



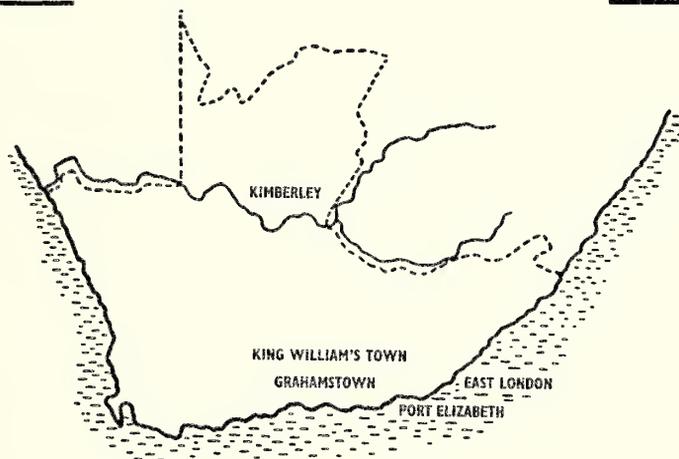


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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 1

30th September 1975

PUBLISHED JOINTLY BY THE

CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA





The ecology of a minnow, *Barbus trevelyani* (Pisces, Cyprinidae) in the Tyume River, Eastern Cape.

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SUMMARY

The minnow *Barbus trevelyani* Günther, is known today only from restricted habitats in the Buffalo River and Tyume River, Eastern Cape. The ecology of this species has been studied and it is concluded that *Barbus trevelyani* is in danger of extinction due to deterioration of the habitat, and the presence of introduced exotic species.

INTRODUCTION

Surveys done by the Albany Museum, Cape Department of Nature Conservation and the Zoology Department of Fort Hare University before 1971 showed that *Barbus trevelyani* has a limited distribution being confined to the Buffalo River between the Maden and Rooikranz Dams (Jubb, 1967; Gaigher, 1970) and the upper reaches of the Tyume River (Visser, 1969).

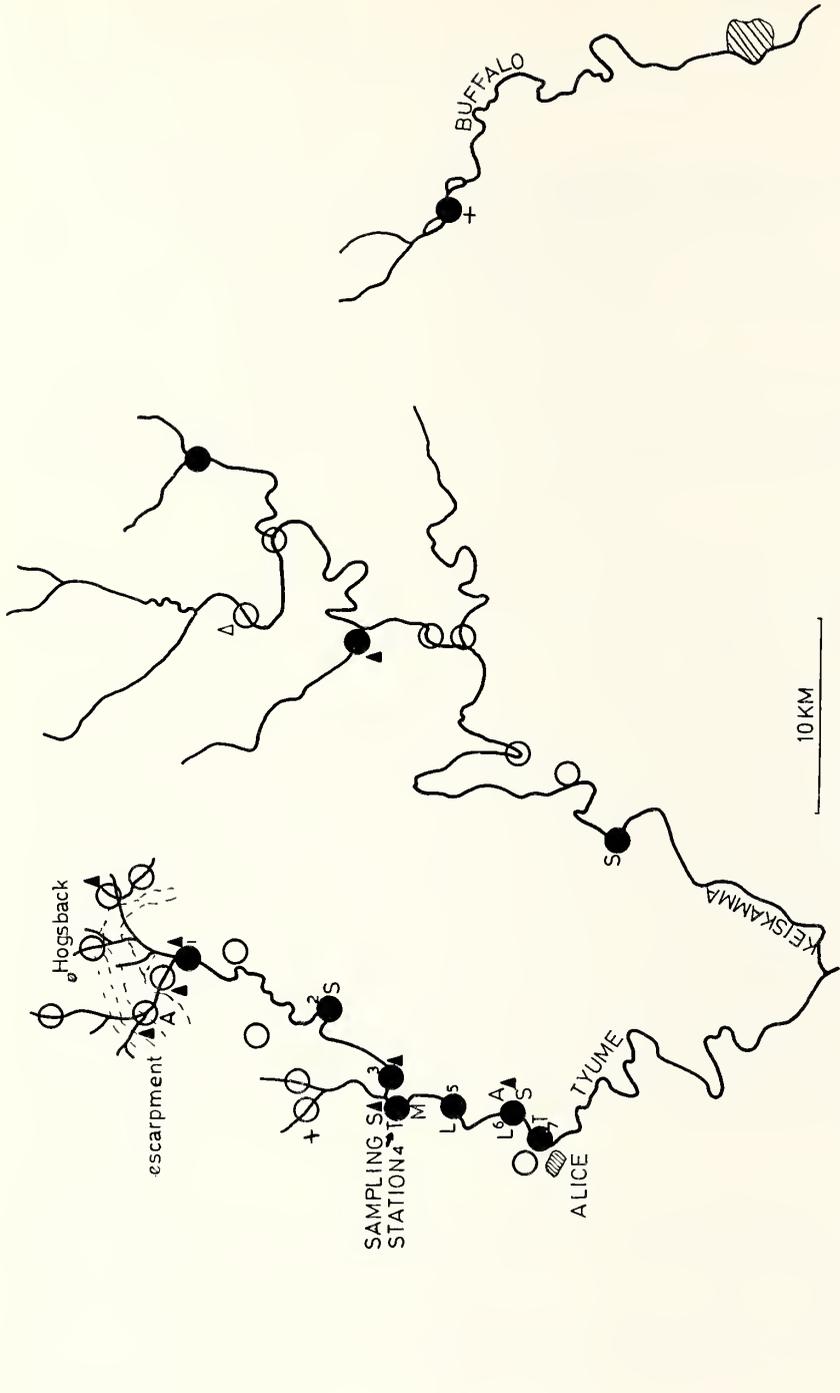
All these rivers have been stocked with trout and other foreign species, and this, together with the effects of the rapidly increasing agricultural and industrial development such as damming, water extraction, silting, pollution, etc. could easily cause the extinction of *B. trevelyani*. For this reason *B. trevelyani* was placed on the I.B.P. list of endangered fish species.

The relationship of *B. trevelyani* to other minnows has not been cleared up, but it certainly belongs to a group that populated the Cape rivers during the Upper Pliocene (Gaigher and Pott, 1973). Its serrated dorsal spine might point toward a close relationship to *B. hospes* of the Lower Orange River and *B. calidus* of the Olifants River (Western Cape), both belonging to this ancient group. However, there is a gap of more than 800 km between the distribution ranges of *B. trevelyani* and *B. calidus*. *B. trevelyani* is also related to the widely distributed *B. paludinosus* (Jubb, 1967) that occurs as far south as the Orange River system. However, there is good evidence to show that *B. paludinosus* only populated the Orange River at a much later stage. More intensive studies are required to solve these problems and valuable clues to the zoogeography and systematics of Cape minnows will be lost if *B. trevelyani* becomes extinct. The objective of this project was therefore to study the distribution and general ecology of *B. trevelyani*, and to implement this knowledge to plan conservation measures if necessary.

METHODS

Specimens were collected with the aid of a 220 V (A.C.) shocking apparatus and a small seine net. Collections were not made at regular time intervals, but as circumstances permitted during the period August, 1972 to October, 1973. After an initial distributional survey a

Editors note: Specimens used in this study have been deposited in the Freshwater fish collection at the Albany Museum. Accession numbers: AM/P 2580—AM/P 2603 inclusive.



- *B. trevelyani* present
- *B. trevelyani* absent
- ▲ *Salmo gairdneri*^x
- △ *S. trutta*^x
- + *Barbus anoplus*

- L *Labeo umbratus*^x
- S *Sandelia bairdii*
- A *Anguilla mossambica*
- T *Ilapia sparrmanii*^x
- M *Lepomis macrochirus*^x

x : introduced

Fig. 1. The distribution of *B. trevelyani*.

suitable stretch of the Tyume River was selected (Collecting site 4 in Fig. 1) and all subsequent collections made there.

After being collected, the fish were preserved whole, in 10% formaldehyde. In the laboratory each specimen was measured, sexed, and the weight of both gonads determined to the nearest 0,001 g. Classification of gonads into maturity stages was impractical due to preservation and the small size of the gonads. Assuming a cubic exponential relationship between length and weight, a gonadal index was calculated for each fish with the equation

$$\text{index} = \frac{G}{L^3} \times 10^5$$

where G = weight of both gonads in grams

and L = fork length of the fish in millimetres.

Each ovary contained small ova of varying sizes, and a certain percentage of "large" ova that were all approximately of the same size. Ten "large" ova of each ovary were measured with the aid of an eyepiece micrometer to the nearest 0,16 mm. The ova had probably shrunk to a certain degree as a result of preservation so that the values do not represent live ova sizes. However, it was still possible to indicate relative changes in ova size in this way.

The ovaries were then placed in a solution of alcohol and acetic acid for a few hours. This solution loosened ovarian tissue and caused the eggs to swell, and so facilitated counting considerably. All ova, except very minute ones, of both ovaries were counted under six times magnification.

Scales of 67 specimens were collected from the side of the body between the origin of the dorsal fin and the lateral line. These were mounted between two microscope slides and examined with the aid of a pamphot microscope. Annuli were identified as areas of the scale where the circuli showed overlapping or interruptions. Annuli were generally not clearly visible and examination was also hampered by the small size of the scales. The stomach contents were so small that their volumes could not be determined accurately. It was, for the same reason, also impractical to classify the stomachs as full, half full, etc. The only alternative was to weigh the contents, and this was done to the nearest 0,001 g. The contents were examined in a drop of water under 6 to 40 x magnification. Due to mastication it was impossible to count individual food items or to identify genera or species. The items were therefore merely classified into major groups such as Ephemeroptera nymphs, etc. The food items were separated, and the percentage each constituted of the whole content estimated. By assuming that all food items have approximately the same wet weight, it was possible to calculate the approximate weight of each food item in each stomach content.

DESCRIPTION OF THE STUDY AREA

The Tyume River rises as several small streams on the Winterberg Mountains near Hogsback, Eastern Cape, at an altitude of approximately 1 500 m (Fig. 1). After flowing for some distance, the tributaries plunge over an escarpment, forming several high waterfalls, down to an altitude of approximately 800 m. It then meanders through hilly country with a gradient of approximately 1:40, to its confluence with the Keiskamma River. The Tyume River receives several annual streams below the escarpment and the size of the river bed and the maximum summer flow therefore increases with decreasing altitude. Because the annual tributaries drain mostly overgrazed tribal land, pools change from sand or rocky bottomed in the higher reaches, to siltladen in the lower reaches. The drainage area above the escarpment and along the slopes of the mountain is covered with plantations or evergreen forests. Cultivation in the Tyume Valley below the escarpment consists mainly of maize lands and

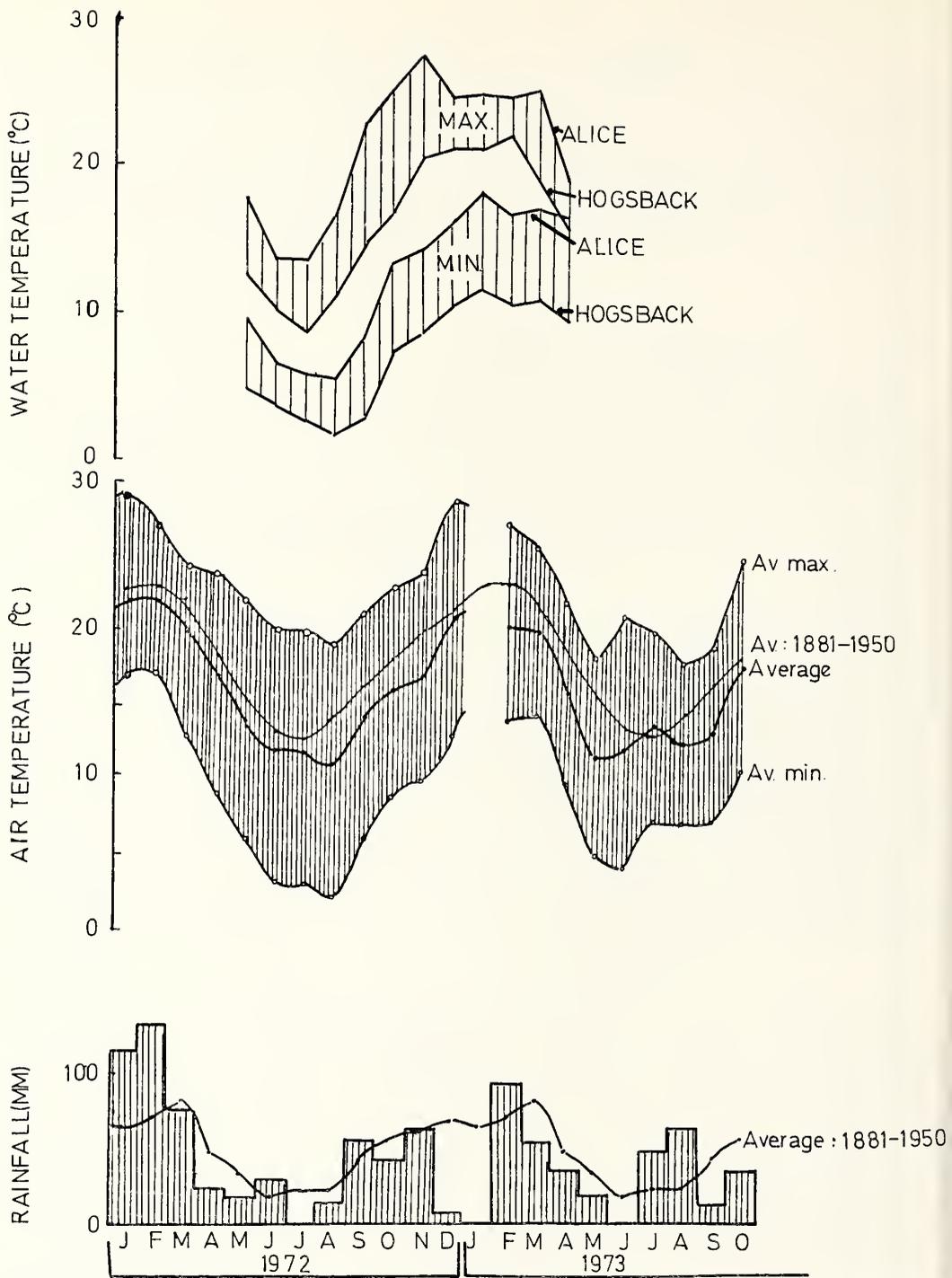


Fig. 2. Rainfall, air and water temperatures at Lovedale (sampling station 6) and water temperatures at Hogsback, 1972-73.

citrus plantations. Several weirs have been erected along the course of the river, damming up large stretches of water.

The rainfall season extends from September to April with maximum downpour from December to March (Fig. 2). Rainfall occurs mostly in the form of soft showers. It often snows on the Winterberg Mountains.

July is the coldest month and temperatures reach a maximum from December to February (Fig. 2). The area is characterized by extreme temperatures and sudden changes in temperature. Water temperatures were measured over a twelve month period with mercury remote thermographs at Hogsback and at Alice by the Zoology Department of Rhodes University (Fig. 2). At Alice it ranged from a minimum of 5,2°C in August, 1972 to a maximum of 27,5°C in November 1972. At Hogsback water temperature ranged from 1,7°C in August, 1972 to 22,0°C in February, 1973. Immediately below the escarpment (at collecting site 1, Fig. 1) the river is perennial and not subject to excessive floods (Fig. 3). Lower down the average monthly runoff is higher, but the river often stops flowing, even during the summer months. During periods of high rainfall the annual tributaries contribute large amounts of water to the river causing exceptional floods (Fig. 3).

Water analysis was done by Ntloko (1973) during 1970, and was therefore not repeated during this survey. He found that the river is free of pollution and that the water has the following physical and chemical composition at Lovedale (collecting site 6): pH: 6,2—8,2; conductivity: 65—362 mmhos, and oxygen: 6,1—7,9 ppm.

RESULTS

Distribution and habitat preference

B. trevelyani is abundant in certain habitats in the Tyume River from the town Alice up to the escarpment (Fig. 1). It was found to be most abundant in the lower half of this section, except in the last few kilometres above Alice where it is scarce. Only one specimen could be found at the collecting sites directly below the escarpment, and only after this part was sampled for a second time. The Tyume River between Alice and its confluence with the Keiskamma River was sampled thoroughly by the Zoology Department of the University of Fort Hare for a different project during 1969 and 1970, without finding any *B. trevelyani*. *B. trevelyani* was collected at three widely spaced sites in the Keiskamma River indicating that it still has a wide distribution in the upper reaches of this river too. It is obviously not abundant in the Keiskamma River because only a few specimens could be found at these three sites, and several other collecting sites yielded nothing.

In the Buffalo River *B. trevelyani* was only found in the river between the Maden and Rooikranz dams. None were found in the Nahoon River.

A survey of the upper reaches of the Fish and Kei Rivers proved that *B. trevelyani* is absent there.

B. trevelyani was found only in the main streams of all the rivers sampled. Several annual tributaries of the Tyume River were sampled when they were flowing, without success, during November, 1971. One tributary, the Gwali River, ceases to flow only during dry years, but even there none were found.

B. trevelyani prefers clear, perennial streams with a stony substratum. It was found mostly in depressions formed around large stones in or near the midstream of rapids. It also occurs in shallow pools with a sandy or rocky bottom, but was never found in deep lentic pools with clay or silt bottoms or in muddy sidepools. It maintained this habitat preference during all seasons of the year. It was never found in dammed up sections above weirs, of which the

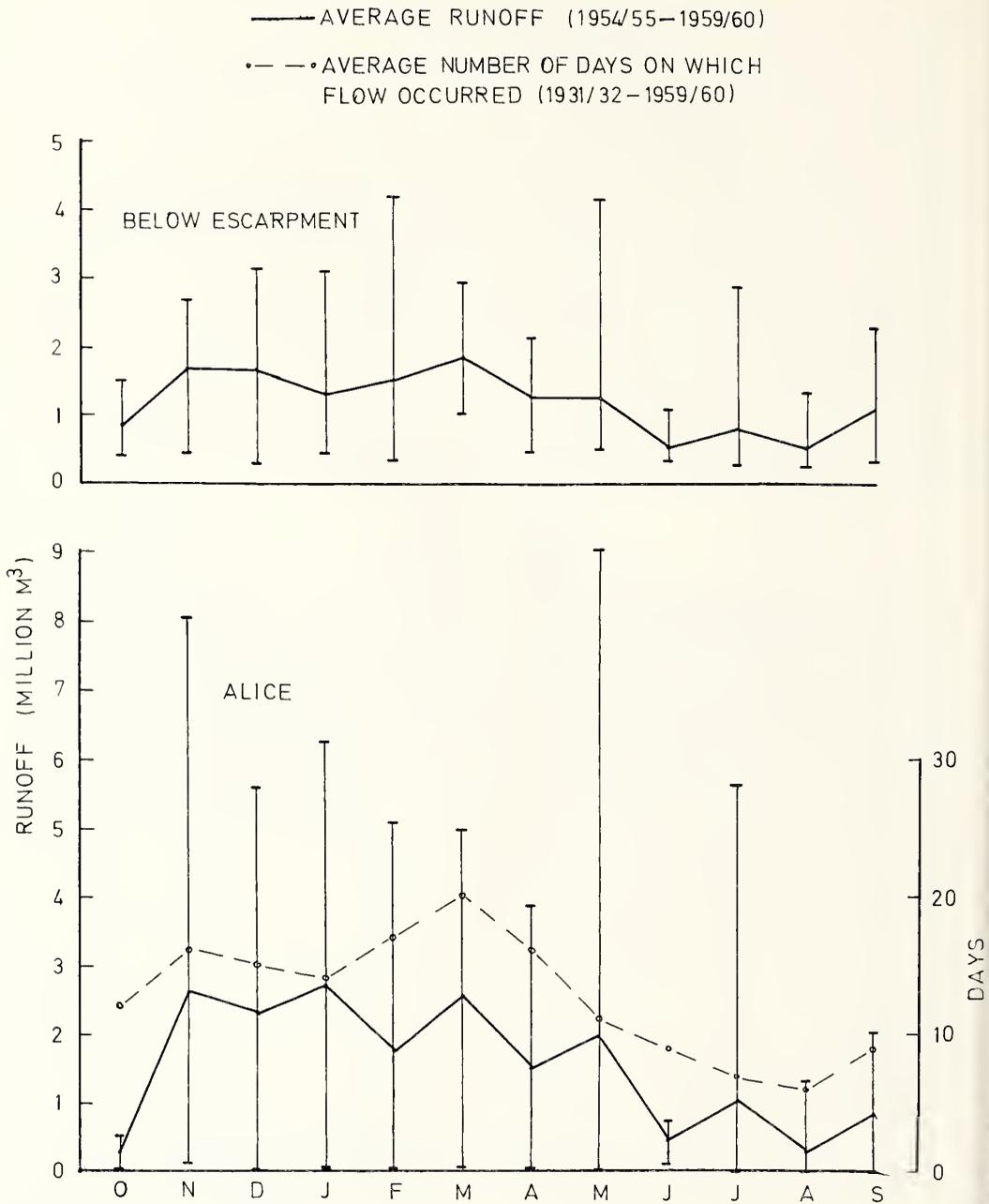


Fig. 3. Monthly runoff of the Tyume River at the town Alice and below the escarpment (at sampling station 1).

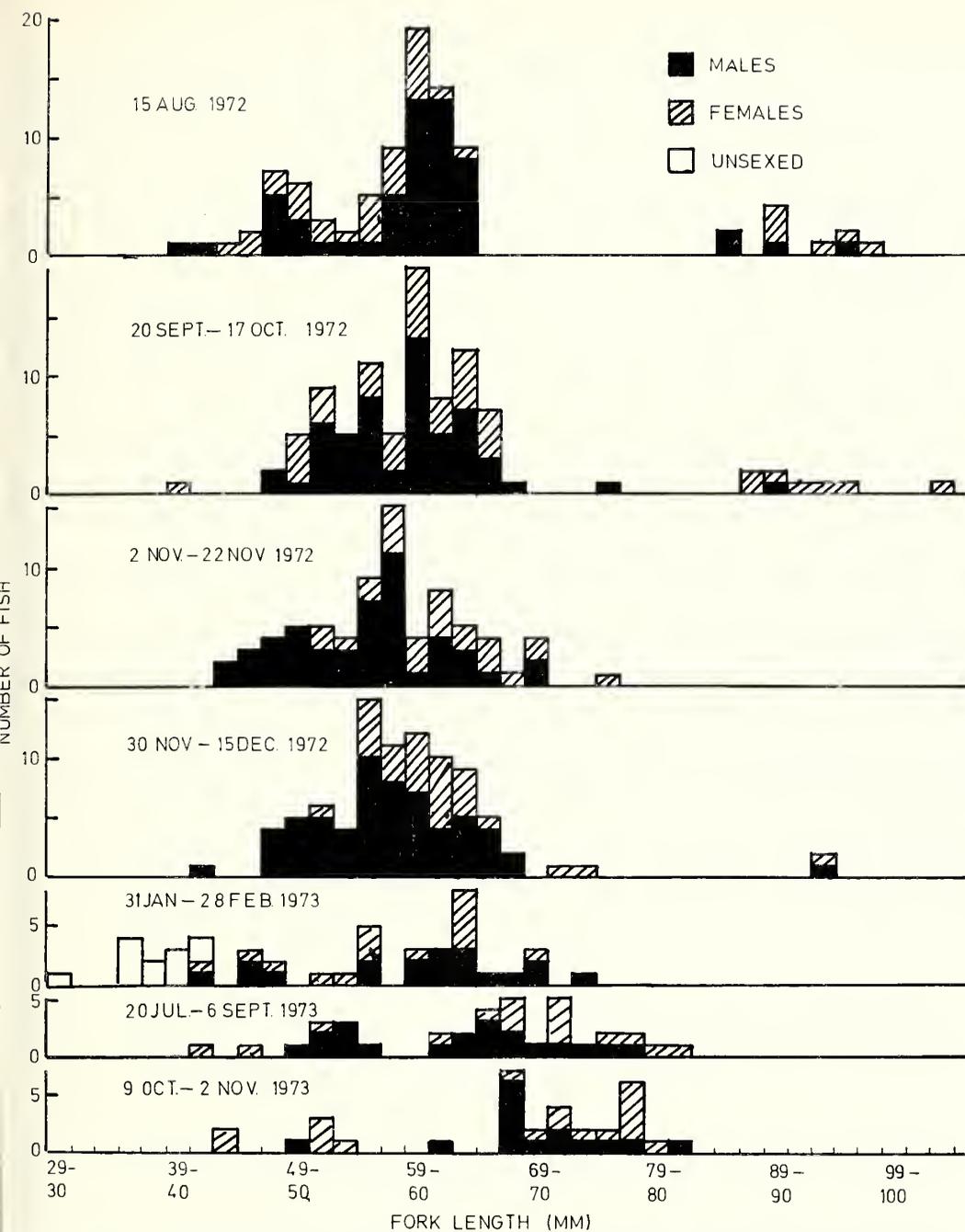


Fig. 4. Length frequency distributions of male and female *B. trevelyani* from the Tyume River, August, 1972 to November, 1973.

substratum is invariably silt-laden. The dependence of *B. trevelyani* on running water is also illustrated by its absence from the Maden and Rooikranz Dams, while it is abundant in the river between the two dams.

It probably frequents this stony midstream habitat mainly for protection against predators such as *Sandelia bainsii*, and because it is where its preferred food is found.

The minimum water temperatures at Hogsback and the maximum at Alice shown in Fig. 2 gives an indication of temperatures under which *B. trevelyani* is able to exist, as these

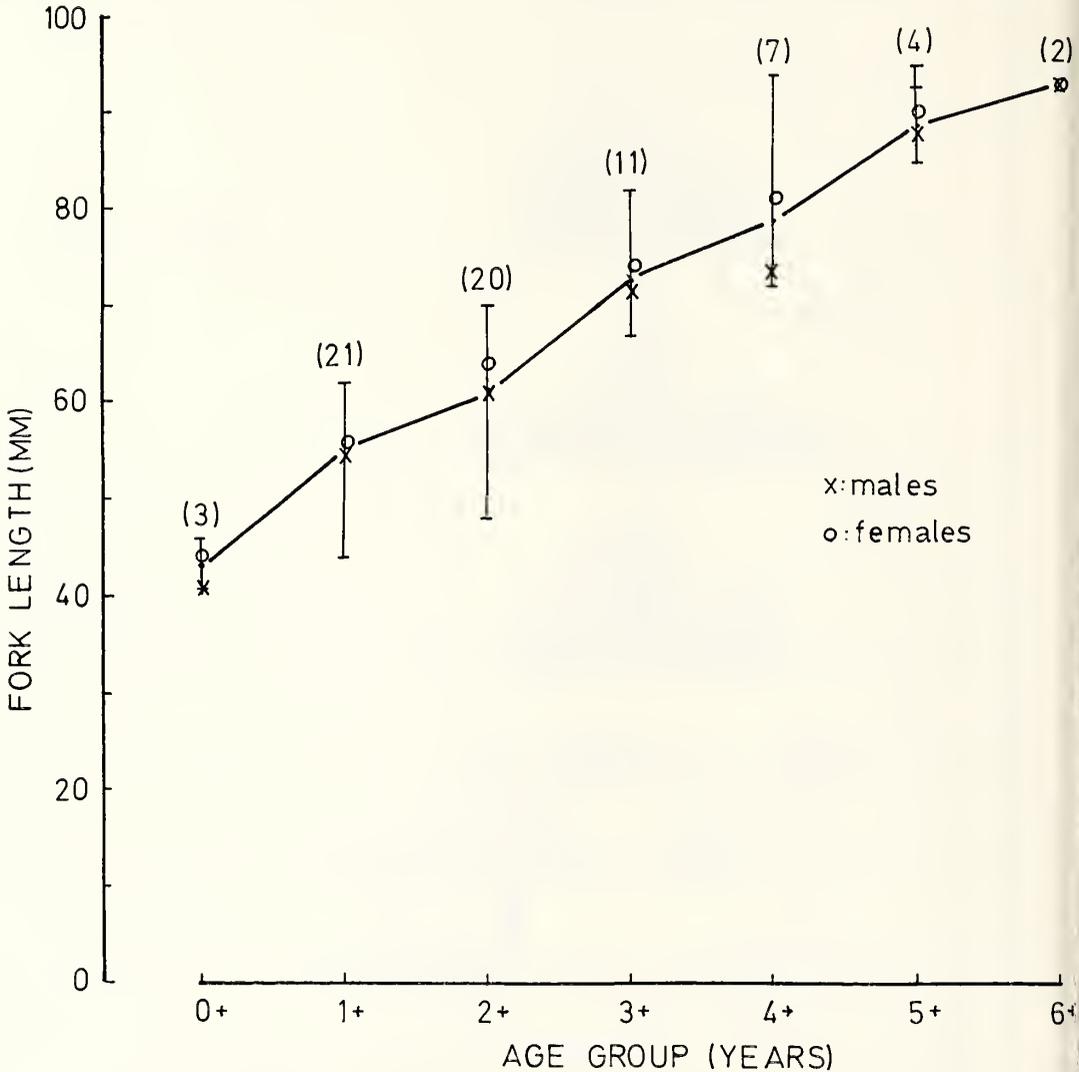


Fig. 5. Growth rate of *B. trevelyani* from the Tyume River.

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measurements were done above and just below its present range of distribution. This does not mean that *B. trevelyani* is not able to withstand temperatures outside this range because other factors already mentioned also limits its distribution. Its upper distribution is halted by the escarpment.

Sudden drops in water temperature, caused by untimely snow, probably causes largescale mortalities from time to time. This was illustrated as follows in March, 1974: It was very hot on the 16th March, (maximum air temperature: 31 °C at Alice). On the 17th March heavy snow fell on the Winterberg Mountains and the temperature at Alice dropped sharply (max: 17; min: 9). On the 18th heavy rain fell on the mountains causing the snow to melt and probably resulting in a sudden drop in water temperature. Sampling station 4 was visited on the 21st March when large numbers of dead *B. trevelyani* were found washed out on the banks. These were already partly dried out and must have been lying in the sun for a day or more. The only explanation for this mortality is that the fish were killed directly by the sudden inflow of cold water.

B. trevelyani was found singly or in shoals up to 25 in number. The shoals were of mixed sexes and consisted of fishes of varying sizes.

No attempt was made to determine the density of *B. trevelyani*. However, it is still the most abundant fish in the areas sampled. An indication of relative abundance is obtained from the numbers of different species collected from collecting site 4. All the fish were collected from a 550 m stretch of the river from August 1972 to October 1973 for ecological data. No attempt was made to remove all fish. During this period 466 *B. trevelyani* were collected together with 83 *S. bainsii*, 13 *Tilapia sparrmanii*, 11 *Salmo gairdneri* and one *Lepomis macrochirus*. Visser (1969) found 27 *B. trevelyani* together with 25 *S. bainsii* in a 710 m² and 42 *B. trevelyani* from a 300 m² surface area of water higher up in the Tyume River at collecting site 2. These figures must be interpreted with caution because *B. trevelyani* is stenoeicous and it is therefore only present in certain sections of the river.

Length frequencies and growth rate

No clear length groups can be distinguished in Figure 4 and therefore few conclusions can be made. The 1972 spawn appears in the graph for Jan./Feb. 1973. The largest fish collected was a female with a length of 103 mm. The graph does show a decline in percentage males with increase in length.

Figure 5 shows that *B. trevelyani* grow rapidly in their first year of life to a length of between 40 and 50 mm. Growth rate then decreases and remains approximately linear at least to their sixth year of life, when they are between 80 and 100 mm in length. The sample is too small for reliable comparison, but it seems as if females have a slightly faster growth rate than males.

REPRODUCTION

Sex ratio

TABLE 1. Sex ratios of *B. trevelyani* of different length groups from the Keiskamma River system, 1972—1973.

Length (mm)	Sample size	% Males
0—50	61	71
51—70	337	63
over 70	76	37
Total	474	60

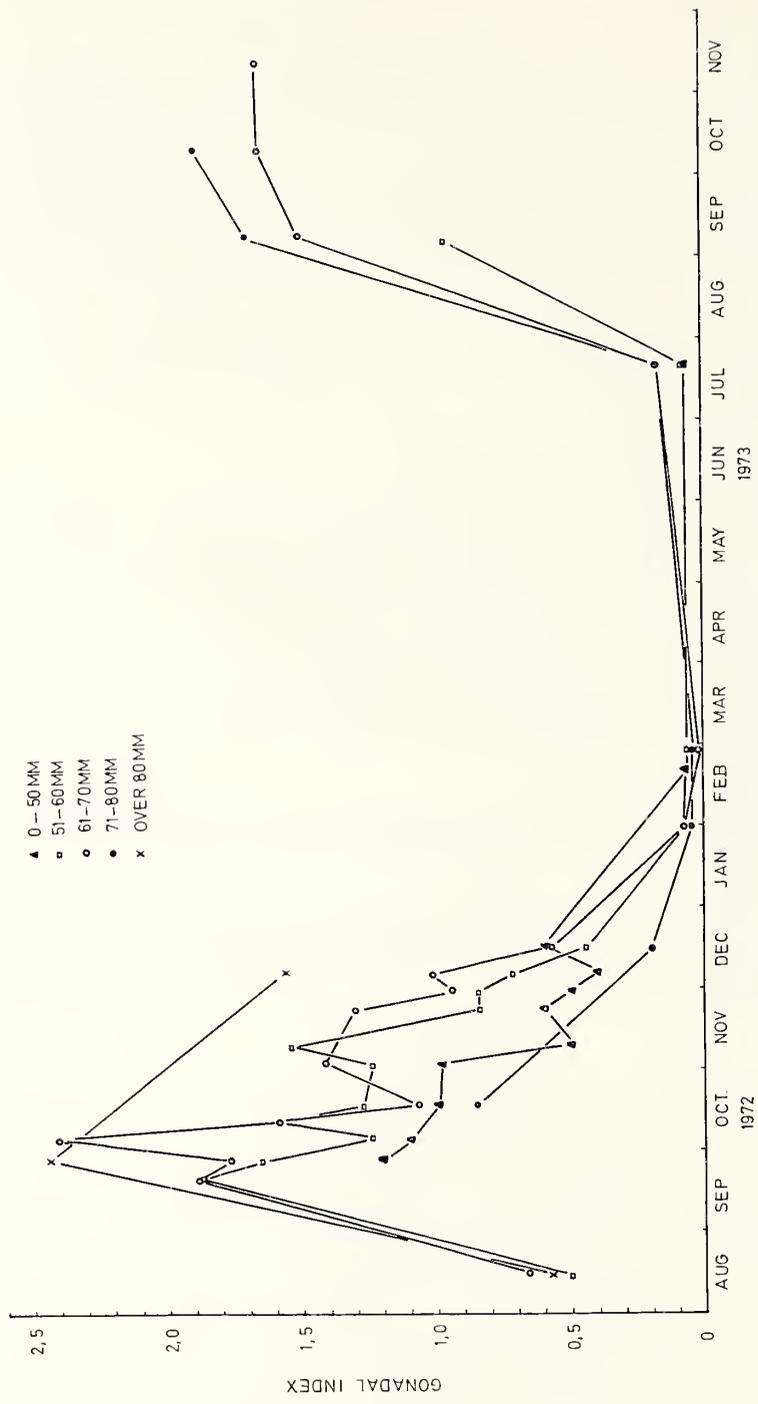


Fig. 6. Monthly change in average gonadal indices of different length groups of male *B. trevelyani* from the Tyume River, August, 1972 to November, 1973.

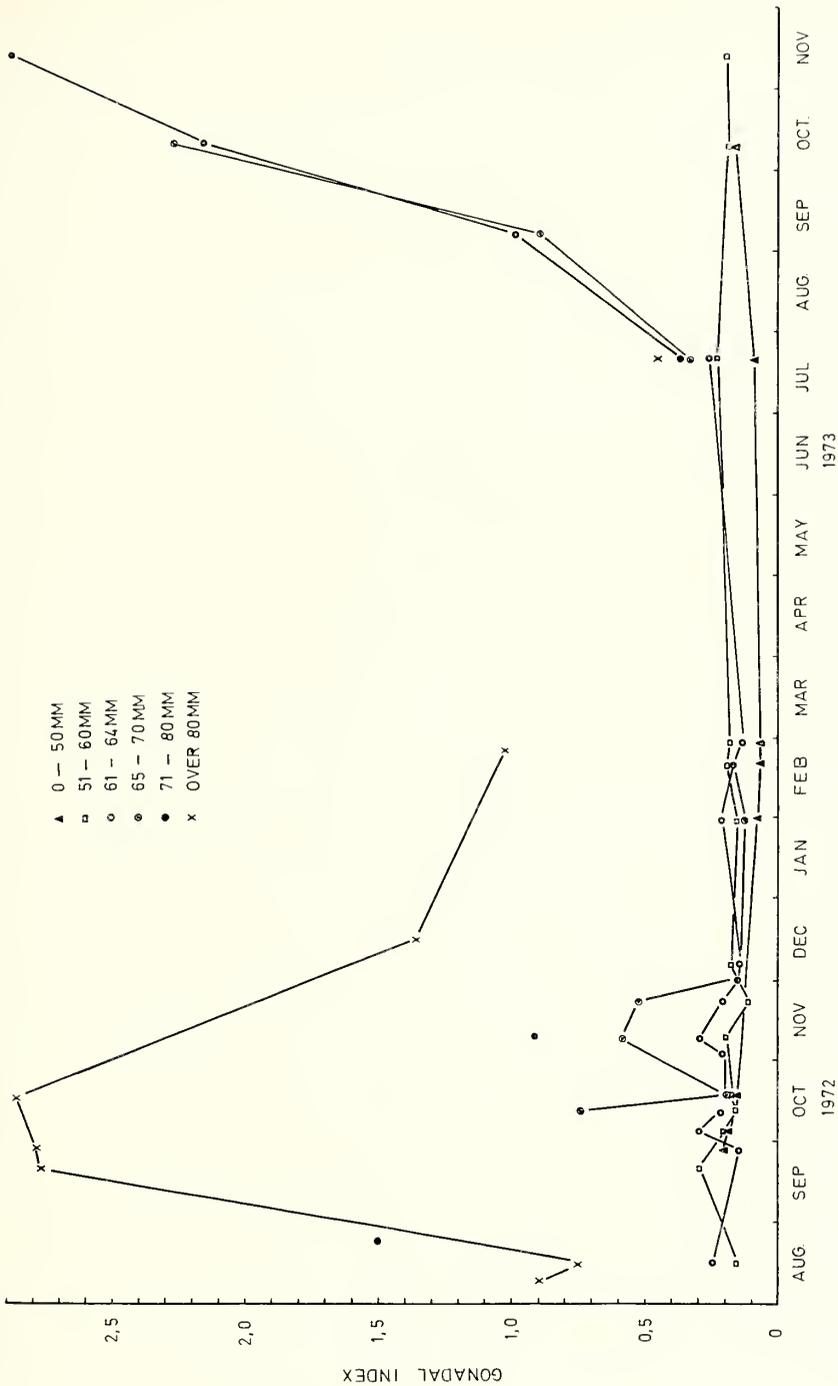


Fig. 7. Monthly change in average gonadal indices of different length groups of female *B. trevelyani* from the Tyume River, August, 1972 to November, 1973.

Sixty per cent of all specimens collected were males. This is in contrast to the expected ratio of 1:1. One would expect a ratio closer to 1:1 at least in smaller fishes, but 71% of fishes under 51 mm in length were males. Females probably have a higher survival rate than males because 63% of fishes over 70 mm in length were females.

Males turn slightly golden in colour during the breeding season, although not as strikingly as in *B. anoplus*.

Spawning season and length at sexual maturity

All the males collected in 1972 were sexually mature showing that they reach this stage at the end of their first year of life (Fig. 6). Females, however, only reach sexual maturity at the end of their third year of life, at a length of between 65 and 75 mm (Fig. 7). In some specimens of this length group gonads increased in weight without producing eggs, or producing only a few (10–20) small eggs.

Figures 6 and 7 show that spawning commences at the end of September. The gonadal indices of both sexes reached a peak at the end of September for all length groups, and then

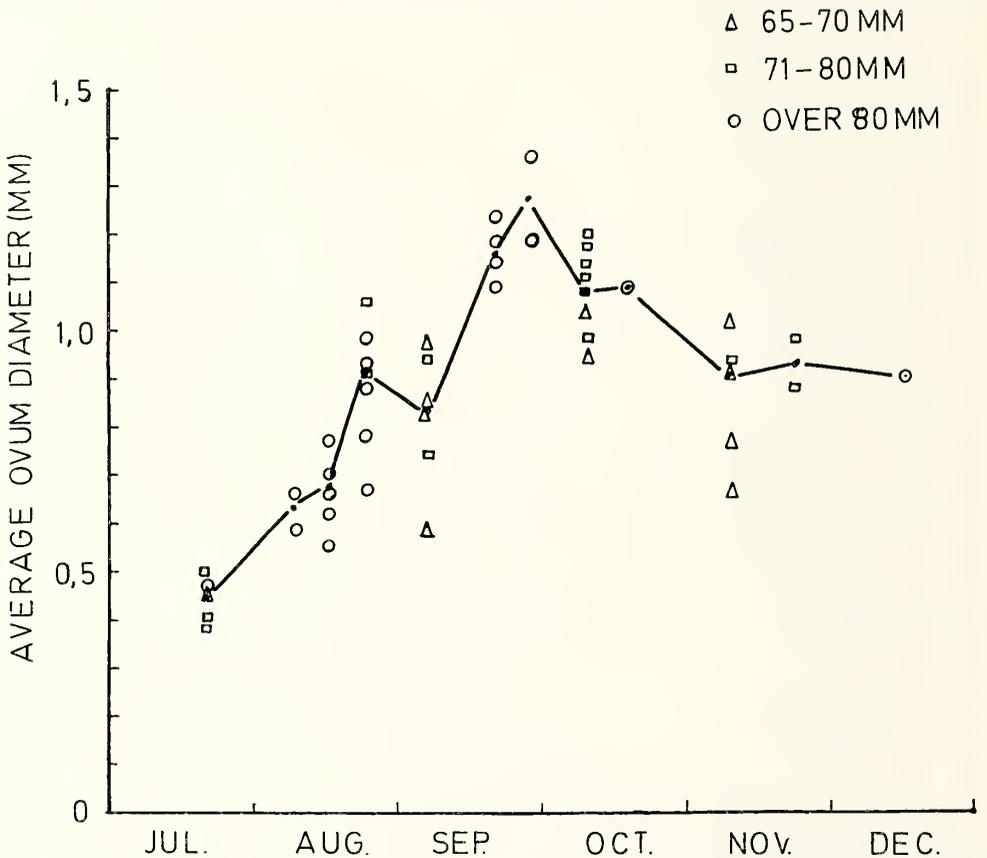


Fig. 8. Monthly change in average diameter of "large" ova of different length groups of *B. trevelyani* from the Tyume River, 1972-73.

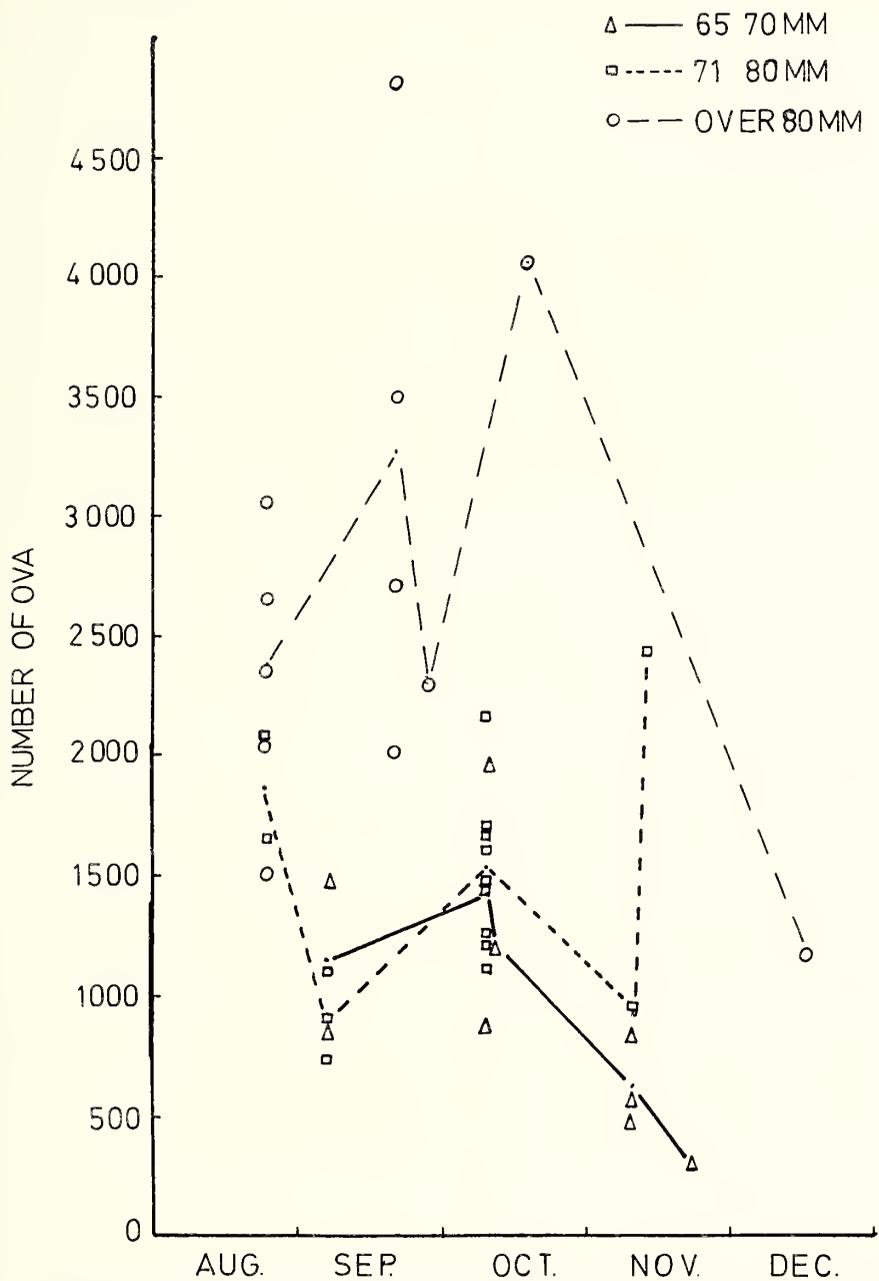


Fig. 9. Monthly change in average number of ova per female of different length groups of *B. trevelyani* from the Tyume River, 1972-73.

gradually declined to reach a minimum in February or March. This finding is substantiated by a maximum ovum diameter in Sept/Oct. (Fig. 8), and, less clearly, by maximum numbers of ova per female for the same period (Fig. 9).

Sept./Oct. is obviously the peak spawning period, but it is not clear, from the available data, whether each female spawns once or more than once each season. The variation in ovum size, gradual decline in gonadal index, length-frequency data and change in average

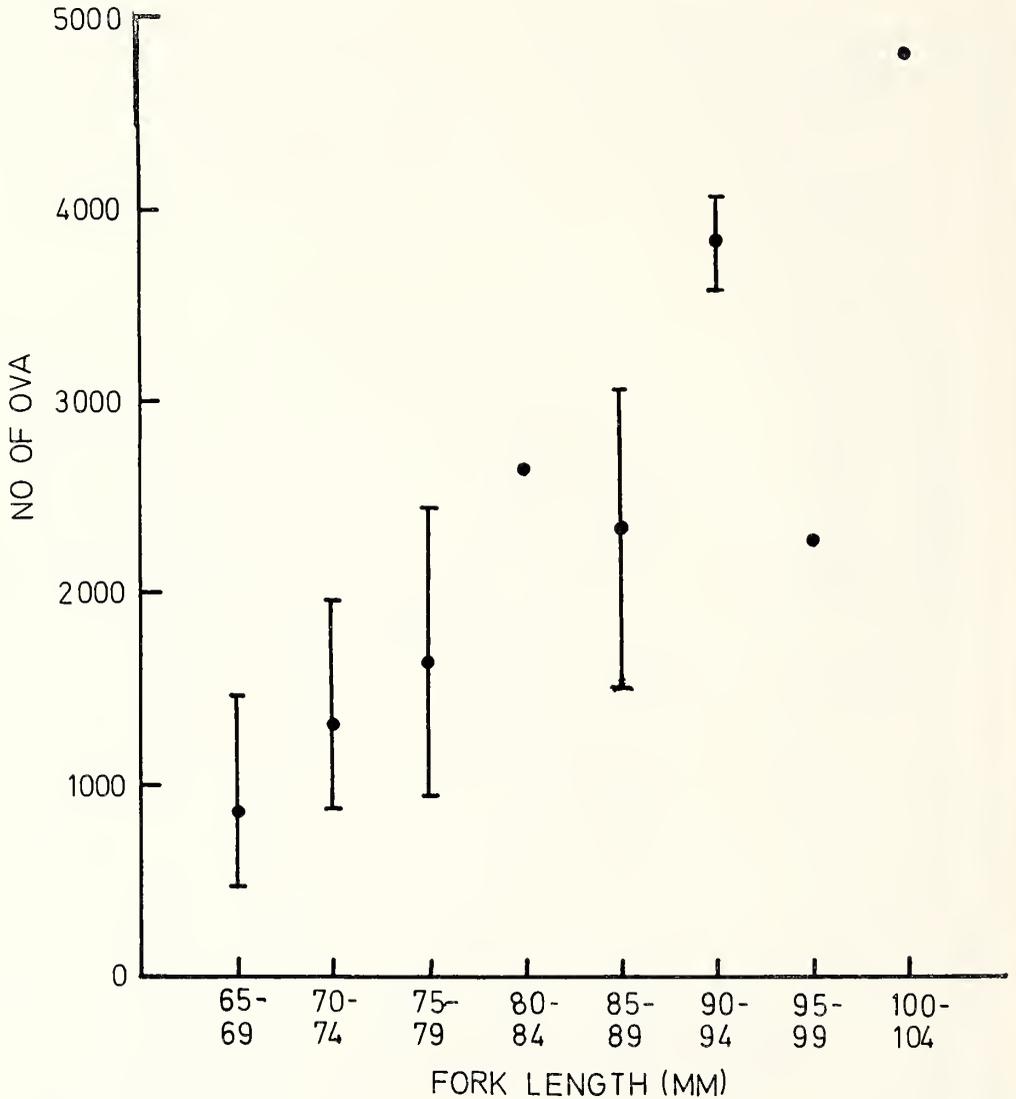


Fig. 10. Relationship between fecundity and fork length of *B. trevelyani* from the Tyume River.

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ova number indicate that each female spawns several times in a season. However, more data is necessary to substantiate this.

Spawning behaviour was not observed, but the nature of its habitat and the following data indicate that *B. trevelyani* spawns in the midstream (on gravel beds as *B. holubi*?) and not on floodplains or submerged plants: No upstream migrations were observed. After the first floods in September and October, 1972 *B. trevelyani* was still present in its preferred habitat. None were found below a cataract or a weir at collecting site 4, both impassable to minnows. If upstream migration took place after the first floods, then one would expect a crowding of fish at these sites.

Fecundity

Fecundity increases with increase in length from an average of about 900 in fish of 65 to 69 cm in length, to between 4 000 and 5 000 for fish over 100 mm in length (Fig. 10). Decrease of life expectancy, and the average length, due to predation by trout or other causes thus has a great influence on the population fecundity, and therefore the survival of *B. trevelyani*.

Food habits (Table 2)

B. trevelyani feeds mainly on aquatic insect nymphs and larvae. Ephemeroptera nymphs was by far the most important food item in the 40 stomachs containing food. It occurred in 87,5% of the stomachs and made up 64,9% of the estimated bulk. It also feeds on terrestrial insects (Hymenoptera and Isoptera in this sample) and bits of aquatic and terrestrial plant material. The plant material consisted of seeds (mostly grass), bits of leaves and filamentous algae. Although plant material was present in 30% of the stomach contents, it only made up 6,6% of the estimated bulk. These bits were probably taken accidentally in its search for animal food. One stomach contained a few grains of sand and a few small nematode parasites were present in two.

The stomachs contained very little food (average weight 0,005 g, range: 0,001—0,016 g) and 44 of the 84 stomachs analysed were empty. All the stomachs were collected between October and November between 0900 and 1200h.

These results show that *B. trevelyani* competes with young trout for food where these are present.

TABLE 2. Food habits of 40 *B. trevelyani* from the Tyume River

<i>Food item</i>	<i>Est. % of weight</i>	<i>% Fr. of occ.</i>	<i>% Dominance</i>
Ephemeroptera nymphs	64,9	87,5	75,0
Chironomidae larvae	14,9	32,5	12,5
Plant material	6,6	30,0	2,5
Terrestrial insects	5,0	12,5	2,5
Simuliidae larvae	0,2	5,0	0
Unid. insects	8,6	10,0	7,5

Tuberculation

Minute tubercles occur in both males and females of *B. trevelyani*, but are much smaller than those of the males of certain other minnows such as *B. motebensis* and *B. burchelli*.

147 Specimens were examined, and their tubercles classified as very small, moderately developed, or well developed. All specimens examined had tubercles, although in some the tubercles were only visible under high magnification.

Tubercles are better developed in males than in females. In 88 males collected between August and February, 25 had very small, 17 moderately developed, and 46 well developed tubercles. Only 3 of 37 females collected during the same period, had well developed, and nine moderately developed tubercles.

Tubercles are best developed during the spawning season. Tubercles were present in specimens of both sexes collected during July, but were much smaller than in specimens collected during the summer months. There is no clear relationship between fish size and tubercle development. Several immature females had moderately, and one had well-developed tubercles.

In well-tubercled specimens the tubercles cover the dorsal and lateral sides of the head, and the body above the lateral line becoming less numerous towards the caudal fin. Tubercles are also present on the dorsal side of the pectoral fin and occasionally on the dorsal fin.

According to Wiley and Collette (1970) who did a thorough study of tuberculation in fishes, tubercles are epidermal structures that function primarily in facilitating contact between individuals during spawning. They are used by some species for defence of nests and territories and perhaps for stimulation of females in breeding.

Parasites

Only two parasite types were found in *B. trevelyani* namely a few small nematodes (in the stomachs of two specimens) and "black spot" caused by the metacercaria of a trematode in the skin of most specimens from the Tyume River. The black spots are similar in appearance to those caused by the genus *Neascus* in European fishes. Only two of 18 specimens collected from the Keiskamma River each had one metacercaria in the skin. Metacercariae were abundant in the integument of *B. trevelyani* from collecting site 4 in the Tyume River. The metacercaria in 125 specimens from this site were counted and the results are shown in Figure 11. There is an increase in infection with increase in length and all specimens over 80 mm in length contained at least two metacercariae. Specimens with more than seven parasites were all over 60 mm in length and specimens less than 50 mm in length all had less than 5 metacercariae. Most fish had from 0 to 3 parasites, but infection could be very high, and one specimen with a length of 75 mm contained no less than 99 metacercariae. The high rate of infection in the Tyume River indicates that this population is not as healthy as it should be.

THE INFLUENCE OF OTHER SPECIES ON *B. TREVELYANI*

Trout

Jubb (*in litt*) found eleven specimens of *B. trevelyani* in the stomach of a large rainbow trout collected from the top end of the Rooikranz dam, which clearly shows that trout do feed on *B. trevelyani*. During this survey, trout were collected together with *B. trevelyani* at three different sites. The stomach contents of five large trout (20, 21, 25, 26 and 29 cm in length) from these sites were analysed. The stomachs contained no fish material and the contents consisted of a variety of other organisms such as aquatic insects, crabs, a frog and some terrestrial insects.

Trout is well established in the Tyume River and spawns naturally. It is abundant in the upper reaches where it is a hazard to *B. trevelyani* through predation and competition for food. *B. trevelyani* is able to avoid predation by *Sandelia bainsii* to a certain extent through its habitat preference, but trout frequents the same habitat and therefore probably has a greater impact.

Sandelia bainsii

S. bainsii is the most abundant fish occurring together with *B. trevelyani* in the Tyume River. Although the two species are sometimes found together, *S. bainsii* prefers a different ha-

bitat, and is mostly found in sidepools or deep midstream pools. Stomach contents of *S. bairnsii* were not analysed, but aquarium studies showed that it does feed on *B. trevelyani*. Specimens of *B. trevelyani* were invariably consumed if placed in an aquarium together with large *S. bairnsii*.

Due to habitat difference *S. bairnsii* probably does not have a great impact on *B. trevelyani* under normal conditions. However, if runoff diminishes, or if flow ceases, *B. trevelyani* is forced to enter the habitat of *S. bairnsii* where it is then more vulnerable.

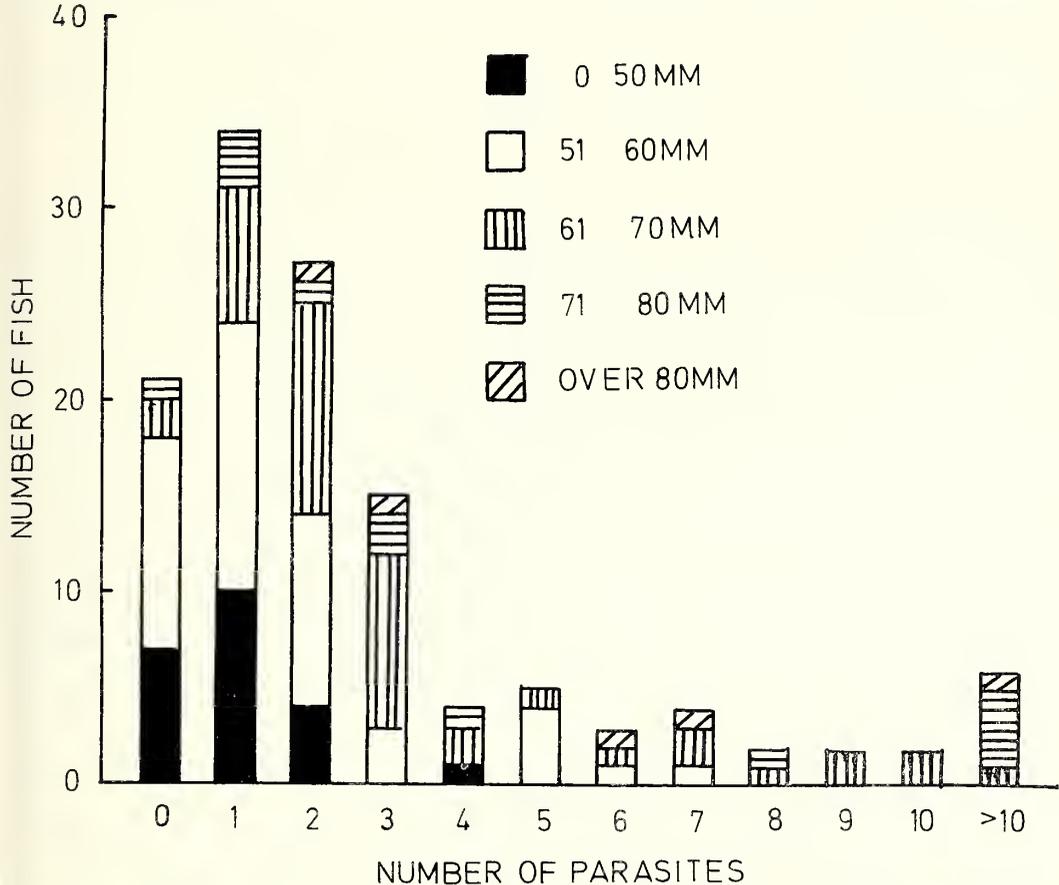


Fig. 11. Frequency of occurrence of "black spot" metacercariae in *B. trevelyani* from the Tyume River, 1972-1973.

Barbus anoplus

B. anoplus is abundant in the Buffalo River between the Maden and Rooikranz Dams together with *B. trevelyani*, showing that these two species are able to occur and thrive together. It is therefore strange that no *B. anoplus* was found in the Keiskamma and Tyume Rivers. A single population of *B. anoplus* was found in a small earthen dam adjacent to the Gwali River, a tributary of the Tyume River (Fig. 1). Although it was not found in the Gwali

River, it probably occurs there too as the pond is filled from the Gwali River, and dries up from time to time.

Other species

Few *Anguilla mossambica* were collected, but it has a wide distribution and often occurs in the same habitat as *B. trevelyani*. Large specimens probably, to a certain extent, feed on *B. trevelyani*.

Both *Tilapia sparrmanii* and *Lepomis macrochirus* are rare and were only found in pools that are not frequented by *B. trevelyani*.

Labeo mbratus is abundant in the Tyume River below collecting site 5 (Fig. 1). Its upper distribution range overlaps that of *B. trevelyani*, but in this area it is relatively rare, and mainly confined to a habitat not frequented by *B. trevelyani*.

DISCUSSION

The objective of this study was to determine which factors are responsible for the limited distribution of *B. trevelyani*. An initial survey showed that it has a wide distribution in the upper reaches of the Keiskamma River system, and that it is still relatively abundant in certain habitats in the Tyume River between Alice and the escarpment. From this it might seem that concern for the existence of *B. trevelyani* has been overrated. A study of its ecology showed, however, that this is definitely not the case and that this unique species is actually in grave danger of extinction.

Where still found, the Tyume River is obviously at the moment the most suitable of the three rivers for *B. trevelyani*. Even here its survival is increasingly endangered by silting, damming, water extraction and predation. Combined with these factors, extreme climatic conditions, that are characteristic for this area, can also cause great mortalities.

Factors causing the decline of *B. trevelyani* cannot be halted as they go hand in hand with agricultural and industrial development. The following is therefore recommended:

1. That part of the rivers in which *B. trevelyani* occurs be proclaimed conservation areas. Gaigher (1970) proposed that the Buffalo River between the Maden and Rooikranz Dams be proclaimed a reserve for this fish. Being one of the few remaining conserved river catchments in the eastern Cape, this is probably the most suitable site, in the present distribution range of *B. trevelyani*. However, as pointed out by Gaigher (1970) this site is also threatened by a plan to raise the wall of the Rooikranz Dam. No other site will be suitable for a reserve in the long run because of factors already mentioned.
2. An intensive study of all aspects of the biology of *B. trevelyani* while sufficient material is still available.
3. An investigation of the possibility of stocking rivers in more suitable areas with *B. trevelyani*.

ACKNOWLEDGEMENTS

The author is greatly indebted to the following:

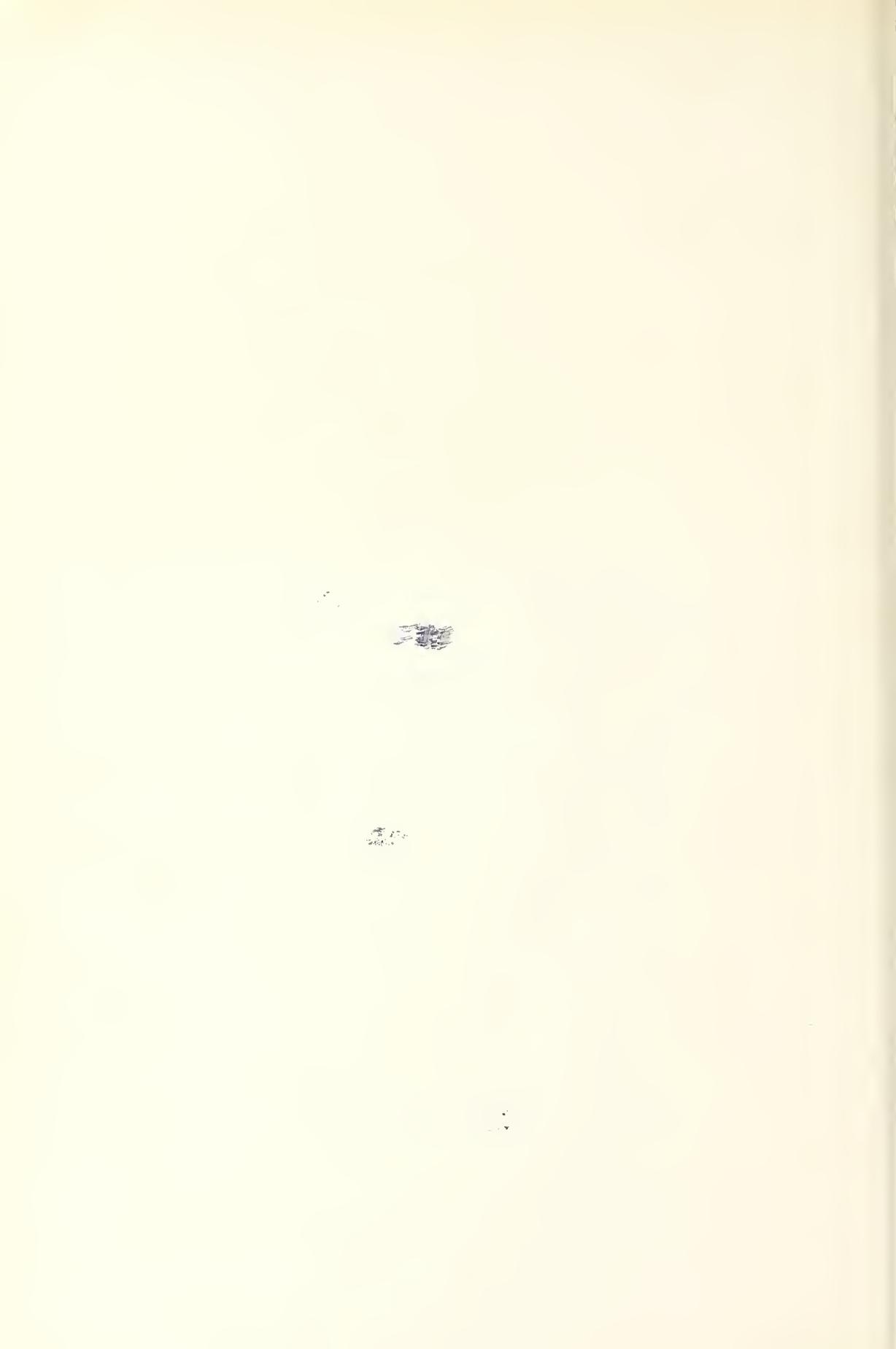
The Council of the University of Fort Hare for permission and facilities to do the study; Professor R. A. van den Berg, Head of the Department of Zoology for his guidance; Mr. D. P. Baird for his help with fieldwork and for valuable discussions; Mr. B. C. Wilmot of the Albany Museum for water temperature data; Mr. P. H. Skelton of the Albany Museum who kindly read this paper; Messrs. P. Kekana and J. Jemar for their assistance during fieldwork.

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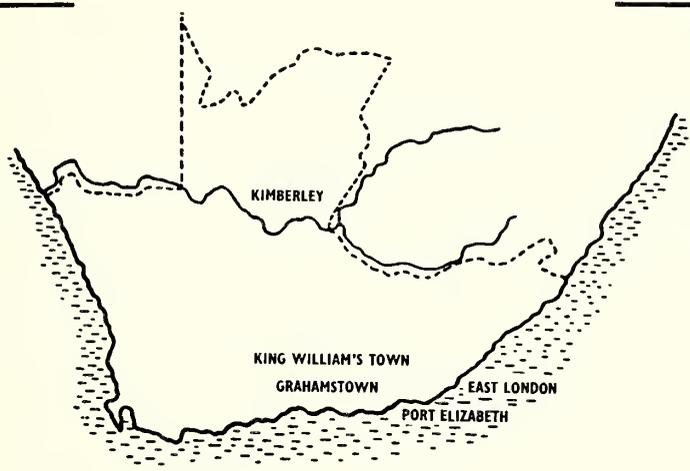


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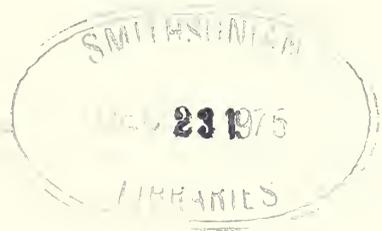
VOLUME 11 • PART 2

30th September 1975

PUBLISHED JOINTLY BY THE

CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN

SOUTH AFRICA



Ethological studies of *Bembecinus cinguliger* (Smith) and *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae), two southern African turret-building wasps.

by

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INTRODUCTION

The ethology of some species of *Bembecinus* Costa, a genus distributed throughout the warmer regions of the world, has in recent years been reviewed by Evans (1955: 295—302 and 1966: 132—143). That author drew attention to the uniformity exhibited by the ethology of those species which had been investigated up to those dates. In a very recent publication by Evans and Matthews (1974: 131) it was again stated that "little diversity in behavior has been demonstrated within the genus". African species have received scant attention and, other than for a record of the prey of a single species (Bridwell, 1937, cited by Evans, 1966: 142), the published information concerning biology is limited to some general remarks by Brauns (1911: 92).

The present paper is concerned with some aspects of the ethology of two southern African species, *B. cinguliger* (Smith) and *B. oxydoreus* (Handl.), which, by lacking the tarsal comb or sand rake usually associated with the fore-legs of these wasps, differ from other African species and indeed, as far as can be ascertained, from all other species of the genus. Correlated with this difference in the structure of the fore-legs is a marked difference in the nature of the soil in which nesting takes place and in the manner in which the subterranean burrow is excavated by the wasps.

Techniques adopted by the authors for examining the subterranean burrow are not discussed here, being similar in most respects to those described previously (Gess and Gess, 1974: 118—119).

GEOGRAPHIC DISTRIBUTIONS

The distributions of both *B. cinguliger* and *B. oxydoreus* appear to be restricted to southern Africa. As far as can be judged from available records *B. cinguliger* is confined to the southern parts of the Cape Province, whereas *B. oxydoreus* which occurs together with *cinguliger* in at least part of the latter's range (the Eastern Cape Province) is far more widely spread, occurring also in the Cape Province north of the Orange River, in Lesotho (formerly Basutoland), the Orange Free State, the Transvaal and Rhodesia. Actual localities of specimens of the two species in the Albany Museum collection are listed below.

B. cinguliger (Smith)

Alice, Alicedale (New Year's Dam), Carlisle Bridge, Ceres, Fullarton, Grahamstown (Hilton, Hounslow, Strowan and Table Farm), near Klipfontein, near Lake Mentz, Tarkastad, Thorngrove (N of Cookhouse), Waterford and Willowmore (all Cape Province). The species probably occurs also at Bloutoring Station (between Touws River and Ladismith) for wasps observed nesting there by the senior author in December, 1962, are believed to have been this species.

B. oxydoreus (Handl.)

Fort Brown, Grahamstown (Hilton), Kimberley, Koonap River (17 miles from Adelaide on Grahamstown road), Queenstown, Willowmore (all Cape Province); Tlametlu River (Lesotho); Aldam, Kroonstad, Senekal (all Orange Free State); Pretoria (Transvaal); Bulawayo (Rhodesia). Other localities from which this species has been recorded include Dunbrody (Cape Province) (Cameron, 1905: 323, as *Stizus Johannis* Cam.) and Bothaville (Orange Free State) (Arnold, 1929: 292).

Flight periods as indicated by the above specimens are October to March for *B. cinguliger* and December to April for *B. oxydoreus*.

LOCALITY AND DESCRIPTION OF NESTING SITES

Field observations in the present study were conducted at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S, 26° 32'E) in the Albany Division of the Eastern Cape Province of South Africa. Lying within the region of overlap in the distribution of the two *Bembecinus* species this locality is well suited to an investigation of these wasps. An account of the climate and vegetation of Hilton has previously been given (Gess and Gess, 1974: 191—192). Most of the observations were made during the summer of 1973—74 but certain observations dating from previous nesting seasons and also from the summer of 1974—75 have been included.

B. cinguliger and *B. oxydoreus* at Hilton showed the same preferences with respect to nesting sites and indeed were in some instances found nesting together. Nesting sites were



Plate 1. Hilton, 6.xi.1973. A nesting site of *B. cinguliger* (Smith)
Plate 2. Hilton, 11 iii.1974. A nesting site of *B. oxydorcus* (Handl.).

without exception found to be localized patches of bare earth occurring in low-lying areas sparsely covered by small, low-growing shrubs, mostly *Pentzia incana* (Th.) O.Ktze (Compositae) (Plates 1 and 2). The soil, derived from the Dwyka Series, was of a reddish brown clayey nature and contained no stones. In all cases nesting sites were found to be situated close to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies and shallow furrows.

Both species were found to nest in pseudo-colonies which might, particularly in the case of *B. cinguliger*, become very populous with nest entrances situated close together. Excavation in the soil of a nesting area was found to bring to light many decapped *Bembecinus* cocoons dating from past nesting seasons, indicating the repeated use of the same nesting areas by successive generations of these wasps, a phenomenon made possible by the very slow regeneration of the plant cover of a denuded area.

FLIGHT SEASONS, MATING DANCE, PERIOD OF ACTIVITY OF ADULT WASPS AT THE NESTING SITES AND ADULT SLEEPING HABITS

The pattern of the build-up and subsequent decline in the numbers of the adult population of one of the species, *B. cinguliger*, at Hilton during a previous summer, that of 1970—71, was established as a by-product of the use of three Malaise traps of the pattern designed by Townes (1972). In the graph (Fig. 1) the average numbers of specimens caught per day between successive clearings of the traps' collecting jars are plotted at points midway in time between the dates of clearing during the four-month period November to February. During this period a total of 1248 specimens (152 males and 1096 females) was captured. Though trapping was continued for a full twelve months, the only occurrence of *B. cinguliger* in the catch was during the above four-month period, clearly showing that the species is univoltine. That the species is proterandrous and that females are present in the field longer than are males, as is clearly indicated in the graph, was borne out by the 1973—74 field observations. Thus the first sighting of a male of that season was on 3.xi.1973 but the first sighting of a female was not until 14.xi.1973. The dates of emergence appear to be remarkably consistent in successive years. Thus during the 1974—75 nesting season first sightings of males and of females were on 8.xi.1974 and on 15.xi.1974, respectively.

No specimens of *B. oxydorcus* were caught in the Malaise trap. Field observations at Hilton during 1973—74 indicate that the flight period of this species starts later in the summer than does that of *B. cinguliger* and that this species is also proterandrous. Thus the first sighting of the season for males was on 2.i.1974 and the first sighting of a female on 7.i.1974.

The end of the 1973—74 flight season of *B. cinguliger* was during mid-March, the last sign of activity being observed on 13.iii.1974; the flight season of *B. oxydorcus* had not yet ended when field work was discontinued on 18.iv.1974.

Although *B. cinguliger* is still flying when *B. oxydorcus* starts nesting and although *B. cinguliger* and *B. oxydorcus* in some cases use the same nesting areas there is little direct competition between them as when nesting in *B. oxydorcus* is reaching its height that of *B. cinguliger* is rapidly falling off. It will be seen from a graph (Fig. 1) that the decline in nesting activity of *B. cinguliger* corresponds with a decline in the number of individuals following a peak in mid-December.

During the early part of the flight season of *B. cinguliger*, from the time of male emergence and lasting through the period of female emergence until some time after the initiation of the season's first nests, the newly emerged wasps execute what the Raus (1918: 9—17), writing about *Bembix nubilipennis* Cresson, so elegantly termed a "sun-dance".

In *B. cinguliger* this activity takes place at the bare patches of earth utilized for nesting by this wasp during season after season. It consists essentially of the proterandrous males patrol-

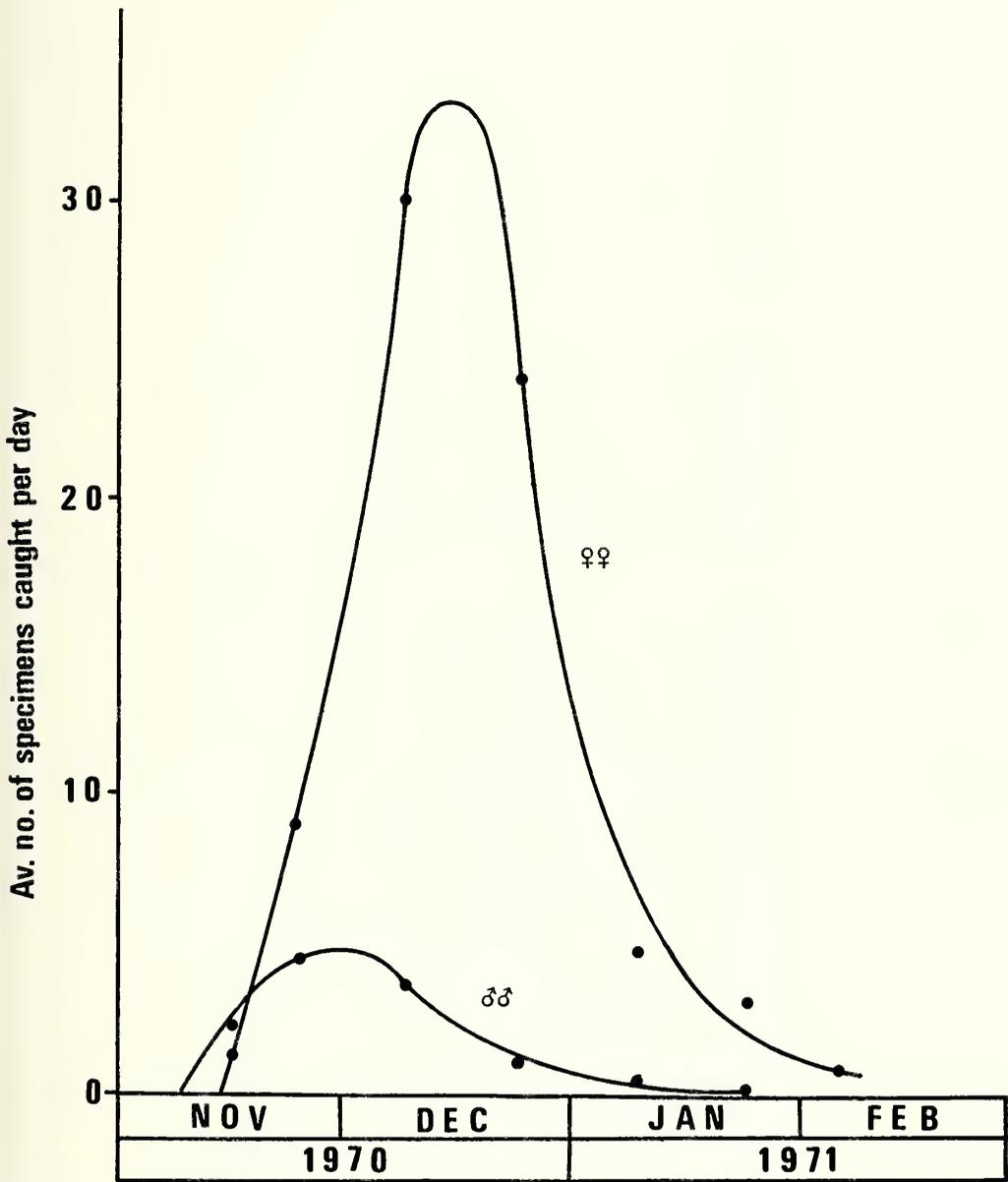


Fig. 1. Graph showing the average numbers of specimens of *Bembecinus cinguliger* (Smith) caught per day by three Malaise Traps at Hilton during the period Nov. 1970 to Feb. 1971.

ling these areas by flying on an irregular path within the confines of the bare patch at a height of 2—8 cm above the ground. When uninfluenced by other individuals, a male executes a slight up and down bobbing movement while flying along his path. However, whenever another individual is spotted the male flies rapidly towards it and the two individuals, possibly joined by further individuals, fly rapidly around each other, sometimes bumping into each other, before resuming their separate flightpaths. Each individual from time to time settles on the ground where it rests with wings folded over the back. An individual flying past causes the settled male to rise up immediately and to follow it, a reaction brought about also by the passage across the dancing area of wasps of other species and even by inanimate objects. Thus the authors found that small objects thrown across the bare area at a low height above the ground were immediately followed by several males, attracted to the objects from their patrolling flights or from their situations on the ground. A distinct humming sound is produced by the wasps flying about in numbers. It is clear that the activity of the males is directed towards locating and mating with the females as these emerge from the ground. Some days after the "dancing" has commenced and at a time when females have emerged, attempts at copulation may be witnessed between dancing wasps. Occasionally successfully copulating pairs may be seen to rise up together to a greater height above the ground and to fly off into the low bushes fringing the bare areas.

The above described "sun-dance" is a very noticeable feature of the beginning of the flight season of *B. cinguliger* at Hilton and has been noticed over a period of five or six years. However, no such activity has been noted for *B. oxydorcus*, probably due to the fact that this species occurs in so much smaller numbers. Clearly the existence of a "sun-dance" in certain species of wasps is dependent upon the formation by these wasps of pseudo-colonies situated in definite nesting areas. Similarly, the level of activity and therefore the degree to which it is noticed is dependent upon the number of individuals participating in the "dancing" which in turn is dependent upon the density of nests within a pseudo-colony.

Activity of the adult wasps at or near the nesting sites was found to be restricted to the hottest part of the day from late mid-morning until early afternoon.

Neither *B. cinguliger* nor *B. oxydorcus* was found to spend the night in the nest, for nests inspected early or late in the day never contained adult wasps. Similarly, wasps were not found sheltering in the nests during the day if the weather was unsuitable for normal nesting activities. Indeed, adult wasps were absent from the nesting areas and not only from the nests themselves during these times.

As reported previously by Brauns (1911: 92) *B. cinguliger* (recorded by Brauns as *Stizus clavicornis* Handl.) is in the habit of forming sleeping clusters. Brauns at Willowmore (Cape Province) reported large assemblages of several thousand individuals, mostly females, forming clusters the size of a small child's head on bushes and low plants growing in sheltered localities.

Jacot-Guillarmod (pers. comm., 1973) reported seeing such a sleeping cluster at Hilton on the evening of 5.xii.1964. A sample taken at the time and now in the Albany Museum collection consists of 62 females and 36 males.

During the present study at Hilton, an extensive search by the authors of a wide area, including the type of situation in which Jacot-Guillarmod made his observation, led to the discovery on the morning of 11.i.1974 of a single sleeping cluster of *B. cinguliger*. Subsequent discussions with Jacot-Guillarmod led to the conclusion that the situation of the present sleeping cluster was virtually identical with that of 1964.

The present sleeping cluster was situated within a large tussock of the coarse grass, *Digitaria macroglossa* Henr., growing on the edge of the bank of a narrow, incised water-course which at the time of discovery contained no water (Plates 3 and 4). The thousands of individuals clustered in the centre of the tussock exhibited no particular orientation except in



Plates 3 and 4. Hilton, 14.i.1974. Grass tussock (*Digitaria macroglossa* Henr.) utilized by *B. cinguliger* (Smith) for sleeping.

so far that those on the outer blades of grass were mostly facing inwards (that is, were orientated facing the basal end of the grass blades). At the time these observations were made (9.30 a.m.) the sky was heavily overcast and there was a cool breeze blowing. Very little movement of the clustered wasps took place when the grass blades were separated by hand in order to obtain a better view of the aggregation within the tussock. Neither on this nor on any of the subsequent occasions on which the sleeping cluster was examined was any aggression shown by the wasps. The few wasps which were disturbed rose up, flew about for a short time and then settled down on the tussock again.

A sample taken on this occasion (11.i.1974) consisted of 136 individuals all of which were females. From the samples taken in the first week of December and the second week of January, albeit in different years, it would appear that a sleeping cluster contains individuals of both sexes during the early stages of the wasps' flight season but only females during the later stages. This change in the composition of the members of a sleeping cluster is probably nothing more than a reflection of the fact that, whereas males are relatively common at the beginning of the flight season, their numbers fall off markedly in the later stages at a time when females are still common (see Fig. 1).

It is noteworthy that the situation of the sleeping place was at a considerable distance from the nearest nesting areas and that the soil near the watercourse was sandy and thus unsuitable for nesting. It appears that the members of the sleeping cluster were drawn from a wide area as the number present was far greater than that in any one nesting area.

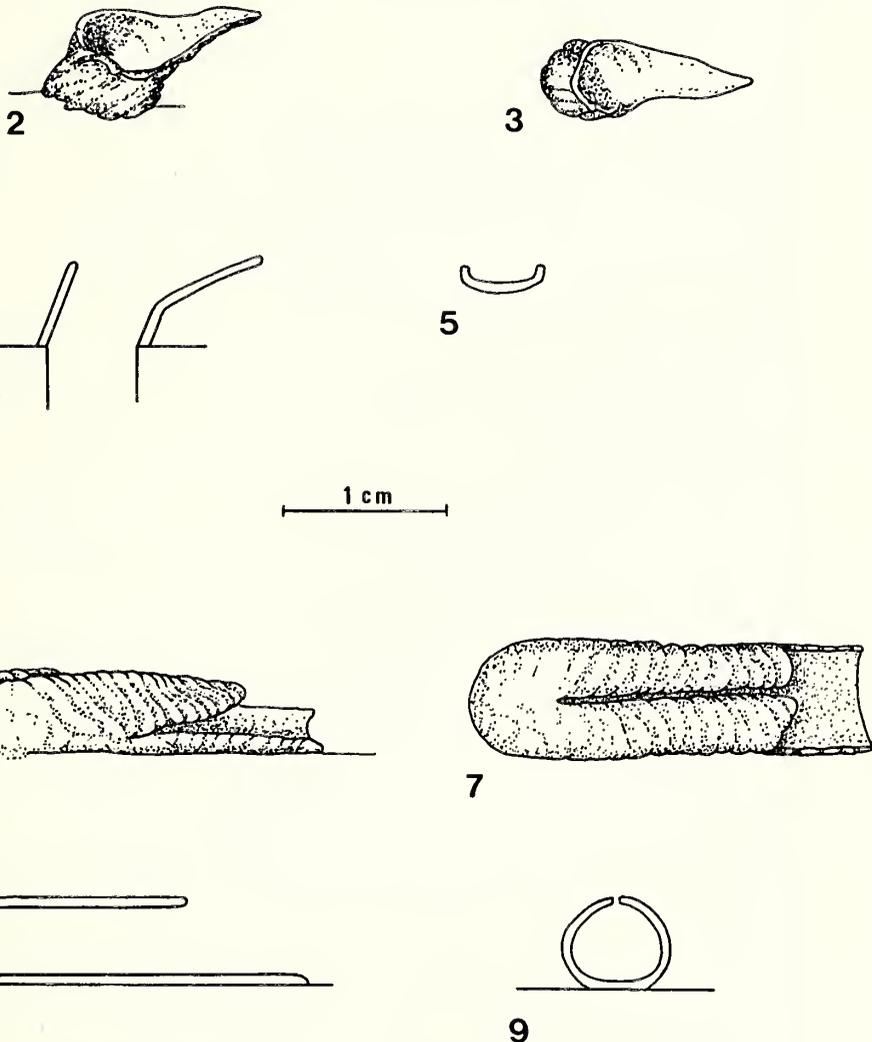
The sleeping cluster was kept under observation for a period of forty-six days, from 11.i.1974 (the date of discovery) until 25.ii.1974. During this period use was made of the same tussock night after night to the exclusion of any other similar tussocks in the vicinity. The tussock utilized by the sleeping cluster was inspected a total of seventeen times in the forty-six days. Thirteen of these inspections were made in the morning, one in the afternoon and three in the evening. It was found that the behaviour of the wasps belonging to the sleeping cluster at the tussock was very strongly influenced by the weather. It was found that 9.25 a.m. on a hot, sunny, dry, windstill morning most of the wasps had already left the vicinity of the tussock, some were sunning themselves on the surrounding vegetation and a few were still in the centre of the tussock. At 10.55 a.m. on a similarly fine day no wasps at all were to be found either in the tussock itself or in the vicinity thereof, all having flown to the nesting areas. At similar times on mornings when the sky was overcast or a cool breeze was blowing most of the wasps of the sleeping cluster were found to have remained in the tussock and only a few individuals were sometimes visible on the outer grass blades. If conditions were slightly better with the sun periodically breaking through the cloud cover, many individuals were found sunning themselves on the outside of the tussock, on the surrounding vegetation and on the ground, particularly the sandy floor of the dry watercourse, and some were found flying about in the immediate vicinity of the tussock. If, as the morning progressed, the weather improved, wasps left to go to the nesting sites. However, if the weather deteriorated, wasps returned from the nesting sites and sheltered in the tussock. If weather conditions remained unfavourable throughout the day, the wasps did not leave the tussock or its immediate vicinity at all.

The time of return to the tussock in the afternoon on fine days was not established but at 6.00 p.m. on a warm sunny evening (13.i.1974) the wasps were found to be inside the tussock with none on the outer blades.

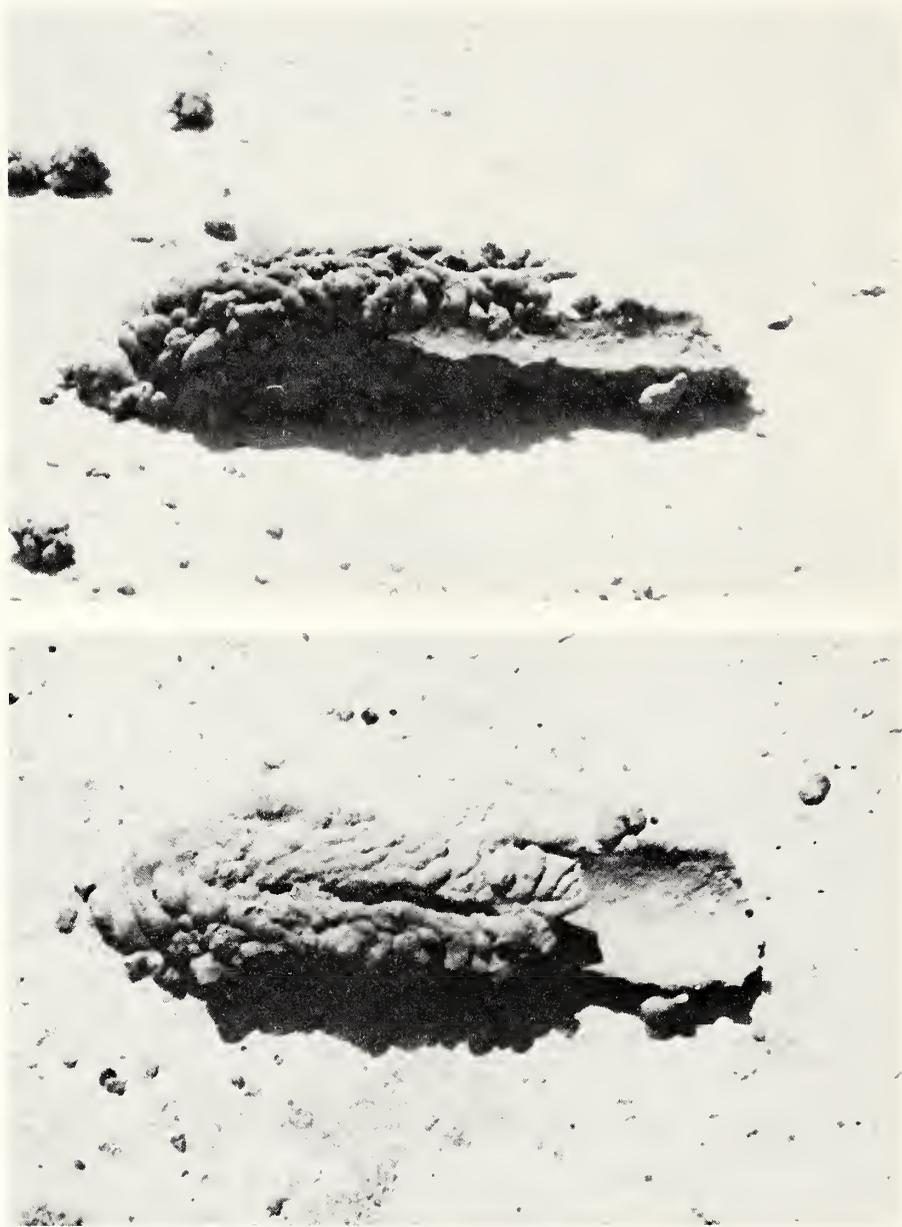
At all times the absence or presence of wasps at the tussock could be correlated with the reverse situation at the nesting sites.

Despite a careful search by the authors no sleeping cluster of *B. oxydorcus* was located though Brauns (1911: 92) reported that individuals of this species at Willowmore assembled in the evening in greater or lesser numbers on vegetation growing at the edge of pools, though never forming the dense clusters formed by *B. cinguliger*. In view of the similarity of behaviour

of *B. oxydorcus* to that of *B. cinguliger* with respect to their absence or presence at the nesting site depending upon the time of day and upon weather conditions it is not surprising that *B. oxydorcus* also forms sleeping aggregations. Taking into account the fact that the numbers of *B. oxydorcus* at Hilton were always far fewer than those of *B. cinguliger*, the aggregations were probably similar in their nature and size to those reported for the former by Brauns. At Hilton



Figs. 2—5. *B. oxydorcus* (Handl.) turret; Figs. 6—9. *B. cinguliger* (Smith) turret.
 Figs. 2 and 6. Side view.
 Figs. 3 and 7. View from above.
 Figs. 4 and 8. Diagrammatic vertical section through long axis.
 Figs. 5 and 9. Diagrammatic vertical section across lip.



Plates 5 and 6. Hilton, 22.i.1975. Nest turret of *B. cinguliger* (Smith) from side and from above. (x3,2)



Plates 7 and 8. Hilton, 11.iii.1974. Nest turrets of *B. oxydorcus* (Handl.) from side. (x1,5)



Plate 9. Hilton, 8 iii.1974. Nest turrets of *B. oxydorcus* (Handl.) from above. That on left open, that on right sealed. (x1,3)



Plate 10. Hilton, 11.iii.1974. *B. oxydorcus* (Handl.) female entering turret. (x3)



Plates 11, 12 and 13, Hilton, 22.iii.1974. Three stages in the sealing of a turret by *B. oxydorcus* (Handl.) (x4)

GESS AND GESS: ETHOLOGICAL STUDIES OF BEMBEVINUS CINGULIGER

a few individuals of *B. oxydorcus* were observed, on an overcast day, "sleeping" on vertical stems of low vegetation growing on the far side of an irrigation furrow bounding one side of a nesting area. However, these individuals being spaced out on the vegetation could not be described as forming an aggregation.

DESCRIPTION OF THE NEST TURRET

Bembecinus oxydorcus and *Bembecinus cinguliger* both construct an aerial mud turret above the subterranean portion of the nest. The turret for each species is distinct and constant in its design (Figs. 2—9 and Plates 5—13).

In both there is an extended lip to one side of the structure. In *B. oxydorcus* this lip is raised above the ground and extends from the edge of the shaft opening at an acute angle with the ground surface. However, in *B. cinguliger* the lip is most commonly in contact with the ground surface along its entire length.

Rising from the edges of the shaft opening and continuous with the base of the lip is a wall which in *B. oxydorcus* forms a short sloping cylinder and in *B. cinguliger* a hood covering the shaft opening. Thus the shaft opening in *B. oxydorcus* is visible from above whereas in *B. cinguliger* it is obscured by the hood.

In addition to this basic structure there is a rim extending along the sides of the lip. In *B. oxydorcus* this rim is barely 1 mm in height whereas in *B. cinguliger* it forms arched sides which almost meet above the lip to form a tunnel, open at its distal end and with in addition a slit opening dorsally along its entire length. For 31 completed *B. cinguliger* turrets measured the total length (measured to the distal end of the lip) averaged 34 mm (range 26—43 mm) and the length of the tunnel-like covered portion averaged 24 mm (range 19—33 mm).

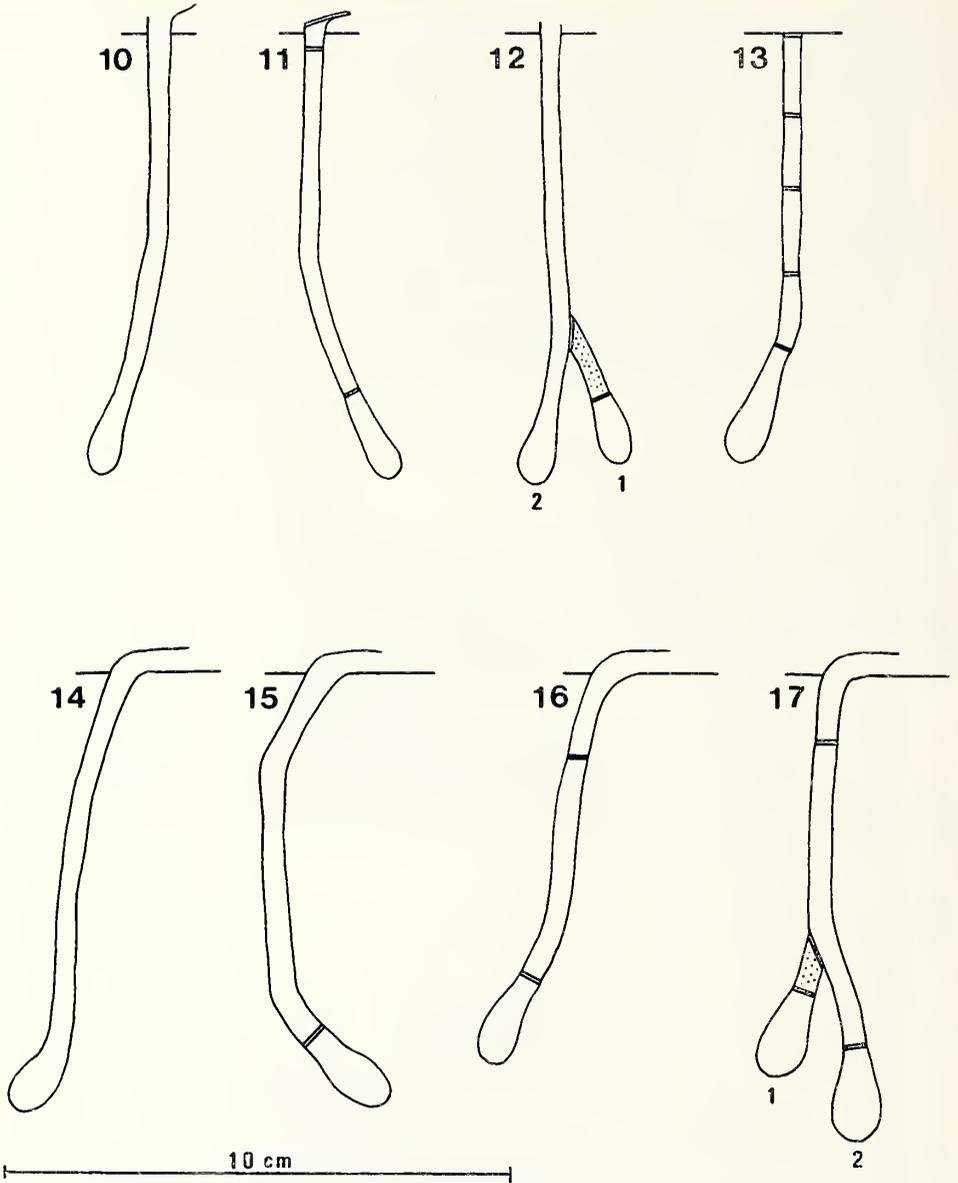
DESCRIPTION OF THE SUBTERRANEAN BURROW

A total of 54 nests in various stages of construction was excavated and investigated during the present study; 34 were those of *B. cinguliger* and 20 those of *B. oxydorcus*. In Table 1 the underground workings of these nests are grouped into three categories according to the number of cells associated with each nest.

TABLE 1. Analysis of the form of the underground workings of 54 nests of *Bembecinus* excavated near Grahamstown

Category	Description of underground workings	Number of nests	
		<i>B. cinguliger</i>	<i>B. oxydorcus</i>
A	Shaft with no cells	0	6
B	Shaft with one cell	29	12
C	Shaft with two cells	5	2
Totals		34	20

The subterranean burrow consists of a shaft terminating in a single cell or branching dichotomously to terminate in two cells (Figs. 10—17). No nest was found with more than two cells.



Figs. 10—17. Plans of underground workings of four nests of *B. oxydorcus* (Handl.) (Figs. 10—13) and four nests of *B. cinguliger* (Smith) (Figs. 14—17).
 Figs. 10 and 14. Nests each showing a single open cell.
 Fig. 15. Nest showing one sealed cell.
 Figs. 11 and 16. Nests showing temporary seals.
 Figs. 12 and 17. Nests each showing two cells and the sequence of their construction.
 Fig. 13. Nest with final seals.

The depth below the ground surface of the bottom of the single cell in nests of category B or of the first-constructed cell in nests of category C varied in *B. cinguliger* from 59 to 90 mm, with an average depth of 75 mm (88% between 65 and 85 mm). In *B. oxydorcus* the depth varied from 72 to 155 mm and averaged 97 mm; however, if two unusually deep nests (130 and 155 mm) are omitted as being atypical, then the depth varied from 72 to 102 mm and averaged 89 mm (75% between 79 and 99 mm).

In those nests having two cells, the second cell always terminated a side branch arising from the main shaft above the sealed first-constructed cell. In both species the depth below the ground surface of the second cell was always in excess of that of the first. In *B. cinguliger* the difference in depth varied from 3 to 10 mm with an average of 7 mm; in *B. oxydorcus*, for which only one measurement was obtained, the difference in depth was 6 mm.

In *B. cinguliger* the length of the cells varied from 12 to 19 mm (average 17 mm) and the width varied from 6 to 8 mm (average 7 mm); in *B. oxydorcus* the corresponding measurements were 15 to 20 mm (average 18 mm) and 6 to 7.5 mm (average 6 mm), respectively. The bore of the shaft was between 4 and 5 mm in *B. cinguliger* and between 3 and 4 mm in *B. oxydorcus*.

In summary, it may be seen that the subterranean burrows of the two species are very similar, the only differences being that the shafts and cells of *B. oxydorcus* are somewhat narrower but longer than are those of *B. cinguliger*.

AN ACCOUNT OF THE METHOD OF BURROW EXCAVATION, TURRET CONSTRUCTION AND NEST CLOSURE

Before the initiation of nest building *B. oxydorcus* females were seen to fly around the nesting area settling from time to time and scraping at the ground with their mandibles and fore-legs, flying up and returning to scrape in the same places.

Nest building in *B. cinguliger* and *B. oxydorcus* is initiated by the collection of a crop-full of water. In both species water is collected when standing on the mud at the water's edge and in *B. cinguliger* less commonly when standing on a floating object or alighting on the water surface itself.

The wasp then flies with this water to the nesting area where she regurgitates it onto the earth. The water and earth are then worked together to form very wet mud. The wasp then starts to excavate the shaft by removing the mud with the mandibles. *B. oxydorcus* places the mud around the opening of the shaft to form a collar of the same diameter as the shaft. To this she adds more pellets evenly but as she always alights and stands on the structure on the same side the portion which supports her gradually slopes away from the shaft opening at an acute angle with the ground and thus a lip develops. The portion furthest from the lip slopes to a lesser degree towards the opening resulting in an off-vertical cylinder bearing the lip on one side. In the structure of *B. cinguliger* this asymmetrical development is very much more marked than in that of *B. oxydorcus*. Most commonly the lip is in contact with the ground along its entire length. However, less commonly it is detached from the surface of the ground and runs parallel to this at a height of approximately 1 mm. Most commonly *B. cinguliger* initially remains standing on the ground and draws the first formed mud back with her mandibles and fore-legs so that the lip initially is in contact with the ground. She then adds mud to form a collar around the shaft opening and connected with the lip. She adds to this collar and to the lip in such a way that the latter is continued along the ground and the portion of the structure further from the lip slopes towards the shaft opening more markedly than in *B. oxydorcus* so that a hood over the opening develops.

When the cylinder of *B. oxydorcus* has almost reached its full height, the wasp starts adding more mud to the lip than to the rest of the structure so that it is extended more rapidly than the off-vertical walls. When adding pellets to the end of the lip the wasp backs out of the turret

along it and steps off the end vibrating her wings rapidly to support herself in hovering flight. Similarly in the *B. cinguliger* construction, once the hood is almost complete considerably more mud is added to the lip than to the hood. In both species pellets are added along the sides of the lip to form a ridge. This ridge is added very evenly, the wasp placing pellets alternately on right and left sides. In *B. oxydorcus* the ridge is complete when about 1 mm high whereas in *B. cinguliger* the wasp continues to add to the ridge in such a manner that it forms sides to the lip which curve over and almost meet above it leaving only a narrow slit opening. Thus a tunnel-like structure is formed and this is extended further by continued additions of pellets to the floor and sides. The additions to the sides always alternate even when extensions to the floor intervene and when building is interrupted by water collection. In order to add mud to the highest parts of the hood and tunnel the wasp leaves the floor and stands upside down on the inside of the structure. This change in position is also noticed in *B. oxydorcus* which plasters the inside of its structure standing on the inner surface of the walls and with its head downwards.

In *B. cinguliger* nesting at a distance of 18 metres from its water source, it was found that the turret was completed within about 45 minutes and that it required about 15 loads of water.

When the turret is completed, the shaft is not yet of its full depth. The additional mud excavated is removed from the shaft in the form of pellets, which are carried out one at a time and dropped 30—40 cm from the nest. In performing this the wasp follows an elliptical flight path. After pellet dropping has started there are still occasional additions to the turret. In the case of *B. cinguliger* it was found that each water load was sufficient for the formation of 13—20 pellets.

B. cinguliger was at times heard to make a buzzing sound when excavating the shaft below the surface of the ground. It is believed that the loosening of the earth at the working face of the excavation was, on these occasions, facilitated by vibrations of the mandibles produced by manipulating the flight mechanisms as described by Spangler (1973) for other Hymenoptera.

As seen from the description of the subterranean burrow plan, a second branch shaft in some cases constructed after the original shaft with its terminal cell has been completed and has been supplied with an egg and fully provisioned. The portion of the original burrow below the opening to the second shaft is found to be filled with earth pellets. As the wasps, at this stage, were not seen to carry pellets into the burrow it is thought that the pellets excavated from the second shaft are probably dropped into the first shaft and not carried out of the nest as was the case in the construction of the latter.

During nest construction there is no regular occurrence of grooming. However, when the regular pattern of water carriage and pellet formation is disturbed, both *B. cinguliger* and *B. oxydorcus* will alight on the ground and groom before continuing building.

B. cinguliger and *B. oxydorcus* were both found to seal their nests at the end of each working day and to open them at the beginning of each successive working day. The temporary seals each consist of a thin mud plate attached around its circumference to the sides of the shaft and positioned at right angles to them. Two such temporary seals are made: one immediately above the cell which is still being provisioned and a second at a depth varying from 3—19 mm below the ground surface. *B. oxydorcus* in addition seals the turret but no such turret sealing was found in *B. cinguliger*. The sealing of the turret in *B. oxydorcus* makes it possible to record the time taken from nest initiation to the completion of that day's temporary closure. It was found that this first day's activity which presumably included at least oviposition was completed in 75 minutes.

The turret seal in *B. oxydorcus* is made by the wasp from the rim of the cylindrical portion of the turret and the ridge on the sides of the lip. The wasp arrives at the nest with a crop-full of

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water and alights on the lip. She first moistens the rim at a point furthest from the lip and draws the resultant mud towards herself. Gradually more of the rim is moistened and drawn across the opening. Mud is consistently taken alternately from right and left sides. When the water in her crop is exhausted, the wasp flies off and fetches a second load. Work is continued in the same way as before until the end of the lip is reached. The builder then steps off buzzing her wings to support herself whilst she completes the sealing at the tip and then flies off. Finally she returns with a third load of water with which she moistens and smooths off the seal. (Plates 11—13)

When opening the nest, the wasp alights on the lip and moves forward onto the lid. She moistens the surface of the lid at a point furthest from the lip, forms a pellet, flies off and drops it. She returns along the lip and repeats the process until the lid is removed. The upper inner seal is then removed in a similar way. Whilst she is engaged in this the tip of her abdomen is visible. Finally pellets are carried out from deeper down out of sight and these are presumably from the lower inner seal. The opening of all three seals is completed in five minutes. As the turret lid is thrown away in the form of pellets the turret must become shorter with each successive day.

In both *B. oxydorcus* and *B. cinguliger*, in nests with two cells, the shaft bearing the original cell is sealed off from the new branch shaft which bears the second cell. The seal separating the two shafts is not at right angles to the shaft wall but is in the same plane as the secondary branch wall so that there is no unevenness in the wall of the shaft terminated by the second cell (Figs. 12 and 17).

After the cell or cells are finally completely sealed the wasp makes two or three further seals at intervals in the shaft (Fig. 13). The spaces between these seals are not filled with earth.

IDENTIFICATION AND COMPOSITION OF THE PREY

Prey that was in a physical condition which allowed identification with respect to family (or superfamily), stage of development and sex was obtained from 31 of the 39 *B. cinguliger* cells excavated and totalled 223 individuals (Table II).

TABLE 2. Analysis of the prey found in 31 cells of *B. cinguliger*

Prey Taxon	Sex and developmental stage				Totals
	Adult Females	Adult Males	Nymph Females	Nymph Males	
HOMOPTERA: AUCHENORRHYNCHA Cicadoidea: Cicadellidae (about 10 species)	91 (4)	57 (3)	22 (1)	9	179
HOMOPTERA: AUCHENORRHYNCHA Fulgoroidea: Family? (2 species)	14	16	0	0	30
DIPTERA Tephritidae (2 species)	Sex not determined		—	—	14
					223

Note: Figures within brackets refer to stylized individuals.

The prey most commonly utilized for provisioning were species of Cicadellidae and 30 of the 31 cells contained individuals of this family, 18 cells being provisioned solely with cicadellids and the remaining 12 being provisioned with other prey in addition. Ten cells contained Fulgoroidea and other prey and six cells contained Tephritidae and other prey. Seven cells were provisioned with a mixture of Cicadellidae and Fulgoroidea, three with a mixture of Cicadellidae and Tephritidae and one with a mixture of Fulgoroidea and Tephritidae. Two cells were provisioned with a mixture of all three prey taxa. It was found that any one cell might contain more than one species of any one or more of the three prey taxa and in the case of the Cicadellidae might contain both adults and nymphs. In length (measured from the front of the head to the end of the abdomen) the Cicadellidae ranged from 1,8—5,4 mm and the Fulgoroidea from 3,9—4,1 mm. The Tephritidae were 2,9 mm long.

With respect to *B. oxydorcus* the number of prey available for examination, obtained from only nine cells, was much smaller but indicated similar prey preferences to those exhibited by its congener. Thus the most commonly utilized prey were species of Cicadellidae of which both sexes and both adults and nymphs were represented. There were no Fulgoroidea in the sample but several Tephritidae were present.

Though no conclusive observations were made on hunting by *Bembecinus* and thus on the source of the prey brought to the nests, circumstantial evidence is very strong that the prey is obtained on the low-growing *Pentzia* bushes which, as noted above, surround the nesting sites. Both *B. cinguliger* and *B. oxydorcus* have been noted flying about among these plants which when swept with an insect net are found to yield many Cicadellidae. It is more than likely that the Tephritidae found in the *Bembecinus* nests are also obtained on the *Pentzia* bushes, where they probably develop in the flowers. Their occurrence in the same niche as the Homopterous prey and their similar size are undoubtedly contributory factors in the atypical acceptance by the wasps of this Dipterous prey.

OVIPOSITION AND PROVISIONING, IMMATURE STAGES

Eggs were found in three nests of *B. cinguliger* and in two nests of *B. oxydorcus*. In the former species two eggs were found in first cells and the third in a second cell; in the latter species both eggs were found in first cells. The eggs of both species were found to be pearly-white and almost straight; those of *B. cinguliger* were about 3,2 mm long and 0,8 mm in diameter; no measurements were recorded for *B. oxydorcus* eggs.

In both species the egg was found on the floor of the cell, in *B. oxydorcus* on loose earth and in *B. cinguliger* at the top of a small cone of earth. In all five cases the cells also contained a single cicadellid prey placed close to the egg. Thus in no case was an egg found in an otherwise empty cell. The only other cells containing but a single prey were two cells (one of each *Bembecinus* species) each containing a very small, newly-hatched larva. All other cells each contained a larva and two or more prey or, in the case of cells with large larvae or larvae in cocoons, the dismembered and fragmentary remains of many prey. The fragmentary nature of the prey remains made it difficult to establish the total number of prey provided for and consumed by each larva but the number appeared to be large. However, an estimate was obtained from a closed cell of *B. cinguliger* in which the larva had not developed (there was a small fly puparium present in the cell) and which contained a total of 41 prey: 19 females, 16 males and 5 female nymphs of the family Cicadellidae, and one male fulgoroid. In both species it was found that the Homopterous prey was without exception so positioned within the cell that the head was directed inwards and the ventral side was up.

Provisioning in both species was found to be progressive, the first prey being brought into the cell shortly after the egg had been laid and the second prey being brought in only after the larva had hatched. Provisioning thereafter appeared to be rapid, prey being brought in at a rate

faster than it was consumed. Thus various cells occupied by small *Bembecinus* larvae and still being provisioned were found to contain as many as from seventeen to thirty identifiable prey in addition to fragments of other, already consumed prey.

In *B. cinguliger* in the field eggs were found to hatch in under 24 hours. Thus four nests of which construction from the beginning was watched during the late morning of 12.xii.1973, and of which the positions were marked, were excavated and examined at the same hour on the following day: one cell contained an egg on the point of hatching together with one prey and the other three cells contained small (2,5—3,0 mm long) larvae together with one, two and three prey respectively.

The cocoons of *B. cinguliger* were found to be narrowly ovoid, from 14,5—16,0 mm in length (average of 11: 15,0 mm) and with a maximum width of from 5,0—6,1 mm (average of 21: 5,4 mm). The anterior end was comparatively wider and more rounded than the narrower and more pointed posterior end. The wall of the cocoon was hard and smooth and coloured like the soil in which the cells had been excavated and it was clear that it was composed of clay. The inside of the clay cocoon wall was lined with a thin layer of fine silk spinings. One (rarely), two (most commonly) or three minute pores were present in the clay wall of each cocoon, situated irregularly around the circumference of the cocoon just about at the middle of the long axis. These pores were fairly easy to spot, the area immediately around them being darker than the cocoon walls generally. Surrounding the hard portion of the cocoon was a loose outer envelope of fairly sparse strands of silk to which adhered the dismembered uneaten remains—hemelytra, legs, head-capsules and other parts of the exo-skeletons of the Homopterous prey. This outer covering of characteristic prey remains renders *Bembecinus* cocoons immediately recognisable in the field. Cocoons dug out of the ground at Hilton on 26.ix.1974 still contained prepupae, indicating that pupation occurs in the spring at some time after this date.

Cocoons of *B. oxydorcus* were found to be very similar to those of *B. cinguliger* but were somewhat smaller—from 12,8—13,8 mm long and with a maximum width of from 4,5—5,0 mm. The three cocoons examined had four pores each. Cocoons dug out of the ground at Hilton on 8.x.1974 still contained prepupae.

PARASITES AND OTHER ASSOCIATED INSECTS

Evidence of only one case of parasitism was found in the 54 nests of both species dug out and examined during the nesting season and in numerous other nests investigated during the end of the winter diapause period. Thus on 31.xii.1973 a sealed cell of *B. cinguliger* was found which contained 41 small homopterous prey and one 2 mm-long dipterous puparium but no egg or larva of the rightful owner of the cell. Unfortunately the puparium was damaged in handling and a more precise identification was thus precluded.

Numerous female Mutillidae of several species were found walking about the nesting site of *B. oxydorcus* during March and April, 1974, and on two separate occasions a female of one of these species was seen entering an open nest during the temporary absence, probably while hunting, of the *B. oxydorcus* female. On the second occasion the *B. oxydorcus* female returned to the nest two minutes after the mutillid had entered it. Twice the sphecid went down into her nest and backed up and out again, then she turned around and went down the burrow backwards. On coming up and out again she was followed by the mutillid which ran out and then stopped a little way off. The sphecid then continued with her normal work.

Foreign Hymenoptera were in several instances observed entering or leaving *Bembecinus* nests and it appears that in some cases at least the nests had been invaded by the former for the purpose of nesting. Thus *B. oxydorcus* nests were found that had been taken over by the

bee *Megachile* (*Eutricharaea*) *meadewaldoi* Brauns (Megachilidae), by *Pison* ?*montanum* Cameron (Sphecidae) and by an unidentified species probably of the family Eumenidae, all species habitually nesting in pre-existing cavities.

The *Megachile* was seen on 8.iii.1974 going down an *oxydorcus* turret carrying something colourful. The bee was captured when it emerged and the burrow when excavated was found to contain four pieces of pink petal introduced by the bee as nesting material. From their colour it was immediately apparent that the pink discs had been cut from the flowers of *Oxalis* sp. (near *stellata* E. & Z.) which grew in numbers in the vicinity of the *B. oxydorcus* nesting site. Examination of the flowers of these plants showed that several petals had holes corresponding in size and shape to the discs.

The *Pison* was seen in association with *B. oxydorcus* nests on three dates during March and April. Several females, two of which were subsequently captured, were observed entering and leaving the turreted nests on 8.iii.1974. On 11.iii.1974 a female carrying an immature spider (Salticidae) held beneath her was observed flying about low over the *B. oxydorcus* nesting area probably trying to locate the nest it had usurped but unable to do so due to the authors sitting on or near it. A further female was observed on 10.iv.1974 regularly visiting an old *B. oxydorcus* nest. Possibly it was preparing the burrow for use for the latter was found on examination to be half filled with loose earth but to contain no prey. Nothing is known concerning the usual nesting habits of *Pison* ?*montanum* Cam. but during the 1973/74 summer the species was found nesting at Hilton in wooden trapnests (4,8 mm and 6,4 mm bore) which the authors had suspended in bushes.

The supposed eumenid which had taken over a *B. oxydorcus* nest was not seen and was known only by its small, lacy, horizontally orientated eumenid-type mud entrance turret with which it had surmounted the opening at the top of the *B. oxydorcus* turret. First observed on 11.iii.1974, the nest furnished with this double turret was excavated two days later but was found to have no cell, egg or provisions.

A female bee, *Tetralonia minuta* Fr. (Anthophoridae) was captured on 12.xii.1973 on emerging from a *B. cinguliger* burrow after it had been observed entering it via the horizontal turret. It is not known what the purpose of this visit to the sphecid nest was, for according to Rozen (1969) this bee itself excavates its burrow. However, another female of this species was captured (11.xii.1973) at Hilton coming out of the emergence hole of a large ground-nesting species of Eumenidae, *Parachilus insignis* (Saussure), whose nesting area abutted that of *B. cinguliger*.

FLOWERS AND NEW PLANT GROWTH VISITED BY ADULT WASPS

During the present study at Hilton *B. cinguliger* (Smith) was observed during the late afternoon of 2.i.1974 foraging in numbers upon the white flowers of *Selago corymbosa* L. (Selaginaceae) and upon the yellow flowers of *Helichrysum ericaefolium* Less. (Compositae). Thirteen females and three males were caught on the former, three females on the latter. Similarly at noon on 15.ii.1974 several females were observed and caught while foraging on the very small yellow flowers of *Pituranthos aphyllus* (Cham. & Schlechtld) Benth. & Hook. f. ex Schinz (Umbelliferae). All three forage plants were at a distance from the nesting areas but close to the sleeping tussock and it is certain that the purpose of the wasps' presence at the flowers was for imbibing nectar and not for catching prey.

At Hilton in previous years *B. cinguliger* was obtained on three occasions on the small, pale-yellow flowers of *Maytenus linearis* (L.f.) Marais (Celastraceae). The records are: 9.xii.1969 (F. W. Gess) 7 males, 11.xii.1969 (F. W. Gess) 6 males and 4 females, 11.xii.1969 (D. W. Gess) 2 females, and 6.xii.1972 (F. W. Gess) 4 males.

In addition to being attracted to the above flowers for the purpose of obtaining nectar, both sexes of *B. cinguliger* were found to be attracted to the glandular exudates associated with the new growth of *Acacia karroo* Hayne (Leguminosae). Thus, a male, the first individual of this species to be spotted during the 1973—74 flight period, was observed and caught on 3.xi.1973 on this new growth of an as yet flower-less *Acacia* bush. On 27.xi.1973 a female was observed and caught visiting the glands but not the flowers of this plant and on 12.xii.1973 an individual of undetermined sex was observed similarly employed.

B. oxydorcus was during the present study likewise found to visit flowers for the purpose of imbibing nectar. Thus on 2.i.1974 a male was captured on *Selago corymbosa* L. (Selaginaceae) where it was foraging in company of both sexes of *B. cinguliger*; on 9.i.1974 a female was captured on the yellow flowers of *Pentzia incana* (Th.) O. Ktze. (Compositae) and on 28.i.1974 five individuals, at least one a male, were observed on the flowers of this latter plant.

The above forage-flower records for the two species have been dealt with in some detail as they are of interest in the light of the statement by Evans (1955: 288) that he knew of no records of any species of *Bembecinus* coming to flowers and that "apparently the adults obtain their nourishment from some other source".

Lest it be construed, however, that *B. cinguliger* and *B. oxydorcus* at Hilton are unusual in this respect, attention is drawn to other flower-visiting records concerning these and other southern African species of *Bembecinus*. These records are listed below under the name of the forage plant.

Zizyphus mucronata Willd. (Rhamnaceae)

<i>Bembecinus braunsi</i> (Handl.)	1 male
<i>Bembecinus cinguliger</i> (Smith)	5 females and 2 males
<i>Bembecinus haemorrhoidalis</i> (Handl.)	1 male
<i>Bembecinus oxydorcus</i> (Handl.)	1 male

at Koonap River, 17 miles from Adelaide on Grahamstown road, 20—22.xii.1972 (C. F. Jacot-Guillarmod).

Foeniculum vulgare Mill. (Umbelliferae)

<i>Bembecinus haemorrhoidalis</i> (Handl.)	1 female (F. W. Gess)
<i>Bembecinus</i> sp. (undescribed)	5 females (F. W. Gess) and 4 females (J. G. H. Londt)

at Belmont Valley, Grahamstown, 17.i.—5.ii.1970.

<i>Bembecinus polychromus</i> (Handl.)	2 females and 1 male
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at Johannesburg (Transvaal), 27.xii.1970 (J. G. H. Londt).

In addition to these records derived from material in the Albany Museum collection, Jacot-Guillarmod has stated (pers. comm., 1973) that he has collected the following species visiting flowers: *B. polychromus* (Handl.), *B. herbsti* (Brauns), *B. haemorrhoidalis* (Handl.) and *B. boer* (Handl.).

Of interest in connection with the attractiveness to *B. cinguliger* of the glandular exudates of *Acacia karroo* Hayne at Hilton are specimens, now in the Albany Museum collection, of three *Bembecinus* species collected by C. F. Jacot-Guillarmod on *Calpurnia intrusa* E. Mey. (Leguminosae) at Mamathes (Lesotho). The species concerned are *B. polychromus* (Handl.) (2 males), *B. herbsti* (Brauns) (3 males) and *B. braunsi* (Handl.) (2 males and 1 female).

Jacot-Guillarmod (1951: 235—236 and 1957: 10—13) has recorded the attractiveness of *Calpurnia intrusa* E. Mey. to Hymenoptera and has drawn attention to the fact that the plant "is most attractive in spring and early summer, when there are many young shoots, but no flowers" and that "when flowers appear it loses its attractiveness except for the flower-visiting wasps . . .". The wasps "seemed to be attracted by the foliage and young shoots which apparently exude some substance that is attractive to them". *Bembecinus* species are not mentioned in these papers but according to Jacot-Guillarmod (pers. comm., 1973) those species recorded from *C. intrusa* were visiting the plant for the exudate and not for the nectar contained in the flowers. The reason for the attractiveness to *Bembecinus* species of the two leguminous plants, *Acacia karroo* Hayne at Hilton and *Calpurnia intrusa* E. Mey. at Mamathes, therefore appears to be the same.

A similar case of feeding on glandular exudates may have been recorded for the males of *B. tridens* (Fabr.) in Switzerland by Lüps (1973: 134). Those males were observed in numbers upon the needles of Scots Pines (*Pinus silvestris*) where they were thought possibly to be imbibing nutriment.

DISCUSSION

Concerning the genus *Bembecinus* Costa, Evans (1966: 132—133) has written that the available data on the more than fifteen species examined to that date "together present a remarkably consistent picture demonstrating that this genus is highly distinctive in its ethology, but suggesting that there are few notable specific differences in behavior within the genus".

The ethology of *Bembecinus cinguliger* (Smith) and of *B. oxydorcus* (Handl.), while conforming to the general pattern of behavior shown by those species of the genus that have hitherto been studied, exhibits some outstanding features which mark off these two species from their congeners and which indeed seem unusual within the Sphecidae.

The fundamental feature in which the present two species differ from other species of *Bembecinus* is that the former choose to construct their nests in soil of a different type from that usually chosen by the genus. Correlated with the difference in the chosen soil type is a well marked morphological difference with respect to the fore-legs of the wasps and the substitution of the usual method of nest excavation and closure practised by *Bembecinus* species by one more suited to the unusual nesting medium.

From the ethological study of the North American *B. neglectus* (Cresson) by Evans (1955: 287—295) and that author's reviews and discussions of the published observations on this and other species of the genus (1955: 295—302) and (1966: 132—143), it appears that, in those species at least, nesting occurs rather locally in restricted sandy areas. In the present authors' experience several southern African species (other than *cinguliger* and *oxydorcus*) similarly nest in sand. In *B. neglectus*, as in the reviewed species, burrow excavation in the sandy medium is essentially by digging, the earth being thrown back beneath the body by the fore-legs, the fore-tarsi being furnished for this purpose with a comb or sand rake. The existence of this tarsal sand rake appears to be typical of virtually all *Bembecinus* species and it may confidently be expected that the possessors of this structure all nest in sandy soil and excavate their burrows in the above indicated manner.

The nesting of *B. cinguliger* and *B. oxydorcus* in a hard clay soil, a nesting medium quite unsuitable for sand-raking (and thus for the great majority of *Bembecinus* species), is clearly correlated in the female wasp with the absence, possibly by secondary loss, of the usual long spines on the fore basi-tarsus which joint instead bears a dense row of short cilia.

Behaviourally the atypical nesting medium and the morphological modification of the fore-tarsi is correlated with the adoption of the use of water for softening the earth and with the habitual utilization of the mouthparts as digging tools and for forming mud pellets in which

form the excavation spoils are removed from the burrow being sunk. While the use of water for the above purpose is entirely foreign to the behaviour of the hitherto observed *Bembecinus* species, if not also to other genera of Sphecidae, the use of the mandibles for removing small pellets of earth from an excavation has been observed by Evans (1955: 290) in *B. neglectus*. That wasp, when the soil it encountered was unusually firm or moist, was seen to carry out pellets which were deposited from one to four centimeters from the nest entrance. Similarly in *B. hungaricus japonicus* (Sonan) the use of the mandibles has been reported by Tsuneki (1969: 8) for assisting the fore-legs in excavating in damp sand and for carrying out of the nest small pebbles encountered during shaft sinking in pebbly ground.

A remarkable feature of the behaviour of *B. cinguliger* and of *B. oxydorcus*, however, is that at least some of the mud pellets derived from the excavation of the burrow are utilized for the construction of a turret surmounting the nest entrance. In this respect these two species are unique not only within the genus *Bembecinus* but also within the Nyssoninae for according to Evans (1966: 422) no member of this subfamily has been recorded to utilize mud in nesting. Indeed, where mud is utilized in nesting by Sphecidae, it is either for the purpose of forming cell partitions and plugs as in some species of *Trypoxylon* or for forming aerial mud nests as in other species of *Trypoxylon* and in *Sceliphron*. As far as can be ascertained by the authors no occurrence of a ground-nesting sphecid surmounting its burrow with a mud entrance turret has yet been recorded.

In the present two species the nature of the soil and the presence of the nest turrets precludes the method of closing the nest with sand as is usually practised by *Bembecinus* species and, in this activity also, mud is prepared and used for constructing seals and plugs.

Clearly the adoption of the use of water for burrow excavation, the utilization of the resulting mud pellets in the construction of a mud entrance turret surmounting the subterranean nest, and the use of mud in sealing the nest is intimately linked with the habit of nesting in clay soil. Similar burrow-excavating, turret-building and nest-sealing techniques in species nesting in clay soils have long been known in the Eumenidae and Masaridae (*Ceramius* species) and have recently (Gess and Gess, 1974) been described for a species belonging to the Pompilidae.

Considering the existence of the above notable points of difference pertaining to certain aspects of the nesting behaviour of sand- and clay-nesting *Bembecinus* species, it is remarkable how similar the two groups are in all other aspects of their behaviour, these not being influenced to any marked degree by the nature of the soil. Thus, in *B. cinguliger* and *B. oxydorcus* large numbers of individuals nest in close proximity giving rise to pseudocolonies, as has also been reported for the American species *B. godmani* (Cameron), *neglectus* (Cresson), *mexicanus* (Handl.), *nanus* (Handl.) and *cingulatus* (Smith) and for the European *tridens* (Fabr.).

In both *B. cinguliger* and *B. oxydorcus* the architecture of that part of the nest that is below the ground is very similar indeed to that described for *neglectus* and other species (Evans, 1966: 138 and Fig. 76), both with respect to nests containing one cell and those containing two. It seems of particular interest that this close similarity in nest plans should exist taking into account the very different soils and excavating techniques. However, these factors may be responsible for the burrows of the present species being subvertical rather than oblique as in the other species.

Like *B. neglectus*, neither *B. cinguliger* nor *B. oxydorcus* spends any time inside the nest when not actually excavating, opening, provisioning, inspecting or closing it and the greater part of the time including the night is spent away from the nest and the nesting area. *B. cinguliger* at least and probably also *B. oxydorcus* share with the South African *B. rhopalocerus* (Handl.) and *rhopaloceroides* (Brauns), the Argentinian *consobrinus* (Handl.) and the North American *godmani* and probably also *neglectus* the habit of spending the night in a sleeping cluster on or in vegetation.

In common with all other species of *Bembecinus* for which prey has been recorded (5 American and 6 Old World), the present two species provision their cells with small Homoptera. Similarly, as in other species, *B. cinguliger* and *B. oxydorcus* practise progressive provisioning. The egg is laid in an empty cell where, in *B. cinguliger* at least, it is glued to the top of a small mound of earth. The first prey is brought in before the egg hatches and is placed in a definite position relative to the mound bearing the egg.

It therefore appears that *B. cinguliger* and *B. oxydorcus* in most respects uphold the uniformity and uniqueness of behaviour exhibited by the genus; that the points of difference are adaptations to meet the challenge of nesting in a soil type otherwise unsuitable for and unexploited by the genus; and that the innovations in nest-building techniques, although apparently unique in the Sphecidae but paralleled in other families of Aculeata, in no way invalidate the inclusion of the two species in *Bembecinus*.

If the number of individuals in a population is any measure of the success of a species, then *B. cinguliger*, easily the most numerous wasp nesting in the clay soil of Hilton, must be considered extremely successful. *B. oxydorcus*, judged by the same criterion, is somewhat less successful at Hilton but may well come into its own at some other locality; its wide distribution in southern Africa certainly indicates success.

It has been shown that the behavioural and morphological departures from the norm manifested by the present two species have allowed them to invade a nesting substrate unsuitable for other species of *Bembecinus*. While this has undoubtedly been of great advantage to the present species, in that competition with their congeners for nesting sites has been eliminated, it must be asked whether the adoption of the clay nesting-substrate has not at the same time imposed any disadvantages or special conditions upon these wasps. Immediately apparent is their utter dependence upon a supply of water without which they are unable to manipulate the clay and the presence of which is thus a prime pre-condition for successful nesting. At Hilton, with its low mean annual rainfall and its generally dry summer months (see Gess and Gess, 1974: 191), the wasps are largely dependent upon ephemeral water, a result of irregular and unpredictable rain, collected in muddy pools, erosion gullies and shallow furrows. To make the best use of such unreliable water supplies it is thus of advantage if nest-building and provisioning can be accomplished rapidly and this indeed is a notable feature in the nesting behaviour of *B. cinguliger* and *B. oxydorcus*. It is fitting that this rapidity is in part made possible by the physical nature of the clay soil which, provided water is available, lends itself to quick manipulation.

As has been noted above, the time taken by *B. oxydorcus* to excavate a new nest, to oviposit in the cell, probably to bring in the first prey, and to seal the nest has been recorded as 75 minutes. Judging from the rapidity with which *B. cinguliger* constructs its nest (45 minutes to turret completion) the time taken by this species is probably similarly short. In contrast the time taken for these activities by the sand-nesting *B. neglectus* is considerably longer. Evans (1955: 290—291) has recorded the time taken by this wasp to dig a nest as averaging two hours and the time taken to seal it and to conceal the entrance as taking at least an hour.

In *B. cinguliger* at least and probably also in *B. oxydorcus* the egg develops very rapidly, the larva hatching in under 24 hours. Provisioning of the nest, apparently begun with a single prey on the day of oviposition, is pursued with rapidity the following day and under favourable weather conditions is probably completed within two days after oviposition. Provisioning is not only rapid but is notable for its economy of effort due to the fact that the nest is kept open from the start to the finish of a working day. In contrast, the nest of *B. neglectus* is invariably closed when the wasp leaves it. Introduction of each prey into the nest by that species is thus preceded by the digging of the earth from the entrance and succeeded by the careful reclosure of the nest from the outside.

In *B. neglectus* the maintenance of a closure at the nest entrance is a measure to keep out parasites. It is thus notable that, despite the fact that the nest of *B. cinguliger* and of *B. oxydorcus* is left open for long periods, the incidence of parasitism appears to be very low. It therefore seems likely that the nest entrance turret serves as a protection against parasites.

Whereas the rapidity of nest-building and provisioning is thus geared to make the fullest use of the short time between the fall of rain and the drying up of the resultant pools, the extended flight period of the females (four months in *B. cinguliger* and over three months in *B. oxydorcus* at Hilton during 1973—74) enables nesting to take place over a considerable period of time whenever water is available. The survival of the species in any one locality in bad years of low rainfall is thus ensured; conversely, in good years of copious rains and ever-available water the population may build up to high levels.

SUMMARY

Some aspects of the ethology of *Bembecinus cinguliger* (Smith) and of *B. oxydorcus* (Handl.) (Hymenoptera: Sphecidae: Nyssoninae) in the Eastern Cape Province of South Africa are described. Particular attention is given to the consequences of these two species choosing to nest in a clay soil and not in sand as is more usual in the genus. Described in detail is the use of water in the construction of the nest which by possessing a mud entrance turret appears to represent a nest-type previously unknown in the Sphecidae. A comparison of *B. cinguliger* and *B. oxydorcus* with their congeners with respect to various aspects of behaviour including the formation of pseudo-colonies, the architecture of the subterranean part of the nest, oviposition, provisioning and adult sleeping habits indicates that despite some notable innovations the present species' inclusion in the genus *Bembecinus* must be upheld.

ACKNOWLEDGEMENTS

The authors wish to thank Mr. T. C. White of the farm Hilton, where all the field work connected with these studies was undertaken, for his much appreciated kindness over the years in allowing them free access to his land.

Thanks are due also to Mr. C. F. Jacot-Guillarmod for helpful comments and discussions, and to Mrs. E. Brink and Miss G. V. Britten, both of the Albany Museum Herbarium for identifying forage plants.

The senior author is grateful to the C. S. I. R. for a grant partly utilized to cover running expenses in connection with the field work involved in the investigations.

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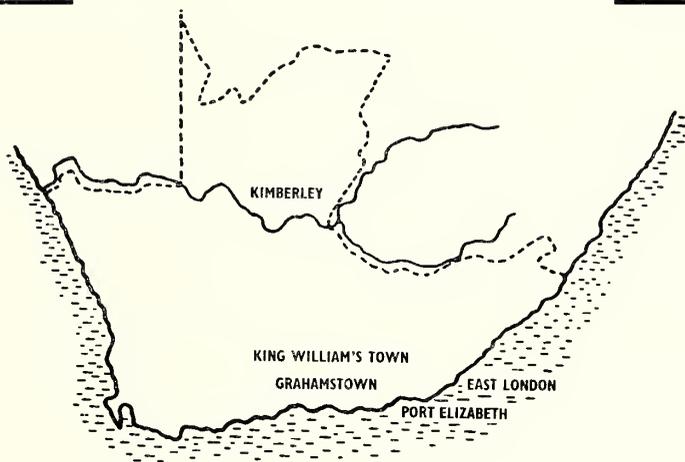


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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 3

31st March 1976

PUBLISHED JOINTLY BY THE

CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN

SOUTH AFRICA

Some aspects of the breeding biology of *Charonia lampas pustulata* (Euthyme, 1889) and *Mayena australasia gemmifera* (Euthyme, 1889) under aquarium conditions. (Gastropoda: Prosobranchiata)

M. J. LATIGAN
(East London Museum)

SYNOPSIS

The egg capsules and pre-planktonic larval development of *C. lampas pustulata* and *M. australasia gemmifera* are described. Notes on the behaviour of adults and brooding females are also presented.

INTRODUCTION

No records can be found in available literature of the embryonic development of any of the South African species of the Cymatiidae. Kilburn (1971) published notes on the family in southern Africa, while Anderson (1959) and Laxton (1969) have described the reproduction of some Australasian species.

METHODS

Studies were carried out on live animals and egg masses in the East London Municipal Aquarium. Periodic visits were made to this institution to examine samples of egg capsules and to photograph the embryos. Microscopic examination and photomicrography of the above material was carried out in our laboratory using 40 X magnification. The adults were collected near East London and were resident in the aquarium during three entire breeding seasons thus obviating possible disturbance on transferring fresh specimens from a natural habitat to an artificial one.

***Charonia lampas pustulata* (Euthyme, 1889)**

Adult behaviour

C. lampas pustulata is South Africa's largest gastropod and exhibits bathymetric variation as well as a wide range of shell colour variation. On two separate occasions copulation was observed, but the females concerned did not lay eggs in the breeding season of the same year. Two other adults were seen in the assumed position of copulation while the female was laying eggs. The male last observed to have paired with the brooding female remained in close proximity to the egg mass for the first few days. Thereafter other adults were seen to move onto and around the eggs with others again on top of them. This phenomenon of communal spawning was observed most markedly during the mid period of egg development. In the final stages the female remained alone on her eggs until hatching commenced. Even when dislodged she sought her way back to the mass. Incubating females were not seen to eat.

One brooding female was removed from her white egg mass and placed in another tank alone, and fifteen days later laid another batch of white eggs. The oxygenation pipe was placed directly under this mass and air bubbled through it. Embryos in both batches developed into veligers but the first batch was abandoned after 31 days and the second after 32 days. Another

female, alone in a tank for some two months except for one adult *Mayena australasia gemmifera*, laid white eggs which she incubated for 50 days. She then abandoned these eggs and laid another batch of pale orange eggs which she incubated for 40 days. In both batches the embryos developed but did not hatch. Thus in the four month period between her introduction to the tank and the laying of the second batch, sperm must have remained viable within her sperm pouch. Females exhibit a preference for laying their eggs in the corners of the tanks and on the vertical surfaces. One mass was laid under rock ledge. Where there were more than one mass in a tank due to having been laid by different females, they were always separated by as much space as the size of the tank would allow.

It would seem that the most probable reason for the female remaining on her eggs during the incubation period would be to protect them from the crustacean *Melita zeylandica* Stebbing, 1904 (Amphipoda). These attacked the capsules of unattended masses, eating the tops away and leaving the ragged lower portions empty. Embryos in capsules removed from a mass and kept in stale unoxygenated water continued their development until putrefaction started after 27 days, thus suggesting that oxygen requirements are minimal.

During brooding, females abandoned their eggs after 32-65 days in 1974, whereas in 1972 and 1973 females were seen to leave their eggs only upon hatching. Shell sizes of brooding females ranged from 13,5 cm to 15,5 cm.

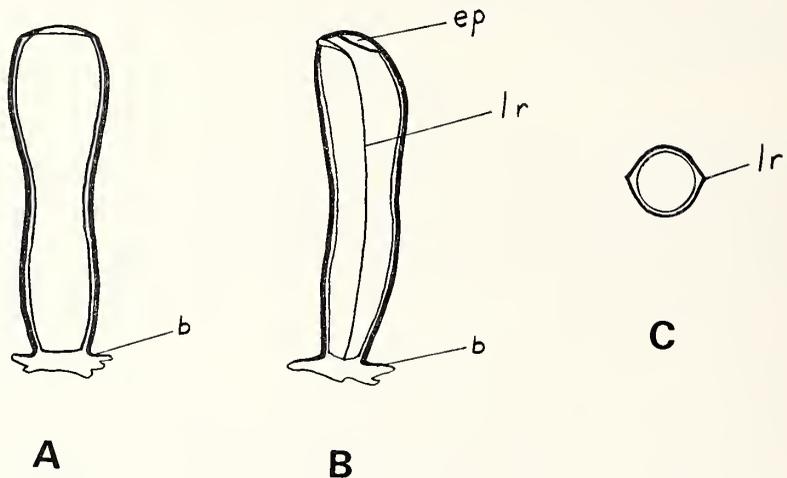


Fig. 1

Fig. 1. The egg capsules of *C. lampas pustulata* X3

View A: front

View B: side

View C: cross section through middle

ep=exit pore lr=lateral ridge b=base

Egg capsules

Egg laying was observed during 1972, 1973 and 1974. Each year the egg capsules appeared from mid July to the beginning of August. Whereas those laid in 1972 and 1973 hatched spontaneously and swam about in the tanks for 2 to 3 days, the 1974 batches did not follow this pattern. Some hatched as early as forty days and others, while incubating to a stage where they normally would have hatched, remained in the capsules until they eventually died.

An entire mass takes 36-48 hours to lay and consists of 90-120 capsules attached vertically to a tough semi-transparent gelatinous base on a rocky substrate. The shape of the mass is loosely circular but is sometimes elongated with no precise pattern. Capsules are transparent and apically rounded, their height being constant throughout the mass. Length of capsules vary from 12-22 mm, being medially constricted and circular in cross section with diameters:

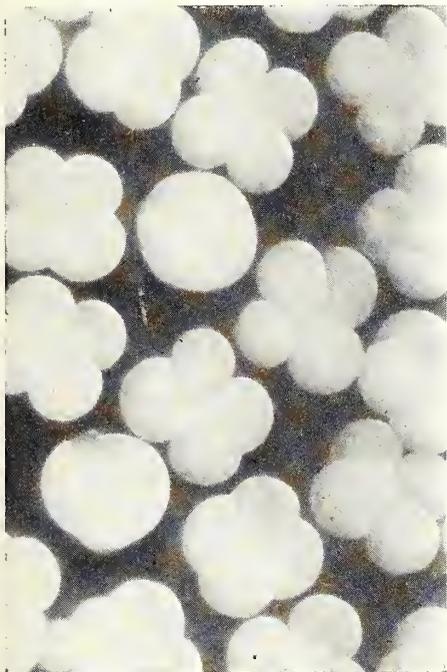


Plate 1. *Charonia lampas pustulata* larvae.
Age: 20 days.

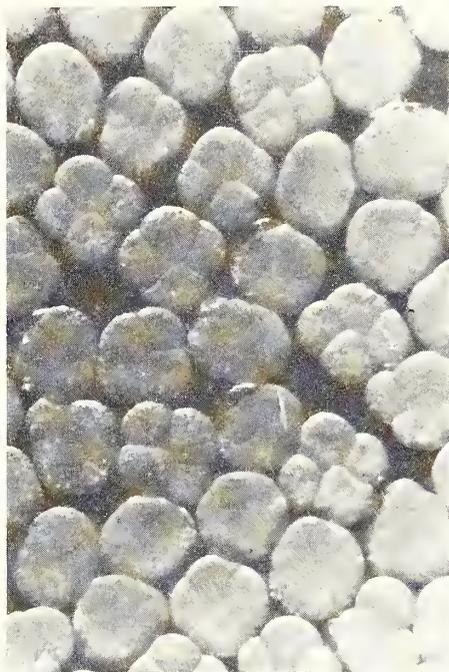


Plate 2. *Charonia lampas pustulata* larvae.
Age: 23 days.

6 mm (top), 3,7-4,4 mm (mid region) and 4,9 mm near base. No apical plug or line of weakness at the exit pore site is evident, and when a capsule had even pressure applied to its sides, it popped open at the base. Contents of two capsules counted showed one to contain 300 eggs and the other 2 000.

Freshly laid egg masses take on the colour of the yolk inside, resulting in the batches ranging from dull white to pale orange and through to dark orange (British Standard 2 660 no. 1-022 colour chart). It was not possible to determine whether the colour of the eggs bore any relation to that of the variable parent shell colouring. As the veligers within the capsules mature, a colour change of the whole mass to brown grey takes place.

Dr. D. J. Brand (pers. com.) gave the following report on specimens in the aquarium of the National Zoological Gardens of South Africa: Copulation was observed for a few days and after 5-7 days eggs appeared which were abandoned by their parents. The colour of the capsules was pearl grey to white. They were kept in artificially constituted sea water at a temperature of $\pm 14^{\circ}$ Celsius. The capsules disappeared after a few days, possibly eaten by some other form of marine life also kept in the tank.

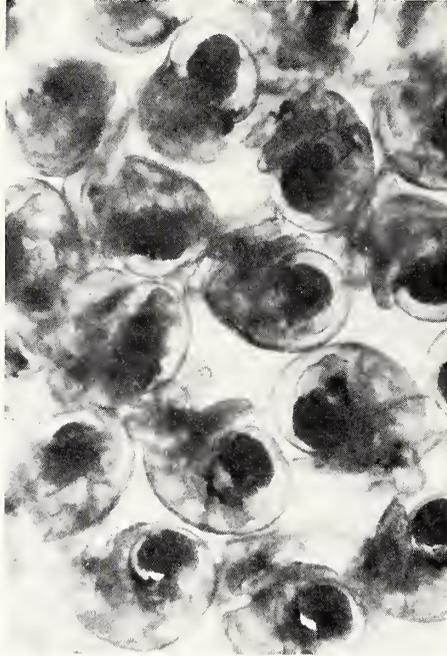


Plate 3. *Charonia lampas pustulata* larvae.
Age: 54 days.

Embryonic development

All eggs observed developed to maturity, but not all developed at precisely the same rate. Initially the eggs are evenly suspended in a clear albuminous jelly but as they develop they settle to the bottom of the capsules. The shape at five days is seen to be distinctly quadrifid and slightly flattened dorso-ventrally, these four large cells being apparently the megameres and not tetrads as described by Laxton (1969).

At 20 days a less pronounced quadrilobed shape is apparent, with some of the eggs showing multiple division of the smaller cells. They soon begin to assume an ovoid shape with the velum vestiges opposite the apex where the smooth shell first appears.

During the next two weeks marked development takes place. The shell is clearly evident and yolk occupies a large part of the visceral mass. The remaining space within the shell appears empty. The velum is developing and has short cilia capable of movement although not sufficient to provide propulsion.

By 50 days the cilia are approximately 0,02 mm long and the veliger moves rapidly. Two black eye spots are present and the foot has lengthened. There is no longer an empty space within the shell and no separate internal embryonic shell can be seen. At this stage the shell has a nautiloid shape and torsion has been completed. On further maturation the yolk mass diminishes in size leaving a considerable open space within the shell when the animal is extended. A pulse is apparent in the visceral area above the yolk mass only when the velum is extended. The definitive shell makes its appearance as an outgrowth on the peristome of the larval shell. Near the axis the definitive shell becomes slightly denser and tinged with brown. Both lobes of the velum are almost circular as seen ventrally, meeting in the area of the mouth. The width of the velum is approximately 0,31 mm and that of the body whorl of the shell as seen laterally approximately 0,35 mm. An operculum was not seen at the magnification used. At this stage complete withdrawal into the shell is possible. The curved beak of the shell described by Fretter and Graham (1962) is not present in this species.

The larvae hatch as free swimming veligers after an average incubation period of 63 days, with the range of variation being 32 to 123 days. Large numbers of hatched larvae were seen swimming in the tanks after hatching in 1972 and 1973. In all cases they died after 2 to 3 days. In 1974 however, this was not noticed due to reductions in the numbers of hatched veligers and the spasmodic rate of hatching.

The shell is smooth and has $1\frac{1}{2}$ whorls on hatching. During the planktonic life another 4 whorls of smooth, horn-coloured shell are produced. An abrupt change to the colour and structure of the adult shell takes place. The width of the last protoconchal whorl is 2,9-3,2 mm and the length of the protoconch is 2,9-3,5 mm. Young shells collected on the beach in May showed 0,75-2 whorls of adult growth after the protoconch.

A sample of apparently intact capsules removed from a mass at 22 days and kept in the laboratory for microscopic examination contained numerous fragments of embryos among the live ones. Also present were small highly motile unidentified crustacea. These were transparent and 0,02-0,05 mm in length.

Aquarium conditions

Supplied food consisted of small pieces of fish flesh. In one of the tanks where live fish were also present a large adult was observed eating a small "blacktail", *Diplodus sargus* Linn., one of the co-inhabitants of the tank. In a different tank algae on the side walls had been removed in long strips. As there were only sessile organisms present apart from *C. lampas pustulata*, it would seem that, at least on occasion, this species is also a grazer.

Water for the aquarium normally came from a rock pool dam and was sand filtered. Temperature records were not kept. It is interesting to note that on 13th August, 1974 a ship was wrecked near the aquarium, and the resulting oil spillage polluted the normal source of the aquarium's water supply. For the next 7 days water was supplied by tanker from the Buffalo River Harbour. As chemical analysis was not carried out it could not be determined if a lack of some essential element was responsible for the unusual hatching pattern exhibited in 1974. Apart from this abovementioned factor, aquarium conditions remained constant during the three seasons of observation.

Discussion

It was not possible to establish from this observational study what effects temperature, diet, water composition and lack of wave action have on the development pattern of this species. The results obtained would indicate that fecundity decreases with the length of time the animals are kept under aquarium conditions as described above. The enigma of the production of the exit pore remains unsolved.

Mayena Australasia Gemmifera (Euthyme, 1889)

Aquarium conditions and methods of study were the same as previously mentioned for *Charonia lampas pustulata*.

Adult behaviour

As there was never more than one female in the same tank, communal spawning was not observed. The female adult was seen to remain stationary on the capsules with tentacles sweeping slowly over them. She was not observed to eat during incubation. The male showed no interest in the egg mass. Copulation was not observed. In one tank *C. lampas pustulata* with egg capsules was also present but no inter-specific competition was observed. The shell size of the brooding female in this tank was 8,2 cm.

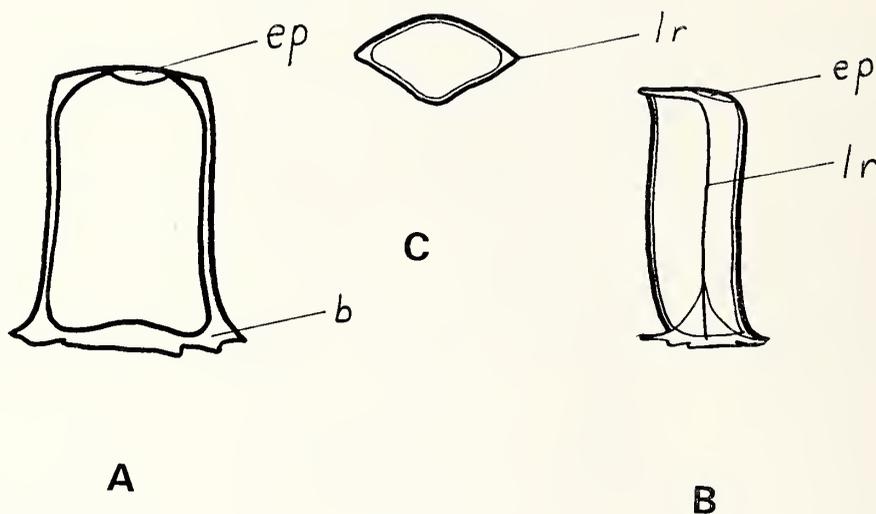


Fig. 2

Fig. 2. The egg capsules of *M. australasia gemmifera* X6

View A: front

View B: side

View C: cross section

ep=exit pore lr=lateral ridge b=base

The Egg Capsules

The eggs are laid once a year from the end of June to the beginning of August, a preference being exhibited for a position just below the waterline of the tank. In one tank a female laid a cluster of eggs which she abandoned following the removal of three capsules for study purposes. The egg mass had been laid three days previously. Two days later she laid another

batch of eggs. The first laid egg cluster developed normally while the second showed no signs of development, and was abandoned after 29 days.

Each capsule is 7,3-8,5 mm in length x 4,3-5,3 mm in lateral diameter x 2-3 mm in posterior-anterior diameter. A ridge on each side becomes a slight but curved extension of the apex, giving the vertex an angle of some 70° from this lateral ridge. The capsule itself is transparent and gelatinous, but takes on a white colour from the yolk of the eggs inside. Each capsule contains 500-600 eggs and there are 115-130 capsules in each cluster. Capsules are tightly packed with their recurved apices all centrally directed. The entire mass is circular in shape, approximately 6 mm in diameter, and takes 24-36 hours to lay. The top surface of the mass is flat and not cup-shaped as in *M. australasia* Laxton (loc. cit.). Only one cluster was seen to be

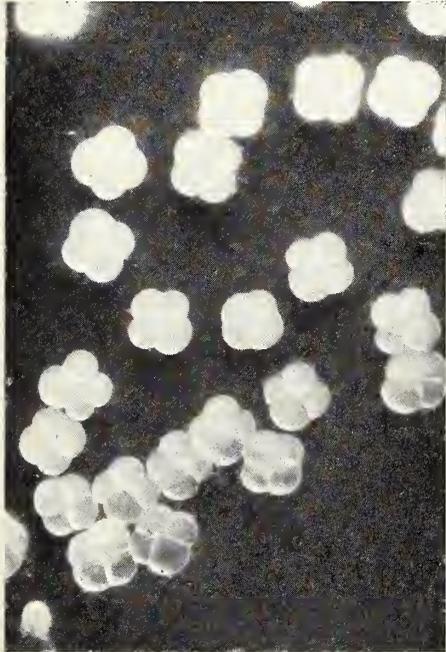


Plate 4. *Mayena australasia gemmifera* larvae.
Age: 5 days.

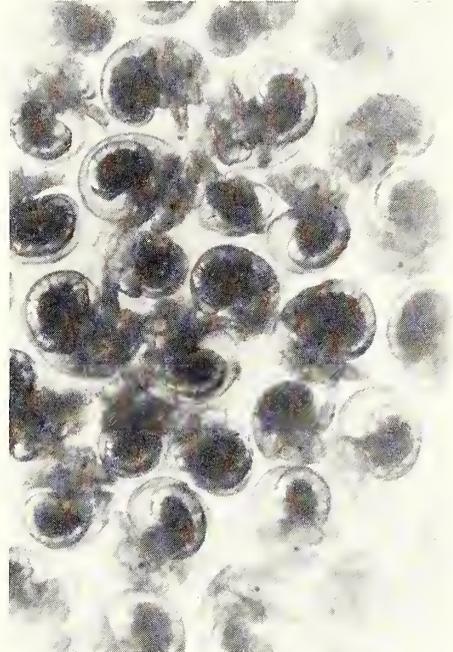


Plate 5. *Mayena australasia gemmifera* larvae.
Age: 70 days.

irregularly shaped and this was seen in 1972. Occasionally a half-sized capsule was seen at the outer edge of the mass.

During the three years of observation of the spawning of this species hatchings were never seen in the tanks although embryos developed into free swimming veligers within the capsules. When capsules were cut open at this stage the larvae lived only for 2-3 days, swimming about during this time.

Embryonic development

Apart from the previously mentioned egg batch laid 5 days after the first by the same female and which failed to develop, all eggs laid were found to develop normally.

At five days four large macromeres are readily noticeable, the egg size being 0,18-0,21 mm. By 18 days the cells lose their four-lobed appearance and are roughly circular in outline, the surface being uneven due to further cell division having taken place. Elongation of the eggs begin at 23 days, the one end becoming smooth, indicating the beginnings of the shell. By 33 days the eggs have all elongated with the rudimentary shell protruding from the end as a transparent projection. A half sized capsule taken from the edge of the cluster at this stage showed the eggs in it to be still round and featureless.

Considerable development is apparent after 51 days. A nautiloid shell of 0,25-0,28 mm in lateral width is present, into which the animal is capable of withdrawal. The yolky viscera fills the base of the shell at this stage, even when the animal is extended. The foot is relatively small and undefined and the operculum is not evident. Two eyespots are visible. The velar lobes are comparatively small and measure 0,18-0,19 mm across both lobes when extended. These are ringed with cilia 0,054-0,068 mm in length.

At 65 days the yolk is diminished in size and the foot has lengthened. The cilia measure 0,10 mm and the velum is approximately 0,3 mm across both lobes. By 70 days an operculum is visible. The lobe of the digestive gland still contains yolk, but is surrounded by intestine which appears empty. There is considerable individual variation in size at this stage, ranging from 0,2-0,35 mm.

The only hatchings which took place in this species occurred in a laboratory specimen bottle after a few capsules had been removed for study. They lived in the bottle for two days swimming about during this time. The veligers were then 50 days old. The remainder left in the tank died in their capsules at 80 days.

The protoconch grows for 4,75-5,25 whorls and is cream to horn coloured and from 3-4 mm in length. The diameter of the widest whorl is between 3,7 and 4 mm. Young shells collected on the beach on 14th May, 1973 showed an average of one adult whorl of growth after the protoconch.

Discussion

It would appear that temperature effects the hatching process. This was demonstrated when the embryos in the bottle hatched as the temperature was raised during transportation. Agitation cannot be ruled out either as the water in the tanks remain calm. Diet may also affect hatching. Although the starfish *Marthasterias glacialis* (Linn.) were present with one pair of *M. australasia gemmifera* in the same tank, the starfish were never eaten. M. Connolly (pers. comm.) states that she has only seen this species eating reef worms (*Gunnarea capensis* (Schm.)).

It is not known how the exit pore is created, but if an enzyme is involved, diet may affect its production. As with *C. lampas pustulata* no plug, line of weakness or putrefaction could be seen at the exit pore site.

From studies of this species M. Connolly (loc. cit.) states that eggs took six weeks to hatch. The eggs were laid in tidy rows under a rock reef about 60 cm below the low tide mark.

The hatching of the specimen-bottle embryos at 50 days and the report of hatchings in natural conditions at 42 days indicate that this sub-species has a shorter incubation period than the nominate species which Laxton (loc. cit.) reported to be three months.

ACKNOWLEDGEMENTS

I would like to thank the Director, staff and Board of Trustees of the East London Museum for their co-operation during this study. The kind help of the Curator and his staff at the East London Municipal Aquarium greatly facilitated work at the Aquarium and

discussion with them clarified many aspects of the observations made. My grateful thanks to Prof. Day of the University of Cape Town for his comments, to Mrs. C. Connolly of Kenwyn, Cape Province for her field data, and to Dr. Brand of the National Zoological Gardens of South Africa in Pretoria for information received about specimens in the aquarium of that institution. I would like to thank Mr. A. McLachlan of the University of Port Elizabeth for kindly reading the manuscript, and Dr. N. A. H. Millard of the South African Museum, Cape Town for identifying the Amphipod.

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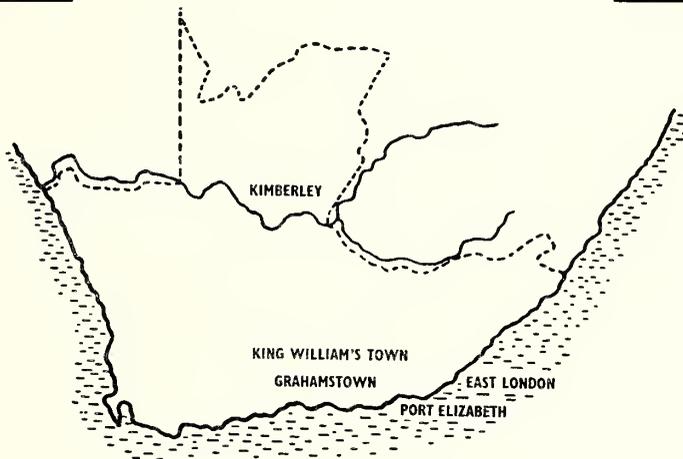
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 4

31st March 1976

PUBLISHED JOINTLY BY THE

CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

An ecological study of rodents in northern Natal, exposed to Dieldrin coverspraying

PIERRE SWANEPOEL

(Kaffrarian Museum, King William's Town)

ABSTRACT

Four grids, each 3,42 ha (4 morgen) in size, were live trapped from April 1967 through May 1969 in two soil and vegetation types near Pongola in northern Natal, to determine the effect of dieldrin coverspraying at a dosage of 87,4 g/ha (2,64 oz/morgen), on rodents. Low population numbers before and especially at the time of spraying made clear-cut conclusions impossible to reach. Rodent numbers (mainly *Praomys (Mastomys) natalensis*, *Saccostomus campestris*, and *Lemniscomys griselda*) were apparently not adversely affected, although *L. griselda* numbers showed a decline which was not in correspondence with that on the control area. This might be ascribed to dieldrin spraying. Relatively higher numbers of *S. campestris* and *L. griselda* numbers were observed during periods of lower *P. natalensis* numbers. Decreases in *P. natalensis* populations coincided with times of food scarcity. *Praomys natalensis* are thus found in association with other rodents when abundant food is available, but seems to give way when competition due to food scarcity occurs.

Reproduction data obtained from the study were too meagre to allow any conclusions concerning the effect of spraying thereon.

Population structure is expressed in terms of frequency per mass class for each season.

Behavioural features of the species captured were also noted.

INTRODUCTION

Large tracts of land in southern Africa are infested by harvester termites, *Hodotermes mossambicus* (Hagen). Although the recommended treatment with sodium fluosilicate bait is effective, implementation of this method on a large scale proved to be impractical. This led to the temporary registration by the Department of Agricultural Technical Services in 1964 of dieldrin coverspraying at a dosage of 87,4 g/ha (2,76 oz per morgen). Due to worldwide concern about the use of organochlorines in general and dieldrin in particular, the permanent registration of dieldrin depended on the outcome of longterm investigations into all its effects on animal life.

In recent years the effect of pesticides on mammals has received increased attention. Pesticides have on occasion been used for the control of rodents although usually at much higher concentrations than when used for insect control (Luckman, 1957; Schneider, 1966 Webb and Horsfall, 1967). More frequently, however, the effect of pesticides on mammals and other vertebrates is a secondary product of attempts to eradicate insect pests.

The effects of persistent pesticides on mammals have been widely studied both in the laboratory and in the field, e.g. Stickel, 1946; Scott, Willis and Ellis, 1959; Bernard and Gaetner, 1964; Ware and Good, 1967; Morris, 1968; Good and Ware, 1969; Korschgen, 1970; Morris, 1970; 1971; Murphy and Korschgen, 1970; Wiese *et al.*, 1970; and 1973.

Resistance to organochlorines, a widely known phenomenon in insects, has now also been demonstrated in the Pine mouse, *Pitymys pinetorum* (Webb and Horsfall, 1967).

In order to appreciate the ecological effects of pesticides, the ecology of the animals and areas studied should be known. Therefore, the present study reports on the effect of dieldrin spraying on the general ecology of wild living rodents occurring on two soil and vegetation types 11 km SSE of Pongola (27° 29'S, 31° 42'E), in northern Natal during the period April 1967 through May 1969.

One of the main aims of ecological work on rodents in South Africa has been to conduct surveys of those species that are involved directly or indirectly in vector-borne diseases of man (Davis, 1963a). A secondary purpose of this study, therefore, was to try to obtain information about those aspects of the ecology of *Praomys (Mastomys) natalensis* and other species occurring in the study area which would assist in understanding, and perhaps preventing, rodent outbreaks and the plague epidemics which sometimes accompany them.

STUDY AREA

The study area is located on the farm Vergeval 644, district Ngotshe, Natal, 11 km SSE of Pongola, at an altitude of approximately 360 m above sea level, and at the coordinates 27° 29'S; 31° 42'E.

An area of 428,3 hectares (500 morgen) was selected for the dieldrin project. One half of this area was sprayed on July 2, 1968 and the other half was used as a control area. Time and duration of trapping on the four grids are indicated in tables 2 to 5.

The climate of the area is subtropical, with a wet summer season followed by a dry winter.

Rainfall figures for the study area and for the Pongola Gorge (27° 26'S, 32° 4'E; 50 km ENE of the study area) are shown in table 1. Due to the fact that rainfall data for the study area were only available from September 1967 on, the Pongola Gorge rainfall figures (January 1966 to May 1969) and the average for Pongola Gorge area (657 mm per annum), were obtained from the Weather Bureau (Department of Transport, Pretoria) for comparison. The rainfall statistics for the nearby Pongola settlement (27° 23'S, 31° 37'E; alt. 274 m), available only for the period 1942 to 1950, can be summed up as follows:

Average over nine years: 718,8 mm.

Max. 977,6 mm (1943)

Min. 497,6 mm (1947) (Weather Bureau, 1954)

When the total rainfall on the study area during 1968, viz. 327,4 mm (the only complete rainfall data for a full year available), and that in the Pongola Gorge during the same period (403,1 mm), are compared with the average over nine years (1942 to 1950) at the Pongola settlement (718,8 mm), it becomes apparent that 1968 was an extremely dry year, the nine-year average rainfall at the Pongola settlement being much higher than the 1968 figures observed on the study area and at the Pongola Gorge Weather Station. The 1968 rainfall on the study area, in fact was even lower than the minimum of 497,6 mm observed at the settlement over the nine year period.

From January to May 1967 the rainfall on the study area was much higher than during the same period in 1968 (records from neighbouring farmers). From July 1968 (the time of spraying) until February 1969, the rainfall was lower than during the same period the previous year. From March to May 1969 the rainfall exceeded that for the previous year (table 1).

The study area, situated in the lowveld veld type (Acocks, 1953) and the Southern savannah biotic zone (Davis, 1962) is composed of two plant communities, viz. *Acacia tortilis*, and *A. nigrescens*. Two grids were situated in each community, grids P46 and P50 in the *A. tortilis*

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TABLE 1: Monthly rainfall (in mm) on the study area between September 1967 and May 1969, and at Pongolo Gorge (27' 26"S, 32' 4"E), between January 1966 and May 1969.

Year	Month	Study area	Pongola Gorge
1966	Jan.	—	251,5
	Feb.	—	83,2
	March	—	19,5
	April	—	18,7
	May	—	21,6
	June	—	8,2
	July	—	0,0
	Aug.	—	17,7
	Sept.	—	5,5
	Oct.	—	15,5
	Nov.	—	60,8
	Dec.	—	55,2
		Total	—
1967	Jan.	—	86,1
	Feb.	—	204,8
	March	—	28,6
	April	—	76,4
	May	—	30,5
	June	—	1,4
	July	—	9,8
	Aug.	—	1,9
	Sept.	18,3	19,3
	Oct.	37,7	49,5
	Nov.	99,1	98,0
	Dec.	26,5	8,9
		Total	—
1968	Jan.	82,1	26,6
	Feb.	67,9	87,8
	March	40,1	105,6
	April	36,0	13,2
	May	1,7	3,0
	June	0,5	3,2
	July	0,0	23,2
	Aug.	16,9	14,4
	Sept.	2,9	1,2
	Oct.	24,3	28,4
	Nov.	45,1	52,0
	Dec.	9,9	44,5
		Total	327,4
1969	Jan.	69,8	73,7
	Feb.	12,7	22,9
	March	156,6	135,1
	April	59,0	76,9
	May	44,7	47,7
	Total	342,8	356,3

community and grids P88 and P89 in the *A. nigrescens* community. This means that a control and a sprayed grid occurred in each plant community.

The study area was grazed during the first three weeks of October 1967 by approximately 1 000 head of cattle, from 9 to 18 May, 1968 by 300 head and from 19 to 31 May, 1968 by 170 head. Thereafter no grazing by cattle took place.

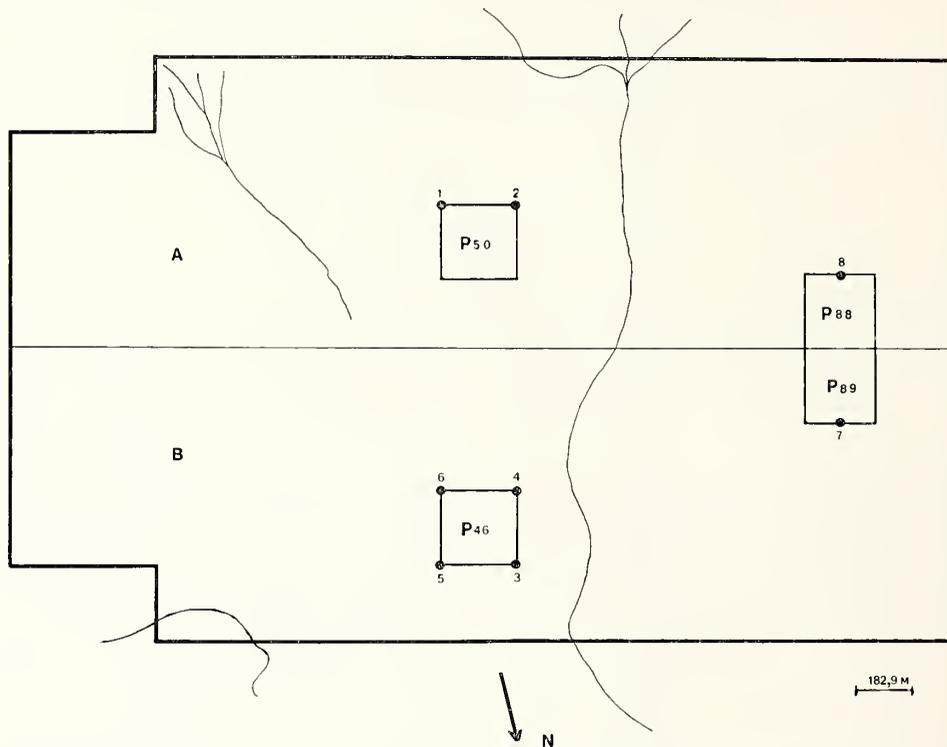


Fig. 1: The positions of the four grids and of the soil samples (numbers 1 to 8) taken on the study area. The dry stream bed cutting through the area from south to north divides the area into two main plant communities viz. *Acacia tortilis* (Grids P46 and P50) and *A. nigrescens* (Grids P88 and P89). A branch of this stream is shown in the north eastern corner of the study area. Area A was dieldrin sprayed and area B was treated as a control. An erosion donga is shown in the south east end of the sprayed half.

At least 100 Impala *Aepyceros melampus*, were present on the area throughout the period of the study, although a much higher population sometimes occurred. Other ungulates present in low numbers were Kudu *Tragelaphus strepsiceros*, Bushbuck *Tragelaphus scriptus*, Steenbok *Raphicerus campestris* and Grey duiker *Sylvicapra grimmia*.

The following small mammals were captured in the course of the study:

Praomys natalensis (A. Smith, 1834) (Multimammate mouse);

Saccostomus campestris (Peters, 1846) (Pouched mouse);

Lemniscomys griselda (Thomas, 1904) (Single-striped grass rat);

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Mus minutoides (Smith, 1834) (Pygmy mouse);
Steatomys pratensis (Peters, 1846) (Fat mouse);
Aethomys (Aethomys) chrysophilus (de Winton, 1897) (Red veld rat);
Tatera brantsi (A. Smith, 1834) (Highveld gerbil);
Otomys angoniensis Wroughton, 1906 (Vlei rat); and
Crocidura hirta (Peters, 1852) (Musk shrew).

The position of the study grids (P46, P50, P88, and P89) in the study area is shown in fig. 1.

The general topography and nature of the habitat of grid P46 during November, 1968 are indicated in fig. 2. The clayish soil varies from dark brown to brownish red in colour. The area is flat and free of stones with *Acacia tortilis* and *A. karroo* the two most common tree species. The most common grass was *Sporobolus smutsii*. In the shade of the acacias, *Panicum maximum* and *P. deustum* were, however, the dominant species. These latter two species were those most damaged by termites through the winter months.

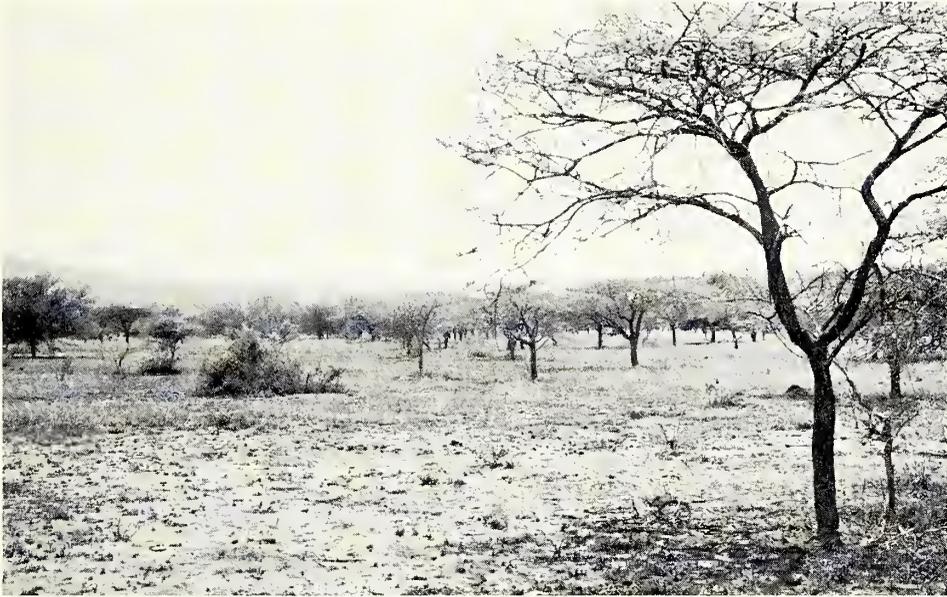


Fig. 2: The general topography and habitat of grid P46. The photo was taken in November 1968.

During April/May 1967 the grass cover was denser than at any other time during the study period. By the end of August (the end of winter), however, the grass cover had been severely damaged by harvester termites, more than on any of the other three grids. During the winter of 1968 (June to August) much less termite activity was observed than during the previous winter.

At the end of the wet season in April/May 1968, the grass stand was far less than at the same time during the previous year. This was due mainly to the much lower rainfall during early 1968 (table 1).

The vegetation cover during late spring (November) of 1968 is shown in fig. 2. From this it can be seen that no new growth had taken place by the end of the spring. No sub-

stantial growth occurred before good rains fell in March, 1969. This was, however, too late to enable any significant rodent population increase to take place before the termination of the study (see Population densities).

The general topography and nature of the habitat of grid P50 during November 1968 are depicted in fig. 3. The clayish soil is brown-red in colour and the area is flat and free of stones, with *A. tortilis* the most common tree.

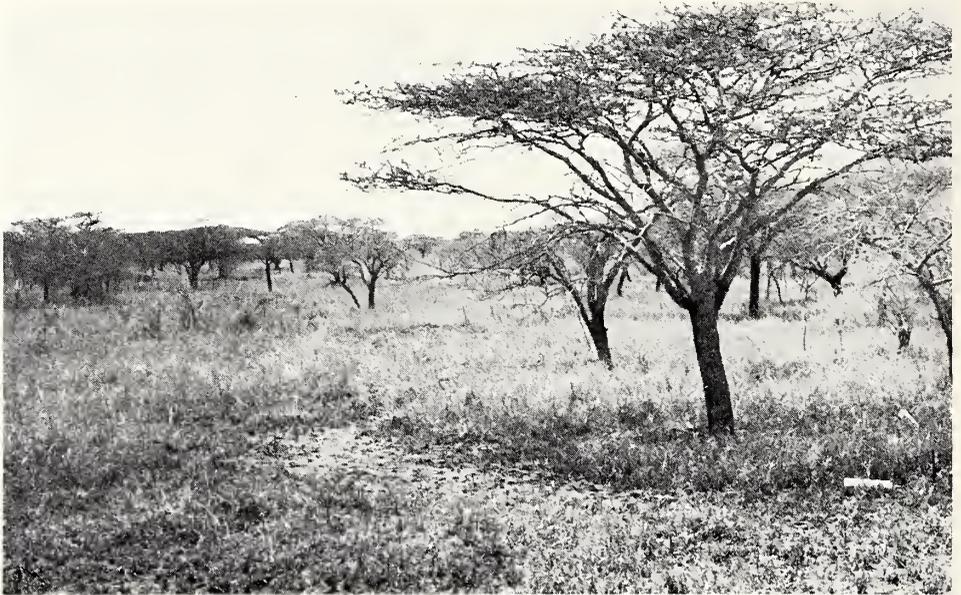


Fig. 3: The general topography and habitat of grid P50. The photo was taken in November 1968.

Panicum maximum and *P. denstun* were less common than on grid P46. These two grass species seemed to be favoured by termites. The most common and less favoured species, *S. smutsii*, remained relatively dense even during winter.

During the 1968/69 rainy season this grid had a relatively better grass cover than did P46 (see figs. 2 and 3). The vegetation cover on this grid, however, was also poor during late spring of 1968 (November) and did not improve before March 1969.

Grids P88 and P89 are situated on a slightly stony slope, sloping downwards from west to east. The soil type is black clay (black turf).

The general topography and nature of the habitat during November 1968 are evident from fig. 4. *A. nigrescens* was the most common tree. *Heteropogon contortus* and *S. smutsii* were the most abundant grasses. *P. maximum* and *P. denstun* were sparsely distributed and are assumed to have played an insignificant role on these two grids.

Grids P88 and P89, on black clay soil, and the vegetation belonging to the *A. nigrescens* community, had a continuous grass cover (fig. 4) in contrast with the *A. tortilis* community (figs. 2 and 3), probably as a result of undergrazing of the *A. nigrescens* community, the conspicuous absence of termites or termite damage, and the soil type.



Fig. 4: The general topography and habitat of grids P88 and P89. The photo was taken in November 1968.

MATERIAL AND METHODS

The four grids, each 3,42 ha in size, were each trapped with 225 Chauvancy live traps spaced 13,1 metres (43 feet) apart, 15 rows with 15 trap stations each, and one trapper section placed within a 1 metre radius of the station marker.

The time and duration of trapping on the four grids are indicated in tables 2 to 5. Grids P46 (19 times) and P89 (16 times) were trapped from May 1967 through May 1969. Grid P88 (16 times) was trapped from April 1967 and grid P50 (18 times) from August 1967, both through May 1969. Each grid was trapped for four successive nights during each trapping period, with all 225 traps operating concurrently. Because of the lower number of animals captured, grids P88 and P89 were sometimes trapped for only 3 nights during a trapping period.

The Chauvancy live trap is made by G. Rousseau and A. Darnet, 64 Avenue Gambetta, Paris, France on a patent of Centre National De La Recherche Scientifique. It is so designed that by touching the bait, attached to a wire trigger, the trap door closes immediately.

A mixture of peanut butter and rolled oats was used as bait. No prebaiting was carried out.

On first capture each rodent was etherized and marked by toe-clipping and/or ear-clipping. In addition, the following data were recorded for each animal at every capture: species; the mass of each animal to the nearest gram, obtained on a triple beam balance; sex; position of testes in males, whether scrotal or abdominal; vagina open or closed in females; pregnancy in females, as detected by palpation; total length in millimetres (animals were stretched out on their backs on a ruler and measured from the tip of the nose to the end of the tail); tail length, by the vertebral method (Coetzee, 1967); and trap number.

After the above data had been recorded the animals were released at their point of capture.

During all the trapping periods from May 21, 1968 to November 1968, traps in grids P46 and P50 were serviced twice daily, in the early morning and again at sundown. This prevented mortality of the diurnal *Lemniscomys griselda*, which otherwise sometimes had to remain in the traps for a day and a night before release. Prior to May 21, 1968 the number of *L. griselda* captured did not warrant this procedure, and their numbers in the other two grids were too low throughout the study to require traps to be serviced twice daily.

For the purpose of population density estimation the afternoon catches were added to those of the following morning. The data thus accumulated were treated as if the traps had only been cleared in the mornings.

Grids P50 and P88 were sprayed from the air on July 2, 1968 with a solution of 13% (weight/weight) technical dieldrin (85 per cent 1,2,3,4, 10-hexachloro-6, 7-epoxy-1,4,4a, 5,6,7,8, 8a-octahydro-exco-1, 4-endo-5, 8-dime-thanonaphthalene, Heod, and 15 per cent related compounds) in a mixture of 70 per cent xylene/styrene polymer and 30 per cent Shellsol R, at the rate of 0,630 litres/hectare (0,95 pints/morgen; 83,0 g per ha). A rate of 0,633 litres/hectares (1,00 pint/morgen) is equal to 87,4 g active material per ha (2,64 oz/morgen). Therefore, slightly less dieldrin was sprayed than was intended. The insecticide was delivered by four two-blade rotary atomisers giving a distribution pattern of 5,77 droplets per cm² (37,2 droplets/in²) (Wiese and Basson, unpublished data).

At intervals of 10, 14, 20, and 60 days after spraying, small mammals were snap-trapped, and whole carcass samples taken for gas-chromatographic determination of dieldrin and photodieldrin (photoisomerization product of dieldrin) residues. As rodent populations were low at the time, all the species occurring were not sampled every time.

Three grass samples for analysis were taken from the sprayed area immediately after spraying and at 1,2, 7, 14, 21, 30, 42, 56, 90, 146, 189, 258, and 380 days after spraying. (Wiese and Basson, unpublished data).

The gas-chromatographic method used for analysis is described by Wiese, Basson, and van der Merwe (1970).

The density during April/May 1967 was estimated by means of the capture-recapture method described by Davis (1956). This was adopted because the method of Jolly (1965), which was used for data from the rest of the study, supplies no population estimate for the first sample.

From August 1967 to May 1969 densities were estimated by means of the stochastic capture-recapture model of Jolly (1965).

The percentage of scrotal males and pregnant females per trapping period was calculated and breeding seasons for the different species were obtained. The relative frequency of animals of different body mass during the four seasons of the year was used to divide the population into different age classes. Behaviour of the species encountered was noted during trapping, handling, and release.

RESULTS AND DISCUSSION

Population densities

The numbers of animals of each species and sex captured, the number of first captures, and the total number captured during each trapping period on all the grids appear in tables 2 to 5. The population density estimates on grids P50 and P46 are illustrated in figs. 5 and 6.

Throughout the study the *A. nigrescens* community (see study area) usually had a denser grass cover than did the *A. tortilis* community, especially during drier periods. It is surprising,

therefore, that grids P88 and P89, adjoining each other in the *A. nigrescens* plant community, consistently supported a relatively much lower rodent population than did grids P46 and P50, situated in the *A. tortilis* community. During the rainy season the new growth in the *A. tortilis* community was better than in the *A. nigrescens* community. Dead grass was always present in the latter but never in the former, suggesting undergrazing in the *A. nigrescens* community.

During April/May 1967 grids P88, P89 and P46 supported the largest rodent population per grid observed at any time during the study, consisting mostly (52% and more) of *P. natalensis*. Grid P50 was not trapped during this period. This high rodent population during the late autumn of 1967 coincided with a rodent population outbreak observed through large parts of southern Africa, extending from late 1966 to early 1969 in some areas (Van der Merwe and Keogh, 1970). After the autumn of 1967, there was no evidence of the outbreak in the study area.

Of this population, only a small breeding stock still remained in August/September 1967 for the 1967/68 breeding season. This can be primarily ascribed to a considerable reduction in amount of vegetation and ground cover during the winter. Grid P46 in particular was largely laid bare by harvester termites between May and August 1967. This grid experienced its most marked decrease in rodent population density during this time (fig. 6).

On grid P88 (table 2) and grid P89 (table 3) *P. natalensis* declined from 17 and 13 individuals per grid respectively in April 1967, through the winter of 1967 and summer of 1967/68 to a low in December 1967 on grid P88, and in April 1968 on grid P89, when only one animal was captured on each grid. Thereafter numbers remained low until the end of the study.

While barely present on these two grids (tables 2 and 3) from September to December 1967, *S. campestris* increased on both to a small peak (six animals) in February 1968. It disappeared from both grids prior to spraying in July 1968. On grid P88, which was sprayed, this species appeared again in July, just after spraying, but never more than one at a time, and on grid P89 (control) it did not appear until May 1969 (three animals).

Lemniscomys griselda numbers on these two grids (tables 3 and 4) stayed consistently low and no clear trend could be discerned.

Aethomys chrysophilus, *Mus minutoides*, and *Steatomys pratensis* were very infrequently present on grid P88 (table 2). Grid P89 (table 3) also supported low numbers of these species. During May and September 1967, however, a relatively high number of *M. minutoides* (three to six animals) was present on this grid.

Mus minutoides and *S. pratensis* appeared sporadically on grid P50 (table 4). One *Otomys angoniensis* was captured on this grid, but *A. chrysophilus* was never observed. *Steatomys pratensis* was never captured on grid P46, while *M. minutoides* seemed to be present more regularly here than on grid P50. *Aethomys chrysophilus* was recorded on grid P46 during February 1968 and April 1969, while *T. brantsi* was recorded from this grid during February and May 1969 (table 5).

According to Veenstra (1958) *P. natalensis* is found in association with other rodents (*Rattus*, *Tatera*, *Mus*, and *Rhabdomys*) when abundant food is available, but when competition leads to food scarcity it gives way. In domestic habitats where *Rattus* or *Mus musculus* have established themselves, *P. natalensis* seems to be driven away (Shortridge, 1934, citing Hewitt, 1918 and 1931). Delany and Neal (1966) report the same phenomenon; after the introduction of *Rattus rattus* in Uganda, *P. natalensis* was driven from its domestic habitat (native huts).

On both grids P50 (fig. 5) and P46 (fig. 6) *S. campestris* experienced a relatively large increase in numbers during the period January/February to early May 1968, before *P. natalensis* started to decline (see below). Although the sample was small, the fact that both grids showed more or less the same trend suggests that the relationship is a real one and not a result of sampling error.

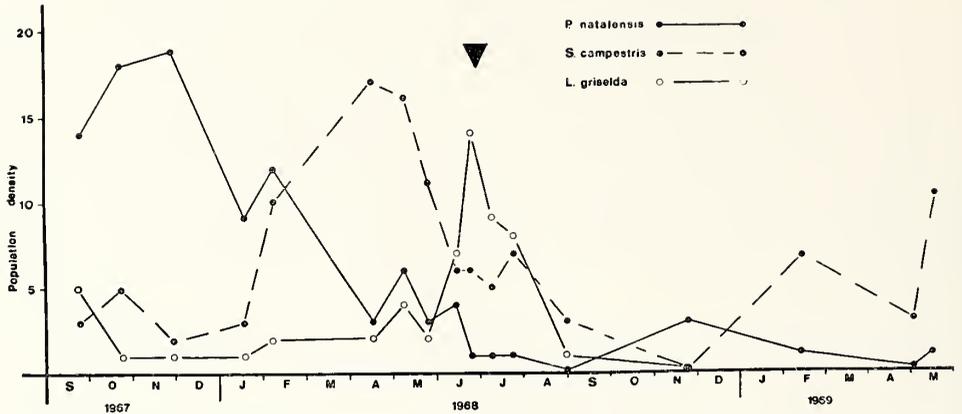


Fig. 5: The estimated population of *Praomys (Mastomys) natalensis*, *Saccostomus campestris* and *Lemniscomys griselda* on grid P50. Time of spraying is indicated by an inverted triangle.

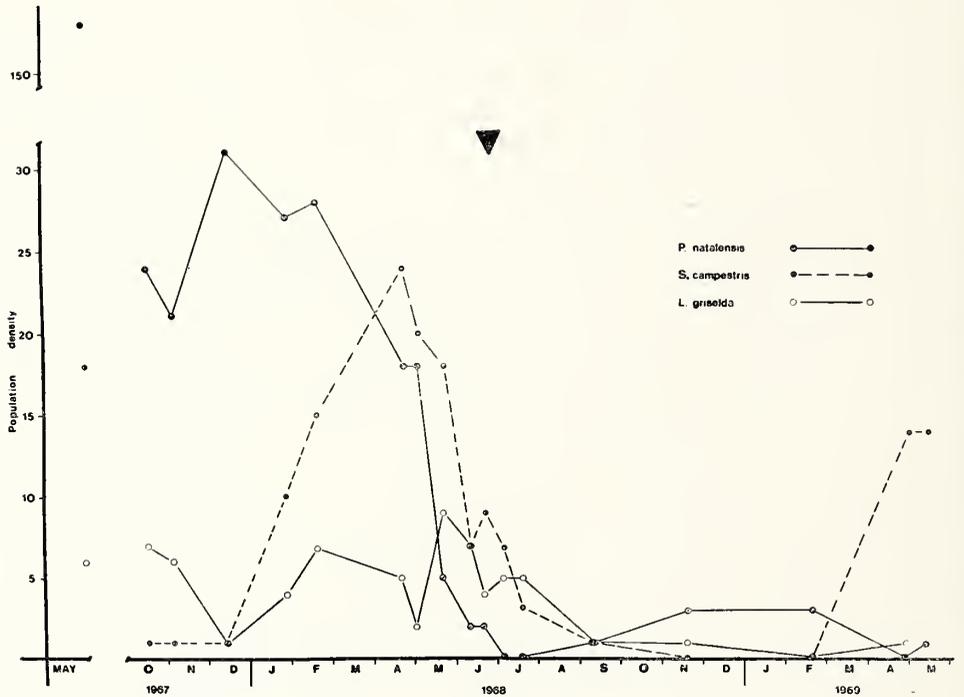


Fig. 6: The estimated population of *Praomys (Mastomys) natalensis*, *Saccostomus campestris* and *Lemniscomys griselda* on grid P46. Time of spraying is indicated by an inverted triangle.

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Relatively higher numbers of *S. campestris* and *L. griselda* than usual were observed during times of lower *P. natalensis* populations. The total population on grid P50 comprised from August 1967 to February 1968 (the time of a *P. natalensis* high) on the average 60% *P. natalensis*, 19% *S. campestris*, and 12% *L. griselda* of the 135 animals captured. While the remaining species comprised 9% of the animals captured. During the subsequent period, towards late July 1968 (time of relatively high *S. campestris* and *L. griselda* numbers), *P. natalensis* averaged 13% of the 110 animals captured, *S. campestris* 45%, and *L. griselda* 41% (table 4). During the following period, towards termination of the study in May 1969, the animals captured comprised 16% *P. natalensis*, 75% *S. campestris*, and 3% *L. griselda*.

During April/May 1967, on grid P46 *P. natalensis* comprised 86% of the 177 animals captured, *S. campestris* 10% and *L. griselda* 3%. From September 1967 to February 1968 *P. natalensis* comprised on the average 67% of the 219 animals captured, *S. campestris* 13%, and *L. griselda* 15%. During the subsequent period, towards late July 1968 (the time of relatively high *S. campestris* and *L. griselda* numbers), *P. natalensis* averaged 28% of 163 animals captured, *S. campestris* 44% and *L. griselda* 22%. The trapping periods from July 1968 to May 1969 yielded 20% *P. natalensis*, 64% *S. campestris* and 9% *L. griselda* (table 5).

These lower *P. natalensis* numbers coincided with times of extreme food scarcity. During the autumn (April/May) of 1967 when the habitat was good, with abundant food, *P. natalensis* numbers were high while *S. campestris* and *L. griselda* numbers were relatively low. During the autumn of 1968 and 1969 *S. campestris* was present in relatively high numbers, coinciding with a time of food scarcity.

In spite of the fact that *P. natalensis* is a very successful rodent in terms of reproduction and distribution, the present data seem to favour the hypothesis that *P. natalensis* gives way during times of food scarcity in autumn and winter.

EFFECT OF DIELDRIN COVERSPrAYING ON RODENT NUMBERS

Grids P88 and P50 were sprayed with dieldrin on 2 July, 1968 while grids P89 and P49 were treated as controls.

After the *P. natalensis* population declined in December 1967 (i.e. before spraying) on grid P88 (sprayed) and P89 (control), *P. natalensis* never again increased on these two grids to such a level as to supply either positive or negative evidence regarding the effect of spraying (tables 2 and 3). On grid P46 (control) the population declined from its peak in December 1967 to zero in early July 1968 (the week of spraying), and thereafter stayed at a low level until termination of the study (fig. 6 and table 5). The number on grid P50 (sprayed), after its highest peak in October 1967, declined progressively to an extreme low just prior to spraying and thereafter showed no increase above this level. Again there is no evidence of a differential decline in numbers which could be ascribed to spraying (fig. 5 and table 4).

This decline in *P. natalensis* numbers must therefore be ascribed to low rainfall and poor habitat as both sprayed and control grids declined to a similar extent.

On grid P88 (table 2) and grid P89 (table 3) *Saccostomus campestris*, after its peak in February 1968, decreased to zero just prior to spraying. It appeared again on grid P88 just after spraying in late July and thereafter stayed at an extremely low level. On the control grid P89, *S. campestris* did not appear again before May 1969. After a population peak in April 1968, the *S. campestris* population on grid P46 (fig. 6) decreased towards early July (the time of spraying). Thereafter it stayed low until a substantial increase occurred in May 1969. The population on grid P50 (sprayed; fig. 5) also showed a peak in April 1968, declined to a low in early July (just after spraying), and thereafter stayed low until a similar increase as on grid P46, was observed in May 1969.

Lemniscomys griselda numbers on grids P88 (table 2) and P89 (table 3) stayed low and no clear trend was apparent. During late May 1968 a peak was observed on grid P46 (fig. 6). At the time of spraying the population had, however, already declined and thereafter declined still further to zero in February 1969. Grid P50 (sprayed; fig. 5) supported a high population from early June 1968 until after spraying in late July, whereafter it declined sharply to zero in November, not to increase again. Although *L. griselda* numbers on the sprayed grid P50 did not decline until after spraying, this was not evident on grid P46 (control), where a decline was already observed prior to spraying. Therefore, the possibility does exist that spraying might have influenced *L. griselda* numbers on grid R50.

RESIDUE ANALYSIS

Dieldrin and photodieldrin residues (mean of three samples) found on the grass at progressive intervals after spraying are shown in table 6 (Wiese and Basson, unpublished data). These data correspond closely with those of Wiese, Basson, and van der Merwe (1970) and Wiese and Basson (unpublished data) for veld treated at the same dosage.

TABLE 6: Dieldrin and photodieldrin residues (in ppm) on the veld at increasing intervals after treatment (mean of three replicates) on the study area (From Wiese and Basson, unpublished data).

Days	Dieldrin	Photodieldrin
0	15,08 ± 1,14	0,12 ± 0,01
1	10,61 ± 1,24	1,67 ± 0,02
2	9,29 ± 1,09	4,05 ± 0,52
7	4,34 ± 0,17	7,3 ± 0,40
14	1,97 ± 0,37	8,37 ± 0,73
21	1,65 ± 0,45	6,65 ± 0,50
30	1,00 ± 0,30	4,57 ± 0,60
42	0,46 ± 0,17	4,26 ± 0,02
56	0,38 ± 0,15	3,20 ± 0,03
90	0,11 ± 0,02	1,40 ± 0,03
146	0,08 ± 0,02	0,67 ± 0,03
189	0,02 ± 0,02	0,35 ± 0,04
258	0,01 ± 0,01	0,20 ± 0,08
380	< 0,01	< 0,01

Immediately after spraying 15,08 ppm dieldrin were present on the grass and it thereafter declined to 4,34 ppm after seven days and 1,00 ppm after 30 days, while photodieldrin (photoisomerization product of dieldrin) increased from 0,12 ppm immediately after spraying to a peak of 8,37 ppm 14 days after spraying and thereafter declined to 1,4 ppm 90 days after spraying. No detectable amount of either dieldrin or photodieldrin was present 380 days after spraying.

Dieldrin and photodieldrin residues (in ppm) obtained from whole small mammal carcasses, are shown in table 7. As the rodent numbers were low, not all species were sampled on each occasion. Samples were obtained only from *Saccostomus campestris*, *L. griselda* and *Crocidura hirta*. *Lemniscomys griselda* (10, 20, and 60 days after spraying) and *S. campestris* carcasses (16 days after spraying) showed very low residues (<1.0 ppm), while one *C. hirta* collected 60 days after spraying, showed 4,66 ppm dieldrin, and 0,21 ppm photodieldrin.

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TABLE 7: Dieldrin and photodieldrin residues (in ppm) in carcasses of rodents exposed to treated habitat on the study area at increasing intervals after treatment. Sample sizes are shown in brackets.

Time elapsed between dieldrin application and sampling (days)	Pesticide	<i>L. griselda</i>	<i>S. campestris</i>	<i>C. hirta</i>
10	Dieldrin Photodieldrin	0,010 (5) 0,000	— —	— —
16	Dieldrin Photodieldrin	— —	0,015 (2) 0,000	— —
20	Dieldrin Photodieldrin	0,054 (6) 0,000	— —	— —
60	Dieldrin Photodieldrin	0,102 (3) 0,000	— —	4,660 (1) 0,206

REPRODUCTION

The study covered two complete breeding seasons, viz. 1967/68 and 1968/69, as well as the end (April/May) of the 1966/67 breeding season. Reproductive activity was observed only in *P. natalensis*, *S. campestris* and *L. griselda*.

Praomys natalensis

Breeding data for grids P88 and P89 were combined because of the small samples obtained from each. At the end of the 1966/67 breeding season (during April/May 1967), scrotal males were observed but no pregnant females. While there was reproductive activity in the 1967/68 season, extending from September 1967 to February 1968 (69% of 29 females pregnant and 62% of 34 males scrotal), there was none in the 1968/69 season.

Grid P50 was not trapped until after the end of the 1966/67 breeding season. Fifty-two per cent of 29 females and 73% of 41 males were in breeding condition during the period September 1967 to April 1968. During the next breeding season no pregnant females were observed amongst three captured and only one scrotal male (collected in November 1968) of two captured.

Reproduction, especially amongst the females, was much lower on grid P46 (control) than on grid P50 (sprayed). Pregnant females were observed only during September and October 1967 (seven of 10 animals captured) while from September 1967 to early May 1968, 65% of 110 males observed were scrotal. No pregnant *P. natalensis* females were observed on grids P46 and P50 during the 1968/69 season. Scrotal males were observed on both but in very low numbers (see above) (grid P46; one male observed during September 1968 not scrotal; one scrotal male of two observed in November 1968; and two scrotal males in February 1969).

When data for the four grids are combined, females in breeding condition (i.e. pregnant) were observed from September to February and males in breeding condition (i.e. scrotal) from September to April.

Brambell and Davis (1941) found breeding females throughout the year in Sierra Leone with the greatest proportion present during October to November (end of wet season/beginning of dry season; autumn in northern hemisphere). Chapman, Chapman, and Robertson (1959) observed pregnant females in Rukwa, Tanzania from February to November with a

peak during April and May (end of wet season/beginning of dry season; autumn in southern hemisphere). Pirlet (1954) found breeding in Katanga also to be at its height during the autumn months. In Uganda during the period June to July 1958, Southern and Hook (1963) found three of seven females collected either pregnant or lactating. Material from Uganda (Delany, 1964a) indicates no pregnant or lactating females during August to December 1961. The same was observed in 19 females during the period 13 July to 13 September 1963 (Delany, 1964b). Delany and Neal (1966 and 1969) observed pregnant females in Uganda during May to July and during October to December, while males with high sperm rating were observed throughout the year. Coetzee (1965 and 1967), studying the breeding season of *P. natalensis* in the Roodepoort area near Johannesburg, reports breeding to be continuous through the spring and summer, reaching a peak in autumn (March to May; end of wet season/beginning of dry season). Thereafter no breeding was observed until July/August (end of winter) in spite of abundant food being present in nearby maize lands.

An autumn reproductive peak at the end of the rainy season was not observed in the present study. Poor rainfall during the study is suspected to be the cause.

Saccostomus campestris

Ten of the 14 males observed on grids P88 and P89 during the 1967/68 season were scrotal. In April 1967 there were few observations, which included less than 5% scrotal animals. The only pregnant female observed on these grids during the study was encountered in May 1969 when one of four females captured proved to be pregnant.

On grid P50 (sprayed) pregnant females were observed in October 1967 (one of two animals), February 1968 (one of four animals) and May 1969 (two of four animals). On grid P46 (control) no pregnant females were observed throughout the study. Scrotal males (68% of 25 animals observed) were present on grid P50 from August 1967 to early May 1968, and from August 1968 to May 1969 (94% of 16 animals observed). Scrotal males were present on grid P46 from October 1967 to June 1968 (50% of 52 observed), in September 1968 (one of one), and during April/May 1969 (70% of 20 animals observed).

When the breeding data from all four grids are combined, the observed breeding activity of males lasted from late August to June while that of females extended from October to February.

A pregnant female *S. campestris* was observed in Uganda during November (Delany and Neal, 1966).

Lenmiscomys griselda

On grids P88 and P89 scrotal males were observed only during April/May 1967 (three of three animals) and during October 1967 (one of one). The only pregnant females encountered were during February 1968 (two of three animals observed).

Grid P50 (sprayed) supported breeding males and females prior to spraying but not afterwards (males: September 1967, the only one captured being scrotal; February to May 1968, all four animals scrotal; females: September 1967, all four females pregnant; and January 1968, the only female captured pregnant). No pregnant females were observed on grid P46 (control) during the study and scrotal males were encountered only before spraying, from September 1967 to February 1968 (53% of the 17 animals observed were scrotal).

Combining the data for the four grids, breeding activity of females extended from September to February and that of males from September to May.

Because of the below average rainfall during the study period and the possible effect of this on the vegetation, the observed extent of breeding activity for the different species might be somewhat aberrant.

Reynolds (1960) reports two peaks of breeding in Merriam's kangaroo rat, *Dipodomys merriami*, corresponding closely with the periods of new vegetation growth in spring and late summer. Bodenheimer and Sulman (1946) report that fresh vegetation has a stimulating effect upon breeding activity, and that the oestrous cycle of the vole *Microtus guentheri* seems to be associated with a gonadotrophic factor found in fresh green plant material which is responsible for increased ovulation.

Bothma (1969) found high temperature and a too low or too high rainfall the apparent limiting factor of the breeding season of Cottontail rabbits *Sylvilagus floridanus*, in South Texas. He found reproductive peaks to correspond to increased growth of vegetation in the spring and autumn.

Stodart and Myers (1966) report green vegetation to be of importance to the maintenance of reproduction in the Australian wild rabbit. The same phenomenon has been observed in North American rabbits (Ingles, 1941; Fitch, 1947; Mossman, 1955; Bothma, 1969).

Bothma (1969) reports the onset of the Cottontail rabbit breeding season to be closely correlated with the initial break in drought. Newsome (1966) reports this reaction to rainfall in the red kangaroo *Megalaia rufus*, while Poole (1960) and Myers and Poole (1962) report it in the Australian rabbit. This response was attributed to estrogens in the growing tips of sprouting vegetation. Therefore the gonadotrophic factor mentioned by Bodenheimer and Sulman (1946) might be estrogen.

According to Measroch (1954) many animals from equatorial regions lack seasonal breeding periodicity. The results obtained by various workers (Brambell and Davis, 1941; Measroch, 1954; Pirlot, 1954; Allanson, 1958; Chapman *et al.*, 1959; Delany, 1964a and 1964b; Coetzee, 1965 and 1967; Dieterlen, 1967; Delany and Neal, 1966 and 1969; and unpublished data), however, indicate that many species of small rodents have a restricted breeding season, in tropical and southern Africa corresponding more or less with the rainy season.

The appearance of green vegetation in the present study area was inhibited by the low rainfall prevailing during the period, and this might have resulted in reduced or delayed breeding activity.

During normal rainfall years on the study area, the *Praomys natalensis*, *S. campestris*, and *L. griselda* breeding season is expected to be from the onset of good spring rains until after the end of autumn rains.

The reproductive data obtained from the present study were too meagre to allow any conclusions concerning the effect of dieldrin coverspraying on the reproductive activity of the animals present in the area.

POPULATION STRUCTURE

Praomys (Mastomys) natalensis

Coetzee (1967) states subadults to have a mass of 15 g to 25 g, adults to be above 25 g and mice above 45 g to be large adults. According to Dieterlen (1967) the juvenile stage ends when the animal reaches a mass of 10 to 20 g (25 to 30 days old) and it becomes adult when it reaches a mass of more or less 40 g (70 to 80 days old). The age classes of Coetzee (1967) are followed here.

The relative frequency of animals of different body mass during the four seasons indicates that during spring (160 animals), all animals present in the population were subadults (47%), and adults (53%) of which 2% are designated as large adults. Males (97 animals) comprised 67% adults and 33% subadults. Three per cent of the adult males were above 45 g in mass (large adults). In the females (63 animals) the opposite was apparent (32% adults, and 68% subadults). No large adult females were observed.

During summer most animals were adults (males: 94% of 73 animals; females 86% of 62 animals; both sexes: 90%). Juveniles (4%) appeared in the population and a substantial decrease in sub-adults from 47% to 5% was observed, probably as a result of the growth of subadults of the previous season to adulthood. In contrast with spring no obvious difference in age-class proportions of the sexes was apparent. This season showed the highest number of large adults (26% of 135 animals; males: 34% of 73 animals; females: 18% of 62 animals).

From summer (135 animals) to autumn (54 animals) there was a relative increase in number of juveniles (4% to 31%) and subadults (5% to 24%) with a decrease in number of adults, including large adults (90% to 44%) and large adults (26% to 4%), indicating high mortality among the adults.

Fewer observations (16 animals, comprising 18% juveniles; 43% subadults; 38% adults; 0% larger adults) during the winter made comparison more difficult, but indicated extensive mortality since the previous season.

Coetzee (1967) reports a comparatively high number of subadults during late autumn and spring. In the present study relatively high numbers of subadults were observed during the spring and winter, although during winter the small sample available could have been a source of error.

Juveniles were recorded throughout the year except during spring, while Coetzee (1967) found no juveniles in winter (July to early August). In both studies juveniles were most frequent during autumn.

The summer population seemed to consist of two mass groups, viz. one with a body mass below 11 g (three males and three females) and another with a body mass of above 19 g (> 23 g in 70 males; and > 19 g in 59 females).

Coetzee (1967) found two mass groups during the autumn, one with mass below 25 g, the other above 35 g. In the present study two autumn groups are also apparent although very indistinct (males: < 21 g, N = 16, and > 24 g, N = 11; females: < 12 g, N = 13, and > 26 g, N = 14). No size groups were observed in the spring material, while the winter sample was too small to allow any meaningful conclusions to be reached.

In late winter and spring (August to October), Coetzee (1967) found apparently young animals, judging from fecundity and moult, with exceptionally heavy molar tooth wear. He suggests either that two species of multimammate mice occurred in the Roodepoort area, or that there was a difference in tooth wear rate during certain times of the year.

A possible alternative explanation may be retarded growth and sexual maturation during the winter and early spring, before the first rain of the season and the appearance of green growth.

It is possible that animals born just prior to the winter may reach subadult stage, remain constant in mass and size until after the first spring rains, and then within a few weeks develop to breeding adults. The animals can, therefore, be as old as four or five months, with teeth correspondingly worn, and still be subadult, while animals born just after the first spring rains could become breeding adults within two to four months, at which time teeth would be rather less worn. In laboratory studies of *P. natalensis*, Johnston and Oliff (1954) report age at first litter to be 130 days, and Coetzee (1967) citing records from the animals house of the Medical Ecology Centre, reports a mean age at first parturition of 94.1 ± 19.18 days with a range of 59 to 149 days. The youngest female to litter in a study by Meester (1960) was 77 days old.

Saccostomus campestris

Three mass classes are recognized, i.e. < 35 g, 35 to 50 g, and > 50 g. These classes are not necessarily assumed to represent a particular age group although they possibly correspond

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roughly to juvenile, subadult, and adult classes. The body mass distribution during the four seasons allows the conclusion that the spring sample consisted mostly (77% of 26 animals) of larger animals (> 50 g). During summer the three mass classes were more or less equally represented (N = 62; < 35 g: 29%; 35 g to 50 g: 39%; > 50 g: 32%), while during autumn and winter, the intermediate size class (35 g to 50 g) comprised the largest proportion of the sample (autumn: 46% of 135 animals; winter: 58% of 36 animals). The relative number of smaller (< 35 g) and intermediate (35 g to 50 g) animals increased progressively from spring to winter.

Lemniscomys griselda

Three mass classes are recognized, i.e. < 30 g, 30 g to 45 g, and > 45 g. The relative frequency of animals of different body mass during the four seasons allows the conclusion that smaller animals (30 g) occurred in low numbers throughout (spring: 0% of 21 animals; summer: 10% of 21 animals; autumn: 10% of 21 animals; winter: 2% of 48 animals).

During spring (24% of 29 animals) and summer (19% of 21 animals), there were relatively fewer animals of intermediate size (30 g to 45 g) than in autumn (62% of 21 animals) and winter (63% of 48 animals). During spring and summer, however, there was a higher number of larger animals (< 45 g; spring: 76%; summer: 71%; autumn: 29%; and winter 35%).

BEHAVIOUR

The following miscellaneous notes on the behaviour of the different species were accumulated in the course of the study.

Praomys (Mastomys) natalensis

Praomys natalensis was observed utilizing natural holes in the ground and termite mounds. Shortridge (1934), Veenstra (1958), and Delany and Neal (1966) report that this species uses the deserted burrows of other animals whenever possible. If forced to do so, it will also burrow, but only when the soil is either soft or cracked (Veenstra, 1958). According to Delany and Neal (1966) animals of this species are good burrowers.

When transferred from the trap into a plastic bag, animals were normally calm, in so far as that they did not jump about in the bag. When released at the trapping site, they would sit for a few seconds at the site of release and then unerringly move towards their holes without further delay. The speed of movement varied from one individual to the next.

They usually attempted to bite when handled unetherized, and did not seem to become tamer with repeated recaptures. When held by the nape and the base of the tail, a stream of air blown into the face caused them to respond with high-pitched squeaks. This was observed also by Veenstra (1958).

Measuring *P. natalensis* accurately when only half etherized or not etherized at all proved impossible, because stretching the animals to their maximum length resulted in rounding of their backs and kicking of their feet.

Veenstra (1958) reports *P. natalensis* to be nervous, quick to escape, conscious of danger, difficult to handle, and likely to bite without provocation.

Multiple captures of *P. natalensis* were observed twelve times on grid P46, but never on any of the other grids. Male/female and female/female multiple captures were each observed three times, while all-male multiple captures were found in six cases. In one of the male/female captures, the female had a mass of 45 g and the male 15 g. It could be that this was a mother with one of her recently weaned young. In the other two cases of male/female multiple captures the mass of the two animals was comparable, e.g. male no. 96 and female no. 97 had a

mass of 22 g and 23 g respectively, and both male no. 113 and female no. 112 had a mass of 12 g. In the latter case the animals could have been siblings at an age of more or less three weeks (Meester, 1960) i.e. both just weaned.

In both all-female and all-male multiple captures the two animals captured were normally of more or less the same size and mass. A mass of 28 g was never exceeded, suggesting that juveniles and subadults were involved in these multiple captures. Animals in a multiple capture, therefore, might have been of the same litter.

All but two multiple captures were in the trapping period 30 May, 1967 to 3 June, 1967, the period of extremely high population densities on grid P46. The other two multiple captures (all-male) were in May 1968 and coincided with a relatively high population density prevailing at that time, although not as high as that of May/June 1967 (see population densities).

The mechanism of the Chauvancy live traps used in this study renders it impossible to catch more than one animal at a time if they do not enter the trap almost simultaneously. Multiple captures could, therefore, indicate any of the following, either separately or in interaction:

- (1) The mice were travelling together and therefore some sort of social relationship existed between them;
- (2) a high degree of competition for food and living space occurred; and
- (3) the mice might have arrived separately at the trap seconds after each other and entered together, as when one chasing the other.

The presence of live and unscarred animals together in the traps would indicate mutual tolerance.

Praomys natalensis and *S. campestris* were the only species of which more than one animal was caught at a time. It seems that *P. natalensis* is tolerant of other rodents, of both its own and other species. Veenstra (1958) remarks that mixed or unisexual groups can live together without fighting and several families can live in one burrow. Shortridge (1934) reports that caged animals of this species are less quarrelsome than most other rodents.

Shortridge (1934), Roberts (1951), Delany and Neal (1966), and Delany and Kansiiimeruhanga (1970) report *P. natalensis* to be omnivorous, with insects comprising about 50% of the diet.

Further evidences for the hypothesis that *P. natalensis* gives way to other species during the time of food scarcity had been obtained in the present study (see Population densities).

Saccostomus campestris

Holes in termite mounds as well as other natural holes were used as home sites in the present study. Roberts (1951) and Waller (1964) report *S. campestris* to dig burrows of their own.

When a storeroom near the study area was demolished in November 1968, a female *S. campestris* was found nesting in a hollow in the sand under the floor, together with a large quantity of *Balanites manghamii* seeds which the animal had most probably been storing there for food. Seeds of three Acacia species, *Acacia tortilis*, *A. nilotica* and *A. karroo*, were found in the cheek pouches of *S. campestris* from time to time during the study. An animal of this species was also observed eating the fruit of *Grewia monticola*. Roberts (1951) reports *S. campestris* to feed on seeds, berries and termites.

These animals did not jump up and down when placed in a plastic bag after removal from the trap, but tried to run up against the side of the bag with characteristic, relatively slow, movements. This behaviour was exhibited for minutes on end if the animal was not released or etherized before then. Calm individuals were, however, also observed.

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Saccostomus campestris were normally slow to seek cover when released, and seemed to find difficulty in orienting themselves in relation to their home sites, judging from the amount of time spent and the detours travelled before reaching their holes.

These animals are known to be extremely docile (Davis, 1963b; Walker, 1964; and Joubert, 1967). If handled, however, even while partly etherized, they would attempt to bite.

Intraspecific aggression is reported by Davis (1963b), and Joubert (1967). Females in oestrus or pro-oestrus have been observed to rip open the scrotum of males or even kill them (Coetzee, pers. comm.).

Because of its slow movements *S. campestris* was easy to catch in enclosed areas. They were, however, not easily handled because of their extremely loose skin and their habit of trying to turn around and bite the handler.

One multiple capture of *S. campestris* was observed on June 3, 1967 on grid P46. This included two males, both having a mass of 20 g, on the same grid and in the same trapping period as the multiple catches of *P. natalensis* during the population high of May/June 1967. Here again, as in *P. natalensis*, the large population size and consequent shortage of food and living space probably played an important role.

Lemniscomys griselda

Lemniscomys griselda a predominantly diurnal animal, used natural holes in the ground as home sites. No burrowing was observed.

When released from the trap into a plastic bag, *L. griselda* would frantically attempt to jump from the bag, bouncing up and down in it.

When released at the trapping site after handling, animals of this species immediately sought cover, many so fast that it was difficult to follow their movements clearly, so that they were easily lost from sight.

On the other hand, members of this species could be measured fairly accurately without being fully etherized, as they did not kick or round their backs as *P. natalensis* did. No attempt was ever made to bite when cautiously handled even when unetherized or only partly etherized.

Shortridge (1934) reports that all specimens from South West Africa were trapped in high grass near swamps or waterholes. In the present study this was not the case.

Lemniscomys griselda appears to feed mainly on vegetable matter and seeds (Shortridge, 1934).

Mus minutoides

Attempts to bite the handler were observed. Animals of this species were twice observed taking refuge in scorpion (*Cheloctonus jonesi*) holes after release. However, several hundred scorpion holes dug up gave no evidence of *Mus minutoides* inhabiting them. Delany (1964b) reports *M. minutoides* to omnivorous.

SUMMARY AND CONCLUSIONS

Under the conditions which prevailed during the study, the *A. tortilis* community was preferred by *P. natalensis*, *S. campestris*, and *Lemniscomys griselda*, all the other species showed no clear preference for either of the two plant communities. *Steatomys pratensis*, however, seemed to appear more regularly in the *A. nigrescens* community (grids P88 and P89). It was never captured on grid P46 and only twice (one animal each time) during September and December 1967 on grid P50.

The findings of Shortridge (1934), Veenstra (1958), and Delany and Neal (1966), regarding competition between *P. natalensis* and other species, sustain those of the present study. In

spite of the fact, therefore, that *P. natalensis* is a very successful rodent in terms of breeding success and distribution, the present data seem to favour the hypothesis that *P. natalensis* gives way during times of food scarcity such as autumn and winter. Whether this phenomenon will be found throughout the range of *P. natalensis* is impossible to say until further studies have been undertaken. The numbers of *P. natalensis* may, however, be affected by habitat and climate, depending on what the optimum environment is for this species.

Wiese *et al* (1970) report spraying at the same concentration as used in the present study to have had no adverse effects on exposed livestock. It was, however, found that dieldrin presents a definite hazard to antelope populations generally, and Blesbuck *Damaliscus dorcas philipsi* and Springbok *Antidorcas marsupialis* in particular. Therefore, its use on open grassland inhabited by antelope has accordingly been withdrawn (Wiese *et al.*, 1973). They conclude, furthermore, that antelope mortality was primarily due to photodieldrin intoxication.

Van Ark and Sheasby (1972) state that it would be unlikely that the ecological status of wood eating termites would be endangered when veld is sprayed at the recommended concentrations. While van Ark and Pretorius (1970), studying the effect of dieldrin cover-spraying on night-flying insect populations in the present study area, conclude that no significant differences could be found between populations before and after spraying.

Wiese and Basson (1967) and Basson (1970a; 1970b; and 1971) found the scorpion *Cheloctonus jonesi*, millipedes *Alloporus* spp., Crowned guinea-fowl *Numida meleagris*, Laughing dove *Stigmatopelia senegalensis*, and Cape sparrow *Passer melanurus*, not to be adversely affected at concentrations simulating that used in the field. Wiese, Basson, van der Vyver, and van der Merwe (1969) report significantly higher egg production of Crowned guinea-fowl exposed to higher dieldrin dietary levels. The viability (weight gain and egg production) of the F1 progeny of these birds was ascribed to a selection (resulting from dieldrin intoxication) for increased vigour.

Swanepoel (1973) considering data from the literature (Wiese and Basson, 1967; Wiese *et al.*, 1969; and Basson, 1971), comes to the conclusion that when large areas (e.g. a few thousand hectare) are to be sprayed at the recommended dosage bird mortality probably will occur in some species. This would probably be mainly caused by photodieldrin or a combination of photodieldrin and dieldrin, as dieldrin alone apparently is proven to be less toxic to most species.

In the present study, *Lemniscomys griselda* and *S. campestris* showed very low dieldrin residues (< 1,0 ppm) after spraying. While one shrew, *Crocidura hirta* (60 days after spraying) yielded a relatively high concentration (4,66 ppm dieldrin, and 0,216 ppm photodieldrin). As shrews feed on insects and other invertebrate and vertebrate animals, they represent a higher level in the food chain than do graminivorous rodents, and can therefore be expected to accumulate higher insecticide residues. The presence of the relatively high residue level in the insect-eating *Crocidura hirta* is an indication that these animals might possibly be adversely affected by spraying. However, whole carcass analysis of insect-eating birds from the same area after spraying did not produce evidence of higher residue levels (unpublished data). In any case, the sample was much too small as it is known that residues in different animals of the same species treated alike may differ considerably (Wiese, pers. comm.).

Comparable low residue levels in rodents were also observed in a similar study near Dendron in Northern Transvaal. While in the laboratory, *Tatera leucogaster* males receiving 100 ppm dieldrin consistently in their diet lived up to 48 days after onset of exposure (unpublished data). This makes it highly unlikely that this rodent species and perhaps others will be adversely effected by the spraying.

Under the circumstances of below average rainfall and consequently poor habitat conditions which had a profound effect on rodent numbers, no final conclusion concerning dieldrin

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coverspraying at 83 g/ha on rodent population densities could be reached. The possibility, however, exists that spraying might have influenced numbers of *Lemniscomys griselda* on grid P50 but evidence for this is very tenuous, as the numbers captured were too low to allow a clear-cut conclusion to be reached.

Furthermore it may be surmised that reproduction in the Pongola rodent population could have been affected by dieldrin coverspraying. Again, however, the reproductive data obtained were too meagre to allow any conclusions to be reached on this score.

Therefore dieldrin in coverspraying at the dosage applied had no apparent influence on rodent populations in the present study.

It has been recommended that spraying for harvester termites need not be done more than once every 10 years, and at the rate dieldrin and photodieldrin break down, as observed in the present study and in similar studies at Dendron in northern Transvaal (Wiese and Basson, unpublished data), and at Lydenburg in eastern Transvaal (Wiese *et al.*, 1970), no accumulation of this pesticide under similar spraying conditions is expected in the environment.

ACKNOWLEDGEMENTS

This work was in part submitted as a M.Sc. thesis to the Zoology Department, University of Pretoria. My sincere thanks go to Prof. J. A. J. Meester, University of Natal, for guidance and constructive criticism during the study; to Dr. J. A. J. Nel, University of Pretoria; to Dr. I. H. Wiese, Plant Protection Research Institute, who was a constant inspiration; to Mr. C. G. Coetzee, State Museum, Windhoek, who made useful suggestions; to my wife Rina who tirelessly helped with the fieldwork and analysis of data; to Mr. Stephens Mothlasedi who helped with the fieldwork; to other members of the Plant Protection Research Institute staff who helped in many ways; and to the Department of Agricultural Technical Services for the opportunity to have done the work while in their service, and for approving and financing the work.

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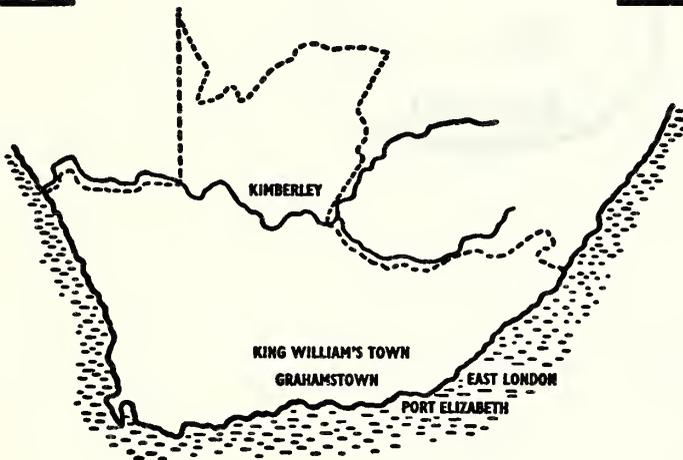
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 5

31st DECEMBER 1976

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA



An ethological study of *Parachilus insignis* (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa

by

F. W. GESS

(Albany Museum, Grahamstown)

and

S. K. GESS

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INTRODUCTION

The genus *Parachilus* Giordani Soika (1960) is restricted in its distribution to the Ethiopian Region and includes eight species, six of which occur in southern Africa and two in East Africa. The southern African *Parachilus insignis* (Saussure), the subject of this paper, is the largest species and is a wasp of very striking appearance.

None of the species of *Parachilus* is well known and the authors' belief that nothing has been recorded concerning the nesting of any of the species belonging to the genus has been confirmed by Giordani Soika (pers. comm., letter dated 30.x.1974).

The present paper is the third of a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW. of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa. In the two previous papers (Gess and Gess, 1974 and 1975) which like the present one dealt with ground-nesting species, an account was given of the climate and vegetation of Hilton as well as of the soil in which the previously studied species excavated their nests. As these descriptions hold good for *P. insignis* also, they will not be repeated here. It should be noted that all the species dealt with to date (that is including *P. insignis*) belong to the community of wasps nesting in clay soil, that all have similar requirements with respect to the availability of water and that as a result all might during the course of the summer be encountered using the same areas for the purpose of nesting.

The greater part of the present study was undertaken during the summer of 1973-4 but certain general observations dating from previous seasons and also from the summer of 1974-5 have been included.

TAXONOMIC HISTORY

Parachilus insignis with five other of the eight species now included in the genus *Parachilus* Giordani Soika was described as a species of the widespread genus *Pterocheilus* Klug. The remaining two species of *Parachilus* were also previously included in *Pterocheilus* to which genus they had been transferred from *Odynerus* Latreille. On account of the absence of long hairs on the labial palps in females of those of the above eight species then known to him, Bohart (1940) excluded these species from *Pterocheilus* and transferred them to the Ethiopian genus *Pseudochilus* Saussure which he characterized as being intermediate between *Odynerus* and *Pterocheilus*. While accepting the exclusion of *P. insignis* and related species from *Pterocheilus*, Giordani Soika (1960) on the grounds of differences in the length of the tongue, in the number of segments composing the maxillary palps, in the proportions of the labial palps, and in the site of the insertion of the basal vein on the subcosta, removed them from *Pseudochilus* and included them in his new genus *Parachilus* with *P. capensis* (Saussure) as the type species.

GEOGRAPHIC DISTRIBUTION

Considering the large size (length up to 23 mm) and the exceptional beauty of *Parachilus insignis* it is remarkable how little is known about its distribution. Described by de Saussure in 1856 from "le Cap de Bonne-Espérance", it was subsequently recorded from Pretoria (Transvaal) by Distant (1892: 210). More recently Giordani Soika (1960: 402) recorded specimens from the following localities: Mamathes (Lesotho); Chicago in the Lindley District and Thaba Nchu (both Orange Free State); Pretoria (Transvaal). In the Albany Museum collection the species is represented from only two localities, separated from each other by a mere 23 kilometres: New Year's Dam, Alicedale (1 female collected by J. G. H. Londt on 22.xi.1970 and 1 female collected by A. S. Greathead on 16.xii.1971) and Hilton, Grahamstown (numerous specimens of both sexes collected by the authors).

DESCRIPTION OF NESTING SITES

Three distinct and well-separated nesting sites of *Parachilus insignis* were located at Hilton over the period of several years that this species was observed. One site was situated on a bare



Plate 1. Hilton. A nesting site of *P. insignis* (Sauss.) on a bare earthen farm road.

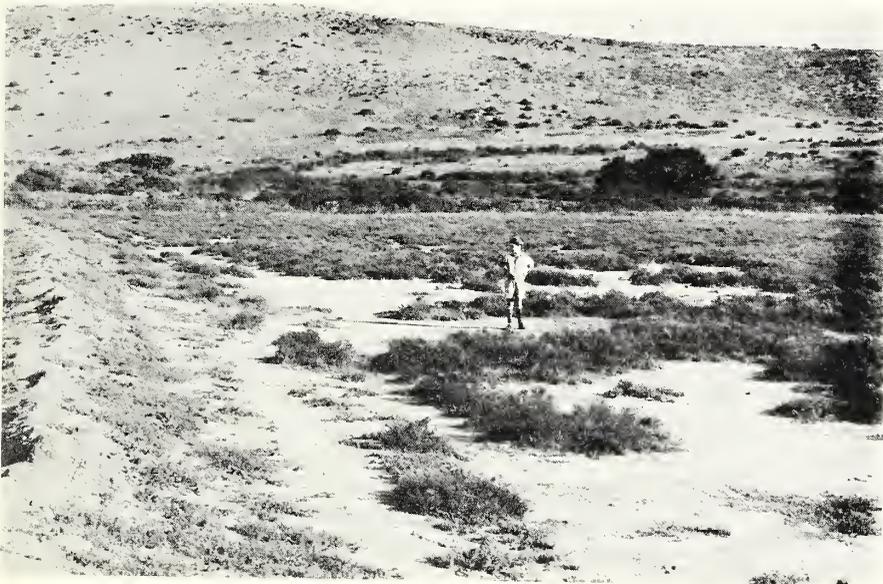


Plate 2. Hilton. A nesting site of *P. insignis* (Sauss.) on a bare area below a water furrow.

earthen farm road (Plate 1), a second on a bare area below a water furrow (Plate 2) and a third on a slightly sloping area denuded of vegetation and topsoil by sheet erosion. All three nesting sites were localized patches of bare clayey earth occurring in low-lying areas sparsely covered by small, low-growing shrubs, largely *Pentzia incana* (Th.) O. Ktze (Compositae) and situated close to temporary sources of water. This water, a result of rain, had collected in muddy pools, erosion gullies and shallow furrows. Its distance from the nesting areas was measured for two of the sites and was from 6–14 metres.

Although the level of activity and thus the number of nests of *P. insignis* in any one of the three nesting areas varied from one nesting season to another it was found that, during the period of observation, the three sites were utilized by this species each year to the exclusion of any other similar bare patches which appeared potentially suitable for nesting. This situation had apparently existed for some considerable time, at least at two of these sites, both of which were subject to slow sheet erosion. There the gradual stripping away of the upper layers of the ground by water and wind action had exposed to the surface the remains of many nest cells excavated by *P. insignis* during the course of its nesting over past years.

The restriction of nesting to these three small nesting sites, the clustering of the nests within a nesting site, and the apparent lack of any appreciable emigration by emerging wasps from the site where they were reared to new nesting areas at a distance was seen to result in the formation and maintenance of well-marked pseudo-colonies at times containing a high density of active nests. Thus on 15.xi.1974 over 45 active nests, clustered in a roughly oval area 224 cm long and 168 cm wide, were counted in one of the nesting sites (that shown in Plate 2). Nest entrances were frequently clustered together as close as 4 cm and even less, the ground between them being littered with discarded pellets (Plates 3 and 4).

FLIGHT SEASON

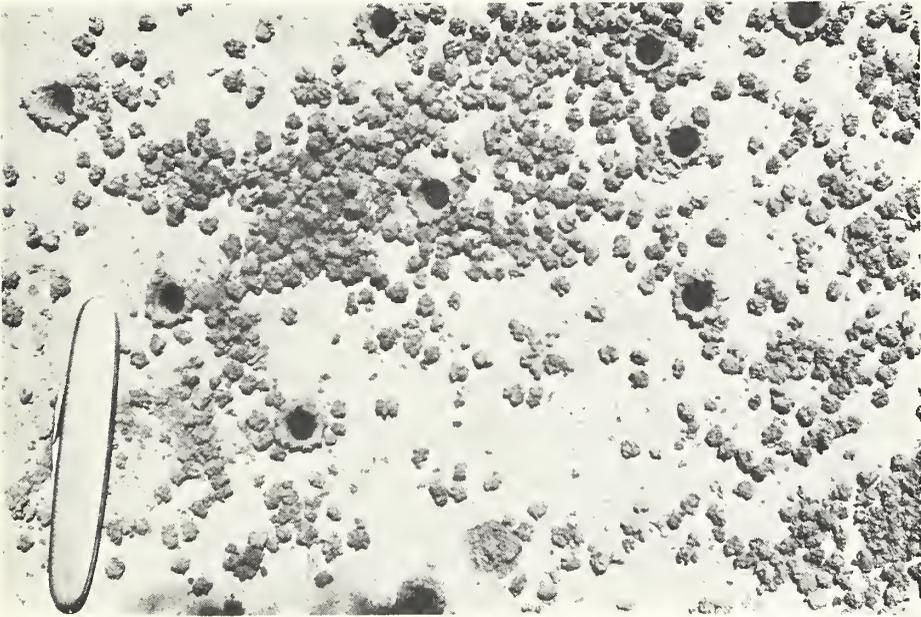
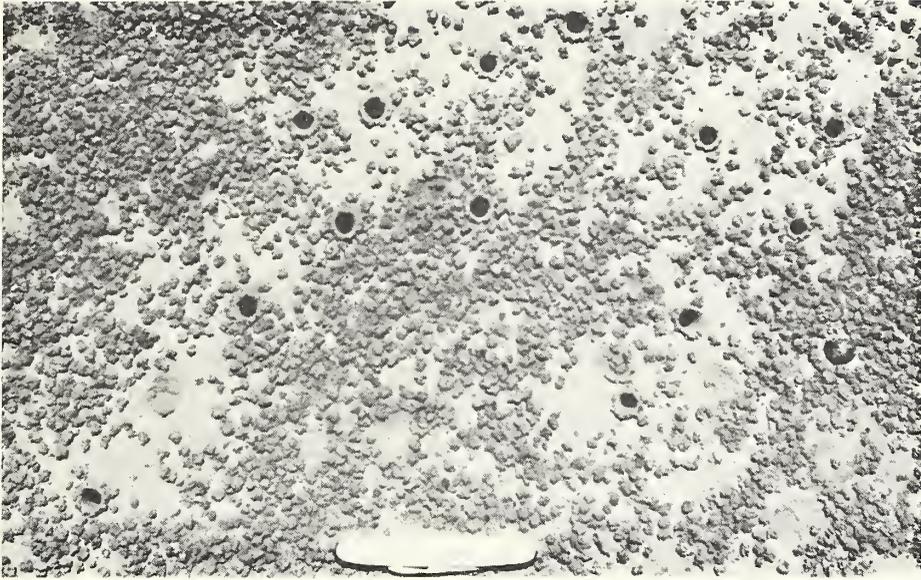
Parachilus insignis is univoltine, the flight season beginning at the very end of October and, depending upon weather conditions, continuing through to early January or even early February. Thus during the 1973–4 summer these wasps were first observed in small numbers on 29.x.1973 and last observed on 7.i.1974, being absent when next looked for on 14.i.1974. During the 1974–5 summer, they were very plentiful by 8.xi.1974 and were still nesting, though only in very small numbers, on 7.ii.1975. It was found that not all individuals emerged at the same time, for on 13.xi.1974, when adults were common and nesting was well under way, 29 sealed cells of the previous season were found on excavation by the authors to contain 15 prepupae and 14 pupae close to turning into adults. Emergence of adult wasps thus probably continues over some time.

BEHAVIOUR OF THE MALES

At the beginning of the flight season, when the nests were widely spaced, it was observed that there were as many males as females present in the nesting areas. The females which were observed building nests each had a male in attendance. Each male was stationed within a radius of about 60 cm from a nest and either rested upon the ground or perched upon a nail used by the authors to mark the position of the nest. He was observed to rise up, fly at and pursue any insect flying in the vicinity of the nest. The female was pursued whenever she emerged from her nest or returned to it but the male did not accompany her on her periodic flights out of the nesting area. Foreign males approaching the vicinity of the nest were pursued, jostled and sometimes engaged in battle on the ground. Other insects including would-be parasites such as bombyliids and chrysidids were similarly attacked and driven off.

As the nesting season advanced and the nests became crowded there was such seething activity that clear-cut male behaviour was no longer observable if it was still taking place.

GESS: PARACHILUS INSIGNIS (SAUSSURE) (HYMENOPTERA: EUMENIDAE)



Plates 3 and 4. Hilton, 13.XI.1974. Portion of a nesting area of *P. insignis* (Sauss.) showing open and sealed nest entrances and discarded pellets. Plate 3 ($\times 0.3$), Plate 4 ($\times 0.5$).

At no time was successful copulation observed. However, males were frequently observed grappling with females on the ground within the nesting areas.

TABLE I. Analysis of the provision found in closed egg and pantry compartments and in complete cells of *P. insignis*.

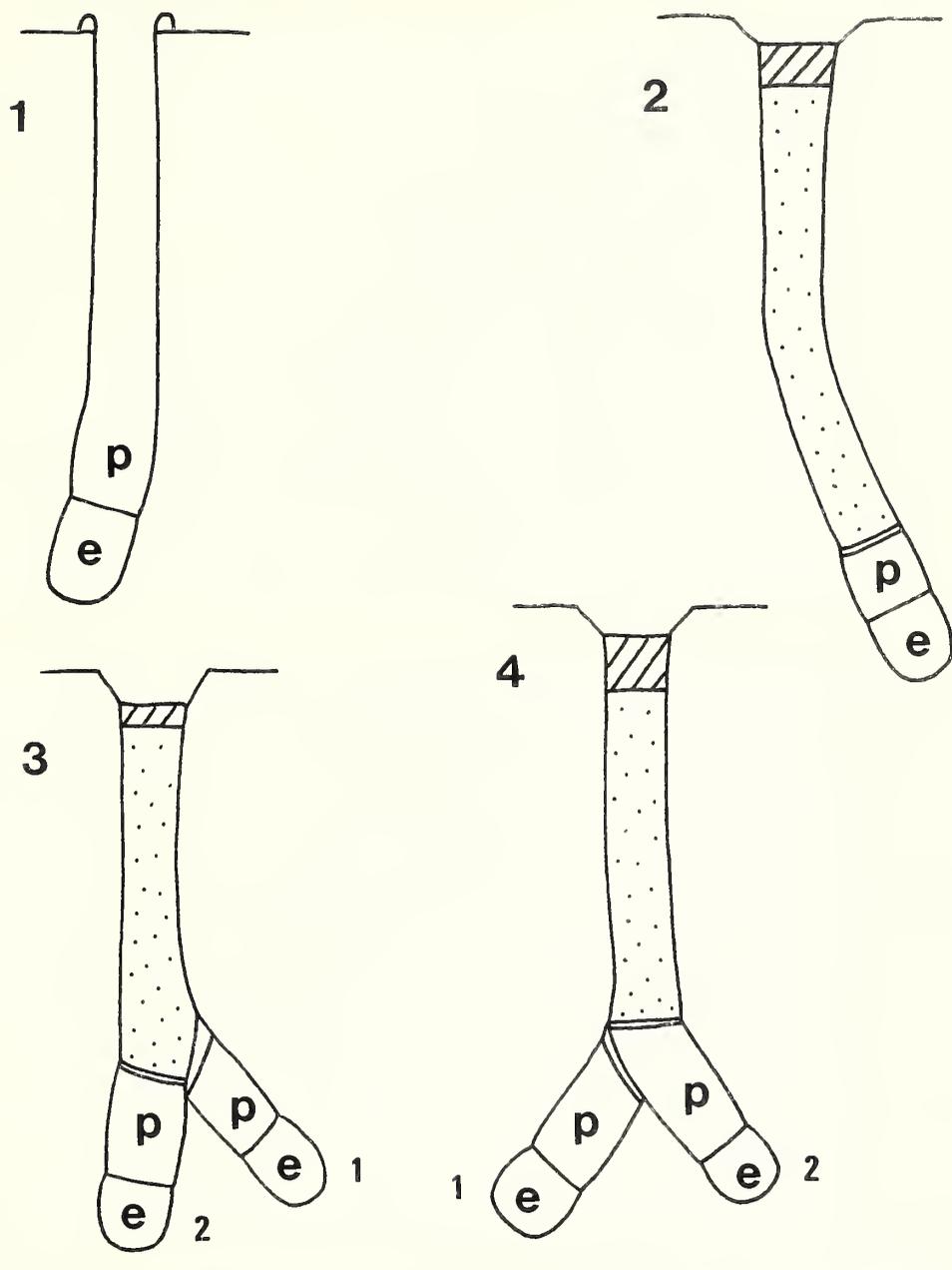
Part of nest	Size of sample	No. of prey constituting provision (range)	No. of prey constituting provision (average)	Mass of provision (range) mg	Mass of provision (average) mg
Closed egg compartment	21	2-4	2,7	125-322	220
Closed pantry compartment	13	5-13	8,0	473-913	703
Complete cells	11	8-17	10,7	832-1210	950

DESCRIPTION AND METHOD OF CONSTRUCTION OF THE NEST

The nest of *Parachilus insignis* consists of a subterranean burrow surmounted by a turret which is little more than a collar. This collar is made from mud pellets cemented together and smoothed on the inner surface only. The subterranean burrow consists of a shaft which is either simple terminating in a cell or in addition bears one lateral branch which leaves the main shaft just above the terminal cell and itself terminates in a cell which usually fills its entire length. Each cell is divided into two compartments, a lower (termed the egg compartment) containing the egg and a small number of prey caterpillars and an upper (termed the pantry compartment) containing a large number of prey caterpillars but no egg (Table I). These two compartments are separated by a thin mud plate. (Figs 1-4)

Water is required for nest-building and is collected by the female from a near-by puddle. She stands on the mud at the edge of the water to fill her crop. Several individuals were timed and took eleven seconds to perform this.

Nest excavation is initiated by the female regurgitating a cropfull of water onto the ground. Using her mandibles she works this water into the earth to form mud. This mud is formed into pellets which she lifts in her mandibles and arranges in a circle (inner diameter 5-7 mm) which is the foundation for the collar and also fixes the diameter of the shaft opening. While working the female stands outside the burrow, head down (Plates 5-7). The wasp adds pellets to the collar whilst rotating through 360° repeatedly so that pellets are added in spiral layering. The collar which is completed at an approximate height of 3 mm is thus built entirely from earth removed from the excavation of the burrow. Shaft excavation is continued but the pellets extracted are carried away from the nest and dropped except for an occasional pellet which is added to the collar. While working the wasp always enters the nest head first and emerges backwards. She leaves the nest in a constant direction, flies off, drops the pellet in a definite pellet-dropping area and before returning to the nest flies in a wide circle around it and finally alights on the collar and



Figs 1-4. Plans of underground workings of four nests of *P. insignis* (Sauss.). e—egg compartment; p—pantry compartment. Fig. 1. Open nest with sealed egg compartment and open pantry compartment. Fig. 2. Sealed nest with a single sealed cell. Figs 3 and 4. Sealed nests each with two sealed cells—sequence of construction of cells indicated.



Plate 5. Hilton, 13.xi.1974. Female *P. insignis* (Sauss.) at the entrance of the nest which she is constructing. (\times circa 1,4). Plate 6. Hilton, 13.xi.1974. Two female *P. insignis* (Sauss.) disputing ownership of nest. (\times circa 1,4).

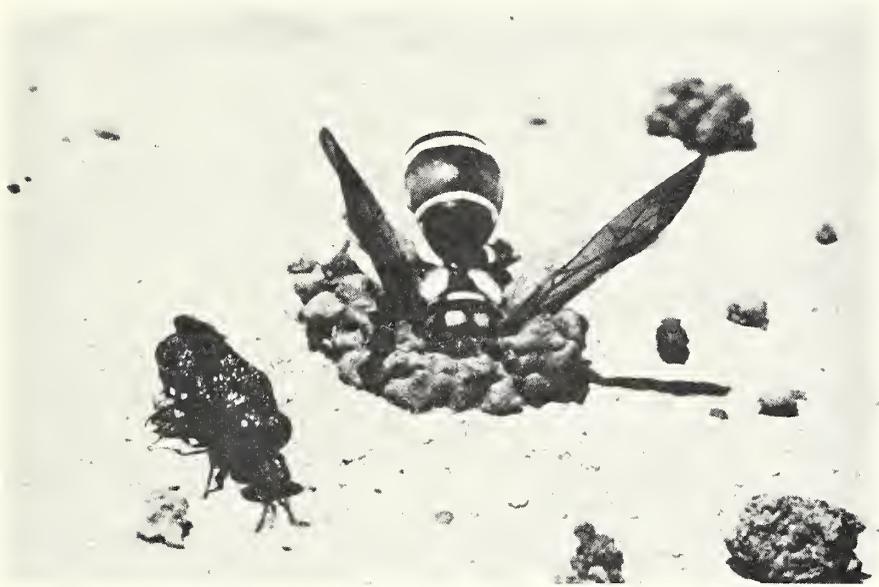


Plate 7. Hilton, 13.xi.1974. Female *P. insignis* (Sauss.) entering her nest and female *Octochrysis vansoni* (Brauns) on the ground close by. (\times circa 2,5). Plate 8. Hilton, 13.xi.1974. Female *Octochrysis vansoni* (Brauns) inspecting nest entrance of *P. insignis* (Sauss.). (\times circa 2,5)

enters the nest facing away from the pellet-dropping area (Fig. 5). All the individuals in a particular nesting site were seen to have their pellet-dropping areas in the same direction and to follow similar flight-paths. Six to eight pellets are excavated for each load of water and six to nine minutes elapse between successive water collections. A sample of 20 pellets was taken and their dry weight was found to be remarkably similar and to average 58 mg. When forming pellets the wasp is seen to rotate in the shaft and thus removes earth evenly ensuring that the shaft is circular in cross section. In one of the nests observed, it was found that the time taken from nest initiation through collar formation to completion of 25 mm of shaft was 36 minutes which indicates that the complete excavation of the nest could easily be accomplished in one working day. If the collar is destroyed by rain or in any other way there is no attempt to replace it. These observations were made early in the nesting season when individual nests, their builders and their pellet-dropping areas could easily be distinguished. Later in the season the nests were closely crowded and therefore pellet-dropping areas were no longer distinct. (Plates 3 and 4).

A total of 35 nests was excavated and drawn. Of this total 20 nests were still open and possessed single cells in various stages of provisioning, and were still being worked upon by adult female wasps. The other 15 nests had been completed and had been sealed. Ten of these sealed nests each possessed a single cell and five each possessed two cells.

All 28 nests (20 open and 8 sealed) excavated over the six-week period from the beginning of the nesting season up to 12.xii.1973 were found to be single-celled whereas five of the seven nests (all sealed) excavated two weeks later (on 27.xii.1973) were found to be two-celled. It therefore appears that single-celled nests are the rule in the first weeks of the nesting season but that two-celled nests may commonly be constructed during the second half of the nesting season at a time when nesting is very active. The fact that the state of development of the wasp young within each of the two-celled nests was in all cases very similar indicates that, at the time of construction of the two-celled nests, there was an abundant supply of prey and that the two cells were constructed and provisioned within a very short time of each other. A similar change during the course of a nesting season from the construction of nests containing one cell to that of nests containing more than one cell has been recorded for a population of *Bembix americana* (Sphecidae) by Alcock (1973) who has fully discussed the probable reasons for the phenomenon.

The depth below the ground of the bottom of the single cell or, in the case of nests with two cells, the bottom of the lower cell ranged from 60–105 mm (average 80 mm, 76 per cent in the 71–90 mm range). The bore of the main shaft at its mouth varied from 5–7 mm but was most commonly in the 6.5–7.0 mm range. As the shaft descended, its bore generally increased slightly and at about half its length (depth) varied from 7–9 mm (average 8 mm). The cells at the ends of the shafts varied in bore from 7–10 mm (average 9 mm). The lower portion of the cell, the egg compartment, varied in height (length) from 6–15 mm (average 10 mm) and the upper or pantry compartment varied from 10–18 mm (average 14 mm). The mud partition between the two cell compartments was very fragile and thin—1 mm or less in thickness, whereas the mud plug, the cell closure, between the upper compartment and the shaft was robust and thicker—about 2 mm.

COMPOSITION, PHYSICAL CONDITION AND TRANSPORT OF THE PREY; PROVISIONING AND OVIPOSITION

Parachilus insignis at Hilton was found to prey exclusively upon larval Psychidae (bagworms). Two species were taken and these could readily be distinguished in the field by the coloration of their heads. Thus in one species the head was uniformly rufous in colour, in the other species it was pale ochreous with brown spots. Whereas the arrival of provisioning wasps with their prey at the nesting sites was frequently observed, the hunting and the method utilized to de-bag the bagworms was unfortunately never witnessed. However, a careful search of the dwarf shrubs which surrounded the nesting sites to a considerable distance revealed that both

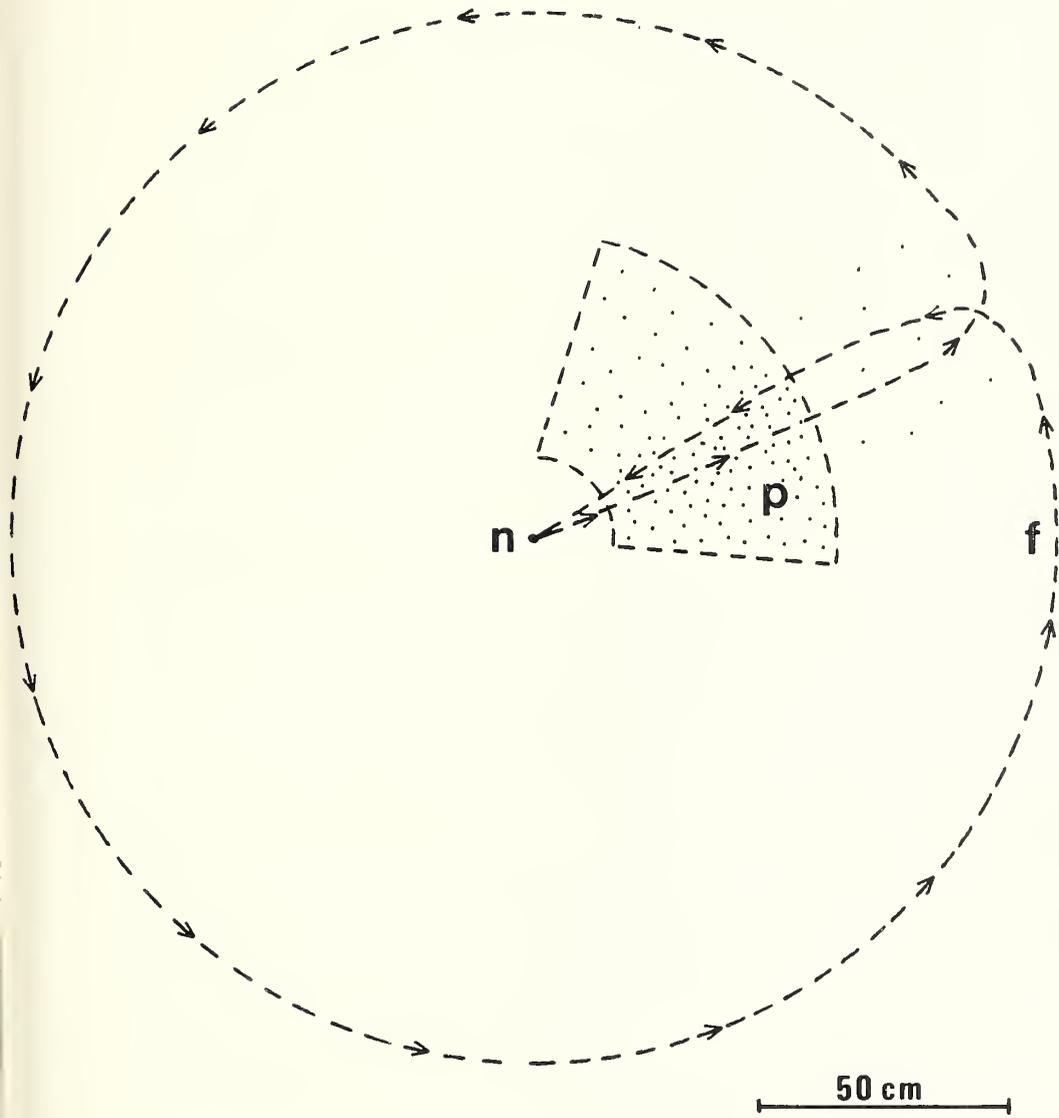


Fig. 5. Diagrammatic plan of pellet-dropping area and of flight-path taken during pellet-dropping phase of nest construction. f—flight path; n—nest entrance; p—pellet-dropping area.

species of prey were to be found occurring on these plants and that the bags constructed by the two species were distinct. The bag of the rufous-headed species was constructed of relatively longer, fine sticks of similar length, orientated parallel to the long axis of the bag. The only specimen found was feeding on a yellow daisy-flower (? *Gazania* sp.) (Compositae). The bag of the species with the pale-ochreous, brown-spotted head was constructed of relatively shorter, fine sticks of varying lengths, orientated tangentially at right-angles to the long axis of the bag. Thus whereas the proximal ends of the sticks were incorporated in the body of the bag the distal portions ($\frac{2}{3}$ to $\frac{3}{4}$ of the length in the case of longer sticks) stuck out to the sides. Seen end-on the bag thus appeared ornamented with whorls of protruding sticks. Five or six specimens were found, all feeding upon the dwarf-shrub *Pentzia incana* (Th.) O. Ktze (Compositae).

Both species were represented in the prey throughout the nesting season but one species was consistently more common than the other. Thus of a total of 318 prey caterpillars examined (258 from opened cells and 60 taken from ants raiding nests) 287 specimens were of the species with the pale-ochreous, brown-spotted head and only 31 specimens were of the rufous-headed species. The two species did not differ from each other in size and taken together prey of both species varied in length from 6–18 mm. Of 156 specimens, the length of which was measured, 73 per cent were in the 9–13 mm range. The average mass was 87 mg.

A total of 144 prey caterpillars was examined with respect to the location of sting sites which were visible as small dark lesions. It was found that each caterpillar was stung in three places on the underside of the thorax: on the prothorax, on the mesothorax and on the metathorax, in all cases in front of the legs. No sting sites were found on the abdominal segments nor anywhere else on the body. The prothorax invariably bore at least one sting. The mesothorax and metathorax in the great majority of cases likewise bore at least one sting though occasionally there were no stings in these two segments. Occasionally any one of the three segments bore more than one sting. The 144 prey examined together bore 158 stings on the prothorax, 180 on the mesothorax and 169 on the metathorax.

Paralysis of the prey was only partial, tactile stimulation resulting in squirming movements. Prey which was for some reason or other not eaten continued to defaecate for some time and remained alive for considerable periods but was generally inactive. Thus of 77 stung prey obtained from provisioned cells on 27.xii.1973 and kept in gelatin capsules, 46 individuals (60 per cent) were still alive on 7.ii.1974 (42 days later), 4 individuals (5.2 per cent) were still alive on 19.iii.1974 (82 days later) and one individual was still alive but very weak on 26.iv.1974 (120 days later). None of these specimens pupated. However, a 13 mm long rufous-headed larva with stings on all three thoracic segments, obtained from a nest cell opened on 27.xi.1973, pupated successfully and emerged as an adult male on 17.iii.1974.

P. insignis flies with its caterpillar prey from the site of capture to the nest. The prey, carried ventral side up and with the head facing the direction of travel, is held closely beneath the wasp's body by the latter's mandibles and legs. On arrival at the nest opening the wasp alights on the ground next to it, relinquishing her hold of the prey with her legs but not her mandibles. Raising the anterior part of her body the wasp then proceeds to work the prey forwards towards the nest opening and lets it drop down the nest shaft. The wasp then flies off to continue the hunt and it is only after several prey have been transported to the nest and dropped down the shaft that the wasp herself goes down the latter to arrange them in the cell. If, on the occasions when the wasp goes down the shaft herself, she is carrying a caterpillar, she does not enter the hole with the prey beneath her but lowers it in ahead of her.

The provision found in closed egg and pantry compartments and in complete cells was analysed and is presented in Table I. When considering the mass of the provision supplied for an egg, it is significant to note the mass of the adult wasp. The mass of females ranged from 135–222 mg and averaged 189 mg for a sample of 11 and the mass of males ranged from 172–275 mg and averaged 230 mg for a sample of 7.

As the wasp is unable to turn around in her cell she enters the nest backwards in order to oviposit. The egg is suspended from the upper surface of the egg compartment by a short filament of average length 4,5 mm. The eggs were all very similar in size. The average length was 3,26 mm and the average width was 0,9 mm. The weight of the only egg weighed was 2 mg.

A total of 39 egg compartments was examined of which 8 were open and 31 sealed. Each of the sealed egg compartments contained 2-4 prey and either an egg (in 23 compartments) or a small larva (in 8 compartments). Two of the 8 open egg compartments contained neither eggs nor prey having been examined before oviposition and provisioning had taken place. Of the remaining open cells one contained an egg and 2 prey and 5 contained prey (1, 1, 2, 7 and 11 individuals) but no egg. Whereas the number of prey in the two compartments containing 7 and 11 prey is so highly aberrant that the absence of an egg cannot be considered significant, the remaining 3 cells must be considered as having contained prey but no egg as it is remarkable that in all the closed cells excavated there is no case of an egg having been overlooked. The sample is however too small for any conclusions to be drawn.

NEST CLOSURE

After the cell or cells have been completed and sealed the shaft is filled with pellets and small crumbs of loose earth and the opening at the surface of the ground closed with a mud plug and smoothed off leaving a shallow depression 10-17 mm in diameter in the surface of the ground (Figs 2, 3 and 4). The earth and mud pellets used for nest closure are derived from the collar, a "quarry", scattered pellets and from loose earth where the ground has been disturbed. In the first case the wasp having filled her crop with water regurgitates it onto the collar and with her mandibles scrapes off and kneads into a pellet a small quantity of the resultant mud. The pellet so fashioned is then dropped down the shaft. The antennae are held close to the mandibles seeming to monitor the progress being made with the pellet. Additional pellets are taken from a "quarry" a short distance from the nest (*circa* 30 cm). Pellets are formed as before and the wasp flies with each pellet and drops it down the shaft. As she returns to quarry further pellets in the same place a small crater develops. In addition previously discarded pellets and loose crumbs of earth lying near the nest may be collected and dropped down the shaft. When the shaft has been entirely filled, the wasp seals the opening by cementing together pellets to form a plug 4,5-9,0 mm in depth. Finally she moistens the surface of the ground on the sides of the depression and draws the resultant mud across the plug to give it a smooth finish. Sealed nests are difficult to distinguish from quarry sites.

PARASITES AND OTHER ASSOCIATED INSECTS

Several species of insects, belonging to different orders, were found in association with *Parachilus insignis*. They included parasites (Meloidae, Chrysididae and Bombyliidae), prey robbers (Formicidae) and users of old burrows (Apoidea).

A species of Meloidae, *Lytta enona* Péringuey was found to be a fairly common cleptoparasite in the nests of *P. insignis* where in its larval stage it feeds upon the stored caterpillars after first destroying the eumenid's egg. The seventeen individuals found in association with *P. insignis* nests are dealt with in an order determined by their developmental stage when found.

A triungulin larva, 1,0 mm in length with a darkly pigmented body and with well developed long legs and long slender cerci was found on 27.xi.1973 in a sealed egg compartment containing two prey and a collapsed *P. insignis* egg still hanging from its filament. In the hope of rearing this larva the contents of the egg compartment were transferred to a gelatin capsule but, unfortunately, the larva died two days afterwards. However, in view of other finds, the authors are satisfied that this larva was that of *L. enona*.

TABLE II. Developmental times for the later stages of the life history of *Lytta enona* Péringuey (Meloidae).

	Date of moult from 4th (scarabaeoid) to 5th (coarctate) instars	Date of moult from 5th (coarctate) to 6th (scolytoid) instars	Date of pupation	Date of full pigmentation and hardening of adult
1	10-20.i.74	24.xi.74	4.xii.74	17.xii.74
2	10-20.i.74	30.xi.74	—	—
3	10-20.i.74	10.xi.74	18.xi.74	7.xii.74
4	10-20.i.74	3.i.75	9.i.75	24.i.75
5	10-20.i.74	24.xi.74	5.xii.74	23.xii.74

On 27.xii.1973 five sealed egg compartments in as many nests were each found to contain a single foreign larva with small but functional thoracic legs. These larvae were feeding upon the provision laid in for the *P. insignis* larvae. In one case the remains of the *P. insignis* egg or newly hatched larva were found in the egg compartment. These foreign larvae were the 3rd (1st scarabaeoid) instar larvae of *L. enona*, the identification being established by the successful rearing through to the adult stage of four of their number. Dates of moulting from the 3rd to 4th instars were not recorded but developmental times for later stages of the life history are given in Table II. The lengths of the larvae when found varied from c. 10- c. 14 mm (average 12,6 mm). During the course of their development in the cell and later in the laboratory the larvae consumed from 6 to 8 caterpillars each between hatching and the end of the 4th (2nd scarabaeoid) instar, after which no further feeding took place. The non-feeding, diapausing 5th (coarctate) instar was characterized by the hardness of the brown-coloured integument and by the rudimentary nature of the legs and mouthparts. The non-feeding 6th (scolytoid) instar, with which development proceeded after the winter and spring months had passed, was softer and paler than the preceding instar but had functional legs. Larvae of this instar kept in Petri dishes moved about restlessly for a period of two to three days after which they lay motionless until they pupated. Pigmentation of the eyes and of the mandibles began six and eight days respectively after pupation.

A diapausing 5th (coarctate) instar larva was found associated with a nest of *P. insignis* excavated by the authors on 26.ix.1974 and six additional specimens were found associated with nests excavated on 13.xi.1973. The first-mentioned larva moulted to the 6th instar two days after collection, pupated on 20.x.1974 and was fully adult on 18.xi.1974.

Four adult beetles were obtained in the field. One of these was found on 13.xi.1974 inside a sealed nest of *P. insignis*, the others were found on different dates (7.xii.1973, 8.xi.1974 and 15.xi.1974) walking about on the ground within the nesting site of *P. insignis*.

Lytta enona Péringuey (1899: 319) was described from Uitenhage, about 120 kilometres from Grahamstown. Whereas the species was subsequently reclassified as belonging in the genera *Cantharis* and *Epicauta* by Péringuey (1909: 266) and by Borchmann (1917: 74) respectively, Kaszab (1953: 484) upheld its original inclusion in the genus *Lytta*. The species appears to be poorly represented in collections and nothing has hitherto been recorded regarding its life-history.

The biology of *L. enona* is unusual in so far that the larva feeds upon the paralysed insect prey with which a hunting wasp has provisioned its cell whereas meloid larvae generally feed either upon the buried egg packets of Orthoptera or upon the provisions laid in by pollen- and nectar-collecting Hymenoptera. When considered in terms of the discussion of the possible behavioural evolution of the Meloidae presented by Paoli (1938) it is clear that the food choice of *L. enona* would place this species in a category previously exemplified solely by the European *Cerocoma schaefferi* L. The larva of that species was found by Fabre (1943b: 268–80) to develop in the nests of a species of *Tachysphex* ("Tachyte manticide" of Fabre) (Sphecidae) where it fed upon small mantids with which the cells had been provisioned.

Two species of Chrysididae (Holonychinae) were found in association with the nests and nesting sites of *P. insignis* at Hilton. The more common of the two, *Octochrysis vansoni* (Brauns), a dark-green species with infuscated wings, was found over several seasons to be a constant attendant at each of the nesting sites and at times appeared to be as common there as *P. insignis* itself. Its appearance in early summer was found to coincide with that of the eumenid and its flight season appeared to be of similar length. The species was never observed anywhere other than at the nesting areas of *P. insignis*. Within the *Parachilus* nesting area *O. vansoni* is to be found resting upon the ground in close proximity to nests which are being worked upon (Plate 7). Every so often the chrysidids take to the wing to inspect open nests left unguarded while the eumenids have flown off to fetch water or to hunt. Having alighted upon the nest collars the chrysidids are seen to probe the nest entrances with rapidly quivering antennae (Plate 8) and occasionally to enter the nests. Remarkably little notice appears to be taken of the chrysidids by the female eumenids.

The very much less common of the two chrysidid species, *Pseudospinolia ardens* (Moc-sary), a ruby coloured form with infuscated wings, does not differ in its behaviour from that described for *O. vansoni*.

It is remarkable that all the specimens (123 of *O. vansoni* and 5 of *P. ardens*) collected at the nesting sites over a period of several seasons appear to be females. These include specimens determined by Linsenmaier in 1972 which were used by the authors in naming subsequently collected material.

No conclusive proof was obtained that either species is a parasite or cleptoparasite of *P. insignis* but to the very suggestive circumstantial evidence may be added the fact that typical chrysidid cocoons of the correct size for either of the species were obtained from *P. insignis* cells excavated on 13.xi.1974. Unfortunately, the diapausing larvae within the cocoons, which were transferred to glass vials, did not develop further and died after several months.

Little is known about either species: *Octochrysis vansoni* was described by Brauns (1928: 388) from two males on a *Euphorbia* sp. at Vanrhynsdorp, Namaqualand (Cape Province, not Transvaal as incorrectly stated by Edney (1954: 637)); *Pseudospinolia ardens* was recorded by Edney (1947: 185) from the Cape Province. No hosts have been recorded for either species.

A single diapausing dipterous larva, identified as the 3rd instar of a species of Bombyliidae was obtained from a cell of *P. insignis* excavated on 13.xi.1974. Pale coloured, weakly curved and about 14 mm in length, the larva was amphipneustic with spiracles on the prothoracic and eighth abdominal segments and bore a pair of minute bristles ventro-laterally on each thoracic segment. Other than for the smaller degree of curvature of the body and the reduced length of the thoracic bristles the larva was very similar to that of a *Systoechus* sp., a locust-egg predator, described and figured by Greathead (1958: 6–10, Fig. 1 and Plate 1). At the time of writing (June 1975) the larva was still in a state of diapause and it was hoped that it might yet continue its development and that a specific identification might be possible.

During December 1973 the bombyliid *Exoprosopa leucothyrida* Hesse was very commonly found either resting on the ground or flying about within the nesting areas of *P. insignis*. Hesse (1956: 658) in his summary of the known biology of the genus *Exoprosopa* showed that the

available evidence indicates that the species of this genus parasitize various species of Hymenoptera. It is thus not impossible that the above-described larva may be that of *E. leucothyrida*.

Some indication of the extent to which *P. insignis* is victim to the various parasites may be seen from an enumeration of the insects found in 38 cells excavated and opened by the authors on 13.xi.1974. Twenty-nine cells contained pupae or diapausing larvae of *P. insignis*, six cells contained coarctate larvae of *Lytta enona*, three cells contained cocoons of Chrysididae and one cell contained a diapausing larva of Bombyliidae.

An important prey robber to which the wasps of one of the nesting sites repeatedly fell victim during the 1973-4 nesting season was the camponotine ant *Plagiolepis steingroeveri* Forel. This pugnacious species which had nested in the ground at the edge of the *Parachilus* nesting area systematically raided the open nests of the wasps and carried off the caterpillars with which the cells were being provisioned. During a raid the provisioning wasps which were powerless to prevent the theft of their prey hovered above their nests and above the ants which appeared to take no notice of them but attacked the wasps when they alighted upon the ground.

It is significant that during the following (1974-5) season this particular nesting area contained but a fraction of the usual number of emergence holes and later showed a most striking reduction in the level of nesting activity when compared with that of previous years.

Several species of solitary bees, mostly Megachilidae, were found associated with open old burrows from which *Parachilus* had previously emerged.

The most regular use of these old burrows was made by *Creightoniella dorsata* (Smith), several females of which were observed to be nesting in them. The completed nest of one of these females, the only one excavated by the authors, was found to contain two 17 mm long cells constructed of leaf cuttings. The closure, also constructed of pieces of leaf was 32 mm in length and came to within 3 mm of the opening of the shaft at ground-level.

Other leaf- or petal-cutting species caught on emerging from old *Parachilus* burrows, which were however not excavated by the authors, were *Megachile (Euricharaea) alicae* Cockerell, *M. (E.) meadewaldoi* Brauns, *M. (E.) semiflava* Cockerell and *M. (E.) stellarum* Cockerell. At Hilton *M. (E.) meadewaldoi* has previously been recorded nesting in the burrow of *Bembecinus oxydorcus* (Handl.) (Gess and Gess, 1975: 40) and *M. (E.) stellarum* in the burrows of *Dichragenia pulchricoma* (Arnold) (Gess and Gess, 1974: 204).

An anthophorid bee, *Tetralonia minuta* Fr., a single female of which was captured on emerging from an old *Parachilus* burrow, has previously been recorded from a *Bembecinus cinguliger* (Smith) burrow at Hilton (Gess and Gess, 1975: 40). In neither case is the nature of the association clear.

SLEEPING AND SHELTERING BEHAVIOUR OF THE ADULT WASPS

Both sexes of *Parachilus insignis* spend the night and periods of unfavourable weather during the day sleeping or sheltering in their burrows. Thus on an overcast and cold morning at the very beginning of the flight season (on 30.x.1973), at a time when there were many open burrows from which wasps had emerged over the previous few days but before new burrows had been excavated by the wasps in any numbers, both males and females were found sheltering in the old (previous season's) burrows. When the sun appeared from behind the clouds at 11.30 a.m and the temperature rose these wasps left the burrows and flew off. It was clear that these wasps were not emerging for the first time but were leaving burrows to which they had returned the previous afternoon in order to spend the night in shelter. In sleeping or sheltering in the burrows the wasps, orientated facing the burrow openings, are situated in the upper part of the main shafts, their heads being about 15 mm below ground-level. A sheltering wasp's head and prothorax are clearly visible from outside and appear to block the shaft completely.

As nesting commences females no longer shelter in old burrows but in burrows which they are excavating or provisioning. Males, however, continue to shelter in the previous season's burrows.

During fine, warm, sunny weather the usual time of emergence by the wasps in the morning was not established but in the afternoon many females returned to their burrows as early as 3.30 p.m. During the day it was very noticeable that, whenever the sun was obscured by heavy clouds, the females backed into the burrows they were excavating or provisioning and sheltered there until the sun reappeared. During overcast, cold or rainy days the wasps remained in their burrows all day.

On 12.xi.1973 after three days of rain (during which time 26 mm fell) it was noted that nest collars and pellet-dumps had been washed away or had melted and that nests the existence of which was known could be located only by reference to marker-nails and by measurement, the nest openings having been filled with earth. As the morning passed some of these blocked-up nests were reopened from within by the sheltering wasps. One nest, opened from the outside by the authors was found to contain a live female sheltering between the filled-in portion and the provisioned and sealed egg compartment of the cell. The cell at a depth of 79 mm below the ground surface was quite dry despite the rain, the soil being damp to a depth of only about 50 mm. Undoubtedly, the presence of the sheltering female in the nest shaft helped in the formation of the earth plug sealing the nest and thus saved the cell from flooding.

DISCUSSION

Parachilus insignis shares with certain species belonging to several other odyneroïd genera (such as *Euodynerus*, *Odynerus*, *Oplomerus*, *Paragymnomerus*, *Pterocheilus* and *Stenodynerus*) the habit of constructing original burrows in level ground.

With the exception of *Pterocheilus* all the genera listed above include species whose nest-building behaviour is similar to that of *P. insignis* in that they utilize water to soften the earth and carry away the excavation spoils in the form of mud pellets. Most but not all the species utilize some of the pellets to build mud turrets. Accounts of nesting behaviour relevant to the discussion include those of the following species: *Euodynerus annulatus annulatus* (Say) by Isely (1914: 277-81) (as *Odynerus annulatus* Say) and by Rau and Rau (1918: 300-12) (as *O. geminus* Cresson); *E. annulatus arvensis* (Saussure) by Isely (1914: 271-6) (as *O. arvensis* Saussure) and by Evans (1956: 267-8) (as *Rygchium annulatum arvense* (Saussure)); *E. dorsalis dorsalis* (Fabricius) by Isely (1914: 281-94) and by Rau and Rau (1918: 312-31) (both as *O. dorsalis* Fabr.); *Odynerus dilectus* Saussure by Linsley and Michener (1942: 27); *Oplomerus* species by Blüthgen (1961: 70-82), by Fabre (1943a: 81-103) (as *Odynerus*), by Grandi (1961: 55-62) (as *Hoplomerus*) and by Spradbery (1973: 48-50) (as *Odynerus*); *Paragymnomerus spiricornis* (Spinola) by Blüthgen (1961: 82); *Stenodynerus fundatiformis* (Robertson) by Evans (1956: 268).

When compared with the various accounts of nesting in the above-listed species, the nesting of *P. insignis* is seen not to deviate to any appreciable degree from the overall pattern but rather to be fairly typical of a ground-nesting, water-utilizing eumenid. Indeed, the similarity between the nesting behaviour of *P. insignis* and that of some of the other species, notably *E. dorsalis dorsalis* is most striking. With respect to the latter species one of the few differences lies in the arrangement of the cells which in contrast to the arrangement in *P. insignis* are built one above the other in the direct line of the burrow.

It is in its habit of dividing each cell into two compartments separated by a thin mud plate that *P. insignis* differs in its nesting behaviour from all the above species and indeed the authors have been unable to discover any instance of this behaviour in any other eumenid. As has already been shown, the cell's lower compartment (termed the egg compartment) contains the egg and a

small number of prey caterpillars and the upper compartment (termed the pantry compartment) contains a large number of prey caterpillars but no egg. For the full development of the wasp larva the provision contained in both cell compartments is required. The young larva after having eaten the relatively small amount of provision present in the egg compartment breaks down the thin mud partition separating the compartments and then feeds upon the main supply of provision stored in the pantry compartment. The relative masses of the provision in the two compartments may be seen in Table I and the inadequacy for full larval development of the provision present in the egg compartment alone is apparent when compared with the mass of adult wasps. In this connection it is of interest that in *P. insignis* the males have a greater average mass and are thus generally of larger size than are the females. In connection with the apparent uniqueness of the physical separation of the cell into two compartments in *P. insignis* it should be noted that the statement by Malyshev (1968: 176) concerning Fabre's description of the cell of *Oplomerus reniformis* (Gmel.) (as *Odynerus*) can be misleading. A close study of Fabre's own account (1943a: 100) indicates that there was no actual separation of the cell into two parts by a wall as in *P. insignis* but that the cell merely had a wide and a narrow part.

In view of the one-time inclusion of *P. insignis* and its present congeners within the genus *Pterocheilus*, it is relevant to draw attention to the marked difference between *Parachilus* (as exemplified by *insignis*) and *Pterocheilus* with respect to the nature of the ground in which nesting takes place and to the method by which the nest is excavated. As has been shown *P. insignis* nests in clay soil which requires softening with water before it can be worked whereas those species of *Pterocheilus* for which nesting data could be found nest in sandy soil or at least in soil the nature of which is such that nest excavation (and nest sealing) can be accomplished without the use of water. Species of *Pterocheilus* whose nesting behaviour was considered in this connection comprise the European *chevrieranus* Saussure (Ferton, 1910 and Ahrens, 1924) and the North American *quinquefasciatus* Say (Isely, 1914: 294-6), *texanus* Cresson (Evans, 1956: 265-7) as well as four other species said to have similar life histories (Bohart, 1940: 164).

The above-indicated differences between the two genera with respect to choice of nesting substrate and method of nest excavation are correlated with morphological differences in the mouthparts of the female wasps which have been used as characters in separating *Parachilus* (and *Pseudochilus*) from *Pterocheilus*. Thus the long and pendulous, fringed labial palpi of *Pterocheilus* (see Bohart, 1940: Pl. 1, Fig. 17) are supposedly used in conjunction with the fringed mandibles to form a basket for carrying loose earth from the nest during its construction (see Evans and Eberhard, 1970: Fig. 55). In contrast, the labial palpi of *P. insignis* are furnished with sparse, short hairs (see Giordani Soika, 1960: Fig. 11) and the mandibles though furnished with a well-developed fringe of stiff hairs have these shorter than those of *Pterocheilus*. No psammophore as seen in *Pterocheilus* is thus present in *P. insignis* but the arrangement of hairs on the mouthparts is suited for holding pellets of mud.

SUMMARY

Some aspects of the ethology of *Parachilus insignis* (Saussure) (Hymenoptera: Eumenidae) in the Eastern Cape Province of South Africa are described. Nesting is dealt with in considerable detail as nothing concerning this activity has hitherto been recorded for any species of *Parachilus*. When compared with the published accounts of the nesting of representatives of several other odyneroid genera, the nesting of *P. insignis* is seen to be fairly typical of a ground-nesting, water-utilizing species. However, the division of each cell into two compartments separated by a thin mud plate marks off the behaviour of the present species from that of other Eumenidae. Whether this feature is unique to *P. insignis* or is common to all *Parachilus* species is unknown at present.

Lytta enona Périnquey (Meloidae) is recorded as a cleptoparasite in the cells of *P. insignis* where in its larval stage it feeds upon the paralysed caterpillars laid in as provision by the wasp.

ACKNOWLEDGEMENTS

The authors wish to thank Mr T. C. White of the farm Hilton, where all the field-work connected with this study was undertaken, for his much appreciated kindness over the years in allowing them free access to his land.

Thanks are due also to Mr C. F. Jacot-Guillarmod, Director of the Albany Museum, for helpful comments and discussions, to Dr A. Giordani Soika of the Museo Civico di Storia Naturale, Venice, for identifying *Parachilus insignis* (Saussure), and to Mr M. A. Meyer for his assistance in re-photographing the authors' colour transparencies in order to produce the black-and-white prints used for Plates 3-8.

The senior author is grateful to the C.S.I.R. for a grant partly utilized to cover running expenses in connection with the field-work involved in the investigation.

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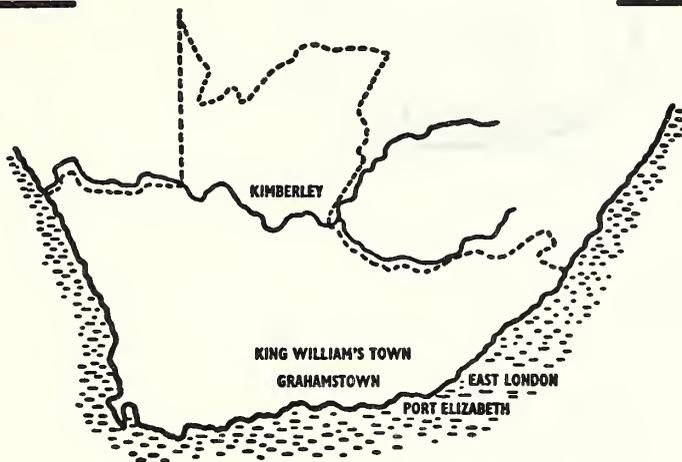


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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 6

31st DECEMBER 1976

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

A new species of *Mastacembelus* (Pisces, Mastacembelidae) from the upper Zambezi River, with a discussion of the taxonomy of the genus from this system

by

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Albany Museum, Grahamstown

INTRODUCTION

The upper Zambezi River sub-system as described by Bell-Cross (1972, 1974) includes the Okavango River and Swamps as well as the Zambezi River itself and its tributaries above the Victoria Falls (Fig. 1). Two *Mastacembelus* species are known and recognized from this region, although only one of the species, listed in recent check-lists of fishes (Bell-Cross 1965, 1972, 1974; Balon 1974; Jubb 1967; Jubb & Gaigher 1971; Jackson 1961, 1975) as *M. mellandi* Boulenger (1914) has been recorded from the upper Zambezi River itself. The second species, *M. mutombotombo* Pellegrin (1936), was described from a single specimen collected in the upper reaches of the Cubango or Okavango River in Angola. Both of these species are characterized by the possession of more or less 30 dorsal spines.

Recent collections of fishes taken from the Zambezi River and its tributary and flood-plain system in the Eastern Caprivi area by Mr B. van der Waal and sent to the Albany Museum, Grahamstown and the Queen Victoria Museum, Salisbury, include a species of *Mastacembelus* which cannot be referred to either *M. mellandi* or *M. mutombotombo*, or any other described species of this genus in Africa. The species is described below as new to science.

Until recently there has been a lack of sufficient suitable material of *Mastacembelus* from the rivers of the southern African region in systematic collections and, as a result, the taxonomy of these southern Africa forms, has not received much attention. Mr van der Waal's collections include specimens not only of the new species, but also specimens which can be referred to as *M. mellandi* (= *frenatus*, *vide infra*). Further specimens of the genus from the Okavango River in Angola have been made available for study and in view of the paucity of published data on the species, morphometric and meristic data are presented and discussed in this paper.

Measurements were taken with vernier callipers to the nearest millimetre in the case of total, standard, pre- and post-anal lengths, and to the nearest 0.1 mm with other measurements. Vertebral and fin ray counts were taken from radiographs and from specimens cleared and alizarin-stained. Due to the specialized morphology of *Mastacembelus* the following notes on the measurements are given. Total length was taken from the tip of the rostral appendage to the extremity of the caudal rays. Standard length excludes the rostral appendage, i.e. is taken from the anterior margin of the premaxilla to the posterior margin of the hypural elements. Head

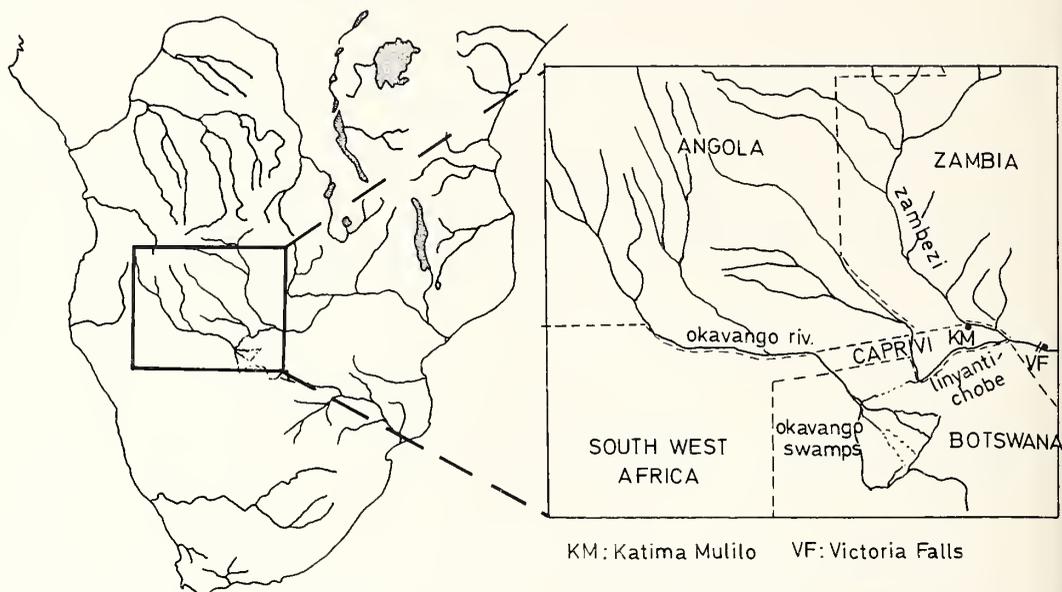


Fig. 1. Maps to show the upper Zambezi River system (as referred to in text).

length is measured from the anterior margin of the premaxilla to the posterior margin of the opercular membrane. Snout length is measured from the anterior margin of the premaxilla to the anterior margin of the eye. Eye length and interorbit distance are as defined in Hubbs and Lagler (1947) with the interorbit distance meaning the least bony width. Dorsal fin to head distance is measured from the base of the first dorsal spine to the posterior occipital margin of the head. Anus to head distance is measured from the vertical through the anus to the vertical through the posterior occipital margin of the head.

Mastacembelus vanderwaali new species (Figs 2 (a) (b), 3) Caprivi spiny eel

Holotype: Male, 153 mm SL AM/P 3183 (a);

Zambezi River mainstream, at Katima Mulilo, Eastern Caprivi. Approximately 17° 30'S., 24° 16'E. Collected by B. van der Waal and P. H. Skelton, 29 September 1975.

Paratypes: 67, males and females, 58,5–151,0 mm SL.

All paratypes collected from the same locality as the holotype. Paratypes registered and collected as detailed below. 11, males and females, 79,0–142,0 mm SL. AM/P 3138 (b) collected with the holotype.

20, males and females, 74,0–151,0 mm SL, AM/P 3450 (5 of these have been sent to the British Museum (Natural History); 5 have been cleared and alizarin-stained). Collected by B. van der Waal, 24 October 1975.

13, males and females, 98,0–142,0 mm SL, AM/P 3449 (5 of these have been sent to the American Museum of Natural History, New York; 3 are deposited in the J. L. B. Smith Institute of Ichthyology, Grahamstown). Collected by B. van der Waal, 8 October 1975.

6, females, 78,0–113,0 mm SL, AM/P 2712 (one cleared and alizarin-stained). Collected by B. van der Waal, 27 November 1974.

3, 1 male and 2 females, 83,0–107,0 mm SL, AM/P 3396. Collected by B. van der Waal, 2 September 1974.

14, males and females, 70,0–134,0 mm SL, QVM reg. No. 3451. Collected by B. van der Waal, 2 September 1974.

TABLE 1

Mastacembelus vanderwaali, new species, Morphometrics (N = 67).

Measurement	Mean	S.D.	S.E.	Range
Standard length (SL) mm	104,7	20,7	2,53	58,5 – 153,0
Total length (mm)	110,1	21,76	2,66	61,5 – 160,0
Body depth (% SL)	7,9	0,61	0,07	6,67 – 9,04
SL/body depth	12,74	0,99	0,12	10,64 – 15,0
Head length (% SL)	16,98	1,0	0,12	14,88 – 20,0
Pre-anal length (% SL)	53,5	1,52	0,19	50,71 – 58,97
Post-anal length (% SL)	46,5	1,52	0,19	41,03 – 49,29
Snout length (% SL)	29,09	1,4	0,17	25,0 – 31,71
Appendage (% eye diam.)	67,87	13,00	1,59	44,44 – 105,0
Eye diameter (% HL)	12,10	1,16	0,14	10,17 – 15,86
Interorbit (%HL)	6,5	0,75	0,09	4,76 – 8,33
Pre-dorsal—head (% SL)	10,84	0,75	0,09	9,08 – 12,86
Pre-dorsal—head (% HL)	64,1	5,11	0,62	51,89 – 73,57
Pectoral fin length (% SL)	25,55	2,51	0,31	20,69 – 32,16
Anal—head length (% SL)	42,09	1,27	0,15	39,79 – 44,35
Anal—head length (% HL)	249,0	14,19	1,73	217,0 – 275,0

Diagnosis: *Mastacembelus vanderwaali* differs from the only other recorded species in the upper Zambezi River, *M. mellandi*, in having fewer dorsal spines (*M. vanderwaali*, 22–26; *M. mellandi*, 27–34); in having fewer vertebrae (*M. vanderwaali*, 78–84; *M. mellandi*, 85–92), a difference which is correlated with different number of vertebrae before the interception of the leading anal pterygiophore; in the head length (*M. vanderwaali* (% SL) 16,98; *M. mellandi*, 13,87); in the head to dorsal fin distance (*M. vanderwaali* (% HL) 64,1; *M. mellandi*, 74,33); in the anal to head distance (*M. vanderwaali* (% HL) 249; *M. mellandi*, 334); and in coloration (see description below for *M. vanderwaali*, and discussion for *M. mellandi*).

Description: Based on the holotype (Fig. 2 (a) and (b)) and 67 paratypes, taken from the mainstream Zambezi River near Katima Mulilo, Eastern Caprivi. Morphometric data is derived from the holotype and 66 paratypes. Six paratypes are cleared and alizarin-stained (after the method of Taylor (1967)) one of which was not previously used for morphometric data. Vertebral counts are taken from radiographs and the 6 cleared and stained specimens. Meristic values are given with the number of individuals preceded by the symbol f in parentheses.

A species of the genus *Mastacembelus* (for generic definition see Boulenger (1916)) of

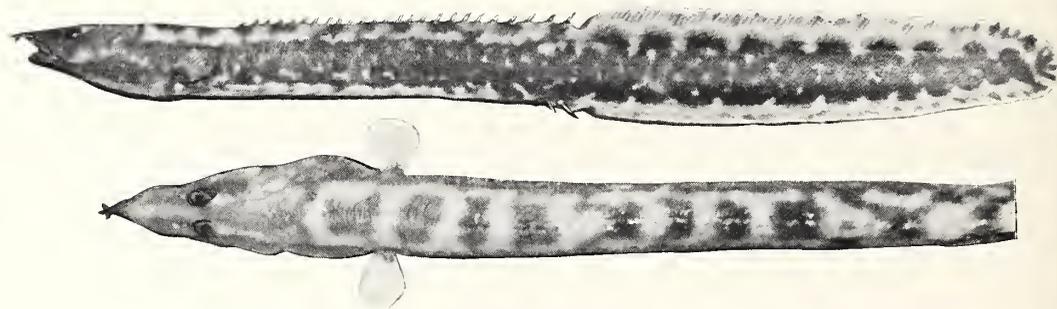


Fig. 2 (a) Holotype *Mastacembelus vanderwaali* n.sp. AM/P 3183 (a) 153 mm SL; (b) Dorsal view of anterior half of specimen. (retouched photographs).

specific morphometric characteristics as listed in Table 1. The maximum size recorded for a male specimen is 153 mm standard length and for females is 134 mm standard length. There is no marked or observed external sexual dimorphism. The body standard length (SL) is, on average, 12,74 times the depth of the body, and between 5 and 6,7 times the length of the head. The anus is closer to the posterior margin of the hypurals than it is to the anterior margin of the premaxillae, and the anal to head distance is on average 2,5 times the length of the head. The snout is 2,4 times the eye diameter and ends in an appendage bearing the anterior nostrils which is usually less than the eye diameter. The posterior fleshy angle of the mouth, when closed, reaches the vertical through the posterior nostril. The lips are well developed, broad and fleshy, and the jaws are endowed along the major portion of the length of the premaxillae and dentaries with numerous sharply pointed, posteriorly inclined teeth up to 3 deep. There are no preorbital or preopercular spines.

The dorsal fin has XXII + I (f1), XXIII + I (f7), XXIV + I (f31), XXV + I (f22) or XXXVI + I (f7) spines increasing posteriorly in size to a maximum in the last externally protruding spine. The additional spine listed above is short and does not protrude externally and is situated immediately anterior to the soft rays of the fin (Fig. 3). The dorsal fin has 64 (f1), 65 (f1), 66 (f3), 68 (f2), 69 (f2), 70 (f2), 71 (f4), 72 (f1), 73 (f1), 74 (f1) or 75 (f1) soft rays. The mean predorsal to head distance is 0,64 times the length of the head but may vary depending on the number of dorsal spines. The anal fin has II + I (f67) spines and 64 (f1), 66 (f2), 67 (f1), 68 (f1), 70 (f5), 71 (f3), 72 (f1), 75 (f3), 78 (f1), and 79 (f1) soft rays. As in the case of the dorsal fin the additional ray recorded is a short reduced non-protruding spine situated between the protruding spines and the soft rays of the fin. The dorsal, caudal and anal fins are confluent and present a varying elliptical profile. The width of the dorsal fin is about 1,5 times the width of the anal fin. The caudal fin has 9 (5 + 4) principal rays. The pectoral fins are small and fan-shaped about 0,25 times the length of the head.

The scales are small, approximately 15–20 occurring between the origin of the soft dorsal and the lateral line. Lateral line pores irregularly spaced from every 3 to 6 scales along the length of the body.

Vertebral column with 78 (f1), 81 (f3), 82 (f5), 83 (f4) or 84 (f3) vertebrae, of which there are 30 (f1), 31 (f1), 32 (f10), 33 (f4) or 34 (f1) vertebrae before the interception of the leading anal pterygiophore and 46 (f1), 47 (f1), 48 (f1), 49 (f2), 50 (f5), 51 (f5) or 53 (f1) vertebrae posterior to the interception of the leading anal pterygiophore. There are 6 (f13) or 7 (f4) vertebrae anterior to the leading dorsal pterygiophore. Each of these latter vertebrae is characterized by a blunt, broad bi- or tri-crested neural spine. There are no predorsal supraneural bones.

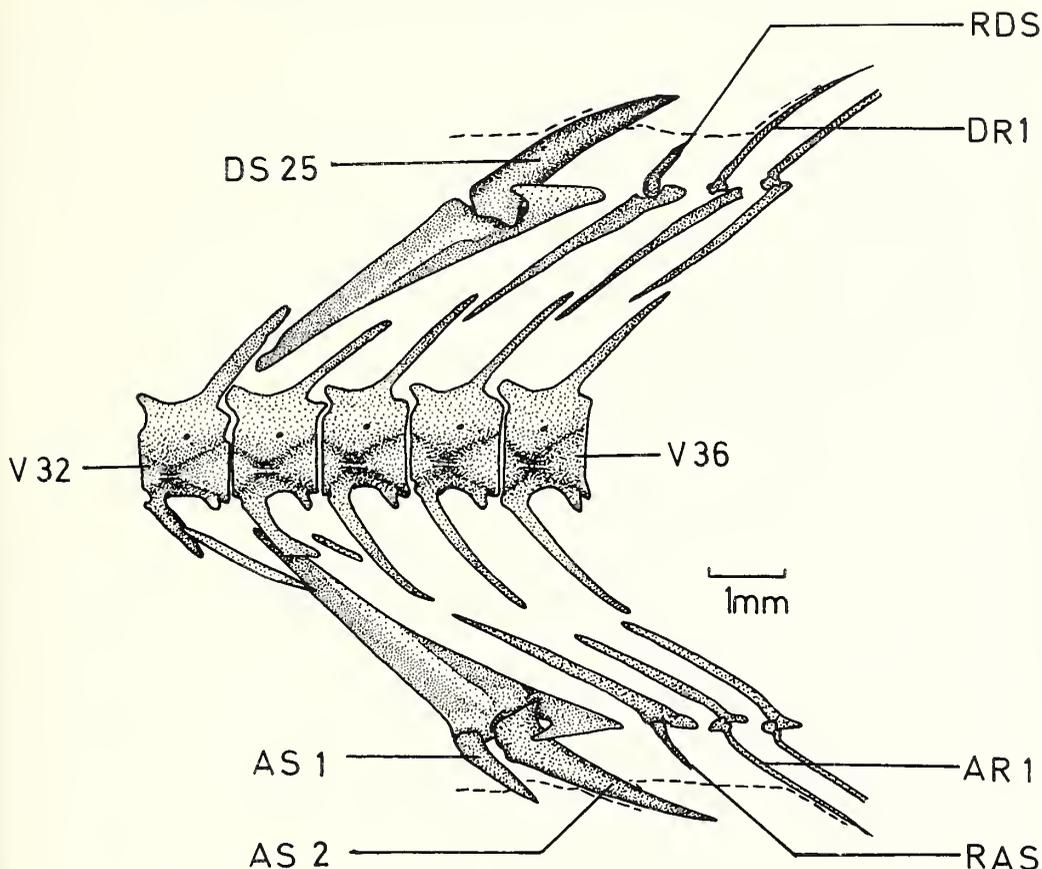


Fig. 3. Section of axial skeleton of *Mastacembelus vanderwaali* n.sp. (paratype AM/P 2712) to show the reduced ultimate spines in the dorsal and anal fins. [Abbreviations: V—vertebra, AS—anal spine, AR1—1st anal soft ray, DS25—25th dorsal spine, DR1—1st dorsal soft ray, RAS—reduced ultimate anal spine, RDS—reduced ultimate dorsal spine.]

The alimentary tract is short with a single recurved loop along its length. The gonads in both sexes extend on average 40 per cent of the length of the body cavity and are usually distally united for slightly less than half of their length. In one female paratype (AM/P 3396; 107 mm SL), in a ripe condition, the formalin-preserved ova have diameters of up to 2.8 mm.

Despite considerable individual variation there is a basic colour pattern discernible in the majority of specimens of the species. The following colour description is based on personal observation of living specimens, colour notes provided by B. van der Waal, and from preserved specimens. The holotype (Fig. 2 (a) and (b)) shows an accentuated and well-developed colour pattern of the basic type. Along the dorsal surface from behind the head to the caudal fin, the colour is predominantly yellow broken along the spiny section of the dorsal fin by a series of blackish-brown approximately rectangular patches which are more or less interconnected anteriorly between the fin and the head. A series of 9–12 dark blackish-brown ocellate reticulations

extend on either side of the soft dorsal fin impinging both on the fin membrane and on the body. A second series of ocellate reticulations occurs in similar fashion along the anal fin. These latter reticulations are slightly smaller than those of the dorsal series but impinge as with the dorsal series both on the fin and the body.

The dorsal and anal fins are predominantly yellowish but are marked with dark dashes running parallel to the rays and which leave a clear yellow margin around each ocellus. Laterally the body is variously marbled or reticulated in yellow and deep blackish-brown. When in a diffused state the colour may appear to be an olive brown and the yellow and blackish-brown contrast can vary considerably. Depending on the degree of pigment diffusion the ventral region anterior to the anal fin may be reticulated or a plain light grey in preserved specimens. In living specimens this region varies from a light cream to yellow through olive to a deep blackish-brown. The head is generally deeply pigmented blackish-brown dorsally, reticulated laterally with a lighter, usually plain ventral surface.

Distribution and habitat: The holotype and paratypes were all collected with electro-fishing gear in the rocky rapids near Katima Mulilo in the Eastern Caprivi (Fig. 1). In addition the species has been collected by B. van der Waal (pers. comm.) in Zambezi rapids near Impalila Island in the south-eastern corner of Eastern Caprivi. It is noteworthy that the species has not been encountered away from the rocky-rapid habitat despite extensive collecting efforts over several years using a wide range of techniques by Mr van der Waal throughout the Eastern Caprivi area. His collecting sites include the Zambezi River mainstream and its Caprivi flood-plain as well as the Kwando/Linyanti/Chobe River and associated flood-plain areas. This indicates that *M. vanderwaali* is probably rocky-rapid-habitat dependant and that its distribution will be governed by the occurrence of such habitats in the system. The rocks which form the rapids near Katima Mulilo are aeolian, being derived from the Kalahari sands which form the geological surface deposits in that area. Consequently the rocks are characterized by jagged rough profiles and contain numerous, often interconnected cavities in which *M. vanderwaali* exists. Long stretches of rapids occur at intervals along the course of the upper Zambezi (Bell-Cross 1974) and it may be anticipated that the species will be found in such stretches in this river sub-system at least. A population of *Mastacembelus* in the Okavango River in Angola is also referred to this species (details given in discussion).

Biology: Of fifty-three paratypes, chosen randomly for sexing by gonad inspection, twenty were males and thirty-three were females. Apart from the previously mentioned ripe female collected in early September 1974, all the specimens varied from an immature to merely active condition. No specimens were collected during the first half of the year, during which the upper Zambezi is annually subjected to flooding, which in the Caprivi area usually reaches a peak between March and May (Curson 1947). Although there is at present a lack of positive data it is possible that the breeding of *M. vanderwaali* is associated with this period of high water.

A preliminary examination of stomach contents indicates that *M. vanderwaali* is predominantly insectivorous, feeding on the macro-benthic rock fauna. Positively identifiable food items include simuliid and chironomid larvae and ephemeropteran and trichopteran nymphs. Odd filamentous algal strands and plant particles are also recorded but are probably incidental items judging from the form of the teeth and alimentary tract of *M. vanderwaali*.

Etymology: The species is named after Mr B. van der Waal, Senior Professional Officer in Charge of Fisheries in the Eastern Caprivi Government Service. Valuable systematic collections of fishes from this area, including this new species, have been submitted to the Queen Victoria and Albany Museum by Mr van der Waal.

DISCUSSION

Certain of the morphological features described above for *M. vanderwaali* are probably of generic and not necessarily of specific significance. Partially fused gonads are features observed in *M. frenatus* (*vide infra*) from the Zambezi system. The reduced spines preceding the soft dorsal and anal fins as described above (Fig. 3) are also present in *M. frenatus*, and would appear to be, in the case of the anal fin, equivalent to the third spine reported for certain species. It is no large difference for such a spine to be protruding or not and the third anal spine of species with three such spines is reduced in size relatively to the second spine (cf. figures in Boulenger 1916; pers. obs.). The lack of predorsal supraneural bones and the broad neural spines of the anterior vertebrae before the dorsal fin are also non-specific characters.

Matthes (1962) examined the type specimens of *Mastacembelus frenatus* Boulenger 1901, *M. taeniatus* Boulenger 1901, *M. victoriae* Boulenger 1903, and *M. mellandi* Boulenger 1914, and concluded that all these species were synonyms of *M. frenatus*. *M. mellandi* was described from a specimen collected from a tributary of the upper Zambezi and was later reported by Boulenger (1916) to be in the Congo (Zaire) River system as well. Despite Matthes's (1962) synonymy the majority of subsequent workers on the Zambezi ichthyofauna have continued to refer to the single known species as *M. mellandi*. By way of exception Lagler *et al.* (1971) in their check-list of fishes from the Kafue River, a middle Zambezi tributary with upper Zambezi ichthyofaunal affinities, followed Matthes (1962) and recorded the *Mastacembelus* species as *M. frenatus*. Elsewhere throughout the range of the species the synonymy has been accepted, e.g. in Lake Victoria by Welcomme (1969), and Lowe-McConnell (1975). Considering the intraspecific variation in coloration, morphometric and meristic characters recorded for various *Mastacembelus* species including *M. frenatus* by Matthes (1962) and in the present paper (Tables 1-4), I am of the opinion that the synonymy of Matthes (1962), in which good reason has been detailed, is valid for the species known as *M. mellandi* in the Zambezi River system, and is adopted hereafter.

In the Caprivi area *M. frenatus* is easily distinguished from *M. vanderwaali* in coloration. Due to a poverty of taxonomic data published for *M. frenatus* from the Zambezi River and for comparative purposes a morphometric (Table 2) and meristic and colour description for the species is offered here. Material examined is recorded in Appendix I, colour was recorded from live fishes and the preserved material, soft ray counts are taken from two cleared and stained specimens and suitable radiographs.

In contrast to the generally bold markings of *M. vanderwaali*, *M. frenatus* from the Caprivi area is either plain or finely spotted or reticulated, becoming more marked posteriorly. The ground colour is brown and a usually outstanding feature is a lighter reddish brown dorso-lateral band extending from the tip of the snout to the latter half of the soft dorsal fin where it progressively merges with the reticulations of this part of the body. The soft dorsal and anal fins have a series of ocellate spots along the bases. Dorsally the reddish band is more or less divided by a series of dark brown markings about the bases of the dorsal spines, a feature well illustrated by a figure of *M. taeniatus* (= *M. frenatus*) in Steindachner (1915). The fin membranes are marked with a series of dashes separated from the ocellate spots anteriorly but merging with them posteriorly to form a reticulated pattern.

The range of variation recorded for dorsal spines as well as dorsal and anal soft rays and for vertebral counts of *M. frenatus* is wide and underlines the caution which must be given in attaching specific significance to these characters alone. Dorsal spines range from XXVII + I (f1) through XXVIII + I (f2), XXX + I (f3), XXXI + I (f9), XXXII + I (f9), XXXIII + I (f4) to XXXIV + I (f1), all individuals having a reduced non-protruding ultimate spine as reported for *M. vanderwaali* above. Anal spine counts were all II + I (f31), likewise in each case with a third non-protruding spine prior to the first soft ray. Accurate soft ray counts are available from two

cleared and stained specimens (AM/P 3295 & AM/P 3250) and suitable radiographs of five specimens (AM/P 3441 (f1), QVM 1843 (f2), QVM 0322 (f1), QVM 2074 (f1). Dorsal soft rays were less than the number of anal soft rays in six of the seven specimens having respective values as follows (dorsal soft rays first): 70-76, 81-83, 69-66, 72-76, 72-76, 72-73, 74-78. It is clear that there is a broad variation in soft fin ray counts for both *M. frenatus* and *M. vanderwaali* and thus there appears to be no specific distinction in this character for these species. Vertebral counts of nine specimens are available: 85 (f1), 86 (f1), 89 (f5), 90 (f1), 91 (f1). As in *M. vanderwaali* there are 6 (f5) or 7 (f4) vertebrae before the interception of the leading dorsal pterygiophore, and from 35 (f1), 36 (f1), 37 (f1), 38 (f2) to 39 (f4) vertebrae before the interception of the leading anal pterygiophore. It would appear from this brief analysis that the larger number of vertebrae recorded for *M. frenatus* than *M. vanderwaali* is due to an increased number of vertebrae before the anal fin, which correlates well with the larger number of dorsal spines in the former species.

Morphometric analysis for *M. frenatus* from the upper Zambezi follows in Table 2.

TABLE 2

Mastacembelus frenatus (= *mellandi*) from the upper Zambezi River system, Morphometric analysis (N = 31).

Measurement	Mean	S.D.	S.E.	Range
Standard length (SL)	138,68	49,74	8,93	62,0 - 235,0
Total length (MM)	144,81	51,89	9,32	64,5 - 242,0
Body depth (% SL)	7,98	0,74	0,13	6,3 - 9,49
SL/body depth	12,62	1,2	0,22	10,53 - 15,84
Head length (% SL)	13,87	1,39	0,25	9,57 - 16,46
Pre-anal length (% SL)	54,89	1,84	0,33	50,65 - 58,33
Post-anal length (%SL)	45,11	1,84	0,33	41,67 - 49,35
Snout length (%HL)	30,78	2,54	0,46	26,47 - 35,0
Appendage (% eye diam.)	84,58	20,57	3,69	55,0 - 146,66
Eye diameter (%HL)	11,5	1,63	0,29	7,5 - 14,63
Interorbit (%HL)	8,28	0,94	0,17	6,52 - 10,57
Pre-dorsal—head (%SL)	10,27	0,93	0,17	8,9 - 13,04
Pre-dorsal—head (% HL)	74,33	7,08	1,27	64,00 - 103,1
Pectoral fin length (% HL)	27,1	2,78	0,5	22,76 - 35,11
Anal—head length (% SL)	45,7	1,47	0,26	42,86 - 49,07
Anal—head length (% HL)	334,0	38,19	7,09	269,0 - 498,0

The morphometric values of *M. frenatus* (Table 2) and *M. vanderwaali* (Table 1) are generally close except with regard to maximum standard (or total length) attained and the anal to head distance (expressed as % head length). With regard to this latter measurement although the range shown by *M. frenatus* apparently overlaps that of *M. vanderwaali* extensively the recorded range is misleading as the individual fish with the range extremes are exceptional and a more reliable range taken from the remaining specimens would be (% HL) 304 to 369, as well beyond the range of *M. vanderwaali*. Again this difference between these species can be correlated to the difference in the number of vertebrae before the anal fin as recorded above. The maximum standard length recorded deserves comment as it appears to be a feature of *M. vanderwaali* to be

a shorter species (when adult) than *M. frenatus*. There are indications that *M. vanderwaali* can be sexually active at less than 100 mm standard length, whereas *M. frenatus* were all larger than this when showing any sign of sexual activity in the state of the gonads. The type specimen of *M. mellandi* with a total length of 310 mm (Boulenger, 1914) is almost twice the length of the largest *M. vanderwaali* from the type series.

Boulenger (1917) described from a single specimen a second species of *Mastacembelus* from the upper Zambezi (taken near Shesheki in, what is now, Zambia), viz. *M. thompsoni*. Jubb (1967) placed *M. thompsoni* in synonymy with *M. frenatus* (= *mellandi*) but did not detail reason for so doing. An examination of the type specimen (SAM 14542) at present housed in the Albany Museum, indicates that the specimen (Table 3) differs from *M. frenatus* (Table 2) significantly only in the body depth to standard length ratio. The high ratio recorded is not due to poor preserved condition as a similar ratio was recorded by Boulenger (1917) in the original description using total length, but may be a reflection of poor condition in life. Not only is the specimen large (i.e. long) (SL 272 mm) but the extensive collecting in the upper Zambezi close to Shesheki by Mr van der Waal indicates that there is only one species growing to this size and with as many dorsal spines, viz. *M. frenatus*. The synonymy is therefore upheld.

TABLE 3

Mastacembelus thompsoni, holotype, Morphometrics (Dec. 1975)

Measurement	
Standard length (SL) mm	272,0
Total length (mm)	281,0
Body depth (% SL)	5,1
SL/body depth	20,0
Head length (% SL)	12,83
Pre-anal length (% SL)	50,36
Post-anal length (% SL)	49,53
Snout length (% HL)	30,3
Appendage (% eye diam.)	116,0
Eye diameter (% HL)	9,09
Interorbit (% HL)	8,48
Pre-dorsal—head (% SL)	8,82
Pre-dorsal—head (% HL)	72,72
Pectoral fin length (% HL)	27,27
Anal—head length (% SL)	43,38
Anal—head length (% HL)	357,0

Pellegrin (1936) described *Mastacembelus mutombo* from a single specimen taken from the upper reaches of the Cubango or Okavango River in Angola. The species was described with a dorsal spine count of 30, well above that encountered for *M. vanderwaali* from the upper Zambezi.

Poll (1967) drew attention to the close resemblance of *M. mutombo* to what was identified as *Mastacembelus batesii* Boulenger (1911). It is noted that Poll's (1967) *M. batesii*

bears a strong resemblance, judging from his figure and description, to the Zambezi form of *M. frenatus*. *Mastacembelus mutombotombo* has not been recorded in southern African collections until recently when specimens collected by the State Museum, Windhoek, in the Okavango River (Cubango) in Angola (fig. 1) were referred to this species. A sample of these specimens was made available for study and an analysis is given below.

The general facies and coloration of these specimens is close to that recorded for *M. vanderwaali* above. Morphometrics of the specimens are recorded in Table 4 below. Dorsal spines range from XXVI + I (f1), XXVII + (f5), XXVIII + (f4) to XXIX + I (f2) and anal spines II + I (F12). The range for dorsal soft rays is 62 to 71 and for anal fin soft rays is 63 to 70. The relationship between the number of dorsal soft rays and anal soft rays appears to be irregular and for the eleven specimens counted the values are as follows (dorsal precedes anal count): 69-69, 62-13, 69-69, 65-66, 62-69, 65-69, 71-70, 66-65, 68-67, 65-70, 71-70. The number of vertebrae range from 83 (f1), 84, (f4), 85 (f2), 86 (f1) to 87 (f3). There are 33 (f1), 34 (f4), 35 (f3) or 36 (f3) vertebrae before the leading anal pterygiophore and from 49 (f1), 50 (f7), 51 (f2) to 53 (f1) posterior to the leading anal pterygiophore.

TABLE 4

Mastacembelus species: Okavango River, Caiundo, Angola (N = 12)

Measurement	Mean	S.D.	S.E.	Range
Standard length (SL) mm	102,0	15,23	4,4	79,0 - 140,0
Total length (mm)	107,0	16,07	4,64	83,0 - 147,0
Body depth (% SL)	7,86	0,76	0,22	7,13 - 9,9
SL/body depth	12,81	1,08	0,31	10,11 - 14,02
Head length (% SL)	16,81	0,52	0,15	16,00 - 17,37
Pre-anal length (% SL)	56,15	1,47	0,42	53,48 - 57,97
Post-anal length (% SL)	43,85	1,47	0,42	43,03 - 46,52
Snout length (% HL)	28,99	1,87	0,54	26,49 - 33,54
Appendage (% eye diam.)	62,00	5,37	1,55	50,0 - 68,42
Eye diameter (% HL)	11,89	0,78	0,23	10,57 - 13,43
Interorbit (% HL)	6,36	0,72	0,21	5,3 - 7,61
Pre-dorsal—head (% SL)	10,75	0,65	0,19	9,8 - 11,67
Pre-dorsal—head (% HL)	63,98	4,3	1,24	56,4 - 70,89
Pectoral fin length (% HL)	21,93	2,13	0,62	19,21 - 25,44
Anal—head length (% SL)	44,19	1,54	0,45	42,17 - 45,92
Anal—head length (% HL)	263,0	12,4	3,6	244,0 - 279,0

The morphometric values for this species of *Mastacembelus* from the Okavango River (Table 4) compare very similarly with those of *M. vanderwaali* (Table 1). Of particular note are the points of similarity between the two samples, which are points of difference between *M. vanderwaali* and *M. frenatus*. The similarity of overall size range is significant in the light of the discussion of this recorded above. Sexually mature specimens are present in the Okavango material which has a sample maximum size of 140 mm SL. Certain differences in the meristic values of *M. vanderwaali* and the Okavango material exist. The vertebral number of the Okavango specimens proceeds higher than for *M. vanderwaali* mainly as a result of increased

number of vertebrae before the anal fin. This increase is reflected in the increased number of dorsal spines of the Okavango specimens, the mode value of which is still less than the mode recorded for *M. frenatus* above. Of particular significance is the similarity of the Okavango specimens in the anal fin to head distance (as % head length) with *M. vanderwaali* and in this same respect its dissimilarity with *M. frenatus*. It is thus concluded that the Okavango specimens are best referred to as a form of *M. vanderwaali* and not of *M. mutombotombo* as described by Pellegrin (1936).

The holotype of *Mastacembelus mutombotombo* Pellegrin (1936) has been received on loan from the Museum National d'Histoire Naturelle, Paris (Registered No. -36-157) and the following analysis and consideration of the specimen and species is thus possible. Table 5 records a morphometric analysis of the specimen. Vertebral and fin ray counts taken from a radiograph are as follows: total vertebrae 91, 37 pre-anal (38 pre-caudal) and 54 post-anal (53 caudal) vertebrae; 6 vertebrae before the dorsal fin, XXX + I dorsal spines, II + I anal spines, 64 dorsal soft rays, 68 anal soft rays. Scale counts are as recorded by Pellegrin (1936) and although the coloration is presently faded, faint traces of the pattern recall that of *M. frenatus* above.

TABLE 5

Mastacembelus mutombotombo, holotype (Mus. Nat. d'Hist. nat., Paris: -36-157)

Measurement	
Standard length (SL) mm	221,0
Total length (mm)	231,0
Body depth (% SL)	7,69
SL/body depth	13,0
Head length (HL) (% SL)	13,12
Pre-anal length (% SL)	52,49
Post-anal length (% SL)	47,51
Snout length (% HL)	28,62
Appendage (% eye diam.)	87,1
Eye diameter (% HL)	10,69
Interorbit (% HL)	6,9
Pre-dorsal—head (% SL)	9,5
Pre-dorsal—head (% HL)	72,41
Pectoral fin length (% HL)	22,07
Anal—head length (% SL)	43,89
Anal—head length (% HL)	334,5

Pellegrin described the coloration as uniformly brown with the fins as greyish or yellowish and darker markings along the soft dorsal and back. Beyond a slight discrepancy in the standard length and possibly a longer snout length the values recorded in Table 5 fit the original description.

The morphometric values for *M. mutombotombo* are also well within the range recorded for *M. frenatus* in Table 2, and there is no disagreement in the dorsal spine count of the specimen with those of *M. frenatus*. The soft ray counts differ from that recorded by Pellegrin (1936) (dorsal 60, anal 60) and although the specimen's counts for the soft fin rays are slightly less than

the values recorded for the six *M. frenatus* specimens above they are sufficiently close and provide no grounds for specific distinction. I consider therefore that *M. mutombotombo* to be a syn. nov. of *M. frenatus*.

It is fairly certain that *M. vanderwaali* is confined to the rocky-rapid environment reported under the habitat of the species above. Although this environment is typical for the genus as shown by Corbet (1961), Lowe-McConnell (1975) and others, the narrow habitat preference of *M. vanderwaali* in contrast to the less demanding *M. frenatus* is reflected in the only recent, yet relatively belated appearance of *M. vanderwaali* to science. The case history of *Clariallabes platyprosopos* a closely sympatric species apparently confined to the same environment gives further explanation to this situation. *C. platyprosopos* was described by Jubb (1964) from a single specimen collected in the upper Zambezi in 1955. No further specimens were collected before it was described (Jubb 1964) and no specimens are known to have been collected or reported on until 1974, when Mr. B. van der Waal submitted specimens collected with electro-fishing gear in the rapids at Katima Mulilo to the Queen Victoria Museum, Salisbury.

The meristic differences between the population in the Okavango River and that from the Zambezi in the Caprivi area lends support to the thesis that the swampy Okavango/Linyanti/Chobe connection between these populations is an effective ecological barrier to the species. In this regard a detail of the habitat in which the Okavango specimens were collected (Penrith *in litt.*) is pertinent "rapid moving water between large rocks and solid rock bed".

The following note is proffered as a point of correction on the spelling and authorship of the genus *Mastacembelus* and which has varied in certain recent southern African publications. The correct spelling in agreement with the family Mastacembelidae is *Mastacembelus*. Correct authorship is given to Scopoli 1777 who was the first to use the name in bi-nomial combination.

ACKNOWLEDGEMENTS

I am grateful to the director of the Albany Museum. Mr C. F. Jacot-Guillarmod, for permission to pursue the study and publish this paper. Mr Ben van der Waal exposed the problem, collected specimens and provided ecological and other information on them. I am also extremely grateful to Mr van der Waal and his wife for their warm hospitality while in the Caprivi. Dr R. A. Jubb and Mrs H. Jubb provided the illustration of the holotype, read the paper and, by discussion, stimulated the research, all of which is gratefully appreciated. Mr J. C. Greig kindly read the paper. Dr P. H. Greenwood of the British Museum (Natural History) provided information on the spelling and authorship of the genus. Mr M. Penrith and Mr G. Bell-Cross provided specimens for study, and X-ray services were generously provided by the J. L. B. Smith Institute of Ichthyology, Grahamstown. The Director, Museum National d'Histoire Naturelle, Paris, kindly loaned the holotype of *Mastacembelus mutombotombo*.

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APPENDIX

Mastacembelus frenatus; material examined.

Abbreviations: AM/P—Albany Museum, Grahamstown.

SAM—South African Museum, Cape Town (note: specimen housed in Albany Museum).

QVM—Queen Victoria Museum, Salisbury.

SMW—States Museum, Windhoek, South West Africa.

PNHM—Museum National D'Histoire Naturelle, Paris.

- QVM 2074 1 specimen (231 mm SL) Luanginga River, Kalabo, Zambezi River system, Zambia. March 1964, R. Japp.
- QVM 1843 2 specimens (183; 198 mm SL) Luanginga River, Kalabo, Zambezi River system, Zambia. March 1964, R. Japp.
- QVM 0322 1 specimen (186 mm SL) Mohembo, Okavango River. 3 December 1958, D. C. Culver-Letter.
- AM/P 34 3 specimens (214; 192; 186 mm SL) Victoria Falls National Park, Zambezi River, Rhodesia. 6 August 1959, R. A. Jubb.
- AM/P 1780 2 specimens (206; 173 mm SL) upper Zambezi River.
- AM/P 2381 1 specimen (140 mm SL) (head damaged) Schuckmannsburg, Eastern Caprivi, Zambezi River system. 12 October 1973, B. van der Waal.
- AM/P 3132 3 specimens (84; 106; 116 mm SL) Drainage channel, Zambezi flood-plain, near Schuckmannsburg, Eastern Caprivi. 27 September 1975, B. van der Waal and P. H. Skelton.
- AM/P 3295 5 specimens (85; 89; 97; 102; *113 mm SL) (*cleared and alizarin-stained) Backwater (mulapo) from Zambezi River, Eastern Caprivi. 30 August 1975, B. van der Waal.

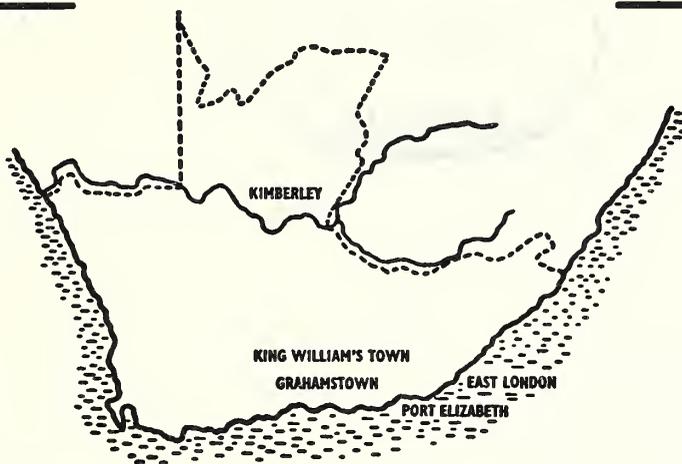
- AM/P 3351 3 specimens (152; 155; 235 mm SL) Zambezi River system. Schuckmannsburg, Eastern Caprivi. 1974-5, B. van der Waal.
- AM/P 3371 1 specimen (123 mm SL) Zambezi River system, Eastern Caprivi. 1974-5, B. van der Waal.
- AM/P 3425 1 specimen (108 mm SL) stream, Impalila, Zambezi River system, Eastern Caprivi. 7 August 1975, B. van der Waal.
- AM/P 3441 2 specimens (105; 170 mm SL) Nabwizu, Eastern Caprivi, upper Zambezi system. 23 July 1975, B. van der Waal.
- AM/P 3350 4 specimens (79; 97; 103; *109 mm SL) (*cleared and alizarin-stained) Malila backwater, Eastern Caprivi, Zambezi River system. 27 August 1975, B. van der Waal.
- AM/P 3554 2 specimens (62; 100 mm SL) Malila backwater, Eastern Caprivi, Zambezi River system. 29 August 1975, B. van der Waal.
- SAM 14542 Holotype, *Mastacembelus thompsoni*, Shesheki, Northern Rhodesia (Zambia). Rev. L. Jalla.
- SMW P.777 *Mastacembelus* cf. *vanderwaali*, 12 specimens Okavango River, Caiundo, Angola. 15 October 1972, M. J. Penrith, J. Baptista.
- PNHM -36-157 Holotype, *Mastacembelus mutombombo*, Cubango River, Angola. Dr Monard.

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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 7

31st DECEMBER 1976

PUBLISHED JOINTLY BY THE

CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

The larval and pupal stages of *Ugandatrichia* Mosely (Trichoptera: Hydroptilidae) from Rhodesia, with the description of a new species

by

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ABSTRACT

A new species of *Ugandatrichia* Mosely, *U. rhodesiensis* (Hydroptilidae), is described from the Chimanimani National Park in Rhodesia, as are its larval and pupal stages. The larval and pupal stages of this genus were previously unknown, as are the immature stages of *Micropstila* Ris, with which it may be synonymous. The relationships of the young stages are briefly discussed.

INTRODUCTION

The specimens described in this paper were collected in the mountains in the Chimanimani National Park near Melsetter in eastern Rhodesia, by Professor (then Dr) A. D. Harrison, who kindly submitted the Trichoptera to me for identification. Dr Harrison informed me (*in litt.* 3.vi.1963), that these mountains are composed largely of old quartzites, and that the water coming from them is acid as in the Western Cape mountains (pH 5.6; conductivity 6.8). The water is clear in the main river and brown in the small side streams.

The collection included imagos, larvae and pupae of two species of Hydroptilidae, one in the genus *Ugandatrichia* Mosely (given as a synonym of *Micropstila* Ris by Schmid, 1960), and one in *Afritrichia* Mosely, synonymized with *Stactobia* McLachlan, also by Schmid (1959). Both are hydropetric species, inhabiting waterfalls on the Bundi River at a considerable altitude (1 580–1 700 m); both appear to be new species. The *Ugandatrichia* is described in this paper, as *Ugandatrichia rhodesiensis* sp. nov., and I hope to describe the *Afritrichia* at a later stage. These were the only Hydroptilidae represented in the collection. The larval and pupal stages of the *Ugandatrichia* are particularly interesting, not only in their own right as being most unusual, but also because the young stages of neither *Ugandatrichia* nor *Micropstila* have to my knowledge as yet been described.

Note: Specimen numbers refer to collections and catalogues in the Albany Museum, Grahamstown, South Africa.

Family HYDROPTILIDAE

Ugandatrichia rhodesiensis n. sp.

MATERIAL STUDIED: Rhodesia: Chimanimani National Park, Bundi River, main waterfall (c. 1 580 m), 17 ♂♂, 4 ♀♀, on rocks beside fall and flying over it (SRE 3D(1)–3D(21)), 24 larvae of various sizes, many damaged, collected from most torrential part of fall (SRE 3G), 9 pupae collected in fall (SRE 3H), all these 19.v.1963; Bundi River, main waterfall pool, 1 ♂ 1 ♀ flying low over pool at dusk (SRE 6C, 17.v.1963); Bundi River, small waterfall about 1.6 km below main fall, 4 pupae collected in splash zone (SRE 4A, 15.v.1963); Bundi River, upper waterfall (c. 1 700 m), 1 ♀ (SRE 5A(1), 16.v.1963). Holotype ♂ (SRE 3D(1)) deposited in the Albany Museum Freshwater Collection, also ♂ paratypes SRE 3D(2)–3D(12) and SRE 6C(1); also ♀♀ SRE 3D(18)–(20), SRE 5A(1) and SRE 6C(2); also larvae and pupae. ♂ paratypes SRE 3D(16) and (17), with ♀ SRE 3D(21), larvae and pupa, to the Smithsonian Institution, Washington, D.C.; ♂ paratype SRE 3D(13) to the British Museum (Natural History); ♂ paratype SRE 3D(14) to the National Museum, Bulawayo, Rhodesia, and ♂ paratype SRE 3D(15) to the Musée Royal de l'Afrique Centrale, Tervuren.

DESCRIPTION OF ♂ HOLOTYPE (in alcohol) (Figs 1–8)

A medium-sized Hydroptilid, length of forewings 4.5 mm, dark brown in colour when first collected, possibly black in life. Insect densely hairy, dorsal surface of abdomen rather less so; forewings covered with both recumbent and stiff, thickened, erect setae; genitalia short, with blackened apices.

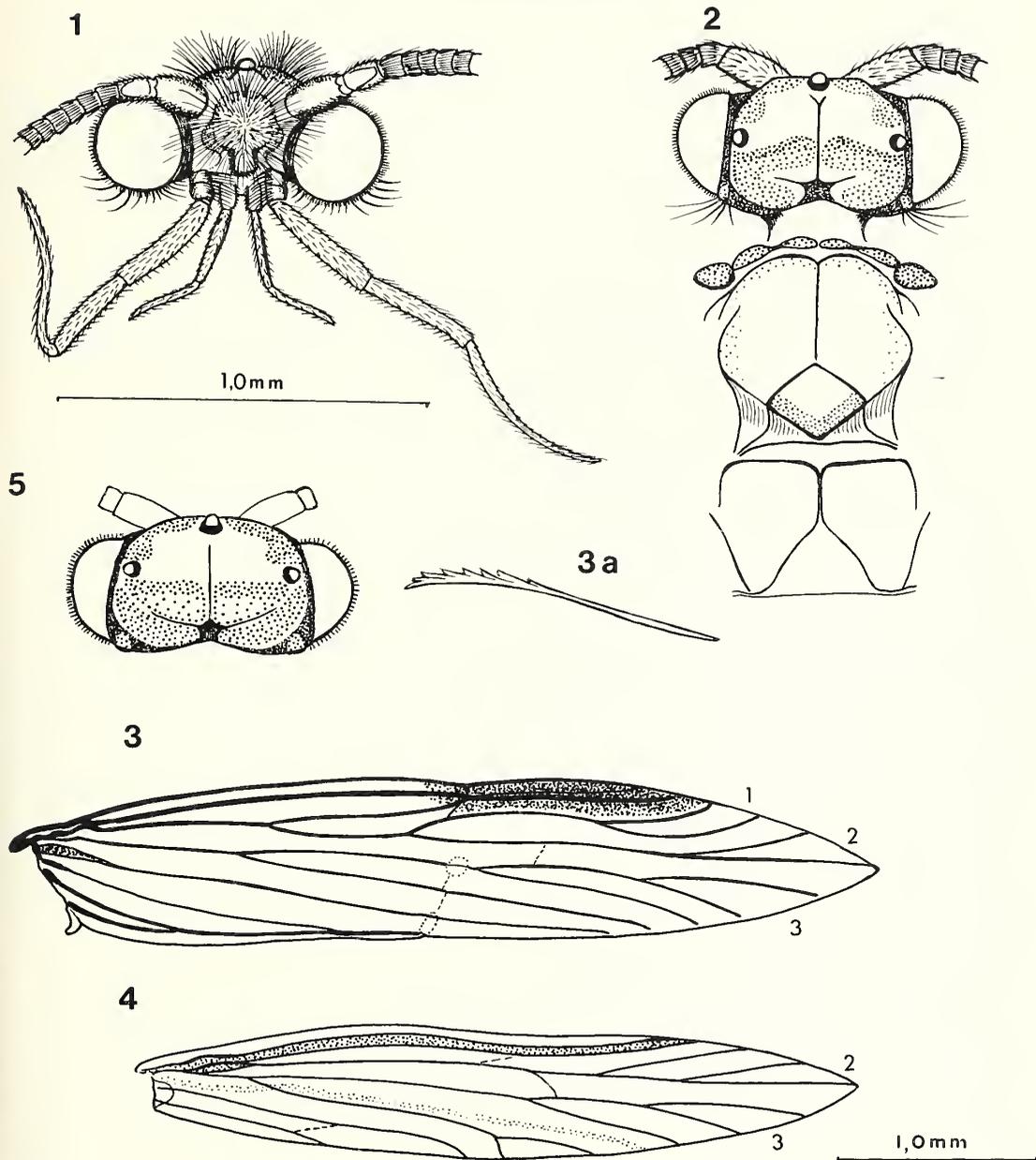
Head (Figs 1, 2): ocelli present, white ringed with dark brown to black, very conspicuous; antennae with 42 segments; eyes large, dark, pubescent; maxillary palps long, dark, first two segments very short, with inner tufts of long setae, third and fourth segments long, considerably longer than one and two together, third slightly longer than fourth, fifth longest, slender, flexible; labial palps considerably shorter, paler, with first segment small, second and third longer, subequal, third flexible.

Tibial spurs 0, 3, 4.

Wings (Figs 3, 4): forewings with forks 1, 2, 3 present; hind wings with forks 2 and 3 only. Wing membrane thickly covered with micro- and macrotrichia; forewings in addition with a dense covering of strong, erect, serrate setae (Fig. 3a). Nearly all veins in the forewing take the form of thickened, pitted bands, the pits indicating the positions of the serrate setae. Sc and Sc+R1 are particularly thick, the latter set in an apical pterostigma. This thickening makes it easy to follow the course of the veins, but the cross-veins are very difficult to distinguish except at the anastomosis where parts are clear (white). In the hind wings, which lack the erect setae, veins are narrow except for Sc+R1, which is very much broadened; there is also a brown streak between M and Cul, running close to the latter and crossing it near its base. No basal cross-veins could be found in either wing, except for one faint vein joining 1A and 2A in the hind wing. In the forewing the veins stop short of the costa along the anal margin.

Abdomen: the terga of abdominal segments II to VII each have two patches of light brown pigment near the proximal margin, on I and VIII these merge to form one diffuse patch; there is a small, pointed, sclerotized ventral process on VII.

Genitalia (Figs 6–9): (cleared in KOH and examined in clove oil), ninth segment short, partially retracted within eighth, proximally emarginate both dorsally and ventrally; a raised membranous dorsal plate with median incision occupying most of the centre, very difficult to see except in lateral view; beneath this can be seen the aedeagus (large, with central canal and an apparently membranous fringe, encircled by a coiled sheath or titillator, see Fig. 9); beneath that again lies the lower penis cover, ending in a pair of curious apical sclerotizations each bearing a



Figs 1-5, *Ugandatrachia rhodesiensis* n. sp., holotype, ♂ (SRE 3D(1)), or paratypes or ♀ if other numbers given. 1. Anterior view of head including palps and bases of antennae. 2. Dorsal view of head, pro-, meso- and metanota. 3. Forewing of paratype SRE 3D(3). 4. Hind wing of paratype SRE 3D(3). 5. ♀, SRE 3D(18), dorsal view of head.

long, horn-like seta. The distal margins of the ninth sidepieces are swollen and heavily studded with long, recurved setae; proximal to each of these on the dorsal side is a smaller, setose bulge, and towards the apex of each, on the inner side, a thumb-like spur, seen in lateral view to be down-turned. On the ventral side the inferior appendages are widely divergent, each terminating in a blackened median boss or knob, and an outer membranous lobe set with large blade-like setae; the appendages themselves are ventrally pubescent and thickly covered with longer setae. Within each a large, stout seta can be seen by transparency. The base of the segment shows a deep, U-shaped emargination, the ninth sternite being narrow. ♂ genitalia are more or less symmetrical, but not entirely so in details.

Comparison with ♂ paratypes

The ♂ Holotype and the 17 ♂ paratypes are all very similar in general appearance, but differ slightly in size, wing length (forewing) ranging from 3,5 to 4,5 mm, and the antennae having from 42 to 45 segments. In most specimens the genitalia are deeply retracted into the eighth segment, or even both eighth and ninth retracted within the seventh; the aedeagus is usually exserted. The shape of the sidepieces varies with the state of retraction of the genitalia.

DESCRIPTION OF ♀ PRESUMED TO BELONG TO ♂ (in alcohol) (Figs 5, 10)

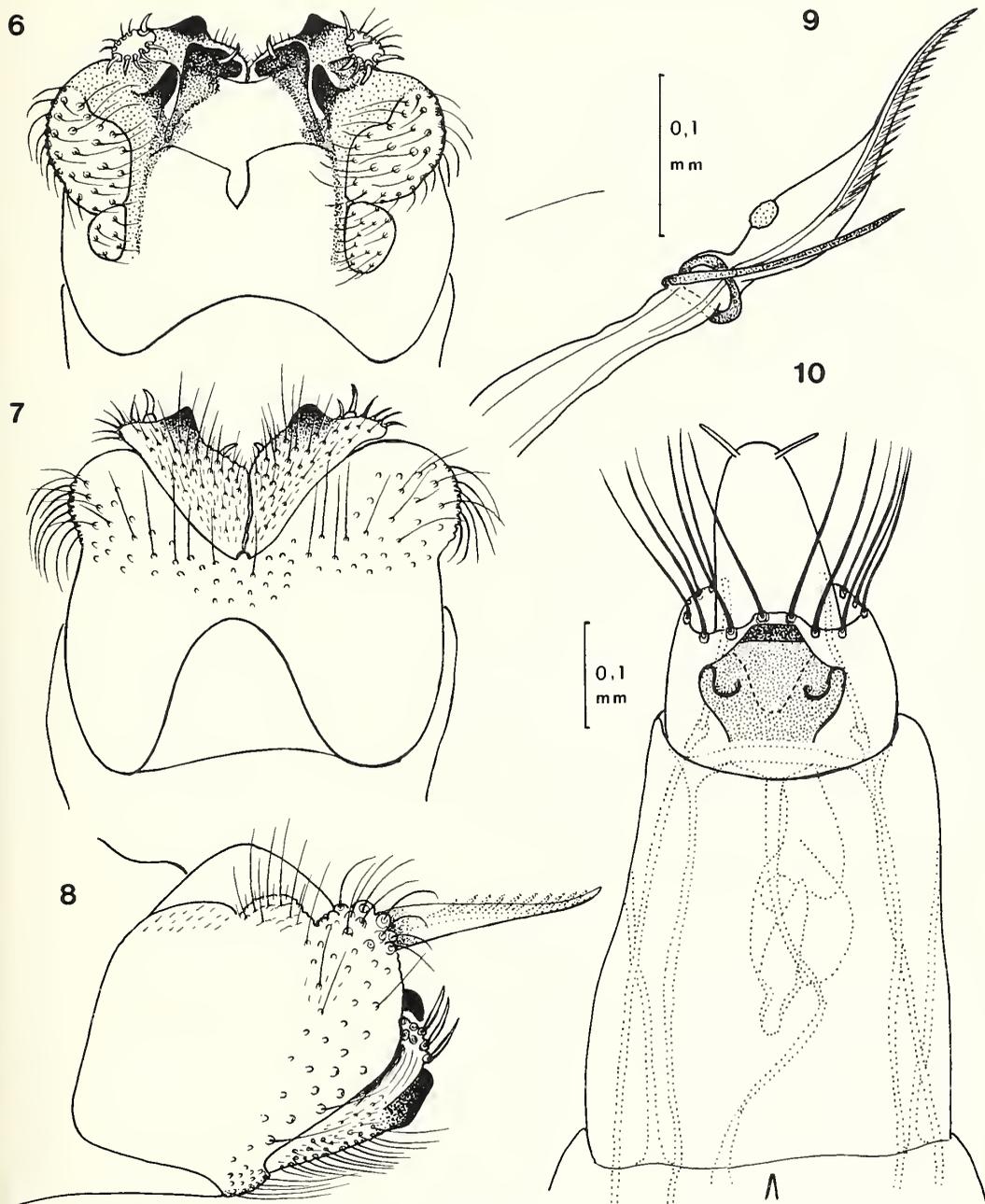
Similar to ♂ in general appearance, also very hairy, size variable as in ♂, description based on the six specimens available. It has been assumed that these are probably the females of *U. rhodesiensis* since they were the only females of the genus *Ugandatrichia* taken, and were taken with the males, but there is as yet no proof. The females show several minor but constant differences from the males. The antennae are shorter (c. 36 segments), and have a conspicuous white section from about segment 13 to 25; the head warts, although very similar, differ in that the basal warts are completely separated (cf. Figs 2, 5); there are also small differences in the proportions of the wing veins.

Abdomen: not as hairy as in the ♂ except apically, where there is a very thick fringe of terminal dorsal and lateral setae on VIII, within which is a circle of widely spaced movable setae round the apex of IX; these may be closed inwards or spread widely outwards like the spokes of an open umbrella (see Fig. 10). In preserved specimens the ♀ genitalia may be so tightly tucked in that the ends of these dense fringing setae are tucked in too, making it difficult to elucidate the genitalia. The abdomen shows the same paired brown patches on the terga as in the ♂, but on the venter there is a thin scattering of brown microscales not seen in the ♂, and the eighth sternite has a large apico-median area densely furred with short setae. There is a small sclerotized process on the seventh sternite. Eighth segment long, ninth short, with a somewhat urn-shaped ventral plate, clearly visible in uncleaned specimens. Tenth segment very lightly chitinized, with oval apex bearing a pair of slender rod-like processes. VIII, IX and X appear to be supported by an internal framework of sclerotized rods as indicated in Fig. 10. Vagina etc. visible by transparency, lying within the framework.

Comparison with Mosely's species of Ugandatrichia

The genus *Ugandatrichia* was described by Mosely (1939) from East Africa, including three species, *U. minor*, ♂, from Thompson's Falls, 7 500 ft., N. of Nakuru, Kenya; *U. nigra*, ♂ and ♀, from Namwamba Valley, 6 500 ft., Ruwenzori, Uganda, and *U. acuta*, ♀ only, from Chania Falls, 4 000 ft., near Nairobi, Kenya.

The present species, *U. rhodesiensis*, clearly falls into the same genus, but does not appear to be any of Mosely's species. The wings of both ♂ and ♀ closely resemble those figured for *U. minor* and *U. acuta*, being closer to the latter in shape, and differing from both only in the thickened pterostigma and the virtual absence of basal cross-veins. In size, and in structure of ♂ genitalia, *rhodesiensis* is close to *nigra*, though showing differences in the wide U-shaped proximal emargination of the ninth tergite and sternite, the expansion of the apico-lateral margins



Figs 6-10, *Ugandatrichia rhodesiensis*, figures of genitalia. 6-8, holotype, ♂, SRE 3D(3). 6. ♂ genitalia, dorsal view, tilted obliquely so that the parts do not obscure one another; aedeagus omitted. 7. ♂ genitalia, ventral view. 8. ♂ genitalia, lateral view. 9. ♂ genitalia: dorsal view of aedeagus (taken from SRE 3D(2), as that of holotype has the titillator uncoiled and atypical). 10. ♀, SRE 3D(18), ventral view of segments VII-X, showing ♀ genitalia (dense fringe of setae surrounding VIII omitted).

of the side-pieces, and in details of the structure of the other parts, including the aedeagus. The ♀ is much closer to *acuta* than to the ♀ of *nigra*, possessing a similar ventral plate, and lacking the forked ventral process of *nigra*. It differs from *acuta* both in the shape of the ventral plate and the absence of the paired ventral patches of scales.

Taken all in all, *rhodesiensis* definitely appears to be a new species, and has been named after its country of origin.

I am aware that Schmid (1960) has synonymized *Ugandatrichia* with *Microptila* Ris, and he may well be correct, although there do appear to be constant differences in wing venation and details of genitalia. I am, however, retaining *rhodesiensis* in *Ugandatrichia* for the present on account of its most interesting and unusual larval and pupal stages, described below. Once the immature stages of *Microptila* have been discovered, the matter can doubtless be satisfactorily settled.

THE IMMATURE STAGES OF *UGANDATRICHIA RHODESIENSIS* n. sp. (Figs 11–22)

When the imago of this species were collected by Dr Harrison, the young stages were fortunately collected at the same time, mainly from the most torrential parts of the waterfall on the Bundi River. This material comprised 24 larvae, including several different instars, and 13 pupal cases. Of the latter, two of the cases contained prepupal larvae, the same as those collected with them, nine contained immature pupae, together with larval sclerites evidently belonging to the same larvae, one was empty, and one contained a mature ♂ pupa, disclosing genitalia like those of the *Ugandatrichia rhodesiensis* described above, and together with them the same larval sclerites. Thus there is a positive and complete correlation between the larvae, pupae and ♂ imago of *Ugandatrichia rhodesiensis*.

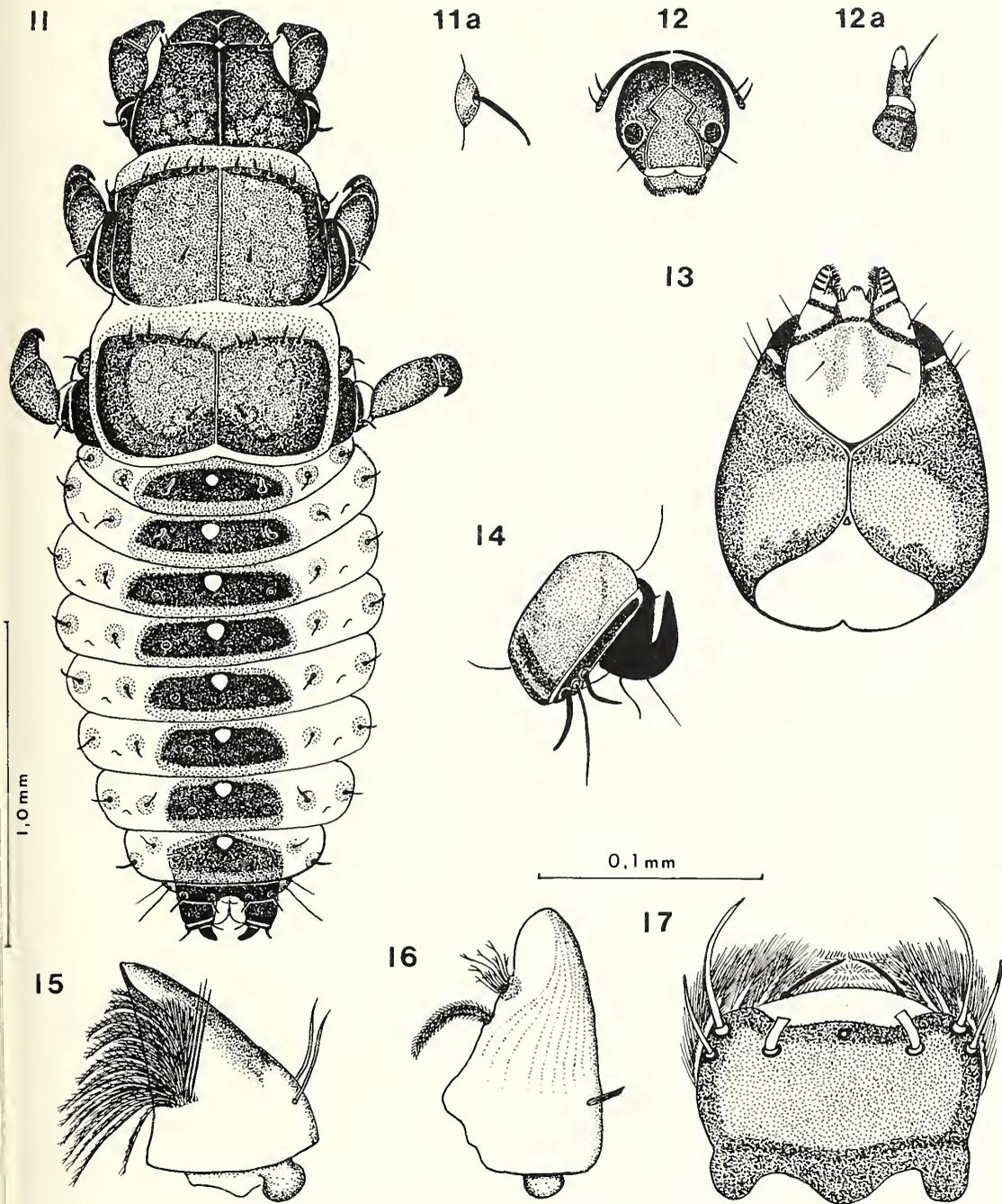
The Trichoptera may be divided into two groups, one with free-living larvae, the other with larvae which construct cases in which to live. The Hydroptilidae are unique among the Trichoptera in that they are free-living in the first five instars, but make cases at the beginning of the sixth and last instar, in which they live, and which they usually modify for pupation. The larvae of *Ugandatrichia rhodesiensis* are therefore particularly interesting because, although Hydroptilids, they are evidently free-living at all stages, and that under the most stringent of living conditions, only making cases when ready to pupate. No doubt in response to their torrential habitat, the larvae are strong, stout and muscular, resembling beetle larvae (particularly those of the Coccinellid *Vedalia*) rather than Trichoptera in general appearance.

DESCRIPTION OF MATURE LARVA

(In alcohol. Figs 11–20). Length 2.5–3.0 mm, abdomen up to 0.8 mm across widest part (segments II–IV); abdomen gradually tapers from IV to VIII, but IX is considerably narrower than VIII. Larvae are blackish in dorsal view as they are heavily sclerotized and all sclerites are dark brown to black in colour.

Head (Figs 12, 13): small, smooth, oval, black; eyes large, dark brown, within paler area and under lens-like modifications of cuticle; frontoclypeus with one pair of deep lateral indentations and seven pairs of setae, sutures, including frontoclypeal stem, clearly marked; tentorial pits obscure, probably due to heavy sclerotization. Antennae (Fig. 12a) situated next to anterolateral corners of frontoclypeal apotome; well developed, with two sclerotized segments, the apical one bearing a seta, and a membranous tip. Ventral surface of head with anterior and posterior ventral apotomes very small, former very narrow with long, slender anterior arms.

Mouthparts (Figs 13, 15–17): labrum large, dark, with two pairs of long dorsal setae, a median short pair (either truncated or broken), and a slender anterior pair (shown black in Fig. 17



Figs 11-17, *Ugandatrichia rhodesiensis*, mature larva. 11. Habitus drawing of mature larva (composite drawing from several mature specimens). 11a. Modified seta, further enlarged. 12. Dorsal view of head, anterior margin of pronotum also shown. 12a. Antenna further enlarged (same magnification as mandibles and labrum). 13. Ventral view of head. 14. Right anal proleg, including claw; lateral view. 15. Left mandible. 16. Right mandible. 17. Labrum: dorsal view.

but actually colourless); extremely dense bushes of setae, apparently arising from basal stems, beneath labrum. Labium with large, clearly visible, maxillary and labial palps. Mandibles with blunt apex, no lateral teeth; left mandible with dense inner brush of feathered spines, also several plain spines and two outer setae; right mandible ridged, with long, apparently double, feathered inner spine and a tuft of shorter bifid spines, also a thick, short outer seta, possibly broken off.

Thorax (Fig. 11): pronotum divided longitudinally, black in colour, narrowed anteriorly, forming a collar round back of head and terminating in triangular antero-lateral points, each bearing two modified setae; there are also four pairs of modified setae towards the middle of the pronotum. Meso- and metanota blackish, also longitudinally divided; they have four pairs of modified setae along the anterior margin and one median pair. All three nota show obscure muscle marks, more evidenced by smooth texture than by a change in colour, though the whole central part of both meso- and metanota is somewhat lighter in colour than the margins, being brownish black rather than shining black. This is more noticeable in the younger of the large larvae than in the oldest ones, in which the sclerites tend to be mainly shining black. Anterior to both meso- and metanota there is a band of sclerotized points. Thoracic nota, bases of legs, and abdominal sclerites bear modified setae, black in colour, thicker than normal, comparatively short, usually curved, blunt-ended and conspicuous (see Fig. 11a); main positions of these setae indicated in Fig. 11. There are also a few small, inconspicuous, colourless, normal setae, not shown in the figure. Thoracic sterna entirely membranous, strongly muscular.

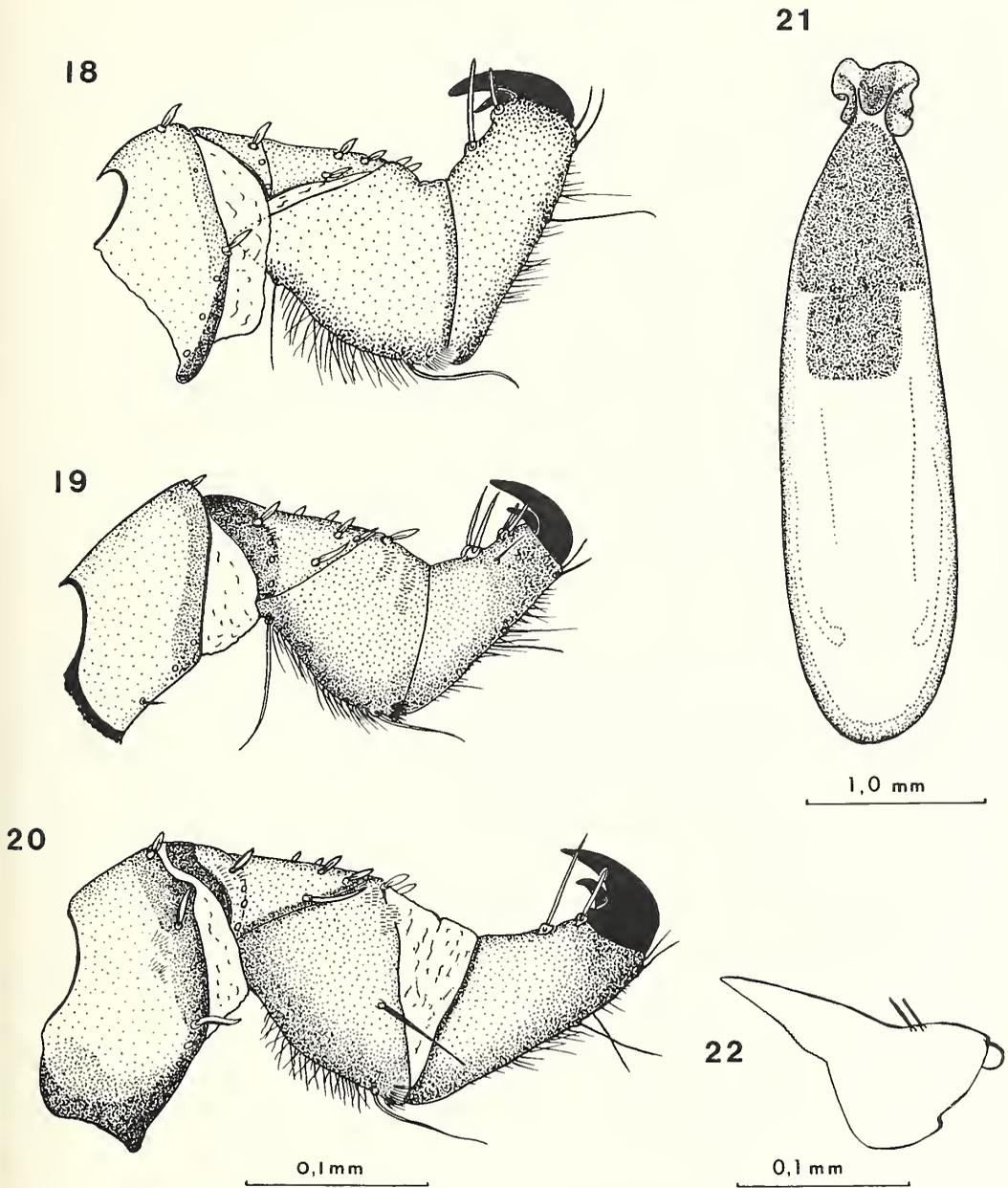
Legs (Figs 18–20): stout, powerful, sclerites blackish, a large modified seta on outer side of coxae, rest of setae comparatively few and small, shown in the figures. Coxa large; trochanter divided, with short blade-like setae; femora large, with a few blade-like setae, fine fringing setae along dorsal margin, and small patches of setulae in the case of mid- and hind legs (also present on trochanter in mid-leg and, in hind leg, on both trochanter and coxa); tibiae and tarsi evidently fused to form a single stout joint, which bears a few dorsal fringing setae in addition to two pairs of long, blade-like setae just proximal to the claws (these are shown double in Fig. 19, of the mid-leg; they are also paired in fore- and hind legs). Pleural sclerites black, comprising pre-episternum (first pleural sclerite), second pleural sclerite and epimeron; the last bears a modified seta.

Abdomen (Fig. 11): gills absent; no anal gills visible. All abdominal segments with large sclerotized tergites, mainly black in colour, with brownish border, a few obscure muscle marks and a central clear spot, oval in shape. Each tergite bears a pair of modified setae and at least three pairs of small, colourless ones. Tergite on IX lacks central clear spot and has an emarginate posterior border, bearing three pairs of large modified setae in addition to the usual pair. The tergite on each segment from I to IX is flanked on each side by two small, round, brownish or blackish sclerites, each bearing a modified seta (Fig. 11a); in the case of IX these sclerites are small and contiguous with or fused to IX, being situated at the posterolateral corners of the tergite. The abdominal segments are clearly demarcated and strongly muscular. On the ventral side of the abdomen, which is dorsoventrally flattened and evidently modified for clinging to the rocks, each segment from II to VIII bears what appears to be a pair of suction pads or suckers, close to the lateral margins.

Anal prolegs (Fig. 14): short, stout, each with a large, partly blackened lateral sclerite, distal to which is a second, narrow, inturned black sclerite bearing two modified setae, between which is a longer, normal one. Anal claws simple, large, hooked, bearing a few small colourless setae.

EARLIER LARVAL INSTARS

Most larvae appear to be in their final or penultimate instar (though the abdomen may be in various stages of expansion), but there are also two younger larvae, which could be in their third and fourth instars respectively; it is these which are particularly reminiscent of *Vedalia* larvae.



Figs 18-22, *Ugandatrachia rhodesiensis*, mature larva and pupa. 18. Right fore-leg of larva: median view. 19. Right mid-leg: median view. 20. Right hind leg: median view; shown extended, with large membranous area visible between femur and tibio-tarsus. 21. Pupal case (showing position of pupa and larval sclerites through case). 22. Mandible of pupa.

Both are basically similar to the mature larvae in appearance, but show the following differences: colour of sclerites brown, not black; thoracic nota each a single sclerite, undivided; modified setae present but relatively larger; each abdominal segment with only one pair of setate lateral sclerites flanking the tergite, not two (and these lateral sclerites are long and oblong or oval, not round); abdominal tergites plain brown, with central spot only faintly visible, as is also a pair of lateral spots (possibly muscle marks, faintly seen as such in older larvae); limb claws and anal claws as in mature larvae, but latter relatively larger.

DESCRIPTION OF PUPA

The pupal material included prepupae, immature pupae, and one mature ♂ pupa, all in cases. Larval sclerites were present within the cases in all instances.

Pupal case (Fig. 21): although the larvae are free-living, they pupate in cases. These cases are made of secretion, are tough and parchment-like in texture, and semi-transparent, so that the black larval sclerites (retained in case) and outline of the pupa can be distinguished through the wall. The cases are sac-like in shape, tubular, not flattened, and anchored to the substratum by a holdfast at one end only.

Pupa (Fig. 22): of usual Hydroptilid type; antennae, palps, tibial spurs as in adult. Dorsal abdominal sclerites all very small in size, rounded to oval in shape, with minute teeth or scabrosities, present on abdominal terga as follows: on abdominal segments III, IV and V, paired pre- and postsegmental sclerites; on segments VI and VII, paired presegmental sclerites only. Mandibles (Fig. 22) blade-like, with rounded base, blade with microscopical serrations along the proximal part, two short, blunt setae on outer margin of base; labrum rounded, not sclerotized.

DISCUSSION

On searching through the literature to find accounts of other free-living Hydroptilid larvae, the only genus that I encountered whose larvae seemed to bear some similarity to those of *Ugandatrichia*, was *Alisotrichia* Flint, a New World genus from Central America and the Caribbean islands. Flint has placed *Alisotrichia* in his subfamily Leucotrichinae (Flint, 1970), and regards it as a unit on its own within that subfamily, chiefly because of its larvae and larval habits, having found them to be unique in that the larvae appear to be free-living up to the end of the last instar; they then spin a silken shelter within which they pupate. The larvae are thus free-living until pupation, just as in the case of *Ugandatrichia*. Whether *Ugandatrichia* larvae spin a shelter under which to pupate or not is unknown, but the form of the pupal case (quite unlike that of *Alisotrichia*) seems to render this unlikely, as it is complete in itself, with its own holdfast.

Dr Flint very kindly sent me some *Alisotrichia* larvae for comparison, and they certainly show strong similarities to—and differences from—those of *Ugandatrichia*. The similarities could well be due, in part at least, to a similar mode of life, as Dr Flint informed me (*in litt.* 15.4.75), that *Alisotrichia* larvae are primarily hydropetric. These resemblances include the habitus of the larvae, the strong limbs, the stout modified setae, the muscular abdomen with sclerotized tergites, the lateral abdominal setate sclerites, and the stout anal claws. Differences are more difficult to define, as a number of species of *Alisotrichia* are known in the larval stage and they cover a wide range of forms, as indeed do the adults; in fact Dr Flint (1970) suggests that they may eventually prove to include several different genera or subgenera. Thus the various features seen in *Ugandatrichia* seem to be found in one or another species of *Alisotrichia*, though not all together. There do, however, seem to be some valid generic differences, which include the following points: in *Ugandatrichia* the head sutures are well developed; the abdominal tergites have a central clear spot instead of a dark area with three pores, and have paired lateral setiferous

sclerites, not single ones (except in the young instars); the legs are much more powerful, and have the tibiae fused with the tarsi; the abdomen appears to have paired ventral suckers, the anal prolegs are short, not long, and the anal claw lacks the enlarged seta.

Imagos of the two genera also show certain resemblances; in both genera there are ocelli, and possible spur counts in *Alisotrichia* include 0, 3, 4. The pronotum in *Ugandatrichia* is not, however, produced dorsally, the mesoscutellum lacks a transverse suture, and the ♂ genitalia are much less complex than most *Alisotrichia* species, though not so far from *A. hirudopsis*. On the other hand, there are two very striking differences: *Alisotrichia* ♂♂ have strongly modified, enlarged, antennae and maxillary palps, quite unlike the simple ones found in *Ugandatrichia*.

None the less, it is extremely interesting that such similar larvae should occur so far apart, unless, as Dr Flint tentatively suggested (*in litt.* 15.4.75), there might be some very old, gondwanan, pantropical pattern being shown here; that is a fascinating speculation, even if it is never proved.

ACKNOWLEDGEMENTS

I am much indebted to Dr Harrison for submitting his very interesting collection to me for identification; although identified many years ago the *Ugandatrichia* is only now being described. I also owe grateful thanks to Dr O. S. Flint, jun., of the Smithsonian Institution, Washington, for the gift of *Alisotrichia* larvae and pupae, and to Mr C. F. Jacot-Guillarmod, Director of the Albany Museum, for accommodation in the Museum, and for reading the manuscript. The permission of the Director of the National Institute for Water Research to publish this work is gratefully acknowledged.

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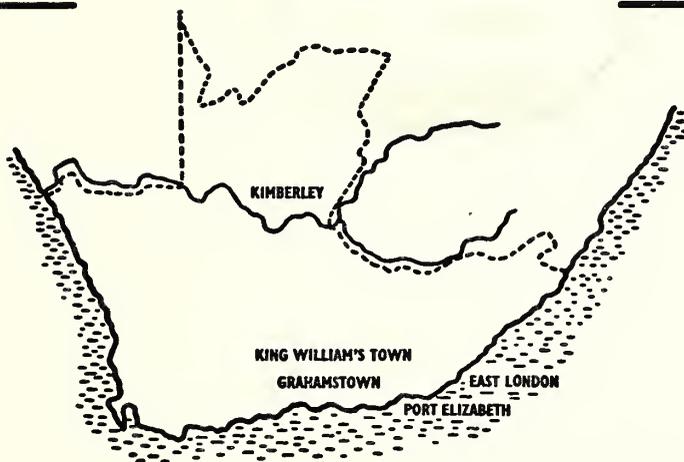
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 8

31st DECEMBER 1976

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

**Ethological notes on *Dichragenia neavei* (Kohl) (Hymenoptera: Pompilidae),
an African spider-hunting wasp building a turreted, subterranean nest**

by

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and

S. K. GESS

INTRODUCTION

In a recent paper Gess and Gess (1974) described the ethology of *Dichragenia pulchricoma* (Arnold) (Pompilidae: Macromerini) in the Eastern Cape Province of South Africa. Of particular interest was the form of the nest which, by possessing a mud entrance turret surmounting the subterranean burrow and cells, was believed to represent a nest type previously unknown within the Pompilidae.

In the present paper an account of some aspects of the ethology of a closely related species, *Dichragenia neavei* (Kohl) **comb. nov.** (syn. *Pseudagenia neavei* Kohl, 1913 and *Pseudagenia mygnimioides* Bischoff, 1913) is presented. *D. neavei*, like *D. pulchricoma*, surmounts its subterranean nest with a mud turret. Mention of turret building by *D. neavei* (as *Pseudagenia mygnimioides* Bischoff) has previously been made by Chapman (1958) in a very brief account based upon the discovery of a single nest in the Rukwa Valley, Tanzania. This record of turret-building in the Pompilidae was overlooked by the present authors when writing their earlier (1974) paper on *Dichragenia* and was not noticed either by Evans and Eberhard (1970, see p. 76). In view of the fragmentary nature of Chapman's data it is considered warranted to publish the present more extensive observations particularly as an opportunity is thus afforded for comparing the nesting of *D. neavei* with that of *D. pulchricoma*.

THE NESTING OF DICHRAGENIA NEAVEI (KOHL)

Dichragenia neavei is similar in size and facies to *D. pulchricoma* and like it has fuscous wings and ferruginous legs. The two species may however readily be distinguished in the field by the coloration of the pronotum, ferruginous in *D. neavei* and black in *D. pulchricoma*.

During the six weeks from 26.x.1972 to 6.xii.1972 within which period the ethology of *D. pulchricoma* was being studied at Hilton and at Clifton, localities near Grahamstown (33° 19'S., 26° 32'E.) in the Eastern Cape Province of South Africa, *D. neavei* was commonly observed in company with the former species at puddles and temporary pools at both localities. It was clear

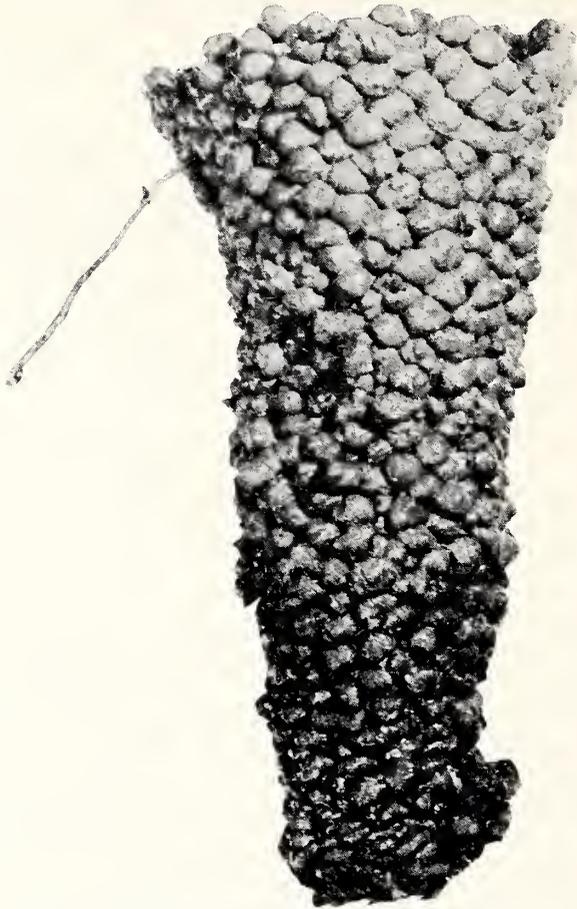


Plate 1. Hilton, 9.i.1974. Turret of *Dichragenia neavei* (Kohl). ($\times 2$).

that the females of *D. neavei*, like those of *D. pulchricoma*, were collecting water and it was assumed, correctly as it later transpired, that it was for the same purpose—namely for nest construction. However, whereas large numbers of nests of *D. pulchricoma* were located and positively identified as being those of that species, no nests of *D. neavei* were found and it was not until the following summer that the first was discovered. Subsequently two further nests of *D. neavei* have been located.

The first nest (Fig. 1) of *D. neavei*, discovered on 9.i.1974, aroused the authors' interest due to its large, upright funnel-shaped turret (Plate 1). In height this turret rose 57 mm above the surface of the ground, in diameter it increased from 12 mm at its extreme base to 28 mm at its distal opening. Seen from above the turret was nearly radially symmetrical. The mud pellets used as building bricks in turret construction were spirally arranged and were closely packed. Small interstices were however left between them, especially distally. Whereas the individual pellets

were very distinct on the outer surface of the turret walls, some smoothing of the pellets had been done on the inner surface. Believed at the time of discovery to be merely an aberrant turret of *D. pulchricoma*, it was nevertheless collected and the nest below it excavated. Two cells were found. The first-constructed, situated at a depth of about 75 mm below the ground surface, was sealed and contained a prey spider with its head orientated towards the shaft-end of the cell. No egg or wasp larva was found. The second cell, situated at a greater depth, was open and had not yet been provisioned. The female nest builder was not seen.

The second nest was spotted on 18.iv.1974. Due to lack of time the turret was not collected nor were the underground workings excavated. The turret was similar to that of the first nest.

The third nest (Fig. 2) was discovered on 10.i.1975 when a female *D. neavei*, seen walking about on the ground, was followed to it. The wasp which entered the turret and went down into the nest below was captured upon re-emerging. The capture of this female enabled the true builder of the funnel-shaped turrets to be identified and ended the long search for the nest of *D. neavei*. The turret was collected and the subterranean part of the nest was excavated. In height this turret rose only 19 mm above the surface of the ground, in diameter it increased from 11 mm at its extreme base to 26 mm at its distal opening. In all other respects it was very similar to the turret of the first nest and like it showed evidence of some smoothing of the inner surface of the walls. Three sealed cells were found near the end of the main nest shaft at a depth of between 130 and 140 mm. Each cell contained a prey spider but in only two cells was a wasp egg found.

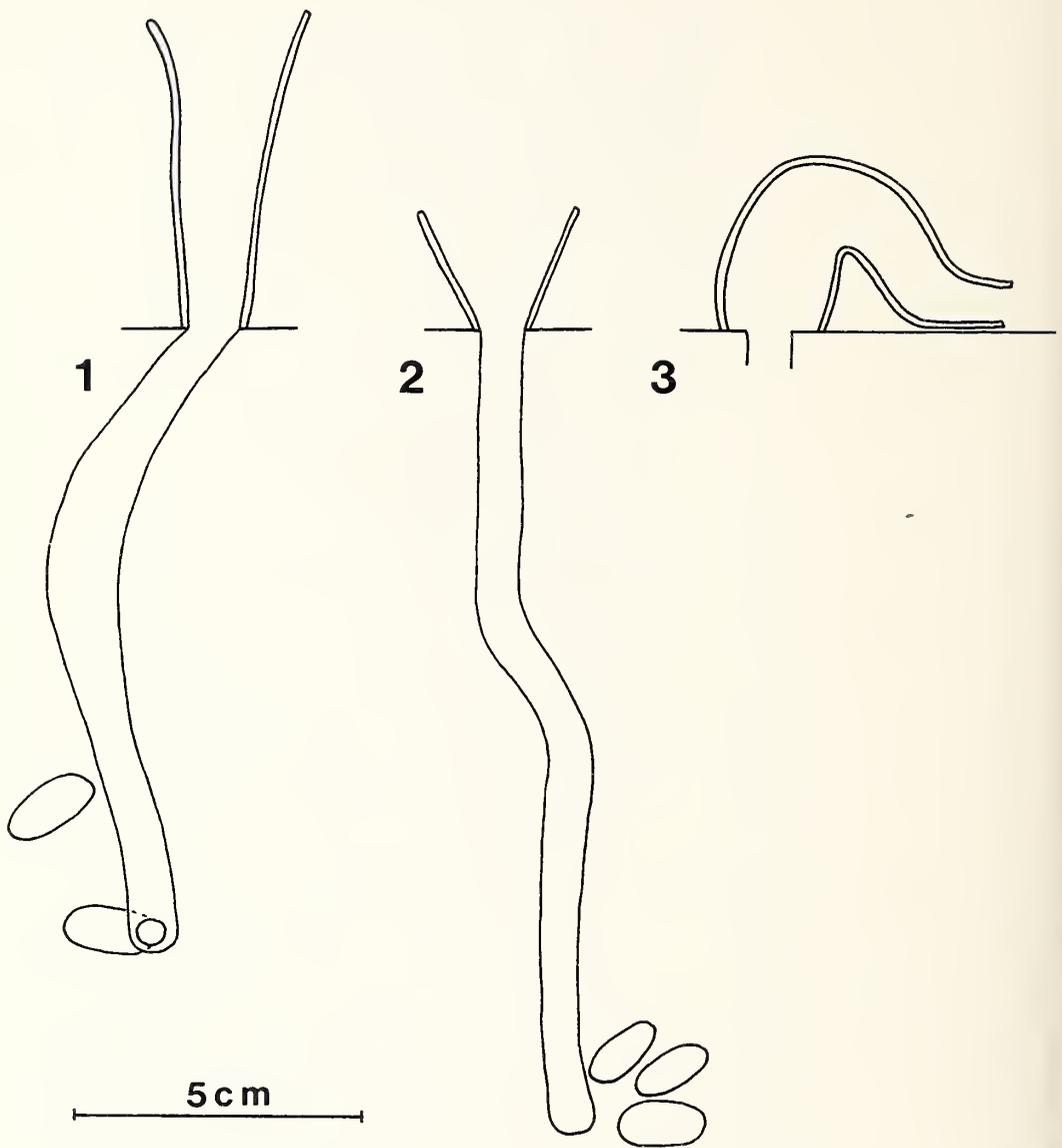
All three nests of *D. neavei* were, like those of *D. pulchricoma*, built in places where the ground had been disturbed and partially denuded of vegetation. Similarly, all three were close to temporary sources of rain-water. The first nest was situated on partially denuded ground flanking a water furrow, the second on the raised bank of earth running parallel to a water furrow and derived from the excavation there of (near site shown in Gess and Gess, 1974: Plate 2), and the third on slightly sloping ground intersected by small erosion gullies in places trapping shallow pools of water (near site shown in Gess and Gess, 1974: Plate 3).

Whereas the mud turrets of *D. pulchricoma* were most often found completely exposed in bare areas and were only occasionally in more protected situations as at the base of dwarf shrubs, all three turrets of *D. neavei* were found to be situated well under or within dwarf shrubs, those of the first and second nests actually having small branchlets passing through the turret walls. These branchlets thus incidentally helped to support the large funnel-shaped structures in an upright position. Owing to their position the turrets of *D. neavei* are much more difficult to spot than are those of *D. pulchricoma*.

A female *D. neavei* was observed transporting its prey at noon on 28.i.1974. The wasp carried its prey across open ground, walking forwards, straddling the prey with its legs. The spider, an immature specimen of indeterminable sex of *Palystes* sp. (Sparassidae), had had all its legs amputated and was carried dorsal side up, head forwards, held by the wasp's mandibles at the base of the right chelicera. No attempt was made by the wasp to fly. Captured and weighed the "dressed weight" of the prey spider was found to be 137 mg whereas the weight of the wasp was a mere 48 mg.

The four prey spiders obtained from the provisioned cells of the first and third nests were all of the family Lycosidae. The first nest contained an adult male and the third an adult male and two immature specimens of indeterminable sex. Three of the spiders had had all the legs amputated at the coxal-trochantal joint and the fourth had one leg (the left front) remaining. In all cases the pedipalps were intact. Three of the spiders were 10 mm long and one was 9 mm long; the width across the carapace was 4 mm and across the carapace to the ends of the leg stumps 5 mm. All the prey spiders were alive and responded to tactile stimulation.

The eggs found on the spiders in two of the cells of the third nest were both attached to the side of the spider's abdomen near the base of the latter, in a position very similar to that shown for the egg of *D. pulchricoma* (see Gess and Gess, 1974: Figs 6, 7). The attachment of the egg



Figs 1 and 2. Vertical plans of the turrets and underground workings of two nests of *Dichragenia neavei* (Kohl) studied at Hilton. Fig. 3. Vertical plan of the turret of a nest of *Dichragenia pulchricoma* (Arnold) studied at Hilton.

was over its entire length with the exception of the extreme anterior end which was sited uppermost. One egg was attached to the left side of the spider's abdomen and the other to the right side. Both eggs were 2,3 mm in length.

DISCUSSION

The ethology of *Dichragenia neavei* (Kohl), as far as can be ascertained from the small number of nests examined and from the few observations made during the present study, appears to be very similar indeed to that of *D. pulchricoma* (Arnold) described and discussed at length by Gess and Gess (1974).

D. neavei, like its congener and indeed like species of other genera of Macromerini (such as *Phanagenia*, *Auplopus* and *Ageniella*) selects for its prey certain errant spiders, the legs of which it amputates at the coxal-trochantal joint prior to removal to the nest. Like *D. pulchricoma* and species of *Phanagenia* and *Ageniella* (but not *Auplopus*) *D. neavei* straddles its prey and walking forwards transports it dorsum up, grasped at the base of a chelicera.

In common with *D. pulchricoma* and a few species such as *Priocnemis minorata* Banks (tribe Pepsini) but in marked contrast to the above three macromerine genera (which construct aerial nests), *D. neavei* constructs a multicellular subterranean nest in clay soil. In the adoption of the use of water to soften the hard soil, in the removal of the spoils of nest excavation in the form of mud pellets and in the use of these mud pellets in the construction of a turret surmounting the nest entrance, the behavior of *D. neavei* closely parallels that of *D. pulchricoma* but differs from that of all other hitherto studied Pompilidae. This similarity in the ethology exhibited by these two species leads to the conclusion that it is probably typical for the genus *Dichragenia* Haupt as a whole.

It is of interest that it is in the architecture of that physical artifact of behaviour, the nest turret, the possession of which by *Dichragenia* at present appears unique within the Pompilidae, that the most notable differences in nesting between the two species are apparent. Thus whereas the turret of *D. neavei* is funnel-shaped (Figs 1 and 2 and Plate 1) that of *D. pulchricoma* is retort-shaped (Fig. 3 and also Gess and Gess, 1974: 195-196, Plates 6-8). Furthermore, whereas the bore of the turret of *D. neavei* is the same at its base as is that of the nest shaft at its top, that of the turret of *D. pulchricoma* in the same position is about three times that of the shaft. A difference is also to be seen in the fact that whereas *D. neavei* turrets exhibit some smoothing of their inner surface no such smoothing is seen in *D. pulchricoma* turrets.

The account of the nesting of *D. neavei* given by Chapman (1958) brief as it is nevertheless raises some interesting questions. According to that author *D. neavei* in constructing its turret uses its jaws, forelegs and the tip of the abdomen to place each pellet. In the present study *D. neavei* was not observed in the act of turret construction but *D. pulchricoma* which was watched for considerable periods on two occasions was seen to use the mandibles only. The tip of the abdomen was never used. Use of the pygidium as a "trowel" for smoothing the surface of a mud structure, the nest, has however been reported for *Auplopus* by Evans and Eberhard (1970: 100 and Fig. 67). Chapman also reported *D. neavei* sealing the nest by filling the shaft with earth and by placing debris, small stones and twigs within the mud turret. The present authors have never observed such behaviour in either *D. neavei* or *D. pulchricoma* and, although in the case of the latter species a total of sixty nests was excavated, no evidence of nest sealing was found. In both species, however, each cell within a nest is individually sealed off from the common shaft by means of a mud plug, the existence of which is strangely not mentioned at all by Chapman. Further observation of *D. neavei* at work is obviously necessary in order to resolve these questions.

The study of the ethology of the present two species has on a generic level yielded taxonomic characters which have confirmed the validity of the genus *Dichragenia*, erected on the

basis of what might be considered rather minor morphological features. At the same time it has clearly indicated relationships with certain other genera. Furthermore it has been shown that the architecture of the nest turrets is a useful character distinguishing the two species. It is clear that further ethological studies of Ethiopian *Macromerini*, of which there are more than 120 described species, would be very rewarding and might well be of great assistance at both the generic and the specific levels in any future revision of this, at present, very confused group.

SUMMARY

Some aspects of the ethology of *Dichragenia neavei* (Kohl) in the Eastern Cape Province of South Africa are described and are compared with the known ethology of *D. pulchricoma* (Arnold). Attention is drawn to some points of variance between the present observations and those made on *D. neavei* by Chapman (1958) in Tanzania.

ACKNOWLEDGEMENTS

The authors wish to thank Mr T. C. White of the farm Hilton for his much appreciated kindness over the years in allowing them free access to his land. Thanks are due also to Mr M. C. Day of the British Museum (Natural History) for confirming the senior author's identification of the wasp and for drawing attention to the synonymy. The senior author is grateful to the C.S.I.R. for a running expenses grant for field-work during the course of which the present observations were made.

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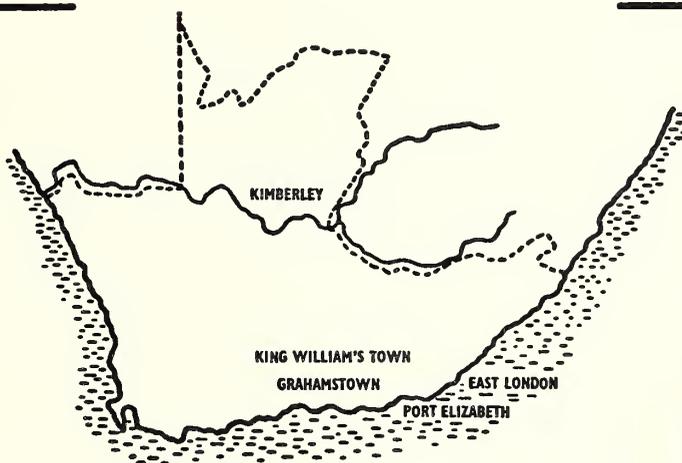
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 ● PART 9

29th APRIL 1977

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

The Taxonomy of Bottlenosed Dolphins *Tursiops* species in South African waters, with notes on their biology.

by

G. J. B. Ross

Port Elizabeth Museum

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ABSTRACT

Material and data from 58 specimens of *Tursiops* from South African waters were examined.

On the basis of cranial characters, supported by external measurements and the post-cranial skeleton, it was shown that two forms of *Tursiops* are present in these waters, identified as *Tursiops truncatus* Montagu and *T. aduncus* (Ehrenberg). The identifications were made by comparison with the published data on the types of *T. absulam* (Ruppell), *T. catalania* (Gray), *T. aduncus* (Ehrenberg) and *Delphinus gadamu* Owen, all of which are considered to represent one species *T. aduncus*, and cranial measurements of 17 *T. truncatus* from British waters.

The available data on growth, reproduction, food and feeding behaviour, parasites, diseases, injuries and mortality are given for South African *Tursiops aduncus*.

INTRODUCTION

In the last few decades the rapid increase and diversification of cetacean research has been made possible by the availability of accessible captive animals in oceanaria throughout the world. For economic reasons these animals have generally been the smaller dolphins and porpoises, though many institutions now possess facilities for keeping some of the larger forms. The most commonly held dolphins are still bottlenosed dolphins, members of the cosmopolitan genus *Tursiops*, which are readily available close inshore, train well and adapt easily to captive life. As a result, much of the groundwork in the various fields of research has been based on this genus, to the point where *Tursiops* could be considered the best-known of all cetaceans.

In the field of systematics, however, research on *Tursiops* has progressed little in the present century and a review of current literature on *Tursiops* species presents an extremely confused picture. During the 19th century cetacean taxonomists were often confronted with single specimens from many parts of the world, and with the lack of comparative material they could take little account of population, age, sex or individual differences in their attempts to classify material. Consequently by the turn of the century, twenty specific names had been applied to members of the genus *Tursiops* (Hershkovitz, 1966) many of them based upon single skulls. At this time, True (1889) published his important revision of the Delphinidae in which he synonymized many of the forms into five species: *Tursiops tursio* (Fabricius), *T. catalania* (Gray), *T. absulam* (Ruppell), *T. gilli* (Dall), and *T. parvimanus* Lütken. He deliberately omitted a discussion of *Tursiops aduncus* (Ehrenberg) since he lacked the original description. Subsequently Lahille (1908) and Andrews (1911) described two new species, *T. gephyreus* and *T. nuuanu* respectively, which True (1914) included in a briefer review of the genus, together with *T. truncatus* (previously *tursio*), *T. parvimanus*, *T. gilli*, *T. absulam*, and *T. catalania*. He also listed *T. aduncus* as a further possible species but suggested that it is probably synonymous with *T. absulam*. True emphasized the need for further material before the real status of each of these species could be assessed. Unfortunately relatively little new material has been described in the literature since True's paper, and though several authors have listed the forms of *Tursiops* in recent years, few have been able to base their opinions on more than a reassessment of the same material and the literature. Present opinions differ widely. Tomilin (1957) suggested that *Tursiops* is represented by a single cosmopolitan species, divided into a number of geographical races. Hershkovitz (1966) held that *T. gilli* and *T. truncatus* were the only valid species, but that the latter embodied two subspecies *T. truncatus truncatus* and *T. truncatus aduncus*. Nishiwaki (1972) included the eight species listed by True (1914) while Van Bree (1966 and *in litt*) suggested that there are two species, *T. truncatus* and *T. aduncus*, each with geographical subspeciation. In the most recent review Pilleri and Gahr (1972a) suggested that *T. truncatus*, *T. aduncus* and *T. gilli* are valid species. The paucity of available material is reflected in this paper, where the authors have based their assessment of *T. aduncus* on data from twelve specimens

published in the literature and three new specimens. These specimens were recorded from Pakistan (3), Australia (2), Natal (5), India (1), China Seas (1), the Red Sea (1), Indian Seas (1) and from an unknown locality (1). Pilleri and Gihir (1972b) also considered *T. gephyreus* to be distinct from the other species.

This confused situation can only be resolved satisfactorily by more detailed regional studies of the limits of variation within populations, based on larger series of specimens. This is particularly true of *Tursiops* in the Indian Ocean where there are few series of specimens from one area.

The present project began as a study of variation in South African bottlenosed dolphins which have been referred to as *Tursiops aduncus* by a number of authors (Ellerman *et al.*, 1953; Barnard, 1954; Van Bree, 1966). The distribution of *aduncus* also includes part of Australia, Sumatra, Java, India and the Red Sea. Very few South African specimens are recorded in the literature. True (1914) gave measurements of five specimens from Natal, while Barnard (1954) recorded another specimen from Noordhoek, Western Cape Province. A seventh skull collected at Mossel Bay in 1904 was re-described as *T. aduncus* by Van Bree (1966). In view of the paucity of material it is not surprising that Barnard referred to the apparent rarity of the species in South African waters. Observations in recent years however show that bottlenosed dolphins are relatively common inshore, particularly in the Eastern Cape, and one of the most frequently stranded cetaceans. As a result it was possible to collect most of the specimens reported on here over the relatively short period of some seven years. As the collection grew, however, it became apparent that a small proportion of the animals differed considerably from the others. A few were larger, with a shorter snout and fewer teeth than the remainder. Superficially the two groups appeared sufficiently different to suggest that two forms of *Tursiops* occurred in South African waters. This possibility prompted the present writer to re-examine the taxonomic status of South African *Tursiops*.

The taxonomic treatment is based primarily on a comparison of skull measurements and non-mensural characters, supported by available data on the post-cranial skeleton, colour pattern and external characters.

Since there appears to be a complete lack of published data on the basic biology of *Tursiops* for any part of the Indian Ocean, the available information on reproduction, feeding and parasites collected during the study are presented in the second part of the report.

MATERIAL

Material from a total of 58 animals including 10 neonatals was examined during the study. The majority, collected in the Eastern Cape and Natal, are registered in the Port Elizabeth Museum collections (PEM specimens). Two skulls (EL 40 and EL 873) were obtained on loan from the East London Museum. A skull presumed to be from the Eastern Cape was also received on loan from Mrs. M. Yates of Port Elizabeth (M.Y.1). Data on five specimens from the Western Cape were collected for the study by Dr. P. Best, South African Museum, Cape Town. Three of these skulls are registered in the South African Museum (SAM specimens), one is owned privately by Miss J. Currie of Constantia, and one by Mr. G. Palmer, of Clovelly. Dr. Best also collected data from a specimen owned by Mr. F. Strohmaier of Swakopmund which was collected at Cape Cross, South West Africa. These skulls were later examined by the author.

The extent to which complete data and material could be collected from each specimen was largely dependent on the circumstances at the time. The author was often dependent upon the public for reports of strandings, and as a result many of the stranded animals were found in a state of decomposition or mutilated by passers-by. Others found on more remote beaches posed transport problems. As a result data on colour patterns and a number of external measurements were often unobtainable, while reproductive material and stomach contents were beyond

collection. In certain cases collection of post-cranial skeletal material was restricted to the caudal vertebrae which were not easily counted in the field.

Details concerning dates, locality, material collected and other data for each specimen are presented in table 17 of the Appendix.

TAXONOMY

Age determination

While the differences noted in the material during collection clearly indicated the possibility that two forms of *Tursiops* were present on the South African coast, an objective separation could not be based on such characters since it was unknown whether they were taxonomically significant or merely extremes of variation within one population. However, a brief comparison of two pairs of animals selected from each of the two apparent groups suggested that age would be a useful guide in the initial separation of the two groups, prior to an analysis of morphological characters.

A female *Tursiops*, "Haig" (PEM 1516/00), had been kept in captivity at the Port Elizabeth Oceanarium for eight years. It was thought to be at least two years old at capture. It had given birth to two calves in the two years prior to its death and was thus sexually mature. Two corpora albicantia were present in the left ovary. It measured a total length of 2 375 mm. A stranded female (PEM 1515/74) measured 2 795 mm in length, and examination of the ovaries revealed no signs of corpora albicantia. As the presence of at least one corpus in the ovaries is the only acceptable criterion of a sexually mature female cetacean at present, this animal is considered sexually immature.

Similarly, a male dolphin, "Dickie" (PEM 1517/72), captured and kept in captivity for two months, showed signs of old age. It was heavily scarred and the teeth were either missing or worn down to the level of the gums. At death the testes weighed a combined total of 1 730 g and were histologically active. The animal's total length was 2 440 mm. A stranded male (PEM 1517/77), 2 605 mm in total length, was found to have histologically inactive testes with a combined weight of 31 g. This weight is similar to those given for sexually immature male *T. truncatus* from Florida by Harrison *et al.* (1972). The difference in the testes weights of the two animals was considered too large to be the effect of seasonal change.

As this form of comparison is limited to certain age classes and could not be extended to specimens lacking reproductive data, an ageing technique applicable to skeletal material was required. The most suitable technique for odontocetes, developed and used by a number of research workers in recent years, is based on the laminar deposition of dentine within the tooth pulp cavity (Jönsgard, 1969).

At birth, the delphinid tooth consists of a thin cone of uniform prenatal dentine, partially covered externally by a cap of enamel. At this time a poorly-calcified translucent layer termed the neonatal line is laid down. It is considered to be the result of disturbed growth during the change from foetal life to a free-swimming existence. After birth the tooth is lengthened by the addition of dentine on the inner surface of the tooth cavity, until the tooth reaches its full length. Deposition of dentine continues with age in a series of translucent and opaque zones until the pulp cavity is completely filled. In some cases, and particularly in the material presently studied, the dentine laid down near to closure of the pulp cavity is generally uniformly-translucent, showing little lamination. It has been termed secondary dentine here (fig. 1).

Since the deposition of dentine is progressive with age, the counts of the number of growth of dentine layers, each consisting of one translucent and one opaque zone, have been used in age-determination studies by a number of authors. In delphinids, the method has been applied to

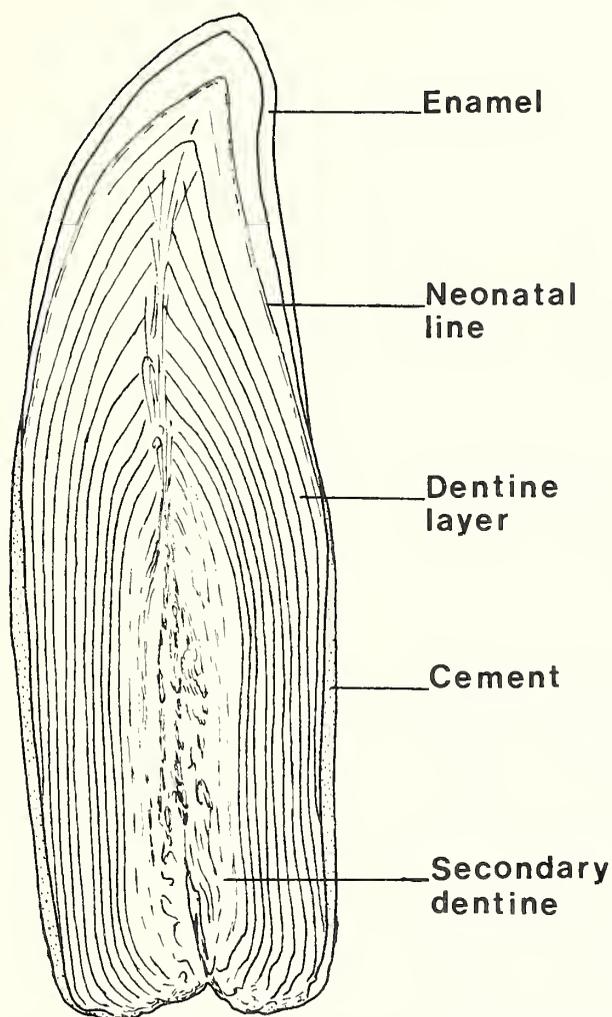


Fig. 1. Diagram illustrating the structure of a delphinid tooth as seen in longitudinal section. Counts of the number of dentine layers are used for age determination. In older South African *Tursiops*, the deposition of weakly layered secondary dentine restricted counts to the outer nine or ten layers.

the Atlantic bottlenosed dolphin *Tursiops truncatus* (Sergeant, 1962) and the euprosyne dolphin *Stenella coeruleoalba* (Kasuya, 1972), while it has also been used in studies on the sperm whale *Physeter catodon*, the white whale *Delphinapterus leucas* and other species by several authors.

At present the reason for the alternate zonation of the dentine is not clear and in many species the number of dentine layers deposited per year is uncertain, or a matter of controversy. Recent work by Sergeant *et al.* (1973) on longterm captive animals from Florida shows that one growth layer per year accumulates in *T. truncatus*. However in the taxonomic part of this study it

is only necessary to determine relative age; available data for South African material on the relationship between the number of dentine layers and absolute age are discussed further in the biological notes.

There are a number of methods of treating teeth in order to demonstrate the growth layers in the dentine. In the smaller delphinids they are best seen in longitudinal section. In this study the layering proved to be fairly indistinct and difficult to count, and various techniques were tried in an attempt to improve the readability of the tooth sections. Polished half teeth were viewed in reflected light or etched in 10 per cent formic acid for up to twelve hours. Thin decalcified

TABLE 1. Numbers of dentine layers counted in longitudinal sections of *Tursiops* teeth from South Africa. Counts made at 10 × magnification in strong reflected sunlight against a black background. Qualitative adjectives under comments refer to the readability of each tooth. Counts were made to the secondary dentine when it was present.

Cat. No.	Counts					Pulp Cavity	Comments	
	1	2	3	4	Average			
<i>Group A</i>								
PEM 1496/73	3,5	3,5	<4	<4	3,5	Open		Poor
PEM 1514/97	8	8	8		8+	Almost closed	Secondary dentine	Fair to Poor
PEM 1514/98	14	13	13	13	13+	Closed	Secondary dentine	Good
PEM 1514/48	6	6	6		6	Open		Good
PEM 1515/55	<1	<1	<1		<1	Open	Minor layers within	Poor
PEM 1515/83	9	10	9	9	9	Open		Poor
PEM 1515/95	6	6	6		6	Open		Good
PEM 1516/00	13	13	13	12	13	Closing	Captive for eight years	Poor
PEM 1516/33	10	10	11	10	10+	Closed	Secondary dentine	Good
PEM 1517/35	2	2	2		2	Open		Fair
PEM 1517/58	9	8	8	8	8+	Almost closed	Secondary dentine	Good
PEM 1517/60	10	10	10		10+	Closing	Dentine	Good
PEM 1517/61	10	11	11	11	11+	Closed	Secondary dentine	Fair
PEM 1517/69	10	11	11	11	11	Closing		Poor
PEM 1517/72	17	16	17	18	17+	Closed	Secondary dentine	Good
PEM 1517/83	10	10	10	9	10+	Closed	Secondary dentine	Poor
PEM 1517/96	11	11	12	11	11	Almost closed		Poor
PEM 1518/27	12	13	12	12	12+	Closed	Secondary dentine	Good
PEM 1518/43	1	1	1	1	1	Open		Fair
PEM 1518/54	13	13	14	13	13+	Almost closed	Secondary dentine	Good
PEM 1518/97	10	10	10		10+	Closed	Secondary dentine	Poor
PEM 1518/98	3,5	3,5	3,5		3,5	Open		Fair
PEM 1519/07	11	12	10		11+	Closing	Secondary dentine	Poor
PEM 1519/08	2,5	2,5	2,5		2,5	Open		Fair
PEM 1519/27	9	9	9		9+	Closed	Secondary dentine	Good
PEM 1519/28	9	9	9		9	Closing		Fair
M.Y.I.	9	9	10	10	10+	Closed	Secondary dentine	Fair
J. Currie	9	9	9		9	Closing		Poor
<i>Group B</i>								
PEM 1515/74	8	7	7	7	7	Closing		Fair to Poor
PEM 1515/94	9	9	9		9+	Closing	Secondary dentine	Good
PEM 1516/06	11	11	12	11	11+	Almost closed	Secondary dentine	Fair to Poor
PEM 1517/77	4	4	4		4	Open		Good
SAM 35104	10	10	11	10	10+	Almost closed	Secondary dentine	Good
SAM 37124	17	17	17		17	Almost closed		Good
G. Palmer	12	11	11	11	11	Closing		Good

longitudinal and transverse sections were stained in Mallory's triple stain, and in haematoxylin and eosin without success. Thin longitudinal sections stained with silver nitrate were unreadable, though with careful regrinding after staining, some layers were visible and this method may prove useful in future studies. Photography of thin sections viewed in transmitted light using high-contrast copy film were also unsuccessful. No improvements in the readability of sections was made by using polarizing or phase-contrast microscopes.

In the method finally used, a longitudinal section was prepared from one of the largest, most uniformly-shaped teeth from each specimen. Each was flattened antero-posteriorly on a fine grindstone prior to hand-grinding on ground glass using 500-grade carborundum powder. The sections were finally polished on glass with 600-grade carborundum powder to a thickness of approximately 0.2–0.3 mm. These were then washed in water, followed by toluene, before mounting under coverslips in Caedax (Merck), a synthetic Canada balsam mounting medium. The dentine layers were counted under a dissecting microscope at 10× magnification using reflected sunlight against a black background. Three, and in some cases four counts were made for each tooth, and the three most consistent taken as the average count. Details of these counts and comments on each specimen are given in table 1.

It will be noted in table 1 that the teeth of the older animals were only counted to the beginning of the secondary dentine, which appears to be formed after approximately 9–11 growth layers, though there are exceptions. Although research workers elsewhere have counted layers throughout the width of the tooth, this was not possible with the South African material. It is not known whether this restriction is a result of the technique employed in this study or a tooth formation peculiar to the present material.

Group Separation

Despite the restrictions in the method of estimating age resulting in minimum counts for older animals, these counts proved useful in separating two groups of animals, by plotting them against a suitable parameter; in this case the total or condylobasal length (CBL) of the skull was chosen as most of the specimen were represented by cranial material. The results of this plot are shown in fig. 2.

In this figure, teeth with open pulp cavities and in which entire layer counts were made, are distinguished by open circles (○); those teeth with open pulp cavities but which were counted to the secondary dentine are distinguished by partially closed circles (◐); those teeth with completely closed pulp cavities, but which were counted to the secondary dentine are distinguished by closed circles (●).

In fig. 2 it is evident that the specimens form two groups differing in skull length with respect to age. Those of the shorter group, A, attain a skull length of less than 500 mm while those on the larger group, B, have a skull length of more than 500 mm (after some four dentine layers have been deposited). A major assumption in this separation is that those specimens in Group A which have skull lengths approaching 500 mm are of an age when relatively little or no further growth will occur. Evidence that this assumption is in fact valid is given by four specimens, PEM 1516/33 (CBL 489 mm, 10 + dentine layers), PEM 1518/54 (CBL 480 mm, 13 + dentine layers), PEM 1518/97 (CBL 458, 10 + dentine layers) and PEM 1519/07 (CBL 477, 11 + dentine layers) in which the completely fused state of vertebral epiphyses to their centra indicates attainment of physical maturity, and thus the completion of growth. In three of these specimens the pulp cavities of the teeth were completely filled; in those of PEM 1519/07 the pulp cavities were still open for one quarter of the tooth length. In a fifth specimen, PEM 1517/60 (CBL 482 mm, 10 + dentine layers) the last twenty caudal and one mid-thoracic vertebrae were collected. The epiphyses of all the vertebrae were fused, indicating physical maturity, but the tooth pulp cavity of this specimen was open for nearly half the length of the

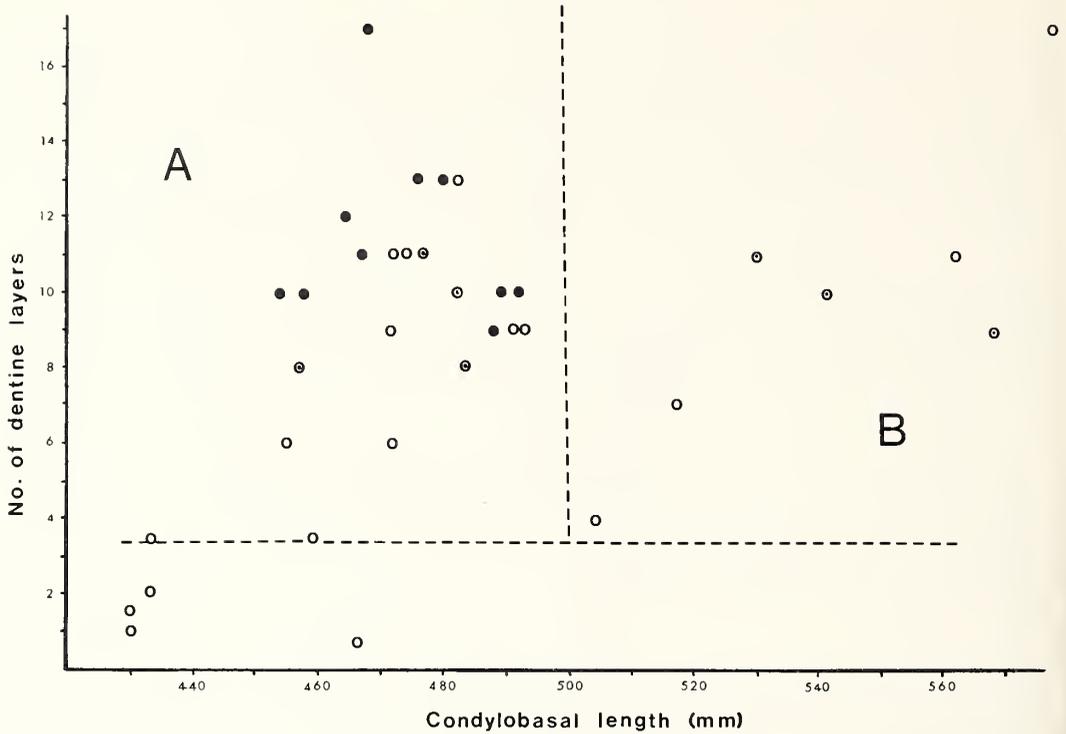


Fig. 2. Illustrating the separation of South African *Tursiops* into groups A and B, based on relative age from dentine layer counts and condylbasal length of the skull. Non-separable specimens below the horizontal dotted line are excluded from the grouping. The dotted line at 500 mm CBL is drawn at two standard deviations above the mean CBL for the 14 group A specimens with secondary dentine in the teeth. O, pulp cavity open, entire count; ⊙, pulp cavity open, counted to secondary dentine; ●, pulp cavity closed, counted to secondary dentine.

tooth. This suggests that other specimens in group A which have teeth with obliterated pulp cavities are also physically mature, and that other specimens with open pulp cavities bordered by secondary dentine may have reached, or are approaching physical maturity.

A statistical comparison of the condylbasal lengths of these fully, or nearly fully grown animals in groups A and B can be made by means of Student's t-test (Campbell, 1967). The resultant t-value ($t_{0.001;4,941}$) is highly significant, stressing the difference between the groups in skull length at maturity. The condylbasal length of PEM 1517/77 (CBL 504 mm, 4 dentine layers) lies close to the 500 mm separation line represented by two standard deviations above the mean condylbasal length for the fourteen group A specimens. However, as mentioned previously this animal is sexually immature, and can be expected to grow considerably, thus placing it within group B. PEM 1496/73 (CBL 459 mm, 3½ dentine layers) is much the same age as PEM 1517/77; yet the difference in skull lengths of the two animals (45 mm) is more than the difference in skull lengths of the smallest and largest mature group A animals (38 mm). As the limits of variation in skull length within a population increase with age, it is unlikely that PEM 1517/77 and PEM 1496/73 belong to the same group, or that the skull length of the latter will increase to beyond 500 mm. This specimen has thus been included with the group A material.

At this stage it is not possible to place specimens with less than four dentine layers into either group with certainty since there are insufficient specimens to indicate growth trends. These specimens have been omitted from the following morphological comparison of the two groups. On the other hand one specimen that was not aged but has a skull length well in excess of 500 mm has been included with the group B specimens in the analysis (SAM 19928, CBL 574 mm).

External Measurements

The external measurements taken in this study (table 2) are based on those listed by Norris (1961) with one addition.

TABLE 2. Descriptions of measurements provided in table 3 and table 18 of the appendix (after Norris, 1961).

-
1. Total length, from tip of upper jaw to deepest part of notch on flukes.
 2. Tip of upper jaw to centre of eye.
 3. Tip of upper jaw to apex of melon.
 4. Tip of upper jaw to angle of gape.
 5. Tip of upper jaw to external auditory meatus.
 6. Centre of eye to ext. auditory meatus.
 7. Centre of eye to angle of gape.
 8. Centre of eye to centre of blowhole.
 9. Tip of upper jaw to blowhole.
 10. Tip of upper jaw to anterior insertion of flipper.
 11. Tip of upper jaw to anterior insertion of dorsal fin.
 12. Tip of upper jaw to tip of dorsal fin.
 13. Tip of upper jaw to midpoint of umbilicus.
 14. Tip of upper jaw to midpoint of genital aperture.
 15. Tip of upper jaw to centre of anus.
 16. Projection of lower jaw beyond upper.
 17. Girth on a transverse plane intersecting axilla.
 18. Maximum girth.
 19. Girth on a transverse plane intersecting anus.
 20. Length of eye.
 21. Length of mammary slits (a) left (b) right.
 22. Length of (a) genital slit (b) anal opening (c) anogenital slit.
 23. Width of blowhole.
 24. Length of flipper, anterior insertion to tip.
 25. Length of flipper, axilla to tip.
 26. Maximum width of flipper.
 27. Height of dorsal fin.
 28. Length of dorsal fin base.
 29. Width of flukes, tip to tip.
 30. Distance from nearest point on anterior border of flukes to notch.
 31. Depth of notch between flukes.
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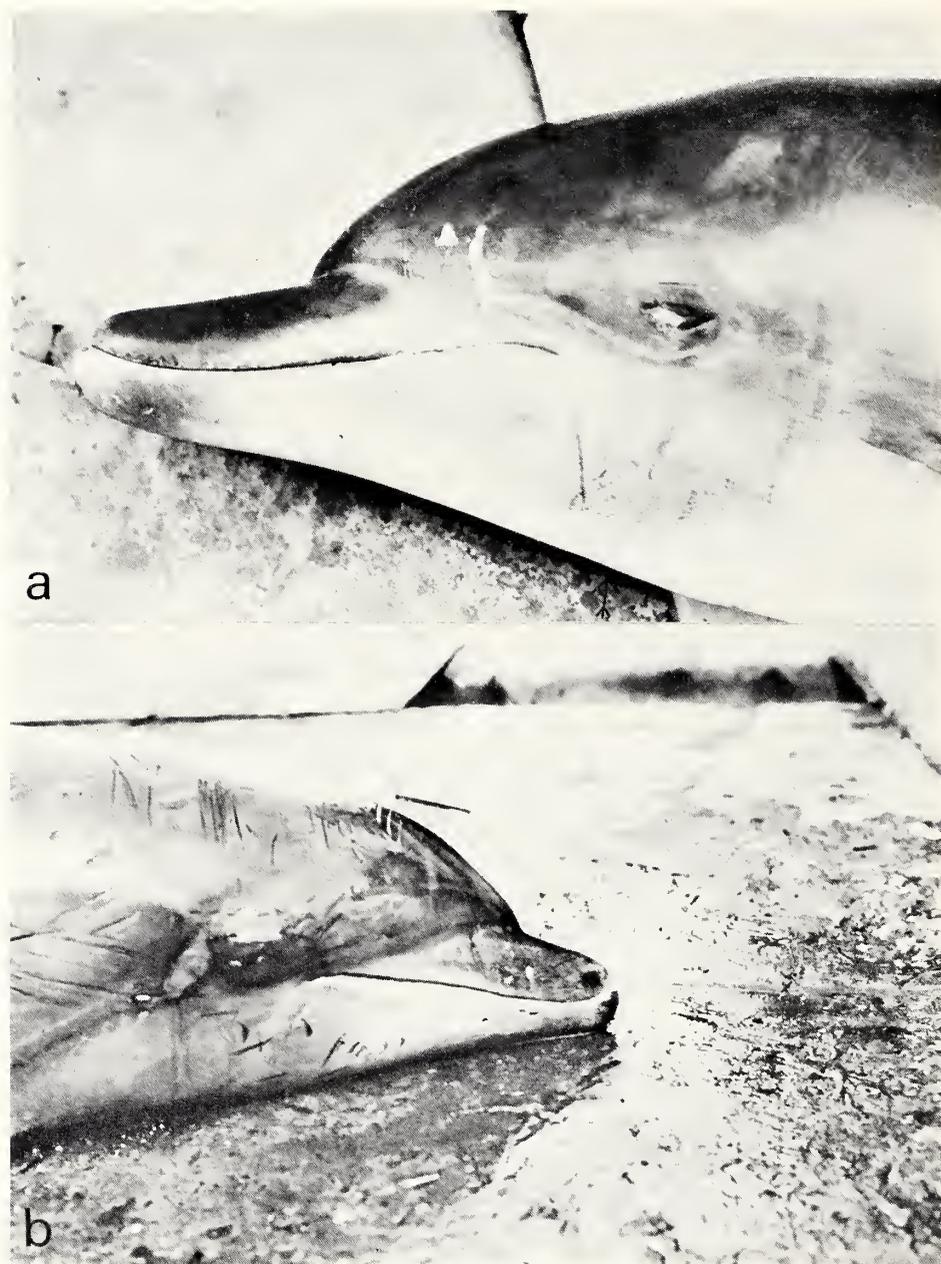


Plate 1. Illustrating the relative beak lengths of (a) a group A female, PEM 1516/00, from Port Elizabeth and (b) a group B female, PEM 1515/74, from Port Elizabeth. Note the sharp demarcation of the throat patch in PEM 1516/00.

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TABLE 3. Analysis of selected body measurements from groups A and B. Total length (no. 1) is given in mm. The other measurements we expressed as percentages of total length. Measurement numbers are keyed to table 2.

No. of measurement	Group A			Group B			U-values
	Limits	Mean	N	Limits	Mean	N	
1	2 020-2 540	2 375	17	2 605-3 270	2 848	4	0***
2	13,5-16,1	14,7	16	13,2-14,6	13,9	4	12,5
3	4,7- 6,0	5,3	17	3,1- 4,7	3,8	4	0,5***
4	11,2-13,4	12,2	17	10,1-12,5	11,5	4	22
7	2,3- 3,2	2,8	15	2,3- 3,1	2,8	4	29
8	8,2- 9,4	8,6	14	7,5- 9,3	7,7	4	13
9	14,2-16,8	15,5	16	12,5-14,6	14,0	4	12
10	20,2-26,5	23,4	17	20,5-22,4	21,5	4	9
12	54,4-62,6	59,9	17	56,4-61,7	59,9	3	25
14	58,3-71,2	64,6	14	60,9-67,7	65,6	4	20,5
15	68,6-76,8	71,0	15	68,2-73,8	71,4	4	24
19	28,9-41,1	34,6	13	26,3-32,4	28,8	4	10
24	15,4-18,2	16,8	17	15,0-15,9	15,4	4	5**
25	11,0-13,3	12,0	17	10,9-11,7	11,2	3	8,5
26	5,2- 7,1	5,5	17	5,0- 5,4	5,2	4	4**
27	7,5-12,5	9,8	16	8,4- 9,1	8,8	3	8,5
28	13,1-19,8	16,7	17	15,9-18,6	17,1	4	30
29	20,1-29,4	24,5	16	18,5-26,2	23,0	4	23
30	6,3-8,6	7,5	16	7,1- 8,3	7,8	4	22,5
31	0,9-2,0	1,6	16	1,3-2,1	1,7	4	30

** Significant in a two-sided test at $\alpha = 0,02$

*** Significant in a two-sided test at $\alpha = 0,002$

Measurements of individual specimens are given in table 18 of the appendix. In table 3 selected data extracted from table 18 are given for specimens in groups A and B. Measurements of apertures, or those for which data are too few, have been omitted from the comparison. In the statistical comparison the non-parametric U-test of Mann-Whitney was used in preference to the Student t-test, since it avoids the assumption of normality embodied in the latter test (Siegel, 1956). The values obtained were tested against tabled critical values at two levels of significance.

At the more stringent level of significance ($\alpha = 0,002$ for a two-sided test) only groups of data which do not overlap differ significantly with sample sizes as small as those tested. Two sets of measurements were found to differ.

Not unexpectedly groups A and B differ in total length (no.1) since this measurement is by its nature associated with the method of group separation. The longest animal recorded in group A was an old male (PEM 1517/83) of 2 540 mm, which is some 65 mm shorter than the youngest animal (PEM 1517/77) included in group B.

The length of the beak (no. 3) is proportionately shorter in group B animals. The short, stubby beak of each group B animal was one of the most noticeable features in the initial examination of these animals. Though it is now known from additional material (see Ross, 1973) that there is relatively little difference in the absolute values for beak length (group A, 110-134 mm; group B, 100-127 mm), the proximal portion of the beak in group B animals is distinctly broader and deeper than that of group A animals, emphasizing its shortness (plate 1). The shape of the beak may prove a useful feature in the identification of free-ranging animals under certain circumstances such as bow-riding.

Tested at a lower level of significance ($\alpha = 0,02$ for a two-sided test) two other

measurements differ significantly in the two groups. These are the length of the flipper, anterior insertion to tip (no. 24) and the maximum width of the flipper (no. 26), which indicate the group B animals have slightly smaller flippers in proportion to group A animals. In absolute values the flippers of group B animals are in fact slightly longer (group A, 350–445 mm; group B, 405–490 mm) and similar in width (group A, 120–178 mm; group B 137–160 mm) to those of group A; the difference in the proportional measurements merely reflect the greater length of group B

TABLE 4. List of cranial measurements provided in Tables 5, 6 and 9, and in Tables 19, 20 and 21 of the appendix.

-
1. Condylobasal length.
 2. Rostrum length.
 3. Rostrum, basal width.
 4. Rostrum, width 60m anterior to antorbital notches.
 5. Rostrum, width at midlength.
 6. Premaxillae, width at midlength of rostrum.
 7. Tip of rostrum to superior nares.
 8. Tip of rostrum to posterior margin of pterygoids near midline.
 9. Preorbital width.
 10. Postorbital width.
 11. Orbital width.
 12. Width of superior nares.
 13. Zygomatic width.
 14. Greatest width of premaxillae.
 15. Width of braincase across parietals.
 16. Number of teeth, upper right.
 17. Number of teeth, upper left.
 18. Length of tooth row, upper right.
 19. Length of tooth row, upper left.
 20. Posterior end of upper tooth row to tip of premaxillae, right.
 21. Posterior end of upper tooth row to tip of premaxillae, left.
 22. Number of teeth, lower right.
 23. Number of teeth, lower left.
 24. Length of lower tooth row, right.
 25. Length of lower tooth row, left.
 26. Posterior end of lower tooth row to tip of mandible, right.
 27. Posterior end of lower tooth row to tip of mandible, left.
 28. Mandible length.
 29. Coronoid height.
 30. Length of mandibular symphysis.
 31. Length of temporal fossa.
 32. Height of temporal fossa.
 33. Rostrum, width at $\frac{3}{4}$ -length.
 34. Cranial height.
 35. Cranial length, internal.
 36. Antero-lateral length of jugal, left.
 37. Antero-lateral length of jugal, right.
 38. Length of tympanic bulla, left.
 39. Length of tympanic bulla, right.
-

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specimens. These two measurements are of little use as taxonomic characters owing to the extent of the overlap in their ranges for each group.

Cranial measurements

Although cranial morphology continues to play an important role in cetacean systematics, the measurements applicable to delphinids still require formal standardization. In this study the measurements used by Dr. F.C. Fraser, British Museum of Natural History, have been applied and are listed in table 4 with four additional measurements (nos. 36–39). The points to which

TABLE 5. Analysis of cranial measurements for sexual dimorphism in group A. Measurements are extracted from table 19. Condylobasal and tympanic bulla lengths are given in mm. Other measurements except tooth counts are expressed as percentages of condylobasal length. Measurement nos. are keyed to table 4.

No. of measurement	Males			Females			U-values
	Limits	Mean	N	Limits	Mean	N	
1	458–493	475	8	433–489	472	8	30
2	55,7–59,3	57,0	8	56,6–58,9	57,9	8	15
3	21,4–26,0	23,7	8	22,9–24,5	23,6	8	30,5
4	16,1–17,3	17,0	8	16,2–17,3	16,7	8	31,5
5	12,9–15,6	14,0	8	13,1–14,6	13,6	8	25
6	6,4– 8,1	7,1	8	6,8– 8,1	7,3	8	25
7	65,3–68,7	66,8	8	66,2–68,6	67,3	8	21
8	65,0–67,2	66,0	7	65,8–69,3	66,8	8	17,5
9	41,6–45,8	43,3	8	41,1–43,9	42,6	8	23
10	47,3–52,3	49,2	8	46,6–49,6	48,1	8	17
11	42,2–46,0	44,1	8	42,3–44,9	43,4	8	23
12	10,6–12,6	11,5	8	10,8–12,0	11,5	8	29
13	47,6–52,3	49,4	7	45,7–49,7	47,7	8	10,5
14	16,6–19,0	17,5	8	16,7–18,7	17,7	8	25
15	35,0–40,4	37,2	8	33,7–36,9	35,8	8	21,5
16	24–26	25,1	7	24–27	25,6	8	28,5
17	24–27	25,6	8	24–28	26,1	8	22
18	44,0–47,3	45,7	8	43,1–48,3	46,0	8	25,5
19	44,6–48,4	45,9	8	43,6–49,4	46,2	8	27
20	45,7–49,8	47,4	8	46,8–49,4	48,0	8	20,5
21	45,7–49,8	47,5	8	47,0–49,9	48,2	8	17
22	23–29	26,3	8	25–28	26,4	8	31
23	23–27	25,6	8	26–28	26,4	8	20,5
24	44,2–49,8	47,7	8	46,5–53,6	48,5	8	29
25	45,4–50,0	47,5	8	46,3–52,9	48,3	8	23
26	44,6–50,4	48,1	8	46,7–54,0	49,2	8	24
27	47,0–50,4	48,0	8	46,7–53,1	48,7	8	25
28	83,5–86,7	84,7	8	83,7–86,3	85,3	8	23,5
29	17,2–18,8	17,7	8	16,4–18,6	17,5	8	26,5
30	12,5–16,7	14,6	8	14,1–17,3	15,0	8	24
31	22,4–23,7	22,8	8	20,8–23,7	22,2	8	20,5
32	16,6–18,4	17,3	8	14,3–17,3	15,8	8	8
33	9,6–12,8	10,7	8	9,6–11,0	10,4	8	31,5
34	28,6–35,5	31,4	8	26,3–32,1	29,8	8	22
35	27,8–32,3	30,9	7	26,7–31,7	29,4	8	14
36	8,5–11,0	9,5	8	8,5–10,0	9,2	6	18
37	7,3–10,2	8,9	8	8,1– 9,5	8,6	8	24
38	35,0–38,0	36,3	7	35,0–37,0	35,7	6	14
39	35,0–38,0	36,5	6	34,0–37,5	35,4	6	8,5

these apply are illustrated in figs. 5–8 of the appendix. Long measurements were taken with calipers transferred to a metre rule, while shorter measurements were taken with vernier calipers. In cases where the rostrum had splayed during preparation, the distal thirds of the maxillae were squeezed to bring the premaxillae into contact or near-contact in the midline, prior to measurement of rostral widths (nos. 3, 4, 5, 6, and 33). Mandibular measurements and temporal fossa length and height were normally measured on the left side. Rudimentary teeth are included in the analysis of tooth counts and their alveoli included in measurements of tooth row length. Cranial measurements are given for individual specimens in tables 19 and 20 of the appendix.

TABLE 6. Analysis of cranial measurements of specimens in groups A and B. Condylbasal and tympanic bulla lengths are given in mm. Other measurements, except tooth counts, are expressed as percentages of condylbasal length. Measurement numbers are keyed to table 4.

No. of measurement	Group A			Group B			U-values
	Limits	Mean	N	Limits	Mean	N	
1	433–493	472	24	504–578	547	8	0***
2	54.7–59.3	57.3	24	55.7–58.3	56.8	8	54.5
3	21.4–25.4	23.7	24	24.5–27.3	26.1	8	8.5***
4	15.9–19.2	16.9	24	18.3–22.5	20.5	8	2***
5	11.6–16.5	13.9	24	14.5–18.3	16.1	8	16.5***
6	6.4– 8.8	7.3	24	7.5– 9.9	8.9	8	10***
7	65.0–68.7	67.1	24	65.9–67.5	66.9	8	86.5
8	63.0–69.7	66.6	23	66.0–69.7	68.0	7	34.5
9	41.0–45.8	42.9	23	43.2–48.4	46.3	8	10.5***
10	46.6–52.3	48.7	23	47.7–53.0	50.7	8	35.5**
11	42.2–46.0	43.7	23	44.2–47.6	46.1	5	9***
12	10.6–12.6	11.5	23	10.9–11.9	11.6	5	52.5
13	45.7–52.3	48.5	21	48.6–52.9	51.6	8	23**
14	16.6–19.0	17.7	24	17.2–19.6	18.6	8	42**
15	33.7–40.4	36.6	24	33.1–37.7	35.0	8	39**
16	24–27	25.3	22	22–25	23.8	8	21.5***
17	24–28	25.8	23	23–25	24.3	8	27.5**
18	43.1–48.3	45.8	23	46.4–49.5	47.7	8	20.5***
19	43.6–49.4	45.9	23	46.4–49.8	47.8	8	23.5***
20	45.5–49.8	47.6	22	47.2–49.1	48.0	4	33.5
21	45.5–49.9	47.7	22	47.2–50.1	48.2	5	40.5
22	23–29	26.1	22	21–23	22.4	8	2.5***
23	23–28	25.9	21	22–24	22.5	8	5***
24	44.2–53.6	47.9	21	45.4–47.7	46.6	8	40
25	45.4–52.9	47.8	21	45.1–47.7	46.3	8	35**
26	44.6–54.0	48.5	21	46.8–47.8	47.3	4	19.5
27	46.6–53.1	48.3	21	46.8–47.4	47.1	4	17.5
28	82.5–87.0	84.9	21	83.8–87.1	85.3	8	79
29	16.4–18.9	17.8	22	17.0–19.3	18.4	8	44
30	12.5–17.3	14.6	22	12.6–15.7	14.2	8	78
31	20.5–24.0	22.5	23	20.6–22.8	21.2	8	33.5**
32	14.3–18.8	16.5	24	14.4–16.6	15.4	8	38.5**
33	8.5–12.8	10.6	24	10.8–14.7	12.2	8	29.5**
34	26.3–35.5	31.0	24	30.2–32.5	31.1	8	93
35	27.3–32.3	30.3	22	30.8–31.7	31.2	4	34.5
36	8.2–11.0	9.5	22	10.1–12.6	11.7	8	5***
37	7.3–10.2	8.8	23	9.7–11.9	10.9	8	2***
38	35.0–38.0	36.1	15	38.0–38.5	38.2	3	1**
39	34.0–38.0	36.0	13	38.0–38.0	38.0	3	1.5**

** Significant in a two-sided test at $\alpha = 0.02$.

*** Significant in a two-sided test at $\alpha = 0.002$.

Comparisons of data for groups A and B extracted from these tables have been tested with the U-test of Mann-Whitney ($\alpha = 0.02$ and $\alpha = 0.002$ for a two-sided test) (Siegel, 1956).

Up to this point, comparisons between groups A and B have excluded possible sexual dimorphism which could affect conclusions drawn from the combined data. Though there are insufficient sexed specimens in group B, eight males and eight females, sexed from reproductive organs, are included in group A. (♂♂:PEM 1515/83, 1515/95, 1517/69, 1517/72, 1517/83, 1518/27, 1518/54, 1518/97; ♀♀:PEM 1516/00, 1516/33, 1517/60, 1517/61, 1517/96, 1518/98, 1519/07, 1519/28.) Data extracted from table 19 are presented for these 16 specimens in table 5.

None of the probabilities associated with the U-values obtained for comparisons in table 5 indicate significant differences between males and females. Henceforth the data for group A specimens have been combined; owing to the lack of material a similar situation has been assumed for group B specimens.

Data for twenty-four group A specimens and eight group B specimens are compared in table 6. Excluding the difference in condylobasal length, the two groups differ significantly in nine measurements at the higher level of significance ($\alpha = 0.002$). Though in each of these comparisons there is a certain degree of overlap in the data, it is felt that this overlap reflects the extremes of variation within each group, without detracting from the taxonomic value of the measurement.

The first four group differences (nos. 3, 4, 5 and 6) indicate that the rostrum is considerably wider, proportionately, in group B than in group A, in the proximal half of its length. The most distinct of these differences is the width of the rostrum 60 mm anterior to the antorbital notches; in group A the margins of the proximal 60 mm of the rostrum taper abruptly, while a more even tapering of the rostrum occurs in group B (plate 2).

The preorbital and orbital widths of group A specimens are proportionately smaller than those of group B animals. The closer similarity of other skull width measurements (nos. 10 and 13) indicate that this difference is not a reflection of a proportionately narrower skull in group A, but results from the lateral compression of the antorbital prominences in this group. In dorsal view the lateral margins of the orbit are inclined antero-mesially (plate 2), while in anterior view the supraorbital plate appears more strongly arched and robust in group A, owing to the large maxillary prominence. In group B the lateral margins of the orbits are sub-parallel, inclined antero-mesially, and in anterior view the antorbital prominence is relatively thin (plate 5).

The upper tooth rows are relatively shorter in group A animals. Though there are slightly more teeth on average in the upper jaws of group A specimens, these teeth are visibly smaller in diameter than those in group B, and the alveoli are set closer together (plate 3). Maximum tooth diameter would probably prove a useful taxonomic character, but it was omitted in this study as the teeth fall free of the jaws during preparation, after which it is impossible to choose teeth originating from a particular part of the tooth series for accurate comparison. Alveolar diameter was discarded as a possible character as it is difficult to measure accurately and changes in form considerably with age.

In the lower jaw, group A animals have considerably more teeth than group B specimens. The combination, however, of more but thinner teeth and more closely spaced alveoli in group A tends to equalize differences in the lengths of tooth rows in the lower jaws of both groups, so that measurements 24 and 25 do not distinguish the two groups. The difference in the number of mandibular teeth is an important character, for it can be applied to material of any age, particularly from young or neonatal animals.

The relatively longer antero-lateral margin of the jugal in group B specimens is indicated by measurements 36 and 37. In lateral view the antorbital prominence of group B skulls has an attenuated appearance, with the thin plate-like jugal extending postero-ventrally to the posterior edge of the relatively robust antorbital process of the frontal. In group A the antorbital prominence has a foreshortened appearance in lateral view (plate 4).

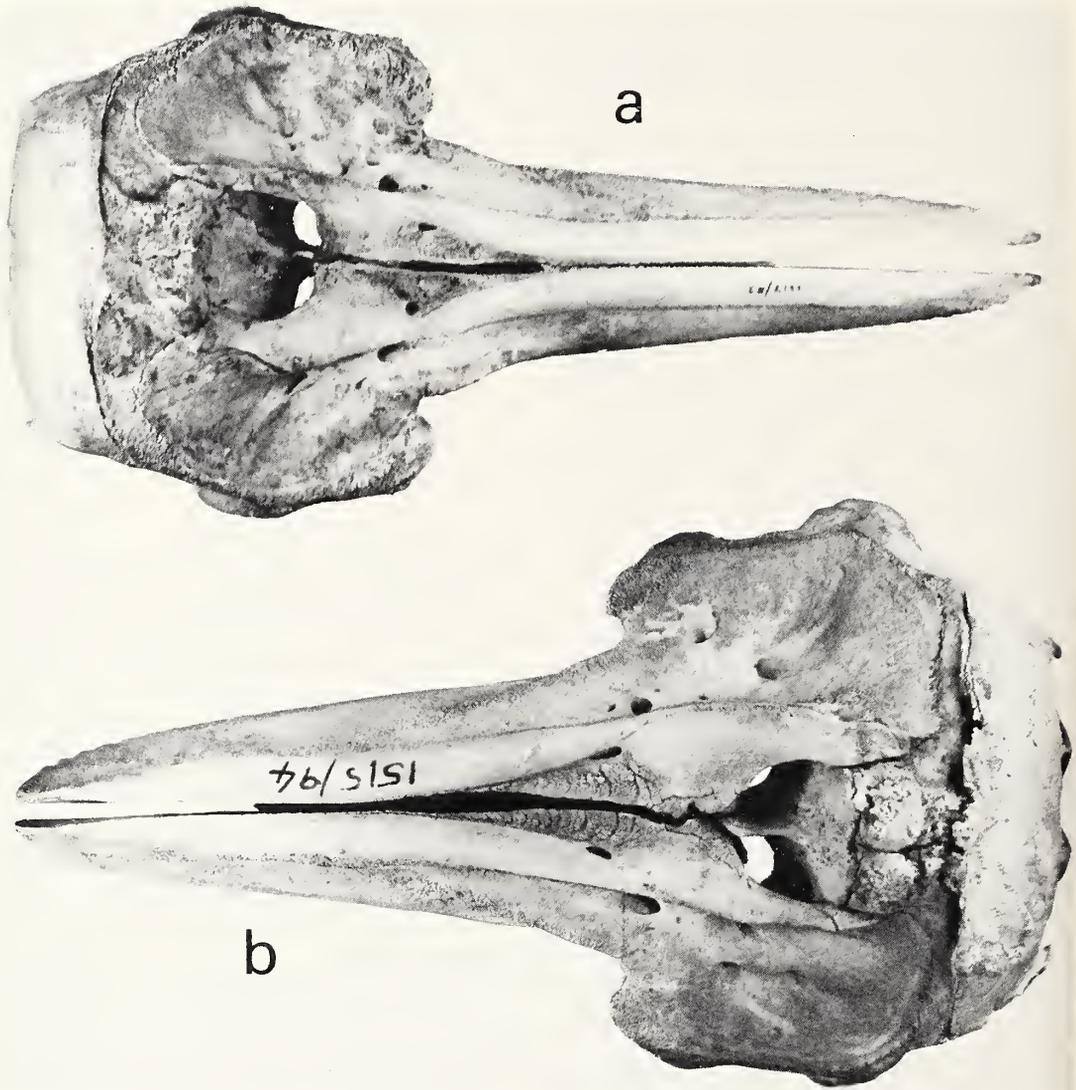


Plate 2. Dorsal views of the skulls of (a) a group A specimen, PEM 1517/83, from Port Elizabeth, and (b) a group B specimen, PEM 1515/94, from Algoa Bay, illustrating differences in the width and tapering of the rostrum and the preorbital width.

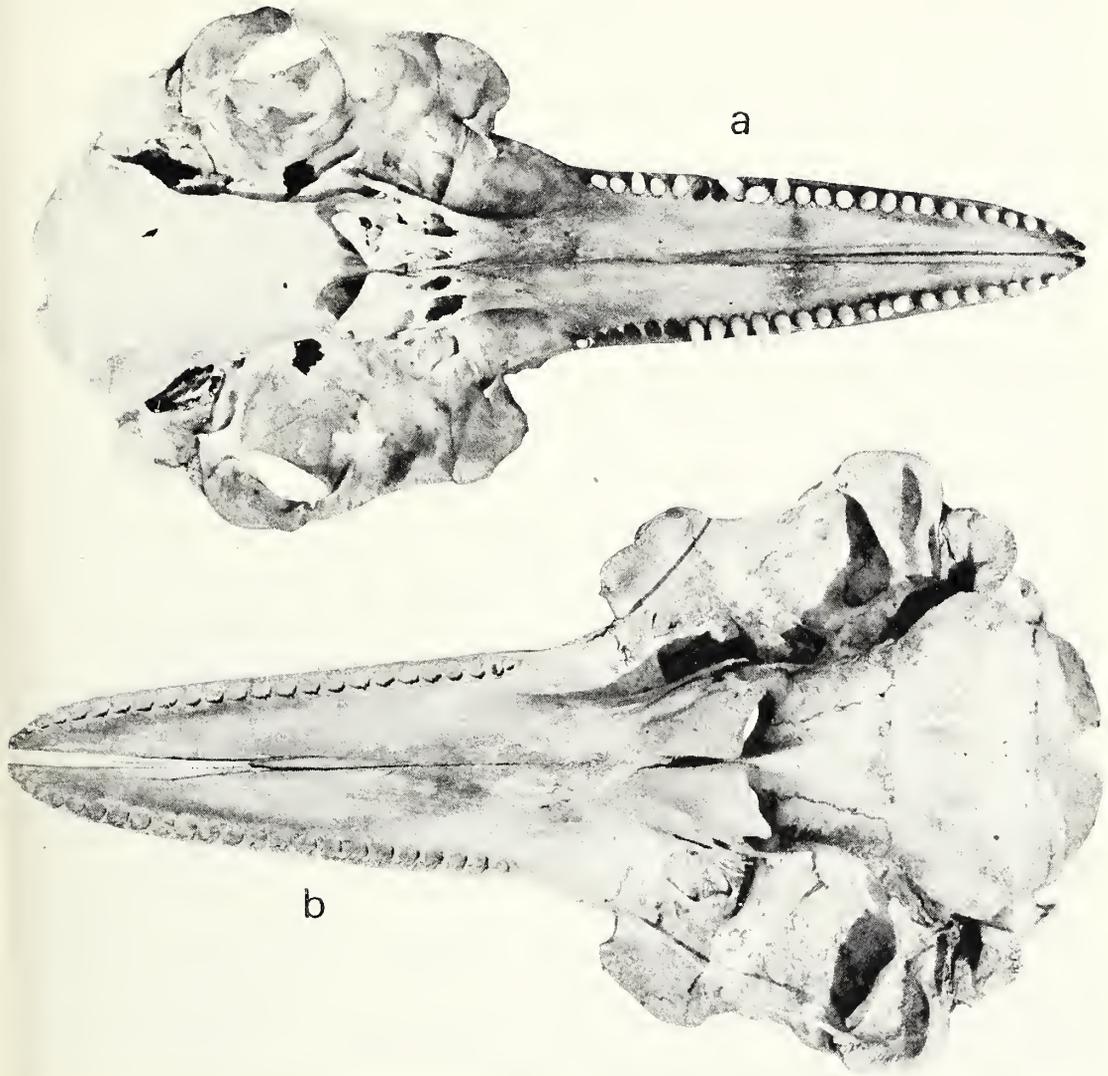


Plate 3. Ventral views of the skulls of (a) a group A specimen, PEM 1517/58, from Natal (?), and (b) a group B specimen, PEM 1515/94, from Algoa Bay, illustrating differences in the spacing of the alveoli, and the shape of the vomer posteriorly. Note the separation of the pterygoids in both skulls.

Table 6 also contains a number of measurements in which the two groups differ significantly at a lower level of significance ($\alpha = 0,02$). Though these are indicative of minor differences in the skull proportions of the groups, it was felt that the degree of overlap in the data precluded their use as taxonomic characters.

Additional cranial characters

Purely morphometric characters lose much of their value in the identification of young or neonatal animals when the data on growth changes are incomplete, as in this study, in which young animals were specifically excluded during group separation. To offset this disadvantage 24 group A skulls and 8 group B skulls were examined for non-mensural characters which could be considered consistent within each group, at all ages. Unfortunately no confirmed young or neonatal group B animals have been collected but the skull of one group A neonate (PEM 1515/02) was available; this animal was the calf of a captive group A female (PEM 1516/00), and has been included in the group A material.

Five characters which appeared potentially useful are listed as propositions against which the material in both groups has been tested.

1. Posterior width of vomer. In ventral view the posterior portion of the vomer is narrow, with parallel or subparallel lateral margins in group A; in group B it is broadened posteriorly with distinctly flaring lateral margins (plate 3).

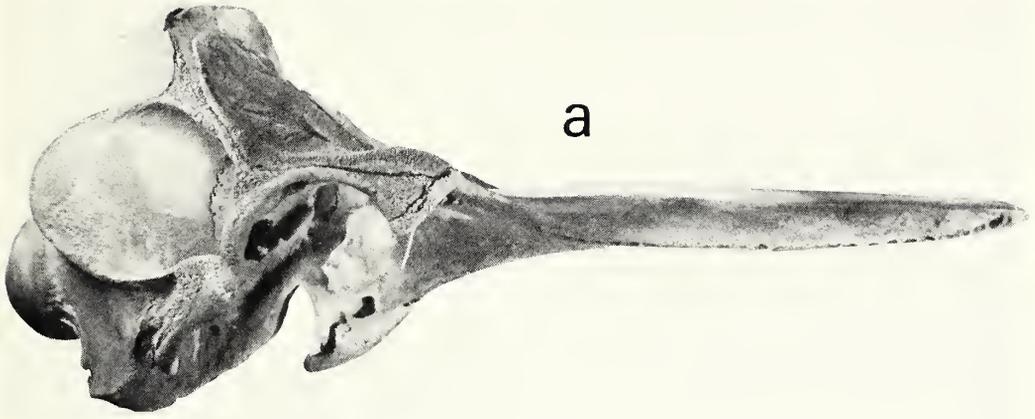
2. Pterygoid notch. In lateral view the pterygoid notch is relatively narrow, and the anterior and posterior margins converge to a sub-acute apex in Group A; in group B the pterygoid notch is broad, and the margins are sub-parallel, converging slightly to a rounded obtuse apex (plate 4).

3. Squamosal. The portion of the squamosal forming the lower wall of the temporal fossa is small, with its apex directed dorsally in group A; in group B it is broader, and more extensive, with its apex directed postero-dorsally (plate 4).

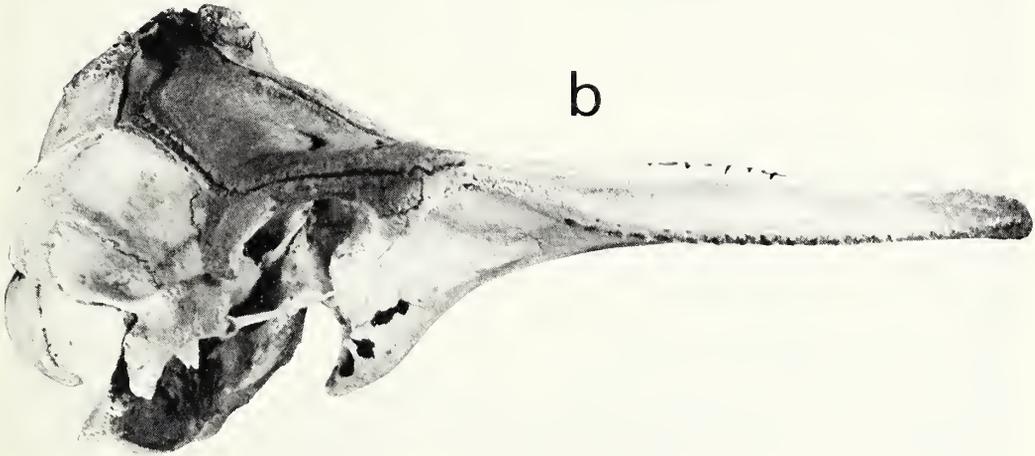
4. Premaxillary convexity. In anterior view the premaxillae are strongly arched in the middle third of the rostrum so that the dorsal surfaces of the premaxillae and maxillae meet at a conspicuous angle in Group A; in group B the premaxillae are less strongly arched so that the dorsal surfaces of the premaxillae and maxillae follow into one another relatively smoothly.

5. Lateral margin of premaxilla. In dorsal view there is little or no strip of cancellous bone bordering the dense bone of the premaxilla laterally, and adjacent to the premaxillary-maxillary suture in the middle third of the rostrum in group A; in group B cancellous bone is present in a broad and conspicuous strip (plate 2).

The results in table 7 show a high proportion of specimens in each group which conform to the characters as proposed for them, indicating that these characters are taxonomically useful. In two cases in group A (MYI; PEM 1515/95), and one in group B (PEM 1516/06) the posterior portion of the vomer had been broken or resorbed beyond definite classification. Two group A skulls (MYI; PEM 1517/83) partially conformed to proposition 2, in having narrow pterygoid notches with obtuse apices. In one group B specimen (SAM 19928) which differed entirely from proposition 3, the squamosal portion of the temporal fossa was far smaller on both sides than any of the group A specimens, and probably should be considered aberrant. The cancellous strip on the lateral margin of the premaxilla is variable in width up to 3 mm in group A specimens; one group B skull (PEM 1517/77) with a narrow strip of 3 mm partially conformed to proposition 5, while the other specimens in the group had considerably wider strips.



a



b

Plate 4. Lateral views of the skulls of (a) a group A specimen PEM 1516/00, from Port Elizabeth, and (b) a group B specimen, PEM 1515/94 from Algoa Bay, illustrating differences in the shape of the lacrimal, the antorbital process, the pterygoid notch, and the portion of the squamosal forming the wall of the temporal fossa.

TABLE 7. The number of specimens conforming to (C), partially conforming to (C?), and differing from (D) for the additional characters as proposed for groups A and B.

Proposition	Group A			Group B		
	C	C?	D	C	C?	D
1	22	1	0	7	1	0
2	23	2	0	8	0	0
3	24	1	0	7	0	1
4	23	2	0	8	0	0
5	23	1	0	7	1	0

The group A neonatal (PEM 1515/02) conformed well to propositions 1, 2 and 3 as proposed for group A, but only partially conformed to proposition 4, where it appeared to be intermediate between groups A and B. This is thought to be the result of distortion in the soft neonatal bones of the rostrum during preparation and assembly. Proposition 5 could not be included for this skull as the entire premaxilla is cancellous in appearance at this age. The conformity of a skull of this age in the first three propositions is encouraging since it suggests that other young and neonatal animals can be grouped on these characters.

Post-cranial Skeleton

In a few cases the complete post-cranial skeleton of an animal could be collected; often however, post-cranial data were limited by circumstances to a vertebral and rib count. In these specimens the number of cervical vertebrae was assumed to be seven and the number of thoracic vertebrae equal to the number of ribs, and thereafter the lumbar and caudal vertebrae were counted together as caudally as possible. The remainder of the caudal vertebrae were collected and preserved. In the vertebral counts the triangular terminal caudal bone is considered to represent two fused vertebrae (True, 1914). Despite precautions, the smaller caudal vertebrae are often lost during preparation, and the number of missing caudal vertebrae in some specimens has been counted by direct comparison with complete specimens. Material from 10 group A and 3 group B skeletons was examined.

The results given in table 8 indicate that groups A and B differ in the total number of vertebrae and in the number of the first caudal vertebra in which the arterial canal in the transverse process appears. Though in the present study these differences could be used as supplementary characters in the identification of younger specimens, there is considerably variation in these small samples, and further material is required before their true taxonomic value can be assessed.

One further feature of the vertebral column which appears to have taxonomic potential is the form of the neural spine of the atlas vertebra. In all seven group A specimens examined, the spine is short and truncated, in four cases bifid and in one case partially bifid terminally. Only two group B specimens are available; in both the spine of the atlas is elongate and tapered, truncate terminally in one animal, and very slightly bifid in the second animal.

X-ray photographs of the flippers of three animals were taken to determine their phalangeal formulae. The variation in the three suggests that they would have little taxonomic value. Inclusive of the metacarpals, the formulae are: PEM 1516/00, I2, II8, III6, IV4, V3 (group A); PEM 1515/74 I2, II8, III6, IV3, V2 (group B); PEM 1516/06 I1, II8, III7, IV4, V2 (group B).

ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS TURSIOPS SPECIES

TABLE 8. Comparison of vertebral data from group A and B specimens. The characters numbered in the first column are listed below the table.

No. of character	GROUP A										GROUP B		
	PEM 1515/83	PEM 1516/00	PEM 1516/33	PEM 1517/69	PEM 1517/72	PEM 1517/83	PEM 1517/96	PEM 1518/54	PEM 1518/97	PEM 1519/07	PEM 1515/74	PEM 1516/06	PEM 1517/77
1	—	61	61	61	61	60	59-60	59	61-62	60	65	64	65
2	—	2	2	1	5	5	7-8	0	2-3	2	4	6	0
3	26	26	26	25	—	—	—	27	26	24	26	26	—
4	22	22	23	22	—	—	—	20	22	21	22	23	—
5	23	27	25	23	—	—	—	25	24	24	26	26	—
6	22-23	23-25	23-25	24	—	—	—	21-22	23-25	23	25-28	24-27	—
7	39	40	38	39	—	40*	38*	38	41	39	43	45	46
8	12	12	12	12	13	13	12	12	13	12	12	12	13

Characters 1: Total number of vertebrae.

2: Number of caudal vertebrae lost in preparation, normally terminals. This has been included to allow assessment of the accuracy of character 1.

3: Serial number of the vertebra with the greatest total height.

4: Serial number of the vertebra with the greatest transverse width.

5: Serial number of the vertebra at which the orientation of the neural spine changes.

6: Serial number(s) of the vertebra(e) at which the orientation of the transverse processes changes.

7: Serial number of first caudal vertebra with an arterial canal through the transverse process.

8: Number of vertebral ribs.

*The serial number of the first of those vertebrae collected. It is possible that more anterior vertebrae also had arterial canals through the transverse processes, but only caudal vertebrae were collected for these specimens.

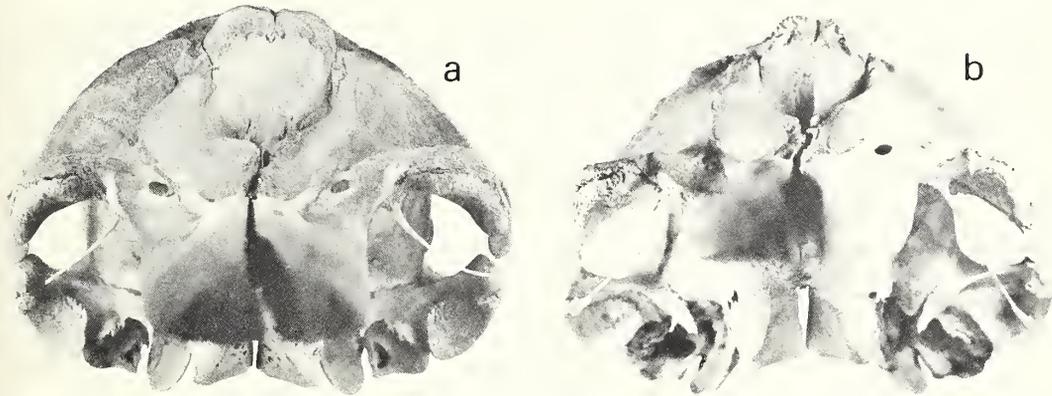


Plate 5. Anterior views of the skulls of (a) a group A specimen PEM 1516/00, from Port Elizabeth, and (b) a group B specimen, PEM 1515/94, from Algoa Bay, illustrating differences in the shape of the antorbital prominences. Owing to the limited depth of field, the photographs do not illustrate the difference in the convexity of the premaxillae in the middle third of the rostrum.

Status and Affinities of Groups

It is clear that groups A and B are morphologically separable by a number of external and skeletal characters, some of which are potentially applicable to all age groups. In the material examined so far, there is no evidence of intermediate forms. There also appear to be differences in the distribution patterns of the two groups which overlap extensively between the Western Cape and Natal; examination of locality data contained in table 17 of the appendix shows that group A predominates on the south-east coast, while group B predominates in the Western Cape and on the west coast. The distribution patterns are dealt with more fully in the discussion. The presence of morphological differences in two closely-related groups, sympatric over a wide area of overlap in distribution clearly indicates two reproductively-isolated groups, each deserving full specific status. Groups A and B are therefore considered to represent separate species (A and B respectively) in South African waters.

Comparison of the characters outlined for species B with published descriptions of other *Tursiops* species (True, 1889, 1914) suggested that species B was closely related to, or identical with *T. truncatus* from the North Atlantic. In order to confirm this similarity, the cranial measurements taken for the 8 species B skulls have been compared to those of a series of 17 *T. truncatus* from British waters. These latter measurements were taken and kindly supplied to the author by Dr. F. C. Fraser, of the British Museum, from specimens housed in that institution. To conform to the restrictions originally placed on the South African material, only specimens with a condylobasal length of more than 500 mm were selected for comparison. Measurements of 17 individual skulls are given in table 21 of the appendix.

Data from the British series and the species B series are given in table 9, and compared with the U-test of Mann-Whitney. The data for the species A series has also been included in table 9, and a group comparison for each measurement made with the Kruskal-Wallis test (Siegel, 1956). Further pair-wise comparison of these groups have been made using Dunn's method.

The British *truncatus* and species B differ significantly ($\alpha = 0,02$) in five skull measurements. The width of the proximal proportion of the rostrum (nos. 3, 5 and 6), the zygomatic width (no. 13), and the greatest width of the premaxilla (no. 14) are all slightly greater in the British material than in species B material. In addition the mandible (no. 28) is slightly longer in the former series. In all of these comparisons however, there is a considerable overlap of data, and none of these could be considered taxonomically significant, particularly at the specific level. At a more stringent level of significance ($\alpha = 0,002$) no significant differences were found.

On these grounds, the South African species B can be considered conspecific with *Tursiops truncatus* of the North Atlantic, though the position will require re-evaluation as more material is collected. There may well be sub-specific differences. For example in all the South African material examined of both species, the pterygoid hamuli are separated in the midline, while in the north Atlantic specimens they are almost invariably in contact (Van Bree, *in litt.*). Until recently, contact between the pterygoid hamuli has been considered characteristic of the genus *Tursiops* (Tomilin, 1957), a character which is now obviously invalid even on the specific level.

The Kruskal-Wallis comparison and the pair-wise contrast of all series supports the conclusions that species B and *T. truncatus* are conspecific, and species B is henceforth referred to as *T. truncatus*. In four measurements (nos. 3, 18, 22 + 23) species A differs significantly from both South African and British *T. truncatus*; in a further eight measurements species A differs from British *T. truncatus*; in the remaining seven measurements there was no significant contrast. In no measurement did South African *T. truncatus* contrast significantly with the British material ($\alpha = 0,01$), although minor differences were found in a direct comparison of these two groups with the U-test.

Comparison of the characters outlined for species A with published descriptions of *Tursiops* species indicate that it identifies with a number of species described from the Indian Ocean,

TABLE 9. Comparison of cranial measurements of British *Tursiops truncatus*, and South African material of species A and B. Condylolbasal length (no. 1) is given in mm, other measurements except tooth counts are expressed as percentages. Measurement numbers are keyed to table 4.

No.	Brit. <i>T. truncatus</i> (C)			Species B (B)			U-value B/C	Species A (A)			Kruskal-Wallis H. values	Dunn* Cont.
	Limits	Mean	N	Limits	Mean	N		Limits	Mean	N		
1	500-575	541	17	504-578	547	8	58.5	433-493	472	24	36.08†	ABC
2	55.4-59.0	57.2	17	55.7-58.3	56.8	8	44	54.7-59.3	57.3	24	3.27	ABC
3	25.6-30.3	27.3	17	24.5-27.3	26.1	8	27.5**	21.4-25.4	23.7	24	35.40†	ABC
5	16.3-20.5	18.2	16	14.5-18.3	16.1	8	16**	11.6-16.5	13.9	24	34.24†	ABC
6	8.5-11.3	10.1	17	7.5- 4.9	8.9	8	18**	6.4- 8.8	7.3	24	36.28†	ABC
7	62.5-68.0	66.3	16	65.9-67.5	66.9	8	44.5	65.0-68.7	67.1	24	1.48	ABC
8	65.9-69.7	67.7	16	66.0-69.7	68.0	7	17.5	63.0-69.7	66.6	23	8.80	ABC
11	43.0-51.7	47.7	16	44.2-47.6	46.1	5	44.5	42.2-46.0	43.7	23	25.64†	ABC
13	48.3-58.4	54.2	16	48.6-52.9	51.6	8	25**	45.7-52.3	48.5	21	25.67†	ABC
14	18.4-20.8	19.7	17	17.2-19.6	18.6	8	23**	16.6-19.0	17.7	24	28.35†	ABC
16	21-25	23.3	13	22-25	23.8	8	44.5	24.0-27.0	25.3	22	17.27†	ABC
17	21-25	23.7	12	23-25	24.3	8	36.5	24.0-28.0	25.8	23	18.30†	ABC
18	44.0-50.1	46.0	17	46.4-49.5	47.7	8	56.5	43.1-48.3	45.8	23	20.93†	ABC
22	21-24	22.7	9	21-23	22.4	8	29.5	23.0-29.0	26.1	22	27.33†	ABC
23	20-25	22.8	9	22-24	22.5	8	29.5	23.0-28.0	25.9	21	28.92†	ABC
26	46.0-50.4	47.8	16	46.8-47.8	47.3	4	30	44.6-54.0	48.9	21	5.75	ABC
28	84.6-90.5	87.1	15	83.8-87.1	85.3	8	16.5**	82.5-87.0	84.9	21	21.33†	ABC
30	11.7-17.1	14.1	16	12.6-15.7	14.2	8	36.5	12.5-17.3	14.6	22	5.16	ABC
31	19.7-26.3	22.8	17	20.6-22.8	21.2	8	32	20.5-24.0	22.5	23	6.84	ABC
32	13.7-19.3	16.6	17	14.4-16.6	15.4	8	32	14.3-18.8	16.5	24	6.57	ABC

* Letters underlined together do not contrast significantly.

** Significant in a two-sided test at $\alpha = 0.02$.

† Significant in a two-sided test at $\alpha = 0.01$.

including *T. aduncus* (Ehrenberg, 1832), *T. absulam* (Ruppell, 1842), *T. catalania* (Gray, 1862) and *Delphinus gadamu* Owen, 1866.

Together with other described species (Hershkovitz, 1966) it has long been suspected by past and modern authors that these species are all synonymous under the specific name of *T. aduncus* though they lacked the confirmatory material. The variation within the present series of species A could provide a means of examining both the status of these species and the specific identity of species A.

In table 10 the published characters of *T. aduncus*, *T. catalania*, *T. absulam*, and *D. gadamu* are compared with those of species A which are considered taxonomically important. Cranial measurements of the types of *T. catalania* and *T. absulam* are taken from True (1889) and the external measurements of *T. catalania* from Gray (1865), while those of *T. aduncus* are taken from True's (1914) translation of the type description. Characters of *D. gadamu* are from Owen's (1866) original description, which refers to the type specimen (British Museum catalogue number 1477b). Skull measurements however are those of a second specimen (cat. no. 1477a) apparently received with the type of *D. gadamu* and listed by True (1899).

The comparison is limited by the lack of published data on these type specimens; on the available evidence there is little against conspecificity of all the compared forms except one or two extralimital proportional measurements. The counts of teeth in the lower jaw strongly suggest that they are in fact conspecific, for all counts, except that of *T. catalania* (1391b) which is limital, distinguish these specimens from *T. truncatus* of British waters, but lie within the limits of species A.

True (1899, 1914) also distinguished *T. absulam*, *T. catalania* and *T. truncatus* on differences in colour pattern. *T. absulam* was described as having dark sea-green upper parts and a spotted belly, while *T. catalania* and *T. truncatus* had lead-coloured upper parts; the belly of *T. catalania* was also described as spotted while that of *T. truncatus* was not.

These differences can be interpreted in terms of the variation seen within the present South African material. Owing to the rapid overall darkening of specimens soon after death, the material discussed is limited to four fresh species A specimens (PEM 1516/00, 1517/61, 1517/83 and 1517/96) and one fresh South African *T. truncatus* (PEM 1515/74). All of these animals were photographed within an hour of death, with the exception of PEM 1517/83 which died in captivity at an unknown time during the night, and was photographed early the following morning.

The colour pattern variation in these specimens can be analysed most conveniently by separating the components of the patterns into the component systems proposed by Perrin (1972). The two major systems are illustrated in fig. 3. The darkly pigmented dorsal cape system is comprised of the upper surface of the beak, the anterior part of the lower jaw, the bridle from the eye and from the blowhole to the apex of the melon, the cape itself broadening posteriorly to a maximum at the level of the anterior insertion of the dorsal fin and terminating mid-dorsally posterior to the fin, the dorsal fin itself and the flukes. Superimposed on the dorsal cape system is the dorsal field overlay, which is laterally more extensive but slightly paler than the dorsal cape system. The dorsal field overlay covers the entire dorsum, extending ventrally to approximately mid-depth on the body. Posteriorly it extends further to meet in the ventral midline posterior to the anus. In addition a broad flipper stripe runs from the eye to the insertion of the flipper and thence includes both surfaces of the flipper.

Perrin (1972) considered that variation in *Tursiops* pigmentation was primarily the result of variation in the extent and darkness of the dorsal field overlay. The present material tends to confirm his conclusions. In three specimens the dorsal field overlay is evenly pigmented (PEM 1515/74, 1516/00 and 1517/96). In two others which were caught from the same school (PEM 1517/61 and 1517/83) the pigment is laid down in numerous closely set streaks and spots giving a streaked appearance to the animal laterally. The degree and form of the ventral extension of the

TABLE 10. Comparison of characters of species A with those of *Tursiops aduncus*, *T. absulam*, *T. catalania* and *Delphinus gadamu*

	Species A South Africa		<i>T. aduncus</i> (Ehrenberg) TRUE, 1914		<i>T. catalania</i> (Gray) GRAY, 1865, TRUE, 1889 syntypes		<i>T. absulam</i> (Rüppell) TRUE, 1889		<i>D. gadamu</i> , Owen OWEN, 1866 TRUE, 1889 type BM 1477a	
	Limits	N	type	BM 1391a	BM 1391b	type	type	type	type	type
Total length (mm)	2020-2540	17	1830	2286	2057	1949	2083	—	—	—
Length of beak (% total length)	4,7-6,0	17	—	—	—	—	—	—	—	—
Condylobasal length (mm)	433-493	24	432	434	413	460	—	—	—	—
Rostrum, basal width (% CBL)	21,4-25,4	24	—	23,2	25,2	20,0*	—	—	—	—
Rostrum, width midlength (% CBL)	11,6-16,5	24	10,3	14,1	14,8	14,3**	—	—	—	—
Pre-orbital width (% CBL)	41,0-45,8	23	—	—	—	—	—	—	—	—
Orbital width (% CBL)	42,0-46,0	23	—	42,6	45,8	40,7	—	—	—	—
Length, upper tooth row (% CBL)	43,1-48,3(R) 43,6-49,8(L)	23	—	49,0	48,4	—	—	—	—	—
No. of teeth, lower jaw	23-29(R) 23-28 (L)	22	22 + 25	25 + 25	23 + 23	26	27 + 28	—	—	—
No. of vertebrae	59-62	9	—	—	—	61	—	—	—	—

*given as 23% by True (1914)

**given as 14,8% by True (1914)



Plate 6. Illustrating variation in the extension of the Dorsal Field Overlay as a series of spots onto the ventral surface of group A specimens. (a) PEM 1517/61, adult female from Port Elizabeth; (b) PEM 1516/33, adult female from Durban.

overlay on to the ventral surface is very variable. In PEM 1516/00 even, pale-grey pigment extends under the lower jaw and throat meeting mid-ventrally, and forming the anterior margin of a sharply demarcated M-shaped throat patch (plate 1). The apex of the M is extended posteriorly as a discontinuous mid-abdominal streak. In the other four specimens this throat patch is hardly discernible at all, as the slight darkening of the ventral surface of the lower jaw is not sharply demarcated from the white of the belly. The dorsal overlay extends ventrally to the midline between the flippers as a series of widely-spaced light grey spots in PEM 1517/83 and 1517/96, while in 1517/61 the spots extend to the ventral midline between the flippers and the umbilicus (plate 6a).

The final stage in the ventral extension of the dorsal overlay as a series of scattered spots, is found in two specimens of species A (PEM 1517/60 and 1516/33) in which the entire ventral surface between the flippers and the anus was covered in dark spots of varying size (plate 6b). Although neither of these specimens was fresh and had blackened dorsally, the spots were quite clear.

In fresh animals, the colour patterns of the South African specimens are composed of different intensities of lead-grey pigment, on a white to off-white background, as in fig. 3. In the living animal the ventral surface may be tinged with pink owing to vasodilation of surface blood vessels. Soon after death, however, the grey pigment rapidly darkens and eventually turns purplish-black in the sun, so that most stranded animals appear black dorsally and off-white ventrally. Later the ventral surface becomes purplish owing to blood seepage. The illustration of the type of *T. absulam* (True, 1889) presents such an appearance, suggesting that this animal had been dead for some time before colour notes were made. Further, in Rüppel's (1845) description of the internal organs, he noted that the spleen was emerald green in colour, and that the reniculi of the kidney were also greenish; these colours suggest that a certain amount of decomposition had already taken place prior to his examination. Thus Rüppel's description of the external coloration as dark sea green dorsally and whitish-flesh coloured ventrally can not be accepted as the normal colour pattern of *T. absulam*. Though most of the "non-fresh" animals examined in this study were purplish-black dorsally, one decomposing but entire specimen of *truncatus* from Durban (PEM 1516/06) had a slight greenish tinge to the dorsal surface, owing to numerous green patches 10–15 mm in diameter on the pigmented areas of the body. The origin or cause of these patches is unknown.

The colour pattern of *D. gadamu* illustrated by Owen (1866) resembles that illustrated in plate 6b for PEM 1518/33.

The colour patterns described by McGillivray (Gray, 1865) of the syntypes of *T. catalania* were both of freshly harpooned animals. The larger of the two animals (B.M. 1391a) is described as "very light lead-coloured above and on the sides, gradually passing into the dirty leaden white of the lower parts which were covered (as also the flippers) with longitudinally elongated blotches of dark lead-colour". The smaller of the two specimens (B.M. 1391b) was lead-coloured dorsally, and whitish ventrally. The sides were marked with small oblong spots of the same colour as the back. No mention is made of ventral spots. Equivalents of both these colour patterns are found in the South African species A material.

Until such time as larger series of specimens can be collected at the type localities of *T. absulam*, *T. catalania* and *T. aduncus* and *D. gadamu*, their true status will be in some doubt. Bearing in mind the variability of the South African material of species A it seems unlikely that these forms represent more than one species. The present writer therefore concurs with previous authors in regarding them and the South African species A as conspecific, for which the earliest available name, despite its poor type description, is *Tursiops aduncus* (Ehrenberg, 1832).

Identity of additional material

The identity of 24 additional specimens omitted from the taxonomic treatment can now be

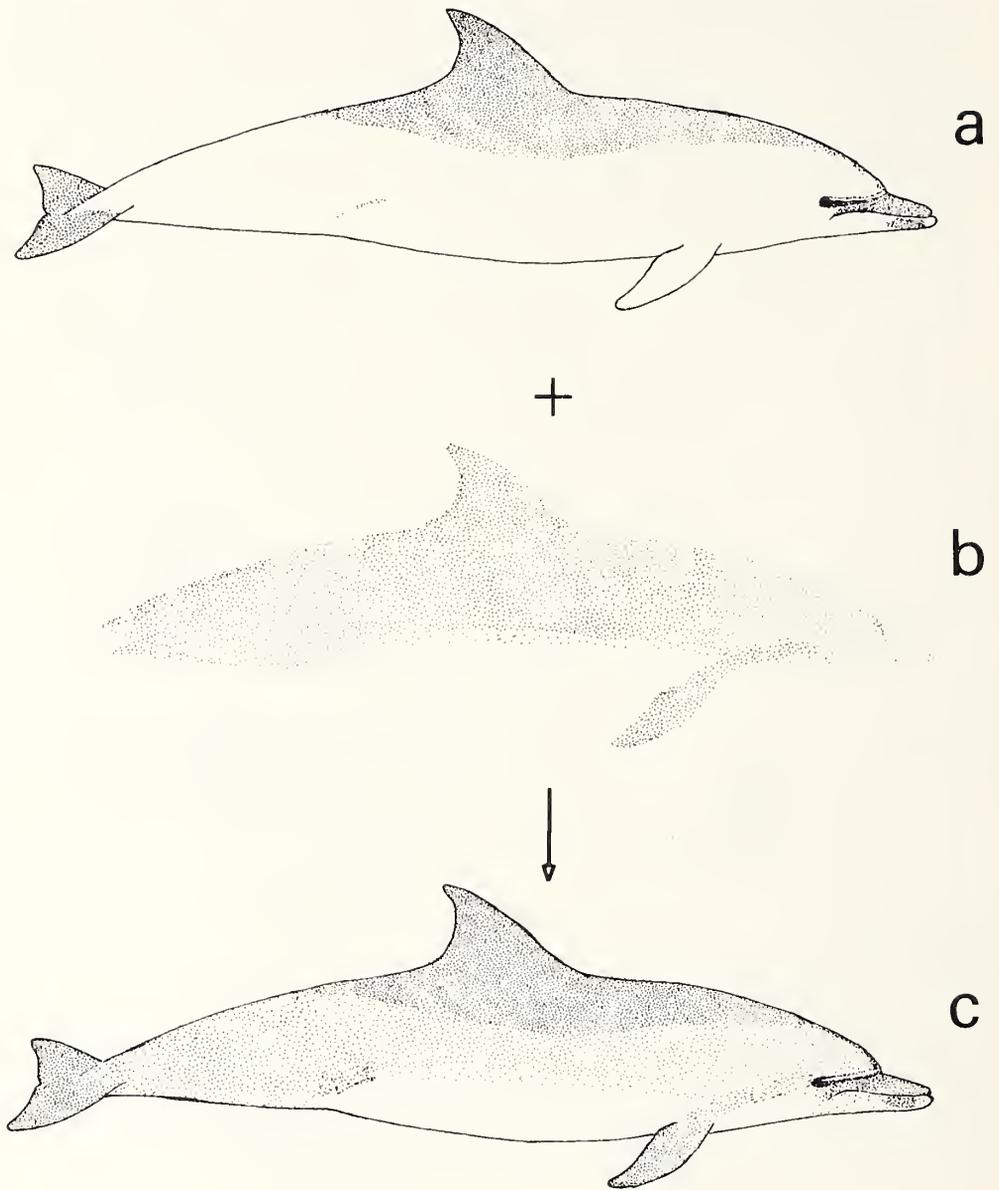


Fig. 3. Illustrating the components of (a) the Dorsal Cape system and (b) the Dorsal Field Overlay, which in combination form (c) the basic colour pattern observed in *Tursiops aduncus* (after Perrin, 1972).

established on the characters separating South African *T. truncatus* and *T. aduncus*. Since many of these specimens are young or neonatal animals, characters based on proportional measurements, have been avoided where possible. Further details concerning these specimens are given in table 17 of the appendix.

In table 11, all but one of the specimens, for which the mandibles were missing, possessed numbers of mandibular teeth within the range of *T. aduncus*. Twelve of those for which data were available conformed to *T. aduncus* on skull characters, while a further three partially conformed on one character of the four. Four specimens partially conformed to, or differed from *T. aduncus* in more than one character; the identity of these four specimens is examined further in table 12 on the basis of cranial measurements.

All of these measurements lie within the range of values found for South African *T. aduncus*, though some (marked with * in table 12) lie within the range of overlap between *T. aduncus* and *T. truncatus*. A combination of the characters in tables 11 and 12 however suggest that these four specimens are *Tursiops aduncus*, and are included as that species in the biological notes where applicable.

There are three other *Tursiops* records for which skeletal material is not yet available, and therefore can not be identified according to the skull characters used above. However the records are important in the distribution pattern and are tentatively identified on the available data kindly supplied by Dr. P. B. Best.

On 3 July 1975 six *Tursiops* of a school of about 40 were netted off the beach at Walvis Bay, South West Africa. Of these, two males over 3 m in length, and a female and calf were released. A second female 2,93 m in length was released a few days later. The last animal, a female 2,43 m in length, measured 390 mm from tip of snout to eye, allowing an estimate of the beak length to be made from a photograph of the head as 113 mm (4,7 per cent body length). On 9 October 1975, a 2,78 m female *Tursiops* stranded at Walvis Bay. The length of the beak was 125 mm (4,5 per cent body length) and there were 21 erupted teeth in each lower jaw. These data are consistent with those given for South African *T. truncatus*.

On 29 January 1974 a 2,25 m male *Tursiops* was collected at 33° 19' S, 43° 51' E, on the Walter Shoal some 950 km S of Madagascar. The beak length was 4,7 per cent of body length, and there were 20 erupted teeth in each jaw. The combined weight of the testes was 27 g, showing clearly that the animal was sexually immature (see further for notes on reproduction) and thus had not reached full length. On the evidence this animal is referred to *T. truncatus*.

BIOLOGICAL NOTES

Published biological data for *Tursiops aduncus* are practically non-existent. Whereas the information collected from the present material is by no means complete, it is offered as a basis on which a more comprehensive study of the biology of this species can be built. Since most of the specimens collected in this study are *Tursiops aduncus*, observations without a specific identification refer to this species. The few data relating to South African *T. truncatus* are specified where applicable.

Growth and development

The length at birth ranges from 838 to 1 120 mm, based on eight neonatal specimens. Five of these were stranded animals at length of 838, 1 002, 1 067, 1 080 and 1 120 mm. Three others were calves born in captivity at the Port Elizabeth Oceanarium, at lengths of 880, 930 and 1 092 mm. A ninth animal was stranded at a length of 1 150 mm; though the birth creases were still visible on its sides, there were numerous healed tooth scars on the skin, suggesting that it was not newly born, but perhaps a month old.

TABLE 11. Characters identifying additional material excluded from the taxonomic treatment. C conforms to, C? conforms partially to, and D differs from the characters as found in South African *Tursiops aduncus*.

Catalogue number	No. of mandibular teeth	Shape of lacrimal	Convexity of premaxilla	Posterior end of vomer	Squamosal of temporal fossa
1514/31	C(24,25)	—	C	C	C
1514/47	—	C?	C	C?	C?
1514/99	C(25,26)	C	C	C	C
1515/02	C(24,25)	C	C?	C	C
1515/08	C(25,24)	—	C	C	C
1515/23	C(26,25)	—	—	—	—
1515/24	C(25,26)	C	C	C	C?
1515/55	C(26,26)	C?	C	C	C?
1515/69	C(25,—)	C	C	C	C
1515/92	C(25,25)	—	—	—	—
1516/34	C(25 + x, 25 + x)	—	—	—	—
1517/35	C(24,24)	C	C?	D	C
1517/44	C(25,25)	C	C?	C?	C
1518/19	C(24,23 + x)	C	C	C	C
1518/26	C(25,25)	—	—	—	—
1518/43	C(25,26)	C	C	C	C
1518/57	C(26,26)	—	—	—	—
1518/99	—	—	C	C	C
1519/13	C(26,26)	C	C	C	C
1519/23	C(23,23)	C	C	C?	C
1519/26	C(24,25)	C	C	C	C
SAM 35062	C(25 + 1?,—)	C	C	C?	C
EL 40	C(25,—)	C	C	C	—
EL 873	C(25,26)	C	C	C	C

TABLE 12. Cranial measurements for four specimens of doubtful identity. Condylbasal length (no. 1) is given in mm. Other measurements are expressed as percentages of condylbasal length. Measurement numbers are keyed to table 4.

Measurement	1	3	4	5	6	9	18	19	36	37
PEM 1514/47	472	24,4	16,5	13,6	8,1*	44,1*	43,9	44,9	9,7	9,1
PEM 1515/55	466	22,3	16,5	13,3	6,7	41,8	—	—	10,3*	9,4
PEM 1517/35	433	21,9	16,9	14,3	7,6*	42,3	43,4	43,4	10,4*	9,7*
PEM 1517/44	430	24,7*	15,6	12,8	7,4	44,7*	—	—	9,8	8,8

*Measurements within the range of variation for *T. aduncus* and *T. truncatus*.

The length at birth in northern hemisphere *T. truncatus* varies widely from 980 to 1 260 mm (Harrison *et al.*, 1969), and the recorded lengths for *T. aduncus* probably represent normal variation. It is apparent that *T. aduncus* is slightly smaller than *T. truncatus* at birth.

Information on post-natal growth is scanty owing to the uncertainty in absolute age determinations from dentine layer counts. The most recent study by Sergeant *et al.* (1973) supports earlier work indicating that one dentine layer is deposited per year in *T. truncatus*. The only South African specimen for which age is partially known is the female *T. aduncus* "Haig" (PEM 1516/00) held captive at the Port Elizabeth Oceanarium for eight years. Her age at capture was unknown but the small size suggested she was subadult. Examination of the teeth showed 13 dentine layers, indicating an accumulation rate of less than two layers per year. With the assumption that the accumulation rate is an integer (Sergeant *et al.*, 1973) this rate must be one layer per year. Until further known-age animals become available, and a better understanding of the mechanism of layer formation is gained, it has been assumed that *T. aduncus* has a similar accumulation rate to *T. truncatus* of one layer per year.

As in other cetaceans (Bryden, 1972), growth in the first post-natal year in *T. aduncus* is rapid. A male calf, "Dolfie", born at the Port Elizabeth Oceanarium in December 1972 was estimated at a little over 1 500 mm in length at an age of 10 months. At 18 months he was measured at 1 950 mm in length, and at 35 months old he was 2 200 mm in length.

A stranded female, PEM 1518/43, with one and a fraction dentine layers measured 1 870 mm in length. Thereafter growth appears to slow considerably; a stranded male, PEM 1517/35, with two dentine layers in the teeth had a total length of 1 960 mm. One specimen of unknown sex, PEM 1515/55, however bears no relation to this outlined sequence, for though it measured 2 030 mm in length, the postnatal dentine in the teeth was extremely thin, appearing to represent less than one dentine layer. In strong transmitted light though, two or three very narrow light and dark zones can be seen within this layer. At present the age of this animal is indeterminate.

A female calf "Dolly", born in the Port Elizabeth Oceanarium in December 1968 was measured in July 1974 at 2 470 mm, aged 67 months, and in November 1975 at 2 550 mm, aged 83 months.

Evidence has been given in the initial group separation that specimens with completely obliterated tooth pulp cavities are more than likely to be physically mature. On this basis the maximum length attained in South African *T. aduncus* is 2 240–2 540 mm with a mean of 2 412 mm in five males, and 2 310–2 465 mm with a mean of 2 371 mm in four females.

Though on average the females appear to be slightly smaller than the males, the largest female specimen recorded, PEM 1517/96, was only 20 mm shorter than the largest male.

It was not possible to determine the maximum age attained, or the age at physical maturity owing to the limitations of the ageing method. However laminations which occur in the cement of the tooth can be counted in very thin ground sections. It has been suggested by Sergeant (1962) in work on the pilot whale *Globicephala melaena* that these layers could be used for ageing after the pulp cavity has closed. Some 47 cement layers could be counted in the teeth of the largest male, PEM 1517/83, 2 540 mm, but until more information is available on the accumulation rate of cement layers, little can be inferred from such counts.

Total weights and organ weights for seventeen *T. aduncus* and two *T. truncatus* from South Africa are listed in table 13; the total weight (kg) of each specimen is plotted against total length (cm) on a logarithmic scale in fig. 4. The relationship between weight and length must be interpreted with caution, for the majority of the specimens were either stranded or animals which died from diseases in captivity. Five netted animals (PEM 1517/61, 1516/33, 1517/69, 1518/98 and 1519/07) may be considered to have normal weight values. The variation in blubber and meat weights in these five animals is considerable. It is clear though that two females, PEM 1516/00 and 1517/60 which were visibly emaciated, have low meat weight values, while one male, PEM 1515/83, has a low blubber weight value. As there are too few females, a regression

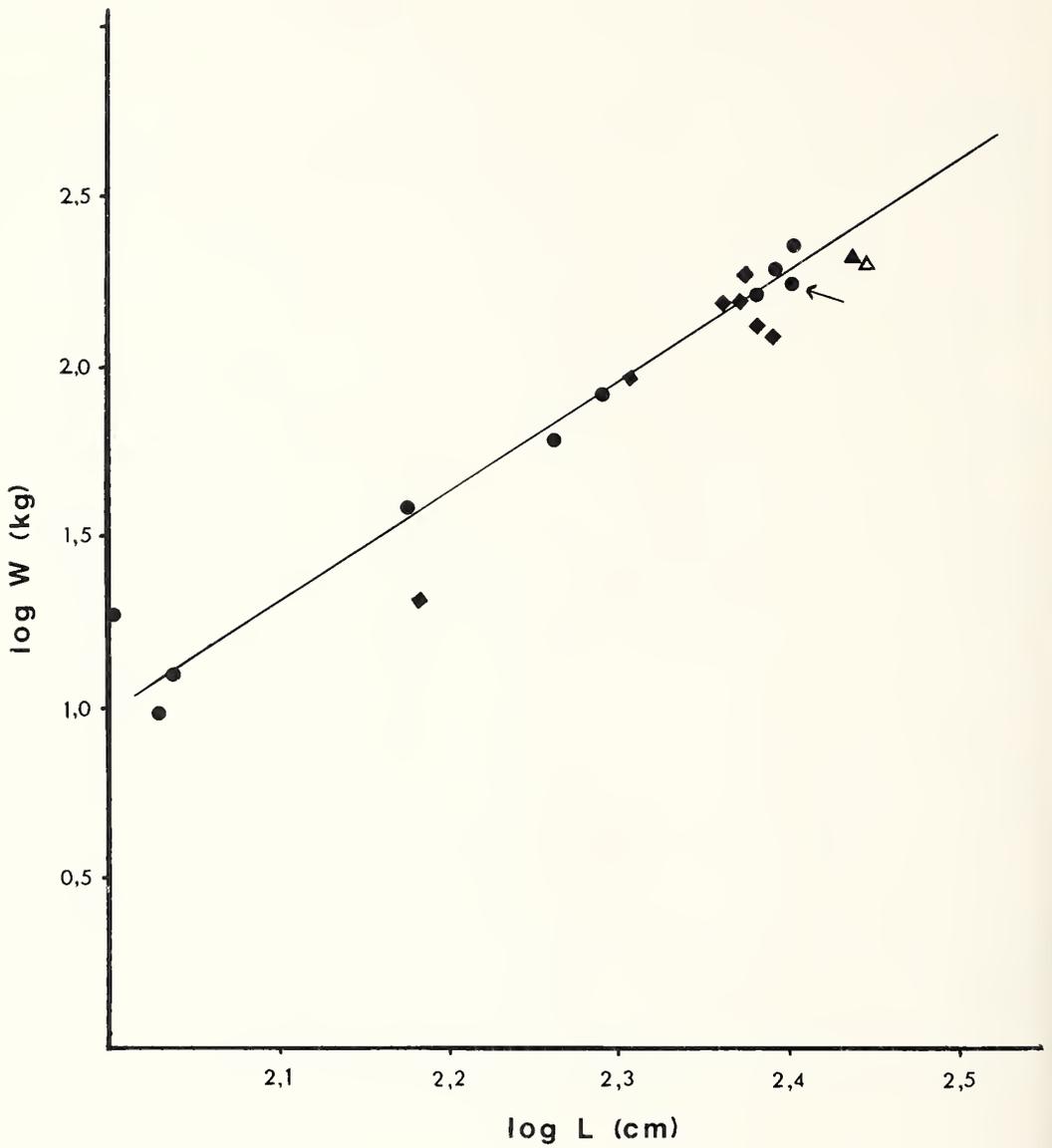


Fig. 4. Illustrating the length/weight relationship for ten male (●) and seven female (■) *Tursiops aduncus*, and one male (▲) and one female (△) *T. truncatus* from South African waters. The regression line is based on nine *T. aduncus* males (excluding the arrowed specimen) and is fitted from the equation $0,3105 \log W + 1,692 = \text{Log } L$ where $W = \text{weight (kg)}$ and $L = \text{length (cm)}$.

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line has been plotted in fig. 4 for nine *T. aduncus* males only, excluding PEM 1515/83. It is possible that other underweight animals are included in this regression, and this factor should be considered in comparing the weight/length relationship of the present series with others.

The equation for the regression line in fig. 4 was calculated by the method of least squares and may be expressed as: $0,3105 \log W + 1,692 = \log L$ ($r = 0,98$) where w = weight (kg) and L = total length (cm).

In addition to the few data presented in table 13 for relative organ weights, the visceral weight in PEM 1517/69 was 13,6 per cent of body weight, while the spleen weights for PEM 1516/00 and 1515/83 were 0,037 per cent and 0,018 per cent of body weight respectively. The length of the intestine in one animal PEM 1519/07 was 19,3 m from pylorus to anus (818 per cent body length).

TABLE 13. Body and organ weights for South African specimens of *T. aduncus* and *T. truncatus*. Total body lengths are in mm, and total body weights in kg; other weights are percentages of total body weight.

Cat. No.	Sex	Total Length	Total Weight	Blubber*	Meat**	Heart and Lung	Heart	Liver	Kidney	Remarks
<i>Tursiops aduncus</i>										
1518/26	♂	1002	13,4							Stranded. Neonate.
1515/08	♂	1067	9,8							Stranded. Neonate.
1515/02	♂	1092	12,5							Born in captivity.
1519/23	♀	1150	20,9							Stranded.
1516/34	♂	1500	39,4	22,4	31,6	3,9	0,63	1,3	0,60	Stranded.
1518/57	♂	1840	49,0							Stranded.
1518/35	♂	1955	83,5	16,6						Stranded.
1518/98	♀	2020	92,1	19,0	32,5					Caught in shark nets.
1517/61	♀	2310	152,4	19,3	29,0					Netted deliberately.
1516/33	♀	2350	156,5	14,5	39,7	3,1		2,3	0,57	Caught in shark nets.
1519/07	♀	2360	181,5	19,3	35,8					Caught in shark nets.
1516/00	♀	2375	136,1	18,6	16,8		0,43			Died in captivity. Emaciated.
1517/69	♂	2390	159,7	15,1	32,1					Caught in shark nets.
1517/72	♂	2440	192,8							Died in captivity.
1517/60	♀	2465	121,6	15,3	23,1					Stranded. Emaciated.
1515/83	♂	2490	174,6	10,9	26,2	4,6	0,65	2,5	0,91	Stranded.
1517/83	♂	2540	226,4							Died in captivity.
<i>Tursiops truncatus</i>										
1516/06	♂	2720	213,2	12,7	30,4	3,3	0,75	2,0		Stranded.
1515/74	♀	2795	201,9	13,7	26,7	3,5	0,72	2,5	0,76	Stranded.

*Weight of blubber removed posterior to the head.

**Weight of epiaxial and hypaxial filets only.

Reproduction

Although direct observation of reproductive events in free-ranging cetaceans is extremely difficult and in most cases impractical, the pattern of these events can be observed indirectly in the morphology of the reproductive organs.

Female cetaceans exhibit a phenomenon which has not yet been observed in any other mammal. The corpora which form after ovulation do not disappear from the ovarian tissue in

mysticetes (Slijper, 1966). In odontocetes the situation is not completely clear. Harrison (1949, *in* Slijper, 1966) considered that corpora in the ovaries of the pilot whale *Globicephala melaena* eventually regressed to a size where they were no longer visible macroscopically. Sergeant (1962) however, in a study of the same species, considered that no corpora disappear, or that only a small percentage of corpora albicantia of ovulation eventually disappear. Evidence presented by Harrison *et al.* (1972) indicates that corpora albicantia of pregnancy can persist for at least ten years and probably for life in *Tursiops truncatus*. Thus examination of the ovaries can provide a considerable amount of data on the reproductive biology of an individual or a population.

The only delphinid for which data on male maturation and testes development are reasonably complete, is the pilot whale *Globicephala melaena*, though the data given by Harrison (1969) and Harrison *et al.* (1972) suggest that the pattern of development in other delphinids is similar. In the pilot whale, Sergeant (1962) showed that the testes increased continually in weight with age. At a body length of approximately 3.9–4.2 m the rate of testis growth increased; he considered that this change in growth rate denoted the onset of sexual maturation. Functional maturation, however, as judged by the presence of sperm in the epididymis, occurred at a mean body length of 4.9 m. There is little evidence that the delphinid testis increases in size seasonally, and though Sergeant (1962) suggested that spermatogenesis was depressed in the pilot whale during September and October, cyclic activity in the testis has not yet been convincingly demonstrated (Harrison, 1969). Though there is no evidence that adult male *Tursiops* are fertile throughout the year, or that they exhibit seasonal activity, plasma testosterone levels in captive males show peaks at times of the year which correlate fairly well with other reproductive events (Harrison *et al.*, 1972).

Females

Reproductive material was collected from six female *T. aduncus* and one *T. truncatus*. The preserved ovaries were separated from connective tissue, weighed, measured, and sliced into sections up to 3 mm thick with a scalpel. Corpora lutea and corpora albicantia were counted and measured macroscopically. Data from the ovaries are presented in table 14. A number of tentative conclusions can be drawn from this extremely limited material.

The length of females at sexual maturity lies between 2 020 and 2 310 mm, based on the presence of corpora albicantia in the ovary. A closer estimate of this length may be obtained indirectly from the length at physical maturity. For instance Laws (1956, *in* Bryden, 1972) showed that the length of the female at puberty is approximately 86 per cent that of the physically mature animal in many marine mammals. Sergeant *et al.* (1973) estimate this figure at 90 per cent in *T. truncatus* from Florida. In the present study three of the females (table 14) are known to be physically mature, from the fused state of the vertebral epiphyses, at lengths of 2 350 mm, 2 360 mm and 2 465 mm, while a fourth is considered to be mature at a length of 2 310 mm. The estimated lengths at puberty of these four females range from 1 990 to 2 120 mm with a mean of 2 040 mm (86%) and 2 080 to 2 220 mm with a mean of 2 134 mm (90%). These ranges are well within the range obtained directly.

A comparison of the lengths of these females with that of the captive female Dolly is intriguing, for at seven years of age she is, at 2 550 mm in length, one of the longest *T. aduncus* on record, surpassed only by her sire, which measured 2 580 mm in length. At this age, Dolly should be close to sexual maturity (see further in this section), when growth is not complete, but would potentially add a further 10 per cent to her body length. It is possible that the relatively easy life in captivity with its ample food supply increases or accelerates normal growth, and that growth studies on captive animals may not be representative of free-ranging animals.

Comparison of the number of corpora albicantia with their sizes indicate that corpora regress

ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS *TURSIOPS* SPECIESTABLE 14. Ovarian data from nine *Tursiops aduncus* and one *T. truncatus* females from South African waters.

Cat. No. (PEM)	Total length (mm)	No. of dentine layers	Ovarian		Corpus luteum diam. (mm)	Corpora albicantia diam. (mm)	Total no. of corpora	Comments
			Length (mm)	Weight (g)				
<i>Tursiops aduncus</i> 1519/23	1 150	1	20	0,75	0	0	0	Neonate. Few deep sulci, otherwise smooth.
			20	0,75	0	0		
1518/43	1 870	1	33	2,3	0	0	0	Sexually immature. Smooth, unscarred.
			35	2,4	0	0		
1518/98	2 020	3,5	35	1,6	0	0	0	Sexually immature. Smooth, unscarred.
			35	1,6	0	0		
1516/00	2 375	13 left right	25	6,6	0	12:9	2	C. albicantia prominent on surface. Small follicles up to 2 mm in dia.
			30	3,0	0	0		
1517/60	2 465	10 + left right	33	6,6	0	9:9:7	3	Three C. albicantia promi- nent on surface. Few follicles up to 1 mm diam.
			30	4,6	0	0		
1519/07	2 360	11 + left right	—	3,9	0	12,5	4	Smooth surface. Few small follicles. Corpus luteum of 9,9 g; solid luteal tissue. Lactating.
			—	14,4	28	7:4		
1517/96	2 520	11 left right	—	20,8	28	9,5:9:9:6,5	5	Corpus luteum of 10 g, jellyfilled centre. Four large follicles up to 5 mm diam. Smooth surface, few fol- licles up to 2 mm diam. Lactating.
			—	3,5	0	0		
1516/33	2 350	10 + left right	27	—	0	9,5:9,5:8:8:7,5 7,5:7,5:7:6	9	Poorly preserved. Few follicles up to 2 mm diam.
			21	—	0	0		
1517/61	2 310	11 + left right	28	2,8	0	7,5:6,5:4,5:4,5: 4:2,5:2,5:2:2	10	Eight corpora visible on surface. Few very small follicles. Lactating.
			27	1,7	0	0		
<i>Tursiops truncatus</i> 1515/74	2 795	7	55	5,2	0	0	0	Sexually immature. Nume- rous follicles up to 2 mm. Largest few up to 2,5 mm.
			61	4,3	0	0		

continually as they accumulate. It is still not known whether corpora eventually regress to a size where they are no longer visible macroscopically (Slijper, 1966). The number of corpora in the ovaries of PEM 1517/61 suggest that corpora remain visible for a considerable period; however, while the smallest corpora measured in the left ovary of this animal may represent the final size of a corpus albicans, the fact that this animal was lactating heavily when caught indicates that she was still reproductively active, and that further regression of corpora could occur as new ones accumulate.

The size of corpora in the physically mature female PEM 1517/60 indicate that no more than three ovulations had occurred in this animal; the presence of some milk in the mammary gland shows that at least one of these ovulations was relatively recent. The ovaries of the physically mature PEM 1519/07 indicate a similar situation. By comparison the younger female PEM 1517/96 has a total of five corpora, showing that either the age at sexual maturity is variable or that ovulation rates vary in individuals; it seems likely that differences in individual ovulation rates are more important in determining the accumulation rate of corpora in an individual than variation in the age at which sexual maturity is attained, for this latter variation is probably not more than two years. Sergeant *et al.* (1973) show that this variation is approximately two years in wild-caught *T. truncatus*.

PEM 1517/96 was both pregnant and lactating when she was examined, at the age of 11 years, assuming one dentine layer is deposited per year. Even if only two corpora in the ovary represent these two pregnancies, the animal would have been, at most, nine years old when she first ovulated. Though the history of the other three corpora is unknown, they indicate that sexual maturity occurred earlier than at nine years of age. Further, if each of these corpora represents one pregnancy, she would have ovulated for the first time at six or less years of age.

The history of the captive female "Haig" PEM 1516/00 is particularly interesting. She was captured on 16 October 1962 and held in the Port Elizabeth Oceanarium until her death on 25 November 1970. Until November 1967, when two bulls were placed in the pool, she had had no contact with male *Tursiops* since her capture. She gave birth to a male calf, PEM 1515/02 on 22 October 1969, and a female calf PEM 1515/92, on 26 October 1970. The first of these survived for about five minutes; the second calf was born at night, and the mother was seen carrying its body the next morning. If the 13 dentine layers counted in Haig's teeth represent 13 years, she would have been five years old at the time of capture, and 11 years old when she first ovulated, as it is almost certain that both corpora in the left ovary represent the ovulations of the two pregnancies.

Though the absence of bulls, or the stress of Haig's capture and training may have suppressed ovulation, Sergeant *et al.* (1973) have presented evidence indicating that captive life only slightly delayed onset of sexual maturity in female *T. truncatus* from a mean of 10 years of age in wild animals to a mean of 12 years of age in captive females. If the same holds true for *T. aduncus*, by comparison with PEM 1517/96, Haig would have reached puberty at least two years, or more, prior to the introduction of males into the tank; yet there is no evidence of ovulation in this period. The inference is that ovulation does not occur spontaneously in the absence of males. The alternative, induced ovulation, which has already been suggested as the pattern of ovulation in captive *T. truncatus* (Harrison *et al.*, 1972) would seem to fit the limited evidence available for *T. aduncus*. The problem can only be adequately resolved when more data from animals of known history become available.

In five of the six sexually mature females the corpora are present in the left ovary only, and in three animals the left ovary is heavier than the right. The preponderance of activity in the left ovary prior to the right is a feature of a number of odontocetes (Harrison *et al.*, 1972), though these authors found corpora in the right ovary only, in three of eighteen *T. truncatus*. Similar variation should be expected in larger samples of *T. aduncus*.

The sample of five wild, sexually-mature female *T. aduncus* is too small to comment on the

frequency of pregnant females. Only one, PEM 1517/96, was found pregnant with a 445 mm male foetus on 29 July 1972. Three others, PEM 1517/60, 1517/61 and 1519/07 were lactating, indicating recent pregnancy. The two pregnancies of Haig are interesting since this is the first confirmation that pregnancy can occur in successive years. In three captive *T. truncatus* in Florida, successive births were always separated by two years, over periods of five, seven and eight years (Essapian, 1963).

A total of 369 days separate the births of Haig's two calves; after the death of the first calf, Haig carried the body for five days, during which time mating did not occur. Thus the gestation period of the second calf was a maximum of 364 days. Mating between Haig, Dimple (a second female) and the two bulls began within days of the bull's introduction into the tank in mid-November 1967. Dimple gave birth to a female calf Dolly, on 12 December 1968, indicating a gestation period of just over a year, though the precise date of conception is unknown. Tayler and Saayman (1972) give a figure of 342 days for this period, and 351 days for the gestation period of Haig's first calf, based on the onset of marked behavioural changes and increase in appetite. These figures are similar to those recorded for captive *T. truncatus* (Tavolga and Essapian, 1957). In the only birth observed to date, Haig's first calf was born tail-first in the normal cetacean pattern.

Stranded neonates of *T. aduncus* have been recorded in October (PEM 1518/26) in Natal, and in November (PEM 1514/31, 1515/08), January (PEM 1515/24), February (PEM 1519/13), March (PEM 1519/23) and June (PEM 1519/26) in the Eastern Cape. The 445 mm foetus of PEM 1517/96 is considered to be approximately mid-term (29 July) and thus would have been born in the summer months. In captivity, two calves were born to Haig in October, and two calves to Dimple in December at the Port Elizabeth Oceanarium. A third calf born to Dimple in November 1975 was thought to be still born and possibly slightly premature. These records show that births can occur throughout the year but predominate in the late spring and summer months. A similar protracted calving season occurs in *T. truncatus* (Harrison *et al.*, 1972).

The length of the lactation period is not known with certainty. One captive animal, born to Dimple, began taking fish from the age of six months; there is evidence, however, that suckling continued for a considerably longer period for at the age of 29 months she released a cloud of milky fluid considered to be milk from her mouth at the observation window (G. S. Saayman, pers. comm.). As this animal habitually presented various objects to observers at the window, her action was interpreted as being deliberate, and not an involuntary regurgitation of some other fluid. Tavolga and Essapian (1957) consider that suckling can continue up to 20 months in *T. truncatus*.

Dimple's second calf, born four years after the first, began taking fish at the age of 11 months, at a length of just over 1 500 mm. A stranded male, PEM 1516/34, 1 500 mm in length had the remains of fish bones in its stomach. As it stranded in October it is likely to have been between eight and 12 months old.

The quantity of milk seen in the cut mammary glands of four lactating females varied. Although volumes were not measured, they could be expressed in relative terms. Three females were considered to be lactating heavily (PEM 1517/96, 1517/61, 1519/07). The milk in PEM 1517/96 which was pregnant, was fairly thin and watery in consistency. The milk in PEM 1519/07 was thick, with a curdled appearance. One mammary gland in this animal measured 400 mm in length, 120 mm in width and 50 mm in depth; it weighed 1.24 kg. The mammary glands of PEM 1517/60 contained a small quantity of milk. One gland in this animal measured 300 mm in length from the anterior tip to the nipple and approximately 35 mm in greatest diameter.

The mammary gland of the sexually immature *T. truncatus* female, PEM 1515/74, measured 185 mm in length.

Males

Reproductive data were collected from 11 male *T. aduncus* and two male *T. truncatus*. Samples from the centre of the testis at mid-length were taken from five *T. aduncus* and one *T. truncatus* for histological examination. These were fixed in 10 per cent formalin and sectioned at 1μ thickness after embedding in wax. The sections were cleared and stained with haematoxylin and eosin. The diameters of 30 tubules were measured with a microscope eyepiece micrometer to obtain the mean tubule diameter. These data are summarised in table 15.

TABLE 15. Reproductive data for eleven *Tursiops aduncus* and two *T. truncatus* males from South African waters.

Cat. No. (PEM)	Total length (mm)	No. of dentine layers	Size of testis (mm)		Weight of testis (g)			Diameter of tubules (μ)	Comments
			Left	Right	Left	Right	Total		
<i>Tursiops aduncus</i>									
1518/26	1 002		60 × 8	40 × 8				33	Neonate Est. age 8-12 months
1516/34	1 500		51 × 10	60 × 10					
1518/57	1 840		64 × 19	67 × 16	9	9	18		
1517/35	1 955	2					16	243	Sperm present in tubules
1518/27	2 240	12+		280 × —	545	727	1 270		
1518/97	2 320	10+		250 × 85		745			
1517/69	2 390	11	215 × 64	203 × 79	357	308	665		
1517/72	2 440	17+	270 × 90	240 × 90	900	830	1 730		
1515/83	2 490	9	254 × 50	267 × 64	385	520	805	189	Sperm absent in epididymis. Few sperm in tub. Sperm numerous in tub. Sperm present in epididymis
1518/54	2 520	13+	220 × —	230 × —	670	760	1 430	252	Sperm in epididymis thin and watery. Sperm numerous in tubules
1517/83	2 540	10+	267 × 83	254 × 89	773	727	1 500		
<i>Tursiops truncatus</i>									
1517/77	2 605	4	78 × 18	76 × 25	12	19	31	47	Interstitial tissue broad, no sperm, immature
1516/06	2 720	11+	190 × 32	140 × 25					

The few data suggest there is relatively little change in testis size or weight in male *T. aduncus* up to a body length of 2 000 mm. On the basis of the few sperm in the tubules, but no sperm in the epididymis, spermatogenesis was beginning in PEM 1517/69 at the age of 11 years, assuming one dentine layer accumulates per year; a comparison of the combined testis weights of this male and PEM 1515/83 suggests that the latter animal was also maturing sexually at nine years of age, particularly as sperm was present in the epididymis. In older animals the weight of the testis is almost double that of the maturing animals, and while there is considerable variation in tubule diameter, active spermatogenesis, based on the numbers of sperm in the tubules, was occurring in all three animals examined histologically. Sergeant *et al.* (1973) found maturing male *T. truncatus* from Florida between seven and 15 years of age, and mature males of 12 or more years of age. More specimens are required to establish the limits in the lengths of maturing and mature males. On the present data, the smallest maturing male is 2 390 mm in length, but the smallest mature male, 2 240 mm in length, would presumably have been slightly smaller when maturing.

Little can be said concerning South African *T. truncatus* males at this point. The size of the testis and tubule diameter of PEM 1517/77, 2 605 mm total length, are intermediate between those given by Harrison *et al.* (1972) for *T. truncatus* from Florida 1 470 to 2 000 mm in length.

By comparison with PEM 1517/77, the present data on *T. aduncus* and figures quoted for *T. gilli* and *T. truncatus* by Harrison *et al.* (1972), the testis sizes of PEM 1516/06 suggest that it is maturing but not fully mature.

Food and feeding

Stomach contents were collected from 13 *T. aduncus* and two *T. truncatus*. Three other *T. aduncus* examined had empty stomachs. In four specimens of *T. aduncus* collected earlier in the study, stomach contents were either preserved entire in formalin prior to examination or the larger items only were removed piecemeal in the field for preservation in formalin. As a result many of the smaller identifiable items in the stomach, such as otoliths, were probably missed or dissolved during preservation. Stomachs from the other, later specimens were removed entire and the contents washed carefully into a tray for closer examination. Otoliths were separated and preserved dry or in 70 per cent alcohol.

Cephalopod beaks and fish otoliths are digested relatively slowly in cetacean stomachs, and are often the last remnants of particular prey items to be found (Fitch and Brownell, 1968; personal observations). The morphology of a cephalopod beak or fish otolith is characteristic, so that provided a comparative collection is available, stomach contents can be identified to a certain extent, on the basis of these remnant. In this study, beaks found in the stomachs of PEM 1516/33 and 1516/06 were identified by Mr. N. McLeod of the National Institute of Oceanography, Britain, while those found in the stomachs of PEM 1517/60, 1517/61, 1517/69 and 1517/77 were identified by Miss M. A. Roevelde of the South African Museum, Cape Town. Beaks in the stomachs of PEM 1518/98 and 1519/28 were identified by comparison with beaks in these previous samples. A comparative otolith collection was recently started at the Port Elizabeth Museum to assist in the identification of stomach contents, and though by no means complete yet, it has been of considerable help in the study.

Of the 13 *T. aduncus* with food remains in the stomach, six contained both fish and cephalopod remains, five contained fish only and two contained only cephalopods. Eight of the nine stomach contents examined after washing the stomach proved to contain fish remains, while four of these also contained cephalopod remains. The contents of nine *T. aduncus* and two *T. truncatus* stomachs are itemised more specifically in table 16.

The prey species which have been identified with reasonable confidence provide a broad outline of the feeding habits of *Tursiops* in Eastern Cape and Natal waters. The conclusions drawn from the data must be considered with caution, for many dolphins were stranded from unknown causes, which may have changed normal feeding patterns. Data from PEM 1516/33, 1517/61, 1517/69 and 1518/98 may be considered as normal as these four animals died accidentally.

Though there is no quantitative information on relative abundance of fish and cephalopods off the Eastern Cape, line and trawl catches give the impression that all the identified fish and *Loligo* found in *T. aduncus* stomachs are common to abundant in this region. In Natal, *Pomatomus saltator* is abundant in this region between August and November (Biden, 1930), the period in which PEM 1516/33 was netted (October). The wide variety of recorded species indicates that *T. aduncus* is catholic in taste, though perhaps it is no accident that many of these species are commercially-valuable food or angling species. In sum, it appears that *T. aduncus* is an opportunistic feeder taking any suitable prey as it is encountered.

The known habits of the prey species, which at present can only be inferred from effective methods of catching them by trawl or lines, or from observations while diving, suggest that *T.*

TABLE 16. Numbers of prey items recorded from stomach contents of nine *Tursiops aduncus* and two *T. truncatus* from South African waters.

	<i>T. aduncus</i>									<i>T. truncatus</i>		TOTAL
	PEM 1516/33	PEM 1517/60	PEM 1517/61	PEM 1517/69	PEM 1518/27	PEM 1518/43	PEM 1518/54	PEM 1518/98	PEM 1519/28	PEM 1516/06	PEM 1517/77	
Synodontidae								1				1
<i>Saurida undosquamis</i>												
Gadidae												
<i>Merluccius capensis</i>					2		1		22		1	26
Bothidae?												
4 (?) unidentified spp.				4								4
Soleidae												
<i>Austroglossus pectoralis</i>									1			1
Carangidae?							1					1
Pomatomidae												
<i>Pomatomus saltator</i>	1											1
Sciaenidae												
<i>Johnius sina</i>								6				6
Unidentified sp.								1				1
Pomadasyidae												
<i>Pomadasys olivaceum</i>			1					121	1			123
<i>Rhonciscus</i> sp.								1				1
Unidentified spp.				2								2
Sparidae												
<i>Pterogymnus laniarius</i>			4									4
<i>Lithognathus mormyrus</i>			2									2
<i>Pagellus natalensis</i>								18				18
<i>Sarpa salpa</i>						5						5
Denticidae												
<i>Cheimereus nufar</i>					1							1
Lepidopidae												
<i>Lepidopus caudatus</i>											6	6
Unidentified fish			3	4		1	1		19			28
Loliginidae												
<i>Loligo</i> sp.	24			2								26
<i>Loligo vulgaris</i> ?		10	13					5	26			54
Enoploteuthidae												
<i>Enoploteuthis</i> sp.										124		124
Enoploteuthid?											6	6
Sepiidae												
<i>Sepia</i> sp.			1*					1				2

*The upper and lower beaks of a *Sepia* were vomited after capture by an adult male caught with PEM 1517/61.

aduncus feeds primarily on benthic or reef-dwelling species. Information on the maximum depths to which these species occur is limited, but the limits given by Barnard (1925) and Smith (1965) for some of the recorded fish species do not exceed 150 m in depth, except in the case of *Merluccius capensis*. *Loligo* is taken commonly in trawls at 60–70 m in Eastern Cape waters (personal observations). Roeleveld (*in litt.*) suggests that the *Sepia* beaks recovered from PEM 1517/61 and its school companion (PEM 1517/72 or 1517/83) were from one of the larger species such as *S. officinalis*, *S. papillata* or *S. simoniana*, which are not recorded beyond 200m in depth (Roeleveld, 1972). The present limited data thus suggest that *T. aduncus* feeds over the continental shelf, perhaps to a depth of 200 m.

Most of the prey items in *T. aduncus* stomachs were estimated at under 200 mm in length. Larger items however include three of the Bothids, which were reasonably complete, at lengths of approximately 230, 300 and 350 mm, and all four *Pterogymnus* otoliths were larger than those of a specimen 230 mm in length. The largest items were one *Merluccius* from PEM 1518/27 and one from PEM 1518/54 whose otoliths matched in size those of fish 600 mm in total length. The stomach contents of PEM 1519/28 include one *Austroglossus* estimated at 310 mm in length, six *Merluccius* up to 500 mm in length, and 16 *Merluccius* up to 500 mm in length, and 16 *Merluccius* under 250 mm in length.

The presence of *Enoploteuthis* and Enoploteuthid (?) squids in the stomach of both *T. truncatus* is interesting, for squids of this family are oceanic, though at least one species may occur over the continental shelf (Clarke, 1966). The presence of six *Lepidopus caudatus* in PEM 1517/77 suggests feeding in an area where this species is common; in South African waters they have been recorded from the surface to a depth of 400 m (Barnard, 1925). In European waters the majority are caught offshore in depths of 100 to 250 m (Wheeler, 1969) though they occur from the surface to 400 m depth. If this fish has similar habits off South Africa, it suggests that *T. truncatus* may feed further off-shore than *T. aduncus*. The depth to which *truncatus* hunts is unknown, though the single *Merluccius* otolith in the stomach of PEM 1517/77 indicates that feeding may occur on or near the bottom.

The *Lepidopus* otoliths recovered from 1517/77 vary in size but the largest pair, together with a set of jaws, were slightly larger than those from a specimen 1 002 mm in standard length and weighing 0,7 kg.

Parasites

The parasitic cirripede *Xenobalanus globicipitis* was found on two *T. aduncus* captured from the same school; on one animal PEM 1517/61 specimens were found on the leading edge of the right flipper (1), the tip of the dorsal fin (1), and the trailing edge of the flukes (6). Barnard (1924) recorded four specimens of this barnacle from the tail of *Tursiops catalaniae* (sic) caught in Natal in 1919.

Macroscopic examinations of 13 *T. aduncus* and two *T. truncatus* were made for internal parasites. In all of these animals the blubber and stomach cavity were checked; other organs including the lungs, liver, kidneys and intestines, were not always examined, so that the frequency of parasite occurrence in these organs is not known.

A few cestode cysts were found in three *T. aduncus*, PEM 1515/83, 1518/27 and 1519/07, localised in the blubber of the anal region. Though these were not identified, they are probably one of the *Phyllobothrium* species, which occur frequently in odontocetes, and are restricted to the blubber in cetaceans (Dailey and Brownell, 1972). These authors state that cysts of *Monorygma* are also common in cetaceans. They are larger than those of *Phyllobothrium* and are always found internal to the blubber. It is probable then that a cestode cyst approximately 20 mm in diameter found retroperitoneally near the rectum of PEM 1517/61 is referable to *Monorygma*.

Nematodes were found in the stomachs of eight of nine *T. aduncus*; the hosts measured between 2 240 and 2 520 mm in total length. There appeared to be no correlation between the age of these hosts and a qualitative estimation of the parasite load. It is interesting that no nematodes were found in the stomachs of four *T. aduncus* between 1 500 and 1 955 mm in total length, which from stomach contents, were known to have been eating fish, and in one case cephalopods.

Nematodes were taken from the stomachs of both *T. truncatus* PEM 1517/77 and 1516/06. Those from the latter animal were kindly identified by Dr. A. Verster, Division of Veterinary Services, Onderstepoort, as immature females of the genus *Anisakis*, which occurs widely in marine mammals.

Unidentified lungworms were recorded in 2 *T. aduncus*. In PEM 1515/83 a few thin elongate nematodes were found in the bronchioles of the lungs. In PEM 1516/34, 1 500 mm in total length, lungworms were found in one lung only, confined to several localized, purulent areas, 10–20 mm in diameter, on the pleural surface of the lung.

Diseases, injuries and mortality

Information on diseases in South African *Tursiops* is restricted to observations on animals in the Port Elizabeth Oceanarium and the results of post-mortems on captive animals performed by veterinarians, and incidental observations of stranded animals.

Erysipelas

Two adult male dolphins PEM 1517/72 and 1517/83, caught on 9 December 1971, died of *erisypelas septicaemia* after two and six months in captivity. Externally both animals showed numerous healed scars and some deep seated swellings bulging under the epidermis which are thought to be healed wounds. The posterior half of the body of PEM 1517/72 was extensively covered with rough, wart-like skin lesions, while the skin of the hard palate was rough, and appeared pale and necrotic. In PEM 1517/83 this roughness was restricted to the palate. Both animals were relatively inactive and off their food on the day preceding death.

The following points are summarized from the post-mortem report on PEM 1517/83.

The lungs were congested, with petechial haemorrhages on the surfaces. The trachea and bronchioles were inflamed, but there were no gross signs of drowning, though froth was found in the trachea.

The heart was congested; haemorrhages found on the epicardium were more prevalent on the left side. The heart valves, though thickened, were not rough or inflamed.

The spleen was enlarged and congested with petechial haemorrhages over the entire surface. There was also slight fatty degeneration of the tissue.

The external vessels of the stomach were enlarged and congested, and the secretory portion of the stomach was haemorrhagic in defined areas. The intestine was congested but not inflamed.

The cortices of the kidney reniculi were congested while the medullary regions were pale.

Blood smears showed small bacilli, and pure cultures of an organism identical to *Erisipelothrix rhusiopathae* were grown from samples of the liver, spleen and kidney.

In culture the organism was found to be sensitive to Penicillin and Furazolidine.

Similar but less profuse skin lesions to those on PEM 1517/72 were found on the left flank and palate of the stranded male PEM 1518/27, but samples were not collected for pathological examination.

A skin lesion known as a "tattoo" has been recorded in *T. truncatus* by Simpson and Gardner (1972), together with small pigmented dots approximately 1 mm in diameter. The causative agent is not known. Skin lesions fitting their descriptions have been noted on captive *T. aduncus* at the Port Elizabeth Oceanarium. Tattoos have occurred on two animals born in captivity. They follow a general pattern of slow growth over several months and are then sloughed off leaving a white patch of similar shape. These patches slowly become repigmented leaving the vague outline of the tattoos. The small pigmented dots have appeared on all five animals in the pool, most extensively on the two animals born in captivity. These dots, originally black, form small white scars which become progressively more diffuse in shape, eventually giving a flecked appearance to an animal with a large number of these dots. Though the presence of a virus has not been confirmed, it is suspected that they are caused by one of the pox viruses (Dr. Baxter, State Veterinarian, Port Elizabeth, pers. comm.).

Lung fibrosis

The captive female Haig, PEM 1516/00, gave birth to a calf on 26 October 1970 which was stillborn or died soon after birth. Haig carried the body for the following 6½ days. Soon after, she became lethargic and refused food; in a relatively short time she was visibly emaciated owing to wasting of the dorsal muscles. On 23 November she was isolated, and treated with acroflavin to stem suspected pyometra, since extremely thick mucoid matter was oozing from the genital slit. Examination of a smear of this matter showed the presence of multitudes of cocci (personal observation). The following day, Dr. H. L. Lucouw, of Port Elizabeth, tentatively diagnosed a respiratory infection, with a differential diagnosis of oesophageal obstructions, but despite treatment, she died on the night of 25 November. On post-mortem examination, Dr. Lucouw found extensive chronic fibrosis of the right lung, with multiple adhesions to the pleura, to such an extent that the lung had to be wrenched free of the pleura for examination. The entire lung was a fibrotic mass and must have been completely non-functional. There were no signs of acute inflammation except in the pharynx. Bacteria cultured from swabs were all non-pathogenic. The chronic condition of the right lung indicated a very old infection, perhaps prior to her capture eight years previously; although Haig was an excellent performer, she lacked stamina and seemed to tire very quickly. (Cited data communicated by Dr. Lucouw.)

“Bloat”

PEM 1517/96 stranded alive in a rocky gully and was kept in the water until her death. When examined approximately one hour after death, the stomach was found to be abnormally bloated, increasing the internal pressure enough to squirt blood briefly from severed neck vessels, and milk from the cut mammary gland. The stomach itself was ballooned with gas, but was otherwise completely empty. Comparison with other live stranded animals examined soon after death suggested that this animal was bloated before stranding. The effect of this bloating on buoyancy and movement may have contributed to the stranding. The only apparent internal abnormality was the peculiar thickening of the apex of the forestomach, which was up to 60 mm thick. Samples of the stomach wall have not yet been examined histologically.

Though tooth-rake scars attributable to intraspecific behavioural encounters occur frequently in specimens, scars resulting from other injuries were not common.

A stranded adult male PEM 1518/27 had a prominent healed scar across the ridge bordering the genital opening on the right side. The original wound appears to have been a deep lateral tear with the removal of a portion of the ridge, and had healed to give a triangular appearance to the genital slit.

When this animal was examined, it was thought initially that cuts on the head, flippers and dorsal fin were made by passers-by. However two shorter cuts on the lower jaw and one long cut behind the eye were parallel and did not resemble the normal pattern of mutilation encountered on stranded animals. It is suggested that these cuts were made by a boat's propeller, which may or may not have made other cuts on the flipper and dorsal fin.

A large healed scar was present on the dorsal surface of the caudal peduncle of PEM 1517/69, which appears to have been partially severed. In healing, the contraction of the tissues had left a distinct, broad indentation in the dorsal profile of the peduncle, and in dorsal view, the dorsal ridge posterior to the scar was distinctly canted to the left, some 50 mm out alignment with the body axis. It is possible that this wound was also made by a propeller.

A large scar approximately 300 mm in diameter, clearly the result of a shark bite, was found on the right flank of a mature female *T. aduncus* PEM 1517/61 (plate 6). A scar 120 mm in diameter attributed to a shark bite was found on the dorsal ridge, posterior to the fin, of a male *T. truncatus* PEM 1516/06 stranded in Natal. In view of the large numbers of sharks present in the inshore waters of Natal and the Eastern Cape it is interesting to note the low incidence of shark bites on *Tursiops*. One other record of a healed shark bite on a male *T. aduncus* caught at Port Elizabeth is given by Tayler and Saayman (1972). Wood *et al.* (1970) have noted the frequent occurrence of scars definitely or possibly attributable to sharks in *T. truncatus* captured alive off the coast of Florida. Twelve of 22 *Tursiops* at Marineland of Florida at the time of their investigation bore such scars. The inshore waters of the south-east coast of South Africa are often discoloured over large areas by river water, in which attacks on dolphins by sharks could well succeed. In this regard it was interesting to note the movements of a school of 30 to 40 *Tursiops* (*aduncus*?) sighted 1 km off Port St. Johns on 4 February 1973. At this time the discharge of muddy, turbid water from the Umzimvubu River extended down the coast for several kilometres and offshore for approximately 1 km. The school of dolphins moved up the coast on the outside of this silt-laden zone, but never in it, until they had passed the river mouth, when they headed inshore to the breaker line. It is possible that avoidance of such silt-laden zones is normal behaviour in South African *Tursiops*.

Evidence of internal injury was seen in an adult male *T. aduncus* PEM 1517/83. The left mandible had a healed fracture posterior to the end of the tooth row. In the same animal, part of the left temporal fossa had also been fractured leaving a healed oval depression some 45 × 35 mm in diameter. The apparent rarity of such injuries suggests that both fractures occurred at the same time, though as the bones of the orbit project beyond the plane of the two fractures, they must have resulted from two blows. A similar injury can be seen in the left mandible of an old *T. aduncus* PEM 1519/27 which has a healed fracture 60 mm in length at the posterior end of the tooth row. The blow causing the fracture led to the loss of the last four teeth and cracked off the two adjacent anterior teeth at the level of the gum.

It is interesting to note that the majority of stranded *T. aduncus* are relatively old animals. There are very few middle-aged and a few young animals. A similar pattern is shown by *Tursiops* stranded in Britain (Fraser, 1966). The low incidence of young stranded animals suggests a relatively low mortality rate in this age group. Conversely predators and scavengers may be able to deal with a smaller animal more effectively than a large animal, so that true mortality rates bear no relation to stranding frequencies of different age classes. More information is required on the age-composition of free-ranging groups to clarify this point.

There are no records of predation by killer-whales *Orcinus orca* on *Tursiops* in South African waters, though on several occasions killers have been sighted very close to the shore. Similarly the incidence of shark attacks is unknown, but as mentioned previously, appears to be low on the basis of scarred animals. Conversely, it is possible that the lack of scarred animals reflects a low escape rate.

Nine animals in the present material were taken from anti-shark nets off the Natal coast. Bottlenosed dolphins are well known for their ability to avoid such obstacles by use of their sonar, so that such deaths are probably uncommon. An explanation was offered in the case of a mass mortality in October, 1964, when 93 *Delphinus delphis*, 1 *Tursiops aduncus* and 1 *Sousa plumbea* were caught in the nets off Durban. At this time unseasonal shoals of pilchards *Sardinops ocellata* were present off Durban. Examination of the dolphins' stomach contents showed that they had been feeding on pilchards. It was suggested that preoccupation with feeding distracted the dolphins' attention, resulting in their entanglement (Anon., 1965). In support of this explanation is the high incidence of *D. delphis* in the nets, a pelagic species, which would not normally encounter such obstacles, while *T. aduncus* and *S. plumbea* both occur commonly close inshore, and would be familiar with obstacles in the water.

GENERAL DISCUSSION AND CONCLUSIONS

It has been shown that the *Tursiops* material collected along the South African coast can be separated into two distinct groups, which, on morphological grounds, are considered sufficiently different to warrant full specific status for each group. Further, comparison of these two species with data on *Tursiops truncatus* from British waters, and other described species of *Tursiops* from the Indian Ocean identified the two South African species as *Tursiops truncatus* (Montagu) and *T. aduncus* (Ehrenberg).

The large overlap in the distribution of these two species has been mentioned briefly. The eight *T. truncatus* specimens have been recorded from South West Africa (1), the Western Cape (3), the Port Elizabeth area (3), and Durban (1). *T. aduncus* has been recorded frequently from Natal and the Eastern Cape, from Mossel Bay (Van Bree, 1966) and twice from the Western Cape.

The stranding and capture dates of *T. aduncus* in the Eastern Cape indicate that this species is present throughout the year in this area. Strandings were recorded in all months except April and September, though the greater number of records in the summer months suggest seasonal fluctuations in numbers. The three Eastern Cape records of *T. truncatus* are in the months of April (1) and October (2). On the available data, it seems likely that both *T. aduncus* and *T. truncatus* are present simultaneously in Eastern Cape waters for at least part of the year, and in fact one stranded *T. truncatus* PEM 1515/94, was found on the same day as a stranded *T. aduncus* PEM 1515/95, only seven miles farther up the beach.

The stranding and capture records of *T. aduncus* from Natal examined in this study occur in the months of May (3), August (1), September (1), October (4) and November (1). The absence of records from December through April may be the result of a seasonal shift in the population or merely a reflection of an inadequate number of records.

Seasonal migrations of delphinids are generally poorly documented, though there is evidence that *T. truncatus* populations shift northwards in summer along the east coast of North America (Tomilin, 1957), while stranding records on the British coast suggest that *T. truncatus* migrates towards Britain from the south-west, reaching peak numbers in summer (Fraser, 1953). The only evidence that such population shifts may occur off the South African coast is provided by numbers of sightings of unidentified dolphin schools by spotter-aircraft during whale marking cruises off Natal and the Eastern Cape. In February 1973, 2 schools of dolphins were sighted in 15 hours flying in Natal waters, in contrast to 28 schools sighted in 57 hours flying in Eastern Cape waters. In February 1971, only 7 schools were sighted in 90 hours flying in Natal waters. These figures suggest a real difference in the numbers of dolphins in the two regions at this time of the year. A comment by one of the whaling skippers that dolphins were more numerous on the Natal whaling grounds during winter suggested that there may be a seasonal shift of dolphin populations along the south-east coast of South Africa (Report of the Whale-marking Cruise of the "Pieter Molenaar", Internal Report, N.I.O. 1973). These observations however were made in offshore waters, mostly beyond the edge of the continental shelf. As *T. aduncus* appears to be an inshore species it is unlikely that movements of *T. aduncus* are reflected in these observations, but they may undertake similar movements.

Sight records of *Tursiops* sp. mapped by Saayman *et al.* (1972) show that the majority of schools were seen within 5 km of the shore in the relatively shallow bay area at Plettenberg Bay, where the water depth is 50 m or less, but within 1 km of the shore off the Tsitsikama coast, where the 50 m depth line is 3 km or less from the shore. While the distance at which dolphins can be reliably identified from the shore limits such observations, dolphins reliably identified as *Tursiops* have been seen at sea more than 15 km offshore on two occasions only in three whale marking cruises off Natal, and two cruises in both Natal and Eastern Cape waters (personal observations). On 21 January 1975, a group of eight dolphins were seen 126 km, 226° from Cape

Receife, near Port Elizabeth. On 24 January 1975 a group of 10 animals bowrode the ship 298 km, 186° from Cape St. Blaize at Mossel Bay. Both positions are well beyond the continental shelf. The animals appeared to have relatively short beaks suggesting that they were *T. truncatus*.

Three other offshore sightings of dolphins identified as *Tursiops* have been kindly provided by Dr. P. B. Best: 28 August 1971, three dolphins, 25 km offshore, 190° from Durban; 2 March 1973, 20–30 dolphins, 34 km offshore, 160° from Durban; 4 April 1973, six dolphins, 102 km offshore, 82° from Durban. The water depths show that these localities are also well beyond the continental shelf, at 600, 450 and over 100 fathoms respectively.

Until a representative series of specimens can be collected at sea, the identity of such sightings cannot be confirmed. At present the only indication that *T. truncatus* occurs further offshore than *T. aduncus* on the south-east coast of Africa is given by the limited data on feeding habits in the two species, and the single *T. truncatus* collected at sea by Dr. Best at 33° 19' S, 43° 51' E. On the west coast, where *T. aduncus* has not been recorded, *T. truncatus* has been caught very close inshore.

Gaskin (1968) has given evidence suggesting that the distributions of dolphin species off the east coast of New Zealand are closely associated with certain temperature ranges and consequently with specific water masses and convergence regions. The distribution of *T. aduncus* is perhaps a reflection of warm water conditions associated with the Agulhas current on the south-east coast. Without further data, it is not possible to associate the distribution of southern African *T. truncatus* with similar oceanographic features. With the peculiar oceanographic conditions pertaining to the South African coast, it is likely that *T. truncatus* and *T. aduncus* meet at least occasionally; as yet there is no evidence of hybridization in the material examined. Very little is known about reproductive isolation in cetaceans, though evidence that isolating mechanisms occasionally fail is provided by three specimens from Ireland, which form a graded series between *T. truncatus* and the related Risso's dolphin *Grampus griseus* (Fraser, 1966). In captivity, a remarkable hybrid was produced by a female rough-toothed dolphin *Steno bredanensis* and a male *Tursiops truncatus*. On current classification systems, this offspring represents an interfamilial hybrid (Dohl, Norris and Kong, 1974).

Further research on the morphology and biology of both species of *Tursiops* in South African waters, and in other regions such as New Zealand, which appears to have two species of *Tursiops* (Gaskin, 1972) should prove most rewarding, particularly with regard to the factors limiting the distribution of these species or populations of them. The taxonomic results of this paper should be viewed as preliminary, pending a global review of the taxonomy of *Tursiops*. It would be most useful to supplement purely morphometric methods of analysis with other forms of data such as blood protein electrophoresis provides. There are numerous *Tursiops* in captivity throughout the world which represent several different populations; if plasma samples could be collected and sent to a central research body for analysis, the results would provide a basis for assessing the morphometric approach to the taxonomy of *Tursiops*.

SUMMARY

Material and data from 58 specimens of *Tursiops* from South African waters were examined. Analysis of cranial data, supported by data on external measurements and the post cranial skeleton, showed that the material was divisible into two groups. These differed sufficiently in several morphological characters to warrant specific recognition. Comparison of the South African material with 17 *T. truncatus* from British waters identified one South African species as *T. truncatus*, with possible subspecific differences between the two populations. Comparison of the second South African species with the available published data on the types of *T. absulam* (Rüppell), *T. catalania* (Gray), *T. aduncus* (Ehrenberg) and *Delphinus gadamu* Owen tends to confirm the opinions of previous authors that all of these species are synonymous

under the name *Tursiops aduncus* (Ehrenberg, 1832). The South African *T. aduncus* is distinguished from South African *T. truncatus* by the following characters.

1. *T. aduncus* is shorter than *T. truncatus*. Greatest body length recorded for *T. aduncus* is 2 540 mm, while CBL of the skull is less than 500 mm. A young *T. truncatus* with four dentine layers exceeded this length, and a male of 3 270 mm was recorded; CBL of skull ranges between 504–578 mm.
2. Beak length in *T. aduncus* is 4,7–6,0% (mean 5,3%) body length; in *T. truncatus* it is 3,1–4,7% (mean 3,8%) body length.
3. The values for the proportionately narrower rostrum of *T. aduncus* are; basal width 21,4–25,4% (mean 23,7%) CBL, width 60 mm anterior to the base 15,9–19,2% (mean 16,9%) CBL, width at mid length 11,6–16,5% (13,9%) CBL, and width of premaxillae at rostral mid length 6,4–8,8% (mean 7,3%) CBL. Corresponding values for *T. truncatus* are 24,5–27,3% (mean 26,1%) CBL, 18,3–22,5% (mean 20,5%) CBL, 14,5–18,3% (mean 16,1%) CBL and 7,5–9,9% (mean 8,9%) CBL.
4. The preorbital width of the skull in *T. aduncus* is 41,0–45,8% (mean 42,9%) CBL, while the orbital width is 42,2–46,0% (mean 43,7%) CBL. The corresponding values for *T. truncatus* are 43,2–48,4% (mean 46,3%) CBL, and 44,2–47,6% (mean 46,1%) CBL.
5. The lengths of the upper tooth rows in *T. aduncus* are 43,1–48,3% (mean 45,8%) CBL and 43,6–49,4% (mean 45,9%) CBL. In *T. truncatus* they are 46,4–49,5% (mean 47,7%) CBL and 46,4–49,8% (mean 47,8%) CBL.
6. There are 21–23 (mean 22,4) and 22–24 (mean 22,5) teeth in the lower jaws of *T. truncatus*. In *T. aduncus* there are 23–29 (mean 26,1) and 23–28 (mean 25,9) teeth.
7. The posterior portion of the vomer is narrow with parallel or sub-parallel margins in *T. aduncus*. In *T. truncatus* the vomer broadens posteriorly.
8. The pterygoid notch is narrow with a sub-acute apex in *T. aduncus*. In *T. truncatus* it is broad with an obtuse apex.
9. The portion of the squamosal forming the wall of the temporal fossa is small with a dorsally-directed apex in *T. aduncus*. In *T. truncatus* it is more extensive, with its apex directed postero-dorsally.
10. In anterior view the premaxillae are strongly arched in the middle third of the rostrum in *T. aduncus*. In *T. truncatus* they are not strongly arched.
11. In dorsal view there is a broad strip of cancellous bone forming the lateral border of the premaxilla in the middle third of the rostrum in *T. truncatus*. In *T. aduncus* this strip is absent or very narrow.
12. The few available data suggest that the total number of vertebrae is 59–62 in *T. aduncus* and 64–65 in *T. truncatus*. The serial number of the first vertebra with an arterial canal through the transverse process is 38–40 in *T. aduncus* and 43–46 in *T. truncatus*.

Specimens which were excluded from the taxonomic treatment were identified on these characters, and included in the biological notes. The following points were concluded from the limited South African material.

1. The length of eight *T. aduncus* at birth ranged from 838 to 1 120 mm.
2. The 13 dentine layers in the teeth of a female *T. aduncus* caught at an unknown age and held captive for eight years suggested that one dentine layer is deposited per year.
3. Five male *T. aduncus* were considered physically mature at body lengths of 2 240–2 540 mm (mean 2 412 mm).
4. Four female *T. aduncus* were considered physically mature at body lengths of 2 310–2 465 mm (mean 2 371 mm). The longest female specimen recorded was 2 520 mm in length.
5. The greatest weight recorded for *T. aduncus* was 226,4 kg for a male 2 540 mm in length. A

regression line of weight on body length based on nine male *T. aduncus* was fitted by the equation

$$0,3105 \log W + 1,692 = \log L.$$

where W=weight (kg) and L=total length (cm).

6. Data from one stranded female *T. aduncus* suggest that it matured sexually at less than nine years of age and possibly as early as six years of age, assuming one dentine layer accumulates per year.
7. The ovulatory pattern shown by one female *T. aduncus* held captive for eight years, of which males were absent for the first five years, suggested that ovulation is induced and not spontaneous.
8. In five of six sexually mature female *T. aduncus* ovulation had occurred in the left ovary only.
9. The two calves of a captive female *T. aduncus* were born in successive years.
10. The gestation period in *T. aduncus* is approximately one year.
11. The calving season in *T. aduncus* is prolonged, with most births in late spring and summer.
12. Calves may take solid food from the age of six months or later in captivity. The length of the lactation period is unknown though evidence is given of sporadic suckling by one *T. aduncus* calf at the age of 29 months.
13. There is little change in testis weight of male *T. aduncus* up to a body length of 2 000 mm.
14. One male *T. aduncus* was considered to be sexually maturing at 11 years of age, while a second male was possibly functionally mature at nine years of age, assuming one dentine layer is deposited per year.
15. The smallest maturing male *T. aduncus* was 2 390 mm in body length, while the smallest mature male was 2 240 mm in body length.
16. Prey items identified in stomach contents of nine *T. aduncus* suggest that this species is an opportunistic feeder, catching predominantly benthic or reef-dwelling fish and cephalopods which are common, probably at depths of less than 200 m.
17. Fish and cephalopods identified in stomach contents of two *T. truncatus* suggest that this species may feed further offshore than *T. aduncus*.
18. Records of parasites in *T. aduncus* include *Xenobalanus globicipitis*, cestode cysts in the blubber (*Phyllobothrium?*) and internally (*Monorygma?*), nematodes in the stomach, and lungworms. Nematodes were found in the stomachs of two *T. truncatus*; these were identified as *Anisakis* sp. in one animal.
19. Records of diseases in *T. aduncus* include erisypelas septicaemia, chronic lung fibrosis, a skin condition known as "tattoo" and a gastric condition resembling "bloat".
20. External scars and a skull injury were noted in *T. aduncus*, while one shark bite scar was found on a male *T. truncatus*. The incidence of shark bites on South African *Tursiops* appears to be low. Incidental mortality in the anti-shark nets off the Natal coast is noted.
21. Stranding and capture dates show that *T. aduncus* is present in the Eastern Cape throughout the year. The three Eastern Cape records of *T. truncatus* are in April and October. On one occasion stranded specimens of both species were found seven miles apart on the same day.
22. Apart from possible differences in feeding habits, mechanisms operative in isolating the two species are unknown.

ACKNOWLEDGEMENTS

I wish to express my thanks to all those people who have assisted in this project. As a full list would be embarrassingly long, I have omitted mentioning numerous people by name. Such omissions however do not imply ingratitude on my part in any way. Particular thanks are due to the following:

Prof. J. Meester, Zoology Department, University of Natal, Prof. J. R. Grindley, formerly of the Port Elizabeth Museum and Prof. T. Erasmus, Zoology Department, University of Port Elizabeth who read and criticized drafts of this paper; Dr. P. B. Best, of Sea Fisheries Branch, Cape Town, who initially suggested the variation study, and supplied data on the material in the South African Museum and in private collections in Cape Town; Dr. F. C. Fraser, formerly of the British Museum, who generously supplied his own measurements of material in the British Museum and who read an initial draft; Dr. P. J. H. van Bree, University of Amsterdam, for much constructive advice and unpublished information given in the initial stages of the project; Dr. A. J. Bass, Dr. G. Hughes, and other staff members of the Oceanographic Research Institute, Durban for collection and freezing of Natal specimens; Mr. N. McLeod and Miss M. A. Roeleveld for the identification of cephalopod beaks; my wife and colleagues at the Port Elizabeth Museum who have assisted in collecting material, and for whom life has held a series of dubious aromas.

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APPENDIX

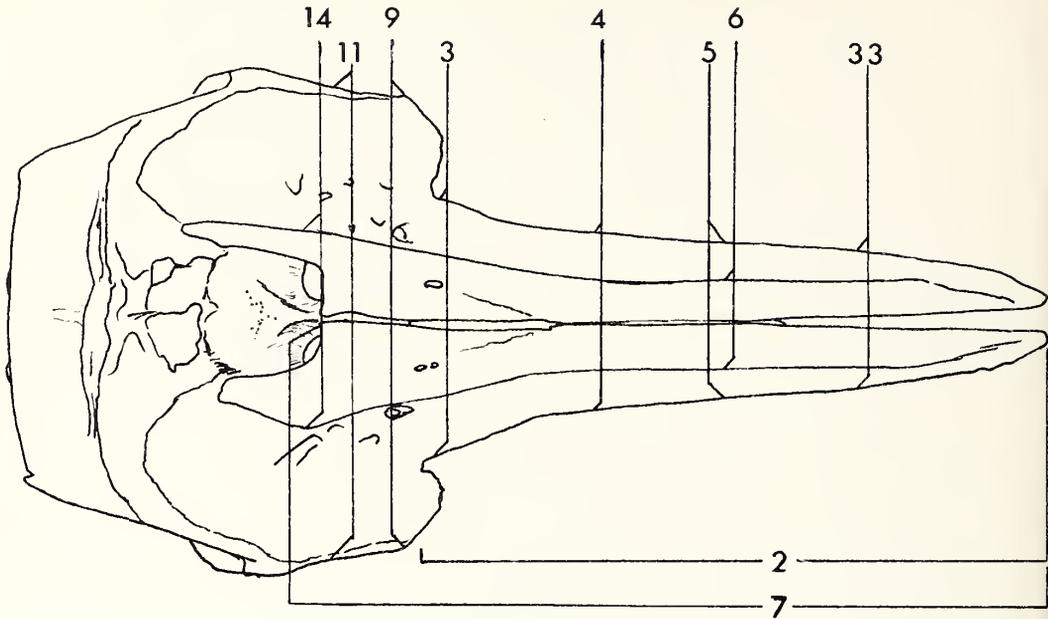


Fig. 5. Illustrating the cranial measurements listed in table 4.

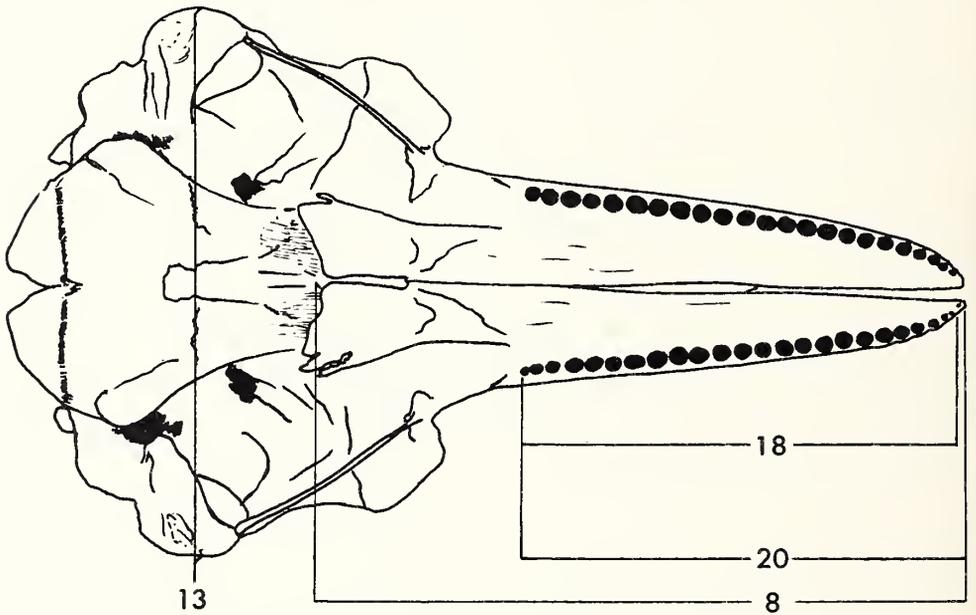


Fig. 6. Illustrating the cranial measurements listed in table 4.

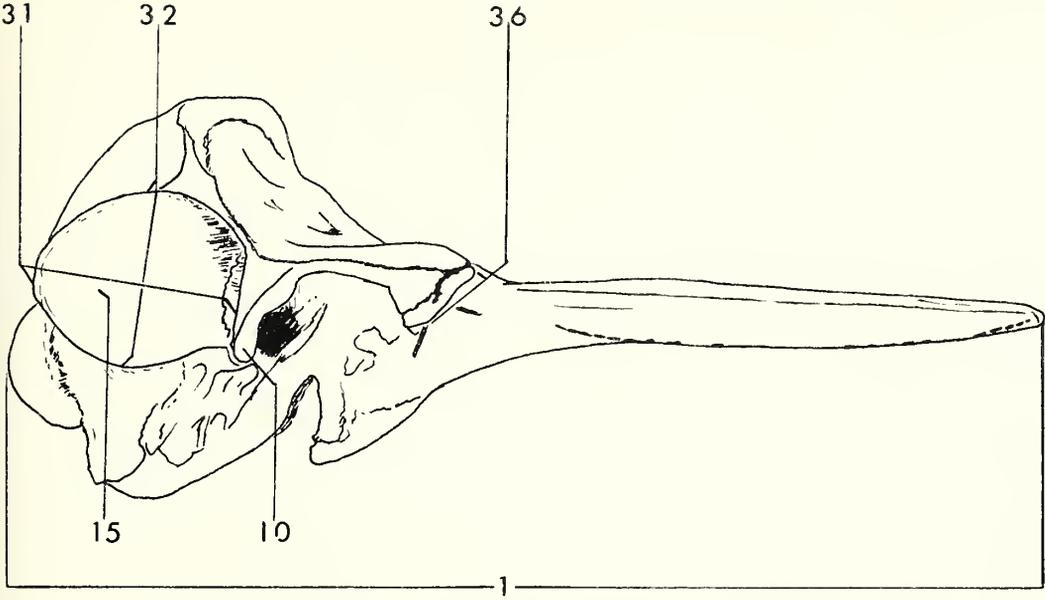


Fig. 7. Illustrating the cranial measurements listed in table 4.

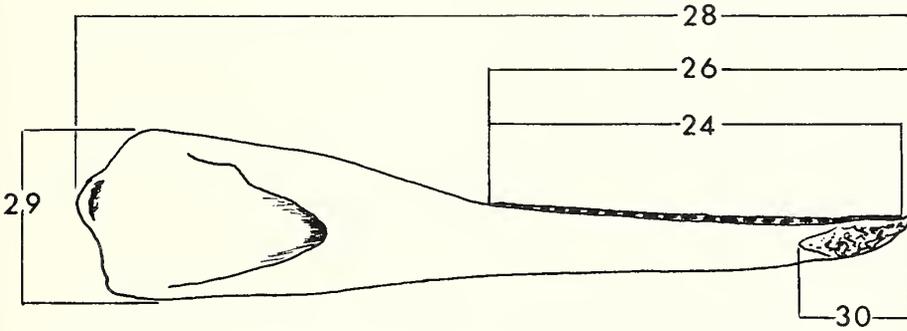


Fig. 8. Illustrating the mandibular measurements listed in table 4.

TABLE 17a. Data and preserved material of South African *Tursiops aduncus* examined in this study. Abbreviations for material and data are: S—skull; M—mandibles; T—teeth; PC—postcranial skeleton; Ph—photographs; E—external measurements; R—reproductive organs; St—stomach contents; F—foetus; P—parasites. Underlining indicates incomplete material.

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Material and data	Comments
PEM 1496/73	♂	838	459	March 1963	Kings Beach, P.E. 35° 58' S; 25° 38' E	S, M, T	Netted with two others
PEM 1514/31				24.11.68	Flat Rocks, P.E. 34° 01' S; 25° 41' E	<u>S</u> , M	Stranded
PEM 1514/47			472	Jan. 1969	Springmount, Algoa Bay 33° 45' S; 26° 12' E	S	Skull found on beach
PEM 1514/48			455	Jan. 1969	Springmount, Algoa Bay 33° 45' S; 26° 12' E	S, M, T	Stranded. Decomposing
PEM 1514/97			483	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	S, T	Anti-shark nets with 1514/98, 99
PEM 1514/98			476	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	S, T	Anti-shark nets
PEM 1514/99			456	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	<u>S</u> , M, T	Anti-shark nets
PEM 1515/02	♂	1 092	266	27.10.69	Oceanarium, P. E.	S, M, T, PC, E	Calf of PEM 1516/00
PEM 1515/08	♂	1 067		9.11.69	Van Stadens River Mouth 33° 58' S; 25° 13' E	S, M, T, E	Stranded. Neonate
PEM 1515/23	♀	2 185		24.11.69	2 km N. Boteler Point, Natal 27° 00' S; 32° 53' E	M, T, Ph, E	Stranded
PEM 1515/24			2 030	9.1.70	Kowie River Mouth 33° 36' S; 26° 54' E	S, M, T	Stranded
PEM 1515/55			466	14.6.70	Pollock Beach, P.E. 33° 59' S; 25° 41' E	S, M, T, PC, E	Stranded
PEM 1515/69				1970?	Durban (?), Natal	S, M, T	Head donated to PEM from Durban
PEM 1515/83	♂	2 490	493	29.10.70	1 km E. Swartkops River Mouth 33° 51' S; 25° 38' E	S, M, T, PC, E	Stranded
PEM 1515/92	♀	930		26.10.70	Oceanarium, P.E.	T, E	2nd calf of PEM 1516/00
PEM 1515/95	♂	2 190	472	12.11.70	29 km E. Sundays River Mouth 33° 43' S; 26° 09' E	S, M, T, E	Stranded
PEM 1516/00	♀	2 375	482	25.11.70	Oceanarium, P.E. 33° 58' S; 25° 38' E	S, M, T, PC, Ph, E, R	Netted at P.E. on 16.10.62 'Haig'
PEM 1516/33	♀	2 350	489	Oct. 1970	Durban, Natal 29° 52' S; 31° 00' E	S, M, T, PC, Ph, E, R, St	Anti-shark nets
PEM 1516/34	♂	1 500		Oct. 1970	Durban, Natal 29° 52' S; 31° 00' E	Ph, E, St, P	Stranded?
PEM 1517/35	♂	1 955	433	11.8.71	The Willows, P.E. 34° 03' S; 25° 35' E	S, M, T, Ph, E	Stranded
PEM 1517/44		430		12.11.63	Kings Beach, P.E. 33° 58' S; 25° 38' E	S, M, T	Netted with two others
PEM 1517/50		457			Presumed Natal Coast	S, M, T	Donated by O.R.I. Durban

ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS TURSIOPS SPECIES

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Material and data	Comments
PEM 1517/60	♀	2 465	482	4.12.71	Sardinia Bay 34° 02' S; 25° 30' E	S, M, T, PC, E, R, St	Stranded
PEM 1517/61	♀	2 310	467	9.12.71	Kings Beach, P.E. 33° 58' S; 25° 38' E	S, M, T, Ph, E, R, St	Died during netting
PEM 1517/69	♂	2 390	472	Oct. 1971	Durban, Natal 29° 52' S; 31° 00' E	S, M, T, PC, E, R, St	Anti-shark nets
PEM 1517/72	♂	2 440	468	3.2.72	Oceanarium, P.E.	S, M, T, Ph, E, R, St	Netted at P.E. on 9.12.71 'Dickie'
PEM 1517/83	♂	2 540	492	17.6.72	Oceanarium, P. E.	S, M, T, Ph, E, R, St	Netted at P. E. on 9.12.71 'Dolfie'
PEM 1517/96	♀	2 520	474	29.7.72	Noordhoek, P.E. 34° 02' S; 25° 39' E	S, M, T, PC, Ph, E, R, F	Stranded alive. Pregnant, lactating
PEM 1518/19				23.8.72	10 km E. Sundays River Mouth 33° 48' S; 25° 58' E	S, M, T	Stranded (immature)
PEM 1518/26	♂	1 002		1.10.72	Umzambe, Natal 30° 37' S; 30° 33' E	T, X-ray of S, M, & PC	Anti-shark nets with adult ♀
PEM 1518/27	♂	2 240	464	4.3.72	4 km W. Cape Recife 34° 02' S; 25° 39' E	S, M, T, Ph, E, R, St	Stranded
PEM 1518/43	♀	1 870	411	6.5.73	Sardinia Bay 34° 02' S; 25° 30' E	S, M, T, PC, Ph, E, R, St	Stranded
PEM 1518/54	♂	2 520	480	10.8.73	Jeffreys Bay 34° 04' S; 24° 56' E	S, M, T, PC, Ph, E, R, St	Stranded
PEM 1518/57	♂	1 840		14.11.68	St. George's Strand, P.E. 33° 50' S; 25° 39' E	E	Stranded
PEM 1518/97	♂	2 320	458	27.5.74	Westbrook, Natal N. Coast 29° 31' S; 31° 13' E	S, M, T, Ph, E, R	Shark nets
PEM 1518/98	♀	2 020	433	27.5.74	Westbrook, Natal Coast 29° 31' S; 31° 13' E	S, M, T, PC, Ph, E, R, St	Shark nets
PEM 1518/99	♂	1 525		27.5.74	Westbrook, Natal N. Coast 29° 31' S; 31° 13' E	S, M, T, PC, E	Shark nets
PEM 1519/07	♀	2 360	477	6.8.74	Umhloti, Natal N. Coast 29° 39' S; 31° 08' E	S, M, T, Ph, E, R, P	Shark nets
PEM 1519/13	♀	1 120		2.2.75	Gamtoos River Beach 33° 59' S; 25° 01' E	S, M, T, Ph, E	Stranded. Neonate
PEM 1519/23	♀	1 150		23.3.75	Sundays River Beach 33° 48' S; 25° 58' E	S, M, T, Ph, E, R	Stranded
PEM 1519/26	♂	1 080		June 1975	2 km E. Woody Cape 32° 46' S; 26° 20' E	S, M, T, Ph, E	Stranded. Neonate
PEM 1519/27		2 520	488	June 1975	1 km W. Cape Padrone 32° 46' S; 26° 27' E	S, M, T, E	Stranded
PEM 1519/28 EL 40	♀	2 340	472	June 1975	1 km W. Kousouga River Mouth 33° 39' S; 26° 44' E	S, M, T, Ph, E, St S, M, T	Stranded
EL 873			454 +20?	4.3.69	East London? East London Harbour 33° 01' S; 27° 55' E	S, M, T	Immature
SAM 35062		464 +10?		4.4.62	Gordons Bay/Strand 34° 08' S; 18° 51' E	S, M, T	Stranded?
M. Y. 1 J. Currie		454 481 +10		Feb. 1970	Port Elizabeth area? Walker Bay, W. Cape 34° 30' S; 19° 20' S	S, M, T S, M, T, PC	Stranded? Stranded

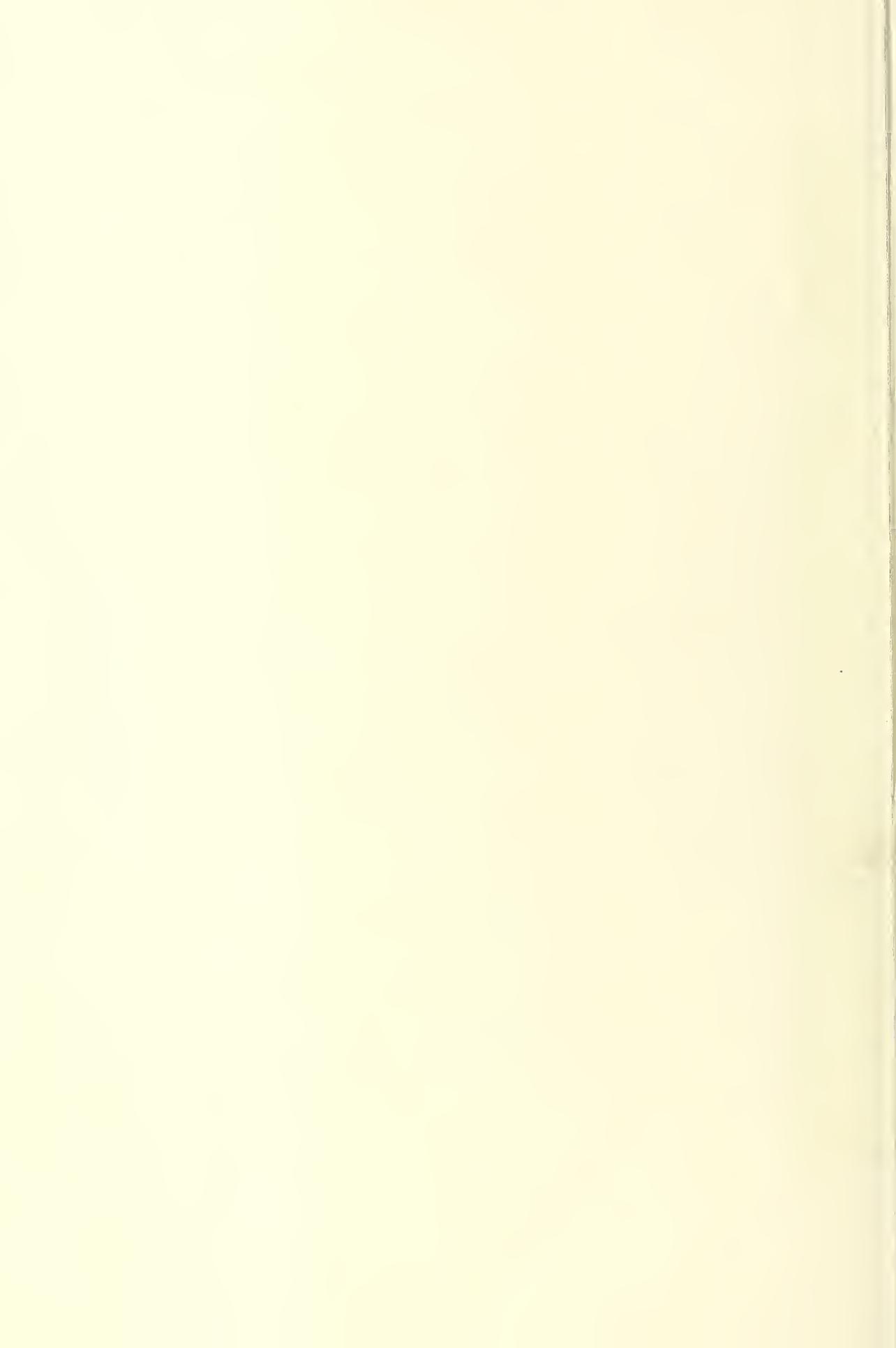


TABLE 17a. Data and preserved material of South African *Tursiops aduncus* examined in this study. Abbreviations for material and data are: S—skull; M—mandibles; T—teeth; PC—postcranial skeleton; Ph—photographs; E—external measurements; R—reproductive organs; St—stomach contents; F—foetus; P—parasites. Underlining indicates incomplete material.

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Material and data	Comments
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PEM 1514/47			472	Jan. 1969	Springmount, Algoa Bay 33° 45' S; 26° 12' E	S	Skull found on beach
PEM 1514/48			455	Jan. 1969	Springmount, Algoa Bay 33° 45' S; 26° 12' E	S, M, T	Stranded. Decomposing
PEM 1514/97			483	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	S, T	Anti-shark nets with 1514/98, 99
PEM 1514/98			476	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	S, T	Anti-shark nets
PEM 1514/99			456	Sept. 1969	Durban, Natal 29° 52' S; 31° 00' E	S, <u>M</u> , T	Anti-shark nets
PEM 1515/02	♂	1 092	266	27.10.69	Oceanarium, P. E.	S, M, T, PC, E	Calf of PEM 1516/00
PEM 1515/08	♂	1 067		9.11.69	Van Stadens River Mouth 33° 58' S; 25° 13' E	S, M, T, E	Stranded. Neonate
PEM 1515/23	♀	2 185		24.11.69	2 km N. Boteler Point, Natal 27° 00' S; 32° 53' E	M, T, Ph, E	Stranded
PEM 1515/24				9.1.70	Kowie River Mouth 33° 36' S; 26° 54' E	S, M, T	Stranded
PEM 1515/55		2 030	466	14.6.70	Pollock Beach, P.E. 33° 59' S; 25° 41' E	S, M, T, PC, E	Stranded
PEM 1515/69				1970?	Durban (?), Natal	S, M, T	Head donated to PEM from Durban
PEM 1515/83	♂	2 490	493	29.10.70	1 km E. Swartkops River Mouth 33° 51' S; 25° 38' E	S, M, T, PC, E	Stranded
PEM 1515/92	♀	930		26.10.70	Oceanarium, P. E.	T, E	2nd calf of PEM 1516/00
PEM 1515/95	♂	2 190	472	12.11.70	29 km E. Sundays River Mouth 33° 43' S; 26° 09' E	S, M, T, E	Stranded
PEM 1516/00	♀	2 375	482	25.11.70	Oceanarium, P. E. 33° 58' S; 25° 38' E	S, M, T, PC, Ph, E, R	Netted at P.E. on 16.10.62 'Haig'
PEM 1516/33	♀	2 350	489	Oct 1970	Durban, Natal 29° 52' S; 31° 00' E	S, M, T, PC, Ph, E, R, St, P	Anti-shark nets
PEM 1516/34	♂	1 500		Oct. 1970	Durban, Natal 29° 52' S; 31° 00' E	Ph, E, St, P	Stranded?
PEM 1517/35	♂	1 955	433	11.8.71	The Willows, P.E. 34° 03' S; 25° 35' E	S, M, T, Ph, E	Stranded
PEM 1517/44			430	12.11.63	Kings Beach, P.E. 33° 58' S; 25° 38' E	S, M, T	Netted with two others
PEM 1517/58			457		Presumed Natal Coast	S, M, T	Donated by O.R.L. Durban

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TABLE 17a continued

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Material and data	Comments
PEM 1517/60	♀	2 465	482	4.12.71	Sardinia Bay 34° 02' S; 25° 30' E	S, M, T, PC, E, R, St	Stranded
PEM 1517/61	♀	2 310	467	9.12.71	Kings Beach, P.E. 33° 58' S; 25° 38' E	S, M, T, Ph, E, R, St	Died during netting
PEM 1517/69	♂	2 390	472	Oct. 1971	Durban, Natal 29° 52' S; 31° 00' E	S, M, T, PC, E, R, St	Anti-shark nets
PEM 1517/72	♂	2 440	468	3.2.72	Oceanarium, P. E.	S, M, T, Ph, E, R, St	Netted at P.E. on 9.12.71 'Dickie'
PEM 1517/83	♂	2 540	492	17.6.72	Oceanarium, P. E.	S, M, T, Ph, E, R, St	Netted at P. E. on 9.12.71 'Dolfie'
PEM 1517/96	♂	2 520	474	29.7.72	Noordhoek, P.E. 34° 02' S; 25° 39' E	S, M, T, PC, Ph, E, R, F	Stranded alive. Pregnant, lactating
PEM 1518/19				23.8.72	10 km E. Sundays River Mouth 33° 48' S; 25° 58' E	S, M, T, Ph, E, R, F	Stranded (immature)
PEM 1518/26	♂	1 002		1.10.72	Umzombe, Natal 30° 37' S; 30° 33' E	T, X-ray of S, M, & PC	Anti-shark nets with adult ♀
PEM 1518/27	♀	2 240	464	4.3.72	4 km W. Cape Recife 34° 02' S; 25° 39' E	S, M, T, Ph, E, R, St	Stranded
PEM 1518/43	♂	1 870	411	6.5.73	Sardinia Bay 34° 02' S; 25° 30' E	S, M, T, PC, Ph, E, R, St	Stranded
PEM 1518/54	♂	2 520	480	10.8.73	Jeffreys Bay 34° 04' S; 24° 56' E	S, M, T, PC, Ph, E, R, St	Stranded
PEM 1518/57	♂	1 840		14.11.68	St. George's Strand, P.E. 33° 50' S; 25° 39' E	E	Stranded
PEM 1518/97	♂	2 320	458	27.5.74	Westbrook, Natal N. Coast 29° 31' S; 31° 13' E	S, M, T, Ph, E, R	Shark nets
PEM 1518/98	♀	2 020	433	27.5.74	Westbrook, Natal Coast 29° 31' S; 31° 13' E	S, M, T, PC, Ph, E, R, St	Shark nets
PEM 1518/99	♂	1 525		27.5.74	Westbrook, Natal N. Coast 29° 31' S; 31° 13' E	S, M, T, PC, E	Shark nets
PEM 1519/07	♀	2 360	477	6.8.74	Umhloti, Natal N. Coast 29° 39' S; 31° 08' E	S, M, T, Ph, E, R, P	Shark nets
PEM 1519/13	♀	1 120		2.2.75	Gamtoos River Beach 33° 59' S; 25° 01' E	S, M, T, Ph, E, R	Stranded. Neonate
PEM 1519/23	♀	1 150		23.3.75	Sundays River Beach 33° 48' S; 25° 58' E	S, M, T, Ph, E, R	Stranded
PEM 1519/26	♂	1 080		June 1975	2 km E. Woody Cape 32° 46' S; 26° 20' E	S, M, T, Ph, E	Stranded. Neonate
PEM 1519/27	♀	2 520	488	June 1975	1 km W. Cape Padrone 32° 46' S; 26° 27' E	S, M, T, E	Stranded
PEM 1519/28	♀	2 340	472	June 1975	1 km W. Kasouga River Mouth 33° 39' S; 26° 44' E	S, M, T, Ph, E, St	Stranded
EL 40			454 +20?		East London?	<u>S</u> , M, T	
EL 873				4.3.69	East London Harbour 33° 01' S; 27° 55' E	S, M, T	Immature
SAM 35062		464 +10?		4.4.62	Gordons Bay/Strand 34° 08' S; 18° 51' E	S, M, T	Stranded?
M. Y. 1		454			Port Elizabeth area?	S, M, T	Stranded?
J. Currie		481 +10		Feb. 1970	Walker Bay, W. Cape 34° 30' S; 19° 20' S	S, M, T, PC	Stranded

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ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS TURSIOPS SPECIES

TABLE 17b. Data and preserved material of South African *Turistops truncatus* examined in this study. Abbreviations for material are listed in table 17a.

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Material and data	Comments
PEM 1515/74	♀	2 795	517	1.10.70	Skoenmakerskop 34° 02' S; 25° 33' E	S, M, T, PC, Ph, E, R	Stranded alive
PEM 1515/94	♂	3 270	568	1.11.70 (Reported) August 1970	2 km W. Woody Cape 33° 41' S; 26° 16' E	S, M, T, E	Stranded
PEM 1516/06	♂	2 720	530	8.4.72	Durban, Natal 29° 52' S; 31° 00' E	S, M, T, PC, Ph, E, R, St	Stranded?
PEM 1517/77	♂	2 605	504	1952	4 km W. Van Stadens River Mouth 33° 58' S; 25° 11' E	S, M, T, PC, Ph, E, R, St	Stranded
SAM 19928			574	10.12.64	Noordhoek, W. Cape 34° 07' S; 18° 23' E	S, M, T, PC	Stranded?
SAM 35104	♂	3 000 est.	541	July 1972	Veldrif, St. Helena Bay 32° 45' S; 18° 05' E	S, M, T, PC	Stranded?
Palmer 18		4 000 est.	562		Noordhoek, W. Cape 34° 07' S; 18° 23' E	S, M, T	Stranded?
Cape Cross			578		16 km S. Cape Cross 21° 56' S; 13° 55' E	S, M, T, PC	Stranded

ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS TURSIOPS SPECIES

TABLE 18. External body measurements of specimens in groups A and B. Total length is given in mm. Other measurements are expressed as percentages of total length. Measurement numbers are keyed to table 2.

No.	Group A										Group B										
	PEM 1518/98	PEM 1515/95	PEM 1518/27	PEM 1517/61	PEM 1518/97	PEM 1519/28	PEM 1516/33	PEM 1519/07	PEM 1516/00	PEM 1517/69	PEM 1517/72	PEM 1517/60	PEM 1515/83	PEM 1517/96	PEM 1519/27	PEM 1518/54	PEM 1517/83	PEM 1517/77	PEM 1516/06	PEM 1515/74	PEM 1515/94
1	2 020	2 190	2 240	2 310	2 320	2 340	2 350	2 360	2 375	2 390	2 440	2 465	2 490	2 520	2 520	2 520	2 540	2 605	2 720	2 795	3 270
2	16.1	15.1	14.7	14.8	14.2	14.9	15.3	14.6	15.2	13.8	13.5	14.4	14.9	14.3	—	14.3	14.5	14.6	14.3	13.6	13.2
3	5.7	5.7	5.6	6.0	4.7	5.1	5.5	5.2	5.6	5.1	5.2	5.2	5.2	5.4	5.0	5.2	5.5	3.9	4.7	3.6	3.1
4	13.4	12.8	12.1	12.6	11.2	11.5	12.3	11.9	12.0	12.0	11.5	12.1	12.0	11.7	11.3	11.9	12.0	11.7	11.7	12.5	10.1
5	—	—	—	18.1	—	—	18.7	—	18.4	—	—	—	—	17.1	—	—	17.0	17.3	17.3	—	—
6	—	—	—	3.3	—	—	3.4	—	3.7	—	—	—	—	3.2	—	—	3.3	2.9	3.3	—	—
7	3.0	2.7	3.1	2.7	—	3.2	3.0	3.0	2.9	2.7	2.6	2.3	2.8	2.8	—	2.8	2.5	2.9	2.8	2.3	3.1
8	9.4	8.2	8.9	8.8	9.1	8.5	8.7	8.1	—	8.8	8.3	8.0	—	8.7	—	8.3	8.8	9.3	7.5	6.8	7.0
9	16.8	15.1	15.2	15.4	14.2	15.0	15.7	15.3	15.0	14.4	14.1	14.7	15.3	14.7	—	14.3	15.0	14.6	14.5	14.5	12.5
10	25.2	26.5	25.0	22.4	21.1	24.4	24.7	21.6	25.7	22.3	23.4	22.7	23.3	23.4	22.6	20.2	23.5	22.4	21.5	21.4	20.5
11	43.6	—	46.9	—	43.5	45.3	—	43.6	—	43.1	45.8	—	—	43.3	42.9	43.7	42.0	44.9	—	—	—
12	58.9	57.5	(60.3)	62.6	59.1	59.0	62.6	61.0	62.6	58.5	61.5	61.3	60.2	58.7	54.4	61.5	58.0	—	61.7	56.4	61.5
13	46.0	—	—	46.2	—	46.1	48.5	47.9	48.1	46.3	—	43.8	43.8	44.4	—	46.0	—	—	49.5	46.4	—
14	66.3	—	65.6	67.0	—	65.8	67.2	71.2	67.4	60.6	62.5	65.5	58.6	(67.5)	—	58.3	61.0	66.3	67.3	67.7	60.9
15	69.8	—	76.8	70.3	72.4	68.8	69.4	73.3	69.5	70.7	74.0	68.6	68.7	(69.8)	—	71.0	72.0	72.7	73.8	70.5	68.2
16	0.4	0.4	0.7	0.3	—	—	0.6	0.5	0.4	0.3	0.5	0.5	0.6	0.5	—	0.6	0.5	0.2	0.4	0.5	—
17	52.0	—	—	54.9	—	—	56.2	—	46.0	54.3	—	—	52.2	52.4	—	55.0	—	55.0	47.7	42.7	—
18	55.4	—	—	57.1	—	—	—	—	(47.1)	—	—	—	—	—	—	57.0	—	—	54.2	46.4	—
19	29.7	—	41.1	35.2	39.7	—	34.0	36.9	30.0	34.0	—	28.9	30.5	—	—	39.7	37.0	26.3	29.9	26.4	32.4
20	—	—	1.1	1.1	—	—	1.4	—	—	0.9	1.0	1.0	1.0	1.0	—	—	1.3	1.0	—	0.9	—
21a	0.6	—	—	1.1	—	—	0.6	0.7	—	—	—	0.8	—	1.2	—	—	—	—	—	0.9	—
21b	0.6	—	—	0.8	—	—	0.6	0.7	1.3	—	—	—	—	1.0	—	—	—	—	—	0.9	—
22a	—	—	(8.9)	6.0	—	—	6.4	—	6.4	4.3	8.3	5.2	—	—	—	5.6	7.0	5.8	5.1	5.5	—
22b	—	—	—	0.4	—	—	—	—	0.4	0.9	2.1	0.5	1.0	—	—	0.4	2.0	2.0	1.9	0.7	—
22c	6.2	—	—	—	—	—	6.4	6.6	—	—	—	—	—	7.9	—	—	—	—	—	—	—
23	1.5	—	1.4	1.4	1.7	—	1.4	1.3	1.5	1.2	—	1.5	1.2	1.4	—	1.2	1.7	1.5	1.4	1.4	—
24	17.3	16.4	17.9	17.6	16.8	15.5	15.7	18.2	16.3	17.6	16.7	17.0	16.9	16.3	15.5	16.3	17.5	15.6	15.9	15.2	15.0
25	12.1	11.0	12.9	12.1	11.1	12.3	13.3	13.3	11.5	13.3	11.5	11.9	11.6	11.1	11.1	11.5	13.0	11.0	11.7	10.9	—
26	6.2	5.5	7.1	6.3	6.5	5.3	6.0	6.8	6.7	6.9	6.5	6.2	5.6	6.2	5.2	5.6	7.0	5.2	5.4	5.3	5.0
27	9.4	9.1	(7.7)	9.9	9.5	(7.7)	11.5	10.8	10.2	10.1	10.4	9.3	9.6	7.5	8.7	10.7	12.5	—	8.4	9.1	8.9
28	16.8	14.6	(17.9)	15.4	17.7	(14.5)	18.7	13.1	19.8	15.4	19.8	15.5	15.3	19.8	13.5	16.7	19.0	16.6	15.9	17.3	18.6
29	22.3	20.1	—	25.3	25.9	20.5	29.4	28.0	25.7	24.5	24.0	23.7	23.3	23.8	23.8	24.6	27.3	18.5	26.2	23.2	23.9
30	6.7	7.3	—	7.7	7.3	6.4	6.8	8.1	7.8	7.4	8.6	7.5	7.2	7.5	6.3	8.3	8.3	7.1	7.1	7.7	8.5
31	1.5	1.6	—	1.9	1.3	0.9	1.5	2.0	1.6	1.3	1.8	1.8	1.6	1.6	1.4	2.0	2.0	1.3	2.1	1.8	1.5

TABLE 19. Cranial measurements of specimens in Group A. Condylobasal and tympanic bulla lengths are given in mm. Other measurements except tooth counts are expressed as percentages of CBL. Measurement nos. are keyed to table 4.

NOS	PEM 1518/98	M.Y.	PEM 1514/48	PEM 1517/58	PEM 1518/97	PEM 1496/73	PEM 1518/27	PEM 1517/61	PEM 1517/72	PEM 1517/69	PEM 1519/28	PEM 1519/95	PEM 1517/96	PEM 1514/98	PEM 1519/07	PEM 1518/54	PEM 1516/00	PEM 1517/60	PEM 1514/97	PEM 1519/27	PEM 1516/33	J. Cmtie	PEM 1517/83	PEM 1515/83	
1	433	454	455	457	458	459	464	467	468	472	472	472	474	476	477	480	482	482	483	488	489	491*	492	493	
2	58.2	57.3	57.1	54.7	55.7	57.5	55.8	57.8	59.0	57.2	58.3	57.4	57.8	57.4	56.6	56.9	58.1	57.7	57.8	57.5	58.9	58.9	57.0	59.3	58.0
3	23.3	23.8	24.2	22.3	26.0	24.2	22.4	23.6	24.4	23.5	24.2	21.4	23.6	23.1	24.5	25.4	23.9	23.9	22.8	25.0	22.3	24.9	24.9	22.9	
4	16.7	17.0	16.7	16.0	16.8	17.4	17.5	16.5	17.1	16.9	17.0	16.1	17.3	16.6	17.2	18.8	16.2	17.0	15.9	16.8	16.4	19.2	17.3	16.8	
5	13.6	15.4	13.8	13.8	14.0	13.8	14.2	13.1	15.4	12.9	14.6	13.1	14.1	13.2	13.8	15.6	13.3	13.5	11.6	14.6	13.1	16.5	13.6	13.6	
6	7.4	7.7	7.3	7.4	7.4	7.4	6.5	8.1	7.7	6.4	7.0	6.6	7.0	6.7	7.8	8.1	7.1	6.8	6.6	7.8	7.0	8.8	7.5	6.7	
7	67.9	67.6	67.0	65.0	66.4	68.2	65.3	66.6	66.0	66.7	67.2	67.2	68.6	66.8	66.7	66.0	67.4	66.2	68.3	66.4	68.1	67.8	68.7	67.3	
8	65.8	67.0	66.4	63.0	65.1	66.2	—	66.4	65.2	67.2	66.1	66.1	66.2	66.8	65.8	65.0	69.3	67.4	68.3	67.6	67.7	69.7	67.1	66.5	
9	41.6	—	44.4	42.2	43.2	43.1	42.7	42.2	44.4	44.7	43.2	42.4	43.9	41.6	42.8	45.8	43.4	42.3	41.0	44.3	41.1	43.2	41.7	41.6	
10	46.7	—	49.0	48.6	49.8	49.2	48.9	47.5	49.6	50.4	49.4	47.7	49.6	47.7	49.3	52.3	48.8	47.3	46.6	49.2	46.6	49.7	47.8	47.3	
11	43.2	43.1	44.8	43.3	43.9	44.0	44.4	42.4	45.3	45.1	44.1	42.8	44.5	42.9	44.9	46.0	43.2	42.5	42.4	43.9	42.3	—	43.1	42.2	
12	12.0	12.5	12.1	11.4	12.0	11.3	11.4	11.1	12.6	11.2	11.4	10.6	10.8	10.9	11.1	12.1	12.0	12.0	11.4	11.3	11.2	—	11.0	11.2	
13	45.7	—	47.9	48.6	—	47.9	48.9	46.9	50.9	49.8	48.7	47.6	48.9	48.9	49.7	52.3	47.9	47.5	47.2	—	46.8	49.1	48.9	47.9	
14	18.7	18.5	18.5	16.8	17.9	19.0	16.6	16.7	19.0	16.9	18.2	16.9	17.1	16.6	17.2	18.3	18.7	17.4	17.4	18.0	17.2	18.3	17.5	17.2	
15	33.7	36.6	38.0	37.2	40.4	36.8	39.7	35.5	35.9	37.7	36.2	36.4	36.9	37.8	36.9	36.5	36.5	36.1	37.5	36.3	34.2	35.2	35.0	35.9	
16	26	24	24	24	24	25	23 + 2 (2)	24	23	24	25	26	26	24	24	24	26	26	26	26	24	25	25	26	
17	27	23	25	24	24	26	25	23 + 1	23	24	25	27	27	24	25	24	27	25	25	25	24	25	25	26	
18	48.3	44.9	45.5	44.0	46.7	46.2	45.9	45.4	44.9	45.3	46.2	44.9	46.8	47.9	45.9	44.0	46.1	46.1	45.8	44.7	24	—	46.7	47.3	
19	49.4	44.7	44.6	44.6	46.1	45.8	46.1	45.4	44.9	45.8	46.8	44.9	45.8	47.9	46.1	44.6	46.1	46.1	46.2	44.3	43.6	—	48.4	47.1	
20	49.4	46.9	—	45.7	47.4	47.5	46.3	48.6	45.7	47.5	47.7	47.0	47.0	49.8	46.8	47.3	48.3	47.9	47.8	45.5	48.3	—	49.8	48.3	
21	49.9	—	47.9	46.0	46.9	47.5	47.0	48.6	45.7	47.7	47.7	47.2	47.5	49.8	46.0	47.3	48.3	47.9	48.2	45.5	48.3	—	49.8	48.3	
22	26 + 2	25 + 1	24 + 2	23 + 1	25 + 1	25 + 1	23	24	24	24	25	26	26	24	25	25	26	24	25	25	26	26	26	26	
23	26 + 2	25 + 1	24 + 2	23 + 1	25 + 1	24 + 1	25	24	23	24	25	26	26	24	24	25	26	24	25	25	26	26	26	26	
24	53.6	49.6	47.7	45.5	46.1	48.4	44.2	46.5	47.4	47.7	47.5	48.3	48.7	—	47.2	49.6	48.3	48.5	—	45.5	47.6	47.5	49.8	48.3	
25	52.9	49.3	47.3	45.7	45.4	48.4	47.0	46.7	46.6	46.6	48.1	48.3	48.3	—	46.3	48.3	48.3	48.5	—	46.5	47.6	47.1	49.8	48.3	
26	54.0	50.0	47.9	45.7	46.3	49.5	44.6	46.7	48.1	49.4	48.5	48.9	48.9	—	47.8	49.8	49.0	49.2	—	47.1	48.3	—	50.4	48.7	
27	53.1	50.0	47.7	46.6	47.2	49.5	47.4	46.7	47.0	47.2	48.7	48.1	48.7	—	47.0	48.8	48.8	48.3	—	46.9	48.3	—	50.4	47.9	
28	86.1	87.0	84.6	82.5	84.5	83.7	83.8	83.7	85.0	84.5	86.0	83.5	85.9	—	84.3	86.3	85.7	84.0	—	85.5	83.5	83.5	85.0	84.6	
29	16.6	18.9	18.0	17.1	17.5	18.1	17.5	16.9	17.9	17.4	18.4	17.2	18.6	—	17.6	18.8	18.3	17.2	—	18.2	16.4	18.7	17.9	17.4	
30	17.3	14.8	13.8	13.6	15.1	15.7	12.5	14.1	14.3	14.6	14.6	14.0	15.4	—	14.3	16.7	14.7	14.7	—	14.4	14.7	13.0	15.2	14.2	
31	20.8	—	22.6	21.0	22.3	20.5	22.4	21.8	23.7	23.5	23.7	22.7	23.6	22.5	22.9	22.5	22.0	22.2	23.2	23.0	20.9	22.6	22.6	22.7	
32	14.3	16.7	17.1	15.3	18.8	16.1	17.2	17.3	16.7	18.4	16.3	16.9	15.6	17.4	17.4	16.7	14.7	15.4	17.2	15.8	15.5	15.3	17.1	16.6	
33	10.6	12.3	9.9	10.3	9.6	9.2	10.1	10.7	12.8	9.7	11.0	10.0	10.5	10.3	10.5	11.5	10.2	9.8	8.5	11.5	9.6	14.5	11.4	10.3	
34	26.3	34.6	33.0	34.8	28.6	31.2	28.7	31.5	35.5	31.4	27.1	32.8	32.1	30.7	27.3	29.0	31.3	31.7	32.7	29.1	30.7	29.3	33.7	31.2	
35	27.3	31.3	31.6	31.3	27.8	31.2	32.3	31.7	32.1	31.4	26.7	31.4	30.0	31.3	27.9	—	30.5	31.3	31.7	30.6	29.1	29.7	29.9	31.2	
36	9.0	9.9	9.7	9.2	8.5	9.6	8.2	9.0	9.8	10.2	8.6	9.3	9.7	9.9	—	11.0	10.0	8.9	9.9	10.6	—	9.0	9.8	9.1	
37	8.3	—	8.8	9.0	8.5	8.7	7.3	8.8	9.2	9.5	8.1	8.9	8.9	9.2	8.8	10.2	9.5	9.1	9.1	9.1	8.6	8.1	8.7	8.7	
38	—	—	37	—	37	—	35	35	35	37	36	38	36	—	37	36	—	35	—	37	35	—	36	—	
39	—	—	—	—	37	—	35	35	—	37	36	38	34	—	37.5	36	—	35	—	36	35	—	36	—	

* 10 mm added to CBL for breakage.

ROSS: TAXONOMY OF BOTTLENOSED DOLPHINS TURSIOPS SPECIES

TABLE 20. Cranial measurements of specimens in group B. Condylbasal and tympanic bulla lengths are given in mm. Other measurements except tooth counts, are percentages of CBL. Measurement nos. are keyed to table 4.

Nos.	PEM 1517/77	PEM 1515/74	PEM 1516/06	SAM 35104	Palmer 18	PEM 1515/94	SAM 19928	SAM 37124
1	504	517	530	541	562	568	574	578
2	56,2	55,7	56,6	56,7	57,1	57,0	58,3	56,4
3	25,2	25,7	24,5	26,8	26,5	27,1	25,8	27,3
4	18,3	20,5	19,6	20,7	22,2	21,5	19,5	22,5
5	14,5	15,5	14,7	16,5	17,3	17,1	15,2	18,3
6	8,3	8,8	8,3	9,4	9,4	9,9	7,5	9,7
7	66,9	66,9	67,0	66,3	67,3	67,5	67,4	65,9
8	67,9	66,0	—	67,6	69,2	68,3	69,7	67,5
9	45,6	47,2	45,5	46,0	46,6	48,4	43,2	47,9
10	50,4	52,2	47,9	51,6	50,5	53,0	47,7	52,1
11	45,4	47,6	44,2	—	—	47,5	—	45,8
12	10,9	11,6	11,9	—	—	11,8	—	11,8
13	51,0	51,8	48,7	52,9	51,8	55,1	48,6	52,9
14	17,5	19,5	19,6	19,4	18,3	18,5	17,2	18,7
15	35,9	37,7	35,5	36,0	33,5	34,9	33,1	33,4
16	22 + 2	22 + 2	22 + 2	24*	25	21 + 2	24	22
17	22 + 2	22 + 2	23 + 2	24*	24	22 + 3	25	23
18	46,6	46,4	48,3	47,7	49,5	47,2	48,7	46,9
19	46,6	46,4	49,4	46,9	49,8	47,5	49,1	46,7
20	47,2	—	49,1	—	—	47,7	—	48,1
21	47,2	48,0	50,1	—	—	47,9	—	47,9
22	21 + 2	21 + 2	21 + 2	23*	22	20 + 1	23	21
23	21 + 2	21 + 1	21 + 1	23*	22	21 + 1	24	22
24	46,8	46,0	45,7	47,7	47,2	45,4	47,6	46,2
25	46,4	45,1	45,7	46,7	47,7	45,4	47,6	46,0
26	47,2	47,8	46,8	—	—	47,2	—	—
27	47,2	46,8	46,8	—	—	47,4	—	—
28	84,5	83,8	84,3	85,3	85,4	87,1	85,4	86,2
29	18,5	19,3	17,0	18,3	18,7	18,8	17,6	19,0
30	14,5	15,7	13,4	12,9	14,1	14,4	15,7	12,6
31	21,0	22,8	20,9	20,7	19,9	22,0	20,6	21,6
32	15,3	15,9	14,7	15,3	14,4	14,4	16,6	16,6
33	11,1	11,2	10,8	12,6	13,5	12,9	11,0	14,7
34	30,9	32,5	31,3	31,4	30,2	32,0	30,3	30,3
35	31,3	31,7	30,8	—	—	30,8	—	—
36	10,5	12,0	11,5	12,2	12,6	12,5	10,1	11,8
37	9,7	11,4	10,9	11,3	11,9	11,3	9,8	10,7
38	38	38	38,5	—	—	—	—	—
39	38	38	38	—	—	—	—	—

* Some alveoli possibly obliterated by ossification.

TABLE 21a. Cranial measurements of *Tursiops truncatus* stranded on British shores, and housed in the British Museum. Condylbasal length is given in mm. Other measurements, except tooth counts, are expressed as percentages of CBL. Measurement nos. are keyed to table 4. Measurements by courtesy of Dr. F. C. Fraser.

Nos.	1935 9.21.1	SW 1934/7	SW 1930/24	SW 1928/34	356a	353d	SW 1915/1	SW 1928/21	353e
1	500	522	526	526	528	533	536	537	537
2	57,6	57,2	55,5	57,4	58,3	55,5	55,4	59,0	58,5
3	26,6	30,3	26,6	26,8	25,6	28,6	27,6	26,8	28,1
5	17,4	20,5	16,9	17,5	16,3	19,3	17,7	17,1	17,9
6	9,2	11,3	8,9	10,5	8,5	11,1	10,1	10,1	10,4
7	66,2	67,0	64,8	66,2	67,6	63,6	62,5	67,4	67,0
8	67,6	67,6	66,9	66,2	69,7	66,8	—	67,0	68,0
11	47,6	51,7	46,2	48,3	43,0	50,7	46,3	48,8	47,1
13	—	58,4	51,9	56,7	48,3	56,7	54,3	56,4	52,9
14	19,6	19,9	19,8	20,0	18,6	20,5	18,8	19,0	20,3
16	23 + 2	22	22 + 1	25	25	—	21 + 1	22 + 2	23 + 2
17	22 + 2	22 + 1	23 + 1	25	25	—	21	22	23 + 2
18*	48,8	47,5	47,9	48,3	48,3	46,0	44,0	47,9	48,4
22	21 + 2	21 + 1	15 + 1-2	23	23	—	21	16 + x	22 + 2
23	—	22 + 1	16 + 1-2	23 + 1	23	—	20	18 + x	21 + 2
26*	47,6	47,1	47,1	50,4	47,0	46,0	46,1	49,2	49,3
28	87,0	87,5	86,5	86,9	86,0	87,2	85,3	90,5	87,2
30	13,6	13,2	14,1	15,6	11,7	13,1	12,9	14,5	15,5
31	22,4	21,6	22,2	24,9	19,7	26,3	22,2	22,9	21,6
32	15,4	17,6	13,7	17,5	15,0	16,9	17,5	16,2	17,1

* Unknown whether measurements refer to left or right.

TABLE 21b. Cranial measurements of *Tursiops truncatus* stranded on British shores, and housed in the British Museum. Condylbasal length is given in mm. Other measurements except tooth counts are expressed as percentages of CBL. Measurement nos. are keyed to table 4. Measurements by courtesy of Dr. F. C. Fraser.

Nos.	SW 1928/40	SW 1931/17	SW 1930/12	1935 9.18.1	SW 1927/21	SW 1918/13	SW 1935/29	353 g
1	545	546	548	551	558	562	575	575
2	57,8	57,9	57,7	57,2	56,1	57,3	57,7	57,0
3	27,3	25,8	27,0	27,9	26,9	28,1	27,5	27,1
5	18,3	—	20,4	18,5	17,7	19,6	19,3	16,9
6	9,9	9,2	10,6	10,9	9,9	10,3	10,4	10,1
7	67,9	66,5	66,1	—	65,9	66,7	66,6	68,0
8	69,7	68,7	67,5	67,3	65,9	68,5	67,1	69,0
11	47,7	44,7	48,0	47,4	—	49,6	48,0	48,0
13	54,1	49,1	54,7	53,5	53,9	56,9	55,3	54,1
14	19,3	19,2	18,4	20,7	20,8	20,3	20,5	19,5
16	—	22 + 2	23 + 1	20 + 1	—	—	21 + 2	20 + 1
17	—	23 + 2	23 + 1	22 + x	—	—	21 + 2	22 + 1
18*	50,1	49,1	47,6	48,1	47,3	48,4	48,3	47,0
22	—	22 + 2	23	—	—	—	—	20 + 1
23	—	23 + 2	23	—	—	—	20 + 3	20 + 1
26*	48,1	48,4	49,5	—	46,6	49,6	46,3	46,4
28	87,3	86,1	87,2	—	84,6	88,8	—	87,7
30	15,6	12,1	15,0	—	13,3	17,1	14,1	14,1
31	25,5	20,1	20,1	24,5	24,6	24,9	22,4	22,4
32	19,3	15,6	16,4	17,8	19,2	17,6	15,3	14,8

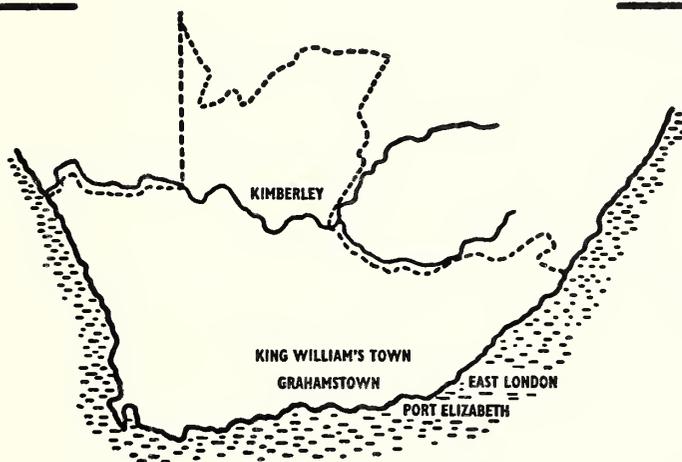
* Unknown whether measurements refer to left or right.

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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 ● PART 10

9th FEBRUARY 1978

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

A selected bibliography of literature on Odonata from Africa and adjacent islands

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This bibliography was compiled to supplement that of Pinhey (1962) which included references to African Odonata up to December 1959. While the vast majority of articles included here are subsequent to this date there are some earlier, non-systematic references omitted by Pinhey. All publications with references to Odonata have been included, whether systematic, ecological, zoogeographical, biological or bibliographic. Since only literature seen by the compilers is included the bibliography cannot claim to be complete and we shall be grateful to readers who send us any references that have been omitted.

The geographical coverage of articles is indicated by a code letter or letters placed after each reference. The code letters and their meanings, after Scott & Scott (1969), are as follows:

- N. North Africa, i.e. Africa north of the Sahara, including oases.
- C. Africa south of the Sahara but north of the Zambesi. This is the largest area, including all the central African countries from the Sudan to Zambia and Senegal to Somalia.
- S. Southern Africa, i.e. Africa south of the Zambesi. This includes South Africa, South West Africa, Rhodesia, Lesotho, Swaziland, Botswana and the southern part of Mozambique.
- I. Islands off the coast of Africa with the exception of those in the Mediterranean Sea which are excluded.
- A. This indicates Africa as a whole and means that the article concerned covers the continent in general.

The relative importance of an article is indicated by the number of asterisks placed after the geographical code of that reference. Following Davies & Davies (1976) the ratings are as follows:

- * only passing reference made to Odonata;
- ** a part of the article deals with Odonata;
- *** the article deals exclusively with Odonata.

An article dealing exclusively with Odonata but with only passing reference to an African species or the African distribution of a species is rated as single asterisk.

The abbreviations of publication titles cited are from the Biosis List of Serials (1975) (CODEN). Titles of publications not included in the Biosis List of Serials are written out in full in italics.

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ACKNOWLEDGEMENTS

Thanks are due to Dr E. C. G. Pinhey of the National Museum, Bulawayo, for allowing us to consult his reprint collection; to Dr K. M. F. Scott of the National Institute of Water Research and Mr C. F. Jacot-Guillarmod, Director of the Albany Museum, for their advice and encouragement; to the staff of the Rhodes University Library for their assistance in resolving bibliographical problems and to Miss R. Couch for typing the manuscript.

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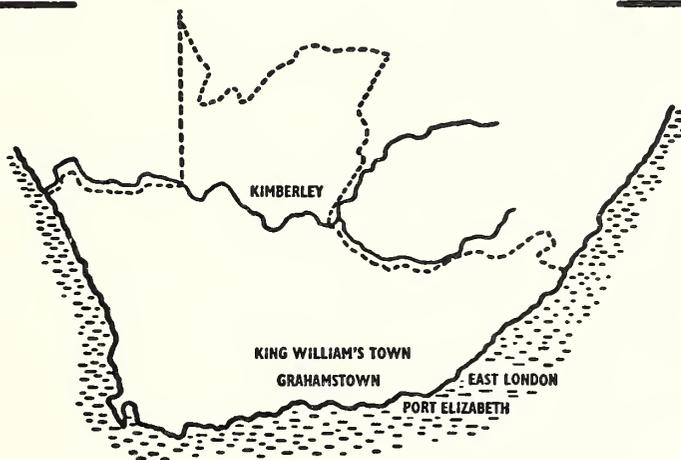
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 11

10th MAY 1978

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

Ethological notes on *Holotachysphex turneri* (Arnold) (Hymenoptera: Sphecidae: Larrinae) in the Eastern Cape Province of South Africa

by

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INTRODUCTION

The genus *Holotachysphex* de Beaumont, 1940 (= *Phytosphex* Arnold, 1951 and *Haplognatha* Gussakovskij, 1952) consists of six species found in Africa, Madagascar, the eastern Mediterranean area, southwestern USSR, and the Oriental Region. Most of these species were originally included in the genus *Tachysphex* Kohl. According to Bohart and Menke (1976: 282) *Tachysphex* and *Holotachysphex* are similar in general facies but the presence of a number of basic differences warrants their separation.

The only hitherto published observations on the nesting of *Holotachysphex* are those by Brauns concerning *H. turneri* (Arnold) at Willowmore in the Cape Province of South Africa. According to Arnold (1923: 166), reporting upon Brauns' observations, this species 'nests in hollow stems of *Aloe*, *Datura*, etc., lying on the ground; the partitions between the cells being formed of earth and little pebbles'. The prey was not recorded. The statement that the stems were lying on the ground indicates that they were dried out. In the case of the *Aloe* the hollow stem is most likely that of an old inflorescence.

In view of the paucity of biological information on the genus it is considered justified to publish the present notes on the nesting of *H. turneri* (Arnold).

THE NESTING OF HOLOTACHYSPHEX TURNERI (ARNOLD)

Information on the nesting of *H. turneri* (Arnold) was obtained as a result of the utilization for nesting purposes by this wasp of five trap-nests of the types described by Krombein (1967 and 1970). All the trap-nests concerned were in the field at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19'S., 26° 32'E.) in the Albany Division of the Eastern Cape Province of South Africa. Hilton is about 270 kilometres E. of Willowmore, the site of Brauns' observations. An account of the climate and vegetation of Hilton has previously been given (Gess and Gess, 1974: 191-192).

All five trap-nests utilized by *H. turneri* were 165 mm long and had a bore of 6.4 mm. All were suspended horizontally from living branches of small trees, one from *Salix mucronata* at a height of 2 metres above the ground and the other four from *Acacia karroo* at a height of a little above 1 metre. Trap-nest A (that on *Salix*) was taken in from the field on 11.i.1974, trap-nests B, C, D and E on 9.xii.1975, 29.xii.1976, 3.i.1977 and 4.ii.1977 respectively, each trap-nest having been utilized by the wasp within the preceding three or four days.

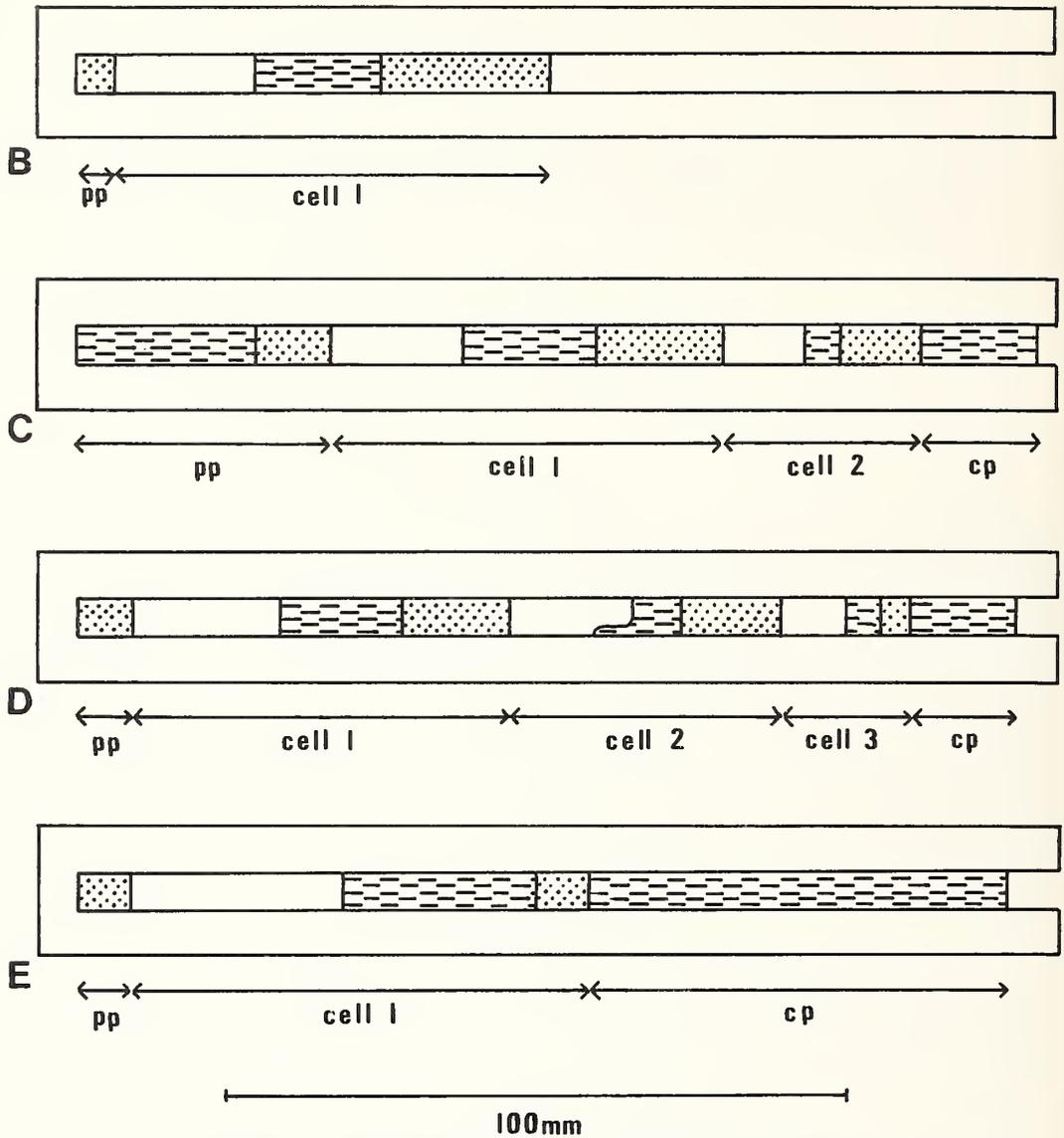


Fig. 1. *Holotachysphex turneri* (Arnold). Plans of nests B-E showing preliminary plugs (pp), cells, and closing plugs (cp) as well as nature of nesting materials: clods of clayey earth (stippled) and coarse detritus (dashed).

Due to the disarrangement of the nesting materials in nest A resulting from a mishap during the splitting open of the trap-nest no accurate measurements were possible and the account of nest architecture is consequently based mainly upon nests B-E (see Fig. 1) all in trap-nests with perspex windows and wooden lids.

H. turneri was found to have constructed a preliminary plug at the inner end of all five trap-nests, no empty space being left between this plug and the blind end of the boring. In nests B, D and E the plug consisted of small clods of clayey earth and was 6, 9 and 8 mm in thickness respectively. In nest C the preliminary plug was much more extensive and consisted of an initial 29 mm of coarse detritus (all derived from *Acacia* and consisting of small bits of bark, short lengths of twigs, seeds and leaflets), available to the wasp on the ground beneath the trap-nests, followed by 12 mm of the usual small clods of clayey earth. Four nests were completed of which nests A and E contained one cell each, nest C two cells and nest D three cells. Nest B was incomplete and contained a single cell. Each cell was capped by a partition consisting of two parts, an inner part composed of detritus and an outer part consisting of clods of earth, the whole plug thus being of the same composite nature as the preliminary plug of nest C. The seven capped cells were 21-75 mm long (mean 53 mm). The partitions closing these cells were 10-49 mm thick (mean 32 mm). The thicknesses of the detritus and of the earth in the partitions were 5-31 mm (mean 16 mm) and 5-29 mm (mean 16 mm) respectively. The closing plugs sealing the completed nests were composed of coarse detritus. The closing plugs of nests C, D and E were 19, 17 and 68 mm thick respectively.

The prey in all five nests consisted of nymphs of a single species of short-horned grasshopper belonging to the family Pyrgomorphidae (Acridoidea) and tentatively determined as *Pyrgomorphella* sp. by the author. A sample was submitted to Dr H. D. Brown who replied that the nymphs "are so small that they are almost impossible to determine with certainty, they could, for example, belong to *Pyrgomorphella*, as you suggest, or they could belong to *Pyrgomorpha* itself".

The number of prey stored in each cell was dependent upon size and varied from four individuals (9-10 mm long with a combined mass of 68 mg) in nest E and five individuals (11-12 mm long) in nest A to thirty-two individuals (3.2-6.7 mm long with a mean length of 4.5 mm) in nest B.

The prey were without exception stored facing the blind end of the trap-nest. Although paralysed, slight twitching movements indicated that the prey grasshoppers were alive. *H. turneri* eggs were found attached to prey in cells 2 and 3 of nest D and feeding larvae were found in cell 1 of that nest, in both cells of nest C and in the cells of nests A and B. No egg or larva was found on any of the prey in nest E. In all cases the anterior end of the egg or the mouth of feeding larva was sited just behind the base of the left prothoracic coxa. The length of the egg or later the body of the larva lay transversely across the thoracic sterna and extended beyond the prey on the right. In the five cells of nests C and D the grasshopper bearing the wasp egg or larva was positioned on its back; other prey in the cells by contrast were positioned on their venters or sides. In all five cells the egg- or larva-bearing prey was situated at the inner end of the cell and it appears that oviposition is probably on the first prey to be introduced into the cell.

Developmental data are limited. However, from the dates of the major events in the life-history given in Table I it appears that about three days elapse between oviposition and egg hatching and that the larva grows to maturity within about six to eight days. Available evidence indicates that the species is probably univoltine.

The cocoon is surrounded by fine silken threads attached to the walls of the cell and in places to the cocoon itself and forming a thin net-like envelope or shroud to which in places adhere fragments of prey exoskeleton, clods of earth and other debris from which the cocoon itself is thus kept isolated. The cocoon is oval about 10 mm long by about 4 mm wide, at its widest, and tapers slightly to the rounded ends, the anterior one being more bluntly rounded than the

TABLE I. Developmental dates for *Holotachysphex turneri* (Arnold) in trap-nests from Hilton.

Trap-nest	Cell	Date of oviposition	Date of egg hatch	Date of larval maturity	Date of cocoon spinning	Date of adult emergence and sex
A	1	?	pre 11.i.74	16.i.74	18.i.74	(died)
B	1	on or pre 9.xii.75	12.xii.75	(died)	—	—
C	1	?	on or pre 29.xii.76	4.i.77	5.i.77	7.ii.78 (♀)
	2	?	on or pre 29.xii.76	5.i.77	6.i.77	6.ii.78 (♀)
D	1	?	on or pre 3.i.77	11.i.77	11.i.77	6.ii.78 (♀)
	2	?	4.i.77	11.i.77	11.i.77	(died, cocoon empty)
	3	probably 2 or 3.i.77	5.i.77	11.i.77	12.i.77	(died, cocoon contained fully developed ♂)
E	1	(no egg or larva found in cell)				

posterior. The walls of the cocoon are composed of fine sand grains, silk and an oral secretion to form a hard shell with a granular but glazed surface.

The identification of the nests as those of *H. turneri* was made possible by the capture on 3.i.1977 of a nesting female which was observed carrying small clods of earth into a newly positioned trap-nest. The earth which was being collected on the ground beneath the branch from which the trap-nest was suspended was carried up to the nest in flight and was being used by the wasp in the construction of the preliminary plug. This female is believed to have been the builder of the nests in trap-nests C (taken in on 29.xii.1976) and D (taken in on 3.i.1977) as both these had in their turn occupied the identical position in the same trap-nest bundle as did the trap-nest being worked upon by the female when she was captured. On 3.i.1977 less than an hour had elapsed between the removal of trap-nest D and the initiation of the preliminary plug in its replacement.

DISCUSSION

The genus *Holotachysphex* was described by de Beaumont (1940: 179) as a subgenus of *Tachysphex* Kohl in which genus five of the six species now placed in *Holotachysphex* were

originally included. Bohart and Menke (1976: 282) state that although the two taxa are similar in general facies and are allied with respect to the form of the genitalia, male subgenital plate, and the pair of supra-antennal tubercles, there are a number of basic differences that warrant the recognition of *Holotachyspex* as a genus. Among these differences, according to the above authors, are: the presence in *Holotachyspex* of lateral carinae on terga I and II, the absence of a foretarsal rake, the absence of a pygidial plate, the generally dense punctation of the body, and the velvety sternal patches of the male.

Other than Brauns' observations (Arnold, 1923: 166) that *H. turneri* (Arnold) nests in hollow stems lying on the ground, nothing has hitherto been published regarding the biology of any *Holotachyspex* species. In contrast, a considerable number of papers on the biology of *Tachyspex* species have appeared, important ones being listed by Bohart and Menke (1976: 270). A useful summary of the known biology of the Palaearctic species has been provided by Pulawski (1971: 16–20). The present observations on the nesting of *H. turneri* enable some basic facets of the biology of this species, as a representative of *Holotachyspex*, to be compared with the biology of species of *Tachyspex*.

The most notable differences in the nesting behaviour shown by *H. turneri* and species of *Tachyspex* pertain to the situation and nature of the nest and to the method employed by the wasp in the manipulation of nesting materials. Thus, with the exception of one species which uses abandoned *Philanthus* burrows or ant tunnels for its nest, all *Tachyspex* species as far as is known dig their nests in the soil. In contrast, *H. turneri*, as has been shown, nests in pre-existing cavities—hollow plant stems and old inflorescences lying on the ground (and in trap-nests 1–2 metres above the ground). Directly associated with these ethological differences are two of the basic morphological differences that according to Bohart and Menke warrant the separation of *Holotachyspex* from *Tachyspex*, namely the presence or absence in the female of a foretarsal rake and of a pygidial plate. Excavation of the nest in the soil by *Tachyspex* species is effected by the loosening of the earth by the mandibles followed by the removal of the loosened earth by the well-developed foretarsal rakes which are usually composed of long, fine, close-set, flexible spines. These tarsal rakes are used also in reopening temporarily closed nests and in sealing nests.

The pygidial plate in *Tachyspex* is believed to aid in nest excavation by acting as an earth pusher. *H. turneri* which nests in pre-existing cavities in horizontal or near horizontal plant stems neither excavates earth nor pushes earth and in common with twig-nesters in other genera of the family Sphecidae lacks a foretarsal rake and a pygidial plate in consequence. As far as is known manipulation of the nesting materials (clods of clayey earth and coarse detritus) by *H. turneri* is effected by the mandibles only.

In marked contrast to the above differences with respect to the nature of the nest and the method employed in the manipulation of nesting materials is the conformity shown by other facets of nesting behaviour, comparison being on a level of gross detail. Thus in both *H. turneri* and *Tachyspex* species the nest is prepared before hunting takes place—that is, in the former a preliminary plug is introduced into the pre-existing nesting cavity and in the latter a burrow is excavated in the ground. In both *H. turneri* and *Tachyspex* species orthopteroid prey is utilized: in the former Pyrgomorphae (Acridoidea); in the latter, according to the species, Acridoidea, Tettigonioidea, Grylloidea (all Orthoptera), Mantidae and Blattidae (both Dictyoptera). In both, the nests may be single-celled or multicellular and each cell is provisioned with an indefinite number of prey: one to eight are recorded for *Tachyspex* species and four to thirty-two for *H. turneri*. Similarly, in both the prey is incompletely paralysed and twitching movements of the antennae, mouthparts and tarsi take place. Furthermore, the egg is positioned on the prey in the identical manner in *H. turneri* and in those species of *Tachyspex* which like the former utilize Acridoidea, namely, transversely across the underside of the prey's body with the anterior end attached immediately behind the base of one of the fore-legs. Whereas in *H. turneri* oviposition

appears to be on the first prey to be introduced into the cell, in *Tachysphex* the prey oviposited upon appears to vary according to the wasp species. Thus Pulawski (1971: 18) records oviposition to be on the first, second or last prey whereas Bohart and Menke (1976: 271) state that the egg is laid after the last provision is stored and that it is often placed on the largest prey.

Comparison of the overall nesting behaviour of *Holotachysphex* (as exemplified by *H. turneri*) with that of *Tachysphex* species indicates a close relationship between the two taxa which is in accord with that shown by the sum of their morphological characters. At the same time, however, *Holotachysphex* in general appears to be specialized or advanced in comparison with *Tachysphex* with respect to those major characters, both morphological and ethological, in which the two taxa differ.

If *Holotachysphex* species are considered to have developed from a *Tachysphex*-like form, as seems possible, then the major ethological advance would have been marked by the abandonment of the construction of a nest in the ground in favour of the utilization for nesting of a pre-existing cavity in a dry twig, stem or inflorescence. Concomitant with this change to twig-nesting would have been the secondary loss of both the foretarsal rake and the pygidial plate. This view is consistent with the conclusions of Bohart and Menke (1976) who hold that the absence of a foretarsal rake is specialized or advanced when it occurs in the Larrinae and that the absence in *Holotachysphex* of a pygidial plate is secondary. With respect to the presence in *Holotachysphex* of lateral carinae on terga I and II it is considered by the same authors that this character too is specialized or advanced and conversely that the absence of these carinae in *Tachysphex* is unspecialized or primitive.

If *Holotachysphex* is considered to have developed from a *Tachysphex*-like form, it appears to be a matter of opinion whether the species included in *Holotachysphex* are sufficiently distinct to warrant generic separation from *Tachysphex* as is advocated by Bohart and Menke (1976) or whether they should rather be seen as advanced species of *Tachysphex* in which case they could be accorded subgeneric separation as suggested by de Beaumont (1940). Of interest in this connection is the fact that the pygidial plate is weakly defined in a few *Tachysphex* and is totally absent in the aberrant Argentinian *T. mendozamus*. According to Bohart and Menke (1976: 270) this species, of which they saw only the female, could be placed in *Holotachysphex* except that it has a well-developed foretarsal rake and lacks the lateral carina on tergum II. Also of interest is the presence in *Tachysphex* and in *H. turneri* of an externoventral notch in the mandible and its absence in the other species of *Holotachysphex*. It may be hoped that ethological information pertaining to species such as *T. mendozamus* and further species of *Holotachysphex* when available will be of use in clarifying the relationship of the two taxa.

SUMMARY

Some aspects of the ethology of *Holotachysphex turneri* (Arnold) (Hymenoptera: Sphecidae: Larrinae) in the Eastern Cape Province of South Africa are described. In the study which was based upon five nests constructed within wooden trap-nests suspended from small trees particular attention is given to nest architecture and nesting materials, to the identity, number and orientation of the prey in each cell, and to the position of the wasp egg on the prey. The nesting of *Holotachysphex* is compared with that of species of *Tachysphex*, a closely allied genus.

ACKNOWLEDGEMENTS

The author wishes to thank Mr T. C. White of the farm Hilton for his much appreciated kindness over the years in allowing him free access to his land. Thanks are due also to Dr H. D. Brown, Head of the Red Locust Control Service, Pretoria for his help with respect to the identity

of the nymphal Pyrgomorphidae. The author is grateful to the C.S.I.R. for a running expenses grant for field work during the course of which the present observations were made.

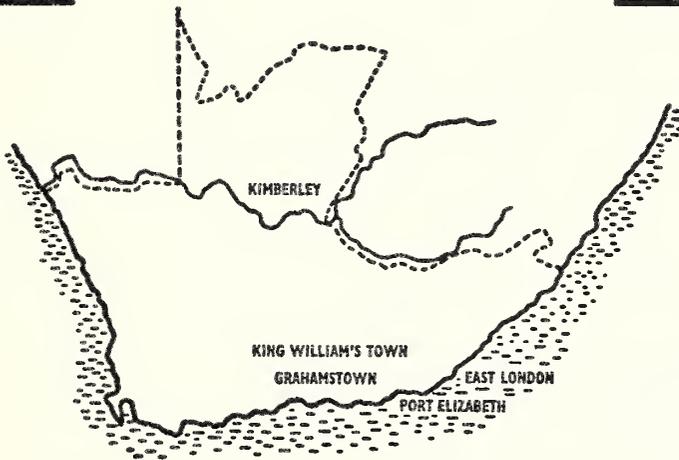
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ANNALS
OF THE
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Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 12

20th JUNE 1978

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

The Re-Excavation of Powerhouse Cave and an Assessment of Dr Frank Peabody's Work on Holocene Deposits in the Taung Area

by

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INTRODUCTION

In 1947 and 1948 the palaeontological part of the University of California and South African Expedition investigated the travertine deposits at Buxton, near Taung in Bophuthatswana. This work was under the direction of Dr Frank Peabody (1954). Interest in the Buxton area was prompted by the fact that this was the type locality of *Australopithecus africanus*. Peabody's investigations were not, however, confined to the geological and palaeontological aspects of the travertines; he also undertook test excavations at a number of rock shelters which yielded Upper Pleistocene and Holocene artefact assemblages. None of these assemblages was ever described in detail and they were identified as either "Middle Stone Age" or "Later Stone Age" (or "Wilton") in terms of the intuitive criteria applied at that time. Recently Prof J. D. Clark (1971) described the Upper Pleistocene artefacts from Witkrans and this represents the first detailed analysis of any of the artefacts recovered by Peabody. The Holocene artefacts became of interest in the context of a research project based on the Kaap Escarpment undertaken by the writer during the period 1973-76 while he was on the staff of the McGregor Museum, Kimberley. Preliminary enquiries revealed that the assemblages excavated by Peabody had been split up between, at least, Johannesburg and Berkeley, U.S.A. (R. J. Mason and J. D. Clark, pers. comm.). It became clear therefore that any re-assessment of the Buxton Holocene assemblages would have to be based upon new excavations. Several of the sites within the Buxton mining area originally investigated by Peabody have been destroyed by the mining operations and only Powerhouse Cave now has potential for reinvestigation. This paper presents the results of the re-excavation of Powerhouse Cave and an assessment of Peabody's work on the "Later Stone Age" in the area.

THE AREA

The Kaap Escarpment is a prominent scarp averaging about 100 m in height and extending for some 280 km in a north-east to south-west direction from 27° 7'S. near Vryburg in the north to 29° 7'S. near Douglas in the south. It is the eastern edge of the Kaap Plateau which is composed predominantly of Precambrian dolomites of the Transvaal System. The escarpment itself is an exhumed early Palaeozoic erosional feature which was subsequently buried under Karoo sediments and then re-exposed by the late Tertiary planation of the Vaal Basin (Butzer 1974: 369). At various points along the escarpment major drainage lines have incised V-shaped gorges (or "kloofs") in which travertine deposits have formed. The Buxton-Witkrans travertines investigated by Peabody are a series of such travertines located on the northern reaches of the Kaap Escarpment (Fig. 1).

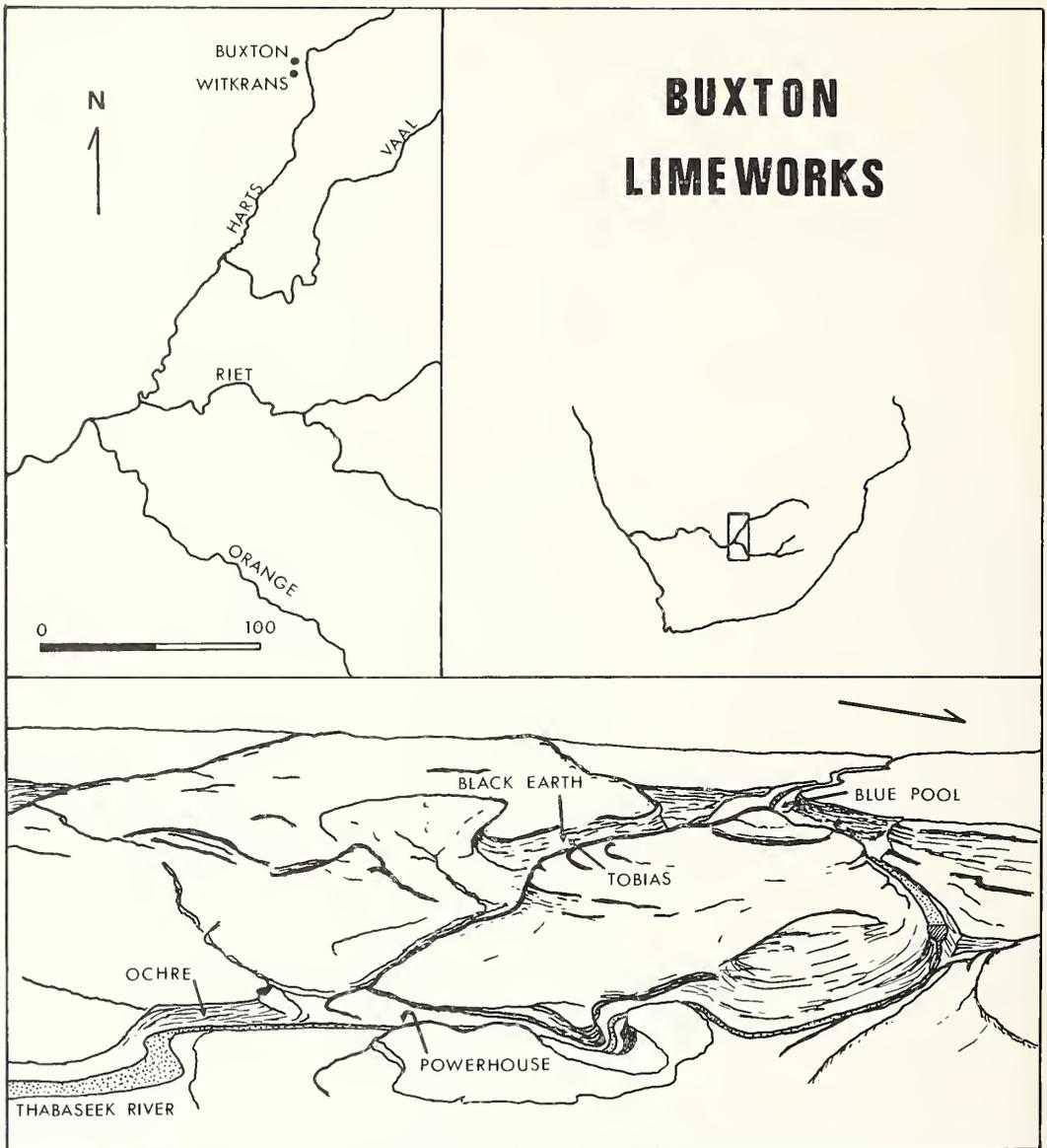


Fig. 1. Locality map. The diagrammatic panorama of the Buxton travertines is from Peabody (1954: Plate 5) and shows the topography before quarrying operations began. The distance from Ochre Cave to Blue Pool is approximately 1,25 km.

The mining settlement of Buxton (or Norlim as it is now called, although for the sake of clarity the old name is retained here) is located at the base of the escarpment overlooking the Harts River valley (27° 37,2'S., 24° 38,5'E.). The Kaap Escarpment is an arid area, with extremes of temperature; in summer the temperature often exceeds 38 °C while in winter there is frost. The average rainfall near Buxton is about 450 mm, most of this falling in the summer months. Much of the rain-water is absorbed by the surficial sediments and it is only after protracted heavy rains that streams develop.

The travertines at Buxton developed with respect to two successive bedrock valleys of the Thabaseek River which now occupies a canyon measuring as much as 200 m from shoulder to shoulder and 50 m in depth (Butzer 1974: 374). The river rises some 30 km to the west and is substantial enough, even today, to have justified the construction of dams. The relationship of the river to the various travertine bodies has been discussed in detail by Butzer (1974) and no repetition is necessary here.

The vegetation in the Buxton area is similar to that occurring on the Kaap Plateau and Escarpment in general. The plateau *Tarchonanthus* veld consists of shrubs and trees on mixed grassland, *Eragrostis*, *Aristida* and *Digitaria* being the main species. The escarpment is covered by trees such as *Celtis* and *Ficus* as well as various types of succulents, with thickets of *Acacia* trees occurring sporadically. The plane down to the Harts River supports sweet veld grasses dominated by *Themeda triandra* (Acocks 1953).

The fauna in the area today is a remnant of a once rich fauna that existed in the past. The records of the early travellers bear testimony to the fact that many species now extinct in the area were present in large numbers in historical times. The possibility of animal migrations from the plateau to the river valley and vice versa according to rainy seasons has been discussed by Clark (1971: 1 226-7). Historical evidence for animal migrations and human adaptations to these patterns lies in remarks made by the Rev John Campbell (1822: 28) in 1820. Further discussion on this interesting hypothesis is not necessary here as it will appear elsewhere (Humphreys, in preparation).

PEABODY'S WORK ON THE HOLOCENE DEPOSITS

Peabody excavated five shelters which yielded Holocene deposits containing "Later Stone Age" artefacts and a sixth which although not "implementiferous" was also ascribed to the "Later Stone Age". These sites may be summarised briefly as follows:

(a) *Blue Pool Cave*

This small cave had already been destroyed by the time Peabody published his report. It was located above the Blue Pool and was formed when the Thabaseek River truncated the Oxland travertine. Excavations revealed a deposit some 1,5 m thick. The lower 60 cm were composed of unconsolidated fluvial sands with occasional bits of charcoal and bones of small vertebrates. Above this was approximately 30 cm of "blocky soil, dark blue black with red streaks" and then a further 30 cm of chalky lime with thin lenses of fluvial sand. The uppermost 30 cm of the deposit was composed of a brown earth overlain by a black earth with a superficial layer of dust and manure. The upper 15 cm contained splintered bones of ungulates, ostrich egg shell fragments and remains of owl pellets. Ash and charred bones were also recovered. These remains suggested to Peabody that "Wilton peoples occasionally used the cave". The fact that the deposits below the 15 cm level appeared to be mainly fluvial in origin indicated that the cave was not suitable for habitation during most of its existence.

(b) *Ochre Cave*

This small cave is still in existence. It was developed along a joint plane in the dolomite bedrock. The mouth opens at the base of a low cliff facing directly onto the bed of the Thabaseek

River. The floor of the cave is only about 1 m above the bed of the river and so the danger of flooding was ever-present. The floor is rubbly with very little deposit. Peabody however sank four test pits to a depth of about 30 cm. The excavation produced worked pieces of yellow and red ochre as well as "Later Stone Age" flakes and a few faunal remains; ostrich egg shell fragments were not present. The most notable fact about Ochre Cave is that it was the source of the ochre recovered in Powerhouse Cave. The limited area with deposit coupled with the lack of information on the location of Peabody's test pits does not justify further excavation at the cave.

(c) *Powerhouse Cave*

Full details on Powerhouse Cave are given below and so only a few comments are necessary here. Peabody seemed less interested in this site than in others as he remarked: "Because Powerhouse Cave is primarily an implementiferous site, Camp and the writer excavated only a few test pits and presented all the material to the Archaeological Survey of South Africa . . . The artefacts include elements only of the Wilton culture of Late Stone Age" (Peabody 1954: 687). The fact that the deposit contained no sign of fluvial action showed that the occupation of the cave began only after the river channel had eroded to approximately its present form. Peabody regarded this as important as it provided archaeological dating for this physiographic feature.

(d) *Witkrans Cave*

This cave and Little Witkrans shelter are located about 5 km south of the main Buxton quarry. The Witkrans Late Pleistocene deposits have been described by Peabody (1954: 690-1) and more recently by Clark (1971: 1 223) and so do not require further discussion here. The Holocene deposit consisted of a thin wedge of light brown, dusty rubble overlying the cemented Late Pleistocene deposit. This deposit contained a few worked flakes, ostrich egg shell fragments and beads which were "confidently correlated with Little Witkrans, Powerhouse Cave and Blue Pool Cave deposits" (Peabody 1954: 693).

(e) *Little Witkrans*

This shelter is a recess under a small travertine cliff and is about 3,6 m deep and 9,0 m wide. Peabody's excavations revealed a deposit 1,2 m thick, unconsolidated except for a fine to coarse agglomerate zone about 15 cm thick on bedrock. Peabody described the deposit as having accumulated under dry conditions except for a temporary wet period evidenced by a thin layer of crusty, white, limy earth about 40 cm below the surface. The uppermost 30 cm of the deposit had a high percentage of ash and also produced most of the artefacts recovered. Artefacts occurred down to about 1,0 m, however, and consisted of microliths, beads, ostrich egg shell and faunal remains.

(f) *Black Earth Cave*

This complex system of galleries yielded scant evidence of Holocene remains. Ash, a single bone awl and a single fragment of decorated ostrich egg shell "indicates the Wilton culture of the Late Stone Age of Africa" (Peabody 1954: 686).

It is clear from these descriptions that the Buxton-Witkrans caves together provided useful evidence of Holocene occupation. It is equally clear that the existing descriptions do not do justice to this evidence and that a reassessment based upon new excavations is necessary to provide a control for the integration of this evidence with the growing body of information on the Holocene of the interior of South Africa. This is the main reason for the re-excavation of Powerhouse Cave.

DESCRIPTION OF THE SITE

Powerhouse Cave is located in the east wall of the Thabaseek River canyon. The name is derived from the fact that the cave lies close to the ruins of an old plant which provided power for the mining operations (Fig. 1; see Peabody 1954: Fig. 2 for precise locality). The cave is part of a subterranean cavity which developed at the contact between the Norlim travertine and bedrock. This cavity was truncated by the Thabaseek River when its present bed was eroded. Traces of this original cavity can be seen directly opposite in the west wall of the canyon. The cave is about 5.0 m above the present bed of the river.

Powerhouse Cave is some 15 m wide at the mouth and 6 m deep; it has a high roof with ample clearance except for within a metre or two of the walls (Fig. 2). At the back of the cave is a narrow passage leading to a large cavity of about the same floor area as the front section but with a low roof making it impossible to stand upright except in the passage area. The floor of the rear cavern is covered in part by a powdery deposit.

The floor of the front section of Powerhouse Cave is more or less level and there is no surface indication of where Peabody conducted his excavations. The high mouth of the cave is such that about a third of the surface area of the deposit is unprotected from even a moderately driving rain; this may have had the effect of concentrating occupational activities further back rather than forward.

The walls of the cave have red ochre smudges and finger strips painted on them. The only design of any note is the so-called "five-rayed asterisk" described by Peabody (1954: 687). Peabody stated that these were the only paintings found in the caves of the Kaap Escarpment. Subsequent research has shown that this is not the case but these may nevertheless have been the only ones occurring in the Buxton-Witkrans area.

THE EXCAVATION

Peabody's published account of his work at Powerhouse Cave gives little on the nature of the deposit beyond the fact that it was "dusty, blackish earth, apparently wind blown, ranging up to 28 inches thick" (Peabody 1954: 687). "A few test pits" is all that is given on the extent of the excavations. Fortunately the writer was able to obtain copies of Peabody's field notes through the kind offices of Prof J. Desmond Clark of the University of California, Berkeley. These notes included a sketch plan showing the approximate positions of the various test pits. These positions have been plotted onto the ground plan of the cave shown in Fig. 2; it must be emphasised that these positions may be inaccurate as there is not a very close correlation between Peabody's sketch plan and the measured ground plan produced by the writer. The various passages in Peabody's diary directly relevant to Powerhouse Cave have been extracted and are presented in Appendix 1.

In the present excavations at Powerhouse Cave an area of 6 m² was laid out in the northern half of the cave (Fig. 2). This area was divided into three major Provenance Units (P.U.'s) and the excavation was to proceed in spits or according to natural layers should such be found to exist although from Peabody's descriptions the latter seemed unlikely.

The surface of the deposit was covered by a few cm of loose dung; below this was a hard deposit of dark grey to brown soil. This soil proved to be entirely featureless except for occasional concentrations of ash but even these were without clearly defined limits gradually fading out on all sides. The deposit was therefore removed in 4 arbitrary spit levels designated Levels S, I, II, and III (Fig. 3); the thickness of the levels was largely determined by the density of artefact and faunal remains. Bedrock was reached at a maximum depth of 60 cm and consisted of a solid shale surface.

On the basis of Peabody's sketch plan of his excavations it appeared that his "north pit" might have been expected to intersect the west side of P.U.-C. There was, however, no evidence

of any earlier disturbance in this area and the artefact and faunal concentrations in this P.U. were essentially similar to those in the other P.U.'s. It is therefore probable that Peabody's "north pit" did not extend as far back as the impression given in his sketch plan, or, alternatively, that it was placed further north than is suggested in Fig. 2.

DATING

Charcoal fragments occurred diffused through the deposit. Most of these were tiny fragments which meant that a sample collected over a relatively wide area would be required for dating purposes. One such sample from Level I in P.U-A was submitted for radio-carbon dating. A second sample consisting of several large pieces of charcoal found on bedrock in P.U-A was also sent to Dr J. C. Vogel of the C.S.I.R. The results were as follows:

P.U-A Level I	Pta 1763	2 250±65 B.P.
P.U-A Level II	Pta 1508	3 680±60 B.P.

These dates indicate that the dark grey to brown soil unit accumulated over a period of about 1 400 years. The fact that no visible evidence of stratigraphic breaks in the unit was found suggests that the deposit may have accumulated slowly but more or less continuously over this period.

STONE ARTEFACTS

(a) DEFINITIONS

All stones showing signs of modification through human agencies were recovered from the excavation. For the purposes of analysis the assemblage was divided into *Tools* and *Waste*. Tools

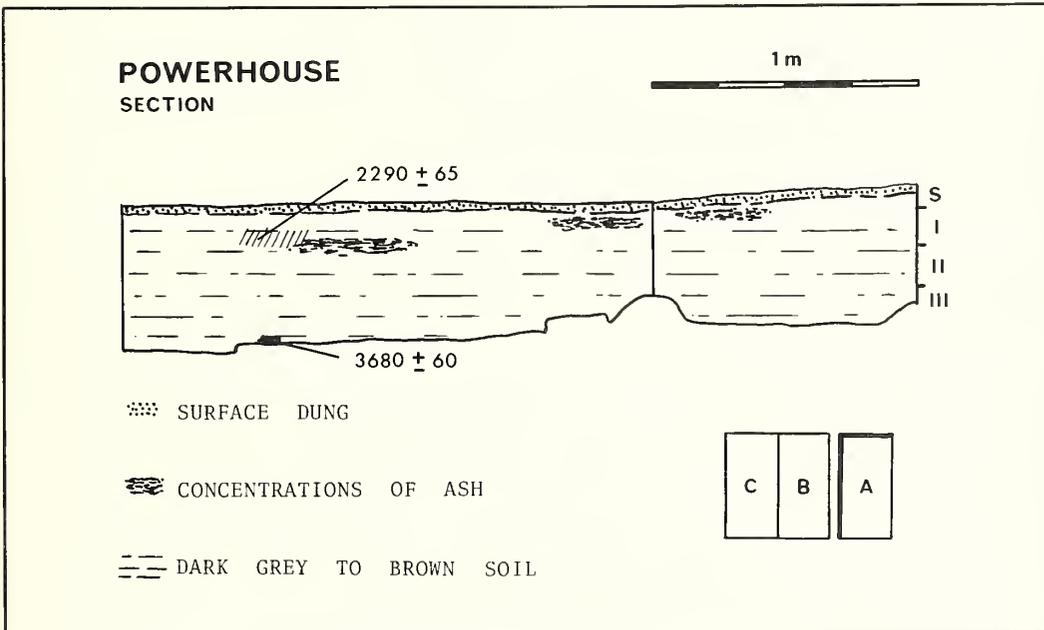


Fig. 3. Section through the excavation in Powerhouse Cave.

include all artefacts showing retouch or utilisation. Waste consists of whole unretouched flakes, flake fragments, flaked chunks and cores. The various classes may be defined as follows:

(i) Tools

(a) *Scrapers*: These are tools with systematic retouch over a portion of the perimeter of a flake. They represent a distinct class of tools that can be recognised even intuitively with a considerable degree of consistency. The scraper class was subdivided and measured according to the method used by J. Deacon (1972). Such an approach is preferred to a detailed typology such as that suggested by Sampson (1967) as it eliminates many of the inconsistencies of sorting which become obvious to anyone handling a series of artefacts from Holocene deposits in the interior of South Africa. Only whole scrapers were used in the analysis for obvious reasons. A broken scraper is recognised by the fact that the fracture cuts through a retouched edge thereby indicating that the retouch must have extended further along the edge of what was originally a larger flake. On the other hand, flakes that were broken before retouch (i.e. the retouched edges are complete) are nevertheless regarded as "whole" scrapers.

(b) *Backed tools*: These are small blades or flakes which have one whole lateral, or part thereof, backed or blunted by steep retouch. This class has been divided into two distinct groups: Backed blades and Crescents. In the case of backed blades the group has been divided into nine classes in a scheme that has been adapted from H. J. Deacon (1976). This typology provides a logical framework related to the manufacture of backed blades. The nine classes are as follows:

- A. Backed blade blank
- B. Blade with partial backing only on distal or proximal end
- C. Totally backed blade
- D. Distal discard
- E. Backed point terminated by break
- F. Backed point terminated by truncation
- G. Segment of backed blade terminated by breaks
- H. Segment of backed blade terminated by break and truncation
- I. Proximal discard including bulb.

The following dimensions were recorded for the back blades—length, breadth and height of backed edge. The distal and proximal discard classes (D & I) were not measured.

The second backed group—crescents—follows the generally used definition: they are backed pieces with a curved back so as to form an orange segment shaped tool. The dimensions recorded were as for the backed blades.

(c) *Other tools*: These consist of three main classes of tools which generally lack formal shape, as well as upper and lower grindstones. The definitions are as follows:

Outils are generally quartz crystals or fragments which show signs of flaking or crushing on one or more edges. These approximate to the generally used class of outil ecailles but they lack any consistency of shape or size; the distinguishing feature is essentially the flaked and crushed edge.

Adzes here describe a class of tools which although exhibiting a similarity of working edge shows no uniformity of shape or size. These pieces consist of a wide range of shapes of flakes and chunks each with a part of its edge having a very steeply flaked and battered area. These edges are similar to those occurring on tools described by others (e.g. Sampson 1967) as adzes but the overall form of individual pieces varies considerably and is not as uniform as implied in other definitions of adzes. The use of the term here is to describe the nature of the working edge rather than the form of the tool.

Trimmed/Utilised Flakes is a general class including all flakes which show signs of miscellaneous retouch or utilisation. Again these pieces lack any uniformity of shape or size but the fact that retouch occurs in places shows that they must have served some purpose.

Upper grindstones/hammerstones are cobbles showing signs of faceting or pitting as the result of use in the hand as a grindstone or hammerstone.

Lower grindstones are flat stones with distinct signs of smoothing resulting from the use of the stone as a grinding surface. This class includes complete as well as fragmentary examples.

(ii) *Waste*

(a) *Whole waste flakes*: These consist of whole flakes showing no sign of utilisation; they represent flaking debris and potentially usable flakes. The length and breadth of these flakes were measured.

(b) *Waste fragments*: These include broken flakes, chips and chunks all of which represent the residue of human activity but which cannot be sorted into any of the other classes recognised.

(c) *Cores*: These are pieces which show a pattern of flaking consistent with the systematic production of flakes. Three types were recognised: bladelet, radial and irregular. Their definitions follow Sampson (1967).

(b) *RAW MATERIALS*

Three major groupings of raw material types used for stone artefact production were recognised: chert, quartz and lydianite. "Chert" includes siliceous types such as chert, agate, chalcedony and jasper, all of which are essentially very fine-grained raw materials. Quartz is equally fine-grained but tends to be very brittle making it less useful for fine working. Lydianite or indurated shale is well known as a raw material used in prehistoric times. Its occurrence at Powerhouse Cave is of interest in that none of the other Kaap Escarpment sites investigated by the writer has produced any trace of lydianite. In this analysis the lydianite category includes a few pieces of quartzite which are too isolated to justify separate listing. Quartzite has been included with lydianite in that it and lydianite occur as relatively large fragments in contrast to the much smaller form of materials such as chert and quartz.

Chert and quartz were readily available in the immediate vicinity of the cave. The source of the lydianite was not found but in view of its abundance at the site it was clearly easily exploitable from the cave.

TABLE I

Powerhouse Cave: Raw Materials

		Chert	Quartz	Lydianite*
Level S	Tools	38,1%	4,8%	57,1%
	Whole flakes	9,9%	1,8%	88,3%
	Waste frags.	9,3%	13,7%	77,0%
Level I	Tools	47,9%	4,2%	47,9%
	Whole flakes	12,8%	0,5%	86,7%
	Waste frags.	5,9%	7,7%	86,4%
Level II	Tools	59,2%	4,1%	36,7%
	Whole flakes	10,4%	0,7%	88,9%
	Waste frags.	9,4%	6,8%	83,8%
Level III	Tools	55,8%	4,7%	39,6%†
	Whole flakes	15,8%	3,8%	80,4%
	Waste frags.	12,7%	10,9%	76,3%

*Includes traces of quartzite

†Includes 7,0% quartzite

The relative proportions of the raw materials used are given in Table 1. In the whole flakes and waste fragments categories lydianite is by far the dominant raw material type. This is probably a reflection of the fact that it occurs in larger forms than other raw material types and there is as a result more wastage. In the tool category, on the other hand, chert is far more important. It is interesting to note, however, that the trend through the sequence is towards a greater use of lydianite for tools until in Level S lydianite is also the dominant tool raw material. This pattern of large proportions of lydianite waste and a trend towards the greater use of lydianite for tools is paralleled in the Middle Orange River area; this point will be taken up again later.

(c) ANALYSIS OF THE ARTEFACTS

The breakdown of the various classes of artefacts is given in Table 2.

Of the tool types represented, only the scrapers and backed tools show real signs of consistency and regularity as the above definitions have indicated. These two types therefore

TABLE 2

Powerhouse Cave: Lithic Artefacts

	LEVELS			
	S	I	II	III
<i>Tools</i>				
Scrapers				
Whole	10	23	21	16
Broken	1	4	2	4
Backed				
Blades	1	4	2	7
Crescents	—	—	1	3
Other				
Outils	—	1	1	1
Adzes	2	6	6	2
T/U Flakes	7	10	16	10
Lower G-stone	—	—	1	—
Upper G-stone	—	—	2	1
<i>Waste</i>				
Whole flakes	111	390	450	444
Fragments	248	1137	631	77
Cores				
Bladelet	1	5	11	13
Irregular	—	1	3	2

HUMPHREYS: POWERHOUSE CAVE AND DR FRANK PEABODY'S WORK ON HOLOCENE DEPOSITS

TABLE 3

Powerhouse Cave: Dimensions of Scrapers (mm.)

	Level	n	Mean	Std. Dev.
<i>Length</i>				
Chert	S	7	20,57	4,69
	I	15	19,67	5,51
	II	20	21,40	4,72
	III	12	20,00	6,59
Lydianite	S	3	60,33	18,01
	I	8	51,25	28,51
	II	1	(length - 122,0 mm)	
All scrapers	III	4	64,80	23,04
	S	10	32,50	21,35
	I	23	30,65	22,68
	II	21	26,19	22,43
	III	16	31,19	23,21
<i>Width</i>				
Chert	S	7	16,00	5,26
	I	15	19,87	4,94
	II	20	16,30	3,66
	III	12	18,67	10,82
Lydianite	S	3	68,33	20,03
	I	8	55,88	29,57
	II	1	(width - 70,00 mm)	
All scrapers	III	4	59,25	26,61
	S	10	31,70	27,33
	I	23	32,39	24,52
	II	21	18,86	12,25
	III	16	28,81	23,60
<i>W/L Ratio</i>				
Chert	S	7	79,06	25,04
	I	15	106,41	33,88
	II	20	78,97	24,01
	III	12	92,30	26,84
Lydianite	S	3	113,63	13,78
	I	8	115,83	51,38
	II	1	(W/L ratio - 57,4)	
All scrapers	III	4	93,18	26,59
	S	10	89,43	27,19
	I	23	109,68	39,89
	II	21	77,94	23,87
	III	16	92,52	25,88
<i>Height of Retouch</i>				
Chert	S	7	4,71	0,95
	I	15	5,00	1,60
	II	20	5,20	1,61
	III	12	4,00	1,21
Lydianite	S	3	3,67	0,58
	I	8	5,75	1,39
	II	1	(Height of retouch - 5,00 mm)	
All scrapers	III	4	6,50	3,00
	S	10	4,40	0,97
	I	23	5,26	1,54
	II	21	5,19	1,57
	III	16	4,63	2,03

have the greatest potential for further analysis. The whole waste flake category is also important in terms of consistency and numerical strength. These classes will be examined below:

(i) *Scrapers*

In the preliminary sorting of the scrapers it became obvious that there was a significant difference in size between those made on chert and those on lydianite. For this reason the scrapers were separated into these two groups and the dimensions for chert and lydianite scrapers and the total sample for each level are given in Table 3. These results demonstrate that the lydianite scrapers are in fact much larger than those on chert. The chert scrapers nevertheless show a greater regularity of size than is evident in the lydianite group (i.e. the standard deviation is smaller). From these figures it is also evident that there is no significant size trend through time as represented by the series of levels. This is demonstrated by the use of the z-test on the chert scrapers:

		length	width	W/L ratio
Level S vs I	z =	0,40 NS	1,64 NS	2,12 S
Level I vs II	z =	0,98 NS	2,35 S	2,67 VHS
Level II vs III	z =	0,64 NS	0,73 NS	1,41 NS

(Critical values: 1,96 at 0,05 probability and 2,58 at 0,01 probability).

The very highly significant difference between Levels I & II in W/L ratio may be accounted for by the fact that Level I includes some Class 9 scrapers as well as a single Class 11 scraper (see below). Similar results were obtained by using the t-test but they are not presented here.

Following J. Deacon's (1972) method the position of scraper retouch classes given in Table 4 were recognised. Except for Level II, Class 6 (end-scrapers) is the dominant class; in all levels Classes 6 & 7 constitute the major scraper types. This indicates in general terms a greater reliance on "end- (or side and end-) scrapers" than on "double" or "side-scrapers".

TABLE 4

Powerhouse Cave: Scraper Classes

		LEVELS			
		S	I	II	III
Class	6	8 (80,0%)	10 (43,5%)	9 (42,9%)	9 (56,3%)
Class	7	2 (20,0%)	8 (34,8%)	11 (52,4%)	6 (37,5%)
Class	8	—	1 (4,4%)	—	—
Class	9	—	3 (13,0%)	1 (4,8%)	1 (6,3%)
Class	10	—	—	—	—
Class	11	—	1 (4,4%)	—	—

(ii) *Backed tools*

Relatively few backed tools were recovered. The sample was too small for detailed analysis but the dimensions of all the specimens are given Table 5. Perhaps the only point worthy of note is that crescents, which are rare in the Kaap Escarpment area, appear to be confined to the lowest levels in the deposit. Whether this has cultural significance or is due to a sampling error is not clear.

(iii) *Whole waste flakes*

The lengths and widths of all the whole waste flakes were measured and the results are summarised in Table 6. As was the case with the scrapers, it was immediately clear that flakes on chert were smaller than those on lydianite and this is demonstrated by the figures quoted in the table. The measurements indicate a trend through time towards larger flakes both on chert and on lydianite and consequently in the waste flake class as a whole. The significance of this trend was tested on an inter-level basis using the z-test. The results indicate that there is a highly significant difference between Levels S & III thus confirming that this time trend has significance within the sequence as a whole. The results in the case of chert do not show any significant breaks except possibly for length between Levels II & III. Lydianite being the dominant raw material directly influences the result for the total whole flake sample and here there are highly significant

TABLE 5

Powerhouse Cave: Dimensions of Backed Artefacts (mm.)

Backed Blades

Level	Class	L	B	Ht	Material
S	G	18,0	7,5	3,0	chert
I	E	14,7	3,9	1,8	quartz
	I	—	—	—	chert
II	I	—	—	—	chert
	E	12,6	4,0	1,8	chert
III	I	—	—	—	chert
	B	16,7	7,1	3,1	chert
	C	16,3	4,3	2,1	lydianite
	C	13,7	3,3	2,0	chert
	C	16,0	7,2	3,5	chert
	C	13,6	7,7	2,6	chert
	E	17,6	6,6	2,3	chert
	E	12,1	4,2	1,6	chert

Crescents

Level	L	B	Ht	Material
II	17,8	7,1	3,3	chert
III	10,5	4,5	2,9	chert
	10,4	4,7	3,8	chert
	—	6,9	2,3	chert

Double Backed Point

Level	L	B	Ht	Material
I	23,8	5,1	2,9	chert

differences both in length and width between Levels II & III, as well as in length between Levels I & II. While the trend towards larger flakes is common, the chert flakes appear to be more stable than the lydianite flakes. This may be of cultural significance in that it could reflect a greater proficiency in the use of chert as opposed to lydianite. The time trend in whole waste flakes contrasts with the stability through time of the scraper sample as demonstrated above.

TABLE 6

Powerhouse Cave: Dimensions of Whole Waste Flakes (mm.)

	n	Length		Width	
		Mean	Std. Dev.	Mean	Std. Dev.
Level S					
Chert	11	24,91	9,59	16,73	3,80
Lydianite	98	28,43	14,66	24,62	10,53
Total	111	27,80	14,25	23,59	10,40
Level I					
Chert	50	20,18	6,64	15,18	6,58
Lydianite	338	28,30	14,77	23,71	11,63
Total	390	27,18	14,22	22,65	11,55
Level II					
Chert	47	19,47	7,54	14,23	6,49
Lydianite	400	25,83	12,95	23,01	11,91
Total	450	25,11	12,62	22,02	11,76
Level III					
Chert	70	16,16	5,75	12,54	5,54
Lydianite	357	24,24	12,43	20,22	10,02
Total	444	22,51	11,94	18,65	9,87

z-tests

		Chert	Lydianite	Total
LEVEL S vs I	L	z = 1,56 NS	z = 0,08 NS	z = 0,41 NS
	W	z = 1,05 NS	z = 0,73 NS	z = 0,82 NS
LEVEL I vs II	L	z = 0,49 NS	z = 2,40 Sig	z = 2,23 Sig
	W	z = 0,71 NS	z = 0,80 NS	z = 0,79 NS
LEVEL II vs III	L	z = 2,55 Sig	z = 1,73 NS	z = 3,17 VHS
	W	z = 1,46 NS	z = 3,53 VHS	z = 4,62 VHS
LEVEL S vs III	L	z = 3,54 VHS	z = 2,59 VHS	z = 3,60 VHS
	W	z = 3,17 VHS	z = 3,70 VHS	z = 4,53 VHS

Critical values: 1,96 at 0,05 probability (Significant) and 2,58 at 0,01 probability (Very Highly Significant).

NON-LITHIC CULTURAL OBJECTS

The non-lithic artefacts are detailed in Table 7 and may be considered under several headings:

(a) *BONE*

Bone was used as a source of raw material for artefact manufacture although it is less well represented at Powerhouse Cave. Two general classes of bone artefacts were recognised: bone points and miscellaneous. Bone points consist of round shafts of bone artificially ground and smoothed to form what are assumed to have been arrowheads and link shafts. The bone points have been divided as follows:

- A. Shaft fragments—broken both ends
- B. Point fragments—a point at one end and a fracture at the other
- C. Ground butt fragments—with fracture at other end
- D. Whole bone points
- E. Link shafts—both ends ground flat.

In all cases the diameter was measured at the centre of the surviving fragment; in the case of complete objects (D & E) the length was also recorded.

The bone points recovered are given in Table 8. The sample is too small for further analysis. One bone point is worthy of note in that it is much larger than the other points which can be

TABLE 7

Powerhouse Cave: Non-Lithic Artefacts

	LEVELS			
	S	I	II	III
BONE				
Points	—	5	3	2
Misc.	—	—	3	1
OSTRICH EGG SHELL				
Beads	10	17	15	23
Broken beads	28	30	23	41
Bored fragments	29	66	53	90
Container mouths	—	2	—	—
Decorated	1	2	3	—
Misc.	—	1	1	—
Fragments	264	578	458	754
METAL				
Fragments	2	1	—	—
WOOD	1	—	—	—
SPECULARITE	—	—	1	—
OCHRE	xxx	xxx	xxx	xxx
SOAPSTONE	1	—	—	—

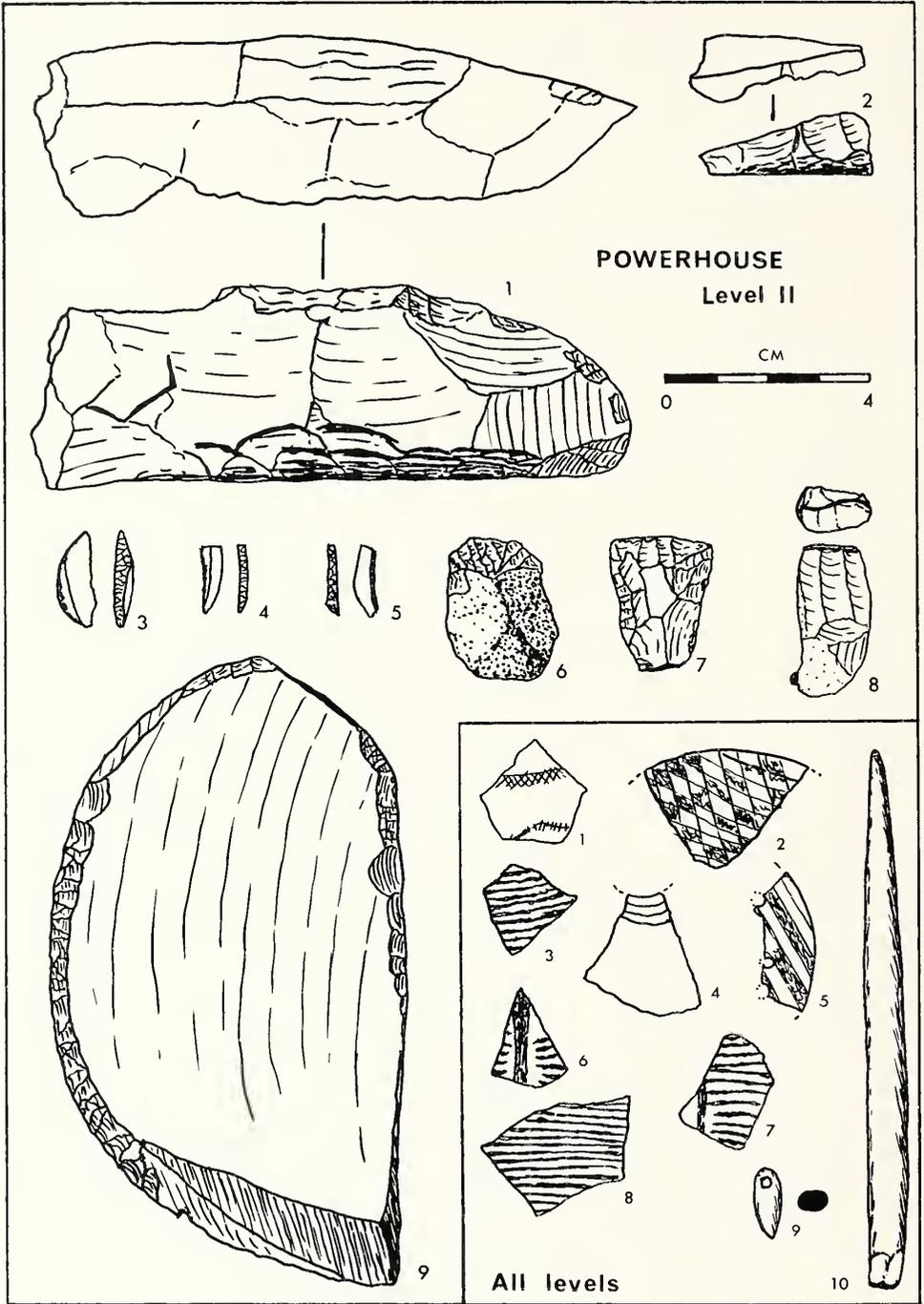


TABLE 8

Powerhouse Cave: Diameters of Bone Points (mm.)

	CLASS				
	A	B	C	D	E
LEVEL S	—	—	—	—	—
I	3,3 2,8	4,1	2,4	7,0	—
II	(split)	3,9	4,4	—	—
III	4,1	—	—	—	4,9

interpreted as arrowheads. This specimen is 105,1 mm in length and 7,0 mm in diameter and is more crudely made than the other points (Fig. 4, inset 10). It may represent an awl or some such tool.

Levels II & III yielded some other bone artefacts of interest. A polished bone pendant was recovered from Level II. It is rounded to a point at the base with a perforation at the top end (Fig. 4, inset 9). The dimensions are 13,5 × 5,5 × 3,8 mm; diameter of perforation 2,0 mm.

A section of a cylindrically shaped polished bone bead was also recovered from Level II. About one third of the bead has survived. The bead is 7,9 mm long with an outside diameter of about 13,5 mm; the diameter of the perforation is 11,8 mm.

Level II produced in addition a whittled and ground fragment of bone. One end of the bone, 93,9 mm long and 10,5 mm in diameter, has been whittled to a blunt point while the other end has been cut off in steps. Signs of grinding are visible along the sides of the shaft. There is no obvious purpose for the object as it is unfinished.

Level III produced a miscellaneous fragment of bone a point and grinding at each end. Length 55,1 mm and thickness 8,0 mm.

(b) BEADS

Ostrich egg shell beads and bored fragments were found throughout the deposit. Their distribution is given in Table 7.

The mean diameters of the whole beads are as follows; they show a remarkable consistency of size:

Level S	4,40 mm
I	4,24 mm
II	4,36 mm
III	4,22 mm

Fig. 4. A selection of artefacts from Level II: 1. Adze (Provincance Unit A, lydianite); 2. Adze (P.U-A, lydianite); 3. Crescent (P.U-B, chert); 4. Class E backed blade (P.U-B, chert); 5. Class I backed blade (P.U-B, chert); 6. Scraper (P.U-C, chert); 7. Scraper (P.U-C, chert); 8. Outil (P.U-B, quartz); 9. Scraper (P.U-A, lydianite).

Inset: Non-lithic artefacts from all levels: 1. Decorated ostrich egg shell fragment (P.U-C, Level S); 2. Ostrich egg shell pendant fragment (BI); 3. Decorated ostrich egg shell fragment (AI); 4. Ostrich egg shell container mouth (AI); 5. Ostrich egg shell pendant fragment (CII); 6, 7, 8. Decorated ostrich egg shell fragments (AII); 9. Bone pendant fragment (BII); 10. Bone point or awl (AI).

(c) *DECORATED OSTRICH EGG SHELL, CONTAINER MOUTHS AND PENDANTS*

Six decorated fragments of ostrich egg shell were recovered. These may be described briefly as follows:

- Level S —fragment with narrow strip of cross-hatching, width \pm 2,8 mm and line with parallel lines. Length 19,9 mm, width 19,6 mm (Fig. 4, inset 1).
- Level I —fragment with parallel lines \pm 1,0 mm apart over entire surface. Width along lines 17,2 mm, length 16,6 mm (Fig. 4, inset 3).
—fragment as above. Length 11,8 mm, width 9,3 mm.
- Level II —fragment as above. Length 21,0 mm, width 27,6 mm (Fig. 4, inset 8).
—fragment as above but with wide bar (2,4 mm) down length of fragment. Length 19,2 mm, width 14,1 mm (Fig. 4, inset 6).
—fragment as above but only small section of bar. Length 21,4 mm, width 18,5 mm.

Two container mouth fragments were recovered from Level I. One of these is a tiny fragment (length 6,6 mm, width 3,4 mm) with the remains of a polished mouth. The second fragment is larger (length 22,6 mm, width 21,1 mm) and has three lines roughly 1,5 mm apart incised below the mouth (Fig. 4, inset 4).

Two decorated fragments, possibly parts of pendants, were recovered. A fragment from Level I has a smoothed and rounded convex edge and is decorated by cross-hatching and filling in of alternate squares. The lines are some 3,5 mm apart; the length of the fragment along the convex edge is 31,0 mm and the width 22,5 mm (Fig. 4, inset 2). The fragment from Level II also has a rounded convex edge but is decorated by parallel lines some 3,0 mm apart with alternate areas filled in. The remains of three perforations are preserved in a line following the curvature of the outer edge and are placed 7,5 mm in from the edge and 9,6 mm and 3,3 mm apart. The perforations are 2,1 mm in diameter (Fig. 4, inset 5).

The decorated fragments are too few to reflect any cultural trends. The fact that they are entirely absent from Level III may or may not be significant.

(d) *OCHRE*

Ochre, mainly red but with odd fragments of yellow, occurred throughout the deposit. The ochre was too widespread and fragmentary for full recovery to have been a proposition. Its abundance at the site is directly related to the fact that Ochre Cave is so close to hand as Peabody pointed out. Its presence at Powerhouse Cave therefore means little more than that the inhabitants were exploiting a highly convenient source. The odd finger strip paintings in the cave testify to one use of this ochre.

(e) *SPECULARITE*

One tiny fragment of specularite (0,84 g) was recovered from Level II. The nearest source of specularite is the Postmasburg area some 115 km to the south-west.

(f) *SOAPSTONE*

A fragment of soapstone (19,2 \times 7,5 \times 5,6 mm) was recovered from Level S. It shows distinct signs of grinding. The nearest source is unknown but the fact that it was from the surface level means that it may be a modern introduction.

(g) *IRON*

Three fragments of iron were found, all from Levels S & I and clearly of modern origin. A metal rod, heavily rusted, but with remains of what appear to have been threads was found in

Level S; length 57,4 mm, diameter 13,4 mm. Level S also yielded a metal disc with rounded edges reminiscent of a bottle crown but without the denticulations; diameter 20,1 mm, height 5,1 mm. The top of Level I produced a tiny (17,0 × 4,2 mm) metal strip with two perforations of unknown origin but certainly intrusive.

(h) *WOOD*

Level S produced a fragment of wood 26,6 mm long and 7,1 mm in diameter showing signs of whittling down one end with a thin piece having been snapped off. In view of the lack of wood in the other levels this specimen must be regarded as being of relatively recent age.

FAUNAL REMAINS

The excavation produced well preserved faunal remains. These were submitted to Dr R. G. Klein of the University of Chicago for analysis and his list is given in Table 9. The assemblage also included a large quantity of microfauna which was extracted and which will receive separate treatment in the future. The fauna identified by Klein shows considerable diversity but it is difficult to establish the minimum number of individuals represented because of the highly fragmentary nature of the sample. This fragmentation is undoubtedly due to the slow build up of the deposit demonstrated by the radiocarbon dates. The low minimum numbers make it impossible to establish any time trends in exploitation patterns. Even a presence/absence criterion reveals nothing; indeed the faunal composition shows remarkable stability over the period of the occupation of the cave. All the species represented in the list are known to exist in the area today or to have existed in historical times. An interesting feature in the list is the exploitation of riverine resources in the form of fish (including barbel), crab and fresh water mussel but with the proximity of the Thabaseek River this is to be expected.

OSTRICH EGG SHELL FRAGMENTS

Ostrich egg shell fragments occurred throughout the deposit but were not as plentiful as in some other Kaap Escarpment sites. The numbers and weights are as follows:

	Total	Weight
Level S	264	136 g
I	578	308 g
II	458	287 g
III	754	381 g

On the basis of these weights the minimum numbers of ostrich egg shells represented in each level are 1,2,1,2 respectively. (For discussion on this calculation see Humphreys 1975: 16.) This minimum number of ostrich eggs represented over a 1 400-year period contrasts with a site like Burchell's Shelter where a shallow deposit covering a very restricted time span produced evidence of a minimum of five eggs (1 405,6 g) (Humphreys 1975: 16).

DATA FROM RELATED SITES

The published data on the sites investigated by Peabody have been outlined above. It has also been pointed out that the artefact assemblages have been split and therefore cannot be readily reanalysed. There are however two further sources of information on the Holocene of the area that have a bearing on the Powerhouse Cave results.

(a) *TOBIAS CAVE*

In the description of his work at Buxton, Peabody (1954: 688) mentioned a rescue excavation carried out by Prof P. V. Tobias in 1952 of what was apparently a "Later Stone Age"

TABLE 9
Fauna from Powerhouse Cave
 (Identification by R G Klein)

	LEVELS			
	S	I	II	III
Chiroptera				
Bats	—	x	x	x
Insectivora				
Shrews	x	x	x	x
Lagomorpha				
Hares (2spp.)	1	2	2	1
Rodentia				
<i>Pedetes capensis</i> , Springhaas	—	1	1	?1
<i>Hystrix africae-australis</i> , Porcupine	1	2	—	—
Others (all very small)	x	xx	xx	xx
Primates				
<i>Papio ursinus</i> , Baboon	1	1	?1	—
Carnivora				
<i>Canis mesomelas</i> , Blackbacked Jackal	1cf.	1cf.	1cf.	?1
<i>Vulpes chama</i> , Cape Fox	—	1	—	—
<i>Mellivora capensis</i> , Honey Badger	—	1	—	—
<i>Cynictis pectinata</i> , Yellow Mongoose	?1	—	1cf.	—
<i>Felis libyca</i> , African Wildcat	—	—	1cf.	—
<i>F. caracal</i> , Caracal	—	—	?1	?1
Hyracoidea				
<i>Procavia capensis</i> , Rock Hyrax	1	2	1	1
Perissodactyla				
<i>Equus quagga</i> , Quagga	1cf.	1cf.	1cf.	—
<i>Diceros bicornis</i> , Black Rhino	1cf.	1cf.	1cf.	—
Artiodactyla				
<i>Phacochoerus aethiopicus</i> , Warthog	—	1	1	1
<i>Redunca fulvorufula</i> , Mountain Reedbuck	1cf.	?1	1	?1
<i>Connochaetes gnou</i> , Black Wildebeest	1cf.	1cf.	1cf.	?1
<i>Antidorcas marsupialis</i> , Springbok	—	1	?1	?1
<i>Sylvicapra grimmia</i> , Grey Duiker	—	?1	—	—
<i>Raphicerus campestris</i> , Steenbok	1cf.	1cf.	2	1cf.
<i>Oreotragus oreotragus</i> , Klipspringer	—	—	1cf.	1cf.
<i>Taurotragus oryx</i> , Eland	—	—	?1	—
Reptilia				
Tortoises	1	2-3	3	1
Snakes	x	x	x	x
Lizards	—	x	x	x
Amphibia				
Frogs or toads	—	x	x	x
Aves				
Mainly small passerines	—	x	x	x
Pisces , Fish (including barbel)	x	x	x	x
Crab	1	2	8	14
Mussel (<i>Unio caffer</i>)	x	x	x	x

? = Determination based on fragmentary post-cranial material of the right size. "Possibly."
 cf. = Determination based on fragmentary cranial (mostly dental) material. "Probably".

deposit exposed by blasting operations. Since Peabody referred only in general terms to a report and various artefacts and faunal remains, including a "Bushman" skull, which were recovered by Tobias, enquiries were made in 1974 in an effort to relocate both the original report and the recovered remains. Through the kind efforts of Prof Tobias and Mr Alun Hughes the original report and the stone artefacts were found in the Anatomy Department of the University of the Witwatersrand; the skull and faunal remains have yet to be relocated.

Tobias's report on the location of the deposit and the rescue excavation is as follows:

Notes on Excavation of Cave Deposit at Buxton

Following blasting operations in Quarry C, on the north bank of the canyon (ancient bed of Thabaseek River), the back of a cave deposit was exposed, from which a small, partly-mineralised pentagonoid skull was blasted, as well as teeth. The roof of the cave had collapsed recently probably from the blast, but its original entrance was found to be facing west, i.e. into the canyon. The deposit apparently corresponds in position with the site marked "black Earth Cave" in Dr Peabody's map of the Buxton area.

A large amount of deposit had spilled down the deposit and from this, numerous remains were recovered on sieving. These comprised:

- (a) Further human teeth.
- (b) Many scrapers (end- and side-), ostrich egg shell beads and fragments.
- (c) Numerous faunal remains—including baboon, a variety of buck, lion and smaller carnivores, warthog, etc.

Excavations were conducted from the exposed face into the deposit. These brought to light a few further human skeletal fragments, more artefacts of Smithfield type, including a well-finished grooved stone and several slender bone points.

The original calvaria, consisting of the complete parietals and most of the frontal bone, is manifestly Bush in physical type with a suggestion of some additional element, not as yet analysed.

P. V. TOBIAS 1952.

The relocated artefacts made available to the writer by Tobias consist of two series—one is the artefacts recovered from the downslope spill caused by the blast (here designated "Dump") and the other is the artefacts actually excavated *in situ* in the surviving deposit ("Excavated"). Of these two series, only the "Excavated" artefacts were analysed; the results are given in Table 10. The "Dump" material consisted of 189 artefacts, 122 ostrich egg shell fragments (weight—145,5 g) and 5 ostrich egg shell beads (mean diameter—10,42 mm). These artefacts were not analysed in detail because of the possibility of mixing with material not derived from the exposed shelter; the very weathered nature of some of the artefacts (in contrast to the fresh "Excavated" material) suggested that such mixing had indeed occurred.

Table 10 shows that scrapers constitute the largest category, even more than waste; they in fact represent 31,3% of the entire assemblage. This is highly suggestive of the fact that during the rescue excavation recovery was selective and by no means total. The scraper sample, however, is reasonably large and therefore amenable to further analysis; the fact that the sample is "mixed" from a stratigraphic point of view (assuming that some stratigraphy existed) does nevertheless limit its usefulness.

When the scrapers were measured it was obvious that the specimens made on lydianite (including a few on Ventersdorp lava) were significantly larger than those made on chert. For this reason the scrapers were grouped according to raw material types when they were measured. The results are as follows:

		Mean	Std. Dev.
CHERT	Length	28,69	13,62
	Width	20,69	7,54
	W/L ratio	77,08	18,87
LYDIANITE	Length	44,20	14,27
	Width	48,60	15,61
	W/L ratio	113,72	36,22

In the absence of stratigraphic evidence it is impossible to interpret the significance of this size grouping, but it is at least obvious that the form of the available raw material directly influenced the size of the scrapers produced.

Other cultural objects recovered included a grooved stone and several bone points but these were not included in the collection examined by the writer and so no comment can be made.

Tobias's report does not make it clear whether faunal remains were recovered from the *in situ* deposit. In any event, however, the faunal remains are at present unlocated. The excavations did produce further human remains but these too have since disappeared.

The main interest in "Tobias Cave" is the fact that human cranial material apparently of Bush type was found in association with artefacts and bone points similar to those found at Powerhouse Cave. The lack of pottery in the assemblage, if real, may be suggestive of a time span comparable to that represented at Powerhouse Cave; at least the deposit would appear to predate the introduction of pottery in the area. Tobias (pers. comm.) has undertaken to obtain a radiocarbon date for the human skeletal material when it is relocated and this should go some way towards resolving the problem of the age of the deposit.

TABLE 10
Tobias Cave: Analysis of Artefacts

	Chert	Lydianite	Quartzite	Other	TOTAL
TOOLS					
Scrapers					
Whole	14	8	—	4	26
Broken	3	2	1	—	6
Backed					
Blades	—	—	—	—	—
Crescents	—	—	—	—	—
Other					
Outils	2	—	—	—	2
Adzes	3	—	1	—	4
T/U flakes	4	9	1	—	14
WASTE					
Whole flakes	—	7	1	—	8
Fragments	6	6	2	5	19
Cores					
Bladelet	—	—	—	—	—
Radial	1	—	1	—	2
Irregular	1	—	1	—	2

Other Artefacts recorded by Tobias: Grooved stone
"Several" bone points

(b) *ANALYSIS OF PEABODY FAUNAL REMAINS*

Peabody (1954: 698-9) published a list of the faunal remains recovered in the course of his excavations. These remains have more recently been reanalysed by Dr H. B. S. Cooke of Dalhousie University and his results are given in Table 11. It is clear from a glance at this list that Peabody did not recover anything like the range actually present at Powerhouse Cave. This must cast doubts on his recovery techniques and also therefore on the usefulness of his artefact assemblages even if they were more easily accessible.

DISCUSSION

The full implications of the findings at Powerhouse Cave will only become clear when the results from all the excavations carried out in the Kaap Escarpment area are available. A few general observations can however be made at this stage.

(a) *THE NATURE OF THE OCCUPATION*

The relatively small area excavated, coupled with the slow build up of deposit and the absence of any stratigraphic breaks makes it difficult to draw conclusions on the nature of the occupation represented by the archaeological remains preserved in the cave. The various excavated levels consist of arbitrary "grabs" within a continuous sequence; the levels are thus part of a serial sequence rather than a series of occupation levels. The occupation of the cave can be viewed only as a dynamic process and not as a series of "snapshots" through time.

The remains clearly relate to occupation by peoples living a hunter-gatherer way of life and their activities are represented by stone artefacts as well as ornamental pieces such as decorated ostrich egg shell, pendants, beads and the use of ochre and specularite. Their diet is represented in part by the faunal remains recovered from the deposit. The low density of finds over the long period of time reflects a very sporadic use of the cave. Because the site is located in what can be described as an optimum position overlooking a river and placed on an ecological divide between the extensive flat plane of the Kaap Plateau and the broad valley of the Harts River, this sporadic use can be interpreted as reflecting a low population density during the period that the deposit accumulated. Given the limitations of the type of evidence preserved at the site, broader interpretations of the life style represented can only be attempted once all the Kaap Escarpment data have been assembled.

There is no evidence for any seasonal pattern in the occupation of the site. The water supply was probably constant and so was not a factor. Clark (1971) has attempted to establish if Witkrans, just south of Powerhouse Cave, was a "home base" or a "transit camp" during "Middle Stone Age" times. This was done by examining the composition of the faunal assemblage excavated by Peabody in order to establish the proportions of migratory and non-migratory animals against the background of the seasonal movements of these animals. While the observational data on animal movements in this area are probably still inadequate for this type of approach to be meaningful, an examination of the Powerhouse Cave fauna using Clark's criteria suggests that the assemblage is roughly equally divided between migratory and non-migratory animals. It is obvious moreover that for such a classification to be meaningful the actual proportions of the different animals within the diet have to be taken into consideration and with the low individual counts from Powerhouse Cave, these data are not available. In this connection it may be noted that even Clark's simple presence or absence count must be regarded as suspect because of the inadequacy of Peabody's faunal samples, as demonstrated above. Whatever the factors involved in the accumulation of the faunal remains in Powerhouse Cave it can however be noted that the archaeological record shows remarkable uniformity throughout the period of occupation.

TABLE 11
Fauna Recovered in Peabody's Excavations.
 (Identification by H B S Cooke).

	Blue Pool Cave	Ochre Cave	Powerhouse Cave	Little Witkrans	Witkrans Cave (Upper)
Chiroptera					
Bats	—	—	x	—	—
Insectivora					
Shrews	—	x	?	—	—
Lagomorpha					
Hares	—	—	?	—	x
Rodentia					
<i>Hystrix africae-australis</i> , Porcupine	—	x	x	—	—
Various (small)	—	—	—	—	x
Primates					
<i>Papio ursinus</i> , Baboon	—	—	—	—	x
Carnivora					
<i>Atilax paludinosus</i> , Mongoose	—	—	—	—	x
<i>Panthera pardus</i> , Leopard	—	—	—	—	x
Hyracoidea					
<i>Procavia capensis</i> , Hyrax	—	x	—	—	x
Perrissodactyla					
<i>Equus burchelli</i> , Zebra	x	x	x	x	x
Artiodactyla					
<i>Phacochoerus</i> sp., Warthog	—	x	—	—	x
<i>Redunca fulvorufula</i> , Mt. Reedbuck	—	x	—	—	x
<i>Syncerus caffer</i> , Buffalo	?	—	—	—	—
<i>Hippotragus equinus</i> , Roan	—	—	—	—	?
<i>Damaliscus</i> cf. <i>pygargus</i> , Bontebok	—	—	—	—	?
<i>Alcelaphus caoma</i> , Hartebeest	—	—	—	—	?
<i>Raphicerus campestris</i> , Steenbok	—	—	—	—	x
<i>Antidorcas marsupialis</i> , Springbok	—	x	—	—	x
Reptilia					
Tortoises	—	—	x	—	x
Lizards	—	—	x	x	x
Amphibia					
Frogs	—	—	x	x	—
Pisces					
Fish	—	—	x	x	x
Mussel	—	—	x	—	—

(b) USE OF THE LOCAL ENVIRONMENT

As appears to be the norm in Holocene sites in the interior of South Africa, only a very biased picture of the subsistence patterns has survived in the archaeological record: while the faunal remains are well represented, evidence of plant exploitation is entirely absent. Even from an artefact point of view hunting is represented by bone points and backed blades while, with the possible exception of grindstones, plant collecting is not evidenced. The low individual counts of the various animal species represented make it impossible to detect any specialisation but it is clear from the list that both large and small animals were hunted; perhaps the game-pits mentioned by the early travellers played a significant part even at that time. The exploitation of riverine resources has already been noted but again low counts make it impossible to assess the importance of this food source within the diet.

The use of lydianite at this site is a reflection of its easy accessibility. It is interesting to note that lydianite was also used by the inhabitants of Tobias Cave (from the same source?) but that it is very rare in the Witkrans assemblage described by Clark (1971) where only two pieces were recovered. Clark's description is of the "Middle Stone Age" artefacts but this rarity may also be a feature of the Holocene artefacts; this is a point that requires confirmation. The Buxton area may therefore have been unique in that it alone (so far as present knowledge goes) provided a source of lydianite in the Kaap Escarpment area. This would explain the larger and less refined artefacts made on lydianite at Powerhouse Cave and Tobias Cave described above; it may have been a type of raw material largely unfamiliar to the peoples occupying the Kaap Escarpment area. Situations such as this could usefully provide data on local and short-term adaptations to specific raw material types.

The ubiquitous ochre is also the reflection of a unique situation, the close proximity of Ochre Cave. Unfortunately there are no data to show the distribution of the use of this ochre source within the area.

(c) COMPARISONS WITH OTHER SITES

Apart from the other Buxton sites, on which there is minimal information, Powerhouse Cave invites comparison with several other interior sites, most notably Blydefontein, Zaayfontein and Riversmead on the Orange River Scheme where there is a direct temporal overlap. The writer has recently reanalysed the assemblages from Glen Elliott and Blydefontein using the approach outlined in this paper and a reassessment of the Middle Orange River sequence is being prepared (Humphreys, in preparation). At this stage it is therefore necessary only to make a few general comments on the comparison between Powerhouse Cave and the Orange River sites.

Blydefontein (Sampson 1970: 87-105) is particularly relevant because Level VIII has produced a radiocarbon date of 3650 ± 120 B.P. (SR-152) (as against 3680 ± 60 for the base of the Powerhouse sequence). Level III at Blydefontein has been dated to 1980 ± 120 B.P. (SR-132) so this means that the lower half of the Blydefontein occupation sequence directly overlaps Powerhouse Cave in time. The tools at Blydefontein are made almost exclusively on lydianite but the scrapers exhibit far greater consistency than is evident at Powerhouse Cave. The scraper dimensions from the basal levels at Blydefontein agree very closely with those of the chert sample from Powerhouse Cave while the Blydefontein sequence as a whole shows the increase in scraper size now well established for the interior of South Africa, so much so in fact that the scrapers from Level I are nearly double the length of those from Level VIII.

Blydefontein has produced a very much larger backed tool assemblage than Powerhouse Cave; it is not clear if this reflects a different hunting strategy. Unfortunately the faunal remains from Blydefontein have not yet been analysed and so comparison between the two sites are not possible. Bone points are common to both sites.

The raw material trends evident in the Middle Orange River sites have been discussed elsewhere (Humphreys 1972). The pattern of raw material usage at Powerhouse Cave is exactly

paralleled by the Middle Orange River data. Common to all sites is the dominance of lydianite in the waste categories while the tools are mainly on chert with a gradual trend through time towards a greater use of lydianite for tool manufacture. As suggested in Humphreys (1972) this trend may reflect the gradual recognition of the tool making potential of lydianite by peoples previously unfamiliar with the raw material.

The comparison between the Kaap Escarpment sites and the Middle Orange River sites will be discussed in detail elsewhere (Humphreys, in preparation) but at this stage it may be noted that the differences between Powerhouse Cave and the Middle Orange River sites are no greater than the differences between any of the individual Orange River sites themselves. This general "uniformity" within the interior of South Africa despite environmental differences has important implications for the use of stone artefact assemblages as meaningful indicators of prehistoric social groupings. The possibility exists that for the interior stone artefact assemblages may not be sensitive enough to distinguish large scale social groupings, let alone more subtle "activity variations". It is anticipated that further research within the Kaap Escarpment Holocene project will throw more light on these problems.

CONCLUSION

This paper has set out to present the results of the re-excavation of Powerhouse Cave and to assess Peabody's work in the area. The significance of Powerhouse Cave will only become apparent when all the data from the Kaap Escarpment are integrated. At this stage, however, a few of the outstanding problems and questions have been outlined and it is already clear that the Powerhouse Cave data will make a significant contribution to Holocene studies in the interior of South Africa.

The limitations of Peabody's work have become apparent as a result of the detailed investigation of Powerhouse Cave. In general terms his observations have proved to be accurate (he recognised, for example, the contrast between the small chert artefacts and the larger lydianite pieces—Appendix 1) but these are clearly inadequate for modern archaeological research. It is obvious that very little is to be gained from reassessing the collections from early excavations however important the sites themselves might have been. Archaeological observation and recovery techniques are continually changing and data recovered from any excavations are generally only useful in the context of the approaches prevailing when those excavations were undertaken. Field observations are as important as laboratory observations and without proper control of the former, the latter are greatly diminished in value.

ACKNOWLEDGEMENTS

The excavation and analysis of Powerhouse Cave was undertaken as part of a project on the late Holocene in the Kaap Escarpment area while the writer was on the staff of the McGregor Museum, Kimberley. Grateful thanks are due to the museum and its staff for providing the necessary facilities and assistance.

Thanks are also due to Prof J. D. Clark of the University of California, Berkeley, for providing copies of Peabody's field notes; to Dr H. B. S. Cooke of Dalhousie University, Canada, for the analysis of the fauna from Peabody's sites; to Prof R. G. Klein of the University of Chicago for analysing the fauna from the present excavation; to Prof P. V. Tobias and Mr Alun Hughes of the University of the Witwatersrand for information on Tobias Cave and for the loan of the collection; to Dr J. C. Vogel of the National Physical Research Laboratory, Pretoria, for the radio-carbon dating. Mr P. Wolf of the Northern Lime Company kindly allowed access to the site.

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APPENDIX 1

Dr. F. Peabody's Diary Entries Concerning His Work at Powerhouse Cave

- p. 653. *Nov. 29th 1947.* Camp, Niel Ray and I went on a tour of the Quarries starting with the Powerhouse Cave where I dug a prospect hole $1\frac{1}{2}' \times 4'$ finding a few tortoise bones, other stuff (not much) and a tiny Wilton microlith.
- p. 724. *Feb. 9th 1948 . . .* In the afternoon the above mentioned trio [i.e. "Sackie, I and a boy"] worked the Powerhouse cave. I started a trench north of our old prospect hole, and in the course of the aft. [-ernoon] we worked out a $6' \times 2'$ by $2'$ deep pit, collecting from 0-4", 4"-14", 14"-24". The middle zone produced more beads than any other digging. A brand new object turned up also in the middle zone. A small water worn pebble has a smoothly polished notch which must have been used to polish a shaft. The notch is over half a diameter deep. Quantities of microliths, especially the thumb nail scrapers were found. Large stuff of black chert—including a core—is mixed in at all levels . . .
- p. 725. *Feb. 10th 1948.* Powerhouse cave: Worked again in the morning, lengthening main pit (north; see diag.) 4-12" level continued to be richest but all stuff peters out toward back wall. 24-28" level lying on floor showed nothing. Continued to find heavy stone tools in top level along with microliths and old jack knife (!) key (all very rusted of course). Most interesting find was a bivalve very like the marine *Venerupis*. The single valve had a neat hole in the beak, as if for suspension by cord around the neck.
- p. 726. The beak area is worn down flat. Position of hole not usual for marine bore—in thickest. With this shell, which comes from 14-24" layer was a crude "lunette" scraper, the only one found in the pit. Started a new pit ("b") but found nothing except a decorated chip of ostrich shell in the 0"-4" level. This is the only one from 38-27 [i.e. Peabody's number for Powerhouse Cave] to my knowledge. Sacky dug a pit up in the gallery ("d") which yielded a piece of zebra lower jaw and other scrap bone. Depth 0-18" hit floor.
North Pit: The middle zone, 4"-14", was the richest especially in beads and drilled chips. Averaged 2 or 3 per sieve full. 14"-24" was poorer even than the surface and 24"-28" was barren. The surface 0-4" was richest in the heavy stone implements and the only level to produce etched shell.
Remains of red painted designs or figures may be seen on the smoother portions of the cave ceiling and walls. Only one design is clear and recognisable. It is an asterisk symbol in broad design . . .

Permission for the above quotation kindly granted by Prof J. Desmond Clark and the Departments of Palaeontology and Anthropology, University of California, Berkeley.

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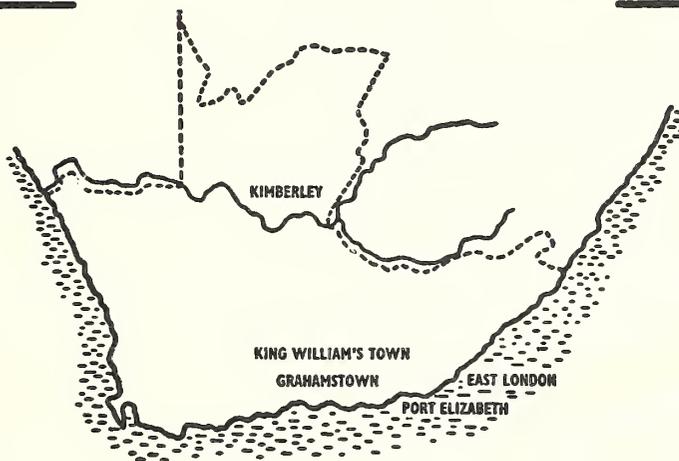
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ANNALS OF THE CAPE PROVINCIAL MUSEUMS

NATURAL HISTORY

Ann. Cape Prov. Mus. (nat. Hist.)



VOLUME 11 • PART 13

30th JANUARY 1979

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

Printed by Cape & Transvaal Printers (Pty.) Ltd., Cape Town

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Une nouvelle espèce de *Pisulia*, son développement et la position systématique de ce genre (Trichoptera)

par

G. MARLIER

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Rue Vautier, 31 1040/Bruxelles
(Avec 7 planches hors texte)

Abstract:

Description of a new species of *Pisulia* (Trichoptera) from Eastern Zaïre in the adult, pupal and larval stages.

From its larval features *Pisulia* fits very well in the family Lepidostomatidae near the genus *Dyschimus* Barnard.

INTRODUCTION

Dans une importante collection faite par le professeur Malaisse (Univ. officielle du Zaïre) dans la rivière Luanza (Shaba) en 1967, se trouvaient des larves, des nymphes et 4 adultes d'une nouvelle espèce du genre *Pisulia* Marlier.

Par suite de l'intérêt de ce genre pour lequel H. H. Ross (1967) a érigé une famille spéciale, les Pisuliidae, cette récolte fait ici l'objet d'une note préliminaire.

En effet, la découverte des stades jeunes de *Pisulia* permet d'en rechercher les affinités systématiques.

Tout ce matériel, larves et adultes, provient des environs de la source de la Luanza, à 1690 m, affluent de la rivière Luizi, elle-même tributaire du Luapula. Le cours de cette rivière est donc situé sur les contreforts orientaux du plateau des Kundelungu. Les adultes furent pris au piège lumineux et les larves sur des feuilles et des morceaux de bois immergés.

Pisulia shabae n.sp.

Matériel étudié

Adultes: 3 mâles et 1 femelle; holotype ♂ en alcool, n° de récolte 5271 c; 2 paratypes ♂ en préparations, même numéro de récolte; 1 ♀ en 3 préparations et 3 ♂♂ paratypes n° 5252 c (mai 1967).

Larves: 19 larves n° 5003 (janvier 1967); 3 larves 5402 a; 3 larves 4959 et 2 larves 5004; 2 nymphes mâles et 1 nymphe ♀ 5003 (mai 1967).

Tout ce matériel se trouve dans les collections de l'Institut Royal des Sciences Naturelles à Bruxelles, apart de 2 paratypes ♂ et de 3 larves qui seront déposés dans les collections de l'Albany Museum, à Grahamstown, Afrique du Sud.

DESCRIPTION

(1) ADULTE

Coloration brun clair, plus foncée au thorax et aux pattes; Face dorsale de la tête presque nue, avec une suture médiane incomplète partant du bord postérieur et s'arrêtant vers le milieu;

entre les antennes une verrue sétigère conique; au bord de l'oeil une rangée de 2-3 soies. A l'arrière du vertex un petit groupe de soies (6-10 de chaque côté); juste derrière l'oeil une petite verrue en croissant; face antérieure de la tête avec 2 zones sétigères triangulaires latérales bordant les yeux et s'étendant près de l'antenne au bord inférieur; labre ovale et assez étroit; haustellum large, trilobé, le lobe médian lui-même indenté au milieu; mandibules membraneuses assez gonflées de forme générale triangulaire; palpes maxillaires du mâle relevés et appliqués contre la face, de 3 articles minces, le dernier peu séparé du deuxième, un peu renflé au bout et terminé par un faisceau de poils; palpes maxillaires de la femelle de cinq articles cylindriques, les deux premiers un peu plus courts que les trois derniers qui sont subégaux; palpes labiaux des deux sexes de trois articles dont le basal porte une forte digitation interne étroite;

Aile antérieure assez large, à bord antérieur convexe, de 6,6 mm de long (mâle) et 8,2 mm (femelle); membrane assez granuleuse densément poilue à nervation épaisse et nette.

Nervation de même type que *P. glabra* Marlier mais la portion commune de la furca 2 (suivant la conception de D. E. Kimmins) ou la base de f3, suivant mon opinion antérieure, est plus longue chez *P. shabae* n.sp. que dans le générotype;

Membrane d'un brun pâle avec une zone hyaline transversale assez courte sur les bases des cellules discoïdale et thyridiale; nygmes bien marqués aux deux ailes; tache thyridiale très nette aux deux ailes antérieures; aile postérieure à membrane brunâtre, moins granuleuse présentant une inflexion du bord dans la région cubito-anale, comme dans l'espèce-type.

Pronotum avec deux grandes verrues sétigères rondes très saillantes se prolongeant sur les côtés par deux lobes ovales également sétigères.

Mésonotum à mésoscutum portant une paire de petites verrues longitudinales étroites et pointues porteuses de 4 soies; mésoscutellum avec une grande verrue ovale élargie et arrondie en avant, bordée par une rangée de soies. Cinquième sternite abdominal avec une paire d'orifices latéraux ouvrant dans une vésicule ovale.

Eperon interne apical des tibias postérieurs normal et velu chez la femelle; modifié chez le mâle en une griffe aiguë, glabre, courbée; formule calcarienne 2/4/3.

Genitalia mâles

Appendices supérieurs longs et étroits non élargis à l'apex avec une double dent basale ventrale, couverts de longues soies à leurs faces ventrale et externe. Neuvième segment étroit en vue dorsale, légèrement saillant au milieu et muni de 10 fortes soies raides postérieures; élargi en vue latérale et portant à mi-hauteur un appendice en forme de saillie bilobée, le lobe dorsal arrondi et mince, l'inférieur anguleux et épais hérissé de longues soies raides; ventralement de longueur modérée, formant une saillie triangulaire sur la ligne médiane.

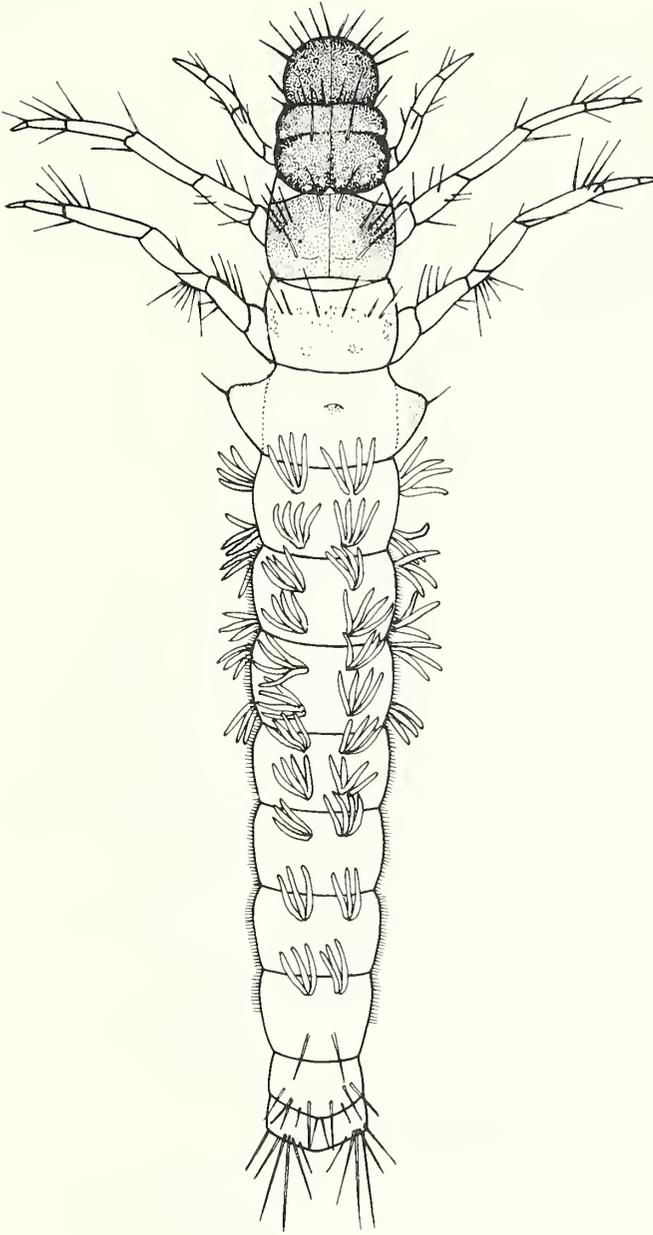
Appendices supérieurs et appendices latéraux fixés sur la membrane qui sépare le neuvième du dixième segment.

Dixième tergite formant, comme chez *P. glabra* un toit allongé bilobé au-dessus du pénis; celui-ci est recourbé vers le bas. De part et d'autre du pénis, on observe une plaque sclérifiée de couleur sombre, de forme plus ou moins triangulaire, munie latéralement d'une échancrure arrondie. Cette plaque semble reliée aux "appendices intermédiaires" (plaque parapénienne).

Appendices inférieurs longs, minces, courbés vers le haut, un peu plus courts que les supérieurs, glabres mais terminés par une touffe de soies.

Affinités

L'espèce diffère nettement de *P. glabra* par ses appendices supérieurs (app. préanaux dans la description originale de *P. glabra*) non élargis et non sinués, par ses appendices intermédiaires beaucoup plus grands et par la plaque parapénienne qui présente une échancrure beaucoup plus petite que chez l'espèce-type de genre (c'est la "gaine" pénienne de la description originale). *P. shabae* est par ailleurs extrêmement différent de *P. hirta* (Marlier) et de *P. pinheyi* (Kimm.), notamment par la longueur des appendices inférieurs.



(2) *LARVE* (fig. dans le texte et pls. III-VI)

Longueur de la larve mûre: 11-14 mm.

Larve éruciforme, cylindrique, semblable à une larve de *Goerodes*. Tête ronde, yeux punctuels latéraux à mi-longueur de la tête; antennes situées au tiers proximal de la distance oeil-base de la mandibule.

Coloration brun-noisette avec une grande plage claire autour de la tache oculaire et des points lenticulaires clairs sur les pleures et le vertex; une zone claire diffuse à l'angle rentrant du clypéus; celui-ci bien échancré au milieu. Soies noires minces et longues sur la tête. Antennes bien formées, de 2 articles; le basal cylindrique, 2,5 fois plus long que sa largeur, le terminal vésiculeux translucide. Tégument céphalique couvert de minuscules spinules disposées en peignes arrondis. Face inférieure de la tête spinuleuse, comme le dessus, dans sa moitié antérieure; moitié postérieure avec de grandes zones lenticulaires translucides; gula triangulaire, aiguë à l'arrière, n'atteignant pas l'ouverture occipitale; précula peu saillante et arrondie. Premier sclérite (stipes) des maxilles, rectangulaire, peu sclérifié, non spinuleux; base du labium bombée rectangulaire, spinuleuse, ne portant pas de sclérisation. Lobe labial conique aigu, inséré un peu avant (ventralement) l'extrémité du mentum, qui est bien développé et arrondi en avant. Palpes maxillaires de 4 articles, palpes labiaux sans doute de 1 article portant 2 bâtonnets sensoriels et une fossette. Mandibules courtes, triangulaires, à dents apicales disposées comme suit: à droite, 2 ventrales, 1 terminale forte et 2 dorsales dont la basale est la plus forte, brosse interne très touffue; à gauche, 5 dents apicales sur une rangée courbée presque verticale, croissant de la proximale (la plus ventrale) à la terminale, la dorsale plus petite; brosse interne à poils longs.

Labre avec échancrure antérieure très large et peu profonde bordée de fins poils serrés et courts, à brosses latérales bien développées; les tormae courts et repliés ventralement.

Pronotum sclérifié, de la même couleur que la tête, orné de points lenticulaires clairs dans sa seconde moitié, avec une rangée de deux fois 5 grandes et 5 petites soies minces, angles antérieurs droits; tiers antérieur séparé du reste par un léger rebord arrondi souligné d'une rangée transversale de 6 longues soies; un sillon oblique, de chaque côté souligné d'un fin liseré brun, séparant les angles postérieurs du segment; un sillon transversal peu accentué après le bord antérieur; la portion située en avant de ce sillon couverte de petits tubercules arrondis, qui deviennent plus allongés derrière le sillon, disparaissant en arrière du milieu et remplacés par une sculpture polygonale étirée transversalement. Bord postérieur avec une fine ligne brune élargie au milieu et près des angles; ceux-ci droits, incurvés vers la face ventrale en arrière des épimères. *Mésanotum* peu sclérifié jusqu'aux 2/3 de la largeur et seulement membraneux en arrière; propleures amples, le trochanter offrant 2 pointes antérieures, l'inférieure la plus forte, conique; épisternum quadrangulaire, épimère subtriangulaire à pointe dirigée vers l'avant. *Métanotum* à sclérites pâles, indistincts, le médian impair. *Prosternum* jaune pâle très mince, peu sclérifié mais luisant. Dans la membrane entre le prothorax et le mésothorax, de chaque côté, un sclérite triangulaire brun foncé. Corne prosternale très développée, aiguë, plus longue que le pronotum, couverte de tubercules et de sétules à la base.

Premier segment abdominal à "bosse" dorsale petite, arrondie, finement plissée transversalement et couverte de très fins poils denses. "Bosses" latérales assez aplaties et à stries plus larges et couvertes de soies courtes et aiguës.

Ligne latérale commençant au dernier cinquième du deuxième segment et s'étendant jusqu'à la moitié du huitième.

Des épines bifides latérales au nombre de 4 sur le IV, 5 sur le V, 5 sur le VI, 5 sur le VII.

Branchies filiformes, en groupes de 2 ou 3 filaments naissant d'une base commune, sur les segments II à VIII, disposées conformément au schéma suivant.

Les nombres de filaments indiqués sont les plus élevés observés et correspondent aux plus grandes larves étudiées.

MARLIER: NOUVELLE ESPÈCE DE *PISULIA*

Segment	Dorsales		Latérales		Ventrales	
	Pré	Post.	Pré	Post.	Pré	Post.
II	4	4	0	4	4	4
III	4	4	6 (4)	4	4	4
IV	4	4	2 (0)	3	4	4
V	4	3 (4)	0	0 (2)	4	4
VI	4	3 (0)	0	0	4	4
VII	3	0			3	3
VIII	3	0			2	0

Segment IX: sans écusson dorsal mais avec 2 longues soies noires postérieures paramédianes et 2 paires de soies latérales plus faibles; à la face ventrale, 1 paire de soies noires paramédianes.

Appendices postérieurs: premier article couvert de spinules denses et aiguës, surtout entre les bases de crochets anaux. Ceux-ci dirigés vers l'extérieur et munis d'une forte griffe aiguë, pliée en angle aigu, avec une dent dorsale très pointue.

PATTES

Pattes antérieures courtes et fortes, médianes: les plus longues, les postérieures de longueur moyenne.

Téguments des pattes densément couverts de spinules disposées en petits peignes.

Patte antérieure à coxa épaisse et conique, fémur épais et déprimé et d'une largeur dépassant la moitié de la longueur avec 2 éperons ventraux, 1 court basal et 1 long distal, les spinules ventrales assez longues et denses entre les éperons. Tibia avec des spinules groupées à l'extrémité du bord ventral. Griffé fort épaisse, assez peu aiguë avec un éperon empodial, presque aussi long qu'elle, translucide.

Patte médiane à coxa allongée spinuleuse, à trochanter portant au bord ventral deux éperons terminaux et une longue soie calcariforme foncée et une dizaine de longues soies articulées en un groupe basal et un groupe terminal contenant un éperon aigu. Fémur long et un peu renflé au bout avec 2 forts éperons ventraux; l'un à la moitié, l'autre à l'extrémité; surface spinuleuse sauf au bord dorsal.

Patte postérieure

Coxa couverte de spinules plus longues qu'aux autres pattes, à la face interne et postérieure; trochanter avec la même garniture que le trochanter II; fémur avec 2 éperons ventraux, le basal avant le milieu; plus court, de largeur 2,4 fois la longueur, couvert de petites spinules, avec une soie dorsale longue juste au-dessus de l'éperon basal; tibia court avec trois longues soies dorsales terminales, faces non spinuleuses mais bord ventral couvert d'un peigne de petites épines et un fort éperon apical; tarse court, spinuleux à l'extrémité ventralement; griffe courbée, forte avec un éperon empodial aussi long qu'elle et transparent.

(3) *NYMPHE* (pl. VII)

Nymphe mince, allongée, à bords parallèles; mâle, à antennes plus courtes que le corps, fourreaux alaires antérieurs atteignant le début de l'abdomen IV, arrondis et ondulés à l'extrémité. Fourreaux des palpes maxillaires courts, cylindriques, divergents. Labre saillant, arrondi, portant 3 paires de longues soies proximales non crochues et une touffe serrée distale de chaque côté de la ligne médiane.

Mandibules faibles, en faucille, sans dents; bord postérieur du premier tergite abdominal avec un rebord corné semblable à celui du genre *Dyschimus* Barnard; plaques de crochets petites, présentes du segment II au segment VII; les présegmentales avec 2 crochets, la postsegmentale du segment V avec 4 crochets bien marqués, équidistants (3-4 chez la ♀).

Neuvième segment sclérifié en une plaque dorsale terminée par un rebord horizontal profondément fendu sur la ligne médiane, chaque demi-rebord largement bilobé, le lobe interne lui-même bidenté.

Branchies nombreuses en houppes, en 2 rangées dorsales, 2 latérales et 2 ventrales.

Segment	Dorsales		Latérales		Ventrales	
	Pré	Post.	Pré	Post.	Pré	Post.
II	4	4	—	4	4	4
III	4	3	5	—	4	4
IV	4	4	3	—	4	4
V	4	3	3	—	4	4
VI	3	1	1	—	4	3
VII	3	—	2	—	2	3

Fourreau nymphal

Fourreau tubulaire de coupe triangulaire, recouvert de morceaux de feuilles imbriquées d'avant en arrière en morceaux grossièrement ovales, au nombre de 4 environ d'avant vers l'arrière.

Grille postérieure à mailles quadrangulaires ou arrondies en soie brune contenant les débris larvaires.

POSITION SYSTEMATIQUE

Comme nous l'avons rappelé plus haut, H. H. Ross (1967) a érigé pour le genre *Pisulia* une nouvelle famille: les Pisuliidae.

Cette famille d'Integripalpia, proviendrait de l'Ancêtre 5, puis de 6 et enfin de 8, Ancêtre de tous les trichoptères coléophores (à l'exception des Glossosomatidae et des Hydroptilidae).

Tous les descendants de l'Ancêtre 8 constituent la superfamille des Limnephiloidea.

Celle-ci présente à son tour deux branches d'évolution; la branche Limnephilidienne (ancêtre 9) et la branche Leptocéridienne (ancêtre 13).

Les Pisuliidae sont placés par H. H. Ross à la base de cette dernière via un ancêtre 14 à mésoscutellum court et ayant perdu les vestiges du supratentorium. Comme le fait remarquer l'auteur de cette hypothèse, la plupart des stades jeunes nous sont inconnus, ce qui implique certaines suppositions dans l'élaboration d'un schéma d'évolution.

Par suite de la découverte des larves et nymphes de *Pisulia* nous pouvons dès maintenant être sûrs que ce genre dérive de l'ancêtre 9 et est donc un Limnephilidien. En effet la seule existence d'une "corne prosternale" bien développée apparente cette larve à l'ancêtre 10. Par ailleurs ni l'adulte, ni les stades jeunes ne diffèrent considérablement des Lépidostomatinae, auxquels se rattache aussi le genre africain *Dyschimus* Barnard.

C'est à cette solution que nous nous tiendrons provisoirement, comme nous l'avons déjà fait lors de la création du genre.

MARLIER: NOUVELLE ESPÈCE DE *PISULIA*

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LISTE DES FIGURES

Figure dans le texte: *Pisulia shabae*, larve

Planche I

PISULIA SHABAE n.sp.

A, B, éperons du tibia postérieur du ♂

C tête et thorax en vue dorsale

D palpe labial

E nervation alaire

Planche II

A PISULIA SHABAE n.sp. genitalia ♂ vue dorsale

B PISULIA SHABAE n.sp. genitalia ♂ vue ventrale

C PISULIA SHABAE n.sp. genitalia ♂ vue de profil

D PISULIA SHABAE n.sp. genitalia ♂ vue oblique ventrale droite

Planche III

PISULIA SHABAE n.sp., larve

A tête vue ventrale

B, C mandibules

D tête vue dorsale

Planche IV

PISULIA SHABAE n.sp.; larve

En haut:

Thorax et premier segment abdominal

En bas: fourreau

Planche V

PISULIA SHABAE n.sp.; larve

pattes, A antérieure

B intermédiaire

C postérieure

Planche VI

PISULIA SHABAE, larve

Extrémité de l'abdomen: à gauche vue dorsale

à droite vue ventrale

Planche VII

PISULIA SHABAE n.sp.

Nymphe. A labra et mandibule

B extrémité de l'abdomen

C Nymphe entière, vue de profil

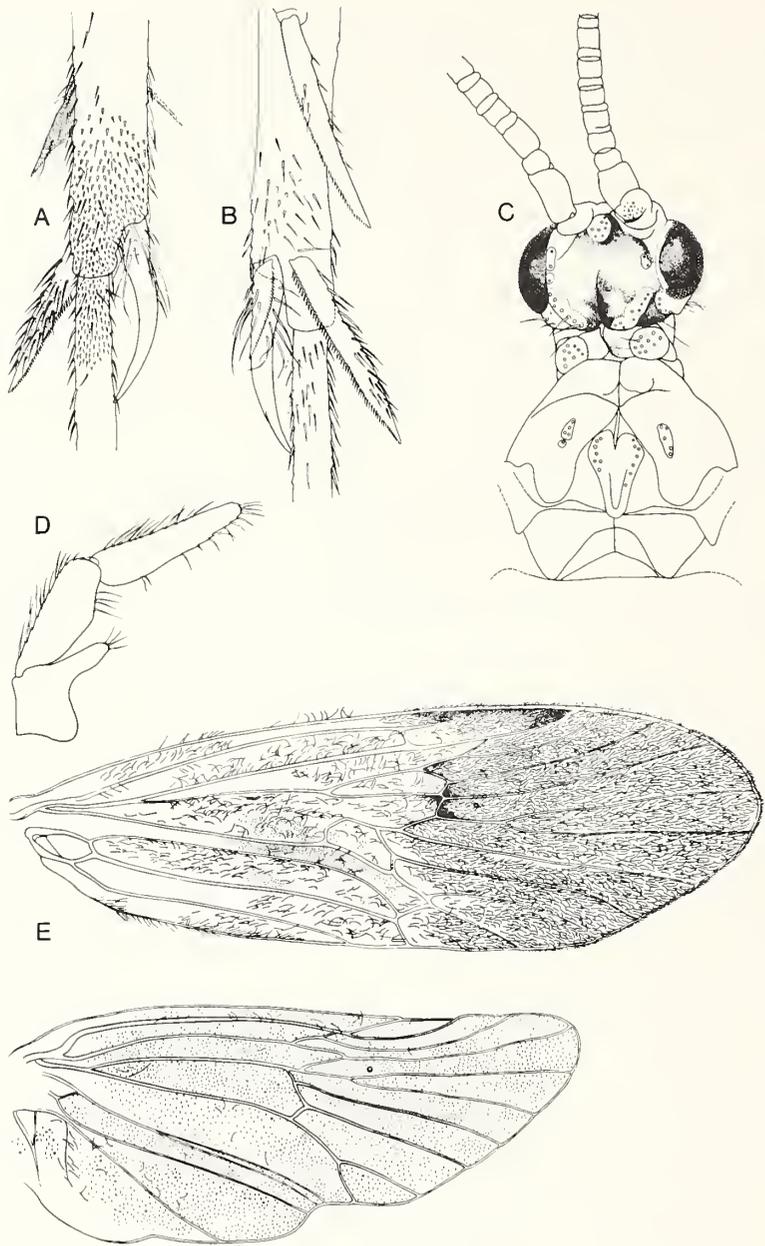


Planche 1

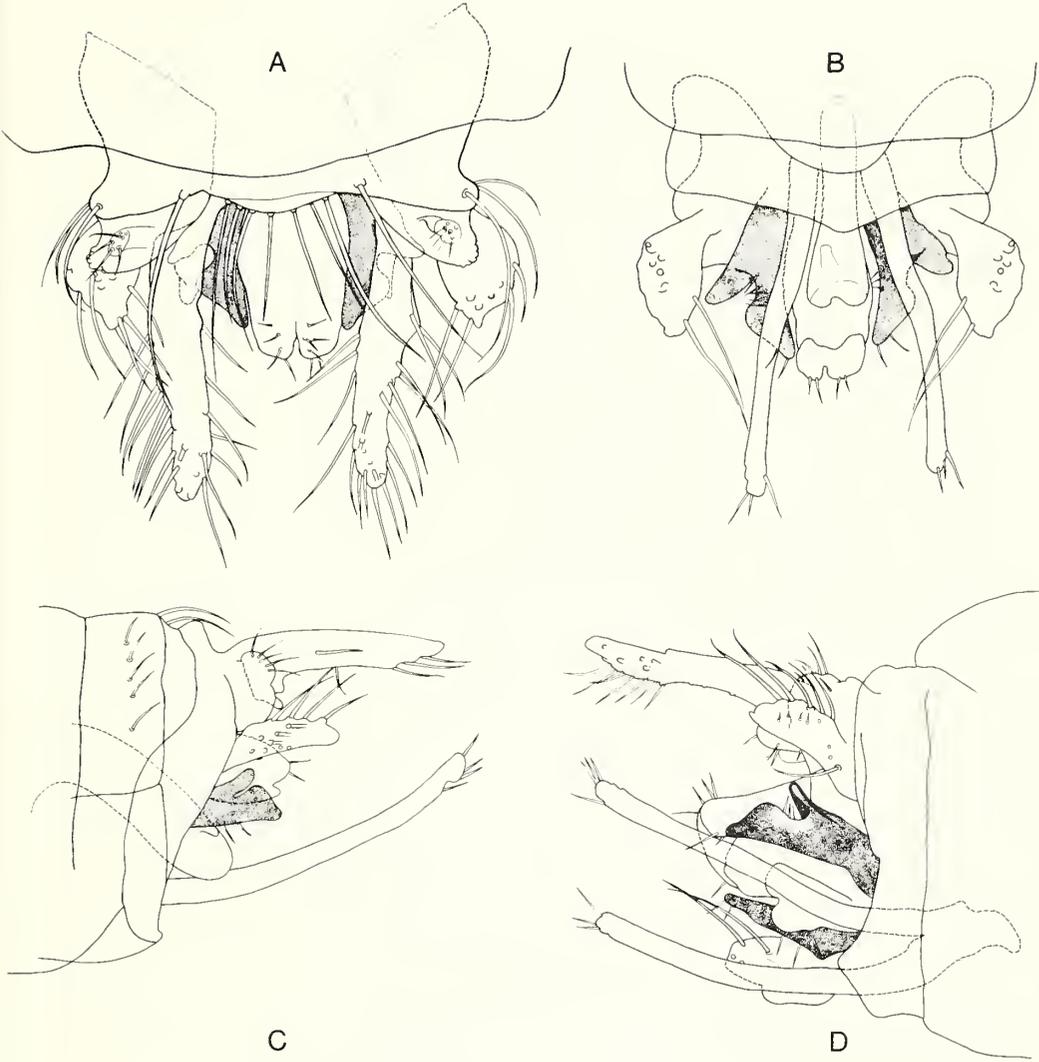


Planche II

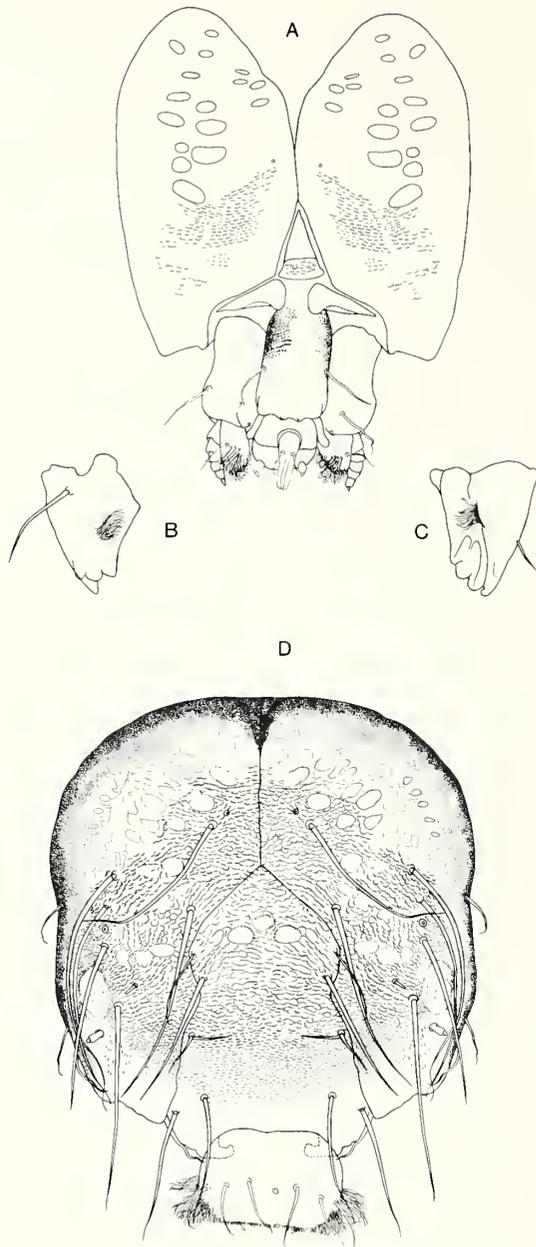


Planche III

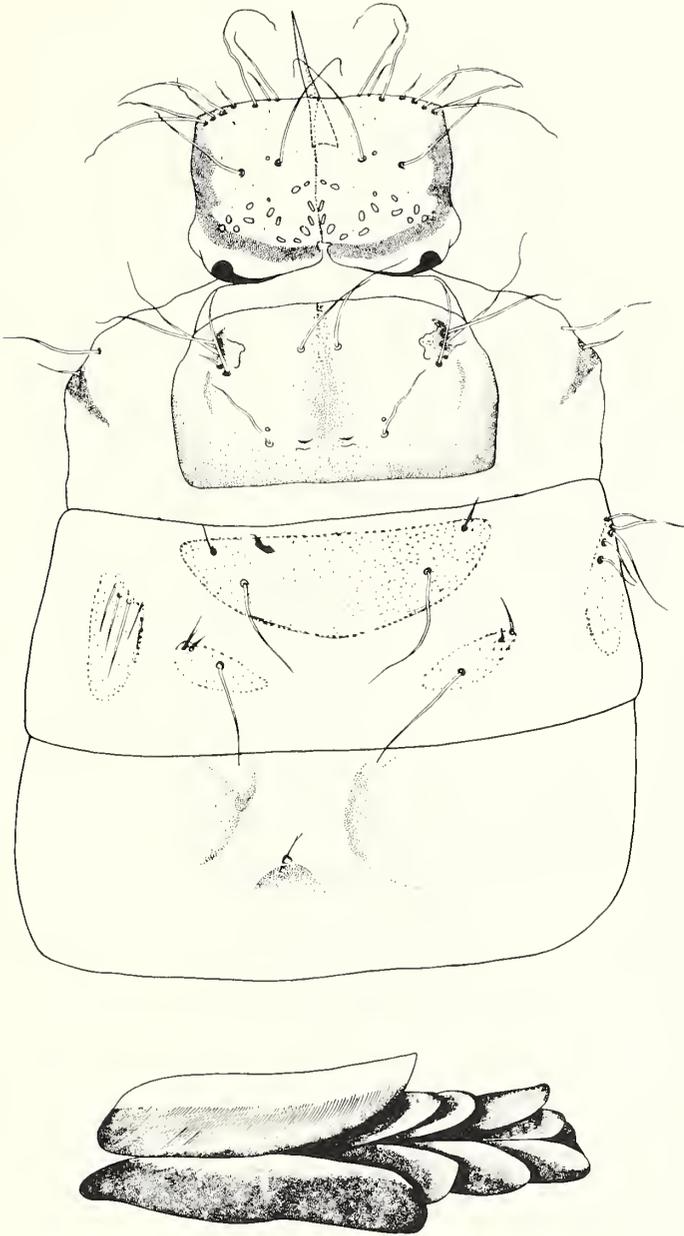


Planche IV



Planche V

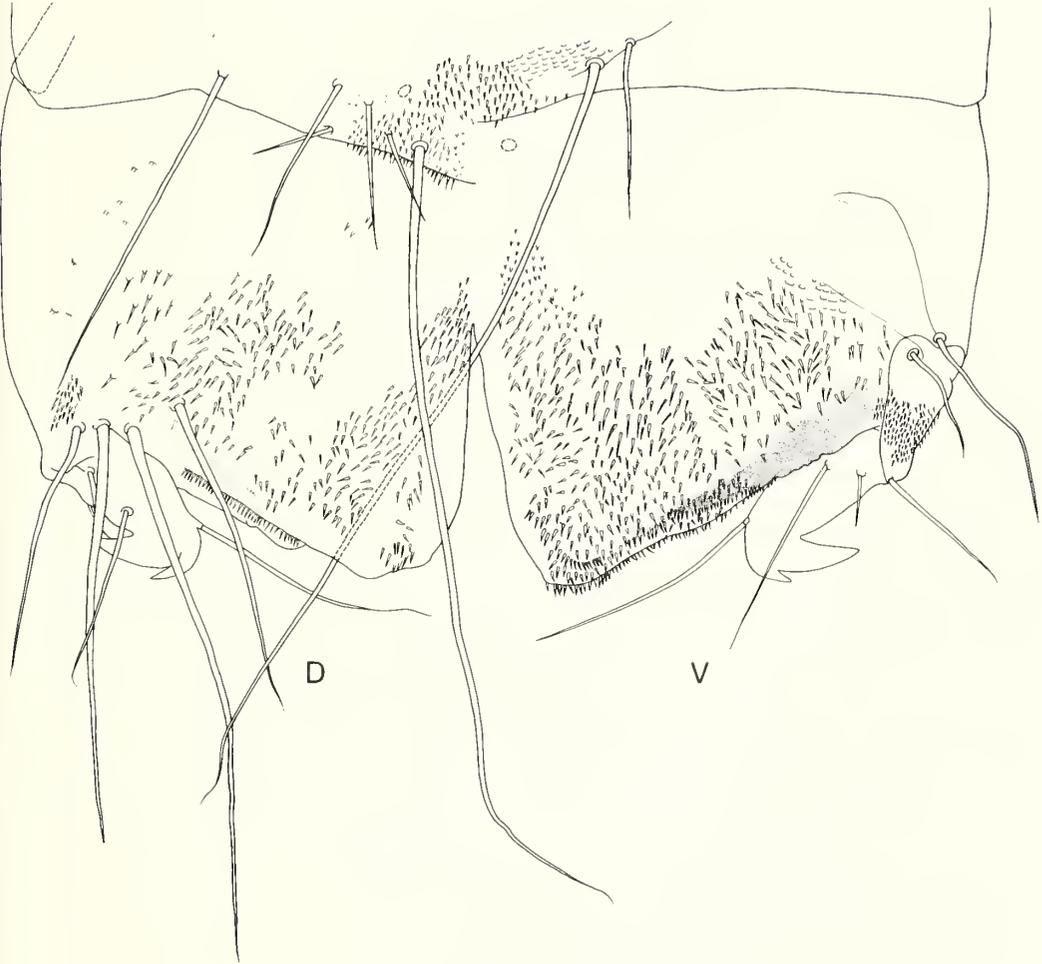


Planche VI

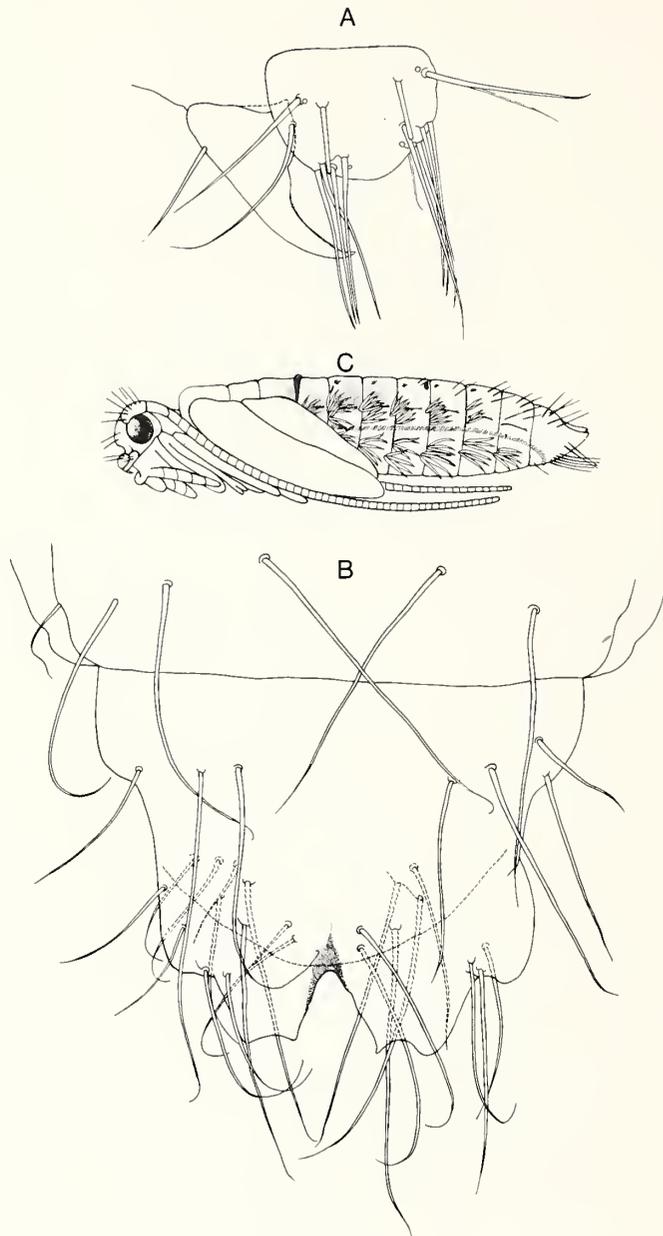


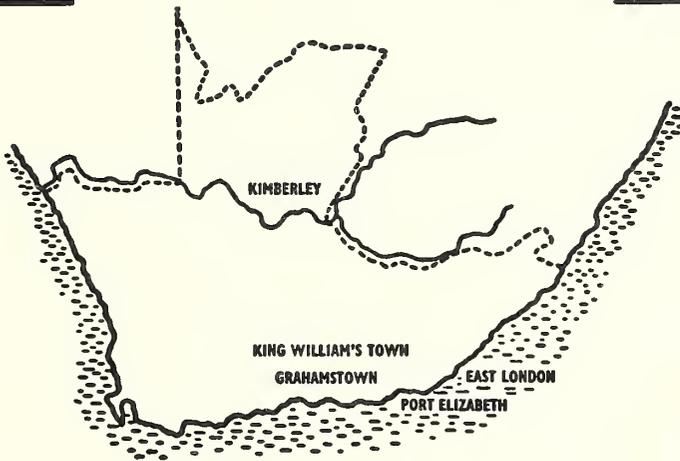
Planche VII

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VOLUME 11 • PART 14

30th JANUARY 1979

PUBLISHED JOINTLY BY THE
CAPE PROVINCIAL MUSEUMS AT THE ALBANY MUSEUM, GRAHAMSTOWN
SOUTH AFRICA

Records of pygmy and dwarf sperm whales, genus *Kogia*, from southern Africa, with biological notes and some comparisons

by

G. J. B. ROSS

(Port Elizabeth Museum, Port Elizabeth)

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ABSTRACT

Sixty-four strandings of pygmy and dwarf sperm whales, genus *Kogia*, representing at least 80 animals have been recorded on the southern African coast up to the end of 1975. Comparison of material of *K. breviceps* and *K. simus* confirmed Handley's (1966) distinction of the two species based on cranial and external characters, with the exception of the relative height of the foramen magnum and the position of the dorsal fin relative to body length, which should be used with caution in specific identification. *K. breviceps* has a longer snout than *K. simus*. Changes in

head shape occur in both species with age. Colour patterns are similar in both species. Longitudinal sections of teeth of *K. breviceps* were prepared for ageing purposes. Dentine layers in *Kogia* teeth form a chevron pattern in longitudinal section and the pulp cavity is open throughout life as in *Physeter*. Dentine layers were counted with some success in teeth of *K. breviceps* but not in those of *K. simus*.

The length at birth of *K. breviceps* is estimated to be 1,2 m. Females attain sexual maturity at about 2,7–2,8 m in length, while males are thought to mature between 2,7 and 3,0 m in length. The gestation period and length of lactation could not be estimated. Stomach contents of 16 animals indicate that cephalopods form the basic diet, supplemented with crustaceans and fish. The distribution of identified cephalopods suggests that *K. breviceps* normally inhabits oceanic waters beyond the edge of the continental shelf. Nematodes collected from the stomachs were identified as *Anisakis simplex* (Rudolphi), *Anisakis physeteris* Baylis, and *Phocanema kogiae* Johnston and Mawson. *K. breviceps* has been recorded from South West Africa to Natal. Analysis of 32 dated records does not suggest seasonal movements off South Africa.

The length at birth of *K. simus* is estimated to be 1 m. Body weights for 11 animals are given and the weight/length relationship $\log Y = 7,31 + 2,86 \log X$ was calculated, where $Y =$ body weight (kg) and $X =$ body length (mm). Both male and female *K. simus* are thought to become sexually mature between 2,1 m and 2,2 m in length. The gestation period could not be estimated. Stomach contents of 21 animals indicate that cephalopods form the basic diet supplemented with fish and some crustaceans. The distribution of identified cephalopods suggests that *K. simus* inhabits the area over the edge of the continental shelf. The same species of nematodes found in *K. breviceps* stomachs were collected from stomachs of *K. simus*. In southern African waters *K. simus* has been recorded from Saldanha Bay (17°E) to East London (27°E). There is little evidence from 27 dated records that *K. simus* migrates seasonally.

A linear relationship between the head length and total length in adult *K. simus*, *K. breviceps* and male and female *Physeter macrocephalus* is demonstrated, and discussed with regard to buoyancy regulation.

INTRODUCTION

In the 140 years that have passed since Blainville (1838) described the first pygmy sperm whale *Kogia breviceps* from a skull collected at the Cape of Good Hope, approximately 150 specimens of this genus have been reported from strandings on shores bordering the temperate and tropical seas of the world. During this period, published information on *Kogia* has been concerned almost entirely with distribution, morphology and specific nomenclature. While as many as seven species of *Kogia* have been described, for many years most workers accepted that there was a single, variable species. Following work by Ogawa (1936) and Yamada (1954), Handley (1966) established that there are two well-defined species, the pygmy sperm whale *Kogia breviceps* Blainville, 1838 and the dwarf sperm whale *Kogia simus* Owen, 1866.

In spite of the number of records, very little is known of the biology of either species. Prior to Handley's (1966) publication, the difficulties of those authors who summarised the meagre available data on reproduction and migration were compounded by the inadvertent combination of information from both species (Allen, 1941; Tomilin, 1957; Duguy, 1966).

There are few published records of *Kogia* from South African waters. Sclater (1901) described three records, including the type of *K. breviceps*, while Barnard (1954) noted 15 records from the south western Cape coast. Both *K. breviceps* and *K. simus* are known to occur off southern Africa (Handley, 1966; Best, 1971). Strandings of both species have occurred fairly frequently since 1954; 64 strandings representing at least 80 animals, have been recorded on the southern African coast from that year to the end of 1975. This paper presents an analysis of material and data from these and previous records with particular regard to the biology of the two species.

MATERIAL AND METHODS

External measurements of 17 *K. breviceps* and 30 *K. simus* were taken in the field. Almost all of the more recent specimens were measured by the author or Dr P. Best (Sea Fisheries Branch, Cape Town) following the standards recommended by Norris (1961). Cranial material was examined and measured in the South African Museum, Cape Town (SAM specimens; 9 *breviceps*, 6 *simus*), the Port Elizabeth Museum (PEM specimens; 11 *breviceps*, 17 *simus*) and the East London Museum (ELM specimens; 2 *breviceps*, 2 *simus*). One *simus* skull was measured in the Zoology Museum, University of Cape Town. Three skulls (2 *breviceps*, 1 *simus*) were identified by Dr Best in the collections of Mr Kleyenstüber, Cape Cross, South West Africa, Mr G. Palmer, Clovelly, Cape Province, and Mr Cairncross, Victoria Bay, George, Cape Province. Measurements to be taken were provided by Dr P. J. H. van Bree, Amsterdam, and are figured in Fig. 16. Measurements of individual skulls are provided in Tables 26 and 27 of the appendix.

Further records were obtained from the files of the Luderitz, South African, Port Elizabeth and East London Museums, and the Oceanographic Research Institute, Durban, as well as a number of newspaper files.

When available, one tooth from each specimen was prepared for age determination. The teeth were flattened antero-posteriorly on a grindstone, and polished to a thickness of 0.2–0.3 mm on ground glass using 500 and 600 grade carborundum powder. Sections were washed in water, and then toluene, before mounting in Caedex (Merck) under coverslips. They were examined by transmitted light at 10–20 × magnification.

Ovaries were weighed after preservation in 10% formalin, and measured in three perpendicular planes. Each ovary was sliced at approximately 2–3 mm intervals with a scalpel. Corpora lutea and corpora albicantia were counted and measured in three perpendicular planes to the nearest 1 mm. Segments or small cubes of tissue from the mid-length of one testis were preserved in 10% formalin. They were embedded in paraffin wax (MP 54° C), sectioned at 5 μ thickness and stained with haematoxylin and eosin. The minimum diameters of 30 tubules were measured with an eyepiece micrometer to determine the mean tubule diameter.

Fish otoliths recovered from stomach contents were identified by Mr J. Fitch, Department of Fish and Game, California, and fish jaws were identified by Dr P. Hulley, South African Museum. Cephalopod beaks from stomachs were separated into upper and lower beaks. The latter were sorted into apparently similar groups, and representatives of each group were sent to Mr N. MacLeod, Institute of Oceanographic Sciences, U.K., for identification. These identified beaks together with some reference specimens obtained from the cephalopod collection of the South African Museum were used to classify the remaining lower beaks from the stomachs. Beaks from lycoteuthid squids were identified as *Oregoniateuthis* from material provided by Mr M. Imber, Wildlife Service, Wellington, New Zealand.

Parasitic helminths were identified by Mr S. Prudhoe, British Museum (Natural History), London.

IDENTIFICATION OF MATERIAL

In his synopsis of the genus, Handley (1966) provided a number of characters for distinguishing *K. breviceps* from *K. simus*. The majority of these differences refer to features of the cranium and mandible, and separate the two species without difficulty when applied to the South African material. The most distinctive cranial characters are the shape of the dorsal sagittal septum near the vertex and the dorsal cranial fossae.

In *K. breviceps* the sagittal septum near the vertex is broad and slopes gradually into the cranial fossa on either side. In *K. simus* the septum is narrow, with near-vertical walls, and is often pinched posteriorly. The minimum width of the septum in 22 South African *K. breviceps*

was 14,5–49 mm (condylobasal length = CBL 237–467 mm); excluding 5 specimens with CBL < 339 mm, the minimum width of the septum was 23–49 mm. The minimum width of the septum in 26 *K. simus* from South Africa was 5–20,5 mm (CBL 201–323 mm); in all but two specimens the minimum width was 15,5 mm or less.

The shape of the dorsal cranial fossae of each species differs in the present material, as described by Handley (1966). In *K. breviceps* the fossae are elongated antero-posteriorly and the posterior wall of each fossa slopes gradually from the dorsal rim of the skull. In *K. simus* the dorsal rim of the cranial fossae is sub-spherical, and the posterior wall of each fossa is steep, giving a cupped appearance to the skull.

The condylobasal lengths of 24 South African *K. simus* ranged from 201–323 mm, and of 22 South African *K. breviceps* from 237–467 mm. Specimens known to be subadult or older from the degree of closure of the tooth pulp cavities, or the extent of the ossification of the mesethmoid at the base of the rostrum, can be identified with some certainty on condylobasal length alone. *Kogia* skulls with a condylobasal length of more than 350 mm are almost certain to be those of *K. breviceps*.

Handley's fourth cranial character refers to the position of the foramen magnum in relation to the height of the skull. He maintained that the foramen magnum was near to the midpoint of skull height in *K. breviceps*, and well below the midpoint in *K. simus*. Two combinations of three measurements were used to quantify this character. The height of the skull (No. 8) was measured perpendicularly from the surface on which the basioccipital processes were resting to the vertex, when the dorsal surface of the rostrum was horizontal. The height of the ventral border of the foramen magnum (No. 12), and the upper margin of the foramen magnum to the vertex (No. 24) were measured with the skull in the same position. The ranges of values obtained for the ratios of measurements 24/8 and 12/8 (from Tables 26 and 27) are given in Table 1, and compared more directly in Fig. 1.

TABLE 1

Ratios between cranial measurements 8,12 and 24 used to determine the position of the foramen magnum in relation to skull height

	<i>K. breviceps</i>	<i>K. simus</i>
Ratio Meas 24/8	0,46–0,55 (<i>n</i> = 21)	0,48–0,62 (<i>n</i> = 23)
Ratio Meas 12/8	0,25–0,37 (<i>n</i> = 22)	0,18–0,32 (<i>n</i> = 25)

Fig. 1 indicates that the wide ranges of values obtained for both ratios are in part the result of growth changes and partly individual variation. While the foramen magnum of *K. breviceps* tends to be closer to the midpoint of skull height than that of *K. simus*, the overlap between the two species precludes the use of this character for identification purposes.

The length and the ventral shape of the mandibular symphysis are particularly useful in separating the two species. In 17 *K. simus* from South Africa the length of the mandibular symphysis varied from 23–51 mm (CBL 207–323 mm). In 15 *K. breviceps* from South Africa the length of the mandibular symphysis varied from 36,5–128 mm including four juvenile animals (CBL < 300 mm); excluding these four, the length varied from 64–128 mm (CBL 333–453 mm). These values are similar to those tabled by Handley (1966). In 17 South African *K. breviceps* examined, the ventral margin of the symphysis was keeled; the maximum depth of the keel was at a point posterior to the mid-length of the symphysis. In 19 *K. simus* examined, the ventral surface of the symphysis was plane in some specimens, or uniformly convex with the maximum convexity at the midpoint of the symphysis.

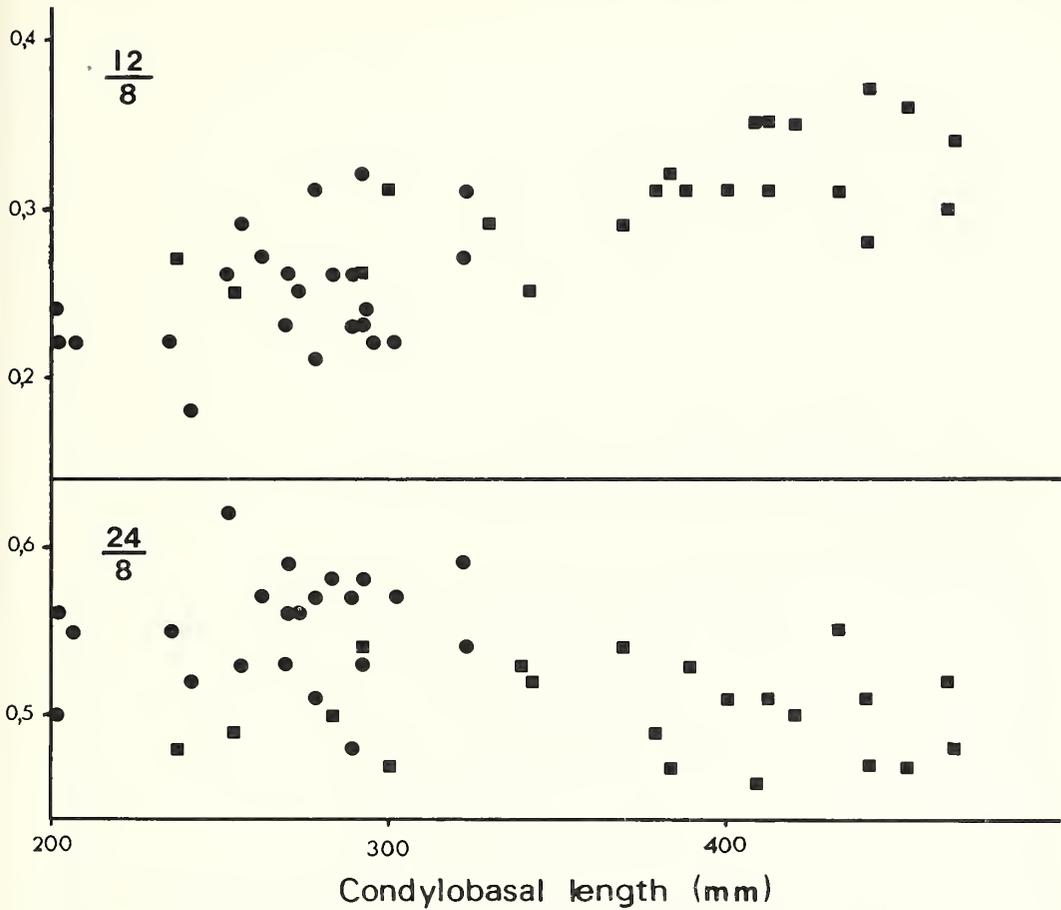


Fig. 1. Illustrating the relative position of the foramen magnum in *K. breviceps* (■) and *K. simus* (●) as a ratio between the height of the ventral border of the foramen (meas. 12) or the distance from the foramen to the vertex of the skull (meas. 23) and total skull height (meas. 8).

The number of mandibular teeth is distinctive for each species. In 8 South African *K. breviceps* the number of alveoli varied from 12–16, with a mean of 13,6. In 16 South African *K. simus* there were 7–12 alveoli with a mean of 9,7. In one immature *K. breviceps* and 4 *K. simus* the number of teeth counted in the flesh and the number of alveoli coincided exactly. In one immature *K. simus* (PEM 1519/59) there was one less tooth on the left side in the flesh than the number of alveoli, while one extra tooth in the flesh on each side was found in two *K. simus* (PEM 1519/62, PEM 1519/72).

The true incidence of maxillary teeth in South African *K. simus* is uncertain. Of 14 animals in which the presence or absence of maxillary teeth was specifically noted in the flesh, 10 had no maxillary teeth. The remaining four had varying numbers of teeth: left/right, 1–0, 2–1, 2–2, and 3–3. No maxillary teeth were found in 6 *K. breviceps* examined specifically for them.

Handley (1966) described the form of *Kogia* teeth and mentioned the use of the degree of tooth pulp closure as an ageing criterion. Comparison of teeth from the present material suggested further that tooth size in conjunction with the degree of pulp closure would be a useful specific character. In Table 2 the measurements of the largest available tooth from 12 *K. breviceps* and 15 *K. simus* are given. Tooth length was measured in a straight line from the tip to the base. The degree of closure of the pulp cavity was measured from a longitudinal section of each tooth as the distance from the tip to the apex of the pulp cavity expressed as a percentage of the tooth length.

TABLE 2

Measurements of the largest available tooth from 12 K. breviceps and 15 K. simus from South Africa

Catalogue No.	CBL (mm)	Length (mm)	Max. Diam. (mm)	Pulp Cavity closure (%)	No. of teeth available	Length Max. Diam.
<i>K. breviceps</i>						
SAM 35550	254	13	2,6	50	33	5,0
PEM 1511/10	300	18	3,7	24	1	4,9
SAM 36980	339	26,5	4,5	56	2+	5,9
PEM 1519/12	341	28	5,6	35	29	5,0
SAM 35522	369	30	7,0	38	12	4,3
SAM 3912	388	31+	5,0	—	18	6,2+
PEM1511/13	400	35	5,6	35	31	6,3
ELM 674	408	37	6,2	94	29	6,0
SAM 35795	433	34	5,0	78	26	6,8
SAM M723	441	39,5	9,0	—	26	4,4
PEM 1516/08	453	38	7,1	89	2	5,4
PEM 1517/76	—	35+	8,0	100	8	4,6+
<i>K. simus</i>						
PEM 1516/51	202	9	1,7	22	11	5,3
PEM 1519/73	207	11	1,9	40	12	5,8
PEM 1519/17	235	12	2,6	42	3	4,6
PEM 1519/59	252	15,5	2,1	52	21	7,4
PEM 1519/61	262	23	2,8	52	21	8,2
PEM 1519/62	270	20	3,0	56	19	6,7
PEM 1517/12	273	20	2,7	90	12	7,4
PEM 1519/72	278	21	3,5	83	21	6,0
SAM 35634	278	20,5	2,8	75	22	7,3
PEM 1519/60	283	18	2,9	75	19	6,2
PEM 1519/09	289	26	3,5	95	9	7,4
SAM 36728	293	24,5	3,3	87	19	7,4
SAM 36677	323	26	3,7	—	12	7,0
PEM 1515/25	—	18,5	4,2	83	2	4,4
PEM 1515/50	—	21	4,2	90	9	5,0

These measurements show that teeth of *K. simus* are shorter and proportionately more slender than those of *K. breviceps*. A *Kogia* tooth longer than 30 mm and more than 4,5 mm in diameter is almost certain to be from *K. breviceps*. Teeth 20–30 mm in length can be assigned to species on the degree of closure of the pulp cavity which is less than 60% in *K. breviceps* and generally more than 60% in *K. simus* for this size range. Teeth of either species that are shorter than 20 mm are too similar to permit accurate identification.

Few differences in the external morphology of the two species have been described. In addition to the greater total length of *K. breviceps*, Handley (1966) described the dorsal fin of *K. breviceps* as being lower, and placed more posteriorly on the back than that of *K. simus*. These characters were used by Raun *et al.* (1970) and Caldwell *et al.* (1971) to identify records from measurements or photographs.

The external measurements of 16 *K. breviceps* and 21 *K. simus* which were identified on cranial or mandibular material are compared in Table 3. Measurements of individual animals are provided in the appendix (Tables 23 and 24).

The length of the longest South African specimen of *K. simus* (2,64 m) is close to the maximum length of 2,7 m given by Handley (1966) for this species, and only two other specimens were longer than 2,6 m. In view of the size of the present sample (14 animals over 2,3 m in length) it seems very unlikely that *K. simus* attains lengths of more than 2,8 m. Hence *Kogia* specimens more than 2,8–2,9 m in length are certain to be *K. breviceps* and have been identified accordingly in this report.

The size of the dorsal fin is distinctly different in the two species. In *K. breviceps* the height of the fin is less than 5% total body length, and more than 5% body length in *K. simus* which also has a slightly longer dorsal fin base. Fin height would be a most useful character for identifying records of *Kogia* based on photographs, provided the height of the fin and the body length could be estimated, or from measured specimens. Photographs showing a portion of the animal only present more of a problem. In Table 4 the height and length measurements of the dorsal fin of 11 *K. simus* and 5 *K. breviceps* from South Africa are expressed as a ratio from actual measurements, and from measurements of outline drawings taken from colour slides.

The results in Table 4 suggest that dorsal fin height to length ratios based on actual measurements may prove a useful supplementary character in identification. Ratios based on measurements taken from outline drawings however are considerably more variable, particularly those of *K. simus*. In at least two cases this variation is a result of using measurements from photographs taken obliquely. The main source of variation stems from the difficulty of pinpointing the limits of the length of the fin base which also affects the measurement of the height. In sum it appears that a qualitative visual impression only of fin shape would be a useful supplementary character in conjunction with more distinctive characters.

The position of the dorsal fin varies considerably in both species. The anterior insertion of the fin in *K. simus* is generally less than 50% of total length from the tip of the snout while that of *K. breviceps* is more than 50%. Despite the overlap in their limits the measurements for the present samples of 6 *K. breviceps* and 10 *K. simus* differed significantly when tested with the Mann-Whitney test ($U = 4$, $\alpha = 0,05$). The distance from the tip of the snout to the tip of the dorsal fin in samples of 12 *K. breviceps* and 18 *K. simus* was not found to differ significantly between the two species. The relatively small differences in the position of the anterior insertion of the fin indicate that this character should be used with caution in identification.

Three other measurements in Table 3 were found to differ significantly between the two species when compared with the Mann-Whitney test ($\alpha = 0,05$). Differences in the length from the tip of the snout to the eye ($U = 25,5$), to the blowhole ($U = 0$), and to the anterior insertion of the flipper ($U = 54$) all indicate that *K. breviceps* has a longer snout than *K. simus*. The length from the tip of snout to the blowhole should prove a particularly useful character since there is no overlap between the two species and it is a relatively accurate measurement.

TABLE 3

External measurements of 16 K. breviceps and 21 K. simus from South Africa. Total length is given in mm; other measurements are percentages of body length

Measurement	<i>K. breviceps</i>			<i>K. simus</i>		
	Limits	Mean	N	Limits	Mean	N
1. Total length	1880-3250	2530	16	1360-2640	2085	21
2. Tip of snout to centre of eye . .	11,2-17,3	14,3	12	8,7-13,3	11,0	20
3. Length of gape	5,2-6,5	5,8	7	2,0-8,3	4,3	18
4. Tip of snout to ext. auditory meatus	17,5-20,8	19,1	2	11,5-19,5	15,1	7
5. Centre of eye to ext. auditory meatus	2,5-3,5	2,8	3	2,8-3,2	2,9	6
6. Centre of eye to angle of gape . .	8,1-10,4	8,9	8	5,3-9,2	8,0	14
7. Centre of eye to blowhole (both)	10,8-11,7	11,2	6	7,9-13,0	10,5	7
Centre of eye to blowhole (left)	9,8-12,4	11,1	2	8,7-10,7	9,6	5
Centre of eye to blowhole (right)	11,5-14,9	13,2	3	11,9-12,7	12,1	6
8. Tip of snout to blowhole	10,4-12,8	11,7	10	7,5-10,1	8,7	16
9. Tip of snout to ant. insertion of flipper	19,5-25,2	22,0	13	16,7-23,3	19,6	20
10. Tip of snout to ant. insertion of dorsal fin	49,0-58,9	52,2	6	42,7-54,0	46,0	10
11. Tip of snout to tip of dorsal fin . .	58,1-67,5	60,6	12	56,4-65,4	59,7	18
12. Tip of snout to umbilicus	40,5-45,5	42,7	6	37,7-46,7	42,8	8
13. Tip of snout to midpoint of genital slit (male)	45,7-58,9	50,2	5	44,5-51,6	47,3	6
14. Tip of snout to midpoint of genital slit (female)	70,3-73,3	71,9	3	66,4-77,2	70,9	10
15. Tip of snout to anus	70,1-77,2	72,7	6	67,3-75,1	71,1	9
16. Projection of snout beyond lower jaw	1,3-7,6	4,5	8	2,5-5,8	3,8	16
17. Girth on transverse plane at axilla	51,7-67,7	58,0	4	53,9-64,9	57,7	8
18. Girth, maximum	59,5-60,2	59,9	2	59,8-67,2	64,8	8
19. Girth on transverse plane at anus	35,1-46,8	41,2	5	36,8-47,0	42,1	12
20. Length flipper, ant. insertion to tip	11,4-15,3	13,9	15	12,9-17,5	15,0	21
21. Length, flipper, axilla to tip . . .	8,1-12,4	10,4	13	9,7-12,1	10,7	21
22. Maximum width of flipper	4,2-6,1	5,0	15	4,4-6,1	5,4	21
23. Height, dorsal fin	2,3-4,7	3,6	12	5,4-10,0	7,5	19
24. Length, dorsal fin	6,1-13,1	10,0	12	10,8-17,5	14,7	19
25. Width of flukes, tip to tip	20,4-27,1	23,8	15	21,2-32,4	26,1	21
26. Anterior border of flukes to notch	6,3-9,1	7,7	12	6,3-9,5	8,1	20
27. Depth of notch	0,8-2,3	1,6	11	1,3-2,9	1,9	20

TABLE 4

Measurements of the dorsal fin height and length of 5 *K. breviceps* and 11 *K. simus* from South Africa expressed as ratios

Cat. No.	Ratio from	
	Direct Measurements	Outline Drawings
<i>K. breviceps</i>		
PEM 1515/70	0,30	0,26
PEM 1511/13	—	0,36
PEM 1516/48	0,35	0,37
PEM 1517/89	0,57 (0,31*)	0,49
PEM 1517/90	0,30	0,31
<i>K. simus</i>		
PEM 1517/12	—	0,27†
PEM 1519/72	0,48	0,42
PEM 1519/73	0,44	0,52
PEM 1513/86	—	0,30†
PEM 1519/09	0,54	0,44
PEM 1519/59	0,50	0,41
PEM 1519/60	0,56	0,43
PEM 1516/97	0,50	0,49
PEM 1516/50	0,41	0,39
PEM 1516/51	0,42	0,42
PEM 1519/61	0,53	0,43
PEM 1519/62	0,50	0,45

*The fin length proved very difficult to measure: maximum and minimum lengths were taken.

†The photographs of the fin were taken from a ventro-lateral aspect.

The shape of the snout at various body lengths is shown in Fig. 2 for 7 *K. breviceps* and Fig. 3 for 12 *K. simus*. In these figures it is clear that distinct changes in the shape of the head occur as the body length increases. In the youngest animals of both species the dorsal margin of the snout slopes noticeably towards the tip, up to body lengths of approximately 2,0 m. In animals longer than 2,0 m the dorsal profile of the snout and that of the neck and back form a smooth, almost straight line. Apart from a more pugged appearance to the snout of *K. simus* there is little to distinguish the head shape of the two species in animals less than about 2,3 m in length. In animals longer than 2,3 m the snout of *K. simus* is distinctly squarish and blunt in lateral view. In *K. breviceps* longer than 2,3 m the snout is distinctly more elongated and sub-rectangular in lateral view, with an almost bulbous appearance in some animals.

The colour patterns of animals identifiable as *K. breviceps* have been described by Boschma (1951), Hubbs (1951) and Hale (1963), while Yamada (1954) described the colour pattern of *K. simus*. In the present study, 3 *K. breviceps* and 8 *K. simus* were examined soon after death before post-mortem changes in colour became extensive. There appear to be no consistent differences in the colour patterns of the two species. The colour pattern of an adult female *K. simus* is illustrated in Plate 1, from colour slides taken at night a few minutes after death. The

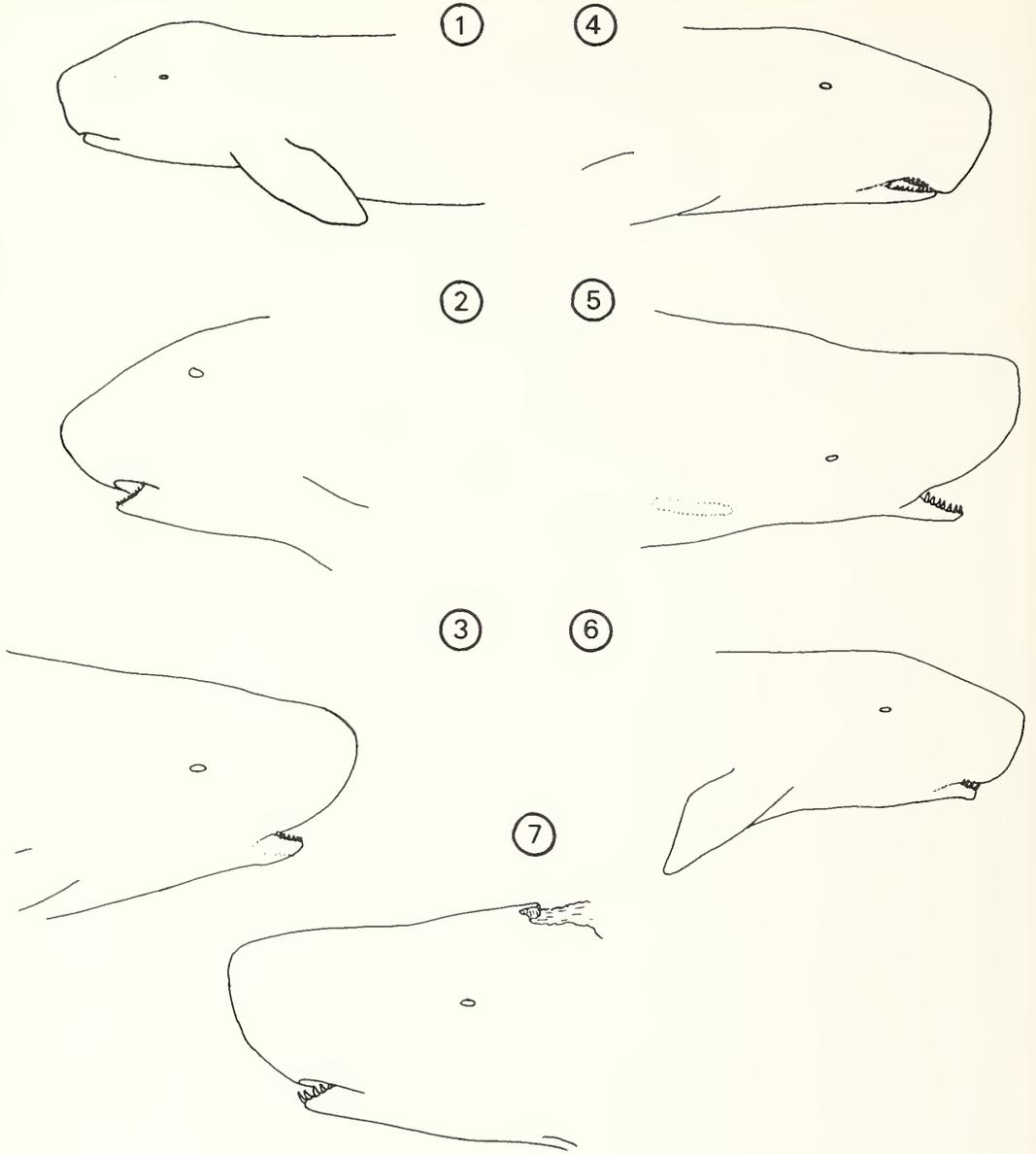


Fig. 2. Changes in the head profile of *K. breviceps* with an increase in total length. 1—PEM 1516/48, 1 135 mm; 2—PEM 1515/70, 1 650 mm; 3—PEM 1517/90, 2 020 mm; 4—PEM 1519/12, 2 340 mm; 5—PEM 1511/13, c. 2 700 mm; 6—PEM 1516/48, 3 050 mm; 7—PEM 1517/89, 3 055 mm.

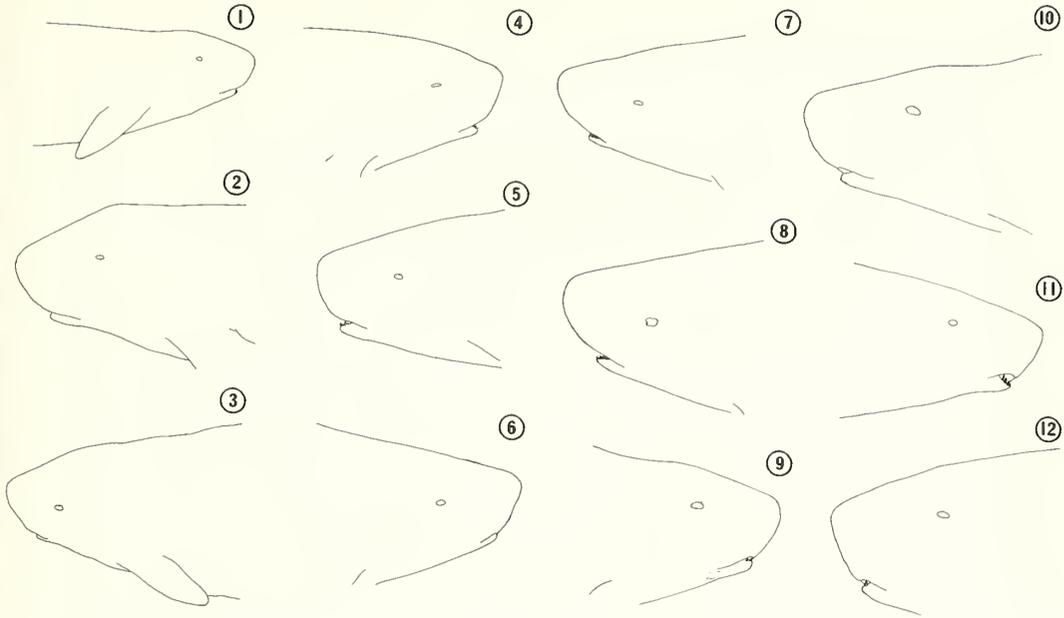


Fig. 3. Changes in the head profile of *K. simus* with an increase in total length. 1—PEM 1516/51, 1 360 mm; 2—PEM 1516/99, 1 525 mm; 3—PEM 1519/73, 1 610 mm; 4—PEM 1519/59, 1 890 mm; 5—PEM 1519/62, 2 040 mm; 6—PEM 1519/60, 2 060 mm; 7—PEM 1519/61, 2 090 mm; 8—PEM 1519/72, 2 240 mm; 9—PEM 1516/97, 2 340 mm; 10—PEM 1517/12, 2 440 mm; 11—PEM 1516/50, 2 440 mm; 12—PEM 1519/09, 2 520 mm.

colour tones of this animal ranged from dark bluish grey dorsally through a pale blue grey zone laterally to the white of the ventral surface. The white bracket-shaped mark behind the eye, as described by Hubbs (1951) and several subsequent authors, was present in all eleven *Kogia* examined and appears to be characteristic of the genus, though it was absent in the specimen figured by Boschma (1951).

Details of all the specimens of *K. breviceps* and *K. simus* recorded from southern Africa and identified on these characters are listed in Tables 5 and 6 respectively. Records of *Kogia* not yet identified to species are listed in Table 7.

BIOLOGY: *KOGIA BREVICEPS*

AGE DETERMINATION

The teeth of *K. breviceps* examined in longitudinal section show a similar basic structure to those of other odontocetes reviewed by Jönsgård (1969). Though an enamel cap is absent, the prenatal dentine is usually easily distinguished by its homogenous appearance and is delineated from the postnatal dentine by a narrow clear neonatal line approximately 15μ thick. In teeth from older animals the prenatal dentine may be worn away. Dentine deposition in the first part of life contributes most of the tooth's total length, and in section the pulp cavity is long, tapering to an acute apex. The pattern of further dentine deposition resembles that of the sperm whale *Physeter* in which dentine increments are deposited forming a chevron pattern in longitudinal section, and is in contrast to those of delphinids in which the pulp cavity becomes completely

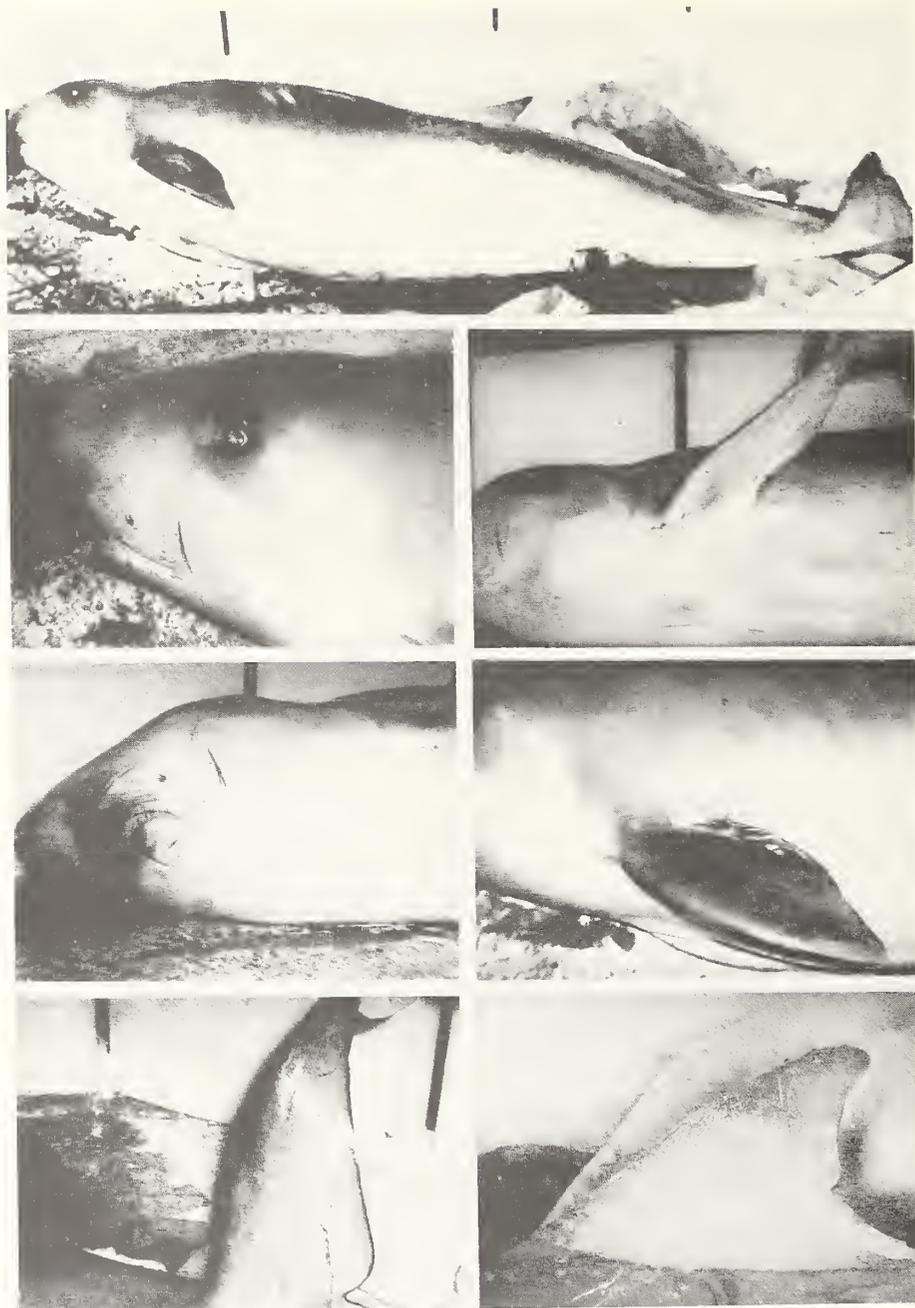


Plate 1. Colour pattern of an adult female *Kogia simus* Owen (PEM 1516/97), from colour slides taken at night a few minutes after death.

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS *KOGIA*

TABLE 5

Records of pygmy sperm whales *Kogia breviceps* from South Africa. Abbreviations for primary identification characters are: C = cranium; S = mandibular symphysis; T = teeth; L = total length; Dh = dorsal fin height; H = head shape

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Identification	Comments
MNHNP 1927:3	—	—	393	1837	Cape of Good Hope	C	Holotype (de Blainville, 1838)
SAM 35074	—	—	—	1880	Buffels Bay, Knysna	ST	Coll. by H. Munro
SAM 3911	♀	1755	—	1896	3404S 2300E Green Point, Table Bay	C	Sclater (1901)
SAM 3912	—	—	388	1899	3454S 1824E Knysna	C	Sclater (1901)
SAM 34018	—	—	441	15/12/30	3402S 2303E Milnerton Beach, Cape Town	C	
SAM 17690	—	—	237	2/8/33	3352S 1829E Table Bay	C	Fishermen reported 2 large animals
—	—	—	—	c. 1940	3353S 1826E Wilderness	C	In collection of Mr Cairncross, Victoria Bay, George
—	♀	c. 3050	—	1951/52	3359S 2235E Plettenberg Bay	L	c. 1 m foetus K. H. Barnard's records
SAM 282	—	—	—	Jan. 1955	3403S 2323E Plettenberg Bay	ST	Lower jaw collected by Mr P. Jones
—	—	c. 3050	—	24/10/56	3403S 2323E Brighton Beach, Durban	LH	Photograph in Natal Mercury 25/10/56
ELM 616/a	♀	—	—	31/5/58	2952S 3100E Mazeppa Bay, Transkei	C	
ELM 674	♂	c. 2750	408	Aug./Sept. 1960	3228S 2839E Nahoon Beach, East London	C	Photographs in ELM files
—	—	c. 2700	—	11/4/62	3359S 2756E Wilderness	Dh, H	Photographs in SAM files
PEM 1496/66	♂	2970	442	20/11/63	3359S 2235E Amsterdamhoek, P.E.	C	Stranded alive
ELM 779	♀	—	412	24/1/64	3352S 2537E East London	C	
—	♂	3305	—	10/6/64	3301S 2755E Begha R. Mouth, East Cape	H	Photographs 213/6-10 ELM
—	♀	c. 3050	—	14/4/65	3320S 2723E Vleesbaai, Mossel Bay	L	
PEM 1511/12	♀	—	383	Oct. 1965	3319S 2155E Nature's Valley	C	Pregnant, with PEM 1511/10
PEM 1511/10	—	—	300	Oct. 1965	3359S 2334E Nature's Valley	C	Stranded with PEM 1511/12
—	—	—	—	Sep. 1966	3359S 2334E Natal North Coast	ST	Stranded with a calf. Photograph of lower jaw in SAM files

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Identification	Comments
—	—	c. 3660	—	Oct. 1966	Lüderitz 2640S 1509E	L	Photographs in Lüderitz Museum files
SAM 35522	♂	2665	369	3/12/66	Hout Bay 3404S 1822E	C	
PEM 1511/13	♂	c. 2700	400	8/3/67	Nature's Valley 3359S 2334E	C	
PEM 1513/87	♂	2935	412	22/7/67	St George's Strand, P.E. 3350S 2539E	C	
SAM 35550	♂	1945	254	30/4/68	Die Plaat, Gansbaai 3435S 1921E	C	One of two animals
PEM 1514/58	—	—	467	Jan. 1969	Woody Cape, Algoa Bay 3341S 2616E	C	Skull found on beach
SAM 35795	♂	3050	433	6/11/69	4 km. W. of Arniston 3440S 2012E	C	An old stranding
PEM 1515/07	♀	1880	292	7/11/69	Begha R. Mouth, East Cape 3320S 2723E	C	Stranded alive
PEM 1515/12	—	3050	420	6/12/69	Beachview, P.E. 3405S 2520E	C	Decomposed
SAM 37126	—	—	465	1969	Cape Cross, S.W. Africa 2146S 1355E	C	Partial Skeleton on beach. Coll. Mr Kleyenstüber
SAM 36721	—	—	—	Jul./Aug. 1970	50 km. W of Cape Infanta 3533S 2024E	ST	One of two animals
PEM 1515/70	—	1965	283	29/8/70	Schoenmakerskop, P.E. 3402S 2533E	C	
PEM 1516/08	♂	3250	453	21/11/70	Van Staden's R. Mouth E. Cape 3358S 2513E	C	Decomposed
—	—	c. 3050	411	Jan./Feb. 1971	7 km. S. of Cape Cross, S.W.A. 2150S 1355E	C	In collection of Mr Kleyenstüber
PEM 1516/48	♀	3050	—	14/3/71	Maitland R. Mouth E. Cape 3405S 2518E	T, H, Dh	1,135 m foetus
PEM 1517/28	♀	2895	—	18/7/71	Schoenmakerskop, P.E. 3402S 2533E	T	Slightly decomposed
PEM 1517/76	—	3275	—	2/4/72	Bushman's R. Mouth, E. Cape 3342S 2640E	ST	Decomposed
PEM 1517/89	♀	3055	—	11/7/72	Coega R. Mouth, E. Cape 3348S 2542E	T	Stranded with PEM 1517/90
PEM 1517/90	♂	2020	—	11/7/72	Coega R. Mouth, E. Cape 3348S 2542E	T	Stranded with PEM 1517/89
PEM 1517/91	♀	3095	—	18/7/72	Schoenmakerskop, P.E. 3402S 2533E	T	Stranded with PEM 1517/92
PEM 1517/92	♂	1970	—	18/7/72	Schoenmakerskop, P.E. 3402S 2533E	T	Stranded with PEM 1517/91
SAM 36980	♀	c. 2360	339	10-11/8/74	Die Plaat, Walker Bay 3430S 1920E	C	Decomposed
PEM 1519/12	♂	2340	341	25/12/74	King's Beach, P.E. 3358S 2538E	C	
SAM 35075	—	—	379	—	—	C	Skull found in collection

C.T. = Cape Town, E.L. = East London, P.E. = Port Elizabeth.

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

TABLE 6

Records of dwarf sperm whales *Kogia simus* from South Africa. Abbreviations of primary identifying characters are: C = cranium; S = mandibular symphysis; T = teeth; L = total length; Dh = dorsal fin height; H = head shape

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Identification	Comments
BM 1952.8.28.1	—	—	—	—	Muizenberg Beach, False Bay 3407S 1828E	C	Donated by Dr Gilchrist, 15/6/25 (Dr van Bree, pers. comm)
—	♂	2 520	—	1954	Buffels Bay, Knysna 3404S 2300E	C	In collection of Mr Cairncross, George
ELM 477	—	—	292	12/1/55	Kaiser's Beach, E.L. 3313S 2737E	C	
—	♂	c. 2 440	—	16/7/60	Eastern Beach E.L. 3301S 2755E	Dh, H	Photographs in ELM files
—	—	—	292	1962?	Bloubergstrand, W.Cape? 3348S 1827E	C	In Zoology Museum, Univ. of Cape Town
SAM 35079	♂	2 470	—	20/5/63	Lynch Point, Saldanha Bay 3303S 1758E	C	Decomposing
PEM 1513/86	—	2 410	269	Apr. 1967	Springmount, Algoa Bay 3345S 2612E	C	
SAM 35634	♂	2 155	278	2/12/68	Bloubergstrand, W. Cape 3348S 1827E	C	Decomposing
PEM 1515/00	♂	2 605	322	20/10/69	Seeköe R. Mouth, E. Cape 3305S 2455E	C	
SAM 35799	♂	1 780	—	30/11/69	Fish Hoek, False Bay 3408S 1826E	Dh, H	
PEM 1515/25	♂	c. 2 540	—	Jan. 1970	Jeffrey's Bay 3404S 2456E	C	
SAM 36024	♂	1 975	270	1/2/70	Woodstock Beach, W. Cape 3355S 1828E	C	
PEM 1515/50	♀	2 310+	—	28/4/70	St. George's Strand, P.E. 3350S 2539E	C	Stranded with PEM 1515/51
PEM 1515/51	—	—	202	28/4/70	St. George's Strand, P.E. 3350S 2539E	C	Stranded with PEM 1515/50
PEM 1515/53	♀	2 305	278	10/5/70	9 km E. Hougham Park, Algoa Bay 3344S 2449E	C	Stranded with PEM 1515/54
PEM 1515/54	—	1 525	201	10/5/70	9 km E. Hougham Park, Algoa Bay 3344S 2449E	C	Stranded with PEM 1515/53
PEM 1516/50	♀	c. 2 440	—	24/3/71	2 km W. Cape Padrone 3346S 2627E	T	Stranded with PEM 1516/51
PEM 1516/51	♀	1 360	—	24/3/71	2 km W. Cape Padrone 3346S 2627E	T	Stranded alive with PEM 1516/51
PEM 1516/97	♀	2 350	289	14/4/71	Amsterdamhoek, P.E. 2452S 2537E	C	Stranded alive with PEM 1516/99
PEM 1516/99	♀	1 525	—	14/4/71	Amsterdamhoek, P.E. 2452S 2537E	Dh, H	Stranded alive with PEM 1516/97
PEM 1517/13	—	—	—	Apr. 1971	Mossel Bay 3411S 2209E	T	Decomposed
PEM 1517/12	♂	c. 2 400	273	2/5/71	Seaview, P.E. 3401S 2522E	C	Tail cut off
—	—	—	—	18/7/71	Fish Hoek, False Bay 3408S 1826E	C	In collection of Mr Palmer, Clovelly, Cape

Cat. No.	Sex	Total length (mm)	CBL (mm)	Date	Locality Co-ordinates	Identification	Comments
PEM 1517/38	♀	c. 2 700	—	4/9/71	Beachview, P.E. 3400S 2520E	S	Decomposed
SAM 36677	—	—	323	13/5/72	Milnerton Beach, W. Cape 3352S 1829E	C	Decomposed
PEM 1518/02	♀	2 400	—	23/8/72	Sundays R. Mouth, E. Cape 3343S 2552E	T	Pregnant, accompanied by a calf c. 1,3 m long
SAM 36728	♀	2 640	293	31/12/72	Blouwaterbaai, Saldanha Bay 3303S 1758E	C	Stranded with a ♂
SAM 36729	—	—	256	—	Muizenberg Beach, False Bay 3407S 1828E	C	Presented to SAM in Aug. 1972
PEM 1518/82	♀	2 150	—	5/2/74	North End, P.E. 3456S 2537E	ST	
PEM 1518/85	♀	1 890	241	26/2/74	King's Beach, P.E. 3457S 2538E	C	
PEM 1519/09	♂	2 520	289	19/8/74	North End Beach, P.E. 3454S 2538E	C	
PEM 1519/16	—	—	301	Feb. 1975	Van Stadens/Gamtoos Beach 3358S 2510E	C	Bleached skull found on the beach
PEM 1519/17	♂	1 810	235	9/2/75	Van Stadens R. Mouth, E. Cape 3358S 2514E	C	Decomposing
PEM 1519/59	♀	1 890	252	10/7/75	Sea Vista, Cape St. Francis 3408S 2450E	C	Stranded with PEM 1519/60, 61, 62
PEM 1519/60	♀	2 060	283	10/7/75	Sea Vista, Cape St. Francis 3408S 2450E	C	Stranded with PEM 1519/59, 61, 62
PEM 1519/61	♀	2 090	262	10/7/75	Sea Vista, Cape St. Francis 3408S 2450E	C	Stranded with PEM 1519/59, 60, 62
PEM 1519/62	♂	2 040	270	10/7/75	Sea Vista, Cape St. Francis 3408S 2540E	C	Stranded with PEM 1519/59, 60, 61
PEM 1519/72	♀	2 240	278	17/9/75	Sundays R. Mouth, E. Cape 3343S 2552E	C	Stranded with PEM 1519/73
PEM 1519/73	♀	1 610	207	17/9/75	Sundays R. Mouth, E. Cape 3343S 2552E	C	Stranded with PEM 1519/72
ELM 524	—	—	295	—	—	C	Found in collection

E.L. = East London; P.E. = Port Elizabeth

obliterated at a relatively early age. In *K. breviceps* the pulp cavity appears to remain open at the base of the tooth throughout life, though in one instance (PEM 1517/76) the pulp cavities had closed in four of the eight available teeth. All of these teeth showed signs of advanced dental decay.

Growth layers are visible in the present material in both the dentine and the cement as alternating opaque and translucent laminae. The distinctness of these two laminae however is very variable in the dentine, even within one growth layer in different parts of a single tooth. The opacity of the teeth also varies so that some teeth may be almost uniformly translucent. In such teeth the growth layers can only be detected as very thin refractive lines in a position corresponding to the junction of two layers. Within a growth layer several lesser or secondary layers can normally be seen, each with thin opaque and translucent laminae or appearing as thin lines in very translucent teeth.

The counts of dentine layers given for 15 *K. breviceps* in Table 8 have been used bearing in mind the limitations of the available material. An estimate of their accuracy can be gauged from the quality given in Table 8 for each count.

TABLE 7

Records of Kogia from South Africa which have not been identified to species

Sex	Total Length (mm)	Date	Locality Co-ordinates	Comments
—	—	Oct. 1904	Schoenmakerskop, Port Elizabeth 3402S 2533E	Accompanied by calf
♀	—	1910	False Bay 3410S 1840E	Material in SAM subsequently lost. With 1,45 m calf
♂	—	1913	Gordon's Bay 3410S 1852E	Material in SAM subsequently lost
♂	—	1918	Muizenberg 3407S 1828E	Material in SAM subsequently lost
—	c. 2 700	1935	Groen R., Namaqualand 3051S 1735E	Accompanied by smaller animal, (K. H. Barnard)
—	—	Jun. 1938	Salt River, W. Cape 3355S 1826E	Three animals (K. H. Barnard)
—	2 510	19/11/49	Kaiser's Beach, East London 3313S 2737E	In <i>Daily Despatch</i> , 19/11/49
♀	—	27/1/50	Kaiser's Beach, East London 3313S 2737E	Photographs in ELM files
—	—	15–16/2/54	Strandfontein, False Bay 3410S 1840E	One animal (K. H. Barnard)
—	—	2/7/62	5 km E. Woody Cape 3346S 2627E	One photograph in PEM files
—	c. 2 130	Aug. 1966	E. of Old Woman's R., E. Cape 3330S 2710E	Decomposed

The time interval represented by one growth layer in *K. breviceps* is not yet known. In the sperm whale *P. macrocephalus* (Best, 1970) and in several delphinids (Sergeant, 1959, 1962; Kasuya, 1972; Kasuya *et al.*, 1974) the rate of layer formation has been studied by examining the condition of the newest dentine growth layer. Their results showed a marked seasonality in the time of formation of opaque or translucent laminae and they concluded that one growth layer was formed per year.

A number of teeth in the present sample of *K. breviceps* had laminae that were too uniform in density to observe the extent of opaque or translucent laminae formation. In consequence, the extent of the last growth layer was estimated as 0–25%, 25–50%, 50–75% or 75–100% of the width of the previous two or three layers in older animals and in young animals by comparison with similar layers in older teeth. The results presented in Table 9 show considerable variation, with little more than a suggestion of seasonal variation in the timing of laminae formation. The method used to group these teeth is probably subject to errors resulting from normal variation in the widths of growth layers which could have a considerable effect in such a small sample, and more material is required to resolve the problem.

TABLE 8

Counts of growth layers in the dentine of 15 K. breviceps from South Africa

Cat. No.	Total length (mm)	No. of Complete Layers	Completion of last Layer (%)	Month of Death	Legibility of tooth
SAM 35550	1 945	—	75-100	April	Fair
PEM 1517/92	1 970	1	0-25	July	Fair
PEM 1517/90	2 020	1	50-75	July	Poor
PEM 1511/10	2 110*	1	0-25	October	Fair
PEM 1519/12	2 340	2	25-50	December	Fair
SAM 36980	2 360	2	75-100	August	Poor
SAM 35522	2 665	4	75-100	December	Poor
PEM 1511/13	c. 2 700	4	0-25	March	Fair
ELM 674	2 870*	12	75-100	Aug/Sept	Poor
PEM 1517/28	2 895	9 (10?)	—	July	Poor
SAM 35795	3 050	7	—	Oct/Nov	Poor
PEM 1516/48	3 050	8	50-75	March	Fair
PEM 1517/89	3 055	11	50-75	July	Poor
PEM 1517/91	3 095	17 (?)	75-100	July	Poor
PEM 1516/08	3 250	10+	75-100	Oct/Nov	Poor

*Calculated from regression of total length of CBL.

TABLE 9

The estimated extent of formation of the last dentine growth layer in the teeth of 13 K. breviceps from South Africa in relation to the month at death

% of Layer Completion	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
50-75			1				2					
75-100				1			1	1	1*		1†	1
0-25			1				1			1		
25-50												1

*August/September

†October/November

GROWTH AND DEVELOPMENT

Length at birth. The largest foetus of *K. breviceps* from South Africa was 1,135 m total length (PEM 1516/48). Duguay (1966) recorded a foetus of 1,10 m from a female stranded at La Rochelle, France and quotes a record of a pregnant female with a foetus 1,23 m in length from Setubal, Portugal. The smallest free-swimming calf from South Africa was 1,88 m in length.

Caldwell and Golley (1965) however record a mother and calf pair of 2.9 m and 1.2 m in length respectively from Sapelo Island, Georgia, while Caldwell *et al.* (1971) give details of a second pair from the same island of 2,845 m and 1,295 m in length. Allen (1941) recorded that the adult female that stranded at Long Beach, Long Island, New York in February 1918 was accompanied by a new-born calf, 1,097 m long. Schulte and Smith (1918) however clearly state that this specimen was a male foetus taken from the adult's body. The lengths of these calves and foetuses suggest that calves of *K. breviceps* are born at approximately 1.2 m in length.

Maximum length and physical maturity. There is some confusion as to the maximum length attained by this species. Beddard (1902) stated that *Kogia* did not exceed 15 feet (4.57 m) in length. Tomilin (1957) gave 4 m as the maximum length, but quoted figures of 3.35 m and 3.20 m as the maximum recorded lengths of 8 males and 8 females respectively. Bryden (1972) gives the length at physical maturity as 4.5 m and 4.0 m for males and females respectively, quoting from Tomilin (1957), and Harrison *et al.* (1969). The longest specimen for which a length has been specified was a 4.25 m female stranded on Sullivan's Island, North Carolina (Caldwell *et al.*, 1971).

Though this animal was measured by a museum staff member after exhumation, 4.25 m seems coincidentally close to 4.267 m, or 14 feet, which may have been the estimated length prior to burial. It should be possible to estimate the total length of this animal from the condylobasal length of the skull if it has been preserved. The second largest specimen recorded in the literature was a 3.5 m pregnant female from Wellington, New Zealand (Dell, 1960). The lengths of *K. breviceps* from South Africa appear to be similar to those recorded by Allen (1941) and Duguay (1966) for animals from the North Atlantic. Apart from an animal stranded at Luderitz in October 1966, with an estimated length of 3.66 m (12 feet), the longest measured South African specimen was 3.28 m (PEM 1517/76). The longest male recorded was 3.25 m and the longest female was 3.095 m.

There is little published information on the lengths of physically mature specimens of *K. breviceps*. Hale (1962) recorded an adult female 2.897 m in length in which the epiphyses were fused to the centra of the first and second thoracic vertebrae, and an adult female 2.98 m in length in which all epiphyses were fused to the centra of the vertebrae. In the present study the vertebral epiphyses of SAM 35795 (total length 3.05 m) were unfused, while those of two anterior thoracic vertebrae collected with PEM 1514/58 were completely fused. The body length of the latter animal is not known, but the skull was the longest examined in the study (467 m CBL), and from the regression of total length on condylobasal length given in Fig. 6, the total length of this animal can be estimated to be about 3.3 m.

Growth curve. A growth curve based on the 15 *K. breviceps* listed in Table 8 is shown in Fig. 4. The curve has been fitted to the data by eye. Though the curve is based on a small sample and may well change with additional data, it is interesting that changes in the rate of growth in the initial part of the curve occur gradually and smoothly, in a similar way to that of the female sperm whale (Best, 1970) and in contrast to the majority of growth curves illustrated by Bryden (1972) for several other marine mammal species.

Relative growth of body and skull. Very little change appears to occur in the external proportions of *K. breviceps* with body lengths of 1.8 m or more. Some growth trends may be masked by the variation shown in a relatively small sample (Fig. 5). If the measurements of the 1.135 m foetus can be considered as representative of a neonatal animal, it appears that the relative height of the dorsal fin and the relative length of the flipper decrease with an increase in body length. In Fig. 6 the condylobasal lengths of 11 *K. breviceps* from South Africa are compared with their respective total lengths. The measurements of 13 *K. breviceps* from South Australia (7) (Hale, 1947, 1962, 1963), Uruguay (1) (Vaz Ferreira and Praderi, 1973), the United States (2) (Gunter *et al.*, 1955; Caldwell *et al.*, 1971) and Europe (3) (Duguay, 1966, 1972; Duguay and Budker, 1972; van Bree and Duguay, 1967) have been included in the plot. Regression

lines fitted to the data by the method of least squares are virtually identical for the South African and combined samples, and fit the equations.

$$Y = - 8,46 + 7,06 X \quad (r = 0,98) \text{ (South African sample)}$$

$$\text{and } Y = - 3,3 + 6,97 X \quad (r = 0,96) \text{ (combined sample)}$$

Where Y = total length (mm), X = condylobasal length (mm).

In the present study estimation of total lengths based on condylobasal length has been made from the combined sample.

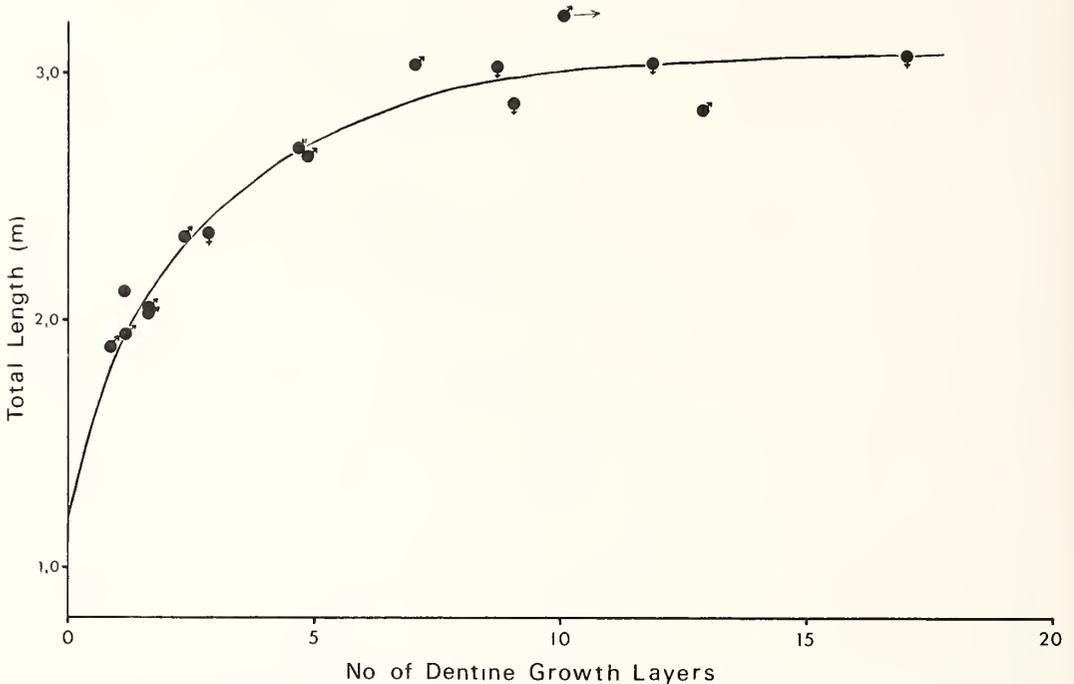


Fig. 4. Growth curve for 16 *K. breviceps* based on counts of growth layers in the teeth. The line has been drawn by eye.

Changes in the proportions of the skull with an increase in skull length are illustrated in Fig. 7. The length of the rostrum tends to increase proportionately with age as is shown by measurements 2, 11 and 16. The mandible tip shows a similar elongation in measurements 17 and 21. The width of the rostrum at mid length (meas. 4), the width of the supraoccipitals (meas. 10) and the width of the occipital condyles (meas. 15) all show a decrease in proportion to increasing skull length. The proportions of all the other skull measurements to the skull length appear to remain static as the skull length increases.

The ossification of the cartilage in the mesorostral canal is progressive with an increase in skull length and proceeds anteriorly. Fig. 7 (meas. 24) shows that the rate of ossification increases quite sharply at a condylobasal length of about 390 mm. From the equation given above, this skull length would correspond to a body length of about 2 715 mm, which, as will be seen in the section on reproduction, approximates the length at which sexual maturity is reached. The significance of this change in growth rate is considered further in the discussion.

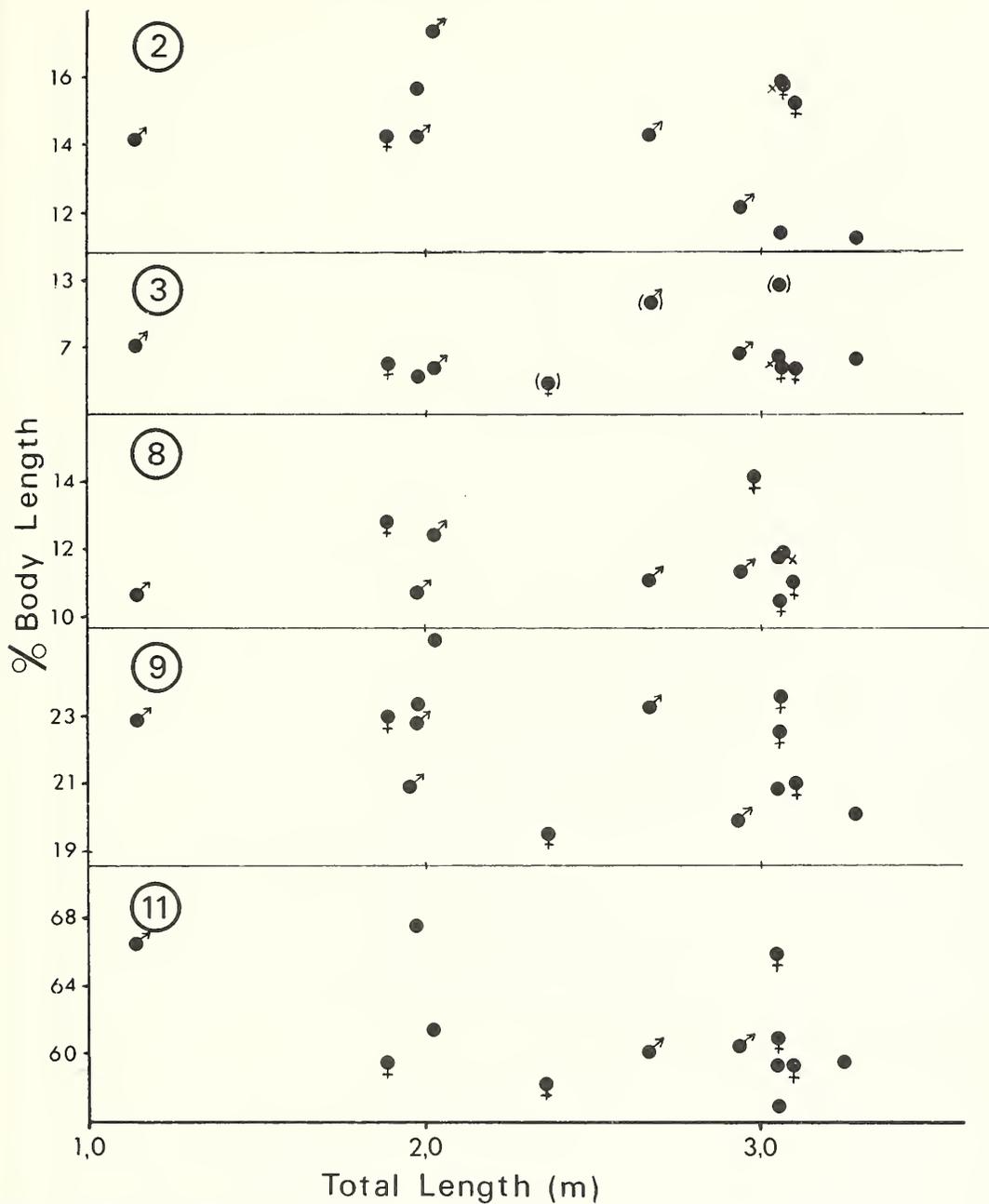


Fig. 5. Relationship between body measurements and total length of *K. breviceps*. Measurement numbers are keyed to Table 3.

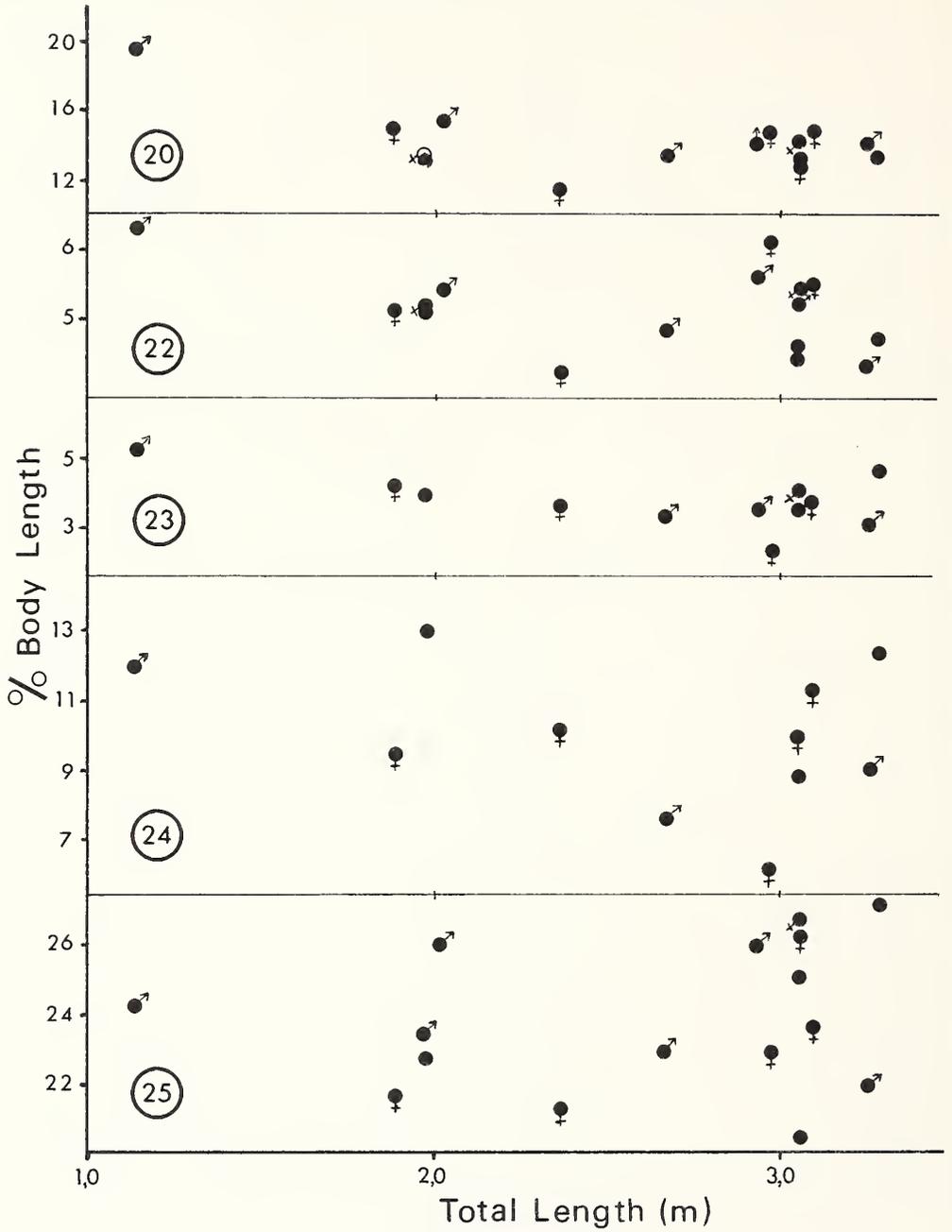


Fig. 5. Continued.

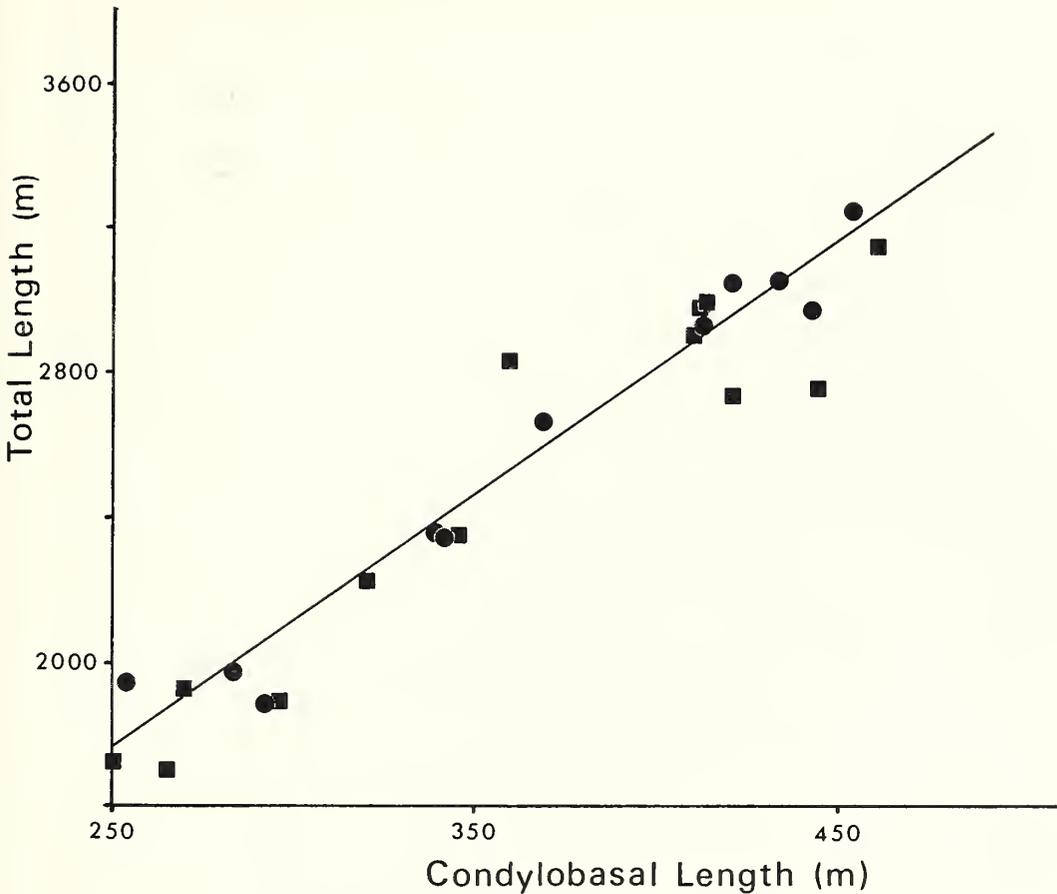


Fig. 6. Relationship between total length and condylbasal length for 24 *K. breviceps*. The regression line was fitted from the equation $Y = -3,3 + 6,97 X$ ($r = 0,96$), where Y = total length (mm) and X = condylbasal length (mm).

Body weight. Relatively few specimens of *K. breviceps* have been weighed, particularly adults, probably owing to the difficulties of handling larger animals. In the present study only two immature animals and one foetus were weighed. These weights are given in Table 10 together with records taken from the literature.

REPRODUCTION

Females. Little information has been published on reproduction in *Kogia*. Allen (1941) summarized the available data, but combined information on *K. breviceps* with that on *K. simus*. Duguy (1966) provided lengths of foetuses of *K. breviceps*. Harrison *et al.* (1972) have described the ovaries of a 3,03 m *K. breviceps* which stranded on Jekyll Island, Georgia.

Ovaries were available from five *K. breviceps* from South Africa. Details of this material are provided in Table 11. The gradation in size of corpora albicantia in these ovaries indicates that they regress in size with age. Though the smallest corpus albicans in the present sample was

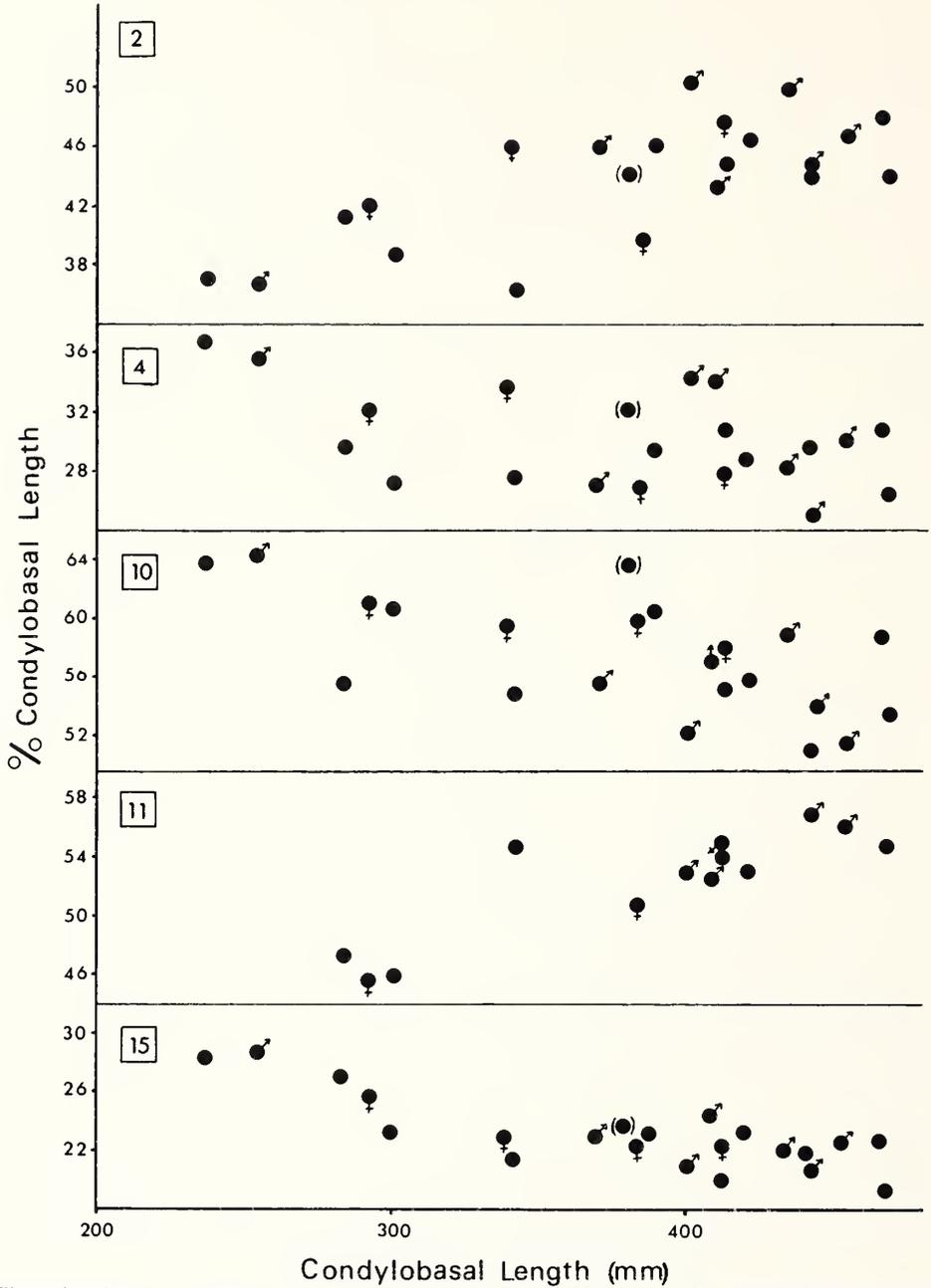


Fig. 7. Illustrating changes in proportions of the skull with increasing skull length in *K. breviceps*. Measurement numbers are keyed to Table 25.

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

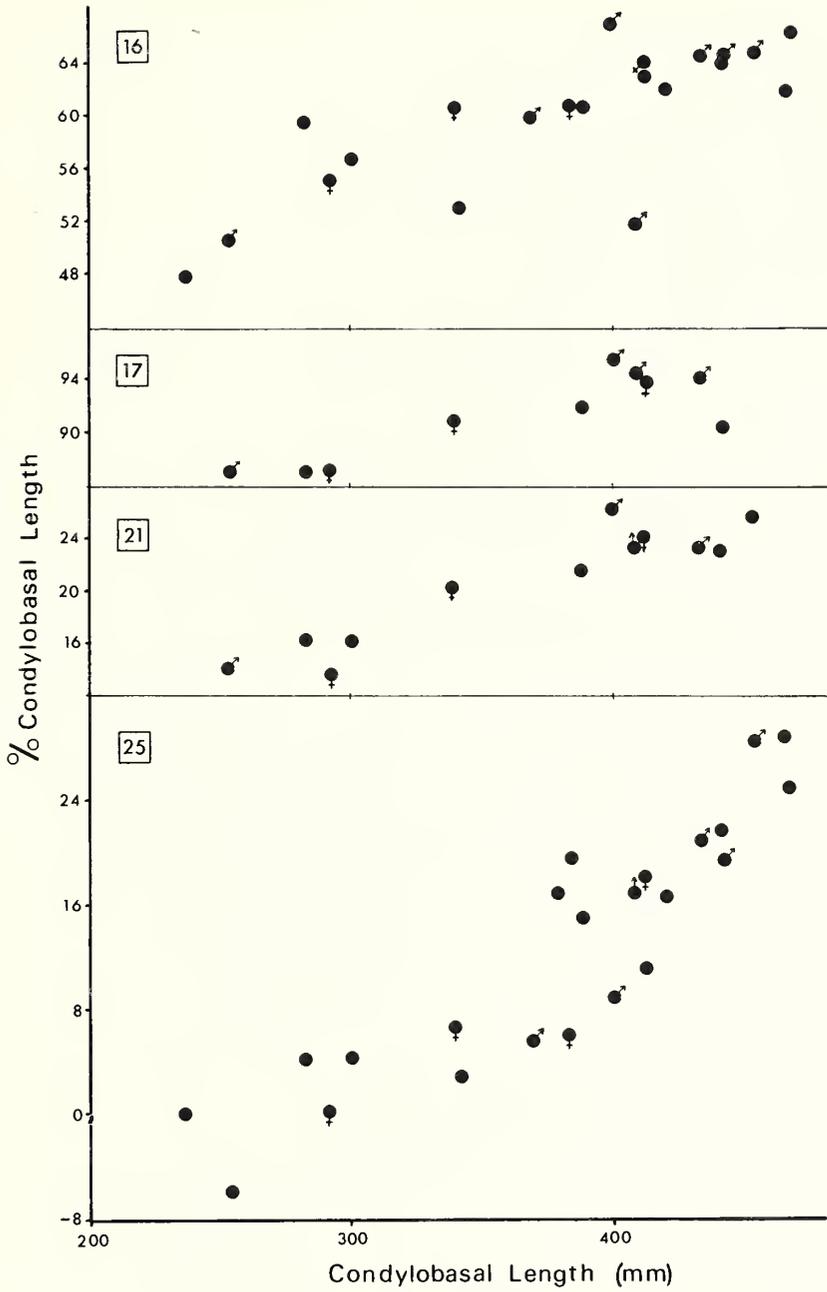


Fig. 7. Continued.

TABLE 10

Body weights of 9 K. breviceps recorded in the literature and from South Africa

Total Length (mm)	Weight (kg)	Source	Comments
1 100	16,1	Duguy, 1966	Foetus
1 135	23,0	present study	Foetus of PEM 1516/48
1 880	83,6	present study	Emaciated
1 948	109,7	Scheffer and Slipp (1948)	
1 970	145,4	present study	Weighed entire
2 220	195	Vas Ferreira and Praderi (1973)	
2 800	342	Carvalho (1966)	Weighed in parts
2 986	417	Tomilin (1957)	
3 020	336,3+	Raun, <i>et al.</i> (1970)	Weighed less viscera

3 × 2 × 2 mm and could perhaps regress further, both ovaries of the female examined by Harrison *et al.* (1972) contained a number of corpora of this size, suggesting that these dimensions may represent the minimum size to which a corpus would regress, and thus for practical purposes corpora would remain visible throughout life, as suggested by Harrison *et al.* (1972).

The dimensions of these ovaries include the corpora lutea which were pedunculated and situated at one pole of the ovary in each case. Two corpora lutea (PEM 1517/89, 1517/91) had very small central cavities filled with tertiary liquor folliculi while the third (PEM 1516/48) was composed of solid luteal tissue. The presence of a corpus albicans beneath the surface of the ovary was not always indicated by a well-defined, wrinkled scar. In section, however, corpora albicantia were generally distinguished by the presence of yellow-brown pigment surrounding a central core of pale fibrous tissue, and particularly by the "capped" appearance of each corpus caused by the eversion of the body onto the surface of the ovary. In this macroscopic examination there was no indication that two types of corpora albicantia might be present representing those formed from corpora lutea of pregnancy and those formed from corpora lutea of ovulation.

Records of female *K. breviceps* known to be sexually mature by the presence of a foetus or accompanied by a small calf are given in Table 12. The mean length at sexual maturity based on the lengths of these females is estimated to lie between 2,7 m and 2,8 m. It should be noted that the length of PEM 1511/12 has been estimated from the condylobasal length of the skull, while the length of the specimen from India (Tomilin, 1957) appears to be a converted figure (2 747 mm = 9 feet) and may have been originally estimated. Pillay (1926) estimated the length of the same animal as 3,05 m (10 feet).

The lengths of the 11 foetuses in Table 12 have been plotted against the month of occurrence in Fig. 8. Two neonatal animals (1,2 m and 1,295 m) have been included in this plot, as it was considered that possible differences in pre- and postnatal growth rates would be minimal in these two cases. The northern and southern hemisphere samples have been combined and the time scales for these have been shifted out of phase by six months, on the assumption that if peaks in breeding activity exist they would occur in similar seasons in both hemispheres. The months of occurrence of small and near-term foetuses indicate that mating and calving seasons extend over a period of approximately seven months from autumn through spring.

TABLE 11
Ovarian data from 5 *K. brevicaeps* from South African waters

Cat. No.	Total length (mm)	No. of dentine layers	Ovarian		Corpus Luteum diam. (mm)	Corpora Albicantia diam. (mm) and index*	Total No. of Corpora	Remarks
			Dimensions (mm)	Weight (g)				
PEM 1517/07	1 880	—	33 × 10 × 12	3,2	—	—	0	Cystic Follicles of 12,8 and 4 mm diam. 1 Cystic Follicle 17 mm diam.
			30 × 20 × 7	2,4	—	—		
PEM 1517/28	2 896	9(10?)	65 × 32 × 15	16,8	—	17(1 360); 6(120); 6(54).	3	Cystic Follicle 16 mm diam. several follicles up to 2 mm diam. Few follicles up to 2 mm diam.
			52 × 27 × 17	11,9	—	8(128); 7(343); 7(294)		
PEM 1516/48	3 050	8	37 × 26 × 10	19,1	46 × 26 × 17	—	1	Numerous follicles up to 3 mm diam. Weight of corpus luteum 13,2 g.
PEM 1517/89	3 055	11	38 × 17 × 14(l)	5,4	—	6(126); 5(50); 4(64)	3	Several follicles up to 3 mm diam. Several follicles up to 3 mm diam. Weight of corpus luteum 9,4 g.
			65 × 25 × 19(r)	13,7	31 × 31 × 16	6(60); 4(64); 4(10)		
PEM 1517/91	3 095	17(?)	40 × 26 × 20(l)	11,7	18 × 17 × 19	9(432); 7(175); 6(120); 6(144); 6(54); 6(72); 5(75)	8	Several follicles up to 5 mm diam.
			50 × 40 × 26(r)	30,6	37 × 38 × 26	8(96); 3(12)		

*Corpus albicans index is the product of the diameter measured in three planes at right angles to one another.

TABLE 12

Details of female K. breviceps, with a foetus, or accompanied by a calf, from South Africa, and from records in the literature

Cat. No.	Length Adult (mm)	Length Foetus (mm)	Sex of Foetus	Length Calf (mm)	Sex of Calf	Date	Region	Source	Remarks
PEM 1511/12	2 695*	195	♀	2 110*	— ♂	Oct. 1965	South Africa	Present study	Squid beaks, crus-taceans in the stomach
SAM 35550	—	—	—	1 945	—	30/4/68	South Africa	Present study	Adult not lactating. Squid beaks, crus-taceans in calf stomach
PEM 1516/48	3 050	1 135	♂	—	— ♂	14/3/71	South Africa	Present study	Squid beaks, crus-taceans in calf stomach
PEM 1517/89	3 055	458	♂	2 020	—	11/7/72	South Africa	Present study	Squid beaks, crus-taceans in calf stomach
PEM 1517/91	3 095	175	♂	1 970	♂	18/7/72	South Africa	Present study	Squid beaks in calf stomach
—	2 747	230	—	—	—	19/12/24	India	Tomilin (1957)	
—	—	1 097	♂	—	—	28/2/18	U.S.A.	Schulte and Smith (1918)	
—	—	—	—	1 600	—	7/11/57	U.S.A.	Caldwell and Golley (1965)	
—	2 900	—	—	1 200	♂	4/6/63	U.S.A.	Caldwell and Golley (1965)	
—	2 845	—	—	1 295	♀	17/8/64	U.S.A.	Caldwell <i>et al.</i> (1971)	
—	2 990	1 100	♂†	—	—	2/3/65	France	Duguy (1966)	
—	2 950	200	—	—	—	13/12/25	Holland	Duguy (1966)	
—	—	1 230	♂	—	—	26/6/56	Portugal	Duguy (1966)	
—	2 800	260	—	—	—	8/10/65	Brazil	Carvalho (1966)	
—	2 897	203	♂	1 710	♀	25/4/37	Australia	Hale (1947)	Adult lactating. Squid beaks in calf stomach
—	2 980	—	—	1 892	♂	28/6/59	Australia	Hale (1962)	Calf reported to be suckling
—	c. 3 500	c. 900	—	—	—	11/1/55	New Zealand	Dell (1960)	

*Calculated from CBL.

†Given as a female by Duguy (1966), but it is clearly a male from his measurements and photograph.

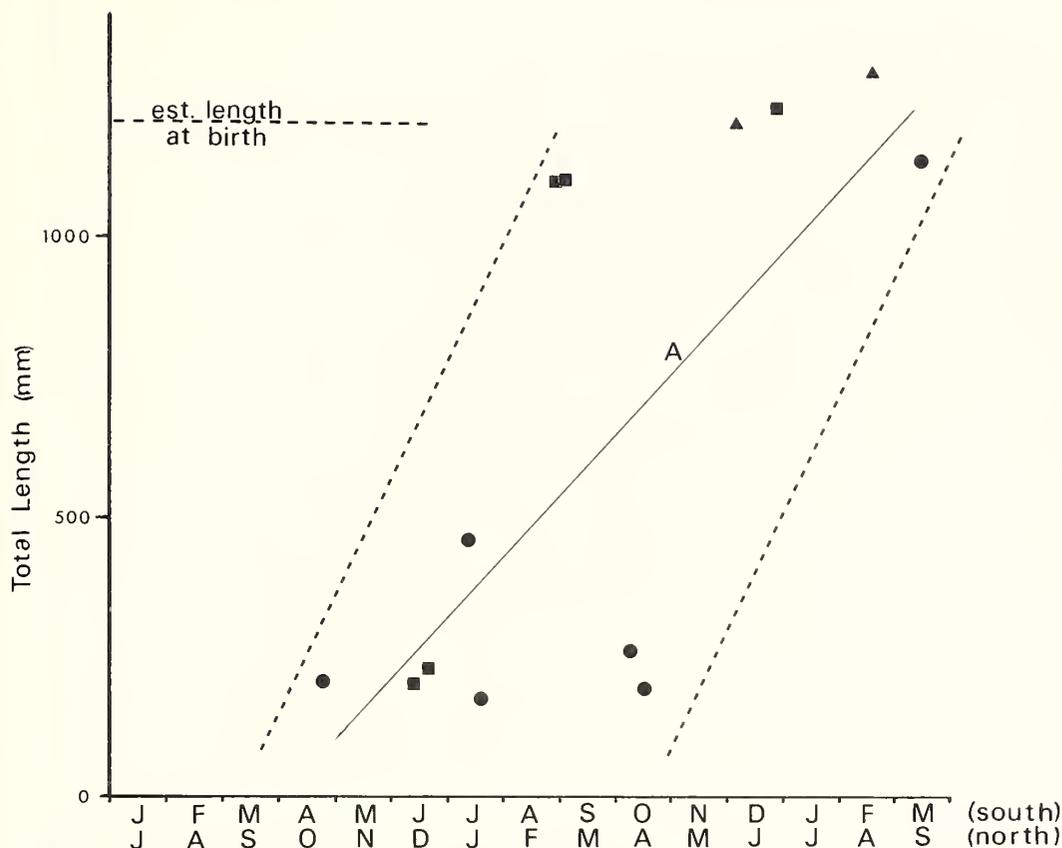


Fig. 8. Plot of lengths of foetuses and neonatal *K. breviceps* against month of occurrence. Records of foetuses (■) and calves (▲) from the northern hemisphere have been moved out of phase with foetuses from the southern hemisphere (●) by six months. Interpretation of the seasonal limits (----) and the regression line A are given in the text.

It has not been possible to estimate the length of the gestation period on the present small sample, owing to the lack of information on mid-term foetuses. If the limits of the seasonal distribution of this sample are representative of the true situation, they would suggest a gestation period of a little over 7 months. However a regression line (line A, Fig. 8) fitted to the present data by the method of least squares would suggest a gestation period of over 11 months.

At least four of the females in Table 12 were simultaneously pregnant and accompanied by a calf, indicating that a reasonable proportion of females conceive in successive breeding seasons. Three of these calves showed less than two dentine growth layers in their teeth. In addition to the South African females in Table 12, three other females listed in Table 5 can be considered sexually mature (Plettenberg Bay, 1951/52; East London, 1944; Vleesbaai, 1965) on the basis of length or the presence of a foetus. Five of these 8 females were pregnant, the ovary of PEM 1517/28 contained a very large corpus albicans, possibly indicating a lost foetus or calf, and the condition of two females was not recorded. These figures suggest a potential pregnancy rate of more than 63%, but the sample is very small, and there is a possibility that pregnant females are more susceptible to stranding than non-pregnant females.

The state of lactation has been recorded for two females only (Table 12). The 2,02 m calf accompanying PEM 1517/89 had apparently ceased suckling, while the 1,71 m calf stranded in South Australia with a lactating adult (Hale, 1947) had not. Hale (1962) reported a mother and calf pair, of which the 1,892 m calf was recorded as suckling, but there is no indication that the mammary glands of the adult had been examined. The presence of squid beaks and other food remains in calves upward of 1,6 m in length (Caldwell and Golley, 1965) indicates that solid food is taken by juveniles for an unknown period before suckling ceases. The two South African calves of 2,02 m and an estimated 2,11 m length are the longest on record of a number of mother and calf pairs, suggesting that the close association between mother and calf probably ends soon after weaning. The presence of a suckling calf with the physically mature female stranded in Australia (Hale, 1962) suggests that the reproductive life span is reasonably long in this species.

Males. Data on the testes of five male *K. breviceps* from South Africa are presented in Table 13, together with available details of five animals recorded in the literature. The dimensions of the testes appear to remain fairly constant up to a body length of about 2,4 m, after which they begin to increase in size. The testes of SAM 35522 should be considered as maturing, since they had not attained the size of those from animals of over 3 m in length, and though the mean tubule diameter had increased, few spermatozoa were being produced. Unfortunately histological details of the 3,02 m animal described by Raun *et al.* (1970) and those of SAM 35795 (3,05 m) are absent, for they would provide confirmation that the testes of these two animals are mature, as seems likely from their dimensions. Until further specimens are collected, it is suggested that male *K. breviceps* mature sexually between 2,7 m and 3,0 m in length.

Sex Ratio. The sex ratios of the fetuses and calves listed in Table 12 appear surprisingly disproportionate. Seven of eight fetuses for which the sex has been determined are males, while five of the seven calves are males. The probability that similar or more disparate ratios would differ from parity due to chance alone is 0,070 for the sample of fetuses (7:1), and 0,035 for the combined sample of fetuses and calves (12:3). The combined ratio differs significantly from parity ($\alpha = 0,05$), and suggests perhaps that there is a larger proportion of successful male conceptions. The sex ratio of adult and sub-adult *K. breviceps* appears to be 1:1 based on all 8 males and all 8 females over 2,6 m in length listed in Table 5. The reality of this ratio relies on the assumptions that the stranding rates of males and females are similar and that there is no observer bias in the sexing of carcasses.

FOOD

Few stomach contents of *K. breviceps* have been examined. The stomach of a 2,95 m female stranded in Holland contained a large number of carapaces of the green crab *Carcinides maenas* and cephalopod beaks, and the stomachs of two other European specimens contained squid beaks (Allen, 1941; Duguay, 1966). Hale (1947, 1962, 1963) recorded numerous beaks of *Sepioteuthis australis* in the stomachs of a 2,73 m male, a 1,192 m animal and a 1,71 m calf. The adult female with the calf appeared to have been eating prawns of the general *Penaeus* and *Hymenodora* (Hale, 1947). Scheffer and Slipp (1948) recorded squid beaks, fish otoliths and bones, a limb segment of a crab and fragments of shrimps of the genera *Pasiphaea*, *Pandalus* and *Pandalopsis* in the stomach of a 1,885 m animal. Raun *et al.* (1971) found numerous squid beaks, including those of the genus *Ommastrephes*, the mysid *Gnathophausia ingens*, and a penaeid shrimp *Aristaeomorpha foliacea* in a 3,02 m male *K. breviceps*, together with some pieces of *Sargassum*. The stomach of a 3,18 m animal examined by Vaz-Ferreira and Praderi (1973) contained a mass of squid beaks. The smallest specimen with squid beaks in its stomach was a 1,6 m calf stranded with an adult female (Caldwell and Golley, 1965).

The contents of the stomachs of 16 *K. breviceps* from South Africa indicated a similar diet to that outlined in the literature. Squid beaks were found in all 16 stomachs examined. Remains

TABLE 13

Reproductive data for ten male K. breviceps

Cat. No.	Total Length (mm)	Testis dimension (mm)	Testis Weight (g)	Tubule Diam. (μ)	Remarks	Reference
—	1 885	90 × 25			Immature	Scheffer and Slipp (1948)
SAM 35550	1 945				Testes small and firm. Immature	
PEM 1517/90	2 020	100 × 17 (L) 110 × 15 (R)	22 (L) 22 (R)	53 (C) 45 (P)	Immature	
—	2 220				Immature histologically	Vaz Ferreira and Praderi (1973)
PEM 1519/12	2 340			36 (C) 32 (P)	Immature	
—	2 345	approx. 100 × 25				Hubbs (1951)
—	2 420	140 × 30		70	No sperm	Harrison <i>et al.</i> (1972)
SAM 35522	2 665	240 × 70 × 40 (L) 260 × 75 × 45 (R)	520 (L) 665 (R)	144 (C)	Few sperm in lumen	
—	3 020	445 × 100				Raun <i>et al.</i> 1970
SAM 35795	3 050	320 × 100 (L)				

Abbreviations. L = left, R = right, C = section at centre of testis at mid length, P = section at periphery of testis at mid length.

of crustaceans were found in 12 stomachs. In 9 of these 12 animals, the mysid *Gnathophausia* was present, and measurements of 18 carapaces preserved from six stomachs ranged from 55 mm to 85 mm in length, with a mean of 75 mm. The stomach of PEM 1517/91 contained two carapaces, and that of SAM 36980 one rostrum identified as those of the carid prawn *Notostomus* (Barnard, 1972). The carapace length of one of these was 72 mm. The stomach of SAM 35795 contained a single specimen of the sand-dwelling benthic crab *Goneplax angulata*, while a single crab megalopa larva was found in the stomach of SAM 36980. Fish remains were found in 4 stomachs only, represented by single fish in each case. Large jaws in PEM 1516/48 and PEM 1517/91 were identified by Dr P. Hulley, South African Museum, as those of the gempylid fish *Rexea solandri*. A single otolith recovered from PEM 1519/12 was identified as that of the myctophid *Scopelopsis multipunctatus*. The fourth fish in the stomach of SAM 35522 was unidentified. The remains of a *Pyrosoma* was found in one animal (PEM 1517/91), and the stomach of PEM 1515/07 was filled with a mass of unidentified objects which could be the remains of numerous *Pyrosoma* tangled together, as well as one metre of string and several pieces of polythene bag.

The identifications of 408 lower beaks of cephalopods from 13 stomachs of *K. breviceps* are given in Table 14. Though the identification of cephalopods based on the beaks alone is a

TABLE 14
Numbers of lower beaks of Cephalopods from 13 stomachs of Kogia breviceps from South Africa

Cephalopods*	Catalogue Numbers													Total number	% of total	Family % of total			
	SAM 35522	SAM 35795	SAM 36980	PEM 1496/66	PEM 1511/13	PEM 1516/48	PEM 1517/28	PEM 1517/76	PEM 1517/89	PEM 1517/90	PEM 1517/91	PEM 1517/92	PEM 1519/12						
Hisiototeuthidae																			
Type 1	9	4			1	8	13			2	2	11			49	12,0			
Type 2	13	6				13	4	1	2	13	6				60	14,7			
Type 3	2	15				6	2			2	1	1			28	6,9			
Type 4		1					2			5	1				8	2,0			
Type 5						4									5	1,2			
Type 6	1	1				1				1					2	0,5			
†Type 7		1						1							3	0,7			
Enplototeuthidae																			
Pyrototeuthis			1									1		1	2	0,5			
Abrialopsis		5								2					7	0,2			
Abrealia															1	0,2			
Ancistrocheirus	2		5			9					2				13	3,2		5,6	
Lycoteuthidae																			
Oregoniateuthis	5		24	1		19	1	1	1	12	1	3	10		78	19,1		19,1	
Psychroteuthidae															1	0,2		0,2	
Cranchiidae																			
Pyrgopsis					1	2		1							4	1,0			
Galiteuthis	2							1			1				4	1,0			
Phasmatopsis	1								1						2	0,5			
Taonius	1					5					1				7	1,7		13,1	
†Type 1	10			1		10		1			1		2		26	6,4			
†Type 2		3		1		2		1		2			1		10	2,5			
Octopoteuthidae																			
Octopoteuthis	4		1	2		26									34	8,3			
Taningia			1	1		1									2	0,5		8,8	

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

Cephalopods*	Catalogue Numbers														Total number	% of total	Family % of total
	SAM 35522	SAM 35795	SAM 36980	PEM 1496/66	PEM 1511/13	PEM 1516/48	PEM 1517/28	PEM 1517/76	PEM 1517/89	PEM 1517/90	PEM 1517/91	PEM 1517/92	PEM 1519/12				
Chiroteuthidae	1			1		2		1	1						6	1,5	4,7
Type 1						4									5	1,2	
Type 2						7		1		1					8	2,0	
†Type 3																	
Onychoteuthidae	1		1			1	1								4	1,0	2,7
Onychoteuthids						1									2	0,5	
<i>Moroteuthis</i> 1	2					3									5	1,2	
<i>Moroteuthis</i> 2																	
Ommastrephidae						2	1								4	1,0	1,7
Ommastrephids										1					3	0,7	
<i>Todarodes</i>											1						
Loligimidae														3	3	0,7	0,7
Vampyroteuthidae															1	0,2	0,2
<i>Vampyroteuthis</i>								1									
Sepiidae															9	2,2	2,5
Octopodidae		11													11	2,7	2,7
															407	100,0	

*Beaks unassignable to any group were found in PEM 1517/76 (1), 1517/90 (1), 1517/92 (3), SAM 35522 (2) and SAM 36980 (1).

†These beaks are tentatively assigned to their respective families.

comparatively new field, the beaks of many families show distinctive features which permit ready classification to the family level (Clarke, 1962). In some cases however relegation of a group of beaks to a family has been tentative, for example, those called Chiroteuthid type 3. In Table 14 the lower beaks of histioteuthid type 7 are typical of the family in the form of the ridge on the lateral wall, but the form of the lateral wall and wing structure is reminiscent of a lycoteuthid beak. Of the beaks grouped with the cranchiid squids, type 1 beaks are very similar to those of *Taonius*, while those of type 2 bear some resemblance to those of gonatid squids. At the generic level, a number of small enoploteuthid beaks were assigned to the genera *Abralia* and *Abraliopsis* by comparison with single specimens of *Abralia veranyi* and *Abraliopsis gilchristi*.

With the exception of some genera accepted as monotypic (*Ancistrocheirus*, *Taningia* and *Vampyroteuthis*) few groups of beaks could be identified to the species level. Lower beaks of histioteuthids type 1 and type 4 are, with some individual variation, identical with specimens of *H. bonnellii* and *H. miranda* respectively, while those of *Todarodes* are identified as *T. sagittatus*. The distinctive lower beaks of *Oregoniateuthis* were identified with beaks taken from intact lycoteuthids obtained from stomachs of yellowfin tuna caught south of Algoa Bay.

These identified food items provide little information on the depth at which *K. breviceps* normally feeds. Excluding the few octopodids and sepiids, some members of most of the families of squids in Table 14 are known to undertake diel vertical migrations, with at least part of the populations appearing in the upper 100 m during the night (Roper and Young, 1975).

Cephalopod families which are considered typical of inshore waters such as octopodids, sepiids and loliginids form a very small portion of the diet of *K. breviceps*. Approximately 75% of the squids recorded in Table 14 are members of families which, with a few exceptions, are entirely oceanic (Clarke, 1966; Young, 1972). *Oregoniateuthis* appears to be common over the continental slope, as discussed in more detail under *K. simus*. The evidence suggests that *K. breviceps* normally inhabits oceanic waters beyond the edge of the continental shelf.

PARASITES

Parasites were recorded in 10 South African *K. breviceps* and noted as absent in the stomach and blubber of one animal (PEM 1515/07). In one further animal, cestode cysticerci were noted as absent from the blubber (PEM 1517/90). Both of these animals were juveniles. In two animals (PEM 1517/89, 1516/48) a few cysticerci were found in the blubber near the anus.

Nematodes were recorded from the stomachs of 10 animals. A qualitative estimate of the parasite load was made in five of these animals: light load—PEM 1517/91 and 1517/92; medium load—PEM 1517/90; heavy load—PEM 1515/70 and 1517/89. This material was identified by Mr S. Prudhoe, British Museum, and found to include three species *Anisakis physeteris* Baylis, 1923, *A. simplex* (Rudolphi, 1809) and *Phocanema kogiae* Johnston and Mawson, 1939. In five cases all three species were found in the same animal (PEM 1511/13, 1517/89, 1517/90, 1517/92 and 1519/12). *P. kogiae* was absent in PEM 1517/91 and PEM 1516/48 in which both species of *Anisakis* occurred but present on its own in PEM 1515/70. *A. physeteris* was present on its own in SAM 35522, and a fragment found in SAM 36980 could not be identified.

Fragments of a large nematode taken from the neck muscles of PEM 1519/12 were tentatively identified as *Crassicauda* sp.

DISTRIBUTION AND MOVEMENTS

Information on the distribution and movements of *K. breviceps* is very limited. Gunter, Hubbs and Beal (1955) have suggested that *Kogia* is absent from the eastern coast of North America during June through August, basing their conclusions on the dates of 31 strandings. Six records of *K. breviceps* stranded in South Australia occur from late autumn to early spring (Aitken, 1971). The absence of summer records may be indicative of an offshore movement at this time.

In southern African waters *K. breviceps* has been recorded from Cape Cross, South West Africa (21°S) to Natal (31°E). While the greatest number of records occur on the south western and south eastern Cape coasts (Table 15) this does not imply that *K. breviceps* is more abundant in these regions. The three records of *K. breviceps* from South West Africa form a substantial proportion of all the small cetacean records from this territory, which has over 1 000 km of uninhabited coastline. Though the coast of Natal has a higher human population, it seems to have a relatively low stranding rate of all species of cetaceans, possibly as a result of the direction of the prevailing winds and current systems, which are largely parallel to the coast line, and the abundance of predators such as sharks which could dispose of carcasses before they could wash ashore. Further, the distribution of records in the Cape reflects the localities of the museums in Cape Town (18°E), Port Elizabeth (25°E) and East London (27°E) which have maintained an interest in stranded cetaceans for many years.

TABLE 15

Number of records of K. breviceps stranded on the southern African coast in relation to longitude (°E)

Longitude	13°–15°	16°–18°	19°–21°	22°–24°	25°–27°	28°–30°	31°–33°
No. of records	3	4	5	8	16	1	2

The changes that occur in the oceanographic conditions between Natal and South West Africa are particularly marked, and the interactions between the cold water of the West Wind Drift/Benguella system and the warm water of the Agulhas Current form an area of mixed water with exceptionally complex conditions off the southern coast of Africa. As *K. breviceps* appears to be distributed across an entire spectrum of oceanographic conditions, in the present study, it seems unlikely that the distribution of this species could be correlated with particular water masses.

Thirty-two dated records of *K. breviceps* given in Table 5 have been plotted by months against longitude in Fig. 9 to establish whether seasonal movements of the population occur off southern Africa. There is little to suggest that *K. breviceps* is more abundant in any one season, at least for the western and eastern Cape coasts for which there are a reasonable number of records, which suggest that the species is non-migratory.

BIOLOGY: *KOGIA SIMUS*

AGE DETERMINATION

The teeth of *K. simus* are similar in structure to those of *K. breviceps*. In longitudinal section the prenatal dentine can be distinguished as a thin translucent line when viewed with transmitted light, and the postnatal dentine is deposited in a similar chevron pattern which becomes progressively more obtuse in older teeth. Dentine deposition appears to continue throughout life, as the pulp cavity was open at the base in all 17 teeth examined from animals of all ages.

Growth layers were visible in the dentine of some teeth as alternating opaque and translucent laminae, but these were not very distinct. Several of the teeth were uniformly translucent, and in these teeth growth increments showed as refractive lines in the dentine.

In all but the smallest teeth examined, counts of the growth increments yielded figures that were obviously too high to represent a number of annual increments, and attempts to distinguish

groups of growth increments that might represent annual increments proved partially possible only in a few younger teeth. As a result of these difficulties and the large risk of inaccurate counts, further attempts to age this species from the teeth have been deferred.

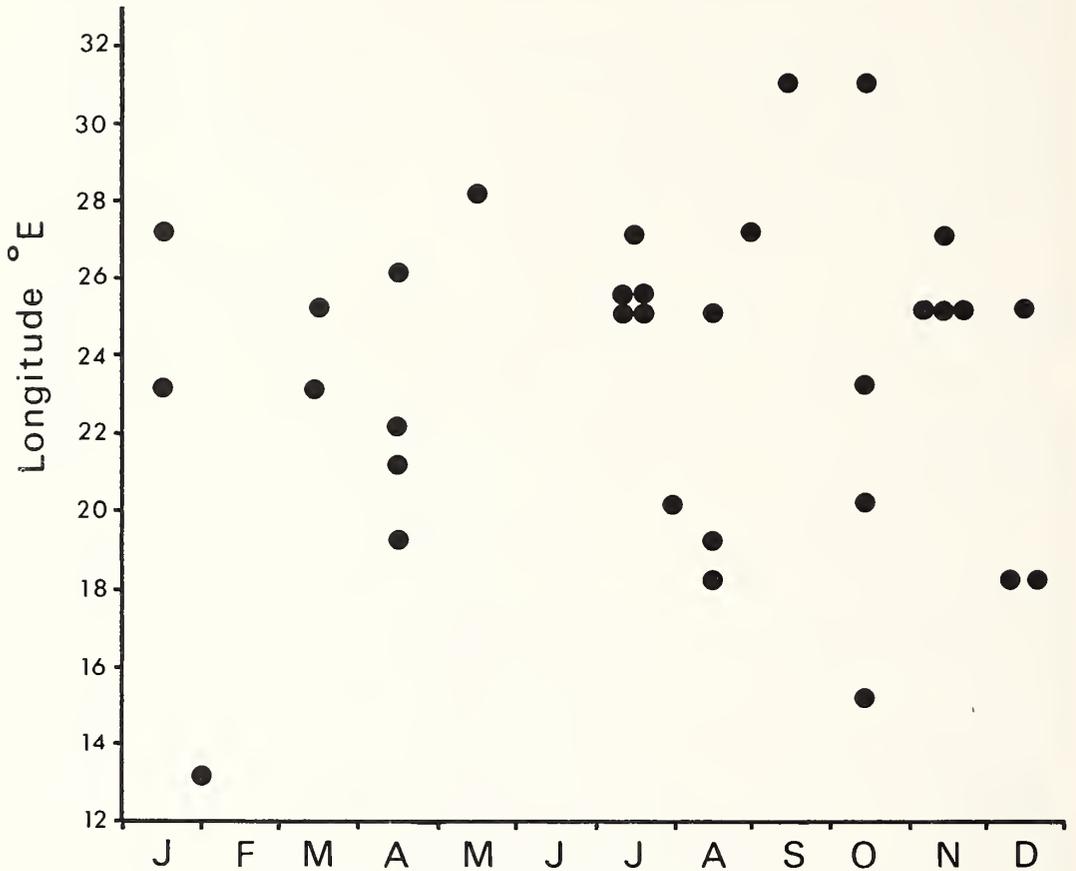


Fig. 9. Seasonal occurrence of *K. breviceps* based on 32 dated records from southern Africa.

GROWTH AND DEVELOPMENT

Length at birth. The length at birth of *K. simus* is not known. The smallest calf of known length was 1,36 m long (PEM 1516/51). However, PEM 1518/02, which is identified as this species by a tooth and from description, was accompanied by a calf estimated at 1,0 m to 1,3 m in length. The adult was also pregnant with a foetus 0,20 m to 0,25 m long. The longest foetus on record was 0,325 m in length (PEM 1519/72). By comparison with the birth length of *K. breviceps* it is suggested that calves of *K. simus* are born at about 1 m in length.

Maximum length and physical maturity. Handley (1966) gives the maximum length of *K. simus* as 2,7 m. The lengths of animals in the present study are in agreement with his figure, for the longest specimen measured accurately was 2,64 m (SAM 36728). PEM 1517/38 was a

decomposed female estimated at 2,7 m in length. The length of SAM 36677 is estimated to be 2,68 m based on the regression of body length on condylobasal length, which is 323 mm in this animal.

The length at which physical maturity is attained varies considerably in spite of the relatively small size of this species. In this study the epiphyses of the centra of the mid thoracic vertebrae of five animals between 1,78 m and 2,09 m in length were unfused to the bodies of the centra. All five animals were sexually immature (SAM 35799, PEM 1519/59-62). Allen (1941) records a 2,21 m pregnant and lactating female from Cape Henry, USA, that was physically mature, based on the "complete union of all epiphyses". Tomilin (1957) quotes a record of a 2,44 m *K. simus* from South Carolina which was physically mature. The vertebral epiphyses of three animals in the present study were entirely fused to the bodies of their centra; their body lengths were 2,47 m (SAM 35079), approximately 2,54 m (PEM 1515/25) and an estimated 2,68 m (SAM 36677).

Relative growth of body and skull. There appears to be very little change in the proportions of the body with an increase in body length in *K. simus* of more than 1,36 m in length. In only one measurement (No. 10, tip of snout to anterior insertion of the dorsal fin) was there a suggestion of an initial decrease in the rate of growth (Fig. 10). There is a great deal of individual variation in the external measurements, some of which undoubtedly results from variable measuring techniques. However an indication of the extent of actual variation is provided by three of four immature animals stranded together and measured at the same time in an identical fashion (total lengths: 2,04 m, 2,06 m, 2,09 m, in Fig. 10.). In several measurements the variation shown by these three animals covers much of the range of variation of the whole sample.

In Fig. 11 the condylobasal lengths of 17 *K. simus* skulls from South Africa have been plotted against their corresponding total lengths (Table 6). The measurements of two animals from Australia (Hale, 1962, 1963), one from California (Roest, 1970) and one from Japan (Yamada, 1954) have also been included in the plot. Regression lines fitted to the data by the method of least squares are very similar for the South African and combined samples, and fit the equations:

$$Y = -433 + 9,63 X \quad (r = 0,91) \text{ (South African sample)}$$

$$\text{and } Y = -407 + 9,55 X \quad (r = 0,91) \text{ (Combined sample)}$$

where Y = total length (mm), X = condylobasal length (mm).

In the present study estimates of total length using condylobasal length have been based on the combined sample.

Changes in the proportions of the skull with increasing condylobasal length are illustrated in Fig. 12. In spite of considerable individual variation, trends are apparent in several measurements. An increase in the proportional length of the rostrum is shown in measurements 2, 11 and 16. There are also slight increases in the proportional length of the mandible (No. 17) and the mandibular symphysis (No. 21). Decreases in the proportional width of the base of the rostrum, the post-orbital width and the supraoccipital width are indicated by measurements 3, 6 and 10, while the relative width of the occipital condyles (No. 15) and the height of the mandible at the coronoid (No. 20) appear to decrease very slightly. The width of the rostrum at mid length, the zygomatic width, the skull height and position of the foramen magnum in relation to skull height, the width of the vertex and the lengths of the tooth rows appear to maintain the same growth rate as the condylobasal length.

The extent of the ossification of the mesethmoid in the mesorostral canal increases anteriorly with age in a similar way to that of *K. breviceps*, though the change in the rate of ossification is perhaps more pronounced. In *K. simus* from South Africa the change in growth rate occurs at a condylobasal length of about 265-275 mm, which corresponds to a total body length of approximately 2,1 m to 2,2 m. Animals of both sexes appear to be reaching sexual maturity at

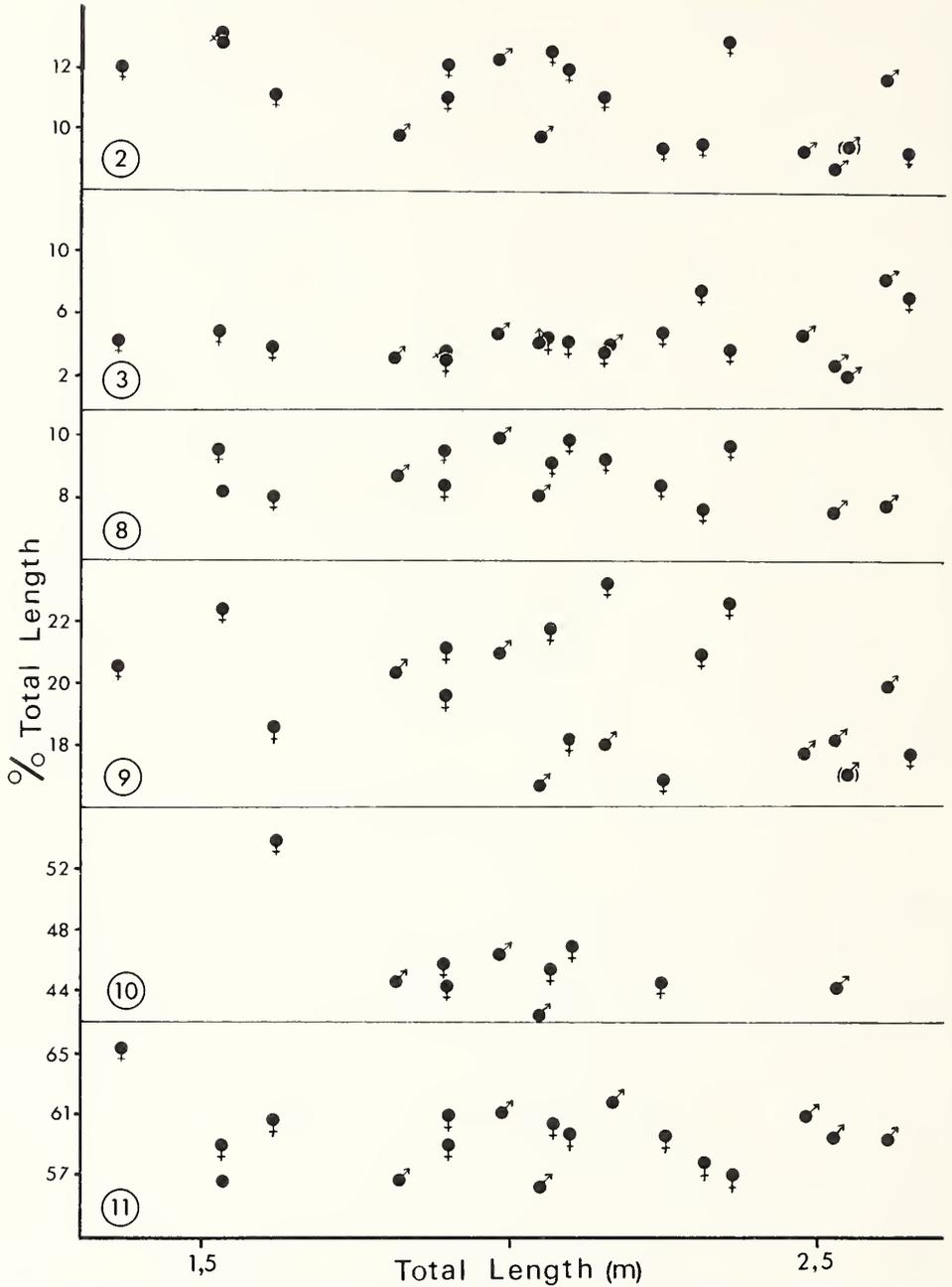


Fig. 10. Relationship between body measurements and total length of *K. simus*. Measurement numbers are keyed to Table 3.

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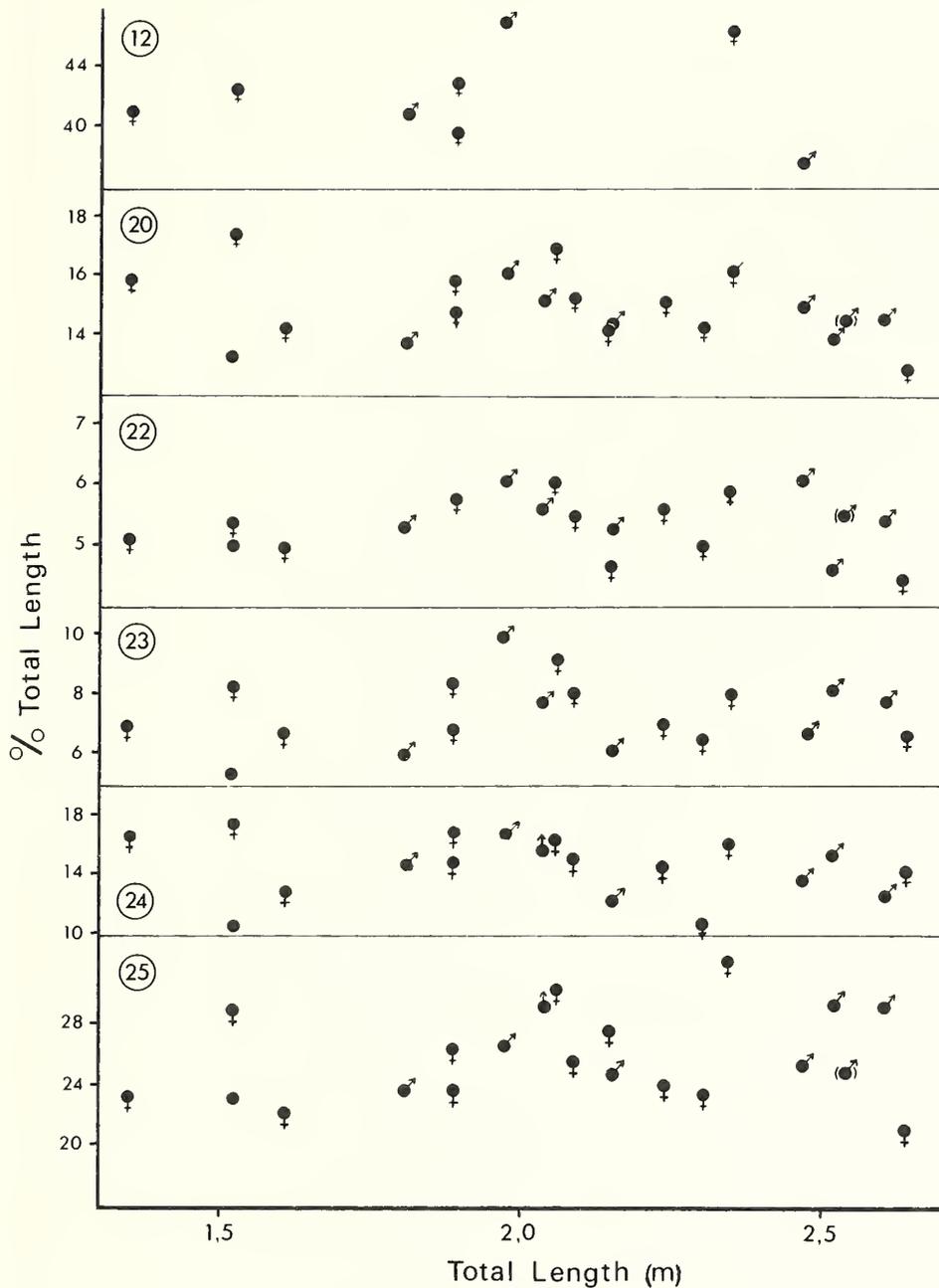


Fig. 10. Continued.

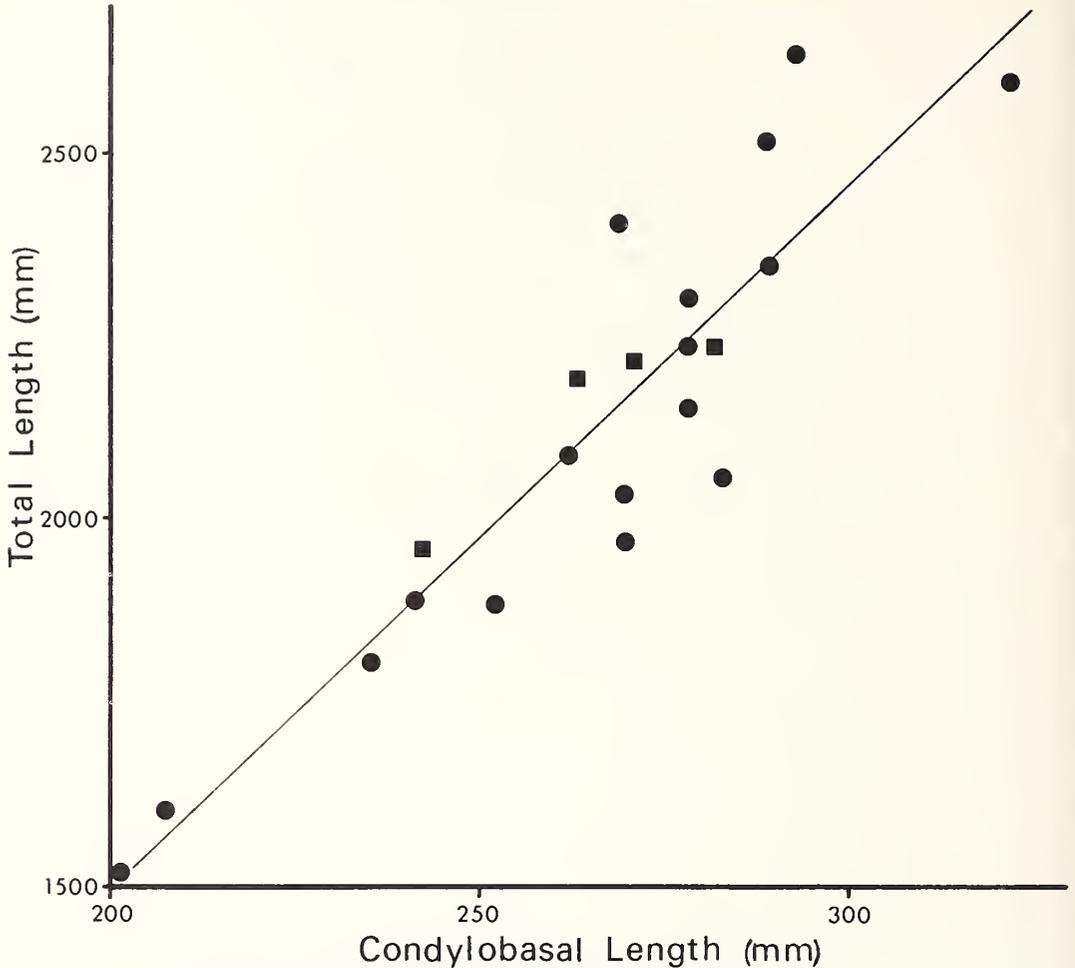


Fig. 11. Relationship between total length and condylbasal length for 21 *K. simus*. The regression line was fitted from the equation $Y = -407 + 9.55X$ ($r = 0.91$) where Y = total length (mm) and X = condylbasal length (mm).

about this length, as is discussed under reproduction. The significance of this change in growth rate of the mesorostral ossification is considered further in the discussion.

Body weights. There appear to be no published records of weights for any specimen of *K. simus*. In the present study weights were taken of 11 animals 1.36 m to 2.47 m in length, and these are presented in Table 16. A logarithmic plot of body weight against body length indicated a strong correlation between them (Fig. 13) and a regression line fitted to the data by the method of least squares was drawn from the equation:

$$\log Y = -7.29 + 2.86 \log X \quad (r = 0.88)$$

where Y = body weight (kg), X = body length (mm)

This equation should be used cautiously as it was derived from measurements of stranded animals which may have been abnormal with respect to weight.

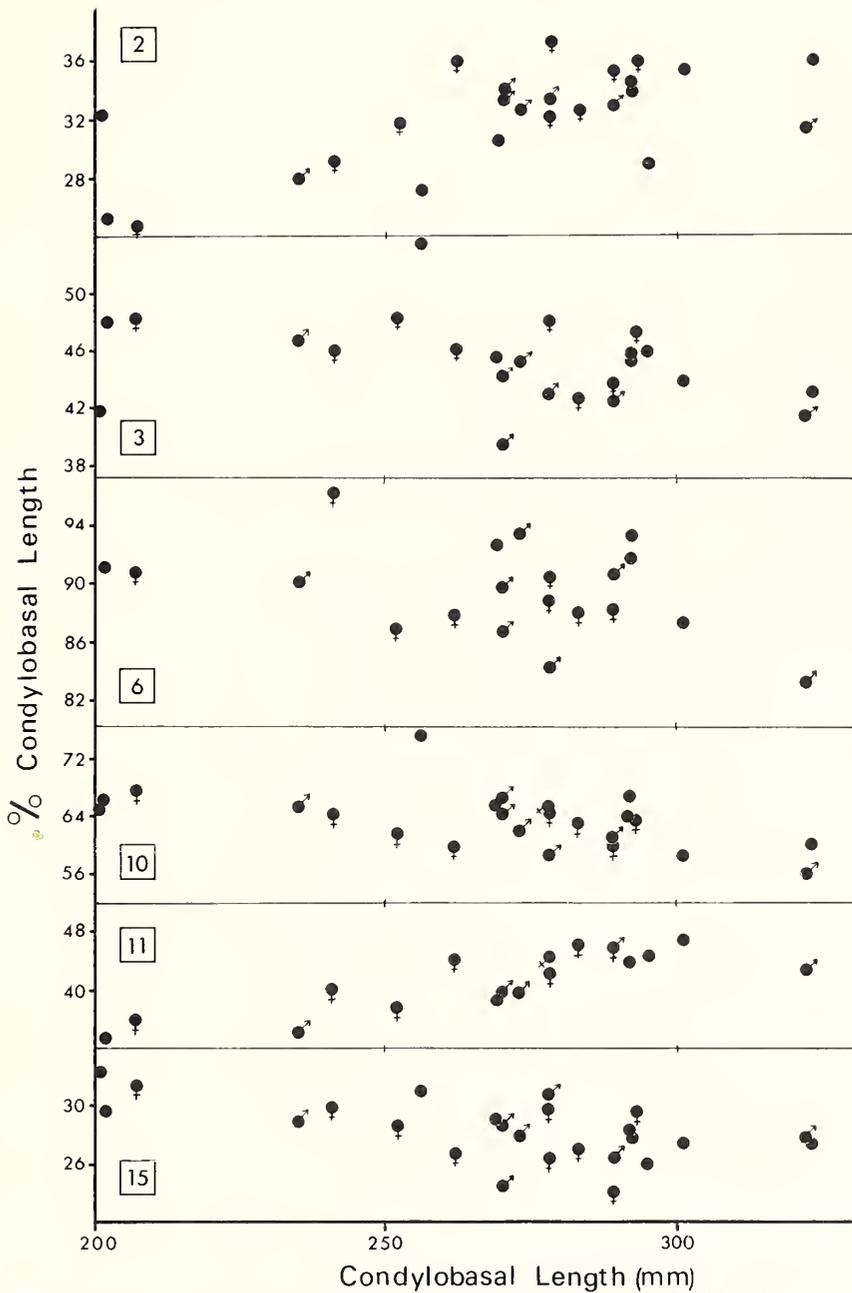


Fig. 12. Illustrating changes in proportions of the skull with increasing skull length in *K. simus*. Measurement numbers are keyed to Table 25.

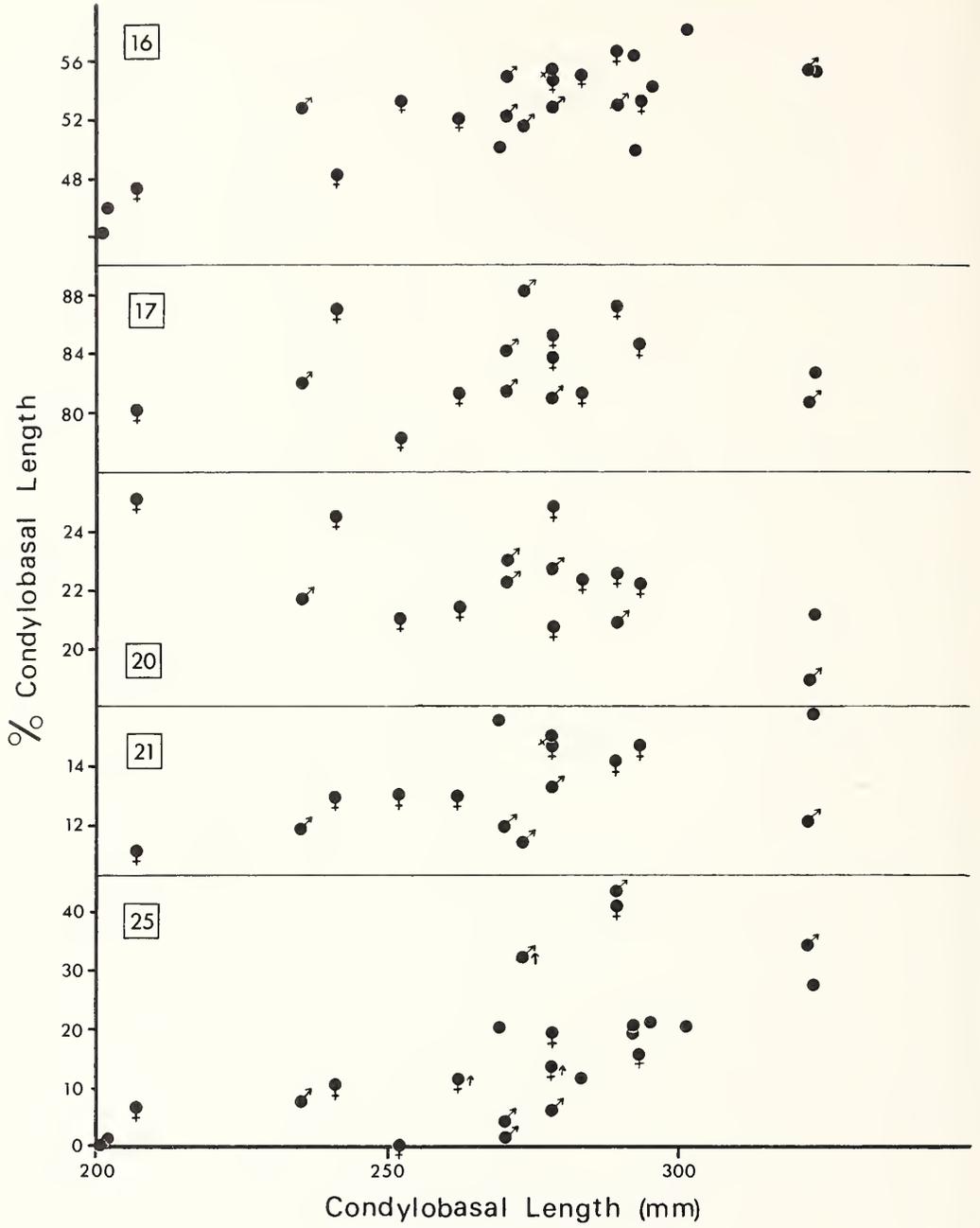


Fig. 12. Continued.

TABLE 16
Total and partial body weights of 11 K. simus from South Africa. Partial body weights are expressed as actual weights (kg) and as percentages of body weight

Cat. No.	Total Length (mm)	Total Weight (kg)	Blubber		Meat		Liver		Heart, Lungs and Trachea		Heart		Kidneys	
			kg	%	kg	%	kg	%	kg	%	g	%	g	%
PEM 1516/51	1 360	47.3	9.5	20.2	9.7	20.5	0.86	1.8	—	—	260	0.55	145*	0.31
PEM 1516/99	1 325	61.8	15.5	25.0	13.2	21.3	1.7	2.8	1.5	2.4	350	0.57	—	—
PEM 1519/73	1 610	59.5	—	—	—	—	—	—	—	—	—	—	—	—
SAM 35799	1 780	104.5	—	—	—	—	—	—	—	—	—	—	—	—
PEM 1518/85	1 890	129.5	26.6	20.6	46.5	35.8	2.3	2.2	1.9	1.8	520	0.50	695	0.67
PEM 1519/59	1 890	113.2	25.5	22.5	38.2	33.7	4.4	3.4	3.2	2.5	—	—	720	0.56
PEM 1519/62	2 040	136.1	34.1	25.0	45.0	33.1	2.64	2.3	2.46	2.2	—	—	755	0.67
PEM 1519/60	2 060	155.9	38.2	24.5	50.9	32.7	31.3	2.0	2.99	1.9	—	—	790	0.51
PEM 1519/61	2 090	142.7	33.2	23.2	49.1	34.4	—	—	—	—	—	—	—	—
PEM 1516/97	2 350	209.1	35.5	17.0	65.5	31.3	6.8	3.3	4.3	2.1	1 140	0.54	—	—
SAM 35079	2 470	—	—	—	—	—	—	—	2.65†	—	—	—	1 390	—

*One kidney only.

†Lungs and trachea only.

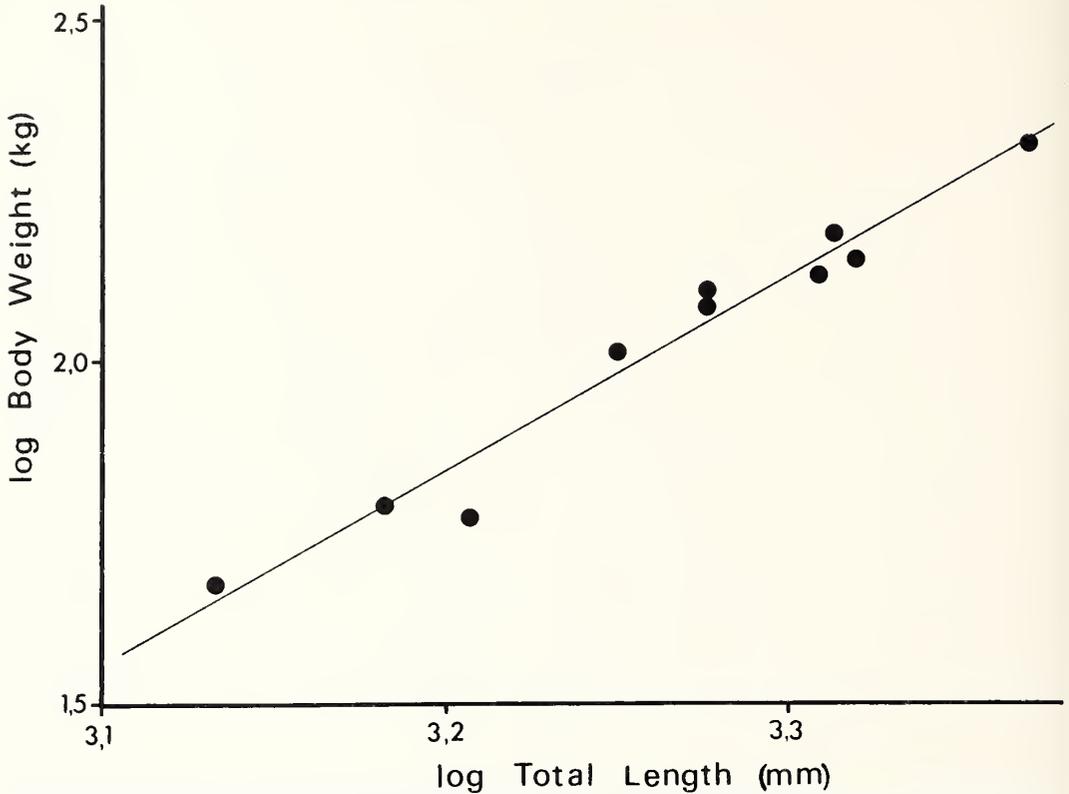


Fig. 13. Length—weight relationship for 10 *K. simus* from data provided in Table 16. The regression line was fitted from the equation $\log Y = -7,29 + 2,86 \log X$ ($r = 0,88$), where Y = body weight (kg) and X = total length (mm).

The blubber weights given in Table 16 represent the weights of blubber removed posterior to the transverse plane intersecting the condyles, while meat weight represents the weight of the epaxial muscle fillets and the hypoaxial fillets posterior to the rib cage.

The pancreas weighed 66 g (0,06% body weight) in SAM 35799 and 95 g (0,07% body weight) in PEM 1518/85.

The total weight of PEM 1518/85 was 129,5 kg. However, the total weight was 125,4 kg when the animal was weighed in pieces. The loss of weight presumably represented loss of body fluids, but the amount seems surprisingly low (3,1% body weight) to account for the total blood volume, even accepting that perhaps only 75% of the blood volume can be drained by direct bleeding (Lockyer, 1976). If the weight loss represented only 50% of the total blood volume, it would still suggest that *K. simus* had a relatively small blood volume. The heart does not seem to be particularly large, and is comparable to that of *Tursiops truncatus* (0,54% body weight) (Ridgeway, 1972). The small blood volume and relatively small heart may indicate *K. simus* is not a very active species, though it appears to be capable of diving to at least 300 m (Fitch and Brownell, 1968).

Intestine Length. The lengths of the large and small intestines were recorded for five animals, and the results are given in Table 17. The variation indicated by the lengths of PEM

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1519/59–62 is natural, for these four animals were measured in an identical fashion by laying out the intestine in rows after freeing it from all mesenteries.

TABLE 17

Intestinal lengths of 5 K. simus from South Africa, expressed as multiples of total body length

Cat. No.	Total Length (mm)	Large Intestine	Small Intestine	Total
PEM 1519/59	1 890	1,59	10,58	12,17
PEM 1519/62	2 040	0,93	13,63	14,56
PEM 1519/60	2 060	2,09	12,97	15,06
PEM 1519/61	2 090	2,06	11,00	13,06
SAM 35079	2 470	1,87	7,49	9,36

REPRODUCTION

Females. Ovaries were available from 10 *K. simus* from South Africa. Details of this material are provided in Table 18. Only four of these ten were sexually mature, and none of these had more than six corpora in both ovaries. Thus while there appears to be a gradation in the size of corpora albicantia as their number increases suggesting that they regress in size with age, it is uncertain that corpora with an index of 20–30 represent the smallest size attained in ovaries with more corpora.

All four corpora lutea were pedunculated, and situated at one pole of the ovary. One corpus luteum (PEM 1515/50) was composed of solid luteal tissue. The corpus luteum of PEM 1516/97 had a small cavity filled with tertiary liquor folliculi, and those of PEM 1518/82 and PEM 1519/72 had irregular cavities up to 6 mm in diameter.

The appearance of surface scars marking the position of corpora albicantia was variable. In PEM 1518/82 the surface scar was a prominent pale patch which contrasted with the grey colour of the ovary. A small crater was visible in the centre of some ten short radiating wrinkles. The surface scars were either absent or unclear in PEM 1519/72 and simply stellate wrinkles in PEM 1516/97. In PEM 1515/50 the scars were well defined and approximately 1 or 2 mm greater in diameter than the major diameter of the corpus underneath, except in one case when no scar was visible (corpus diameters $4 \times 3 \times 2$ mm). In section the corpora albicantia were characterized by a central white fibrous core surrounded or outlined by yellow-brown pigment. Eversion of the tissue of the corpus at the surface produced a capped effect in all but one case (PEM 1515/50, $3 \times 3 \times 3$ mm).

Several bodies were found in the ovaries of PEM 1516/97 and PEM 1515/25 which were classified as corpora atretica. These were of two types, though both were characterized by their small size, and a thin line of yellow pigment around the periphery. One form was spherical, about 1 mm in diameter and usually occurred deep in the ovarian tissue. The second form was cylindrical, about 1 mm in diameter and up to 3 mm in length perpendicular to and generally reaching the surface.

Records of female *K. simus* known to be sexually mature by the presence of a foetus or accompanied by a small calf are given in Table 19. The smallest sexually mature female was PEM 1518/82 which measured 2,15 m in length. However, the length of the physically mature female described by Allen (1941) was only 2,21 m. The length at sexual maturity in marine mammals has been estimated at 86% of the length at physical maturity (Laws, 1956), which

TABLE 18
Ovarian data from 10 female *K. simus* from South Africa

Cat. No.	Total length (mm)	Ovarian		Corpus Luteum diam. (mm)	Corpora Albicantia diam. (mm) and index*	Total No. of Corpora	Remarks
		Dimensions (mm)	Weight (g)				
PEM 1516/99	1 524	24 × 12 × 8	1,0	—	—	0	Several tiny follicles up to 1 mm. Smooth unscarred surface
		24 × 12 × 7	1,3				
PEM 1519/73	1 610	20 × 13 × 8	1,1	—	—	0	Several tiny follicles up to 1 mm. Smooth unscarred surface
		20 × 13 × 8	1,2				
PEM 1518/85	1 890	36 × 24 × 14	6,6	—	—	0	Very numerous follicles many 2-4 mm diam. Surface of ovary dimpled by follicles and spongy to touch
		32 × 23 × 13	5,7				
PEM 1519/59	1 890	24 × 14 × 8	1,9	—	—	0	Numerous follicles up to 2 mm diam. Surface smooth unscarred
		22 × 17 × 8	2,0				
PEM 1519/60	2 060	37 × 20 × 13	5,1	—	—	0	Numerous follicles up to 3-4 mm diam
		34 × 25 × 9	5,6				
PEM 1519/61	2 090	32 × 22 × 10	3,8	—	—	0	Numerous follicles up to 3,5 mm diam. Several form dimples on the smooth surface of the ovary
		30 × 21 × 14	5,1				
PEM 1518/82	2 150	47 × 28 × 13	14,2	28 × 20 × 11	7 (245)	2	Numerous follicles 2-3 mm diam. Corpus luteum 3,8 g
		41 × 23 × 14	7,6				
PEM 1519/72	2 240	46 × 12 × 15 (l)	9,7	23 × 21 × 19	7 (175) 6 (150)	2	Corpus luteum 5,8 g. 325 mm foetus. Very few follicles up to 2 mm.
		35 × 15 × 11 (r)	3,2				
PEM 1516/97	2 350	37 × 18 × 14 (l)	6,0	—	5 (100); 5 (40) 4 (48)	3	Few follicles up to 2 mm diam.
		31 × 20 × 14 (r)	10,9				
PEM 1515/50	2 310+	40 × 17 × 12	4,5	—	3 (27)	1	Several follicles up to 1 mm. 2 corpora atretica
		63 × 20 × 13	13,6				
				26 × 21 × 16	7 (252); 6 (72) 4 (24); 4 (24)	5	Corpora luteum 5,3 g. Follicles up to 2 mm. 3 corpora atretica. Foetus lost

*This index is the product of the diameter of the corpus measured in three planes at right angles to each other.

TABLE 19
Records of female K. simus with a foetus, or with a calf, from South Africa and from the literature

Cat. No.	Total length (mm)	Length of foetus (mm)	Sex of foetus	Length of calf (mm)	Sex of calf	Date	Region	Source	Remarks
PEM 1515/50	2 310+	?	—	c. 1 520*	—	28/4/70	South Africa	Present study	Adult lactating. Foetus lost
PEM 1515/53	2 305	—	—	1 525	—	Apr/May 1970	South Africa	Present study	Adult lactating moderately
PEM 1516/50	c. 2 440	—	—	1 360	♀	24/3/71	South Africa	Present study	Adult lactating heavily
PEM 1516/97	2 350	72	♀	1 525	♀	15/4/71	South Africa	Present study	Foetal and calf lengths are rough estimates
PEM 1518/02	c. 2 400	c. 200–250	—	c. 1 000–1 300	—	23/8/72	South Africa	Present study	
PEM 1519/72	2 240	325	♀	1 610	♀	17/9/75	South Africa	Present study	Adult's state of lactation not checked
—	2 185	?	—	—	—	1/3/1853	India	Owen (1866, 1867)	Type of <i>K. simus</i>
—	2 220	—	—	—	—	23/7/51	Japan	Yamada (1954)	Lactating
—	2 210	c. 300	—	c. 1 500	♂	21/4/39	U.S.A.	Allen (1941); Barbour (1950)	Adult lactating physically mature

*Estimated from CBL.

would give an estimated length at sexual maturity of about 1,9 m for this particular female. Five of the ten females in Tables 17 and 18 that are sexually mature are less than 2,24 m in length, while the longest immature females are 2,06 m and 2,09 m in length. On this evidence it is estimated that most female *K. simus* become sexually mature between 2,1 m and 2,2 m in length.

There are too few records to provide information on the length of gestation, or to establish whether there is a distinct breeding season. The lengths and dates of the first four and last two calves in Table 18 suggest an extended calving season of at least five or six months.

Five of the six females known to be pregnant have been accompanied by calves, two of which were known to have been suckling, which suggests that a large proportion of the mature females fall pregnant in successive seasons. Of the nine sexually mature females known from South Africa four were pregnant, two were suckling calves, one was too badly cut to determine if a foetus had been present though a small corpus luteum was present, and the state of the last two is unknown (PEM 1517/38, SAM 36728). The presence of the foetus and suckling calf in the physically mature female described by Allen (1941) suggests an extensive reproductive life span.

It appears from Table 18 that suckling continues until the calf is over 1,5 m in length. The shortest immature animal, which was associated with three other immature animals, and therefore had almost certainly ceased suckling, was 1,89 m in length (PEM 1519/59). SAM 35799 was only 1,78 m in length and though stranded alone, it may have become separated from an adult. The stomachs of the calves of PEM 1519/72 (1,61 m) and PEM 1516/97 (1,525 m) contained squid beaks, while that of the 1,36 m calf of PEM 1516/50 contained a single nematode, indicating that it had eaten solid food.

Males. Data on the testes of 9 male *K. simus* from South Africa are presented in Table 20, with published information of four other males. Males less than 1,9 m in length are immature, but reach puberty at about 2,0 m. The dimensions of the testes, the tubule diameter and the presence of sperm in the epididymis all suggest that males of more than 2,2 m are fully sexually mature, and that most males probably mature between 2,1 m and 2,2 m.

Sex Ratio: The number of mature males and females recorded as strandings should reflect the sex ratio of the adults, with the assumption that longevity and susceptibility to stranding is equal for both sexes, and that there is no observer bias in sexing the carcasses. There are 9 females and 8 males more than 2,1 m in length listed in Table 6, which is a ratio of 1,13:1. In the present small sample this ratio is not considered significantly different from parity.

FOOD

The stomachs of 24 *K. simus* were examined in the present study, of which three proved to be empty except for a few nematodes.

Cephalopods form the basis of the diet of *K. simus* judging by the number of beaks collected from the stomachs. Over 1 400 beaks were collected from 18 stomachs. These have been assigned to families and genera with the same reservations applied to the identification of the beaks recorded from *K. breviceps*, and are listed in Table 21.

With a few exceptions the types of squids recorded from these *K. simus* stomachs are the same as those found in *K. breviceps* (Table 14). However the frequency of occurrence of the squid families differs considerably in these two whales. In Table 21 the percentages of oceanic forms, particularly histioteuthids, cranchiids, octopoteuthids and chiroteuthids are less than one fifth of those recorded in *K. breviceps*, while nearly 70% of the cephalopods recorded from *K. simus* are sepiids, which are typically inhabitants of the continental shelf, and along the south coast of South Africa seldom recorded beyond 100 m depth (Roeleveld, 1972). These percentages are affected by the large numbers of sepiids found in four of the stomachs examined, which may give a false impression of the importance of sepiids in the diet of *K. simus*. However in *K. simus* the average number of beaks per stomach of oceanic families such as histioteuthids and cranchiids is still less than half that found in *K. breviceps*.

The percentage frequency of occurrence of *Oregoniateuthis* is approximately the same in both whales, though the average number of beaks per stomach in *K. simus* (13) is more than double that in *K. breviceps* (6). Imber (1975) has pointed out that nearly all records of lycoteuthid squids have been from over a continental slope or oceanic ridge. South of Algoa Bay, yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* are caught by sport fishermen from 10 to 50 miles south of Cape Recife. Examination of stomachs containing food from 49 yellowfin and 20 skipjack tuna showed that 86.5% of 559 cephalopod lower beaks in the yellowfin tuna and 55% of 22 lower beaks in the skipjack tuna were from *Oregoniateuthis* (Ross, unpublished data). A total of 43 intact or partially digested *Oregoniateuthis* indicating recent ingestion, were recorded from tuna caught between 25 and 37 miles south of Cape Recife, over water depths ranging from 120 m to over 250 m.

Unfortunately no data are available on stomach contents of tuna caught much further from the edge of the continental shelf in this region. However, no specimens of *Oregoniateuthis* were found in 136 stomachs of four species of tuna (*T. thynnus*, *T. alalunga*, *T. albacares* and *T. obesus*) caught beyond the 200 m depth contour off the Cape west coast (de Jager *et al.*, 1963).

The evidence supports Imber's (1975) suggestion and suggests that *Oregoniateuthis* occurs on the edge of the continental shelf and the upper part of the continental slope in the region south of Algoa Bay, perhaps associated with the sharp temperature gradient between the cooler inshore waters and those of the Agulhas Current. If this is true, the predominance of *Oregoniateuthis* and sepids in the diet of *K. simus* may indicate that this whale also inhabits the area over the edge of the continental shelf.

Ten stomachs were flushed thoroughly with water to collect any fish otoliths present. Otoliths were found in this way in two stomachs only (PEM 1519/09, PEM 1519/17). The stomach of PEM 1519/09 contained a large number of fish jaws which have been identified by Dr P. Hulley as those of *Photichthys argenteus*, *Chauliodus ?sloani*, *Stomias boa*, and an unidentified gempylid fish. The otoliths were identified by Mr J. Fitch as follows, with minimum numbers of each species in parenthesis: *Photichthys argenteus* (26), *Nansenia* sp (3), *Melamphaes* sp (2), *Benthodesmus* sp (2), *Sudis* cf. *hyalina* (2), stomiatoids cf. *Chauliodus* (12), a macrourid (?), three species of *Lampanyctus* (14, 7 and 1), two species of *Myctophum* (2,1), *Scopelopsis multipunctatus* (12), 9 unidentified myctophids and one other unidentified otolith. Dr Hulley estimated that the jaws of *Photichthys* were from specimens about 300 mm SL or more in length. The stomach of PEM 1519/17, contained the otoliths of one *Merluccius capensis* and a juvenile *Helicolenus*. The egg case of a skate was found in the stomach of PEM 1516/97, together with squid beaks and a polythene bag, while a single fish jaw was found in a male stranded with SAM 36728.

Fitch and Brownell (1968) have recorded fish taken from stomachs of 3 *K. simus* captured off Japan, including *Nansenia*, macrourids and myctophids, and concluded that these *K. simus* had been feeding 250 m or more below the surface. These authors noted that *Nansenia* seldom approaches within 200 m of the surface, while macrourids are bathypelagic. *Scopelopsis multipunctatus* is generally found from 200 m down to 2 000 m (Dr P. Hulley, in litt.) and *Merluccius capensis* is considered to be a benthic rather than a mid-water species. Remains of crustaceans were found in 11 of the 24 stomachs examined. The mysid shrimp *Gnathophausia* was found in three stomachs only (PEM 1515/50, 1519/09, 1519/59) and the carapace lengths of the 8 preserved carapaces ranged from 45 mm to 85 mm with a mean of 72 mm. Decapod crustaceans were identified in three stomachs from features of the carapaces (Barnard, 1972). A single specimen of *Acantheephyra eximia* (carapace length 41 mm) was found in the stomach of PEM 1519/09, while four specimens of *Solenoceras* sp. (carapace lengths 28, 26, 24, 22 mm) were found in the stomach of PEM 1518/82. In the stomach of PEM 1519/72 were two specimens of *Parapenaeus fissurus* (carapace lengths 49, 36 mm) and one penaeid tentatively

TABLE 20
Reproductive data for thirteen male K. simus.

Cat. No.	Total length (mm)	Testis dimension (mm)	Testis Weight (g)	Tubule Diam. (μ)	Sperm in Epididymis	Remarks	Reference
SAM 35799	1 780	160 x 30 (L) 160 x 30 (R)	54 (L) 55 (R)	40 (C)		Immature	
PEM 1519/17	1 810	190 x 20 (L) 185 x 20 (R)					
—	1 890	165 x 25 (L) 155 x 30 (R)			Absent		Harrison <i>et al.</i> (1972)
SAM 36024	1 975		75 (L) 100 (R)	44 (C)		Immature	
PEM 1519/62	2 040	250 x 50 (L) 260 x 40 (R)	200 (L) 222 (R)	101 (C) 89 (P)	Moderately numerous	Few sperm in some tubules	
SAM 35634	2 153	210 x 60 (L) 220 x 50 (R)					
PEM 1517/12	2 200*	395 x 85 (L) 375 x 80 (R)	1 500 (L) 1 140 (R)	123 (C)	Present	Sperm numerous in tubules	
—	2 240	approx. 400					Roest, 1970

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Cat. No.	Total length (mm)	Testis dimension (mm)	Testis Weight (g)	Tubule Diam. (μ)	Sperm in Epididymis	Remarks	Reference
—	2 420	475 × 70 (L) 500 × 75 (R)			Absent		Harrison <i>et al.</i> (1972)
—	2 460	465 × 95 (L) 430 × 95 (R)		200	Present		Harrison <i>et al.</i> (1972)
SAM 35079	2 470	370 × 90 × 35 (L) 400 × 85 × 30 (R)	925 (L) 995 (R)				
PEM 1519/09	2 520	560 × 80 (L) 560 × 80 (R)	2 180 (L) 1 725 (R)	160 (C) 121 (P)	Numerous	Sperm numerous in tubules	
PEM 1515/00	2 605	380 × 90 (L) 380 × 90 (R)					

Abbreviations. L = left, R = right, C = sampled at centre at mid-length of testis, P = sampled at periphery at mid length of testis.
*Length estimated from regression of Total Length on CBL.

TABLE 21
Numbers of Lower Beaks of Cephalopods from 18 stomachs of Kogia simus from South Africa

Cephalopods*	Catalogue Numbers														Total number	% of total	Family % of total				
	SAM 35079	SAM 35634	SAM 35799	SAM 36024	SAM 36728	PBB 72/16	PEM 1516/97	PEM 1516/99	PEM 1517/12	PEM 1518/85	PEM 1519/09	PEM 1519/17	PEM 1519/59	PEM 1519/60				PEM 1519/61	PEM 1519/62	PEM 1519/72	PEM 1519/73
Histioteuthidae																					
Type 1	3	1	3	—	1	—	1	—	10	—	3	—	—	—	—	—	—	—	23	1,6	
Type 2	34	3	—	—	1	—	—	—	—	—	2	—	2	2	—	—	—	—	44	3,1	
Type 3	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	9	0,6	
Type 4	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	0,1	
Type 5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	< 0,1	
Type 6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	< 0,1	
†Type 7	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	0,3	
†Type 8	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	< 0,1	
Enoploteuthidae																					
<i>Abraliopsis</i>	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	< 0,1	< 0,1
Lycoteuthidae																					
<i>Oregoniateuthis</i>	18	3	2	—	12	1	—	11	—	124	4	9	1	—	—	—	14	35	234	16,3	16,3
Cranchiidae																					
<i>Pyrogopsis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	< 0,1	< 0,1
<i>Galliteuthis</i>	—	—	2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	2	0,1	0,1
<i>Phasmatopsis</i>	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	3	0,2	0,2
<i>Taonius</i>	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	0,2	0,2
†Type 1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	0,4	0,4
†Type 2	1	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	1,0	1,0
†Type 3	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	2	0,1	0,1

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

Cephalopods*	Catalogue Numbers													Total number	% of total	Family % of total					
	SAM 35079	SAM 35634	SAM 35799	SAM 36024	SAM 36728	FBB 72/16	PEM 1516/97	PEM 1516/99	PEM 1517/12	PEM 1518/85	PEM 1519/09	PEM 1519/17	PEM 1519/59				PEM 1519/60	PEM 1519/61	PEM 1519/62	PEM 1519/72	PEM 1519/73
Octopoteuthidae <i>Octopoteuthis</i>	—	—	1	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	3	0,2	0,2
Chiroteuthidae Type 1	—	—	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	< 0,1	< 0,1
Type 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	0,3	0,3
†Type 3	2	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	4	0,3	0,3
Onychoteuthidae <i>Moroteuthis 1</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	< 0,1	0,1
Ommastrephidae Ommastrephids	—	—	—	62	—	—	—	—	—	—	—	—	—	—	—	—	—	—	62	4,3	4,3
<i>Todarodes</i>	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	< 0,1	< 0,1
Loliginidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	4	0,3	0,3
Vampyroteuthidae <i>Vampyroteuthis</i>	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	< 0,1	< 0,1
Sepiidae	—	—	1	—	—	6	11	—	—	—	—	183	190	14	46	14	303	299	997	69,5	69,5
Octopodidae	—	—	—	—	—	—	—	—	—	—	—	3	2	—	—	—	—	1	6	0,4	0,4
																			1 436	99,6	99,6

*Beaks unassignable to any group were found in PEM 1518/85 (2), 1519/73 (1), 1519/09 (1) and SAM 36728 (1).

†These beaks are tentatively assigned to their respective families.

placed in the genus *Metapenaeus* (carapace length 53 mm). One stomach contained a single megalopa larva (SAM 36024), and five stomachs held unidentified crustacean fragments.

PARASITES

Examinations for stomach and blubber parasites were made in 26 *K. simus* from South Africa. The lungs and liver of 9 specimens and the kidneys of 6 of these were examined without finding parasites.

Nematodes were recorded from the stomachs of 24 animals. A qualitative estimate of the parasite load was made in 16 of these animals as follows: light load—PEM 1515/53, 1515/70, 1516/51, 1518/82, 1519/73, SAM 36728 and its companion; medium load—PEM 1516/97, 1519/59, 1519/62, 1519/72 and SAM 35799; heavy load—PEM 1519/60, SAM 35079, and SAM 36024. Material from 17 stomachs was found to contain the same three species as were found in *K. breviceps*. In nine cases all three species *Anisakis physeteris*, *A. simplex* and *Phocanema kogiae* were found together in the stomach. In four stomachs, *A. physeteris* and *P. kogiae* occurred together, and in four stomachs, *A. physeteris* occurred on its own.

There appears to be no correlation between the parasite load and the number of species of nematode present in the eleven stomachs for which the data were available.

Cestode cysticerci were found in the blubber of 12 specimens and noted as absent or not seen in 6 animals. Numbers ranged from one or two to a few, often near the anus in the caudal blubber. One cysticercus from the blubber of PEM 1518/85 was identified as *Phyllobothrium delphini* (Bosc, 1802).

Two small nematodes were removed from the aorta of SAM 36024, but have not been identified.

DISTRIBUTION AND MOVEMENTS

The only published information on the possible movements of *K. simus* was given by Yamada (1954) who recorded that catches of *Kogia* were confined to the summer season off Japan, presumably because a migration took place. Some, but not necessarily all of the *Kogia* he referred to were *K. simus*, however *K. breviceps* may have been caught as well.

In southern African waters *K. simus* has been recorded from Saldanha Bay (18°E) to East London (28°E) with the majority of records (20 of 30 for which the locality is known) from the eastern Cape. As in *K. breviceps*, the largest number of specimens have been recorded in regions with interested museums, and it seems quite likely that the known range of *K. simus* on the southern African coast would be extended with more interested observers on the west coast. The coast between the present limits of distribution borders on the area of mixed water systems formed by the interactions of the Agulhas and Benguella current systems, and it is possible that the conditions in this region play a part in determining the distribution of *K. simus*.

Twenty-seven dated records of *K. simus* given in Table 6 have been plotted in Fig. 14. It is fairly clear that *K. simus* is present in eastern Cape waters throughout the year, and perhaps also in waters off the western Cape. The paucity of records for the coastline between Cape Town and Port Elizabeth is almost certainly due to the lack of observers. There seems to be little evidence that *K. simus* migrates onshore or along the shore at any season.

SCHOOLING BEHAVIOUR

As there are so few sightings of either *Kogia* species on record, very little is known of their school size and structure, or behaviour.

The first report of school size in *Kogia* was reported by Bullen (1906) who harpooned five "short headed cachalots" from a school near the Aldabra islands. The specific identity of these whales can not be established.

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

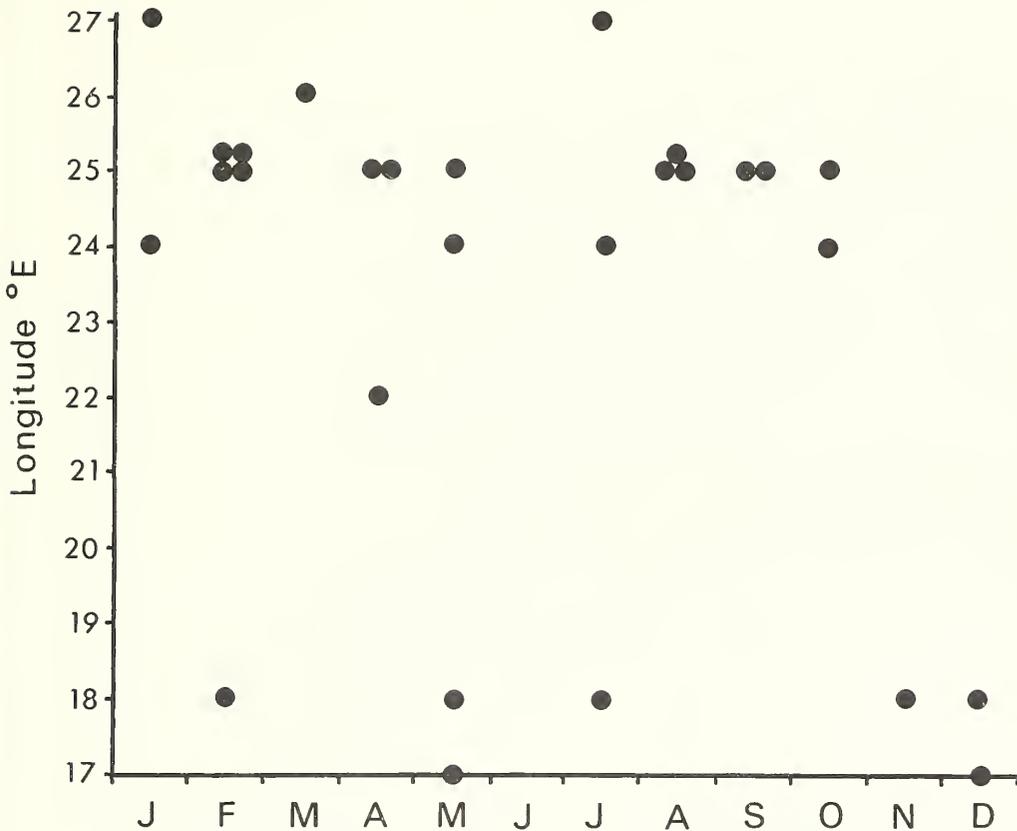


Fig. 14. Seasonal occurrence of *K. simus* based on 28 dated records from southern Africa.

The remaining published reports refer to *K. simus*. Hale (1963) recorded that a school of "porpoise-like" animals was noted off Leighton Beach, Western Australia, the day before a 2,2 m female *K. simus* stranded alive on the beach. Hale (1959) also recorded a 1,93 m male with a second animal estimated at 2,13 m in length at Largs Bay, South Australia.

Two of the whales described by Yamada (1954) were harpooned from a group of 6 to 7 whales. These were No. 5, a male with an estimated total length of 2,30 m (CBL 284 mm) and No. 4, a lactating female 2,22 m in length. A second male (No. 6) estimated at 2,43 m in length (CBL 297 mm) was taken from a group of 2 or 3 whales. Yamada notes that kogiids are often found basking on the surface of the sea and are easy to approach. This habit is reflected in the ancient Japanese name "Uki-Kujira" or "floating whale" given to *Kogia*.

Caldwell *et al.* (1973) reported two crania of *K. simus* collected from the small cetacean fishery at St Vincent, Lesser Antilles. The condylobasal lengths of the two crania were 195 mm and 175 mm, from which the total lengths of the animals are estimated to have been about 1,46 m and 1,27 m respectively. From data in this report both animals would have been suckling still and it seems probable that they accompanied adult females, though no other animals were believed to have been present by the authors. The fishermen reported that they had encountered the species

about a dozen times in the past, usually in small groups, and they referred to them as "rat porpoises".

In the present study four sexually immature animals stranded together at Sea Vista, Cape St Francis (PEM 1519/59-62). At least one of these was alive when the group was found. They were spread over about 800 m of shallow-sloping beach in the order: male, 2,04 m; female 2,09 m; female, 2,06 m; female, 1,89 m. SAM 36728, a 2,64 m female, stranded with a male estimated at 2,45 m in length. They were reported to have been fighting before stranding, and fresh tooth marks were found on the caudal peduncle behind the dorsal fin of one animal.

The data suggest that the school size of *K. simus* is probably 10 animals or less. The known or inferred ages of the groups stranded or captured suggest that females accompanied by calves may group together (Caldwell *et al.*, 1973), immature animals may form schools (present study, and possibly the two animals recorded by Hale, 1959), and sexually mature males and females can be found in the same school (present study, and Yamada, 1954).

It is interesting to note that all the specimens of *Kogia* that have been taken in small cetacean fisheries with sufficient frequency that they have a common name, have been *K. simus*, including the type specimen which was captured by fishermen at Waltair, India, where they were known by the name of "Wonga" (Owen, 1866). This may be because *K. simus* occurs closer inshore than *K. breviceps*, as inferred on the basis of stomach contents in this report.

DISCUSSION

The shape of the head in the three extant physeterids is one of the most distinctive features of the family. The function of the massive head of the sperm whale *Physeter*, and that of the spermaceti organ within it, has been the subject of discussion for many years. Recently Clarke (1970) proposed that the spermaceti organ assists in maintaining neutral buoyancy at great depths, when cooling of the spermaceti oil increases its density and compensates for the positive buoyancy effect of the denser sea water on the whale at depth. Rewarming of the spermaceti by vasodilation of blood vessels in the head would give the whale a positively-buoyant "head-up" attitude which would greatly assist the whale in its return to the surface.

Clarke's hypothesis was criticized by Ridgeway (1971) who maintained that reduction in body volume due to thoracic collapse at depth would increase the density of a sperm whale sufficiently to retain neutral buoyancy. It seems more likely that both mechanisms operate, in a co-ordinated fashion, for an increase in density in the head without a corresponding increase in that of the body will produce a rotary downward movement about the centre of gravity which would be a disadvantage in horizontal swimming.

A further hydrostatic mechanism has been discussed by Schenckan and Purves (1973) who have examined the nasal tract of *Kogia* and *Physeter* in detail.

They concluded that during a dive negative pressure develops in the right naris due to the buoyancy of the spermaceti organ and adipose cushion in *Kogia* and the spermaceti organ in *Physeter*.

This negative pressure gradually evacuates the lungs, and residual thoracic air is shared by the trachea, larynx, and the right nasal air cavities. During the "head-down" attitude and at depth, all of the air in the right nasal tract would be squeezed into the naso-frontal sac. In the "head-up" attitude and reduced hydrostatic pressure the air would tend to move forward into the anterior chambers of the right naris. These authors considered that this periodic shift in the centre of buoyancy would have some hydrodynamic importance in *Physeter* but less in *Kogia* since the head is much shorter in this genus.

It has been shown in the present study that the snout of *K. simus* is shorter than that of *K. breviceps*, and bearing in mind that the head length of female *Physeter* is less than that of male *Physeter*, the possibility arose that a relationship between head length and total body length existed throughout the family.

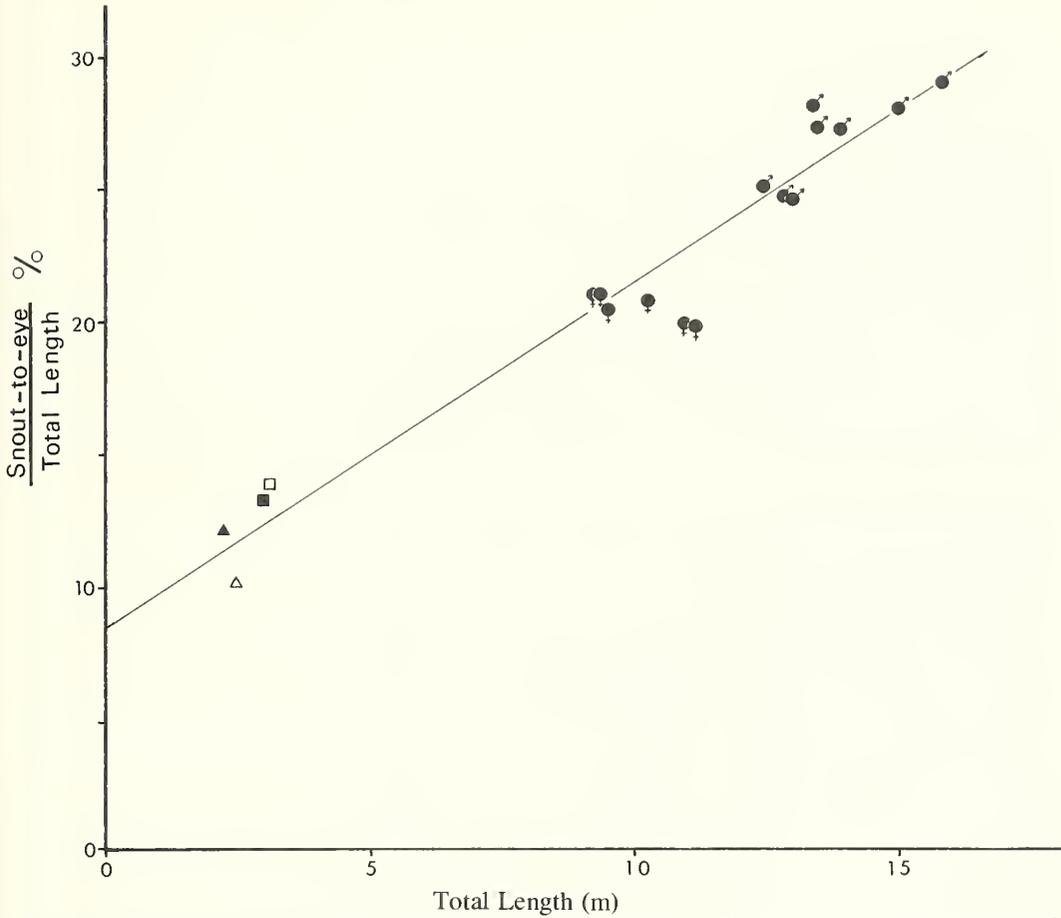


Fig. 15. Illustrating the relationship between snout-to-eye and body lengths in *K. simus* from South Africa (Δ) and elsewhere (\blacktriangle), *K. breviceps* from South Africa (\square) and elsewhere (\blacksquare) and male (σ) and female (φ) *Physeter macrocephalus* from a number of localities (Table 22). The regression line is fitted from the equation $Y = 8,59 + 1,296 X$, where $Y = \frac{\text{Snout—Eye}}{\text{Total Length}} \times 100\%$ and $X = \text{Total length (m)}$.

The length from the tip of the snout to the eye was chosen as the most convenient expression of head length. Data on the snout-to-eye length and total length have been taken from Machin (1974) for adult *Physeter* from South Africa, South Georgia, Antarctica, Bonin Is, Japan, and the South East Pacific region. Data for *K. breviceps* over 2,6 m in length are from the present study (8 animals), and from 12 animals in the literature (Allen, 1941; Caldwell *et al.*, 1971; Carvalho, 1966; Duguay, 1966; Hale, 1947, 1962; Raun *et al.*, 1970). Data for *K. simus* over 2,1 m in length are from the present study (9 animals) and from 4 animals in the literature (Allen, 1941; Yamada, 1954).

These data have been plotted as separate points in Fig. 16 from Table 22. The distribution of the points suggested that a linear relationship did exist, and a regression line was fitted by the method of least squares to the equation:

$$Y = 8,59 + 1,296 X \quad (r = 0,973)$$

where $Y = \frac{\text{Snout-Eye}}{\text{total length}} \times 100 (\%)$ and

$X = \text{total length (m)}$.

The significance of this relationship is not known, but if the head is involved in regulating buoyancy during diving one might expect its size to be in proportion to the body mass on which it is to act. In this respect it is interesting to note that while the snout-to-eye body length proportion appears to change very little with age in both *K. breviceps* and *K. simus* (Fig. 5.11) there are distinct changes in the shape of the head at different body lengths. These changes seem to occur at similar lengths in both species rather than in relation to biological ages such as length at sexual maturity, implying that physical size is an important factor in the change. In *Physefer* the head increases in length with age and also changes shape, apparently increasing the volume (Nishiwaki *et al.*, 1963). Accurate measurements of head and body volumes in all three species would demonstrate whether these conclusions are correct or not.

If Schenckan and Purves (1973) are correct in their interpretation of the movements of air in the right nasal tract during diving, the effect of the positive buoyancy given by air in the anterior chambers of the right naris would be proportional to the distance from the centre of gravity in

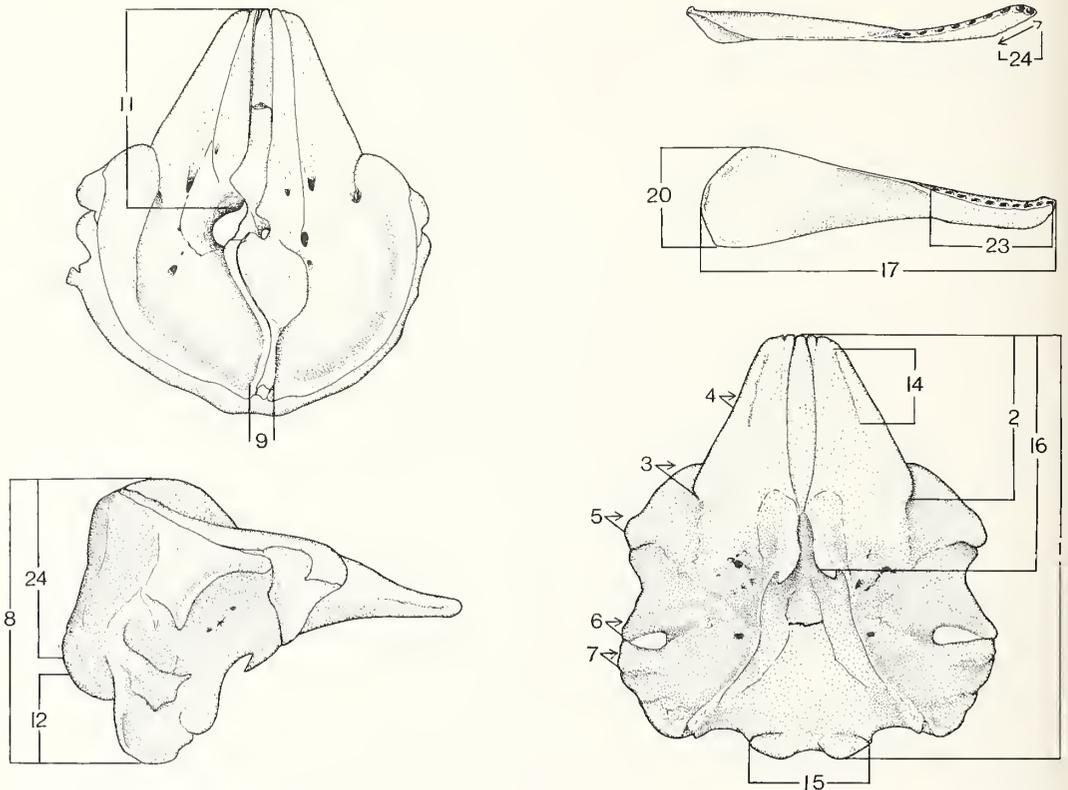


Fig. 16. Illustrating the cranial and mandibular measurements listed in Table 25.

maintaining the "head-up" attitude during the ascent from a dive, and to the body mass. In heavier animals presumably this optimum distance would be greater than in smaller animals.

More measurements of the weight of spermaceti and its proportion to body weight in all three species would also be useful. Schenckan and Purves (1973) have pointed out that the spermaceti organ in *Kogia* was so small that it could not serve the same hydrostatic function in this genus as in *Physeter*. Clarke (1970) estimated that a 13 m male sperm whale weighing 31 435 kg possessed about 1 450 kg of spermaceti oil. This represents 4,6% of the total body weight. In the present study, the spermaceti of a 1 965 m immature *K. breviceps* (total weight 145,5 kg) weighed approximately 1,13 kg or 0,7% body weight. Even if adult *Kogia* have a higher proportion of spermaceti than this immature it is unlikely that it would be comparable to that of *Physeter*.

The change in the rate of growth of the mesorostral ossification towards the tip of the rostrum appears to take place at the time of sexual maturation in both species. The significance of this change is not known, but the mesorostral canal has been implicated as a wave guide in the transmission of sounds used in echolocation (Norris, 1975), and the change may indicate a functional change in the animal's echolocation at this time.

TABLE 22

Total lengths and snout-to-eye lengths of *Physeter macrocephalus*, *K. breviceps* over 2,6 m in length and *K. simus* over 2,1 m in length. Sources of measurements are provided in the text

	Total length (m)	$\frac{\text{Snout-to-eye}}{\text{Total length}} =$ % length	N	Region
<i>P. macrocephalus</i> ♂♂	13,33	28,3	17	South Africa
	15,72	29,1	32	South Georgia
	14,94	28,1	50	Antarctic
	13,83	27,4	12	Paita
	12,76	24,8	8	Pisco
	12,36	25,2	5	Iquique
	13,39	27,2	34	Bonin Is.
	12,93	24,7	63	Japan
	♀♀	10,2	20,8	13
9,46		20,5	9	Paita
9,31		21,1	7	Pisco
9,2		21,1	3	Iquique
10,85		20,0	2	Bonin Is.
11,01		19,9	23	Japan
<i>K. breviceps</i>	3,023	13,9	8	South Africa
	2,935	13,3	12	see text
<i>K. simus</i>	2,425	10,2	9	South Africa
	2,186	12,1	4	see text

ACKNOWLEDGEMENTS

I wish to thank the Directors of the South African Museum, Cape Town, the East London Museum, the Lüderitz Museum, and the Oceanographic Research Institute, Durban for permission to examine material and data housed in their institutions. I am particularly grateful to Dr P. B. Best, Branch Sea Fisheries, Cape Town, for his generous provision of data on *Kogia* from the western Cape and South West Africa.

Identifications of material were kindly provided by Mr J. Fitch, California Fish and Game (fish otoliths), Dr P. A. Hulley, South African Museum (fish jaws), Mr N. MacLeod, Institute of Oceanographic Sciences, U.K., and Mr M. Imber, Wildlife Service, Wellington, New Zealand (cephalopod beaks).

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TABLE 23

External measurements of 1 foetal and 16 postnatal K. breviceps from South Africa. Total body lengths are expressed in mm. Other measurements are expressed as a percentage of body length. Measurement numbers refer to measurements listed in Table 3

	PEM 1516/48	PEM 1515/07	SAM 35550	PEM 1515/70	PEM 1517/92	PEM 1517/90	SAM 36980	SAM 35522	PEM 1513/87	PEM 1496/66	PEM 1515/12	SAM 35795	PEM 1516/48	PEM 1517/89	PEM 1517/91	PEM 1516/08	PEM 1517/76
1	* 1135	1880	1945	1970	1970	2020	† (2360)	2665	2935	2970	(3050)	3050	3050	3055	3095	3250	3280
2	14,1	14,2	—	15,6	14,2	17,3	9,3	14,3	12,1	—	15,8	11,3	15,8	15,7	15,2	—	11,2
3	6,9	6,1	—	5,2	(5,1)	5,7	4,7‡	11,4‡	6,5	—	12,5‡	—	6,3	5,6	5,5	—	(6,2)
4	18,1	—	—	—	—	20,8	—	—	—	—	—	—	—	17,5	—	—	—
5	4,0	—	—	—	—	3,5	—	—	—	—	—	—	—	2,5	—	—	—
6	9,7	8,1	—	10,4	(7,6)	9,9	8,9	—	—	—	9,2	—	8,8	8,2	8,1	—	(8,5)
7 Unsidcd	11,5	11,5	—	11,7	—	—	11,0	—	—	—	10,8	—	11,3	—	11,0	—	—
7 (left)	—	—	—	—	—	12,4	—	—	—	—	—	—	—	9,8	—	—	—
7 (right)	—	—	—	—	—	14,9	—	—	—	—	—	—	—	11,5	—	—	13,2
8	10,6	12,8	—	—	10,7	12,4	8,9	11,0	11,3	14,1	11,7	—	10,4	11,8	11,0	—	(9,3)
9	22,9	23,0	20,9	23,4	22,8	25,2	19,5	23,3	19,9	—	—	20,8	22,5	23,6	21,0	—	20,2
10	—	—	54,9	—	—	49,0	—	—	—	50,5	—	50,0	—	58,9	50,1	—	—
11	66,5	59,5	—	67,5	—	61,4	58,1	60,0	60,4	—	59,2	56,7	60,8	65,9	59,2	59,4	(59,3)
12	43,2	40,5	—	44,2	41,6	45,5	41,1	—	—	—	—	—	43,3	—	—	—	—
13	46,7	—	48,4	—	47,2	51,0	—	45,7	58,9	—	—	—	—	—	—	—	—
14	—	70,3	—	—	—	—	—	—	—	—	—	—	73,3	72,0	—	—	—
15	68,7	71,6	—	70,1	—	77,2	—	72,4	70,1	—	—	—	75,0	—	—	—	—

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

	PEM 1516/48	PEM 1515/07	SAM 35550	PEM 1515/70	PEM 1517/92	PEM 1517/90	SAM 36980	SAM 35522	PEM 1513/87	PEM 1496/66	PEM 1515/12	SAM 35795	PEM 1516/48	PEM 1517/89	PEM 1517/91	PEM 1516/08	PEM 1517/76
16	4,4	—	—	6,5	—	5,0	—	—	3,5	7,6	5,0	1,3	3,8	3,3	—	—	—
17	58,1	54,1	—	67,7	—	—	58,5	—	—	—	—	—	51,7	—	—	—	—
18	65,2	59,5	—	—	—	—	60,2	—	—	—	—	—	—	—	—	—	—
19	39,6	35,1	—	46,8	—	43,6	37,3	—	—	—	—	—	43,3	—	—	—	—
20	19,4	14,9	—	13,0	13,7	15,3	11,4	13,3	14,1	14,8	14,2	13,3	14,2	13,7	14,9	14,1	13,2
21	13,2	9,5	—	11,0	9,6	12,4	8,1	10,0	—	—	11,7	10,4	10,8	10,8	12,0	9,4	9,7
22	6,3	5,1	—	5,2	5,1	5,4	4,2	4,8	5,6	6,1	4,6	4,4	5,2	5,4	5,5	4,3	4,7
23	5,3	4,1	—	3,9	—	(4,5)	3,6	3,3	3,5	2,3	—	3,5	3,5	4,1	3,7	3,1	4,7
24	11,9	9,5	—	13,0	—	(14,9)	10,2	7,6	—	6,1	8,8	8,8	10,0	13,1 (7,2)	11,3	9,0	12,4
25	24,2	21,6	—	22,7	23,4	25,9	21,2	22,9	26,0	22,9	25,0	20,4	26,7	26,2	23,6	21,9	27,1
26	9,3	9,1	—	7,8	8,1	8,4	6,8	—	—	—	9,9	6,3	7,9	8,5	8,1	6,6	7,6
27	1,8	1,7	—	2,3	(1,5)	2,0	1,5	—	—	—	0,8	1,0	2,3	2,1	1,6	1,2	1,2

* = Foetus.

† = Tip of snout damaged.

‡ = Decomposed animal.

() = Approximate measurement.

TABLE 24

External measurements of 21 K. simus from South Africa. Total lengths are expressed in mm. Other measurements are expressed as a percentage of body length. Measurement numbers refer to measurements listed in table 3

Meas.	PEM 1516/51	PEM 1515/54	PEM 1516/99	PEM 1519/73	PEM 1519/17	PEM 1518/85	PEM 1519/59	SAM 36024	PEM 1519/62	PEM 1519/60	PEM 1519/61	PEM 1518/82	SAM 35634	PEM 1519/72	PEM 1515/53	PEM 1516/97	SAM 35079	PEM 1519/09	PEM 1515/25	PEM 1515/00	SAM 36728
1	1360	1525	1525	1610	1810	1890	1890	1975	2040	2060	2090	2150	2155	2240	2305	2350	2470	2520(2540)	2605	2640	
2	12,1	12,9	13,3	11,2	9,9	12,2	11,1	12,3	9,8	12,6	12,0	3,7	—	9,4	9,6	13,0	9,3	8,7	9,5	11,7	9,3
3	4,2	—	5,0	4,0	3,3	3,2	3,7	4,8	4,2	4,9	4,3	—	4,1*	4,9	7,7*	3,8	4,7	2,8	2,0	8,3	7,2
4	—	—	16,3	—	—	—	13,7	—	13,5	15,3	—	—	—	—	—	16,2	—	11,5	—	19,5	—
5	—	—	2,9	—	—	—	2,9	—	2,9	2,9	—	—	—	—	—	3,2	—	2,8	—	—	—
6	8,4	—	8,8	8,1	8,8	—	8,2	—	8,6	9,2	8,1	—	—	8,0	—	8,6	5,3	7,9	7,0	7,8	—
7 (un- sided)	—	9,6	10,0	13,0	—	12,7	—	—	10,3	—	—	—	—	—	10,2	—	7,9	—	—	—	—
7 (left)	—	—	—	—	—	—	—	—	—	10,2	—	10,7	—	9,8	—	—	—	8,7	8,8	—	—
7 (right)	12,1	—	—	—	12,7	—	12,2	—	—	—	12,0	12,1	—	—	—	11,9	—	—	—	—	—
8	9,3	8,3	9,6	8,1	8,8	9,5	8,5	10,0	8,1	9,2	10,1	—	—	8,5	7,7	9,7	—	7,5	—	7,8	—
9	20,6	—	22,5	18,6	20,4	21,2	19,6	21,0	16,7	21,8	18,2	23,3	18,0	17,0	20,9	22,7	17,8	18,3	17,0	20,0	17,8
10	—	—	—	54,0	44,8	46,0	44,4	46,5	42,7	45,6	46,9	—	—	44,6	—	—	—	44,4	—	—	—
11	65,4	56,7	59,2	60,9	56,9	59,3	60,9	61,3	56,4	60,7	59,8	—	61,9	59,8	57,9	57,3	61,1	59,5	—	59,5	—
12	41,1	—	46,7	—	40,9	42,9	39,7	47,1	—	—	—	—	—	—	—	46,5	37,7	—	—	—	—
13	—	—	—	—	46,4	—	—	51,6	46,7	—	—	—	49,6	—	—	—	44,5	45,2	—	—	—
14	66,4	—	73,3	68,3	—	73,0	67,7	—	—	77,2	73,7	—	—	71,9	68,0	69,2	—	—	—	—	—

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

Meas.	PEM 1516/51	PEM 1515/54	PEM 1516/99	PEM 1519/73	PEM 1519/17	PEM 1518/85	PEM 1519/59	SAM 36024	PEM 1519/62	PEM 1519/60	PEM 1519/61	PEM 1518/82	SAM 35634	PEM 1519/72	PEM 1515/53	PEM 1516/97	SAM 35079	PEM 1519/09	PEM 1515/25	PEM 1515/00	SAM 36728
15	67,3	—	—	—	71,3	75,1	—	72,3	71,1	—	—	71,4	—	—	—	72,4	69,2	—	—	70,2	—
16	3,7	4,2	5,8	—	3,9	4,8	4,2	5,5	1,5	3,9	3,4	3,7	—	2,7	3,3	4,3	—	—	2,5	3,9	—
17	59,8	—	60,0	—	—	—	56,1	—	53,9	57,3	55,0	—	—	—	—	64,9	54,3	—	—	—	—
18	59,8	—	65,0	—	—	—	63,5	—	66,1	67,0	64,6	—	—	—	—	64,9	67,2	—	—	—	—
19	41,1	—	40,0	—	—	43,4	43,4	—	39,7	43,7	36,8	—	—	43,8	41,9	41,1	47,0	—	—	42,9	—
20	15,9	13,3	17,5	14,3	13,8	15,9	14,8	16,1	15,2	17,0	15,3	14,4	14,5	15,2	14,3	16,2	15,0	13,9	14,5	14,6	12,9
21	10,7	10,8	11,7	9,9	9,9	10,3	11,1	11,9	10,3	11,9	11,5	12,1	9,7	10,3	9,9	10,8	11,3	10,3	10,0	11,2	9,5
22	5,1	5,0	5,4	5,0	5,3	5,8	5,8	6,1	5,6	6,1	5,5	4,7	5,3	5,6	5,0	5,9	6,1	4,6	5,5	5,4	4,4
23	7,0	5,4	8,3	6,8	6,1	6,9	8,5	10,0	7,8	9,2	8,1	—	6,2	7,1	6,6	8,1	6,7	8,3	—	7,8	6,8
24	16,8	10,8	17,5	13,0	14,9	14,8	16,9	16,8	15,7	16,5	15,3	—	12,4	14,7	11,0	16,2	13,8	15,5	—	12,7	14,4
25	23,4	23,3	29,2	22,4	23,8	23,8	26,5	26,8	29,4	30,6	25,8	27,9	24,8	24,1	23,7	32,4	25,5	29,4	25,0	29,3	21,2
26	7,9	6,7	9,2	7,5	7,7	7,9	9,5	9,4	8,8	9,2	8,6	8,8	—	7,4	6,9	9,2	6,9	8,3	7,3	8,5	6,3
27	2,3	1,7	2,1	1,2	1,7	1,9	2,6	1,9	2,2	2,9	2,4	1,4	—	1,8	1,9	2,4	2,0	1,6	1,3	2,0	1,3

*Decomposed animal.
() denotes approximate measurement.

TABLE 25

Cranial and mandibular measurements taken on Kogia material from South Africa. Reference points for the majority of these are illustrated in Fig. 16

1. Total (condylobasal) length.
2. Rostrum length.*
3. Rostrum, basal width.*
4. Rostrum, width at its middle.*
5. Breadth across pre-orbital angles of supra-orbital processes.
6. Breadth across post-orbital processes.
7. Zygomatic width.
8. Height to vertex.
9. Width of vertex.
10. Width of supra-occipital at narrowest part between posterior margins of temporal fossae.
11. Tip rostrum—left naris.
12. Height of ventral border of foramen magnum.
13. Length maxillary toothgroove—right.
14. Length maxillary toothgroove—left.
15. Width outer margins occipital condyles.
16. Tip rostrum—hind margin pterygoids.
17. Length of mandible.
18. Number of alveoli—left.
19. Number of alveoli—right.
20. Height mandible at coronoid.
21. Length mandibular symphysis.
22. Length lower toothrow—left.
23. Length lower toothrow—right.
24. Height dorsal border of foramen magnum to vertex.
25. Length, anterior margin mesorostral ossification to anterior border of left naris.

*Measured ventrally.

TABLE 26

Cranial and mandibular measurements of 22 K. breviceps from South Africa. The condylobasal length is expressed in mm. Other measurements are percentages of condylobasal length. Measurement numbers are keyed to Table 25

1	SAM 17690	237*	254*	PEM 1515/70	PEM 1515/07	PEM 1511/10	SAM 36980	PEM 1519/12	SAM 35522	SAM 35075	PEM 1511/12	SAM 3912	PEM 1511/13	ELM 674	ELM 779	PEM 1513/87	PEM 1515/12	SAM 35795	SAM 723	PEM 1496/66	PEM 1516/08	SAM 37126	PEM 1514/88
2	37,1	36,7	41,3	36,7	35,6	38,7	46,0	36,4	46,1	44,3	41,7	46,1	50,5	43,4	47,8	45,1	46,7	49,9	44,0	44,9	46,8	48,1	44,1
3	39,2	41,9	36,7	35,6	40,0	39,8	39,8	40,8	35,2	45,9	41,5	44,8	43,7	41,9	45,9	43,7	43,3	40,0	35,8	43,4	40,6	39,6	40,0
4	36,9	35,5	29,7	32,2	27,3	33,6	33,6	27,6	27,1	32,2	26,9	29,4	34,5	34,1	27,9	30,8	29,0	28,2	29,7	25,1	30,0	30,8	26,5
5	81,4	90,0	—	—	83,0	84,4	84,4	88,6	79,1	—	85,6	87,1	87,0	89,0	87,9	80,8	88,3	86,6	80,7	83,5	84,1	84,7	83,9
6	80,6	87,6	85,5	—	85,0	81,4	—	—	80,0	88,7	86,2	86,6	88,5	88,5	88,3	83,7	91,2	86,6	77,1	84,4	84,5	81,1	83,9
7	82,3	88,8	80,6	80,1	81,7	86,7	86,7	85,0	82,4	91,0	84,1	88,7	85,5	83,8	87,9	81,3	85,7	88,9	81,0	81,0	—	84,7	80,9
8	69,6	66,8	59,4	59,6	60,6	67,3	67,3	64,2	62,3	67,3	56,1	66,5	62,3	61,8	63,1	60,0	55,2	65,8	55,6	57,9	58,9	62,8	57,8
9	6,1	5,6	6,0	8,2	7,3	5,0	5,0	7,0	6,8	6,1	6,8	10,3	6,8	11,8	11,9	9,7	5,7	7,6	6,2	8,4	7,3	5,6	10,1
10	63,7	64,1	55,5	61,0	60,6	59,3	59,3	54,8	54,5	63,6	59,7	60,3	52,0	57,1	57,8	55,1	55,7	58,7	50,8	53,8	51,4	58,7	53,5
11	—	—	47,3	45,5	46,0	—	—	47,2	—	—	50,9	—	53,0	52,7	55,1	54,1	53,1	—	—	57,0	56,1	—	54,8
12	18,6	17,0	15,2	15,4	19,0	19,8	19,8	15,8	17,1	21,1	17,8	20,4	19,5	21,8	22,1	18,7	19,5	20,3	15,6	21,5	21,0	18,9	19,9
13	19,4+	—	28,3	21,9	—	37,8	37,8	18,2	28,2	20,6	21,4	28,4	32,0	27,7	27,9	27,9	33,8	27,0	20,4	33,0	23,0	26,2+	38,5
14	—	—	26,1	20,9	—	39,5	39,5	18,8	29,8	23,7	24,8	—	21,0	—	27,9	28,9	32,6	28,2	25,6	34,2	21,4	28,2	38,5
15	28,3	28,6	26,9	25,7	23,3	23,0	23,0	21,4	23,0	23,7	22,2	23,2	20,8	24,3	22,3	20,1	23,3	21,9	21,8	20,6	22,7	22,6	19,3
16	47,7	50,6	59,4	55,1	56,6	60,5	60,5	52,8	59,6	—	60,8	60,6	66,8	51,2	64,1	62,9	61,9	64,4	63,9	64,5	64,7	61,9	66,2
17	—	86,9	86,9	87,0	(87,3)	90,9	90,9	(97,4)	85,4+	—	(80,0)	92,0	95,5	94,6	93,7	—	94+	94,0	90,2	—	88,3+	—	—
18	9+	—	12+	12	11+	14	14	12+	6+	—	9+	12	16	15	—	—	12+	13	13	—	—	—	—
19	9+	—	—	10+	13	13+	13+	12+	6+	—	9+	12	15	14	15	—	14+	13	13	—	14	—	—
20	—	25,9	23,3	(22,9)	—	20,9	20,9	23,2	22,0	—	(21,9)	22,9	25,3	22,3	23,5	—	24,5	22,4	20,4	—	—	—	—
21	—	14,1	16,3	13,7	16,3	20,4	20,4	(27,6)	—	—	16,2+	21,6	26,3	23,5	24,3	—	21,4+	25,4	23,1	—	—	—	—
22	—	32,8	(35,0)	34,9	(34,3)	34,2+	34,2+	(47,5)	—	—	—	33,8	43,0	44,1	—	—	36,9+	36,5	37,9	—	—	—	—
23	—	34,0	(34,6)	33,7	37,3	34,8+	34,8+	(48,1)	—	—	—	33,8	42,3	41,7	42,7	—	39,3+	37,2	37,9	—	—	—	—
24	33,3	32,8	29,7	32,2	28,3	35,6	35,6	33,1	33,3	32,7	26,4	35,6	31,5	28,7	—	30,3	27,4	36,3	28,3	27,4	27,8	32,9	28,1
25	0,0	-6,2	4,1	0,0	4,3	6,5	6,5	2,6	5,4	16,9	6,0	14,9	8,8	16,7	18,0	9,0	16,7	20,8	21,5	19,3	28,3	20,6	24,8

*5 mm added for breakage. () denotes approximate measurement.

TABLE 27

Cranial and mandibular measurements of 25 K. simus from South Africa. The condylobasal length is expressed in mm. Other measurements are percentages of condylobasal length. Measurement numbers are keyed to Table 25

Meas. No.	PEM 1515/54	PEM 1515/51	PEM 1519/73	PEM 1519/17	PEM 1518/85	PEM 1519/59	SAM 36729	PEM 1519/61	PEM 1513/86	PEM 1519/62	SAM 36024	PEM 1517/12
1	201	202	207	235	241	252	256*	262	269*	270	270	273
2	36,3	29,2	28,5	31,9	33,2	35,7	30,9	40,1	34,6	38,1	37,4	36,6
3	41,8	48,0	48,3	46,8	46,1	48,4	53,5	46,2	45,7	44,4	39,6	45,4
4	(36,3)	39,1	28,5	33,6	31,5	29,4	40,2	33,2	30,5	35,6	31,1	35,2
5	79,6	89,1	86,5	88,1	88,8	82,9	—	85,1	89,2	85,9	84,8	87,9
6	—	91,1	90,8	90,2	96,3	86,9	—	87,8	92,6	89,6	86,7	93,4
7	—	—	87,9	85,9	(93,4)	83,3	—	86,3	88,5	85,6	90,0	89,1
8	63,2	65,8	61,8	63,8	58,5	61,5	—	60,3	65,8	59,3	65,9	63,0
9	3,7	5,2	3,4	5,5	2,1	3,2	(3,9)	6,9	4,1	3,5	4,4	3,3
10	64,7	66,3	67,6	65,1	64,3	61,5	75,0	59,9	65,4	64,4	66,3	61,9
11	34,3	33,7	36,2	34,5	40,2	37,7	—	44,3	38,7	40,0	—	39,6
12	15,4	14,4	13,5	14,0	10,8	15,9	23,0	16,4	14,7	13,3	17,0	15,8
13	17,9	17,8	27,1	26,4	23,2	17,5	—	28,6	—	—	16,7+	—
14	14,4	16,8	25,1	26,4	21,6	18,7	—	32,4	—	—	13,0	—
15	32,3	29,7	31,4	28,9	29,9	28,6	30,9	26,7	29,0	28,5	24,4	27,8
16	44,3	46,0	47,3	52,8	48,1	53,2	—	51,9	50,2	52,2	54,8	51,6
17	—	—	80,2	82,1	87,1	78,2	—	81,3	—	81,5	84,1	88,3
18	—	—	9	12	9	12	—	10	9	9	10	11
19	—	—	10	10	9	12	—	10	8	9	10	11
20	—	—	25,1	21,7	24,5	21,0	—	21,4	(25,3)	22,2	23,0	(21,6)
21	—	—	11,1	11,9	12,9	13,1	—	13,0	15,6	(10,4)	11,9	11,4
22	—	—	28,1	34,9	32,4	32,9	—	30,5	30,9	(32,2)	30,3	30,0
23	—	—	28,1	33,2	31,1	31,3	—	30,9	30,5	(32,2)	28,1	32,6
24	31,8	36,6	34,3	34,9	30,7	38,5	43,0	34,4	34,9	33,0	38,9	35,2
25	0,0	1,5	6,8	7,7	10,4	0,0	—	11,5+	20,4	4,1	1,8	32,4

ROSS: PYGMY AND DWARF SPERM WHALES, GENUS KOGIA

anial and mandibular measurements of 25 *K. simus* from South Africa. The condylobasal length is expressed in mm. Other measurements are percentages of condylobasal length. Measurement numbers are keyed to Table 25

SAM 35634	SAM 1515/53	PEM 1519/72	PEM 1519/60	PEM 1516/97	PEM 1519/09	UCT†	ELM 477	SAM 36728	ELM 524	PEM 1519/16	PEM 1515/00	SAM 36677
278	278	278	283	289	289	292	292	293	295	301	322	323
37,4	41,4	36,3	36,7	39,4	37,0	38,0	38,7	40,3	32,9	39,5	35,4	40,2
43,1	—	48,2	42,8	43,9	42,6	45,4	45,9	47,4	46,1	43,9	41,6	43,3
29,5	28,8	29,9	27,2	39,8	32,5	34,9	31,2	35,2	31,9	27,2	27,3	35,6
80,6	83,5	88,5	82,3	83,7	84,8	91,1	84,9	84,6	87,1	81,0	81,4	84,8
84,2	90,6	88,8	88,0	88,2	90,7	91,8	93,2	—	—	87,3	83,2	—
86,3	86,7	85,6	83,8	84,1	—	91,8	88,7	—	—	84,7	79,8	89,2
66,2	63,7	59,4	60,8	60,6	61,9	65,4	66,8	69,6	60,3	56,5	57,5	63,5
3,6	2,5	2,5	3,4	2,8	4,2	6,8	4,1	7,0	2,0	2,0	4,7	4,8
58,6	64,7	65,1	62,9	60,2	60,9	64,0	66,8	63,5	—	58,8	56,2	60,1
—	—	42,4	46,6	46,4	46,0	—	43,8	—	44,7	47,2	42,2	—
13,7	19,4	12,6	15,9	15,6	14,5	14,7	21,2	16,7	13,6	12,6	15,5	19,5
30,6	19,1	33,8	26,9	32,2	—	31,5	30,1	30,7	26,7	26,2	30,7	23,5
29,9	16,5	32,7	27,6	32,2	—	31,5	33,9	30,7	35,3	28,6	30,7	24,1
30,6	26,3	29,5	26,9	23,9	26,3	28,0	27,7	29,4	25,8	27,2	27,6	27,2
52,9	54,7	55,4	55,1	56,7	52,9	50,0	56,2	53,2	54,2	58,1	55,3	55,1
80,9	83,8	85,3	81,3	87,2	—	—	—	84,6	—	—	80,7	82,7
9+	8	11	9	9	8+	—	—	9	—	—	—	11
9+	7	11	9	8	8+	—	—	10	—	—	10	10
22,7	24,8	20,7	22,3	22,5	20,8	—	—	22,2	—	—	18,9	21,1
13,3	15,1	14,7	(13,4)	14,2	—	—	—	14,7	—	—	12,1	15,8
28,4+	31,3	31,3	31,4	32,9	—	—	—	34,1	—	—	—	28,2
28,8+	28,4	29,5	32,2	32,5	—	—	—	34,1	—	—	28,6	29,4
37,4	32,4	33,8	35,3	29,1	35,3	37,7	36,0	—	(35,6)	32,2	34,2	34,4
6,1	13,7+	19,4	11,7	41,5	43,3	19,2	20,9	16,0	21,4	20,6	34,5	27,6

*3 mm added for breakage; ‡15 mm added for breakage;
 () denotes approximate measurement; †UCT = Zoology Museum, University of Cape Town.

TABLE 27

Cranial and mandibular measurements of 25 *K. simus* from South Africa. The condylobasal length is expressed in mm. Other measurements are percentages of condylobasal length. Measurement numbers are keyed to Table 25

Cranial and mandibular measurements of 25 *K. simus* from South Africa. The condylobasal length is expressed in mm. Other measurements are percentages of condylobasal length. Measurement numbers are keyed to Table 25

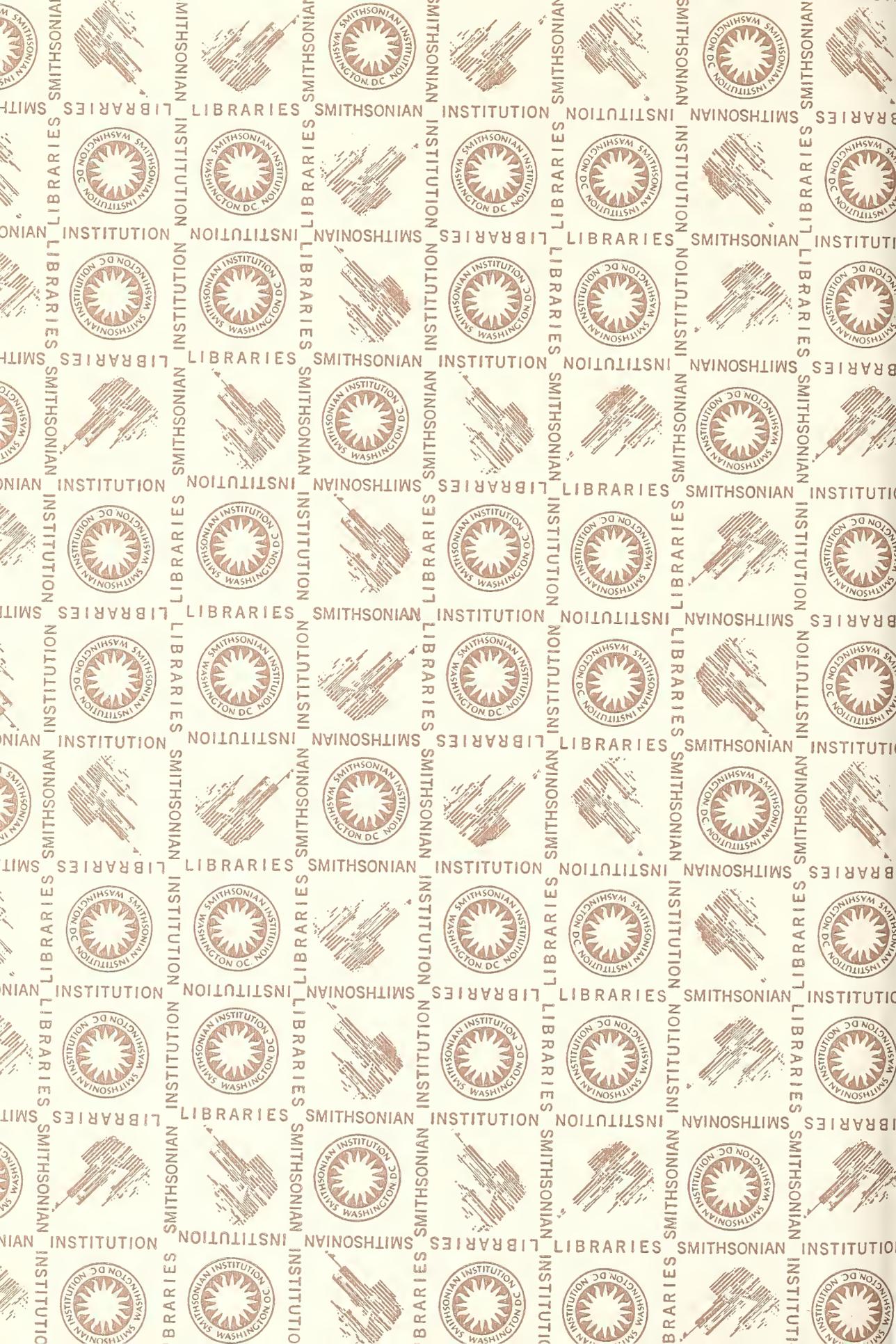
Meas. No.	PEM 1515/54	PEM 1515/51	PEM 1519/73	PEM 1519/17	PEM 1518/85	PEM 1519/59	SAM 36729	PEM 1519/61	PEM 1513/86	PEM 1519/62	SAM 36024	PEM 1517/12	SAM 1515/53	PEM 1519/72	PEM 1519/60	PEM 1516/97	PEM 1519/09	UCT†	ELM 477	SAM 36728	ELM 524	PEM 1519/16	PEM 1516/90	SAM 36677
1	201	202	207	235	241	252	256*	262	269*	270	270	2734	278	278	283	289	289	292	292	293	295	301	322	323
2	36,3	29,2	28,5	31,9	33,2	35,7	30,9	40,1	34,6	38,1	37,4	36,6	41,4	36,3	36,7	39,4	37,0	38,0	38,7	40,3	32,9	39,5	35,4	40,2
3	41,8	48,0	48,3	46,8	46,1	48,4	53,5	46,2	45,7	44,4	39,6	45,4	—	48,2	42,8	43,9	42,6	45,4	45,9	47,4	46,1	43,9	41,6	43,3
4	(36,3)	39,1	28,5	33,6	31,5	29,4	40,2	33,2	30,5	35,6	31,1	35,2	28,8	29,9	27,2	39,8	32,5	34,9	31,2	35,2	31,9	27,2	27,3	35,6
5	79,6	89,1	86,5	88,1	88,8	82,9	—	85,1	89,2	85,9	84,8	87,9	83,5	88,5	82,3	83,7	84,8	91,1	84,9	84,6	87,1	81,0	81,4	84,8
6	—	91,1	90,8	90,2	96,3	86,9	—	87,8	92,6	89,6	86,7	93,4	90,6	88,8	88,0	88,2	90,7	91,8	93,2	—	—	87,3	83,2	—
7	—	—	87,9	85,9	(93,4)	83,3	—	86,3	88,5	85,6	90,0	89,1	86,7	85,6	83,8	84,1	—	91,8	88,7	—	—	84,7	79,8	89,2
8	63,2	65,8	61,8	63,8	58,5	61,5	—	60,3	65,8	59,3	65,9	63,0	63,7	59,4	60,8	60,6	61,9	65,4	66,8	69,6	60,3	56,5	57,5	63,5
9	3,7	5,2	3,4	5,5	2,1	3,2	(3,9)	6,9	4,1	3,5	4,4	3,3	2,5	2,5	3,4	2,8	4,2	6,8	4,1	7,0	2,0	2,0	4,7	4,8
10	64,7	66,3	67,6	65,1	64,3	61,5	75,0	59,9	65,4	64,4	66,3	61,9	64,7	65,1	62,9	60,2	60,9	64,0	66,8	63,5	—	58,8	56,2	60,1
11	34,3	33,7	36,2	34,5	40,2	37,7	—	44,3	38,7	40,0	—	39,6	—	42,4	46,6	46,4	46,0	—	43,8	—	44,7	47,2	42,2	—
12	15,4	14,4	13,5	14,0	10,8	15,9	23,0	16,4	14,7	13,3	17,0	15,8	19,4	12,6	15,9	15,6	14,5	14,7	21,2	16,7	13,6	12,6	15,5	19,5
13	17,9	17,8	27,1	26,4	23,2	17,5	—	28,6	—	—	16,7+	—	19,1	33,8	26,9	32,2	—	31,5	30,1	30,7	26,7	26,2	30,7	23,5
14	14,4	16,8	25,1	26,4	21,6	18,7	—	32,4	—	—	13,0	—	16,5	32,7	27,6	32,2	—	31,5	33,9	30,7	35,3	28,6	30,7	24,1
15	32,3	29,7	31,4	28,9	29,9	28,6	30,9	26,7	29,0	28,5	24,4	27,8	26,3	29,5	26,9	23,9	26,3	28,0	27,7	29,4	25,8	27,2	27,6	27,2
16	44,3	46,0	47,3	52,8	48,1	53,2	—	51,9	50,2	52,2	54,8	51,6	54,7	55,4	55,1	56,7	52,9	50,0	56,2	53,2	54,2	58,1	55,3	55,1
17	—	—	80,2	82,1	87,1	78,2	—	81,3	—	81,5	84,1	88,3	83,8	85,3	81,3	87,2	—	—	—	84,6	—	—	80,7	82,7
18	—	—	9	12	9	12	—	10	9	9	10	11	8	11	9	9	8+	—	—	9	—	—	—	11
19	—	—	10	10	9	12	—	10	8	9	10	11	7	11	9	8	8+	—	—	10	—	—	10	10
20	—	—	25,1	21,7	24,5	21,0	—	21,4	(25,3)	22,2	23,0	(21,6)	24,8	20,7	22,3	22,5	20,8	—	—	22,2	—	—	18,9	21,1
21	—	—	11,1	11,9	12,9	13,1	—	13,0	15,6	(10,4)	11,9	11,4	15,1	14,7	(13,4)	14,2	—	—	—	14,7	—	—	12,1	15,8
22	—	—	28,1	34,9	32,4	32,9	—	30,5	30,9	(32,2)	30,3	30,0	31,3	31,3	31,4	32,9	—	—	—	34,1	—	—	—	28,2
23	—	—	28,1	33,2	31,1	31,3	—	30,9	30,5	(32,2)	28,1	32,6	28,4	29,5	32,2	32,5	—	—	—	34,1	—	—	28,6	29,4
24	31,8	36,6	34,3	34,9	30,7	38,5	43,0	34,4	34,9	33,0	38,9	35,2	32,4	33,8	35,3	29,1	35,3	37,7	36,0	—	(35,6)	32,2	34,2	34,4
25	0,0	1,5	6,8	7,7	10,4	0,0	—	11,5+	20,4	4,1	1,8	32,4	13,7+	19,4	11,7	41,5	43,3	19,2	20,9	16,0	21,4	20,6	34,5	27,6

*3 mm added for breakage; †15 mm added for breakage;
() denotes approximate measurement; UCT = Zoology Museum, University of Cape Town.

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