ANNALS OF THE
SOUTH AFRICAN MUSEUM

VOLUME 52

ANNALS

OF THE

SOUTH AFRICAN MUSEUM

VOLUME 52

PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
1968–1969

PRINTED IN SOUTH AFRICA BY
THE RUSTICA PRESS, PTY., LTD., WYNBERG, CAPE

LIST OF CONTRIBUTORS

NEW GENERIC NAMES PROPOSED IN THIS VOLUME

Namamurex Carrington & Kensley, 1969 (Muricidae), 197
Zorillodontops Cluver, 1969 (Scaloposauridae), 187

INDEX TO GENERA AND SUBGENERA

(Synonyms in italics)

INDEX TO GENERA AND SUBGENERA

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

Volume **52** Band
October **1968** Oktober
Part **1** Deel

THE TUNAS OF THE GENUS *THUNNUS* IN SOUTH AFRICAN WATERS

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Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

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Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

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van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad
(Kontant met bestelling, posvry)

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.-p.i.), 5(2, 5, 7–9), 6(1, t.-p.i.), 7(1, 3), 8, 9(1–2), 10(1–3), 11(1–2, 7, t.-p.i.), 21, 24(2), 27, 31(1–3), 38, 44(4).

Price of this part/Prys van hierdie deel

R2.00

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

THE TUNAS OF THE GENUS *THUNNUS* IN SOUTH AFRICAN WATERS.

PART I. INTRODUCTION, SYSTEMATICS, DISTRIBUTION AND MIGRATIONS

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(With 8 figures)

[*MS. received* 19 *August* 1964]

Contents

Introduction

In South Africa research on the tunas lagged far behind that in European countries, the Americas, and especially Japan. Prior to 1945 tunas were considered by ichthyologists to be only rare migrants to South Africa.

Tunas were first recorded from South Africa by Günther (1860). Other early records were those of Gilchrist (1902) and Thompson (1918), and later Barnard (1927), Biden (1930), Smith (1935) and Barnard (1939). All considered tunas to be rare in South Africa; only Biden suggested that they might be present in greater quantities than indicated by the records.

In March 1941, tuna were reported to be common in False Bay (newspaper reports), but the species was not identified. In December 1945, large numbers of tuna reported to be small *Thunnus thynnus* (newspaper reports in which the fishes were stated to have been identified by Molteno) were caught from the shore near Cape Point, False Bay. Sport fishing recovered after the war, and by 1952 fishing for tuna off the Cape Peninsula was firmly established. Several thousands of troll-caught tuna were being landed each summer season. Up to

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Ann S. Afr. Mus. **52** (1), 1968: 1–41, 8 figs.

1960 there was no commercial exploitation (Talbot & Penrith, 1960).

At the time of the beginning of the present survey (1960) the possibility of subsurface populations being present was not known, tuna were thought to be absent from the Cape in winter, and nothing was known of their biology from this area. Molteno (1948) had published a useful list of species known and to be expected from South Africa, with biological data based on work in other parts of the world, and Smith (1949) considered the species known at that time, giving a key for their identification in his treatise on South African marine fishes.

The present survey was conducted in two parts, as an eighteen-month survey in the south-western Cape (1960–1) and a two-month survey in the south-western Indian ocean (August 1962; February 1963). A ship, crew, and equipment were supplied by Irvin & Johnson Ltd. for the Cape survey, and by the South African Navy and the South African Council for Scientific and Industrial Research for the Indian ocean. Scientists were supplied by the South African Museum and the Council for Scientific and Industrial Research. It was decided that of the four possible methods for obtaining tuna samples (surface trolling, pole-and-line fishing, long-lining, and purse seining) only long-lining would be used, as this method required the least ship modification.

Aims of the survey

It was decided that priority should be given to the following problems, which were considered to be of particular interest:

(*a*) Systematics. In 1960 the taxonomy of tuna throughout the world was very confused; for example, the Atlantic and Indo-Pacific yellowfin, which were indistinguishable when placed side by side, were put in different genera. This was the case with many of the tunas, and matters had reached such a point, where, for clarity, the common names were being used rather than the scientific. It was felt that specimens from the Cape, being situated at the boundary between the Indo-Pacific and Atlantic oceans, could be of value in solving some of these systematic problems.

(*b*) Distribution. As three very different water masses meet at the Cape, attention was aimed at local distribution, and the relationship between distribution and hydrographic factors.

(*c*) Feeding. Practically nothing was known about feeding of tuna in South African waters. Troll-caught tuna fed mainly on pilchards (*Sardinops ocellata*) and squid (*Loligo reynaudi*) (personal observations) and the only published statements were by Horne (1959) on the finding of a grunter (*Pomadasys operculare* Playfair) in the stomach of a large *Thunnus thynnus* netted in False Bay. There was no knowledge of possible food preferences and competition between species in this area.

(*d*) Breeding. Nothing was known about the breeding of the tuna found off South Africa. The breeding times and size of maturity were unknown; it was not even known whether tuna did breed in South African waters. From the findings of sports fishermen it was assumed that the tuna left to breed elsewhere

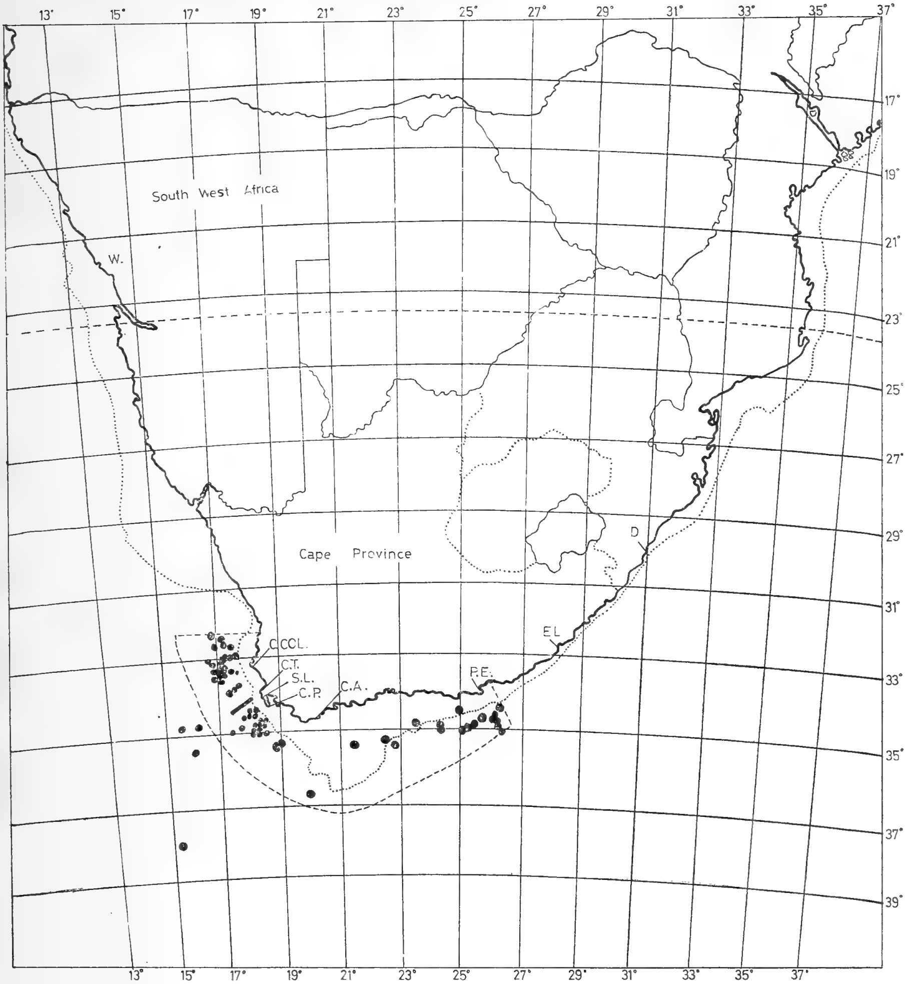

Fig. 1. Area of survey. Each dot represents one station, except off Slangkop, Cape Peninsula, where the solid line represents 51 stations.

during the southern winter (May–September), as no tuna were caught during these months. It was hoped that detailed examination of the gonads could give give some indication of when the breeding period occurred, and possibly whether breeding took place locally or not.

(*e*) Age and growth. It was proposed to use the length frequency method of determining growth, and to examine scales or some part of the skeleton (e.g. otoliths or vertebrae) in an attempt to find growth rings which could be correlated with any modes found in the length frequency curves.

The results bearing on (*a*) and (*b*) above are reported on in this paper.

Area of study

It was decided that, rather than cover a wide area in an overall search for subsurface fishes, it would be more valuable to concentrate the survey in one area, so that any changes during the year would be more comparable. The survey was concentrated in a line running out magnetic west from Slangkop for two reasons: firstly, surface tuna were known to occur in the area in large numbers at certain times of the year (Horne, 1954), and secondly, the University of Cape Town research vessel *John D. Gilchrist* had a monthly series of hydrographic and plankton stations on the same line. It was also known that sudden changes in surface temperature occur along this line, a factor widely known as a good indicator for tuna (Thompson, 1917; Powell *et al.*, 1952; Murphy & Shomura, 1955). Figure 1 is a map of the area surveyed, indicating the stations at which long-lines were fished.

Sixteen cruises of between four and fifteen days' duration were made. During four of the cruises fishing was undertaken off the east coast, but on all four occasions the fishing was severely hampered by storms. In addition to these cruises, two cruises, each of a month, were made in the south-west Indian Ocean, one in summer and one in winter. A complete list of stations is given in Appendix A.

Description of methods used

One basket of gear with components and lengths is sketched in figure 2. Each basket was 200 fathoms long. 8 mm Kuralon was used for the main line and droppers. In order to study depth distribution the normal catenary curve of the line was accentuated by keeping the outer droppers short, and lengthening the middle droppers.

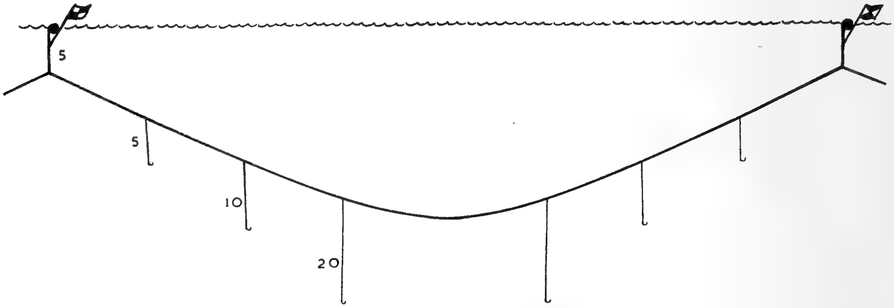

Fig. 2. Diagrammatic representation of one basket of long-line as used in the present survey. Lengths in fathoms.

Setting was begun before dawn (5.00–6.30 hours) throughout the year, as tuna seem to be mainly dawn and dusk feeders (Nakamura, 1949; Powell, 1950; Powell *et al.*, 1952). Bait used was whole pilchards (*Sardinops ocellata*), frozen or lightly salted. Usually twenty baskets of long-line were set at a time, this taking some forty minutes.

At the completion of setting, a bathythermograph cast was made, water samples and temperatures taken. Three water samples and temperatures were made, at 0, 30 and 150 metres, using a Petterson-Nansen insulated bottle fitted with a Negretti and Zambra thermometer. The two subsurface depths were chosen as being at above the level of the shallowest and deepest hooks. Salinity determinations were made by the Division of Sea Fisheries using a salinometer. Hauling of the long-line was done at about 10.30 a.m., after the line had been in the water for about 4–5 hours. The condition of each hook was listed as it was hauled (baited, no bait, fish).

Immediately after completion of hauling the fish were all washed, spread out on the deck, and the identification in the hook log checked. The fork-length of all fish was then measured using a 2·5 metre long pair of calipers, and morphometric measurements according to the method of Marr & Schaefer (1949) were made on as many fish as possible. Measurements other than fork-length were not made on albacore (*T. alalunga*).*

The gonads and stomach contents of all fish (other than shark-damaged specimens) were removed and preserved. Formalin of 10% strength was used so as to stop the process of digestion as rapidly as possible and to harden the forage organisms which had become soft due to digestion.

Notes on sampling

Selectivity

No fishing gear is completely unselective, and the long-line is no exception. The factors that might influence selection are discussed below.

(*a*) Hook size

The Japanese hook (size 3, 6 cm high, 3 cm wide) was chosen because it was the middle of the size range offered. It was found, however, that hook size is only of minor importance, as tuna from 5 to 400 lb were landed, as well as other larger fish which had much larger mouths than any tuna (large sharks, e.g. *Prionace glauca* and marlins, *Makaira* spp., of up to 1,460 lb), and exceptionally small-mouthed fishes such as *Brama raii* and a pilot fish *Naucrates ductor* weighing less than 1 lb. It is not possible to disprove selection due to hook size, but the wide size range of fishes taken suggests it was not a major factor.

(*b*) Sampling depth

There was a very marked selection due to the sampling depth. Surface trolling by game-fishing vessels off the Cape Peninsula results in a catch consisting almost exclusively of yellowfin tuna (*T. albacares*), whereas in the survey *T. albacares* accounted for only 11·6% of the total tuna catch, and in the Cape

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* In South Africa *T. alalunga* has the common name longfin tuna. The name albacore is used for the carangid *Seriola lalandii*.

Peninsula area 8·8%. Conversely, the long-line took large numbers of other tuna species that had only rarely been taken by surface trolling. This makes it difficult to attempt to assess the true relative abundance of the various species, but subsurface long-lining did capture fair numbers of four species, whereas surface trolling or pole-and-line fishing could be expected to take only two species. Long-lining also in general captures larger fish than surface trolling; *T. alalunga* of over 950 mm fork-length are rare using the latter method but are commonly taken on long-lines. Presumably this is due to swimming depth of various sizes of tunas.

(*c*) Hunger and seasonal feeding changes

By its nature a baited line will normally only take feeding fish. Sampling error caused by this, and possibly also by seasonal changes in food requirements, could not be assessed.

Faults and advantages of the sampling method used

The major fault of long-lines for obtaining samples of tuna is that only the subsurface populations are sampled. Surface trolling has shown much larger populations of *T. albacares* in the area surveyed than the results from the long-lining.

Another disadvantage was the lack of any knowledge of actual depth of capture. The work of Kamimura (1957) has suggested that most tuna are caught at a depth shallower than the maximum to which the hook sinks. It was not known in the present survey exactly how deeply the hooks did sink. Some workers, especially at the U.S. Bureau of Commercial Fisheries at Hawaii, used a rangefinder or radar to measure the distance between the buoys and, knowing the length of the line between them, could calculate the catenary of the line. This, however, does not take into consideration the effects of bowing or slanting of the line due to subsurface currents or the action of hooked fish. It was planned to attach Kelvin sounding tubes to certain of the droppers to find the catenary of the line, but their use was discontinued owing to the very contradictory results obtained (see also Murphy & Shomura, 1953). Graham & Stewart (1958) have shown that the line may go deeper during hauling than it normally hangs. Attempts to locate the line by means of echo-sounding were unsuccessful. On one occasion off Port Elizabeth several of the hooks did touch the bottom, bringing up bits of coral, from 78 to 80 fathoms, showing that the deepest hooks at least reach this depth.

It was assumed that the outside hooks of the basket with 5-fathom droppers fished at 15–20 fathoms, the 10-fathom droppers at 35–45 fathoms, and the long centre dropper of 20 fathoms at 75–80 fathoms.

In general it can be stated that the long-line, in spite of the above disadvantages, is probably the best method of estimating the abundance and size-range of large subsurface fishes.

Systematics

Starks (1910) was the first to notice the presence of a prootic pit in the skull of certain of the Scombridae, and proposed the subfamily Thunninae to contain the genera *Thunnus*, *Auxis*, *Katsuwonus* and *Euthynnus*, which possessed it. Kishinouye (1923), after his careful anatomical studies on the Scombridae, on the basis of the prootic pit and the subcutaneous blood system which he found to be present in the fishes contained in Starks's Thunninae, proposed that these four genera (much subdivided by him), should be separated into the order Plecostei, having equal rank with the order Teleostei, which would contain all the other bony fishes. It is perhaps best to consider Kishinouye's work as a brilliant monograph on scombrid anatomy, but to ignore the final section on classification. Berg (1940) in his definitive work unfortunately leaned heavily on Kishinouye. Berg's order Thunniformes (being Kishinouye's Plecostei) is removed from the suborder Scombroidei in the order Perciformes. This step is not quite so drastic as that proposed by Kishinouye, but any attempt to separate the tunas and mackerels into even separate families does not seem warranted.

Since 1950 several reviews of the Scombridae have appeared. Fraser-Brunner (1950) proposed a straightforward classification, having two subfamilies, Gastrochismatinae and Scombrinae, and sinking many of Kishinouye's genera to subgeneric level. Ginsburg (1953) and Godsil (1954) agreed with Fraser-Brunner that the Thunniformes and Scombroidei (of Berg) were so closely related that they should be kept in one family. This has been done also by Collette & Gibbs (1963*a*, 1963*b*), and has been followed here.

Many generic names have been suggested for the large tunas, and *T. alalunga*, *T. obesus*, *T. albacares* and *T. tonggol* have all been placed in monotypic genera at various times. Most authors now consider that the genera *Germo*, *Neothunnus*, *Kishinoella* and *Parathunnus* should be dropped (Fraser-Brunner, 1950; Ginsburg, 1953; Godsil, 1954; De Sylva, 1955; Collette & Gibbs, 1963*a*) but the names have remained in general use because they were the names used by many tuna biologists in Japan and the United States. There are a number of reasons for placing all the large tunas in a single genus, the main one being the arbitrary nature of any divisions within the group, depending upon what characters are used. The following choices of grouping indicate this. Watson (1963) has shown on the basis of osteology that there can be two groups, *T. obesus* being similar to *T. thynnus* and *T. alalunga*, while *T. albacares* is similar to *T. tonggol* and *T. atlanticus*. De Sylva has suggested, also on the basis of osteology, that *T. albacares* and *T. obesus* are closely related. Beebe & Tee-Van (1936) claimed on the basis of external morphology that *T. obesus* and *T. atlanticus* are closely related. This indicates that such groupings give little information on the phyletic history of the tunas. A single genus with several species seems the best arrangement of the group.

Genus THUNNUS South, 1845

Description: Body robust; abdomen without median groove for pelvic fins; adults with body completely scaled, anterior scales larger, forming a corselet; juveniles not necessarily fully scaled (Moore, 1951); interpelvic process bifid; teeth small, conical, in a single row in each jaw; vomer and palatines toothed; no strongly developed adipose eyelids; well developed lateral keel on each side of caudal peduncle and two smaller keels on tail above and below hind end of larger keel; gill-rakers 20–42 (both arches); dorsal fins almost contiguous; dorsal spines 13–15, rays 22–23, some posterior rays separated as separate finlets; anal rays 21–22, with posterior finlets as in dorsal; vertebrae 39, first reduced and firmly articulated to the skull; well developed subcutaneous blood-vessels on sides; skull with deep prootic pits.

The number of species in the genus is still in some doubt (Rivas, 1961; Roedel & Fitch, 1961) but a number of authors such as Collette (1961), Collette & Gibbs (1963*a*), Mather (1963*a*), and Watson (1963) consider that there are six species. Here we provisionally recognize seven species, of which five occur in South Africa waters.

Thunnus albacares (Bonnaterre)

Yellowfin

Scomber albacares Bonnaterre, 1788:140.
Neothunnus itosibi: Smith, 1935:207. Molteno, 1948:33.
Germo albacora: Molteno, 1948:20. Smith, 1949:299.
Germo itosibi: Smith, 1949:299.
Thunnus albacares: Talbot & Penrith, 1960:1, 1961*a*:1, 1962:558, 1963*a*:617. Talbot, 1964:205. De Jager, 1963:589. De Jager *et al.*, 1963:11.

Liver without striations on its ventral surface, and with the right lobe longer than the central and left lobes. Pectoral fins long, reaching to or beyond the origin of the soft dorsal except in large individuals. Dorsal and anal lobes exhibiting marked allometric growth and becoming extremely elongated in large specimens, reaching even beyond the caudal fin. Gill-rakers 11 + 19–20. (See table 1, for morphometric data.) Swim bladder present. A dense rod of connective tissue running down the dorsal wall of the body cavity presses into

Thunnus albacares

Fork-length	594	614	935	1145	1230	1505
Height D^2	65	79	151	215	321	514
Height anal	68	77	154	218	236	594
Length pectoral	171	190	266	318	315	371
Head	169	175	253	300	312	370
Snout—D^1	186	194	273	329	350	399
Snout—D^2	320	341	491	601	628	738
Snout—anal	358	371	531	654	695	832
Depth	153	158	245	300	327	366
Length maxilla	65	71	102	118	120	148

TABLE 1. Morphometric data for *Thunnus albacares* caught off the Cape Peninsula.

the swim bladder. Body shape, when compared with *T. obesus*, less deep. Reaches about 400 lb in weight. Colour royal blue on back, white or silver on belly, separated by a lateral golden stripe some 5 cm wide in a fish of 1 metre. Dorsal lobe dark at its base, golden yellow above this, with a white tip in large specimens. Anal lobe similar to dorsal, but with a silver-white base. Dorsal and anal finlets bright orange yellow, with or without a thin black border.

This species has an extensive synonymy, due in large measure to the marked allometric growth of the dorsal and anal lobes. This aspect has been discussed fully by Cunningham (1910), Kishinouye (1923), Beebe & Tee-Van (1936), Schaefer & Walford (1950), Schaefer (1952), and particularly by Royce (1961, 1965).

Following Collette (1961), Collette & Gibbs (1963*a*), Royce (1961, 1965) we recognize one world-wide species of yellowfin tuna.

A consideration of the taxonomic status of the bluefin tunas

We have decided not to consider the southern Indo-Pacific and Atlantic bluefin tuna as subspecies of *Thunnus thynnus*, as suggested by Collette & Gibbs (1963*a*), and previously by ourselves (Talbot, 1964; Talbot & Penrith, 1963*a*). We have done this after a careful consideration of the position in South African waters, where these two forms overlap in distribution.

There are clearly at least three series of populations, one series being found in the Atlantic and Mediterranean, another in the northern Indian and Pacific oceans and a third in the southern Atlantic and Indo-Pacific. They can be distinguished from each other in almost all individuals on a number of characters, including gill-raker counts, skeletal differences, and coloration.

The large bluefins found in summer at the Cape have the typical characteristics of the populations known from the Atlantic Ocean, the clearest being a high gill-raker count. The large populations of smaller bluefin found in the area in winter have the characteristics of southern Indo-Pacific fishes (low gill-raker counts and bright yellow peduncle keels). It is therefore likely that these fishes belong to the North Atlantic and southern Indo-Pacific groups of populations respectively and return to them. Until these fish are actually marked and recovered this must remain an assumption.

Given this assumption there is a reasonable case for separating the bluefins at the Cape into two species. Gill-raker counts, coloration, and skeletal differences are clearly marked between the summer and winter populations. No merging of differences or different combinations of characters are found, although the two forms are sympatric at one time of year. Two isolating mechanisms seem to have developed. There is a difference in breeding times, with the southern fishes feeding at the Cape in the southern winter, with completely inactive gonads, so apparently breeding in the southern summer, and with the northern fishes present in the Cape in the southern summer with again completely inactive gonads, and apparently breeding elsewhere in the southern winter. These characteristics indicate that different behavioural characteristics have developed which keep them genetically apart in spite of their sympatry during some part of the year at the Cape. We consider that there is sufficient genetic isolation, causing visible morphological differences, to justify accepting the two bluefins found at the Cape as separate species, although the division of the bluefins is clearly of more recent date than that of the other species.

The earliest name available for a southern ocean species is *Thunnus maccoyii* (Castelnau, 1877).

The position of the third bluefin, the northern Indo-Pacific species, at times referred to as *T. orientalis*, is beyond the scope of this paper. Nakamura (1965) appears to consider it to be no more than a subspecies of *T. thynnus*, a position retained in the authoritative work of Gibbs & Collette (1967).

Thunnus thynnus (Linnaeus)
Atlantic Bluefin Tuna

Scomber thynnus Linnaeus, 1758: 297.
Thunnus thynnus: Barnard, 1927:798. Molteno, 1948:16. Smith, 1949:298. Talbot & Penrith, 1962:558, 1963*a*:637.

Entire ventral surface of liver covered with blood-vessels forming dense striations. Pectoral relatively short, not reaching past the eleventh or twelfth dorsal spine. Length of dorsal and anal lobes short. Gill-rakers (South African specimens) 12 – 15 + 26 – 31, total 37 – 44 (see table 2). (Morphometric data given in table 3.)

Gill-rakers	31	32	33	34	35	36	37	38	39	40	41	42	43	44
T. maccoyii	1	2	3	5	1	1								
T. thynnus											1		1	1

TABLE 2 (South African specimens only)

Colour of body dark blue-black above, with white below, in life or freshly dead said to be separated by a yellow or iridescent blue band (Migdalski, 1958; Tiews, 1963). Pectoral fin dark silver at base, dark grey or black distally with red patches. Dorsal lobe dark, with yellow and red near tip. Anal lobe silver with red and yellow as dorsal lobe. Finlets yellow with broad black edging. Caudal fin dark with red or yellow posterior edge. Peduncle keels dark. Reaches 1,600 lb (Crane, 1936), and reputedly 2,000 lb. South African specimens were all adult.

Thunnus thynnus

Fork-length	2151	2671	Snout—D¹	585	740
Height D²	362	422	Snout—D²	1075	1345
Height anal	353	366	Snout—anal	1220	1537
Length pectoral	402	400	Depth	522	695
Head	558	675	Length maxilla	220	258

TABLE 3. Morphometric data for *Thunnus thynnus* caught off the Cape Peninsula.

The distribution and taxonomy of Atlantic bluefins have been the subject of much controversy. Storer (1867) differentiated western Atlantic fishes from those on the European side under the name *T. secundodorsalis*. The validity of *secundodorsalis* was questioned by Jordan & Everman (1926) and Godsil & Holmberg (1950), but they did not formally suppress the name. Ginsburg (1953), however, claimed the two populations were distinct on morphometric and meristic grounds. His meristic characters show slight differences in means, but it is not certain whether these would disappear with larger samples.

Rivas (1954) considered there to be one Atlantic species, with two separate breeding populations racially or subspecifically distinct. Sella's (1927, 1929) suggestions that an exchange of fish took place across the Atlantic has now been thoroughly proved by Mather's tagging studies (1960, 1962, 1963). Tagging returns indicate that *T. thynnus* can cross from America to Europe, and is, therefore, quite capable of swimming to the Cape.

Thunnus maccoyii (Castelnau)
Southern Bluefin Tuna

Thynnus maccoyii Castelnau, 1872:109.
Thunnus maccoyii: Nakamura, 1965:18. Penrith, 1967:535
Thunnus thynnus (*non* Linnaeus) Talbot & Penrith, 1962:558.
Thunnus thynnus maccoyii: Serventy, 1956*a*:13.
Thunnus thynnus orientalis non Temminck & Schlegel, 1844:94. Talbot & Penrith, 1963*a*:630. Talbot, 1964:201. De Jager, 1963:589. De Jager *et al.*, 1963:11.

Liver completely striated ventrally. Pectoral short, scarcely reaching the origin of the second dorsal. Dorsal and anal lobes short. (Table 4 gives morphometric data.) Gill-rakers 30–38 in total, but usually 33–34 (see table 2). Swim bladder variable, usually being better developed in large fishes. Colouring in general similar to *T. thynnus*, but no trace of yellow on the dorsal and anal lobes and the pelvic in fishes examined by us. The peduncle keels are usually bright yellow, sometimes darker, but always with a translucent, almost hyaline, look, unlike the solid black of *T. thynnus*. Finlets yellow with a thin black edge.

	Thunnus maccoyii			
Fork-length	1045	1202	1235	1351
Head	30·4	30·2	29·2	29·1
Snout—D^1	31·5	31·7	33·1	30·4
Snout—D^2	55·3	54·7	55·7	53·9
Snout anal	60·2	60·3	63·4	58·7
Depth	26.7	26·5	26·2	26·9
Length pectoral	23·1	20·4	23·6	21·6
Height D^2	12·9	12·6	14·1	11·6
Height anal	13·3	13·0	13·6	11·6
Length maxilla	12·2	12·2	12·1	11·3
Gill-rakers	33	34	33	34

TABLE 4. Morphometric data for *Thunnus maccoyii* caught off the Cape Peninsula.

Thunnus alalunga (Bonnaterre)
Longfin, Albacore

Scomber alalunga Bonnaterre, 1788:139 (based on a description by Cetti, 1777).
Thynnus alalonga: Günther, 1860:366. Gilchrist, 1902:128. Thompson, 1918:108.
Germo alalunga: Smith, 1949:299. Molteno, 1948:29.
Germo alalonga: Barnard, 1927:799.
Thunnus alalunga: Talbot & Penrith, 1960:1, 1962:558, 1963*a*:609. Talbot, 1964:199. De Jager, 1963:589. De Jager *et al.*, 1963:11.

Ventral surface of liver densely covered with striations. Pectoral fins sabre-shaped and elongate, reaching to or beyond the first anal finlet. Dorsal and anal lobes low. Gill-rakers 8–9 upper, 19–21 lower, 28–30 total. Back dark metallic blue, belly silver-white, separated by an iridescent blue band, which disappears after the fish is gaffed. Pectoral fin black, ventral and dorsal lobes dusky. First dorsal lobe colourless, anal lobe silver. Posterior edge of caudal fin white, dorsal finlets pale yellow with dusky edges, ventral finlets dark. Reaches 80 lb, usually smaller. Flesh paler than other species. (See table 5.)

Thunnus alalunga

Fork-length	818	864	892	975	993
Height dorsal^2	93	111	118	128	128
Height anal	94	107	122	134	130
Length pectoral	352	387	409	397	408
Head	233	254	273	290	289
Snout—dorsal^1	271	287	320	232	321
Snout—dorsal^2	482	502	574	573	583
Snout—anal	514	535	610	631	631
Depth	203	220	257	277	255
Length maxilla	90	97	104	112	105
Gill-rakers:					
upper	20	21	21	21	20
lower	10	9	9	9	10
Total	30	30	30	30	30

TABLE 5. Morphometric data for *Thunnus alalunga* caught off the Cape Peninsula.

This is considered to be one widely ranging species and while little is known of its movements in the Indian or Atlantic oceans, it has been shown to make trans-Pacific migrations (Blunt, 1954; Otsu, 1960; Uchida & Otsu, 1961; Clemens, 1961, 1963).

Thunnus obesus (Lowe)
Bigeye

Thynnus obesus Lowe, 1839:78.
Thunnus obesus: Talbot & Penrith, 1960:1, 1961*a*:1, 1961*b*:240, 1962:558, 1963*a*:624. Talbot, 1964:203. De Jager, 1963:589. De Jager *et al.*, 1963:11.

Liver showing patches of peripheral striations. Pectoral fin one quarter to one sixth of total length, reaching the end of the dorsal lobes, becoming relatively shorter with increased size. Dorsal and anal lobes short compared with *T. alba-*

Thunnus obesus

Fork-length	1172	1356	1483	1582	1784
Height D²	170	223	220	285	301
Height anal	175	214	213	271	290
Length pectoral	319	356	369	410	422
Head	337	391	395	446	493
Snout—D¹	362	401	447	469	518
Snout—D²	652	747	828	836	946
Snout—anal	652	853	924	937	1057
Depth	325	367	392	415	468
Length maxilla	141	152	172	182	199

TABLE 6. Morphometric data for *Thunnus obesus* caught off the Cape Peninsula.

cares. Gill-rakers 7–9 upper, 18–20 lower, 26–28 total. (See table 6 for morphometric data.) Swim bladder with very deep paired pits anteriorly, and no central thick connective tissue ridge pressing down into the swim bladder as in *T. albacares*. In spite of the name the eye of the bigeye tuna is not much larger than in the other tunas. The eye of *T. alalunga* is actually greatest in relation to fork-length (5·3–5·7). The eyes of both *T. albacares* (3·2–6·2%) and *T. maccoyii* (3·1–4·1%) may occasionally reach the size range of *T. obesus* (3·5–4·6%) at the same size. (See also Mather, 1963.)

Key to the genus Thunnus

The following key has been constructed to include all species which may be found to comprise the genus *Thunnus*:

1	(*a*)	Pectoral fin reaching beyond posterior margin of anal fin	2
	(*b*)	Pectoral fin not reaching beyond posterior margin of anal fin, although it may reach anal fin insertion	3
2	(*a*)	Posterior edge of caudal fin with a distinct white edging; ventral surface of liver dark and densely striated	*T. alalunga*
	(*b*)	No white edging on posterior edge of caudal fin; liver pale and at most only slightly striated (juvenile tuna)	3
3	(*a*)	Liver without striations ventrally	4
	(*b*)	Liver with distinct striations ventrally	6
4	(*a*)	Total gill-raker count over 25 (usually 27–31); all fins bright yellow including the first dorsal	*T. albacares*
	(*b*)	Total gill-raker count less than 25	5
5	(*a*)	Body deep (depth over 27% of fork-length); distance snout to anal fin more than 56% of fork-length. Small air bladder present	*T. atlanticus**
	(*b*)	Body slender (depth under 26% of fork-length); distance snout to anal fin less than 60% of fork-length. No air bladder	*T. tonggol**
6	(*a*)	Total gill-rakers more than 38; often over 400 lb weight	*T. thynnus*
	(*b*)	Total gill-rakers 36 or less; usually less than 500 lb	7
7	(*a*)	Ventral striations on liver in groups near margin. Peduncle keel dark, pelvic fin with red and yellow markings	*T. obesus*
	(*b*)	Ventral surface of liver fully striated	8
8	(*a*)	Peduncle keels bright yellow or hyaline; no yellow markings on pelvic fin. Deep lateral pocket in pectoral region of roof of body cavity	*T. maccoyii*
	(*b*)	Peduncle keels opaque black, yellow markings on pelvic fins. Shallow lateral depression in pectoral region of roof of body cavity	*T. orientalis**

* Not known from South African waters.

Distribution and Migrations

Hydrography

Before the detailed distribution of tunas in the areas surveyed can be discussed, some knowledge of the physical environment is required. The coastline of southern Africa is shown in figure 1, together with the positions of the stations fished. The distribution of water masses in the region of the Cape of Good Hope is complex and variable, although the broad pattern of the currents is known (fig. 3).

Offshore the coasts are ringed by subtropical water; inside this subtropical water, the waters of the east and south coasts are warm and saline, whereas the waters bounding the west coast are cold and of low salinity, although rich in nutrients.

The major water masses in the South African region which were fished during this survey are:

(*a*) South Atlantic Subtropical Surface Water

This water mass is part of the South Atlantic anti-cyclonic gyral. To the south it is bordered by the West Wind Drift, from which it is separated by the Subtropical Convergence at about 37°–40°S. Eastwards it is bordered by the Agulhas Current south of the African continent and the surface waters of the Indian ocean, but there is often no sharp boundary between these waters, and the South Atlantic Subtropical Surface Water may move as far east as Cape Agulhas or further when the force of the Agulhas Current is weak. The temperature and salinity decrease southwards; at 20°S they are of the order of 23°C; 36$^{\circ}/_{\circ\circ}$, while at 34°–35°S they have dropped to 15°–21°C; 35·4–35·9$^{\circ}/_{\circ\circ}$ (Clowes, 1950).

(*b*) Benguela Current

The Benguela Current has recently been discussed in great detail by Hart & Currie (1960), who have shown that the current is caused by local southerly winds inducing an offshore movement of surface water in a north-westerly direction, which in turn causes upwelling. This upwelled water is separated from the north and west-flowing waters of the South Atlantic gyral by a convection cell. It was formerly thought (Clowes, 1950) that the upwelled water had its origin in the Antarctic Intermediate Water, but Hart & Currie have shown that the upwelled water has its origin at 200–300 metres, far above the depth of the Intermediate Current, and originates from Atlantic Central Water. The water inshore of the convection cell is cold (9°–15°C), the temperature depending largely on the degree of upwelling, and of relatively low salinity (34·5–35·1$^{\circ}/_{\circ\circ}$), although rich in phosphates, silicates, and nitrates. It is quite common during calm weather in summer for the surface waters to warm up and a marked thermocline to exist. At station 3425 in February 1958 *Africana II*, a research vessel belonging to the Division of Sea Fisheries, found surface water of 17·55°C and salinity 34·97$^{\circ}/_{\circ\circ}$, while at 30 metres, although the salinity remained con-

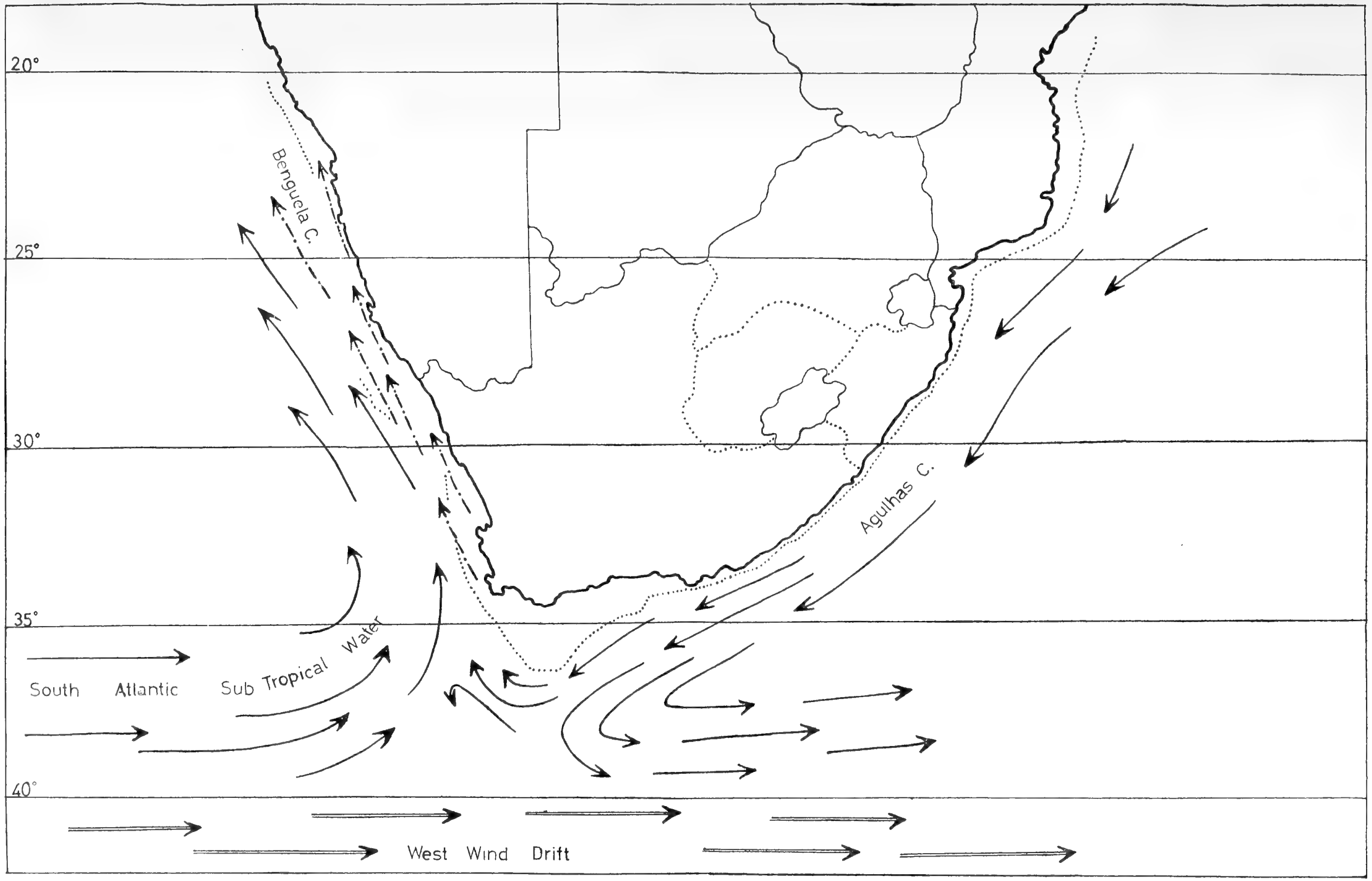


Fig. 3. Current systems around South Africa under typical summer conditions.

stant, the temperature had dropped to 12·14°C. Other stations in the area showed the same effect (Div. Sea Fish. Ann. Rep. 1960).

(*c*) Central Water

The origin of this water is believed to be the sinking of surface water at the Subtropical Convergence (Sverdrup *et al.* (1942) although Clowes (1950) suggests that it is the direct result of mixing between surface subtropical water and the underlying Intermediate Water. In the present survey only Atlantic Central Water which contributes to the Benguela Current is involved. The temperature range is 5°–12°C, and the salinity 34·3–35·1°/₀₀ (Sverdrup *et al.*, 1942). It lies below the surface waters at 150–500 metres (Hart & Currie, 1960).

(*d*) Agulhas Current

The Agulhas Current forms part of the South Indian ocean gyral, being derived from the southern branch of the South Equatorial Current, flowing down the west side of Madagascar, and down the southern African coast to the tip of Africa. The currents in the Mozambique Channel are thought to be variable, but may contribute at certain times of year to the Agulhas Current. The speed of the current is considered to be 3–4 knots (*African Pilot*). When the current reaches the Agulhas Bank, it swings away from the South African coast, following the edge of the bank, moving in a south-westerly direction, and then turning eastwards as the Agulhas Return Current.

There is indication that a varying amount of Agulhas Current water may cross the Agulhas Bank, or round its tip, to mingle with the South Atlantic Subtropical Water in the area of the survey, its temperatures generally being in the region of 20°–24°C and the salinity 35·4–35·6°/₀₀, although both may decrease near the coast, but are not known to fall below 17°C; 35·3°/₀₀. The inshore water between the Agulhas Current and the coast, where the current is often northward flowing (Gilchrist, 1903), was not fished, as the water depth was not sufficient for the type of gear used.

(*e*) South Indian Ocean Subtropical Water

This water mass is analogous with the South Atlantic Subtropical Water and, although in general slightly less saline, is several degrees warmer. *Discovery II* found a temperature of 26·58°C and salinity of 35·31°/₀₀ at 21° 44′ E south of the Cape in April (Clowes, 1950). In the south-west Indian ocean, temperatures during this survey ranged from 18·7°–23·2°C in August 1962 and from 22·7°–26·7° in February 1963. This water is separated from the South African coast by the Agulhas Current.

Clowes (1950) has discussed the hydrography of South African seas in detail, and much of the above is based on his work, except that upwelled water off the coast is considered to be Central Water (after Hart & Currie, 1960) rather than Antarctic Intermediate Water. Clowes also gave T/S curves for each 5° of longitude from 5°W to 45°E within latitudes 30°–35°S. The curves

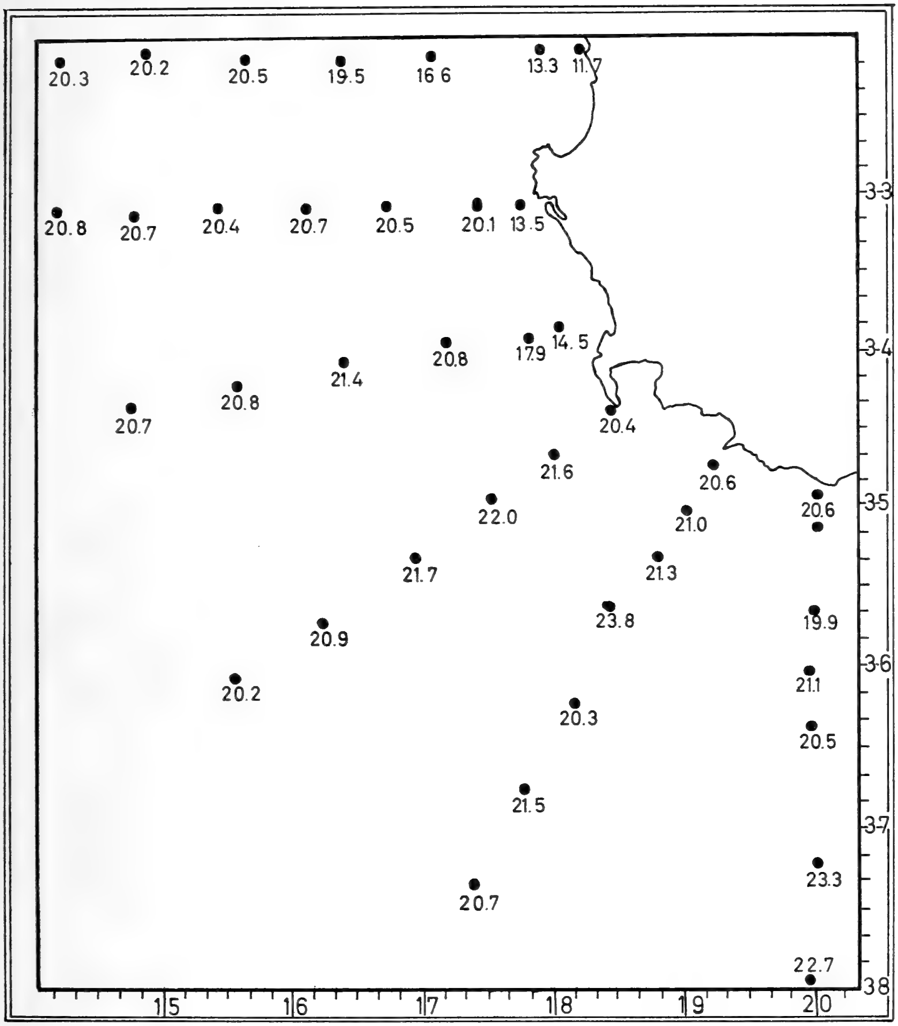


Fig. 4. Temperatures of the surface water off the western Cape in March. Taken from data in the Annual Report Division of Sea Fisheries, 1957–1958.

for the region 5°W to 15°E show clear differences from those for the region 25°–45°E, although crossing several times. Clowes considers the water west of 15°E to be purely Atlantic and that east of 25°E to be purely Indian. In the area 15°–25°E, however, there is a great deal of mixing, both between Atlantic and Indian surface water, and between surface water and upwelled Central Water.

In winter the Agulhas Current is weakened and due to the prevailing winds off the Cape at this time being westerly, the Atlantic water may penetrate eastwards, often to or even beyond Cape Agulhas, and deflect the Agulhas Current south and east (Buys, 1959; De Jager *et al.*, 1963). In summer, however, the conditions are reversed; the Agulhas Current is flowing strongly, the prevailing winds are southerly and easterly and tend to blow the surface water away from the coastline along the west coast. This results in upwelling, and inshore the South Atlantic Surface Water becomes mixed with Central Water. A portion of the Agulhas water appears to continue into the Atlantic (Dietrich, 1935), and there is often in summer a broad band of very warm water (over 20°C) right round the Cape from the Atlantic to the Indian ocean outside the cold upwelled water. Figure 4 shows surface temperatures and salinities prevailing off the Cape in March 1958 (drawn from data in Div. Sea Fish. Ann. Rep. 1960). It clearly shows in this case that, while there is cold upwelled water close inshore from Cape Point westwards, there is very warm water outside, while salinities suggest that Agulhas water is only reaching Danger Point; between it and Cape Columbine there is an area of lower salinities, suggestive of mixed water between the Agulhas water and the Atlantic surface water.

Temperature Tolerance of Tuna

Much work in the field of temperature tolerance of tuna, especially *T. alalunga*, has been done off the Californian coast. As long ago as 1917 Thompson (1917, 1919) suggested that small changes in water temperature might cause marked changes in the distribution of oceanic fishes, as did Hubbs & Schultz (1929) and Walford (1931). Statistics of the Californian tuna industry show great fluctuations in catch; after several good years there are one or two bad ones. In 1925 the catch of tuna was 25 million lb, and in 1926 it dropped to 3 million lb, for instance. Hubbs (1948) was the first to investigate the problem, and concluded that *T. alalunga* had a temperature range of 15·5°–18·4°C, and that when this temperature range did not occur in the fishing area during the tuna season, the fishery did not develop. Later workers (Clemens, 1957, 1958, 1961; Craig, 1959, 1960; Powell & Hildebrand, 1950; Powell *et al.*, 1952; Neave & Hanovan, 1960; Radovich, 1960, 1961) found slightly different limits, but all agreed that the absolute limits for a fishery to develop were above 14·4°C and below 20°C. Occasional fish could still be taken at temperatures above 20°C, but only one fish was recorded below the minimum (Schaefers, 1953). Clemens (1958), Craig (1959, 1960), and Radovich (1960, 1961) found that small fluctuations in surface temperature were of great importance, since a slight rise above the normal, which would result in a northward movement of the isotherms beyond their normal latitude during the tuna season, would cause the fish to move north of their usual area. They found that the best fishing area for the season could be accurately determined by means of a pre-season temperature survey of the usual area, and so successful has this forecasting proved in the last few years that Johnson (1960) could state: 'The value of the sea temperature as a forecasting tool of albacore (*T. alalunga*) distribution has been amply demonstrated during the last four years.' In the Californian area similar temperature effects were found for all other tuna species. Uda (1961*a*, *b*) has made similar observations for the western Pacific ocean.

The temperatures quoted in literature are almost invariably surface, and not ambient temperatures, because of the difficulty of obtaining the latter. Even with fishes caught on long-lines whose depth is more or less known, catches may be made while hooks are sinking or rising. Squire (1963) gives both surface temperatures and those at the hook depth. Surface temperatures are used here,

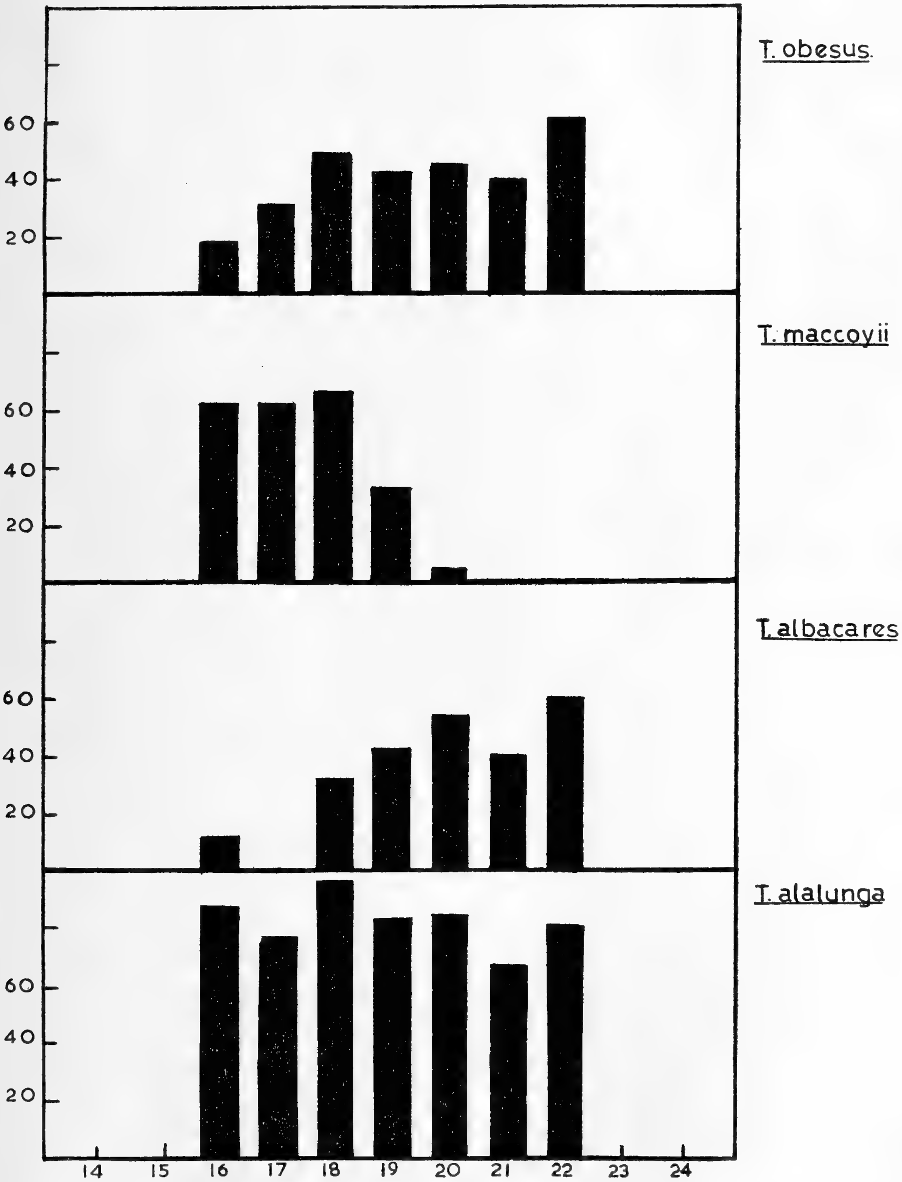


Fig. 5. Percentage of successful stations for each species at various water temperatures (to the nearest 1·0°C). Only temperatures at which more than five stations were occupied are given.

but in appendix A subsurface temperatures are given for all stations where known.

There seems to be a range of temperatures within which a species of tuna is usually found in any one area, but occasionally it may also be found outside this range. We are calling the normal range the 'optimum range', merely on the basis of the fact that the fishes are usually found within it.

The correlation between catch and surface temperature is shown in the histogram in figure 5.

T. alalunga

As shown above, *T. alalunga* off the Californian coast has a normal temperature range of 14·4°–20°C. In other areas, however, slightly different temperatures may be preferred. Alverson (1961) found off British Columbia that the population of north Pacific *T. alalunga* with which he was dealing had an optimum temperature range of 13·3°–16·1°C (54°–61°F). In equatorial regions, on the other hand, there are tuna fisheries taking *T. alalunga* in water of up to 21°C according to Rosa & Laevastu (1961) and Laevastu & Rosa (1963) as shown by their histogram although their chart of fishing areas shows fishing up to the Equator in surface temperatures over 25°C. According to Kishinouye (1923) *T. alalunga* is found in the region of Japan in water of 13°–24°C. Squire finds a range of 11·5°–28·2°C.

Attempts have been made to find the optimum surface temperature (as defined above) for *T. alalunga* (as well as the other species present) during the survey off the Cape. Unfortunately to do this requires a large number of samplings at a wide range of temperatures, which the 111 stations occupied during the present survey did not have. Observations in the centre of the range were adequate, but this was not the case at the possible extremes. The correlation between catch and temperature is shown in the histogram in figure 5.

T. alalunga was taken almost throughout the range of temperatures. Only at temperatures above 22°C was this species never taken. The only stations fished at temperatures higher than 22°C were off the east coast, however, where *T. alalunga* was never found, perhaps for other reasons. On the basis of our observations at the 91 stations at which this species was taken, *T. alalunga* has an optimum range of 16°–22°C, and is occasionally taken in temperatures as low as 14°C.

T. maccoyii

Relatively little work has been done concerning the temperature requirements of *T. maccoyii*. None of the authors who have studied the populations off the Australian coast have published temperature observations of this species, except Robins (1963), who mentioned that adults are seldom found at temperatures above 21°C, and 'juveniles' do not occur above 19°C.

By referring to figure 5 it may be seen that *T. maccoyii* is only rarely taken at temperatures above 19°C in the Cape area, the drop-off in catch rate above this temperature being very marked. The lower limit of *T. maccoyii* is unfortunately not clear; below 15·5°C it seems to become less common.

T. thynnus

According to Mather (1963) and Tiews (1963) *T. thynnus* has a wide temperature range of 12–25°C. In False Bay, Cape Town, this species is only found in water above 20°C.

T. albacares

More observations on the temperature requirements of this species have been made than for most other species, except perhaps *T. alalunga*. Kishinouye (1923) gave a total range for this species of 14°–27°C, but gave as an optimum temperature range 22°–24°C.

In the Pacific ocean, Kamimura & Honma (1963) have shown that the best catches of *T. albacares* are made in the equatorial area between 5°N and 10°S, with the centre of distribution just south of the Equator, where the temperature range is 22°–26°C. Schaefer *et al.* (1963) agree that this species is usually found in water above 20°C, but add that they may occasionally be found in water below 20°C. *T. albacares* in the north-east Pacific is, like *T. alalunga*, affected by small changes in the surface temperature of its normal area, moving polewards during periods of warm water both off California and South America (Blackburn, 1960; Schaefer, 1961), and suggesting that *T. albacares* may avoid water which has a temperature of over 25°C.

Squire (1963) found that in the north-west Atlantic the yellowfin could be found in water ranging from 18·4° to 28·8°C, with an average temperature at which fish were caught of 25·2°C.

Tsuruta (1961) found *T. albacares* in the south-west Indian ocean in water with a range of temperature of 19·0°–25·3°C.

Off the Cape (fig. 5), the histograms suggest that the sampling was conducted at the lower end of the temperature range, since in all figures, both of percentage catch rate and successful stations, the catch seems to be increasing with increase in temperature. Little fishing was done in warmer water, however. It is worth noting, too, that *T. albacares* has a wide range of temperature tolerance, since off the Cape it was the only species to occur over the whole range of temperatures fished (13·8°–24°C); there was, however, no sign of an optimum temperature. There is some indication that the optimum temperature range of *T. albacares* is higher in this area than that of the other species, an observation that is in agreement with the findings of Squire (1963) for the north-west Atlantic, and the tentative conclusions reached by De Jager (1963) and De Jager *et al.* (1963) for the Cape. Figure 5 suggests that *T. albacares* is normally found only in water above 17·5°C.

T. obesus

While *T. obesus* is in general a species of low latitudes, being found in its greatest quantities just north of the Equator (Kamimura & Honma, 1963), it does have a very wide range of temperature tolerance. In the Japanese area Kishinouye (1923) recorded that the temperature range was 13°–25°C with an optimum of 22°–24°C. Tsuruta (1961), in the south-west Indian ocean, found this species in water ranging in temperature between 17°C and 25°C. Other wide ranges of temperature recorded are 12·2°–28·8°C (54°–84°F) in the eastern Pacific (Alverson & Peterson, 1963) and 13·5°–27·3°C in the north-west Atlantic (Squire, 1963).

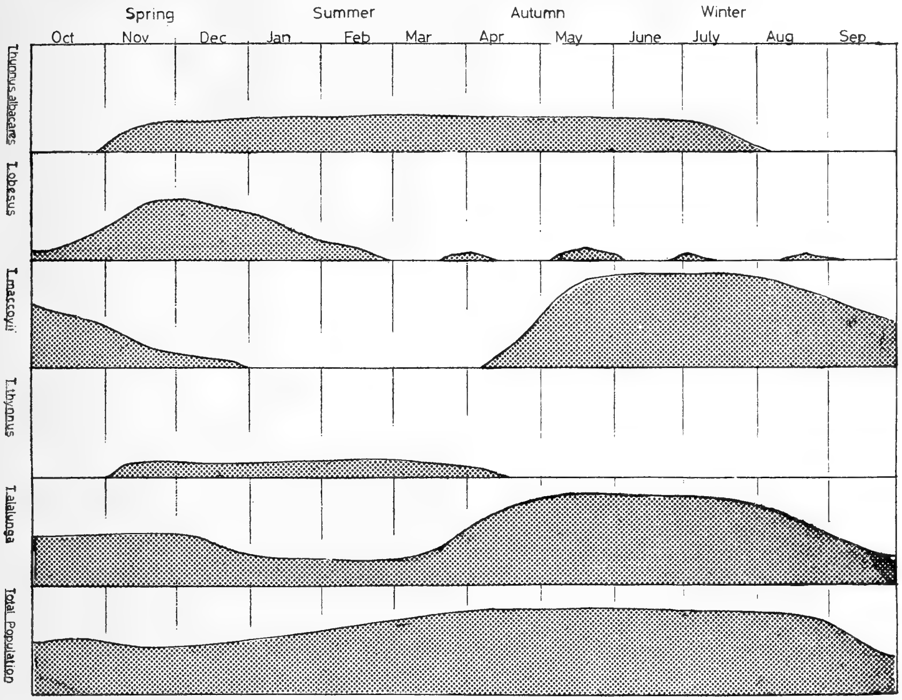
During the survey very few *T. obesus* were taken, too few to give a true picture of their temperature range in this area; also, like *T. albacares*, there were too few stations occupied in warm water, above 21·5°C.

In conclusion, it can be said that, although the tuna found off the Cape have a wide range of temperature tolerance, they are usually found within a restricted range of temperature, which in *T. maccoyii* is low (below 19°C) and in *T. obesus* and *T. albacares* higher (above 17·5°C). *T. alalunga*, however, seems to have a wide optimum temperature range.

Changes in the tuna population

Prior to 1960 the opinion was widely held that tuna were found off the Cape during the summer months only (Horne, 1959), although whaling skippers working off Cape Columbine in the winter of 1957 reported seeing tuna. During the summer months (November to April) the sport fishing vessels took large numbers of *T. albacares* and a small number of *T. alalunga* (Horne, 1959). In some years small numbers of what were probably large *T. thynnus* were also taken by beach seines at this time, as well as smaller specimens by anglers off the rocks at Rooikrantz, near Cape Point (*Cape Times*, 31/12/1945, 5/1/1946, and South African Museum records). In addition, two specimens of *T. obesus* were caught in November 1959 by trolling off Slangkop, Cape Peninsula (Talbot & Penrith, 1961*b*).

It was therefore confidently expected that during the winter months long-lining would produce few or no tuna, and doubts were expressed as to the desirability of continuing the survey during the winter. It was thus extremely surprising to find that during the winter period the catches, far from showing any tendency to diminish, actually increased, though changing in species composition. The change is shown diagramatically in figure 6. Referring to figure 6 it may be seen that *T. alalunga* is the only species present off the south-western Cape at all times of the year. During the months October to May, what may be termed the summer population of tunas is present off the Cape. This is composed of *T. albacares*, *T. obesus*, *T. alalunga* (in the main comprising small fish of less than 950 mm fork-length of this species), and a small number of *T. thynnus*. During May to November a different population of tunas is present, being composed of *T. maccoyii* and *T. alalunga*, but the latter species is more abundant than during the summer due to the addition of large numbers of larger individuals of over 950 mm fork-length. During the winter occasional specimens of *T. albacares* and *T. obesus* are found, but in such small numbers that they may be


Cape West Coast

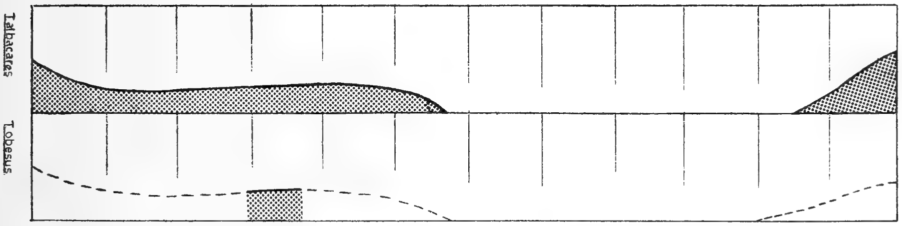

Cape East Coast

Fig. 6. Annual changes in tuna populations in the waters west of Cape Town and on the South African south-east coast. Only *Thunnus albacares* and *T. obesus* were taken in the latter area. Height of shaded area is proportional to the catch per hundred hooks of long-line gear, as shown by our survey.

presumed to have been individuals which did not migrate from the Cape with the main population.

Off the east coast, in the area surveyed, between Cape Agulhas and Cape Recife, there was a marked difference both in the species composition and in the numbers of tuna present in comparison with the western Cape. No *T. alalunga*, *T. thynnus* or *T. maccoyii* were found, nor have they ever been definitely recorded from this area. Only two species, *T. obesus* and *T. albacares* are definitely found in this area. During summer *T. obesus* and presumably *T. albacares* were present, but owing to bad weather only two stations could be fished in this area in summer; at these stations four *T. obesus* were taken. In late summer both species were found in small quantities, while in winter, although stations were occupied in warm water, no tuna of any sort were caught. At the end of April 1960 large quantities of *T. albacares* and a smaller number of *T. obesus* were caught between Cape St. Francis and Cape Recife in water of 18°–20·3°C, although off Cape Infanta, in water of similar temperature (18·3°C) no tuna were found.

In the south-west Indian Ocean so few fish were caught during the two cruises on the S.A.S. *Natal* that no clear results could be obtained. Noteworthy was the finding of *T. alalunga* close inshore east of Durban, from where it had been recorded only once previously (Molteno, 1948). It was also found that there seemed to be a marked difference in the number of tuna present in summer (February 1963) and in winter (August 1962). During winter tunas were found in fairly small quantities on the stations east of Durban, *T. alalunga* and *T. albacares* being the species present. During the summer tunas were almost completely absent in the area surveyed, only two *T. albacares* and one *T. obesus* being found. As in the area further south, no *T. thynnus* were obtained.

To our knowledge the first survey of the area south of Madagascar and east of Durban was done in January 1961, by the R.V. *Koyo-Maru* belonging to the Shimonoseki College of Fisheries, Japan. She obtained catch rates of 2·0% for *T. albacares*, 1·1% for *T. alalunga*, and 0·2% for *T. obesus* (Tsuruta, 1961), a total catch rate far in excess of the total catch rate for the February *Natal* cruise of 0·3%. A possible reason for this seeming anomaly is patchy distribution. Tsuruta's data suggest small shoals very widely separated, and since the *Koyo-Maru* used a far longer length of long-line than the *Natal*, thus sampling a far greater area of the sea, this may partly account for the apparent difference in results.

This area has, however, become a commercial fishing area since the survey of the *Koyo-Maru*, and, judging by the aerial sightings of vessels off Durban (Pinkerton, pers. comm.) and by landings of frozen tuna at Durban by Japanese long-liners (Durban Customs, pers. comm.), most of the fishing in this area is done in winter. It seems therefore that the indication given by the cruises on S.A.S. *Natal*, that tuna are more plentiful in the south-west Indian ocean in winter than in summer, is correct, although based on scanty evidence at present.

The Distribution of Tuna in Relation to Hydrographic Conditions

Off the Cape there are both marked annual changes in tuna populations and great annual changes in the hydrographic conditions of the surface water masses. The tuna populations change at the same time as the water masses, suggesting a causal relationship. The main determinants of horizontal distribution in a pelagic open-ocean fish such as tuna are probably the necessity to find available food, the necessity to remain within suitable hydrographic conditions, the necessity to satisfy the particular, usually more narrowly selected, hydrographic conditions during the breeding season, and also behavioural factors such as schooling behaviour and inherent migratory urges. It would be naïve to consider the spatial position of tuna to be anything but the result of a complex inter-relationship of a number of these factors at any one time. Nevertheless, given adequate feeding at a non-breeding season, temperature (which has been considered by Yabe *et al.* (1963), to be the most important factor determining the suitability of the hydrographic environment) may be closely linked to distribution.

Food and feeding will be discussed in a later section, but it should be noted that the Cape area, owing mainly to the upwelling of the water forming the Benguela Current, is exceptionally rich in phosphates, nitrates and silicates, and is biologically one of the richest areas of the oceans (Steemann-Nielsen, 1956), supporting vast quantities of potential tuna forage organisms such as *Sardinops ocellata*, *Maurolicus muelleri* and *Loligo reynaudi*.

Tuna require a very uniform body of water within which to breed, with no sudden changes or fluctuations in temperature. The temperature, too, must be high (24°C or higher according to Yabe *et al.*, 1963). These conditions are not met with off the Cape.

If the catch rate of fish per hundred hooks is considered as a measure of abundance, which over a series of stations fished at different times is a fair assumption, the different water masses around the Cape have very different populations of tuna. In figure 7 the populations have been expressed in number caught per hundred hooks in the different water masses. The upwelled water that forms the Benguela Current changes little in temperature from summer to winter, although it is more clearly defined in summer because of the off-shore wind systems at that time of year (fig. 3). The South Atlantic Subtropical Surface Water changes considerably, however, from summer to winter in temperature. Because of this, and the fact that species of tuna move from the Cape at different times to breed the water masses have been considered separately for summer and winter.

In summer there is much mixing of the Agulhas Current water (which rounds the Cape under certain wind conditions) and the South Atlantic Subtropical Surface Water in the area west of Cape Town where the main sampling effort of the survey was concentrated (fig. 3). These surface waters have rather similar temperature and salinity characteristics, and this, plus the problem of mixed water, makes it difficult to decide in many cases in what water a station was placed. They have therefore been considered together (fig. 7) in summer, but in winter, where there is no rounding of the Cape by the Agulhas Current, and the South Atlantic Subtropical Surface Water is much colder, they can be clearly differentiated, and we have been able to consider them separately. Summer has been considered to be from December to May inclusive, as these

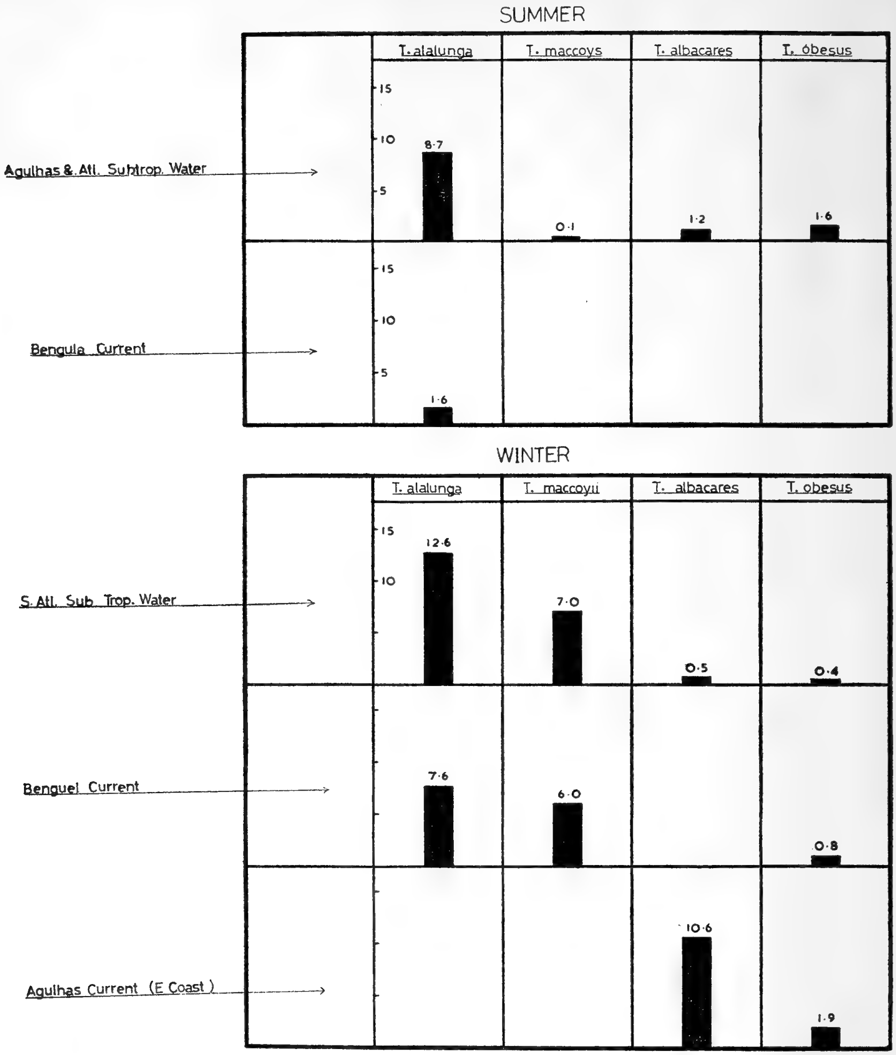


Fig. 7. Catch rate of tuna in summer and winter in the various water masses sampled. Catch rate is expressed as number of fishes taken per hundred hooks laid, and is stated above each histogram.

months showed warmer water (over 20°C) than the months June to November (below 20°C) during the eighteen months of the survey.

The Benguela Current lies inshore of the warm Agulhas Current/South Atlantic Subtropical Surface Water in summer, and is often so clearly demarcated from the latter that there is a change in surface temperature of as much as 5°C over a hundred yards, and also a change from greenish water with a high plankton concentration to clear blue warm water. Only *T. alalunga* was found in the Benguela Current in the few stations occupied in summer. In winter, when *T. maccoyii* has reached the Cape, both this species and *T. alalunga* are found in this water mass. A few *T. obesus* were also taken in it in winter, presumably being some of the very few fish of this species that remain through the winter in the area. At 4 stations, however, all in summer, at the border of the Benguela Current, and apparently just within it, both *T. albacares* and *T. obesus* were taken in quantity. Stations further into the Benguela water at the same time gave none of these species. These stations were not included in figure 7, and are mentioned here to indicate that on rare occasions the warmer water species may move just into the borders of the Benguela, presumably to feed on the rich stocks of forage species.

In the Agulhas Current/South Atlantic Subtropical Surface Water in summer the dominant species is *T. alalunga*, and both *T. albacares* and *T. obesus* are common (fig. 7). *T. maccoyii* is absent from the Cape during summer; its presence in this water mass (fig. 7) is due to a few specimens being taken on 7 and 8 December 1960, and on 21 and 22 June 1961, i.e. just outside the limits of 'summer' as defined here. Although the two water masses are here considered together, in comparing temperature/salinity curves at the stations with those of Clowes (1950) there was an indication that *Thunnus albacares* and *T. obesus* were mostly in water of Agulhas Current origin, while *T. alalunga* was found in both waters, but mostly in South Atlantic Subtropical Surface Water. The only specimen of *T. thynnus* was taken in this water mass in December 1960. From the catches of commercial long-line boats which began operating after this survey it has become clear that at least in some summers *T. thynnus* is very much more common than this single record indicates. In the summer of 1963–4, as well as in subsequent years, a large number of this species was also taken by sports fishermen in False Bay. As they were using a technique new in the area (chumming and whole bait), it is possible that this species may have been here in other years.

In the South Atlantic Subtropical Surface Water which lies offshore from the western Cape in winter the dominant species are *T. alalunga* and *T. maccoyii.* The occasional finding of *T. albacares* and *T. obesus* in this water mass in winter suggests that a small proportion of these predominantly summer fish do not leave but overwinter at the Cape.

Migrations of South African Tunas

Tunas are known to occur off Angola (Molteno, 1948; Schaefer & Walford, 1950; Vilela & Monteiro, 1959) and Zanzibar (Copley, 1947; Morrow, 1954; Williams, 1956, as well as the south-west Indian ocean (Tsuruta, 1961). Off Angola *T. albacares*, *T. alalunga* and *T. obesus* have been recorded, but no *T. thynnus*, although this species is known from St. Helena Island (Molteno, 1948). *T. albacares* is the dominant species off Zanzibar, together with a few *T. alalunga*, but Williams (pers. comm.) has not recorded *T. obesus* or *T. thynnus.* In the south-west Indian ocean off Durban *T. obesus*, *T. albacares* and *T. ala-*

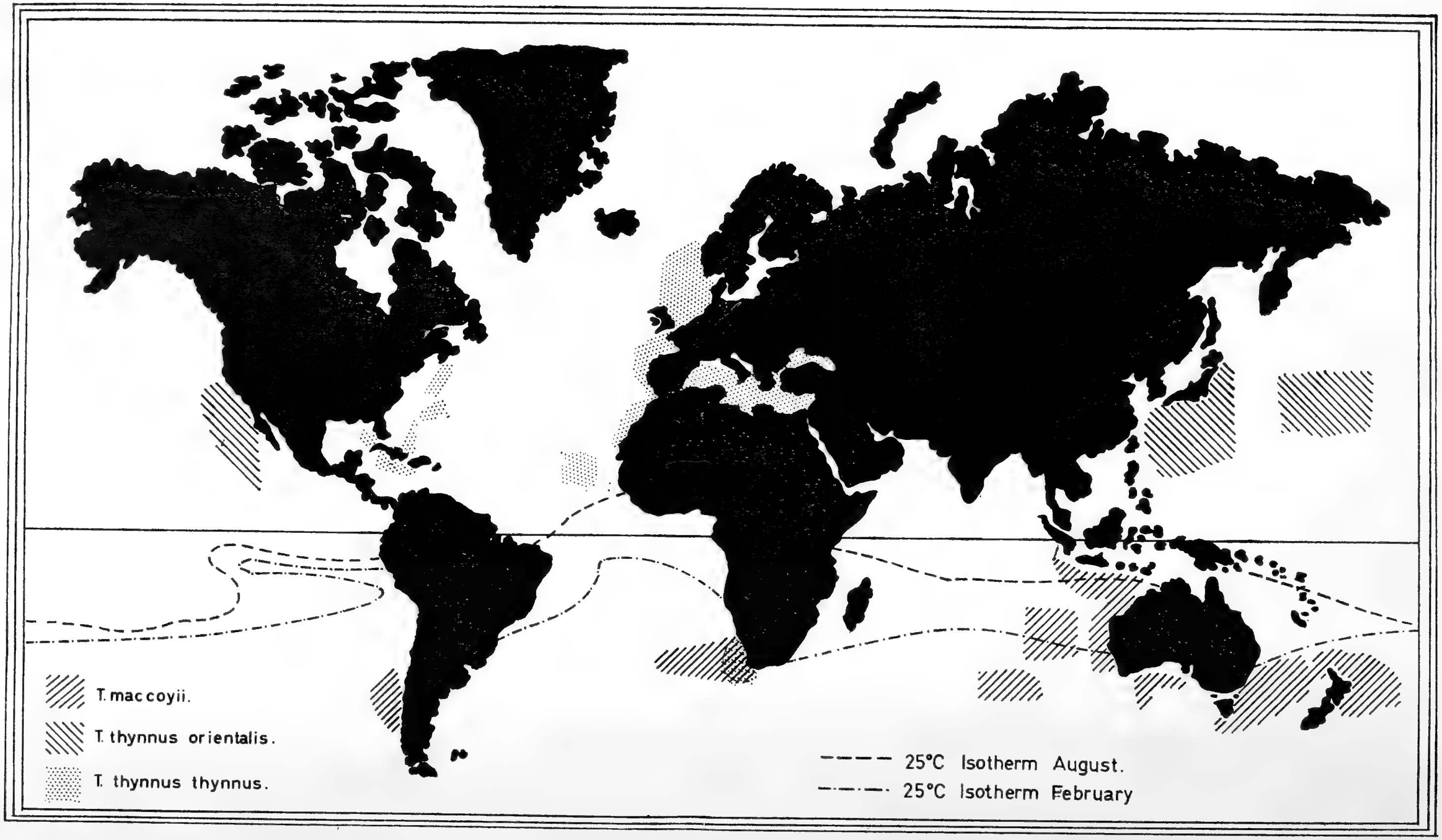


Fig. 8. World distribution of the three probable species of bluefin tuna *Thunnus thynnus*, *T. maccoyii* and *T. orientalis*.

lunga are found (Molteno, 1948; Tsuruta, 1961; and the present survey).

The major annual changes in the tuna populations of the Cape have already been discussed, but which ocean the South African populations are derived from, and what their migrations are in these oceans has always been in doubt. The work of Rivas (1955), Clemens (1961), Hamre (1962) and Mather (1962) have shown that tuna are capable of long migrations at a relatively high average speed (up to 3–5 knots). Mather has shown that *T. thynnus*, of both large and small size, cross the Atlantic. Long distance migrations of albacore across the Pacific have also been shown to occur by the U.S. Fish and Wildlife Service (Otsu & Uchida, 1963).

(*a*) *Thunnus thynnus*

Thunnus thynnus has never been recorded on the Indian ocean side of the Cape, and it seems probable that the small number of this species which occurs off Cape Town during summer have their origin in the Atlantic.

(*b*) *Thunnus maccoyii*

T. maccoyii had never been recorded in the Atlantic until this survey, and is an Indo-Pacific species. The fishes of this species found off the Cape normally have bright yellow peduncle keels, and the only other population of bluefin tuna which is stated in the literature to have this feature occurs in the waters off Australasia (Serventy, 1956*a*). Mimura (1961) described the main fishing areas for this form, off the Australian west coast, mentioning two areas, the 'Old ground' 20°–30°S, 100°–110°E, and the 'New ground' 10°–18°S, 115°–120°E. In addition to these, Laevastu & Rosa (1963) show a third area, 32°–38°S, 80°–95°E, which they state is fished for 'bluefin'. Mimura states that *T. maccoyii* is found only from October to April in the 'New ground', and September to March in the 'Old ground'. It is significant that this is the time during which *T. maccoyii* is absent from the Cape. It is possible that the fish occurring off the Cape may have their origin off the Australian coast. The results of tagging of *T. alalunga* in the north Pacific (Otsu & Uchida, 1963) and of *T. thynnus* in the Atlantic and Pacific (Hamre, 1963; Mather, 1963*a*) have shown that an annual migration of this magnitude is not impossible.

Subsequent to this survey, however, *T. maccoyii* has been found to occur in the south Atlantic at Vema seamount (31° 38′S 8° 20′E) (Penrith (1967) and later personal catches from the R.V. *Thomas B. Davie* belonging to the University of Cape Town), and Shingu (1967) has shown that *T. maccoyii* is found over a wide band of the south temperate zone, but probably avoids the warm water of the Agulhas Current.

(*c*) *Thunnus alalunga*

The distribution of *T. alalunga* around the South African coast shows a strange break in continuity. The species is common off Angola, St. Helena Island, Walvis Bay, Stompneus Bay (outside the Benguela Current), and from

Cape Columbine to Danger Point. The species is then, as far as is known, absent from waters off the South African south-east coast, but reappears off Durban and, although found by Tsurutu (1961) to be present well off the African coast to 35°S, is not plentiful in this area (Kataoka, 1957; Laevastu & Rosa, 1963). It seems therefore very reasonable to assume that the population of *T. alalunga* found off the Cape is of Atlantic origin, and is the south-eastern limit of a large population which is known in the South Atlantic from 10°–35°S, according to Laevastu & Rosa (1963).

(*d*) *Thunnus obesus* and *T. albacares*

The origin of *T. obesus* and *T. albacares* is less clear. The two species are common off Angola and are also found in the south-west Indian ocean off Durban. Mention was made earlier of the extremely large catch of *T. albacares* made at three stations between Cape St. Francis and Cape Recife at the end of August 1960, together with smaller numbers of *T. obesus*. It is felt that these catches were highly significant for two reasons. Firstly, August was approximately one month before the two species began to appear off the Cape Peninsula in the long-line industry catches (Bacon, pers. comm.); and secondly, the large numbers of fish obtained (almost half the *T. albacares* obtained during the entire survey were taken during the three days) suggests a compact migrating population rather than a widespread feeding population. It seems, therefore, in the absence of any valid evidence to suggest an Atlantic origin for *T. albacares* and with it *T. obesus*, that they are probably of Indian ocean origin. The presence of fair numbers of *T. albacares* off Durban in winter and their almost complete absence in summer cannot be explained. It might be speculated that their absence is due to their having migrated southward owing to high temperatures found in the region in summer (similar to the situation off North America, as noted by Radovich, 1961), and that they are actually part of the same population as occurs off the Cape. Alternatively, however, they could have migrated northward to spawn during the summer.

One further point must be discussed in connection with the migration of *T. albacares*. It is common knowledge among Cape anglers that the best catches of *T. albacares* off the Cape Peninsula are made at the beginning and end of the season; during the middle of the season catches in this area tail off somewhat, and at the same time the fish are sometimes found at Mossel Bay. This, in the opinion of Horne (1962) suggests an Atlantic origin for the species. The species is said to come from the Atlantic, reach the Peninsula, then migrate up the east coast to Mossel Bay, and then turn and come back to the Peninsula. If this were true one would expect large numbers of the fish to be caught off Mossel Bay, not the small numbers that are actually found. It is far more likely that large compact migratory schools (such as were found off the east coast during this survey) should reach the Cape (and since they are large and near the surface are easily spotted during trolling) and then break up, so that anglers' catches decline. Some of these fish will feed on the Agulhas Bank, where they often are seen during summer by trawler crews (Barker, pers. comm.). It is probable that some of these fish enter Mossel Bay. At the end of summer the migratory schools will re-form, and again anglers' catches off the Cape will show a marked increase.

Genetic exchange between Atlantic and Indo-Pacific Tunas

The waters to the south of the Cape are probably the only place where genetic exchange between Atlantic and Indo-Pacific populations of *T. alalunga*, *T. albacares*, and *T. obesus* could take place.

As has been shown, the closely allied *T. thynnus* and *T. maccoyii* occur at the Cape, but these are found at different seasons, and neither breeds in the area.

The other three species, *T. alalunga*, *T. albacares*, and *T. obesus* do not show, in the adult form at least, any great differences between Atlantic and Indo-Pacific populations. This suggests (although does not prove) that there is some genetic interchange between the Atlantic and Indo-Pacific populations. While the migratory patterns discussed above are thought to be the major ones, it is probable that there are smaller migrations of *T. obesus* and *T. albacares* from the Atlantic and *T. alalunga* from the Indian ocean to the Cape, and contact between Atlantic and Indo-Pacific ocean populations takes place.

The possibility of both Atlantic and Indian ocean tunas being present off the Cape in summer, at least, is strengthened by the finding, in the water off the Cape in summer, of marlins which are indigenous to the Indo-Pacific (*Makaira indica* and *Makaira audax*) as well as a marlin known only from the Atlantic (*Tetrapturus albidus*) (Talbot & Penrith, 1962, 1963*b*). The problems of the origin and migration of the Cape tuna population can be elucidated only by the inauguration of a large scale tagging programme on the tunas off the Cape.

ACKNOWLEDGEMENTS

This survey would not have been possible without the generous help and co-operation received from Irvin & Johnson (Pty.) Ltd. who supplied all equipment, boat and crew for the eighteen-month Cape survey. Many persons associated with Irvin & Johnson assisted the museum in various ways, but Mr. C. S. Milford, Mr. K. McKay and Mr. C. Linnigar deserve special thanks. The high degree of co-operation received at sea from Skipper G. Barker and the crew of the M.T. *Cape Point* contributed much towards the success of the survey.

That portion of the survey conducted in the south-west Indian ocean was done from S.A.S. *Natal* by courtesy of the South African Navy. The co-operation of the hydrographer, Capt. J. K. Mallory, and the captain and crew of S.A.S. *Natal* is appreciated. The cost of the long-lining equipment used on S.A.S. *Natal* was covered by a grant from the Council for Scientific and Industrial Research as part of the South African participation in the International Indian Ocean Expedition.

Mr. N. Bacon, manager of the Atlantic Tuna Corporation (Pty.) Ltd. and Mr. C. Horne, a keen angler and author of several books on angling in South Africa, gave much help and information.

We are grateful to Dr. J. R. Grindley and Mr. S. X. Kannemeyer of the South African Museum, Mr. A. J. de Freitas of the Instituto de Investigaçao Cientifica de Moçambique and Mr. W. Nussey of Cape Town for assistance at sea.

Mr. F. Williams, formerly of the East African Marine Fisheries Research Corporation in Zanzibar, kindly made unpublished data on *T. albacares* available.

The Division of Sea Fisheries analysed all water samples and loaned many journals not available in the museum library.

We are grateful to the South African Marlin and Tuna Club for making arrangements for us to measure large numbers of yellowfins caught during their championships.

We are grateful to Professor J. H. Day, Dr. B. B. Collette and Dr. R. H. Gibbs for reading and criticizing the manuscript.

The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research for a grant to publish this paper.

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Date	C.P. No.	Bearing	Landmark	Distance Miles	Water Temperature			Salinity OM	Hooks Used	Catch in %				Total	
					OM	30M	150M			LF	YF	BF	BE	No.	%
1960															
16/2	1	W	Slangkop	40	20·40	—	—	—	48	—	—	—	—	—	—
4/3	2	W	Slangkop	43	18·82	16·60	12·18	35·40	60	—	—	—	8·3	5	8·3
5/3	3	W.S.W.	Slangkop	79	20·04	19·82	13·60	35·54	66	7·6	—	—	1·5	6	9·1
6/3	4	W	Slangkop	35	20·04	—	11·03	35·47	66	7·6	—	—	—	5	7·5
7/3	5	W	Danger Point	40	20·38	20·30	9·86	35·46	66	9·4	—	—	—	7	9·4
9/3	6	W	Slangkop	45	20·19	20·19	12·33	35·47	66	7·6	—	—	—	5	7·6
9/3	7	W	Slangkop	45	20·20	20·19	12·35	35·47	66	1·5	1·5	—	—	2	3·0
10/3	8	W.S.W.	Slangkop	75	20·43	20·14	13·96	35·55	66	6·0	1·5	—	—	5	7·6
26/3	9	S	Cape Recife	45	23·80	20·83	11·15	35·37	66	6·0	3·0	—	—	2	3·0
28/3	10	S	Cape Recife	60	18·80	18·62	10·40	35·35	180	—	2·8	—	·5	6	3·3
30/3	11	S	Cape Recife	62	20·40	—	—	—	180	—	3·3	—	—	6	3·3
2/4	12	W	Danger Point	55	19·30	19·29	12·56	35·55	60	5·0	—	—	1·7	4	6·7
27/4	13	W	Slangkop	30	18·24	18·13	15·31	35·53	54	7·1	1·8	1·8	1·8	7	12·5
28/4	14	W	Slangkop	50	18·11	18·09	13·07	35·53	90	1·1	2·2	—	—	3	3·3
30/4	15	W.N.W.	Dassen Island	35	13·83	13·64	11·61	35·06	30	10·0	6·6	3·3	3·3	7	23·4
1/5	16	W.N.W.	Cape Columbine	30	16·66	14·52	10·88	35·38	36	—	—	—	—	—	—
2/5	17	W.N.W.	Cape Columbine	60	15·68	15·23	12·63	35·22	30	—	—	—	—	—	—
3/5	18	W.N.W.	Dassen Island	40	14·85	13·90	11·88	35·17	114	28·0	—	—	—	32	28·0
3/6	19	S.S.W.	Yzervark Point	65	21·98	20·91	14·57	35·47	114	—	—	—	—	—	—
4/6	20	S	Knysna	55	21·04	21·02	11·93	35·48	114	—	—	—	—	—	—
5/6	21	S	Cape St. Francis	25	21·10	19·23	11·11	35·47	42	—	—	—	—	—	—
11/6	22	W	Cape Point	30	17·25	17·21	11·83	35·47	114	6·1	—	2·6	·9	11	9·6
12/6	23	W	Slangkop	45	17·30	17·23	11·64	35·49	36	—	—	13·9	—	5	13·9
13/6	24	W	Slangkop	65	17·36	17·21	13·30	35·48	150	11·3	—	31·3	—	64	42·6
15/7	25	W	Slangkop	50	16·80	—	—	—	36	5·5	—	2·8	—	3	8·3
17/7	26	W	Slangkop	75	16·70	16·30	13·05	35·43	108	6·5	—	2·8	—	10	9·3
18/7	27	W	Slangkop	45	15·58	15·31	12·24	35·43	90	15·5	—	14·5	—	27	30·0
19/7	28	W	Slangkop	30	16·48	16·01	11·97	35·47	54	40·7	—	—	—	22	40·7
20/7	29	N.W.	Cape Columbine	37	15·58	15·50	13·14	35·43	120	—	—	—	—	—	—
21/7	30	W.N.W.	Dassen Island	35	14·48	14·47	9·31	35·26	120	·8	·8	9·2	—	13	10·8
22/7	31	W.N.W.	Table Mountain	45	17·81	17·45	13·24	35·50	120	20·0	·8	24·2	—	54	45·0
28/8	32	S.E.	Cape Infanta	100	18·50	—	—	—	120	—	—	—	—	—	—

Date	C.P. No.	Bearing	Landmark	Distance Miles	Water Temperature			Salinity OM	Hooks Used	Catch in %				Total	
					OM	30M	150M			LF	YF	BF	BE	No.	%
1960															
29/8	33	S.E.	Cape St. Francis	60	19·23	18·98	11·06	35·47	150	—	28·0	—	1·4	44	29·8
31/8	34	S.S.E.	Cape Recife	50	17·95	17·31	11·82	35·42	120	—	15·0	—	·8	19	15·8
1/9	35	S.S.E.	Cape Recife	60	20·15	19·97	16·23	35·44	90	—	22·2	—	4·5	24	26·7
1/10	36	W.N.N.	Dassen Island	35	16·32	16·30	13·96	35·51	114	24·6	—	4·4	—	33	29·0
2/10	37	W.N.W.	Cape Columbine	45	16·48	16·41	13·87	35·53	114	4·4	—	1·8	—	7	6·2
3/10	38	W.N.W.	Cape Columbine	60	16·41	16·38	13·42	35·54	114	13·2	—	—	—	15	13·2
4/10	39	W	Slangkop	45	16·59	16·58	12·52	35·53	114	12·3	—	12·3	·9	29	25·5
5/10	40	W	Slangkop	45	16·70	—	—	—	66	21·2	—	9·1	1·5	21	31·8
6/10	41	W	Slangkop	30	16·70	—	—	—	42	9·5	—	—	4·8	6	14·3
8/10	42	W	Slangkop	55	16·38	16·13	12·21	35·51	150	9·3	—	6·7	—	24	16·0
2/11	43	W	Slangkop	40	18·20	—	—	—	60	1·7	—	—	1·7	2	3·3
3/11	44	W	Slangkop	60	18·14	17·77	—	35·48	120	3·3	—	3·3	·8	9	7·5
3–4/11	45	W	Slangkop	45	18·20	—	—	—	60	1·7	—	1·7	—	2	3·3
4/11	46	W	Slangkop	45	18·02	17·57	13·78	35·54	120	10·8	—	2·5	—	16	13·3
5/11	47	W	Cape Point	30	18·00	—	—	—	90	18·9	5·5	5·5	—	27	30·0
6/11	48	W.N.W.	Danger Point	40	18·59	18·54	12·29	35·50	114	1·8	—	4·4	—	7	6·2
7/11	49	W	Danger Point	50	17·64	17·85	12·29	35·53	120	14·2	—	2·5	1·7	22	18·2
8/11	50	W	Cape Point	40	17·98	17·93	13·01	35·53	120	10·0	—	5·8	·8	20	16·7
9/11	51	W	Cape Point	30	18·10	—	—	—	54	16·7	—	5·6	—	12	22·2
9/11	52	W	Cape Point	30	18·10	—	—	—	72	6·9	4·2	—	—	8	11·1
10/11	53	W	Slangkop	45	18·40	—	—	—	150	4·7	—	1·3	1·3	11	7·3
7/12	54	W	Cape Columbine	30	17·80	—	—	—	120	23·4	—	·8	1·7	31	25·8
8/12	55	W.N.W.	Dassen Island	35	18·10	—	—	—	120	2·5	—	1·7	10·0	17	14·2
9/12	56	W.N.N.	Table Mountain	50	17·80	—	—	—	120	12·5	—	·8	2·5	19	15·8
10/12	57	W	Slangkop	45	20·50	—	—	—	120	5·8	—	—	3·3	11	9·2
10/12	58	W	Slangkop	45	20·50	—	—	—	90	6·6	—	—	3·3	9	9·9
11/12	59	W	Slangkop	60	21·40	—	—	—	120	5·0	—	—	3·3	10	8·3
11/12	60	W	Slangkop	60	21·50	—	—	—	90	11·0	—	—	6·6	16	17·6
12/12	61	W	Hout Bay	18	15·90	—	—	—	120	—	7·5	—	—	9	7·5
1961															
3/1	62	S	Cape Recife	45	21·31	19·39	13·83	35·31	120	—	—	—	1·7	2	1·7
3/1	63	S	Cape Recife	45	21·31	19·39	13·83	35·31	60	—	—	—	3·3	2	3·3

8/1	64	S	Danger Point	40	21·42	21·23	—	35·49	120	5·8	4·2	—	·8	13	10·8
9/1	65	W	Slangkop	45	19·50	—	—	—	120	2·5	·8	—	13·3	20	16·7
9/1	66	W	Slangkop	45	19·60	—	—	—	9	—	1·1	—	7·7	8	8·8
11/3	67	W	Slangkop	15	14·70	—	—	—	—	—	—	—	—	—	—
12/3	68	W	Slangkop	30	19·60	—	—	—	120	2·5	2·5	—	·8	7	5·8
13/3	69	W	Slangkop	45	21·21	21·21	14·49	35·47	120	1·7	·8	—	—	3	2·5
14/3	70	S.W.	Danger Point	55	21·42	21·31	11·87	35·43	120	10·0	15·8	—	—	31	25·8
14/3	71	S.W.	Danger Point	55	21·42	21·31	11·87	35·43	60	1·7	3·3	—	—	3	5·0
15/3	72	W×S	Danger Point	50	21·60	—	—	—	120	—	·8	—	1·7	3	2·5
15/3	73	W×S	Danger Point	50	21·60	—	—	—	60	15·8	—	—	5·0	12	20·8
16/3	74	W	Slangkop	45	21·59	21·54	13·65	35·45	120	2·5	1·7	—	—	5	4·2
16/3	75	W	Slangkop	40	21·59	21·54	13·65	35·45	60	6·7	—	—	—	4	6·7
17/3	76	W.N.W.	Dassen Island	40	19·50	—	—	—	120	17·5	—	—	1·7	23	19·2
17/3	77	W.N.W.	Dassen Island	40	19·40	—	—	—	60	6·7	—	—	—	4	6·7
18/3	78	W.N.W.	Table Mountain	40	15·90	—	—	—	120	5·8	—	—	—	7	5·8
16/4	79	W	Cape Columbine	40	20·64	19·34	12·82	35·56	102	9·8	—	—	—	10	9·8
17/4	80	W	Cape Columbine	60	20·01	18·95	14·37	35·52	120	15·8	·8	3·3	2·5	27	22·5
17/4	81	W	Cape Columbine	60	20·00	18·95	14·37	35·52	60	15·0	—	—	—	9	15·0
18/4	82	W.N.W.	Dassen Island	45	19·80	19·69	14·83	35·52	120	15·0	2·5	—	—	21	17·5
18/4	83	W.N.W.	Dassen Island	45	19·80	19·69	14·83	35·52	60	3·3	3·3	—	—	4	6·6
19/4	84	W	Slangkop	45	19·79	19·75	13·56	35·50	120	40·0	—	—	—	48	40·0
19/4	85	W	Slangkop	45	19·79	19·75	13·56	35·50	60	31·7	—	—	—	19	31·7
20/4	86	W	Slangkop	18	16·23	15·07	11·16	35·44	120	5·0	·8	—	—	7	5·8
20/4	87	W	Slangkop	18	16·23	15·07	11·16	35·44	60	3·3	—	—	—	2	3·3
21/4	88	W	Slangkop	40	19·03	19·01	11·98	35·37	120	19·2	—	—	—	23	19·2
21/4	89	W	Slangkop	40	19·03	19·01	11·98	35·37	60	28·3	1·7	—	—	18	30·0
22/4	90	W	Slangkop	55	18·95	18·92	12·76	35·39	120	15·0	1·7	—	—	20	16·7
23/4	91	W	Slangkop	60	19·25	19·02	12·95	35·46	120	5·8	—	—	—	7	5·8
23/4	92	W	Slangkop	60	19·25	19·02	12·95	35·46	48	20·6	—	—	—	11	20·6
20/5	93	W	Danger Point	40	20·40	—	—	—	120	·8	2·5	—	—	4	3·3
21/5	94	W	Danger Point	55	20·60	—	—	—	120	20·0	5·0	—	—	30	25·0
22/5	95	W	Cape Point	20	19·70	—	—	—	120	25·0	—	—	5·0	36	30·0
23/5	96	W×S	Slangkop	60	20·90	—	—	—	120	25·0	1·7	—	—	32	26·7
24/5	97	W	Slangkop	120	20·53	19·61	14·95	—	120	14·2	·8	—	·8	19	15·8
25/5	98	W×S	Slangkop	20	17·60	—	—	—	120	4·2	—	1·7	1·7	9	7·5
26/5	99	W	Slangkop	45	19·70	—	—	—	120	10·0	·8	—	1·8	14	11·7
21/6	100	W.N.W.	Dassen Island	45	19·10	—	—	—	120	16·7	4·2	13·3	·8	42	35·0

Date	C.P. No.	Bearing	Landmark	Distance Miles	Water Temperature			Salinity OM	Hooks Used	Catch in %				Total	
					OM	30M	150M			LF	YF	BF	BE	No.	%
1961															
22/6	101	W	Cape Columbine	45	19·22	19·21	13·58	—	108	21·3	·9	18·5	·9	45	41·6
23/6	102	W.N.W.	Dassen Island	45	18·99	18·96	13·41	—	108	26·9	—	13·9	—	44	40·8
24/6	103	W	Slangkop	35	18·30	—	—	—	108	22·2	—	—	—	24	22·2
25/6	104	W×N	Slangkop	40	17·80	—	—	—	108	10·2	—	—	—	11	10·2
26/6	105	S.W.	Cape Point	40	17·94	17·86	12·43	—	102	19·6	—	3·9	—	24	23·5
28/8	106	W	Cape Columbine	45	15·90	—	—	—	84	11·9	—	7·1	—	16	19·1
29/8	107	S.W.	Cape Columbine	50	16·19	16·12	13·40	—	84	9·5	—	13·1	—	19	22·6
30/8	108	W.N.W.	Dassen Island	40	16·20	—	—	—	84	4·8	—	1·2	—	5	6·0
2/9	109	W	Slangkop	30	16·40	—	—	—	84	9·5	—	15·5	2·4	23	27·4
3/9	110	W.S.W.	Slangkop	25	15·80	—	—	—	78	9·0	—	1·3	1·3	9	11·6
5/9	111	W×S	Slangkop	20	15·80	—	—	—	66	13·6	—	1·5	1·5	11	16·7

Appendix A (i)

Summary of stations occupied by m/t *Cape Point* during the tuna survey off the south and west Cape coast 1960–61.

L.F. = *T. alalunga;* Y.F. = *T. albacares;* B.F. = *Thunnus maccoyii;* B.E. = *T. obesus*

The bearings given are the course steered by the vessel from the landmark.

Only tuna are listed in the catch, other fish (sharks, billfish, etc.) are not recorded.

Positions of the landmarks listed are:

	S	E
Slangkop lighthouse . .	34° 09′	18° 19′
Danger Point lighthouse .	34° 38′	19° 18′
Cape Recife lighthouse .	34° 02′	25° 42′
Dassen Island lighthouse .	33° 26′	18° 05′
Cape Columbine lighthouse	32° 49′	17° 50′
Yzervark Point . . .	34° 23′	21° 44′

	S	E
Knysna Heads	34° 05′	23° 04′
Cape St. Francis lighthouse . .	34° 13′	24° 50′
Cape Point lighthouse . . .	34° 21′	18° 30′
Table Mountain (Maclear's Beacon)	33° 58′	18° 25′
Hout Bay (Duiker Point) . .	34° 02′	18° 18′

Date	Station LLN	Position S	Position E	Watertemp. Surface	Hooks	Catch in % LF	Catch in % YF	Catch in % BE	Total	
1962										
11/8	1	32° 03′	32° 49′	21·1	120	4·2	5·0	—	11	9·2
12/8	2	32° 30′	35° 16′	20·1	120	3·3	·8	—	5	4·1
15/8	3	31° 58′	43° 45′	18·0	120	·8	1·7	—	3	2·5
15/8	3(a)	31° 58′	43° 45′	18·0	120	—	—	—	—	—
18/8	4	26° 44′	44° 19′	22·7	120	—	—	—	—	—
19/8	5	26° 24′	40° 44′	22·8	120	—	—	—	—	—
19–20/8	6	25° 56′	39° 31′	23·1	120	—	—	—	—	—
21–22/8	7	26° 25′	33° 44′	23·0	120	—	—	—	—	—
23/8	8	30° 00′	31° 42′	21·9	120	—	9·2	—	11	9·2
23/8	8(a)	30° 00′	31° 42′	21·9	120	3·3	8·3	—	14	11·9
1963										
15/2	9	32° 06′	35° 25′	20·0	120	—	·8	—	1	·8
19/2	10	31° 50′	44° 11′	24·0	120	—	—	·8	1	·8
21/2	11	27° 10′	45° 45′	26·1	120	—	—	—	—	—
22/2	12	26° 56′	42° 11′	26·3	120	—	—	—	—	—
25/2	13	26° 42′	35° 00′	27·3	120	—	—	—	—	—
26/2	14	29° 46′	32° 25′	26·2	120	—	·8	—	1	·8
26/2	14(a)	29° 46′	32° 25′	26·2	120	—	—	—	—	—

Appendix A (ii)
Summary of stations occupied by S.A.S. *Natal* during the tuna survey in the south west Indian Ocean. 1962–63.

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

MANUSCRIPT

To be typewritten, double spaced, with good margins, arranged in the following order: (1) Heading, consisting of informative but brief title, name(s) of author(s), address(es) of author(s), number of illustrations (plates, figures, enumerated maps and tables) in the article. (2) Contents. (3) The main text, divided into principal divisions with major headings; subheadings to be used sparingly and enumeration of headings to be avoided. (4) Summary. (5) Acknowledgements. (6) References, as below. (7) Key to lettering of figures. (8) Explanation to plates.

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To be reducible to 4¾ in. × 7 in. (7½ in. including caption). A metric scale to appear with all photographs.

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Examples (note capitalization and punctuation)

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

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

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. Polyphacophora, 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.

ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs. 5 *a*, *b*; Liste: 11. Turton, 1932: 80

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **52** Band
October **1968** Oktober
Part **2** Deel

NEW QUATERNARY FOSSIL SITES NEAR SWARTKLIP, CAPE PROVINCE

By

Q. B. HENDEY & HÉLÈNE HENDEY

Cape Town Kaapstad

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Price of this part/Prys van hierdie deel

R1.75

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

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By

Q. B. Hendey

South African Museum, Cape Town

&

Hélène Hendey

(With 7 plates and 2 figures)

[*MS received* 10 *September*, 1967]

Contents

Introduction

During April, 1966, students from the Department of Geology, University of Cape Town, discovered an horizon containing fossil bone in the sand- and limestone cliffs near Swartklip on the False Bay coast. Subsequent investigations revealed the existence of fossil-bearing deposits at three localities—Site I, the most prolific occurrence, and Sites II and II Extension, two separate exposures of a single horizon (fig. 1).

Earlier, Singer & Fuller (1962) had reported on an assemblage of fossil bone from a fallen block of the cliff-face in the Swartklip (Zwartklip) area. This discovery is herein referred to as the 'Singer/Fuller Occurrence'.

All the fossil material recovered from these occurrences is almost certainly at least broadly contemporary, and it is the purpose of the present report to place on record the material from the three new sites which had been recovered up to July, 1966. The fossils, which are housed in the South African Museum (Natural History), Cape Town, have in many cases been incompletely classified, largely because of the lack of adequate comparative material. It is hoped

Ann. S. Afr. Mus. **52** (2), 1968: 43–73, 7 pls., 2 figs.

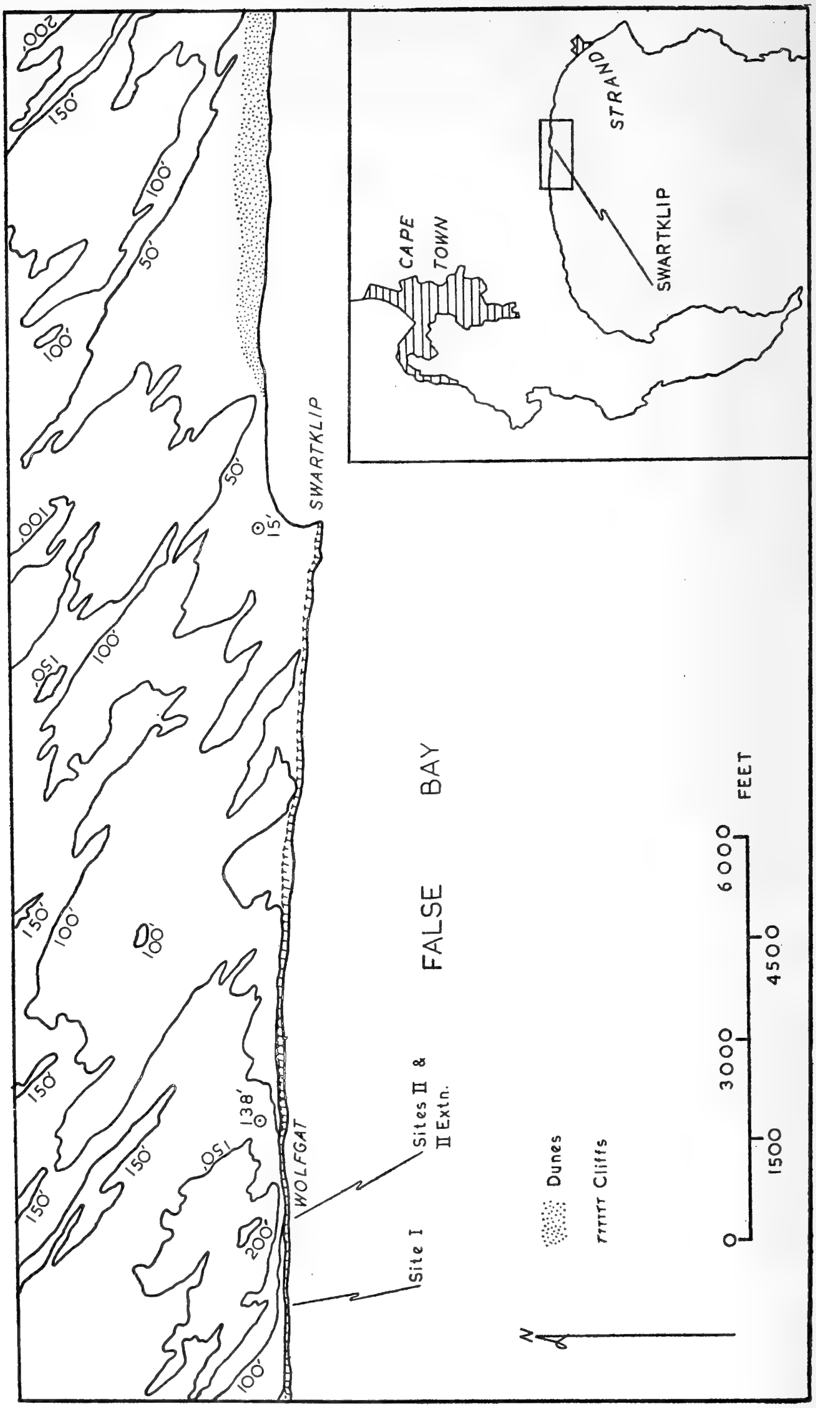

FIG. 1. Map showing location of new fossil sites near Swartklip, C.P. (Adapted from Trig. Survey Sheet no. 3418 B6).

to refer back to these specimens as detailed osteological studies of their modern and fossil counterparts progress.

GEOLOGICAL ASSOCIATIONS OF THE FOSSILS

The geology of the Swartklip deposits has already been recorded in some detail (Singer & Fuller, 1962). The fossils at the new sites occur in an irregular horizon of unbedded calcareous sand and grit, at approximately 60 feet above sea-level. At Site I an extensive talus slope has developed from beneath the small overhang in which the fossil horizon is exposed, and it was from the rubble of this scree that most of the fossils were recovered (pl. 1A, B). The deposits are, for the most part, incompletely consolidated, and their instability limited the collection of *in situ* fossils.

The fossiliferous horizon at Site I is clearly distinguishable from the overlying and underlying horizontally bedded deposits (fig. 2), and it appears to fill what was once a low cave. Comminuted marine shells occur in great quantities throughout the deposits incorporating the fossil horizon, and they are clearly marine in origin, although they may well have been redistributed in part by subsequent wind action. Their age is uncertain, but Singer & Fuller consider that they cannot post-date the 'Riss/Würm' interglacial. It is unlikely that they are older, since they would have had to withstand marine erosion during the high sea-level of that period, which is improbable in view of their relatively unconsolidated nature. The fossil deposits are clearly younger, but geological evidence can provide no closer estimate of age.

Overlying the horizontally bedded sands are discontinuously developed horizons of calcrete ('calcareous tufa' of Singer & Fuller) and calcareous sands, partially consolidated reddish-brown sand and unconsolidated white sand, all of which reflect the more recent geological and pedological history of the area. Shells of land snails occur within these deposits, which are aeolian in origin, and the calcareous and ferruginous characters reflect chemical changes within the soil body subsequent to its accumulation. The calcrete has resulted from the induration of the calcareous sands.

The geology at Sites II and II Extension is similar in most respects.

Singer & Fuller concluded that the fossils recovered by them probably came from a crevice in the cliff formation and that the occurrence post-dated the cliff sands, but pre-dated the calcrete. Observations at the new sites confirm the former speculation, but do not necessarily support the latter. At none of the sites is there evidence for a vertical opening through the deposits which has been sealed by the calcrete. At Site I there is a strong suggestion that the 'cave' opening was in a gully to the east of the fossiliferous deposit. The formation of the calcrete, therefore, had no direct effect on the 'cave' opening, and the fossils do not necessarily pre-date its formation.

ARCHAEOLOGICAL ASSOCIATIONS OF THE FOSSILS

A single undiagnostic silcrete flake was recovered from the talus slope at Site I, but no material of an archaeological nature was found definitely asso-

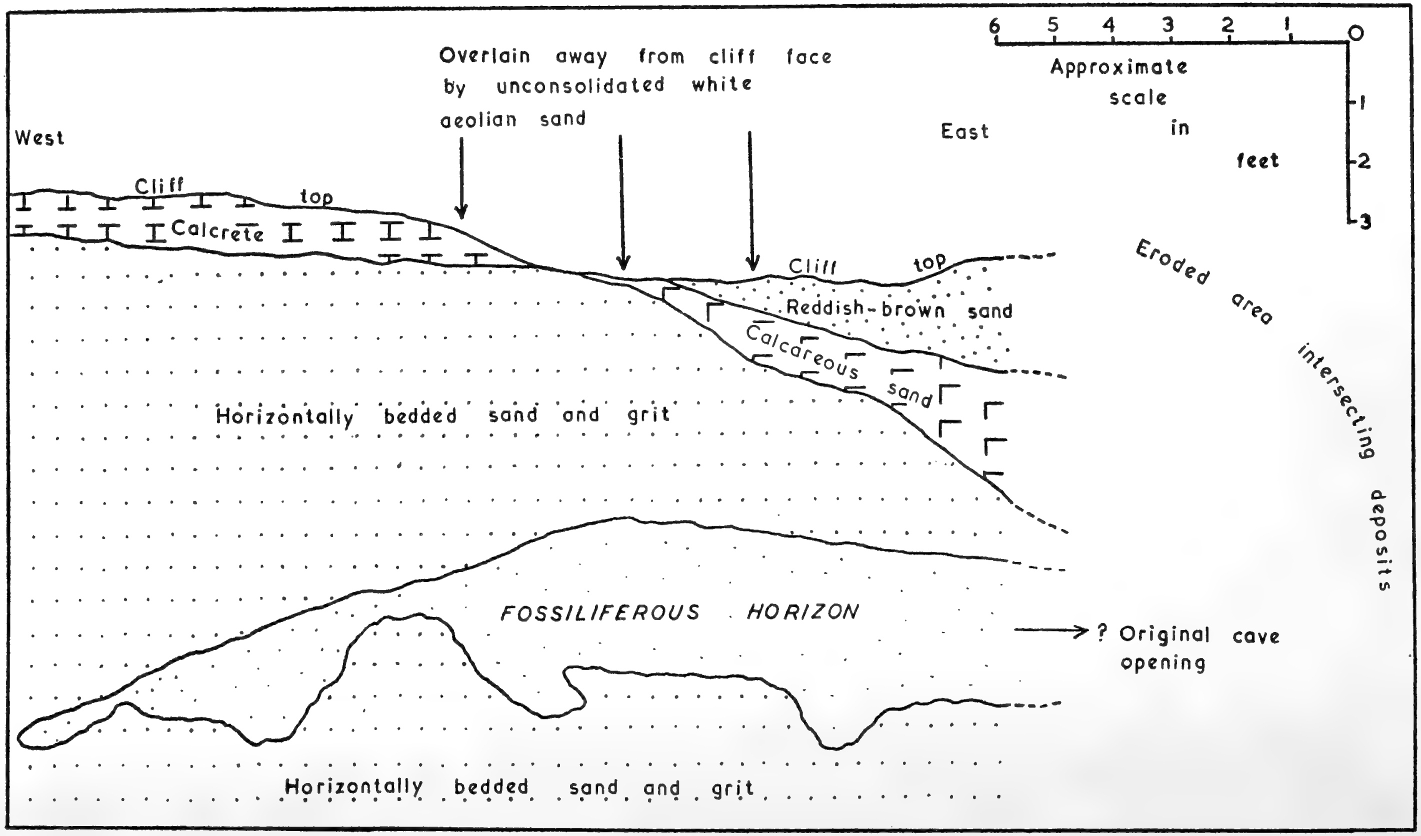

Fig. 2. Sketch section of Site I.

ciated with the fossils at this locality.

At Site II Extension, approximately 2 feet above the fossils, is a clearly defined horizon, apparently an old land surface, from which several flakes and numerous marine shells were recovered. This midden dates probably from the Late Stone Age, and may be indirectly associated with the fossils (*vide infra*).

From Site II a complete ostrich-egg, with a single perforation on its surface, was recovered (pl. 1C), and this resembles the 'water-containers' known from Late Stone Age contexts, and still used today by the Bushmen of the Kalahari Desert. The perforation is irregular and appears to have been made by being chipped away with a sharp object. This is the technique commonly employed in the manufacture of ostrich-egg water containers (Maggs, 1966), although in the present instance the perforation has not been rounded out.

If indeed this specimen is a water-container, its association with the fossils might be coincidental, having been buried into the fossil horizon from the Late Stone Age living floor immediately above.* These containers were, and still are, buried when being stored.

None of the fossils show any evidence of human interference, neither artificially produced fractures (spiral fractures, punctate marks, flaking, etc.), nor wear through use having been observed.

There is, therefore, no certain evidence for associating the fossils with human activity.

THE FOSSILS RECOVERED

The fossils were, in general, extremely well preserved. This is accounted for by the alkali nature of the deposits, and by the original protection afforded them in the caves from natural destructive agencies such as wind, water and temperature changes.

Damage to the specimens has been largely post-fossilization, and occurred mainly as a result of the collapse of deposits from the cliff-face, and their subsequent exposure to the atmosphere. Absorption of salts from the sea air, and their later crystallization within the fossils has resulted in lamination and cracking of some specimens.

The fossils are not heavily mineralized, and this rendered the preparation of those specimens in well consolidated matrix very difficult.

They occurred most commonly towards the base of the horizon, with several pockets of concentration, and usually lay horizontally in the deposit. Several instances were noted where elements of the skeleton were in articulation or only slightly separated. Since no systematic excavation was undertaken it was not possible to assess the frequency with which this occurred. This feature is a further indication of accumulation under protected conditions.

---

* The living floor was not actually detected at Site II, but since it and Site II Extension are exposures of the same horizon on either side of a small spur, it is almost certainly present.

Origin of the Fossils

The lack of positive cultural associations, taken in conjunction with the small size of the caves, indicates that some agency other than man was responsible for the bone accumulations. The nature of the fossils described by Singer & Fuller (1962) prompted the observation that, 'they could well have been deposited on the floor of a small cave or rock shelter used as a lair'. This view is supported by observations made in the present study.

In southern Africa an animal lair containing bones immediately suggests that the porcupine (*Hystrix africaeaustralis*) is, or was, the occupant. In the present instance this possibility was discounted, since the assemblages contained no gnawed bones. Porcupine lairs contain a high proportion of bones which show gnaw marks (Hendey & Singer, 1965).

Alternatives were sought among the Carnivora. One of the most striking features of the assemblages was the variety of carnivores represented. In the mammalian fauna of a region the numbers and types of carnivores form a relatively small percentage of the total, and this balance is usually reflected in the faunal assemblages of fossil sites (table 1). The situation at Swartklip suggests that the lairs were inhabited by a number of carnivores over a period of time, and that the assemblages contain the remains of animals which died there.

Table 1

THE VARIETIES OF CARNIVORA FROM SITE I COMPARED WITH THOSE FROM OTHER SITES IN THE CAPE PROVINCE

	Swartklip Site 1	Open Sites		Cave Sites*	
		Melkbos	Hopefield	A.K. 1	A.K. 2
Animal lairs	×				×
Human activity evident . .		×	×	×	
Varieties of carnivora . .	7	3	12	6	2
Other mammals (excl. microfauna)	8	14	38	11	11
Carnivora as % of total . .	47	18	24	35	18

* Hendey & Singer, 1965.

Perhaps the most significant evidence in support of the 'lair theory' is provided by the official name, Wolfgat, of the area in which the sites are located (fig. 1). This Afrikaans word, which literally translated is 'wolf-hole', but in free translation means 'hyena-lair', is an example of the naming of localities after animals, an extremely common practice amongst the early European settlers in South Africa (Sargent, 1954). The use of the term 'wolf' for hyenas is now largely an anachronism, but it does persist in the common Afrikaans names of these animals, i.e. 'gevlekte wolf' or 'tierwolf' =*Crocuta crocuta*; 'strandwolf' = *Hyaena brunnea*; 'aardwolf' = *Proteles cristatus*.*

---

* Often classed in a separate family, the Protelidae, but undoubtedly considered a true hyaenid by early non-scientific observers.

Dart (1949) states that 'most South African carnivora, such as the lion, jackal and spotted hyena, actually avoid caverns and live out in the veld, killing their prey and consuming it in the open country. Two South African types, namely the leopard and brown hyena, are attracted by the protection of rock shelters and of fissures. . . .' Remains of the brown hyena occur in both the Site I and Site II assemblages, and since it is also well known as a scavenger on sea-shores, it is the animal considered most likely to have given rise to the name 'Wolfgat'. Furthermore, the presence in the assemblages of isolated bones of large animals, such as the rhinoceros, suggests that at least one of the inhabitants of the lair was a scavenger.

The suggestion that the brown hyena was one of the 'bone-collectors' must, however, be accepted with reservations. Dart (1956) has gone to great lengths to prove that it does not accumulate bones in its lairs, and that it does not defecate in its lairs. Both Sites I and II Extension have yielded coprolites, and although the animal responsible for these was not identified, they were of a size sufficient at least to suggest the brown hyena.

The aardwolf also inhabits burrows, and although it is unlikely to have been responsible for the bone accumulations, being largely insectivorous, it is reported also to be a carrion eater (Miller, 1954; Maberly, 1963).

In any event, it is certain that within historic times there was a lair of a 'hyaenid' in the area where the fossil sites are located. Whether or not this can be related to the fossil occurrences is a matter for conjecture.

Speculations on other possible occupants of the lairs have proved equally inconclusive. The African hunting dog (*Lycaon pictus*), recorded from Site I, does not normally inhabit lairs, but the females do occupy burrows during the natal and early post-natal periods.

The lion (*Felis leo*), although not an occupier of lairs today, must be considered as a possibility simply because of the number of individuals recorded. Remains of the lion are extremely rare at fossil sites in South Africa, whereas at least five individuals are represented in the relatively small Swartklip assemblages.

Fragments of ostrich-eggshell were recovered at all three sites, and unless these are all from broken water containers, which is considered highly unlikely, their presence suggests that eggs formed part of the diet of one of the occupants.

The presence of fossils at and near the top of the fossiliferous horizon is an apparently anomalous situation in the lair theory. There would, however, have been some fall of sand from the walls and roof of the caves, and with the accumulation of sand, bones and other debris in the lair, the occupying animal would have been forced to clear the floor from time to time. In the clearing of new living space, bones would have been thrown up and in some cases reached roof level. This regular disturbance would also account for the completely amorphous character of the sand constituting the fossiliferous horizon.

It is possible that the lair at Sites II and II Extension was occupied at the time that the land surface on which the midden accumulated was in existence (*vide supra*). If this was the case, there may well be some tenuous link between human activity and the fossils, such as, for example, the scavenging of food remains from nearby human occupation sites by the animal inhabiting the lair at that time.

The Faunal Assemblages

An analysis of the material recovered confirms the observation of Singer & Fuller (1962) on the great diversity of faunal types represented in a relatively small total assemblage from a limited area (table 2).

Of the new sites, Site I was the most productive (table 3).

Table 2

	Site I	Site II	Site II Extn.	Singer/Fuller Occur.
Class *MAMMALIA*				
Order ARTIODACTYLA				
Family **Bovidae**				
Redunca cf. *arundinum*	×	×	×	×
Hippotragus cf. *leucophaeus*	×			
cf. *Connochaetes* sp.	×			×
Antidorcas marsupialis australis n. subsp.	×	×	×	×
Raphicerus sp.	×	×		×
Family **Hippopotamidae**				
cf. *Hippopotamus* sp.	×			
Order PERISSODACTYLA				
Family **Rhinocerotidae**				
Diceros simus	×			
Incertae sedis	×	×		×
Family **Equidae**				
Equus sp.	×			
Order CARNIVORA				
Family **Hyaenidae**				
Hyaena brunnea	×	×		
Family **Felidae**				
(?) *Felis serval*	×			
Felis leo	×	×		
Family **Canidae**				
Lycaon pictus	×			
cf. *Canis* sp.	×	×		
Canis cf. *mesomelas*	×	×		×
Family **Viverridae**				
(?) *Herpestes ichneumon*	×			
Family **Mustelidae**				
Mellivora capensis	?			×
Aonyx sp.				×
Incertae sedis (+1)	×	×		
Order RODENTIA				
Family **Bathyergidae**				
Bathyergus suillus	×			
Incertae sedis (3)	×			

	Site I	Site II	Site II Extn.	Singer/Fuller Occur.
Class *AVES*				
Order **STRUTHIONIFORMES**				
Family **Struthionidae**				
Struthio australis	×	×	×	
Class *REPTILIA*				
Order **CHELONIA**				
Incertae sedis		×		

TABLE 3

THE FOSSIL MATERIAL RECOVERED FROM THE THREE SITES

	Cranial pieces	Min. no. indiv. based on skull	Identified post-cranial pieces	Min. no. indiv. based on Postcranial skeleton	Unident frags.	Complete ostrich egg	Frags. ostrich-eggshell	Frags. tortoise carapace	Coprolites
Site I	270	45	700	25	1630	—	199	—	7
Site II	12	8	100	12	119	1	33	1	—
Site II Extn.	6	3	13	3	34	—	2	—	5
Totals	288	56	813	40	1783	1	234	1	12

SYSTEMATIC DESCRIPTION OF FAUNAL TYPES

The specimen numbers are those in the accession registers for the Swartklip area in the Subdepartment of Quaternary Palaeontology, South African Museum, and all comparative material referred to is in the collections of this museum.

Unless otherwise stated the material described is from Site I. Measurements are in millimetres.

Where possible the nomenclature follows that of Ellerman *et al.* (1953). An exception to this is the use of the generic name *Felis* for the lion, in place of *Panthera* (Hershkovitz, 1959).

Family **Bovidae**

Tribe *Reduncini*

Redunca cf. *arundinum* Boddaert

Reedbuck

At Site I a minimum of six individuals were represented, while there was at least one from both Sites II and II Extension.

ZW 376—(♂) (table 4, pl. 2A, B)—This is the skull of an adult, with the braincase almost intact, but having lost the tympanic bullae, most of the basioccipital, the sphenoid, the zygomatic arches, and parts or all of other delicate features from the base of the skull. Both horn cores have lost part of their distal extremities. The frontals are largely intact above the supraorbital foramina, but those parts forming the roof of the orbits have been lost.

TABLE 4

DIMENSIONS OF ♂ *Redunca arundinum* SKULLS COMPARED WITH THOSE OF TWO FOSSIL SPECIMENS FROM SWARTKLIP

	Fossil Specimens		Modern *R. arundinum* (♂)		
	ZW 376	ZW 1316	Mean	Range	No. Measured
Postorbital constriction ..	c75·0	76·0	69·5	—	1
Max. length across occipital condyles	59·5	58·8	57·2	56·5–57·7	4
Max. skull width in occipital plane	102·5	102·1	98·2	94·7–101·0	4
Height from most superior point of foramen magnum to lambda*	35·0	36·8	37·5	36·8–38·6	4
Dimensions of horn pedicle: Ant./Post. ..	35·9	35·5	35·1	31·9–38·0	4
Dimensions of horn pedicle: Transverse ..	38·0	34·0	34·3	32·2–36·6	4
Skull width at horn pedicles ..	102·4	105·6	99·7	95·4–102·0	4

* Point on median line contact of occipital and parietal.

ZW 1316—(♂) (table 4, pl. 2C)—The skull of an adult from Site II. It corresponds closely in size and morphology to ZW 376. Except for the horn cores, of which only the bases remain, it is more complete than ZW 376, and lacks only the facial region, the zygomatic arches, the tympanic bullae and rims of the orbits.

The braincases of these two specimens have distinctly flattened dorsal surfaces, with the nuchal crests not as strongly arched as in the comparative specimens. This morphological difference is not clearly expressed by the skull dimensions, the width/height ratio being 1 : 2·8 in the fossil specimens and 1 : 2·6 for the mean of the comparative series. It has clearly resulted from an upward expansion of the braincase on either side of the median line. In all other observable respects the two fossil skulls were similar to those of the comparative series.

ZW 74—(♀) (tables 5 & 6, pl. 2D)—The almost intact skull of a young adult, with the M^3 incompletely erupted. It lacks the nasals, the premaxillae and parts of the maxillae, and is slightly damaged in the parietal and occipital regions. All the molars are present and well preserved, as is the left P^4. The specimen ZW 712, a fragment of right maxilla with the P^2, P^3, and P^4 belongs almost certainly to ZW 74.

TABLE 5

DIMENSIONS OF ♀ *Redunca* cf. *arundinum* SKULL FROM SWARTKLIP (ZW 74)

Postorbital constriction	70·2
Length between external occipital protuberance and bregma	76·3
Width between external alveolar margins at midpoints of M^1	71·7
Height from basioccipital to most superior point of occipital	56·4

No female *R. arundinum* skulls were available for comparison, and consequently no conclusions could be drawn as to the relative size and morphology of the fossil specimen.

In addition twenty-two isolated upper teeth and maxillary fragments were assigned to *Redunca*. These included deciduous teeth. The permanent teeth were, without exception, longer than those of the comparative specimens, while the breadths were greater than, or near the top of the range of the comparative series (table 6). The six modern *R. arundinum* skulls examined were those of males with horn lengths ranging from 24 cm to 30 cm along the front curve. They were, therefore, above average size for the species (Ward, 1899).

TABLE 6

DIMENSIONS OF UPPER TEETH OF *Redunca arundinum* COMPARED WITH THOSE OF FOSSIL SPECIMENS FROM SWARTKLIP

		Fossil Specimens				Modern *R. arundinum* (♂)		
		ZW 74	ZW 712	ZW 80	ZW 392	Mean	Range	No. Measured
P^2	l	—	7·0	—	—	6·4	5·5–7·2	2
	b	—	5·9	—	—	5·2	4·8–5·4	2
P^3	l	—	c9·5	—	—	8·6	7·9–9·1	4
	b	—	8·0	—	—	8·5	8·3–9·0	4
P^4	l	11·0	10·9	—	—	9·1	8·3–9·7	5
	b	9·4	9·1	—	—	8·7	7·8–9·1	4
M^1	l	c16·5	—	—	17·5	12·2	10·4–13·8	6
	bm	12·8	—	—	10·7	11·2	10·7–11·7	3
	bd	12·1	—	—	9·4	10·9	10·1–12·2	5
M^2	l	17·9	—	—	18·0	13·9	12·1–15·0	6
	bm	12·1	—	—	9·9	10·9	9·8–11·7	6
	bd	10·8	—	—	8·0	10·2	9·5–10·8	4
M^3	l	17·2	—	17·9	—	15·3	13·3–17·3	6
	bm	10·4	—	11·3	—	10·0	8·8–10·8	5
	bd	9·2	—	9·7	—	8·5	7·8–9·1	5

Sixteen mandibles, mandible fragments, and isolated lower teeth of *Redunca* were also included in the assemblages, but since no mandibles of the modern reedbuck were available for comparison, they were not studied in detail.

The available evidence suggests that the Swartklip *Redunca* is at least subspecifically distinct from the extant form. In view of the inadequate range of comparative material, the degree of difference could not be accurately assessed, and the fossil material is therefore only tentatively assigned to *R. arundinum*.

Tribe *Hippotragini*

Hippotragus cf. *leucophaeus* Pallas

Blue Antelope

The remains of at least four individuals were recovered at Site I.

The tentative conclusion on the presence of the recently extinct blue antelope was based on three specimens, which belong almost certainly to a single individual.

ZW 355—(tables 7, 8 & 9, pl. 5A, B)—A right mandible with a complete set of moderately worn cheek teeth.

ZW 375—An incomplete left mandible with P_4—M_3.

ZW 357—RP^2.

The incisal alveolar region of ZW 355 is missing, as is much of the ascending ramus, and that part of the mandible in the region of the angle. The teeth and remainder of the corpus are well preserved. The teeth are clearly hippotragine, but differ significantly from those of the extant roan (*H. equinus*) and sable (*H. niger*) antelopes. They do, however, closely resemble the teeth of the type specimen of *H. problematicus* Cooke (1947). This specimen is from Bloembos, near Darling, about 50 miles north of Swartklip.

In *H. problematicus* (SAM 661A & B) the premolar series is proportionately longer than the molar series, the premolars resembling those of the roan antelope, while the molars are intermediate between those of the roan and sable antelopes (Cooke, 1947). This feature is also exhibited by the Swartklip specimen (table 7).

TABLE 7

THE LENGTHS OF THE CHEEK TEETH SERIES OF THE SWARTKLIP *Hippotragus*, COMPARED WITH THOSE OF OTHER HIPPOTRAGINES

	ZW 355	*H. problematicus** (S.A.M. 661A)	*H. equinus** (Mean)	*H. niger** (Mean)
$P_2 - P_4$ length	51·2	53·0	51·0	45·0
$M_1 - M_3$ length	70·2	71·0	78·0	68·0

* Cooke, 1947.

In general the teeth of ZW 355 correspond closely to those of the *H. problematicus* type specimen in size, although the M_2 and M_3 are slightly narrower (table 8). Morphologically the differences are also slight. The anterior accessory cusp of the P_2 of SAM 661A is seen on the lingual surface as a clearly defined vertical pillar, whereas in that of ZW 355 the base of the cusp broadens out posteriorly and is not as well defined as an 'accessory' feature. The P_4 of ZW 355 has a small accessory cusp developed on the anterior part of the buccal surface, and this is not present on the P_4 of SAM 661A. In ZW 355 the anterior enamel folds are more strongly developed than those of SAM 661A. In the M_2 of ZW 355 the external accessory pillar between the lobes is separated from the folds of buccal enamel, whereas in SAM 661A it has been incorporated. Usually this might be ascribed to different degrees of wear, but the teeth of the two specimens have very similar crown heights.

TABLE 8

DIMENSIONS OF THE LOWER TEETH OF THE SWARTKLIP *Hippotragus*, COMPARED WITH THOSE OF THE TYPE SPECIMEN OF *H. problematicus*

		ZW 355	S.A.M. 661A
P_2*	l ..	15·0	14·8
	b ..	11·9	11·6
P_3*	l ..	17·0	17·4
	b ..	14·0	14·3
P_4*	l ..	18·6	19·1
	b ..	14·8	14·1
M_1†	l ..	20·0	19·3
	bm ..	13·1	13·7
	bd ..	12·1	c12·0
M_2†	l ..	22·5	23·0
	bm ..	11·9	13·4
	bd ..	12·0	12·8
M_3†	l ..	28·7	30·1
	bm ..	11·2	12·5
	bd ..	10·8	11·8

* Maximum dimensions midway up crown.

† Dimensions at occlusal surface.

The two specimens differ most widely in the relative sizes of their mandibular corpora, the Swartklip specimen being considerably more robust (table 9). This is possibly a reflection of a difference in sex.

Cooke (1947) suggested that *H. problematicus* may prove to be a synonym of *H. leucophaeus* Pallas, which became extinct in the Cape Province at the end

TABLE 9

DIMENSIONS OF THE MANDIBULAR CORPUS OF THE SWARTKLIP *Hippotragus*, COMPARED WITH THOSE OF THE TYPE SPECIMEN OF *H. problematicus*

	ZW 355	S.A.M. 661A
Height below midpoint of M_3* ..	c62·0	—
Height below midpoint of M_1* ..	53·4	44·0
Height below midpoint of P_2* ..	40·0	30·9
Distance between post. end of mental foramen and ant. end of P_2	46·8	40·0

* Measured on lingual surface.

of the eighteenth century. Later he expressed reservations on this question as a result of information supplied him by the late Robert Broom (Cooke, 1955), but as far as can be determined Broom's opinion remains unsubstantiated.

Nevertheless, in view of the geographical position of Swartklip and the relatively recent age of the fossils (*vide infra*), it is considered that sufficient justification exists for tentatively assigning the Swartklip hippotragine material to *H. leucophaeus*.

The specimen ZW 357 (RP^2) is considerably larger than the corresponding teeth of the roan and sable antelope comparative specimens, having a maximum length of 18·3 and a maximum breadth of 22·1 mm.

Tribe *Alcelaphini*

cf. *Connochaetes* sp.

The minimum number of alcelaphines represented was three. All the specimens recovered were assigned to the genus *Connochaetes* (*sensu lato*) (pl. 5D).

In general the material showed greater affinities to *C. gnou*, rather than *C.* (*Gorgon*) *taurinus*, but owing to the lack of adequate comparative information, no conclusion on the specific rank of the fossil form was reached.

Tribe *Antilopini*

Antidorcas marsupialis australis n. subsp.

Diagnosis

An *Antidorcas* differing from the extant *A. marsupialis* principally in the size and shape of the horn cores of the male. They are notably more slender in the fossil form, being intermediate in size between those of the male and female of the modern form. Although lyrate in shape they show no indication of an inward curve towards the tip. They rise vertically above the orbits as in the modern form, but then have only a slight backward sweep. The braincase of the fossil specimens is slightly longer and lower than that of the extant springbok, but in general its morphology is similar. A notable exception is that the basioccipital and body of the sphenoid of the new subspecies lie in a plane with the inferior margin of the occipital condyles, whereas in the modern springbok the sphenoid curves upwards fairly sharply immediately anterior of the basilar tubercles.

Morphologically the teeth of the modern and fossil forms are indisinguishable, although those of the new subspecies tend to be rather narrow.

Material

ZW 66—(♂) (table 10, pl. 3)—The skull of an adult consisting of a complete braincase and frontlet. The left horn core is intact, but only the base of the right core is preserved. The braincase has suffered some slight superficial damage, and delicate parts such as the tympanic bullae have been lost. The left horn core, from which the extreme tip is missing, is damaged on the

TABLE 10

DIMENSIONS OF THE SKULLS OF *Antidorcas marsupialis australis* n. subsp. FROM SWARTKLIP COMPARED WITH THOSE OF THE MODERN SPRINGBOK

	ZW 66	ZW 67A	ZW 402	ZW 1317	*A. marsupialis* ♀ Mean	Range	No. measured	*A. marsupialis* ♂ Mean	Range	No. measured
Max. skull width at horn pedicles ..	67·8	c64·0	c65·0	74·7	58·5	52·5–61·6	3	75·3	70·2–79·8	9
Width between horn cores	19·0	c19·0	c21·0	c21·0	28·0	25·0–31·9	3	18·6	16·0–21·8	6
Dimensions of horn pedicle { Ant./Post.	28·7	28·8	27·0	c32·5	18·9	14·0–22·7	3	37·2	33·0–40·1	9
Dimensions of horn pedicle { Transverse	24·0	21·2	22·2	27·3	15·6	12·7–18·8	3	29·7	25·9–32·3	8
Height from base of foramen magnum to top of external occip. protuberance	40·3	—	c40·0	—	38·9	—	1	42·5	41·0–43·8	4
Length between ext. occip. protuberance and bregma	70·0	—	66·5	—	60·8	—	1	64·4	64·0–65·0	4
Max. length across occip. condyles ..	44·0	—	c46·0	—	40·0	—	1	43·6	41·6–47·0	4
Max. skull width at mastoid processes ..	79·0	—	—	—	69·2	—	1	79·7	77·8–82·9	4
Max. width across parietals	68·8	—	c66·0	—	62·8	—	1	66·1	61·6–67·5	4

anterior surface of the proximal end. There is, however, no indication of transverse ridges on this, or any of the other horn cores.

ZW 402—(♂) (table 10, pl. 4A)—The skull of an adult consisting of the frontlet, left and right horn cores and incomplete braincase. The tip of the left horn core is missing. The base and sides of the braincase are extensively damaged, and approximately fifty fragments of bone from this region were not restored to the skull. The largest of these fragments includes the basioccipital with the right occipital condyle, and the sphenoid. This specimen compares remarkably closely with ZW 66 in all observable respects.

ZW 67a—(♂) (table 10, pl. 4B)—The right horn core and part of the frontal of an adult. It corresponds closely with ZW 66 and ZW 402 in all observable respects.

ZW 1317—(♂) (table 10)—An incomplete and heavily weathered skull from Site II, with only the base of the horn cores and part of the frontal and parietal remaining. The dimensions of the horn cores correspond more closely with those of the comparative specimens than do any of the others.

ZW 48—(♀)—The only female specimen known from Swartklip, having come from the Singer/Fuller Occurrence, and referred to *Antidorcas marsupialis* or *Gazella wellsi* Cooke by them. The specimen consists of an incomplete left horn core and part of the frontal. Owing to its condition, accurate measurements were not possible, but it appears to fall within the range of variation of the female springbok.

ZW 68—A fragment of the roof of a braincase, very similar to the corresponding parts of ZW 66 and ZW 402.

ZW 69, ZW 70 & *ZW 71*—Horn core fragments, indistinguishable from the corresponding parts of the more complete specimens.

ZW 151 & *ZW 161*—LM^3 and incomplete RM^3, indistinguishable from the M^3 of the modern springbok.

ZW 1571—LM^1 from Site II Extension, somewhat smaller than the M^1 of the comparative specimens.

ZW 81 & *ZW 82*—(table 11, pl. 4C)—Incomplete left mandibles, with the P_3 lost from both specimens. As is characteristic of *Antidorcas* there is no P_2. In all respects these specimens correspond closely to the comparative series.

Discussion

The minimum number of individuals represented in the Site I assemblage was four, while there was at least one from both Site II and II Extension.

Three subspecies of *Antidorcas marsupialis* Zimmerman are generally recognized: *marsupialis* in the Transvaal, Orange Free State and south of the Orange River; *angolensis* in the Kaokoveld and northern Namib Desert; and *hofmeyri* in Great Namaqualand and the Kalahari Desert (Roberts, 1951; Ellerman *et al.*, 1953).

TABLE 11

DIMENSIONS OF THE LOWER TEETH OF THE FOSSIL *Antidorcas* FROM SWARTKLIP COMPARED WITH THOSE OF THE MODERN SPRINGBOK

				Modern springbok (3 specimens)	
		ZW 81	ZW 82	Mean	Range
P_4	l	—	8·6	8·9	7·7–10·0
	b	—	5·0	5·3	4·4–6·0
M_1	l	13·0	12·5	13·1	11·7–14·0
	bm	6·1	6·4	6·8	6·5–7·0
	bd	6·7	6·9	7·8	6·9–8·2
M_2	l	14·5	14·9	14·9	12·8–16·4
	bm	6·2	7·1	7·4	7·3–7·4
	bd	6·4	7·3	7·7	7·3–8·4
M_3*	l	20·4	21·4	23·2	22·9–23·8
	bm	5·5	7·0	7·2	6·7–7·8
	bd	5·7	7·2	7·6	6·9–8·3
$M_1 - M_3$		48·1	47·6	50·0	46·1–53·0

* M_3 of ZW 81 incompletely erupted.

Unfortunately the localities from which the comparative specimens came were not all known, but at least three of the males were from South West Africa. These were, therefore, probably either *angolensis* or *hofmeyri*, while most of the others were almost certainly *marsupialis*. Blaine (quoted by Roberts, 1951) in his definition of *angolensis* stated that the horns of this subspecies are not as stout at the base as those of *marsupialis*, while the skull is, 'relatively longer, narrower and vertically less deep'. This description could apply to the new subspecies, but Thomas (1926) in his definition of *hofmeyri* stated that it has the 'same long heavy horns' of *angolensis*. Consequently since the horns of these two subspecies are apparently similar, and since the comparative series included specimens of at least one of them, the characteristics defined by Blaine are obviously not of a degree sufficient to make the horns of *angolensis* comparable in size to those of the new subspecies.

Clearly then the horns of the males of the extant subspecies, although variable, differ significantly from those of the fossil specimens. These are gracile, not heavily ridged, do not have the marked sweep posteriorly, and do not appear to recurve inwards towards the tip. They show a considerably greater divergence in character to those of the extant subspecies than these show relative to one another.

Gentry (1964) has shown the importance of the transverse compression of horn cores in the classification of gazelles, and applying his method of quantitatively expressing this feature, it was found that the horn cores of the Swartklip *Antidorcas* correspond very closely to those of the modern springbok (table 12). In this respect at least, the horns of the modern and fossil forms are similar.

The angulation of the sphenoid relative to the basioccipital in the modern springbok is a feature which relates directly to the size and orientation of the horns. Gentry (1964) has indicated the relationship between the degree of development of the basilar tubercles and horn size in gazelles, and in the slender-horned Swartklip *Antidorcas* these tubercles are indeed less pronounced than in the modern springbok. With the marked backward sweep of the horns in the latter, an adaptation of the angle of attachment of the neck muscles to the skull would be necessary to compensate for the relative posterior shift in weight of the horns. This requirement could be met by the downward movement of the basioccipital relative to the sphenoid. The basioccipital of the new subspecies is somewhat more rectangular than that of the modern springbok and this feature, together with the slightly shorter and lower braincase, are probably related expressions of the same factor.

TABLE 12

THE TRANSVERSE COMPRESSION* OF THE SWARTKLIP *Antidorcas* HORN CORES COMPARED WITH THAT IN A SERIES OF MODERN SPRINGBOK

	$\frac{\text{Transverse diameter}}{\text{Antero-posterior diameter}} \times 100$		
	Mean	Range	No. measured
Swartklip specimens	80·85	73·6–84·0	4
Modern *A. marsupialis* ♂	80·56	75·7–87·3	8
Modern *A. marsupialis* ♀	83·47	76·9–90·7	3

* Gentry, 1964.

Recently Gentry (1966) has recorded from Beds I and II at Olduvai Gorge, a series of gazelline horn cores (his Group (B): 65–66, pl. 2C) which, as far as can be determined, compare closely to those of the Swartklip *Antidorcas*. He refers these specimens tentatively to *Gazella*, but concludes that they are unlike the horn cores of any living gazelle. The illustrated specimen (1953, SHK II, 285) in lateral view is very similar to the Swartklip horn cores, and its dimensions (28·2 × 23·1 mm) fall within the range of variation of the Swartklip specimens. If this Olduvai Gorge form is indeed the same as that from Swartklip, it indicates a wide temporal and geographical range for the animal. It is also almost certainly present at the Elandsfontein (Hopefield) site, where a number of horn cores and dentitions of this and other Antilopini have been recovered.

The taxonomic status of the Swartklip *Antidorcas* does, in part, hinge on the question of the geographical distribution of this genus. The extant subspecies of the springbok are plains-dwelling animals confined largely to the inland plateau and the western coastal region of southern Africa (Ellerman *et al.*, 1953; Roberts, 1951). The natural pattern of their distribution has been extensively disrupted by human settlement, and while the springbok may have occurred in the south-western Cape during the seventeenth century, no historical records to this effect could be located. If it was indeed present, there will certainly be no adequate descriptions of the physical character of the local form available, and reference to the fossil record must therefore be made. The Swartklip fossils do indicate the presence of a springbok differing slightly from the subspecies occurring further north.

In the light of available evidence it is concluded that the Swartklip *Antidorcas* is at least a geographical variant of the extant species, and in view of the location of the sites, the taxon *Antidorcas marsupialis australis* is proposed. However, if the suggested wider relationships of this form can be convincingly demonstrated, its elevation to the species level will need to be considered.

Tribe: *Neotragini*

Raphicerus sp.

The minimum number of neotragine antelope represented in the Site I assemblage was six, while a single individual was represented at Site II.

The two extant South African species of *Raphicerus*, namely *campestris* (steenbok) and *melanotis* (grysbok), cannot be satisfactorily distinguished on osteological grounds. Both are found in the south-western Cape Province today, and the Swartklip specimens show no significant differences from the living forms.

Singer & Fuller (1962) stated that the *Raphicerus* specimens recovered by them had closer affinities to the recent forms than to the fossil form from the Elandsfontein site.

Family **Bovidae:** *Incertae sedis*

Almost one hundred skull fragments and isolated teeth, mostly incomplete, from the Site I assemblage were not classified, but none suggested the presence of an antelope other than those already listed.

Family **Hippopotamidae**

cf. *Hippopotamus* sp.

A single unerupted (? deciduous) tooth, doubtfully ascribed to the hippopotamus, was included in the Site I assemblage.

Family **Rhinocerotidae**

Diceros (*Ceratotherium*) *simus* Burchell

White Rhinoceros

Remains of the rhinoceros were rare in all the assemblages, and only a single unerupted RP^3 (ZW 192) from Site I was identified positively as belonging to *Diceros simus*. This species was not recorded in the south-western Cape Province during historic times, but has been recorded from the Langebaanweg, Hopefield and Melkbos fossil sites.

Diceros sp.

The only other cranial remains of the rhinoceros recovered were four tooth fragments. Owing to their condition it was not possible to assign them to any species.

Six elements of the postcranial skeleton were recovered from Sites I and II, including a radius and ulna (ZW 292 and ZW 1120) found in close association at Site I.

It is generally considered impossible to distinguish the white from the black rhinoceros on the basis of their postcranial skeleton (Hooijer & Singer, 1960), but the specimens from Site I compared closely in size with corresponding elements of the skeleton of a white rhinoceros in the South African Museum (SAM 21379). However, the postcranial material recovered may belong in part, or entirely to the black rhinoceros (*Diceros bicornis*), which was recorded in the area during historic times, and which is commonly found at other fossil sites in the area.

Family **Equidae**

Equus sp.

No cranial remains of this genus were recovered, but several elements of the postcranial skeleton were included in the Site I assemblage. They represent the remains of at least two individuals, an adult and a juvenile.

Family **Hyaenidae**

Hyaena brunnea Thunberg

Brown Hyena

The minimum number of individuals represented in the assemblages was three.

ZW 394—A right premaxilla, probably of an immature adult, with only the I^2 remaining in position. This tooth is fully erupted, but unworn.

ZW 1311—(table 13, pl. 6A, B)—An incomplete skull of an immature individual from Site II, with associated right and left mandibles (ZW 1312 & ZW 1313). The facial part of the skull is largely intact, but most of the braincase has been lost. The teeth preserved are as follows:

Left: Roots of I^1 and di^3; I^2 and I^3 about to erupt; root and damaged crown of $d\underline{c}$; P^1; dp^2; dp^3; dp^4; P^4 about to erupt; M^1 just erupted.

Right: As above, except that the I^1 is intact, only the posterior root of the dp^2 remains, and the P^1 has been lost.

The right mandible (ZW 1312—pl. 6C) has the following teeth present: I_1; $d\bar{c}$; dp_2; dp_3; dp_4; and M_1 partially erupted.

The left mandible (ZW 1313) is incomplete, and only the dp_3 and part of the dp_2 are preserved.

TABLE 13

DIMENSIONS OF THE TEETH OF AN IMMATURE *Hyaena brunnea*, SPECIMEN (ZW 1311) FROM SWARTKLIP

P^1		dp^2		dp^3		dp^4		M^1		
l	b	l	b	l	b	l	b	l	b	$P^1 - dp^4$
7·3	7·6	13·5	c7·2	24·1	13·3	9·6	14·2	c12·5	6·4*	51·5

* At midpoint of tooth.

No skulls of immature brown hyenas were available for comparative purposes, but the permanent teeth present corresponded closely with those of the adult comparative specimens.

A fragment of right maxilla (ZW 141) with the dp^3 and dp^3 from Site I, closely resembled the corresponding part of ZW 1311 in all observable respects.

Family **Felidae**

? *Felis serval* Schreber

Serval Cat

At least two individuals were represented in the Site I assemblage.

ZW 110—(table 14, pl. 7C)—An incomplete skull of a small felid consisting of the braincase, the posterior part of the palate and left maxilla, and the left carnassial. This tooth was somewhat shorter than those of modern serval cats (Roberts, 1951), but since it is poorly preserved the dimension given may be inaccurate. An isolated felid P^4 from the Site I assemblage (ZW 183) has a length of 14·0 mm, which is within the range of variation for this species.

TABLE 14

DIMENSIONS OF THE SKULL OF A ? *Felis serval* FROM SWARTKLIP COMPARED WITH THOSE OF MODERN SPECIMENS

		Felis serval subsp.*					
				3 adult ♂			
	ZW 110	♂	♀	Min.	Max.	♂	♂
Intertemporal constriction	30·8	—	30·0	29·5	35·0	32·5	35·2
Braincase width	52·2	—	49·7	52·5	56·0	52·5	52·6
Bullae—greatest diameter	c24·5	26·5	23·5	25·5	27·5	26·5	25·0
P^4 length	c12·0	16·0	13·0	13·9	15·3	14·0	14·8

* Roberts, 1951.

ZW 377—The anterior part of the snout of a small felid, with the LI^1, LI^2, RI^2, RI^3 and RC.

Owing to the lack of comparative material these specimens are only doubtfully referred to *Felis serval.*

Felis leo Linnaeus

Lion

A minimum of four individuals was represented in the Site I assemblage, and one in the Site II assemblage.

ZW 100—(pl. 7A)—An incomplete skull consisting of the braincase and part of the frontals. The occipital is intact except for that part in the region of the left mastoid process. The right tympanic bulla is slightly damaged and the left completely absent. The right temporal is complete and both the articular groove and postglenoid process are present. The basioccipital and sphenoid are largely intact. The left side of the braincase is damaged and most of the parietal and temporal have been lost.

This specimen was morphologically indistinguishable from the skulls of the modern lion examined, and in size fell within the range of variation of the comparative series.

ZW 101—An incomplete braincase lacking the top of the nuchal crest, the sagittal crest and immediately adjacent parts. It compares closely in all observable respects with ZW 100, but is less well preserved.

ZW 131 (& *ZW 174*)—An incomplete left maxilla with the dp^3, dp^4 and the M^1 just erupting. The $\underline{C}$, P^3 and P^4 are present but unerupted. The unerupted teeth and the M^1 were similar in all respects to those of the comparative series.

ZW 106—(pl. 7B)—A left maxillary fragment with the dp^2 and dp^3, and the unerupted P^4.

Eight other isolated deciduous or unerupted permanent teeth were recovered, in addition to a fragment of right maxilla (ZW 144), which belongs almost certainly with ZW 106.

The deciduous teeth show all the characteristics of those of the modern lion (Broom, 1949).

Few elements of the postcranial skeleton were recovered. A first phalanx (ZW 237), two fragments of a right radius (ZW 350 and ZW 526) and the distal end of an ulna (ZW 1209) were the only postcranial remains of adults recovered, the last-mentioned from Site II. A single metapodial (ZW 261) of an immature individual came from Site I. None of these specimens, with the possible exception of the ulna, was of unusual size.

Family **Canidae**

Lycaon pictus Temminck

African Hunting Dog

Two isolated teeth, a LI^2 (ZW 137) and an incomplete RI^3 (ZW 177), were assigned to this species. They were indistinguishable in all respects from the corresponding teeth of the comparative series.

cf. *Canis* sp.

ZW 1314—A left maxillary fragment with the P^4 and M^1 from Site II. While the teeth resemble those of *Canis* morphologically, they fall beyond the size range of variation of the two extant South African jackals (*C. mesomelas* and *C. adustus*).

ZW 108—A canine which is significantly larger than those of the two extant jackals, but appreciably smaller than that of *Lycaon pictus*.

Canis cf. *mesomelas* Schreber

Black-backed Jackal

This was the most commonly represented carnivore at Site I, the remains of at least six individuals being present.

The tentative diagnosis of the specimens was based principally on the size of the lower carnassials, and the carnassial: molar ratio (Ewer, 1956*a*), which excluded the possibility of the material belong to the side-striped jackal (*C. adustus*) (tables 15, 16).

Table 15

DIMENSIONS OF THE LOWER TEETH OF *Canis* cf. *mesomelas* FROM SWARTKLIP COMPARED WITH THOSE OF A SERIES OF TEN *C. adustus* AND FOURTEEN *C. mesomelas*

	Swartklip specimens			*C. adustus**		*C. mesomelas**	
	Mean	Range	No. measured	Mean	Range	Mean	Range
P_1 l	4·2	—	2	3·4	2·9–4·0	4·0	3·4–4·8
b	3·3	—	2	2·3	2·0–2·7	2·7	2·3–3·2
P_2 l	8·5	8·1–8·9	3	7·6	7·2–8·2	8·0	7·2–9·0
b	4·0	3·8–4·4	3	3·1	2·8–3·5	3·3	2·4–3·8
P_3 l	9·4	9·1–9·7	4	8·6	8·0–9·0	8·8	7·1–10·0
b	4·4	4·1–4·6	4	3·4	2·8–4·4	3·5	3·0–4·0
P_4 l	10·9	10·5–11·3	4	9·8	9·3–10·6	10·3	9·2–11·5
b	4·9	4·4–5·4	4	4·2	3·7–4·7	4·3	3·6–4·8
M_1 l	20·5	19·6–21·0	5	16·2	15·0–17·4	18·8	16·5–20·7
b	8·7	8·4–9·3	5	6·1	5·1–6·8	7·2	6·5–8·2
M_2 l	8·7	8·0–9·4	6	9·4	8·7–10·0	8·5	7·4–9·6
b	6·7	6·0–7·1	6	6·5	5·2–7·0	6·3	5·7–7·0
M_3 l	4·5	—	1	4·6	4·3–5·0	4·2	3·5–4·9
b	4·1	—	1	3·9	3·5–4·5	3·8	3·3–4·3
$P_1 - P_4$ l	35·9	34·6–38·0	3	35·0	31·7–36·4	34·8	31·5–37·1
M_1: M_2 l	2·46	2·35–2·58	3	1·73	1·60–1·81	2·21	1·99–2·57

* Ewer, 1956*a*.

Although available evidence indicates the presence of *C. mesomelas* in the assemblages, it may prove on closer examination that *all* the canid material from the Swartklip sites belongs to an extinct member of the family.

TABLE 16

DIMENSIONS OF THE UPPER TEETH OF *Canis* cf. *mesomelas* FROM SWARTKLIP COMPARED WITH THOSE OF A SERIES OF TEN *C. adustus* AND FOURTEEN *C. mesomelas*

	Swartklip specimens			*C. adustus**		*C. mesomelas**	
	Mean	Range	No. measured	Mean	Range	Mean	Range
I^2 l ..	5·0	—	1	3·6	2·9–4·1	4·4	3·8–5·0
b ..	4·8	—	1	—	—	—	—
I^3 l ..	6·4	6·0–7·1	5	4·4	3·8–5·0	5·3	4·6–6·3
b ..	5·2	4·9–5·8	5	—	—	—	—
P^1 l ..	5·0	—	1	4·1	3·4–4·9	5·0	4·1–5·8
b ..	3·5	—	1	2·5	2·2–2·8	3·0	2·2–3·5
P^2 l ..	9·5	—	1	7·7	7·2–9·0	8·6	7·4–9·6
b ..	4·2	—	1	—	—	—	—
P^3 l ..	10·5	—	1	9·2	8·5–9·8	9·6	8·7–11·0
b ..	4·9	—	1	—	—	—	—
P^4 l ..	18·5	—	1	14·4	12·8–15·6	17·1	15·0–19·1
b ..	9·7	—	1	6·7	5·5–7·7	7·8	6·8–8·7
M^1 l ..	11·0	—	1	11·7	10·4–12·7	11·8	10·3–13·7
b ..	15·0	—	1	12·5	10·7–13·3	13·7	11·7–15·5
M^2 l ..	7·3	—	1	7·7	7·0–8·6	6·8	6·2–7·8
b ..	10·9	—	1	10·4	9·3–11·8	10·5	9·8–11·5

* Ewer, 1956*a*.

Family **Viverridae**

? *Herpestes ichneumon* Linnaeus

Egyptian Mongoose

A single specimen (ZW 111) (pl. 7D) was doubtfully assigned to this species. It is the crushed skull of a large viverrid which lacks the braincase, the left P^1, P^4, M^1 and M^2 and the right P^2. No comparative material was available and the identification is based on published information (Ewer, 1956*b*; Roberts, 1951). The teeth of the specimen compare fairly closely in size with those of the extant *H. ichneumon* (table 17).

TABLE 17

DIMENSIONS OF THE TEETH OF A ? *Herpestes ichneumon* FROM SWARTKLIP COMPARED WITH THOSE OF THE MODERN FORM

	ZW 111	*Herpestes ichneumon**			
C—M^2 length ..	c41·4	38·0	39·1	38·8	40·0
P^4 length ..	c10·3	11·0	11·9	10·7	11·3

* Roberts, 1951.

As far as can be determined this species has not been recorded in the south-western Cape Province during historic times, but is known to occur in the coastal region further east.

Family **Mustelidae**

? *Mellivora capensis* Schreber

Honey Badger

A left maxillary fragment (ZW 142) from Site I was doubtfully assigned to this species. It is intact up to and including the most anterior part of the orbit. Only the P^2 remains, but the alveolus of the $\underline{C}$ and the anterior part of the alveolus of the P^3 are preserved.

It corresponds closely in size and general morphology with modern *Mellivora capensis* skulls, and also with fossil specimens from Swartklip (ZW 1, Singer/Fuller Occurrence) and Elandsfontein. However, in ZW 142 the P^2 is situated posterior to the $\underline{C}$ and is set parallel to the margin of the maxilla, whereas in all the comparative specimens it is at an angle to this margin and overlaps with the posterior margin of the $\underline{C}$ on its lingual surface.

The alveoli of the $\underline{C}$ and P^3 were comparable in size to those of the comparative specimens, although the P^2 was large compared with the mean of the comparative series (table 18).

TABLE 18

DIMENSIONS OF THE P^2 OF THE ? *Mellivora capensis* FROM SWARTKLIP COMPARED WITH THOSE OF A SERIES OF MODERN AND FOSSIL SPECIMENS

		Mellivora capensis						
			Hopefield specimens			Modern specimens		
	ZW 142	ZW 1	E.C.14	20916A	8640D	3325	19940	3326
P^2 l ..	6·3	5·3	5·1	5·3	5·1	5·3	6·6	5·8
P^2 b ..	4·4	3·8	3·5	4·0	3·4	3·8	4·3	3·4

CARNIVORA: *Incertae sedis*

The following specimens were not classified:

ZW 178—An incomplete left mandible with an incisor, canine and premolar of a small carnivore of uncertain affinities.

ZW 143—An incomplete left mandible of an immature individual, with an unerupted canine and premolar, probably belonging to a small felid.

ZW 109—The anterior part of a right mandible with an incomplete deciduous dentition, belonging to a small carnivore.

ZW 136—A canine (?) of a carnivore of uncertain affinities, with an extremely long root relative to the crown height.

ZW 1315—An incomplete canine, possibly belonging to a lion.

Family **Bathyergidae**

Bathyergus suillus Schreber

Cape Dune Mole

The remains of at least two individuals were present in the Site I assemblage.

ZW 123—An incomplete right mandible with the incisor, both premolars and the first of the molars.

ZW 398—An incomplete left mandible with only the first of the premolars remaining.

ZW 1112—A fragment of left mandible.

ZW 190—A fragment of a left upper incisor.

These specimens were indistinguishable from the corresponding parts of *Bathyergus suillus*, which occurs commonly in the area today.

RODENTIA: *Incertae sedis*

Three incisors (ZW 169, ZW 1205 and ZW 1206) representing three distinct types of rodent other than *Bathyergus* were recovered at Site I.

Family **Struthionidae**

Struthio australis

Ostrich

In addition to the egg and eggshell fragments already mentioned, the following bones of the ostrich were recovered from Site I:

ZW 208—The shaft of a tibia.

ZW 714—The shaft of a femur.

ZW 948—An incomplete right metatarsal of an immature individual.

ZW 1124 A, B, C—Fragments of the distal end of a femur.

Morphologically the specimens were indistinguishable from the corresponding parts of the extant ostrich, but the tibia shaft was somewhat longer than those of the comparative specimens.

CHELONIA: *Incertae sedis*

A single fragment of carapace (ZW 1208) was recovered at Site I.

THE POSTCRANIAL REMAINS

Approximately 86% of all the identified postcranial bones recovered came from Site I (table 2), and a summary of the analysis of this material (excluding non-mammalian remains) is given in table 19.

One of the most striking features emerging from this analysis was the scarcity of postcranial remains relative to the number of individuals represented. In the case of the lion, for example, the disparity was very marked. The appendicular skeleton of the lion is made up of approximately 110 bones, excluding the innominates, patellae and sesamoids. With four individuals represented at Site I, theoretically at least 440 bones should have been

Table 19

THE MAMMALIAN POSTCRANIAL REMAINS FROM SITE I

ZOOLOGICAL GROUPS		Scapulae	Humeri	Ulnae/Radii	Metacarpals	Innominate	Femora	Tibiae	Metatarsals	Carpal/Tarsal	Undifferentiated metapodials	Phalanges	Sesamoids & patellae	Vertebrae	Ribs	Unidentified fragments	TOTALS
CARNIVORA	Felidae—*Felis leo* . .			2							1	1					4
	Other carnivora . .		5	20			7	3		4	22	16					77
PERISSODACTYLA	Equidae		1	1						1		2					5
	Rhinocerotidae . .			2	1				1		1	2					7
ARTIODACTYLA	Bovidae		19	43	21			17	24	33	35	68					260
RODENTIA	. . . . . .		2	1			2	1		2							8
UNDETERMINED	. . . . . .	20	10	19		66	46	30		9			7	122	10	1630	1969
	TOTALS	20	37	88	22	66	55	51	25	49	59	89	7	122	10	1630	2330

Note: Numbers do not necessarily indicate complete bones.

recovered. There were in fact only parts of three bones recovered—less than 1 % of the theoretical total. Other figures calculated on this basis ranged up to 20% in the case of the appendicular skeleton of antelope.

The presence of incomplete skeletons at fossil sites is quite common, and many factors might be responsible. Recent work by Brain (1967) is of special interest in the present instance. He has demonstrated by careful field observation that disproportionate occurrences of bones and parts of bones can result from the destructive chewing of small carnivores—domestic dogs in the study undertaken by him. Since carnivores are thought to have been responsible for the fossil assemblages at Swartklip, they were probably also responsible for the destruction of much of the original assemblage. The main objection to this theory is that none of the bones showed signs of tooth marks. The possibility that subsequent weathering has removed all traces of these is considered unlikely, in view of the excellent state of preservation of the specimens.

Clearly allowance must be made for the method of collection, which resulted in only part of the entire deposit being handled. However, this factor alone cannot adequately account for the persistent shortage of postcranial remains of all categories.

In addition there was almost certainly some selective collecting of bone by the inhabitants of the lairs.

It is probably a combination of these factors which has given the assemblage its present character.

A second feature of the postcranial assemblage was the 'completeness' of the bones. A frequently characteristic feature of bone accumulations resulting from the activities of man is the highly fragmented state of the bone (cf. Dart, 1957, for details and references). There are two basic reasons for man's deliberate fragmentation of bone—firstly, to obtain pieces suitable for the manufacture of tools, and secondly, to remove all edible soft tissue. Although the bones from the Swartklip assemblages were often incomplete, this was the result mainly of post-fossilization damage, and as a whole the assemblages lacked large numbers of small bone fragments and splinters. In this respect at least the assemblages had the appearance of animal lair residues, rather than human occupation site debris (Hendey & Singer, 1965: 212).

Age of the Assemblages

The fauna of the sites is essentially 'modern' in character. No extinct genera are present, and most of the forms are indistinguishable from, or closely related to extant species. The fauna clearly post-dates that of the Elandsfontein site, which is usually termed 'late Middle/early Upper Pleistocene' (Boné & Singer, 1965), and corresponds most closely with that of the Melkbos fossil site (Hendey, in press).

Singer and Fuller (1962) suggested that the assemblage described by them was late Upper Pleistocene, and the present study tends to confirm this, although the possibility that the fauna is post-Pleistocene cannot be discounted.

The application of the name 'Wolfgat' to the area in which the sites are located, suggests the possibility that the lairs in which the fossils accumulated were still being occupied after the arrival of the first settlers from Europe in 1652. It is uncertain when this name was first used but it is most likely to have been during the late seventeenth or early eighteenth centuries. However, even by 1649, before the first permanent European settlement, the indigenous fauna of the Cape Peninsula area was much depleted (Sargent, 1954), and it is concluded from the variety of faunal types represented, that at least part of the assemblages accumulated in prehistoric times.

All the available evidence points to the Swartklip fossils being late Upper Pleistocene or Recent in age.

Conclusion

The importance of the Swartklip sites lies chiefly in the fact that they have provided the largest range of later Quaternary fossils known from the south-western Cape Province to date. Information on the Quaternary fauna of this region is now coming from the Early or Middle Pleistocene deposits at Langebaanweg, the Middle/Upper Pleistocene site at Elandsfontein and the more recent Melkbos and Swartklip sites. Consequently there is now a proven potential in this limited geographical region for establishing a succession for the Quaternary fauna of southern Africa, a situation unparalleled elsewhere in the subcontinent.

Furthermore the fossils at Swartklip come from sealed deposits where the danger of admixture of earlier and later elements is excluded. This is not the case with the other major sites of the region. The excellent state of preservation of the specimens makes detailed morphological studies of them possible, and there is no doubt that the future exploitation of the sites, and a closer examination of the material already recovered, will provide a great deal of unique and valuable information.

They are potentially the most important fossil occurrences of their kind discovered in southern Africa in recent years.

Summary

The fauna of three recently discovered fossil sites in the south-western Cape, South Africa, is described, accounts being given of nineteen mammalian types, including one new subspecies, *Antidorcas marsupialis australis*.

Brief accounts of the geological and archaeological associations of the fauna are given, and the suggestion made that the fossils accumulated in carnivore lairs.

It is concluded that the assemblages are late Upper Pleistocene or Recent in age.

Acknowledgements

We are indebted to Dr. E. Middlemost of the University of Cape Town, who first drew our attention to the sites, and to Dr. Middlemost, Mr. R. R.

Inskeep and students of the Department of Geology, University of Cape Town, who were responsible for much of the original collecting of material.

Members of the Western Cape Local Centre of the South African Archaeological Society and the University of Cape Town Archaeology Field Club undertook most of the later collecting, and we are especially grateful to Miss E. Speed, who arranged these collecting trips.

Prof. L. H. Wells of the University of Cape Town kindly offered opinions and suggestions on some of the material. Mr. C. E. Gow of the South African Museum took the photographs of the specimens, and our thanks go also to him. Much of the preparation of specimens was competently undertaken by Mr. M. Jacobs.

Finally we wish to thank Dr. Ronald Singer and Dr. E. C. Olson of the University of Chicago, who kindly checked the manuscript and made many useful suggestions.

This study was supported in part by the U.S. Public Health Service grant no. GM 10113 to Dr. Singer, and the National Science Foundation grant no. B 2453 to Dr. Olsen.

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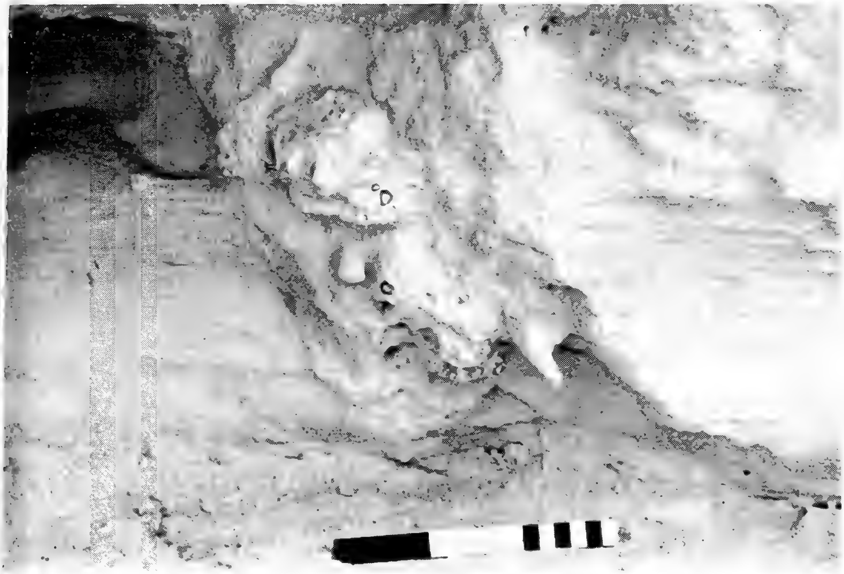
Plate 1

A



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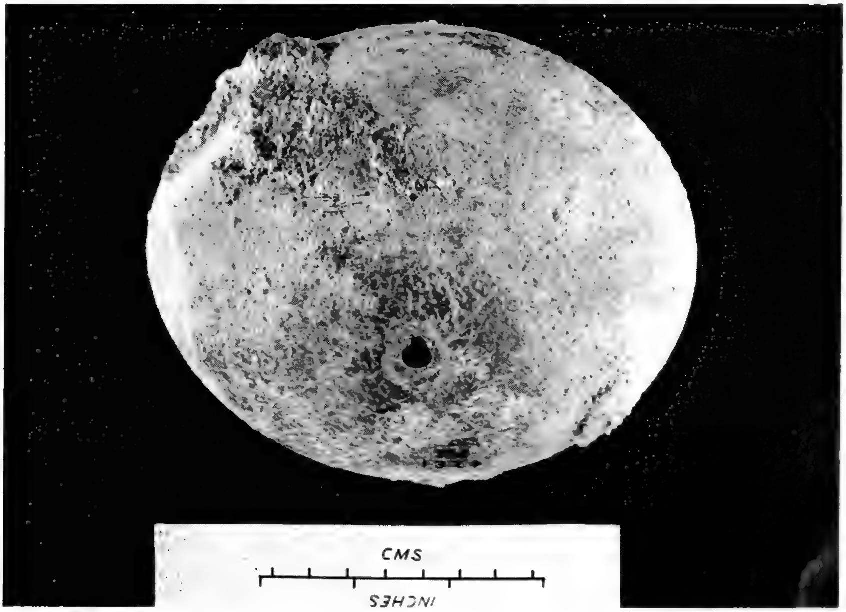
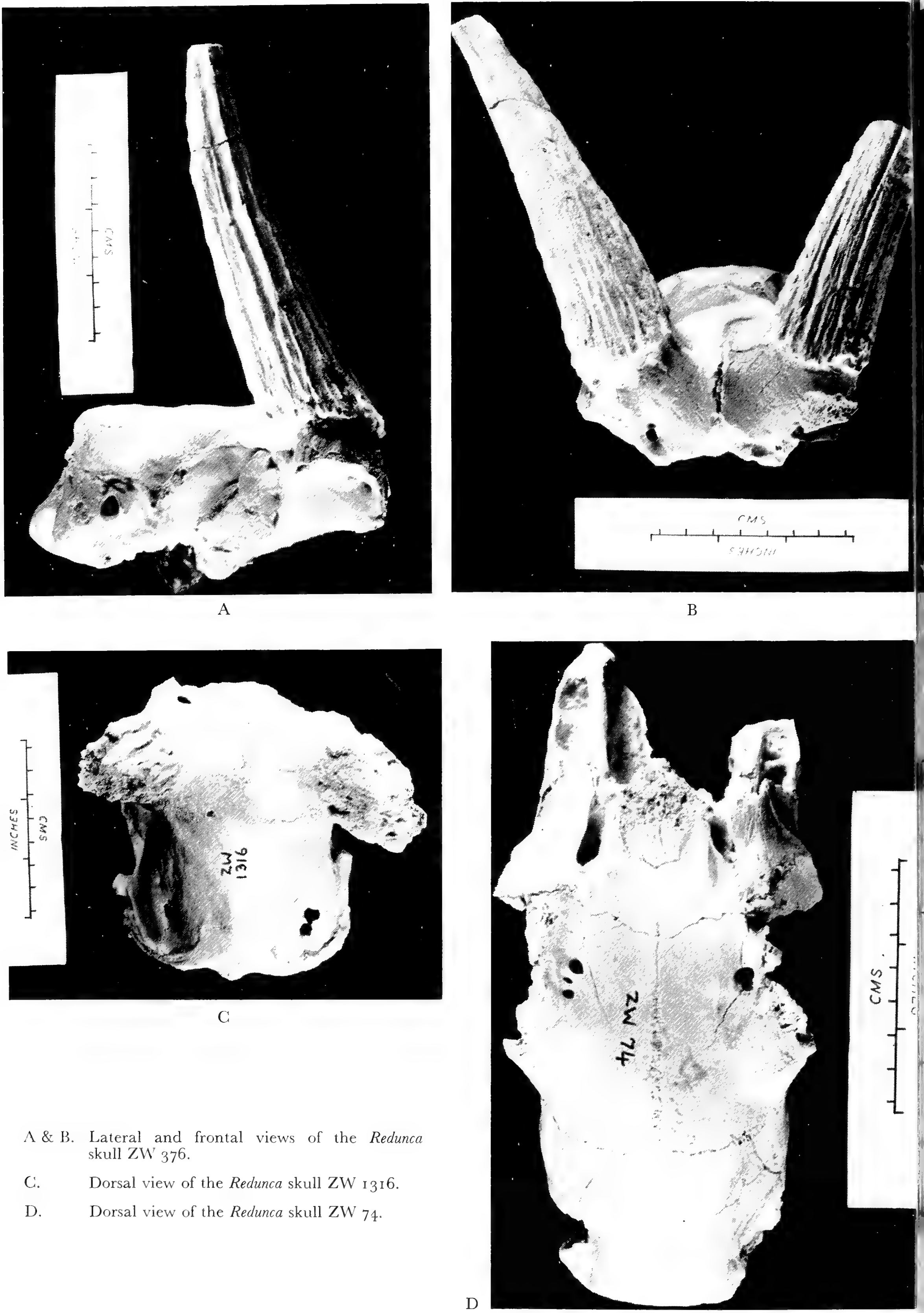


C

A. The overhang and talus slope at Site I, viewed from the east.

B. The fossiliferous horizon and underlying horizontally bedded sands at Site I.

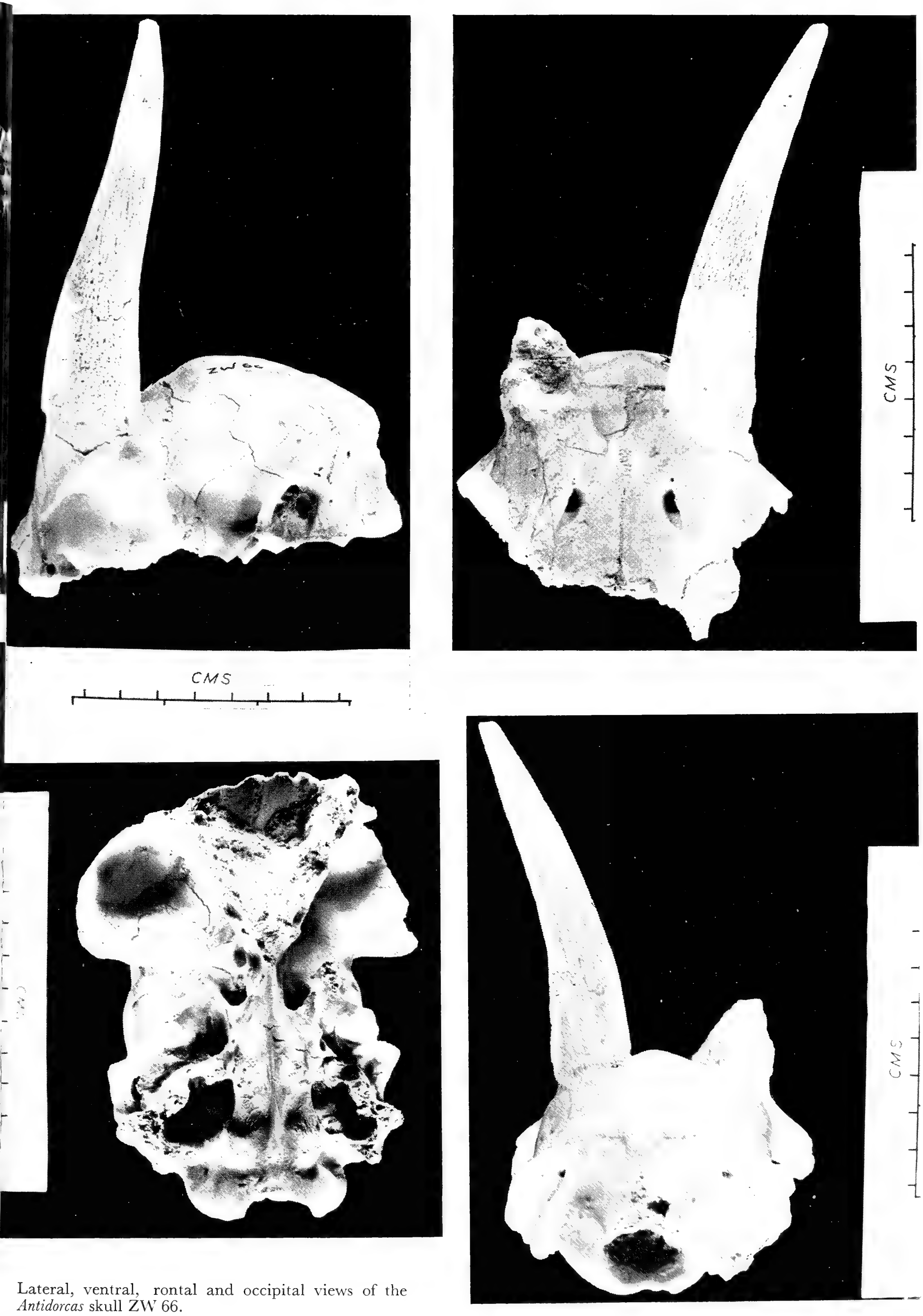
C. The perforated ostrich-egg from Site II.



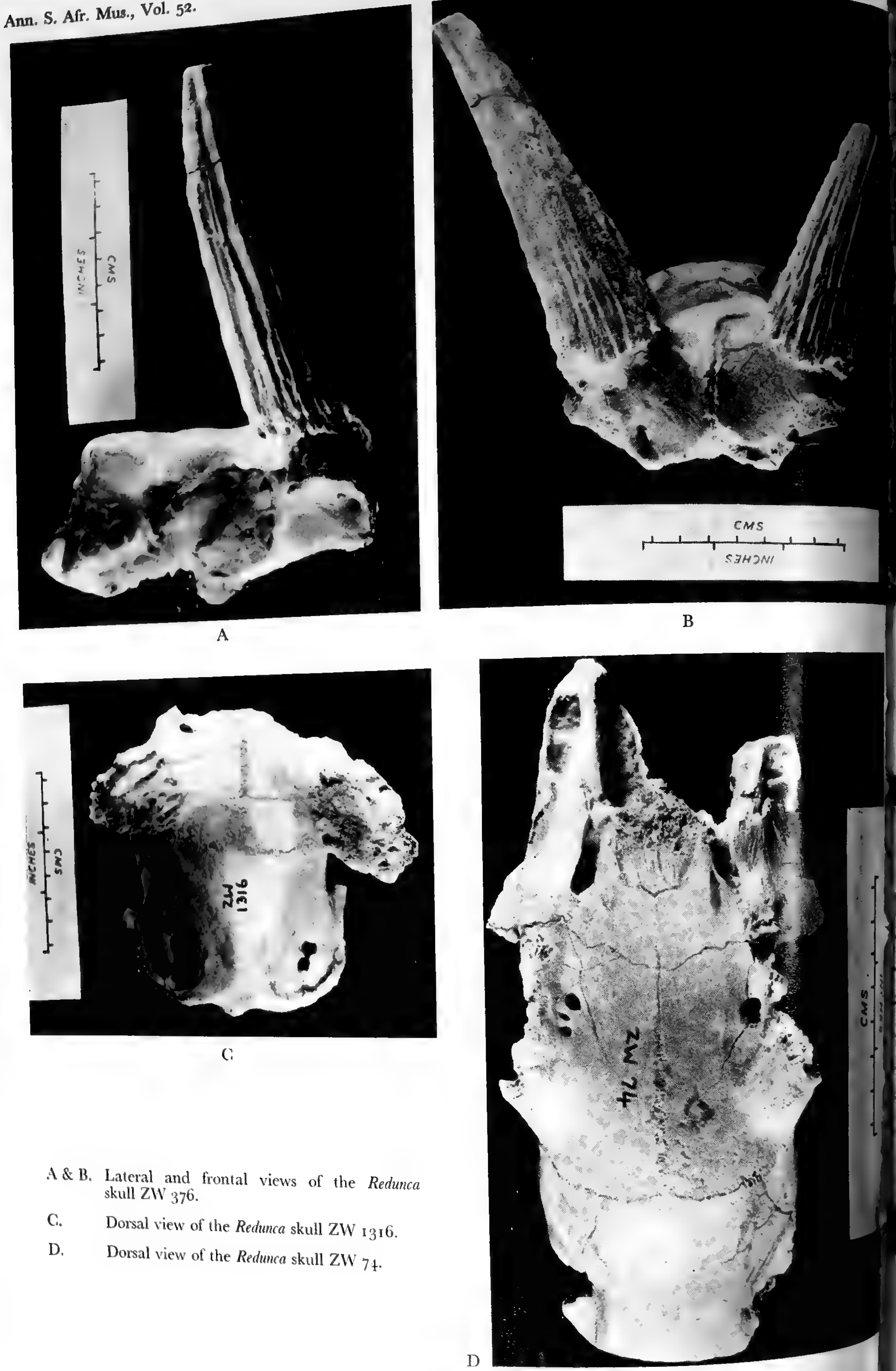
A & B. Lateral and frontal views of the *Redunca* skull ZW 376.

C. Dorsal view of the *Redunca* skull ZW 1316.

D. Dorsal view of the *Redunca* skull ZW 74.



Lateral, ventral, rontal and occipital views of the *Antidorcas* skull ZW 66.

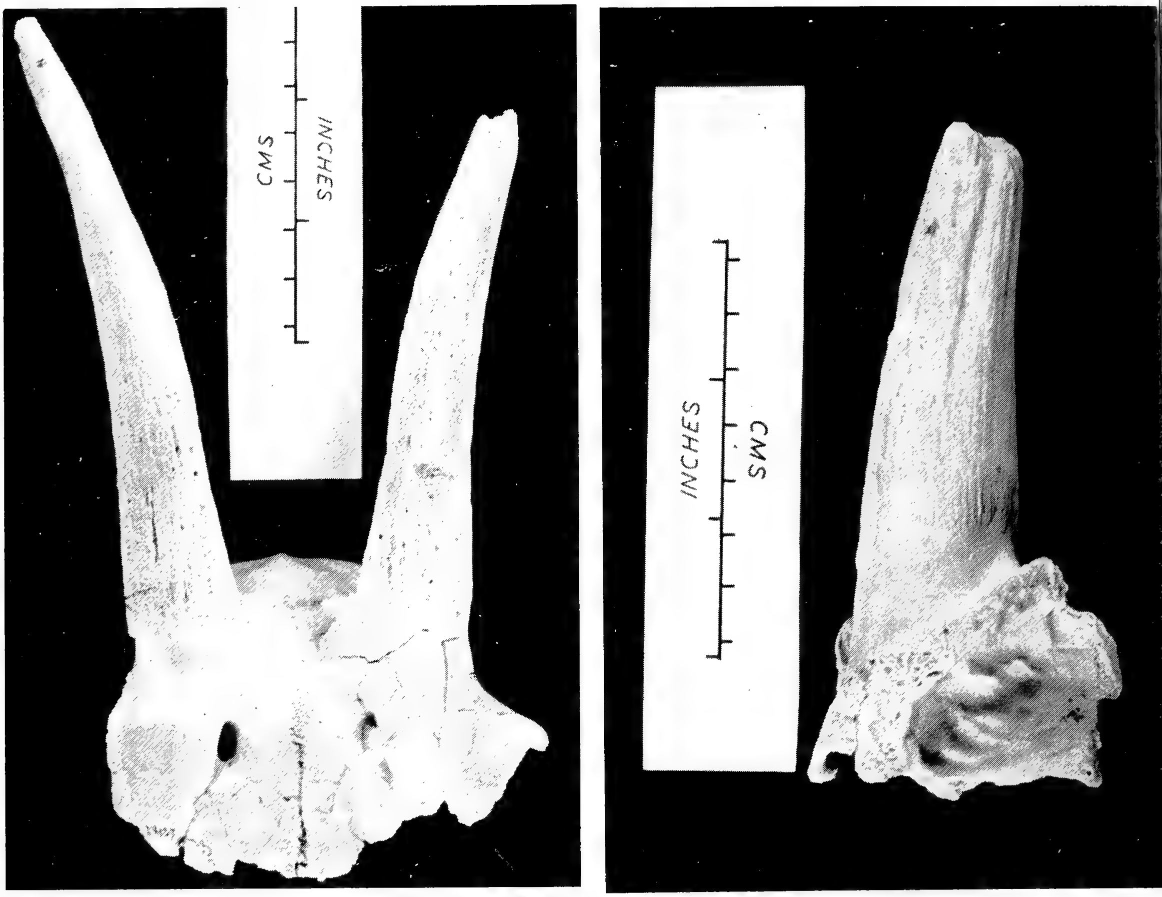


A & B. Lateral and frontal views of the *Redunca* skull ZW 376.

C. Dorsal view of the *Redunca* skull ZW 1316.

D. Dorsal view of the *Redunca* skull ZW 74.

Lateral, ventr[illegible] [illegible]rontal and occipital views of the *Antidorcas* skul[illegible] [illegible]56.



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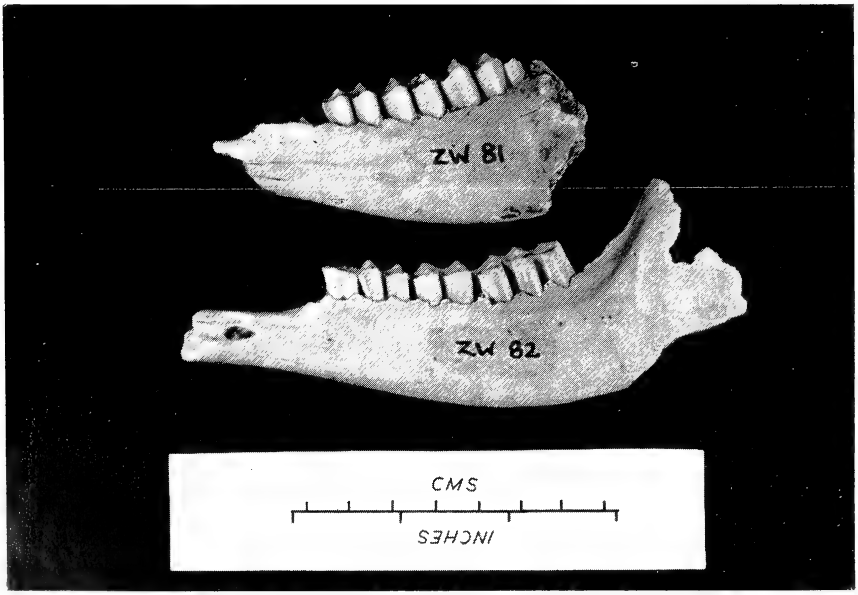
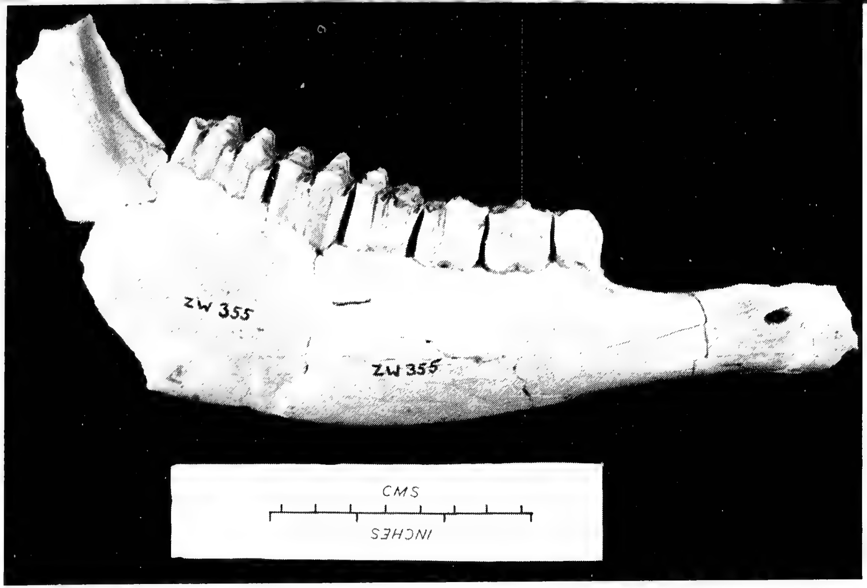


C

A. Frontal view of the *Antidorcas* skull ZW 402.

B. Medial view of the *Antidorcas* horn core ZW 67a.

C. Buccal view of the *Antidorcas* mandibles ZW 81 and ZW 82.



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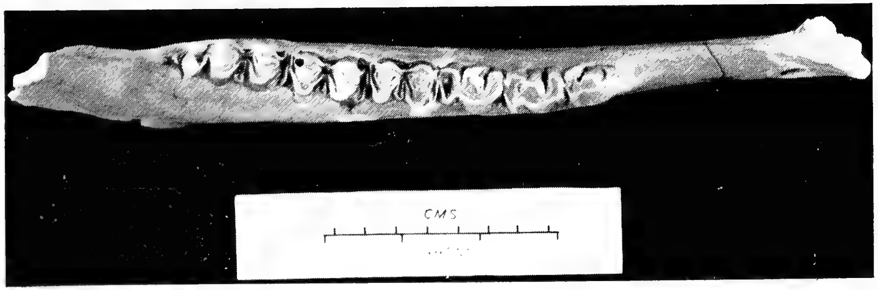

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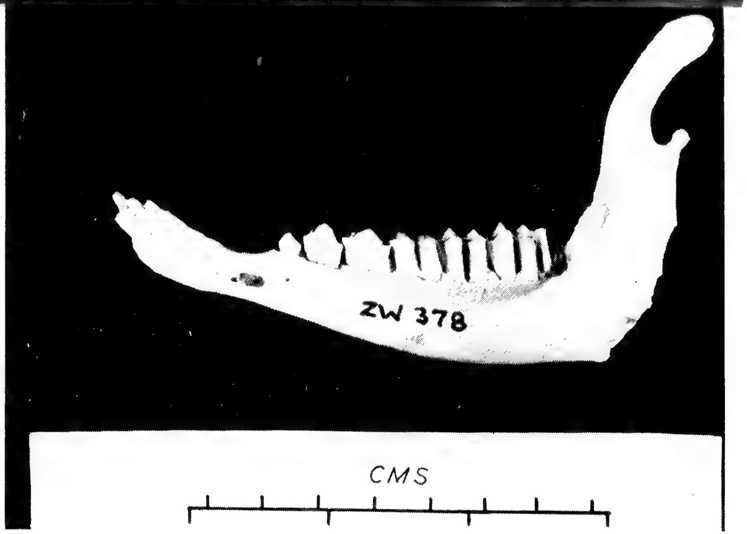

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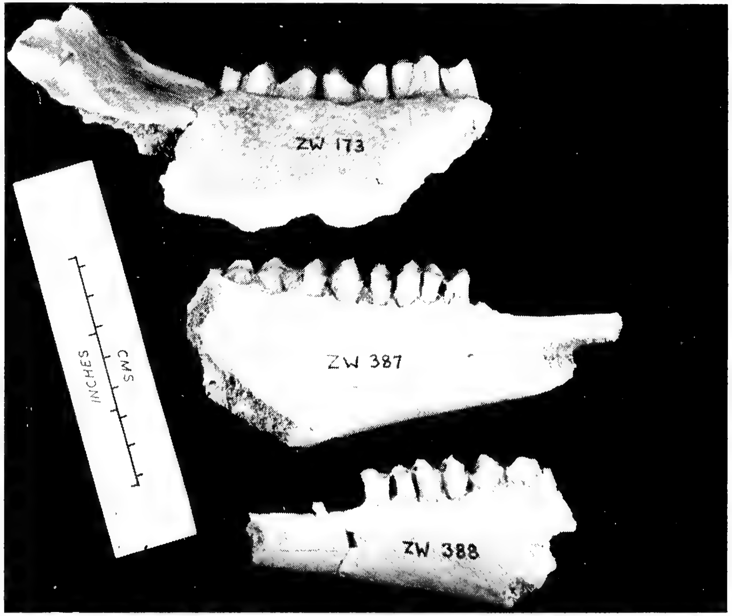
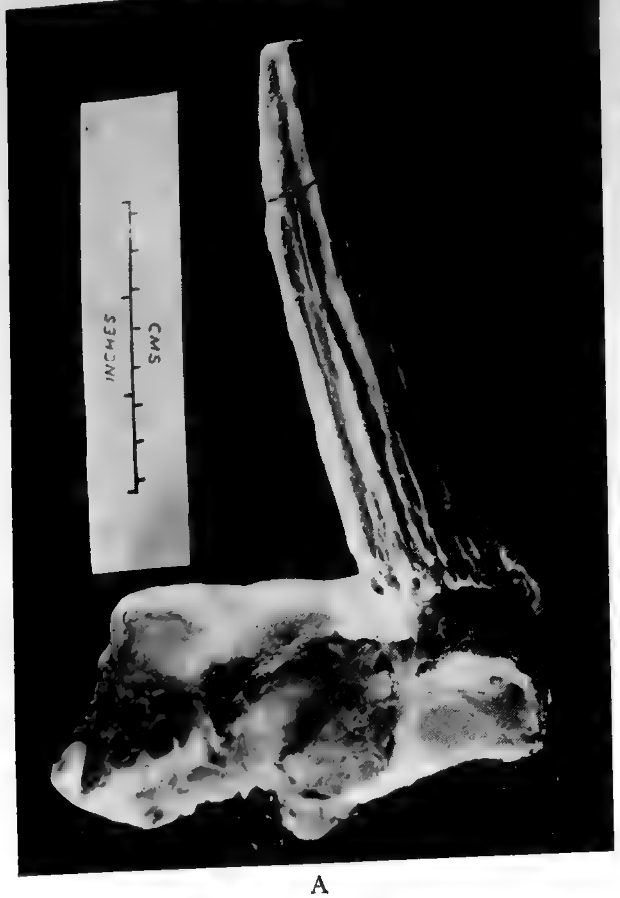


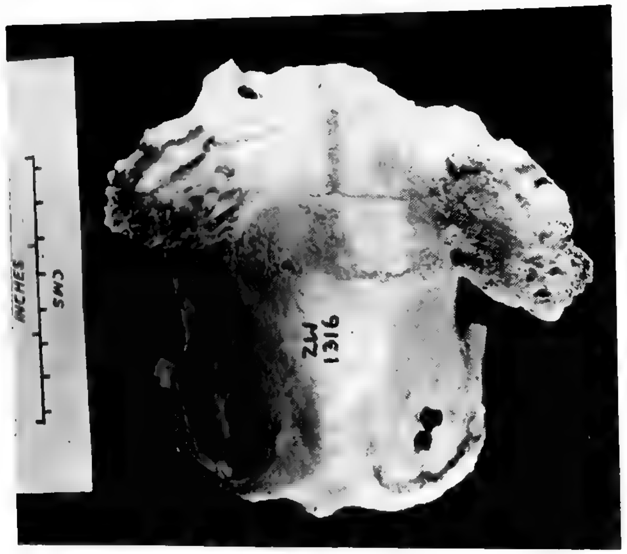
D

A & B. Buccal and occlusal view of the *Hippotragus* mandible ZW 355.
C. Buccal view of the *Raphicerus* mandible ZW 378.
D. Buccal view of the *Connochaetes* mandibles ZW 173, ZW 387 and ZW 388. Note anomalous premolar in ZW 388.



A

B



C

D

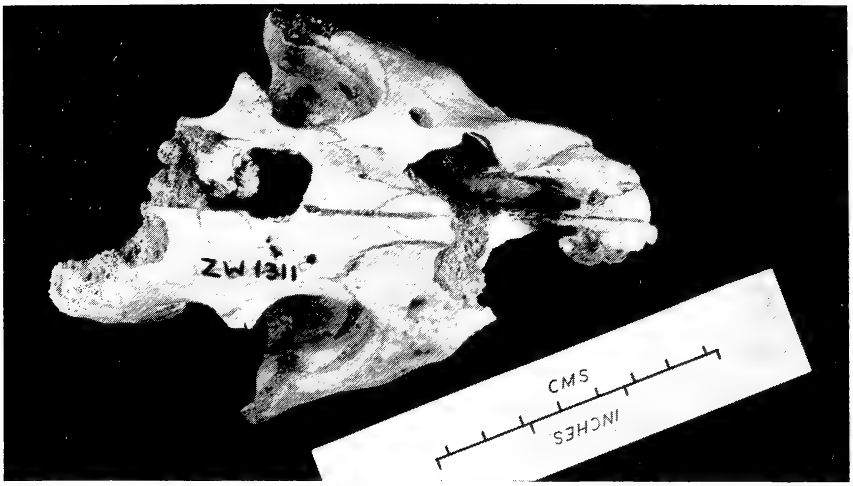
A & B. Lateral and frontal views of the *Redunca* skull ZW 376.

C. Dorsal view of the *Redunca* skull ZW 1316.

D. Dorsal view of the *Redunca* skull ZW 74.

Lateral, ventral, frontal and occipital views of the *Antidorcas* skull ZW 66.

A



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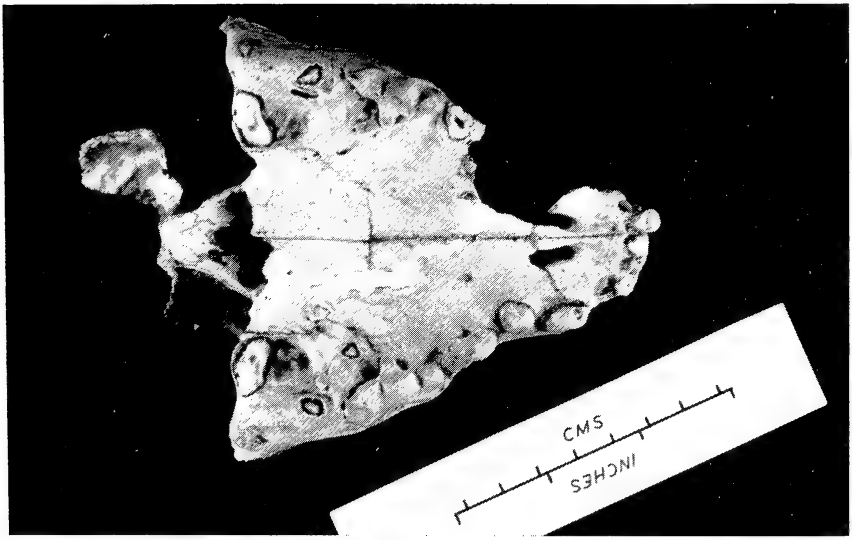

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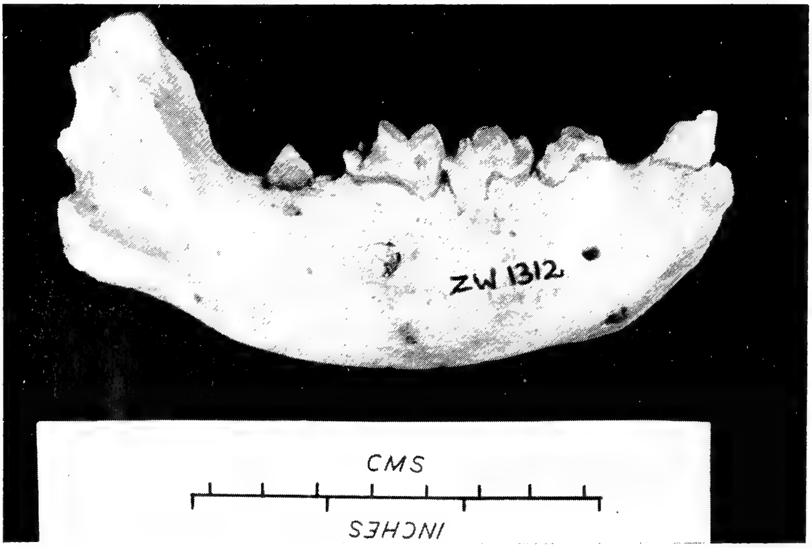
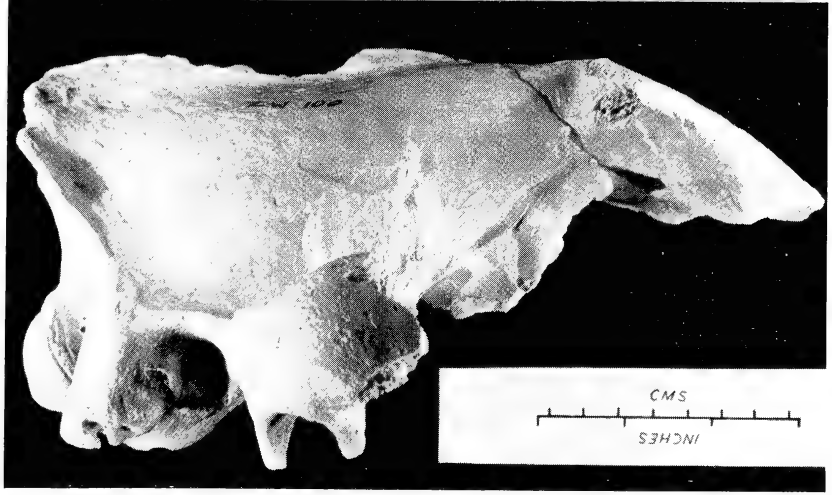


A & B. Dorsal and ventral views of the *Hyena* skull ZW 1311.

C. Buccal view of the *Hyena* mandible ZW 1312.

A



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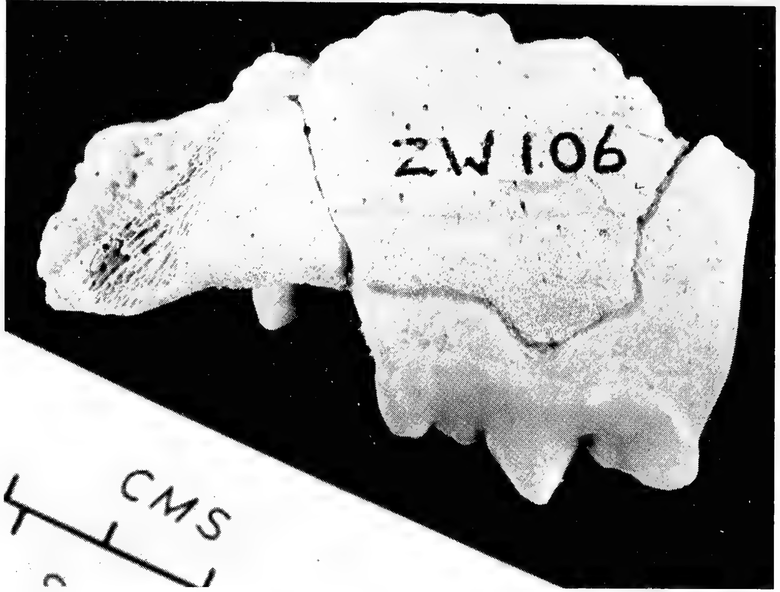

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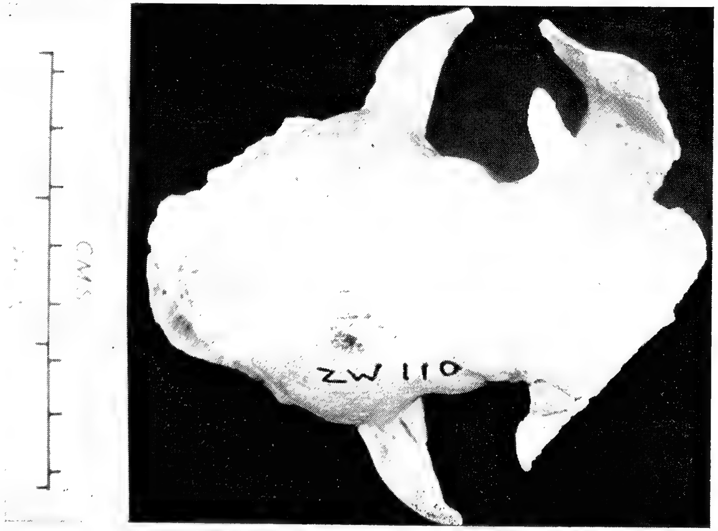
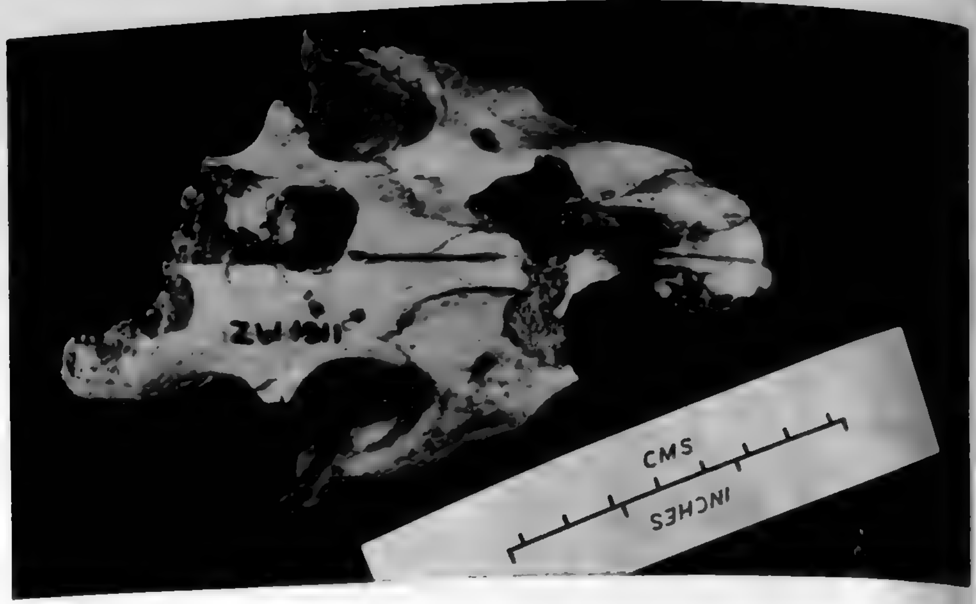


D

A. Lateral view of the *Felis leo* skull ZW 100.
B. Buccal view of *Felis leo* maxilla ZW 106.
C. Dorsal view of ?*Felis serval* skull ZW 110.
D. Lateral view of ?*Herpestes ichneumon* skull ZW 111.

A



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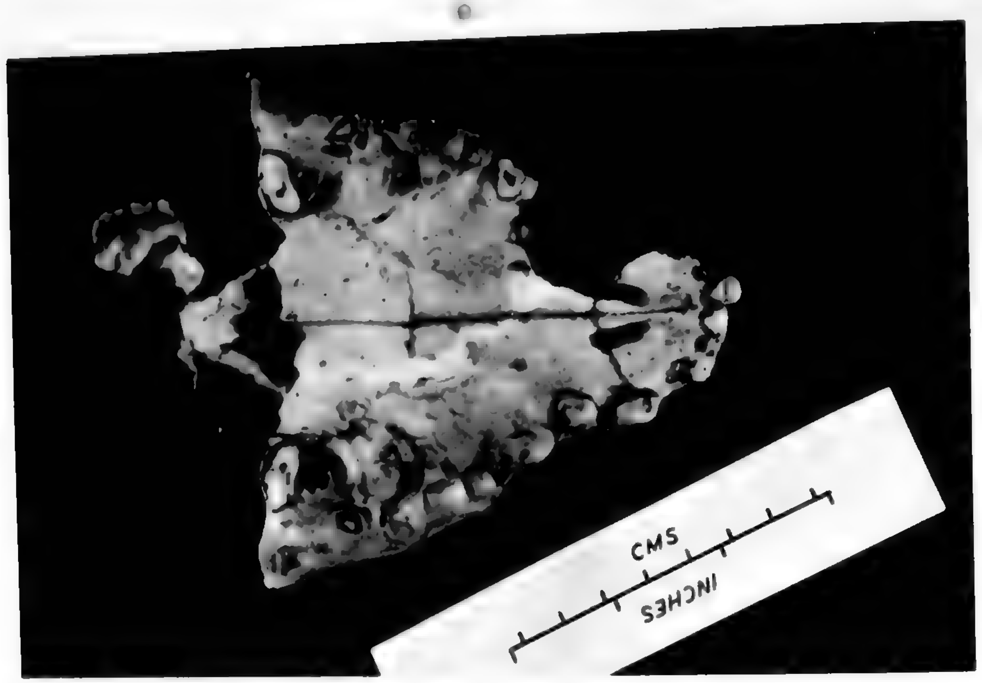

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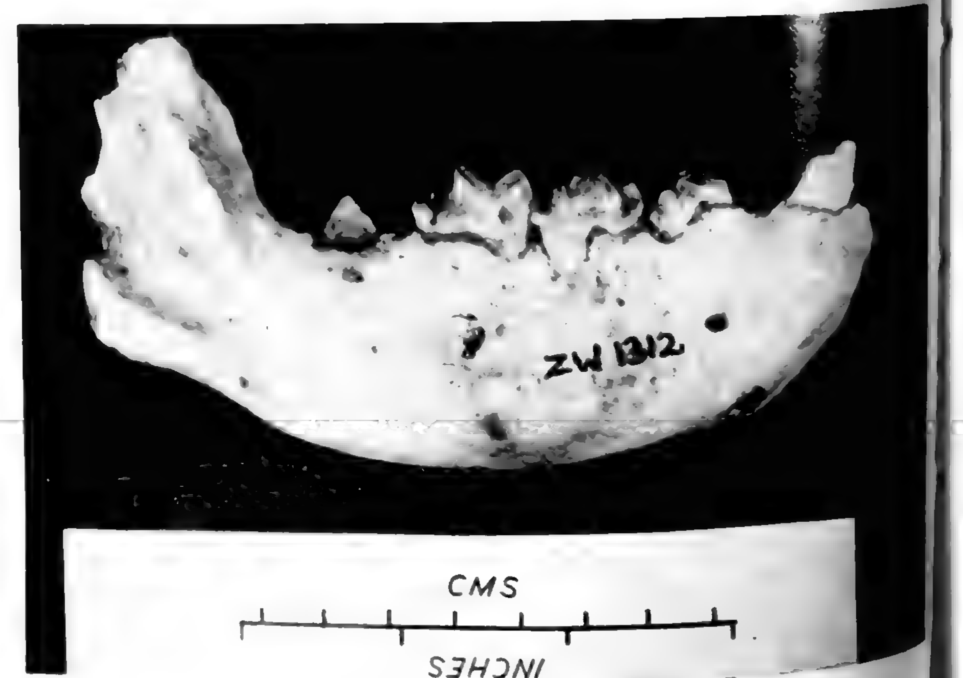
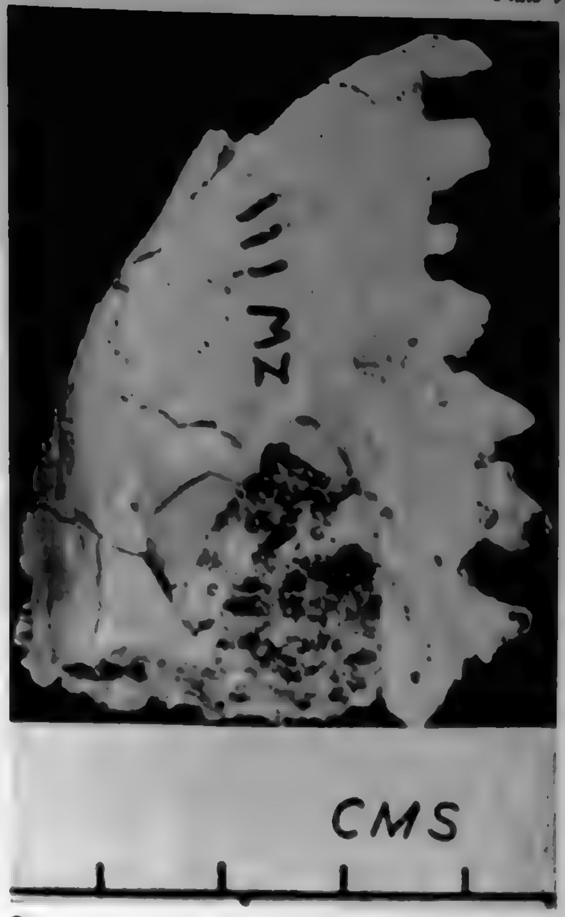


A & B. Dorsal and ventral views of the *Hyena* skull ZW 1311.

C. Buccal view of the *Hyena* mandible ZW 1312.

B



D

A

C

A. Lateral view of the *Felis leo* skull ZW 100.
B. Buccal view of *Felis leo* maxilla ZW 106.
C. Dorsal view of ?*Felis serval* skull ZW 110.
D. Lateral view of ?*Herpestes ichneumon* skull ZW 111.

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Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Fischer, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

Fischer, P.-H., Duval, M. & Raffy, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

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. Polyphacophora, 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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Example

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Volume 52 Band
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Part 3 Deel

TWO NEW SPECIES OF *ACHAEUS* (CRUSTACEA, DECAPODA, MAJIDAE) FROM SOUTH AFRICA

By

D. J. G. GRIFFIN

Cape Town Kaapstad

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The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
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By

D. J. G. Griffin

Australian Museum, Sydney, Australia

(With 4 text-figures)

[*MS. received* 15 *January* 1968]

Contents

Introduction

The small, long-legged spider crabs of the genus *Achaeus*, belonging to the majid subfamily Inachinae, have most recently been reviewed by Griffin & Yaldwyn (1964), who considered that about 20 species were known. A more detailed count (Griffin, unpublished) shows that 27 species of good status are at present placed in the genus; two of these have recently been described from the south Atlantic by Forest & Guinot (1966). Three others are of uncertain status. Two of these are from South Africa and were discussed by Barnard (1950): '*Achaeus* cf. *lorina* Adams and White' and '*Achaeus* cf. *affinis* Miers'. Re-examination of the material studied by Barnard shows that both these are distinct, unnamed species of *Achaeus*. The first is similar in some ways to a few species of the genus *Macropodia*. Examination of the holotype of *A. lorina*, of a specimen of that species from the Philippines and of one specimen from the series recorded by Rathbun (1911) from Amirante in the Indian Ocean permits a further diagnosis of *A. lorina* and reveals that Rathbun's material is probably referable to *A. fissifrons* (Haswell). Barnard's '*A.* cf. *affinis*' is similar to *A. brevirostris* (Haswell).

In the present paper the new species are described and figured and compared with other species of *Achaeus*. The terminology and system of measurements used follow Griffin & Yaldwyn (1964). In general, carapace length is abbreviated as c.l.

Ann. S. Afr. Mus. **52** (3), 1968: 75–87.

SYSTEMATIC ACCOUNT

Achaeus spinosissimus n.sp.

(Figs 1, 2, 4*a*, *b*)

Achaeus cf. *lorina*: Barnard, 1950: 22–23, fig. 3*g*.
[*non*] *Inachus lorina* Adams & White, 1848.

Holotype: Male, c.l. 10·0 mm, off Hood Point (East London), South Africa (S. Afr. Mus. reg. A8309)—South African Museum, Cape Town.

Description: Carapace elongate subtriangular (length 1·3 times width), narrowed anteriorly, not markedly constricted behind orbits, branchial regions swollen, lateral margins and dorsal surface armed with numerous spines and spinules and a few scattered short hairs; regions moderately well defined. Surface of carapace, sternum, abdomen and third maxillipeds coarsely granular.

Rostrum of two very short, slender, blunt spines separated by a narrow slit.

Supraorbital eave bearing midway along a long, slender, weakly curved, acuminate spine directed outwards, upwards and forwards; eave otherwise unarmed. Postorbital region with about four short spines laterally, one longer than others, and two or three dorsal spinules near lateral margin. Eyestalks stout, a narrow process extending above cornea terminating in a small tubercle; a small pointed spinule on anterior surface close to cornea; cornea large, ovoid, obliquely terminal.

Hepatic region not greatly expanded, with four or five spines on margin, one longer spine on dorsal surface posteriorly and some spinules anteriorly.

Dorsal surface of carapace with two prominent short, blunt tubercles in mid-line, one spinous gastric and a blunt one on tumid cardiac region; a low swelling behind cardiac tubercle. Protogastric regions each with a curved spine just in front of hepatic regions with one or two spinules at its base. Branchial regions with six spines on, or close to, margin; eight or nine spines and spinules on outer slope of each mesobranchial region and a very low swelling on metabranchial region above last legs.

Basal antennal article very slender, armed with four equidistant, broad-based, long, subacute spines mostly directed outwards situated towards lateral border. First segment of flagellum short, with an outwardly-directed terminal spine. Second segment long, with a small spinule laterally. Flagellum of moderate length, with a few long hairs.

Antennular fossae large, longitudinally subovate; basal segment of antennules bearing medially a row of seven prominent spinules; inter-antennular spine slender, projecting downwards as an obtuse, triangular process; anterior process of epistome extremely slender.

Epistome about as wide as long with several spinules laterally, two behind antennal article and others near anterolateral angle of mouthfield. Pterygostomian regions with a spine midway along lateral border. Several spinules ventrally on branchial regions.

Third maxillipeds almost meeting in midline, spinous and hairy. Ischium

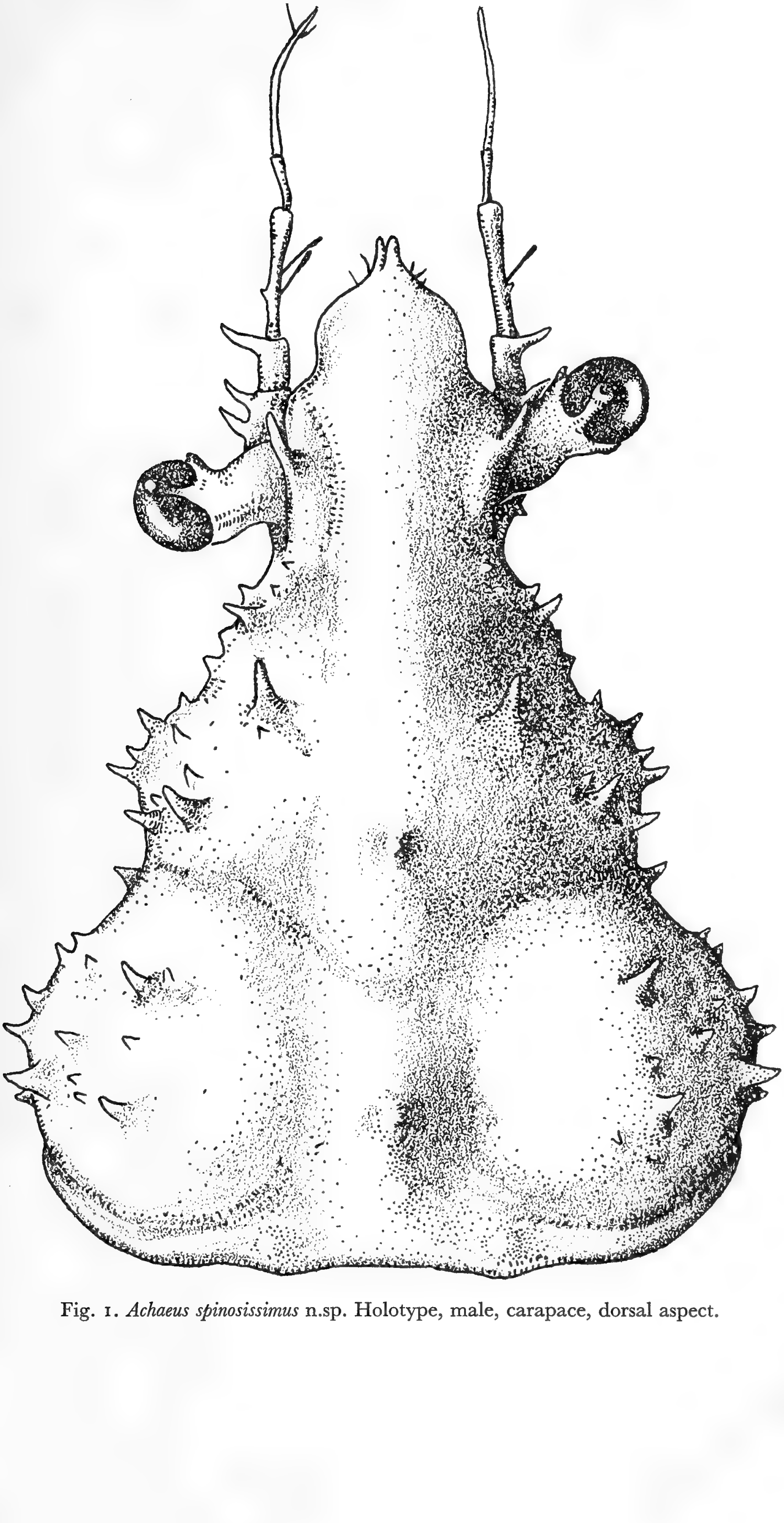

Fig. 1. *Achaeus spinosissimus* n.sp. Holotype, male, carapace, dorsal aspect.

bearing spines in two oblique rows, one row of two or three laterally and a central row of seven similar spines; medial edge finely toothed, overlaid by long hairs. Merus narrow, subovate, with four spines near medial edge, three in a central row and two smaller ones at anterolateral angle; several long hairs arising from medial edge. Palp long and stout, dactyl as long as carpus and propodus together, carpus and propodus each with a spine near distal border on medial surface; long hairs arising from medial surface and tips of all three segments.

Chelipeds long and stout, with numerous spines and spinules more or less in longitudinal rows, and long sparse hairs. Ischium with several spines. Merus subcylindrical, swollen, bearing numerous spinules and curved spines largest along outer lateral surface where five, larger than others, stand in a row. Carpus subcylindrical, with numerous curved spines which are generally longest laterally. Chela about half total length of cheliped, compressed, fingers not much shorter than palm which is deep, dorsally weakly convex and ventrally strongly convex; dorsal surface and dorsal part of outer surface with short, curved spines and blunt tubercles in poorly defined rows in proximal two-thirds; a few, similar but smaller, spinules and tubercles on ventral part of outer surface and along ventral surface; distal part of outer surface smooth. Fingers stout, very widely gaping for about proximal two-thirds; fixed finger with a very large, apically truncate tooth proximally filling gape, its straight apex spinulate, remainder of inner edge denticulate, strongly concave proximally, obtusely angled at distal end of gape. Dactyl with large truncate tooth, smaller than, and just beyond, that on fixed finger, remainder of inner edge irregularly dentate. Chela with long hairs dorsally, ventrally, on outer surface of palm distally, along both fingers and filling gape.

Ambulatory legs very long, slender, with curled hairs arising singly on dorsal surface of propodi and long hairs, especially on distal two-thirds of propodi and on dactyls; first leg the longest, remainder decreasing to last; bases of all legs and ischia of first with some spinules ventrally, meri of all with a terminal dorsal spine; dactyls almost straight in first pair and unarmed, second with a single, strong, subterminal, curved spinule ventrally, dactyls of third and fourth legs short, weakly curved with several small denticles and two curved, subterminal spines ventrally, the distal the longer.

Sternum with spinules in transverse rows opposite base of each leg and two on each side along margin of abdominal fossa anteriorly at base of chelipeds.

Abdomen in male of six segments, segments 6 and 7 coalesced. All segments wider than long, first segment the longest, second very short, remainder subequal in length, third and last a little longer than others. Abdomen widest about middle of laterally convex third segment, lateral margin concave to just beyond base of last segment, then tapering rapidly, apically rounded but with surface deeply concave and appearing bilobate in ventral view. Surface with a broad medial elevation distally in segments 1–5 and proximally in last, each bearing a pair of long hairs. Third segment with two oblique rows of three spines on each side of midline on swollen lateral surfaces. Proximal part of last segment laterally swollen.

Male first pleopod moderately stout, uniformly tapering apically, curved outwards, terminally blunt; aperture terminal, a narrow slit at end of groove along medial surface; lacking hairs except for several at base laterally.

Measurements: Carapace length 10·0 mm, carapace width 7·1 mm, rostral length 0·5 mm, rostral width 0·5 mm, cheliped length 17·5 mm, chelar length 8·4 mm, chelar height 3·6 mm, dactyl length 5·1 mm, first ambulatory leg length 26·2 mm.

Remarks: This new species agrees with Adams & White's original description and figures only in a number of general features, including shape of the carapace, presence of two tubercles in the midline, presence of a larger tooth near the base of each finger of the chela, setose anterior ambulatory legs and curved dactyls on the posterior ambulatories.

Examination of drawings of the holotype (a male, c.l. 11 mm (approx.), 'Eastern Seas', in the British Museum (Natural History)) of *Inachus lorina* by Dr. A. L. Rice and the availability of a specimen from the United States National Museum collections—1 ovigerous female, c.l. 10·5 mm (reg. no. 49837), *Albatross* Philippine Expedition 1907–1910, Sta. 5355, North Balabac Strait, 44 fms—which is certainly conspecific with the holotype, show that the diagnostic features of *A. lorina* include the weakly bilobed, apically rounded rostrum, acute but not markedly expanded hepatic regions, single gastric elevation, two small tubercles side by side on elevated cardiac region, a small spine or tubercle close to posterior margin above last ambulatory leg, supraorbital eave without spines or tubercles, eyestalks with a sharp tubercle, basal antennal article with a spine centrally and an apical spine. The Philippine specimen possesses a small spinule at the base of the basal antennal article and there is an oblique row of three low tubercles on the branchial regions medially extending forward from opposite the cardiac prominence; neither of these features are apparently obvious in the holotype. The third maxillipeds are of the usual form in this genus and are spinous and hairy; there is one longitudinal row of spines on the ischium, the surface of which is weakly excavate immediately lateral to the spines; there are two spines not far from the lateral edge, one proximal, one distal; the merus is also weakly excavate centrally and lateral to this there are three sharp spines; the medial and anterolateral edges bear sharp spines and the carpus and propodus each bear a single, slender spine. The slender chelipeds are spinous and hairy, long spines and hairs arising from the ventrolateral edge of the merus, the dorsomedial surface of the carpus and the ventral edge of the palm of the chela; there are long hairs and shorter spines along the dorsal surface of the merus and palm of the chela; fringes of long hairs continue on to the dorsal edge of the dactyl and the ventral edge of the fixed finger. The ambulatory legs are extremely long and slender and the propodus and dactyl of all bear very long hairs; the dactyl of the last ambulatory leg is weakly falcate with a double row of short spines on the proximal two-thirds and three longer back-

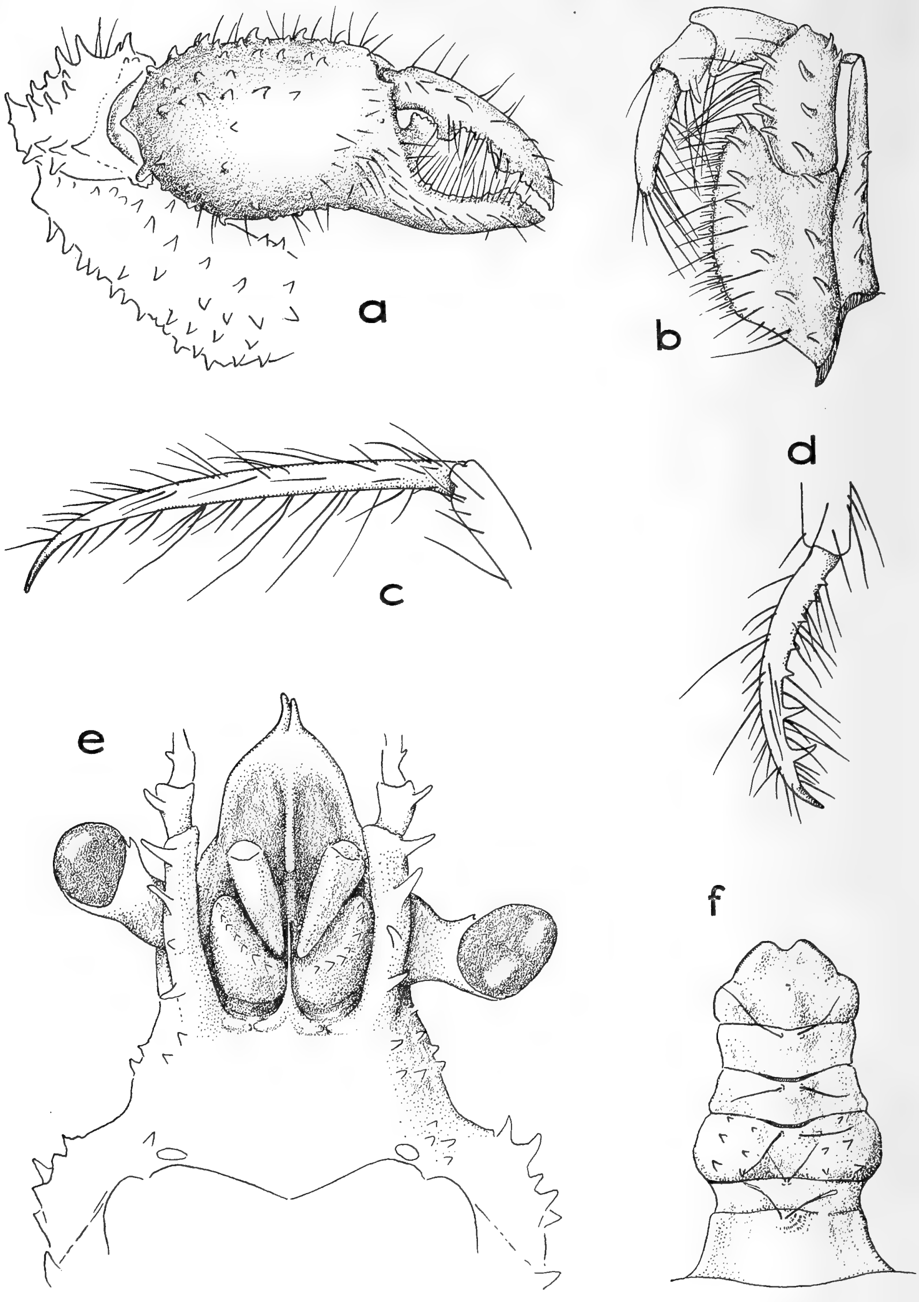

Fig. 2. *Achaeus spinosissimus* n.sp. Holotype, male: a, right cheliped; b, left third maxilliped; c, left first ambulatory dactyl; d, left fourth ambulatory dactyl; e, front of carapace, ventral aspect; f, abdomen.

wardly curved spines, equally spaced, distally, the last distant from the tip; there is a short spine just beyond the penultimate large spine.

Thus, *A. spinosissimus* differs from *Achaeus lorina* notably in the presence of a supraorbital spine, larger spines on the dorsal surface of the carapace, particularly the protogastric ones, more numerous spines on the hepatic and branchial margins, in the form of the rostrum and in the presence of much larger spines on the basal antennal article. As Barnard (1950) states, this species agrees reasonably well with the description of *Achaeus lorina* given by De Man (1902) of specimens from Ternate and Halmahera in Indonesia. However, none of the most notable features of this species are present in the holotype of *Achaeus lorina*. The material reported on by De Man may be conspecific with *A. spinosissimus*.

Examination of one specimen—an ovigerous female, c.l. 5·9 mm (reg. no. 1912:2:10:82), Percy Sladen Trust—*Sealark* Expedition to the Indian Ocean Sta. E14, Amirante, 34 fms—in the collections of the British Museum (Natural History) from the series recorded by Rathbun (1911:244) as *Achaeus lorina* shows that this identification by Rathbun was incorrect. The specimen is definitely not conspecific with *A. lorina* but possesses the general features of the carapace, orbit, maxillipeds and cheliped of *A. fissifrons* (Haswell) (see Griffin & Yaldwyn, 1964: 38–41, figs. 1–8) except that the eyestalks are much longer, the postorbital spinules are minute and the palm of the chela possesses fewer spinules on the dorsal and ventral surfaces than does *A. fissifrons*. The fact that the specimen is a female without ambulatories makes precise determination difficult. Positive identification of Rathbun's series thus awaits further study.

Among the known species of *Achaeus*, *A. spinosissimus* appears to be most closely related to those such as *A. inimicus* Rathbun, *A. akanensis* Sakai, *A. anauchen* Buitendijk, *A. fissifrons* (Haswell) and *A. cadelli* Alcock, in which the supraorbital eave possesses 1–3 large spines. From these it is distinguished by its more spiny carapace and chelae, the form of the rostrum and the presence of long spines on the basal antennal article. The closely approximated rostral spines are reminiscent of species of *Macropodia* in which, however, the rostrum is nearly always much longer. The species of *Macropodia* most similar to *A. spinosissimus* is *M. formosa* Rathbun (see Barnard, 1950: 17, figs 2*g*–*i*).

Achaeus barnardi n.sp.

(Figs 3, 4*c*–g)

Achaeus cf. *affinis*: Barnard, 1950: 19–20, figs 3*d*–*f*.
[*non*] *Achaeus affinis* Miers, 1884 (= *A. brevirostris* (Haswell)—see Griffin & Yaldwyn, 1964: 46–48).

Holotype: Male, c.l. 8·5 mm, chelipeds and legs missing, off Cape Morgan, South Africa (S. Afr. Mus. reg. A1392)—South African Museum, Cape Town (this is the specimen figured previously by Barnard).

Paratypes: Two males, c.l. 6·7, 5·5 mm, 1 female (ovig.) c.l. 7·0 mm, same data as for holotype—South African Museum, Cape Town.

Description: Carapace elongate subtriangular, narrowed anteriorly, not markedly constricted behind orbits, branchial regions swollen, lateral margins and dorsal surface with a few tubercles, regions well defined. Surface of carapace, sternum, abdomen and third maxillipeds coarsely granular.

Rostrum of two short, slender, subacute lobes separated apically by a very narrow, V-shaped slit.

Supraorbital eave with up to six or seven very small, sharp spinules anteriorly on dorsal surface near margin. Postorbital region unarmed. Eyestalks stout, a narrow process extending above cornea terminating in a small but prominent tubercle; anterior surface with a prominent rounded or subacute lobe midway along; cornea large, ovoid, obliquely terminal.

Hepatic region not greatly expanded, with a small tubercle at summit and one or two tubercles or spinules in front of this.

Branchial regions smooth or with three very low tubercles laterally in a shallow arc, one anteriorly, one just forward of cardiac prominence and one close to posterior margin on metabranchial region above last leg; anterolateral margins with two or three small tubercles, posterior margins laterally with some minute spinules.

Dorsal surface of carapace with four low tubercles in midline, one far back on mesogastric region, two small tubercles side by side surmounting tumid cardiac region and a low tubercle on posterior slope.

Protogastric regions smooth or with a small, low tubercle on each side just in front of marginal hepatic tubercle.

Basal antennal article with surface weakly convex, oblique, smooth or with up to four very small tubercles in a row centrally. First segment of flagellum stout, short, a small, apically curved spine laterally midway along and two smaller spines ventrally, one midway along and one apically; second segment almost three times as long. Flagellum of moderate length, with a few long hairs.

Antennular fossae large, longitudinally subovate, distal part of lateral edge slightly outwardly splayed; basal segment of antennules with a row of spinules medially; interantennular spine and anterior process of epistome slender, the former projecting down as an obtuse lobe.

Epistome slightly longer than wide, with one or two spinules just lateral to opening of green gland, otherwise smooth.

Third maxillipeds almost meeting in midline, spinulous and hairy. Ischium bearing spinules in two oblique rows, one laterally and one centrally bordering a broad, shallow groove; medial edge coarsely toothed. Merus narrow, subovate, with four or five spinules centrally in proximal half, a similar number of spinules close to medial margin and three spinules on anterolateral angle. Palp long and stout.

Chelipeds long and stout in male, short and slender in female, tuberculate or spinous. Ischium tuberculate. Merus subcylindrical, bearing three sharp tubercles dorsally in both sexes, two proximal, one distal and a row of tubercles ventrally which are blunt in male and become small distally but sharp in female

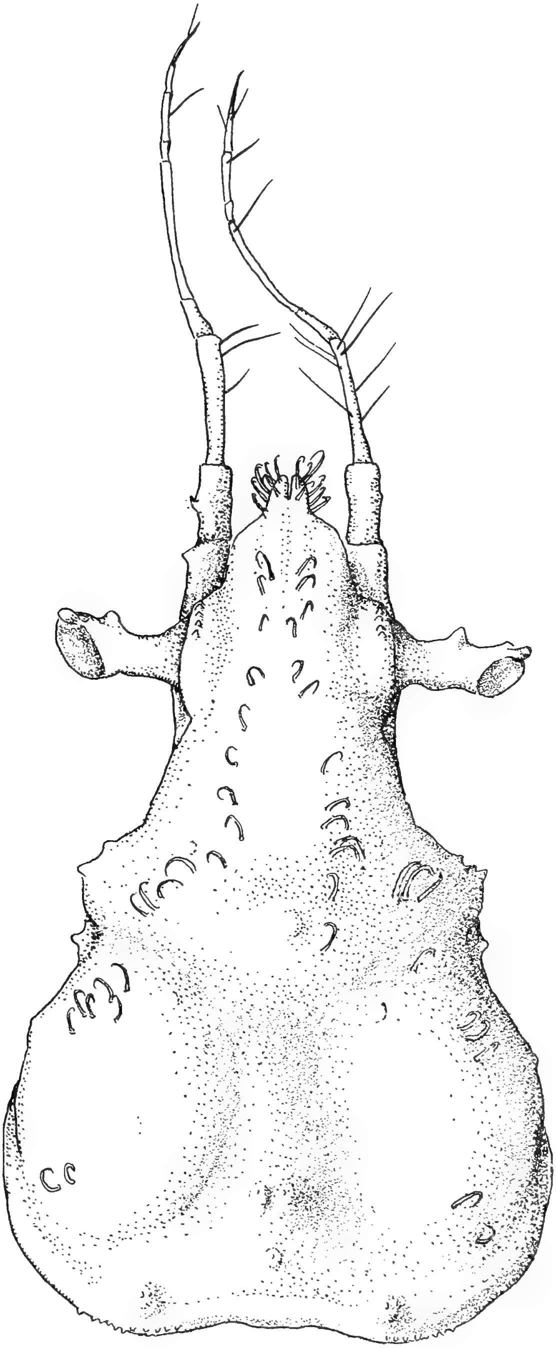

Fig. 3. *Achaeus barnardi* n.sp. Holotype, male, carapace, dorsal aspect.

and of equal length throughout. Carpus medially bearing about five sharp spinules. Chela in male about half length of cheliped, compressed, robust, palm dorsally weakly convex and ventrally strongly convex, outer surface granular, dorsal and ventral surface with a few small spinules proximally, without spines or tubercles; fingers as long as palm, stout, very widely gaping for proximal half, fixed finger with a narrow, apically truncate tooth proximally almost filling gape, remainder of inner edge strongly concave in proximal half, obtusely angled at distal end of gape; dactyl with a small truncate tooth, slightly shorter than, and just beyond, that on fixed finger, a broader, minutely dentate tooth near distal part of gape, distal half of inner edge irregularly dentate; a few short hairs on both fingers extending into gape. Chelae slender in female, fingers with inner edges adjacent for entire length.

Ambulatory legs very long, slender, with curled hairs arising singly on dorsal surface of propodi, long hairs on distal two-thirds of propodi and on dactyls; first leg the longest, remainder decreasing to last, all legs without spines; dactyls almost straight in first and second pair, strongly falcate to semicircular in last two legs, third dactyl with strong spinules ventrally along whole length, last dactyl with strong spinules for distal half to two-thirds.

Sternum with tubercles in transverse rows along each sternite; anterior margin of sternum subtruncate, bearing spinules close together.

Abdomen in male of six segments, segments 6 and 7 coalesced. All segments wider than long, last segment the longest, almost as long as wide, first slightly shorter, second the shortest; fifth also short, third and fourth subequal, about half length of last. Abdomen widest about middle of laterally convex third segment, lateral margin concave to just beyond base of last segment, then tapering to subtruncate, weakly concave distal edge. Surface with a broad medial elevation distally in segments 1–5 and proximally in last segment. Third segment with small spinules in three ill-defined longitudinal to oblique rows on swollen lateral surfaces; proximal part of last segment laterally swollen.

Male first pleopod moderately stout, uniformly tapering apically and outwardly curved, terminally blunt; aperture subterminal, a broad slit at end of groove on medial surface; lacking hairs.

Measurements (paratype male): carapace length 6·7 mm, carapace width 4·8 mm, rostral length 0·5 mm, rostral width (at base) 0·9 mm, chelar length 5·0 mm, chelar height 1·5 mm, dactyl length 3·0 mm, first ambulatory leg length 21·0 mm.

Remarks: This species is very similar to *A. brevirostris* (Haswell) (of which *A. affinis* Miers is a synonym). Comparison with the series from Australia examined by Griffin & Yaldwyn (1964: 46–47) shows the following differences. In *A. brevirostris* the carapace is narrower, the rostral lobes are somewhat broader, usually more widely separated and blunter, the supraorbital lobe lacks spinules or tubercles, the cardiac elevation is usually very much more prominent, the branchial margin is without tubercles or spinules, the merus and carpus of the cheliped in both sexes are tuberculate but without spines, the fourth ambulatory

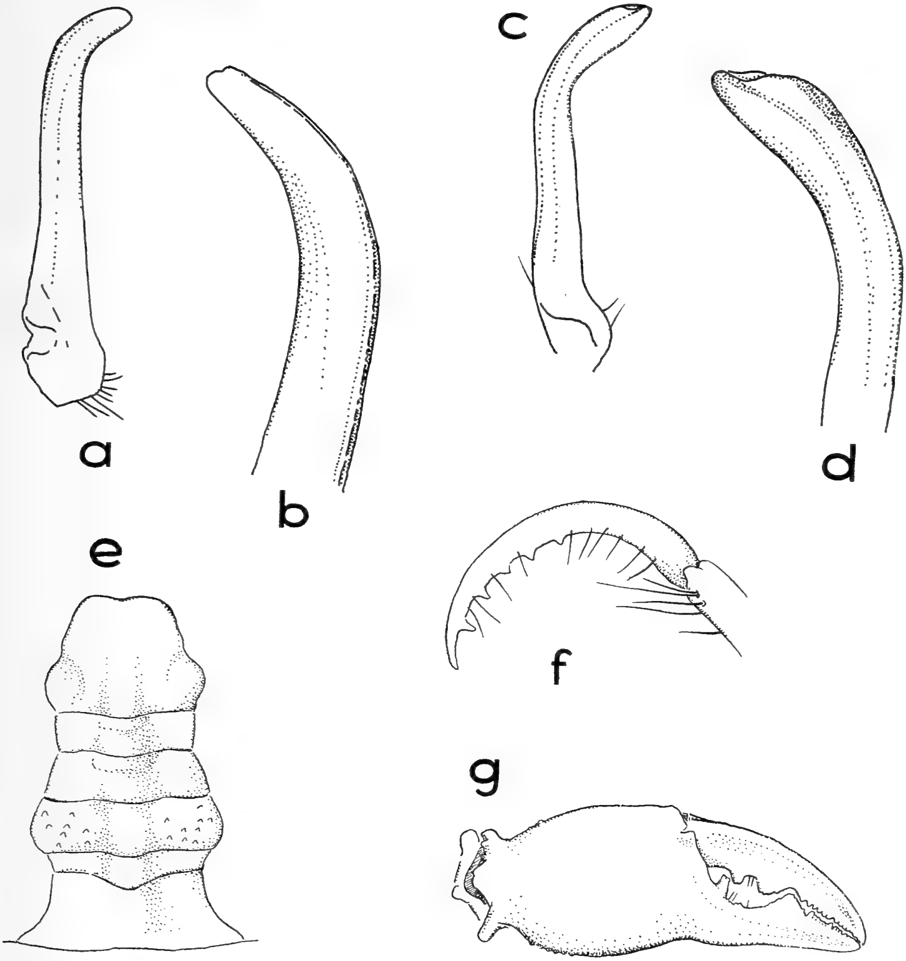

Fig. 4. *Achaeus spinosissimus* n.sp. Holotype, male, left first pleopod (a, b): a, abdominal aspect; b, tip, sternal aspect. *Achaeus barnardi* n.sp. (c–g): c, holotype, male, left first pleopod, abdominal aspect; d, tip of same, sternal aspect; e, abdomen of holotype; f, fourth left ambulatory dactyl, posterior aspect, of male paratype, c.l. 6·7 mm; g, right chela, outer aspect, of male paratype.

dactyl is falcate but not semicircular and possesses spinules ventrally along the whole length, and the sternum in the male is anteriorly weakly convex and bears only minute spinules or lacks spinules altogether. Lastly, the male first pleopod is almost straight, not curved distally.

Barnard's description of this species is in error only in the following particulars. He did not mention the mesogastric tubercle or the spinules on the anterior part of the supraorbital eave and he described and illustrated the third ambulatory dactyl in mistake for the fourth. He also stated that the male first pleopod resembled that of *Macropodia falcifera*. In that species, however, the distal part is rather abruptly bent, not smoothly curved as in this species.

The new species is named for the late Keppel Harcourt Barnard, former director of the South African Museum, Cape Town, who made so many notable contributions to what is known of South African Crustacea.

Discussion

The total number of species of *Achaeus* in South African waters is four. These are *A. spinosissimus* and *A. barnardi*, described in this report, *A. lacertosus* Stimpson and a species which is almost certainly *A. laevioculis* Miers (*A.* cf. *laevioculis* of Barnard). Re-examination of the three specimens which Barnard identified tentatively as this species and comparison with Miers's (1884: 520, pl. XLVI, figs A, *a*) description does not suggest that the South African species is distinct. However, the following remarks are necessary: Barnard figures one specimen with the rostrum bearing denticles on the anterior margin—the other two specimens have the rostrum medianly divided apically, the lobes rounded and entire with a submarginal fringe of hairs; the hepatic margin bears a few low tubercles; the anterior tubercle near the medial margin of the branchial regions has one or two small tubercles near by; the lateral margin of the branchial regions possesses spinules anteriorly; there is a very low tubercle near the posterior margin above the base of the last legs; the meri of the chelipeds have one dorsal tubercle and several tubercles ventrally, especially along the ventrolateral edge; the carpi of the chelipeds possess a few tubercles dorsally; and the palm of the chela has tubercles on the dorsal and ventral edges distally.

Of these four species the two described in this report are restricted to South African waters, *A. laevioculis* is known from the western Indian Ocean and *A. lacertosus* is widespread in the Indo-Pacific, from Australia and Japan through the Gulf of Siam and the Gulf of Martaban to India and the Iranian Gulf.

Summary

A re-evaluation of the material from South African waters, of two species of majid spider crab belonging to the genus *Achaeus* discussed recently by Barnard shows that they are distinct and previously unnamed species. The two species are described and figured and compared with closely related species. Additional descriptive notes are given on *A. lorina* (Adams & White) which is known with certainty only from Indonesia and the Philippines and the material recorded from the western Indian Ocean by Rathbun as *A. lorina* is considered to belong to the widespread *A. fissifrons* (Haswell). The new species appear to be confined to South Africa; one other species, *A. laevioculis* Miers, is found in other parts of the western Indian Ocean whilst *A. lacertosus* Stimpson is found throughout most of the Indo-West Pacific.

ACKNOWLEDGEMENTS

I wish to thank the Director and Mr. B. Kensley of the South African Museum, Cape Town, for making this material available. I am grateful also to Dr. A. L. Rice, British Museum (Natural History), and Dr. R. B. Manning, United States National Museum, for information about material in their collections and for the loan of comparative material and Dr. J. C. Yaldwyn, Australian Museum, for helpful discussion and for commenting on the manuscript.

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Volume **52** Band
December **1968** Desember
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By

Q. B. HENDEY

Cape Town Kaapstad

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The Rustica Press, Pty., Ltd.
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South African Museum, Cape Town

(With plates 8–10 and 3 figures)

[*MS received* 10 *September* 1967]

Contents

Introduction

In the collections of the South African Museum (Natural History), Cape Town, is an assemblage of fossils recovered from a site near the coast north of the town of Melkbosstrand (fig. 1). The first recorded discovery of fossils at this locality was made in 1956 by Mr. J. Rudner of Cape Town. Thereafter small collections were made from time to time, and much of the material recovered found its way to the Anatomy Department of the University of Cape Town. In 1962 this material was presented to the South African Museum and forms the nucleus of the assemblage presently to be described.

The limits of 'the Melkbos site', as it has become known, are not clearly defined, fossil and cultural material having been recovered from an area about 1½ miles long and a few hundred yards wide, beginning about 3 miles north of the mouth of the Sout (Klein Sout) River. The fossils have been exposed by erosion in, and associated with, an horizon of calcareous sandstone ('calcrete') and sand in the area, which forms part of the Sandveld region (Talbot, 1947) (pl. 8A).

Pleistocene fossil occurrences are known from several localities along the Table Bay and False Bay coasts. These include Milnerton and Ysterplaats (Broom, 1909; Cooke, 1955), Paarden Eiland, Strandfontein and Swartklip (Singer & Fuller, 1962; Hendey & Hendey, 1968). The Melkbos site has been one of the most productive of these occurrences, and the South African Museum's collection at present includes over 600 specimens from the site. However, its true wealth can never be accurately assessed, since it is easily accessible and

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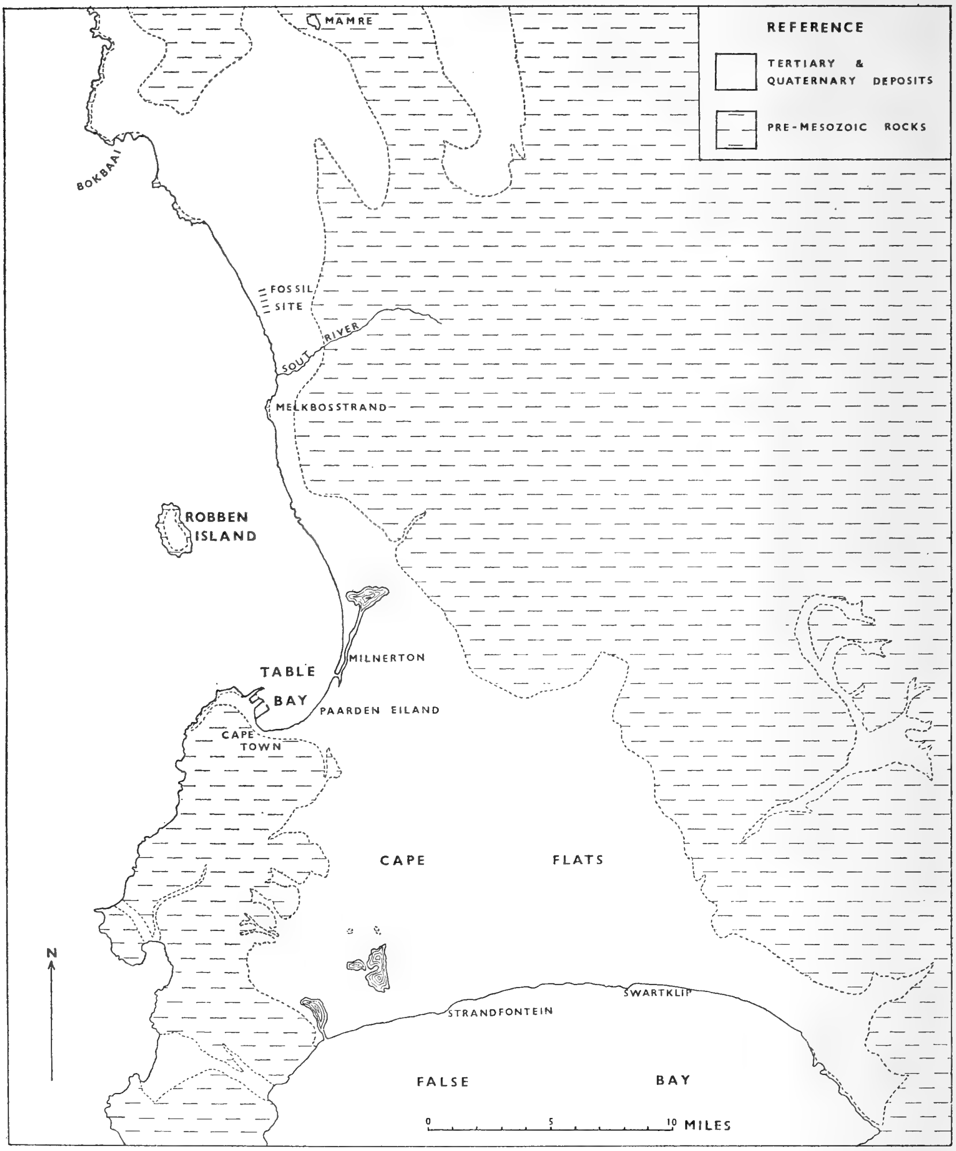


Fig. 1. The location of the Melkbos fossil site.

extensive collecting by visitors to the area takes place. In addition, the fossils are rapidly destroyed by weathering once they have been exposed.

The purpose of this report is to place on record the presence of the site, its relationship to other south-western Cape fossil sites and to give a preliminary account of the more important specimens thus far recovered.

Geological Associations and Nature of the Occurrence

The deposits in the area can conveniently be divided into two categories.

Firstly, there are Recent aeolian sands, which have resulted from the weathering and erosion of pre-existing deposits. These are, in places, vegetated and fairly stable, but elsewhere are in the form of mobile barchan dunes. Where they have been stabilized they are sometimes found in association with Late Stone Age middens. They are discontinuously developed and clearly post-date the period of fossil accumulation.

The second category of deposits are the Pleistocene sands, calcrete and ferricrete, with which the fossils are associated. They have a long and complex history, the sands probably having been laid down during the Tertiary, and been transported and redeposited several times since. No systematic excavations have been undertaken in the area, and the sequence of events suggested below is based only on surface observations.

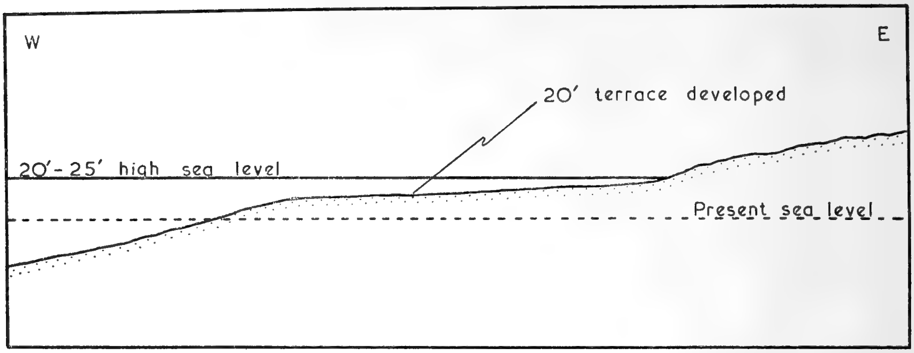
In the area between the fossil occurrence and the sea, a fairly extensive platform is exposed, almost certainly 'wavecut', with an elevation of about 20 feet above sea-level. Krige (1927) refers this platform to his 'Minor Emergence', stating that 'the overgrown flats at Melkbosch Strand suggests a terrace of the right order'. Assuming correspondence to the European Pleistocene sea-level changes, and in the present instance there is no reason to believe that such a correlation is invalid, this terrace is Late Monastirian (= Tyrrhenian III) in age (Zeuner, 1959; Oakley, 1964).

The fossiliferous deposits at Melkbos overlie the 20-foot terrace, and therefore post-date it (fig. 2).

Mabbutt *et al.* (1955) recorded a succession at Bok Baai (fig. 1) which includes a calcrete, almost certainly equivalent to that at Melkbos, overlying 'Minor Emergence' beaches and related cliff slopes.

The Early Würm interstadial, with which the Late Monastirian is correlated (Oakley, 1964), has been assigned a chronometric date of about 40,000 years B.P. (Emiliani, 1961). The Chatelperronian industry of the Upper Palaeolithic of Europe has been related, in time, to this interstadial and the industry has been dated to about 32,000 B.C. at Arcy sur Cure, France (Oakley, 1964). The South African Middle Stone Age/Second Intermediate industries, with which the Melkbos fauna has suggested associations (*vide infra*), has been dated variously between 44,000 B.P. to 2540 B.C., with 'the Middle Stone Age *in sensuo* [*sic*] *stricto* . . . later than 40,000 years B.P.' (Deacon, 1966).

The Melkbos fauna is therefore considered to be no earlier than 30,000 to 40,000 years B.P. No upper age limit was determined, but a date of late Upper



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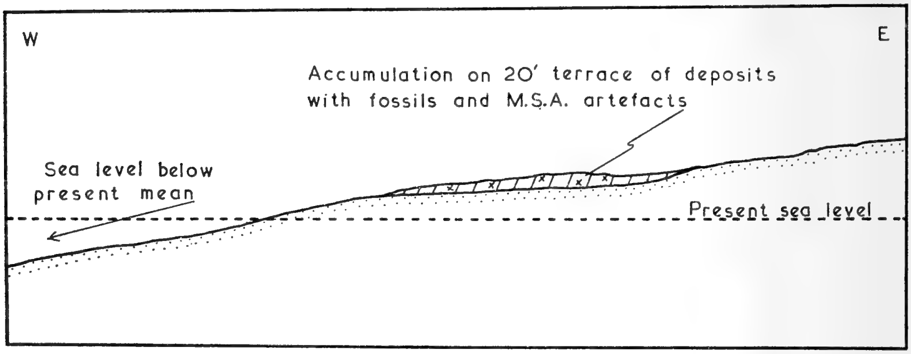

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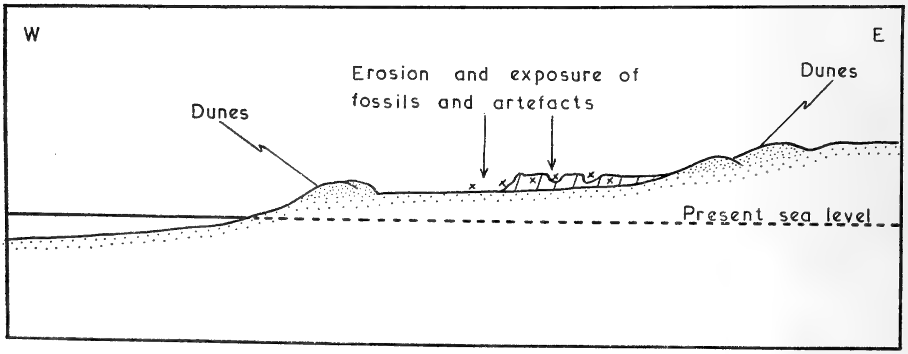

3. RECENT

Fig. 2. Diagrammatic representation of the suggested sequence of events at the Melkbos site.

Pleistocene is proposed for the fauna. This will serve adequately to place it chronologically, until such time as a more definite chronometric date is established.

It was not evident from the surface observations whether single or multiple fossiliferous horizons exist. The fossils appeared to be preserved only in association with the calcrete, i.e. the original lime-rich horizon of the Upper Pleistocene palaeosol. A few very poorly preserved specimens were found in the more acid horizons of the palaeosol, which are now marked by the exposures of ferricrete.

Gradual concentration of the calcium carbonate in the lime-rich horizon, and induration following its exposure, has given rise to the calcrete in its present form. The outer surfaces of the exposures are extremely hard, but the degree of induration diminishes away from the exposed areas (cf. Du Toit, 1917: 12). The calcrete is, therefore, not strictly speaking Pleistocene in age since some of its characters are still being developed, but it had its beginnings at the time of the development of the soil body overlying the 20-foot terrace and after the fossils were already in place.

The site is exposed to both south-easterly and north-westerly gales which are prevalent in the region in summer and winter respectively, and wind erosion of the area is perennial and severe. The exposed fossils suffer extensive sand-blasting, and develop a deep red or dark brown colour and a very characteristic glazed patination, reminiscent of the 'desert varnish' of rocks in arid regions. Bone fragments litter the site, but diagnostic material is much less common (pl. 8B).

Archaeological Associations of the Fossils

No positive association between cultural material of a known period and the fossils has been demonstrated.

The fossils predate the Late Stone Age middens which often occur on or within the Recent aeolian sands. They have been found in surface association with undoubted L.S.A. artefacts, but this is considered to be fortuitous.

No Early Stone Age material has been recorded from the site.

Undiagnostic silcrete flakes have on occasion been found during the excavation of fossils in the unconsolidated deposits, and on rare occasions there have been 'flakes' of dubious authenticity found embedded in the calcrete. The former, at least, were considered to be genuine archaeological associations. Several finely worked bifacial points of a rather small size, and flakes with prepared striking platforms, all in a silcrete similar to that of the excavated material have been recovered from the surface of the site. This lithic material, undoubtedly dates from the Middle Stone Age or Second Intermediate, and an association between it and the fossils is suggested.

The Faunal Assemblage

The nomenclature, with a few exceptions, follows that of Ellerman *et al.* (1953).

Class *MAMMALIA*
- Order **CARNIVORA**
  - Family **Hyaenidae**
    - *Hyaena* cf. *brunnea*
  - Family **Felidae**
    - *Felis leo* aff. *spelaea*
  - Family **Canidae**
    - *Canis* cf. *mesomelas*
- Order **PINNIPEDIA**
  - Family **Otariidae**
    - ? *Arctocephalus pusillus*
- Order **PROBOSCIDEA**
  - Family **Elephantidae**
    - ? *Loxodonta africana*
- Order **PERISSODACTYLA**
  - Family **Rhinocerotidae**
    - *Diceros simus*
    - *Diceros bicornis*
  - Family **Equidae**
    - *Equus* sp.
- Order **ARTIODACTYLA**
  - Family **Hippopotamidae**
    - *Hippopotamus amphibius*
  - Family **Bovidae**
    - *Syncerus* sp.
    - *Tragelaphus* cf. *strepsiceros*
    - *Taurotragus oryx*
    - *Redunca arundinum*
    - cf. *Hippotragus* sp.
    - *Connochaetes* sp.
    - *Raphicerus* sp.
    - cf. *Antidorcas* sp.
- Order **RODENTIA**
  - Family **Bathyergidae**
    - *Bathyergus suillus*

Class *REPTILIA*
- Order **CHELONIA**
    - *Incertae sedis*

Class *AVES*
- Order **STRUTHIONIFORMES**
  - Family **Struthionidae**
    - *Struthio australis*

Systematic Description of the Fauna

Class *MAMMALIA*

Family **Hyaenidae**

Hyaena cf. *brunnea* Thunberg

Brown Hyaena

The only hyaenid remains recorded from the site are an incomplete mandible (Mb 116) and an incomplete maxilla (Mb 117), which belong almost certainly to the same adult individual (pl. 9). Both specimens are from the left side.

Mb 116—(table 1)—The mandible has lost that part of the corpus posterior to the P_4, and has suffered extensive post-fossilization weathering. The I_3 root, incomplete $\overline{C}$, P_2 and P_4, and the almost intact P_3 are preserved. It exhibits characteristics of the genus *Hyaena* as defined by Ewer (1954), although it differs slightly from the *H. brunnea* mandibles of the comparative series.

Table 1

DIMENSIONS OF MELKBOS *HYAENA* CF. *BRUNNEA* TEETH AND MANDIBLE, COMPARED WITH THOSE OF A FOSSIL SPECIMEN FROM ELANDSFONTEIN AND TWO SERIES OF MODERN SPECIMENS.

	Mb 116	E'f'tein 16686	Modern *H. brunnea*† Mean	Range	Modern *H. brunnea** Mean	S.D.
C l	19·6	19·5	18·3	17·5–19·8	17·16	1·14
b	12·6	13·5	12·9	12·0–13·4	13·35	0·84
P_2 alveolar l	16·7	17·3	14·7	13·4–15·3	—	—
alveolar b	8·0	9·5	7·8	6·7– 8·4	—	—
P_3 l	21·0	22·2	20·9	20·3–21·5	21·17	0·40
b	c15·0	15·0	14·4	13·6–15·0	14·40	0·60
P_4 l	c23·7	24·7	22·7	22·4–22·9	23·59	0·56
b	c13·7	14·2	13·4	12·9–13·7	13·80	0·51
P_2–P_4 alveolar l	c60·0	61·6	56·8	56·6–57·0	—	—
Diastema length	8·7	8·2	11·8	10·8–13·1	—	—
Corpus height below P_3	40·0	41·0	36·3	34·1–38·5	—	—
Corpus width below P_3	21·0	24·1‡	18·7	17·4–19·5	—	—
Distance between LP_3 and RP_3	c58·0	c62·0	57·5	55·0–59·1	—	—

† Sample of four specimens.
* Ewer & Singer, 1956; sample of thirteen specimens.
‡ Measurement somewhat high due to a pathological condition in this region of the mandible.

The diastema is appreciably shorter and the P_2 and P_4 slightly longer than those of the comparative specimens. However, the P_4 length corresponds closely to the mean of a series of 13 measurements given by Ewer and Singer (1956) for *H. brunnea.*

The corpus is very robust, and falls beyond the size range of the comparative series. The estimated inter-corporal width falls within the range observed in *H. brunnea.*

Mb 117—(table 2)—The maxilla has only the damaged crown of the P^3 preserved, while little more than the roots of the P^2 and P^4 remain. It shows greater differences from the *H. brunnea* comparative series than does the mandible, although it clearly belongs to *Hyaena* rather than *Crocuta.*

TABLE 2

DIMENSIONS OF MELKBOS *HYAENA* cf. *BRUNNEA* UPPER TEETH, COMPARED WITH THOSE OF A SERIES OF FOUR MODERN SPECIMENS.

		Mb 117	Modern *Hyaena brunnea*	
			Mean	Range
P^1–P^4 alveolar length		80·0	77·2	75·9–78·5
P_2	alveolar l	17·5	15·5	15·1–15·7
	alveolar b	9·0	8·3	7·8– 8·8
P_3	l	22·9	23·2	22·6–23·8
	bm	c14·4	14·7	13·0–15·5
	bd	15·5	15·8	15·0–16·9
P_4	alveolar l	33·0	32·8	30·0–34·2
	alveolar b	18·6	19·3	18·0–20·5

The length of the anterior alveolus of the P^4 expressed as a percentage of the total alveolar length of this tooth, is 39·4, as against a mean of 43·6 for the *H. brunnea* series and 29·4 for the *C. crocuta* series.

The alveolus of the P^1 is small, almost circular in shape and overlaps the distal end of the $\underline{C}$ alveolus on its lingual side. The position of the P^1 relative to the $\underline{C}$ of the comparative specimens was variable, but none exhibited an overlapping of these teeth. With the $\underline{C}$ set back so far relatively, the canine fossa is very pronounced, and descends steeply from the infra-orbital foramen to the alveolar margin. These features, taken in conjunction with the relatively short mandibular diastema indicate an overall foreshortening of the anterior region of the snout. The lengths of the cheek tooth rows are greater than those of the comparative specimens, indicating that the foreshortening is confined to the canine/incisor region.

The P^2 is both longer and broader than those of the comparative series, while the P^3 falls within the size range of variation. The latter differs from the P^3 of the comparative series in that an anterior accessory cusp is present in the form of a small but clearly defined projection from the cingulum.

Discussion

Owing to the condition of the fossil specimens, the fact that they represent only a single individual, and in view of the limited number of comparative specimens, there are insufficient grounds for separating the Melkbos *Hyaena* specifically or subspecifically from the extant *H. brunnea.*

The possibility that it is not an isolated aberrant specimen is lent some support by a recently discovered *Hyaena* mandible and P^3 (16686 and 16687) from the Elandsfontein (Hopefield) site. These specimens exhibit some of the unusual features observed in Mb 116 and Mb 117. *H. brunnea* has already been recorded from the Elandsfontein site (Ewer & Singer, 1956), but the new specimens differ from those previously described in much the same way as those from Melkbos differed from the comparative series. The mandibular corpus of 16686 is extremely robust and corresponds closely in size to that of Mb 116. The diastema is slightly shorter than that of Mb 116 (table 1). The P^3 (16687) has a small anterior accessory cusp identical in development to that of Mb 117. The teeth of the Elandsfontein and Melkbos specimens are similar in size.

Family **Felidae**

Felis leo aff. *spelaea* Goldfuss

The lion is represented in the assemblage by four specimens, which belong to at least two individuals. Postcranial remains include the distal half of a right radius (Mb 561) and the proximal half of a left fourth metacarpal (Mb 576). Cranial remains include a fragment of a right mandible (Mb 603) and an incomplete left mandible (Mb 143).

Mb 143—(pl. 10; table 3)—This is the right mandible of an adult individual which lacks the ascending ramus, the angular process and those parts of the corpus anterior to the P_4. The P_4 and M_1 are largely intact and well preserved.

The P_4 has lost the most mesial portion of the anterior cusp. In spite of this, its estimated length was significantly greater than the length of corresponding teeth in a series of 17 modern lion specimens. The breadth falls within the range observed in this series, although it is greater than the mean.

The M_1 shows slight wear on the shearing blades. Its length is slightly above the maximum of the comparative series, and the estimated breadth is near the upper limit of the observed range.

Morphologically the teeth are indistinguishable from those of the modern lion, although the 'talonid' of the M_1 is slightly more pronounced in the fossil specimen.

On discovery the specimen was embedded in a block of calcrete with only the lingual surface of the corpus and the M_1 exposed. This area has been heavily weathered, and the mandibular canal and anterior root of the M_1 have been exposed. The vertical wall of the masseteric fossa and inferior margin of the corpus posterior to the M_1 have been lost.

The corpus is extremely robust, but differs most notably from those of the comparative specimens in the region of the masseteric fossa. The superior and anterior walls of the fossa are steep, while the inferior wall becomes progressively more U-shaped posteriorly, with the development of a ridge of bone along the buccal surface of the inferior margin. On a line 20 mm behind the posterior end of the M_1, the height measured from the top of this ridge to the inferior margin of the mandible is + 26·0 mm. The mean for corresponding measurements in 10 comparative specimens was 18·4 mm, with a maximum of only 22·0 mm. Towards the posterior limit of this ridge and immediately below

TABLE 3

DIMENSIONS OF MELKBOS *FELIS LEO* TEETH AND MANDIBLE, COMPARED WITH THOSE OF A SERIES OF 17 MODERN SPECIMENS, AND A SERIES OF *FELIS LEO SPELAEA* TEETH FROM BRITAIN.

	Melkbos		Modern African *Felis leo*			Pleistocene *F. leo spelaea**		
	Mb 143	Mb 603	Mean	Range	S.D.	Mean	Range	No. measured
P_4 l	c32·0	+25·0	26·85	23·1–29·5	2·07	30·13	22·9–33·0	9
P_4 bm	11·9	+11·0	10·60	8·7–12·2	0·89	—	—	—
P_4 bd	14·9	+13·0	13·54	10·8–15·5	1·32	13·74	10·4–16·3	9
M_1 l	31·0	—	28·12	25·7–30·6	1·35	30·33	26·2–33·0	7
M_1 b	c16·0	—	14·18	12·2–16·2	1·19	14·12	10·2–15·2	6
Corpus height below P_4	52·8	—	45·46	32·8–52·8	5·86	—	—	—
Corpus height below M_1	53·7	—	45·64	34·4–54·5	5·92	—	—	—

*Dawkins & Sanford (1866–1872); measurements of both 'large' and 'small' forms.

it, there arises a horizontally projecting ridge which curves downwards in the direction of the missing angular process. Although there was considerable variation in the nature of this region of the mandible in the comparative specimens, none showed the pronounced development of the features observed in Mb 143. This suggests that the masseter muscle was very powerfully developed, a factor which is in keeping with the relatively large size of the specimen.

Mb 603—(table 3)—This poorly preserved specimen, a fragment of a right mandible, retains only a damaged P_4. Although accurate measurements of this tooth are not possible, it appears to be larger than the mean of the comparative series.

Mb 561—(table 4)—This specimen, the distal portion of a right radius, is poorly preserved and has lost the styloid process and much of the brachioradialis tuberosity. Morphologically it is indistinguishable from the radius of the modern lion, but was significantly larger than the three comparative specimens available. It corresponds closely in size to a series of four felid radii from the Elandsfontein site, which are thought to belong to a large extinct lion (*vide infra*).

TABLE 4

DIMENSIONS OF MELKBOS *FELIS LEO* RADIUS, COMPARED WITH THOSE OF A SERIES OF THREE MODERN LIONS, AND A SERIES OF FOUR FOSSIL SPECIMENS FROM ELANDSFONTEIN.

		Elandsfontein		Modern *F. leo*	
	Mb 561	Mean	Range	Mean	Range
Transverse diameter*	40·0	41·0	37·0–44·0	31·5	28·4–34·0
A/P diameter* ...	23·5	22·3	20·5–23·0	22·7	21·8–23·8

* Measured immediately above brachioradialis tuberosity.

Mb 576—A metacarpal fragment, which although heavily weathered, clearly belonged to a lion of substantial proportions.

Discussion

The Melkbos lion, while being of robust proportions, cannot on available evidence be separated specifically from the extant *F. leo*. The few previously described fossil lions from South Africa (Broom, 1939 & 1948; Ewer, 1956*a*) are known only from fragmentary remains, and their specific rank is open to some doubt. In respect to size and the development of the M_1 'talonid', the Melkbos lion is similar to the '*Panthera shawi*' from Kromdraai (Ewer, 1956*a*), but the remains of both forms are too scanty to allow conclusive comparisons.

It is probable that a close relationship exists between the Melkbos lion and the as yet undescribed form from Elandsfontein, which is appreciably larger than the extant form.

The relatively abundant lion remains from Swartklip (Hendey & Hendey, 1968) represent a form indistinguishable from the extant *F. leo*, and it is probably at least subspecifically distinct from that from Melkbos. Possible relationships of both these forms to the recently extinct Cape Lion (*Felis leo melanochaitus* Smith) were considered, but owing to the lack of information on the osteology of the latter, the question remained inconclusive.

The relatively large size of the Melkbos lion invites speculation on its possible relationship to the 'giant' felines of the Pleistocene of the Northern Hemisphere. These include the giant 'jaguar' of North America (*Felis atrox*) (Merriam & Stock, 1932; Simpson, 1941; Kurtén, 1965*a*), the 'tigers' of the Asian Pleistocene (*F. tigris* subspp.) (Hooijer, 1947) and the European cave lion (*F. leo spelaea*) (Dawkins & Sanford, 1866–72). It is with the latter that the Melkbos lion is tentatively identified, although the basis for comparison is limited by the fragmentary remains from Melkbos. Both the size and character of the teeth, and the overall size of the animals suggest a close relationship between the two forms (fig. 3, table 3).

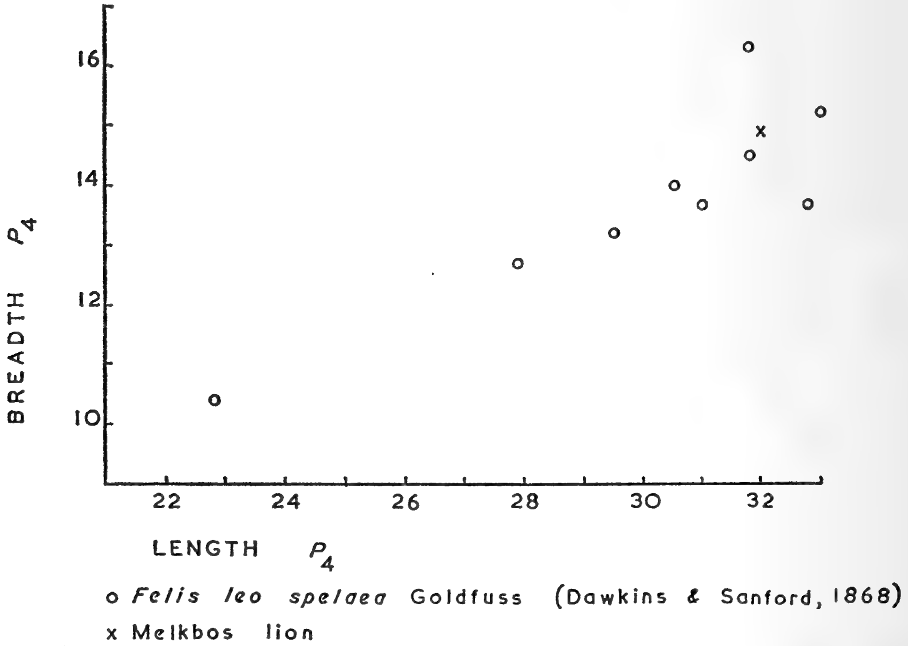

Fig. 3. The length/breadth relationship of the P_4 of the Melkbos lion, compared with those of a series of *Felis leo spelaea* specimens from Britain.

The great distance between Melkbos and the known limit of distribution of *F. leo spelaea* makes it necessary to express reservations on the identification. The question can clearly not be resolved until such time as a greater number of more complete specimens are known from South Africa. However, even the extant subspecies of large felines are not easily distinguished on osteological grounds alone. This is true of the African and Indian lions (Todd, 1966) and the tigers of south-east Asia (Hooijer, 1947). In the case of the latter there is a marked decrease in size towards the periphery of the area of distribution. This is a parallel of the situation observed in many carnivores during the Pleistocene, where a marked decrease in size occurred with the passage of time (Kurtén, 1965*b*). The variations in the size of carnivores in both time and geography obviously limit the use of this factor alone as a taxonomic discriminant.

Family **Canidae**

Canis cf. *mesomelas* Schreber

Black-backed Jackal

The jackal is represented in the assemblage by a single M_1 (MB 556), which is well preserved and in a moderately advanced state of wear. Morphologically this tooth is not distinguishable from the corresponding teeth of the two extant South African jackals, *C. mesomelas* and *C. adustus*. However, metrically it corresponds more closely to the former, being only slightly larger than the maximum of a range given for this species by Ewer (1956*b*) (table 5).

Table 5

DIMENSIONS OF THE M_1 OF *CANIS* CF. *MESOMELAS* FROM MELKBOS, COMPARED WITH A SAMPLE OF TEN *C. ADUSTUS* AND FOURTEEN *C. MESOMELAS* SPECIMENS (EWER, 1956B).

		C. adustus		*C. mesomelas*	
	Mb 556	Range	Mean	Range	Mean
M_1 l	21·0	17·4–15·0	16·2	20·7–16·5	18·8
M_1 b	9·7	6·8– 5·1	6·1	8·2– 6·5	7·2

In a study of the *C. mesomelas* remains from the Elandsfontein site, Ewer and Singer (1956) found that several of the fossil teeth exceeded the known size range of the modern species.

Since then newly discovered material from the Elandsfontein and Swartklip sites has suggested the presence of a jackal in the south-western Cape during the Pleistocene of somewhat greater proportions than the extant *C. mesomelas*.

It may prove that the Melkbos specimen has affinities with this extinct form, but at present there is no adequate reason for separating it from the species *mesomelas*.

Family **Otariidae**

? *Arctocephalus pusillus* Schreber

Cape Fur Seal

A single fragment of the distal end of a humerus (Mb 546) is tentatively ascribed to this species. Only the medial epicondyle and part of the trochlea are preserved. It compares closely in size and morphology to the humeri of female *A. pusillus* specimens. The proximity of the site to the coast in an area where this seal occurs today, lends some support to its suggested affinities.

Family **Elephantidae**

?*Loxodonta africana* Blumenbach

African Elephant

Three fragments of a cheek tooth (Mb 513 A & B, and Mb 514) are the only elephant cranial remains recorded from the site. Their condition precludes positive diagnosis, but there is no reason to believe that they belong to a form other than *L. africana.*

Two fragments of a right scapula (Mb 78 & Mb 515), belonging almost certainly to the same bone, compare closely in all observable respects to the corresponding parts of scapulae of *L. africana.*

In view of the fragmentary nature of these remains, they are only tentatively ascribed to *L. africana.*

The recently described lower molar of '*Archidiskodon*' cf. *transvaalensis* (Hendey, 1967), recovered near the mouth of the Klein Sout River, has no apparent associations with the main Melkbos fossil site.

Family **Rhinocerotidae**

Diceros simus Burchell

White Rhinoceros

The White Rhinoceros was identified in the assemblage from a series of upper teeth of a single immature individual.

Mb 511A—(table 6)—LM^2, lacking the roots and in which the protoloph and metaloph have been reconstructed. The crochet is slightly worn, but the crista is still below the grinding surface. All the outer cement covering has been lost, but some remains in the medi- and postfossettes.

TABLE 6

DIMENSIONS OF *DICEROS SIMUS* TEETH FROM MELKBOS, COMPARED WITH THOSE OF TWO MODERN SPECIMENS.

	Mb 511A	Mb 511B	Modern *D. simus* 21379	21381
M_2 l	66·1	—	69·0	71·4
M_2 b	c45·0	—	41·0	45·5
M_1 l	—	c67·0	69·6	61·5
M_1 b	—	c42·5	44·5	43·5

Mb 511B—(table 6)—LM^1, lacking the roots and outer cement covering, and in which the ectoloph, protoloph and distal portion of the metaloph have been reconstructed. The medifossette is separated from the prefossette by the uniting of the crista and crochet.

Mb 511C—LP^4, very poorly preserved, and either completely unworn or in a very early stage of wear.

Mb 511D—LP^3, and least well preserved of the teeth.

In size and morphology this series of teeth corresponds closely to those of two modern *D. simus* specimens, and the degree of wear indicates an order of eruption normally found in the rhinoceros, i.e. M^1, M^2, P^3, P^4 (Cooke, 1950).

A skull fragment (Mb 591) was also tentatively assigned to *D. simus*.

Diceros bicornis Linnaeus

Black Rhinoceros

This species is represented in the assemblage by an incomplete mandible (Mb 125). It consists of a large part of the right corpus and the symphyseal region. The right P_3 and P_4 are largely intact, and the RM_1 is partially preserved. Only the roots of the other right molars, and the LP_1 and LP_2 remain. The symphyseal region is of the characteristic *D. bicornis* type and in size (table 7) and morphology the teeth are indistinguishable from those of the modern species.

TABLE 7

DIMENSIONS OF *DICEROS BICORNIS* TEETH FROM MELKBOS, COMPARED WITH THOSE OF A SERIES OF FIVE MODERN SPECIMENS.

		Modern *D. bicornis*	
	Mb 125	Mean	Range
P_2–M_3 alveolar length	285·0	272·0	253·0–297·0
P_3 l	35·0	37·0	33·0– 39·1
P_3 b	c31·0	31·9	30·8– 34·6
P_4 l	42·5	44·6	41·9– 46·9
P_4 b	c34·0	35·8	34·3– 38·0

Diceros sp.

Two tooth fragments (Mb 179 & Mb 583) and two mandible fragments (Mb 154 & Mb 427) were not identified as to species.

Rhinoceros postcranial remains are abundantly represented in the assemblage, but owing to the difficulty of distinguishing the two extant African species on the basis of their postcranial skeletons, no attempt was made to categorize these specimens specifically.

Family **Equidae**

Equus sp.

Equid remains are rare at the site, and only three teeth and five elements of the postcranial skeleton have been recovered.

Mb 120—A left M^2, the best preserved of the teeth, which corresponds closely in size to the M^2 of the *Equus helmei* type specimen (Dreyer & Lyle, 1931), but which does not exhibit the same complexity in the enamel pattern of the occlusal surface.

Mb 121 & Mb 137—Right upper and lower premolars, respectively, and both poorly preserved.

In view of the present unsatisfactory classification of South African fossil Equidae, and the number and condition of the Melkbos specimens, no specific diagnosis is proposed.

Family **Hippopotamidae**

Hippopotamus amphibius Linnaeus

The hippopotamus is represented in the assemblage by an incomplete M_3, of which only the hypoconid and entoconid are preserved.

Family **Bovidae**

Tribe *BOVINI*

Syncerus sp.

One of the most commonly represented bovids at the site is a large syncerine buffalo.

Material

Mb 610—An incomplete and highly fragmented skull, which consists of the base of the horn cores and frontal region, nasals and part of the left maxilla. Although observations on the skull characters were limited by the condition of the specimen, it proved to be considerably more robust than the *Syncerus caffer* comparative specimens (table 8).

The nasals correspond fairly closely in size to those of *Homoioceras* specimens from the Elandsfontein site. They are flattened rather than arched, and when articulated with the single remaining maxillary fragment it was apparent that in general appearance and proportions, the facial region of this specimen is similar to that of '*Homoioceras*'.

Table 8

DIMENSIONS OF *SYNCERUS* SP. SKULL FROM MELKBOS, COMPARED WITH THOSE OF *SYNCERUS CAFFER* SPECIMENS.

		*Syncerus caffer**			
		♂			♀
	Mb 610	Mean	Range	No. measured	35445
Maximum width across nasals	+86·0	63·8	54·5–72·0	6	c60·0
Maximum A/P width of horn core bosses ...	+247·0	220·7	207·0–230·0	3	156·0
Minimum distance between left and right bosses	c25·0	29·7	27·0–34·0	3	c77·0
Maximum distance between left and right bosses	c33·0	48·3	41·0–52·0	3	—

* Specimens in collections of S.A. Museum (Nat. Hist.)

However, the morphology of the frontal region corresponds more closely to that of *Syncerus*. The roof of the skull above the frontal sinuses is heavily rugose, far more so than in *S. caffer*, but clearly quite unlike the condition in '*Homoioceras*', in which the bases of the horns are not bossed. The median 'valley' separating the bosses is narrower in the Melkbos specimen than in any of the *S. caffer* comparative specimens, which is a factor in keeping with the greater overall size of the former. The anterior edge of the horn cores above the orbits parallels the condition in *Syncerus* exactly, the only difference being in degree of development. The antero-posterior diameter of the horn cores could not be measured accurately, since their posterior margins have been lost, but the remaining part of the left boss apparently comes close to the posterior point of recurvature. It measures 247 mm, 17 mm more than the maximum of the *S. caffer* comparative series. The males of this series were all hunting trophies and almost certainly above average size for the species.

There were two features in which the horn cores differed from the comparative specimens. The bosses did not display the marked dorsal antero-posterior convexity present in *Syncerus*, and secondly, although little of the horn cores beyond the bosses remains, it is clear that they do not have a pronounced downward sweep of the horns beyond the bosses. Roberts (1951) states that, 'as we go northward in the continent the horns of Buffaloes dip downward less and less until . . . they are on the top of the skull with only an outward and upward trend'. Consequently, the sweep of the horns in Mb 610, although not typical of the southern African *S. caffer*, is apparently the normal condition in their northern relatives.

Mb 15, and associated fragments Mb 89, 93 & 96—The horn core fragments of a second individual, which parallel in all observable respects the features of Mb 610, indicating that the latter is not a single atypical specimen.

Mb 608 & Mb 609—(tables 9 & 10)—Right and left mandibles of a single individual, the former with a complete set of cheek teeth, and the latter with the M_1, M_2 and incomplete M_3. The corpora of both halves are incomplete.

TABLE 9

DIMENSIONS OF *SYNCERUS* SP. MANDIBULAR CORPORA FROM MELKBOS, COMPARED WITH THOSE OF A *SYNCERUS CAFFER* SPECIMEN.

	Mb 67	Mb 144*	Mb 608	M 147‡
Maximum height below M_3	81·0	c75·0	89·0	67·6
Maximum width below M_3	43·2	c36·0	c47·0	30·7
Maximum height below P_3	64·4	—	—	57·2
Maximum width below P_3	32·5	—	—	23·4

* Immature individual.

‡ Large ♂ *Syncerus caffer*.

Mb 67—(table 9)—The almost intact corpus of a right mandible lacking all the teeth.

Mb 144—(tables 9 & 10)—A left mandible, lacking that part of the corpus anterior to the M_1, but otherwise intact. The M_1, M_2 and M_3 are well preserved but incompletely erupted.

Mb 4—(table 10)—An incomplete right mandible with the M_2 and M_3 preserved.

Mb 220—Incomplete left mandible with poorly preserved M_2 and M_3.

Mb 465—(table 10)—An incomplete left mandible with P_3, P_4 and M_1, and associated M_2 (Mb 464A) and M_3 (Mb 464B).

In addition to the above material, ten isolated lower and four upper teeth belonging to this genus were recovered.

A large number of elements of the postcranial skeleton were also recovered, but they were not studied in detail.

Morphologically the lower teeth of the Melkbos buffalo are indistinguishable from those of the extant *S. caffer*.

The premolars were similar in size to those of the single comparative specimen available, but the molars were, in general, significantly larger (table 10). The mandibular corpora of the fossil specimens were considerably more robust than that of the single comparative specimen, which belongs to a large male. The greatest size difference was in the region posterior to the premolar series. None of the lower teeth approached those of '*Homoioceras*' in size, but the posterior parts of the corpora corresponded fairly closely to those of the smaller '*Homoioceras*' specimens from Elandsfontein.

Discussion

Published records of the fossil buffaloes of southern Africa are very limited, although a large amount of material is available for study. The Pleistocene longhorned forms from this region are now almost invariably referred to '*Homoioceras bainii*', in spite of the fact that the original description of this species ('*Bubalus*' *bainii* Seeley, 1891) is very inadequate, and the generic designation (Bate, 1949 & 1951) is based on inference rather than actual study of available material.

The relationship between the southern African '*Homoioceras*' and the extant *Syncerus* is not at all clear, and consequently speculations on the affinities of the Melkbos buffalo to these two forms are somewhat premature at this stage. There is, however, little doubt that the Melkbos material will be of great importance in any future consideration of the phylogeny of the African buffaloes. The admittedly inadequate comparisons with *S. caffer* and '*Homoioceras*' specimens made in the course of the present study, suggest that it is 'intermediate' between the two forms in many respects. A more detailed comparative study must inevitably be hampered by the limited amount and condition of the cranial material from Melkbos, but a clearer appreciation of the characteristics

TABLE 10

DIMENSIONS OF *SYNCERUS* SP. LOWER TEETH FROM MELKBOS, COMPARED WITH THOSE OF A *SYNCERUS CAFFER* SPECIMEN.

	P_2		P_3		P_4		M_1			M_2			M_3		
	l	b	l	b	l	b	l	bm	bd	l	bm	bd	l	bm	bd
Mb 608	15·5	10·8	20·6	15·6	23·4	17·1	33·5	21·3	22·2	34·7	23·4	23·0	45·2	21·7	c20·0
Mb 464 A	—	—	—	—	—	—	—	—	—	33·2	21·1	21·8	—	—	—
Mb 464 B	—	—	—	—	—	—	—	—	—	—	—	—	c44·7	22·1	21·2
Mb 465	—	—	18·4	13·9	22·1	c17·0	29·2	—	—	—	—	—	—	—	—
Mb 144 (^{1})	—	—	—	—	—	—	c35·0	20·0	21·1	39·9	19·7	20·1	c50·0	—	c20·0
Mb 4 (^{1})	—	—	—	—	—	—	—	—	—	34·7	—	—	c40·0	—	—
Mb 604	—	—	20·2	14·9	—	—	—	—	—	—	—	—	—	—	—
Mb 557	—	—	c19·5	c14·3	—	—	—	—	—	—	—	—	—	—	—
M 147*	16·0	9·4	21·7	12·9	22·8	16·8	c24·8	16·3	18·4	30·0	19·2	20·3	42·9	19·4	19·7

(1) Dimensions given are not true maxima since teeth incompletely erupted; on all other teeth maximum dimensions taken near base of crown.
* Large ♂ *Syncerus caffer*.

and status of the Elandsfontein buffalo will enable a more objective analysis of the Melkbos material to be made.

It was considered that adequate grounds exist at present for assigning this material to the genus *Syncerus*. The size differences alone cannot justify an alternate conclusion, and while other critical differences may be revealed when more complete skulls are known, the available evidence suggests that the material belongs to what is merely an extremely robust buffalo of the *Syncerus* type.

Family **Bovidae**

Tribe *TRAGELAPHINI*

Tragelaphus cf. *strepsiceros* Pallas

The specimens tentatively assigned to this species are few in number, and almost all are poorly preserved. They are, however, of particular interest since they provide an additional record of an apparently extinct form of koodoo, which inhabited the south-western Cape in later Pleistocene times.

Material

Mb 134—The incomplete horn cores and frontlet of a large male, rather poorly preserved and reconstructed in part. The horn cores are robust, their diameter at the pedicle being comparable to those of the largest of the modern Greater Koodoo (*T. strepsiceros*) specimens available. Although only a part of their original length is preserved, it is evident that the helices had a considerably shorter pitch than those of the modern species. This feature is also apparent in the koodoo horn cores recovered at the Elandsfontein site.

Mb 24—The fragment of a left horn core, also with a tighter spiral than that of *T. strepsiceros.*

Mb 388—The fragment of a left frontal and horn core.

Mb 135 A–E—(table 11)—A series of left upper cheek teeth (P^3–M^3), recovered in association with Mb 134, and belonging almost certainly to the same large male. Comparison with the upper cheek teeth of three male *T. strepsiceros* specimens revealed that morphologically the teeth are indistinguishable, but that they are significantly shorter, with the exception of the P^4. A similar disparity in tooth size is observed in the Elandsfontein koodoo material.

Discussion

The limited amount and condition of the material available precludes the possibility of establishing the specific status of the Melkbos koodoo. The differences from the extant *T. strepsiceros*, which it shares with material from the Elandsfontein site, strongly suggest that it belongs to a form at least subspecifically distinct from the modern southern African koodoo. It clearly has greater affinities with this form than with the Lesser Koodoo (*T. imberbis.*)

A detailed study of the Elandsfontein material, which is more abundant and, in general, better preserved, should resolve the question of the classification of this fossil form.

TABLE 11

DIMENSIONS OF MELKBOS *TRAGELAPHUS* CF. *STREPSICEROS* UPPER TEETH, COMPARED WITH A SERIES OF THOSE OF THREE MODERN KOODOO.

		Mb 135	*Tragelaphus strepsiceros*	
			Mean	Range
P^3	l	14·8	17·5	16·9–18·0
	b	16·0	16·7	—
P^4	l	14·0	14·8	13·8–16·1
	b	16·3	17·6	16·9–18·7
M^1	l	18·4	21·7	20·0–22·7
	bm	20·2	20·6	19·1–22·4
	bd	19·9	20·3	19·2–21·7
M^2	l	23·4	26·5	25·9–26·9
	bm	23·1	23·3	22·0–24·8
	bd	21·7	22·4	21·7–23·3
M^3	l	25·0	28·7	28·0–30·1
	bm	21·7	22·8	22·0–23·5
	bd	17·8	21·1	20·8–21·3

Family **Bovidae**

Tribe *TRAGELAPHINI*

Taurotragus oryx Pallas

Eland

The eland is poorly represented in the assemblage, and only four specimens, none of which show appreciable differences from the extant form, were assigned to this species.

Mb 70—(table 12)—The complete horn cores and frontlet of a large adult individual, and the best preserved of all the antelope cranial material recovered at the site.

TABLE 12

DIMENSIONS OF MELKBOS *TAUROTRAGUS ORYX* HORN CORES AND FRONTLET.

		Mb 70
Skull width at horn pedicles		170·0
Base of right horn core	A/P diameter	77·0
	Transverse diameter	66·0
Distance between tips of horn cores		350·0
Maximum length of left horn core		510·0

Mb 589—A horn core fragment.

Mb 11—A mandible fragment with a single damaged molar.

Mb 10—A mandible fragment with incomplete M_1 and M_2.

Family **Bovidae**

Tribe *REDUNCINI*

Redunca arundinum Boddaert

Reedbuck

The reedbuck is the most commonly represented antelope in the assemblage. Eighteen horn cores, mostly incomplete, were recovered, and these did not differ in any observable respect from those of the extant species (table 13) Also recovered were an incomplete M^1 or M^2, and a fragment of mandible (Mb 215A & Mb 123).

Table 13

DIMENSIONS OF MELKBOS *REDUNCA ARUNDINUM* HORN CORES, COMPARED WITH THOSE OF A SERIES OF FOUR MODERN SPECIMENS.

	Melkbos specimens			Modern *R. arundinum*	
	Mean	Range	No. measured	Mean	Range
A/P diameter	33·4	28·0–38·0	6	35·1	31·9–38·0
Transverse diameter ...	33·8	30·0–38·7	13	34·3	32·2–36·6

This material may well have affinities with the reedbuck from the Swartklip sites (Hendey & Hendey, 1968), which, although on the basis of horn cores is indistinguishable from the modern species, appears to differ from it in other respects. However, at present there are no adequate grounds for separating the Melkbos reedbuck from *R. arundinum.*

Family **Bovidae**

Tribe *HIPPOTRAGINI*

cf. *Hippotragus* sp.

Two specimens in the assemblage were doubtfully ascribed to the genus *Hippotragus.*

Mb 122—A right dp_4 in an advanced state of wear, and which corresponds fairly closely in most respects to the dp_4 of a mandible from the Elandsfontein site (12209) that has been tentatively ascribed to *Hippotragus.*

Mb 1—(table 14)—An incomplete right mandible with the M_2 and M_3, roots of the P_4 and M_1, and alveoli of the P_2 and P_3. The ascending ramus and the most anterior part of the corpus have been lost. In size the corpus and teeth are similar to those of a *Syncerus caffer* specimen (M 147, see tables 9 and 10), but the teeth are hippotragine rather than syncerine in character. The mesial enamel plication of the M_2 and M_3, a characteristic of hippotragines but not present in *Syncerus*, does not extend through the entire crown height, and would have become less pronounced as wear on the teeth progressed and would have disappeared completely even when an appreciable amount of the crowns remained. In all the hippotragine comparative specimens examined, this accessory fold extended through the entire crown height.

TABLE 14

DIMENSIONS OF MELKBOS CF. *HIPPOTRAGUS* SP. TEETH AND MANDIBLE.

	Mb 1			Mb 1
Height of corpus below M_3	73·5	M_2	l	c32·4*
Width of corpus below M_3	c33·3		bm	15·7 (20·8)‡
Height of corpus below M_1	55·7		bd	15·6 (19·0)
Width of corpus below M_1	34·0	M_3	l	c37·5
Height of corpus below P_3	48·3		bm	14·5 (18·0)
Width of corpus below P_3	25·9		bd	15·5 (17·8)
		P_2–M_3 alveolar	l	161·7

* Measurements at the occlusal surface.
‡ Maximum dimensions near base of crown.

A giant hippotragine is known from the Pleistocene of Africa (*Hippotragus gigas* Leakey, 1965), and this species is thought to be present in the Elandsfontein assemblage. It is possible that the specimen Mb 1 has affinities with this form.

Family **Bovidae**
Tribe *ALCELAPHINI*
cf. *Connochaetes* sp.

A total of six horn core fragments and seven teeth from the assemblage were tentatively assigned to the genus *Connochaetes* (*sensu lato*). Attempts to place this material specifically were inconclusive.

Family **Bovidae**
Tribe *NEOTRAGINI*
Raphicerus sp.

The neotragine group of antelopes is represented in the assemblage by a single poorly preserved horn core (Mb 29). It is indistinguishable in all observable respects from the horn cores of the extant species, *R. campestris* and *R. melanotis*, both of which occur in the south-western Cape today.

Family **Bovidae**
Tribe *ANTILOPINI*
cf. *Antidorcas* sp.

A pair of incomplete horn cores (Mb 177 E and F) were doubtfully ascribed to the genus *Antidorcas*. Little of the right horn core is preserved and observations were confined to that from the left (Mb 177E).

The antero-posterior axis of the horn core is at an angle to the median line of the skull, the orientation in this respect being as in *A. marsupialis*. In the vertical sense its angulation begins as in *A. marsupialis*, but unlike this species it does not curve posteriorly, remaining instead remarkably straight along its entire length. In this respect it corresponds more closely to the form of the horn cores of *A. marsupialis australis* from Swartklip (Hendey & Hendey, 1968).

It also corresponds closely in size to the horn cores of the males of the Swartklip subspecies, having an anteroposterior diameter of c27·5 mm and a transverse diameter of c24·0 mm at the pedicle. The transverse compression of the core expressed as a percentage (Gentry, 1964) is 87·3, which is within the range of variation encountered in the modern *A. marsupialis*. In vertical section the inter-frontal plane is almost identical to that of the Swartklip specimen ZW 67*a*.

Only the marked straightness of this specimen is not in keeping with the horn cores of *Antidorcas*, and it is possibly a feature of an isolated aberrant individual, but until other specimens are recovered, the tentative diagnosis must stand.

Family **Bovidae**

Incertae sedis

In addition to the material already described, sixteen incomplete teeth, two incomplete mandibles and two horn core fragments were recovered. None of these specimens suggest the presence of a form other than those already listed.

No attempt was made to classify the large number of bovid postcranial bones recovered at the site.

Family **Bathergidae**

Bathyergus suillus Schreber

Cape Dune Mole

An almost complete skeleton (Mb 173) and an isolated lower incisor (Mb 49) of *Bathyergus* were recovered at the site. Although the condition of these specimens resembled that of the other fossils, it is possible that they are recent intrusive elements in the assemblage. The dune mole is common in the area today, and skeletons, or parts thereof, of recently dead individuals have been recovered at the site. It is possible that such remains which become buried may take on the appearance of the other fossils simply by becoming discoloured.

Intrusive elements at surface sites such as Melkbos can often not be detected without resort to chemical analyses, and since none were carried out in conjunction with the present survey, the status of these questionable elements in the assemblage remains uncertain.

Class *REPTILIA*

Order **CHELONIA**

Incertae sedis

Fifty fragments of carapace, probably all belonging to land tortoises, were included in the assemblage, but no attempt was made to classify them.

Class *AVES*

Family **Struthionidae**

Struthio australis

Ostrich

The ostrich is represented in the assemblage by two first phalanges (Mb 496 A & B), which are indistinguishable in all observable respects from those of the extant species.

Discussion of the Fauna

There are a number of sites in the south-western Cape Province which have yielded mammalian fossils, and while the study of the fauna of these sites is still in progress, it is apparent that in time they span the greater part of the Quaternary. Most attention has been focused upon the fossil occurrences at Langebaanweg, Elandsfontein (Hopefield), Melkbos and Swartklip, and the fauna of these sites is now moderately well known (table 15).

The Langebaanweg sites are both the earliest and potentially the most important of them all. They date probably from 'the earliest phases of the Pleistocene' (Boné & Singer, 1965), and have yielded a number of archaic forms, such as *Hipparion*, *Anancus*, *Stegolophodon*, an agriotheriine bear and a nimravine. The fossils have been recovered in the course of the mining of phosphate by the African Metals Corporation (Singer, 1961), and most of the material recorded to date has come from three quarries, viz. Baard's, 'E' and 'C' Quarries. The deposits in Baard's Quarry are apparently largely fluviatile, those in 'E' Quarry are estuarine and in 'C' Quarry there is a mixture of marine and estuarine sediments. The mammalian faunas from the three quarries are apparently at least broadly contemporary. The fossils have no known archaeological associations.

The fauna of the Elandsfontein site is the best known in the region (cf. Singer, 1962 for references), and the geology and archaeology of the site have recently been the subject of intensive study (H. J. Deacon and J. Wymer, in preparation). The fauna includes a number of extinct genera and species, but modern forms, or forms only subspecifically distinct from them, are well represented. The date usually used in reference to the fauna of this site is late Middle / early Upper Pleistocene (Boné & Singer, 1965), but it is possible that later elements occur in accidental association with the main body of fossils (Inskeep & Hendey, 1966). Artefacts of three industrial complexes have been recovered at the site, with the main faunal element apparently associated with an evolved Acheulian ('Fauresmith') industry (Howell & Clark, 1963; J. Wymer, pers. comm.).

The sites at Swartklip, which are late Pleistocene or Recent in age, have yielded a fauna made up almost entirely of modern forms (Hendey & Hendey, 1968). These sites have no certain cultural associations, but tenuous links with the Late Stone Age and historic times (Post-1652 A.D.) have been suggested.

TABLE 15

THE FAUNA OF THE PRINCIPAL FOSSIL SITES OF THE SOUTH-WESTERN CAPE PROVINCE.

	Langebaanweg			Elandsfontein (Hopefield)	Melkbos	Swartklip
	Baard's Quarry	'C' Quarry	'E' Quarry			
Class *MAMMALIA*						
Order ARTIODACTYLA						
Family **Hominidae**						
**Homo sapiens rhodesiensis*				×		
Family **Cercopithecidae**						
**Simopithecus oswaldi hopefieldensis*				×		
Order PHOLIDOTA						
Manis sp.				×		
Order CARNIVORA						
Family **Mustelidae**						
Mellivora capensis				×		×
**Aonyx* sp.						×
Family **Canidae**						
Subfamily **Caninae**						
Canis mesomelas				×	cf.	cf.
Canis adustus				×		
**Canis* sp.				cf.		cf.
**Canis* sp.			×			
Subfamily **Simocyoninae**						
**Lycaon pictus magnus*				×		
Lycaon pictus						×
Family **Ursidae**						
Subfamily **Agriotheriinae**						
*cf. *Agriotherium* sp.			×			
Family **Viverridae**						
Herpestes ichneumon				×		×
Family **Felidae**						
Subfamily **Felinae**						
Felis serval				×		cf.
Felis caracal				×		
**Felis* sp.			×			
Felis leo						×
**Felis leo* aff. *spelaea*				×	×	
Subfamily **Machaerodontinae**						
**Megantereon* cf. *gracile*				×		
Subfamily **Nimravinae**						
**Dinofelis* sp.			×			
Family **Hyaenidae**						
Hyaena brunnea				×	cf.	×
**Hyaena* sp.		×	×			
**Crocuta crocuta spelaea*				×		
Order PINNIPEDIA						
Family **Otariidae**						
? *Arctocephalus pusillus*					×	
*cf. *Arctocephalus* sp.	×	×	×			

Table 15 — *cont.*

	Langebaanweg			Elandsfontein (Hopefield)	Melkbos	Swartklip
	Baard's Quarry	'C' Quarry	'E' Quarry			
Order PROBOSCIDEA						
Family **Gomphotheriidae**						
**Anancus* sp.			×			
Family **Elephantidae**						
**Stegolophodon* sp.	×					
**Stegodon* sp.	○	○				
*cf. '*Archidiskodon*' sp.	○	○				
*'*Archidiskodon*' *broomi*				×		
*'*Loxodonta*' *zulu*				×		
? *Loxodonta africana*					×	
Order PERISSODACTYLA						
Family **Rhinocerotidae**						
Diceros bicornis	×		×	×	×	
Diceros simus	×			×	×	×
* ? *Diceros* sp.	×					
Family **Equidae**						
**Hipparion albertense baardi*	×	×	cf.			
**Equus plicatus*				×		
**Equus helmei*	○	○		×		
Equus sp.					×	×
Order ARTIODACTYLA						
Family **Suidae**						
**Mesochoerus lategani*				×		
**Mesochoerus paiceae*				×		
**Tapinochoerus meadowsi*				×		
**Incertae sedis* (2)			×			
Family **Hippopotamidae**						
Hippopotamus amphibius	cf.	cf.		×	×	cf.
Family **Giraffidae**						
**Libytherium olduvaiense*	×		×	×		
**Giraffa gracilis*			cf.	cf.		
Family **Bovidae**						
**Tragelaphus* cf. *strepsiceros*				×	×	
Taurotragus oryx				×	×	
*'*Homoioceras bainii*'				×		
**Syncerus* sp.					×	
Redunca arundinum				×	×	
Redunca cf. *arundinum*						×
**Redunca* sp.	○	○	×			
**Hippotragus* cf. *leucophaeus*						×
**Hippotragus* spp.			cf.	×	×	
**Damaliscus* sp.	○	○				
**Damaliscus* sp.				×		
cf. *Connochaetes* sp.				×	×	×
**Lunatoceros* cf. *mirum*				×		
**Megalotragus* sp.				×		
cf. *Oreotragus* sp.	○	○				
Raphicerus sp.				×	×	×

Table 15 — *cont.*

	Langebaan-weg			Elandsfontein (Hopefield)	Melkbos	Swartklip
	Baard's Quarry	'C' Quarry	'E' Quarry			
Family **Bovidae** (*cont.*)						
**Antidorcas marsupialis australis*						×
**Antidorcas* sp.				×	cf.	
**Gazella* cf. *wellsi*				×		
**Gazella* spp.	×		×	×		
**Incertae sedis* (+1)			×	×		
Order **CETACEA**						
Incertae sedis			×			
Order **LAGOMORPHA**						
Lepus capensis				×		
Lepus sp.			×			
Order **RODENTIA**						
Family **Bathyergidae**						
Bathyergus suillus				×	×	×
Georychus cf. *capensis*				×		
Family **Hystricidae**						
Hystrix cf. *africae-australis*				×		
Family **Muridae**						
Otomys cf. *saundersiae*				×		
Parotomys cf. *brantsi*				×		
Incertae sedis (+1)			×			×
Class *REPTILIA*						
Order **CHELONIA**						
Incertae sedis (+1)	×	×	×	×	×	×
Class *AVES*						
Order **STRUTHIONIFORMES**						
Struthio australis			×	×	×	×
Incertae sedis (+1)			×	×		
Class *CHONDRICHTHYES*						
Several genera and species		×				
Class *OSTEICHTHYES*						
Several genera and species		×	×			

* Extinct forms.

○ Recorded from 'Langebaanweg'; from either Baard's Quarry, 'C' Quarry or both.

The Melkbos fauna has essentially the same 'modern' character as that from Swartklip, but it includes elements such as the lion, hyaena and koodoo, which have affinities to forms from Elandsfontein. In addition, the buffalo and ? hippotragine antelope from Melkbos are extinct forms not represented in the Swartklip assemblage, and it is concluded that the Melkbos fauna predates that from Swartklip. The archaeological associations of these two sites, while too dubious to be of real value, do at least suggest an age difference in the right order. Since none of the extinct genera of the Elandsfontein fauna (*Simopithecus*, *Mesochoerus*, *Megantereon*, etc.) occur at Melkbos, the fauna of the latter site almost certainly post-dates the main Elandsfontein fauna.

These four sites have yielded widely different numbers of specimens, ranging between about 600 from Melkbos to about 20,000 from Elandsfontein, and they have been studied with varying degrees of thoroughness. Nevertheless, it is concluded that there are sufficient grounds for considering Melkbos to be intermediate in age between Elandsfontein and Swartklip, and that these three occurrences date from the latter part of the Quaternary. The Langebaanweg fauna takes a more isolated position in the earlier part of the Pleistocene.

Acknowledgements

Over the years many persons have presented fossils they had collected at the Melkbos site to the South African Museum. Without their interest and generosity this report would not have been possible. In this connection I wish particularly to mention Prof. R. Singer of the University of Chicago and Messrs. J. Rudner, H. G. A. Craye, R. R. Inskeep and G. Hoehn, all of Cape Town.

Prof. Singer kindly assisted and encouraged in many ways and I am especially grateful to him.

I wish also to thank Prof. L. H. Wells of the University of Cape Town for many helpful discussions.

Dr. E. C. Olson of the University of Chicago kindly read the manuscript and offered many useful suggestions.

The conclusions reached in this report do not necessarily reflect the views of any of these people.

Finally I wish to thank my wife who was a constant source of encouragement.

This study was supported in part by the U.S. Public Health Service grant no. G.M. 10113 to Prof. R. Singer, and the National Science Foundation grant no. B2453 to Dr. E. C. Olson.

Summary

The location, geological and archaeological associations, and fauna of a fossil site north of the town of Melkbosstrand, Cape Province is discussed. The remains of eighteen types of mammals, one bird and one tortoise are described or mentioned. It is concluded that the site dates from the latter part of the Upper Pleistocene, that it post-dates that at Elandsfontein (Hopefield), and is earlier than the Swartklip fossil sites.

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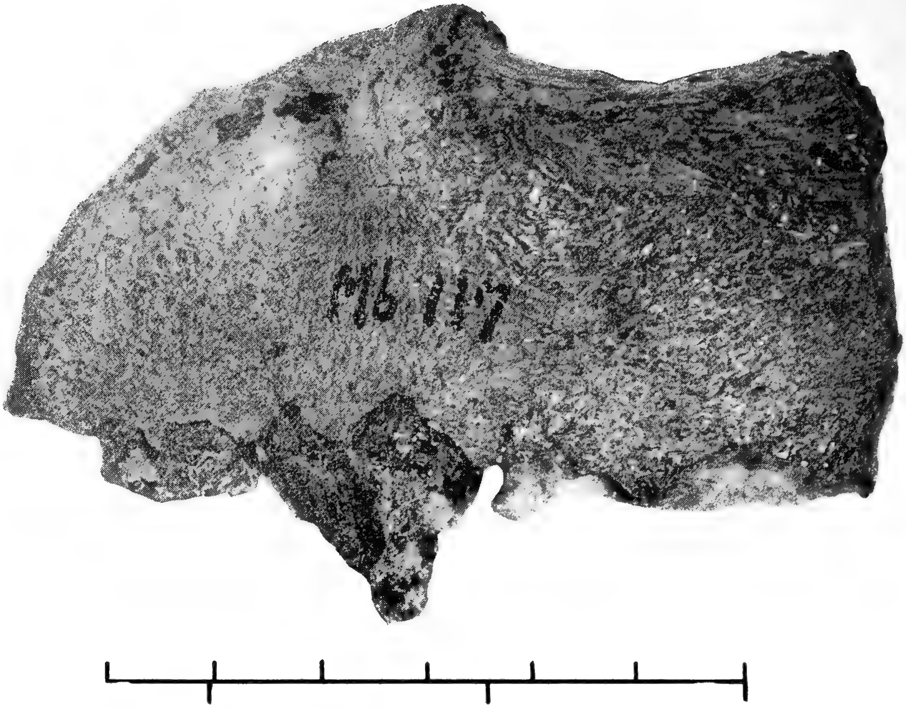
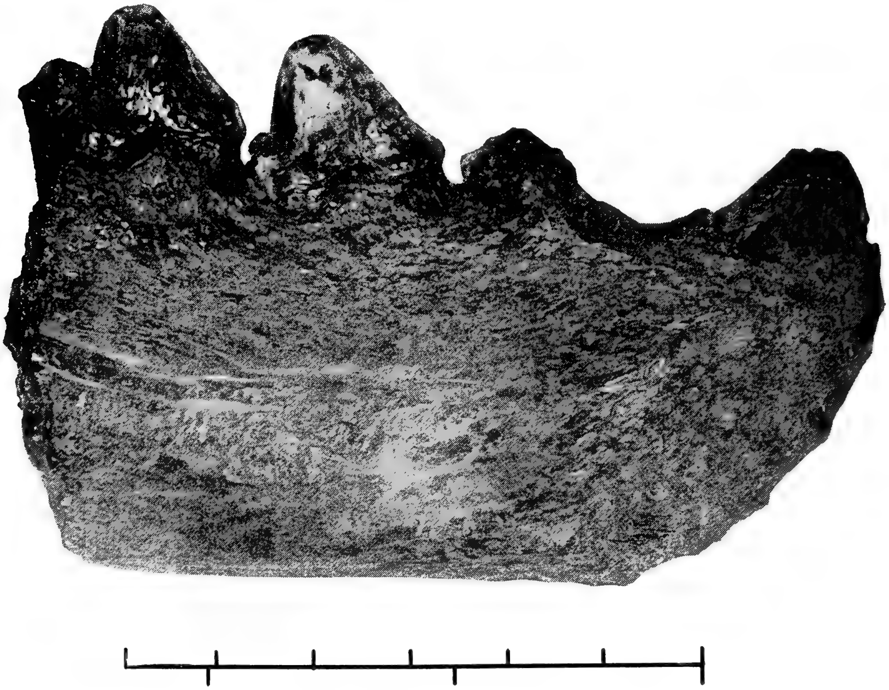
A—A view of the site showing recent dunes (background and left), and exposures of calcrete.

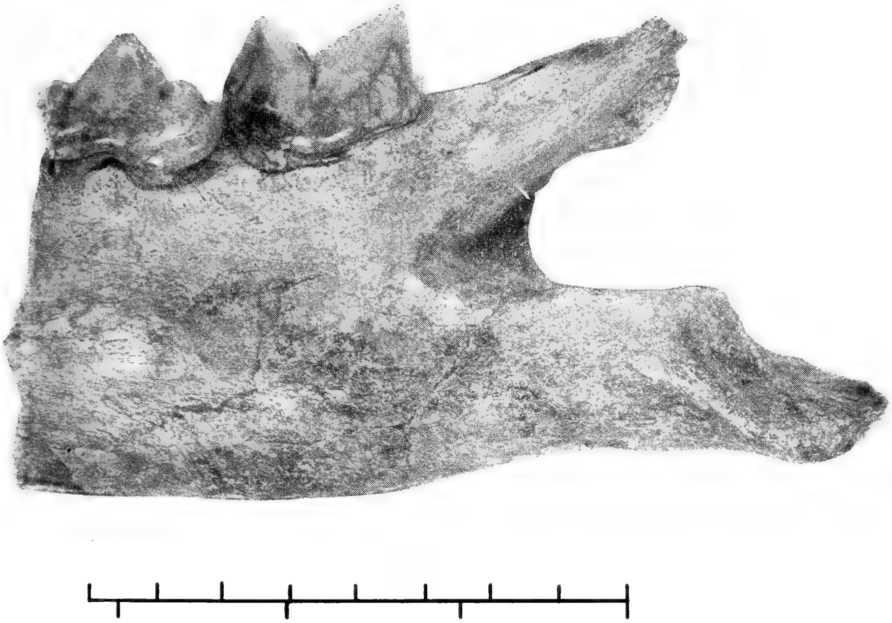
B—A typical surface on the site showing bone fragments and blocks of calcrete (top left).



A—Buccal view of *Hyaena* cf. *brunnea* maxillary fragment (Mb 117). (Scale in centimetres and inches.)



B—Lingual view of *Hyaena* cf. *brunnea* mandible fragment (Mb 116).



Buccal view of *Felis leo* aff. *spelaea* mandible fragment (Mb 143).

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Example

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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad
(Kontant met bestelling, posvry)

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(2, 5, 7–9), 6(1, t.–p.i.), 7(1, 3), 8, 9(1–2), 10(1–3), 11(1–2, 7, t.–p.i.), 21, 24(2), 27, 31(1–3), 38, 44(4).

Price of this part/Prys van hierdie deel

R1.85

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

A DOLPHIN (*STENELLA ATTENUATA*) FROM DURBAN, SOUTH AFRICA

By

Peter B. Best

South African Museum, Cape Town

(With plates 11–17 and 1 figure)

[*MS. received* 15 *January* 1968]

Contents

Introduction

On 4 July 1964, a female dolphin seven feet and half an inch long was stranded on Battery Beach, Durban, South Africa. Mr. J. Wallace of the Oceanographic Research Institute recognized the unusual appearance of the specimen and so preserved it entire in a deep-freeze. With the kind co-operation of the Institute, this dolphin was eventually presented to the South African Museum (catalogue number 35515) in September 1966, where on examination it proved to be a specimen of the narrow-snouted dolphin *Stenella attenuata* (Gray, 1846), the first recorded from South Africa for nearly 100 years.

External Appearance

Colour pattern. Mr. Wallace took several black and white photographs of the specimen while it was still fresh, and also made a pencil sketch of the distribution of pigment. Although the dolphin was subsequently in a frozen state for over two years, and was in fact pure black on arrival at the museum, immersion in water rapidly caused most of the original colour pattern to reappear. The distribution of pigment, therefore, has been accurately recorded, but less confidence can be placed in the colour tones attributed to these pigmented areas after two years in cold storage.

The dolphin was basically a dark slate-grey above and a light slate-grey below, the border between the two being fairly sharply defined in the anterior half of the body but less defined in the area behind the dorsal fin (fig. 1). A light grey band began just behind the apex of the melon and ran back above the eye,

Ann. S. Afr. Mus. **52** (5), 1969: 121–135, 7 pls, 1 fig.

Fig. 1

where it joined a similar-coloured band from the angle of the gape. This common band then passed back above the flipper, subsequently spreading out to cover the entire ventral surface as far as the base of the tail. There was no darkening or lightening of the grey pigment along the centre of the belly. The upper border of the light grey area continued along the body from the side of the head in a gradually downward-curving sweep, which in the region between flipper insertion and dorsal fin levelled out more than half-way down the side. Thereafter it curved up sharply at the level of the dorsal fin, the grey colour from each side meeting over the back about half-way between the dorsal fin and the tail. The portion of the back just anterior to the tail-stock, however, was dark slate-grey, giving the area of light grey pigment behind the dorsal fin the appearance of an upward-curving band. The remainder of the upper and lower surfaces of the tail flukes was dark slate-grey.

Both surfaces of the flippers were similarly coloured, and a dark streak ran from the flipper insertion to just below the angle of the gape, whence it extended as a black margin along the lower jaw to meet the corresponding band of the other side towards the jaw tip. The eye was ringed with dark slate-grey, and this extended forward as a narrow streak along the base of the melon. From each side of the apex of the melon a light grey streak ran back to the lateral margin of the blowhole, narrowing all the way.

The throat was chiefly light slate-grey in colour, but with yellowish-pink mottling extending as a widening band from each angle of the gape, forming a 'bridle' round the throat. The extreme tips of both upper and lower jaws were yellow-grey flecked with black, as were the inner margins of the lips and the palate, where the black flecks were larger. The tongue was a bright pink.

Small white flecks, mostly elongated in an anterior-posterior direction, and on average about three-sixteenths of an inch in diameter, were scattered over most of the body surface. They were less abundant on the throat and belly as far as the genital aperture, but were particularly numerous on the sides behind the dorsal fin and on the ventral caudal peduncle. There were no such markings on the rostrum or either side of the flippers and tail flukes, but there were a few at the base of the dorsal fin. A narrow area on the back from head to dorsal fin was also largely devoid of flecks.

Although the colour pattern in many *Stenella* species is either unknown or poorly described, this specimen was clearly separate from forms which are typified by a dark stripe down the side, such as *S. euphrosyne*, *S. lateralis*, *S. caeruleoalba* and *S. styx*. It also seemed distinct from *S. plagiodon*, which has a pure white belly and no stripe from the flipper to the angle of the mouth, and *S. graffmani*, which is coal black all over except for many whitish-grey spots, particularly on the back. Among other forms in which the colour pattern is known in some detail, the specimen most closely resembled *S. frontalis*, as described by Fraser (1950), and *S. attenuata*, as described by Nishiwaki, Nakajima & Kamiya (1965).

The colour description of the *Atlantide* dolphin, identified by Fraser (1950) as *S. frontalis*, agreed closely with the Durban specimen in both the distribution of major pigment zones and the colour values assigned to them. Thus the *Atlantide* dolphin was described as black above and a dark grey below, the boundary between the two zones following the same curve down the body as in the Durban specimen. The colour of the dorsal fin, tail flukes and flippers was identical in the two animals, and the *Atlantide* dolphin also had a dark stripe from the flipper to the angle of the mouth, and a dark ring round the eye which extended forward to the base of the snout. Similar irregular light grey flecks covered the back, and white flecks were present on the belly.

The two specimens differed, however, in the colour of the snout and lower jaw. Whereas the *Atlantide* dolphin had the distal third of the snout whitish-pink in colour, only the extreme tip of the snout of the Durban dolphin was light in colour, being a yellowish-grey flecked with black. Similarly, the forward end of the lower jaw was described as white with dark spots posteriorly in the *Atlantide* dolphin, whereas the Durban specimen only had the extreme tip of the lower jaw yellowish-grey flecked with black. In both dolphins, however, the light colour anteriorly was continued as a narrow band along the margin of upper and lower jaws as far as the angle of the gape.

The band of yellowish-pink mottling on the throat of the Durban specimen was absent in the *Atlantide* dolphin.

Apart from these differences in the colour of the snout and lower jaw, the only other features of body coloration that differed were the presence of abundant dark spots on the belly and a narrow band of lighter grey mid-ventrally, both of which were present on the *Atlantide* dolphin but not seen on the Durban dolphin.

Nishiwaki, Nakajima & Kamiya (1965) described a number of dolphins from Arari, Japan, which they identified as *S. attenuata*. The colour pattern as figured and described for these dolphins agreed in almost every detail with that of the Durban specimen. The only discernible difference appeared to be in the extent of light pigment on the snout and lower jaw, which was greater in the Arari dolphins but at the same time was considerably less than in the *Atlantide* dolphin. Nevertheless, this was a variable feature, Nishiwaki *et al.* remarking that such white tips to the snout were absent in foetuses and new-born calves. Consequently both the Arari and Durban dolphins differed from the *Atlantide* specimen in the extent of white on the snout, in having a 'bridle' of light mottling, and in lacking dark spots on the belly and a lighter mid-ventral area. *Body proportions.* In general shape the Durban dolphin resembled many other species of *Stenella* and *Delphinus* in possessing a slender, streamlined body, a narrow beak clearly separated from the rest of the head, small curved flippers and a centrally-placed, recurved dorsal fin. A series of 32 body measurements were made of the Durban specimen, and these, expressed as percentages of the body length, have been compared with similar measurements recorded for the *Atlantide* dolphin (Fraser, 1950) and for the Arari dolphins (Nishiwaki *et al.*, 1965) in table 1.

All but two measurements of the Durban dolphin fell within the range of the Arari dolphins, but in nearly every case they were nearer the lower end of the range. The two exceptions were the length of the dorsal fin base and the width of the tail flukes, the first of which was less and the second of which was greater than that recorded for any Arari dolphin. The base of the dorsal fin in the Durban dolphin was prolonged posteriorly as a narrow ridge along the caudal region, and so its actual length was extremely hard to judge. For this reason the posterior end of the base was arbitrarily fixed as that point immediately below the tip of the dorsal fin, and so this measurement was probably not directly comparable to that recorded for the Arari or *Atlantide* dolphins. The relative width of the tail flukes in other dolphins is known to increase with the size of the animal, and as the Durban specimen was larger than any measured at Arari this probably accounts for the greater width of the tail flukes. In most respects, therefore, the Durban dolphin could be considered as indistinguishable in body proportions from those collected at Arari.

Ignoring the length of the dorsal fin base, the *Atlantide* dolphin apparently differed from both the Durban and Arari dolphins in having a shorter beak (measurement number 3) and an anus situated farther forward. However, the position of the latter was fixed differently in the *Atlantide* specimen, the measurement being taken from the notch of the flukes rather than from the tip of the snout, and this may have introduced some disparity. Nevertheless, the *Atlantide* dolphin seems to be clearly separated from the Durban and Arari dolphins by its shorter beak.

Skeleton

Skull. The skull and mandibles of the Durban dolphin are shown in plates 11 and 12.

The right premaxilla extended back about 15 mm farther than the left, and was considerably wider at its termination. Unlike the *Atlantide* dolphin, neither premaxilla came into contact with the nasal bones posteriorly, there being a clear wedge of the maxillary bone 4 to 5 mm wide between the tip of the right premaxilla and the nasal. As in the *Atlantide* dolphin, the prenarial triangle was concave and the apical portions roughened. The lateral margins of the triangle were also elevated above and overhung the adjacent areas of the maxillae, particularly at the level of the anterior margin of the superior nares, Body measurements of the Durban dolphin with those of *S. frontalis* and *S. attenuata* for comparison.

Measurement	Durban dolphin ♀		*Atlantide* dolphin (*S. frontalis*) Fraser, 1950 ♂	Arari dolphins (*S. attenuata*) Nishiwaki *et al*., 1965 ♂♂		♀♀	
	in.	%	%	% Range	Mean	% Range	Mean
1. Total length	84·5	100	100	—	100	—	100
2. Tip of snout to centre of eye	12·0	14·2	14·3	13·5–16·3	15·3	14·0–17·7	15·7
3. Tip of snout to apex of melon	4·5	5·3	4·5	5·3–6·4	5·9	5·5–7·7	6·2
4. Tip of snout to blowhole	12·5	14·8	14·8	14·2–17·1	15·6	14·2–17·7	15·4
5. Tip of snout to angle of gape	10·3	12·2	12·0	11·0–14·4	12·9	11·7–14·5	13·3
6. Tip of snout to anterior insertion of flipper	15·8	18·7	19·1[1]	—	—	—	—
7. Tip of snout to tip of dorsal fin	48·5	57·4	—	—	—	—	—
8. Tip of snout to centre of genital aperture	59·5	70·4	—	—	—	—	—
9. Tip of snout to centre of anus	62·3	73·7	70·0[2]	73·5–74·8	74·3	72·8–74·8	73·7
10. Centre of eye to angle of gape	2·3	2·7	—	—	—	—	—
11. Centre of eye to centre of blowhole	5·8	6·9	—	—	—	—	—
12. Projection of lower jaw beyond upper	0·3	0·4	c. 0·25	—	—	—	—
13. Girth, at axilla	36·0	42·6	—	—	—	—	—
14. Girth, maximum (3 feet from snout)	40·5	47·9	46·5[3]	—	—	—	—
15. Girth, at anus	24·3	28·8	—	—	—	—	—
16. Flipper, anterior insertion to tip	10·8	12·8	12·0	14·4–15·1	14·8	12·0–15·2	13·6
17. Flipper, axilla to tip	7·4	8·8	8·5	10·1–10·7	10·4	8·5–10·4	9·5
18. Flipper, maximum width	3·6	4·3	4·5	5·0–5·3	5·2	4·2–5·3	4·7
19. Dorsal fin, height	7·1	8·4	8·0	8·2–9·7	9·0	7·8–9·4	8·4
20. Dorsal fin, length of base	10·0[4]	11·8	16·5	12·1–14·4	13·5	12·4–14·2	13·3
21. Tail flukes, width, tip to tip	20·0	23·7	22·0	21·6–22·5	22·1	21·3–23·5	22·4
22. Tail flukes, notch to nearest point on anterior border	4·5	5·3	—	—	—	—	—
23. Tail flukes, depth of notch	0·9	1·1	—	—	—	—	—
24. Eye, height	0·5	0·6	—	—	—	—	—
25. Eye, length	1·0	1·2	—	—	—	—	—
26. Right mammary slit, length	1·1	1·3	—	—	—	—	—
27. Left mammary slit, length	1·0	1·2	—	—	—	—	—
28. Ano-genital slit, length	6·0	7·1	—	—	—	—	—
29. Ano-genital slit, length including anterior groove	9·3	11·0	—	—	—	—	—
30. Anal opening, length	0·8	0·9	—	—	—	—	—
31. Blowhole, width	1·0	1·2	—	—	—	—	—
32. Blowhole, length	0·4	0·5	—	—	—	—	—

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[1] Obtained by subtracting length of flipper from distance 'tip of snout to tip of flipper'. [2] Obtained by subtracting distance 'notch of flukes to anus' from total length. [3] Site of measurement not recorded. [4] Distance from anterior insertion of dorsal fin to point vertically below fin tip (see text).

where they formed distinct promontories. The smooth rostral portions of the premaxillae were arched more prominently than either their roughened lateral portions or the adjacent maxillae. At the base of the rostrum the lateral margins of the maxillae were raised into a roughened ridge, as described for the *Atlantide* dolphin.

The palate conformed to the normal *Stenella* pattern in lacking a pair of longitudinal grooves. At its extreme anterior tip the palate was concave, and in profile curved slightly downward. The central region, however, was noticeably concave, bearing a strong median groove, but this closed up about 30 mm anterior to the hindmost tooth. The palate was then almost flat, but thereafter the centre rose rapidly as a prominence bearing the pterygoid bones. The pterygoids were closely apposed in the midline, their posterior margin being roughly bracket-shaped. The ventral surface of each bone was raised into a slight ridge which diverged posteriorly and became less prominent on the pterygoid wing. These ridges did not seem to be as well developed as in the *Atlantide* dolphin, and were placed nearer the midline. The inner edge of each tooth alveolus was raised up as a little cone-like ridge, and these formed a more or less continuous band along the whole tooth-row, being marked off anteriorly from the rest of the maxilla by a shallow groove.

The lower jaws were not ankylosed at the symphysis. The mandibular rami in lateral view seemed to be more curved than those figured for the *Atlantide* dolphin, and the tips were more tapered.

The dental formula, expressed in such a way as to indicate the normal-sized teeth and the smaller anterior teeth, was

$$\mathrm{R}\,\frac{37+4}{38+2} \qquad \mathrm{L}\,\frac{37+4}{37+2},$$

which hardly differed from that of the *Atlantide* dolphin, and fell well within the range of $\frac{38–45}{36–43}$ given for the Arari dolphins.

A series of 20 measurements were made of the skull and mandibles of the Durban dolphin (table 2).

In a comparison of the skull of the *Atlantide* dolphin with 30 other similar specimens, among them the types of *Delphinus attenuatus*, *Steno capensis*, *Delphinus doris*, *Delphinus frontalis* and *Delphinus fraenatus*, Fraser (1950) was able to separate the skulls into two groups from the shape of the rostrum distally: this was best expressed by the width of the rostrum at a quarter its length from the tip. One of these groups, including the types of *frontalis*, *fraenatus* and *doris* and the *Atlantide* specimen, could be distinguished by a distinctive range in six other measurements from the second group which included the types of *attenuatus* and *Steno capensis*. In this way it was possible to state that in the *frontalis* group the rostrum at the middle, the zygomatic, preorbital, postorbital widths and the premaxillary width proximally were all greater than in the *attenuata* group, and the height of the mandible at the coronoid process also seemed to be greater in the *frontalis* group.

TABLE 2

Skull measurements of the Durban dolphin with those of *S. attenuata*, *S. frontalis* and *S.* cf. *capensis* for comparison.

Measurement	Durban dolphin		Arari dolphins (*S. attenuata*) Nishiwaki *et al.*, 1965		*S. attenuata* group Fraser, 1950		*S. frontalis* group Fraser, 1950		*S.* cf. *capensis* (St. Helena) Fraser, 1966	
	mm	%	% Range	Mean	% Range	Mean	% Range	Mean	% Range	Mean
1. Total length	415	100	—	100	—	100	—	100	—	100
2. Rostrum length	251	60·5	57·8–61·5	59·9	59·5–61·9	61·1	56·2–60·0	57·9	56·7–61·3	58·7
3. Rostrum width at base	87	21·0	21·5–23·3	22·4	19·9–22·3	21·1	20·3–24·0	22·1	20·0–23·9	21·6
4. Rostrum width at middle	45	10·8	10·8–12·1	11·3	9·0–10·9	9·9	11·1–13·8	12·3	—	—
5. Rostrum width 60 mm in front of antorbital notches	62	14·9	14·2–15·4	14·9	13·0–15·8	14·0	14·2–17·2	15·6	13·2–16·1	14·2
6. Rostrum width ¾ length	32	7·7	7·5–8·1	7·7	6·1–7·1	6·6	7·9–10·1	8·9	—	—
7. Preorbital width	154	37·1	38·7–42·8	40·0	35·4–38·2	36·8	38·4–42·7	40·3	35·6–42·0	38·0
8. Postorbital width	177	42·7	42·2–45·9	43·7	39·5–42·9	41·2	43·7–47·7	45·4	40·7–45·1	42·7
9. Zygomatic width	177	42·7	37·3–42·6	39·7	39·4–42·1	40·9	43·4–47·7	45·2	39·7–45·1	42·4
10. Parietal width	138	33·3	35·3–39·1	36·8	32·1–36·3	34·0	34·1–39·5	37·1	32·3–39·1	35·2
11. Maximum width of premaxilla proximally	68	16·4	16·6–18·4	17·6	15·5–16·7	16·0	17·4–21·0	18·6	15·8–18·4	17·0
12. Tip of rostrum to ant. margin superior nares	289	69·6	68·0–70·5	69·3	68·9–72·4	71·1	65·8–69·6	67·5	—	—
13. Tip of rostrum to end of pterygoid	299	72·1	70·1–73·0	71·4	69·7–73·2	71·7	67·6–71·2	69·6	—	—
14. Temporal fossa, length	70	16·9	13·4–14·7	14·1	14·4–18·2	15·9	15·2–19·3	17·1	—	—
15. Temporal fossa, height	56	13·5	8·1–10·2	9·0	10·2–13·7	11·6	11·5–15·3	12·9	—	—
16. Hinder end of tooth row to tip of premaxilla (R)	216	52·1	48·7–52·6	51·0[1]	51·5–53·4	52·4	46·3–52·5	49·9	47·0–53·5	50·0
do. (L)	217	52·3	48·0–52·3	50·9[1]					47·0–53·0	49·9
17. Mandible length (R)	347	83·6	83·8–90·3	85·8[1]	84·2–85·8	84·9	81·3–86·3	84·3	82·1–88·3	84·4
do. (L)	347	83·6	84·1–89·8	85·8[1]					81·6–88·0	84·5
18. Coronoid height (R)	62	14·9	14·3–15·4	14·8[1]	13·5–14·6	14·0	14·7–16·4	15·4	13·6–16·4	14·6
do. (L)	61	14·7	14·0–15·2	14·7[1]					13·2–16·0	14·4
19. Hinder end of tooth row to tip of mandible (R)	207	49·9	49·3–51·6	50·5[1]	49·1–52·6	50·9	46·9–52·0	48·7	46·7–53·5	49·4
do. (L)	208	50·1	49·5–51·9	50·5[1]					46·1–53·5	49·2
20. Length of symphysis	81	19·5	16·0–18·8	17·3	—	—	—	—	13·6–19·2	16·7

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[1] Maximum reading for each specimen, whether right or left.

When the measurements of the skull and mandibles of the Durban specimen, expressed as percentages of the skull length, were compared with those recorded for the *frontalis* and *attenuata* groups by Fraser (1950), it was immediately obvious that the specimen had a greater affinity to the *attenuata* group. Of 18 of the measurements, nine fell exclusively within the range recorded for the *attenuata* group, while five were shared by both groups. Only two measurements (numbers 17 and 18) fell exclusively within the range of the *frontalis* group, both being measurements referring to the mandible. However, two of the skull proportions used by Fraser to distinguish between the two groups, the zygomatic width and the rostrum width at three-quarters of its length, fell between the ranges for *frontalis* and *attenuata*.

When the skull measurements of seven dolphins from Arari (Nishiwaki *et al.*, 1965) were compared with the ranges recorded for the *frontalis* and *attenuata* groups, a similar overlap was found between the ranges of both groups in 13 of the 18 measurements. These included four of the proportions found by Fraser to be of diagnostic value in separating *attentuata* from *frontalis*: the rostrum width at the middle, the postorbital width, the premaxillary width proximally and the coronoid height of the mandible. Three additional measurements could be related only to the *attentuata* group, including the zygomatic width, while two were referable only to the *frontalis* range: the preorbital width and the rostrum width at three-quarters of its length.

The close similarity in external appearance between the Durban and Arari dolphins has already been established. Nevertheless, nine of the skull proportions of the Durban dolphin fell outside the range recorded for the Arari dolphins. These included three of Fraser's diagnostic measurements, the postorbital and zygomatic widths and the premaxillary width proximally. Consequently it appeared that the Durban skull bore a closer similarity to the specimens in Fraser's *attenuata* group than to the Arari dolphins. Neither the Durban nor the Arari dolphins, however, fully conformed with the skull proportions found by Fraser to be typical of *frontalis* or *attenuata*, the Arari specimens in fact appearing to occupy an intermediate position between the two groups.

Fraser (1966) has listed the skull proportions of a series of *Stenella* cf. *capensis* from around St. Helena in the South Atlantic. Twelve of the proportions recorded for the Durban dolphin, for which there were comparable data from St. Helena, fell within the range of the *S.* cf. *capensis* specimens. The only exception, the length of the mandibular symphysis, was a measurement which Fraser had stated to be only really useful for distinguishing species in which it is widely divergent. Seven of the 12 proportions in fact fell within the standard deviation of the means recorded for the St. Helena dolphins. Unfortunately, however, the external appearance of the St. Helena dolphins was unknown, but there seemed to be a close similarity between the skulls from this locality and the Durban specimen. It should be added that all of the skull proportions of *S.* cf. *capensis* straddled the ranges recorded for the *attenuata* and *frontalis* groups by Fraser (1950), even in the six measurements considered by Fraser to be of value in distinguishing between *frontalis* and *attenuata*.

Vertebral column. There were 78 vertebrae, the vertebral formula being as follows —cervical 7, thoracic 16, lumbar 19 and caudal 36. This contrasted with the number given by Fraser (1950) for the *Atlantide* dolphin, 81, composed of 7 cervical, 15 thoracic, 23 lumbar and 36 caudal, but was in close agreement with the formula given for the Arari dolphins (Nishiwaki *et al.*, 1965). According to these authors individual variation in the vertebral formula was very little, the typical column consisting of 7 cervical, 15–16 thoracic, 18–19 lumbar and 37 caudal, or a total of 78 vertebrae.

The epiphyses were fused to their centra throughout the vertebral column, indicating that the Durban dolphin had attained full physical maturity.

The atlas had a breadth of 84 mm between the outer margins of the articulating surfaces. The lateral processes were 25 mm long, and the length of the neural spine from its tip to the nearest point on the anterior edge of the neural canal was 47 mm. The neural spine bore a prominent central ridge about 3 mm high (maximum), and on each dorsal extremity of the articulating surfaces there was a sharp spine 4–5 mm long which projected towards the anterior edge of the neural canal (pl. 13).

The axis was fused with the atlas, only the neural arch being free laterally, as in both the *Atlantide* and Arari dolphins. The axis had a short, pointed lateral process to each side which was directed obliquely backwards and slightly upwards. These processes measured 6–7 mm in length, and so were somewhat shorter than those described for the *Atlantide* dolphin (13 mm).

Unlike the latter specimen, both the neural arch and centrum of the third cervical vertebra were free of the axis in the Durban dolphin. Such also appeared to be the case in the Arari dolphins. Cervical vertebrae 3 to 6 all had small neural spines, whereas the neural arch of cervical 7 was not complete but had a gap mid-dorsally and thus no spine: this feature is recorded for the *Atlantide* dolphin but not for the Arari dolphins. Nevertheless, evidence given by Fraser (1950) indicated that an incomplete neural arch to cervical 7 has been recorded for *Stenella graffmani* and *Delphinus delphis*, and so has little taxonomic significance. There were short lateral processes from the base of neural arches 3, 4 and 7, with only the very slightest indications of one on vertebrae 5 and 6. The process on cervical 7 was the largest of all, and the whole of the lateral wall of the neural arch was greatly widened. Lateral processes from the side of the centrum were clearly present in cervicals 5 and 6, with the faintest trace of one on cervical 3. Cervical 7 bore a lateral process low down on the right hand side of the centrum. As in the *Atlantide* and Arari dolphins, the lateral process on cervical 6 was the largest, being directed anteriorly and 10–12 mm in length. Cervical 7 also bore a facet on the centrum for the articulation of the first rib.

The neural spines of the remainder of the vertebral column sloped backwards as far as lumbar 8 (31 in the column), the ninth being vertical (pl. 14).

From lumbar 10 to caudal 15 (57 in the column), the spines were directed anteriorly, but caudal 16 was vertical. From there till caudal 25, which was the last vertebra bearing a distinguishable neural spine, they again sloped backwards. These facts agreed closely with the description for the *Atlantide* dolphin (Fraser, 1950).

The height of the neural spines increased rapidly from thoracic 1 to 15, but then remained more or less constant at 83–85 cm until lumbar 13, when their height decreased, slowly at first but rapidly after caudal 19. The spines on the thoracic vertebrae tended to be larger than in the *Atlantide* dolphin, those on the first, second, third, tenth and last respectively being 33, 43, 51, 70 and 83 mm, as compared to 29, 37, 47, 59 and 76 for the *Atlantide* dolphin.

Metapophyses were absent on the first two thoracic vertebrae, but slight prominences appeared in the relevant position on the third. This contrasted with Fraser's (1950) statement that metapophyses were lacking from the first three thoracic vertebrae of the *Atlantide* specimen. From thoracic 4 to 7 the metapophyses were well developed and separate from the prezygapophyses, but from thoracic 8 onwards these two processes were fused and have been termed metapophyses thereafter. They were developed as far back as lumbar 7 (30 in the column), and remained only as traces from lumbar 8 to 17. Metapophyses reappeared, however, on lumbar 18, and persisted as separate processes until caudal 17 (59 in the column). From caudal 18 onwards the processes from each side tended to fuse together, and the last vertebra bearing a trace of a metapophysis was caudal 23 (65 in the column, as in the *Atlantide* dolphin). The Durban specimen, therefore, seemed to have developed metapophyses on more vertebrae than the *Atlantide* dolphin, the central area of column where they persisted only as traces being ten vertebrae as opposed to 22 vertebrae (Fraser, 1950). The Arari dolphins seemed to have a similar greater development of metapophyses from the plates figured by Nishiwaki *et al.* (1965).

Transverse processes on the first four thoracic vertebrae were almost straight transverse, but from thoracic 5 onwards they projected obliquely backwards, particularly so in the caudal region. The last traces of transverse processes were found on caudals 18 and 19 (60 and 61 in the column). Fraser (1950) found the last traces of transverse processes on the 61st and 62nd vertebrae of the *Atlantide* specimen.

Arising close to the tip of the transverse process on the last lumbar vertebra there was a prominent ridge which ran obliquely backwards. On successive posterior vertebrae this ridge was situated closer to the centrum, and from caudal 7 onwards placed on the body of the centrum, rising dorsally to occupy a position either side of the base of the neural arch. The last trace of this ridge was found on caudal 22 (or 64 in the column). On caudals 2 to 6 the ridge was accompanied by a small anterior projection to the leading edge of the transverse process. A similar ridge and process has been described for the *Atlantide* dolphin (Fraser, 1950).

Vertically perforating foramina for blood vessels started on caudal 13

(55 in the column), as compared to the 56th vertebra of the *Atlantide* specimen.

The first chevron bone was found immediately below the centrum of the 44th vertebra in the column, but appeared from its position and structure to consist of two adjacent chevron bones fused in an anterior-posterior direction. Consequently, the first caudal vertebra was considered as number 43 in the column. This first chevron bone was not fused in the midline, as has also been recorded for the Arari and *Atlantide* dolphins. The last three pairs of chevrons also consisted of two separate halves (as in the Arari dolphins), and were located on the 70th to 72nd vertebrae in the column. As a result, there must have been a total of 29 chevron bones, the first consisting of two fused together. This was closer to the total of 28 bones recorded for the Arari dolphins than to that of 24 recorded for the *Atlantide* dolphin, though in the latter case the smallest of the chevrons appeared to be absent.

Ribs. The Durban dolphin had 16 pairs of ribs, two of which were free: according to Fraser (1950), the *Atlantide* specimen had 15 pairs of ribs, one being free, and the Arari dolphins were recorded as having 15 to 16 pairs, one or two of which were free (Nishiwaki *et al.*, 1965). The first six pairs of ribs were double-headed, numbers 7 to 14 possessing only a tubercle, as in the *Atlantide* dolphin. The first pair of ribs was very strongly compressed, their transverse breadth being 14–24 mm but their thickness only 5 mm. The second pair was similarly compressed but to a lesser extent, the corresponding measurements being 14–15 mm and 5 mm. As described by Fraser (1950) for the *Atlantide* dolphin, each of the remaining ribs had a sharp, posteriorly-projecting keel on the dorsal surface which extended from the tubercle to the front where the rib bent round laterally. However, by the 13th rib this had become a mere trace, and was absent from the last three ribs.

Sternum. The sternum of the Durban dolphin consisted of two parts, the manubrium fused with the first mesosternal element, and the second mesosternal element as a separate, smaller bone (pl. 15). The third mesosternal element appeared to be absent. This contrasted with the sternum described for both the *Atlantide* and Arari dolphins, in which the manubrium, first and second mesosternal elements were fused, and in which the third mesosternal element was present as a separate bone. The manubrium of the Durban dolphin had a central foramen measuring 5·5 by 3·5 mm, similar to that figured for the Arari dolphins, whereas the *Atlantide* dolphin had no trace of a foramen. The measurements of the sternum were as follows: manubrium breadth in front of the first rib articulations 48 mm, behind these 65 mm, and between the ends of the lateral processes 76 mm. Behind these processes the manubrium was 38 mm wide. In general shape, therefore, the manubrium was very similar to that of the *Atlantide* dolphin, but was relatively wider behind the lateral processes. The first mesosternal element was about 50 mm long and 19 mm wide at the middle, and the second mesosternal element 35 mm long and 17 mm wide. Both elements were also relatively wider than in the *Atlantide* dolphin.

There were only nine pairs of sternal ribs present in the Durban dolphin, as against 11 pairs in both the Arari and *Atlantide* dolphins. This was probably correlated with the reduction of one mesosternal element in the Durban dolphin. All but the last two pairs of sternal ribs bore faceted ends which indicated that they were probably articulated with the sternum.

Hyoid bones. The basihyal was only partly fused to the thyrohyals, the basihyal length being 31 mm and its width about 28 mm. There was no median notch to the basihyal anteriorly as in the *Atlantide* dolphin, and in fact the anterior edge of the basihyal had a slight, V-shaped projection (pl. 16), a feature which was also figured for the Arari dolphins (Nishiwaki *et al.*, 1965). The basal breadth of the thyrohyal was 19 mm and its length 56 mm. The stylohyal length was 71 mm and its thickness 12 mm.

Pelvic bones. The pelvic bones were simple and rod-like in shape, measuring 69 mm in length with a transverse width of about 7 by 4 mm (pl. 16).

Scapula. The scapula was small and very similar in general outline to that figured for the Arari dolphins. The shape of the acromion, however, was different (pl. 17), its distal margin being straight and forming a much acuter angle with the axis of the acromion than that figured for either the *Atlantide* or Arari dolphins, although there is apparently considerable intra-specific variation in this feature (Fraser, 1950). The head of the coracoid was longer than that figured for the Arari dolphins, and the dorsal margin was more curved. The measurements of the scapula were as follows:

Greatest antero-posterior length—151 mm.
Height from anterior margin of acetabulum to upper margin of scapula—103 mm.
Greatest length of acromion—37 mm.
Greatest breadth of acromion—27 mm.
Greatest length of coracoid—30 mm.

Fore limb. The flipper was of the same general outline as those figured for the *Atlantide* and Arari dolphins. The measurements of the flipper bones were as follows:

Greatest length of humerus—51 mm.
Greatest breadth of humerus distally—37 mm.
Greatest length of radius—67 mm.
Greatest breadth of radius distally—33 mm.
Greatest length of ulna—62 mm.
Transverse breadth of proximal row of carpals—61 mm.

There were three bones in the proximal carpal series, identified as the scaphoid (in contact with the radius), the lunar (in contact with both radius and ulna) and a bone in contact with the ulna which appeared to consist of the cuneiform fused with the pisiform (pl. 17). Fraser (1950) stated that the pisiform was completely absent in the *Atlantide* dolphin. The distal series of carpals also consisted of three bones, the trapezium (in contact distally with the first metacarpal), the unciform (in contact distally with the third and fourth metacarpals) and a bone between the two in contact with the second and third metacarpals which seemed to represent the fusion of the trapezoid with the magnum. In the *Atlantide* dolphin the trapezoid was still present as a separate but very small element, whereas in the Arari dolphins the distal carpal series seemed to consist of only three bones as in the Durban dolphin.

Distal to the carpals were five metacarpals, of which the first is fused with the first phalanx in the right flipper only (pl. 16). The number of phalanges was as follows; first digit one, second digit nine, third digit six, fourth digit two and fifth digit one. Alternatively, if all the joints distal to the carpals were considered to be phalangeal, the formula became I:2, II:10, III:7, IV:3 and V:2, which compared with I:2, II:9, III:6, IV:3 and V:2 for the *Atlantide* dolphin and I:2, II:9, III:7, IV:3 and V:2 for the Arari dolphins. Intraspecific variation in the phalangeal formula, however, is known to be considerable for other odontocete species.

ADDITIONAL NOTES

The Durban dolphin was an adult female in anoestrus. There was no milk in the mammary glands, which from a histological examination proved to be in a resting state. The diameters of the uterine cornua differed considerably, the left horn (24 mm) being larger than the right horn (17 mm). This was associated with a similar difference in the size of the ovaries, the left one (3·87 g) being considerably larger than the right (1.93 g—preserved weights). As discussed by Ohsumi (1964), members of the genus *Stenella* seem to ovulate exclusively from the left ovary until about nine corpora have accumulated, when the right ovary may begin to function. This effect is responsible for the greater development of the left side of the reproductive tract in the Durban dolphin, for macroscopically the left ovary appeared to contain the scars of about 16 corpora whereas the right had none. There was no trace of a functional or recent corpus luteum, and no enlarged Graafian follicle was found.

The contents of the stomach consisted of a mass of small fish bones and one squid beak.

A post-mortem examination of the lungs revealed that the dolphin was suffering from a form of necrotizing pneumotitis at the time of death. An ulcer, probably of traumatic origin, was present in the lining of the first stomach.

SUMMARY

Evidence from the skull proportions of the Arari and St. Helena dolphins indicates that the *frontalis* and *attenuata* groups distinguished by Fraser (1950) are not as exclusive as was at first thought, and this has further complicated the identification of dolphins apparently belonging to the *frontalis*/*attenuata* complex.

In external appearance the Durban dolphin was closest to the Arari dolphins, although the appearance of *S.* cf. *capensis* from St. Helena is at present unknown. In skull proportions, however, the Durban specimen was rather different from those from Arari, was more closely related to Fraser's *attenuata* group, and was apparently closest to *S.* cf. *capensis* from St. Helena. Data from the post-cranial skeleton is difficult to evaluate because so little is known of the amount of intra-specific variation within any of the relevant species. Indeed, the skeleton of *S.* cf. *capensis* is completely unknown. In most features the post-cranial skeleton of the Durban dolphin resembled that figured for the Arari dolphins. The vertebral formula, free third cervical vertebra, greater development of metapophyses, the shape of the hyoid bones and arrangement of the carpal series in the fore limb all showed a greater similarity to the Arari specimens than to the *Atlantide* dolphin. As in the skull, however, the skeleton of the Durban dolphin had certain other characters apparently unlike either the Arari or *Atlantide* specimens, notably in the development of the sternum and associated sternal ribs.

Until more information on the external appearance and skeleton of the *Stenella* species around St. Helena is available, it seems that the Durban dolphin must be referred to *Stenella attenuata* (Gray, 1846). As such, it is the first specimen of the species to be recorded from South Africa since the type skull of *Steno capensis* was sent to the British Museum in 1865 by E. Layard of the South African Museum (Gray, 1866). This skull, the locality of which was recorded as the Cape of Good Hope, has subsequently been included in *Prodelphinus attenuatus* by Flower (1885) and True (1889), and in the *Stenella attenuata* group by Fraser (1950). To date, these two specimens represent the only records of *S. attenuata* from South African seas.

Acknowledgements

I am indebted to the Trustees of the Oceanographic Research Institute, Durban, for presenting the dolphin to the South African Museum, so enabling me to examine it, and also for their permission to publish this paper.

I must also thank Professor C. J. Uys of the Pathology Department, University of Cape Town Medical School, for undertaking a post-mortem examination of material collected from the dolphin, and Mr. Sidney Kannemeyer of the South African Museum for preparing the skeleton and photographing it.

Dr. F. C. Fraser of the British Museum (Natural History) was kind enough to read and comment on this manuscript.

The Trustees of the South African Museum thank the South African Council for Scientific and Industrial Research for a grant in aid of publication.

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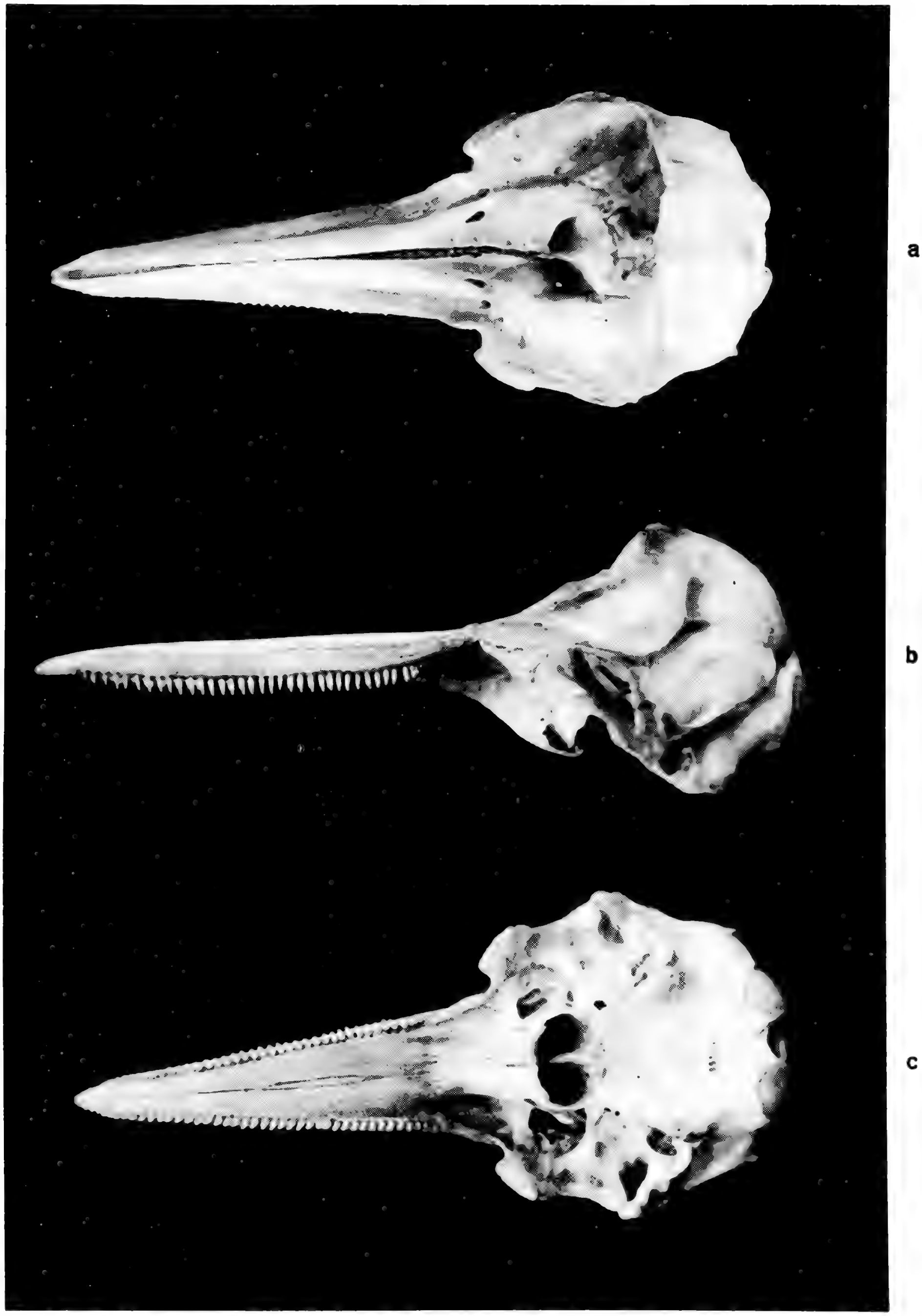
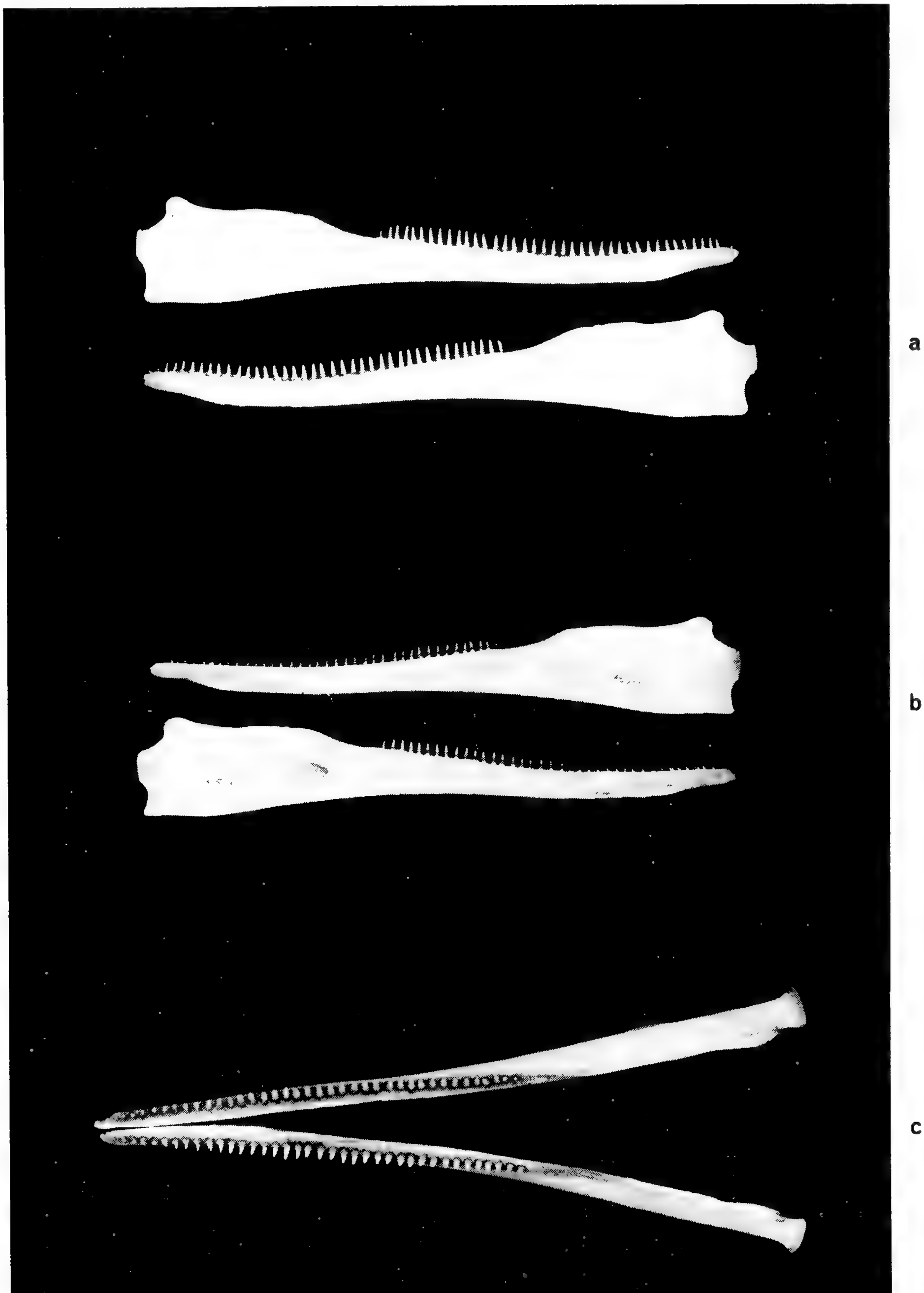
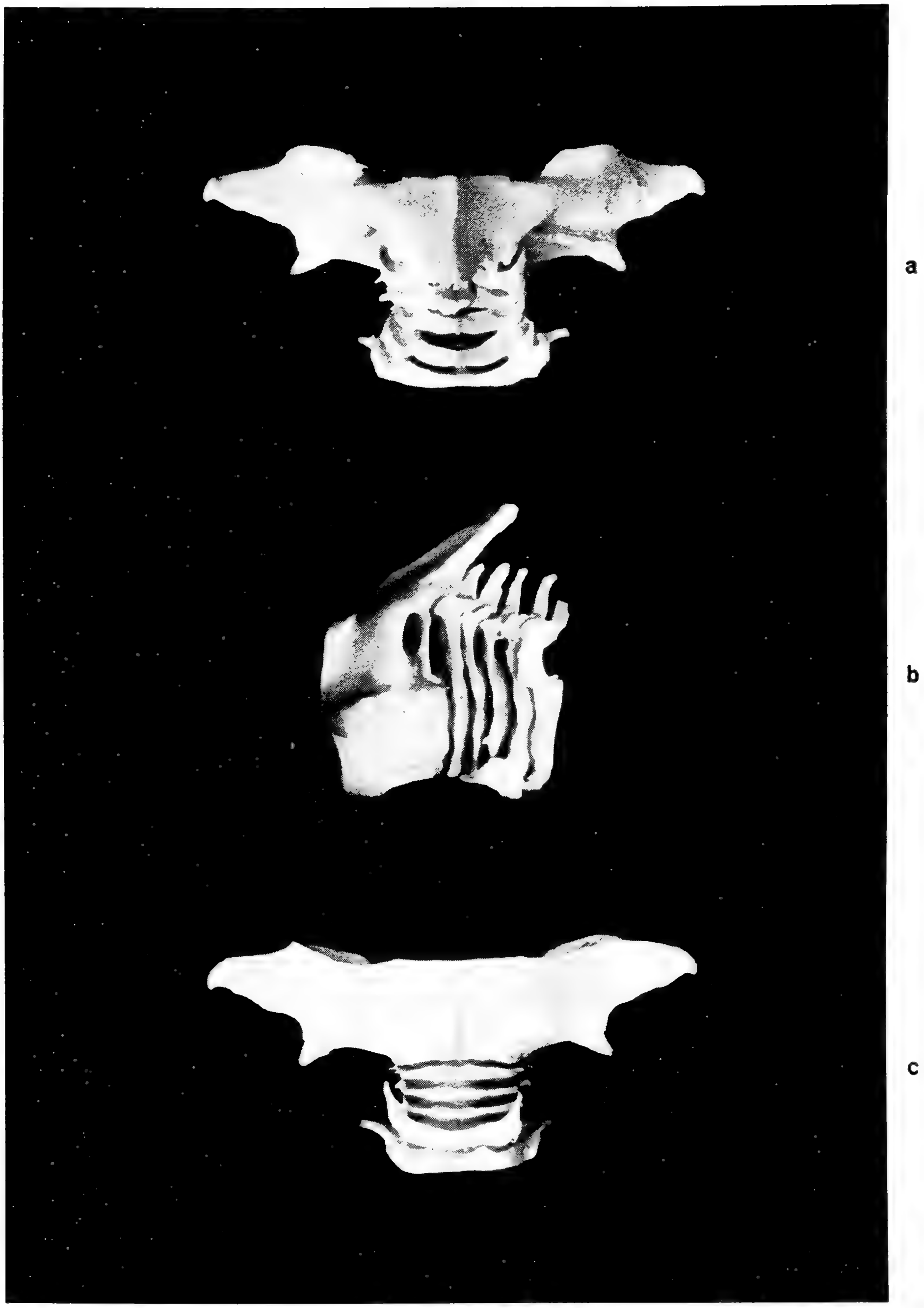


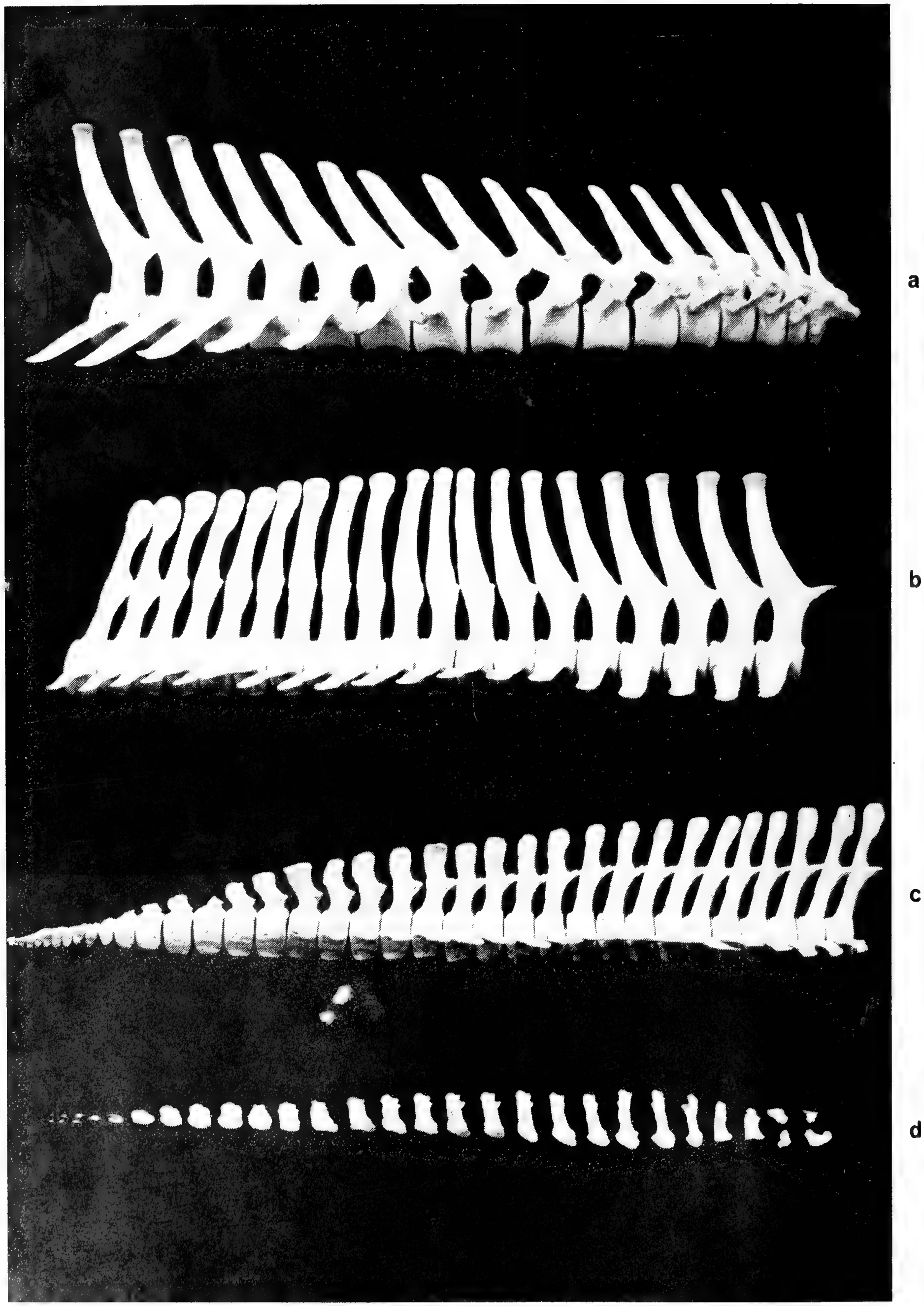
a. Skull, dorsal view. *b*. Skull, lateral view. *c*. Skull, ventral view.



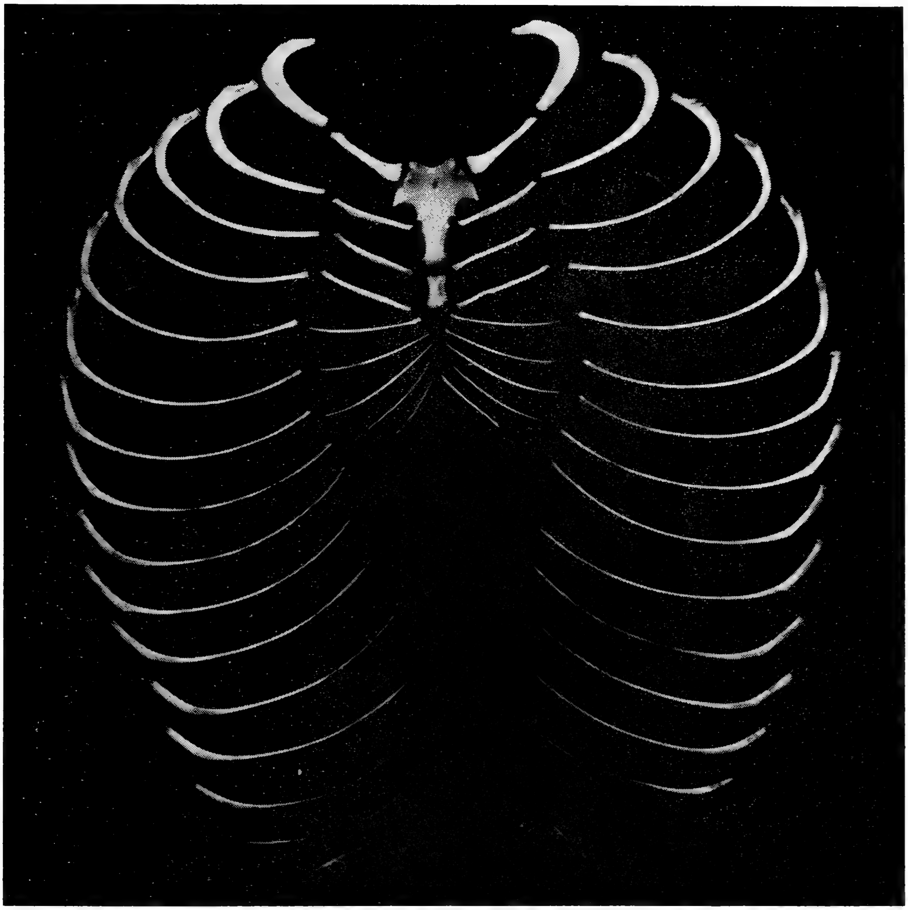
a. Mandibles, lateral view, external aspect. *b*. Mandibles, lateral view, internal aspect. *c*. Mandibles, dorsal view.



a. Cervical vertebrae, dorsal view. *b*. Cervical vertebrae, lateral view. *c*. Cervical vertebrae, ventral view.

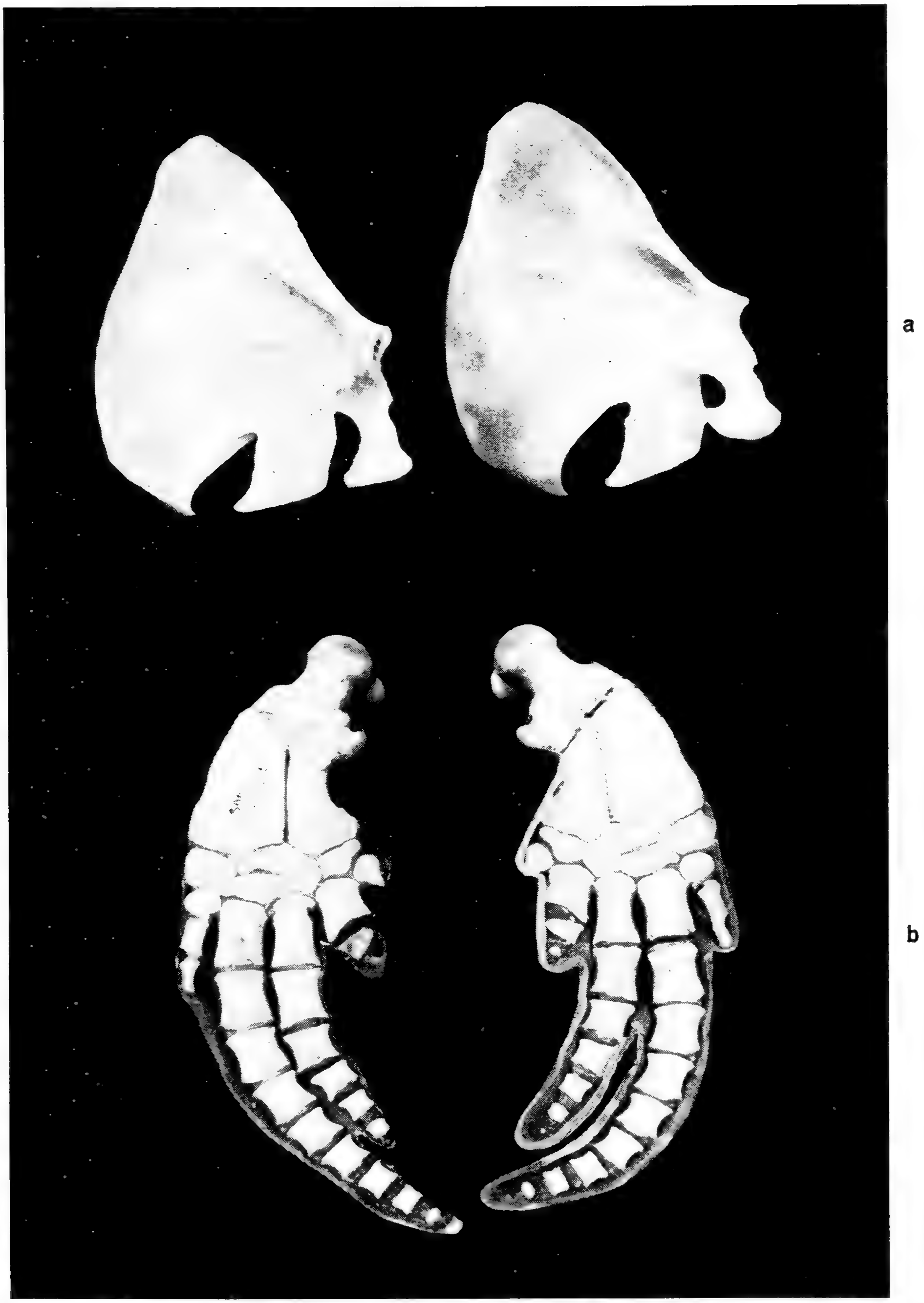


a. Thoracic vertebrae, lateral view. *b*. Lumbar vertebrae, lateral view. *c*. Caudal vertebrae, lateral view. *d*. Chevron bones.



Ribs, sternum and sternal ribs.

a. Hyoid bones. *b*. Pelvic bones. *c*. X-ray photograph of right flipper.



a. Scapulae. *b*. Left and right flippers.

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THE RELATIONSHIP BETWEEN *RAJA MIRALETUS* LINNAEUS AND *RAJA OCELLIFERA* REGAN BASED ON A STUDY OF THE CLASPER

By

P. A. HULLEY

Cape Town Kaapstad

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South African Museum, Cape Town

(With 3 figures)

[*MS. received* 27 *September*, 1967]

Contents

Introduction

Bigelow & Schroeder (1953) have pointed out that several South African skates seem to be indistinguishable from European species from the corresponding latitudinal belt in the northern hemisphere. These species are *Raja pullopunctata* Smith, 1964 and *Raja batis* Linnaeus, 1758; *Raja rhizacanthus* Regan, 1906 and *Raja clavata* Linnaeus, 1758; and *Raja alba* Lacépède, 1803, which is recorded as such from both regions. These pairs seem to represent cases of masked bipolarity (Ekman, 1953). Besides the brief references given by Norman (1935), little work has been done on the comparison of the specimens from the two regions. On the basis of the clasper structure of mature males, Hulley (1966) has shown that *R. rhizacanthus* Regan is synonymous with *R. clavata* Linnaeus, while *R. pullopunctata* Smith is distinct from *R. batis* Linnaeus.

A more interesting relationship is shown by the pair *R. miraletus* Linnaeus, 1758 and *R. ocellifera* Regan, 1906. *R. miraletus* (fig. 1) has been recorded from the Mediterranean (Italy, Adriatic, Nice, Tunis, Tripoli: Clark, 1926), and this species extends southwards along the north-west African and west African coasts, being recorded from Morocco (Clark, 1926), Cape Bojador (Murray & Hjort, 1912), Rio de Oro, Cape Blanc to Cape Verde (Pellegrin, 1914), Senegal (Cadenat, 1950) and from Cape Lopez in Gabon to Baie les Tigres in Angola (Fowler, 1936; Poll, 1951). The species *R. ocellifera* is known to extend from

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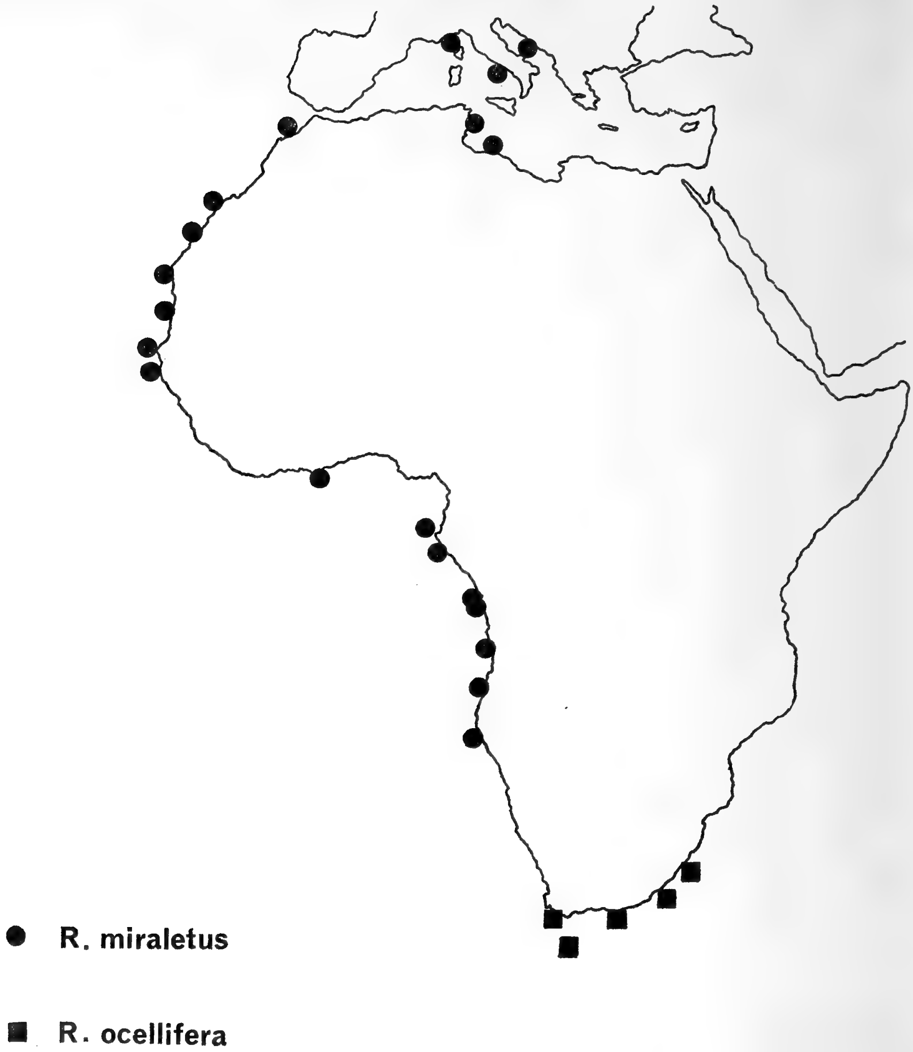

Fig. 1

Map showing the distribution of *R. miraletus* and *R. ocellifera.*

False Bay and the Agulhas Bank northwards to Natal (Barnard, 1925; Smith, 1961). It has not been recorded along the west coasts of South Africa and South West Africa. *R. ocellifera* has also been reported from the Kerala coast, in southern India (Samuel, 1963).

Norman (1935) has pointed out that *R. ocellifera* from South African waters is closely related to *R. miraletus* from the Mediterranean and the west coast of Africa, so much so that specimens taken from Cape St. Blaize, near Mossel Bay, have been identified as *R. miraletus* by Boulenger (Von Bonde & Swart, 1923) and as *R. ocellifera* by Norman (1935). Furthermore, specimens obtained by both the *Discovery* and by the Belgian South Atlantic Expedition off the Congo and Angola, approximate to the South African form, but have been referred to *R. miraletus* on the basis of a somewhat longer tail, a longer snout, narrower interorbital distance, fewer teeth in the upper jaw, and a circular ocellus.

The genus *Raja*, however, shows great variability in its morphological characters, which vary with age and/or sex in the individuals within a species, so that a more critical method of examination needs to be employed. The purpose of this paper is to re-examine the relationship between *R. miraletus* and *R. ocellifera* in the light of the structure of the claspers of mature males.

Leigh-Sharpe (1920–6) has shown that the species of the genus *Raja* may be recognized by the morphological structure of their claspers, and Ishiyama (1958) has pointed out that the clasper structure is the most reliable basis for the systematics of this group, since both the external and internal structures of the claspers are species-specific without exception. On this basis, Hulley (1966) has employed the structure of the clasper for comparing geographically separated species. However, differences in the external and measurable characters of the species must also be taken into account.

Clasper Structure

Comprehensive anatomical studies have been carried out on the claspers of European and Japanese rajids, so that the nomenclature used in this paper is in accordance with Petri (1878), Jungersen (1899), Huber (1901), Leigh-Sharpe (1920–6) and Ishiyama (1958).

The claspers of three adult specimens of *R. ocellifera*, trawled in Algoa Bay and Jeffrey's Bay, one adult specimen of *R. miraletus* obtained by the Belgian South Atlantic Expedition (Station 15: 05°50′ S, 11° 32′ E, WNW Banana, in 210 metres), and two specimens of *R. miraletus* from the north-west coast of Africa (*Walther Herwig* Station 125/1964; 08° 32′ N, 14° 09′ W, in 44–48 metres) were examined. Although the latter two specimens were small and had only just reached maturity, the external characters of the claspers could be recognized.

External anatomy

The shape of the claspers is the same in both *R. miraletus* and *R. ocellifera* (fig. 2A). The clasper is comparatively short: proximally, it is cylindrical, but from about two-thirds its length, it becomes dorso-ventrally flattened, especially on the ventral surface. It tapers gradually towards its distal end and terminates in a pointed, spatulate tip. The ventral surface is pale, while the dorsal surface of the clasper tones with the general coloration of the upper surface of the disc.

The apopyle is situated dorsally, some little distance behind the vent, and the appendix groove arising at this point runs laterally outwards towards the margin of the clasper, before turning to run parallel with this margin, almost to the distal end of the organ (fig. 2A).

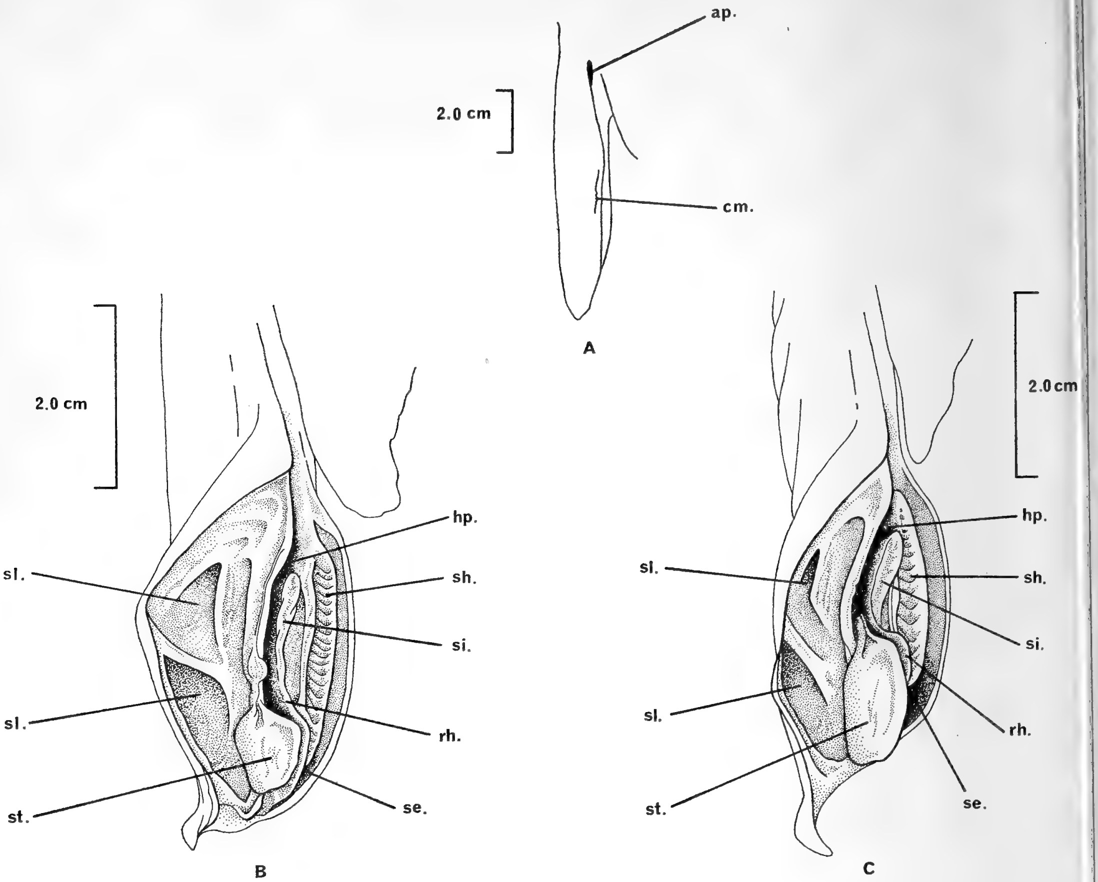

Fig. 2

A. External view of the right clasper from the dorsal side.
B. *R. ocellifera:* lateral view of the right clasper opened to show the structural features of the glans.
C. *R. miraletus:* lateral view of the right clasper opened to show the structural features of the glans.
ap.–apopyle; cm.–pecten; hp.–hypopyle; rh.–rhipidion; se.–sentina; sh.–shield; si.–signal; sl.–slit; st.–sentinel

Adjacent to the groove and situated at a point about midway along the length of the clasper, there is a row of four to six small, sharp protuberances, the pecten. This is the result of the projection of the outer lateral margin of the dorsal terminal 2 cartilage (fig. 3B) through the skin of the clasper. Although the pecten is present in both *R. ocellifera* and the Angolan specimen of *R. miraletus*, it was found to be absent in the two *Walther Herwig* specimens. This is probably due to the fact that these specimens are only just mature and no calcification of the clasper cartilages has taken place.

Apart from a difference in the size of the sentinel, the structures of the clasper glans were the same in all specimens examined (figs 2B, 2C). It should be noted that the slight differences in these figures is due to the fact that the clasper has been more fully opened in *R. ocellifera.*

The spade-shaped sentinel is strongly developed and is situated at the distal end of the glans, slightly dorsal to the line of the appendix groove. It is covered by epithelium, but its outer lateral margin is knife-like and exposed. The spike lies ventrally just beneath the sentinel, which completely obscures it from sight. A sentina is present. The fleshy pad, situated in the mid-region of the organ and ventral to the appendix groove, is the signal. This is capable of some rotational movement about the longitudinal axis of the clasper. The fleshy pad extends distally as a plate-like structure, the rhipidion. The ventral shield is narrow, but is well developed, especially on its inner lateral margin, where it is somewhat raised into a longitudinal ridge. The shield extends from the proximal region to about three-quarters the length of the glans. In mature specimens, the shield is covered by pleated epithelium (figs 2B, 2C), but this is so thin along the outer lateral margin that the sharp edge of the ventral terminal cartilage is exposed. Two pouches, the slits, are present in the dorsal surface of the concavity of the clasper glans. They are shallow depressions, but are well demarcated from each other by a cartilaginous shelf. The proximal slit has a raised inner margin, due to the prominence of the axial cartilage in this region.

Internal anatomy

The following descriptions and relevant diagram (fig. 3) are based on the dissection of the claspers of *R. ocellifera.*

Axial, dorsal marginal and ventral marginal cartilages (figs 3A–E)

The axial cartilage is stout and cylindrical at its junction with the b_2-cartilage, but it becomes broader and dorso-ventrally flattened from about half of its length to the distal end, terminating in a broadly rounded tip. On the ventral surface of the axial cartilage, there is a short, shallow groove, which runs from almost the flat tip of this cartilage to about one-quarter its length from the distal end (fig. 3E). This groove accommodates the accessory 2 cartilage.

The marginal cartilages are more heavily calcified than the axial and can easily be distinguished from it. The marginal cartilages border the appendix groove dorsally and ventrally, and are somewhat scrolled. The origin of the dorsal marginal cartilage is more proximal than that of the ventral marginal, so that the interspace between the two marks the position of the apopyle. The dorsal marginal extends proximally for about half the length of the axial, and is tightly bonded to this cartilage, except at its distal end. Here the dorsal marginal turns laterally outwards and terminates in a blunt point (fig. 3A). At a point about two-thirds along its length, the dorsal marginal possesses a step, into which fits the dorsal terminal 2 cartilage (fig. 3A).

The ventral marginal cartilage is bonded to the axial along the whole of its inner lateral margin. It is ventrally concave, so that its outer lateral margin is raised into a thin ridge, which runs along the whole of the appendix groove. Distally, the ventral marginal cartilage is obliquely truncate.

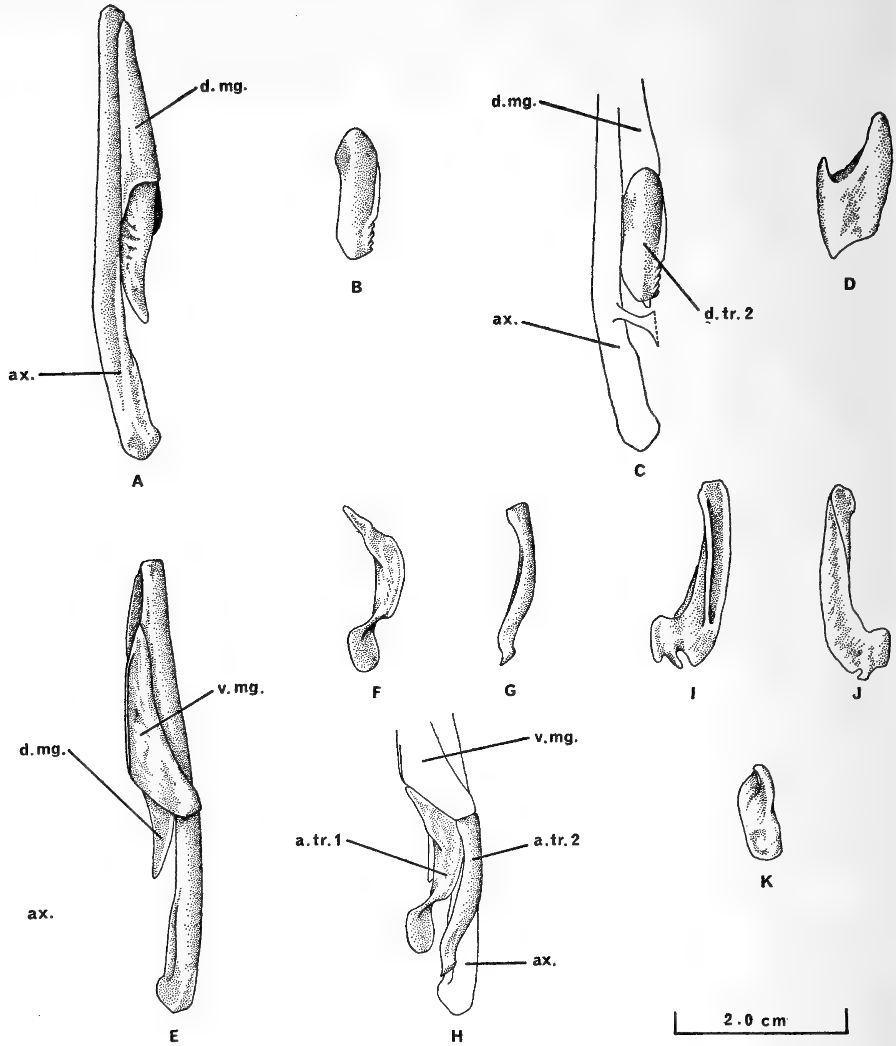

Fig. 3

R. ocellifera: cartilages of the terminal group of the clasper.

A. axial and dorsal marginal (dorsal view); B. dorsal terminal 2 (dorsal view); C. dorsal terminal 2 cartilage *in situ* (dorsal view); D. dorsal terminal 1 (dorsal view); E. axial and ventral marginal (ventral view); F. accessory terminal 1 (ventral view); G. accessory terminal 2 (ventral view); H. accessory 1 and 2 cartilages *in situ* (ventral view); I. ventral terminal (dorsal view); J. ventral terminal (ventral view); K. accessory terminal 3 (dorsal view).

ax.–axial; d.mg.–dorsal marginal; v.mg.–ventral marginal; d.tr.2–dorsal terminal 2; a.tr.1–accessory terminal 1; a.tr.2–accessory terminal 2.

Dorsal terminal 1 *cartilage* (fig. 3D)

This is a flatly-rounded, shield-like cartilage occurring on the dorsal side of the clasper. It is curved proximally and elongated into a blunt point along its outer lateral margin. This outer lateral margin fits into the slight groove in the dorsal terminal 2 cartilage (fig. 3B). From this point, and running in a curve, is a slight shelf, which serves as the area of insertion of the *m. dilatator*. Distally, the cartilage is somewhat pointed on its inner lateral margin. This is slightly curved and wraps around the body of the clasper.

Dorsal terminal 2 *cartilage* (figs 3B, 3C)

The dorsal terminal 2 cartilage is dorsally convex, with a broadly rounded anterior end. This end fits into the step of the dorsal marginal cartilage (fig. 3C). Along the distal edge of its outer lateral margin, the dorsal terminal 2 is serrate, the serrations being raised into small, sharp points. These are associated with the development of the pecten. Distal to the dorsal terminal 2 cartilage and in the covering of the connective tissue, there is a cartilaginous 'rib', which joins the axial at about two-thirds along its length (fig. 3C). This rib forms the shelf which separates the two dorsal slits.

Ventral terminal cartilage (figs 3I, 3J)

This is a J-shaped cartilage, which is attached to the distal end of the ventral marginal cartilage. It is somewhat curved medially, so that it runs around the inner lateral side of the axial cartilage. The ventral terminal is bluntly rounded anteriorly, but posteriorly and distally there is a small point. The elongated region of the cartilage possesses a shelf and a broad ridge on its dorsal side, while ventrally the cartilage is slightly concave. The shelf on the dorsal side, which is associated with the shield, is thin and has a knife-like outer lateral edge.

Accessory 1 *cartilage* (figs 3F, 3H)

The cartilage is S-shaped, with its distal end curved laterally outwards and expanded into a thin, flat plate. This is the sentinel of the clasper glans. The proximal end of the accessory 1 cartilage is dorso-ventrally flattened and terminates in a blunt point. This point and the adjacent portions are attached to the distal end of the ventral marginal cartilage. There is a slight ridge along the inner lateral side of the accessory 1 cartilage. This fits into a groove on the outer lateral edge of accessory 2.

Accessory 2 *cartilage* (figs 3G, 3H)

This cartilage is attached to the inner, truncate edge of the ventral marginal cartilage (fig. 3H). It has a broad anterior end and is more or less cylindrical in shape. It curves laterally outwards to form a hook at its distal end. This hook is the spike of the clasper glans. Along its outer lateral edge, the accessory 2 cartilage possesses a slight groove, into which fits the accessory 1 cartilage (fig 3H).

Accessory 3 *cartilage* (fig. 3K)

The accessory 3 cartilage consists of a single cartilaginous element, which manifests itself in the clasper glans as the signal. Ventrally, this cartilage is flat, but dorsally, it is raised into an anteriorly directed ridge. The accessory 3 is attached to the distal end of the ventral marginal cartilage, more ventrally than the attachment of the accessory 1 and 2 cartilages.

The cartilaginous elements of the clasper glans of *R. miraletus* were examined by X-ray photography. The structure of these elements proved to be identical to that of *R. ocellifera*, as given above.

External Characters

While the clasper structure may be used as a means of comparison between geographically separated species, it is as well to examine the external and measurable characters of the species concerned. As already pointed out, South African specimens have been referred to *R. ocellifera* Regan rather than to *R. miraletus* Linnaeus, because of differences in the length of the tail, the length of the snout, the interorbital distance, the number of rows of teeth in the upper jaw and the nature of the ocellus.

Table 1: A comparison of the external and measurable characters of specimens of *R. miraletus* from the Mediterranean, Sierra Leone and Angola, with specimens of *R. ocellifera* from South Africa.

		R. miraletus		*R. ocellifera*
	Mediterranean	Sierra Leone	Angola	South Africa
Tail length in disc width	1·1	1·1	1·1	1·2–1·4
Middle of vent to 1st dorsal origin in snout to middle of vent	Not given	1·2–1·3	1·1–1·2	1·1–1·4
Snout length in disc width	5·0–5·7	5·0–5·2	5·5–5·6	5·1–6·1
Interorbit in disc width	22·0–24·0	16·6–18·5	16·8–20·4	14·0–17·1
Interorbit in snout length	4·2–4·4	3·3–3·6	3·5–3·6	2·3–3·0
Interorbit in internasal	2·3–2·5	1·9–2·1	1·8–2·3	1·7–2·2
No. of teeth in upper jaw	40–42	45–47	47–52*	42–50
No. of precaudal vertebrae	Not given	49–51	52–54	49–53

*Poll (1951)

The following comparison (table 1) of these characters is based on 24 specimens of *R. ocellifera* (disc width 84–354 mm) taken in South African waters from False Bay to Algoa Bay; 2 specimens of *R. miraletus* (disc width 305, 343 mm) trawled off the coast of Angola; and 2 specimens of *R. miraletus* (disc width 196, 204 mm) taken off the coast of Sierra Leone (*Walther Herwig* Station 125/1964). Measurements given by Clark (1926) for Mediterranean *R. miraletus* have also been employed.

As has been pointed out (Norman, 1935), there is a difference in the ocellus. In *R. miraletus*, the ocellus is circular in shape, while in *R. ocellifera*, it tends to be horizontally ovate. The ocellus of *R. miraletus* consists of a number of concentric rings of colour: a blue-black centre spot, surrounded by a dark black ring, which is in turn surrounded by a complete brownish-yellow outer ring. In *R. ocellifera*, the outer brownish-yellow ring is usually incomplete and consists of a number of spots of the colour, which are narrowly united.

DISCUSSION

The structural features and lay-out of the clasper glans are the same in both *R. miraletus* and *R. ocellifera*. The two dorsal slits are shallow in both species and the sentinel completely covers the spike. The slight difference in the size of the sentinel is probably due to an age difference, since the shape of the sentinel and the nature of the corresponding cartilage (accesory 1) are the same in both species. Furthermore, the presence of the comb confirms that the claspers of *R. ocellifera* are identical to those of *R. miraletus*.

Since the cartilaginous elements of the claspers are directly related to the external characters of the glans, it would be expected that these would be similar. This is true at least for the accessory 1 and 2 cartilages, where the author is unable to detect any appreciable difference. As these cartilages are species-specific without exception (Ishiyama, 1958), it is reasonable to assume that the species *R. ocellifera* Regan is synonymous with the species *R. miraletus* Linnaeus.

There are differences in the external and measurable characters of the two 'species' (table 1). The tail is comparatively shorter in *R. ocellifera* than in *R. miraletus*, as shown by the measurement of the tail length in the disc width. In *R. ocellifera* this measurement varies from 1·2 to 1·4, while in *R. miraletus*, it is more or less constant at 1·1. However, Ishiyama (1952) has pointed out that a more reliable method for comparing tail length is the determination of the number of precaudal vertebrae. These counts are not always useful in the separation of species. In *R. ocellifera*, the count is from 49 to 53, and in *R. miraletus*, from 49 to 54, so that the number of precaudal elements in *R. ocellifera* is within the range for *R. miraletus*. This is confirmed externally by the measurement of the distance from the middle of the vent to the 1st dorsal origin (*R. ocellifera* 1·1–1·4; *R. miraletus* 1·1–1·3).

The snout appears to be somewhat longer in *R. miraletus*. It would seem from table 1 that there is a slight decrease in the snout length from the Mediterranean specimens to the west African specimens of *R. miraletus*. Similarly, the interorbital distance appears to be less in *R. miraletus*. These two differences are particularly noticeable in the measurement of the interorbital distance in the snout length.

The author is unable to detect any difference in the number of teeth in the upper jaw, since the range for *R. miraletus* covers that of *R. ocellifera*. The most easily distinguishable difference between the two 'species' is the nature of the ocellus. This has been shown above. However, the systematic importance of such a character is unknown.

It is therefore concluded that these external and measureable differences are probably of secondary importance in the systematics of this group, and that since the structures of the claspers are identical, and the number of precaudal vertebrae is similar, *R. ocellifera* and *R. miraletus* should be regarded as two extremes of one varietal species.

This being the case, it is interesting to note the distribution of the species. It is present along the whole of the west African coast, from the Mediterranean to the southern border of Angola, absent from the region Walvis Bay to Cape Point, and again present along the east coast of South Africa. It is suggested that the cold water of the Benguela Current, in the region Walvis Bay to Cape Point, acts as a temperature barrier. Since some gene flow must occur from west to east and *vice versa*, the species probably moves off-shore. A similar occurrence is found in *R. clavata* (Hulley, 1966: fig. 8), but in this temperate species, it is warmer water which acts as the barrier.

Summary

After detailed studies of the anatomy of the claspers of the males, and consideration of the external features, it is concluded that *Raja ocellifera* Regan is synonymous with *Raja miraletus* Linnaeus.

Acknowledgements

My thanks are due to Dr. G. Krefft of the Institut für Seefischerei in Hamburg and Mr. J. P. Gosse of the Institut Royal des Sciences naturelles de Belgique for the loan of the *R. miraletus* specimens, and to the late Prof. J. L. B. Smith of Rhodes University for specimens of *R. ocellifera*. I am also grateful to Mrs. E. Cluver and Mr. S. X. Kannemeyer of the South African Museum for assistance with the X-ray photographs.

The Trustees of the South African Museum thank the Council for Scientific and Industrial Research for a grant in aid of publication.

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Volume **52** Band
April **1969** April
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By

B. F. KENSLEY

Cape Town Kaapstad

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Printed in South Africa by
The Rustica Press, Pty., Ltd.
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B. F. Kensley
South African Museum, Cape Town

(With 16 figures)

[*MS. received* 30 *July* 1968]

Contents

Introduction

The material dealt with in this paper comes from several sources. The greatest proportion was collected on the seventh cruise of the R/V *Anton Bruun*, in 1964, as part of the International Indian Ocean Expedition. The station numbers of the *Anton Bruun* are designated by the letters BRU, while catalogue numbers of the Zoology Department, University of Cape Town, are designated either as NAD (off the Natal coast) PED (off Moçambique coast), MDD (off the south-western coast of Malagasy Republic), or WBS (Walter's Shoal). This latter is a shallow area about 400 nautical miles south of the Malagasy Republic, and about 600 miles off the coast of South Africa. A final report of the expedition was published by the U.S. Program in Biology, I.I.O.E., in 1965, to which body I am indebted for the opportunity of examining the material.

Other sources of material include the collections made by the R/V *Vema* (station Vema 6) off the Natal coast, the *John D. Gilchrist* (station GIL 56–58) off Natal, and the S.A.S. *Natal* (station NGY) off Natal.

Type material is housed at the South African Museum, and catalogued with South African Museum (S.A.M.) numbers. All other material is in the Zoology Department of the University of Cape Town.

Ann. S. Afr. Mus. **52** (7), 1969, 149–181, 16 figs.

Abbreviations

Sampling gear:

AD—Agassiz Dredge
CG—Campbell Grab 0.6 m^2
MT—Menzies Trawl
RD—Rock Dredge

Substrata:

c—coarse
Calc. Alg.—Calcareous Algae
Crl—coral
d—dark
f—fine
G—gravel
gn—green
G.O.—Globigerina Ooze
gy—grey
M—mud
R—rock
S—sand
Sh—shell
St—stone

Station List

Station Number	*Date*	*Position*	*Depth (m)*	*Bottom*	*Gear*
GIL 56	13.7.59	29°53′S/31°06′E	20	SM	RD
GIL 58	13.7.59	29°53′S/31°04′E	71	M	RD
NGY 21	17.5.58	30°47′S/30°29′E	44	St	
NGY 17	16.8.58	29°53′S/31°04′E	38	CI	D
NGY 59	12.8.58	29°58′S/31°27′E	49		
NGY 63	13.8.58	30°47′S/30°27′E	36		
Vema 6	23.4.58	29°46′S/31°17′E	110–130		
BRU 356 B	29.7.64	29°11′S/31°37′E	18	R	RD
BRU 356 J	29.7.64	29°10′S/31°51′E	43	S	MT
BRU 357 B	30.7.64	29°11′S/32°02′E	70	R Sh	RD
BRU 358 C	30.7.64	29°21′S/31°58′E	370	gn S M	MT
BRU 363 P	5.8.64	23°17′S/43°33′E	12–25	gn M	AD
BRU 363 W	12.8.64	23°19′S/43°36′E	82		AD
BRU 370 G	18.8.64	24°40′S/35°28′E	347	Sh	AD
BRU 371 E	18.8.64	24°46′S/35°20′E	132	R Sh S	RD
BRU 371 F	18.8.64	24°46′S/35°18′E	110	c S R	RD
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BRU 373 B	22.8.64	26°00′S/33°05′E	135	R Sh	RD
BRU 381 A–C	30.8.64	33°13′S/43°51′E	38–46	Calc. Alg.	RD
BRU 389 G	8.9.64	29°57′S/31°31′E	700	G O	AD
BRU 390 C	8.9.64	29°45′S/31°40′E	440	S	AD
BRU 390 E	8.9.64	29°42′S/31°38′E	350	S M	AD
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BRU 390 R	9.9.64	29°35′S/31°42′E	138	Gr Crl	CG
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BRU 391 B	9.9.64	29°29′S/31°45′E	86	M	CG
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BRU 391 F	9.9.64	29°26′S/31°46′E	77	gn M	AD
BRU 391 H	9.9.64	29°21′S/31°35′E	57	c M S Sh	AD
BRU 391 J	9.9.64	29°31′S/31°35′E	57	M S Sh	AD
BRU 392 F	10.9.64	29°16′S/31°32′E	35	d M	CG
BRU 392 G	10.9.64	29°14′S/31°31′E	18	f gy S	CG
BRU 392 H	10.9.64	29°13′S/31°31′E	18	gy f S	AD
BRU 392 K	10.9.64	29°19′S/31°26′E	38	c S	AD

Species List

* — new record for the southern African region
ovig — ovigerous
juv — juveniles

Species	♂	♀	*Juv*	*Station*	*Catalogue number*
BRACHYURA					
Achaeopsis spinulosus Stimpson	1	3 ovig	—	Vema 6	NAD 11 B
Achaeopsis thomsoni (Norman)	2	1 ovig	—	372 Q	PED 20 Y-Z
	1	—	—	371 F	PED 7 B
Achaeus lacertosus (Stimpson)	7	2 ovig	—	372 G	PED 16 N
Achaeus cf. *affinis* Miers	—	1		372 G	PED 16 N
	—	3 ovig	—	NGY 21	NAD 3 Z
Actaea rueppellii (Krauss)	1	—	—	NGY 21	NAD 3 X
Calappa lophos (Herbst)	1	—	—	363 W	MDD 1 D
Carcinoplax longimanus (de Haan)	—	1	15	390 H	NAD 31 C
	3	—	—	371 G	PED 8 Y
Charybdis cf. *annulata* (Fabricius)	—	1 ovig	—	NGY 17	NAD 8 L
Conchoecetes artificiosus (Fabricius)	8	6	—	391 J	NAD 62 L
Dorippe lanata (Linnaeus)	1	3 ovig	1	391 C	NAD 51 E
	—	—	2	390 L	NAD 35 E
	1	4 ovig	—	GIL 58	NAD 26 R
Ebalia (*Lithadia*) *barnardi* Stebbing	1	—	—	391 B	NAD 55 N-Q
Ebalia (*Ebalia*) *tuberculata* Miers	4	2 ovig	—	Vema 6	NAD 11 E
	1	—	—	390 S	NAD 45 N
	2	1	—	390 S	NAD 45 L
	—	—	1	358 C	ABD 1 C
Ebalia (*Ebalia*) *tuberculosa* f. *postulans* (Stebbing)	1	—	—	371 G	PED 8 V
Ebalia (*Ebalia*) *tuberculosa* f. *scandens* Stebbing	3	2	—	NGY 63	NAD 14 M
	1	1	—	390 E	ABD 15 K
	5	1 ovig	—	370 G	ABD 8 Z
	4	—	—	358 C	ABD 1 B
Ebalia sp.	1	—	—	390 E	ABD 15 L
**Ethusa sinespina* n.sp.	—	1 ovig	—	390 E	S.A.M. A12648
	—	1	—	358 C	S.A.M. A12649
	1	—	—	390 S	NAD 45 K
Eumedonus granulosus MacGilchrist	1	—	—	372 G	PED 16 Z
Eurynome aspera (Pennant)	3	1 ovig	—	NGY 21	NAD 3 S
Goneplax angulata (Pennant)	5	3	—	390 H	NAD 31 E
Gonioneptunus africanus (Shen)	10	17+2 ovig	—	390 L	NAD 35 D
	2	1 ovig	—	372 L	PED 19 N
Homola barbata (Fabricius)	—	1	—	381 A-C	WSS 3 D
Hyastenus spinosus Milne-Edwards	4	1 ovig	—	391 J	NAD 62 B
	2	—	—	372 G	PED 7 C
Inachus cf. *dorsettensis* (Pennant)	1	—	—	370 G	ABD 9 A
Inachus guentheri (Miers)	2	1 ovig	—	371 F	PED 7 C
	1	3 ovig	—	Vema 6	NAD 11 B
Inachus sp.	—	—	3	370 G	ABD 9 A
Leucosia marmorea Bell	—	1 ovig	—	391 J	NAD 62 K

	♂	♀	*Juv*	*Station*	*Catalogue Number*
Lophozozymus dodone (Herbst)	1	—	—	NGY 21	NAD 3 W
Lupocyclus tugelae Barnard	—	1 ovig	—	372 G	PED 16 K
Macropodia formosa Rathbun	4	—	—	NGY 59	NAD 18 T
	2	1 ovig	—	372	PED 19 T
	1	—	—	381 A-C	WSS 3E
**Nursilia dentata* Bell	1	—	—	371 F	PED 6 Z
**Palicus sexlobatus* n.sp.	1	—	—	371 F	S.A.M. A12642
**Paratergatis longimanus* Sakai	—	1	—	372 L	PED 19 M
	2	—	—	391 C	NAD 51 C
	2	—	—	390 P	NAD 40 K
Philyra globosa (Fabricius)	2	—	—	392 H	NAD 73 B
Philyra globulosa Milne-Edwards	13	8 ovig	—	391 C	NAD 51 A
	—	1 ovig	2	356 J	NAD 86 D
	2	2 ovig	—	392 K	NAD 75 E
Pilumnus hirsutus Stimpson	1	3	—	372 C	PED 12 Q-R
	2	1	—	372 G	PED 16 F-G
Pilumnus longicornis Hilgendorf	1	—	—	371 G	PED 8 X
	—	1	—	356 B	NAD 80 X-Y
	2	4	—	NGY 21	NAD 3 Y
Pinnotherids (Unidentified)	1	—	—	363 W	MDD 1 C
	1	—	—	372 L	PED 19 K
	1	—	—	390 S	NAD 45 J
	1	—	—	372 G	PED 16 H
Platylambrus quemvis Stebbing	5	7+2 ovig	—	391 J NGY 59	NAD 62 A NAD 18 R
Platypodia cf. *granulosa* (Rüppell)	—	1	—	381 A-C	WSS 3 C
Portumnus mcleayi Barnard	1	1 ovig	—	372 C	PED 12 N
	1	—	—	391 J	NAD 64 W
Ranina ranina (Linnaeus)	1	—	—	372 G	PED 16 E
**Retropluma planiforma* n.sp.	2	4	—	390 H	NAD 31 D S.A.M. A12643-5
Thalamita woodmasoni Alcock	—	1 ovig	—	NGY 21	NAD 3 R
Thalamita sp.	—	1 ovig	—	NGY 21	NAD 3 R
Thalamita sp.	2	—	—	Vema 6	NAD 11 C
Xanthias tuberculidens Rathbun	1	—	—	390 S	NAD 45 G
	—	1	—	390 R	NAD 49 R
	—	1	—	371 E	PED 2 D
	1	—	—	356 B	NAD 80 X-Y
	2	—	—	NGY 21	NAD 3 V
? *Xanthias* sp. (Immature)	—	—	2	372 G	PED 16 L
Xanthids (Unidentified)	—	—	5	381 A-C	WSS 3 B
ANOMURA					
PAGURIDEA					
Anapagurus hendersoni Barnard	1	—	—	390 L	NAD 35 G
	1	1	—	390 S	NAD 45 R
	1	—	—	390 C	ABD 14 L
Dardanus arrosor (Herbst)	1	—	—	391 J	NAD 62 T
	—	1+1 ovig	—	GIL 58	NAD 26 S
Dardanus euopsis (Dana)	1	—	—	372 G	PED 16 R-T
Dardanus setifer (Milne-Edwards)	1	—	—	NGY 59	NAD 20 V
	1	—	—	NGY 21	NAD 3 N

	♂	♀	*Juv*	*Station*	*Catalogue Number*
Diogenes brevirostris Stimpson	1	1	—	372 C	PED 12 S
Diogenes costatus Henderson	2	—	—	NGY 59	NAD 18 Y
		many		356 J	NAD 86 A
				392 H	NAD 73 K
				392 K	NAD 75 H
				391 J	NAD 62 S
				391 F	NAD 58 J
				391 C	NAD 51 N
				391 H	NAD 67 C
Diogenes custos (Fabricius)	5	2	—	392 H	NAD 73 J
**Nematopagurus gardineri* Alcock	1	—	—	390 S	NAD 45 P
**Nematopagurus squamichelis* Alcock	2	1	—	370 G	ABD 8 V
Pagurus spinulentus (Henderson)	5	3	—	392 K	NAD 75 J
				GIL 56	NAD 24 D
				NGY 59	NAD 18 V
	1	—	—	356 J	NAD 87 W
	13	7 ovig	—	391 J	NAD 62 N
Pagurus sp.	1	—	—	372 C	PED 12 V
	1	—	—	390 S	NAD 45 Q
	—	—	1	370 G	ABD 8 W
	—	2 ovig	—	372 G	PED 16 R-T
Between *Pagurus & Pylopagurus*	1	—	—	372 G	PED 16 R-T
Parapagurus pilosimanus Smith	2	1	—	358 C	ABD 1 E
? *Pylopagurus* sp.	1	—	—	371 E	PED 2 G
GALATHEIDEA					
Galathea dispersa Bate	2	1	—	357 B	NAD 20 S
	—	1 ovig	—	371 G	PED 8 U
	2	1 ovig	—	372 L	PED 19 L
	—	—	1	371 F	PED 23 D
Galathea intermedia Liljeborg	5	5	—	NGY 59	NAD 20 S
	—	—	2	390 G	NAD 33 N
	—	1	—	NGY 21	NAD 3 Q
	1	4	—	372 G	PED 17 W
Munida sanctipauli Henderson	—	1 ovig	—	373 B	PED 23 Z
	—	1	—	389 G	ABD 13 L
Munida semoni Ortmann	1	1+1 ovig	1	372 L	PED 19 Q
	—	1 ovig	—	373 B	PED 23 C
	—	1+2 ovig	—	371 F	PED 6 X
	2	1	—	372 G	PED 16 C
	10	12	—	390 P	NAD 40 L
	—	2	—	391 C	NAD 51 G
	7	2	—	390 S	NAD 45 B
	11	6	—	390 H	NAD 31 A
Munida cf. *semoni* Ortmann	—	1 ovig	—	371 F	PED 6 X
**Petrolisthes militaris* (Heller)	5	3	—	372 G	PED 16 A
	1	—	—		ABD 82 M
Porcellana dehaanii Krauss	—	—	2	356 B	NAD 80 Z
Porcellana streptocheles Stimpson	2	2	—	357 B	NAD 91 J
	—	1	—	356 B	NAD 82 M
	3	—	—	NGY 21	NAD 3 P
	—	—	1	372 C	PED 12 T
	4	6	—	372 G	PED 16 A
THALASSINIDEA					
**Axius* (*Neaxius*) sp.	1	—	—	357 B	NAD 91 N
	—	1	—	356 B	NAD 81 A

	♂	♀	*Juv*	*Station*	*Catalogue Number*
Callianassa sp.	1	—	—	390 H	NAD 31 B
Callianassa sp.	—	1	—	390 H	NAD 31 B
MACRURA					
PENAEIDEA					
Acetes erythraeus Nobili	5	3	2	NGY 21	NAD F
	2	13	—	392 H	NAD 73 F-H
	—	1	—	392 K	NAD 75 N
**Gennadas propinquus* Rathbun	1	—	—	363 P	ABD 5 A
Macropetasma africana (Balss)	1	10	—	392 H	NAD 73 E
Metapenaeopsis adamanensis (Wood-Mason)	—	1	—	390 S	NAD 45 T
Metapenaeopsis cf. *stebbingi* Nobili	—	—	1	392 H	NAD 73 F-H
Parapenaeus fissurus (Bate)	1	—	—	390 P	NAD 40 R
	—	1	—	391 C	NAD 51 M
	—	—	1	390 L	NAD 35 N
Penaeopsis rectacuta (Bate)	—	1	—	370 G	ABD 8 T
Penaeus japonicus Bate	1	—	—	392 H	NAD 73 D
Sergestes prehensilis Bate	1	—	—	390 C	ABD 14 R
Solenocera africanum Stebbing	1	—	—	390 P	NAD 40 S
	—	1	—	390 H	NAD 31 G
Solenocera ? *pectinata* (Bate)	1	—	—	390 P	NAD 40 R
Solenocera sp.	?1	—	—	390 L	NAD 35 Q
CARIDEA					
Alpheus frontalis Milne-Edwards				390 G	NAD 33 K
**Alpheus nonalter* n.sp.	sev.	sev.	—	390 H	NAD 31 H, S.A.M. A12650–1
	sev.	sev.	—	390 P	NAD 40 M
				391 C	NAD 51 H-J
	1	—	—	372 L	PED 19 P
**Alpheus waltervadi* n.sp.	4	2 ovig	6	381 A-C	WSS 2 Y, S.A.M. A12646–7
Alpheus sp. (damaged)	1	—	—	391 J	NAD 62 V
	1	—	—	NGY 59	NAD 20 Q
				390 P	NAD 40 N
				392 K	NAD 75 P
				390 N	NAD 43 B-C
Chlorotocus crassicornis (Costa)	—	1	3	390 L	NAD 35 M
	—	1	—	390 C	ABD 14 T
	1	1 ovig	—	390 P	NAD 40 U
	—	1	—	372 L	PED 19 Y-Z
Eualus ctenifera (Barnard)	?4	2 ovig	—	381 A-C	WSS 2 Z
**Heterocarpus woodmasoni* Alcock	—	1	—	370 G	ABD 8 U
Hippolysmata vittata Stimpson	—	1	—	356 B	NAD 81 B-E
Latreutes mucronatus (Stimpson)	5	3 ovig	sev.	356 B	NAD 81 B-E
	?1	—	—	372 C	PED 12 U
	?1	—	—	372 G	PED 16 X-Y
Leptochela pugnax de Man	—	1	—	392 F	NAD 72 P
Leptochela robusta Stimpson	—	1 ovig	—	371 E	PED 2 C
Nikoides cf. *danae* Paulson	1	1	—	356 J	NAD 86 F
**Oplophorus spinicauda* Milne-Edwards	—	?1	—	363 P	ABD 5 C
Periclimenes (*Periclimenes*) sp.	?3	—	—	356 B	NAD 81 B-E
Periclimenes sp.	?1	—	—	373 B	PED 22 U

	♂	♀	*Juv*	*Station*	*Catalogue Number*
**Plesionika* cf. *acanthonotus* (Smith)	2	—	—	390 P	NAD 40 T
	1	1	—	390 H	NAD 31 F
Plesionika martia (Milne-Edwards)	—	?1	—	392 H	NAD 73 F-H
	2	—	—	358 C	ABD 1 D
Pontocaris cataphracta (Olivi)	—	1 ovig	—	372 L	PED 19 W
	1	1 ovig	—	372 G	PED 16 U
	1	—	—	391 F	NAD 58 H
	1	1 ovig	—	391 J	NAD 62 W
	1	—	—	390 P	NAD 40 Q
	3	—	—	391 C	NAD 51 S
Pontocaris lacazei (Gourret)	2	—	—	390 C	ABD 14 P
	—	1	—	390 L	NAD 35 P
Processa austroafricana Barnard	2	4+5 ovig	1	390 L	NAD 35 L
	—	1 ovig	—	390 P	NAD 40 V
	—	—	1	356 B	NAD 81 B-E
Processa sp.	—	1 ovig	—	372 G	PED 16 X-Y
Stylodactylus bimaxillaris Bate	—	1 ovig	—	372 L	PED 19 Y-Z
	—	—	1	390 P	NAD 40 W
Synalpheus anisocheir Stebbing	—	3+3 ovig	4	NGY 21	NAD 4 B
	?1	—	—	NGY 59	NAD 20 Q
Synalpheus jedanensis de Man	—	1+2 ovig	—	372 G	PED 16 V-W
Synalpheus cf. *jedanensis* de Man	—	1	—	357 B	NAD 91 M
Tozeuma armata (Paulson)	?1	—	—	371 G	PED 8 Z

Systematic Discussion

BRACHYURA

Family **Parthenopidae**

Eumedonus granulosus MacGilchrist, 1905

Fig. 1 a–b

Eumedonus granulosus MacGilchrist, 1905: 253. Rathbun, 1911: 259. Flipse, 1930: 90. Barnard, 1954: 96.

Previous records: Amirante, Persian Gulf, Zanzibar, Delagoa Bay.

Material: 1 ♂, carapace length (including rostrum) 4 mm, carapace breadth (including lateral spines) 3·8 mm. Station BRU 372 G. Depth, 55 metres.

Remarks: The present specimen appears to differ from the original description of *E. granulosus* only in the degree of granulation of the carapace. From MacGilchrist's description and figures (latter in *Illustrations of the zoology of the R.I.M.S. 'Investigator'*, 1907, plate 77, figs 2, 2a), it would seem that the whole integument is granulated, whereas in the present specimen it is granulated only in the antero-lateral region. The specimen recorded by Barnard (1954) has the carapace granulated in the mid-region only. The carapace grooves of the type are more distinct than in this specimen. Body proportions are similar. Unfortunately, all the pereiopods and chelipeds are missing. The differences mentioned may be due to the immaturity of the specimen, as the type measures 11·5 × 11·5 mm.

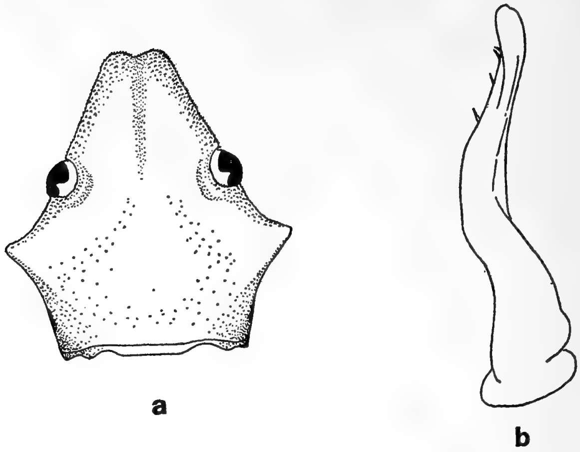

Fig. 1. *Eumedonus granulatus* MacGilchrist
a. Carapace. *b*. First pleopod, male.

Family **Xanthidae**

Paratergatis longimanus Sakai, 1965

Paratergatis longimanus Sakai, 1965*a*: 98, fig. 1; 1965*b*: 128, fig. 16.

Previous records: Sagami Bay and near-by Japanese islands.

Material: 1 ♀, carapace length 12·0 mm, carapace breadth 19·0 mm. Station BRU 372 L. Depth, 112 metres. 2 ♂♂, carapace lengths 10·6 mm, 6·0 mm, carapace breadths 17·0 mm, 7·0 mm. Station BRU 390 P. Depth 118 metres. 2 ♂♂, carapace lengths 12·0 mm, 5·0 mm, carapace breadths 19·0, 8·0 mm. Station BRU 391 C. Depth 86 metres.

Remarks: There can be no doubt that this is the same species as that recorded by Sakai (1965*a*, *b*). This would appear to be the first record of this monotypic genus outside Japanese waters.

Family **Palicidae**

Cympolidae: Rathbun, 1918: 182. Sakai, 1939: 607.
Palicidae: Holthuis & Gottlieb, 1958: 104.

Palicus sexlobatus n.sp.

Fig. 2 a–e

Description: Carapace wider than long, dorsally convex, granular, with larger scattered tubercles, margins crenulate. Fronto-orbital margin with 2 pairs of spines, inner 2 more slender, longer than outer spines, set slightly lower than latter. 3 supra-orbital teeth, innermost broadest, outer 2 acutely triangular. External orbital tooth largest of 6 antero-lateral teeth, latter decreasing in size posteriorly. Postero-lateral margin of carapace concave at origin of 5th pereiopod. (Latter dorsal in position.) Posterior margin with 6 separated flattened lobes. Gastric region tuberculate, with anterior row of 4 larger transverse tubercles, 2 posterior transverse tubercles. Gastric region separated from cardiac and branchial regions by well-defined grooves. Cardiac region with row of 4 transverse flattened tubercles, inner 2 larger. Branchial regions with scattered tubercles. Lower orbital margin formed by 2 broad rounded crenulated lobes.

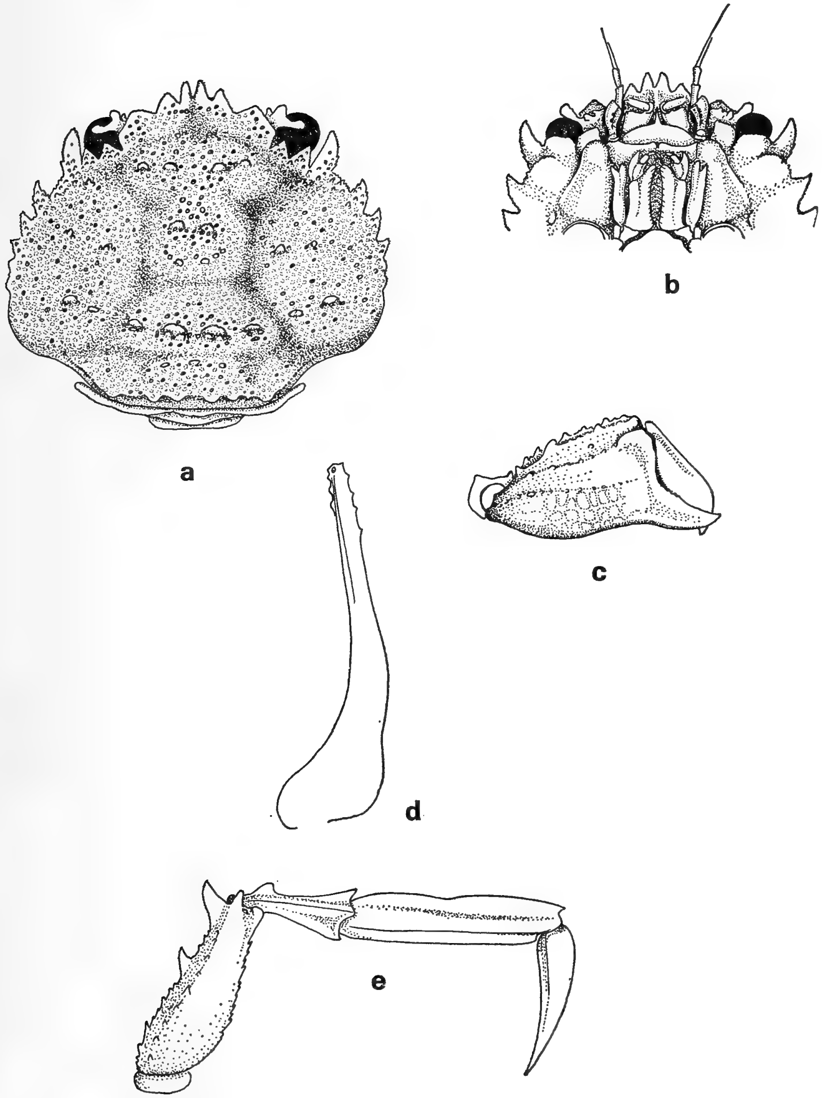

Fig. 2. *Palicus sexlobata* n.sp.
a. carapace, dorsal view. *b*. Antero-ventral region of carapace. *c*. Right cheliped. *d*. First pleopod, male. *e*. Second pereiopod.

Distal portion of basal joint of antenna wider than proximal part, with 3 small ventral tubercles. 2nd and 3rd joints of peduncle slender, equal in length. Eye wider than stalk, latter with 3 dorsally visible lobes. 4th joint of endopod of maxilliped 3 with external curved flattened portion. Right cheliped stout, (left missing), upper surfaces of propodus, carpus, merus tuberculate. Finger and thumb flattened, tips overlapping, cutting edge entire. Pereiopods stout, meri granulate, upper surface with 2 large spines, more anterior of which largest, plus several smaller flattened spines. Lower surface with many small spines. Carpus half length of merus, slightly flattened, proximally with a flattened rounded lobe on upper edge, distally with an acute flattened spine. Propodus and dactylus flattened, lower edge of latter entire. Abdomen with 7 segments, first 2 very short, with prominent transverse raised ridge. 3rd segment twice length of 2nd, also with raised ridge, all 3 ridges dorsally visible.

Material: 1 ♂, holotype, S.A.M. A12642, carapace length (including rostral spines) 8·6 mm, carapace breadth 10 mm. Station BRU 371 F. Depth 110 metres.

Remarks: This species would seem to be most closely related to *P. investigatoris* (Alcock), but differs in the arrangement of the larger tubercles of the carapace, also in the posterior carapace ridge. The latter has 6 flattened lobes in *P. sexlobatus*, 8 in *P. investigatoris*. The ambulatory pereiopods differ in that the propodi and dactyli of *P. investigatoris* are denticulate on their lower edges, entire in *P. sexlobatus*. This appears to be the first record of this cosmopolitan genus from the Moçambique Channel.

Family **Retroplumidae**

Alcock & Anderson, 1894: 180. Gill, 1894: 1044. Doflein, 1904: 29. MacGilchrist, 1905: 266. Tesch, 1918: 29. Rathbun, 1932: 33. Sakai, 1948: 606.

Retropluma planiforma n.sp.

Fig. 3 a–g

Description: Carapace more or less flattened, almost naked, slightly granular. Carapace divided into 3 parts by 2 transverse carinae. Entire carapace margin crenulated. Anterior portion sloping forward to slender apically rounded rostrum. Latter slightly shorter than basal antennular peduncle joint. Supraorbital border smoothly contoured, unarmed. External orbital angle a rounded forwardly projecting lobe. Antero-lateral border sloping obliquely outward from external orbital lobe to more anterior lateral carapace lobe. Latter is extension of anterior transverse carina. Lateral margin of middle carapace portion with a convex rounded lobe. Second carapace carina slightly curved. Carapace wider than long (excluding rostrum). Postero-lateral angles rounded. Eyestalks free, directed laterally, upper surface granular. Base of eyestalks wider than cornea. Infra-orbital spine prominent, forwardly directed, margins crenulated, reaching to middle of second joint of antennal peduncle. Latter

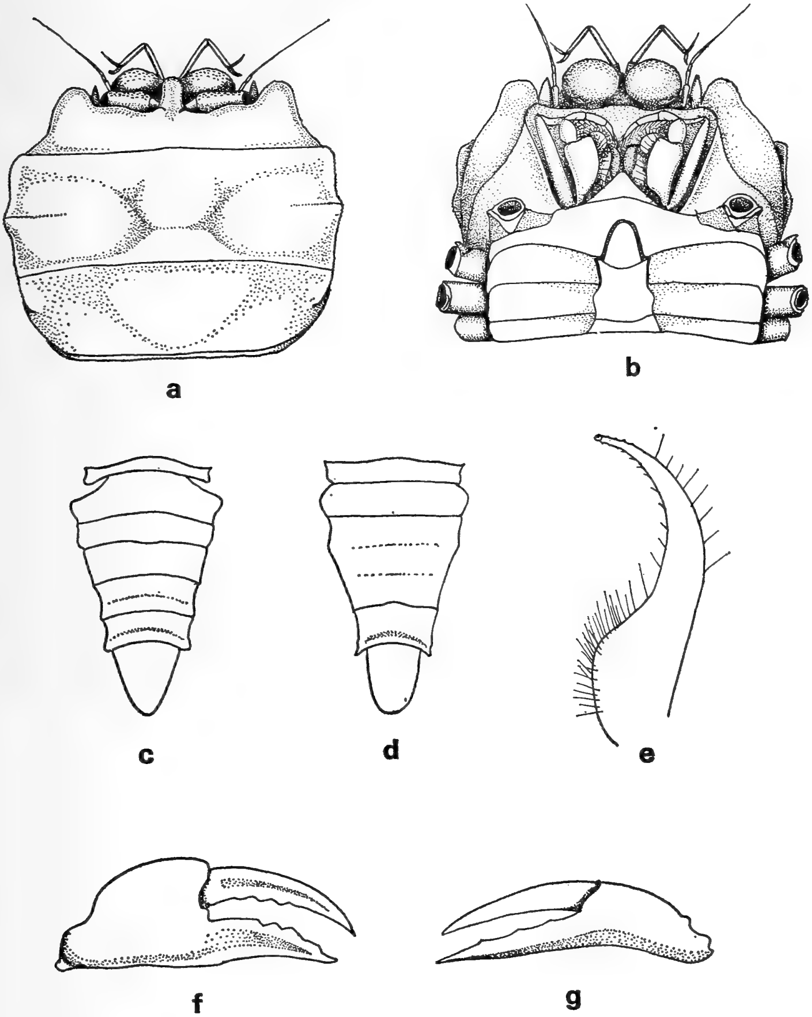

Fig. 3. *Retropluma planiforma* n.sp.
a. Carapace, dorsal view. *b*. Carapace, ventral view. *c*. Abdomen, female. *d*. Abdomen, male. *e*. First pleopod, male. *f*. Right chela. *g*. Left chela.

half length of basal joint. Flagellum of antenna with 19 or 20 joints. Basal antennular joint globular, inflated, granular. 2nd joint arising at antero-mesial corner of basal joint. Bases of antennae, antennules and infra-orbital spines in a line. Chelipeds equal in length, right stouter than left, palm higher, equal in length to finger. Palm of left chela shorter than finger, upper borders of both chelae smooth. Fingers wide at base, compressed. A gap between fingers of right chela. Fingers of latter with 3 (possibly 4) teeth, on sharp cutting edge

Cutting edge of left chela only slightly denticulate. All pereiopods fringed with feathered hairs. Ambulatory pereiopods (i.e. 2, 3, 4) long and slender, 2nd pair longest. Dactyli slender, slightly curved, equal in length to outer margin of propodus of same pereiopod. Anterior margins of propodi and carpi, anterior and posterior margins of meri finely denticulate. Distal denticles of carpi and proximal denticles of propodi particularly well developed. 5th pereiopods reduced, almost dorsal, prominently fringed with feathered hairs. Entire 5th pereiopod equal in length to merus of 4th. Abdomen of male and female triangular. Abdomen of female 7-jointed, 7th longest, apically rounded. 6th segment with lateral notch, distal blunt tooth, a raised ridge between the notches. Abdomen of male 5-jointed, 3rd joint largest (consisting of fused segments 3–5), 6th joint with posteriorly directed lateral tooth, also with raised ridge. 7th segment apically rounded. Pleopods of female sometimes protruding from beneath abdomen.

Material: Holotype, S.A.M. A12644, paratypes, S.A.M. A12643, A12645.

	♀ carapace			♂ carapace		Station	Depth (m)
	length	breadth		length	breadth		
Holotype	7·0	9·1	Paratype	5·8	7·9	BRU 390 H	200
Paratype	5·4	6·5		5·4	7·0		
	6·8	9·0					
	4·5	6·0					

Remarks: The genus *Retropluma* is represented by 5 species, viz. *notopus* (Alcock & Anderson, 1894), from the eastern Indian Ocean, *chuni* Doflein, 1904, from the Andaman Islands, *plumosa* Tesch, 1918, from the Kei Islands in the Banda Sea, and *denticulata* Rathbun, 1932, from Japan. *Retropluma eocenica* Via Boada, 1959, has been recorded from the Eocene of Spain. The present species differs from *notopus* and *denticulata* in having rounded lobes on the lateral margins of the carapace and an apically rounded rostrum. *R. notopus* has no lateral extrusions, neither has *denticulata*. The rostrum is apically bifid in *notopus*, a mere point in *denticulata*. *R. planiforma* differs from *chuni* in that while the latter has acute lateral carapace spines and a tapering rostrum, the former has rounded lobes and a rostrum with parallel sides. *R. planiforma* most closely resembles *plumosa* in the rounded carapace lobes, the shape of the male abdomen and the granulate character of the integument, especially that of the appendages. The main differences include the shape of the rostrum (tapering in *plumosa*) the externo-orbital angles (angular in *plumosa*, rounded in *planiforma*), the denticulate nature of the ambulatory pereiopods in *planiforma* (granulate but not noticeably denticulate in *plumosa*). The antennal flagellum has fewer segments (25 in *plumosa*, 19–20 in *planiforma*). A very obvious difference is the lack of specialized hairs found on the appendages in *plumosa*. These hairs are scattered amongst the plumose hairs and are inflated and membranous. *R. planiforma* has only plumose hairs.

Family **Dorippidae**

Ethusa sinespina n.sp.

Fig. 4 a–c

Ethusa spp. Alcock, 1896: 281–286. Doflein, 1904: 27–32.

Description: Carapace slightly longer than broad, finely and evenly granulate, anterior portion with fine scattered hairs. Frontal indentation forming angle of about 60°. Front bilobed, 4-toothed, inner teeth slightly longer than outer, smooth rounded indentation separating the 2 teeth. Supra-orbital angle acute. External orbital spine acute, directed slightly outward, not reaching to tip of outer frontal spine. Carapace regions not very well demarked, cardiac and branchial regions with indistinct delimiting grooves. Branchial regions very slightly convex in dorsal view. Antennal peduncle slightly longer than frontal spines. Eyestalks stout, movable. Efferent branchial canals ending just behind frontal notch. Chelipeds small, finger and thumb equal in length to palm. Finger and thumb separated by gap, each with 4 small teeth on cutting edge. Dactylus of 3rd leg longer than propodus, equal in length to merus. Abdomen 7-jointed, 3rd and 4th joints widest. Distal segment apically rounded.

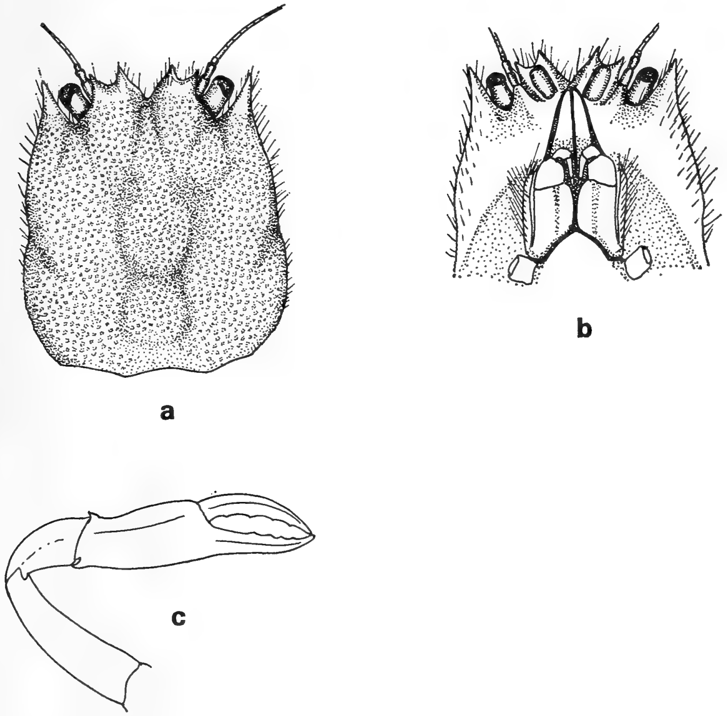

Fig. 4. *Ethusa sinespina* n.sp.
a. Carapace, dorsal view. *b*. Carapace, antero-ventral region. *c*. Right cheliped.

Material: 1 ♀, paratype, S.A.M. A12649 carapace length, 5·8 mm, carapace breadth 5·2 mm. Station BRU 390 S. Depth 138 metres. 1 ♀, ovigerous, Holotype, S.A.M. A12648, carapace length 7·5 mm, carapace breadth 6·8 mm. Station BRU 390 E. Depth 350 metres. 1 ♀, carapace length 4 mm, carapace breadth 3·5 mm. Station BRU 358 C. Depth 370 metres.

Remarks: These specimens are most closely related to *E. zurstrasseni* Doflein, recorded by the *Valdivia* from the East African coast, but differ from this species in that there is no minute spine between the pairs of frontal spines. The external orbital spine is not dorso-ventrally flattened. The grooves defining the carapace regions are not so well defined as in *zurstrasseni.*

Family **Leucosiidae**

Nursilia dentata Bell, 1855

Fig. 5 a–e

Nursilia dentata Bell, 1855: 309. Alcock, 1896: 260. Rathbun, 1911: 203.

Description: Entire carapace finely and evenly granular, roughly hexagonal. Front with large raised supra-orbital lobes, with single smaller ventro-lateral exorbital tooth. Indistinct mid-dorsal carapace carina, stretching from base of supra-orbital lobes to 1st median spine in cardiac region. 4 blunt prominent spines in median cardiac region, most anterior of which largest, flanked by

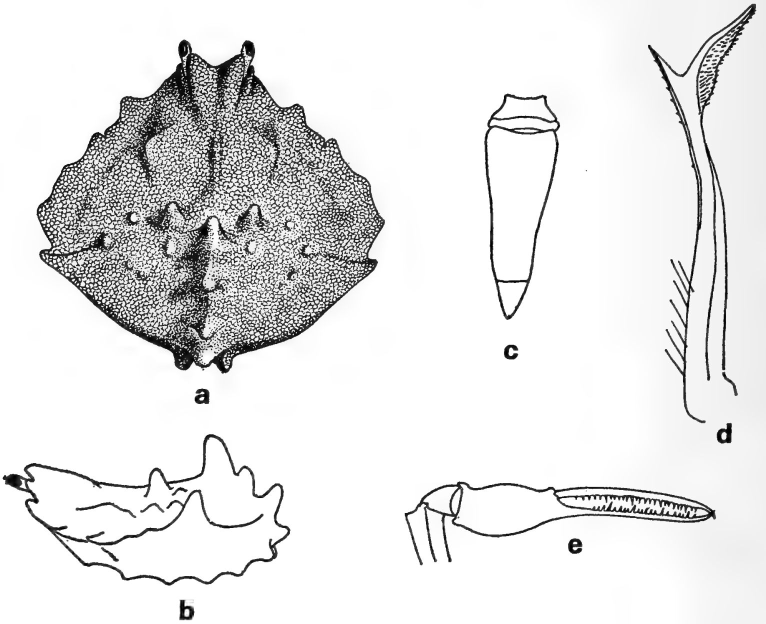

Fig. 5. *Nursilia dentata* Bell.
. Carapace, dorsal view. *b.* Carapace, lateral view. *c.* Abdomen, male. *d.* First pleopod, male. *e.* Right chela.

pair of blunt knobs on posterior gastric region. Lateral carapace margin slightly upturned, with 5 teeth, most posterior of which largest. Between largest lateral tooth and median line, 4 or 5 slight knobs. Abdomen of 4 segments, first 2 narrow, 3rd largest, latter three times longer than broad, with single forwardly directed median spine near distal margin; distal segment triangular, apically rounded. Palm of left chela slightly inflated, two-thirds length of fingers. Latter slender, with about 25 large and small teeth on cutting edge.

Previous records: Andaman Sea, off Ceylon, Madras coast, off Maldives, Seychelles, Malabar coast, Cargados Carajos.

Material: 1 ♂, carapace length 7 mm, carapace breadth 8 mm. Station BRU 371 F. Depth 110 metres.

ANOMURA

Family **Paguridae**

Nematopagurus squamichelis Alcock, 1905

Fig. 6 a–d

Nematopagurus squamichelis Alcock, 1905: 113, pl. 12, fig. 1.

Description: Carapace breadth three-quarters that of length, broadest in branchial region. Latter clearly defined dorsally by 2 ridges. Cervical groove distinct. Rostrum lacking, frontal margin smoothly curved. Eyes much wider than eyestalks, latter stout, one-third of carapace length. Ocular scales tiny. Chelipeds equal in length, right stouter than left. Tips of finger and thumb corneous, entire hand and fingers and carpus of chelae covered with flat imbricating squamae. Vas deferens of male protruding on right side, slender and elongate, ending in coiled filament. Vas deferens of left side protruding as short conical papilla.

Previous records: Andaman Sea.

Material: 2 ♂♂, carapace length 7·5 mm, 8·0 mm, 1 ♀, carapace length 5·5 mm. Station BRU 370 G. Depth 347 metres.

Nematopagurus gardineri Alcock, 1905

Fig. 6 e–h

Nematopagurus gardineri Alcock, 1905: 110, plate 12, fig. 2.

Description: Carapace breadth half length. Cervical groove and ridges defining branchial regions well marked. Rostrum lacking, frontal margin smoothly rounded, tiny supra-antennal spine present. Ocular scale minute. Eyes wider than eyestalks. Chelipeds thickly pilose, especially on outer surface of propodus and carpus. Right chela slightly longer, much stouter than left. Cutting edges and tips of finger and thumb corneous. Upper edge of carpus and propodus spinous, denticulate. Outer surface with median longitudinal row of spines.

Previous records: Maldive Islands.

Material: 1 ♂, carapace length 4·8 mm. Station BRU 390 S. Depth 138 metres.

Remarks: Easily distinguished from the previous species by the pilose and spinous nature of the chelipeds.

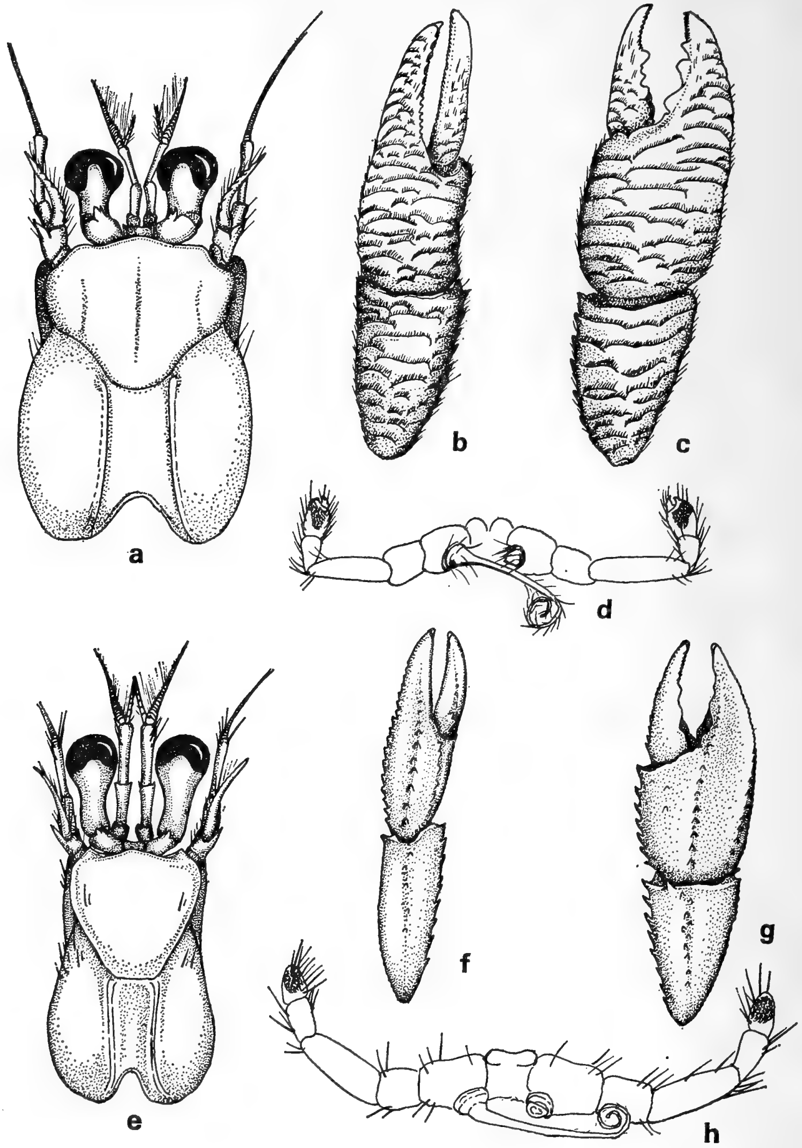

Fig. 6. *Nematopagurus squamichelis* Alcock.
a. Carapace, and anterior appendages. *b.* Left chela and carpus. *c.* Right chela and carpus.
d. Sternum and 5th pair pereiopods, male.

Nematopagurus gardineri Alcock.
e. Carapace and anterior appendages. *f.* Left chela and carpus. *g.* Right chela and carpus.
h. Sternum and 5th pair pereiopods, male.

Family **Galatheidae**

Munida semoni Ortmann, 1894

Munida semoni Ortmann, 1894: 24, plate 1, fig. 4. Barnard, 1950: 491, fig. 92c.

Material: see page 153 of species list.

Remarks: The present specimens agree closely with *semoni*, but differ in the following respects: the 2nd abdominal segment has 8 spines on the anterior margin, the posterior portion of segments 2 and 3 with only 1 setose transverse groove (2 in *semoni*), 4th joint of maxilliped 3 with only 2 strong spines (3 in *semoni*). In smaller specimens, there are sometimes 2 spines on the anterior margin of the 3rd abdominal segment.

Petrolisthes militaris (Heller, 1862)

Fig. 7 a–d

Petrolisthes militaris (Heller), Miyake, 1943: 56. Haig, 1964: 357.

Description: Carapace length (including rostrum) equal to breadth. Frontal margin broadly triangular, apically rounded, base (between supra-orbital teeth) just less than twice length, margin finely crenulated. Prominent supra-

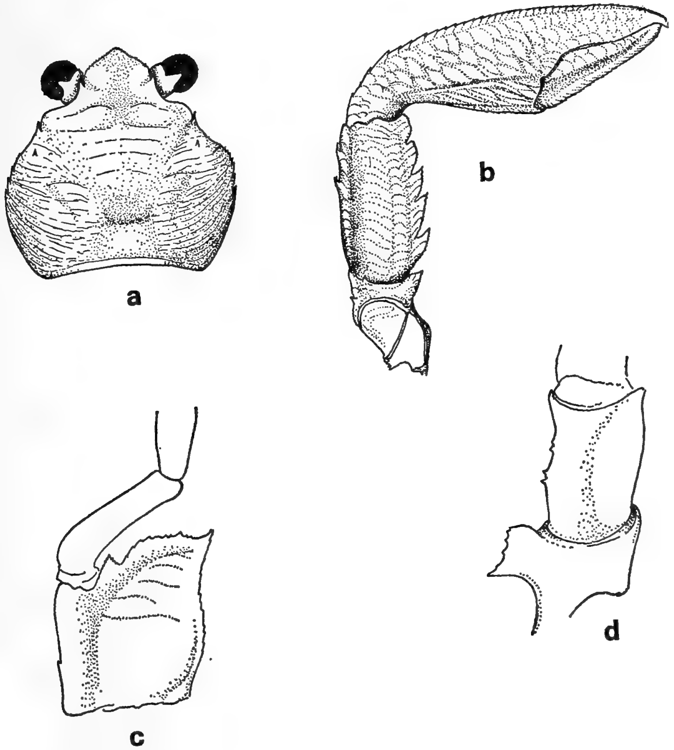

Fig. 7. *Petrolisthes militaris* (Heller).
a. Carapace. *b.* Left cheliped. *c.* Basal joint of antennule. *d.* Basal joints of antenna.

orbital spine present. Epibranchial spine present. Just posterior to latter, small spine in antero-branchial region. Lateral branchial margin with 2 or 3 largish spines, anterior to which, 2 or 3 minute spines. Gastric and branchial regions covered with transverse rugae. Basal joint of antennule with distal toothed keel. 1st free peduncular joint of antenna with distal slightly flattened denticulate lobe. Chela longer than carapace. Merus, carpus, propodus, and dactylus of cheliped covered with flattened rugae. Merus with large crenulated tooth on inner distal angle. Carpus with 5 crenulate flattened teeth on anterior margin, distal 2 apically blunt. Posterior margin of carpus with 3 small distal spines. Proximal posterior margin of chela slightly denticulate, denticles decreasing in size distally. Meri of ambulatory pereiopods with flattened rugae. Propodi cylindrical, about twice length of carpus. Dactylus with 3 sharp spines on lower margin, ending in acute curved talon.

Distribution: Widespread throughout Indo-Pacific region.

Material:

♂ carapace length	♀ carapace length	Station	Depth (m)
4·0	4·5	BRU 372 G	55
4·0	5·0		
4·6	6·0		
5·0			
6·0			
3·5			

Remarks: These specimens would appear to constitute the most south-westerly record for the species.

THALASSINIDEA

Family **Axiidae**

Axius (*Neaxius*) sp.

Fig. 8 a–b

Description: Rostrum triangular, breadth equal to length, apically notched, margin with 4 spines. Prominent exorbital spine, region between latter and base of rostrum smooth. Lateral margin of anterior carapace region with 13 to 14 spines. Very prominent cervical groove. Anterior two-thirds of flattened part of carapace with scattered spines. Telson slightly broader than long, without transverse carinae.

Material: 1 ♂, carapace length 4 mm, overall length 9·5 mm. Station BRU 357 B. Depth 70 metres. 1 ovigerous ♀, dimensions as ♂. Station BRU 256 B. Depth 18 metres.

Remarks: As many of the appendages are missing, it is difficult to be definite about the specific position of these specimens. *Axius acanthus* var. *mauritianus* Bouvier, 1914, has been recorded from Mauritius. This species has a telson with 2 transverse carinae, poorly developed lateral carapace spines, and no scattered carapace spines. The present specimens lack the telson carinae, while possessing scattered spines on the carapace, and well-developed antero-lateral carapace spines.

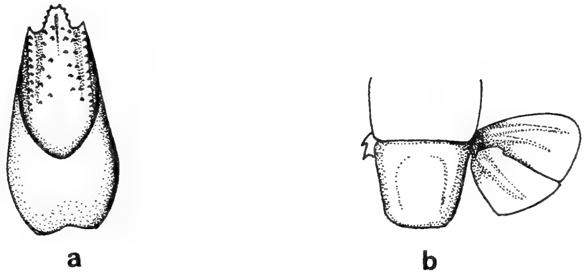

Fig. 8. *Axius* (*Neaxius*) sp.
a. Carapace. *b*. Telson and uropod.

PENAEIDEA

Family **Penaeidae**

Gennadas propinquus Rathbun, 1906

Fig. 9

Gennadas propinquus Rathbun, 1906: 907. Barnard, 1950: 634.
Gennadas scutatus Kemp, 1910: 178, *non* Bouvier, 1908: 42.
Gennadas scutatus indicus Balss, 1927: 259.

Previous records: Indian Ocean, off Hawaii.

Material: 1 ♂, carapace length (including rostrum), 9 mm. Station BRU 363 P. Depth 1225 metres.

Fig. 9. *Gennadas propinquus* Rathbun. Petasma.

CARIDEA

Family **Pasiphaeidae**

Leptochela pugnax de Man, 1920

Fig. 10 a–c

Leptochela pugnax de Man, 1920: 26. Kemp, 1925: 255. Barnard, 1958: 6 (In *L. robusta*).

Description: Rostrum slender, reaching beyond eyes to 2nd antennular peduncle segment. Small antennal spine present. Rostral carina not continued posteriorly along carapace. Dactylus of 2nd pereiopod with about 19 spines, finger of propodus with about 21 spines. 5th abdomimal segment not dorsally carinate, unarmed. Pleurae of 3rd, 4th, 5th abdominal segments ventrally rounded, each with small tooth in anterior region. 6th abdominal segment with long ventro-lateral spine about two-thirds from anterior end, followed by several setae. Posterior margin of 6th segment with prominent lateral spine. Anterior part of telson with 1 pair of dorsal spines, 1 pair of lateral spines at about the mid-point. Telson with 5 pairs of apical spines.

Previous records: Maldives, Andamans, Nicobars, Mergui Archipelago.

Material: 1 ♀, carapace length 4 mm, overall length 13 mm. Station BRU 392 F. Depth 35 metres.

Remarks: The present species closely resembles *L. robusta* Stimpson, which has

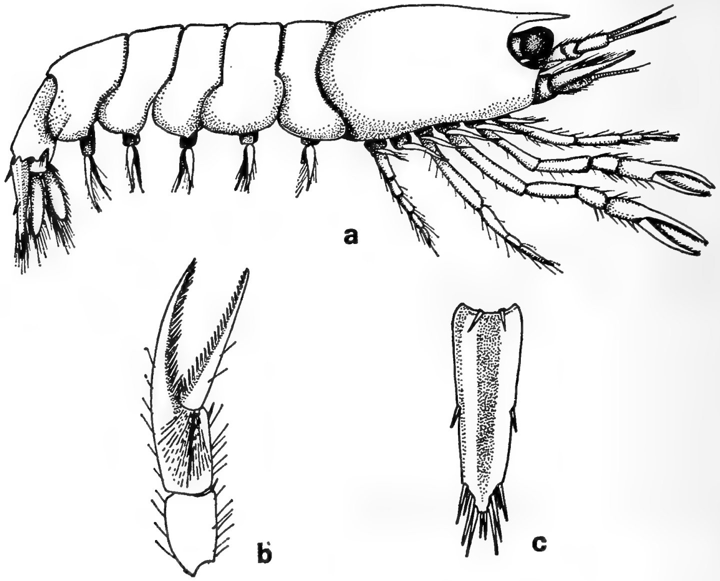

Fig. 10. *Leptochela pugnax* de Man.
a. Lateral view. *b*. First chela. *c*. Telson.

been recorded from Inhambane, but differs in the possession of an antennal spine, and one pair of lateral telson spines and not two as in *robusta*.

Family **Oplophoridae**

Oplophorus spinicauda Milne-Edwards, 1883

Fig. 11

Oplophorus spinicauda Milne-Edwards, 1883: plate 29. de Man, 1920: 48. Chace, 1940: 184.

Description: Postero-lateral angle of carapace lacking tooth. 2nd, 3rd, 4th abdominal segments ending in long spines. Telson terminating in end piece, latter armed laterally with spines.

Previous records: East coast of U.S.A., West Indies, off Morocco, north of Malagasy Republic, off Indian coast, Philippines, Hawaii.

Material: 1 ? ♀, carapace length (excluding rostrum) 5·5 mm. Station BRU 363 P. Depth 1225 metres.

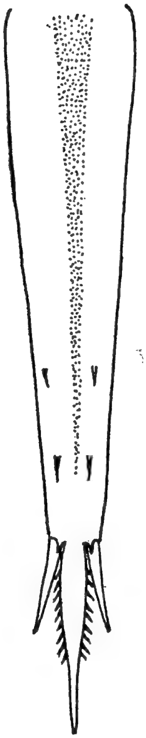

Fig. 11. *Oplophorus spinicauda* M.-Ed.
Telson.

Family **Pandalidae**

Heterocarpus woodmasoni Alcock, 1901

Fig. 12

Heterocarpus woodmasoni Alcock, 1901: 108. de Man, 1920: 156.

Description: Rostrum one and a half times longer than carapace, 10 dorsal, 7 ventral teeth. Rostral carina produced almost to posterior margin of carapace, posterior portion indistinct. Carapace with prominent post-antennular and post-antennal carinae, starting with prominent antennal and branchiostegal spines respectively. Antennal scale two-thirds carapace length. 1st pereiopods equal in length to 3rd maxillipeds, ending in minute dactyl. 2nd pereiopods both chelate, right shorter than left. Right chela slightly larger than left, carpus of former with 12 segments, carpus of latter with about 20 segments. 3rd, 4th, 5th pereiopods similar, with slender dactyls. Abdominal segments 1 and 2 dorsally smooth, 3rd with flattened hook-like tooth, 4th, 5th, 6th dorsally smooth. Telson elongate, tapering, equal in length to outer branch of uropod, apically pointed, with 2 pairs of subapical spines.

Previous records: Bali Sea, Makassar, Kei Islands, Madura Straits, Andaman Sea.

Material: 1 ♀, carapace length (excluding rostrum) 9 mm, overall length 43 mm. Station 370 G. Depth 347 metres.

Remarks: This appears to be the most southerly record of this very distinctive Indian Ocean species.

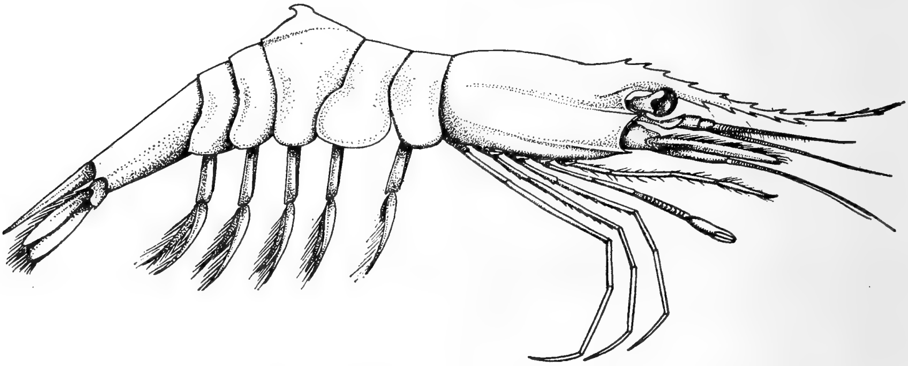

Fig. 12. *Heterocarpus woodmasoni* Alcock.
Lateral view.

Plesionika acanthonotus (Smith, 1882)

Fig. 13 a–b

Pandalus acanthonotus Smith, 1882: 61, plate 13, figs 10, 11.
Plesionika acanthonotus (Smith), de Man, 1920: 105. Holthuis, 1951: 62, fig. 13 b-t.

Description: Rostrum two-thirds carapace length, compressed, spines variable (11/5, 12/4, 12/5). Prominent antennal and branchiostegal spines. Basal joint of antenna with prominent spine on lower distal angle. Antennal scale seven-eighths carapace length, rostrum two-thirds antennal scale length. Carapace and abdomen with minute scales. 1st pereiopod with microscopic dactyl, very slender, propodus half length of carpus, 2nd pereiopods equal in length, reaching beyond antennal scale. Chela about one-eighth length of carpus. Latter consisting of about 21 jointlets. Merus and ischium equal in length, each slightly more than half length of carpus. Dactyl of 3rd pereiopod one-third length of propodus, merus reaching to end of antennal scale. Posterior margin of merus with 11 spines. 4th pereiopod similar to 3rd. 5th pereiopod longest, midpoint of carpus reaching to end of antennal scale. Merus armed with 8 spines. Pleuron of 5th abdominal segment with tooth on postero-ventral angle. Telson with 3 pairs lateral spines, slightly shorter than inner branch of uropod, latter slightly shorter than outer branch. Outer margin of outer branch with tooth some way behind apex.

Previous records: East coast of U.S.A., off Portugal, Spain, Brazil, Angola.

Material: 1 ♂, carapace length (excluding rostrum) 6 mm, 1 ♀, carapace length 5 mm. Station BRU 390 H. Depth 175–200 metres. 2 ♂♂, carapace lengths 8 mm, 7·5 mm. Station BRU 390 P. Depth 118 metres.

Remarks: From de Man's 1920 key to the genus *Plesionika*, this specimen falls into the group characterised by a rostrum shorter than the carapace, 2nd pereiopods equal in length. The species in this group, viz. *hypanodon* Doflein,

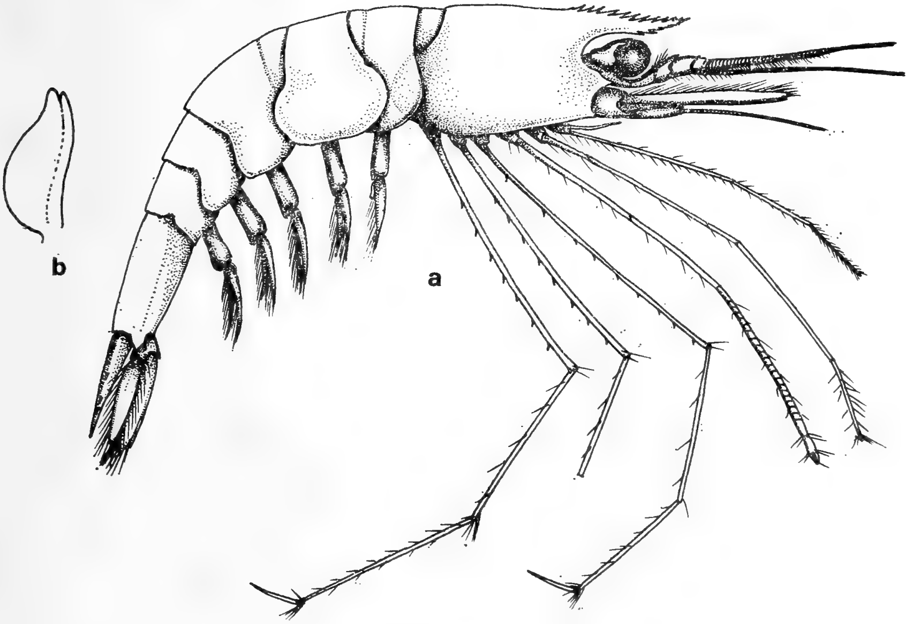

Fig. 13. *Plesionika acanthonotus* (Smith).
a. lateral view. *b.* Endopod of pleopod one.

and *brevis* (Rathbun) bear little resemblance to the present species, which more closely resembles the *ortmanni* Doflein, *longipes* (Milne-Edwards), *sindoi* (Rathbun) group, in spite of the short rostrum. This species most closely resembles *P. acanthonotus* (Smith). The rostra of the 2 species are very similar, being shorter than either the carapace or the antennal scale. The variation in number of the rostral teeth in this species is similar to that of *acanthonotus*. The shape of the telson, abdomen, and antennular peduncle also agree closely. The pereiopods are similar in both species, including the number of jointlets of the carpus of the 2nd pereiopods. The mouthparts are identical. The antennal scale of this species appears proportionally more slender than *acanthonotus*, while the endopod of the 1st pleopod in the male differs in shape. It seems unusual that such a typically Atlantic species should occur in the Indian Ocean. Without further material it is not possible to be more definite regarding the status of this species, but if not *acanthonotus*, it is certainly very closely related.

Family **Processidae**

Processa sp.

Fig. 14

Description: Rostrum apically bidentate, reaching to posterior part of orbit. Lateral process of basal joint of antennule smoothly rounded, with a slightly elongate inner rounded angle. Antennal scale apically rounded, spine on outer margin slightly longer than apex. Palm of chela of right 1st pereiopod almost twice length of finger and thumb. Dactylus of left 1st pereiopod about one-third length of propodus. Postero-inferior angle of pleuron of 5th abdominal segment with a small tooth.

Material: 1 ovigerous ♀, carapace length (including rostrum) 4·5 mm, overall length 16 mm. Station BRU 372 G. Depth 55 metres.

Remarks: This specimen closely resembles *P. australiensis* Baker, 1907, in the shape of the carapace, rostrum, telson and 5th abdominal pleuron, but differs in possessing a smoothly rounded process on the basal antennular joint. *P. australiensis* has this process with a spine on the outer angle. The 2nd–5th pereiopods appear to be more slender than in *australiensis*. Without more material it is difficult to give this specimen definite status.

Family **Alpheidae**

Alpheus nonalter n.sp.

Fig. 15 a–d

Description: No supra-orbital spines. Rostrum reaching about two-thirds along basal antennular peduncle joint. Latter with swollen base, spine on external distal angle reaching just beyond end of joint. 2nd antennal peduncle segment 3 times length of 3rd. Antennal scale reaching beyond antennular peduncle. Larger chela with palm about 4 times longer than broad. No notch at base of

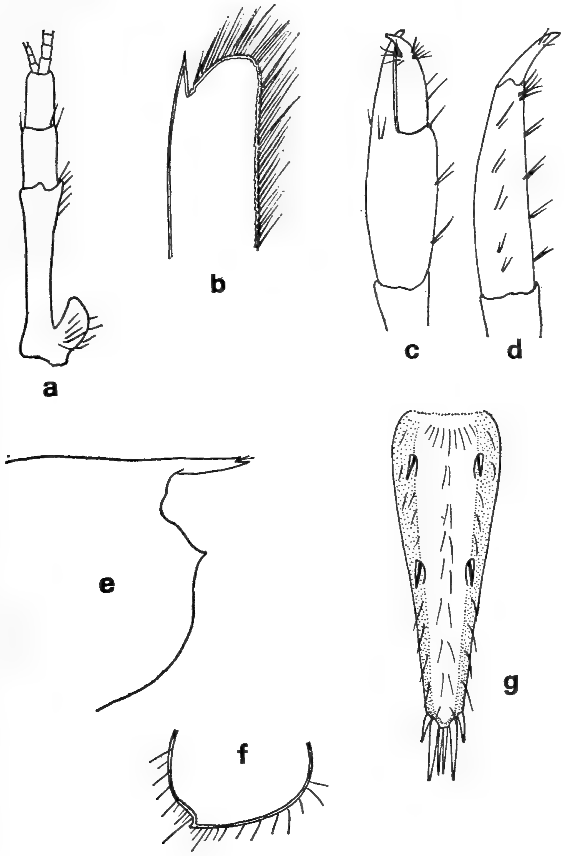

Fig. 14. *Processa* sp.

a. Peduncle of antennule. *b*. Tip of antennal scale. *c*. Chela of first right pereiopod. *d*. Dactyl and propodus of left first pereiopod. *e*. Antero-lateral portion of carapace. *f*. Pleuron, 5th abdominal segment. *g*. Telson.

dactyl, but shallow notch at base of fixed finger. Latter longer than movable finger. Both chelae granulous. Smaller chela with fingers half to two-thirds length of palm. Latter cylindrical, six times longer than wide. Movable finger slightly balaeniceps-like. Meri and ischia of both chelae with inner margin denticulate, former with spine on inner distal angle. Carpus of 2nd pereiopod of 5 jointlets, 2nd joint two-thirds length of 1st, equal in length to jointlets 3, 4, 5 together. Pereiopods 3, 4, 5 with simple flattened dactyls. Propodi, carpi, and meri equal in length. Ischia with single ventral spine. Telson length twice basal width.

Material: 3 ovigerous ♀♀, carapace lengths (including rostrum) 8·0, (holotype, S.A.M. A12650), 8·0, 9·0 mm. 7 ♂♂, carapace lengths, 6·0, 7·0, 7·4, 7·5 (paratype, S.A.M. A12651), 8·0, 8·0, 8·0 mm. 18 damaged specimens. Station BRU 390 P. 118 metres. 1 ♀, carapace length 7·5 mm. 1 damaged. Station BRU 391 C. 86 metres. 4 ♀♀, carapace length 7·5, 8·0, 8·0, 8·0 mm. 4 ♂♂, 6·0, 6·0, 7·0, 8·0, 15 damaged, 4 juveniles. Station BRU 390 H. 175–200 metres.

Remarks: The unarmed meri of the third pereiopods, the balaeniceps-like smaller chela of the male, the simple lanceolate-like dactyls of the last 3 pairs of pereiopods and the lack of supra-orbital spines place this species in the *Brevirostris* group of de Man (1911). This species is most closely related to *A. acutocarinatus* de Man, and *A. macrosceles* Alcock & Anderson. It differs from

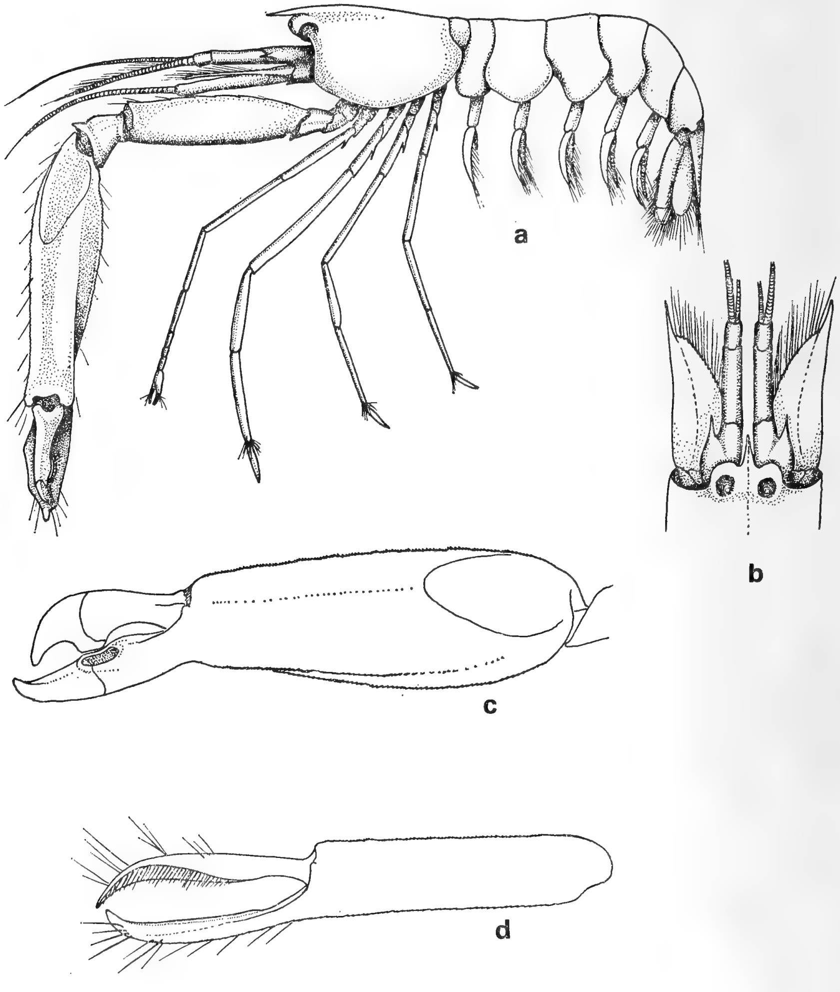

Fig. 15. *Alpheus nonalter* n.sp.
a. Lateral view. *b.* Anterior carapace and appendages, dorsal view. *c.* Large chela. *d.* Small chela.

A. acutocarinatus in that it lacks a prominent post-rostral carina and the tubercle or tooth just behind the orbital hood. It differs from *A. macrosceles* (which has a subcylindrical chela) in having a slightly flattened larger chela. The smaller chela of *A. macrosceles* is not balaeniceps-like, as in this species; both fingers meet when shut.

Alpheus waltervadi n.sp.

Fig. 16 a–c

Description: Rostrum reaching to middle of 1st antennular peduncle segment, supra-orbital spines slightly shorter. 2nd antennular peduncle segment twice length of 1st, 1⅓ length of 3rd. 1st antennular peduncle segment basally broad, with external spine reaching to end of segment. Apical spine of antennal scale reaching beyond 3rd antennular peduncle segment. Larger chela of 1st pereiopods with distinct deep notch in upper margin of palm behind dactyl. Notch followed distally by raised flattened lobe, distal end of which armed with forwardly directed tooth. Latter overhangs dactyl. Carpus one quarter length of merus, latter triangular in cross section, distally ending in 3 lobes at the angles, margins unarmed. Smaller chela only slightly shorter than other, fingers equal in length to palm. Spine at distal end of palm overhangs dactyl. Latter with concave inner edge. Carpus of 2nd pereiopods consisting of 5 jointlets, 1st largest. Ischium only slightly longer than merus. Dactyls of pereiopods 3, 4, 5, biunguiculate. Carpi two-thirds length of propodi, latter armed ventrally with 8 spines. Carpus with distal lobe overlapping propodus, otherwise unarmed, merus with flattened spine on ventral distal margin. Telson 1½ times longer than basal width, with 2 pairs lateral spines dividing the appendage into thirds.

Material: 2 ovigerous ♀♀, carapace lengths 5·5 (paratype, S.A.M. A12647), 4·1 mm (holotype, S.A.M. A12646). 4 ♂♂, carapace lengths 3·4, 4·0, 4·1, 4·1 mm. 6 juveniles, 5 damaged, station BRU 381 A-C, 38–46 metres (Walter's Shoal).

Remarks: According to de Man's 1911 classification of the genus *Alpheus* (taken from Coutiere, 1899), this species belongs to the *Megacheles* group, characterized by the presence of supra-orbital spines, a grooved and notched first chela, unarmed meri of the 3rd pereiopods and biunguiculate dactyls for the last three pairs of pereiopods. This species is very closely related to the following: *A. hailstonei* Coutiere, and its varieties *assimulans* de Man, *laetabilis* de Man, and to *A. paradentipes* Coutiere. It differs from *hailstonei* in that the larger chela is proportionally more robust and shorter and differently shaped. The supra-orbital spines are not as pronounced as in *hailstonei.*

It differs from *hailstonei* var. *assimulans* in the detailed shape of the larger chela, the stockier meri of the third pereiopods and in the 4th joint of the carpus of the 2nd pereiopods being only half as long as the 2nd. (These are equal in *assimulans.*) It differs from *hailstonei* var. *laetabilis* in lacking the spinous merus of the larger chela characteristic of this variety. It differs from *paradentipes*, which it most closely resembles, in the shape of the larger chela, in having much less prominent supra-orbital spines, and no spines on the carpi of the last three pairs of pereiopods. Further investigation may well prove this species to be synonymous with an already established one. This is, however, a preferable situation to incorrectly assigning them to an already established species.

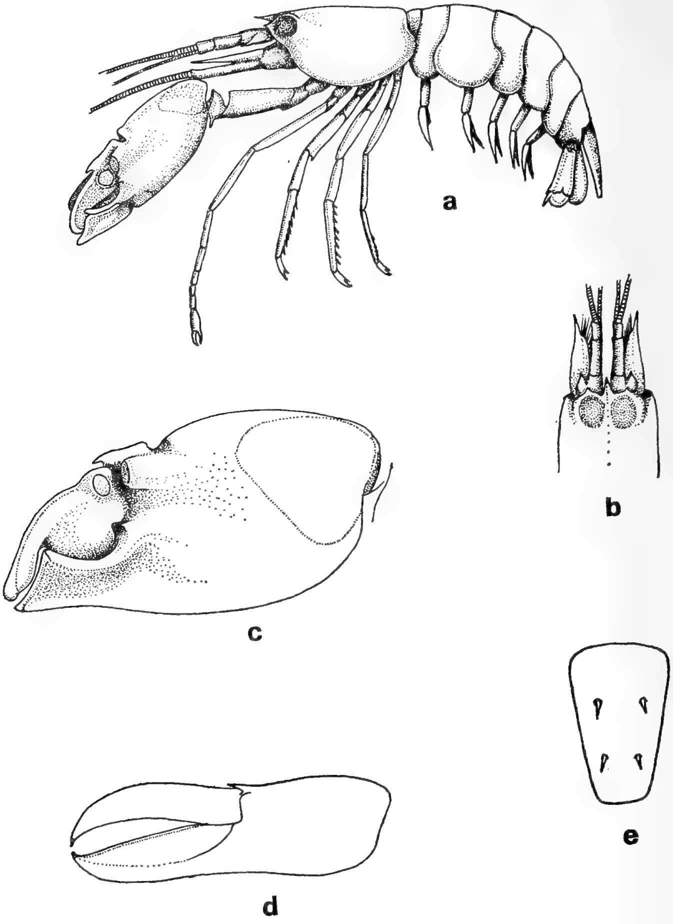

Fig. 16. *Alpheus waltervadi* n.sp.
a. Lateral view. *b*. Anterior carapace and appendages, dorsal view. *c*. Large chela. *d*. Small chela. *e*. Telson.

Distribution

In the following table the geographical distribution of all the species in this collection is given. All are automatically included in the Indo-Pacific region. The South African region includes the area from Cape Point east to about Durban. The Atlantic region includes the area west from Cape Point. It can be seen from this table that the majority of animals have Indo-Pacific affinities, while only about 21 species occur in all three regions.

Species	Indo-Pacific	South African	Atlantic
BRACHYURA			
Achaeopsis spinulosus	×		
Achaeopsis thomsoni	×	×	×
Achaeus lacertosus	×		
Achaeus cf. *affinis*	×	×	
Actaea rueppellii	×		
Calappa lophos	×		
Carcinoplax longimanus	×	×	
Charybdis cf. *annulata*	×		
Charybdis variegata	×		
Conchoecetes artificiosus	×		
Dorippe lanata	×	×	×
Ebalia barnardi	×	×	
Ebalia tuberculata	×	×	×
Ebalia tuberculosa f. *postulans*	×	×	
Ebalia tuberculosa f. *scandens*	×	×	
Ethusa sinespina	×		
Eumedonus granulosus	×		
Eurynome aspera	×	×	×
Goneplax angulata	×	×	×
Gonioneptunus africanus	×	×	
Homola barbata	×	×	×
Hyastenus spinosus	×		
Inachus cf. *dorsettensis*	×		
Inachus guentheri	×	×	
Leucosia marmorea	×		
Lophozozymus dodone	×	×	
Lupocyclus tugelae	×	×	
Macropodia formosa	×	×	
Nursilia dentata	×		
Palicus sexlobatus	×		
Paratergatis longimanus	×		
Philyra globosa	×	×	
Philyra globulosa	×	×	
Pilumnus hirsutus	×	×	
Pilumnus longicornis	×		
Platylambrus quemvis	×		

Species	Indo-Pacific	South African	Atlantic
Platypodia granulosa	×		
Portumnus mcleayi	×	×	
Ranina ranina	×		
Retropluma planiform	×		
Thalamita woodmasoni	×		
Xanthias tuberculidens	×	×	
ANOMURA			
PAGURIDEA			
Anapagurus hendersoni	×	×	
Dardanus arrosor	×	×	×
Dardanus euopsis	×		
Dardanus setifer	×		
Diogenes brevirostris	×	×	×
Diogenes costatus	×	×	
Nematopagurus gardineri	×		
Nematopagurus squamichelis	×		
Pagurus spinulentus	×	×	
Para-pagurus pilosimanus	×	×	×
GALATHEIDEA			
Galathea dispersa	×	×	×
Galathea intermedia	×	×	×
Munida sanctipauli	×	×	×
Munida semoni	×		
Porcellana dehaanii	×		
Porcellana streptocheles	×	×	
MACRURA			
PENAEIDEA			
Acetes erythraeus	×		
Gennadas propinquus	×		
Macropetasma africana	×	×	×
Metapenaeopsis adamanensis	×		
Metapenaeopsis stebbingi	×		
Parapenaeus fissurus	×		
Penaeopsis rectacuta	×		
Penaeus japonicus	×	×	
Sergestes prehensilis	×	×	
Solenocera africanum	×	×	×
Solenocera pectinata	×		

Species	Indo-Pacific	South African	Atlantic
CARIDEA			
Alpheus nonalter	×		
Alpheus waltervadi	×		
Alpheus frontalis	×		
Chlorotocus crassicornis	×	×	×
Eualus ctenifera	×	×	
Heterocarpus woodmasoni	×		
Hippolysmata vittata	×		
Latreutes mucronatus	×		
Leptochela pugnax	×		
Leptochela robusta	×		
Nikoides cf. *danae*	×		
Oplophorus spinicauda	×		×
Plesionika cf. *acanthonotus*	×		
Plesionika martia	×	×	×
Pontocaris cataphracta	×	×	×
Pontocaris lacazei	×	×	×
Processa austroafricana	×	×	
Stylodactylus bimaxillaris	×	×	×
Synalpheus anisocheir	×	×	×
Synalpheus jedanensis	×		
Tozeuma armata	×		

SUMMARY

A collection of brachyuran, anomuran and macruran decapod Crustacea is described. The material is from the south-west Indian Ocean, i.e. off the coasts of Portuguese East Africa, Natal and Malagasy Republic, and includes approximately 110 species, of which 15 are new records, and 5 previously undescribed.

ACKNOWLEDGEMENTS

Thanks are due to the Zoology Department of the University of Cape Town, and particularly to Mr. J. Field, for making the material available. Thanks are also due to Mr. C. Berrisford and Miss L. Joubert for preliminary identifications of some of the material and to Dr. M.-L. Penrith for helpful comments and criticisms.

The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research for a grant towards the publication of this paper.

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Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.

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ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 52 Band
May 1969 Mei
Part 8 Deel

ZORILLODONTOPS, A NEW SCALOPOSAURID FROM THE KAROO

By

M. A. CLUVER

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM
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1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(2, 5, 7–9), 6(1, t.–p.i.), 7(1, 3), 8, 9(1–2), 10(1–3), 11(1–2, 7, t.–p.i.), 21, 24(2), 27, 31(1–3), 38, 44(4).

Price of this part/Prys van hierdie deel
R0.50

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

ZORILLODONTOPS, A NEW SCALOPOSAURID FROM THE KAROO

By
M. A. Cluver
South African Museum, Cape Town

(With 2 figures)

[*MS. received* 11 *September*, 1968]

Contents

Introduction

The South African Museum has recently acquired the major part of the fully articulated skeleton of a small therocephalian reptile (S.A.M. No. K 1392), collected by the late Mr. J. J. Pansegrouw at Edenville in the Orange Free State, from Middle Beaufort beds, most probably those of the *Lystrosaurus* zone. Preparation has revealed the entire right side of the skull and most of the right shoulder girdle and limb. Also most of the vertebral column and parts of the pelvic girdle and right hind-limb have been exposed. The specimen is embedded in a soft, green mudstone matrix.

Description of the Material

The skull has suffered some lateral compression, but it nevertheless seems that in its natural state it was relatively deep and narrow. From the dorsal, supraoccipital border of the foramen magnum to the tip of the premaxilla it measures 44 mm, making it one of the smallest therocephalians yet recovered from the Karoo. The short temporal fossa and relatively large orbit both measure 10 mm in length. The preorbital length is 19 mm, and is thus a little less than half of the total skull length.

Lateral compression appears to have resulted in an artificial median crest above the orbit and temporal fossa. In figure 2 allowance has been made for this and the dorsal midline has been drawn slightly lower than in the actual specimen. It does not, however, seem likely that a flat, intertemporal plate (as in *Scaloposaurus*) was ever present. One side of the intertemporal region has been damaged, but there are no indications of a pineal foramen in the rest of the region. The parietal separates the squamosal from the postorbital,

Ann. S. Afr. Mus. **52** (8), 1969: 183–188, 2 figs.

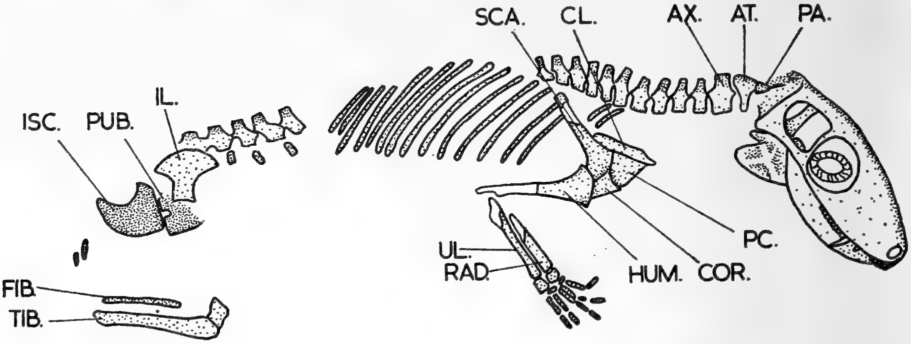

FIG. 1. *Zorillodontops gracilis*, gen. et sp. nov. (S.A.M. No. K1392). Lateral view of preserved portions of the skeleton × $\frac{5}{8}$. The unshaded areas represent bone impressions in the matrix. AT—atlas. AX—axis. CL—clavicle. COR—coracoid. FIB—fibula. HUM—humerus. IL—ilium. ISC—ischium. PA—proatlas. PC—procoracoid. PUB—pubis. RAD—radius. SCA—scapula. TIB—tibia. UL—ulna.

which forms only a short part of the dorsal border of the temporal fossa. The squamosal descends fairly far ventrally towards the quadrate. A triangular postfrontal lies wedged between the postorbital and the frontal. The postorbital bar is complete but slender.

The prefrontal is small and does not separate the nasal from the lacrimal. This condition has been found in *Scaloporhinus angulorugatus* (Boonstra, 1953). At the anterior extremity of the snout the sutures between the premaxilla, septomaxilla and nasal are not clear.

The premaxilla carries six incisors, the first two being indistinct and the last one very small. The premaxillary alveolar border meets the maxillary alveolar border smoothly, and there is no premaxillary 'step'. There are two canines, the first one small and separated by a diastema from the second, large canine. There is a clear diastema between the last incisor and the anterior canine. Eight small postcanine teeth follow closely on the canine. The postcanines are shorter and broader than the incisors and there appear to be minute anterior and posterior cusps on some of them. Unfortunately, the posterior three teeth have been badly damaged and show no details.

The occiput has been laterally compressed and displaced so that in lateral view the supraoccipital, exoccipital and opisthotic are visible. The tabular lies above the post-temporal fenestra, closely apposed to the squamosal. Beneath the opisthotic the stapes is visible, abutting against the inner surface of the quadrate.

The epipterygoid is a flat sheet of bone, expanded ventrally but not dorsally, and is not hour-glass shaped.

A complete ring of approximately 18 extremely delicate scleral plates is present within the orbit, giving an indication of the size of the eyeball. In the type specimen of *Scaloporhinus angulorugatus* scleral plates are also visible.

The lower jaw is drawn up tightly inside the maxilla, and no mandibular teeth could be exposed. The dentary is slender and smoothly curved and the coronoid process projects into the temporal fossa. The large angular wing projects below the level of the dentary and bears a system of prominent radiating ridges. The surangular and articular are also partly visible, but show few details.

The small size of the new specimen suggests the possibility of its being an immature individual. However, the dermal bones of the skull appear to be tightly knit and the scleral plates fully ossified. Furthermore, the posterior canine is fully developed and relatively powerful.

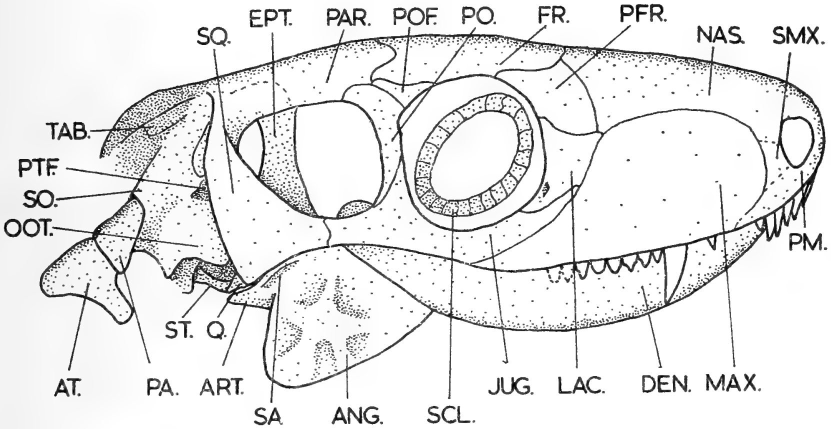

FIG. 2. *Zorillodontops gracilis*, gen. et sp. nov. (S.A.M. No. K1392) × 2. Lateral view of skull with occipital distortion uncorrected.

ANG—angular. ART—articular. AT—atlas. DEN—dentary. EPT—epipterygoid. FR—frontal. JUG—jugal. LAC—lacrimal. MAX—maxilla. NAS—nasal. OOT—opisthotic. PA—proatlas. PAR—parietal. PFR—prefrontal. PM—premaxilla. PO—postorbital. POF—postfrontal. PTF—post-temporal fenestra. Q—quadrate. SA—surangular. SCL—scleral plates. SMX—septomaxilla. SO—supraoccipital. SQ—squamosal. ST—stapes. TAB—tabular.

A fairly broad and robust proatlas is present on each side between the atlas and the side of the foramen magnum. The atlas shows few details, but the axis bears its characteristic enlarged neural spine. From the eighth vertebra back the spines are decreased in height and become posteriorly slanted. Beyond this there is no sudden transition between the cervical and thoracic portions of the vertebral column. Little can be seen of the column posterior to the fifth or sixth thoracic vertebra. Four 'lumbar' vertebrae, relatively more robust than the thoracic vertebrae, are preserved.

Twenty ribs of the right side can be made out, the first two of which are short and meet the sixth and seventh vertebrae. Anterior to the ilium there are three short, stout 'lumbar' ribs.

Most of the right side of the pectoral girdle has been preserved. The scapula appears to have been slender dorsally but it broadens ventrally to meet the large procoracoid and coracoid (the latter slightly displaced). The ventral part of the clavicle lies up against the anterior edge of the scapula and procoracoid. The proximal portion of the right humerus is preserved in articulation with the slightly distorted glenoid cavity. This portion is only moderately expanded. Distally, the humerus is indicated as an impression, but it is possible to estimate the length as 25 mm. Radius and ulna are present, proximally indicated as bone impressions. The length of the ulna is approximately 19 mm.

The manus was exposed but is incomplete. A radiale and ulnare are clearly present, as are what I take to be two centrals. There is an indication of a fourth or fifth distal, but no sign of the first three distals. All five metacarpals are present, followed by five elongated proximal phalanges similar to *Ericiolacerta* (Watson, 1931). The second and third digits have a further anterior, similarly elongated phalanx each, but no other phalanges or terminals could be found.

Posteriorly the expanded blade-like right ilium is preserved, but the right pubis and ischium have been lost. Preparation, however, exposed the inner surfaces of the left ischium and pubis, indicating their general outline. The obturator foramen can be made out as a notch in the posterior edge of the pubis, closed off posteriorly by the ischium. There is a fairly strong tibia and a thin, reduced fibula alongside it. Of the hind-foot, only a few small, scattered bones and what appear to be two phalanges are left.

Discussion

In the following discussion the division of the Therocephalia used by Haughton & Brink (1954) has been followed.

Owing to its small size, slender, smoothly curved dentary, single large canine and small anterior canine, short temporal fossa and lack of a raised temporal crest, our skull does not correspond to any members of the Pristerognathidae, Lycosuchidae or Alopecodontidae. It is also manifestly distant from the specialized Whaitsiidae, Lycideopsidae and Euchambersidae.

Among the Ictidosuchidae, both *Ictidosuchus* and *Ictidodraco* have one canine. Broom (1920, 1932) found two anterior canines in *Ictidosuchoides* but Boonstra (1934) could find only two unerupted precanines. This family is, moreover, characterized by a long temporal fossa and a raised intertemporal crest.

The Akidnognathidae have a small anterior canine tooth and a postfrontal, but the skull is much larger. In *Akidnognathus* the first canine follows immediately on the powerful incisors, whereas in our specimen a considerable diastema separates the incisors and canines. *Ictidosaurus* resembles our specimen more in this respect, but is from the *Tapinocephalus* zone and is much larger. There is, moreover, a marked premaxillary 'step', which occurs also in *Scylacosaurus*. *Trochosuchus* has only four postcanine teeth.

The new specimen must therefore fall under the Scaloposauridae.

It should be noted that Romer (1956, 1966), divides the Scaloposauridae of Haughton & Brink (1954) into several new families which, together with the Lycideopsidae and Ictidosuchidae, he places in another infraorder, the Bauriamorpha. According to Haughton & Brink (1954), the Scaloposauridae can be defined as follows:

> 'Skull small. Snout usually long. Intertemporal bar fairly broad. Postorbital bar either complete or incomplete, but always feeble. Secondary palate in process of development. Teeth numerous and pointed, with one or two small canines in front of the main canine. Pineal foramen present or absent' (p. 141).

The presence of a postfrontal is uncommon in this family, but has been found in *Ictidostoma hemburyi* (Broom, 1932), which is from the *Endothiodon* zone. For the rest, the small size, slender dentary, weak postorbital, small precanine tooth, short temporal fossa (and possible absence of a pineal foramen) are characteristics found within the scaloposaurids.

Silpholestes jackae (Broom, 1948) from the *Cistecephalus* zone is only slightly larger than the new specimen, and has the same general proportions. There is an enlarged canine and a small anterior canine, but there are thirteen postcanines (as against eight postcanines in our specimen) and the first canine is not separated from the incisors and large canine by diastemas. The postorbital is figured as being complete (although Broom was uncertain of this). Further points of difference are the large prefrontal and the apparent absence of a postfrontal in *Silpholestes*.

Among the other scaloposaurids *Scaloporhinus* (Boonstra, 1953) has a similar large ornamented angular and short prefrontal, while *Ictidostoma* (Broom, 1912, 1932) resembles our specimen in its dentition and the presence of a postfrontal. *Ericiolacerta* (Watson, 1931) is also from the *Lystrosaurus* zone.

On the basis of these similarities and differences, it seems justified to regard our specimen as representative of a separate genus in the family Scaloposauridae, and I propose for it the name *Zorillodontops gracilis*, gen. et sp. nov. *Zorillodontops* is probably related to *Silpholestes* and can be taxonomically defined as follows:

Class	Reptilia
Subclass	Synapsida
Order	Therapsida
Infraorder	Therocephalia
Family	Scaloposauridae

ZORILLODONTOPS n.gen.

Diagnosis: Skull small, lacrimal meets nasal, postfrontal present, postorbital bar complete but slender, 6 incisors, 2 canines of which posterior one is enlarged, 8 postcanines, reflected lamina large with radiating ridges.

Zorillodontops gracilis n.sp.

Holotype: Skull with major part of postcranial skeleton, S.A.M. No. K1392.

Horizon and locality: Lystrosaurus zone, Edenville, Orange Free State, South Africa.

Diagnosis: As for genus.

If Romer's (1956) classification is followed, *Zorillodontops* would be included in the family Silpholestidae of the infraorder Bauriamorpha.

ACKNOWLEDGEMENTS

I am indebted to Dr. P. J. Rossouw of the Geological Survey of South Africa for information regarding the geological horizon from which the fossil was recovered, and to Mr. D. Pansegrouw, who presented the specimen to the South African Museum.

The Trustees of the South African Museum thank the South African Council for Scientific and Industrial Research for a grant in aid of publication.

SUMMARY

The skull and major part of the skeleton of a small, new *Lystrosaurus* zone therocephalian, *Zorillodontops gracilis*, is described. It is concluded that *Zorillodontops* is a scaloposaurid and is unusual in having a postfrontal. The new genus is in several respects similar to *Silpholestes*, a small scaloposaurid from the *Cistecephalus* zone.

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Example

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

Volume 52 Band
July 1969 Julie
Part 9 Deel

PLEISTOCENE MOLLUSCS FROM THE NAMAQUALAND COAST

By

A. J. CARRINGTON & B. F. KENSLEY

Cape Town Kaapstad

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Price of this part/Prys van hierdie deel
R3.00

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

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South African Museum, Cape Town

(With plates 18 to 29 and 11 figures)

[*MS. received* 1 *October* 1968]

Contents

Introduction

In the course of an examination of the Tertiary to Recent sediments of the Namaqualand coast, being carried out by one of the authors (A.J.C.), a collection of fossil molluscs was assembled from the Pleistocene horizons encountered in the area.

The purpose of this paper is to introduce and describe some twenty species from this collection, including forms new to the South African palaeontological literature.

In the case of a number of these species, the present geographic ranges of the genera to which they are assigned suggests that, in the Lower Pleistocene at least, the Namaqualand coast was washed by waters markedly warmer than those which presently bound this shore.

In the areas examined, the local Archean metamorphics are overlain by a succession of marine, fluviatile and terrestrial sediments of Tertiary to Recent age.

The marine elements of this succession extend some three to five miles east of the present coastline and are the result of a series of geologically fairly recent transgressions by the sea on to the land.

The oldest sediments present, fluviatile clays, silts and sands occupying a system of partly confluent channels deeply incised in the gneissic bedrock, are succeeded by isolated remnants of a profoundly indurated phosphatic siltstone and sandy clay horizon carrying an abundance of shell casts and moulds.

Overlying these fossiliferous silts is a succession of compact, poorly cemented, marine sands and gravels associated with a series of high-level beaches, developed during Pleistocene fluctuations of sea-level resulting from the periodic wasting and renewal of high latitude, continental ice-sheets. That this succession of marine sands is of Pleistocene age seems certain. In this area, where there is no evidence of tectonic instability in Pleistocene-Recent

Ann. S. Afr. Mus. **52** (9), 1969: 189–223, 12 pls, 11 figs.

times, the series of fossil beaches, testifying to repeated marine transgression during which sea-levels reached altimetric maxima of 75–90 (oldest), 45–50, 29–34, 17–21, 7–8, 5 and 2 (youngest) metres, accords very nearly with the well documented succession of Pleistocene strands along the Atlantic coast of Morocco (Biberson, 1963; Butzer, 1966).

Although the coarse, porous, marine sands of the 75–90 m transgression have, so far, proved to be barren of animal remains, the succeeding beaches are abundantly fossiliferous. The oldest of these shell-bearing beds, laid down during the 45–50 m inundation, has yielded more than 120 species of molluscs of which only seventeen of the twenty forms here described, plus the previously recorded *Chamelea krigei* Haughton and *Fissurella robusta* Sowerby, are not found living in the seas surrounding the coasts of South Africa.

The stratigraphic correlation alluded to earlier, the high proportion (84%) of species extant in the present seas, the low degree of lithification and the extraordinary 'fresh' appearance of the invertebrate remains together militate against the acceptance of an age other than Pleistocene for these sands and gravels laid down during the 45–50 m transgression.

Comparison with the Mediterranean and Moroccan marine Pleistocene successions, based solely on altimetric evidence, suggests a date equivalent to the Maarifian (Morocco) or Milazzian (Mediterranean) for this high sea stand.

Succession

	Thickness	*Suggested age*
Loose surface sand	0–4 m	Recent
—*unconformity*—		
2 m Transgression complex		
Highly fossiliferous sands and gravels; berm sands	2–7+m	
—*unconformity*—		Upper Pleistocene[1]
5 m Transgression complex		
Slightly calcareous sands and shelly granule gravels	2–3 m	
—*unconformity*—		
7–8 m Transgression complex		
Stabilised berms; calcareous, often highly garnetiferous marine sands over well-developed boulder gravels	3–5+m	
—*unconformity*—		
Terrestrial sands		(to Recent in part) Middle Pleistocene[1]
Sheet wash deposits	2–7 m	
—*unconformity*—		
17–21 m Transgression complex		
Coarse sands and grits over massive, basal boulder gravels	10–15 m	
—*unconformity*—		
29–34 m Beach		
Thin, discontinuous, shelly gravel beach	uncertain	
—*unconformity*—		
45–50 m Transgression complex		
Aeolianite and coarse regressive facies overlying locally fossiliferous, fine-grained, transgressive sands	5–25+m	Lower Pleistocene[1]
—*unconformity*—		

75–90 m Transgression complex		
Regressive aeolianite overlying coarse, marine sands and thin gravels	35+m	Basal Pleistocene[1]
—unconformity—		
Fossiliferous phosphatic siltstones	0–1 m	Pliocene
—unconformity—		
Fluviatile beds		
Linear deposits of clays and clayey sands. Unfossiliferous	up to 20 m	Mio-Pliocene?
—unconformity—		
Basement gneiss		Archean Complex

[1] Subdivision of the Pleistocene after Butzer, 1966.

Details of the succession given above and dating of the component horizons are based on the results of the geological survey at present being carried out by A.J.C. It is hoped that a fuller description of the geology and palaeontology of this area will be given at a later date.

The fossil species described in this paper were collected from the three localities indicated in figure 1. With the exception of a new species of *Fissurella*, all were recovered from sands deposited during the 45–50 m marine transgression.

The extreme dissimilarity in lithological character of sediments from the 45–50 m and the 17–21 m inundations is a notable feature. Typically, the shelly fore-beach deposits of the 45–50 m transgression are constituted of extremely fine-grained, moderately rounded and sorted sands and silts. Fine to laminar bedding structures are apparent and the faunule includes a strong complement of sand-dwelling bivalves of the families Mactridae, Tellinidae and Veneridae. The sedimentary characteristics of these beds, which locally yield an abundance of a new species of *Donax*, and the prevalence of burrowing bivalves point to a quiet depositional environment with low rates of both provenance and accumulation of sediment.

Conversely, the extremely coarse sediments of the 17–21 m transgression, granular, well sorted and rounded, frequently cross-bedded and with a paucity of sand-dwelling bivalve species, suggest that a more rigorous, abrasive environment with a high rate of sediment accumulation was current during the deposition of these beds.

In at least one species, it is suggested that adaption to the profound shift in the nature of the environment, inferred from the change in lithology, has progressed so far and has engendered such physical change that the final product of these adaptive trends should be accorded a separate, specific identity.

Systematic Discussion

Key to abbreviations

L. = length
B. = breadth
D. = greatest diameter
A. = altitude
W. = width

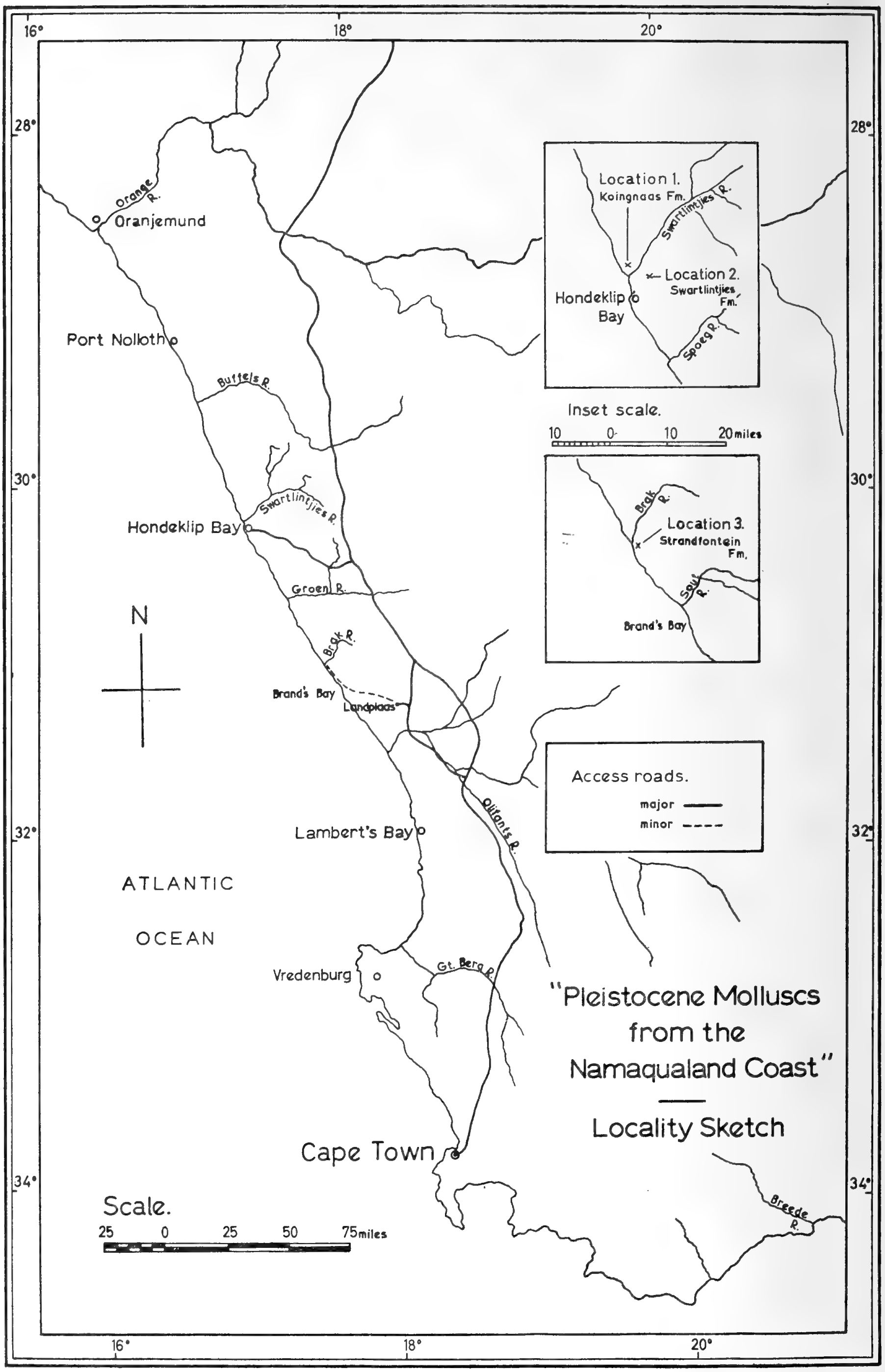
16°
18°
20°
28°
30°
32°
34°
Orange R.
Oranjemund
Port Nolloth
Buffels R.
Swartlintjies R.
Hondeklip Bay
Groen R.
Brak R.
Brand's Bay
Landplaas
Olifants R.
Lambert's Bay
Vredenburg
Gt. Berg R.
Cape Town
Breede R.
N
ATLANTIC
OCEAN
Scale.
25 0 25 50 75 miles
Location 1.
Koingnaas Fm.
Swartlintjies R.
Location 2.
Swartlintjies Fm.
Hondeklip Bay
Spoeg R.
Inset scale.
10 0 10 20 miles
Brak R.
Location 3.
Strandfontein Fm.
Sout R.
Brand's Bay
Access roads.
major
minor
"Pleistocene Molluscs from the Namaqualand Coast"
Locality Sketch

Fig. 1

Family **Turridae**

‘*Turris*’ ***nigrovitta*** n.sp.

Pl. 18

Location 1. 45–50 m Transgression complex.
Fore-beach environment.

Description

Protoconch eroded, possibly 1½ whorls. Postnatal whorls 5. 1st whorl with 7 axial ribs, 5 spiral lirae, 2nd whorl with 8 axial ribs, 5–6 lirae, 3rd whorl with 8 axial ribs, 7–8 lirae, 4th whorl with 7 axial ribs, 7–8 lirae, body whorl with 7–8 axial ribs, spiral lirae obscured by erosion. Axial ribs broad. Lower body whorl and anterior canal with about 11 lirae. No sinus on outer lip. Inner area of outer lip with 8 or 9 elongate plicae. Anterior canal subequal to aperture, latter equal in length to spire.

Named from location – ‘Swartlintjies’, Afrikaans – ‘black ribbons’.

Material

Holotype:	S.A.M.	K1443	L. 27 mm	B. 12 mm
Paratype:	S.A.M.	K1444	20 mm	8 mm

Remarks

With only the shell available, it is difficult to decide on generic status for this species. The main diagnostic features relating to the shell are the shape of the outer lip sinus, and the anterior canal. As there is no trace of a sinus in the present shells, choice of a subfamily is made almost impossible. The axial sculpture is similar to that found in *Turris saldanhae* Barnard and *Surcula scalaria* Barnard, but there are no other similarities. Without more material being available, the species is placed in the genus ‘*Turris*’ merely for convenience.

Family **Fasciolariidae**

Fasciolaria sp.

Pl. 18

Location 1. 45–50 m Transgression complex.
Beach environment.

Description

Aperture slightly shorter than spire. Shell 5½ whorls, protoconch and first 3 whorls eroded. 9–10 spiral lirae commencing on latter part of 3rd whorl, 11–12 on 4th whorl, 12–15 on 5th whorl. Outer lip with 28–32 lirae, internally plicate in the larger shell. Exact number of lirae on outer lip difficult to determine as lirae divide into two at upper and lower portions of whorls and each may again divide. Latter divisions not as obvious in middle portion of whorl where erosion has occurred. Profile of whorls smoothly convex, lower two with very slight shoulder. No columella pleats present, no axial sculpture apart from irregular growth lines.

Material

S.A.M.	K1445	L. 61·0 mm	B. 26·5 mm	(outer lip broken)
S.A.M.	K1446	66·0 mm	33·0 mm	(very worn)

Remarks

In general shape, these shells are typical of the genus *Fasciolaria* and resemble *F. lugubris* Reeve very closely. There are, however, several points of difference. The columella is not as sinuous anteriorly as in *F. lugubris*. The latter usually has several columella pleats in the region of the anterior canal while near the suture of the body whorl with the preceding one, there are usually several small pleats on the columella. In the present shells there is only a slight nodule on the upper columella. The sculpturing differs from *F. lugubris*, which usually has the outer lip with 22 broad spiral lirae, alternating with finer lirae. The broad lirae are each made up of 5–7 fine lirae while the narrow lirae are made up of 2–3 finer ones. The 4th whorl has 9 broad lirae. The present species, however, has 28–32 lirae on the outer lip, 11–12 on the 4th whorl, while each lira is made up of 2 finer ones, or, if the lirae are split, 4 each.

The present shells are perhaps a form of *F. lugubris* which has been recorded from the Pleistocene deposits of the Saldanha Bay area, but without more material being available, their status is difficult to determine.

Fusus faurei Barnard, 1959
Pl. 18

Fusus faurei Barnard, 1959: 94.

Location 1. 45–50 m Transgression complex.
Beach environment.

Material

One specimen: L. 42·2 mm B. 20·5 mm

Previous records

Alive, off Cape Point.

Remarks

The present shell agrees almost exactly with the description of *F. faurei* Barnard, the only difference being in the number of axial ribs. The penultimate whorl of *F. faurei* Barnard has 14–15 axial ribs, while the present shell has 12–14 ribs. The earlier whorls also have fewer ribs. The spiral sculpture is, however, almost identical and there can be no doubt that this shell is a form of *F. faurei* Barnard.

Family **Nassidae**

Nassa litorafontis n.sp.

Pl. 18

Location 3. 45–50 m Transgression complex.
Early transgression beach.

Description

Protoconch 1–1½ whorls, 4½–5 post-natal whorls, first four post-natal whorls with strong axial sculpture, about 20–24 axial ribs on 1st whorl, crossed by 4 spiral lirae. 2nd whorl with 25–30 axial ribs, 4 main lirae, very fine intermediate lirae starting between major ones. 30–35 ribs on 3rd whorl, 6–7 lirae. 4th whorl with about 28 axial ribs, becoming broader and rounder and less distinct, finally obsolete on body whorl. Latter with about 25–27 lirae on outer lip, upper ones broad, lower ones narrow. Axial ribs in general stronger on the lower part of the whorls than on the upper. Aperture slightly shorter than spire. Inner margin of outer lips smooth except near junction with columella, where a single nodule is followed by a very low, smooth ridge. Columella smooth; just below junction with body whorl, an acute raised ridge, just opposite the nodule of the outer lip. Anterior end of columella carinate. Outer lip excavate at anterior junction of columella.

Named from location – coastal farm Strandfontein – 'Strandfontein', Afrikaans – 'beach fountain'.

Material

Holotype:	S.A.M.	K1441	L.	28·0 mm	B.	12·5 mm
Paratype:	S.A.M.	K1442		22·0 mm		10·0 mm

Remarks

In general shape, the present species most closely resembles one of the South African representatives of the genus *N. bicallosa* Smith, recorded from the Natal coast, although the figure given with the original description (Smith, 1876) is of a more squat shell. The sculpture of axial whorls is similar but *N. bicallosa* has fewer ribs (13–17, as opposed to up to 35 in *N. litorafontis*). In *N. bicallosa* there is both an external parietal callus and an internal callus, while the columella is denticulate, and the outer lip plicate. *N. litorafontis* has a single callus, a smooth columella, and no plications on the outer lip. In the latter species, the single ridge near the fusion of the outer lip and the columella is more developed than in *N. bicallosa*.

Latiaxis sp.

Pl. 19

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Shell broken, very eroded, 4 whorls extant. Aperture longer than existing spire. Profile of whorls with prominent angular shoulder. Sutures undulate. Very faint indications of axial ribs on earlier whorls. Strong parietal callus, narrow umbilicus. Rostrum present, but very worn.

Material

S.A.M. K1447 L. 62·5 mm B. 37 mm (outer lip missing)

Remarks

This specimen agrees with Thiele's (1929) definition of the genus. Specific status, however, cannot be accorded this shell, due to its very incomplete state. In general shape it resembles *Latiaxis tortilis* H. & A. Adams, which has been recorded once in the South African region, from west of Cape Point. None of the characteristic axial and spiral sculpture of this species is discernible in the present shell. The undulations of the sutures may seem to indicate that there were fairly strong axial ribs present. The genus appears to be characteristic of the Indo-Pacific region. Barnard (1959) remarked on the unusualness of the occurrence of *L. tortilis* from the west coast of the Cape Peninsula. This record from the Namaqualand coast would serve as yet another indication of the presence of a warm-water fauna on this coast during the period under discussion.

Family **Muricidae**

Tritonalia bonaccorsii n.sp.

Pl. 19

Location 1. 45–50 m Transgression complex.
Back-beach environment.

Description

Spire slightly longer than aperture. Protoconch of 2–2½ whorls, 4–4½ post-natal whorls. First 3 whorls bicarinate, the 2 carinae formed by 2 strong spiral lirae. 4–5 fine lirae between upper carina and suture. 3rd whorl with 3 fine lirae between the 2 major lirae, 2 fine lirae between lower carina and suture. Cancellate sculpture on first three whorls formed by axial ribs crossing lirae. 1st whorl with 10–12 axial ribs, 11–12 on 2nd and 3rd whorls. Lower carina on last whorl not stronger than rest of lirae, body whorl therefore unicarinate. Body whorl with 9 lirae above the carina, 16–19 below. Outer lip with about 8 plicae on inner margin. Short open anterior canal, strong parietal callus, very slight umbilicus, slight rostrum with 3 worn squamae.

Named after donor, Dr. G. Bonaccorsi.

Material

Holotype: S.A.M. K1436 L. 34·2 mm B. 17 mm

Remarks

The strong spiral sculpture, which forms a cancellate decoration with the axial ribs, is characteristic of several genera of the Muricidae. The tall spire, egg-shaped aperture, very convex body whorl, and short anterior canal bent to the left would seem to indicate the genus *Tritonalia.* The present shell lacks the strong axial sculpture of *T. decussata* Gmelin or *T. fasciata* Sowerby of west Africa and *T. kieneri* (Reeve) and *T. scrobiculata* (Dunker) of the South African region. Similarly, *T. bonaccorsii* lacks the axial sculpture of *T. purpuroides* (Reeve), known from the Pleistocene deposits of Saldanha Bay. The early whorls of this latter species, however, resemble the earlier whorls of the present shell in possessing a cancellate sculpture, and two strong spiral lirae per whorl. *T. sperata* (Cossman) of the east coast has a much longer anterior canal; this, and a nodulose axial sculpture, separates it from the present shell. The latter most closely resembles *T. puncturata* (Sowerby), recorded from the east coast as well as from the west coast of the Cape Peninsula. This latter species occasionally shows a tendency towards carination, particularly in the earlier whorls, where the sculpture is cancellate. The aperture of *T. puncturata* is usually more elongate, while the penultimate and body whorl never have so strong a carina as in *T. bonaccorsii.*

There is a superficial similarity between the present shell and *Cancellaria lyrata* (Brocchi), but the former lacks the columella pleats and prominent spined axial ribs of the latter species. There is also a slight, superficial similarity between *Latiaxis rosaceus* Smith and the present shell but the former is more squat, and has blunt, nodulose axial ribs. From the above, it is obvious that some doubt exists as to the generic status of this shell. Without more material being available, greater certainty is not possible.

NAMAMUREX n.gen

Description

Shell of 4 or 5 whorls. Varices 3 per whorl, connecting with those of previous whorls. No sculpture between varices. Outer lip with 8 submarginal nodules, one prominent erect tooth near base of nodules. Aperture longer than spire. Anterior canal open, slightly shorter than rest of aperture.

Generic name in part a contraction of the general location – Namaqualand.

Discussion

The presence of strong varices, a well-marked anterior canal, a toothed outer lip, and a prominent tooth on the lower outer lip, make it seem certain that this shell is a member of the family Muricidae.

The presence of a spine on the outer lip is characteristic of several genera of the Muricidae, viz. *Acanthina, Ceratostoma, Pterorytis, Jaton.*

The genus *Acanthina* is known living from the west coast of North and South America, especially from the Californian coast. Apart from the presence of the spine on the outer lip, the present shells bear little resemblance to any of the forms of *Acanthina,* all of which are rather *Thais*-like.

The genus *Ceratostoma,* as defined by Vokes (1964), includes the species *C. nuttalli* (Conrad) from the Californian coast, which the present shells most closely resemble. *C. nuttalli* has three well-developed almost foliose varices per whorl, and in addition, single elongate axial nodules between the varices. The absence of these nodules in the present shells, as well as the absence of the prominent spiral ridges, excludes these shells from the genus *Ceratostoma.* The latter genus invariably has a closed anterior canal, quite different from *Namamurex.* The genus *Ceratostoma* is a Pacific form, being found on the west coast of North America, and in the Japanese region (Hall, 1959).

The genera *Jaton* and *Pterorytis,* both of which have a denticulate outer lip, are typical Atlantic forms. The former, having 3 or 4 wide transverse plications separated by deep, slightly striated grooves, contains the single species, *J. decussata* (Linnaeus) from west Africa (*vide* Vokes, 1964: 21). *Pterorytis,* defined as being fusiform, with 6 prominent recurved foliated ribs, and having a closed anterior canal, is known only from the Miocene and Pliocene of the Atlantic coastal plain of the United States. The present shells are thus eliminated from both these genera, and as they conform with none of the recognized general of the Muricidae, it is necessary to erect a new genus, as defined above.

Namamurex odontostoma n.sp.

Pls 20–21

Location 2. 45–50 Transgression complex.
Fore-beach environment.

Description

Shell of 4 or 5 whorls, protoconch eroded. 3 prominent varices per whorl, continuous with those of previous whorls. Outer lip, at formation of varix, having 8 slightly raised nodules on inner margin. Near base of latter nodules, a prominent erect spine. Latter spine also visible on two earlier varices, slightly embedded in following portion. A shallow groove, becoming almost a line, running from tooth along following portion of whorl. Profile of earlier whorls with slight shoulder, later whorls becoming smoothly rounded. No sculpture other than faint growth lines.

Material

Holotype:	S.A.M.	K1437	L. 55·0 mm	B. 30·0 mm	
			Aperture	L. 36·4 mm	

Other specimens:		L. 54·0 mm	B. 36·0 mm
		64·5 mm	40·5 mm
		51·0 mm	35·5 mm
		39·0 mm	25·0 mm
		(Latter two specimens with 4 varices per whorl on earlier whorls, varices not meeting, shoulder between varices almost joining to form a ridge.)	
S.A.M.	9925	L. 68·0 mm	B. 43·0 mm
		(Collected by Haughton, very eroded, 3 varices per whorl.)	

Family **Eratoidae**

Subfamily *Eratoinae*

Hespererato oppenheimeri n.sp.
Pl. 19

Location 3. 45–50 m Transgression complex.
Early transgression beach.

Description

Shell small, sub-conical, inflated posteriorly, attenuated anteriorly. Posterior extremity of outer lip angular and projecting.

Spire small, eroded in the present specimens, but quite definitely projecting above the terminal whorl; apparently non-granulate.

Surface smooth, possibly glossy in life; non-sulcate.

Outer lip sharply incurved, attaining its greatest thickness in the central region; externally thickened at margin. Incurved marginal area bearing a series (*circa* 10) of equal, regularly spaced, plicate ridges, giving a denticulate aspect to outer lip.

Posterior canal very poorly defined, virtually obsolete; ill-defined oblique ridge marking the left border.

Aperture slightly curved, rather narrow posteriorly, becoming considerably wider anteriorly before being constricted by the terminal flexure of the columella lip.

Anterior edge of columella lip obliquely truncated, bounded by two closely spaced terminal ridges.

A series (*circa* 8) of elongate subequal plicae, regularly spaced, traverses the columella lip of the labrum. Plicae approximately at right angles to the axial plane of the shell, their alignment markedly dissimilar to the oblique trend of the terminal ridges, tending to be discontinuous along the central portions, forming two parallel rows of elongate columella and labral denticles. Between the most anterior of these denticles and the terminal ridges, a distance of approximately one fifth the length of the inner lip, the columella is smooth and non-denticulate. The series of plicae persists to the posterior end of the columella lip, being there less strongly developed, the columellar denticles becoming subordinate to those on the labrum.

Extreme anterior area of shell squarely terminated, no obvious concavity, fossula obsolete.

Named after the late Sir Ernest Oppenheimer, past Chairman of Anglo American Corp. S.A.

Material

Holotype:	S.A.M.	K1428	L.	12 mm	B.	8 mm
Paratype:	S.A.M.	K1429		13 mm		9 mm
Other specimen:				10 mm		7 mm

Remarks

The general shape of the shell, the numerous transverse denticles arming the columella and labrum, the character of the aperture, which is not axial, and the form of the spire, which projects above the terminal whorl, suggest that the present species should most properly be assigned to the sub-family Eratoinae (Eratoidae) rather than to the genus *Persicula* (Marginellidae), or to the sub-family Triviinae (Eratoidae).

In his monograph on the Eratoinae, Schilder (1933) recognizes four genera and three sub-genera. Regarding the generic position of the present species within the sub-family, the following characters of this species appear to be of diagnostic importance:

(i) dorsum smooth;
(ii) fossula almost obsolete;
(iii) two terminal ridges on columella lip;
(iv) columellar denticles transverse, quite definitely not parallel with terminal ridges;
(v) anterior columellar denticles develop some distance away from the terminal ridges.

Characters (i)–(iv) suggest that the present species best fits into the genus *Hespererato* Schilder.

It is notable that the hiatus between the terminal ridges and the columellar denticles (v) seen in the present species is a character held in common by a number of species within the genus *Hesperato* and one which is not apparent in any of the three other genera in this sub-family. Similarly, a sinuous columellar outline and an outer lip bearing fewer but larger denticles are features borne by several species within this genus.

Of the 99 fossil and living species listed by Schilder, none is exactly similar to the present form. The strongest resemblance is to *H. vitellina* (Hinds), a Californian form, and the type species of the genus. Representatives of this genus are known from Miocene to Recent and range from the west coast of the Americas to France and Italy.

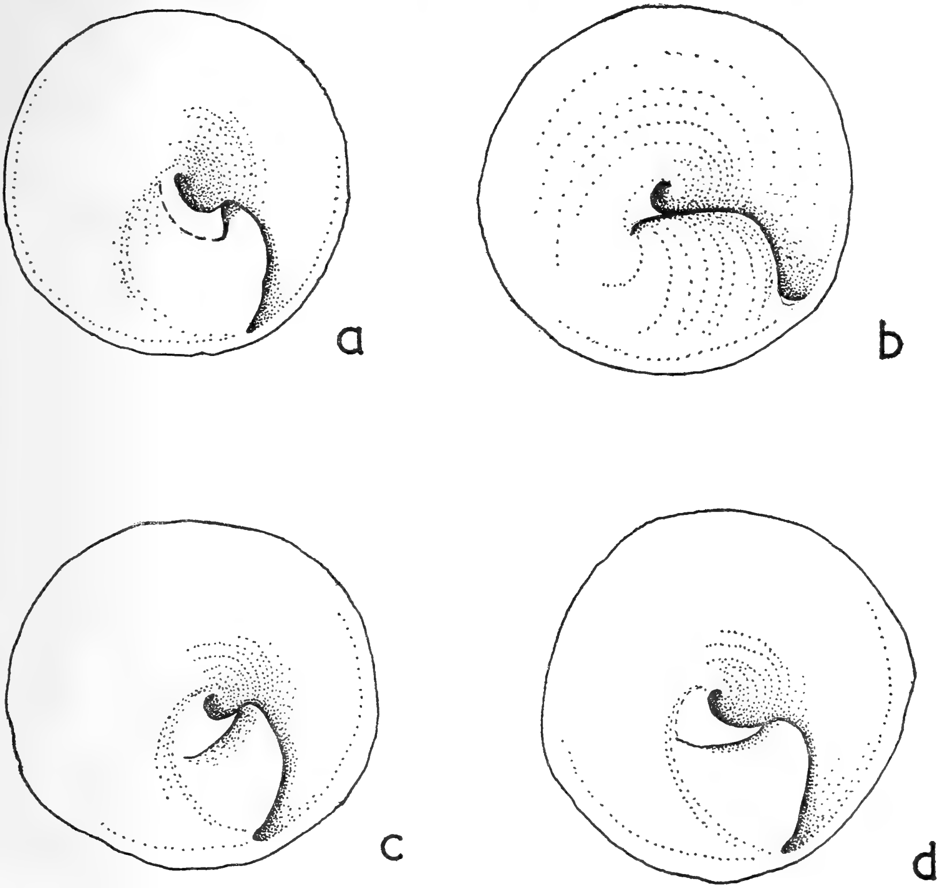

Fig. 2. Ventral views: a. *Calyptraea viridarena* n.sp. Holotype. b. *C. helicoidea* (Sowerby). c. *C. aurita striata* n.subsp. Holotype. d. *C. aurita* Reeve.

It is of interest to note that the local contemporary form *Proterato* (*P.*) *sulcifera* (Sowerby) is a member of the sub-genus *Proterato* Schilder, found only in the Indo-Pacific and Australasian areas. The presence of apparently generically different forms in Lower Pleistocene and Recent seas around the South African coasts and the surprising distribution of the genus *Hespererato* (west coast of America, Antilles, and Europe) may perhaps suggest that the phylogenetic aspects of one, at least, of these generic divisions are not of profound significance.

Family **Calyptraeidae**

Calyptraea aurita striata n.subsp.

Pl. 22 & Fig. 2

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Basal circumference circular. Protoconch eroded. Post-natal whorls indistinct, possibly 3. External sculpturing consists of fine, oblique, radiating ribs. Shelf loosely reflexed upon itself at the columella, forming a wide elongate umbilicus. Margin of the shelf slightly incised at its fusion with the shell periphery.

Material

Holotype: S.A.M.	K1433	D.	19·6 mm	A.	8·1 mm
Other specimens:			24·8 mm		10·0 mm
			24·0 mm		11·5 mm

Remarks

The only difference between the present shells and *C. aurita* Reeve lies in the external sculpture. The usual sculpture of *C. aurita* consists of irregular, radial rows of hollow, squamiform prickles. This subspecies lacks these prickles but has very fine radial ribs. While the present subspecies is seen to be fairly common, no examples of *C. aurita* have been recovered from any of the locations visited. *C. aurita* has been recorded alive from the warm waters of Algoa Bay and St. Francis Bay, while fresh dead shells have been reported from Struis Bay, Cape Recife and Cape St. Blaize.

Calyptraea viridarena n.sp.

Pl. 22 & Fig. 2

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Basal circumference of shell circular. Protoconch eroded. Post-natal whorls 3–4. External sculpture consisting of strong oblique radiating ribs, close together. Internal shelf reflexed on itself at junction with columella, forming a slit-like umbilicus. Reflexed portion about 0·3–0·4 of length of shelf at its widest. Outline of shelf curved. Shelf somewhat incised at peripheral junction.

Name descriptive of the colour characteristic of the enveloping sands.

Material

Holotype: S.A.M.	K1432	D.	27·8 mm	A.	10·1 mm
Other specimens:			27·5 mm		12·0 mm
			29·9 mm		13·0 mm
			22·5 mm		9·5 mm
			20·0 mm		7·0 mm

Remarks

The present species differs significantly from living southern African representatives of the genus. The sculpturing is very similar to that of *C.*

helicoidea (Sowerby), but with the radiating ribs relatively stronger and closer together. The whorls are less clearly demarcated than in *C. helicoidea*, which is a proportionally higher shell, with a more obvious spire and with a better developed protoconch. The following measurements indicate the relative differences in height of shells of similar size of the two species:

C. helicoidea	D. 27·0 mm	A. 14·0 mm
	23·0 mm	11·3 mm
C. viridarena n.sp.	27·5 mm	12·0 mm
	22·5 mm	9·4 mm

The structure of the shelf and columella more closely resembles that of *C. chinensis* (Linnaeus) than *C. helicoidea*. In the latter, the reflexed portion is very short and forms a wider umbilicus than in the present species, while there is no incision at the fusion with the periphery, as in the present species.

Family **Trochidae**

Clanculus murrayi n.sp.

Pl. 23 & Fig. 3

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Shell trochoid in form, somewhat depressed; periphery angular, accentuated by strong carina, carinate sculpture lending a turreted aspect to the outline.

Eroded protoconch nucleus, plus apparently four whorls.

Suture non-canaliculate, umbilicus open and deep.

A single carina on the early whorls, located slightly below the midline, accompanied on the penultimate and last whorls by a second carina, developing from the suprasutural lira on the penultimate whorl and forming the shell periphery on the last whorl. Carinae equal to sub-equal in strength; where subequal, the upper, non-peripheral member always the stronger. Carinae composed of closely spaced oval to sub-rectangular granules with long axes sub-parallel to the vertical axis of the shell; granules slightly inclined on earlier whorls. Granulate radial lirae apparently present on all whorls; granules sub-circular on earlier whorls becoming more elongate along the vertical axis and eventually oval to sub-rectangular on the final whorl. In the largest specimens, areas between lirae with raised threads. On the 2nd whorl, approximately 5 lirae and a single carina; on the 3rd, 5–6 lirae and 2 carinae; 4th whorl 4–5 supra-carinate lirae, 2 carinae separated by 2–3 lirae with approximately 7 lirae on base of shell.

Specimens show a tendency for the body whorl to drop away from the periphery of the preceding whorl.

Outer lip of aperture strongly plicate, bearing 10–15 dentiform plicae. A prominent, ridged denticle present at the anterior end of the inner lip, protruding into the aperture; a second, smaller denticle, also pointing into the aperture on the posterior portion of the inner lip. Two small denticles, often elevated on a narrow ridge running into the umbilicus, on the median portion of the inner lip, pointing away from the aperture. On the larger specimens, dentiform plicae present on the margin of the umbilicus.

Named after Dr. L. G. Murray, Consulting Geologist, Anglo American Corp. S.A.

Material

Holotype:	S.A.M.	K1434	D. 17·6 mm	A. 11·8 mm
Paratype:	S.A.M.	K1435	17·0 mm	14·0 mm

Remarks

The trochoid form, open umbilicus and denticulate aperture suggest that this species should be assigned to the genus *Clanculus*, having strong affinities with the local species *C. miniatus* (Anton).

The present species differs from all the South African representatives of the genus in having a generally depressed form and a strongly turreted outline. The presence of strongly developed carinae distinguishes the present species from the non-carinate *C. atricatena* Tomlin and *C. puniceus* (Philippi), both of which exhibit a more complex and pronounced plication of the aperture lips. The non-canaliculate suture, amongst other features, serves to distinguish the present species from *C. waltonae* Sowerby, and *C. mixtus* Smith. In *C. miniatus*, carinate forms are common. However, such forms carry only a single carina

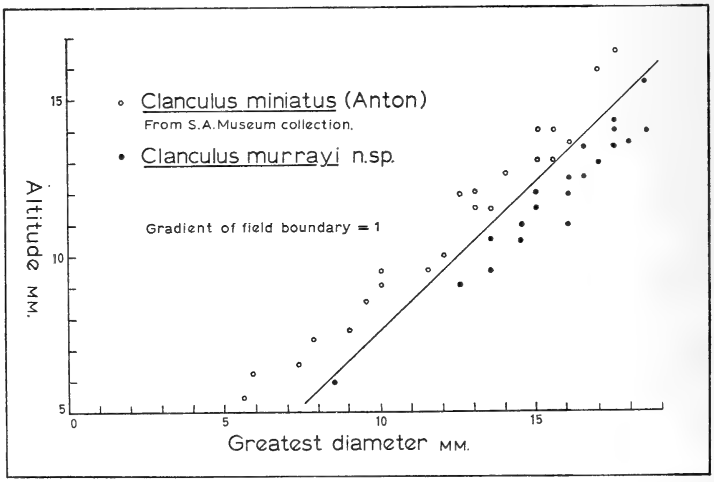

Fig. 3. Comparison of altitude/diameter ratios in *Clanculus miniatus* (Anton) and *C. murrayi* n.sp.

on the last whorl, at the shell periphery. In some of the specimens of *C. miniatus* examined, the mid-whorl granules on the last whorl are more strongly developed than their neighbours but are never sufficiently prominent to produce a bicarinate aspect. It is notable that in the present species, where the carinae are subequal, the mid-whorl member is always the stronger.

The depressed form of the present species in comparison with *C. miniatus* is illustrated by figure 3 and is possibly linked to the fewer whorls borne by this new species.

C. villanus Phillipi, reported from Angola by Paes-da Franca (1960), is another elevated member of the genus having a denticulate aperture but lacking the single, large, prominent tooth on the anterior area of the columella lip.

The new form shows little affinity with the west African representatives of the genus (*C. kraussi* Philippi, and *C. guineensis* Gmelin) noted by Nicklès (1950), both of which lack a prominent denticle on the inner lip and a strong peripheral carina.

Calliostoma depressa n.sp.

Pl. 23

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Shell a wide cone, apical angle greater than 90°, profile straight. Protoconch smooth, 2 whorls, $4\frac{1}{2}$–5 post-natal whorls. Profile of body whorl smoothly rounded. Sculpture consisting of very fine growth lines and spiral lirae. Latter formed by single strand of knobs connected by a low ridge. Body whorl with 19 lirae (counted at aperture). Penultimate whorl and preceding whorl with 7 lirae, first two postnatal whorls with 4–5 lirae, latter all of equal strength. Each lira separated from the next by a definite regular space. Each knob distinct, not touching the following or preceding one. Umbilicus closed, columella smooth.

Material

Holotype:	S.A.M.	K1440	D.	21 mm	A.	15 mm
Paratype:	S.A.M.	K1453		37 mm		30 mm

Remarks

Compared with the known living forms of this genus from southern Africa, this species is a much flatter shell with fewer whorls, most of the other species having 6–8 post-natal whorls. The sculpture, spiral lirae with knobs, is typical of the genus. The present species, in general shape, most resembles *Calliostoma eucosmia* Bartsch, particularly the 'low' form mentioned by Barnard (1963). The latter, however, is a more elevated shell, with the lirae much closer together and usually having strong lirae alternating with weaker ones, the knobs crowded on each other. *C. eucosmia* usually has a definite shoulder to the last whorl, although some forms approach the present species in having an almost smoothly rounded body whorl. The latter type of body whorl is characteristic of *C. multiliratum* (Sowerby), but the sculpture of this species is distinctive and very different from *C. depressa.* In the latter only a suggestion of a shoulder is present where the outer lip joins the preceding whorl. *C. africanum* Bartsch has sculpturing similar to the present shell, but with the knobs closer together. In the older shells of *C. africanum* the knobs tend to coalesce to form a solid raised lira. In *C. depressa,* the knobs remain distinct. There is little similarity between this shell and any of the west African, Angolan, or Moçambique species. Apart from *C. perfragile* Sowerby, which has been taken alive from the west coast of the Cape Peninsula, the genus is not known from the west coast of South or South West Africa. Further north the genus is again encountered in warm Angolan waters, where it is represented by *C. granulatum.*

Family **Fissurellidae**

Fissurella glarea n.sp.

Pl. 24

Location 3. 29–34 m Beach.

Description

Margin of shell egg-shaped, anterior end narrower than posterior. Lateral margins ventrally convex. Foramen elongate oval, lateral margins slightly concave, situated anterior to midline. Sculpture only of concentric irregular growth lines. No sign of radial sculpture. Dark radiating bands (*circa* 23–26) imposed on lighter background, stretching from foramen to margin.

Name descriptive of the gravelly nature of the enveloping sediment.

Material

Holotype:	S.A.M.	K1438	L.	39·0 mm	B.	27·5 mm
Paratype:	S.A.M.	K1439		76·0 mm		59·5 mm

Remarks

The following are the species of *Fissurella* which have been recorded from the South African region:

F. robusta Sowerby, known only as a fossil from the Pleistocene deposits of the west coast and Algoa Bay.

F. mutabilis Sowerby, known living from the west coast, False Bay, east coast, Madagascar, etc. Fossil from Pleistocene of Algoa Bay and Little Brak River.

F. natalensis Krauss, known living from the east coast, fossil from the Pleistocene of Algoa Bay.

The present species most closely resembles *F. robusta,* of which several undamaged specimens are available. This resemblance is most apparent in the young stages, older shell being obviously different. The marginal outline is very similar, the foramen is in the anterior portion of the shell in both species, and the sculpturing is similar. There are, however, several differences. The foramen in *F. robusta* has slightly convex sides, whereas in the present species, the sides are slightly concave (this portion of the shell is particularly subject to erosion, resulting in a variety of shapes, the true form being apparent only in unworn specimens). The profile of *F. robusta,* from posterior margin to foramen, is never straight. In younger specimens it is slightly convex, while in older specimens, the shells are distinctly arched, almost 'humped'. The posterior profile of the present species is never curved. *F. robusta* is a proportionally higher and heavier shell than the present species, which seems, if anything, to become flatter with age. Young specimens of *F. robusta* occasionally show faint radial lines. These are not apparent in the present species. The dark radial bands of the outer layers of the shell of the present species are not apparent in *F. robusta,* except in one specimen, which has a slightly curved posterior profile.

F. glarea differs from *F. mutabilis* Sowerby, which has radial costae, and no convexity of the margins, i.e. the entire margin touches a flat substrate. The shape of the foramen also differs. *F. mutabilis* does not have the dark radial bands of the present species.

F. natalensis is a rugose shell with almost nodulose radial costae, and with fine concentric lines, subordinate to the radial sculpture; all very different from *F. glarea.* Further differences include the overall shape of the shell (*F. natalensis* rests on the anterior and posterior ends of the shell), and the shape of the foramen.

F. dubia Reeve, from Moçambique, also has radial costae and the foramen is placed more or less centrally.

F. tanneri Verril, from Angola, has fine radial lines and an almost circular foramen. Both *F. coarctata* King and *F. nubecula* Linnaeus of west Africa have strong radial sculpture.

Family **Arcidae**

Arca avellana Lamarck, 1819

Pl. 25

Arca avellana Lamarck, Barnard, 1961: 192; 1964: 369. Boshoff, 1965: 109.
Arca acuminata Krauss, 1848: 14.
Navicula kraussii (Philippi), Cox, 1930: 154.

Location 3. 46–50 m Transgression complex
Early transgression beach.

Description

Cardinal area flat, triangular, the angle at the umbo 90°, marked with divergent ligament grooves. Umbo eroded in all except youngest valve.

Material

L. 44·00 mm (broken valve)
29·6 mm
28·2 mm
28·0 mm
20·0 mm
19·6 mm

Previous records

Living: Inhaca Island, Inhambane, Bazaruta, Durban.
Fossil: Pleistocene: Redhouse, Zwartkops River.
Post Pliocene: Inhambane.
Pliocene: Zwartkops.

Remarks

Cox (1930) described an abnormal right valve of *Navicula krausii* (Philippi) from the Pliocene deposits of Zwartkops, near Port Elizabeth. The present valves (with the exception of the smallest) all agree with Cox's description, in hinge details, sculpture, and general shape. The smallest valve is a typical *Arca avellana* without any distortion. All the complete valves show, to some degree, the septum-like platform in the anterior corner, as was noted in Cox's specimen. The ventral marginal area is narrow and concave, forming a large byssal gape. Boshoff (1965) notes that as this species frequents crevices, the valves are often distorted.

This species, in its present geographic distribution, is restricted to the warm waters of the Indian Ocean.

Arca* (*Acar*) *halmyrus n.sp.

Pl. 24

Location 3. 46–50 m Transgression complex.
Early transgression beach.

Description

Shell longer than high, umbo anterior to middle of shell. Fairly prominent posterior ridge present. Well-developed concentric and radial sculpture. Nearer the umbo, radial ribs more prominent than concentric lines. Anterior 7 or 8 ribs strong, increasing in thickness ventrally. Posterior 6 or 7 radial ribs similarly prominent, the largest forming the posterior ridge. Where concentric ridges cross anterior and posterior ribs, distinct knobs formed. Radial ribs of mid-region fine, an almost cancellate sculpture formed with the concentric growth lines. Intermediate radial ribs developing as growth proceeds. Cardinal area very narrow, 5 narrow, oblique grooves in posterior region, ending just posterior to umbo. Hinge slightly curved dorsally with 12 or 13 anterior teeth, the most anterior 4 or 5 being oblique. Median teeth reduced and almost absent in some. 10 or 11 posterior teeth, almost all oblique. Inner surface of valves with fine radiating lines. Inner margin of shell crenulate.

Named from the location – 'Brak', Afrikaans – 'brack' river.

Material

Holotype: S.A.M.	K1448	L.	26 mm	A.	15 mm
Other specimens:			23 mm		11 mm
			21 mm		12 mm
			16 mm		8 mm

Remarks

These shells are placed in the subgenus *Acar* as defined by Thiele (1929), as there is a posterior ridge present, the sculpture being knobbed, the umbo anterior to the midline of the shell, the dorsal plane small, the median hinge teeth weak/rudimentary and the outer teeth oblique. The present species differs from *Arca* (*Acar*) *plicata* Dillwyn, which it most strongly resembles, in the following respects: the present shell is flatter than *A.* (*A.*) *plicata* and has well-developed anterior and posterior radiating, nodulose ribs which *A.* (*A.*) *plicata* lacks. In the region of the posterior ridge, *A.* (*A.*) *plicata* usually has prominent squamae instead of the nodules of the present species. In the hinge area, the dorsal plane of *A.* (*A.*) *plicata*, which is wider than in the present species, has 10 or more oblique/elongate grooves, the more medial ones extending the entire length of the hinge area; *A.* (*A.*) *halmyrus* however, has only about 5 oblique grooves, none extending beyond the umbo. The angle of the posterior ribs radiating from the umbo differs considerably in these species.

Family **Condylocardiidae**

Carditella calipsamma n.sp.

Fig. 4

Location 1. 45–50 m Transgression complex.
Back-beach environment.

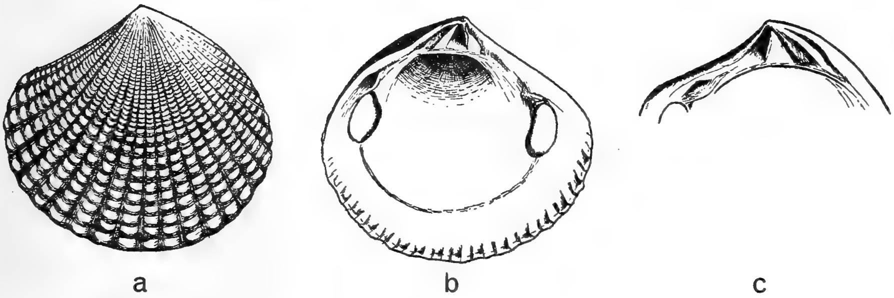

Fig. 4. *Carditella calipsamma* n.sp. Holotype. a. Right valve in external view. b. Right valve in internal view. c. Hinge of left valve.

Description

Valves equilateral, prodissoconch eroded. 23–27 radial ribs with low nodules. Latter oval near apex, becoming transversely rectangular nearer margin. Grooves between ribs becoming wider and shallower towards margin. Very fine concentric growth lines present, more apparent in grooves on younger portion. 4–5 growth lines per nodule. Ventral inner margin of shell crenulate, mantle line uninterrupted. Left valve with two cardinal teeth, anterior tooth a low ridge, posterior tooth prominently triangular. Right valve with 2 cardinal teeth, separated by a deep triangular pit. Low ridge present in front of anterior tooth. Each valve with a single anterior and posterior lateral tooth.

Name descriptive of the local lithology.

Material

Holotype:	S.A.M.	K1449	L.	11·9 mm	A.	12·3 mm
Paratype:	S.A.M.	K1450		9·2 mm		9·2 mm
Other specimens:				12·8 mm		12·8 mm
				12·5 mm		12·7 mm
				11·8 mm		12·2 mm

Remarks

The sculpture of this species resembles that of *Carditella similis* Jaeckel & Thiele, *Carditopsis dartevellei* Nicklès and to some extent *Cuna gambiensis* Nicklès. *C. gambiensis* differs from the present species in that the grooves separating the radial ribs are relatively narrower. The dorsal profile of *C. gambiensis* is more acute (90° as compared with *circa* 110°). The west African species also appears to lack lateral teeth (see Nicklès, 1955). The present species is more closely related to *Carditopsis dartevellei* Nicklès, 1952, recorded from the Quaternary deposits of Gabon, but this differs in possessing fewer rays (14–16) and in being a much smaller shell (2·5 × 2·6 mm being the largest). The adductor muscle scars of the present species are not as obviously reniform as those in *C. dartevellei*. *Carditella similis* differs from the present species in possessing fewer ribs (20–21), in the older nodules being more obviously rectangular and flattened and in being a smaller shell (3·5 × 7·3 mm being the largest).

Family **Mactridae**

Standella* (*Eastonia*) *namaquensis n.sp.

Pl. 26 & Fig. 5

Location 1. 45–50 m Transgression complex.
Back beach environment.

Description

Ovate, inequilateral, equivalve, transversely elongate. Umbones small, slightly incurved, located anterior to mid-line of shell. Anterior end rounded,

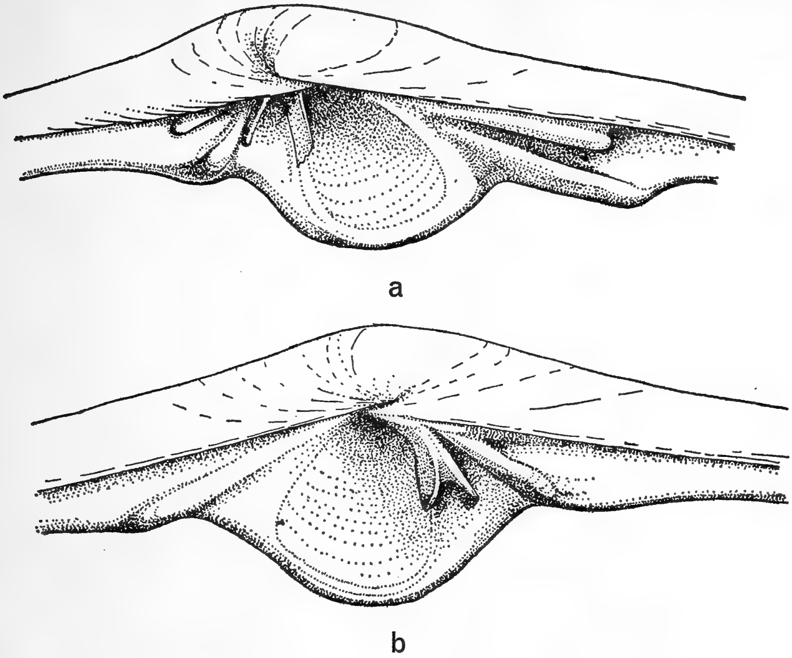

Fig. 5. *Standella* (*Eastonia*) *namaquensis* n.sp. Hinge details: a. Right valve. b. Left valve.

posterior end subtruncate. Dorsal outline, posterior to umbones, very slightly concave. Valve interior moderately concave; posteriorly the concavity diminishes, the posterior termini becoming flattened, with a narrow gape. A weak dorsal ridge runs from the umbo to the posterior end of the shell, fairly close to the postero-dorsal angle. Lunule poorly defined. Outline non-crenulate.

Sculpture of concentric growth lines, raised and sub-lamelliform on the ventral periphery. Radial sculpture of numerous, very fine, plicate ribs, irregularly spaced, slightly sinuous, often showing random bifurcation and fusion, frequently discontinuous across growth ridges. The radial and concentric sculpture together produce a very fine, highly irregular, reticulate pattern. Posteriorly, the surface becomes slightly rugose, the growth lines correspondingly more sinuous.

Hinge plate robust, carrying a chondrophore projecting backwards but torted towards the median area of the ventral margin. Distal outline of chondrophore smoothly rounded. Hinge of right valve with 2 elongate, posterior lateral teeth; the larger ventral tooth erect, the dorsal tooth suberect. 3 anterior dental elements present; a thin cardinal lamella, running the length of the anterior margin of the chondrophore, leaning slightly towards the mid-line to cover a small segment of that hinge component, a narrow lateral aligned close to the dorsal margin of the hinge plate and a large, erect, apparently bilobed, cardio-lateral tooth. This last element appears to be compounded of a small, dorsally situated, trigonal cardinal fused to a much larger, longer, subtrigonal, lateral tooth. The suture marking this fusion is clearly evident when viewed from the anterior aspect. The compound cardio-lateral tooth is separated from the cardinal lamella by a narrow, triangular pit.

In the holotype, the cardinal lamella has broken away but the scar is apparent. The lamella is preserved on a second specimen (paratype S.A.M. K1425).

Hinge of left valve with a single, elongate, posterior lateral ridge extending to the hinge plate margin. In front of the chondrophore, 2 anterior cardinal teeth fused to form a Λ-shaped compound tooth which extends approximately half way across the hinge plate. In the holotype, the Λ-shaped tooth is suberect, the crest deflected some 20–30° from the vertical; in smaller specimens the degree of deflection is somewhat greater. The two branches of the Λ-tooth diverge at about 30°, the posterior branch overhanging the chondrophore. A narrow, linear depression separates this compound tooth from a single, large, erect lateral.

Pallial sinus deep, sub-parallel; terminus well rounded, extending to the level of the extreme posterior edge of the chondrophore.

Examination of other specimens from the type locality indicates that the outline and decoration show some variation. In the smaller specimens, the valves are less elongate and slightly donaciform. In some specimens the sculpture is apparently muted with concentric growth lines dominant. Examination of such forms indicates that the fine, radial elements of the reticulate sculpture have been preserved in depressions in the somewhat rugose surface of the extreme posterior areas of the valves. It is supposed that the destruction of these delicate plicate ribs is the result of abrasion encountered during transport of the valves along the beach. It is notable, in this context, that discrete, separated valves are more profoundly affected in this respect than the holotype, recovered with both valves together.

Named from the general location – Namaqualand.

Material

Holotype:	S.A.M. K1424	L. 68 mm	A. 43 mm	W. 28 mm (both valves)
Other specimens:		51 mm	34 mm	
		43 mm	31 mm	
Paratype (hinge fragment):	K1425			

Remarks

As regards dentition, the present species more closely resemble Lamy's figure (1918: 383) of *Eastonia rugosa* (Helbling) than it does his figure (p. 382) of *Standella pellucida* (Chemnitz). The two branches of the Λ-shaped compound cardinal tooth in the left valve as noted above, diverge at an acute angle, the posterior branch overhanging a segment of the chondrophore. Despite the degree of fusion, it is suggested that the compound anterior cardio-lateral tooth in the right valve of the present species more nearly resembles the closely apposed anterior cardinal and lateral teeth of *E. rugosa* than it does the continuous, bilobed, anterior cardio-lateral element in *S. pellucida.*

For the above reasons the present species is assigned to the sub-genus *Eastonia.*

S. (*E.*) *namaquensis* is unlike the only South African representative of the sub-genus, viz. *Standella* (*Eastonia*) *solanderi* (Gray). (Barnard (1964) suggests that *S. nicobarica* (Gmelin) falls outside the limits of the sub-genus.) In *S.* (*E.*) *solanderi,* which is a far smaller form bearing a strong radial ornament of relatively regular, continuous ribs, the Λ-shaped tooth occupies the full width of the hinge-plate; the divergence of the branches of this tooth being greater than in the present species.

The similarity in hinge detail between *S.* (*E.*) *namaquensis* and the west African representative *S.* (*E.*) *rugosa* has been noted above. The two species differ as regards decoration, the last named, according to Nicklès' figure (1950: 210), possessing a strong radial ornament of regular, closely spaced costae. In this figure, the terminus of the pallial sinus attains the level of the anterior edge of the chondrophore.

In Lamy's figure (p. 383) of *S.* (*E.*) *rugosa,* the anterior lateral tooth in the left valve appears oblique, not erect as in the present species.

S. (*E.*) *rugosa* is a Mediterranean species extending into the Atlantic ocean along the Portuguese and west African coasts. It is known from the Pliocene and Pleistocene of France.

Nicklès (1950: 210) suggests, by his terminology, that *S. senegalensis* Philippi is not to be included in the sub-genus. The outline and decoration of this shell is markedly different from the present species.

The Philippine forms *S.* (*Merope*) *plicatilis* (Deshayes) and *S.* (*Merope*) *capillacea* (Deshayes), according to Deshayes (1854: 69), have an irregular, reticulate sculpture of fine plicate ribs like that possessed by the present species. In *M. plicatilis* however, the pallial sinus is trigonal, terminating at an obtuse angle.

Family **Donacidae**

Donax haughtoni n.sp.

Pls 27–28 & Figs 6–9

Location 2. 45–50 m Transgression complex.
Fore-beach environment.

Description

Shell equivalve, inequilateral, greatest pre-umbonal length longer than greatest post-umbonal length. Shell anteriorly smooth, posterior ridge not very distinct, with fine concentric lines sometimes posteriorly present; rest of shell

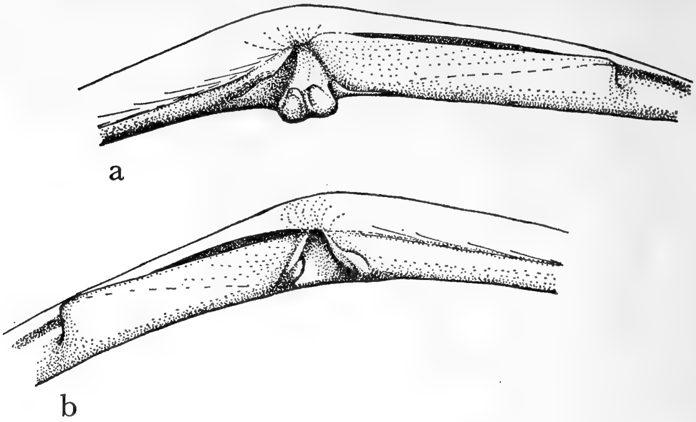

Fig. 6. *Donax haughtoni* n.sp. Hinge details: a. Right valve. b. Left valve.

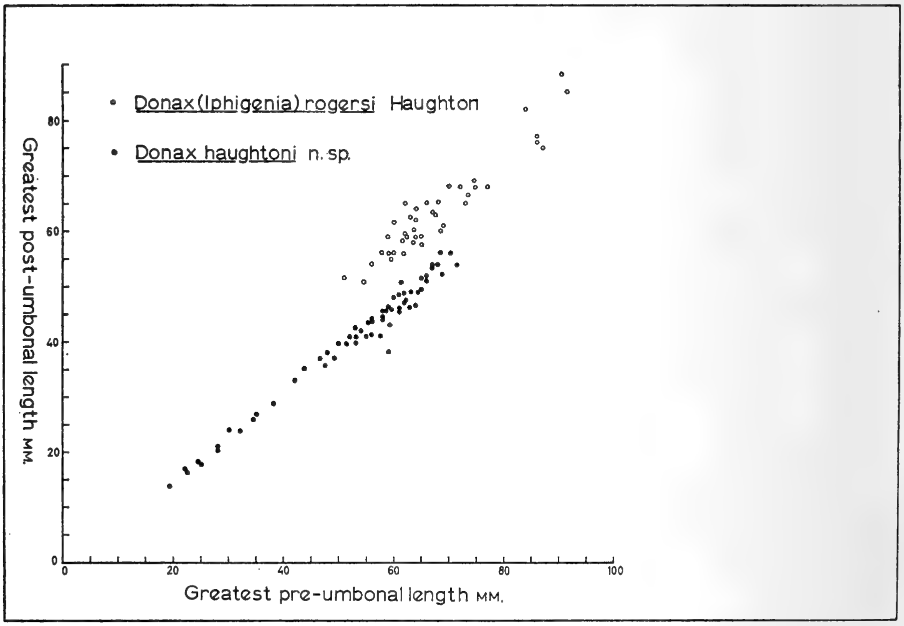

Fig. 7

surface smooth. Inner margin smooth. Antero-ventral margin smoothly rounded, postero-ventral margin with a slight corner in older valves. Hinge of left valve with 2 cardinal teeth with triangular pit between. Anterior tooth slightly broader than posterior. Hinge of right valve with a low anterior ridge and a prominent, broad cardinal tooth. Latter apically bifid. Rectangular flattened process, posterior to umbo in both valves, at least three times longer than wide.

Named after Dr. S. H. Haughton.

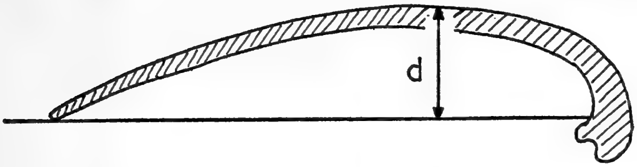

Fig. 8. *Donax haughtoni* n.sp. Diagrammatic cross-section of valve to illustrate distance d—greatest width, hinge excluded.

Material

Holotype: S.A.M. K1430 L. 97·0 mm A. 61·0 mm
Paratype: S.A.M. K1431 70·5 mm 44·0 mm
(A complete range of valves from 20 mm to 97 mm in length, in the South African Museum.)

Remarks

This species most closely resembles *Donax* (*Iphigenia*) *rogersi* Haughton, from the coastal deposits of Doornbaai. Haughton's material in the South African Museum, however, includes both *D.* (*I.*) *rogersi* and *D. haughtoni.* Haughton (1931: 36), states that the smaller shells obtained from The Point, Van Rhynsdorp, have the umbo well in advance of the midline of the shell but that the umbo's position 'accords well with that in equivalent growth stages of the larger shells from Doornbaai and Alexander Bay, and these specimens fall therefore within the limits of the species'. With more material now available it would seem that this smaller and more elongate form mentioned by Haughton is the present species and not a young form of *D.* (*I.*)

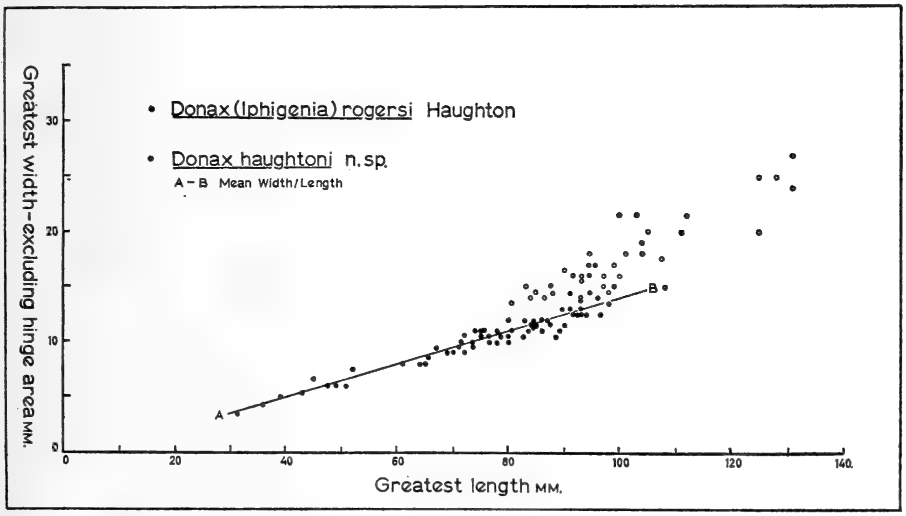

Fig. 9. Comparison of greatest length/greatest width (hinge excluded) ratios in *Donax* (*I.*) *rogersi* Haughton and *D. haughtoni* n.sp.

rogersi. Figure 7 graphically illustrates the relationship of valve proportions in the two species. It can be seen that in *D. haughtoni* the proportion between the greatest pre-umbonal length and the greatest post-umbonal length is fairly constant. Specimens of *D.* (*I.*) *rogersi*, although more variable, usually have a more equilateral shell. There is a distinct separation of the two species in the region of the graph where shells of similar size are recorded. The elongate anterior region of *D. haughtoni* is thus an almost constant feature of the species.

Other differences between the species include the strength of the posterior ridge, hinge details, and relative thickness of the shell.

In *D.* (*I.*) *rogersi* the posterior ridge is far more pronounced than in *D. haughtoni*. This results in a relatively wider shell. In an attempt to illustrate this graphically, total shell length was plotted against the width of the shell. This latter parameter, the distance 'd', was measured at right angles to a line connecting the ventral and dorsal margins but excluding the immediate hinge areas, as the teeth especially are subject to erosion. Figure 9 illustrates this relationship. This character would seem to be rather variable, especially in *D. rogersi*. Almost all the *D.* (*I.*) *rogersi* lie above a line representing the mean for *D. haughtoni*, thus showing that *D. rogersi* usually has a relatively wider shell.

Although Haughton in his description of *D.* (*I.*) *rogersi* stated that the central tooth of the right valve was not bifid, examination of less eroded material shows that this tooth is indeed bifid, but not as markedly so as in *D. haughtoni*.

The rectangular process just posterior to the cardinal teeth in *D.* (*I.*) *rogersi* is about twice as long as wide. All the specimens of *D.* (*I.*) *rogersi* are massive shells, much thicker than shells of comparable size of *D. haughtoni*. The stratigraphical distribution of the two forms is perhaps the most telling point in favour of according a specific identity to Haughton's '*young growth stages of D.* (*I.*) *rogersi*'.

In fore-beach environments associated with the 45–50 m strand line, *D. haughtoni* has been recovered in extraordinary abundance (see pl. 28). Here, owing to this super-abundance and to the excellent preservation, a very large number of individuals may be examined and a complete range of growth stages recovered. From this wealth of material, not a single specimen of *D.* (*I.*) *rogersi* was located. A large percentage of the individuals examined were grouped in the largest size range, length 80 mm to 95 mm, which probably represents the dimensions normally attained by mature adults of the species. Growth stages from length 20 mm upwards to the adult length were examined and found to exhibit no major variation in form, differing from one another in size alone. If, as has been suggested previously, *D. haughtoni* is merely the juvenile form of *D.* (*I.*) *rogersi* and that only mature or senescent forms of this latter species are characterised by a thickening of the shell, an apparent shift of the umbones to a median position and the development of a strong posterior ridge, then a few at least of such 'mature' forms might reasonably be expected to appear in the assemblage. None was apparent.

In the transgressive gravels and the coarse back-beach sediments of the

45–50 m strand, representatives of the genus were not commonly found, those located were usually fragmental. Of these, the few entire individuals and occasional shards collected could all be assigned to *D. haughtoni*. Fragments or entire valves of *D.* (*I.*) *rogersi* were not recorded.

At the localities investigated, the species *D.* (*I.*) *rogersi* is found associated with the extremely coarse, granular to pebbly, back-beach deposits relating to the 17–21 m sea stand. At this elevation numerically large concentrations of individuals of this species are met with (pl. 28), all such individuals being ascribed to the species *D.* (*I.*) *rogersi*; not a single individual of the proposed *D. haughtoni* was noted. The degree of preservation of the shells is rather poor, much of the material being chipped or badly broken and often of a fragile, powdery or flaky consistency. The fractured nature of the shells, from coarse breakage to fine comminution, may be attributed to the extremely rigorous environment which existed during the time of entombment and is testified to by the coarse grain size of the sediments. The powdery, fragile condition of the shells points to subsequent leaching of carbonate by solutions percolating through the very coarse, highly permeable, enveloping granular sediment.

It is suggested that this compounding of rigorous depositional environment and post-depositional leaching is, in large measure, responsible for the virtual absence of young growth stages of *D.* (*I.*) *rogersi* in the assemblages.

It seems apparent that there are stratigraphical as well as purely morphological differences between *D.* (*I.*) *rogersi* and the proposed *D. haughtoni* – the former flourishing at the time of the 17–21 m marine transgression, the latter being prevalent during an earlier encroachment by the sea on to the land.

It is possible that *D. haughtoni* eventually gave rise to *D.* (*I.*) *rogersi*, the change being conditioned by a profound shift in environment indicated by the widely different character of the sediments in which the two species are found.

As suggested in the opening remarks, the nature of the 45–50 m transgression sediments may indicate a slow accumulation of very fine grained material producing an environment favourable to sand dwelling bivalves and one allowing fairly thin-walled, elongate shells to flourish.

In the case of those sediments comprising the 17–21 m beach, the abundance of coarse, granular horizons up to 5 m above the basal gravel suggests that molluscs inhabiting the littoral during those times were obliged to withstand a rigorous, abrasive environment, characterized by a rapid accumulation of coarse sediment.

In this habitat, the thin-shelled form would be under stress and liable to breakage. Accordingly, by a process of selection, communities containing individuals tending towards a more robust and resistant form became dominant. The shell of the average individual became thicker, with a powerful hinge placed at the mid-dorsal point of the shell, producing a structure more suited to withstand vertical stresses in a plane at right angles to the surface of the shell. Similarly, stresses parallel with the short axis of the shell were countered by the development of the strong posterior ridge.

The placing of *D. rogersi* in the subgenus of *Iphigenia* must now be considered in the light of this new information. If *Donax* (*Donax*) *haughtoni* gave rise to the later *D.* (*I.*) *rogersi*, it would seem unlikely that the same subgenus (*Iphigenia*) would also occur in the Miocene deposits of Venezuela, where *D.* (*I.*) *olssoni* Hodson, 1931, was recorded. The subgenus *Iphigenia* is also represented by the living *D.* (*I.*) *rostrata* Römer, *D.* (*I.*) *laevigata* (Gmelin) and *D.* (*I.*) *truncata* (Monterosato) in west Africa.

In this particular case, it would seem that the division of the southern African members of the genus *Donax* is an artificial one and that *D. rogersi* probably does not fall into the subgenus *Iphigenia.*

Paes-da Franca (1960) records the discovery at Baia dos Tigres, Angola, of a single valve, 77 mm long, of *Donax serra* Chemnitz. The accompanying plate portrays a sub-donaciform shell having a smooth, non-crenulate ventral outline. The angle between the postero-dorsal and antero-dorsal margins is rather high, certainly greater than that normally exhibited by *D. serra.* The arena behind the dorsal ridge is fairly smooth, prominent crenulation of the growth lines in this region, so typical of *D. serra*, being apparently absent. It is suggested that Paes-da Franca has recovered a valve of *D. haughtoni*, probably washed out of a local Pleistocene horizon and not a specimen of *D. serra.*

Family **Tellinidae**

Gastrana rostrata n.sp.

Pl. 29 & Fig. 10

Location 1. 45–50 m Transgression complex.
Fore-beach environment.

Description

Shell moderately large, thin-walled, elongate, inequilateral, equivalve. Anteriorly rounded, posteriorly strongly rostrate. Median areas of valves vaulted, posteriorly the degree of concavity reduced, the rostrate regions becoming flattened along a plane separating the valves, forming a small gape. Dorsal outline behind umbones concave; ventral outline smooth.

Umbones small, not inflated, slightly forward of the median dorsal area; external surface of shell hardly visible in interior view. A weak dorsal ridge running from the umbonal region to the posterior ventral angle.

Lunules moderately long, narrow, and well-defined; ligament mainly external.

Sculpture of concentric growth lines which become raised to sub-lamelliform towards the periphery, also microscopic radial striae, entirely subordinate to the concentric sculptural elements.

Hinge areas extremely small in relation to the size of the shell.

Left valve with 2 cardinal teeth, very unequal in size. Posterior tooth small, erect, lamelliform, situated very close to the anterior end of the ligament and obliquely set. Anterior cardinal tooth centrally situated on hinge plate, relatively large, wedge shaped, squarely set pointing just anterior to the median portion of the ventral outline. A deep, narrow groove running along the upper surface, giving a profoundly bifid appearance to the tooth. 2 raised processes, separated by this groove, situated on the extreme distal portion of the tooth. Terminal area of this large cardinal not projecting beyond the hinge plate and obliquely truncated, sloping posteriorly. Cardinal teeth separated by a deep triangular pit.

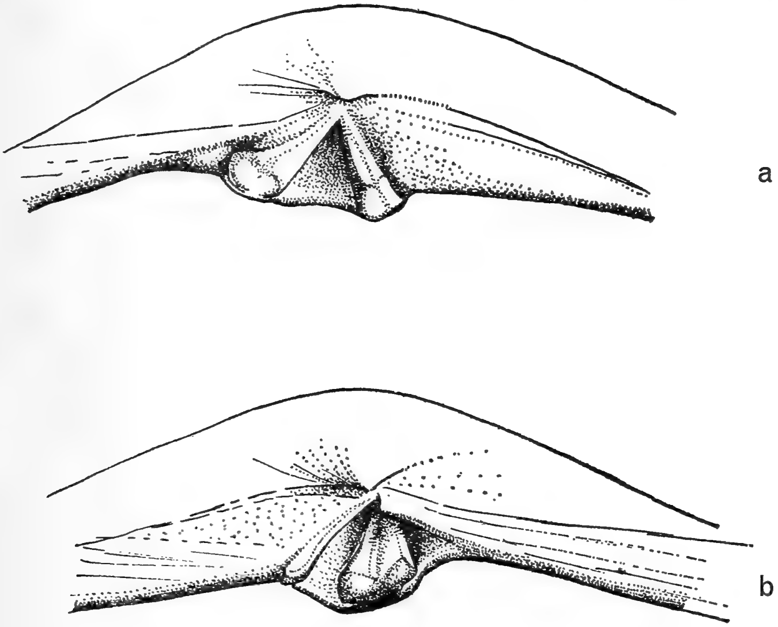

Fig. 10. *Gastrana rostrata* n.sp. Hinge details: a. Right valve. b. Left valve.

Right valve with 2 moderately large, divergent cardinal teeth; sub-equal, the anterior member somewhat broader; both erect, narrowly wedge-shaped and patently bifid, each with a longitudinal groove on the upper surface. A broad, deep triangular pit, accommodating the large cardinal tooth of the left valve, separating the two teeth.

Pallial sinus deep, passing beyond the level of the hinge; sides not parallel, the dorsal margin sloping steeply downwards; terminus poorly rounded. Ventral margin running close to, and parallel with, pallial line.

Material

Holotype:	S.A.M.	K1426	L.	67·0 mm	A.	39·5 mm
Paratype:	S.A.M.	K1427		64·5 mm		43·5 mm

Paratype: S.A.M. K1445 L. 62·0 mm A. 68·0 mm
Paratype: S.A.M. K1446 66·0 mm 43·0 mm

Remarks

The presence of two cardinal teeth in each valve, the absence of laterals, the gross inequality of the cardinal teeth in the left valve, the bifid nature of the teeth and the form of the ornament and the pallial sinus suggest that this new species should be assigned to the genus *Gastrana* Schumacher.

The present species shows affinities with *G. abildgaardiana* (Spengler) and with *G. matadoa* Gmelin, all three forms having a similar pallial sinus form and a basically similar dental design.

The former species is an inhabitant of the southern and eastern coasts of South Africa and is recorded from the local Pleistocene deposits; Sedgefield (Martin); Knysna (Schwarz) and Saldanha Bay (Haughton). The latter lives along the west African coast as far south as the Congo.

G. matadoa and the present species are dissimilar in regard to shape and ornament, the former being generally oval in outline and decorated with more massive concentric ridges, becoming very strongly developed on the peripheral parts of the shell. In the left valve of the west African species, the central tooth is relatively larger, projects slightly beyond the hinge-plate margin and carries a broad shallow trench rather than a deep, narrow groove on the upper surface.

The sculpture of *G. abildgaardiana* is very similar to that of the present species. The two forms show definite differences in shape (*G. abildgaardiana* being ovato-cuneiform) and in dentition. In Spengler's species the triangular central cardinal tooth in the left valve is a relatively massive structure, very broad and occupying a larger area of the hinge region. In this large tooth, which projects well beyond the hinge margin, the bifid condition is only poorly developed.

In the right valve the subequal cardinals show only poor bifidity. In both *G. matadoa* and *G. abildgaardiana* the umbones are moderately inflated.

The difference in shape and size of the dental elements suggests that the present form is specifically different from both *G. abildgaardiana* and *G. matadoa* and not simply an aberrant rostrate form of one or the other. In this context it is interesting to note that the present species is to be found in abundance in certain localities at the horizon noted above. From these localities, *G. abildgaardiana* has not been recovered; a single, small, left valve of *G. matadoa* has, however, been found amongst the hundreds of individuals of *G. rostrata*. This valve bears the ovato-cuneiform outline and the strong, concentric sculpture ridges of the contemporary *G. matadoa* as figured by Nicklès (1950: 220, fig. 426). A broad, shallow groove runs along the upper surface of the central cardinal tooth which projects beyond the hinge-plate margin.

Deeply abraded, exceptionally thick-walled and heavy, ovate specimens of *G. abildgaardiana* are found in the very coarse sediments of the 17–21 m beach.

Family **Aloididae**

Aloidis palaegialus n.sp.

Pl. 25 & Fig. 11

Location 3. 45–50 m Transgression complex.
Early transgression beach.

Description

Inequilateral, umbo in front of middle. Inequivalve, right valve larger than left, strongly vaulted. Both valves posteriorly with blunt carina stretching from umbo to margin, posteriorly slightly beaked. Antero-ventral margin smoothly rounded. Ventral edge of right valve very thin, overlapping left valve, mainly in posterior region. Sculpture of not very regular, fine, concentric ridges, becoming stronger ventrally. Umbonal region almost smooth. Internally,

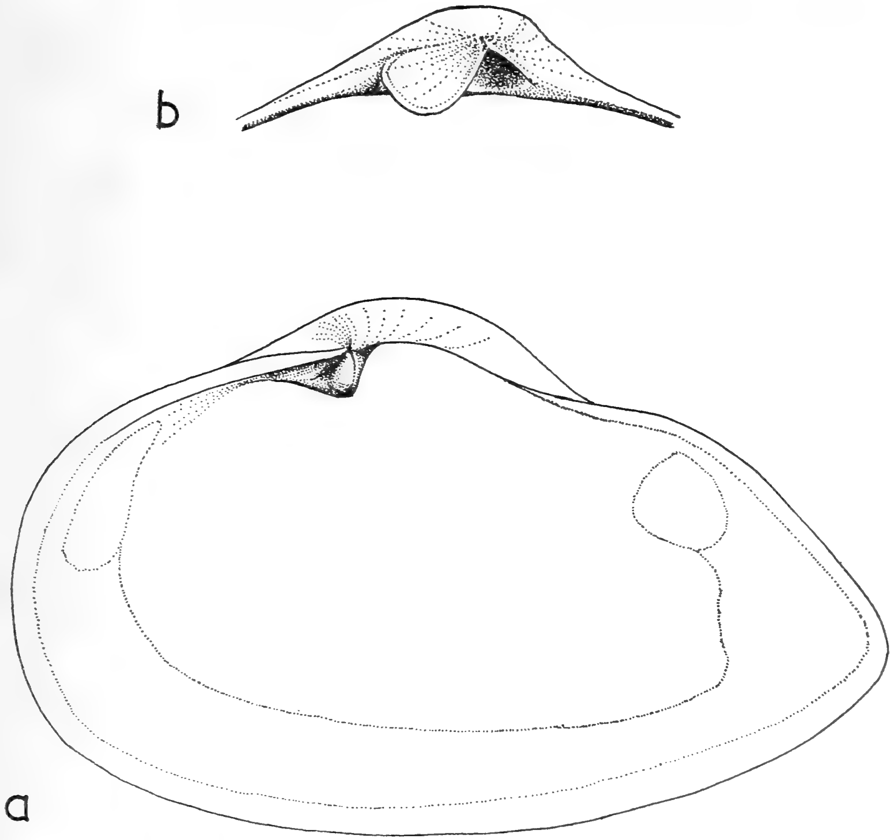

Fig. 11. *Aloides palaegialus* n.sp. Hinge details: a. Right valve. b. Left valve.

overlapping portion of right valve clearly demarcated from rest of valve. Anterior and posterior muscle scars present, pallial line uninterrupted, no pallial sinus; posteriorly, pallial line turns upwards at right angles, to meet the posterior adductor muscle scar. Hinge of right valve with prominent triangular tooth, a low ridge running anteriorly. Just posterior to the strong cardinal tooth, a deep ligamental pit, set well under the umbo. Hinge of left valve with an anterior triangular pit (to accommodate the cardinal tooth of the right valve) just posterior to which, a large, spatulate, triangular ligament support.

Material

Holotype:	S.A.M.	K1451	L.	15·5 mm	A.	9·8 mm
Paratype:	S.A.M.	K1452		16·2 mm		10·0 mm

Remarks

This species is very similar in shape to *Aloides striatissima* Lamy, known living from Angola to Senegal and as a fossil from the Pleistocene of Gabon (Nicklès, 1952). The concentric sculpture appears identical in the two species. In most of the available descriptions of *A. striatissima* mention is made of very fine radiating lines, particularly on the anterior portion of the valves. The present species bears no sign of radiating sculpture. No figures or description of the hinge of Lamy's species is at present available.

ACKNOWLEDGEMENTS

The authors wish to express their appreciation of the assistance rendered by the Management of De Beers Consolidated Mines Ltd., Namaqualand Venture. They are indebted to Dr. G. Bonaccorsi, who kindly donated the holotypes of *Standella* (*E*) *namaquensis* and *Tritonalia bonaccorsii* and to Mr. S. Kannemeyer (South African Museum) from whose photographs plates 18–27 and 29 are derived.

The Trustees of the South African Museum thank the South African Council for Scientific and Industrial Research for a grant in aid of publication.

SUMMARY

During the course of a geological survey of the Tertiary to Recent sediments of the Namaqualand coast, a suite of fossil molluscs was recovered from Pleistocene horizons at three locations along this coastal strip. The paper describes some twenty species and subspecies from this collection, seventeen of which are new, the remaining three being new records for the west Coast.

The generic affinities of the new species and the present geographic ranges of the previously recorded forms, here described, suggest that, in Lower Pleistocene times at least, the waters bounding this coast were considerably warmer than those presently washing this shore.

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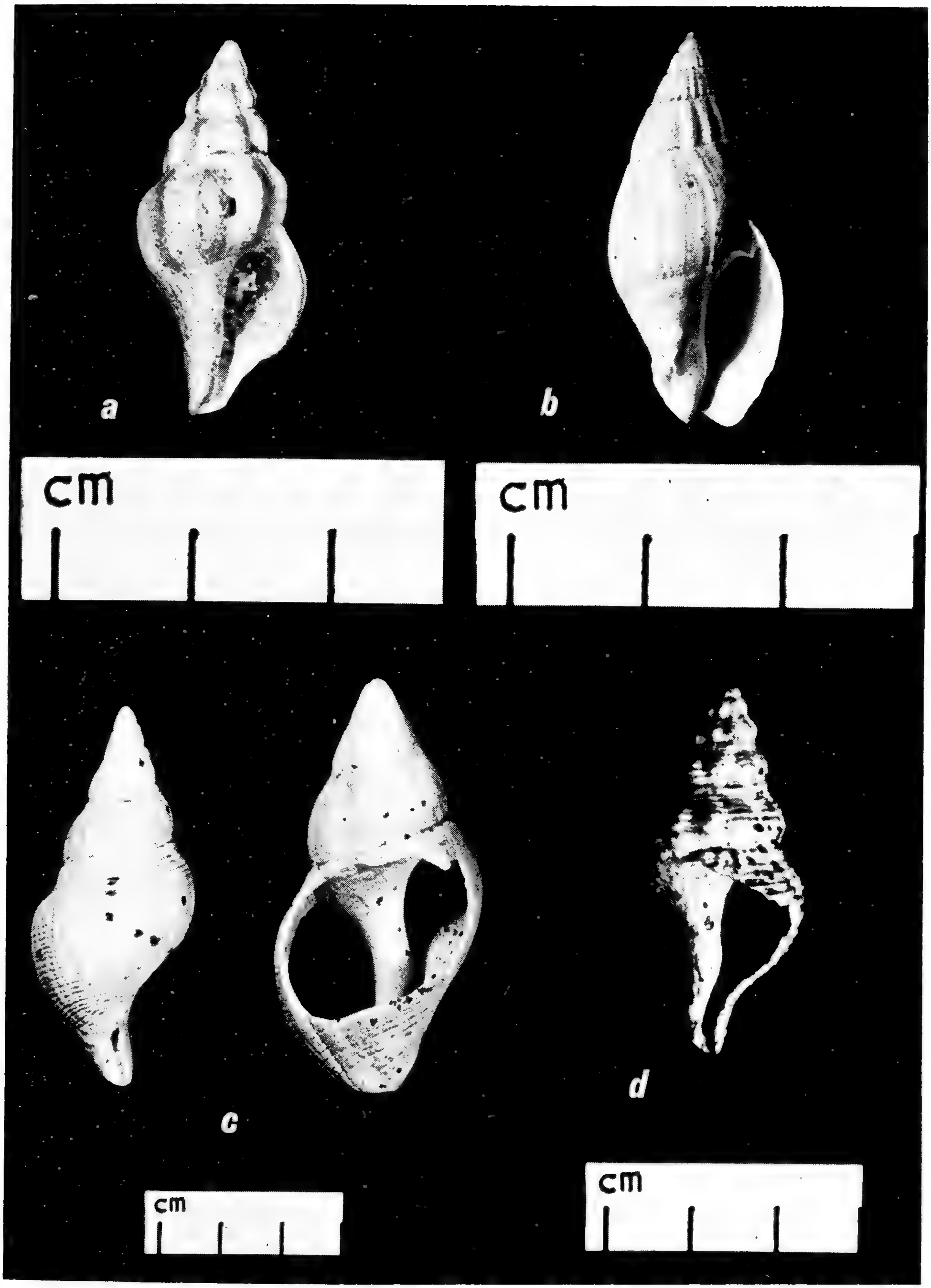
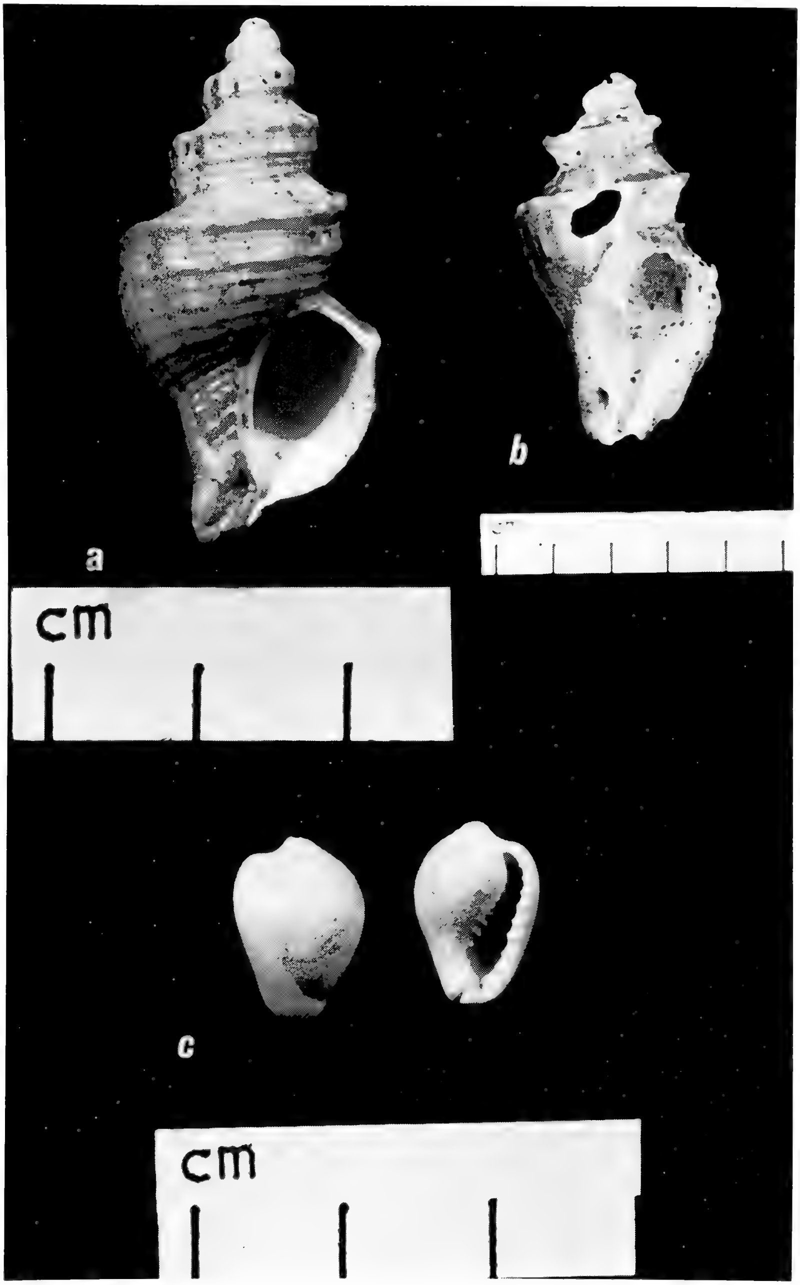


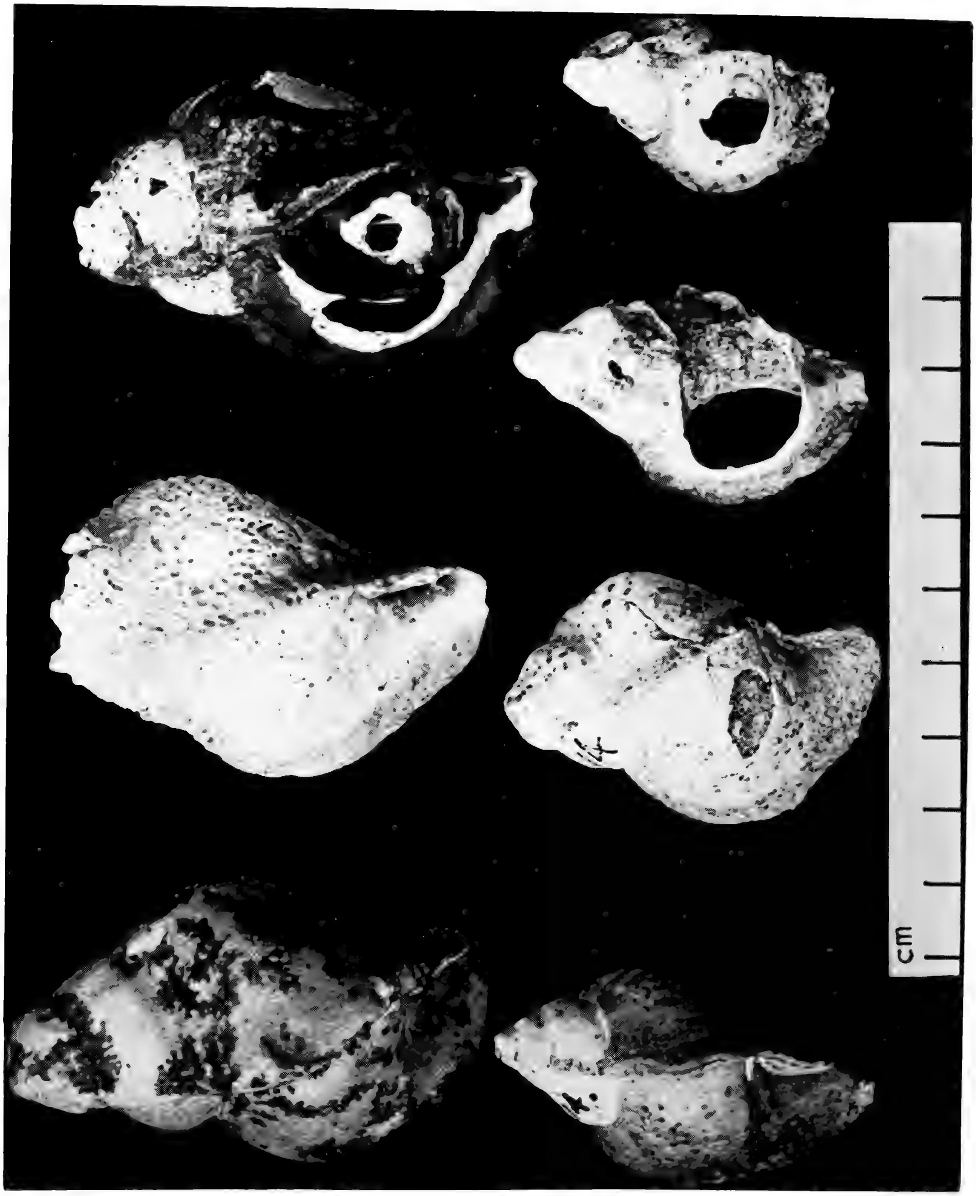
(Note: on all plates, one division of the scale = 1 cm.)

a. '*Turris*' *nigrovitta* n.sp. Holotype
b. *Nassa litorafontis* n.sp. Holotype
c. *Fasciolaria lugubris* Reeve
d. *Fusus faurei* Barnard

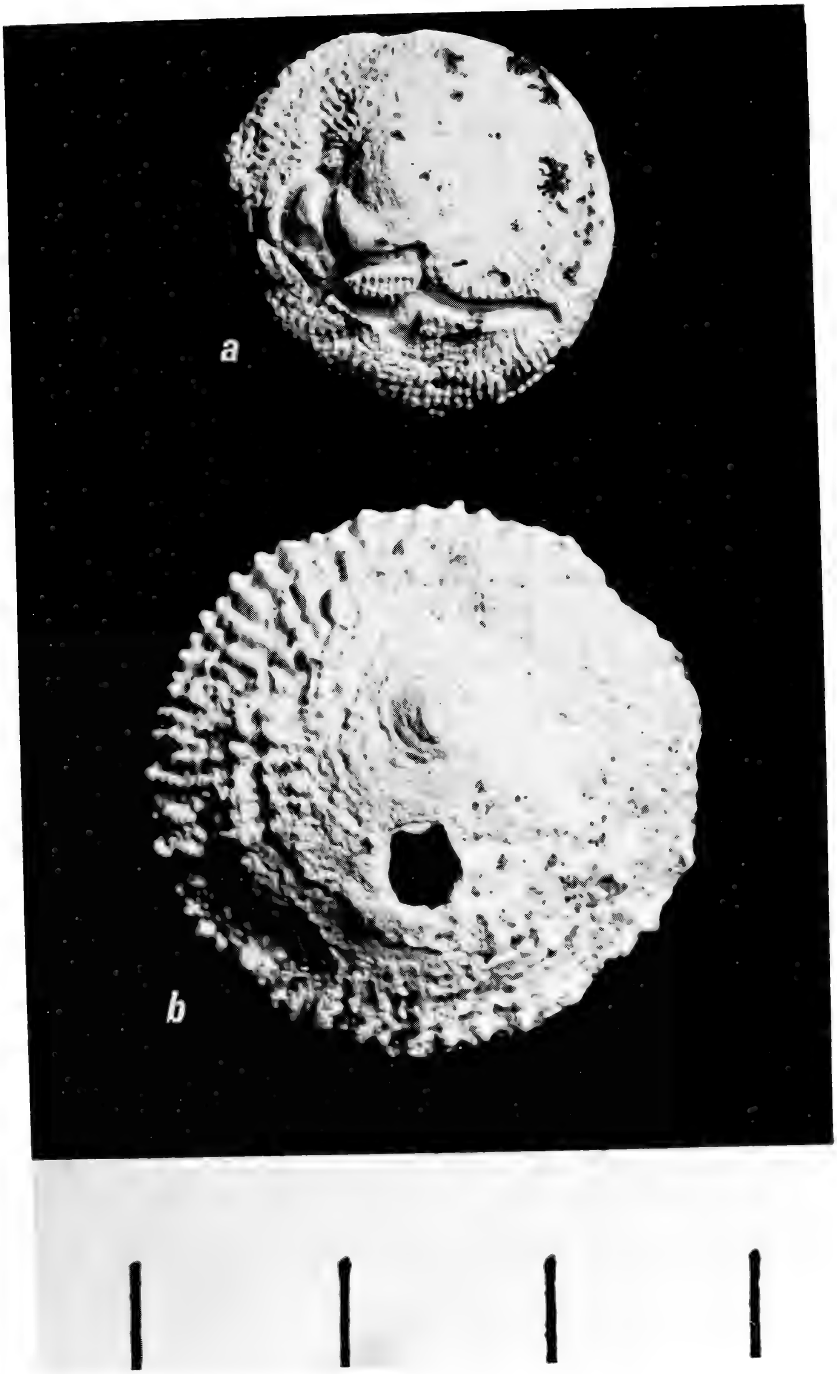


a. *Tritonalia bonaccorsii* n.sp. Holotype
b. *Latiaxis* sp.
c. *Hespererato oppenheimeri* n.sp. Holotype

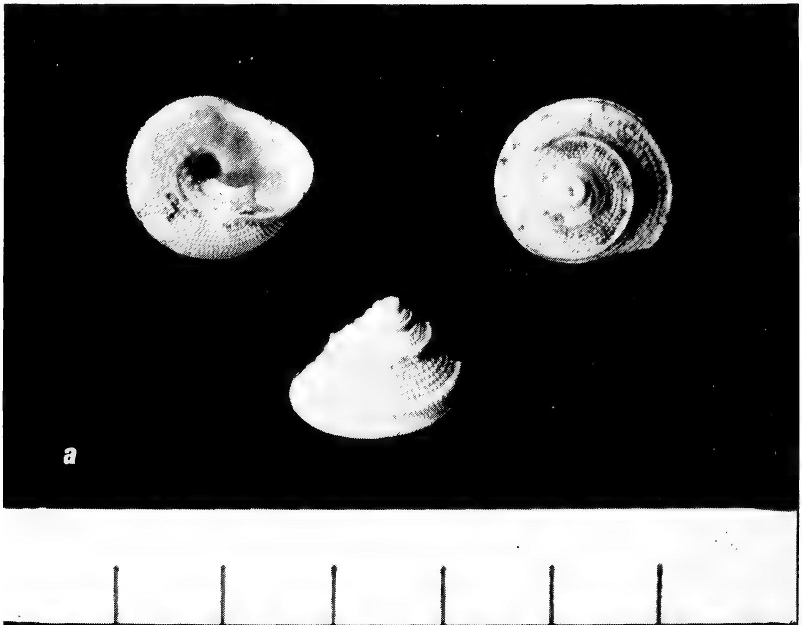
Namamurex odontostoma n.gen. et sp. Holotype

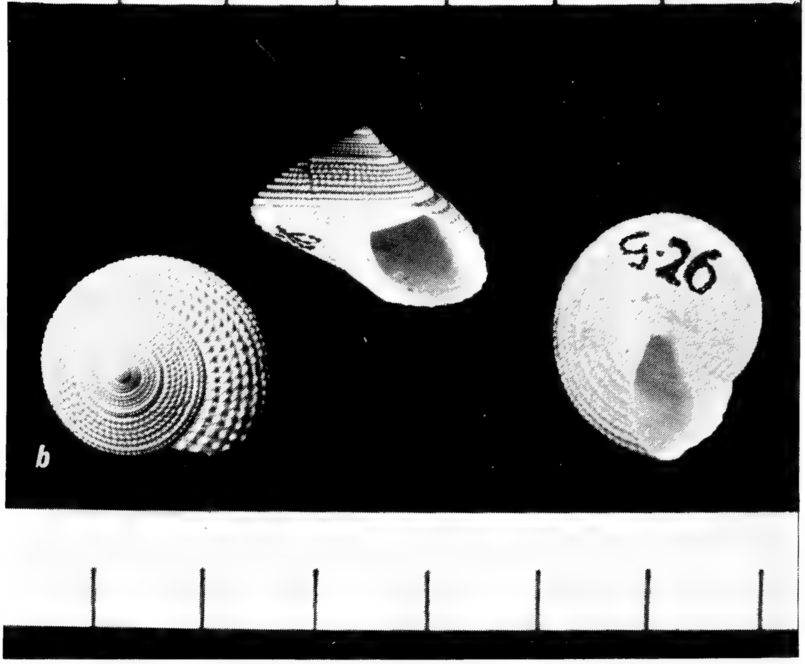


Namamurex odontostoma n.gen. et sp. Size range
Top left—Haughton's specimen
Bottom left—Holotype

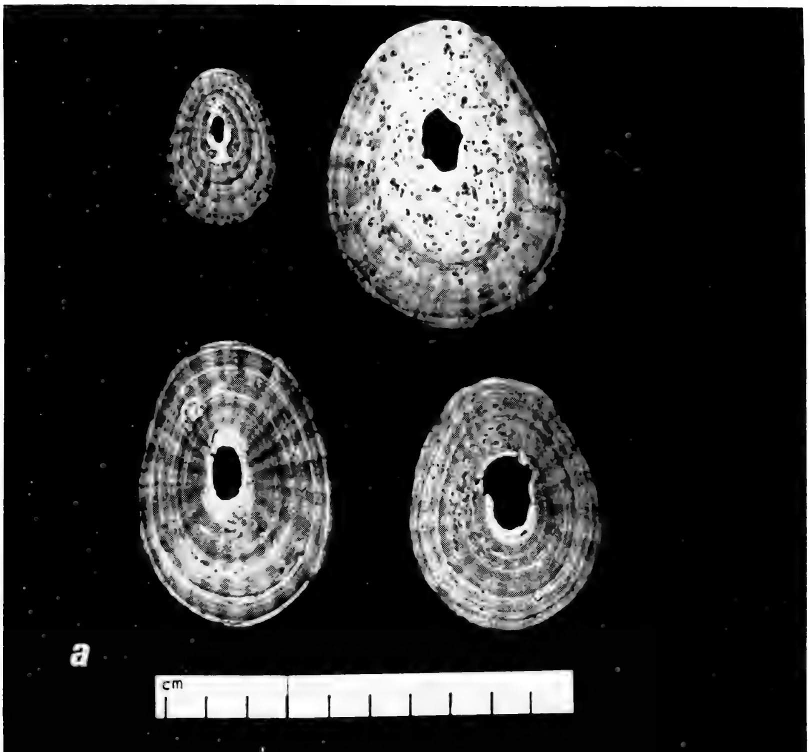


a. *Calyptraea aurita striata* n. subsp. Dorsal view, Holotype
b. *Calyptraea viridarena* n.sp. Dorsal view, Holotype

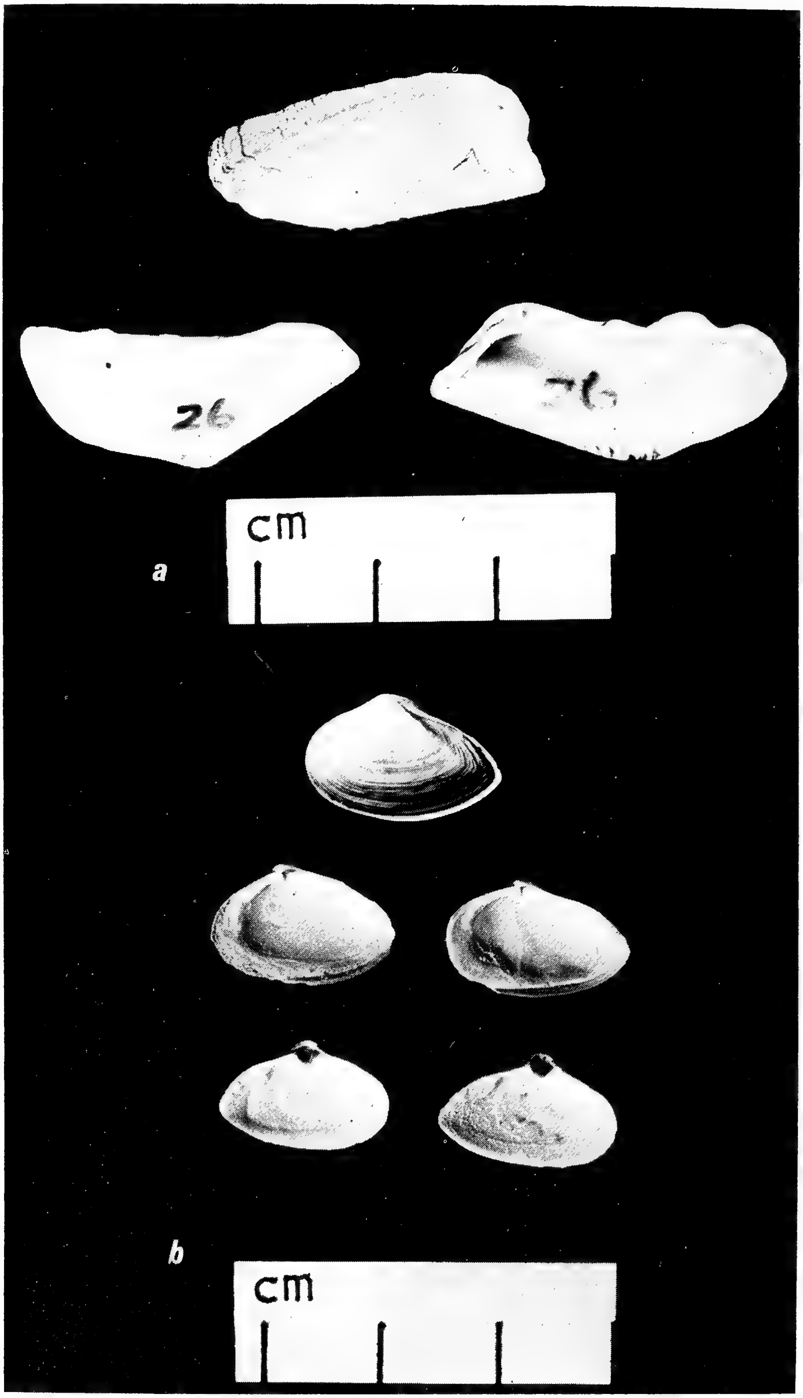




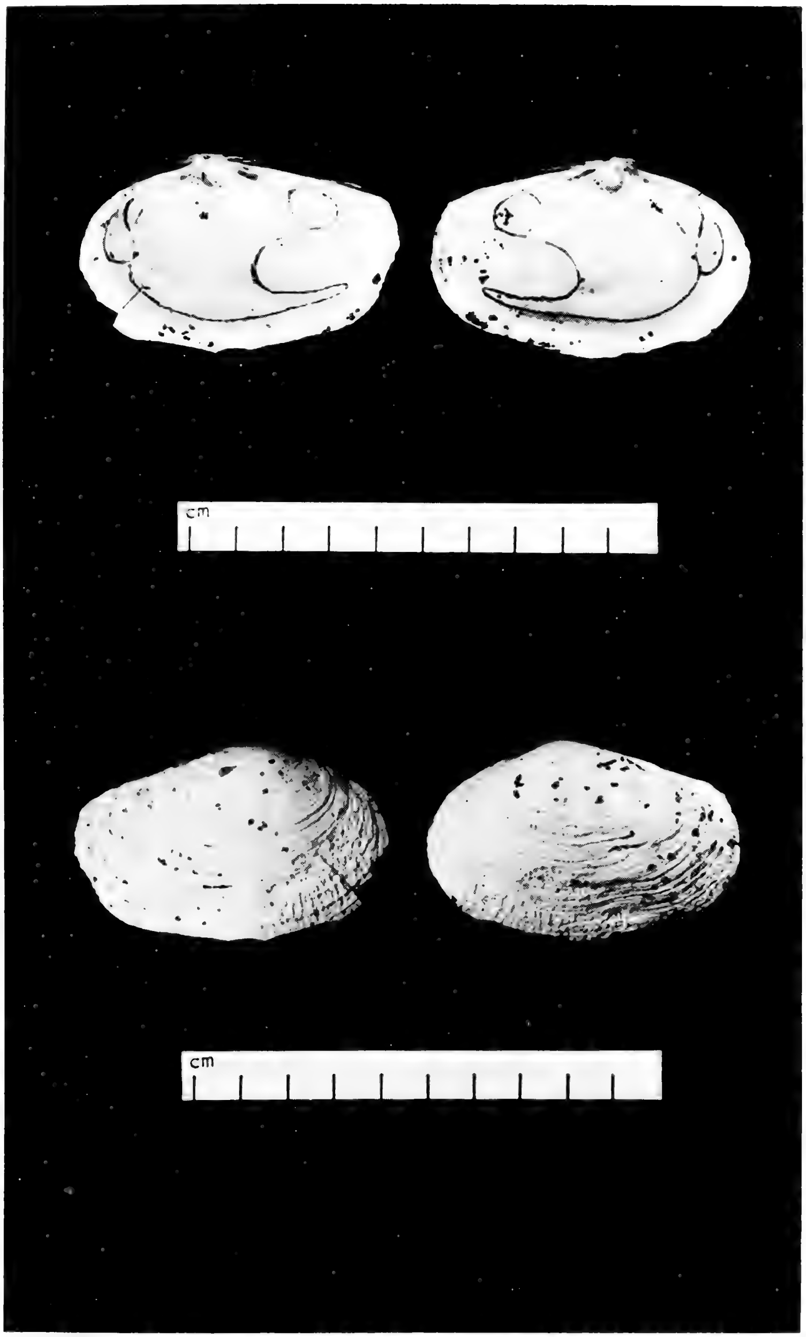
a. *Clanculus murrayi* n.sp. Holotype, upper right
Paratype, upper left
b. *Calliostoma depressa* n.sp. Holotype



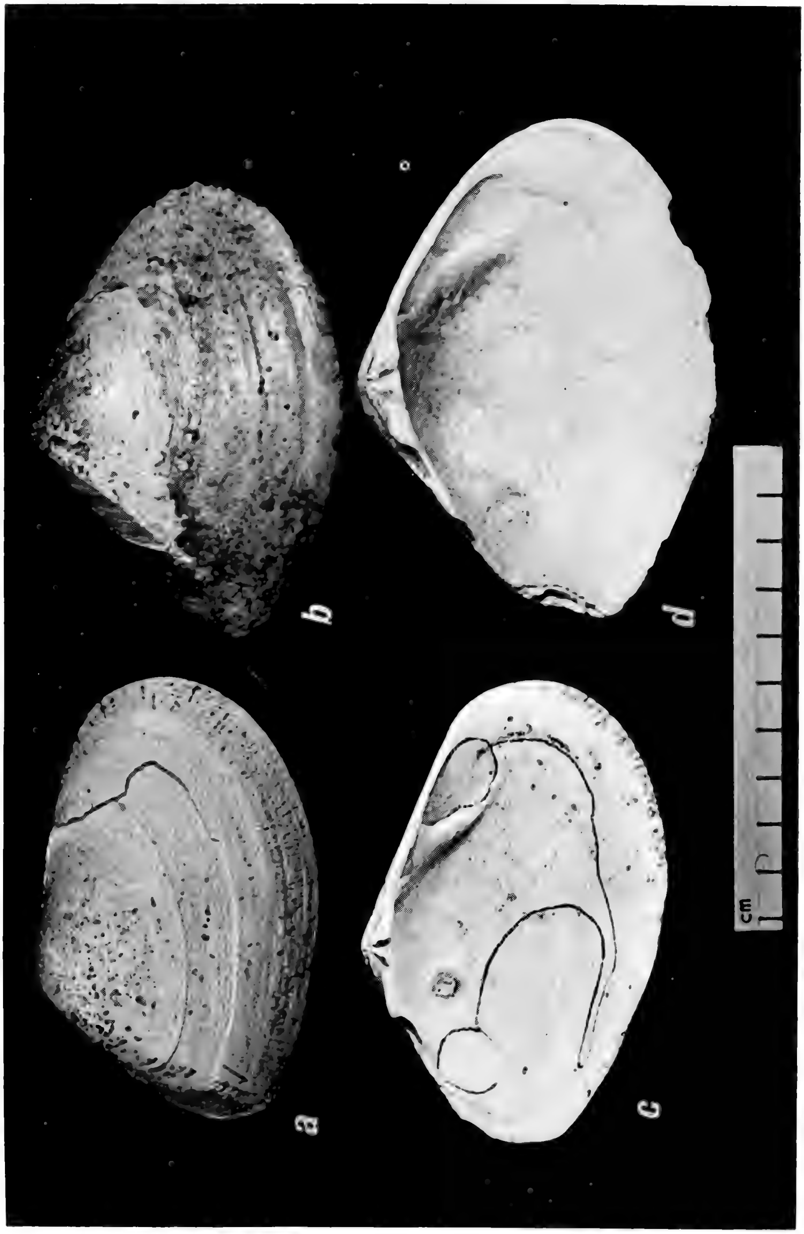
a. *Fissurella glarea* n.sp. Size range, Holotype bottom left
b. *Arca* (*Acar*) *halmyrus* n.sp. Holotype



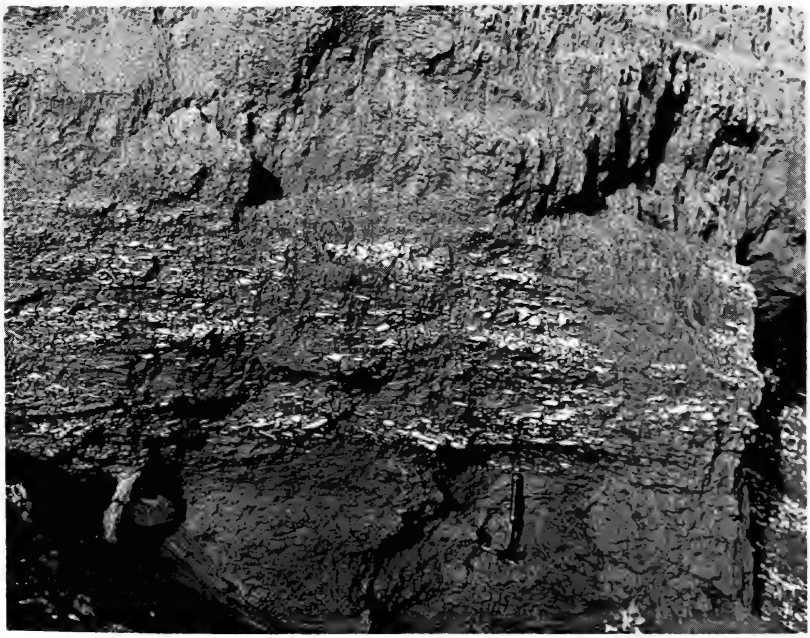
a. *Arca avellana* Lamarck
b. *Aloidis palaegialus* n.sp. Holotype, top



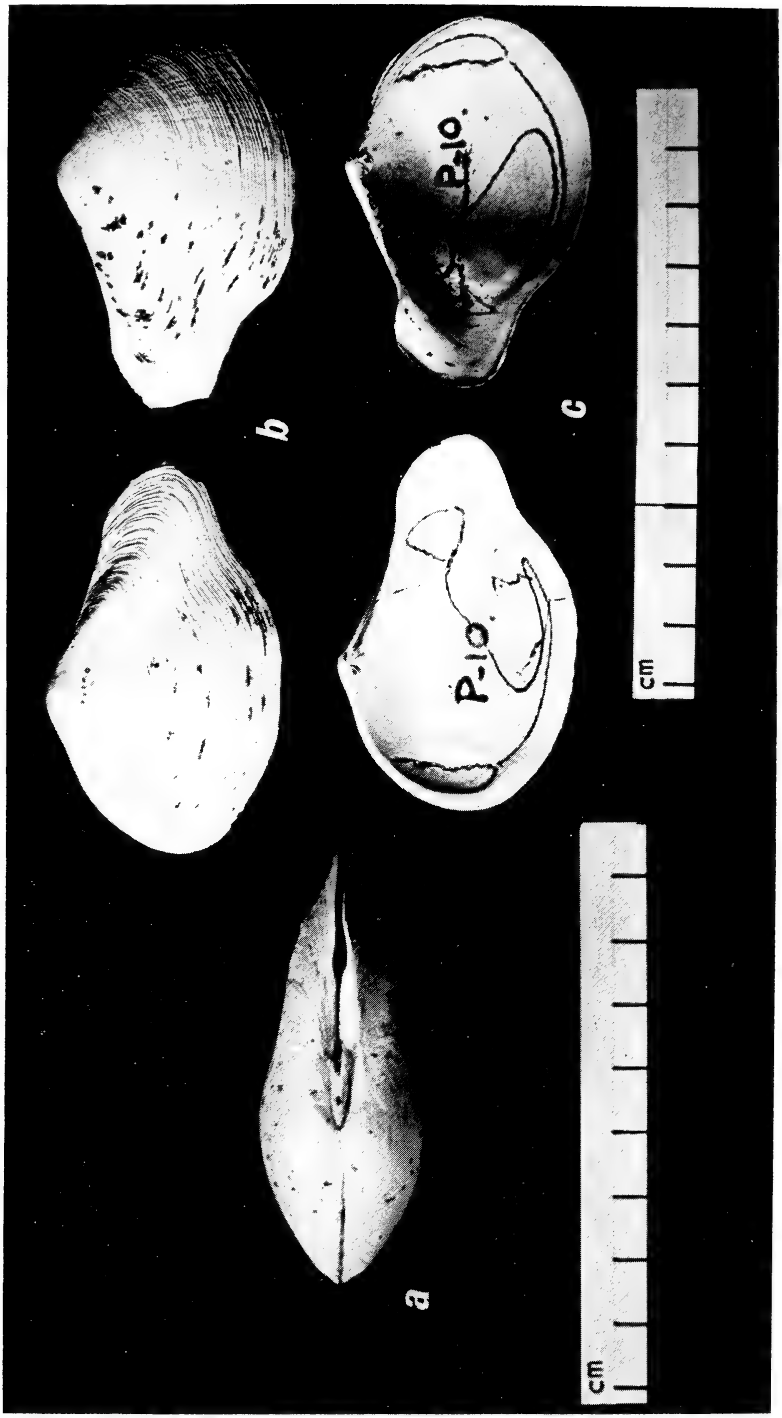
Standella (*Eastonia*) *namaquensis* n.sp. Holotype



a. *Donax haughtoni* n.sp. Holotype, external view of right valve
b. *Donax rogersi* Haughton. External view, right valve
c. *Donax haughtoni* n.sp. Holotype, internal view of left valve
d. *Donax rogersi* Haughton. External view of left valve



Top. *Donax haughtoni* n.sp. Location 2
Bottom. *Donax rogersi* Haughton. Location 1



Gastrana rostrata n.sp.
a. Dorsal view, Paratype
b. External view, Holotype
c. Internal view, Paratype

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

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FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

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. Polyphacophora, 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.

ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.

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

Volume 52 Band
November 1969 November
Part 10 Deel

THE BEHAVIOUR OF CAPTIVE CAPE ROCK LOBSTERS, *JASUS LALANDII* (H. MILNE EDWARDS)

By

NELLIE F. PATERSON

Cape Town Kaapstad

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Price of this part/Prys van hierdie deel

R2.50

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

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NELLIE F. PATERSON

South African Museum, Cape Town

(With 4 figures and 15 tables)

[*MS. received* 12 *September* 1968]

CONTENTS

INTRODUCTION

Various problems concerning the habits and the biology of *Jasus lalandii* have been investigated by Gilchrist (1913, 1918), Von Bonde & Marchand (1935), Von Bonde (1936), Matthews (1962), Heydorn (1965, 1966), and Lazarus (1967). However, the results of field and laboratory observations indicate that clarification of some aspects is still desirable.

Ann S. Afr. Mus. **52** (10), 1969: 225–264, 4 figs, 15 tables

It has generally been accepted that the adults moult once a year, but differences between the moulting frequencies of feral and captive animals are suggested in several reports. In certain holding experiments, Gilchrist (1913) showed that two ecdyses a year occurred in some mature females, and recent observations (Paterson, 1968; 1969*a*) have confirmed the prevalence of biannual ecdyses in captive animals.

There is little information regarding the mating behaviour in *J. lalandii*, and the method of insemination has been a matter of speculation. Based on the nature of the membranes of freshly-laid eggs and on the supposed absence of external spermatophores, Von Bonde (1936) concluded that fertilization probably takes place in the oviducts. This opinion has received some support from Fielder (1964*c*) and Heydorn (1966), but it has been noted (Paterson, 1968) that the external genital apparatus of *J. lalandii* resembles that of some Scyllaridae, in which family external spermatophores have been described by Matthews (1954*a*). It has also been implied (Paterson, 1968) that the mating behaviour of *J. lalandii* and the Natal rock lobster, *Palinurus gilchristi* Stebbing, may prove to be similar and that in both species the eggs are probably fertilized externally.

In pursuit of further information on the general behaviour of *J. lalandii*, various specimens were maintained at the Sea Point Aquarium from March 1966 to July 1968. During the course of the study, a soft, transparent, external spermatophoric mass was detected behind the gonopores of one experimental female. It is considered that this fact contributes towards an understanding of the process of fertilization in the Cape rock lobster.

Material and Methods

As soon as possible after their capture, the animals were placed in glass-fronted tanks filled with aerated sea water operating from a closed circuit. The largest experimental tank measured 72 in. × 69 in. × 48 in. and had a built-in rocky background. Frequent use was also made of ten smaller tanks, each of which was approximately 42 in. × 20 in. × 18 in. in size and had a fair depth of sand and loose stones on the bottom. In addition, a large exhibition tank, measuring 102 in. × 48 in. × 72 in. and accommodating a variable number of mature and immature rock lobsters, was also available for general observations.

From time to time, adult males and females were generously supplied by Dr. A. E. F. Heydorn, Mr. G. G. Newman and their colleagues, who collected the animals by hand during routine diving operations off Robben Island in Table Bay. Random specimens in each batch of animals were dissected to check whether the gonads were mature. In most of the experiments the sexes were paired and, as the females were generally smaller than the males, they appeared to be suitable for mating. More information concerning the habits of captive animals was gained from 24 juvenile females, which were selected from a large number of immature animals introduced into the Aquarium in July 1966.

To avoid overcrowding, only five pairs of mature animals were placed in the largest experimental tank and usually two pairs of adults and no more than a dozen juveniles were kept in the smaller tanks. The animals were handled carefully and as seldom as possible, yet several of them lost some of their appendages at times when there was no outside interference. Most of the maimed animals were replaced by more perfect specimens, but it is probable that, had they been retained, regeneration of the injured limbs would subsequently have taken place.

The animals were maintained successfully on a daily meal of pieces of stockfish, *Merluccius capensis* Castlenau, supplemented by quantities of the mussels, *Aulacomya magellanica* (Chemnitz), various species of *Patella*, and the kelp, *Ecklonia*.

At 6 p.m. each day the electric lights in the Aquarium were regularly switched off and all the tanks were in total darkness until 9 a.m. on the following day. In an endeavour to make the conditions as normal as possible, the artificial illumination of the rock lobster tanks was dispensed with and it was found that sufficient subdued natural light reached the tanks from the outside windows of the building.

After their introduction into the tanks, the animals were inspected at least once or twice during the day, and visits of varying duration and frequency were made at night when torchlight was used for the observations. During these visits the habits of individual animals were studied.

Using steel calipers, the total cephalothoracic length (T.C.L.) was measured in millimetres from the tip of the rostrum to the postero-dorsal edge of the carapace. Heydorn (1965) has concluded that the males and females may become sexually mature when the T.C.L. is 6·0 to 6·5 cm and 7·0 cm or more respectively. In the present study few small males were handled and most of the adult females were at least 70 mm in T.C.L.

Exuviation, which usually took place at night, was seen on a number of occasions. Records of the ecdyses of individual animals were used to determine the growth rate and the length of the intermoult periods.

As few of the captive females produced eggs, attempts were made to inseminate several specimens by artificial means. In another inquiry into the possible intromission of sperm, the histology of the reproductive organs was examined. Sections were cut of part of the ovary and the entire oviduct of an ovigerous female and of portions of the testis and the vas deferens of a mature male. The sections were 10 μ thick, and alternate slides were stained with Mallory's triple stain or with Heidenhain's iron haematoxylin and eosin. Smears of seminal matrix, fixed either in osmic acid fumes or in Zenker's fluid and stained with Heidenhain's haematoxylin, were used as an additional check for possible traces of spermatophoric material in sections of the female organs.

General Observations

After becoming acclimatized to their surroundings, most of the rock lobsters established territorial rights to certain rock niches or corners in the tanks and adopted a belligerent attitude towards other animals attempting to usurp their chosen retreats. The individuals varied in their habits from day to day and, while some remained dormant for long periods, others in the same tank were often fairly active. Some degree of activity was therefore frequently observed during the day and at night in one or more of the tanks.

Most of the specimens devoted some considerable time to the diligent cleaning of the appendages or various parts of the surface of the body. The antennulary flagella seemed to receive most attention, being repeatedly drawn through the apposed medial setose margins of the third maxillipeds. The latter were then rubbed together and apparently cleaned after the antennulary flagella had been released.

Occasionally some of the legs of one side were hooked over and drawn as far as possible along the antennal flagellum of the same side, the surface of which was presumably brushed by the spines and setae on the dactyls. The antennal peduncles, the eyes, and parts of the cephalothorax were most frequently cleaned by the dactyls of the second or the fourth pereiopods.

In both sexes the dactyls of the fifth legs were employed to scrape the surfaces of the abdomen and the pleopods. As remarked by Gilchrist (1913), Von Bonde & Marchand (1935), Von Bonde (1936), and Fielder (1964*b*), ovigerous females habitually used the chelae of the fifth legs to groom the incubation chamber. The loosened debris was probably cleared by the subsequent vigorous flapping of the pleopods, which at times was also instrumental in releasing swarms of larvae.

When not engaged in grooming, many of the animals rested on the bottom of the tanks, usually supported by the flexed tail-fan and the posterior legs, while the other legs swayed leisurely to and fro. Such limb movements appeared to be rather aimless, but they were doubtless of consequence in maintaining the stream of respiratory water entering the branchial chambers at the bases of the legs.

Occasionally some individuals were observed drawing the anterior legs through the sand, and several specimens seemed to be fastidious about their resting-places. Some of the occupants of the smaller tanks dug pits in the sand in which they later rested. Fairly heavy loose stones lying in front of the bottom rock recesses in the large tank were often forcibly removed, probably to make the retreats more accessible.

Locomotor and Feeding Activities

From June to September 1966, a study was made of the locomotor and feeding activities of ten pairs of adult rock lobsters which had been in captivity for two months before the observations began. The T.C.L. of the animals

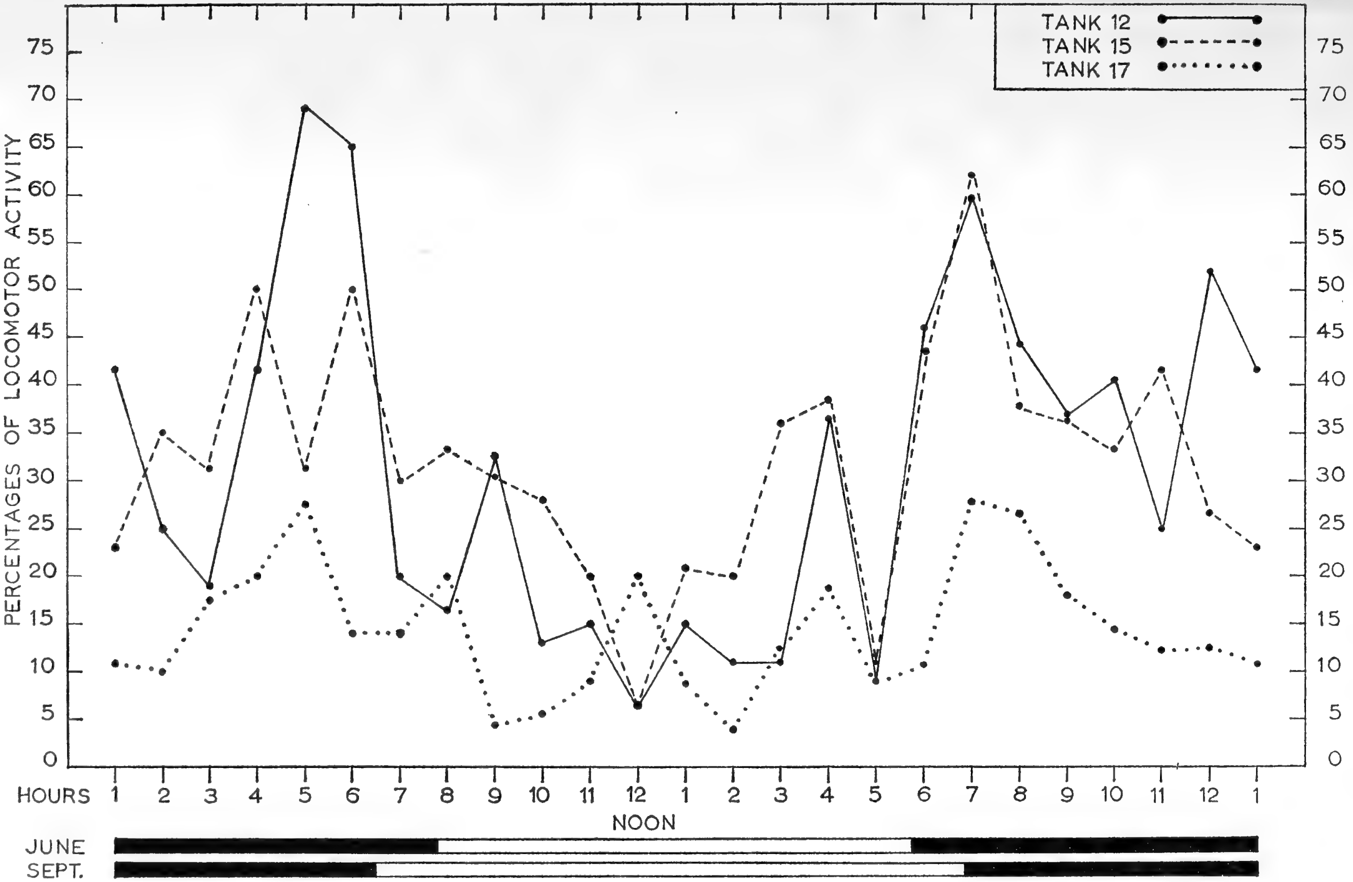

FIG. 1. The hourly variations in the locomotor activity of three groups of adult rock lobsters for the period 1 June to 30 September 1966. Tanks 12 and 15 measured about 42 in. × 20 in. × 18 in. and each contained two pairs of animals. Tank 17 measured 72 in. × 69 in. × 48 in. and contained five pairs of animals. Food was supplied regularly each day between 3 and 4 p.m. The hourly counts of active animals are expressed as percentages of the number of animals present. The black bands represent the average hours of darkness in June and September.

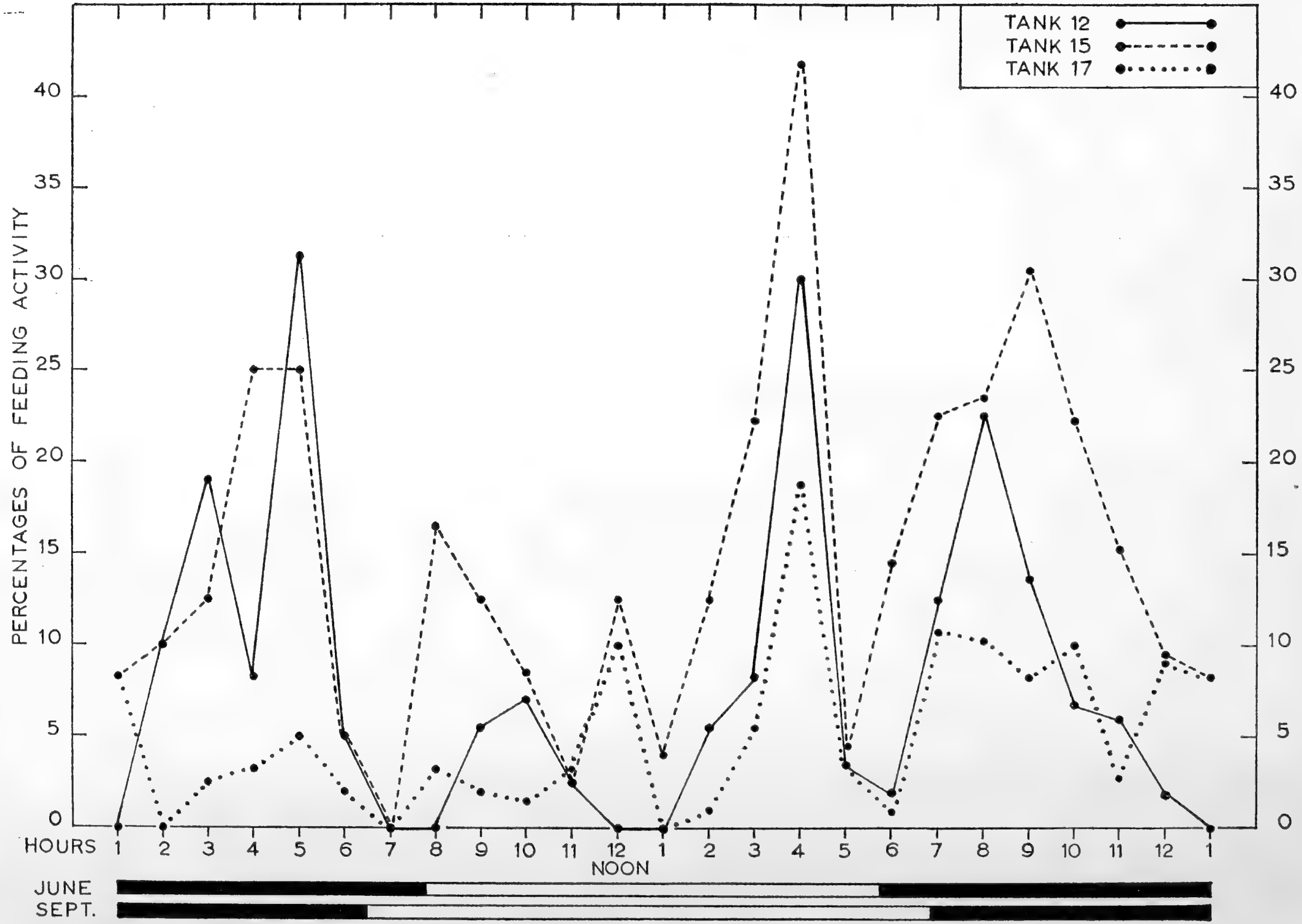

Fig. 2. The hourly variations in the feeding activity of the same animals and for the same period as in figure 1. The hourly counts are also expressed as percentages of the number of animals present. A high level of activity was evident during the afternoon when food was introduced into the tanks.

ranged from 78 to 122 mm in the males and from 83 to 100 mm in the females. Exploratory movements away from an established niche were regarded as locomotor activity, while actual seizure and consumption of food were recorded as feeding activity.

Intermittent observations of the tanks were made at least twice an hour during the day and at night, and the hourly counts of the animals active were expressed as percentages of the total number of animals present. These percentages were used to determine the mean hourly variations in the locomotor and the feeding behaviour during the four months in question (figs 1, 2).

From the above figures a comparison may be made between the hourly activities of 18 animals located in two of the smaller tanks (nos 12, 15) and the larger experimental tank (no. 17). The results suggest that the four animals in each of the two smaller tanks were generally more active than the ten animals in the larger tank. Although the animals in the smaller tanks were by no means cramped, they probably disturbed one another more frequently than did the animals in the larger tank, in which some specimens remained quiescent in their rock shelters for relatively long periods.

The graphs shown in figures 1 and 2 may also be used to illustrate the hourly levels of activity over a period of four months. Three main peaks of locomotor and feeding activity are indicated, one occurring before sunrise, another between 3 and 4 p.m., and a third after sunset.

The normal rhythms of foraging and feeding were doubtless disturbed by the daily introduction of fish into the tanks between 3 and 4 p.m. Consequently, the marked afternoon increase in activity appears to be anomalous. If, however, the responses to artificial feeding are excluded, a bimodal rhythm seems to be suggested in both the locomotor and the feeding activity.

A somewhat similar bimodal cycle has been reported by Kubo & Masuda (1964) in the feeding habits of captive specimens of *Panulirus japonicus*. It was established that the twilight peaks roughly corresponded with those found in fishing experiments, but the dawn peak of the latter was two hours later than the corresponding peak in the captive animals.

On the other hand, in captive *Jasus novaehollandiae* (*lalandii*), Fielder (1965) observed that the maxima for both the locomotor and the feeding activity occurred at dusk. This may imply that the normal rhythm is unimodal in this species.

Following procedures suggested by Sutcliffe's (1956) experiments on captive *Panulirus argus*, the hourly counts of activity in 18 to 20 animals formed the basis of a comparison between the day and the night locomotor and feeding activities (table 1). The observations covered the same period of four months indicated in figures 1 and 2, but, in addition to the previously mentioned 18 animals, another pair was maintained in a separate tank during June and July. The means are represented as percentages of the quotients of the total number of animals present and the number of active animals observed in hourly counts throughout the whole period.

Table 1

Summary of counts of the diurnal and the nocturnal locomotor and feeding activities of 18 to 20 adult rock lobsters for the period June to September 1966. The means are expressed as percentages of the total number of animals present.

Time	*No. of hourly counts*	*No. of animals present*	*No. of animals foraging*	*Mean % of locomotor activity*	*No. of animals feeding*	*Mean % of feeding activity*
Day	149	2850	414	14·5	194	6·8
Night	194	3748	1093	29·2	423	11·3

Applying Hoel's (1962) formula for testing the difference between two proportions to the data in table 1, an assessment was made of the respective day and night proportions of activity relative to the number of animals present.

The values of z were 14·1 and 6·2 with regard to the locomotor and feeding activities respectively. This means that in both foraging and feeding the difference between the day and the night activity was significant at the 1 % level.

It has been concluded that, although the daily introduction of food during the afternoon affected the diurnal counts, there was an increase in both types of activity at night.

Ecdysis

Most of the animals were soft to the touch about two weeks before ecdysis, but in a few large males proecdysis apparently began nearly three weeks before the animals moulted. During this time the animals tended to become gradually more quiescent, but they had occasional periods of restiveness. Feeding was usually suspended for approximately five to seven days before ecdysis and was resumed in four to eight days after the event.

As has been indicated in *Panulirus* by Travis (1954) and other investigators, the first obvious sign of proecdysis was the appearance of a resorptive line running somewhat obliquely backward and downward along the branchiostegite to its posterior articulation with a condyle on the last thoracic epimeron. This line is probably more noticeable in species of *Panulirus* than in *J. lalandii*, in both sexes of which a longitudinal pale streak is commonly present on the branchiostegite more or less in the position of the suture along which calcium resorption takes place during proecdysis.

About four to seven days before ecdysis the resorptive line was most clearly seen by torchlight at night. It resembled a shining, greasy-looking marking along each branchiostegite with an additional, short, broad band extending downward at the junction of the branchial and the prebranchial chambers. Even though the resorptive line became progressively more marked, it was less obvious in the adult males than in mature females, but was very distinct in both sexes of juvenile animals.

As the time for exuviation approached, the animals usually became very restless and the body had a somewhat deformed appearance owing to an apparent loosening of the parts at the junction of the thorax and the abdomen. This was often evident about 24 hours before ecdysis and was associated with the gradual exposure of the first abdominal tergum and a widening of the gap between the carapace and the flange on the first abdominal segment. The abdomen was then frequently held in the fully extended position, but the animals were still able to move about fairly rapidly, although rather clumsily.

About two to three hours before exuviation in the juveniles and 45 to 75 minutes in the adults, the animals seemed to be more perturbed and were noticeably hostile towards other rock lobsters in the tank. As they roamed about, the antennae were held aloft and the pleopods, which were often pendent at this stage, were swung leisurely to and fro. During short periods of rest, the antennulary flagella were drawn vigorously through the apposed margins of the third maxillipeds. The pereiopods and even the eyes were moved restlessly in various directions, and at intervals the first abdominal segment was thrust forward below the posterior margin of the carapace. Travis (1954) has suggested that similar activities in *Panulirus argus* probably help to loosen the old exoskeleton from the underlying new one.

Immediately before ecdysis began, the animal became more agitated and attempted to brace itself on the bottom of the tank or over a loose stone, occasionally exhibiting convulsive movements. If, as frequently occurred, it happened to be disturbed by other individuals at this juncture, it was still able to evade them by darting swiftly backward through the water.

As in other species, the movements in *J. lalandii* were accompanied by the gradual and extraordinary swelling of the thoraco-abdominal intertergal membrane which, according to Drach (1939) and subsequent observers, is effected by water absorption and increased pressure in the pericardial pouches.

The distension of the membrane seemed to be less rapid in the juveniles than in the adults. In the former the membrane began to stretch at least 80 minutes before ecdysis, while in the adults it was usually first visible about 30 to 40 minutes before actual exuviation. When the dorsal membrane became markedly stretched, the animal seemed to be less sensitive to light. It settled down fully extended, supported on the tips of the pereiopods and the edge of the tail-fan and often with the antennae directed forward.

The preliminary step of exuviation was the detachment of the lower margin of the old branchiostegite from the new exoskeleton, as a result of which the posterior border of the old carapace was slightly raised. Thereafter, the dorsal intersegmental membrane became progressively more taut until eventually the posterior edge of the new carapace was clearly visible through the membrane. At the same time, the bracing action of the limbs and the somewhat telescopic movements of the abdominal segments probably created additional pressure required for the implementation of ecdysis.

Rupture of the fully stretched membrane was sudden, and the old carapace began to rise quickly and almost imperceptibly until it was tilted forward at an angle of about 90 degrees. After the eyes had been withdrawn, the animal seemed to find purchase against the anterior and lower parts of the old exoskeleton while the antennae, the legs, and the successive abdominal segments were freed from their previous casings. Almost simultaneously, the sternum and the old endoskeleton were released and, with a sudden convulsive movement, the animal extricated itself from its former skeleton.

Most of the young rock lobsters were inclined to dart out from the right side of the exuviae, but in the adults the procedure seemed to be more normal and they emerged dorsally through the wide gap between the raised carapace and the first abdominal tergum of the old exoskeleton. Once the animal had moulted, it appeared to be unusually excited and very sensitive to light, and its rather flexible antennal flagella were swept through the water with considerable force.

Ecdysis usually took place at night, but was also recorded before noon in two adult males and one female. The exact time of ecdysis was somewhat variable, and in observations of 11 juveniles and seven adults (fig. 3) it ranged from 22 minutes before sunset in the largest specimen to over six hours after sunset in one immature female.

In both the juveniles and the adults exuviation was generally completed in three to five minutes and there appeared to be no direct correlation between the size of the animal and the duration of ecdysis. Nor did the time of the year have any obvious effect on the period required for emergence. Eight of the observations below were made in spring, six in summer, two in autumn, and two in winter. It may also be remarked that one of the summer ecdyses was that of a female (T.C.L. 77 mm) which had produced eggs in captivity 140 days before this particular ecdysis.

The mean duration of exuviation in the 18 animals was 4·4 ± 0·95 minutes. This average includes the exceptional time of seven minutes recorded in one immature animal (T.C.L. 58 mm) which required short periods of rest between frenzied efforts to free its legs. During the struggle, the old exoskeleton was torn asunder, and in several unsuccessful ecdyses of adult animals the exuviae were found to be similarly dismembered.

The main difference between ecdysis in *J. lalandii* and the process described in other Decapoda is in the time taken for the withdrawal of the animals from their exuviae. Drach (1939) observed that the period required in Brachyura was 10 to 30 minutes, while in *Panulirus* it seems to vary with the species. Several accounts show that it is about 15 minutes in *P. japonicus* (Nakamura, 1940), three to five minutes in small specimens and five to ten minutes in somewhat larger individuals of *P. argus* (Travis, 1954), 11 to 18 minutes in *P. interruptus* (Lindberg, 1955), and eight to ten minutes in *P. cygnus* (Thomas, 1966). In figure 3 it is evident that the normal duration of ecdysis in the

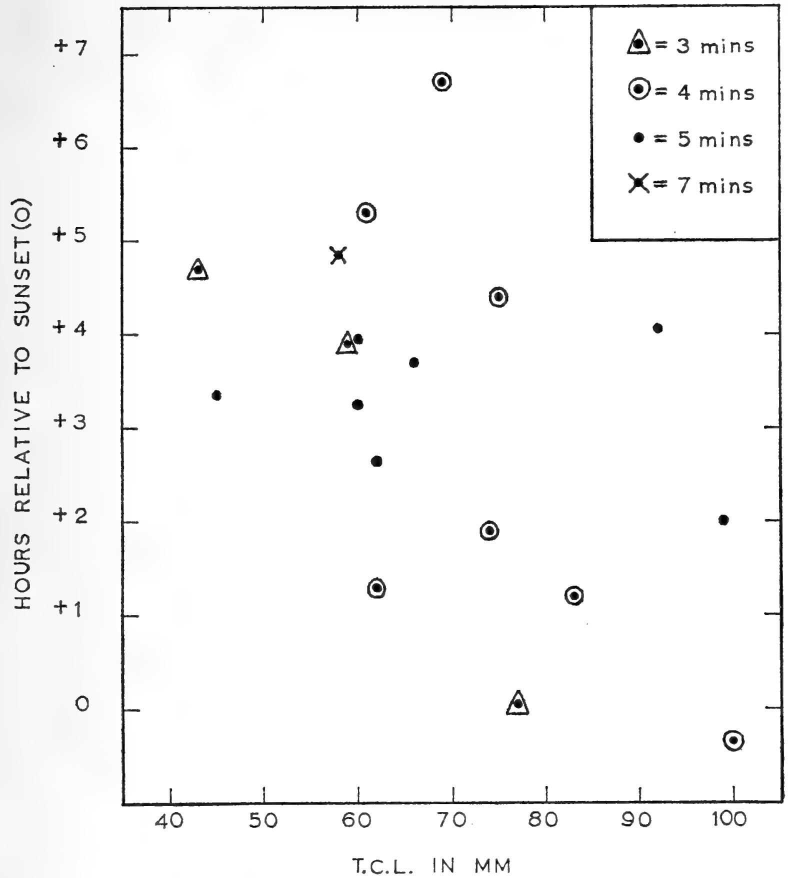

FIG. 3. Starting times of ecdysis in 18 animals, plotted to the nearest minute before or after sunset (o). The duration of ecdysis is indicated by the symbols shown in the key. The T.C.L. of the individuals ranged from 43 to 100 mm.

juveniles of *J. lalandii* is comparable to that observed by Travis (1954) in young forms of *P. argus*, but in the adults it is shorter than in other palinurids.

During 1967 some records were also kept of ecdysis in a number of males of *J. tristani* exhibited at the Sea Point Aquarium. The exuviation of three specimens with cephalothoracic measurements of 83 mm, 105 mm, and 119 mm occurred about two hours after sunset and took four minutes, five minutes, and seven minutes respectively. The process was similar to that of *J. lalandii*, except that before and during ecdysis the animals were more composed than moulting specimens of the local species and withdrawal from the exuviae was effected with a minimum of effort. Such deliberate action was, however, consistent with the habits of these fairly large rock lobsters which were generally more placid than the captive juveniles and adults of *J. lalandii*.

Several investigators have stated that during ecdysis in palinurids the old exoskeleton fractures along the resorptive lines but, as in *Panulirus argus* (Travis, 1954), this does not eventuate in *J. lalandii* or in *J. tristani*. The sutures along the branchiostegites are softened by calcium resorption and, although they are easily broken while handling the exuviae, they normally remain intact and simply serve as pliable seams along which the side flaps of the otherwise rigid exoskeleton are able to bend slightly when the carapace is raised during ecdysis.

From an examination of exuviae, it is further evident that the carapace becomes detached from the thoracic epimeral plates and that it is hinged at the base of the epistoma. As Drach (1939, 1950) has shown in his comprehensive studies of ecdysis, withdrawal of the animal is also facilitated by extensive resorption of the medial elements of the endoskeleton. The resultant gaps in the old endoskeleton are not only essential for the speedy release of the sternum and the thoracic appendages, but their presence also accounts for the obvious weakness of animals in the so-called 'soft old shell' stage.

All newly shed exuviae are provided with a thin slimy lining which, according to Drach (1939) and Passano (1960), is formed during proecdysis from a membranous layer adjacent to the epidermis. As these authors have suggested that this lining may serve as a lubricant for the easy withdrawal of the animal, it seems likely that a deficiency of mucilage may be one of the causes of death during ecdysis. Failure to extricate the appendages and the exposure of some of the gills and epipodites appeared to be common reasons for fatalities during or shortly after ecdysis in some of the present animals.

In most of the captive animals the new integument seemed to be fairly hard about three weeks after ecdysis, but the time required under natural conditions is not known. Drach (1939) has shown that some of the calcium necessary for the reconstruction of the new exoskeleton is derived from food intake and from reserves in the digestive gland (hepatopancreas). He has also concluded that calcium absorption from the sea water, particularly during the first stages of the moulting cycle, is of great importance in the consolidation of the new exoskeleton. A calcium deficiency in the external medium would therefore be detrimental to postecdysial animals in that hardening of the exoskeleton would be retarded. Chemical tests of the water in the rock lobster tanks indicated, however, that the calcium level was satisfactory.

Regeneration of the Appendages

Renewal of appendages, which had been lost either before or shortly after the animals were captured, also accompanied ecdysis in some adult and juvenile specimens. The amputation of an injured pereiopod invariably took place at the fracture plane between the basipodite and the ischiopodite, and the extremity of the stump was then sealed by an obvious black scab.

At the next ecdysis, all the segments of the limb had been reformed, but they were always shorter and thinner than normal. Dissections of several animals which died during exuviation showed that the soft regenerating limbs were neatly folded within the stumps of the old limbs.

Occasionally an antennal flagellum, which had fractured close to the peduncle, was partly regenerated during one intermoult period, but usually it was no more than half its normal length. In one specimen, in which the antenna had apparently been severely injured, a short bifurcated antennal flagellum was produced when the animal moulted. In another specimen, which had lost the right middle pereiopod and the left antennal flagellum, two ecdyses were required before the limb had regained its natural proportions and strength. The left antennal flagellum, however, only became subequal to the one on the other side after three ecdyses.

This fairly rapid replacement of injured appendages in *J. lalandii* is compatible with Bradstock's (1950) observations of autotomy and autospasy of the pereiopods and autospasy of the antennae of *J. edwardsii* (*lalandii*), in which an antennal flagellum became fully regenerated within a year.

Cannibalism

From time to time cannibalism of recently-moulted juveniles occurred in the large exhibition tank. It was common when the animals were somewhat crowded and a greater competition for food was likely.

In one instance, a young, newly-moulted female (T.C.L. 52 mm) was relentlessly attacked by two other rock lobsters of a similar size and died within half an hour. One assailant immediately tore out the eyes and at the same time presumably destroyed the brain, while the second cannibal confined its attention to the posterior end of the body. This observation is of interest inasmuch as Carlisle (1953) has reported that prawns kept under crowded conditions devour the eyestalks of dead specimens before eating other parts of the body.

Cannibalism was not observed among immature and adult experimental animals which were less confined and probably better nourished than the other captive rock lobsters. In some of the tanks, however, the exuviae were occasionally partly eaten before they could be removed.

From all accounts, the consumption of exuviae is usual in Crustacea and is not confined to captive animals. Its occurrence in the latter may indicate an inadequate supply of their natural food which could lead to cannibalism in hungry animals and result in a reduction of the stock. Drach (1939) has indicated that certain species eat exuviae as a source of calcium for accelerating the hardening of the exoskeleton after ecdysis. He has, however, also remarked that some animals will consume exuviae, not because of a need for calcium, but because no other food is available.

Average Rate of Growth

The exoskeleton was allowed to harden for about three weeks before the average growth rate was determined by comparing the premoult and the postmoult cephalothoracic measurements of individual specimens. The moult increments in T.C.L. for the juvenile females, the adult males, and the adult females are considered separately in tables 2 to 4.

TABLE 2

Average growth rate per moult in juvenile females

T.C.L. in mm	*No. of specimens*	*Increase in mm*	*Mean increase in mm*	*Mean % increase*
20–29	3	2·25–2·5	2·4	8·8
30–39	4	2·5–3·0	2·6	7·5
40–49	3	2·5–3·0	2·8	6·5
50–59	12	0·0–4·0	2·5	4·4
60–69	9	0·0–4·25	2·8	4·4

TABLE 3

Average growth rate per moult in adult males. No specimens with a T.C.L. of 80 to 89 mm were available

T.C.L. in mm	*No. of specimens*	*Increase in mm*	*Mean increase in mm*	*Mean % increase*
70–79	7	1·5–3·0	2·4	3·1
90–99	9	2·0–3·0	2·4	2·6
100–109	8	1·0–3·5	2·3	2·2
110–119	3	2·0–3·0	2·3	2·0

TABLE 4

Average growth rate per moult in adult females

T.C.L. in mm	*No. of specimens*	*Increase in mm*	*Mean increase in mm*	*Mean % increase*
70–79	9	0–2·0	1·8	2·4
80–89	20	0–3·0	2·1	2·5
90–99	8	0–3·0	2·1	2·2
100–109	3	0–3·0	1·7	1·7

An examination of the above percentage increases in length in the various size classes shows that the growth rate decreases as the animals become larger. A somewhat similar gradation in the growth rate of a greater number of specimens of *J. novaehollandiae* has been reported by Fielder (1964*a*).

The increase in the T.C.L. of the adults was usually 2·0 or 3·0 mm at each ecdysis, but in some individuals the increments fluctuated at successive ecdyses and occasionally little or no difference in size was noted. In a few of the adults the growth of the body was probably moderated by the necessary regeneration of one or more injured appendages, but relatively low values were also common in a number of perfect specimens.

Although there is no relationship between the T.C.L. and the growth increments in the present small samples, an attempt was made to examine the difference between the mean increments of the adult males and females on the one hand and the adult females and the juvenile females on the other hand. The relevant statistics are summarized in table 5.

TABLE 5

Estimated mean increases in T.C.L. per moult in captive animals, together with the standard deviations and the *t* values

	No. of specimens	*Mean increase in mm*	*Standard deviations*	t *values*	
Adult males	27	2·37	·64	1·83	
Adult females	40	2·02	·86		2·50
Juvenile females	31	2·62	1·07		

From the statistical information in table 5, it has been calculated that:

1. In the ratio of the adult males to the adult females, with 65 degrees of freedom, a *t* value of 1·83 is significant at the 10% level only. Thus, no appreciable difference in the growth increments of the captive adult males and females was apparent.

2. In the comparison between the adult females and the juvenile females, with 69 degrees of freedom, a *t* value of 2·5 is significant at the 5% level. It is therefore probable that the T.C.L. moult increments of the juvenile females slightly exceeded those of the adult females.

It may be remarked that the increments shown in tables 3 and 4 are lower than those in Heydorn's (1966) field observations, in which the natural growth rate of 19 tagged adults of *J. lalandii* ranged from 2·0 to 8·5 mm per moult. None of the present experimental adults increased by more than 3·5 mm in T.C.L. after any one ecdysis, and a diminution of the growth rate was evident at the consecutive ecdyses of several animals. Some confirmation of Lindberg's (1955) suggestion that growth is probably retarded in captive animals may therefore be indicated.

At the same time, some of the length increments recorded by Heydorn (1966) appear to be greater than would be expected at a single ecdysis. His results are obviously based on the conclusion that there is an annual ecdysis in the adults of *J. lalandii*, but it was found that biannual ecdyses were common in the present captive animals. If it should later be established that there is more than one ecdysis a year in the field, it is probable that the average growth rates of captive and free-living rock lobsters may prove to be more compatible than is at present apparent.

INTERMOULT PERIODS

From May 1966 to July 1968, 109 ecdyses (table 6) were recorded at different times of the year in 75 adults, comprising 28 males (T.C.L. 71 to 122 mm) and 47 females (T.C.L. 66 to 102 mm). During much the same period, 38 ecdyses (table 6) occurred in 18 immature females (T.C.L. 26 to 69 mm).

TABLE 6

Summary of the number of seasonal ecdyses in captive rock lobsters from May 1966 to July 1968

Specimens	*Autumn*	*Winter*	*Spring*	*Summer*
Adult males	4	8	17	10
Adult females	12	17	18	23
Immature females	8	7	15	8

Of the 75 adults, 18 males and 29 females either died or were abandoned after their first ecdysis. Thirteen of the 29 females, including one with a T.C.L. of 66 mm, had been collected in berry during the winter breeding season, and all of them moulted the following spring or summer after the eggs had hatched.

As indicated in a brief account of the ecdyses of captive rock lobsters (Paterson, 1969*a*), the remaining 28 adults were maintained for a year or longer (table 7) and usually moulted in autumn or winter and again in spring or summer.

TABLE 7

Summary of the plural ecdyses in individual adult rock lobsters from May 1966 to July 1968

	Four ecdyses in 24 months	*Three ecdyses in 18 months*	*Two ecdyses in 12 months*
Males	0	1	9
Females	1	3	14

Most of the females which survived two or more ecdyses failed to spawn, but three of them moulted in captivity before producing eggs and each had a second ecdysis five or six months later.

In 26 of the 28 animals enumerated in table 7 definite spring/summer to autumn/winter and autumn/winter to spring/summer intermoult periods occurred (tables 8, 9). The two exceptional animals were females, in one of which (T.C.L. 72 mm) there was a short spring to summer intermoult period of 119 days and in the other (T.C.L. 85 mm) a winter to early spring intermoult period of 105 days. These two intermoult periods have been omitted in tables 8 and 9.

TABLE 8

Duration of the spring/summer to autumn/winter intermoult period in adult males and females

T.C.L. in mm	*No. of intermoult periods*		*Intermoult periods in days*		*Mean duration of intermoult periods in days*
	Males	*Females*	*Males*	*Females*	
70–79	1	1	154	201	177·5
80–89	0	4	0	176–220	191·2
90–99	1	1	147	213	180·0
100–109	1	0	207	0	

TABLE 9

Duration of the autumn/winter to spring/summer intermoult period in adult males and females

T.C.L. in mm	*No. of intermoult periods*		*Intermoult periods in days*		*Mean duration of intermoult periods in days*
	Males	*Females*	*Males*	*Females*	
70–79	0	3	0	120–185	148·3
80–89	0	6	0	143–188	158·3
90–99	3	4	166–198	146–166	164·1
100–109	4	2	161–186	150, 188	171·6
110–119	1	0	173	0	

Although the number of examples is small, it seems obvious that in the adults the interval between the spring/summer and the autumn/winter ecdyses is the longer of the two intermoult periods.

Ecdysis was irregular in the immature females, but some correlation between the size of the animals and the length of the intermoult periods is indicated in table 10.

TABLE 10

Intermoult periods in the various size classes of juvenile females

T.C.L. in mm	*No. of intermoult periods*	*Intermoult periods in days*	*Mean duration of intermoult periods in days*
20–29	2	72, 81	76·5
30–39	3	71–107	87·7
40–49	2	85, 102	93·5
50–59	8	87–223	157·8
60–69	4	152–234	185·2

In the 50 to 59 mm size class short periods of 87, 120, and 127 days were referable to three animals measuring 53 to 57 mm in T.C.L. The other animals in this and in the 60 to 69 mm size class underwent two ecdyses a year, one in spring or summer and the other in autumn or winter. Two distinct intermoult periods were thus recognized in several animals (tables 11, 12).

TABLE 11

Duration of the spring/summer to autumn/winter intermoult period in juvenile females

T.C.L. in mm	*No. of specimens*	*Intermoult periods in days*	*Mean duration of intermoult periods in days*
50–59	3	203–223	211·7
60–69	3	152–234	195·3

TABLE 12

Duration of the autumn/winter to spring/summer intermoult period in juvenile females

T.C.L. in mm	*No. of specimens*	*Intermoult periods in days*	*Mean duration of intermoult periods in days*
50–59	2	141, 151	146
60–69	1	155	

As in the adults, there is a difference between the mean duration of the two intermoult periods in the juvenile females, but too few specimens were handled for a true assessment to be made of the length of either period. In agreement with Fielder's (1964*a*) observations on *J. novaehollandiae*, however, a progressive lengthening of the intermoult period is indicated (table 10) as the animals increase in size. Fielder (1964*a*) has also ascertained that in 33 *J. novaehollandiae*, measuring from 5·0 to 5·9 cm in T.C.L., the average intermoult period was 137 days from July to December and 158 days from January to June.

Moulting Frequencies and Annual Rate of Growth

No observations were made of the behaviour of captive immature male rock lobsters, but some information was gained regarding the consecutive ecdyses of several juvenile females and adult males and females.

Although the records are somewhat meagre, a tentative estimate of the mean annual frequency of moulting may be obtained from a consideration of the duration of the intermoult periods in the various size classes (tables 13, 14). In addition, the probable annual increase in T.C.L. has been appended to each size class in tables 13 and 14.

In collating the data, the two short intermoult periods of 119 and 105 days, which were omitted in tables 8 and 9, have been included in table 13 in the mean intermoult periods of the 70 to 79 mm and 80 to 89 mm size classes respectively.

Table 13

Mean frequency of moulting and annual increase in T.C.L. in captive female rock lobsters

T.C.L. in mm	*No. of specimens*	*Mean intermoult in days*	*Mean frequency of moulting per annum*	*Mean increase per moult in mm*	*Annual increase in T.C.L. in mm*
20–29	2	76·5	4·8	2·4	11·5
30–39	3	87·7	4·2	2·6	10·9
40–49	2	93·5	3·9	2·8	10·9
50–59	8	157·8	2·3	2·5	5·8
60–69	4	185·2	2·0	2·8	5·6
70–79	5	153·0	2·4	1·8	4·3
80–89	11	165·5	2·2	2·1	4·6
90–99	5	164·8	2·2	2·1	4·6
100–109	2	169·0	2·2	1·7	3·7

Table 14

Mean frequency of moulting and annual increase in T.C.L. in captive adult male rock lobsters. No specimens were available in the 80–89 mm size class

T.C.L. in mm	*No. of specimens*	*Mean intermoult in days*	*Mean frequency of moulting per annum*	*Mean increase per moult in mm*	*Annual increase in T.C.L. in mm*
70–79	1	154·0	2·4	2·4	5·8
90–99	4	171·2	2·1	2·4	5·0
100–109	5	179·8	2·0	2·3	4·6
110–119	1	173·0	2·1	2·3	4·8

The moulting frequencies seem to be rather variable, but it may be concluded that, as the animals increase in size, they undergo fewer ecdyses a year. It is also apparent that there is a corresponding diminution in the annual growth rate.

The above results indicate that the smallest rock lobsters may moult at least four times a year and that, correlated with the lengthening of the intermoult periods in the larger size classes, the number of ecdyses is reduced to three and then to two a year.

Two or more ecdyses a year occurred in only ten of the experimental juvenile females, and direct observations suggest that the transition from three to two annual ecdyses may take place in animals with T.C.L. measurements of 53 to 57 mm. The occurrence of biannual ecdyses in the 60 to 69 mm size class is of interest and may denote that the moulting rhythm of young animals approaching puberty is similar to that of the adults.

A higher moulting frequency in immature than in mature specimens of *Jasus* has been reported by Hickman (1945) and Bradstock (1950). More recently, Fielder (1964*a*) has found that in *J. novaehollandiae* the average number of annual ecdyses is three in specimens with a rostrum-carapace length of 5·0 to 7·9 cm and two in the 8·0 to 8·9 cm size class.

As shown in table 7, two ecdyses a year took place in 28 adults which survived their first ecdysis in captivity. It may also be remarked that, in the few animals which moulted more than twice, the cyclical sequence (Paterson, 1969*a*) was sufficiently regular to warrant the conclusion that a definite and recurrent moulting rhythm is established in individual rock lobsters.

It was suggested by Gilchrist (1913) that the adults of *J. lalandii* probably moult once a year, the males in spring (September and October) and the females in mid-winter. In four captive females, however, he observed that two of them moulted annually, while two ecdyses a year occurred in the other two animals. Except for the omission of the annual dates, the table and comments published by Von Bonde & Marchand (1935) are similar to Gilchrist's (1913) findings and provide no further information as to the frequency of ecdysis in mature females.

More recent observations by Matthews (1962) and Heydorn (1965) on populations of adult rock lobsters off the west coast of South Africa have not determined that there is more than one ecdysis a year. From his investigations on the biology of *J. lalandii* found off Robben Island, Heydorn (1966) has concluded that most of the adult females moult in late autumn or early winter (May and June) before mating begins and that there is a marked increase in the ecdysis of adult males during late spring and summer (November to February).

It has also been inferred by Heydorn (1966) that captive 'unfertilized females undergo an untimely moult four or five months after the normal annual moult'. Nevertheless, biannual ecdyses were indicated in both sexes of the present captive animals (tables 7–9), and a spring/summer ecdysis took place, not only in unmated females, but also in females which had previously been in berry.

Investigations by Crawford & De Smidt (1922), Nakamura (1940), Sutcliffe (1953), Lindberg (1955), George (1962), and Sheard (1949, 1962) have also proved that the mature females of various species of *Panulirus* undergo two ecdyses a year, one before mating and the other after the eggs have hatched. It is even more pertinent to the present study that Grua (1964) has reported the occurrence of winter and summer ecdyses in the females of *Jasus paulensis*.

Ovigerous Setae

After it was found that the captive adults moulted twice a year, more attention was paid to the condition of the ovigerous setae. During a period of two years, 70 observations were made of the setal arrangement at the successive ecdyses of 33 females which either possessed ovigerous setae when they were collected or acquired them at their first ecdysis in captivity.

If, as is detailed in the appendix, the presence and absence of the ovigerous setae are respectively represented by plus and minus signs, the following definition of the setal history relative to the biannual ecdyses is obtained:

Autumn/winter ecdyses: $+ = 31$; $- = 5$
Spring/summer ecdyses: $+ = 3$; $- = 31$

In an analysis of 37 pairs of ecdyses referable to the 33 females (see appendix), the sequence of setal (+) and a-setal (−) ecdyses was found to be:

$(+, -) = 30$; $(+, +) = 2$; $(-, +) = 1$; $(-, -) = 4$

The above summaries show that, whereas 31 of the females possessed ovigerous setae at the autumn/winter ecdysis, only three females produced setae at the spring/summer ecdysis. It is also apparent that in most of the females there was an almost regular biannual development and loss of the ovigerous setae.

There is no doubt that the ovigerous setae are acquired when the females attain sexual maturity. Consequently, if the alternation of the setal and the a-setal phases observed in captive females is normal, it suggests that in a large population of rock lobsters there may sometimes be a number of mature females which lack ovigerous setae. Such females could be described as being in a state of sexual rest and would resemble immature animals if the setae had been shed at an ecdysis following the incubation of the eggs.

Little is known about this aspect of *J. lalandii* in the field, but Bradstock (1950) has concluded that a relatively high percentage of the females of *J. edwardsii* retain the ovigerous setae after the eggs have hatched. In *Panulirus*, on the other hand, accounts by Nakamura (1940), Sutcliffe (1953), and George (1962) indicate that the females moult and shed the ovigerous setae after the breeding season.

In *J. lalandii* large ovaries containing brick-red or orange eggs are typical of females possessing long ovigerous setae. It was therefore of interest that apparently mature ovaries were observed in three unmated females after a lengthy period of captivity and upon renewal of the ovigerous setae at the winter ecdysis. By contrast, in a number of unmated and post-ovigerous females, which lost the ovigerous setae at the spring/summer ecdysis, the ovaries were narrow and only slightly folded and the eggs were small and white.

Apart from some observations by George (1958) and Fielder (1964*b*), the correlation between the condition of the ovaries and the setal arrangement in the Palinuridae seems to have been hardly investigated. The significant results of experiments performed by Charniaux-Cotton (1960) on *Orchestia gammarellus* may, however, be mentioned in this connexion. In this amphipod it has been shown that the oostegites revert to the juvenile state and have shorter ovigerous setae when the ovaries are inactive. It has been concluded that the ovigerous setae of *Orchestia* are temporary sexual characters associated with the incubation of the eggs and that their growth is induced by an ovarian hormone which is secreted during vitellogenesis.

It seems reasonable to suppose that similar conditions may prevail in some palinurids and that the absence of ovigerous setae is connected with the immature state of the eggs between one reproductive cycle and the next. At such a time, hormonal control of the external secondary sexual characters would be precluded and, if an ecdysis ensues shortly after the eggs have hatched, it is unlikely that ovigerous setae will be formed at this ecdysis. It thus appears that, even though the moulting frequencies of experimental animals suggest that the mature females of *J. lalandii* may moult twice a year, only one incubatory period will be possible if the ovigerous setae are shed at one or the other of the two ecdyses.

Grua (1964) has concluded that the damaged setae of post-ovigerous females of *Jasus paulensis* are replaced at a summer ecdysis which is quite distinct from the one that precedes mating. The present observations indicate, however, that in most captive *J. lalandii* females the ovigerous setae are renewed only at the premating ecdysis. There is also a strong probability that the latter takes place in late autumn or winter in some females (31 in the present study) and in spring in other females (3 in the present study).

If this opinion is correct, it may explain why one of the captive females in Gilchrist's (1913) experiments spawned on two different occasions after the second ecdysis, while another female spawned after the first ecdysis. As the moulting cycles of these two females are more or less comparable with the present findings, it is surmised that the ovigerous setae were developed at the second ecdysis in Gilchrist's first female and at the first ecdysis in the second female.

Although most of the females of *J. lalandii* are apparently equipped for carrying eggs after the autumn/winter ecdysis, it has been shown that a considerable number of the captive females discarded their ovigerous setae at the spring/summer ecdysis. It may be noted, however, that two females, which were captured in berry towards the end of winter, did not moult until the following autumn and the ovigerous setae were again renewed and not lost. As these females were included in an independent tagging experiment, they have been omitted from the above considerations. Nevertheless, if their behaviour was normal, it introduces the possibility that in some females the post-incubatory ecdysis may be omitted and that the premating ecdysis may occur at slightly different times in consecutive years.

REPRODUCTION

Most of the mature females were provided with apparently suitable partners, but mating was not observed and only five females produced eggs. Two of the females were soft when collected and, as they became ovigerous in 11 and 18 days after their capture, it was assumed that mating had taken place in captivity some considerable time after they had moulted in the field.

The other three females moulted in captivity and spawned respectively in 9, 20 and 63 days after ecdysis. Two of them (T.C.L. 72, 79 mm) were of interest in that they spawned in spring and were consistent with Heydorn's (1966) conclusion that the smaller females are usually in berry later in the year than the larger females.

These few results suggest that the interval between ecdysis and egg-production is variable. The period of 9 to 20 days recorded in four of the females is probably more normal than the delay of 63 days observed in the fifth individual. At all events, it was noticed that most postmoult females appeared to avoid the males for several days, and it is surmised that the females are probably too weak to spawn immediately after ecdysis. Contrary to the opinions of some observers, it has been inferred that ecdysis and spawning are not necessarily closely associated in *J. lalandii.*

Retrogression of the ovaries and autolysis of the eggs have been suggested as probable causes of sterility in several species of captive decapods. Resorption of yolk from the eggs of *Homarus americanus* has been cited by Allen (1895) and has also been reported in *Orconectes limosus* (*Cambarus affinis*) by Andrews (1906), in *Diogenes pugilator* by Bloch (1935), and in *J. lalandii* by Heydorn (1966).

It is possible that similar processes may have contributed to the negative results obtained in most of the present breeding experiments. Nevertheless, in at least three females the ovaries were large and no yolk resorption was apparent when they were examined macroscopically after an ecdysis at which long ovigerous setae were developed. As two of the females were in captivity for over a year and had survived three ecdyses, it seems that, although they did not spawn, the sexual cycle had not been markedly affected. No sections of the ovaries of these animals were prepared, and it is not known if the eggs were fully mature. Until further information on this aspect is available, a decline in the fertility of the females during long periods of captivity cannot be excluded.

From current observations, it is also doubtful if young females become mature in captivity. A few small females were maintained for two years, by which time the T.C.L. was 69 to 71 mm. Even though females smaller than this have occasionally been collected in berry, none of the young experimental females acquired ovigerous setae and the ovaries were immature. A likely explanation is that maturation of the ovaries may be delayed or inhibited by a lack of factors essential to vitellogenesis.

Another reason for the persistent sterility in most of the captive adult females may have been the approximate coincidence of their ecdyses with those of the males. As the captive males also moulted twice a year, it is feasible that they are subject to periods of sexual impotence and that, unless they moult some time before the females are furnished with ovigerous setae, mating will not take place.

When soft-bodied males were placed in tanks containing females, which had moulted and were known to have ovigerous setae, no eggs were produced. Assuming that metabolic changes correlated with moulting had affected the male sexual behaviour, it is possible that the proper stimulus for mating was lacking.

The association of freshly-collected, hard-shelled males and females, which had either recently moulted or which moulted in the presence of the males, was equally ineffectual. Although the females possessed ovigerous setae, no sexual activity was displayed.

As most of the females moulted successfully but failed to reproduce, some of them may have been either too large or too small for the available males. In one experiment, however, a female (T.C.L. 79 mm), which had moulted in isolation, spawned six days after a male (T.C.L. 100 mm) was introduced into the tank. Similarity in the size of the partners may, therefore, not be an essential attribute to successful mating, but intercourse between small males and larger females seems unlikely.

Attempts at Artificial Insemination

When it became apparent that reproduction had failed in most of the experiments during the first half of 1966, the following four rather crude attempts were made to inseminate a number of freshly-collected mature females. All the females were soft when captured and the semen was removed directly from the vasa deferentia of mature males.

1. Spermatophoric material was smeared on the sterna behind the gonopores of three females (T.C.L. 82, 82, 83 mm).

2. Seminal substance was pressed with a spatula into the gonopores of three females (T.C.L. 75, 77, 80 mm).

The above females were captured on 26 June 1966 and were isolated for about three weeks to ensure that they had not mated recently in the field.

In the next two experiments, injection syringes with blunted fine and coarse needles were used to introduce spermatophoric matrix into the oviducts of four females. These females were isolated for nine days after their collection on 26 July 1966.

3. Pure spermatophoric material was injected into the oviducts of two females (T.C.L. 82, 84 mm).

4. As some difficulty was experienced in drawing sufficient quantities of the viscous, transparent spermatophoric mass into the syringes, a dilution of equal parts of seminal material and sea water was injected into the oviducts of two females (T.C.L. 73, 77 mm).

In each experiment the treated animals and control females of similar sizes and condition of shell were placed in separate tanks. They were observed for at least a fortnight, but none of them produced eggs.

All the females seemed to be unusually restless for several days after treatment. They moved about, either with the abdomen fully extended and with the pleopods pendent, or with the abdomen tightly flexed and simulating the ovigerous posture.

The somewhat rough handling of the specimens appeared to have no ill effect. One female, which moulted in captivity before the experiments, survived two further ecdyses. Another female moulted 36 hours after the injection of diluted seminal fluid into the oviducts and had a second ecdysis six months later. The other females had obviously moulted in the field before their capture and, although most of them were maintained for several months in tanks containing males, reproduction did not take place.

Assuming that artificial insemination would have induced spawning, one reason for the negative results could have been the time lapse between the winter ecdysis of the females and the beginning of the experiments. Nevertheless, previous comments (p. 247) show that *J. lalandii* females are capable of reproduction some time after they moult.

It has also been suggested (p. 246) that in mature females a period of sexual quiescence occurs after the breeding season and coincides with the immature condition of the ovaries and the loss of the ovigerous setae. All the females in these experiments possessed long ovigerous setae, and it was assumed that they had not been in captivity long enough for the production of any radical changes in the state of the ovaries. Physical contact and sexual stimulation by hard-shelled males may, however, be essential to successful reproduction in this species.

Several tests indicated that the spermatophoric substance remains soft and simply disintegrates after being immersed in sea water for a few days. It is therefore probable that most of the spermatophoric material which was applied to the sterna of the first three females was washed off the surface soon after the animals were returned to the tanks.

Another factor which seemed to militate against the possible fertilization of the internal eggs of the females used in the other experiments was the rapid expulsion of the injected seminal matter through the gonopores, presumably by internal pressure either within the body cavity or in the oviducts. Thus, even if the females had been capable of reproduction at this juncture, it is doubtful if sufficient spermatophoric material was retained in the oviducts to impregnate the eggs.

No valid conclusions concerning the method of fertilization in *J. lalandii* can be drawn from these simple experiments. However, if true copulation takes place, it is still uncertain how sperm intromission is effected. It is also questionable if there is adequate provision for the storage of spermatophoric material in the oviducts. On the other hand if fertilization is external, the consistency and the rapid deterioration of the exposed contents of the vasa deferentia suggest that the eggs must be laid shortly after mating.

Histology of the Reproductive Organs

Histologically the gonads of both sexes of *J. lalandii* seem to be practically identical with those of *J. novaehollandiae* (Fielder, 1964*b*). In both species the testes are intricately coiled tubes and the parts of the vasa deferentia are sharply differentiated. In the present material they are divisible into three regions, the first and third of which are similar to the proximal and distal vas deferens of *J. novaehollandiae*.

The slender, convoluted proximal portion of the vas deferens (fig. 4*A*) is oval in section and its lumen is reduced to a narrow, keyhole-shaped slit by the arrangement of the columnar epithelium into small cells at the poles and elongate, very narrow cells along the two sides.

The middle and distal parts of the vas deferens are wider than the first part and each has a thick muscular wall. The slightly coiled middle region (fig. 4*B*) is lined by a villiform glandular epithelium which is produced into a conspicuous typhlosole. The latter underlies a surface streak, called the hyaline line by Matthews (1951, 1954*a*, 1954*b*), along which the wall appears to be somewhat thinner and less muscular. Some similarity is evident between sections of this region and those of the enlarged swollen part of the vas deferens

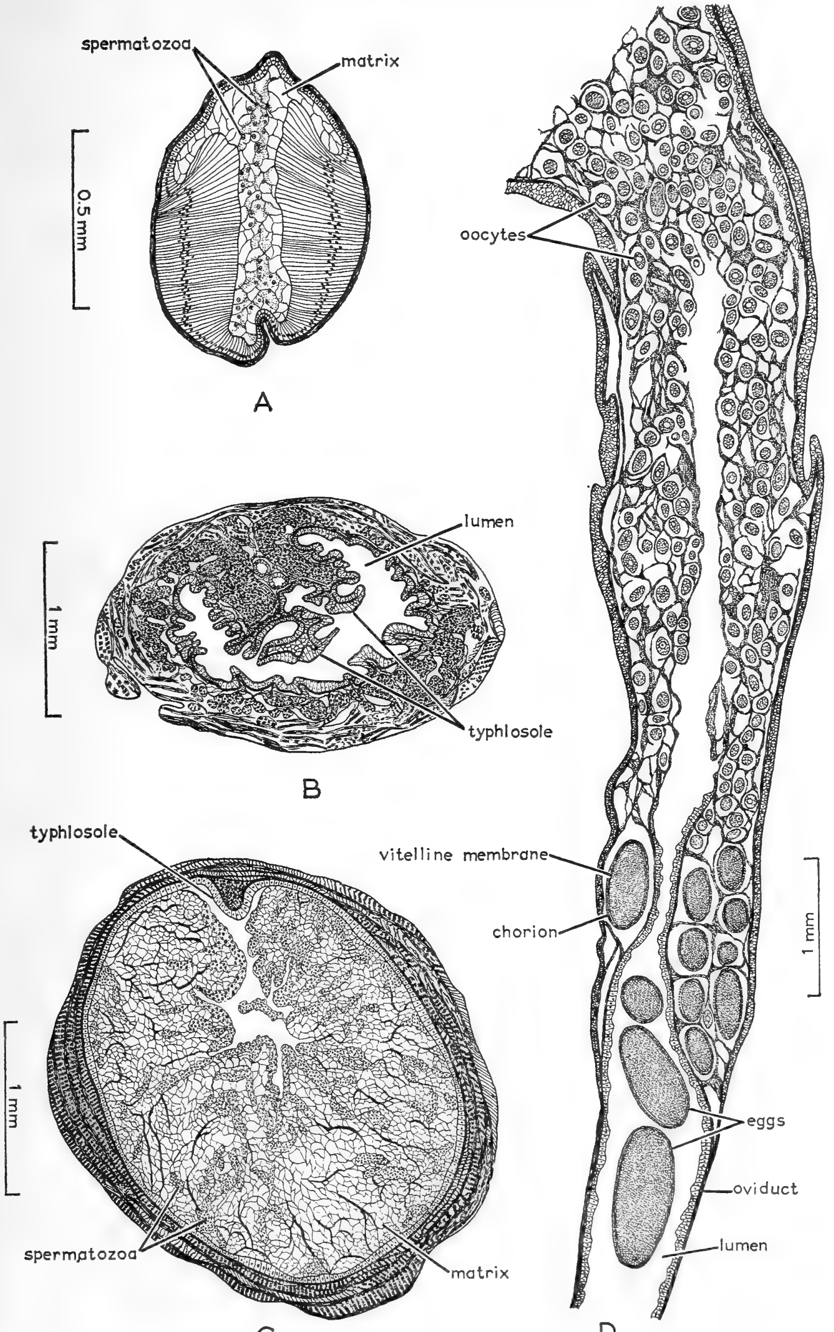

FIG. 4. Diagrammatic sections of the organs of a mature male (T.C.L. 110 mm) and an ovigerous female (T.C.L. 85 mm).

A. Transverse section through the proximal portion of the vas deferens.
B. Transverse section of the middle region of the vas deferens.
C. Transverse section of the distal part of the vas deferens.
D. Longitudinal section passing through the junction of the ovary and the oviduct.

of *Panulirus penicillatus* depicted by Matthews (1951).

The structure of the longer, straighter, and more cylindrical tube (fig. 4*C*), which passes to the gonopore, is comparable with that of the distal part of the vas deferens of *J. novaehollandiae* (Fielder, 1964*b*). The epithelium is flatter than that of the middle region, and the typhlosole is small and conical in section. The wide lumen is filled with a reticulated, folded matrix, the sinuous edges of which are charged with spermatozoa. The definite spermatophoric wall and the 'putty-like' basis of the matrix, described in *P. penicillatus* (Matthews, 1951), seem to be lacking. It is believed by Matthews (1951, 1954*a*, 1954*b*) and Fielder (1964*b*, 1964*c*) that most of the spermatophoric matrix is secreted by the typhlosole. In the present sections the matrix is absent from the middle part of the vas deferens (fig. 4*B*), but occurs in the other two regions of the duct and also in the lumen of the testis.

In sections of the testis and the vas deferens and in smears of the spermatophoric matrix of mature males the spermatozoa are small spherical bodies measuring 6·8 to 13·5 μ in diameter. As in *Palinurus elephas* (*vulgaris*) (Bloch, 1935), each spermatozoon has a distinct cupular nucleus and a globular capsule. It seems unlikely that the spermatozoa are immature but, even in thin smears, the characteristic radiating processes are indeterminate. Comparatively few spermatozoa are furnished either with one or with four to six delicate filaments measuring about 7 to 11 μ in length, and it is possible that some of these are artefacts. Heydorn (1965) has, however, detected up to five spines projecting from the spermatozoa of *J. lalandii*, and Matthews (1951) has mentioned the presence of rayed spermatozoa in *Panulirus penicillatus*.

From a number of ovigerous females examined, the one selected for microscopic study of the gonads contained mature eggs in the ovaries and the oviducts. In section, the ovary (fig. 4*D*) presents some of the features of the ovaries of *J. novaehollandiae* and *J. lalandii*, described respectively by Fielder (1964*b*) and Heydorn (1966). Numerous oocytes with a maximum diameter of 120 μ are visible. Each is enclosed in a delicate vitelline membrane and a layer of follicle cells, and in many of the oocytes the large nucleus contains a conspicuous nucleolus.

The mature eggs in the ovary and in the oviduct measure from 400 to 500 μ in diameter. In addition to the thin vitelline membrane, each is surrounded by a thicker envelope, the chorion (fig. 4*D*), which is cribriform in section. It has been shown by Herrick (1911) that the ripe eggs of *Homarus americanus* are invested by a chorion which is secreted by the egg follicle. Bloch (1935) has also suggested that, as the mature ovarian eggs of *Diogenes pugilator* are furnished with both a vitelline membrane and a chorion, the latter is not a product of the oviduct. Von Bonde's (1936) conclusion that fertilization is internal in *J. lalandii* is based on the supposition that the 'chitinous' egg membrane is secreted by the lower part of the oviduct, but his interpretation of the egg membranes may be somewhat erroneous.

The external eggs of *J. lalandii* are approximately 750 μ in diameter and are enclosed in an additional cuticular membrane which is continuous with the egg-stalk and is believed by several authorities to be secreted by the tegumental glands of the pleopods.

Although the residual mature eggs of ovigerous females are probably destined to be resorbed, it seems logical to assume that, if intromission takes place, traces of the seminal material will remain for some time in the oviducal lumen. In the present serial sections of the oviduct, however, no spermatozoa or any substance resembling the spermatophoric matrix could be detected.

In support of Von Bonde's (1936) assumption that the eggs of *J. lalandii* are fertilized in the proximal part of the oviduct, Fielder (1964*c*) has proposed that the spermatozoa could be lodged in the folds of the oviducal wall after the dissolution of the spermatophoric matrix. This hypothesis has been accepted by Heydorn (1966) but has not been confirmed in the present investigation.

FERTILIZATION

Various accounts of mating and reproduction in macrurous Reptantia have shown that spermatophoric masses are deposited by the male on the sternum of a recently-moulted, soft-bodied female. It has also been suggested that in *Panulirus* the sperm are released when the female uses the chelae of the fifth pereiopods to scarify the hardened spermatophoric mass on her sternum.

In the absence of resistant external spermatophores in *J. lalandii*, it appears that the main function of the chelae is to groom the abdomen and the pleopods in both unmated and ovigerous females. Sexual dimorphism of the fifth pereiopods of this species was not apparent in small females with a T.C.L. of 26 mm. As the females increased in size, however, the process of the propodite, which forms an essential part of the chela, gradually became more pronounced.

Failure to detect the usual palinurid external spermatophores has been one of the most puzzling features in the reproductive biology of *J. lalandii*, and it has often been assumed that fertilization is internal. Microscopic examination of the reproductive organs and attempts to induce spawning by artificial insemination suggest that this supposition is unlikely.

Dissections of a number of mature females at different times of the year proved that no spermathecal enlargements occurred on the oviducts. It was also observed that, in freshly-collected, soft females possessing long ovigerous setae, the oviducts were distended with mature eggs awaiting extrusion. Moreover, the male has no intromittent organs, and no support has been found for Von Bonde's (1936) theory that the eggs are fertilized in the oviducts.

The following observation is considered to be significant in that it seems to indicate how fertilization is accomplished externally. It concerns an experiment with a female (T.C.L. 89 mm) and two hard-shelled males (T.C.L. 90, 100 mm). The smaller male had been in captivity for a month and the larger male was a recent introduction.

On 25 July 1967, 36 days after the female had moulted, she was observed in a crouched position about an hour after sunset. Mating had probably just taken place, and it appeared that spawning was imminent. The abdomen was strongly flexed and the tail-fan was fully expanded beneath the cephalothorax. An immediate examination of the female's sternum behind the gonopores revealed the presence of a fairly thick layer of colourless, gelatinous matter resembling the spermatophoric matrix.

Stained smears of some of the material, which had been kept overnight in sea water, were somewhat unsatisfactory, but the nature of the deposit was established by the identification of a number of spermatozoa. These were comparable in size to the spermatozoa observed in fixed preparations of the contents of the vasa deferentia. It was also of interest that several freshly-laid eggs were found in the vessel in which the material had been stored.

In trying to evade capture, the female had obviously been greatly disturbed at a critical period and much of the extraneous matter was dislodged in handling her. By the following morning all traces of the hyaline deposit had disappeared and, so far as is known, no more eggs were produced.

Although this isolated incident requires further confirmation, it suggests that a soft, transparent spermatophore is placed on the female's sternum during the brief act of mating. If, however, the eggs are extruded almost immediately after its application, the spermatophore will virtually be obscured. (A short report of this opinion has been submitted in a letter to the Editor of the *South African Journal of Science*, Paterson, 1969*b*.)

In several females it was observed that a considerable number of eggs were still adherent to the sternum shortly after spawning had taken place. Presumably, these eggs were embedded in the remains of the colourless, viscous spermatophoric mass. It is therefore probable that the eggs are fertilized on the female's sternum before they pass into the incubation chamber, where they become attached by stalks to bundles of the ovigerous setae on the endopodites of the pleopods.

Incubatory Period

The period of incubation, during which the eggs are carried externally and cared for by the females, was studied in 22 specimens, 19 of which were captured in berry. As it was noted that in many of the broods some larvae emerged earlier than others, a distinction has been made between the start and the completion of hatching (table 15). The average interval between spawning and the first signs of larval eyes in the incubating eggs is also indicated.

It was observed that the incubatory period differed somewhat in individual females, but its duration may depend upon the size of the animal and on the number of eggs carried. Although no regular pattern was evident, clearance of the pleopods was generally effected sooner in some of the smaller than in the larger females in each size class.

TABLE 15

Summary of the development of the larval eyes and the length of the incubatory period in the eggs of captive females

T.C.L. in mm	*No. of specimens*	*Development of larval eyes*		*Start of hatching*		*Completion of hatching*	
		No. of days	*Mean in days*	*No. of days*	*Mean in days*	*No. of days*	*Mean in days*
60–69	1	32	32·1 ±2·6	44	62·2 ±11·4	81	94·2 ±8·4
70–79	5	31–37		51–81		77–102	
80–89	7	29–37		61–81		78–102	
90–99	8	28–37		51–81		85–102	
100–109	1	32		67		90	

The eyes of the developing larvae in the eggs of females which were collected in berry were apparent in 29 to 32 days. This compares with 28 to 37 days observed in the eggs of the present females which spawned in captivity. It is therefore reasonable to suppose that most of the ovigerous females had been captured shortly after the eggs were laid. On this premise, it has been concluded that the incubation of the broods was generally completed in approximately three months. Occasionally, however, the development of some embryos was retarded, and a few females moulted in spring or summer before all the larvae had hatched.

Gilchrist (1913) considered that the eggs of *J. lalandii* are carried for about five months, but in his holding experiments a shorter period of two to four months is indicated. The latter time is more consistent with an incubatory period of three to four months reported by Von Bonde & Marchand (1935).

The length of the incubatory period also appears to be variable in species of *Panulirus*. While Allen (1916) estimated that in *P. interruptus* hatching was completed in nine or ten weeks, a period of 18 days was recorded for *P. argus* by Crawford & De Smidt (1922). Contrasted with these findings, it is thought that the embryonic development lasts about a month in *P. japonicus* (Terao, 1929; Nakamura, 1940) and in *P. argus* (Sutcliffe, 1952).

DISCUSSION

Most of the important biological and ecological facts concerning *J. lalandii* have been acquired either by regular experimental trawling or tow-netting (Gilchrist, 1913, 1918; Von Bonde & Marchand, 1935; Matthews, 1962;

Lazarus, 1967) or by direct underwater observations of the animals (Heydorn, 1965, 1966). A few aquarium experiments have also been performed by some of these investigators.

The primary object of the present study was an inquiry into the mating behaviour and the process of fertilization, but several side-issues have also proved of interest. Some of these are discussed in an attempt to correlate the behavioural patterns of captive *J. lalandii* with the data obtained in the field by other workers.

Locomotor and feeding activities

As in other Decapoda, the Cape rock lobsters are more active at night than during the day, and the suggestion of a bimodal rhythm in the locomotor and feeding activities is partly substantiated by reports that the highest catches of rock lobsters are obtained by local fishermen just before daybreak.

Foraging and feeding were also observed in some captive animals during the day, and it seems unlikely that all the animals in thickly populated areas will remain strictly nocturnal in their habits. Active feeding on the sea bed has been observed during the day by Heydorn (1966), and some measure of diurnal activity also appears to be implied in the successful day-time hauls of rock lobsters described by Gilchrist (1913, 1918) and Von Bonde & Marchand (1935).

It is well known that rock lobsters are easily caught in traps or hoop nets baited with dead fish and, while the captive animals became accustomed to feeding on a daily supply of pieces of fresh stockfish, live fish and other active animals are probably not included in their normal diet.

A few small klipfish, *Clinus superciliosus* (Linnaeus), and a number of crabs, *Plagusia chabrus* (Linnaeus), lived unharmed for several months in a tank containing eight juvenile rock lobsters. It was only when the klipfish became moribund after an overnight failure of the water and air circuits that they were partly eaten by the rock lobsters. On other occasions, some klipfish and crabs were introduced into tanks containing adult rock lobsters and, although the crabs were often seen perched on the carapace of the rock lobsters, no attempts were made to attack or dislodge them.

The cardiac stomach of freshly-collected animals usually contained fragmented mollusc shells. Sometimes pieces of the exoskeleton of rock lobsters, the byssus threads and complete shell valves of small mussels, *Aulacomya magellanica* (Chemnitz), were also observed. It is therefore likely that their natural food consists mainly of sedentary organisms such as *Aulacomya*, which are said to be plentiful in rock lobster grounds. Omnivorous feeding is suggested by the preference shown by captive animals not only for lamellibranchs, but also for small limpets and kelp. They were, however, also attracted to the dead bodies and the exuviae of other rock lobsters, and cannibalism, which only occurred among crowded immature specimens, is probably resorted to when other food is scarce.

Moulting frequencies

Based on field investigations, it has been assumed that in *J. lalandii* there is an annual ecdysis which takes place in late spring or summer in the males and in late autumn or early winter in the females. Nevertheless, Gilchrist (1918) recorded the capture of a number of soft-bodied males in winter and soft females in summer. Moreover, in a study of *J. novaehollandiae*, Hickman (1945) remarked that, although most of the males moulted in spring, some catches taken during autumn and winter contained a few soft males. It is likewise pertinent that a winter ecdysis is indicated in the males of *J. tristani*, 17 of which were maintained for several months at the Sea Point Aquarium during 1967. Five of the specimens died between 15 June and 23 August just before ecdysis and, of the remaining animals, one moulted in May, five in July, three in August, and three in September.

Biannual ecdyses were common in the captive adult males and females of *J. lalandii*, and a similar frequency seems to be implied in Fielder's studies of *J. novaehollandiae*. He established (1964*a*) that animals with a rostrum-carapace length of 8·0 to 8·9 cm moulted twice a year. It was also noted (1964*c*) that four females moulted between August and October but, like most of the present specimens, they did not reproduce.

Ecdysis and spawning

As it is generally agreed that ecdysis of the females precedes spawning, the prevalence of a spring/summer ecdysis in the captive females is of interest, more particularly because in some females it was correlated with the loss of the ovigerous setae and the diminution of the ovaries. It has therefore been inferred that the annual period of sexual activity in the females is characterized by the development of long ovigerous setae and is followed by an ecdysis which marks the beginning of a period of sexual quiescence.

The presence of the ovigerous setae, either at the autumn/winter ecdysis or at the spring/summer ecdysis, suggests that two overlapping incubatory periods are possible in a given population of *J. lalandii*, one occurring from winter to spring in some females and the second from spring to summer in other females. This supposition is partly confirmed by Gilchrist's (1913) observations of captive animals and by his conclusion (1918) and that of Matthews (1962) that spawning takes place later in some areas than in others.

Two distinct breeding communities are likewise suggested by Heydorn's (1966) field observations which have shown that, while the larger females reproduce in winter, some smaller ovigerous females may still be found during the following summer. The existence of separate spawning populations has also been considered by Lazarus (1967) as a possible explanation of the occurrence of 'winter' and 'summer' hatching peaks associated with the distribution of the phyllosoma larvae of *J. lalandii*.

As embryonic development probably lasts about three months, the presence of ovigerous females throughout several seasons obviously indicates that the females are not all fertile at the same time and that the pre-mating ecdysis of the females must likewise be staggered over five or six months.

The relatively high percentages of ovigerous females recorded in the field during spring therefore seem to be significant. They may support the theory that the population is roughly divisible into two groups, one of which spawns earlier than the other. The numbers of animals in the two groups may be disproportionate but, if the incubatory periods of some females in each subdivision happen to coincide in spring, an increase in the percentages of ovigerous females collected at that time will be expected.

The cycles of ecdyses recorded in the field do not altogether disprove this opinion, since minor peaks of ecdysis seem to be evident in spring and summer in some of the areas so far investigated. As the pre-mating ecdysis of the females is undisputed, it may be postulated that the general patterns of moulting and ovigerous females should be more equable than is apparent in most field observations, some of which hardly reflect the ecdyses of the females that spawn in spring. Moreover, the spring/summer ecdysis frequently recorded in captive unmated and post-ovigerous females has not been corroborated in the field, but it is conceivable that it corresponds to the post-incubatory ecdysis described in species of *Panulirus*.

Mating

Several investigators have indicated that in some captive Decapoda the ovaries degenerate and that reproduction is consequently suspended, yet Gilchrist (1913) demonstrated that mating recurred annually in a few experimental specimens of *J. lalandii*. In later observations, however, Gilchrist (1918) found that after a year in captivity a number of females became sterile. He tentatively suggested that spawning might occur biennially, but this seems unlikely. Most of the present females were also infertile, although post-mortem examinations of a few specimens, which had been captive for some time, showed that the ovaries looked mature and apparently had not been permanently impaired.

It has been surmised that the sexual activity of captive males was limited by their biannual ecdyses and that some were therefore unsuitable for mating with the available females. The choice of physiologically adjusted partners is doubtless a deciding factor in effective breeding experiments. When selecting hard-shelled male rock lobsters, however, it is difficult to determine whether they have already moulted in the field or whether they will moult during the reproductive period of the females.

Gilchrist (1913) gave no particulars concerning the males used in his experiments, but it is possible that the successful results were obtained by the annual introduction of new hard-shelled males. No real support for this conjecture was evident in the present study. It has been shown (p. 247) that five females produced eggs after mating with fresh hard-shelled males, but it must be noted that four of the females were also fairly recent acquisitions. The fifth female spawned in spring after four months of captivity, but other females, which had been held for even longer periods, remained barren. It is therefore possible that reproduction in some of the females was inhibited by factors in the environmental conditions to which they were subjected.

It has usually been assumed that the annual reproductive cycle in *J. lalandii* is actuated by the ecdysis of the female and that successful mating is dependent upon the soft condition of the female. Judging by the present observations, this conclusion seems doubtful. An unusually long interval of 63 days occurred between ecdysis and spawning in one female. In four other individuals the eggs were laid in 9 to 20 days after ecdysis and while hardening of the exoskeleton was in progress.

Variations in the time between the ecdysis of the female and spawning are also evident in other reports on the biology of *J. lalandii*. An analysis of Gilchrist's (1913) experiments indicates that one female spawned on two occasions shortly after ecdysis. In other females the interval between ecdysis and mating was about 14 days and, when the time of mating was not recorded, there were periods of 38 to 47 or 48 days between ecdysis and egg-production. Matthews (1962) has also suggested that spawning probably takes place about three weeks after the females have moulted.

From these accounts, it would seem that mating in *J. lalandii* is possible when the exoskeleton has begun to harden. This conclusion is, however, at variance with the views of Von Bonde & Marchand (1935), who considered that mating and oviposition are accomplished shortly after the female has moulted. In this connexion, it is of interest that Sutcliffe (1952, 1953) has observed that in *Panulirus argus* mating may take place when both the males and the females are hard shelled.

Fertilization

Elsewhere (Paterson, 1968) it has been suggested that the male genital apparatus of *J. lalandii* resembles that of the Natal rock lobster, *Palinurus gilchristi* Stebbing. There is also a marked difference between the male gonopores of these two species and those of the east coast rock lobster, *Panulirus homarus* (Linnaeus), in an account of which firm external spermatophores have been described by Heydorn (1966).

Hard external spermatophores comparable to those of *Panulirus* have not been detected in *J. lalandii*, but some importance is attached to the discovery of a colourless gelatinous mass behind the gonopores of one of the present captive females. As this substance contained spermatozoa and resembled the transparent viscid contents of the vasa deferentia of mature males, it is believed that in *J. lalandii* a soft external spermatophore is deposited on the female's sternum. It is also anticipated that a similar external spermatophore will be found in *Palinurus gilchristi*.

The latter expectation seems to be reasonable enough, because, according to Brocchi (1875) and Bloch (1935), one investigator (Coste, 1860) reported the presence of external spermatophores in the langouste, *Palinurus elephas* (Fabricius). In addition, some early workers were convinced that true copulation did not take place in *Palinurus* and other Macrura. It was postulated that intromission of sperm would hardly be effective in fertilizing the large number of eggs produced by each female.

A similar argument would be equally cogent in speculations regarding the method of insemination in *J. lalandii* but is no longer considered to be necessary. The present conviction that a soft external spermatophore occurs in this species confirms previous conjectures (Paterson, 1968) that fertilization is external and not internal, as has formerly been supposed. The spermatophore of *J. lalandii* apparently lacks the 'putty-like' matrix described in species of *Panulirus*, and the fact that it is transparent and transient probably explains why it has hitherto been overlooked.

Summary

Some aspects of the behaviour of juvenile females and adult males and females of the Cape rock lobster, *Jasus lalandii* (H. Milne Edwards), were studied in holding experiments at the Sea Point Aquarium, Cape Town, from March 1966 to July 1968.

Shortly after their introduction into the tanks, the animals established territorial rights to particular corners or rock niches and defended them against intruders.

Reference is made to some of the grooming operations frequently observed.

Direct observations of 18 to 20 adults over a period of four months suggested the presence of a bimodal diurnal rhythm in the locomotor and feeding activities. The normal behaviour was probably affected by the daily introduction of food during the afternoon but, even so, the levels of activity were generally higher at night than during the day.

Ecdysis, which usually took place at night, was observed in eleven juveniles and seven adults of *J. lalandii* and also in three males of *J. tristani*. An account is given of the process which is essentially similar to that described by several authors in *Panulirus*. Actual exuviation was completed in three to five minutes in *J. lalandii* and in four to seven minutes in *J. tristani*.

No significant difference was found in the average growth rates of the adult males and females, but the mean increments in the T.C.L. of the juvenile females were probably slightly higher than those of the adult females. As the animals increased in size, a progressive decrease in the growth rate was observed.

The mean moulting frequency decreased from 4·8 to 2·0 per annum as the animals became larger. Biannual ecdyses, one in autumn or winter and the other in spring or summer, occurred in the 60 to 69 mm T.C.L. size class of juvenile females and in both sexes of the adults.

A study of the ecdyses of 33 mature females revealed that the ovigerous setae were frequently developed at the autumn/winter ecdysis and were shed at

the spring/summer ecdysis. Only three of the females acquired ovigerous setae at the spring/summer ecdysis. The loss of the ovigerous setae was correlated with a diminution in the size of the ovaries.

Apparently compatible males and females were selected for breeding experiments, but most of the females failed to spawn. The coincidence of the ecdyses of the captive males and females and degeneration of the ovaries may have contributed to the persistent sterility in the adult females. Maturation of the ovaries also seemed to be delayed or inhibited in young captive females and was probably occasioned by the unnatural environmental conditions.

Mating and spawning were not observed, but four females produced eggs in 9 to 20 days after ecdysis. In a fifth female, which reproduced in spring, there was a period of 63 days between ecdysis and spawning. It has been concluded that the soft condition of the female is not necessarily a prelude to mating and egg-production.

The assumption that fertilization is internal in *J. lalandii* has not been confirmed. Attempts to inseminate several mature females gave negative results, and serial sections of the ovary and the oviduct of an ovigerous female showed no traces of spermatophoric material.

In one female, which had probably just mated and which seemed about to spawn, a transparent seminal mass, resembling the viscous contents of the vasa deferentia of mature males, was found applied to the sternum behind the gonopores. It is believed that a soft, transient spermatophoric mass occurs in *J. lalandii* and that the eggs are fertilized externally on the female's sternum shortly after mating takes place.

Acknowledgements

The writer is greatly indebted to the Director of the Division of Sea Fisheries, Cape Town, for permission to use the facilities at the Sea Point Aquarium; to Dr. A. E. F. Heydorn of the Oceanographic Research Institute, Durban, and to Mr. G. G. Newman and his colleagues at the Division of Sea Fisheries for supplying the experimental animals and for useful discussions of some of the problems involved in their maintenance; to Mr. S. E. Hope, Division of Sea Fisheries, for checking the mathematical calculations; to Mr. G. G. Newman for valuable suggestions concerning the interpretation of the statistical results; and to the South African Council for Scientific and Industrial Research for financial support during the prosecution of this study.

The Trustees of the South African Museum thank the C.S.I.R. for a grant in aid of publication.

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APPENDIX

Summary of the incidence of ovigerous setae in captive females.

Animal No.	*Aut/Wint* 1966	*Spr/Sum* 66/67	*Aut/Wint* 1967	*Spr/Sum* 67/68	*Aut/Wint* 1968
5	+	−			
6	+	−			
18		+	+	−	
20		+	+		
27	+	−	+		
28	+	−			
29	+	−			
30	+	−			
31	+	−			
32	+	−			
33	+	−			
34	+	−			
35	+	−	−		
36	+	−			
37	+	−			
38	+	−			
39	+	−			
40	+	−			
46			−	−	
47			−	−	
49			+	−	
51			+	−	
55			+	−	−
57			+	−	
59				+	−
67			+	−	
68			+	−	
69			+	−	
70			+	−	
74			+	−	
75			+	−	
76			+	−	
77			+	−	

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Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.