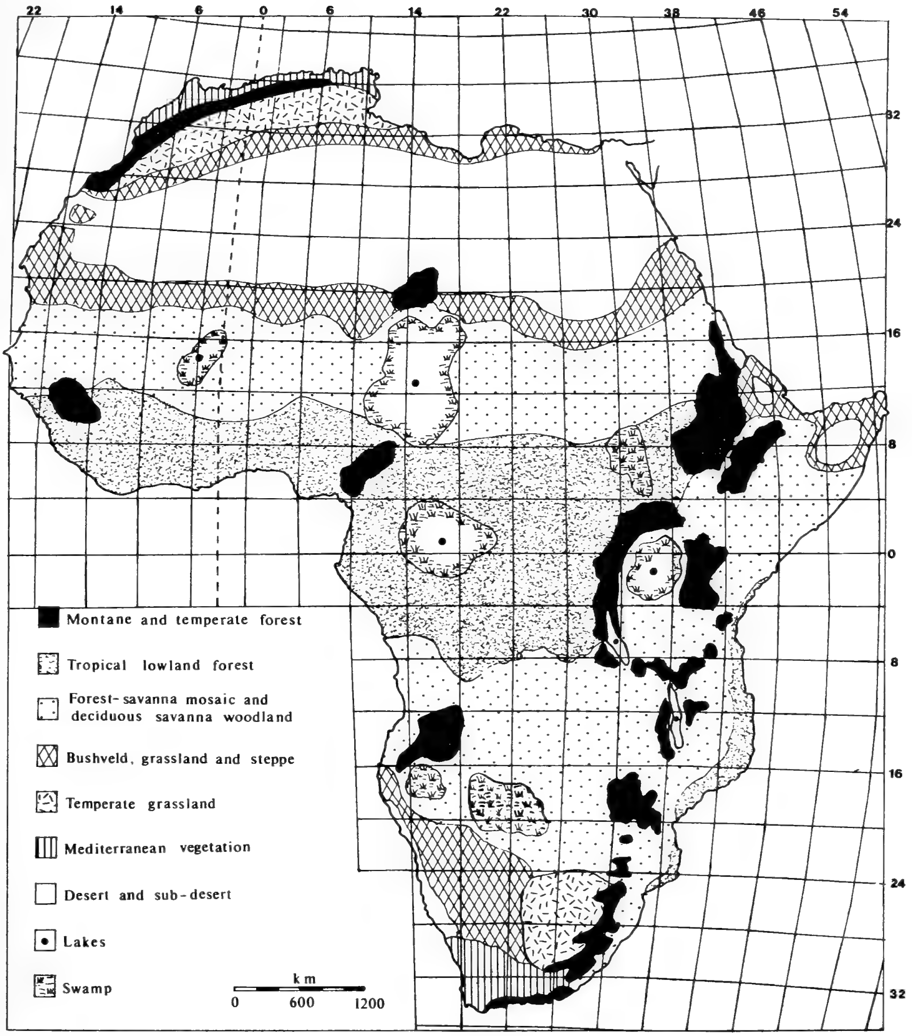

Fig. 5. Hypothetical vegetation map of Africa during a wetter period.

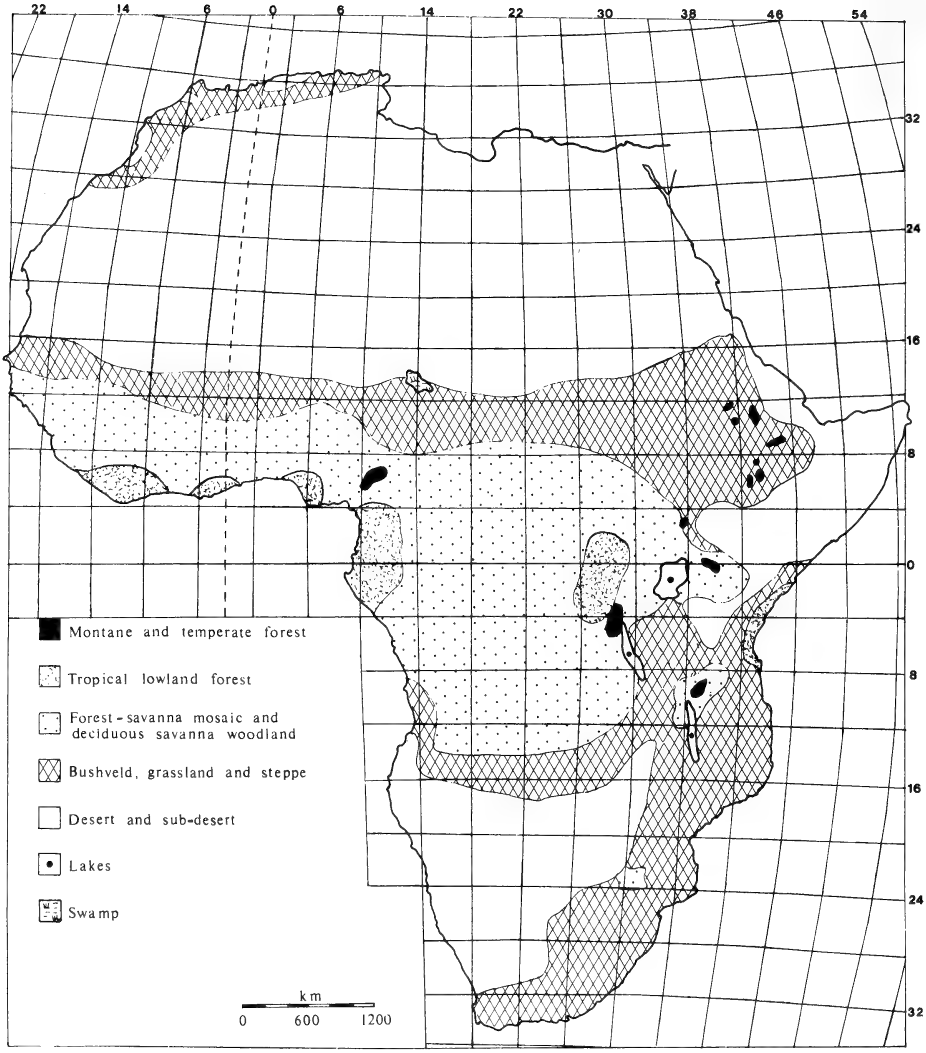

Fig. 6. Hypothetical vegetation map of Africa during a drier period.

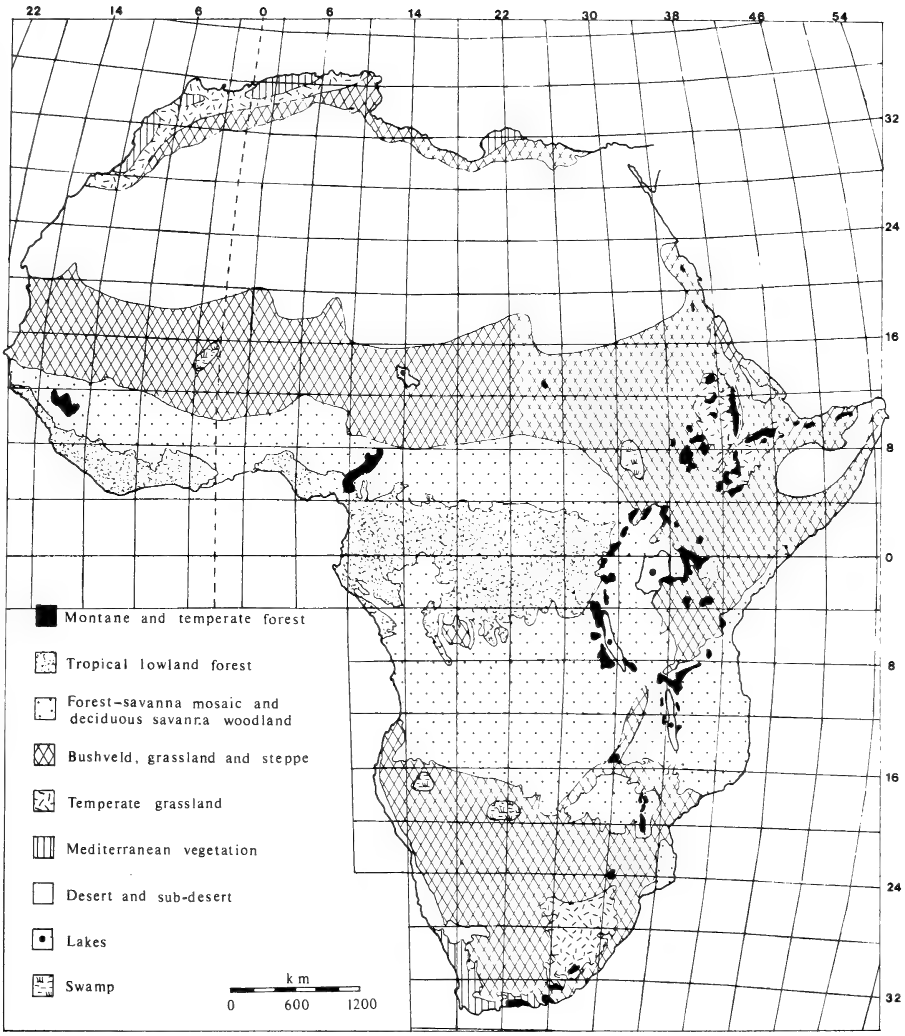

Fig. 7. Present-day vegetation map of Africa.

guinea-fowl are sedentary, stenotopic animals, the distribution of a given taxon should reflect the geographical limits and temporal stability of its associated biome. If a taxon has a vicariated distribution, it is likely that the vicars (see Udvardy 1969) were isolated as a result of past partitioning of its biome. However, if a taxon shows little geographic variation, its biome probably has not been fragmented in the past. In this study, the boundaries of recognized genera, species and subspecies were used to formulate an hypothetical avifaunal map of Africa. Boundaries of taxonomically homogeneous genera (i.e. with no subspecies) were used to delimit African avian subregions in this map. In other words, a subregion is any biome which has presented its associated guinea-fowl taxa with a sufficiently consistent selective regime to produce a monotypic genus, or a genus composed of monotypic species. Species boundaries were used to delimit provinces, and subspecies boundaries to delimit districts, following a similar reasoning used in defining subregions.

RESULTS, DISCUSSION AND CONCLUSIONS

TAXONOMY

GENERA

There are fourteen groups of guinea-fowl specimens (Table 2) which possess unique combinations of the qualitative characters listed in Appendix 1. These groups are termed operational genera (OG). In the light of habitat preference information summarized by Crowe & Snow (1978), the results of a cluster analysis of the OG (Fig. 8) suggest that there are four genera in the Numidinae. These are labelled A–D in Figure 7, and become apparent at the similarity level of eleven shared characters. In Table 1, genus A corresponds to the genera *Agelastes* Bonaparte, 1850, and *Phasidus* Cassin, 1857; genus B to *Guttera*; genus C to *Acryllium*; and genus D to *Numida*. Genus A must be named *Agelastes*. The following section consists of a taxonomic summary including taxonomic conclusions, brief descriptions and mensural statistics, and a discussion of taxonomic conclusions when deemed necessary. All recognized genera are said to be largely restricted to broad 'niches' (Crowe & Snow 1978). The genus *Agelastes* is found only in dense tropical lowland forest. The genus *Guttera* is also limited to forest areas, but inhabits riverine forest and the forest edge as well as tropical lowland forest. The genus *Acryllium* is confined to the subdesert steppe of north-eastern Africa. The genus *Numida* can be found in virtually all areas of non-forested Africa outside of desert, Mediterranean and montane vegetation.

SPECIES AND SUBSPECIES

The genus *Acryllium* appears to be monotypic. A cluster analysis of 43 *Acryllium* specimens (Fig. 9) according to 7 quantitative characters (nos 1–5, 41–42 in Appendix 2) yields only one OTU. Six individuals from Mt Kunchurro, Boran, Ethiopia (*c.* 4°30′N 38°E), link to form a cluster at a level (indicated

TABLE 2

Operational genera derived from analysis of qualitative character states listed in Appendix 1.

Character	Operational genera													
no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	3	3	2	2	2	2	2	2	4	4	4	4	4
2	5	5	1	3	3	3	3	3	4	2	5	2	5	2
3	1	4	4	4	3	4	4	4	4	2	1	2	2	2
4	1	1	2	2	2	2	1	2	2	2	2	2	2	2
5	1	1	2	2	2	1	1	2	2	2	2	2	2	2
6	1	1	1	1	1	2	2	2	1	1	1	1	1	1
7	1	1	1	2	2	1	1	1	1	3	3	2	2	3
8	1	1	2	2	2	2	2	2	2	1	2	3	3	1
9	1	1	1	1	1	1	1	1	1	1	2	1	2	1
10	1	7	6	5	5	2	5	2	2	4	3	3	5	3
11	1	1	2	3	3	3	3	3	4	2	2	2	2	2
12	1	1	2	2	2	2	2	2	2	2	2	2	2	2
13	1	1	1	2	2	2	2	2	2	2	2	2	2	2
14	1	1	2	1	1	1	2	2	2	1	1	1	1	1
15	1	1	3	2	2	2	2	2	2	4	4	4	4	4
16	1	1	1	2	2	2	2	2	2	1	1	1	1	1
17	?	?	2	1	1	1	1	1	1	1	1	1	1	1
18	1	1*	2	4	4	4	4	4	4	3	3	3	3	3

* Only in the juvenile bird.

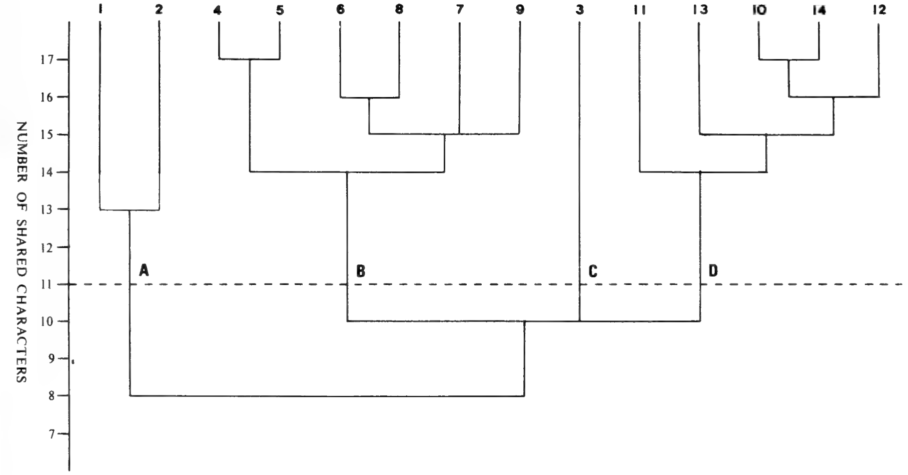

Fig. 8. The results of a cluster analysis of OG in Table 2. A. *Agelastes*. B. *Guttera*. C. *Acryllium*. D. *Numida*.

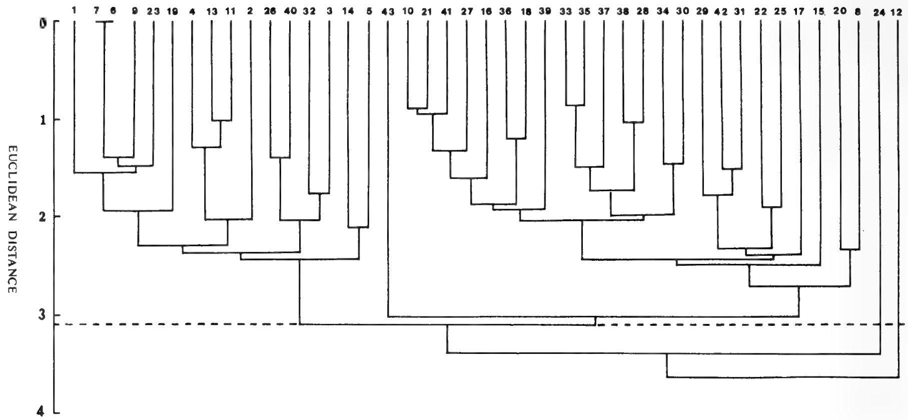

Fig. 9 The results of a cluster analysis of forty-three specimens of *Acryllium.*

by the dashed line in Fig. 9) lower than does any combination of specimens from the remainder of the distribution of the genus. Thus, for the characters investigated, variation in a single population is as great as that found throughout the range of the genus. Accordingly, in agreement with all previous studies (Table 1), one monotypic species, *Acryllium vulturinum*, is recognized. The distribution of this species is plotted in Figure 10.

The genus *Agelastes* is composed of two monotypic species. A cluster analysis of 49 specimens according to 11 quantitative characters (nos 1–5, 23–24, 41–44 in Appendix 2) yields two OTUs, labelled A and B in Figure 11. The dashed line in the figure indicates the level at which eight individuals from Kribi, Cameroons (2°50′N 10°5′E), link to form a cluster. A discriminant functions analysis of the two OTUs reveals no intermediate specimens. Therefore the OTUs are recognized as species. In Table 1, OTU A corresponds to

Table 3

Similarity matrix showing number of shared qualitative character states between OG derived and listed in Table 2.

OG no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	—	13	5	2	2	3	3	1	2	5	5	4	4	5
2		—	7	3	2	4	4	2	3	5	4	4	4	5
3			—	6	6	6	6	8	9	7	7	7	6	7
4				—	17	14	13	14	13	8	8	9	9	8
5					—	13	12	13	12	8	8	9	9	8
6						—	15	16	15	6	6	6	5	6
7							—	15	12	4	4	4	4	4
8								—	15	6	6	6	5	6
9									—	7	7	7	6	7
10										—	13	15	13	17
11											—	13	14	14
12												—	15	16
13													—	13
14														—

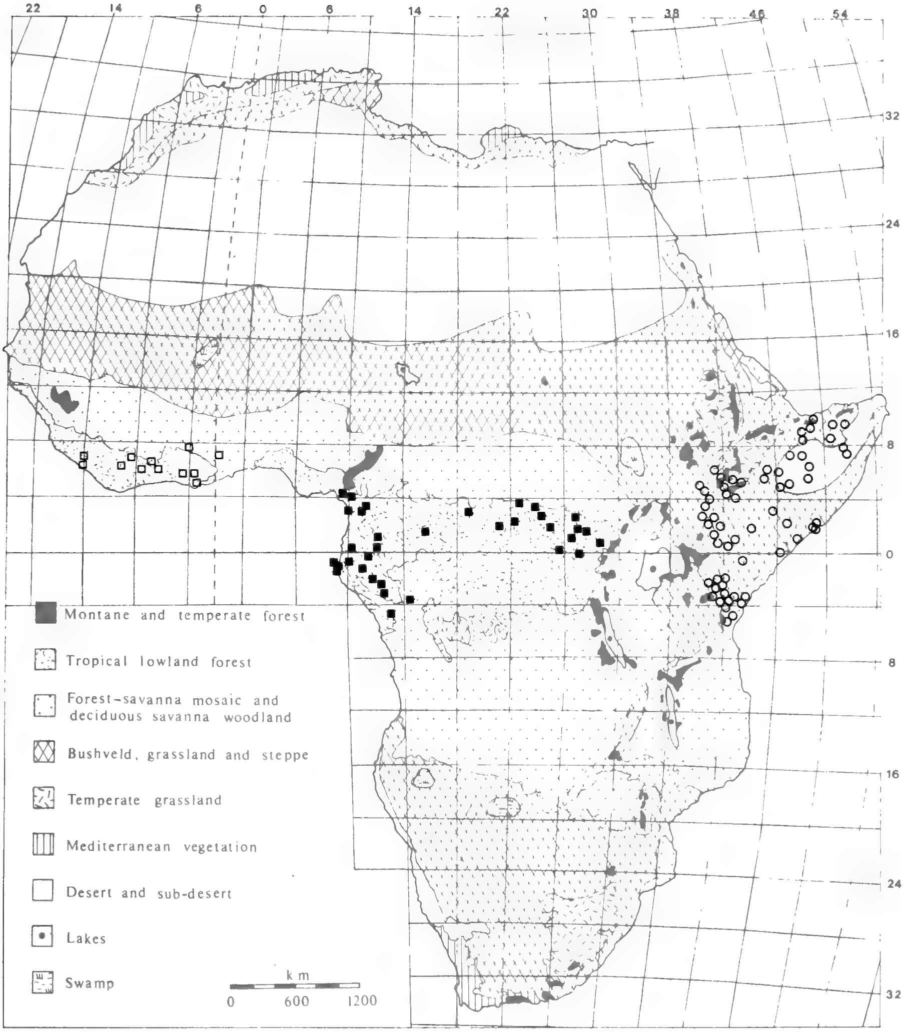

Fig. 10. The distributions of *Agelastes meleagrides* (□), *Agelastes niger* (■), and *Acryllium vulturinum* (○).

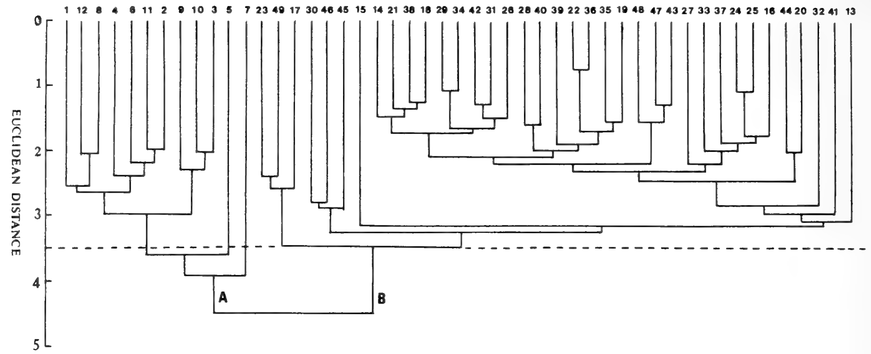

Fig. 11. The results of a cluster analysis of forty-nine specimens of *Agelastes*. A. *A. meleagrides*. B. *A. niger*.

Agelastes meleagrides and OTU B to *A. niger*. The distributions of these species are plotted in Figure 10.

The remaining two genera are taxonomically more complex than are the first two. The results of a cluster analysis of 494 *Guttera* specimens according to 24 quantitative characters (nos 1–5, 22–40 in Appendix 2) are summarized in Figure 12A. The dashed line in Figure 12A indicates the level at which twelve individuals from Ngayu, Zaïre (1°45′N 27°15′E), link to form a cluster. Seven OTUs are recognized. A discriminant functions analysis (Fig. 13) suggests that there are two groups of OTUs between which there are no intermediate individuals. These OTU groups are recognized as species. The first species, comprising OTUs 1 and 2, corresponds to *G. plumifera* in Table 1. The second species, comprising OTUs 3–7, corresponds to two commonly recognized species, *G. pucherani* (Hartlaub), 1860, and *G. edouardi* (Hartlaub), 1867 (Table 1). Following the law of priority, this species must be named *G. pucherani*.

The two OTUs comprising *Guttera plumifera* partition the distribution of that species into eastern and western portions. The distributions of these OTUs (Fig. 14) are delineated by patterns of variation in fifteen of the sixteen quantitative characters which vary in *G. plumifera*. Contour maps of variation in these characters, and of the total COV for six areas (Fig. 15) within the distribution of *G. plumifera* are given in Figures 16 and 17. Two types of character variation, 'mountain–valley' and clinal variation, are apparent in these contour maps. 'Mountain-valley' variation occurs when eastern and western OTUs have similar values, and are separated by a transition area(s) with higher ('mountains') or lower ('valleys') values. Characters which show 'mountain–valley' variation are: bill length (Fig. 16B), wing length (Fig. 16C), tarsometatarsus length (Fig. 16D), wattle length (Fig. 16F), crest frontal length (Fig. 16G), crest basal length (Fig. 17J), dorsal spot number (Fig. 17K), total spot barbs (Fig. 17M), and total within-spot barbs (Fig. 17N). Characters which show clinal variation are: occipital fold (Fig. 16A), wattle basal width (Fig. 16E), crest rear length (Fig. 16H), dorsal spot size (Fig. 17L), ear patch

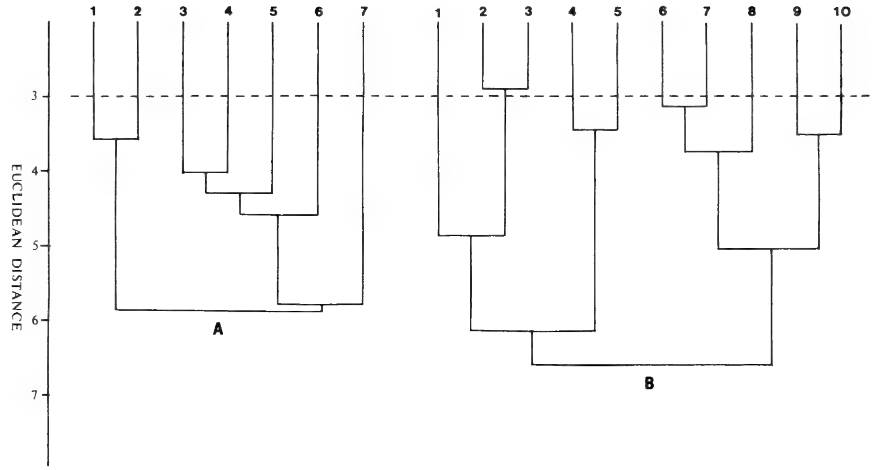

Fig. 12. The results of a cluster analysis. A. *Guttera* specimens B. *Numida* specimens.

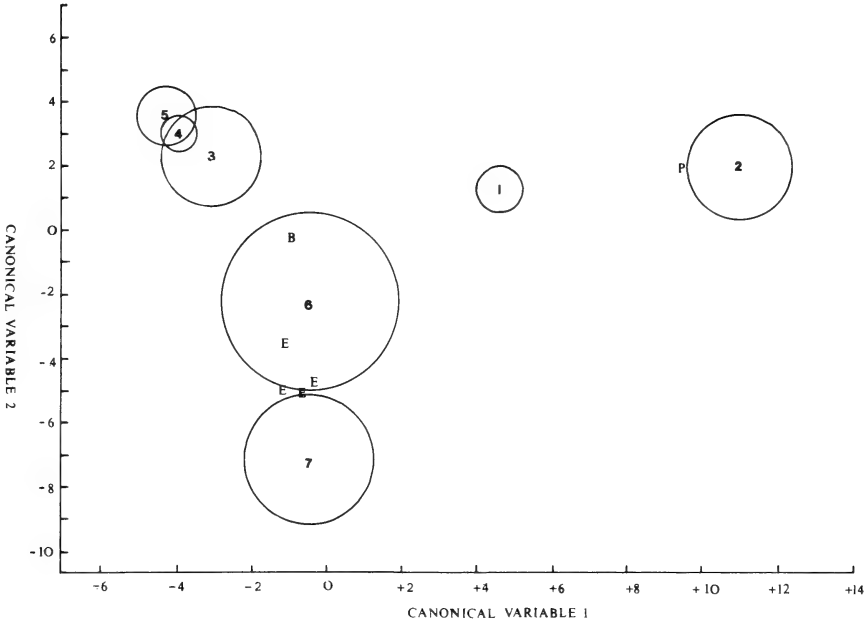

Fig. 13. A discriminant functions analysis of *Guttera* OTUs. Circles encompass 90 per cent of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. B — intermediate between OTUs 5 and 6; E — intermediate between OTUs 6 and 7; P — intermediate between OTUs 1 and 2.

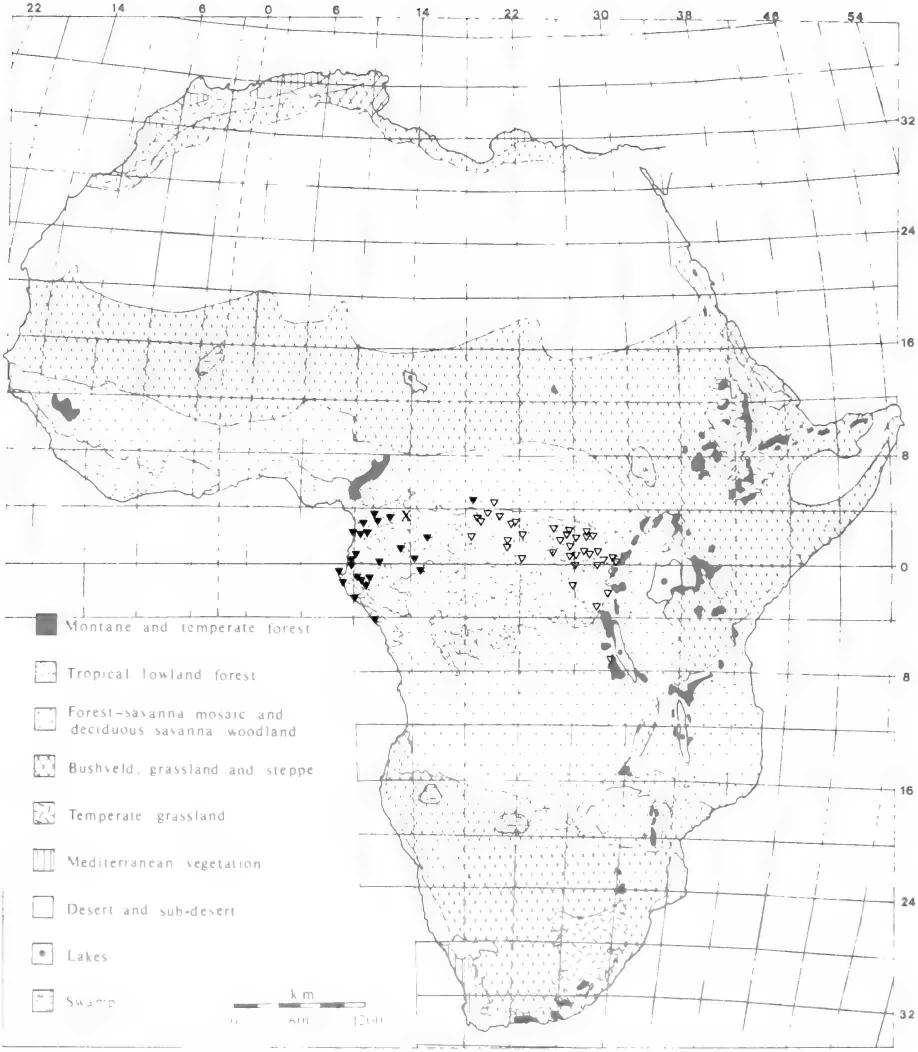

Fig. 14. The distribution of *Guttera plumifera plumifera* (▼) (= OTU 2), *G. p. schubotzi* (▽) (= OTU 1), and a single intergrade (×).

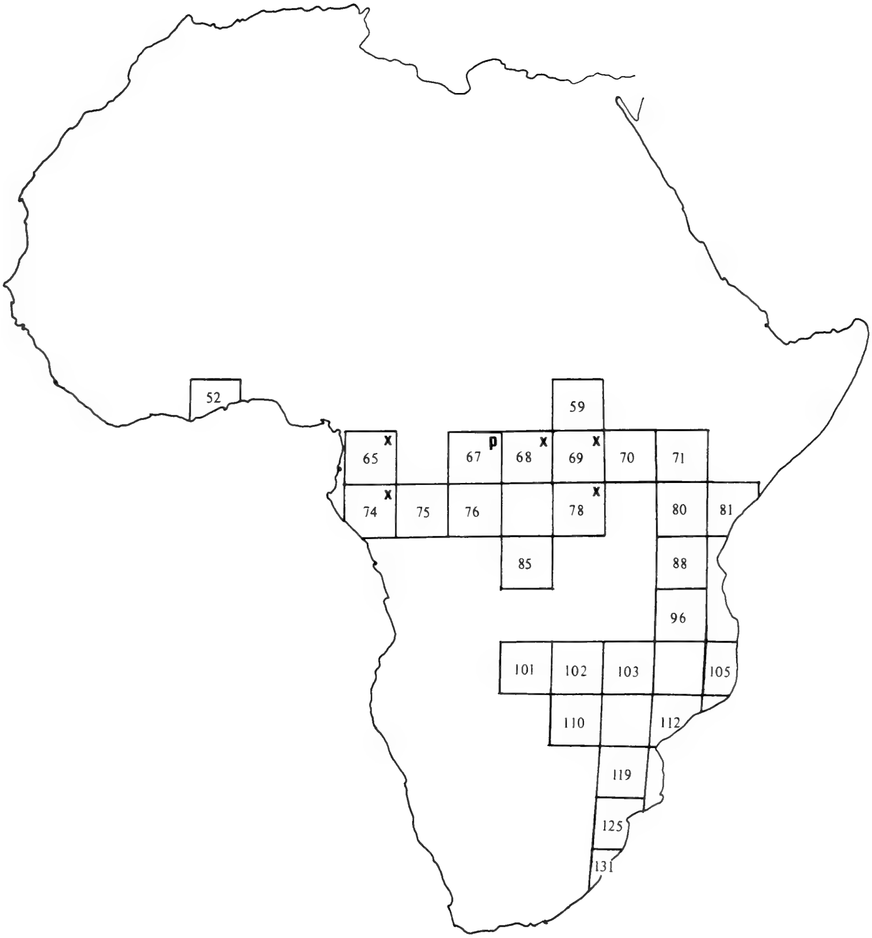

Fig. 15. Areas used in contour map analysis of *Guttera* spp. Those areas marked with an 'X' have data for both species. Those marked with a 'P' have data for *G. plumifera* only, and those without notation for *G. pucherani* only.

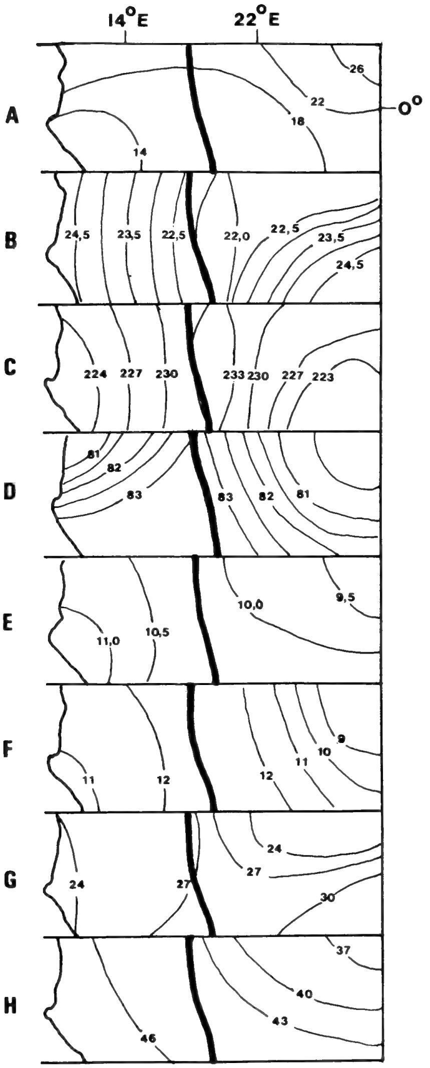

Fig. 16. Contour maps of character variation in *Guttera plumifera*. A. Occipital fold. B. Bill length. C. Wing length. D. Tarso-metatarsus length. E. Wattle width. F. Wattle length. G. Crest frontal length. H. Crest rear length. OTU boundaries are indicated by thick lines.

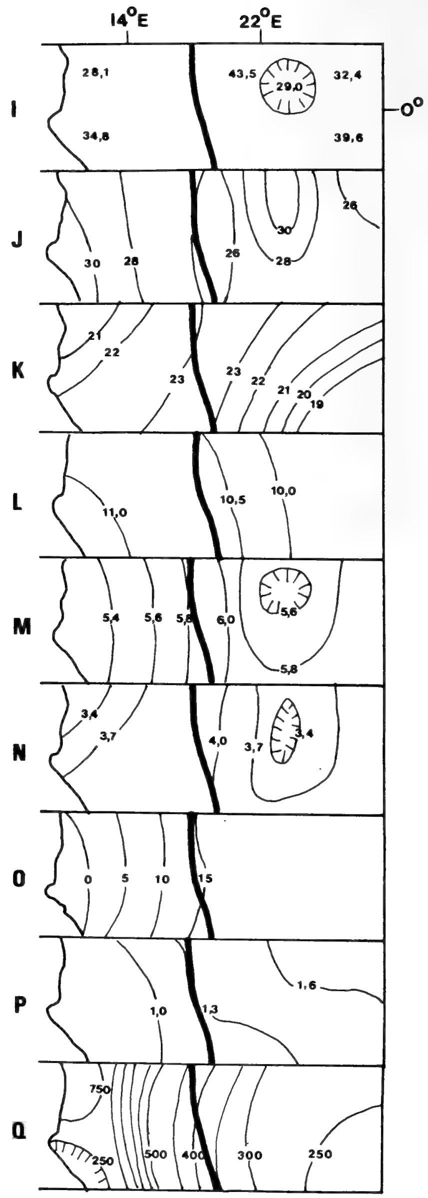

Fig. 17. Contour maps of character variation and total COV for *Guttera plumifera*. I. Crest central height. J. Crest basal length. K. Dorsal spot number. L. Dorsal spot size. M. Total spot barbs. N. Total within spot barbs. O. Ear patch. P. Spot barb blueness. Q. Total COV. OTU boundaries are indicated by thick lines.

(Fig. 17O), and spot barb blueness (Fig. 17P). These well-defined OTUs each have a region of relatively low total COV (*c*. 250) within their distributions, and are separated by a transition area with a relatively high total COV (*c*.750) (Fig. 17Q). Thus, both OTUs meet the criteria set for subspecies (see *Taxonomic methodology*). In Table 1, the western subspecies (OTU 2) corresponds to *G. p. plumifera*, and the eastern subspecies (OTU 1) to *G. p. schubotzi*. In statistical comparisons, these subspecies differ significantly ($P \leq 0{,}05$; *t* test) in eight characters. *Guttera plumifera plumifera* has significantly higher values for bill length, wattle basal width, wattle length, crest rear length, and crest basal length. *Guttera plumifera schubotzi* has higher values for occipital fold, ear patch, and spot barb blueness. Means and standard deviations for these and other characters are given in the section below.

Approximate geographic distributions of the five OTUs comprising *G. pucherani* are shown in Figure 18A. Contour maps of twenty-three characters which vary in this species (nos 1–5, 22–31, 33–40 in Appendix 2) are given in Figures 19–30A. In these maps, the distributions of all five OTUs are delineated from those of their neighbours by statistically significant patterns of variation in six to seventeen of the characters analysed. The results of all possible pairwise statistical comparisons (*t* tests) between neighbouring OTUs are summarized in Tables 4 and 5. A contour map of variation in total COV for twenty-five areas (Fig. 15) within the distribution of *G. pucherani* is given in Figure 30B. This figure shows that the distributions of all five OTUs enclose or fall within a region of relatively low total COV (200–400). For all OTU distributions but one, that of OTU 4, the region of relatively low total COV is bordered by a region(s) of relatively high total COV (e.g. 600–800). Thus, all OTUs ascribed to *G. pucherani* satisfy the criteria specified for subspecies (see *Taxonomic methodology*). The lack of a high total COV interface between the low COV regions of OTUs 3 and 4 is attributed to poor sampling and the small geographic distribution of OTU 4. Assuming that *G. edouardi* is a synonym of *G. pucherani* in Table 1, and following the law of priority, OTU 3 corresponds to *G. p. verreauxi*, OTU 4 to *G. p. sclateri*, OTU 5 to *G. p. pucherani*, OTU 6 to *G. p. barbata*, and OTU 7 to *G. p. edouardi*. The geographic distributions of these subspecies, and of intermediate populations, are shown in Figure 31.

The results of a cluster analysis of 704 *Numida* specimens according to characters 1–22 in Appendix 2 are summarized in Figure 12B. Nine well-defined, and one borderline OTU are recognized. The dashed line indicates the level at which eight individuals from the vicinity of Gassam, Senegal (14°50′N 15°20′W), link to form a cluster. Only 704 specimens could be analysed in this cluster analysis due to computer storage limitations. However, those specimens analysed were chosen so as to ensure uniform sampling of the sexes and collection localities. A discriminant functions analysis including all 1 245 *Numida* specimens (Fig. 32) reveals intermediate individuals between all parapatric OTUs. Therefore only one species is recognized. Following the law of priority, this species is named *Numida meleagris*.

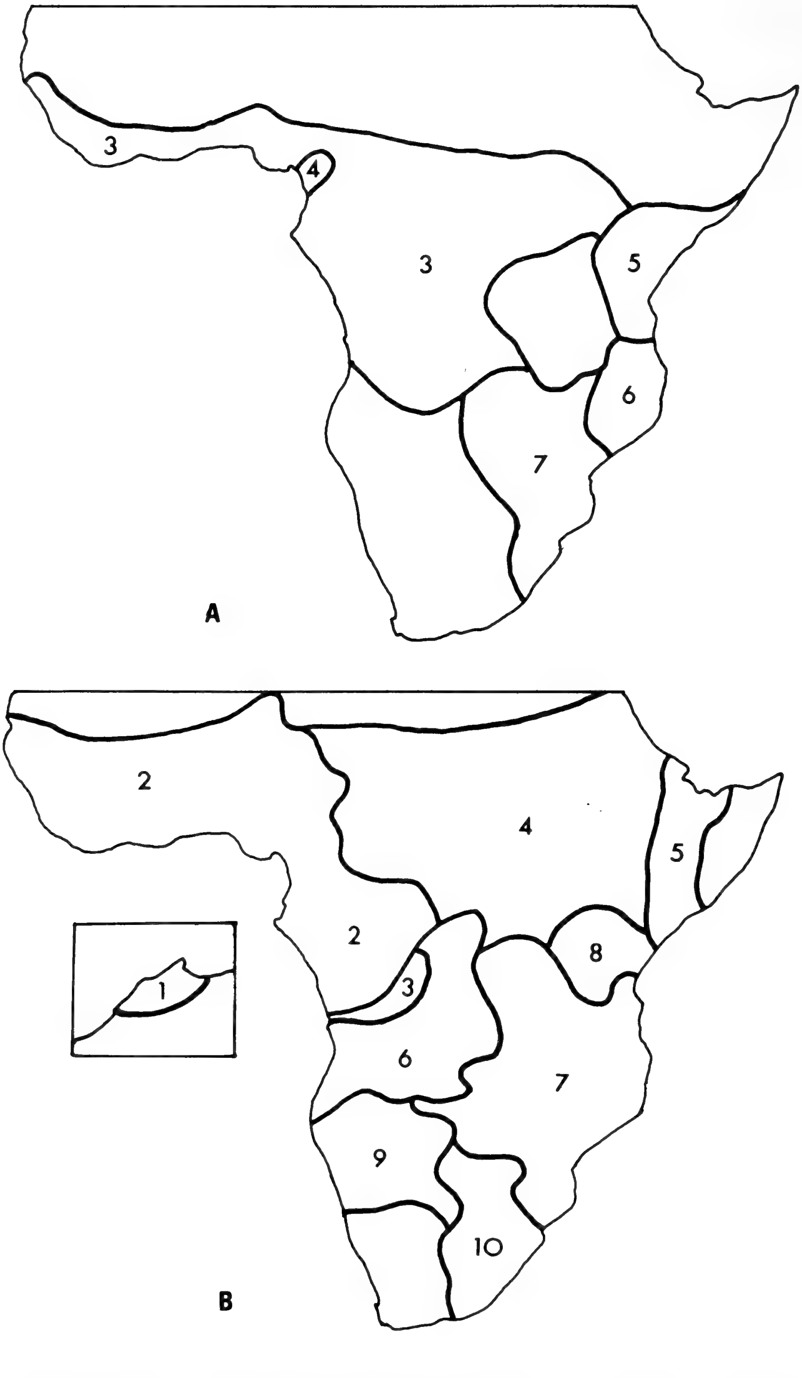

Fig. 18. The geographic distributions of OTUs comprising A. *Guttera pucherani* and B. *Numida meleagris*.

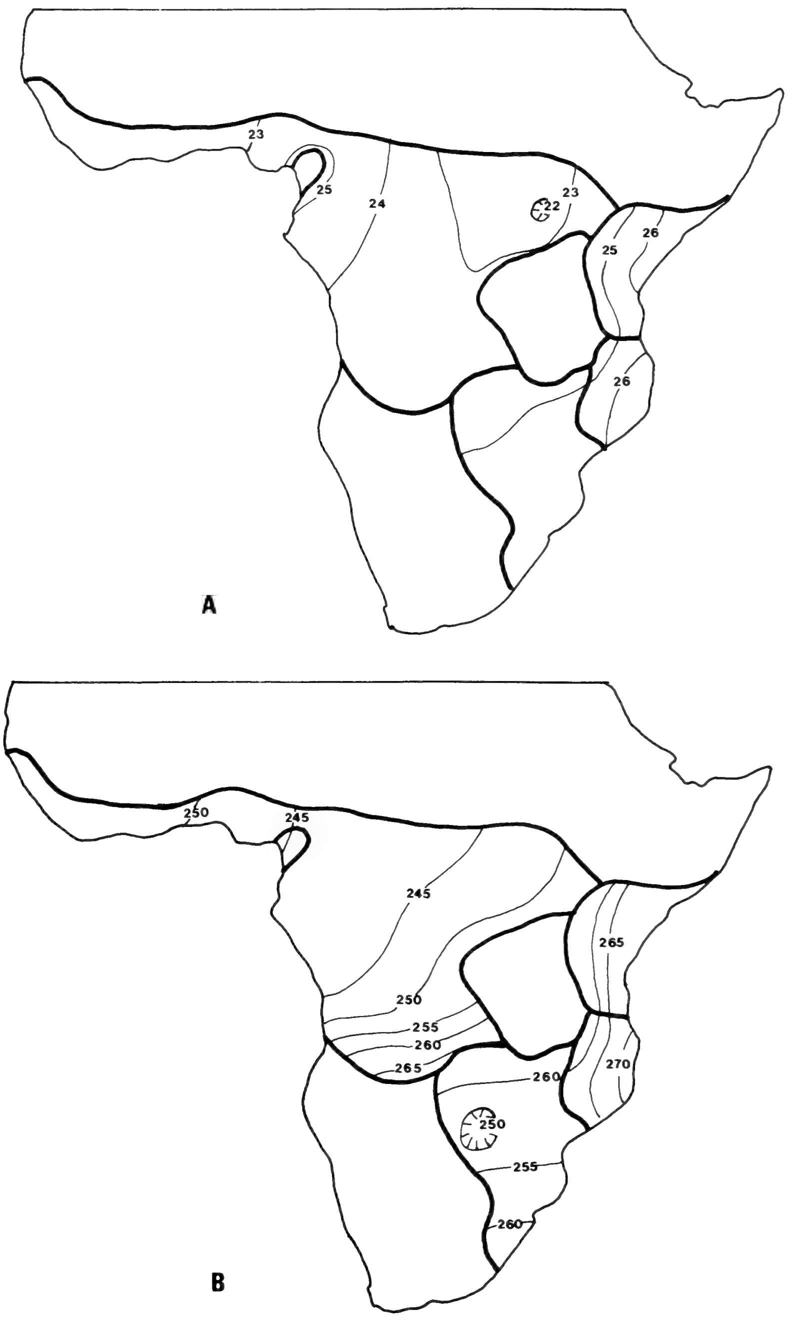

Fig. 19. Contour maps of character variation in *Guttera pucherani*. A. Bill length. B. Wing length. OTU boundaries are indicated by thick lines.

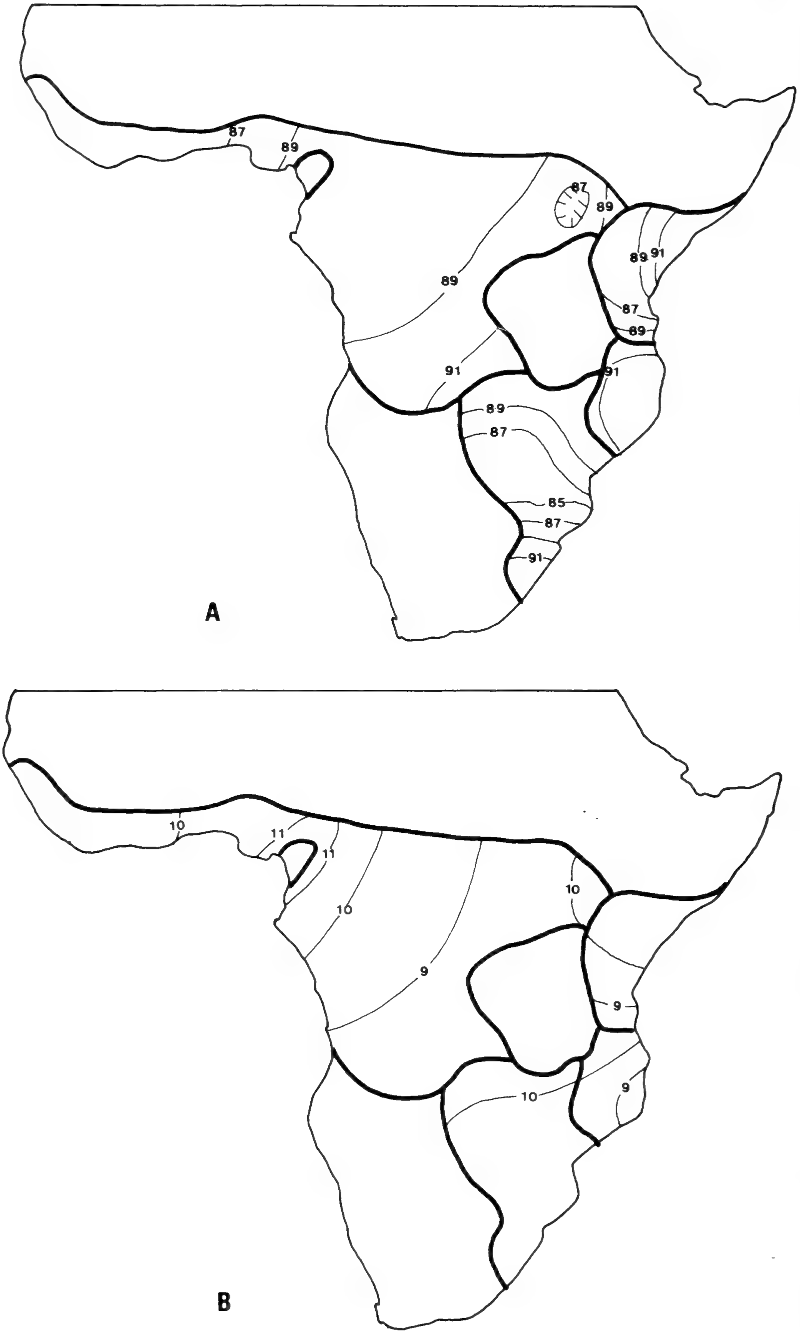

Fig. 20. Contour maps of character variation in *Guttera pucherani*. A. Tarso-metatarsus length. B. Wattle basal width. OTU boundaries are indicated by thick lines.

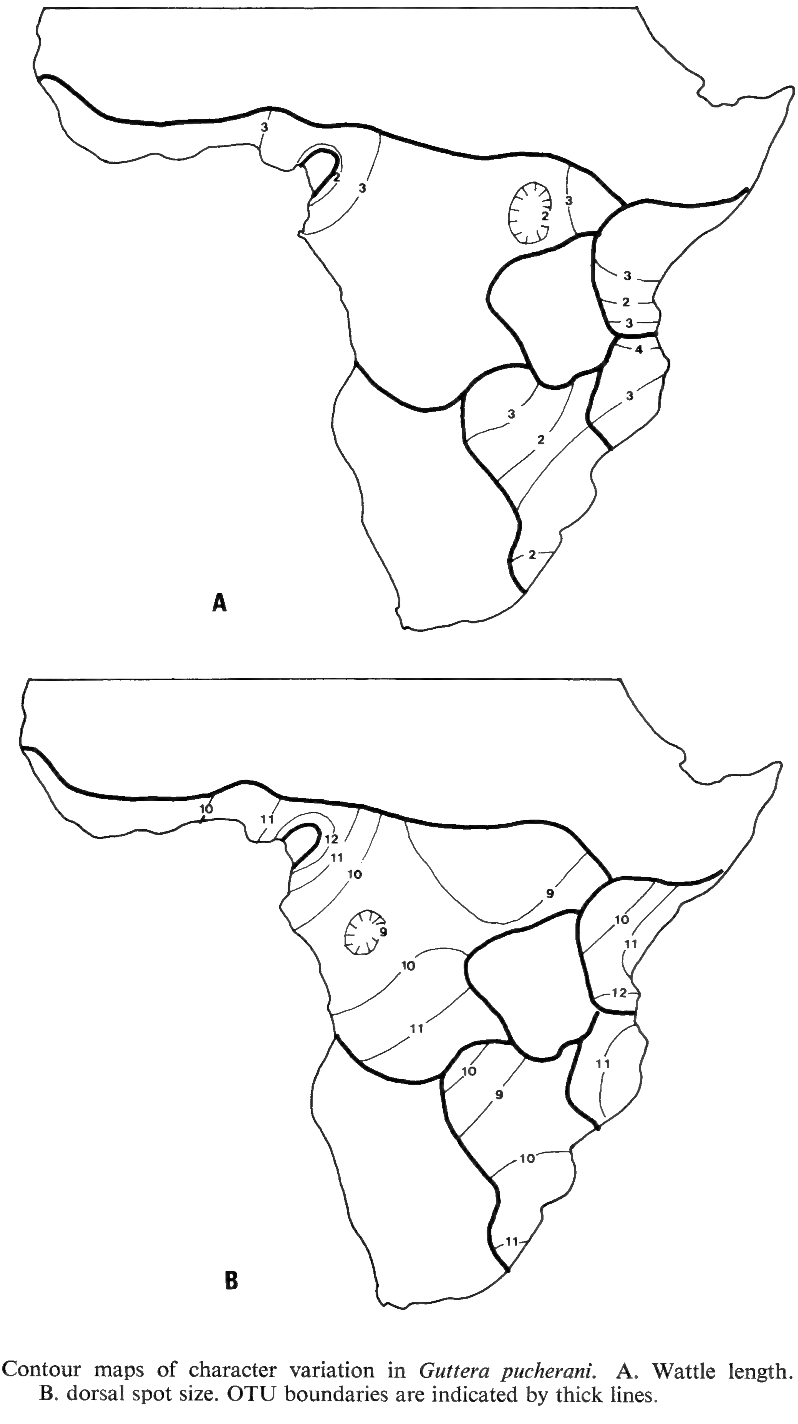

Fig. 21. Contour maps of character variation in *Guttera pucherani*. A. Wattle length. B. dorsal spot size. OTU boundaries are indicated by thick lines.

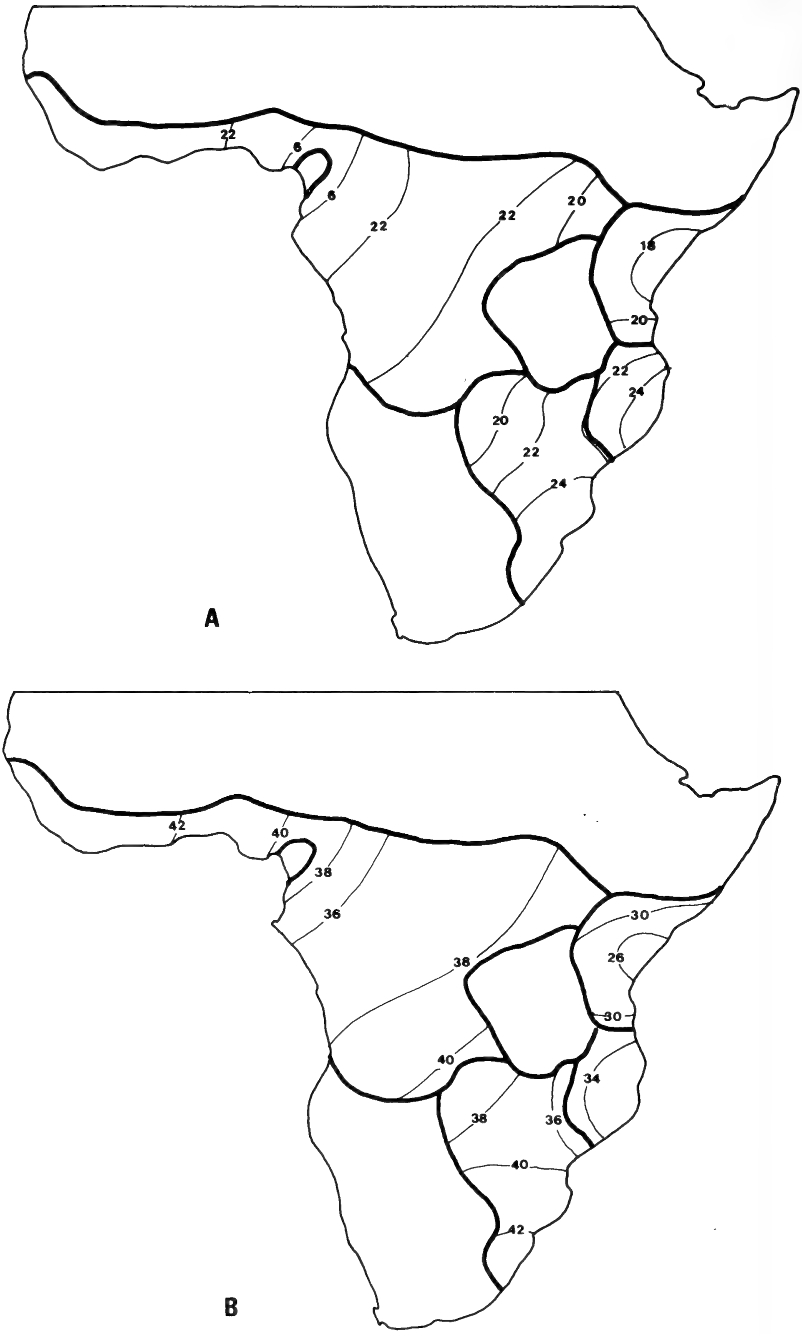

Fig. 22. Contour maps of character variation in *Guttera pucherani*. A. Crest frontal length. B. Crest rear length. OTU boundaries are indicated by thick lines.

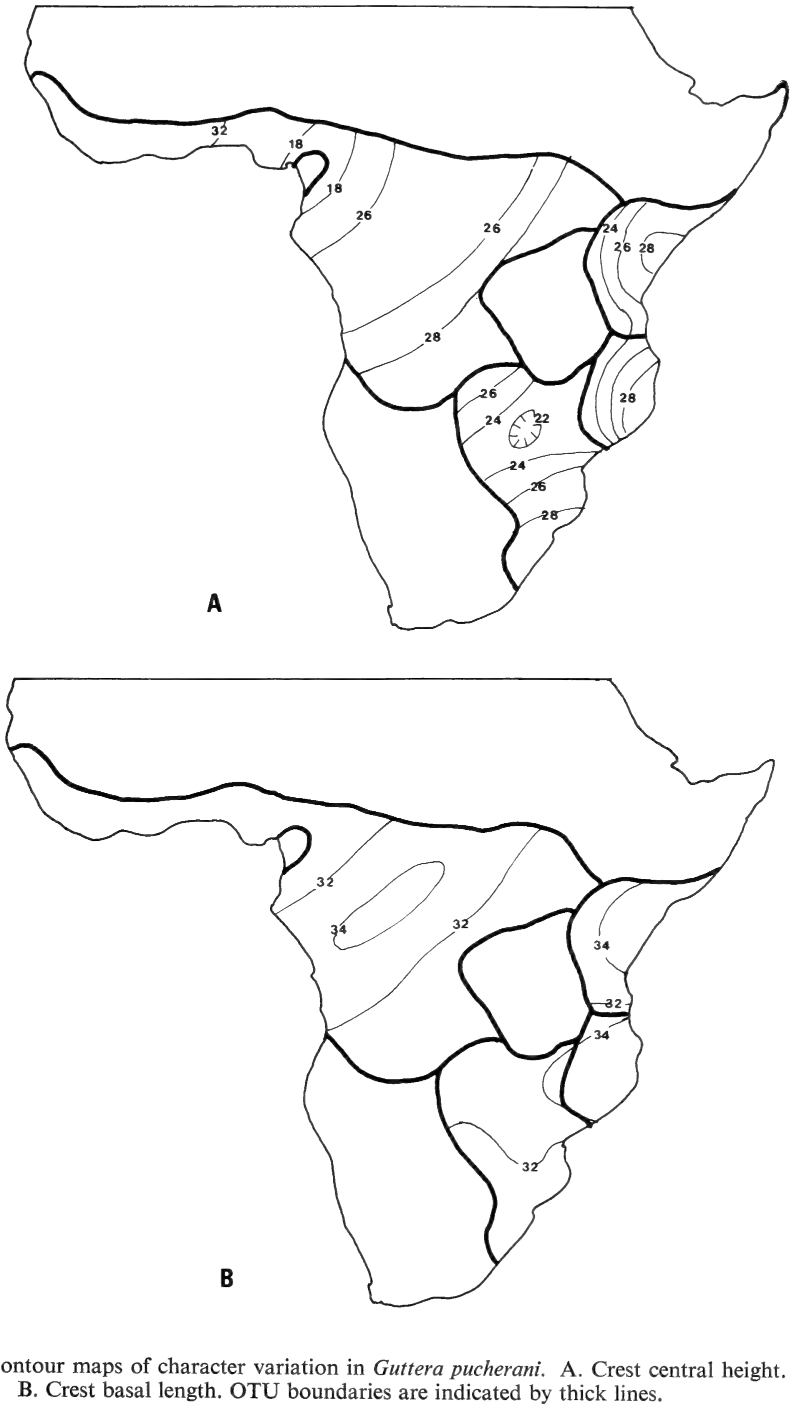

Fig. 23. Contour maps of character variation in *Guttera pucherani*. A. Crest central height. B. Crest basal length. OTU boundaries are indicated by thick lines.

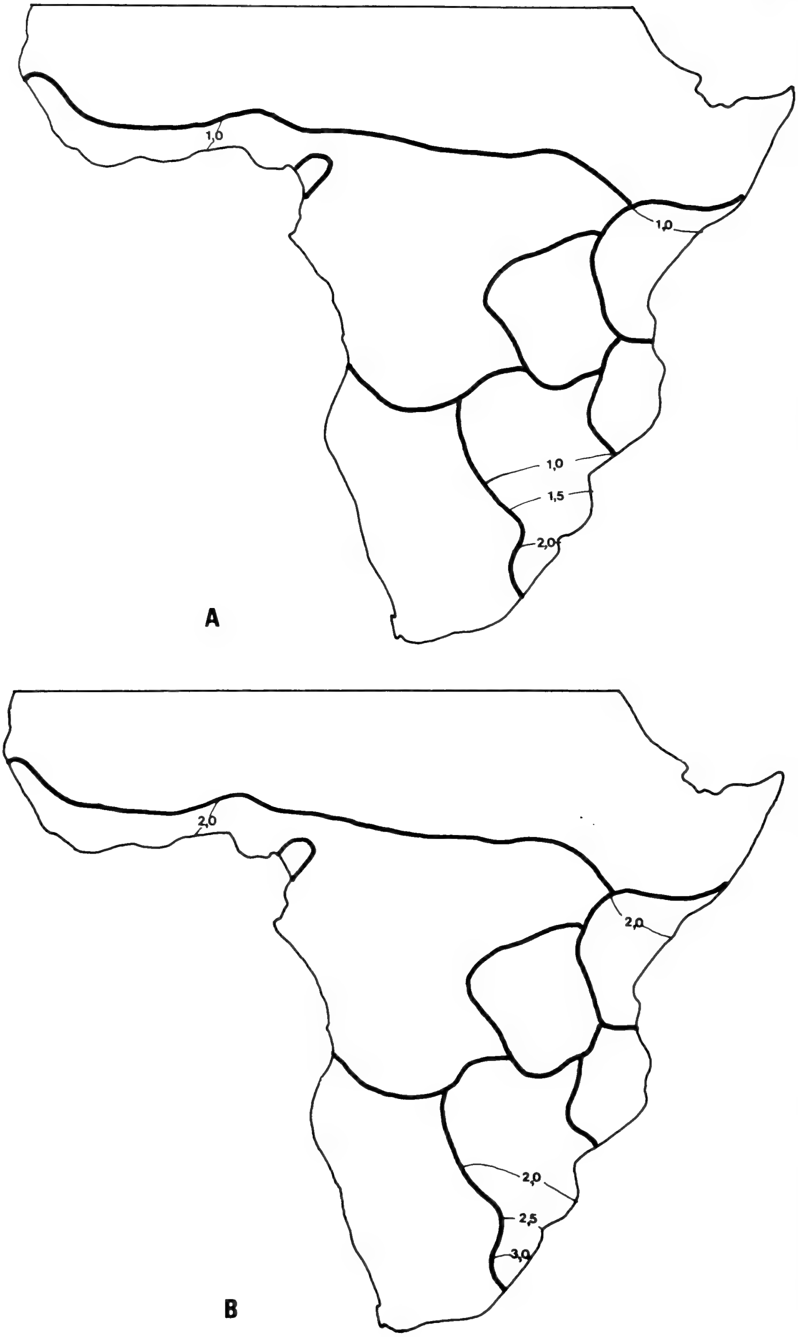

Fig. 24. Contour maps of character variation in *Guttera pucherani*. A. Anterior crest curliness. B. Posterior crest curliness. OTU boundaries are indicated by thick lines.

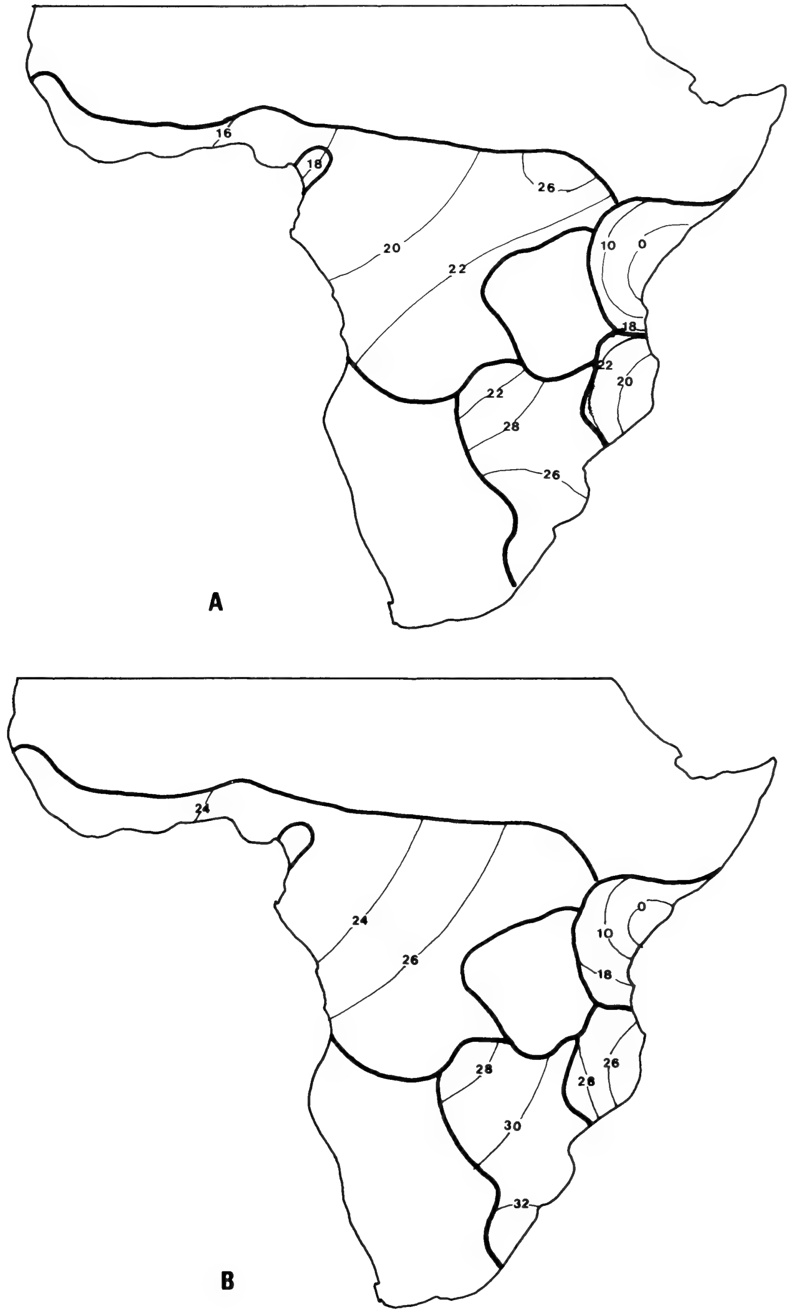

Fig. 25. Contour maps of character variation in *Guttera pucherani*. A. dorsal black collar. B. Ventral black collar. OTU boundaries are indicated by thick lines.

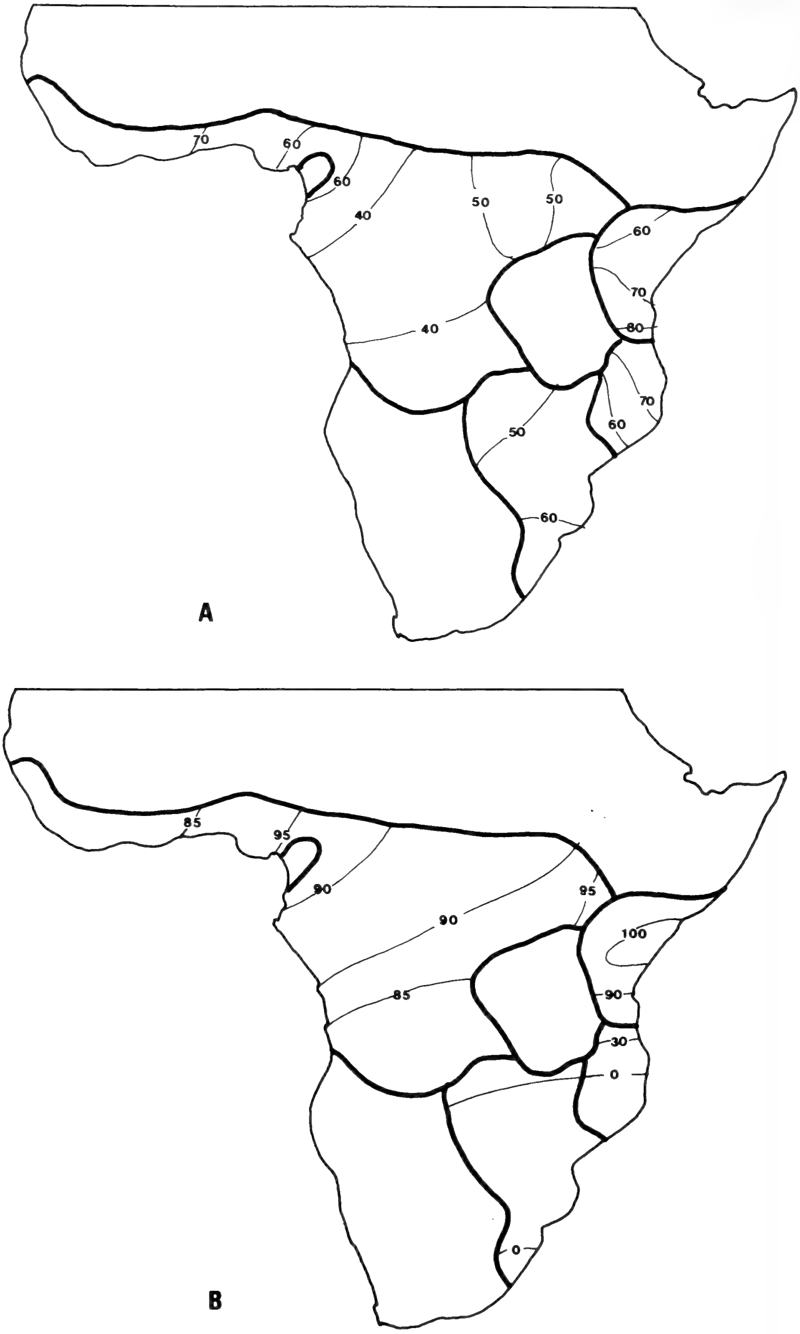

Fig. 26. Contour maps of character variation in *Guttera pucherani*. A. Occipital fold. B. Throat red. OTU boundaries are indicated by thick lines.

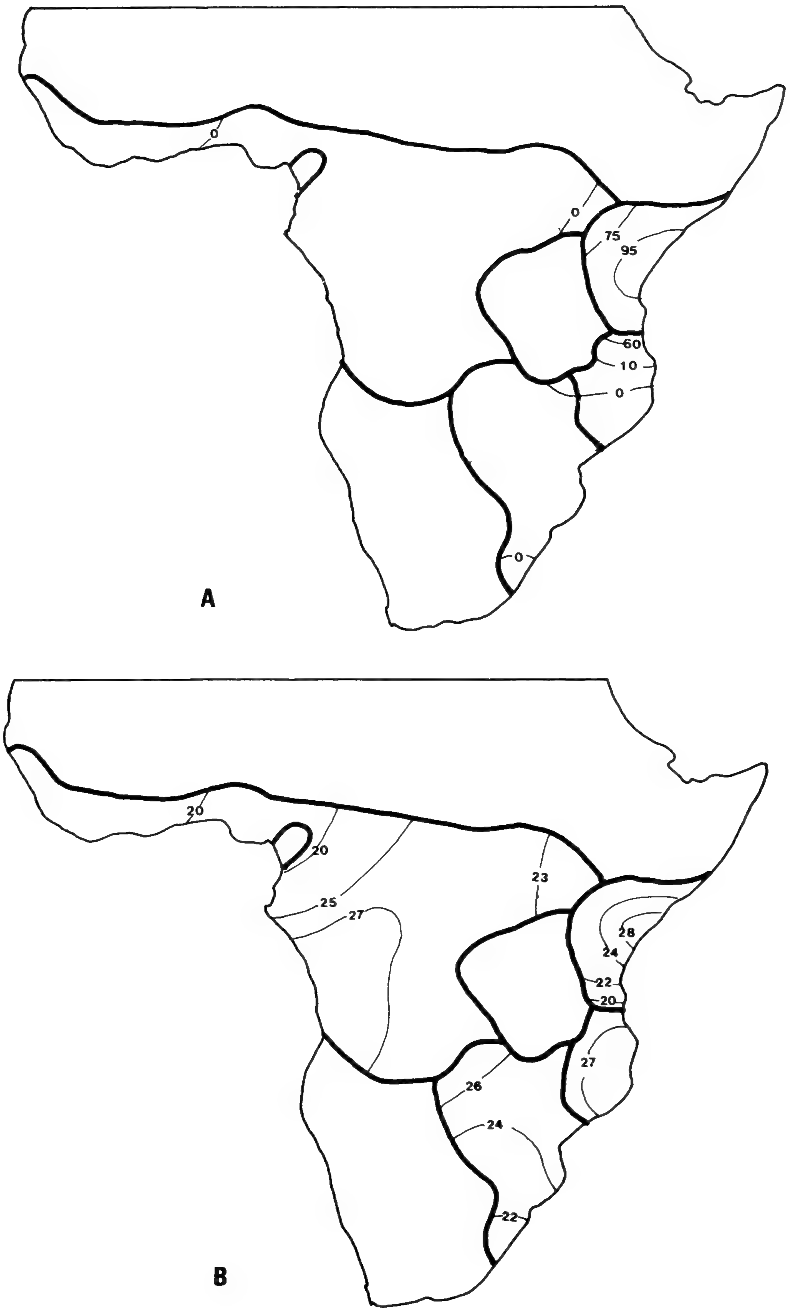

Fig. 27. Contour maps of character variation in *Guttera pucherani*. A. Orbital red. B. Dorsal spot number. OTU boundaries are indicated by thick lines.

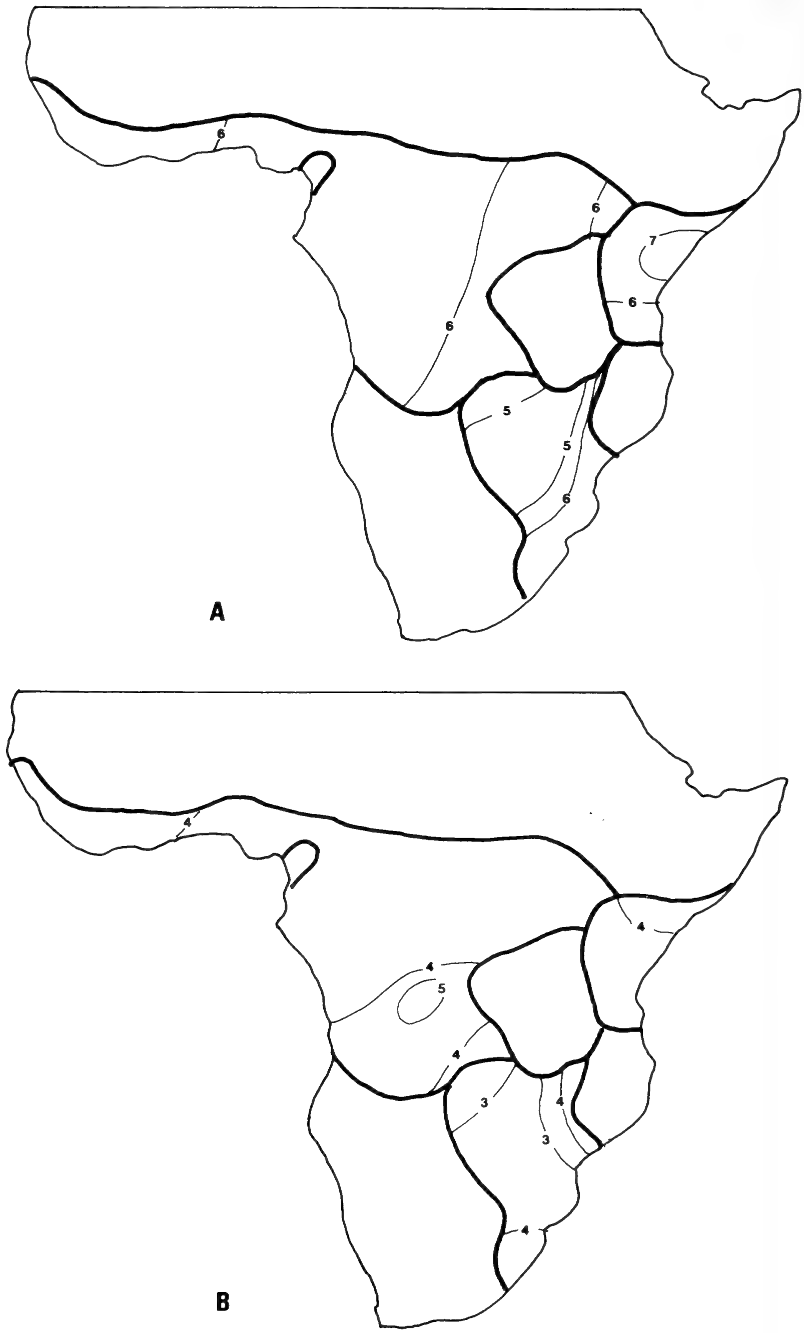

Fig. 28. Contour maps of character variation in *Guttera pucherani*. A. Total spot barbs. B. Total within spot barbs. OTU boundaries are indicated by thick lines.

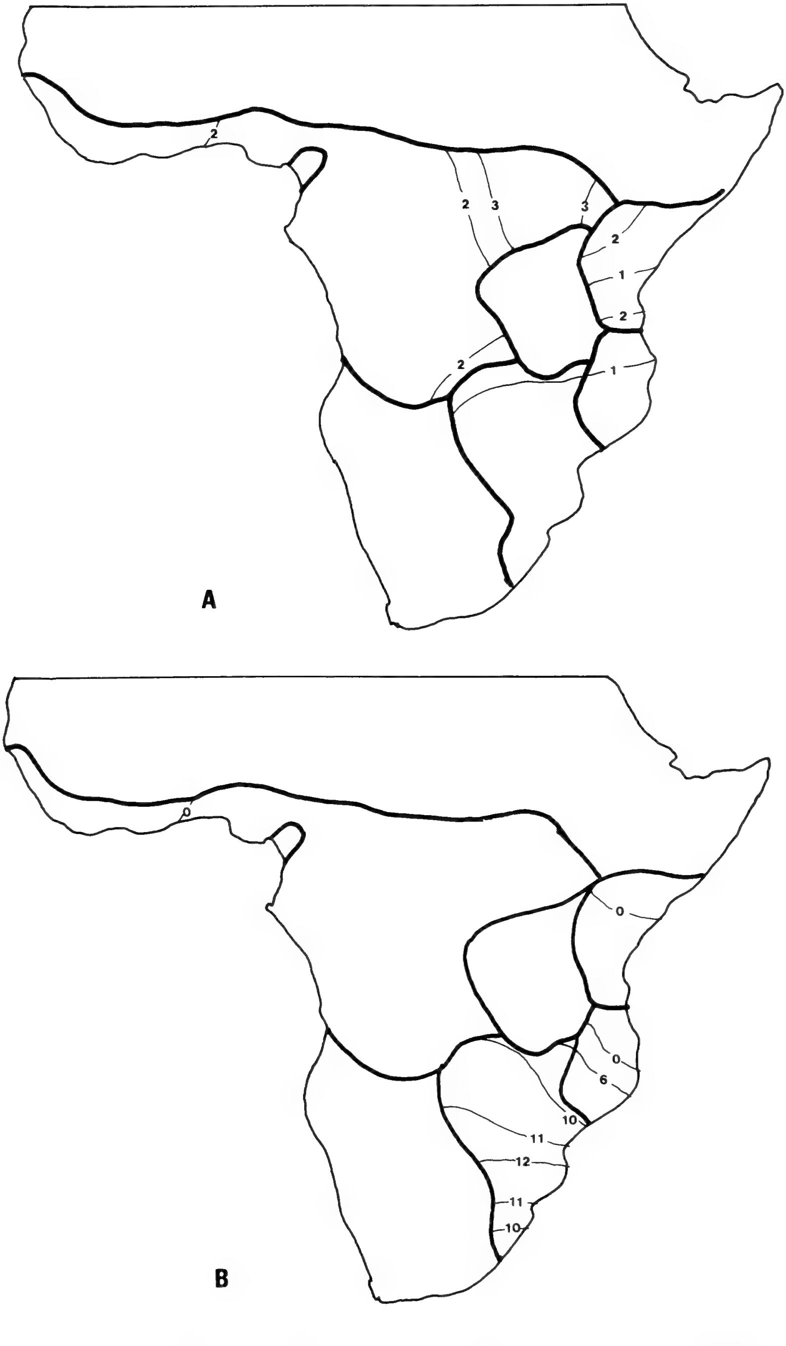

Fig. 29. Contour maps of character variation in *Guttera pucherani*. A. Spot barb blueness. B. Chestnut blotch size. OTU boundaries are indicated by thick lines.

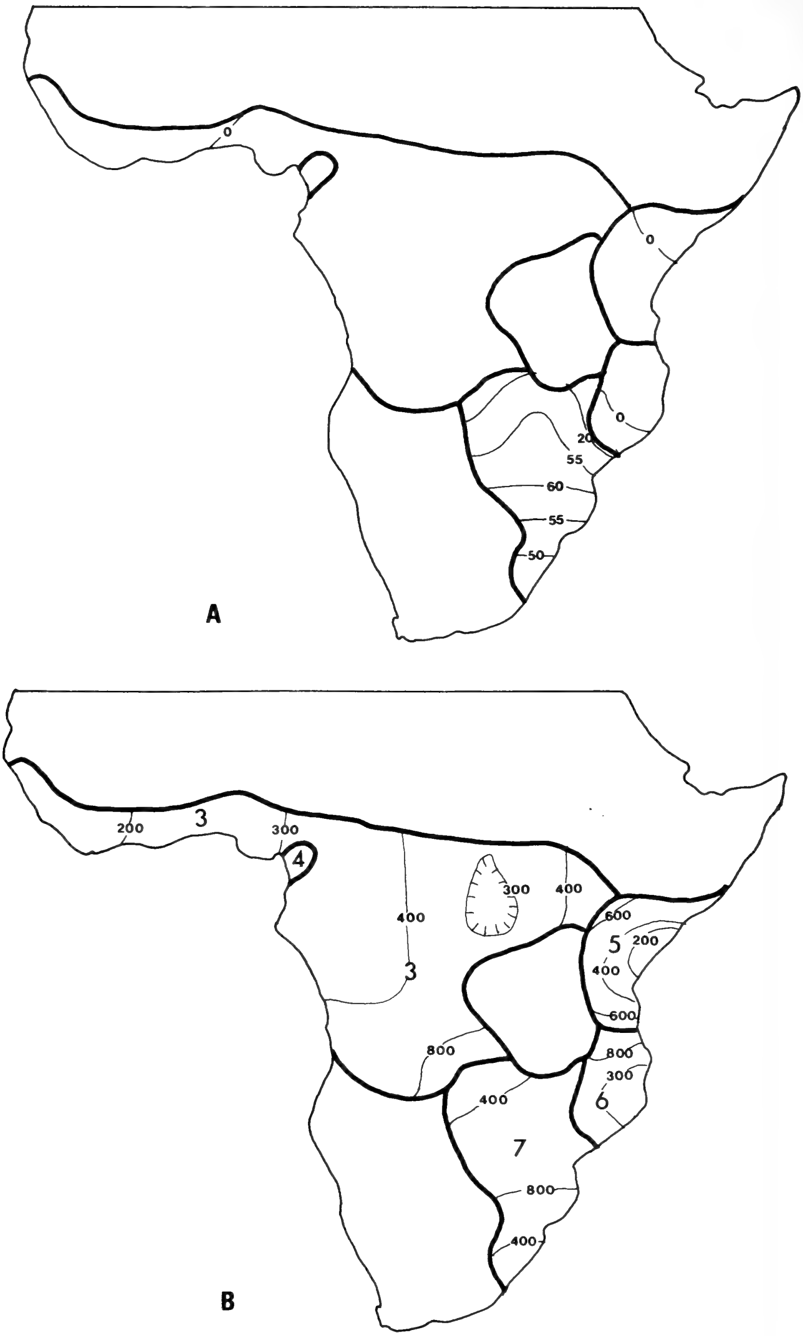

Fig. 30. Contour maps of character variation in *Guttera pucherani*. A. Chestnut blotch extent. B. Total COV. OTU boundaries are indicated by thick lines. Larger numbers in B. refer to OTU numbers shown in Figure 18A.

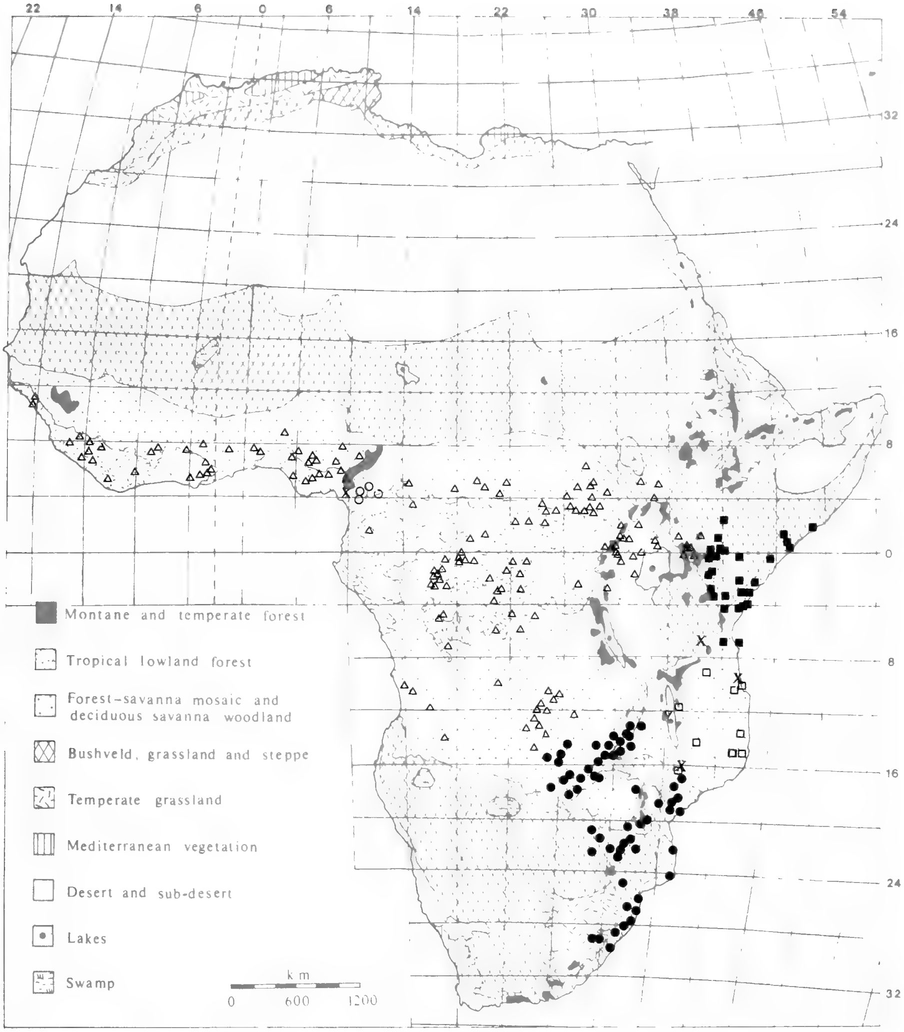

Fig. 31. The distributions of *Guttera pucherani* subspecies. *G. p. pucherani* (■). *G. p. verreauxi* (△). *G. p. sclateri* (○). *G. p. barbata* (□). *G. p. edouardi* (●). Intergrades (×).

TABLE 4

A comparison of OTU 3 for *G. pucherani* with OTUs 4, 5 and 7. × — not significantly different ($P \leq 0{,}05$; *t* test); + — OTU 3 significantly greater; — — OTU 3 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTU* 4	5	7	*Contour map Figure no.*
Bill length	—*	—*	—*	19A
Wing length	×	—*	—*	19B
Tarso-metatarsus length	×	×	+	20A
Wattle basal width	—*	×	—*	20B
Wattle length	+*	×	+*	21A
Dorsal spot size	—*	—*	—*	21B
Crest frontal length	+*	+*	—*	22A
Crest rear length	×	+*	×	22B
Crest central height	+*	×	×	23A
Crest basal length	×	—*	—	23B
Anterior crest curliness	×	×	—*	24A
Posterior crest curliness	×	×	—*	24B
Dorsal black collar	×	+*	—*	25A
Ventral black collar	+	+*	—*	25B
Occipital fold	—	—*	—*	26A
Throat red	×	—*	+*	26B
Orbital red	×	—*	×	27A
Dorsal spot number	+	×	×	27B
Total spot barbs	×	—*	+*	28A
Total within spot barbs	×	—	+*	28B
Spot barb blueness	+	+*	+*	29A
Chestnut blotch size	×	×	—*	29B
Chestnut blotch extent	×	×	—*	30A

[1] See Appendix 2 for character descriptions.

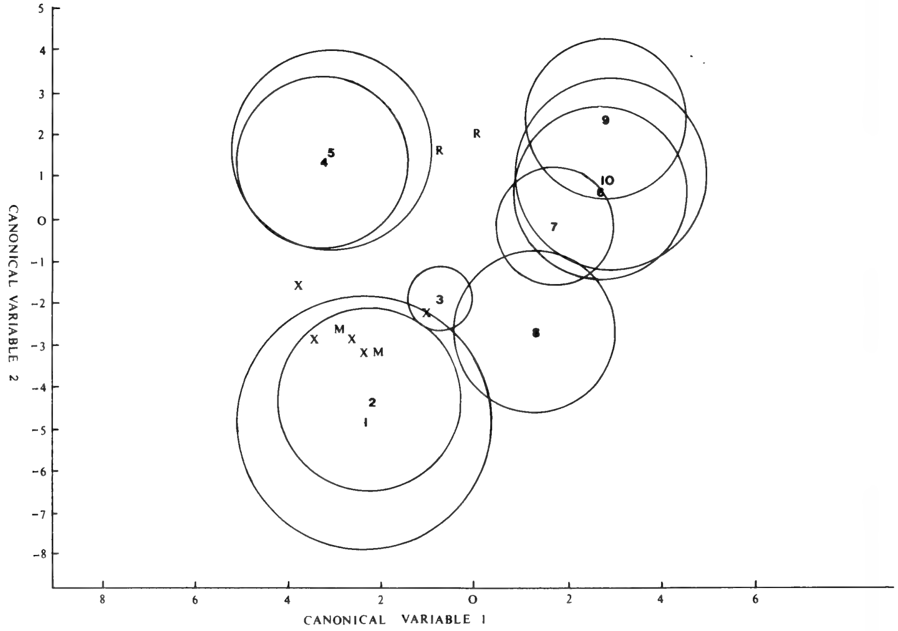

Fig. 32. A discriminant functions analysis of *Numida* OTUs. Circles encompass 90 per cent of the individuals assigned to each OTU. Only intermediate specimens between non-overlapping OTUs are plotted. M — intermediate between OTUs 4 and 7; R — intermediate between OTUs 4 and 8; X — intermediate between OTUs 4 and 2.

TABLE 5

A comparison of OTU 6 for *G. pucherani* with OTUs 5 and 7. × — not significantly different ($P \leq 0,05$; *t* test); + — OTU 6 significantly greater; — — OTU 6 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTU*		*Contour map*
	5	7	*Figure no.*
Bill length	×	×	19A
Wing length	×	+*	19B
Tarso-metatarsus length	×	+*	20A
Wattle basal width	×	—*	20B
Wattle length	×	+*	21A
Dorsal spot size	×	+*	21B
Crest frontal length	+*	×	22A
Crest rear length	+*	—*	22B
Crest central height	×	×	23A
Crest basal length	×	+*	23B
Anterior crest curliness	×	—*	24A
Posterior crest curliness	×	—*	24B
Dorsal black collar	+*	—*	25A
Ventral black collar	+*	—*	25B
Occipital fold	×	+*	26A
Throat red	—*	+	26B
Orbital red	—*	+	27A
Dorsal spot number	×	+*	27B
Total spot barbs	×	+	28A
Total within spot barbs	×	+*	28B
Spot barb blueness	—*	+	29A
Chestnut blotch size	+	—*	29B
Chestnut blotch extent	+	—*	30A

[1] See Appendix 2 for character descriptions.

The approximate geographic distributions of the ten OTUs comprising *N. meleagris* are shown in Figure 18B. Contour maps of variation in twenty-two quantitative characters analysed for this species (nos 1–22 in Appendix 2), and of the total COV for forty-eight areas (Fig. 33) are given in Figures 34–44. In these contour maps, the distributions of all ten OTUs but one, that of OTU 3, are delineated from those of their neighbours by statistically significant patterns of variation in nine to seventeen of the twenty-two characters analysed (Tables 6–11). Results of all possible pairwise statistical comparisons (*t* tests) between neighbouring OTUs are summarized in Tables 6–11. The distribution of OTU 3, the borderline OTU in Figure 11B, is delineated from those of its neighbours (OTUs 2 and 6) by at most two characters (Tables 7, 9). In the contour map of total COV (Fig. 45), the distribution of all OTUs, except again OTU 3, enclose a region of relatively low total COV (*c.* 400–500) bordered by a region(s) of relatively high total COV (*c.* 700–1000). Thus, all OTUs ascribed to *N. meleagris*, except OTU 3, satisfy the criteria set for subspecies (see *Taxonomic methodology*). In Table 1, following the law of priority, OTU 1 corresponds to *N. m. sabyi*, OTU 2 to *N. m. galeata*, OTU 4 to *N. m. meleagris*, OTU 5 to *N. m. somalienses*, OTU 6 to *N. m. marungensis*, OTU 7 to *N. m. mitrata*, OTU 8 to *N. m. reichenowi*, OTU 9 to *N. m. damarensis*, and OTU 10 to *N. m. coronata*.

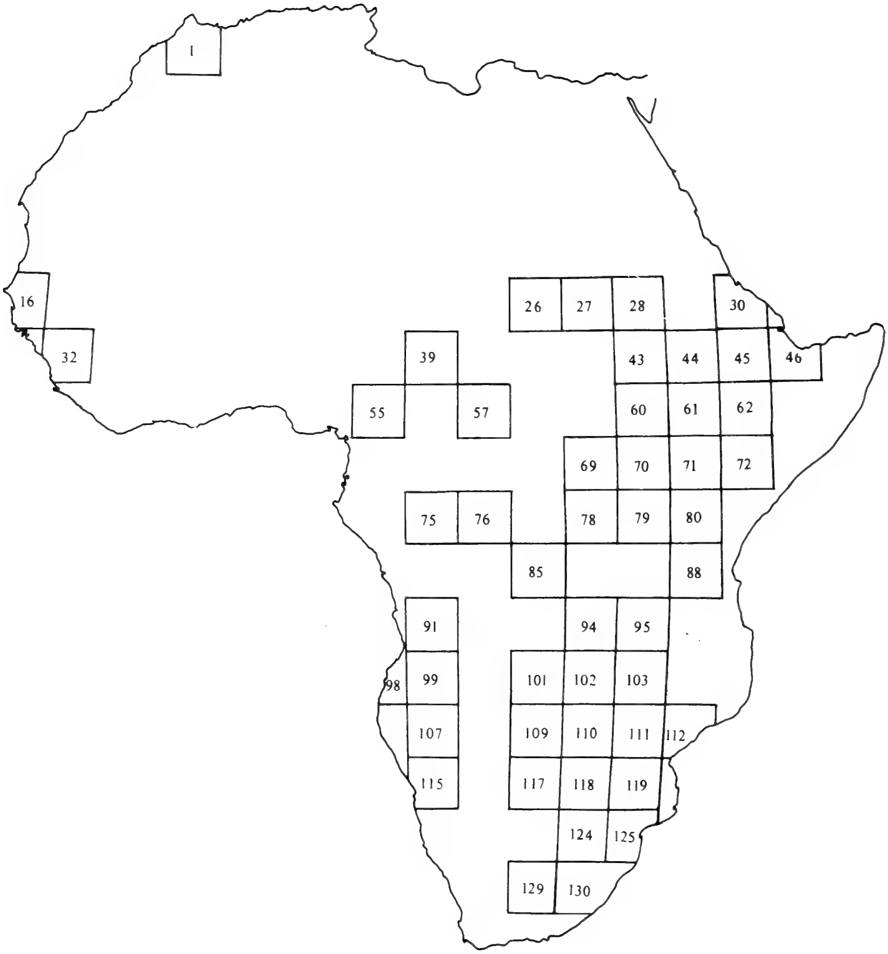

Fig. 33. Areas used in contour map analysis of *Numida meleagris*.

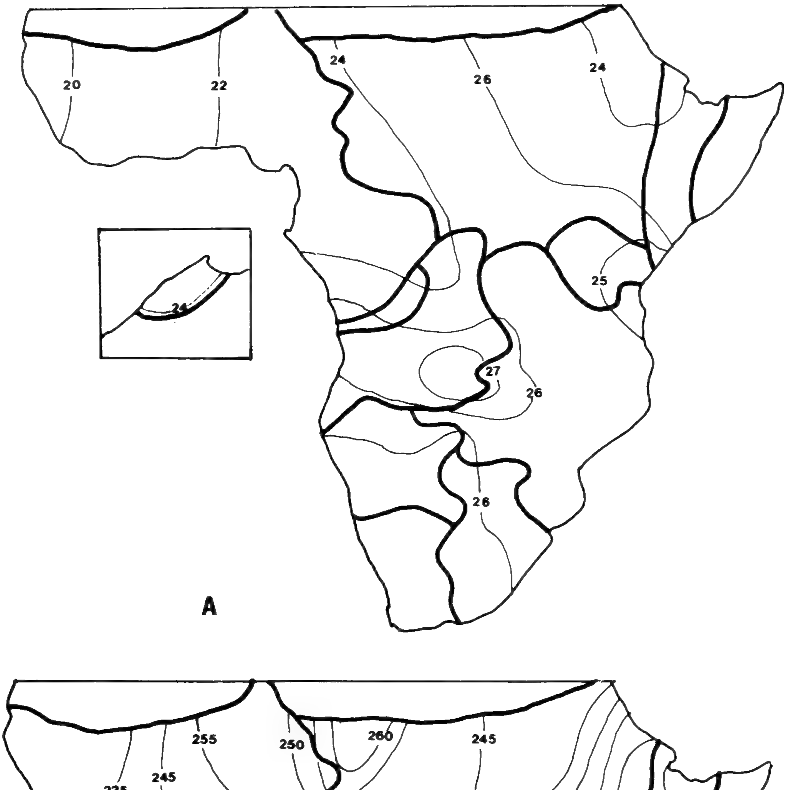

Fig. 34. Contour maps of character variation in *Numida meleagris*. A. Bill length. B. Wing length. OTU boundaries are indicated by thick lines.

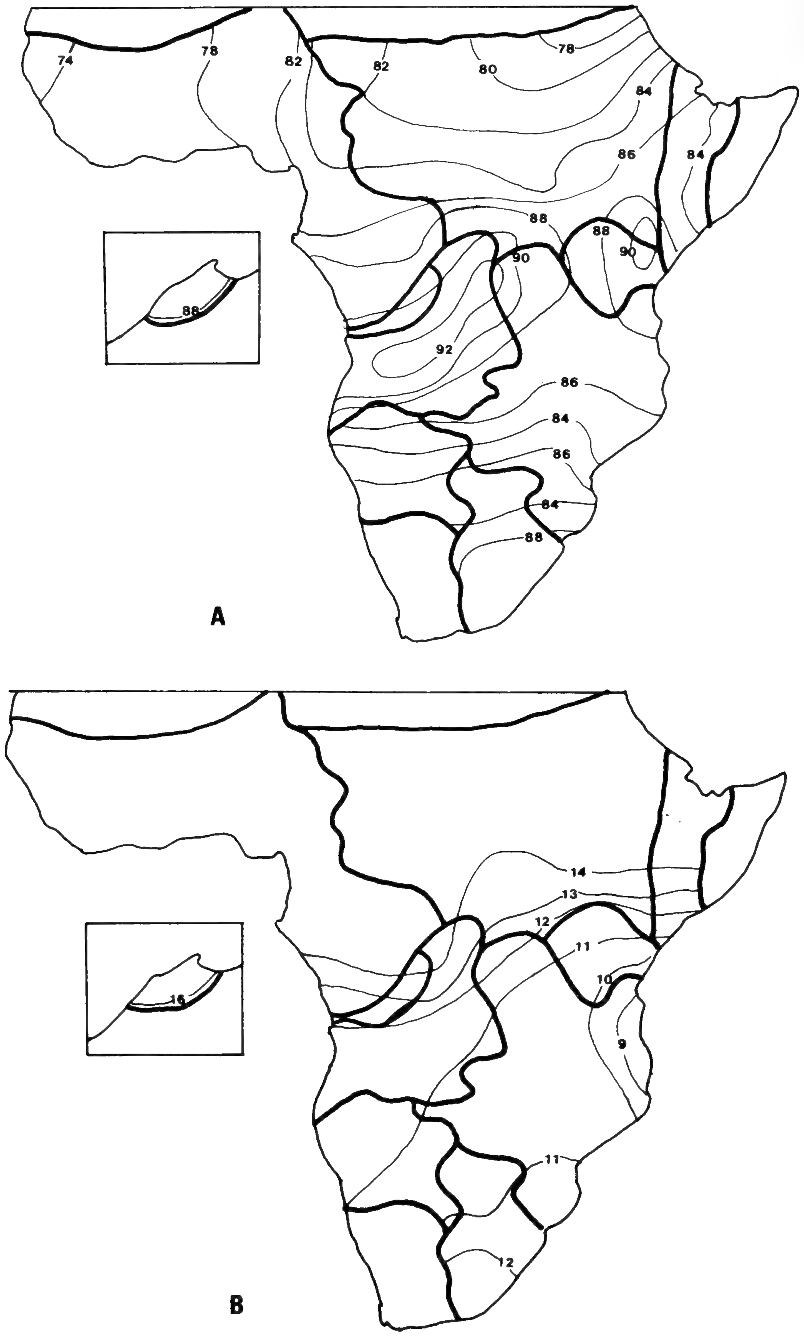

Fig. 35. Contour maps of character variation in *Numida meleagris*. A. Tarso-metatarsus length. B. Wattle basal width. OTU boundaries are indicated by thick lines.

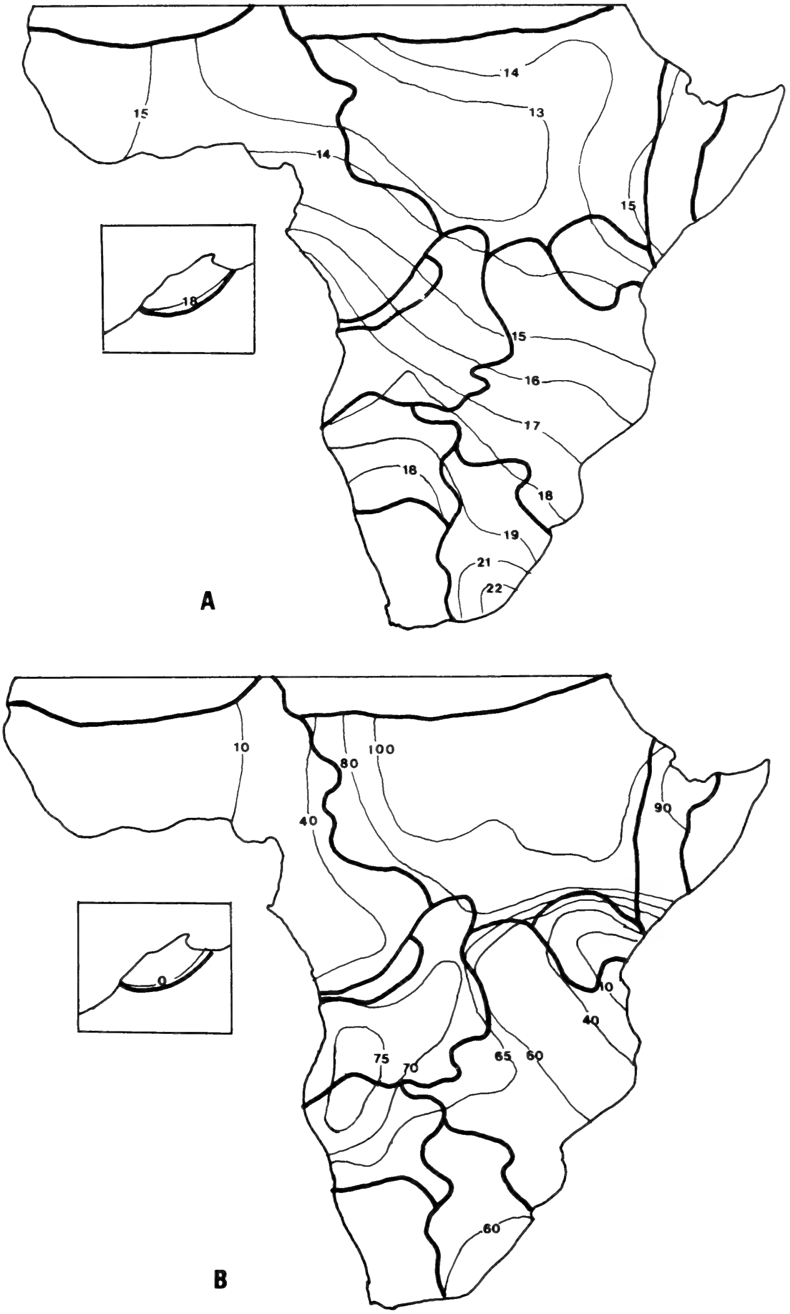

Fig. 36. Contour maps of character variation in *Numida meleagris*. A. Wattle length. B. Wattle per cent blue. OTU boundaries are indicated by thick lines.

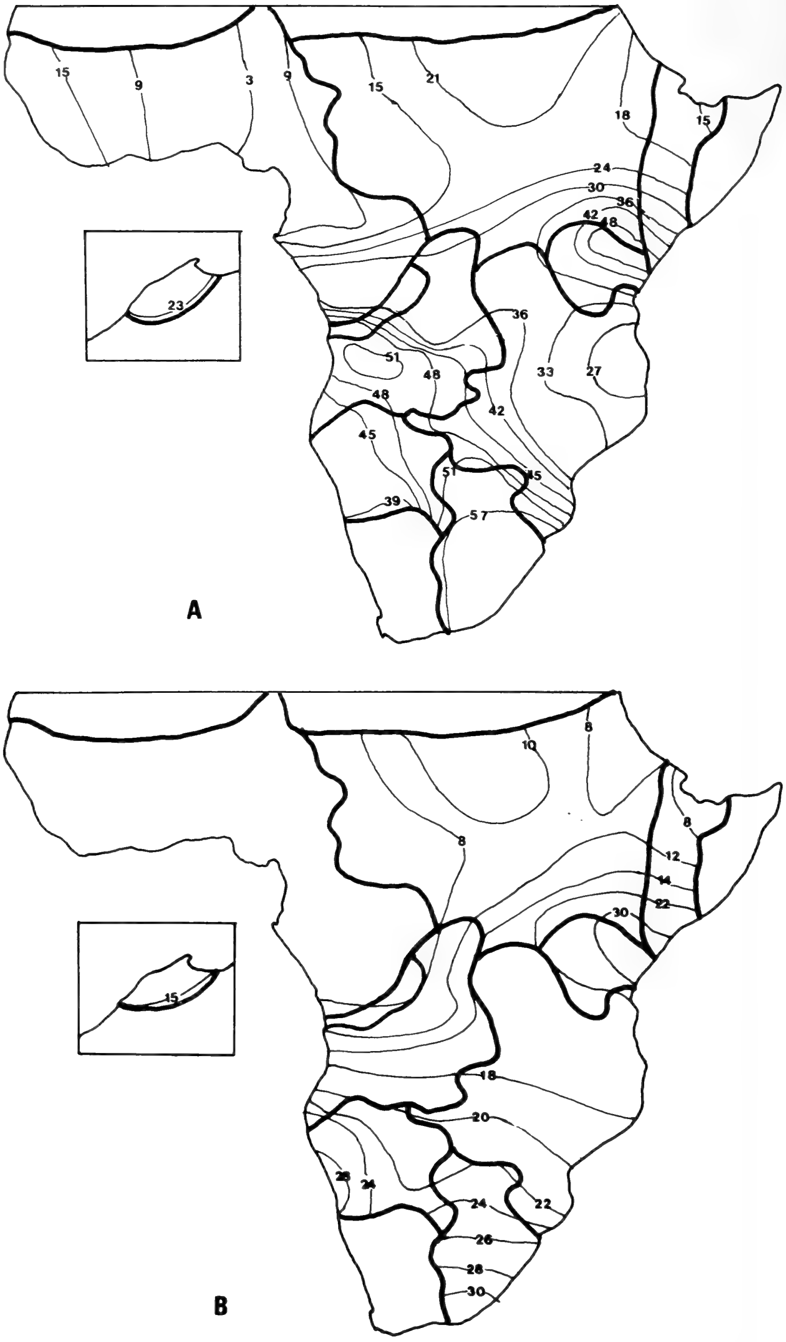

Fig. 37. Contour maps of character variation in *Numida meleagris*. A. Helmet frontal length. B. Helmet rear length. OTU boundaries are indicated by thick lines.

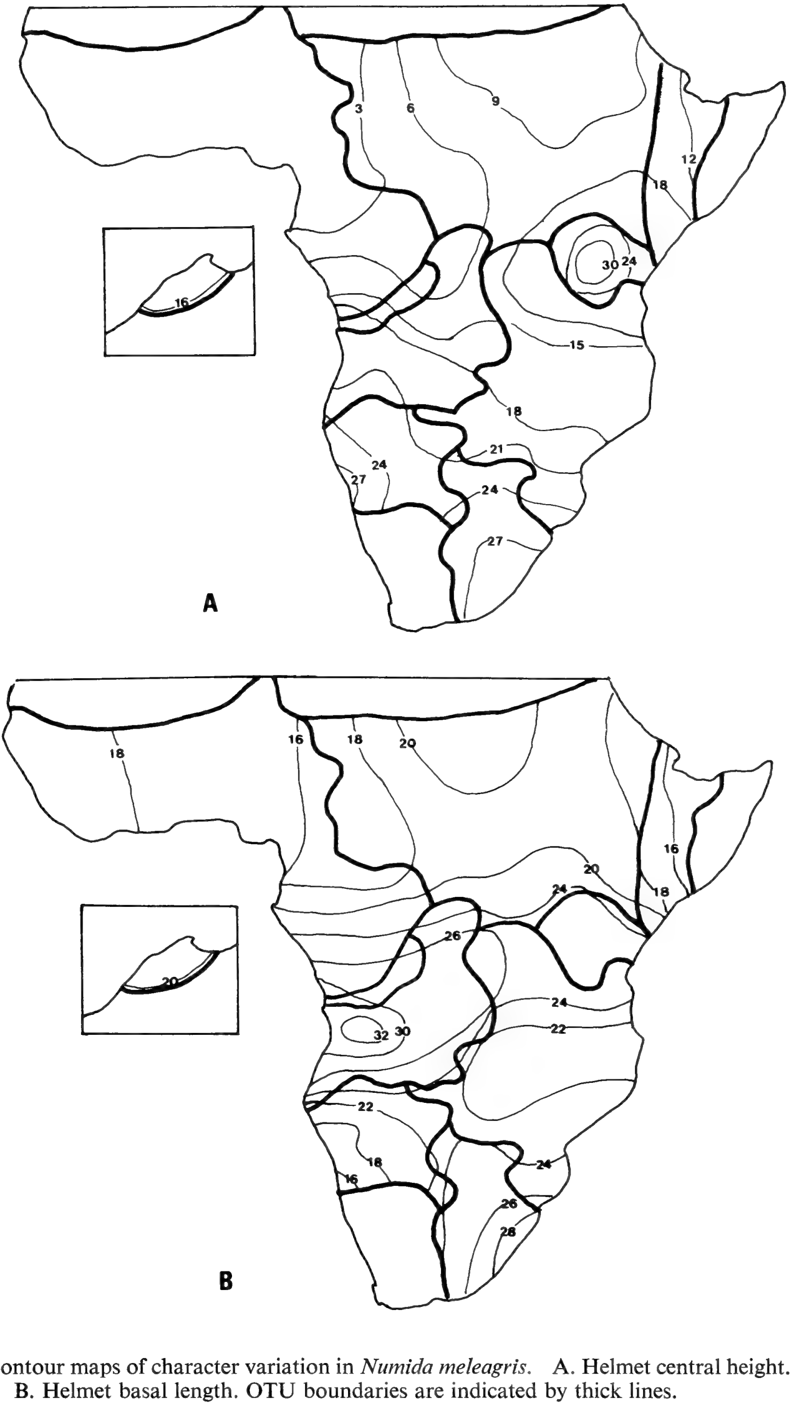

Fig. 38. Contour maps of character variation in *Numida meleagris*. A. Helmet central height. B. Helmet basal length. OTU boundaries are indicated by thick lines.

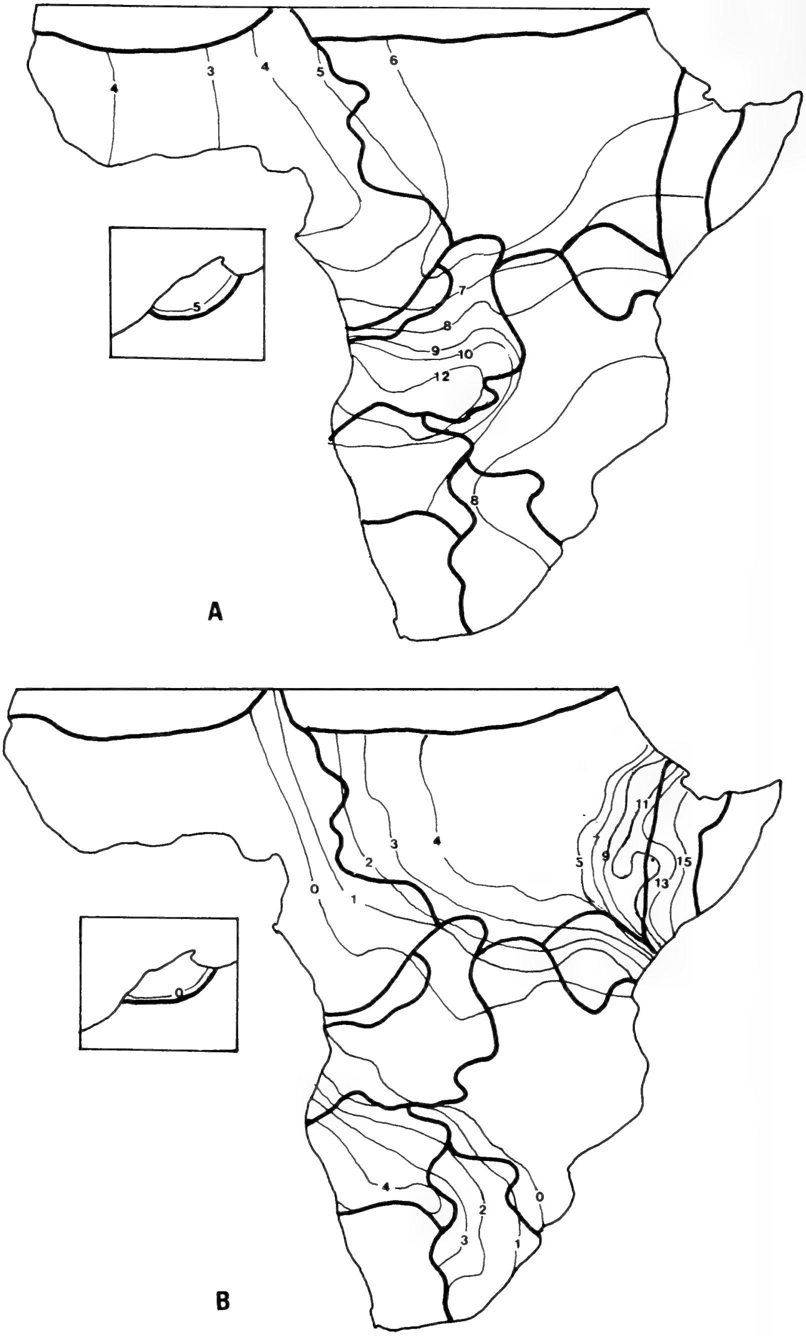

Fig. 39. Contour maps of character variation in *Numida meleagris.* A. Helmet thickness. B. Cere structure length. OTU boundaries are indicated by thick lines.

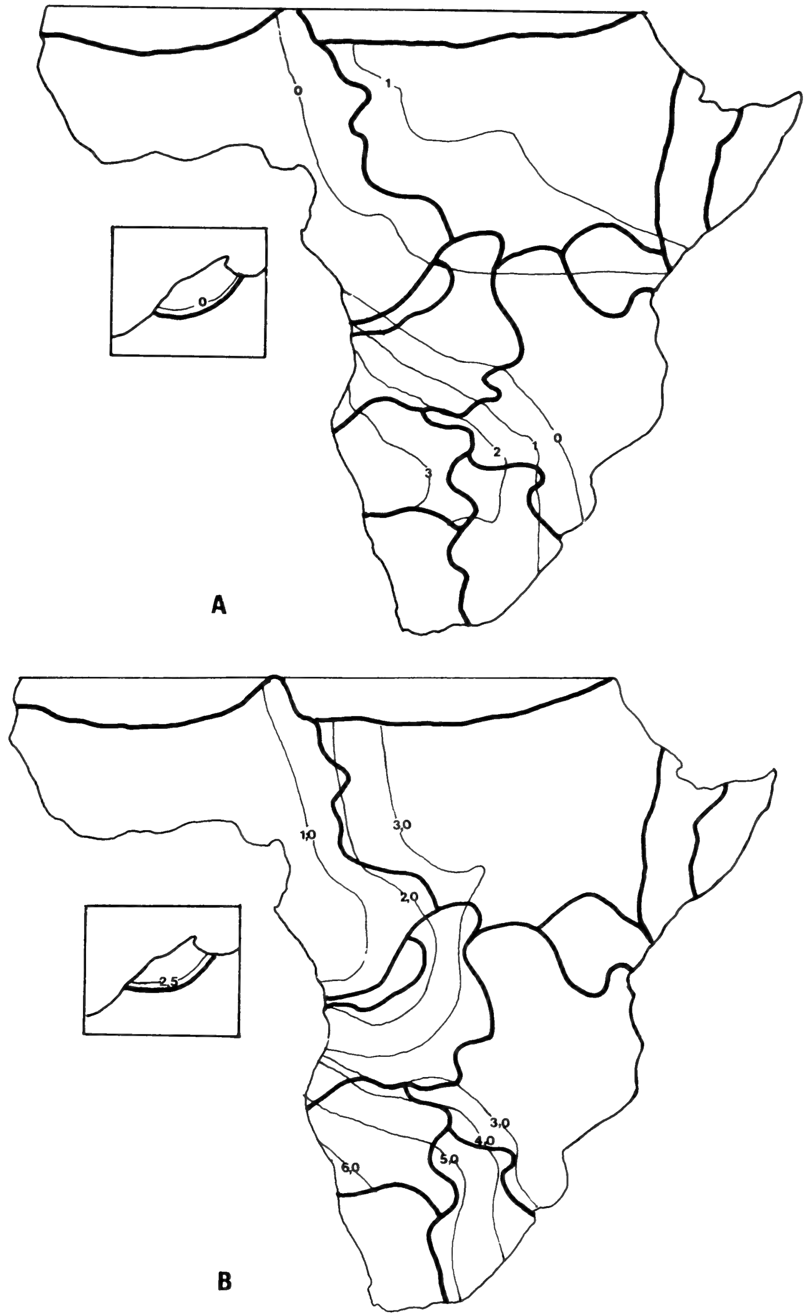

Fig. 40. Contour maps of character variation in *Numida meleagris*. A. Cere structure thickness. B. Collar plumage. OTU boundaries are indicated by thick lines.

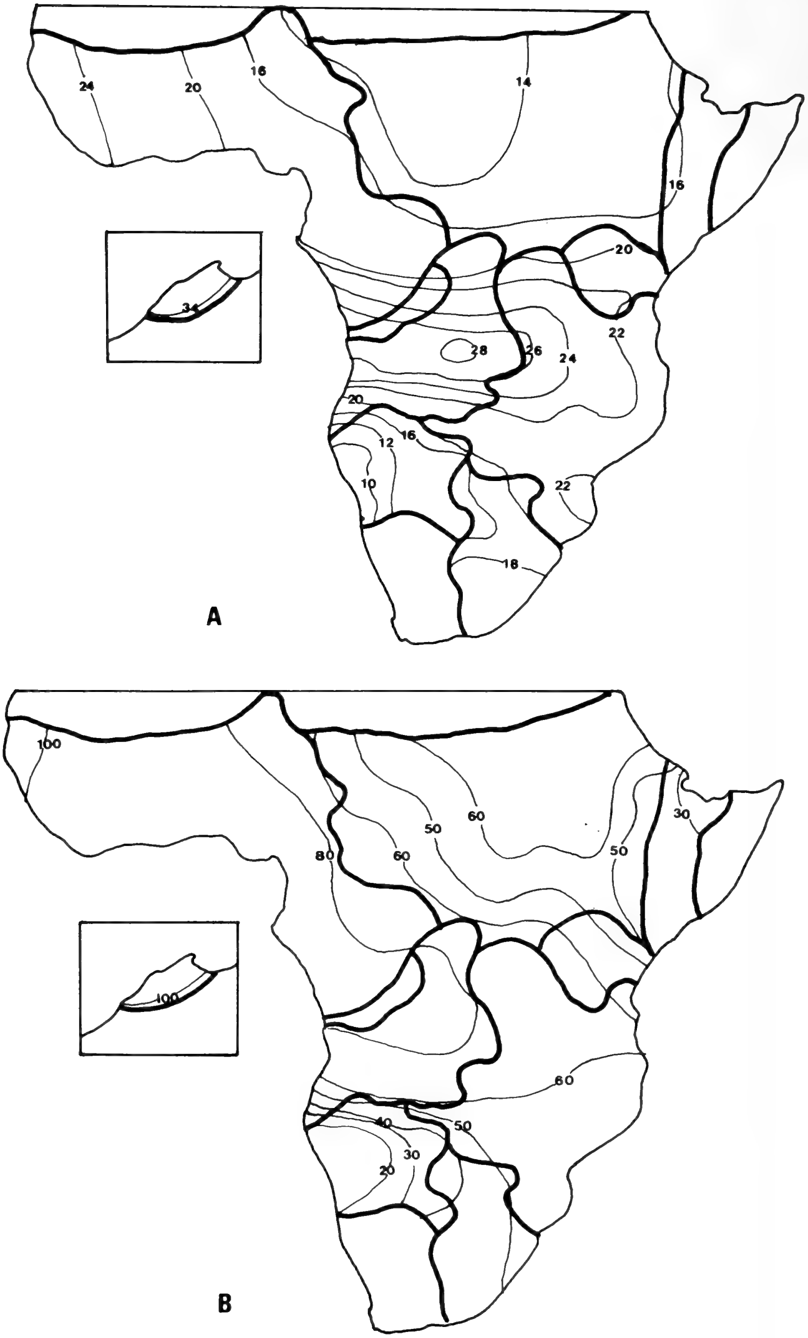

Fig. 41. Contour maps of character variation in *Numida meleagris*. A. Nape filoplume length. B. Nape anteroposterior coverage. OTU boundaries are indicated by thick lines.

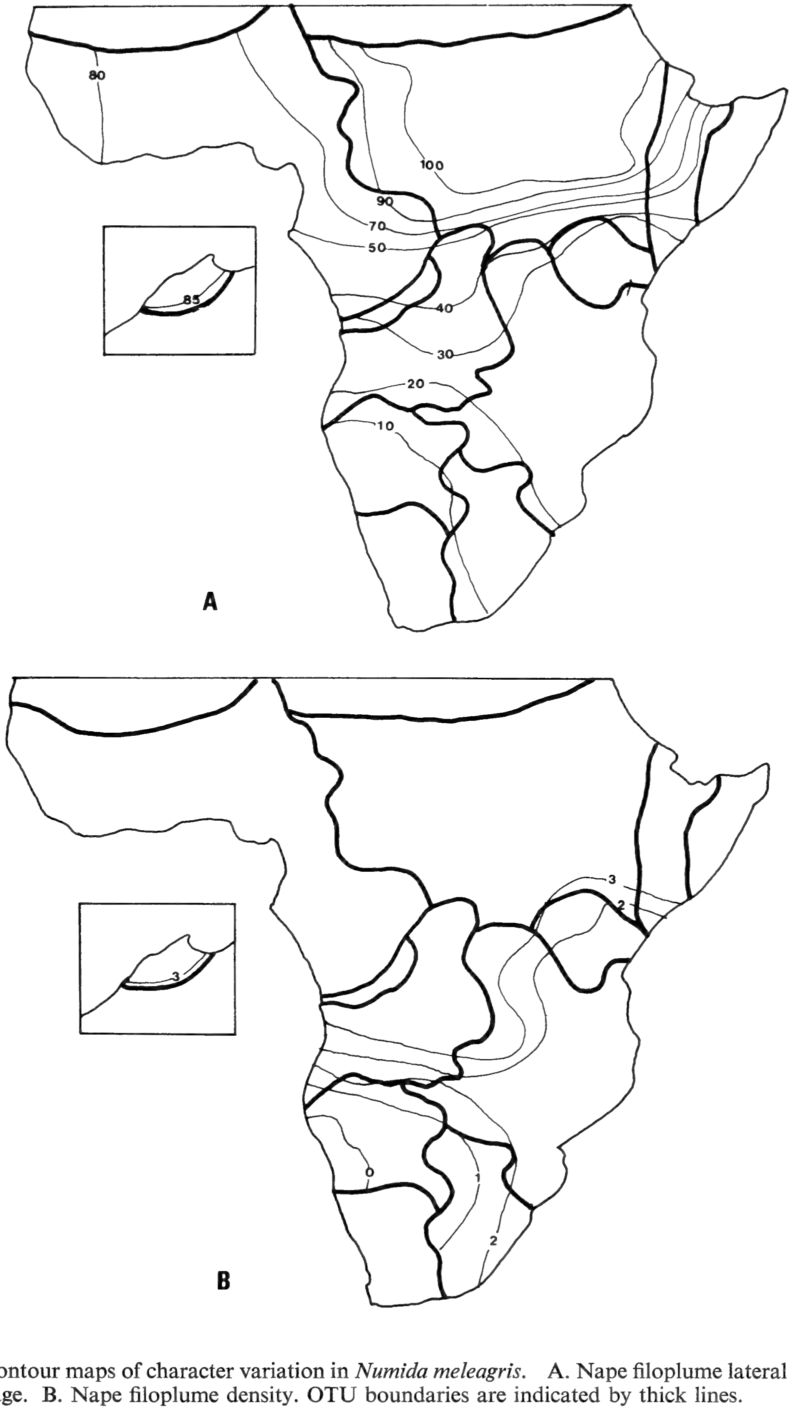

Fig. 42. Contour maps of character variation in *Numida meleagris*. A. Nape filoplume lateral coverage. B. Nape filoplume density. OTU boundaries are indicated by thick lines.

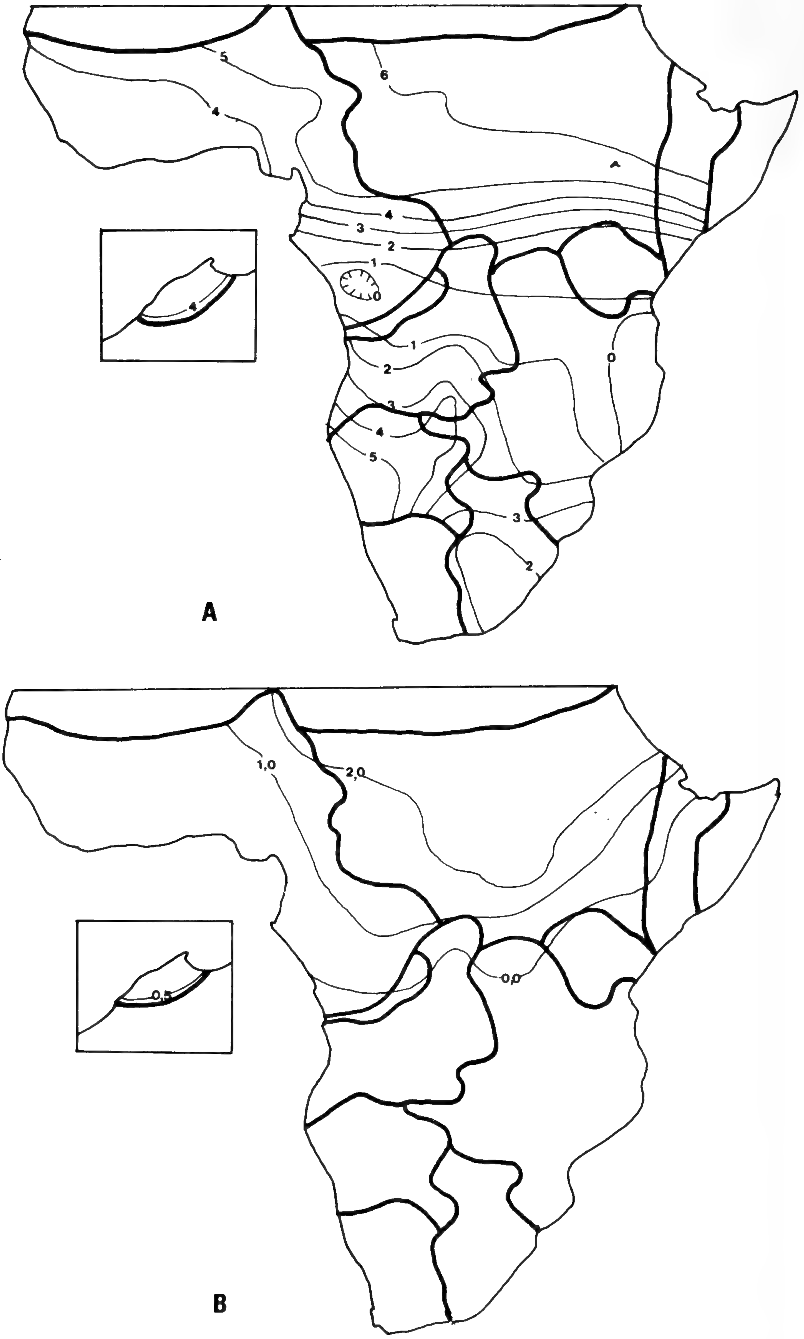

Fig. 43. Contour maps of character variation in *Numida meleagris*. A. Secondary remex outer web vermiculation. B. Wing covert barring. OTU boundaries are indicated by thick lines.

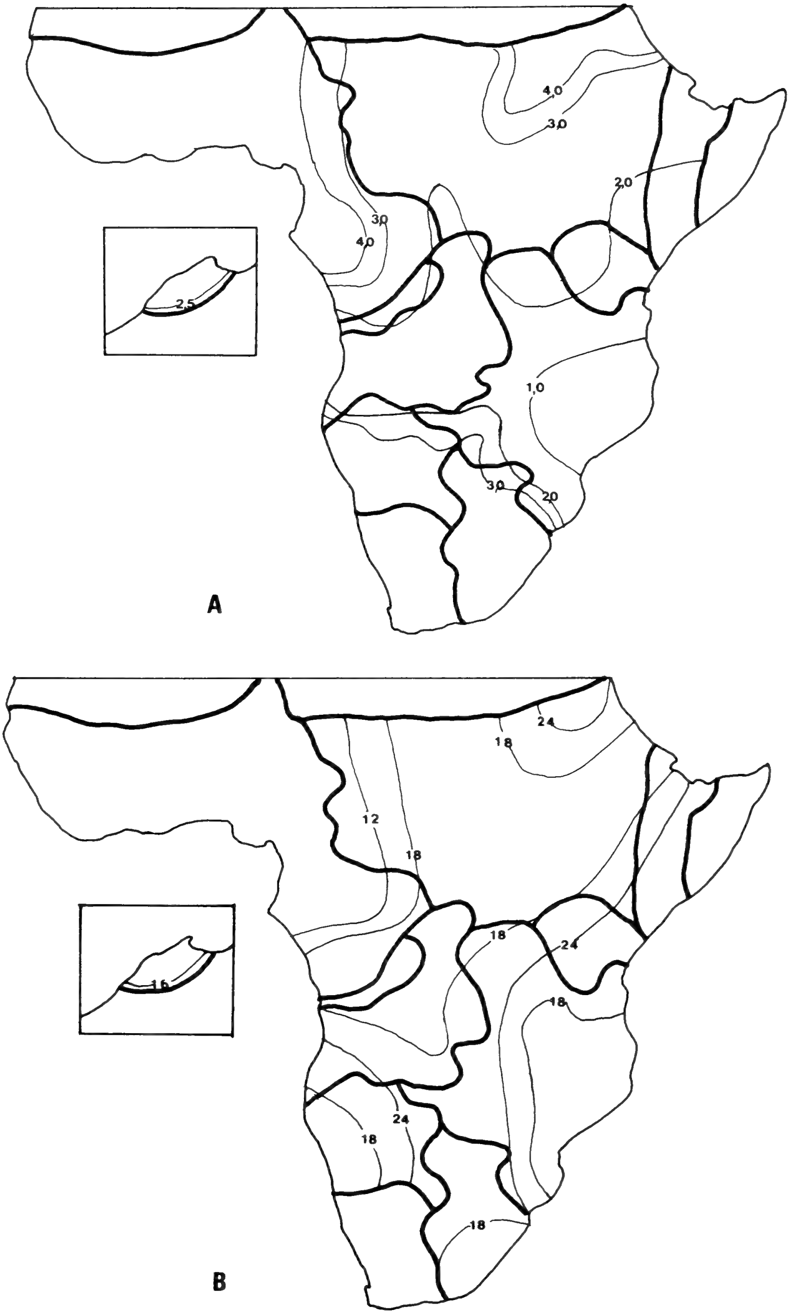

Fig. 44. Contour maps of character variation in *Numida meleagris*. A. Dorsal vermiculation. B. Dorsal spot size. OTU boundaries are indicated by thick lines.

TABLE 6

A comparison of OTU 4 for *N. meleagris* with OTUs 2, 5, 6, 7 and 8. × — not significantly different ($P \leq 0,05$; *t* test); + — OTU 4 significantly greater; — — OTU 4 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTU*					*Contour map*
	2	5	6	7	8	*Figure no.*
Bill length	+*	×	—*	—	×	34A
Wing length	+	×	—*	—*	—*	34B
Tarso-metatarsus length	+*	×	—*	—	—*	35A
Wattle basal width	×	×	+*	+*	+*	35B
Wattle length	—	—*	—*	—*	+	36A
Wattle per cent blue	+*	+*	+*	+*	+*	36B
Helmet frontal length	+*	×	—*	—*	—*	37A
Helmet rear length	+*	×	—	—	—*	37B
Helmet central height	+*	×	—	—*	—*	38A
Helmet basal length	×	+*	—*	—*	—*	38B
Helmet thickness	+*	×	—*	—*	—	39A
Cere structure length	+*	—*	+*	+*	+	39B
Cere structure thickness	+*	×	+*	+*	+*	40A
Collar plumage	+*	×	×	—	×	40B
Nape filoplume length	—*	—*	—*	—*	—*	41A
Nape filoplume anteroposterior coverage	—*	+*	—*	×	×	41B
Nape filoplume lateral coverage	+*	+*	+*	+*	+*	42A
Nape filoplume density	×	×	×	+	+*	42B
Secondary remex outer web vermiculation	+*	+	+*	+*	+*	43A
Wing covert barring	+*	+*	+*	+*	+*	43B
Dorsal vermiculation	—*	+	+*	+*	+	44A
Dorsal spot size	+*	—*	—	×	—*	44B

[1] See Appendix 2 for character descriptions.

TABLE 7

A comparison of OTU 2 for *N. meleagris* with OTUs 1, 3 and 6. × — not significantly different ($P \leq 0,05$; *t* test); + — OTU 2 significantly greater; — — OTU 2 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTUs*			*Contour map*
	1	3	6	*Figure no.*
Bill length	×	—	—*	34A
Wing length	—*	—	—*	34B
Tarso-metatarsus length	—*	—	—*	35A
Wattle basal width	×	×	+*	35B
Wattle length	×	×	—	36A
Wattle per cent blue	+*	—*	—*	36B
Helmet frontal length	—*	—	—*	37A
Helmet rear length	—*	—	—	37B
Helmet central height	—*	—	—	38A
Helmet basal length	×	—	—*	38B
Helmet thickness	×	—	—*	39A
Cere structure length	×	+	×	39B
Cere structure thickness	×	+	×	40A
Collar plumage	—*	—*	—*	40B
Nape filoplume length	—*	×	—*	41A
Nape filoplume anteroposterior coverage	×	×	+	41B
Nape filoplume lateral coverage	×	+	+	42A
Nape filoplume density	×	×	×	42B
Secondary remex outer web vermiculation	×	+	+	43A
Wing covert barring	+*	+	+*	43B
Dorsal vermiculation	+*	+	+*	44A
Dorsal spot size	+*	—	—	44B

[1] See Appendix 2 for character descriptions.

Table 8

A comparison of OTU 8 for *N. meleagris* with OTUs 5 and 7. × — not significantly different; ($P \leq 0{,}05$; *t* test); + — OTU 8 significantly greater; — — OTU 8 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTUs*		*Contour map Figure no.*
	5	7	
Bill length	×	—*	34A
Wing length	+*	+*	34B
Tarso-metatarsus length	+*	+*	35A
Wattle basal width	—	+	35B
Wattle length	—	—	36A
Wattle per cent blue	—*	—*	36B
Helmet frontal length	+*	+*	37A
Helmet rear length	+*	+*	37B
Helmet central height	+*	+*	38A
Helmet basal length	+*	+*	38B
Helmet thickness	+	+	39A
Cere structure length	—*	+	39B
Cere structure thickness	—	+	40A
Collar plumage	×	—	40B
Nape filoplume length	+*	—*	41A
Nape filoplume anteroposterior coverage	+	×	41B
Nape filoplume lateral coverage	—	+	42A
Nape filoplume density	—*	×	42B
Secondary remex outer web vermiculation	—*	+*	43A
Wing covert barring	—	+	43B
Dorsal vermiculation	×	+	44A
Dorsal spot size	×	+	44B

[1] See Appendix 2 for character descriptions.

Table 9

A comparison of OTU 6 for *N. meleagris* with OTUs 3, 7 and 9. × — not significantly different ($P \leq 0{,}05$; *t* test); + — OTU 6 significantly greater; — — OTU 6 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTUs*			*Contour map Figure no.*
	3	7	9	
Bill length	+	+*	+*	34A
Wing length	+	+*	+*	34B
Tarso-metatarsus length	×	+*	+*	35A
Wattle basal width	—	+*	+	35B
Wattle length	+	×	—	36A
Wattle per cent blue	+*	+*	+	36B
Helmet frontal length	+	+*	+*	37A
Helmet rear length	+	—	—*	37B
Helmet central height	+	×	—	38A
Helmet basal length	+	+*	+*	38B
Helmet thickness	+	+*	+*	39A
Cere structure length	+	×	—*	39B
Cere structure thickness	+	×	—*	40A
Collar plumage	+	×	—*	40B
Nape filoplume length	+	+*	+*	41A
Nape filoplume anteroposterior coverage	—	+*	+*	41B
Nape filoplume lateral coverage	—	+	+*	42A
Nape filoplume density	×	+*	+*	42B
Secondary remex outer web vermiculation	—	—	—*	43A
Wing covert barring	—	×	×	43B
Dorsal vermiculation	—	—	—*	44A
Dorsal spot size	+	+	×	44B

[1] See Appendix 2 for character descriptions.

TABLE 10

A comparison of OTU 10 for *N. meleagris* with OTUs 7 and 9. × — not significantly different ($P \leq 0,05$; *t* test); + — OTU 10 significantly greater; − — OTU 10 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTUs*		*Contour map Figure no.*
	7	9	
Bill length	−	+	34A
Wing length	−	−	34B
Tarso-metatarsus length	×	+	35A
Wattle basal width	×	×	35B
Wattle length	+*	×	36A
Wattle per cent blue	−	−*	36B
Helmet frontal length	+*	+*	37A
Helmet rear length	+*	+*	37B
Helmet central height	+*	+*	38A
Helmet basal length	+*	+*	38B
Helmet thickness	+	×	39A
Cere structure length	+	−*	39B
Cere structure thickness	+	−*	40A
Collar featheration	+*	−*	40B
Nape filoplume length	−*	+*	41A
Nape filoplume anteroposterior coverage	−	+*	41B
Nape filoplume lateral coverage	−	+*	42A
Nape filoplume density	−	+*	42B
Secondary remex outer web vermiculation	+*	−*	43A
Wing covert barring	×	×	43B
Dorsal vermiculation	+*	×	44A
Dorsal spot size	+	−*	44B

[1] See Appendix 2 for character descriptions.

TABLE 11

A comparison of OTU 7 for *N. meleagris* with OTU 9. × — not significantly different ($P \leq 0,05$; *t* test); + — OTU 7 significantly greater; − — OTU 7 significantly lower; * — differences delineate OTUs in contour maps.

Character name[1]	*OTU* 9	*Contour map Figure no.*
Bill length	+	34A
Wing length	+	34B
Tarso-metatarsus length	+	35A
Wattle basal width	×	35B
Wattle length	−*	36A
Wattle per cent blue	×	36B
Helmet frontal length	−*	37A
Helmet rear length	−*	37B
Helmet central height	−*	38A
Helmet basal length	+*	38B
Helmet thickness	−*	39A
Cere structure length	−*	39B
Cere structure thickness	−*	40A
Collar featheration	−*	40B
Nape filoplume length	+*	41A
Nape filoplume anteroposterior coverage	+*	41B
Nape filoplume lateral coverage	+*	42A
Nape filoplume density	+*	42B
Secondary remex outer web vermiculation	−*	43A
Wing covert barring	×	43B
Dorsal vermiculation	−*	44A
Dorsal spot size	−*	44B

[1] See Appendix 2 for character descriptions.

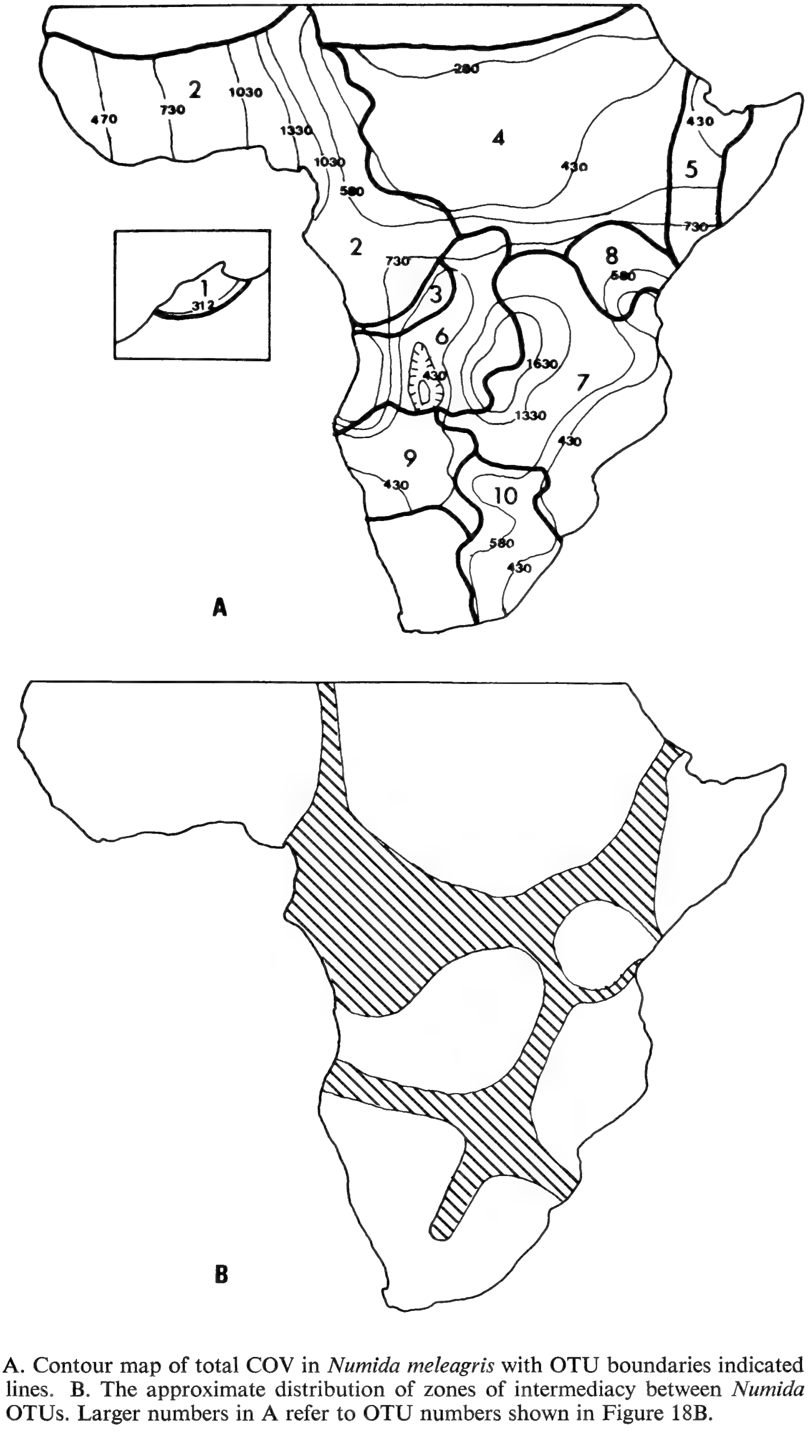

Fig. 45. A. Contour map of total COV in *Numida meleagris* with OTU boundaries indicated by thick lines. B. The approximate distribution of zones of intermediacy between *Numida* OTUs. Larger numbers in A refer to OTU numbers shown in Figure 18B.

The distributions of these subspecies are plotted in Figure 46, and zones of intermediacy are shown in Figure 45B.

TAXONOMIC SUMMARY

In the following classification, verbal descriptions are brief, focusing on more obvious differences and similarities with respect to the qualitative and quantitative characters analysed. For each subspecies, reference is made to its OG or OTU number and the appropriate page(s), tables and figures summarizing its taxonomic relationships and quantitative comparisons with other subspecies. If a synonymized taxon is not discussed, it must be assumed that it did not emerge as an OTU in the cluster analyses. In other words, it was not taxonomically distinct above a level attributable to individual variation in a relatively homogenous population. Subspecies which are mentioned in Table 1, but are not recognized or synonymized, are taken to be intergrades. Herein, an intergrade is a group of taxonomically indeterminable, phenotypically highly variable populations. A population is taken to be taxonomically indeterminable if many of its component individuals show affinities to two or more subspecies (i.e. are classed as intermediates) in discriminant analyses. A population is taken to be highly variable phenotypically if it has a high total COV. See the section on *Taxonomic methodology* for a detailed discussion of OTUs, discriminant analyses and total COV.

Genus *Agelastes*

Agelastes Bonaparte, 1850

Fig. 8(OG1–2)

Agelastes meleagrides Bonaparte, 1850

Figs 1A, 8(OG1)

Agelastes meleagrides Bonaparte, 1850: 145.

Description

Small overall size; no crown, occipital, cere, nape or throat adornments; rudimentary red gape wattles; no feathers on head or neck, skin colour of head and neck red; collar plumage white; body plumage black with faint vermiculations; tarso-metatarsus covered with imbricated scales in rows, and usually with a well-developed spur(s); iris brown; outer margins of secondaries black with faint vermiculations; furcula blade-shaped; abdominal plumage white.

Statistics for quantitative characters (N = 12)

Character	$\bar{X}$	S.D.
Bill length	16,8 mm	1,7
Wing length	205,0 mm	4,8
Tarso-metatarsus length	80,9 mm	3,6
Wattle basal width	6,5 mm	1,2

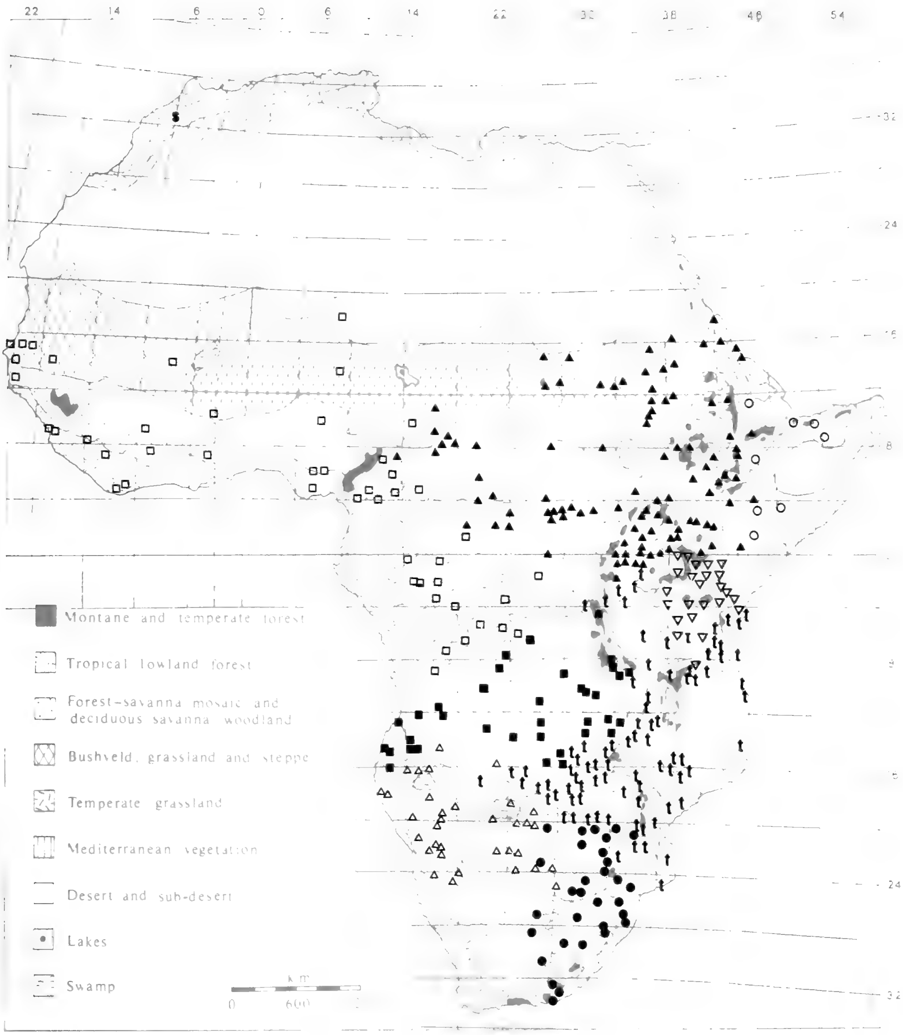

Fig. 46. The distribution of *Numida meleagris*. *N. m. meleagris* (▲). *N. m. sabyi* (**s**). *N. m. galeata* (□). *N. m. somaliensis* (○). *N. m. marungensis* (■). *N. m. reichenowi* (▽). *N. m. mitrata* (*t*). *N. m. damarensis* (△). *N. m. coronata* (●).

Character	X̄	S.D.
Wattle length	2,7 mm	0,7
Tarsal structure number	0,8	0,6
Tarsal structure length	4,8 mm	3,5
White collar	100,0 %	0,0
Facial filoplumes	0,0	0,0

Distribution

See Figure 10.

Discussion

White collar and facial filoplumes are used as quantitative characters in cluster and discriminant analyses to demonstrate the qualitative distinctness of this taxon from *A. niger*.

Agelastes niger (Cassin, 1857)

Figs 1B, 8(OG2)

Phasidus niger Cassin, 1857: 322.

Description

As *A. meleagrides* except: crown surmounted by a short crest of feathers; nape covered by short, sparsely distributed, black downy feathers; face covered with sparsely distributed filoplumes; collar and abdominal plumage black with faint vermiculations, abdominal plumage white in juveniles.

Statistics for quantitative characters (N = 39)

Character	X̄	S.D.
Bill length	16,9 mm	1,5
Wing length	203,0 mm	7,3
Tarso-metatarsus length	79,2 mm	3,4
Wattle basal width	6,5 mm	1,2
Wattle length	2,4 mm	0,6
Tarsal structure number	1,1	0,7
Tarsal structure length	3,4 mm	2,4
White collar	0,0 %	0,0
Facial filoplumes	9,8	0,2

Distribution

See Figure 10.

Discussion

Hall (1961) also advocates the synonomy of *Phasidus* in *Agelastes*, basing her argument largely on analysis of juvenile characters.

Genus *Guttera*

Guttera Wagler, 1832

Fig. 8(OG4–9)

Guttera plumifera plumifera (Cassin, 1857)

Figs 1C, 12A(OTU2), 13(OTU2)

Numida plumifera Cassin, 1857: 321.

Description

Larger than *Agelastes* spp.; crown surmounted by a crest of long, straight, bristly feathers; small occipital fold of blue-black skin; no nape, throat or cere adornments; well-developed, pointed, blue gape wattles; orbital and throat skin blue-black; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris brown; outer margin of secondaries white; furcula blade-shaped; caecum up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters (N = 26)

(See p. 65 for statistical comparisons with *G. p. schubotzi.*)

Character	$\bar{X}$	S.D.
Bill length	24,5 mm	1,7
Wing length	225,6 mm	5,9
Tarso-metatarsus length	81,7 mm	3,1
Wattle basal width	10,7 mm	1,2
Wattle length	11,6 mm	2,2
Dorsal spot size	10,7 units	1,0
Crest frontal length	24,6 mm	3,7
Crest rear length	46,9 mm	5,6
Crest central height	31,8 mm	6,7
Crest basal length	30,0 mm	2,6
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	18,3 %	7,5
Ear patch	0,4 mm	0,6
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	3,7
Total spot barbs	5,4	0,6
Total within spot barbs	3,5	0,6

Character	X̄	S.D.
Spot barb blueness	0,8	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 14.

Guttera plumifera schubotzi Reichenow, 1912

Figs 1D, 12A(OTU1), 13(OTU1)

Guttera plumifera schubotzi Reichenow, 1912: 320.

Description

As *G. p. plumifera*, except that the base of the nape and an area anterior to the ear are covered by patches of orange-yellow skin.

Statistics for quantitative characters (N = 71)

(See p. 65 for statistical comparisons with *G. p. plumifera*)

Character	X̄	S.D.
Bill length	22,8 mm	1,4
Wing length	227,2 mm	8,2
Tarso-metatarsus length	80,7 mm	3,4
Wattle basal width	9,6 mm	1,5
Wattle length	8,9 mm	2,4
Dorsal spot size	10,0 units	1,4
Crest frontal length	24,3 mm	5,9
Crest rear length	38,4 mm	4,8
Crest central height	32,4 mm	6,4
Crest basal length	25,9 mm	2,4
Anterior crest curliness	1,0	0,0
Posterior crest curliness	1,0	0,0
Dorsal black collar	0,0 %	0,0
Ventral black collar	0,0 %	0,0
Occipital fold	24,0 %	8,5
Ear patch	15,1 mm	2,8
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	21,2	2,9
Total spot barbs	5,7	0,6
Total within-spot barbs	3,7	0,5
Spot barb blueness	1,6	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 14.

Discussion

The one intermediate specimen between *G. p. schubotzi* and *G. p. plumifera* is more *schubotzi* in appearance, but the patches of orange on the nape and ear are much reduced in extent.

Guttera pucherani pucherani (Hartlaub, 1860)

Figs 1E, 12A(OTU5), 13(OTU5), Tables 4–5 (OTU5)

Numida pucherani Hartlaub, 1860: 341.

Description

Larger than *G. plumifera*; crown surmounted by a long crest of relatively curly, downy feathers; well-developed occipital fold of blue-black skin; no nape and cere adornments; orbital and throat skin red; throat skin folded; rudimentary, relatively short blue wattles at gape; collar plumage spotted; body plumage spotted without vermiculations; tarso-metatarsus without spurs, scales pentagonal, not in rows; iris red; outer margin of secondaries white; furcula hollow; caecum length up to 150 mm; abdominal plumage spotted bluish-white without vermiculations.

Statistics for quantitative characters (N = 64)

(See Tables 4–5 for statistical comparisons with other subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,5 mm	1,8
Wing length	261,6 mm	14,8
Tarso-metatarsus length	90,2 mm	6,9
Wattle basal width	9,2 mm	1,5
Wattle length	2,7 mm	0,7
Dorsal spot size	11,3 units	1,3
Crest frontal length	19,4 mm	3,9
Crest rear length	29,5 mm	3,7
Crest central height	26,4 mm	6,6
Crest basal length	34,7 mm	3,2
Anterior crest curliness	1,0	0,2
Posterior crest curliness	2,0	0,2
Dorsal black collar	5,3 %	7,5
Ventral black collar	7,4 %	10,4
Occipital fold	74,6 %	19,5
Ear patch	0,0 mm	0,0
Throat red	98,0 %	12,7
Orbital red	95,4 %	2,4

Character	X̄	S.D.
Dorsal spot number	26,0	4,3
Total spot barbs	6,3	1,3
Total within spot barbs	4,3	0,7
Spot barb blueness	1,9	0,9
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Discussion

From breeding experiments with captive birds, Ghigi (1936) demonstrated complete interfertility between individuals ascribed to *G. edouardi* and *G. pucherani*. He also found that red throat and orbital skin, characters used to distinguish *G. pucherani*, were invariably absent among F1 hybrids. This suggests that these character states may be recessive. Ghigi (1936) further hypothesized that *Guttera edouardi suahelica* (Neumann 1908: 14) and *G. e. granti* (Elliot 1871: 584), subspecies described from specimens collected in southern Tanzania, are in fact intergrades between *G. p. pucherani* and *G. p. barbata*. The results of this study support that hypothesis, since *pucherani–barbata* intermediates in discriminant analysis (Fig. 13) almost invariably fit descriptions of these taxa, and the distribution attributed to them falls in the high total COV region between the suggested parental subspecies (Fig. 30B).

Guttera pucherani verreauxi (Elliot, 1870)

Figs 1F, 12A(OTU3), 13(OTU3), Table 4(OTU3)

Numida verreauxi Elliot, 1870: 300.
Guttera cristata sethsmithi Neumann, 1908: 13.
Guttera pallasi Stone, 1912: 208.
Guttera edouardi schoutedeni Chapin, 1923: 73.
Guttera edouardi chapini Frade, 1926: 139.
Guttera edouardi kathleenae White, 1943: 19.

Description

As *G. p. pucherani*, except crest longer; less well-developed occipital fold; orbital skin colour blue; collar plumage black with no vermiculations; spotting with stronger blue hue; iris brown.

Statistics for quantitative characters (N = 159)

(See Table 4 for statistical comparisons with other subspecies.)

Character	X̄	S.D.
Bill length	23,8 mm	1,6
Wing length	249,2 mm	11,2

Character	X̄	S.D.
Tarso-metatarsus length	89,2 mm	4,2
Wattle basal width	9,2 mm	1,2
Wattle length	2,7 mm	0,8
Dorsal spot size	9,5 units	1,5
Crest frontal length	21,1 mm	4,2
Crest rear length	37,4 mm	6,0
Crest central height	26,5 mm	5,8
Crest basal length	31,9 mm	2,6
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,0	0,2
Dorsal black collar	21,1 %	6,6
Ventral black collar	27,5 %	6,8
Occipital fold	47,1 %	18,4
Ear patch	0,0 mm	0,0
Throat red	91,7 %	13,3
Orbital red	0,0 %	0,0
Dorsal spot number	24,1	3,8
Total spot barbs	6,0	0,7
Total within-spot barbs	3,9	0,7
Spot barb blueness	2,3	0,6
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Guttera pucherani sclateri Reichenow, 1898

Figs 1G, 12A(OTU4), 13(OTU4), Table 4(OTU4)

Guttera sclateri Reichenow, 1898*b*: 115.

Description

As *G. p. verreauxi*, except anterior crest much shorter.

Statistics for quantitative characters (N = 12)

(See Table 4 for statistical comparisons with other subspecies.)

Character	X̄	S.D.
Bill length	25,2 mm	2,2
Wing length	245,6 mm	10,4
Tarso-metatarsus length	89,9 mm	4,5
Wattle basal width	10,4 mm	1,2
Wattle length	2,3 mm	0,5
Dorsal spot size	11,5 units	1,5
Crest frontal length	5,8 mm	2,7

Character	X̄	S.D.
Crest rear length	40,8 mm	7,2
Crest central height	18,5 mm	4,2
Crest basal length	32,1 mm	4,1
Anterior crest curliness	1,1	0,3
Posterior crest curliness	2,1	0,3
Dorsal black collar	18,0 %	2,7
Ventral black collar	23,5 %	5,1
Occipital fold	62,5 %	17,6
Ear patch	0,0 mm	0,0
Throat red	95,3 %	6,6
Orbital red	0,0 %	0,0
Dorsal spot number	21,3	2,1
Total spot barbs	6,3	0,8
Total within-spot barbs	4,3	0,8
Spot barb blueness	1,8	0,5
Chestnut blotch size	0,0 units	0,0
Chestnut blotch extent	0,0 %	0,0

Distribution

See Figure 31.

Guttera pucherani barbata Ghigi, 1905

Figs 1H, 12A(OTU6), 13(OTU6), Table 5(OTU6)

Guttera barbata Ghigi, 1905: 194.

Description

As *G. p. pucherani*, except crest longer; throat and orbital skin blue; collar plumage black with no vermiculation; body plumage spots occasionally interspersed with chestnut blotches.

Statistics for quantitative characters (N = 28)

(See Table 5 for statistical comparisons with other subspecies.)

Character	X̄	S.D.
Bill length	25,3 mm	1,3
Wing length	264,7 mm	11,0
Tarso-metatarsus length	90,2 mm	4,5
Wattle basal width	9,4 mm	1,3
Wattle length	2,8 mm	0,8
Dorsal spot size	10,9 units	1,2
Crest frontal length	23,3 mm	3,7
Crest rear length	32,2 mm	3,9
Crest central height	26,9 mm	8,5
Crest basal length	34,6 mm	2,9

Character	X̄	S.D.
Anterior crest curliness	1,1	0,3
Posterior crest curliness	1,9	0,3
Dorsal black collar	21,4 %	4,5
Ventral black collar	26,5 %	5,5
Occipital fold	76,4 %	11,3
Ear patch	0,0 mm	0,0
Throat red	6,9	25,8
Orbital red	0,3	3,9
Dorsal spot number	25,9	4,9
Total spot barbs	5,9	0,7
Total within-spot barbs	4,0	0,5
Spot barb blueness	1,5	0,7
Chestnut blotch size	2,7 units	1,1
Chestnut blotch extent	4,8 %	2,6

Distribution

See Figure 31.

Discussion

Ghigi (1936) mentions *G. p. barbata* specimens with brown irides. This is further evidence of gene flow between the brown-eyed western and red-eyed eastern subspecies of *G. pucherani.*

Guttera pucherani edouardi (Hartlaub, 1867)

Figs 1I, 12A(OTU7), 13(OTU7), Tables 4–5(OTU7)

Numida edouardi Hartlaub, 1867: 36.
Guttera lividicollis Ghigi, 1905: 195.
Guttera edouardi symonsi Roberts, 1917: 3.

Description

As *G. p. barbata,* except crest curlier; occipital fold is of whitish skin; no throat fold; black collar plumage extensively covered with chestnut blotching.

Statistics for quantitative characters (N = 34)

Character	X̄	S.D.
Bill length	25,6 mm	4,9
Wing length	255,8 mm	7,4
Tarso-metatarsus length	86,9 mm	4,8
Wattle basal width	9,9 mm	1,0
Wattle length	2,5 mm	0,6
Dorsal spot size	9,9 units	1,0
Crest frontal length	22,6 mm	4,7
Crest rear length	38,0 mm	4,1

Character	X̄	S.D.
Crest central height	25,9 mm	5,3
Crest basal length	32,8 mm	2,4
Anterior crest curliness	1,5	0,7
Posterior crest curliness	2,1	0,3
Dorsal black collar	27,4 %	4,8
Ventral black collar	32,8 %	4,7
Occipital fold	55,8 %	9,6
Ear patch	0,0 mm	0,0
Throat red	0,0 %	0,0
Orbital red	0,0 %	0,0
Dorsal spot number	23,7	4,2
Total spot barbs	5,2	0,7
Total within-spot barbs	3,5	0,6
Spot barb blueness	0,8	0,5
Chestnut blotch size	10,8 units	3,4
Chestnut blotch extent	54,2 %	19,7

Distribution

See Figure 31.

Genus *Acryllium*

Acryllium Gray, 1840

Fig. 8(OG3)

Acryllium vulturinum (Hardwicke, 1834)

Fig. 1J

Numida vulturina Hardwicke, 1834: 52.

Description

The largest guinea-fowl species; no crown, nape, throat or cere adornments; occiput covered by short, dense, downy chestnut-coloured feathers; rudimentary blue-grey wattles at gape; orbital and throat skin blue-grey; well-developed collar hackle; body plumage spotted with vermiculations; tarso-metatarsus usually with bump(s), scales pentagonal, not in rows; iris red; outer margins of secondaries lavender; furcula blade-shaped; caecum longer than 200 mm; abdominal plumage blue.

Statistics for quantitative characters (N = 43)

Character	X̄	S.D.
Bill length	28,5 mm	2,0
Wing length	293,3 mm	10,1
Tarso-metatarsus length	106,0 mm	6,9
Wattle basal width	7,2 mm	1,1

Character	X̄	S.D.
Wattle length	2,2 mm	0,6
Tarsal structure number	1,8	1,4
Tarsal structure length	2,6 mm	1,9

Distribution

See Figure 10.

Genus *Numida*

Numida Linne, 1766

Fig. 8(OG10–14)

Numida meleagris meleagris (Linne, 1758)

Figs 1K, 12B(OTU4), 32(OTU4), Table 6(OTU4)

Phasianus meleagris Linne, 1758: 158.
Numida ptilorhyncha var. *major* Hartlaub, 1884: 217.
Numida ptilorhyncha omoensis Neumann, 1904: 407.
Numida ptilorhyncha toruensis Neumann, 1904: 410.
Numida ptilorhyncha macroceras Erlanger, 1904: 97.
Numida ptilorhyncha neumanni Erlanger, 1904: 97.
Numida ptilorhyncha var. *inermis* DuBois, 1915: 18, 27.

Description

Larger than *Guttera* spp.; crown surmounted by a bony helmet; no occipital or throat adornments; well-developed, rounded, blue gape wattles; nape covered by short, downy feathers; orbital and throat skin blue; cere surmounted by a tuft of cartilaginous bristles; collar black, finely barred with white; body plumage spotted with vermiculations; tarso-metatarsus lacks spurs, scales pentagonal, not in rows; iris brown; outer margins of secondaries banded black and white with vermiculations; furcula blade-shaped; caecum less than 150 mm; abdominal plumage spotted with faint vermiculations.

Statistics for quantitative characters (N = 311)

(See Table 6 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	25,0 mm	1,7
Wing length	262,2 mm	12,2
Tarso-metatarsus length	84,3 mm	5,2
Wattle basal width	14,1 mm	1,7
Wattle length	13,5 mm	3,0
Wattle per cent blue	97,1 %	12,1
Helmet frontal length	22,6 mm	10,2
Helmet rear length	11,8 mm	7,5
Helmet central height	11,7 mm	8,0

Character	X̄	S.D.
Helmet basal length	19,2 mm	3,0
Helmet thickness	6,4 mm	1,7
Cere structure length	6,0 mm	3,6
Cere structure thickness	1,1 mm	0,4
Collar plumage	2,9	0,6
Nape filoplume length	14,9 mm	2,7
Nape filoplume anteroposterior coverage	58,3 %	17,4
Nape filoplume lateral coverage	95,6 %	15,7
Nape filoplume density	2,9	0,3
Secondary remex outer web vermiculation	5,8	0,7
Wing covert barring	1,5	0,7
Dorsal vermiculation	3,0	0,7
Dorsal spot size	18,8 units	5,7

Distribution

See Figure 46.

Discussion

Two taxa, *N. m. strasseni* (Reichenow, 1911: 82) and *N. m. blancoui* (Grote 1936: 158), have been described from the region in which *N. m. galeata* and *N. m. meleagris* meet. Specimens attributed to these taxa are invariably intermediate between *galeata* and *meleagris* in discriminant analysis, and their collection sites fall in the region of high total COV between the parental forms (Fig. 45A). They are treated as intergrades.

Numida meleagris sabyi Hartert, 1919

Figs 1L, 12B(OTU1), 32(OTU1), Table 7(OTU1)

Numida sabyi Hartert, 1919: 69.

Description

As *N. m. meleagris*, except gape wattles red; nape featheration long filoplumes restricted to the mid-dorsal line; no cere adornment.

Statistics for quantitative characters (N = 4)

(See Table 7 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	24,0 mm	0,8
Wing length	267,3 mm	10,3
Tarso-metatarsus length	88,3 mm	3,1
Wattle basal width	15,5 mm	1,0
Wattle length	17,8 mm	1,7
Wattle per cent blue	0,0 %	0,0

Character	X̄	S.D.
Helmet frontal length	22,5 mm	3,0
Helmet rear length	15,0 mm	6,5
Helmet central height	16,3 mm	2,6
Helmet basal length	20,0 mm	3,4
Helmet thickness	5,3 mm	0,5
Cere structure length	0,0 mm	0,0
Cere structure thickness	0,0 mm	0,0
Collar plumage	2,5	0,6
Nape filoplume length	34,0 mm	7,1
Nape filoplume anteroposterior coverage	100,0 %	0,0
Nape filoplume lateral coverage	85,0 %	17,9
Nape filoplume density	3,0	0,0
Secondary remex outer web vermiculation	3,8	1,5
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,5	0,6
Dorsal spot size	7,2	0,5

Distribution

See Figure 46.

Discussion

Although this taxon is represented by only four specimens, its validity was upheld owing to its isolation and correspondence with criteria set for subspecies.

Numida meleagris galeata Pallas, 1767

Figs 1M, 12B(OTU2), 32(OTU2), Tables 6–7(OTU2)

Numida galeata Pallas, 1767: 13, 15.
Numida marchei Oustalet, 1882: 1.

Description

As *N. m. sabyi*, except smaller with collar plumage grey to blue-grey.

Statistics for quantitative characters (N = 137)

(See Tables 6–7 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	22,3 mm	1,8
Wing length	251,4 mm	14,6
Tarso-metatarsus length	81,8 mm	6,4
Wattle basal width	14,2 mm	1,9
Wattle length	15,5 mm	2,9
Wattle per cent blue	8,3 %	4,3

Character	X̄	S.D.
Helmet frontal length	15,5 mm	5,8
Helmet rear length	7,0 mm	2,5
Helmet central height	5,8 mm	2,9
Helmet basal length	18,6 mm	3,3
Helmet thickness	4,9 mm	1,5
Cere structure length	0,3 mm	0,9
Cere structure thickness	0,3 mm	1,6
Collar plumage	0,1	0,3
Nape filoplume length	20,4 mm	4,3
Nape filoplume anteroposterior coverage	90,9 %	16,0
Nape filoplume lateral coverage	70,8 %	33,3
Nape filoplume density	2,8	0,4
Secondary remex outer web vermiculation	4,4	1,3
Wing covert barring	0,6	0,2
Dorsal vermiculation	3,6	0,6
Dorsal spot size	12,2 units	3,8

Distribution

See Figure 46.

Numida meleagris somaliensis Neumann, 1899

Figs 1N, 12B(OTU5), 32(OTU5), Tables 6, 8(OTU5)

Numida somaliensis Neumann, 1899: 25.

Description

As *N. m. meleagris,* except gape wattles blue with red tips; cere tufts much longer and more numerous; and nape featheration long filoplumes restricted to the middorsal line.

Statistics for quantitative characters (N = 44)

(See Tables 6, 8 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	25,1 mm	1,4
Wing length	265,5 mm	11,0
Tarso-metatarus length	84,2 mm	4,2
Wattle basal width	13,6 mm	2,4
Wattle length	14,6 mm	3,3
Wattle per cent blue	87,5 %	14,9
Helmet frontal length	20,0 mm	7,6
Helmet rear length	10,3 mm	6,0
Helmet central height	12,9 mm	12,3

Character	X̄	S.D.
Helmet basal length	17,4 mm	3,9
Helmet thickness	6,6 mm	1,3
Cere structure length	13,3 mm	7,6
Cere structure thickness	1,0 mm	0,1
Collar plumage	3,0	0,7
Nape filoplume length	15,8 mm	3,1
Nape filoplume anteroposterior coverage	41,5 %	20,7
Nape filoplume lateral coverage	53,3 %	34,0
Nape filoplume density	2,8	0,5
Secondary remex outer web vermiculation	5,2	2,0
Wing covert barring	0,8	0,6
Dorsal vermiculation	2,4	0,9
Dorsal spot size	23,6 units	6,5

Distribution

See Figure 46.

Numida meleagris marungensis Schalow, 1884

Figs 1O, 12B(OTU6), 32(OTU6), Tables 6–7, 9(OTU6)

Numida coronata marungensis Schalow, 1884: 105.
Numida marungensis maxima Neumann, 1898: 21.

Description

The largest subspecies; helmet characteristically thicker and longer basally; long gape wattles, blue with red tips; no cere adornment, and wattles pointed.

Statistics for quantitative characters (N = 97)

(See Tables 6–7, 9 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	26,7 mm	1,4
Wing length	283,5 mm	11,1
Tarso-metatarsus length	90,2 mm	4,7
Wattle basal width	11,8 mm	1,5
Wattle length	16,6 mm	3,1
Wattle per cent blue	73,6 %	8,5
Helmet frontal length	47,7 mm	8,5
Helmet rear length	13,4 mm	5,1
Helmet central height	18,7 mm	3,8
Helmet basal length	39,2 mm	3,7
Helmet thickness	12,4 mm	2,6
Cere structure length	0,3 mm	0,7
Cere structure thickness	0,3 mm	0,9

Character	$\bar{X}$	S.D.
Collar plumage	2,9	0,7
Nape filoplume length	26,3 mm	3,3
Nape filoplume anteroposterior coverage	77,3 %	17,5
Nape filoplume lateral coverage	29,6 %	17,5
Nape filoplume density	2,9	0,4
Secondary remex outer web vermiculation	0,9	1,0
Wing covert barring	0,0	0,0
Dorsal vermiculation	1,5	0,8
Dorsal spot size	23,5 units	4,5

Distribution

See Figure 46.

Discussion

N. m. frommi (Kothe 1911: 13) and *N. m. rikwae* (Reichenow 1900: 40) have been described from the region between *N. m. marungensis* and *N. m. mitrata*, and *N. m. callewaerti* (Chapin 1932*b*: 1) from the region between *N. m. galeata* and *N. m. marungensis*. Specimens attributed to these three forms are invariably intermediate between two subspecies in discriminant analyses, and their collection localities fall within regions of high total COV (Fig. 45A). They are treated as intergrades.

Numida meleagris reichenowi Ogilvie-Grant, 1894

Figs 1P, 12B(OTU8), 32(OTU8), Tables 6, 8(OTU8)

Numida reichenowi Ogilvie-Grant, 1894: 536.

Description

Similar to, and nearly as large as *N. m. marungensis*; except wattles rounded and red, helmet taller and sabre-shaped, and nape featheration less dense.

Statistics for quantitative characters (N = 121)

(See Tables 6, 8 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	24,7 mm	1,6
Wing length	282,2 mm	9,1
Tarso-metatarsus length	90,7 mm	11,4
Wattle basal width	11,9 mm	1,4
Wattle length	12,8 mm	2,5
Wattle per cent blue	12,9 %	29,2
Helmet frontal length	44,2 mm	10,9
Helmet rear length	29,5 mm	9,8
Helmet central height	29,5 mm	9,0

Character	X̄	S.D.
Helmet basal length	24,9 mm	2,9
Helmet thickness	8,3 mm	1,7
Cere structure length	0,7 mm	1,8
Cere structure thickness	0,4 mm	0,8
Collar plumage	2,9	0,5
Nape filoplume length	20,5 mm	3,6
Nape filoplume anteroposterior coverage	63,8 %	49,2
Nape filoplume lateral coverage	30,0 %	21,3
Nape filoplume density	2,5	0,6
Secondary remex outer web vermiculation	2,3	1,3
Wing covert barring	0,2	0,5
Dorsal vermiculation	2,4	0,7
Dorsal spot size	23,2 units	3,5

Distribution

See Figure 46.

Discussion

N. m. intermedia (Neumann 1898: 21), and *N. m. ansorgei* (Hartert 1899: 331) have been described from the transition area between *N. m. meleagris* and *N. m. reichenowi*. *N. m. uhehensis* (Reichenow 1898*a*: 88) has been described from the transition area between *N. m. mitrata* and *N. m. reichenowi*. For reasons given in other such instances, these forms are treated as intergrades.

Numida meleagris mitrata Pallas, 1767

Figs 1Q, 12B(OTU7), 32(OTU7), Tables 6, 8–10(OTU7)

Numida mitrata Pallas, 1767: 18.

Description

Smaller than the last two subspecies; phenotype as *N. m. marungensis* except that helmet less well developed.

Statistics for quantitative characters (N = 293)

(See Tables 6, 8–10 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	25,7 mm	1,3
Wing length	275,4 mm	8,2
Tarso-metatarsus length	86,1 mm	4,2
Wattle basal width	10,9 mm	1,5
Wattle length	16,8 mm	3,0
Wattle per cent blue	64,6 %	9,3

Character	$\bar{X}$	S.D.
Helmet frontal length	38,3 mm	9,5
Helmet rear length	18,8 mm	5,1
Helmet central height	19,4 mm	7,9
Helmet basal length	23,3 mm	3,8
Helmet thickness	8,3 mm	2,0
Cere structure length	0,2 mm	0,8
Cere structure thickness	0,2 mm	0,7
Collar plumage	3,1	0,6
Nape filoplume length	23,0 mm	3,9
Nape filoplume anteroposterior coverage	59,1 %	19,7
Nape filoplume lateral coverage	23,0 %	8,3
Nape filoplume density	2,5	0,7
Secondary remex outer web vermiculation	1,5	1,3
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,2	0,7
Dorsal spot size	19,4 units	4,5

Distribution

See Figure 46.

Numida meleagris coronata Gurney, 1868

Figs 1R, 12B(OTU10), 32(OTU10), Table 10(OTU10)

Numida coronata Gurney, 1868: 253.
Numida transvaalensis Neumann, 1899: 26.
Numida papillosa limpopoensis Roberts, 1924: 77.

Description

As *N. m. marungensis*, except smaller overall size; decidedly thinner and taller helmet, collar plumage more streaked than barred with white.

Statistics for quantitative characters (N = 136)

(See Table 10 for statistical comparisons with neighbouring subspecies.)

Character	$\bar{X}$	S.D.
Bill length	25,1 mm	1,7
Wing length	270,9 mm	7,0
Tarso-metatarsus length	85,6 mm	5,2
Wattle basal width	11,0 mm	1,5
Wattle length	18,7 mm	3,2
Wattle per cent blue	61,5 %	10,0
Helmet frontal length	54,8 mm	9,6
Helmet rear length	25,1 mm	5,8
Helmet central height	24,7 mm	5,3
Helmet basal length	25,8 mm	2,9

Character	X̄	S.D.
Helmet thickness	8,8 mm	2,1
Cere structure length	0,4 mm	0,7
Cere structure thickness	0,3 mm	0,4
Collar plumage	4,2	1,1
Nape filoplume length	18,5 mm	4,6
Nape filoplume anteroposterior coverage	40,0 %	22,8
Nape filoplume lateral coverage	15,3 %	4,9
Nape filoplume density	1,2	0,8
Secondary remex outer web vermiculation	2,5	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,6
Dorsal spot size	20,4 units	5,6

Distribution

See Figure 46.

Discussion

Numida meleagris papillosa (Reichenow 1894: 145) has been described from the region south of Lake Ngami, i.e. the transition area between *N. m. damarensis* and *N. m. coronata*. For reasons given in other instances this form is taken to be an intergrade.

Numida meleagris damarensis Roberts, 1917

Figs 1S, 12B(OTU9), 32(OTU9), Tables 9–11(OTU9)

Numida papillosa damarensis Roberts, 1917: 2.

Description

As *N. m. coronata*, except well-developed papilli at cere; collar spotted; helmet less well developed.

Statistics for quantitative characters (N = 102)

(See Tables 9–11 for statistical comparisons with neighbouring subspecies.)

Character	X̄	S.D.
Bill length	24,6 mm	1,6
Wing length	273,2 mm	7,6
Tarso-metatarsus length	83,4 mm	3,9
Wattle basal width	11,1 mm	1,3
Wattle length	18,9 mm	2,8
Wattle per cent blue	64,4 %	8,5
Helmet frontal length	45,2 mm	7,5
Helmet rear length	22,9 mm	4,6
Helmet central height	22,3 mm	4,3

Character	$\bar{X}$	S.D.
Helmet basal length	19,7 mm	3,1
Helmet thickness	9,2 mm	1,3
Cere structure length	3,7 mm	1,5
Cere structure thickness	2,9 mm	0,3
Collar plumage	4,9	1,0
Nape filoplume length	12,3 mm	8,5
Nape filoplume anteroposterior coverage	24,7 %	27,2
Nape filoplume lateral coverage	9,7 %	8,0
Nape filoplume density	0,5	0,7
Secondary remex outer web vermiculation	3,8	1,4
Wing covert barring	0,0	0,0
Dorsal vermiculation	2,6	0,5
Dorsal spot size	22,5 units	8,5

Distribution

See Figure 46.

PHYLOGENY

PRIMITIVE AND DERIVED CHARACTER STATES

The following hypothetical primitive-derived sequences are postulated for the characters listed in Appendix 1. The number in parentheses following each character name is its number in Appendix 1.

Crown (1), *occipital* (2), *nape* (3), *and throat* (6) *adornments*

All francolins and guineafowl-phasianid hybrids have feathered crowns, occiputs and napes. Very few francolins have crests, and then only rudimentary ones. No francolin has a throat fold. Therefore, a naked crown, nape or occiput is taken to be derived relative to the feathered condition. Among guinea-fowl with feathered crowns, a well-developed crest of downy feathers is taken to be derived relative to a short crest of downy feathers, and a well-developed crest of bristly, erect filoplumes derived relative to a well-developed crest of downy feathers. The latter assumption is based on the idea that a modification of a downy, drooping crest to an erect bristly crest allows species or individual recognition in social encounters. Also, among guinea-fowl which have these regions unfeathered, any likely secondary elaboration of the unfeathered condition (e.g. a helmet, long filoplumes, patches of skin of contrasting colour, folds of skin) is taken to be derived, since these structures may be adaptive in a social (individual and species identification) or physio-ecological (thermoregulation, crypsis) context (Brown 1963; Reynolds 1977). Finally, folded throat skin is taken to be derived relative to the unfolded condition.

Orbital (4), *throat* (5), *and gape wattle* (8) *skin colour*

In nearly all francolins, areas of naked skin on the head and throat are red. Therefore, red is taken to be the primitive condition relative to any other colour for the above characters.

Gape adornment (7)

No francolin has a gape wattle, and guineafowl-phasianid hybrids have at most rudimentary wattles. Therefore, well-developed gape wattles are taken to be derived.

Cere adornment (9)

No francolin or guineafowl-phasianid hybrid has an adornment at the cere. Therefore, any cere adornment is taken to be derived.

Collar (10), *body* (11) *and abdominal* (18) *plumage*

The plumage of francolins and guineafowl-phasianid hybrids is usually dark, often streaked, barred or vermiculated with lighter colours. Moreover, none of the above possesses an elaborate collar-hackle. Therefore, among guinea-fowl, white or blue plumage is taken to be derived relative to dark plumage, and spotted plumage derived relative to barred, streaked or vermiculated plumage. Among guinea-fowl with spotted plumage, spotted plumage without peripheral vermiculation is taken to be derived relative to that with vermiculation. Also, regardless of plumage pattern, an elaborate collar hackle is taken to be derived relative to an undifferentiated collar.

Tarso-metatarsal scales (12) *and adornment* (13)

All francolins have their posterior tarso-metatarsus covered by small imbricated scales in rows. In nearly all francolins, the male at least possesses spurs. Therefore, among guinea-fowl any modification of the spurred condition (e.g. naked tarsi or tarsal bumps), and any scalation pattern other than that described above are taken to be derived conditions.

Iris colour (14)

Nearly all francolins have brown eyes. Therefore, among guinea-fowl, a red iris is taken to be derived.

Outer margins of secondaries (15)

In most francolins the secondaries are brown to grey, sometimes faintly streaked or vermiculated with white. In only a few francolins do the outer margins of these feathers appear to be strikingly different from the general body plumage. Therefore, among guinea-fowl, secondaries that contrast with the general body plumage pattern, i.e. character states 2–4, are taken to be derived.

Furcula (16)

All francolins have blade-shaped furculas. Therefore, a hollow furcula is taken to be derived.

Caecum length (17)

In francolin and guinea-fowl of the genera *Numida* and *Guttera* caecum length is about 16 per cent that of the large and small intestines combined (Beddard 1898). There is no information on caecum length for *Agelastes* spp. In *Acryllium vulturinum*, the length of this organ is more than 23 per cent that of the intestines (Beddard 1898). Therefore, among guinea-fowl a relatively long caecum is taken to be derived.

PHYLETIC ANALYSIS

The most parsimonious guinea-fowl phylogeny based on primitive-derived character sequences is given in Figure 47. In this figure, the four shared derived character states comprising character suite 1 delineate the subfamily Numidinae from francolin-like phasianids. These derived character states, common to all guinea-fowl taxa (Ghigi 1936), and their primitive counterparts (in parentheses) are:

1. large size (small size);
2. third and fourth sacral vertebrae with robust transverse processes (only third vertebra with such a process);
3. second metacarpal lacks a backward process (process present);
4. largely naked head with at least rudimentary wattles (feathered head, and no wattles).

Agelastes sp., with their preponderance of primitive character states, probably more closely resemble the proto-guinea-fowl than does any other member of the subfamily. These two species share only one derived character state, white abdominal plumage. Adult *A. niger* (Fig. 1B) shows primitive character states for all characters investigated except for its naked occiput. The white abdominal plumage linking it to *A. meleagrides* (Fig. 1A) is present only in juvenile birds. It is also possible that the additional derived character states attributable to *Agelastes* due to the naked head and neck of *A. meleagrides* are the result of convergent evolution, and do not suggest any closer affinity to other guinea-fowl genera.

Character suite 2 consists of three shared derived character states (spotted body plumage, non-imbricated, pentagonal scalation of the posterior tarso-metatarsi, unspurred tarso-metatarsi) which link the three remaining genera. Character suite 3 consists of three shared derived character states (unfeathered crown, blue orbital and throat skin) which link *Acryllium* (Fig. 1J) and *Numida* (Fig. 1K–S). Character suite 4 consists of four shared derived character states (folded occipital skin, white outer secondary margins, body plumage spotted without peripheral vermiculation, hollow furcula) which link the two *Guttera* species (Fig. 1C–I), and distinguish them from *Acryllium* and *Numida*. Character suite 5 consists of four derived character states (helmeted crown, naked occiput, well-developed wattles, cere with tufts or papilli) which distinguish *Numida* Fig. 1K–S) from *Acryllium* (Fig. 1J). Character suite 6 consists of three

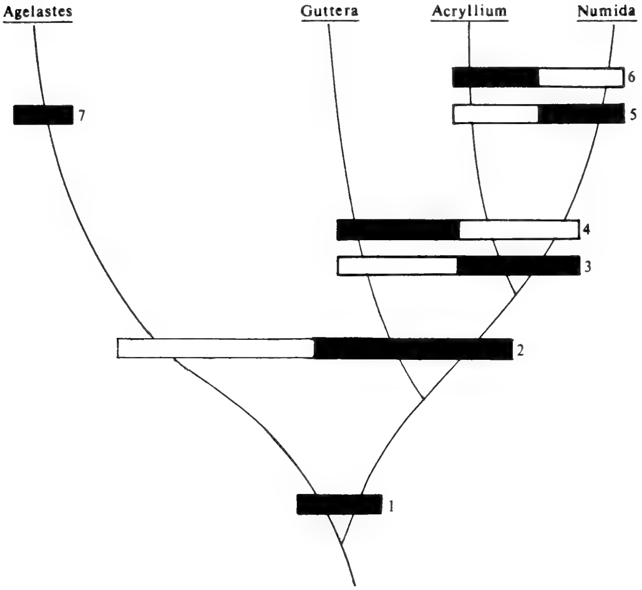

Fig. 47. An hypothetical phylogeny for the Numidinae. Each monophyletic lineage is characterized by a suite of derived character states (■), the primitive counterparts of which (□) are found in members of the co-ordinate sister-group.

derived character states (hackled collar, long caecum, red eye) which distinguish *Acryllium* from *Numida*.

SPECIATION

ORIGIN AND DERIVATION OF THE NUMIDINAE

Several hypotheses have been offered concerning the origin and evolution of the Numidinae. Ghigi (1936) states that the proto-guinea-fowl originated in Africa, and probably was derived from a francolin ancestor. This hypothesis is based on the fact that guinea-fowl are found only in Africa (Arabian and Malagasy populations being probably the result of introductions by man), and phenotypic similarities between the most primitive guinea-fowl (*Agelastes* spp.) and *Francolinus* spp. Cracraft (1973), in support of his hypothesis of a Gondwanaland origin for the Galliformes, suggests a North American origin from New World quails. Olson (1974), suggests a possible Asiatic origin from a pheasant-like bird, based on analysis of a single Eocene fossil femur from Mongolia. This bone is intermediate in shape between femurs of extant pheasants and *Agelastes niger*. However, it is only about 70 per cent the length of an *Agelastes* femur, i.e. well within the size range of many extant francolins (Mackworth-Praed & Grant 1952, 1962, 1970).

There is no compelling evidence favouring any of these three hypotheses. When, and if, sufficient information comes to the fore, it will probably support elements of all three. Accordingly, the working hypothesis taken herein is: the Numidinae are derived from a francolin-like Asiatic phasianid; but evolution and radiation of extant guinea-fowl has occurred solely in Africa.

EVOLUTION OF GENERA

The first opportunity for colonization of Africa by Asiatic faunal elements arose with the mid-Miocene (*c.* 17–18 m.y.B.P.) union of the African and Asian plates (Axelrod & Raven 1978). At this time, forest was much more extensive in Africa than at present, possibly even exceeding limits depicted in Figure 5. However, the colonization corridor connecting these two continents was covered by relatively arid savanna vegetation in the mid-Miocene, and has almost certainly not had more lush vegetation since then (Axelrod & Raven 1978). Thus, any Asiatic ancestral guinea-fowl was probably a bird which lived in savanna habitat, and, upon its arrival in Africa, encountered vast forest, and much less extensive savanna adaptive zones. Since *Agelastes* spp. possess so few derived character states (see above), it is likely that radiation of proto-*Agelastes* into the forest took place soon after colonization.

With the joining of the two continents, the mild climate that favoured widespread forest vegetation throughout the late Cretaceous and early Tertiary began to deteriorate. Africa became progressively more arid; and savannah and desert–steppe biomes expanded, at the expense of forest, throughout the latter Miocene and Pliocene (Axelrod & Raven 1978). Moreover, this period was characterized by widespread uplifting, rifting and tectonic activity adding considerable topographic diversity to the continent, and partitioning its expanding and contracting biomes (Axelrod & Raven 1978). These conditions would have favoured radiation in and into expanding forest-edge, savanna and desert–steppe biotopes; and it is possible that proto-*Guttera*, *Numida*, and *Acryllium* were the result of such Mio-Pliocene radiations.

EVOLUTION OF SPECIES AND SUBSPECIES

After the uniformly arid Pliocene, the relatively rapid wet–dry climatic fluctuations and continuing rifting and mountain building during the Pleistocene provided additional opportunities for radiation in Africa (Moreau 1966; Hamilton 1974; Livingstone 1975; Axelrod & Raven 1978). Expanding forest and wetlands in relatively moist phases would have divided savanna biome into more or less isolated tracts, and restricted desert to relatively small refugia in Somalia, northern and south-western Africa. If wet-phase forest and wetlands were distributed as in Figure 5, *Acryllium vulturinum* (Fig. 10) and sub-Saharan subspecies attributed to *Numida meleagris* herein (Fig. 46) would have had the opportunity to diverge in isolation, since portions of their present-day ranges are encompassed by isolated tracts of savanna and desert–steppe refugia. Also, expanding forest may have favoured a second radiation into relatively widespread lowland forest, culminating in *Guttera plumifera*.

During arid phases, forest-living guinea-fowl, and Moroccan *N. meleagris*, would have been restricted to island-like refugia. If vegetation were distributed as in Figure 6, *N. m. sabyi* (Fig. 46), *Agelastes meleagrides* (Fig. 10), *A. niger* (Fig. 10), *Guttera plumifera plumifera* and *G. p. schubotzi* (Fig. 14) and, to a lesser extent, forest-edge taxa (subspecies attributed to *G. pucherani*) had the opportunity to diverge in allopatry, since portions of their present-day ranges would have had access to refuges of suitable biotope. Thus, we need look no further than the Pleistocene for biogeographic events which could have allowed allopatric evolution of extant guinea-fowl species and subspecies.

BIOGEOGRAPHY

RESULTS

A map of hypothetical African avifaunal zones drawn from evolutionary patterns found in guinea-fowl is given as Figure 48. Zonal boundary lines in this map agree remarkably well with those in Chapin's (1932*a*) faunal map (Fig. 49) based on distribution patterns of 'many species and races of birds', and with species and subspecies boundaries in distribution maps of selected francolin species and subspecies (Figs 50–51). In the hypothetical avifaunal map, subregion boundaries are those of the relatively phenotypically homogeneous (i.e. no subspecies) genera, *Agelastes* and *Acryllium* (Fig. 10). Provincial boundaries coincide closely with those of species, and district boundaries with those of subspecies (Figs 14, 31 and 46). Chapin neither lists the taxa whose ranges form the basis of his map, nor specifies criteria used in distinguishing subregions, provinces and districts. The hypothetical map differs markedly from Chapin's in that it:

1. restricts the forest subregion (commonly labelled ① in Figs 48–49) to an area somewhat larger than Chapin's province no. 1;
2. divides his province no. 4 into eastern and western, rather than northern and southern districts;
3. divides his district 1B into two districts (1A and 1B in Fig. 48).
4. reapportions territory within the commonly labelled province no. 6;
5. divides his district no. 6E into two provinces (7 and 8 in Fig. 48);
6. does not recognize montane provinces.

The only differences between the hypothetical map and the francolin distribution maps are relatively minor shifts in boundary lines, and a still finer subdivision of districts by francolins. Also, district boundaries, which separate guinea-fowl subspecies, often delimit francolin species.

DISCUSSION

It is impossible to resolve differences between the two avifaunal maps in zonal boundaries and hierarchical assessments, since Chapin does not specify the data base and methodology underlying his map. His decision to unite the continuous block of lowland forest with the surrounding forest–savanna mosaic to form subregion ① (Fig. 49) is probably due to the abundance, in

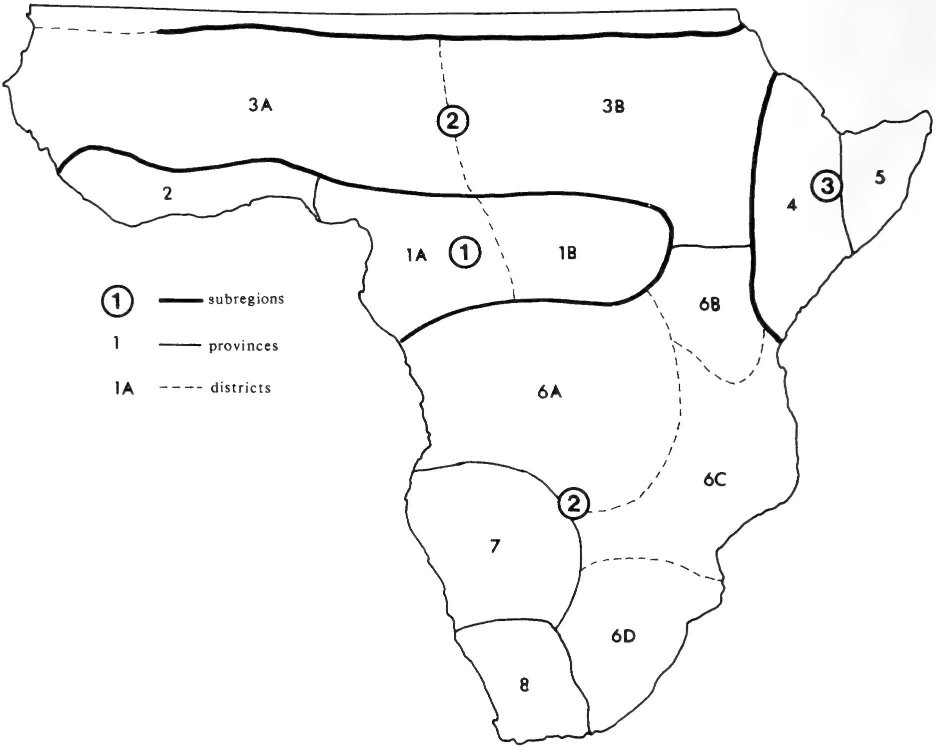

Fig. 48. Hypothetical African avifaunal zones based on evolutionary patterns found in guinea-fowl.

the latter, of relict patches of lowland forest and gallery forests, which provide suitable habitats for forest birds. Indeed, when distributional data are lacking or equivocal, Chapin (1932*a*) and other zoogeographers (e.g. Davis 1962; Moreau 1966) seem to have relied on the distribution of vegetation as a predictor of bird distributions. The division of Chapin's province no. 4 and district 1B into east–west districts in the hypothetical map is due to effects (on guinea-fowl evolution) of probable past forest–wetland and savanna barriers that bisected these zones during the Pleistocene (see Figs 5–6). The reapportionment of territory to districts in the commonly labelled province no. 6 may reflect a lack of clear-cut avian distributional patterns within that province, a possibility already suggested by Benson & Irwin (1966). The necessity of partitioning Chapin's district no. 6E was anticipated by that author (Chapin 1932*a*: 89), and has been done by other authors (Moreau 1952; Davis 1962). The lack of montane avifaunal zones in the hypothetical map is certainly due to the submontane altitudinal limitation of guinea-fowl.

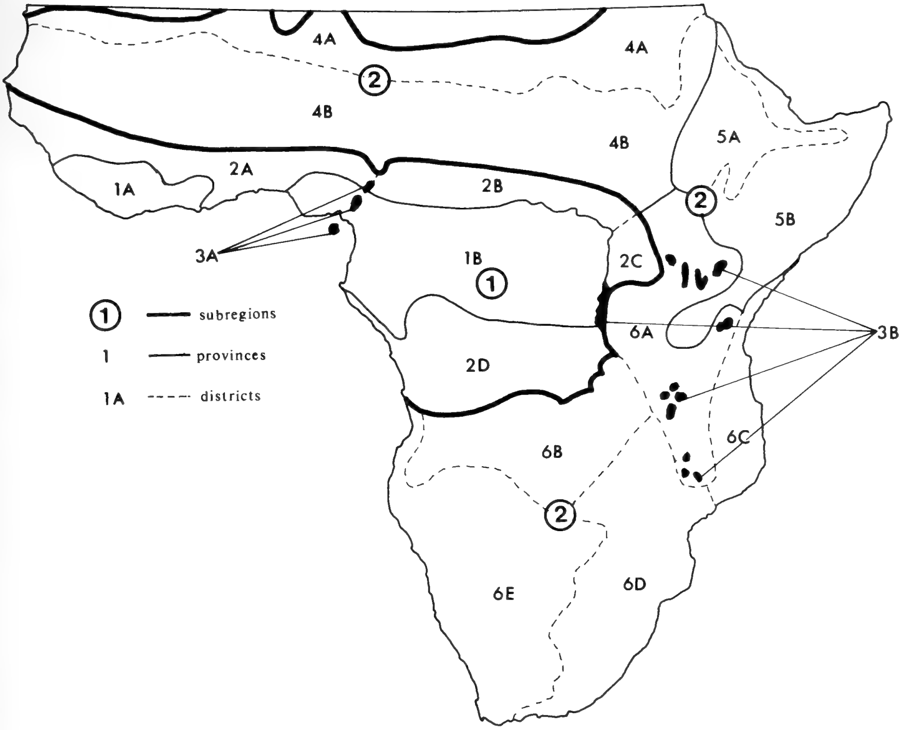

Fig. 49. African avifaunal zones based on analysis of bird species and subspecies distributions (after Chapin 1932*a*).

CONCLUSIONS

The results of comparisons of the hypothetical avifaunal map with Chapin's map and francolin distribution maps suggest three tentative conclusions, which can serve as hypotheses in future evolutionary and biogeographic studies.

1. Distribution patterns found in guinea-fowl can be used as models for broad patterns exhibited by African bird species and subspecies other than those dependent on montane habitats.

2. At least some francolin species and subspecies have evolved as a result of factors that have been important in the evolution of guinea-fowl.

3. Physical and ecological barriers which have allowed only subspeciation in guinea-fowl have been sufficient to bring about speciation in francolins.

The first hypothesis is being tested by a cluster analysis (Hagemier & Stults 1964; Sneath & Sokal 1973) of 119 equally sized areas of Africa according to 1 099 passerine species and well-marked subspecies in Hall & Moreau (1970) (Crowe in prep.). The preliminary results of this study, summarized in Figure 52, are consistent with that hypothesis. The second and third hypotheses can be tested, if patterns of character variation in francolin taxa are analysed using

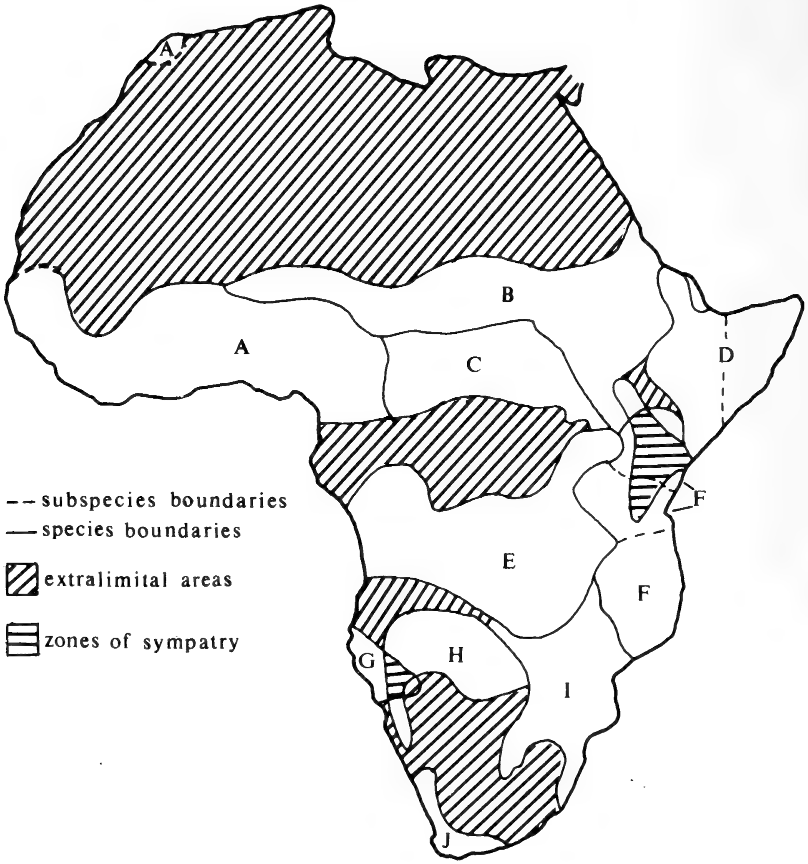

Fig. 50. Distributions of selected non-forest francolin species and subspecies (after Hall 1963 and Mackworth-Praed & Grant 1952). A. *Francolinus bicalcaratus ayesha.* B. *F. clappertoni.* C. *F. icterorhynchus.* D. *F. leucoscepus.* E. *F. afer cranchii, intercedens* and *harterti.* F. *F. hildebrandti.* G. *F. hartlaubi.* H. *F. adspersus.* I. *F. natalensis.* J. *F. capensis.*

methodology outlined herein, and the results are compared to those for guinea-fowl.

SYNTHESIS

Taxonomy, phylogeny, speciation and biogeography are intimately related aspects of guinea-fowl evolution. Their necessary separation under different headings in the present study has been somewhat detrimental to the understanding of each. Accordingly, this section attempts to synthesize the author's conception of evolution in guinea-fowl (summarized in Fig. 53).

Guinea-fowl are characteristically African birds. Although the likely ancestral guinea-fowl was an Asiatic francolin-like phasianid which could live in arid savanna habitat, the evolution that has led to extant guinea-fowl taxa occurred solely in Africa. Moreover, biogeographic patterns derived from

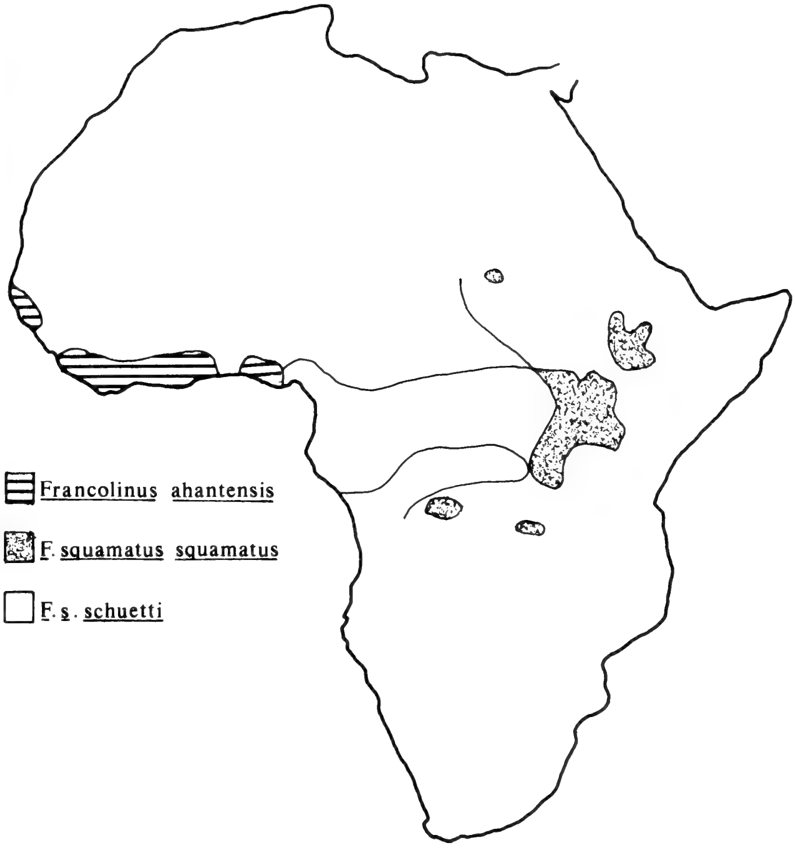

Fig. 51. Distributions of selected forest-living francolin species and subspecies (after Hall 1963).

guinea-fowl species and subspecies boundaries closely parallel broad patterns found in African birds as a whole. The Asiatic ancestral guinea-fowl probably traversed the arid-savanna corridor linking Asia and Africa soon after the mid-Miocene union of the two continents. This savanna-living bird encountered an African continent dominated by forest, possibly unoccupied by potential competitors. Such conditions favoured radiation into the forest, and it is likely that *Agelastes*, the most primitive (i.e. most francolin-like) guinea-fowl genus is a result of an early radiation into forest.

Relatively soon (on a geological time scale) after this successful invasion of forest, the climate of Africa became more arid. Throughout the latter Miocene and Pliocene savanna and desert biomes expanded at the expense of forest. Such a situation favoured radiation in non-forest biomes, and into the expanding forest-edge biotope, and it is possible that proto-*Numida*, *Acryllium* and

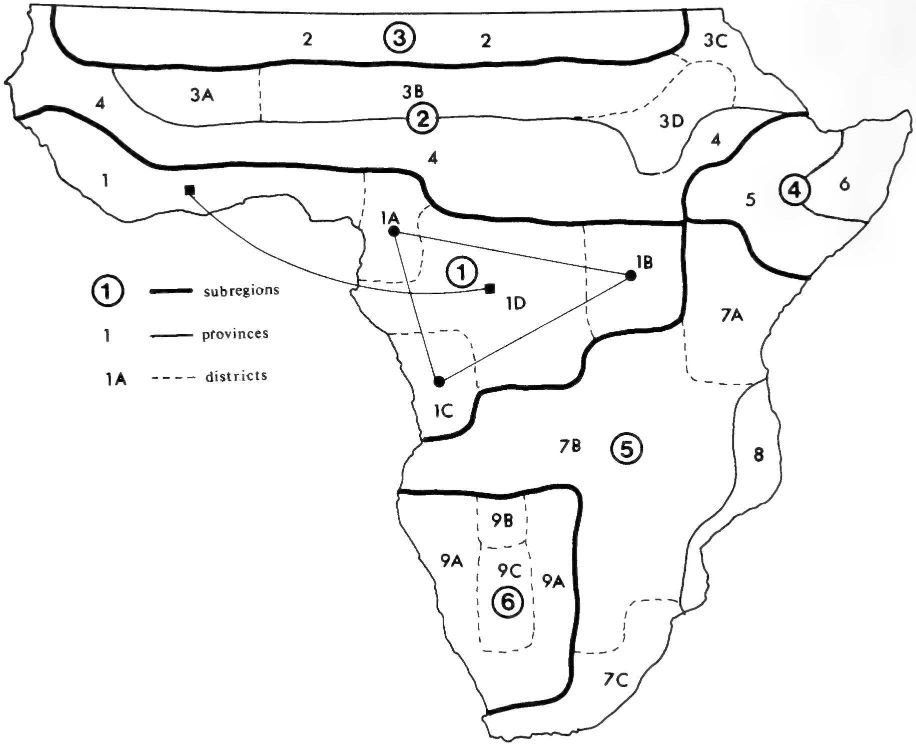

Fig. 52. Hypothetical African avifaunal zones based on a cluster analysis of 119 equally sized blocks of Africa according to 1 099 species and subspecies in Hall & Moreau (1970).

Guttera were the result of such radiations. The relatively uniformly arid conditions of the Pliocene subjected these four lineages to strongly divergent selective pressures, and it is probable that the genera recognized herein were already well defined at the beginning of the Pleistocene.

The arid climate of the Pliocene was replaced by a fluctuating wet–dry climate in the Pleistocene. These climatic fluctuations had profound effects on the distribution of African biomes. During moist phases, the forest biome expanded considerably beyond its present extent, partitioning non-forested biomes into more or less isolated tracts. Desert biome was confined to relatively small areas, and savanna biome bridged the western Sahara, allowing dispersal of *N. meleagris* into north Africa. Sub-saharan subspecies of *N. meleagris* are the result of divergence in these wet-phase isolated tracts. Also, expanded forest during mesic phases could have allowed a second radiation into lowland forest, culminating in *Guttera plumifera.* During arid phases, the forest contracted into island-like refugia, and *N. m. sabyi* was isolated, and presumably diverged from sub-Saharan populations. The species *Agelastes meleagrides* and *A. niger*,

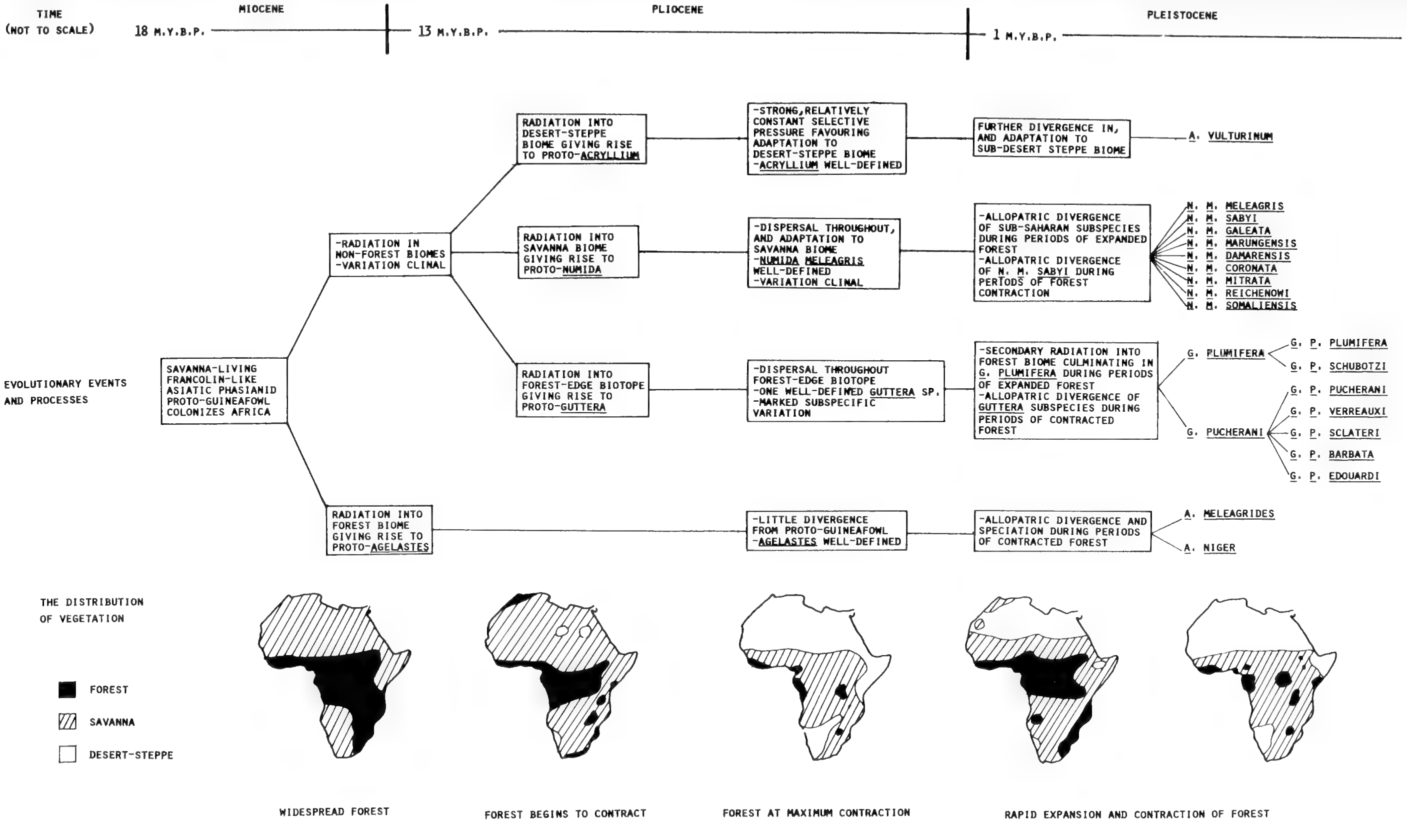

Fig. 53. An hypothetical evolutionary history of guinea-fowl.

and subspecies in the genus *Guttera*, are also a result of divergence in these refugia. The fact that *Guttera* subspecies are much more well marked than are those of *N. meleagris* suggests that isolation in forest refugia has been more effective than in tracts of savanna partitioned during wet phases.

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Appendix 1

Qualitative characters and character states analysed in this study.

No.	*Character name*	*States*
1	Crown adornment	1 — short crest of feathers
		2 — long crest of feathers
		3 — none, only naked skin
		4 — bony helmet
2	Occipital adornment	1 — short, dense, chestnut-coloured downy feathers
		2 — long filoplumes confined to a mid-dorsal line
		3 — fold of blue to black skin
		4 — fold of whitish skin
		5 — none, only naked skin
3	Nape adornment	1 — short downy feathers
		2 — long filoplumes confined to a mid-dorsal line
		3 — patch of orange-yellow skin at base, similar patch anterior to ear
		4 — none, only naked skin
4	Orbital skin colour	1 — pink to red
		2 — light blue to black
5	Throat skin colour	1 — pink to red
		2 — blue to black
6	Throat adornment	1 — no fold of skin
		2 — fold of skin
7	Gape adornment	1 — rudimentary wattles
		2 — well-developed and pointed wattles
		3 — well-developed and rounded wattles
8	Gape wattle colour	1 — pink to red
		2 — blue to blue-grey
		3 — blue with red tips
9	Cere adornment	1 — none
		2 — cartilaginous tufts or papilli
10	Collar plumage	1 — black with faint vermiculations
		2 — black with no vermiculations
		3 — black, finely barred with white
		4 — grey to blue-grey
		5 — spotted
		6 — well-developed hackle
		7 — white
11	Body plumage	1 — black with vermiculations
		2 — spotted with vermiculations
		3 — spotted without vermiculations
		4 — as 3, with chestnut blotching between spots

No.	*Character name*	*States*
12	Tarso-metatarsal scales	1 — imbricated and in a row 2 — pentagonal, not in rows
13	Tarso-metatarsal adornment	1 — spurs or bumps 2 — none
14	Iris colour	1 — brown 2 — red
15	Outer margins of secondaries	1 — brown to black with faint vermiculation 2 — white 3 — lavender 4 — alternating bands of black and white with varying degrees of black and white vermiculations
16	Furcula	1 — blade-shaped 2 — hollow, cup-shaped; found in guineafowl with long crests (Chapin 1932*a*)
17	Caecum length	1 — up to 150 mm 2 — greater than 200 mm; in all specimens conforming to the description of *Acryllium vulturinum* (Beddard 1898)
18	Abdomen plumage	1 — white 2 — blue 3 — white spots with faint vermiculations 4 — bluish-white spots without vermiculations

APPENDIX 2

Quantitative characters analysed in this study. See Figures 1–4 for a pictorial representation of many of the characters.

No.	*Name*	*Units*	*Description*
1	Bill length	mm	the chord measured from the base of the cere to the tip of the maxilla
2	Wing length	mm	the chord of the unflattened folded wing from the farthest anterior tip of the wrist joint to the tip of the longest primary
3	Tarso-metatarsus length	mm	the diagonal chord from the posterior point of articulation of the tarsometatarsus with the tibia to the most distal undivided tarsal scute on the dorsal surface of the middle toe
4	Wattle basal width	mm	the chord from the most anterior to posterior points of juncture of the wattle with the cheek
5	Wattle length	mm	the chord from the juncture line of the wattle to the most distal point along the wattle margin
6	Wattle per cent blue	%	a subjective estimate of the surface area of the wattle covered by blue pigment. It is possible to assess the amount of this colour in preserved material since, although natural colour is lost soon after death, the demarcation between red and blue can be determined because red areas revert to a yellow or translucent amber state, and blue areas to an opaque blue-grey
7	Helmet frontal length	mm	the curvilinear distance, as measured with a flexible tape, along the anterior margin of the bony helmet from the point of juncture with the skull to the apex

No.	*Name*	*Units*	*Description*
8	Helmet rear length	mm	the curvilinear distance along the posterior margin of the helmet from the point of juncture with the skull to the apex
9	Helmet central height	mm	the chord perpendicular to the line of juncture with the skull to the highest point along the margin of the helmet
10	Helmet basal length	mm	the chord from the anterior to posterior juncture points of the helmet with the skull
11	Helmet thickness	mm	the maximum lateral width of the helmet at its base
12	Cere structure length	mm	the chord from the base of the cere to the distal tip of the longest tuft or papilla
13	Cere structure thickness	mm	the maximum thickness of the thickest tuft or papilla
14	Collar plumage	0–6	0 = grey; 1 = blue/violet; 2 = black, barred white with a blue wash; 3 = black, barred white; 4 = black, barred white with faint longitudinal streaking; 5 = black, barred white with some spotting; 6 = spotted
15	Nape filoplume length	mm	the chord from the base to the tip of the longest straightened nape filoplume
16	Nape filoplume antero-posterior coverage	%	the percentage of the nape, at the mid-dorsal line, from the occiput to the upper-most collar feathers, covered by filoplumes
17	Nape filoplume lateral coverage	%	the percentage of the nape covered laterally by nape filoplumes at the mid-point of the anteroposterior coverage
18	Nape filoplume density	0–4	a subjective estimate, based on a comparison with reference specimens encompassing the range of variation, of density of the nape filoplumes on a scale of increasing density. 0 = filoplumes not present, 4 = covered by a mat of filoplumes
19	Secondary remex outer web vermiculation	0–6	0 = absent; 1 = extends $\frac{1}{5}$ way along the white bands; 2 = extends $\frac{2}{5}$ way along the white bands; 3 = extends $\frac{3}{5}$ way along the white bands; 4 = extends $\frac{4}{5}$ way along the white bands; 5 = extends to full length of white bands; 6 = outer edge of white bands obliterated by vermiculation
20	Wing covert barring	0–2	0 = not present; 1 = present but faint; 2 = present
21	Dorsal vermiculation	0–4	a subjective estimate, as with character no. 18, 0 = faint, graded subjectively to 4 = dense
22	Dorsal spot size	units 6 = 1 mm	the maximum width, as measured with a dissecting microscope fitted with an ocular grid, of a particular spot on a randomly selected feather from the mid-dorsal region
23	Crest frontal length	mm	the chord from the base to the tip of the longest straightened crest feather within 5 mm of the cere
24	Crest rear length	mm	the chord from the base to the tip of the longest straightened crest feather within 5 mm of the most posterior extent of the crest

No.	*Name*	*Units*	*Description*
25	Crest central height . .	mm	the chord perpendicular to the line of crest juncture with the skull from the base of the crest feathers to the highest point along the margin of the unstraightened crest
26	Crest basal length . .	mm	the chord from the anterior to posterior juncture points of the crest with the skull
27	Anterior crest curliness .	1–3	a subjective estimate as with character no. 18. 1 = straight; 2 = moderately curly; 3 = very curly
28	Posterior crest curliness .	1–3	as with character no. 27
29	Dorsal black collar . .	%	the percentage of black plumage extending from the most anterior dorsal aspect of the collar to the base of the tail
30	Ventral black collar . .	%	as with character no. 29 but the ventral surface
31	Occipital fold . . .	%	a subjective estimate of the lateral extent of the occiput covered by a fleshy fold
32	Ear patch	mm	the maximum width of any patch of non-blue/black skin anterior to the ear
33	Throat red	%	a subjective estimate of the anteroposterior extent of red pigmented skin between the throat and the ventral base of the neck. As with character no. 6, this character may be assessed since the red colour reverts to a yellow state after preservation.
34	Orbital red	%	a subjective assessment of the amount of red pigmented skin around the eye
35	Dorsal spot number . .	count	the maximum number of spots falling within a circle of 1 cm radius superimposed over the dorsal feather discussed in character no. 22
36	Total spot barbs . . .	count	the number of non-black barbs associated with the spot measured in character no. 22
37	Total within spot barbs .	count	the number of barbs encompassed by the spot measured in character no. 22
38	Spot barb blueness . .	0–3	a subjective assessment of the amount of blue in the spot. 0 = white; 1 = faint blue; 2 = medium blue; 3 = darkest blue
39	Chestnut blotch size . .	units 6 = 1 mm	the maximum width of any chestnut blotch, as measured with a dissecting microscope fitted with an ocular grid, found on the feather examined for character no. 22
40	Chestnut blotch extent .	%	the extent of the spotted area of the feather examined for character no. 22 covered by chestnut blotching
41	Tarsal structure number .	count	the number of spurs or bumps on the tarsus
42	Tarsal structure length .	mm	the chord measured from the juncture line of the longest tarsal bump or spur with the tarso-metatarsus to the apex of the structure
43	White collar . . .	%	the percentage of white plumage in the collar
44	Facial filoplumes . .	0–10	a subjective estimate of the extent of the head, other than the occiput, nape and crown, covered by filoplumes

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

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

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

T. M. CROWE

THE EVOLUTION OF GUINEA-FOWL (GALLIFORMES, PHASIANIDAE, NUMIDINAE) TAXONOMY, PHYLOGENY, SPECIATION AND BIOGEOGRAPHY

VOLUME 76 PART 3 AUGUST 1978 ISSN 0303-2515

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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

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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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SOUTHERN AFRICAN CUMACEA

PART 3

FAMILIES LAMPROPIDAE AND CERATOCUMATIDAE

By

JENNIFER DAY

Cape Town Kaapstad

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SOUTHERN AFRICAN CUMACEA
PART 3
FAMILIES LAMPROPIDAE AND CERATOCUMATIDAE

By

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Zoology Department, University of Cape Town

(With 16 figures and 1 table)

[*MS. accepted 20 June 1978*]

ABSTRACT

The Lampropidae in southern Africa are represented by eleven species in five genera. Seven species are new: *Platysympus camelus, P. depressus, P. compressus, P. phylloides, Paralamprops margidens, Hemilamprops glabrus* and *Hemilamprops* sp. *Hemilamprops pellucidus* and *Bathylamprops calmani* are redescribed and new figures are given. Adult males of *Paralamprops* (formerly *Platytyphlops*) *peringueyi* and *Stenotyphlops spinulosus* are described and figured for the first time. The generic diagnosis of *Paralamprops* is altered to accommodate information obtained from adult males of *P. peringueyi*, while the genus *Platytyphlops* is invalidated.

Keys are given to the genera of the Lampropidae, the southern African members of the family, the world species of *Paralamprops*, *Platysympus*, *Bathylamprops*, and *Ceratocuma*, and to the species of *Hemilamprops* from the southern hemisphere.

The general distribution of lampropids is discussed and a more detailed account given of the southern African representatives. It is concluded that lampropids are bipolar in distribution, preferring deep and/or cold waters and avoiding the tropics. No member of the family is found at depths of less than 188 m in these waters.

The only southern African member of the Ceratocumatidae, *Ceratocuma horridum*, is redescribed and refigured and is considered to belong to a local subspecies, *C. horridum australe*, which is polymorphic. The ceratocumatids are too poorly known to generalize effectively about their distribution, but they all appear to be deep-water, essentially Atlantic forms. None has been found at depths of less than 196 m or further from the Atlantic than the south-east coast of South Africa and Kerguelen.

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Ann. S. Afr. Mus. **76** (3), 1978: 137–189, 16 figs, 1 table.

INTRODUCTION

This is the third in a series of papers on the Cumacea (Crustacea) of southern Africa. The first two deal with the family Bodotriidae (subfamily Vaunthompsoniinae (Day 1975), subfamily Bodotriinae (Day 1978)). The reader is referred to the first of these for a discussion of the morphology and terminology of the group as a whole.

Since the Lampropidae are essentially cold-loving forms, the only species occurring in these waters are found at depths greater than 188 m where temperatures are uniform and generally low (less than 12°C in these latitudes). Only four species have previously been described from the southern African region: *Hemilamprops pellucidus* Zimmer, 1908, *Platytyphlops peringueyi* Stebbing, 1912, and *Stenotyphlops spinulosus* Stebbing, 1912, from southern Africa and *Bathylamprops natalensis* Jones, 1969, from the South-western Indian Ocean. The other species previously known from the African continent is *Bathylamprops calmani* Zimmer, 1908, from deep waters off equatorial east Africa. A further six species are described here, bringing the total number of named species for southern Africa to ten. There is a further species (probably of *Hemilamprops*), but all the individuals are too badly damaged to allow adequate description.

The Ceratocumatidae, a family known until recently (Jones 1969) from a single species, appear to occur only in waters deeper than 196 m. One of the two findings of the type species, *Ceratocuma horridum* Calman, 1904, was recorded by Stebbing (1912) from Natal. Further individuals are now available but they are morphologically variable and until more material is forthcoming it will not be possible to say with certainty whether all individuals belong to Calman's species.

MATERIAL AND STATION DATA

The vast bulk of the material available to the author was provided by the South African Museum (SAM). Part of it was obtained by the S.S. *Pieter Faure* in 1898–1907 from deep waters round the coast of South Africa, and the remainder was collected aboard the R.V. *Meiring Naude* in 1976–1977 during a survey conducted by the Museum in deep waters off the east coast of South Africa. A few of the samples come from the deepest stations of transects conducted by the Zoology Department of the University of Cape Town (UCT) aboard the University's Research Vessel, the R.V. *Thomas B. Davie*, off Still Bay and Lambert's Bay.

Depth records for some of the *Pieter Faure* stations are approximate and have been estimated from charts. Newly available information on depths off the Cape Peninsula shows that the depth for SAM–A10602 is about 800 m, rather than 400 m as previously estimated.

Figure 1 shows the positions at which lampropids and ceratocumatids were found. The code letters used are as follows:

South African Museum	SAM:	*Pieter Faure* samples
	SM:	*Meiring Naude* samples
Zoology Department, University of Cape Town	LBT:	transect at Lambert's Bay, 200 km north of Cape Town
	SST:	transect at Still Bay, 270 km east of Cape Town
	WCD:	benthic survey off the western Cape Province

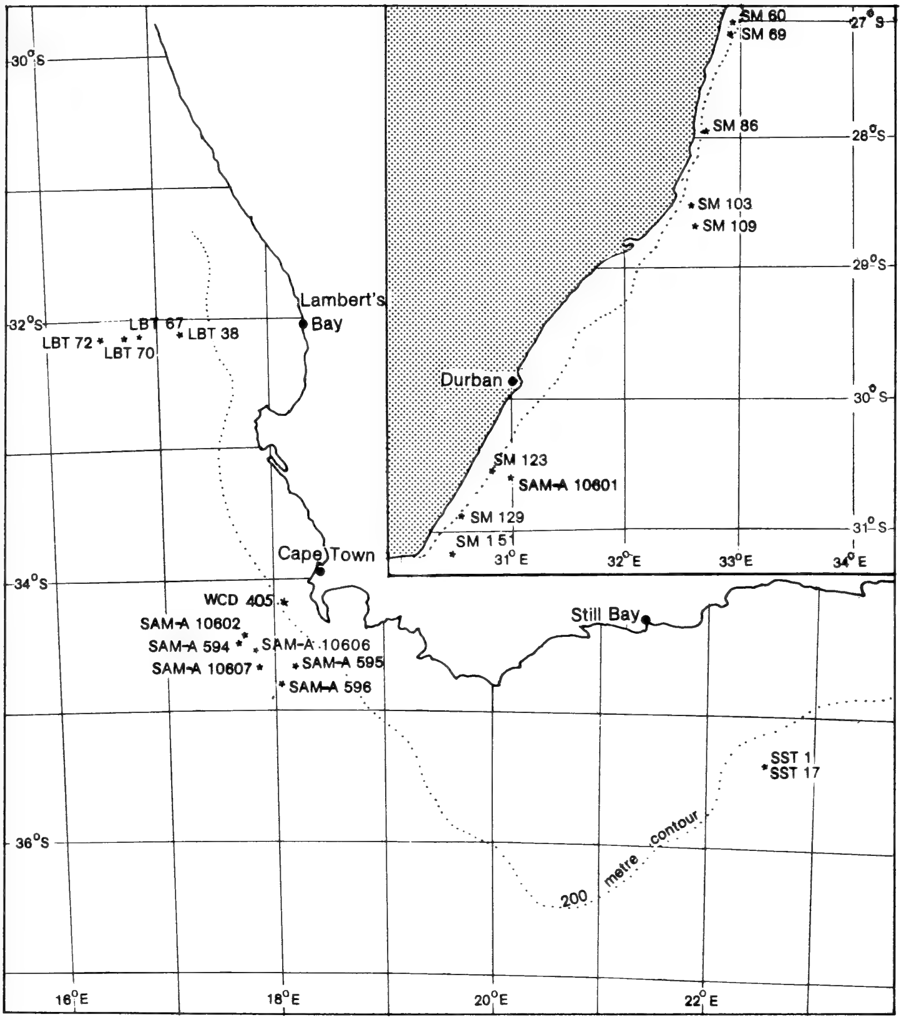

Fig. 1. Coastline of the Cape Province showing positions of stations at which lampropids and ceratocumatids were collected. Inset: coastline of Natal.
Dotted line indicates 200 m depth contour. See text for explanation of code letters.

METHODS

Collections: a variety of gear was used for sampling: dredges in the *Pieter Faure* and *Meiring Naude* programmes, and Van Veen grabs and Cape Town dredges in the *Thomas B. Davie* programmes.

Length measurements were made from the anterior tip of the carapace to the posterior tip of the telson. Exhalant siphons and uropods were excluded in every case.

KEY TO THE SOUTHERN AFRICAN LAMPROPIDAE AND CERATOCUMATIDAE

It should be noted that this key is designed to assist in the identification even of damaged animals and those of varying ages in which the sex may be difficult to determine. For this reason it should always be used in conjunction with the generic keys for final identification.

1 Telson small, semicircular, lacking apical spines (may be deflected over anal valves) (Fig. 15B); carapace sculptured into numerous rounded (Fig. 15A) or digitiform (Fig. 16A) processes .... *Ceratocuma horridum australe* (Figs 15 & 16)

– Telson large, elongate, with at least three apical spines (Fig. 2I); sculpturing variable but not as above 2

2 Carapace rounded, more or less circular in cross-section, totally devoid of marginal or lateral carinae or longitudinal ridges on posterior half at least (Fig. 11A)............. 3

– Carapace dorsoventrally flattened anteriorly at least, marginal or lateral carinae or longitudinal ridges present on most or all of carapace (Figs. 2A, 4A).................... 6

3 Carapace with irregular transverse rows of minute denticles; pseudorostrum almost one-fifth total length of carapace..................... *Bathylamprops calmani* (Fig. 10)

– Carapace without transverse rows of denticles; pseudorostrum distinctly less than one-fifth total length of carapace (Fig. 11A) 4

4 Pseudorostrum truncate anteriorly with short, poorly defined ventrolateral carinae; telson with five spines apically and none laterally............. *Hemilamprops glabrus* (Fig. 13)

– Pseudorostrum pointed anteriorly, without lateral carinae (Fig. 11A); telson with three apical and at least five pairs of lateral spines 5

5 Anterolateral corner of carapace with several long, slender spines; telson less than half length of peduncle of uropod............................. *Hemilamprops* sp. (Fig. 14)

– Anterolateral corner of carapace smooth or minutely denticulate; telson at least two-thirds length of peduncle of uropod................. *Hemilamprops pellucidus* (Figs 11 & 12)

6 Carapace extraordinarily flat and leaf-like, almost as wide as abdomen is long......... *Platysympus phylloides* (Fig. 6)

– Carapace rounded or flattened but not leaf-like, not nearly as wide as abdomen is long (Fig. 8A) 7

7 Carapace and body with a number of longitudinal ridges formed by rows of small denticles; carapace almost rectangular in dorsal outline; fifth pereiopod reduced to two segments *Stenotyphlops spinulosus* (Figs 2 & 3)

– Carapace with a single sharp marginal carina; square or oval in dorsal outline; fifth pereiopod consisting of at least four segments.. 8

8 Abdomen twice as long as cephalothorax; carapace almost square in dorsal view........ *Paralamprops peringueyi* (Fig. 4)

– Abdomen subequal in length to cephalothorax; carapace oval in dorsal view (Fig. 7B).... 9

9 Marginal carina of carapace strongly dentate; exopod present on pereiopod 2 of female *Paralamprops margidens* (Fig. 5)

– Marginal carina of carapace not dentate (Fig. 6A, C); exopod absent from pereiopod 2 of female 10

10 Carapace smoothly oval or with a few small, rounded projections; not laterally compressed dorsal to marginal carina; middorsal carina hardly evident........................ *Platysympus depressus* (Fig. 7)

– Carapace smooth, laterally compressed dorsal to marginal carina (Fig. 8A); middorsal carina evident (Fig. 8B)..11

11 Dorsal edge of carapace smoothly arched; pseudorostrum pointed anteriorly in lateral view *Platysympus compressus* (Fig. 8)

– Dorsal edge of carapace sinusoidal; pseudorostrum dorsoventrally truncate anteriorly in lateral view.. *Platysympus camelus* (Fig. 9)

Family **Lampropidae** Sars, 1878

Diagnosis

Antenna 1 with flagellum well developed. Antenna 2 of male with short segments, of female with at least three segments. Mandibles of normal (boat) shape. Palp of maxilla 1 absent or bearing one or two filaments. Exopods present on maxilliped 3 and pereiopod 1 in both sexes and on pereiopods 2 to 4 in male. Exopods present on pereiopod 2 and rudimentary on pereiopods 3 and 4, or absent from all three, in female. Pleopods in male 0 to 3 pairs, with an outer process to the inner ramus. Telson moderate to large, well developed post-anally, with three to five apical spines.

Type genus

Lamprops Sars, 1863.

Remarks

The presence of a well-developed telson with at least three apical spines together with the well-developed first antenna is characteristic of the family.

Earlier workers tended to distinguish a greater number of families than are now accepted. The families Chalarostylidae, Paralampropidae, Platysympodidae, Pseudodiastylidae and Lampropidae of Stebbing (1913) are now all included in the larger family Lampropidae.

The family is well defined and consists at present of ten genera, five of which are represented in the present collection. One of these (*Stenotyphlops* Stebbing, 1912) is known only from southern Africa.

A problematic feature of the taxonomy of the family is the fact that, being deep-water forms for the most part, relatively few species are known and many of these are represented by only one sex. Since the major distinction between some genera (notably *Lamprops*, *Mesolamprops* and *Hemilamprops*) is the number of pairs of pleopods present in adult males (zero, two and three pairs respectively), females and juveniles cannot always be placed in a genus with any certainty. This in turn makes it difficult to construct a useful key to the genera. In the key below, an attempt has been made to use characters other than those found only in adult males, but these are not very clear-cut. The geographic distribution of the species of *Lamprops*, however, shows that it is essentially a shallow-water genus confined to high latitudes of the Northern hemisphere. The distribution of *Hemilamprops*, on the other hand, is much wider and its species tend to occur in deeper waters. Thus there is little doubt that the species from deep water in the Southern hemisphere for which only females are known—*H. lotusae* Băcescu, 1969, *H. ultimaespei* Zimmer, 1921, *H. glabra* sp. nov. and *Hemilamprops* sp.—are, indeed, members of the genus *Hemilamprops*. The single specimen of *Lamprops? comata* Zimmer, 1907, from Tierra del Fuego is a fragmentary female, so that its systematic position must remain indeterminate for the present.

The presence in the collection of adult males of both *Stenotyphlops* and *Platytyphlops* with three pairs of pleopods throws some light on the relationship between these genera and closely allied ones. Details of the findings are presented in the discussion of *Paralamprops* on page 147.

The genera of the family as a whole are morphologically unremarkable for the most part, but for the fact that in several cases the carapace is very strongly flattened dorsoventrally, with a single, sharp lateral carina encircling the entire carapace apart from the posterior edge (and here called a *marginal carina* to distinguish it from the more usual lateral carinae found widely in several families). The reason for this adaptation is not clear, but since all the species exhibiting this character are deep-water forms, it may have evolved as a means of increasing the surface area to prevent sinking into the oozy mud of the seafloor.

A singular genus, described by Băcescu (1972), is *Archaeocuma*. It is monotypic and known only from the Peruvian Trench. It is distinguished by the presence in both sexes of a single pair of pleopods. In all other characters it is typically lampropid.

KEY TO THE GENERA OF LAMPROPIDAE

All males have three pairs of pleopods unless otherwise stated.

1 Antenna 1 with third segment no longer than second and accessory flagellum minute; telson and peduncle of uropods more than four times length of telsonic somite .... *Pseudodiastylis* Calman, 1905

– Antenna 1 with third segment no longer than second and accessory flagellum well developed *or* with third segment elongate and accessory flagellum very small; telson and peduncle of uropod no more than four times length of telsonic somite..........................2

2 Telson small, subequal in length to telsonic somite and a third length of peduncle of uropod (female unknown).......................................*Chalarostylis* Norman, 1879

– Telson distinctly longer than telsonic and at least half length of peduncle of uropod......3

3 Pereiopod 5 reduced to a minute, 2-segmented projection; a single filament on palp of maxilla 1..*Stenotyphlops* Stebbing, 1912

– Pereiopod 5 normal, or if reduced, at least 4-segmented; palp of maxilla 1 absent or with two filaments...4

4 Basis of pereiopod 4 longer than entire length of pereiopod 5.........................5

– Basis of periopod 4 subequal to, or shorter than, entire length of pereiopod 5...........6

5 Basis of maxilliped 3 much shorter than remaining segments together; male and female both with one pair of pleopods..........................*Archaeocuma* Băcescu, 1972

– Basis of maxilliped 3 not shorter than remaining segments together; male with three pairs of pleopods and female with none...........................*Paralamprops* Sars, 1887

6 Maxilla 1 lacking palp; exopods absent from pereiopods 2–4 in female; carapace with strong marginal carina..................................*Platysympus* Stebbing, 1912

– Palp of maxilla 1 with two filaments; exopods normal on pereiopod 2 and rudimentary on pereiopods 3 and 4 in female; number of pairs of pleopods in male 0, 2 or 3; carapace without marginal carina 7

7 Pseudorostrum at least a fifth of total length of carapace; third segment of antenna 1 longer and considerably more slender than second .... *Bathylamprops* Zimmer, 1908

– Pseudorostrum distinctly less than a fifth total length of carapace; third segment of antenna 1 not much longer or much more slender than second 8

8 Male without pleopods; antennal notch small but distinct; eye present; basis of pereiopod 1 approximately equal in length to rest of limb .... *Lamprops* Sars, 1863

– Male with two pairs of pleopods; antennal notch present or absent; eye present or absent; basis of pereiopod 1 shorter than rest of limb .... *Mesolamprops* Given, 1964

– Male with three pairs of pleopods; antennal notch usually absent; eye present or absent; basis of pereiopod 1 distinctly shorter than rest of limb .... *Hemilamprops* Sars, 1883

Stenotyphlops Stebbing, 1912

Generic diagnosis

Carapace not strongly flattened. Eye absent. Both flagella of antenna 1 well developed. Palp of maxilla 1 with one filament. Exopods of pereiopods 3 and 4 of female rudimentary. Pereiopod 5 reduced to a minute, 2-segmented projection. Male with three pairs of pleopods.

Type species

S. spinulosus Stebbing, 1912 (by monotypy).

Remarks

The genus is monotypic and the single species is known only from southern Africa. The combined presence of a single filament on the palp of maxilla 1 and the greatly reduced fifth pereiopod is diagnostic. The adult male described below is the first known for the genus. The presence of three pairs of pleopods confirms *Stenotyphlops* as typically lampropid, while the extreme reduction of the fifth pereiopod and the nature of maxilla 1 clearly separate it from the other genera in the family. In general morphology it is otherwise very close to *Paralamprops*.

Distribution of Stenotyphlops

Deep water off southern Africa.

Stenotyphlops spinulosus Stebbing, 1912

Figs 2–3

S. spinulosus Stebbing, 1912: 162–163, pl. 60.

Records

SAM–A10602 (PF 17440)	34°25′S 17°45′E	800 m	1 ♂: 10,5 mm; 3 ♀♀: 11,2 mm and damaged; 4 juvs
SAM–A10607 (PF 16982)	34°40′S 17°50′E	1 200 m	1 adult ♂: 13,8 mm; 1 damaged adult ♀
SM 60	27°09′S 32°58′E	800 m	1 damaged ♂
SM 103	28°32′S 32°34′E	680 m	1 damaged ♂; 1 ovig. ♀: 12,5 mm
SM 123	30°33′S 30°48′E	690 m	2 ♀♀: 7,0 mm and damaged
SM 129	30°53′S 30°32′E	850 m	1 ♂: 9,6 mm; 1 ♀: 9,9 mm

Previous records

Holotype only.

Holotype

Adult female, deposited by Stebbing in the British Museum (Natural History). Type locality: approximately 370–550 m, off the Cape Peninsula (34°25′S 17°50′E).

Description

Ovigerous female, length 12,5 mm (SM 103). Integument slightly translucent, armed with very small denticles. Carapace (Fig. 2A) slightly flattened anteriorly and inflated posteriorly with three longitudinal rows of denticles on either side and two on the anterior sinus. Middorsal carina evident anteriorly

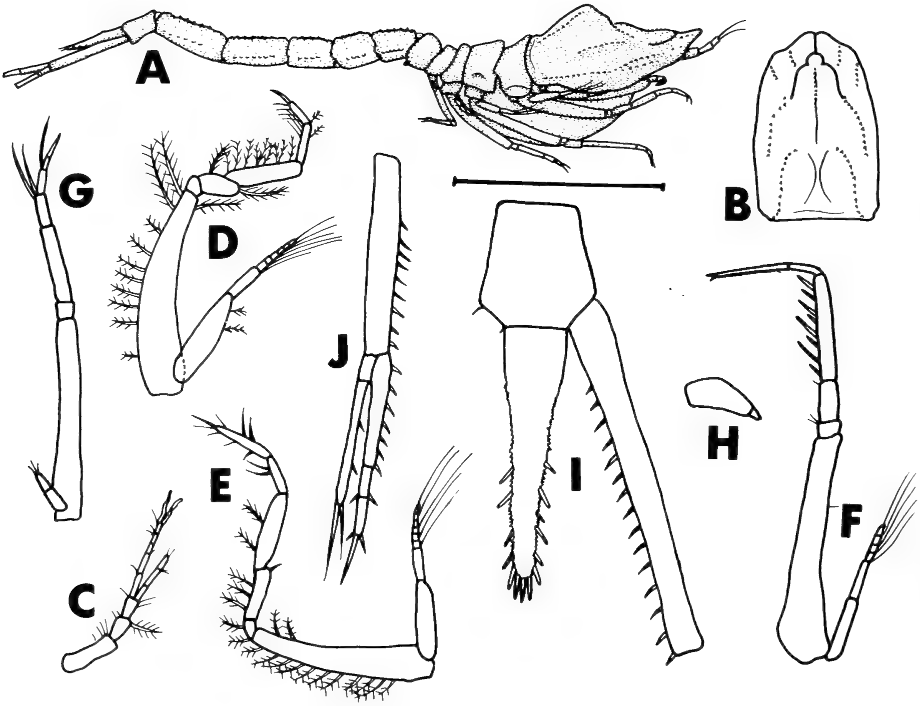

Fig. 2. *Stenotyphlops spinulosus*

Ovigerous female. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Maxilliped 3. E. Pereiopod 1. F. Pereiopod 2. G. Pereiopod 3. H. Pereiopod 5. I. Telson and peduncle of uropod.

Young female. J. Uropod.

Scale line = 4 mm for A–B; 2 mm for C–G; 1 mm for I–J; 0,5 mm for H.

(Fig. 2B) behind eyelobe, minutely denticulate. Eyelobe eyeless. Carapace inflated posterodorsally on either side of middorsal depression. First three thoracic somites flanged laterally. Abdominal somites cylindrical. Cephalothorax and abdomen subequal in length.

Antenna 1 (Fig. 2C) of moderate size; first segment subequal in length to next two together. Both flagella well developed.

Palp of maxilla 1 with a single filament.

Maxilliped 3 (Fig. 2D) fairly stout, basis subequal in length to rest of limb. Carpus long and parallel-sided, propodus and dactyl slender.

Pereiopod 1 (Fig. 2E) not elongate, basis subequal in length to next four segments together. Ischium small, merus and carpus elongate. Propodus and dactyl cylindrical.

Pereiopod 2 (Fig. 2F) elongate. Basis subcylindrical, carpus long and stout, armed with a row of spines on inner edge. Exopod small and slender.

Pereiopods 3 (Fig. 2G) and 4 similar. Basis subequal in length to rest of limb, merus longest of remaining segments. Dactyl minute. Exopod very small, 2-segmented.

Pereiopod 5 (Fig. 2H) reduced to a minute, 2-segmented stump.

Telson (Fig. 2I) distinctly wider proximally than distally, about three-quarters of length of peduncle or uropod, distally armed with five to six pairs of spines laterally and three single spines terminally. Rami of uropod damaged in adult female. Peduncle of uropod of young female (Fig. 2J) subequal in length to endopod. First segment of exopod much shorter than second. First segment of endopod nearly twice length of second and third together. Endopod longer than exopod by one segment.

Adult male, length 13,8 mm (SAM–A10607). As female, except as follows: carapace (Fig. 3A) less flattened anteriorly and less inflated posteriorly. Ridges on carapace more distinct, not always denticulate. Lateral flanges of thoracic somites scalloped (Fig. 3B).

First segment of flagellum of antenna 1 (Fig. 3C) bearing numerous short aesthetascs. Antenna 2 reaching about half way along length of body. Palp of maxilla 1 (Fig. 3D) illustrated. Segments distal to basis of maxilliped 3 and pereiopod 1 missing. Exopod of pereiopod 2 larger. Pereiopod 3 (Fig. 3E) stouter, dactyl minute and apparently continuous with small terminal spine. Pereiopod 5 (Fig. 3G) longer, but still 2-segmented. Three pairs of normal pleopods present.

Telson (Fig. 3F) shorter, about half length of peduncle of uropod. Armature of peduncle and proximal part of endopod of uropod more extensive. Distal portions missing.

Remarks

No adult males have previously been described. The differences between the female described here and Stebbing's holotype are slight, and the differences between adult male and adult female are within the limits expected between

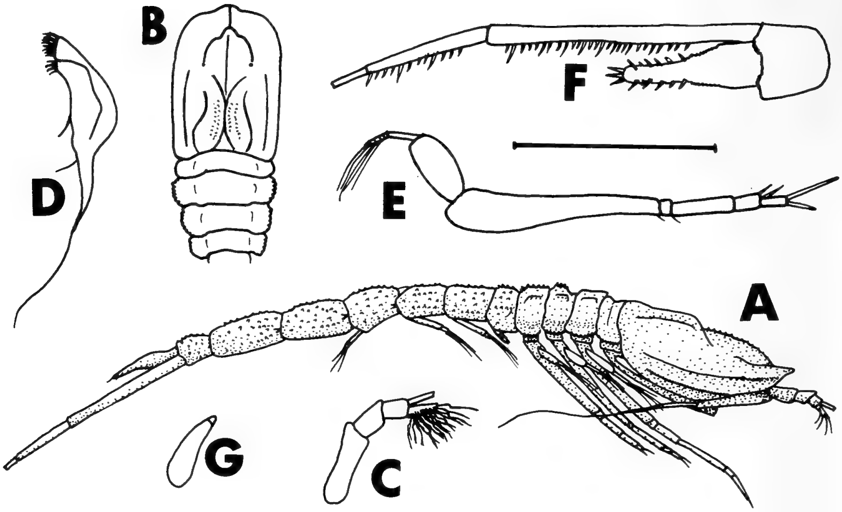

Fig. 3. *Stenotyphlops spinulosus*
Adult male. A. Lateral view. B. Dorsal view of cephalothorax. C. Antenna 1. D. Maxilla 1. E. Pereiopod 3. F. Uropod and telson. G. Pereiopod 5.
Scale line = 4 mm for A–B; 2 mm for C, E–F; 1 mm for D, G.

sexes. Stebbing figures his female with a slightly narrower carapace and a larger first segment of antenna 1. The flagellum of his female has four segments and the present one five. The greatest difference is in the telson: Stebbing figures it as being not very much longer than the telsonic somite and little more than half the length of the peduncle of the uropod. The telsons of both male and female figured here are twice the length of the telsonic somite and in the female is nearly as long as the peduncle of the uropod. In the male the peduncle is much longer, nearly twice as long as the telson. However these differences may simply be due to individual variation since the lengths of the peduncle and telson vary somewhat among the individuals available at present. Apart from this, they agree well with Stebbing's figures and there is little doubt that they belong to the same species.

Distribution

From Cape Point (about 500 to 1 200 m) to Natal (680 to 850 m).

Paralamprops Sars, 1887

Generic diagnosis

Carapace slightly or strongly depressed dorsoventrally with a marginal carina or at least one pair of lateral carinae. Antenna 1 with both flagella well developed. Palp of maxilla 1 absent or with two filaments. Exopods of pereiopods 3 and 4 of female rudimentary or absent. Pereiopod 5 small to rudimentary, no longer than basis of pereiopod 4. Male with three pairs of pleopods. Telson well developed.

Type species

Paralamprops serratocostata Sars, 1887.

Remarks

The genus has consisted up to now of seven species: *P. serratocostata* Sars, 1887, *P. orbicularis* Calman, 1904, *P. aspera* Zimmer, 1907, *P. semiornata* Fage, 1928, *P. grimaldi* Fage, 1928, *P. arafurensis* Jones, 1969, and *P. rossi* Jones, 1971. The genus *Platytyphlops* was established by Stebbing (1912) on the basis of several specimens including a fragmentary ovigerous female and at least one young male. He decided that the male was probably mature and therefore characterized the genus as having no pleopods in the male and a greatly reduced fifth pereiopod in both sexes. One fully adult and several subadult males of the same species are now available, however, and possess three pairs of normal pleopods. They should thus be placed in *Paralamprops*. It also turns out that the reduction of the fifth pereiopod is less evident in the adult male than in immature males or adult females in *P. peringueyi* and that, in fact, the limb is reduced to some extent in all species of *Paralamprops*. But the degree of reduction varies considerably, reaching its limit in *P. peringueyi*. Thus the generic diagnosis of *Paralamprops* has been slightly altered accordingly.

The genus is morphologically rather variable. The first maxilla in *P. serratocosta* and *P. margidens* sp. nov. lacks a palp while in *P. orbicularis*, *P. semiornata*, *P. grimaldi* and *P. peringueyi* there is a normal palp with two filaments. In these last four species and in *P. rossi* the carapace is very strongly flattened with a single, sharp marginal carina forming a wide, flat, flange encircling the entire carapace apart from the extreme posterior edge. The first maxilla is not described for *P. rossi*, *P. aspera* or *P. arafurensis*, all of which are known from single specimens which would have been badly damaged by dissection of the anterior mouthparts. In *P. serratocostata*, which lacks a maxillary palp, the carapace is not strongly flattened dorsoventrally but, in common with *P. arafurensis* and *P. aspera*, does possess a number of longitudinal ridges. *P. margidens* also lacks a maxillary palp, but the carapace is somewhat flattened and bears a single dentate marginal carina, thus being intermediate between the two types described above.

Calman (1912) was of the opinion that the absence of a palp on maxilla 1 was 'so important and unexpected that it might justify the creation of a new genus'. The present author agrees that this character is of considerable significance and suggests that in the future *Paralamprops* may well be split into two genera on the combined characters of the first maxilla and the carapace. However, as Jones (pers. comm.) has pointed out, the practical difficulty of examining the maxilla in rare species and the lack of information on the adults of many of the species under discussion, precludes the splitting of the genus at present.

Stenotyphlops, distinguished by a single filament on the palp of maxilla 1, a greatly reduced fifth pereiopod and several longitudinal ridges on the carapace, is very close to *Paralamprops*, as is *Archaeocuma*, which is distinguished by a single pair of pleopods. The most closely allied genus of all is *Hemilamprops*. In fact, it is difficult to find a really satisfactory set of characters to distinguish *Hemilamprops* from some members of *Paralamprops*, other than the roundness of the carapace and shortness of the abdomen in *Hemilamprops*, and the fact that there is little or no reduction of the fifth pereiopod in this genus. However, these characters are easily distinguishable and seem to be uniform. In order to avoid making *Hemilamprops* unwieldy and even more diverse than it is at present, the two genera must be kept apart for convenience' sake.

Hemilamprops mawsoni Hale, 1937, which was not a satisfactory member of that genus, can, however, now be placed in *Paralamprops*, where it is very similar to *P. rossi*. This brings the total number of species of *Paralamprops* to ten.

Distribution of Paralamprops

Known at depths from 232 to 3 789 m in the Atlantic, Antarctic and East Indies.

KEY TO THE SPECIES OF *PARALAMPROPS*

1 Carapace with a single, sharp marginal carina..2
– Carapace with at least three pairs of lateral and/or dorsolateral carinae 8
2 Carapace no more elevated posteriorly than anteriorly.............................3
– Carapace more elevated posteriorly than anteriorly.................................4
3 Telson little longer than telsonic somite; second and third segments of antenna 1 subequal in length; ischium of pereiopod 1 about as wide as long
P. orbicularis Calman, 1904—N. Atlantic
– Telson more than twice length of telsonic somite; third segment of antenna 1 half length of second; ischium of pereiopod 1 much wider than long
P. semiornata Fage, 1928—W. Portugal
4 Telson nearly equal in length to last two somites together...........................5
– Telson about half length of last two somites together...............................7
5 Marginal carina strongly dentate.............................*P. margidens* sp. nov.
– Marginal carina smooth 6
6 Minute exopods on pereiopods 3 and 4 of female; carapace not transversely ridged in mid-dorsal gutter; pseudorostrum pointed anteriorly in dorsal view
P. mawsoni (Hale, 1937)—Antarctic
– No exopods on pereiopods 3 and 4 of female; carapace lightly ridged transversely in mid-dorsal gutter; pseudorostrum rounded anteriorly in dorsal view
P. rossi Jones, 1971—Ross Sea
7 Fifth pereiopod 5-segmented (female) or 6-segmented (male), much less than half length of pereiopod 4; basis of pereiopod 2 shorter than rest of limb.......................
P. peringueyi (Stebbing, 1912)—South Africa
– Fifth pereiopod 7-segmented, as long as basis of pereiopod 4; basis of pereiopod 2 longer than rest of limb.................................*P. grimaldi* Fage, 1928—Azores
8 Middorsal carina not serrate; telson little narrower posteriorly than anteriorly with five spines transversely across apex..................*P. arafurensis* Jones, 1969—East Indies
– Middorsal carina serrate; telson distinctly narrower posteriorly than anteriorly with three apical spines 9
9 Telson no more than twice length of telsonic somite............................
P. serratocostata Sars, 1887—Kerguelen
– Telson three times length of telsonic somite..........*P. aspera* Zimmer, 1907—Antarctic

Paralamprops peringueyi (Stebbing, 1912)

Fig. 4

Platytyphlops peringueyi Stebbing, 1912: 159–161, pls 58–59.

Records

SAM–A596 (PF 17585)	34°48′S 18°03′E	369–554 m	3 ♀♀: 9,3 mm, 9,9 mm, damaged (paratypes)
SAM–A10602 (PF 17440)	34°25′S 17°45′E	800 m	1 adult ♂: 14,7 mm; 1 damaged subadult ♂; 3 ♂♂: 7,7–10,6 mm; 3 ♀♀: 8,0–16,0 mm; 2 damaged juvs
SAM–A10606 (PF 16769)	34°37′S 17°50′E	1 394 m	1 ovig. ♀: 14,7 mm

Previous records

Type locality only.

Holotype

Not designated: syntypes include ovigerous female and young males from two samples (PF 17585 and PF 17643), deposited in the British Museum (Natural History). Type locality: between 370 and 550 m, off Cape Point (34°48′S 18°03′E).

Description

Adult male, length 14,7 mm (SAM–A10602). Integument with minute triangular denticles. Sides of carapace strongly depressed (Fig. 4A), marginal carina very evident; median part of carapace compressed laterally, slightly more elevated posteriorly than anteriorly. Middorsal line defined anteriorly by extremely well-developed carina and posteriorly by a narrow gutter flanked by a pair of flattened dorsal elevations, denticulate on their anterior edges and bent outwards slightly (Fig. 4B). Eyelobe small, eyeless, flanked by flattened, upturned, lateral extensions of pseudorostral lobes. Carapace slightly longer than wide.

First pedigerous somite exposed dorsally only; second to fourth slightly flanged laterally, fifth cylindrical. Cephalothorax more than three-quarters length of cylindrical abdomen.

Antenna 1 (Fig. 4C) fairly large; first segment longer than next two together. Flagellum elongate, 4-segmented. Accessory flagellum 5-segmented with numerous short aesthetascs on basal segment.

Palp of maxilla 1 with two filaments.

Maxilliped 3 (Fig. 4D) short, leg-like. Merus slightly expanded, carpus and propodus cylindrical, subequal in length.

Basis of pereiopod 1 (Fig. 4E) stout, ischium slightly expanded. Carpus slightly longer than ischium and merus together. Part of propodus and dactyl missing. Exopod large and stout, basal segment almost circular.

Basis of pereiopod 2 (Fig. 4F) fairly short, carpus longer than ischium and

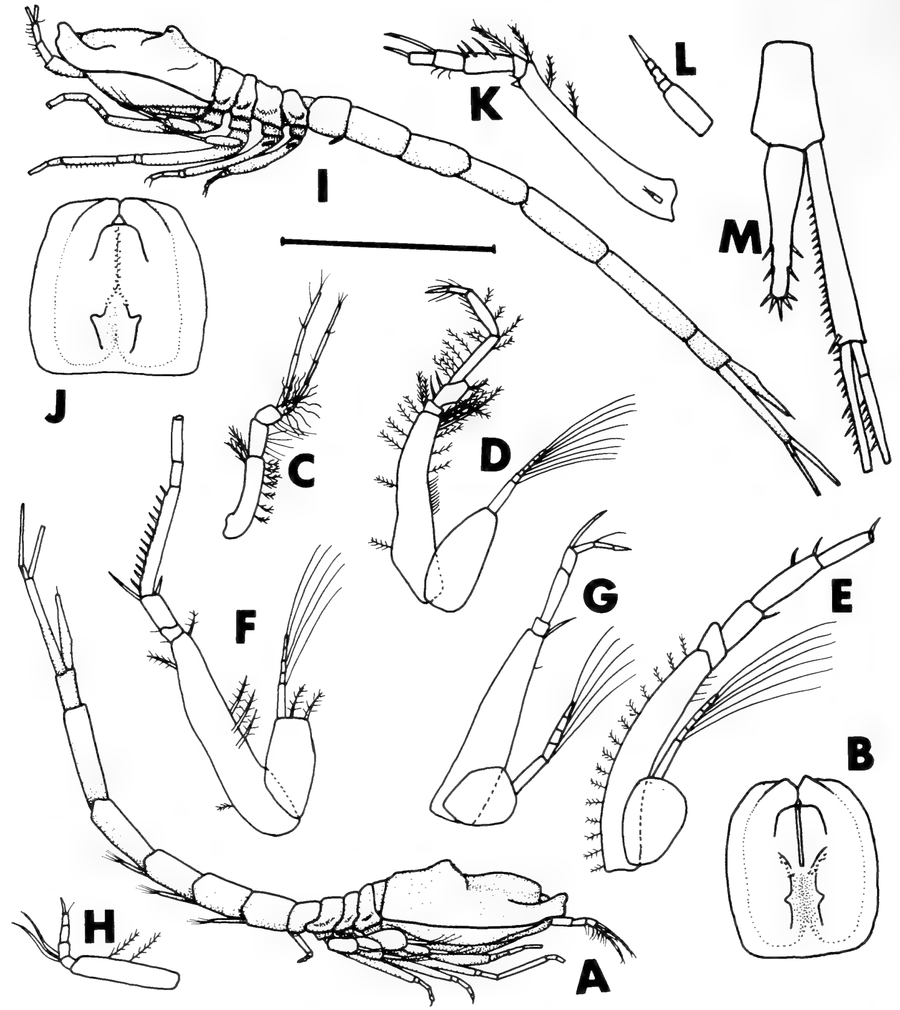

Fig. 4. *Paralamprops peringueyi*
Adult male. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Maxilliped 3. E. Pereiopod 1. F. Pereiopod 2. G. Pereiopod 3. H. Pereiopod 5.
Adult female. I. Lateral view. J. Dorsal view of carapace. K. Pereiopod 3. L. Pereiopod 5. M. Uropod and telson.
Scale line = 4 mm for A–B, I–J; 2 mm for C–H, K, M; 0,5 mm for L.

merus together, armed with a row of sharp spines. Dactyl incomplete. Exopod large.

Pereiopods 3 (Fig. 4G) and 4 similar, basis very large in comparison with rest of limb, of which merus is longest.

Pereiopod 5 (Fig. 4H) very small, 6-segmented. All segments distal to basis subequal in length. Entire limb less than half length of basis of pereiopod 4.

Three pairs of pleopods present.

Uropods and telson as in female (Fig. 4M) except that telson has three pairs of lateral spines, not two.

Adult female, length 16,0 mm (SAM–A10602). As male, except as follows: posterodorsal elevations of carapace narrower and curling over laterally (Fig. 4I). Middorsal carina much less well developed, minutely denticulate. Carapace almost as wide as long (Fig. 4J). First pedigerous somite visible laterally as well as dorsally.

Antenna 1 with third segment slightly longer, first segment of flagellum without aesthetascs. Second antenna 4-segmented. Exopod of pereiopod 2 smaller. Basis of pereiopods 3 (Fig. 4K) and 4 relatively smaller, distal segments larger and stouter; exopods minute. Pereiopods 5 (Fig. 4L) minute, 5-segmented, with a stout terminal spine.

Telsonic somite (Fig. 4M) nearly twice as long as broad, two-thirds length of telson. Telson with two pairs of lateral spines and five terminally. Peduncle of uropod slightly longer than telson with numerous small spines on inner edge. Rami of uropods incomplete.

Remarks

The adult male has not previously been described but corresponds well with the female in most respects. The female differs slightly from that described by Stebbing (1912), mainly because his was considerably smaller and less mature. In particular the carapace is square, not rounded, in dorsal view and the carpus and propodus of maxilliped 3 are smaller in the present specimens. The exopods of the thoracic limbs of Stebbing's male are smaller, again because it is immature. Nevertheless these characters are of little specific significance and there is no doubt that all individuals belong to the same species. It should be noted that there is some individual variation in the degree to which the median part of the carapace is elevated, particularly in some of the younger individuals.

P. peringueyi is characterized by the very great reduction of the fifth pereiopod, particularly in the female. It is most similar to *P. grimaldi*, from which it may be distinguished by this character.

Distribution

Only known off the Cape Peninsula from about 369 to 1 394 m.

Paralamprops margidens sp. nov.

Fig. 5

Records

SAM–A595 (PF 15785)	34°39′S 18°10′E	500 m	1 ♀: 6,1 mm
SAM–A10602 (PF 17440)	34°25′S 17°45′E	800 m	2 ♀♀: 6,1 mm (holotype + 1); 3 ♂♂: 5,8–6,1 mm

Holotype

Young female, in the South African Museum, SAM–A15721, collected by the S.S. *Pieter Faure* in about 1900. Type locality: 800 m, off the Cape Peninsula (34°25′S 17°45′E).

Description

Young female, holotype, length 6,1 mm. Integument lightly calcified, reticulate on body and very slightly denticulate on some limbs. Carapace (Fig. 5A) slightly wider than deep, nearly twice as long as deep, somewhat depressed immediately behind eyelobe. Marginal carina strongly dentate. Middorsal carina shallow, serrate anteriorly. Branchial regions somewhat inflated. No anterolateral angle (Fig. 5B). Pseudorostral lobes short in dorsal view (Fig. 5C). Eyelobe triangular, eyeless.

First three pedigerous somites denticulate laterally. Abdominal somites subcylindrical. Cephalothorax subequal in length to abdomen.

Antenna 1 as in male (Fig. 5N), but third segment slightly longer and flagellum 4-segmented. Accessory flagellum damaged in all females.

Antenna 2 (Fig. 5D) of moderate size, 4-segmented, with the last two segments relatively long.

Maxilla 1 (Fig. 5E) with no sign of palp.

Maxilliped 3 (Fig. 5F) leg-like, basis subequal in length to rest of limb. Ischium small, merus slightly expanded on outer edge with two large terminal spines. Carpus inserting subterminally on merus, subequal in length to last two segments together. Exopod well developed.

Pereiopod 1 (Fig. 5G) very long, basis half length of rest of limb. Merus and carpus subequal in length, propodus almost as long as merus and carpus together, dactyl slightly shorter with several terminal spines. Exopod well developed.

Pereiopod 2 (Fig. 5H) long and slender. Basis subequal in length to next four segments together. Carpus stout with six large spines on lower edge. Last two segments slender. Only basal segment of exopod present.

Pereiopods 3 (Fig. 5I) and 4 similar, basis of pereiopod 4 relatively shorter. Basis of pereiopod 3 very slender, more than twice length of rest of limb. Exopod very small, 2-segmented.

Pereiopod 5 (Fig. 5J) hardly more than half length of basis of pereiopod 4.

Telsonic somite (Fig. 5K) wider than long, little more than a third length of telson. Telson tapering evenly from base, armed with five pairs of short spines laterally and three longer ones terminally. Peduncle of uropod slightly longer than telson. Exopod reaching end of second segment of endopod. Endopod 3-segmented, first armed with fine setae on inner edge.

Subadult male, paratype, length 6,1 mm. As female, except as follows: carapace (Fig. 5L) somewhat shallower, denticles slightly larger. No depression behind eyelobe. Middorsal serrations (Fig. 5M) larger and extending further back. Third and fourth pedigerous somites denticulate dorsally.

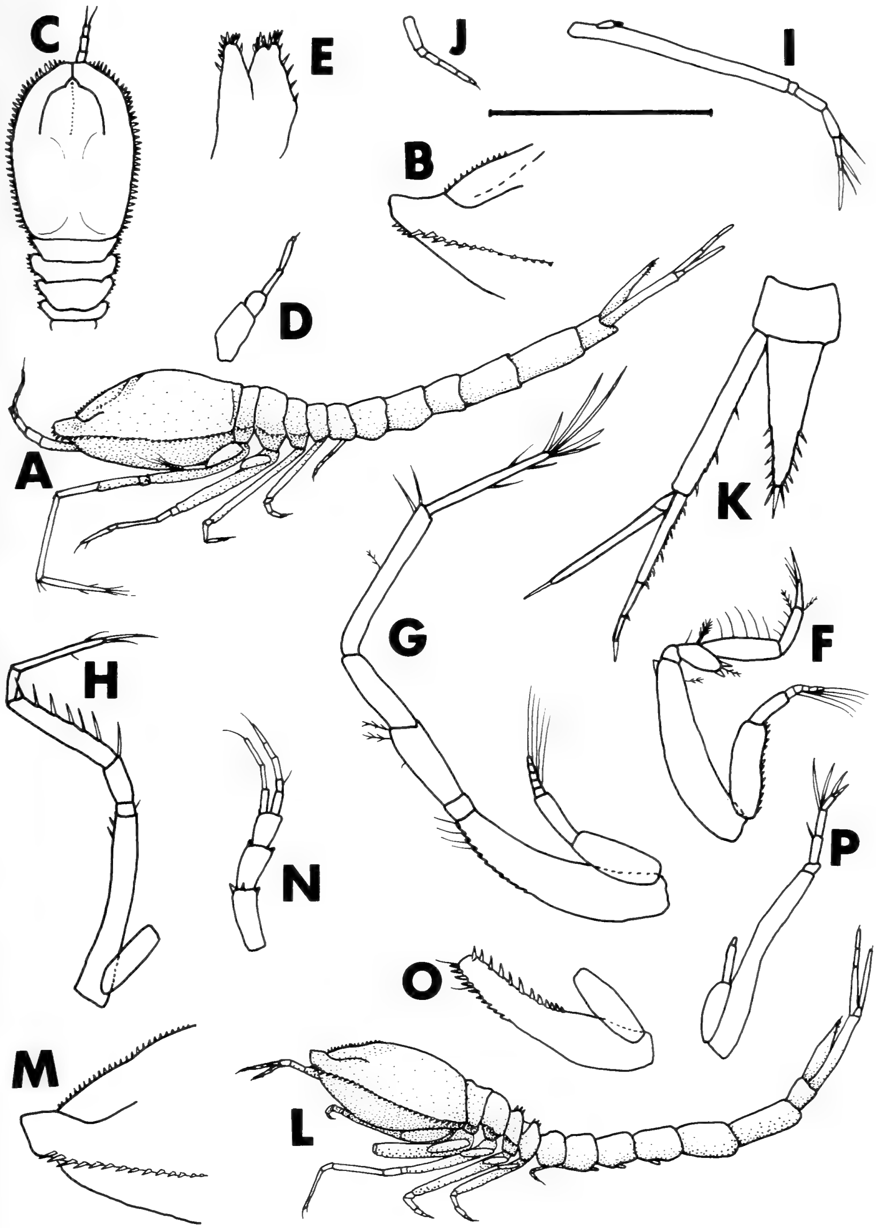

Fig. 5. *Paralamprops margidens* sp. nov.
Adult female, holotype. A. Lateral view. B. Detail of anterior end of carapace. C. Dorsal view of carapace. D. Antenna 2. E. Maxilla 1. F. Maxilliped 3. G. Pereiopod 1. H. Pereiopod 2. I. Pereiopod 3. J. Pereiopod 5. K. Uropod and telson.
Subadult male, paratype. L. Lateral view. M. Detail of anterior end of carapace. N. Antenna 1. O. Basis of pereiopod 1. P. Pereiopod 3.
Scale line = 2 mm for A, C, L; 1 mm for B, F–K, M, O–P; 0,5 mm for D–E, N.

Each segment of antenna 1 (Fig. 5N) slightly longer than succeeding one; flagellum 5-segmented, accessory flagellum 3-segmented. Basis of pereiopod 1 (Fig. 5O) strongly dentate. Distal segments of exopods missing from pereiopods 1 and 2. Bases of pereiopods 3 (Fig. 5P) and 4 shorter and stouter, exopods 3-segmented. Basis of pereiopod 5 slightly longer. Armature of uropods reduced (but possibly lost due to age).

Remarks

Lacking a palp on maxilla 1, *P. margidens* falls within the *serratocostata–aspera–arafurensis* group of *Paralamprops*. It is easily distinguished from these and from the South African *P. peringueyi* by the denticulate marginal carina.

Distribution

Known only from about 500 to 800 m off the Cape Peninsula.

Platysympus Stebbing, 1912

Platyaspis Sars, 1869: 158 (preoccupied name).

Generic diagnosis

Carapace strongly flattened dorsoventrally with strong marginal carina. Both flagella of antenna 1 well developed. Maxilla 1 without palp. Pereiopods 2 to 4 of female without exopods. Male with three pairs of pleopods. Telson well developed.

Type species

Platyaspis typicus Sars, 1869.

Remarks

The genus is well-defined and easily recognizable due to the very characteristic flattened carapace with a strong marginal carina. The absence of exopods on pereiopods 2 to 4 in the female is unique in the family although in other genera they may occasionally be absent from pereiopods 3 and 4. The presence of four new species in southern African waters brings the total number for the genus to seven.

Distribution of Platysympus

Europe from 226 to 1 100 m; North Atlantic from 219 to 957 m; Antarctic at 385 m; South Africa from 188 to 1 200 m.

KEY TO THE SPECIES OF *PLATYSYMPUS*

1 Carapace with three longitudinal ridges dorsal to marginal carina......................
P. tricarinatus Hansen, 1920—N. Atlantic
– Carapace with middorsal and marginal carinae forming only major longitudinal ridges....2
2 Pereiopod 5 half length of pereiopod 4; female with rudimentary exopods on pereiopod 2
*P. brachyurus** Zimmer, 1907—Antarctic
– Pereiopod 5 more than half length of pereiopod 4; pereiopod 2 of female without exopod..3

3 Carapace remarkably flattened and leaf-like: almost circular in dorsal view and wider than abdomen is long . . . . *P. phylloides*, sp. nov.
– Carapace flattened but not leaf-like: longer than wide in dorsal view and considerably narrower than abdomen is long 4
4 Dorsal outline of carapace undulating sinusoidally, forming two evenly-spaced elevations; bases of pereiopods 1 and 2 with flattened, scale-like edges . . . . *P. camelus* sp. nov.
– Dorsal outline of carapace smooth or with several low, unevenly-distributed tumidities; bases of pereiopods 1 and 2 without flattened, scale-like edges 5
5 Dorsal third of carapace strongly compressed laterally, forming a very deep middorsal carina; basis of pereiopod 5 less than half length of rest of limb . . . . *P. compressus* sp. nov.
– Dorsal third of carapace not strongly compressed laterally, middorsal carina negligible or incorporating much less than a third of its depth; basis of pereiopod 5 more than half length of rest of limb 6
6 Middorsal carina distinct over whole length of carapace; carapace of female smooth; merus, carpus and propodus of pereiopod 1 wide and flattened . . . . *P. typicus* (Sars, 1869)—Europe
– Middorsal carina of carapace only evident posteriorly; carapace of female with several tumidities and depressions; merus, carpus and propodus of pereiopod 1 not wide or flattened *P. depressus* sp. nov.

**P. brachyurus* is known only from one incomplete female individual. Some characteristics suggest that when further material is available the species will be found to fit better in *Paralamprops*.

Platysympus phylloides sp. nov.

Fig. 6

Records

SAM–A10607 (PF 16982)	34°40′S 17°50′E	1 200 m	1 adult ♀: 7,2 mm (holotype); 1 damaged ♀
SM 129	30°54′S 30°51′E	850 m	2 ovig. ♀♀: 7,4 and 7,7 mm (both damaged)

Holotype

Adult female, in the South African Museum, SAM–A15682, collected by the *Pieter Faure* in about 1900. Type locality: approximately 1 200 m, off the Cape Peninsula (34°40′S 17°50′E).

Description

Adult female, holotype, length 7,2 mm. Integument very delicate and translucent. Carapace (Fig. 6A) remarkably flat and leaf-like, almost circular in dorsal view (Fig. 6B) with middorsal carina faintly evident anteriorly. Eyelobe small, rounded and eyeless. Carapace flattened and paper-thin at edges forming an almost transparent wide flange extending round entire edge except where attached to abdomen. Posterolaterally, extensions of this carina form flaps overlapping third pedigerous somite on each side and leaving a gap on either side of second somite. All cephalothoracic appendages except fifth pereiopod entirely covered by carapace (Fig. 6C); bases of maxilliped 3 and pereiopod 1 pointing forward and attached underneath carapace by a thin membrane, being thus quite immobilized.

All five pedigerous somites free, last four wider than deep. Carapace wider than abdomen is long. Cephalothorax about half as long again as cylindrical abdomen.

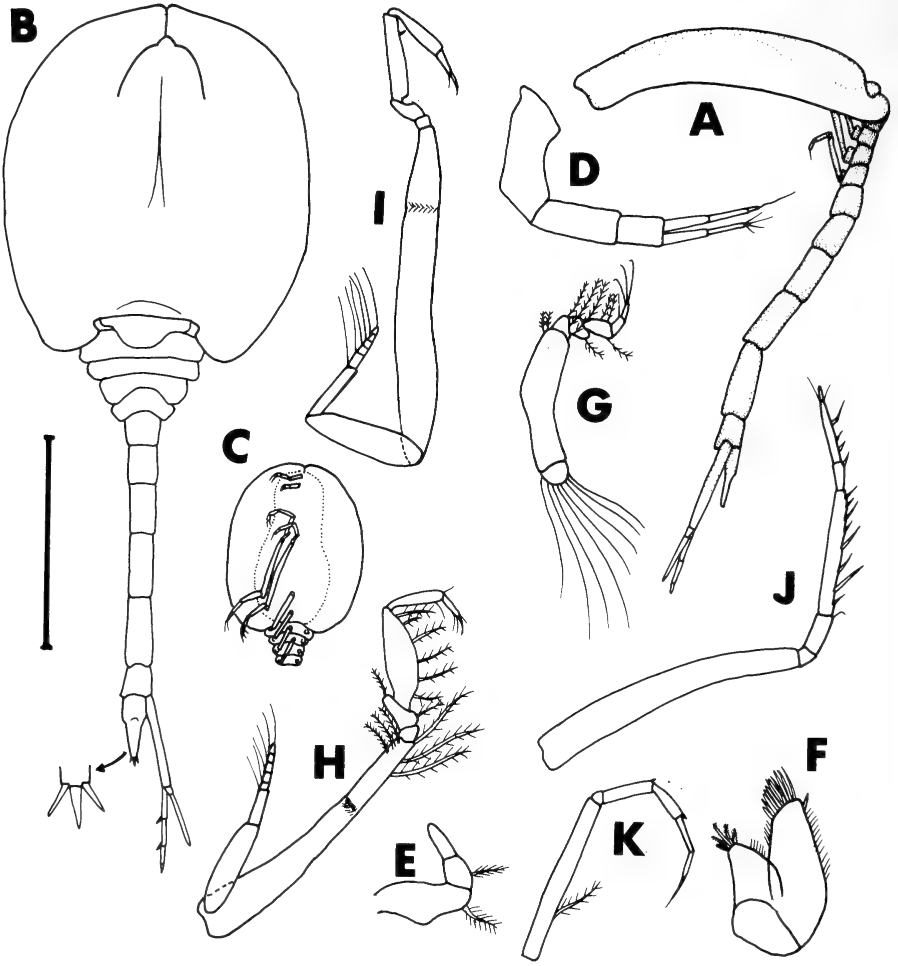

Fig. 6. *Platysympus phylloides* sp. nov.
Adult female, holotype. A. Lateral view. B. Dorsal view. C. Ventral view of cephalothorax. D. Antenna 1. E. Antenna 2. F. Maxilla 1. G. Maxilliped 2. H. Maxilliped 3. I. Pereiopod 1. J. Pereiopod 2. K. Pereiopod 3.
Scale line = 4 mm for C; 2 mm for A–B; 1 mm for G–K; O,5 mm for D–F.

Antenna 1 (Fig. 6D) small, first segment subequal in length to next two together. Both flagella short but well developed, main flagellum 3- and accessory flagellum 2-segmented.

Antenna 2 (Fig. 6E) reasonably large, 3-segmented.

Maxilla 1 (Fig. 6F) without palp.

Maxilliped 2 (Fig. 6G—from ovigerous female, not holotype) with distal segments short. Oostegal setae long and numerous.

Basis of maxilliped 3 (Fig. 6H) very flexible but immobile, being attached to the ventral surface of the carapace. Exopod normal but setae very small and poorly setulose. Ischium small; merus slightly expanded; carpus large and stout; propodus and dactyl slender.

Basis and exopod of pereiopod 1 (Fig. 6I) as in maxilliped 3. Ischium small. Carpus elongate, subequal in length to propodus and dactyl together.

Pereiopod 2 (Fig. 6J) lacking exopod. Basis slender, subequal in length to rest of limb. Carpus long and well armed.

Pereiopods 3 (Fig. 6K) to 5 all similar, lacking exopods. Limbs slender, basis subequal in length to rest of limb; merus, carpus and propodus subequal in length.

Telson (Fig. 6B) twice length of telsonic somite, armed with only three small apical spines. Peduncle of uropod subequal in length to last somite and telson together, unarmed. Exopod unarmed, about two-thirds length of endopod. Each segment of endopod armed with a single small spine distally on inner edge.

Males have not been found.

Remarks

In the absence of male individuals it is not possible to state with certainty that this species belongs to *Platysympus*. It is certainly quite distinctive in the nature of the carapace, but apart from this, the appendages are very similar to other members of the genus. It may be that this is merely the ultimate condition in a genus in which the carapace is always flattened, and that the peculiarities of its morphology are necessary to overcome problems associated with a greatly flattened carapace. For example, the exopods, on those limbs which have them, are reduced and it is difficult to see that they would be of any use if they were present. Pleopods would seem to be unimportant as a means of locomotion in such a flattened animal and it may prove that none are present even in the adult male. If this should be so, then the species will have to be placed in a separate genus.

The peculiar attachment of the third maxilliped and first pereiopod to the floor of the carapace is presumably also an adaptation to the overhanging carapace, as is the presence of the inhalent aperture on either side of the second pedigerous somite.

Distribution

Cape Point at 1 200 m and Natal at 850 m.

Platysympus depressus sp. nov.

Fig. 7

Records

SAM–A10602 (PF 17440)	34°25′S 17°45′E	800 m	1 adult ♂: 5,8 mm (holotype); 2 subadult ♂♂: 5,4 mm; 2 young ♂♂: 4,5 mm, 4,8 mm; 3 ovig. ♀♀: 5,8–6,4 mm; 6 ♀♀: 5,1–6,4 mm

SM 86	27°59′S 32°40′E	550 m	1 subadult ♂: 5,4 mm
SM 103	28°31′S 32°34′E	680 m	1 adult ♂: 7,0 mm; 1 damaged ♀
SM 129	30°54′S 30°31′E	850 m	1 young ♂, 2 ♀♀, all damaged
LBT 38J	32°07′S 16°31′E	440 m	1 ♂: 4,8 mm

Holotype

Adult male, in the South African Museum, SAM–A15683, collected by the *Pieter Faure* in about 1900. Type locality: 800 m, off the Cape Peninsula (34°25′S 17°45′E).

Description

Adult male, holotype, length 5,8 mm. Integument fairly thin and translucent without obvious denticles or reticulations. Carapace (Fig. 7A) dorsoventrally depressed with a single marginal carina around entire periphery except posteriorly. Dorsal outline low and smoothly arched. Middorsal carina faintly evident posteriorly only (Fig. 7B). Eyelobe small, eyeless. Pseudorostral lobes short and expanded laterally.

All five pedigerous somites visible, first four slightly flanged laterally. Abdominal somites cylindrical, together slightly shorter than cephalothorax.

Antenna 1 (Fig. 7C) fairly large. Flagellum 4-segmented, first bearing numerous short aesthetascs. Accessory flagellum 3-segmented.

Antenna 2 (Fig. 7D) fairly short, reaching beyond posterior edge of carapace. Segments short and poorly setose.

Maxilla 1 without palp.

Maxilliped 3 (Fig. 7E) fairly short. Basis unexpanded distally, subequal in length to rest of limb. Merus slightly expanded, carpus large. Propodus and dactyl slender.

Basis of pereiopod 1 (Fig. 7F) longer than rest of limb. Ischium as wide as long, next three segments subequal in length.

Pereiopod 2 (Fig. 7G) slender, carpus longer than propodus and dactyl together, armed with four stout spines.

Pereiopods 3 (Fig. 7H) and 4 similar. Basis slightly shorter than rest of limb in pereiopod 3 and slightly longer in pereiopod 4. Exopods present. Distal segments of pereiopod 5 missing.

Three pairs of normal pleopods present.

Uropods and telson as in female: parts of uropods missing from holotype.

Adult female, paratype, length 6.4 mm. As male, except as follows: carapace (Fig. 7J) with a number of slight swellings and depressions, slightly more elevated dorsally; middorsal carina better defined. No wider anteriorly than posteriorly in dorsal view. First pedigerous somite wider and third narrower.

Distal segments of flagella of antenna 1 missing. Antenna 2 (Fig. 7K) 4-segmented. Distal segments of pereiopod 1 flatter and wider. Pereiopods 2 to 4 without exopods. Pereiopod 2 much more slender, carpus longer; bases of pereiopods 3 and 4 longer and slightly thinner. Pereiopod 5 (Fig. 7I) very

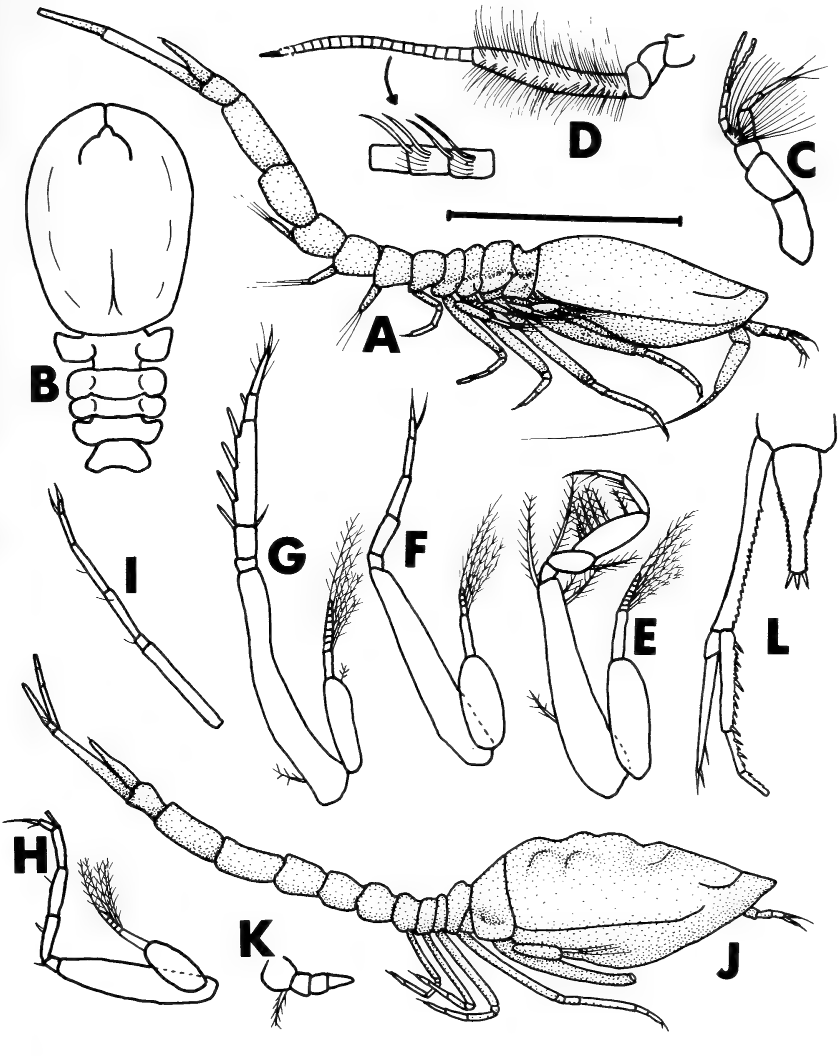

Fig. 7. *Platysympus depressus* sp. nov.
Adult male, holotype. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Antenna 2. E. Maxilliped 3. F. Pereiopod 1. G. Pereiopod 2. H. Pereiopod 3. I. Pereiopod 5. Adult female, paratype. J. Lateral view. K. Antenna 2. L. Uropod and telson. Scale line = 2 mm for A–B, J; 1 mm for C–I, K–L.

slender, basis equal in length to next three segments together; merus and carpus subequal in length.

Telson (Fig. 7L) nearly twice length of preceding somite, wider proximally than distally and serrated on edges; armed only with three small spines apically. Peduncle of uropod longer than telson, subequal in length to endopod, serrated on inner edge. Second segment of exopod with three slender distal spines. First segment of endopod longer than next two together.

Remarks

P. depressus is most similar to *P. typicus* (Sars, 1869) and *P. compressus* sp. nov. It may be distinguished from both in that it lacks a middorsal carina on the carapace and from *P. compressus* by the latter being laterally rather than dorsoventrally compressed, lacking low protuberances on the carapace of the female and having a larger first antenna in the male. *P. depressus* differs from *P. typicus* mainly in the shape of the carapace: the dorsal and marginal carinae are better defined and the female lacks low protuberances on the carapace in *P. typicus*. Also in this species the first antennae are smaller, the distal segments of pereiopod 1 are flattened and the second pereiopod is more slender with a longer dactyl.

Distribution

From Lambert's Bay to northern Natal at depths from 440 to 850 m.

Platysympus compressus sp. nov.

Fig. 8

Records

SAM–A10601 (PF 12605)	30°33′S 30°58′E	805 m	1 subadult ♂: 4,8 mm
SM 60	27°09′S 32°58′E	800 m	1 adult ♂: 5,5 mm (holotype); 3 ♂♂: 5,8–6,1 mm; 3 ovig. ♀♀: 5,8–6,1 mm

Holotype

Adult male, in the South African Museum, SAM–A15681, collected by the *Meiring Naude*, 19 May 1976. Type locality: 800 m, off northern Natal (27°09′S 32°50′E).

Description

Adult male, holotype, length 5,5 mm. Integument smooth without reticulations or denticles. Carapace (Fig. 8A) smooth with marginal carina as in *P. depressus*, dorsoventrally depressed for the most part but the dorsal third strongly compressed laterally, forming a very distinct, narrow middorsal carina. Pseudorostral lobes narrowed anteriorly in lateral view, rounded and fairly short in dorsal view (Fig. 8B). Eyelobe small, rounded and eyeless.

All pedigerous somites exposed, all of similar length. Abdominal somites subcylindrical, together shorter than cephalothorax.

Antenna 1 (Fig. 8C) large, first two segments slightly serrated. Second segment much wider distally than proximally, wider than long. Third segment short and subconical. Accessory flagellum missing. First segment of flagellum with numerous short aesthetascs, last three short and subequal in length.

Maxilla 1 without palp. Maxilliped 3 and pereiopods 1 and 2 represented by bases only.

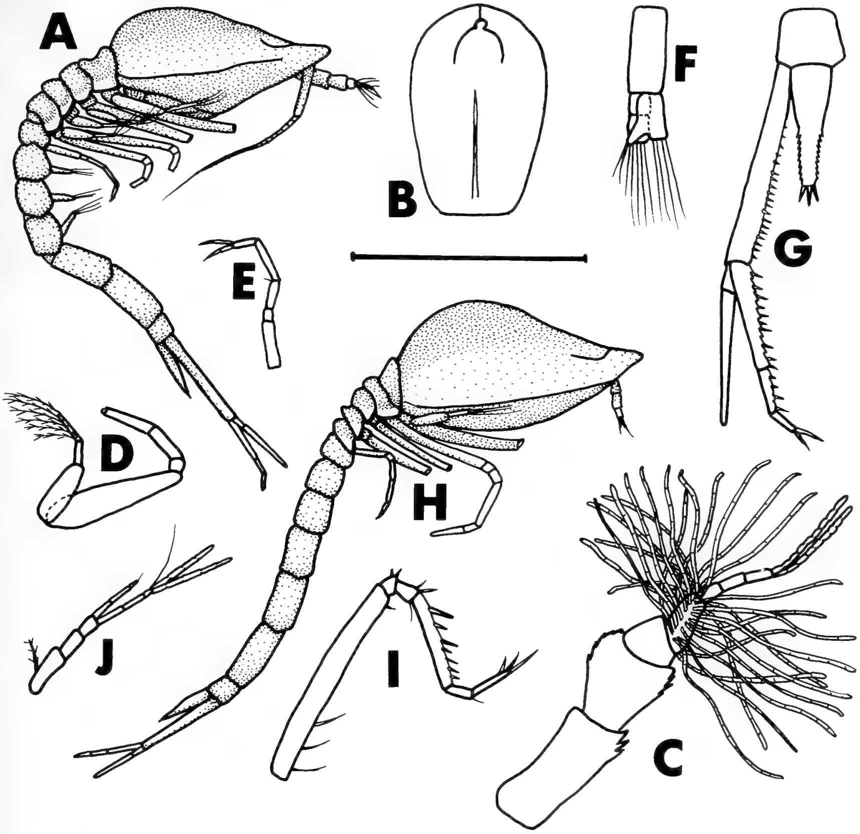

Fig. 8. *Platysympus compressus* sp. nov.
Adult male, holotype. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Pereiopod 3. E. Pereiopod 5. F. Pleopod 2. G. Uropod and telson.
Ovigerous female, paratype. H. Lateral view. I. Pereiopod 2. J. Antenna 1.
Scale line = 2 mm for A–B, H; 1 mm for D–E, G, I–J; 0,5 mm for C, F.

Pereiopods 3 (Fig. 8D) and 4 similar, last two segments of each missing. Basis stout, ischium short, merus and carpus subequal in length. Exopods moderately large.

Pereiopod 5 (Fig. 8E) short and slender.

Three pairs of pleopods present. (Fig. 8F)

Last abdominal somite as wide as long, less than half length of preceding one. Telson (Fig. 8G) slightly more than half length of peduncle of uropod, serrated distally on lateral edges and with three small sharp spines apically. Peduncle of uropod fairly stout, subequal in length to endopod with numerous small sharp spines distally on inner edge. Exopod slightly longer than first two segments of endopod, unarmed. First segment of endopod longer than next two together with several small spines on inner edge. Second segment longer than third.

Ovigerous female, paratype, length 6,1 mm. As male, except as follows: carapace (Fig. 8H) slightly deeper, pseudorostral lobes less narrowed in lateral view. Pedigerous somites shorter, abdominal somites together subequal in length to cephalothorax. Marsupium small.

Antenna 1 small, segments not expanded. Flagella both 2-segmented. Pereiopod 2 slender, without exopod; carpus longer than last two segments together. Segments distal to basis missing from maxilliped 3 and pereiopods 1, 3 and 4. Pereiopods 3 and 4 without exopods. Telson relatively longer—two-thirds as long as peduncle of uropod—but otherwise as in male.

Remarks

Although the appendages of none of the individuals are complete, the carapace is distinctively different from that of the other species in the genus. The lateral compression of the dorsal part of the carapace is characteristic, as is the large, wide first antenna in the male.

Distribution

Known only from depths between 800 and 810 m off northern Natal.

Platysympus camelus sp. nov.

Fig. 9

Records

SM 86	27°59′S 32°40′E	550 m	1 adult ♂: 6,8 mm (holotype); 3 ovig. ♀♀: 6,1–6,8 mm
WCD 450D	34°11′S 18°05′E	188 m	1 subadult ♂: 3,9 mm; 1 ♀: 4,8 mm; 1 damaged ovig. ♀
SST 1K	35°22′S 22°31′E	200 m	1 ♀: 3,9 mm
SST 17N	35°22′S 22°31′E	200 m	1 damaged adult ♂; 1 subadult ♂: 4,1 mm; 4 ♀♀: 4,1 mm

Holotype

Adult male, in the South African Museum, SAM–A15684, collected by the *Meiring Naude*, 22 May 1976. Type locality: 550 m, off northern Natal (27°59′S 32°40′E).

Description

Adult male, holotype, length 6,8 mm. Integument smooth, slightly translucent. Carapace (Fig. 9A) strongly dorsoventrally depressed at edges; slightly compressed laterally in midline forming distinct dorsal carina undulating in lateral view due to two rounded elevations, one middorsally and one posterodorsally. Marginal carina strong, forming a flattened flange around entire carapace except posteriorly. Eyelobe (Fig. 9B) small, rounded and eyeless. All

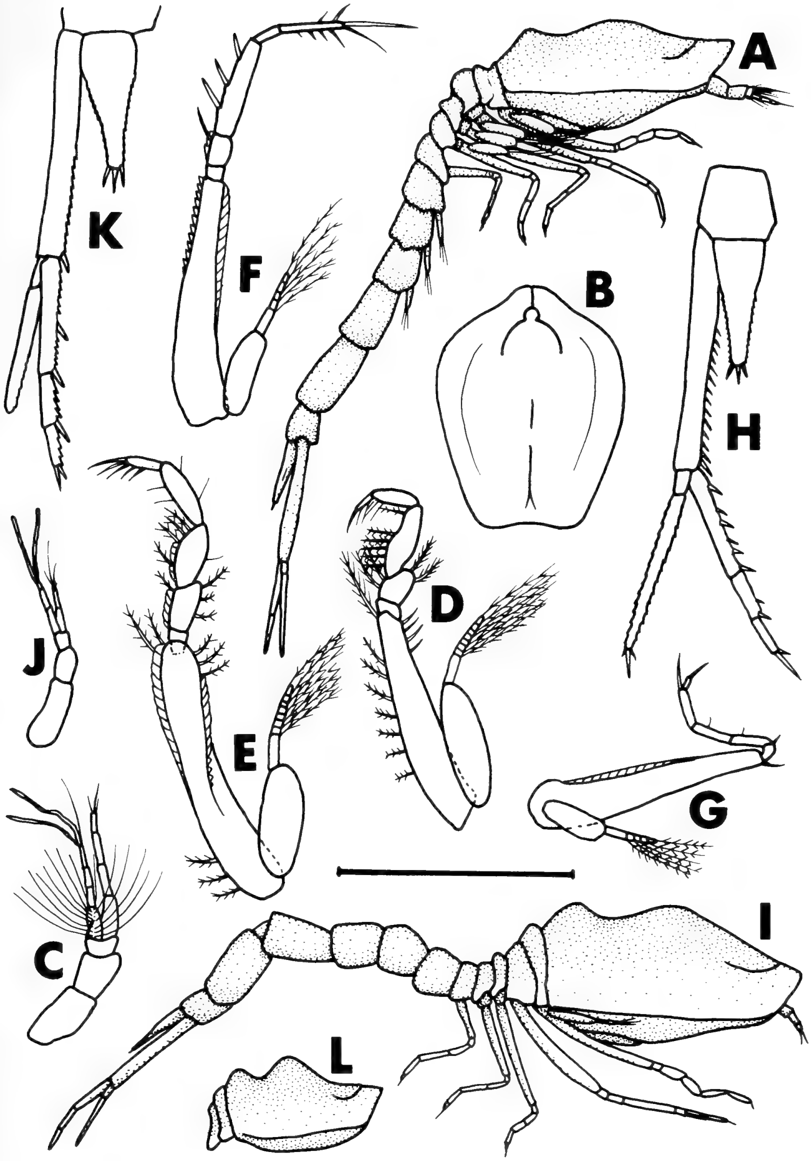

Fig. 9. *Platysympus camelus* sp. nov.

Adult male, holotype. A. Lateral view. B Dorsal view of carapace C. Antenna 1. D. Maxilliped 3. E. Pereiopod 1. F. Pereiopod 2. G. Pereiopod 3. H. Uropod and telson. Ovigerous female, paratype. I. Lateral view. J. Antenna 1. K. Uropod and telson. Juvenile. L. Lateral view of carapace.

Scale line = 2 mm for A–B, I, L; 1 mm for C–H, J–K.

pedigerous somites visible, of approximately equal length. Abdominal somites fairly large, rounded, together subequal in length to cephalothorax.

Antenna 1 (Fig. 9C) fairly large and stout; third segment wider than long. Both flagella 4-segmented, first segment of main flagellum surrounded by numerous short aesthetascs.

Maxilliped 3 (Fig. 9D) short and fairly stout. Basis longer than rest of limb, ischium wider than long. Carpus longer than ischium and merus together.

Bases of pereiopods 1 to 4 flattened, edges expanded by means of flat, transparent scales fusing to form flanges. Basis of pereiopod 1 (Fig. 9E) slightly longer than rest of limb, both inner and outer edges flanged distally. Ischium small, merus and carpus subequal in length, both flanged on inner edge; propodus slightly longer, dactyl short and cylindrical.

Basis of pereiopod 2 (Fig. 9F) flanged distally on both edges. Ischium half length of merus, together about half length of carpus. Propodus and dactyl short and cylindrical.

Pereiopods 3 (Fig. 9G) and 4 similar, inner edges flanged. Basis distinctly longer and stouter than rest of limb, of which merus, carpus and propodus are subequal in length and cylindrical.

Basis of pereiopod 5 about half length of basis of pereiopod 4, distal segments the same.

Three pairs of pleopods present.

Telsonic somite as wide as long, less than half length of telson. Telson (Fig. 9H) tapering evenly from base, little more than half length of peduncle of uropod, serrated distally on both edges and with three small apical spines. Peduncle of uropod with several small sharp spines distally on inner edge. First segment of exopod unarmed, second slightly serrated on both edges with three small terminal spines. First segment of endopod slightly longer than subequal second and third segments together.

Ovigerous female, *paratype*, length 6,8 mm. As male, except as follows: carapace (Fig. 9I) relatively larger, undulations of dorsal surface more marked. Pedigerous somites shorter, the first deeper. Carapace almost round in dorsal view. First segment of antenna 1 (Fig. 9J) larger, third narrower. Both flagella with three segments. Merus of maxilliped 3 longer and thinner, carpus stouter. Distal segments of pereiopod 1 less flattened, edges not flanged, together slightly longer relative to basis. Pereiopods 2 to 4 without exopods. Basis of pereiopod 2 more slender, remaining segments longer and thinner. Bases of pereiopods 3 and 4 more slender. Uropod slightly shorter and stouter, inner edges of peduncle and rami serrated and with fewer spines.

Remarks

The peculiar flanged edges of the bases of pereiopods 1 to 4 and the undulating dorsal edge of the carapace clearly distinguish this species from the others in the genus. It should be noted that this undulation is most marked in juveniles

(Fig. 9L) and least evident in adult males, although these are none the less easy to distinguish.

The flanges on the pereiopods are occasionally found in members of other families of Cumacea (e.g. *Ceratocuma horridum*, Fig. 16D). The functional significance of this feature is uncertain. It may be to increase the surface area (for digging?) with the smallest possible increase in weight.

Distribution

Northern Natal to the Cape Peninsula at depths from 188 to 550 m.

Bathylamprops Zimmer, 1908

Generic diagnosis

Carapace not flattened. Pseudorostral lobes large and acutely produced. Eye absent. First and third segments of antenna 1 elongate, accessory flagellum minute. Palp of maxilla 1 with two filaments. Pereiopods 3 and 4 of female with small exopods. Male with three pairs of pleopods. Telson large and well developed.

Type species

Bathylamprops calmani, Zimmer, 1908.

Remarks

The genus consists of three closely allied deep-water species, *B. calmani* Zimmer, 1908, and *B. natalensis* Jones, 1969, both of which are known only from the east coast of Africa, and *B. motasi* Băcescu & Muradian, 1976, found off Florida. The genus is clearly recognized by the greater development of the pseudorostrum than is usual in the family, and the large first antenna with the minute accessory flagellum. It undoubtedly has close links with *Hemilamprops*, which it resembles in general morphology.

Distribution of Bathylamprops

Deep waters between 1 300 and 3 800 m off the east coasts of Africa and the United States.

KEY TO THE SPECIES OF *BATHYLAMPROPS*

1 Telson more than three times length of telsonic somite; carapace with numerous low, denticulate transverse ridges...... *B. calmani* Zimmer, 1908—east and south-east Africa

– Telson no more than two and a half times length of telsonic somite; carapace minutely denticulate or smooth but without ridges.. 2

2 Basis of maxilliped 3 twice length of remaining segments together, carpus no wider than merus; exopod of uropod shorter than telson; uropodal rami subequal in length........ *B. natalensis* Jones, 1969—Natal

– Basis of maxilliped 3 little longer than remaining segments together, carpus much wider than merus; exopod of uropod longer than telson and longer than endopod........... *B. motasi* Băcescu & Muradian, 1976—Florida

Bathylamprops calmani Zimmer, 1908

Fig. 10

B. calmani Zimmer, 1908: 173–175, figs 60–70.

Records

SM 109	28°41′S 32°36′E	1 300 m	1 adult ♀: 15,4 mm

Previous records

Off Dar-es-Salaam, 2 959 m (Zimmer 1908); off Durban, 2 720–3 530 m (Jones 1969).

Holotype

Damaged adult female, deposited by Zimmer in the Berlin Zoologisches Museum. Type locality: 2 959 m, off Dar-es-Salaam (6°12′S 41°17′E).

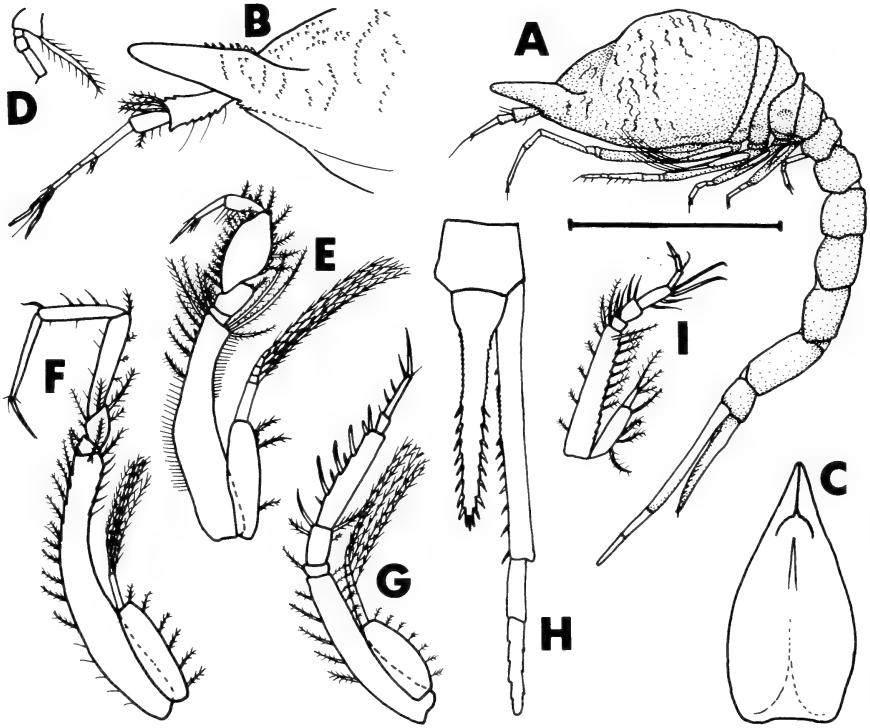

Fig. 10. *Bathylamprops calmani*

Adult female. A. Lateral view. B. Detail of anterior end of carapace. C. Dorsal view of carapace. D. Antenna 2. E. Maxilliped 3. F. Pereiopod 1. G. Pereiopod 2. H. Telson and uropod. I. Pereiopod 4.

Scale line = 4 mm for A–B; 2 mm for C–I.

Description

Adult female, length 15,4 mm. Carapace (Fig. 10A) large, strongly vaulted posteriorly and pointed anteriorly. Integument of carapace minutely denticulate (Fig. 10B) forming numerous transverse ridges, particularly anteriorly. Pseudorostral lobes elongate, denticulate immediately in front of eyelobe; denticles also forming an indistinct and very short lateral carina behind the small and indistinct anterolateral angle. Carapace narrow in dorsal view (Fig. 10C), slightly depressed between a pair of large posterolateral expansions. Middorsal carina present for a short distance behind the eyelobe. Eyelobe very small and eyeless. Pseudorostrum about one-fifth of total length of carapace.

All five pedigerous somites short, visible. Cephalothorax slightly longer than abdomen.

Antenna 1 (Fig. 10B) elongate, first segment more than twice length of second, third slightly longer than second. Accessory flagellum minute, 2-segmented. Flagellum elongate, 3-segmented.

Antenna 2 (Fig. 10D) short, 4-segmented. First segment stout, second and third small, fourth elongate (distal tip missing).

Maxilliped 3 (Fig. 10E) very stout. Basis slightly longer than rest of limb; ischium much wider than long; merus short and slightly expanded; carpus very large and expanded; propodus and dactyl small and cylindrical.

Pereiopod 1 (Fig. 10F) elongate, basis longer than rest of limb. Ischium small, merus slightly longer. Carpus, propodus and dactyl cylindrical and elongate.

Pereiopod 2 (Fig. 10G) stout, basis shorter than rest of limb. Ischium small; carpus long with several strong spines; propodus and dactyl small, narrow.

Pereiopods 3 (Fig. 10I) and 4 similar, basis and exopod of pereiopod 4 shorter. Exopod very well developed for a female, 2-segmented.

Pereiopod 5 shorter and more slender than pereiopod 4.

Telsonic somite (Fig. 10H) slightly wid~~er tha~~n long. Telson well developed, more than three times as long as telsonic somite; pre-anal part short, distinctly wider proximally; eight pairs of sharp spines distally on lateral edges and three short ones terminally. Peduncle of uropod slightly longer than telson with several small spines on inner edge. Exopod missing. First two segments of endopod present, first unarmed, second very slightly serrated on both edges.

Adult males are unknown.

Remarks

From the shape of maxilliped 3 and the sculpturing of the carapace it is clear that the present specimen belongs to the same species as Zimmer's. However he figures the pseudorostrum of his unique, damaged specimen as being somewhat shorter than that figured here. It is difficult to say if his was distorted due to mutilation or whether the length is variable.

B. calmani is very similar to both *B. natalensis* and *B. motasi*. However, in both of the latter the carapace lacks transverse rows of denticles, the exopods of pereiopods 3 and 4 are much smaller and the telson is shorter. In *B. natalensis*, too, the carpus of maxilliped 3 is not expanded and the fifth pereiopod is larger.

Distribution

Confined to deep waters off the east coast of Africa from northern Natal to Dar-es-Salaam at depths from 1 300 to 3 530 m.

Hemilamprops Sars, 1883

Generic diagnosis

Carapace not strongly dorsoventrally flattened. Eye present or absent. Pseudorostrum short. Flagella of antenna 1 well developed. Palp of maxilla 1 with two filaments. Exopods on pereiopods 3 and 4 of female rudimentary. Male with three pairs of pleopods. Telson well developed.

Type species

Not designated: Sars included *H. rosea* (Norman, 1863), *H. cristata* (Sars, 1870), *H. uniplicata* (Sars, 1872) and *H. assimilis* Sars, 1883, in his first description of the genus in 1883.

Remarks

Hemilamprops Sars, 1883, *Mesolamprops*, Given, 1964, and *Lamprops* Sars, 1863, are very closely-related genera, differing mainly in the number of pairs of pleopods in the adult male: none in *Lamprops*, two pairs in *Mesolamprops* and three pairs in *Hemilamprops*. This is the only character which invariably separates the species of the three genera but there are some other differences which are usually reliable in distinguishing them. For example, there is a small but usually distinct antennal notch in *Lamprops*; it may be present or absent in *Mesolamprops* and is usually absent in *Hemilamprops*. An eye is present in *Lamprops*, variable in *Mesolamprops* and usually absent from *Hemilamprops*. The proportions of the basis of pereiopod 1 to the rest of the limb are perhaps most reliable. In *Lamprops* the basis is approximately equal in length to the rest; in *Mesolamprops* it is slightly shorter and in *Hemilamprops* it is distinctly shorter. Although this character appears to be constant, it is not always of practical value since the distal segments of the pereiopods are frequently lost or damaged, particularly in deep-water forms. However the combination of the characters mentioned above should allow most individuals to be placed in the correct genus. But it should be stressed that *only* the number of pleopods in the male is genuinely diagnostic.

Distribution

The genus consists of 22 species, widespread in the Arctic, Antarctic, Pacific, Atlantic and Southern Indian Oceans. The depth distribution is also wide, from 8 to 2 725 m.

The species occur in three distinct groups geographically: one group of eight species is found in the North Pacific, another of five species in the North

Atlantic and Arctic and the remaining group of eight species in southern oceans. Three species (two of which are new) in the last group are found in southern African waters.

There are no records for tropical or subtropical waters and no species is found both north and south of the tropics.

KEY TO THE SPECIES OF *HEMILAMPROPS* FROM THE SOUTHERN HEMISPHERE

Since the tropics form a very distinct boundary between Northern and Southern hemisphere species, a key is given only to those species occurring south of 30°S.

1 Carapace somewhat carinate ventrolaterally, more than one and a half times as broad as deep.. *H. lata* Hale, 1946—Australia
– Carapace not carinate ventrolaterally, less than one and a half times as broad as deep....2
2 Telson longer than peduncle of uropod; carapace robust, subtruncate anteriorly; pseudorostral lobes not meeting anterior to eyelobe........... *H. diversa* Hale, 1946—Australia
– Telson shorter than peduncle of uropod; carapace delicate and elongate; pseudorostral lobes meeting for some distance anterior to eyelobe................................3
3 Telson with ten to twelve pairs of lateral spines; middorsal carina of female finely serrate; carpus of pereiopod 2 long and slender, distinctly more than half length of basis; pseudorostrum pointed anteriorly in lateral view.... *H. pellucidus* Zimmer, 1908—Southern Ocean
– Telson with no more than six pairs of lateral spines; middorsal carina and pseudorostrum variable; carpus of pereiopod 2 less than half length of basis.........................4
4 Anterior tip of pseudorostrum slightly uptilted; anterolateral edge and middorsal carina bearing long, slender spines; telson less than half length of peduncle of uropod with five pairs of small spines laterally and three long ones terminally........ *H.* sp.—South Africa
– Anterior tip of pseudorostrum not uptilted; carapace without spines middorsally or laterally (may be denticulate); telson as long or almost as long as peduncle or uropod with zero to six pairs of spines laterally and three to five terminally............................5
5 Telson with five long spines terminally and none laterally; carapace fairly broad and truncate anteriorly in dorsal view; basis of maxilliped 3 widely expanded, carpus very large and expanded .... *H. glabrus* sp. nov.
– Telson with three long spines terminally and one to six pairs laterally; carapace fairly slender and pointed anteriorly in dorsal view; neither basis nor carpus of maxilliped 3 much expanded 6
6 Peduncle of uropod subequal in length to endopod.... *H. lotusae* Băcescu, 1969—Argentine
– Peduncle of uropod subequal in length to exopod.................. 7
7 Telson with six pairs of lateral spines; carapace finely denticulate middorsally...........
H. serrulata Ledoyer, 1977—Kerguelen
– Telson with three pairs of lateral spines; carapace smooth middorsally.................
H. ultimaspei Zimmer, 1921—Tierra del Fuego

Hemilamprops pellucidus Zimmer, 1908

Figs 11–12

H. pellucidus Zimmer, 1908: 172–173, figs 53–59; 1913: 456–457. Stebbing 1912: 144–145, pl. 52. Jones 1963: 52–53, figs 192–201; Jones 1969: 119.

Records

SAM–A594 (PF 17386)	34°27′S 17°42′E	849 m	1 subadult ♂: 7,4 mm; 1 ♀: 8,0 mm
SAM–A595 (PF 15785)	34°39′S 18°10′E	500 m	4 subadult ♂♂: 5,8–8,0 mm; 4 ovig. ♀♀: 8,3–8,6 mm; 9 ♀♀: 6,1–9,0 mm

SAM–A10601 (PF 12605)	30°33′S 30°58′E	805 m	1 subadult ♂: 6,8 mm
SAM–A10602 (PF 17440)	34°25′S 17°45′E	800 m	2 subadult ♂♂: 7,0–8,0 mm; 1 ♂: 6,9 mm; 2 ovig. ♀♀: 8,6–9,9 mm; 1 juv. 4,6 mm
SM 60	27°09′S 32°58′E	800 m	1 adult ♂: 7,8 mm; 2 subadult ♂♂: 5,8–7,0 mm; 3 ♀♀: 6,4–9,6 mm
SM 69	27°12′S 32°56′E	660 m	1 damaged ♂
SM 86	27°59′S 32°40′E	550 m	6 adult ♂♂: 7,4–8,6 mm; 6 subadult ♂♂: 6,1–7,7 mm; 5 ♂♂: 5,8–6,4 mm; 5 ovig. ♀♀: 9,0–11,2 mm; 5 ♀♀: 5,4–8,3 mm; 5 juvs: 3,8–5,4 mm
SM 109	28°41′S 32°36′E	1 300 m	1 subadult ♂: 7,4 mm; 1 ♀: 7,4 mm
SM 129	30°53′S 30°31′E	850 m	1 damaged ♂; 2 ovig. ♀♀: 9,0–9,3 mm
SST 17P	35°22′S 22°31′E	200 m	1 ♀: 6,4 mm
LBT 67A	32°04′S 17°12′E	200 m	1 subadult ♂: 6,7 mm; 3 ♀♀: 5,8–7,0 mm
LBT 70C	32°07′S 17°12′E	330 m	1 juv.: 5,1 mm
LBT 72D	32°07′S 17°31′E	400 m	3 subadult ♂♂: 5,8–7,7 mm

Previous records

Agulhas Bank, 126 to 596 m (Zimmer 1908, 1921); Chatham Rise, 238 to 535 m (Jones 1963); Antarctic, 2 725 m (Zimmer 1913); Great Australian Bight, 1 320 to 1 340 m (Jones 1969); off Recife, Brazil, >1 000 m (Jones pers. comm.).

Holotype

Not designated: young male and female syntypes deposited in the Berlin Zoologisches Museum. Type locality: 564 m, on the Agulhas Bank (35°09′S 18°32′E).

Description

Adult male, length 7,4 mm (SM 86). Integument thin, pellucid, finely reticulate. Gut-contents black. Carapace (Fig. 11A) elongate, twice as long as deep. Pseudorostral lobes short, roundly pointed anteriorly. Antennal notch a slight excavation below pseudorostrum. Eyelobe (Fig. 11B) small, pointed, with several small denticles in midline. Carapace swollen posteriorly on either side of shallow middorsal depression. Middorsal carina evident anteriorly, denticulate only on eyelobe. Carapace less than half length of rest of body. Pedigerous somites all visible, not flanged laterally. Abdominal somites cylindrical.

First segment of antenna 1 (Fig. 11C) longer than next two together. Flagellum 4-segmented with several small aesthetascs at base; accessory flagellum 3-segmented.

Flagellum of antenna 2 (Fig. 11D) reaching almost to end of body.

Palp of maxilla 1 with two filaments.

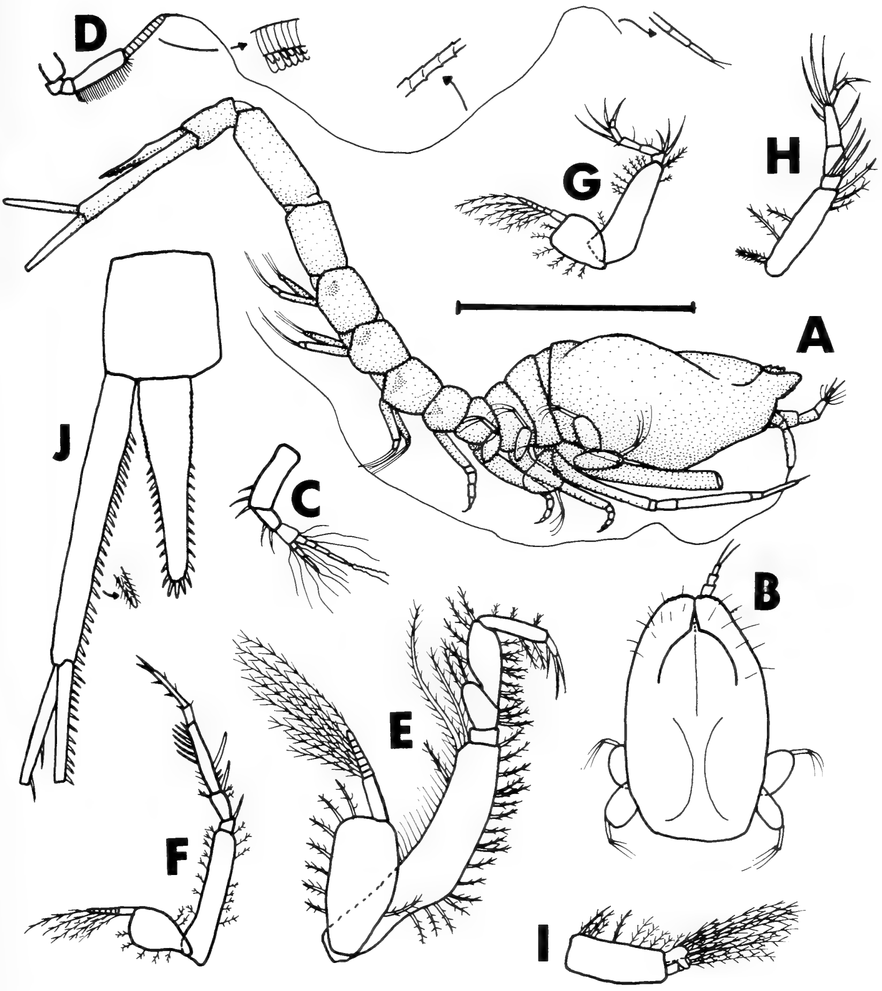

Fig. 11. *Hemilamprops pellucidus*

Adult male. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Antenna 2. E. Maxilliped 3. F. Pereiopod 2. G. Pereiopod 3. H. Pereiopod 5. I. Pleopod 2. J. Uropod and telson.

Scale line = 4 mm for A–B; 2 mm for C–J.

Basis of maxilliped 3 (Fig. 11E) slightly longer than rest of limb. Carpus stout and slightly expanded. Propodus about twice length of dactyl.

Distal segments of pereiopod 1 missing from all specimens. Exopod large and very well developed.

Basis of pereiopod 2 (Fig. 11F) little more than half length of rest of limb. Carpus elongate with several fine spines. Exopod large and almost circular in outline.

Pereiopods 3 (Fig. 11G) and 4 similar. Basis of pereiopod 3 very large and stout, of pereiopod 4 less so.

Pereiopod 5 (Fig. 11H) shorter, basis subequal in length to rest of limb.

Three pairs of typical pleopods present (Fig. 11I).

Telsonic somite (Fig. 11J) less than half length of preceding somite, about two-thirds length of peduncle of uropod. Pre-anal part of telson less than half of total length, serrated laterally. Post-anal part narrower with ten to twelve pairs of small lateral spines and three terminally.

Peduncle of uropod slender with many fine spines on inner edge. Distal portions of both rami missing from all males.

Adult female, length 11,2 mm (SM 86). As male, except as follows: eyelobe (Fig. 12A) without serrations; middorsal carina very finely serrate. Carapace (Fig. 12B) considerably wider posteriorly than anteriorly.

Antenna 1 (Fig. 12C) smaller, without aesthetascs. Antenna 2 (Fig. 12D) 3-segmented. Maxilliped 3 (Fig. 12E) stouter, carpus relatively longer. Exopods of pereiopods much smaller. Basis of pereiopod 1 (Fig. 12F) strongly serrate, subequal in length to next four segments together; propodus and dactyl long, slender and subequal in length. Basis of pereiopod 2 (Fig. 12G) shorter, carpus

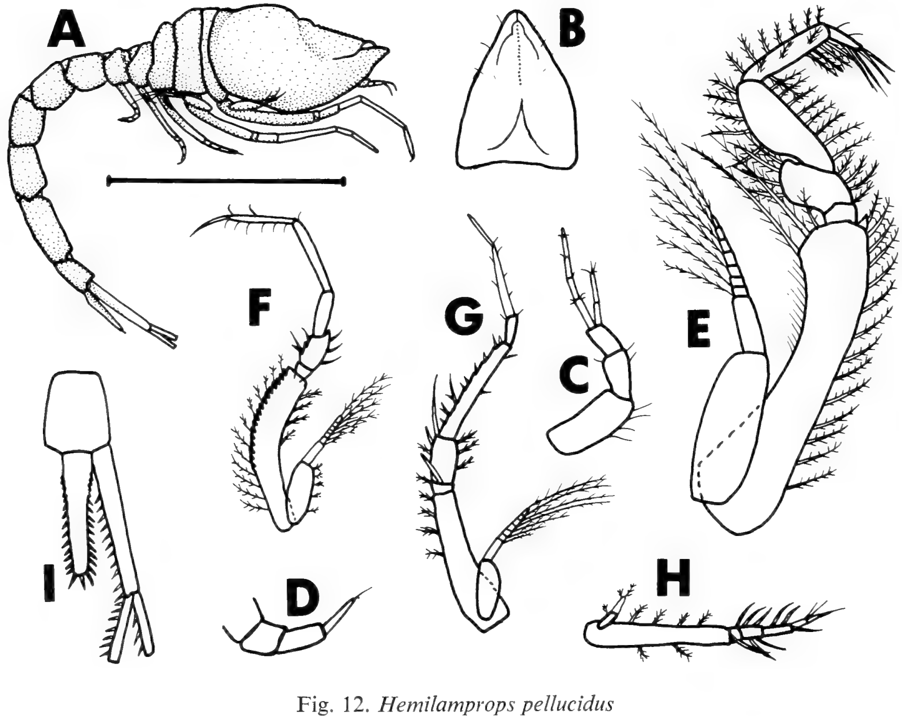

Fig. 12. *Hemilamprops pellucidus*

Adult female. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Antenna 2. E. Maxilliped 3. F. Pereiopod 1. G. Pereiopod 2. H. Pereiopod 3. I. Uropod and telson. Scale line = 4 mm for A–B; 2 mm for F–I; 1 mm for C–E.

longer. Bases of pereiopods 3 (Fig. 12H) and 4 shorter and more slender; exopods 2-segmented.

Telson (Fig. 12I) slightly longer, peduncle of uropod with fewer spines.

Remarks

This species is readily identifiable by the pellucid nature of the integument, nearly always resulting in the gut being clearly visible: in the present specimens it is black or dark brown. It closely resembles a number of other species in which the carapace is of similar shape, but may be distinguished from them as follows: *H. cristata* (Sars, 1869), *H. glabrus* sp. nov., *H. ultimaespei* Zimmer, 1921, *H. lotusae* Băcescu, 1969, *H. serrulata* Ledoyer, 1977, and *Hemilamprops* sp. all have no more than five pairs of lateral spines on the telson. *H. normani* Bonnier, 1896, has a shorter telson and uropodal peduncle and the middorsal carina is slightly serrated in the male. *H. pellucidus* most closely resembles *H. tanseiana* Gamô, 1967, differing from it in the greater number of lateral spines on the telson, the reduced serrations on the middorsal carina, the longer uropod and telson and the larger and more expanded merus and carpus of maxilliped 3 in *H. pellucidus*.

The individuals figured by Stebbing (1912) and Zimmer (1908) differ in several respects from each other and also from those figured here. The shape of the carapace in subadult males differs slightly, as does the length of the telson and its number of lateral spines. Adult males also have a longer telson and more, but smaller, spines on the peduncle of the uropod in the present specimens. Other differences can be attributed to varying age and sex. The adult female differs from that figured by Zimmer in the length of the propodus and dactyl of pereiopod 1 and from Stebbing's as well as from Zimmer's in the slightly longer and stouter telson. However, it seems that the specimens from SAM–A594 are the selfsame ones described and figured by Stebbing, and in fact these fit well within the range of variation of the other individuals available for examination. Thus it is clear that the present specimens can be referred to Zimmer's *H. pellucidus* without any great doubt.

Distribution

This is one of the few species of Cumacea which occurs in southern African waters without being endemic. It appears to be widespread throughout the southern oceans at depths from 126 to 2 725 m.

Hemilamprops glabrus sp. nov.

Fig. 13

Records

SM 109	28°41′S 32°36′E	1 300 m	1 ovig. ♀: 7,0 mm (holotype); 2 ♀♀: 6,4–7,2 mm; 2 mancas: 2,9–3,2 mm

Holotype

Ovigerous female, in the South African Museum, SAM–A15680, collected by the *Meiring Naude*, 25 May 1976. Type locality: 1 300 m, off northern Natal (28°41′S 32°36′E).

Description

Ovigerous female, holotype, length 7,0 mm. Integument rather thin and translucent. Carapace (Fig. 13A) fairly short, swollen posteriorly on either side of shallow middorsal depression. Pseudorostral lobes short and truncate anteriorly with an indistinct anterolateral carina running posteriorly for a short distance, bearing a few denticles above. Carapace in dorsal view (Fig. 13B) slightly flattened, distinctly broader than deep. Eyelobe small, rounded and

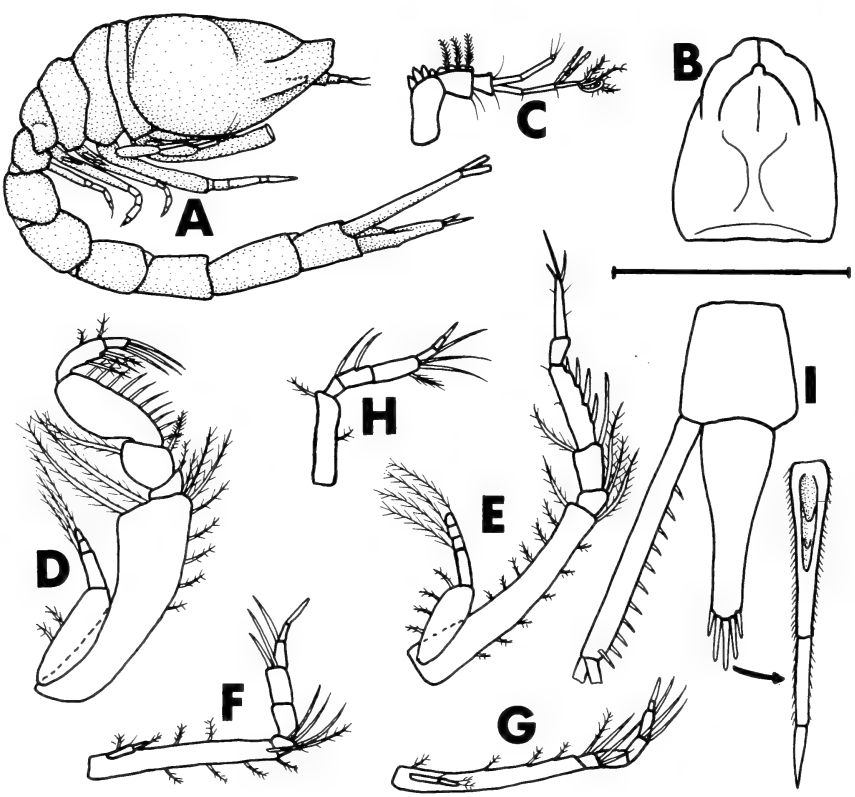

Fig. 13. *Hemilamprops glabrus* sp. nov.

Ovigerous female, holotype. A. Lateral view. B. Dorsal view of carapace. C. Antenna 1. D. Maxilliped 3. E. Pereiopod 2. F. Pereiopod 3. G. Pereiopod 4. H. Pereiopod 5. I. Uropod and telson.

Scale line = 2 mm for A–B; 1 mm for C–I.

eyeless. Pedigerous somites rather deep, all visible. Abdominal somites cylindrical, together subequal in length to cephalothorax. Marsupium small.

Antenna 1 (Fig. 13C) fairly short, both flagella 3-segmented, third segment of accessory flagellum very short.

Palp of maxilla 1 with two filaments.

Basis of maxilliped 3 (Fig. 13D) very stout, slightly shorter than rest of limb: no more than three times as long as wide and particularly expanded distally. Merus wide, carpus large and flattened.

Segments distal to basis missing from pereiopod 1 in all specimens.

Pereiopod 2 (Fig. 13E) slender, basis subequal in length to rest of limb; carpus relatively short, subequal in length to propodus and dactyl together.

Pereiopods 3 (Fig. 13F) and 4 (Fig. 13G) similar. Exopods very small, 2-segmented.

Pereiopod 5 (Fig. 13H) short, basis shorter than rest of limb.

Telsonic somite (Fig. 13I) almost square in dorsal outline, more than half length of telson. Telson slightly shorter than peduncle of uropod, wider proximally; lateral edges entirely smooth; apex with five long stout complex spines. Peduncle of uropod with several small sharp spines on inner edge. Rami missing from all specimens.

Males are not available.

Remarks

It has already been remarked that without mature males it is not possible to place species conclusively in *Lamprops*, *Mesolamprops* or *Hemilamprops*. In this case the first pereiopod cannot be used either since the distal segments are missing in all specimens. However, the general appearance of the specimens, together with their locality, strongly suggests that they should be placed in *Hemilamprops*. In some respects, they do bear a slight resemblance to *Lamprops ? comata* Zimmer, 1907 from deep water off Tierra del Fuego, but since this species is known only from a single fragmentary female, no reasonable comparison is possible.

Within *Hemilamprops*, *H. glabrus* is easily distinguished by the short, stout basis of maxilliped 3 and the shape of the carapace. From those species which it most closely resembles it may be distinguished as follows: from *H. pellucidus* Zimmer, 1908, *H. cristata* (Sars, 1869), *H. tanseiana* Gamô, 1967, *H. normani* Bonnier, 1896, *H. serrulata* Ledoyer, 1977, and *Hemilamprops* sp. by the absence in *H. glabrus* of lateral spines on the telson and denticles on the mid-dorsal carina; from *H. ultimaespei* Zimmer, 1921, and *H. lotusae* Băcescu, 1969, in that it has five terminal spines on the telson and none at all laterally and that its carapace is much broader and truncate anteriorly.

Distribution

Known only from the type locality: northern Natal at 1 300 m.

Hemilamprops sp.

Fig. 14

Records

SAM–A10607 (PF 16982)	1 200 m	34°40′S 17°50′E	2 ovig. ♀♀: 9,6–10,2 mm; 1 ♀: 9,1 mm; 1 damaged ♀

Remarks

Although four individuals of this species are available, all of them are too badly damaged to allow an adequate description. Figure 14A is a composite drawing of the undamaged parts of both ovigerous females.

None the less the carapace and telson are quite distinct from those of any other known species. In particular, the denticles anteriorly along the mid-dorsal carina and on the anterolateral margin of the carapace (Figs 14A and 14B) are longer and sharper than those of any known species, while the telson (Fig. 14C) is characteristically short, with the three terminal spines particularly long and slender. In these characters it is unique in the genus, so that it should not prove difficult to identify further specimens as belonging to the same species.

It is tentatively placed in *Hemilamprops* for the same reasons as those given above for *H. glabrus*. However, the same cautionary note must be sounded until adult males are available to confirm its generic position.

Distribution

Known only from a single sample from a depth of 1 200 m off the Cape Peninsula.

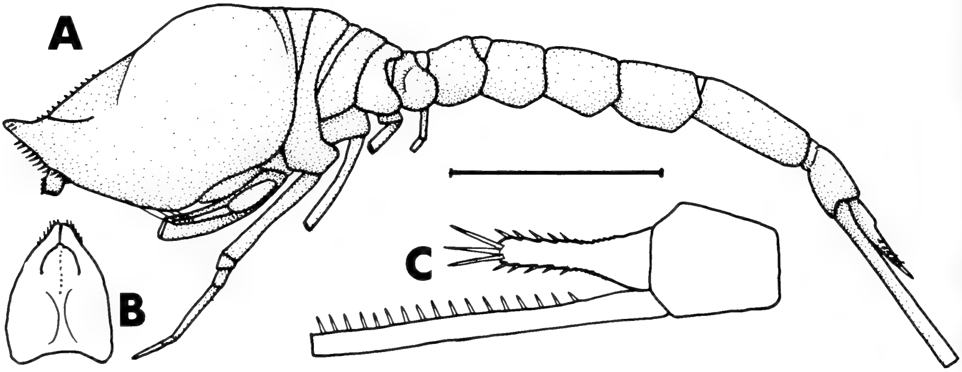

Fig. 14. *Hemilamprops* sp.
Adult female. A. Lateral view. B. Dorsal view of carapace. C. Uropod and telson.
Scale line = 4 mm for B; 2 mm for A; 1 mm for C.

DISTRIBUTION OF LAMPROPIDAE

With only fifty-eight species, the family is rather small, constituting less than 10 per cent of known species of Cumacea. Table 1 details the world-wide distribution of lampropids according to latitude and depth. It can be seen that the family is generally confined to deep and/or cold waters and has a bipolar distribution. 58 per cent of the species-records are from latitudes north of 20°N, 6 per cent between 20°N and 20°S and 36 per cent south of 20°S. Thus very few species are known from the tropics: one of these is recorded from 390 m and the rest from depths greater than 800 m, where temperatures are considerably lower than on the surface. This pattern of distribution shows a direct contrast to that of the Bodotriidae where 38 per cent of the species are found in the tropics (between 20°N and 20°S) (Day 1978).

TABLE 1. Distribution of Lampropidae according to depth and latitude (data mainly from Jones 1969). Species may be entered more than once if they have been recorded from widely different depths or localities. The entry marked * is also entered under '5–200 m' and is, therefore, excluded from the total count of species.

	Shore–5 m		5–200 m		200–2 000 m		> 2 000 m		Total	
	no.	%	no.	%	no.	%	no.	%	no.	%
N of 70°N . . .	1	1+	1	1+	0	0	0	0	2	3
50–70°N . . .	1	1+	12	18	9	13	0	0	22	32
20–50°N . . .			11	16	3	5	2	3	16	23
20°N–20°S . . .			0	0	3	5	1	1+	4	6
20–50°S			3	5	12	18	1	1+	16	24
50–70°S			2	3	0	0	0	0	2	3
S of 70°S . . .			1	1+	2	3	3	5	6	9
Total no. of records	2	3	30	44	29	43+	7	10+	68	100
Total no. of species	1*	1+	26	44	25	42	8	13	59	100

Assuming that the distribution of the lampropids is indeed limited by water temperature, then those species living in shallow water (less than 200 m) would be expected to occur at higher, cooler latitudes. This is shown by the fact that there are no records for shallow waters between 20°N and 20°S, which is not merely a reflection of collecting effort, since 36 per cent of bodotriids are found in the same situation.

Similarly it can be shown that the lampropids preponderate in northern waters, since there are nearly twice as many species (58 %) recorded north of 20°N as there are south of 20°S (36 %). Percentages for the bodotriids are again in inverse proportion to this: 24 per cent occur north of 20°N and 37 per cent south of 20°S.

Fully 55 per cent of lampropids are recorded from depths greater than 200 m (less than 8 % for bodotriids) and 12 per cent below 2 000 m (less than 1 % for bodotriids).

Thus the lampropids form a bipolar group, preferring deep, cold water and avoiding the tropics. Because the collecting effort has been minimal in deep waters, it is suggested that the number of species of lampropid is artificially low. It is predicted that the number of new species in this family will increase rapidly if more collecting is done in deep waters. This prediction is supported by the fact that in the present paper, of the ten species described, six are new.

Of the eleven genera, four (*Mesolamprops* Given, 1964, from California, *Archaeocuma* Băcescu, 1972, from Peru, *Chalarostylis* Norman, 1879, from the North Atlantic and *Stenotyphlops* Stebbing, 1912, from South Africa) are monotypic and their distribution need concern us no further.

Bathylamprops Zimmer, 1908, consists of three species from deep waters, two off the east coast of Africa and one off Florida, and *Pseudodiastylis* Calman, 1905, of two species from deep tropical waters. The remaining genera together consist of fifty species.

Lamprops Sars, 1863, contains twelve species, all from shallow waters at depths less than 200 m and all from the northern hemisphere. Three of these occur mainly between 20° and 50°N and the rest are found north of 50°N, particularly in the region of the Bering Strait. The possible affinities of *Lamprops? comata* are discussed above. *Lamprops fasciata* is the only species in the family to have been found intertidally.

Hemilamprops Sars, 1883, consisting of twenty-one species, is very widespread, representatives being found from the Arctic to the Antarctic, from the Pacific, Atlantic, Indian and southern oceans at depths from 8 to more than 2 000 m. The species fall into three groups: 8 species occur in the North Pacific (Japan to California), 5 in the North Atlantic and Arctic and 8 around South America, South Africa and Australasia. None occurs between 30°N and 30°S. The genus is bipolar, and follows the distribution pattern shown by the family as a whole.

Platysympus Stebbing, 1912, now consists of 7 species, all from waters deeper than 200 m. 2 species are known from the North Atlantic and Norway, and 5 from the Southern hemisphere—1 from the Antarctic and the 4 new species from South Africa.

Paralamprops Sars, 1887, consists of 10 deep-water species. 3 occur in the North Atlantic from 600–3 789 m, 6 in the southern ocean from South Africa to the Antarctic at 232–3 423 m, and 1 in the East Indies at 390 m.

Many of the species are known only from a single record and since so little collecting has been done in deep water where many species normally occur, it is predictable that the actual distribution of species will prove to be much wider than it appears at present.

DISTRIBUTION OF THE SOUTHERN AFRICAN LAMPROPIDAE

Eleven species of lampropid are now known from these waters. Since they are found only at depths greater than 200 m (with a single exception at 188 m), and very little collecting has been done in deep water off southern Africa, it is difficult and perhaps misleading to distinguish any clear distribution patterns.

The frequency of occurrence is also uncertain, because earlier records are incomplete and Cumacea are not caught in all samples, sometimes because the substratum is unsuitable (rock or very coarse sand) or simply because cumaceans are scanty for some other unknown reason. There is also the simple fact that no sampling has been done off the west coast north of Lambert's Bay or off Mozambique at depths greater than 200 m. However, of the 12 grabs taken by UCT at these depths around the coast, 6 contained lampropids, as did 7 of the ten SM samples which contained any Cumacea at all. The incompleteness of the early *Pieter Faure* records is such that it is not possible to determine the exact type of collecting gear nor the number of stations. But from the previous two sets of figures it seems that lampropids are not at all uncommon deep-water forms, although they are entirely absent from waters shallower than 188 m.

In this way the South African lampropids differ from the Northern hemisphere species, of which more than 60 per cent are shallow-water forms. This is no doubt due to the fact that shallow waters in southern Africa are relatively warm.

The southern African species do not fall into any obvious groups: temperature conditions in waters deeper than 200 m do not vary much round the coast and there are many stretches of coast which have been sampled poorly or not at all. In fact, there are only five rather small regions in which sampling has been at all comprehensive. These are off Lambert's Bay, the Cape Peninsula, Still Bay, Durban, and in a fairly wide area off northern Natal.

Two species occur throughout the range: *Platysympus depressus* (21 specimens) and *Hemilamprops pellucidus* (79 specimens), which are also the two most common species in most samples. (This indicates, incidentally, that breaks in the ranges of most species are due to a paucity of numbers rather than the realistic limits of very confined ranges.) Two further species occur from the Cape Peninsula to northern Natal: *Stenotyphlops spinulosus* (17 specimens) and *Platysympus camelus* (14 specimens). The other six species, *Paralamprops peringueyi* (14 specimens), *Paralamprops margidens* (6 specimens), *Platysympus phylloides* (4 specimens), *Platysympus compressus* (8 specimens), *Bathylamprops calmani* (1 specimen), *Hemilamprops glabrus* (5 specimens) and *Hemilamprops* sp. (4 specimens) occur in only one or two regions and are therefore of little value in zoogeographic terms. The only one for which there is some little evidence for a really restricted range is *Paralamprops peringueyi* which is not uncommon off the Cape Peninsula (14 specimens in 3 samples) but has not yet been found anywhere else.

Only two of the ten species are known outside South African waters: the type specimen of *Bathylamprops calmani* was found off Dar-es-Salaam, and Jones (1969) has since recorded three specimens off Durban. The type locality is at a depth of 2 959 m and the other depth records are 2 720 and 3 530 m, suggesting that the present specimen from 1 300 m was at about the upper depth limit for the species. *H. pellucidus* is one of the most widespread of southern African Cumacea, occurring in southern oceans from the Chatham Rise, the

Antarctic, Brazil and the Great Australian Bight as well as being by far the most common lampropid in local waters, constituting half of the individuals in the present collection.

Little can be deduced about depth distributions. In some cases there is a slight tendency for individuals to occur in shallower waters off the cold west coast (*P. depressus* at 440 m off Lambert's Bay, and 550 to 680 m off northen Natal; *P. camelus* at 188 m off the Cape Peninsula, and 550 m off northern Natal; *H. pellucidus* at 200 to 400 m off Lambert's Bay, and 550 to 1 300 m off northern Natal). However, collecting on the west coast has generally been in shallower waters than on the east coast so the differences may be more apparant than real.

There is a slight indication of a change in the fauna at very roughly 800 and 1 400 m. Four species (*Platysympus depressus. P. compressus, P. camelus* and *Paralamprops margidens*) occur only at depths less than 850 m; three species (*S. spinulosus, P. peringueyi* and *P. phylloides*) are found between 300 and 1 400 m and three (*B. calmani, H. glabrus* and *Hemilamprops* sp.) at 1 200 m or more. Here again valid conclusions are limited by the fact that the greatest depth at which sampling occurred was 1 400 m.

The species-diversity of the family is fairly high. In comparison with the Bodotriidae (which are by far the most abundant locally in terms of numbers, both of individuals and of species (Day 1978)) the figures are as follows: the Bodotriidae, with 4 582 specimens, 42 species and 649 records have a ratio of 7,1 individuals per record and a specimen : species ratio of 109. The Lampropidae, with 169 specimens, 11 species and 39 records have a ratio of 4,3 individuals per record and a specimen : species ratio of 15,4. Thus lampropids occur in fewer samples and are far less abundant where they do occur, but they are far more diverse than are the bodotriids.

Family **Ceratocumatidae** Calman, 1904

Diagnosis

Five free pedigerous somites. Mandibles narrow (boat-shaped) at base. Maxillipeds 2 and 3 elongate, 7-segmented, basis not produced distally. Exopods present at least on maxilliped 3 and pereiopod 1 in both sexes. Propodus of pereiopod 1 with two lobular setose processes. Male with four to five pairs of pleopods. Telson small, unarmed and flap-like, hinged to cover anal valves. Endopod of uropod 1-segmented, exopod 2-segmented with first segment very short.

Type genus

Ceratocuma Calman, 1904.

Remarks

This is the smallest and most recently erected of the seven cumacean families. The combination of four or five pairs of pleopods in the male, together with a small telson and the setose lobes on the propodus of the first pereiopod, is quite characteristic. However, the telson is very small and is often held flapped over the anal valves so that it is sometimes difficult to detect.

Until 1969, the family was known from four specimens of a single species in two records, one from the north-western coast of Ireland at 705 m and one from about 800 m off Durban. Examination of material from deep waters in the Atlantic has increased numbers dramatically in the last few years so that the family is now known from hundreds of specimens in seven species and two genera. It is expected that further exploration of deep and abyssal waters will continue to provide useful information on this family.

Ceratocuma Calman, 1904

Generic diagnosis

Body elongate, carapace dorso-ventrally flattened with protuberances. Exopods present on pereiopod 1 in both sexes and on pereiopod 2 in the male. Pereiopods 2 to 4 very long and slender, pereiopod 5 absent. Uropods slender and elongate.

Type species

Ceratocuma horridum Calman, 1904.

Remarks

Ceratocuma is easily distinguished from *Cimmerius*, the only other genus in the family, the generic diagnosis of which reads as follows: Body not elongate. Carapace rounded, reminiscent of *Campylaspis*. Exopods present on pereiopods 1 to 4 in both sexes, reduced on pereiopod 4 in female. Pereiopod 5 present. Pereiopods and uropods not particularly elongate or slender.

In general appearance the two genera are quite different, although they both possess the familial characteristics.

Distribution of Ceratocuma

The four species are all known from the Atlantic and southern Indian oceans: one from Ireland and Natal, one from the Puerto Rico Trench, one from the Azores, and one from Panama, but all at depths of 680 m or more.

KEY TO THE SPECIES OF *CERATOCUMA*

1 About eighteen pairs of long, sharp, slender spines on carapace, others on posterior somites; carapace oval in dorsal view and rounded anteriorly (ignoring spines); telsonic somite less than half length of peduncle of uropod .... *C. reyssi* Jones, 1973—Azores

– Protrusions of carapace (about ten pairs or fewer) and posterior somites confined to blunt spines or rounded tubercles; carapace more or less rectangular in dorsal view; telsonic somite half length of peduncle of uropod or more 2

2 Carapace without paired dorsolateral tubercles or blunt spines: at most with three pairs of very low but extensive rounded protrusions .... *C. amoena* Jones, 1969—Puerto Rico Trench, off Surinam, Bay of Biscay

– Carapace with several pairs of dorsolateral protrusions, tubercles or blunt spines 3

3 Carpus of pereiopods 3 and 4 twice length of propodus; ischium and merus of pereiopod 1 together about half length of carpus.. *C. panamensis* Băcescu & Muradian, 1974—off Panama

– Carpus and propodus of pereiopods 3 and 4 subequal in length; ischium and merus of pereiopod 1 together subequal in length to carpus..................................4

4 All tubercles on carapace, including anterior ones, sharply hooked..................... *C. horridum horridum* Calman, 1904—North Atlantic

– Tubercles on anterior half of carapace low and bluntly rounded, on posterior half blunt or sharply hooked.....................................*C. horridum australe* subsp. nov.

Ceratocuma horridum Calman, 1904

C. horrida Calman, 1904: 37–40, pl. 55 (figs 57–75). Stebbing, 1913: 51–52.

Holotype

Not designated: three male syntypes, two of them mature, deposited by Calman in the British Museum (Natural History). Type locality: 705 m, off Northern Ireland.

Ceratocuma horridum australe subsp. nov.

Figs 15–16

C. horridus: Stebbing, 1912: 142–143.

Records

SM 103	28°31′S 32°34′E	680 m	1 adult ♂: 3,5 mm (holotype); 2 subadult ♂♂: 2,9 mm; 1 ovig. ♀: 3,7 mm; 2 juvs: 2,8 mm
SM 129	30°53′S 30°31′E	850 m	1 adult ♂: 4,5 mm; 1 damaged ovig. ♀
SM 151	30°14′S 30°27′E	900 m	1 ovig. ♀: 5,1 mm; 1 ♀: 3,7 mm

Previous records

Natal, 805 m (Stebbing, 1912).

Holotype

Adult male, in the South African Museum, SAM–A15722, collected by the R.V. *Meiring Naude*, 24 May 1976. Type locality: 680 m, off northern Natal (28°31′S 32°34′E).

Description

Adult male, holotype, length 3,5 mm (SM 103). Integument pale and thin, brittle, faintly reticulate. Carapace (Fig. 15A) large, slightly flattened dorsoventrally, somewhat wider than deep and nearly twice as long as deep; irregularly sculptured to form a number of low, rounded projections. In lateral view, nine pairs visible: one large pair posterodorsally, four closely-adjacent pairs posterolaterally, one pair anterolaterally, one pair immediately above the anterolateral angle, one pair middorsal and one pair midlateral. The same protuberances visible dorsally (Fig. 15B), the four outermost pairs forming the lateral edges of the carapace and causing the lateral outline to be broken;

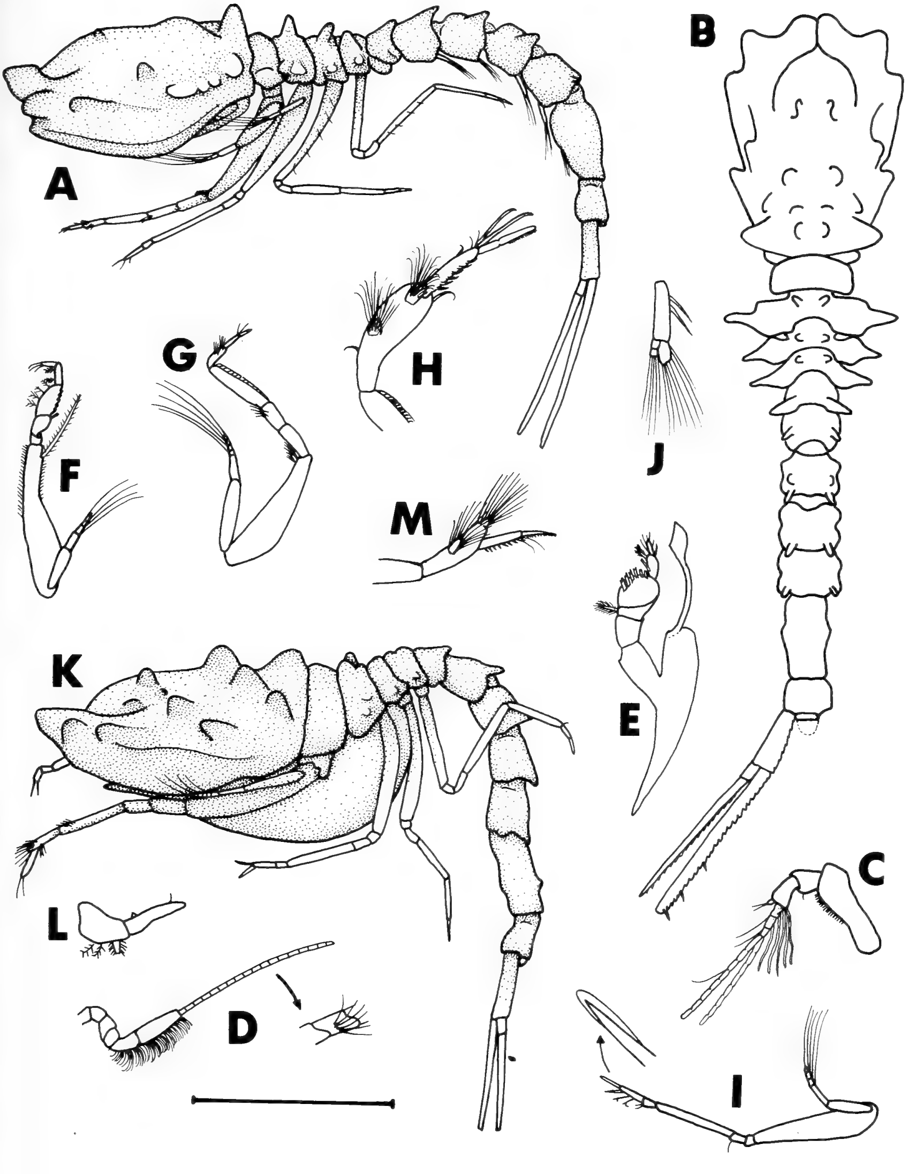

Fig. 15. *Ceratocuma horridum australe* subsp. nov. (SM 103)

Adult male. A. Lateral view. B. Dorsal view. C. Antenna 1. D. Antenna 2. E. Maxilliped 1. F. Maxilliped 3. G. Pereiopod 1. H. Distal tip of pereiopod 1. I. Pereiopod 2. J. Pleopod 3. Ovigerous female. K. Lateral view. L. Antenna 2. M. Distal tip of pereiopod 1.

Scale line = 1 mm for A–B, D, F–G, I, K; 0,5 mm for C, E, J, L–M; 0,3 mm for H.

slightly medial to these are two pairs and the last three pairs are arranged in longitudinal rows just lateral to midline. Middorsal carina absent. Eyelobe small and eyeless. Carapace slightly less than twice length of pedigerous somites together.

All five pedigerous somites visible, first slightly wider than deep without lateral expansions; second, third and fourth expanded ventrolaterally forming wide, pointed lateral extensions and dorsolaterally forming smaller, low protuberances. Last pedigerous somite without appendage, small and similar to abdominal somites. First four abdominal somites produced to slight points dorsolaterally, fifth elongate, sixth small and wider than long or deep. Cephalothorax longer than abdomen.

Antenna 1 (Fig. 15C) short, first segment longer than next two together. Accessory flagellum very small, 1-segmented. Flagellum short, 3-segmented with two aesthetascs.

Antenna 2 (Fig. 15D) shorter than carapace with short, poorly-setose segments.

Palp of maxilla 1 with two filaments.

Maxilliped 1 (Fig. 15E) with a single branchial leaflet; carpus very widely expanded.

Maxilliped 3 (Fig. 15F) normal, merus and carpus very slightly expanded.

Basis of pereiopod 1 (Fig. 15G) subequal in length to next three segments together. Ischium longer than merus, together subequal in length to carpus. Carpus elongate with laminar expansion on inner edge. Propodus (Fig. 15H) with two setose lobes, one at midlength and one subterminally. Dactyl narrow, shorter than propodus, with a number of small spines.

Pereiopod 2 (Fig. 15I) elongate with small exopod. Basis shorter than rest of limb; ischium very short, merus little longer. Carpus elongate, half length of propodus and dactyl together, unarmed. Terminal spine on dactyl with flattened tip.

Pereiopods 3 and 4 elongate, without exopod. Pereiopod 5 lacking (suppressed).

Telson very small, usually folded over anal valves; rounded when extended.

Peduncle of uropod much shorter than rami, serrated on inner edge. Both rami serrated on inner edge, otherwise poorly armed: both appear broken at tip.

Ovigerous female, paratype, length 3,7 mm (SM 103). As male, except as follows: carapace (Fig. 15K) with protuberances better developed, also nine pairs: one large pair posterolaterally; two sets of three pairs arranged transversely, the most dorsal pair in each case also being most anterior; two pairs laterally immediately behind anterolateral corner. First two pedigerous somites wider and deeper, all with much reduced lateral expansions, and dorsal expansions hardly evident. Marsupium large and well developed.

Antenna 2 (Fig. 15L) small and apparently 2-segmented. Second and third segments of antenna 1 slightly smaller. Propodus of pereiopod 1 (Fig. 15M) smaller, one of the setose lobes at distal tip; dactyl inserting subterminally about a third of total length from distal tip. Pereiopod 2 without exopod. Telson slightly rounder and broader. Rami similar but distal tips missing.

Adult male, length 4,5 mm (SM 129). At first glance the two individuals from SM 129 and the ovigerous female from SM 151 look very different from the rest. However, these differences appear to be confined to the sculpturing of the carapace, and the appendages (except for the distal segments of pereiopod 1) are identical in all important respects. The sizes of the individuals also vary quite considerably. But it does not seem possible to pinpoint any really significant differences which would allow specific differentiation and it would therefore seem that we are dealing with a single polymorphic species.

The adult male from SM 129 (Fig. 16A) differs from that figured in Fig. 15A as follows: the five posterior pairs of protuberances on the carapace are drawn out to form distinct points and the anterior pairs are either very much reduced or absent. The tips of these points are very delicate, almost transparent and very easily broken off, so that the apparent degree of development of these may not be of great significance. The expansions of the second and third pedigerous somites and the first four abdominal somites are very much better developed: these too are easily damaged and one is broken off. In dorsal view (Fig. 16B) the second lateral pair of protuberances from the anterior end is

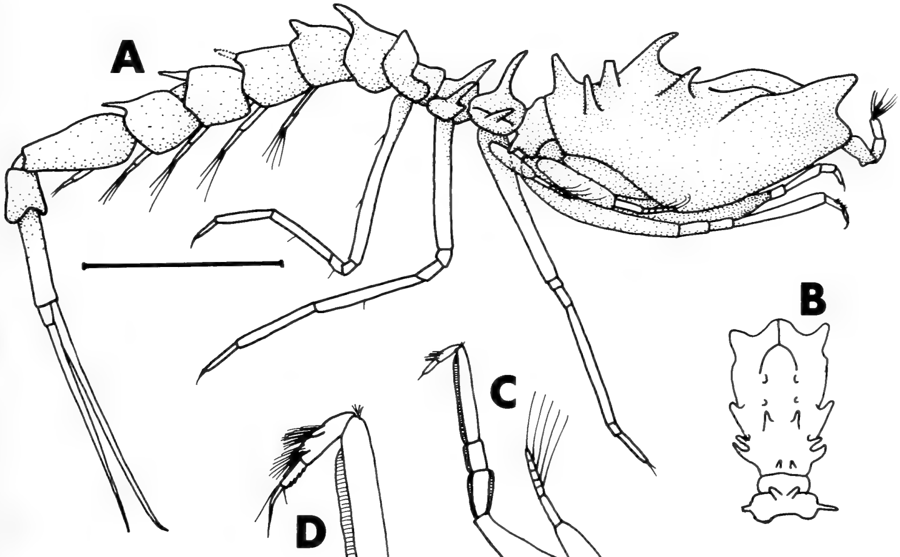

Fig. 16. *Ceratocuma horridum australe* subsp. nov. (SM 129)
Adult male. A. Lateral view. B. Dorsal view of carapace. C. Pereiopod 1. D. Distal tip of pereiopod 1.
Scale line = 2 mm for B; 1 mm for A, C; 0,5 mm for D.

much smaller, the third and fourth better defined and more pointed, as are the two posterodorsal pairs. The ovigerous female is the same in all respects as the male.

Pereiopod 1 of the male (Fig. 16C) differs slightly in that the inner edge of the ischium, merus and carpus have laminar expansions, the carpus is nearly one and a half times the combined length of the ischium and merus and the propodus is shorter (Fig. 16D). The peduncle of the uropod is also slightly longer relative to the fifth abdominal somite.

Remarks

The systematic position of these individuals is not indisputable. The appendages of all four species known so far are very similar, while the sculpturing of the carapace in particular and the rest of the body in general varies quite considerably. *C. reyssi* Jones, 1973, from the Azores, can easily be distinguished by the numerous long, slender spines, not only on the carapace but also on the first, fourth and fifth pedigerous and all abdominal somites except the last. The pseudorostrum, too, is pointed anteriorly without a broad, flanking projection on either side. There are other minor differences in the proportions of the limbs as well, so that this species is clearly distinct from the others.

C. amoenum was described by Jones (1969) on the basis of the cephalothorax of a single male from the Puerto Rico Trench. He has since (pers. comm.) found undamaged specimens of the same species from Surinam and the Bay of Biscay in which the sculpturing of the carapace is the same as that figured and which species he confirms to be easily distinguishable from *C. horridum* in all cases. It is further distinguished by 'the uropod peduncles being relatively long (compared with *C. horridum*) in proportion to the rami', and some fully adult males have only four pairs of pleopods. *C. amoenum*, then, is also clearly distinct.

C. panamensis Băcescu & Muradian, 1974, from north-east of Panama, differs from *C. horridum* in the smaller number of protuberances on the carapace and thorax and the proportions of the distal segments of the pereiopods. As the authors point out, it is very close to *C. horridum*; certainty about the validity of the species will have to await the collection of adult males.

C. horridum was described by Calman (1904) on the basis of three males, two of which were mature. Jones (pers. comm.) has since found large numbers in the North Atlantic and off Surinam, all of which clearly belong to Calman's species. Stebbing (1912) identified (but did not figure) a single specimen from Durban as *C. horridum*, saying that it differed from Calman's description and figures only 'in a small bulbous expansion of the base of [the] peduncle (of the uropod)'. The several other specimens now available from South Africa are problematical. Some approach *C. amoenum* in having low protuberances on the carapace, while others are very similar to Calman's description of *C. horridum*, having long, slender spine-like processes. However, close comparison of the structure and positioning of the protuberances in the present specimens shows them to be very similar to each other, although the magnitude of the sculpturing differs considerably. The sculpturing—in the form of sharp digitiform processes in some cases and merely raised bumps in others—is very similar in arrangement to that figured by Calman for *C. horridum.* The structure of the limbs is almost identical in both South African forms and in the description of *C. horridum,* confirming that they are very similar. It therefore seems appropriate to consider these specimens as belonging to *C. horridum.*

Even in those specimens in which the carapace most closely approaches that figured by Calman, the sculpturing is greatly reduced anteriorly and the dactyl of pereiopod 1 inserts terminally on the propodus. In those specimens with all the sculpturing reduced, the dactyl inserts subterminally, as it does in Calman's figure. Since the central and northern Atlantic form of the species seems to be quite uniform, it is proposed to distinguish the local specimens subspecifically as *C. horridum australe.* Due to the considerable variation within as well as between samples, even the subspecies must be considered at least to be highly polymorphic. Whether this polymorphism will prove sufficient for erecting two species or subspecies in the place of *C. horridum australe* will have to await the collection of a much larger number and wider range of individuals. At such time, it should also be possible to determine the relationship between the local subspecies and *C. horridum sensu* Calman.

Distribution

Natal from 680 to 900 m.

DISTRIBUTION OF CERATOCUMATIDAE

With the family consisting of only seven species in two genera, it is not possible to draw many inferences from its distribution. It is worth noting, however, that all seven species appear to be confined to the Atlantic and south-western Indian Ocean (including Kerguelen). They are cold- and deep-water forms, the depth at which they are found being reciprocal to the latitude, except in records from the deepest waters.

Anatomically, *Ceratocuma* appears to form a cline of species differing mainly in the sculpturing of the carapace but its distribution in the Atlantic is rather haphazard and available evidence shows no relationship between morphology and geographical distribution.

ACKNOWLEDGEMENTS

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

JENNIFER DAY

SOUTHERN AFRICAN CUMACEA

PART 3

FAMILIES LAMPROPIDAE AND CERATOCUMATIDAE

VOLUME 76 PART 4 AUGUST 1978 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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

2. LAYOUT should be as follows:

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

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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

Footnotes should be avoided unless they are short and essential.

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

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

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

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

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

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

'Smith (1969) describes . . .'
'Smith (1969: 36, fig. 16) describes . . .'
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Note: no comma separating name and year
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FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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THREE NEW SPECIES OF HARPACTICOIDA (CRUSTACEA, COPEPODA) FROM SANDY BEACHES IN ALGOA BAY, SOUTH AFRICA, WITH KEYS TO THE GENERA *ARENOSETELLA*, *HASTIGERELLA*, *LEPTASTACUS* AND *PSAMMASTACUS*

By

ANTON McLACHLAN
&
COLIN G. MOORE

Cape Town Kaapstad

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Isle of Man, and Zoology Department, University of Port Elizabeth,
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(With 7 figures)

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ABSTRACT

A new species of harpacticoid copepod of the family Ectinosomatidae, *Arenosetella fimbriaticauda* sp. nov., is described from Algoa Bay, South Africa. It appears related to *A. duriensis* Galhano and *A. littoralis* Bodin from which it differs in the setation of the endopodites of the walking legs. It is proposed that *Hastigerella palpilabra* Nicholls and *A. monensis* Moore are synonymous with *H. tenuissima* (Klie) which is transferred to the genus *Arenosetella*. Two new species of the family Cylindropsyllidae are also described. *Leptastacus naylori* sp. nov. differs from all described species of *Leptastacus* in the setation of the walking legs, while *Psammastacus erasmusi* sp. nov. appears closely related to *P. ghanai* (Chappuis & Rouch) from which it differs in the setation of the fourth leg and the structure of the fifth leg and furcal rami. Keys to all these genera are provided.

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Ann. S. Afr. Mus. **76** (4), 1978: 191–211, 7 figs.

PART 1

INTRODUCTION

During investigations of the meiofauna of sandy beaches in Algoa Bay, South Africa, specimens were collected of an interstitial harpacticoid of the family Ectonisomatidae Sars, 1903, genus *Arenosetella* Wilson, 1932, thought to be new to science. This species, referred to as *Hastigerella* sp. A by McLachlan & Furstenberg (1977), is abundant around the high tide level on King's Beach and has also been recorded on Sunday's River Beach, Algoa Bay. The physical characteristics of these exposed sandy beaches have been described by McLachlan (1977).

SYSTEMATIC DESCRIPTION

Family **Ectinosomatidae** Sars

Arenosetella fimbriaticauda sp. nov.

Material

A number of specimens were extracted from fine sand collected at the spring high tide level on King's Beach (25°39′E 33°57′S) and preserved in 5 per cent buffered formalin. For examination adult male and female specimens were dissected in lactic acid and mounted in polyvinyl lactophenol.

Holotype

1 dissected ♀ (SAM–A15708) deposited with the South African Museum Cape Town, South Africa.

Allotype

1 adult ♂ (SAM–A15712) in the South African Museum.

Paratypes

2 ♂♂ (SAM–A15710 and 15711) and 1 ♀ (SAM–A15709) in the South African Museum.

Other specimens are in the first author's collection.

Description of adult female

Length 0,30–0,32 mm from base of rostrum to base of furcae. Body (cf Fig. 1A) vermiform, cylindrical, with subtriangular pointed rostrum. Cephalothoracic shield rectangular in dorsal view, with striations and bearing fine hairs anteriorly. Cephalothorax about half as long as four free thoracic somites combined; cephalothorax and thorax together slightly longer than abdomen. Hyaline frill striated; cephalothorax and first two free thoracic somites fully-incised obtusidigitate becoming acutidigitate (Moore 1976*a*) posteriorly; penultimate somite (Fig. 1C–D) semi-incised subulate with small pseudoperculum dorsally and similar lobe ventrally; remaining somites deeply-incised subulate (Fig. 1B). Cuticle of anal somite drawn out into rows of weak spinuli-

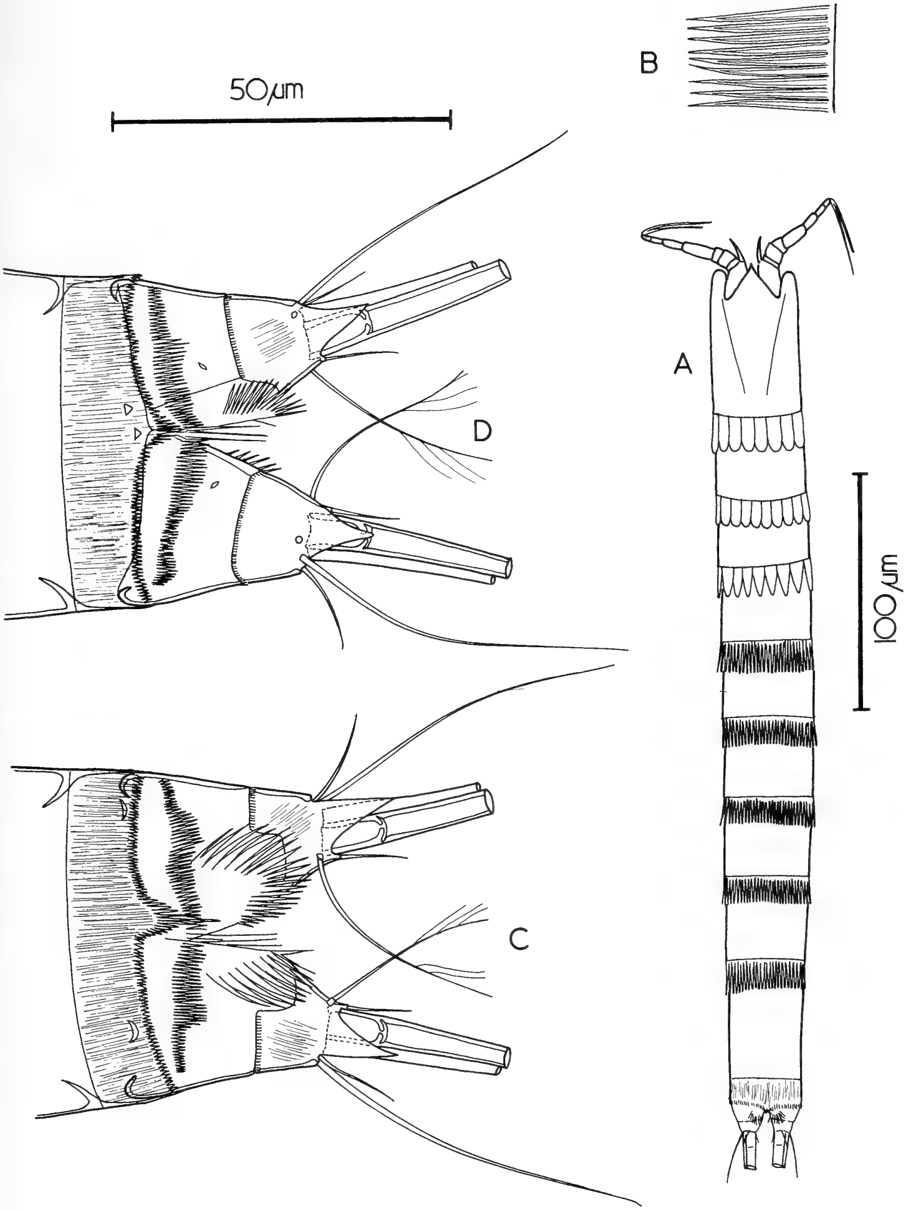

Fig. 1. *Arenosetella fimbriaticauda* sp. nov.
A. ♂ dorsal. **B.** ♀ abdominal hyaline frill. **C.** ♀ furcae dorsal. **D.** ♀ furcae ventral.

form lappets; anterior row present dorsally and ventrally and apparently continuous inside median somitic cleft; posterior row of larger lappets curving from the inner surface of the cleft onto the dorsal surface. Posterior margin of anal somite with row of minute spinules. Genital double somite without obvious signs of subdivision.

Furcal ramus (Fig 1C–D). Striated, slightly wider than long and tapering distally (the specimen from which the drawings were made was slightly flattened). Two principal terminal setae, inner one about as long as abdomen and free thoracic somites combined and twice as long as outer one; accompanied to the outside by one long and one short fine seta and to the inside by one short and one longer, distally-plumose, fine seta. Distal margin of furca drawn out into one dorsal and one ventral triangular lappet.

Antennule (Fig. 2A). Five-segmented, but segment five may possibly be composed of a short proximal and a longer distal component. First segment with a large plumose seta at anterior distal corner and a transverse row of fine spinules on anterior surface. Third and terminal segments each supplied with one aesthetasc.

Antenna (Fig. 2B). Exopodite three-segmented; first segment bearing one terminal seta; second segment shortest and with one terminal seta; distal segment with two terminal setae and a transverse row of spinules. Endopodite two-segmented; first segment longer and slightly curved; second segment with two transverse rows of spinules, anterior margin with some spinules near proximal corner and two juxtaposed, spinulose setae; distal margin with six spinulose spiniform setae.

Mandible (Fig. 2C). Coxa-basis with three setae near anterior distal corner. Exopodite furnished with one lateral and two terminal setae. Endopodite same length as coxa-basis and armed with three outer, three distal and two inner setae.

Maxillula (Fig. 2D). Arthrite of praecosa armed with one slender and four strong unguiform spines. Basis with four setae, endopodite with four setae, exopodite with two setae.

Maxilla (Fig. 2E). Syncoxa with two endites, each with two setae. Basis with three setae near proximal inner edge. Endopodite with two strong geniculate setae and four slender setae.

Maxillipede (Fig. 2F). First endopodite segment longer than second and with a row of long hairs along inner edge. Second segment with two fine setae on inner edge, the proximal one longer, and two fine apical setae of different lengths.

Leg 1 (Fig. 3A). Coxa and basis each with outer distal spinule row and basis with strong inner seta. Rami three-segmented, spinulose along outer edges. Exopodite extending to middle of distal endopodite segment; second segment with inner seta modified with branched tip. Endopodite with median and distal transverse rows of spinules on first segment and short distal row on second segment.

Legs 2–4 (Fig. 3B–D). Coxa and basis each with outer distal spinule row.

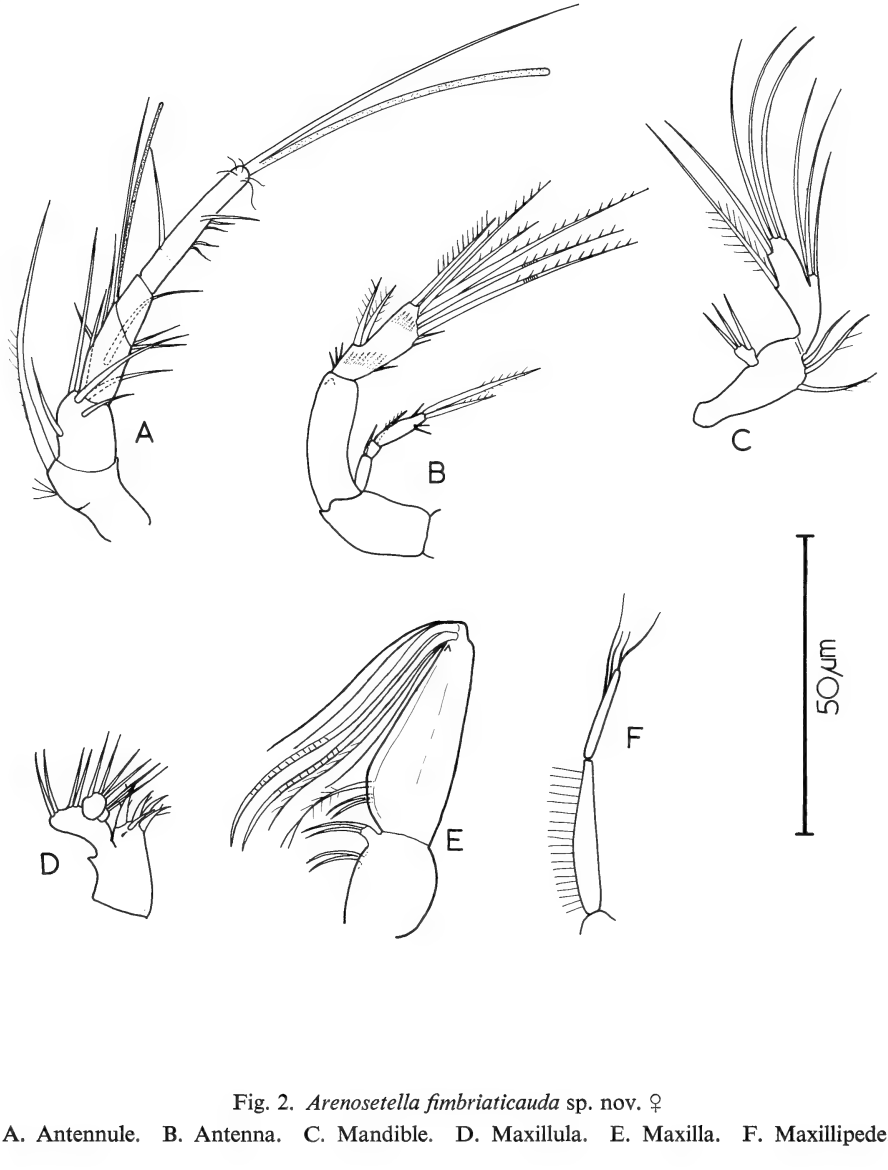

Fig. 2. *Arenosetella fimbriaticauda* sp. nov. ♀
A. Antennule. B. Antenna. C. Mandible. D. Maxillula. E. Maxilla. F. Maxillipede.

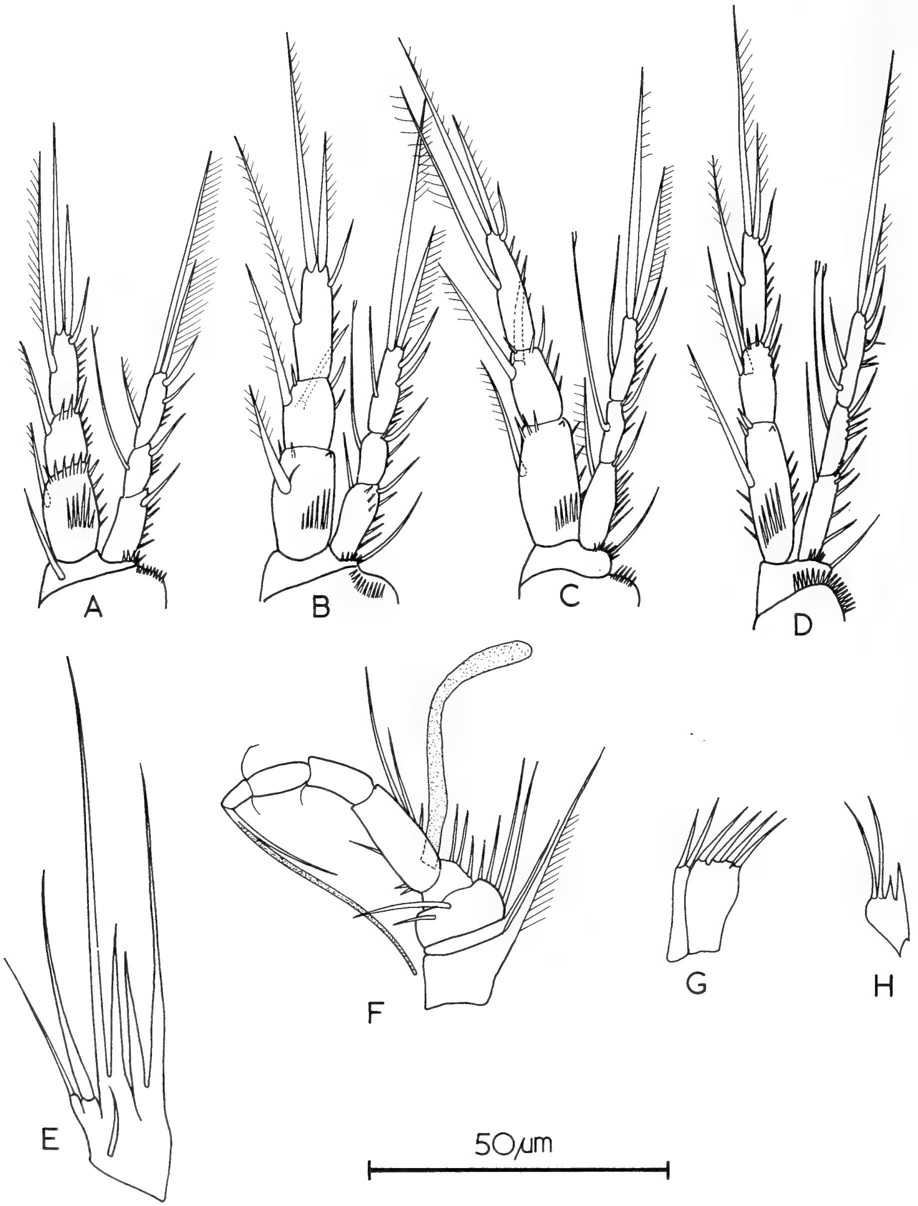

Fig. 3. *Arenosetella fimbriaticauda* sp. nov.
A. ♀ P1. B. ♀ P2. C. ♀ P3. D. ♀ P4. E. ♀ P5. F. ♂ antennule. G. ♂ P5. H. ♂ P6.

Rami three-segmented, more or less spinulose along outer margins. Exopodite extending past second endopodite segment; middle segment with modified inner seta, such a seta also being present on the inner margin of the distal segment of the P4. Endopodite with transverse row of spinules on first segment; second segment bears, in addition to the inner seta, a short, thick, weakly-chitinized seta on the posterior surface just inside the inner margin.

The setal formula is:

	Exopodite			Endopodite		
	1	2	3	1	2	3
P1	0	1	1 2 2	1	1	1 2 1
P2	1	1	1 2 2	1	2	1 2 1
P3	1	1	1 2 2	1	2	1 2 1
P4	1	1	2 2 2	1	2	1 2 1

Leg 5 (Fig. 3E). Rami indistinctly defined. Accessory seta issuing near base of limb. Exopodite with three marginal setae; outer seta issuing from small lobule, middle seta longest. Inner expansion of basoendopodite extending almost to end of exopodite; inner seta more than twice as long as outer seta.

Description of adult male

Length 0,32–0,34 mm. Agrees with female apart from the following features.

Antennule (Fig. 3F). Eight-segmented; first segment bearing stout plumose seta at anterior distal corner; second segment very short; fifth segment longest and furnished with a large aesthetasc; terminal segment with long, slender aesthetasc.

Leg 5 (Fig. 3G). The structure could not be definitively interpreted. All setae subequal. Inner part of basoendopodite apparently distinct, bearing two distal setae and extending to about the end of the expodite. Exopodite with three marginal setae and no sign of an accessory seta.

Leg 6 (Fig. 3H). Bearing two inner spines and two outer setae.

Variability

Only slight variation in size was noted.

Etymology

The specific name alludes to the presence of the rows of fringing lappets on the anal somite.

DISCUSSION

Arenosetella fimbriaticauda shows affinities with *A. duriensis* (Galhano 1970) and *A. littoralis* (Bodin 1978) from which it differs by the setation of the distal endopodite segments of P2–P4. These three species, with their anal rows of spinules or lappets, and *A. balakrishnani* (Bozic 1966) with four dorsal pairs of spines on the anal somite, differ from most other members of the genus which have claw-like structures. Lang (1965) distinguished *Arenosetella* from *Hastigerella* solely by the presence of these anal claws. Wells (1976), however, broadened the definition to include under *Arenosetella* forms with setae or spines (as well as claws) on the dorsal surface of the anal somite as opposed to the naked state in *Hastigerella.*

Whether all these anal structures are homologous is open to question, as is their derivation. Chappuis (1953) believed that the anal claws are homologous to the anal operculum present in most other harpacticoids. Thus, the last copepodite stage of *Arenosetella incerta* Chappuis, 1953, possesses an operculum armed with long spines, which in the adult are replaced by the claws. The ornamentation of *A. fimbriaticauda,* however, suggests an alternative origin: the position of the inner posterior row of lappets in *A. fimbriaticauda* is occupied by a row of hairs or spinules in many harpacticoid species in several families (e.g. *Pseudobradya pulchera* Lang, 1965; *Arenolaophonte stygia* Lang, 1965). *Arenosetella fimbriaticauda* may well represent an intermediate stage in the development of this row, which is further modified into the laminar spines of *A. kaiseri* Lang, 1965, and eventually into the unguiform claws of *A. germanica* Kunz, 1938, and several other species.

The anal ornamentation was examined in several species of *Hastigerella,* viz. *H. palpilabra* Nicholls, 1935, from the type locality (Millport, Scotland), *H. tenuissima* (Klie, 1929) and *H. leptoderma* (Klie, 1929) from the Island of Sylt, Germany. Careful examination, using phase contrast microscopy, failed to reveal any dorsal armature of the anal somite in *H. leptoderma*; however, both *H. palpilabra* and *H. tenuissima* were found to exhibit a pair of bifid appendages identical to those of *A. monensis* Moore, 1976*b*. These are markedly weaker than those found in *A. germanica* (see Moore 1976*b*) and are consequently easily overlooked. Further examination showed these three species to be identical, the apparent setational differences of the pereiopods recorded in the literature being due to variance of interpretation. *A. incerta* sensu Bodin, 1971, also appears conspecific. The senior synonym, *H. tenuissima* must, therefore, be placed in the genus *Arenosetella* and it is suggested that *H. leptoderma* replaces *H. palpilabra* as the type-species of *Hastigerella.*

The following are a key to *Arenosetella* updated from Moore (1976*b*) and a key to *Hastigerella* based partly on the keys of Lang (1965), Apostolov (1974) and Wells (1976).

KEY TO *ARENOSETELLA* WILSON

1. Last somite dorsally with two simple appendages 2
— Last somite dorsally with two bifid appendages, each appendage furnished with an accessory spine 3
— Last somite dorsally with two trifid appendages . . . spec. aff. *incerta* Noodt, 1958
— Last somite dorsally either with two bifid appendages without accessory spines or with two overlapping spines on each side of middle line 4
— Last somite dorsally with four pairs of spines . . . . . *balakrishnani* Bozic, 1966
— Last somite with two rows of spinuliform lappets or spinules entirely or partly on the dorsal surface 8

2. Appendages not fused at base; last segment exopodite P4 with 2 inner setae *spinicauda* Wilson, 1932
— Appendages fused at base; last segment exopodite P4 without inner setae *indica* Krishnaswamy, 1957
3. Accessory spine situated on outer side above bifurcation; last segment endopodite P4 with 4 setae and spines in all . . . . *fissilis* Wilson, 1932
— Accessory spine situated on inner side on a level with bifurcation; last segment endopodite P4 with 3 setae and spines in all . . . . *incerta* Chappuis, 1953
4. Last segment endopodite P3 and P4 each with 5 setae and spines in all *madagascariensis* Lang, 1965
— Last segment endopodite P3 and P4 each with 4 setae and spines in all 5
— Last segment endopodite P3 and P4 each with 3 setae and spines in all 7
5. Middle segment endopodite P4 with 1 seta . . . . *bidentata* Ito, 1972
— Middle segment endopodite P4 with 2 setae 6
6. Appendages of last somite bifid, unguiform . . . . *germanica* Kunz, 1938
— Appendages of last somite straight . . . . *kaiseri* Lang, 1965
7. First segment exopodite P2 and P3 each with 1 inner seta . . . . *rouchi* Lang, 1965
— First segment exopodite P2 and P3 each with no inner seta. . *tenuissima* (Klie, 1929)
8. Last segment endopodite P2–P4 with 4 setae and spines in all . *fimbriaticauda* sp. nov.
— Last segment endopodite P2–P4 with 5 setae and spines in all 9
9. Middle segment exopodite P2–P4 with 1 inner seta . . . . *duriensis* Galhano, 1970
— Middle segment exopodite P2–P4 with 2 inner setae . . . . *littoralis* Bodin, 1978

KEY TO *HASTIGERELLA* NICHOLLS

1. Last segment exopodite P3 with 8 setae and spines in all . . . *soyeri* Bodin, 1976
— Last segment exopodite P3 with 7 setae and spines in all 2
— Last segment exopodite P3 with 6 setae and spines in all 3
— Last segment exopodite P3 with 5 setae and spines in all 7
2. Last segment exopodite P2–P4 with 7–7–7 setae and spines in all *meridionalis* (Chappuis, 1954)
— Last segment exopodite P2–P4 with 6–7–7 setae and spines in all . *unisetosa* (Wells, 1965)
— Last segment exopodite P2–P4 with 7–6–6 setae and spines in all . *chappuisi* Soyer, 1974
3. Last segment endopodite P2–P4 with 4 setae and spines in all 4
— Last segment endopodite P2–P4 with 5 setae and spines in all 5
— Last segment endopodite P2–P4 with 6 setae and spines in all . . *scheibeli* Mielke, 1975
4. A1 with 6 segments; penultimate abdominal somite with posterior ventral spinule row . . . . *abbotti* Lang, 1965
— A1 with 7 segments; penultimate abdominal somite with no posterior ventral spinule row . . . . *bozici* Soyer, 1974
5. Middle segment endopodite P2–P4 with 2 inner setae . *noodti* (Rao & Ganapati, 1969)
— Middle segment endopodite P2–P4 with 1 inner seta 6
6. Furca longer than broad . . . . *bodini* Apostolov, 1974
— Furca broader than long . . . . *psammae* (Noodt, 1955)
7. Middle segment endopodite P1 with 2 inner setae 8
— Middle segment endopodite P1 with 1 inner seta 9
8. Last segment endopodite P1–P4 with 3 setae and spines in all *clavata* (Rao & Ganapati, 1969)
— Last segment endopodite P1–P4 with 5 setae and spines in all . *leptoderma* (Klie, 1929)
9. Last segment exopodite P1 with 6 setae and spines in all *monniotae* (Guille & Soyer, 1966)
— Last segment exopodite P1 with 5 setae and spines in all 10
— Last segment exopodite P1 with 4 setae and spines in all . . *bengalensis* Rao, 1972
10. Middle segment endopodite P2–P4 with 1 inner seta. . *setosa* (Rao & Ganapati, 1969)
— Middle segment endopodite P2–P4 with 2 inner setae . *grandimandibularis* Wells, 1967

PART 2

INTRODUCTION

Two new species of harpacticoid copepod of the family Cylindropsyllidae Sars, Lang, thought to be new to science, have been collected between mean and low tide levels on a high energy sandy beach in Algoa Bay. A species of *Leptastacus* T Scott is common around the mean tide level and a species of *Psammastacus* Nicholls is abundant around the spring low tide level (McLachlan & Furstenberg 1977).

SYSTEMATIC DESCRIPTIONS

Family **Cylindropsyllidae** Sars, Lang

Leptastacus naylori sp. nov.

Material

Specimens were extracted from fine sand (median particle diameter 240 μm) on Sunday's River beach (25°53′ E 33°43′S) and preserved in buffered formalin. Six adults were examined, two being dissected in lactic acid and mounted in polyvinyl lactophenol.

Holotype

1 ♀ (SAM–A15713) deposited in the South African Museum Cape Town, South Africa.

Allotype

1 adult ♂ (SAM–A15716) in the South African Museum.

Paratypes

1 ♀ (SAM–A15714) and 1 ♂ (SAM–A15715) in the South African Museum.

Description of adult female

Length 0,32–0,36 mm from base of rostum to base of furcae. Body (Fig. 4A) vermiform, cylindrical with a short rostrum. Cephalothorax rectangular in dorsal view. Genital double-somite without obvious signs of subdivision. Anal operculum a rectangular plate with spinulose posterior margin.

Somitic ornamentation. Somites with a fine fully-incised subulate hyaline frill. Anal somite with ventral rows of spinules along posterior edge.

Furcal ramus (Figs 4B, 4I). Two times as long as broad and with an inner row of ventrally-directed spinules; two terminal setae, inner much longer than outer; one inner seta and two dorsal setae; distal end with a ventrally-directed spine.

Antennule (Fig. 4C). Seven-segmented, with an aesthetasc on segments four and seven. Segment two the longest and segments five and six the shortest.

Antenna (Fig. 4D). Coxa and allobasis devoid of ornamentation. Exopodite

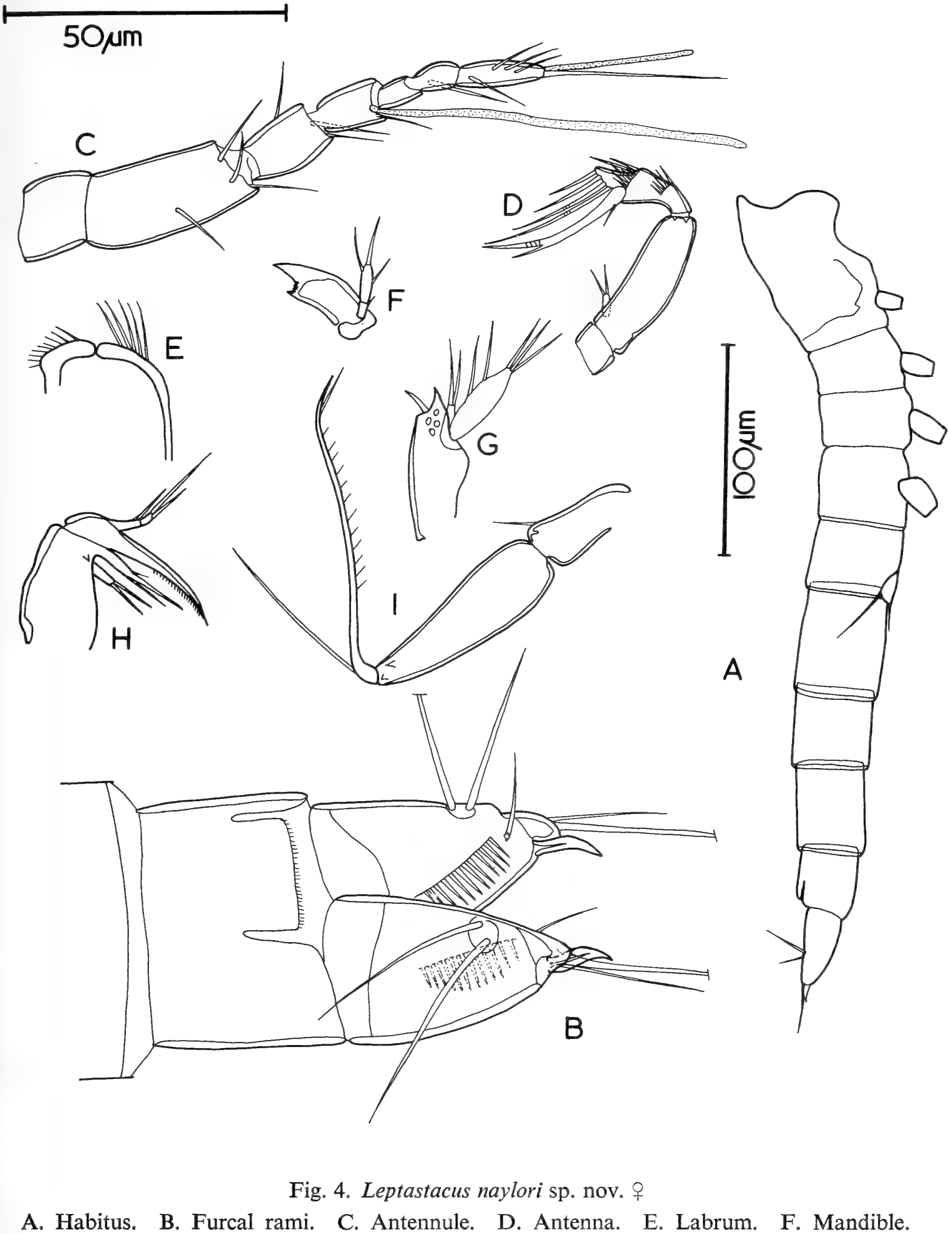

Fig. 4. *Leptastacus naylori* sp. nov. ♀

A. Habitus. B. Furcal rami. C. Antennule. D. Antenna. E. Labrum. F. Mandible. G. Maxillula. H. Maxilla. I. Maxillipede.

one-segmented, with two small apical setae. Endopodite furnished with two transverse rows of spinules on surface, two juxtaposed spines on anterior edge and distal edge with two plain setae and three geniculate setae, the most posterior sharing its base with a setule.

Mandible (Fig. 4F). Praecoxa with unidentate pars incisiva and a number of small teeth along cutting edge. Palp two-segmented, segment one with one spinule and segment two with one terminal and two lateral setae.

Maxillula (Fig. 4G). Arthrite of praecoxa with one claw and five spines. Coxa with two apical setae. Basis with three terminal and two lateral setae.

Maxilla (Fig. 4H). Syncoxa with two endites, proximal one with two setae, distal one with an unguiform spine and two setae. Basis with a large unguiform spine. Endopodite two-segmented; first segment with one seta, second segment with two apical setae.

Maxillipede (Fig. 4I). First endopodite segment elongate; second segment with a long, slender, pennate claw and a slender seta.

Leg 1 (Fig. 5A). Exopodite three-segmented, shorter than endopodite. Endopodite of two subequal segments.

Legs 2–4 (Fig. 5B–D). Exopodite three-segmented, spinulose along outer margin of first two segments. Endopodite of two subequal segments, shorter than exopodite and spinulose along outer margin.

The setal formula is:

	Exopodite			Endopodite	
	1	2	3	1	2
P1	0	0	0.2.1.	1	0.1.1.
P2	0	0	0.2.1.	1	0.1.0.
P3	0	0	1.2.1.	1	0.1.1.
P4	0	1	2.2.1.	0	0.1.0.

Leg (Fig. 5E). A triangular plate with one outer seta and spinule (or setule), two distal setae and some spinules along inner margin.

Description of adult male

Length 0,28–0,33 mm. Agrees with female apart from the following features. First two abdominal somites distinct.

Antennule (Fig. 5F). Haplocerate, eight-segmented. A very large aesthetasc on segment four and a small one on segment eight. Segment two the longest and segment five the shortest.

Leg 3. Second endopodite short and with one terminal seta.

Leg 5 (Fig. 5G). A plate with two marginal setae and a spinuliform projection.

Leg 6 (Fig. 5H). A plate with two setae.

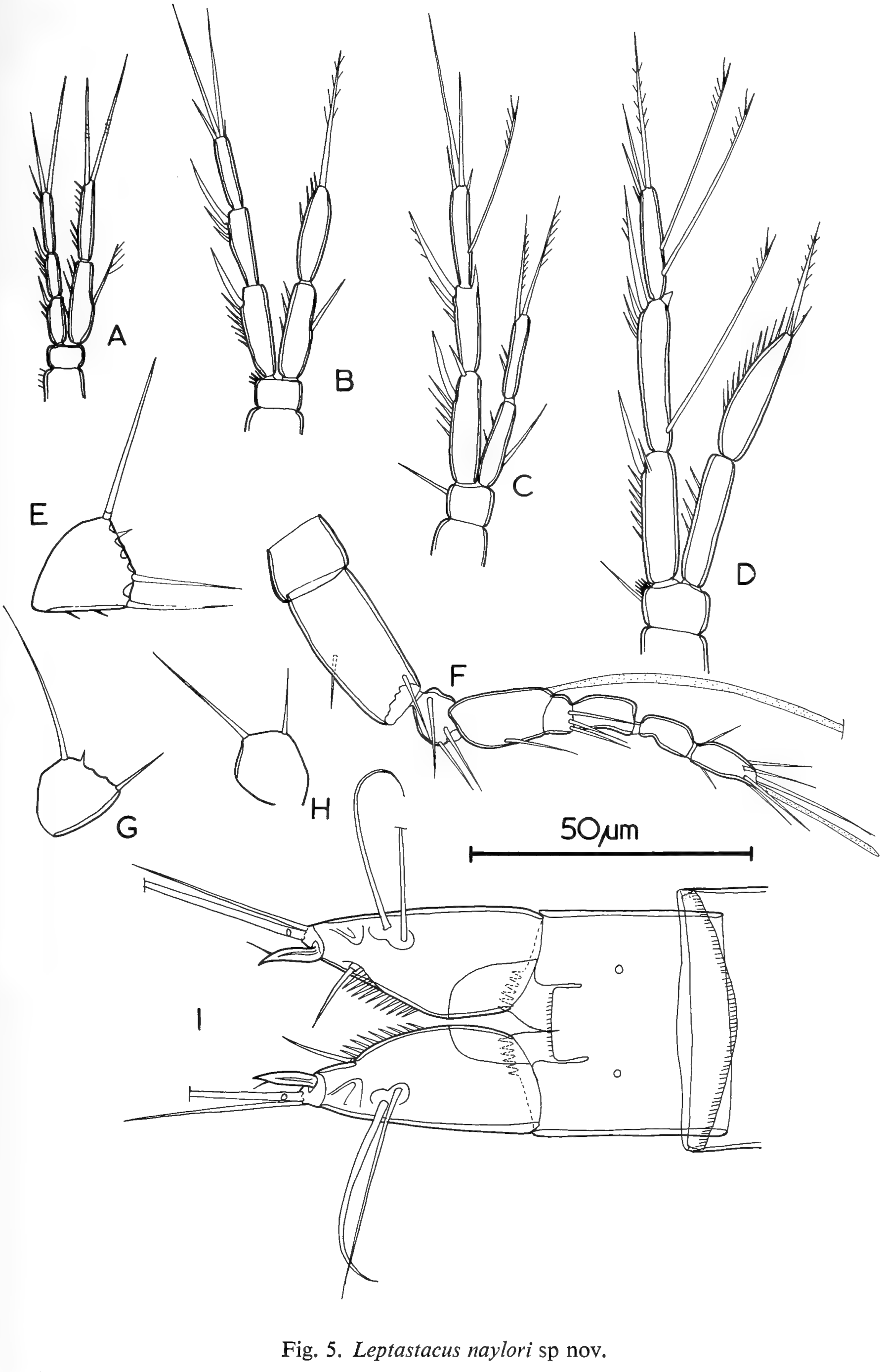

Fig. 5. *Leptastacus naylori* sp nov.
A. ♀ P1. B. ♀ P2. C. ♀ P3. D. ♀ P4. E. ♀ P5. F. ♂ antennule. G. ♂ P5. H. ♂ P6.
I. ♀ furcal rami.

Etymology

This species is named in honour of Prof. Ernest Naylor of the Department of Marine Biology, University of Liverpool, Isle of Man.

Psammastacus erasmusi sp. nov.

Material

Numerous specimens collected from medium sand (median particle diameter 260 μm) at low tide level on Sunday's River beach, preserved in 5 per cent formalin and mounted in polyvinyl lactophenol.

Holotype

1 ♀ (SAM–A15717) in the South African Museum.

Allotype

1 ♂ (SAM–A15718) in the South African Museum.

Paratypes

7 ♀♀ (SAM–A15719) in the South African Museum.

Description of adult female

Length 0,38–0,49 mm from base of rostrum to base of furcae. Body (Fig. 6A) vermiform, cylindrical with an elongate pointed rostrum (Fig. 6B). Cephalothorax rectangular in dorsal view. Genital double-somite without obvious signs of subdivision. Anal operculum a rectangular plate with spinulose posterior margin not easily visible.

Somitic ornamentation. Somites with a fine fully-incised subulate hyaline frill and circumscribed by a row of rectangular thickenings on the abdomen.

Furcal ramus (Fig. 7A). 1,5 times as long as broad and with an inner row of ventrally directed spinules; two terminal setae of unequal lengths; one inner articulated seta, one middorsal seta and one outer lateral seta; distal end with a strong, straight spine ventrally and a smaller, hooked spine dorsally.

Antennule (Fig. 6C). Seven-segmented with a large, annulated aesthetasc on segment four. Segment two the longest and segment five the shortest.

Antenna (Fig. 6D). Coxa and allobasis devoid of ornamentation. Exopodite one-segmented with two small apical setae. Endopodite furnished with two transverse rows of spinules on surface, two outer juxtaposed spines and two spines and three geniculate setae along distal edge; largest geniculate seta confluent at base with a fine seta.

Mandible (Fig. 6F). Praecoxa with unidentate pars incisiva and a number of small teeth along cutting edge. Palp two-segmented with one lateral and two terminal setae on second segment.

Maxillula (Fig. 6G). Praecoxal arthrite with one seta and five spines. Palp of one segment with two lateral and three terminal setae.

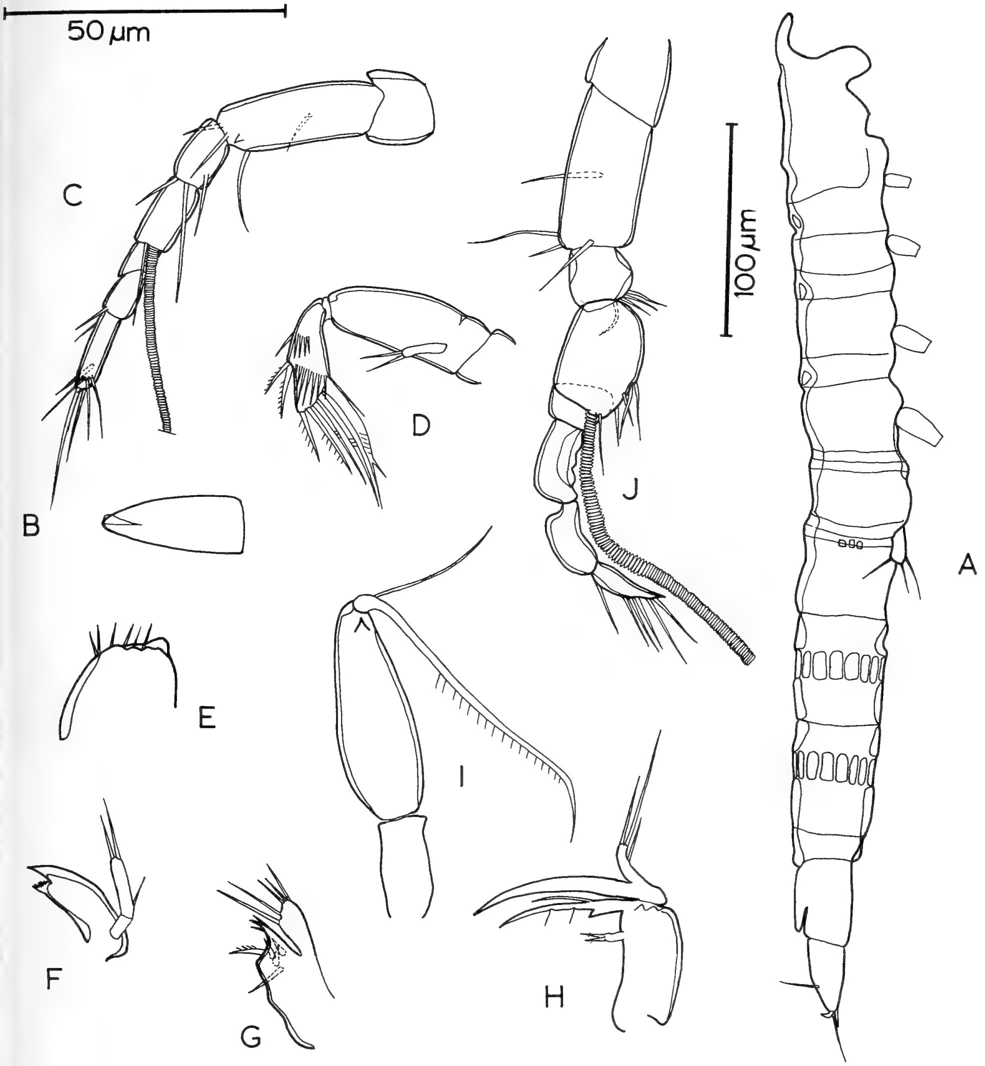

Fig. 6. *Psammastacus erasmusi* sp. nov.
A. ♀ habitus. B. ♀ rostrum. C. ♀ antennule. D. ♀ antenna. E. ♀ labrum. F. ♀ mandible. G. ♀ maxillula. H. ♀ maxilla. I. ♀ maxillipede. J. ♂ antennule.

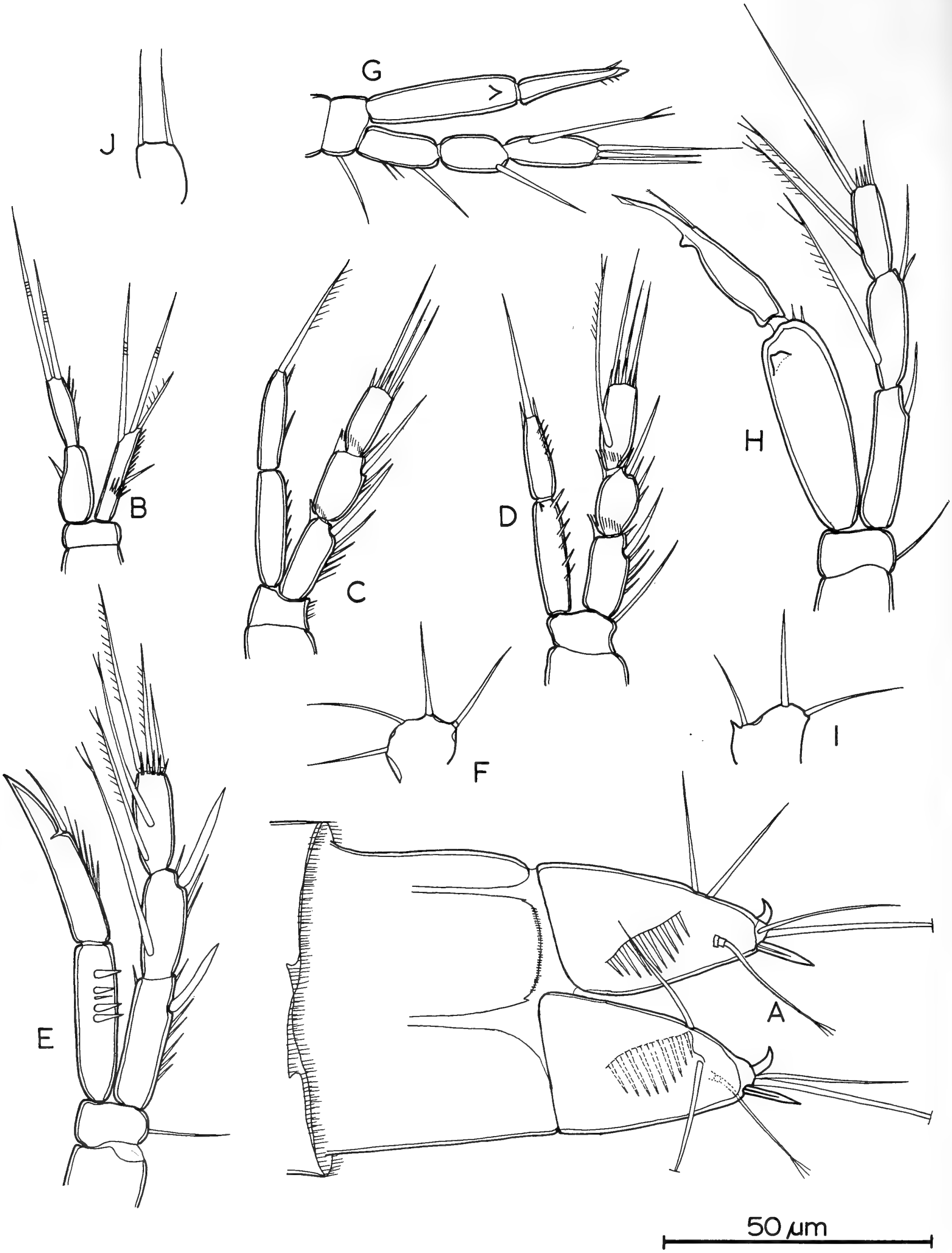

Fig. 7. *Psammastacus erasmusi* sp. nov.
A. ♀ furcal rami. B. ♀ P1. C. ♀ P2. D. ♀ P3. E. ♀ P4. F. ♀ P5. G. ♂ P3. H. ♂ P4. I. ♂ P5. J. ♂ P6.

Maxilla (Fig. 6H). Syncoxa with two endites; smaller one with two small setae; larger one with a seta and an unguiform spine. Basis with a terminal unguiform spine. Endopodite with one lateral and two terminal fine setae.

Maxillipede (Fig. 6I). First endopodite segment elongate; second segment with a long, slender, pennate claw and a slender seta.

Leg 1 (Fig. 7B). Exopodite a single segment slightly longer than first endopodite segment; with three terminal setae and one outer spine midway along ramus. Endopodite of two subequal segments, the first with an inner median spine and the second with two terminal setae.

Legs 2–4 (Fig. 7C–E). Rami more or less spinulose along outer margins. Exopodite three segmented, with distal row of spinules; segments with a well-developed appendicular hyaline frill. Endopodite a little shorter, two-segmented. Fourth leg much the largest; inner distal spine of endopodite very stout and partly confluent at base.

The setal formula is:

	Exopodite			Endopodite	
	1	2	3	1	2
P1	–	–	0.2.2.	1	0.2.0.
P2	0	0	0.2.1.	0	0.1.0.
P3	0	0	1.2.1.	0	0.1.0.
P4	0	1	2.2.1.	0	0.2.0.

Leg 5 (Fig. 7F). A small plate with four setae.

Description of adult male

Length 0,37–0,47 mm. Agrees with female apart from the following features. First two abdominal somites distinct.

Antennule (Fig. 6J). Haplocerate, eight-segmented with an annulated aesthetasc on segment four. Segment six with three chitinous thickenings along anterior margin.

Leg 3 (Fig. 7G). As in female but without terminal seta on distal endopodite segment.

Leg 4 (Fig. 7H). As in female but inner distal spine of endopodite of different construction.

Leg 5 (Fig. 7I). A small plate with 3 setae and a short spinuliform projection at inner distal corner.

Leg 6 (Fig. 7J). A very small plate with two setae.

Etymology

This species is named in honour of Prof. Theunus Erasmus of the Zoology Department, University of Port Elizabeth.

DISCUSSION

Leptastacus naylori differs in the setation of the swimming legs from all the described species of *Leptastacus* T. Scott. In this respect it is closest to *L. macronyx* (T. Scott, 1892) and *L. laticaudatus* Nicholls, 1935, from which it differs in the presence of an extra inner seta on the distal segment of the endopodite of the third leg.

The following key to the females of the genus *Leptastacus* is based partly on the key of Lang (1965) and the setal formula table of Lindgren (1975). Here, because of inadequate descriptions, *L. nichollsi* Krishnaswamy, 1951, *L. acuticaudatus* Krishnaswamy, 1957, *L. euryhalinus* Krishnaswamy, 1957, and *L. macronyx* pontica Griga, 1962, have been omitted.

Apostolov (1973) gives drawings of a form from the Black Sea he ascribes to *L. laticaudatus* Nicholls, 1935 *intermedius* Kunz, 1938. However, as the fifth leg clearly differs from Kunz's (1938) original description of this subspecies, the Black Sea form is given in the key as *L. laticaudatus intermedius* sensu Apostolov.

KEY TO THE FEMALES OF *LEPTASTACUS* T. SCOTT

1.	P2 endopodite with an inner seta on segment 1	2
—	P2 endopodite without an inner seta on segment 1	10
2.	P3 endopodite with an inner seta on segment 1	3
—	P3 endopodite without an inner seta on segment 1	*minutus* Chappuis,1954
3.	P4 endopodite with 1 seta on terminal segment	4
—	P4 endopodite with 2 setae on terminal segment	8
4.	P3 endopodite with 1 seta on terminal segment	5
—	P3 endopodite with 2 setae on terminal segment	*naylori* sp. nov.
5.	P5 foot-shaped at tip	6
—	P5 not foot-shaped at tip	7
6.	P5 with 2 inner setae	*laticaudatus laticaudatus* Nicholls, 1935
—	P5 with 3 inner setae	*laticaudatus intermedius* Kunz, 1938
7.	P5 produced distally into short projection with rounded tip; furca about 3 times as long as wide	*laticaudatus intermedius* sensu Apostolov, 1973
—	P5 produced distally into long pointed projection; furca at least 4 times as long as wide	*macronyx* (T. Scott, 1892)
8.	P5 produced distally into long pointed projection	9
—	P5 not produced distally into long pointed projection	*incurvatus* Lang, 1965
9.	P3 endopodite with 1 seta on terminal segment	*rostratus rostratus* Nicholls, 1939
—	P3 endopodite with 2 setae on terminal segment	*rostratus taurica* Marinov, 1973
10.	Segment 2 exopodite P4 with no inner seta	*aberrans* Chappuis, 1953
—	Segment 2 exopodite P4 with 1 inner seta	11
11.	Terminal segment endopodite P4 with 2 setae and spines in all	*operculatus* Masry, 1970
—	Terminal segment endopodite P4 with 1 seta	12
12.	Terminal segment endopodite P3 with 2 setae and spines in all	14
—	Terminal segment endopodite P3 with 1 seta	13
13.	P5 with 5 setae	*delamarei* Rouch, 1962
—	P5 with 4 setae	*waltairensis* Rao & Ganapati, 1969
14.	P5 with no setae on inner margin	*jenneri* Lindgren, 1975
—	P5 with 1 seta on inner margin	15
—	P5 with 2 setae on inner margin	*wieseri* Chappuis, 1958
15.	Principal furcal setae confluent at base	*japonicus* Ito, 1968
—	Principal furcal setae not confluent at base	16

16.	Inner distal corner of furca produced into spiniform projection	*mozambicus* Wells, 1967
—	Inner distal corner of furca not produced	*constrictus* Lang, 1965

The setation of legs one to four of *Psammastacus erasmusi* agrees only with *P. spinicaudatus* Rao & Ganapati, 1969, and *P. remanei* Noodt, 1964. However, the sexual dimorphism of the third and fourth legs shows the species to be closest to *P. ghanai* Chappuis & Rouch, 1960. These two species differ in the setation of the fourth leg and in the structure of the fifth leg and furcal rami.

The modification of the endopodite of the fourth leg of the female in *P. erasmusi* is unique in the genus. Moreover, the annulated structure of the antennular aesthetascs has not been observed by the authors in any other species of harpacticoid copepod.

The following key to the genus is valid for both sexes.

KEY TO *PSAMMASTACUS* NICHOLLS

1.	Third segment expodite P4 with 2 inner setae	2
—	Third segment expodite P4 with 1 inner seta	6
2.	Exopodite P1 with 3 setae and spines in all	*perplexus* Wells & Clark, 1965
—	Exopodite P1 with 4 setae and spines in all	3
3.	Exopodite P1 with outer spine midway along ramus	4
—	Exopodite P1 with no such spine midway along ramus	*spinicaudus* Wells, 1967
4.	Inner distal corner exopodite P4 prolonged into stout spine	*erasmusi* sp. nov.
—	Inner distal corner exopodite P4 with no such spine	5
5.	Fifth legs partly fused along midline	*spinicaudatus* Rao & Ganapati, 1969
—	Fifth legs distinct along midline	*ramanei* Noodt, 1964
6.	Endopodite P4 with 1 apical seta	7
—	Endopodite P4 with 2 apical setae	8
7.	Furca broader than long	*brevicaudata* Nicholls, 1935
—	Furca longer than broad	*confluens* Nicholls, 1935
8.	P5 with 2 setae	*acuticaudatus* Krishnaswamy, 1957
—	P5 with 4 setae	*ghanai* (Chappuis & Rouch, 1960)

ACKNOWLEDGEMENTS

We thank Dr W. Scheibel who originally identified to genus specimens of all three species, Drs W. Mielke and I. Barclay for supplying specimens, and Dr Ph. Bodin for critical reading of part of the initial manuscript. The first author gratefully acknowledges financial assistance from the British Council, the South African Council for Scientific and Industrial Research and the University of Port Elizabeth.

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

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

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

ANTON McLACHLAN
&
COLIN G. MOORE

THREE NEW SPECIES OF HARPACTICOIDA (CRUSTACEA, COPEPODA) FROM SANDY BEACHES IN ALGOA BAY, SOUTH AFRICA, WITH KEYS TO THE GENERA *ARENOSETELLA*, *HASTIGERELLA*, *LEPTASTACUS* AND *PSAMMASTACUS*

VOLUME 76 PART 5 SEPTEMBER 1978 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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

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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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

Footnotes should be avoided unless they are short and essential.

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

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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)

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THE SKELETON OF THE MAMMAL-LIKE REPTILE *CISTECEPHALUS* WITH EVIDENCE FOR A FOSSORIAL MODE OF LIFE

By

MICHAEL A. CLUVER

Cape Town Kaapstad

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MICHAEL A. CLUVER

South African Museum, Cape Town

(With 20 figures)

[*MS. accepted 21 June 1978*]

ABSTRACT

A full description of the skeleton of *Cistecephalus*, based on a number of specimens, is given. A skeletal reconstruction shows that *Cistecephalus* was probably the most aberrant member of the infraorder Dicynodontia, and comparison with living animals suggests that the osteological modifications of, in particular, the shoulder girdle and forelimb represent adaptations to powerful and frequent digging activities.

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INTRODUCTION

The cranial morphology of the Upper Permian dicynodont *Cistecephalus* has been made well known through a succession of papers following Owen's original description of the genus in 1876. Chief among these are those of Seeley (1894), Broom (1932, 1948), Broili & Schröder (1935), Brink (1950, 1952), Keyser (1973) and Cluver (1974). As details of the skull structure were established, it became clear that *Cistecephalus* was a highly specialized animal showing a number of fundamental departures from the usual dicynodont condition. As these specializations must represent adaptations to a specific way of life, *Cistecephalus* has been the subject of some speculation by a number

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of authors. Aquatic habits were proposed by Broom (1948) and Brink (1950), but the latter author later (Brink 1952) maintained that the structure of the manus indicated adaptations to digging activities. Keyser (1973) thought that the orientation of the orbits and possible opposability of digits of the manus pointed to commitments to arboreality, but included digging activities as part of the animal's general way of life. Cluver (1974) compared the skull of *Cistecephalus* with that of the related *Kawingasaurus*, for which genus Cox (1972) had produced convincing evidence of powerful digging or fossorial habits, and also with skulls in living and extinct fossorial mammal groups, and concluded that *Cistecephalus* was in all likelihood an accomplished digger.

Since only tantalizingly little of the cistecephalid postcranial skeleton has been described in the literature (Brink 1952, Keyser 1973, Von Huene 1942, Cox 1972), it seemed worth while to investigate available material of the genus in order to determine whether the peculiarities in the cranial structure are matched by specializations in the axial and appendicular parts of the skeleton. As a result of this exercise, it has been possible to establish a complete reconstruction of the cistecephalid skeleton, which shows that the living animal was probably the most specialized and aberrant member of the infraorder Dicynodontia, in itself a highly modified division of the order Therapsida.

Studies on the postcranial skeleton of Permian dicynodonts are regrettably few; in this investigation use was made chiefly of the accounts by Watson (1960), Cox (1959, 1972) and Boonstra (1966).

MATERIAL

SAM–10665. *Cistecephalus* sp. Ou Plaas, Murraysburg, Cape Province. The skull, complete but slightly compressed dorsoventrally, has been fully prepared. The lower jaw, lacking the posterior part of the right ramus, has been separated from the skull and also fully prepared.

BPI 4086. *Cistecephalus* sp. Bloukop, Roggevlei boundary between Richmond and Victoria West, Cape Province. An almost complete skeleton, showing the skull and lower jaw, the vertebral column and ribs, the right scapula, humerus, radius and partial manus, a complete left hind limb and the right femur and distal ends of the tibia and fibula. The atlas and last caudal vertebrae are absent.

BPI 696. *Cistecephalus* sp. Aasvogelkrans, Murraysburg, Cape Province. A skull and lower jaw with associated but largely disarticulated postcranial skeleton. The right scapula, left humerus and ulna and partial left manus are well displayed, as well as the pelvic girdle, sacral and caudal vertebrae.

BPI 2915. *Cistecephalus* sp. Beeldhouersfontein, Murraysburg, Cape Province. A skull and lower jaw with cervical vertebrae, pectoral girdle and complete left forelimb and manus.

BPI 506. *Cistecephalus* sp. Towerwater, Murraysburg, Cape Province. A skull and lower jaw with anterior vertebrae, a complete pectoral girdle and a good left humerus.

BPI 2450. *Cistecephalus* sp. Klipplaat, Murraysburg, Cape Province. A skull and partial lower jaw with isolated ribs and the right half of the pelvic girdle.

BPI 4120. *Cistecephalus* sp. Modderfontein, Victoria West, Cape Province. Skull and anterior part of vertebral column, pectoral girdle and articulated forelimbs.

RC 298. *Cistecephalus* sp. Tweefontein, Graaff-Reinet, Cape Province. Good skull and lower jaw with anterior part of vertebral column and ribs, a nearly complete pectoral girdle and a good left humerus with the proximal part of the ulna in articulation.

BPI 2124. *Cistecephalus* sp. Kraaifontein, Murraysburg. Skull and lower jaw with pectoral girdle and right and left forelimbs in near-natural articulation. Left manus seen in ventral view.

GS K224. *Cistecephalus* sp. Steilkranz, New Bethesda. Skull and lower jaw with articulated anterior part of postcranial skeleton. Manus of left and right sides seen in ventral view.

SAM–11114. *Oudenodon* sp. Melton Wold, Victoria West. Skull, lower jaw, pectoral girdle and left and right forelimbs.

All specimens are from Upper Permian, *Cistecephalus* zone localities.

THE SKELETON OF *CISTECEPHALUS*

Skull and lower jaw

The *Cistecephalus* skull and lower jaw have been fully described by Keyser (1973) and need not be considered in detail here. Some features of functional significance may, however, be mentioned. As suggested by Cluver (1974), the broad intertemporal region and rounded occiput may reflect forward extension and hence increased size of the neck and shoulder musculature, such as is found in many burrowing mammals. The basicranial region is strengthened by a meeting in the ventral midline between the pterygoids, vomer and the base of the presphenoid, with the obliteration of the interpterygoidal vacuity.

The lower jaw is short, deep and robust. The dentary symphysis is extended as a sharp transverse blade which met the premaxillary part of the secondary palate during mastication. This scoop-like anterior edge of the lower jaw is narrower than the secondary palate, and it is likely that the lower jaw could be moved laterally across the secondary palate while crushing food in the mouth. The short lower jaw did not meet the blunt anterior edge of the premaxilla at any time during the masticatory cycle.

In Figure 20 skull details are derived from SAM–10665 and BPI 4086. Detailed drawings of cistecephalid skulls have been published by Keyser (1973) and Cluver (1974).

Vertebral column

In RC 298 the atlas, axis and succeeding 6 cervical vertebrae are preserved in natural or near-natural articulation (Figs 1–2). The right half of the atlas neural arch lies slightly displaced upon the odontoid process of the axis, and

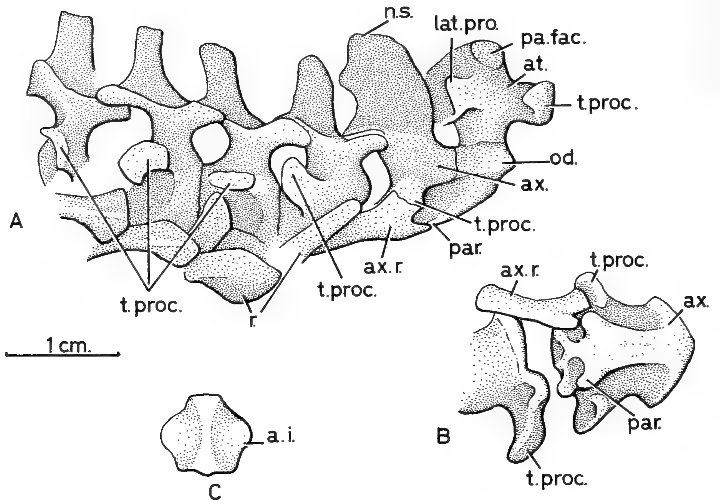

Fig. 1. *Cistecephalus* sp. RC 298. A. Cervical vertebrae in right lateral view. B. Axis and 3rd cervical vertebra in ventral view. C. Atlas intercentrum in ventral view.

carries a strong anteroposteriorly elongated transverse process. The facet for the proatlas is situated on a distinct raised platform. The body of the atlas arch carries a large posteromedially facing facet that articulates with the odontoid process, and an anteromedially facing facet that meets the occipital condyle. An isolated atlas intercentrum is present. The element is transversely expanded and carries a ventral longitudinal crest. Little can be seen of the articulatory facets for the odontoid and occipital condyle, but it appears that the bone is flatter than that of *Lystrosaurus* (Cluver 1971).

The axis is well preserved. The neural arch is indistinguishably fused to the centrum, and bears a broad spine, higher than those of the succeeding vertebrae. The postzygapophysis is tightly articulated with the prezygapophysis of the next vertebra, but the prezygapophyseal region is damaged, evidently as a result of the displacement of the atlas. The centrum of the axis carries a distinct transverse process and is apparently fused with the odontoid element. There is a smaller process, the parapophysis, low down on the centrum directly beneath the transverse process, serving for the articulation of the capitulum of a short but stout axial rib.

Six vertebrae are preserved in articulated position behind the axis, the last two incompletely exposed. The three immediately behind the axis have narrower spines than the fourth, and could represent true cervicals. Including atlas and axis, this would mean a total of five cervical vertebrae in the column. The third cervical carries a long, backwardly and dorsally directed transverse process, much more prominent than those of the axis or the succeeding vertebrae; the transverse processes of the last two cervicals are directed laterally and only slightly posteriorly. The zygapophyses of the cervicals, particularly the last two, are set close to the neural spine and are tightly interlocked. In what is regarded as the first dorsal vertebra, the transverse process is short and excavated posteriorly, so that in lateral view the distal surface of the process is arcuate in outline.

In BPI 4086 the vertebral column is complete except for the atlas and the most posterior tail vertebrae. In this specimen, too, a total of five cervicals can be recognized. The first three cervicals, including the axis, are articulated, but

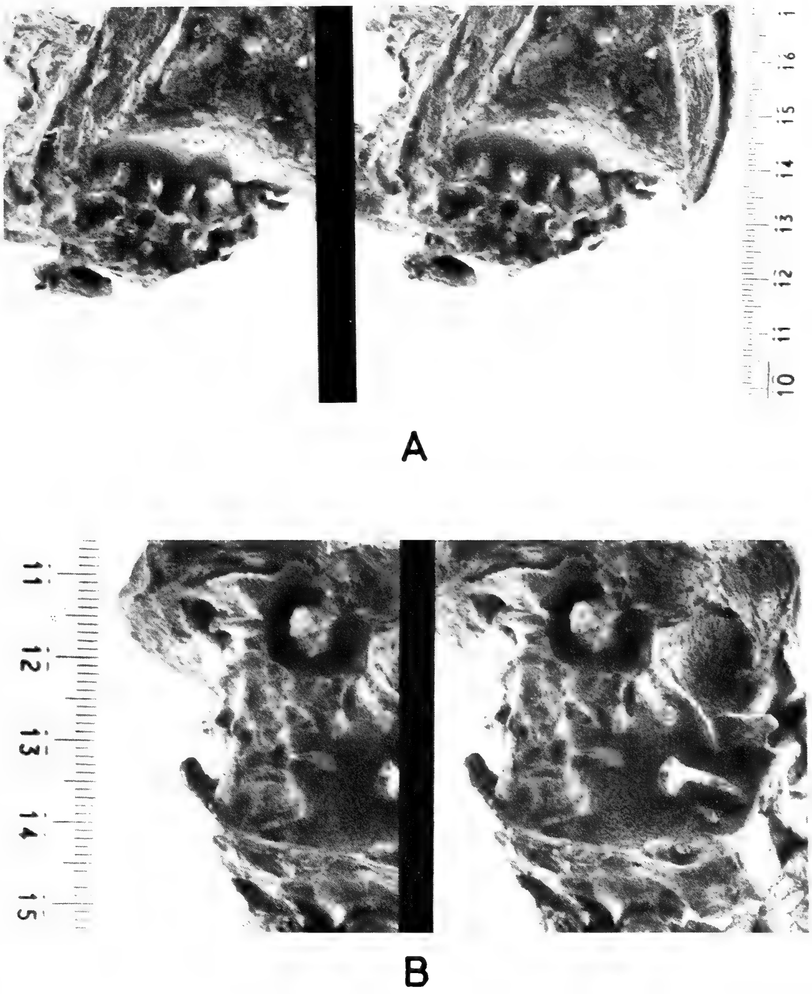

Fig. 2. *Cistecephalus* sp. RC 298. Stereophotographs of anterior cervical vertebrae. A. Right lateral view. B. Ventral view.

the fourth and fifth in the row are loose from each other and from the sixth, from which point the column is again fully articulated. The fourth in the row (fifth cervical) is more complete than the anterior vertebrae; the spine appears narrower than that of the succeeding vertebra, which differs, too, in the stouter transverse process carried higher on the neural arch. This latter vertebra can be regarded as the first dorsal (see p. 219). A total of twenty-five dorsals is present. All are damaged to some extent, and the twenty-first and twenty-second dorsals have become separated from each other. As far as can be made out, the dorsals have broader neural spines than the cervicals, and in some instances this width becomes extreme. The twenty-second dorsal has a very broad anteroposteriorly inflated spine; the adjoining vertebrae are too damaged to give any indication of the breadth of their spines. In all the vertebrae, including the cervicals, the zygapophyses articulate at steep angles to the horizontal.

Three sacral vertebrae are present in BPI 4086, each apparently indistinguishably fused to its pair of ribs (Fig. 16A). The first sacral rib is very deep, as is the second, but the third is less strongly developed. All three sacral vertebrae are damaged and many details are lacking, but it seems that the spine of the second slopes back to a much greater degree than does that of the last dorsal.

In BPI 696 the two halves of the pelvis are in near-natural position relative to each other and sacral and caudal vertebrae are preserved. The first sacral vertebra is partially exposed and its right rib is seen in anteroventral view. The rib is short and wide distally and is not fused to the vertebra, which it meets close to the body of the centrum. The centra of three vertebrae are visible in ventral view behind the first sacral; the last of these is that of the first caudal. In this specimen the remaining caudal vertebrae have folded over to lie upon the dorsal spines of the sacral vertebrae, obscuring them from view. Only the ventral surfaces of the centra, and in some cases the ribs, of the caudal vertebrae are visible. A total of fifteen caudals is present, the last being a mere fleck of bone and it seems likely that this represents a complete or near-complete series, although it is possible that members of the series may be missing at the point of dislocation from the sacral series.

In BPI 4086 four caudal vertebrae, all damaged and the last very incomplete, are present. The second caudal has a fairly long laterally directed rib.

As far as can be seen, the zygapophyses of all vertebrae examined meet each other at steep angles to the horizontal, and it is likely that only dorsoventral flexure or rotation between vertebrae could have been possible, even in the neck region. No horizontal or near-horizontal articulations are present anywhere in the column.

Ribs

The anterior ribs are best seen in RC 298. There is no indication of an atlantal rib, but a short, stout and double-headed axis rib is present (Fig. 1). The second rib present, that of the third cervical, is poorly preserved and it is not possible to determine whether a double head was present; there is, however, no clear parapophysis for attachment of the capitulum, as in the axis. In the fourth cervical a short and relatively slender double-headed rib is present. In the fifth cervical the rib is incomplete but longer than that of the fourth. The capitulum and tuberculum lie close to each other and are separated by a very shallow notch. The next two ribs are almost complete, and lie crossed over each other with the ventral ends meeting the side of the sternum in what appears to be a natural association. The sixth vertebra carries the anterior of these two ribs and can be regarded as the first dorsal, an identification supported by characters of the vertebrae themselves (see p. 218). The head of the first dorsal rib is incomplete, but that of the second dorsal is wide and a separate capitulum and tuberculum cannot be made out. It seems likely (see below) that in this specimen at least three ribs are attached to the sternum.

In BPI 4086 ribs are preserved from the first dorsal vertebra to the twenty-fourth dorsal vertebra. Ribs are very short in the posterior region and are longest between the sixth and eleventh dorsal, but it should be noted that none of the ribs is absolutely complete. As shown above, the second caudal vertebra carries a simple, laterally directed rib. In BPI 696 the first three caudals in the dislocated portion of the row have short, slender ribs; there is no sign of haemal arches in this series, and the base of the tail was probably clearly demarcated from the rest of the body.

Pectoral girdle and forelimb

In RC 298 there is an almost complete left scapula, procoracoid and coracoid, a complete clavicle on both sides, an interclavicle and a sternum (Figs 3–5). The left humerus is present in natural articulation with the glenoid, but is damaged proximo-anteriorly. The olecranon portion of the ulna is preserved in contact with the left humerus. On the right side the clavicle articulates with the acromian process of the scapula, which is complete below the level of this process. The proximal part of the humerus is preserved in position in the glenoid cavity. A complete coracoidal plate is also present, but is slightly obscured by the overlying clavicle.

The scapula is a long, relatively slender bone. The acromian process, situated low down close to the level of the glenoid, is a continuation of the anterior edge of the scapula blade and is formed more by an excavation of the anterior edge of the blade than by a separate bony projection (see Watson (1960) fig. 12). The upper half of the scapular blade is bent back relative to the lower half and the bone can thus be divided into an acromian section and an upper section, lying at about 25° to each other. Below the acromian process the base of the scapula is turned sharply inwards to meet the procoracoid. The glenoid is a well-defined hollow bounded by a sharp, flared rim, and faces laterally rather than posterolaterally as in other dicynodonts (Watson 1960).

The procoracoid/coracoid plate is more complete on the right side, but is partially obscured by the clavicle. There are no clear boundaries between the

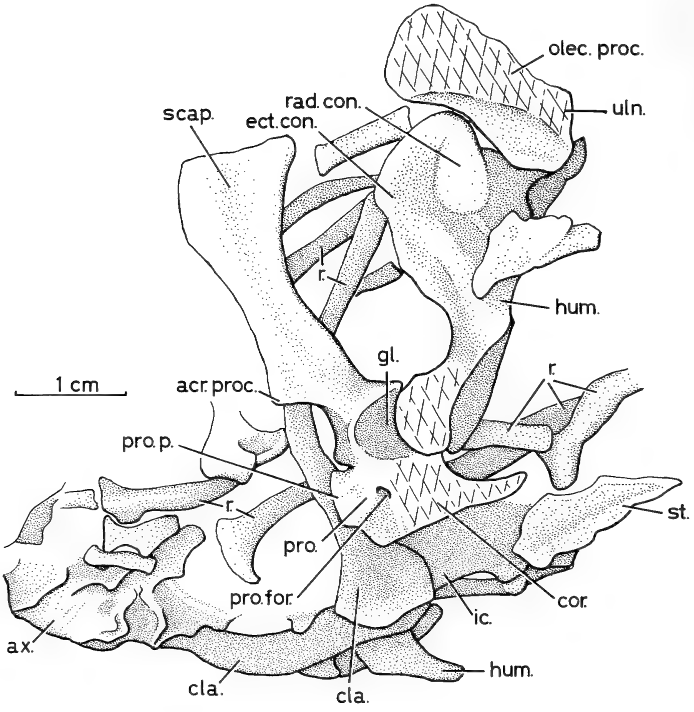

Fig. 3. *Cistecephalus* sp. RC 298. Semi-articulated pectoral girdle in left lateral view.

two elements making up the plate, but a ridge running forward from the rear of the glenoid cavity may indicate a large coracoid, forming most of the ventral part of the glenoid cavity. The anterior edge of the procoracoid is expanded to form a fairly robust process which abutted against the clavicle of its side. A procoracoid foramen is present half-way between the ventral limit of the anterior procoracoid process and the ventral rim of the glenoid cavity.

The clavicle is a fairly stout bone with a wide contact with the inner surface of the scapula at the level of the acromian process, and a broad ventral meeting with the clavicle of the other side in the ventral midline. Along the midline each clavicle is dorsoventrally expanded, so that the pair meet over a wide area. This connection seems to have been a strong one and is preserved in most specimens. The median plate formed by the two clavicles in the ventral midline is overlain by the front of the interclavicle, less robust in comparison. Half-way down the posterolateral surface of its shaft the clavicle carries a recess, bounded laterally by a thin crest of bone, which in size and position is suited for articulation with the anterior procoracoidal process. This articulation would have served to strengthen the connection between clavicle and scapulocoracoid, and prevent forward and inward displacement of the scapulocoracoid resulting from forces at the glenoid.

The partially exposed interclavicle is seen as a flat, rectangular sheet with its anterior end obscured by the meeting between the clavicles, and its posterior end lying above the sternum. The sternum is fully exposed and most of its structure can be made out. It is wide and flat-edged anteriorly and tapers posteriorly to a fairly narrow median spine. A prominent ventral median crest

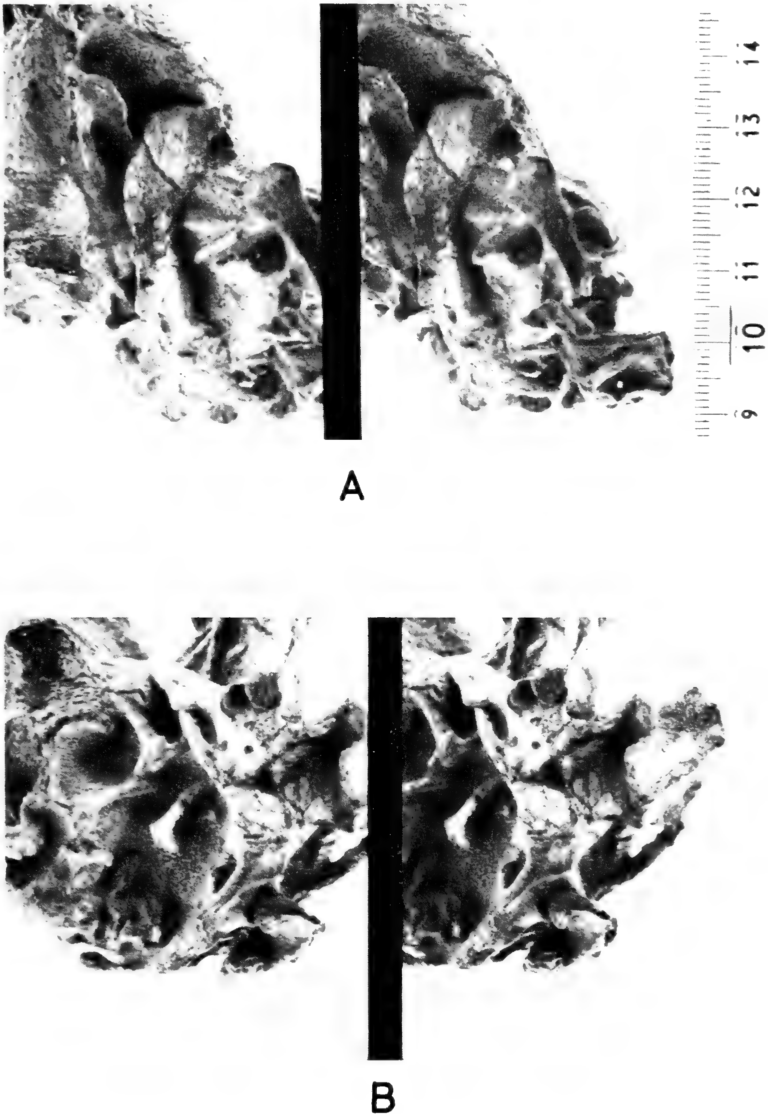

Fig. 4. *Cistecephalus* sp. RC 298. Stereophotographs. A. Left scapulocoracoid in lateral view. B. Pectoral girdle in ventral view.

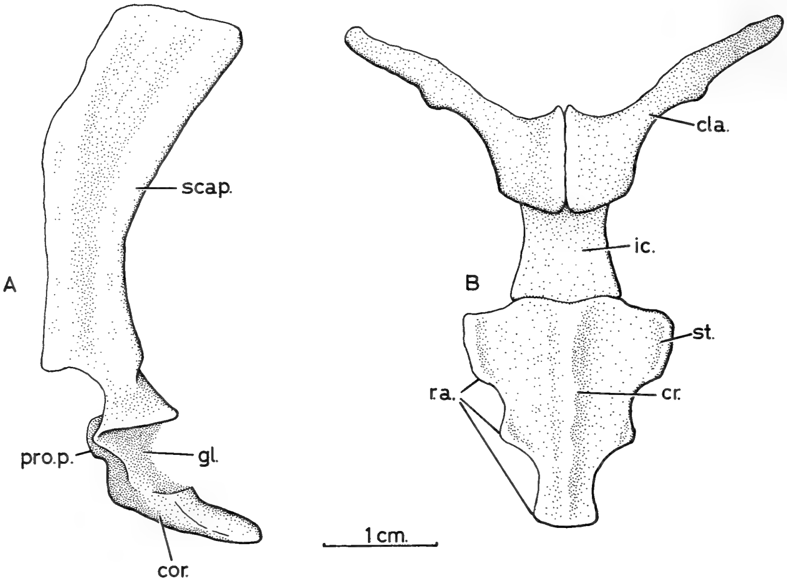

Fig. 5. *Cistecephalus* sp. RC 298. A. Left scapulocoracoid in lateral view. B. Pectoral girdle in ventral view.

runs the length of the bone. On each side three processes for the attachment of ribs can be made out, one behind the anterolateral corner of the bone, one half-way down the side and one on the posterolateral corner. On the right side two ribs are in near natural articulation with the two most anterior processes. The distances separating the three processes are approximately the same.

Several additional specimens show further details of the pectoral girdle. In BPI 2915 a good scapula, with cleithrum, is present, differing from that in RC 298 in that it extends straight dorsally without a posterior twist in the dorsal half. On the left side the coracoid and procoracoid have become detached from the scapula, and the suture between the two ventral elements can be seen running vertically and transversely through the middle of the ventral part of the glenoid. The procoracoid foramen is situated in the centre of the procoracoid, well away from the glenoid cavity. In BPI 696 the right scapula, of which the dorsal part is damaged, shows the acromian region well. The procoracoid is present, though apparently incomplete, and where the two bones have moved slightly apart it can be seen that the scapula extends ventrally for a considerable distance on the inside of the procoracoid. In BPI 4086 and BPI 2124 the scapula is bent towards the rear as in RC 298.

In BPI 2915 a distinct cleithrum is present, and this appears to have been the case in the other specimens as well. Von Huene (1942) described this element in material later referred to *Kawingasaurus* by Cox (1972).

In GS K224 (Fig. 12A) the interclavicle is not completely preserved and the sternum has apparently been eroded away. Seen in the midline above where the sternum would have lain are the bases of the coracoids, meeting over the anterior parts of their inner surfaces in what appears to be a natural relationship; all the remaining postcranial elements in this specimen are in natural articulation with each other. In BPI 2915 a similar meeting of the coracoids in the midline, over the rear of the interclavicle and the front of the sternum, seems likely.

The best humerus is that of the right side in BPI 4086 (Figs 7–8), but the bone is also well preserved in BPI 506 (Fig. 9) and BPI 696 (Fig. 10). The bone is almost as broad as it is long, and is characterized by greatly enlarged processes serving for muscle attachment. There is a clearly demarcated head (*caput humeri*), forming the most proximal corner of the bone and facing dorsally as a prominent, slightly rounded condyle. The head is especially strongly developed in BPI 506. Behind this the posterior corner of the humerus is extended as a powerful posteromedial process, which consists of a neck portion and an expanded terminal portion. In front of the humeral head the inner, anterior edge of the bone is drawn forward as a broad, thin deltopectoral crest, with a thickened leading edge.

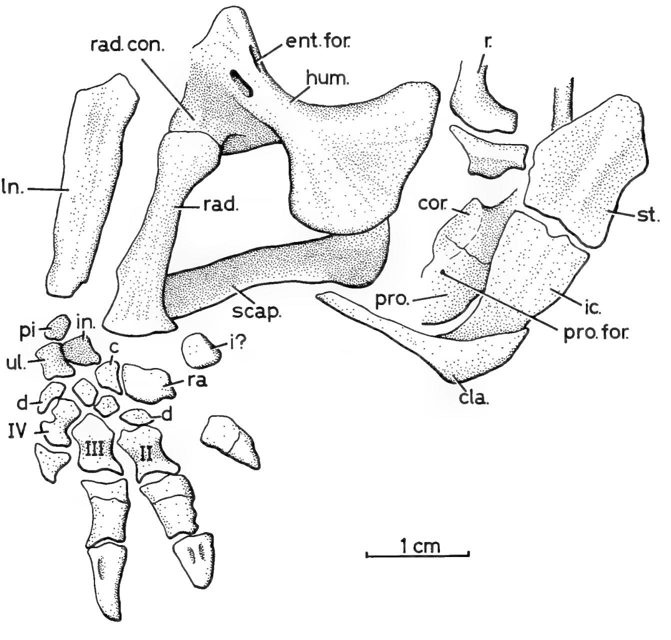

Fig. 6. *Cistecephalus* sp. BPI 2915. Partial pectoral girdle and left forelimb. Manus seen in ventral view.

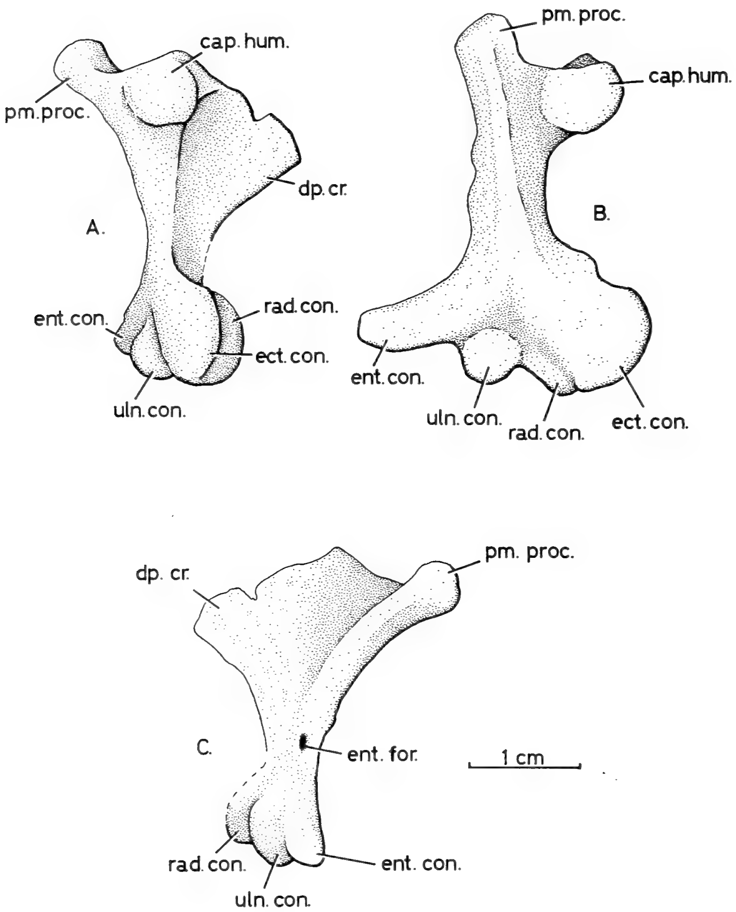

Fig. 7. *Cistecephalus* sp. BPI 4086. Right humerus. A. Dorsal view. B. Posterior view. C. Ventral view.

The proximal part of the humerus is convex dorsally and concave ventrally. The distal half is twisted so that the plane in which the distal edge lies is at right angles to the plane in which the deltopectoral crest and posteromedial process lie. In this way, when the proximal part of the humerus is brought to lie in the horizontal plane, the articulatory surfaces for the radius and ulna on the distal edge face forward and laterally. With the distal edge in the horizontal plane, the most anterior part is formed by the broad ectepicondyle. A thin crest leads medially from the ectepicondyle to merge with the body of the humerus near the waist of the bone. Below and behind the ectepicondyle is a prominent, rounded condyle for the radius, separated from the ectepicondyle by a distinct groove. Behind this is a smaller but equally distinct condyle for the ulna; the distal edge of the humerus is thinner in this region, and the ulnar condyle stands clear of both the dorsal and ventral surfaces of the bone, while on the dorsal surface there is a slight depression medial to the condyle. This depression is deepest in BPI 506, where the condyles are very powerfully developed. Posterior to the ulnar condyle the humerus is extended as a long, relatively slender entepicondyle. At the base of this process, near the waist of the bone, the humerus is pierced by the entepicondylar foramen.

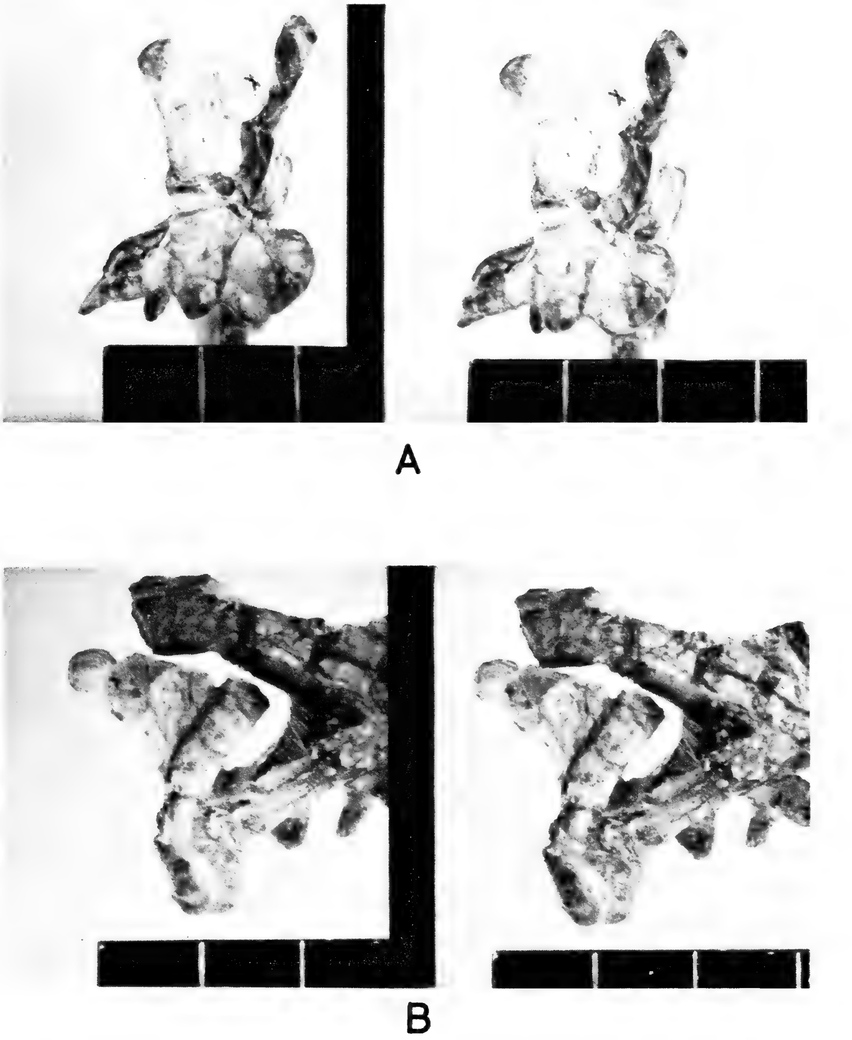

Fig. 8. *Cistecephalus* sp. BPI 4086. Stereophotographs of right humerus. A. Posterior view. B. Dorsal view.

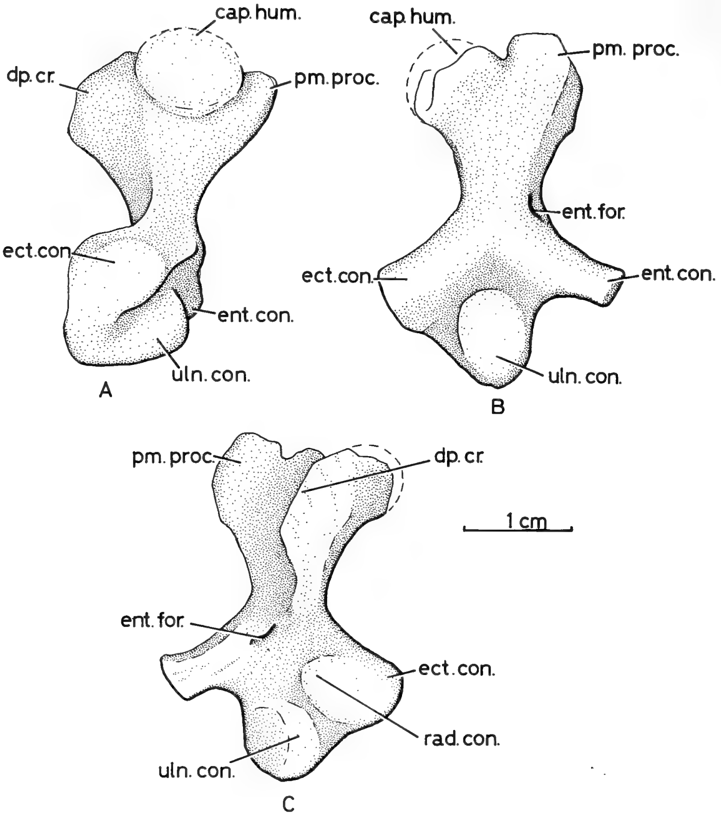

Fig. 9. *Cistecephalus* sp. BPI 506. Left humerus. A. Dorsal view. B. Posterior view. C. Ventral view.

The radius is well preserved in BPI 2915 (Fig. 6) and BPI 2124 (Fig. 11). The length of the bone in BPI 4086 is equal to that of the humerus between the humeral head and the outside surface of the radial condyle. The ulna is fairly robust, widened proximally for the meeting with the humerus and flared distally to meet the bones of the carpus over a fairly broad area. A posterior crest on the distal end gives the bone a triangular cross-section where it meets the carpus.

The ulna (Figs 6, 10–11) is present in BPI 2915, BPI 696 and BPI 2124. It is characterized by a wide and powerful olecranon process extending up above a notch for articulation with the ulnar condyle on the humerus. The shaft of the ulna is slender, and the distal extremity is rounded in section and narrower than that of the radius. On the posterior surface a deep groove extends down the shaft from the level of the articulatory facet for the humerus.

The carpus is best seen in BPI 2915 (Figs 6, 13), where the ventral surfaces of the bones are exposed. The radius and ulna are separated from the carpus by a slight gap, within which three small bones lie alongside the ulna. The one nearest the ulna can be regarded as a pisiform, drawn medially during the pulling apart of the wrist, while of the other two the lateral one probably represents an ulnare, and the medial element the intermedium. The remainder of the carpus is still undisturbed and the bones can be identified with a fair amount of certainty. There are a large medial radiale and a centrale, followed distally by a row of four distalia. In BPI 2124, the specimen described by Brink (1952), an ulnare, an intermedium and a large radiale are present, as well as four, possibly five, distalia (Fig. 11). A centrale is also present. The doubtful fifth distal is the most median one, which may actually be part of the radiale. The middle distale is smaller than figured by Brink, who mistook part of the third metacarpal as being part of it. The most lateral distale, behind the fourth

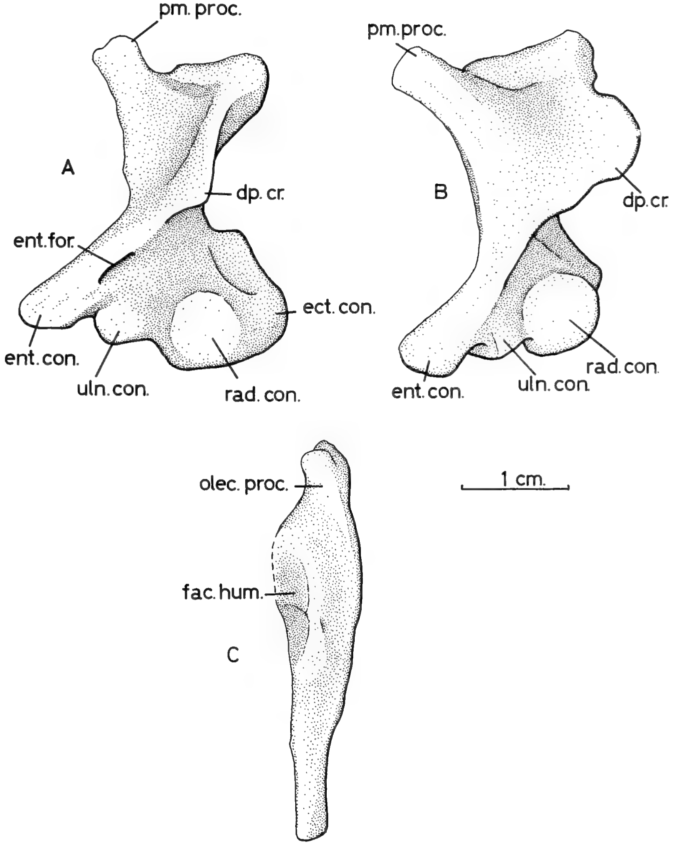

Fig. 10. *Cistecephalus* sp. BPI 696. Left humerus. A. Anteroventral view. B. Ventral view. C. Left ulna in anterior view.

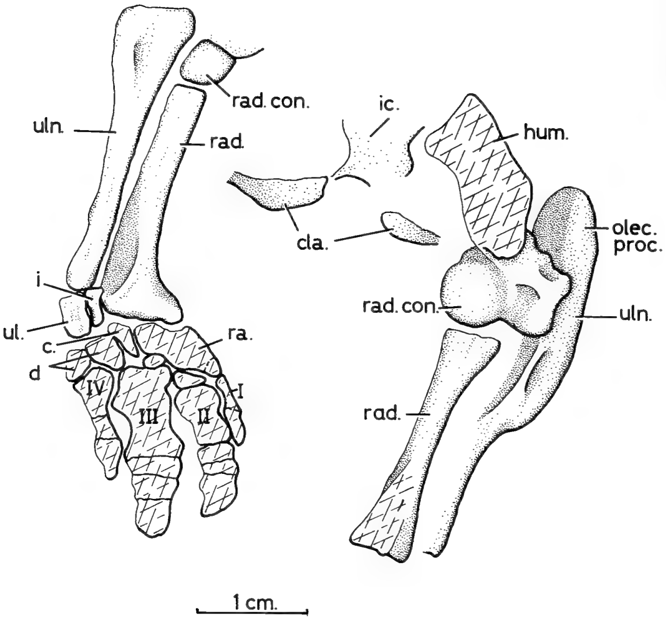

Fig. 11. *Cistecephalus* sp. BPI 2124. Left and right forelimbs as preserved. Left manus in ventral view, radius and ulna of both sides in posterior view.

metacarpal, was regarded by Brink as metacarpal V. In BPI 4120 a row of four distalia is seen.

In BPI 4120 (Fig. 12B) four metacarpals are present in the right manus, the two middle ones being the largest. These are interpreted as being, from medial to lateral, the first to fourth metacarpals; a small bone close inside the fourth metacarpal may be a reduced fifth metacarpal. Four metacarpals are present in BPI 2124 (Fig. 11), Brink's (1952) specimen, these being nos. I, II, III and IV. In BPI 696, where the carpus is very incomplete, a splint of bone alongside the fourth digit may represent a fifth metacarpal. Three metacarpals are in position in BPI 2915 (Figs. 6, 13A). These have been identified as nos. II, III and IV. A loose, damaged element lying medial to the rest of the wrist bones may possibly be a dislodged first metacarpal.

A digital formula can be obtained in GS K224, the specimen described by Keyser (1973). This is the only specimen to show a hand with five digits (Figs 12A, 13B). The left hand, seen in ventral view, is best preserved. The first digit is reduced but appears complete, with the two phalanges separated by only a narrow line of fusion. There is a small metacarpal. Digits 2 and 3 are robust, also with the first and second phalanges fused, and are provided with powerful ungual phalanges. The ungual phalanx of digit 2 is damaged but was clearly of a size comparable with that of 3. The fourth digit is reduced in size, and about the size of the first, while the fifth is also small. Here there is an ungual phalanx smaller than that of 4, and a single phalanx is preserved behind this. The right manus is also preserved, and preparation of digit 5 shows that it is complete; it is smaller than the others but consists of an ungual phalanx and fused first and second phalanges. The digital formula of this specimen is thus 2,3,3,3,3.

Several other specimens show details of the manus. In BPI 2915 (Figs 6, 13A) three digits are present, two of them nearly complete. In two digits, regarded as the second and third, the first and second phalanges are immovably united, and can be distinguished from each other only by a thin line of fusion. Medially a third fused pair of phalanges lies separated from the radiale by a space large enough to accommodate a metacarpal; this probably represents the first digit, with the first and second phalanges fused. The ungual phalanges of the second and third digits are damaged, but that of the third digit is of

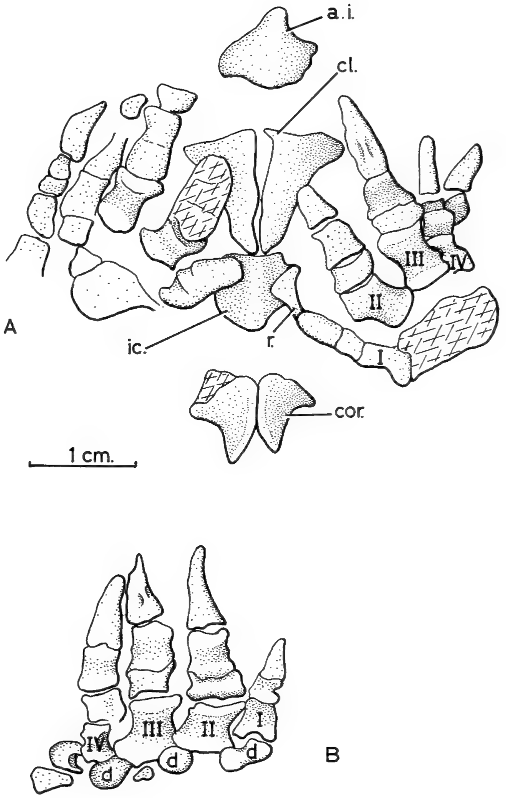

Fig. 12. *Cistecephalus* sp. A. GS K224. Left and right manus in ventral view, as preserved. B. BPI 4120. Right manus in ventral view.

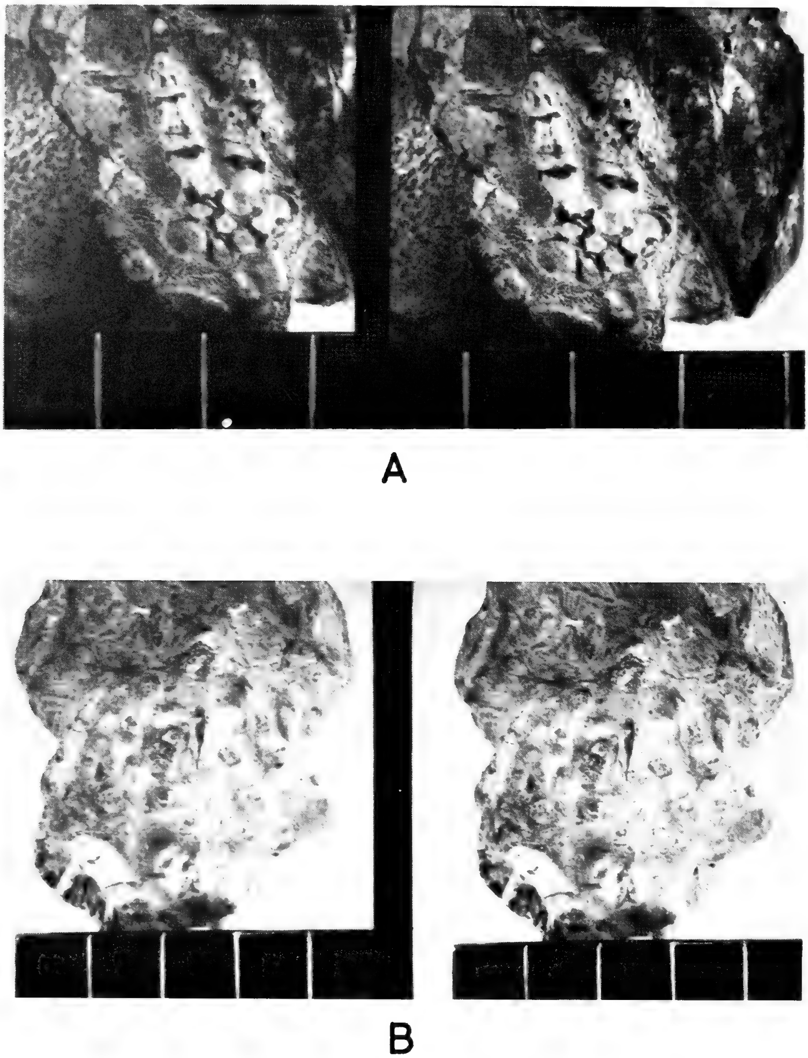

Fig. 13. *Cistecephalus* sp. A. Stereophotographs of BPI 2915, left manus in ventral view. B. Stereophotograph of GS K224. Left and right manus in ventral view.

considerable length. Only a fragment of the first phalanx of the fourth digit is preserved. In BPI 4120 (Fig. 12B) four digits are present, these being the first, second, third and fourth. In all the first and second phalanges are closely united but in only the first digit have the two reached the stage of semi-fusion found in the case of BPI 2915. The ungual phalanges are long and sharp-pointed, particularly that of the second digit. In the second, third and fourth digits the first phalanx is shortened to almost disc-like proportions. In overall appearance the manus is short, wide and powerful.

In BPI 696 a left manus, with a very incomplete wrist, is preserved. As interpreted, the first, second, third and fourth digits are present. In the first digit the first and second phalanges are fused, while in the other digits this is the condition in the first two phalanges, the ungual phalanx being movable on the distal tip of the second phalanx. In Brink's (1952) specimen, BPI 2124, a part of the first metacarpal is preserved, and possibly part of the first phalanx (Fig. 11). Digits 2 and 3 are complete, and the first two phalanges of each are firmly united and separated by a line of fusion. The fourth digit is very incomplete, but at least one phalanx is present.

The absence of a fifth digit in all but one of the specimens available is probably best regarded as being due to accidents of preservation resulting from this digit's relatively delicate structure.

Pelvic girdle and hind limb

The pelvic girdle is preserved in BPI 696 (Fig. 14B), BPI 2450 (Fig. 16B) and BPI 4086 (Figs 14A, 16A). The ilium lies well forward in relation to the other pelvic bones with the blade forming a strong anterior process. A posterior process is clearly demarcated from the base of the bone. Above the acetabulum the base of the ilium is drawn out as a buttress terminating in a laterally directed process, while in front of the acetabulum its anterior surface is broad and flat. The pubis forms the ventral part of the acetabulum and the anterior wall of the obturator foramen. Ventrally it carries a low keel set off laterally to the ventral border of the bone. The ischium forms a lower rim for the acetabular socket which is not as strongly developed as the iliac buttress. The acetabulum is shallowest on the ischium and deepest on the ilium, where the iliac buttress overhangs the socket. All three bones are firmly united and the puboischiadic plate lies at an angle to the ilium, suggesting that the two ischia approached each other in the ventral midline. There is, however, no indication of a bony or cartilaginous symphysis between the two halves of the pelvis.

In BPI 2450 two clear depressions and a third less distinct one on the inside of the iliac blade mark the points of attachment of the sacral ribs. The most anterior of these lies some way behind the anterior tip of the ilium and is shallow and fairly long. The second is deep in comparison and lies above the anterior border of the acetabulum. The third depression may mark the attachment of the last sacral; it lies close behind the preceding one. If the sacral vertebrae were held horizontally, these depressions, which lie some distance below the dorsal border of the iliac blade, show that the pelvis must have been rotated so that the puboischiadic plate lay largely behind the acetabulum.

The ilium of BPI 2450 (Fig. 16B) differs in some respects from that of BPI 696 and BPI 4096. The iliac blade is shorter than in BPI 696, and the anterior border of the anterior process is turned out laterally and descends to meet the highest point of the acetabular buttress well behind the anterior edge of the bone. As a result, the iliac blade is laterally concave. There is no sign of a separate posterior process at the base of the ilium, but the dorsal crest of the bone does extend back a short way. In overall view, therefore, the ilium is a high, narrow bone. The acetabulum appears to be deeper than in BPI 696, and bounded by a more prominent rim; the posteroventral, ischial part of the rim is almost as strongly developed as the anterodorsal, iliac part.

The structure of the hind limb can be determined in BPI 4096 (Figs 15, 16). Both femora are preserved, the right one being the better exposed. The bone is a remarkable one, with a strongly developed head carried medial to the inner border of the shaft and standing well forward of the anterior surface of the bone. The greater trochanter is confined to the lateral corner of the proximal part of

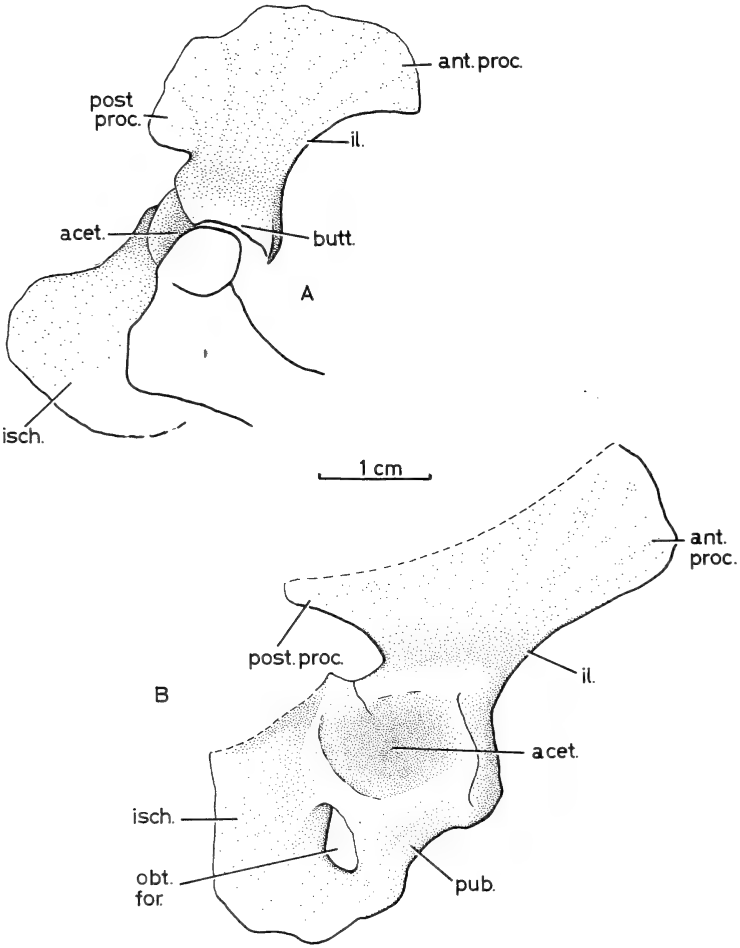

Fig. 14. *Cistecephalus* sp. Pelvic girdle in right lateral view. A. BPI 4086. B. BPI 696.

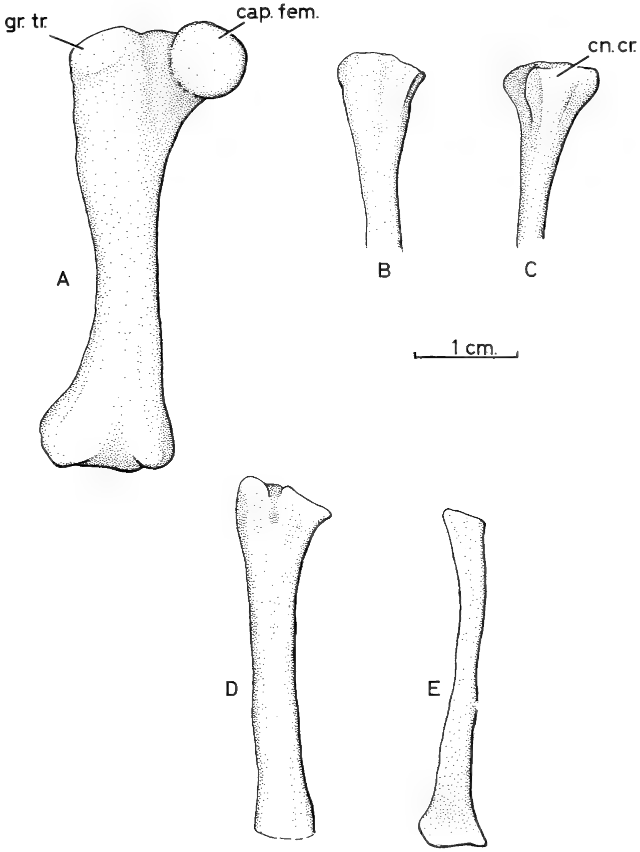

Fig. 15. *Cistecephalus* sp. BPI 4086. A. Right femur in anterior view. B. Right tibia in medial view. C. Right tibia in anterior view. D. Left tibia in lateral view. E. Left fibula in ?lateral view.

the bone, and does not extend down the shaft as a separate crest. The anteroposteriorly compressed shaft is slightly rounded anteriorly but almost perfectly flat behind. Distally the bone is expanded for the articulatory areas with the tibia and fibula. The proximal end of the bone between the head and expanded greater trochanter is essentially as narrow as the shaft.

The proximal ends of the tibia and fibula are preserved on the right side but both bones are fully exposed on the left side, except where the distal end of the tibia is partially obscured by the foot. The tibia is a well-ossified bone with the proximal articular surface roughly triangular in outline. There are two clear areas for articulation with the condyles of the femur, forming two corners of a triangle completed by an anterior cnemial crest. Proximally the lateral

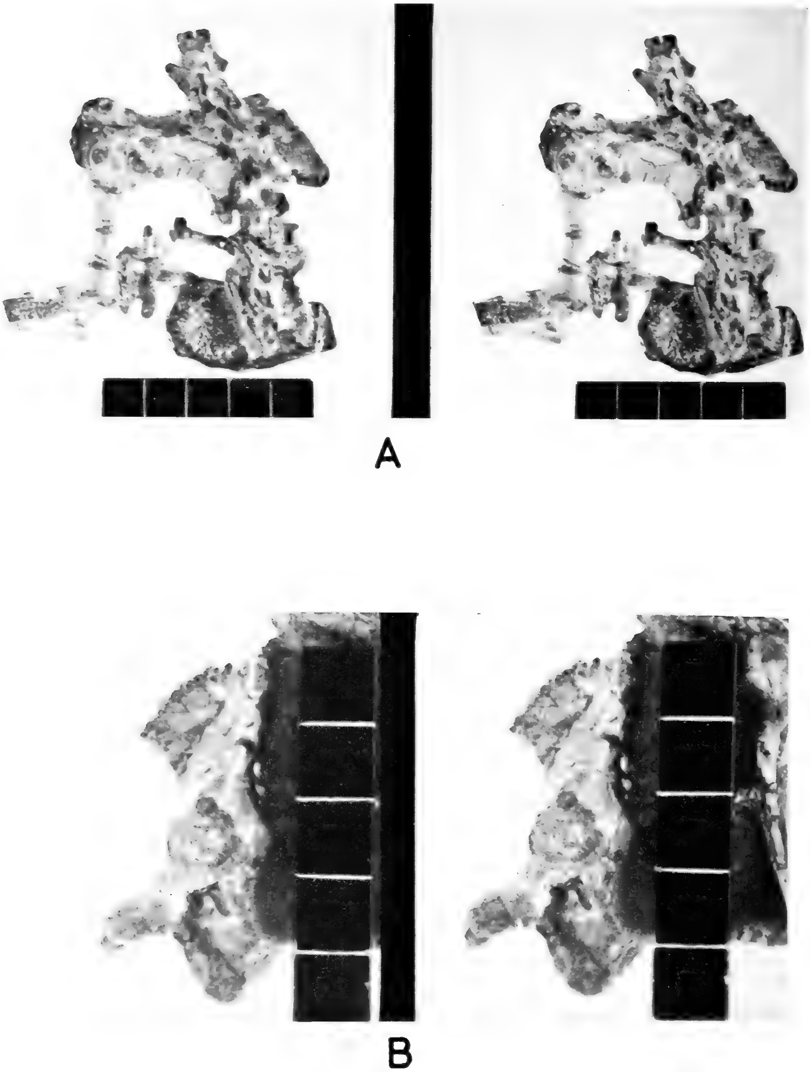

Fig. 16. *Cistecephalus* sp. A. Stereophotograph of BPI 4086. Right ilium, femur and proximal part of tibia and fibula. Left astragalo-calcaneum in proximal (dorsal) view. B. Stereophotograph of BPI 2450. Right half of pelvic girdle in lateral view.

surface of the bone bears a groove which may have received the dorsal part of the fibula (see Watson 1960). Distally the shaft becomes narrower and lateromedially compressed, but it widens again to form a rounded condyle for articulation with the tarsus.

The slender fibula is slightly expanded proximally where it lay up against the lateral side of the tibial head. It could not have had more than a small area of articulation with the femur, but distally it widens to form a small, flat articulatory surface for the tarsus.

The left tarsus and pes, slightly separated from the tibia and fibula, are preserved nearly complete and are seen in ventral view (Figs 16–17). The astragalus and calcaneum appear to be unique among dicynodonts in that the two bones are united and can be distinguished from each other only by a notch and a line marking the fusion between them. Their proximal surfaces combine to form a wide, concave articulatory area for the tibia and fibula. The largest

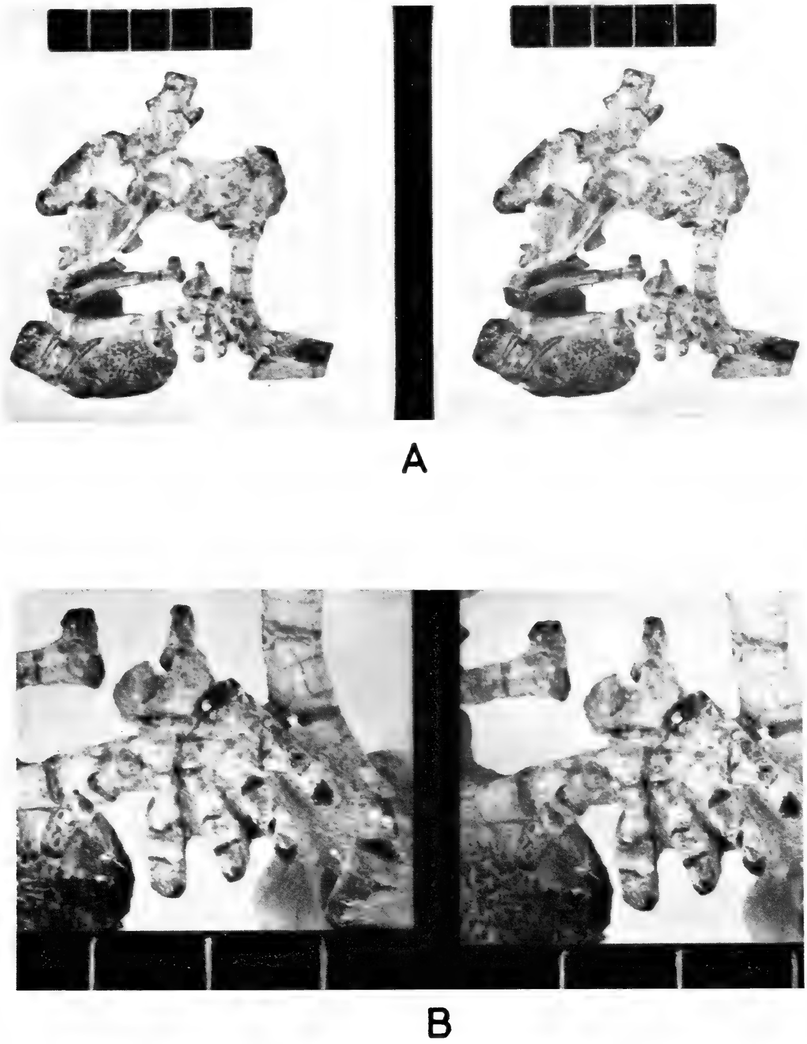

Fig. 17. *Cistecephalus* sp. BPI 4086. Stereophotographs. A. Left ilium, femur, tibia, fibula and pes. B. Left astragalo-calcaneum and pes in ventral view.

part of this surface is formed by the astragalus and is more concave than the smaller calcaneal surface which met the fairly flat distal part of the fibula. The distal surface of the calcaneum, more extensive than that of the astragalus, is rounded for its meeting with the tarsal bones. The size and strength of the structure, and its well-developed articulation with the tibia and fibula, are surprising in a reptile such as *Cistecephalus*, and suggest considerable movement at the ankle joint, including rotation between the astragalo-calcaneum and the tibia and the fibula, and flexure and extension between astragalo-calcaneum and the foot.

In front of the astragalo-calcaneum are two proximal tarsal bones, one seen only very indistinctly. These probably met the medial part of the calcaneum and the lateral part of the astragalus. Following on these is a row of four distal tarsals. The most medial of these meets the first metatarsal and part of the second metatarsal; the third meets the third metatarsal while the fourth and largest touches the base of both fourth and fifth metatarsals. The metatarsals of the second, third and fourth digits are short and fairly slender. Only in the fifth digit can three phalanges be distinguished, and these are not very clearly shown. The rest of the digits have suffered varying amounts of damage. Only two phalanges are found in the second, third and fourth digits, while in the first digit only one separate phalanx could be identified. In this digit, a small bony flake might represent part of a terminal phalanx.

RANGE OF MOVEMENTS AND MUSCULATURE OF THE LIMBS

Attempts at reconstructing musculature and limb movements in extinct reptiles, particularly in the case of forms which have no living descendants, inevitably involve some degree of speculation, but if this shortcoming is clearly borne in mind the exercise can be a useful and informative one. In the following, only general features in the bony structure and only those main muscle groups which are expected to be present in all terrestrial reptiles are considered (see Romer 1922, 1944). Cox (1972) has given a more detailed account of the musculature and possible range of movement in the forelimb of *Kawingasaurus*, where the material included separated bones which could be manipulated and where the relations between the joints could be better determined than was possible in the case of the *Cistecephalus* material available for the present study.

Pectoral girdle and forelimb

The pectoral girdle of *Cistecephalus* is unusual in several respects. The girdle as a whole lies well forward, leaving a short neck with the scapula relatively close behind the skull. The glenoid cavity faces almost straight laterally while the blade itself, instead of sloping slightly forward, is vertical or even posteriorly inclined in its upper half. The base of the scapula has rotated forward and the acromian process, rather than being a separate projection, is part of the general anterior edge of the scapular blade. The clavicle appears to have lain at an angle of approximately 45°, from an acromian connection

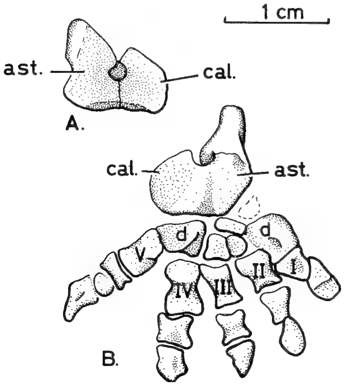

Fig. 18. *Cistecephalus* sp. BPI 4086. A. Left astragalo-calcaneum in proximal (dorsal) view. B. Left pes in ventral view.

straight down to a second support at the anterior edge of the procoracoid. This may be associated with the forward position of the shoulder girdle as a whole relative to the vertebral column and skull. Besides being strongly braced by scapulae and procoracoids, the clavicles also meet in the ventral mid-line in an extensive face-to-face contact.

These features of the pectoral girdle can be interpreted in terms of resistance to strong lateral forces which were imposed upon the forwardly rotated glenoid region of the scapulocoracoid. Such forces would have been transmitted internally on to the clavicle which, instead of bracing the scapulocoracoid against stress from a posterolateral direction, had to support that bone against forces of almost purely lateral origin. To help counter these forces, the acromian articulation was extended dorsally so that the clavicle enjoyed an extensive dorsoventral overlap with the scapula; at the same time the ventral part of the clavicle rotated back to meet the anterior edge of the procoracoid in an extra point of support. The substantial meeting between the clavicles in the ventral mid-line may be regarded as a further strengthening device.

The relationship between the glenoid cavity and humerus is also of significance. The glenoid is a well-finished socket, with a sharp dorsal rim on the supraglenoid buttress. The humerus carries a distinct humeral head, set off as a dorsal condyle on the proximal part of the bone, and it is evident that all movement between humerus and glenoid took place about its slightly convex articulatory surface. With the humeral head dorsally oriented the deltopectoral crest faces forwards, and the twist of the humerus along its long axis is such that the condyles for the radius and ulna are directed forward at an approximate angle of 45° to the horizontal. With the head of the humerus facing forward in the glenoid cavity the distal condyles of the humerus face straight down. Judging by the relations between the head of the humerus and the glenoid, this 45° rotation, accompanied by forward and back swing, was the most general movement of the upper arm.

The highly developed articulations between the radius and ulna and the humerus indicate that considerable movement between upper and lower forearm was characteristic of the animal. While the radius seems restricted to a rocking motion against the radial condyle of the humerus, the ulna is notched for articulation with the ulnar condyle and distal edge of the humerus. The depression on the humerus immediately proximal to the ulnar articulation suggests, too, that the ulna could be straightened on the upper arm by the action of muscles attaching on its high olecranon process.

Powerful extension of the forearm on the humerus, best explained as a digging or scraping movement for which the broad, powerfully constructed manus with its fused phalanges and strong claws was clearly suited, would account for the lateral forces directed on to the glenoid region of the scapulocoracoid. A consideration of some of the chief muscles associated with the pectoral girdle and forelimb supports this interpretation.

In a dicynodont such as *Cistecephalus* it is expected that the main muscles bracing the scapula on the side of the trunk were the trapezius muscle anteriorly, inserting on the anterior edge of the bone and on the cleithrum, and the levator scapulae superficialis muscle. These arose from the posterior and posterodorsal part of the rounded occipital area of the skull and from the ligamentum nuchae. Posteriorly the scapula would have been held in position by the serratus anterior superficialis muscle, arising from the spines of the dorsal vertebrae and inserting on the dorsal edge of the scapula. The backward slope of the dorsal part of the scapula in some specimens may indicate a division of the insertional areas of these three muscles: the levator scapulae superficialis anteroventrally, the trapezius anterior anterodorsally and the serratus anterior superficialis posterodorsally.

Muscles which are generally responsible for movement of the humerus are, superficially, the latissimus dorsi, arising from the surface of the back and flank behind the pectoral girdle, and the deltoideus group, arising from the scapula and clavicle as the scapular and clavicular deltoid muscles. In *Cistecephalus* the area for insertion of the deltoideus is clearly marked off from the head and more posterior part of the humerus by a crest running from the base of the head to the ectepicondyle. The pectoralis muscle normally arises from the sternum and ribs and inserts on a process below the proximal end of the humerus. In *Cistecephalus* the insertion areas of both the deltoideus muscles, pulling the humerus forward and up, and the pectoral muscle, pulling the humerus back and down, are greatly expanded as a powerful deltopectoral crest, giving both muscle groups added leverage on the upper arm and reflecting their increased size. Another muscle important in locomotion is the subcoracoscapularis, which arises from inside the girdle to insert near the head of the humerus and which serves to pull the humerus back—in *Cistecephalus* the prominent medially oriented internal process marks the point of insertion of this muscle, and is evidence of its increased importance during locomotion. Cox (1972) suggests that due to the similar medial position of the internal process relative to the condyle in *Kawingasaurus*, contraction of the subcoracobrachialis would also have resulted in a downward thrust of the humerus. Other muscles inserting on the humerus would have been the scapulohumeralis anterior, arising from the forward part of the girdle and inserting near the head of the bone, and the supracoracoideus, extending from the anterior part of the coracoid plate to the underside of the humerus.

Movement of the forelimb is brought about by the triceps muscle dorsally and the biceps and brachialis muscles ventrally. In *Cistecephalus* the areas of origin of the triceps on the humerus were the posteromedially extended internal process and the expanded area behind the ectepicondyle which, as shown above, is demarcated from the deltoideus insertion area by a crest. The third triceps head arose from the scapula. In *Cistecephalus* the insertional area of the muscle, the olecranon process, is greatly enlarged over the normal dicynodont condition, and it is evident that the triceps, though short, was a muscle of considerable size and able to exert powerful extension forces on the lower arm.

Besides extension and flexion movements of the forearm on the humerus, it is likely that anteroposterior swing of the forearm was possible (see Cox 1972). Such movements would have been controlled by flexor and extensor muscles arising from the ectepicondyle and entepicondyle of the humerus; in *Cistecephalus* these are powerfully developed and extend well in front of and behind the condyles for articulation with the radius and ulna.

Seen in its entirety, the structure of the pectoral girdle and forelimb in *Cistecephalus*, characterized by strong processes for muscle attachments and well-finished joints and articulations carrying a minimum of cartilaginous lining, suggests that the animal was capable of using its forelimbs in controlled movements of considerable power. As suggested above, these movements may be interpreted as forming part of habitual digging or scraping activities.

Pelvic girdle and hind limb

In the hind limb all joints and articulations are, as in the forelimb, characterized by well-ossified and smooth bony surfaces. The relationships of the femur to the pelvic girdle and lower hind limb are of particular significance. The prominent, rounded femoral head projects medially and forward on the narrow proximal part of the bone, and it is clear that a considerable range of movement was possible at the acetabulum. The offset head suggests that the femur was held with the lower end drawn in close to the body in a mammal-like fashion, with movement taking place mainly in a vertical, parasagittal plane. In addition, the fact that much of the articulatory surface on the head faces forward as well as inward suggests that the femur could rotate medially along its long axis so that the anterior part of the head came to lie deeper within the acetabulum. In this position the greater trochanter on the proximolateral corner of the bone is turned forward, while the condyles for the tibia face slightly outward, turning the lower leg away from the body. Since the condyles on the femur for articulation with the tibia face distally as well as posteriorly, it is likely that the lower limb could have been extended far forward on the femur.

The strengthened astragalo-calcaneum provided a single, large articulatory surface for movement between the foot and the tibia and fibula. The rounded distal end of the tibia has a radius of curvature smaller than that of the broadly concave astragalus, but the fibula terminates in a relatively flat articulatory surface which coincides more closely with the surface of the calcaneum. Movement between the astragalo-calcaneum and the tibia and fibula must have involved considerable rotation and even sliding between the bones of the lower limb and tarsus.

Increased rotatory movement between the lower leg and the pes could be the result of the femoral rotation discussed above, during which the lower leg was directed away from the long axis of the body. For example, if the femur were rotated inwards along its long axis while in the forward position, the lower leg could have been flexed back and away from the body in a scraping movement; however, rotation of the femur would have resulted in lateral displacement of the lower end of the tibia and fibula, and could have occurred only if compensatory movements were possible between the lower leg and pes while the pes was firmly placed on the ground. Thus, longitudinal rotation of the femur and the development of a broad articulatory surface on the astragalo-calcaneum in *Cistecephalus* are probably related phenomena, and are indications of unusual hind limb function in the living animal.

Although areas of muscle attachment are less clearly marked on the bones of the hind limb than on those of the forelimb, some observations can nevertheless be made regarding the possible arrangement of the hind limb musculature. In reptiles several muscles are responsible for movement of the femur. The puboischiofemoralis internus arises from the lumbar region and inner surface of the girdle and inserts on the femur near its head. In *Cistecephalus* a large, forward-facing area on the base of the ilium probably served for the origin of part of this muscle, which served to pull the femur forward. The iliofemoralis muscle in reptiles arises from the ilium and inserts on the upper surface of the femur, drawing it back; in *Cistecephalus* a distinct greater trochanter on the proximolateral corner of the bone shows that the muscle inserted in a primitive mammal-like fashion. Other muscles which generally draw the femur back are the caudifemoralis muscles arising from the tail, but the tail in *Cistecephalus* and other dicynodonts is weak and it is unlikely that these muscles were very important—no trochanter for their insertion is found on the femur. However, backward pull on the femur would have been provided by the ischiotrochantericus (obturator internus) running from the inside of the ischium to the head of the femur. In addition, an adductor femoralis arising from the pubo-ischiadic plate would have attached down the ventral surface of the femur and served to pull the leg back.

For the lower leg a group of extensor muscles, the iliotibialis and femurotibialis, run from the girdle and femur to insert on the tibia. A distinct cnemial crest on the *Cistecephalus* tibia indicates a well-developed femurotibialis, while the distally placed tibial condyles on the femur show that the lower limb could have been almost fully straightened upon the femur. Flexor muscles for the lower leg would have included the puboischiotibialis, running from the pelvic girdle to the lower leg.

The hind limb has clearly been modified in a different way to the forelimb. While the humerus has become broad and robust, with enlarged processes for the attachment of muscles, the femur is slender in comparison with other dicynodonts. The manus is relatively immobile and powerfully constructed, while the pes again is small but very mobile on the lower leg. In terms of length there are also significant differences between the bones of the forelimbs and hind limbs. Thus, the femur and tibia are both longer than their counterparts in the forelimb, the total length of the humerus and radius being approximately 73 per cent of the total length of femur and tibia. Although the point of articulation between the humerus and glenoid cavity is lower on the body than is the articulation between the almost vertically held femur and the acetabulum, it appears that the pelvic region of the body was held higher off the ground than the pectoral region during ordinary locomotion.

DISCUSSION

In its skull and jaw, axial skeleton, pectoral and pelvic girdles as well as in its appendicular skeleton, *Cistecephalus* shows a wide range of modifications which together make it probably the most aberrant of dicynodonts. It follows that *Cistecephalus* was adapted to a very distinctive mode of life, and that the general nature of the animal's habits should be indicated by these skeletal modifications. The peculiarities of the skeleton are all related to strengthening of individual bones or functionally integrated groups of bones and reflect increase in the size and power of various parts of the musculature. The clearly defined and in some cases enlarged areas of articulation between bones of the limbs and girdles, and the distinct articular condyles, with a minimum of cartilaginous capping, on the humerus and femur, all point to a high degree of muscular control over the limbs during movements of considerable power. Indications are that the forces exerted during these movements were far in excess of the requirements for normal locomotion, and it can be deduced that the limbs were frequently used during additional activities that formed an integral part of the animal's life. Moreover, the overall similarities between the skulls of *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*, and between the pectoral girdle and forelimb of *Cistecephalus* and *Kawingasaurus*, suggest that the family Cistecephalidae was adapted to a broadly uniform way of life.

Cox (1972) concluded on the basis of available material that *Kawingasaurus* was an active digger, and it is now possible to assign a similar way of life to *Cistecephalus* and, by inference, to *Cistecephaloides*. Compared with living

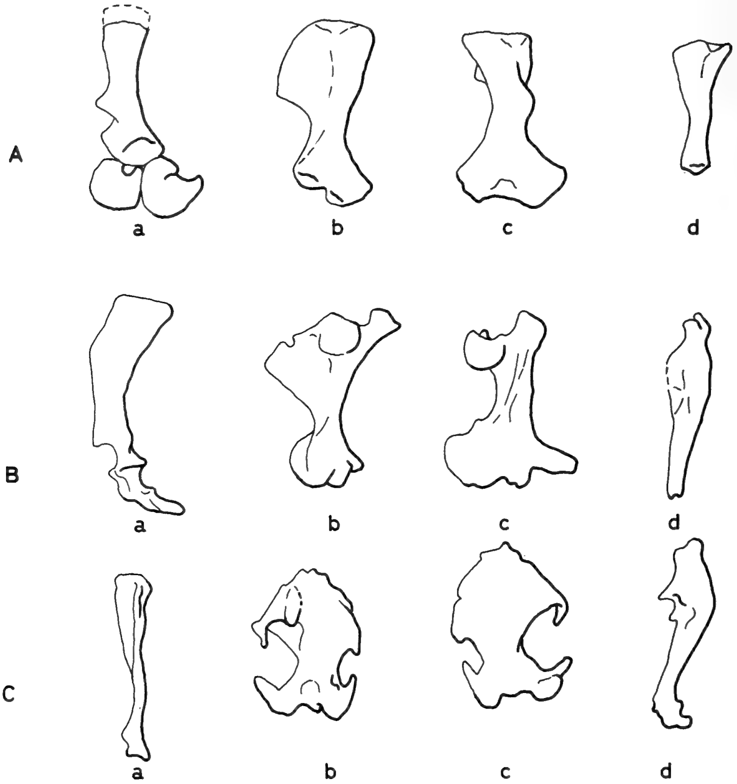

Fig. 19. Left scapulocoracoids, humeri and ulnae. Not to scale. A. *Oudenodon* sp., SAM–11114: a—scapulocoracoid in lateral view, b—dorsal view of humerus with proximal end horizontal, c—dorsal view of humerus with distal end horizontal, d—ulna in anterior view. B. *Cistecephalus* sp., from several specimens: a—scapulocoracoid in lateral view, from RC 298, b—dorsal view of humerus with proximal end horizontal, from BPI 4086 (drawn from right side), c—dorsal view of humerus with distal end horizontal, from BPI 4086 (drawn from right side), d—ulna in anterior view, from BPI 696. C. *Talpa europaea:* a—scapula in lateral view, b—humerus in posterior view, c—humerus in anterior view, d—ulna in anterior view.

mammal groups, the skeletal anatomy of *Cistecephalus* bears the closest overall resemblances with those forms which are adapted to a digging or burrowing way of life (Hisaw 1923, Yalden 1966, Reed & Turnbull 1965). Such features as a rounded occipital region, the broad humerus with powerful processes for muscle attachment, and a greatly enlarged olecranon process in *Cistecephalus* are found in analogous form in the European mole *Talpa europaea* and the Cape Golden mole *Chrysochloris asiatica* (Fig. 19). In these living forms the rounded occiput is related to increased size of the shoulder and neck muscles, while the robust humerus and high olecranon process reflect the increased power of muscles used during burrowing. The broad manus of *Ciste-*

cephalus, with three enlarged digits and fused phalanges, is suited to scraping or digging, with the highly mobile pes shovelling loosened soil to the rear and side of the animal.

The limbs and limb girdles provide the strongest evidence for digging or burrowing activities, but other features of the skeleton can also be interpreted in terms of this way of life. Thus strengthening of the skull by broadening the skull roof and eliminating the interpterygoidal vacuity in the basicranial girder, and loss of mobility between the cervical and dorsal vertebrae could indicate resistance to forces encountered by the skull and transmitted to the vertebral column during burrowing. The anterior position of the pectoral girdle relative to the vertebral column is also a feature found in both the true moles (Talpidae) and the Cape Golden mole (Chrysochloridae) (Campbell 1938, 1939) and it is significant that outward rotation of the hind limb is a characteristic of the true mole *Talpa* (Yalden 1966).

The family Cistecephalidae, including *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*, therefore represents a dicynodont radiation into a burrowing or fossorial way of life. Food sources such as plant roots and small invertebrates become available to animals capable of powerful digging, while the true bur-

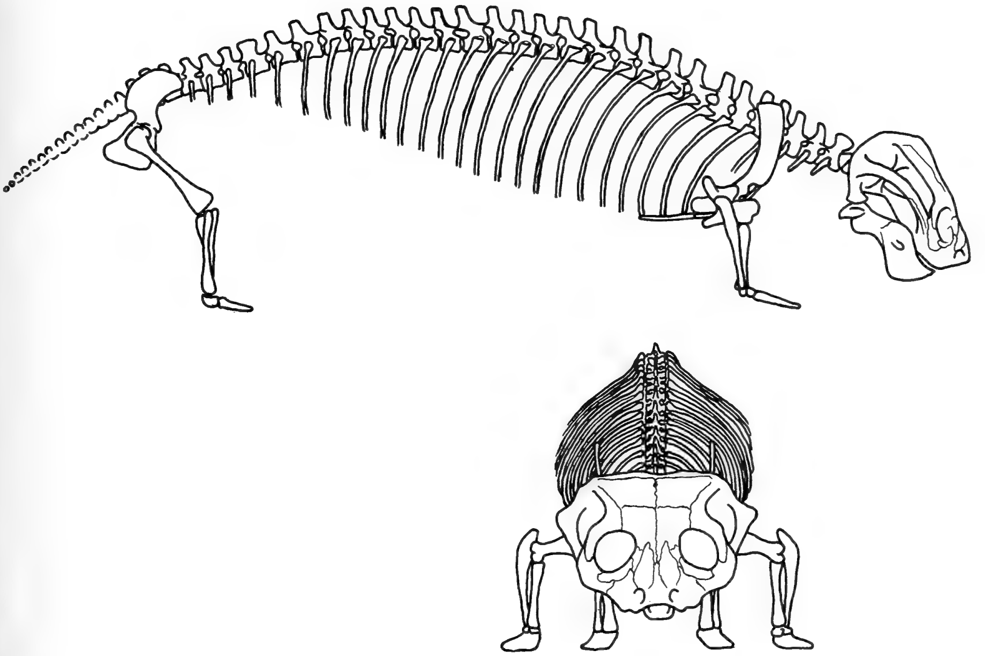

Fig. 20. Formal reconstruction of *Cistecephalus* in lateral and anterior views, mainly from BPI 4086 and SAM–10665. Approximately ⅜ natural size.

rower has available an effective means of escape from predators. The degree of burrowing characteristic of the various cistecephalid genera will remain uncertain until further more definite discoveries are made; for instance, the discovery of a complete skeleton in an in-filled burrow would establish a highly-developed fossorial way of life for the particular species. Also, material at present available does not allow the actual nature of the cistecephalid burrowing activity to be identified and compared with the 'swimming' burrowing style of *Talpa* and its allies, or the 'running' style of the Chrysochloridae (Hisaw 1923, Yalden 1966, Campbell 1938). It is, however, clear at this stage that the Cistecephalidae were committed to intensification of digging or burrowing activities which probably formed only a minor part of the general way of life of other dicynodont groups.

SUMMARY

In both its cranial and postcranial skeleton *Cistecephalus* shows evidence of adaptations to a very specific mode of life. The skull is structured within the characteristic dicynodont framework, but its many substantial modifications appear to be linked with specialized features of the postcranial skeleton. Seen in its entirety, the skeleton of *Cistecephalus* represents an osteological extreme in dicynodont evolution, and all indications are that the living animal, committed as it was to at least semi-fossorial habits, was a highly unusual member of South Africa's Upper Permian fauna.

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ABBREVIATIONS

acet.	acetabulum
acr. proc.	acromian process
a.i.	atlas intercentrum
ant. pro.	anterior process of ilium
ast.	astragalus
at.	atlas
ax.	axis
ax. r.	axis rib
butt.	buttress of ilium
c.	centrale
cal.	calcaneum
cap. fem.	caput femoris
cap. hum.	caput humeri
cla.	clavicle
cn. cr.	cnemial crest
cor.	coracoid
cr.	crest
d.	distal carpal, tarsal
dp. cr.	deltopectoral crest
ect. con.	ectepicondyle
ent. con.	entepicondyle
ent. for.	entepicondylar foramen
fac. hum.	facet for humerus
gl.	glenoid
gr.	groove

hum.	humerus
i.	intermedium
ic.	interclavicle
il.	ilium
isch.	ischium
lat. pro.	lateral process
n.s.	neural spine
obt. for.	obturator foramen
od.	odontoid
olec. proc.	olecranon process
pa. fac.	facet for proatlas
par.	parapophysis
pi.	pisiform
pm. proc.	posteromedial process
post. proc.	posterior process of ilium
pro.	procoracoid
pro. for.	procoracoid foramen
pro. p.	procoracoid process
pub.	pubis
r.	rib
ra.	radiale
r.a.	rib articulation
rad.	radius
rad. con.	radial condyle
scap.	scapula
st.	sternum
ul.	ulnare
uln.	ulna
uln. con.	ulnar condyle
BPI	Bernard Price Institute for Palaeontological Research, Witwatersrand University, Johannesburg
GS	Geological Survey, Pretoria
RC	Rubidge Collection, Wellwood, Graaff-Reinet
SAM	South African Museum, Cape Town.

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

Note punctuation in the above example:
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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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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

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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
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(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

MICHAEL A. CLUVER

THE SKELETON OF THE MAMMAL-LIKE REPTILE *CISTECEPHALUS* WITH EVIDENCE FOR A FOSSORIAL MODE OF LIFE

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ANNALS

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CAPE TOWN

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

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(continued inside back cover)

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THE DEVELOPMENT OF *XENOPUS GILLI* ROSE & HEWITT (ANURA, PIPIDAE)

By

R. E. RAU

Cape Town Kaapstad

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By

R. E. RAU

South African Museum, Cape Town

(With 10 figures)

[*MS. accepted 6 July 1978*]

ABSTRACT

Tadpoles of the Cape clawed frog *Xenopus gilli* can be distinguished from those of *Xenopus laevis* by the distribution of melanophores and differences in dimensions. *Xenopus gilli* breeds in cooler water and is less tolerant of rising water temperatures. The species seems to be more abundant in mountainous terrain than in the low-lying Cape Flats. The breeding period largely coincides with that of *Xenopus laevis*, but indications are that it starts and ends earlier in the year. Where both species occur together some specimens appear to be hybrids.

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INTRODUCTION

The Cape clawed frog, as it should preferably be called (Mertens 1970), was recognized as a new species and described as *Xenopus gilli* by Rose & Hewitt in 1927. The type locality of this pretty and easily distinguishable species is the Silvermine Stream near Clovelly, Cape Peninsula. A smaller, more pointed head, the absence of the subocular tentacle and the distinctive coloration render it quite different from the more common *Xenopus laevis*, which reaches a much greater maximum size. Both species often occur together, and the validity of the species *X. gilli* has sometimes been questioned.

Recently *X. gilli* has been confirmed as a true species. H. Kobel (*in litt.* 1977) of the Zoology Department of the University at Geneva succeeded in breeding *Xenopus gilli*, and also in cross-breeding *X. gilli* with *X. laevis*. The male hybrids proved to be sterile, while the female crosses could reproduce when mated with either *X. gilli*, *laevis* or *muelleri* (see Kobel & Du Pasquier 1975; Wabl & Du Pasquier 1976).

In the sandy Cape Flats only a few metres above sea-level, one specimen of

Ann. S. Afr. Mus. **76** (6), 1978: 247–263, 10 figs.

Xenopus gilli is occasionally found amongst approximately 1 000 *X. laevis* which are being caught commercially for export as laboratory animals (J. Wood pers. comm.). Sometimes, during the dry season, several specimens of *X. gilli* have been found hibernating together under logs, etc., or encapsulated into the mud of dried-up vleis in the Cape Flats.

There are two specimens, male and female, in the collection of the South African Museum (ZR18914), which were collected at Citrusdal, in approximately 1937. Several *Xenopus* specimens, originally considered to be *X. laevis*, were reidentified after the establishment of *X. gilli* as belonging to that species (Mertens 1970), as well as a male specimen at the South African Museum (ZR2346) collected at Willemsrivier (31°21′S 19°06′E) west of Calvinia in 1898.

Both Citrusdal and Willemsrivier are within the winter-rainfall area of the south-western Cape. These localities have not been reconfirmed, however, nor has *Xenopus gilli* been recorded between the Cape Flats and the already-mentioned northern localities. The reason might be that a thorough search for this species has not yet been conducted in the area. In addition, *Xenopus gilli* is usually not easily found as the frogs hide in the mud or leaf-layer at the bottom of the pond. Occasional migration over land of this aquatic species, as is known to happen with *Xenopus laevis,* probably does occur. This could perhaps explain why in a given locality *Xenopus gilli* is found in one year and not in the following years.

It is also possible that the two northern localities represent isolated occurrences, especially if *Xenopus gilli* is a relict of a formerly more widely distributed form. *Xenopus laevis* lives in both acidic and alkaline waters (Nieuwkoop & Faber 1956) ranging from clear, cold, fast-running mountain streams to shallow, warm, muddy vleis. If, indeed, the essentially tropical *Xenopus laevis*, which occurs in most of eastern and southern Africa from the Red Sea to the western Cape (Mertens 1970), has invaded the range of the winter-rainfall species *Xenopus gilli*, the obviously greater tolerance to environmental changes of *X. laevis* might well be detrimental to the more specialized *Xenopus gilli.*

A clarification of the present range of *Xenopus gilli* and the question of possible competition with *Xenopus laevis*, especially in view of possible protective measures, is desirable. As described above, the presence of *Xenopus gilli* is not easy to establish when depending, as hitherto, on the fully developed frog alone. This suggested the use of the larval stages for distribution investigation. While the development of *Xenopus laevis* is fully documented (Nieuwkoop & Faber 1956), both eggs and larvae of *Xenopus gilli* remained unknown (Wager 1965).

Investigations during the past few years revealed that in several ponds and dams within the plateau of the mountainous Cape Point Nature Reserve *Xenopus gilli* is comparatively common. This in all probability is due to the curious fact that *Xenopus laevis* is comparatively rare in these localities.

To establish whether *X. gilli* can be identified in its larval stages and also to prove or disprove the species validity through cross-breading with *Xenopus* *laevis*, breeding experiments were undertaken by the author during 1976 at the South African Museum and by S. McVeigh at the Fauna and Flora Section of the Cape Department of Nature and Environmental Conservation. While the females responded to the hormone treatment by laying eggs, the males showed no reaction. One female, 5,3 cm in length (snout to vent), laid approximately 270 eggs within a few hours with a yolk-size of 1,4–1,8 mm. Thus the larval stages still remained undescribed.

MATERIALS AND METHOD

The natural breeding season of *Xenopus laevis* is given as September to December for the Stellenbosch–Cape Town area (Nieuwkoop & Faber 1956). It was thought that, since *Xenopus gilli* is a true western Cape winter-rainfall species, its breeding season could well start as early as winter. *Xenopus* tadpoles were caught during metamorphosis in January–February 1976 in the Cape Point Reserve. They completed development in an aquarium and proved to be *Xenopus gilli.* This, and the dominance of *Xenopus gilli* over *Xenopus laevis* in the reserve, led to the checking of various water accumulations in the reserve on 31 July 1977. *Xenopus* larvae, approximately 12–15 mm in length, were found in coffee-coloured water with a pH of 5, and with a temperature of 12°C at 11h00 at a depth of 25 cm.

Some of these larvae were reared in an aquarium in the open, and the ponds in the Cape Point Reserve were checked periodically for new spawnings and to record the development of the tadpoles in natural conditions. Several tadpoles of various stages were kept in a plastic gauze cage 1 m × 0,5 m × 0,5 m, which was fixed between poles at the edge of a pond, leaving the upper edge 10 cm above the water. This facilitated observations on the development of specific, free-living individuals. In addition, approximately 100 preserved larvae and young frogs of *Xenopus gilli*, collected in the same area and fixed in Lenhossek fluid or alcohol, were used for the study.

For comparison the following material of *Xenopus laevis* was examined: preserved larvae and young frogs collected by N. A. H. Millard in the Cape Flats during the 1940s and by the author in the Cape Flats during 1977; a series of stage-determined larvae collected by Hubrecht Laboratory, Utrecht, Holland, at Stellenbosch in 1949–50 and housed in the South African Museum; and live larvae reared in an aquarium during 1977.

In the following description, which is the object of this paper, the stage numbers refer to those of the Normal Table of *Xenopus laevis* laid down by Nieuwkoop & Faber (1956).

DEVELOPMENT

While there are changes in body-proportions and pigment-distribution throughout development, free-swimming larvae of *Xenopus gilli* can be distinguished from those of *Xenopus laevis* by their unpigmented longitudinal bands on the dorsal surface of the head (Fig. 1A). These occur, one on either side, a short distance lateral to the central nervous system (seen by transparency). The bands embrace the eyes from where they run in an S-shape inwards then backwards towards the trunk. The two bands together form a lyre shape, which, even in the water, is very conspicuous, the rest of the body being very dark. From approximately Stage 45 onwards isolated melanophores begin to appear

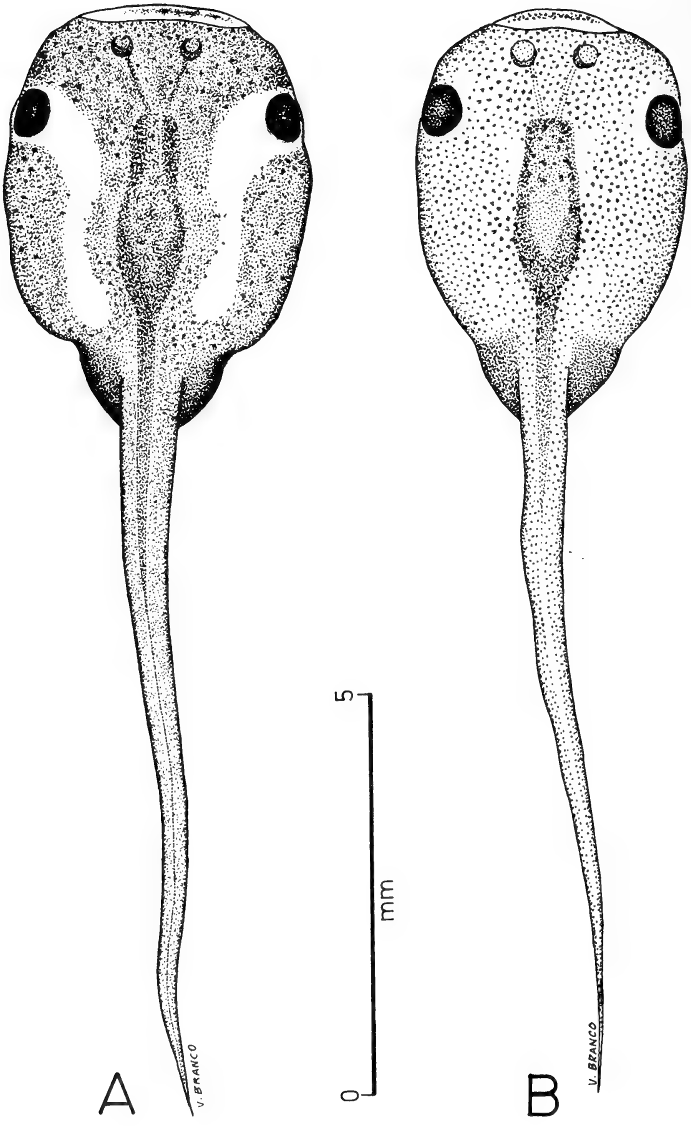

Fig. 1. A. *Xenopus gilli* larva, Stage 45–46, dorsal. B. *Xenopus laevis* larva, Stage 45–46, dorsal.

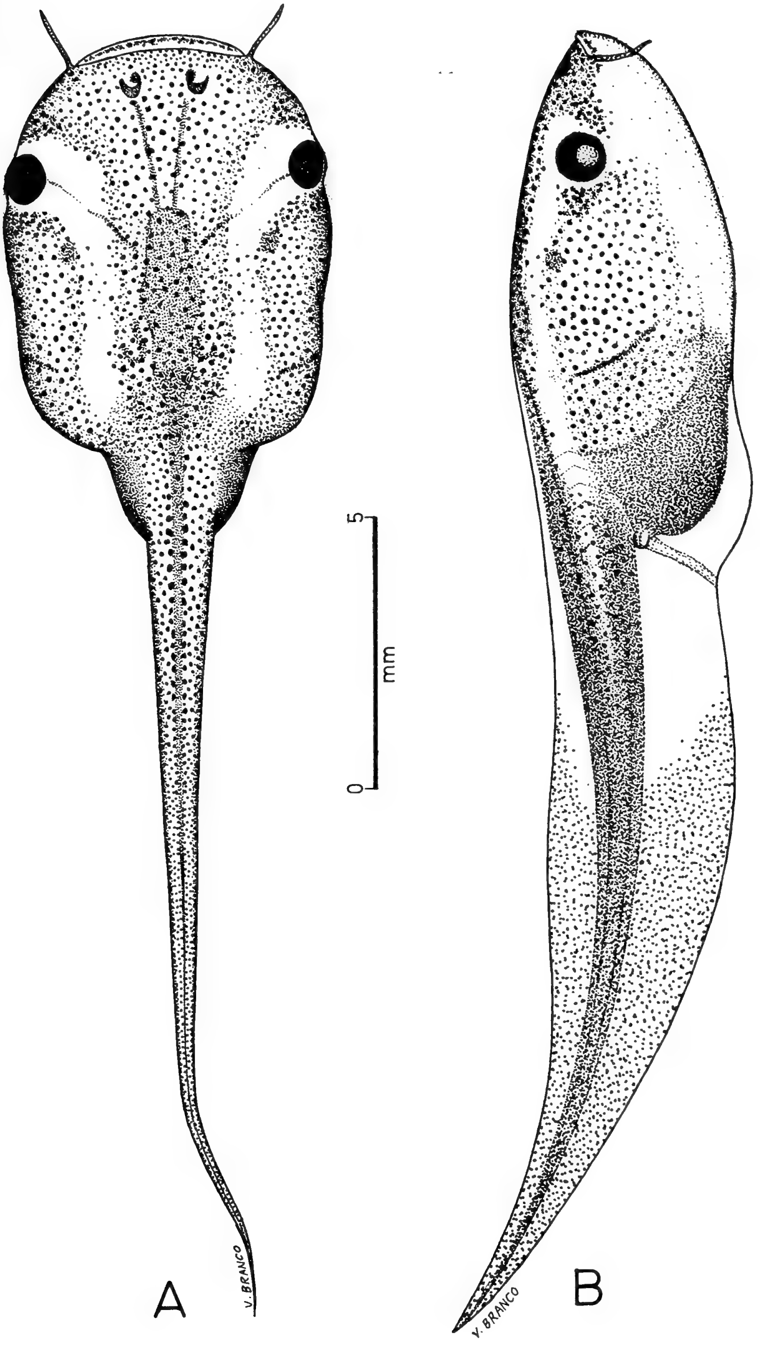

Fig. 2. *Xenopus gilli* larva, Stage 51. A. Dorsal. B. Lateral.

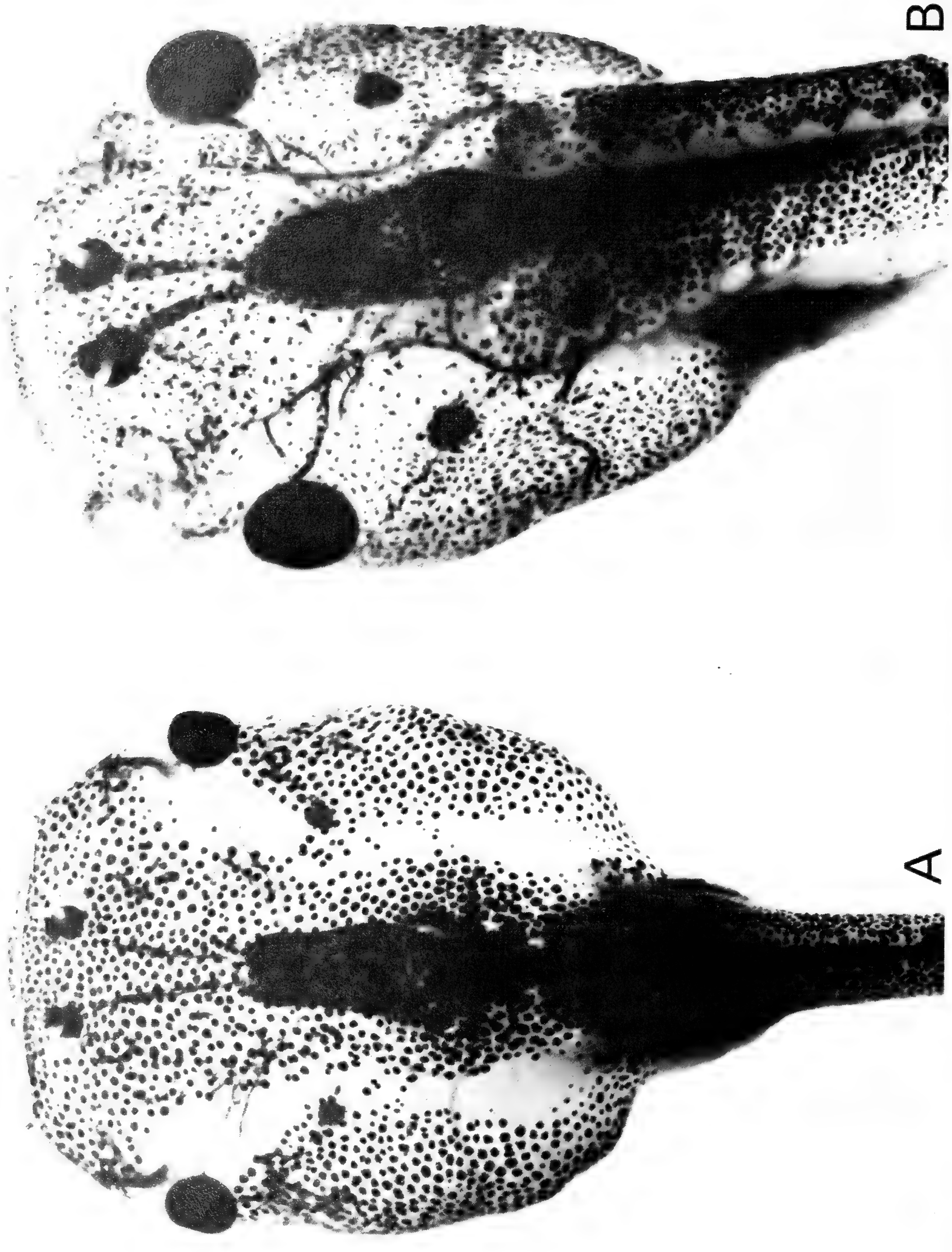

Fig. 3. Photographs of heads of live larvae, Stage 51, dorsal. A. *Xenopus gilli.* B. *X. laevis.*

in the lyre in the thymus gland region. They increase in number during further development, but never seem to reach the density of the centre portion and the sides of the head (Figs 2, 3A). The posterior third of the lyre remains unpigmented until at least Stage 56, while the areas surrounding the eyes can become somewhat pigmented from Stage 55 onwards (Fig. 5). However, in most specimens the lyre, although partly obscured, remains distinguishable well into metamorphosis (Fig. 5).

In contrast, *Xenopus laevis* larvae from an early stage usually have a more or less uniform distribution of pigment on the dorsal surface of the head (Fig. 1B), except sometimes in a position corresponding to the last portion of the lyre, which may be unpigmented. However, in very young *Xenopus laevis* larvae (free-swimming, but before Stage 44) there may be some unpigmented areas on either side of the central nervous system, which remind one of the lyre of *X. gilli*, though the anterior part is quite different (Fig. 6). This condition was found in ten out of twenty specimens of the same batch and size. But even in these specimens the posterior portion of the 'lyre' usually becomes pigmented very early and is often indistinct at Stage 46, when the areas between eyes and central nervous system have usually also become pigmented (Fig. 1B). In the water the only dark portions which show up are the central nervous system, the eyes and the abdomen.

The thymus gland, which is situated between eye and ear just below the surface, and which becomes pigmented in both species at Stage 49, is more conspicuous in *Xenopus laevis*, appearing almost like a second pair of eyes (Figs 3, 4). In *Xenopus gilli*, this gland is situated just outside the lyre and is somewhat obscured by the heavy pigmentation in the layers above it.

The pigmentation in the dorsal and ventral tail-fins starts at the hind end and increases in an anterior direction. In *Xenopus gilli* the pigmentation of the ventral fin extends as a narrow band along the edge, and reaches the cloaca at Stages 55–56 (Fig. 5), while in *Xenopus laevis* the only fin pigmentation near the cloaca is an isolated patch which appears at Stage 56 (Nieuwkoop & Faber 1956).

While melanophores appear on the hind-limb buds of *Xenopus laevis* at Stage 51, in *Xenopus gilli* the hind-limb buds are already pigmented at Stage 48. At the same stage in *X. gilli*, and sometimes earlier, a whitish spot becomes visible above the anterior portion of the central nervous system. In later stages the 'Stirnorgan', in the form of a spherical opaque structure which pushes up the skin above it, can be observed in this spot (Fig. 5). In *Xenopus laevis* an unpigmented spot is said to appear above the 'Stirnorgan' at Stage 57. The 'Stirnorgan' is developed from the pineal body and lies between the epidermis and the skull (Nieuwkoop & Faber 1956).

The naso-lachrymal duct is indicated in *Xenopus gilli* tadpoles at Stages 55–56 when the pigment begins to part along a line roughly parallel to the upper lip, from the outer corner of the nostril to where it meets a triangular, unpigmented area in front of the eye (Fig. 5). This unpigmented line is very

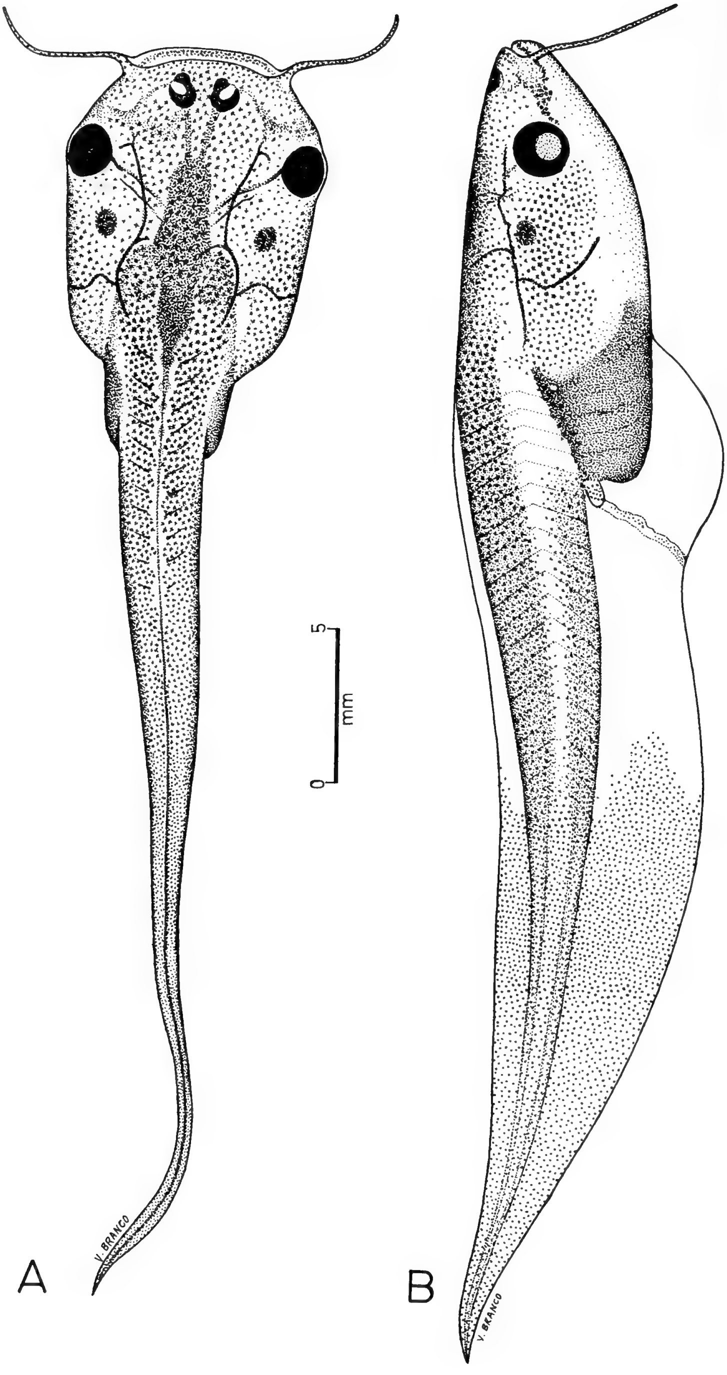

Fig. 4. *Xenopus laevis* larva, Stage 51. A. Dorsal. B. Lateral.

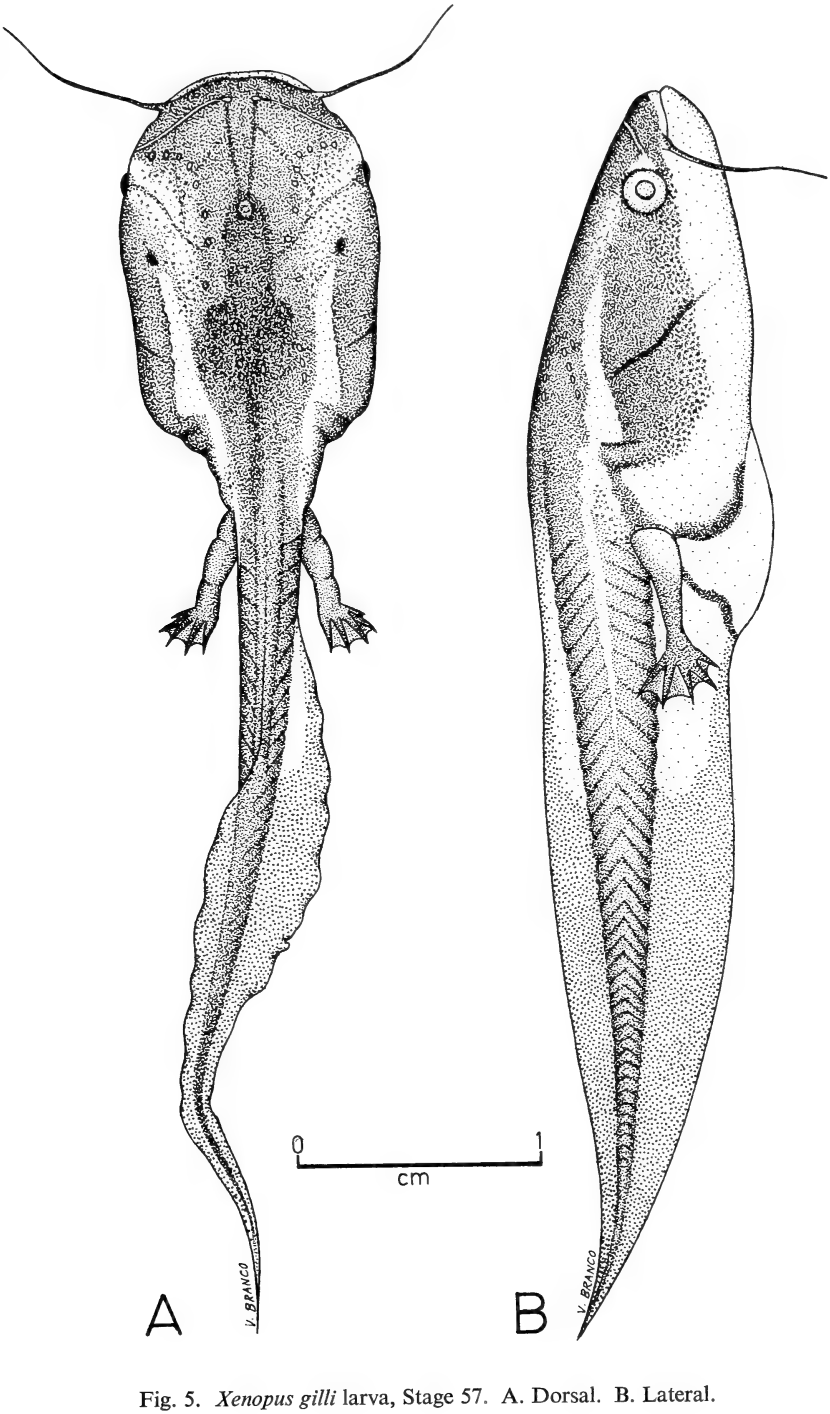

Fig. 5. *Xenopus gilli* larva, Stage 57. A. Dorsal. B. Lateral.

clear and narrower than the olfactory nerve at Stages 57 and 58, after which melanophores shift over it again. At Stage 60 it is nearly invisible. A somewhat irregular protuberance appears at Stage 61 at the point where the nasolachrymal duct meets the pre-orbital triangle on the lateral wall of the head. The protuberance shifts in a ventro-caudal direction, coming closer to the eye, and reaches its final position ventral to the eye, almost in line with the circumorbital lateral line sensory organs, at Stage 64 (Fig. 7). Two depressions appear on it which at the end of metamorphosis have become oval apertures, facing in a slightly caudal direction. Due to its size and position this raised area bearing the

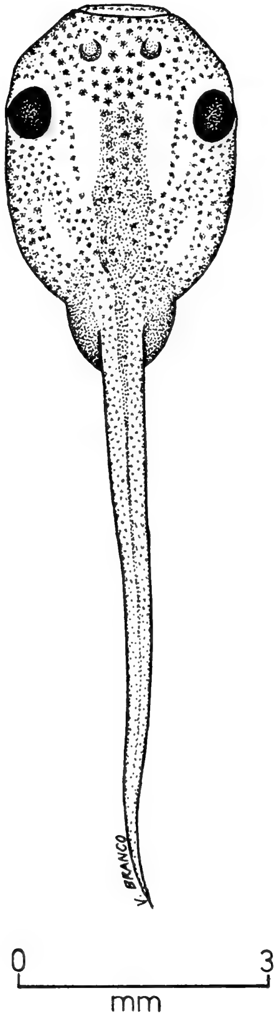

Fig. 6. *Xenopus laevis* larva, pre Stage 44, dorsal.

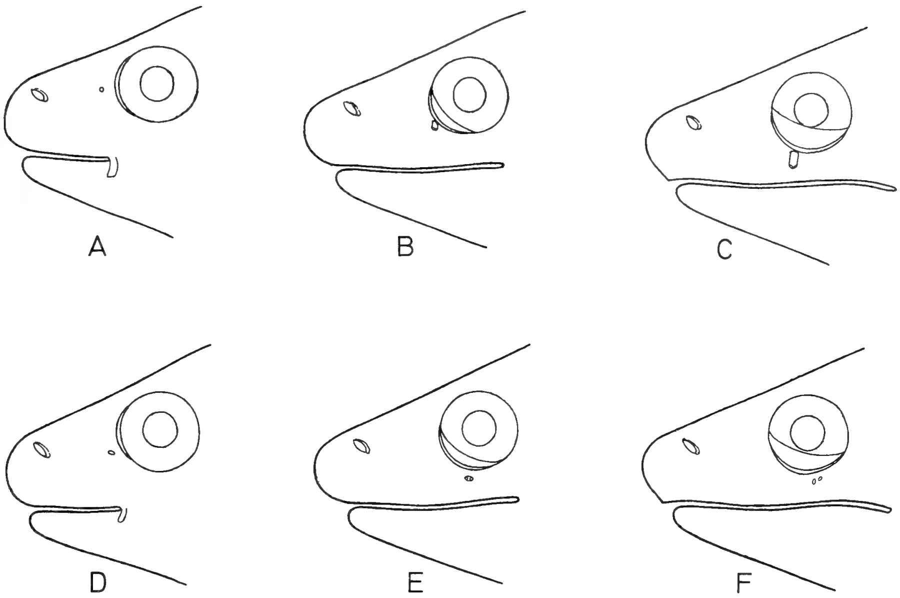

Fig. 7. Development of nictitating membrane and external aperture of nasolachrymal duct, Stages 62, 64, 66 (metamorphosis completed). A–C. *Xenopus laevis.* D–F. *Xenopus gilli.*

external openings of the nasolachrymal duct can easily be mistaken for one of the sensory organs. However, in adult stages the protuberance is usually flattened out and only two openings remain.

Föske (1934 from Paterson 1939*b*) believed that the nasolachrymal duct develops within a very short period from the lower layer of the epidermis. He was, however, unable to find a developmental stage in support of this view. It is likely that the parting of the pigment above the future nasolachrymal duct in *X. gilli,* as described above, supports Föske's view.

The nictitating membrance ('eyelid') forms parallel with this development. In *Xenopus gilli* at Stage 59 the posterior margin of the unpigmented pre-orbital triangle becomes raised and shows a vertical fold close to the eye. The fold lengthens during further development and shifts along the ventral margin of the eye in a caudal direction, absorbs the unpigmented triangle and becomes the nictitating membrane (Fig. 7).

In *Xenopus laevis* the development of the 'eyelid' is similar. The posterior end of the nasolachrymal duct is first visible at Stage 62, when a small, indented semicircular protuberance appears near the anterior tip of the unpigmented pre-orbital triangle (Fig. 7A). At Stage 64 this protuberance is longer than wide, oval in cross-section and has two apertures at its tip, separated by a short septum. It increases in length, comes closer to the eye and, together with the nictitating membrance, shifts ventrad to the eye, where it reaches its final position at Stage 65, forming the subocular tentacle (Fig. 7).

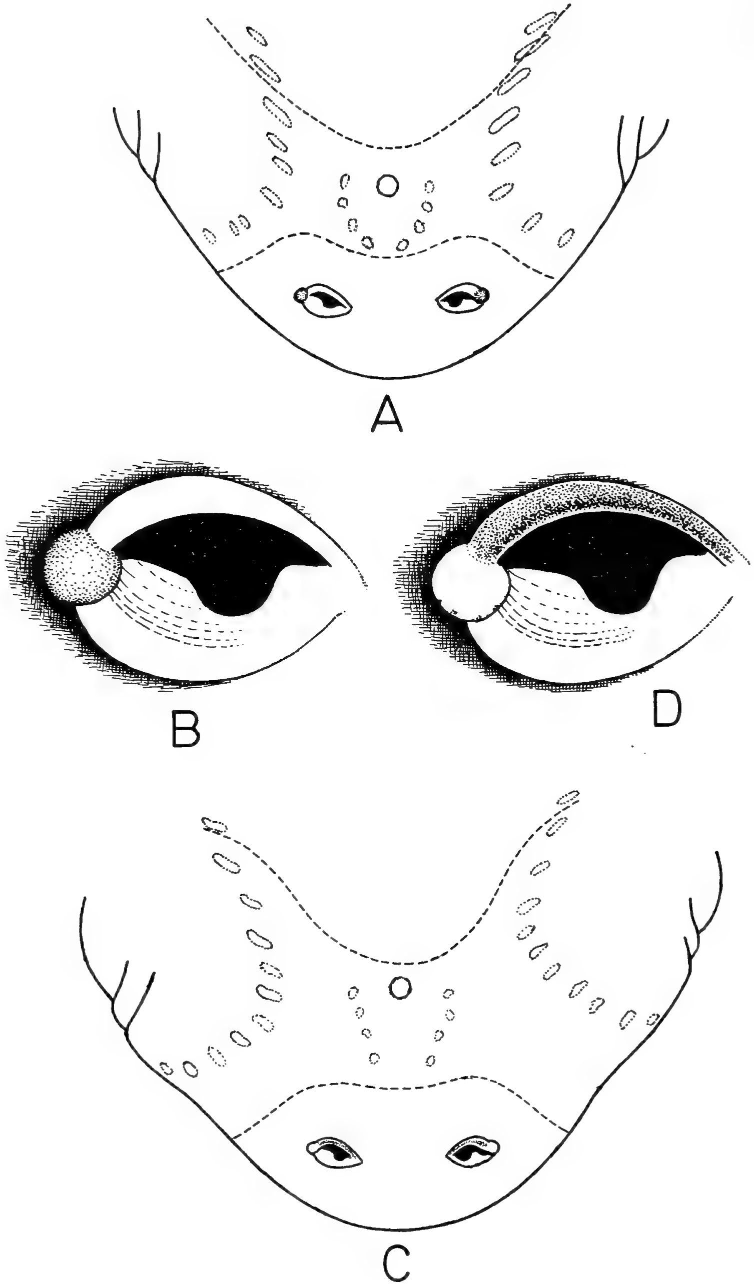

Fig. 8. Head and nostril, Stage 59 onwards, dorsal.
A–B. *Xenopus laevis*. C–D. *Xenopus gilli*.

This so-called subocular tentacle, which is not a true tentacle (Paterson 1939*a*, 1939*b*) sometimes retains both openings in mature frogs. Often, possibly through wear, the short septum disappears so that the two openings unite partially or fully.

Contrary to expectation the nasolachrymal duct in both species has no contact with the orbital capsule. Paterson (1939*b*) concluded that had there been movable eyelids the duct would have been directed inwards towards the eye and its aperture would then have been comparable with the punctum lacrimale of higher forms. Observation of living adult *Xenopus laevis* reveals that the slightly opaque nictitating membrane can move in an upward direction, over the surface of the eye, to its upper margin. This, however, seems to happen only when irritation is felt.

At Stages 55–56 of *X. gilli* the nostril has its outer corner well sunk below the surface of the head. Its caudal margin begins to develop a cone-like protrusion, roughly where the olfactory nerve meets it. This protrusion shifts outwards and becomes situated at the outer corner at Stage 59, where it remains. During these stages the margins of the nostril become raised progressively towards the outer corner, so that at Stage 59 the inner corner is level with the head-surface, while the outer is raised well above it. The lip-like raised margins are now pigmented while the 'knob' is unpigmented (Fig. 8C–D). Soon after the completion of metamorphosis the 'knobs' at the outer corners of the nostrils become pigmented and the darkish belly-dotting appears. At the completion of metamorphosis the frogs measure approximately 15 mm from snout to vent.

This development of nostril and nasolachrymal duct is much the same as in *Xenopus laevis*. However, in the latter the 'knob' is usually pigmented, while the 'lips' are almost unpigmented (Fig. 8A–B).

Thus, while identification of *Xenopus gilli* tadpoles by the lyre becomes less easy in advanced stages, the reversed pigment-pattern of the nostril-margins provides a useful character.

At Stage 60 a light dorsal midline appears on the head and body of *Xenopus gilli*, beginning roughly between the eyes and ending roughly between the hind legs. The typical *gilli*-pattern of more or less complete longitudinal dark bands, two on the back and a weaker, more broken one, on either side, is fully differentiated at Stage 62 (Fig. 9A).

FURTHER OBSERVATIONS ON LIVING LARVAE

The duration of development from the fertilized egg to the end of metamorphosis probably varies. For *Xenopus laevis*, reared in the laboratory, it is given as approximately 58 days (Nieuwkoop & Faber 1956). *Xenopus gilli* larvae examined here were first seen when at Stage 45–46 (probably one week old) on 31 July 1977. On 6 November 1977 approximately 15 per cent of the larvae in the ponds had reached Stage 62. On 20 November some had completed metamorphosis. The development thus required approximately 120 days. This much longer period was probably partly due to the low water temperature, which

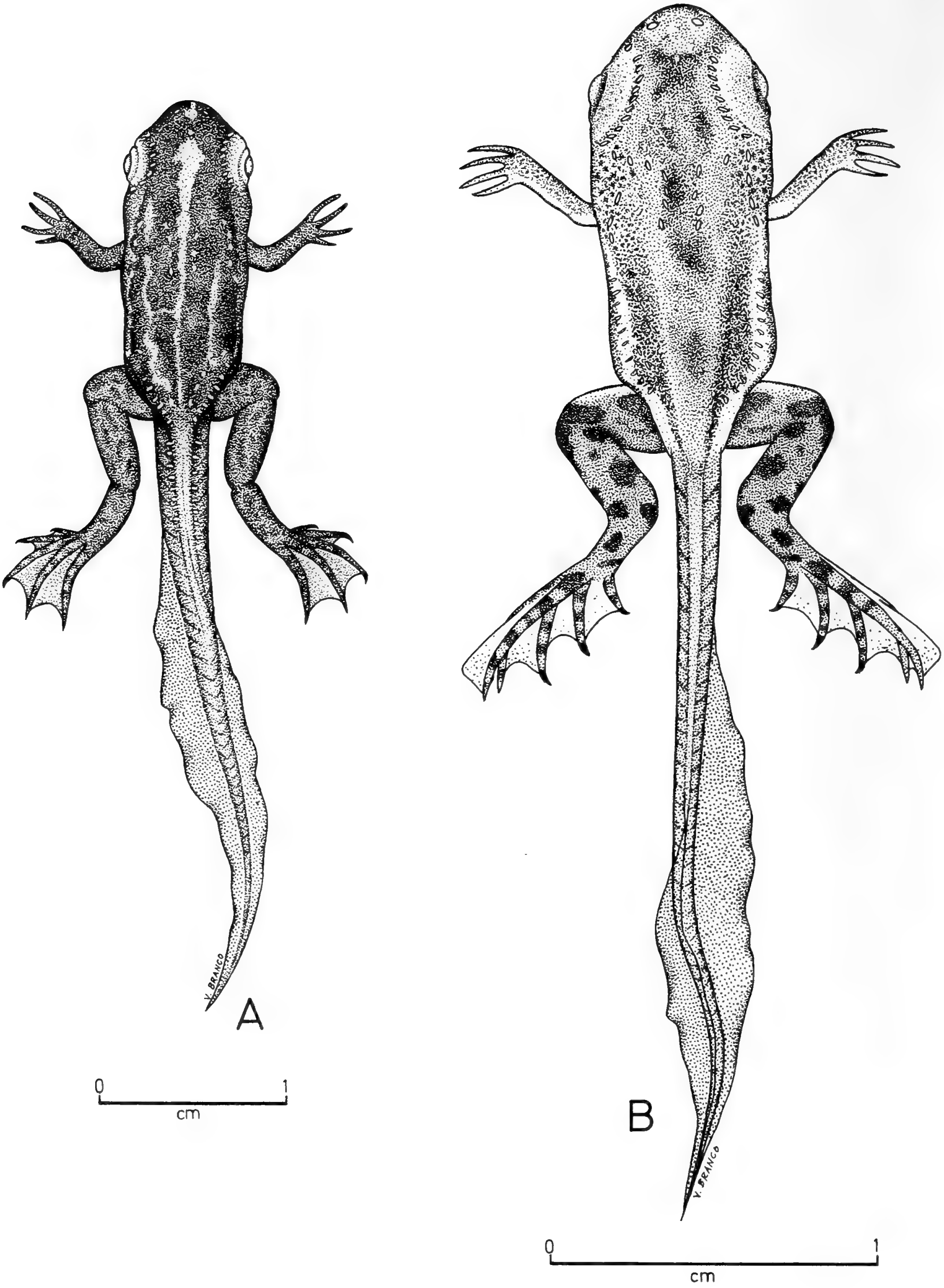

Fig. 9. A. *Xenopus gilli* larva, Stage 62, dorsal.
B. *Xenopus laevis* larva, Stage 62, dorsal.

on 6 November 1977, a warm, sunny day, measured only 20°C at 11h00 in 25 cm depth, whereas Nieuwkoop & Faber retained the water temperatures for their developing larvae at 22–24°C throughout. All larvae observed in three different ponds in the Cape Point Reserve on 31 July and 7 August 1977 were of roughly the same size and stage. During subsequent examinations small and more advanced larvae were encountered together, indicating additional spawning. However, on 6 November the smallest larvae were in Stage 48–49, probably indicating that spawning had ceased. In February 1976 *Xenopus gilli* larvae from Stage 54 to the end of metamorphosis had been collected in the biggest pond where the temperature might have remained sufficiently low. *Xenopus gilli* larvae show signs of discomfort when the water temperature reaches 27°C. They remain at the bottom and try to go even deeper. At 31°C they make sporadic attempts to swim, but balance-disturbance causes them to tumble, often sinking to the bottom, where they remain motionless, sometimes lying on the side or back. In contrast, *Xenopus laevis* larvae still behave normally at a temperature of 34°C. Only when 36°C is reached, do they show signs of dying.

During the night the larvae of both species darken considerably. The tail-fin especially appears practically black when suddenly brought into light.

Larvae reared in an aquarium show retarded growth, although the development seems to progress normally, thus producing smaller frogs. Two *Xenopus gilli*, which were caught near the end of metamorphosis in February 1976 in the Cape Point Reserve, were kept indoors thereafter and did not develop the typical *gilli* belly-dotting and ochrous undersurfaces of the thighs. The nostril 'knob', too, remained unpigmented as in advanced *Xenopus gilli* larvae. In all other respects they showed the *gilli* characteristics and measured approximately 43 mm from snout to vent in November 1977.

Occasionally, when both species occur together, some specimens appear to be hybrids. Their size and general shape is that of *Xenopus laevis*, and so is the presence of the subocular tentacle just ventral to the eye. Both dorsal and ventral coloration is that of *Xenopus gilli*, the longitudinal dark bands being sometimes more complete than in some specimens of *Xenopus gilli*.

A specimen (SAM–ZR44317), collected by B. Deyer in March 1975 in the Lotus River near the entry into Zeekoevlei and donated to the museum by R. Boycott in March 1977, is peculiar in some aspects: its general shape, the lack of a subocular tentacle, the dense pigmentation of the webbing of the feet and the dark belly dotting are typical of *Xenopus gilli*; the teeth in the upper jaw are, as in *Xenopus gilli*, long and protrude well beyond the edge of the mouth; however, the dorsal surface of the animal is of a more or less even, greyish colour with no pattern; the general colour is lighter than is usual in *Xenopus gilli* and the claws on both feet are unpigmented (some unpigmented claws do occur occasionally in both species). The specimen, with a snout-to-vent length of 67 mm, exceeds the maximum size given for *Xenopus gilli* (Poynton 1964).

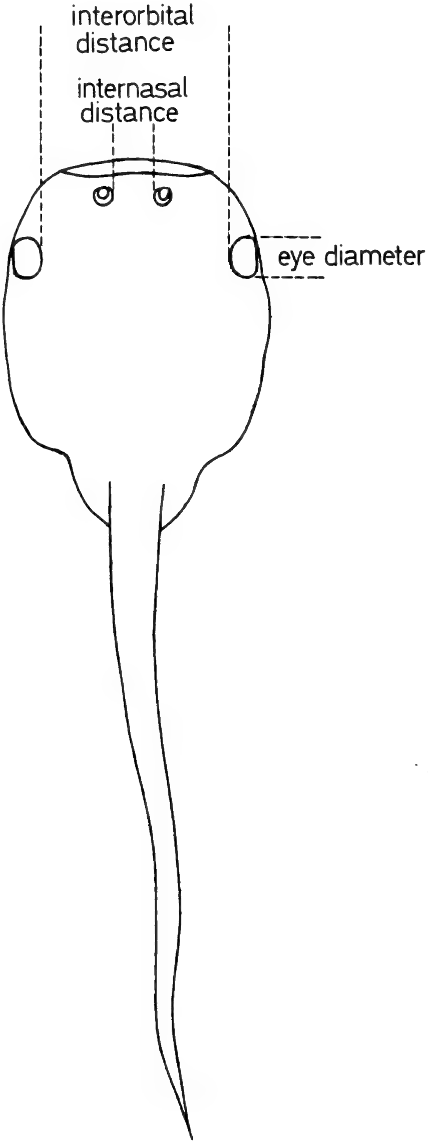

Fig. 10. Diagram to illustrate dimensions used to distinguish *Xenopus gilli* from *Xenopus laevis* larvae.

SUMMARY OF DISTINGUISHING FEATURES OF *X. GILLI* AND *X. LAEVIS* LARVAE

It should be noted that the material on which the dimensions are based consists of freshly preserved specimens in the case of *X. gilli*, and in *X. laevis* of both freshly preserved specimens and specimens which have been preserved for about 30 years.

	X. gilli	*X. laevis*
1.	Tadpoles very dark with unpigmented lyre.	Tadpoles light with more or less even pigmentation.
2.	Thymus gland and blood-vessels on head-body not conspicuous.	Thymus gland and blood-vessels on head-body conspicuous.
3.	Eyes comparatively small; eye diameter/ interorbital distance, Stage 45–46: 0,20–0,32 $\bar{x}_{20}$ 0,26; Stage 50–51: 0,18–0,22 $\bar{x}_{15}$ 0,20 (see Fig. 10).	Eyes comparatively large; eye diameter/ interorbital distance, Stage 45–46: 0,30–0,54 $\bar{x}_{16}$ 0,34; Stage 50–51: 0,23–0,46 $\bar{x}_{15}$ 0,33.
4.	Nasal capsules comparatively far apart; internasal distance/eye diameter, Stage 45–46: 0,83–1,40 $\bar{x}_{20}$ 1,04; Stage 50–51: 0,62–0,90 $\bar{x}_{15}$ 0,74 (see Fig. 10).	Nasal capsules comparatively close together; internasal distance/eye diameter, Stage 45–46: 0,43–0,88 $\bar{x}_{16}$ 0,63; Stage 50–51: 0,38–0,80 $\bar{x}_{15}$ 0,53.
5.	Nostril 'knob' unpigmented; raised margin of nostril pigmented.	Nostril 'knob' pigmented; raised margin of nostril unpigmented.
6.	Pigmentation of ventral tail-fin reaching cloaca from Stage 55 onwards.	Pigmentation of ventral tail-fin not reaching cloaca but forming an isolated patch near cloaca at Stage 56.

ACKNOWLEDGEMENTS

I wish to express my thanks to the chief warden, Mr G. E. P. Wright, and the rangers of the Cape Point Nature Reserve for co-operation; to my colleagues, Mr L. R. Swartz and Mr G. Esau for assistance in the field; to Mr V. Branco for the drawings made with the aid of a camera lucida; to Mr G. X. Kannemeyer for the photographing of tadpoles; and to Dr N. A. H. Millard for encouraging discussion and help with the manuscript.

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

R. E. RAU

THE DEVELOPMENT OF *XENOPUS GILLI* ROSE & HEWITT (ANURA, PIPIDAE)

VOLUME 76 PART 7 SEPTEMBER 1978 ISSN 0303-2515

ANNALS OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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

2. LAYOUT should be as follows:

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

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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

Footnotes should be avoided unless they are short and essential.

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

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

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Fischer, P.-H., Duval, M. & Raffy, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

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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.

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LATE TERTIARY HYAENIDAE FROM LANGEBAANWEG, SOUTH AFRICA, AND THEIR RELEVANCE TO THE PHYLOGENY OF THE FAMILY

By

Q. B. HENDEY

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South African Museum, Cape Town

(With 11 figures and 4 tables)

[*MS. accepted 11 July 1978*]

ABSTRACT

The Hyaenidae are divided on phylogenetic grounds into the '*Hyaena* group' and the '*Percrocuta* group', both of which are represented by fossil forms from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg, South Africa, four species being assigned to the *Hyaena* group and one to the *Percrocuta* group. The latter species is *Adcrocuta australis*, while the others are *Ictitherium preforfex*, *Hyaena abronia*, *Hyaenictitherium namaquense* and an unnamed species of *Euryboas*. They reflect a pattern of representation established during the late Miocene, although individual species are more advanced than their Eurasian late Miocene counterparts, and they fill an important temporal gap in the recorded history of the family. *Chasmaporthetes* is regarded as a member of the *Percrocuta* group and not as a close relative of *Euryboas*.

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INTRODUCTION

There are only four hyaenid species still extant and they comprise a relatively uncommon element in the faunas of Africa and southern Eurasia. The species are the striped hyaena (*Hyaena hyaena*), the brown hyaena (*Hyaena brunnea*), the spotted hyaena (*Crocuta crocuta*) and the aardwolf (*Proteles cristatus*). The latter is an aberrant insectivorous species, while the others are well adapted to a scavenging role, although they may also be actively predacious.

The family, which stemmed from the Viverridae during the Miocene, was formerly more diverse and widespread, and, although hyaenas are rare as fossils in North America, they are sometimes abundantly represented in late

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Cenozoic deposits in the Old World. In spite of this, opinions on hyaenid interrelationships and phylogeny are almost as numerous as papers dealing with these subjects, some recent examples being Thenius (1966), De Beaumont (1967), Ficcarelli & Torre (1970), Hendey (1974*a*), Schmidt-Kittler (1976), and Galiano & Frailey (1977). There is, however, one important point about which there does appear to be general agreement. Evidently hyaenids evolved from viverrids on more than one occasion, and on phylogenetic grounds the family is divisible into at least two major groups. These two groups have yet to be accorded formal nomenclatural recognition, and they are here informally termed the '*Percrocuta*' and '*Hyaena*' groups.

The former was the first to be differentiated, having evolved from an as yet undetermined viverrid ancestor (or ancestors) early in the Miocene. The genera (or subgenera) constituting this group are *Percrocuta*, *Dinocrocuta* and *Adcrocuta* (see Schmidt-Kittler 1976). For reasons which will be explained later, the genus *Chasmaporthetes* is also included here. Members of the group appear in Africa and Eurasia as progressive hyaenas late in the middle Miocene. They may have had their origins in Africa where the Miocene fossil record is comparatively poor. Certainly the superior Eurasian record includes no appropriate links with the Viverridae.

By contrast, the evolution of the *Hyaena* group is well documented by Eurasian fossils. The stem genera were the 'Vindobonian' *Protictitherium* and *Miohyaena* (Schmidt-Kittler 1976), which were apparently descended from the late Oligocene *Herpestides* (De Beaumont 1967). The group radiated during the late Miocene and a number of small- to medium-sized species occurred together as a characteristic element in Eurasian '*Hipparion* faunas' (i.e. Turolian in Europe and Turolian equivalent in Asia). There is as yet no consensus on the nomenclature of the late Miocene taxa. The genera recognized here are *Plioviverrops*, *Ictitherium*, *Palhyaena*, *Hyaenictitherium*, *Hyaenictis*, and *Lycyaena*. Numbers of species and subspecies have been named, but the complexities of the situation will not be explored.

Many of the recorded late Miocene hyaenids of Eurasia were separated from one another temporally and/or geographically, but there are well-documented examples of the contemporary occurrence of several species at a single locality. Pikermi in Greece is perhaps the most extreme case, its fauna including five members of the *Hyaena* group (i.e. *Plioviverrops orbignyi*, *Ictitherium robustum*, *Palhyaena hipparionum*, *Hyaenictis graeca*, and *Lycyaena chaeretis*), and a percrocuta (*Adcrocuta eximia*) (Pilgrim 1931). A similar association is evident at several localities in China, where there are three *Hyaena* group species (*Ictitherium gaudryi*, *Palhyaena wongii*, and *Hyaenictitherium hyaenoides*), and a percrocuta (a variety of *A. eximia*) (Zdansky 1924; Kurtén 1953).

The diversity of hyaenids in Eurasia during the late Miocene is a reflection of the wealth of the fauna as a whole at that time. It is a period of which Kurtén (1971: 135) has said 'may well be regarded as the climax of the entire Age of

Mammals'. This probably applies in the case of Africa as well, but the late Miocene fauna of the continent is not well known.

It is, however, becoming increasingly clear that African faunas of the very late Miocene and early Pliocene were as spectacular in character as the Eurasian 'Hipparion faunas', which predate them. The African faunas in question include those from Mpesida (Bishop *et al.* 1971), Lothagam 1 (Smart 1976), Lukeino (Pickford 1975), Sahabi (Petrocchi 1952), 'E' Quarry at Langebaanweg (Hendey 1976) and Kanapoi (Behrensmeyer 1976). Smart (1976) has already pointed out that climatic and environmental changes, which adversely affected Eurasian faunas towards the end of the Miocene, had less of an impact in Africa. Indeed, they may have had the effect of increasing mammalian migration from Eurasia to Africa.

In spite of the improving situation in Africa, the very late Miocene/early Pliocene fossil record in the Old World is generally poor. This was a period for which recorded fossil occurrences are few in number, widely dispersed and have often yielded faunas of limited size. There is a considerable improvement in the record throughout the Old World during the late Pliocene, a tendency which continues into the succeeding Pleistocene epoch.

The Old World late Tertiary record is thus characterized by both temporal and geographical irregularities, which complicate interpretations of the origins and history of mammals that lived during this period. The problem is particularly acute in the case of those mammalian groups, such as the Hyaenidae, which were both diverse and widespread. Consequently any fossil occurrence which dates from a poorly known part of the record, and which produces good samples of material, could make a significant contribution towards the understanding of the history of such groups.

'E' Quarry at Langebaanweg is an occurrence of this kind. Deposits exposed in this quarry are comprised largely of the latest Miocene/early Pliocene Varswater Formation, which has produced a fossil assemblage of size and diversity unequalled by contemporary occurrences elsewhere in Africa (Hendey 1976). One of the more remarkable features of this fauna is the number and variety of carnivores which are represented (Hendey 1974*a*, 1976, 1977), and, of the terrestrial species, Hyaenidae occur most commonly. At least five hyaenid species are represented, which is in marked contrast to the situation at other late Miocene/early Pliocene localities in Africa (Table 1).

Before proceeding to an account of the hyaenids, a few further observations on the 'E' Quarry fauna and deposits are necessary to place them in perspective.

Evidence which indicates an early Pliocene age for the Varswater Formation was recently reviewed (Hendey 1978: 2). The dating of this formation is based on comparisons between certain of its taxa with their counterparts in the east African sequence, for which there are some radiometric dates. The suggested age limits of 4 to 5 million years (m.y.) for the Varswater Formation are, however, not securely established. The 4 m.y. limit has already been questioned (Hendey 1978), and there is now reason to believe that the older limit may have

TABLE 1

Late Miocene/early Pliocene Hyaenidae of Africa.

LOCALITY	AGE	TAXA	REFERENCES
Kanapoi	early Pliocene	*Hyaena* sp.	Behrensmeyer 1976
Langebaanweg ('E' Quarry)	latest Miocene/ early Pliocene	*Ictitherium preforfex* *Hyaena abronia* *Hyaenictitherium namaquense* *Euryboas* sp. *Adcrocuta australis*	This report
Sahabi	late Miocene or early Pliocene	Hyaenidae gen. et sp. indet.	—
Lukeino	late Miocene	cf. *Crocuta* sp.	Pickford 1975
Lothagam 1	late Miocene	aff. *Euryboas* sp.	Smart 1976

been underestimated. This matter will be dealt with in detail elsewhere, but in the meantime the former practice of referring to the age of the Varswater Formation and its fossils as 'early Pliocene' is here replaced by the reference, 'latest Miocene/early Pliocene'.

It is nevertheless perfectly clear that the Varswater Formation fauna as a whole postdates the classic Eurasian late Miocene faunas such as those from Pikermi and lower Samos, which are between 7 and 10 m.y. old, but predates the Old World late Pliocene/early Pleistocene faunas, which are younger than 3,5 m.y. In other words, it dates from a period towards the end of the Tertiary when the Old World fossil record is generally poor.

Another important point about the Langebaanweg ('E' Quarry) fauna relevant to the present study is that it comes from the most southerly part of Africa and is thus geographically far removed from those faunas with which it is here compared and contrasted. It is therefore possible that the 'E' Quarry fauna, like that of the near-by Baard's Quarry, includes regional variants of more widespread taxa, endemic taxa and even late surviving members of lineages which were elsewhere extinct (Hendey 1978). If there are regional peculiarities in the fauna and these are not recognized, this could result in incorrect interpretations of the relationships of such taxa. Furthermore, the populations to which the Langebaanweg species belonged were probably not directly ancestral to later ones elsewhere.

The Cenozoic terrestrial faunas of the most southerly parts of Africa may characteristically have contributed little in the way of emigrants to regions further north. Instead the composition of the local faunas is likely to have been changed largely by immigration from the north and some endemic speciation, while local extinctions were not necessarily coincident with those elsewhere. The region may thus be viewed as a terminus in a zoogeographic sense. Nevertheless, local populations may have exhibited all the characteristics of their more northerly counterparts from which subsequent populations did evolve. Thus, when Langebaanweg species are suggested as ancestors of later ones, they were themselves not directly ancestral, but simply represent the kinds of animals from which later ones were derived (i.e. 'structural ancestors').

The observations in the preceding paragraphs are conveniently summarized if the Langebaanweg ('E' Quarry) fauna is visualized as a younger southern African counterpart of the classic '*Hipparion* faunas' of Eurasia. It differs from such faunas because it is separated from them by the width of a continent and a few million years in time. In spite of this, its composition is of an essentially similar pattern. The 'E' Quarry fossil assemblage, with its eighty mammalian species, provides the best evidence yet that the Old World late Tertiary 'climax of the entire Age of Mammals' persisted over much, if not all, of Africa long after it had passed in Eurasia.

A final point about the 'E' Quarry fauna relevant to the present report is that it includes species from a variety of habitats (Hendey 1976: 222–230). As a general rule terrestrial carnivores such as hyaenids are not as tied to particular habitats as are, for example, herbivores such as bovids. However, the contemporary occurrence at Langebaanweg of several closely related hyaenids suggests that the species concerned did occupy different habitats. A similar association of three hyaenid species in China during the late Miocene led to the suggestion by Kurtén (1953: 45) that one was a 'steppe form', one a 'forest form', and the third an 'intermediate'.

The situation at Langebaanweg, and indeed elsewhere, cannot be completely explained by habitat preference, since there were more hyaenid species than major habitat types. The co-existence of more than one species in a given environment is made possible by different behaviour patterns in the species concerned. This no doubt applies in the case of certain of the Langebaanweg hyaenids, but the habitat preference factor is almost certainly significant as well, since certain species occur commonly in, or are restricted to, deposits of particular kinds (e.g. river channel, floodplain). It is thus possible that while some species lived in the immediate vicinity of what was then a river estuary, others lived further inland and the remains of individuals were transported to the area of deposition by the river. While it is not possible to relate individual species to major habitat types (e.g. riverine woodlands, open plains), it is nevertheless significant that elements of the faunas from such habitats were incorporated in the Varswater Formation.

To sum up, the 'E' Quarry fossil occurrences are a potentially important source of information on Hyaenidae for the following reasons:

1. the fauna dates from a period which has a comparatively poor fossil record in the Old World;
2. the occurrences are situated on a continent for which the whole late Tertiary record is poor, but which may well have played a more important role in hyaenid evolution than has hitherto been supposed;
3. the sample sizes of individual taxa are reasonably good;
4. elements from more than one major habitat type are included in the fauna.

THE LANGEBAANWEG HYAENIDAE

INTRODUCTION

Five hyaenid species were described in a recent study of material from 'E' Quarry (Hendey 1974*a*). They were identified as follows: *Hyaenictis preforfex*, *Hyaena abronia*, *Hyaena* sp. B, *Hyaena* sp. E, and *Percrocuta australis*.

Hyaena sp. E is known only from a mandible fragment of an immature individual and, since its status is uncertain, it is excluded from the discussions which follow. Each of the remaining four species is known from cranial remains of three or more individuals and incomplete postcranial skeletons of at least two individuals. In addition, there is one undescribed species, a *Euryboas*, which is represented by the cranial remains of several individuals and an incomplete postcranial skeleton of one individual. The present situation in respect of individual species is now reviewed.

The smallest of the Langebaanweg hyaenids, that identified previously as *Hyaenictis preforfex*, has proved to be a problematical species. The type specimen is the damaged skull and incomplete postcranial skeleton of an aged individual (Hendey 1974*a*) from bed 3aS of the Pelletal Phosphorite Member (Hendey 1976: 226–230, 1978: 3). Additional specimens assigned to this species have since been found in bed 3aN of the same member and, although of comparable size, the new specimens differ from the holotype in certain dental characters. The differences are here regarded as more apparent than real and are ascribed to the aged condition of the holotype. Certain of the characteristics of the species mentioned in this report are evident in the bed 3aN sample but not in the holotype. They include a prominent M_1 metaconid, a feature which suggests that the genus concerned was not *Hyaenictis*. The reassessment of this species also suggests that it may not have been ancestral to the Transvaal '*Hyaenictis*' *forfex* as indicated earlier.

The additional '*Hyaenictis*' *preforfex* specimens show that this species was more similar to the second of the Langebaanweg hyaenids, *Hyaena abronia*, than had previously been supposed. Specimens which are unequivocally assigned to *H. abronia* are from the Quartzose Sand Member, which underlies the Pelletal Phosphorite Member, and are from floodplain deposits, whereas all the '*H.*' *preforfex* specimens are from river channel deposits. *H. abronia* is perhaps the least problematical of the Langebaanweg hyaenids in terms of its status and relationships.

The third, and next largest, of the species is the unnamed *Hyaena* sp. B, which is known only from the floodplain deposits of the Quartzose Sand Member. At least two additional individuals of this species are now represented and there is no longer any doubt that it is distinct from *H. abronia*. The possibility that species B and the poorly known '*Hyaena*' *namaquensis* from Kleinzee (Stromer 1931) were closely related was mentioned earlier (Hendey 1974*a*: 147). The additional species B specimens have made a close relationship seem more than just possible. The only observable difference between '*H.*' *namaquensis* and species B is that the M_1 of the former is slightly longer and narrower. In spite of this, species B is here identified with '*H.*' *namaquensis* since the small M_1 size difference is outweighed by the general size similarity, comparable tooth morphology, the proximity of the Langebaanweg and Kleinzee occurrences and the likelihood that they are broadly contemporaneous.

Many of the specimens belonging to the three species already mentioned were excluded from the present study because the general similarity in the characteristics of the species creates the potential for incorrect identification. Only the best preserved and most complete specimens, that is, those which undoubtedly belong to the species concerned, were taken into account. In addition, each sample was limited to specimens from a single stratigraphic unit. The specimens examined were as follows:

'*Hyaenictis*' *preforfex*—7 individuals from bed 3aN of the Pelletal Phosphorite Member (SAM–PQ–L33046, L31028, L31333, L32893, L33520, L33842, L34778).

Hyaena abronia—4 individuals from the Quartzose Sand Member (L14186, L20984, L21009, L22202).

'*Hyaena*' *namaquensis*—3 individuals from the Quartzose Sand Member (L12848, L21008, L25026).

These three species are clearly closely related members of the *Hyaena* group and are distinguished from one another principally on the basis of size. They are characterized by the presence of P_1 and M^2_2, although M^2 is sometimes absent in *H. abronia*, and are generally similar in terms of tooth morphology (Figs 1–2).

The fourth species is the undescribed *Euryboas*. It is similar in overall size to '*H.*' *namaquensis*, but is distinguished by the absence of P_1, the occasional absence of M_2, shorter M^1, reduction or loss of the M_1 metaconid, smaller and simpler M_1 talonid and longer but narrower P^2_2 to P^4_4 and M_1 (Fig. 6, Table 2). The Langebaanweg *Euryboas*, which is apparently the earliest and most primitive known member of the genus, will be fully described elsewhere. Remains of only two individuals were taken into account in the present study (L21000, L21788). Both are from deposits in the Quartzose Sand Member which were probably laid down close to, or even in, a river channel. Other specimens probably belonging to this species are from river channel deposits of the Pelletal Phosphorite Member.

The fifth and largest of the 'E' Quarry hyaenids is a member of the *Percrocuta* group and, although described as a *Percrocuta*, it is now referred to *Adcrocuta* (i.e. *A. australis*). This is done because a close relative and possible ancestor, the Eurasian '*Percrocuta*' *eximia*, is now generally regarded as an *Adcrocuta* (Ficcarelli & Torre 1970; Schmidt-Kittler 1976). *A. australis* has some characters in common with the *Euryboas*, but is distinguished by its larger size, lower crowned and stouter canines, occasional presence of anterior accessory cusps on P_2 and P_3, longer carnassials, and unicuspid M_1 talonid. The *A. australis* sample used in this study was derived from the Quartzose Sand

Fig. 1. Lateral views of hyaenid hemimandibles from Langebaanweg. A. '*Hyaenictis*' *preforfex* (L33046). B. *Hyaena abronia* (L14186) (reversed). C. '*Hyaena*' *namaquensis* (L25026).

Fig. 2. Occlusal views of hyaenid hemimandibles from Langebaanweg. A. '*Hyaenictis*' *preforfex* (L33046). B. *Hyaena abronia* (L14186) (reversed). C. '*Hyaena*' *namaquensis* (L25026).

Member, but it is also known from the Pelletal Phosphorite Member and is apparently not confined to deposits of a particular type.

The 'E' Quarry hyaenids appear to be unique in providing evidence of a progression in an evolutionary sense from Eurasian late Miocene hyaenids, while at the same time maintaining the pattern of their representation. In other words, there is apparently no other Old World fauna of comparable age which includes a variety of hyaenid species which are reminiscent of the Eurasian late Miocene. In order to justify this observation recorded Eurasian late Miocene taxa are compared and contrasted with those from Langebaanweg.

THE *HYAENA* GROUP

Plioviverrops orbignyi is the smallest of the Eurasian species and one which evidently does not have a counterpart at Langebaanweg. This species may have become extinct without issue, although Thenius (1966) suggested it as a possible ancestor of *Proteles cristatus*, a species whose fossil history is largely unknown except for a Pleistocene species from the Transvaal (Hendey 1974*b*).

The European *Ictitherium robustum* and Chinese *I. gaudryi* have long been recognized as closely related forms and they may be conspecific. The situation in respect of *Palhyaena hipparionum* and *P. wongii* is similar. By contrast, the Chinese *Hyaenictitherium hyaenoides* apparently had no European counterpart, but together with *Ictitherium* and *Palhyaena* is part of a close-knit combination within the *Hyaena* group which has been thoroughly examined by Kurtén (1954), amongst others.

Schmidt-Kittler (1976) cast some doubt on the status of *Hyaenictitherium*, claiming that it does not even merit separate subgeneric status. *H. hyaenoides* is nevertheless distinguishable from the classic *Palhyaena*, the taxon which Schmidt-Kittler regards as the stem form. The classification of taxa in such situations is prone to be controversial and Schmidt-Kittler's 'lumping' is justifiable. However, the evolution of this group of hyaenids is here interpreted as successive branching from a primary lineage, with each additional branch representing a new genus (Fig. 3).

This arrangement can be justified only if later, well differentiated representatives of individual branches are recognized. Thus the earliest member of a new lineage, although essentially similar to the stem form, is distinguished at the genus level if it can be established that it had descendants whose characteristics are clearly different from those of members of the stem lineage. Certain of the Langebaanweg hyaenids are relevant to the recognition here of *Ictitherium*, *Palhyaena* and *Hyaenictitherium* as distinct genera.

The '*Hyaenictis*' *preforfex*/*Hyaena abronia*/'*Hyaena*' *namaquensis* combination at Langebaanweg is reminiscent of the Eurasian trio referred to above. In

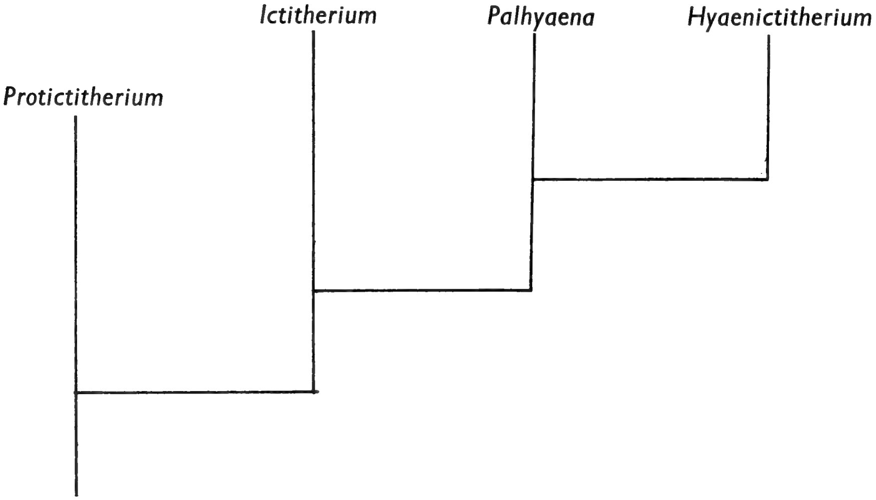


Fig. 3. Suggested phylogenetic relationships of some late Tertiary members of the *Hyaena* group.

each case size differences of no great magnitude are combined with differences in tooth proportions to distinguish associated species of the two combinations of taxa. In general, the Langebaanweg species are more advanced than those of the Eurasian late Miocene. For example, in the Langebaanweg species the molars (i.e. M^1, M_1 talonid, M^2_2) are reduced relative to those of the Eurasian species. In addition, the species of the Langebaanweg series are larger than those of the Eurasian series, that is, '*H.*' *preforfex* is larger than *Ictitherium*, *H. abronia* is larger than *Palhyaena* and '*H.*' *namaquensis* is larger than *Hyaenictitherium*.

The simplest phylogenetic interpretation of the preceding observations would be to regard *Ictitherium* as the ancestor of '*H.*' *preforfex*, *Palhyaena* the ancestor of *H. abronia*, and *Hyaenictitherium* the ancestor of '*H.*' *namaquensis*, with the ancestral forms possibly being African counterparts of the recorded Eurasian species.

Having established this as a working hypothesis, the suggested interrelationships can be examined in more detail. Superficially there is nothing which would positively preclude the suggested relationships. Indeed they seem eminently feasible. For example, one of the more striking features of the two series of taxa is that in each case it is the smallest member which is the most primitive (i.e. viverrid-like).

In a study of the Eurasian taxa Kurtén (1954: 16–17, Fig. 9) used a ratio diagram of certain tooth lengths to illustrate similarities and differences. A similar ratio diagram for the Langebaanweg species is equally revealing (Fig. 4). Kurtén used *Palhyaena wongii* as a standard and in the case of the Langebaanweg series *Hyaena abronia* was selected since it is the suggested descendant of *Palhyaena*. It is worth noting that a ratio diagram using tooth breadths revealed an essentially similar pattern.

There are some remarkable similarities between the ratio diagrams of the Langebaanweg and Eurasian series. In their proportions the teeth of '*Hyaenictus preforfex* and '*Hyaena*' *namaquensis* differ from the *Hyaena abronia* standard in much the same way as *Ictitherium robustum* and *Hyaenictitherium hyaenoides* differ from *Palhyaena wongii*. Interestingly, a much closer approach to the '*H.*' *preforfex* graph is achieved when the *I. robustum* and *I. gaudryi* samples are combined by drawing a new graph on Kurtén's Figure 9 equidistant from the graphs of the two *Ictitherium* species. This may not be a valid statistical procedure since the unpublished primary data for the two species should be combined in order to calculate accurate ratios for the combination. Nevertheless, the experiment must have produced a graph which is approximately correct.

The similarity between the ratio diagrams of the Langebaanweg and Eurasian samples strongly suggests that the three Langebaanweg species are interrelated in a manner which is comparable to the interrelationships between the Eurasian *Ictitherium*, *Palhyaena* and *Hyaenictitherium*. This is here interpreted as evidence in support of the ancestor/descendant relationships postulated earlier.

Not surprisingly the two ratio diagrams also differ in certain respects. For

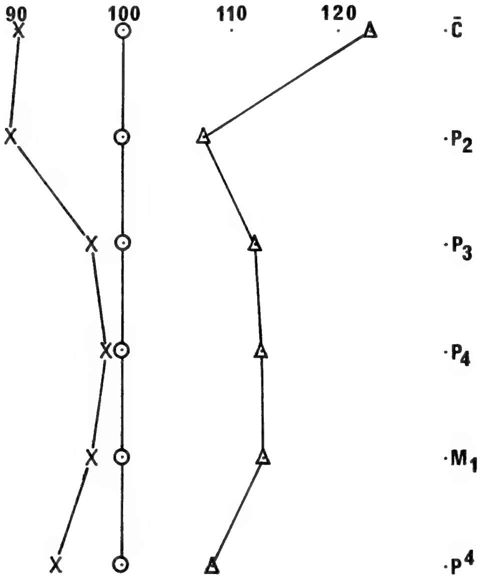


Fig. 4. Ratio diagram comparing mean lengths of lower teeth and P⁴ in certain Langebaanweg Hyaenidae: '*Hyaenictis*' *preforfex* (×), '*Hyaena*' *namaquensis* (△). Standard of comparison (100%): *Hyaena abronia* (○).

example, in terms of its tooth proportions '*H.*' *preforfex* is closer to *H. abronia* than are either of the Eurasian *Ictitherium* species to P. *wongii*. This applies particularly in the case of the posterior premolars (P_3, P_4). This is also illustrated by a second ratio diagram (Fig. 5), in which the lower cheektooth lengths of the Langebaanweg species are plotted against an *I. robustum* sample as standard.

Figure 5 illustrates even more clearly than Figure 4 that the tooth proportions of '*H.*' *preforfex* and '*H.*' *namaquensis* are essentially similar and that *H. abronia* differs from them principally in its premolar development. An increase in premolar size is one of the more general rules in hyaenid evolution and their marked size increase in '*H.*' *preforfex* and '*H.*' *namaquensis* relative to the condition in *I. robustum* is not surprising, since the latter species is a generalized form which presumably resembles the common ancestor of this group of hyaenids. Evidently the situation in respect of premolar development in *H. abronia* was somewhat different. A possible explanation for this situation emerges from an examination of the hypothetical lineage which includes *H. abronia*.

This lineage, which has *Ictitherium* as the stem form and with *Palhyaena*, *H. abronia* and the living *Hyaena hyaena* as subsequent members (Hendey 1974*a*, this report), may well prove to be less controversial than others suggested here.

There is little difference in overall body size and tooth characters in later members of the lineage, that is, *H. abronia* through to living *H. hyaena*. This suggests that the evolution of at least some characters had virtually ceased by the time an *H. abronia*-like stage had been reached. Since some recorded *Palhyaena* specimens seem to be little different from the Langebaanweg *H. abronia*, the lineage had evidently reached an 'optimum' stage relatively early. In other words, the '*Hyaena*' condition was achieved precociously.

Evidently the same did not apply to the *Ictitherium*–'*H.*' *preforfex* and *Hyaenictitherium*–'*H.*' *namaquensis* lineages, where development of characters such as premolar size continued. They were thus slower in reaching an 'optimum' condition.

Another important point which is clearly illustrated by the accompanying ratio diagrams concerns the development of the canines. Kurtén (1954: 16) found *Hyaenictitherium hyaenoides* to be 'fairly similar' in tooth proportions to *Palhyaena* 'with the exception of the powerful canines'. This is also the character which most readily distinguishes the Langebaanweg '*H.*' *namaquensis* from its two contemporary near relatives. The implication is that *H. hyaenoides* and '*H.*' *namaquensis* had the development of large canines as a character in common and, consequently, that they were, indeed, closely related.

There is, however, a complication with this interpretation of the data. Judging from Figure 5, canine size in the Langebaanweg species is approximately proportional to the overall size of the species concerned, something which is also evident, although perhaps less obvious, in Kurtén's (1954) ratio

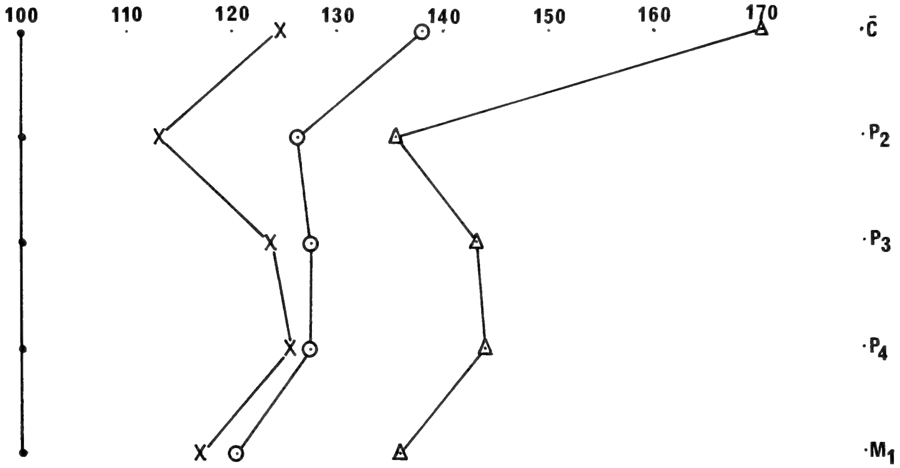


Fig. 5. Ratio diagram comparing mean lengths of lower teeth in certain Langebaanweg Hyaenidae: '*Hyaenictis*' *preforfex* (×), *Hyaena abronia* (○), '*Hyaena*' *namaquensis* (△). Standard of comparison (100%): European *Ictitherium robustum* (Kurtén 1954).

diagram. It is therefore possible that the large canine size in *H. hyaenoides* and '*H.*' *namaquensis* is due not to a phylogenetic connection, but simply to the fact that they are the largest members of their respective series. This means that canine size, and indeed the overall similarities in tooth proportions in the two series, may be coincidental.

Coincidence can, of course, not be ruled out, but it must be highly improbable. Not only do the two series have similar patterns in tooth proportions which go together with evolutionary advances in tooth morphology (e.g. reduced molar size in the Langebaanweg series), but in the case of the *Palhyaena–H. abronia* lineage at least, there is evidence of advances in the postcranial skeleton as well (Hendey 1974*a*: 116, table 20). Furthermore, if the Langebaanweg series did not evolve from the suggested late Miocene taxa, alternatives must be sought and certainly none are obvious.

Whereas the evolution of *H. hyaena* from the *Palhyaena–H. abronia* combination appears likely, the subsequent histories of the *Ictitherium*–'*H.*' *preforfex* and *Hyaenictitherium*–'*H.*' *namaquensis* lineages are obscure. The former almost certainly has no living descendant, but the latter could be ancestral to *Hyaena brunnea.*

The first fully mature '*H.*' *namaquensis* specimen from Langebaanweg (SAM–PQ–L25026) is similar in overall size to living *H. brunnea.* The fossil species differs in some body proportions such as, for example, having longer hind limbs. This difference is similar to one which distinguishes *H. abronia* from *H. hyaena* (Hendey 1974*a*: 116–118). There are also some marked differences in the dentitions of '*H.*' *namaquensis* and *H. brunnea.* For example, the former retains P_1 and M^2_2 and has lower crowned and more slender premolars. These, and other differences, all indicate the primitive state of '*H.*' *namaquensis* and all are likely to have been present in an early ancestor of *H. brunnea.* Consequently, there is apparently nothing to preclude an ancestor/descendant relationship between these taxa.

The situation is reminiscent of that which exists between *H. abronia* and *H. hyaena*, although in this instance the differences are less marked and there is an appropriate late Pliocene/early Pleistocene intermediate form recorded (i.e. *H. hyaena makapani*). It was suggested above that the hypothetical *Hyaenictitherium*–'*H.*' *namaquensis* lineage had apparently not reached an 'optimum' evolutionary state by the early Pliocene. If evolutionary advances continued during this epoch, they may well have been in the direction of an *H. brunnea*-like species. This would account for the fact that *H. brunnea* is the more specialized (advanced) of the two living *Hyaena* species. While a direct relationship between '*H.*' *namaquensis* and *H. brunnea* is here suggested as a possibility, more evidence is needed to test the hypothesis.

Whereas *Ictitherium*, *Palhyaena* and *Hyaenictitherium* form a close-knit unit within the late Miocene *Hyaena* group of Eurasia, the group apparently has at least two additional members, namely, *Hyaenictis* and *Lycyaena.*

For a reason given earlier, the Langebaanweg '*Hyaenictis*' *preforfex* is no longer regarded as a member of that genus. There is, however, another of the Langebaanweg species which may be related to *Hyaenictis* or *Lycyaena*. This is the undescribed species of *Euryboas*.

The late Miocene ancestor of the Langebaanweg *Euryboas* is likely to have had the following amongst its characteristics:

1. M^2 reduced or absent.
2. M_1 metaconid present, although possibly smaller than in *Ictitherium*, *Palhyaena* and *Hyaenictitherium*;
3. M_1 talonid bicuspid;
4. M_2 persistently present, but P_1 absent or sometimes absent;
5. Postcranial skeleton similar in overall size to larger members of the *Ictitherium/Palhyaena/Hyaenictitherium* subgroup.

The last character is important in suggesting that *Euryboas* belongs to the *Hyaena* group rather than the *Percrocuta* group, since the late Miocene percrocutas were evidently relatively large, heavily-built animals. The other characters combine to suggest that *Euryboas* was derived from *Hyaenictis* or *Lycyaena*, rather than the *Ictitherium/Palhyaena/Hyaenictitherium* subgroup. Both *Lycyaena* (De Beaumont 1967) and *Hyaenictis* (Thenius 1966) have previously been suggested as possible *Euryboas* ancestors.

In the case of *Hyaenictis*, *H. graeca* is the species of appropriate age to be ancestral to a primitive *Euryboas*. This species apparently fulfils most of the required criteria for this role, but it does lack the M_1 metaconid. This is not necessarily a serious objection since this cusp is sometimes variably developed in hyaenid species (Kurtén 1956: 12–14), and the M_1 of *H. graeca*, like that of the Langebaanweg *Euryboas*, may sometimes have had a small metaconid. Alternatively, this cusp may have been present in an as yet unknown African counterpart of *H. graeca*.

The Eurasian late Miocene representative of *Lycyaena* is *L. chaeretis*, for which a similar complication exists. According to Pilgrim (1932) this species lacks M_2, a tooth which is sometimes present in the Langebaanweg *Euryboas*. Zapfe (1948) has, however, recorded a *L. chaeretis* from Austria in which a small M_2 was present. The presence of M_2 may have characterized certain late Miocene populations of *Lycyaena*, including an African one, if it existed.

On balance the other recorded characteristics of *Lycyaena* appear to be more *Euryboas*-like than those of *Hyaenictis* and the former is here regarded as the likely ancestor of *Euryboas*.

Later species of *Euryboas* are recorded from elsewhere in Africa and in Europe. Some of the specimens previously included in this genus were recently referred instead to *Chasmaporthetes* (Galiano & Frailey 1977).

THE *PERCROCUTA* GROUP

The last of the 'E' Quarry hyaenids, *Adcrocuta australis*, was once thought to be the least problematical of the species, since its large size and certain specialized dental characters readily distinguished it from its contemporaries.

The increase in the sample size has revealed that there is appreciable variation in this species, which may be due at least in part to sexual dimorphism, and some cranial material apparently belonging to *A. australis* resembles specimens assigned to *Euryboas*.

Even when allowance is made for marked sexual dimorphism, and problematical fragmentary specimens are excluded from consideration, the material assigned to *A. australis* is more variable than that belonging to other Langebaanweg hyaenids. Indeed, there are grounds for suspecting that the material may belong to two species. An essentially similar situation was encountered by Zdansky (1924) when he studied the Chinese *A. eximia variabilis*. His decision to recognize only one variable species has been generally supported (e.g. Pilgrim 1931; Kurtén 1957). With this precedent in mind, and since *A. eximia* is regarded as the structural ancestor of *A. australis* (Hendey 1974*a*), the material assigned to the latter is left undivided.

The Langebaanweg *A. australis* and *Euryboas* have certain dental characters in common. For example, their cheekteeth are generally similar in morphology (Fig. 6) and in proportions (Fig. 7). These two species are readily distinguished from the other Langebaanweg hyaenids, and this raises the possibility that the *Euryboas* belongs in the *Percrocuta*, rather than *Hyaena* group. Although this possibility cannot be dismissed, it is not favoured since *A. australis* does have some specialized characters not evident in *Euryboas*, which suggests that the two species belong to lineages which had had a long, separate history. For example, *A. australis* was a large animal with robustly proportioned postcranial bones, whereas the *Euryboas* was smaller and more lightly built. *A. australis* is also distinguished by specialized dental characters such as sometimes having prominent anterior accessory cusps on P_2 and P_3 and in having a unicuspid M_1 talonid.

The similarities between *A. australis* and the *Euryboas*, which are here ascribed to parallel evolution, will be discussed again in a later section of this report.

NOMENCLATURE

Having reviewed the status and relationships of the 'E' Quarry hyaenids, the taxonomic implications of the conclusions reached here can be considered.

Since '*Hyaenictis*' *preforfex* is regarded as a descendant of late Miocene *Ictitherium*, and since the subsequent history of the lineage is not known, the Langebaanweg species is referred to *Ictitherium* on the principle that members of a single lineage are congeneric.

The situation in respect of *Hyaena abronia* remains unchanged, although a new complication now arises. In this instance both ancestral (*Palhyaena*) and descendant (*H. hyaena*) forms are recognized and, in order to conform to the principle stated above, *Palhyaena* should be sunk into *Hyaena*, the latter being the name which has priority. This step is, however, not formally proposed since there is no point in synonymizing a name in common use if the reason for doing

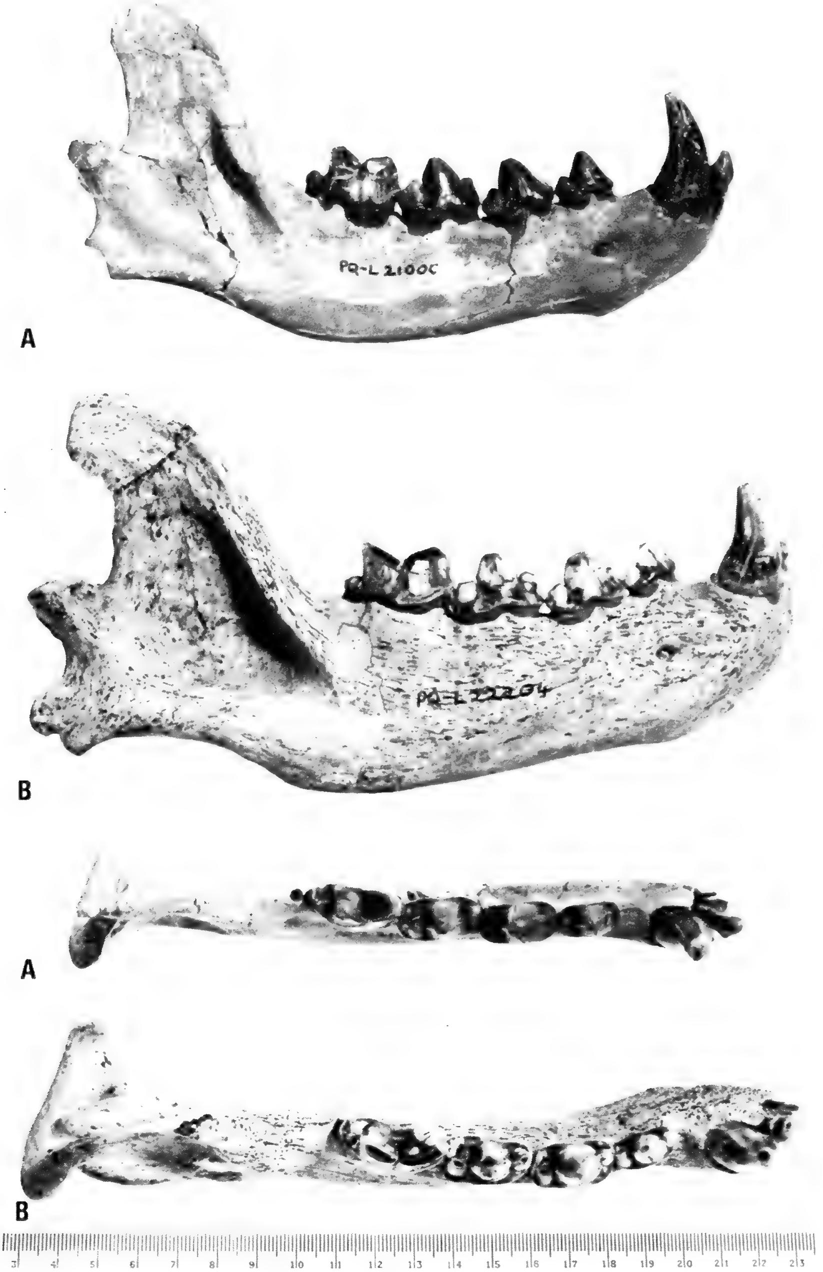


Fig. 6. Lateral and occlusal views of hyaenid hemimandibles from Langebaanweg. A. *Euryboas* sp. (L21000) (immature adult). B. *Adcrocuta australis* (L22204).

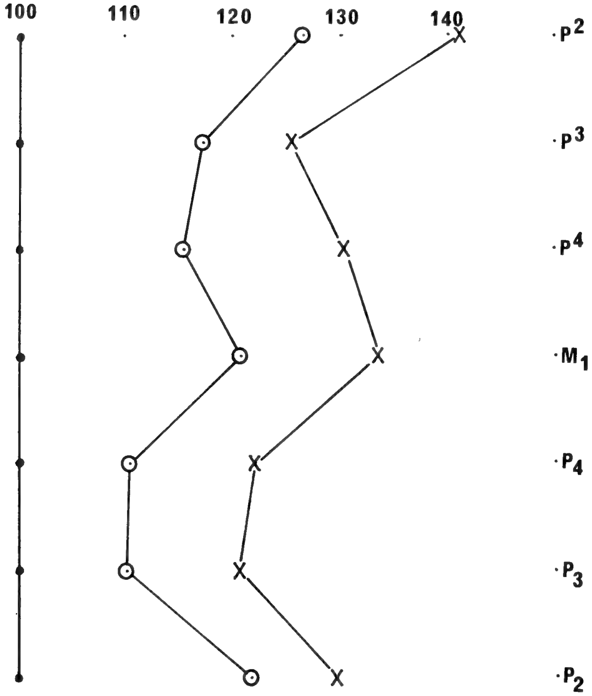


Fig. 7. Ratio diagram comparing mean lengths of upper and lower teeth of Langebaanweg *Euryboas* sp. (○) and *Adcrocuta australis* (×). Standard of comparison (100%): *Hyaena hyaena.*

so is not generally accepted. A decision can await reactions to the suggestion.

'*Hyaena*' *namaquensis*, like *Ictitherium preforfex*, is referred to its supposed ancestral genus, in this instance, *Hyaenictitherium*. The name becomes *Hyaenictitherium namaquense*. If substantiated, the suggestion that *H. namaquense* is ancestral to *Hyaena brunnea* will provide a solution to the problem of the generic name of the latter. At least twice in recent years it has been indicated that the relationship between *H. hyaena* and *H. brunnea* is distant enough to warrant nomenclatural distinction above the species level (Hendey 1974*a*: 148–149; Galiano & Frailey 1977: 11–12). *Hyaenictitherium* probably has priority over any other generic name available for '*Hyaena*' *brunnea*.

In spite of the problems and doubts about relationships mentioned earlier, no name changes are proposed in the cases of *Adcrocuta australis* and the unnamed *Euryboas* species.

The Langebaanweg ('E' Quarry) hyaenids now recognized are listed in Table 1. The suggested relationships of the taxa already discussed are summarized in Figure 8. In all instances the ancestral forms are merely recorded species in an appropriate evolutionary state for this role and they need not have been in the actual ancestral position. For example, the Chinese *Hyaenictitherium hyaenoides* was almost certainly not a direct ancestor, but was simply a structural ancestor of the South African *H. namaquense*. It is much more likely that the latter stemmed from an as yet unknown African late Miocene *Hyaenictitherium* which resembled *H. hyaenoides*, but which was not necessarily conspecific with it.

The tooth sizes of the samples used in this study are recorded in Table 2.

RELATIONSHIPS OF *CHASMAPORTHETES*

In a recent note on the origins of North American *Chasmaporthetes*, the Chinese late Miocene *Adcrocuta eximia variabilis* was suggested as a likely ancestor (Hendey 1975). In recording what they regard as the first Asiatic *Chasmaporthetes* (*C. kani*), Galiano & Frailey (1977: 9) concluded that this genus 'was apparently generically distinct before its entry into North America and shares a number of derived characters with *Euryboas* rather than with *Percrocuta*'. This conclusion was based on a cladistic analysis of the Hyaenidae other than the percrocutas.

The omission of the percrocutas was justified on the grounds that they retain 'a number of primitive characters' in association with others that are 'highly derived', which sets them apart from other hyaenids, including *Chasmaporthetes* (Galiano & Frailey 1977: 9). The derived characters mentioned are a reduced P^4 protocone and contact between the premaxillary and frontal

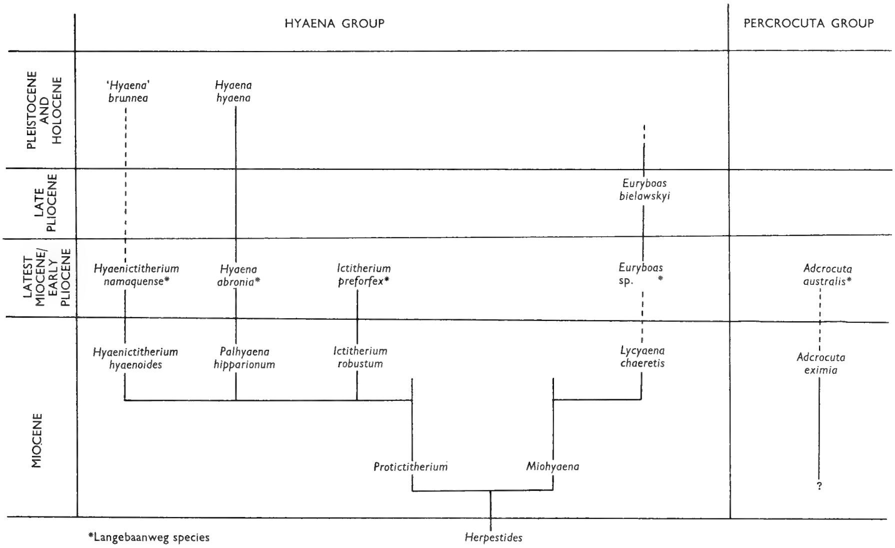


Fig. 8. Tentative phylogeny of some Hyaenidae.

TABLE 2

Mean dimensions of Langebaanweg Hyaenidae teeth.

	$\underline{C}$		P^1		P^2		P^3		P^4		M^1		M^2	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
Ictitherium preforfex (n = 7)	12,1	9,1	5,6	4,7	13,8	7,7	18,7	11,4	26,3	15,3	7,9	13,1	3,6	5,3
Hyaena abronia (n = 4)	11,9	9,8	6,2	5,1	14,4	8,2	18,9	11,4	28,0	15,7	9,3	15,0	4,0	5,3
Hyaenictitherium namaquense (n = 3)	15,3	11,4	7,9	6,7	16,4	9,2	21,4	13,6	30,3	17,8	9,3	16,5	—	—
Euryboas sp. (n = 2)	15,7	11,8	7,0	7,3	20,0	11,5	23,9	14,5	34,7	19,5	7,8	15,8	0	0
Adcrocuta australis (n = 8)	16,8	12,6	8,1	8,7	22,3	12,2	25,6	16,1	39,2	20,2	—	—	?0	?0

	$\overline{C}$		P_1		P_2		P_3		P_4		M_1		M_2	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b
Ictitherium preforfex (n = 7)	12,1	9,2	3,2	3,4	12,1	7,3	16,7	9,6	18,3	9,6	20,2	9,3	4,5	4,2
Hyaena abronia (n = 4)	13,4	10,2	4,1	3,7	13,5	7,6	17,2	9,6	18,6	9,8	20,8	10,3	5,2	4,5
Hyaenictitherium namaquense (n = 3)	16,5	11,7	3,8	4,6	14,5	8,3	19,3	10,9	21,0	11,2	23,5	10,7	5,6	5,2
Euryboas sp. (n = 2)	15,5	11,4	0	0	16,9	9,1	20,9	11,2	22,8	11,7	25,2	12,0	—	—
Adcrocuta australis (n = 8)	17,6	12,8	0	0	18,0	9,9	22,9	12,3	25,0	12,7	27,9	12,7	—	—

bones of the skull, while the only primitive character mentioned was the presence of a large metacarpal I. While the omission of most percrocutas on these grounds may be justified, this does not apply in the case of *A. eximia variabilis.*

A large metacarpal I, which amongst living taxa is found only in *Proteles*, undoubtedly is a 'primitive' character, but it was a feature of most, if not all, late Tertiary hyaenids. This certainly applies in the case of all five species recorded from 'E' Quarry.

Although the P^4 protocone generally is reduced in the percrocutas (Kurtén 1957), *A. eximia variabilis* is exceptional in having this cusp of variable size (Zdansky 1924: 96; Pilgrim 1931: 117; Kurtén 1957: 399). Evidently in the case of certain individuals at least, the P^4 protocone was not necessarily any smaller than that in *C. kani*, in which this cusp is also somewhat reduced (Galiano & Frailey 1977: fig. 1).

The contact between the premaxillaries and frontals is not a constant character in *A. eximia variabilis*, Zdansky (1924) having recorded one specimen in the series he studied in which there was no such contact. This character is also variable in some other hyaenids. For example, a series of 13 *Crocuta crocuta* skulls in the South African Museum includes 7 specimens in which there is no contact between these bones, 1 specimen in which there is contact on one side only, and 5 specimens in which there is contact. Galiano & Frailey were thus mistaken both in regarding the maxillary-frontal contact in *A. eximia variabilis* as constant, and in regarding it as unique.

Since there are now no recorded grounds for dismissing the possible phylogenetic link between *A. eximia variabilis* and *Chasmaporthetes*, it is here examined in some detail.

North American *Chasmaporthetes* undoubtedly had an Asian ancestor, and Galiano & Frailey (1977) have provided evidence that the Chinese *C. kani* is an appropriate candidate for this role, at least in terms of morphology. Consequently the theory that *Chasmaporthetes* and *Adcrocuta* are closely related can most conveniently be tested by comparing *C. kani* with the Chinese *A. eximia variabilis* described by Zdansky (1924). The comparison is facilitated by the fact that both species are represented by fairly complete and well-preserved specimens belonging to several individuals.

In the comparisons which follow account is also taken of the undescribed *Euryboas* from Langebaanweg. It is relevant because if Galiano & Frailey are correct in concluding that *Chasmaporthetes* and *Euryboas* were closely related, then the Langebaanweg species should, because of its age relative to recorded *Chasmaporthetes*, be a more appropriate structural ancestor of the latter than is *A. eximia variabilis*. Mention will also be made of the Langebaanweg *A. australis* since it is evidently intermediate in age between *A. eximia variabilis* and *C. kani*, and, if the latter two taxa are phylogenetically related, *A. australis* should also have characters in common with *C. kani*.

The skulls and mandibles of *C. kani* and *A. eximia variabilis* are superficially similar morphologically and little different in size. The mandible of *Euryboas* may, on average, be more slender than those of the other two taxa, but this possible difference has yet to be substantiated. There is certainly a greater similarity between the mandible of *C. kani* and certain of the Langebaanweg *A. australis* specimens than between that of the former and the Langebaanweg *Euryboas.*

One of the more striking characteristics of the mandible in *Euryboas* is that the corpora are remarkably straight, the two halves being steadily divergent from the symphysis. Viewed ventrally the mandible is V-shaped. In this respect *Euryboas* resembles all other members of the *Hyaena* group, living and fossil, examined during the course of the present study. By contrast, at least some of the mandibles of *A. australis*, *A. eximia* (e.g. Schmidt-Kittler 1976: pl. 3, fig. 6) and North American *Chasmaporthetes* (e.g. Stirton & Christian 1940: fig. 1) have markedly curved corpora and, viewed ventrally, are almost U-shaped. This also applies to some specimens in the available series of living *C. crocuta* specimens, in which four out of seven specimens have curved jaws.

Since mandibular curvature is not constant in any one species, it is an unreliable distinguishing character. However, it may be significant that curved mandibles were observed only in species which are, or which might be, members of the *Percrocuta* group. *Adcrocuta* and *Chasmaporthetes* are here regarded as percrocutas, while *C. crocuta* may be, even though it is generally included in the *Hyaena* group (e.g. Thenius 1966; Galiano & Frailey 1977). This may be an instance where a character (i.e. curved mandibles) is indicative of one group only (i.e. the percrocutas), whereas the opposite condition (i.e. straight mandibles) is found in both groups of hyaenas. Further observations are required to test this hypothesis.

Jaw shape is usually an indication of the shape of the cheektooth rows, although there are instances where straight jaws (viewed ventrally) occur together with curved cheektooth rows. This applies in the case of, for example, '*Hyaena*' *brunnea.* Toothrow curvature has, therefore, to be considered as a separate character.

Galiano & Frailey (1977) have pointed out that in *Euryboas* the cheektooth rows are straight, whereas in *Chasmaporthetes* they are curved. The latter condition is evident in both *A. eximia variabilis* and *A. australis*, even when the jaws are straight. The primitive Langebaanweg *Euryboas*, like later forms, has straight cheektooth rows, which is an indication that this was a characteristic of the lineage for most, and probably all, of its history. The implication is that *Euryboas* and *Chasmaporthetes* had evolved independently at least since late in the Miocene.

As with the mandibles, there is a greater similarity between the teeth of *C. kani* and *A. australis* than between those of the former and *Euryboas*. In addition, there is a general similarity between the teeth of these three taxa and those of *A. eximia variabilis*, although it is on the differences which do exist that the question of interrelationships hinges.

Ratio diagrams are used to illustrate some of the similarities and differences in tooth proportions in *A. eximia variabilis*, *C. kani* and the Langebaanweg *Euryboas* (Fig. 9). There is a basic similarity in the patterns of tooth length in the three taxa. The premolars of *C. kani* are only slightly shorter than those of *A. eximia variabilis*, whereas the carnassials are appreciably shorter (Fig. 9A). By contrast, the carnassials of *C. kani* and the *Euryboas* are of comparable length, whereas the anterior premolars of the latter are longer (Fig. 9B). Thus if the *Euryboas* represents the structural ancestor of *C. kani*, then the evolutionary trend in respect of cheektooth length was reduction of premolar length. Alternatively, if *A. eximia variabilis* was the ancestor, then the trend was reduction of carnassial length.

One of the metrical characters not illustrated in the accompanying ratio diagrams is crown height of the canines. The canines of *A. eximia* and North American *Chasmaporthetes johnstoni*, and possibly also *C. kani*, are unremarkable, relatively low-crowned teeth, whereas the canines of the Langebaanweg *Euryboas* are relatively high-crowned. The length: crown height ratio for the $\overline{C}$ of specimen SAM–PQ–L21000 is 1 : 2, which compares closely to the ratio

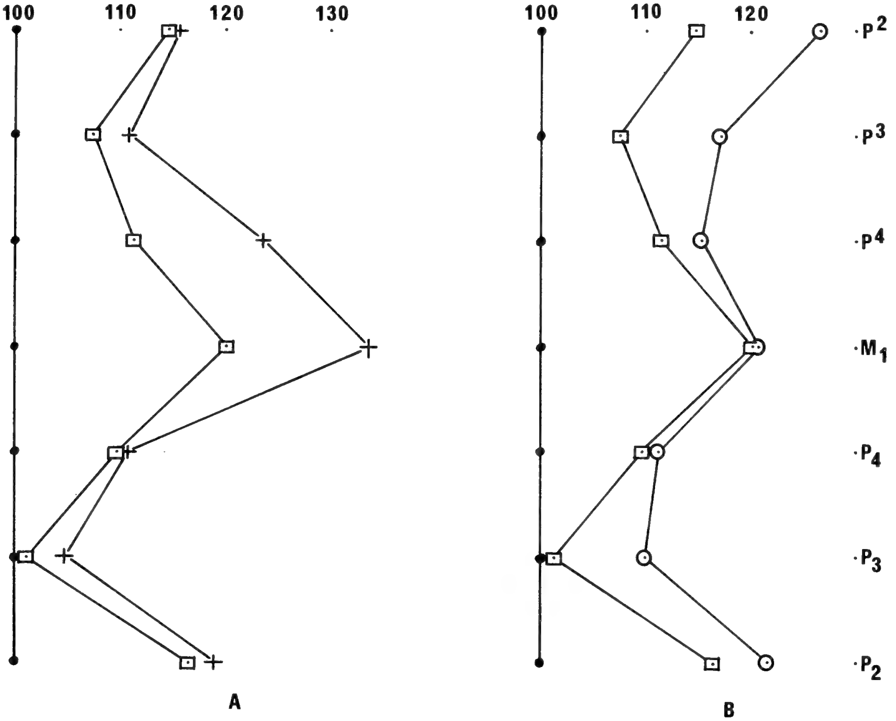


Fig. 9. Ratio diagrams comparing mean lengths of upper and lower teeth of *Adcrocuta eximia variabilis* (+) (Kurtén 1957), *Chasmaporthetes kani* (□) (Galiano & Frailey 1977), and the Langebaanweg *Euryboas* sp. (○). Standard of comparison (100%): *Hyaena hyaena*.

of 1 : 1,97 in the *E. bielawskyi* from Roccaneyra (Schaub 1941). The ratio in *C. johnstoni* is 1 : 1,79, while in one of the Langebaanweg *A. australis* specimens (L22204) it is 1 : 1,63. The canine height in *Euryboas* is clearly a specialized character, which is not shared by at least some, and perhaps all, species of *Adcrocuta* and *Chasmaporthetes*. Thus in terms of canine development *Adcrocuta* is more appropriate than *Euryboas* as an ancestor for *Chasmaporthetes*.

C. kani differs from *A. eximia variabilis* in having a slightly larger P^1. Galiano & Frailey (1977: 6) are of the opinion that the P^1 of *C. kani* 'is proportionally larger than in any other hyaenid genus'. No explanation of this character is offered but, since it is apparently unique, it must be regarded as a specialization. By curious contrast in view of their conclusion on relationships, Galiano & Frailey record the absence of P^1 as one of the characteristics of *Euryboas*. In fact, this tooth is present in the primitive Langebaanweg species. Since this species was ancestral to forms which had lost P^1, it is perhaps unlikely that it should also be the ancestor of another (i.e. *C. kani*) in which this tooth was unusually well developed. No such anomaly exists in respect of *Adcrocuta*, which would, therefore, be a more appropriate ancestral form for *C. kani*.

C. kani also differs from *A. eximia variabilis* in lacking P_1, a tooth which is usually present in the latter. The reduction and eventual loss of P_1 is a general rule in hyaenid evolution, so in respect of this tooth *C. kani* could well have evolved from *A. eximia variabilis*, a species in which loss of P_1 was already being manifested. On the other hand, the Langebaanweg *Euryboas* would be an equally appropriate structural ancestor since, like *C. kani*, it lacks P_1.

The P^2_2, P^3_3 and P_4 of *C. kani* and *A. eximia variabilis* are of comparable length, but those of *C. kani* are narrower (Table 3), the latter being a difference

TABLE 3

Mean dimensions of *Chasmaporthetes kani* and *Adcrocuta eximia variabilis* teeth.

	P^1		P^2		P^3		P^4		M^1	
	l	b	l	b	l	b	l	b	l	b
Chasmaporthetes kani[1]	8,8	7,8	18,1	11,3	21,9	13,7	32,6	18,0	7,6	16,4
Adcrocuta examia variabilis[2]	7,1	7,4	18,1	12,5	22,6	16,0	38,4	19,0	6,1	13,6

	P_1		P_2		P_3		P_4		M_1	
	l	b	l	b	l	b	l	b	l	b
Chasmaporthetes kani[1]	0	0	15,8	9,0	19,2	10,7	22,3	11,8	25,1	11,4
Adcrocuta eximia variabilis[2]	5,3	5,9	16,4	11,8	19,7	14,2	22,2	13,8	27,5	13,1

[1] Galiano & Frailey 1977.
[2] Zdansky 1924.

not shown on the ratio diagram (Fig. 9A). The Langebaanweg *Euryboas* has premolars comparable in breadth to those of *C. kani* but which are, with the exception of P_4, slightly longer. Advanced *Chasmaporthetes*, like *Euryboas*, has narrow, sectorial premolars as a major distinguishing characteristic. It follows that while derivation of *C. kani* from *A. eximia variabilis* would be logical in terms of the relative development of their premolars, derivation of the former from the Langebaanweg *Euryboas* is not, since even this primitive *Euryboas* was already more specialized in terms of premolar proportions.

Also relevant here is the observation by Galiano & Frailey (1977: 2) that the 'anterior accessory cusps of P_2 and P_3 [in *C. kani* are] relatively weak as compared with other *Chasmaporthetes* species'. In this respect *C. kani* occupies a position intermediate between *A. eximia variabilis* and advanced *Chasmaporthetes*, an appropriate position in the hypothetical *Adcrocuta*-North American *Chasmaporthetes* lineage. Assuming that Galiano & Frailey were correct in reassigning some Old World hyaenids to *Chasmaporthetes*, then it appears that *Euryboas* never did develop prominent anterior accessory cusps on the anterior premolars. This need not necessarily exclude the Langebaanweg *Euryboas* from the role as structural ancestor of *Chasmaporthetes* but, as in the case of P^1, it would be another instance where descendant forms evolved different characteristics.

The shapes of the anterior lower premolars are also significant. In *Chasmaporthetes* these teeth tend to be ovate in occlusal view, whereas in *Euryboas* they are more or less rectangular in outline. This is most obvious in the case of P_3. In *A. eximia variabilis* and *A. australis* the P_3's are rectangular, and in this respect they resemble most, if not all, contemporary hyaenids. Rectangularity in the lower premolars is thus a primitive condition, and their ovate shape in *Chasmaporthetes*, combined with the narrowness of these teeth, appears to be unique amongst hyaenids.

The carnassials of *C. kani* differ from those of *A. eximia variabilis* by being shorter and, in the case of M_1, in having a simple unicuspid talonid. The M_1 talonid in *A. eximia variabilis* is variably developed, but both entoconid and hypoconid may be prominent. The fact that the talonid is variable in this taxon suggests that it was already evolving away from the more complex condition characteristic of primitive hyaenids and tending towards that evident in *C. kani*. The significance of carnassial shortening in the hypothetical *A. eximia variabilis*–*C. kani* lineage is not known. Possibly the development of the premolars as more effective shearing teeth in *C. kani* reduced the demand on the carnassials for this function.

Galiano & Frailey (1977) record the absence of the metaconid and presence of a unicuspid talonid on M_1 as characteristics of *Euryboas*. This does not apply in the case of the primitive Langebaanweg species, which has a bicuspid talonid and sometimes has a metaconid. These features would not, however, exclude this species as a structural ancestor of *C. kani*.

Relevant here is the nature of the M_1 in the Langebaanweg *A. australis*.

Although this species, like *A. eximia variabilis*, exhibits appreciable variation in certain characters, its M_1 typically lacks the metaconid and has a unicuspid talonid. Thus *A. australis* and *C. kani* are similar in terms of M_1 morphology, whereas the Langebaanweg *Euryboas* is, in this respect, more primitive in an evolutionary sense. These comments also apply with respect to the anterior accessory cusps of the anterior lower premolars. This is here interpreted as a further indication that the relationships of *Chasmaporthetes* lie with *Adcrocuta* rather than with *Euryboas*.

The M^1 of *C. kani*, like the P^1, is a little larger than that of *A. eximia variabilis*. As a general rule, hyaenid evolution is characterized by a reduction in the size of upper molars. Consequently, the increase in the size of the *C. kani* M^1 relative to that of its hypothetical *A. eximia variabilis* ancestor is an anomaly which requires explanation. A similar situation exists in the case of the *Euryboas* lineage and it will be discussed first.

The M^1 of the Langebaanweg *Euryboas* is relatively large and more transversely elongated compared with those of other members of the *Hyaena* group from Langebaanweg. The transverse elongation is emphasized by the reduction of the metastyle and the root which supports it. Judging from a cast of the Val d'Arno *E. bielawskyi* maxillary fragment described by Schaub (1941), the M^1 of this species was even more transversely elongated, while the metastyle and supporting root were apparently absent. Indications are that the transverse elongation of M^1 was a progressive character in the *Euryboas* lineage and must, therefore, have been of functional advantage in the otherwise essentially sectorial dentition of this genus.

In primitive or unspecialized hyaenids, of which the living *Hyaena hyaena* is an example, the M^1 occludes with the posterior parts of M_1, food being crushed between the occlusal surfaces of the M^1 and the M_1 talonid. In specialized species such as *Crocuta crocuta* the shearing blades of the carnassials are highly developed, the M_1 talonid is small and the M^1 reduced or absent. *Euryboas* is clearly quite different from either of the above examples since the M^1 appears disproportionately large in relation to the size of the M_1 talonid.

The M^1 in carnivores is not necessarily used only for crushing food. Even in such groups as the Felidae, in which the cheekteeth are highly sectorial and the M_1 talonid is absent in all but primitive forms, an M^1 is present. In such cases the M^1 also has a shearing function. As the jaws are closed the apex of the M_1 protoconid passes across the P^4 metastyle in a manner normal for carnivore carnassial shear. Thereafter it comes into contact with the anterior edge of M^1 and the posterior keel of the protoconid slides along this edge with a slicing action, which is at right angles to the main carnassial shear. Presumably it is occlusion of this kind which had developed to a high degree in *Euryboas*. In this instance there was the added refinement provided by the M_1 talonid, itself sectorial in advanced species, which slid across the occlusal surface of the M^1, probably with a cutting, rather than crushing, action.

The Langebaanweg *Euryboas* was relatively primitive in having a bicuspid

M_1 talonid and, in addition, it sometimes had a small M_2. Thus, in this species the crushing function of the molars had not yet been completely replaced by the shearing function evident in later *Euryboas*.

The situation in the hypothetical *Adcrocuta–Chasmaporthetes* lineage was probably essentially similar and the relatively large M^1 of *C. kani* may be interpreted as a specialized, rather than primitive, character.

The M^1 of the Langebaanweg *Euryboas* is comparable in size to that of *C. kani* and this may be yet another indication that there was no direct phylogenetic link between them. There evidently was transverse elongation (i.e. size increase) in M^1 on the Langebaanweg *Euryboas–E. bielawskyi* lineage, but nothing comparable in the case of *C. kani* if it, too, stemmed from a *Euryboas* resembling that from Langebaanweg. This would be yet another example of possible descendants of the Langebaanweg *Euryboas* following different evolutionary trends. While this is, of course, not impossible, it is unlikely.

The postcranial skeleton of *Chasmaporthetes* has yet to be recorded but, since the dentition of this genus deviates markedly from those of most hyaenids and in some respects resembles that of *Euryboas*, it is possible, and perhaps even likely, that the postcranial skeleton also differed from those of 'conventional' hyaenids, and that it shared the specializations evident in *Euryboas*.

To sum up, the observable similarities and differences between the taxa discussed here combine to weight the evidence in favour of an *Adcrocuta* rather than *Euryboas* origin for *Chasmaporthetes*. All those characters in which the dentition of early Pleistocene *C. kani* differs from that of late Miocene *A. eximia variabilis* may be interpreted as advanced and none would exclude the latter from an ancestral role. Most of the differences reflect stages in the development of the highly sectorial postcanine dentition characteristic of North American *Chasmaporthetes*, and *C. kani* is, in an evolutionary sense, in an intermediate position in the hypothetical *A. eximia variabilis*–North American *Chasmaporthetes* lineage suggested earlier (Hendey 1975). The similarities between *A. eximia variabilis*, *C. kani*, and North American *Chasmaporthetes* also point to a close relationship between these taxa.

By contrast, the latest Miocene/early Pliocene *Euryboas* from Langebaanweg is less well suited to the role as structural ancestor of *Chasmaporthetes*, and a direct phylogenetic connection between these taxa is, at the very least, highly improbable. On the other hand, the Langebaanweg *Euryboas* is in every respect ideally suited to be the ancestor of the late Pliocene/early Pleistocene *E. bielawskyi* of Europe.

The earlier view that *Chasmaporthetes* and *Euryboas* evolved independently, with the latter being an essentially African genus which also spread into southern Europe (Hendey 1975), is here maintained.

In considering the origins and relationships of *Chasmaporthetes* and *Euryboas*, another important species which has to be taken into account is '*Hyaena*' *borissiaki* from the Pliocene of Moldavia in the Soviet Union (Khomenko 1932). De Beaumont (1967) believed it to be an intermediate between *Lycyaena* and various species now assigned to *Chasmaporthetes* and *Euryboas*. More recently Galiano & Frailey (1977: 9) noted that it has characters in common with both these genera, but concluded that '*H.*' *borissiaki* 'appears to be referable to *Chasmaporthetes senso stricto*'.

'*H.*' *borissiaki* is evidently broadly contemporary with the hyaenids from Langebaanweg, although the actual ages of the Moldavian and South African species are not known. The relative ages of these hyaenids could be crucial to the interpretation of their relationships. '*H.*' *borissiaki* has characters in common with both *Adcrocuta australis* and the *Euryboas* from Langebaanweg. For example, both '*H.*' *borissiaki* and the *Euryboas* have straight cheektooth rows and jaws, while their cheekteeth are comparable in both size and morphology. On the other hand, '*H.*' *borissiaki* resembles *A. australis* in cheektooth morphology, most significantly in having a reduced P^4 protocone. In this respect, and in the occasional presence of P_1, it is also similar to *A. eximia variabilis*.

In terms of the interrelationships postulated here, '*H.*' *borissiaki* may be visualized either as an intermediate between *A. eximia variabilis* and *Chasmaporthetes*, or as an early *Euryboas* which was not conspecific with the Langebaanweg species. The first of these alternatives is perhaps the more likely and, following Galiano & Frailey (1977), '*H.*' *borissiaki* is here tentatively regarded as an early *Chasmaporthetes*.

Nevertheless, the similarities to *Euryboas* are striking and, as a further alternative, *Chasmaporthetes? borissiaki* may be interpreted as the species from which both *Euryboas* and *Chasmaporthetes* were derived. This possibility would be strengthened should it transpire that *C.? borissiaki* predates the Langebaanweg *Euryboas*. In the case of this alternative, the stem form might either have been *Lycyaena*, as De Beaumont (1967) suggested, or *Adcrocuta*, as indicated above.

While the phylogenetic position of *C.? borissiaki* is uncertain, it is clearly a species of great significance in the matter of 'hunting hyaena' interrelationships.

Judged on available evidence the hypothetical *Adcrocuta–Chasmaporthetes* transition took place in Asia some time between the late Miocene and early Pleistocene. Members of this lineage dispersed eastwards into North America by way of the Bering Land Bridge, and westwards into Europe and perhaps also Africa.

A problem which arises in connection with this theory concerns the age of *C. kani*, which was given as 'Early Pleistocene' by Galiano & Frailey (1977: 2). If this was indeed the case, then *C. kani* must be younger than at least some of the European and North American specimens assigned to *Chasmaporthetes*, even though it is more primitive in an evolutionary sense. Either *C. kani* is older than Galiano & Frailey suppose, or it was a conservative species, little different from a Pliocene form from which late Pliocene/early Pleistocene European and North American *Chasmaporthetes* must have been derived. In other words, the latter are likely to have stemmed from a *C. kani*-like ancestor of Pliocene rather than early Pleistocene age. *C.? borissiaki* could possibly be the species in question.

The actual dates when *Chasmaporthetes* first appeared in Europe and North America have yet to be firmly established. If the Plio/Pleistocene boundary is taken at about 2 m.y. before present, then migration to North America must have been during the late Pliocene, since *Chasmaporthetes* is recorded from the 'early Blancan' (Repenning 1967), which is of late Pliocene age (Kurtén 1971). The Olivola and Senéze faunas of Europe, which include *C. lunensis* (Galiano & Frailey 1977), date from the latter part of the Villafranchian (Kurtén 1968), which postdates the early Blancan. The migration to Europe may thus have been later than that to North America.

The ranges of *Chasmaporthetes* and *Euryboas* overlap both temporally and geographically in Europe and, in view of their shared characteristics, they may well have competed with one another. It is not known which of the two taxa survived longest in Europe, but that honour may go to *Chasmaporthetes*.

The situation in Africa is somewhat obscure, the basic problem being to which of the two genera material from the Transvaal caves and undescribed specimens from east Africa (e.g. Howell & Petter 1976) belongs. The best

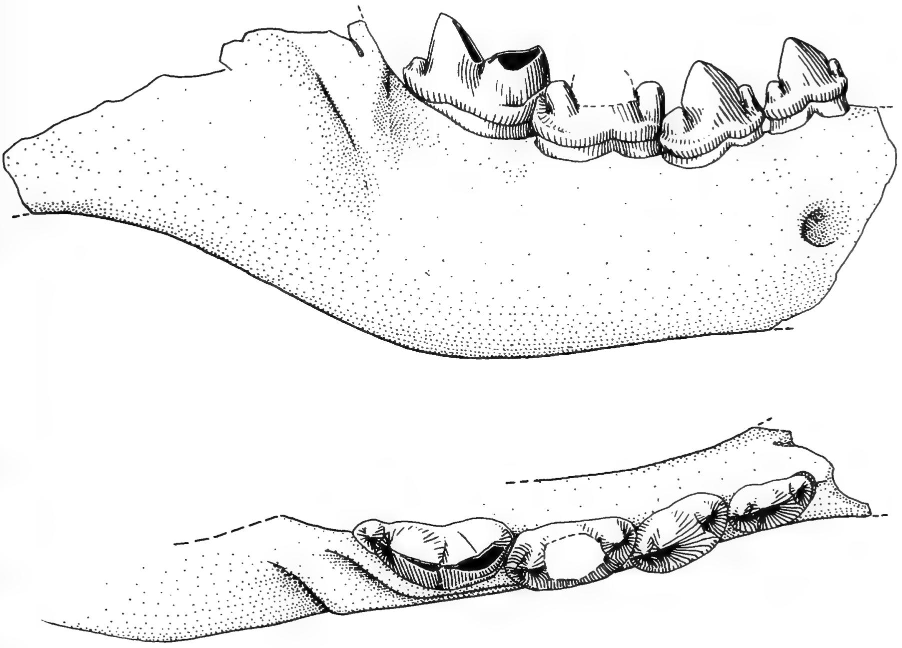


Fig. 10. Lateral and occlusal views of *Chasmaporthetes nitidula* hemimandible from Swartkrans (Transvaal Museum SK14005). (80% of natural size.)

TABLE 4

Some characteristics of the lower teeth and jaws in *Adcrocuta*, *Chasmaporthetes* and *Euryboa*

	late Miocene *Adcrocuta eximia variabilis* (China)	latest Miocene/ early Pliocene *Adcrocuta australis* (Langebaanweg)	'Early Pleistocene' *Chasmaporthetes kani* (China)	late Plioce *Chasmaporth* *lunensis* (Saint-Valli
Shape of jaw (ventral view)	straight (?or curved)	straight or curved	?	curved
Shape of cheektooth row (occlusal view)	curved	curved	curved	curved
Canine height	low	low	?	low
Shape of P_3	rectangular	rectangular	ovate	ovate
Anterior accessory cusps of P_2 and P_3	sometimes absent	sometimes absent	sometimes absent	present
M_1 talonid	bicuspid or unicuspid	unicuspid	unicuspid	unicuspid

represented of the later African forms is '*Euryboas*' *nitidula* from Swartkrans, which Galiano & Frailey (1977) believe may be a *Chasmaporthetes*. In their view referral to this genus would be more certain if 'the condition of P^1 and the degree of curvature of the tooth rows' were known (Galiano & Frailey 1977: 9). The condition of P^1 is still not known, although it may well have been absent, but the tooth rows, and jaws, are curved (Fig. 10), as in *Chasmaporthetes*. The case for referral of '*E.*' *nitidula* to *Chasmaporthetes* is thus strengthened and the Swartkrans species is here recognized as *Chasmaporthetes nitidula*.

The date when *Chasmaporthetes* entered Africa is not known, but it may have postdated its entry into Europe. That unit of the Swartkrans fauna which includes *C. nitidula* dates back about 1,5 m.y. (Vrba 1976), which makes it one of the youngest records of the genus, another being the *C. ossifragus* from Inglis IA in Florida (Webb 1974). There is thus evidence that in Africa *Chasmaporthetes* survived longer than *Euryboas*.

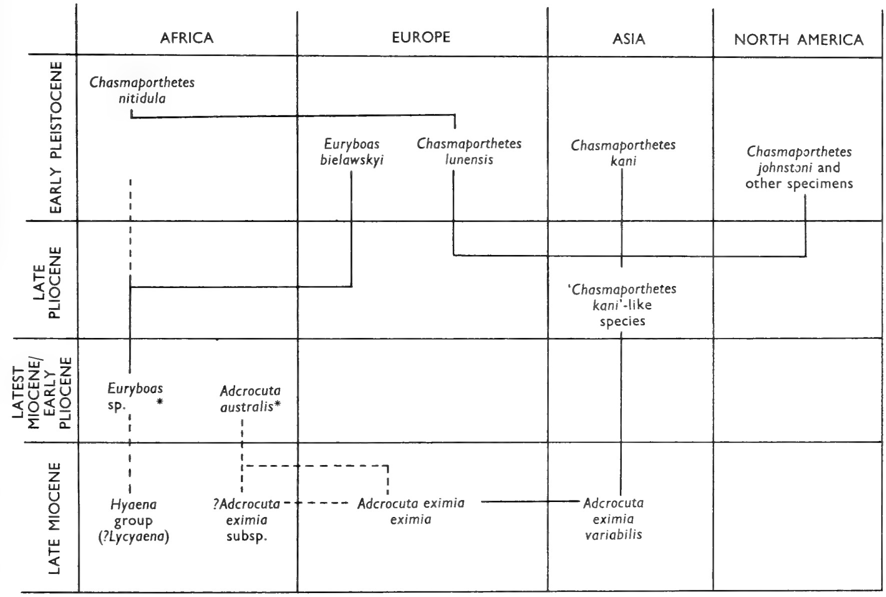
Present indications are that *Chasmaporthetes* was the more widespread, and ultimately also the more successful of the two 'hunting hyaena' genera. It was, in fact, the most widely distributed of all hyaenids, having occurred over much of North America as well as the Old World.

The interrelationships of *Adcrocuta*, *Chasmaporthetes* and *Euryboas* as interpreted here are summarized in Figure 11, while some of their more significant characters from a phylogenetic point of view are listed in Table 4. *Chasmaporthetes ? borissiaki* is omitted owing to the uncertainties surrounding it.

The discovery of additional specimens of different ages and from different geographical locations, and accurate dating of specimens already known, should allow testing of the opinions expressed in this paper. The recent dis-

te Pliocene *smaporthetes* *johnstoni* ta Canyon)	early Pleistocene *Chasmaporthetes* *ossifragus* (Inglis IA)	early Pleistocene *Chasmaporthetes* *nitidula* (Swartkrans)	latest Miocene early Pliocene *Euryboas* sp. (Langebaanweg)	late Pliocene *Euryboas* *bielawskyi* (Roccaneyra)
ved	curved	curved	straight	straight
ved	curved	curved	straight	straight
	?	low	high	high
te	ovate	ovate	rectangular	rectangular
sent	present	present	absent	absent
cuspid	unicuspid	unicuspid	bicuspid	unicuspid

coveries at Langebaanweg and identification of the first Asiatic *Chasmaporthetes* have already clarified the situation to some extent and no doubt more relevant material will still come to light.



*Langebaanweg species

Fig. 11. Tentative phylogeny of *Euryboas* and *Chasmaporthetes*.

TABLE 4

Some characteristics of the lower teeth and jaws in *Adcrocuta*, *Chasmaporthetes* and *Euryboas*.

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Shape of jaw (ventral view)	straight (?or curved)	straight or curved	?	curved	curved	curved	curved	straight	straight
Shape of cheektooth row (occlusal view)	curved	curved	curved	curved	curved	curved	curved	straight	straight
Canine height	low	low	?	low	low	?	low	high	high
Shape of P_3	rectangular	rectangular	ovate	ovate	ovate	ovate	ovate	rectangular	rectangular
Anterior accessory cusps of P_2 and P_3	sometimes absent	sometimes absent	sometimes absent	present	present	present	present	absent	absent
M_1 talonid	bicuspid or unicuspid	unicuspid	unicuspid	unicuspid	unicuspid	unicuspid	unicuspid	bicuspid	unicuspid

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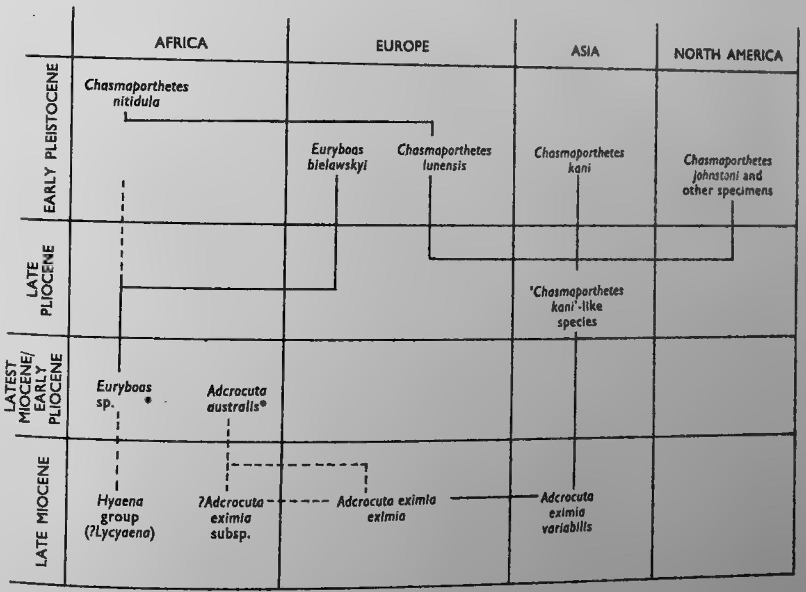

*Langebaanweg species

Fig. 11. Tentative phylogeny of *Euryboas* and *Chasmaporthetes*.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

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

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

Note punctuation in the above example:
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figures of plates are enclosed in parentheses to distinguish them from text-figures
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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
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(c) Scientific names, but not their vernacular derivatives
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Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

Q. B. HENDEY

LATE TERTIARY HYAENIDAE FROM LANGEBAANWEG, SOUTH AFRICA, AND THEIR RELEVANCE TO THE PHYLOGENY OF THE FAMILY

VOLUME 76 PART 8 SEPTEMBER 1978 ISSN 0303-2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

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

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(e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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(continued inside back cover)

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A FRAGMENTARY SPECIMEN OF *SAURICHTHYS* SP. FROM THE UPPER BEAUFORT SERIES OF SOUTH AFRICA

By

JOHN GRIFFITH

Cape Town Kaapstad

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A FRAGMENTARY SPECIMEN OF *SAURICHTHYS* SP. FROM THE UPPER BEAUFORT SERIES OF SOUTH AFRICA

By

John Griffith

Westfield College, University of London

(With 1 figure)

[*MS. accepted 18 July 1978*]

ABSTRACT

The tip of an elongate jaw, found in association with the holotype of the amphibian *Capitosaurus africanus*, is identified as belonging to the actinopterygian genus *Saurichthys*. This is the first record of the family Saurichthyidae from the mainland of Africa; an additional point of interest is its almost certain freshwater provenance.

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INTRODUCTION

The specimen was discovered by Mrs Ione Rudner of the South African Museum during preparation of the holotype of the amphibian *Capitosaurus africanus* Broom, 1909 (SAM–2360). It lay in the right interpterygoid vacuity of the amphibian skull roughly at the same level as, but not in contact with, the ventral surface of the palatal bones. The protection so afforded is probably responsible for its preservation, but it is not possible to determine if there is any other significance in the association.

The specimen was subsequently freed of matrix by Mrs Rudner and tentatively identified as belonging to the genus *Saurichthys* by Dr J. Cosgriff, of Wayne State University, Detroit, U.S.A.

LOCALITY AND HORIZON

The *Capitosaurus* skull was collected by Broom from the *Cynognathus* beds of Farm Vaalbank, near Burgersdorp (Broom 1909). The Cynognathus zone comprises the whole of the Upper Beaufort Series (Broom 1932; Hotton 1967) and, according to Harland *et al.* (1967), is of Lower Triassic (Olenekian) age.

Ann. S. Afr. Mus. **76** (8), 1978: 299–307, 1 fig.

DESCRIPTION

Order SAURICHTHYIFORMES
Family **Saurichthyidae**

Genus *Saurichthys* Agassiz, 1834
Saurichthys sp. indet.

The specimen (SAM–2360*a*) consists solely of the incomplete tip of an elongate jaw. It measures 11,8 mm in length and roughly 3,6 mm in width. In dorsal and ventral view (Fig. 1) the anterior end appears roughly rounded and behind this the two sides are more or less parallel. In lateral view the jaw is slightly curved and decreases in height anteriorly so that, whereas the tooth-bearing surface is almost flat, the opposite surface shows a more pronounced curvature that increases towards the anterior end.

The external surfaces show traces of a weak ornamentation of short, mainly longitudinal, ridges. There is no sign of a sensory canal.

The oral surface bears a narrow median ridge that projects slightly above the general level of the bone and, in places, seems to show an indistinct longitudinal suture-line. On either side of this ridge lie four large teeth or tooth-bases, arranged more or less symmetrically, and between these a number of less regularly arranged, smaller teeth. All, except one of the smallest, were damaged or missing before fossilization.

The larger teeth lie in pairs, one on each side of the midline. Their bases occupy the whole width between the median ridge and the edge of the jaw. They are conical in shape and inclined away from the sagittal plane but with a slight medial curvature so that their apices must have lain vertically above, or below, the jaw edge. The anterior pair, in addition, project slightly forwards. The remains of the best preserved large tooth measure 2,8 mm in height; when intact it must have been at least 0,5 mm taller. The apical part of the tooth is more transparent than the rest and is ornamented with fine, closely-spaced, parallel striations running in an apical-basal direction. This part is marked off from the remainder of the tooth by a barely visible groove and is estimated to have accounted for slightly more than one-third of the total height. The surface of the rest of the tooth is practically smooth except for moderate plication near the region of attachment to the underlying bone.

The small teeth are less than half the height of the large ones, about twice as numerous, and occur either singly or in groups of two or three along the edge of the jaw in the gaps between the large teeth. They appear to have been similar in shape and structure to the larger teeth but all except one are broken and abraded. The smallest tooth of all (arrowed in Fig. 1) is intact and, though no surface detail can be made out in this tooth either, examination by transmitted light with the specimen immersed in cedar-wood oil reveals some details of its internal structure. There is a distinct apical cap of clear material which is moderately birefringent and contains few tubules and is therefore identified as enameloid (Schaeffer 1977) or modified dentine (Peyer 1968). The remainder of the tooth consists of orthodentine with the characteristic, numerous, closely-spaced dentine tubules radiating from a central pulp cavity. This part shows only very slight optical activity between crossed polarizers. The pulp cavity, in its distal half at least, is relatively narrow and ends just short of the amelodentinal junction. The proximal part of the tooth is too opaque for much detail to be distinguished.

The broken end of the specimen is roughly D-shaped with a single, small,

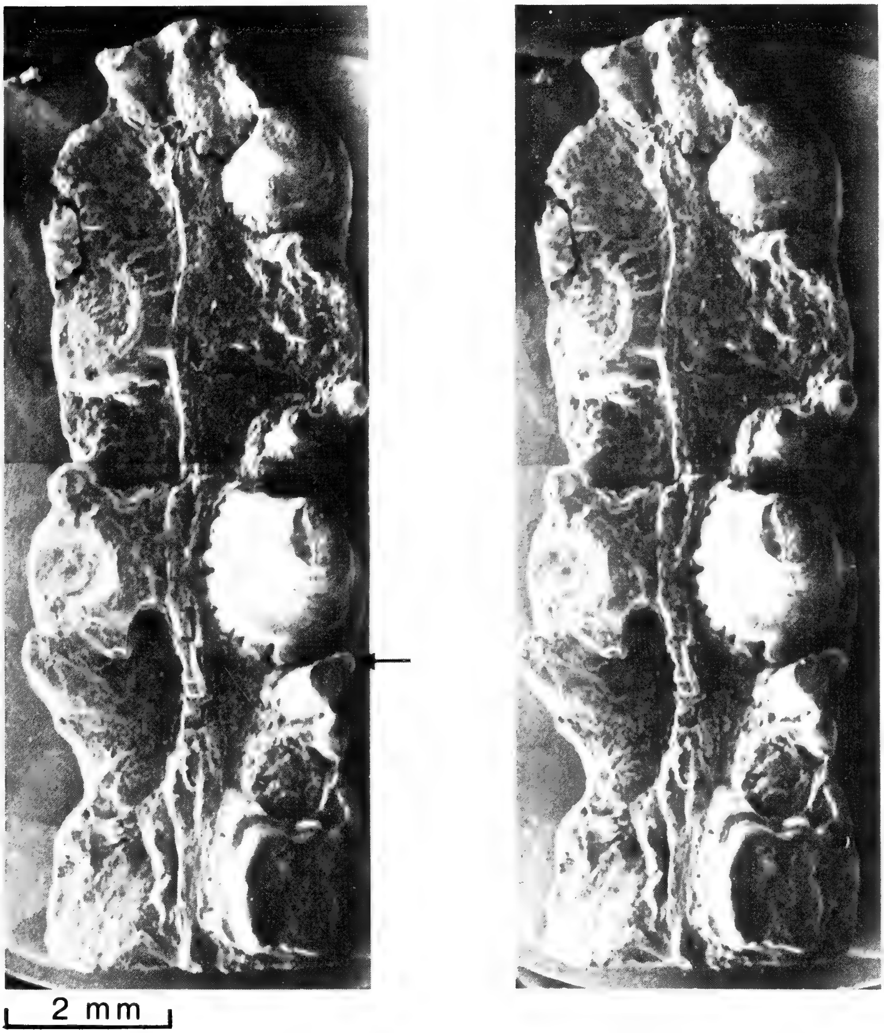

Fig. 1. Stereoscopic pair of scanning electron microscope photographs of specimen SAM–2360*a* in oral view. The arrow points to the small tooth referred to in the text.

nearly circular central cavity infilled with calcite. The bone is relatively thick but compact and shows no sign of endochondrial origin.

IDENTIFICATION

The presence of a distinct apical cap of enameloid or modified dentine clearly shows that the specimen belongs to an actinopterygian fish (Peyer 1968). With this and the conspicuous elongation of the jaw in mind there appear to be only four reasonable possibilities, that it is from: (i) a saurichthyid; (ii) an aspidorhynchid; (iii) an early representative of one of the several groups of long-jawed euteleosts; or (iv) a species unrelated to any of the known fishes with elongate jaws. These alternatives will be considered in order.

(i) In the family Saurichthyidae the two jaws are more or less equal in length. The anterior end of the upper jaw appears to be composed almost entirely of the premaxillae (rostalo-premaxillaries in Stensiö's (1925) nomenclature). These are curved transversely so as to form a tapering, hollow half-cylinder that is completed ventrally by the horizontal dental lamellae which extend medially to meet the lateral edges of the slender vomers. The resulting structure has a single cavity, as in specimen SAM–2360*a*. It seems unlikely that the vomers extended right to the tip of the jaw, and here the two premaxillae must have met ventrally as well as dorsally. Stensiö (1925) suggests that separate rostral and, or, postrostral elements were also involved but, whatever the ontogeny of this region, none of the numerous specimens belonging to several species examined by the author shows any sign of sutures dorsally though suggestions of a midventral suture are occasionally visible. The anterior end of the lower jaw appears to have been formed in a closely analogous manner from the dentaries (dentalosplenials) with a minor contribution from the coronoids (mixicoronoids) paralleling that of the vomers to the upper jaw. According to Stensiö (1925) in *Saurichthys hamiltoni* the two mandibular rami meet in a very long, rigid symphysis but do not coalesce and a distinct median ventral suture persists. However, in most species in which this region is known no sutures are visible and the tip of the mandible is so similar, apart from its inversion, to the corresponding part of the upper jaw that it is impossible to distinguish them on morphological grounds alone.

The ethmoidal and mandibular sensory canals have never been traced right to the tips of the jaws in any species and may have ended some distance short of this.

In nearly all species in which the dentition is known each half of each jaw carries a single series of fairly evenly spaced, large teeth interspersed with less regularly arranged, smaller teeth and these tooth-rows extend right to the tips of the jaws. Again there is no observable difference between upper and lower jaws. The teeth themselves do show some interspecific differences but in general are perfectly compatible in shape, proportions, ornamentation and structure with those of the specimen described above.

There are, at present, four valid genera in the family Saurichthyidae:

Saurichthys; *Saurorhynchus* Reis, 1892; *Brevisaurichthys* Beltan, 1972; and *Systolichthys* Beltan, 1972.

The genus *Saurichthys*, which contains at least thirty-five species ranging throughout the Triassic, has never been adequately defined because of the fragmentary nature of the material of the type species, *Saurichthys apicalis* Agassiz, 1834. However, several of the species ascribed to this genus are known in some detail and nothing that the author has been able to discover suggests that the specimen SAM–2360*a* does not belong to this genus.

The genus *Saurorhynchus* contains two Lower Jurassic species. Though not a diagnostic character, as it is shared with at least one species of *Saurichthys*, both species of *Saurorhynchus* show the presence of 'incissivlucken', distinct depressions in the bone of the jaw into which the apices of the large teeth of the opposite jaw fitted in occlusion. The absence of this feature in the specimen under discussion argues against it belonging to this genus.

The genera *Brevisaurichthys* and *Systolichthys* were erected by Beltan (1972) each to contain a single new species from the Middle Triassic (? Ladinian) of Spain. In both of these genera the elongation of the head is noticeably less than in *Saurichthys* and *Saurorhynchus* and the relatively obtuse ends to the jaws make it unlikely that SAM–2360*a* belongs to either.

(ii) In the family Aspidorhynchidae the upper and lower jaws are dissimilar in structure. In most species the head is continued beyond the anterior limit of the mouth as a slender, tapering rostrum which is roughly circular in cross-section and is toothless for all, or nearly all, of its length. In a few species, e.g. *Aspidorhynchus tenuirostris* Agassiz, 1833, there is no rostrum, strictly speaking, and both jaws extend to the anterior end of the head. In these species the major part of the upper jaw is formed, as in the Saurichthyidae, from the elongated premaxillae but each premaxilla is rolled into a complete, hollow cylinder and, though these meet and fuse dorsally, they remain separated ventrally for most, if not all, of their length, so forming a median groove for the reception of the presymphysial teeth. The detailed structure of the extreme tip of the upper jaw of these species is poorly known but appears to consist of a half-cylinder grooved ventrally and with its interior filled with spongy (? endochondrial) bone; a short distance behind the tip the paired, cylindrical premaxillae can clearly be recognized, so that in cross-section the upper jaw shows either two cavities or none at all. The dentition of the upper jaw differs from that of the saurichthyids and of specimen SAM–2360*a* in the segregation of the teeth into rows or groups within which all neighbouring teeth are of roughly similar size. Thus the fused premaxillae bear two principal tooth-rows composed of relatively large teeth posteriorly and these decrease in size gradually and evenly towards the tip of the jaw; smaller teeth are present on the posterior part of the premaxillae in some species but these are confined to separate rows flanking the larger teeth and never extend into the anterior part of the bone.

The anterior end of the lower jaw is formed by a single, median presymphysial bone which carries a highly distinctive dentition consisting of a single, median row of large teeth flanked posteriorly, in some species only, by one or two separate rows of much smaller teeth on either side.

The earliest known aspidorhynchid comes from the Bathonian Stage of the Middle Jurassic which does leave an appreciable time-gap, but quite apart from this it seems fairly obvious on anatomical grounds that specimen SAM–2360*a* cannot possibly belong to an aspidorhynchid.

(iii) The Euteleostei (Division III of Greenwood *et al.* 1967) include a number of fishes in which the jaws show conspicuous elongation.

In the living Belonidae (garfishes) the jaws are roughly equal in length and toothed throughout. The anterior end of the upper jaw is narrower than the corresponding part of the lower jaw and fits partly within it during occlusion. The upper jaw is formed, as in the other families described above, mainly from the elongate premaxillae, each of which is completely rolled upon itself prior to joining with its fellow so that in cross-section this jaw displays two cavities, one on each side of the midline, and, moreover, is roughly oval in shape. The lower jaw is roughly W-shaped in section with a well-developed median ridge separating two deep channels into which the teeth of the upper jaw fit. The teeth, though sharply pointed, are all relatively small and confined to the edges of the jaws. As in the Aspidorhynchidae, larger and smaller teeth are segregated and do not intermingle in the same row, and the smaller teeth do not extend to the anterior ends of the jaws. In the closely related Hemirhamphidae (half-beaks) only the mandible is elongated and this projects beyond the upper jaw as a toothless pseudorostrum. The geological record of the suborder Exocoetoidei, to which these fishes belong, is only known with certainty to extend back to the Middle Eocene though there is a doubtful record from the Cretaceous (Maestrichtian) (Patterson 1967).

The extinct suborder Alepisauroidei Rosen, 1973, contains several Upper Cretaceous genera with greatly elongated jaws. In *Ichthyotringa* Cope, 1878, *Apateopholis* Woodward, 1891, and *Dercetis* Agassiz, 1834, the two jaws are of roughly equal length; in *Rhynodercetis* Arambourg, 1944, the upper jaw is considerably longer than the lower and so forms a true rostrum. In all, the anterior part of the upper jaw is formed largely from the premaxillae with contributions from the mesethmoid, vomer and palatines, and the anterior part of the lower jaw from the dentaries (Goody 1969). The dentition in all four genera is unlike that of specimen SAM–2360*a*. In *Ichthyotringa* each half-jaw has a row of modestly-sized conical teeth and lateral to this a completely separate marginal row of minute teeth. In *Apateopholis* the premaxillary and dentary teeth are all extremely small. *Dercetis* has small, needle-like hollow teeth with peculiar apecies, and on the dentary these teeth are arranged in clusters not rows. *Rhynodercetis* has no teeth at all on the premaxillae and only small teeth on the dentary.

The Xiphiidae (swordfishes) and Istiophoridae (marlins and sailfishes) have conical rostra which project for some distance beyond the mandibles. Their lower jaws are slightly elongated but remain more or less normal in appearance and the anterior ends do not resemble SAM–2360*a*. The premaxillae are toothless for all or most of their length. Dentary teeth are either minute or absent.

The extinct family Palaeorhynchidae, grouped with the xiphiids and istiophorids in the suborder Scombroidei, contains two Lower Tertiary genera: *Palaeorhynchus* Blainville, 1818, with jaws of roughly equal length; and *Hemirhynchus* Agassiz, 1844, in which the lower jaw is shorter than the upper. In both genera the anterior parts of upper and lower jaws are circular in cross-section, solid and completely devoid of teeth.

The Upper Cretaceous and Eocene Blocidae are poorly known and, though they, too, were at one time included in the suborder Scombroidei, Patterson (1973) regards their affinities as uncertain. The upper jaw is extended into a rostrum which, according to Woodward (1901), 'resembles a pair of tubes pressed together'. The mandible is only about two-thirds of the length of the upper jaw and rostrum; very little is known of its structure. Teeth are either very minute or absent altogether.

None of the above shows sufficient resemblance to specimen SAM–2360*a* to indicate close affinity and, in any case, none can be traced backwards in time beyond the Upper Cretaceous, and it seems extremely unlikely that a representative of one of these groups, or indeed any euteleost, should have been in existence in Lower Triassic times.

(iv) The specimen may not be closely related to any of the groups discussed above. It could belong to a specialized offshoot of a group of more normal-shaped fishes, or may represent a hitherto unknown group of long-jawed fishes. As the only derived character shown by the specimen, namely the great elongation of the jaw, appears to have been independently acquired in a number of phyletic lines such speculations are impossible to prove or disprove. On the other hand, as all the observed features can be accounted for by the assumption that the specimen belongs to a species of the genus *Saurichthys* (see (i) above), these hypotheses are unnecessary and must be rejected in the interests of parsimony.

In conclusion, in all of the observed features specimen SAM–2360*a* agrees with, or falls within the range of structure shown by, the genus *Saurichthys*. There is not sufficient information to determine if it is part of an upper or of a lower jaw, to identify it as belonging to a known species of *Saurichthys*, or to warrant its description as a new species of that genus. It differs from each of the other taxa considered above in at least one character. It is unnecessary to postulate that it belongs to some previously unknown genus. The specimen is therefore determined as *Saurichthys* sp. indet.

REMARKS

There are two points which are perhaps worthy of brief comment:

(i) This is the first record of the Saurichthyidae from the mainland of Africa. According to the palaeocontinental maps produced by Smith & Briden (1977) the geographically nearest occurrences (in Triassic times) so far known are, in order: *Saurichthys madagascariensis* Piveteau, 1944, and *S. stensioi* Lehman, 1952, from the Lower Triassic (Induan) of Madagascar; *S. gigas* and *S. gracilis* (both first described by Woodward in 1890) from the Lower or Middle Triassic, and *S. parvidens* Wade, 1935, from the Middle Triassic of New South Wales, Australia; numerous Lower, Middle and Upper Triassic and Lower Jurassic species from Europe. The saurichthyids appear to have had an almost world-wide distribution and their previous absence from records for South Africa probably merely reflects the paucity of fossiliferous marine deposits of suitable age.

(ii) The Upper Beaufort Series are generally accepted as being continental freshwater fluviatile and lacustrine deposits and, though Hotton (1967) suggests that these conditions alternated with persistent deltaic ones, Rayner (1971) regards this hypothesis as untenable. The saurichthyids appear to have been predominantly marine though a few species have been recorded from deposits thought to have been laid down under fresh or 'brackish' water conditions. Specimen SAM–2360*a* could have been reworked from earlier, marine beds such as the marine phases of the Ecca or Dywka Series, but as no saurichthyid has ever been recorded there this seems improbable. It therefore appears that some species of saurichthyid were at least capable of temporary excursions into fresh water and may even have lived there permanently.

ACKNOWLEDGEMENTS

I wish to record my gratitude to the Director of the South African Museum for the loan of the specimen and to Dr M. A. Cluver for bringing it to my attention and for a helpful correspondence. I am also indebted to Mrs M. Petri for taking the scanning electron microscope photographs reproduced here as Figure 1.

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

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figures of plates are enclosed in parentheses to distinguish them from text-figures
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Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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

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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) . . .'

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Reference to the author should be expressed in the third person

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

JOHN GRIFFITH

A FRAGMENTARY SPECIMEN OF *SAURICHTHYS* SP. FROM THE UPPER BEAUFORT SERIES OF SOUTH AFRICA

VOLUME 76 PART 9 SEPTEMBER 1978 ISSN 0303-2515

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(c) *Table of contents* giving hierarchy of headings and subheadings
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TWO NEW SPECIES OF *GASTROSACCUS* (CRUSTACEA, MYSIDACEA) FROM SANDY BEACHES IN TRANSKEI

By

T. WOOLDRIDGE

Cape Town Kaapstad

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TWO NEW SPECIES OF *GASTROSACCUS* (CRUSTACEA, MYSIDACEA) FROM SANDY BEACHES IN TRANSKEI

By

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Department of Zoology, University of Port Elizabeth

(With 8 figures)

[*MS. accepted 2 August 1978*]

ABSTRACT

Sampling by means of a sledge from the low-water mark out to a depth of 1,5 m showed clear peaks of maximum distribution for *Gastrosaccus bispinosa* sp. nov. which was more abundant at the upper limit of the low-water mark. *Gastrosaccus longifissura* sp. nov. was more common in the breaker zone. Both species were also collected in the more sheltered waters along the edge of the sandbank inside the mouth of the Mgazana estuary.

The known distribution of *Gastrosaccus psammodytes* Tattersall, 1958, is extended further eastwards as far as Kei Mouth. The appearance of *G. psammodytes* in off-shore plankton samples is discussed. A note on the distribution and a key to the species of *Gastrosaccus* recorded in southern Africa are given.

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INTRODUCTION

Two new species of *Gastrosaccus* (Crustacea, Mysidacea) from sandy beaches in Transkei are described and illustrated. *G. psammodytes* is described from South Africa (Tattersall, O. S. 1958) while other sandy beach mysids are known from various parts of the world. *G. vulgaris* is reported from Japan (Nakazawa 1910) while Gauld & Buchanan (1956) have recorded *G. spinifer* on sandy beaches in Ghana. Macquart-Moulin (1977) notes the distribution of *G. mediterraneus* and *G. spinifer* along Mediterranean sandy shores. *G. sanctus* is known from sandy beaches in the northern hemisphere (Băcescu 1934; Tattersall, W. M. 1927; Tattersall & Tattersall 1951; Moran 1972). In southern Africa *G. sanctus* is recorded from inshore waters (Lazarus 1975) and off-shore waters only (Tattersall, O. S. 1957). Other reports of mysids from sandy beaches are noted by Brown & Talbot (1972).

The two new species reported here are recorded from sandy beaches at Mbotyi (31°28′S) and at Mgazana (31°41′S) on the Pondoland coast, Transkei

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(Fig. 1). *G. longifissura* sp. nov. is also recorded from Kei Mouth (32°41′S), South Africa (Fig. 1), where it occurred with *G. psammodytes*.

The present species overlapped along a 70 m transect into the breaker zone. Sampling was done with a sledge from the low-water mark out to a depth of 1,5 m. Beyond the 1,5 m depth contour, sampling with the sledge apparatus was not possible due to excessive turbulence. Along the transect clear peaks of maximum distribution were evident for each of the two species. *G. bispinosa* sp. nov. was more abundant at the upper limit of the low-water mark, while *G. longifissura* sp. nov. was more common in the breaker zone.

Both species were also collected along the edge of the sandbank inside the mouth of the Mgazana estuary. At night they were taken in the breaker zone with a plankton net (WP 2 net of 190 micron aperture towed by hand in water of 1 to 1,5 m depth). They were absent in surface plankton samples taken at

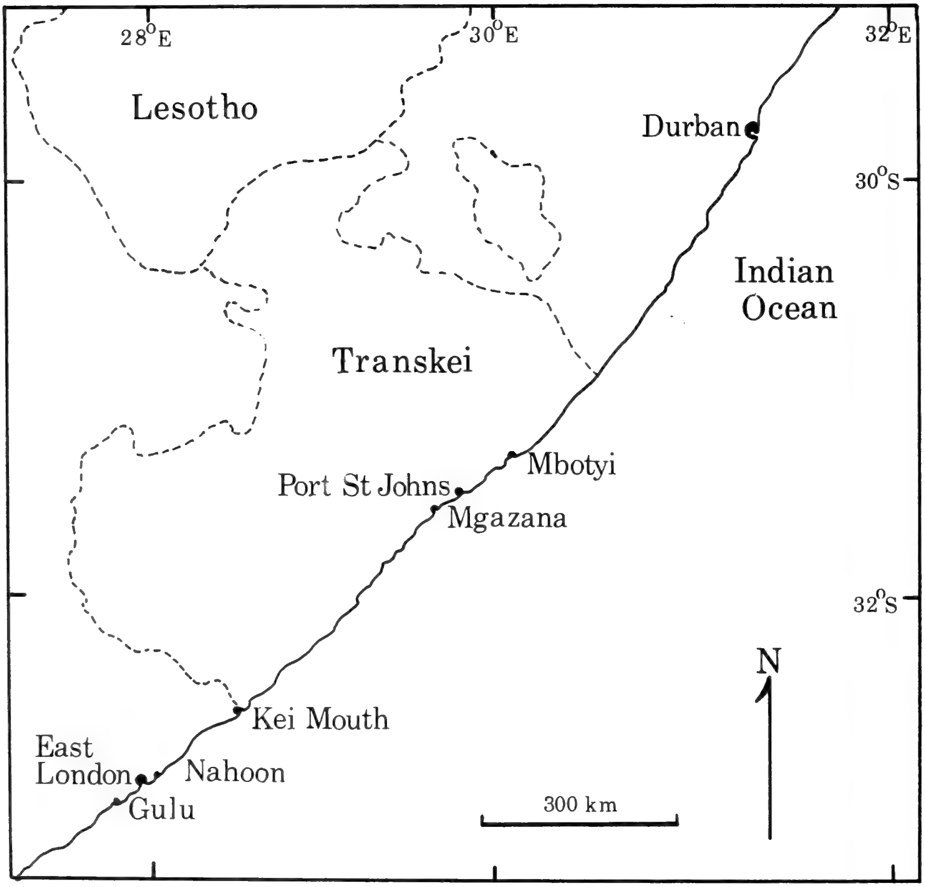

Fig. 1. Map of the coastline indicating the position of the localities mentioned in the text.

night in the mouth channel of the estuary (samples collected on ten occasions between 1971 and 1973), except in September 1972 when two specimens of *G. bispinosa* sp. nov. were captured (Wooldridge 1977).

DESCRIPTION OF MATERIAL

Gastrosaccus bispinosa sp. nov.

Figs 2–5

Holotype

SAM–A15749 lodged in the South African Museum, Cape Town. Adult female from Mgazana beach (31°42′S), collected by T. Wooldridge, 30 September 1977.

Paratypes

SAM–A15750 lodged in the South African Museum, Cape Town. Numerous adult males and adult females from Mgazana beach (31°42′S), collected by T. Wooldridge, 30 September 1977.

Description

Carapace long, anterior margin produced into a triangular rostrum not covering the eyestalks (Fig. 2A). Apex smoothly rounded. Posterior margin of carapace emarginate, exposing the last thoracic somite. Posterior half of this emargination forming a forwardly directed lobe which overlaps the more proximal portion of the emargination on each side. In lateral view carapace extends posteriorly to cover the whole of the thorax and the first abdominal somite.

Antennule (Fig. 4A), first segment of peduncle slightly shorter than second and third combined. Five or six small setae on outer distal angle. Second segment of peduncle short and armed with three strong spines set obliquely along its outer margin. Inner distal corner with a fine seta. Third segment relatively slender, bearing a curved finger-shaped process on dorsal side at the anterior end. A small spine present just posterior to the process. Outer flagellum swollen at the base and bearing relatively long, flattened setae. In the male the usual hirsute lobe present.

Antennal peduncle extending slightly beyond the distal end of the second segment of the antennular peduncle (Fig. 2A). The second segment of antennal peduncle about two and a half times as long as the third, bearing five plumose setae on the inner margin and two setae on the inner distal angle (Fig. 2B). Third segment with four plumose setae on inner margin and four and two smaller plumose setae on the inner and outer distal corners respectively. Antennal scale as long as peduncle and about three times as long as broad. Outer margin straight, naked, terminating in a strong spine which does not extend beyond the rounded apex of the scale. Inner margin convex and setose (Fig. 2B).

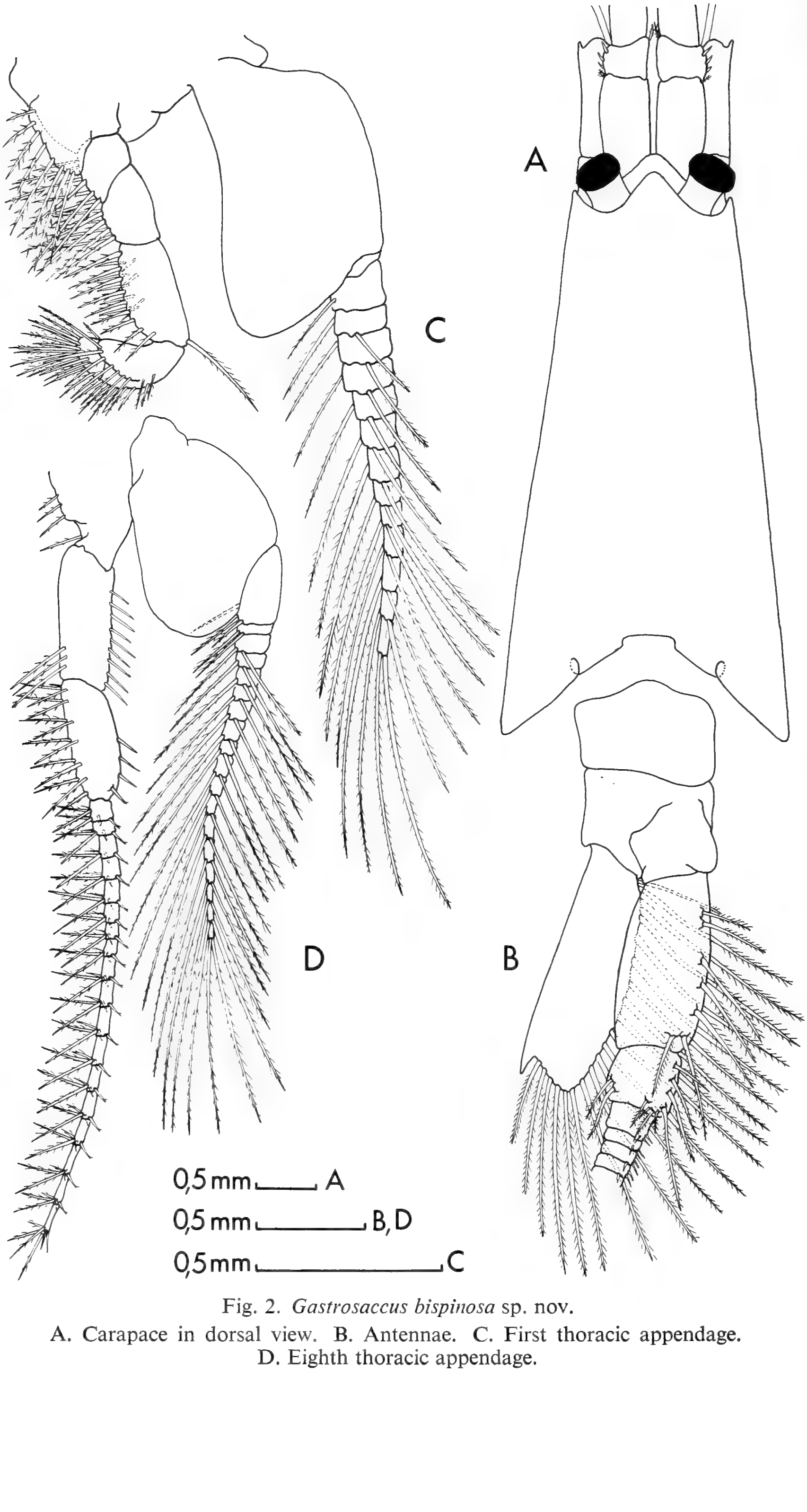

Fig. 2. *Gastrosaccus bispinosa* sp. nov.
A. Carapace in dorsal view. B. Antennae. C. First thoracic appendage. D. Eighth thoracic appendage.

Mandible (Fig. 3A) well developed without spine row. Palp long and slender, first segment unarmed. Second and third segments extremely setose, the third segment with a terminal comb-like process and two strong apical spines.

Maxillule (Fig. 3B) three segmented, first and second segments appear to be fused. Lobe from first segment with three short serrated spines and three longer spines armed with a row of fine setae and four to six teeth distally. Third segment drawn out into a well-developed lobe which is armed with a close group of short, strong, spinous and slightly curved spines. Row of six serrated spines along the inner, sub-terminal margin which are setose proximally.

Maxilla (Fig. 3C) typical of the genus.

First thoracic limb with well-developed endite on basal segment (Fig. 2C). Endopod short and robust, densely setose along inner margin. A well-developed seta present on outer distal angle of carpus segment. Dactylus well developed, without claw. First segment of exopod large and expanded, the outer distal angle smooth (exopod twisted in figure). Flagellum fourteen-segmented, each segment with one or two long plumose setae.

Second thoracic limb similar in form to first, dactylus of endoped with claw. First exopod segment with a small tooth on outer distal angle.

Third to eight thoracic limbs similar in form, but becoming progressively stronger and longer posteriorly. Carpus and propodus of endopod fused and divided into many short subsegments. The number of these subsegments increases posteriorly as follows: in the third limb, ten; in the fourth, eleven; in the fifth, twelve; in the sixth, thirteen; in the seventh, sixteen; in the eighth, eighteen (Fig. 2D). Each subsegment bears a small brush of setae and a small spine on the inner distal angle, and a small spine on the outer distal angle. The first segment of exopod in third to seventh pairs of thoracic limbs large and armed with a strong tooth on outer distal corner. In the eighth pair of appendages this angle is smoothly rounded (Fig. 2D). Flagellum sixteen- to eighteen-segmented, each segment with one or two long plumose setae.

First pleoped of female (Fig. 4B) with long, slender sympod armed proximally with three, and distally with nine, long plumose setae. Exopod about twice as long as wide, armed with one spine-like seta, nine short plumose setae and two relatively long plumose setae at the distal end. Endopod almost four times as long as wide, armed with nine plumose setae distally. Remaining pleopods in the female in the form of simple, unjointed plates, becoming progressively longer on the posterior somites.

First pleopod of the male (Fig. 4D) with swollen sympod, outer margin armed with thirteen long plumose setae. Endopod short, unsegmented, with two terminal plumose setae and a single subterminal spine-like seta. Seven short plumose setae also present, their relative position illustrated in Figure 4D. Exopod composed of thirteen or fourteen segments, each segment armed with two unequal plumose setae.

Second pleopod of the male (Fig. 5A) with large rectangular sympod which

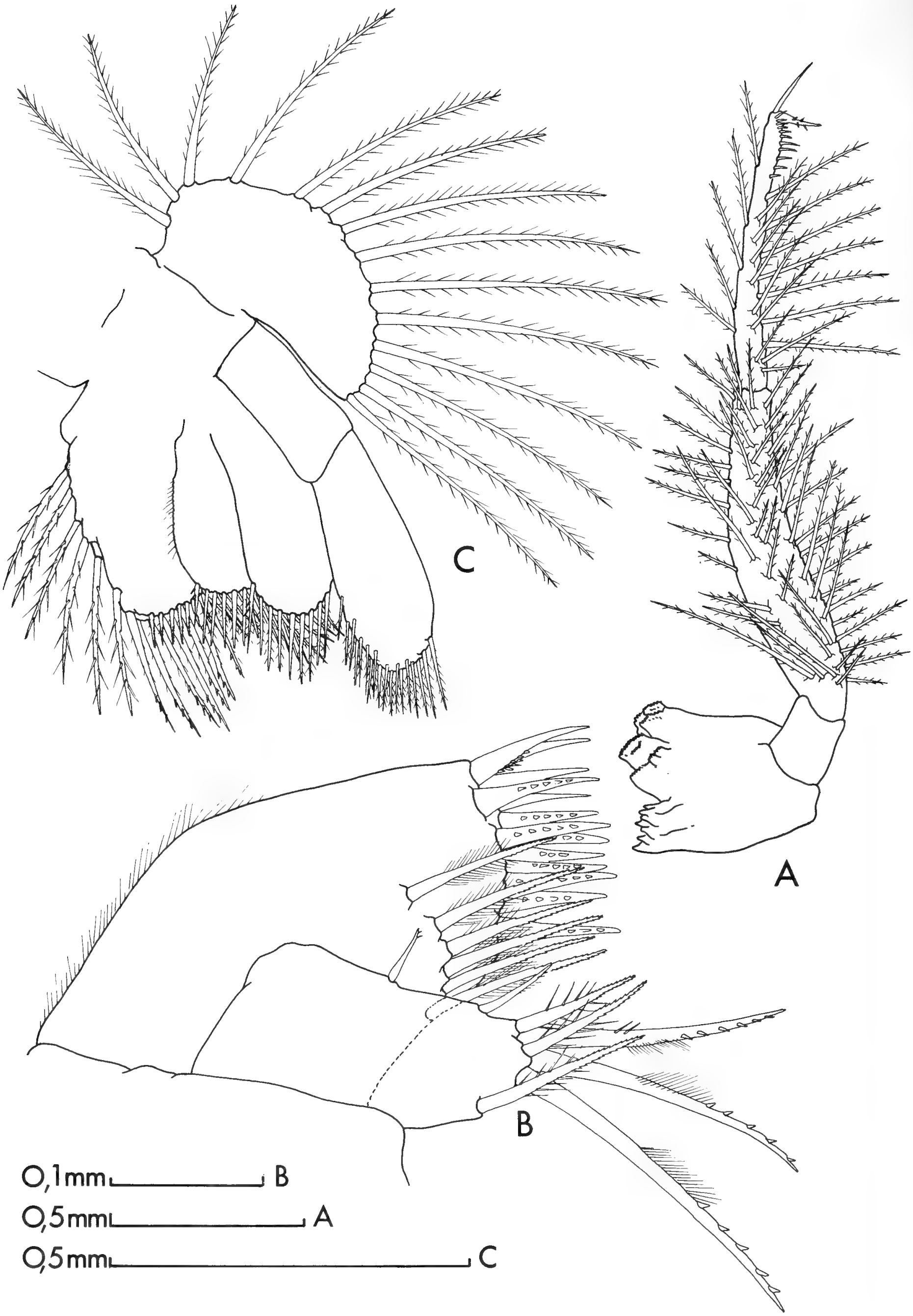

Fig. 3. *Gastrosaccus bispinosa* sp. nov.
A. Mandible. B. Maxillule. C. Maxilla.

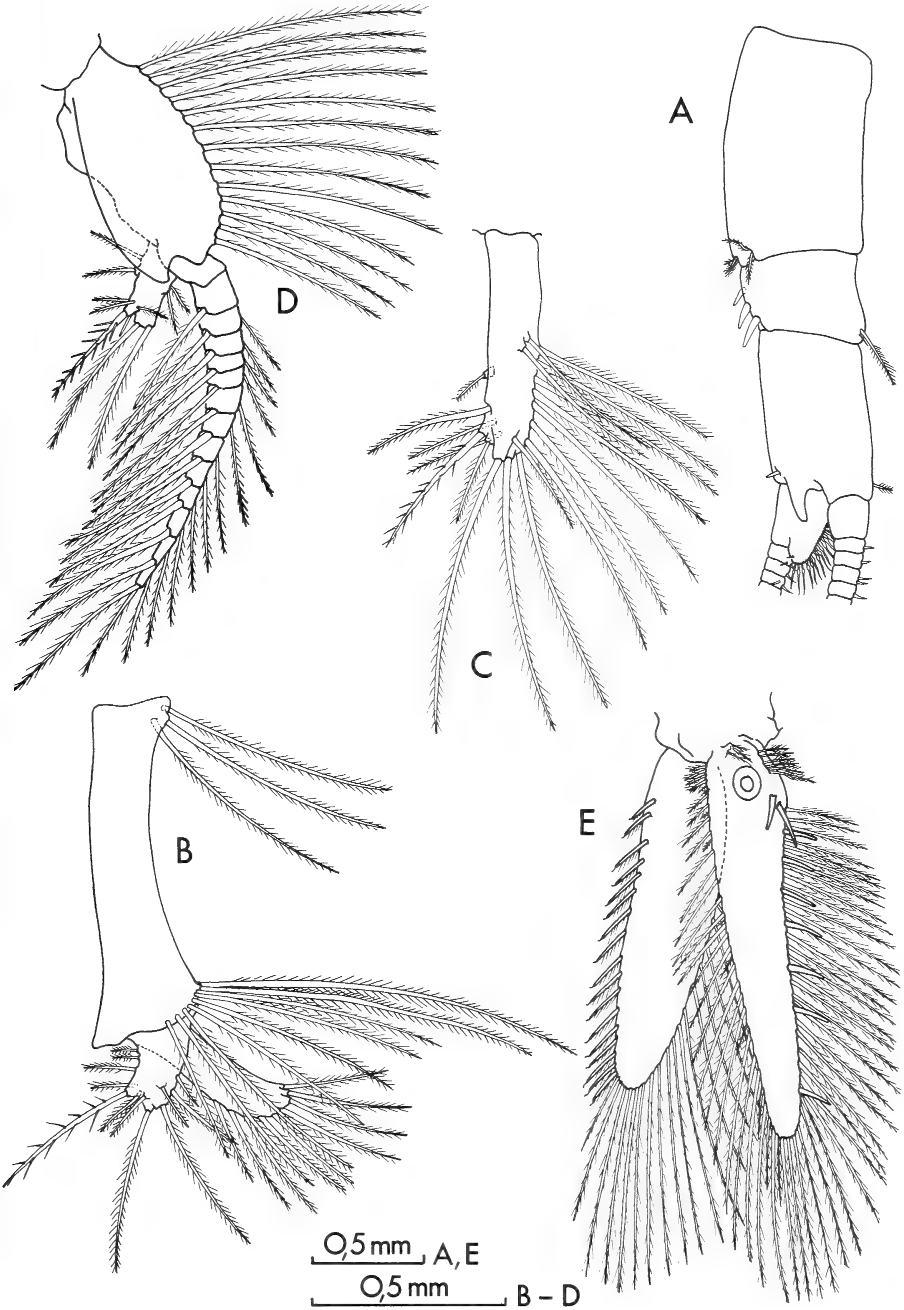

Fig. 4. *Gastrosaccus bispinosa* sp. nov.
A. Antennule. B. First pleopod of female. C. Second pleopod of female.
D. First pleopod of male. E. Uropod.

is indented on distal margin. Endopod eight-segmented and slender, subequal in length to sympod. A well-developed pseudobranchial lobe at base of first endopod segment, armed with a number of small plumose setae and one spine-like seta. Exopod robust, almost twice as long as endopod, setae along inner margin considerably shorter than those on outer margin.

Third pleopod of the male (Fig. 5B) with four-segmented endopod, the first segment large and bulbous, bearing a well-developed pseudobranchial lobe which is armed with a number of small plumose setae and a single spine-like seta. Second and third endopod segments small, each armed with two short plumose setae. The terminal segment of endopod reaching midpoint of first exopod segment, bearing two relatively long plumose setae. Exopod four-segmented, extending backwards to proximal end of the telson. First segment subequal in length to the second, which is about twice the length of the third. Fourth segment equal in length to the first segment. In some specimens a prominent protrusion along concave margin. Apex armed with two strong, barbed setae, the barbs of the one seta thin and spine-like, those on the other seta robust and considerably smaller in the distal half (Fig. 5C). Remaining pleopods in the male small, endopod reduced to a single segment.

Uropods (Fig. 4E) extending a short distance beyond telson. Exopod subequal in length to endopod, armed along outer margin with seventeen strong, regular spines which are finely plumose along the posterior margins. Apex of these spines with a short curved tip. Endopod more slender than exopod, tapering distally with seven long, curved irregularly-spaced spines amongst setae on inner margin. Two posteriorly directed spines present on inner side of statocyst. Anterior to the statocyst a row of small, graduated, closely set setae and a row of three small setae present. Outer margin of endopod with a row of plumose setae which increase in length posteriorly. Along the outer margin and set irregularly amongst the longer setae are a number of extremely short plumose setae.

Telson (Fig. 5D) about three times longer than its width at the base. Lateral margins armed with six strong spines of which the distal two on each side are longer than the others. Apical spines long and strong. Spaces between the last three lateral and terminal spines occupied with one to six small spinules which become more numerous distally. A strong spine present on each side of the cleft on the dorsal side. Cleft one-quarter of the length of the telson and armed with twenty to twenty-five spinules on either side. Spinules increase in length and robustness posteriorly.

Length

Adult female 13,3–17,5 mm
Adult male 11,0–14,5 mm

Remarks

Gastrosaccus bispinosa shows small affinities to *Gastrosaccus gordonae* Tattersall, 1952. It is readily distinguished, however, by the prominent spine on

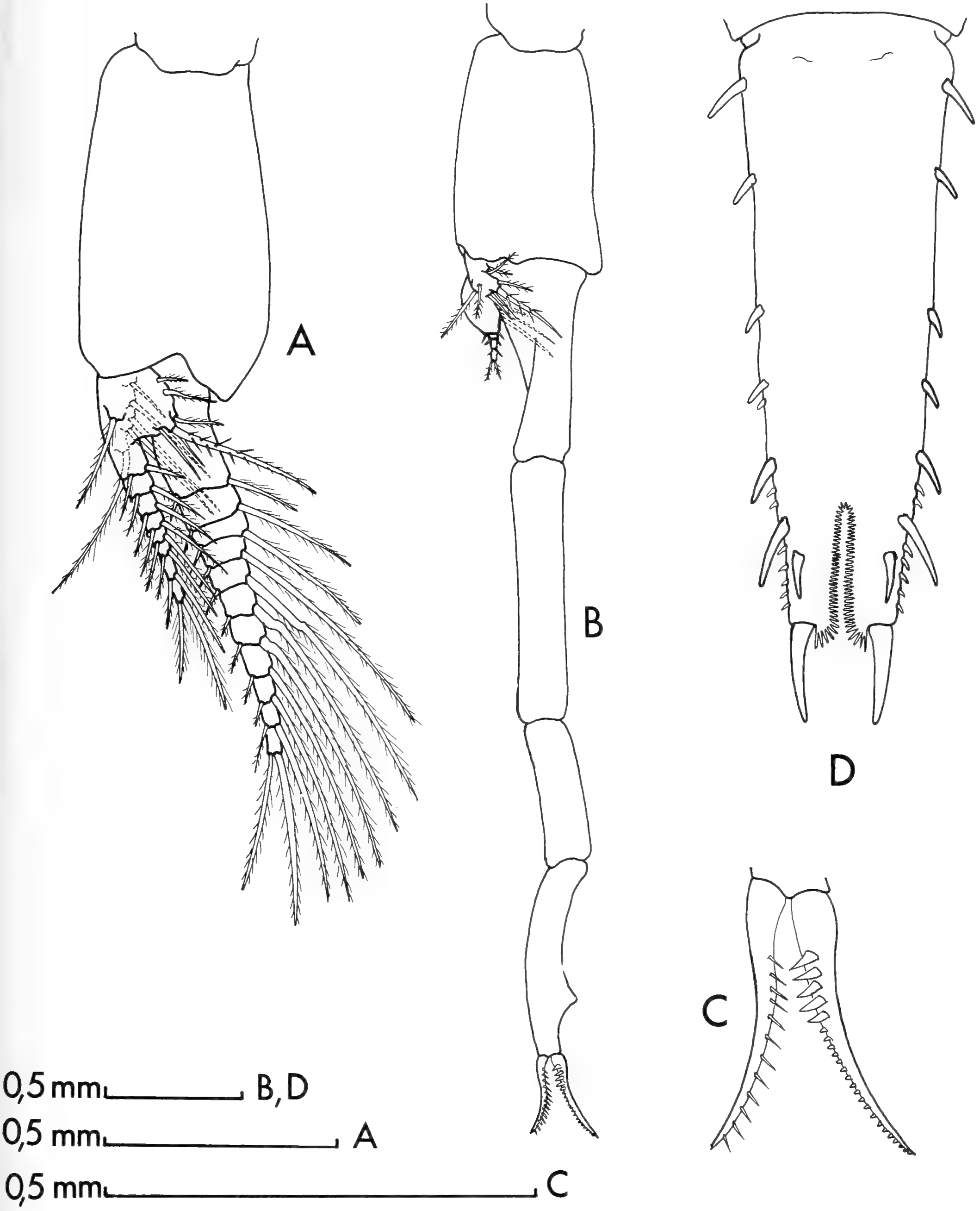

Fig. 5. *Gastrosaccus bispinosa* sp. nov.
A. Second pleopod of male. B. Third pleopod of male. C. Terminal setae of third pleopod of male. D. Telson.

each side of the cleft and the armature along the lateral margins of the telson. There is some diversity in the armament of the small spinules between the last three pairs of lateral and terminal spines. In some specimens the spinule in the space between the anti-penultimate and penultimate lateral spine was absent, while in others it was present on one side only. The number of spinules distal to the last pair of lateral spines also varied slightly and numbered either five or six on each side.

The species may also be identified by the form of the third pleopod of the male. The endopod is composed of only four segments, while the armature of the barbed setae at the base of the fourth exopod segment is characteristic.

Gastrosaccus longifissura sp. nov.

Figs 6–8

Holotype

SAM–A15751 lodged in the South African Museum, Cape Town. Adult female from Mgazana beach (31°42′S), collected by T. Wooldridge, 30 September 1977.

Paratypes

SAM–A15752 lodged in the South African Museum, Cape Town. Numerous adult males and adult females from Mgazana beach (31°42′S), collected by T. Wooldridge, 30 September 1977.

Description

Carapace (Fig. 6A) with anterior margin produced to form a triangular rostrum, acutely rounded. Posterior margin deeply and narrowly emarginate, exposing the last thoracic somite. The emargination is notched proximally, forming a forwardly directed lobe which overlaps the anterior portion of the emargination laterally. In lateral view the carapace extends posteriorly to cover the thorax entirely as well as the first abdominal somite.

Antennule (Fig. 6B), first segment of peduncle slightly shorter than second and third peduncular segments combined, outer distal angle with four or five plumose setae. Second segment of peduncle short, armed with three slender spines set obliquely along the outer margin. Inner distal corner with a fine setae. Third segment almost twice as long as broad, with a slender, curved, finger-shaped process dorsally on the outer distal corner. Outer flagellum swollen at the base and bearing long flattened setae. In the male a well-developed hirsute lobe present.

Antennal peduncle relatively long and extending forward almost to mid-point of the third segment of antennular peduncle (Fig. 6C). Second segment of antennal peduncle about two and a half times as long as broad, with four plumose setae on the inner lateral margin and two or three plumose setae at the distal corner. Third segment about one-third the length of second segment, with

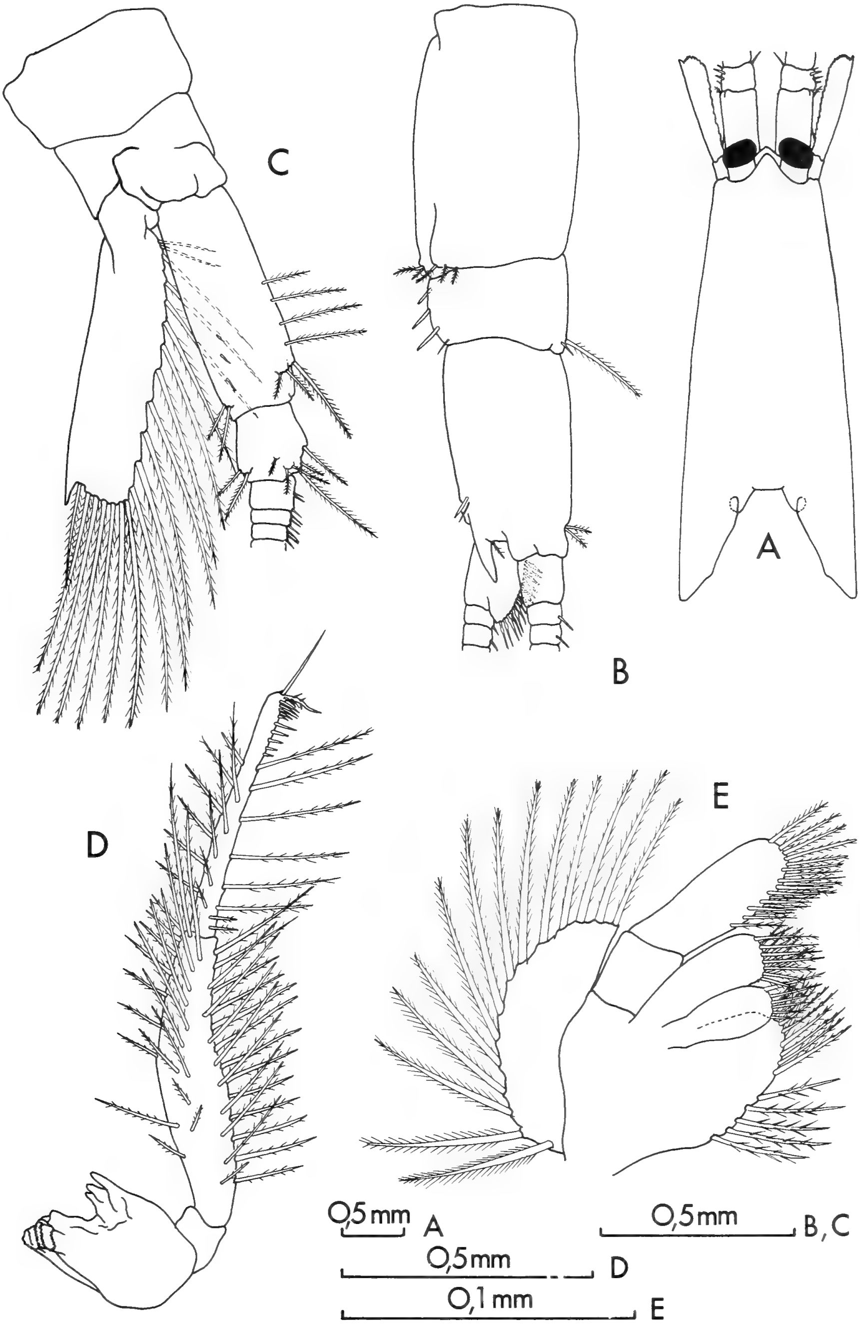

Fig. 6. *Gastrosaccus longifissura* sp. nov.
A. Carapace in dorsal view. B. Antennule. C. Antennae. D. Mandible. E. Maxilla.

eight plumose setae at the distal end. Antennal scale as long as peduncle and about four times as long as broad. Outer margin naked, terminating in a strong spine which does not extend beyond rounded apex of scale. Inner margin setose.

Mandible (Fig. 6D) without spine row. Palp long and slender, first segment unarmed. Setation of second and third segments as in Figure 6D. Third segment with a terminal comb-like process and two apical spines.

Maxillule (Fig. 7A), lobe from first segment with five relatively short spines and three long terminal spines, the armature of the shorter spines as in Figure 7A. Three terminal spines about twice as long as the shorter spines, each armed distally with about four strong teeth. Lobe from third segment armed with a close group of short, strong, spinous, slightly curved spines. A row of six spines along inner, subterminal margin, serrated distally and plumose proximally.

Maxilla (Fig. 6E), lobe from coxal segment with many well-developed spine-like setae, those at the apex shorter and more closely set. Lobe from basis incised to base, armed with many short setae along inner margin in the distal half and at the apex. Exopod with outer margin markedly convex, armed with about fourteen plumose setae.

First thoracic limb with well-developed endite on basal segment (Fig. 7B). Endopod short, robust, densely setose along inner margin of first segment. A single seta on outer distal angle of carpus. Propodus armed on outer margin only. Dactylus with many spine-like setae, without claw. First exopod segment large and expanded, the outer distal angle smooth (exopod twisted in figure). Flagellum fourteen-segmented, each segment with one or two plumose setae.

Second thoracic limb similar in form to first, dactylus of endopod with claw. First exopod segment with a well-developed tooth on outer distal angle.

Third to eighth thoracic limbs similar in form, but becoming progressively stronger and longer posteriorly. Carpus and propodus of endopod fused and divided into many short, subsegments. The number of these subsegments increases posteriorly as follows: in the third limb, eight; in the fourth, nine; in the fifth, ten; in the sixth, eleven; in the seventh, fourteen; in the eighth, sixteen. Each subsegment bears a brush of small setae and a single spine on the inner distal angle and a small spine on the outer distal angle. The first exopod segment in the third to seventh pairs of thoracic limbs armed with a strong tooth on the outer distal angle. In the eighth pair of appendages (Fig. 7C) this angle is smoothly rounded (exopod twisted in figure). Flagellum of exopod fourteen- to sixteen-segmented, each segment with one or two long plumose setae.

First pleopod of female (Fig. 7D) with long, slender sympod armed proximally with three, and distally with seven long plumose setae. Exopod about three times as long as wide, armed with one spine-like seta, seven short plumose setae, and two relatively long plumose setae at the distal end. Endopod

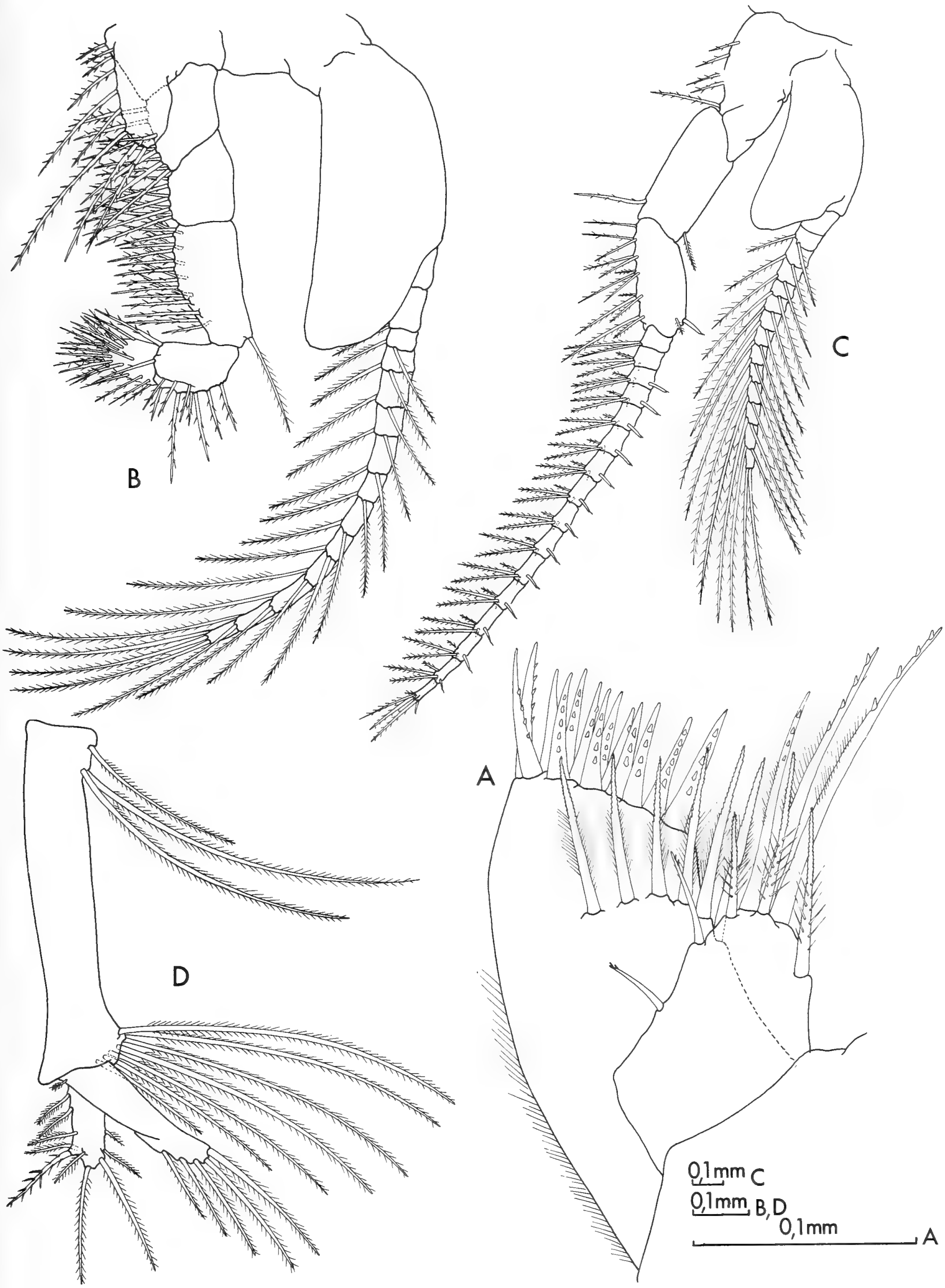

Fig. 7. *Gastrosaccus longifissura* sp. nov.
A. Maxillule. B. First thoracic appendage. C. Eighth thoracic appendage.
D. First pleopod of female.

almost four times as long as wide, armed with five plumose setae in the distal half. Remaining pleopods in the female becoming progressively longer on the posterior somites, each armed with many plumose setae and a single spine-like seta.

First pleopod of the male (Fig. 8B) with swollen sympod, the outer margin armed with ten long plumose setae. Endopod short, unsegmented, with two terminal plumose setae and a subterminal spine-like seta. Seven short plumose setae present, their relative positions illustrated in Figure 8B. Exopod with eight segments, the first almost twice as long as endopod. Each segment armed with two unequal setae except the last which has two equal terminal setae and a single sub-equal lateral seta.

Second pleopod of the male with sympod twice as long as wide (Fig. 8C). Endopod slender and five-segmented, almost three-quarters as long as sympod. A well-developed pseudobranchial lobe on first endopod segment, armed with a number of small plumose setae and one spine-like seta. Exopod robust, almost twice as long as endopod, setae along inner margin considerably shorter than those on the outer margin.

Third pleopod of the male with three-segmented endopod (Fig. 8D). The first segment large and bulbous, bearing a well-developed pseudobranchial lobe which is armed with a number of plumose setae and a single spine-like seta. Second and third endopod segments small, the terminal segment reaching almost one-third along the length of the first exopod segment and armed with two relatively long plumose setae. Exopod four-segmented, extending backwards to proximal end of telson. Exopod segments become progressively shorter distally. First segment more than twice as long as the fourth, which bears two non-plumose setae at the proximal end. Apex armed with two curved, barbed setae, one of which is two and a half to three times the length of the other. The longer seta is armed in the proximal half only. Remaining pleopods in the male small, endopod reduced to a single segment.

Uropod (Fig. 8E) extending a short distance beyond telson. Exopod as long as endopod and armed on the outer margin with sixteen strong, regular spines which are finely plumose along the posterior margins. Apex of these spines with a short, curved tip. Endopod more slender than exopod, tapering distally, with seven long, curved, irregularly spaced spines amongst setae on inner margin. A single posteriorly directed spine present on inner side of statocyst. Two rows of small, closely set setae present anterior to statocyst on dorsal side. Outer margin of endopod with a row of eight short plumose setae opposite statocyst. Outer margin of endopod armed posteriorly with a row of graduated plumose setae, which are interspersed with a number of short plumose setae.

Telson (Fig. 8F) about three times as long as broad at the base. Lateral margins armed with seven strong spines of which the distal two on each side are longer than the others. The spaces between the last three pairs of lateral and terminal spines occupied with two, three or four small spinules which become more numerous distally. Apical spines long and strong, cleft slightly less than

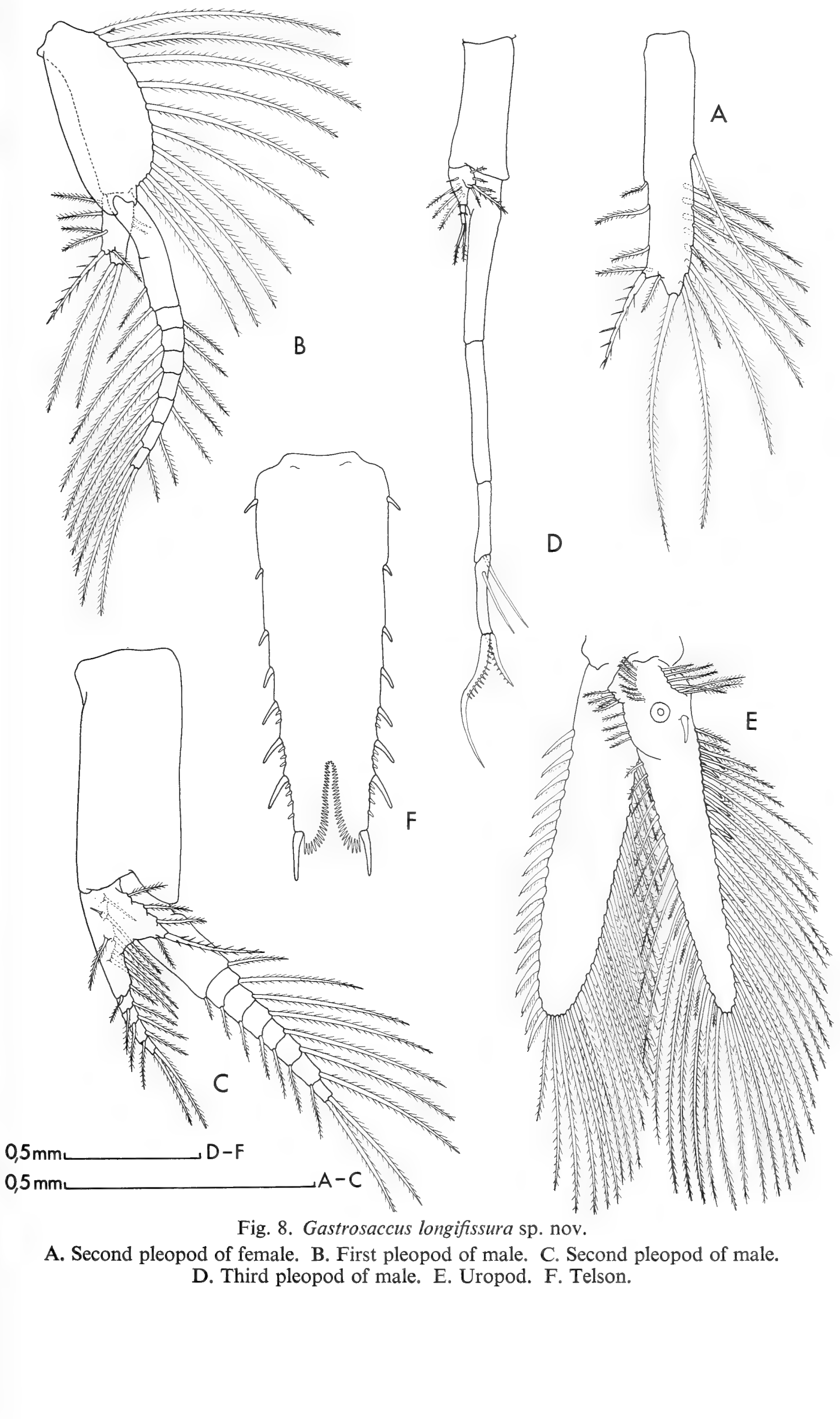

Fig. 8. *Gastrosaccus longifissura* sp. nov.
A. Second pleopod of female. B. First pleopod of male. C. Second pleopod of male. D. Third pleopod of male. E. Uropod. F. Telson.

one-quarter of the length of the telson. Cleft armed with twenty to twenty-five small spinules on either side.

Length

Adult female, 8,5–10,5 mm
Adult male, 8,2–9,8 mm

Remarks

G. longifissura shows affinities to *G. bispinosa* sp. nov. and *G. gordonae* Tattersall, 1952. It is distinguished from *G. bispinosa* by the absence of a spine on each side of the cleft on the dorsal side of the telson. The third pleopod of the male is also characteristic for each species. The endopod is four-segmented in *G. bispinosa* and three-segmented in *G. longifissura.* The terminal setae on the fourth exopod segment are subequal in length in *G. bispinosa.* In *G. longifissura* one of the seta is two and a half to three times the length of the other, while the fourth exopod segment also bears two non-plumose setae at the proximal end. These setae are absent in *G. bispinosa.*

G. longifissura is distinguished from *G. gordonae* mainly in the form of the telson. In *G. gordonae*, there are eight large spines on the lateral margin of the telson (the terminal spine is not grouped with the lateral spines in the present work), with the spaces between the third to the terminal spine occupied with three to six small spinules on each side. In *G. longifissura* the lateral margin of the telson is armed with seven large spines. The spaces between the fifth to the terminal spines are occupied with two to four spinules.

Important differences between the two species are also found on the uropods. In *G. gordonae*, the endopod is armed on the inner side of the statocyst with two unequal, posteriorly directed spines. The inner margin is armed with a row of ten small, unequal spines extending from the statocyst to half-way along the margin. In the distal half there are three long, widely-spaced spines. In *G. longifissura* there is only one posteriorly directed spine on the inner side of the statocyst and seven long, irregularly spaced spines among the setae on the inner margin.

Differences are also apparent on the third pleopod of the male. In *G. gordonae* the endopod is well developed and seven-segmented, extending well beyond the midpoint of the first exopod segment. The fourth exopod segment is armed midway along its outer margin with one simple seta. In *G. longifissura* the endopod is three-segmented and extending about one-third along the length of the first exopod segment. The fourth exopod segment bears two simple setae at the proximal end.

The second male pleopod in *G. gordonae* has an eight-segmented endopod, while the setae on the outer distal corners of the second to the fourth exopod segments are modified, being thickened and having their proximal margins serrated. In *G. longifissura* the endopod is five-segmented, with no modifications to the outer setae on the exopod segments.

DISTRIBUTION OF *GASTROSACCUS* RECORDED IN SOUTHERN AFRICA

Five species of *Gastrosaccus* are so far recorded from southern Africa. *G. dunckeri* is recorded from the Morrumbene estuary in Mozambique (Tattersall, O. S. 1958; Day 1974). *G. gordonae* is also reported from estuaries on the east coast (Tattersall, O. S. 1952; Scott *et al.* 1952; Day *et al.* 1954; Grindley & Wooldridge 1974), and from Saldanha Bay and Stompneus Bay on the West Coast (Lazarus 1975). *G. brevifissura* is recorded from estuarine and coastal waters (Tattersall, O. S. 1952; Day *et al.* 1954; Milland & Harrison 1954; Day 1958; Tattersall, O. S. 1962; Connell 1974; Lazarus 1975; Grindley 1977; Wooldridge 1976, 1977) as well as the intertidal zone (Tattersall, O. S. 1962). *G. sanctus* has been collected on several occasions off the coast of South Africa (Tattersall, O. S. 1957; Brown & Talbot 1972; Lazarus 1975).

G. psammodytes is the only species so far reported from sandy beaches in southern Africa and was until recently collected only in the intertidal and surf zone (Tattersall, O. S. 1958; Day 1958; Brown & Talbot 1972). McLachlan *et al.* (1978) have shown that numbers of *G. psammodytes* collected at night in the upper surf zone were significantly lower than numbers collected during the day and have suggested a general emergence from the sand after dark when the animals become planktonic in deeper waters. Samples collected at night (unpublished data) on a number of occasions in Algoa Bay with a WP–2 plankton net have shown them to be present in surface waters 250–300 m off shore, while Lazarus (1975) collected a number of specimens at night in vertical plankton samples off the west coast of South Africa. Similar activity patterns of diurnal burrowing and a nocturnal pelagic life have been shown for *G. sanctus* (Băcescu 1934; Moran 1972) and for *G. mediterraneus* and *G. spinifer* (Macquart-Moulin 1977). The most easterly extension of *G. psammodytes* is given as Kleinmond (33°33′S) in the eastern Cape Province (Brown & Talbot 1972). During the course of the present study it was collected at Gulu (33°08′S) and Nahoon (32°59′S) near East London, and at Kei Mouth (32°41′S).

Past workers divided the genus *Gastrosaccus* into two groups based on the form of the endopod of the third pleopod of the male. In the *Spinifer* group the endopod is multiarticulate, while in the *Normani* group it is reduced to a single segment or lacking. All species of *Gastrosaccus* from southern Africa are members of the *Spinifer* group with the exception of *G. dunckeri*. In this species the endopod of the third male pleopod is completely lacking.

A further broad separation of the species can be found in the form of the posterior margin of the carapace. Members of the genus from the southern African region belong to that group in which the posterior margin of the carapace is notched, forming an overlapping lobe on either side, or where the posterior margin of the carapace is produced to form a pair of lappets which are reflexed forward.

KEY TO THE SPECIES OF *GASTROSACCUS* RECORDED IN SOUTHERN AFRICA

Characteristics common to both sexes are used where possible.

1. Posterior margin of carapace cleft in the median line. Margins on each side of the cleft produced into two lappets which are reflexed forward 2
— Posterior margin of carapace forming an overlapping lobe on either side of the emargination, not reflexed 3
2. Endopod of third pleopod of the male eight-segmented; *Spinifer* group. Telson with five lateral spines and no spinules between them . . *G. sanctus* (van Beneden), 1861
— Endopod of third pleopod of the male lacking; *Normani* group. Telson with about ten to twelve lateral spines. No spinules between them . . *G. dunckeri* Zimmer, 1915
3. Cleft in telson deep, one-quarter to one-sixth the length of the telson 4
— Cleft in telson shallow, in some specimens little more than an emargination *G. brevifissura* Tattersall, 1952
4. Telson with six lateral spines not interspersed with small spinules, or at most one or two spinules between the larger spines on each side . . *G. psammodytes* Tattersall, 1958
— Telson with six, seven or eight lateral spines interspersed with at least six to eight small spinules between the larger spines on each side 5
5. Telson with eight lateral spines. Spaces between last six pairs of lateral and the terminal spines occupied with three to six spinules. Endopod of uropod with thirteen spines among setae along inner margin . . . . *G. gordonae* Tattersall, 1952
— Telson with six or seven lateral spines. Spaces between last three pairs of lateral and the terminal spines occupied with one to five spinules. Endopod of uropod with seven spines among the setae along the inner margin 6
6. Telson with a strong spine on each side of the cleft on the dorsal side *G. bispinosa* sp. nov.
Telson without a spine on each side of the cleft on the dorsal side *G. longifissura* sp. nov.

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

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

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

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

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '. . . the Figure depicting *C. namacolus* . . .'; '. . . in *C. namacolus* (Fig. 10) . . .'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

T. WOOLDRIDGE

TWO NEW SPECIES OF *GASTROSACCUS* (CRUSTACEA, MYSIDACEA) FROM SANDY BEACHES IN TRANSKEI

VOLUME 76 PART 10 SEPTEMBER 1978 ISSN 0303–2515

ANNALS
OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN

INSTRUCTIONS TO AUTHORS

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

2. LAYOUT should be as follows:

- (a) *Centred masthead to consist of*
  - Title: informative but concise, without abbreviations and not including the names of new genera or species
  - Author's(s') name(s)
  - Address(es) of author(s) (institution where work was carried out)
  - Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
- (c) *Table of contents* giving hierarchy of headings and subheadings
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- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
- (f) *Summary*, if paper is lengthy
- (g) *Acknowledgements*
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3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2,5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

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

Footnotes should be avoided unless they are short and essential.

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

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

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

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

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Fischer, P.-H., Duval, M. & Raffy, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.
Kohn, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.
Kohn, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.
Thiele, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* Schultze, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

(continued inside back cover)

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LATE TERTIARY MUSTELIDAE (MAMMALIA, CARNIVORA) FROM LANGEBAANWEG, SOUTH AFRICA

By

Q. B. HENDEY

Cape Town Kaapstad

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By

Q. B. Hendey

South African Museum, Cape Town

(With 11 figures and 10 tables)

[*MS. accepted 2 August 1978*]

ABSTRACT

The Mustelidae of the latest Miocene/early Pliocene Varswater Formation in 'E' Quarry, Langebaanweg, are described. They are identified as *Plesiogulo monspessulanus* Viret, 1939, which is the southernmost record of a wolverine, *Mellivora benfieldi* sp. nov., which is a likely ancestor of the living *M. capensis*, and *Enhydriodon africanus* Stromer, 1931, which is a structural and temporal intermediate between *E. lluecai* and *E. sivalensis*.

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INTRODUCTION

Since publication of an account of the Carnivora from the Varswater Formation in 'E' Quarry, Langebaanweg, Cape Province (Hendey 1974*b*), a great deal of additional material belonging to this order has been discovered (Hendey 1976*b*, 1977, 1978*c*). Although the original species list has not been substantially altered, the additional material does include specimens belonging to species not previously known from this locality and some which have led to revision of earlier identifications. Others have served simply to confirm original identifications.

Each of these situations applies in the case of the Mustelidae, a family which is comparatively poorly represented in the 'E' Quarry fauna, both in terms of numbers of species and numbers of specimens. Three species are recognized. The undescribed mustelid is the first African record of the extinct wolverine, *Plesiogulo* (Hendey 1976*b*: 239), the species previously incorrectly identified is a honey badger, *Mellivora* (Hendey 1974*b*: 68), while the species whose identity is confirmed is an otter, *Enhydriodon* (Hendey 1974*b*: 72).

The 'E' Quarry fauna, of which these three mustelids are a part, has generally been regarded as early Pliocene (4–5 Ma) in age. This dating is, however, insecure and present indications are that the outside age limits are 3,5 and 7 Ma, that is, the fauna dates from the very late Miocene and/or early Pliocene (Hendey 1978*c*).

Ann. S. Afr. Mus. **76** (10), 1978: 329–357, 11 figs, 10 tables.

The fossils dealt with in this report are from three distinct stratigraphic units in the Varswater Formation. They are, in descending order of age, the Quartzose Sand Member and beds 3aS and 3aN of the Pelletal Phosphorite Member (Hendey 1976*b*, 1978*a*). The durations of the intervals which elapsed between deposition of these units are not known, but they may have been appreciable. There is evidence, some of which will be presented below, that certain taxa show evolutionary advances over counterparts from lower units in the succession, although the differences are relatively slight and generally would not warrant taxonomic distinction at species level.

The material described is housed in the South African Museum, and catalogue numbers are prefixed SAM–PQ–, which identifies the institution and department concerned. This lettering is omitted from the text.

SYSTEMATIC DISCUSSION

Family **Mustelidae**

Subfamily Mellivorinae

Plesiogulo monspessulanus Viret, 1939

Material

L21570. Remains of an adult individual including: incomplete right mandible with P_3 to M_2; right I_1 and I^2; left I_1 and I^3. Part of right pes including most tarsal bones, and metatarsals I to V lacking distal ends.

L40042. Remains of an adult male including: fragmented and incomplete skull and mandible with right P^1 to P^4, right P_2 to P_4, several worn incisors and fragments of other teeth. Elements of the vertebral column, limb girdles and all four limbs, most larger bones being incomplete.

L28394. Left mandible fragment with M_1 and M_2.

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. L21570 and L28394 are from the Quartzose Sand Member; L40042 is either from the Quartzose Sand Member or the lowermost level of bed 3aS of the Pelletal Phosphorite Member.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

The most striking characteristic of this species is its large size. It was apparently only a little smaller than *Megalictis ferox* of the North American Miocene (Matthew 1907), which was the 'largest of all mustelids [reaching] the size of a black bear' (Kurtén 1971 : 119). The Langebaanweg species is generally similar to the living wolverine, *Gulo gulo*, in terms of its dental and osteological characters.

The skull of L40042 was badly damaged by a mechanical excavator and useful observations can be made only on the upper and lower premolars, and parts of the braincase, right maxilla and left mandible.

The maxillary fragment is comprised only of the bone immediately adjacent to the four premolars (Fig. 1). Parts of the alveoli of the $\underline{C}$ and M^1 are preserved. The premolars are large and relatively broad compared with those of living

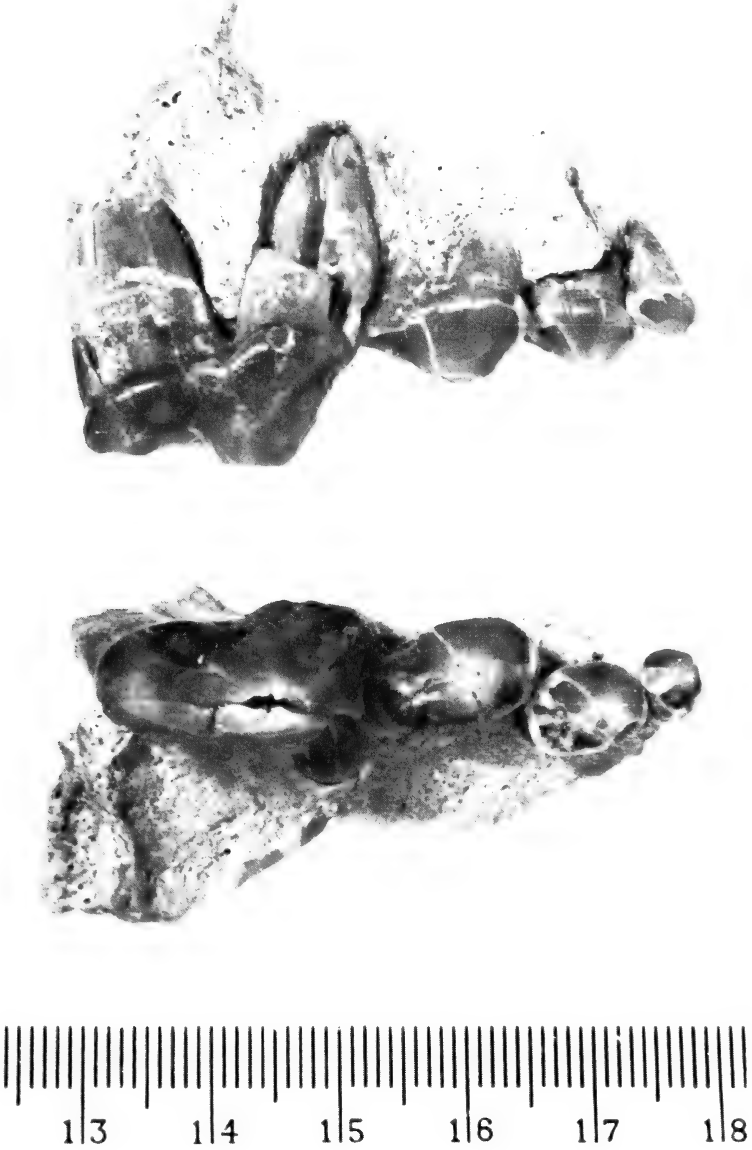

Fig. 1. Buccal and occlusal views of *Plesiogulo monspessulanus* maxilla (L40042) from Langebaanweg.

TABLE 1

Dimensions of the teeth of *Gulo gulo* and *Plesiogulo* species.

		P^1		P^2		P^3
		l	*b*	*l*	*b*	*l*
Gulo gulo—Scandanavia (n = 11—15)*		4,0–4,6	—	6,2–7,2	—	9,6–11,2
Plesiogulo 'major'—China†		—	—	—	—	—
Plesiogulo monspessulanus—Europe† . . .		—	—	—	—	—
Plesiogulo monspessulanus—Langebaanweg	L40042	*c.* 5,2	6,0	9,7	7,2	13,9
	L21570	—	—	—	—	—
	L28394	—	—	—	—	—
Plesiogulo crassa—China (means)†		—	—	8,2	5,9	11,0

* Data provided by E. Anderson (Denver, Colorado).
† Kurtén 1970.

Gulo gulo (Table 1). They are positioned as in the living species, except that P^2 and P^3 overlap, which is unlike the fore-aft arrangement in the two available *G. gulo* comparative specimens and some illustrated examples (e.g. Anderson 1977, fig. 4; Novikov 1962, fig. 128; Kurtén & Rausch 1959, figs 3–4). Morphologically the teeth are similar to those of *G. gulo* in all observable respects. The infraorbital foramen of L40042 is more posteriorly situated than that of *G. gulo*. It opens above the apex of the P^4 paracone, whereas in the living species the opening is above the anterior end of P^4.

The features of the posterior parts of the skull of L40042 (Fig. 2) are essentially similar to their counterparts in *G. gulo*. The fossil skull is, however, very large (Table 2), with processes and crests greatly exaggerated. The sagittal crest is particularly prominent, being about 20 mm high along that part which is preserved. This crest terminates posteriorly above the level of the occipital condyles, whereas in *G. gulo* it usually, or always, projects further back. By contrast, the paroccipital process of the fossil projects further back than that of *G. gulo*.

The less posteriorly protruding sagittal crest is one manifestation of the relatively shorter braincase of the fossil. The distance between the external auditory meatus and most posterior part of the sagittal crest is about 30 mm in L40042, whereas in two *G. gulo* specimens it is 36 mm (SAM–ZM36095 ♂) and 40 mm (SAM–ZM38641 ♀). This difference is also indicated by the orientation of the nuchal crest in lateral view. In L40042 the lower part of this crest is at an angle of about 70° above the horizontal, whereas in the *G. gulo* comparative specimens the angle is about 50°.

In *G. gulo* the zygomatic process of the squamosal rises vertically above the level of the glenoid fossa so that the inferior margin of this process is elevated

P^4	P_2		P_3		P_4		M_1		M_2	
b	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*
11,0–12,8	5,7–6,8	—	7,7–9,6	5,3–6,6	10,5–12,4	6,2–7,8	19,7–22,5	8,4–10,0	5,0–6,5	4,3–5,5
—	8,9	—	12,5	—	14,3	—	30,5	11,3	—	—
—	—	—	10,0	—	14,0	—	28,0	10,5	—	—
c. 15,6	9,1	6,7	12,6	8,1	16,0	9,5	—	—	—	—
—	—	—	11,4	7,3	15,2	9,2	28,3	c11,0	11,4	c8,5
—	—	—	—	—	—	—	*c.* 27,5	11,4	*c.* 7,5	c6,7
12,9	7,4	5,9	9,8	6,6	13,0	7,8	23,9	9,6	7,7	6,6

well above the glenoid fossa and external auditory meatus. In L40042 the process is much less elevated and its inferior margin is actually below the level of the auditory meatus.

Lower teeth of all three fossil individuals are preserved and the only elements not represented are I_2 to P_1. The lower teeth, like the uppers, are generally similar to their counterparts in *G. gulo*, although they are larger (Table 1, Fig. 3). The P_2 of L40042 differs from its counterpart in *G. gulo* in being single-rooted, a possibly significant character from a phylogenetic point of view and one which will be discussed later.

The M_1's of both L21570 and L28394 are damaged and it cannot be established for certain whether or not a metaconid was present. Judging from the less damaged M_1 of L28394, this cusp was either very small or absent. The M_1 of the fossil does differ from that of *G. gulo* in having a relatively longer talonid.

The M_2's of L21570 and L28394 are strikingly different in both size and morphology. The M_2 of the latter is slightly damaged, but it was evidently similar to that of *G. gulo* in proportions. By contrast, the M_2 of L21570 is anteroposteriorly elongated, with the trigonid and talonid distinguishable, although none of the individual cusps is prominently developed. The elongated M_2 of L21570 may be an individual peculiarity, rather than being typical of the Langebaanweg species. The $M_1 : M_2$ length ratio in L28394 (1 : 0,27) is comparable to the ratio in both living *G. gulo* (1 : 0,28 — n = 2) and the relatively primitive late Miocene *Plesiogulo crassa* (1 : 0,33—Kurtén 1970), whereas the ratio in L21570 is quite distinct from either (1 : 0,40).

The mandible of L21570 lacks much of the coronoid process and symphyseal region (Fig. 3). The latter region was affected by a pathological condition

TABLE 1

Dimensions of the teeth of *Gulo gulo* and *Plesiogulo* species.

		P^1		P^2		P^3		P^4		P_2		P_3		P_4		M_1		M_2	
		l	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*	*l*	*b*
Gulo gulo—Scandanavia (n = 11–15)*		4,0– 4,6	—	6,2– 7,2	—	9,6– 11,2	5,7– 6,9	8,3– 1,2	11,0– 12,8	5,7– 6,8	—	7,7– 9,6	5,3– 6,6	10,5– 12,4	6,2– 7,8	19,7– 22,5	8,4– 10,0	5,0– 6,5	4,3– 5,5
Plesiogulo 'major'—China†		—	—	—	—	—	—	—	—	8,9	—	12,5	—	14,3	—	30,5	11,3	—	—
Plesiogulo monspessulanus—Europe† . . .		—	—	—	—	—	—	—	—	—	—	10,0	—	14,0	—	28,0	10,5	—	—
Plesiogulo monspessulanus—Langebaanweg	L40042	*c.* 5,2	6,0	9,7	7,2	13,9	9,0	3,2	*c.* 15,6	9,1	6,7	12,6	8,1	16,0	9,5	—	—	—	—
	L21570	—	—	—	—	—	—	—	—	—	—	11,4	7,3	15,2	9,2	28,3	c11,0	11,4	c8,5
	L28394	—	—	—	—	—	—	—	—	—	—	—	—	—	—	*c.* 27,5	11,4	*c.* 7,5	c6,7
Plesiogulo crassa—China (means)†		—	—	8,2	5,9	11,0	6,9	9,5	12,9	7,4	5,9	9,8	6,6	13,0	7,8	23,9	9,6	7,7	6,6

* Data provided by E. Anderson (Denver, Colorado).

† Kurtén 1970.

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In *G. gulo* the zygomatic process of the squamosal rises vertically above the level of the glenoid fossa so that the inferior margin of this process is elevated well above the glenoid fossa and external auditory meatus. In L40042 the process is much less elevated and its inferior margin is actually below the level of the auditory meatus.

Lower teeth of all three fossil individuals are preserved and the only elements not represented are I_2 to P_1. The lower teeth, like the uppers, are generally similar to their counterparts in *G. gulo*, although they are larger (Table 1, Fig. 3). The P_2 of L40042 differs from its counterpart in *G. gulo* in being single-rooted, a possibly significant character from a phylogenetic point of view and one which will be discussed later.

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The mandible of L21570 lacks much of the coronoid process and symphyseal region (Fig. 3). The latter region was affected by a pathological condition

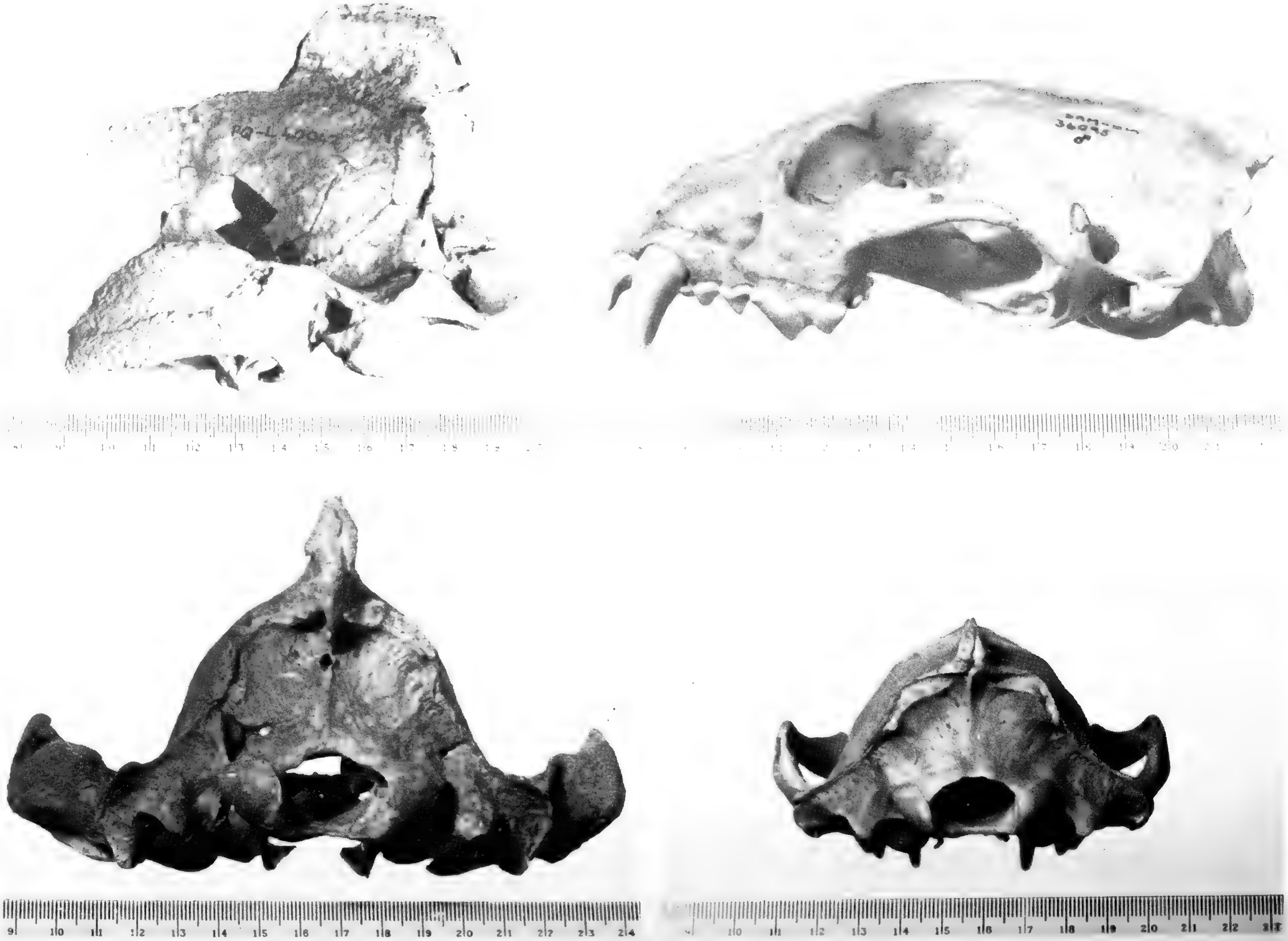

Fig. 2. Lateral and posterior views of *Plesiogulo monspessulanus* skull (L40042) from Langebaanweg (left) and *Gulo gulo* skull (ZM36095) (right).

TABLE 2

Dimensions of the skull and mandible of the Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo*.

	Plesiogulo monspessulanus			*Gulo gulo*	
	L40042	L21570	L28394	ZM36095	ZM38641
Braincase length (postorbital constriction to occipital condyles)	81,0	—	—	69,5	65,5
Width across occipital condyles .	50,8	—	—	37,8	35,7
Mastoid width	108,2	—	—	88,8	81,4
Zygomatic width	158,5	—	—	103,7	95,0
Occiput height (occipital condyles to top of sagittal crest) . .	80,5	—	—	50,9	52,6
Depth of mandible below M_1 .	*c.* 39,0	39,0	37,5	23,3	22,3
Height of ascending ramus (angle to top of coronoid process) .	68,7	—	—	50,9	47,1
Transverse diameter of condyle .	44,1	41,4	—	25,7	24,7

Fig. 3. Occlusal and buccal views of *Plesiogulo monspessulanus* mandible (L21570) from Langebaanweg.

which has left the remaining bone spongy in texture. The abnormality extends along the alveolar margins of the cheekteeth, becoming less pronounced posteriorly. The area of insertion of the occipito-mandibularis muscle in the subangular region is marked by V-shaped ridges of bone which diverge posteriorly, that on the buccal side being more prominent and irregular in outline. The counterparts of these ridges in L28394 and L40042 are only slightly developed, although the latter apparently belonged to a more aged individual, judging from wear on the cheekteeth. The ridges in L21570 may be a further manifestation of the mandibular pathology of the individual concerned.

The fossil mandibles are generally similar to corresponding parts of the mandibles of the *G. gulo* comparative specimens, except that the condyles are remarkably long and tubular in shape (Table 2, Fig. 4).

A feature of the dentition of L21570 which is evidently related to the pathological condition of the mandible is that, although the cheekteeth are only slightly worn, the preserved incisors are well worn. Similar pathology in one of the *G. gulo* comparative specimens (SAM–ZM38641) is accompanied by broken canines and heavily worn incisors. According to E. Granqvist of the Zoological Museum of the University, Helsinki (letter to R. Rau), damaged symphyseal teeth, and pathology of the adjacent parts of the jaws, are not uncommon in wolverines. Presumably this results from the aggressive behaviour and indis-

Fig. 4. Posterior view of *Plesiogulo monspessulanus* mandible (L40042) from Langebaanweg.

criminate feeding habits of the species. The condition of L21570 suggests that the late Tertiary wolverine from South Africa had habits similar to its living relative.

Ten of the vertebrae of L40042 are reasonably intact and all are distinguished from their modern counterparts only by their very much larger size. In general this also applies to other known postcranial bones of the fossil (Figs 5–6, Tables 3–6). The limb bones, and particularly the metapodials, are relatively less elongated, but much more stoutly proportioned than the corresponding bones in *G. gulo*. These differences, and possibly all others, are presumably due to the size difference between the species concerned. For example, the humerus of L40042 has a much deeper supratrochlea fossa and longer lateral condyloid crest, which reflect the stoutness and more heavily-muscled state of this bone. One of the differences for which no explanation can be offered is the marked curvature of the radius and ulna of L40042 (Fig. 6).

The relatively short and stout metapodials of the fossil go together with differences in proportions of certain carpal and tarsal bones. For example, the fossil calcanea and astragali are also relatively short and stout. Possibly the fossil species was more perfectly plantigrade than the living wolverine.

Postcranial bones of both L40042 and L21570 show signs of an arthritic condition, something which is not uncommon amongst the fossil carnivores from Langebaanweg (Hendey 1974*b*).

Fragments of the baculum of L40042 are preserved. They are similar in shape to corresponding parts of the baculum of *G. gulo*.

Discussion

The Mellivorinae are known from late Tertiary and Quaternary contexts through much of the Old World and North America. They are a heterogeneous group for which a subdivision into tribes has been suggested, and Webb (1969) visualized the subfamily as follows:

Mellivorini	Gulonini	Brachypsalini
Aelurocyon Peterson, 1906	*Ischyrictis* Helbing, 1930	*Paroligobunis* Peterson, 1906
Megalictis Matthew, 1907	*Hadrictis* Pia, 1939	*Brachypsalis* Cope, 1890
Perunium Orlov, 1947	*Plesiogulo* Zdansky, 1924	*Brachypsaloides* Webb, 1969
Eomellivora Zdansky, 1924	*Gulo* Frisch, 1775	
Promellivora Pilgrim, 1932		
Mellivora Storr, 1780		

At least one additional genus belonging to this subfamily (*Ferinestrix* Bjork, 1970) has since been described, while *Promellivora* has been regarded as a synonym of *Mellivora* (Hendey 1974*b*). The latter opinion may not have been warranted (see below).

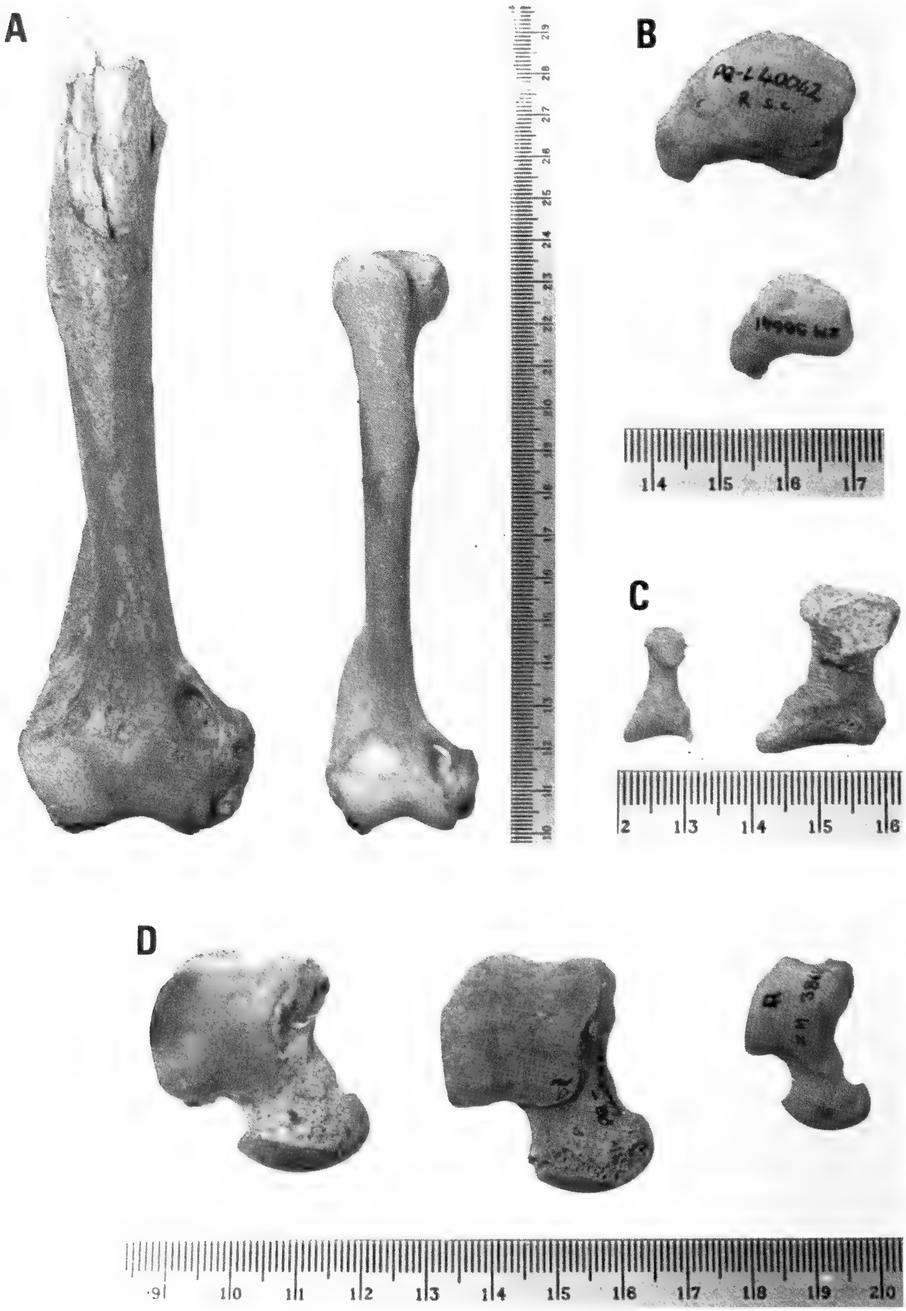

Fig. 5. *Plesiogulo monspessulanus* from Langebaanweg and *Gulo gulo* (ZM38641). A. Humeri. B. Scapholunars. C. Pisiforms. D. Astragali. All specimens of *P. monspessulanus* belong to L40042, except the left astagalus which is of L21570.

TABLE 3

Dimensions of Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo* long bones.

	HUMERUS			RADIUS			ULNA		
	Gulo gulo		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*
	6129*	ZM38641	L40042	6129*	ZM38641	L40042	6129*	ZM38641	L40042
Max. length	—	—	—	—	—	—	145,0	136,8	186,0
Max. ant.-post. diameter, proximal end .	—	—	—	12,2	10,4	c15,5	—	—	—
Max. transverse diameter, proximal end .	—	—	—	17,5	16,3	c24,0	—	—	—
Max. ant.-post. diameter, distal end .	22,4	19,8	36,8	15,5	14,5	21,7	—	—	—
Max. transverse diameter, distal end .	39,8	36,6	54,5	23,2	22,0	34,1	14,4	12,5	c19,5

	FEMUR			TIBIA			FIBULA		
	Gulo gulo		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*
	6129*	ZM38641	L40042	6129*	ZM38641	L40042	6129*	ZM38641	L40042
Max. length	14,9	137,8	c215,0	142,0	137,5	c185,0	129,0	124,3	162,0
Max. ant.-post. diameter, proximal end .	—	—	—	32,0	30,0	c50,0	—	—	—
Max. transverse diameter, proximal end .	40,0	33,5	59,0	—	—	—	—	—	—
Max. ant.-post. diameter, distal end .	—	—	—	17,5	15,7	26,4	14,0	14,8	19,6
Max. transverse diameter, distal end .	—	—	—	23,8	22,4	34,1	8,9	7,3	12,1

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

TABLE 4

Dimensions of Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo* carpal and tarsal bones.

		Gulo gulo		*Plesiogulo monspessulanus*	
		6129*	ZM38641	L40042	L21570
SCAPIO-LUNAR	Max. transverse diameter . . .	20,0	18,5	28,5	—
	Max. diameter proximal end to distal end	11,0	9,7	14,4	—
PISIFORM	Max. length	17,4	17,8	25,4	—
	Max. ant.-post. diameter, articular end	7,8	7,5	11,4	—
	Max. transverse diameter, articular end	11,9	10,5	18,5	—
CALCANEUM	Max. length	43,5	41,7	55,7	55,8
	Max. transverse diameter . . .	22,0	22,0	33,1	33,2
	Max. dorsoventral diameter . . .	22,4	21,0	31,7	—
ASTRA-GALUS	Max. length	27,0	26,8	36,1	36,4
	Max. transverse diameter, tibial facet	14,9	13,3	22,2	20,0
NAVICULAR	Max. length (dorsoventral diameter) .	15,8	—	23,3	22,3
	Max. transverse diameter . . .	12,6	—	18,3	18,9

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

Fig. 6. Ulnae of *Plesiogulo monspessulanus* from Langebaanweg (L40042) and *Gulo gulo* (ZM38641).

TABLE 5

Dimensions of Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo* metacarpals.

	METACARPAL I			METACARPAL II			METACARPAL IV		
	Gulo gulo		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*	*Gulo gulo*		*Plesiogulo*
	6129*	ZM38641	L40042	6129*	ZM38641	L40042	6129*	ZM38641	L40042
Max. length	28,9	30,5	36,3	40,5	41,2	50,0	49,8	49,2	62,1
Max. ant.-post. diameter, proximal end .	6,8	7,0	12,1	8,7	8,8	14,4	10,2	9,4	15,0
Max. transverse diameter, proximal end .	8,8	8,0	11,0	7,4	7,0	11,1	7,4	7,4	12,0
Max. ant.-post. diameter, distal end .	6,4	6,2	9,0	7,9	7,1	12,2	8,6	7,5	12,2
Max. transverse diameter, distal end .	7,7	7,4	9,1	9,3	9,0	13,1	9,8	9,2	13,7

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

TABLE 6

Dimensions of Langebaanweg *Plesiogulo monspessulanus* and living *Gulo gulo* metatarsals.

	METATARSAL I				METATARSAL II			
	Gulo gulo		*Plesiogulo monspessulanus*		*Gulo gulo*		*Plesiogulo monspessulanus*	
	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042	L21570
1. Max. length	—	—	—	—	49,9	50,4	56,2	—
2. Max. ant.-post. diameter, proximal end	9,5	8,3	—	10,2	9,2	9,0	13,8	14,6
3. Max. transverse diameter, proximal end	10,6	9,1	—	10,4	6,2	6,0	9,3	11,3
4. Max. ant.-post. diameter, distal end .	6,6	5,9	8,1	—	7,7	7,2	11,0	—
5. Max. transverse diameter, distal end .	7,8	7,3	9,7	—	9,4	8,9	12,6	—

	METATARSAL III				METATARSAL IV				METATARSAL V		
	Gulo gulo		*Plesiogulo monspessulanus*		*Gulo gulo*		*Plesiogulo monspessulanus*		*Gulo gulo*		*Plesiogulo monspessulanus*
	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042	L21570	6129*	ZM38641	L40042
1.	57,0	56,6	66,2	—	60,4	58,9	69,1	—	53,1	53,4	c59,0
2.	13,0	11,6	—	17,6	12,6	11,6	c17,0	17,8	—	—	—
3.	8,9	9,9	11,1	12,7	9,2	8,5	c12,0	12,5	—	—	—
4.	8,1	7,4	12,0	—	8,2	7,3	11,4	—	8,2	7,3	11,0
5.	10,0	9,4	13,2	—	10,1	9,3	12,9	—	10,0	9,0	11,9

* U.S. Geological Survey, Menlo Park, Branch of Paleontology & Stratigraphy.

With the exception of *Mellivora* and *Gulo*, all the recorded genera are late Tertiary in age and they are generally not well represented. As a result their inter-relationships are somewhat obscure. Webb (1969: 66) concluded that there was apparently 'an early Miocene radiation of mellivorine stock which gave rise to the *Aelurocyon–Megalictis* and *Paroligobunis–Brachypsalis–Brachypsaloides* lineages in North America and the *Ischyrictis–Hadrictis–Plesiogulo* lineage in Europe'. Later Mellivorini were confined to the Old World.

Plesiogulo, the genus with which the Langebaanweg wolverine is identified, was widespread in Eurasia during the late Miocene and Pliocene (Kurtén 1970), and was also present in North America (Kurtén 1970; Bjork 1970). Its presence at Langebaanweg near the southern tip of Africa means that it must have been distributed over much of this continent as well. Both Kurtén (1970) and Anderson (1977) regard *Plesiogulo* as the ancestor of *Gulo*.

Until recently large mellivorines were not known from Africa, but now, in addition to the Langebaanweg species, there is an as yet unidentified species recorded from the Omo Group deposits in Ethiopia (Howell & Petter 1976). The relationships between the Langebaanweg and Omo species have yet to be determined.

Of the described species of *Plesiogulo*, the one from Langebaanweg most closely resembles the broadly contemporaneous *P. monspessulanus* from Europe and *P. major* from China. These Pliocene species are the largest and most recent representatives of the genus. They are distinguished from one another only by the fact that *P. major* has an M_1 metaconid and Kurtén (1970: 12) concluded that they 'were obviously closely related'. They should, perhaps, be regarded as conspecific, with *P. monspessulanus* being the senior synonym. If this step is taken, then it becomes immaterial whether or not the Langebaanweg species had an M_1 metaconid, since there are no obvious grounds for separating it from its European and Chinese counterparts and all three may be identified with *P. monspessulanus*.

Geographical factors alone are sufficient to preclude the Langebaanweg *P. monspessulanus* from the role as direct ancestor of *Gulo*. In addition, it was noted above that the only preserved P_2 of this species is single-rooted and if this was characteristic of the Langebaanweg population, rather than just an individual anomaly, then it, too, indicates the lack of a direct phylogenetic connection with *Gulo*, in which P_2 is double-rooted. The P_2 of the Eurasian populations of *P. monspessulanus* has yet to be recorded.

Mellivora benfieldi sp. nov.

Holotype

L42838. Right mandible fragment with $\overline{C}$ and P_2 to M_1.

Referred material

L6385. Left mandible fragment with P_4 and M_1 (Hendey 1974*b*: 68–72, fig. 6).

L31273. Right mandible fragment with M_1.

L50443. Right mandible fragment with P_4 and M_1.

L50541. Right M^1.

A left ulna (L40080) and right radius (L45384) are tentatively assigned to this species.

Other poorly preserved and/or fragmentary specimens were excluded from the present study.

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. The holotype (L42838), L6385 and L40080 are from bed 3aS, and the remaining specimens are from bed 3aN, both units of the Pelletal Phosphorite Member.

Etymology

Named for Graham Benfield, formerly geologist and mine superintendent at the Chemfos Ltd mine at Langebaanweg, whose contributions to the Langebaanweg Research Project were of inestimable value.

Diagnosis

A species of *Mellivora* a little smaller than the extant *M. capensis*; P_1 and M_2 absent; P_2 to M_1 relatively narrow; principal cusps of P_2 to P_4 sharp-pointed, with sharp anterior and posterior keels; anterior and posterior accessory cusps of P_4 relatively small; M_1 talonid relatively short, narrow and sectorial; internal lobe of M^1 only slightly expanded, lacking prominent cingulum round the protocone; mandibular condyle not elevated above cheekteeth.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

L6385 has already been described and discussed in detail (Hendey 1974*b*), and the paragraphs which follow summarize and supplement the earlier account of the Langebaanweg *Mellivora*.

The lower canine and cheekteeth of *Mellivora benfieldi* are superficially similar to those of the living honey badger, *M. capensis*. They differ in being smaller and narrower (Table 7), with cusps more sharp-pointed and keels more sharp-edged (Fig. 7). In these respects *M. benfieldi* is clearly the more primitive (less specialized) of the two species. They resemble one another in the number and arrangement of the teeth in the jaw and in the cusps on individual teeth. The P_4 accessory cusps are, however, smaller in *M. benfieldi*, while the M_1 talonid is smaller, narrower and without the basin-shaped depression situated lingually in *M. capensis*.

The internal (lingual) lobe of the isolated M^1 (L50541), like the M_1 talonid, is relatively small (Fig. 7). Its length (5,2 mm) is only slightly greater than that of the buccal lobe (4,2 mm), whereas in *M. capensis* the corresponding figures are 8,3 and 4,4 mm (n = 8). The expansion of the internal lobe in the M^1 of *M. capensis* is due to the development of a prominent cingulum round the protocone, a feature which is lacking in L50541. The fossil tooth is also narrower

Fig. 7. A. Occlusal and buccal views of *Mellivora benfieldi* holotype (L42838). B. Occlusal view of M^1 (L50541). Both from Langebaanweg.

TABLE 7

Dimensions of mandibles and lower teeth of *Mellivora* species.

			$\bar{C}$		P_2		P_3		P_4		P_4 *l* : *b*	M_1		M_1 *l* : *b*	P_2–M_1	Depth of corpus below M_1
			l	*b*	*l*	*b*	*l*	*b*	*l*	*b*		*l*	*b*		*l*	
Mellivora capensis (n = 8)		Mean	8,9	7,2	5,2	4,1	6,9	5,2	10,0	6,5	1 : 0,65	14,4	7,0	1 : 0,49	35,4	15,4
		Range	7,6–10,1	6,0–8,4	4,5–5,7	3,4–4,7	6,3–7,5	4,7–5,6	9,5–10,9	6,0–7,6	1 : 0,60–1 : 0,70	13,7–16,3	6,4–8,0	1 : 0,46–1 : 0,51	33,7–38,0	13,7–17,8
Mellivora benfieldi	bed 3aN	L50443	—	—	—	—	—	—	8,4	5,2	1 : 0,62	12,6	6,0	1 : 0,48	—	c14,5
		L31273	—	—	—	—	—	—	—	—	—	13,5	6,1	1 : 0,45	—	14,6
	Bed 3aS	L42838	6,5	4,6	4,6	3,4	6,2	4,4	8,4	4,8	1 : 0,57	11,5	5,3	1 : 0,46	30,2	13,4
		L6385	—	—	—	—	—	—	9,4	5,3	1 : 0,55	14,1	6,0	1,043	—	15,8
*Mellivora punjabiensis** . .			11,6	8,5	5,3	—	6,1	4,2	8,4	6,2	1 : 0,74	—	6,0	—	—	18,3

* Pilgrim 1932

than the M^1 of *M. capensis*, measuring 9,5 mm as against the mean of 10,9 mm in the comparative series.

The inferior margins of the fossil mandibles are slightly convex, whereas in the *M. capensis* comparative series they are straight or slightly concave. In both species the number and position of mental foramina are variable. In *M. benfieldi* there is only a slight elevation of the inferior margin towards the angle and the condyle is not raised above the level of the cheekteeth as in *M. capensis*. The larger of the fossil mandibles presumably belonged to males and are comparable in size to the smaller mandibles in the *M. capensis* comparative series, which belong to females.

The ulna, L40080 (Fig. 8), and radius, L45384, are the only postcranial bones in the Langebaanweg fossil assemblage which have so far been tentatively assigned to *Mellivora*. They are essentially similar to their counterparts in *M. capensis*, but are relatively short and stout (Table 8). Their size is in keeping with that of the lower jaws described above.

Discussion

It was earlier concluded that the 'E' Quarry *Mellivora* was closely related to, and possibly conspecific with, the Indian Mio/Pliocene *M. punjabiensis* (Hendey 1974*b*). It is now clear that the two species are not conspecific. *M. benfieldi* differs in having a smaller canine and shallower mandibular corpus, it lacks P_1 and has a narrower P_4.

The loss of P_1 is an advanced character in mellivorines and in this respect at least, *M. benfieldi* is closer to *M. capensis*. Since the only known canine of *M. benfieldi* is probably that of a female (L42838), while the *M. punjabiensis* holotype could be a male, the canine size difference is not necessarily as great as would appear at first sight. Nevertheless, the difference is probably more than would be encountered in a single species. The large canine and relatively deep

Fig. 8. Ulnae of *Mellivora benfieldi* (L40080) from Langebaanweg and *M. capensis* (ZM36867).

TABLE 8

Dimensions of *Mellivora* species radii and ulnae.

	RADIUS			ULNA		
	Mellivora capensis ZM35574	*Mellivora capensis* ZM36867	*Mellivora benfieldi* L45384	*Mellivora capensis* ZM35574	*Mellivora capensis* ZM36867	*Mellivora benfieldi* L40080
Max. length	106,8	101,4	80,4	139,0	130,5	106,5
Max. ant.-post. diameter, proximal end	12,1	11,7	9,4	—	—	—
Max. transverse diameter, proximal end	15,9	16,3	13,6	—	—	—
Max. ant.-post. diameter, distal end	13,9	14,2	13,4	13,5	14,8	13,3
Max. transverse diameter, distal end	24,0	22,7	17,8	8,5	8,6	9,0

mandibular corpus may also be primitive characters in *M. punjabiensis*, since they are features of *Eomellivora*, the genus from which *M. punjabiensis* may have been derived. The relatively short and broad P_4 of the latter is, however, more specialized than that of *M. benfieldi*.

To sum up, *M. punjabiensis* is an inappropriate structural ancestor for *M. benfieldi* and there was probably no direct phylogenetic connection between them. On the other hand, *M. benfieldi* is suitable in all observable respects to be ancestral to *M. capensis*. It follows that the suggestion, first made by Pilgrim (1932), that *M. punjabiensis* may have been an early ancestor of *M. capensis*, can now be dismissed. It also follows that the suggestion that the original separate generic status of '*M.*' *punjabiensis* was unwarranted (Hendey 1974*b*), is no longer acceptable. This species should once again be identified as *Promellivora punjabiensis*. The origins of *Mellivora* will be discussed again below.

The *M. benfieldi* sample is divisible into two units on stratigraphic grounds. The holotype (L42838) and L6385 are from bed 3aS of the Pelletal Phosphorite Member, while L31273 and L50443 are from the stratigraphically higher (and younger) bed 3aN. It was mentioned earlier that the interval between deposition of these beds may have been appreciable and that evidence exists of evolutionary changes in taxa common to both.

This applies in the case of *M. benfieldi*, since the P_4's and M_1's of the bed 3aN specimens are intermediate in breadth between those of the bed 3aS specimens and modern *M. capensis* (Table 7). In the case of M_1's there are overlaps in the ranges of the three samples, but the mean figures show a breadth increase from the 3aS sample (1 : 0,45), through the 3aN sample (1 : 0,47), to *M. capensis* (1 : 0,49). The differences are thus in the expected order given the relative ages of the three samples. Although the mean values for both P_4 and M_1 are discrete, the differences are small and appreciable overlaps in ranges would be expected of larger samples.

It is worth noting here that the P_4 length : breadth ratio in *Promellivora punjabiensis* (1 : 0,74) sets this species apart from the *M. benfieldi–M. capensis* combination.

The new *Mellivora* specimens from 'E' Quarry confirm the earlier conclusion that the 'E' Quarry species is definitely not conspecific with the *Mellivora* from the nearby Baard's Quarry (Hendey 1974*b*, 1978*a*). The latter is clearly more advanced and closer to, if not conspecific with, *M. capensis*.

Subfamily Lutrinae

Enhydriodon africanus Stromer, 1931

Material

L9138. Right mandible fragment with part of P_4 (Hendey 1974*b*: 72–74, fig. 7).

L50000. Left mandible fragment with P_4 to M_2 and isolated left P^4.

Various postcranial bones, including a femur (L41523), distal radii (L50001) and an astragalus (L50117), are tentatively assigned to this species.

Locality and horizon

Varswater Formation, 'E' Quarry, Langebaanweg. L9138 and L41523 are from bed 3aS, and the remaining specimens are from bed 3aN, both units of the Pelletal Phosphorite Member.

Age

Langebaanian (latest Miocene/early Pliocene), between 3,5 and 7 Ma.

Description

The mandible L9138 was described earlier and identified with *Enhydriodon africanus*, a species otherwise known only from Kleinzee, which is also on the west coast of the Cape Province, but about 400 km north of Langebaanweg (Hendey 1974*b*).

The new mandible, L50000, is a better specimen than L9138 and has served to confirm the identification with *E. africanus*, since it is very similar to the type specimen of this species. It lacks P_1, has a single-rooted P_2 and a double-rooted P_3. The P_4 has a principal cusp, a posterior accessory cusp and a prominent cingulum round its circumference. The P_4 of L9138 is higher crowned and has a more prominent posterior accessory cusp than those of L50000 (Fig. 9) and the *E. africanus* holotype. The significance of this difference will be discussed below.

The M_1 of L50000 is large, with the paraconid, protoconid and metaconid more or less equally developed (Table 9, Fig. 9). These cusps are low-crowned and bulbous. The talonid is large and basin-shaped, with the hypoconid covering about half its area. There is a prominent cingulum encircling the paraconid and extending posteriorly to the talonid on the buccal margin of the tooth. The M_2 is single-rooted and slightly elongated transversely, with little relief on the occlusal surface.

The isolated P^4 (Table 9, Fig. 10), which evidently belongs to the same individual as the new mandible, is an important specimen since the P^4 of *E. africanus* was not previously known. It has a small parastyle, the paracone is the most prominent cusp, the metastyle is very short, the protocone is large and nearly as prominent as the paracone and it is flanked posteriorly by a large, but low hypocone. There is a prominent cingulum encircling much of the tooth.

The various postcranial bones tentatively identified with *E. africanus* are similar to corresponding bones of the living clawless otter, *Aonyx capensis*. They are distinguished principally by their larger size. For example, the femur, L41523 (Fig. 11), has an overall length of 165 mm, compared with a mean length of 114 mm in a series of four *A. capensis* specimens.

Discussion

Repenning (1976) has dealt in detail with recorded representatives of *Enhydriodon* and concluded that there were two late Tertiary lineages of this genus. One led to *E. sivalensis* and 'can be characterized by the presence of a

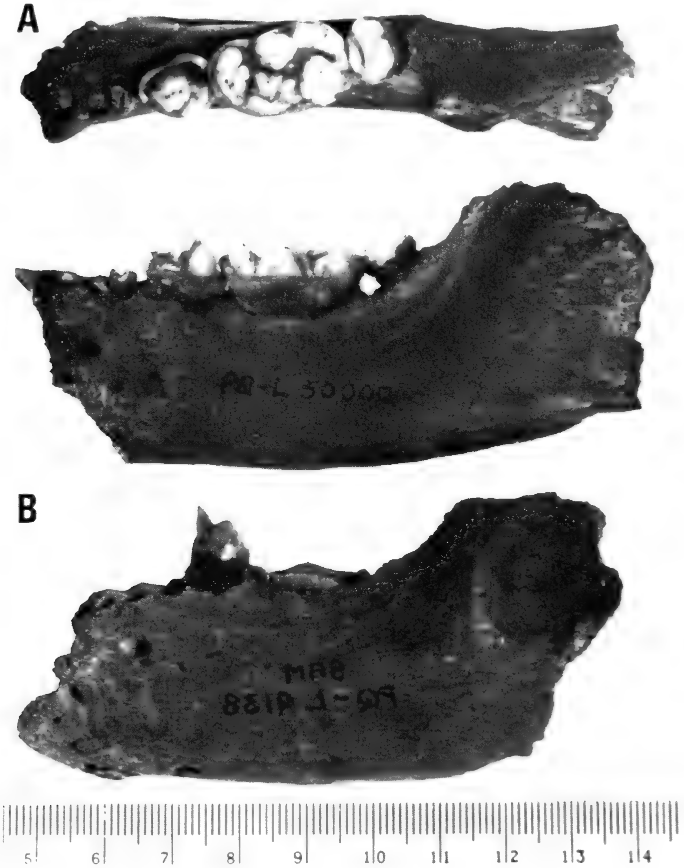

Fig. 9A. Occlusal and buccal views of *Enhydriodon africanus* mandible (L50000). B. Buccal view of *E. africanus* mandible (L9138) (reversed). Both from Langebaanweg.

parastyle on P^4 and by the location of the protocone of this tooth which is located as far lingually as the hypocone' (Repenning 1976: 305). The second lineage led to the living sea otter, *Enhydra lutris*.

On the basis of the P^4 characters, *E. africanus* evidently belongs with the group which includes *E. sivalensis*, a conclusion already reached by Repenning (1976) on other evidence. *E. sivalensis* is the more advanced of the two species, since it has a broader P^4 (Table 9), with a more quadrate outline due to a greater development of the hypocone. In addition, the cheekteeth of *E. africanus* apparently have more strongly developed cingula, which is a primitive condition in the *Enhydriodon*/*Enhydra* group.

E. africanus is here regarded as a structural and temporal intermediate

TABLE 9

Dimensions of the teeth and mandibles of *Enhydriodon* species.

	P^4		P^4 *l* : *b*	P_4		M_1		M_2		P_2–M_2 alveolar	Depth of corpus below M_1	Breadth of corpus below M_1
	l	*b*		*l*	*b*	*l*	*b*	*l*	*b*	*l*		
*Enhydriodon sivalensis** . .	16,2	18,4	1 : 0,88	—	—	21,6	12,7	—	—	—	—	—
Enhydriodon africanus† (Kleinzee)	—	—	—	11,9	8,6	22,0	+12,0	c9,5	—	57,0	27,0	14,8
E. africanus (Langebaanweg) bed 3aN L50000	16,9	17,2	1 : 0,98	12,3	9,4	21,2	13,5	8,5	10,3	55,0	26,5	14,0
bed 3aS L9138	—	—	—	c13,0	10,0	c22,0	c12,5	—	—	c55,0	30,1	17,7
*Enhydriodon lluecai** . . .	13,0	12,8	1 : 1,02	—	—	—	—	—	—	—	24,0	—

* Repenning (1976). M_1 is GSI D161—dimensions from Pilgrim (1932).
† Stromer (1931).

Fig. 10. Occlusal and buccal views of *Enhydriodon africanus* P^4 (L50000) from Langebaanweg.

between the late Miocene *E. lluecai* and the late Pliocene or early Pleistocene *E. sivalensis*.

A general trend in the evolution of *Enhydriodon* cheekteeth was towards inflation of the cusps and lowering of crown height, culminating in 'the low bulbous, or mastoid, tooth cusps', which are characteristic of *Enhydra* (Repenning 1976: 306). The fact that the P$_4$ of the bed 3aN L50000 has lower crowned and more bulbous cusps than the bed 3aS L9138 may therefore be interpreted as an indication that the former belongs to a more advanced form of *E. africanus*. This is further evidence which indicates that there was a lengthy

Fig. 11A. Femur of *Enhydriodon africanus* (L41523) from Langebaanweg. B. Femur of *Aonyx capensis* (ZM36254).

interval between deposition of beds 3aS and 3aN. The bed 3aN *E. africanus* is apparently morphologically closer to the Kleinzee representative of this species than is the one from bed 3aS.

GENERAL DISCUSSION

The Mustelidae comprise a relatively small element in the carnivore fauna of the Varswater Formation, being made up of only 3 of the approximately 29 recorded species (Table 10). In terms of the numbers of specimens known they form an almost insignificant part of the assemblage of carnivore material. Further collecting, and analysis of collected specimens, is unlikely to change this pattern of representation. Mustelids are a relatively uncommon element in the Pleistocene and Recent faunas of Africa as well.

The presence in the Langebaanweg fauna of an otter and a honey badger is not surprising, since both have counterparts in the modern fauna of the region, and Pleistocene representatives of these animals are also known (Hendey 1974*b*). The post-Pliocene species concerned are *Aonyx capensis* and *Mellivora capensis*, both of which were first recorded from the 'Cape of Good Hope' (Ellerman *et al.* 1953), the type specimens probably having come from the region in which Langebaanweg is located.

The only other mustelid, living or fossil, from this region is the musteline, *Ictonyx striatus*. It is still one of the more commonly occurring small carnivores in the vicinity of Langebaanweg. Small carnivores are well represented in the Varswater Formation fauna, but all are viverrids and the apparent absence of even one musteline is notable.

Wolverines are today known only from Arctic and sub-Arctic regions, so the presence of a fossil wolverine at Langebaanweg at about 33°S would seem at first sight to be extraordinary. It is, however, but one of several species in the Varswater Formation which have living counterparts on continents other than Africa. Other examples are a bear (Hendey 1972, 1977) and a peccary (Hendey 1976*a*). Such species belong to groups which had a much wider distribution in the Old and New Worlds during the late Tertiary than was the case subsequently. There was evidently appreciable faunal interchange between Africa and Eurasia at certain times during the late Tertiary. Greater climatic uniformity and differences in the pattern of zoogeographic barriers contributed to the existence of a more widespread and cosmopolitan fauna at that time.

The wolverines of that period were obviously not inhabitants of cold regions as they are today, and no satisfactory explanation can be offered for their failure to maintain their position other than in northern high latitudes. The living wolverine is a remarkably strong and resourceful animal, and one of the more extreme examples of an opportunistic feeder. It is difficult to conceive of its large late Tertiary forebears becoming extinct through unsuccessful competition with other carnivores or because of a decline and extinction of a preferred prey species. Similarly, since the wolverine today flourishes in the most rigorous of climates, the climatic deterioration late in the Tertiary, and subsequently, is unlikely to have adversely affected its viability. The failure of the bear-like wolverine, and of true bears, to survive in Africa is one of the more curious aspects of the later history of mammals on this continent.

No such problems exist in the case of the honey badgers. *Mellivora capensis* is still found over much of Africa and parts of southern Asia (Dorst & Dandelot

TABLE 10

Carnivora of the Varswater Formation, Langebaanweg.

	Quartzose Sand Member	Pelletal Phosphorite Member	
		bed 3aS	bed 3aN
Canidae			
Vulpes sp.		×	×
Ursidae			
Agriotherium africanum		×	×
Mustelidae			
Plesiogulo monspessulanus	×	?	
Mellivora benfieldi		×	×
Enhydriodon africanus		×	×
Phocidae			
Prionodelphis capensis	×	×	×
Viverridae			
Viverra leakeyi	×	×	×
Genetta sp.	×		
Herpestes sp. A	×	×	
Herpestes sp. B	×	×	
Herpestinae spp. C, D, E	×		
Herpestinae (not studied)		×	×
Hyaenidae			
Adcrocuta australis	×	?	?
Ictitherium preforfex		×	×
Hyaena abronia	×	×	×
Hyaenictitherium namaquense	×		
Euryboas sp.	×	×	×
Hyaenidae sp. E		×	
Hyaenidae (not studied)		×	×
Felidae			
'*Machairodus*' sp.	×		
Homotherium sp.	×	×	
Felis sp. (small)	×		
Felis aff. *issiodorensis*	×	×	
Felis obscura		×	
Dinofelis aff. *diastemata*	×	×	×
Felidae (not studied)		×	×
Unclassified Carnivora			
Gen. et sp. indet. (Canidae or Viverridae)	×		
Gen. et sp. indet. (?Procyonidae)	×		
Gen. et sp. indet. (?Lutrinae)	×		
Gen. et sp. indet. (?Otariidae)		×	

1970), although it is probably nowhere common. *Mellivora* has a poor fossil record, but the genus has probably had an uninterrupted tenure in Africa since late in the Miocene. Apart from the Langebaanweg species and Pleistocene representatives of the genus in South Africa (Hendey 1974*a*, 1974*b*), there is an approximately 10 m.y. old *Mellivora* recorded from the Ngorora Formation in Kenya (Bishop & Pickford 1975). The Ngorora species is undescribed, but it is apparently the earliest record of the genus anywhere. This, together with the suggestion made above that Asian *Eomellivora* and *Promellivora* were not directly related to *Mellivora*, suggests that the latter genus may have had its origins in Africa. The ultimate origins of *Mellivora* are obscure, but there is now a middle Miocene mellivorine recorded from South West Africa (Hendey 1978*b*), which probably is a suitable structural ancestor. This animal, which is tentatively identified with *Ischyrictis*, might also be ancestral to *Plesiogulo*.

Unlike the situation with *Plesiogulo*, the extinction of *Enhydriodon* in the late Pliocene or early Pleistocene could be explained by unsuccessful competition. The appearance in Africa of both *Lutra* and *Aonyx* was apparently more or less coincident with the disappearance of *Enhydriodon*. Otters are, however, not common as fossils in Africa and much has yet to be learnt of the history of the subfamily on this continent.

The 'E' Quarry mustelids provide little information on the problem of the age of the Varswater Formation. The three species are consistent with a post-'Pikermian' and pre-'Villafranchian' age, but only when their broadly contemporaneous counterparts from securely dated contexts elsewhere are better known will they be useful for relative dating purposes.

On the other hand, *Mellivora benfieldi* and *Enhydriodon africanus* are significant in providing evidence that there was an appreciable time interval between deposition of beds 3aS and 3aN of the Pelletal Phosphorite Member. Other supporting evidence has yet to be published and it is intended to delay a detailed consideration of this matter until more of the taxa common to these units have been studied. There is little prospect yet of being able to establish the duration of the time interval, but this may change as more is learnt of late Miocene and Pliocene faunas elsewhere in Africa.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

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

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

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

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

Holotype

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

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

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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

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as
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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

Q. B. HENDEY

LATE TERTIARY MUSTELIDAE (MAMMALIA, CARNIVORA) FROM LANGEBAANWEG, SOUTH AFRICA