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LIST OF CONTENTS

	Page
BOONSTRA, L. D.	
Discard the names Theriodontia and Anomodontia: a new classification of the Therapsida (published September 1972)	315
BOONSTRA, L. D.	
The early therapsids (published December 1971)	17
HAIGH, E. H.	
Development of <i>Trachurus trachurus</i> (Carangidae), the South African maasbanker (published May 1972)	139
HAIGH, E. H.	
Larval development of three species of economically important South African fishes (published March 1972)	47
HENDEY, Q. B.	
The evolution and dispersal of the Monachinae (Mammalia: Pinnipedia) (published March 1972)	99
HENDEY, Q. B. & REPENNING, C. A.	
A Pliocene phocid from South Africa (published March 1972)	71
HENDEY, Q. B.	
A Pliocene ursid from South Africa (published March 1972)	115
HOOIJER, D. A.	
A Late Pliocene rhinoceros from Langebaanweg, Cape Province (published August 1972)	151
McKENZIE, K. G.	
A new species of <i>Paradoxostoma</i> (Crustacea, Ostracoda) from South Africa (published May 1972)	133
MAIER, W.	
Two new skulls of <i>Parapapio antiquus</i> from Taung and a suggested phylogenetic arrangement of the genus <i>Parapapio</i> (published December 1971)	1
ROELEVELD, M. A.	
A review of the Sepiidae (Cephalopoda) of southern Africa (published September 1972)	193

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TWO NEW SKULLS OF *PARAPAPIO ANTIQUUS*
FROM TAUNG AND A SUGGESTED PHYLOGENETIC
ARRANGEMENT OF THE GENUS *PARAPAPIO*

By

WOLFGANG MAIER

Cape Town Kaapstad

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1971

TWO NEW SKULLS OF *PARAPAPIO ANTIQUUS* FROM TAUNG
AND A SUGGESTED PHYLOGENETIC ARRANGEMENT
OF THE GENUS *PARAPAPIO*

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(With 1 plate, 4 figures, 3 tables)

[*Ms. accepted 30 July 1971*]

CONTENTS

	PAGE
Introduction	1
Description	2
Discussion	4
Classification of the genus <i>Parapapio</i>	11
Summary	14
Acknowledgements	14
References	14

INTRODUCTION

The travertine caves near Taung, Cape Province, are the type locality of *Australopithecus africanus*. In addition, some Pleistocene cercopithecoids and a considerable number of other fossil animals were found there. The fossil material, however, was not collected systematically and is not as well known as that of the australopithecine-bearing dolomite caves of the Transvaal. Peabody (1954) has compiled a faunal list for the Taung sites.

The fossil cercopithecoids from Taung were first mentioned by Houghton (1925), who proposed the name *Papio antiquus* for the material available at that time. Gear (1926), describing these and additional new specimens in more detail, distinguished another species, *Papio izodi*. Broom (1940) included both species in the genus *Parapapio*, which had been created by Jones (1937) for a primitive baboon-like form from Sterkfontein. Only Freedman (1957) recognized the clearcut differences between both taxa; he considered that only the first species belonged to *Parapapio*, *P. antiquus* Houghton, 1925, while the latter was a primitive true baboon, *Papio izodi* Gear, 1926. In 1957 Freedman also described the colobid *Cercopithecoides williamsi* and the small *Parapapio jonesi* from Taung, and in 1961 the same author described *Papio wellsi*, another true baboon found at this site.

Unfortunately most of the Taung caves were mined out by the early fifties and consequently have yielded no further fossil material. In 1952, however, Mr. James Kitching of the Bernard Price Institute for Palaeontological Research, Johannesburg, was able to rescue the last few primate specimens from the Taung dumps. The present author was kindly allowed to prepare this material, which appeared to consist of two fairly complete female skulls

of *Parapapio antiquus*. These two new specimens were embedded in a fine-grained pinkish breccia, which seems to be more calcified in M.3079 than in M.3078, the hardness of the former approximately corresponding to that of the pink cercopithecoid breccia (Brain's Upper Phase I) of the Makapansgat Lime-works. Both specimens are housed at the Bernard Price Institute for Palaeontological Research, Johannesburg.

DESCRIPTION

The measurements of the two new specimens are incorporated in Tables 1 and 2, which at the same time provide comparative data. Unless otherwise stated, the technique of measuring is in accordance with the definitions of Freedman (1957), and most of the comparative data have been extracted from the publications of the same author.

(1) Specimen M.3078 (Pl. 1)

This is a fairly complete and undistorted cranium with the third molars only newly erupted and not having been in occlusion. The muzzle is complete as is the left half of the braincase; the right half of both the upper face and the braincase together with most of the cranial base have been eroded away. The incisors, the canines and the right P³ were lost before fossilization, but their alveoli have been preserved. The remaining teeth are in relatively good condition. The morphology and size of both skull and teeth indicate that this was a young female of *Parapapio antiquus*.

The proportions of this cranium are similar to those of Tvl. 639 (Transvaal Museum, Pretoria; Freedman 1957: Fig. 48), the muzzle being short in relation to the braincase. The braincase itself is fairly flat in the frontal region, but drops relatively steeply in the parietal region. The nuchal plane is therefore situated deeply in the backward prolongation of the alveolar margins. As far as can be seen, the mastoid processes must have been well developed, whereas nuchal crests are absent. The nuchal line runs backward as a straight continuation of the jugal arch, the inion therefore being in a lowered position. The temporal crest shows the typical course met with in other specimens of *Parapapio antiquus*: it is well pronounced in its frontal part, exhibiting only a slight notch behind the orbit; hence, it overhangs the postorbital constriction of the lateral wall of the braincase (temporal fossa), resulting in a wide post-orbital breadth when seen in dorsal view. On the parietal bone the faint temporal line very gradually converges toward the midline, but approaches to within only about 15 mm of it.

The anterior root of the jugal arch starts above the distal half of the second molar. The zygomatic part of the jugal arch is comparatively strong and broad, showing clearly the area for the insertion of the masseter muscle. The temporal part of the arch is narrower, but exhibits a strongly developed tubercle fronto-lateral to the articular fossa. This fossa is remarkably deep and distinctly concave transversely. Posteriorly it is bounded by a very small postglenoid process.

Medially, the glabellar region is very undeveloped, the nasal line running as a nearly straight continuation of the frontal outline. Laterally there exist shallow excavations between the supraorbital arcus and the cranial vault. The arcus are barely prominent, but possess distinct supraorbital notches. The left orbit does not seem to be disproportionately large and is fairly well rounded. The interorbital and nasal region show a straight contour, which is a typical feature of *Parapapio antiquus* as compared with female skulls of the other species of this genus.

The muzzle appears to be quite narrow and slender in this specimen, because the maxillary crests are not strongly developed. Hence, although the muzzle dorsum drops steeply towards the sides, the canine fossae are comparatively well excavated. There are 4 to 5 infraorbital foramina on each side, opening separately just at the posterior end of the maxillary crests. The premaxilla protrudes considerably, indicating a well-developed incisor row; the lateral wings of the premaxilla do not reach the nasal bone. The nasal aperture shows a typical ovoid outline.

The maximum breadth of the muzzle and of the ovoid tooth arch lies across the anterior half of the second molars. The palate seems to be short, the posterior margin lying between the last molars. The greater palatine foramina are slit-like and they are situated between the second and the third molars. The incisive fossa opens between the canines. The angle between the pharyngeal face of the base of the braincase and the palate is 135° ; in two new female skulls of *Parapapio broomi* (M.3056 and M.3070) it is 127° and 122° .

Due to the immaturity of the new specimen, the alveolar processes are quite undeveloped, resulting in a comparatively low facial height.

The alveoli of the (missing) medial incisors are about 5,5 mm in breadth, but those of the lateral incisors only about 4 mm, thus indicating the specialized broadening of the former ones. The alveoli of the canines measure about 6 by 7 mm; in the male specimen T.22 (Transvaal Museum, Pretoria) of *Parapapio antiquus* these dimensions are 9 by 9 mm, proving that the present skull is that of a female. Both premolars are well developed and comparatively elongated. In the last two upper molars, the distal pair of cusps, and particularly the disto-buccal cusps are conspicuously reduced in size.

(2) Specimen M.3079

This specimen is not as complete as the first one. It comprises only a fairly well-preserved facial skeleton and the frontal part of the calvaria. The few remaining teeth are very worn and although damaged to some degree, show that it was a very old animal. The front teeth were lost before fossilization, but their alveoli are still visible. The canine alveoli are comparatively small, thus indicating that the present cranial fragment is that of a female. The skeletal parts show some minor cracking, probably causing some slight distortion.

The muzzle of this specimen appears to be altogether heavier and stouter than that of the first specimen. The maxillary crests are more prominent, the

muzzle dorsum consequently being broader and more flattened, as is typical for the species (Freedman 1957). Most breadth measurements of this fragmentary cranium are distinctly greater than in M.3078, whereas the length measurements are very similar. The degree of excavation of the canine fossae is nearly identical in both specimens. In the present cranium the orbits seem to be more flattened and the supra-orbital arcus more developed, resulting in a more conspicuous ophryonic groove. These features are shared with specimen Tvl. 639, which also represents an old female. The temporal crests are very strong in M.3079, resulting in a very great intertemporal breadth. The zygomatic bone of the left side is partly damaged, but appears to have been very strong. The anterior root of the jugal arch, as in Tvl. 639, is also situated above the anterior part of the third molar; the tooth rows of these two old specimens were thus shifted relatively more forward than in the younger specimen. The same age differences are to be observed in the height of the face, the older specimens being distinctly higher. In living primates this downward and forward growth of the alveolar processes is well known to occur during adulthood (Scott 1967).

There is only one premolar left in the present cranium, and this has been partly damaged; it is fairly similar to those of M.3078 and T. 17 (Transvaal Museum, Pretoria). The existing first molar is very worn and extruded and thus comparatively long. However, M² and M³ are also very long, and they belong to the top of the known size range for this species. As far as can be seen in both of these posterior molars, there is considerable reduction in the breadth of the distal cusps, which is typical for *Parapapio antiquus*.

DISCUSSION

The two new skulls, described above, add in many respects to our knowledge of the fossil species *Parapapio antiquus*, which so far has been found only at Taung. These two specimens confirm that the peculiar shape of the muzzle, with its straight nasal and its well-developed maxillary crests and canine fossae, is very characteristic for this taxon. As the material comprises a young adult and a very old female skull, we can appreciate some of the morphological differences due to age. In the young specimen the muzzle is more slender and the face is narrower and less high than is the case in old specimens (Figs 1 and 2). Skull M.3078 exhibits, for the first time, morphological details of the articular and infratemporal fossae of *P. antiquus*.

The lateral and oblique position of the temporal crests in *P. antiquus* indicates a backward-orientation of the temporal muscle, which may be correlated with some specialization of the masticatory function, i.e. a stressing of more anterior parts of the dentition. Interestingly, some of the tooth characters of *P. antiquus* seem to support this kind of functional interpretation (see below). This specific course of the temporal crests is already met with in the comparatively young animal M.3078, whereas the typical flattening of the muzzle dorsum is not yet evident.

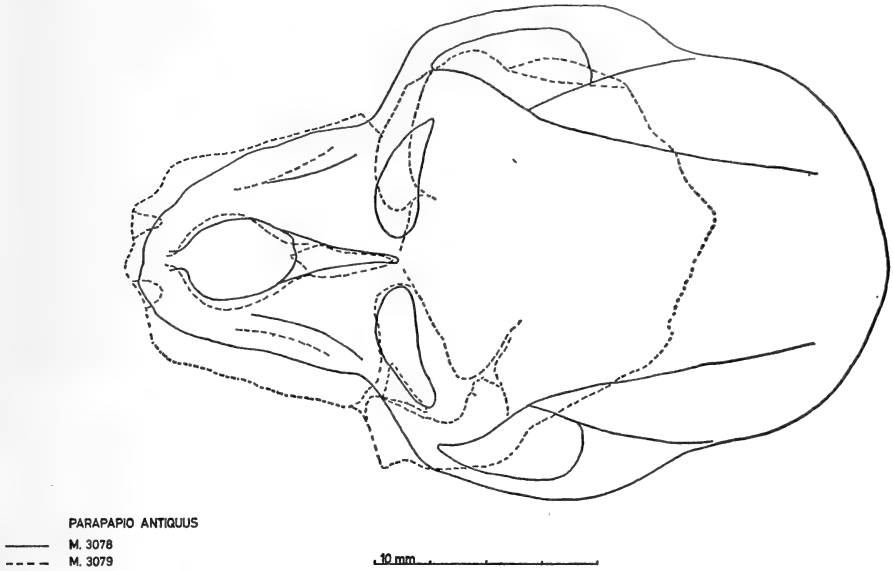


FIG. 1. Pantographs of the young female specimen M.3078 and of the old female M.3079 are superimposed to show differences due to age. Both are shown in norma dorsalis, being orientated on the occlusal plane.

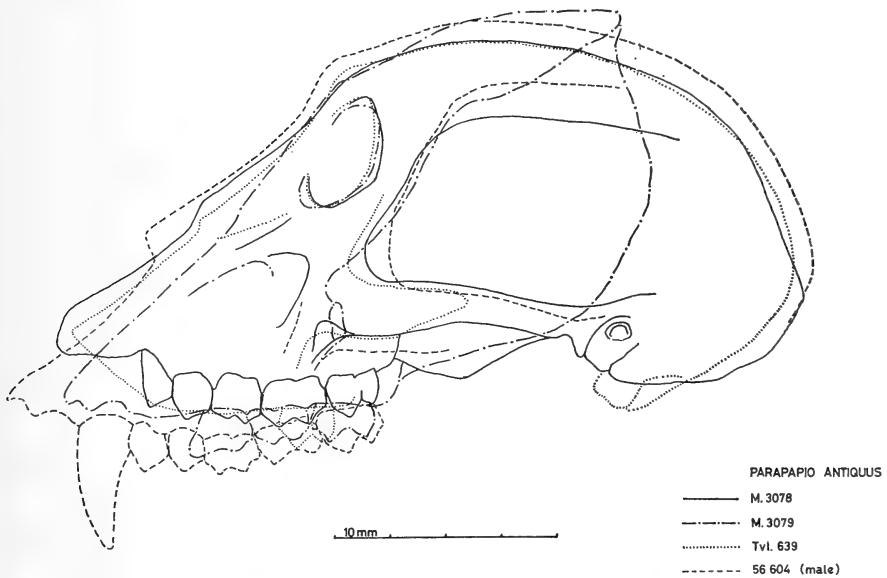


FIG. 2. Pantographs of four of the most complete skulls of *Parapapio antiquus* are superimposed in norma lateralis. Specimens Tvl. 639 and 56 604 are reversed. The picture demonstrates an increasing degree of tooth row declination and facial height with increasing age; it shows also the small degree of sexual dimorphism in the known specimens.

TABLE 1. Cranial measurements of *Parapapio antiquus* and *P. broomi*.

	<i>Parapapio antiquus</i>						<i>Parapapio broomi</i> *			
	females			males			females**		males	
	M.3078	M.3079	T.17	T.11	Tvl.639	56 694*	n	X	n	X
Maximum length	135	—	—	(141)	(140)	—	3	139	1	(150)
Basal length	—	—	—	—	(100)	—	1	100	—	—
Bizygomatic breadth	(88)	—	—	—	—	—	1	(88)	1	96
Basion - Bregma	(56)	—	—	—	62	—	1	59	—	—
Basion - Glabella	(70)	—	—	—	73	—	2	72	—	—
Minimum interfrontal	(53)	(61)	—	53	54	52	5	55	1	57
Maximum temporal	(70)	—	—	—	72	—	2	71	1	73
Inion - Glabella	92	—	—	(90)	91	—	3	91	1	96
Muzzle height ant. P ³	17	16	18	—	19	15	5	17	2	23
Muzzle breadth ant. M ³	45	48	47	—	—	46	4	47	1	48
Muzzle breadth ant. P ³	34	39	—	—	37	35	4	36	1	36
Muzzle breadth dors. M ²	30	37	35	30	35	—	4	33	1	38
Nasion - Prosthion	66	(66)	—	(68)	(71)	68	5	68	2	79
Staphylion - Prosthion	54	54	(62)	—	(64)	—	4	59	1	66
Nasion - Rhinion	(30)	(30)	—	33	32	—	4	31	1	41
Interorbital breadth	8	(10)	—	7	9	9	5	9	1	9
External orbital breadth	(69)	(76)	—	68	73	70	5	71	2	77
Orbital height	22	20	—	22	23	22	5	22	2	24
Orbital breadth	24	26	—	26	26	25	5	25	2	27
Nasal aperture breadth	15	16	17	16	17	19	6	17	1	17
Nasal aperture height	27	(26)	25	27	29	—	5	27	2	27
Vertical height of face (Alveolar line - torus s.)	51	53	—	—	62	—	3	55	2	62
Alveolar l. - infraorb. margin	30	34	34	—	36	—	4	34	2	35

* After Freedman 1957.

** Including two new skulls from Makapansgat.

Although the morphology of the female skull of *P. antiquus* is fairly well known, metrical data are still poor, and the present knowledge of the male skull is very unsatisfactory (Table 1). In overall size, female skulls of *Parapapio antiquus* are very similar to those of *P. broomi*, whereas male skulls of the latter species are considerably larger than those of the former, suggesting a lesser degree of sexual dimorphism for *P. antiquus* (Maier 1971). Figure 2 shows a craniogram of the most complete male skull known so far (University of California, Museum of Paleontology Specimen No. 56 604; unfortunately still partly embedded; see Figure 4 in Freedman 1965); the muzzle is only slightly longer and more declined than in the super-imposed female craniogram.

The relatively large numbers of teeth permit a statistical analysis to be made. This is, however, true only for premolars and molars, the front teeth still being virtually unknown. Table 2 provides comparative data for the other species of *Parapapio*. Although the length of the tooth row is very similar in *P. antiquus* and *P. broomi*, there seem to be some discrepancies in the dimensions of individual teeth. P^4-M^2 are distinctly longer in *P. antiquus*, whereas

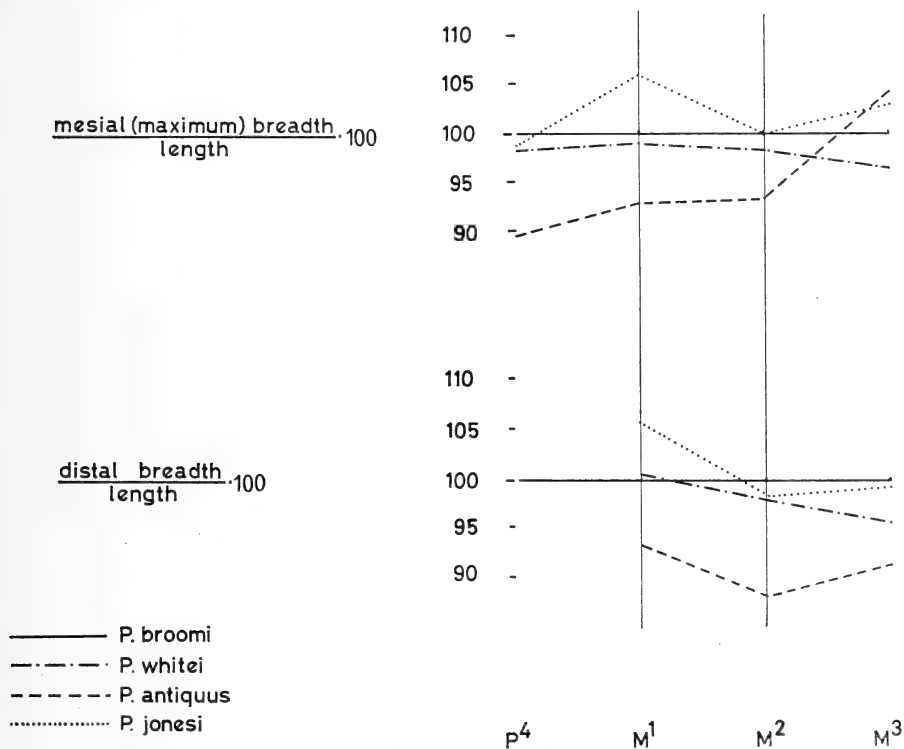


FIG. 3. Breadth/length indices of the last upper premolar and the upper molars in the four species of the genus *Parapapio*. The values for *P. broomi* are considered to be 100; those of the other species are related to *P. broomi*. The diagrams demonstrate the aberrant tooth proportions of *P. antiquus*. For exact data see Table 2.

TABLE 2. Measurements in mm of upper teeth in females of various *Parapapio* species¹

	<i>Parapapio antiquus</i>										<i>P. broomi</i> *			<i>P. whitel</i> *			<i>P. jonesi</i> *		
	M.3078	M.3079	T.17	T.16	T.25*	56 608*	56 694*	n	X	B/L 100	n	X	B/L 100	n	X	B/L 100	n	X	B/L 100
I ¹	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
i :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
b :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
h :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
101,5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
I ²	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
i :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
b :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
h :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
124,4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
i :	—	—	(6,2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
b :	—	—	(6,3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
h :	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
103,4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P ³	9,8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
b :	7,4	—	7,9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
112,1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P ⁴	6,9	(6,8)	7,1	—	7,7	6,8	6,7	6	7,0	(117,7)	8,4	6,4	6,4	6	6,9	6,9	6	6,0	(n=7)
b :	8,3	(8,0)	(8,0)	—	—	8,2	—	4	(8,1)	117,7	8,4	8,4	131,5	6	8,7	129,1	5	7,7	129,8
M ¹	10,0	11,0	(9,8)	10,9	10,3	9,2	(8,9)	7	10,0	(n=5)	9,5	9,6	(n=15)	6	10,7	(n=5)	6	8,7	(n=6)
mb :	8,5	(9,2)	(9,5)	10,6	—	9,1	—	5	9,4	92,3	12	9,5	99,3	5	10,5	98,5	5	8,8	105,1
db :	8,0	(9,0)	(8,8)	10,0	—	7,7	—	6	8,7	85,4	10	8,8	91,2	5	9,8	91,7	5	8,0	96,5
M ²	11,5	12,1	(11,7)	11,5	11,6	11,0	10,9	7	11,5	(n=6)	11,1	11,1	(n=22)	6	12,7	(n=7)	4	10,3	(n=5)
mb :	10,5	(10,4)	—	11,5	11,0	10,5	11,3	6	10,9	95,2	12	11,1	101,7	6	12,4	100,3	2	10,5	101,6
db :	9,1	9,5	—	9,8	9,2	9,1	9,6	6	9,4	82,1	13	10,1	93,1	6	11,4	91,7	2	8,9	91,4
M ³	10,3	10,9	10,4	11,3	10,4	9,6	9,8	7	10,4	(n=7)	11,0	11,0	(n=21)	2	13,3	(n=2)	3	9,6	(n=8)
mb :	10,2	(10,7)	11,1	11,5	10,4	10,4	10,9	7	10,7	103,6	11	10,7	99,3	1	12,8	96,0	2	10,5	102,7
db :	7,6	7,8	8,3	9,5	7,2	7,2	7,7	7	7,9	76,0	10	8,8	82,8	1	11,0	79,3	3	7,9	82,1
P ⁴ -M ³	37,1	(37,0)	37,5	—	38,8	35,9	35,8	6	37,0	—	7	36,3	—	2	39,6	—	3	33,3	—
C — M ³	(49)	(48)	49,6	—	—	—	—	3	(48,9)	—	3	48,6	—	1	51,7	—	1	43,1	—

¹ Indices comprise males and females including specimens from Maier 1971.

* Figures from Freedman 1957.

n = number of specimens.

X = average value.

B = tooth breadth.

L = tooth length.

TABLE 3. Statistical analysis of the tooth lengths of P⁴, M¹, M² and M³ in the females of *Parapapio antiquus* and *P. broomi*

	Standard deviation s ² *		Student's t-Test for the sample means*	Degrees of freedom	Significance probabilities*	
	<i>Parapapio antiquus</i>	<i>P. broomi</i>	t	df	t.99	
P ⁴	0,136	0,070	3,9	18	2,878	0,01
M ¹	0,743	0,366	1,4	19	2,861	0,2-0,1
M ²	0,169	0,252	1,7	22	2,819	0,1
M ³	0,345	0,226	3,0	17	2,898	0,01

* After Simpson, Roe & Lewontin 1960.

M³ seems to be reduced. The Student t-test proved these differences to be significant for P⁴ and M³ (Table 3).

The breadths of the premolars and molars being nearly identical in both taxa, the breadth/length index could be expected to express the different degrees of elongation (or reduction). The index also makes possible a comparison with the other species, *P. jonesi* being absolutely smaller and *P. whitei* larger than the previous two. Figure 3 shows the relations diagrammatically, the indices of *P. broomi* being expressed as 100. *P. jonesi* exhibits comparatively high values, especially for M¹ and M³, this possibly being a primitive feature. *P. whitei* is very similar to *P. broomi*, showing a slight tendency to elongation, especially in M³. Again, *P. antiquus* appears to be very aberrant with its gradual increase of the index in mesio-distal direction. The indices for the distal breadths of the molars show that *P. antiquus* possesses the highest degree of reduction of the distal cusps in all molars. Absolutely this reduction is most pronounced in M³, whereas the relative value is lowest for M².

Judging from tooth size and morphology, *P. jonesi* could tentatively be regarded as the most primitive of the fossil cercopithecids of South Africa, possibly being closely related to their common ancestor. New finds of male skulls, however, show clearly that this taxon was well advanced in some respects: its high degree of sexual dimorphism would exclude it from being a direct for-runner of *P. antiquus* and its well-pronounced maxillary crests and different cranial proportions from being a direct ancestor of both *P. broomi* and *P. whitei* (Maier 1971).

On its teeth alone, however, *P. jonesi* provides a model for understanding the evolutionary alterations within the genus *Parapapio*. Compared with *P. jonesi*, *P. antiquus* shows P⁴ and M¹ very much elongated; M² being still longer, while M³ is very similar in both taxa—apart from the conspicuous reduction of the distal cusps in *P. antiquus*, which cannot be understood simply as a consequence of small size.

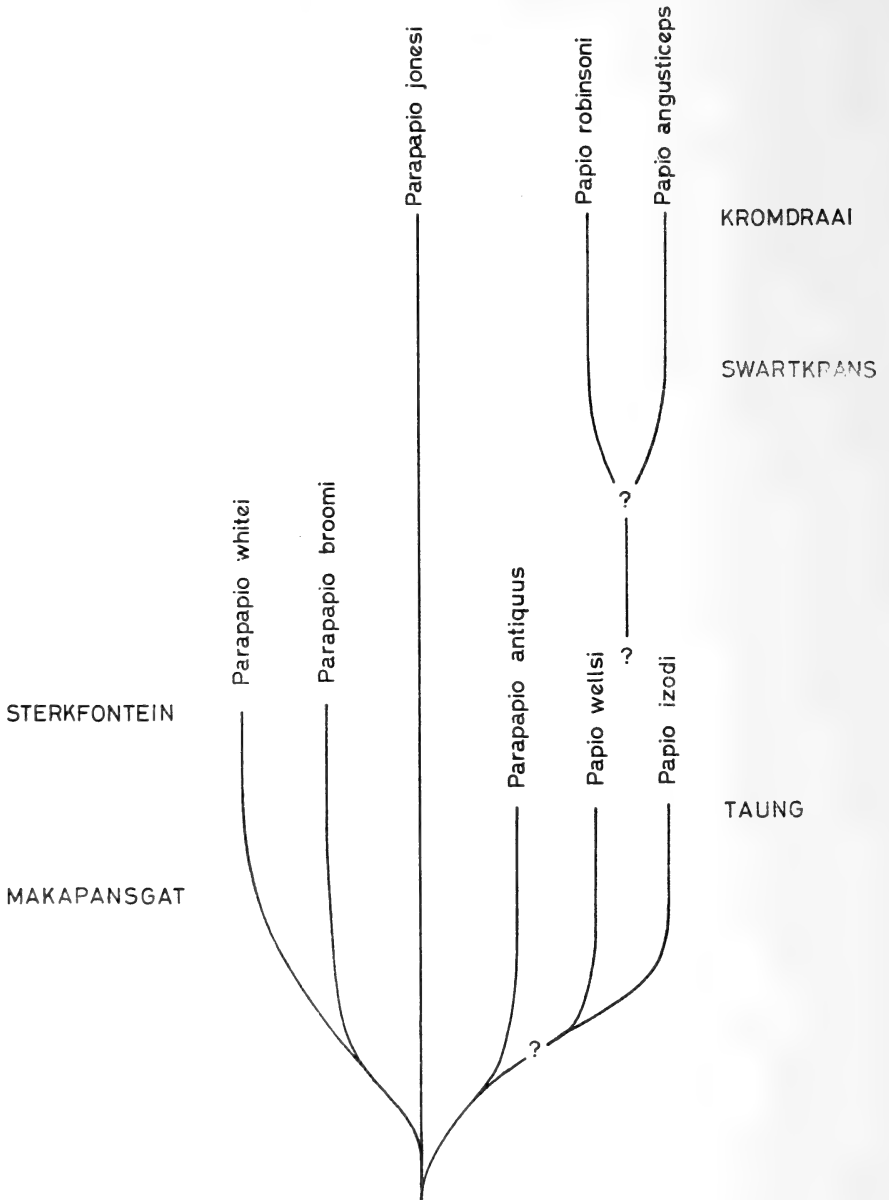


FIG. 4. Phylogenetic diagram of the genus *Parapapio* and the hypothetical origin of the genus *Papio*. The diagram is based on the South African evidence only. *P. jonesi* occurs at all the mentioned sites; the forms on the left side occur only at Sterkfontein and Makapansgat, those on the right only at Taung, Swartkrans and Kromdraai. Less important sites have been disregarded.

P. broomi and *P. whitei* are very similar in tooth indices, underlining the close coincidences in their cranial morphology. Both these taxa are similar to *P. jonesi* in the proportions of P^4 and M^2 , whereas M^1 and M^3 seem to be distinctly elongated. Summarizing, one can state that *P. antiquus* shows a progressive elongation of the ' P^4/M^2 -field' of the tooth row, whereas in both *P. broomi* and *P. whitei* it is mainly the third molar which is increased. In some regards, these conclusions need to be confirmed by additional observations.

These peculiarities of the dentition could possibly be interpreted functionally: in *P. antiquus*, the centre of gravity of the chewing activity is shifted forward as compared with that of the related species. This would necessitate a more oblique direction of the temporal muscle, and would, in turn, explain not only the morphology of the temporal crests but possibly even the low position of the occipital region of the braincase as observed in *P. antiquus*.

CLASSIFICATION OF THE GENUS *Parapapio*

Present mammalian systems are based mainly on the methods of comparative morphology and this is especially true for fossil forms. The classification of fossil cercopithecoids is fraught with many difficulties, and even that of the extant taxa has not yet been satisfactorily established. External and soft-part characters have proven most valuable for systematic purposes within this superfamily (Pocock 1925), the teeth and the skeletons being very uniform within the whole group (Remane 1960; Schultz 1970). As far as possible, ecological and functional aspects should be considered also and, in the case of fossils, it is important that there be an appreciation of the time factor as well. The present state of knowledge as to the classification of the Cercopithecoidea was discussed recently by the present author (Maier 1970).

All attempts to obtain absolute data on the ages of the South African australopithecine caves have so far been unsuccessful (Tobias & Hughes 1969). However, recent finds have resulted in surprising changes of the chronology of the North and East African Pliocene and Pleistocene fossil sites. Olduvai Bed I has been dated at about 1,8 m.y., while the deposits at Omo, Kairo, Kanapoi, Koobi Fora, Chemeron and Laetolil might reach back some 3 to 4 m.y. (Maglio 1970). These sites with their varied fossil faunas provide a good basis for comparison with the richly fossil-bearing cavern breccias in southern Africa, but not much work has so far been done in this field. Hendey (1970) has pointed out the major difficulties in comparing South African fossil faunas at the present stage of knowledge.

Whereas Kurtén (1960, 1968) suggested a Middle Pleistocene age for the South African ape-man cave deposits, we must now contemplate a Lower Pleistocene age for them. Ewer (1963: 343) reviewed the then available evidence and concluded that 'Kromdraai and Swartkrans may correspond to the gap between [Olduvai] I and II, while Makapan and Sterkfontein belong to the period covered by the older deposits of Olduvai I and Omo'. This tentative

correlation was repeated by the same author in 1967. According to Cooke (pers. comm.) the pigs and elephants from Makapansgat compare well with forms from Kanapoi and Lower Omo beds, indicating an absolute age of some 2,5–3,5 m.y. for that site. Sterkfontein is estimated by Cooke to be about 2,5 m.y. and Swartkrans about 2,0 m.y. As in East Africa, the Pleistocene sites of South Africa will, most probably, have to be dated further back than was previously thought.

This evidence, so far based mainly on Suidae, Elephantidae and Carnivora, seems to be supported by the primate evidence. (Unfortunately, the rich East African cercopithecoid material has not yet been described comprehensively, but Mrs. Meave Leakey of the Kenya National Museums will shortly publish a monograph.) Arambourg (1947) recorded *Dinopithecus brumpti* from the Omo deposits, Butzer (1971) added *Colobus* sp., *Cercopithecus* sp., *Parapapio* sp., *Papio* sp. and *Simopithecus* sp. from this site. R. E. F. Leakey (1969) described *Papio baringensis* from the Chemeron Beds which shows much similarity with *Papio robinsoni*, and in 1970 the same author recorded from Koobi Fora (\pm 2,5 m.y.) *Cercopithecus* sp., *Papio* sp. and *Simopithecus* sp. According to L. S. B. Leakey (1965), large forms of *Papio* and *Simopithecus* are known from Olduvai Beds I–IV. As far as I could see during a recent visit to the Kenya National Museums, Nairobi, the genus *Parapapio* occurs as well, both at Olduvai and Koobi Fora, the material most probably belonging to the species *P. jonesi*. A mandible from Kanapoi (\pm 4 m.y.) has recently been referred to this species as well (Patterson 1968). A few small teeth from Lothagam would fit approximately some specimens from the 'grey breccia' of Makapansgat, being referred also to *P. jonesi*. Most of these better known sites seem to have three cercopithecoid forms side by side: a small *Parapapio*, a large *Papio* (*Dinopithecus* and *Gorgopithecus* possibly being only synonyms) and a very large *Simopithecus*.

The South African cave deposits show a different arrangement, which may, however, be due partly to geographical separation and a different mode of deposition (Ewer 1967). The older sites at Makapansgat and Sterkfontein have so far yielded only various types of *Parapapio* and a comparatively small and primitive *Simopithecus* (Maier, in press), but no true baboon of the genus *Papio* whatsoever (Freedman 1957). Very small and primitive forms of baboons appear only at Taung, while, besides *Parapapio* and *Simopithecus*, *Papio* is abundantly represented in the younger sites of Swartkrans and Kromdraai. The fossil colobids of both East and South Africa are too different for useful comparisons to be made.

Pending more detailed information about the cercopithecoid material from the Lower Pleistocene of East Africa, the preliminary evidence seems to suggest rough contemporaneity of the more important South African faunas.

The faunal comparison of the South African sites is complicated by their geographical distance and by evident palaeo-ecological differences in the surroundings of the ancient deposits (Ewer 1956a). Thus, at Makapansgat the environment was probably more varied and less dry (Ewer 1956b; Wells 1967),

whereas Taung 'was distinctly more desert-like than . . . the other deposits' (Ewer 1957: 139). Zoogeographically Makapansgat shows more affinities with central Africa than the other sites. Considering these difficulties, Ewer (1957: 141) concluded: 'The probable time sequence of the deposits is Sterkfontein and Makapansgat close together, with the former very probably being the earlier; then Swartkrans and lastly Kromdraai, while the Taung deposit is most probably closest in time to Sterkfontein and Makapan.' From the morphological evidence of the cercopithecoids, Freedman (1957) considered the Taung deposit to be the oldest, followed in order by Sterkfontein, Makapansgat, Swartkrans and Kromdraai. Wells (1967) and Cooke (1967) seem to assume that Taung is slightly younger, the latter author giving a sequence Makapansgat, Sterkfontein and Taung for his 'Sterkfontein Faunal Span' (see his Table I).

Recently Wells (1969) more clearly expressed his conviction that Makapansgat may be earlier than Sterkfontein, whereas Taung may be even closer to the Swartkrans-Kromdraai 'faunal span'. It seems to be very necessary that the newly prepared elephant material from Makapansgat be studied by experts who are well acquainted with the East African forms.

Freedman (1957: 248) stated that the more important South African fossil sites originate from 'a geologically short period just following the Plio-Pleistocene boundary', the time of depositing between the oldest (Taung) and the youngest (Kromdraai and Cooper's) breccias not being longer than about 250 000 years. As, according to Simpson (1944), the minimum time span for the evolution of a new species amounts to about 0.5 m.y., Freedman (1957: 244) concluded: 'Therefore . . . it seems quite obvious that the faunal changes between the sites could not be due to *in situ* evolution' and that 'it would therefore seem that the most obvious and probable cause of the faunal replacements was successive migrations into and out of the areas as a result of local and/or distant environmental changes'. The recently suggested evidence of the very great age and long duration of these deposits would yield, however, a satisfactory temporal frame to explain the evolution and radiation of the numerous Pleistocene Cercopithecoidea in South Africa, without entirely discarding the possibility of some faunal shifting.

The existing classification of the genus *Parapapio* was elaborated in the studies of Broom (1940) and Freedman (1957). Based mainly on the occurrence of different-sized molars, these authors established four species: the small-sized and, as it appears now, widespread *Parapapio jonesi*, two medium-sized forms, *P. antiquus* and *P. broomi*, which 'are remarkably similar in tooth size but differ very considerably in skull shape' (Freedman 1957: 158), and finally the large-sized *P. whitei*.

The small *Parapapio jonesi* could easily represent the generalized common ancestor of the Papionini *sensu stricto*. Its small teeth are unspecialized as compared with progressive features in the other species of *Parapapio*. Occurring in all of the australopithecine caves of South Africa, this taxon has now been recorded from various places in East Africa as well, probably covering some

2-3 m.y. of the Pleistocene fossil record. New finds have shown, however, that the male skull is quite advanced, although retaining its primitive teeth (Maier 1971).

In cranial shape, tooth specialization and the small degree of sexual dimorphism, *Parapapio antiquus* seems to differ more from *P. jonesi* than does *P. broomi*, and might thus be an earlier offshoot, possibly being somehow adapted to the drier ecological conditions prevailing at Taung. Such an environment could also have stimulated the evolution of the small true baboons *Papio wellsi* and *P. izodi*: '*Parapapio antiquus* is very similar in size and dental morphology to *Papio izodi*, and these two species may represent a morphological stage not far from the point at which the genera *Parapapio* and *Papio* started diverging from a common stem' (Freedman 1957: 245).

The nature of the molar specializations and the very similarly elongated male crania indicate a monophyly of both *Parapapio broomi* and *P. whitei*. The teeth of the latter species seem to be relatively larger than in the similarly sized *P. broomi*. Further material may close the existing size gap, but since both forms occur in the same blocks of the 'Upper Phase I' breccia of Makapansgat, they cannot form a chronocline. As we do not know their postcranial skeleton, it is not possible at the moment to assign different ecological niches to these apparently sympatric species. In Figure 4 an attempt is made to plot the evidence in the form of a phylogenetic diagram.

SUMMARY

Two new female skulls of the fossil cercopithecoid *Parapapio antiquus* from Taung, Cape Province, South Africa, are described and discussed. The teeth of this species especially show some significant differences from the other three species of *Parapapio*. A phylogenetic arrangement of the genus is suggested.

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Parapapio antiquus M.3078 (female) lateral and basal view. Note the straight contour of the muzzle dorsum, the low position of the occiput and the reduction of the third molar. Scale unit 10 mm.

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L. D. BOONSTRA

South African Museum, Cape Town

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CONTENTS

	PAGE
Introduction	17
Diversity	18
Structural variations	
Temporal fenestra	19
Position of the quadrate	23
Insertion of the temporal muscle	24
Reflected lamina of the angular	25
Marginal teeth	25
Palate	26
The locomotor apparatus	26
Diverse structures	29
Morphological series	
Series I	31
Series II	33
Series III	35
Series IV	36
Summary of morphological series	40
Early therapsid history	41
Subsequent history	41
References	44

INTRODUCTION

As early therapsids I consider those forms that have been recovered from Zones I and II of the Russian succession and from the *Tapinocephalus* zone of the Beaufort beds of the Karroo System. They thus range from the top of the Lower Permian to the end of the Middle Permian.

In this paper I am stressing, firstly, the great diversity of forms with which we are so suddenly confronted in one of the many explosive faunal developments that have so repeatedly occurred during the long history of animal life and apparently gainsaying the dictum *natura non facit saltum*.

Secondly, I shall attempt to arrange this assemblage into a number of morphological series, before attempting a phylogenetic arrangement, because I feel that this is a safer procedure, bearing in mind that this fauna with which we are confronted as a *fait accompli* consists of contemporaries and geologically speaking of the same age with no one the ancestor of any other.

Thirdly, I shall consider the derivation of these therapsids from the antecedent fauna of pelycosaur with which in similar fashion we are confronted in Carboniferous-Permian times.

DIVERSITY

Of the pre-Upper Permian assemblage of therapsids we know at least 70 well-established genera which have on taxonomic criteria been brigaded into 19 families. This explosive radiation is much greater than the earlier Carboniferous—earlier Permian radiation of the pelycosaurs with its 8 families.

In the early therapsids the size variation is as much as that between a rat and a hippopotamus, with weights from about 500 g to two tons. In shape they vary from light and slender to massive and plump. Some are agile, others ponderous. There are long as well as short tailed forms, long snouted and extremely short snouted species lived side by side; locomotion varied from slinking, walking to running, with the body slung between the spread-eagled limbs or carried fairly high on more upright supports. A few were insectivorous, some carrion eaters, others predaceous carnivores and many herbivores; some feeding on soft marsh plants, whereas others, roaming on to higher ground, subsisted on more fibrous shrubs. In one group the teeth were largely replaced by horny sheaths analogous to those of tortoises.

This diverse assemblage has been classified into the following 19 families:

1. Eotitanosuchidae
2. Brithopidae
3. Anteosauridae
4. Titanosuchidae
5. Tapinocephalidae
6. Styracocephalidae
7. Estemmenosuchidae
8. Phthinosuchidae
9. Hipposauridae
10. Galesuchidae
11. Otsheriidae
12. Venyukoviidae
13. Dromasauridae
14. Endothiodontidae
15. Dicynodontidae
16. Alopecodontidae
17. Pristerognathidae
18. Lycosuchidae
19. Scaloposauridae

The various authors who have established these 19 discrete families have done so on the basis of determined differences of a structural nature.

These differences, although often considerable, are also limited, and it is because of these limitations accompanied by certain basic similarities and trends that these families have been brigaded into one order—the Therapsida.

A profitable evaluative discussion can best be started by considering firstly those points of basic similarity and then the extent of the differences and variations.

Structural features common to all the known early therapsids are:

1. A single temporal fenestra lying below the posterior process of the post-orbital, but the participation of this process and of the various other bones forming the temporal border varies.
2. The pterygoids tend to meet in the middle line behind the interpterygoid vacuity, which is thereby variously reduced, and applied to the basicranium with consequent loss of the primitive freely movable joint and the development of a longitudinal basicranial girder.
3. The jaw articulation never lies in a plane posterior to that of the occipital condyle and the anteriorly directed slope of the occiput is reduced, often becoming nearly vertical or even sloping backwards.
4. There is always a reflected lamina of the angular.
5. The septomaxilla, with a foramen, has a more or less well-developed lateral facial exposure but small in *Otsheria* and brithopids and phthinosuchids and not exposed laterally in dicynodonts.
6. There is no supratemporal and the anterior coronoid is always lost and sometimes both are absent.
7. The lacrimal never reaches the nostril.
8. The maxilla is always deep.
9. The squamosal flares out laterally and posteriorly to various degrees.
10. The quadrate ramus of the pterygoid reaches the quadrate.
11. The vertebrae are amphicoelous and there are no dorsal intercentra.
12. The girdles and limbs are adapted for an early stage of a quadrupedal gait. The main adaptations are: loss of the supraglenoid buttress and foramen, loss of one central in the tarsus and one distal, number of phalanges reduced to varying degree, the glenoid is reduced in length and the humerus untwisted to varying degrees, the iliac blade is heightened, and an anterior process developed to varying degrees, the femur loses the Y system of ridges and develops a greater trochanter.

STRUCTURAL VARIATIONS

TEMPORAL FENESTRA

It is obvious that the origin of the m. capiti-mandibularis in the captorhinomorphs (and all other anapsids) could only have been from the inner or under surface of the temporal or cheek bones. Fox has reported that in a captorhinid examined by him the central part of the temporal covering is composed of very thin bone with a concomitant thickening peripherally of this weak area and infers that the attachment of the muscle was mainly on the thickened parts and that the thinning centrally was due to this area becoming non-functional and thus liable to fenestration.

Such fenestration has in fact taken place in the pelycosaurs. The area of bone-resorption is mainly situated at the junction of squamosal and jugal, but the fenestration in the pelycosaurs has been far from uniform. In fact in one species of *Ophiacodon* there is not a single but a double fenestra. Moreover, there

is considerable variation in the participation in the border of the fenestra by the bones of the cheek. The dorsal border or upper temporal arch is always formed by the postorbital and the squamosal. The lower border or zygomatic arch is mostly formed by the jugal and squamosal in varying proportions, but in all the three suborders there are forms in which the quadratojugal enters the lower border of the fenestra. Is this of sufficient importance to query the homology of the temporal fenestra?

The temporal fenestrae of the pelycosaurs lie mainly laterally in the cheeks and are separated from one another by a broad flat intertemporal skull table. In the pelycosaurs the original capiti-mandibularis has divided into a major medial mass, the temporal and a lateral mass, the masseter. The temporal originated from the inner face of the bones above the fenestra, viz. parietal, postorbital, postfrontal and squamosal. The masseter arose from the inner face of the zygomatic arch, i.e. from the jugal and squamosal lying below the fenestra. The function of the fenestra is undoubtedly to enlarge the adductor chamber for the bulging of the temporal muscle during contraction.

The temporal fenestra of the earliest therapsids, apparently homologous to that of the higher sphenacodonts, when first encountered already shows a number of modifications in divergent directions.

In *Hipposaurus* the fenestrae are still small and are separated by a wide intertemporal table, the posterodorsal flange of the postorbital, meeting the squamosal, lies in a horizontal plane with the temporal muscle originating, in part, from its ventral face.

In the early Galesuchidae the fenestra is larger both in length and width, but otherwise essentially as in the higher sphenacodonts.

In *Phthinosuchus* the fenestra is greatly enlarged both in height and length due to the outflaring of the squamosal laterally as well as posteriorly. (It extends forward into the jugal.) The postero-dorsal flange of the postorbital lying horizontally is, however, shortened and laterally flanked by a horizontally disposed lappet of the squamosal which on its ventral face provides a large area of the origin for the temporal muscle.

In *Eotitanosuchus* the fenestra is enlarged, extending forward into the jugal, and a groove on the outer edge of the postorbital indicates that the temporal in part arose from the lateral face of this bone.

In the Brithopidae, and even more so in the Anteosauridae, the fenestra is enlarged by a lateral as well as a posterior outflaring of the squamosal which greatly increases the size of the adductor chamber. The dorsal flange of the postorbital now shows a well-developed lateral face and the temporal muscle now arose in part from a ridge on the dorsal edge of the postorbital, confluent with a postero-lateral edge on the squamosal. Moreover, in the Brithopidae and Anteosauridae, the intertemporal skull table is much reduced in width and the original horizontally lying upper face of the postorbital now faces appreciably laterally and is practically excluded from the skull table.

In the Titanosuchidae the temporal fossa is only of moderate size. The

posterior flange of the postorbital, lying mainly vertical and applied to the outer face of the parietal, is greatly reduced and lying low down in the skull reaches the squamosal as a tapering splint.

The intertemporal skull table is reduced in width and the parietals form a fairly wide and fairly high sagittal crista.

The origin of the temporal muscle mass is mainly from the outer face of the posterior postorbital flange and extends up the lateral face of the parietal to the edge of the crista and posteriorly to the upper part of the squamosal, whose lateral edge is continued as a ridge on to the parietal.

The jugal is excluded from the fairly deep lower temporal arch, apparently due to the downgrowth of the strong postorbital.

In the Tapinocephalidae the greatly varying pachyostotic thickening of the skull bones affects the nature of the temporal fenestra, the adductor chamber and the degree of participation of the bones forming the borders of the fenestra.

As to position of the fenestra, the one extreme is seen in *Riebeeckosaurus* where the two fenestrae are separated by only a sharp parietal crista; in the other extreme the intertemporal width is so great in *Criocephalus* that the fenestra is not visible in dorsal view. In all the lower arch, formed solely by the squamosal, is very deep so that the fenestra is situated high up in the cheek. In general the strong postorbital bar makes the distance between orbit and fenestra great. As to shape, the fenestra is slitlike in some moscopines and tapinocephalines with the fore-aft diameter one-third of the dorso-ventral, whereas in *Avenantia* it is longer than high, with the struthiocephalines in an intermediate position.

The adductor chamber is roomy in *Avenantia*, moderately so in the struthiocephalines but antero-posteriorly compressed in the tapinocephalines and in *Moschops* and *Criocephalus*. As to the circum-fenestral bones, the Tapinocephalidae have one feature in common in that the jugal is wholly excluded from the lower arch, being pushed anteriorly by the thick postorbital bar and the forward growth of the squamosal due to the quadrate moving anteriorly.

In the tapinocephalids considerable variations occur in the upper temporal arch. In some of the struthiocephalines (where the pachyostosis is moderate) the dorso-posterior flange of the postorbital and the upper flange of the squamosal do not meet, being thus separated by the parietal. In the other tapinocephalids (where the pachyostosis is greatly developed) the junction of the postorbital and squamosal is pushed down to the lower half of the fenestra.

In the tapinocephalines (where the pachyostosis is great) abnormal overgrowth of both the frontal and postfrontal bones caused these bones to enter the dorso-anterior part of the rim of the fenestra.

In the moscopines (where the pachyostosis is in some respects even greater) only the postfrontal enters the dorso-anterior part of the rim of the fenestra. In all the tapinocephalids the main origin of the temporal muscle

mass is from the lateral surfaces of those parts of the parietal, postorbital and squamosal lying well within the upper part of the temporal fossa.

The rim of the fenestra thus lies lateral to the area of origin, i.e. the more fibrous part of the temporal muscle, and any bulging of the muscle mass on contraction could hardly have occurred through the fenestra, which is in any case small. The body or fleshy part of the muscle lies lower down and is covered by the deep lower arch (squamosal). The fenestra thus seems to have lost its primary function! The forward position of the lower jaw articulation with the concomitant great depth of the squamosal arch greatly lengthens the muscle mass and this increased length would compensate for a decreased ability to bulge locally.

In the Styracocephalidae the pachyostosis has caused a great reduction of the size of the temporal fenestrae, which are situated widely apart. Differential bone thickening has resulted in the rim of the fenestra being formed solely by the postorbital and squamosal.

A forward shift of the jaw articulation as in the tapinocephalids with the deep squamosal low arch has affected the working of the temporal muscles as described above for the tapinocephalids.

In the Estemmenosuchidae the fenestra is large particularly in length due to a forward extension into the jugal as well as a posterior outflaring of the squamosal. The dorsal flange of the postorbital lying in the skull table is shortened and fails to reach the squamosal. The intertemporal width is large. The temporal muscle thus in part originates from the lateral face of the parietal.

In the Otsheriidae the temporal fenestra is large, due to the outflaring of the squamosal both laterally and posteriorly as well as the reduction of the width of the intertemporal skull table. It is still primitively bounded by the three bones—postorbital, squamosal and jugal, but both the upper and the lower arch are modified.

In the upper arch the posterior flange of the postorbital only provides a narrow edge to bound the upper border of the fenestra and the temporal muscles arise in part from the latero-ventral edge of this splint-like flange.

The lower arch is fairly shallow but is deeper than broad, thus lying vertically, with a large contribution from the jugal. The postero-ventral corner of the squamosal is prolonged ventrally in the form of a pedicel to hold the quadrate in a position low down in the skull and also far posteriorly. The adductor chamber is roomy and the temporal muscles short but bulky.

In the Dromasauridae a single skull of *Galeops* from the *Tapinocephalus* zone is inadequately known.

The temporal fossa is short but deep and apparently bounded by the postorbital, squamosal and jugal.

The squamosal has a long ventrally directed pedicel similar to that of *Otsheria*.

In the Endothiodontidae and Dicynodontidae the oldest known forms from low down in the *Tapinocephalus* zone already have the temporal region,

which is so typically unique for all the Dicynodontia and basically retained throughout the long history of this group.

Of all the early therapsids the Endothiodontidae and Dicynodontidae show the greatest modification in the temporal region from the primitive pelycosaur condition.

The temporal fenestra is greatly enlarged. The fore-aft diameter is uniquely lengthened due to the anterior position of the orbit accompanied by the slenderness of the postorbital bone and the posterior flaring of the squamosal. The medio-lateral diameter is enlarged due to the reduction of the intertemporal width of the skull table.

The upper postorbital-squamosal arch is fairly primitive except for the greatly lengthened dorsal flange of the postorbital which is somewhat bent down laterally from the horizontal. The temporal muscle arises in part from the lateral edge and under surface of the postorbital and the upper edge of the squamosal.

The greatest modification is seen in the structure of the squamosal.

In the zygoma the squamosal, originally lying in a vertical plane, is bent down laterally to lie in a horizontal plane with the original dorsal edge now forming the lateral edge of the bar. In addition the squamosal extends far anteriorly to terminate in a plane ventral to the orbit and the jugal is almost completely excluded from the lateral face of the zygoma.

The downward growth of the postero-ventral corner of the squamosal to form a pedicel, first seen in *Otsheria*, is also greatly modified. In *Otsheria* the face of this pedicel is lateral. In the Dicynodontia this face is now directed much anteriorly with the original posterior edge turned outwards to form a sharp lateral edge. To the lower part of this oblique face the quadratojugal is applied. Above the quadratojugal is the area of origin of the masseter mainly from fascia attached to the sharp lateral squamosal edges.

In all the four early therocephalian families (Pristerognathidae, Lycosuchidae, Alopecodontidae and Scaloposauridae) the temporal fenestra is large and faces more dorsally than laterally and the adductor chamber is very roomy. Here also the posterior flange of the postorbital is greatly reduced and lies as a small splint lying vertically and applied to the lateral face of the parietal, which now forms the greatest part of the upper border of the temporal fenestra.

The intertemporal width is greatly reduced and this part of the skull table is normally developed into a sagittal crista of varying width and height.

Here the temporal muscle had its main origin from the lateral face of the parietal.

POSITION OF THE QUADRATE

The foregoing comparison of the temporal fenestra and its arches in the early therapsids drew our attention to the origin of muscles of the capitimandibularis mass.

The function of these adductors is related to the position of the jaw articulation and the insertion on the lower jaw. These two aspects will now be considered. In the pelycosaurs the quadrate is situated far posteriorly just posterior to the plane of the occipital condyle.

In the earliest Gorgonopsia the quadrate lies just anterior to the plane of the occipital condyle.

In the Eotitanosuchidae the quadrate apparently lies in the plane of the condyle.

In the Brithopidae the quadrate has shifted somewhat anteriorly to the plane of the condyle.

In the Anteosauridae the quadrate has shifted still further anteriorly and due to the backward tilt of the occiput lies very far anterior to the upper edge of the occiput.

In the early therocephalian families the quadrate still lies in the primitive posterior position.

In the Titanosuchidae, Tapinocephalidae, Styracocephalidae and Estemmenosuchidae the quadrate lies very far forward of the plane of the condyle and still more of the plane of the upper occipital edge.

In the Otsheriidae the quadrate would appear to have been situated somewhat anterior to the plane of the condyle.

This is also the position of the quadrate in the early Endothiodontidae and Dicynodontidae.

INSERTIONS OF THE TEMPORAL MUSCLE

The primitive nature of the insertions of the *m. capitimandibularis* is still evident in the sphenacodonts and this condition is basically retained in the early therapsids.

The most significant change is seen in the Gorgonopsia and the Therocephalia, where the dentary developed a prominent free-standing dorso-posteriorly directed coronoid process for the reception of the temporalis.

No forms are known in which this development is incipient. Low down in the *Tapinocephalus* zone it is simply there fully developed in the oldest Gorgonopsia and Therocephalia.

As has already been mentioned above, the origin of the subdivided capitimandibularis is in the early Gorgonopsia still of primitive nature, but that in the earliest therocephalians it is already highly specialized in a mammalian direction. This very definite difference in origin of the muscles is remarkably not accompanied by any noteworthy change in the insertion.

The development of the coronoid process in these two groups thus appears to have been caused by a pull exerted by the adductors in a primitive way in the case of the gorgonopsians on the one hand and by an advanced mammal-like way in the therocephalians.

The presence of a coronoid in the Gorgonopsia can thus at most be considered as a parallel development and not one in a mammalian direction.

THE REFLECTED LAMINA OF THE ANGULAR

This structure is a feature common to all the early therapsids and is concerned with the insertion of the anterior pterygoid and superficial masseter muscles.

This is also the condition in the higher sphenacodonts and held as strong evidence of their consanguinity with the therapsids.

In the early Dicynodontia the structure of the reflected lamina differs somewhat from that of the other early therapsids. This is probably associated with a difference in the origin of the anterior pterygoid muscle for we know that in the early Endothiodontidae and Dicynodontidae, but not in the Otsheriidae, the lateral pterygoidal flange is greatly reduced.

THE MARGINAL TEETH

Of the oldest therapsid families, 10 have a carnivorous dentition and 7 are herbivorous, with the adaptations showing a quite remarkable diversity.

In the primitive pelycosaur the tooth row is long and consists of simple pointed teeth. In the maxilla a pair of teeth well back in the row are enlarged as 'canines'. The replacement is distichial.

In the advanced sphenacodonts the enlarged 'canines' are situated near the front of the maxillary row. The functional replacement is by a member of the same tooth family but the upper canines are replaced alternately.

In the early therapsids the tooth row is reduced in all the carnivorous families, but is secondarily lengthened in the herbivorous Titanosuchidae, Tapinocephalidae and Styracocephalidae. In the Otsheriidae and Venyukoviiidae the row is still fairly long but highly specialized. In the Endothiodontidae and Dicynodontidae development of horny sheaths radically reduces the marginal teeth.

In the early therapsids the upper canine when present is the first tooth in the maxilla in all the families, except the Scaloposauridae and Alopecodontidae.

A lower canine is present, except where secondary lost as in the herbivorous Endothiodontidae, Dicynodontia and Tapinocephalidae but persists in the herbivorous Titanosuchidae and Styracocephalidae. In the Lycosuchidae there are a pair of upper canines replaced alternately but functionally by a member of the same family.

In the pelycosaur there appears to be no limit to the tooth replacement. This is also the case in the Titanosuchidae and probably also in the Tapinocephalidae. In the other families there is evidence of limited replacement in the Gorgonopsia and Therocephalia. The condition in the other early therapsid families is unknown.

In the early therapsids the upper teeth in occlusion lie lateral of the lower teeth, but in the Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracocephalidae the incisors intermesh, so do the canines in the Titanosuchidae and the whole battery in the Tapinocephalidae.

In the sphenacodonts the teeth are simple and pointed.

In the early therapsids considerable variations have arisen.

In the Eotitanosuchidae the primitive condition is retained.

In the Brithopidae and Anteosauridae the incisors are progressively lengthened and in the latter the postcanines become bulbously spatulate.

In the carnivorous gorgonopsian and therocephalian families the distal edge of the incisors, canines and post-canines becomes serrated.

In the herbivorous Titanosuchidae, Tapinocephalidae and Styraocephalidae the incisors develop a talon and heel; in the Tapinocephalidae the canine and the postcanines develop a similar talon and heel, but in the Styraocephalidae only the postcanines. The canine remains fairly normal in the Titanosuchidae and Styraocephalidae. In the Titanosuchidae the long row of postcanines are spatulate with serrated edges.

In *Otsheria* and *Venyukovia* the teeth become bluntly conical.

In the Dicynodontia the incisors disappear, the upper canines present or absent and the lower canine always absent. There are no postcanines in the Dicynodontidae and in the Endothiodontidae they are reduced, and displaced medially from the jaw margin.

PALATE

In the sphenacodonts the pterygoids do not meet in the median line posterior to the interpterygoid vacuity. The quadrate ramus is deep and strong. The transverse ramus is strong, prominent and dentigerous. The choana is long and situated anteriorly. There is no suborbital foramen or fenestra. The posterior end of the vomers is spatulate and the vomerine bar lies low down in the skull.

The early therapsids manifest considerable variations from the primitive pelycosaur palatal structure. They all have one advance in common, viz. that the basiptyergoid joint is no longer freely movable. The quadrate ramus becomes weaker in the Gorgonopsia, Therocephalia and Dicynodontia. The anterior ramus is (generally) reduced; greatly so in the Dicynodontia. The transverse ramus is progressively weakened in the series *Otsheriidae*–*Venyukoviidae*–*Dicynodontia* and becomes edentulous in practically all the therapsids.

The choana is somewhat shortened in the Brithopidae and Anteosauridae but in the dicynodontian families it is both shortened and pushed backwards by the enlarged palatal process of the premaxilla. Only in the therocephalian families is a well-developed suborbital fenestra present.

Only in the Eotitanosuchidae, Gorgonopsia and Dicynodontia is the vomer well raised above the general palatal level.

THE LOCOMOTOR APPARATUS

In the 19 known families of early therapsids the structure of the girdles and limbs is not adequately known in 11 of these families. Any comparative consideration must thus be tentative.

An overall picture of the locomotor apparatus in the other 8 families discloses considerable adaptive radiations, but in all there is an advance

beyond the crawling habit of the pelycosaurs to a slinking habit in the brithopids, anteosaurids and hipposaurids and a more upright walking gait in the endothiodontids, dicynodontids, the 3 therocephalian families and the titanosuchids and tapinocephalids.

We may commence by attempting to give a picture of the diversity exhibited in the structure of the girdles and limbs in these early therapsids.

In the hipposaurids the procoracoid has not been ousted from the glenoid; in all the others it has been ousted.

The procoracoid is enlarged in the hipposaurids and the Dinocephalia, small in the Dicynodontia and moderate in the other families.

Only in the Dicynodontia is an acromion process developed on the scapula. This feature, typical of the mammals, is however no evidence of affinity of the Dicynodontia to the mammals, but rather a case of parallelism as it is also found in the contemporary Pareiasauridae—a cotylosaur family with no affinity to the mammals. An ossified sternum is developed in the Dicynodontia and Gorgonopsia but in none of the other groups. In all the early therapsids the axial muscles have been forced off the outer face of the ilium and the iliac height is increased.

The anterior iliac process is incipient in the hipposaurids, moderate in the pristerognathids and brithopids and anteosaurids, well developed in titanosuchids and tapinocephalids and great in the endothiodontids and dicynodontids but undeveloped in the dromasaurids.

Only in the endothiodonts and dicynodontids has the acetabulum moved to the anterior pelvic border.

The pubo-ischiatic plate retains its great primitive length in hipposaurids, pristerognathids and anteosaurids. The pubic part is shortened in titanosuchids and tapinocephalids and greatly so in endothiodontids and dicynodontids, where a pubo-ischiatic fenestra replaces the pubic foramen present in all the other families.

The pelvic symphysis is strongly ossified in the hipposaurids, pristerognathids and anteosaurids but weak in all the other families.

Humerus

All the early therapsids have lost the primitive strap-like caput of the humerus and there has been an untwisting of the proximal and distal ends relative to each other. These ends remain expanded to various degrees, but are greatly reduced in hipposaurids.

In hipposaurids no epicondylar foramina are present. In endothiodontids, dicynodontids, Tapinocephalidae and Anteosauridae there is no ectepicondylar foramen but it is present in brithopids, titanosuchids and Therocephalia.

Femur

In all the early therapsids there has been a preaxial shift and a shortening of the caput femoris but to varying degrees in the various families. The distal condyles have shifted to lie in the same plane and this distally so that the knee

joint becomes a simple hinge well adapted to a more upright disposition of the limb.

Only in the Titanosuchidae and Tapinocephalidae has the femur become greatly broadened.

Forefoot

The primitive phalangeal formula of 2, 3, 4, 5, 3 has been reduced to 2, 3, 4, 4, 3 in the hipposaurids and to 2, 3, 4, 3, 3 in the anteosaurids and to 2, 3, 3, 3, 3, in all the other families of the early therapsids.

Hindfoot

In the tarsus the primitive medial central has been lost in all the early therapsids, where this structure is known, and the phalangeal formula reduced from the primitive 2, 3, 4, 5, 4 to 2, 3, 4, 4, 3 in the hipposaurids, 2, 3, 4, 3, 3, in brithopids and anteosaurids and 2, 3, 3, 3, 3 in all the other early therapsids.

In the pristerognathids the astragalus tends to overlies the calcaneum and in the hipposaurids a *sustentaculum tali* is developed as well as a *tuber calcis*.

Now, what does this rather great diversity in the structure of the locomotor apparatus signify?

The main variations are apparently towards the acquisition of a greater degree of active movement than that of crawling—on the one hand that possible in a slinking habit and on the other in a more upright walking habit.

Is the improved locomotor ability correlated in any way with an improved masticatory ability?

In the herbivorous families the achievement of a walking gait would increase the area that can be grazed and the ability to reach higher ground would bring these reptiles into contact with hardier and more fibrous plants than those flourishing in more marshy terrain.

In the Otsheriidae and Venyukoviidae the bluntly conical teeth appear to be adapted to a coarser fare.

The horny jaw sheaths and plates of the Endothiodontidae and Dicyodontidae together with the fore-and-aft sliding of the lower jaw would greatly help in the shearing and milling of fibrous vegetable matter.

In the Titanosuchidae and Tapinocephalidae and Styracocephalidae the intermeshing talon-and-heel teeth showing considerable abrasion are obviously well adapted for piercing and crushing tough fibrous plants.

In the *Eotitanosuchus-Anteosaurus* series of carnivores the progressive development of a formidable battery of long pointed intermeshing incisors together with the strong canines would enable these reptiles to execute a strong piercing and jerking bite into the flesh of the larger herbivores. The progressive decrease in the role of the postcanines would accompany this method of biting.

A slinking habit of locomotion indicates that these carnivores did not run after their prey but rather lay in ambush and then pounced.

The early gorgonopsians with their moderate anterior teeth and reduced postcanine series and slinking but agile locomotory ability probably pounced on the small contemporary Dicynodontia or could have at times been carrion eaters.

The early therocephalians with their limbs well adapted to a more upright walking and running gait could pursue and overcome even some of the larger herbivores. With the postcanines greatly reduced in some genera, the front part of the jaws was mostly in action pulling and tearing out lumps of flesh.

The scaloposaurids with a long tooth row and small canines and with some cuspidate postcanines were better adapted as insectivores.

The variations in the adductor muscles in the above groups of early therapsids appear to be well correlated to both the varied dentitions and modes of locomotion.

DIVERSE STRUCTURES

The quadratojugal has variable relations in the early therapsids. In all it is, however, much reduced in size and never enters the lower temporal arch as it does in some members of all three of the pelycosaurian suborders.

Primitively a surface bone of the postero-lateral corner of the skull, flanking the quadrate, it first tends to move medially in some of the higher sphenacodonts to rest on the quadrate above the lateral condyle as a bone of reduced size.

This process is seen continued in the Gorgonopsia, Therocephalia, Brithopidae and Anteosauridae. Whereas in the Dicynodontia the quadratojugal becomes a plate applied to the antero-lateral face of the everted squamosal, in the Titanosuchidae and Tapinocephalidae the quadratojugal, variable in size and shape, still forms part of the lateral skull surface. Does this indicate an origin from different pelycosaurian ancestors?

The lacrimal, primitively a long bone stretching from orbit to nostril, is reduced to an anterior circumorbital bone in all the therapsids. It is reduced in some sphenacodonts but also in the edaphosaurian, *Mycterosaurus*.

The supratemporal is absent in all therapsids and in all one coronoid is lost, but both coronoids are absent in the Dicynodontia.

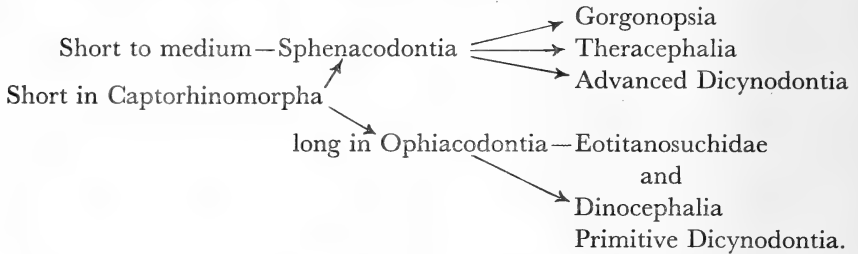
In the early therapsids the preparietal is a new acquisition in only the Endothiodontidae and Dicynodontidae as well as the Hipposauridae and Galesuchidae. In the primitive dicynodontian family, Otsheriidae, there is however no preparietal. It is also absent in the possible gorgonopsian forerunner, *Eotitanosuchus* and *Phthinosuchus*.

In the early Gorgonopsia the preparietal lies anterior to the pineal foramen, but forms its anterior border in the early Dicynodontia which implies a different *raison d'être*.

The dorsal process of the premaxillaries varies in length in the pelycosaurs, being long in ophiacodonts, short to medium in sphenacodonts and edaphosaurs.

It is also variable in the early therapsids, being long in eotitanosuchids, brithopids and anteosaurids; very long in the Titansuchidae and Tapinocephalidae. In the dicynodontian families it is long in the primitive Otsheriidae and Venyukoviidae, but short in the more advanced early Endothiodontidae and Dicynodontidae.

Arranged into series as to length of premaxillary process we have:



Together with the development of a reflected lamina of the angular we see a reduction in the role of the posterior mandibular bones in the higher sphenacodonts and in all the early therapsids and this reduction is more pronounced in those therapsids where the dentary develops a coronoid process.

The braincase has its sidewall largely open in the Therocephalia and Dicynodontia, but much less so in the Anteosauridae, Titanosuchidae and Tapinocephalidae. In the Therocephalia there is no downward directed flange of the parietal whereas in all the other early therapsids, where known, it is present.

The sphenethmoidal complex is weakly ossified in the early Therocephalia but well developed in the Dinocephalia and in those early Dicynodontia where it has been studied. In the Dicynodontia it lies far anteriorly and has no contact with the prootic, whereas in the Dinocephalia contact is made above the lateral fenestra.

The fenestra ovalis lies low down in the skull in all the early therapsids, but there are considerable variations in the structure of the stapes. The dorsal process of the stapes is reduced in the Tapinocephalidae and absent in all the other early therapsids. A stapedia foramen usually present is absent in the hipposaurids, brithopids, anteosaurids and in all the early Dicynodontia where the stapes has been described.

The exoccipital apparently does not enter the floor of the braincase in *Captorhinus*. This is definitely the case in the early Endothiodontidae and Dicynodontidae and the early Gorgonopsia, whereas in *Dimetrodon* and all the Dinocephalia it forms the whole posterior part of the brain floor.

The prootics do not meet in the middle line in *Captorhinus*, but do meet in *Dimetrodon*. They meet in all the Dinocephalia, where known, but not in the Dicynodontia and just meet in the Therocephalia.

The dorsum sellae is very high in *Captorhinus* and high in *Dimetrodon*. In the former it is formed by the basisphenoid, whereas in the latter by the prootic.

In the Dinocephalia the upper part of the dorsum sellae is formed by the prootic, and in the Therocephalia the prootic just enters, whereas it is excluded in the early Dicynodontia. The sella turcica is deep in *Captorhinus* and *Dimetrodon*. This is also the case in all the Dinocephalia but is shallow in the Therocephalia and Dicynodontia.

The quadrate ramus of the pterygoid is strong in the sphenacodonts and is greatly strengthened in the Dinocephalia but weakened in Therocephalia, Gorgonopsia and Dicynodontia.

MORPHOLOGICAL SERIES

In the foregoing the extent of the variations observed in the assemblage of early therapsids has been given in some detail. The result being that one cannot see the wood for the trees.

We must now consider whether these divergencies can be arranged in some orderly manner on a basis of possible consecutive ascending morphological stages.

The early therapsids form a fauna of discrete types of animals living together during a definite interval of time. They can thus, broadly speaking, be considered as contemporaries and thus some cannot be conceived as being ancestral to others.

What we can, however, attempt to do is to determine the possibility of arranging the animals exhibiting these various structural features in series, one derivable from the others in a morphological sense.

SERIES I

Captorhinidae → Pelycosauria → Eotitanosuchidae → Brithopidae → Anteosauridae.

Consecutive steps in the following features:

(a) *Temporal fenestra*

Absent in captorhinids → small or double in pelycosauria → large in eotitanosuchids → larger in brithopids → very large in anteosaurids. This progressive increase is mainly due to lateral and posterior outflaring of the squamosal.

(b) *Intertemporal skull table*

Wide in pelycosauria → still wide in *Eotitanosuchus* → greatly reduced in brithopids → but less reduced in anteosaurids.

(c) *Posterior process of postorbital*

Horizontal surface bone in pelycosauria → just starting to tilt down in *Eotitanosuchus* → tilting progressively increased in brithopids and anteosaurids to culminate as a bone lying nearly vertically flanking the parietal inside the temporal fossa.

(d) Area of origin of the temporal muscle on the postorbital

Under surface of postorbital in pelycosaur → moving to lateral edge and dorsal face in *Eotitanosuchus* → on the morphological dorsal face in brithopids and anteosaurids which progressively becomes a functionally lateral face.

(e) Insertion of temporal muscle

Notwithstanding the changes in the origin of the muscle in this series, the insertion on the mandible remains constant from sphenacodontid to anteosaurid.

(f) Jaw articulation

In captorhinids this lies posteriorly in a plane with the occipital condyle and level with the alveolar border → this is still the position in most pelycosaur, but in the higher sphenacodonts it has shifted downwards → posterior and low in eotitanosuchids → shifted both anteriorly and ventrally in brithopids and anteosaurids.

(g) Reflected lamina of the angular

Absent in captorhinids → still absent in most pelycosaur, but developed in the higher sphenacodonts → progressively better developed in eotitanosuchids, brithopids and anteosaurids.

(h) Marginal tooth row and 'canines'

In captorhinids the tooth row is long, without 'canines' → in pelycosaur long to very long, canines absent or variously present in the three pelycosaur groups, but strong in *Eothyris* and most sphenacodontids → row reduced in eotitanosuchids, but strong definite canine present → progressive reduction of number of post-canines in brithopids and anteosaurids, canines very strong and incisors progressively lengthened to culminate in the very long inter-meshing set of *Anteosaurus*.

(i) Septomaxilla, maxilla and lacrimal

In captorhinids the septomaxilla is intranarial, the lacrimal enters the narial border and the maxilla is low → these relations are retained in nearly all the pelycosaur but in *Mycterosaurus*, *Sphenacodon* and *Dimetrodon* the lacrimal fails to reach the naris and the maxilla becomes high. This may be related to the greater development of 'canines' in these three genera, but other pelycosaur have enlarged 'canines' without affecting the primitive relations of the maxilla → in eotitanosuchids, brithopids and anteosaurids the septomaxilla extending backwards becomes a bone of the lateral surface, the lacrimal fails to reach the nostril and the maxilla is high.

(j) Dorsal process of the premaxilla

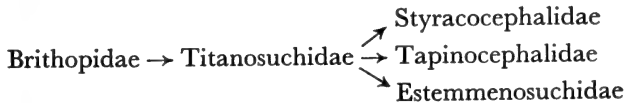
Short in captorhinids → moderately lengthened in some pelycosaur but still fairly short in sphenacodonts → greatly lengthened in eotitanosuchids, brithopids and anteosaurids.

(k) Braincase

Insufficiently known in this series, but in both *Dimetrodon* and *Anteosaurus* the sphenoidal complex is well ossified and the exoccipital and the prootic enter the floor of the braincase and the prootics meet in the middle line in the dorsum sellae.

(l) Locomotor apparatus

Insufficiently known, but in all brithopids and anteosaurids the femur has become a long, slender curved bone.

SERIES II*(a) Temporal fenestra*

In brithopids large → slightly reduced in titanosuchids → moderately to very greatly reduced in tapinocephalids (except in *Avenantia* and *Riebeeckosaurus*).

(b) Intertemporal skull table

Moderately wide in brithopids → so also in titanosuchids → moderately to enormously widened in tapinocephalids (except in *Avenantia* and *Riebeeckosaurus*).

(c) Posterior process of the postorbital

In brithopids long and high with good contact with the squamosal → in titanosuchids reduced to a splint and just meeting the squamosal → in tapinocephalids shortened still further so that in some forms it fails to reach the squamosal.

(d) Area of origin of the temporal muscle on the postorbital

In brithopids from the fairly large tilted (dorsal) face → in titanosuchids this area is reduced and the origin transferred more on to the parietal → this is carried further in the tapinocephalids where the total area is small (except in *Avenantia* and *Riebeeckosaurus*).

(e) Insertion of temporal muscle

The primitive pelycosaurian position is retained throughout the series.

(f) Jaw articulation

In brithopids anterior to the plane of the occipital condyle → in titanosuchids still further anteriorly → in tapinocephalids very far anteriorly.

(g) Marginal teeth

In brithopids moderately long pointed incisors, well-developed canines, fairly long postcanines row of bluntly conical teeth.

In titanosuchids we find a radical change to a herbivorous dentition; strong pointed canine is retained, the strong intermeshing incisors have developed a piercing talon and crushing heel and the very long postcanine row has cuspidate spatulate crowns.

In tapinocephalids this process is carried further in that the canine has disappeared as such and the very long series consists of isodont talon-and-heel teeth, all intermeshing but the anterior teeth are weaker than the incisors of the titanosuchids.

(g) *Dorsal process of the premaxilla*

In brithopids this is of moderate length intercalated between the nasals, greatly lengthened in both titanosuchids and tapinocephalids and nearly reaching the frontal.

(h) *Braincase*

Little known in the brithopids.

In both titanosuchids and tapinocephalids the lateral wall is well ossified and the sphenoidal complex strongly ossified; the exoccipital and prootic enter the floor of the braincase; the prootics meeting in the middle line form part of the dorsum sellae.

(i) *Locomotor apparatus*

In brithopids the girdles and limbs are fairly lightly built whereas in both titanosuchids and tapinocephalids they are massive to very massive.

Styracocephalidae

With a persistent canine and the development of weak talon-and-heel incisors and postcanines and a secondary broadened intertemporal skull table and reduced temporal fossa. *Styracocephalus* can be derived from the titanosuchids as a branch somewhat divergent from the tapinocephalid branch.

Estemmenosuchidae

It is difficult to place *Estemmenosuchus*. The shagreen of palatal teeth is reminiscent of early pelycosaurs.

The broad intertemporal region with the upper part of the postorbital lying on the dorsal surface overhanging the temporal fenestra are eotitanosuchid features as is the large temporal fenestra. The incisors and canines are like those of the brithopids.

The great downward and forward shift of the quadrate and the long series of postcanines parallel features of both the titanosuchids and the tapinocephalids.

SERIES III

Pelycosauria → *Phthinosuchidae* → *Hipposauridae* → *Galesuchidae*.

(a) *Temporal fenestra*

This is small or double in the pelycosaurs → suddenly very large in *Phthinosuchus* → but only moderately enlarged in *Hipposaurus* → then again large in the galesuchids. Clearly not a consecutive series.

(b) *Intertemporal skull table*

Wide in pelycosaurs → remains wide in *Phthinosuchus* → becomes very wide in *Hipposaurus* → but somewhat reduced in the galesuchids. Again not a consecutive series.

(c) *Posterior process of the postorbital*

In the whole series it persists as a horizontal surface bone overhanging the temporal fenestra. Long in pelycosaurs → short in *Phthinosuchus* → very long in *Hipposaurus* → long in galesuchids. In *Phthinosuchus* it is almost entirely excluded from the edge of the skull table due to the development of a lappet of the squamosal extending far anteriorly and lying laterally of the postorbital.

(d) *Area of origin of the temporal muscle on the postorbital*

In the whole series the origin remains on its under surface, but in *Phthinosuchus* also from the under surface of the squamosal lappet.

(e) *Insertion of the temporal muscle*

Partially inserted on the upper and outer face of the dentary in pelycosaurs → this primitive insertion retained in *Phthinosuchus* → but in hipposaurids and galesuchids mainly on the strongly developed coronoid process.

(f) *Jaw articulation*

Posterior position in pelycosaurs → shifted anteriorly in *Phthinosuchus*, *Hipposaurus* and galesuchids. But situated far ventrally in *Hipposaurus*.

(g) *Dorsal process of the premaxilla*

Moderately long in pelycosaurs → unknown in *Phthinosuchus* → very short in *Hipposaurus* and the galesuchids.

(h) *Marginal teeth*

Postcanines progressively reduced in the series. A single well developed canine present in *Phthinosuchus*, *Hipposaurus* and the galesuchids.

(i) *Locomotor apparatus*

Unknown in *Phthinosuchus* and the early galesuchids. In *Hipposaurus* the anterior iliac process remains weak as in pelycosaurs, an ossified sternum is developed;

the limbs have become long and slender as in anteosaurids. The tarsus is greatly specialized with the development of a *tuber calcis* and a *sustentaculum tali*; the phalangeal formula only slightly reduced, probably 2, 3, 4, 4, 3.

(j) *Preparietal*

Absent in pelycosaurs and in *Phthinosuchus*, suddenly present in *Hipposaurus* and all other gorgonopsians.

(k) *Vomer*

Lying in general plane of palate with broad posterior end in pelycosaurs → raised or vaulted, with broad posterior end in *Phthinosuchus* → raised or vaulted in *Hipposaurus* and galesuchids, posterior end tapering and intercalated between palatines.

SERIES IV

Pelycosauria → *Otsheriidae* → *Endothiodontidae* → *Dicynodontidae*.

(a) *Temporal fenestra*

In pelycosaurs small or double, bounded by postorbital, squamosal and jugal in the higher sphenacodonts → in *Otsheria* large, bounded by postorbital, squamosal and jugal → in endothiodonts and dicynodonts very large mainly due to posterior outflaring of the squamosal, with jugal participation in its border reduced.

(b) *Intertemporal skull table*

Wide in pelycosaurs → moderate in *Otsheria* and in endothiodonts and dicynodonts.

(c) *Posterior process of the postorbital*

A horizontal surface bone in pelycosaurs and fairly long → in *Otsheria* showing only an edge as a surface bone and fairly long → in endothiodonts and dicynodonts slanting downwards laterally and very long.

(d) *Area of origin of the temporal muscle on the postorbital*

In pelycosaurs from its undersurface → in *Otsheria* from its latero-ventral edge → in endothiodonts and dicynodonts from the dorsal surface now lying at a slant.

(e) *Squamosal*

In most pelycosaurs the postero-lateral corner of the squamosal lies in the plane of the alveolar border, but in the higher sphenacodonts (and *Edaphosaurus*) it lies far ventrally and the lower temporal arch, in which the jugal plays a large part, lies in a vertical plane.

In *Otsheria* the process of the squamosal lies far ventrally and the lower arch, in which the jugal plays a large part, still lies in a vertical plane.

In endothiodonts and dicynodonts both these features are suddenly radically changed. The ventral process, still extending far ventrally, is uniquely everted to present a sharp lateral edge and an anterior face to which the quadratojugal is applied as a flat sheet of bone. The anterior process of the squamosal, now forming most of the lower temporal arch, is also everted and now lies in a nearly horizontal plane with its morphological dorsal edge facing laterally.

(f) *Temporal muscles*

In sphenacodonts the origin of the temporal muscles is mainly from the under surface of the bones of the skull roof → in *Otsheria* it is partly shifted to the edge of the postorbital → in the early endothiodonts and dicynodonts the unique and radical changes in the nature of the squamosal is due to the radical changes in the areas of origin of both the temporal and masseter. Noteworthy is that the masseter lying medially of the zygomatic arch in the pelycosaurs now has its origin from the antero-lateral face of the squamosal below the zygomatic arch.

The insertion of these muscles has not changed much from the pelyosaur condition and no coronoid process is developed, but there is already an indication of a lateral flange on the dentary well developed in some later Dicynodontia.

(g) *Reflected lamina of the angular*

In the higher sphenacodonts we have the first development of this structure → it is unknown in *Otsheria*, but in *Venyukovia* it is well developed → it is present in the early endothiodonts and dicynodonts but in nature differs considerably from that in the other contemporary therapsids indicating a difference in the insertion of the anterior pterygoid muscle. A fenestra in the lower jaw is known in *Ophiacodon* but in no other pelyosaur; it is also present in *Venyukovia* and the endothiodonts and dicynodonts.

In some pelycosaurs with 'canines' the maxilla is high → but in *Otsheria* without canines it is suddenly very high as it is in endothiodonts with or without canines. If the increase in maxillary height is due to the presence of canines, as has been maintained, then *Otsheria* must have inherited this feature from an ancestor with canines.

(h) *Jaw articulation*

This lies posteriorly in the series pelyosaur → *Otsheria* → endothiodonts and dicynodonts.

In pelycosaurs it lies high up (except in the higher sphenacodonts and *Edaphosaurus*) → very far ventrally in *Otsheria* and endothiodonts and dicynodonts.

(i) *Septomaxilla, lacrimal and maxilla*

In pelycosaurs the septomaxilla lies internarily → in *Otsheria* there is a small lateral face → but in the endothiodonts and dicynodonts it is again internarial.

The lacrimal fails to reach the naris in some pelycosaurs (e.g. *Dimetrodon*

and *Mycterosaurus*) → in *Otsheria* it is greatly shortened (but still long in *Venyukovia*) → in endothiodonts and dicynodonts it has become a short bone of the anterior orbital border.

(j) *Snout*

In nearly all pelycosaurians the snout is long with the orbit and nostril far apart → in *Otsheria* it is greatly shortened (but still fairly long in *Venyukovia*) → in the early endothiodonts and dicynodonts the snout is very greatly shortened with the naris very near the orbit.

(k) *Dorsal process of the premaxilla*

Moderately long in pelycosaurians → long tapering intercalation between nasals in *Otsheria* (and *Venyukovia*) → but very short in endothiodonts and dicynodonts.

(l) *Palatal face of the premaxilla*

Absent in pelycosaurians and choana extending far anteriorly → well developed in *Otsheria* and choana pushed posteriorly but not reaching the palatine (very well developed in *Venyukovia*, choana pushed back but still long, makes contact with the palatine) → well developed in endothiodonts and dicynodonts, choana pushed backwards and greatly shortened, it sometimes makes contact with the palatine.

(m) *Vomer*

In pelycosaurians paired and lying in general plane of palate broadened posteriorly → unpaired in *Otsheria* lying low down broad posteriorly (paired in *Venyukovia*) → raised above (vaulted) general plane of palate, reaching interpterygoid vacuity in Dicynodontia.

(n) *Lateral ramus of pterygoid*

Strongly developed in pelycosaurians → quite strong in *Otsheria* (but weak in *Venyukovia*) → absent in endothiodonts and dicynodonts.

(o) *Marginal teeth*

In pelycosaurians the tooth row is long, with 'canines' in some forms, pointed in most → moderately long row in *Otsheria*, with incisors enlarged, no 'canine', postcanines spatulate (in *Venyukovia* 'canine' present, teeth bluntly conical, some with crushing face) → in early endothiodonts and dicynodonts the anterior part of the jaws is edentulous with development of horny sheaths, strong upper canines present or absent, reduced postcanines shifted away from jaw margin in endothiodonts but absent in dicynodonts.

(p) *Braincase*

The exoccipital and prootic form floor of braincase in *Dimetrodon* and prootics meeting in middle line in the dorsum sellae → unknown in *Otsheria* → in early endothiodonts and dicynodonts the exoccipital and prootic do not enter the floor and the prootic does not enter the dorsum sellae.

The sphenoidal complex is well developed in *Dimetrodon*, situated far posteriorly but the lateral wall is widely open → unknown in *Otsheria* → very well developed in endothiodonts and dicynodonts but situated very far anteriorly with the result that the lateral wall is widely open because in addition the prootic has little anterior development.

(q) *Locomotor apparatus*

Primitive in pelycosaurs → unknown in *Otsheria* → in the earliest endothiodonts and dicynodonts it is already highly specialized. The scapula has a well-developed acromion process; there is a strongly developed ossified sternum, the ilium has an enormous anterior iliac process; the pubis is greatly reduced; there is a large pubo-ischiatic fenestra; the phalangeal formula is reduced to 2, 3, 3, 3, 3.

Galeops

This very imperfectly known form from the *Tapinocephalus* zone shows a few features similar to those of the early Dicynodontia.

The temporal fenestra is short but high; the squamosal has a long downwardly directed process; in the lower jaw there is no coronoid process but a reflected lamina of primitive form is developed and a fenestra pierces the jaw; the jaws are edentulous.

With its large procoracoid and the absence of an acromion process *Galeops* is more primitive than the other early dicynodonts.

Terocephalia

We, as yet, know no forms that could provide a morphological step intermediate between the pelycosaurs and the four earliest therocephalian families (Alopecodontidae, Lycosuchidae, Pristerognathidae and Scaloposauridae).

The big morphological gap will be evident if we, in summary, list the advances shown in these early therocephalians.

The temporal fenestra is immediately very large with outflaring squamosals, and the parietal is always intercalated between the postorbital and squamosal; the intertemporal skull table is narrow and developing a sagittal crista; the posterior process of the postorbital is reduced to a small splint applied to the lateral parietal face; the temporal muscle no longer arising from the under surface of the roof bones and is inserted on a strong coronoid process; one or two strong canines developed (except in the scaloposaurids); small teeth anterior to the large canine in alopecodonts but absent in the other families and the tooth row generally shortened sometimes radically; dorsal process of premaxilla always very short; jaw articulation shifted slightly forwards; but the exoccipital and prootic less prominent in the brain floor than in *Dimetrodon* and the sphenoidal complex less developed; a large sub-orbital fenestra present; the whole locomotor apparatus well developed in adaptation to a more upright walking gait and the phalangeal formula reduced to 2, 3, 3, 3, 3.

SUMMARY OF MORPHOLOGICAL SERIES

The series primitive sphenacodont (*Haptodus?*), eotitanosuchids, brithopids to anteosaurids, undoubtedly forms a morphological ladder with its bottom end resting further down among the captorhinomorphs with *Anteosaurus* on the highest rung.

The series primitive brithopid (*Sydon?*), titanosuchids to tapinocephalids, styracocephalids and estemmonosuchids, is clearly a line closely related to but diverging from the first series. That this series started from a primitive brithopid appears very probable but can be queried. The tapinocephalids are a very mixed lot but undoubtedly closely related and in various ways a rung up the ladder above the titanosuchids, but the picture is complicated by the developments seen in the other two related forms—*Styracocephalus* and *Estemmenosuchus*. This series also terminates at the top of the *Tapinocephalus* zone.

In the series primitive sphenacodont, *Phthinosuchus*, *Hipposaurus* to galesuchid gorgonopsians, the position of *Phthinosuchus* as intermediate between sphenacodonts and hipposaurids is very uncertain but a fairly close but less specialized form than *Phthinosuchus* would fit the bill. Moreover, *Hipposaurus* does not quite fit in as an antecedent stage to the galesuchids.

If those objections are valid then the phthinosuchids, hipposaurids and galesuchids form a triradiate branch arising from a sphenacodont group close to that from which the Dinocephalia is derived.

In the dicynodont series the morphological step from any known pelycosaur to *Otsheria* is very great and I find it difficult to visualise how such a step could have taken place; but the transition from *Otsheria* to endothiodonts and dicynodonts is small and obvious.

In the pelycosaur—therocephalian series no intermediate stages are known and the gap is very wide, but nothing that the discovery of some more primitive forms would not bridge.

In short, the Dinocephalia and Gorgonopsia can be derived from a sphenacodont near to *Haptodus* and the Dicynodontia and Therocephalia from two other as yet unknown primitive pelycosours.

The foregoing morphological analysis can also be presented in numerical form. For the various groups under consideration here I have tabulated the primitive reptilian characters determinable in each.

Arranging these in numerical order we get the following percentages:

Captorhinomorpha	100
Sphenacodontia	88
Eotitanosuchia	68
Dinocephalia	60
Gorgonopsia	56
Therocephalia	52
Otsheriidae	40
Dicynodontia	32

EARLY THERAPSID HISTORY

From the foregoing there is no doubt that on purely morphological grounds the therapsids must be derived from the captorhinomorphs by way of the sphenacodont pelycosaurs.

Now, does this fit in with the known history of the early tetrapods?

We can begin the story with the primitive anthracosaurs which were the first tetrapods to successfully achieve an amphibious life. These are best known from the Lower Carboniferous of Scotland where the prevailing climate was warm and moist and eminently suitable for an existence partly in water and partly on land.

At the close of the Lower Carboniferous times the Scottish climate changed radically. The elevation caused by the Hercynian Foldings made the climate arid and thus unsuitable for these amphibians.

We now find the amphibian history continuing in central Europe and North America where during Upper Carboniferous times swampy conditions in a warmer climate prevailed.

Swampy conditions continued into Lower Permian times in central Europe and North America, but slowly changed to drier conditions and this sparked off the explosive development of the earliest cotylosaurs especially in North America, closely followed by the rise of the pelycosaurs also mainly in North America but with representatives in central Europe.

At the end of the Lower Permian the climate over North America became more and more arid and the cotylosaur—pelycosaur explosion came to an abrupt end.

In parts of Europe, however, the Lower Permian climate remained cool and favourable for the continued existence of the sphenacodonts and during the Middle Permian this cool climate continued in Cisuralian Russia where the first therapsids made their appearance in deltaic conditions and from there spread to southern Africa where the favourable flood plain conditions existed in a fairly cool to warm climate.

It would thus appear that for every major step in the phylogeny a change of scene was necessary.

This seeming capriciousness can, however, be reasonably accounted for.

During Carboniferous—Permian times the western part of the northern hemisphere formed a single continent—Laurentia—and, notwithstanding the upheavals caused by the Hercynian Foldings and the presence of Tethys, there would at this time have been fewer barriers for the transmigration of tetrapods than at the present time.

SUBSEQUENT HISTORY

Arising in late Ecca (Lower Permian) times the therapsids formed a firmly established order of reptiles with four distinct suborders at the beginning of early Beaufort (*Tapinocephalus* zone—Middle Permian) times.

During the whole of the *Tapinocephalus* zone (2 200 m of sediments) little further development took place.

The Dinocephalia were fully developed at the base of the zone—only *Styracocephalus* is first encountered above the lowest of the tripartite subdivisions of the zone. This greatly diversified suborder dominated the vertebrate life of the Middle Permian, consisting as it did of a family of large carnivores (Anteosauridae) and three families of large herbivores (Titanosuchidae, Tapinocephalidae and Styracocephalidae). Life during this time must have been easy with a cool moist climate in an area of low relief consisting of large expanses of fresh-water pools separated by low uplands with periodic floodings. But abruptly at the end of *Tapinocephalus* zone times the life span of the Dinocephalia was cut short, thus ending one of the first four developmental trends of the early therapsids.

This sudden extinction was apparently not caused by any radical change in the environmental conditions. The succeeding *Endothiodon* zone lies conformably on the *Tapinocephalus* zone without any radical change in lithological character—the only noteworthy feature being the increase of the number of purplish bands indicating more periods of somewhat drier conditions. There was also no sudden development of competitors or antagonists.

The only reason for the sudden extinction of the Dinocephalia I can advance is that they went to seed in too favourable living conditions, aggravated by the pathological pachyostosis induced by a pituitary hypertrophy.

The Gorgonopsia, represented by two families from low down in the *Tapinocephalus* zone, had by then already developed all the characters typical of this suborder and during the Middle Permian show no further development. They constituted a very minor element in the fauna of these times. This suborder of rather primitive therapsids is represented in the higher zones of the Beaufort beds to form a much more important element in the fauna.

The Hipposauridae, forming a very distinctive family, is not represented in the *Endothiodon* zone, but in the *Cistecephalus* zone we know three further genera. Thus they become extinct at the top of the Upper Permian.

The suborder is further represented in the *Endothiodon* zone by 13 genera and in the *Cistecephalus* zone, by 48 genera and these have been subdivided into as much as 17 discrete families, indicating that during the Upper Permian this suborder really went to town and during this period constituted an important element of carnivorous forms in the fauna.

Their span of life came to an abrupt end at the close of the Permian.

This second developmental trend of the early therapsids thus had a life-span extending through the whole of the Middle and Upper Permian. During this period the gorgonopsians manifest but minor variations and retain such a uniform morphological pattern that the subdivision into separate families can at most be considered as of taxonomic convenience.

They form an interesting group of fairly long-lived primitive therapsids suddenly present at the beginning of the Middle Permian with their distinctive

cachet fully developed in one bound and wholly sterile.

It is of interest to note that the gorgonopsians, apparently of Cisuralian origin, have only three genera in the Russian Upper Permian. *Inostrancevia* is a giant gorgonopsian, whereas the aberrant *Proburnetia* is very similar to *Burnetia* of the Karoo.

The Dicynodontia, with two families in the Middle Permian, numerically rich in individuals, formed a significant element in the fauna as the sole assemblage of small herbivores preyed on by the smaller to medium sized carnivores of those times. With a fully developed morphological pattern from the base of the Middle Permian they waxed exceedingly until becoming extinct in the Middle Trias.

The basic pattern, fully developed at the beginning of the Middle Permian, remains unchanged during their long span of life. But in the Upper Permian a mass of small variations occur as witnessed by the fact that over 200 species have been named. During these times the dicynodonts were extremely abundant, by far outnumbering all their contemporary therapsids and constitute the bulk of the herbivores on which the gorgonopsians preyed.

In the Lower Trias the lystrosaurids were very nearly the only herbivores preyed on by some small cynodonts and the predaceous *Chasmatosaurus*.

In *Cynognathus* zone times we get the kannemeyeriids forming the end of this line of development, which during its long span of life continued basically unchanged and sterile.

The Dicynodontia, with the Cisuralian form *Otsheria* as starting point, had but five descendant genera in Russia, but since the Upper Permian have spread to Scotland, China, Indo-China, North and South America, India and Antarctica.

Thus, notwithstanding their innate inability to escape from their confining basic structural pattern they were very adaptable herbivorous reptiles, well able to fit into all the vicissitudes of the environmental changes encountered from the moist Middle Permian to deep into the arid Trias in six of our present continents.

The Therocephalia with four families and 18 genera in the *Tapinocephalus* zone form an important element of the contemporary fauna forming the small to medium sized insectivores and carnivorous predators of their time.

The Pristerognathidae continue into the Upper Permian with three genera in the *Endothiodon* zone and one in the *Cistecephalus* zone.

The Alopecodontidae have no representatives in the *Endothiodon* zone but there are two genera in the *Cistecephalus* zone.

The Scaloposauridae continue into the Trias with two genera in the *Endothiodon* zone, 14 in the *Cistecephalus* zone and one in the *Lystrosaurus* zone.

In the Upper Permian five new families make their appearance, indicating a continued virile variability. In *Euchambersia* we have the first poisonous reptile with a poison gland and an appropriate fang.

In the specialized Whaitsiidae we find a tendency towards the develop-

ment of a secondary palate and the closure of the suborbital fenestra.

Of the Akidnognathidae and Ictidosuchidae there are in the Upper Permian nine genera of small advanced therocephalians.

In the *Cynognathus* zone there are nine genera of small to medium-sized Bauridae more advanced than the Scaloposaurids from which they arose.

In the Red Beds there follow the Tritylodontidae and in the Cave Sandstone we have the Diarthrognathidae.

The Cynodontia, appearing for the first time in the *Cistecephalus* zone, if not developed independently and directly from the pelycosaurs can only be derived from the Therocephalia.

In this versatile assemblage the later branches exhibit various trends towards the mammalian condition particularly in regard to the braincase, the dentition, the secondary palate, the reduction of the posterior mandibular bones and the establishment of an articulation of the dentary directly to the squamosal.

Of the four suborders of the therapsids, developed from pelycosaur ancestors before the beginning of the Middle Permian, the Dinocephalia, Gorgonopsia and Dicynodontia have been proved phylogenetically sterile.

Only the more plastic and versatile Therocephalia developed upper branches approaching structural levels very close to that of the first mammals and it seems reasonable to assume that one or more of these trends did actually culminate in the first mammals.

This phylogenetic success of the Therocephalia can be attributed to a number of factors. In the initial stages most of the primitive conservative structural patterns were bred out and a great amount of plasticity was retained by developing at a moderate tempo without any extravagant variations. In some of the later branches, as exemplified by *Euchambersia* and the whaitsiids, such sterile developments were however not avoided, but there was always a plastic core retained.

From the start excessive size was avoided, except in some pristerognathids and lycosuchids which soon petered out. Together with the small size there was the acquisition of an agile locomoter potential and this ability to live an active mobile life ensured their ultimate success.

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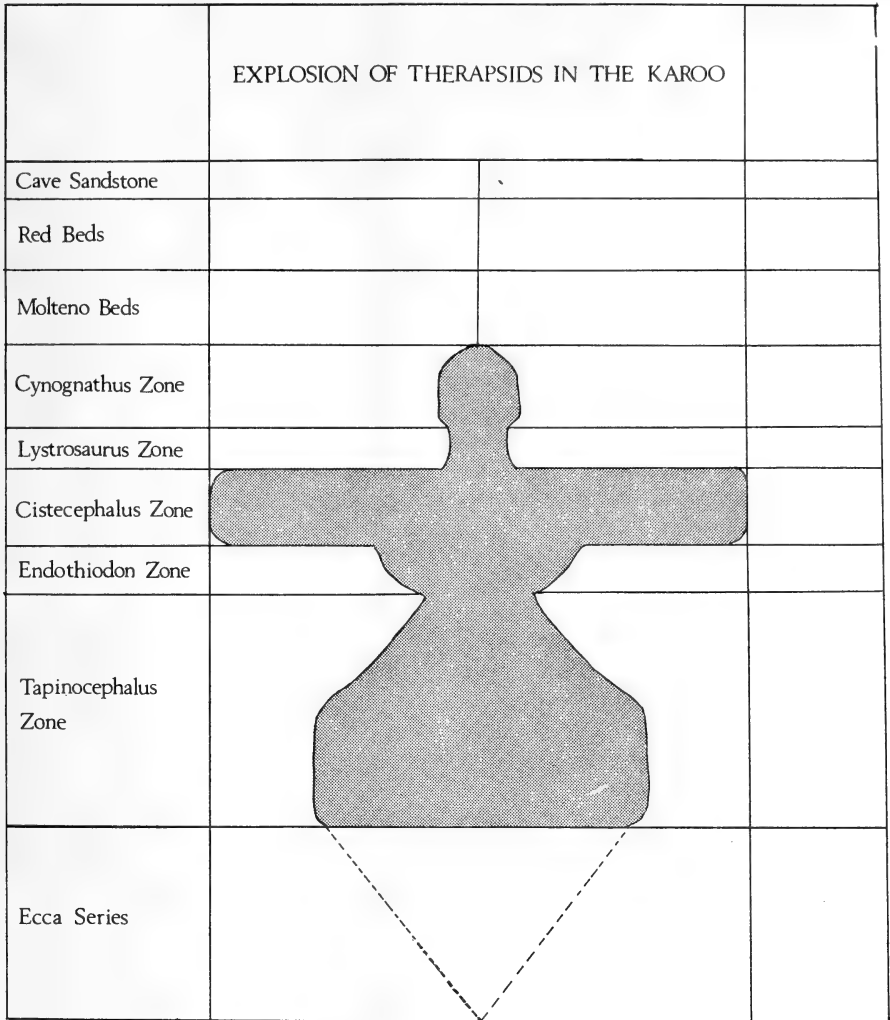


FIG. 1. The therapsid explosion in the Karoo.

This diagram very effectively illustrates the main features of the faunistic history of the therapsids during Permo-Triassic times.

The therapsids, arising in Cisuralian Russia in the Lower Permian, spreading southwards entered the Karoo Basin at the beginning of the Middle Permian as a well-established and diversified order of reptiles. In the cool, moist, equitable climate then prevailing in the Karoo they quickly established themselves as the dominant land vertebrates.

This initial burst slackened off towards the end of the Middle Permian.

But in the Upper Permian, with its more varied climate, in which periods of warmer drier conditions alternated with fairly cool and moist periods, in a further and greater expansive burst the therapsids attained their maximum faunistic development.

With the drastic ecological changes in the *Lystrosaurus* zone (lowest Triassic) with its heavy rains and marshes in a warmer climate, the therapsids all but petered out.

Later in the Triassic, in drier and sometimes arid conditions, only those therapsids far advanced in a mammal direction extended the life span of the therapsids, but now they were faunistically overshadowed by the sauropsid explosion which then came under way.

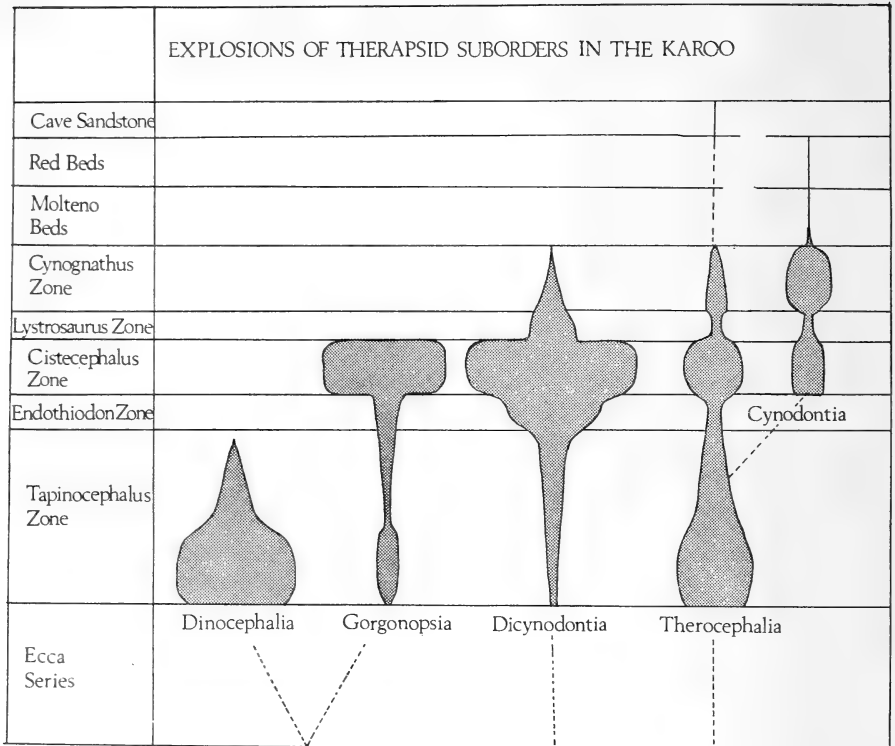


FIG. 2. The explosion of the therapsid suborders in the Karoo.

The Dinocephalia, arising in Russia in the late Lower Permian, entered the Karoo Basin as a diversified suborder and immediately became the dominant therapsids. But they quickly shot their bolt and from the middle of the Middle Permian declined rapidly to become extinct before the Upper Permian. Thus ended the first sterile therapsid trend towards an actively mobile life on firm land of some altitude.

The Gorgonopsia and Dicynodontia, entering the Karoo Basin fully fledged, but in a subordinate faunistic role, became the dominant therapsids in the Upper Permian. The predatory Gorgonopsians came to an abrupt end as the second sterile trend towards life on drier ground when the marshes of the *Lystrosaurus* zone made life for their herbivorous prey impossible on dry land, coupled with the predators' inability to pursue the surviving lystrosaurids into the marshes. The herbivorous Dicynodontia, adapted to upland life, found the swampy conditions of the *Lystrosaurus* zone all but impossible and only the lystrosaurids could adapt themselves, but this temporary success proved their final undoing and in the later dry to arid Triassic only the kannemeyeriids could eke out an existence.

Thus ends the third therapsid attempt towards an active mobile life on firm land.

The Therocephalia entered the Karoo Basin as a diversified suborder with two families in a strong predaceous role and two in an insectivorous role. The predators flourished in the Middle Permian but were ousted from this role by the gorgonopsians in the Upper Permian. The more insectivorous families continued successfully into the later Triassic, but were overshadowed faunistically (except for their cynodont offshoot) by the upsurging sauropsids. This fourth trend of the therapsids towards upland active life proved to be genetically fertile in that they gave rise to the first mammals in the Upper Triassic.

Tapinoceph

Dicynodontid



St



Endothiodontid



diagrammatic phylogeny of the early therapsids.
 phenacodontid represented by *Haptodus*
 protitanosuchid represented by *Eotitanosuchus*
 lithopid represented by *Syodon*
 anteosaurid represented by *Anteosaurus*
 tanosuchid represented by *Jonkeria*
 styracocephalid represented by *Styracocephalus*
 tapinocephalid represented by *Tapinocephalus*
 phthinosuchid represented by *Phthinosuchus*
 hipposaurid represented by *Hipposaurus*
 alesuchid composite of the early genera
 trochosuchid represented by *Trochosaurus*
 asterognathid represented by *Glanosuchus*
 blattoidealestes represented by *Blattoidealestes*
 otsheriid represented by *Otsheria*
 dicynodontid represented by *Dicynodon*
 endothiodontid composite of early genera
 tomasaurid represented by *Galeops*.

Otsheriid



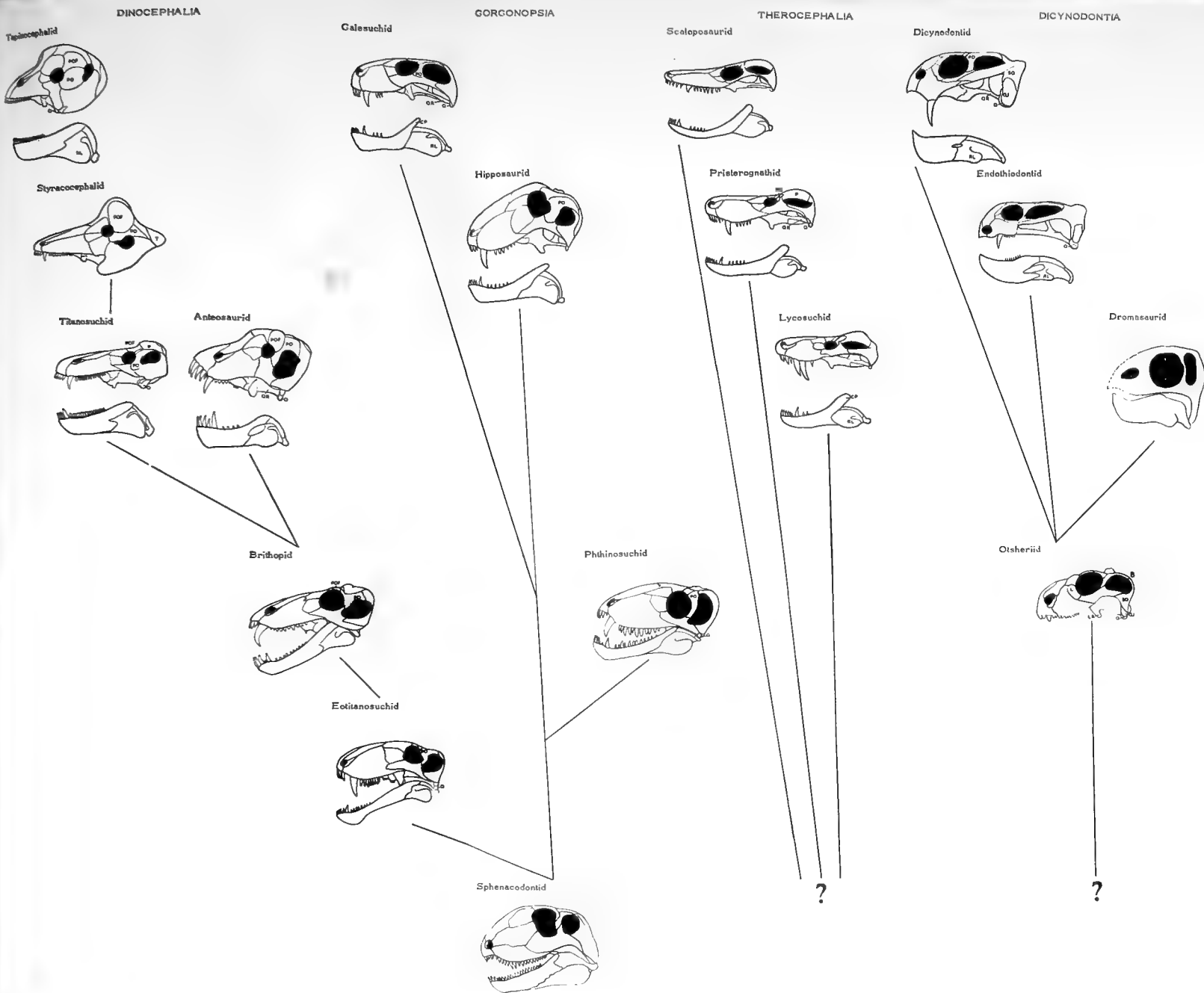


FIG. 3. A diagrammatic phylogeny of the early therapsids. Sphenacodontid represented by *Haptodus*. Eoitanosuchid represented by *Eoitanosuchus*. Brithopid represented by *Syodon*. Anteosaurid represented by *Anteosaurus*. Titanosuchid represented by *Jonkeria*. Styraecocephalid represented by *Styraecocephalus*. Tapinocephalid represented by *Tapinocephalus*. Phthinosuchid represented by *Phthinosuchus*. Hipposaurid represented by *Hipposaurus*. Galesuchid composite of the early genera Lycosuchid represented by *Trochosaurus*. Prieterognathid represented by *Glanosuchus*. Scaloposaurid represented by *Blattoidealestes*. Otsheriid represented by *Otsheria*. Dicynodontid represented by *Dicynodon*. Endothiodontid composite of early genera Dromasaurid represented by *Galops*.

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- (4) Summary.
- (5) Acknowledgements.
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LARVAL DEVELOPMENT OF THREE SPECIES
OF ECONOMICALLY IMPORTANT
SOUTH AFRICAN FISHES

By
E. H. HAIGH

Cape Town Kaapstad

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By
E. H. Haigh

South African Museum, Cape Town

(With 11 figures and 9 tables)

[MS. accepted 1 September 1971]

CONTENTS

	PAGE
Introduction	47
Material and methods	49
Description	50
<i>Merluccius capensis</i>	50
<i>Thyrsites atun</i>	55
<i>Helicolenus dactylopterus</i>	60
Distribution	69
Summary	69
Acknowledgements	69
References	69

INTRODUCTION

This paper is the first of a series of studies on larval fish development. Mainly economically important species will be described although other species of interest will also be included.

The species described in this paper are *Merluccius capensis*, the Cape stockfish, *Thyrsites atun*, the snoek, and *Helicolenus dactylopterus*, the jacobever.

The Cape stockfish or hake is of great economic importance in South Africa. The annual trawled catch has ranged from 68 019 223 to 70 686 775 kilo over the five years from 1961 to 1965 (*Ann. Rep. Div. Sea Fish. S. Afr.* 33). At the end of 1970 the trawled landings were reported to be 64 million kilo. Irvin & Johnson (1963) give an account of the economic importance and habitat of the adult. Although the adult is almost exclusively demersal, the larvae are caught in plankton nets, indicating a pelagic mode of life. However, the number of larvae, especially the older, larger forms, is relatively small in the samples.

The snoek is an important predator of the pilchard *Sardinops ocellata* and related pelagic fish. It is a large rapacious carnivore, with excellent, firm flesh and thus also an important seasonal food fish in South African waters. Annual catches vary between 7,2-9 million kilo per annum.

The jacobever is uncommon in fishmarkets around the coast, the larger number being caught in trawls and used in fishmeal manufacture. Between 1961 and 1965 the landings ranged between 857 427 and 1 487 624 kilo (*Ann.*

Rep. Div. Sea Fish. S. Afr. 33). Smith (1953) reports its flesh to be palatable. However it does not constitute a major portion of the fishing resources of the country.

Davies (1949) states that *Helicolenus* inhabits waters between 90 and 360 metres. It is a bottom-dwelling fish usually on the continental shelf. Superficially it is very like the Tristan da Cunha scorpaenid *Sebastichthys capensis* and several authors have reported both genera to be viviparous. Specimens between 3.5 and 4.2 mm standard length had well-developed jaws (indicating functionality) and several head spines. Davies (1949) suggests a November spawning season, Ahlstrom (1961) on the other hand suggests a winter and early spring release of young of *Sebastodes* spp. on the west coast of the United States. Moser (1967) states that there are two broods released in *Sebastodes paucispinis*, one in autumn and one in spring. The majority of samples in our collection were caught in late spring, October. These represent a complete range in sizes. As the collection is not very large, no conclusions can be drawn from this.

The three species described in this paper are classified as follows:

Order:	Gadiformes	Perciformes	Scorpaeniformes
Suborder:	Gadoidei	Scombroidei	Scorpaenoidei
Family:	Merlucciidae	Gempylidae	Scorpaenidae
Genus:	<i>Merluccius</i>	<i>Thyrsites</i>	<i>Helicolenus</i>
Species:	<i>capensis</i>	<i>atun</i>	<i>dactylopterus</i>
	Castelnau 1861	Euphrasen 1791	Delaroche 1809

The family Merlucciidae is distinguished by a separate caudal fin. According to Norman (1937, 1966) it has one genus comprising seven species, three in the northern and four in the southern temperate zones. Although Gilchrist (1921) and Barnard (1925) doubt the distinction made between the European species *Merluccius merluccius* and *M. capensis*, Norman (1937) confirms Regan's (1908) distinction. Ginsburg (1954) sheds more light on the American species of the Merlucciidae.

The Gempylidae is a small family comprising 10 genera each with only a small number of species. Its taxonomic history seems to have been untroubled.

The taxonomy of the family Scorpaenidae needs world-wide revision. Eschmeyer (1969) gives a good review of the Atlantic Scorpaenidae, synonymizing *Helicolenus maculatus* with *H. dactylopterus* and separating the Tristan da Cunha species from *H. dactylopterus*. However, he does state that the gradient in characters is rather disjointed and that a conclusive synonymy needs a more comprehensive study of material.

Eggs and larvae of *Merluccius merluccius* have been described by Ehrenbaum (1909) and D'Ancona (1933); of *M. bilinearis* by Kunz & Radcliffe (1917); of *M. productus* by Ahlstrom & Counts (1955). Marak (1967) describes the early pro-larvae of *M. albidus* and distinguishes them from the pro-larvae of *M. bilinearis*. Fischer (1959) describes eggs and pro-larvae of *M. gayi* from Chile

as do Santander & Castillo (1969) from the coast of Peru. Hart & Marshall (1951) report a larval *Merluccius capensis* between 19° and 22°S, extending the possible range further north than this present survey. Matthews & De Jager (1951) described the development of the egg and pro-larva of 2,35 mm for *M. capensis*. Larvae of the genus *Merluccius* show a basic similarity in pigmentation, allowing for easy recognition.

Larvae of species of the family Gempylidae have been described: *Gempylus serpens* by Jones (1960); *Nesiarchus nasatus* and *Gempylus* spp. by Voss (1954) and *Thyrsites atun* by Regan (1914-16). De Jager (1955) described the development of artificially fertilized eggs and resultant larvae of *Thyrsites atun* up to the age of nine days and a length of 3,9 mm. In the present paper the development from 4,6 mm to 25 mm is described, thus completing the description of *Thyrsites atun* development.

In the family Scorpaenidae larval development of two species of *Sebastodes* has been described by Ahlstrom (1963) and *Sebastes marinus* has been described by Bigelow & Welch (1924). A paper on the distribution of *Sebastodes* spp. in Californian waters was published by Ahlstrom in 1961. In this paper he discussed briefly the distinguishing features of some scorpaenid larvae in the eastern North Pacific. However, Moser (1967) gives the complete development of *Sebastodes paucispinis* and gives illustrations and a list of characters of early stages for 14 further species.

MATERIAL AND METHODS

Specimens were obtained by research vessels of the Division of Sea Fisheries, Cape Town, using N100B and N100H plankton nets, from 1950 to 1967. Samples were fixed and stored in formalin which was replaced by 70% ethyl-alcohol. Specimens were stained, using the methods of Hollister (1934), Davies & Gore (1935) and Moran (1956) but modified slightly by reducing the clearing time in KOH and reducing the concentration of the KOH used. This was done in order to preserve the pigment of the specimens. As pigments are inclined to fade, more than one larva in the size range was used in order to obtain the most characteristic pigmentation pattern. Stained specimens were preserved in glycerin and ethyl-alcohol.

Measurements were taken as follows:

- standard length (s.l.): tip of lower jaw to caudal peduncle
- snout: tip of lower jaw to anterior edge of eye
- eye diameter
- head length: tip of snout to posterior edge of cleithrum
- trunk: tip of snout to posterior edge of anus and not to anal fin insertion
- depth: at pelvic fin insertion
- pelvic and first dorsal spine lengths for *Thyrsites atun* only

All proportions presented as percentage of standard length. All lengths cited in text are the standard lengths of the specimen.

Some specimens that should have been well ossified did not absorb stain properly. This was most probably due to decalcification of the bone by formalin. Vertebral counts include urostylar complex which is counted as two.

DESCRIPTION

Merluccius capensis

Merluccius capensis is characterized by 130–140 scales in longitudinal series, 13–14 gillrakers in lower part of anterior arch and a pectoral with 13–14 rays reaching to beyond the origin of the anal, while the pelvic extends nearly to the vent. Depth is 60% of length and headlength is 32–36% of length. The maxillary extends to below the posterior edge of the pupil or beyond and is less than half of head-length. D:10–11; 35–40. A:37–40 (Norman 1937).

Pigmentation

The general pigmentation pattern of *M. capensis* is similar to that of *M. merluccius* as described by Ehrenbaum (1909) and D'Ancona (1933). The major pigmentation on the head consists of one or two large stellate melanophores situated at the postero-dorsal edge of the brain and anterior to the first dorsal fin—occipital spot. The dorsal peritoneal wall is always darkly pigmented with both stellate and closed chromatophores.

The tails of most larvae examined bear three areas of pigmentation. An anteropostanal spot situated latero-ventrally just behind the anus; a larger mediopostanal spot, covering the whole lateral surface of the tail, midway between the anus and the caudal fin; and one or two stellate melanophores comprising the caudal spot situated latero-ventrally on the caudal peduncle.

These pigmented areas are characteristic of the species and are to a greater or lesser extent augmented by smaller stellate and contracted melanophores at the dorsal aspect of the head and ventral aspect of the abdomen. These vary a great deal in intensity within a size group but generally increase in size with age during larval life.

In the early post-yolk-sac stage larvae (Fig. 1a) the head bears a pigment spot on the anterior edge of the brain which becomes obscured as the larvae get larger and ossification commences. The cerebral area of the head is further dotted with a varying number of melanophores. With further development, melanophores may also appear on the jaw, around the eyes and on the opercular surface of the head (Figs 1d, 2a).

Peritoneal pigmentation remains fairly constant throughout development. The melanophore anterior to the first dorsal fin becomes augmented by smaller stellate melanophores along the sides of the first dorsal and later the second dorsal fin.

The anteropostanal, mediopostanal and caudal spots remain relatively the same size throughout the larval life but in prejuvenile and juvenile stages,

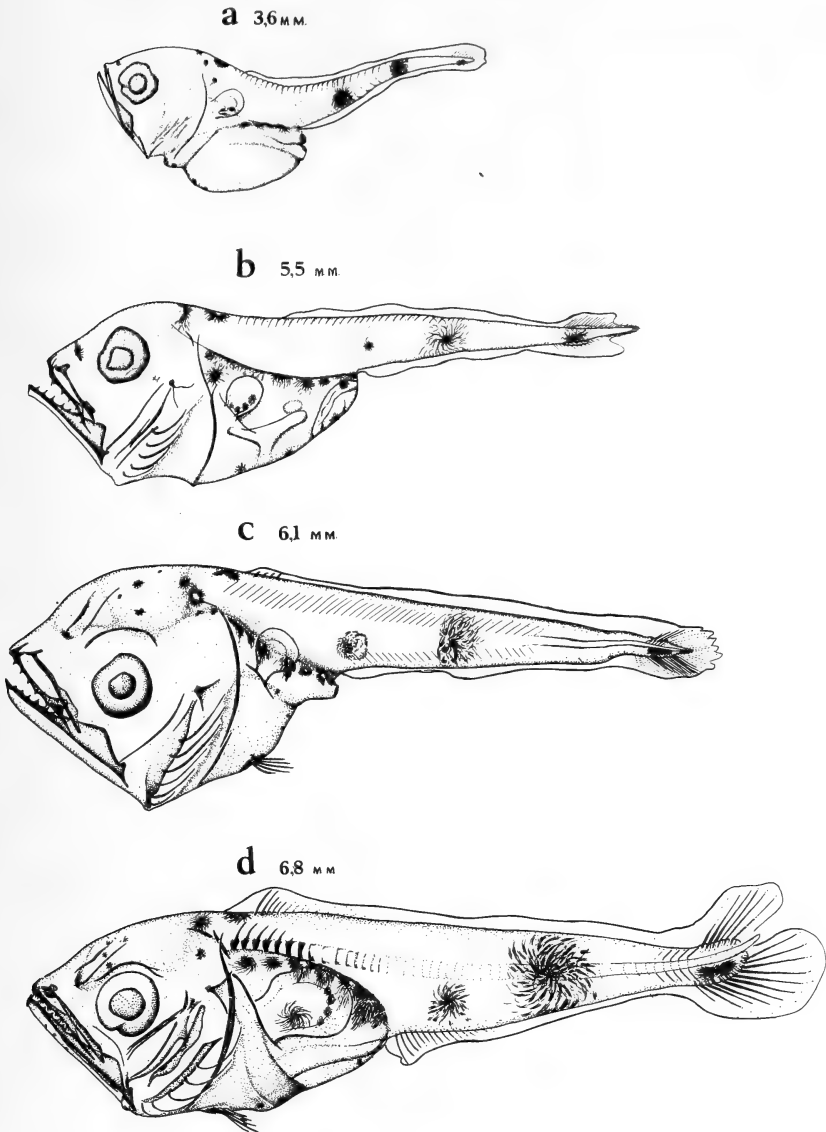


FIG. 1. *Merluccius capensis*

Early larval stages showing position of major pigmentation areas and ossification development. Measurements indicate standard length.

they appear to become smaller and more discrete. They probably break up to form the smaller melanophores that abound on the dorsolateral sides of the juvenile (Fig. 2c).

Small, discrete pigment spots are present on the pectoral and pelvic fin-

buds of some of the larvae. As soon as ossification of the pelvic fins is complete, pigmentation appears on both fins. No caudal fin pigmentation was observed.

Pigment spots appeared on the dorsal fin late in the larval and early juvenile stages. Pigmentation was also present on the dorsal head and abdominal surfaces in juveniles.

Ossification

The premaxilla, maxilla, mandible and cleithrum are ossified in larvae 3,6 mm long. The first traces of the gill-arches can be seen in slightly larger specimens. The branchiostegal rays then ossify progressively from dorsal to ventral (Fig. 1b). The premaxilla at 5,5 mm has between four to six teeth and the dentary four to six. The supracleithrum and posttemporal appear as slender rods. By 6,1 mm the epiphyal and ceratohyal are well formed and bear six branchiostegal rays. The first traces of the preopercle, cranial and opercular ridges are ossified and there are eight mandibular teeth. By 7 mm the hyomandi-

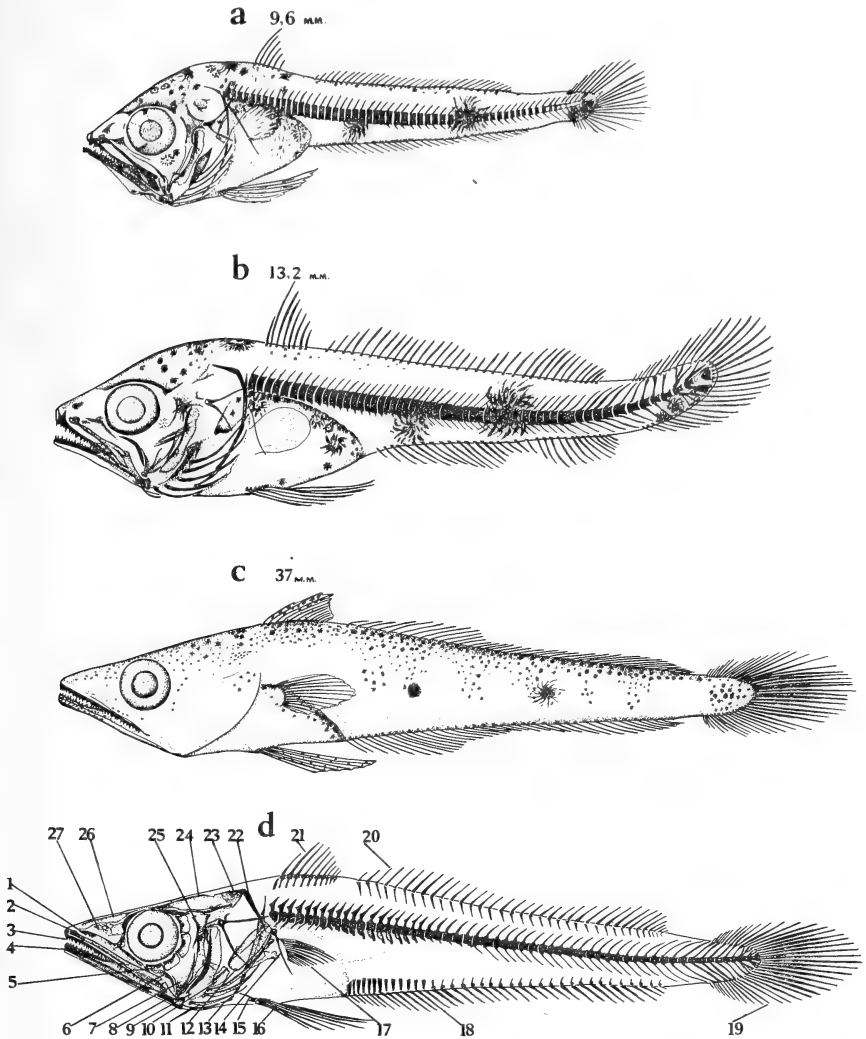
TABLE 1

Ossification of skeletal elements of *Merluccius capensis*

Size in mm	I		II		Vertebrae	Neural spines	Haemal spines	Pectoral rays	Pelvic rays
	Dorsal	Dorsal	Anal	Caudal					
4,5	—	—	—	—	—	3	—	—	—
5,4	—	—	—	6	—	4	—	—	2
6,0	—	—	—	8	—	6	—	—	3
6,6	2-3	—	—	12-14	8-13	8-10+2-5	3-5	—	5
6,9	3	—	—	15	12+5	8+5	4	—	6
7,8	5-7	6-8+4-5	15-17+	20-21	41-42	50-54	24-25	—	7
			5-7						
9,0	6-7	26	30	19-21	47-49	54	24	—	9
10,2	8	34	33	28	57	54	27	—	9
12,0	9	35	35	30	57	54	29	—	9
14,1	11	32	39	40	57	54	29	7	9

bular can be clearly distinguished and the quadrate has started ossifying in the articular region. The pterygoid has also started forming and the seventh branchiostegal is complete. Other bones have thickened and widened considerably. By 9,6 mm parietal and frontal bones are well formed, the nasals have started ossifying and so have the lacrymals. The first trace of the operculum is present, underlying the opercular ridges. The visible bones in the head have now been fully laid down and further development takes place to reach the juvenile stage between 14 and 16 mm (Fig. 2d).

The anterior neural spines ossify first, followed by the anterior centra. At 6,8 mm the first seven centra and five to eight haemal spines are formed. However, neural and haemal spines of some of the caudal vertebrae also show signs of ossification at this stage. During this growth-period the centra are rapidly laid down and at 9,6 mm all the vertebrae except the five preceding the last centrum have been fully formed. The last vertebra is ossified but the urostyle is still cartilaginous. At this stage the hypural and epural elements show some degree of ossification. Haemal spines are only found from the 26th

FIG. 2. *Merluccius capensis*

a-b. Late larval stages. c. Juvenile. d. Lateral view: 1. Lacrimal. 2. Maxilla. 3. Premaxilla. 4. Dentary. 5. Circumorbitals. 6. Pterygoid. 7. Quadrate. 8. Articular. 9. Preopercle. 10. Subopercle. 11. Branchiostegal rays. 12. Opercle. 13. Cleithrum. 14. Postcleithrum. 15. Pelvic girdle. 16. Pelvic rays. 17. Pectoral rays. 18. Anal rays. 19. Caudal rays. 20. Second dorsal fin. 21. First dorsal fin. 22. Supracleithrum. 23. Posttemporal. 24. Cranial bones. 25. Hyomandibular. 26. Frontal. 27. Nasal.

centrum at this stage, indicating the first 24 to 25 vertebrae to be abdominal. By 13,2 mm all the parapophyses of the abdominal vertebrae, except the first six, have enlarged somewhat. In the juvenile there are 18 abdominal vertebrae bearing parapophyses expanded lateroventrally (Fig. 2d).

Fin formation takes place in the following sequence: pectoral fin bud, caudal buds and pelvic bud between 3,0 and 5,0 mm. In size range 5,0 to 6,0 mm the pelvic rays ossify, then the caudals start, followed by the first dorsals at between 5,5 and 6,8 mm. The anal and second dorsal rays follow almost immediately. Pectoral rays only appear much later. By 6 mm the first five pelvic rays have appeared in the pelvic bud. The caudal buds appear at about 4,5 mm. The ventral caudal rays appear first, followed at 6 mm by the dorsal caudal rays. Several caudal rays seem to ossify simultaneously. In some larvae of 6 mm the basal buds of the first four dorsal rays are also evident.

Although the anal fin starts ossifying only after the first dorsal, its development proceeds faster and by 6,8 mm between six and eight rays are ossified in the anal while only five dorsal rays can be distinguished. The pelvic now has six ossified rays and the caudal has 14.

The pelvic attains its full complement of seven rays at approximately 9 mm. The caudal, dorsal and anal fins have an almost complete number of rays at 13,2 mm but as so few larvae over this size were obtained there is no certainty about the exact size when full ray number is attained. Ahlstrom & Counts (1955) give 16 mm as the size where the full complement of both dorsal and anal fin rays is present in *M. productus*.

Seven pectoral fin rays were observed at 14,1 mm. The juvenile of 37 mm has a full number of 14. *M. productus* larvae only develop pectoral fin rays at 24 mm and later (Ahlstrom & Counts, 1955).

Changes in body form and growth rate

The eye diameter is larger than the snout length in the earlier stages but this difference is gradually diminished and by 6,0 mm they are approximately equal in length. The snout becomes longer than the eye diameter from 10,5 mm s.l.

TABLE 2
Mean measurements in mm and proportions (% of s.l.) of *Merluccius capensis*

Size group	No.	Snout l.		Eye diameter		Head l.		Trunk l.		Depth	
			%		%		%		%		%
2,5-3,49	2	0,13	4,57	0,31	11,12	0,64	22,44	1,71	63,33	0,98	33,05
3,5-4,49	9	0,25	6,57	0,32	8,10	1,07	25,70	1,73	43,35	1,06	26,60
4,5-5,49	21	0,48	9,91	0,53	11,07	1,43	28,39	2,86	46,69	1,40	29,55
5,5-6,49	11	0,62	10,32	0,62	10,32	1,89	31,08	2,80	48,65	1,69	30,60
6,5-7,49	18	0,65	8,65	0,65	8,65	1,96	27,10	3,23	46,54	1,66	26,09
7,5-8,49	13	0,71	9,67	0,73	9,36	2,30	30,24	3,66	46,61	2,03	25,81
8,5-9,49	1	0,90	10,00	0,90	10,00	2,40	26,66	4,20	46,66	2,10	23,33
9,5-10,49	8	0,97	8,86	0,90	9,22	2,92	30,01	4,60	47,55	2,40	25,02
10,5-11,49	6	1,05	9,73	0,90	8,33	3,20	30,09	4,90	45,35	2,40	22,71
† —											
13,5-14,49	3	1,30	9,33	1,10	7,88	3,70	26,57	6,20	44,63	3,00	21,60
* 20,40	1	1,80	8,82	1,50	7,35	6,60	32,35	9,60	47,05	4,20	20,58
26,60	1	2,10	7,89	1,80	6,76	7,20	27,06	11,40	42,85	5,10	19,17
36,30	1	3,80	10,46	2,80	7,71	11,30	31,12	17,00	46,83	7,50	20,66
41,00	1	4,50	10,97	3,00	7,31	13,00	31,70	19,00	46,34	8,00	19,51
46,00	1	5,00	10,86	3,00	6,52	13,50	29,34	21,20	46,08	8,00	17,39

† Two size groups not obtained in the samples.

* Specimens no longer fall into size groups.

The head is 24% of the standard length in the smallest stages (2,9 to 4,4 mm), increasing to 28% at 4,5 to 5,4 mm and remaining 25 to 32% of standard length for the rest of development from 5,5 to 46 mm. The head shows an average rate of increase of 0,36 mm for each millimetre increase in standard length.

The proportion of the trunk to the standard length varies between 42 and 48% but is usually about 45% throughout development and can be used as a taxonomic character (Ahlstrom & Counts, 1955). The trunk shows an average increase of 0,47 mm/mm increase of standard length. Up to a length of 9,75 mm the depth increases 0,23 mm/mm increase in standard length, but between 9,75 mm and 13,2 mm the increase is only 0,127 mm/mm increase in standard length. Thus the hake changes from a rather deep tadpole-like post-larva to a slender, evenly sloping juvenile (Fig. 2c).

Thyrsites atun

The snoek is characterized by the maxilla reaching slightly beyond the anterior border of the eye, the long mandible projecting the upper jaw and reaching to the posterior third of the eye. Both jaws carry large canines. The caudal is deeply forked.

D: 18-21 + 10-12 + 6. A: 1-2 + 8-11 + 6. Pectoral: 2 + 11. Pelvic: 1 + 5. Vertebrae: 34-35. Depth \pm 7 (Smith 1953; Fowler 1936; Beaufort & Chapman 1951: 199).

Pigmentation

Standard pigmentation in larvae of *Thyrsites atun* between 4,0 and 10,0 mm consists of a variable number of small stellate and closed melanophores over the snout and cerebral areas of the head. A dark area of pigmentation, standard in all larvae, is found on the antero-dorsal and lateral areas of the peritoneum. Small scattered spots are also to be found posteriorly, above the anus. The pigmentation is darker in smaller specimens of four to six millimetres, becoming more diffuse and evenly distributed as the fish grows larger. When the snoek larvae are 11 to 15 mm long, abdominal pigmentation consists of scattered stellate melanophores.

Most characteristic and stable are the two areas of tail pigmentation. On the ventral surface of the tail, midway between anus and anal fin, is a smaller spot consisting of only one melanophore. Also ventrally situated is the posterior pigment area between the anal and caudal fin. This spot consists of several stellate melanophores clustered together, and covers two to three times the area of the anterior pigment spot. However, these areas of tail pigmentation do not appear in the specimens figured by De Jager (1955). I have had occasion to examine the specimens of De Jager and his figures agree reasonably well with the specimens. It would appear that rapid migration of pigment takes place in early larval life. The pigment pattern described above is only evident in the last stage of De Jager's larvae at 3,9 mm but unfortunately is not obvious

in his Figure 18. The two tail pigment areas only disappear in juveniles over 16 mm and constitute a good diagnostic feature for the larvae of the species.

The characteristic black dorsal pigmentation of the adult snoek begins to show up in larvae of 6,0 mm. On each side of the dorsal spines a thin line of black pigment appears, which becomes thicker and more obvious as the larvae grow. This line is characteristic of the Gempylidae. None of the fins shows pigmentation during development (Fig. 3).

Ossification

At 4,6 mm the premaxilla with four teeth, the maxilla, and the mandible with two teeth are ossified as well as the cleithrum. Ossification of the preopercle has begun and two spines may be distinguished on the margin as well as one small spine originating in the middle of the preopercle in line with the

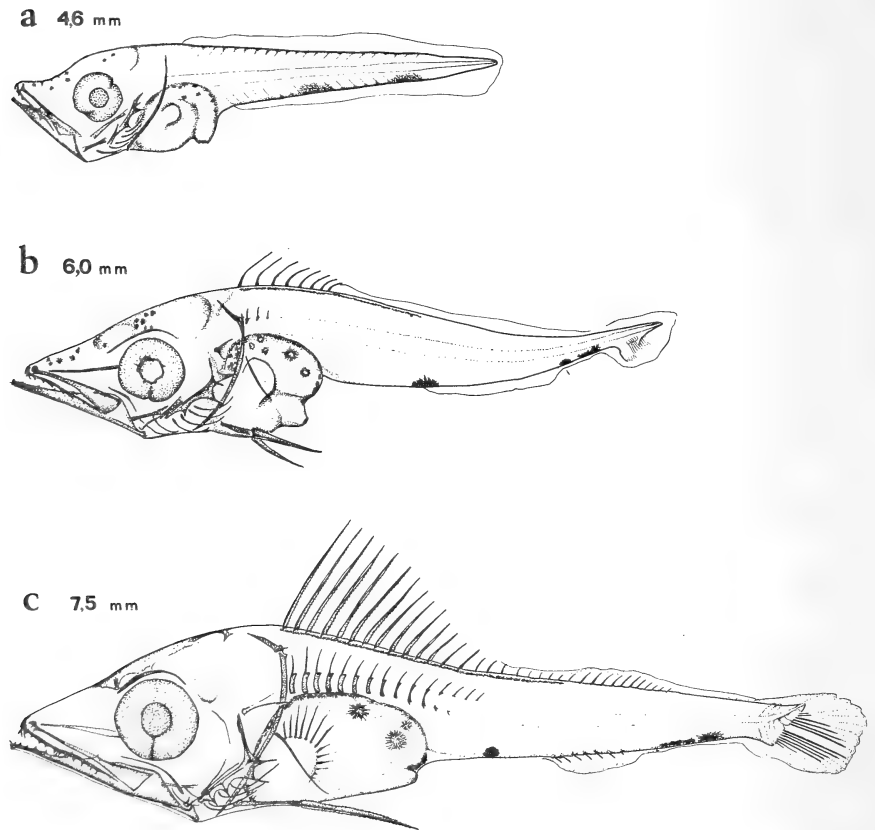


FIG. 3. *Thyrsites atun*

Early larval stages showing position of major pigmentation areas and ossification development. Measurements indicate standard length.

most dorsal spine. The first gill arches and five branchiostegals are formed.

Between 5 and 6 mm the premaxilla develops four more teeth and the anterior canines also start developing. The mandibular teeth increase to six. The palatine is clearly visible. Preopercular spines increase to four and the branchiostegals to six. Traces of the pterygoid, quadrate, symplectic, and opercle are ossified as well as the posttemporal and postcleithrum. The ceratohyal can also be faintly discerned. By 8 mm traces of the hyomandibular are laid down and the preopercular spines increase to five. By 10 mm palatine teeth develop. The cranial bones have by now become clearly ossified and traces of the subopercle are present. By 11,5 mm traces of the nasals can be seen, the fangs are well developed (two on each side) and three palatine teeth are present. The subopercle is quite clear and the hyomandibular is well formed. By 20,0 mm the jaws are heavily ossified, the preopercle has assumed a more median position and the six preopercular spines are not as obvious as before. The quadrate is well ossified, obscuring part of the symplectic. Frontal and parietal bones are well formed but there are still wide gaps between them. The bones of the pectoral girdle have become much wider and flanges have developed on the posttemporal and cleithrum.

There are no traces of ossification in the vertebral column at 4,6 mm, but between 5,4 and 6,0 mm the basic elements of the neural spines appear in some specimens. At 6,6 mm at least three, usually more, neural spines are ossified. Between 6,6 and 7,2 mm the first centra of the vertebrae become ossified and by 9,75 mm at least 18 vertebrae are ossified. By 8,15 mm the first haemal spines appear. The ossification of the vertebral spines exceeds that of the centra. The full complement of the haemal spines is ossified at 11,4 mm. Of these, 11 are shorter abdominal and 14 to 15 are larger caudal spines. Only at 13 to 14 mm is the full complement of neural spines laid down and by 14 mm the vertebral centra are also fully ossified.

The vertebral centra ossify from the dorsal and ventral peripheries inward, except for the last three vertebrae where ossification proceeds dorsally from the ventral periphery. In these three vertebrae the neural spines also form later than in the other vertebrae. The snoek has 21 abdominal and 13 to 14 caudal vertebrae.

The urostyle begins to turn up at 7,2 mm and the first traces of urostyle and hypural ossification are evident at 9,0 mm. At 11,0 mm the urostyle is fully ossified and bears two dorsal and three ventral hypural elements. The haemal spines of the ultimate and penultimate vertebrae have broadened to support the caudal fin.

The pectoral lobe is evident at 4,5 mm but the first fin ossification appears in the pelvic spine at 5,4 mm. By 6,0 mm the initial ossification of the pelvic girdle has started and by 8,15 mm the pelvic spine has achieved its characteristic serrate appearance and proportional full length. The pelvic rays develop gradually until the full complement of five is attained at 14,0 mm.

The first dorsal fin starts ossifying anteriorly between 5,5 and 6,0 mm

and this proceeds rapidly posteriorly. At 7,2 mm there are 10 to 13 rays present, the most anterior having become hard and serrate. The second dorsal fin has traces of 10 to 15 rays ossified at 8,15 mm and at 9,5 mm the distinction between the first and second dorsal is clear. There are 19 to 20 spines and 12 to 16 soft rays. However it is not until later in the juvenile stage that the finlets differentiate from the second dorsal. The only distinction that can be made, even at 20 mm, is that the last five rays are more widely separated than the rest.

TABLE 3

Table of skeletal elements of *Thyrsites atun* larvae at different stages

Size in mm	No. of specimens	Pectoral	Pelvic	Caudal	Dorsal		Anal	Haemal spine	Neural spine	Vertebrae
					I & II					
5,1	2	0	0	0	0	0	0	0	0	0
5,4	6	0	0	0	0	0	0	0	0	0
6,0	5	0	1	0	4-8	0	0	0	0	0
6,6	6	0-4	1	0-4	9-13	0	0	0	0-3½	0
7,2	6	4-6	1	5-8	10-13	0	3-6	0	7	6
8,0	6	7-9	1	10	15	+10	7-10	5-10	17	15
9,5	6	12	1	17	19	+14	11-12	16-19	20-27	18-20
11,4	5	13	1+2	17+5	19	+17	13	23-25	28-32	25-28+2
14,0	1	13	1+5	17+12	19-20+16-17		1-2+14	23-25	34	34-36
20,0	1	14	1+5	17+10	21	+16	2+15	26	35	36-37

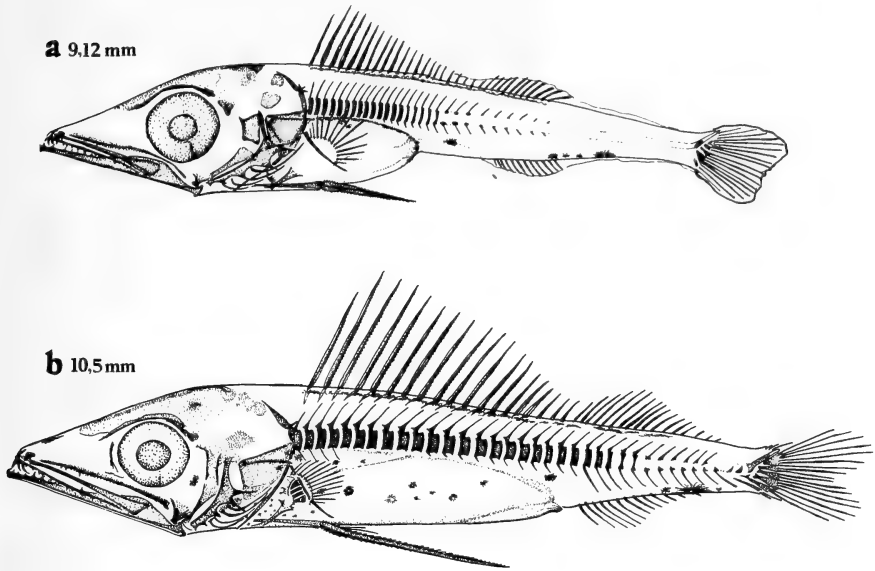
The next fin-rays to ossify are those of the caudal and pelvic fins which do so almost simultaneously between 6,0 mm and 6,6 mm. At 8,0 mm there are seven to nine pectoral rays and at 9,5 mm 11 to 13, while the pectoral girdle has started to ossify. At 11,5 mm the coracoid, scapula and radials have formed. In the caudal fin the ventral fin-rays are completed first, followed shortly after by the dorsal rays at 9,5 mm. Between 10 mm and 15 mm the secondary caudal rays appear. By 14 mm the caudal fin is fully ossified except for some small secondary fin-rays. The caudal has eight ventral and nine dorsal primary rays.

The last fin to start ossifying is the anal fin. By 7,2 mm only traces of the first three to six rays are laid down and by 8,15 mm at least the first seven rays are ossified. The full complement of 16 rays is only laid down by 14 mm. In the specimens examined, the large majority had only one anal spine; a few had anal fins with two spines. As with the second dorsal fin, the anal finlets are not differentiated until late in the juvenile development.

The dorsal spines increase rapidly in actual and relative length between 6 and 7,5 mm and remain at 13 to 14% of standard length till 14 mm length is reached. After this the relative length decreases somewhat to about 8% of standard length by 21 mm.

Changes in body form

The very young snoek larva has a large head and short abdomen with a fairly long tail (Fig. 4a). The head is 30,6% of standard length at 5,4 mm and increases to 35,2% by 8,5 mm, more or less retaining that proportion till the juvenile stage is reached where it diminishes proportionately as standard length increases. The head increases by 0,42 mm/mm increase in standard length

FIG. 4. *Thyrsites atun*

Larvae showing increase in size of area occupied by viscera.

between 4,08 and 14,25 mm. After this size is reached, increase in head length appears to decrease and reach 0,225 mm/mm increase in length.

The snout is 37% of the head length. Initially the snout is only 0,09 mm longer than the eye diameter, but this difference increases with age until at 21,0 mm the snout length is 1,05 mm greater than the eye diameter (Table 4).

TABLE 4

Mean proportions of *Thyrsites atun* larvae presented as % of s.l.

Size range of standard length in mm	No. of larvae	Head	Depth	Trunk	1st Dorsal
4,08-5,49	11	30,6	21,4	42,0	—
5,5-6,49	7	32,6	21,2	45,1	7,4
6,5-7,49	22	32,6	20,6	47,9	11,0
7,5-8,49	13	35,2	21,0	55,2	13,2
8,5-9,49	11	37,8	20,8	64,8	14,7
9,5-10,49	7	36,8	20,0	66,03	13,7
10,5-11,49	3	37,5	19,7	71,2	14,7
12,6	1	35,7	20,2	69,0	13,0
13,5	1	35,5	18,8	64,4	13,3
14,0	2	36,2	21,2	74,8	13,8
20,17	2	33,0	16,2	76,2	11,1
21,0	1	31,4	16,1	73,3	8,5

The ante-anal length or trunk length is initially 42,0% of the standard length. This, however, does not remain constant but increases as shown in Table 4. As far as can be judged from material available, the area occupied

by the intestine and viscera increases rapidly as the larva reaches 7 mm (Fig. 5 and Table 4). This rapid increase of an average of 0,98 mm/0,95 mm increase in standard length continues till 11 mm s.l. is reached when the rate of increase of the trunk slows down somewhat. At this stage (11 mm s.l.) the anus has reached the origin of the anal fin, i.e. its juvenile position. It is possible that the rapid rate of visceral increase is linked to the change in the diet of the larvae. The larvae cease to feed on phytoplankton and become predatory on other fish. Head and eyes of larval fish have been found in the gut of snoek larvae as small as 8 mm.

Proportional depth of the snoek larvae remains fairly constant, between 18 and 21% of standard length, until 14,0 mm is reached, then it drops gradually to 16% of standard length at 21,0 mm. Actual depth increase is of the order of 0,17 mm for each mm of standard length increase up to 13 mm s.l. After this, accuracy of calculation breaks down due to the small number of available specimens, but the rate appears to be less and in the order of 0,056 mm/mm increase in s.l. Generally the larvae seem to become slimmer as they reach the juvenile stage.

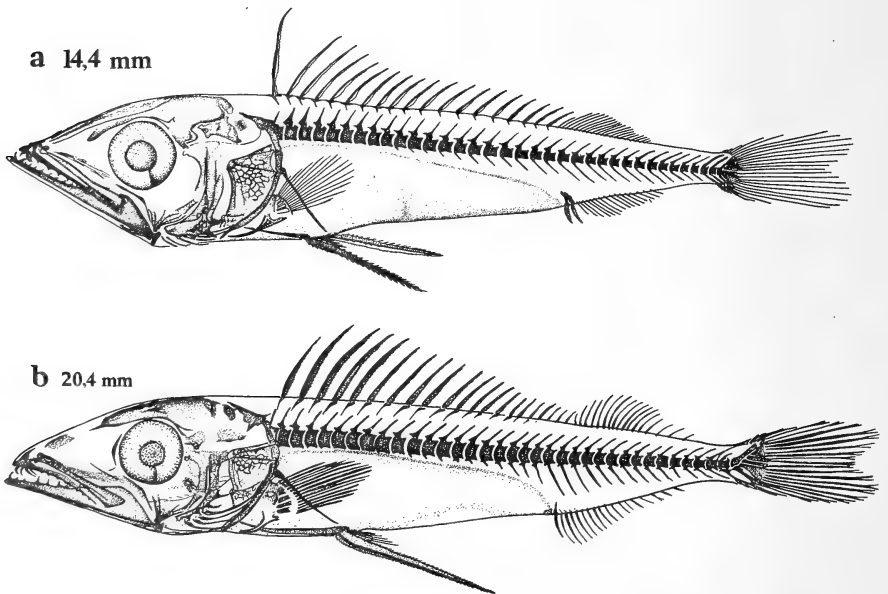


FIG. 5. *Thyrsites atun*
Late larval and juvenile stages. Measurements indicate standard length.

Helicolenus dactylopterus

The pectoral of *Helicolenus dactylopterus* is emarginate on the dorsal edge, with two unbranched rays followed by eight branched and nine unbranched

rays, the latter being free from the membrane for at least one-third of their length. Suborbital keel smooth with one spine small or absent, the mouth large with villiform teeth on the jaws, vomers and palatine. The maxilla reaches to below the hind margin of the eye. The spination of the adult head is as follows: 1 nasal, 2 supraorbital, 2 parietal, 1 pterotic, 2 posttemporal, 2 opercular, 1 small suborbital, 5 preopercular, second the longest (Fig. 6c). Soft dorsal higher than spinous dorsal. Pelvic reaches almost to vent. D: 12 + 12-13. A: 3 + 5. Pelvic: 1 + 5. Vertebrae: 24-25.

Smaller specimens have black pigments near the end of the spinous dorsal. Pigment on body of juveniles in vertical bands (Eschmeyer 1969: 92-99).

Pigmentation

All specimens from 3.5 mm have a clearly pigmented peritoneum with scattered melanophores on the posterior aspect of the head. This peritoneal colouring is still visible at 20 mm on the dorsal surface of the peritoneum. The pectoral fins in this species are unpigmented whereas some other scorpaenid larvae in the collection have variously pigmented pectoral fins.

Ossification

Even the smallest larvae obtained had well ossified head spines and jaws as well as a cleithrum. By 4.5 mm (Fig. 7a) the premaxilla and maxilla are clearly defined, as is the lower jaw. The parietal, pterotic and posttemporal head spines are developed. The opercle is small and lightly ossified while the preopercle has three well-developed primary spines on the outer edge and two secondary spines on the median ridge. The middle of the primary spines is the longest. Four branchiostegal rays are present.

By 6.0 mm the frontal, parietal and pterotic bones are ossified but still easily distinguished. The hyomandibular has developed and the cleithrum is wider and better ossified than the 4.5 mm stage. A small subopercle is present.

TABLE 5
Mean measurements of *Thyrsites atun* larvae in mm

Size range of standard length	No. of larvae	Standard length s.l.	Head	Snout	Eye diameter	Depth	Snout to anus	Length pelvic spine	Longest dorsal spine
4.08-5.49	11	4.08-5.4	1.55	0.588	0.501	1.08	2.12	—(0.3)	—(0.3)
5.5-6.49	7	5.7-6.0	1.80	0.681	0.608	1.26	2.69	0.35	0.45
6.5-7.49	22	6.6-7.35	2.30	0.860	0.680	1.43	3.34	0.77	0.76
7.5-8.49	13	7.5-8.42	2.88	0.93	0.87	1.70	4.52	1.24	1.09
8.5-9.49	11	8.55-9.45	3.42	1.32	0.96	1.88	5.84	1.73	1.32
9.5-10.49	7	9.6-10.24	3.60	1.52	1.12	1.97	6.48	2.01	1.34
10.5-11.49	3	10.5-10.8	4.00	1.56	1.04	2.11	7.60	2.26	1.58
11.5-13.5	2	12.6	4.50	1.80	1.14	2.55	8.70	2.10	1.65
		13.5	4.80	1.80	1.65	2.55	8.70	2.40	1.80
13.5-15.5	2	13.8	4.8	2.10	1.26	3.00	10.20	2.40	1.80
		14.25	5.4	1.95	1.56	2.95	10.80	3.00	2.10
15.5 & over	3	20.10	6.6	2.46	1.68	3.40	15.9	2.4	1.8
		20.25	6.75	2.70	1.65	3.15	15.85	3.45	2.7
		21.0	6.80	2.70	1.65	3.40	15.40	2.80	1.80

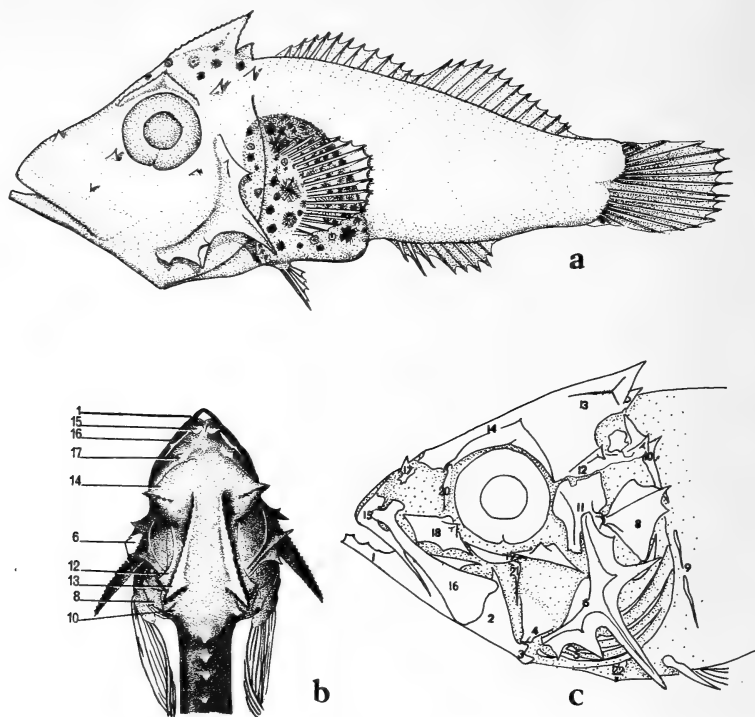


FIG. 6. *Helicolenus dactylopterus*

a. Larva at 10 mm standard length showing external features only. b. Dorsal view of head showing position of spines. c. Lateral view of head showing position of cranial bones and spines: 1. Dentary. 2. Angular. 3. Articular. 4. Quadrate. 5. Branchiostegal rays. 6. Preopercle and five spines. 7. Subopercle. 8. Opercle. 9. Postcleithrum. 10. Posttemporal and spines. 11. Hyomandibular. 12. Pterotic and spine. 13. Parietal and spines. 14. Frontal and supraorbital spine. 15. Premaxilla. 16. Maxilla. 17. Nasal and spine. 18. Lacrymal and suborbital spine. 19. Circumorbitals. 20. Prefrontal. 21. Pterygoid. 22. Cleithrum.

Gillrakers and gill-arches have started ossifying. A ceratohyal, quadrate and traces of the pterygoid are visible.

By 6,6 mm the lacrymal and endopterygoid are formed and the lacrymal bears a spine. Frontal and parietal are fused. Supratemporal and spine are evident. Six branchiostegal rays are ossified. By 7,35 mm the lacrymal is larger and bears two spines while the first and second suborbital are well ossified, obscuring the pterygoid to some extent. Thirteen gillrakers are present and the sutures between parietal, pterotic, posttemporal and hyomandibular have become indistinct. In the size range 6,6 to 7,35 mm the head spines present are: supraocular, parietal, pterotic, supratemporal, preorbital, suborbital, three primary and two secondary preopercular. Between 7,35 and 9,0 mm ossification of the head proceeds to near juvenile condition. New elements added include nasal spines, two extra primary preopercular spines and traces of a preopercular

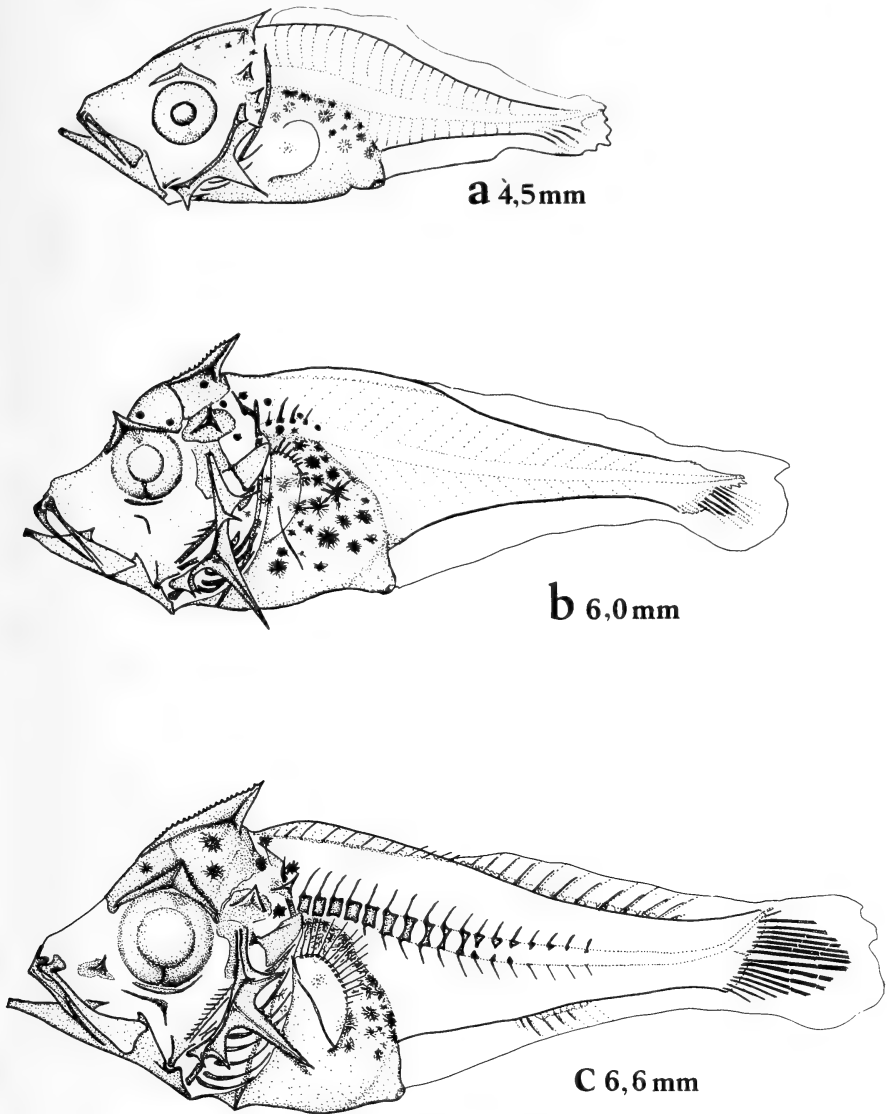


FIG. 7. *Helicolenus dactylopterus*

Early larval stages showing position and relative length of head spines. Measurements indicate standard length.

spine. By 10,2 mm the parietal spine has become bifid as in juveniles. Two opercular spines become evident at the posterior edge of the opercle as in adults. From late larval stage at 10,0 mm and juvenile stage between 15 and 20 mm the relative size of the head spines decreases and they become far less conspicuous. The secondary spines on the preopercular disappear and the

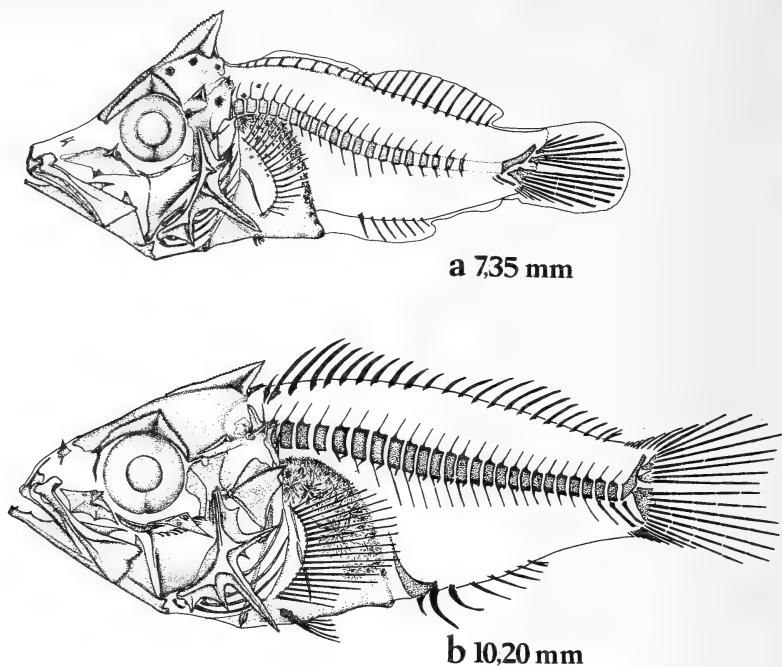


FIG. 8. *Helicolenus dactylopterus*

a. Larva. b. Early juvenile showing completed major ossification. Measurements indicate standard length.

second primary spine lengthens considerably to become as long as the third and eventually the longest spine, as in the adult condition. A small spine develops behind the supraorbital, also behind the supratemporal. Rows of villiform teeth develop on the upper and lower jaws in the late larval stage.

In the trunk and tail ossification of the neural spines commences between 5,0 and 5,4 mm while that of the centra starts between 5,5 and 6,0 mm and that of the haemal spines soon after. Ossification proceeds anteroposteriorly in sequence.

At 5,4 mm there are two neural spines and at 6,0 mm 5 to 18. Between 6,0 and 6,6 mm ossification proceeds rapidly and 17 to 20 neural spines and 14 to 16 haemal spines are formed, as well as 15 to 20 complete and 2 to 3 incomplete centra (see Table 6). Twenty vertebrae are fully ossified at 7,35 mm (Fig. 9d) and by 8,5 mm 24 centra, with a full complement of 18 to 19 haemal and 23 neural spines ossified by standard length 9,5 mm. Between 10,0 mm and the juvenile stage the neural arches ossify completely and the spines become broader and stouter.

At 4,8 mm there are four ossified caudal rays, five or six at 6,0 mm. The notocord becomes heterocercal at 6,6 mm. The full complement of 15 primary caudal rays is ossified by 7,35 mm as well as five to six secondary rays. The

TABLE 6

Range of skeletal elements in vertebral column of *Helicolenus dactylopterus*

Length mm	Haemal spine	Neural spine	Vertebrae	No. of specimens
5,4	—	0-3	—	1
5,7	0-9	0-15	0-5+0-10($\frac{1}{2}$)	3
6,0	0-13	5-18	5-6+5-9($\frac{1}{2}$)	6
6,6	14-16	19-23	15-21+2($\frac{1}{2}$)	3
7,2	16-17	19-23	20-24+2($\frac{1}{2}$)	4
7,9	15-18	19-23	21-24+2($\frac{1}{2}$)	2
8,1	13-19	18-23	23-24	2
9,0	19	23-24	24-26	2
10,5	19	24-25	26-27	4
15,0	19	24-25	26-27	5

($\frac{1}{2}$) refers to partly ossified vertebrae.

TABLE 7

Average number of ossified elements in fins of *Helicolenus dactylopterus* larvae

Size in mm	Caudal	Dorsal		Anal		Pectoral lobe	Pelvic
		Spines	Rays	Spines	Rays		
4,00	4	—	—	—	—	—	—
5,40	6	—	—	—	3	4	—
6,60	2+15+3	8	11 $\frac{1}{2}$	1	6	12	—
7,60	3+15+3	8	3+12	2	6	17	1+3
8,50	4+15+5	5	8+12	2	6	17	1+4
9,50	6+15+6	12	+ 13	3	+5	18	1+5
10,50	8+15+9	12	+ 13	3	+5	19	1+5

(Bold face denotes present but unerupted spines)

urostyle and four hypural elements also ossify between 6,6 and 7,35 mm. By 10,2 mm the caudal fin takes on a juvenile aspect and more secondary rays are present (Table 7).

The pectoral fin starts ossifying between 5,0 and 5,4 mm. Ossification proceeds dorsoventrally and is completed by 10,2 mm when there are 19 pectoral rays. Differentiation into the characteristic *Helicolenus* pattern of two unbranched plus 8 to 9 branched plus 8 to 9 unbranched rays only takes place in late juvenile or early adult stage.

Dorsal and anal fins ossify between 6,0 and 6,6 mm. At 6,6 mm 11 to 12 dorsal rays are lightly ossified and 6 to 10 dorsal spines visibly ossified but not erupted. The anal fin has six lightly ossified rays and one unerupted spine. Three posterior dorsal spines have erupted by 7,35 mm and by 10,0 mm the unpaired fins have become fully differentiated; all the dorsal spines have erupted between 9,0 and 9,5 mm. The 12 dorsal spines are shorter and stouter than the 12 to 13 dorsal rays while the three anal spines are as long as the five rays except for the second spine which is longer. Between 10,0 mm and 15 to 17 mm the fin supports develop fully.

The pelvic fin is evident at 7,0 mm and the spine is first to ossify. One spine and three rays are complete at 7,35 mm. One spine and five rays present the full complement and are present at 10,2 mm. Ossification of skeletal parts seems to proceed at widely differing rates but as little is known about prevailing conditions under which growth took place, no deduction can be made.

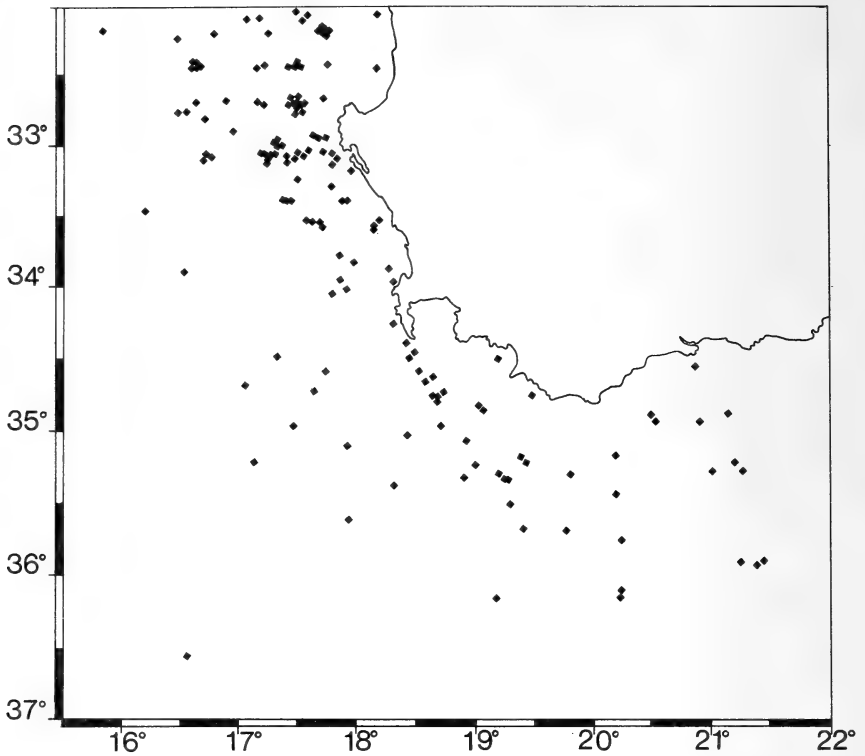


FIG. 9

Distribution of *Merluccius capensis* from 1951 to 1966.

TABLE 8

Average measurements of *Helicolenus dactylopterus* larvae in mm

Size range of s.l.	No. of specimens	Standard length	Head length	Snout length	Eye diameter	Depth	Trunk length
3,50-4,49	15	3,99	1,38	0,37	0,42	1,36	2,04
4,5-5,49	27	4,82	1,81	0,57	0,60	1,68	2,51
5,50-6,49	10	5,92	2,28	0,91	0,78	2,13	3,21
6,50-7,49	14	6,92	2,70	0,94	0,92	2,48	3,70
7,50-8,49	9	8,10	3,23	1,10	1,06	2,86	4,66
8,50-9,49	4	8,92	3,20	1,12	1,20	3,60	5,30
9,50-10,49	2	9,90	4,05	1,35	1,50	3,60	6,00
10,50-11,49	4	11,10	4,27	1,42	1,18	3,82	6,75
11,50-12,45	2	12,00	4,05	1,65	1,50	4,20	7,35
12,50-14,95	1	12,60	4,20	1,20	1,50	4,20	7,20
16-17	1	17,10	6,00	1,80	2,40	6,00	10,80
18-19	2	—	6,90	1,95	2,40	6,30	11,25
20-21	2	—	7,20	2,10	2,85	6,60	13,05

TABLE 9

Body proportions of *Helicolenus dactylopterus* larvae in % of standard length

Size range in mm	Snout %	Eye %	Head %	Trunk %	Depth %	No. of specimens
3,5-4,49	8,6	10,7	34,9	51,7	34,3	16
4,5-5,49	14,2	12,8	36,4	50,5	33,9	23
5,5-6,49	13,6	13,1	38,6	54,2	36,0	11
6,5-7,49	13,6	13,3	39,1	53,6	35,9	14
7,5-8,49	11,9	13,1	40,0	57,8	35,0	9
8,5-9,49	12,6	13,4	36,1	59,6	40,3	4
9,5-10,49	13,6	15,2	40,9	60,3	36,4	3
10,5-11,49	12,8	12,8	38,5	60,8	34,5	2
11,5-12,49	13,7	12,5	33,7	61,0	40,0	4
12,5-13,49	9,5	11,9	33,3	57,1	33,3	1
16,5-17,5*	10,5	14,0	35,1	63,1	35,1	5
18,5-19,5*	8,2	11,8	32,5	61,8	30,9	
20,5-21,6	10,0	13,5	34,2	62,1	31,4	

* Size ranges not available in collection.

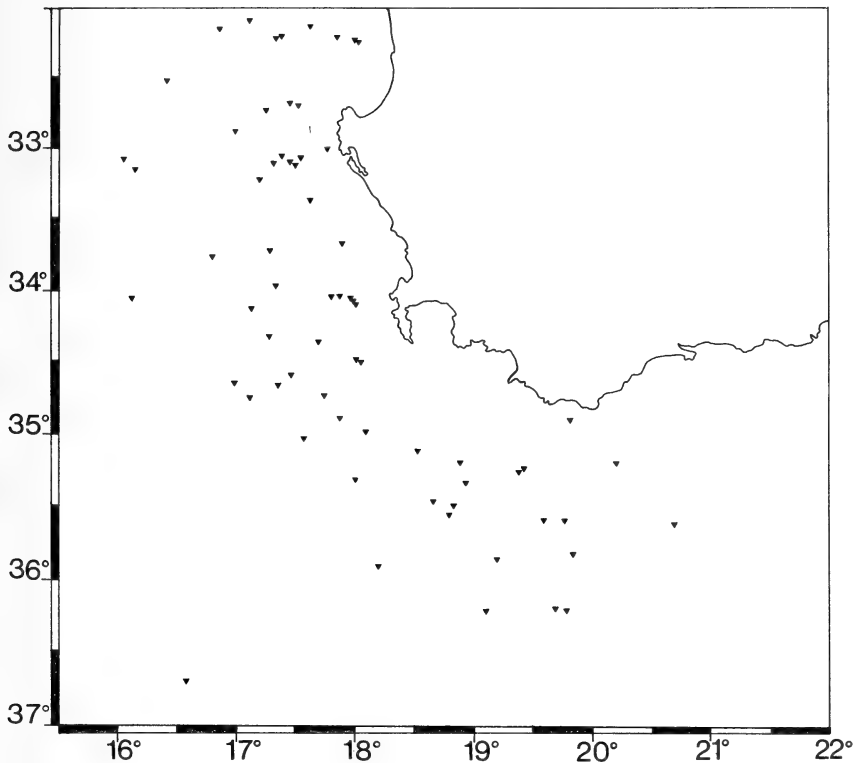


FIG. 10

Distribution of *Thysites atun* from 1951 to 1956 and 1960 to 1965.

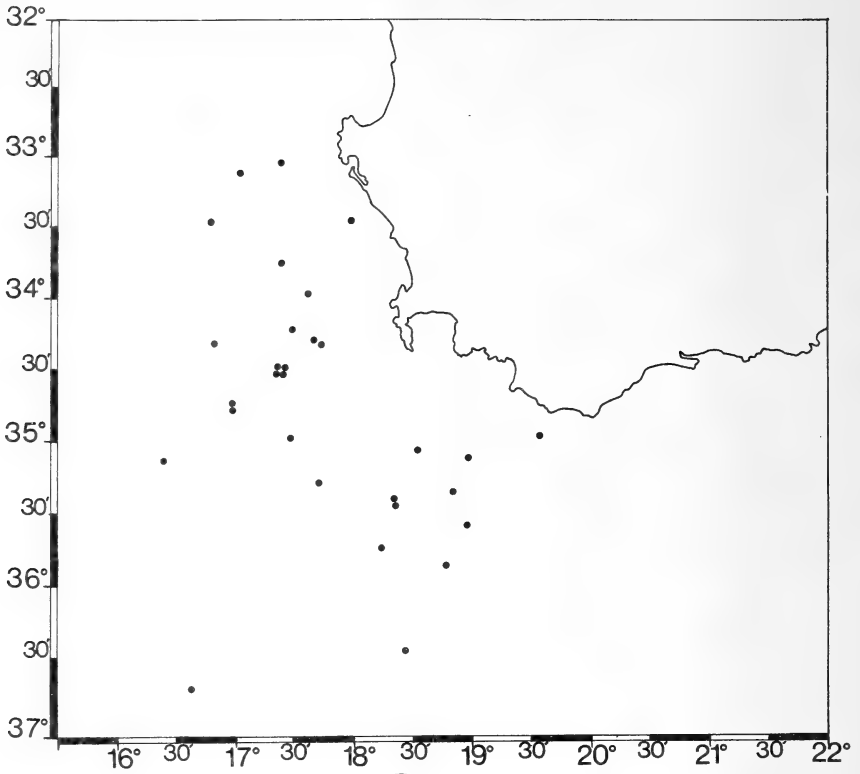


FIG. 11

Distribution of *Helicolenus dactylopterus* from 1962 to 1965.

Changes in body form

During development the body form changes from a rather deep anteriorly large to a more evenly proportioned shape with a depth approximately 30% of the standard length. The relative head length remains fairly constant during development, varying between 34 and 40% of the standard length. Head length increases $\pm 0,39$ mm for each mm increase in standard length. The snout is 8 to 14% of standard length and eye diameter 11 to 15% of s.l., both remaining constant throughout development. The rapid increase in snout length during size range 3,4 to 5,49 mm could however indicate the growth and ossification of jaw elements. The trunk length increases 0,6 mm per mm increase in s.l., increasing to 0,9 mm per mm increase in s.l. at 9,0 to 10,0 mm s.l. Relative trunk length increases gradually during development from 50 to 51% of standard length between sizes of 4 and 5 mm, to 61 to 62% of s.l. at 19 to 21 mm.

DISTRIBUTION

The area covered by the research vessels of the Division of Sea Fisheries on the pilchard research programme has varied since its inception. During 1951 and 1952 the area worked lay between 32° and 35°30'S and was delimited by the 200 fathom depthline to the west. Approximately the same area was worked between 1953 and 1957. In 1958 the eastern limit of the work area was extended round Cape Point to 19°30'E. This area was worked until the end of 1960, when the eastward delimitation was extended to 21°E. During these years the westward delimitation extended to 16°31'E. From July 1963 to December 1965 the area covered by the research vessels was between 32°10' to 36°10'S and 16° to 21°30'E. Stations lists are obtainable from the Annual Reports of the Division of Sea Fisheries for the relevant years.

SUMMARY

The larval stages of *Merluccius capensis*, *Thyrsites atun* and *Helicolenus dactylopterus* are described. All three species are economically important in South Africa. The taxonomy of each species is revised according to latest opinions. A brief description of distribution is included.

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(With plates 2-18, 2 figures and 7 tables)

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CONTENTS

	PAGE
Introduction	71
Systematics	73
The Langebaanweg seal	74
Description	
The skull	76
The postcranial skeleton	83
Discussion	92
Summary	96
Acknowledgements	96
References	96

INTRODUCTION

Although Illiger recognized the basic features of the seals of the world in 1811 by separating them from the sirenians and placing them in a separate order, the Pinnipedia, their classification is still in a state of flux. In 1880 Allen divided the pinnipeds into two major groups: the 'walkers' and the 'wrigglers' which Smirnov (1908) subsequently named the superfamilies Otarioidea and the Phocoidea. The Phocoidea contains only one family, the Phocidae (Gray 1825, but defined with its present contents by Brookes, 1828), usually known as the 'earless seals' or 'true seals'. Subsequent to Kellogg's (1922) introduction of the subfamily Lobodoninae (respelled Lobodontinae by Hay, 1930) to include the Antarctic phocids, the family Phocidae was considered to include four sub-families: Phocinae for the northern seals, Monachinae for the genus *Monachus*, Cystophorinae for the genera *Cystophora* and *Mirounga*, and Lobodontinae. Scheffer (1958) reduced the rank of the Antarctic phocids to that of a tribe, Lobodontini, within the family Monachinae. King (1966), in possibly one of the most detailed explanations of a change in pinniped classification, abandoned the subfamily Cystophorinae, placing the genus *Cystophora* in the Phocinae and the genus *Mirounga* in the Monachinae. Most recently (at this writing) McKenna

(1969), in possibly one of the briefest explanations of a change in pinniped classification, stated that the formal taxon order Pinnipedia has been abandoned.

As here used, the order Pinnipedia contains three families: Odobenidae, the walruses; Otariidae, the sealions; and Phocidae, the true seals who must 'wriggle' on their bellies in terrestrial locomotion, their hind limbs permanently extended behind them. The family Phocidae contains two distinct subfamilies, the Phocinae, inhabiting temperate and arctic waters of the Northern Hemisphere, and the Monachinae, inhabiting parts of most oceans except the Arctic Ocean.

For the most part, the characters identified by King (1966) may be used to separate the living members of the two phocid subfamilies. Since it is assumed that the two subfamilies derive from a common ancestor, it is to be expected that fewer of these characters will be useful for familial identification in the fossil ancestors of the living true seals. Such is the case with the Pliocene phocid from South Africa.

Since 1958, when the first discoveries from the quarries of the African Metals Corporation were recorded by Singer & Hooijer (1958), tens of thousands of vertebrate specimens have been recovered from these Pliocene phosphate deposits near Langebaanweg, Cape Province. At least 60 mammalian species, as well as a full complement of birds and cold-blooded vertebrates, have been recognized (Hendey, 1970a, 1970b). The fauna is both marine and terrestrial, apparently representing accumulation during a prolonged period of marine, estuarine, and terrestrial deposition in the area.

The dating of the Langebaanweg fauna is a major problem presently being investigated (Hendey, 1970b; Maglio & Hendey, 1970). On the basis of an admittedly limited number of comparisons with faunal elements from better-dated localities in East Africa, we believe the Langebaanweg deposits bearing the main body of higher vertebrate remains to be perhaps 4 to 5 million years old. The most recent interpretation of the most reasonable definition of Pleistocene, and the approximation of its beginning between 2.6 to 3 million years ago (Savage & Curtis, 1970), suggest that the Langebaanweg fauna should probably be called late Pliocene.

The Langebaanweg fauna includes a pinniped which was first reported by Boné & Singer (1965). These authors tentatively referred it to the otariid genus *Arctocephalus*, but more recently discovered specimens show clearly that it is a monachine phocid which belongs to a previously unrecorded species of the extinct genus *Prionodelphis*, heretofore known only from Pliocene deposits in Argentina. In many respects this seal from Langebaanweg is similar to the extant *Monachus* and its ancestors, notably *Pliophoca etrusca* from the late Pliocene of Italy (Tavani, 1942). However, similarities to the extant phocids of the Antarctic seas are equally well marked.

In view of the small number of recorded specimens of *Prionodelphis rovereti* (Frenguelli, 1922, 1926), from Argentina, the Langebaanweg seal, represented

by a wide variety of specimens, is clearly important in that it provides the first good evidence of the antiquity and ancestry of the monachine seals in the Southern Hemisphere.

SYSTEMATICS

As here used, the subfamily Monachinae includes the same genera of living seals that were included in this subfamily by King (1966). Except for the addition of the genus *Mirounga*, this agrees with the definition of the subfamily as originally defined by Trouessart (1897:373).

As noted by Scheffer (1958:111), when he reduced the Lobodontinae to tribal rank within the Monachinae, the major difference between these Antarctic seals and *Monachus* is one of geography. King (1966) omitted reference to Scheffer's tribe Lobodontini when discussing the monachine relationship of *Mirounga*, with good reason as the genus does not conform to the geographic distinction mentioned by Scheffer. Recognition of any tribal subdivision of the Monachinae now seems pointless.

King (1966:397) noted that with some features otherwise typical of the monachine seals *Monachus* was an exception and regarded this genus as being not quite so advanced. Such exceptions to otherwise typical features of the Monachinae are even more evident in the Pliocene seal from Langebaanweg. At this stage in the evolution of the phocid seals the subfamily Monachinae can be distinguished from the subfamily Phocinae by the following characters of the skull.

Subfamily **Monachinae**

Diagnosis. Seals having a mastoid bone without a prominent posterolaterally projecting rounded crest but, instead, having a posterolateral surface curving uniformly from the region of the parietal suture down to the region of the stylomastoid foramen; mandible with an extensive symphyseal surface that is elongate and smoothly oval in outline and that firmly articulates over the entire depth of the chin.

As will be shown in the following report, some postcranial bones of the Langebaanweg seal exhibit monachine features while other are simply phocid, with no subfamilial characteristics.

GENUS *Prionodelphis*

Type. *Prionodelphis rovereti* Frenguelli, 1922.

Known distribution. Pliocene of the South Atlantic Ocean.

Comment. The type species, *Prionodelphis rovereti*, was described as a squalodont cetacean from a few isolated teeth found in Pliocene deposits in Entre Rios in Argentina. A mandibular fragment bearing one tooth was later found at the same locality which led Cabrera (1926:390) to the conclusion that the animal was a pinniped, a conclusion supported by others (Frenguelli, 1926;

Kraglievich, 1934; Kellogg, 1942). We are aware of no additional material.

The material from South Africa now makes it possible to provide a better definition of the genus.

Diagnosis. A generalized monachine seal lacking the shortened rostrum and crowded teeth of *Monachus monachus* and the squared premaxillaries with aligned, upper incisors of *M. tropicalis* and *M. schauinslandi*; postcanine teeth low-cusped as in *M. schauinslandi*, *M. tropicalis* and *Pliophoca etrusca* and distinctly narrower in occlusal outline than those of *M. monachus*; upper fifth postcanine¹ with recurved crown; ascending ramus of premaxilla strong, terminating against nasals and prominently visible in lateral view separating maxilla from nasal aperture; pre-orbital processes prominent; forehead broad in supra-orbital region; osseous nasal septum strongly developed; dental formula 2.1.5/2.1.5; tympanic bulla covers petrosium.

THE LANGEBAANWEG SEAL

Prionodelphis capensis n.sp.

Holotype. An incomplete skull with left canine and fourth postcanine, and right third postcanine (South African Museum No. L 15695).

Referred material. An incomplete skull (L 12695); temporal bone (L 15652); mandible fragments (L 7556, L 12299); one lower and two upper incisors; three lower and four upper canines; and nine lower and ten upper postcanines.

Various elements of the postcranial skeleton have been recovered, of which the following have been selected for description: vertebrae (L 7563, L 15689, L 15849A1 & A2, L 15396, L 15857); scapula (L 2160); humeri (L 2157, L 4638); ulnae (L 2161, L 15682); radii (L 2935, L 12869), innominate (L 15849A), femur (L 10131); tibiae (L 2138, L 10128/9); calcaneum (L 10118); astragali (L 10130, L 10993); navicular (L 15851); entocuneiform (L 10134); metapodial (L 10996); first phalanx (L 10999); second phalanx (L 10205).

All specimens are housed in the South African Museum, Cape Town. Except for the two incomplete skulls, which are too fragile to cast, casts of the more significant specimens are housed in the U.S. Geological Survey, Pacific Coast Center, Menlo Park, California.

Locality and horizon. The holotype and most of the referred material is from horizon 2, 'E' Quarry, Langebaanweg. Some postcranial elements are known from horizon 1. These horizons are thought to be broadly contemporaneous (Hendey, 1970b). A few fragmentary remains from 'C' and Baard's Quarries are excluded from this report, but they apparently represent the same species.

Comparative material. Skulls of all living phocid species except *Pusa caspica* have been available for comparison either in the South African Museum or in the Pacific Coast Center of the U.S. Geological Survey. Postcranial material has been somewhat less available, but comparisons were made with postcranial

¹ Called P₁ by Frenguelli, 1922: 496.

elements of *Monachus schauinslandi*, *Hydrurga leptonyx*, *Lobodon carcinophagus*, *Mirounga angustirostris*, *M. leonina*, and all living phocine genera.

Diagnosis. *Prionodelphis capensis* differs from the type species in that it has only one anterior accessory cusp on the lower postcanines instead of two, and there is a greater reduction in size of the posterior root in the second to fourth upper postcanines. The cheek-teeth of the South African species approach more closely a three-cusped tooth pattern, and in addition, are slightly larger and more laterally compressed (Table 1).

TABLE 1. Average length-width ratios for postcanines 2 to 4 of some phocids.

	Length	Width	W/L × 100	Upper/ Lower
<i>Hydrurga leptonyx</i>				
Upper (N = 6)	18,0 mm	8,8 mm	49	0,925
Lower (N = 6)	17,6	9,3	53	
<i>Prionodelphis capensis</i>				
Upper (N = 7)	13,8	7,5	54	1,200
Lower (N = 8)	15,0	6,8	45	
<i>Prionodelphis rovereti</i> ¹				
Upper (N = 1)	12,25	8,0	65	1,204
Lower (N = 2)	13,0	7,0	54	
<i>Monachus schauinslandi</i>				
Upper (N = 6)	12,0	7,9	66	1,047
Lower (N = 6)	12,1	7,6	63	
<i>Monachus monachus</i>				
Upper (N = 6)	12,9	9,1	70	1,111
Lower (N = 6)	12,9	8,0	63	

¹ From Frenguelli, 1922.

DESCRIPTION

The assessment of the fossil remains listed above is somewhat hampered by their fragmentary nature. The holotype is composed of about 60 individual pieces, including three teeth, found scattered over a wide area in the excavation No. LBW 1969/1 (South African Museum departmental records). Numerous small pieces could not be restored to the skull, although they undoubtedly belong, and others presumably remain in unexcavated parts of the deposit.

The second partial skull (L 12695) was similarly fragmented. Although the partially restored snout region is less complete than that of L 15695, parts of the braincase of the second specimen were also recovered. Many of the individual pieces are extensively abraded, probably having suffered in a manner similar to that described for an alcelaphine skull recovered near by (Hendey, 1970a: 82).

As with much of the referred material, the temporal bone (L15652) also came from the excavation LBW 1969/1, but from approximately 75 cm below the holotype. It probably belongs to another individual.

Most of the isolated teeth were recovered intact, and they vary from unworn to extremely worn.

Few elements of the postcranial skeleton were recovered intact, but in some cases sufficient numbers of a particular bone are known to enable a complete assessment of its characteristics.

THE SKULL

The skull of the Langebaanweg pinniped is in many ways unique, and it exhibits a set of characteristics which makes it impossible to assign it to any previously known phocid species (Plates 2-8).

As a whole, the skull appears convincingly to be that of a monachine seal. The lack of swollen or crested mastoids, the broad and flat dorsal surface of the petrosal apex, and the deep and oval mandibular symphysis rule out any known phocine seal, while the incisor formula and cheek-tooth pattern strongly suggest a monachine seal. Although the postcranial bones in general also appear monachine, they possess some features that are characteristic of living phocine seals, such as an entepicondylar foramen on the humerus.

In general features, the skull most resembles those of *Monachus* and *Hydrurga*, although it is considerably more gracile and less elongated than the latter. Of all extant genera its teeth most resemble those of *Monachus*. However, except for the lack of great vertical exaggeration of the cusps, the teeth are also quite similar to those of *Hydrurga*. Of the extinct genera they are, as far as comparisons are possible, most similar to *Prionodelphis rovereti* and, less so, to *Pliophoca etrusca*. The basic pattern of the cheek-teeth appears to be that of earlier members of the family Phocidae.

Unlike the usual pattern in the Antarctic monachines, the premaxilla terminates against the nasal bone. Although it shares this characteristic with *Monachus* and several phocine seals, it differs markedly, as does *Pliophoca etrusca*, in the massiveness of the ascending ramus of the premaxilla. When the

TABLE 2. Dimensions of the skull of *Prionodelphis capensis* from Langebaanweg.

	L15695	L12695	L7556	L12299
Rostral width	48,0*	61,0*	—	—
Distance between pre-orbital processes of maxilla	94,0*	—	—	—
Minimum diameter of inter-orbital region	36,0*	—	—	—
Distance between pre-maxillary projections and posterior limit of nasal aperture	58,0*	51,0*	—	—
Lengths of nasals	62,0*	—	—	—
Distance between external alveolar margins of fifth postcanines	74,5*	87,0*	—	—
Alveolar length of upper postcanine series	72,5	72,5*	—	—
Alveolar length of lower postcanine series	—	—	66,5	—
Depth of mandible behind M ₁	—	—	27,9	31,6

* Estimated.

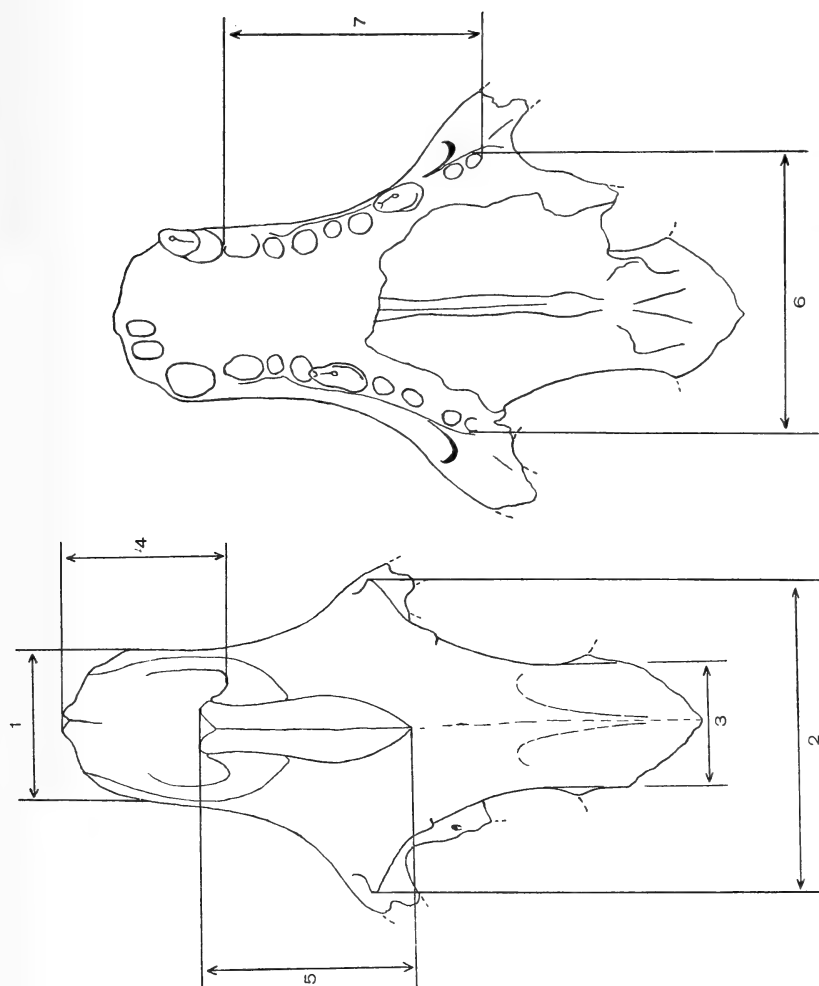


FIG. 1. Diagram of cranial measurements: 1. Rostral width. 2. Distance between pre-orbital processes of maxilla. 3. Minimum diameter of inter-orbital region. 4. Distance between premaxillary projections and posterior limit of nasal aperture. 5. Length of nasals. 6. Distance between external alveolar margins of fifth postcanines. 7. Alveolar length of upper postcanine series.

skull is viewed laterally the premaxilla is visible along its entire length rather than being partly hidden behind the maxilla, largely within the nasal opening, as in living monachines. The nasal opening is elongated antero-posteriorly, and of the southern phocids most resembles *Hydrurga* and *Lobodon*, rather than *Leptonychotes* and *Ommatophoca* in which there is foreshortening of the anterior part of the snout. In this respect it is also similar to *Monachus* and *Pliophoca*. The two halves of the premaxilla have fairly prominent projections at their most anterior point of contact, dorsal to the incisors. Of the extant monachines *M. tropicalis*, *M. schauinslandi* and *Hydrurga* have similar projections, but in *Hydrurga* inflation of the alveolar region of the incisors renders the projections less prominent, and in the two *Monachus* species the projections are quite widely separated. In the fossil species there is a marked step between the most anterior maxilla-premaxilla contact and the premaxillary projection. This is best seen in the specimen L 12695.

Judging from the size of the alveoli, the lateral incisor is only slightly larger than the medial one. The latter is situated slightly anterior to the other. The relative size and position of the upper incisors are as in *M. monachus* and *Hydrurga*, and unlike the specialized condition found in *Lobodon* and *Leptonychotes*, in which genera the lateral incisor is much larger than the medial one and is situated in line with it.

Two upper incisors are known, both left medials judging from their size. The structure of the crown resembles that of the incisors of *M. monachus* and *Pliophoca etrusca*. The cross-section of the canines is only slightly elongated antero-posteriorly, and in this respect *P. capensis* differs markedly from the Antarctic phocids. The canines L 11686 (Plate 9B) and L 12695 have large bulbous roots, a feature also seen in some of the postcanines. This is a characteristic of old age in most or all pinnipeds.

There are five upper postcanines and at least one specimen of each dental category is known from the assemblage. The first, and smallest, is single rooted (Plate 9C). The remainder are all double rooted, with the posterior root being larger than the anterior one in the second, third, and fourth teeth, and the sizes reversed in the fifth. The latter is also the second smallest of the teeth and is set slightly separate from the others immediately below the infra-orbital foramen. The postcanine tooth rows curve outwards posteriorly as in *Ommatophoca*, and are not diverging straight lines as in *Leptonychotes* and *Hydrurga*; this pattern is rather close to that of *M. schauinslandi* as well as some other phocid species.

The postcanines resemble those of *Pliophoca etrusca*, although narrower and more gracile, and except for being much less massive, they are also similar to those of *M. monachus* (Plate 9D). They are quite distinct from the highly specialized teeth of extant Antarctic phocids; of this group the teeth of *Leptonychotes* are closest to the fossils, but they are nevertheless significantly different. The basic pattern of the first to fourth postcanines is similar to the corresponding teeth of *M. monachus*. There is a prominent central cusp with two smaller cusps situated anteriorly and posteriorly, with an additional small projection on the

most posterior part of the cingulum. The enamel is generally rugose, a condition which is found in all monachine seals except *Mirounga*, but which is also found in some phocine seals. The second, third and fourth upper postcanines have a marked inflation of the postero-internal cingular region, a condition also evident in some teeth of *P. rovereti*, and *P. etrusca*, and these teeth are broader posteriorly than they are anteriorly. The first upper postcanine has the internal cingulum inflated, and the maximum transverse diameter is at about the mid-point of the tooth. The upper postcanine of *P. rovereti* described by Frenguelli (1922:493 and figs. 1b, 1c) is shorter and relatively broader than those of *P. capensis*. It lacks the distinct anterior accessory cusp present in the latter species and has a larger posterior root.

The fifth postcanine of *P. capensis* lacks the posterior accessory cusp and cingular projection, and the anterior accessory cusp is much reduced, being barely discernible; the principal cusp is strongly recurved (Plate 9E). It resembles the cheek teeth of *Leptonychotes* in this respect. Both the fifth postcanines recovered to date are completely unworn, and it seems probable that this tooth did not occlude with the lower fifth postcanine. *Leptonychotes* also has a non-occluding upper fifth postcanine. This tooth, in *P. capensis*, is very similar to one of the original *P. rovereti* specimens illustrated (as a P_1) by Frenguelli (1922: fig. 2A). The principal differences are in the smaller size of the *P. rovereti* specimen, in that its anterior accessory cusp is situated higher up the crown, and also in that there is no cingulum on the buccal surface of the Langebaanweg specimens. The two *P. capensis* specimens differ from one another only in that one is slightly shorter and somewhat broader than the other. In the postcanines such differences distinguish upper from lower teeth, but judging from the size of alveoli in mandibles and maxillae known, these teeth can only be upper fifth postcanines.

Of the seven second, third and fourth upper postcanines known, two are unworn and five show wear angled from the principal cusp to the posterior cingulum.

The general features of the maxilla of *P. capensis* correspond most closely to those of *Hydrurga*. The fossil seal has very prominent preorbital processes. The one preserved in the holotype projects outwards and downwards as in *Hydrurga*, although in L 12695 it has an outwards and upwards inflection. The presence and form of the preorbital process is variable throughout the Pinnipedia, but within the monachine seals it is virtually absent in *M. schauinslandi*, *M. tropicalis* and *Leptonychotes* and present but variably developed in other extant monachine species.

In the Antarctic phocids the jugal terminates lateral to the infra-orbital foramen, whereas in *P. capensis*, *P. etrusca*, *Monachus* and several other seals it terminates above this foramen.

The infra-orbital foramen is oval shaped as in *Hydrurga* and *Lobodon*, but the orientation of the longitudinal axis of the foramen differs in that it is directed upwards and outwards in *P. capensis*, whereas the axis is upwards and inwards in *Hydrurga* and *Lobodon*.

The shape of the nasals is not perfectly known, but from a reconstruction of this region in the holotype (Plate 2), it appears that they do not correspond in shape to those of other monachines. Instead they are broader in the frontal region than between the maxillae.

The osseous nasal septum is a very stout bone which terminates at or near the most anterior limit of the nasals. Its proportions resemble those of *M. schauinslandi*, *M. tropicalis*, *Hydrurga*, *Ommatophoca* and *Mirounga*, but not *M. monachus*, *Lobodon* and *Leptonychotes*.

The supra- and post-orbital regions of the frontal bones are essentially similar to those of *Hydrurga*, *Lobodon* and *Ommatophoca*, and are not parallel-sided as in *Monachus*, *Leptonychotes* and *Mirounga*, nor as in *P. etrusca*. In the holotype there are the beginnings of a sagittal crest towards the posterior part of the frontals. There are two step-like projections on the frontals above and behind the preorbital processes of the maxilla. Similar features are present in *Ommatophoca* and are less distinctly represented in *Hydrurga*.

The second partial skull (L 12695) belongs to an aged individual and is somewhat more robust than that of the holotype (Plate 5). The difference in size of the two specimens may in part be due to the ages of the individuals concerned, but may also reflect sexual dimorphism in the species. Apart from size, the most striking difference between the two specimens is in the form of the nasal aperture. That of L 12695 is actually slightly shorter than that of L 15695, although it is, as would be expected, wider and higher. A similar and probably related allometric feature is the correspondence in the length of the postcanine tooth rows.

The braincase of *P. capensis* is not known, although parts of the nuchal region of L 12695 were recovered. The nuchal crest is fairly well developed, being more similar to that of *Hydrurga* than other species, although, like the sagittal crest, it is considerably less prominent than that of *Hydrurga*. Unlike *Hydrurga* there is no marked concavity of the supra-occipital. As in the Antarctic seals, *Monachus monachus*, and *Pliophoca etrusca*, the nuchal crest extends anteriorly across the temporal, terminating near the external acoustic meatus, rather than uniting with an enlarged jugular process of the exoccipital as in *M. schauinslandi* and *M. tropicalis*.

The basi-cranium is largely unknown, but a number of specimens of the well-ossified temporal bone have been recovered. The most complete (L 15652) has the mastoid and most of the tympanic intact, and the post-glenoid process is still attached (Plate 6). That part of the ectotympanic which projects under the acoustic meatus has been broken off and lost.

Although the general appearance of the tympanic region is most reminiscent of *Monachus* because of the slight inflation of the bulla, some of its features strongly indicate a relationship between *Prionodelphis capensis* and the Antarctic phocids. These include the posterior extent of the bulla and the rounded apex of the petrosium.

As noted by King (1966:387), the posterior wall of the bulla in phocine

seals (except some individuals of *Erignathus*), and in species of *Monachus*, is located rather far forward so that the posterior part of the petrosium is exposed in ventral aspect (without recourse to peering through the posterior lacerate foramen), whereas in the Antarctic monachine seals, including *Mirounga*, the bulla covers the petrosium and essentially separates the mastoid from the posterior lacerate foramen by almost contacting the exoccipital. The latter condition is very evident in *P. capensis*, strongly suggesting an affinity with the Antarctic seals.

The dorsal (cerebellar) surface of the temporal resembles that in some living Antarctic seals (Plate 7). The apex of the petrosium is broad and rounded with low relief, as in *Lobodon* and *Leptonychotes*, and differs greatly from the pointed apex found in *Monachus*. It is not the globular structure typical of the phocine seals. However, the petrosal apex of *P. capensis* is smaller than in the living Antarctic seals, suggesting that this seal was less well adapted for directional underwater hearing, according to the interpretation of Repenning (in press). The cerebellar fossa is relatively large, as in *Leptonychotes*, and as in the latter, the squamosal extends medially to the edge of the cerebellar fossa and to the internal facial canal.

The ventral (external) side of the temporal most resembles that in *Hydrurga*. The external opening of the carotid canal is located well forward of the posterior limit of the bulla, as in *Hydrurga*, *Leptonychotes* and *Lobodon*, but in contrast to the more posterior location in *Ommatophoca*, *Mirounga* and *Monachus*. In *P. capensis* this foramen faces noticeably ventrally, as in *Hydrurga*, but the general outline of the bulla is more similar to that in *Lobodon*. The stylomastoid foramen is rather widely separated from the external cochlear foramen (Burns & Fay, 1970:374). A similarly wide separation is found in *Hydrurga*.

Dissection of the middle ear was not undertaken.

The mandible is rather unspecialized and resembles that of *Hydrurga* and *Monachus* (Plate 8). It differs from that of *Hydrurga* in its smaller size and in having the symphyseal region relatively narrower transversely. In *Hydrurga* the two lower incisors are situated side by side, but in the fossil the medial incisor lies in an almost horizontal position above and behind the lateral incisor, in a manner comparable to that in most other species of phocid seals.

A single isolated lower medial incisor (L 15444A) is known. It is similar in size to that of *Leptonychotes* but has a pronounced step on the lingual surface of the crown which, in lateral view, resembles that of *Monachus*.

The lower canines are similar to the uppers, but have a straighter root and are more rounded in cross section.

The five lower postcanine teeth are situated close to one another: the alveolar walls between the teeth are as narrow as, or narrower than, those between the two roots of one tooth. In the mandibular ramus L 7556, the teeth are positioned in much the same way as in the *P. etrusca* specimen described by Tavani (1943: fig. 6a). The first postcanine is single rooted, and the remainder, which are more or less equal in size, have two roots. These teeth apparently all

have a crown pattern similar to the first to fourth upper postcanines (Plate 9G). Nine isolated lower postcanines are known, one of which is identified as a first lower and two are thought to be second lowers. Both the latter are worn on their posterior surfaces. Of the remainder, three show most wear on their anterior surfaces, and four, including the first lower, show no perceptible wear at all. Judging from the wear on the upper and lower postcanines, it appears that they functioned as crushing agents, although two of the lower teeth show signs of a transverse shearing action.

The lower teeth are differentiated from the uppers by the fact that they are more slender, with little or no inflation of their internal cingula. The lower postcanines of *P. rovereti* (Frenguelli, 1922:499, figs. 2B, 2C) are shorter and relatively broader than those of *P. capensis*, and have a variably developed second anterior accessory cusp which is not present in the Langebaanweg species.

TABLE 3. Dimensions of the teeth of *Prionodelphis capensis* from Langebaanweg.

	UPPER				LOWER		
	No.	A-P diameter	Transverse diameter		No.	A-P diameter	Transverse diameter
Incisors Med. Med.	L 11689 L 15381B	6,1 6,3	5,3 5,2	Incisors Med.	L 15444A	3,8	3,2
Canines	L 11686 L 15241 L 15630B/2 L 15695	10,1 c. 10,2 c. 10,1 10,1	7,5 7,5 c. 8,0 7,4	Canines	L 15437 L 15743 L 13152	9,2 9,0 9,6	7,4 7,3 7,8
Post-canines 1st 2nd 3rd 4th 5th 5th ? ? ? ?	L 11687 L 15611 L 15695 L 15695 L 12562 L 15429 L 12557 L 12556 L 15630B/2 L 15664	9,0 13,9 14,5 13,4 9,8 10,4 12,9 13,7 13,8 14,1	6,1 c. 7,0 7,5 7,4 6,4 5,5 8,1 7,8 7,2 7,8	Post-canines 1st 2nd ?2nd ? ? ? ? ? ?	L 15580 L 15680B/2 L 15736A L 15429/1 L 15413B L 10160 L 15444B L 15771 L 12124	9,7 14,5 14,2 c. 15,0 15,4 14,8 15,2 15,0 16,0	5,6 6,4 6,5 6,5 6,4 7,2 7,0 7,1 7,3

The proportions of the upper and lower cheek teeth to one another are similar in *P. capensis* and *P. rovereti*, and differ from some extant monachines (Table 1).

The height of the mandibular corpus is fairly constant between the poste-

rior limit of the symphysis and the fifth postcanine (Plate 8). In the mandible fragment L 12299, the masseteric fossa begins about 20 mm behind the fifth postcanine, and the ascending ramus begins inclining at about this point. There is no corresponding upward inflection of the inferior margin of the corpus as there is in *Leptonychotes*, and the fossil resembles most other phocid species in this respect.

The symphysis of the mandible is short relative to that of some monachine seals, and terminates below the posterior root of the second postcanine. It is typically monachine, however, and has a strong, oval articular surface over the entire depth of the jaw. The mandibular condyle is not known.

There are multiple mental foramina towards the anterior part of the corpus.

THE POSTCRANIAL SKELETON

While the skull characters of *Prionodelphis capensis* show its relationships to lie with the Monachinae, certain features of the postcranial skeleton are more commonly found among the Phocinae (see King, 1966). Presumably, the 'phocine' characteristics are inherited from the primitive ancestral stock, and are features which were lost by the Monachinae during their later development. Characteristics which are typically monachine are also evident.

Vertebrae

Associated with the innominate to be described later (L 15849), were a number of vertebrae, most of which were badly crushed and incomplete. However, two lumbar (L 15849A1 and A2) and one caudal vertebra (L 15857) were reasonably well preserved although still incomplete (Plate 10C, D, F). Other vertebrae recorded are an axis (L 7563), one other cervical (L 15689), and a sacral (L 15396) (Plate 10B, E), all of which are damaged, and a number of other fragmentary specimens.

Only the centrum of the second cervical vertebra is preserved. The odontoid process is prominent, with a length of 16 mm and a maximum transverse diameter of 17,7 mm. The total length of the centrum is 53 mm, and the transverse diameter of the anterior articular end is estimated to be about 55 mm. The other cervical vertebra, probably a fourth, consists of the centrum, parts of the left transverse processes enclosing the vertebrarterial canal, and part of the left half of the neural arch. The centrum is 47,6 mm long and the transverse diameter of the anterior epiphysis is 31,4 mm. Both these specimens have the reduced transverse processes which characterize the Phocidae (King, 1964:98).

The two lumbar vertebrae, a second or third and a fifth, are similar in size to those of *Pliophoca etrusca* (see Ugolini, 1902, and Table 4). The transverse processes of the fifth lumbar vertebra are very prominent, which is characteristic of all Phocidae (King, 1964:99).

Although the sacral vertebra, a third, is from an adult individual it was not fused to the second. However, the anterior end of the preserved right transverse process is markedly rugose, suggesting that there was a strong cartilaginous

TABLE 4. Dimensions of lumbar vertebrae of *Prionodelphis* and *Pliophoca*.

	<i>Prionodelphis capensis</i>		<i>Pliophoca etrusca</i>		
	2nd or 3rd	5th	2nd	3rd	5th
Length of centrum	60,4	55,4	62,0	61,5	55,5
Transverse diameter of anterior epiphysis	41,0	42,2	41,0	40,0	44,0

attachment between it and the posterior end of the second sacral transverse process. This specimen is unusual in that it lacks the left transverse process, and the anterior end of the centrum and neural arch are, as a result, asymmetrical with the dorso-ventral median axis directed from right to left at a slight angle to the normal line. The length of the centrum is estimated to be 38 mm, while that of a *Pliophoca etrusca* specimen is 36 mm (Ugolini, 1902).

In the caudal vertebra, a first, much of the centrum is lost, apparently having been gnawed away. Crushing, punctures, and gnaw-marks resulting from grasping and chewing by carnivores are a not uncommon feature of the fossils from Langebaanweg. Both anterior and posterior zygapophyses of the caudal vertebra are well developed, and the distance between their anterior and posterior limits is 47 mm. The transverse diameter of the anterior epiphysis of the centrum is approximately 25 mm.

Anterior Limb

Scapula

A single incomplete pinniped scapula (L 2160) is known from Langebaanweg (Plate 10A). This specimen consists of the articular end, neck and lower parts of the blade. The acromion and internal margin of the articulation are damaged.

The glenoid cavity is markedly elongated and concave; the concavity as well as the breadth/length ratio being comparable only to that of *Lobodon* and *Monachus* (67,9% for L 2160, 72,0% for one *Lobodon* scapula, and 67,1% for one *Monachus schauinslandi* scapula). Other monachine genera have shallower and more nearly equidimensional scapular glenoid fossae.

Also most comparable to *Lobodon* and particularly *Monachus*, the neck of the fossil scapula is extremely short and has an antero-posterior diameter of 45,8 mm. The spine is strongly developed for a monachine seal, but might not exceed the development of that of *Lobodon*. Too little is preserved to be certain. The sharp scapular notch, where the anterior margin of the coracoid process turns into the inferior border of the suprascapular fossa, suggests that the anterior border of the scapula may have been straight and vertical as in the Antarctic monachines.

The medial surface of the subscapular fossa is divided into two parts by a prominent ridge most resembling that of *Monachus* in its prominence and location. The ridge is more prominent than in *Monachus*, however, and is better developed than in any living phocid. Although the scapula differs greatly in other respects, the prominence of this subscapular ridge is equalled only by the

Miocene *Phoca vindobonensis* Toula (1897: pl. 9, fig. 15a).

Humerus

All fourteen humeri recovered to date in which the distal end is preserved have an entepicondylar foramen. The supinator ridge is well developed in all specimens (Plate 11). These features are characteristic of the extant Phocinae (King, 1966), but in at least one extinct monachine, *Monotherium*, an entepicondylar foramen was present (see Van Beneden, 1877). This is a characteristic of particular significance in the interpretation of the relationships of *Prionodelphis capensis*.

Because of the rather startling phocine appearance of the humerus of *P. capensis*, it is appropriate to examine this bone in greater detail. Plate 12 shows the right humeri of *Monachus schauinslandi*, *P. capensis* and *Cystophora cristata*. The humerus of *Cystophora* was selected because it, of all phocine genera, most resembles that of the fossil. The humerus of another phocine, *Erignathus barbatus*, is shown with those of *P. capensis* and *M. schauinslandi* in Figure 2. It is immediately evident that the *P. capensis* humerus exhibits not only phocine, but also monachine characteristics.

Apart from the two characters already mentioned, there is also a considerable difference between phocine and monachine humeri in the region of the deltoid crest. In all pinnipeds the pectoralis muscle is prominent, and its insertion on the humerus is strengthened. In the phocine seals this has been accomplished by an anteriorly directed enlargement of the medial edge of the deltoid crest toward the enlarged lesser tubercle, so that the intertubercular groove becomes circular in cross-section, coming to within 40° of completely encircling the bicipital tendon in some species. In the otarioid seals, the pectoral insertion is similarly strengthened in this area, and the intertubercular groove becomes trenchant, although the lesser tubercle remains 'lesser'. Strengthening of the pectoral insertion on the phocine humerus does not take place by extending the insertional area distally along the shaft of the humerus but, rather, the insertional area terminates abruptly at a strong process on the distal end of the deltoid crest. Beyond this point the anterior margin of the phocine humerus shaft is concave as it curves to meet the distal articulation, and is devoid of muscle scars.

The transverse development of the deltoid crest of phocine humeri is also in evidence laterally, where a lip of bone overhangs the area of insertion of the deltoid muscle.

In the monachine seals anterior enlargement of the deltoid crest is minimal, the intertubercular groove remains widely open, and there is no overhanging of bone on the lateral edge of the crest. The pectoralis insertion on the humerus is strengthened by extending its area distally down the shaft toward the radial fossa (much reduced in monachine seals) and the distal articulation. The anterior margin of the monachine humerus is, therefore, straight or even convex, and muscle scars are prominent where the deltoid crest blends distally into the shaft. A similar elongation of the pectoral insertion is also present in the otarioid

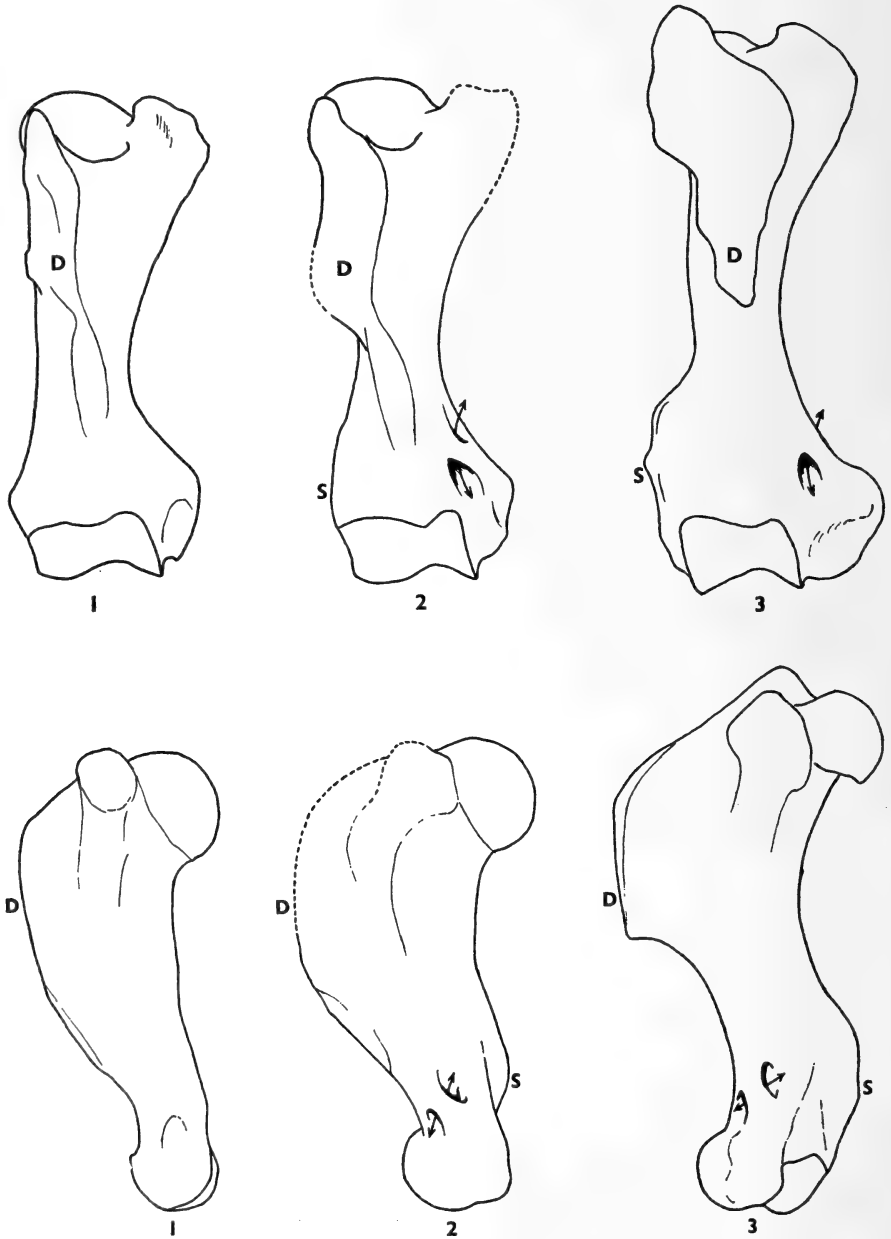


FIG. 2. Anterior and medial views of the right humeri of *Monachus schauinslandi* (1), *Prionodelphis capensis* (2), and *Erignathus barbatus* (3). (D - deltoideus crest; S - supinator ridge.)

seals, consistent with the greater development of the pectoral muscles in that group.

In the *P. capensis* humerus, the bicipital or intertubercular groove is widely open, the deltoid crest blends smoothly into the distal part of the shaft, and the muscle scars are prominent on the shaft below the deltoid crest. In these respects it is typically monachine. It does, however, have the lateral overhanging of the deltoid crest similar to that of the phocines. The deltoid crest is as a result, more prominently developed than in modern monachines.

It is concluded that the pattern of strengthening of the pectoral muscle insertion is a more useful character in classifying phocids than the two characters given by King (1966), which apply to modern species only. In the *P. capensis* humerus the loss of the entepicondylar foramen, a reduction in the size of the supinator ridge and reduction of the lateral development of the deltoid crest, would reduce it to an almost exact replica of that of *M. schauinslandi*.

The humerus of *P. capensis* is stoutly proportioned, and the most complete specimen known (L 4638) has a total length of 138 mm between the head and median condyle. The transverse diameter of the distal end is 52.7 mm (mean of 8 specimens). It is stouter than that of living *Monachus* and *Leptonychotes*, and some fossil monachines such as *Pliophoca etrusca* and *Monotherium aberratum*; comparable in stoutness to the humerus of living *Hydrurga* and fossil *Palaeophoca nystii*; it is less stout than that of living *Lobodon* and *Ommatophoca*. Relatively shorter and stouter humeri suggest more pelagic adaptations in living phocids.

Ulna

According to King (1966:390) there are no consistent differences between the ulnae of phocines and monachines. In our sample of ulnae from living species there is a suggestion that the tuberosity for insertion of the internal anconeal muscle (Howell, 1929:75) is much more produced and somewhat more posterior in location in the phocine seals. In the monachine seals, if any anconeal tuberosity can be said to exist, it is continuous with the triceps insertion at the anterodorsal apex of the olecranon (ulnar orientation is here considered to be with the long axis vertical, as in fissiped carnivores). There also appears to be slight but persistent sigmoid flexure of the phocine ulnar shaft, in anterior or humeral aspect, because of a lateral curve distal to the radial notch, whereas the shaft of modern monachine seals is straight distal to the radial notch.

Of these two suggestive characters, the nature of the anconeal insertion is not preserved on the ulnae of *P. capensis*, but there appears to be a slight phocine outward curvature of the shaft in the vicinity of the interosseous crest, distal to the radial notch. It thus seems possible that the straight shaft of the living monachine seals has been recently acquired.

Except for the slight curvature of the shaft, the ulna of *P. capensis* (Plate 13) greatly resembles that of *M. schauinslandi*. The proportions are nearly equal and both are characterized by an extremely elongated posterior process of the olecranon, giving the bone a very hatchet-like appearance.

There is considerable generic variation, and no subfamilial differentiation, in the configuration and relative location of the humeral and proximal radial articulation on the phocid ulna. In these articular facets *P. capensis* also resembles living *Monachus*. The radial facet has minimal medial offset and distal separation from the facet for the humerus, and faces anteriorly rather than anterolaterally as in other phocids. The humeral facet has a distinct medial curvature, as does that of many other phocids. It also seems possible, therefore, that the lateral positioning of the head of the radius, as reflected in its articulation with the ulna, may be a rather recent development, at least in the monachine seals.

The total length of the ulna of *P. capensis*, estimated from two incomplete specimens, is about 170 mm.

Radius

Reflecting the more anterior orientation of the radial articulation of the ulna, the radius of *Prionodelphis capensis* (Plate 14) was orientated more anteriorly from the ulna than is that of some living monachines and apparently all living phocines. As a result, the radial tuberosity lies distinctly on the medial side of the radius, as on the radius of living *Monachus*, and not on the posteromedial surface as is the case of the radius of living phocines.

King (1969: fig. 31) has pointed out that the distal articulations of the radii of *Hydrurga* and *Ommatophoca* have convex surfaces that curve on to the medial (flexor) side of the radius at or near the anterior (preaxial) limit of the articular surface. The radius of *Halichoerus* has this medially curving segment of the articulation about midway between the anterior and posterior limits of the articular surface. The condition in the latter produces a moderate indentation in the medial margin of the articular facet when viewed distally.

The pattern of distal articulation on the radius of *Halichoerus* seems to be a characteristic of all extant Phocinae. The radii of living monachine seals follow the patterns shown by King (1969) for *Ommatophoca* and *Hydrurga*. In *Ommatophoca* and *Mirounga* the distal articular surface is roughly rectangular, and the anteromedial quarter curves on to the medial surface. In *Hydrurga*, *Lobodon* and *Monachus* the anteromedial corner of the articulation is extended so that the part of the surface that curves on to the medial side of the radius is almost a separate articulation (see King, 1969: fig. 31b).

In *Prionodelphis capensis* the distal articulation of the radius (L 2935) most resembles that of *Mirounga*. In general configuration the radius is markedly spatulate with a prominent anterior crest for insertion of supinator and pronator teres muscles, most closely resembling in this respect, *Hydrurga* and *Ommatophoca* of the living monachines.

The total length of the radius of *P. capensis*, estimated from two incomplete specimens, is about 145 mm with the greatest anteroposterior diameter of the shaft being 51,4 mm. The dimensions of the proximal end are 30,8 by 23,4 mm (mean of seven specimens).

Posterior Limb

Innominate

The most complete innominate known (L 15849A) lacks the most anterior part of the ilium, and the posterior parts of the ischium and pubis (Plate 15). There is, however, sufficient of this bone remaining to enable a fairly confident assessment of its characteristics.

The ilium is weakly everted, approximately to the extent of that of *Erignathus* and most monachine seals. *Erignathus* is atypical of the Phocinae, the remainder of which have a strongly everted ilium 'with a deep lateral excavation' (King, 1969:392); the latter character is absent in *P. capensis*.

Comparison of the post-acetabular proportions of the entire innominate is precluded by the incompleteness of the specimens. However, a comparison of the distance between the centre of the acetabulum and the apex of the ischiatic spine, to the width of the obturator foramen ventral to the ischiatic spine (not always maximum width), results in an equally distinct separation between monachine and phocine seals (Table 5). Interestingly, measurements of photographs and drawings published by King (1956, 1966, 1969), also conform quite well.

TABLE 5. Innominate proportions of some phocids.

Species	O = Width of obturator foramen		O/A × 100
	A = Acetabulum center to tip of ischiatric spine	center to tip of ventral to ischiatic spine	
<i>Monachus m.</i> ¹	37,1	18,3	49,3
<i>Prionodelphis capensis</i>	90,8	39,8	43,8
<i>Hydrurga l.</i>	132,8	57,8	43,5
<i>Hydrurga l.</i> ²	25,6	9,9	38,7
<i>Leptonychotes w.</i> ²	24,0	9,5	39,6
<i>Leptonychotes w.</i> ¹	44,4	15,9	35,8
<i>Monachus s.</i>	95,6	36,5	38,2
<i>Ommatophoca r.</i> ²	22,5	8,2	36,4
<i>Lobodon c.</i>	95,0	33,4	35,2
<i>Cystophora c.</i>	132,8	44,4	33,4
<i>Pagophilus g.</i>	93,8	30,3	32,3
<i>Halichoerus g.</i> ²	23,3	6,9	29,6
<i>Halichoerus g.</i> ¹	34,9	9,4	26,9
<i>Phoca v.</i>	97,9	28,6	29,2
<i>Erignathus b.</i>	141,2	39,1	27,7
<i>Erignathus b.</i> ²	28,5	7,7	27,0

¹ From photo in King, 1956.² From drawing in either King, 1966, or King, 1969.

As with the living Antarctic monachines (but not *Monachus schauinslandi*) and some phocine seals, the innominate of *P. capensis* appears rather thick across the acetabulum. It appears similarly thick in available specimens of *Pagophilus* and *Cystophora*. This appearance is caused by a relatively small acetabulum.

Femur

Only the distal end of the femur of *P. capensis* is known (L 10131) (Plate 16A). The patellar facet is somewhat broader than tall, as in the monachine seals, while a fairly marked pit for the popliteus muscle on the lateral epicondyle shows resemblance to the phocine seals.

Tibia

The tibia of *P. capensis* is remarkable for the development of pronounced fossae on the posterior and antero-lateral surfaces. In the specimen L 10128/9 (Plate 16B, C, D) the thickness of bone between these two fossae is as low as 0,75 mm. This condition most resembles that in the tibia of *Halichoerus*. King (1966) states that the post-tibial fossa is more pronounced in the Phocinae than in the Monachinae.

Distally, the tibia of *P. capensis* is conspicuously broad and anteroposteriorly flattened (Plate 16E, F), a condition very similar to *Pliophoca etrusca* (Tavani, 1942: fig. 18). The fibular contact is sharply angled outward suggesting that the fibula was rather markedly bowed.

Pes

A calcaneum (L 10118), two astragali (L 10130, L 10993), one navicular (L 15851), one entocuneiform (L 10124), one metatarsal V (L 10996) and two phalanges (L 10999, L 10205) of *Prionodelphis capensis* are known (Plates 17 & 18). At first glance it seems obvious that *P. capensis* has long metatarsal bones relative to the size of the astragalus, and in fact, a sampling of the relative sizes of these two bones in seven living genera seems to bear this out (Table 6). The Langebaanweg seal appears to have relatively longer metatarsals than those of the compared living genera except *Monachus*.

TABLE 6. Tarsal-metatarsal comparison of some phocids.

Genus	(1) Greatest length of MT V	(2) Greatest length of astragalus	(3) Greatest length of cuboid-MT IV facet	(2/1)	(3/1)
<i>Phoca</i> . . .	70,7 mm	59,7 mm	28,2 mm	0,84	0,398
<i>Lobodon</i> . . .	98,2	75,0	35,2	0,76	0,358
<i>Cystophora</i> . . .	94,6	69,9	32,4	0,74	0,342
<i>Mirounga</i> . . .	129,5	90,5	47,8	0,70	(0,369)
<i>Hydrurga</i> . . .	120,2	82,0	40,8	0,68	0,339
<i>Pagophilus</i> . . .	85,6	57,7	25,9	0,67	(0,302)
<i>P. capensis</i> . . .	89,5	57,5	30,4	0,64	0,339
<i>Monachus</i> . . .	98,0	56,3	30,2	0,57	0,308

As the fossil astragali and metatarsal V were not found in association, they could represent different sized individuals, creating a false impression of relative metatarsal size. To check this possible error a similar comparison of the cuboid-metatarsal IV articular facet on metatarsal V, to the total length of the

the metatarsal was also made (Table 6). Comparable results were achieved, except for *Mirounga* and *Pagophilus* whose relative proportions were not consistent. It therefore appears probable that *P. capensis* did indeed have relatively elongated metatarsal bones and hence had relatively large hind flippers.

King (1966:393-394) has suggested that the more distal articular facet between the astragalus and the calcaneum is relatively long in the phocine seals and short in the monachines. Although there is no exception in the monachine specimens available, there seems to be great variation in the form of this facet on the astragalus of the phocine seals. Our specimen of *Cystophora* appears decidedly 'monachine' in this character: astragali of *Erignathus* appear to vary from distinctly 'monachine' to distinctly 'phocine'. This articular surface on *P. capensis* is distinctly elongated and hence 'phocine' to the extent that the character is valid.

In all respects other than their mutual lower articulation, the astragalus and calcaneum of *P. capensis* are extremely similar to those of *M. schauinslandi*. If the tibial articulation of the astragalus is arbitrarily taken to be dorsal, so that the fibular articulation is vertical, these surfaces are low relative to the body of the astragalus and the fibular articulation extends about to the most ventral limit of the bone. Among living monachines a similar condition is found in both *Monachus* and *Mirounga*, which differ greatly in this respect from *Hydrurga*. Wide variation is found also in the phocine seals: the astragalus of *Pagophilus* is perhaps most similar to that of *P. capensis*, while that of *Phoca* differs the most.

The tibial articulation is cylindrical, as in *Mirounga*, *Monachus* and *Lobodon*, rather than spherical as in *Hydrurga*. No angular boundary separates the distal articulation for the navicular from the adjacent articulation for the calcaneum. The astragalus is rather short-necked and has a short calcaneal process.

The dimensions of the calcaneum L 10118 (Table 7) are remarkably similar to that of a *M. schauinslandi* specimen recorded by Robinette & Stains (1970: table 1), while its proportions are clearly monachine rather than phocine (Robinette & Stains, 1970: table 2). The metrical data presented in Table 7 confirms the observations on the similarities between the calcanea of *P. capensis*, *Monachus* (especially *M. schauinslandi* and *M. tropicalis*) and *Mirounga*, and also illustrates differences from those of *Hydrurga*, *Leptonychotes* and *Ommatophoca*.

The posterior¹ astragalal articulation of the calcaneum of *P. capensis* is narrow relative to its length. This contrasts with that facet of the calcaneum of *Hydrurga* and *Monachus schauinslandi*, in which it is nearly as wide as it is long. Robinette and Stains (1970:535) state that the facet is narrower on the calcaneum of *M. tropicalis* than on that of *M. schauinslandi*.

The facet of the navicular, for articulation with the entocuneiform, is notably equidimensional and flat. The articular surface on the entocuneiform, for contact with metatarsal I, is notably elongated, suggesting a more slotted

¹ As used by Robinette & Stains (1970: fig. 1); this is the anterior articulation of King (1966: 393).

TABLE 7. Dimensions of calcaneum of *Prionodelphis capensis* from Langebaanweg, compared with those of some modern monachines.

Species	N	TL	W	DVH	W/TL	DVH/TL	DVH/W
<i>Monachus monachus</i> †	1	63,2	29,8	30,0	47	47	101
<i>Mirounga angustirostris</i> †	6	79,0*	40,9*	38,7*	52	49	95
<i>Monachus schauinslandi</i> †	1	59,1	31,9	30,3	54	51	95
<i>Monachus tropicalis</i> †	1	54,9	27,3	28,5	50	51	104
<i>Prionodelphis capensis</i>	1	58,4	30,7	30,4	53	52	99
<i>Hydrurga leptonyx</i> †	1	74,5	38,7	42,0	52	56	108
<i>Leptonychotes weddelli</i> †	1	71,5	38,2	41,9	53	58	110
<i>Ommatophoca rossi</i> †	1	56,0	30,4	34,6	54	61	114

† From Robinette & Stains, 1970.

TL = total length.

DVH = dorsoventral height.

* Average figures.

W = width.

proximal articulation rather than the basined articulation on metatarsal I of most living seals. Although both the navicular and the entocuneiform appear large relative to the known astragali and calcaneum, they appear to be undiagnostic of subfamily affinities.

As has been mentioned, metatarsal V appears to be relatively elongated. The two known phalanges also appear to be conspicuously elongated and slender when compared with those of living phocids. Otherwise they seem to have no distinctive features.

DISCUSSION

In assigning the Langebaanweg phocid to the genus *Prionodelphis*, it is recognized that reassessment may be required when more material of *P. rovereti* is found. Generic identity is based upon the remarkable similarity of the few fragments from Argentina to the South African material and on the belief that the lack of greater knowledge is a stronger argument against the establishment of a new genus than it is against tentative assignment to the same genus.

The similarity of the cheek teeth of *P. rovereti* and *P. capensis* is very strong. The transverse narrowness of the cheek-teeth, more evident in the latter species, and a posterointernal shelf on the upper cingula only, are features found only in some of the Antarctic genera of the monachine seals. As mentioned, the tooth proportions and cingular shelf are most similar to the condition in *Hydrurga*. In addition, the greatly reduced and distinctly recurved last upper postcanine, of both species of *Prionodelphis* is singularly suggestive of a close relationship, and is not known in other monachine seals, although there is some resemblance to the more anterior cheek teeth of *Leptonychotes*, and to a lesser extent also *Ommatophoca*.

Apart from differences in the dimensions of the teeth of *P. capensis* and *P. rovereti*, some differences in morphology are also evident. Other than the upper

fifth, the only known upper postcanine of *P. rovereti* (Frenguelli, 1922: fig. 1), differs from the second to fourth upper postcanines of *P. capensis* in having a far larger posterior root, which is at least partially divided longitudinally. This feature of the Argentinian species, as well as its slightly broader cheek-teeth, can be interpreted as being less advanced characteristics. The anterior part of the crown of this tooth of *P. rovereti* lacks a distinct accessory cusp, which is present in all the known postcanines of *P. capensis*. The anterior part of the *P. rovereti* tooth is markedly convex, and the lingual view (Frenguelli, 1922: fig. 1c) shows a small step more or less where an accessory cusp might be expected. It is possible, therefore, that this specimen has the anterior accessory cusp masked by some individual variation, and that normally such a cusp was present. The lower postcanines of *P. rovereti* (Frenguelli, 1922: fig. 2B, C) are illustrated as having not one, but two anterior accessory cusps, with the anterior and posterior parts of the teeth being almost mirror images of one another. In none of the postcanines of *P. capensis* is a second anterior accessory cusp known, and its development in the Argentinian species could be a more advanced specialization.

The age of the Argentinian species is even more uncertain than that from Langebaanweg. The Entre Rios deposits, from which the specimens of *P. rovereti* came, appear to be of Pliocene age (Langston, 1965: table 3) and would seem, therefore, to be roughly the same age as those from Langebaanweg. However, most often these deposits have been referred to as being late Miocene or early Pliocene, and the latter age is given by Romer (1966).

Discussion on the relationship of *P. capensis* to *P. rovereti* will be more meaningful when more specimens of the latter are known, but the observed differences between the two sets of specimens, the possibility of a temporal difference in the deposits from which they come, and their geographical separation suggest a distinction between the South African and Argentinian fossils at least at the species level.

The relatively poor fossil record of the Phocidae in general renders interpretation of the wider relationships of *P. capensis* equally problematical. Some features of the fossil seal from South Africa are found, among the living seals, only in the Phocinae. However, a number of features are clearly monachine and these suggest that the dichotomy from the primitive phocid into the two extant subfamilies was a result of two distinctly different patterns of specialization to better adapt to pelagic existence. These adaptations relate to, amongst other things, greater swimming ability and underwater hearing. As has been pointed out throughout the description, in all of these adaptations *P. capensis* has clearly followed the monachine pattern.

To judge from the comparisons between *P. capensis* and the living phocine and monachine seals, differences in adaptation toward greater swimming ability appear most evident in the proximal limb elements. Subfamilial differences in the structure of the humerus related to the strengthening of the pectoralis muscle have been outlined in the discussion of this bone. In the Phoci-

nae the pectoralis insertion has been strengthened by exaggeration of the deltoid crest, and in the Monachinae strengthening of this same muscle has been accompanied by a distally extended insertional area on the humerus shaft.

One might infer that the phocid ancestral to the living subfamilies had a humerus of relatively slender proportions showing a moderate development of both types of pectoralis insertion, such as seen on the humerus of '*Phoca vindobonensis* Toulou (1897: pl. 1, fig. 16) or *Leptophoca lenis* True (1906: pl. 75). Such fossil phocids as *Monotherium aberratum* Van Beneden (1877: pl. 17, figs. 1-4) appear to have the insertional area extended so far distally on the shaft that a monachine condition seems indisputable, while others such as *Phocanella pumila* Van Beneden (1877: pl. 14, figs. 1-4), have clearly evolved the phocine condition by strengthening the deltoid crest and eliminating all pectoralis insertion on the shaft distal to the crest. In addition, the presence of an entepicondylar foramen on the humerus appears to be a primitive feature. It is present in all of these fossil seals, including *Prionodelphis capensis*, and is retained in the living phocine seals as well. Only at the stage of evolution evident in the living phocids does the presence of this foramen become diagnostic of subfamily affinity.

Consideration of the subfamilial differences in swimming adaptations which might be found in the pelvic limbs has been hampered in this study by the lack of a complete specimen of the femur of *P. capensis*. Nevertheless, King (1966:392) has pointed out that, except for the genus *Erignathus*, the phocine seals may be recognized by their extremely everted ilium. Both leverage and strength of the insertion of the massive muscles of the back, the iliocostalis system, are benefited by this structure, as well as are most of the gluteus group which directly transfers the forces of the back to the femur to produce the characteristic phocid swimming motion. The advantages of this structure seem so obvious that it is puzzling why none of the monachine seals have developed it, or why it developed so late in the history of the phocid seals. Few fossil seals in which the pelvis is known, exhibit the phocine everted ilium.

The interpretation of the functions of osteological characters in the phocine and monachine ear regions is subjective, but according to one interpretation (Repenning, in press), two of these differences relate to improved underwater hearing.

The presence of a more or less horizontal crest on the external surface of the mastoid bone in all phocine seals is correlated with a greater directional selectivity of sounds in water originating above or below the head; this crest is not present in the monachine seals, including *P. capensis*.

The development of an enlarged petrosal apex in all seals is correlated with a greater sensitivity to sound in water, and this development is conspicuously less in *P. capensis* than in the living Antarctic seals. The enlargement of the petrosal apex is in the form of a globular mass in the phocine seals, while in the monachine seals, with the exception of *Mirounga*, the apex is enlarged as a rather low and broad structure. In this respect *P. capensis* is clearly monachine.

It should also be noted that broadening is slight in *Hydrurga*, and that enlargement of the apex is partly accomplished by thickening; the structure does not appear globular as in the phocine seals, however. Furthermore, enlargement of a petrosal apex is minimal in *Monachus*, less than in *P. capensis*; in this respect *Monachus* might be expected to be most similar to the ancestral phocid from which the extant subfamilies evolved.

Monachus is the least specialized of the living monachine seals in the enlargement of the petrosal apex, strengthening of the humerus, distal broadening of the radius, enlargement of the ilium, strengthening of the femur and modification of the dentition. Except for the condition of the femur, which is unknown in the South African fossil, and possibly the enlargement of the ilium, which is incompletely preserved, *Monachus* is also less specialized in these features than *P. capensis*.

From the preceding consideration of *Prionodelphis capensis* and related seals, the following features appear most likely to be those that would characterize the ancestral protophocid from which the two modern subfamilies, the Phocinae and the Monachinae, evolved: dentition with primary cusp flanked by one accessory cusp anteriorly and one posteriorly, much the same as seen in *Praepusa pannonica* Kretzoi (1941: fig. 1), ear region much as in living *Monachus*, and postcranial skeleton unspecialized as in '*Phoca*' *vindobonensis* Toulou (1897).

The relationship of *P. capensis* to the Antarctic monachines is evident in a broad sense, but it is not clearly ancestral to any of the four living genera. The highly modified dentitions of the living genera differentiate them most strikingly from the Pliocene fossil. The great reduction of the last upper postcanine tooth of *P. capensis* seems to preclude the possibility of it being ancestral to *Hydrurga* or *Lobodon*, while the great simplification of the teeth of *Leptonychotes* and *Ommatophoca* leave little basis for interpretation. *Hydrurga*, *Lobodon* and *Ommatophoca* are all clearly better adapted to pelagic life in their postcranial specializations than was *P. capensis*. All of the Antarctic seals, and *Leptonychotes* in particular, have a greater development of the petrosal apex than does *P. capensis*, which indicates that the latter had less acute hearing underwater. In all these respects *P. capensis* is less advanced than the Antarctic seals, but more advanced than *Monachus*.

It seems probable that *Prionodelphis*, presently known only by the species *P. rovereti* and *P. capensis*, was not the only Pliocene monachine of the southern seas, and that some or all of the modern Antarctic genera derive from a related but unknown form.

All previously described fossil phocids are known from incomplete remains and a good many from a very few, or even one bone. The humeri and femora are the most commonly described because they are among the more durable bones of the body, and, presumably, their size lends them to discovery. Excluding mandibular fragments, *Pliophoca etrusca* Tavani (1942; a skull), *Phoca pontica* Eichwald (1853; a cranium) and *Phoca pontica* Alekseev (1924; a rostrum) are the only fossil phocids of which the skulls are even partially known. Despite its

fragmentary nature, *Prionodelphis capensis* is one of the most completely known fossil phocids, and since the systematic investigation of the Langebaanweg deposits is still in its early stages, it can be expected that much more material will become available for study in the future.

SUMMARY

Pinniped remains from the late Pliocene deposits at Langebaanweg in South Africa are described. The material is referred to *Prionodelphis capensis* n. sp. (family Phocidae, subfamily Monachinae). On the basis of this material, the genus *Prionodelphis* Frenguelli 1922 is defined. The relationships of the Langebaanweg species to extant and fossil monachines are discussed, and morphological characters, by which fossil Phocinae and Monachinae can be differentiated are suggested.

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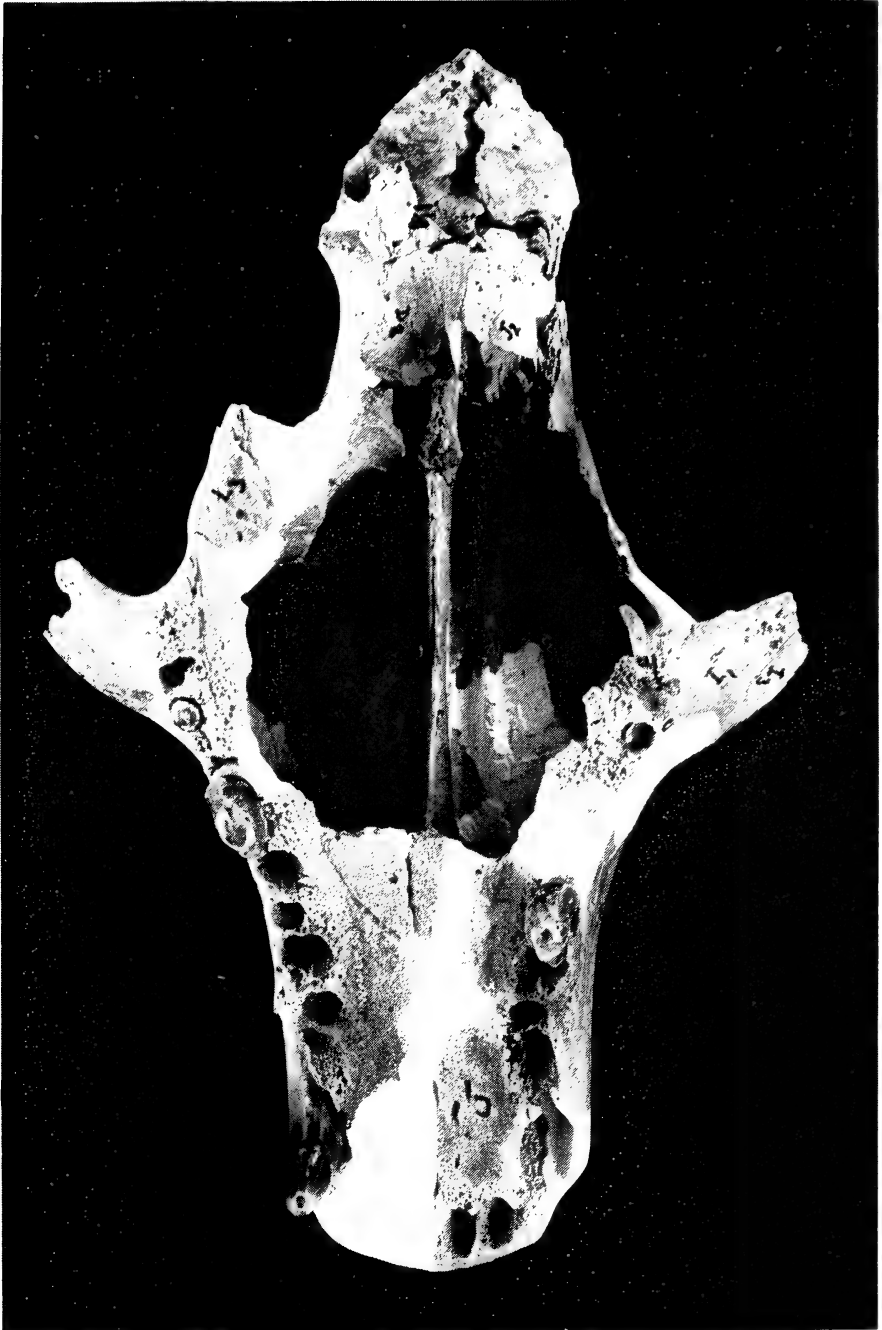
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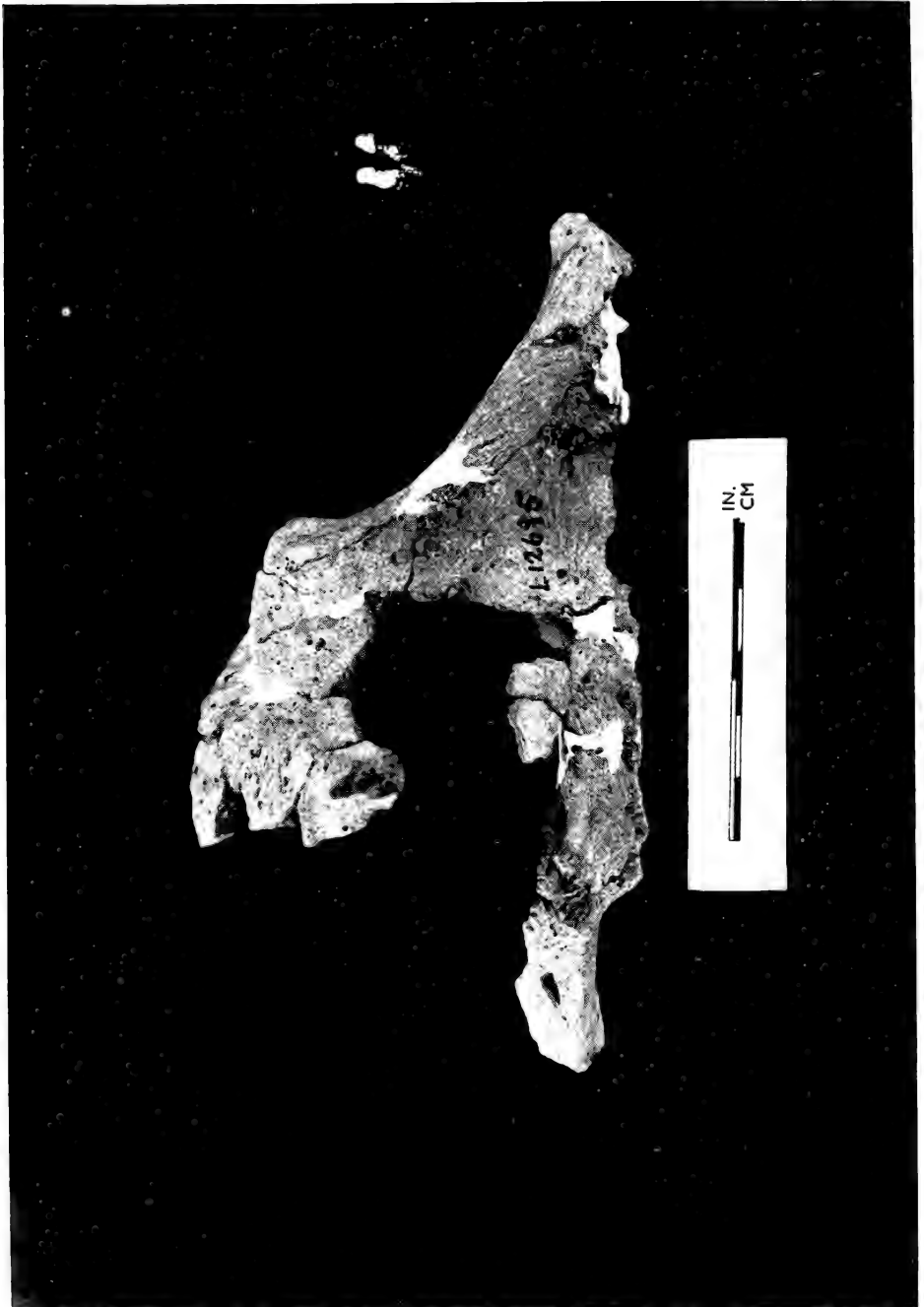
Dorsal view of skull L 15695. Scale represents 5 cm.



Lateral view of skull L 15695. Scale represents 5 cm.



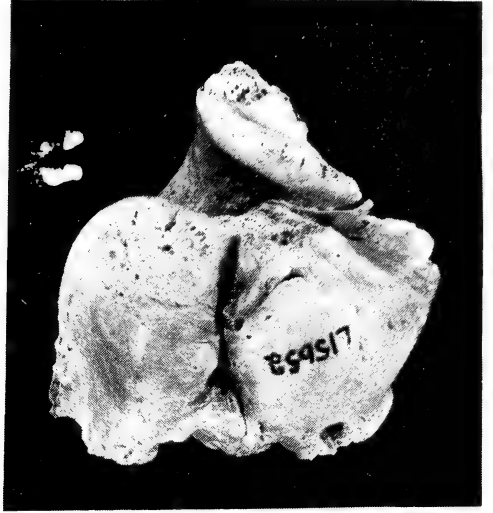
Ventral view of skull L 15695. Scale represents 5 cm.



Right lateral view of rostrum L 12695.



A



B



C

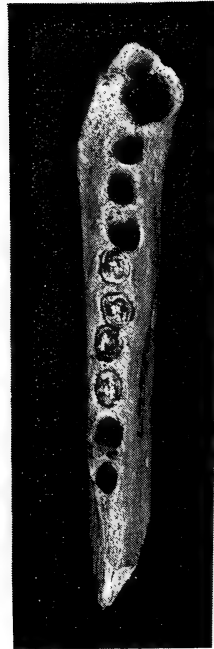
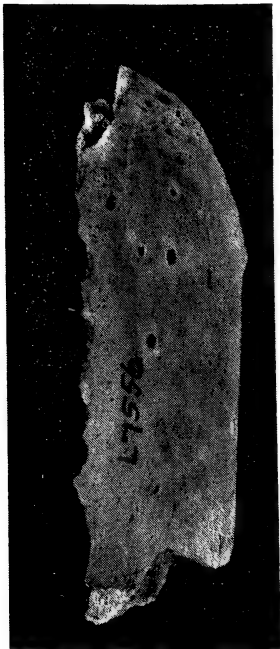
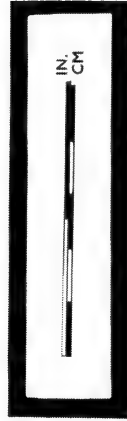


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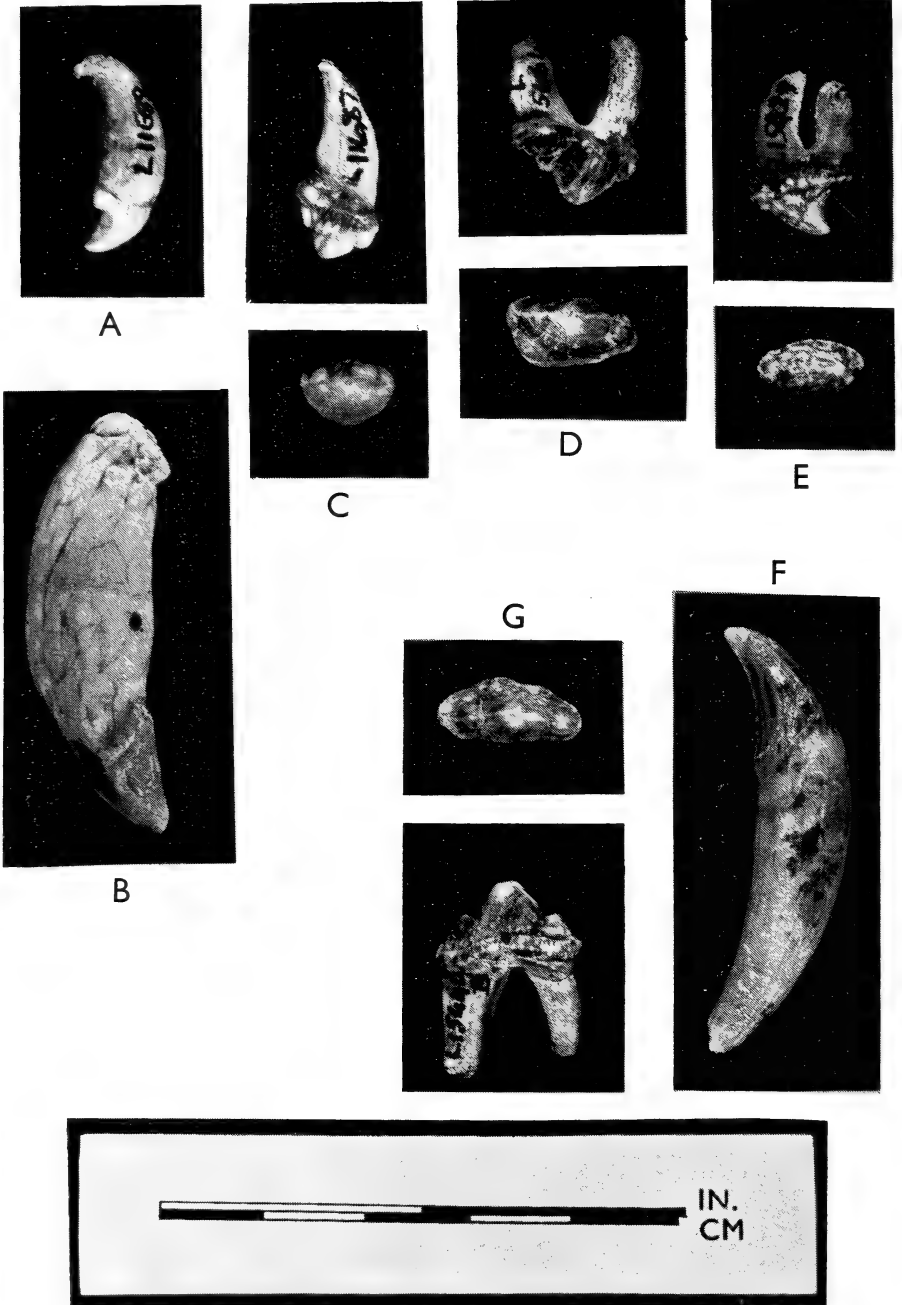
A, B, C & D. Dorsal, ventral, lateral and internal views of temporal L 15652.



Dorsal views of the temporals of *Monachus schauinslandi* (A), *Prionodelphis capensis* (B) and *Leptonychotes weddelli* (C).
 Abbreviations: c.a. - cochlea aqueduct; c.c. - carotid canal; c.f. - cerebella fossa; f.c. - facial canal; pa.a - petrosal apex; s.m. - squamosal margin; Vc.f. - vestibulocochlea fossa.
 Scale slightly reduced.



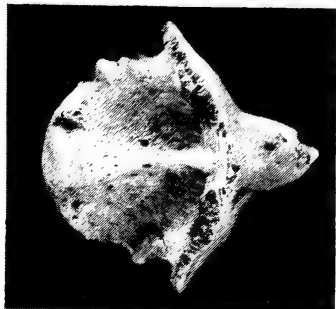
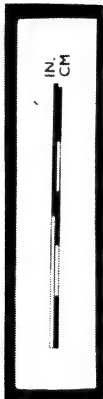
A, B & C. Lateral, internal and dorsal views of mandible L. 7556.



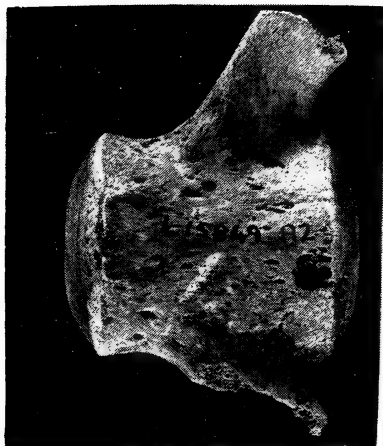
- A. Lateral view of upper incisor L 11689.
- B. Lateral view of upper canine L 11686 (aged individual).
- C. Buccal and occlusal views of first upper postcanine L 11687.
- D. Buccal and occlusal views of second, third or fourth upper postcanine L 15664.
- E. Lingual and occlusal views of fifth upper postcanine L 15429.
- F. Lateral view of lower canine L 13152 (young individual).
- G. Buccal and occlusal view of lower second, third, fourth or fifth postcanine L 15444B.



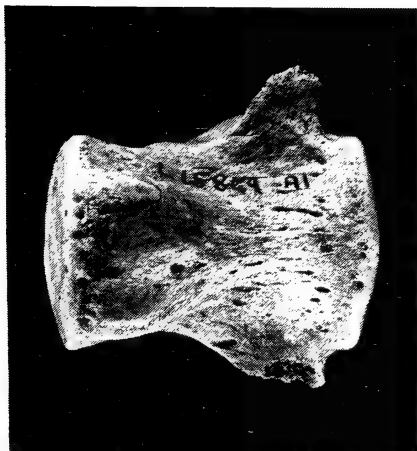
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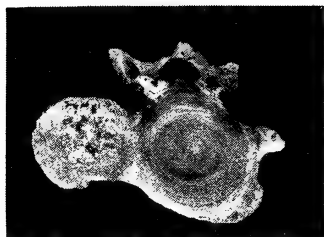
B



C



D



E

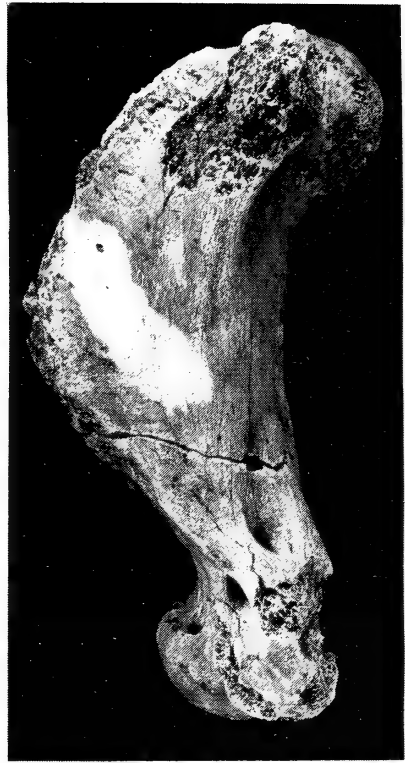


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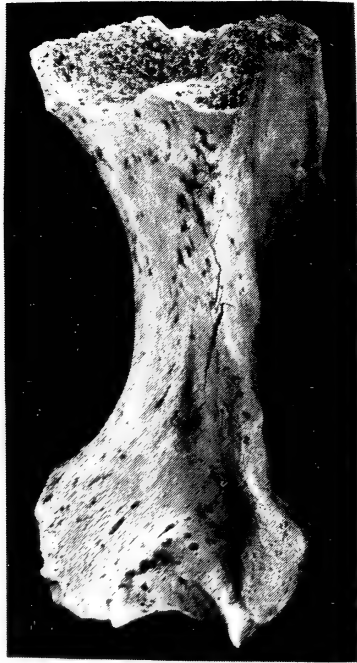
- A. Lateral view of scapula L 2160.
- B. Lateral and ventral views of second cervical vertebra L 7563.
- C. Ventral view of a second or third lumbar vertebra L 15849 A2.
- D. Ventral view of fifth lumbar vertebra L 15849 A1.
- E. Anterior view of third sacral vertebra L 15396.
- F. Anterior view of first caudal vertebra L 15857.



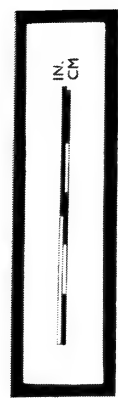
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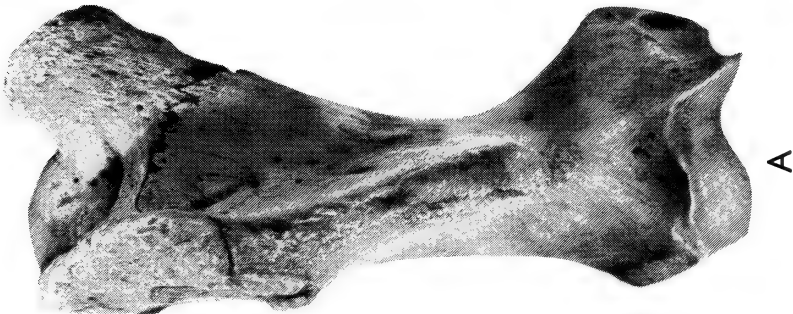
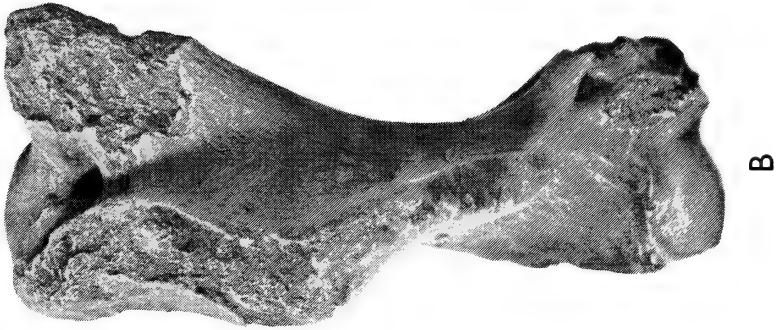
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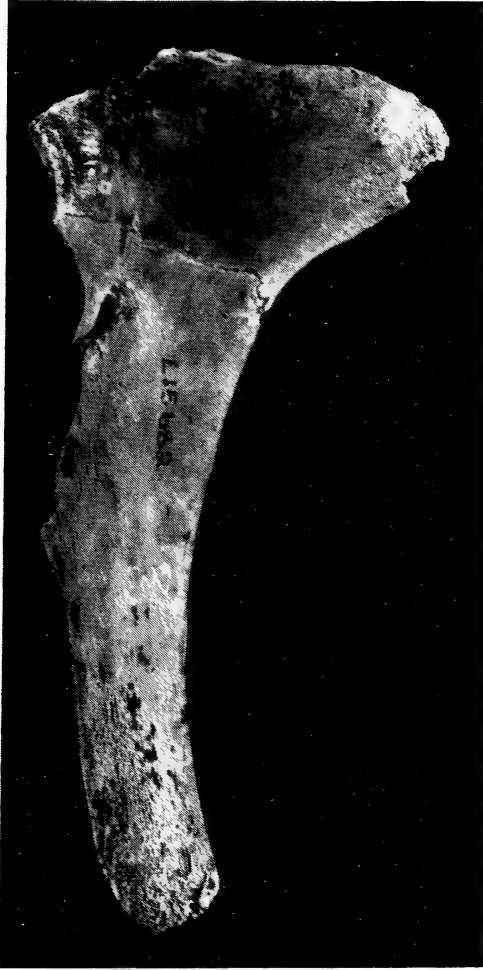
B



A & B. Anterior and posterior views of humerus L 2157.
C. Medial view of humerus L 4638.



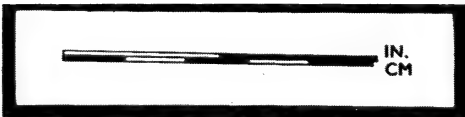
Anterior views of the right humeri of *Monachus schauinslandi* (A), *Prionodelphis capensis* (B) and *Cystophora cristata* (C). Scale approximately $\times \frac{1}{2}$.



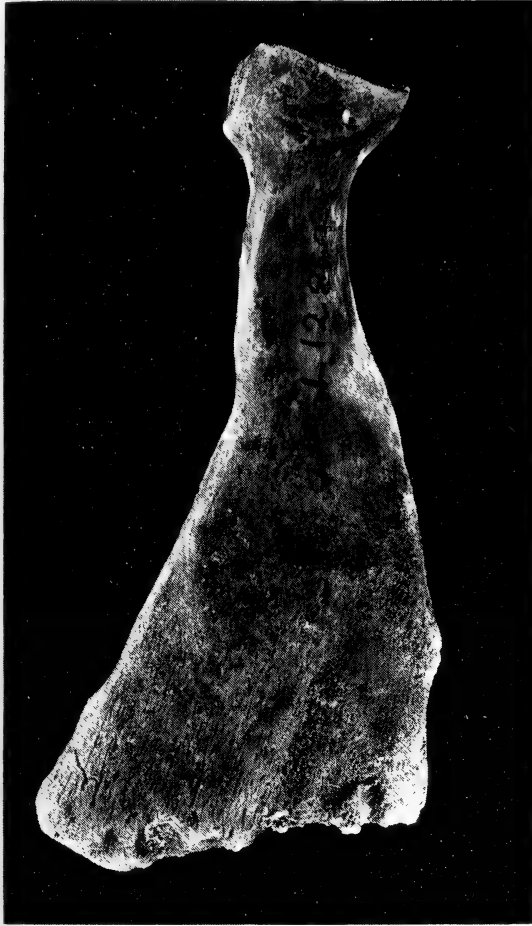
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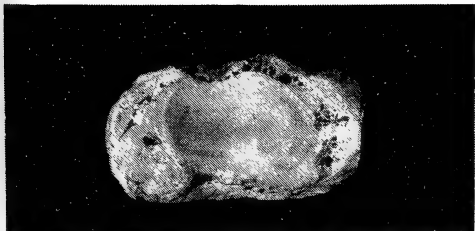
B



A. Lateral view of left ulna L 15682.
B. Medial view of right ulna L 2161.



A



B



A. Lateral view of right radius L 12869.

B. View of distal articulation of right radius L 2935 (anterior parts of specimen are lost).



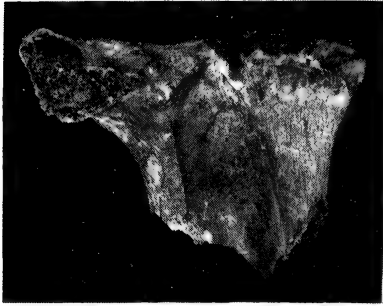
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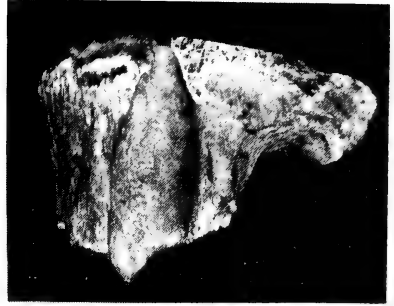
B



A & B. Dorsal and lateral views of left innominate L 15849A.



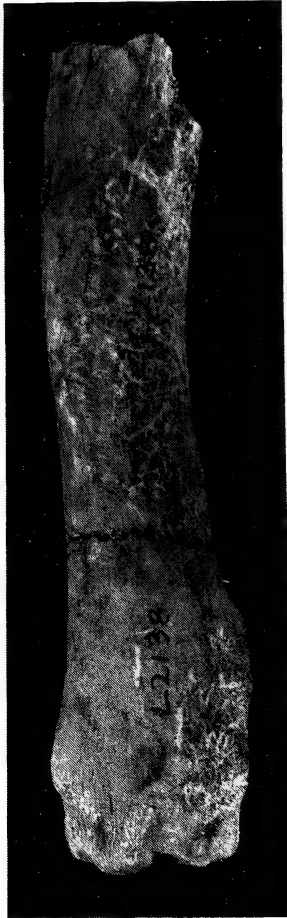
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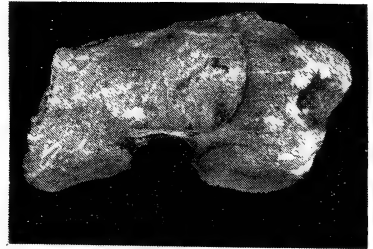
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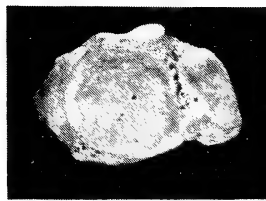
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E

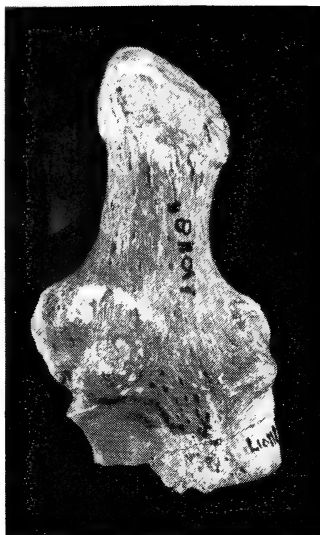


A

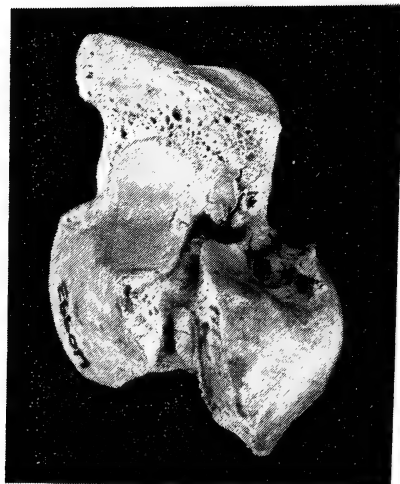


F

A. Distal view of femur L 10131.
B, C & D. Posterior, anterior and proximal views of right tibia L 10128/9.
E. Posterior view of left tibia L 2138.
F. View of distal articulation of right tibia L 10128/9.

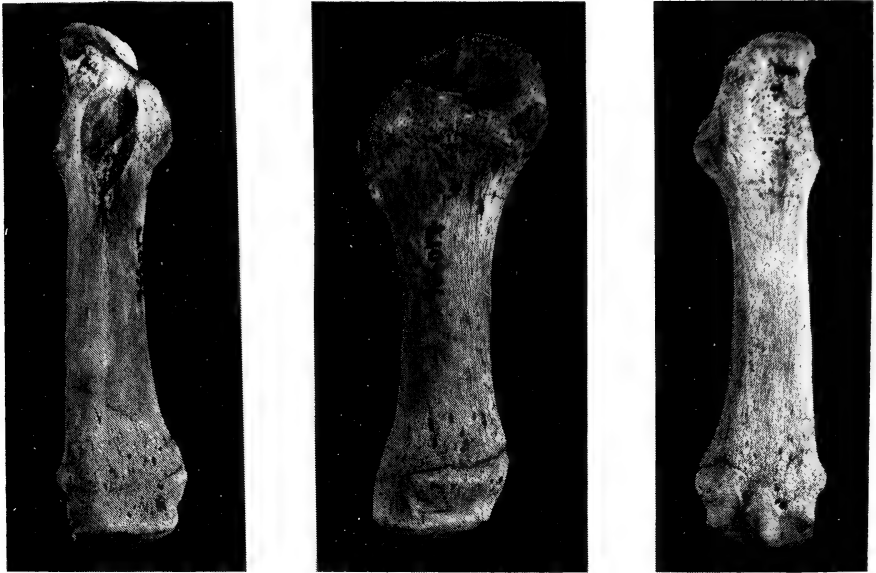


A



B

A. Lateral, ventral and medial views of right calcaneum L 10118.
B. Dorsal and ventral views of left astragalus L 10993.



A



B

A. Dorsal, lateral and ventral views of left metatarsal V, L 10996.
B. Dorsal view of phalanges L 10205 and L 10999.

INSTRUCTIONS TO AUTHORS

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Style manual for biological journals. Washington: American Institute of Biological Sciences.

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

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med-naturw. Ges. Jena* **16**: 269-270.

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Example

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MONACHINAE (MAMMALIA: PINNIPEDIA)

By
Q. B. HENDEY

Cape Town Kaapstad

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South African Museum, Cape Town

(With 2 figures)

[Ms. accepted 15 November 1971]

CONTENTS

	PAGE
Introduction	99
The monk seals	100
The Antarctic monachines	105
The elephant seals	107
Discussion	108
Conclusion	111
Summary	111
Acknowledgements	112
References	112

INTRODUCTION

The recent description of a late Pliocene monachine seal from Langebaanweg in South Africa (Hendey & Repenning 1972) included a discussion on the possible relationships of this species (*Prionodelphis capensis*) to other Monachinae. It is the purpose of the present paper to enlarge upon this topic, and also to comment on the phylogeny and zoogeography of the Monachinae.

The origin and evolution of the Pinnipedia have been the subject of numerous publications (e.g. McLaren 1960; Sarich 1969 etc.) and of all the subfamilies of this order, the Monachinae is probably that with the poorest fossil record, and consequently the one whose evolution is least well understood.

A number of fossil monachines ranging in age from Miocene to Pleistocene have been recovered from localities in Europe, while there are Pleistocene records of monk seals from the south-eastern United States (King 1964). The Pliocene monachine from South Africa is only the second Southern Hemisphere record of its kind, the other being the poorly known *Prionodelphis rovereti* Frenguelli 1922 from the Pliocene of Argentina. There are later Pleistocene and Holocene records of Monachinae from the southern continents, but these are all of species still extant, and are from areas within, or near to, the present ranges of the species concerned. For example, remains of seals have been found preserved by icy conditions in Antarctica, although none of these specimens is more than a few thousand years old (Crane & Griffen 1968). There are also late Pleistocene and Holocene records of *Mirounga leonina* from coastal human occupation sites in South Africa, an area where occasional stray individuals of this species are still found.

The sparse fossil record of the Monachinae in the southern continents is curious, since modern representatives of this subfamily are found mainly in the higher latitudes of the Southern Hemisphere. The only extant northern monachines are the comparatively small and widely scattered populations of monk seals (*Monachus monachus*, *M. tropicalis* and *M. schauinslandi*) and the northern elephant seal (*Mirounga angustirostris*).

Modern monachine distribution is one of the more remarkable features of this subfamily, and in speculating on phyletic relationships within the group it is convenient to consider the possibilities under three separate headings.

THE MONK SEALS

Modern monk seals occur in the Mediterranean area and adjacent coast of north-west Africa (*Monachus monachus*), the Caribbean area (*M. tropicalis*, which may now be extinct), and in the Leeward chain of islands north-west of Hawaii (*M. schauinslandi*). On the basis of the admittedly poor fossil record, it seems probable that this group, and the subfamily as a whole, originated from a generalized phocid in the western Europe and Mediterranean areas.

The earliest record of a monachine seal anywhere is *Monotherium aberratum* Van Beneden 1877 from the late Miocene of Belgium. As far as can be seen from the fragmentary remains known, this species is little different from other generalized phocids of the Miocene. In the absence of any other monachines of comparable age, with the possible exception of *M. maeoticum* Nordmann 1860 from southern Russia, it can conveniently be regarded as ancestral to the rest of the subfamily. Indeed, there is nothing in the morphology of known skeletal elements of *M. aberratum* which would preclude it from being ancestral to later Monachinae.

Other European fossil monachines include *Pliophoca etrusca* Tavani 1942 from the later Pliocene of Italy, and *Palaeophoca nystii* Van Beneden 1877 from the Pleistocene of Belgium. The status of the Pliocene *Pristiphoca occitana* Gervais & Serres 1847 is uncertain, although Kellogg (1922: 78) states that it 'certainly belongs to the same genus, and possibly to the same species, as the fossil form from the Orciano in Italy' (i.e. *Pliophoca etrusca*). *P. etrusca* is very similar to the extant *M. monachus*, and it was in fact originally described as a fossil *M. albiventer* (= *monachus*) by Ugolini (1902). Whatever the correct nomenclature of the Italian fossils, they are clearly closely related to *M. monachus*, as is also *Monotherium maeoticum* (Kellogg, 1922). Several other species of *Monotherium* have been described (Kellogg 1922; King 1964).

This sparse and taxonomically confused fossil record clearly does not allow an unequivocal statement to be made on the phyletic relationships of the species concerned. However, the *Monotherium aberratum* - *Monachus monachus* lineage is here taken to include *Pliophoca etrusca* as an intermediate form, and *Palaeophoca nystii* as an offshoot.

Elsewhere in the areas of distribution of modern monk seals, the fossil record is extremely poor or non-existent. Nevertheless, some inferences can be

drawn from the few available records of fossil monk seals and related forms.

Although the South African *Prionodelphis capensis* does exhibit certain characteristics which are typical of modern Antarctic seals, in totality of characters there is a more marked resemblance between it and the monk seals and their ancestors. However, it differs from *Pliophoca*, *Palaeophoca* and *Monachus* in at least one important anatomical detail, and that is the presence of an entepicondylar foramen in the humerus. This feature is also present in the humerus of *Monotherium aberratum*. It is therefore concluded that the dichotomy of the European monachine lineage, and the lineage which includes *P. capensis*, occurred in the late Miocene or early Pliocene.

Similarly, in view of the late Pliocene date of the fossils from Langebaanweg, it is certain that the southern lineage was established in the south Atlantic sometime earlier in this epoch, or perhaps even during the late Miocene.

Having taken Europe as the centre for monachine evolution, the possible routes followed by early monachines into the South Atlantic need to be considered. When intercontinental migrations of seals took place, it is reasonable to suppose that these would be successful where distance between landfalls was least, and prevailing ocean currents favourable. The role of ocean currents in pinniped migrations may well be more complex than appears at first sight. For example, a factor directly related to ocean currents is that of water temperatures. King (1964) has noted a connection between pinniped distribution and water temperatures, and thus also ocean currents. It is to be expected that pinnipeds undertaking long migrations would follow prevailing ocean currents, not only because these would facilitate long-term directional movements, but also because water temperatures remain more equable within a single current system. Temperature is important in determining the ecosystem of any oceanic environment, and since pinnipeds are simply one element of such a system, their dispersal in the past is likely to have been influenced by sea temperature and ocean current patterns.

Pliocene to Recent records of monk seals in the Atlantic Ocean are as follows:

- M. monachus* and its ancestors—Europe and north-west Africa
- M. tropicalis*—Caribbean
- P. rovereti*—Argentina
- P. capensis*—South Africa

With Europe and north-west Africa taken as the centre from which the Monachinae dispersed, the other records can be accounted for in a number of ways.

However, bearing in mind the factors already mentioned, the pattern of dispersal outlined below is considered the most probable of the alternatives.

While east to west crossings of the Atlantic could conceivably have taken place in both hemispheres, it is simpler to suppose that some time in the late Miocene or early Pliocene a single such crossing took place, starting from the

north-west coast of Africa to the most easterly parts of South America. Even today *M. monachus* occurs as far south as Cape Blanc in Mauritania, and historic records indicate its presence even further south in Senegal (Van Wijngaarden 1962). Assuming a similar distribution for an early ancestor, an east to west crossing following the prevailing ocean currents by way of the Canary Islands at the shortest distance between Africa and South America would not have been difficult to achieve.

Once established in South America, these early monachines could have spread both north and south, the former to give rise eventually to *M. tropicalis* in the Caribbean, and the latter to give rise to *P. rovereti* in Argentina. All the monachines involved in these movements would have been species adapted to warm water conditions.

An early monachine population adapting itself to colder waters and moving into the far south of South America would then have been ideally situated for further dispersal into Antarctic regions, eventually to give rise to modern Antarctic monachines. This same group could also have undertaken another Atlantic crossing, this time from west to east, by way of islands near the Antarctic convergence and the prevailing ocean currents of the southern mid-latitudes, to South Africa. The presence of *P. capensis* at Langebaanweg is thus accounted for, and while Europe is regarded as the centre from which all later Monachinae were dispersed, the east coast of South America is here regarded as the centre from which the southern monachines arose (Fig. 1).

Palaeontological evidence relating to the date of arrival of the ancestors of *M. tropicalis* in the Caribbean is inconclusive. While there are Pleistocene records of *M. tropicalis* in Florida and South Carolina (King 1964), early forms of this species must have been present in this area before the Pleistocene. This is a statement which is also based on inference rather than direct evidence.

Since the two records of *Prionodelphis* both date from the Pliocene, and only one east to west crossing of the Atlantic has been indicated, it suggests that ancestors of *M. tropicalis* were present in the Caribbean during the Pliocene as well.

There is further indirect evidence to substantiate this statement. It is well known that there is greater morphological correspondence between *M. tropicalis* and *M. schauinslandi* than exists between either of these species and *M. monachus*, which indicates that these two species have had a common ancestor more recently than the genus as a whole. In order that this common ancestor could give rise to the two modern species, it must have been present in both the Atlantic and Pacific Oceans.

Bearing in mind the existing distribution of *M. tropicalis* and *M. schauinslandi*, the most probable Atlantic-Pacific link penetrated by the common ancestor, was that which existed before the North and South American continents were linked by the isthmus of Panama. Once established on the Pacific coast of Central America, the dispersal of ancestors of *M. schauinslandi* to islands in the central Pacific would have been facilitated by the prevailing currents in the north equatorial region of this ocean (Fig. 1).

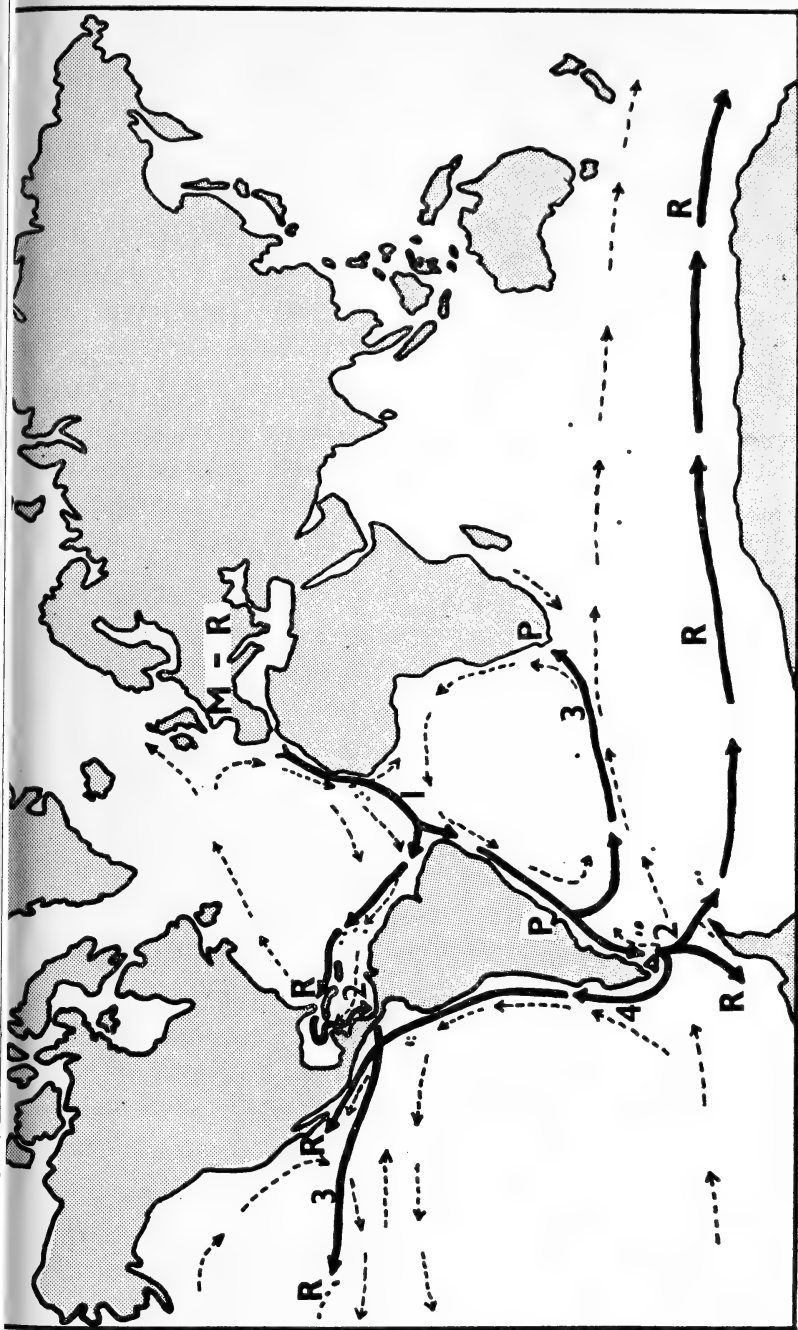


FIG. 1. Suggested dispersal routes of monachine seals.

Light arrows—Some of the principal surface currents of the oceans.

Dark arrows—Suggested dispersal routes of the Monachinae.

M—Miocene records of monachines.

P—Pliocene records of monachines.

R—Recent records of monachines.

Northern Hemisphere dispersal:

1. Crossing to east coast of South America in late Miocene or early Pliocene.

2. Arrival of ancestors of *Monachus tropicalis* in Caribbean during the late Miocene or early Pliocene, and crossing to Pacific coast of Central America.

3. Spread of ancestors of *Monachus schauinslandi* to central Pacific.

Southern Hemisphere dispersal:

1. Crossing to east coast of South America in late Miocene or early Pliocene.

2. Arrival of ancestors of modern southern monachines in Antarctic regions, probably during the Pliocene.

3. Crossing of South Atlantic of *Prionodelphis* during the Pliocene.

4. Spread of *Mirounga* along west coast of South America to North America, probably during the late Pliocene.

The last time a crossing of the Central American region by pinnipeds was possible is not known for certain. Olsson (1932) has stated that the first evidence for a separation between marine invertebrates of northern Peru and the Caribbean was in the late Miocene. This suggests that the common ancestor of *M. tropicalis* and *M. schauinslandi* must have crossed somewhere near the present isthmus of Panama by this time. However, Simpson (1950) has referred to the Pliocene mammals migrating between the two New World continents as 'island hoppers', and indicates that the final North and South American land connection was achieved in the late Pliocene, a view supported by Whitmore & Stewart (1965). A Pliocene Atlantic to Pacific crossing by early monachines would seem more reasonable in view of the late Miocene date for the earliest monachine in Europe. Even though the movement of marine invertebrates between the Atlantic and Pacific may not have been possible since the late Miocene, the movement of pinnipeds across the area between Central and South America during the Pliocene is probable. It is possibly the imprecise relative dating of the fossils and deposits referred to in the preceding discussion that causes the discrepancy in the evidence provided by invertebrate and vertebrate fossils. Gabunia & Rubinstein (1968) give an indication of the difficulties encountered in the relative dating of deposits at the period of time which is critical in the present instance.

The preceding interpretation of the evolution and dispersal of the monk seals can be summed up as follows:

1. *Monachus monachus* evolved from a late Miocene monachine, largely in the area in which it is found today.
2. In the late Miocene or early Pliocene an early monachine crossed the Atlantic from the west coast of Africa to the east coast of South America.
3. One group of these immigrants moved southwards along the east coast of South America and gave rise to *Prionodelphis rovereti*.
4. This southward movement of monachines continued into Antarctic regions, while at least one population crossed the South Atlantic to South Africa and gave rise to *Prionodelphis capensis*.
5. A second group of the original immigrants to South America moved northwards into the Caribbean, and also across into the Pacific before the final linking of the North and South American continents. They eventually gave rise to *Monachus tropicalis* and *M. schauinslandi*, ancestors of the latter having moved from the Pacific coast of Central America to the central Pacific.

The monk seals are a remarkably conservative group. Although the three modern species have had a history independent of one another, perhaps dating back to the Miocene, and certainly dating back to the Pliocene, they are still morphologically very similar to one another. It seems that having once adapted to their environment they received little, if any, pressure to cause adaptive change. This conservative, low latitude group survives today, effectively isolated from other pinnipeds.

THE ANTARCTIC MONACHINES
(Excluding the southern elephant seal)

Before dealing with the evolution and dispersal of Antarctic monachines, it is necessary to consider in detail their possible phyletic relationships to the two species of *Prionodelphis*, based on considerations of comparative morphology.

A detailed study of the known remains of *Prionodelphis capensis* revealed that there is an undoubted connection between this species and the Antarctic monachines in general (Hendey & Repenning 1972). However, it was also clear that no definite phyletic connection between the South African species and any one of the modern Antarctic seals could be demonstrated. In some respects *P. capensis* is morphologically intermediate between the genus *Monachus* and the Antarctic seals. Such features of *P. capensis* as the relatively narrow cheekteeth, the flat and broad petrosal apex of the tympanic, and the relatively stout humerus and spatulate radius, suggest a stage of development from the ancestral monachine condition (exhibited by the conservative *Monachus*) towards *Hydrurga*, *Lobodon*, *Leptonychotes* and *Ommatophoca*.

The highly modified dentitions of the Antarctic monachines are the features which differentiate them from *P. capensis* most strikingly. On the basis of their dentitions it is improbable that either *Hydrurga* or *Lobodon* could be derived from a *P. capensis*-like ancestor, since this would have necessitated the reversal of at least one evolutionary trend.

Both species of *Prionodelphis* have a reduced upper fifth postcanine, with only the vestiges of a single anterior accessory cusp remaining, this apparently having derived from the basic three-cusped pattern still evident in *Monachus*. Both *Hydrurga* and *Lobodon* have little reduction of this tooth, which in both cases has well-developed accessory cusps anteriorly and posteriorly. While it is not impossible that lost features can be redeveloped (Kurtén 1963), this is not usual, and the possibility of a phyletic connection between *Prionodelphis* and both *Hydrurga* and *Lobodon* becomes more improbable.

The multiplication of accessory cusps in *Lobodon* is yet another complicating factor. The lower postcanines of *P. rovereti* have two anterior and two posterior accessory cusps, but even this does not match the proliferation of posterior cusps in the second to fifth postcanines of *Lobodon*. Cusp development in this genus is variable, and additional accessory cusps appear to develop as buds from the principal cusp and as projections from the cingulum. There is no evidence to suggest that the archetype monachine cheektooth had an array of cusps such as is seen in *Lobodon*. Consequently, although deviation from the basic three-cusped pattern may not have been difficult to achieve, in the case of the *Prionodelphis* upper fifth postcanine it would require an even more complex reversal of the trend already mentioned.

In addition, *Lobodon* differs from other Antarctic monachines in having teeth which are relatively broad. A comparison of the cheekteeth of *P. rovereti*, *P. capensis* and *Hydrurga* shows a progressive narrowing of the teeth (Hendey

& Repenning 1972: Table 1), and a similar transverse compression is also evident in the teeth of *Leptonychotes* and *Ommatophoca*. The teeth of *Lobodon* are more like the ancestral monachine condition in this respect.

Kellogg (1942: 453) has already suggested that *P. rovereti* might be ancestral to *Leptonychotes*. This suggestion is not affected by the one that *P. capensis* is a derivative of the Argentinian species. The phyletic connection between the two species of *Prionodelphis* is indicated partly by the inferred manner of dispersal of southern monachines, the earlier suggestion that in some respects *P. capensis* has more advanced characteristics (Hendey & Repenning 1972: 93), and that the Entre Rios deposits are early Pliocene (Romer 1966), while those at Langebaanweg are late Pliocene (Hendey 1970).

Prionodelphis capensis could be regarded as intermediate between *P. rovereti* and *Leptonychotes* in view of the reduction in the size of the posterior root in its upper postcanines, the reduction in the number of cusps in its lower postcanines, and in the greater transverse compression of its cheekteeth. Much the same can be said in the case of *Ommatophoca*, but in this instance the differences between the cheekteeth of *P. capensis* and *O. rossi* are far greater, and changes would have needed to be at a greatly accelerated rate. Perhaps the feature most suggestive of a connection between *Prionodelphis* and *Leptonychotes* is the recurved crown and virtual lack of accessory cusps in the upper fifth postcanine of the former genus, characteristics which are matched in most of the cheekteeth of *Leptonychotes*. To a lesser extent these characteristics are evident also in the cheekteeth of *Ommatophoca*.

Thus on the basis of teeth alone, it appears that *Prionodelphis* is more likely to be ancestral to *Leptonychotes* and *Ommatophoca*, although *P. capensis* itself is probably not on a direct line to these species, but merely paralleled the trends which led to them. On the other hand *Hydrurga* and *Lobodon* are likely to be derived from an even more generalized monachine—a proto-*Prionodelphis*.

Looking once more at the distribution of the southern monachines, it is clear that, other factors aside, *P. capensis* was not geographically well situated to give rise to the Antarctic monachines, and *Leptonychotes* and *Ommatophoca* in particular.

In view of the suggestion that *Hydrurga* and *Lobodon* arose from a 'proto-*Prionodelphis*', it is possible that early representatives of these genera reached Antarctica before the ancestors of *Leptonychotes* and *Ommatophoca*. Since the latter two genera have a more southerly distribution than *Hydrurga* and *Lobodon* (King 1964), it is likely that their ancestors entered Antarctica from the southern tip of South America (55°S) via the South Shetland Islands to the Palmer Peninsula of Antarctica itself. The most likely route into Antarctica from South Africa (34°S) would, because of prevailing ocean currents, have been by way of the south Indian Ocean, via islands near the Antarctic convergence and the pack ice to the Antarctic continent. In addition to being a more difficult route, it would have necessitated the crossing of an area (the outer fringes of the pack ice) which may already have been inhabited by the ancestors of *Hydrurga* and

Lobodon. While the four modern Antarctic species do not compete for food, this must become progressively less so further back in time when their respective ancestors were more generalized.

A final point concerning the possibility of a phyletic connection between *P. capensis* and one or more of the modern Antarctic monachines, concerns the age of *P. capensis*. Since *P. capensis* is considered to date back 4–5 million years (Hendey 1970), it would be required that the marked morphological differences between it and, say, *Leptonychotes* be developed in this period of time. If the early Pliocene date for *P. rovereti* is correct, the period of time for similar changes to occur might be two or three times as long. In itself this is meaningless, but clearly the greater the time involved, the greater the possibilities for radical morphological change.

In the absence of convincing evidence to the contrary, it is probable that differentiation and evolution of the Antarctic monachines took place in the high latitudes in which they occur today. The more extreme climate and climatic changes in high latitudes during the Pliocene and Pleistocene may well have provided the mechanism for accelerated changes in the Antarctic monachines, the nature of the environment acting as a stimulant to adaptive change. Owing to the lack of deposits of Pliocene and Pleistocene age in Antarctica, except for those beneath the Antarctic Ocean, it is very improbable that the nature of the development of Antarctic seals will ever be known from fossil remains. Thus with this group of pinnipeds, interpretations of their evolutionary history will probably remain speculative.

It is clear that there was a far more rapid evolution of specialized characters in the southern monachines than was the case with the monk seals, even though the independent history of the four southern species was probably no longer than that of the three monk seals. Thus the Antarctic seals contrast with the monk seals by being a high latitude and highly specialized group, as opposed to a low latitude and conservative group.

THE ELEPHANT SEALS

The genus *Mirounga* has long been the subject of controversy as to its relationships. It is now included in the Monachinae (King 1966) but anatomically and in its distribution it does still to some extent stand apart from other monachines.

While some conclusions on relationships can be drawn from comparisons between the cheekteeth of other monachines, the peg-like teeth of *Mirounga* are singularly uninformative. Burns & Fay (1970: 389), however, concluded that, 'craniologically *Mirounga* is more like other phocids of the Southern Hemisphere than is *Monachus*'. The mere fact that *Mirounga* is a highly specialized genus makes it probable that it would have closer connections to the diversified Antarctic monachines, rather than with the conservative monk seals. In other words, it is suggested that adaptive radiation in the Monachinae is confined to the southern high latitude group, to which *Mirounga* must therefore belong.

Furthermore, the distribution of the two modern species is more readily accounted for in assuming a southern origin for the genus. This is already suggested by the fact that *M. angustirostris* maintains a pattern of breeding (in the northern winter) which is typical of Southern Hemisphere phocids (King 1964).

The present distribution of the southern elephant seal includes the extreme southern end of South America, but within historic times it has been reported as far north as the Juan Fernandez Islands, which is in fact the type locality. A wider spread along the west coast of South America during the past, in a manner comparable to that of modern *Arctocephalus australis*, is conceivable owing to prevailing ocean currents and water temperatures of that coast. This would have brought the southern and northern ranges into far closer proximity, and indeed have allowed the southern species, or an ancestor, to reach the area in which the northern species occurs today. A split in this distribution, centred in low latitudes, of a single population of *Mirounga*, and a gradual retreat in its range in the south, would then account for the present pattern of elephant seal distribution. *Mirounga angustirostris* can thus be regarded as a relict species, surviving in isolation far from the origins of the genus.

Since there is an early Pleistocene record of *Mirounga* in California (C. A. Repenning, pers. comm.), it is probable that the genus arose during the Pliocene, and the present pattern of elephant seal distribution developed during the Pleistocene.

The suggested phyletic relationships of modern and some fossil Monachinae are illustrated in Figure 2.

DISCUSSION

The present pattern of monachine distribution is perhaps the most unusual of any of the pinniped subfamilies. The Otariinae and Arctocephalinae, which are taken by some to be a single subfamily (Mitchell 1968), have essentially similar distributions, with the eastern Pacific shorelines providing the closest links between the species of the two hemispheres. The Odobeninae and Phocinae are purely Northern Hemisphere groups, largely confined to high latitudes. The Monachinae alone can be subdivided into two geographically widely separated groups, while a third subdivision includes two equally widely separated species of a single genus.

King (1964) has discussed pinniped distributions as they relate to ocean currents and water temperatures, and has remarked upon the correlation with colder waters. The monk seals are one of the few exceptions to the general rule that, 'the 20°C summer isotherm in either hemisphere, where it approaches continental coasts forms a reasonable pointer to the limits of where one might expect to find seals' (King 1964: 89). The critical temperature for the monk seals is higher. By contrast the Antarctic seals are limited to waters with a maximum temperature of 3-4°C. The southern elephant seal also occurs in

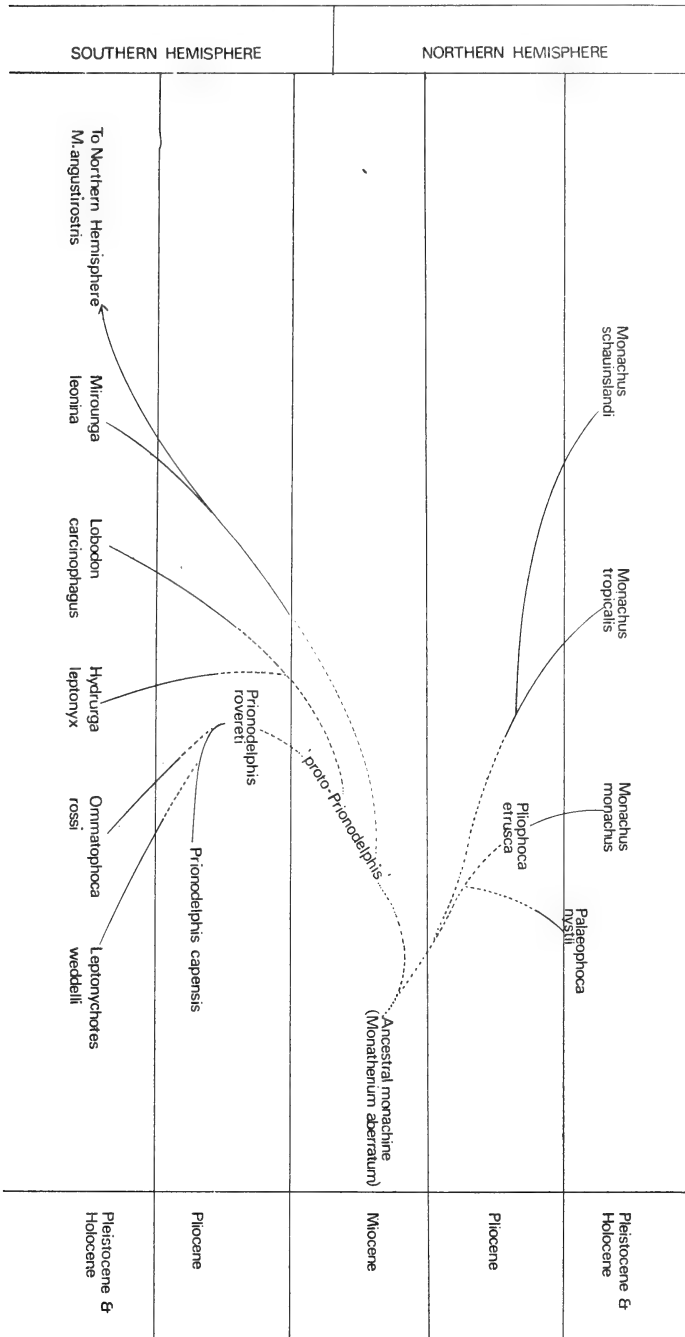


FIG. 2. Suggested relationships of some monachine seals.

the cold waters of the far south, while its northern relative conforms to the general rule quoted above.

It is reasonable to suppose that at one time the monachines had a less interrupted distribution, and the records of *Prionodelphis* give an indication that this was indeed the case. In order to explain the curious pattern of modern distributions, it is necessary to refer to the occurrence of other pinnipeds. It is found that the southern fur seals (genus *Arctocephalus*) and southern sea lion (genus *Otaria*) inhabit much of the intervening area which is suitable for occupation by seals. Bearing in mind the suggested manner of dispersal of early monachines, it is probable that much of their range during the Pliocene, and perhaps part of the Pleistocene as well, included the areas in which at least some of the species of *Arctocephalus* and also *Otaria* occur today. The indications are, therefore, that there has been replacement of monachines by otariids, especially in the Southern Hemisphere.

The earliest Southern Hemisphere records of the Otariidae are *Otaria fischeri* Gervais & Ameghino 1880 from Argentina, a *Phocartos hookeri* from New Zealand (Berry & King 1970), and '*Arctocephalus williamsi* from Australia (King 1964). The two Australasian species are Pliocene in age, and while King (1964) listed the Argentinian record as '? Miocene', it too probably dates from the Pliocene (Davies 1958). Excluding Pleistocene records, other recorded fossil otariids are from either the west coast of North America or Japan. Thus it is probable that while the Phocidae had the Atlantic Ocean as the centre for their evolution, the early history of the Otariidae was confined to the Pacific. The indications are, therefore, that the Otariidae only reached southern Africa after they had become established in Australasia and South America, i.e. the two southern continents bounding the Pacific Ocean. It must have been very late in the Pliocene, or perhaps only in the Pleistocene that the otariids became established in southern Africa. Although the fossil record is not conclusive on this point, it does seem likely that the extinction of *Prionodelphis* in South America and South Africa was more or less synchronous with the advent of otariids in these regions.

The present distribution of the two species of *Mirounga* discussed earlier, may at least be partly determined by the presence of *Arctocephalus australis* populations on the South American coast. King (1964) states that even though *M. leonina* and *A. australis* have a common diet they appear to co-exist without difficulty, but she also notes that when breeding season conflicts occur 'the fur seal usually wins' (King 1964: 25). The fact that *M. leonina* distribution has become considerably less in recent times suggests that the sympatric existence of these two species may be in a state of delicate balance, and, if upset, *A. australis* is in a position of dominance.

Unsuccessful competition by monachines with otariids cannot be proven, but the present distribution of these two groups suggests that there is a mutually exclusive inter-relationship between them.

The possible influence of climatic changes on monachine distribution

cannot, of course, be ignored. For example, *M. leonina* may be more sensitive to increasing temperatures than *Arctocephalus*, and the virtual disappearance of this species from the South African coast in the Holocene may be due to the general warming of conditions during this epoch. It is unlikely that prehistoric man played any significant role in the disappearance of the South African *Mirounga*, although this possibility cannot be entirely discounted. Late Pleistocene coastal hominid occupation sites are all below present sea-level, and the relative importance of *Mirounga* and *Arctocephalus* in diets of the hominids of the time is not known.

It is probable that the radiation of the otariids, coupled with changes in climate, jointly determined the nature of the present distribution of the Monachinae, which survive as isolated populations in low latitudes, and as firmly entrenched populations only in the southern high latitudes.

In reviewing the evolution of the Monachinae as outlined above, it is evident that this group does not conform exactly to some widely accepted principles. Crowson (1970: 133) lists certain 'rules' 'for determining the areas of origin of systematic groups from the patterns of distribution of their present-day members'. He states that it 'has been suggested that any group should be considered to have originated in that area where (a) it is represented by the greatest number of existing species . . . or (d) its most primitive living forms occur'. Crowson's conclusion that these 'rules' can be misleading is substantiated by the Monachinae, since the greatest number of living species (the Antarctic seals) are far removed from the most primitive living forms (*Monachus*). In this case 'rule' (d) applies.

CONCLUSION

There are undoubtedly alternatives to the speculations outlined in this report. However, since the facts which form its basis are so limited, their interpretation must to a large extent be subjective. This is inevitable when dealing with a group of mammals with a poor fossil record which is supplemented only at very infrequent intervals. The only two Southern Hemisphere records which throw any light on the early history of the southern Monachinae are *Prionodelphis rovereti* from Argentina and *P. capensis* from South Africa, the descriptions of which were published nearly 50 years apart.

Given such a situation it seems preferable to speculate now, rather than wait for further significant discoveries to be made.

If this paper serves to stimulate better reasoned interpretations of the limited fossil record of the Monachinae, it will have served a purpose. Whatever is finally accepted, it is clear that a reassessment of the taxonomy of the monk seals and all fossil Monachinae is necessary.

SUMMARY

The fossil record of the Monachinae is outlined, and it is concluded that this pinniped subfamily arose in the western Europe-Mediterranean area. It

is concluded that the monk seals, and the early ancestors of the Monachinae as a whole, are an essentially low-latitude and conservative group, from which arose the high-latitude and specialized 'southern' monachines, which include *Mirounga angustirostris*. It is suggested that the latter group underwent their differentiation in the high latitudes in which they are most commonly found today, having arisen from *Prionodelphis* and 'proto-*Prionodelphis*' populations which spread into Antarctic regions from South America. It is suggested that the decline of the Monachinae in southern mid-latitudes was due at least partly to the rise of the Otariidae in these regions.

ACKNOWLEDGEMENTS

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REFERENCES

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Example

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A PLIOCENE URSID FROM
SOUTH AFRICA

By
Q. B. HENDEY

Cape Town Kaapstad

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A PLIOCENE URSID FROM SOUTH AFRICA

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South African Museum, Cape Town

(With plates 19–20, 2 figs and 3 tables)

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CONTENTS

	PAGE
Introduction	115
The family Ursidae	116
Intra-familial categories within the Ursidae	119
The Langebaanweg bear.	126
Description	126
Discussion	130
Summary	131
Acknowledgements.	131
References	131

INTRODUCTION

There are few mammal-bearing deposits of Pliocene age known in Africa (Kurtén 1971: 134) and consequently occurrences which date from this epoch are of significance in that they may produce records of species which are of special phylogenetic and zoogeographic interest. The only Pliocene occurrences presently being investigated in southern Africa are those at Langebaanweg in the Cape Province (Hendey 1970a, 1970b), and one of the more remarkable records from this locality is that of an agriotheriine ursid (Hendey 1969). It was the first record of an agriotheriine in Africa, and is still the only ursid known from sub-Saharan Africa.

The Agriotheriinae, which in the most restricted sense may be taken to include the genera *Agriotherium* and *Indarctos*, are known from a number of late Tertiary and early Pleistocene occurrences in Eurasia and North America, and the South African record adds a new dimension to concepts of the evolution and dispersal of this group. In general, the recorded species are represented by rather fragmentary material and, unfortunately, this is also the case with the Langebaanweg form. However, the significance of the material is not diminished, although the description which follows might well require revision if more specimens are recovered in the future.

The terrestrial mammal fauna with which the Langebaanweg agriotheriine is associated includes a number of species which are unexpected in an African context. For example, one of the hyaenids is referred to *Percrocuta*, a genus which is otherwise known in Africa only from the Algerian Miocene (Thenius

1966). It was, however, widely distributed in Eurasia during the late Tertiary (Kurtén 1957a). A second unusual species is an as yet unnamed boselaphine antelope, which apparently derives from the Miocene *Protragocerus labidotus* of Kenya (Gentry 1970). The boselaphines were also common in Eurasia during the late Tertiary.

Other significant, although not unexpected, records from Langebaanweg include an early ancestor of *Hyaena hyaena*, a primitive form of *Mammuthus subplanifrons* which is one of the earliest of the true elephants (Maglio & Hendeby 1970), and an ancestor of the white rhinoceros, *Ceratotherium simum* (Hooijer, in press).

The Langebaanweg deposits are unique amongst the major late Cenozoic fossiliferous occurrences of sub-Saharan Africa in that a marine fauna is associated with the terrestrial vertebrate fossils. Vertebrates linked with the marine environment include the first recorded fossil penguin from Africa (Simpson 1971) and an unusual monachine seal, *Prionodelphis capensis* (Hendeby & Repenning 1972), which has shed some light on the origins of the Antarctic seals (Hendeby 1972).

Viewed in relation to the fauna as a whole, the agriotheriine is but one of a series of important additions to the fossil record of the late Cenozoic of Africa.

In order that this species might be placed in taxonomic perspective, its description is preceded by a brief review of the Ursidae.

THE FAMILY URSIDAE

The Ursidae are a comparatively recently evolved mammalian group, with a relatively small number of constituent genera, and they have received a considerable amount of attention from palaeontologists and neontologists alike. Despite this they have proved an extremely controversial group and it is only recently that a measure of agreement has been reached on their phyletic and intra-familial relationships.

The most comprehensive account of the Ursidae is that of Erdbrink (1953), and this has provided an invaluable basis for more recent work on the family. Since the appearance of Erdbrink's monograph much attention has been focused upon the ursine bears (the genus *Ursus* and closely related forms). Their phylogeny is now one of the best known of all mammalian groups and this successful study has been largely due to the work of Kurtén (1957b, 1958, 1964, etc.) and Thenius (1959a). Much the same can be said of the tremarctine bears (the genus *Tremarctos* and its close relatives) (Kurtén 1966, 1967), although the origin of this group remains obscure.

The taxonomic position of the giant panda, *Ailuropoda melanoleuca*, has been a matter of controversy for more than a century owing to its combination of ursid and procyonid characteristics. Davis (1964) presented what is perhaps the definitive study of the anatomy of this animal, and he held the view that it is indeed a bear. While this conclusion is still not universally accepted, *Ailuropoda* is regarded as an ursid in the present study.

The Tertiary ursids, excluding the immediate ancestors of the ursine group, can conveniently be placed in two categories. The first includes those genera which bridge the evolutionary gap between the Canidae and 'true' bears. They are *Cephalogale*, *Hemicyon* and *Dinocyon*. Secondly, there is a more advanced group in which many specialized ursid characteristics were developed. This group includes *Agriotherium* and *Indarctos*. Not surprisingly these two groups may be broadly differentiated on temporal as well as morphological grounds, the former being essentially Miocene in age, and the latter dating largely from the Pliocene. The Tertiary ursids are not as well known as the Quaternary forms because they are less well represented in the fossil record. There are also many uncertainties regarding the relative ages of some members of the groups.

Frick (1926) separated these Tertiary forms from both the Canidae and Ursidae, placing them in a single unit which he called 'Hemicyoninae'. Subsequently Pilgrim (1932) referred them all to the Ursidae and this arrangement is generally followed today.

There have been many differences of opinion concerning formal subdivisions within the family. For example, Kraglievich (1926) proposed separation into three subfamilies, which Simpson (1945: 225) argued was 'of very doubtful theoretical validity and of little or no practical convenience'. Indeed, he even appeared to be in some doubt as to whether the bears merited family rank. Erdbrink (1953) was another not in favour of having subfamilies within the Ursidae. Today it has become fairly widely accepted that subfamilial grouping is both reasonable and desirable and the arrangement usually followed is that of Thenius (1959*a*), who recognized the Hemicyoninae, Agriotheriinae, Tremarctinae and Ursinae.

In spite of the formal system of zoological nomenclature, there is a strong element of personal opinion in the definition of many taxa. The inclusion or exclusion of the Hemicyoninae from the Ursidae appears to depend largely upon whether a 'vertical' or 'horizontal' system of classification (Simpson 1945) is favoured. An excellent example of this basic difference in approach is afforded by the controversy which has surrounded the taxonomy of early Pleistocene Hominidae. Reed (1967) has given a concise summary of the two points of view, and states that 'as gaps in the fossil record . . . have been filled, the tendency has been . . . to shift from a horizontal (grade) type of classification to a vertical (clade) type'.

While the general pattern of ursid evolution has long been appreciated, the intra-familial groupings have tended to emphasize morphological rather than phylogenetic aspects of the family. An attempt has been made here to classify the ursids according to their phylogeny, although this was hampered by the fact that there are still certain critical points in ursid evolution which are not satisfactorily resolved. The intra-familial classification to be given presently follows that of Thenius (1959*a*), but is modified on the basis of the tentative phylogeny presented in Figure 1. This phylogeny is based on the work of

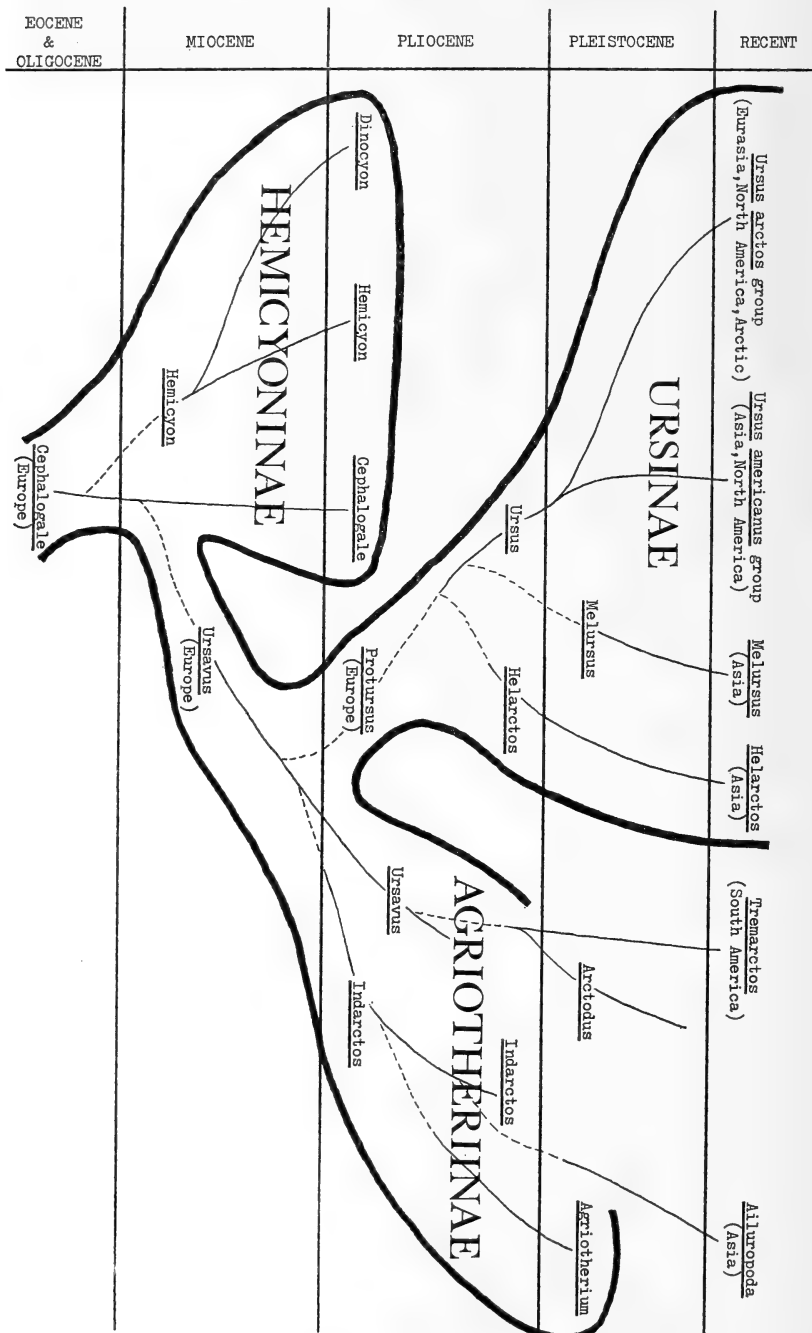


FIG. 1. Tentative phylogeny of the Ursidae.

Erdbrink, Kurtén and Thenius, and the morphological characters, temporal range and geographical distribution of each genus was taken into consideration.

The pattern which emerges is one of three distinct radiations within the family, each successive radiation cutting out the one preceding temporally and/or geographically. In each case the stem genus is recorded in Europe, and dispersals were largely confined to the northern continents. The intra-familial classification arrived at is as follows:

<i>Subfamily</i>	<i>Tribe</i>	<i>Genera included</i>
Hemicyoninae ..	Hemicyonini ..	<i>Cephalogale, Hemicyon, Dinocyon</i>
Agriotheriinae ..	Agriotheriini ..	<i>Ursavus, Indarctos, Agriotherium</i>
	Ailuropodini ..	<i>Ailuropoda</i>
	Tremarctini ..	<i>Arctodus, Tremarctos</i>
Ursinae	Ursini	<i>Protursus, Ursus, Helarctos, Melursus</i>

The replacement of the Hemicyoninae by the Agriotheriinae, and the latter in turn by the Ursinae, can be accounted for in general by assuming that there was competition between better and lesser adapted groups. Such competition would, of course, have taken place at the species level, but would ultimately have been manifested in higher taxonomic categories as well.

Kurtén (1957c: 224) has concluded that the replacement of a species by an ecologically related species may occur in one of three ways:

- (1) 'The extinction of the earlier form has no causal connection with the immigration of the later form. Both result from the action of other factors, for instance climatic.'
- (2) 'The extinction of one species permits the subsequent immigration of another.'
- (3) 'The immigrating form is adaptively superior to the local form, and ousts it through competition.'

While the third alternative is the one concluded to be the most generally applicable in the present instance, it was almost certainly not the sole factor involved in the extinction of ursids. Furthermore, competition was probably not confined only to members of the family, and some ursids probably became extinct as a result of competition with members of other families. This might well have been the case with the somewhat aberrant ursid *Agriotherium*.

INTRA-FAMILIAL CATEGORIES WITHIN THE URSIDAE

Subfamily **Hemicyoninae**

Diagnosis (adapted from Pilgrim 1931). Ursidae with the upper profile of the skull almost rectilinear; snout relatively long and narrow; infra-orbital foramina rather remote from orbits; temporal fossae long and deep; occiput low; sagittal and lambdoidal crests prominent; zygomatic arches relatively narrow; P² and P³ double-rooted; P⁴ situated behind infra-orbital foramen,

and antero-posterior diameter equal to or slightly exceeding that of M^1 ; P^4 with prominent protocone situated towards the midpoint of the tooth, and parastyle absent; M^1 larger than M^2 , with the transverse diameter of these teeth exceeding antero-posterior diameter, and with internal cusps crescentic inwards; M^3 always absent; mandible with premasseteric fossa and full complement of teeth; P_2 to P_4 double-rooted; M_1 large with talonid becoming prominent; M_2 smaller than M_1 , double-rooted with antero-posterior diameter slightly greater than transverse diameter; M_3 small, single-rooted and slightly elongated antero-posteriorly; postcranial skeleton a cursorial type, feet digitigrade; humerus with entepicondylar foramen.

Discussion. In general there was an increase in body size with time, and some later Hemicyoninae were as large as the biggest of modern bears. Although probably carnivorous on the whole, at least one genus (*Cephalogale*) apparently became progressively more omnivorous, and it is regarded as the ancestor of all ursids.

Early in their history the Hemicyoninae were confined to the Old World and only spread to North America at the peak of their radiation in the late Miocene. Although they were a restricted group generically, they were widespread and apparently very successful in the northern continents during the Miocene. They became extinct early in the Pliocene when the radiation of the Agriotheriinae was beginning.

Subfamily **Agriotheriinae**

Tribe *Agriotheriini*

Diagnosis. Ursidae with the upper profile of the skull rather convex; snout fairly short and broad; infra-orbital foramina close to orbits; occiput moderately high; sagittal crest not prominent; zygomatic arches becoming broad; P^4 situated below or slightly anterior to infra-orbital foramen, with antero-posterior diameter approximately equal to that of M^1 ; P^4 protocone becoming progressively larger and sometimes with accessory cusps developed anterior to it; P^4 parastyle develops and becomes progressively larger; M^1 roughly square; M^2 sometimes with talon; M^3 always absent; mandible sometimes with premasseteric fossa; M_1 usually large and sectorial; M_2 elongated; M_3 usually circular or very slightly elongated; postcranial skeleton progressively more heavily built; humerus (usually) with entepicondylar foramen.

Tribe *Ailuropodini*

Diagnosis. Ursidae with upper profile of skull convex; snout short and broad; infra-orbital foramina close to orbits; sagittal crest not prominent; P^1 vestigial or absent; P^4 large with prominent protocone and antero-internal cusp (protocone lobe), and prominent parastyle; P^4 situated below infra-orbital foramen, with antero-posterior diameter slightly greater than that of M^1 ; M^1 roughly square with prominent internal cingulum; M^2 elongated with

prominent internal cingulum and talon on which multiple cusplets are developed; M^3 always absent; mandible without premasseteric fossa; P_1 vestigial; M_1 large, elongated and non-sectorial; M_2 large and slightly elongated with multiple cusplets on occlusal surface; postcranial skeleton robustly proportioned; non-cursorial; humerus with entepicondylar foramen.

Tribe *Tremarctini*

Diagnosis. Ursidae with the upper profile of the skull rather convex; snout relatively short and broad; infra-orbital foramina close to orbits; sagittal crest sometimes prominent; zygomatic arches moderately broad; P^4 situated anterior to infra-orbital foramen, with antero-posterior diameter usually less than that of M^1 ; P^4 protocone prominent and parastyle absent; M^1 roughly square or slightly elongated; M^2 elongated with prominent talon; M^3 always absent; mandible with premasseteric fossa; M_1 large, elongated and non-sectorial; M_2 elongated, antero-posterior diameter approximately equal to that of M_1 ; M_3 moderately large and slightly elongated; postcranial skeleton robustly proportioned; non-cursorial; humerus with entepicondylar foramen.

Discussion. As here defined the Agriotheriinae are the most diverse of the ursid subfamilies. It includes the genus *Ursavus* which is the earliest member of the family which is unmistakably 'bear-like', and which is regarded as the stem genus of the ursids by those who include the Hemicyoninae in the Canidae (e.g. Kurtén 1966). It is known only in Europe.

An apparent off-shoot from *Ursavus* was *Indarctos*, a genus which is first recorded in the early Pliocene of Europe. It is uncertain which species of *Indarctos* is the earliest. One possibility is *I. vireti* Villalta & Crusafont 1945 from Spain, while another is the agriotheriine from the lignites of Monte Bamboli in Italy (Erdbrink 1953). The transition from *Ursavus* to *Indarctos* appears to be principally a matter of an increase in size.

A number of other species of *Indarctos* have been recorded in the Pliocene of the northern continents. European species are *I. arctoides* Deperet 1895, *I. atticus* Dames 1883 and *I. ponticus* Kormos 1913, while *I. lagrelli* Zdansky 1924 is from China, *I. punjabiensis* Lydekker 1884 from India and *I. oregonensis* Merriam *et al* 1916 from North America. In general the recorded specimens of *Indarctos* are rather fragmentary, and consequently definitions of the species are often inadequate. Pilgrim (1931) noted the similarity between *I. ponticus* and *I. lagrelli*, and Kurtén (1957c) regarded them as conspecific. Probably the recovery of additional material and a review of the genus would result in further synonymies being recognized.

Much the same can be said of *Agriotherium*, except that this genus survived into the Villafranchian of Europe (Kurtén, 1968), and as the new record from Langebaanweg shows (*vide infra*), it also became established in Africa. As far as could be determined there is no early Pliocene record of this genus. Species include *A. insigne* Gervais 1853 from Europe, *A. maraghanus* Mecquenien 1925

from Iran, *A. palaeindicus* Lydekker 1878 and *A. sivalensis* Falconer & Cautley 1836 from India, and *A. gregoryi* Frick 1921 from North America.

Probably the best published account of the differences between *Agriotherium* and *Indarctos* is that of Pilgrim (1932). He was apparently the first person to conclude that *Agriotherium* is the more advanced of the two genera, although only in some respects and he stated that *Indarctos* was a development from *Agriotherium*. This is a traditional point of view which is still widely held, and *Agriotherium* has often been referred to as a link between the Canidae and Ursidae.

The present study led to the conclusion that the characteristics of *Agriotherium* are not primitive, but rather the result of the development of specializations. *Agriotherium* is regarded as a derivative of *Indarctos* in which there was a trend towards the development of more carnivorous habits. The alternative view that *Indarctos* was derived from *Agriotherium* is rendered a little unlikely by the known temporal ranges of the two genera, and the possibility that both are descended from a hypothetical common ancestor is an unnecessary theory.

The general trend in ursid evolution has been towards the development of characters suited to an omnivorous or herbivorous diet. There is at least one well-documented reversal of this trend. The polar bear, *Ursus maritimus*, is a purely carnivorous form which still retains many of the characters of *U. arctos*, the species from which it is derived (Kurtén 1964). This anomalous development may have come about during one of the Pleistocene glaciations when an *U. arctos* population adapted to life in a vegetation-less peri-glacial environment. Since the dichotomy of *U. maritimus* and *U. arctos* took place comparatively recently, the dentitions of the two species are still essentially similar. Given sufficient time the *U. maritimus* dentition would become increasingly modified, with the carnassials developing at the expense of the molars.

Agriotherium was probably just such an exception to the general rule in ursid evolution, but in this instance the carnivorous habits are reflected by the nature of the dentition. The numerous references to its 'primitive' and 'canid-like' characteristics imply 'carnivore-like', which is not necessarily primitive at all. In fact Erdbrink (1953: 582) referred to the upper carnassial of *Agriotherium* as being 'very carnivorous in aspect'.

The most important characters which distinguish *Agriotherium* from *Indarctos* are to be found in the dentitions, and basically the differences are centred on the emphasis of the carnassials and the reduction of the other cheekteeth in *Agriotherium* (Pilgrim 1932: 42).

In *Agriotherium* the anterior premolars in both maxilla and mandible are reduced in size and sometimes number. This is not necessarily an indication of a carnivorous diet, since many ursines also have the anterior premolars reduced or lost, but in this group the molars are correspondingly enlarged and the reduction also affects the carnassials. This is not so in *Agriotherium*.

This genus differs from *Indarctos* in having the lingual margins of M¹ and M² shorter than buccal margins as a result of the paracones and metastyles

being more strongly developed than the protocones and hypocones. Since the buccal cusps are higher than lingual ones it is possible for them to act as shearing as well as crushing agents. The crushing function of the M^2 of *Indarctos* is further indicated by the presence of a talon, and in this genus the M^2 is always longer than M^1 . By contrast the M^2 of *Agriotherium* is nearly always smaller than M^1 and lacks the talon. Erdbrink's (1953: 571) conclusion that there is 'at best a beginning of a talon . . . in *A. insignis*' is probably incorrect, and the talon in this species is regarded as vestigial.

The 'carnivorous aspect' of the upper carnassial of *Agriotherium* has already been mentioned, and this tooth is also the most important in so far as the inferences on the ancestry of the genus are concerned. It is characterized by the presence of a prominent parastyle, a cusp which is not found in any of the Canidae, Hemicyoninae or species of *Ursavus*. It is, however, present but small in some species of *Indarctos* (e.g. *I. punjabiensis*). This suggests a progressive development of a P^4 parastyle in the Agriotheriinae as follows:

Ursavus (absent)—*Indarctos* (small)—*Agriotherium* (prominent).

In *Ailuropoda*, which is here regarded as another descendent of *Indarctos*, it is also prominent.

The lower carnassial of *Agriotherium* also exhibits 'carnivorous' characteristics. The talonid is reduced relative to the trigonid and the hypoconid is higher than the entoconid, which makes it a more efficient shearing tooth than that of *Indarctos*.

The reasons for the development of an apparently carnivorous lineage stemming from *Indarctos* are not known, but this might have been in response to competition with early Ursinae. By the late Pliocene when the ursine radiation was getting under way in Europe, *Agriotherium* was the only agriotheriine surviving in this area and it only became extinct in the early Pleistocene. It follows that if it was indeed a purely carnivorous form, its ultimate extinction in Europe and elsewhere cannot be explained in the same way as the extinction or limitation of other Agriotheriinae. In this instance competition with other fissiped carnivores may be the answer, although other undetermined factors might have been involved.

In the late Pliocene *Indarctos* was still present in Asia, an area in which the Ursinae had not yet become common, and it is only in Asia that *Ailuropoda* is recorded. Those authors who have accepted *Ailuropoda* as an ursid have invariably suggested its descent from the *Agriotherium/Indarctos* group (see Davis 1964), and *Indarctos* appears to be the only known fossil form from which *Ailuropoda* can be satisfactorily derived. Since *Ailuropoda* was well established early in the Pleistocene, and since it is a good deal more advanced than *Indarctos*, its differentiation must have taken place during the Pliocene, probably at about the time that *Indarctos* itself was nearing extinction.

Much of the controversy about the status of *Ailuropoda* seems to stem from the fact that it is almost always compared with modern ursine bears, from which it does indeed differ quite markedly. However, if it is taken into account

that their common ancestor was a Miocene form (Fig. 1), the differences are hardly surprising. The differences between the European early Pleistocene *Ursus minimus* and *Agriotherium insigne* are as great, or even greater, than those between modern ursines and *Ailuropoda*, yet the referral of *Agriotherium* to the Ursidae is no longer questioned.

In order to illustrate that on dental evidence alone *Indarctos* could be ancestral to both *Ailuropoda* and *Agriotherium*, a list of some characters of the upper cheekteeth of these three genera is given in Table 1. On the one hand the dentition is modified for a herbivorous diet (*Ailuropoda*), and on the other a carnivorous dentition is developed (*Agriotherium*).

TABLE 1. Some characters of the upper dentitions of *Ailuropoda*, *Indarctos* and *Agriotherium*.

<i>Ailuropoda</i>	<i>Indarctos</i>	<i>Agriotherium</i>
Herbivorous lineage	Ancestral genus	Carnivorous lineage
<i>Anterior premolars</i>		
P ¹ sometimes absent	P ¹ present	P ¹ present (?)
P ² & P ³ double-rooted	P ² & P ³ double-rooted in early forms (?)	P ² & P ³ single-rooted
<i>Carnassial</i>		
P ⁴ with prominent parastyle and antero-internal cusp	P ⁴ parastyle absent or small, antero-internal cusp small	P ⁴ with prominent parastyle, antero-internal cusp usually absent
<i>Molars</i>		
M ¹ square with prominent lingual cingulum, four main cusps and smaller cusplets	M ¹ square, four main cusps only	M ¹ narrower lingually, four main cusps only
M ² elongated with prominent talon, four main cusps and many cusplets	M ² slightly elongated with small talon and four main cusps	M ² nearly square, talon vestigial or absent, usually four main cusps only

The range of *Ailuropoda* diminished considerably during the Quaternary and it now survives in a natural state only in isolated areas in China. During the Pleistocene it was widely distributed in China, and is also recorded from Burma (Smith-Woodward 1915). It was during the Pleistocene that the Asiatic radiation of the Ursinae took place and this suggests that *Ailuropoda* may have been an unsuccessful competitor with this group. It is therefore another agriotheriine whose decline is attributed to the Ursinae.

The decision to include the tremarctines in the Agriotheriinae is not easily justified. Superficially at least, there are similarities between the extant *Ailuropoda melanoleuca* and *Tremarctos ornatus*, and both differ from *Ursus*. There are resemblances in general skull morphology, both being 'short-faced' forms, and Davis (1955: 29) states that, 'Except for the pre-masseteric fossa, the features that distinguish the skull of *Tremarctos* from the skull of *Ursus*, although much less exaggerated, are similar to the features that distinguish the skull of the

giant panda (*Ailuropoda*)'. Kurtén (1967) mentioned the similarity between the tremarctine *Arctodus* and *Indarctos*.

However, the teeth of the tremarctines are much closer to those of *Ursus* than any other agriotheriine. The P⁴ lacks a parastyle and the molars are similar to those of *Ursus*.

Its ancestry may lie with the agriotheriine *Ursavus*, and the problematical (?) *Ursavus pawniensis* Frick 1926 from the North American Miocene may be the ancestral form. Erdbrink (1953) suggested that the tremarctines are not a homogeneous group, and he derived *Tremarctos* from ursine stock, but the 'arctotheres' (*Arctodus*) from *Indarctos*. However, Kurtén (1966: 7) found that although the 'earlier history of *Arctodus* is poorly documented . . . there can be little doubt that it is a tremarctine'.

Another significant characteristic of tremarctines is the entepicondylar foramen of the humerus. This is a feature also present in the humerus of *Indarctos* (e.g. *I. oregonensis*), *Ailuropoda* and the Hemicyoninae from which the Agriotheriinae are derived. It is, however, not present in the humerus of the Ursinae. It is here regarded as a primitive characteristic retained in at least two agriotheriine lineages (*Indarctos*—*Ailuropoda* and ?*Ursavus*—Tremarctini), but lost in the Ursinae and perhaps also the *Indarctos*—*Agriotherium* lineage.

The conclusion reached here is that the tremarctines do belong in the Agriotheriinae, having stemmed from an *Ursavus*-like ancestor, and having paralleled the Ursinae in some respects.

As with *Ailuropoda*, the only surviving tremarctine, *Tremarctos ornatus*, occurs isolated from the Ursinae, in this instance in South America. Both *Ailuropoda* and the tremarctines co-existed with ursines for much of the Pleistocene, and in the case of the tremarctines for part of the Pliocene as well (Bjork 1970), so their inferred replacement by the ursines was a slow process. However, the fact remains that they were definitely in decline by the end of the Pleistocene, whereas the Ursinae were still remarkably successful. But for the advent of human civilization the Agriotheriinae might well have become extinct while the Ursinae might have remained a prominent part of the world's fauna.

Subfamily **Ursinae**

Diagnosis (see Pilgrim 1931).

Discussion. There is an extensive literature on modern and fossil ursids and a substantial proportion is devoted to the Ursinae. It is the best known and least controversial of the ursid subfamilies and only in the case of the sun bear, *Helarctos*, and the sloth bear, *Melursus*, are there any real doubts about ancestry. The subfamily apparently stems from the early Pliocene *Protursus* (Kurtén 1971), and the genera *Ursus* and *Helarctos* are first recorded in the late Pliocene, while *Melursus* is known only from the Quaternary.

Four categories may be distinguished within the subfamily. The first two are the *Helarctos* and *Melursus* groups, both of which are represented by a single

extant species, and in neither case is there a good fossil record. The genus *Ursus* can conveniently be divided into two groups. The first comprises *U. americanus* and *U. thibetanus*, the North American and Asiatic black bears, and the second is the brown bear group, *U. arctos* and related forms. The latter includes the polar and grizzly bears as well as a number of extinct species such as the giant *U. spelaeus*. They are an extremely successful group and at one time or another they have been distributed through much of the Northern Hemisphere, including the Arctic and North Africa.

THE LANGEBAANWEG BEAR

Agriotherium africanum n.sp.

Holotype. A left maxillary fragment with P⁴ (South African Museum No. L 2045).

Referred material. A part of an ulna (L 2154) and isolated teeth as follows:
L 1868A—E: I₃, I₁, ?P³ and parts of P⁴ and M¹.

L 12637: M².

L 1844 & L 3141: I₂ and I₃.

L 12561: M₃.

Locality. All the specimens are from 'E' Quarry, Langebaanweg.

Diagnosis. A species of *Agriotherium* of large size, in which the P⁴ has a prominent parastyle and a well-developed protocone lobe, the latter consisting of the protocone, an antero-internal cusp and a small intermediately situated cusp; the protocone lobe projects and is flattened posteriorly where it functions as a shearing surface additional to that of the paracone and metastyle. The M² is smaller than M¹ and is without a talon. The antero-buccal surface of M₃ is inflated.

Etymology. The specific name is given in recognition of the fact that this is the first agriotheriine recorded from Africa.

DESCRIPTION

Only two of the specimens, the ?P³ and M₃ are complete in all respects, while the referred P⁴, M¹ and M² are so poorly preserved that not a single standard measurement could be taken on them. The latter are important, however, since they do give an indication of the morphology of the teeth concerned. In general the Agriotheriinae are not well represented in the fossil record, but the Langebaanweg species can be less adequately defined than most of the recorded species of the subfamily.

The ?P³ (L 1868C) (Plate 19 F, G) is referred to this species since it was found in association with the other L 1868 specimens, which unquestionably do belong to *Agriotherium*. In size (10,8 × 7,8) it is comparable to the P³ of an *Indarctos atticus* specimen described by Thenius (1959b), and it resembles this

tooth in being broadest anteriorly. It is a simple, low-crowned tooth with a barely perceptible principal cusp from which arise keels, one running posteriorly and the other antero-internally. The crown is supported by a single antero-posteriorly elongated root.

The carnassial fragment L 1868D is incomplete, but what remains matches corresponding parts of the holotype P⁴ (Plate 19 A-E). This tooth differs in some respects from those of previously described specimens of *Agriotherium* and *Indarctos*, although in size (Table 2) and general appearance it is similar to the P⁴ of these genera.

TABLE 2. Dimensions of the P⁴ of some species of *Agriotherium*

	<i>A. insigne</i> France (1)	<i>A. sp.</i> Spain (1)	<i>A. palaeindicus</i> India (2)	<i>A. sivalensis</i> India (2)
length . . .	29,1	30,0	28,0	33,0
breadth . . .	21,0	23,0	21,0	19,8

	<i>A. gregoryi</i> N. America (1)		<i>A. africanum</i> South Africa
	UC 24027	AM 18121A	L 2045
length . . .	23,3	35,4	32,5
breadth . . .	21,7	25,8	25,5

(1) Frick (1926)

(2) Lydekker (1884)

The crown consists of a parastyle, which is damaged, paracone and metastyle, which are flanked lingually by a large protocone lobe made up of a protocone, antero-internal cusp and a small, intermediately situated cusp. There are two roots on the buccal side of the tooth and another supporting the protocone lobe. Although the parastyle is damaged, sufficient remains to indicate that it was large and made up about 25% of the total length of the tooth. In this respect it is typical of the P⁴ of *Agriotherium* in which the parastyle is always large, whereas in *Indarctos* it is usually not as well developed. The paracone and metastyle are approximately equal in length and make up the remaining 75% of the total length of the tooth. Shear facets have been worn on the lingual surfaces of these cusps.

The Langebaanweg P⁴ differs most markedly from previously described *Agriotherium* and *Indarctos* carnassials in the size and morphology of the protocone lobe. Its length (22,5 mm) can be measured accurately since its anterior

and posterior limits are clearly defined. In most other *Agriotheriinae* this is not the case as the posterior limit of the protocone merges gradually with the lingual surface of the metastyle, but in any case they all have shorter protocone lobes. In addition, the protocone lobe of L 2045 differs from other species of *Agriotherium* in that it has a fairly prominent antero-internal cusp, although this cusp is present in *Indarctos*. It is small in *I. punjabiensis*,* but quite large in *I. lagrelli* (Zdansky 1924) and *I. atticus* (Thenius 1959b).

The protocone itself is unique in that instead of being conical, it has its apex elongated antero-posteriorly and compressed towards the paracone and metastyle. The elongation of the protocone lobe as a whole is largely due to the shape of the protocone. The functional advantage of this elongation is readily evident, since the posterior part of the protocone has developed on it a shear facet which is supplementary to that of the paracone and metastyle. Of all the *Indarctos* and *Agriotherium* upper carnassials presently known, that of the Langebaanweg species seems the best adapted to a shearing function.

Another unusual feature of the protocone lobe is the small cusp situated between the antero-internal cusp and the protocone. The cusp itself has been all but worn away, but its presence is marked by a circular patch of exposed dentine. It, and the most anterior part of the protocone have almost horizontal wear facets, indicating that the P⁴ served a crushing function as well.

Parts of the enamel of this tooth show the 'wrinkling' or rugosity said to be characteristic of *Agriotherium* (Erdbrink 1953).

In its general morphology the P⁴ of the Langebaanweg species is not dissimilar to that of *Ailuropoda*.

A small part of the maxilla of the holotype is preserved. The most anterior part of the alveolus of M¹, and part of the antero-external root of this tooth are present. The M¹ must have had a transverse diameter of at least 30 mm, which is in keeping with the size of this tooth in *Agriotherium* and *Indarctos*. The inferior margin of the infra-orbital foramen is also present and it is situated above and slightly posterior to the P⁴.

Little of the M¹ (L 1868E) is preserved. Parts of the roots supporting the paracone and protocone are present, and that root beneath the protocone is large, antero-posteriorly elongated and inserted at an angle to the plane of the palate. The other preserved root is smaller, transversely elongated and inserted vertically into the maxilla. It presumably matched the now missing root which supported the metastyle. Most of the crown is lost and the only enamel preserved is near the paracone. Judging from the preserved parts of the crown and the roots, this tooth appears to have been narrower lingually. The transverse diameter is estimated to have been 30 mm, which is comparable to the figure inferred for the missing M¹ of the holotype. The antero-posterior diameter must also have been about 30 mm.

* This cusp was shown in Lydekker's (1884) illustration, but others (e.g. Matthew 1929) apparently overlooked it.

The M^2 (L 12637) is an important specimen, since although it is incomplete, its morphology indicates that the affinities of the Langebaanweg agriotheriine lie with *Agriotherium* rather than *Indarctos*. It consists of a paracone and metastyle which are equal in size, situated parallel to a protocone and hypocone which are also similar in size. The latter cusps are lower than the paracone and metastyle. The enlarged and posteriorly elongated talon which characterizes the M^2 of *Indarctos* is not in evidence. This tooth is appreciably smaller than the M^1 and its dimensions are estimated to be 25×25 mm. It is thus smaller than the M^2 of previously described species of *Agriotherium* (see Frick 1926: 81).

A reconstruction of the posterior upper dentition of the Langebaanweg agriotheriine is illustrated in Figure 2.

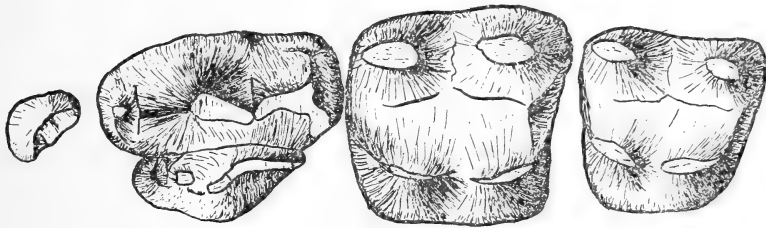


FIG. 2. A reconstruction of the posterior upper dentition of *Agriotherium africanum* based on the specimens L 1868C, L 2045, L 1868E and L 12637 (Natural size).

Little can be said of the lower incisors which are preserved (L 1868A, B, L 1844, L 3141) (Plate 20 A) other than that they are large and agree in all morphological respects with the corresponding teeth of *Indarctos lagrelli* (Zdan-sky 1924) and an *Indarctos* specimen from Samos (Helbing 1932). No descriptions or illustrations of the lower incisors of *Agriotherium* could be located, but presumably they are essentially the same as those of *Indarctos*.

The M_3 (L 12561) (Plate 20 B) is a single-rooted and low-crowned tooth with an almost circular and flat occlusal surface. The antero-buccal part of the crown is inflated and there is a wear facet in this region angled from the occlusal surface across the inflation towards the cingulum. This presumably results from occlusion with the lingual surface of the paracone or metastyle of M^2 . This is an indication that the post-carnassial teeth of this species functioned as shearing as well as crushing agents. The M_3 measures $16,5 \times 16,9$ mm.

The ulna (L 2154) (Plate 20 C, D), which lacks the distal end, lower part of the shaft and anconeus process, is far too large to be confused with the ulna of any other carnivore species in the Langebaanweg assemblage. It compares closely in size (Table 3) and morphology with the ulna from Pikermi referred to *Indarctos atticus* by Pilgrim (1931).

TABLE 3. Dimensions of the Langebaanweg *Agriotherium* ulna, compared with that of an *Indarctos* (?) cf. *atticus* specimen from Pikermi (Pilgrim, 1931).

	L 2154	Pikermi
Dorso-ventral diam. at coronoid process . . .	87,0	85,0
Transverse diam. at coronoid process . . .	59,0	61,0
Transverse diam. at proximal end . . .	50,0	52,0

DISCUSSION

The genera *Agriotherium* and *Indarctos* share many dental and osteological characteristics, but it is clear that the Langebaanweg agriotheriine has greater affinities to the former genus. It is regarded as a species distinct from those previously recorded since it exhibits certain apparently unique characteristics, and in addition it is the most geographically isolated record of the genus.

Agriotherium africanum differs from previously described species in the size of M^2 and in the nature of its P^4 and M_3 . All the species of *Agriotherium* are known from single, or perhaps a few individuals and it has therefore not been possible to assess the range of variation in any of them. However, R. H. Tedford (pers. comm.) has found 'considerable variation [in the P^4] within and among populations of Hemphillian *Agriotherium* from the United States', although none of the North American specimens matched the *A. africanum* P^4 . If the Langebaanweg species is conspecific with a known species, then it is likely that it would be one of the Eurasian forms, which presumably also had variable upper carnassials.

In this connection the geographical location of *A. africanum* is probably significant. Of the 18 species of fissiped carnivores known from Langebaanweg, only four have affinities with contemporary Eurasian species. Much the same applies to the non-carnivorous mammals. Consequently it is probable that although there is a general similarity between the late Pliocene mammal faunas of Eurasia and Africa, each area was represented by its own lineages. For example, although the Langebaanweg *Percrocuta* is fairly similar to the Eurasian *P. eximia*, it is sufficiently different to warrant the status of a separate species. Similarly the boselaphine from Langebaanweg resembles *Tragoportax salmontanus* from the Siwaliks of India, but the two are clearly not conspecific.

Even if larger numbers of individuals of the Eurasian species of *Agriotherium* become available in the future, it seems unlikely material matching that from Langebaanweg will be recorded. It was on this basis that the decision was made to refer the Langebaanweg *Agriotherium* to a new species.

Probably it is just a matter of time before more agriotheriine remains are recovered elsewhere in Africa, especially in view of the attention presently being focused on Pliocene deposits in East Africa. It is also possible that more material of *A. africanum* will be found at Langebaanweg, since some of the deposits from which present specimens were derived remain unexcavated. Consequently more adequate definition of *A. africanum* might still be possible, and its phyletic relationships might yet be more accurately determined.

SUMMARY

An account of the family Ursidae (Mammalia: Carnivora) is given and a new ursid species, *Agriotherium africanum*, is described.

ACKNOWLEDGEMENTS

The first draft of this manuscript was completed in 1967 and at that time I benefited greatly from correspondence with Dr. Björn Kurtén (University of Helsinki) and Dr. Richard H. Tedford (American Museum of Natural History). Both were very generous in sharing their knowledge of the Ursidae, and any merits which this paper may possess are due largely to them. Its shortcomings are, however, entirely of the author's own making.

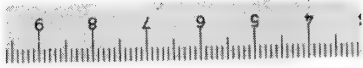
The current investigations at Langebaanweg are being supported by the South African Council for Scientific and Industrial Research, Chemfos Ltd. (a subsidiary of the African Metals Corporation) and Shell South Africa (Pty.) Ltd. The Wenner-Gren Foundation for Anthropological Research, New York, provided the vehicle used in the field work at Langebaanweg (Grant no. 2752-1834).

I am indebted to the management of Chemfos Ltd, and also Mr. H. Krumm and Mr. G. Benfield for their unfailing assistance in the recovery of fossils from the quarries at Langebaanweg.

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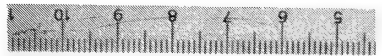
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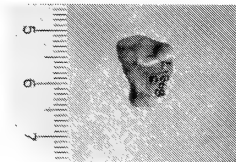
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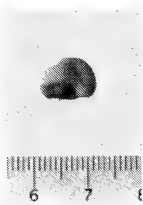
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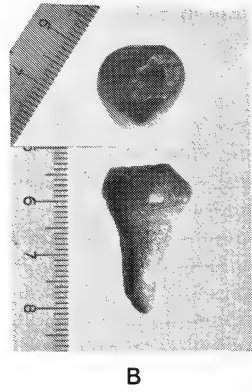
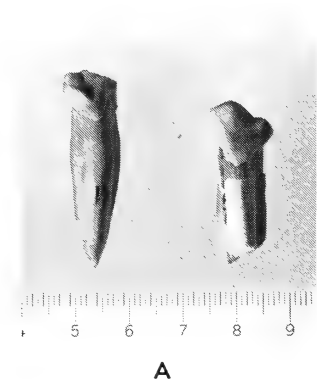


F



G

A-E Buccal, anterior, occlusal, lingual and oblique views of the *Agriotherium africanum* holotype L 2045.
F & G Lingual and occlusal views of the ?P³ of *Agriotherium africanum* L 1868C.



A Lingual view of the I₃ of *Agriotherium africanum* L 3141 and L 1868A.
B Occlusal and posterior views of the M₃ of *Agriotherium africanum* L 12561.
C & D Anterior and medial views of the ulna of *Agriotherium africanum* L 2154.

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Style manual for biological journals. Washington: American Institute of Biological Sciences.

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KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med-naturw. Ges. Jena* **16**: 269-270.

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Example

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FROM SOUTH AFRICA

By
K. G. McKENZIE

Cape Town Kaapstad



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A NEW SPECIES OF *PARADOXOSTOMA* (CRUSTACEA, OSTRACODA)
FROM SOUTH AFRICA

By
K. G. MCKENZIE

British Museum (Natural History), London

(With 12 figures)

[MS. accepted 30 November 1971]

CONTENTS

	PAGE
Introduction	133
Systematics	133
Summary	137
References	137

INTRODUCTION

During a working visit to the South African Museum in September 1970, I was shown a marine sample which had been collected at Sea Point, near Cape Town, by the late Dr. K. H. Barnard and which included a large population of a *Paradoxostoma* species. This species has proved to be new.

I am very grateful to the Director of the South African Museum, Dr. T. H. Barry, for making its facilities available; to Mr. B. F. Kensley, Curator of Crustacea, who drew my attention to the sample; to the National Institute for Water Research, Pretoria, and to my own Museum for financial support; and to Mr. D. Goode, the Transvaal Museum, who inked my original drawings.

Types are stored at the South African Museum under register number SAM A 11014 and some paratypes are at the British Museum (Natural History) under register number BM(NH) 1971.10.13.1-25.

SYSTEMATICS

Paradoxostoma kensleyi n. sp.

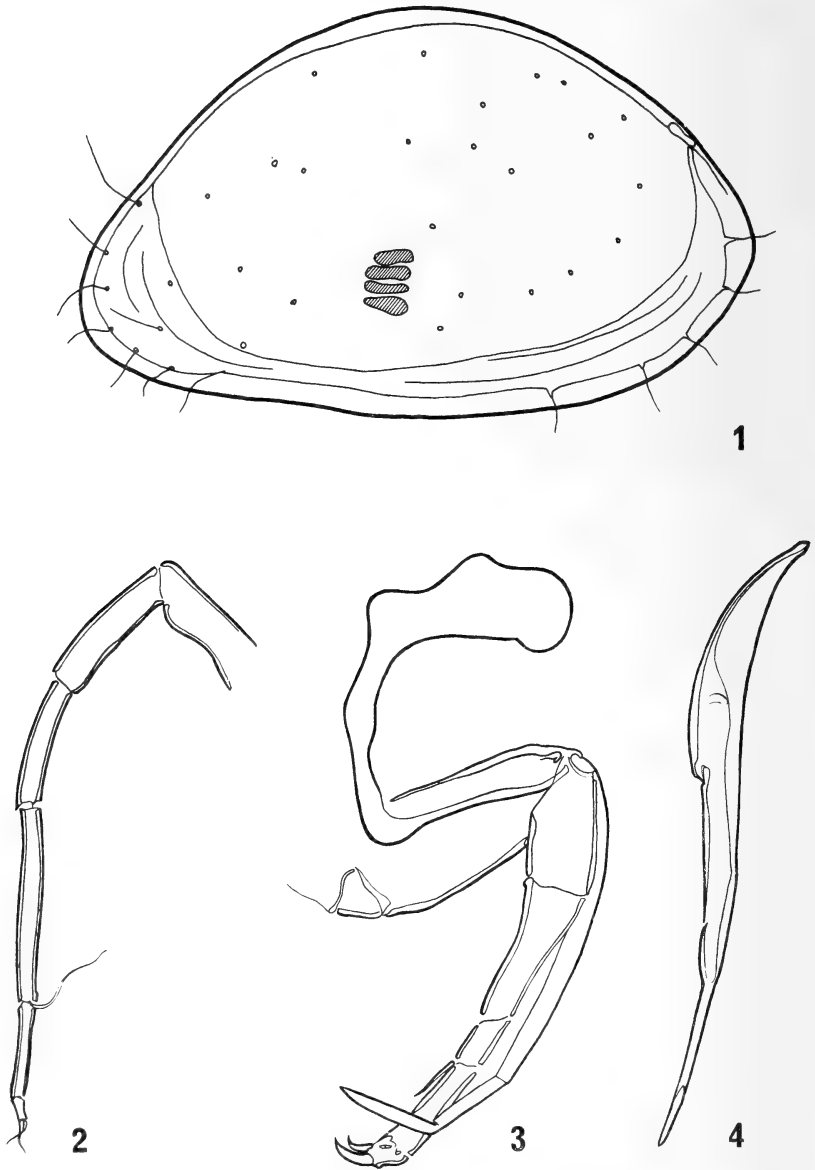
Figures 1-12

Derivation of name

For Mr. B. F. Kensley, who drew my attention to the sample and who has contributed several papers on the crustaceans of South Africa.

Diagnosis

In lateral view, carapace ovate-subtriangular; of medium size (length up to about 0.65 mm); smooth; without conspicuous colour patches in the specimen dissected (possibly, such coloration was present in life but disappeared



Paradoxostoma kensleyi n. sp., ovigerous ♀, paratype

FIG. 1. Internal view of right valve, $\times 300$. FIG. 2. Antennule, $\times 750$. FIG. 3. Antenna with lobate antennal gland, $\times 750$. FIG. 4. Mandible coxale, $\times 750$.

following preservation); anterior margin subacuminate anteroventrally; dorsal margin strongly convex with a weak anterodorsal flexure in the right valve; posterior margin subacuminate posterodorsally, broadly rounded ventrally; ventral margin weakly inflexed in the vicinity of the oral cone; greatest height medial and about 60% of the length. In dorsal view, compressed; evenly elliptical. Internally, inner margin regular; line of concrescence also regular; vestibule continuous; radial pore canals few (about 7 anteriorly and 5 posteriorly) unbranched, short and straight; normal pore canals fairly numerous, scattered, simple; hinge adont or modified adont, with a weak terminal posterior projection in the right valve and a corresponding accommodation in the left valve; muscle scars comprising four adductors in a subvertical series, others not observed (Fig. 1). Carapace sex dimorphism weak.

Antennule (A1) 6-segmented; length ratios of the last four segments 18:27:13:3 (Fig. 2). Antenna (A2) 5-segmented, the penultimate segment appears to be sutured in its proximal half; length ratio of the terminal claws is about 3:2; the flagellum (Spinnborste) extends beyond the tips of the claws and is jointed at about $\frac{2}{3}$ its length from the proximal end; the gland to this Spinnborste is large, and lobate proximally (Fig. 3). Mandible with a styliform coxale (Fig. 4); palp two-segmented with 5 terminal bristles (Fig. 5). Oral cone present, with the characteristic suctorial modification (Fig. 6). Maxilla lacking a palp, trilobate (one lobe hidden in Fig. 7); epipod with about 13 Strahlen and with two downwards-pointing setae. First thoracic leg (P1) pediform, four-segmented; protopod armed with a powerful dorsodistal claw-like spine (Fig. 8). Second and third thoracic legs (P2 and P3) also pediform but with dorsodistal bristles instead of claw-like spines on their protopods (Figs 9, 11). None of the terminal claws on these legs are strongly spinose. Posterior of the body (♀) extended into a caudiform process with a terminal spine (Fig. 10). Hemipenis of male as illustrated (Fig. 12).

Material

A very large population comprising numerous mature individuals and juveniles of both sexes.

Locality

Sea Point, near Cape Town, Republic of South Africa.

Collector and date collected

The late Dr. K. H. Barnard; March 1928.

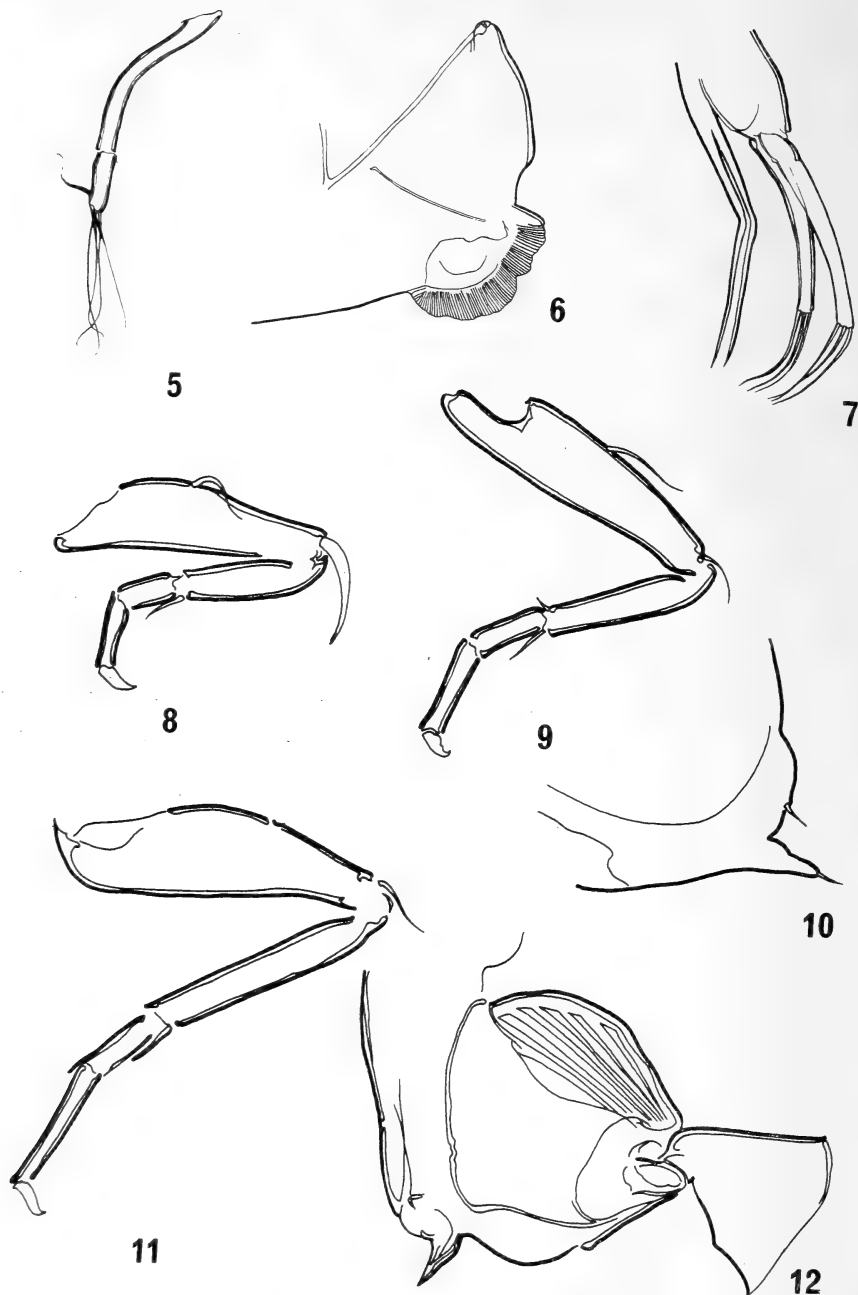
Dimensions

Holotype (♂) Length=0,52 mm; Height=0,31 mm; Breadth=0,18 mm.

Allotype (♀) Length=0,56 mm; Height=0,34 mm; Breadth=0,20 mm.

Discussion

Of the previous workers on Recent South African marine Ostracoda (Brady 1880; Müller 1908; Klie 1940; Benson & Maddocks 1964) only Klie



Paradoxostoma kensleyi n. sp., ovigerous ♀, paratype
(same specimen as in Figs 1-4)

FIG. 5. Mandible palp, $\times 750$. FIG. 6. Oral cone with suctorial disc, $\times 750$. FIG. 7. Maxilla, two lobes plus the downwards-directed setae, $\times 750$. FIG. 8. P1, $\times 750$. FIG. 9. P2, $\times 750$. FIG. 10. Posterior of body, $\times 750$. FIG. 11. P3, $\times 750$.

Paradoxostoma kensleyi n. sp., mature ♂, paratype

FIG. 12. Hemipenis, muscles only illustrated in the upper region, $\times 750$.

described any paradoxostomatids. He keyed six species in a Table (Klie 1940: 447) from which it appears that *P. kensleyi* is closest to the Klie species *P. auritum* and *P. reflexum* in characters based on the first four paired limbs (antennule, antenna, mandible, maxilla) and because it lacks pilosity on the ventral margin of the P₃ third segment. But *P. kensleyi* differs from both these species in maximum size and has a different shape to that of *P. reflexum*. Apart from the maximum size difference, *P. kensleyi* has a different hemipenis to that of *P. auritum* and although similar in general carapace shape also appears to have a different line of conrescence (Klie 1940: 444). Another similar species is *P. hypselum* Müller 1908, which was described from the sub-Antarctic. I have recently determined a specimen which probably belongs to this species (USNM 137380) and the spines on the distal claws of the thoracic legs, for the P₃ in particular, are distinctive, as pointed out by Müller (1908: 118, 119). Such distinct spines do not feature on the distal claws of the thoracic legs in *kensleyi*. Further, *hypselum* (length ♀ 0,72 mm, ♂ 0,68 mm) is a slightly larger species than *kensleyi*.

Summarizing, the known paradoxostomatid fauna of South Africa now comprises 7 species, namely: *Paradoxostoma caeruleum* Klie 1940, *P. griseum* Klie 1940, *P. angustissimum* Klie 1940, *P. auritum* Klie 1940, *P. reflexum* Klie 1940, *P. semilunare* Klie 1940 and *P. kensleyi* n.sp. It is likely that Dr. G. Hartmann, of the Zoologisches Museum und Staatinstitut, Hamburg, will describe further species when he monographs his large Recent South African collections.

SUMMARY

Paradoxostoma kensleyi, a new marine ostracode collected near Cape Town, South Africa, is described and compared with previously described South African paradoxostomatids.

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DEVELOPMENT OF *TRACHURUS TRACHURUS*
(CARANGIDAE),
THE SOUTH AFRICAN MAASBANKER

By
E. H. HAIGH

Cape Town Kaapstad



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By

E. H. HAIGH

South African Museum, Cape Town

(With 4 figures and 3 tables)

[MS. accepted 29 November 1971]

CONTENTS

	PAGE
Introduction . . .	139
Materials and methods . . .	141
Description . . .	141
Distribution . . .	148
Summary . . .	149
Acknowledgements . . .	149
References . . .	149

INTRODUCTION

The systematics of the genus *Trachurus* of the family Carangidae seem to be rather confused and need revision, based on an adequate world-wide collection. Berry (personal communication) is of the opinion that there are two species in South African waters. However, his review paper on the genus *Trachurus* is only to appear in three or four months. The present larval fish collection is not geographically wide enough for accurate comparison of the two possible species and as the distinguishing features are essentially adult characters, the designation *Trachurus trachurus* for these specimens is felt to be the most accurate, at the same time indicating the similarity of these larvae to European *Trachurus trachurus* larvae.

Several papers describing the larval development of specimens bearing either the generic or specific name *Trachurus* have appeared since late in the nineteenth century and this seems an opportune time to review what is known about larvae of this genus.

The description of *Caranx trachurus* by Holt (1898) does not give details and the illustrations in *Annales du Musée d'Histoire Naturelle de Marseille* (5, 1899: 27-32, figs 53-63) to which he refers were not available. However, Ehrenbaum (1909: 27-30) reviews Holt's publications as do Heincke & Ehrenbaum (1900).

All authors seem to be satisfied as to the identity of the egg of *Trachurus trachurus* and describe it as having a diameter of 0,7 to 1,09 mm, a totally segmented yolk and an oil globule of 0,19 to 0,28 mm diameter with yellowish to brownish pigment around it which remain in the anterior part of the yolk

until resorbed. South African maasbanker eggs that have been measured are seldom larger than 1 mm in diameter—usually about 0,9 mm with an oil globule of 0,2 mm diameter. This falls within the range mentioned above.

Ehrenbaum (1909) gives a short description and six rather inadequate figures of *Trachurus trachurus*, but these do serve to confirm the basic similarity to the larvae described by Schnakenbeck (1931). Unfortunately Schnakenbeck fails to provide adequate dimensional data. By modern standards Schnakenbeck's size groups are rather large, but comparative reworking of measurements in the present paper produces values which approximate these.

Delsman (1926) described eggs and early larval stages from the Pacific round the Indonesian islands under the name *Caranx kurra*. However, both eggs and larvae are so similar to descriptions by Ehrenbaum (1909) that they could easily be larvae of the genus *Trachurus*, probably *maccullochi*, which Nichols (1940) put as a race of *Trachurus trachurus*.

The description of *Trachurus symmetricus* larvae from the Pacific coast of America by Ahlstrom & Ball (1954) again shows the small differences between species of *Trachurus*. *Trachurus symmetricus* larvae can perhaps be separated from *Trachurus trachurus* larvae by the very slight difference in degree of pigmentation, the former being less pigmented. However, degree of pigmentation hinges to a very large extent on the length and method of preservation, and perhaps also on the time of capture, be it daylight or after dark. Pigmentation is thus an unreliable characteristic for the distinction of species so closely related.

Aleev (1957) described a good developmental series of *Trachurus mediterraneus ponticus* Aleev. Unfortunately his diagrams do not show ossification details or pigmentation patterns and can thus not be successfully compared with the figures published by Dechnik & Seniokova in 1964 of *Trachurus mediterraneus* (?).

In 1969 Zhudova published three figures of *Trachurus* larvae described as *T. trachurus* and a distribution map giving distribution of *Trachurus* larvae between 5°N to 12°S and 10°E to 14°W in the Gulf of Guinea and in 1970 Kiliachenkova published several good figures of eggs and larvae up to 8,9 mm in length caught along the West African west coast between 24° and 15°N and 19°50' and 17°50'W.

The adult maasbanker is found in most parts of the Atlantic down to a depth of 400 metres. It occurs abundantly on the west coast of southern Africa, where, with *Sardinops ocellata* (Pappe, 1853), the South African pilchard, it forms the basis of the fishmeal industry. Like the pilchard, it is a plankton feeder, its diet consisting mainly of zooplankton including amphipods, euphausiids and fish larvae.

Eggs and larvae are usually found in deep seas (see section on distribution), while juveniles are found mostly in sheltered bays close inland. Several authors report the clustering of small and juvenile *Trachurus* under jellyfish (Ehrenbaum 1909) and floating debris and seaweed (Delsman 1926). Apparently this habit is common to the Carangidae.

MATERIALS AND METHODS

Specimens were obtained by research vessels of the Division of Sea Fisheries, Cape Town, using N100B and N100H plankton nets, from 1950 to 1967. Samples were fixed and stored in formalin which was replaced by 70% ethyl alcohol. Specimens were stained, using methods of Hollister (1934) but modified slightly by reducing the clearing time in KOH and reducing the concentration of the KOH used. This was done in order to preserve pigment in specimens. As pigment is inclined to fade with time, more than one larva in the size range was used in order to obtain the most characteristic pigment pattern. Stained specimens were preserved in glycerin.

Measurements were taken as follows:

Standard length (s.l.):	tip of lower jaw to end of caudal peduncle
snout:	tip of lower jaw to anterior margin of eye
eye diameter:	the eye being essentially round, could be measured in any direction
head length:	tip of snout to cleithrum
trunk length:	tip of snout to posterior end of anus, measured along the midline with verticle to snout and anus
depth:	taken at posterior edge of head

All proportions are presented as percentage of standard length.

All lengths cited in text are the standard length.

DESCRIPTION

The adults and juveniles of *Trachurus* are distinguished from other genera of the family Carangidae by the absence of separate anal and dorsal finlet, the presence of laterally expanded scutes over the full length of the lateral line and a procumbent spine before the spinous dorsal fin. As far as the distinctive South African species is concerned, Smith (1953) says that *Trachurus trachurus* has between 70 and 90 scutes on the lateral line, a depth of 45% and more than 30 dorsal rays.

Among later larval stages, dorsal fin-count of 8 + 31-33 and anal fin-count of 3 + 27-29 combined with distinctive pigmentation pattern will serve to separate *Trachurus* larvae from *Decapterus* larvae which have a darkly pigmented area on the head.

Ossification

The smallest specimens show slight ossification of the premaxilla, dentary and cleithrum. The three horizontal, one corner and one vertically situated preopercular spines are lightly ossified (Fig. 1A). Between 3.0 mm and 4.5 mm ossification takes place rapidly. The premaxilla with four fine teeth is well formed. The maxilla is lightly ossified. The dentary and angular can be clearly distinguished and there are six ossified branchiostegal rays. The preopercle now

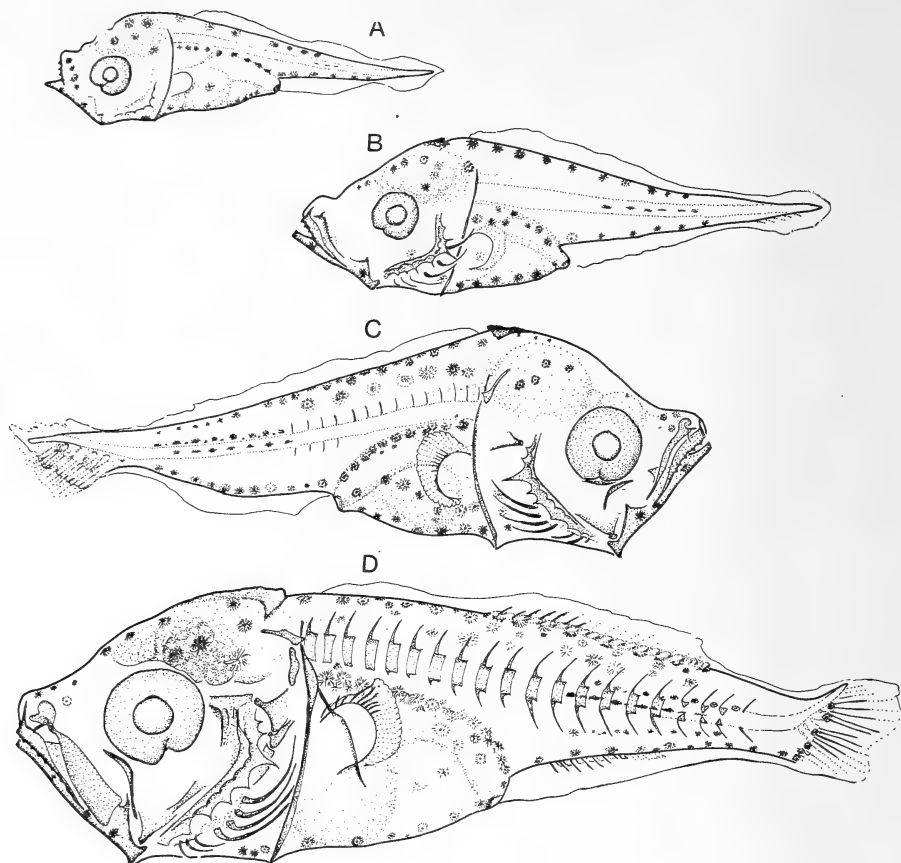


FIG. 1. *Trachurus trachurus*. Early larval stages showing pigmentation, pattern and position and degree of bone development. Measurements indicate standard length.

A. 3,30 mm. B. 4,50 mm. C. 5,80 mm. D. 7,2 mm.

bears four spines on the horizontal arm, the corner spine has become very long and there are two spines on the vertical arm. The number of spines laid down between this stage and 5,4 mm is usually the number that remains for the rest of the development. There is a spiny ridge on the outer anterior edge of the preopercle with six to seven small spines on it.

The cleithrum broadens very gradually and by 5,4 mm the supracleithrum has appeared as have the first traces of the opercle, the quadrate and the pterygoid. There are now seven branchiostegals. Between 5,4 mm and 6,6 mm further ossification takes place, all above-mentioned bones becoming heavier, darker and broader. New bones make their appearance, i.e. the frontal, sphenotic and parietal as well as the supra-occipital crest over the brain region. Laterally from this is the first indication of the pterotic and behind the pterotic

what appear to be the first traces of the exoccipital. The hyomandibular and symplectic can be clearly distinguished as can the opercle, the subopercle and interopercle. The epiphyal and ceratohyal show the first traces of ossification. The articular and dentary have become fairly well amalgamated. By 7,8 mm the pterygoid has become fairly extensive (Fig. 2A) and traces of the lacrimal and nasal can be seen. The postcleithral bones which first become evident at about 6 mm are now joined by traces of the scapula and the pelvic girdle is also evident. Ceratohyal and epiphyal can be easily seen.

The cranial ossification proceeds rapidly after 7,8 mm. The whole brain region becomes ossified and bones join up. The post-temporal appears above the supracleithrum and there are several centres of ossification in the supra-temporal region. The circumorbital bones are evident but the nasal region is still fairly unossified. The maxilla has now become the major bone in the upper jaw, almost completely obscuring the dentary, when the mouth is closed. The spines on the preopercle are less prominent. Ceratohyal and epiphyal are well ossified but still separate. The pectoral girdle elements present are scapula and three pterygials while the pelvic girdle is well ossified.

TABLE I

Average meristic counts during development of *Trachurus trachurus*.

Average s.l.	Dorsal		Anal		Vertebrae trunk tail	Neural spines	Haemal spines	Pectoral fin	Pelvic fin	Caudal. fin
	spines	rays	spines	rays						
4,25	—	—	—	—	0-10+ 0-1	3-16	4-6	0-3	—	1-5+1-5
6,03		0-4	—	0-5	0-10+ 0-4	0-18	0-8	0-5	—	3-5+3-5
6,82	0-6+	0-17	0-1	0-14	0-10+ 0-12	2-20	3-10	3-8	—	1-9+2-8
8,34	0-7+	3-24	1-2	7-22	10+10-14	20-22	11-13	6-14	1-3	8-9+8
9,16	6-8+	13-25	1-3	12-19	10+11-14	20-22	11-13	8-15	3-4	9+8
9,80	5-8+	20-30	3	16-24	10+13-14	22	12-13	9-17	3-5	9+8
11,61	8+1+	28-33	2+1+	26-28	10+14	22	13	16-19	1+4-5	9+8
13,51	8-9+1+	25-33	2+1+	23-28	10+14	22	13	7-18	1+5	9+8
15,37	8+1+	31-32	2+1+	26-27	10+14	22	13	18-21	1+5	9+8
26,00	8+1+	30	2+1+	26	10+14	22	13	1+21	1+5	9+8
29,25	8+1+	33	2+1+	29	10+14	22	13	1+20	1+5	9+8
34,54	8+1+	34	2+1+	30	10+14	22	13	1+21	1+5	9+8
48,50	8+1+	33	2+1+	30	10+14	22	13	1+21	1+5	9+8

In the postcranial region ossification starts at about 4,5 mm in some specimens while others show only the first traces of the haemal and neural spines at about 6,0 mm. The ossification of the vertebral column appears to start anteriorly with two to three neural spines, then some haemal and neural spines ossify medially, and after this the neural spines over the intestinal sac ossify, followed by the posterior haemal and neural spines. Between 5,4 mm and 6,6 mm the vertebral centra ossify rapidly, and apparently several at once, from the anterior, with the result that by 6,6 mm there can be as many as

ten trunk centra and up to twelve tail centra partly or fully ossified. The urostyle ossifies before the penultimate vertebra.

By 7,8 mm ten tail centra are ossified, and by 9,9 mm the full complement of ten trunk and fourteen tail centra, including the urostyle, is ossified. The neural and haemal spines have broadened by now, especially in the caudal plate where three haemal and two neural spines support the caudal fin rays. Schnackenberg (1931) gives an extensive account of the caudal ossification of European species and ossification in the specimens described follows the same pattern.

The median fin rays are first evident between 5,8 and 6,6 mm and those in the dorsal and anal fins are formed simultaneously. Between 6,5 mm and 7,8 mm the dorsal and anal spines appear. The third anal spine is associated with the soft anal and only becomes thickened at about 9,1 mm. The middle dorsal spines appear first then the most posterior and the seventh and eighth spines last of all, usually between 9,0 and 10,0 mm. The small procumbent dorsal spine is formed only during juvenile stage. The spine of the soft dorsal becomes thickened only at about 8,5–9,0 mm. The rays of the anterior and midsections of both fins are formed first and ossification proceeds posteriorly gradually until both fins are fully ossified at about 11,0 mm s.l. Between 9 mm and 12 mm the fin supports of both fins are formed.

The pectoral lobe is present even in smaller specimens and ossification of the rays starts as early as 5,2 mm in a few specimens but in the majority of specimens examined general pectoral fin ray ossification commences between 6,0 and 6,50 mm at the most dorsal aspect of the fin and proceeds round the periphery ventrally in sequence. Ossification takes place rapidly and by 10,0 mm there are usually about 17 rays ossified. The full complement of 22 rays with the most anterior ray considerably thickened can be seen only in juveniles of over 20,0 mm.

There are no evident pelvic lobes and the first ray appears only at 7,5 mm but by 9,8 mm there can be as many as five rays ossified and by 10,0 mm the outermost ray has become noticeably thickened. The full number of one spine and five rays is present at 11,0 mm.

The caudal fin ossification starts very early on in development, as soon as jaws and cleithrum have ossified, and well before the urostyle has turned up. Rays ossify from the middle outward and by 6,5 mm some specimens show the full complement of nine dorsal and eight ventral primary caudal rays. Secondary caudal rays start ossifying almost immediately after this size and proceed gradually until well into the juvenile stage. The urostyle turns up gradually at about 6,0 mm s.l.

Juvenile ossification takes place mainly in terms of consolidation of bones although there is of course a tremendous amount of growth taking place. The juvenile stage is reached between 10,0 and 12,0 mm although the lateral line scutes, a major distinguishing feature of the species, appear only between 18 and 19 mm.

Ossification of *Trachurus trachurus* larvae does not take place at the same rate in all specimens and commencement also varies considerably. If position of capture, time of year and water temperature are considered, it appears that larvae of similar sizes caught in the same latitudes will show different degrees of ossification, depending upon whether they were caught early or late in spring or summer. Larvae of 6,5 mm were caught in water temperatures of 15,79° and 22,18°C. Those caught in 15,79°C (August) showed far less vertebral ossification than those caught at 22,18°C (January).

Pigmentation

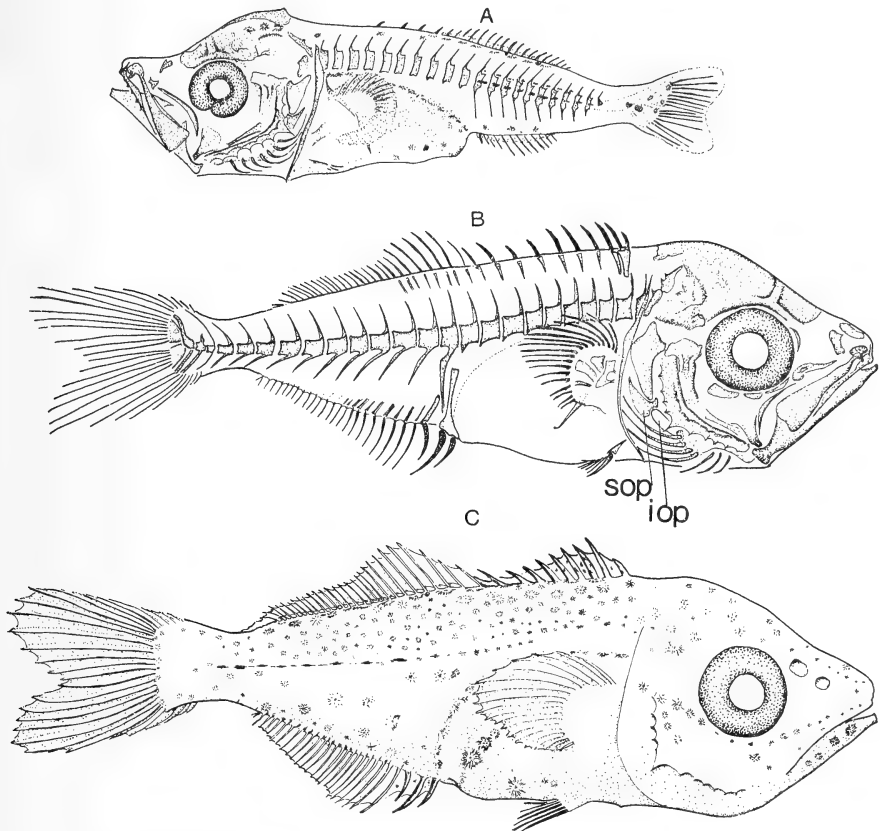


FIG. 2. *Trachurus trachurus*. Late larval stages with ossification nearing completion. A. 8,4 mm standard length. B. 10,5 mm standard length showing ossification. sop. subopercle. iop. interopercle. C. Same specimen showing pigmentation pattern.

The pigmentation pattern in *Trachurus* species from the southern African region is much the same as that described for European specimens by Ehrenbaum (1909) and Schnakenbeck (1931) as well as that of *Trachurus symmetricus*, described by Ahlstrom & Ball (1954).

In the early larvae (Fig. 1A-B) the pigment is distributed in three main areas, dorsally along the edge of the body and over the brain area, medio-laterally along the peritoneal wall and over the medioposterior region of the chorda and ventrally along the edge of the trunk and tail with a few scattered melanophores on the upper and lower jaws and in the region of the cleithrum. The dorsal pigmentation is soon augmented (Fig. 1C) by melanophores appearing on the dorsolateral sides of the body musculature. The median row of elongated contracted melanophores in the lateral line region which is so characteristic of many carangid larvae, becomes darker and more distinct. A second row of pigment appears directly over the notochord. On the peritoneum pigment darkens dorsally and scattered melanophores appear laterally. Chromatophores are still present on the nose, the jaws and underneath the branchiostegal rays. By 6,6 mm (Fig. 1D) a second pigmentation on the caudal plate itself has become more clearly defined. Between 7 mm and 10 mm the body wall thickens and fins are formed obscuring much of the deeper-lying pigmentation. The balance of pigmentation changes rapidly, the dorsal aspect of the fish becoming far more heavily pigmented than the ventral (Fig. 2C). There are large and small melanophores on the dorsolateral aspect. The more dorsally situated ones seem to be far larger than those on the lateral side.

The dorsal aspect of the head has also become pigmented to uniformity with the body. There are still chromatophores on the jaws and nose but none is visible on the trunk region. The ventral aspect of the tail still bears widely scattered melanophores but the caudal plate and unpaired fins have become pigmented. Both spiny sections of the median fins are pigmented, while the rayed parts are clear. The lateral line row of melanophores is still very distinct and remains so until the juvenile stage is reached.

Changes in body-form

The earliest stages of *Trachurus* sp. present in these collections have the yolk-sac absorbed and intestine with one fold developed at 2,45 mm. The eye has become pigmented but the snout is shorter than eye diameter (7,7% v.s. 10,0% of s.l.). During the next millimetre increase in length the head increases proportionately rapidly from 25% to 33,5% of standard length and the depth remains constant at about 30%. However, this depth is measured at the region where the head joins the trunk and it is noticeable (Table 2) that this original proportion is slightly but definitely decreased in the larger stages. This is no doubt due to rapid increase in the head during early development and the increase in tail size in later development. If larvae shown in Figures 1 and 2 are compared, it will be noticed that the younger stages are proportionately much deeper anteriorly than posteriorly while the later stages are of more even proportions.

The larval development of *Trachurus* sp. is thus characterized by a smooth and gradual development. Fins form in adult positions and body proportions change gradually and slightly.

TABLE 2
Mean measurements of *Trachurus trachurus* in mm.

Size range	Average size	No.	Snout	Eye	Head	Trunk	Depth
2,5- 3,5	3,17	5	0,25	0,33	0,90	1,70	0,95
3,5- 4,5	4,04	29	0,45	0,40	1,43	2,40	1,30
4,5- 5,5	4,93	45	0,53	0,50	1,65	2,80	1,55
5,5- 6,5	5,84	32	0,70	0,60	2,00	3,40	1,80
6,5- 7,5	6,92	32	0,75	0,75	2,50	4,00	2,30
7,5- 8,5	8,15	29	0,95	0,95	3,00	4,90	2,60
8,5- 9,5	9,04	16	1,05	1,05	3,20	5,30	2,80
9,5-10,5	10,01	13	1,15	1,10	3,40	5,80	3,05
10,5-11,5	10,89	6	1,20	1,25	3,70	6,20	3,20
11,5-12,5	11,28	17	1,40	1,40	4,10	6,80	3,65
12,5-13,5	12,99	3	1,60	1,40	4,60	7,20	3,90
13,5-14,5	13,90	7	1,50	1,50	4,80	7,70	4,00
14,5-15,5	15,31	6	1,50	1,70	5,20	8,40	4,50
15,6-16,6	—	0	—	—	—	—	—
16,6-17,6	16,90	3	2,00	1,80	5,80	9,70	4,80
17,6-18,6	18,20	1	1,80	2,00	5,90	9,80	5,50
18,6-19,6	18,88	4	2,10	1,90	6,40	9,80	5,20
19,6-20,6	20,15	2	2,20	2,00	6,50	10,50	6,10
20,6-21,6	21,01	4	2,10	2,20	6,70	11,10	6,00
23,67	23,67	1	2,27	2,27	7,80	12,02	5,85
24,05	24,05	1	2,27	2,60	7,80	11,30	6,20
25,67	25,67	1	2,60	2,92	8,45	13,65	6,82
29,00	29,00	1	3,00	3,00	9,50	14,60	7,50

TABLE 3
Mean body proportions of *Trachurus trachurus* larvae as % of standard length.

Size range in mm	Average size in mm	No.	Snout	Eye	Head	Trunk	Depth
2,5- 3,5	3,17	5	7,5	10,0	25,0	54,0	30,0
3,5- 4,5	4,04	29	10,5	9,5	33,5	56,0	30,5
4,5- 5,5	4,93	45	11,0	10,5	32,0	57,0	31,5
5,5- 6,5	5,84	32	11,5	10,5	35,0	53,0	31,0
6,5- 7,5	6,92	32	11,0	11,0	36,0	59,5	32,0
7,5- 8,5	8,15	29	13,0	11,5	36,0	59,5	31,5
8,5- 9,5	9,04	16	12,0	11,5	35,0	58,0	31,0
9,5-10,5	10,01	13	11,5	11,0	34,0	58,0	31,0
10,5-11,5	10,89	6	10,5	11,5	34,0	57,0	29,0
11,5-12,5	11,28	17	11,5	11,5	34,5	57,0	30,5
12,5-13,5	12,99	3	12,0	10,5	35,0	55,5	30,0
13,5-14,5	13,90	7	10,5	11,0	34,5	55,5	29,0
14,5-15,5	15,31	6	9,6	11,0	34,0	54,5	29,0
16,6-17,6	16,90	3	11,0	11,0	34,0	57,0	28,0
17,6-18,6	18,20	1	10,0	10,5	32,0	53,5	30,5
18,6-19,6	18,88	4	11,0	10,0	33,5	52,0	27,5
19,6-20,0	20,15	2	11,0	10,5	32,5	53,0	30,0
20,0-21,0	21,01	4	10,0	10,0	32,0	52,5	28,5
23,67	23,67	1	9,5	9,5	33,0	51,0	24,5
24,05	24,05	1	9,5	11,5	32,5	47,0	25,5
25,67	25,67	1	10,0	11,5	33,0	53,0	26,5
29,00	29,00	1	10,5	10,5	32,5	50,5	26,0

The air-bladder starts as a small clear patch behind the cleithrum and extends rapidly posteriorly until it occupies about 50% of the dorsal longitudinal distance of the peritoneum.

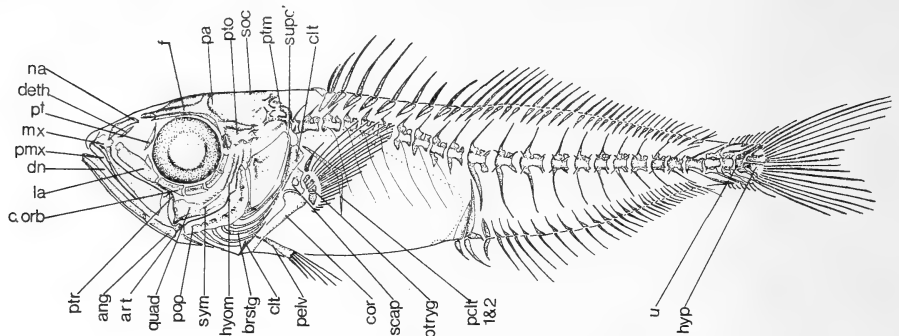


FIG. 3. *Trachurus trachurus* juvenile

ang.	angular	hyp.	hypurals	ptm.	post-temporal
art.	articular	la.	lacrimal	pto.	pterotic
brstg.	branchiostegal rays	mx.	maxilla	ptr.	pterygoid
clt.	cleithrum	na.	nasal	ptryg.	pterygials
cor.	coracoid	pa.	parietal	quad.	quadrate
c. orb.	circumorbitals	pctl. 1 & 2	postcleithra	scap.	scapula
deth.	dermethmoid	pelv.	pelvic girdle	soc.	supraoccipital
dn.	dentary	pf.	prefrontal	supcl.	supracleithrum
f.	frontal	pmx.	premaxilla	sym.	symplectic
hyom.	hyomandibular	pop.	preopercle	u.	urostyle

DISTRIBUTION

The area covered by the research vessels of the Division of Sea Fisheries on the pilchard research programme has varied since the inception of the programme. During 1951 and 1952 the area worked lay between 32° and 35° 30'S and was delimited by the 200 fathom depthline to the west. Approximately the same area was worked between 1953 and 1957. In 1958 the eastern limit of the work area was extended round Cape Point to 19° 30'E. This area was worked until the end of 1960 when the eastward delimitation was extended to 21°E. During these years the westward delimitation extended to 16° 31'E. From July 1963 to December 1965 the area covered by the ships was between 32° 10' to 36° 10'S and 16° to 21° 30'E. Station lists are obtainable from the Annual Reports of the Division of Sea Fisheries, for the relevant years. Figure 4 shows positions where larvae and juveniles were captured from 1951 to 1965. The most productive year was 1964 when *Trachurus* sp. were caught at 81 stations visited, followed by 1965 when 68 stations yielded *Trachurus* sp.

Trachurus larvae were caught throughout the year, the smallest number of stations yielding larvae in July and the largest number during October, that is late spring in the Southern Hemisphere. The spring months, August, September and October, yielded the largest collection of larvae while the three other seasons yielded far fewer and were not markedly different.

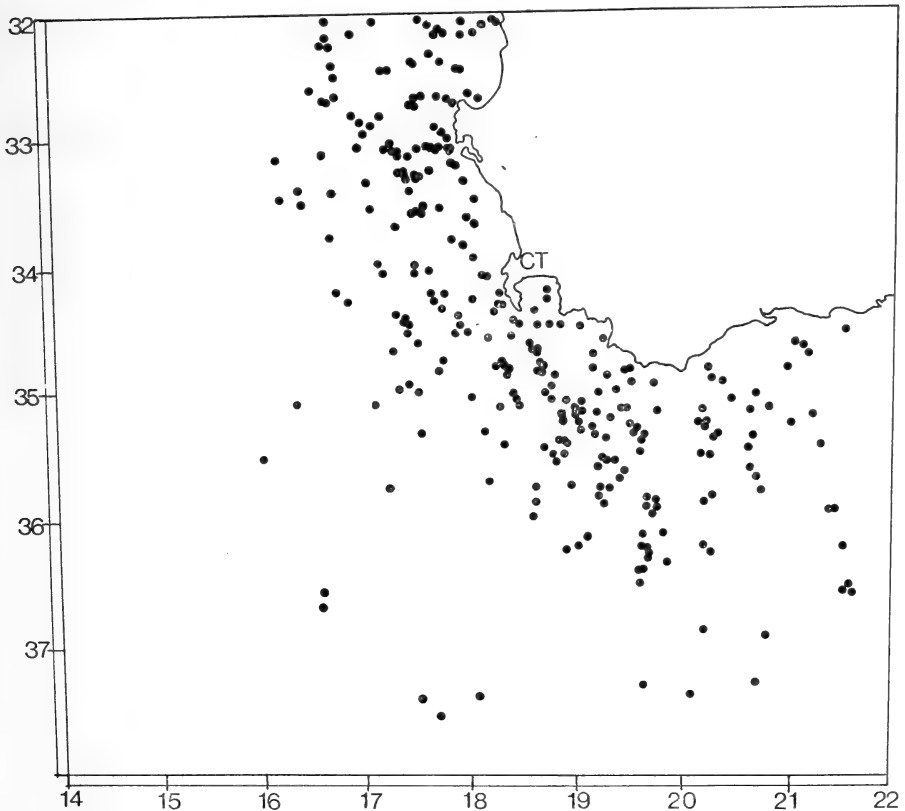


FIG. 4. Distribution of *Trachurus trachurus* larvae in the research area between 1951 and 1965.

SUMMARY

The development of the South African larvae of *Trachurus trachurus* is described and a general map of the distribution of the larvae provided.

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LANGEBAAWEG, CAPE PROVINCE

By
D. A. HOOIJER

Cape Town Kaapstad

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Rijksmuseum van Natuurlijke Historie, Leiden

(With plates 21-34 and 51 tables)

[MS. accepted 14 February 1972]

CONTENTS

Introduction	151
<i>Ceratotherium praecox</i> Hooijer & Patterson	152
Dentition and skull	153
Postcranial skeleton	168
Other <i>C. praecox</i> sites in East and South Africa	187
Summary	190
Acknowledgements	190
References	191
Explanation of the plates	191

INTRODUCTION

The rhinoceros remains described in the present paper are from the 'E' Quarry at Langebaanweg, situated approximately 32°58'S, 18°9'E in the Sandveld region of the south-western Cape Province, some 105 km N.N.W. of Cape Town. They are more abundant than those of any other large mammal in the Langebaanweg fauna. The literature on the geology and palaeontology of the Langebaanweg deposits is reviewed in Henzey (1970a); the geological age is discussed in Henzey (1970b) and Maglio & Henzey (1970). The 'E' Quarry rhinoceros has been cited as *Diceros* aff. *bicornis*, but I found it to be a very early *Ceratotherium*, the same as that from Kanapoi, Ekora and Lothagam-1 in N.W. Kenya described as *Ceratotherium praecox* Hooijer & Patterson (1972). This species is still very close to a *Diceros* like *D. bicornis* (L.) in some dental characters which take the eye even at a cursory look, such as the transversely placed proto- and metaloph, absence of medifossettes, well-developed paracone style, and angular antero-internal crown corners. In these as well as other characters the fossil teeth from Langebaanweg and those of *D. bicornis* differ from those of *Ceratotherium simum* (Burchell), which has obliquely placed proto- and metalophs, medifossettes, no paracone style, and rounded antero-internal crown angles. We believe that *Ceratotherium praecox* is directly ancestral to the living *C. simum*, and its occurrence at the Kenya sites, near the 4 million year level (Maglio 1970; Cooke & Maglio 1971; Bishop 1971a: 511) is perfectly in accordance with the Late Pliocene age that is now becoming accepted for the Langebaanweg deposits.

Abbreviations used in this paper are:

K.N.M.	Kenya National Museum
L.M.	Leiden Museum
M.C.Z.	Museum of Comparative Zoology, Harvard University
S.A.M.	South African Museum

CERATOTHERIUM PRAECOX HOOIJER & PATTERSON

Ceratotherium praecox Hooijer & Patterson 1972: 19.

The present species was based on three incomplete skulls and mandibles with teeth, some fragments without teeth, an upper molar and an imperfect humerus from Late Pliocene sites in north-western Kenya. The Langebaanweg rhino collection comprises four upper dentitions, parts of three skulls and ten mandibles (mostly with teeth), 100 isolated upper and 50 isolated lower cheek teeth, 3 upper incisors, 20 deciduous cheek teeth, and 650 postcranial bones. The cranial and dental characters of the Langebaanweg rhinoceros are the same as those of the Kenya collection already described, but the Langebaanweg collection adds to our knowledge of the species information on the upper incisors and milk teeth which were unknown before, and the postcranial characters which were virtually unknown until the Langebaanweg material became available. The data provided in the present paper show the amount of individual variation within a single species of Pliocene rhinoceros. It is not saying too much now that *C. praecox* odontologically and osteologically is better known than its extant descendant, although, of course, its external characters are for ever lost to us.

The cranial characters of the present species are as follows: dorsal surface more concave, posterior portion less extended behind, occiput less posteriorly inclined, nuchal crest less thickened than in *Ceratotherium simum*. The premaxillae bear two incisors each, about 10 mm in diameter. The symphyseal part of the mandible is narrower than in *C. simum*, and similar to *D. bicornis*. The premolars and molars (upper as well as lower) are more hypsodont than those in *D. bicornis*, but decidedly less so than in *C. simum*. The flattened ectoloph, marked protocone folds in the molars, strong internal cingula in the premolars, angular antero-internal corners of the crowns in premolars and molars alike, the posterior bulging of the protocones, which make up three-fifths of the internal crown faces, the medifossettes that rarely occur (mostly in P²⁻³ and M³, if at all), and the mediusinus and postsinus depths being very nearly equal, all these are characters shared by the Kanapoi and the Langebaanweg *C. praecox*.

The species in question is rather *Diceros*-like in skull and dentition, the teeth differing in their relatively higher crowns, with a flattened ectoloph on which the paracone style is almost completely suppressed, the postsinus being very nearly as deep as the mediusinus, and the posterior protocone bulge slightly more marked. In these points the Kanapoi and Langebaanweg rhinoceros is evolving toward the Quaternary *Ceratotherium simum*, in which the crown height

is still greater, the paracone style completely suppressed and the parastyle raised, forming a concave area on the ectoloph where the paracone style had been, medifossettes are common, formed by the union of crochet and crista, postsinus and medisinus are equal in depth, the protocone bulge is more marked, the protoloph is obliquely placed and the antero-internal crown angles are rounded. In the early subspecies *C. simum germanoaffricanum* (Hilzheimer), which is indistinguishable from the extant *C. simum simum* cranially, and which occurs at Laetolil, the basal Olduvai Beds, and Chemeron Formation locality J.M.90 (=91), the crowns are not quite so hypsodont and the metaloph is still transverse in its course rather than oblique as in the modern form, although the rounded antero-internal crown angles and the medifossettes of *C. simum germanoaffricanum* are as in *C. simum simum*. In my earlier paper on Pleistocene East African rhinoceroses (Hooijer 1969), published at a time when I had not yet studied the material from Kanapoi, Lothagam-1 and Ekora, I referred specimens from the Chemeron Formation, locality J.M.507, and from the Mursi Formation of the Omo Basin (=lower level of the Omo collection made by Mr. R. E. F. Leakey in 1967) to *C. simum germanoaffricanum* which I now recognize as belonging to *Ceratotherium praecox* instead; this will be dealt with in the final section of this paper. The discovery of *Ceratotherium praecox* vindicates the view of Thenius (1955) that *Ceratotherium* split off from the *Diceros* stock sometime in the Pliocene.

DENTITION AND SKULL

The individually youngest upper dentition, L13035, comprises P²-M³ from the right side as well as M¹⁻³ sin. (Pl. 21). The crowns of P³ and M² dext. only are virtually complete. There was a DM¹ or P¹ as there is an anterior facet on P².

P² is worn down to a height of 28 mm externally. The external enamel layer is missing for the most part; only the metastyle portions remain. There is a very marked internal cingulum, rising on the protocone and the hypocone from its lowest point at the medisinus entrance. The internal portions of protoloph and metaloph are connected at their bases by a small ridge; there is a small pit between it and the internal cingulum. The medisinus is slightly deeper than the postsinus, and there is a very small crochet, hardly more than a point.

P³, worn to 45 mm from the base externally, has a very prominent internal cingulum, reaching its lowest point at the entrance to the medisinus, which is narrow and V-shaped. There is a very weak crochet, and no crista or antecrochet. Medisinus and postsinus are equal in depth. The ectoloph is flattened, with a weak cingulum; there is no parastyle fold or paracone style. The protoloph is hardly indented anteriorly, but there is a vertical groove in the metaloph marking off the hypocone.

P⁴, with an external height as worn of 60 mm, has the flattened ectoloph detached from the remainder of the crown, which shows the narrow, V-shaped

medisinus entrance, the heavy internal cingulum, weak crochet, and the medisinus depth equal to that of the postsinus, as in P^3 . An internal view of P^{2-4} dext. of L13035 is given in Plate 25, top.

M^1 , the right of which lacks most of ectoloph and protoloph, and the left of which is entire but for the antero-external angle, is worn to a height of 52 mm externally. The lingual entrance to the medisinus is V-shaped, and there is an anterior fold in the metaloph marking off the hypocone. This molar, in contrast to the premolars, has a deep fold anteriorly in the protoloph marking off the protocone (the protocone fold), a strong crochet extending all across the medisinus, not receding near the base, and the internal cingulum hardly marked except along the protocone and for a tubercle at the entrance to the medisinus. The inner portion of the protoloph is recurved backward, forming three-fifths of the internal surface. The ectoloph is flattened, without styles, and medisinus and postsinus are of the same depth.

M^2 , nearly entire on both sides, is worn to 75 mm from the external base. This is clearly a hypsodont tooth, the anteroposterior diameter of the crown being 62 mm externally. A weak paracone style is seen in the upper part of the crown only, to 60 mm from the base, flattening out further rootward. There is no groove marking off the hypocone, but the description of M^1 would otherwise fit the M^2 .

M^3 of dentition L13035, both incomplete behind, are 90 mm high as worn and the length of the outer surface is about 75 mm. The marked protocone fold, internal protocone cingulum, and strong, even bifid crochet, are as in the other molars of this individual. The paracone style is weak but discernible, reaching from the top of the crown to approximately 50 mm from the crown base.

Another upper dentition, L2519, likewise consists of isolated teeth, which are P^2-M^3 dext. and P^3-M^1 sin. (Pl. 22). They are rather well preserved although a number of crown angles are missing.

P^2 is just 20 mm high as worn externally. The medisinus is still open internally. It shows a crochet united with a small crista so that a medifossette is formed. The same feature is seen in both P^3 , which are worn down externally to 35 mm from the crown base. The protocone fold, which is preserved only in P^3 dext., is more marked than that in P^3 of dentition L13035. The postsinus is almost as deep as the medisinus; the ectoloph is just as flattened, with a weak cingulum, and the internal cingulum is just as prominent as that in P^3 of L13035. P^4 , present on both sides in L2519, is 45 mm high as worn externally, and the right specimen has an imperfectly formed medifossette, while the left has a bifid crochet and a small crista that do not join. There is no difference in depth between the postsinus and the medisinus, and the ectoloph and the internal cingulum are as in P^3 .

M^1 , on both sides, has a particularly powerful crochet, nearly twice as thick as that in M^1 of L13035, but no crista. The external crown height is 35 mm, as worn. In addition to the anterior protocone fold there is an internal indenta-

tion in the protocone as seen in M^1 sin. The posterior bulging of the protocone is such that it forms three-fifths of the internal crown face. There is a distinct hypocone fold, visible in both the right and the left molar. The internal cingulum is not preserved in these molars but externally there is a very weak cingulum, mainly posteriorly, as in all the molars. The ectoloph is flattened, and the narrow postsinus appears to be slightly less deep than the medisinus.

The M^2 dext. of L2519, 50 mm high as worn, has a crochet that is not thickened; it is recurved outward at the apex but the crista is just barely indicated and no medifossette is formed. The posterior bulging of the protocone is such that it occupies 27 out of the 45 mm long internal basal anteroposterior diameter. The lingual entrance to the medisinus is V-shaped, and the protocone is indented lingually. The portion of the crown that would have shown the protocone fold is missing; the hypocone fold is weakly developed, and so is the internal cingulum; the ectoloph is flattened, without styles. The two sinuses are equally deep.

M^3 dext. of L2519 lacks most of the outer surface (ecto-metaloph) so that no measurements can be given. It has a crown height as worn of about 60 mm. There is a very marked protocone fold, and a weak cingulum on the depressed internal surface of the protocone. The crochet is well-developed and there is a crista, too. These projections, however, remain separate down to the bottom of the medisinus. On this rather worn molar there is no trace of a paracone style such as we see on less worn specimens; the paracone style is no longer visible in the basal 50–60 mm of the crown.

The next upper dentition to be described is L13747 (Pl. 23). Of this set of teeth the small anterior premolar P^1 , or a persisting DM^1 , is preserved on the right side, as the teeth are still *in situ* in the maxillary. It is about 23 mm anteroposteriorly, and about 20 mm transversely; nothing can be said about its structure as the crown is worn flat.

P^2 is nearly entire on both sides. Although the worn crown height is the same as that in P^2 of L2519 (20 mm) the valley between protocone and hypocone is closed as wear has reached the bottom of the sinus in between. There is a rather strong internal cingulum, and a pit is formed between it and the joint bases of proto- and hypocone, as in P^2 of L13035. Postsinus and medisinus are of equal depth. There is a crochet but no crista.

P^3 lacks the entire outer surface on the left side, and has only the antero-external angle on the right. The protocone fold is weakly developed. The internal cingulum is very marked, continuous with that on the anterior surface, and it carries a series of tubercles. It extends all along the protocone, reaching its lowest point at the narrow medisinus entrance, and rises along the hypocone, i.e. the same development that we noticed in the premolars of the two upper dentitions dealt with above. There is only a crochet, which is not very prominent, making the central portion of the medisinus rather wide. The depth of this portion of the medisinus is the same as that of the postsinus.

P⁴, the worn ectoloph height of which is 40 mm, is rather damaged on the left but well preserved on the right side. There is a paracone style, which is rather more developed than that in the less worn dentitions L13035 and L2519; in these teeth there is no trace left of the paracone style, but in L13747 it continues to about 20 mm from the crown base. There is a weak external cingulum along the posterior moiety of the ectoloph. The posterior bulging of the protocone occupies three-fifths of the internal surface of the crown. The internal cingulum is less developed, and the crochet more prominent than that in P³. The protocone fold is hardly shown. The medisinus is as deep as the postsinus and has a narrow, V-shaped entrance.

M¹, which is between 20 and 25 mm in worn ectoloph height, has the protocone fold well marked. The protocone takes up 30 out of the 50 mm of internal anteroposterior crown diameter, and is slightly indented internally. The bottom of the narrow internal medisinus entrance is almost reached by wear, but its central portion is still about 15 mm deep, which is also the depth of the postsinus. The very thick crochet is free from the ectoloph at the level of wear. In M¹ dext. it would have closed off a medifossette with the small crista if wear had proceeded some 5 mm more, but in M¹ sin. no medifossette would have been formed in this way. In this advanced stage of wear no trace remains of the paracone style; the internal cingulum is so weak as to be practically absent.

M² is 40 mm high at the worn ectoloph. M² dext. has a vertical fracture in the ectoloph, but the external surface of M² sin. is undamaged although detached from the remainder of the crown. The paracone style is shown as a weak bulge only along the worn edge of the crown. The protocone fold is very distinct, and the internal indentation of the protocone shows just as it does in the M¹. The protocone occupies 40 out of the 65 mm of internal anteroposterior crown diameter. The crochet is narrower than that in M¹ and does remain free at its apex so that no medifossette is formed. There is hardly any trace of an internal cingulum.

M³, incomplete on both sides, has the external surface worn down to 50 mm; the paracone style is shown only in the apical 15 mm. The anterior fold, internal indentation, and posterior bulging of the protocone are as in M². The crochet extends all across the medisinus but does not close off a medifossette.

Whereas the two dentitions first described (L13035 and L2519) are rather similar in dimensions (see Table 1) dentition L13747 is larger, but there are no significant differences in structure. The only point worth making is that the paracone style is slightly more marked in these large teeth than in those earlier described.

A crushed skull, L6658, has a good portion of the palate with P⁴-M² dext. and P²-M² sin., and the two last molars detached (Pl. 24). The dental dimensions are more or less intermediate between those of L2519 and L13747

(Table 1). There is a small portion of the anteriormost premolar, on the left side. P² sin. is incomplete internally and much worn down: the ectoloph height is reduced to 15 mm, and the medisinus is cut off from the lingual border. There is a tiny medifossette, which would have disappeared with a little more wear. P³ sin. has a medifossette too; its external height as worn is almost 30 mm, and no paracone style is shown. The medisinus is just closed off lingually. The internal cingulum, with its lowest point at the junction of protocone and hypocone, is well developed. It is slightly less marked in P⁴, present on both sides, with a worn ectoloph height of 40 mm. The crochet is bifid in P⁴ dext., and single in P⁴ sin. The premolars P³ and P⁴ agree in the postsinus being as deep as the medisinus, the posterior bulging of the protocone forming three-fifths of the internal surface (21 out of 35 mm in P³, and 27 out of 45 mm in P⁴), and in their weak protocone folds.

M¹, lacking the antero-external angle on both sides, is some 25 mm high as worn externally. The protocone fold is very marked, and there is an internal indentation in the protocone, which occupies three-fifths of the internal border. The lingual cingulum is weakly developed, the lingual medisinus entrance very narrow, and the crochet is rather thick, as usual in first molars. M², the right of which is partially embedded in the bone, has a worn ectoloph height of 45 mm, and does not show the paracone style any more. The characters are those of M¹; only the crochet is more slender. The M³, of which the left is virtually complete, is 60 mm high as worn externally. The paracone style can be traced in the apical 15–20 mm only. The crochet extends all across the medisinus, and joins the posterior wall of the protoloph, thus cutting off the external portion of the medisinus. The protocone fold is strongly marked, the internal cingulum very weak.

TABLE I

Measurements of upper teeth of *Ceratotherium praecox* from Langebaanweg (mm)

No. of specimen	L13035	L2519	L13747	L6658
P ² , ant.post.	c. 35	33	36	32
ant.transv.	—	40	44	37
post.transv.	c. 45	—	50	40+
P ³ , ant.post.	45	46	—	43
ant.transv.	58	57	66	62
post.transv.	54	—	—	58
P ⁴ , ant.post.	48	51	53	50
ant.transv.	—	65	75	67
post.transv.	—	60	73	63
M ¹ , ant.post.	—	58	c. 60	57
ant.transv.	70	70	80	73
post.transv.	64	c. 64	72	—
M ² , ant.post.	62	64	68	64
ant.transv.	72	72	82	74
post.transv.	67	65	c. 70	69
M ³ , ant.post.(int.)	65	—	67	66
ant.transv.	72	—	78	73
length outer surface	c. 75	—	79	83
Length P ² –M ³	c. 300	c. 300	330	305
Length P ² –P ⁴	c. 135	130	135	125
Length P ⁴ –M ³	c. 230	c. 225	245	235

To dentition L13035 belongs a skull portion, giving a zygomatic width of 390 mm, very near to the maximum, observed by Heller (1913) in modern *Ceratotherium simum*, viz., 384 mm. The length from M^3 to the back of the postglenoid process is *c.* 220 mm, slightly less than the length P^4-M^3 (*c.* 230 mm). In subadult skulls of *C. simum* in which M^3 has not erupted yet the length P^4-M^3 exceeds the postdental length from M^3 to the back of the postglenoid process (e.g., S.A.M. 21381: P^4-M^3 *c.* 225 mm; postdental length *c.* 190 mm). In skulls with M^3 slightly worn the two lengths are subequal (S.A.M. 21382: P^4-M^3 215 mm; postdental length 200 mm; S.A.M. 21379: P^4-M^3 225 mm; postdental length 210 mm). In fully adult *C. simum* skulls with M^3 well worn down the length P^4-M^3 is exceeded by the postdental length (M.C.Z., Dept Mamm. 24917 and 34850: P^4-M^3 190–205 mm; postdental length 270–275 mm). In the holotype skull of *Ceratotherium praecox* from Kanapoi, which is quite adult, the postdental length is the larger of the two, though not to the extent seen in the recent species (Kanapoi P^4-M^3 205 mm; postdental length 230–250 mm).

The premaxillaries of L13747 are preserved, and they show two alveoli on each side, one behind the other. The anterior alveolus holds a tooth crown that is unerupted, about 12 mm anteroposteriorly and 9 mm transversely. The posterior alveolus is of the same size but empty; its depth is only 7 mm. The specimens are shown in Plate 28, top. The occurrence of rudimentary upper incisors in *C. praecox* is interesting, as the recent species of *Ceratotherium* no longer shows them. An isolated I^1 has a rounded crown and a strong, posteriorly recurved root. The height of the crown and root combined is 37 mm, while the crown diameter is 11 mm (Pl. 28, top right).

The nasal horn boss of L6658 is crushed, but its width is about 180 mm. The nasal portion of another skull, L2520, is 180 mm wide at the horn boss; this width is 170–208 mm in adult males, and 146–173 mm in adult females of recent *Ceratotherium simum* (Heller 1913). The frontal region of the skull L2520 shows the second horn boss, on the frontals, but the upper borders of the orbits are not preserved. Dorsal views of skulls L2520 and L6658 are given in Plate 27.

Skull L13747 is broken in many pieces; the right half of the top of the skull has been reassembled (Pl. 26). Although the angle between the dorsal and the occipital planes cannot be exactly measured it is approximately 60° . This is 65° in skull K.N.M. KP30 from Kanapoi, against $65-80^\circ$ in *Diceros bicornis*, and $45-50^\circ$ in *Ceratotherium simum*. These figures tend to show that in the fossil *C. praecox* the occiput is less posteriorly inclined relative to the dorsal surface than in *C. simum*, and rather resembles *D. bicornis* in this respect. In keeping with the less marked posterior inclination of the occiput, the nuchal crest in *C. praecox* is not as thickened as it is in modern *C. simum*, in which it is quite massive, overhanging the occipital condyles.

The mandible L13035 is nearly entire, lacking only part of the ventral border of the left horizontal ramus and the right coronoid process (Pl. 30).

P₃-M₃ dext. and P₂-M₃ sin. are in situ; an internal view of the right ramus is given in Plate 31. Mandible L11849 has the symphysis as well as P₂-M₃ dext., somewhat more worn than L13035 (Pl. 32, right). There is further a symphyisial portion of the mandible, L6058, with the alveoli for P₂ (Pl. 33). There appear to be small alveoli for incisors in the symphyses examined, but none of these elements has been found. The premolars and molars of the Langebaanweg *Ceratotherium* do not show the tendency toward obliqueness of the lophids, or that toward fossettoid formation seen in *Ceratotherium simum*.

The length of the mandible, L13035, is 570 mm; this measurement is 565-635 mm in adult males, and 550-588 mm in adult females of recent *C. simum* (Heller 1913). The length of the symphysis is 125 mm in L13035 and 145 mm in L11849; 129-155 mm in adult males, and 128-147 mm in adult females of *C. simum*. The fossil specimens agree with the recent in both length measurements. However, the width at the symphysis is 60 mm in L11849 and 65 mm in L6058, which is decidedly less than that in recent males (96-125 mm) and females (91-111 mm) of *C. simum* (Heller 1913). It follows from this that in *C. praecox* the symphysis is relatively (and absolutely) narrower than in *C. simum*. It is in *D. bicornis* that we find such a narrow symphysis: S.A.M. 35658 has a length of symphysis of 105 mm by a width at symphysis of only 45 mm.

In the height at M₁, 125 mm, the fossil mandible L13035 equals *C. simum* (S.A.M. 21379), whereas in *D. bicornis* (S.A.M. 35658) this height is only 85 mm. The distance from the dental foramen to the base of the posteromedial articular surface is 160 mm in L13035, against 230 mm in *C. simum* and 135 mm in *D. bicornis*; the jaw orientation in the fossil was evidently nearer to that in *D. bicornis* than to that in *C. simum*. The condyles in L13035 are not entire, but the condylar area appears to be more massive, and wider below the condyle than in *C. simum*. The medial surface below the condyle is more hollowed than in either of the two living species. These are also the characters of the Kanapoi *C. praecox*.

TABLE 2
Measurements of lower teeth of *Ceratotherium praecox* (mm)

No. of specimen	L13035	L11849		L13035	L11849
P ₂ , ant.post.	30	—	M ₁ , ant.post.	(54)	—
ant.transv.	15	17	ant.transv.	32	35
post.transv.	17	17	post.transv.	32	37
P ₃ , ant.post.	—	—	M ₂ , ant.post.	63	56
ant.transv.	—	24	ant.transv.	36	37
post.transv.	27	—	post.transv.	34	37
P ₄ , ant.post.	48	45	M ₃ , ant.post.	c. 64	60
ant.transv.	30	31	ant.transv.	35	35
post.transv.	32	32	post.transv.	32	34
			Length P ₂ -M ₃	290	290
			Length M ₁ -M ₃	175	170

Dental measurements of the two mandibles are given in Table 2. Isolated lower teeth to be recorded further on considerably expand the variation ranges in size.

Among the isolated teeth from Langebaanweg there are a few unworn or very slightly worn crowns showing the degree of hypsodonty; these will be mentioned in the following pages.

An unworn P⁴ sin., L13760 (Pl. 25, bottom left) has an ectoloph height of 90 mm by a greatest anteroposterior length of the ectoloph, in the apical third of the crown, of 55 mm, which gives a height/length index of 164. An unworn recent P⁴ of *Diceros bicornis* (Leiden Museum, cat.ost.e) has the same greatest ectoloph length by an ectoloph height of 80 mm, giving a height/length index of 145. On the other hand, an unworn P⁴ of recent *Ceratotherium simum* (S.A.M. 21382) has an ectoloph height of 103 mm by a greatest anteroposterior ectoloph length of 46 mm, giving a height/length index of 224.

Among the last upper molars in particular there are several nearly unworn crowns, as follows: an M³ dext., L6696 (Pl. 25, middle), an M³ sin., L7106, of the same individual; an M³ dext., L6291 (Pl. 25, middle), an M³ sin., L6461, of the same individual as L6291; an unworn M³ dext., L6638, incomplete basally and a very slightly worn M² sin., L6636. In L6696 the total height of the outer surface is 94 mm by a length of the outer surface of 78 mm, giving a height/length index of 121. The paracone style is a narrow ridge, which fades away in the basal 35 mm of the ectoloph. L6291 has a height of the outer surface of 85 mm; the length of the outer surface is 70 mm, giving a height/length index of 121. Finally, L6638 has a height of the outer surface of 96 mm by a length of this surface of approximately 80 mm; height/length index *c.*120. This is just about the height/length index of M³ in modern *Diceros bicornis* (outer surface height 64 mm, outer surface length 54 mm, height/length index 119: Hooijer 1969: 87), but the Pleistocene *Diceros bicornis* from the Omo Beds is lower-crowned than the living form (two specimens of M³, height of unworn outer surface 56–59 mm, length of outer surface 55–58 mm, height/length index 102: Hooijer 1969: 87). In modern *Ceratotherium simum* M³ is 120–130 mm high (Dietrich 1945: 59), and a slightly worn recent M³ (S.A.M. 21379) is 100 mm high at the outer surface, while an unworn recent M³ (S.A.M. 21382), the outer surface of which is not quite fully calcified at base, is just over 100 mm high at the incompletely formed external surface. In these recent M³ there is no paracone style but a depression behind the parastyle instead.

The M² from Langebaanweg, L6636, slightly worn, has an ectoloph height at the metaloph origin of 98 mm by a greatest anteroposterior ectoloph length of 73 mm; its height/length index is 134. The hypsodonty of *Ceratotherium praecox* M² has already been demonstrated in a slightly worn M² from Lothagam-1 (K.N.M. LT89 in Hooijer & Patterson 1972) that has an ectoloph height at the metaloph origin of 74 mm by a greatest anteroposterior ectoloph length of 63 mm, giving a height/length index of 117. In modern *Diceros bicornis* M² (two specimens) the ectoloph is not so much higher than wide, although the difference is small: M.C.Z., Dept Mamm., no. 51479, height at metaloph origin 56 mm, length 54 mm, height/length index 104, and Leiden Museum, cat.ost.b, height 74 mm, length 68 mm, height/length index 109.

Since the Omo M³ of *Diceros bicornis* (Pleistocene) is less hypsodont than the modern M³, the same doubtless holds for the M². In the fossil M² from Langebaanweg the paracone style is present on the apical half of the crown only.

There are two very slightly worn P₄ in the Langebaanweg collection, L5356 and L6693, both from the right side. They are rather similar in dimensions (Table 3), and intermediate in height/length indices between recent *Diceros bicornis* (first column) and recent *Ceratotherium simum* (last column of Table 3). The discrepancy in height/length indices is the same as that found in P⁴.

TABLE 3
Measurements of P₄ in *Diceros* and *Ceratotherium* (mm)

No. of specimen	<i>D. bicornis</i>	<i>Ceratotherium praecox</i>		<i>C. simum</i>
	L.M.cat.e	L5356	L6693	S.A.M.21382
Greatest length of outer surface	44	49	48	47
Height of metalophid	63	74	70	94
Height of hypolophid (b)	55	68	65	88
Height/length index (a)	143	151	146	200
Height/length index (b)	125	139	135	187

Four isolated lower molars, either M₁ or M₂, are unworn or very slightly worn. These are L6667 and L2526, from the right side, and L6664 and L6680, from the left. The height of the anterior (meta-) lophid, taken from the external base of the crown, varies from 70 to 80 mm; the hypolophid height varies between the same limits. Unworn M₁₋₂ of recent *D. bicornis* are c. 55 to 65 mm high, and those of *C. simum* c. 80 to 100 mm.

The isolated upper premolars and molars from Langebaanweg are enumerated in the tables that follow.

Of P² we have nine specimens (Table 4) the first three of which are from the right side, the others from the left. There is a double crochet in L6649, a medifossette in L6751, L4750, and L6648, while a bifid crochet is shown in L6623.

TABLE 4
Measurements of P² of *Ceratotherium praecox* (mm)

No. of specimen	L6649	L6751	L4750	L6648	L9124	L11957
Ant.post.	38	c. 34	35	—	34	c. 40
Ant.transv.	41	40	42	39	44	39
Post.transv.	40	—	46	41	45	40
No. of specimen	L6623	L6629	L9129			
Ant.post.	c. 37	c. 34	c. 40			
Ant.transv.	38	37	44			
Post.transv.	41	41	46			

P³ is represented by nineteen specimens (Table 5) the first eight of which are from the right side, the others (starting with L11801) from the left. In L6630 there is seen a slender crista extending to the tip of the crochet; the internal cingulum is rather weak in this specimen as well as in L6627. L6625 and L5665 have a bifid crochet, L5665 has in addition a very small crista.

TABLE 5

Measurements of P³ of *Ceratotherium praecox* (mm)

No. of specimen	L6629	L6630	L6631	L5444	L6625	L6295	L6646
Ant.post.	48	c. 50	47	40	43	40	c. 45
Ant.transv.	65	c. 67	64	59	60	60	62
Post.transv.	58	—	56	52	55	57	58
No. of specimen	L13765	L11801	L6639	L11996	L6627	L5695	
Ant.post.	45	45	43	—	47	44	
Ant.transv.	58	64	62	60	68	61	
Post.transv.	51	57	58	56	61	58	
No. of specimen	L5671	L9114	L5451	L6640	L5665	L13099	Aterir
Ant.post.	45	—	50	46	48	44	45
Ant.transv.	60	64	66	63	65	61	58
Post.transv.	54	58	63	57	59	56	54

There are twenty specimens of P⁴ (Table 6) the first eleven of which are from the right side, the others (from L11132 onward) from the left. L2525 has a crista joining the crochet. L11132 belongs to the same individual as L11121, has a double crochet the lateral part of which is joined to a crista, thus forming a medifossette (Pl. 29, bottom). L6655, slightly worn, shows a double crochet and a crista (Pl. 29, bottom). L13760 shows the full height of the ectoloph, with a height/length index of 164 (Pl. 25, bottom left). Medifossette formation is very rare in P⁴ and M¹⁻², one in twenty or three in forty Langebaanweg teeth.

TABLE 6

Measurements of P⁴ of *Ceratotherium praecox* (mm)

No. of specimen	L6717	L2525	L6652	L6299	L11167	L6619	L6635
Ant.post.	51	54	49	49	51	50	50
Ant.transv.	70	74	70	70	75	71	76
Post.transv.	63	69	61	61	67	61	70
No. of specimen	L6739	L5696	L3454	L11121	L11132	L6618	
Ant.post.	c. 57	51	47	48	48	c. 52	
Ant.transv.	75	69	67	68	68	71	
Post.transv.	64	63	56	62	62	66	
No. of specimen	L6632	L6296	L4612	L6622	L13760	L13099	
Ant.post.	—	48	50	c. 50	47	48	
Ant.transv.	69	70	71	68	68	64	
Post.transv.	63	64	68	63	62	60	

TABLE 7

Measurements of M¹ of *Ceratotherium praecox* (mm)

No. of specimen	L6626	L6624	L6703	L5445	L9113	L6628	L11798
Ant.post.	58	55	—	57	60	52	55
Ant.transv.	73	72	73	72	74	71	72
Post.transv.	68	67	66	65	65	63	67
No. of specimen	L5912	L6293	L12039	L5311	L6647	L5418	L6621
Ant.post.	55	—	c. 52	56	56	61	—
Ant.transv.	68	67	66	69	73	72	75
Post.transv.	65	60	61	65	68	68	—
No. of specimen	L6465	L4749	L5919				
Ant.post.	c. 53	54	58				
Ant.transv.	69	70	70				
Post.transv.	66	61	65				

M¹ is represented by seventeen specimens (Table 7) the first eight of which are from the right side, the left specimens beginning with L6293. Medifossettes are not formed; L6626 has a double crochet (Pl. 28, bottom right).

There are twenty-four specimens of M² (Table 8) the first ten of which are from the right side, the remaining specimens (starting with L6636) from the left. A true medifossette, formed by the union of crochet and crista, is shown only in L9116, L5916 (external surface broken off: Pl. 28), and L10983. A small crista is seen in L5917, L6617 (in which the crochet makes a contact with a small projection on the posterior face of the ectoloph: Pl. 28), L6746, L6654, L6641, L6644A, and L12360. L9118 consists of ectoloph and crochet only; the crista is in contact with the crochet apically (Pl. 29). L6636 is the specimen with the ectoloph slightly worn, and a height/length index of 134, already referred to above.

TABLE 8

Measurements of M ² of <i>Ceratotherium praecox</i> (mm)								
No. of specimen	L5917	L6617	L6694	L9116	L6631	L6634	L5911	L6746
Ant.post.	c. 50	67	c. 62	62	c. 60	61	63	c. 64
Ant.transv.	75	82	82	75	79	77	79	74
Post.transv.	68	75	69	73	71	72	—	—
No. of specimen	L6637	L6643	L6636	L5916	L9118	L6654	L6645	L10983
Ant.post.	—	—	c. 60	—	—	c. 55	56	55
Ant.transv.	80	80	73	—	—	76	78	71
Post.transv.	72	73	66	—	—	68	67	67
No. of specimen	L6644B	L6654	L6641	L6644A	L11898	L12360	L6653	L9115
Ant.post.	c. 62	63	67	65	65	c. 55	c. 55	—
Ant.transv.	74	70	75	79	77	73	71	77
Post.transv.	67	65	67	72	68	70	65	68

We have seventeen specimens of M³ (Table 9) the first ten of which are from the right side, the remaining (to begin with L7106) from the left. L6696 is a slightly worn specimen with a height/length index of 121 (Pl. 25); L6291 is a somewhat smaller specimen likewise slightly worn and with the same index (Pl. 25). The left M³ L7106 belongs to the same individual as L6696, and the left M³ L6461 belongs to the same individual as L6291. The specimen L6638 is unworn but incomplete at the base of the crown; its height/length index is c. 120.

TABLE 9

Measurements of M ³ of <i>Ceratotherium praecox</i> (mm)							
No. of specimen	L6696	L6291	L6638	L6294	L6620	L5666	L10984
Ant.post. (int.)	66	58	c. 65	56	58	61	61
Ant.transv.	71	65	75	68	69	74	66
Length outer surf.	78	70	c. 80	78	75	75	70
No. of specimen	L6641	L6290	L11997	L7106	L6461	L13614	
Ant.post. (int.)	64	61	72	—	58	60	
Ant.transv.	71	75	75	—	65	73	
Length outer surf.	76	81	80	78	c. 70	72	
No. of specimen	L6289	L6642	L11091	L6466			
Ant.post. (int.)	60	57	58	66			
Ant.transv.	67	69	69	72			
Length outer surf.	75	73	68	74			

These specimens have already been referred to above. L6294 has a crochet extending all across the medisinus; L6641 and L11997 have a very large crochet, and L10984 has a small crista and an internal projection at the base of the crochet.

Some of the remaining lower cheek teeth are *in situ* in incomplete mandibles, as follows: L6615, a right mandibular ramus, has the posterior portion of P₄ and the three molars; the lengths are reduced as a result of interproximal wear, their transverse diameters slightly exceed those in L13035 and L11849 (Table 2), and the height at M₁ is 130 mm. P₂-M₂ sin. and P₂-P₄ dext. of one and the same individual, L6659, are narrower-crowned, as are those recorded in Table 2. A right and a left mandibular ramus with the much worn M₁-M₃ on either side (L6612, L6614), give an M₁-M₃ length shorter than that in the less worn dentitions. The height of the ramus at M₁ is 125 mm. L6793 is a right mandibular ramus with P₂-M₂; L11989 is a right ramus fragment with M₁, M₂, and part of M₃. Two parts of right rami, L13759 and L13805, have M₂, and M₃, respectively, *in situ*. The measurements of these teeth are given in Table 10.

TABLE 10
Measurements of lower teeth of *Ceratotherium praecox* (mm)

No. of specimen	L6615	L6659	L6612	L6793	L11989	L13759 L13805
P ₂ , ant.post.	—	—	—	—	—	—
ant.transv.	—	18	—	—	—	—
post.transv.	—	20	—	—	—	—
P ₃ , ant.post.	—	(47)	—	—	—	—
ant.transv.	—	24	—	—	—	—
post.transv.	—	28	—	—	—	—
P ₄ , ant.post.	—	52	—	(43)	—	—
ant.transv.	—	29	—	31	—	—
post.transv.	—	31	—	—	—	—
M ₁ , ant.post.	(40)	57	(44)	—	55	—
ant.transv.	37	32	37	—	35	—
post.transv.	—	34	36	—	—	—
M ₂ , ant.post.	(51)	65	(52)	(54)	59	—
ant.transv.	38	—	37	37	37	36
post.transv.	—	—	39	37	38	37
M ₃ , ant.post.	59	—	58	—	—	63
ant.transv.	38	—	—	—	—	37
post.transv.	38	—	35	—	—	38
Length M ₁ -M ₃	160	—	150	—	—	—

There are seven isolated specimens of P₂ (Table 11) the first four of which are from the right side. The first and the last specimen are decidedly larger than the P₂ in the two mandibles of Table 2.

TABLE 11
Measurements of P₂ of *Ceratotherium praecox* (mm)

No. of specimen	L11812	L6684	L6676	L11999	L11959	L6665	L11815
Ant.post.	33	(30)	—	(27)	30	32	34
Ant.transv.	20	18	17	17	18	17	21
Post.transv.	23	23	21	18	20	18	23

There are ten isolated specimens of P_3 (Table 12) the first three of which are from the right side.

TABLE 12
Measurements of P_3 of *Ceratotherium praecox* (mm)

No. of specimen	L12107	L11810	L6671	L6681	L6669	L11811
Ant.post.	(40)	(44)	(41)	48	(45)	(38)
Ant.transv.	25	27	24	25	28	24
Post.transv.	28	30	31	26	28	26
No. of specimen	L2525	L5698	L11809	L5697		
Ant. post.	(42)	(42)	(43)	50		
Ant.transv.	25	24	27	27		
Post.transv.	30	28	30	28		

P_4 is represented by eight specimens (Table 13) the first two of which are from the right side. L6687, L12108, and L11804 are larger, especially wider, than their homologues in the dentitions of Tables 2 and 10.

TABLE 13
Measurements of P_4 of *Ceratotherium praecox* (mm)

No. of specimen	L6687	L12108	L11804	L11816	L6762
Ant.post.	49	53	51	(45)	50
Ant.transv.	33	33	33	30	29
Post.transv.	34	34	37	31	31
No. of specimen	L6670	L4751	L6662		
Ant.post.	(47)	55	(49)		
Ant.transv.	28	—	31		
Post.transv.	35	31	33		

Fourteen isolated lower molars represent either M_1 or M_2 (Table 14); the first eight are from the right side, the remaining six (beginning with L6672) from the left.

TABLE 14
Measurements of M_1 and M_2 of *Ceratotherium praecox* (mm)

No. of specimen	L6678	L6679	L2525	L6690	L6302	L5690	L11894
Ant.post.	(56)	58	60	(57)	60	65	(50)
Ant.transv.	34	30	31	34	35	34	37
Post.transv.	35	33	33	35	34	34	37
No. of specimen	L6677	L6672	L4752	L9126	L5669	L6689	L13390
Ant.post.	62	60	—	60	(55)	(49)	65
Ant.transv.	38	37	38	38	38	35	38
Post.transv.	36	39	35	37	37	37	36

The last lower molar, M_3 , is easily distinguishable from M_1 or M_2 by its reduced posterior cingulum; in well-worn specimens the absence of a posterior pressure scar of course is characteristic for M_3 . There are eight isolated M_3 (Table 15) the first two of which are from the right side.

TABLE 15
Measurements of M_3 of *Ceratotherium praecox* (mm)

No. of specimen	L5667	L11802	L6613	L11989	L9609	L9125	L9110	L9120
Ant.post.	68	66	(55)	65	67	65	65	(57)
Ant.transv.	38	40	37	42	41	39	36	36
Post.transv.	34	37	36	37	35	34	34	34

In Tables 10 to 15, inclusive, the anteroposterior diameter is in parentheses when it is much reduced because of interproximal wear.

There are a number of teeth belonging to the milk dentition of *Ceratotherium praecox*. Deciduous teeth were not present among the material of this species described from Kanapoi, Lothagam-1 and Ekora (Hooijer & Patterson 1972). Therefore, the Langebaanweg milk teeth are compared below with those of the two living African species. The differential characters of the milk molars of *Diceros bicornis* and *Ceratotherium simum* are recorded in Hooijer (1959). In a collection from Late Pleistocene sites near Swartklip, Cape Province, reported upon by Hendey & Hendey (1968), there are milk molars of *C. simum*, which have been used for comparison.

The maxillary milk dentition of *Ceratotherium praecox* comprises two isolated and much worn DM¹, both from the left side, L6674 and L6675, measuring 22 mm anteroposteriorly and 23 mm transversely. In *C. simum* DM¹ is more elongated anteroposteriorly than in *D. bicornis* because of the greater forward projection of the parastyle in the former, but this character is lost in much worn specimens like those from Langebaanweg and a distinction cannot be made at this stage of wear.

Of DM² there are two specimens in the Langebaanweg collection, L4608 (Pl. 29) and L5664, both from the left side. DM³ is represented only by a single specimen, L9105B (Pl. 29), from the left side and lacking most of the ectoloph. Finally, of the last upper milk molar, DM⁴, we have three specimens, one right lacking the outer surface, L6727, one entire left DM⁴, L13818, and another left specimen, much worn down, L6651 (Pl. 29). The upper milk molars in *C. simum* are distinguished from those in *D. bicornis* by the more prominent parastyle, suppression of paracone style, greater crown height, absence of inner cingula, stronger crista joining the crochet and forming a medifossette, and the postsinus being approximately as deep as the medisinus instead of shallower. The inner portion of the protoloph is more distinctly curved backward in *C. simum* than in *D. bicornis*, but this difference is more marked in the posterior milk molars than in DM², in which it is not or hardly evident. Upper milk dentitions of *C. simum* and of *D. bicornis* have been described from the Early Pleistocene Makapansgat caves (Hooijer 1959); they tend to be on the large side but otherwise indistinguishable from their recent homologues. Variation ranges in dimensions of the milk teeth of the recent species are presented in Table 16 along with the measurements of the Langebaanweg specimens and those from Swartklip in the South African Museum; the Swartklip specimens conform to those of *C. simum* in every respect (they bear catalogue numbers preceded by ZW).

The DM² of *Ceratotherium praecox*, L4608, has a prominent parastyle as in *C. simum* but has an internal cingulum along the protocone, as in *D. bicornis*. There is a tubercle at the medisinus entrance that is absent in L5664; both specimens have a well-developed crista joining the crochet and forming a

medifossette. The postsinus is almost as deep as the medisinus; these are, again, *C. simum* characters.

TABLE 16

Measurements of upper milk molars of *C. praecox* and recent species (mm)

DM ² , no. of specimen	L4608	L5664	<i>D. bicornis</i>	<i>C. simum</i>	ZW192	ZW2610
Greatest length ectoloph	42	—	38-41	41-51	41	42
Antero-transverse	37	35+	33-39	36-41	36	34
Postero-transverse	42	38+	35-40	35-43	—	33
DM ³ , no. of specimen	L9105B	<i>D. bicornis</i>	<i>C. simum</i>	ZW1842		
Greatest length ectoloph	—	45-52	53-61	53		
Antero-transverse	—	40-50	46-48	46		
Postero-transverse	—	39-47	44-46	45		
DM ⁴ , no. of specimen	L13818	L6651	<i>D. bicornis</i>	<i>C. simum</i>		
Greatest length ectoloph	60	54+	50-55	66-68		
Antero-transverse	56	53	45-53	c. 54-55		
Postero-transverse	53	52	40-51	52-60		

L5664 is incomplete internally, but the minimal transverse diameters can be given. The Langebaanweg DM² tally well in size with those of *C. simum*. The two Swartklip specimens of DM², ZW192 and ZW2610, both from the right side, lack the internal cingulum, display well-formed medifossettes, and have the postsinus as deep as the medisinus, as in *C. simum* to which they belong. The same holds good for the Swartklip DM³, ZW1842, which is from the left side. In the Langebaanweg collection there is but one DM³, L9105B, wanting most of the ectoloph. There is a slender crista, not joining the crochet, hardly any trace of an inner cingulum (except at the medisinus entrance), but the postsinus is less deep than the medisinus, as in *D. bicornis*. No measurements can be given. Of DM⁴ we have three Langebaanweg specimens, one right, lacking the outer surface, and two from the left side, as listed above. The entire specimens show the absence of the paracone style, the formation of a medifossette, and the absence of an inner cingulum, as in *C. simum*, although the postsinus is decidedly less deep than the medisinus, as in *D. bicornis*. Thus, the *C. praecox* milk molars combine characters found in *C. simum* and *D. bicornis*, whereas in size they are intermediate between the two.

Of the mandibular milk dentition there are the following specimens: L6686, DM₂ dext., slightly worn; L9105C, DM₃ dext., unworn (Pl. 32), metalophid height 41 mm, and hypolophid height 38 mm; L6301, DM₃ dext., slightly worn; L9105A, DM₄ dext., unworn, metalophid height 50 mm, and hypolophid height 46 mm; L6689, DM₄ dext., much worn down; L6795, left ramus with incomplete DM₃₋₄; L6660, DM₄ dext. in ramus fragment, slightly worn (Pl. 32), crown not fully erupted, anteroposterior diameter 54 mm, as in L9105A; L2524, DM₄ sin. in ramus fragment, crown edge broken, lingual base not exposed; L12870 and L6757, both DM₄ sin., slightly worn.

As shown in Table 17, the Langebaanweg lower milk molars are larger than those in *D. bicornis*, as were the upper milk molars, but they correspond rather well with those from Swartklip, which represent *C. simum*. These Swartklip specimens are: ZW1837, DM₂₋₄ dext. in ramus fragment; ZW2036,

DM₂₋₃ dext.; ZW1867, DM₂ dext.; ZW1876, DM₃ dext., and ZW1966, DM₃ sin., unworn, metalophid height 45 mm, hypolophid height 42 mm. The DM₃ of *C. praecox* that is unworn, L9105C, has the anteroposterior diameter

TABLE 17
Measurements of lower milk molars of *C. praecox* and recent species (mm)

DM ₂ , no. of specimen	L6686				ZW 1837	ZW 2036	ZW 1867	<i>D. bicornis</i>
Ant.post.	41				40	40	39	27-33
Ant.transv.	16				16	—	—	13-15
Post.transv.	18				20	—	—	15-18
DM ₃ , no. of specimen	L9105	L6301	L6795		ZW 1837	ZW 1876	ZW 1966	<i>D. bicornis</i>
Ant.post.	48	46	c. 47		46	45	44	38-41
Ant.transv.	20	—	c. 23		22	—	22	19-20
Post.transv.	22	21	25		23	—	23	20-22
DM ₄ , no. of specimen	L9105	L6689	L12870	L6757	ZW 1837			<i>D. bicornis</i>
Ant.post.	54	(46)	51	51	48			41-45
Ant.transv.	23	23	25	25	—			22-23
Post.transv.	26	25	27	23+	—			23-25

longer than that in the unworn DM₃ of *C. simum*, ZW1966 (48 against 44 mm), whereas both in metalophid height and in hypolophid height L9105C is less than is ZW1966 (41 and 38 mm against 45 and 42 mm). It follows from this comparison that the milk tooth of *C. praecox* is less hypsodont than that of *C. simum*; we got the same result from the unworn permanent premolars and molars.

POSTCRANIAL SKELETON

The postcranial material, which is very abundant at the Langebaanweg 'E' Quarry, is listed in the tables of measurements that follow (18 through 50). Measurements of the bones of *D. bicornis* and *C. simum* have been given in previous papers (Hooijer & Singer 1960; Hooijer 1969) from skeletons in the South African Museum, Cape Town, and in the Osteology Department, National Museum Centre for Prehistory and Palaeontology, Nairobi, respectively. In both cases the *C. simum* skeleton is larger than that of *D. bicornis*, with more massive metapodials (higher width/length ratios), but other than that no skeletal differences between the two extant species are apparent. Most of the Langebaanweg bones are larger than their homologues even in *C. simum*.

Eleven proximal portions of scapulae are in the Langebaanweg collection (Table 18) the first five of which are from the right side.

TABLE 18
Measurements of scapula (mm)

No. of specimen	L8244	L11773	L11524	L8245
1. Ant.post. diameter of collum scapulae	135	—	—	c. 130
2. Ant.post. diameter over tuber scapulae and glenoid cavity	c. 170	155	—	c. 170
3. Ant.post. diameter of glenoid cavity	c. 110	c. 100	c. 110	c. 105
4. Transverse diameter of idem	c. 95	c. 90	95	95
5. Transverse diameter of tuber scapulae	—	55	—	60

No. of specimen	L8306	L13857	L8288	L8287	L8290	L8266	L13779
1.	—	125	120	130	125	—	135
2.	—	165	c. 155	165	165	165	175
3.	c. 105	105	c. 100	105	105	105	—
4.	95	c. 90	c. 90	100	—	—	—
5.	—	65	65	c. 60	c. 60	c. 70	—

No. of specimen	<i>D. bicornis</i>	<i>C. simum</i>
1.	100	130
2.	130	160
3.	85	105
4.	80	100
5.	45	60

The mid-portion of the shaft of a right humerus, L3421, has a width at the deltoid tuberosity of 170 mm, and a least width of 85 mm, as in *C. simum* (Hooijer 1969: 91). There are further only distal portions of the humerus, nine in all (Table 19) the first six of which are from the right side.

TABLE 19
Measurements of humerus (mm)

No. of specimen	L6886	L6977	L13559	L6947	L6878	L6899
1. Least width of shaft	90	80	c. 90	85	—	90
2. Greatest distal width	—	190	—	—	c. 180	c. 190
3. Width of trochlea	135	130	130	c. 130	125	125

No. of specimen	L3423	L6965	L13463	<i>D. bicornis</i>	<i>C. simum</i>
1.	80	—	80	60	70-85
2.	185	—	—	150-155	180
3.	120	125	—	100	120

A radio-ulna dext., L12818, is slightly damaged proximo-medially; the radius is longer than any of the fossil radii, four of which are nearly entire (Table 20); only the last specimen in this table, L4967, is from the left side.

TABLE 20
Measurements of radius (mm)

No. of specimen	L12818	L7997	L6375	L8114
1. Median length	400	375	c. 370	385
2. Proximal width	—	125	130	130
3. Proximal ant.post. diameter (medial side)	—	80	85	85
4. Least width of shaft	75	75	70	70
5. Greatest distal width	120	120	115	—
6. Width distal articular surface	105	100	100	95

No. of specimen	L4967	<i>D. bicornis</i>	<i>C. simum</i>
1.	390	345-350	365-380
2.	135	100	120-125
3.	90	60	75
4.	75	45-55	65-70
5.	—	95	120
6.	105	80	100

There are twenty-one proximal portions of the radius (Table 21); the first seven are from the right side.

TABLE 21
Proximal measurements of radius (mm)

No. of specimen			L13175	L6371	L6370	L3425	L9981	L7983
2. Proximal width			135	130	125	125	120	c. 130
3. Proximal ant.post. diameter (medial side)			90	c. 80	80	85	c. 85	90
4. Least width of shaft			—	65	65	—	—	—
No. of specimen	L7934	L7968	L8017	L8007	L4205	L13845	L12888	
2.	130	—	125	c. 125	115	125	130	
3.	90	c. 95	80	—	85	85	90	
4.	—	—	—	65	70	65	70	
No. of specimen	L7986	L4959	L9978	L2229	L8015	L2289	L7958	L9988
2.	125	130	135	c. 125	125	125	125	c. 120
3.	80	85	c. 90	85	80	c. 80	c. 85	80
4.	75	70	80	70	—	—	—	—

Distal radius portions number thirty-three (Table 22), fifteen from the right and eighteen from the left side.

TABLE 22
Distal measurements of radius (mm)

No. of specimen	L6369	L6367	L7973	L6177	L4202	L13843	L5234
4. Least width of shaft	65	70	70	—	—	65	—
5. Greatest distal width	120	120	120	120	c. 115	c. 110	110
6. Width distal articular surface	100	105	105	110	95	90	95
No. of specimen	L9985	L7911	L8010	L7961	L6362	L6173	L3065
4.	—	—	—	—	—	—	—
5.	120	120	c. 115	120	120	c. 120	120
6.	100	105	105	105	100	105	100
No. of specimen	L5174	L8012	L13842	L2290	L2293	L2291	L9733
4.	—	70	70	70	65	65	65
5.	c. 120	110	c. 120	115	—	120	—
6.	95	90	105	105	100	100	90
No. of specimen	L9986	L4203	L9730	L6170	L4194	L6372	L3067
4.	—	—	—	—	—	—	—
5.	115	115	c. 115	110	c. 115	120	110
6.	105	100	100	95	100	100	100
No. of specimen	L7924	L8006	L4957	L7920	L4200		
4.	—	—	—	—	—		
5.	120	c. 105	110	110	115		
6.	95	100	90	90	100		

The ulna of the radio-ulna dext., L12818, is the only entire ulna in the Langebaanweg collection; it has a maximum length of 530 mm (*D. bicornis* 450 mm; *C. simum* 510 mm), and a length from the processus anconaeus (beak) to the extremity of the olecranon of 175 mm (*D. bicornis* 140 mm; *C. simum* 165 mm). Further measurements are given in Table 23. In this table, twenty proximal and distal ulna portions are listed; the first twelve are from the right side, the remaining eight (beginning with L8052) from the left.

TABLE 23
Measurements of ulna (mm)

No. of specimen	L12818	L8060	L13836	L8038	L8071	L8055	
1. Width at semilunar notch	—	—	c. 95	95	c. 105	105	
2. Greatest distal diameter	90	—	—	—	—	—	
3. Ant.post. diameter distal articular surface	60	—	—	—	—	—	
No. of specimen	L4210	L7984	L7959	L8029	L8025	L7985	L8041
1.	—	—	—	—	—	—	—
2.	85	c. 80	c. 80	c. 80	c. 70	85	—
3.	60	55	c. 50	55	55	55	55
No. of specimen	L8052	L13833	L9994	L6251	L13839	L12891	L3554
1.	105	110	105	105	—	—	—
2.	—	—	—	—	80	85	90
3.	—	—	—	—	60	60	60
No. of specimen	L7927	<i>D. bicornis</i>	<i>C. simum</i>				
1.	—	90	110				
2.	80	75	90				
3.	55	60	65				

There are twenty-six scaphoids (Table 24) the first ten of which are from the right side.

TABLE 24
Measurements of scaphoid (mm)

No. of specimen		L6010	L6012	L6003	L6009	L9477	
1. Posterior height		63	60	58	57	60	
2. Anterior height		58	60	59	59	61	
3. Proximal width		55	56	54	55	54	
4. Proximal ant.post. diameter		75	73	74	70	78	
5. Maximum diameter, distal facets		70	70	69	68	71	
No. of specimen	L11767	L7850	L11768	L5284	L9483	L13472	L6218
1.	63	60	65	62	60	66	62
2.	62	60	63	61	58	64	59
3.	55	61	57	60	53	55	61
4.	74	76	79	77	75	77	77
5.	75	77	75	79	75	73	75
No. of specimen	L7809	L6014	L6008	L7849	L5986	L3569	L7803
1.	60	67	60	63	67	63	65
2.	59	60	63	63	64	64	59
3.	55	60	57	58	60	55	57
4.	75	87	73	84	80	74	78
5.	75	78	72	75	77	74	76
No. of specimen	L7735	L7826	L4290	L13616	L7861	L7738	L5282
1.	66	65	61	64	64	67	57
2.	63	65	59	60	63	68	58
3.	60	60	56	55	59	59	54
4.	76	79	73	81	82	77	68
5.	73	75	69	75	80	77	68
No. of specimen		<i>D. bicornis</i>	<i>C. simum</i>				
1.		50	62				
2.		54-60	58-65				
3.		55	60				
4.		63	75				
5.		62-70	73-78				

Of the lunar there are thirty-six specimens (Table 25), and the first eighteen are from the right side.

TABLE 25
Measurements of lunar (mm)

No. of specimen	L4253	L12379	L6006	L7853	L7829	L7882	
1. Anterior height	64	61	65	69	61	61	
2. Proximal width	67	61	64	68	63	62	
3. Greatest ant.post. diameter	79	83	81	87	78	80	
No. of specimen	L5281	L4270	L3049	L4787A	L9475	L4287	L13828
1.	65	57	58	60	59	60	63
2.	68	58	66	58	61	60	60
3.	75+	72	76	78	78	77	77
No. of specimen	L5290	L13823	L7737	L7755	L5975	L13824	L12187
1.	62	62	58	64	59	66	63
2.	64	60	59	62	56	66	66
3.	79	78	76	80	75	78	82
No. of specimen	L11596	L7885	L7822	L7771	L13727	L9184	L9183
1.	66	58	61	60	58	63	62
2.	65	60	63	60	66	64	63
3.	86	76	76	78	76	83	81
No. of specimen	L5293	L11598	L7896	L4286	L5972	L7890	L9457
1.	60	58	64	63	61	65	66
2.	60	63	65	63	63	65	63
3.	75	75	80	81	79	78	82
No. of specimen	L3806	L7774	<i>D. bicornis</i>	<i>C. simum</i>			
1.	59	64	44-48	54-60			
2.	58	65	48	58-62			
3.	77	80	64-68	75			

Fifteen specimens of the cuneiform are in the Langebaanweg collection (Table 26), ten right and five left; L9465 is presented in anterior view in Pl. 33 (bottom).

TABLE 26
Measurements of cuneiform (mm)

No. of specimen		L12765	L3405	L5218	L4265	L5286	
1. Anterior height		57	51	52	47	61	
2. Distal width		56	48	46	49	51	
3. Proximal ant.post. diameter		51	47	44	43	46	
4. Greatest horizontal diameter		68	63	58	58	61	
No. of specimen	L7808	L7833	L7869	L7898	L13821	L9254	L7749
1.	55	53	56	57	56	45	59
2.	—	44	50	51	c. 47	43	50
3.	48	41	43	47	45	43	49
4.	61	56	61	64	60	57	64
No. of specimen	L3566	L9471	L9465	<i>D. bicornis</i>	<i>C. simum</i>		
1.	59	52	53	50	56-58		
2.	52	50	53	38-40	45-59		
3.	51	43	48	38-40	48-51		
4.	67	57	62	53	66		

Three pisiforms, one right, L6004, and two left, L7854 and L7892, are in the Langebaanweg collection (Table 27); L7892 is presented in anterior view in Plate 33 (bottom). The bones have the two facets, for ulna and cuneiform.

TABLE 27

Measurements of pisiform (mm)

No. of specimen	L6004	L7854	L7892	<i>D. bicornis</i>	<i>C. simum</i>
1. Length	71	72	67	61	60
2. Distal height	51	49	43	35	36

An exceptional bone is L7823, a cuneiform sin. with the pisiform completely ankylosed to it. The part representing the cuneiform is normal in shape, but it forms a solid mass with the pisiform, and the ulnar facets of the two bones are confluent (Pl. 33, middle). The greatest horizontal diameter of the anomalous bone is just over 110 mm (the distal extremity of the pisiform is incomplete). For comparison a cuneiform and a pisiform are figured along with the cuneipisiform (Pl. 33, bottom).

The trapezium, the radial of the distal row of carpal bones, with facets for the scaphoid and the trapezoid, is represented in the Langebaanweg collection by a single specimen, L3497; it is from the right side. In Table 28 the fossil bone is shown to be larger than its homologue in *C. simum*, as is usual for Langebaanweg bones.

TABLE 28

Measurements of trapezium (mm)

No. of specimen	L3497	<i>D. bicornis</i>	<i>C. simum</i>
1. Height	35	31	35
2. Proximal diameters	33 × 22	25 × 15	29 × 17

The trapezoid is represented in the Langebaanweg collection by five specimens, three from the right and two from the left side (Table 29).

TABLE 29

Measurements of trapezoid (mm)

No. of specimen	L7798	L11881	L13999	L4263	L4267	<i>D. bicornis</i>	<i>C. simum</i>
1. Anterior width	35	37	37	35	38	30	35
2. Anterior height	38	45	34	39	38	31	32
3. Posterior height	35	50	33	36	37	29	36
4. Ant.post. diameter	51	55	49	48	52	41	49

Of the magnum we have twenty-one specimens (Table 30) the first ten of which are from the right side.

TABLE 30
Measurements of magnum (mm)

No. of specimen			L7793	L4244	L12824	L4078	L5568
1. Anterior width			59	59	65	58	56
2. Anterior height			40	40	38	34	42
3. Proximal ant.post. diameter			83	80	83	68	76
4. Greatest diameter			103	104	115	c. 85	96
No. of specimen	L9473	L9460	L9459	L6013	L4264	L5184	L6217
1.	62	61	57	52	56	56	56
2.	38	45	41	38	40	40	41
3.	80	85	84	74	77	82	78
4.	—	—	—	—	—	105	107
No. of specimen	L7876	L5259	L7743	L11592	L9476	L4283	L7745
1.	59	c. 60	57	60	c. 55	54	57
2.	38	42	45	43	42	40	c. 40
3.	77	86	88	—	80	77	78
4.	94	105	112	101	101	—	—
No. of specimen	L7797	L7759	<i>D. bicornis</i>	<i>C. simum</i>			
1.	51	c. 55	44-49	57-58			
2.	34	40		38			
3.	77	82	63-67	70-71			
4.	—	—	77-85	84-85			

There are forty specimens of the unciform in the Langebaanweg collection (Table 31), twenty from the right, and the same number from the left side.

TABLE 31
Measurements of unciform (mm)

No. of specimen	L7762	L7812	L12824	L9193	L12766	L5262	L7747	
1. Anterior height	58	64	65	57	62	56	61	
2. Anterior width	81	87	83	77	81	75	83	
3. Greatest diameter	103	112	107	100	108	98	105	
No. of specimen	L11590	L6016	L4240	L9461	L9201	L6005	L7879	L11597
1.	62	62	55	60	56	55	63	61
2.	85	81	76	78	72	80	88	85
3.	111	105	102	100	98	96	c. 115	103
No. of specimen	L9456	L7855	L5260	L7870	L9184	L4076	L11097	L7837
1.	56	64	55	60	57	58	56	62
2.	72	87	73	77	75	83	75	83
3.	98	108	98	102	95	109	97	105
No. of specimen	L4285	L12826	L9468	L5973	L13829	L11591	L7840	
1.	57	61	60	54	58	63	58	
2.	76	79	81	76	83	91	85	
3.	100	105	102	96	108	112	110	
No. of specimen	L4789A	L4256	L11600	L5263	L5258	L7742	L9469	
1.	55	63	53	55	65	60	57	
2.	74	85	78	77	82	80	80	
3.	104	107	95	99	106	102	108	
No. of specimen	L5257	L9466	L9464	<i>D. bicornis</i>	<i>C. simum</i>			
1.	57	60	57	49-51	51-55			
2.	74	84	79	63-65	74-78			
3.	100	106	105	84-90	99-100			

There are twenty entire second metacarpals (Table 32) the first five of which are from the right side. The ratio middle width/median length in the fossil series varies from 0,21 to 0,28, which includes the observations on the recent Mc.II (taken from Hooijer & Singer 1960, and Hooijer 1969).

TABLE 32
Measurements of second metacarpal (mm)

No. of specimen							
1. Median length			L3066	L4890	L5934	L12819	L5988
2. Proximal width			173	177	167	172	160
3. Proximal ant.post. diameter			42	39	43	44	38
4. Middle width			52	c. 50	55	54	50
5. Middle ant.post. diameter			43	40	42	—	38
6. Greatest distal width			24	23	23	—	21
7. Width distal trochlea			50	49	56	56	50
8. Distal ant.post. diameter			44	43	45	46	44
9. Ratio middle width/length			51	49	49	50	48
			0,25	0,23	0,25	—	0,24
No. of specimen	L9225	L7111	L7129	L7109	L7072	L9395	L7083
1.	175	158	172	167	159	172	176
2.	45	37	44	40	37	41	41
3.	55	55	53	51	47	58	51
4.	45	37	42	36	35	41	37
5.	25	20	23	23	21	25	24
6.	53	52	49	46	47	52	56
7.	46	44	45	42	42	45	47
8.	48	48	48	47	45	51	45
9.	0,26	0,23	0,24	0,22	0,22	0,24	0,21
No. of specimen	L7093	L7090	L4104	L7064	L7154	L4132	L6064
1.	162	176	176	158	183	157	163
2.	42	40	42	40	41	40	38
3.	c. 50	52	57	49	53	54	51
4.	41	39	41	35	45	39	35
5.	19	26	29	22	23	24	24
6.	50	53	53	47	57	52	50
7.	42	46	42	42	46	45	45
8.	45	47	48	43	51	48	45
9.	0,25	0,22	0,23	0,22	0,25	0,25	0,21
No. of specimen	L7071	<i>D. bicornis</i>		<i>C. simum</i>		Chemeron	
1.	166	147	148	160	160	165	
2.	—	32	40	44	45	c. 45	
3.	58	46	36	44	49	c. 50	
4.	47	33	31	40	40	42	
5.	28	19	18	20	24	23	
6.	57	39	37	45	50	—	
7.	48	33	—	—	40	—	
8.	50	41	38	43	45	—	
9.	0,28	0,22	0,21	0,25	0,25	0,25	

The third metacarpal is represented in the Langebaanweg collection by twenty-two entire specimens (Table 33), eleven right and eleven left. The bone L3070 is a diseased specimen, somewhat like the second metatarsal of *Dicerorhinus leakeyi* Hooijer (1966, pl. 15) from Rusinga Island.

TABLE 33

Measurements of third metacarpal (mm)

No. of specimen		L5962	L11356	L7086	L7081	L7100	
1. Median length		186	206	192	198	185	
2. Proximal width		67	78	65	76	71	
3. Proximal ant.post. diameter		58	67	55	65	63	
4. Middle width		57	66	56	63	57	
5. Middle ant.post. diameter		27	31	27	28	26	
6. Greatest distal width		74	78	70	78	73	
7. Width distal trochlea		63	72	62	69	65	
8. Distal ant.post. diameter		51	57	52	58	51	
9. Ratio middle width/length		0,31	0,32	0,29	0,32	0,31	
No. of specimen	L7080	L13750	L3070	L6215	L2275	L6045	L2276
1.	193	186	195	187	203	194	200
2.	70	64	69	65	72	67	74
3.	56	57	—	57	—	58	57
4.	58	54	c. 60	58	61	59	61
5.	30	24	—	27	27	26	31
6.	75	67	—	69	80	70+	78
7.	63	58	65	62	67	62	68
8.	51	50	—	54	55	50	54
9.	0,30	0,30	—	0,31	0,30	0,30	0,31
No. of specimen	L7001	L12822	L5937	L5931	L4149	L13756	L9381
1.	183	195	182	188	188	206	192
2.	72	77	70	72	78	69	71
3.	57	61	57	56	58	58	54
4.	63	66	55	58	64	63	57
5.	25	28	24	27	26	24	24
6.	73	—	73	71	75	71	73
7.	61	66	61	58	64	60	62
8.	—	56	53	50	54	54	51
9.	0,34	0,34	0,30	0,31	0,34	0,31	0,30
No. of specimen	L9408	L7085	L13580	<i>D. bicornis</i>		<i>C. simum</i>	
1.	186	183	192	162	166	173	176
2.	72	78	77	59	60	70	68
3.	58	61	60	48	51	55	52
4.	64	64	58	46	45	56	58
5.	27	30	30	22	22	24	28
6.	—	82	74	61	52	66	71
7.	69	64	60	51	—	—	59
8.	—	52	53	44	41	48	48
9.	0,34	0,35	0,30	0,28	0,27	0,32	0,33

The variation range in width/length ratio in the Langebaanweg Mc.III, 0,29 to 0,35, is such that it includes the observations of *C. simum* but the two *D. bicornis* metapodials are relatively more slender than the fossil specimens, although the difference is small.

There are sixteen entire fourth metacarpals in the Langebaanweg collection (Table 34), the first five of which are from the right side. In this metacarpal, only one of the two *D. bicornis* is below the variation range in width/length ratio in the fossil specimens.

TABLE 34
Measurements of fourth metacarpal (mm)

No. of specimen	L6631	L7084	L5936	L5949	L7098	L12820	
1. Median length	148	147	155	151	149	157	
2. Proximal width	53	50	54	55	53	58	
3. Proximal ant.post. diameter	47	52	51	48	50	50	
4. Middle width	39	42	40	37	40	44	
5. Middle ant.post. diameter	24	24	24	23	27	25	
6. Greatest distal width	50	58	—	48	52	55	
7. Width distal trochlea	46	49	46	42	42	45	
8. Distal ant.post. diameter	46	45	—	42	44	46	
9. Ratio middle width/length	0,26	0,29	0,26	0,25	0,27	0,28	
No. of specimen	L2285	L9411	L7078	L4131	L9246	L7089	L7102
1.	150	153	147	160	161	163	155
2.	54	50	51	57	57	58	51
3.	50	—	49	53	52	55	51
4.	39	39	40	36	38	43	37
5.	23	21	24	22	25	24	26
6.	54	48	50	51	51	52	51
7.	46	43	42	43	45	42	42
8.	44	41	42	43	46	44	45
9.	0,26	0,25	0,27	0,23	0,24	0,26	0,24
No. of specimen	L7095	L9401	L7101	<i>D. bicornis</i>		<i>C. simum</i>	
1.	156	145	157	136	135	145	143
2.	64	57	59	43	38	55	54
3.	53	49	51	43	44	51	50
4.	42	38	38	33	30	40	41
5.	25	25	26	18	19	23	23
6.	58	47	52	43	35	48	52
7.	47	46	46	37	—	—	42
8.	48	43	44	38	34	43	45
9.	0,27	0,26	0,24	0,24	0,22	0,28	0,29

The fifth metacarpal of *Ceratotherium praecox* is reduced, mammiform, as it is in the recent species. There is one specimen in the Langebaanweg collection, L11606, with the two facets for the unciform and Mc.IV. It is 46 mm in length, and 35 by 29 mm in proximal diameters. In *D. bicornis* these diameters are 35 mm, and 27 by 26 mm; in *C. simum* the bone is larger, as usual, viz., length 45 mm, and 33 by 26 mm proximally.

Of the femora in the Langebaanweg collection there is only one that is nearly entire, L12292, from the left side, lacking portions of the caput and of the trochanter major, and most of the medial part of the trochlea (first column in Table 35). In length from caput to medial condyle it exceeds the femur of *C. simum*, but in diameter of the caput it is just as large as the larger of the two *C. simum* femora. There are two isolated femur heads, L12632 and L12676, with the same diameter as L12292. The width across the third trochanter, 175 mm, is also found in a mid-shaft portion of a left femur, L13254. There are several juvenile shaft portions showing the third trochanter, viz., L13831, L13867-13869, and L3409. Three distal portions of femora, L8118 and L12681 from the right side, and L11758 from the left, complete the list of femora in the Langebaanweg collection (Table 35).

TABLE 35
Measurements of femur (mm)

No. of specimen	L12292	<i>D. bicornis</i>		<i>C. simum</i>	
1. Greatest length	590	440	460	510	530
2. Diameter of caput	110	80	85	110	95
3. Width across third trochanter	175	—	140	155	—
4. Greatest distal width	c. 175	120	125	155	150
5. Distal ant.post. diameter, medial side	—	160	165	190	190
6. Distal ant.post. diameter, lateral side	155	—	125	155	—
No. of specimen	L8118	L12681	L11758		
4. Greatest distal width	175	180	165		
5. Distal ant.post. diameter, medial side	210	225	c. 200		
6. Distal ant.post. diameter, lateral side	c. 160	c. 175	c. 145		

Twenty-one entire patellae are in the Langebaanweg collection (Table 36), nine from the right, and eleven from the left side. All of them are larger than the recent bones even of *C. simum*.

TABLE 36
Measurements of patella (mm)

No. of specimen	L14035	L13725	L11589	L9210	L4250	L11387	L3069
1. Length	130	115	105	110	115	130	c. 135
2. Width	120	110	105	105	105	120	125
No. of specimen	L6226	L6060	L4268	L7766	L7895	L7739	L4061
1.	130	115	120	125	120	115	130
2.	110	110	110	110	105	105	110
No. of specimen	L12833	L13968	L7787	L4246	L5817	L5927	
1.	135	120	120	115	110	115	
2.	125	110	115	105	105	100	
No. of specimen	L5926	<i>D. bicornis</i>		<i>C. simum</i>			
1.	115	95	100	105	105		
2.	105	85	90	90	95		

Of the tibia there are no entire specimens in the Langebaanweg collection; the most complete specimen, L1805, has only the medial portion of the proximal articular surface, and distally the lateral portion is damaged. The length, measured along the medial surface, is 355 mm, and the greatest length was probably 380 mm (*D. bicornis* 335 mm, *C. simum* 350–380 mm). There are five proximal portions of the tibia (Table 37), the first three of which are from the right side.

TABLE 37
Proximal measurements of tibia (mm)

No. of specimen	L9702	L12619	L7934	L13174	L7944
1. Proximal width	—	150	140	150	155
2. Proximal ant.post. diameter	115	145	120+	—	c. 135
3. Least width of shaft	70	—	—	75	80
No. of specimen	<i>D. bicornis</i>		<i>C. simum</i>		
1.	110	115	135	140	
2.	—	120	—	145	
3.	—	55	—	65	

There are no less than forty-one distal portions of the tibia (Table 38); the first nineteen from the right side, and the remaining twenty-two (starting with L13477) from the left.

TABLE 38
Distal measurements of tibia (mm)

No. of specimen	L7947	L7908	L6171	L7953	L1806	L4968	
3. Least width of shaft	80	75	70	55	70	65	
4. Distal width	105	100	95	90	95	100	
5. Distal ant.post. diameter	100	90	85	85	80	90	
No. of specimen	L11770	L7909	L4963	L4742	L9980	L3073	L6167
3.	—	—	—	—	—	—	—
4.	95	100	105	100	c. 95	95	100
5.	90	95	95	90	85	85	95
No. of specimen	L7910	L7930	L6174	L6373	L6374	L7948	L13477
3.	—	—	—	—	—	—	75
4.	90	100	90	100	105	100	100
5.	85	95	80+	90	95	—	95
No. of specimen	L4965	L13858	L7941	L7940	L4969	L2262	L6165
3.	65	—	70	85	75	70	—
4.	95	95	95	100	95	95	100
5.	90	90	85	100	—	85	95
No. of specimen	L7946	L7914	L7950	L7931	L7947	L7951	L7912
3.	75	—	—	—	—	—	—
4.	90	95	100	105	100	95	100
5.	90	90	95	100	85	85	90
No. of specimen	L2264	L7926	L6366	L11529	L4186	L4187	
3.	—	—	—	—	—	—	
4.	100	95	90	95	100	90	
5.	90	95	85	90	—	—	
No. of specimen	L7921	<i>D. bicornis</i>		<i>C. simum</i>			
3.	—	—	55	—	65		
4.	90	85	95	95	115		
5.	—	70	95	80	85		

The astragalus is represented in the Langebaanweg collection by sixty-seven entire specimens (Table 39), thirty-six from the right side, and thirty-one (beginning with L4166) from the left. The astragalus is the numerically best represented bone in the Langebaanweg collection, to which its solid build undoubtedly contributed.

Like the other bones from Langebaanweg, the astragali are on the large side when compared with their homologues in the living African species. Twenty-six out of the sixty-seven Langebaanweg astragali exceed the larger of the two *C. simum* astragali in all dimensions taken. The ratio medial height/total width varies between much wider limits in the Langebaanweg series (0,74-0,91) than it does in the few recent bones of *D. bicornis* and *C. simum*, as may be expected. However, the variation range in this ratio in the *Ceratotherium praecox* series does not overlap with that in the Miocene brachypotheres of Africa and Europe (*Brachypotherium heinzlini* and *B. brachypus*: 0,64-0,73; cf. Hooijer 1966: 148). In nearly all of the Langebaanweg astragali the trochlea width is

TABLE 39
Measurements of astragalus (mm)

No. of specimen	L5886	L5891	L5929	L4169	L5888	L4173	
1. Lateral height	93	96	89	91	94	94	
2. Medial height	90	94	88	81	85	90	
3. Total width	110	110	104	101	110	116	
4. Ratio medial height/total width	0,82	0,85	0,85	0,80	0,84	0,78	
5. Trochlea width	103	95	93	95	98	105	
6. Width of distal facets	86	90	82	90	93	92	
No. of specimen	L5928	L7222	L7230	L7226	L7209	L7207	L7204
1.	85	88	84	85	96	90	90
2.	88	85	83	80	94	87	87
3.	109	100	103	99	111	106	115
4.	0,81	0,85	0,81	0,81	0,85	0,82	0,76
5.	102	96	93	92	103	96	100
6.	82	86	83	82	90	78	95
No. of specimen	L7211	L7212	L7195	L4865	L1803	L7197	L7198
1.	95	90	94	80	83	92	94
2.	92	89	94	80	81	85	85
3.	110	108	119	104	100	115	111
4.	0,84	0,82	0,79	0,77	0,81	0,74	0,77
5.	103	99	103	89	90	102	96
6.	90	84	95	83	78	80	92
No. of specimen	L7200	L11577	L11903	L6349	L13822	L4161	L6209
1.	100	88	91	95	91	88	94
2.	89	92	94	96	92	88	90
3.	120	116	112	116	111	115	112
4.	0,74	0,79	0,84	0,83	0,83	0,77	0,80
5.	104	95	98	98	102	97	97
6.	98	94	93	94	92	93	88
No. of specimen	L11581	L5427	L4874	L2267	L4868	L4864	L7196
1.	93	91	87	91	105	89	92
2.	94	84	84	89	98	84	88
3.	117	113	107	111	122	113	112
4.	0,80	0,74	0,79	0,80	0,80	0,74	0,79
5.	103	99	96	97	105	96	102
6.	88	86	85	81	103	87	87
No. of specimen	L9489	L12515	L4166	L4162	L4168	L6065	L5890
1.	88	88	88	93	85	77+	86
2.	87	88	89	95	84	87	89
3.	105	103	109	112	103	107	115
4.	0,83	0,85	0,82	0,85	0,82	0,81	0,77
5.	93	90	102	100	90	94	105
6.	82	79	93	90	77	83	87
No. of specimen	L4167	L7213	L7225	L7215	L7216	L5930	L9492
1.	87	86	94	88	91	88	90
2.	86	91	91	87	92	94	88
3.	116	115	120	110	107	115	111
4.	0,74	0,79	0,76	0,79	0,86	0,82	0,79
5.	99	105	105	96	98	108	98
6.	83	96	95	87	82	88	95
No. of specimen	L12655	L7488	L9495	L7219	L5717	L7208	
1.	85	87	80	86	83	85	
2.	92	82	81	85	80	88	
3.	104	105	98	107	105	108	
4.	0,88	0,78	0,83	0,79	0,76	0,81	
5.	90	90	87	95	94	92	
6.	83	83	80	84	83	85	

No. of specimen	L7210	L7203	L7206	L11578	L11583	L4164
1.	91	88	85	87	92	84
2.	87	91	87	93	92	92
3.	107	100	110	120	106	103
4.	0,81	0,91	0,79	0,78	0,87	0,89
5.	92	91	98	105	100	92
6.	86	79	86	101	86	84
No. of specimen	L11582	L5889	L5869	L4870	L9491	L4863
1.	85	94	87	87	85	83
2.	93	97	93	90	82	84
3.	114	108	108	104	106	100
4.	0,82	0,89	0,86	0,87	0,77	0,84
5.	94	97	96	93	90	92
6.	91	88	85	83	84	86
No. of specimen	L9486	<i>D. bicornis</i>		<i>C. simum</i>		
1.	92	65	71	74	76	
2.	94	68	70	75	84	
3.	114	86	83	95	104	
4.	0,82	0,79	0,84	0,79	0,81	
5.	99	78	78	83	87	
6.	87	73	72	85	88	

greater than the medial height, although in some by a narrow margin only; in three specimens (L7203, L4164, and L5889) the trochlea width equals the medial height, and in one (L12655) the trochlea width is just a little less than the medial height. This evidently exceptional condition in *C. praecox* is the rule in *Aceratherium* and *Dicerorhinus* (Hooijer 1966: 173); in *Brachypotherium* trochlea width exceeds medial height, as it does also in *Paradiceros* (Hooijer 1968: 89) and *Chilotheridium* (Hooijer 1971: 377).

The calcaneum is represented in the Langebaanweg collection by fifty specimens, twenty-four right and twenty-six left (Table 40). In greatest height all of these exceed the recent bones used for comparison; in anteroposterior diameter thirty-six fossil calcanea exceed the recent.

TABLE 40
Measurements of calcaneum (mm)

No. of specimen	L11584	L11771	L5867	L4174	L7186	L5980	
1. Greatest height	149	153	143	140	141	145	
2. Greatest width	85	90	—	—	—	—	
3. Ant.post. diameter	—	83	76	72	73	76	
No. of specimen	L5893	L5855	L5982	L5981	L4177	L5851	L3052
1.	142	144	134	146	143	148	140
2.	83	81	81	—	—	82	—
3.	70	78	69	75	76	76	73
No. of specimen	L3052	L4881	L7180	L7169	L7184	L5856	L7190
1.	140	143	146	142	149	152	146
2.	—	—	—	—	95	97	88
3.	73	74	76	73	77	88	79
No. of specimen	L7182	L7198	L7181	L7191	L7166	L6348	L13804
1.	145	157	153	150	152	146	148
2.	90	95	—	94	—	—	—
3.	77	81	77	81	80	76	76

No. of specimen	L5892	L3536	L3149	L7194	L6055	L5853	L9503
1.	144	145	140	156	153	151	145
2.	83	—	87	—	—	84	83
3.	78	76	70	84	80	79	72
No. of specimen	L4175	L5461	L7175	L3790	L8654	L7188	L7187
1.	150	145	152	142	143	141	147
2.	—	—	—	90	—	—	85
3.	73	77	79	c. 75	80	80	77
No. of specimen	L7177	L7171	L7172	L4179	L11585	L6054	L1802
1.	143	145	140	146	161	141	141
2.	—	79	—	—	c. 95	85	83
3.	75	70	73	77	83	72	74
No. of specimen	L9501	L7192	L13825	<i>D. bicornis</i>		<i>C. simum</i>	
1.	152	153	138	110	110	125	125
2.	82	83	—	65	70	80	82
3.	75	82	79	60	65	75	66

The naviculars in the Langebaanweg collection number twenty-seven (Table 41), the first fifteen of which are from the right side.

TABLE 41
Measurements of navicular (mm)

No. of specimen	L9516	L7775	L5567	L3675	L9515	L9512	L9181	
1. Anterior height	35	32	34	37	31	31	34	
2. Total width	56	62	58	54	57	63	60	
3. Ant.post. diameter	71	72	82	75	72	76	80	
No. of specimen	L7852	L7854	L7888	L11623	L6064	L4242A	L6067	L4251
1.	32	31	32	30	33	33	34	33
2.	56	57	61	53	60	55	59	54
3.	76	72	73	69	76	69	72	74
No. of specimen	L7757	L9507	L6065	L9510	L5241	L4242B	L4257	L5264
1.	33	32	32	30	37	30	32	34
2.	66	58	58	56	60	52	53	54
3.	70	72	69	72	78	70	76	75
No. of specimen	L12627	L7889	L7841	L6066	<i>D. bicornis</i>		<i>C. simum</i>	
1.	33	33	33	33	24	29	29	
2.	60	58	55	63	45	55	55	
3.	73	76	66	78	56	62	62	

There are twenty-nine cuboids (Table 42), the first eleven of which are from the right side.

TABLE 42
Measurements of cuboid (mm)

No. of specimen	L6221	L3804	L4262	L3676	L3496	L9482	L12823
1. Anterior height	53	49	49	48	51	50	54
2. Anterior width	53	48	54	49	47	49	58
3. Greatest ant.post. diameter	77	75	76	69	75	73	86
No. of specimen	L4269	L7796	L11750	L4069	L6223	L4260	L7871
1.	51	55	51	51	53	49	46
2.	49	54	50	49	53	44	48
3.	76	79	73	78	82	73	70

No. of specimen	L9458	L9474	L6620	L4068	L7785	L12008	L7803
1.	48	52	52	52	46	50	53
2.	51	—	51	52	49	54	54
3.	72	71	81	83	76	78	87
No. of specimen	L9472	L7770	L5273	L4289	L5287	L5288	L5280
1.	49	52	55	44	50	55	47
2.	44	50	48	43	44	47	53
3.	77	79	78	73	71	76	78
No. of specimen	L5294	<i>D. bicornis</i>	<i>C. simum</i>				
1.	48	37	43				
2.	46	44	52				
3.	73	65	80				

The cuboid of *Ceratotherium praecox* is higher than wide anteriorly in sixteen specimens, and wider than high in nine. We find the same variation in *Aceratherium* and *Dicerorhinus* (Hooijer 1966: 176); it is in *Brachypotherium* and *Chilotherium* that the width is distinctly greater than the height, and this is true to a lesser extent in *Chilotheridium* (Hooijer 1971: 380).

Eight ectocuneiforms, six right and two left (Table 43), have the anterior width about two times the anterior height, as in the recent African species, *Aceratherium* and *Dicerorhinus*, and *Chilotheridium*; in *Chilotherium* the width is three times the height (Hooijer 1966: 177; 1971: 380-381).

TABLE 43
Measurements of ectocuneiform (mm)

No. of specimen	L4075	L9514	L9517	L7820	L4053	L4070
1. Anterior height	30	32	28	30	27	27
2. Anterior width	60	56	54	57	53	55
3. Ant.post. diameter	71	59	57	57	51	56
No. of specimen	L7749	L7773	<i>D. bicornis</i>	<i>C. simum</i>		
1.	33	33	24	27		
2.	57	58	45	57		
3.	58	59	53	54		

One mesocuneiform, from the left side, is the remaining tarsal bone in the collection (Table 44).

TABLE 44
Measurements of mesocuneiform (mm)

No. of specimen	L12663	<i>D. bicornis</i>	<i>C. simum</i>
1. Height	24	14	19
2. Width	24	24	22
3. Ant.post. diameter	45	34	43

A set of right metatarsals, L13548-13550, belong to one and the same individual (Pl. 34). Their measurements are given in the first columns of Tables 45-47.

Of the second metatarsal there are fifteen entire specimens (Table 45), the first seven of which are from the right side. The variation range in width/

length ratio is rather small, 0,18–0,22 only, and one of the *D. bicornis* metapodials remains below these limits, that is, it is more slender in build.

TABLE 45
Measurements of second metatarsal (mm)

No. of specimen	L13550	L2279	L4118	L4886	L13802
1. Median length	176	166	161	164	162
2. Proximal width	41	35	37	35	37
3. Proximal ant.post. diameter	—	49	55	51	54
4. Middle width	32	32	30	33	29
5. Middle ant.post. diameter	32	30	29	26	29
6. Greatest distal width	49	45	—	44	—
7. Width distal trochlea	44	41	39	39	—
8. Distal ant.post. diameter	52	43	44	45	43
9. Ratio middle width/length	0,18	0,19	0,19	0,20	0,18

No. of specimen	L5943	L7075	L11772	L6052	L4109	L4127	L9380
1.	174	158	162	153	160	168	162
2.	43	33	36	33	33	33	39
3.	56	51	58	50	50	54	56
4.	35	29	30	28	32	30	35
5.	33	27	32	24	27	30	30
6.	48	43	49	41	41	44	48
7.	43	38	42	39	38	38	44
8.	48	43	45	42	44	48	45
9.	0,20	0,18	0,19	0,18	0,20	0,18	0,22

No. of specimen	L7097	L11904	L4142	<i>D. bicornis</i>	<i>C. simum</i>
1.	157	153	160	129	135
2.	38	35	39	25	24
3.	56	51	55	42	33
4.	32	33	32	25	22
5.	30	30	31	19	20
6.	46	45	44	33	31
7.	45	40	41	29	—
8.	47	44	48	36	35
9.	0,20	0,22	0,20	0,20	0,16

There are twenty entire third metatarsals (Table 46), ten from the right and ten from the left side. The range of variation in width/length ratio of the fossil bones (0,26–0,33) is very nearly the same as that in the four recent bones.

TABLE 46
Measurements of third metatarsal (mm)

No. of specimen	L13548	L6048	L4138	L13752	L13754
1. Median length	198	192	179	181	171
2. Proximal width	70	62	62	61	55
3. Proximal ant.post. diameter	—	57	57	56	53
4. Middle width	60	53	55	54	47
5. Middle ant.post. diameter	35	31	30	30	25
6. Greatest distal width	82	68	—	71	58
7. Width distal trochlea	69	57	54	58	54
8. Distal ant.post. diameter	55	50	50	—	49
9. Ratio middle width/length	0,30	0,28	0,31	0,30	0,27

No. of specimen	L7068	L7065	L7062	L12615	L11855	L5960	L6043
1.	191	187	182	180	188	198	186
2.	63	64	57	61	62	67	58
3.	61	55	—	57	55	c. 60	51
4.	54	52	53	52	57	62	49
5.	29	29	26	31	27	33	28
6.	67	67	—	68	70	80	—
7.	59	56	56	56	60	66	53
8.	52	51	—	51	51	58	49
9.	0,28	0,28	0,29	0,29	0,30	0,31	0,26
No. of specimen	L7000	L5932	L4148	L13801	L13749	L9379	L7152
1.	180	171	178	190	183	177	182
2.	59	58	58	59	59	61	60
3.	53	52	55	—	54	51	53
4.	48	53	49	55	53	54	60
5.	26	29	28	29	31	31	29
6.	66	64	66	71	—	68	74
7.	55	54	55	59	55	59	62
8.	50	46	48	54	51	49	51
9.	0,27	0,31	0,28	0,29	0,29	0,31	0,33
No. of specimen	L7092	<i>D. bicornis</i>		<i>C. simum</i>		Aterir	
1.	183	148	152	160	169	180	
2.	59	48	50	59	55	58	
3.	—	48	45	47	49	50	
4.	50	40	40	51	48	49	
5.	28	21	19	22	25	24	
6.	65	54	45	56	66	68	
7.	57	47	—	—	51	—	
8.	50	42	40	46	47	45	
9.	0,27	0,27	0,26	0,32	0,28	0,27	

There are sixteen entire fourth metatarsals in the Langebaanweg collection (Table 47), eight right and eight left. The width/length ratio does not vary a

TABLE 47
Measurements of fourth metatarsal (mm)

No. of specimen	L13549	L3555	L4888	L7073	L3785		
1. Median length	170	166	153	166	155		
2. Proximal width	65	54	52	53	48		
3. Proximal ant.post. diameter	52	44	46	48	43		
4. Middle width	33	32	33	31	27		
5. Middle ant.post. diameter	48	40	38	38	32		
6. Greatest distal width	—	43	42	41	37		
7. Width distal trochlea	—	39	39	41	35		
8. Distal ant.post. diameter	49	44	41	45	41		
9. Ratio middle width/length	0,19	0,19	0,22	0,19	0,17		
No. of specimen	L7114	L7070	L7063	L4111	L4151	L4158	L13748
1.	162	157	156	160	163	158	174
2.	54	50	49	53	49	53	53
3.	46	42	46	50	48	55	48
4.	35	27	29	30	31	32	34
5.	38	33	32	35	35	38	40
6.	47	40	40	41	42	40	47
7.	41	38	34	37	39	40	40
8.	45	42	40	43	43	43	46
9.	0,22	0,22	0,19	0,19	0,19	0,20	0,20

No. of specimen	L5942	L9390	L9241	L7099	<i>D. bicornis</i>		<i>C. simum</i>	
1.	152	157	155	154	125	127	138	146
2.	49	57	45	49	42	39	44	49
3.	46	55	56	46	40	40	47	45
4.	29	30	30	27	26	26	35	29
5.	35	40	34	33	24	23	26	28
6.	38	42	40	41	36	31	44	39
7.	34	36	36	38	33	—	—	37
8.	39	39	42	40	38	34	41	41
9.	0,19	0,19	0,19	0,18	0,21	0,20	0,25	0,20

great deal (0,17–0,22). One of the recent bones (the first under the head *C. simum*) is not within these limits but above them; it is more massively built than the other recent, and the fossil fourth metatarsals.

There are nineteen first phalanges of median digits (Table 48), whether from the manus or from the pes I am unable to tell.

TABLE 48
Measurements of phalanx I, median digit (mm)

No. of specimen	L3046	L8418	L6099	L8416	L4214	L9250	
1. Median length	38	41	40	43	38	42	
2. Proximal width	66	67	67	66	64	60	
No. of specimen	L8417	L5276	L9520	L8415	L5326	L8420	L6216
1.	43	44	37	37	37	40	42
2.	61	64	58	61	—	60	57
No. of specimen	L8419	L9251	L5993	L13767	L5275	L7252	
1.	39	37	40	44	39	—	
2.	65	57	61	64	57	71	
No. of specimen	<i>D. bicornis</i>		<i>C. simum</i>				
	manus	pes	manus	pes			
1.	31	33	42	41			
2.	51	49	58	63			

Four second phalanges of median digits are available (Table 49).

TABLE 49
Measurements of phalanx II, median digit (mm)

No. of specimen	L8426	L9253	L9518	L11607	<i>D. bicornis</i>		<i>C. simum</i>	
					manus	pes	manus	pes
1. Median length	30	33	34	26	26	28	30	30
2. Proximal width	64	62	53	64	55	56	65	73

There is one third phalanx of a median digit (Table 50).

TABLE 50
Measurements of phalanx III, median digit (mm)

No. of specimen	L8427	<i>D. bicornis</i>		<i>C. simum</i>	
		manus	pes	manus	pes
1. Median length	32	26	28	—	34
2. Greatest width	93	84	80	—	107

Five bones (L8421, L8422, L9256, L9519 and L11879) represent first phalanges of lateral digits; they vary in median length from 35 to 37 mm, and in proximal width from 42 to 50 mm. A third phalanx of a lateral digit, L9257, has a median length of *c.* 30 mm, and a greatest diameter of 51 mm. Two proximal sesamoids remain to be recorded; the larger bone, L7364, length 41 mm, width 21 mm, presumably belonged to a median digit, while the smaller, L4074, length 28 mm, width 17 mm, may have belonged to a lateral digit.

OTHER *C. PRAECOX* SITES IN EAST AND SOUTH AFRICA

We have evidence of the occurrence of *Ceratotherium praecox* at sites other than Kanapoi, Ekora and Lothagam-1 in Kenya, and Langebaanweg in the Cape Province. Fragmentary teeth from the Mursi Formation of the Omo Basin in southern Ethiopia and from the Chemeron Formation in Kenya, previously referred to *Ceratotherium simum germanoaffricanum* (Hooijer 1969: 86, 77), in the light of the discovery of *Ceratotherium praecox* at Kanapoi and Langebaanweg, should be identified as *C. praecox*. The teeth from the 'lower level' (Mursi Formation), which had been collected by R. Leakey in 1967, were re-examined by me in July 1971 at the Centre for Prehistory and Palaeontology, National Museum, Nairobi. There are a P⁴ sin. and a M²⁻³ sin. in palatal portions (Hooijer 1969, pl. 5, figs 4-5) displaying, as far as preserved, an angular antero-internal corner. In M³ there is a true medifossette, whereas in P⁴ and M² the crochet extends across the medisinus without uniting with a crista to form a medifossette. P⁴ shows the internal indentation of the protocone also seen in M². The internal face of M² is 50 mm anteroposteriorly, and 30 mm of this are taken up by the protocone. Although all the teeth are incomplete externally the basal external crown outline is preserved, and the transverse diameters can be approximately given (Table 51). They are within the limits of their homologues in the Langebaanweg collection. Although the ectoloph of the Mursi Formation specimens cannot be studied, in all observable characters these teeth agree with those of *Ceratotherium praecox*; the medifossette is not normally formed in this species, and its presence in the Mursi M³ is exceptional. The Chemeron maxilla with M¹⁻³ (Hooijer 1969, pl. 2, fig. 1), from locality J.M.507, do not have medifossettes, and M² has a distinct antero-internal crown angle. The teeth are very much worn down, and M¹ and M³ are so fragmentary that the width cannot be determined, but those of M² are approximately the same as those in the Mursi specimen (Table 51). The skull from J.M.91, Chemeron Formation (Hooijer 1969: 76, pl. 1) is more advanced in its dentition and shows the rounded antero-internal crown angles, the medifossettes, and the posterior extension of the protocone characteristic of the modern species; this specimen moreover has the backwardly inclined occiput, extending beyond the occipital condyles, characteristic of *C. simum germanoaffricanum*, and as such it was identified in my earlier paper. The presence of both *Ceratotherium praecox* and *Ceratotherium simum germanoaffricanum* in the Chemeron Formation is puzzling,

for the mammalian fossils in the Chemeron Formation were found so closely together (Dr. W. W. Bishop, pers. comm.) as to make it unlikely that they were not of the same age. The Chemeron locality J.M.90 (=J.M.91) is placed by Cooke & Maglio (1971, fig. 2) at the 2 million year level, whereas the remainder of the Chemeron Formation is left at the 4 million year level. This arrangement is in accordance with the evidence provided by the rhinoceroses. Bishop (1971*b*), with a faunal list, gives the age of the Chemeron Formation as greater than 2,0 m.y. and less than 5,4 m.y.

A metapodial of a rhinoceros from the Chemeron Formation, locality J.M.511, is a left second metacarpal. Whether it represents *C. praecox* or *C. simum* I am unable to tell; the measurements have been added to Table 32 and agree with those of either of the two species.

From locality J.M.511 of the Chemeron Formation there is a P⁴ dext. of a large chalicothere, a new element to the Chemeron Formation fauna (cf. Bishop 1971*b*). It was collected on 5 August 1967; I found it in the Chemeron collection of the Department of Geology at Bedford College, London, on 18 November 1971, and it was given to me for study by Dr. W. W. Bishop. The specimen is of considerable interest as it adds to the younger elements of the Chemeron Formation fauna, and chalicothere teeth are rare anyway. The specimen is referable to *Ancylotherium hennigi* (Dietrich), a species recorded before from Laetolil and Bed I at Olduvai (Dietrich 1942: 105; Butler 1965: 226). It is very well preserved and not much worn; the lingual cusp is only just touched by wear, and the height of the worn ectoloph is 33 mm. The crown measures 28 mm anteroposteriorly and 31 mm transversely, and has all the characters of *Ancylotherium* (Thenius 1953: 98 and fig. 1). The Olduvai material consists of a few carpals, metacarpals and phalanges only, but among the Laetolil collection there is an M² (Dietrich 1942, pl. IV, fig. 37; pl. XII, fig. 79), measuring 55,0 mm anteroposteriorly and 40,0 mm transversely. The newly found P⁴ and the Laetolil M², when compared with their homologues in an upper dentition of *Ancylotherium pentelicum* (Gaudry & Lartet) as figured by Thenius, prove to be on a par for size. In the *A. pentelicum* dentition P⁴ measures 33,3 by 37,5 mm, and M² 67,2 by 50,5 mm (Thenius 1953: 105); the Chemeron P⁴ and the Laetolil M² are both one-sixth smaller in dimensions than the corresponding teeth in *A. pentelicum*. Laetolil and Olduvai Bed I are around the 2 million year level (Maglio 1970; Cooke & Maglio 1971), and that is where part of the Chemeron Formation (locality J.M.90 and 91) was placed by Cooke & Maglio. However, as stated above, in the opinion of geologist Dr. Bishop, the geological evidence does not support a time gap of 2 million years between some Chemeron sites (J.M.90, 91) and others. The tooth of *Ancylotherium hennigi* (locality J.M.511) as well as the skull of *Ceratotherium simum germanoaffricanum* (locality J.M.91) and stage 2 or 3 of *Elephas recki* (Cooke & Maglio 1971) suggest an age for the Chemeron Formation closer to 2 million years than to 4 million years. On the other hand we have elements like the maxillary of *Ceratotherium praecox* (locality J.M.507) in addition to *Loxodonta adaurora* Maglio, *Mammuthus*

subplanifrons (Osborn), *Anancus* cf. *kenyensis* (Cooke & Maglio 1971) or *Anancus* sp. (Bishop 1971b), and *Nyanzachoerus* species 'A' of Cooke & Ewer, which are suggestive of an age around 4 million years. If the Chemeron Formation fauna is really unified as to age, it may tentatively be placed around the 3 million year level, as suggested to me by Dr. W. W. Bishop. However this may be, further faunal studies are needed, and the record of *Ancylotherium hennigi* from locality J.M.511 of the Chemeron Formation is here given as a contribution for that end.

TABLE 51
Measurements of upper teeth of *Ceratotherium praecox* (mm)

	Langebaan- weg	Mursi Fm.	Chemeron Fm. J.M.507	Swartlintjes Farm, Namaqua- land
P ⁴ , ant.post.	47-c. 57	—	—	—
ant.transv.	65-76	c. 68	—	—
post.transv.	56-73	c. 60	—	—
M ² , ant.post.	c. 50-68	—	—	—
ant.transv.	70-82	c. 75	c. 75	74
post.transv.	65-75	c. 65	c. 65	70
M ³ , ant.post. (int.)	56-72	c. 60	—	—
ant.transv.	65-78	c. 67	—	—
length outer surface	68-83	—	—	—

The Aterir Beds in the Baringo area, Kenya, which are placed by Maglio (1970), Cooke & Maglio (1971) and Bishop (1971b) near the 4 million year level (as is the Mursi Formation = Yellow Sands), contain material of *C. praecox*. The inner portion of an upper right molar, marked 5/B₄/6, has the marked protocone fold, internal indentation of the protocone, slight internal cingulum, a crochet but no medifossette, and the marked antero-internal crown corner characteristic of the present species. No measurements can be given, but in its internal anteroposterior diameter, nearly 50 mm (of which 28 mm for the protocone), and the massive crochet it is nearest to M¹. Another Aterir specimen, an upper left premolar, marked 5/B₁, again with the angular antero-internal corner, no medifossette, and a very weak paracone style, has the dimensions of P³ in dentition L13035. Its measurements have been added to Table 5. There is further in the Aterir collection a right third metatarsal (marked 1/18 and 1/23) indistinguishable from its Langebaanweg homologue; its measurements have been added to Table 46: Finally, there is a proximal sesamoid, presumably of a median digit, marked 5/B₁. This Aterir specimen is 41 mm long and 20 mm wide, just about as large as the Langebaanweg sesamoid L7364.

An isolated, rolled M² dext., lacking the antero-external and postero-external angles, and originating from Swartlintjes Farm, Hondeklipbaai, Namaqualand, C.P. (about 160 km north of Langebaanweg), represents the same species of *Ceratotherium* as that from Langebaanweg. According to the geologist who presented the specimen to the South African Museum, Mr. A. J. Carrington, the fossil molar came from ill-sorted angular felspathic fluvial gravels at an elevation of c. 18 m. The gravels overlie what are taken

as Lower Pleistocene marine sands, and would be Upper Pleistocene. However, it is difficult to reconcile this view with the characters of the rhinoceros molar, which are those of the Late Pliocene *Ceratotherium praecox*. Its rolled condition suggests that it was derived from an earlier deposit. The specimen is figured in Plate 25 (bottom right), and bears the South African Museum number Q1771. The ectoloph is 77 mm high as worn. There is a well-marked protocone fold and internal indentation of the protocone, an angular antero-internal crown corner, and further there are a weak cingulum internally at the protocone, a strong but relatively slender crochet, no crista, and a postsinus very nearly as deep as the medisinus. The antero-transverse diameter is 74 mm, the postero-transverse 70 mm, very close to those in L6658.

The Namaqualand site is the only one in the Cape Province other than Langebaanweg from which *Ceratotherium praecox* is recorded, and this species is further known only from north-western Kenya and southern Ethiopia. It is already proving useful in African correlations, and may become more so if and when found in other parts of Africa.

SUMMARY

Numerous remains of an extinct species of rhinoceros have been obtained by parties of the South African Museum at the 'E' Quarry of the Langebaanweg site, 104 km north-northwest of Cape Town, C.P. They are more abundant than those of any other large mammal in the Langebaanweg fauna; there are remains of seven skulls, ten mandibles (most of them with teeth *in situ*), 170 isolated teeth, and 650 postcranial bones. This material is referred to *Ceratotherium praecox* Hooijer & Patterson described from the Late Pliocene of Lothagam-1, Kanapoi, and Ekora in north-western Kenya. *Ceratotherium praecox* is little removed from the point of divergence of the genus *Ceratotherium* and the genus *Diceros*, and is held to represent the immediate ancestor of the modern white rhinoceros, *Ceratotherium simum*. The species is further recorded in the Cape Province from Swartlintjes Farm, Hondeklipbaai, Namaqualand (approximately 160 km north of Langebaanweg). It is also known from the Mursi Formation in southern Ethiopia, and the Chemeron Formation and the Aterir Beds in the Baringo area, Kenya, all deposits dated around the 4 million year level. The discovery of this species is proving most useful in inter-African correlation and adds to the evidence already available that the 'E' Quarry Langebaanweg site is Late Pliocene in age.

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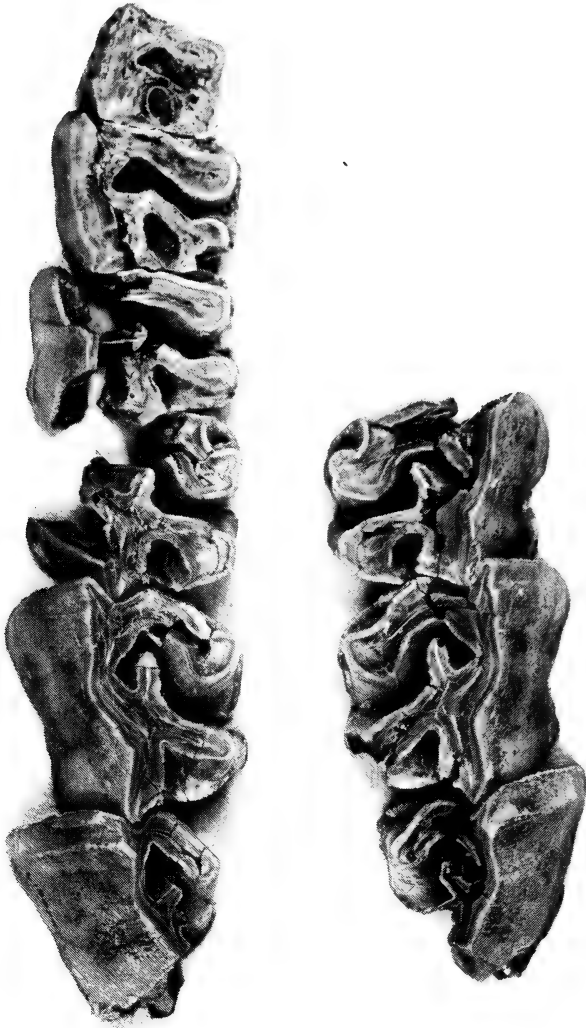
East Rudolf, Kenya, rhinoceroses, and to Mr. Neville Eden who took the photographs. My journey to South Africa has been made possible by a grant from the Wenner-Gren Foundation for Anthropological Research, Inc., New York.

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EXPLANATION OF THE PLATES

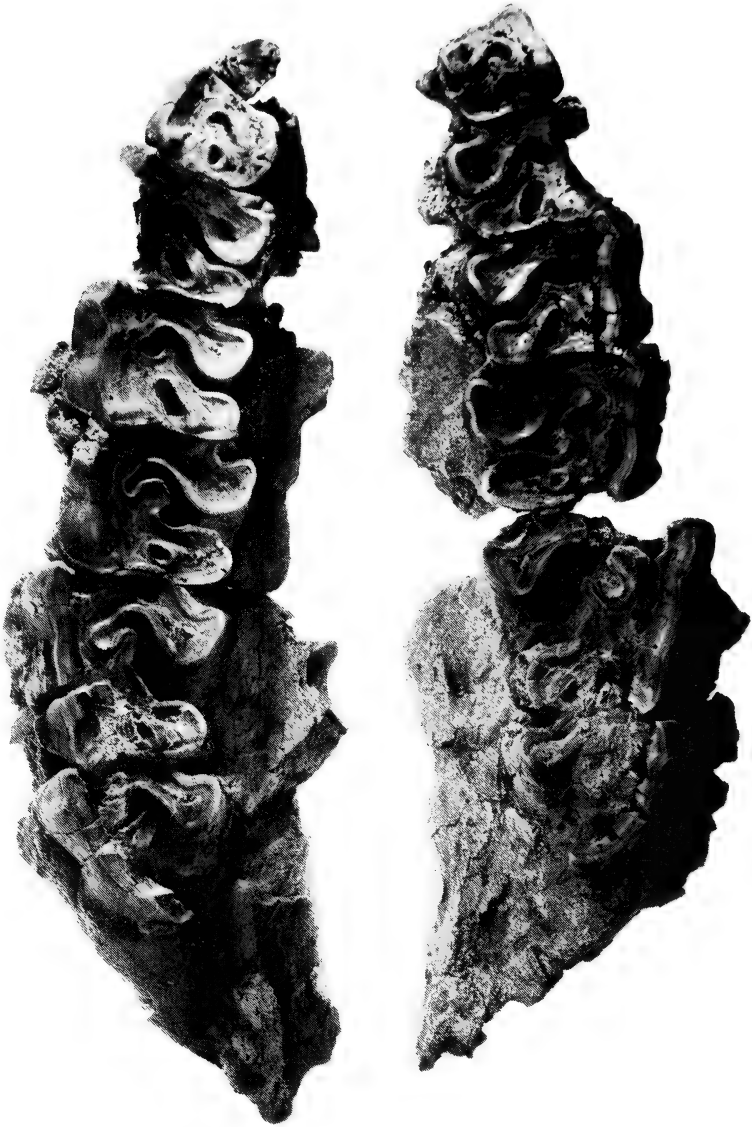
Note. All specimens are *Ceratotherium praecox* Hooijer & Patterson from Langebaanweg, except Plate 25, bottom right, which is from Swartlintjes Farm, Namaqualand.



Upper dentition, L13035, crown view, $\times 0.44$.



Upper dentition, L2519, crown view, $\times 0,52$.



Upper dentition, L13747, crown view, $\times 0,35$.



Skull, L6658, palatal view, $\times 0.37$.



Top, P²⁻⁴ dext., L13035, internal view, $\times 0,78$.

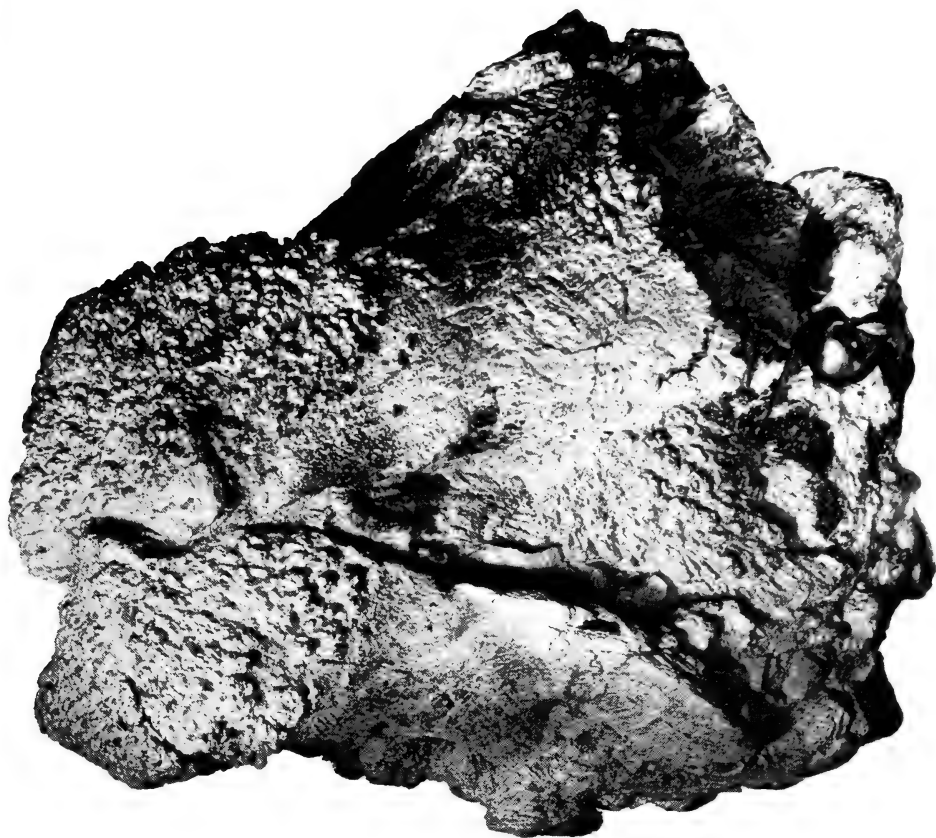
Middle, outer surfaces of M³ dext., L6291 and L6696, external views, $\times 0,57$.

Bottom left, ectoloph of P⁴ sin., L13760, external view, $\times 0,56$.

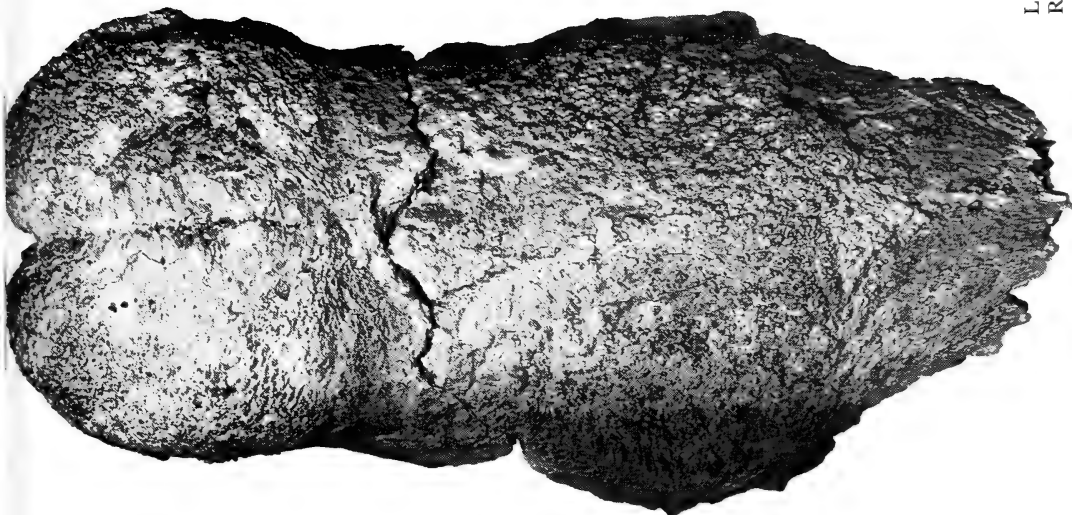
Bottom right, M² dext., Swartlintjes Farm, Namaqualand, S.A.M. Q1771, crown view, $\times 0,82$.



Top of skull, L13747, right lateral view, $\times 0.67$.

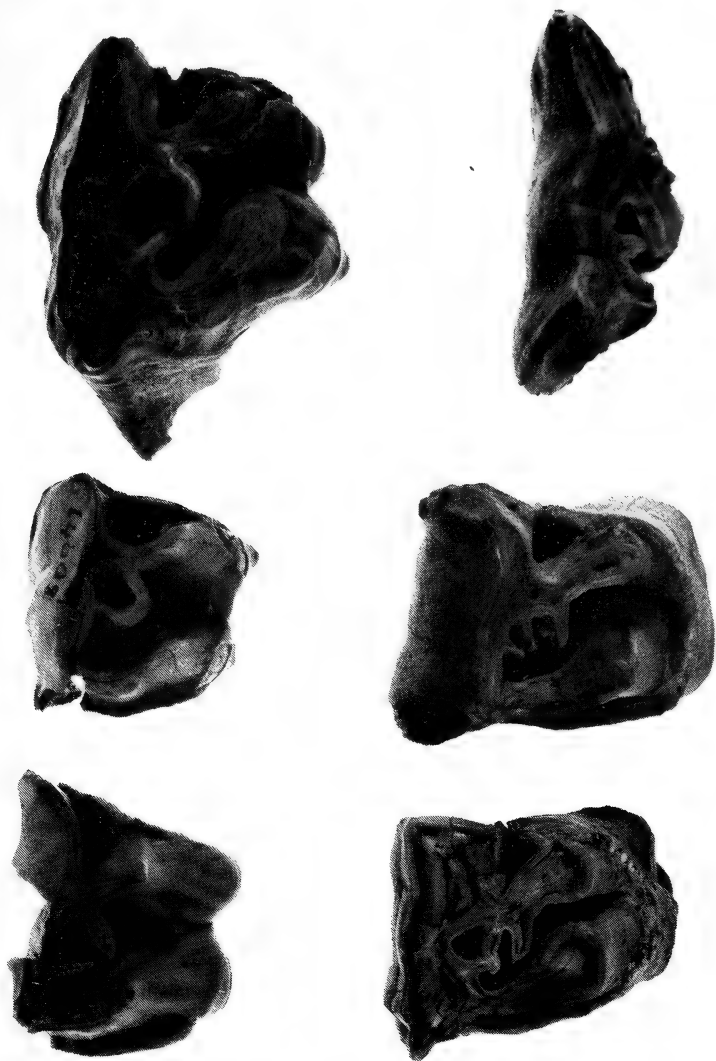


Left, top of skull, L2520, dorsal view, $\times 0.33$.
Right, skull, L6658, dorsal view, $\times 0.35$.





Top left, premaxillaries of skull L13747, palatal view, $\times 0,55$.
Top right, isolated upper I, with skull L13747, lateral view, $\times 1,00$.
Bottom row, from left to right, M² sin., L5916, M² dext., L6617, and M¹ dext., L6626, crown views, $\times 0,52$.



Top row, from left to right, DM³ sin., L9105B, DM² sin., L4608, and DM¹ sin., L6651, crown views, $\times 0.78$.

Bottom row, from left to right, P⁴ sin., L11132, P⁴ sin., L6655, and ectoloph of M² sin., L9118, crown views, $\times 0.67$.



Mandible, L13035, top view, $\times 0,28$.



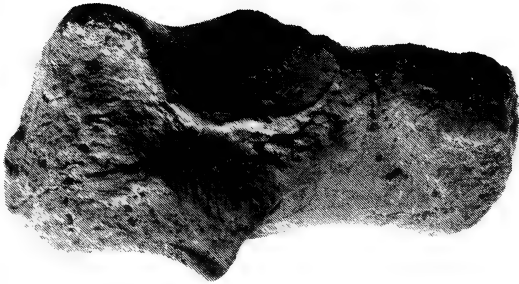
Right mandibular ramus, L.13035, internal view, $\times 0.27$.



Top left, DM₃ dext., L9105C, crown view, $\times 0,99$.

Bottom left, DM₄ dext. in ramus fragment, L6660, crown view, $\times 0,73$.

Right, mandible, L11849, top view, $\times 0,36$.



Top, symphysis of the mandible, L6058, top view, $\times 0,67$.

Middle, ankylosed cuneiform and pisiform sin., L7823, anterior view, $\times 0,61$.

Bottom, cuneiform sin., L9465, and pisiform sin., L7892, as they articulate, anterior views, $\times 0,61$.



Metatarsals II, III and IV dext., L13548-13550, articulated, front view, $\times 0.61$.

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Example

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



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A REVIEW OF THE SEPIIDAE (CEPHALOPODA)
OF SOUTHERN AFRICA

By
MARTINA A. ROELEVELD

Cape Town Kaapstad

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MARTINA A. ROELEVELD
South African Museum, Cape Town

(With plates 35-45, 20 figures and 53 tables)

[MS. accepted 1 March 1972]

CONTENTS

Introduction	194
Methods	194
Abbreviations and glossary	196
Key to the Sepiidae of southern Africa	197
Key to shells only	199
Systematic discussion	
Diagnoses of family and genera	200
Description of southern African species	
<i>Sepia zanzibarica</i> Pfeffer, 1884	202
<i>Sepia officinalis vermiculata</i> Quoy & Gaimard, 1832	204
<i>Sepia acuminata</i> Smith, 1916	208
<i>Sepia confusa</i> Smith, 1916	210
<i>Sepia incerta</i> Smith, 1916	213
<i>Sepia burnupi</i> Hoyle, 1904	217
<i>Sepia joubini</i> Massy, 1927	221
<i>Sepia adami</i> n. sp.	224
<i>Sepia australis</i> Quoy & Gaimard, 1832	227
<i>Sepia tuberculata</i> Lamarck, 1798	231
<i>Sepia papillata</i> Quoy & Gaimard, 1832	235
<i>Sepia simoniana</i> Thiele, 1920	240
<i>Sepia angulata</i> n. sp.	242
<i>Sepia hieromis</i> (Robson, 1924)	243
<i>Sepia insignis</i> Smith, 1916	248
<i>Sepia robsoni</i> (Massy, 1927)	250
<i>Sepia faurei</i> n. sp.	251
<i>Sepia (Hemisepius) typica</i> (Steenstrup, 1875)	257
<i>Sepia (Hemisepius) dubia</i> Adam & Rees, 1966	264
<i>Sepiella cyanea</i> Robson, 1924	266
Discussion	
Relationships	268
Geographical distribution	271
Vertical distribution	276
Growth	278
Summary	280
Acknowledgements	280
References	280
Appendix: Tables 9-53	283

INTRODUCTION

The aim of this paper is to collate and extend, where possible, the knowledge of the Sepiidae of southern Africa (defined by Day 1967: vii, as Africa south of the twentieth parallel of latitude). Hitherto, the sepiids have been described in various papers dealing with South African cephalopods (e.g. Robson 1924*a, b*; Massy 1925, 1927, 1928; Voss 1962*b*, 1967) and in some detail by Adam & Rees (1966) in their excellent review of the family. The collection in the South African Museum, however, comprises some 664 animals and 411 shells, belonging to 18 species, and these specimens provide a number of interesting additions to our knowledge of the southern African Sepiidae. Three new species and the female animal of *Sepia insignis* (previously known only by its shell) are described.

All but two of the species have been redescribed from the specimens available and compared with previous descriptions. Unfortunately the collection is poor in species occurring off the Natal coast (called here the 'dorato-sepion' group). This gap has been filled to some extent by the donation of a few Sepiidae caught off the Moçambique coast by the Oceanographic Research Institute, Durban, and by the loan of some Sepiidae from the Natal Museum, Pietermaritzburg. Most of the latter specimens have previously been described by Miss A. L. Massy (1925, 1928). No specimens were available for *Sepia robsoni* and *S. (Hemisepius) dubia*. Only one specimen, the type, is known of each of these two species; these types are deposited in the British Museum (Natural History), and are not sent out on loan.

Before his death Dr. K. H. Barnard compiled notes on the South African Sepiidae and constructed a rough key to the species. But since several specimens have been added to the collection in the interim, and the notes include a number of errors, the present work was not based on his notes, but was started afresh. Some points of interest found in Barnard's notes are discussed under the relevant species.

This paper was submitted in partial fulfilment of the requirements of the Degree of Master of Science in Zoology at the University of Stellenbosch.

METHODS

All animals in reasonable condition were measured with dividers and millimetre rule. Each dimension was calculated as a percentage of dorsal mantle length for animals and of shell length for shells. For animals of mantle length less than 25 mm, only mantle dimensions were recorded, as the animals are too small to handle without damaging them. Measurements of southern African Sepiidae previously published by other authors were included where possible to increase the numbers to a significant level. Tables of all relative dimensions are given at the end of the paper. For some of the more significant dimensions (mantle width, head width, fin width, length of tentacular club and shell dimensions) ranges and arithmetic means were calculated. Calculations

for male and female animals of each species were carried out separately, but shell dimensions of both sexes were combined, since in the case of a shell found on the beach, the sex of the animal by which it was secreted cannot be determined (except perhaps in the case of *Sepiella cyanea*).

The dimensions of preserved specimens are affected by a number of factors. The relative mantle width is generally greater in dead animals than in live ones, as the mantle collapses and flattens out. However, since all animals measured were dead and fixed in formalin, one may assume the error to be fairly constant. Relative arm lengths are not considered to be of much significance, since they vary considerably, depending on the extent of contraction. However their ranges and means were calculated for comparative purposes, where only large differences may be considered significant. The length of the tentacles is similarly affected, but more so, as the tentacles seem to be more contractile than the arms. In addition, some animals were preserved with the tentacles retracted, and these tentacles were sometimes difficult to straighten out for measuring. Similarly the presence or absence of keels on the arms frequently appears to depend on the condition of the animal at the time of preservation.

In most cases coloration is an unreliable guide within the Sepiidae, as these animals are masters of the art of camouflage, and can show a wide range of colour patterns. Generally the background is a pale cream, overlaid by brown-black and orange-red chromatophores. By progressive expansion of these chromatophores, the animal can assume a range of colours from black, through purple to reddish-brown, over all or part of the body. With complete contraction of the chromatophores only the pale background is seen.

Five of the species described below, namely *Sepia confusa*, *S. incerta*, *S. burnupi*, *S. joubini* and *S. adami*, have been called the 'doratosesion' group for convenience, since these species seem to be closely related and are frequently discussed as a group or compared with each other in the text. Most of these species have been included at some time in Rochebrune's genus *Doratosesion*. This genus was created for Sepiidae with an elongated body, short arms with biserial suckers, short tentacular clubs with unequal suckers, a very elongated shell with two posterior wings and a spine. Whilst Rochebrune's classification of the Sepiidae has been rejected by Adam (1944) and Adam & Rees (1966) with good reason, 'doratosesion' is used here as a collective name for the abovementioned five species. Its use, however, in no way implies the retention of the genus *Doratosesion*.

Distribution ranges have been constructed from localities of specimens in the South African Museum collection and from published records, and have in some cases been extended by locality records from the University of Cape Town Ecological Survey. In the distribution figure (Fig. 18) only localities of animals are recorded. Shell localities cannot be considered to extend the distribution range of a species, since sepiid shells are known to drift over long distances, and their place of origin is thus unknown.

Finally, it should be noted that the Natal Museum has listed the shells of

animals in the collection under separate numbers, e.g.:

N.M.956: *S. incerta*, 1 ♂ from Natal coast, in stomach of Ground Shark.

N.M.957: *S. incerta*, 1 ♂ from the same locality.

N.M.958: shells of the above two specimens (and one shell of *S. burnupi*, presumably added later).

ABBREVIATIONS AND GLOSSARY

- MLd —dorsal mantle length along midline
 MLv —ventral mantle length along midline
 MW —maximum mantle width (excluding fins)
 HL —head length dorsally (from anterior tip of nuchal cartilage to edge of dorsal interbrachial membrane)
 HW —maximum head width (usually across the eyes)
 FL —length of single fin along curve of mantle
 FW —width of single fin, from lateral edge of mantle to free edge of fin
 AL I-IV —arm length measured from inner base of most proximal sucker to tip of arm
 TL —length of tentacle, from point of emergence from tentacular sac to tip of club
 Tcl —length of tentacular club, from basal sucker to tip of club
- Shell:
- L —total length of shell, excluding posterior spine (where present)
 W —maximum width of shell
 Th —maximum thickness of shell, along midline
 Str z —length of striated zone
- km —kilometres
 m —metres
 mm —millimetres
 N —number of specimens measured
 N.M. —Natal Museum
 O.R.I. —Oceanographic Research Institute
 P.F. —Cape Fisheries survey vessel *Pieter Faure*
 S.A.M. —South African Museum
 U.C.T. —University of Cape Town Ecological Survey
- acuminate —forming an acute angle
 arm length formula —comparative lengths of the arms in decreasing order
 attenuated —suddenly becomes very slender distally (usually referring to arm tips)
 'doratosepion' group —includes *Sepia confusa*, *S. incerta*, *S. burnupi*, *S. joubini* and *S. adami*. See page 195 for definition.
 emarginate —with a broad semicircular or rectangular notch (usually referring to anterior mantle margin ventrally)

KEY TO THE SEPIIDAE OF SOUTHERN AFRICA

Figures 1 and 2 illustrate the external morphology of *Sepia* and its shell, and most of the terms used in the keys. *Sepia angulata* is not included in the first key as this species is known only by its shell.

- 1 Posterior gland present, opening via a pore situated between the posterior extremities of the fins (genus *Sepiella*) *Sepiella cyanea*
 Posterior gland absent (genus *Sepia*) 2
- 2 Tentacular club with numerous subequal suckers (Figs 14c, 17b) 3
 Tentacular club with a few median suckers enlarged (Fig. 11) 11
- 3 Mantle produced dorsally 4
 Mantle convex dorsally 7
- 4 Mantle ventrally entire 5
 Mantle ventrally emarginate *S. insignis*
- 5 Dorsal arms with biserial suckers *S. hieronis*
 Dorsal arms with quadriserial suckers 6
- 6 Buccal membrane with a few small suckers *S. zanzibarica*
 Buccal membrane without suckers *S. acuminata*
- 7 Mantle ventrally entire *S. simoniana*
 Mantle ventrally emarginate 8
- 8 Tips of dorsal arms finger-like, devoid of suckers (Fig. 16a) 9
 Tips of dorsal arms normal, with suckers to the tips 10
- 9 Few or no papillae dorsally along outline of shell and on head *S. robsoni*
 Densely papillose dorsally (Fig. 15a) *S. faurei*
- 10 About 12 pairs of pores in the ventral mantle surface (Fig. 17b) *S. (Hemisepius) typica*
 No pores in the ventral mantle surface *S. (Hemisepius) dubia*
- 11 Skin tuberculate dorsally; ventrally with two large wrinkled patches on the mantle (Fig. 12) 12
 Skin smooth dorsally; no ventral wrinkled patches 13
- 12 Diameter of large tentacular suckers approximately equal to width of club (Fig. 11b) *S. papillata*
 Diameter of large tentacular suckers less than width of club (Fig. 11a) *S. tuberculata*
- 13 Shell ovate, width 32-46% length; inner cone well developed, reflexed and completely fused to outer cone (Pls 35c, d, 36a, b) *S. officinalis vermiculata*
 Shell elongate; inner cone reduced, with narrow limbs 14
- 14 Shell broadly elongate, width 29-37% length; no posterior wings on outer cone (Pl. 39a, b). 'Light organ' in mantle cavity *S. australis*
 Shell narrow elongate, width 14-26% length; outer cone with posterior wings (Fig. 2). No 'light organ' in mantle cavity. ('doratosepion' group) 15
- 15 Males (male of *S. adami* not known) 16
 Females. The females of the 'doratosepion' group are difficult to separate, and this part of the key is very tentative 19
- 16 Dorsal arms normal 17
 Dorsal arms modified (Figs 6c, 8e) 18
- 17 Fins rounded posteriorly *S. joubini*
 Fins extended posteriorly to form 'tail' (Fig. 4) *S. confusa*
- 18 Ventral arms with hectocotylyzed region and distal cirri (Fig. 8c, d); fins extended into points posteriorly *S. burnupi*
 Ventral arms without hectocotylyzed region or cirri; fins rounded posteriorly *S. incerta*

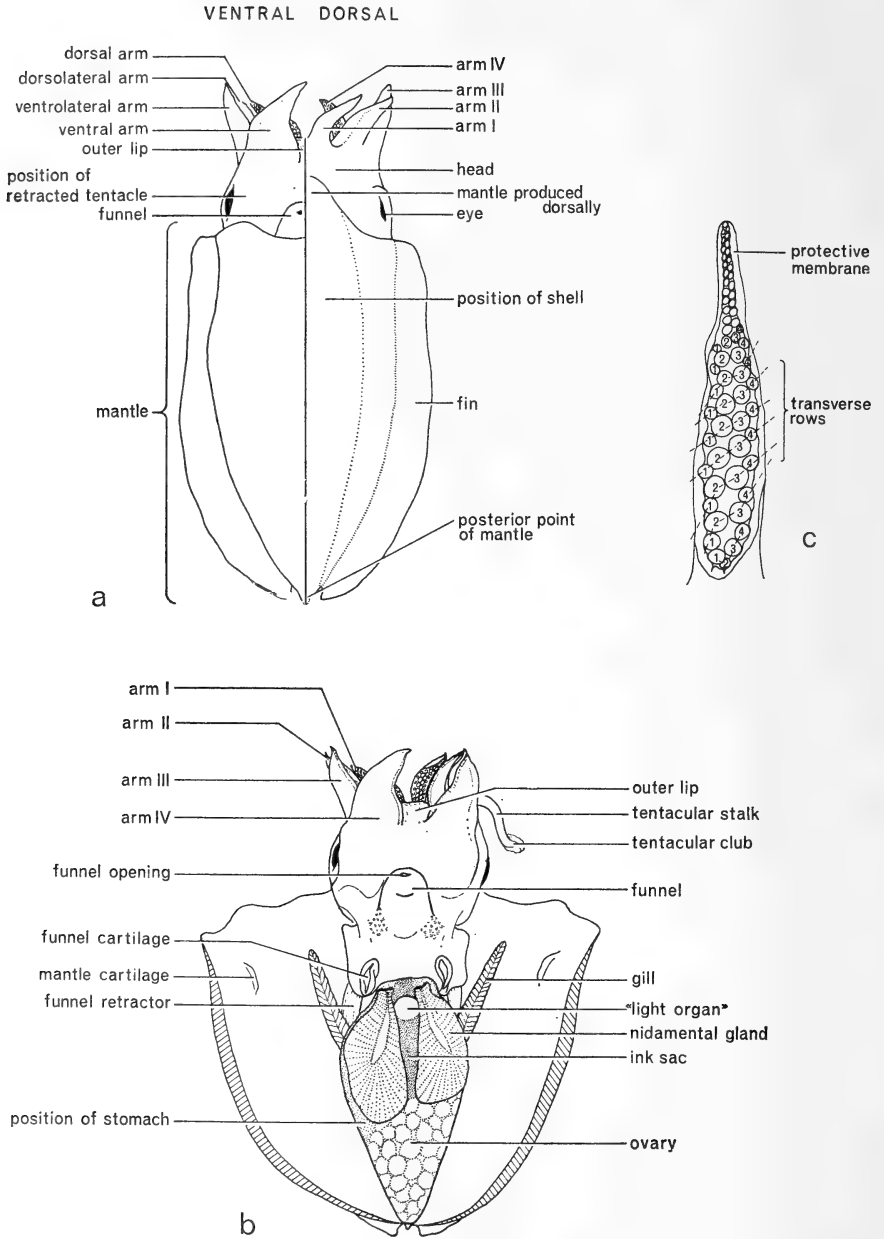


FIG. 1. General morphology of the Sepiidae, illustrated by *Sepia australis*. a. External features; b. the mantle cavity (the 'light organ' is characteristic of *S. australis* and does not occur in other Sepiidae); c. dorsal arm, to show the quadriserial arrangement of the suckers. Longitudinal series numbered 1-4. The suckers of series 1 and 4 are obscured distally by the protective membranes.

- 19 Lateral arms attenuated distally 20
 Lateral arms not attenuated distally *S. adami*
- 20 Lateral arms attenuated over their distal half; distal suckers biserial 21
 Lateral arms attenuated over less than half the arm length; distal suckers quadriserial 22
- 21 Protective membranes on distal part of dorsal arms expanded *S. joubini*
 Protective membranes on distal part of dorsal arms not expanded *S. confusa*
- 22 Shell with inner cone raised posteriorly; striated zone convex; striae convex (Fig. 6d) *S. incerta*
 Shell with inner cone low posteriorly; striated zone Λ -shaped; striae angular (Fig. 8a, Pl. 4d) *S. burnupi*

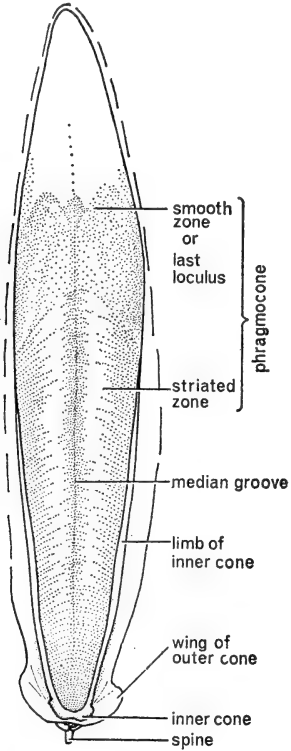


FIG. 2. Ventral view of the shell of *Sepia joubini* (A30141) showing some of the features mentioned in the descriptions. Length 37 mm.

KEY TO SHELLS ONLY

Sepia robsoni is not included in this key, as its shell is insufficiently known.

- 1 Posterior spine present 2
 Posterior spine absent 9
- 2 Ventral part of inner cone well developed 3
 Ventral part of inner cone reduced 4

3	Ventral part of inner cone not reflexed (Pl. 35b)	<i>S. zanzibarica</i>
	Ventral part of inner cone reflexed and completely fused to outer cone (Pls 35d, 36b)	<i>S. officinalis vermiculata</i>
4	Outer cone with posterior wings (Fig. 2)	5
	Outer cone without posterior wings	8
5	Inner cone raised posteriorly, forming a deep pocket over the end of the phragmocone (Pls 37d, 39b)	6
	Inner cone low posteriorly (Pl. 38d)	7
6	Posterior part of inner cone with a deep longitudinal groove (Fig. 6d)	<i>S. incerta</i>
	Posterior part of inner cone rounded, without longitudinal groove (Fig. 5)	<i>S. confusa</i>
7	Limbs of inner cone raised, lying on the phragmocone; striae \wedge -shaped (Pl. 38d, Fig. 8a)	<i>S. burnupi</i>
	Limbs of inner cone not raised, lying at sides of phragmocone; striae convex (Figs 2, 10a)	* <i>S. joubini</i> , <i>S. adami</i>
8	Shell rhomboidal, posterior spine not keeled (Pl. 37a, b)	<i>S. acuminata</i>
	Shell elongate oval, posterior spine keeled (Pl. 39a, b)	<i>S. australis</i>
9	Phragmocone considerably shorter than dorsal shield	10
	Phragmocone almost as long as dorsal shield	12
10	Anterior margin of phragmocone transverse, not parallel with corresponding margin of dorsal lamella (Fig. 17d)	11
	Anterior margin of phragmocone convex, more or less parallel with corresponding margin of dorsal lamella (Fig. 16c)	<i>S. faurei</i>
11	Shell dorsally chitinous, inner cone indistinct (Fig. 17c, d)	<i>S. (Hemisepius) typica</i>
	Shell dorsally calcified, inner cone distinct	<i>S. (Hemisepius) dubia</i>
12	Outer cone expanded posteriorly, inner cone reduced (Pl. 42d) (genus <i>Sepiella</i>) <i>Sepiella cyanea</i>	
	Outer cone narrow posteriorly, inner cone well developed and completely reflexed	13
13	Shell rounded anteriorly	14
	Shell acuminate anteriorly	17
14	Ventral surface flat or concave (Pls 39d, 40d)	<i>S. tuberculata</i>
	Ventral surface convex	15
15	Limbs of inner cone fairly broad, narrowing gradually anteriorly	16
	Limbs of inner cone broad posteriorly, narrowing suddenly anteriorly (Pl. 42b) <i>S. simoniana</i>	
16	Shell very broad (width 50–60% length) (Pl. 45); angle between striated zone and smooth zone pronounced in lateral view (Pl. 10d)	<i>S. angulata</i>
	Shell elongate oval (width 37–55% length) (Pl. 41); no pronounced angle between striated zone and smooth zone in lateral view	<i>S. papillata</i>
17	Limbs of inner cone lie at sides of phragmocone (Pl. 43)	<i>S. hieronis</i>
	Limbs of inner cone raised, lying on phragmocone	<i>S. insignis</i>

SYSTEMATIC DISCUSSION

DIAGNOSES OF FAMILY AND GENERA

Family **Sepiidae**

Mantle short, oval or rounded, dorso-ventrally flattened; fins lateral, occupying almost entire lateral margin of mantle; eye covered by a continuous membranous lid; arm suckers usually quadriserial, occasionally biserial; left

* On the available specimens no constant differences could be found between the shells of these two species.

ventral arm of male usually hectocotylized; tentacles completely retractable, tentacular club distinct from stalk, with subequal or unequal suckers. Shell internal, usually calcareous; phragmocone retained; conotheca reduced ventrally, represented by inner cone; posterior spine present or absent.

Genus *SEPIA* Linnaeus, 1758

Diagnosis as for family. Posterior gland absent; tentacular club with subequal or unequal suckers; locking apparatus simple, oval (Fig. 3a). Outer cone of shell not expanded posteriorly.

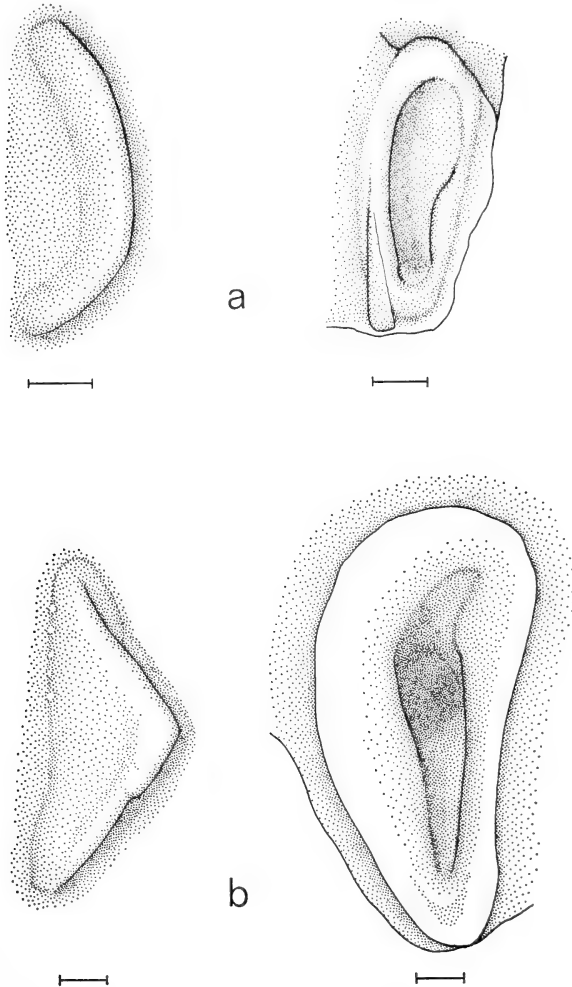


FIG. 3. Comparison of the mantle locking apparatus of a. *Sepia* (*S. australis*, ♀, A30154) and b. *Sepiella* (*S. cyanea*, ♂, A6526). Left, mantle component; right, funnel component. Scale = 1 mm.

Subgenus *Sepia* s.s.

Mantle slender to moderately broad; arm suckers biserial or quadriserial; tentacular suckers subequal or unequal. Shell slender to broadly oval, length approximately equal to dorsal mantle length; phragmocone occupies almost all dorsal shield; posterior spine present or absent.

Subgenus *Hemisepius* Steenstrup, 1875

Mantle very broad; arm suckers biserial; tentacular suckers subequal. Shell very thin, phragmocone shorter than dorsal shield; posterior spine absent.

Subgenus *Metasepia* Hoyle, 1885

Mantle broadly oval; arm suckers quadriserial; tentacular club with few unequal suckers. Shell rhomboidal, much shorter than mantle; posterior spine absent. (No southern African representatives.)

Genus *SEPIELLA* Gray, 1849

Posterior gland present; tentacular club with numerous subequal suckers; locking apparatus with tubercle on mantle component and corresponding depression in funnel component (Fig. 3b). Shell without posterior spine; outer cone expanded posteriorly.

DESCRIPTION OF SOUTHERN AFRICAN SPECIES

Sepia zanzibarica Pfeffer, 1884

(Pl. 35a, b. Tables 9, 10)

Sepia zanzibarica Pfeffer, 1884: 9, fig. 11, 11a. Hoyle, 1886: 22, 217. Smith, 1916: 21. Tomlin, 1923: 40. Massy, 1925: 211. Voss, 1962b: 248. Adam & Rees, 1966: 7, pl. 2, figs 9-11, pl. 41, fig. 247.

Type locality

Zanzibar.

Distribution

Animals: Zanzibar (Pfeffer 1884: 9), German East Africa (Massy 1925: 211).
Depth not known.

Shells: Mombasa (Adam & Rees 1966: 7) to Tongaat, Natal (Smith 1916: 21); also Malagasy (Adam & Rees 1966: 7).

Material

N.M. 959, 960, German East Africa (det. A. L. Massy); 1 ♂
S.A.M. A2141, Chinde, mouth of Zambezi River; 2 shells
Locality unknown; 1 shell

Description

Male (N.M.959) originally described by Massy (1925: 211), now in rather poor condition.

Mantle broadly oval, anterior mantle margin produced dorsally, ventrally entire. Fins narrow, rounded, separate posteriorly. 'The buccal membrane has a single sucker on five of its tips' (Adam & Rees 1966: 8). These not clearly visible in male, due to distorted state of buccal membrane.

Skin smooth, except for few tiny papillae mid-dorsally on mantle. Colour dark purple dorsally, with paler fins. Narrow dark purple line along fin bases. Colour ventrally lighter purple laterally on mantle, fading to mottled buff-purple mid-ventrally.

Arms unequal in length; shortest dorsally, longest ventrally, of formula 4.3.2.1. In female, arms I to III subequal, arms IV considerably longer (Pfeffer 1884: 9). Arms joined by shallow interbrachial web, except between ventral pair. All arms keeled, provided with well-developed protective membranes folding over inner surface; arm tips attenuated.

Suckers on all arms quadriserially arranged to tips. Chitinous rings of suckers smooth.

Left ventral arm hectocotylized. Basal two-thirds of arm bearing quadriserial suckers; suckers minute over six rows on distal third (as described by Massy 1925: 211). Adam & Rees (1966: 8) were mistaken in presuming that the hectocotylus was situated on the proximal third of the arm. Three dorsal series of minute suckers in normal position, ventral series displaced, leaving naked, grooved region on arm; tip of arm bearing normal quadriserial suckers.

Tentacular club long, bearing numerous subequal suckers in rows of about six, 'but probably form oblique transverse rows of eight' (Adam & Rees 1966: 8). Of these, three median series of suckers a little larger than others. In addition, three larger distal suckers partially concealed by reflexed tip of club. Chitinous rings of tentacular suckers finely dentate. Protective membranes well developed, remaining separate proximally and continuing along tentacular stalk for some distance. Natatory membrane a little longer than club.

Shell (N.M.960) of male specimen badly damaged. Three other shells (Pl. 35a, b) in fairly good condition, but somewhat worn.

Shell broadly oval, tapering anteriorly and posteriorly. Dorsal surface roughly granular posteriorly, more finely so anteriorly. Median ridge ill-defined. Two fairly well defined dorsal grooves diverging from posterior end correspond with position of ventral limbs of inner cone. Posterior spine short but strong, directed dorsally and coloured blue; spine not keeled. Striated zone long ventrally, occupying two-thirds to three-quarters shell length. Striae broad Δ -shaped, becoming somewhat more rounded anteriorly. Median groove broad, with phragmocone raised on either side. Inner cone very well developed posteriorly, free, curving over posterior part of striated zone to form a pocket. Limbs of inner cone broad, curving over lateral edges of phragmocone. Outer cone of present shells damaged, but according to Pfeffer's figure (fig. 11a) it broadens somewhat posteriorly without actually forming wings. Shell thickest on either side of midline, near anterior end of striated zone.

Remarks

It is not certain if this may be considered a southern African species, since only shells have been found on our coasts.*

Tomlin (1923: 40) mentions a specimen, presumably a shell, from Isipingo, but gives no details.

Sepia officinalis vermiculata Quoy & Gaimard, 1832

(Pls 35c, d, 36a, b. Tables 1, 2, 11-13)

Sepia vermiculata Quoy & Gaimard, 1832: 64, pl. I, figs 1-5. Férussac & d'Orbigny, 1835-1848: 279, pl. IIIbis. Gibbons, 1888: 202. Bartsch, 1915: 250. Smith, 1916: 20. Robson, 1924a: 12. Massy, 1925: 209; 1928: 91.

Acanthosepion vermiculatum Rochebrune, 1884: 113. Adam, 1944: 234.

Acanthosepion vermiculata: Robson, 1924b: 639. Massy, 1927: 156.

Sepia officinalis vermiculata Adam, 1940: 130; 1941: 99, 102, 106, pl. IV, fig. 1; 1962: 11. Voss, 1962b: 248, 249. Adam & Rees, 1966: 30, pl. 10, figs 55, 56, pl. 45, fig. 271.

? *Sepia jousseaumi* Rochebrune, 1884: 117. Smith, 1916: 22. Adam, 1941: 108, pl. IV, fig. 3; 1944: 235.

? *Sepia jousseaumi*: Bartsch, 1915: 250.

? *Sepia hierredda* (*non* Rang) Turton, 1932: 2.

Type localities

Cape of Good Hope (*S. vermiculata* and *S. jousseaumi*).

Distribution

Animals: 30° 42'S, 15° 59'E (Voss 1962b: 250) to Delagoa Bay, Moçambique (Massy 1927: 156; Adam 1962: 11). Depth 0-248 m.

Shells: Saldanha Bay to Chinde (S.A.M.).

Material

S.A.M. A2143, Chinde, mouth of Zambezi River; 1 shell

A2144, Durban; 1 shell

A30125, S 2° W of Cape Point, 23 km, 156 m; 4 juveniles

A30128, SE of Cape St. Blaize, 9 km, 62 m; 1 juvenile

A30129, Swartkops; 1 juvenile

A30130, Algoa Bay fishing grounds; 1 ♂

A30131, Table Bay; 1 ♀

A30182, locality unknown; 1 ♂

A30183, locality unknown; 1 ♀

A30483, Still Bay; 1 shell

A30487, locality unknown (det. A. L. Massy); 1 shell

A30496, locality unknown; 1 shell

A31238, off Hartenbos, near Mossel Bay, 18-24 m; 5 ♀

A31292, 33° 01'S, 17° 58'E (Saldanha Bay); 1 ♀

* Voss (personal communication) has two females caught off Beira in 1964 by the U.S. Indian Ocean Expedition. The localities are 19° 51'S, 36° 21'E, 62 m, and 20° 30'S, 35° 49'E, 32 m. The latter locality is within the limits of southern Africa as defined on page 194.

Locality unknown; 1 ♀
 Knysna estuary; 30 ♂, 18 ♀
 Durban Bay; 1 ♂, 6 ♀
 Ysterfontein beach; 1 shell
 Nature's Valley; 1 shell, discarded
 Breede River mouth; 1 shell
 Krom River mouth, Cape St. Francis; 12 shells
 Saldanha Bay; 2 shells

Description

Mantle broadly oval, anterior margin somewhat produced dorsally, ventrally entire. Head short and broad; fins broad and rounded but separate posteriorly. Mantle slightly more slender and fins slightly wider in males than in females.

Skin smooth, except in one male (A30130), which is sparsely papillose dorsally, mainly on head. No indication in any specimens of long ridge-shaped tubercles near fins, as mentioned by Massy (1925: 210), although some have pale pink round spots in this region. Colour dark dorsally, pale ventrally and some specimens show the well-known transverse zebra-like stripes dorsally on mantle and on fourth arms, or at least at fin bases. Three specimens (males A30130 and A30182 and female, locality unknown) with pale stripes on dark background, but one female (A30183) with dark stripes on pale background.

Arms longest ventrally, shortest dorsally, with arm length formula 4.3.2.1. Arms joined by shallow web; arms III and IV keeled, arms II sometimes keeled, arms I usually not—depending on manner of preservation. Arm tips somewhat attenuated. Suckers quadriseriably arranged on all arms to tips, decreasing regularly in size from arm base. All sucker rings finely dentate, distal teeth being longer than proximal ones. Protective membranes well developed.

Left ventral arm of male hectocotylized basally. About six normal suckers at base of arm followed by 9–12 rows of modified suckers. The latter much smaller and separated by transverse ridges on arm. Arm normal distally.

Tentacular club bearing small distal suckers in oblique rows of eight. Suckers on proximal part of club variously enlarged: from ventral side, first series of suckers of normal size, second series 1.5–2 times as big as first series, third series 2.5–3 times as big as first series, fourth series 1–1.5 times as big as first series, fifth series same size as first series. Rings of large club suckers smooth, those of smaller suckers toothed distally. One sucker at tip of club concealed by reflexed tip; immediately below this, two suckers, about twice as big as their proximal neighbours, partly concealed by tip. Protective membranes of club not meeting proximally; natatory membrane a little shorter than club.

Shell (Pls 35c, d, 36a, b) broadly oval, tapering somewhat anteriorly and posteriorly; posterior spine present. Posterior end of shell and base of spine covered with horny covering. Dorsal surface of shell tuberculate, with fairly broad chitinous margin. No marked dorsal ridge. Ventral striated zone fairly

long (about half total length), with median longitudinal ridge. Anterior border of striated zone convex on either side of median ridge. Inner cone broad, reflexed and fused to broad outer cone.

Seven shells from Durban Bay have two deep lateral grooves in ventral surface (Pl. 35d). These grooves do not occur in any other shells, and it is strange that all seven shells should have them, as these animals, though from the same locality, were not all caught at the same time (two were caught in February 1970 and the other five in April 1970).

Remarks

Adam (1941: 104) has shown that *Sepia officinalis* in the eastern Atlantic Ocean is represented by four geographic races:

S. o. officinalis Linnaeus, 1758: from the Atlantic coast of France to Rio de Oro (Cap Blanc).

S. o. filliouxii Lafont, 1868: from the Atlantic coast of France to the southern coast of Scandinavia.

S. o. hierredda Rang, 1837: from south of the Baie du Lévrier (Mauritania) to the coast of Angola.

S. o. vermiculata Quoy & Gaimard, 1832: southern Africa.

In addition a fifth race, *S. o. mediterranea* Ninni, 1884, lives in the Mediterranean Sea (Adam & Rees 1966: 32).

TABLE 1. A comparison of the relative dimensions (as % MLD) of the animals of the races *Sepia officinalis vermiculata* and *Sepia officinalis hierredda*. Only animals with dorsal mantle length greater than 100 mm are included. The figures for *S. officinalis hierredda* were calculated from relative dimensions given by Adam (1941).

		Females		Males	
		Range	Mean	Range	Mean
MW	<i>S. o. vermiculata</i>	43,8-63,1	55,0	38,4-57,4	49,9
	<i>S. o. hierredda</i>	41-51	46,0	40-51	44,1
HW	<i>S. o. vermiculata</i>	34,9-50,0	43,4	36,9-46,3	41,5
	<i>S. o. hierredda</i>	31-42,5	35,3	28-36	31,9
AL I	<i>S. o. vermiculata</i>	27,7-55,0	38,9	28,8-46,3	37,3
	<i>S. o. hierredda</i>	26,5-33,5	30,2	26,5-40	34,1
AL II	<i>S. o. vermiculata</i>	29,8-57,9	42,7	34,1-49,3	39,4
	<i>S. o. hierredda</i>	28-36,5	31,3	30-40	36,1
AL III	<i>S. o. vermiculata</i>	31,9-60,3	44,0	35,7-54	43,3
	<i>S. o. hierredda</i>	28,5-37,5	33,8	33,5-43	39,2
AL IV	<i>S. o. vermiculata</i>	37,2-79,3	53,6	40,5-63,2	48,9
	<i>S. o. hierredda</i>	32,5-48	39,5	40-63	50,2
Tcl	<i>S. o. vermiculata</i>	25,7-38,2	30,4	23,8-34	28,2
	<i>S. o. hierredda</i>	20,5-24,5	23,0	19-23	22,2

Adam (1941: 103) was able to show some differences in the shells of the Atlantic races, but could find no marked differences in the forms of the animals. He observed that *S. o. vermiculata* differs from *S. o. hierredda* in that the shell is relatively wider and thicker and is more strongly tuberculate dorsally. Adam & Rees (1966: 32) added that the posterior part of the shell of *S. o. vermiculata* seems to be more broadly rounded than that of *S. o. hierredda*.

A comparison of the measurements of the *S. o. vermiculata* specimens described above, with those given for *S. o. hierredda* by Adam (1941: 157-159), shows that there are indeed some differences, but only in specimens having a dorsal mantle length exceeding 100 mm. The most marked differences between the two races is observable in the tentacular clubs (Table 1). The clubs of *S. o. vermiculata* are relatively longer than those of *S. o. hierredda*, and there is apparently no overlap in the ranges of this dimension for the two races. The differences in the other relative dimensions are less marked, but *S. o. vermiculata* has a relatively wider mantle and head, and longer arms (except the fourth arm in the males) (Table 1). The relative dimensions of the shells also show some differences between the two races (Table 2). The shells of *S. o. vermiculata* are relatively wider and thicker and have a slightly shorter striated zone. These differences become more marked, the larger the shells.

TABLE 2. Comparison of relative shell dimensions (as % L) of *S. officinalis vermiculata* and *S. o. hierredda*. Only shells of length greater than 100 mm are considered. The figures for *S. o. hierredda* were calculated from relative dimensions given by Adam (1941).

		Range	Mean
Width	<i>S. o. vermiculata</i>	32,8-41,7	38,5
	<i>S. o. hierredda</i>	30-36,5	34,0
Thickness	<i>S. o. vermiculata</i>	9,1-15,2	12,5
	<i>S. o. hierredda</i>	9,4-12,6	11,1
Length of striated zone	<i>S. o. vermiculata</i>	40,5-74,8	50,3
	<i>S. o. hierredda</i>	43,5-70,5	57,5

The males of *S. o. vermiculata* and *S. o. hierredda* cannot be distinguished by their hectocotyli. The hectocotylus of *S. o. hierredda* has 8-13 transverse rows of modified suckers (Adam 1941: 106). In the present specimens of *S. o. vermiculata* the hectocotylus has 9-12 rows of modified suckers. The extent of sucker modification seems to increase with the size of the animal. Massy (1925: 210) reported a large male of *S. o. vermiculata* (MLd 6½ inches = 165 mm) having 17 rows of modified suckers on the hectocotylus.

The southernmost record of *S. officinalis hierredda* is the Baia dos Tigres, Angola (about 15° 20'S); *S. officinalis vermiculata* is known to occur as far north as 30° 42'S (north of the Olifants River) off the west coast of southern Africa

(Fig. 18). Dr. M.-L. Penrith (personal communication) points out that no sepiid shells were found on any but the northernmost beaches of South West Africa, although much other debris was washed up. In Angola, where *S. o. hierredda* is known to occur, sepiid shells were present on the beaches. The apparent paucity of Sepiidae off the South West African coast suggests that there may be no region of overlap between *S. o. hierredda* and *S. o. vermiculata*.

On the east coast, animals of *S. o. vermiculata* have been found as far north as Delagoa Bay (Massy 1927: 156; Adam 1962: 11). Barnard collected a shell (A2143) from Chinde, near the mouth of the Zambezi River; but this cannot be considered a reliable locality, since sepiid shells have been known to drift over long distances.

It is of interest to note that *Sepia officinalis* is the only species of *Sepia* known to occur in estuaries in southern Africa. This, its wide geographic distribution and its division into several geographic races, indicate that it is a very adaptable species.

Sepia acuminata Smith, 1916

(Pl. 37a, b. Tables 14-16)

Sepia acuminata Smith, 1916: 21, pl. II, fig. 3 (*partim*). Tomlin, 1923: 40. Robson, 1924a: 12. Massy, 1928: 91, pl. VIII, figs 1-7. Turton, 1932: 1. Voss, 1962b: 248. Adam & Rees 1966: 53, pl. 16, figs 91, 92, pl. 43, fig. 261.

non Sepia acuminata Smith, 1916: *non* pl. II, fig. 4 (= *S. hieronis*).

Rhombosipion acuminata Robson, 1924b: 643.

Sepia sp. Adam, 1941: 121, pl. IV, fig. 6.

Type localities

Port Elizabeth; Tongaat beach, Natal (shells only).

Distribution

Animals: 29° 54'S, 31° 15'E (Robson 1924b: 643, Sta. 103) to Punta Zavora, Moçambique (S.A.M.). Depth 64-369 m.

Shells: Cape St. Francis (S.A.M.) to ? Mombasa (Adam & Rees 1966: 53).

Material

S.A.M. A30147, locality unknown; 1 ♂

A31398, Corner, Moçambique, 25° 15'S, 35° 10'E, ± 266 m; 1 ♂, 1 ♀

A31399, Corner, Moçambique, 25° 15'S, 35° 10'E, 248 m; 1 ♂

A31400, Corner, Moçambique, 25° 15'S, 35° 10'E, 257 m; 1 juvenile

A31401, Punta Zavora, Moçambique, 24° 35'S, 35° 25'E, 220-257 m;

1 ♂

N.M. 964, 965, off Tugela River, 48 km out, 64 m (det. A. L. Massy); 1 ♂, 1 ♀

Krom River mouth, Cape St. Francis; 1 shell (broken)

Umngazana River mouth, west Pondoland; 1 shell

Description

Mantle broadly oval, anterior margin produced to fairly sharp point dorsally, halfway along eyes or more; ventrally entire. Fins narrow, rounded and separate posteriorly.

Skin smooth. Coloration (described from recently caught specimens from Moçambique; other specimens considerably faded): dense concentration of purple chromatophores dorsally on mantle, head and arms; fins pale at edges. Chromatophores less dense ventrally, resulting in paler purple colour near fins and brownish colour medially on mantle. Ventral surface of head and arms almost white.

Arms short (less than half MLd), but somewhat longer in females than in males. Arms I to III subequal in length, arms IV somewhat longer. Shallow interbrachial web present, except between arms IV. All arms keeled to some extent and bear moderately well developed protective membranes.

Arm suckers globose, quadriserially arranged to tips of arms. Chitinous rings of suckers finely toothed distally, with nodular surface; adjacent skin of suckers wrinkled.

Left ventral arm of male hectocotylized distally. Six or seven rows of normal suckers on basal third of arm, followed by nine to ten modified rows, in which all suckers greatly reduced in size. Two dorsal series of modified suckers in normal position, but the two ventral series have moved close together on ventral edge of sucker-bearing surface, almost forming single line. Thus two dorsal series widely separated from two ventral series by naked, wrinkled region. Distal third of arm with normal suckers, decreasing in size to arm tip.

Tentacular club recurved, bearing numerous small subequal suckers in transverse rows of eight. Reflexed tip of club obscures two somewhat larger suckers. Sucker rings toothed distally; protective membranes separate proximally; natatory membrane somewhat longer than club.

Shell (Pl. 37a, b) broadly elongate, sharply pointed anteriorly, rounded posteriorly, bearing spine with tip directed dorsally; spine not keeled. Dorsal surface of shell usually pink in colour, with broad chitinous margins laterally and with median ridge sometimes sunken below level of rest of dorsal surface. Striated zone long ventrally (about two-thirds total length); median groove very faint or absent; striae regularly convex. Inner cone not much thickened posteriorly, with narrow limbs curving over lateral edge of striated zone. Outer cone only slightly calcified and mostly chitinous posteriorly, where it curves sharply in ventral direction. Shell thickest at anterior end of striated zone.

Remarks

In Smith's (1916: 21) original description, he mentioned and figured (pl. II, fig. 4) one specimen from Tongaat Beach which differed from the other examples of *S. acuminata*. From the figure, this specimen is clearly *S. hieronis* (cf.).

The shell from the 'Ph. Dautzenberg' collection, illustrated by Adam (1941, pl. IV, fig. 6) looks very much like that of *S. acuminata*.*

Adam & Rees (1966: 53) reported some broken shells, almost certainly pertaining to *S. acuminata*, from Mombasa. This identification is the more probable since *S. acuminata* is now known to occur as far north as Moçambique, and is apparently a subtropical species. The male specimen reported by Adam & Rees from the U.C.T. Ecological Survey, AFR 1051 K, comes from 29° 54'S, 31° 13'E, 369 m (ex U.C.T. catalogue).

Sepia confusa Smith, 1916

(Pl. 37c, d. Figs 4, 5. Tables 17-19)

Sepia burnupi Hoyle, 1904: 27, pl. I, fig. 192 (*partim*).

Sepia confusa Smith, 1916: 24, pl. II, figs 7, 8. Tomlin, 1923: 41. Robson, 1924a: 12. Turton, 1932: 1. Voss, 1962b: 248. Adam & Rees, 1966: 65, pl. 18, figs 112, 113, pl. 42, fig. 248.

Doratosepion confusa Massy & Robson, 1923: 435, figs 1-3. Carleton & Robson, 1924: 259, pl. 3, figs 1-6.

Doratosepion confusum: Robson, 1924b: 647.

Sepia (Doratosepion) confusa Massy, 1925: 221, pl. XIII, figs 20, 21, 24-28, pl. XIV, fig. 38; 1928: 93.

Type localities

Port Elizabeth; Tongaat beach, Natal (shells only).

Distribution

Animals: 29° 52'S, 31° 17'E (off Durban) (Robson 1924a: 12, 1924b: 647, Sta. 95) to 5° 39'S, 39° 16'E (Zanzibar area) (Adam & Rees 1966: 65). Depth 64-352 m.

Shells: Port Elizabeth (Hoyle 1904: 27) to Chinde, mouth of Zambezi River (S.A.M.).

Material

S.A.M. A2140, Chinde, mouth of Zambezi River; 1 shell

A6516, off Tugela River, 116-134 m; 1 ♂

A30292, 35 km S of Tugela River, 116-134 m; 2 ♂, in poor condition

A31402, Corner, Moçambique, 25° 15'S, 35° 10'E, ± 266 m; 4 ♂

A31403, Corner, Moçambique, 25° 15'S, 35° 10'E, 257 m; 1 ♀

A31404, Punta Zavora, Moçambique, 24° 35'S, 35° 25'E, 220-257 m; 2 ♂

N.M. 961, 962, 48 km off Tugela River, 64 m (det. A. L. Massy); 2 ♂

N.M. 963, Natal coast (det. A. L. Massy); 2 shells

Description

Mantle elongate, anterior margin strongly produced dorsally, ventrally slightly emarginate. Fins of male very broad, especially towards posterior end, and extended to form 'tail' beyond posterior end of mantle (Fig. 4). 'Tail'

* This identification has been confirmed by Adam (personal communication).

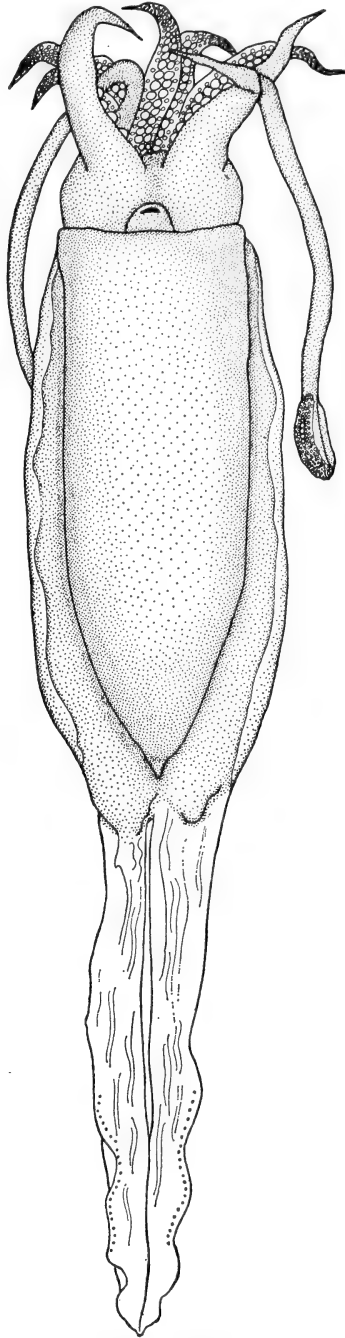


FIG. 4. Ventral view of *Sepia confusa* male, to show 'tail'-like extension of fins. Modified after Massy & Robson (1923).

length approximately equal to or greater than MLd. Fins of female rounded and separate posteriorly, not forming 'tail'.

Skin smooth, except in one male (A6516) which has few small papillae mid-dorsally on mantle. Colour dark purple mid-dorsally on mantle and above eyes. Rest of body paler pinkish-brown, where chromatophores less expanded. Ventral surface of head almost white.

Arms relatively short (not more than half MLd). Dorsal arms of males slightly longer than others, which are subequal in length. Arms of female subequal. Interbrachial web deepest between arms III and IV, absent between fourth pair. Arms I to III slightly keeled, arms IV more strongly so. Protective membranes fairly well developed, especially along attenuated part of arms, where membrane curves over, partially covering suckers. Arms attenuated at tips in males, over about half arm length in female. No sign of hectocotylization in males.

Arm suckers globose, with smooth rings; quadriserially arranged to tips of arms in males. Proximally, two median series of suckers much larger than lateral series, but on attenuated part of arm all suckers minute and of same size. In female, suckers as those of males proximally, but becoming biserial and widely spaced over flattened attenuated part of arm.

Tentacular club slightly recurved, with distal suckers in oblique rows of eight, and with nine median suckers variously enlarged. Of these, five much larger, other four grading to normal size. Three slightly larger suckers partially concealed by reflexed tip of club. Sucker rings broad and nodular, with finely dentate inner edge. Protective membranes of club moderately well developed, separate proximally. Natatory membrane a little longer than club.

Shell (Pl. 37c, d, Fig. 5) very narrow, pointed anteriorly, with posterior spine directed dorsally. In male specimens from Mozambique, delicate keel runs from base of spine and for some distance along dorsal face of shell; dry shells show no indication of keel on spine. Dorsal surface of shell with narrow, heavily calcified region medially, coloured pink; shell chitinous laterally. Distinct broad median ridge, narrowing posteriorly, limited by lateral grooves. Whole dorsal surface shows concentric striae, \wedge -shaped. Ventral striated zone just over half total length. Striae wavy, anterior border of striated zone angular on either side of midline (\wedge -shaped). Median longitudinal groove distinct. Inner cone forms free ledge posteriorly (Fig. 5) and has long narrow limbs. Outer cone broad and deep posteriorly, forming chitinous wings. Shell thick, ventral surface strongly convex; maximum thickness occurring immediately anterior to striated zone.

Remarks

Detailed structure and possible function of the 'tail' are discussed by Massy & Robson (1923) and by Carleton & Robson (1924).

The male of *S. confusa* is distinguished from the other 'doratosepion' species by its 'tail'-like extension of the fins. The female may be separated from all

except *S. joubini* by the biserial sucker arrangement on the attenuated part of the arms. It is distinct from the latter species in that the protective membranes on the tips of the dorsal arms are not expanded as they are in *S. joubini*.

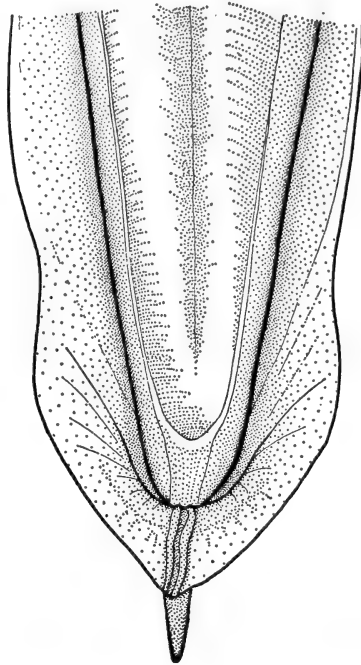


FIG. 5. *Sepia confusa* male (A31402). Detail of posterior end of shell, ventral view.

Sepia incerta Smith, 1916

(Pls 38a, b, 39a, b. Fig. 6. Tables 20–22)

Sepia burnupi Hoyle, 1904: 27, pl. I, figs 190, 191 (*partim*).

Sepia incerta Smith, 1916: 23, pl. II, fig. 6. Tomlin, 1923: 41. Voss, 1962b: 248. Adam & Rees, 1966: 67, pl. 19, figs 114, 115, pl. 41, fig. 241.

Sepia (Doratossepion) incerta Massy, 1925: 219, pl. XIII, figs 22, 23, 29–36, pl. XIV, figs 40, 43.

Sepia (Doratossepion) burnupi (*non* Hoyle) Massy, 1925: 215, pl. XII, figs 12–19, pl. XIV, figs 39, 41, 42; 1928: 94. Barnard, 1962: 252, fig. 4.

? *Sepia incerta*: Turton, 1932: 1.

Type localities

Port Elizabeth; Tongaat beach, Natal (shells only).

Distribution

Animals: 33° 07'S, 27° 56'E* (East London area) (Barnard 1962: 252) to Durban (Adam & Rees 1966: 67). Depth 70–79 m.

* Not 33° 04'S, 27° 54'E, 27 fm., as stated by Barnard (1962: 252).

Shells: Port Elizabeth (Hoyle 1904: 27) to Tongaat beach, Natal (Smith 1916: 23).

Material

S.A.M. A30143, 33° 07'S, 27° 56'E,* 79 m; 5 ♂, 1 ♀

A30480, locality unknown; 2 shells

S.A.M. S1, Punta Zavora, Moçambique; 9 shells

N.M. 956, 957, 958 A, B, Natal coast, in stomach of Ground Shark (det. A. L. Massy); 2 ♂, 2 shells

N.M. 969, 970, Cape Henderson (det. A. L. Massy); 1 ♀, 3 shells

Description

Mature males: mantle elongate, about three times as long as wide. Anterior mantle margin produced dorsally, emarginate ventrally. Fins narrow, fused posteriorly over tip of mantle.

Chromatophores densest mid-dorsally, fewer towards fins and sides of head; ventrally sparse, forming spots on mantle and, in one large specimen, larger spots on funnel. Series of large spots present along dorsal midline of each fin.

Arm lengths unequal (formula 1.4.2 = 3). Dorsal arms longest, modified (Fig. 6c): proximal quarter bearing 10–18 normal suckers basally, then 8–10 suckers on thickened transverse ridges on arm. Above this, protective membranes expanded over about half arm length, supported by transverse thickenings in the membrane. Membranes joined over inner surface, distal to sucker bearing portion of arm; ventral membrane more expanded than dorsal one and forming lamella with maximum width of 10–20 mm, about three-fifths from arm base. Distal quarter of arm attenuated, with protective membranes rapidly reduced towards arm tip.

Lateral and ventral arms bearing suckers quadriserially arranged almost to tips; median suckers larger than lateral suckers, situated on protective membranes. Suckers on these arms decrease gradually in size towards tip—none enlarged. No sign of hectocotylyzation on either ventral arm in any males.

Suckers globose; rings very finely serrated, almost smooth. Skin wrinkled immediately adjacent to chitinous rings of suckers.

Arms joined by shallow web, deepest between arms III and IV; no web between ventral pair.

Tentacular club recurved, bearing numerous small suckers distally in obliquely transverse rows of eight. Four or five suckers at proximal end of one of the median rows much enlarged. Large club suckers with finely serrated rings, small ones with toothed rings. Natatory membrane extends a little beyond proximal limit of club; protective membranes separate distally.

Young male (A30143, MLd 93 mm): dorsal arms shorter than ventral arms, but modified to some extent. Protective membranes well developed,

* See footnote on p. 213.

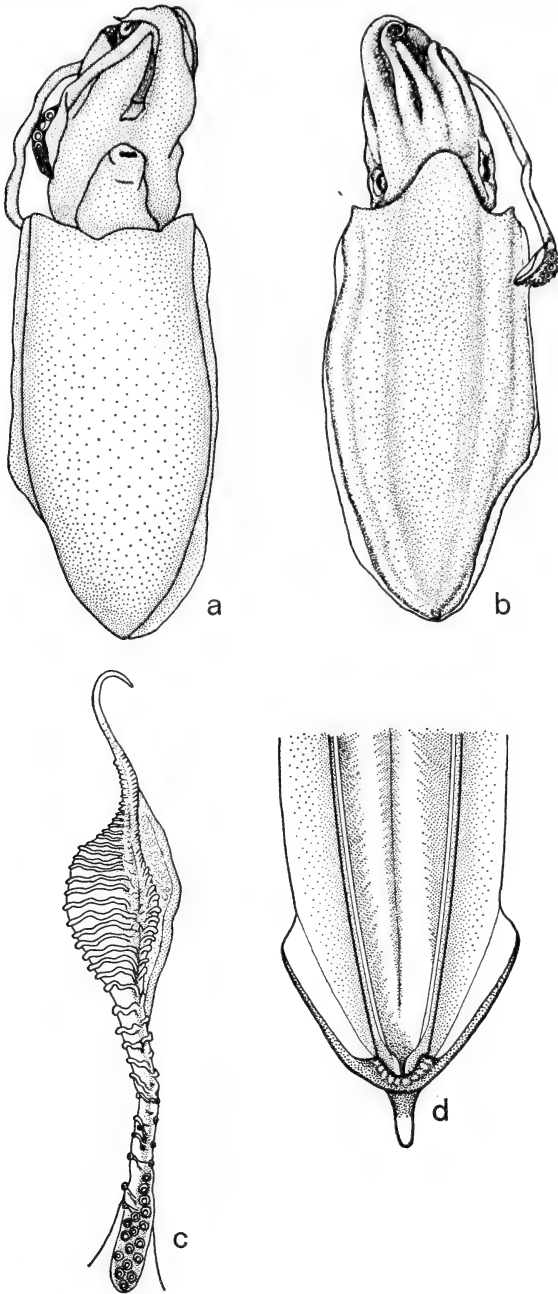


FIG. 6. *Sepia incerta*. a. Ventral and b. dorsal views of female (A30143). c. Right dorsal arm of male; d. detail of posterior end of shell (δ , A30143), ventral view. c. Modified after Barnard (1962); a. b. and d. original.

increasing gradually in width towards distal end, but not forming marked lamellate expansions found in mature males. Protective membranes only 3 mm wide at maximum width, but already fused over inner surface of arm. On proximal two-fifths, 14 normal suckers and 10–12 suckers on transverse ridges. Ventral arms relatively shorter than in mature males.

Females (Fig. 6a, b): small in comparison with large males, but mature. Ovary well developed, containing numerous oval eggs. Well developed nidamental glands present. Females differ from males in that dorsal arms not modified; arm formula variable. Lateral arm pairs not equal in length, unlike those of males. Dorsal arms of female with well developed protective membranes, but these not expanded into lamellae. All arms of female bear quadriserial suckers. Arm tips (less than half arm length) attenuated, bearing quadriserial suckers and having well-developed protective membranes folding over inner surface of arm.

Shell (Pls 38a, b, 39a, b) narrow, elongate, acuminate anteriorly and posteriorly. Dorsally with wide chitinous margins and three median longitudinal ridges, pink in colour, separated by two longitudinal grooves. Median ridge broad anteriorly, narrowing posteriorly; two lateral ridges narrow and indistinct anteriorly, but broader and more marked posteriorly. Ventrally with shallow longitudinal median groove. Striated zone long and anteriorly convex. Striae \wedge -shaped posteriorly, becoming more convex anteriorly. Inner cone with long narrow limbs lying at sides of striated zone; inner cone raised posteriorly to form ledge over end of striated zone. Centre of this posterior ledge bisected by deep longitudinal groove (Fig. 6d). Outer cone forming posterior, chitinous wings, and thickened over base of spine. Spine not keeled; directed dorsally.

Remarks

The soft parts of *Sepia incerta* were first described by Massy (1925: 215, 219). She described two males as *S. burnupi* and two females as *S. incerta*, but a re-examination of the shells of these specimens has indicated that in fact all four specimens are referable to *S. incerta*. Barnard (1962: 252) described another six specimens of *S. incerta* under the name *S. burnupi*.

S. incerta is distinguished from the other species of the 'doratossepion' group as follows: The male of *S. incerta* is characterized by its modified dorsal and unmodified ventral arms. The female is distinct from those of *S. confusa*, *S. joubini* and *S. adami* in that less than half the arm length is attenuated distally, and the suckers on the attenuated part are quadriserial. From the female of *S. burnupi* it can only be separated by the differences in the shells (and the larger size of the animals).

The shell of *S. incerta* differs from those of *S. burnupi*, *S. joubini* and *S. adami* in that the inner cone is raised posteriorly, forming a deep pocket over the end of the striated zone, as in *S. confusa*. It differs from the latter species in having a deep longitudinal groove in the centre of the raised posterior portion of the inner cone.

Sepia burnupi Hoyle, 1904

(Pl. 38c, d. Figs 7, 8. Tables 23, 24)

Sepia burnupi Hoyle, 1904: 27, pl. I, figs 188, 189 (*partim*). Bartsch, 1915: 250. Smith, 1916: 23, pl. II, fig. 5. Voss, 1962b: 248. Adam & Rees, 1966: 81, pl. 20, figs 127, 128.

non Sepia burnupi Hoyle, 1904: *non* pl. I, figs 190, 191 (= *S. incerta*), *non* pl. I, fig. 192 (= *S. confusa*).

Sepia exsignata Barnard, 1962: 250, fig. 3.

non Sepia burnupi: Barnard, 1962: 252, fig. 4 (= *S. incerta*).

? *Sepia burnupi*: Turton, 1932: 1.

Type localities

Umkomaas, Natal (*S. burnupi*, shells only); off Umhlanga River, Natal, 40–48 m (*S. exsignata*).

Distribution

Animals: Off Umhlanga River, Natal (Barnard 1962: 252). Depth 40–48 m.

Shells: ? Port Alfred (Turton 1932: 1) to Tongaat beach, Natal (Smith 1916: 23).

Material

S.A.M. A2147, Scottburgh, Natal; 3 shells

A6525, off Umhlanga River, Natal, 40–48 m; 1 ♂, 1 ♀ (holotype and allotype of *S. exsignata*)

N.M.958 C, ? Natal coast; 1 shell

N.M.4073, off Umhlanga River, Natal, 40–48 m; 1 ♂ (paratype of *S. exsignata*)

Description

Mantle elongate oval, anterior margin somewhat produced dorsally, emarginate ventrally. Mantle pointed posteriorly. Fins beginning at anterior mantle edge, fairly wide. Fins of male drawn out into overlapping points posteriorly (Fig. 7b); rounded ventrally and meeting in midline in female (Fig. 7a).

Skin sparsely papillose dorsally over head and mantle, with a series of elongate tubercles along fin bases dorsally. Skin smooth ventrally, except for longitudinal dermal fold on each side of mantle, between midline and fin bases.

Colour dark dorsally, particularly between eyes and on that part of mantle covering shell; fins pale. Ventral surface pale, but with scattered chromatophores between dermal folds and fins. In addition, female has four oval silvery-blue spots dorsally between eyes.

Arms of female subequal in length, except ventral pair, which a little longer. Arm tips somewhat attenuated; arms III and IV keeled. Suckers on all arms quadriserial, decreasing in size towards tips. Median series of suckers somewhat larger than lateral series.

In male, dorsal and ventral arms modified. Dorsal arms (Fig. 8e) bearing long cirriform processes laterally, and shorter ones on dorsal margin, supporting broad protective membranes. Basally, suckers normal and quadriserial, but rapidly decreasing in size distally, where cirriform processes extend further

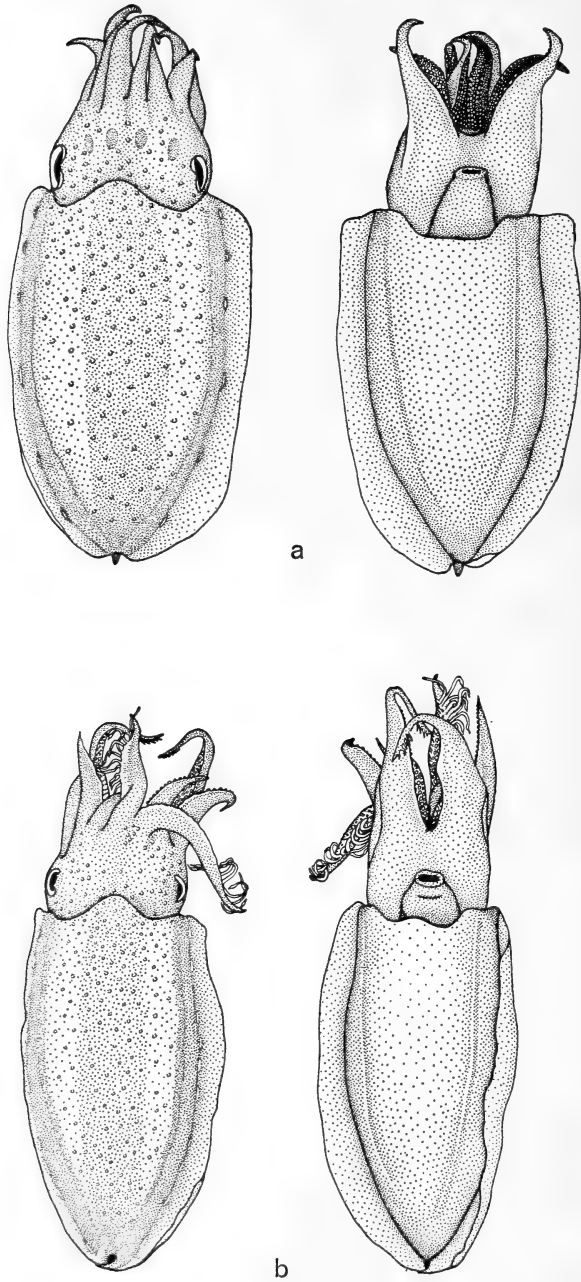


FIG. 7. *Sepia burnupi*, A6525. a. Female (allotype of *S. exsignata*), b. male (holotype of *S. exsignata*). Left: dorsal and right: ventral views.

towards midline of arm, until at distal end they alternate medially with minute, biserial suckers. Tips of lateral cirri swollen. Distal tip of arm (about 2 mm) bare, without suckers or cirri.

Right ventral arm of male with normal quadriserial suckers over most of its length, decreasing markedly in size distally, followed by short bare portion of the arm. Tip bearing short cirri, of which dorsal cirri better developed than ventral ones (Fig. 8d). There are a few small suckers between the cirri. Left ventral arm (Fig. 8c), the hectocotylus, basically like right ventral arm; but in second quarter of arm, ventral protective membrane very well developed, thrown into folds, and ventral series of suckers absent.

Lateral arms like those of female, with quadriserial suckers decreasing in size towards attenuated arm tips. In both sexes, sucker rings without teeth, nodular on upper surface.

Tentacular club of both sexes slightly recurved (Fig. 8b), bearing small suckers in oblique rows of eight, and five suckers greatly enlarged. Two suckers at tip larger than their neighbours, partly covered by reflexed tip of club. All tentacular sucker rings finely dentate. Protective membranes well developed, approximating very closely at base of club, without fusing. Natatory membrane only a little longer than club.

Shell (Pl. 38c, d, Fig. 8a) narrowly elongate, pointed anteriorly and posteriorly. Dorsally, shell calcified only along narrow median strip; laterally with broad chitinous margins. Calcified region finely granular, coloured pink, with fairly well defined median ridge. Posterior spine directed dorsally, not keeled. Deep median ventral groove present over whole length of shell. In region of striated zone, ventral surface highest at limbs of inner cone, shelving to lowest point at median groove, giving ventral surface Λ -shape in cross-section. Striated zone long, with acuminate anterior border. Striae Λ -shaped. Inner cone has curved around lateral edges of striated zone, covering its sides with very thin layer (through which striae can be seen) and having, like *S. insignis*, its limbs lying on the phragmocone and not at its sides. Inner cone only very slightly raised posteriorly, not forming ledge. Outer cone fairly narrow, but forming wings posteriorly. Shell thickest just anterior to striated zone.

Remarks

Hoyle (1904: 27) originally described *S. burnupi* on the basis of five shells. Smith (1916: 23), on re-examining these shells, and with additional material, separated them into three species, *S. burnupi*, *S. incerta* and *S. confusa*.

The first animals referred to *S. burnupi* were two male specimens described by Massy (1925: 215), but these in fact pertain to *S. incerta*. Barnard (1962: 250) described two males and one female (S.A.M. A6525, N.M. 4073) as a new species, *Sepia exsignata*. Adam & Rees (1966: 83), going only by Barnard's description, suggested that *S. exsignata* is probably synonymous with *S. burnupi*. The decalcified shell of *S. exsignata* was examined and, despite its rather poor

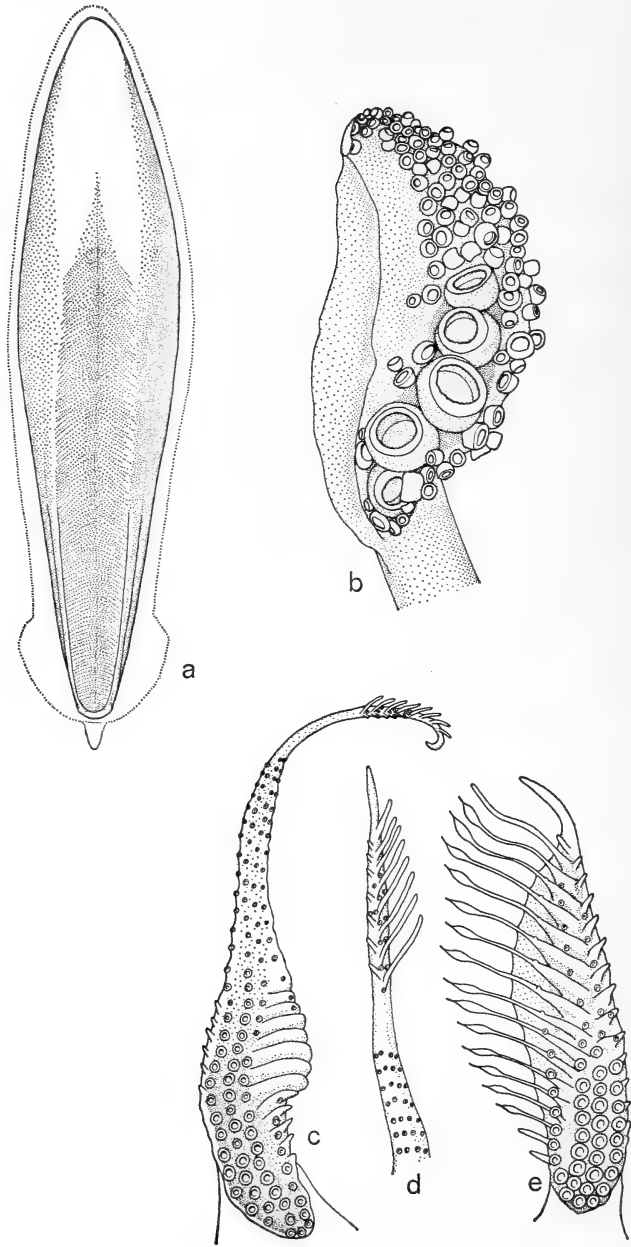


FIG. 8. *Sepia burnupi*, A6525. a. Ventral view of shell of female; b. left tentacular club of male; c. hectocotylized left ventral arm of male; d. tip of right ventral arm of male; e. modified dorsal arm of male. c. d. e. Modified after Barnard (1962); a. and b. original.

condition, was found to be identical with that of *S. burnupi*. The two species are here formally synonymized.

The shell of *S. burnupi* differs from those of *S. confusa* and *S. incerta* in that the inner cone is low posteriorly and does not form a deep pocket over the end of the phragmocone. It differs from *S. joubini* and *S. adami* in the Λ -shape of the striated zone, with the raised limbs of the inner cone lying near the peaks of the Λ and by the angular shape of the striae.

The male of *S. burnupi* is distinguishable from those of the other species of the 'doratoscion' group by the modified tips of the ventral arms. The female is distinct from *S. confusa*, *S. joubini* and *S. adami* in that the arms are attenuated over less than half their length, and the suckers on the attenuated portion of the arms are quadriserial; from *S. incerta* it can be separated only by the shell.

Sepia joubini Massy, 1927

(Figs 2, 9. Tables 3, 25, 26)

Sepia (Doratoscion) joubini Massy, 1927: 161, pl. XVIII, figs 1-10.

Sepia joubini: Voss, 1962b: 248. Adam & Rees, 1966: 70, pl. 43, fig. 257.

Type localities

Tugela River mouth, NW by N $\frac{3}{4}$ N, 25 km, 66-77 m; Cape Natal, W by N, 10.5 km, 99 m.

Distribution

Animals: Off Tugela River mouth to Cape Natal (Massy 1927: 161, and S.A.M.). Depth 66-134 m.

Material

S.A.M. A30141, off Cape Natal, S 79°E 10.5 km, 99 m; 1 ♂, 15 ♀

A30142, 35 km S of Tugela River mouth, 116-134 m; 1 ♂, 2 ♀

A30172, S 11°E of Tugela River mouth, 29 km, 84-101 m; 4 ♂, 1 ♀

A31393, off Cape Natal, S 79°E 10.5 km, 99 m; 11 ♂

Description

Animals small. Mantle elongate, anterior margin produced dorsally, slightly emarginate ventrally. Posterior end pointed. Fins narrow, widening somewhat posteriorly, where rounded and separate.

Skin smooth in most specimens, but some (A30172) have a few dark papillae dorsally. Colour pale, with sparse chromatophores. Dark area dorsally over shell, and oval orange tubercles at fin bases. Pale silvery-blue areas present dorsally in front of and behind eyes, and sometimes also between eyes. These silvery regions not visible in all specimens. Ventral mantle surface pale, with somewhat darker region between midline and fin base. Also a few tubercles present on lateral margin of this area. Head translucent under and on either side of funnel, but beige at arm bases. Males with distinct red spot on lateral side of each dorsal arm, near base. Smaller red spot present on lateral side of

ventral arm, and sometimes small spots also present on other arms. These red spots absent in females.

Arms short (about one-third MLD or less). In males arms subequal in length, attenuated only at tips. Suckers on dorsal arms arranged in about three pairs basally, then quadriserial to arm tip. Suckers on lateral arms arranged in oblique quadriserial rows, except for few irregularly arranged suckers basally. Minute suckers on extreme tip of arm biserial for a few rows. Right ventral arm bearing large irregularly arranged suckers on basal half; suckers much smaller distally, arranged quadriserially. Left ventral arm hectocotylyzed, somewhat longer than its right counterpart. Suckers large basally, variously arranged. Distal hectocotylyzed region obscure and not always recognizable as such. Protective membranes expanded and small suckers arranged quadriserially but widely spaced over about eight rows. Distal tip of arm bearing minute quadriserial suckers.

In female, lateral arms longer than dorsal and ventral ones. Dorsal arms not markedly attenuated, bearing quadriserial suckers separated distally by deep median longitudinal groove. Protective membranes very well developed near arm tip and folded over inner surface of arm. Lateral arms attenuated over about half their length. Proximal part of arm bearing suckers arranged quadriserially, except a few irregular ones basally. Distally, suckers become minute and biserial, separated by longitudinal groove. Ventral arms not attenuated, bearing quadriserial suckers to tips.

Suckers globose in both sexes, having smooth rings. Dorsal and ventral

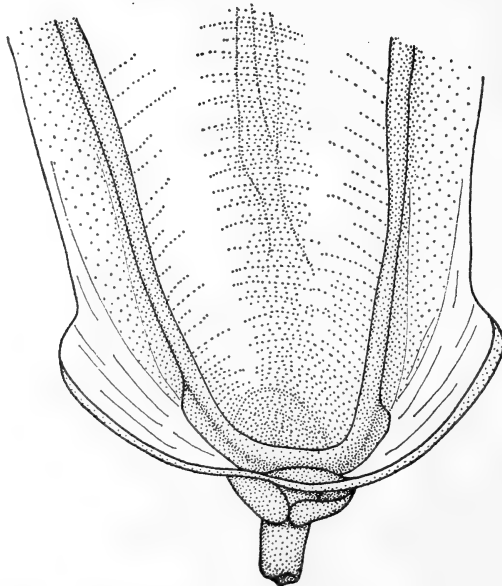


FIG. 9. *Sepia joubini*, A30172. Detail of posterior part of shell, ventral view. See also Figure 2.

arms keeled; interbrachial web highest between lateral arms, absent between fourth pair.

Tentacular club with many small subequal suckers distally in obliquely transverse rows of eight, and four median basal suckers greatly enlarged. All tentacular suckers with finely toothed rings. Tip of club reflexed, partly concealing two somewhat larger suckers. Natatory membrane extending beyond club.

Shells all decalcified, and damaged when removed. Shape of shell (Fig. 2) narrow elongate, pointed anteriorly. Indication of median longitudinal ridge dorsally; posterior spine present, not keeled, directed dorsally (Fig. 9). Median longitudinal groove present ventrally. Striated zone long (about two-thirds shell length), convex on either side of median groove, becoming flattened posteriorly. Striae convex and wavy, becoming more angular anteriorly. Inner cone with long narrow limbs, forming low ledge posteriorly. Outer cone forming posterior wings. Shell thickest in region of anterior end of striated zone. Not known if peculiar structure at base of posterior spine (Fig. 9) occurs in all specimens.

Remarks

The specimens A30141 are topotypes, since they were from the same haul as Massy's syntypes (P.F.10715). These topotypes were not seen by Massy.

Barnard stated in his notes: 'the whip-like tips (of the arms, in the female)

TABLE 3. *Sepia joubini* females: increase in arm length and extent of attenuation of the dorsolateral arm with increase in size.

	MLd (mm)	Arm II Length (mm)	Attenuated part	
			Length (mm)	% Arm II
A30141	26	8	3	37.5
A30141	28	8	3	37.5
A30141	29	8	2	25.0
A30141	30	11	5	45.5
A30141	32	11	4	36.4
A30142	32	13	7	53.8
A30141	34	10	4	40.0
A30142	35	14	7	50.0
A30141	35	13	7	53.8
A30141	36	13	7	53.8
A30141	36	15	10	66.7
A30141	37	14	8	57.1
A30141	37	17	9	52.9
A30172	38	20	12	60.0
A30141	39	16	9	56.3
A30141	39	17	9	52.9
A30141	40	13	7	53.8
A30141	43	17	9	52.9

begin to develop from 30 mm mantle length; below this length the whip is not clearly demarcated from the proximal portion and specimens may be difficult to separate from *australis*. The latter in fact occurred in the same haul. The whip becomes longer relatively to the proximal portion, and may become a little longer than the latter.'

Table 3 shows the extent of attenuation of the dorsolateral arm in females of 26 to 43 mm dorsal mantle length. In the smallest females, the tips of the lateral arms already show some degree of attenuation, but the suckers on the attenuated part are quadriserial. The degree of attenuation of the arm increases with growth of the animal, to a mantle length of about 36 mm, then levels off, although the increase in arm length with growth appears to be linear. In the larger specimens the suckers on the attenuated part of the arm are arranged biserially, although this probably corresponds to a crowding of the quadriserial condition.

The '*australis*' specimens caught in the same haul as *S. joubini* (A30141) are in fact *S. adami* (A30149, A31394). In any case, young *S. joubini* without attenuated lateral arms may be distinguished from *S. australis* by the absence of a 'light organ' in the mantle cavity, and by the differences in the shells. *S. australis* shells are less narrow and elongate; they have a more marked dorsal rib and have a spine with a strong dorsal keel, whereas *S. joubini* shells have an unkeeled spine. The outer cone forms posterior wings in *S. joubini* but not in *S. australis*.

The male of *S. joubini* may be distinguished from the other 'doratosiepien' species by the red spots on the arms, the unmodified dorsal arms and rounded fins. The female is characterized by the expanded protective membranes distally on the dorsal arms.

Sepia adami n. sp.

(Fig. 10. Table 27)

Type locality

S 79°E of Cape Natal 10,5 km, 99 m.

Material

S.A.M. A31394, S 79°E of Cape Natal 10,5 km, 99 m (P.F.10717, 14 December 1900); 1 ♀ (holotype)

A30149, same locality as holotype; 5 ♀ (paratypes)

Description

Only females of this species known.

Mantle elongate oval, sharply pointed posteriorly (Fig. 10c, d). Anterior mantle margin produced dorsally to about anterior level of eyes in large specimens (a little less in smaller ones); ventrally entire or slightly emarginate. Head short and broad. Fins beginning a few mm behind mantle margin, narrow and rounded posteriorly, but fused over posterior tip of mantle.

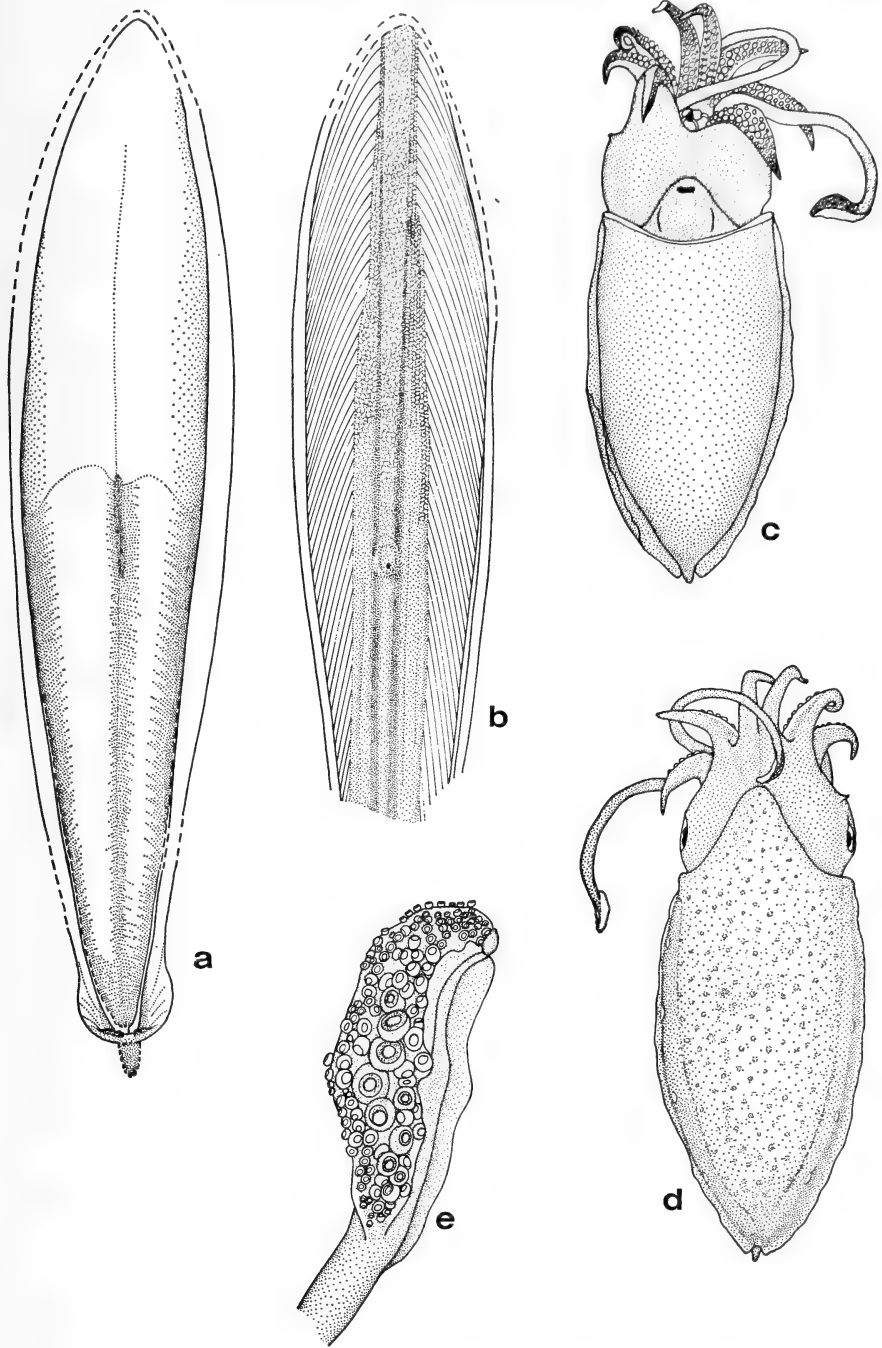


FIG. 10. *Sepia adami* female, A31394 (holotype). a. Ventral view of shell; b. dorsal view of anterior part of shell; c. ventral view of holotype; d. dorsal view of holotype; e. right tentacular club.

Skin sparsely papillose dorsally on head and mantle. Raised lunate tubercles along fin bases dorsally. Colour (of preserved specimens) pale cream, with somewhat darker region mid-dorsally over shell and over eyes. Scattered reddish-brown spots present on arms. Ventral surface pale. Sometimes also a line of pale lunate tubercles in this region (not in type specimen).

Arms subequal in length, joined by shallow web except between ventral arms. All arms keeled. Suckers globose, quadriserial on all arms from base to tip. The two median series of suckers much larger than the lateral ones; but on tips of arms all suckers the same size and markedly smaller than basal suckers. Sucker rings smooth.

Tentacular club (Fig. 10e) short, slightly recurved, with about five median suckers enlarged and smaller distal suckers in five to six longitudinal series. Two suckers at tip of club slightly larger than their neighbours and partially concealed by reflexed tip of club. Rings of large club suckers finely toothed distally, those of small suckers toothed right round. Natatory membrane broad, extending a little beyond club proximally. Protective membranes separate at base of club.

Shells of all specimens very soft and difficult to remove undamaged. Only shell of holotype extracted in reasonably complete state (shell length 59 mm, including spine). Unfortunately, this shell is somewhat abnormal, having apparently been damaged and repaired, since outgrowth present mid-dorsally, corresponding with deep cleft in mid-ventral region. These do not occur in other shell examined by dissection.

Shell (Fig. 10a, b) narrow, elongate, broadest in anterior third, tapering sharply towards posterior end. Shell calcified only in median region dorsally; calcified part consisting of flat median ridge, broadest anteriorly, narrowing posteriorly, and two lateral ridges, narrow and indistinct anteriorly, broadening posteriorly to about twice width of median ridge. Posterior part of shell somewhat damaged dorsally, but ridges apparently fuse and become less distinct in this region. Calcified part of shell pale pink in colour, partially rugose. Rest of shell chitinous dorsally. Posterior spine directed dorsally, not keeled.

Striated zone occupies just over half ventral surface of shell. Anterior border of striated zone convex, with invagination at median groove. But this apparently due to repair outgrowth mentioned above, since anterior border \wedge -shaped in other shell. Inner cone forming shallow pocket posteriorly over striated zone, but not markedly raised. Limbs of inner cone long and narrow, but it is not certain exactly how far they extend. Outer cone widens posteriorly, forming small wings. Shell thickest anterior to striated zone.

Remarks

These specimens were found in the collection of the South African Museum, labelled *Sepia australis*, and indeed they do superficially resemble this species. *S. adami* differs from *S. australis* in the following ways:

1. The shell is markedly different in that it is more elongate, thicker, has posterior wings and a spine without keels.
2. There is no 'light organ' in the mantle cavity.
3. The arm tips are more slender than in *S. australis*.
4. The colour is much paler than that of *S. australis* and there is no indication of an orange band in the region of the fin bases.

With the six female specimens of *S. adami* described above were caught eleven males which almost certainly pertain to *S. joubini*, and have been given a separate catalogue number (A31393). The females of *S. adami* certainly differ from those of *S. joubini*. In *S. adami* the suckers on the dorsal arms are clearly quadriserial to the tips, whereas in *S. joubini* females the suckers on the dorsal arms appear to be biserial, although in fact they are in very oblique rows of quadriserial suckers. Neither are the tips of the dorsal arms provided with expanded protective membranes, as in *S. joubini*. In the latter species the lateral arms are very attenuated over at least half their length, and the suckers on the attenuated portion of these arms are biserial. In *S. adami* the lateral arms are not attenuated and bear quadriserial suckers to the tips of the arms.

Distinctive characters

1. Tentacular club with unequal suckers
2. Shell with unkeeled spine and posterior wings
3. Arms subequal, with quadriserial suckers

This species apparently falls into the 'doratosepion' group, and is most closely related to the other species of this group, viz. *S. confusa*, *S. incerta*, *S. burnupi* and *S. joubini*. It differs from the females of all these species in that the arms are not attenuated distally.

Sepia adami has been named after Professor Dr. W. Adam of the Institut Royal des Sciences Naturelles de Belgique, in recognition of his extensive work on the Sepiidae.

Sepia australis Quoy & Gaimard, 1832

(Pl. 40a, b. Figs 1, 3a, 21. Tables 28-30)

Sepia australis Quoy & Gaimard, 1832: 70, pl. 5, figs 3-7. Hoyle, 1912: 281, fig. 8. Bartsch, 1915: 250. Smith, 1916: 24, pl. II, fig. 9. Tomlin, 1923: 41. Robson, 1924a: 11. Turton, 1932: 2. Adam, 1941: 117, pl. IV, fig. 5; 1942: 10; 1959: 149, fig. 10. Voss, 1962b: 248, 252; 1967: 64. Adam & Rees, 1966: 89, pl. 21, figs 138-142, pl. 45, fig. 270.

Sepia capensis d'Orbigny, 1845a: 283. Férussac & d'Orbigny, 1835-1848: 278, pl. VII, figs 1-3, pl. XII, figs 7-11, pl. XVII, figs 18, 19. Tryon, 1879: 198, pl. 94, figs 440-442. Hoyle, 1886: 23, 217. Gibbons, 1888: 202. Bartsch, 1915: 250. Thiele, 1920: 438, pl. LII, fig. 14, pl. LIII, figs 1-5.

Sepia sinope Gray, 1849: 106.

Rhombosepion australe Rochebrune, 1884: 85. Adam, 1944: 223.

Rhombosepion capense Rochebrune, 1884: 85. Robson, 1924b: 641, fig. 24. Adam, 1944: 222.

Sepia (Doratosepion) australis Massy, 1925: 214.

Rhombosepion australis: Massy, 1927: 156.

non *Sepia australis*: d'Orbigny, 1845a: 294. Férussac & d'Orbigny, 1848: 285, pl. VII, fig. 4. Hoyle, 1886: 22, 220. (= *S. novaehollandiae*).

non *Sepia capensis* d'Orbigny, 1826: Gray, 1849: 110 (= *S. cultrata*).

Type localities

Agulhas Bank (*S. australis*), Cape of Good Hope (*S. capensis*), ? China (*S. sinope*).

Distribution

Animals: South African coast, from 31° 43'S, 16° 13'E (off the Olifants River) (Adam & Rees 1966: 89) to S 73°E of Rame Head, 5 km (near Port St. Johns) (S.A.M.).

Red Sea (Rochebrune 1884: 85; Adam 1942: 10, 1944: 222, 1959: 149).

Depth 2-459 m.

Shells: South African coast, from Braak River (Namaqualand coast) (S.A.M.) to Port Alfred (Turton 1932: 2).

? China (Gray 1849: 106).

Material

S.A.M. 2727, Kalk Bay; 17 shells

A8982, Hout Bay, 17-37 m (det. A. L. Massy); 2 ♂, 3 ♀, in poor condition

A8984, S 78°W of Lions Head 19 km, 110 m (det. A. L. Massy); 2 ♂

A8986, south of Knysna Heads 16 km, 95 m; 25 ♂, 34 ♀, 51 juveniles, all in poor condition

A8988, N 48°W of Lions Head 80 km, 422 m; 4 specimens in poor condition

A8992, S 42°W of Cape St. Blaize 17,5 km, 2-6 m (det. A. L. Massy); 1 ♀ in poor condition

A8994, N 87°E of Cape Point lighthouse 15 km, 59 m (det. A. L. Massy); 11 specimens in poor condition

A8997, mouth of Hout Bay, 73-92 m (det. A. L. Massy); 1 ♀ in poor condition

A29627, 11 km W of Slangkop, 128 m (det. G. L. Voss); 1 ♂, 1 ♀

A29734, west of Slangkop, 100 m (det. G. L. Voss); 2 ♀

A29801, False Bay, 59 m; 1 ♀

A29802, False Bay, 59 m; 1 ♂

A30148, S 57°W of Cape Point lighthouse 11 km, 147 m; 10 ♂, 9 ♀

A30150, S 54°W of Gericke Point 21,5 km, 79 m; 7 ♂, 35 ♀

A30151, S 11°W of Great Fish Point lighthouse 5 km, 73 m; 4 ♂, 6 ♀

A30152, S 6°E of Cape Infanta 21,5 km, 77 m; 1 ♂, 1 ? ♀

A30153, 33° 04'S, 27° 54'E, 50 m; 4 ♀, 2 ? ♀

A30154, 34° 19'S, 18° 32'E (Buffels Bay), 59-64 m; 6 ♂, 12 ♀

A30155, SE of Cape St. Blaize 9 km, 62 m; 1 ♀

A30156, Mossel Bay, 34° 14'S, 22° 23'E, 66 m (det. A. L. Massy); 1 ♂

A30157, S 37°W of Cape Hangklip 45,5 km, 183 m; 2 ♂, 4 ♀

A30158, S 70°W of Cape Infanta 8 km, 64 m (det. A. L. Massy); 1 ♀

A30159, S of Knysna Heads 16 km, 95 m; 3 ♂, 1 ♀

- A30160, S 79°W of Table Mt. 64 km, 459 m; 1 ♂, 6 ♀
 A30161, S 16°W of Cape Point light 16 km, 156 m; 2 ♂, 5 ♀
 A30162, S 34°W of Cape Infanta 30 km, 84 m; 1 ♂, 1 ♀, 2 juveniles,
 all in poor condition
 A30163, S 73°E of Rame Head 5 km, 79 m; 2 ♂
 A30164, S 62°E of Bird Island light 13,5 km, 72 m; 7 ♂, 3 ♀
 A30165, S 70°W of Cape Infanta 8 km, 64 m (det. A. L. Massy);
 1 ♂, 2 ♀
 A30166, S 20°E of Sebastian Bluff 15,5 km, 73 m; 1 ♀
 A30167, S 48°W of Cape St. Blaize 43 km, 81–84 m; 2 ♂
 A30168, off Buffels Bay (False Bay), 55 m; 2 ♂, 4 ♀
 A30169, S of Cape St. Blaize 57,5 km, 99 m (det. A. L. Massy);
 5 specimens in poor condition
 A30170, S 37°W of Cape Infanta 7 km, 68 m; 1 ♂, 1 ♀
 A30171, S 14°W of Gericke Point 8 km, 64 m; 3 ♀
 A30173, S 6°E of Cape Infanta 21,5 km, 77 m; 2 ♂, 1 ♀ in poor
 condition
 A30175, S 42°E of Cape St. Blaize 9,5 km, 66 m; 2 ♂, 2 ♀
 A30190, Salt River power station (Cape Town); 1 ♀
 A30263, N 87°E of Cape Point lighthouse, 59 m (det. A. L. Massy);
 5 specimens in poor condition
 A30264, S 14°W of Gericke Point 8 km, 64 m (det. A. L. Massy);
 1 ♂, 1 ♀, in poor condition
 A30266, S 59°E of Sebastian Bluff 13,5 km, 62 m (det. A. L. Massy); 1 ♂
 A30267, S 34°W of Cape Infanta 30 km, 84 m (det. A. L. Massy);
 1 ♂, 1 ♀, in poor condition
 A30334, S 11°W of Cape Point 15 km, 149–160 m; 1 ♀
 A30504, Bloubergstrand; 1 shell
 A30555, Bloubergstrand; 2 shells
 A30564, Between Strandfontein and Muizenberg; 1 ♂
 A30604, 32° 24'S, 17° 28'E, 193 m; 13 ♂, 53 ♀, all in poor condition
 Ysterfontein beach; 1 shell
 Mossel Bay (south of Slangkop on Cape Peninsula); 22 shells
 Olifantsbosbaai (Cape Point Reserve); 7 shells
 Millers Point, Simonstown; 6 shells
 48 km N of Olifants River; 2 shells
 Strandfontein (False Bay); 1 shell
 Bloubergstrand; 1 shell
 Between Strandfontein and Muizenberg; 11 shells
 Namaqualand coast, between Sout and Braak Rivers; 1 shell
 Simonstown; 2 shells
 Arniston; 2 shells
 Still Bay; 40 shells
 Krom River mouth, Cape St. Francis; 1 shell (broken)

Description

Mantle elongate oval, anterior margin dorsally produced, ventrally entire or slightly emarginate. Head short and broad, fins narrow and rounded but separate posteriorly.

Skin smooth. Colour dark purple dorsally on head and mantle, with slightly paler area medially over shell, and narrow reddish-brown to orange line at bases of fins. This line broadens posteriorly, but not meeting in the midline. Fins pale yellow, with small purple spots. Mantle as dark ventrally as dorsally, with purple chromatophores more concentrated near fin bases and posteriorly on mantle. Fins pale ventrally, without chromatophores; head pale ventrally except for some chromatophores on keeled edges of ventral arms.

Arms subequal in length, joined by shallow interbrachial web, deepest between arms II and III, absent between ventral pair. Protective membranes fairly well developed, especially at arm bases. Arms III moderately, arms IV well keeled.

Suckers globose, quadriserially arranged, with the two median series much larger than the lateral ones. Enlargement of median sucker series more marked in male than in female. Arm tips relatively blunt (definitely not attenuated), bearing minute suckers still arranged quadriserially. In male, distal suckers with long teeth on distal part of rings; rings on proximal suckers smooth on arms I and II, finely dentate proximally on arms III and IV. In female, rings finely dentate in distal suckers, smooth in proximal suckers. Sucker rings nodular on upper surface in both sexes, and adjacent skin of suckers wrinkled.

Left ventral arm of male hectocotylyzed over proximal two-thirds: five or six normal suckers at base, followed by six to seven rows of minute suckers. The two dorsal series of modified suckers arranged in normal positions, but the two ventral series merged to form a single series of 12-14 minute suckers situated on edge of ventral protective membrane. Distal third of arm normal. Modified suckers described by Adam & Rees (1966: 90) as consisting of '13 slightly alternate pairs of smaller ones'. This in fact corresponds to 6-7 quadriserial rows of suckers, of which two ventral series have merged to form a single series, as mentioned above.

Tentacular club somewhat recurved, with small distal suckers in rows of about five. Four median suckers at base enlarged, and two suckers at tip a little larger than their neighbours, partially concealed by reflexed tip of club. Large suckers with smooth rings, smaller ones finely dentate. All rings broad and nodular. Natatory membrane very broad, a little longer than club. Protective membranes not meeting proximally.

Shell (Pl. 40a, b) broadly elongate, somewhat pointed anteriorly, more sharply so posteriorly. Posterior spine with dorsal keel, continuing along dorsal surface of shell for some distance. Shell with broad median rib dorsally, limited on either side by lateral groove. Striated zone long ventrally (about three-quarters shell length); striae wavy. Anterior border of striated zone also wavy and may be sharply pointed or rounded medially. Ventral surface raised in

middle to form broad ridge on either side of distinct median longitudinal groove. Lateral to these ridges, shell concave. Inner cone not well developed posteriorly but raised to form deep pocket; limbs of inner cone narrow. Outer cone narrow, not forming posterior wings. Shell thickest and widest near anterior border of striated zone.

Remarks

In the past there has been considerable confusion in the naming of this species. *Sepia australis* was first described from a specimen from the Cape of Good Hope by Quoy & Gaimard in 1832. Later d'Orbigny claimed that he had described the same species as *Sepia capensis* in 1826, and used the name *S. australis* for an Australian species. Hoyle (1909: 266) could find no confirmation of the use of *S. capensis* prior to 1832, and upheld Quoy & Gaimard's name *S. australis*, renaming *S. australis* d'Orbigny as *Sepia novaehollandiae*.

Regarding *Sepia sinope*, Smith (1916: 24) remarked: 'The name *S. sinope* was substituted by Gray for the *S. australis*, Q. & G. (*non* d'Orb.), and he quoted a single imperfect shell in the British Museum collection which was labelled "China". No information concerning its acquirement is attached to the specimen, and consequently in all probability the locality cannot be relied upon. It certainly belongs to the present species' (i.e. *S. australis*).

S. australis is one of the commonest Sepiidae along the coast of the western Cape and its shells are found in abundance on the beaches. Turton (1932: 2) mentioned that this species is rare at Port Alfred, and indeed not many records are known east of Port Elizabeth.

The University of Cape Town Ecological Survey has a record of *S. australis* from Durban. Unfortunately the animals were discarded and their identity cannot be checked. Since *S. australis* has been confused with *S. joubini* and *S. adami* in the past, this record remains doubtful.

Adam & Rees (1966: 89) report a shell from Grahamstown, Natal. But the only Grahamstown in South Africa known to the author is in the eastern Cape, and is 64 km from the sea.

Voss (1962*b*: 252, 1967: 64) is mistaken in stating that *S. australis* is known only from southern Africa, since Rochebrune (1884: 85) and Adam (1942: 10, 1944: 222, 1959: 149) have reported this species from the Red Sea. The occurrence of *S. australis* in China (Gray 1849: 106) is doubtful (see above).

Sepia tuberculata Lamarck, 1798

(Pls 39c, d, 40c, d. Fig. 11a. Tables 4, 31-33)

Sepia tuberculata Lamarck, 1798: 130; 1799: 9, pl. I, figs 1A-B; 1822: 668; 1845: 372. Bosc, 1802: 45. Montfort, 1805: 274, pl. vii, figs 1-6. Blainville, 1825: 368, pl. I, fig. 2; 1827*a*: figs 2-6; 1827*b*: pl. 1, figs 2-6. Deshayes, 1832: 945. Férussac & d'Orbigny, 1835-1848: 277, pl. VI, figs 1-4. d'Orbigny, 1845*a*: 281; 1845[-47]*b*: pl. 3, fig. 11; 1845[-47]*c*: pl. 3, fig. 11. Hoyle, 1886: 24, 217. Gibbons, 1888: 202. Smith, 1903: 356. Adam, 1941: 113, pl. III, fig. 8. Voss, 1962*b*: 248. Adam & Rees, 1966: 106, pl. 26, figs 169, 170, pl. 27, figs 171, 172, pl. 28, figs 173, 174, pl. 44, figs 265, 268.

? *Sepia mammilata* Leach, MS. Férussac & d'Orbigny, 1835-1848: 277 (*S. mamillata*), pl. IVbis (*S. mammilata*).

Spathidosepion tuberculatum Rochebrune, 1884: 93, pl. IV, fig. 3. Adam, 1944: 226.

Hemisepius (?) *tuberculatus* Smith, 1916: 25.

non *Sepia tuberculata*: Férussac & d'Orbigny, 1835-1848: non pl. XVII, figs 13-15. Steenstrup, 1875: IV, pl. I, figs 20, 21, pl. II, fig. 6. Hoyle, 1910: 265, figs 9, 10, pl. Va, figs 4-14. (= *S. papillata*).

Type locality

?

Distribution

Animals: Melkbosstrand (S.A.M.) to Knysna (U.C.T.). Depth 0-3 m.

Shells: Kommetjie, Cape Peninsula to Nature's Valley (S.A.M.) and Malagasy (Adam, 1941: 114).

Material

S.A.M. A29781, Mossel Bay; 1 ♀

A29867, Strandfontein; 1 ♀

A30121, David's Kraal (near Cape Hangklip); 1 ♂

A30123, Simonstown Harbour, 3 m; 1 ♀

A30139, locality unknown; 1 ♀

A30180, Melkbosstrand; 1 ♀

A30279, locality unknown; 1 ♂

A30485, Simonstown; 1 shell (of juvenile)

A30493, Simonstown; 1 shell

A30500, Gordon's Bay; 2 shells

A30511, Dalebrook; 2 ♀, 1 juvenile ? ♀

A30559, Dalebrook; 1 ♀

A30600, Millers Point, Simonstown; 2 ♂

A31235, locality unknown; 1 ♂

Nature's Valley; 6 shells, discarded

Between Strandfontein and Muizenberg; 3 shells

Millers Point, Simonstown; 3 shells

Betty's Bay; 1 shell

Strandfontein (False Bay); 1 shell

Kommetjie; 1 shell

Die Kelders; 1 shell, discarded

? Cape Agulhas; 4 shells

? Milnerton; 2 shells

? Pearly Beach, S of Gansbaai; 4 shells

? Die Kelders; 1 shell

? 11 km NW of Cape Agulhas; 7 shells

Description

Mantle short and broad, anterior mantle margin convex dorsally (not produced), ventrally entire; mantle rounded posteriorly. Fins wide, beginning a few mm behind anterior mantle margin, rounded but separate posteriorly.

Skin densely tuberculate on dorsal surface of head, arms, mantle and fin bases. Ventral surface smooth except for large oval wrinkled area on each side of mantle and on ventral surfaces of fourth arms. Colour dark purple dorsally, pale buff ventrally.

Arms subequal in length, about half dorsal mantle length. Tips of all arms except ventral pair attenuated. Interbrachial membrane present, except between ventral arms. Arms III and IV keeled.

Suckers not globose; with finely dentate horny rings. Protective membranes well developed. Suckers quadriserial on all arms to tips.

Left ventral arm of male hectocotylized basally. Dorsal series of suckers normal, but the two ventral series are widely separated from these by a broad naked area with transverse ridges. Distal half of arm normal.

Tentacular club long, slightly recurved, bearing small distal suckers arranged in very oblique rows of eight. Four or five median suckers enlarged. Suckers at tip of club no larger than their neighbours. Horny rings of large suckers smooth, those of small suckers dentate. Protective membranes meeting proximally. Natatory membrane extending a little beyond club.

Shell (Pl. 40c, d) oval but somewhat angular anteriorly. Dorsal surface finely granular. Median ridge faint or absent. No posterior spine or knob, but only a small hump present in this position. No distinct median groove ventrally. Striated zone long, striae wavy with overall convex shape. Inner cone completely reflexed and fused to outer cone, but not well developed posteriorly;

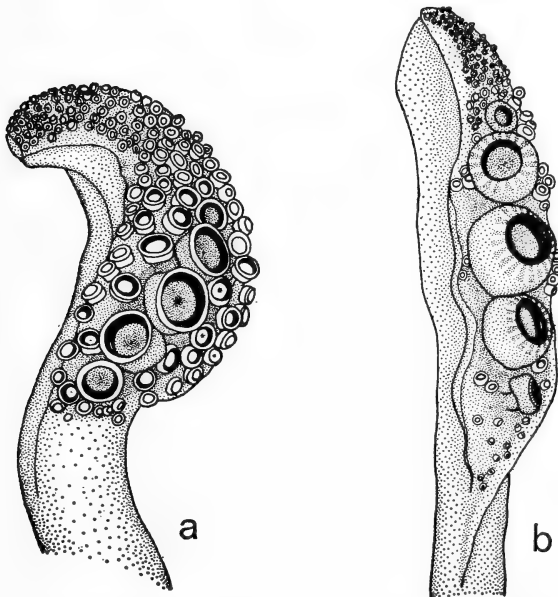


FIG. 11. Comparison of tentacular clubs of a. *Sepia tuberculata* (A30139) and b. *S. papillata* (A30124).

limbs of inner cone long and narrow. Outer cone broad laterally, narrowing sharply posteriorly so that inner cone almost reaches posterior margin of shell. Shell generally very thin, ventral surface flat or slightly concave.

Several shells (indicated with query in list of material) (Pl. 39c, d), found on beaches, with markedly longer striated zone, and sometimes also with somewhat wider outer cone.

Remarks

This species was synonymized with *S. papillata* by Férussac & d'Orbigny (1835-1848: 277), but the two were rightly separated by Rochebrune (1884: 93-95). Hoyle (1910: 267), following Férussac & d'Orbigny's synonymy, described a specimen of *S. papillata* under the name *S. tuberculata*. In fact the differences between the two species are quite clear (Table 4), the most marked being the relative sizes of the large tentacular suckers. The two specimens mentioned by Steenstrup (1875: IV) almost certainly also pertain to *S. papillata* (cf.).

Adam (1941: 114) has mentioned a specimen of *S. tuberculata* from Port Dorey, New Guinea. The correctness of this locality is doubtful (Adam, personal communication), and has not been included in the distribution lists.

The wrinkled areas on the ventral surfaces on the mantle and fourth arms are apparently used to hold on to a hard substratum such as rocks. *S. tuberculata* kept in aquaria have been observed to use these wrinkled areas to cling to the glass walls.

TABLE 4. Comparison of *Sepia tuberculata* with *S. papillata*.

		<i>S. tuberculata</i>	<i>S. papillata</i>
Dorsal mantle margin		Convex	Produced
Tips of arms I-III		Attenuated	Not attenuated
Tentacular club	Large suckers	Diameter less than width of tentacular club	Diameter approximately equal to width of tentacular club
	Protective membranes	Joined proximally	Separate proximally
Shell	Dorsal surface	No median ridge; no posterior knob	Median ridge and posterior knob present
	Ventral surface	Flat or concave; no distinct median groove	Convex; median groove present
	Inner cone	Not well developed posteriorly; limbs narrow	Well developed posteriorly; limbs usually broad (but see description)
	Thickness	Mean 6,6% shell length	Mean 10,1% shell length

The shells with an exceptionally long striated zone (70.0–88.5% shell length) show no other differences from those of *S. tuberculata* (striated zone 54.1–73.9% shell length) and may constitute an extension of the known range of striated zone length for this species, or may be distinct. No decision can be made on their status until the soft parts can be studied.

Sepia papillata Quoy & Gaimard, 1832

(Pl. 41a–d. Figs 11b, 12. Tables 4, 34–37)

Sepia papillata Quoy & Gaimard, 1832: 61, pl. I, figs 6–14. Férussac & d'Orbigny, 1835–1848: pl. III^{ter}, figs 1–5. Bartsch, 1915: 250. Tomlin, 1923: 40 (*partim*). Massy, 1925: 211; 1928: 92. Turton, 1932: 1. Adam, 1939a: 55, pl. III, fig. 6; 1941: 112. Voss, 1962b: 248, 251. Adam & Rees, 1966: 108, pl. 28, figs 175–178.

Spathidosepien papillatum Rochebrune, 1884: 94. Adam, 1944: 226.

Sepia tuberculata (non Lamarck) Férussac & d'Orbigny, 1835–1848: pl. XVII, figs 13–15. Steenstrup, 1875: IV, pl. I, figs 20, 21, pl. II, fig. 6. Gibbons, 1888: 202. Hoyle, 1910: 265, figs 9, 10, pl. Va, figs 4–14.

non *Sepia papillata*: Smith, 1916: 22, pl. II, figs 1, 2 (= *S. simoniana*).

Type locality

Cape of Good Hope.

Distribution

Animals: Lüderitzbucht (Angra Pequena) (Hoyle 1910: 265) to Natal coast, off Tugela River and Umvoti River (Massy 1928: 92). Depth 26–127 m.

Shells: Orange River mouth (S.A.M.) to ? Tongaat, Natal (Tomlin 1923: 40).

Material

S.A.M. A30118, Woodstock power station, Cape Town; 2 ♂ (one shell missing)
A30119, S 62–79°E of Bird Island lighthouse 15 km, 73–48 m; 1 ♀ (shell missing)

A30120, Woodstock power station, Cape Town; 1 ♂

A30124, locality unknown; 1 ♀ (shell missing)

A30136, S 87°E of Cape St. Blaize 9 km, 51 m; 1 ♀

A30137, Hout Bay, 37–73 m; 1 ♂

A30138, N 3°E of Green Point lighthouse 4 km, 40 m; 1 ♂

A30140, S 8–17°E of Maalgaten River mouth 11–14 km, 61–64 m; 1 ♀

A30476, Bloubergstrand; 1 shell

A30482, S 62–79°E of Bird Island lighthouse 15 km, 73–48 m; 1 shell

A30497, locality unknown; 1 shell

A30507, Elandsbaai beach, after red tide; 2 ♂, 2 ♀

A30509, Elandsbaai beach, after red tide; 1 ♂

A30553, Orange River mouth; 2 shells

A30554, Bloubergstrand; 1 shell

A31250, Castle Rock, False Bay; 1 ♂

Ysterfontein; 1 shell

Nature's Valley; 1 shell, discarded
 Between Strandfontein and Muizenberg; 14 shells
 Mossel Bay (S of Slangkop on Cape Peninsula); 1 shell
 Olifantsbosbaai (Cape Point Reserve); 1 shell
 Millers Point, Simonstown; 2 shells
 48 km N of Olifants River; 4 shells
 Strandfontein (False Bay); 6 shells
 Betty's Bay; 1 shell
 Umngazana River mouth, west Pondoland; 2 shells
 Muizenberg; 2 shells
 Kommetjie; 4 shells
 Milnerton beach, Cape Town; 2 shells
 Namaqualand coast, between Sout River and Braak River; 1 shell
 Still Bay; 8 shells
 Simonstown; 2 shells
 Arniston; 2 shells
 Die Kelders; 3 shells, discarded
 Krom River mouth, Cape St. Francis; 32 shells

Description

Mantle broadly oval, anterior margin somewhat produced dorsally, slightly emarginate ventrally. Fins broad, beginning a few mm behind mantle margin; posteriorly rounded and separate.

Skin tuberculate dorsally and laterally on head, arms and mantle, but smooth ventrally except for two large wrinkled patches on mantle, and smaller patches along ventral surfaces of fourth arms, as in *S. tuberculata*. Colour dark reddish-brown to purple dorsally on tuberculate surfaces, pale ventrally with scattered chromatophores, which are somewhat more dense on fins.

Arms subequal in length, about 50% MLd; arms I to III attenuated over about distal quarter. All arms keeled, and joined by fairly deep interbranchial web, which may attain half arm length.

Suckers not globose; with finely toothed chitinous rings. In the female, suckers quadriserially arranged on all arms. Suckers on attenuated arm tips minute, but still quadriserial. In the males, suckers quadriserial over most of arm, but attenuated tip broader and flatter than in female, and minute suckers arranged in eight series. Ventral arms not much attenuated at tips, but suckers also show multiplicity, although less extensively than on other arms.

Left ventral arm of male hectocotylized proximally. Basally about 13 suckers arranged normally, followed by modified region, consisting of eight quadriserial rows of suckers. In this region the two dorsal series are separated from the two ventral series by a naked region with transverse ridges. Modified suckers described by Massy (1925: 212) as '15 rows of diminutive suckers placed 2 in a row, in zigzag order, with shallow grooves between them'. This in fact corresponds with a quadriserial condition in which two series come close

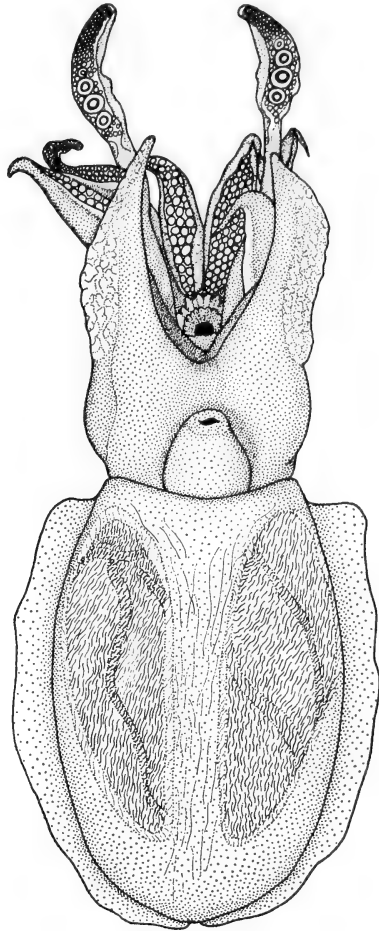


FIG. 12. *Sepia papillata* male, A30137.
Ventral view to show wrinkled areas on
mantle and ventral arms.

together (on either side of median grooved section of arm) until apparently forming single longitudinal zigzag series on each side. Suckers normally quadriserial distally, but at arm tip (which is slightly attenuated), minute suckers arranged in oblique rows of eight.

Tentacular club long, bearing small distal suckers in oblique rows of eight. Four suckers enlarged medially; of these, the middle two extremely large, with diameters equal to width of sucker-bearing surface of club. Chitinous rings of large suckers smooth, those of small suckers dentate. Protective and natatory membranes very well developed; protective membranes not meeting basally, natatory membrane extending a little beyond club.

Barnard (unpublished notes) discovered that there are two forms of shells

belonging to *S. papillata*. Both shell forms (Pl. 40a-d) broadly oval, tapering somewhat anteriorly. Dorsal surface rugose, with faint, broad median ridge, broadening anteriorly. Usually no spine posteriorly, but a broad rounded knob present. In a few shells, however, this knob continues as small spine lying close to shell surface and thus directed ventrally. Spine not exceeding posterior margin of shell. Striated zone long ventrally, with narrow smooth area on either side of it anteriorly. Striae wavy, with overall \wedge -shape. Median longitudinal groove distinct. Shape of inner cone different in the two forms, but completely reflexed and fused to outer cone in both. Outer cone broad laterally. Inner cone frequently (but more often in form A than B) drawn out posteriorly, almost reaching edge of shell, as in *S. simoniana*.

Shell form A (Pl. 40a, b) with broad inner cone; difficult to distinguish from *S. simoniana* in extreme cases. Phragmocone of this form generally thicker at anterior region of striated zone, on either side of midline. Shell form B (Pl. 40c, d) differs in that inner cone narrow and thicker, with limbs forming narrow raised ridges, as in *S. tuberculata*. Phragmocone generally thinner than in form A, but always convex to some extent.

Remarks

As mentioned above, the animals of this species have frequently been confused with those of *S. tuberculata*, but they are in fact distinct (see Table 4).

Of the two shell forms, form A (having a broad inner cone) markedly resembles the shell of *S. simoniana*, but the animals differ primarily in that *S. simoniana* has a tentacular club with numerous subequal suckers, and has a smooth skin, whereas *S. papillata* has a tentacular club with very unequal suckers, and has a tuberculate skin. Shell form B of *S. papillata* closely resembles the shell of *S. tuberculata*, but the differences between the two species are as listed in Table 4. A comparison of the relative dimensions of shell forms A and B of *S. papillata* revealed no statistically significant differences. The present collection includes six male and four female animals having shells of form A, and only two males with shells of form B. No differences could be found between the animals having either shell form, and all undoubtedly belonged to *S. papillata*. The significance of these shell forms is at present unknown, but they may reflect a relationship with *S. simoniana* on the one hand and *S. tuberculata* on the other.

Steenstrup (1875: IV) mentioned two specimens (male and female) of *Sepia* which he thought to be *S. tuberculata*. He illustrated the buccal view of the female (pl. II, fig. 6), suckers (pl. I, fig. 21) and an arm with minute suckers at the tip arranged in eight series (pl. I, fig. 20). As *S. tuberculata* and *S. papillata* have so often been confused, we may assume that Steenstrup's specimens could belong to either species, since neither tentacular club nor shell were illustrated. But of these two species only the male of *S. papillata* has the minute suckers at the tips arranged in eight series. Hence the male specimen was almost certainly *S. papillata*, and presumably the female belonged to the same species.

As mentioned above, Hoyle's (1910: 265) three female specimens, described as *S. tuberculata*, were in fact *S. papillata*. This can clearly be seen from his figures (pl. IVa, figs 4-6). In the description, Hoyle said that the arms are about as long as the mantle, but according to his measurements, they are only half as long, as also in the present specimens.

The description of *S. papillata* shells given by Smith (1916: 22) could cover both *S. papillata* and *S. simoniana*, and indeed he stated that 'It should be noted also that the limbs of the inner cones are rather variable. Sometimes, as in the *Astrolabe* figure, they do not expand much posteriorly. On the contrary, in some specimens they spread considerably, and become rather pointed posteriorly.' The shell in Smith's figure (pl. II, fig. 1) is that of *S. simoniana*. Unfortunately, he does not give a list or the number of specimens examined, but mentions only that there were shells from Port Elizabeth (Ponsonby, Spencer) and Tongaat beach, Natal (Burnup). One of the specimens presented to the British Museum by Spencer was 134 mm long and 60 mm wide.

Adam (1941: 113) lists one of Smith's specimens (length 134 mm, width 45%* length) from Port Elizabeth in a table of measurements of *S. papillata* shells, but does not mention a shell from Port Elizabeth in his list of material examined.

Adam & Rees (1966) do not include Smith (1916) in the synonymy for *S. papillata*, but included in the list of material for *S. simoniana* are three shells from Port Elizabeth (Ponsonby) and three shells (of which one is doubtful) from Port Elizabeth (Spencer). These are presumably the same shells as originally examined by Smith. Of the specimens donated to the British Museum by Spencer, one shell is recorded by Adam & Rees as being 137 mm long, with a width of 44% of the length. This must be the shell measured by Smith. Presumably Adam reconsidered his opinion of 1941 of Smith's specimens, and now considers them all to pertain to *S. simoniana*. Adam & Rees (1966: 109) in fact state that the shell figured by Smith (1916, pl. II, figs 1, 2) as *S. papillata* belongs to *S. simoniana*.

Tomlin's (1923: 40) localities listed for *S. papillata* were obviously quoted from Smith (1916), and thus refer to *S. simoniana* (with the exception of Quoy & Gaimard's locality of the type of *S. papillata*).

Massy (1925: 211) is the only author to have previously described a male of *S. papillata*, but she does not mention the presence of multiplicity of the suckers on the arm tips. Since this condition occurs in all the present male specimens, Massy probably overlooked it in hers.

Voss (1962b: 251) was mistaken in saying that *S. papillata* 'was not reported from South Africa by either Massy or Robson and may be an uncommon species'. *S. papillata* was described by Massy in 1925, and mentioned again in 1928. In fact the species appears to be very common, at least around the western Cape, since the shells are commonly washed up on the beaches.

* Not 57% (Adam, personal communication).

Sepia simoniana Thiele, 1920

(Pl. 42a, b. Tables 38-40)

Sepia simoniana Thiele, 1920: 436, pl. LII, figs 5-13. Odhner, 1923: 7. Tomlin, 1926: 285.

Voss, 1962b: 248, 250. Adam & Rees, 1966: 109, pl. 29, figs 179-182, pl. 42, fig. 254.

Sepia natalensis Massy, 1925: 212, pl. XI, figs 1-11, pl. XIV, fig. 37.*Sepia tuberculata* (non Lamarck) Gray, 1849: 101, 102.*Sepia papillata* (non Quoy & Gaimard) Smith, 1916: 22, pl. II, figs 1, 2. Tomlin, 1923: 40 (*partim*).*Type localities*Simons Bay (*S. simoniana*); 25,5 km NE of Bird Island (*S. natalensis*).*Distribution*

Animals: Simons Bay (Thiele 1920: 436) to off Tugela River (S.A.M.).

Depth 14-134 m.

Shells: 48 km N of Olifants River mouth (S.A.M.) to Tongaat beach, Natal (Smith 1916: 22).

Material

S.A.M. A30127, locality unknown; 1 ♂

A30132, 34° 12'S, 18° 36'E, 40 m; 1 ♀

A30133, Simons Bay; 1 ♀

A30134, locality unknown; 1 ♀

A30135, 35 km S of Tugela River mouth, 116-134 m; 1 ♀

A30179, Millers Point, Simonstown; 1 juvenile

A30498, Table Bay; 1 shell

A30499, Still Bay; 1 shell

A31239, Sunny Cove, False Bay, 14 m; 2 juveniles

A31251, Castle Rock, False Bay; 2 ♂

Between Strandfontein and Muizenberg; 4 shells

Simonstown; 2 shells

48 km N of Olifants River mouth; 1 shell

Betty's Bay; 2 shells

Strandfontein (False Bay); 2 shells

Umngazana River mouth, west Pondoland; 4 shells

Still Bay; 15 shells

Arniston; 4 shells

Die Kelders; 1 shell, discarded

Krom River mouth, Cape St. Francis; 46 shells

Description

Mantle broadly oval, anterior mantle margin somewhat produced dorsally, entire ventrally. Fins fairly narrow, beginning a few mm behind anterior mantle margin, rounded and separate posteriorly.

Skin very finely papillose dorsally on head and mantle. Skin somewhat wrinkled ventrally on mantle in some specimens, but this is possibly due to preservation. One juvenile (A30179), however, has distinct wrinkled oval

patches ventrally on mantle, as in *S. papillata* and *S. tuberculata*. Wrinkled areas usually also present on ventral surfaces of fourth arms. Colour pinkish-brown dorsally, pale ventrally, with sparse chromatophores, except for two slightly darker regions on either side of midline, beginning at anterior mantle margin and fading towards posterior.

Arms subequal in female, about half dorsal mantle length, with third arms a little longer than others. In males, arms unequal in length, of formula 3.2.1.4. All arms except ventral pair somewhat attenuated over about distal quarter. Depth of interbrachial web approximately half arm length, except between ventral pair, where web absent. Third and fourth arms keeled.

Suckers on all arms quadriserial to tips; suckers largest about one-third from arm base, then decrease in size to tips, where they suddenly become minute. On fourth arms, although tips not attenuated, distal suckers also minute. Rings of large suckers smooth, those of smaller ones very finely dentate. Suckers of male more globose than those of female.

Left ventral arm of male hectocotylized proximally. About five to nine normal suckers at base of arm, followed by modified region, where two dorsal series of suckers smaller than usual and separated from the two ventral series by naked region with transverse ridges. Suckers in the two ventral series minute. Distal half of arm normal. According to Thiele's (1920: 438) description of the hectocotylus, second longitudinal series of suckers almost lacking in modified region, although in one specimen this absence was less extensive. But in the present specimens, second series of suckers complete, though smaller, and it seems probable that in Thiele's specimens some suckers were lost after capture.

Tentacular club very long, occupying about half length of tentacle. Club bears very many minute subequal suckers, and four (not two, as stated by Voss 1962*b*: 250) somewhat larger suckers, partly concealed by reflexed tip of club. Protective membranes very well developed, also bearing suckers, except at outer edge. Rings of small suckers with well defined teeth; those of four larger suckers at tip of club smooth. Protective membranes joined basally. Natatory membrane well developed, somewhat shorter than club.

Shell (Pl. 42a, b) broadly oval, tapering a little anteriorly. Dorsal surface finely granular. At most a faint indication of median longitudinal ridge dorsally, broadening anteriorly. Longitudinal grooves on either side of median ridge ill defined. Spine absent posteriorly, but broad knob present, sometimes tapering into small point, but not attaining posterior margin of shell. Striated zone long, about two-thirds shell length. A narrow smooth area present on either side of striated zone. Striae wavy, with overall \wedge -shape. Deep median longitudinal groove present ventrally, with convex striated zone on either side. Striated zone most strongly convex near its anterior end. Inner cone well developed, reflexed and fused to outer cone. Limbs of inner cone very broad, usually narrowing suddenly anteriorly, giving characteristic shape. Inner cone drawn out posteriorly, almost reaching posterior margin of shell. In some shells,

however, anterior narrowing of limbs not as sharp, and these shells are difficult to separate from those of *S. papillata* form A.

Remarks

As has been pointed out above, shell form A of *S. papillata* is very similar to that of *S. simoniana*, but the animals differ markedly.

A shell from the Cape of Good Hope, identified by Gray (1849: 102) as *S. tuberculata*, belongs in fact to *S. simoniana*, according to Adam & Rees (1966: 109), who re-examined the shell.

As mentioned above, the specimens described by Smith (1916: 22) as *S. papillata* are probably *S. simoniana*.

S. simoniana Thiele and *S. natalensis* Massy are indubitably synonymous, as has already been remarked by Voss (1962b: 251) and by Adam & Rees (1966: 109).

***Sepia angulata* n. sp.**

(Pls 44d, 45a-d. Table 41)

Type locality

Bloubergstrand (shells only).

Distribution

Shells: Bloubergstrand to Still Bay (S.A.M.).

Material

S.A.M. A31317, Bloubergstrand (coll. Roeleveld, 9 November 1969); 1 shell (holotype)

A31318, Milnerton beach (coll. Kensley, 29 January 1969); 3 shells

A31319, Still Bay (coll. Du Preez, April 1969); 2 shells

A31320, Still Bay (coll. Du Preez, October 1969); 3 shells

A31395, Bloubergstrand (coll. Roeleveld, 9 November 1969); 3 shells

Description

Only shells of this species known.

Shell (Pls 44d, 45a-d) broadly oval, rounded anteriorly and posteriorly. Dorsally, part of dorsal shield covering phragmocone clearly distinguishable from outer cone: the former brown in colour; the outer cone white. Dorsal surface finely granular, becoming somewhat more coarsely so posteriorly; entire dorsal surface with iridescent sheen. Faint indication of dorsal longitudinal rib, widening anteriorly. No posterior spine or knob.

Ventrally, striated zone fairly short, flat from side to side,* except at extreme lateral edges, which are slightly rounded. Striated zone rises rapidly from posterior to anterior. Then smooth zone, also flat, descends sharply towards anterior, forming distinct obtuse angle between striated and smooth zones (Pl. 44d). A number of shallow grooves radiate over striated zone from

* In one specimen (A31319, length 63 mm) the striated zone is concave.

posterior end in holotype; median longitudinal groove no more distinct than others. Striae wavy over the grooves, with overall convex shape. In some shells, however, radiating grooves less distinct than median groove, and in these shells, striae more regularly convex.

Inner cone completely reflexed, fused to outer cone; posteriorly well developed, forming transverse ridge. Limbs of inner cone broad, as in *S. papillata* form A. Outer cone very broad and deep laterally and posteriorly, giving shell its characteristic tubby shape. Slight fold present in outer cone on each side, near posterior end, from inner cone to margin.

Remarks

This species somewhat resembles *S. papillata* and *S. simoniana*, but the shell of *S. angulata* is somewhat shorter and broader, differing also in that the median ventral groove is indistinct, and the striated zone and last loculus are remarkably flat and form an angle at the point of meeting, about halfway along the shell. *S. angulata* differs from *S. tuberculata* in that it is relatively broader, the phragmocone is much thicker, particularly at the anterior end of the striated zone, and the outer cone is much broader posteriorly. The inner cone is also more strongly developed in *S. angulata*.

S. angulata has been so named after the angle formed between the striated and smooth zones in lateral view (*angulatus*, L.—angular).

Distinctive characters

1. Shell very broad (50–60% length)
2. Obtuse angle between striated and smooth zones, in side view
3. Both striated zone and smooth zone very flat from side to side

Sepia hieronis (Robson, 1924)

(Pl. 43a–d. Fig. 13. Tables 5, 42–44)

Sepia acuminata Smith, 1916: 21, pl. II, fig. 4 (*partim*).

Sepia sp. A Robson, 1924a: 13.

Rhombosepion hieronis Robson, 1924b: 645, pl. II, figs 9, 11. Massy, 1927: 158.

Sepia hieronis Voss, 1962b: 248, 251; 1967: 64. Adam & Rees, 1966: 112, pl. 30, figs 187, 188, pl. 43, fig. 262.

Type localities

S.S. *Pickle*, Sta. 2: 33° 03'S, 17° 42'E, 215 m

Sta. 7: 32° 32'S, 17° 42'E, 206 m

Sta. 8: 32° 33'S, 17° 29'E, 231 m

Sta. 33: 32° 54'S, 17° 25'E, 275 m

Distribution

Animals: West coast: 30° 13'S, 15° 18'E* (Adam & Rees 1966: 112, g) to west of Slangkop (Voss 1967: 64). Depth 43–457 m.

East coast: Monte Belo, Moçambique (S.A.M.). Depth 431–459 m.

Shells: Bloubergstrand (S.A.M.) to Tongaat beach, Natal (Smith 1916: 21).

* Not 30° 09'S, 19° 02'E, as stated by Adam & Rees.

Material

- S.A.M. Ag000, 80 km N 42°W of Lions Head, 422 m (det. A. L. Massy);
 1 ♂, 1 juvenile, in poor condition
 A29728, west of Slangkop, 250 m (det. G. L. Voss); 1 ♂
 A30145, locality unknown; 1 ♀
 A30146, S 76°W of Lions Head 45 km, 257 m; 1 ♂
 A30260, N 48°W of Lions Head 80 km, 422 m (det. A. L. Massy);
 2 specimens in poor condition
 A30268, N 51°W of Lions Head 75 km, 321 m (det. A. L. Massy);
 1 ♂ in poor condition
 A30563, 34° 04'S, 17° 45'E, 275 m; 1 ♂
 A31243, 32° 15'S, 17° 08'E, 283 m; 1 ♂
 A31405, Monte Belo, Moçambique, 25° 35'S, 33° 30'E, 431-455 m; 1 ♂
 A31406, Monte Belo, Moçambique, 25° 35'S, 33° 30'E, 440-459 m; 1 ♂
 A31407, Monte Belo, Moçambique, 25° 35'S, 33° 30'E, 459 m; 1 ♂
 Mossel Bay (S of Slangkop on Cape Peninsula); 19 shells, broken
 Olifantsbosbaai (Cape Point Reserve); 1 shell, broken
 Millers Point, Simonstown; 1 shell, broken
 Bloubergstrand; 2 shells, slightly damaged

Description

The specimens previously described by Massy (1927: 158) now very shrivelled and cannot be measured or properly examined. Remaining specimens (seven males and one small female) in good condition.

Mantle ovate, anterior mantle margin produced to fairly sharp point dorsally between eyes in males, less strongly produced in small female (about half as much as in males). Ventrally, anterior mantle margin entire in males, emarginate in female. Fins narrow, beginning a few mm behind mantle margin, rounded and separate posteriorly.

Colour generally mottled reddish-brown dorsally (but in two males and in female chromatophores contracted to small spots on pale background). Mantle ventrally pale in middle, somewhat darker laterally towards fin bases, where chromatophores more dense. Skin sparsely papillose dorsally on head and mantle in female; smooth in males.

Arms generally shortest dorsally, longest ventrally, having formula 4.3.2.1, but varying somewhat in different specimens (female measured by Adam & Rees 1966: 113, had subequal arms). Interbranchial web present, except between ventral arm pair, and is deepest between arms II and III.

In males, dorsal arms attenuated over about distal third, bearing biserial suckers gradually diminishing in size towards tips, where suckers minute. Sucker arrangement on lateral arms very characteristic. On dorsolateral arms, suckers of basal two-thirds biserial, sometimes becoming somewhat irregularly arranged or even quadriserial for a few rows on middle third of arm, then three to five pairs of greatly enlarged suckers. Of these, middle ones have diameter

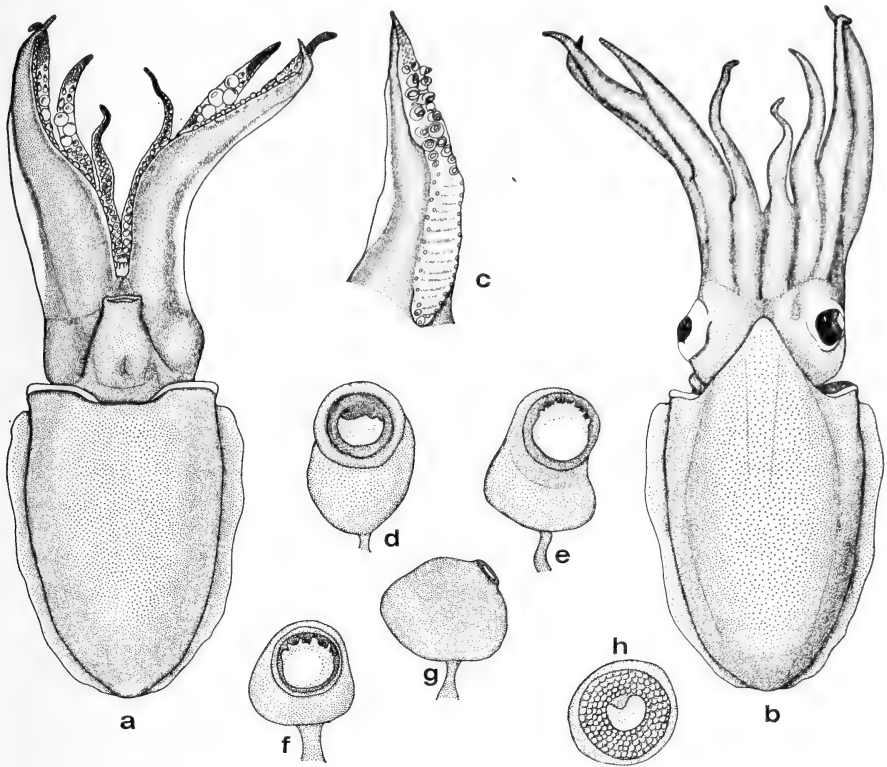


FIG. 13. *Sepia hieronis* male, A30563. a. Ventral view; b. dorsal view; c. hectocotylus; d. sucker from the base of a lateral arm, diameter about 1 mm; e. one of the suckers distal to the enlarged suckers on arms II to IV, diameter about 1 mm; f. one of the enlarged suckers on the distal part of the hectocotylus, diameter about 1 mm; g. enlarged sucker from one of the lateral arms, diameter about 2 mm; h. oral view of sucker from the tentacular club, diameter about 0,2 mm.

about twice that of basal suckers. The more distal enlarged suckers of peculiar shape (Fig. 13e), being elongated and attached by long stalks. Distal suckers minute, arranged quadriserially. Arrangement of suckers on ventrolateral arms generally the same as that on dorsolateral arms, but a number of quadriserial rows of suckers present on middle third of arm. Enlarged suckers not as large (relative to those at arm base) as on dorsolateral arms. On right ventral arm, suckers on basal third arranged as on lateral arms. Quadriserial suckers present on middle third, followed by three to eight biserial rows; then about five biserial rows of suckers larger than those immediately proximal to them, but not as large as basal suckers. Minute suckers at tip of arm also biserial, unlike those of lateral arms.

Left ventral arm of male hectocotylized. One to three normal suckers at base followed by modified region, extending approximately half way along arm, which is transversely wrinkled and bears minute suckers laterally: seven pairs of

minute suckers on dorsal border; ventrally, the two series of suckers have moved together to form a single series of 14 suckers situated on extreme ventral edge of arm. Suckers biserial distally; the more proximal of these suckers (9-10 pairs) large, those on the tip minute.

In the female, all arms attenuated distally. Skin wrinkled basally on arms, next to sucker-bearing surface. This apparently not due merely to preservation, and has not been observed in any other *Sepia* species. Suckers on all arms biserial, and diminish gradually in size from base to tip. No enlargement of suckers on middle third of arms as found in males (Adam & Rees 1966: 113, however, found that females may also have enlarged suckers on the arms. See below).

Tentacular club small and recurved, with numerous subequal suckers in transverse rows of about eight. Rings of suckers without teeth, but covered with numerous small knobs. Protective membranes separate proximally. Natatory membrane extends along tentacular stalk for a distance a little less than half club length.

Shell (Pl. 43a-d) ovate, acuminate anteriorly, narrowing and rounded posteriorly. Dorsal surface usually pink in colour, finely granular posteriorly. Chitinous margins broad in smaller shells. Distinct rounded median rib present dorsally, broadening somewhat anteriorly. Rib limited by distinct lateral grooves. Spine absent posteriorly, but pronounced rounded knob present. Behind this, shell bends sharply towards ventral. Striated zone long, with narrow concave region laterally, raised and flattened medially. Striae convex to angular (\wedge -shaped), but with notch on either side, corresponding with point of meeting of raised middle region of striated zone with concave lateral areas. Median groove usually very faint, sometimes almost indistinguishable, but in a few shells is quite marked. Outer cone broad and deep.

TABLE 5. *Sepia hieronis*: a comparison of the relative dimensions (as % shell length) of the shells from the east and west coasts of southern Africa.

	West coast			East coast		
	N	Mean	Range	N	Mean	Range
Width . . .	4	39,1	38,3-40,4	3	42,4	40,7-45,7
Thickness . .	4	11,0	9,6-11,7	3	14,3	13,0-15,2
Striated zone	4	72,2	70,0-73,1	3	65,6	64,8-66,7

Shells from east and west coasts show some marked differences, although having an overall similar appearance. In shells from west coast (Pl. 43a, b), inner cone not as well developed posteriorly, and with narrow limbs. In eastern shells (Pl. 43c, d), on the contrary, inner cone well developed posteriorly, reflexed and fused to outer cone, and with broad limbs. Eastern shells wider and thicker, have shorter striated zone, and median region of striated zone is more markedly raised than in western shells (Table 5). Yet differences between the

two shell forms are those of degree, and do not suggest different species (except perhaps differences of inner cones). No differences could be found between animals from the two coasts. Differences in relative dimensions of shells from east and west coasts possibly due to size, since shells from east coast generally smaller than those from west coast. Alternatively, differences may be due to contrasting environmental conditions on east and west coasts.

Remarks

Smith (1916: 21), in the original description of *S. acuminata*, mentioned and figured (pl. II, fig. 4) a shell from Tongaat beach, Natal, which differs from the other examples of *S. acuminata*. From the description and figure, this specimen clearly belongs to *S. hieronis*, and differs from *S. acuminata* in that there is no spine, but only a posterior knob (just visible in Smith's figure), the outer cone is well developed posteriorly, the striated zone is more raised, and is divided into three distinct regions: one flat median and two concave lateral areas.

The arrangement of the suckers seems to vary considerably in *S. hieronis*, since every author describes them somewhat differently. But all are agreed that there are a number of pairs of enlarged suckers on the lateral arms of the males.

Robson (1924*b*: 646) described the hectocotylus as having one series of suckers ventrally in the modified region. This in fact corresponds to two series which have moved together to form a single series, as mentioned above. In one of the present specimens the hectocotylized arm is contracted, and the ventral series has become a zig-zag line, illustrating its origin from two longitudinal series of suckers.

According to Massy (1927: 159) the distal suckers on the lateral arms are biserial, but in the present male specimens they are quadriserial.

Adam & Rees (1966: 113), in the description of the male, mention that the suckers of all the arms are proximally quadriserial, and imply that those of the dorsal arms are quadriserial throughout. In the present males, the suckers of the dorsal arms are biserial from base to tip, and on the lateral arms are biserial over at least part of the proximal half, although these conditions are sometimes rendered less clear due to contraction of the arms.

In one female (MLd 61 mm) described by Adam & Rees (1966: 113) the dorsolateral arms have four pairs of enlarged suckers in the middle, minute suckers quadriserially arranged distally; 'the tips of all the arms, except the dorsal ones, seem to have the quadriserial arrangement of the suckers, but we are not sure that this is not due to contraction and that, in fact, all the suckers are biserial'. The female syntype has no enlarged suckers on the dorsolateral arms. In another female the enlarged suckers are well developed on the lateral and even on the ventral arms. In the present female (A30145, MLd 33 mm) all the arm suckers are biserial, and none is enlarged. It is possible that the sucker enlargement only develops as the animals grow to maturity.

Previously, animals of *S. hieronis* were known only from the west coast of

South Africa, from 30° 13'S, 15° 16'E to west of Slangkop (Robson 1924a: 13, 1924b: 645; Massy 1927: 158, 159; Voss 1962b: 251, 1967: 64; Adam & Rees 1966: 112). Adam & Rees (1966: 53, 112) found one shell of *S. hieronis* with specimens of *S. acuminata* from Stations 95 and 103 (Robson 1924a: 12, 13, 1924b: 643). These localities are approximately 30°S, 31°E, which is off the Natal coast, near Durban. Smith's (1916: 21) shell from Tongaat beach, Natal, was the only other record of *S. hieronis* from the east coast.

The present specimens from Monte Belo, Moçambique, are the first records of *S. hieronis* animals from the Indian Ocean. These specimens undoubtedly pertain to *S. hieronis*, although the shells show some differences from those found off the west coast. It is strange that neither the shell nor the animal of *S. hieronis* has so far been recorded between Cape Point and Durban.

Sepia insignis Smith, 1916

(Pl. 44a-c. Fig. 14. Tables 45, 46)

Sepia insignis Smith, 1916: 25, pl. II, fig. 10. Tomlin, 1923: 41. Voss, 1962b: 248. Adam & Rees, 1966: 114, pl. 31, figs 189-191.

Type locality

Tongaat beach, Natal (shells only).

Distribution

Animal: 34° 15'S, 18° 47'E (False Bay) (S.A.M.). Depth 42 m.

Shells: Bloubergstrand (S.A.M.) to Tongaat beach, Natal (Smith 1916: 25).

Material

S.A.M. A30486, locality unknown; 1 shell

A31236, Kommetjie; 1 shell

A31241, Simonstown; 3 shells (1 broken)

A31247, 34° 15'S, 18° 47'E, 42 m; 1 ♀

A31248, between Strandfontein and Muizenberg; 1 shell

Still Bay; 1 shell

Bloubergstrand; 1 shell, broken

Description

Female specimen rather badly preserved, with mantle compressed laterally.

Mantle elongate oval, anterior margin produced dorsally, emarginate ventrally. Head short and broad. Fins rather wide, beginning a few mm behind anterior margin of mantle, rounded and separate posteriorly.

Skin sparsely papillose dorsally with concentric chromatophores on head and mantle. Mantle very wrinkled ventrally, but this may be due to preservation. Colour dark purple dorsally on head and mantle; chromatophores on mantle concentrated mid-dorsally, less dense laterally towards fins. Fins pale, with a few scattered chromatophores both dorsally and ventrally. Mantle pale mid-ventrally, with band of chromatophores on each side along bases of fins.

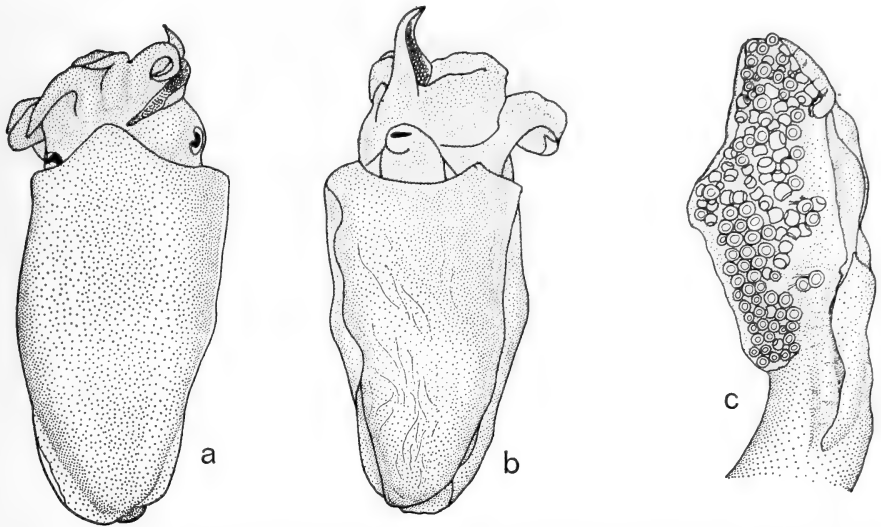


FIG. 14. *Sepia insignis* female, A31247. a. Dorsal view; b. ventral view; c. right tentacular club.

Arms I and II subequal in length, about one-third MLD, arms III a little shorter, arms IV longer, very well developed, and wrinkled ventrally. Shallow interbrachial web present, except between ventral arms. Dorsal arms attenuated distally over about half arm length. Arms III and IV strongly keeled. Protective membranes well developed on all arms, and wide enough to meet over inner surface of arm.

Arms unfortunately rather distorted, and some suckers lost, especially from delicate dorsal arms. Suckers on dorsal arms biserially arranged from base to tip. On arm II, five pairs of suckers basally followed by very oblique quadriserial rows to arm tip. On arm III, two pairs of suckers basally, then one or two to fill in gap before obliquely quadriserial suckers, which continue to tip. Suckers on ventral arms very obliquely quadriserial, with one row of three suckers basally. Quadriserial rows so oblique that suckers appear to be almost biserial. None of the suckers enlarged; size of suckers decreases gradually from base to tip on all arms. Suckers globose, with nodular rings which have irregular but not toothed edges.

Tentacular club fairly small, bearing a number of subequal suckers in transverse rows of about eight. Suckers have large rings with nodular surface and smooth edge. Natatory membrane well developed, continuing a little beyond club. Protective membranes well developed; ventral membrane curves around base of club, but not meeting dorsal membrane, which ends just before base of club. Upper surface of club with a number of transverse rows of chromatophores.

Shell (Pl. 44a-c) elongate, fairly narrow, sharply acuminate anteriorly, then about same width over approximately two-thirds of its length; rounded

posteriorly. Posterior spine absent. Shell a pale pink colour dorsally. Mid-dorsal longitudinal ridge present, but not limited by lateral grooves. Ridge ends posteriorly in blunt knob, whereafter shell curves sharply to ventral. Striated zone long, narrowing markedly posteriorly; striae \wedge -shaped between limbs of inner cone. Well defined median longitudinal groove present over striated zone, continuing along last loculus, where it is less distinct. Inner cone well developed posteriorly, completely reflexed and fused to outer cone. Inner cone curved over sides of striated zone laterally, as in *S. burnupi*, and limbs of inner cone lie on phragmocone. In smallest shell, limbs of inner cone much nearer edges of phragmocone than in larger shells. It would appear that limbs of inner cone move towards middle of shell in older shells. Outer cone broad laterally.

Remarks

Until now only shells of *S. insignis* were known. The present female was found in the collection of the University of Cape Town Ecological Survey, and is now lodged in the collection of the South African Museum.

The shell from Bloubergstrand (Pl. 44c) must have measured about 55 mm when whole, and is the largest shell known of *S. insignis*.

This species seems to be related to *S. hieronis*. The shells of the two species show some resemblance, and the animals are similar in that both species have subequal tentacular suckers and biserial suckers on the dorsal arms.

Sepia robsoni (Massy, 1927)

(Tables 6, 50)

Rhombosepion robsoni Massy, 1927: 159, pl. XVII, figs 1-8.

Sepia robsoni Voss, 1962b: 248. Adam & Rees, 1966: 120, pl. 46, fig. 279.

Type locality

Hout Bay, 17-37 m.

Description

Only one specimen (male) ever caught, and was not available for examination. Following description after Massy (1927: 159) and Adam & Rees (1966: 120).

Animal small. Mantle broadly oval, anterior mantle margin dorsally slightly convex (Adam & Rees 1966: 120), very slightly produced in the centre (Massy 1927: 160), ventrally deeply emarginate. Fins wide, beginning three mm behind mantle margin, separate posteriorly.

A few tubercles present dorsally along outline of shell and on head. Fleishy ridge present on either side on mantle ventrally, near fin bases, as in *S. typica*, but pores absent. Flesh-colour to pale brown, with minute dark chromatophores dorsally, extending partly on to fins. Ventrally with a few chromatophores along fin base.

Arms subequal in length, with ventral arms slightly longer than dorsal ones. Interbrachial web well developed between arms I to III, attaining half

arm length, lower between arms III and IV, absent between ventral pair. Suckers globose, with smooth rings; skin adjacent to rings grooved; suckers biserially arranged, none enlarged.

Dorsal arms with finger-like tips, devoid of suckers, and with eight pairs of suckers proximal to naked tips. Dorsolateral arms with eight pairs of large subequal suckers and a few small suckers distally. Ventrolateral arms with nine pairs of large subequal suckers. Right ventral arm with seven pairs of large suckers, of which suckers of ventral series larger than those of dorsal series, and much larger than those of other arms. Left ventral arm hectocotylized over basal three-quarters of its length, bearing ten pairs of minute suckers on modified region.

Tentacular club crescent shaped, bearing about 53 more or less subequal suckers, in transverse rows of four to six, median suckers being slightly larger than others. Rings of tentacular suckers papillose (? nodular), dentate on at least part of the ring (Massy 1927: 160). Natatory membrane very broad, extending beyond base of club for a distance equal to about half club length; dorsal protective membrane very broad at base of club.

Shell completely chitinized (? decalcified), in poor condition. Anterior part strongly acuminate, resembling that of *S. hieronis*.

Remarks

According to Massy (1927: 159), *Sepia robsoni* resembles *S. hieronis*, but differs from the latter in having grooved suckers (smooth rings) biserially arranged on all the arms, and none is enlarged in the male. 'The shell somewhat resembles that of *S. insignis*, but the latter is even more acuminate anteriorly and seems to be much wider in its posterior part' (Adam & Rees 1966: 121).

S. robsoni also resembles *S. dubia* (for comparison, see Table 6) in that all the arm suckers are biserially arranged, the mantle is very broad, and the ventral mantle surface has fleshy keels without pores. The hectocotylus is like that of *S. typica*, and the interbrachial web is well developed. The tentacular club is exactly like that of *S. typica* (Adam & Rees 1966: 121). *Sepia robsoni* differs, however, from both *S. typica* and *S. dubia* in its shell, which presumably has the phragmocone covering almost the entire dorsal lamella (since it is compared with those of *S. hieronis* and *S. insignis*) and in the dorsal arms with the tips devoid of suckers. In this latter feature *S. robsoni* resembles *S. faurei*.

Sepia faurei n. sp.

(Figs 15, 16. Tables 6, 50)

Type locality

S 14°E of Cape Seal 88 km, 168 m.

Material

S.A.M. A30144, S 14°E of Cape Seal 88 km, 168 m; 1 ♀ (holotype)

Description

Animal small. Mantle broadly oval, anterior mantle margin convex dorsally (not markedly produced), emarginate ventrally. Fins narrow, beginning a few mm behind mantle margin, separate posteriorly.

Colour uniform brown on head and mantle dorsally, with small darker spots on arms. Skin densely papillose dorsally. Fleshy ridge present on either side of mantle ventrally, near fin bases, as in *S. typica*, but pores absent.

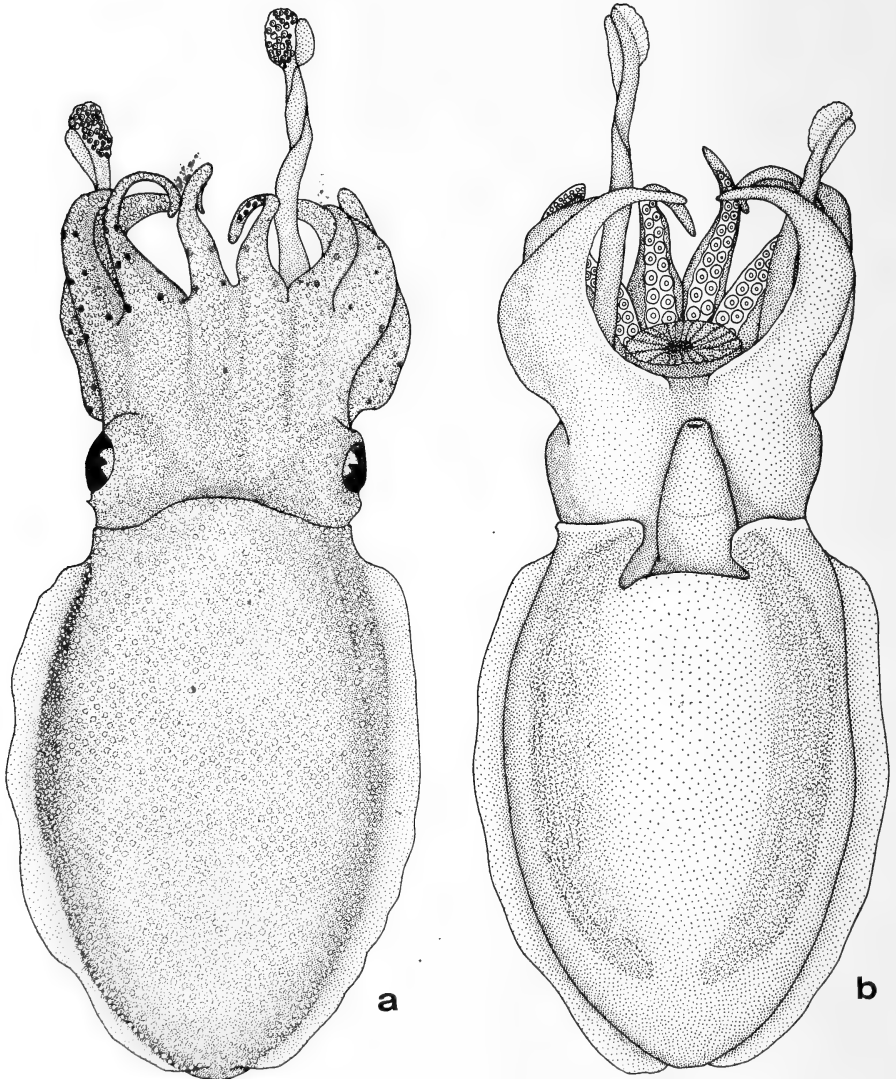


Fig. 15. *Sepia faurei* female, A30144 (holotype). a. Dorsal view and b. ventral view.

Arms subequal in length; interbranchial web high dorsally, attaining about half arm length, but low between ventrolateral and ventral arms, and absent between ventral pair. Suckers globose, without teeth on chitinous rings, but these covered with numerous raised knobs. Suckers on all arms biserially arranged. Distally all arms except ventral pair attenuated over about half arm length; suckers on attenuated portion (about six pairs on arm I, 17 pairs on arm II, and 16 pairs on arm III) minute, and protective membranes very well developed. Tips of attenuated distal half of dorsal arms finger-like, devoid of suckers and protective membranes (Fig. 16a). Six to nine pairs of subequal suckers proximally (nine pairs on arm I, six pairs on arm II, and seven pairs on arm III), of which last pair somewhat smaller. Ventral arms not markedly attenuated distally, bearing eight pairs of subequal suckers proximally, and about 12 pairs of minute suckers on tips.

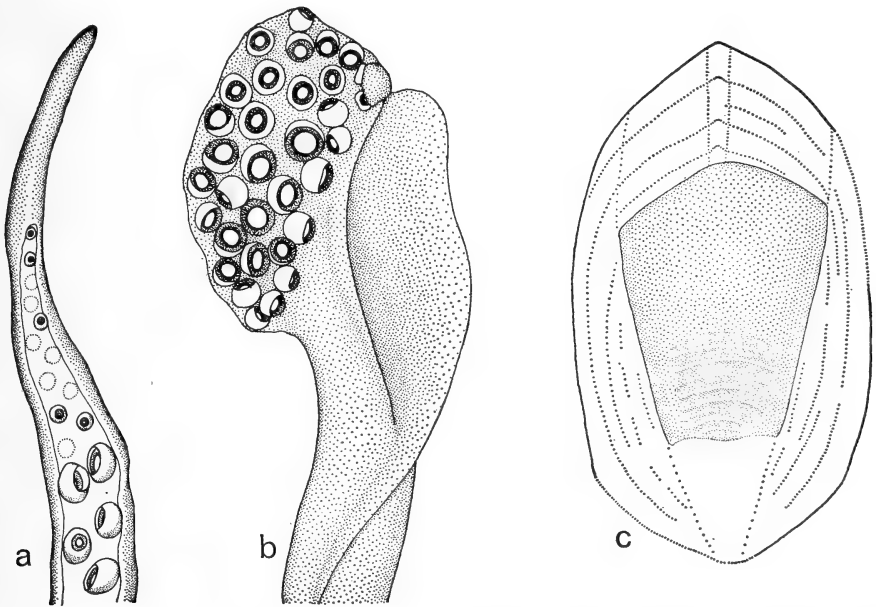


Fig. 16. *Sepia faurei* female, A30144 (holotype). a. Detail of distal part of dorsal arm. Position of missing suckers indicated by dotted rings. b. Right tentacular club. c. Ventral view of shell (incomplete).

Tentacular club broad, slightly recurved, bearing 33 subequal suckers in transverse rows of four to six (Fig. 16b). Median suckers a little larger than lateral suckers. Sucker rings not toothed, with nodular surface. Dorsal protective membrane well developed, separate from ventral membrane proximally. Natatory membrane broad, continuing along tentacular stalk for a distance equal to club length.

Shell (Fig. 16c) not calcified, very thin, as in *S. typica*, broadly ovate,

TABLE 6. Comparison of the main characters of *Sepia robsoni* (Massy), *S. dubia* Adam & Rees and *S. faurei* n. sp.

	<i>S. robsoni</i>	<i>S. dubia</i>	<i>S. faurei</i>
Sex	male	female	female
MLd	17 mm	17 mm	21 mm
Anterior mantle margin	Dorsally slightly convex, ventrally deeply emarginate	Dorsally slightly convex, ventrally deeply emarginate	Dorsally convex, ventrally emarginate
Dorsal papillae	A few tubercles along the outline of the shell and on the head	Dorsal surface of mantle, head and arms covered with well-spaced round papillae, creating a very rugose appearance. Mid-dorsally on the mantle there are two oval patches of contracted papillae, one on each side of the median line, and a third one anteriorly near the mantle margin	Skin dorsally on head, mantle and arms densely covered with small papillae
Ventral mantle surface	Much like that of <i>Hemisepius typicus</i> with the fleshy ridge, but there is no trace of any pores	Smooth, with a thick fleshy keel parallel to the outer margin, as in <i>H. typicus</i> , but without pores	A fleshy ridge on either side near the fin bases, but no pores
Arm lengths	Arms subequal in length	Arms subequal in length	Arms subequal in length
Interbrachial web	The web reaches halfway up the arms between arms I, II and III; between arms III and IV it is much lower and is completely lacking between arms IV	The web is very high between arms I, II and III, reaching halfway up the arms; it is much lower between arms III and IV and non-existent between arms IV	Web does not attain half arm length between arms I, II and III; it is even lower between arms III and IV, and is absent between arms IV
Arm suckers	Suckers globose; biserially arranged on all the arms	Rather small and biserial	Globose; biserial on all arms

Dorsal arms	<p>'The distal portions are thickened and end in rounded knobs without suckers. When observed laterally the surface is seen to be folded as if suckers might be in the course of formation. The appearance may therefore be due to accident' (Massy 1927). But in Massy's figures (pl. XVII, figs 1, 2) the dorsal arms appear slender at the tips. According to Adam & Rees (1966), who re-examined the specimen, 'the dorsal arms have finger-like tips, devoid of suckers'. They do not mention any thickening</p>	<p>The suckers on the dorsal arms continue to within 0.4 mm of the tips (Taylor 1968, personal communication)</p>	<p>The tips of the attenuated distal half of the dorsal arms are finger-like and devoid of suckers and protective membranes</p>
Tentacular club	<p>About 53 suckers arranged in transverse rows of 4-6. About 3 median rows have larger suckers than the rest. Dorsal protective membrane very broad at base of club. Natatory membrane very broad and extending beyond base of club for about half the length of the club</p>	<p>Minute subequal suckers arranged in 4 or 5 longitudinal series (Adam & Rees 1966). There are in fact 54 suckers, of which the median ones are slightly larger (Taylor 1968, personal communication). Dorsal protective membrane wide and separated from the ventral one at base of club. Natatory membrane well developed, extending beyond base of club for about half its length</p>	<p>33 subequal suckers in transverse rows of 4-6, the middle ones a little larger than the marginal ones. Dorsal protective membrane well developed, separate from the ventral one proximally. Natatory membrane broad, and continues along the stalk for a distance equal to the club length</p>

continued overleaf

TABLE 6 (continued)

	<i>S. robusti</i>	<i>S. dubia</i>	<i>S. faurei</i>
Shell	<p>Completely chitinized (? decalcified); in poor condition. Its anterior part is strongly acuminate and resembles that of <i>S. hieronis</i></p>	<p>Shell broadly oval, acuminate anteriorly, but less so than in <i>H. typicus</i> and is broadly rounded behind. It is a low dome-shape in the middle but is flatter near the margins. Nearly the whole dorsal surface is calcareous, with a reticulate pattern. No spine. Ventral surface strongly concave and spoon-shaped. The central part has a reversed conical shape and is slightly higher than the surrounding part; it occupies a little more than half the shell length, as in <i>H. typicus</i>. Last locus trapezoid, widest at anterior margin. This last locus represents about half the length of the striated area. Behind the last locus, the striated area occupies only the central third portion of the whole inner zone and is flanked by two broad, smooth, marginal areas. The striae, about 15 in number, are widely spaced, transverse, nearly straight, being only slightly wavy. There is a distinct inner cone, brownish in colour in alcohol, with rather broad limbs, that are completely fused to the outer cone; its posterior part surrounds a very shallow depression. The broad outer cone surrounds completely the inner cone</p>	<p>Shell completely chitinous. It is broadly oval, somewhat acuminate anteriorly. The ventral phragmocone roughly triangular in shape, and does not cover the anterior part of the dorsal lamella. Last locus, which has a convex anterior border, probably covered about half the length of the phragmocone. The striated zone occupies the central region of the phragmocone. On either side of the striated zone there is a smooth marginal area. The striae are transverse, and slightly rounded. Unfortunately the posterior part of the shell has been lost, and no indication of the inner cone remains</p>

somewhat acuminate anteriorly. Posterior end damaged. As in *S. typica*, phragmocone not covering anterior part of dorsal lamella. Anterior border of last loculus convex. Striae fewer and last loculus longer than in *S. typica*. Striated zone occupying central region of phragmocone; smooth marginal area present on either side of striated zone. Striae transverse, slightly convex in shape. No indication of inner cone remains.

Remarks

Sepia faurei resembles *S. robsoni* in the absence of suckers distally on the dorsal arms. It resembles both *S. robsoni* and *S. dubia* in that the mantle is very broad and has fleshy keels, without pores ventrally, and the arm suckers are biserially arranged. The three species are compared in Table 6.

The shell of *S. faurei* is similar to those of *S. typica* and *S. dubia*, being very thin, with the phragmocone not covering the entire dorsal lamella. In *S. typica* and *S. dubia*, however, the anterior border of the phragmocone is not parallel to the corresponding sides of the dorsal lamella, whereas in *S. faurei* it is more nearly so, and the phragmocone is somewhat longer in the latter species.

Sepia faurei, showing relationships with both *S. robsoni* and *S. dubia*, seems to represent an intermediate link in the transition from *Sepia* to *Hemisepius*. On the one hand it is related (by virtue of the dorsal arms) to *S. robsoni*, which apparently has a *Sepia*-like shell with the phragmocone covering almost the entire dorsal lamella anteriorly, and on the other hand *S. faurei* is related to *S. (Hemisepius) dubia* and *S. (Hemisepius) typica* with a *Hemisepius* shell, in which the phragmocone is much shorter than the dorsal lamella.

Distinctive characters

1. Tips of dorsal arms finger-like, devoid of suckers and protective membranes
2. Suckers biserially arranged on all arms
3. Mantle very broad, with fleshy keels ventrally
4. Skin densely papillose dorsally on head, mantle and arms
5. Shell with phragmocone considerably shorter than dorsal lamella, but with anterior margin of phragmocone convex in shape

The holotype of *Sepia faurei* was collected during one of the cruises of the Cape Fisheries survey vessel *Pieter Faure* (P.F.14290, 19 February 1902), after which this species has been named.

Sepia (Hemisepius) typica (Steenstrup, 1875)

(Fig. 17. Tables 7, 47-49)

Hemisepius typicus Steenstrup, 1875: 468, pl. I, figs 1-10, pl. II, fig. 1. Hoyle, 1886: 26, 217; 1912: 281. Gibbons, 1888: 202. Smith, 1903: 356; 1916: 25. Chun, 1915: 411, figs 33, 34. Massy, 1927: 164. Thore, 1945: 50, fig. 1. Voss, 1962b: 248, 252; 1967: 64.

Hemisepiion typicum: Rochebrune, 1884: 78, pl. 3, fig. 1.

Rhombosepion sp. A Massy, 1927: 161.

Hemisepius typicus var. *chuni* Thore, 1945: 50.

Sepia (Hemisepius) typica Adam & Rees, 1966: 117, pl. 32, figs 192-195, pl. 33, figs 196, 197.

Type localities

Table Bay; St. Francis Bay (var. *chuni*).

Distribution

Animals: Saldanha Bay (Hoyle, 1912: 281) to Cape Natal, W by N, 10 km (Massy 1927: 161). Depth 2–156 m.

Material

- S.A.M. A8989, locality unknown; 1 ♂ in poor condition
 A29608, south side of Schaapen Island, Saldanha Bay, 4 m; 3 ♀
 A29717, SSE of Ystervarkpunt, 92 m (det. G. L. Voss); 7 ♂, 6 ♀
 A29783, Saldanha Bay, 7 m; 15 ♂, 31 ♀
 A30176, S 34°W of Cape Infanta 30 km, 84 m; 5 ♂ (of which two in poor condition), 2 ♀
 A30177, 34° 14'S, 22° 23'E (Mossel Bay), 60 m; 5 ♂, 4 ♀
 A30269, S 16°W of Cape Point lighthouse 16 km, 156 m; 1 ♂, 4 ♀, all in poor condition
 A30484, locality unknown; 1 shell in poor condition

Description

Animals small; largest specimen in present collection being a female of MLd 25 mm; largest male has MLd 21 mm.

Mantle very broadly oval, almost as wide as long. Anterior mantle margin convex dorsally, emarginate ventrally. Ventral surface of mantle bearing two fleshy ridges near fin bases; each ridge with a number of pores anteriorly (most commonly 10–12 on each side, but the number may vary between five and 15. Number of pores not always the same on both sides). Ridges becoming less distinctive posteriorly. No evidence of longitudinal groove linking pores, as described by Steenstrup (1875: II).

Head short and broad. Fins narrow, beginning a few mm behind anterior mantle margin, fused posteriorly.

Colour dark reddish-purple dorsally on head, arms and mantle, with darker diamond-shaped region mid-dorsally over shell. Two pale round tubercles with concentric chromatophores present in middle of darker region. Fins pale dorsally with scattered dark chromatophores, most dense near fin bases. In some cases short transverse orange bands present on fins. Colour pale ventrally, except for darker colour of ridges bearing pores, and sparse chromatophores between ridges and fin bases; a few chromatophores present laterally on funnel.

Skin very sparsely papillose dorsally, a few papillae around eyes being the most marked. Mid-dorsal tubercles on mantle very flattened.

Arms subequal in length, fairly short (about 40–50% MLd). Interbrachial web deep, attaining half arm length, but absent between ventral arms. All arms triangular in cross section, but only well developed ventral arms keeled.

Suckers on all arms biserial, globose, not flattened and disc-shaped, as described by Steenstrup (1875: II). Chitinous rings smooth edged, with nodular

surface. In female, size of suckers decreases gradually from base, but suckers suddenly become much smaller at tips of arms; about six to eight pairs of minute biserial suckers present. In male, one to four pairs of suckers near tips of arms I to III enlarged. No enlargement occurs on ventral arms, but in some cases suckers of dorsal series of right ventral arm larger than those of ventral series. Thore (1945: 52) found, however, that suckers of 12th to 18th rows on right ventral arm were enlarged in his specimens from Table Bay and Oukraal (Oude Kraal). One male from Saldanha Bay (A29783) shows abnormal arrangement of suckers on third arms, perhaps due to contraction. Middle of right arm III bears three rows of suckers in irregular quadriserial arrangement, and one row of three suckers. Left arm III has one row of three suckers, four very oblique quadriserial rows, then a single dorsal sucker medially. These arms normal distally.

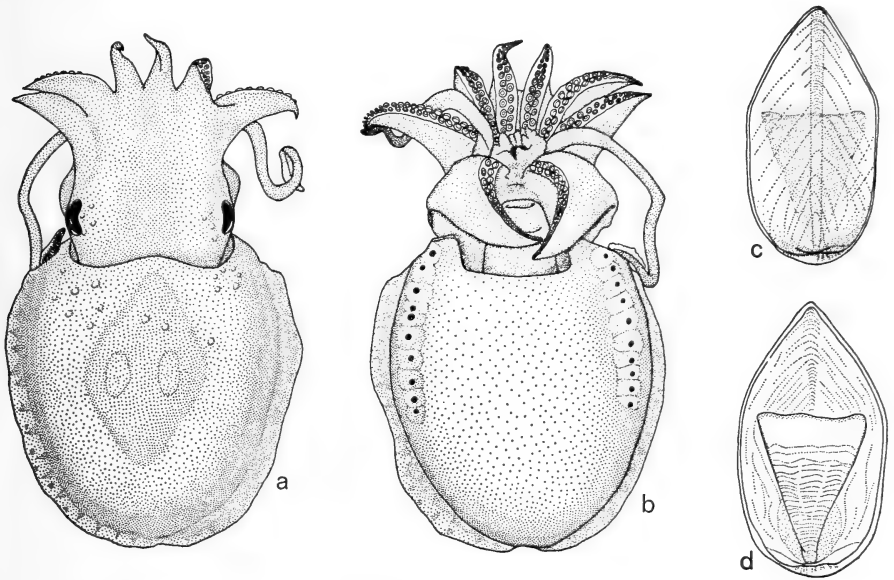


FIG. 17. *Sepia (Hemisepius) typica*. a. Dorsal and b. ventral view of female, A29783. c. Dorsal and d. ventral view of shell of female, A29608.

Left ventral arm of male hectocotylized. Basal half or more of arm modified, bearing nine to 13 pairs of minute suckers arranged in two widely spaced series separated by fleshy transverse ridges on arm. Distal half of arm normal, bearing five to six pairs of normal suckers, then about eight pairs of minute suckers on arm tip. A few basal modified suckers sometimes larger than the rest.

Tentacular club small and straight, bearing numerous subequal suckers in oblique transverse rows of six. Rings of suckers broad and nodular, without teeth. Protective membranes separate proximally. Natatory membrane very

well developed, continuing along stalk for a distance from one-half to once club length.

Shell (Fig. 17c, d) not calcified, very thin and fragile. One shell, successfully dissected out (A29608), has dimensions: length 19,5 mm, width 10,5 mm, length of striated zone 10 mm. It is broad, pointed anteriorly, rounded posteriorly. No posterior spine or knob, and no median dorsal ridge present. Phragmocone very short, triangular in shape, with last loculus constituting base of triangle anteriorly. Last loculus not covering anterior part of dorsal shield. No median longitudinal groove ventrally. Striated zone occupies most of phragmocone; striae wavy. Inner cone barely discernible, completely fused with outer cone; forming, together with its limbs, a circle about posterior point of striated zone. Outer cone broad.

Remarks

When first describing this species, Steenstrup (1875: 468) created a new genus for it, on the basis of the following characters:

1. The ventral mantle surface has deep pores, which in *Hemisepius typicus* are arranged in two lines of 12 pores each.
2. The shell is poorly developed, with very rudimentary, calcareous loculi not covering the anterior part of the dorsal lamella, and their anterior border is not parallel to the corresponding sides of the extremely thin lamella.
3. All arms with biserial suckers, which are very flattened, almost smooth, disc-like.

Until recently, these characters clearly separated *H. typicus* from all the remaining Sepiidae (although the number of pores was found to vary somewhat, and the suckers are not flattened, but globose) and the genus was valid. But a recently discovered species, *Sepia dubia*, first described by Adam & Rees (1966: 119), shows a number of characters which bridge the gap between the genera *Hemisepius* and *Sepia*, and Adam & Rees relegated *Hemisepius* to subgeneric status.

Chun (1915: 412) first described the male of *S. typica*, and illustrated the hectocotylus. He found that most of the suckers in the ventral series of the modified region were absent, but these had probably been lost, since all the males in the present collection have a complete ventral series on the hectocotylus.

Smith (1916: 26) suggested the possibility that *S. tuberculata* be identical with *S. typica*. It is difficult to understand how Smith came to this supposition, since both the shells and the animals of these two species are very different. The only possible similarities in the shells are the general outline and the thinness (although the shell of *S. typica* is much broader and very much thinner than that of *S. tuberculata*). As remarked by Adam (1941: 116), the suggestion is clearly untenable.

Thore (1945: 50) found that his specimens of *S. typica* from Table Bay and Oukraal (MLd 22-27 mm) were larger than that described by Chun (1915: 412)

(MLd 17 mm) from a more easterly locality, St. Francis Bay, but comparable with those of Steenstrup (from Table Bay) and of Massy (1927: 164) (from False Bay and Hout Bay). On the basis of this, he stated: 'I think we have to postulate a constant difference in size between the eastern and western form of *Hemisepius*, the latter being the largest' (Thore 1945: 50), and proposed that the eastern forms be named *H. typicus* var. *chuni*.

Thore found that his western male specimens also differed from that described by Chun in the number and size of the suckers on the ventral arms. The hectocotylus of Thore's specimens differed from that figured by Chun in that the dorsal row of suckers was separated from the edge of the arm by a distinct longitudinal groove; the proximal suckers in the ventral row were not enlarged; the second-last sucker of the dorsal row (in the modified region) was not enlarged; the enlarged suckers distal to the modified region were about 12 in number (five in Chun's specimen) and there were about 20 minute suckers at the tip of the arm (13 in Chun's specimen).

In all, only three specimens of *S. typica* are known from localities east of 24°E: one male (MLd 17 mm) from St. Francis Bay (Chun 1915: 412), one female (MLd 18 mm) from east of Port Elizabeth (Voss 1962b: 252) and one male (MLd 13 mm) from Cape Natal (*Rhombosipion* sp. A, Massy 1927: 161, determined as *S. typica* by Adam & Rees 1966: 117). In the male from Cape Natal, the suckers distal to the modified region of the hectocotylus were absent, presumably lost. This leaves one eastern male with which to compare the western specimens. A comparison of the specimens of Thore and Chun is given in Table 7, together with the specimens in the collection of the South African Museum.

From observations on the specimens and the data in the table, the following points become apparent:

1. Chun's specimen from St. Francis Bay is not unusually small, as it falls into the size ranges of mature specimens from Saldanha Bay and Mossel Bay, and is larger than those from Cape Infanta and Ystervarkpunt.
2. The number and position of enlarged suckers on arms I to III apparently varies randomly; there is no correlation with mantle length or the locality of the specimens. The distal suckers on arms III are not always markedly enlarged.
3. Right arm IV: the total number of suckers increases with the size of the animal, but the specimens from Ystervarkpunt have fewer suckers than those of the same size from other localities; Chun's specimen has an unusually low number of suckers for its size—a specimen of MLd 17 mm from Mossel Bay has 21 pairs of suckers on the fourth right arm. The position of the distal enlarged suckers is not closely related to the total number of suckers, but some enlarged distal suckers are almost always present; in this, Chun's specimen again differs. There are usually three pairs of enlarged suckers basally, but occasionally two or

TABLE 7. *Scpia typica* males. Comparison of number and enlargement of arm suckers. Only specimens with a recognizable hectocotylus are included.

	Saldanha Bay (A29783)	Table Bay (Thore 1945)	Off Cape Infanta (A30176)
Dorsal mantle length	11-19 mm	22-27 mm	11-16 mm
Arm I	Variable enlargement of suckers from 8-12th rows, usually including those of 9-10th rows	Enlargement of 10th sucker pair, and variable enlargement of 2-3 pairs of distal suckers, or of some suckers of one series	Variable enlargement of suckers from 8-11th rows, usually including those of 9th row
Arm II	Variable enlargement of suckers from 8-12th rows, usually including those of 10-11th rows	As arm I	Variable enlargement of suckers from 7-11th rows, usually including those of 9th row
Arm III	Variable enlargement of suckers from 12-16th rows, usually including those of 13-14th rows	Distal enlargement of suckers (which rows not specified)	Variable enlargement of suckers from 10-12th rows, usually including those of 10-11th rows
Total number	19-27 pairs	About 30 pairs	21-22 pairs
Enlarged distally	Variable enlargement from 11-17th rows	12th to 18th pairs	12th to 14th pairs
Enlarged proximally	Basal 3 or 4 pairs	Basal 3 pairs	Basal 2 to 3 pairs
Number minute distally	10-20	About 20	12-19
Number enlarged between modified region and minute distal suckers	8-10	12	8-9
Suckers on right arm IV			
Suckers on hectocotylus (left arm IV)			

TABLE 7 (continued)

	Off Ystervarkpunt (A29717)	Mossel Bay (A30177)	St. Francis Bay (Chun 1915)
Dorsal mantle length	10-15 mm	14-21 mm	17 mm
Arm I	Variable enlargement of suckers from 6-9th rows, usually including those of 7-8th rows	Variable enlargement of suckers from 7-11th rows, usually including those of 9th row	10th pair enlarged
Arm II	Variable enlargement of suckers from 6-10th rows, usually including those of 8th row	Variable enlargement of suckers from 8-13th rows, usually including those of 9-10th rows	10th pair enlarged
Arm III	Variable enlargement of suckers from 10-12th rows, usually including those of 10-11th rows	Variable enlargement of suckers from 9-14th rows	No enlargement reported
Total number	16-21 pairs	21-26 pairs	13 pairs, gradually decreasing in size from base to tip
Enlarged distally	9-14th pairs	11-16th pairs	
Enlarged proximally	Basal 2-3 pairs	Basal 3-4 pairs	
Number minute distally	8-12	16-20	13
Number enlarged between modified region and minute distal suckers	6-10	8-12	5 (or 8?)
Suckers on right arm IV			
Suckers on hectocotylus (left arm IV)			

four pairs; Chun's description does not preclude the possibility that these were also present in the specimen from St. Francis Bay.

4. Hectocotylus: the number of minute distal suckers of Chun's specimen is within the normal range for its size. The number of enlarged distal suckers in Chun's specimen is unusually small; from the figure (Chun 1915, fig. 34), Thore deduced that the penultimate sucker of the dorsal series on the modified region is enlarged, and that there are five enlarged suckers distal to the modified region of the hectocotylus. An alternative interpretation is that this single enlarged dorsal sucker is part of the group of distal enlarged suckers, of which the second pair has failed to become enlarged. A similar case was observed in a specimen (MLD 16 mm) from Cape Infanta, in which one sucker of the second pair of enlarged suckers has remained minute. The longitudinal groove separating the dorsal series of suckers from the edge of the modified surface, as reported by Thore, was observed in some specimens but not in others, and apparently depends on the state of preservation of the specimens. The three enlarged proximal suckers in the ventral row on the modified region, as illustrated by Chun, are absent in Thore's specimens. In the present specimens the proximal suckers of the dorsal and/or ventral row were sometimes found to be somewhat larger than the more distal suckers on the modified region of the hectocotylus. But the proximal enlargement is not marked, and the size of the suckers of the modified region gradually diminishes distally. The number of large suckers, and their position, apparently varies randomly.

Thus Chun's specimen differs from those from more westerly localities only in that it has fewer suckers on the right arm IV, of which none are enlarged distally. Whether or not this constitutes a valid character for separating eastern and western forms of *S. typica* cannot be decided on the basis of the presently known specimens, and a decision must await the collection of further specimens from the eastern coast of South Africa. In any case, the 'variety' is no longer recognized as a valid taxon within the system of nomenclature, and should be replaced by the term subspecies, provided the eastern and western forms of *S. typica* are found to differ sufficiently.

Sepia (Hemisepius) dubia Adam & Rees, 1966

(Tables 6, 50)

Sepia (Hemisepius) dubia Adam & Rees, 1966: 119, pl. 34, figs 198–201, pl. 46, fig. 272, text fig. 1.

Type locality

False Bay, 34° 11'S, 18° 27'E, 25 m.

Description

The only known specimen (female) was not available for examination. Following description after Adam & Rees (1966: 119) and Taylor (personal

communication), who kindly supplied some additional information about the type specimen.

Animal small. Mantle broadly oval, anterior mantle margin slightly convex dorsally, deeply emarginate ventrally.

Dorsal surface of mantle, head and arms covered with well spaced round papillae; in addition, three oval patches of contracted papillae present medially: one on either side of median line, and third one anteriorly near mantle margin. Ventral mantle surface smooth, with thick fleshy keel, parallel to outer margin, as in *S. typica*, but without pores.

Arms subequal in length, laterally compressed, keeled on outer sides; protective membranes narrow. Web very high between dorsal and lateral arms, attaining half arm length; lower between arms III and IV, absent between ventral pair. Arm suckers rather small; biserially arranged.

Tentacular club small, crescent shaped, bearing 54 minute subequal suckers arranged in four or five longitudinal series (according to Taylor, personal communication, the median suckers are slightly larger than the others). Natatory membrane well developed, extending beyond base of club for a distance equal to about half club length. Dorsal protective membrane wide, separated from ventral membrane at base of club.

Shell broadly oval, somewhat acuminate anteriorly, broadly rounded posteriorly. Almost whole dorsal surface calcareous, with reticulate pattern. Posterior spine absent. Ventral surface strongly concave, spoon shaped. Phragmocone has reversed conical shape, occupying a little more than half shell length, as in *S. typica*. Last loculus trapezoid, widest at anterior margin. Striated zone about twice as long as last loculus, but occupying only central third of width of phragmocone; broad smooth marginal area present on either side of striated zone. About 15 widely spaced, transverse, slightly wavy striae present. Inner cone distinct, brownish in colour, with rather broad limbs, completely fused to outer cone. Posterior part of inner cone surrounds shallow depression. Outer cone broad, completely surrounding inner cone.

Remarks

Sepia dubia resembles *S. typica* in that it has biserial suckers on the arms, the tentacular clubs are the same, and the shell is very similar, with a very short phragmocone, whose anterior border is not parallel to the corresponding sides of the thin dorsal lamella. The shell differs however, in that it has a calcareous covering of the dorsal surface, and a distinct inner cone. *Sepia dubia* has fleshy keels on the ventral mantle surface, but there are no pores. It also differs from *S. typica* in that the skin is not smooth, but is covered with well spaced papillae dorsally.

Whilst *S. dubia* is obviously closely related to *S. typica*, the differences between the two species include a character (pores in the ventral mantle surface) listed by Steenstrup (1875: II) as defining the genus *Hemisepius*, and led Adam &

Rees (1966: 143) to state that 'the genus or subgenus *Hemisepius* may be maintained for *H. typicus* and *H. dubius*, but its separation from other Sepiidae has become less distinct'. In the taxonomic section of their review (Adam & Rees 1966: 117, 119) they have relegated *Hemisepius* to subgeneric status for *S. typica* and *S. dubia*.

Sepiella cyanea Robson, 1924

(Pl. 42c, d. Fig. 3b. Tables 51-53)

Sepiella cyanea Robson, 1924a: 13; 1924b: 648, figs 25-27, pl. II, fig. 6. Adam, 1939b: 109, figs 14A-B, pl. IV, figs 3, 4. Voss, 1962b: 248. Adam & Rees, 1966: 121, pl. 36, figs 208-215.

Sepia sp. a Voss, 1962a: 3.

? *Sepiella obtusata* (non Pfeffer) Massy, 1928: 95.

Type locality

S.S. Pickle, Sta. 476: 29° 17'S, 31° 33'E, 51 m (lectotype, designated Adam & Rees 1966: 121).

Distribution

Animals: Port Elizabeth (Adam & Rees 1966: 121) to 29° 17'S, 31° 33'E (off Tugela River) (Robson 1924a: 14, Sta. 476) and Nosy N'Tangam (Malagasy) (Adam & Rees 1966: 121). Depth 51-73 m.

Shells: Port Elizabeth (Adam & Rees 1966: 121) to ? Tongaat (Massy 1928: 95) and Ambavanibé, Malagasy (Adam 1939b: 109).

Material

S.A.M. A6526, Port Alfred; 1 ♂, 5 shells

Description

Mantle elongate oval, anterior mantle margin produced dorsally to eye level, emarginate ventrally. Mantle bluntly rounded posteriorly and posterior gland (characteristic of genus) opens via pore situated between and just below posterior extremities of fins. Fins fairly wide, beginning a few mm from mantle margin, rounded and closely approximated posteriorly. Posterior region of fins somewhat damaged in present specimen, but according to Adam & Rees (1966: 122), fins fused at base.

Skin smooth; colour of head and mantle dark blue-purple mid-dorsally, paler towards fins, on each of which a series of dark wedge-shaped patches present in male. Ventral surface pale, with sparse chromatophores medially, more concentrated near fins.

Arms fairly short, with arm length formula 4.3.1.2, and joined by low interbrachial web, also present between ventral arms (but Adam & Rees 1966: 123, report that web absent between ventral arms). All arms keeled. Arm tips attenuated. Suckers quadriserially arranged on all arms; chitinous rings of suckers toothed distally with about 12 long teeth.

Left ventral arm hectocotylized over basal half. Minute suckers in modified region arranged in one dorsal, one medio-dorsal and two ventral series. Arm surface between dorsal and ventral series is transversely ridged, and suckers of medio-dorsal and dorsal series are situated on the ridges. Middle and distal parts of arm somewhat mutilated, but distal part apparently normal, with quadriserial suckers.

Tentacles of present specimen missing. According to Adam & Rees (1966: 123) 'the tentacular stem is triangular in cross-section with a rounded keel on the outer side and a flat, transversely-striated, inner surface, which is limited by two membraneous ridges, these being the continuation of the protective membranes of the club. The swimming-membrane of the latter is not very broad and barely reaches the base of the club. The protective membranes are narrow. The minute, subequal suckers are arranged in about 12 longitudinal series in both sexes (pl. 36, fig. 215). Their chitinous rings are each armed with a few, blunt, spaced teeth.' Robson (1924b: 648) also observed two enlarged suckers at the extremity of the club.

Shell (Pl. 42c, d) elongate oval, somewhat narrower anteriorly, but not sharply acuminate; posteriorly rather broadly rounded. Dorsal surface calcareous, with median longitudinal ridge and lateral grooves. Chitinous margin fairly broad. No posterior spine, but slight hump present over posterior extremity of striated zone. Broad shallow groove present, running from hump to posterior margin. Striated zone long, fairly broad posteriorly. Anterior margin of striated zone broadly convex, somewhat wavy. Last loculus continues along sides of striated zone to meet limbs of inner cone. Anterior part of smooth zone shows some compression in most shells. Faint indication of median longitudinal groove over striated zone only. Inner cone forms knob posteriorly, and has very short narrow limbs. Outer cone very broad.

Females differ from males in that arms are relatively much shorter, protective membranes on arms better developed, covering distal suckers (Adam & Rees 1966: 123) and sucker rings almost smooth (Robson 1924b: 648). Shell of female broader, ventral surface thinner, inner cone more developed and outer cone broader (Adam & Rees 1966: 123) and striated zone less pointed (Robson 1924b: 649).

Remarks

The genus *Sepiella* is represented by only one known species, *S. cyanea*, in southern African waters. Together with *S. ornata* and *S. weberi*, it differs from the other species of *Sepiella* in the number of sucker series (10–14) on the tentacular club (*S. melwardi* from Australia is known only by its shell).

Sepiella ornata (from West Africa) differs from *S. cyanea* in that the shell is narrower, the striated zone is shorter, and the posterior part of the shell is less broad; in *S. weberi* (from Timor and Soemba) the posterior part of the striated area is less acuminate than in *S. cyanea* (Adam & Rees 1966: 123).

DISCUSSION

RELATIONSHIPS

The genus *Sepia* was created by Linnaeus (1758) to include all cephalopods without an external shell. Of these, the only true *Sepia* included in the genus was *S. officinalis*. The genus was restricted by Lamarck (1799: 4) to include only those cephalopods with an internal calcareous shell. At that time, the only known species were *S. officinalis* and *S. tuberculata*.

Gray (1849: 106) first used the name *Sepiella* for a group of shells which are 'oblong, posterior end expanded, produced, cartilaginous, not beaked, convex beneath'. Steenstrup (1875: 468) created the genus *Hemisepius*, with *H. typicus* as the type species. This author (1880: 347) redescribed the group *Sepiella* and on the basis of the characters of both the shell and the soft parts raised *Sepiella* to generic status.

With the discovery of numerous species of *Sepia* in the course of time, several attempts were made to divide the genus into subgeneric groups, mainly on the basis of sucker arrangement on the sessile arms and tentacular clubs, and on the structure of the shell (d'Orbigny 1845a: 261-298; Gray 1849: 96-112). Attempts have also been made to split up the genus *Sepia* into several genera, mostly without success. Rochebrune (1884: 74) divided the Sepiidae into ten genera, mainly on shell characters. This classification has been shown to be extremely contradictory and unnatural (Adam 1944). More recently, Iredale (1954: 81) divided the Australian Sepiidae into three families, four subfamilies and 13 genera! Criticisms of this classification are given by Adam (1964: 265) and Adam & Rees (1966: 132). These authors have suggested a more reasonable classification,* retaining only the genera *Sepia* and *Sepiella*, which is outlined below in slightly modified form, together with the southern African representatives of each group:

- I. Shell with well-developed posterior spine; ventral part of inner cone strongly developed. Tentacular suckers subequal, in 8-20 series.
Sepia zanzibarica
- II. Shell with well-developed posterior spine; inner cone well developed, with wide limbs, but completely reflexed on to and fused with the outer cone. Tentacular suckers unequal, usually in eight longitudinal series. *Sepia officinalis vermiculata*
- III. Shell with posterior spine which is generally not keeled, but may be keeled dorsally, ventrally, or on both sides; inner cone more reduced, with narrow limbs; in most of these species the outer cone has two posterior wings which form, in the narrower shells, a typical cup-like expansion. Tentacular suckers nearly always arranged in eight longitudinal series.

* Adam (pers. comm.) says that he and Rees do not attach any systematic value to these groups. Where, however, a genus contains as many species as does *Sepia*, the use of some such grouping of similar species greatly facilitates the study of interspecific relationships.

- a. Outer cone without wings; posterior spine with or without keels. Tentacular suckers minute and subequal or slightly unequal. *Sepia acuminata*
 - b. Outer cone with wings; posterior spine not keeled. Tentacular suckers subequal. No southern African representatives
 - c. Outer cone with wings; posterior spine without keels. Tentacular suckers unequal. In some species the ventral part of the inner cone forms a short, rounded ledge. *Sepia confusa*, *S. incerta*, *S. burnupi*, *S. joubini* and *S. adami*
 - d. Outer cone with or without wings; posterior spine keeled. Tentacular suckers unequal or subequal. *Sepia australis*
 - e. Outer cone with wings; posterior spine absent. Tentacular suckers subequal or unequal. No southern African representatives
- IV. Shell relatively broad, with a more or less developed inner cone and without posterior wings at the outer cone; posterior spine absent. Tentacular suckers unequal or subequal. *Sepia tuberculata*, *S. papillata*, *S. simoniana*, *S. angulata*, *S. hieronis* and *S. insignis*
- V. Form of shell not well known. Tentacular suckers subequal; dorsal arms with finger-like tips, devoid of suckers. *Sepia robsoni* and *S. faurei*
- VI. Subgenus *Hemisepius*: Shell very thin, without posterior spine; phragmocone considerably shorter than dorsal shield; inner cone reduced. *Sepia typica* and *S. dubia*
- VII. Subgenus *Metasepia*: Shell rhomboidal, much shorter than the mantle, with a completely chitinous dorsal surface. Tentacular suckers very few in number, unequal. Inner cone very narrow; posterior spine absent. No southern African representatives
- VIII. Genus *Sepiella*: Mantle with a posterior gland and characteristic locking apparatus (Fig. 3b). Tentacular suckers subequal, in 8-32 longitudinal series. Shell with outer cone expanded, inner cone reduced; posterior spine absent. *Sepiella cyanea*

The degree of affinity within the different groups varies. The southern African species falling into group IIIc, the 'doratosepion' group (*Sepia confusa*, *S. incerta*, *S. burnupi*, *S. joubini* and *S. adami*) show close interrelationships and a marked resemblance in the characters mentioned above (p. 195) as defining Rochebrune's genus. Not all the suckers on the sessile arms are biserial, but in most of these species there is a biserial arrangement of suckers on some part of the arms in one or both sexes. These species are also remarkable in that nearly all show sexual dimorphism, such as the 'tail' in males of *S. confusa*, the modified dorsal arms in the male of *S. incerta*, and the modified dorsal and ventral arms in the male of *S. burnupi*. The males of *S. joubini* are less remarkable, being distinguished from the females (apart from the hectocotylization of the left ventral arm) mainly by the red spots on the arms. The male of *S. adami* is not known.

The southern African 'doratosepion' species fall into two orders of size. *S. confusa* and *S. incerta* attain dorsal mantle lengths of 85–90 mm in the females and about 150 mm in the males. *S. burnupi*, *S. joubini* and *S. adami* attain dorsal mantle lengths of 36–59 mm in the females and 41–45 mm in the males (the male of *S. adami* is not known). All these species occur off the east coast of southern Africa.

Sepia australis (group III*d*) shows a superficial resemblance to the smaller 'doratosepion' species, and particularly to *S. joubini* and *S. adami*. But the shell is wider, has a keeled spine and no posterior wings on the outer cone. Its distribution also differs, and this species has been assigned to the Cape faunistic province (see below).

Sepia acuminata (group III*a*) differs markedly from the other species of group III. The animal is generally broader and the shell is not narrow elongate but broad, almost rhomboidal, with no posterior wings on the outer cone.

The affinities between the southern African representatives of group IV (*Sepia tuberculata*, *S. papillata*, *S. simoniana*, *S. angulata*, *S. hieronis* and *S. insignis*) are much less clear than those of group III. Whilst there are similarities between some of these species, the only characters common to all are the absence of the posterior spine and wings on the outer cone of the shell, and the well developed inner cone which is completely reflexed and fused to the outer cone. The shell of *S. papillata* (Pl. 41*a–d*) is similar to that of *S. tuberculata* (Pls 39*c*, *d*, 40*c*, *d*) on the one hand, and on the other hand to that of *S. simoniana* (Pl. 42*a*, *b*), from which it is sometimes almost indistinguishable, and to that of *S. angulata* (Pls 44*d*, 45*a–d*). The shells of *S. hieronis* (Pl. 43*a–d*) and *S. insignis* (Pl. 44*a–c*) are very different to these and to each other in general shape. A consideration of the tentacular suckers, however, divides these species differently: *S. tuberculata* and *S. papillata* have unequal tentacular suckers, whereas in *S. simoniana*, *S. hieronis* and *S. insignis* they are subequal. The soft parts of *S. angulata* are not known. The distribution of these species also varies (Fig. 18, Table 8), but all occur in the Cape–South West African province.

Only two species, *S. typica* and *S. dubia*, fall into group VI, and both are southern African. These small animals show a close affinity in general appearance and in the shells. *S. typica* has previously been separated from the other Sepiidae in the genus *Hemisepius*, but the discovery of *S. dubia* has rendered the separation of *Hemisepius* from *Sepia* less clear. The distribution of these species, and those of group V, falls under the Cape–South West African province.

The systematic position of *Sepia robsoni* and *S. faurei* (group V) seems to be intermediate between those of groups IV and VI. Both species show a relationship with the species of group VI in general shape (animal very small, mantle very broad, with fleshy keels ventrally); other similarities between the species of groups V and VI include the similarity of hectocotylus of *S. robsoni* and *S. typica* (those of *S. faurei* and *S. dubia* not known), the biserial arrangement of the suckers on all the arms, and the similarities of the tentacular clubs, bearing

subequal suckers. The shell of *S. robsoni*, of which little is known, apparently resembles those of *S. hieronis* and *S. insignis* (group IV). The shell of *S. faurei*, on the other hand, approaches the *Hemisepius*-like shell: it is very thin and chitinous, and the phragmocone is considerably shorter than the dorsal lamella, but is not as short as those of *S. typica* and *S. dubia*. The shell of *S. faurei* differs from those of group VI in that the anterior margin is more nearly parallel to the corresponding margins of the dorsal lamella.

An evolutionary series leading to the *Hemisepius* condition can be traced as follows: *Sepia robsoni* (shell *Sepia*-like, dorsal arms with bare tips, fleshy keels on mantle ventrally, pores absent) to *S. faurei* (shell approaching *Hemisepius* condition, dorsal arms with bare tips, fleshy keels on mantle ventrally, pores absent) to *S. dubia* (*Hemisepius*-like shell, dorsal arms normal, fleshy keels on mantle, no pores) to *S. typica* (*Hemisepius*-like shell, dorsal arms normal, fleshy keels with pores).

It is impossible at this stage to draw any further conclusions regarding the phylogenetic relationships between the sepiids. Adam (1939a: 92) concluded that the shell and tentacular club present the best features for distinguishing the species, and Adam (1964: 268) and Adam & Rees (1966: 135) have suggested that the following characters are probably primitive: a well-developed ventral part of the inner cone; the presence of a posterior spine; arm suckers of equal size and quadriserially arranged; subequal tentacular suckers, arranged in eight longitudinal series; and the presence of minute suckers on the buccal membrane (of the species described here, only *S. zanzibarica* has buccal suckers). But an arrangement of species according to shell structure does not agree with an arrangement of a series according to the structure of the tentacular club, e.g. a comparison between *S. papillata* and *S. simoniana*, whose shells are very similar, but whose tentacular clubs are very different.

GEOGRAPHICAL DISTRIBUTION

Sepiids are cephalopods inhabiting the continental shelf and slope, and in some cases the intertidal zone. Although they are capable of active swimming they apparently spend most of their time on the bottom and do not move over very wide areas or go far beyond the continental shelf (sepiids are not generally found deeper than about 500 metres*). This is borne out by the distribution of the individual species; it is found that although sepiids occur around the coasts of Europe, Africa, Asia, the Indo-Pacific islands and Australia, there are no known cosmopolitan species. On the other hand, the number of endemic species is high.

The earliest fossil record of sepiids is that of *Voltzia palmeri* Schevill, from Upper Jurassic deposits. Apart from this, sepiids are known almost exclusively through the Tertiary to the present. Five genera have been recorded from the Eocene (Bülow-Trummer 1920; Roger 1952): *Archaeosepia*, *Belosepia*, *Pseudosepia*,

* Three known exceptions are *Sepia elliptica*, *S. hedleyi* and *S. pharaonis*, which have been collected from depths to 1 000 metres.

Sepia and *Stenosepia*, but of these only *Sepia* has been recorded from later Tertiary deposits (Oligocene, Miocene, Pliocene) and still occurs in recent times. Thus it would appear that *Voltzia* became extinct in the Jurassic, and *Archaosepia*, *Belosepia*, *Pseudosepia* and *Stenosepia* in the Eocene. All recent sepiids were presumably derived from the fossil genus *Sepia*.

All but three of the fossil sepiids were found in European deposits. The three exceptions are *Voltzia palmeri* Schevill from Cuba (Upper Jurassic), *Belosepia incurvata* Cossmann & Pissaro from West Pakistan (Sind Region; Eocene) and *Belosepia ungula* Gabb from North America (Texas, Missouri, Alabama; Eocene).

The absence of sepiids from New Zealand and both coasts of the American continent today is apparently due to the separation of these land masses by extensive, deep oceans and/or very cold water in the regions where migration could otherwise occur. The ocean between Australia (where numerous species of Sepiidae occur) and New Zealand is wide and deep, and the currents are adverse to a crossing in this direction.

TABLE 8. Distributional categories of the Sepiidae of southern Africa (in the same order as in figure 18).

Moçambique-Malagasy province	Natal province	Cape-South West African province
<i>Sepia confusa</i>	<i>Sepia acuminata</i> <i>Sepia joubini</i> <i>Sepia burnupi</i> <i>Sepia adami</i> <i>Sepia incerta</i> <i>Sepiella cyanea</i>	<i>Sepia faurei</i> <i>Sepia simoniana</i> <i>Sepia insignis</i> <i>Sepia dubia</i> <i>Sepia robsoni</i> <i>Sepia tuberculata</i> <i>Sepia typica</i> <i>Sepia officinalis vermiculata</i> <i>Sepia papillata</i> <i>Sepia australis</i> <i>Sepia hieronis</i> ? <i>Sepia angulata</i>

At least two species of fossil sepiids have been recorded from America, the most recent from the Eocene. The absence of later fossil evidence suggests that these species became extinct, and that recolonization was prevented, perhaps by the low temperatures prevailing in the only relatively shallow areas via which Sepiidae could migrate from Asia or Europe, viz. the Bering Straits or via the Faeroe Islands, Iceland and Greenland.

In the waters around southern Africa, 19 species of Sepiidae are known to occur. Of these, 16 are endemic, one is tropical, one is an Atlantic species and the remaining species has an interrupted distribution.

The tropical species, *Sepia confusa*, enters southern African waters at the southern end of its range. It is known to occur from Zanzibar to Durban, and is

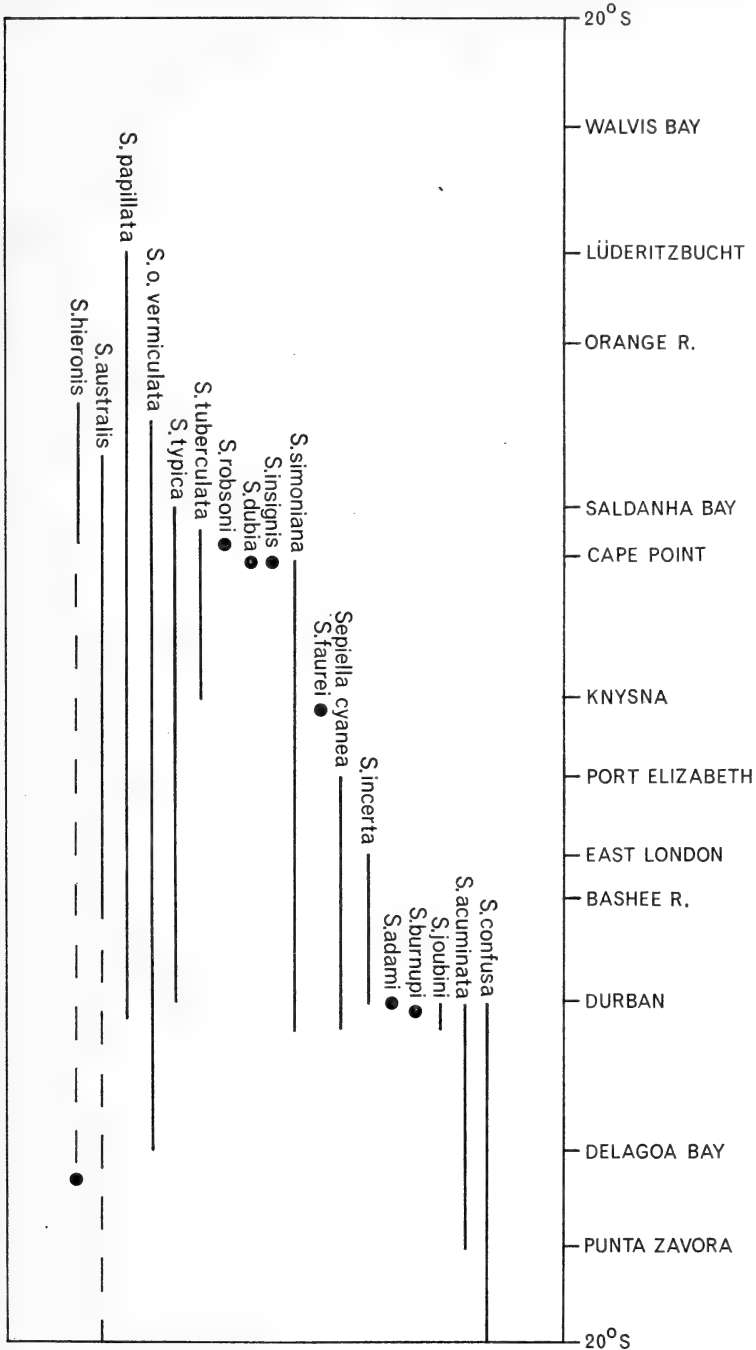


FIG. 18. Distribution ranges of the Sepiidae of southern Africa.

related to other sepiids of the 'doratosepion' group occurring off the east coast of southern Africa.

One Atlantic species, *Sepia officinalis*, enters southern African waters. It occurs from Scandinavia to Delagoa Bay (Moçambique), but the subspecies *S. officinalis vermiculata* is endemic to southern Africa, occurring from off the Groene River mouth on the west coast to Delagoa Bay on the east coast.

Sepia australis has an interrupted distribution, occurring in southern African waters from the Olifants River on the west coast to Rame Head, near Port St. Johns, on the east coast, but is also found in the Red Sea.

The endemic species are divided into two groups: the subtropical species restricted to the east coast of southern Africa, and the temperate species, occurring from the west coast round to the south coast and gradually diminishing along the east coast.

Stephenson (1948: 228), on the basis of extensive surveys of the intertidal fauna, divided southern Africa into three faunistic provinces, namely the subtropical population of Natal, the warm temperate fauna of the south coast and the cold temperate fauna of the west coast. Day (1967: 11) found, however, that these divisions do not apply to shelf fauna, since the change in temperature at, say, 100 m is not as marked as it is in the intertidal zone. Thus the surface temperature of the south coast (Bashee River to Cape Point) ranges from 15° to 20°C, whereas on the west coast (Cape Point to South West Africa) the surface temperature range is about 12° to 15°C. At 100 m, however, the bottom temperature is far more constant, the range being about 12° to 14°C from Port Elizabeth to Lüderitzbucht (Day 1967: 12).

Day (1967: 12) suggests the following faunistic provinces to include both intertidal and shelf fauna:

1. The Moçambique-Malagasy province, reaching Delagoa Bay; dominated by tropical species.
2. The Natal province, from Delagoa Bay to Bashee River; many tropical species, but also fair numbers of endemics and Atlantic species.
3. The Cape-South West African province, from Bashee River to about Cape Frio; dominated by endemics but with a few tropical species and several other components. The intertidal fauna of this province differs on the Indian and Atlantic coasts, i.e. are separated into warm temperate and cold temperate forms.

The distribution of the Sepiidae of southern Africa agrees with Day's faunistic provinces, except that the boundary between the Natal and the Cape-South West African species seems to lie a little further south, between Port Elizabeth and East London (Fig. 18). The species of Sepiidae arbitrarily assigned to the various provinces are listed in Table 8.

1. *The Moçambique-Malagasy province*: only one tropical sepiid species, *Sepia confusa*, is known to occur here. It also occurs further south, as far as Durban. *Sepia hieronis* has been caught in this region, but as it has also been recorded off

the west coast, this is not a tropical species but an endemic one with a peculiar interrupted distribution. *Sepia acuminata*, a subtropical species, enters this province at the northern end of its range.

2. *The Natal province*: all the species of this category are endemic, and are restricted to the east coast of southern Africa; they do not extend further south than Port Elizabeth. The main component of this group of subtropical species is the 'doratosepion' group, including *Sepia incerta*, *S. burnupi*, *S. joubini* and *S. adami*. These species are very similar anatomically and are obviously closely related. *S. confusa* (see above) also belongs to the 'doratosepion' group, but it is not endemic to southern Africa, as it has been recorded as far north as Zanzibar. Since, however, the waters off the east African coast have not been extensively sampled, further collection may well show that the sepiids of the Natal province occur further north than is known at present.

Two other species, *Sepiella cyanea* and *Sepia acuminata*, are found in the Natal province. The latter species extends into the Moçambique province, and has been recorded as far north as Zavora. *Sepiella cyanea* has also been recorded from Nosy N'Tangam, Malagasy (Adam & Rees 1966: 121).

Several species from the Cape-South West African province extend into the Natal province (see below).

3. *The Cape-South West African province*: Sepiids do not seem to enter South West African waters to any marked degree. Only one Cape species, *S. papillata*, has been recorded from South West Africa. The apparent absence of Cape Sepiidae from South West African waters does not seem to be due to temperature, since this varies little along the west coast of southern Africa. It may however be due to the difference in coastal conditions, since the South West African shores consist largely of long sandy beaches, with pounding surf and very little kelp. Rocky outcrops are few and far apart. According to Penrith & Penrith (1969: 100), fishes of the genus *Lithognathus* show a similar break in distribution off the South West African coast. *L. lithognathus* occurs from Natal to the Orange River mouth, but has not been recorded off South West Africa, where the species is replaced by *L. aureti* and *L. olivieri* off the northern half of South West Africa. No species of *Lithognathus* have been recorded off the southern half of South West Africa, between Sandwich Harbour (on the tropic of Capricorn) and the Orange River mouth.

Of the Cape species of Sepiidae, *Sepia tuberculata* occurs from Melkbosstrand to Knysna. The relatively short range of this species may be linked with its shallow-water habitat (depth range 0-3 m).

S. papillata and *S. typica* have wider ranges of distribution, extending into the Natal province (to Durban). On the west coast, *S. papillata* has been recorded as far north as Lüderitzbucht—one of the few rocky areas on the South West African shore; *S. typica* does not seem to occur north of Saldanha Bay.

As mentioned above, *S. officinalis vermiculata* is endemic, and occurs in the

Cape faunistic province. It has been recorded from Groene River mouth to Delagoa Bay, the latter being the northernmost record for temperate Cape species of Sepiidae along the east coast (except perhaps *S. hieronis*).

Sepia simoniana is the only Cape species which does not occur off the west coast. It has been recorded from False Bay to the Tugela River mouth.

Other endemic species of the Cape province are *Sepia insignis*, *S. robsoni*, *S. faurei* and *S. dubia*, each known from only one locality, and *S. angulata*. The soft parts of the latter species are as yet unknown; it is not included in Figure 18. *S. hieronis* has provisionally been allocated to the Cape species, although it has not so far been recorded from the south coast; it is known to occur off the west coast (from Hondeklip Bay to Slangkop) and off Monte Belo, Moçambique.

VERTICAL DISTRIBUTION

The vertical distributions of the southern African sepiids are not well known. Many records give no indication of the depths at which the specimens were caught, and others, where open trawls were used, are unreliable. In the latter case the depth at which the trawl was hauled is given, but the specimens could as easily have been caught while the trawl was raised or lowered. However, since sepiids tend to live on or near the bottom, the depth over which the trawl was fished probably gives a fairly good indication of the depth at which the sepiids were living. The depth records available (Fig. 19) show some interesting features.

Off the south coast, where the continental shelf is very wide (about 220 km at the widest point), few sepiids have been recorded below 100 m. Off the east and west coasts the continental shelf is much narrower (maximum about 40–50 km) and sepiids have been recorded as deep as 460 m, that is, some way out beyond the edge of the shelf.

Sepia officinalis vermiculata is unusual in that it is found in shallow water in estuaries and sheltered bays (Saldanha Bay, Breede River mouth, Knysna lagoon, Bushmans River mouth and Durban Bay). Strangely it has not so far been found in False Bay. This subspecies is not limited to shallow water, however, and has also been recorded from depths to 249 m off the Natal coast (Massy 1925: 209).

Sepia tuberculata is apparently more closely restricted to the inshore waters, and has been collected mainly from rock pools. There is also one record from Simonstown harbour, at a depth of 3 m. Many of the records do not give any reference to depth, and this species is not included in Figure 19.

Sepia typica is common in fairly shallow water in Saldanha Bay, but elsewhere it is found somewhat deeper. In Table Bay and False Bay this species is found below 17–18 m, off the south coast below 40 m, and off Durban at 99 m. Similarly the upper depth limit of *S. simoniana* is deeper off the east coast (116–134 m) than off the south coast (below about 10 m in False Bay). *S. papillata* and *S. australis* show a similar though less marked trend at the eastern end of their distribution ranges.

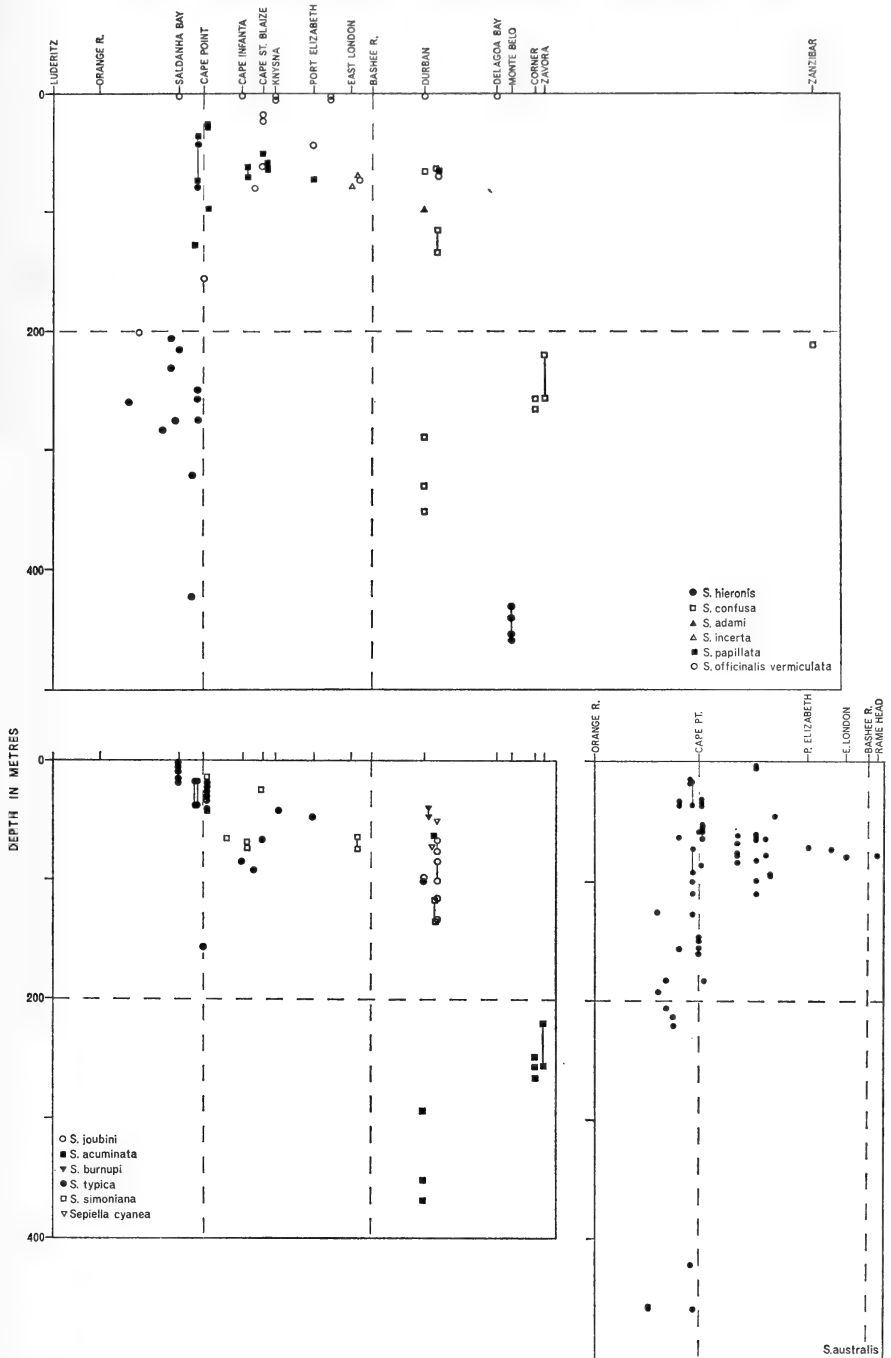


Fig. 19. Vertical distribution of the Sepiidae of southern Africa. Linked symbols indicate continuous hauls between the indicated depths.

The east coast sepiids also show a tendency to occupy deeper water further northwards, as the climate becomes hotter, though the absence of records from shallow water off the Moçambique coast may well be due to insufficient sampling. The east coast species are generally caught below 60 m off the Natal coast and below 200 m off the Moçambique coast. Two exceptions are *S. burnupi*, caught at 40–48 m off the Umhlanga River, and *Sepiella cyanea*, recorded from 51 and 73 m off the Tugela and Umvoti Rivers. For both these species, these are the only available depth records.

GROWTH

For each species the relative dimensions were calculated for as many specimens as possible, and the ranges and means were calculated for those dimensions thought to be of some significance. Tests for correlation between various relative dimensions and the standard length (MLd or shell L) were performed for species where ten or more specimens had been measured (males and females being considered separately), to test if there is any change in relative body (or shell) dimensions with growth. In general the results of the correlation tests were disappointing, due to the great variation in measurements.

The only species giving significant correlations for most of the body measurements was *Sepia australis*, and even here the scatter about the regression lines is wide, though 59 males and 77 females were measured. Figure 20 shows the scatter diagrams for most of the dimensions of *S. australis* males and shells. Where correlation was found to be statistically significant, the regression lines were calculated by the least squares method. These lines are included in Figure 20 for interest, but they clearly do not fit the scatter diagrams well, since the variation is very wide. Trends can, however, be observed. With growth, the mantle becomes much narrower relative to its length; the head becomes relatively shorter and narrower, and the fins also become relatively narrower. The change in relative length of the tentacular club is small, but the arms become relatively longer. In fact there seems to be a general trend to elongation with growth, producing a more streamlined body, perhaps enabling faster locomotion.

Growth of the *S. australis* females is very similar to that of the males, except that the arms are relatively shorter than those of the males, although also becoming longer in larger animals.

The shell dimensions also show a wide scatter, despite the fact that the shell is a rigid structure and is not subject of contractility as are the soft parts. The shell is however secreted by the animal and the variation in its dimensions suggests that the wide scatter of the relative dimensions of the soft parts is not solely due to their contractility. The shell becomes relatively narrower and slightly thinner with growth, and the striated zone becomes relatively longer.

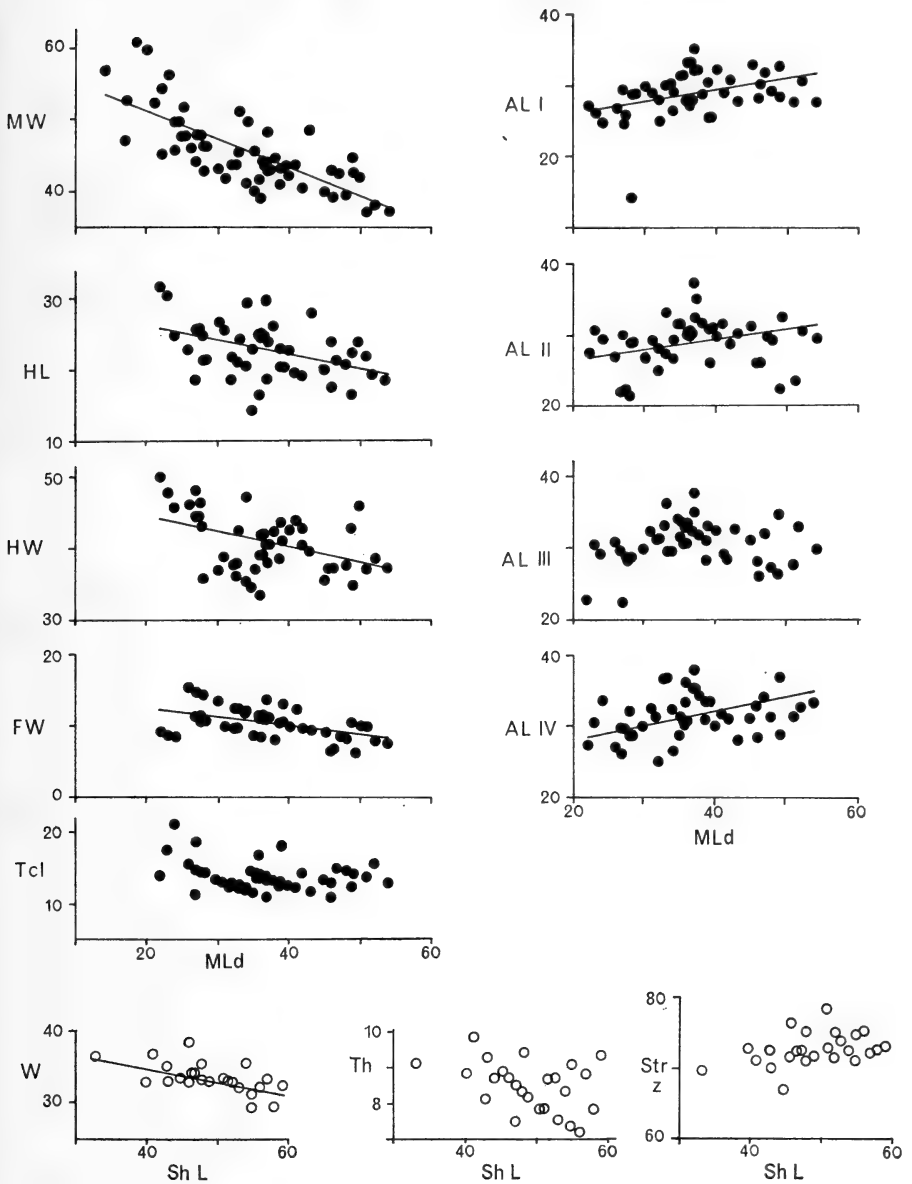


FIG. 20. *Sepia australis* males and shells. Change in dimensions (expressed as % MLd or % shell length) with growth (increase in MLd or shell length). The straight lines through the scatter diagrams indicate the calculated regression lines, where a statistically significant correlation was found to obtain.

SUMMARY

A complete synonymy, distribution and depth ranges, and descriptions of external morphology are given for each of 20 species. Three species, *Sepia adami*, *S. angulata* and *S. faurei*, are new. The soft parts of *S. insignis* (previously known only by its shell) are described for the first time. The animals and shells described by Massy (1925) as *S. incerta* and *S. burnupi* have been re-examined, and all are found to pertain to *S. incerta*. The first known animals of *S. burnupi* (formerly the types of *S. exsignata*) have been redescribed, and the first recorded specimens of *S. hieronis* from the east coast are described. Keys to the soft parts and to the shells are provided. The relationships of the southern African Sepiidae, their geographical and vertical distribution, and their growth, are discussed.

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APPENDIX

TABLE 9. *Sepia zanzibarica*. Relative dimensions as % MLD.

	N.M.959 ♂	Holotype ♀ (Adam & Rees 1966)
MLd in mm . . .	163	168
MLv	71,8	89
MW	52,1	42
HL	33,1	21
HW	31,9	32
FL	103,1	92
FW	10,4	9
AL I	39,9	30
AL II	42,3	30
AL III	43,6	33
AL IV	46,0	40
TL	128,2	92
Tcl	26,4	21

Table 10. *Sepia zanzibarica* shells.
Relative dimensions as % shell length.

	A2141		Mean
L in mm	189	164	
W	31,2	33,5	32,4
Th	8,5	8,5	8,5
Str z	68,8	75,0	71,9

TABLE 12. *Sepia officinalis vermiculata* females and juveniles. Relative dimensions as % MLd.

	A30131	A30183	A31292	Locality unknown	Knysna Estuary						Durban Bay	
					103	105	100	102	98	96	156	172
MLd in mm . . .	208	287	188	242	103	105	100	102	98	96	156	172
MLv	88,5	87,5	88,8	86,4	99,0	93,3	90,0	87,3	92,9	89,6	91,7	92,4
MW	43,8	50,9	44,7	55,8	63,1	50,5	50,0	56,3	53,1	54,2	59,6	59,9
HL	—	24,4	23,9	34,3	25,2	20,0	27,0	25,5	29,6	26,0	33,3	33,1
HW	—	37,6	38,8	39,3	47,6	43,8	42,0	44,1	44,9	47,9	48,7	50,0
FL	101,0	107,3	109,0	110,7	119,4	106,7	104,0	—	105,1	110,4	110,3	113,4
FW	12,0	12,2	16,0	16,5	19,4	12,4	16,0	—	12,2	17,7	13,5	16,3
AL I	31,7	29,6	27,7	55,0	40,8	34,3	32,0	42,2	40,8	35,4	40,4	42,4
AL II	33,7	32,8	29,8	57,9	40,8	34,3	31,0	43,1	40,8	38,5	50,0	47,7
AL III	—	36,6	31,9	60,3	42,7	36,2	36,0	44,1	38,8	42,7	44,2	48,8
AL IV	—	44,3	37,2	79,3	53,4	44,8	42,0	52,0	52,0	51,0	56,4	50,0
TL Rt	101,0	158,5	85,1	203,3	—	—	—	—	—	—	105,8	116,3
TL Lt	117,8	163,1	74,5	159,1	—	—	—	—	—	—	115,4	104,7
Tcl	26,4	27,9	26,6	36,0	29,1	25,7	31,0	38,2	34,7	30,2	31,4	32,0

	Durban Bay (cont.)				Adam 1962	Adam & Rees 1966	N ♀	Mean ♀	Range ♀	A30128 juvenile	A30129 juvenile
	162	149	172	168	147	120					
MLd in mm . . .	162	149	172	168	147	120	—	—	—	50	39
MLv	91,4	89,9	92,4	89,9	90	85	18	90,3	85-99,0	90,0	87,2
MW	58,0	62,4	56,4	58,3	52	54	18	54,6	43,8-63,1	52,0	61,5
HL	31,5	32,9	29,7	32,1	31	33	17	29,0	20,0-34,3	28,0	30,8
HW	49,4	48,3	34,9	36,9	46	42	17	43,7	34,9-50,0	48,0	48,7
FL	113,6	117,4	104,7	114,3	100	98	17	108,5	98-119,4	106,0	97,4
FW	14,8	15,4	17,4	14,9	10	13,5	17	14,7	10-19,4	12,0	10,3
AL I	38,9	41,6	39,5	44,0	42	33	18	38,4	27,7-55,0	22,0	23,1
AL II	46,3	52,3	46,5	49,4	—	33	17	41,6	29,8-57,9	28,0	30,8
AL III	48,1	49,7	47,1	47,2	46	33	17	43,1	31,9-60,3	26,0	30,8
AL IV	56,8	59,7	54,7	58,3	58	46	17	52,7	37,2-79,3	30,0	38,5
TL Rt	104,9	117,4	173,3	157,7	—	150	21	129,3	74,5-203,3	100,0	117,9
TL Lt	112,3	107,4	148,8	138,1	—	—	17	—	—	100,0	125,6
Tcl	28,4	28,9	29,1	33,3	—	32	21	30,6	25,7-38,2	20,0	20,5

TABLE 13. *Sepia officinalis vermiculata* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z		L in mm	W	Th	Str z									
A30129	37	45.9	8.1	43.2	Knysna Estuary (cont.)	86	38.4	11.0	51.2									
A30130	214	36.9	13.1	49.5		81	39.5	11.7	53.1									
A30182	193	33.2	10.9	63.2	79	40.5	12.7	49.4										
A30183	278	38.5	12.6	69.1	77	40.3	12.3	49.4										
Breede River	45	44.4	10.0	46.7	78	39.7	12.2	50.0										
					74	40.5	12.2	48.6										
					72	40.3	12.5	48.6										
Knysna Estuary	120 95 126 98 94 92 56 127 125 102 97 61 112 110 109 105 105 101 103 102 100 95 96 96 93 89 91 85	38.3 37.9 38.1 38.8 39.4 39.1 41.1 33.1 32.8 41.2 38.1 41.0 40.2 39.1 38.5 39.0 41.0 41.6 37.9 39.2 40.0 40.0 39.6 40.6 40.9 40.4 38.5 38.8	11.7 12.6 12.3 11.2 11.7 11.4 11.6 9.8 10.0 12.7 11.3 13.1 12.5 11.7 11.5 12.4 12.9 12.9 11.7 12.7 12.5 12.1 11.5 12.5 11.8 12.9 11.5 12.4	50.0 49.5 47.6 44.9 47.9 47.8 50.0 43.3 41.6 47.1 46.4 52.5 47.3 47.3 48.6 48.6 48.6 46.5 50.5 48.0 46.0 50.5 49.0 47.9 47.3 50.6 49.5 48.2	69	40.6	11.6	49.3										
					68	42.6	13.2	52.9										
					63	41.3	12.7	47.6										
					63	41.3	11.9	52.4										
					62	41.9	12.9	51.6										
					63	41.3	11.9	49.2										
					58	39.7	12.1	51.7										
					56	41.1	12.5	50.0										
					54	42.6	13.0	53.7										
					50	42.0	12.0	50.0										
					45	42.2	10.0	48.9										
					Saldanha Bay	139 165	41.7 34.5	10.1 9.1	74.8 69.1	Krom River	157	39.5	14.0	47.8				
															Durban Bay	148 164 157 138 127 169 168	39.2 39.0 39.5 — 40.2 39.6 40.5	14.2 15.2 14.0 15.2 15.0 14.2 13.7
					N . .	60	61	61										
					Mean .	39.7	12.2	49.7										
					Range .	32.8- 45.9	8.1- 15.2	40.5- 74.8										

TABLE 14. *Sepia acuminata* males. Relative dimensions as % MLD.

	A30147	A31398	A31399	N.M.964	Massy 1928	Adam & Rees 1966	N	Mean	Range
MLd in mm	89	67	89	78	80	67			
MLv	83,1	80,6	80,9	82,1	80,0	78	6	80,8	78-83,1
MW	44,9	68,7	60,7	64,1		49	5	57,5	44,9-68,7
HL	27,0	34,3	36,0	37,2		25	5	31,9	25-37,2
HW	40,4	52,2	48,3	42,3	41,3	36	6	43,4	36-52,2
FL	95,5	86,6	82,0	94,9		87	5	89,2	82,0-95,5
FW	11,2	6,0	7,9	9,0		9	5	8,6	6,0-11,2
AL I	25,8	38,8	39,3	33,3	42,5	25	6	34,1	25-42,5
AL II	24,7	35,8	36,0	29,5	41,3	27	6	32,4	24,7-41,3
AL III	24,7	38,8	42,7	35,9	40,0	28	6	35,0	24,7-42,7
AL IV	27,0	50,7	44,9	43,6	51,3	33	6	41,8	27,0-51,3
TL Rt	44,9	—	—	135,9	145,0				
TL Lt	60,7	182,1	—	—	—	105	6	112,3	44,9-182,1
Tcl	11,2	22,4	—	15,4	15,0	13	5	15,4	11,2-22,4

TABLE 15. *Sepia acuminata* females and juveniles. Relative dimensions as % MLD.

	A31398	N.M.964	Adam & Rees 1966	N	Mean	Range	A31400 juv.
	♀	♀	♀	♀	♀	♀	
MLd in mm	92	92	79				39
MLv . . .	73,9	82,6	83	3	79,8	73,9-83	87,2
MW . . .	65,2	54,3	53	3	57,5	53-65,2	59,0
HL . . .	38,0	31,5	29	3	32,8	29-38,0	38,5
HW . . .	51,1	40,2	40	3	43,8	40-51,1	48,7
FL . . .	76,1	90,2	89	3	85,1	76,1-90,2	82,1
FW . . .	6,5	12,0	11	3	9,8	6,5-12,0	7,7
AL I . . .	40,2	29,3	32	3	33,8	29,3-40,2	35,9
AL II . . .	44,6	38,0	32	3	38,2	32-44,6	35,9
AL III . . .	40,2	37,0	32	3	36,4	32-40,2	33,3
AL IV . . .	50,0	41,3	35	3	42,1	35-50,0	48,7
TL Rt . . .	—	137,0					—
TL Lt . . .	155,4	105,4	95	4	123,2	95-155,4	202,6
Tcl . . .	22,8	18,5	13	3	18,1	13-22,8	23,1

TABLE 16. *Sepia acuminata* shells. Relative dimensions as % shell length.

	A31398	A31399	A31400	West Pondo-land	N.M.965		N	Mean	Range
L in mm	72	92	±39	±108	101	±77			
W . . .	38,9	38,0	±48,7	±43,5	±35,6	±39	6	40,6	35,6-48,7
Th . . .	9,7	9,2	±10,3	±10,2	9,9	±10,4	6	10,0	9,2-10,4
Str z . . .	59,7	68,5	±64,1	±64,8	64,4	±61	6	63,8	59,7-68,5

See opposite for Table 17

TABLE 18. *Sepia confusa* females. Relative dimensions as % MLD.

	A31403	Adam & Rees 1966				N	Mean	Range
MLd in mm . . .	±53	77	85	80	84			
MLv	73,6	80	79	75	81			
MW	49,1	36	33	35	33	5	37,2	33 -49,1
HL	26,4	22	23	19	18			
HW	32,1	31	33	30	33	5	31,8	30 -33
FL	79,2	87	79	81	80			
FW	5,7	13	13	12,5	8,5	5	10,5	5,7-13
AL I	45,3	38	33	34	30	5	36,1	30 -45,3
AL II	45,3	34	32	35	32	5	35,7	32 -45,3
AL III	49,1	34	32	32	32	5	35,8	32 -49,1
AL IV	50,9	36	33	35	34	5	37,8	33 -50,9
TL	—	—	82	—	—			
Tcl	—	13,5	14	—	—	2	13,8	13,5-14

TABLE 19. *Sepia confusa* shells. Relative dimensions as % shell length.

	A2140	N.M.961	A31402			A31403	Adam & Rees 1966	N	Mean	Range
L in mm	88	±141	106	±105	±93	±104	84			
W	19,3	15,6	17,9	18,1	19,4	19,2	19	8	19,1	15,6-24,5
Th	9,1	6,4	8,5	7,6	8,6	7,7	9	8	8,5	6,4-11,3
Str z	55,7	65,2	54,7	58,1	59,1	—	—	6	59,1	54,7-65,2
							±62			

TABLE 17. *Sepia confusa* males. Relative dimensions as % MLD.

	A65:16	N.M.:961	N.M.:962	A31402			Adam & Rees 1966		Massy 1925	Massy 1928	N	Mean	Range
MLd in mm	140	141	133	106	105	93	104	90	±105	±100			
MLv . . .	77.9	75.2	75.9	65.1	70.5	72.0	69.2	72	71	70			
MW . . .	32.1	38.3	39.1	38.7	42.9	48.4	49.0	38	36	35		39.8	32.1-49.0
HL . . .	20.0	21.3	29.3	24.5	23.8	31.2	21.2	22	24	25			
HW . . .	25.7	24.8	21.1	33.0	34.3	34.4	36.5	32	27	28			
FL . . .	85.7	90.1	86.5	75.5	81.0	80.6	81.7	—	—	—		28.6	20.9-36.5
FW . . .	17.9	12.8	11.3	7.6	8.6	9.7	13.5	14.5	12.5	13			
AL I . . .	35.7	41.1	46.6	49.1	43.8	—	52.9	33	35	35		12.1	7.6-17.9
AL II . . .	26.4	36.9	35.3	40.6	32.4	43.0	48.1	28	29	30		42.2	33-52.9
AL III . . .	27.1	32.6	38.3	40.6	42.9	43.0	38.5	28	29	28		36.1	26.4-48.1
AL IV . . .	30.7	41.1	37.6	45.3	42.9	48.4	45.2	28	31	30		35.4	27.1-43.0
TL Rt . . .	67.1	123.4	—	—	—	—	—	—	85	90		38.9	28-48.4
TL Lt . . .	65.7	—	105.3	166.0	—	—	146.2	—	—	—			
Tcl . . .	10.7	9.9	10.5	15.1	—	—	16.3	—	13	14		12.2	9.9-16.3
'Tail' . . .	95.0	125.5	38.3+	77.4+	82.9+	80.6+	—	—	—	—			
									96.3	135.1+			
										125.0			
										100.0			
										10.1			
										10.0			

TABLE 20. *Sepia incerta* males. Relative dimensions as % MLD.

MLD in mm .	N.M.956		N.M.957		A30143				Massy 1925	Massy 1928	Adam & Rees 1966	N	Mean	Range			
	148	84,5	146	82,2	120	127	127	142	93	136	125				150	147	135
MLV . . .	84,5		82,2		85,0	83,5	81,1	78,9	83,9			85,3	83,7	67	74		
MW . . .	34,4		34,3		35,0	30,7	35,4	31,7	35,6					37	34		30,7-37
HL . . .	22,3		23,3		19,2	18,9	16,5	21,8	18,3					27	21		
HW . . .	23,0		23,3		21,7	25,2	28,4	23,2	24,8					24	25		20,4-28,4
FL . . .	95,4		93,8		95,0	93,7	91,3	83,1	94,7					—	—		
FW . . .	9,5		6,2		8,3	10,2	10,2	9,2	9,7					—	—		
AL I . . .	85,8		93,8		75,0	76,4	68,5	88,0	32,3	127,9	107,2	92,7	91,8	11	11		6,2-11
AL II . . .	38,5		37,0		40,8	38,6	39,4	35,2	30,1	61,8	47,8	42,7	41,5	81	84		68,5-127,9*
AL III . . .	37,2		36,3		40,0	39,4	37,8	37,3	33,4	62,5	45,6	49,3	40,1	37	39		35,2-61,8*
AL IV . . .	66,9		66,5		63,3	60,6	66,1	63,4	38,7	102,2	74,4	74,0	74,1	38	39		36,3-62,5*
TL Rt . . .	66,9		—		81,6	107,9	—	96,5	73,1	130,1	138,4	67,3	74,1	59	63		59 -102,2*
TL Lt . . .	61,5		82,2		—	83,5	—	—	—	—	—	65,3	74,8	96	86		
Tcl . . .	12,8		14,4		15,8	15,8	—	13,4	15,1	22,1	19,2	12,7	12,2	15	14		12,2-22,1

* Young male (MLD 93 mm) not included.

TABLE 21. *Sepia incerta* females. Relative dimensions as % MLd.

	A30143	Massy 1925		N	Mean	Range
MLd in mm	82	90	80			
MLv . . .	85,4					
MW . . .	36,6	48,9	53,8	3	46,4	36,6-53,8
HL . . .	18,3					
HW . . .	26,8	33,3	30,0	3	30,0	26,8-33,3
FL . . .	92,7					
FW . . .	8,5					
AL I . . .	26,8	54,4	45,0	3	42,1	26,8-54,4
AL II . . .	22,0	57,8	61,3	3	47,0	22,0-61,3
AL III . . .	31,7	64,4	56,3	3	50,8	31,7-64,4
AL IV . . .	35,4	60,0	62,5	3	52,6	35,4-62,5
TL Rt . . .	87,8					
TL Lt . . .	67,1	142,2	—			
Tcl . . .	14,6	16,7	—	2	15,7	14,6-16,7

TABLE 22. *Sepia incerta* shells. Relative dimensions (approximate) as % shell length. Many of the shells are broken.

	Massy 1925		N.M.958		N.M.970		Punta Zavora				N	Mean	Range
	No. 8	No. 16	A	B	B	C							
L in mm	135	125*	148*	146*	81	65	106	77	66	49	10	18,3	13,7-22,4
W . . .	17	16,8	14,9	13,7	19,8	20,0	17,9	20,8	19,7	22,4			
Th . . .		8	6,1	5,5	7,4	7,7	7,5	7,8	7,6	8,2			
Str z . . .	? 70	? 66	57,4†	47,9†	67,9	56,9	69,8	62,3	56,1	63,3	8	64,0	56,1-? 70

* Length of shell if complete

† Part of striated zone missing; percentage should be higher. These dimensions excluded from the calculation of the mean relative length of striated zone for this reason.

TABLE 23. *Sepia burnupi*. Relative dimensions as % MLd.

	A6525 ♂	N.M.4073 ♂	Mean ♂	A6525 ♀
MLd in mm . . .	44	45		36
MLv	90,9	91,1	91,0	88,9
MW	40,9	40,0	40,5	47,2
HL	25,0	24,4	24,7	27,8
HW	36,4	35,6	36,0	38,9
FL	102,3	97,8	100,1	100,0
FW	11,4	11,1	11,3	11,1
AL I	43,2	33,3	38,3	30,6
AL II	31,8	24,4	28,1	33,3
AL III	38,6	28,9	33,8	30,6
AL IV	54,5	46,7	50,6	38,9
TL Rt	—	—		
TL Lt	68,2	71,1	69,7	83,3
Tcl	11,4	11,1	11,3	11,1

TABLE 24. *Sepia burnupi* shells. Relative dimensions (approximate) as % shell length.

	A2147			N.M.958 C	N	Mean	Range
L in mm . . .	47*	41*	55*	50*			
W	25,5	24,4	23,6	24	4	24,4	23,6-25,5
Th	7,4	6,1	6,4	7	4	6,7	6,1-7,4
Str z	85,1	78,0	81,8	74	4	79,7	74-85,1

* Anterior tip of shell missing.

TABLE 25. *Sepia joubini* males. Relative dimensions as % MLd.

	A30141		A30142		A30172				Massy 1927		A31393		
MLd in mm . .	29	34	36	36	41	39	39		40	33	35	41	41
MLv	79,3	85,3	75,0	80,6	80,5	79,5	84,6				77,1	82,9	75,6
MW	37,9	41,2	38,9	41,7	31,7	38,5	38,5				40,0	36,6	36,6
HL	24,1	26,5	22,2	22,2	24,4	20,5	15,4				22,9	19,5	22,0
HW	34,5	35,3	33,3	33,3	31,7	28,2	30,8		30,0	36,4	34,3	31,7	31,7
FL	79,3	82,4	83,3	86,1	85,4	87,2	84,6				82,9	80,5	80,5
FW	5,2	8,8	5,6	8,3	9,8	7,7	7,7				8,6	7,3	7,3
AL I	24,1	32,4	22,2	30,6	24,4	25,6	28,2		40,0	—	25,7	24,4	24,4
AL II	24,1	29,4	22,2	30,6	24,4	23,1	30,8		37,5	—	22,9	22,0	22,0
AL III	20,7	29,4	25,0	27,8	19,5	23,1	25,6		40,0	39,4	22,9	22,0	22,0
AL IV	17,2	32,4	22,2	25,0	22,0	23,1	25,6		45,0	45,5	25,7	24,4	22,0
Tl Rt	110,3	—	—	91,7	—	117,9	125,6		—	—	91,4	100,0	78,0
Tl Lt	89,7	—	—	—	73,2	102,6	—		—	121,2	94,3	104,9	82,9
Tcl	10,3	—	—	13,9	12,2	10,3	7,7		—	12,1	10,0	9,8	9,8

	A31393 (cont.)								N	Mean	Range
MLd in mm . .	39	36	34	33	26	30	21	20			
MLv	74,4	77,8	76,5	75,8	76,9	76,7	76,2	70,0			
MW	35,9	38,9	38,2	42,4	42,3	40,0	47,6	35,0	18	39,0	31,7-47,6
HL	17,9	22,2	20,6	21,2	23,1	20,0					
HW	30,8	30,6	32,4	36,4	42,3	36,7			18	33,4	28,2-42,3
FL	82,1	77,8	82,4	78,8	80,8	80,0					
FW	5,1	5,6	5,9	6,1	11,5	6,7			16	7,3	5,1-11,5
AL I	25,6	27,8	20,6	21,2	26,9	26,7			17	26,5	20,6-40,0
AL II	20,5	25,0	20,6	21,2	26,9	23,3			17	25,1	20,5-37,5
AL III	20,5	25,0	20,6	21,2	30,8	23,3			18	25,5	19,5-40,0
AL IV	23,1	27,8	23,5	24,2	34,6	23,3			18	27,0	17,2-45,5
Tl Rt	94,9	100,0	105,9	75,8	—	86,7					
Tl Lt	102,6	102,8	111,8	—	—	106,7					
Tcl	10,3	13,9	11,8	12,1	—	13,3			14	11,3	7,7-13,9

TABLE 26. *Sepia joubini* females. Relative dimensions as % MLd.

	A30141											
	40	27	29	28	31	35	33	35	35	38	38	39
MLd in mm . . .	40	27	29	28	31	35	33	35	35	38	38	39
MLv	77,5	81,5	82,8	82,1	80,6	82,9	81,8	80,0	82,9	81,6	81,6	82,1
MW	35,0	40,7	41,4	42,9	41,9	40,0	39,4	40,0	37,1	36,8	36,8	35,9
HL	22,5	25,9	20,7	25,0	25,8	25,7	24,2	22,9	25,7	23,7	21,1	20,5
HW	32,5	40,7	37,9	39,3	38,7	34,3	36,4	34,3	34,3	28,9	31,6	33,3
FL	82,5	81,5	79,3	82,1	83,9	82,9	84,8	77,1	82,9	81,6	78,9	76,9
FW	5,0	7,4	10,3	7,1	6,5	7,1	9,1	5,7	5,7	—	5,3	6,4
AL I	25,0	33,3	27,6	28,6	29,0	31,4	27,3	28,6	31,4	31,6	28,9	33,3
AL II	35,0	25,9	31,0	28,6	25,8	34,3	30,3	31,4	45,7	36,8	39,5	41,0
AL III	37,5	25,9	31,0	28,6	29,0	37,1	30,3	28,6	42,9	39,5	39,5	43,6
AL IV	30,0	29,6	31,0	32,1	29,0	31,4	33,3	28,6	34,3	31,6	34,2	30,8
TL Rt	90,0	140,7	—	107,1	112,9	94,3	87,9	114,3	100,0	—	78,9	—
TL Lt	92,5	107,4	96,6	110,7	—	122,9	87,9	105,7	100,0	84,2	84,2	100,0
Tcl	10,0	14,8	13,8	14,3	12,9	14,3	12,1	14,3	12,9	10,5	13,2	10,3

	A30141 (cont.)		A30142		A30172		Massy 1927 (Adam & Rees 1966) PF11741 PF10715		N	Mean	Range
	40	40	43	36	32	39	47	36			
MLd in mm	40	40	43	36	32	39	47	36			
MLv	82,5	80,0	76,7	86,1	87,5	82,1	83				
MW	35,0	32,5	32,6	38,9	40,6	38,5	32		19	37,8	32-42,9
HL	20,0	22,5	20,9	30,6	40,6	20,5	25				
HW	30,0	27,5	—	33,3	34,4	33,3	30	30,6	19	33,8	27,5-40,7
FL	80,0	80,0	76,7	80,6	90,7	87,2	85				
FW	7,5	7,5	9,3	5,6	6,3	7,7	8,5		18	7,1	5,0-10,3
AL I	30,0	30,0	27,9	27,8	43,8	30,8	30	38,9	20	30,8	25,0-43,8
AL II	37,5	37,5	37,2	38,9	43,8	43,6	38	47,2	20	36,5	25,8-47,2
AL III	37,5	37,5	37,2	38,9	31,3	43,6	38	47,2	20	36,2	25,9-47,2
AL IV	32,5	30,0	27,9	30,6	43,8	28,2	—	38,9	19	32,0	27,9-43,8
TL Rt	90,0	95,0	81,4	—	—	94,9					
TL Lt	97,5	107,5	74,4	—	93,8	92,3	72	127,8			
Tcl	15,0	15,0	11,6	—	15,6	12,8	9,5	13,9	19	13,0	9,5-15,6

TABLE 27. *Sepia adami* females. Relative dimensions as % MLd.

	A31394		A30149				N	Mean	Range
	59	47	44	28	24	25			
MLd in mm	59	47	44	28	24	25			
MLv	76,3	74,5	72,7	78,6	75,0	80,0			
MW	40,7	38,3	38,6	39,3	45,8	44,0	6	41,1	38,3-45,8
HL	22,0	23,4	20,5	25,0					
HW	35,6	36,2	36,4	39,3			4	36,9	35,6-39,3
FL	86,4	80,9	77,3	82,1					
FW	6,8	6,4	6,8	7,1			4	6,8	6,4-7,1
AL I	32,2	29,8	27,3	25,0			4	28,6	25,0-32,2
AL II	30,5	25,5	25,0	21,4			4	25,6	21,4-30,5
AL III	28,8	29,8	25,0	25,0			4	27,2	25,0-29,8
AL IV	32,2	29,8	31,8	25,0			4	29,7	25,0-32,2
TL Rt	98,3	63,8	—	85,7					
TL Lt	78,0	78,7	88,6	92,9					
Tcl	13,6	12,8	12,5	14,3			4	13,3	12,5-14,3

TABLE 28. *Sepia australis* males. Relative dimensions as % MLD.

	A30148										A30150			
	20	27	28	25	39	47	52	42	50	49	39	40	27	27
MLd in mm
MLv	70,0	81,5	82,1	84,0	84,6	85,1	82,7	83,3	88,0	87,8	82,1	85,0	77,8	81,5
MW	60,0	48,1	46,4	52,0	43,6	42,6	38,5	40,5	42,0	42,9	43,6	42,5	48,1	44,4
HL	. . .	25,9	21,4	. . .	23,1	21,3	19,2	19,0	24,0	22,4	20,5	22,5	25,9	18,5
HW	. . .	48,1	46,4	. . .	43,6	42,6	38,5	40,5	46,0	42,9	41,0	42,5	44,4	44,4
FL	. . .	77,8	71,4	. . .	100,0	85,1	73,1	81,0	82,0	83,7	84,6	80,0	77,8	81,5
FW	. . .	14,8	14,3	. . .	16,3	8,5	7,7	9,5	10,0	10,2	12,8	10,0	11,1	11,1
AL I	. . .	29,6	28,6	. . .	25,6	31,9	30,8	31,0	—	32,7	25,6	32,5	25,9	22,2
AL II	. . .	29,6	28,6	. . .	30,8	29,8	30,8	28,6	—	32,7	25,6	30,0	22,2	22,2
AL III	. . .	29,6	28,6	. . .	30,8	31,9	32,7	28,6	—	34,7	28,2	32,5	22,2	22,2
AL IV	. . .	29,6	32,1	. . .	33,3	34,0	32,7	31,0	—	36,7	33,3	30,0	25,9	29,6
Rt	. . .	111,1	—	. . .	102,6	97,9	98,1	102,4	—	75,5	92,3	102,5	111,1	100,0
TL	. . .	114,8	—	. . .	107,7	112,8	103,8	100,0	—	89,8	102,6	—	111,1	107,4
Tcl	. . .	18,5	—	. . .	17,9	14,9	15,4	14,3	—	14,3	12,8	12,5	11,1	14,8

	A30150 (cont.)			A30151			A30152			A30154			A30156		
	28	22	21	37	36	37	18	17	25	14	24	25	26	30	38
MLd in mm
MLv	78,6	81,8	76,2	86,5	80,6	83,8	88,9	82,4	84,0	85,7	83,3	92,0	88,5	86,7	86,8
MW	42,9	45,5	52,4	43,2	44,4	48,6	61,1	47,1	48,0	57,1	50,0	48,0	46,2	43,3	44,7
HL	. . .	21,4	. . .	24,3	25,0	29,7	23,1	26,3
HW	. . .	42,9	. . .	40,5	38,9	41,7	46,2	42,1
FL	. . .	85,7	. . .	91,9	88,9	83,8	88,5	89,5
FW	. . .	10,7	. . .	10,8	8,3	11,1	15,4	7,9
AL I	. . .	14,3	. . .	35,1	27,8	33,3	30,0	28,9
AL II	. . .	21,4	. . .	37,8	30,6	35,1	26,9	31,6
AL III	. . .	28,6	. . .	37,8	30,6	35,1	30,8	31,6
AL IV	. . .	28,6	. . .	37,8	36,1	35,1	26,9	34,2
TL	. . .	110,7	. . .	108,1	102,8	111,1	76,9	83,3
Rt	. . .	—	. . .	94,6	86,1	113,9	80,8	100,0
Tcl	. . .	14,3	. . .	13,5	13,9	16,7	15,4	13,2

TABLE 28 (continued)

	A30157		A30159		A30160		A30161			A30163		A30164	
MLD in mm	45	51	17	24	32	48	46	23	24	34	22	36	36
MLv	84.4	82.4	80.6	82.4	81.3	81.5	85.4	87.0	87.0	88.2	81.8	83.3	80.6
MW	40.0	37.3	41.9	45.8	43.8	37.0	39.6	39.1	56.5	50.0	54.5	41.7	44.4
HL	20.0	21.6	25.8	25.9	21.9	18.5	20.8	30.4	30.4	29.4	31.8	25.0	16.6
HW	35.6	37.3	38.7	45.8	37.5	37.5	37.5	47.8	45.8	47.1	50.0	38.9	41.7
FL	75.6	66.7	77.4	75.8	81.3	79.6	77.1	78.3	75.0	88.2	81.8	91.7	83.3
FW	8.9	9.8	9.7	9.4	9.4	7.4	8.3	6.5	8.3	11.8	9.1	11.1	11.1
AL I	33.3	27.5	29.0	26.1	28.1	27.8	29.2	28.3	26.1	29.4	27.3	27.8	33.3
AL II	31.1	23.5	29.0	30.4	28.1	29.6	29.2	26.1	30.4	29.4	27.3	30.6	30.6
AL III	31.1	27.5	32.3	31.3	31.3	29.6	27.1	28.3	30.4	29.4	22.7	30.6	33.3
AL IV	31.1	31.4	32.3	31.3	31.3	33.3	31.3	32.6	30.4	26.5	27.3	30.6	30.6
TL Rt	111.1	—	87.1	102.7	93.8	83.3	100.0	97.8	126.1	79.4	90.9	88.9	75.0
TL Lt	122.2	103.9	90.3	102.7	90.6	103.7	104.2	115.2	104.3	76.5	90.9	80.6	77.8
Tcl	13.3	13.7	12.9	13.5	12.5	13.0	14.6	13.0	17.4	11.8	13.6	13.9	13.9

	A30164 (cont.)		A30165		A30167		A30168		A30170		A30175		A30266		A30564		Range	
MLD in mm	39	34	35	37	33	28	32	41	49	46	35	43	43	59	45.7	37.0-61.1		
MLv	82.1	85.3	80.0	86.5	78.8	78.6	78.1	87.8	73.5	78.3	77.1	83.7	83.7	59	45.7	37.0-61.1		
MW	41.0	41.2	40.0	43.2	45.5	46.4	43.8	43.9	44.9	43.5	45.7	48.8	48.8	47	40.5	33.3-50.0		
HL	20.5	20.6	14.3	18.9	21.2	25.0	18.8	19.5	16.3	17.4	22.9	27.9	27.9	47	40.5	33.3-50.0		
HW	38.5	35.3	34.3	37.8	36.4	35.7	37.5	43.9	34.7	37.0	37.1	39.5	39.5	47	40.5	33.3-50.0		
FL	84.6	88.2	83.9	89.2	84.8	85.7	84.4	90.2	71.4	73.9	82.9	88.4	88.4	47	40.5	33.3-50.0		
FW	10.3	11.8	11.4	13.5	12.1	10.7	9.4	12.2	6.1	6.5	8.6	9.3	9.3	47	10.3	6.1-15.4		
AL I	30.8	26.5	31.4	32.4	30.3	28.6	25.0	29.3	28.6	30.4	31.4	27.9	27.9	46	28.9	14.3-35.1		
AL II	30.8	26.5	31.4	32.4	27.3	28.6	25.0	31.7	22.4	26.1	31.4	30.2	30.2	46	29.0	21.4-37.8		
AL III	33.3	29.4	34.3	32.4	33.3	28.6	31.3	29.3	26.5	26.1	31.4	32.6	32.6	46	30.5	22.5-37.8		
AL IV	30.8	32.4	28.6	35.1	36.4	28.6	25.0	31.7	28.6	28.3	31.4	27.9	27.9	46	31.4	25.0-37.8		
TL Rt	89.7	82.4	80.0	102.7	75.8	85.7	90.6	90.2	102.0	80.4	85.7	95.3	95.3	45	13.7	10.8-20.8		
TL Lt	97.4	70.6	—	—	75.8	96.4	—	92.7	100.0	76.1	77.1	95.3	95.3	45	13.7	10.8-20.8		
Tcl	12.8	11.8	14.3	13.5	12.1	14.3	12.5	12.2	12.2	12.2	11.4	11.6	11.6	45	13.7	10.8-20.8		

TABLE 29 (continued)

	A30154 (cont.)										A30155			A30157					A30159	
	39	36	38	39	31	30	29	22	19	17	38	49	42	30	33	46	84,8			
MLd in mm . . .	87,2	86,1	84,2	87,2	89,9	86,7	82,8	90,9	89,5	82,4	84,2	79,6	83,3	83,3	81,8	84,8				
MLv	43,6	47,2	44,7	46,2	48,4	50,0	51,7	54,5	52,6	47,1	44,7	42,9	42,9	46,7	45,5	43,5				
MW	23,1	19,4	18,4	20,5	22,6	26,7	27,6				21,1	20,4	23,8	20,0	24,2	19,6				
HL	38,5	38,9	36,8	41,0	41,9	40,0	41,4				39,5	34,7	38,1	40,0	39,4	34,8				
HW	89,7	94,4	89,5	92,3	90,3	93,3	89,7				89,5	67,3	71,4	66,7	69,7	84,8				
FL	12,8	13,9	13,2	12,8	12,9	13,3	13,8				5,3	8,2	11,9	6,7	9,1	8,7				
FW	25,6	25,0	28,9	25,6	25,8	26,7	27,6				23,7	28,6	26,2	20,0	24,2	23,9				
AL I	25,6	27,8	28,9	23,1	29,0	26,7	27,6				26,3	28,6	26,2	23,3	24,2	26,1				
AL II	25,6	27,8	28,9	25,6	29,0	26,7	27,6				23,7	28,6	23,8	23,3	27,3	26,1				
AL III	25,6	27,8	28,9	28,2	29,0	30,0	27,6				26,3	30,6	28,6	26,7	27,3	23,9				
AL IV	87,2	61,1	68,4	82,1	106,5	93,3	93,1				—	100,0	109,5	110,7	—	80,4				
TL Rt	84,6	52,8	65,8	84,6	100,0	100,0	86,2				—	108,2	128,6	110,0	100,0	84,8				
Tcl	15,4	13,9	15,8	15,4	16,1	16,7	13,8				—	12,2	11,9	13,3	18,2	10,9				

	A30160					A30161					A30164			A30165	
	39	41	41	20	15	51	24	26	25	12	38	40	44	42	43
MLd in mm . . .	87,2	84,6	75,6	78,0	86,7	86,3	79,2	84,6	80,0	75,0	84,2	80,0	88,6	81,0	79,1
MLv	43,6	38,5	48,8	46,3	60,0	43,1	50,0	50,0	52,0	66,7	47,4	45,0	43,2	42,9	46,5
MW	23,1	17,9	22,0	19,5		23,5	29,2	26,9	28,0		21,1	25,0	22,7	23,8	18,6
HL	35,9	35,9	36,6	36,6		37,3	45,8	46,2	48,0		36,8	40,0	34,1	38,1	39,5
HW	—	84,6	85,4	80,5		84,3	75,0	73,1	72,0		89,5	92,5	88,6	85,7	93,0
FL	12,8	10,3	7,3	9,8		9,8	8,3	11,5	12,0		13,2	15,0	11,4	11,9	11,6
FW	23,1	20,5	22,0	24,4		29,4	29,2	30,8	28,0		26,3	30,0	27,3	28,6	27,9
AL I	28,2	20,5	26,8	26,8		27,5	20,8	30,8	24,0		31,6	30,0	27,3	26,2	25,6
AL II	25,6	23,1	22,0	26,8		33,3	29,2	30,8	24,0		26,3	30,0	29,5	28,6	25,6
AL III	30,8	23,1	22,0	26,8		33,3	29,2	30,8	28,0		28,9	30,0	27,3	28,6	27,9
AL IV	94,9	120,5	85,4	104,9		68,6	104,2	107,7	96,0		—	82,5	—	88,1	93,0
TL Rt	87,2	107,7	92,7	117,1		76,5	116,7	96,2	116,0		68,4	80,0	61,4	85,7	79,1
Tcl	12,8	12,8	14,6	14,6		11,8	16,7	19,2	16,0		14,5	15,0	11,4	11,9	11,6

TABLE 29 (continued)

	A30166	A30168		A30170	A30171		A30175		A30190	A30334	N	Mean	Range
Mld in mm	43	43	23	49	45	43	43	48	54	58			
MLv . . .	81,4	81,4	82,6	83,7	86,7	83,7	83,7	77,1	88,9	86,2			
MW . . .	41,9	44,2	47,8	40,8	42,2	44,2	44,2	39,6	40,7	39,7	77	46,0	37,5-66,7
HL . . .	25,6	16,3		20,4	17,8	20,9	18,6	18,8	24,1	19,0			
HW . . .	39,5	34,9		36,7	37,8	37,2	39,5	35,4	41,7	37,9	66	39,5	24,1-48,1
FL . . .	88,4	88,4		81,6	91,1	86,0	86,0	72,9	77,8	84,5			
FW . . .	11,6	11,6		10,2	11,1	9,3	9,3	6,3	9,3	12,1			
AL I . . .	27,9	25,6		24,5	26,7	23,3	25,6	25,0	29,6	29,3			5,3-15,0
AL II . . .	25,6	25,6		26,5	26,7	27,9	25,6	22,9	25,9	29,3			19,6-34,0
AL III . . .	25,6	25,6		28,6	28,9	30,2	25,6	20,8	24,1	27,6			16,0-34,5
AL IV . . .	27,9	27,9		26,5	26,7	25,6	23,3	22,9	25,9	27,6			20,0-35,4
Rt . . .	51,2	58,1		83,7	82,2	79,1	76,7	91,7	101,9	69,0			19,0-37,9
TL Lt . . .	69,8	72,1		77,6	93,3	76,7	67,4	87,5	101,9	—			
Tel . . .	16,3	14,0		12,2	11,1	11,6	11,6	12,5	13,0	12,1	64	14,1	9,5-19,2

TABLE 30. *Sepia australis* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z	
2727	33	36,4	9,1	69,7	
	47	34,0	8,5	72,3	
	48	35,4	8,3	75,0	
	47	34,0	7,4	72,3	
	46	34,8	8,7	71,7	
	49	32,7	8,2	71,4	
	51	33,3	7,8	72,5	
	43	32,6	8,1	69,8	
	48	33,3	9,4	70,8	
	51	—	7,8	78,4	
	54	35,2	8,3	72,2	
	A30504	41	36,6	9,8	70,7
	Mossel Bay (Cape Peninsula) . .	52	32,7	8,7	75,0
58		29,3	7,8	72,4	
North of Olifants River . . .	57	33,3	8,8	71,9	
	55	29,1	7,3	74,5	
Strandfontein to Muizenberg . .	45	33,3	8,9	66,7	
	46	32,6	8,7	76,1	
Millers Point	55	30,9	9,1	70,9	
	52	32,7	8,7	71,2	
	43	34,9	9,3	72,1	
Namaqualand coast	59	32,2	9,3	72,9	
Simonstown	40	32,5	8,8	72,5	
Arniston	53	32,1	7,5	73,6	
	56	32,1	7,1	75,0	
N		24	25	25	
Mean		33,2	8,5	72,5	
Range		29,1-36,6	7,1-9,8	66,7-78,4	

TABLE 31. *Sepia tuberculata* males. Relative dimensions as % MLD.

	A30121	A30279	A30600		A31235	Adam & Rees 1966	N	Mean	Range
MLd in mm	25	42	27	33	51	47			
MLv . . .	92,0	85,8	96,3	90,9	90,2	92			
MW . . .	64,0	69,0	63,0	66,7	58,8	66	6	64,6	58,8-69
HL . . .	48,0	50,0	59,3	57,6	37,3	60			
HW . . .	60,0	52,4	70,4	63,6	47,1	53	6	57,8	47,1-70,4
FL . . .	104,0	85,8	96,3	103,0	103,9	96			
FW . . .	16,0	16,7	18,5	15,2	19,6	15+	5	17,2	15,2-19,6
AL I . . .	52,0	—	70,4	72,7	47,1	57	5	59,8	47,1-72,7
AL II . . .	48,0	—	70,4	66,7	43,1	60	5	57,6	43,1-70,4
AL III . . .	56,0	45,3	66,7	66,7	49,0	57	6	56,8	45,3-66,7
AL IV . . .	52,0	52,4	55,6	54,5	47,1	57	6	53,1	47,1-57
TL . . .	76,0	—	140,7	127,3	49,0	106			
Tcl . . .	32,0	—	37,0	30,3	21,6	23,5	5	28,9	21,6-37,0

See page 302 for Table 32

TABLE 33. *Sepia tuberculata* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A29867	69	43,5	8,7	73,9
A30279	39	46,2	5,1	71,8
A31235	45	44,4	6,7	64,4
A30511	55	45,5	5,5	63,6
	45	46,7	6,7	62,2
A30559	32	46,9	6,3	62,5
A30600	27	48,1	5,6	55,6
	22	50,0	6,8	63,6
Strandfontein to Muizenberg . . .	62	—	5,6	71,0
	38	47,4	5,3	73,7
	39	48,7	7,7	56,4
Betty's Bay	37	48,6	8,1	54,1
Kommetjie	40	52,5	7,5	62,5

TABLE 33 (continued)

	L in mm	W	Th	Str z
Adam 1941	55.5 50.5 41.5 46 ±68 61 39 51	52 48.5 50.5 49 54.5 54 51 55		
Adam & Rees 1966	60	45	6.7	55
Cape Agulhas	57 58 49 53	50.9 48.3 51.0 47.2	4.4 5.2 6.1 4.7	77.2 81.0 83.7 77.4
Milnerton	64 68	54.7 51.5	7.0 8.1	84.4 80.9
Pearly Beach	±49 ±50 47 ±54	49.0 52.0 48.9 48.1	5.1 6.0 6.4 5.6	— 80.0 72.3 74.1
Die Kelders	65	50.8	7.7	78.5
Beach 11 km NW of Cape Agulhas .	58 54 52 51 41 46 40	46.6 48.1 48.1 47.1 46.3 43.5 47.5	5.2 5.6 5.8 5.9 4.9 5.4 5.0	87.9 79.6 88.5 76.5 80.5 73.9 70.0
N		39	32	31
Mean		48.9	6.1	72.2
Range		43.5-55	4.4-8.7	54.1-88.5

TABLE 32. *Sepia tuberculata* females. Relative dimensions as % MLD.

	A29781	A29867	A30123	A30139	A30180	A30511	A30559	Adam 1941	Adam & Rees 1966	N	Mean	Range
MLD in mm .	30											
MLV . . .	80,0	75	71	82	70	48	36	56	64			
MW . . .	80,0	89,4	97,2	89,0	90,0	96,0	97,2	84	92	12	69,0	61 -80,0
HL . . .	46,7	66,7	77,5	73,2	68,6	66,7	63,9	62,5	70			
HW . . .	60,0	45,4	46,5	45,0	53,0	50,0	52,8	46,5	47	12	52,5	41,5-61,1
FL . . .	113,3	49,4	53,6	41,5	53,0	58,4	61,1	44,5	55			
FW . . .	16,7	112,0	121,1	109,8	118,6	112,5	105,6	89	102			
AL I . . .	43,3	17,3	18,3	23,2	17,2	20,8	19,4	10,7	19	11	17,4	8,2-23,2
AL II . . .	50,0	48,0	67,6	55,0	55,8	46,0	61,1	52	53	12	52,5	43,3-67,6
AL III . . .	46,7	58,7	66,2	52,5	63,0	64,6	58,3	50	52	12	55,4	39,5-66,2
AL IV . . .	50,0	57,3	67,6	50,0	57,2	64,6	58,3	—	52	11	54,5	45,5-67,6
TL . . .	76,7	46,7	63,4	46,4	53,0	58,4	52,8	46,5	59	12	51,4	43,5-63,4
Tcl . . .	33,3	106,7	107,0	89,0	190,0	114,5	108,3	82	117			
		30,7	43,7	30,5	37,2	33,4	36,1	25	31	12	33,8	25 -46,6
								30	28,5			

TABLE 34. *Sepia papillata* males. Relative dimensions as % MLD.

	A30118		A30120	A30137	A30138	A30507		A30509	A31250	N	Mean	Range
MLd in mm	100	115	112	100	110	115	105	105	113			
MLv . . .	95,0	87,0	±69,6	87,0	86,4	78,3	81,0	90,5	87,6			
MW . . .	68,0	60,9	62,5	60,0	59,1	59,1	76,2	64,8	58,4	9	63,2	58,4-76,2
HL . . .	50,0	38,3	35,7	44,0	40,9	26,1	41,0	33,3	46,9			
HW . . .	50,0	46,1	42,9	42,0	45,5	34,8	52,4	43,8	46,0	9	44,8	34,8-52,4
FL . . .	113,0	117,4	89,3	105,0	100,0	95,7	104,8	±100	104,4			
FW . . .	20,0	26,1	14,3	15,0	13,6	13,0	28,6	—	17,7	8	18,5	13,0-28,6
AL I . . .	53,0	62,6	42,0	54,0	52,7	47,8	56,2	—	64,6	8	54,1	42,0-64,6
AL II . . .	57,0	56,5	42,0	55,0	57,3	47,8	61,9	—	64,6	8	55,3	42,0-64,6
AL III . . .	64,0	61,7	42,9	55,0	65,5	47,8	64,8	—	58,4	8	57,5	42,9-65,5
AL IV . . .	65,0	55,7	56,3	48,0	50,9	43,5	54,3	57,1	52,2	9	53,7	43,5-65,0
TL . . .	105,0	64,3	160,7	75,0	77,3	—	—	—	167,3			
Tcl . . .	38,0	30,4	30,4	30,0	32,7	—	—	—	30,1	6	31,9	30,0-38,0

TABLE 35. *Sepia papillata* females. Relative dimensions as % MLD.

	A30119	A30124	A30136	A30140	A30507		Hoyle 1910	N	Mean	Range
MLd in mm .	130	115	95	140	120	135	115			
MLv . . .	92,3	91,3	88,4	82,1	91,7	88,9				
MW . . .	63,8	82,6	61,1	60,7	75,0	66,7	62,6	7	67,5	60,7-82,6
HL . . .	42,3	60,0	46,3	44,3	58,3	44,4				
HW . . .	42,3	56,5	44,2	37,9	43,3	44,4	46,1	7	45,0	37,9-56,5
FL . . .	115,4	124,3	106,3	103,6	116,7	88,9				
FW . . .	15,4	21,7	13,7	17,9	20,8	18,5	11,3	7	17,0	11,3-21,7
AL I . . .	50,0	63,5	54,7	42,9	58,3	40,7	47,8	7	51,1	40,7-63,5
AL II . . .	50,0	64,3	58,9	46,4	58,3	44,4	48,7	7	53,0	44,4-64,3
AL III . . .	55,4	65,2	57,9	46,4	66,7	48,1	56,5	7	56,6	46,4-66,7
AL IV . . .	50,0	68,7	49,5	45,0	52,5	45,9	47,8	7	51,3	45,0-68,7
TL . . .	161,5	234,8	194,7	107,1	140,8	139,3	113,0			
Tcl . . .	44,6	55,7	42,1	38,6	29,2	25,9		6	39,4	25,9-55,7

TABLE 36. *Sepia papillata* shells (form A). Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A30118	110	46,4	8,6	72,7
A30482	134	—	9,7	68,7
A30507	131	45,8	9,5	61,1
	94	47,9	9,0	61,7
A30509	104	42,3	8,7	65,4
A30553	100	48,0	10,0	67,0
	117	43,6	9,0	68,4
Strandfontein to Muizenberg . .	124	—	10,5	69,4
	100	42,0	10,0	69,0
	103	—	9,2	71,8
	100	46,0	11,5	55,0
Betty's Bay	103	48,5	8,3	70,9
Strandfontein	95	49,5	12,1	57,9
	92	52,2	11,4	60,9
Milnerton beach	122	46,7	12,3	59,0
	123	45,5	9,8	69,1
Arniston	92	45,7	10,3	64,1
Hoyle 1910	103	47,6	12,4	—
N_A		15	18	17
Mean _A		46,5	10,1	65,4
Range _A		42,0-52,2	8,3-12,4	55,0-72,7

TABLE 37. *Sepia papillata* shells (form B). Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A30497	57 41	47,4 48,8	9,6 9,8	61,4 53,7
Strandfontein to Muizenberg . .	109 88	45,9 43,2	9,2 9,7	75,2 68,2
Olifantsbosbaai	97	45,4	10,3	76,3
Strandfontein	76	48,7	9,9	64,5
Namaqualand coast	92	44,6	8,2	68,5
Still Bay	70	50,0	7,9	72,9
Arniston	71	45,1	8,5	74,6
Adam 1941	65,5	48	—	—
Adam & Rees 1966	108	43,5	10	±66
N_B		11	10	10
Mean _B		46,4	9,3	68,1
Range _B		43,2-50,0	7,9-10,3	53,7-76,3

TABLE 38. *Sepia simoniana* males. Relative dimensions as % MLd.

	A30127	A31251		N	Mean	Range
MLd in mm .	116	141	144			
MLv . . .	92,2	91,5	87,5			
MW . . .	62,9	63,1	57,6	3	61,2	57,6-63,1
HL . . .	49,1	43,3	44,4			
HW . . .	37,1	49,6	42,4	3	43,0	37,1-49,6
FL . . .	94,8	113,5	109,0			
FW . . .	—	15,6	16,0	2	15,8	15,6-16,0
AL I . . .	62,9	59,6	55,6	3	59,4	55,6-62,9
AL II . . .	63,8	66,0	63,2	3	64,3	63,2-66,0
AL III . . .	73,3	70,9	68,8	3	71,0	68,8-73,3
AL IV . . .	60,3	53,2	54,9	3	56,1	53,2-60,3
TL Rt . . .	—	177,3	172,2			
Lt . . .	—	173,8	160,4			
Tcl . . .	—	70,2	63,2	2	66,7	63,2-70,2

TABLE 39. *Sepia simoniana* females. Relative dimensions as % MLd.

	A30132	A30133	A30134	A30135	Adam & Rees 1966	Massy 1925	N	Mean	Range
MLd in mm	174	172	139	111	180 165 162 140	147			
MLv . .	87,4	92,4	87,8	87,4	83 90 87 84		8	56,9	53 -60,4
MW . .	53,4	57,6	57,6	60,4	53 58 59 56				
HL . .	46,0	43,6	40,3	37,8	42 51 44 49				
HW . .	40,2	47,7	41,7	45,0	41 39 41 41	39,5	9	41,8	39 -47,7
FL . .	100,0	116,3	105,8	100,0	94 97 99 ±93				
FW . .	10,9	15,1	10,8	9,0	11 — 12 ±8,5		6	11,5	9,0-15,1
AL I . .	43,7	52,3	39,6	38,7	47 — 40 39	45,6	8	43,2	38,7-52,3
AL II . .	43,1	53,5	41,0	41,4	44 — 40 43	40,8	8	43,4	40 -53,5
AL III . .	44,3	55,8	45,3	46,8	50 — 43 46	54,4	8	48,2	43 -55,8
AL IV . .	41,4	54,1	43,2	41,4	47 — 43 43	51,0	8	45,5	41,4-54,1
TL Rt . .	103,4	142,4	89,9	101,8	122 — 99 —	187,1			
TL Lt . .	100,6	127,9	73,4	111,7					
Tcl . .	48,9	55,2	51,8	51,4	49 — 56 —	60,5	7	53,3	48,9-60,5

See opposite for Table 40

TABLE 41. *Sepia angulata* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A31317 (Holotype) .	60	56,7	13,3	51,7
A31395	57 61 ±46	57,9 50,8 56,5	14,0 13,1 13,0	47,4 47,5 52,2
A31318	66 ±75 25	53,0 56,0 60,0	15,2 14,0 16,0	50,0 50,5 60,0
A31319	63 67	57,1 52,2	11,9 11,9	60,3 61,2
A31320	41 35 34	56,1 60,0 52,9	12,2 14,3 11,8	58,5 54,3 58,8
N		12	12	12
Mean		55,8	13,4	54,4
Range		50,8-60,0	11,8-16,0	47,4-61,2

TABLE 40. *Sepia simoniana* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A30127	113	42,5	10,6	67,3
A30132	169	45,6	10,1	71,6
A30133	166	47,6	9,6	78,3
A31239	23	52,2	8,7	56,5
Strandfontein to Muizenberg . .	185	43,8	9,2	79,5
	141	—	10,6	71,6
Simonstown	127	43,3	9,4	71,7
	152	46,1	8,2	71,1
Betty's Bay	181	44,8	11,0	79,6
Strandfontein	98	46,9	10,2	60,2
Umngazana River mouth . . .	73	46,6	—	—
Still Bay	100	44,0	10,0	65,0
	104	42,3	8,7	62,5
	80	46,3	10,0	70,0
Arniston	38	47,4	9,2	63,2
Adam & Rees 1966	137	44	11,5	±59
	131	38	9	±64
	121	43	10	±65
	120	45	12,5	±71
	114	49	12,5	±70
	112	44	10	±62
	111	48	14,5	—
	107	47	12	±70
	105	41	11	±62
	90	43	13	63
	N.		24	24
Mean		45,1	10,5	68,7
Range		38 -52,2	8,2-14,5	56,5-79,6

TABLE 42. *Sepia hieronis* males. Relative dimensions as % MLd.

	A29728	A30146	A30563	A31243	A31405	A31406	A31407	N	Mean	Range
MLd in mm .	59	54	62	61	47	56	48			
ML _v . . .	69,5	70,4	75,8	82,0	83,0	76,8	93,8			
MW . . .	49,2	55,6	56,5	65,6	70,2	55,4	62,5	7	59,3	49,2-70,2
HL . . .	37,3	37,0	37,1	50,8	44,7	44,6	45,8			
HW . . .	44,1	42,6	43,5	50,8	46,8	37,5	54,2	7	45,6	37,5-54,2
FL . . .	78,0	79,6	82,3	90,2	78,7	80,4	83,3			
FW . . .	10,2	5,6	6,5	9,8	8,5	7,1	8,3	7	8,0	5,6-10,2
AL I . . .	30,5	26,0	38,7	55,7	34,0	39,3	41,7	7	38,0	26,0-55,7
AL II . . .	33,9	26,0	35,5	62,3	42,6	37,5	47,9	7	40,8	26,0-62,3
AL III . . .	37,3	31,5	38,7	60,7	46,8	41,1	58,3	7	44,9	31,5-60,7
AL IV . . .	49,2	46,3	45,2	68,9	48,9	35,7	52,1	7	49,5	35,7-68,9
TL . . .	127,1	101,9	90,3	114,8	142,6	121,4	185,4			
Tcl . . .	11,9	14,8	14,5	13,1	12,8	14,3	14,6	7	13,7	11,9-14,8

TABLE 43. *Sepia hieronis* females. Relative dimensions as % MLd.

	A30145	Adam & Rees 1966	N	Mean
MLd in mm .	33	61		
ML _v . . .	78,8	74		
MW . . .	60,6	54	2	57,3
HL . . .	48,5	38		
HW . . .	51,5	51	2	51,3
FL . . .	84,8	85		
FW . . .	9,1	8	2	8,6
AL I . . .	18,2	38	2	28,1
AL II . . .	24,2	38	2	31,1
AL III . . .	30,3	38	2	34,2
AL IV . . .	45,5	38	2	41,8
TL . . .	157,6	—		
Tcl . . .	12,1	10	2	11,1

TABLE 44. *Sepia hieronis* shells. Relative dimensions as % shell length.

		L in mm	W	Th	Str z
West coast	A29728	60	38,3	11,7	70,0
	A30146	52	40,4	9,6	73,1
	A30563	62	38,7	11,3	±72,6
	A31243	67	38,8	11,2	73,1
East coast	A31405	46	45,7	15,2	65,2
	A31406	54	40,7	14,8	66,7
	A31407	54	40,7	13,0	64,8
N . . .			7	7	7
Mean . . .			40,5	12,4	69,4
Range . . .			38,3-45,7	9,6-15,2	64,8-73,1

TABLE 45. *Sepia insignis* female.
Relative dimensions as % MLd.

	A31247
MLd in mm	44
MLv	90,9
MW	± 52,3
HL	27,3
HW	45,5
FL	95,5
FW	6,8
AL I	36,4
AL II	36,4
AL III	29,5
AL IV	45,5
TL Rt	68,2
TL Lt	75,0
Tcl	13,6

TABLE 46. *Sepia insignis* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A30486	29	34,5	10,3	55,2
A31236	29	37,9	10,3	55,2
A31241	34 17,5	35,3 37,1	8,8 —	61,8 60,0
A31247	44	31,8	11,4	63,6
Still Bay	± 32	31,3	10,9	65,6
Adam & Rees 1966 .	26	33	16,5	65
N		7	6	7
Mean		34,4	11,4	60,9
Range		31,3-37,9	8,8-16,5	55,2-65,6

TABLE 48. *Sepia typica* females. Relative dimensions as % MLd.

	A29608			A29717						A29783		
MLd in mm	22	21	18	9	10	12	8	10	11	23	25	19
MLv . . .	93,2	100,0	94,4	88,9	90,0	83,3	75,0	80,0	72,7	91,3	92,0	89,5
MW . . .	72,7	76,2	77,8	88,9	80,0	75,0	75,0	70,0	72,7	82,6	64,0	89,5
HL . . .	63,6	81,0	61,1	66,7	70,0	66,7	—	60,0	63,6	56,5	48,0	57,9
HW . . .	54,5	57,1	55,6	66,7	70,0	66,7	—	60,0	63,6	52,2	48,0	57,9
FL . . .	113,6	109,5	105,6	100,0	100,0	100,0	—	110,0	90,9	113,0	104,0	110,5
FW . . .	9,1	9,5	11,1	—	—	12,5	—	—	—	10,9	12,0	10,5

	A29783 (cont.)											
MLd in mm . . .	15	18	20	14	11	14	10	10	11	10	13	14
MLv	86,7	88,9	90,0	92,9	81,8	85,7	90,0	90,0	90,9	80,0	84,6	85,7
MW	80,0	77,8	80,0	85,7	72,7	78,6	80,0	90,0	81,8	90,0	69,2	85,7
HL	60,0	55,6	50,0	50,0	63,6	57,1	60,0	70,0	63,6	80,0	61,5	57,1
HW	60,0	55,6	55,0	64,3	63,6	50,0	70,0	70,0	63,6	70,0	53,8	57,1
FL	100,0	100,0	105,0	71,4	100,0	107,1	100,0	110,0	109,1	90,0	100,0	107,1
FW	—	—	—	—	—	—	—	—	—	—	15,4	10,7

	A29783 (cont.)											
MLd in mm . . .	14	15	15	15	16	15	16	18	17	14	18	19
MLv	85,7	86,7	93,3	86,7	87,5	93,3	93,8	88,9	88,2	92,9	83,3	94,7
MW	78,6	73,3	80,0	86,7	81,3	80,0	81,3	77,8	82,4	85,7	77,8	84,2
HL	57,1	53,3	60,0	66,7	62,5	66,7	62,5	66,7	64,7	64,3	66,7	68,4
HW	57,1	60,0	60,0	60,0	56,3	60,0	56,3	50,0	58,8	57,1	55,6	52,6
FL	107,1	93,3	106,7	106,7	112,5	100,0	106,3	100,0	111,8	114,3	105,6	100,0
FW	7,1	—	—	—	—	—	18,8	8,3	11,8	7,1	13,9	—

	A29783 (cont.)		A30176		A30177				N	Mean	Range
MLd in mm	18	17	18	15	19	20	15	15			
MLv	88,9	94,1	94,4	86,7	100,0	78,9	93,3	93,3	44	79,3	64,0-90,0
MW	77,8	82,4	72,2	73,3	78,9	75,0	80,0	86,7			
HL	61,1	64,7	55,6	66,7	63,2	55,0	66,7	66,7			
HW	55,6	58,8	55,6	60,0	52,6	60,0	60,0	66,7			
FL	105,6	105,9	100,0	66,7	110,5	110,0	113,3	—	43	59,0	48,0-70,0
FW	—	5,9	—	10,0	—	—	—	—			
									17	10,9	5,9-18,8

TABLE 49. *Sepia typica* shells. Relative dimensions as % shell length.

	L in mm	W	Th	Str z
A29608	19,5	53,8	—	51,3
Adam & Rees 1966 .	21	57,1	—	—
Mean		55,5		

TABLE 50. *Sepia robsoni*, *S. faurei* and *S. dubia*. Relative dimensions as % MLd (or shell length).

	<i>S. robsoni</i> (Massy 1927 & Taylor*)	<i>S. faurei</i> A30144	<i>S. dubia</i> (Adam & Rees 1966 & Taylor*)
	♂	♀	♀
MLd in mm	17	21	17
MLv	87,1	85,7	91,7
MW	±76,5	66,7	68,5
HL	33,5	42,9	53,6
HW	57,1	42,9	52,4
FL	72,9	90,5	91,1
FW	8,8	7,1	9,5
AL I	64,7	38,1	—
AL II	70,6	38,1	—
AL III	70,6	38,1	—
AL IV	76,5	42,9	—
TL	60,6	81,0	68,5
Tcl	17,6	±9,5	16,1
Shell L in mm . . .			14,5
W			62,1

* Taylor, personal communication.

TABLE 51. *Sepiella cyanea* males. Relative dimensions as % MLd.

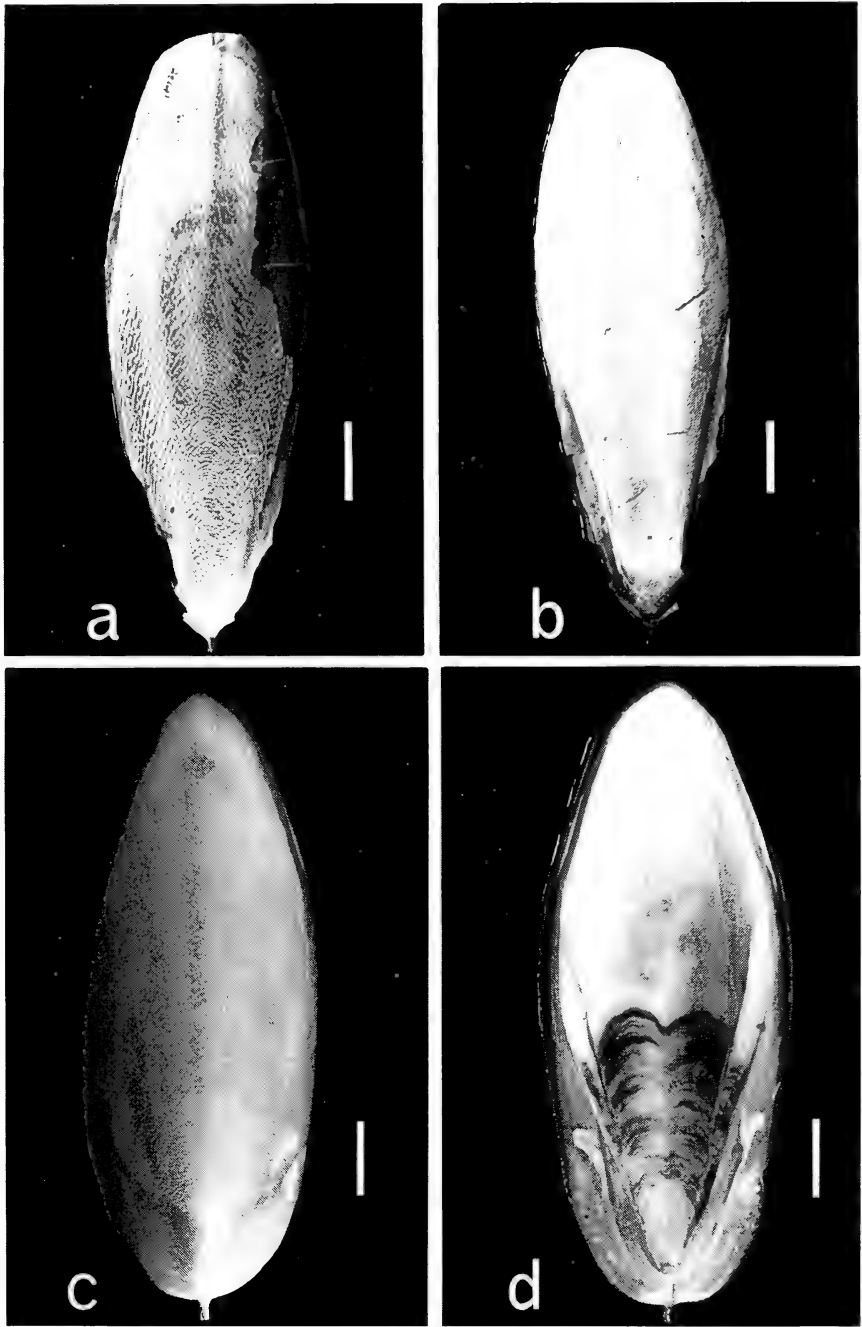
	A6526	Adam & Rees 1966								N	Mean	Range
		74	75	56	55	53,5	50	48	86			
MLd in mm	62	74	75	56	55	53,5	50	48				
MLv	75,8	74	81	88	87	86	86	86				
MW	40,3	45	41	57	56	60	58	60	8	52,2	40,3-60	
HL	19,4	23	24	25	25	26	26	27				
HW	41,9	41	39	52	49	49	52	50	8	46,7	39 -52	
FL	80,6	93	85	100	98	98	98	92				
FW	8,1	15	9,5	19,5	18	20	20	12,5	8	15,3	8,1-20	
AL I	35,5	41	41	36	35	36	38	40	8	37,8	35 -41	
AL II	33,9	41	41	36	36	36	38	40	8	37,7	33,9-41	
AL III	41,9	47	45	46	44	43	48	50	8	45,6	41,9-50	
AL IV	46,8	61	55	54	49	50	54	56	8	53,2	46,8-61	
TL	—	81	106	—	—	—	—	—				
Tcl	—	19	17,5	23	22	20	24	21	7	20,9	17,5-24	

TABLE 52. *Sepiella cyanea* females. Relative dimensions as % MLD.

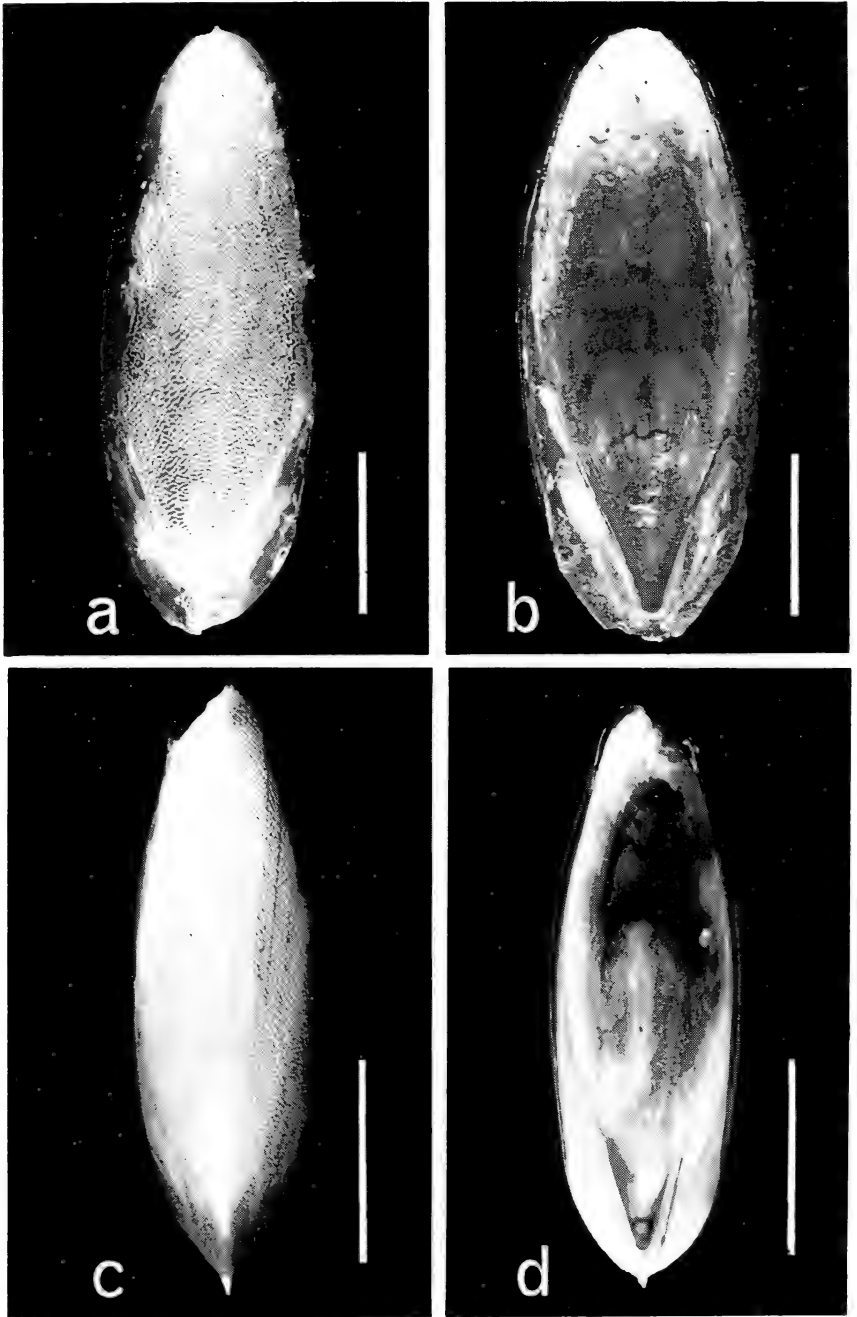
	Adam & Rees 1966							N	Mean	Range
	75	71	69	37	37	37	29			
MLd in mm	75	71	69	37	37	37	29			
MLv	80	84	86	87	87	84	89			
MW	53	45	52	65	59	65	64	7	57,6	45 -65
HL	24	27	25	27	27	27	31			
HW	40	42	49	51	51	51	55	7	48,4	40 -55
FL	87	95	100	100	100	95	91			
FW	13,5	14	19	19	19	16	12	7	16,1	12 -19
AL I	36	38	29	27	27	27	28	7	30,3	27 -38
AL II	33	39	29	27	27	27	28	7	30,0	27 -39
AL III	36	39	30	27	27	27	31	7	31,0	27 -39
AL IV	47	48	38	35	38	38	35	7	39,9	35 -48
TL	146	—	—	—	—	—	—			
Tcl	22,5	22,5	24,5	—	24	—	—	4	23,4	22,5-24,5

TABLE 53. *Sepiella cyanea* shells. Relative dimensions as % shell length.

	Sex	L in mm	W	Th	Str z
A6526	♂	61	31,1	11,5	50,8
Adam & Rees 1966	♂	69	29	10	58
	♂	54	33	14	56
	♀	74	30,5	11	51
	♀	70	31,5	12	53
	♀	69	35,5	13	58
A6526	?	77	33,8	11,7	54,5
	?	76	32,9	11,8	52,6
	?	62	32,2	11,3	54,8
	?	±75	30,7	12,0	61,3
Adam & Rees 1966	?	80	32,5	12	60
	?	76	31,5	12,5	58
N _{total}			12	12	12
Mean _{total}			32,0	11,9	55,7
Range _{total}			29 -35,5	10 -14	50,8-61,3
N _♂			3	3	3
Mean _♂			31,0	11,8	54,9
Range _♂			29 -33	10 -14	50,8-58
N _♀			3	3	3
Mean _♀			32,5	12	54
Range _♀			30,5-35,5	11 -13	51 -58



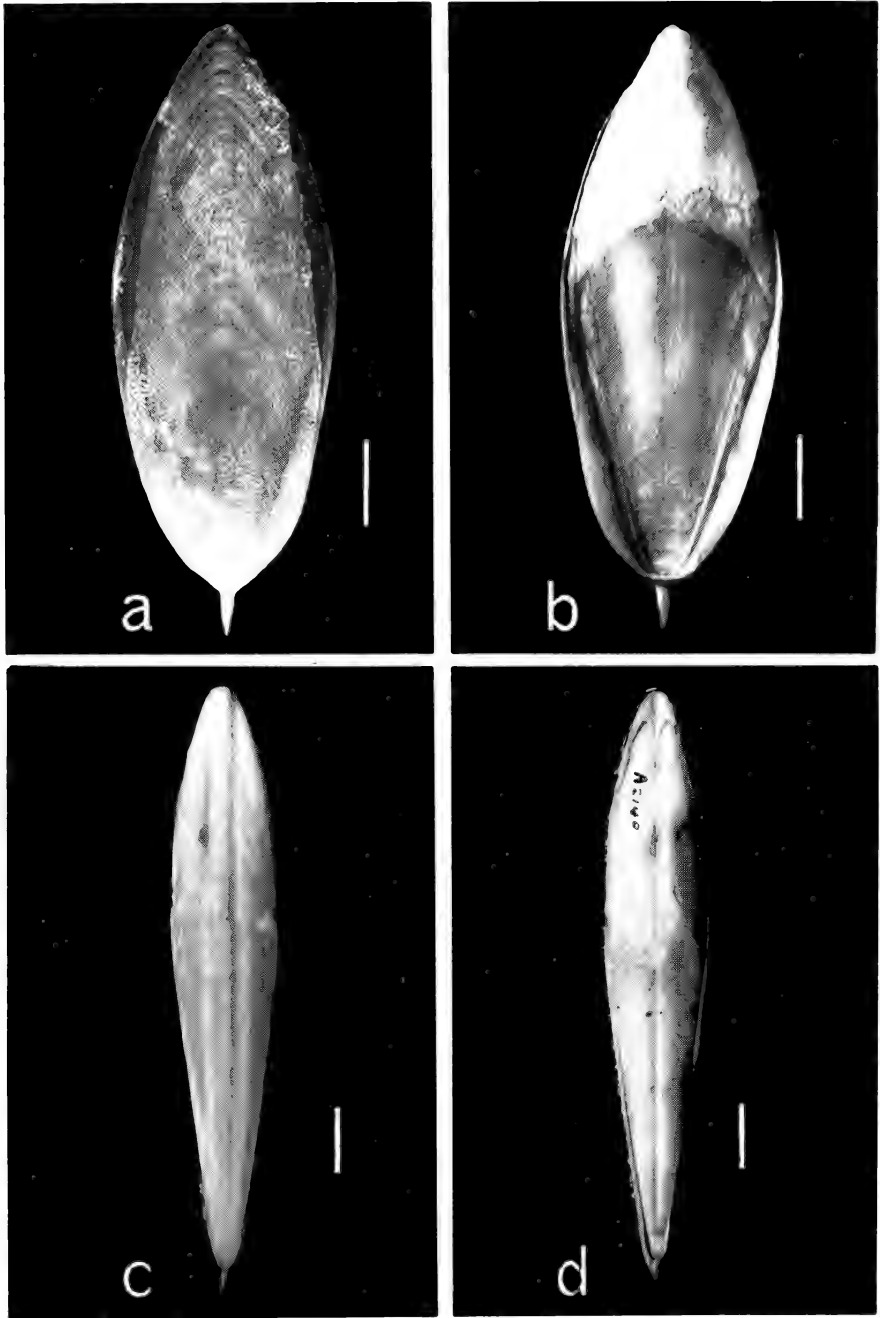
Sepia zanzibarica Pfeffer, A2141: a. Dorsal and b. ventral views of shell.
Sepia officinalis vermiculata Quoy & Gaimard, ♀ from Durban: c. Dorsal and d. ventral views of shell.
Scale = 20 mm.



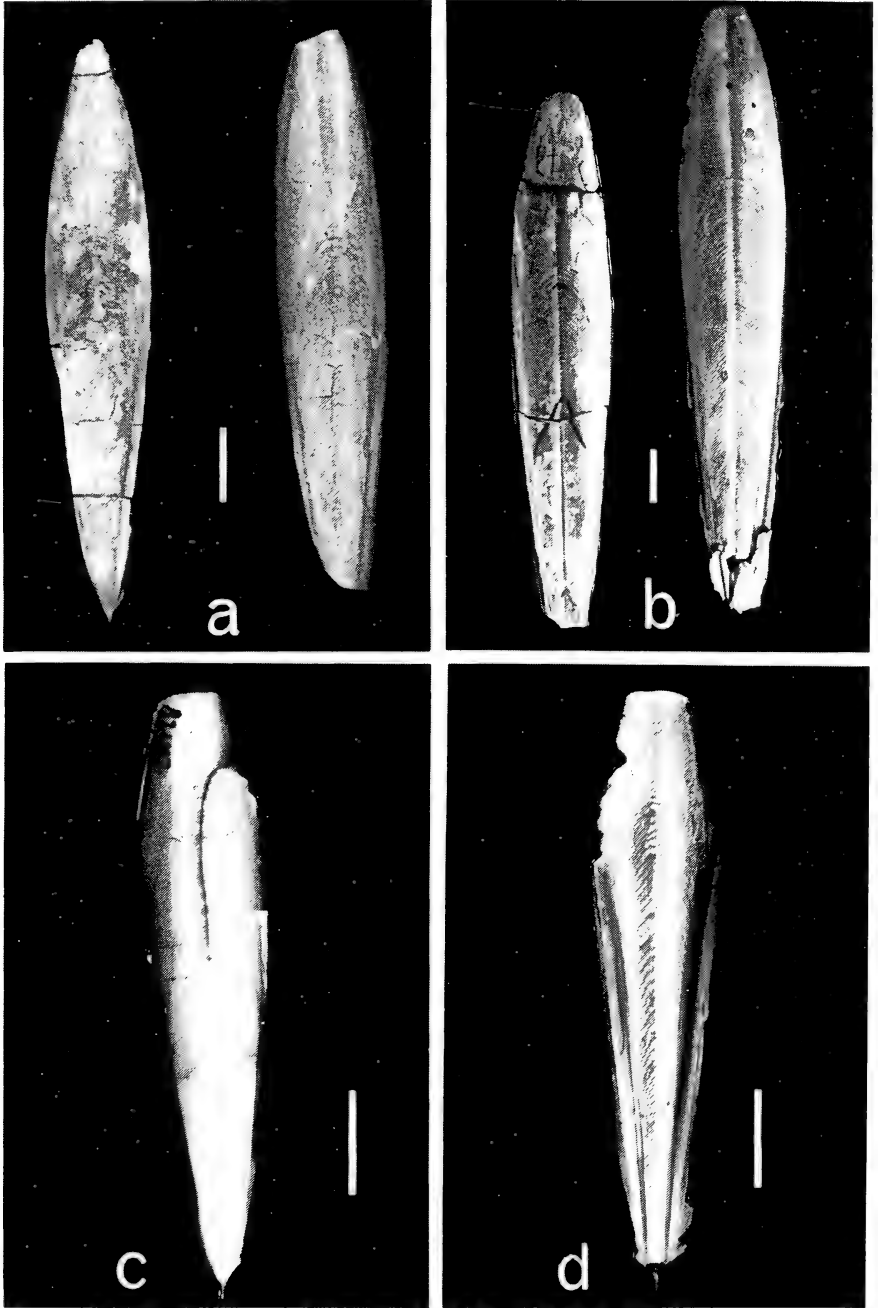
Sepia officinalis vermiculata Quoy & Gaimard, ♀, A30183: a. Dorsal and b. ventral views of shell (posterior spine broken).

Sepia officinalis hierredda Rang, ♂, A31291, from Baia de Cabo Negro, Angola: c. Dorsal and d. ventral views of shell of comparable size to the above.

Scale = 100 mm.



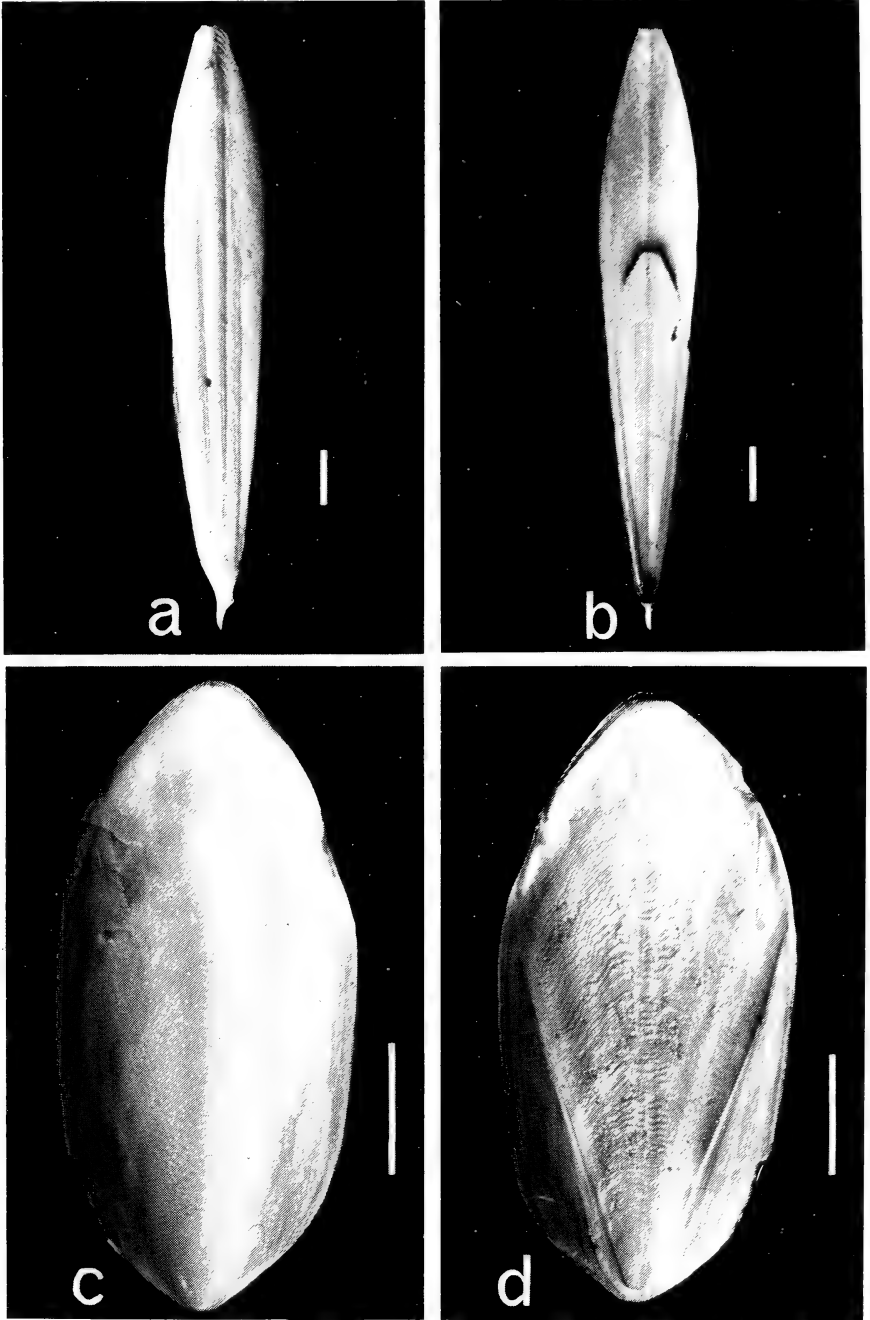
Sepia acuminata Smith, ♂, A31398: a. Dorsal and b. ventral views of shell.
Sepia confusa Smith, A2140: c. Dorsal and d. ventral views of shell.
Scale = 10 mm.



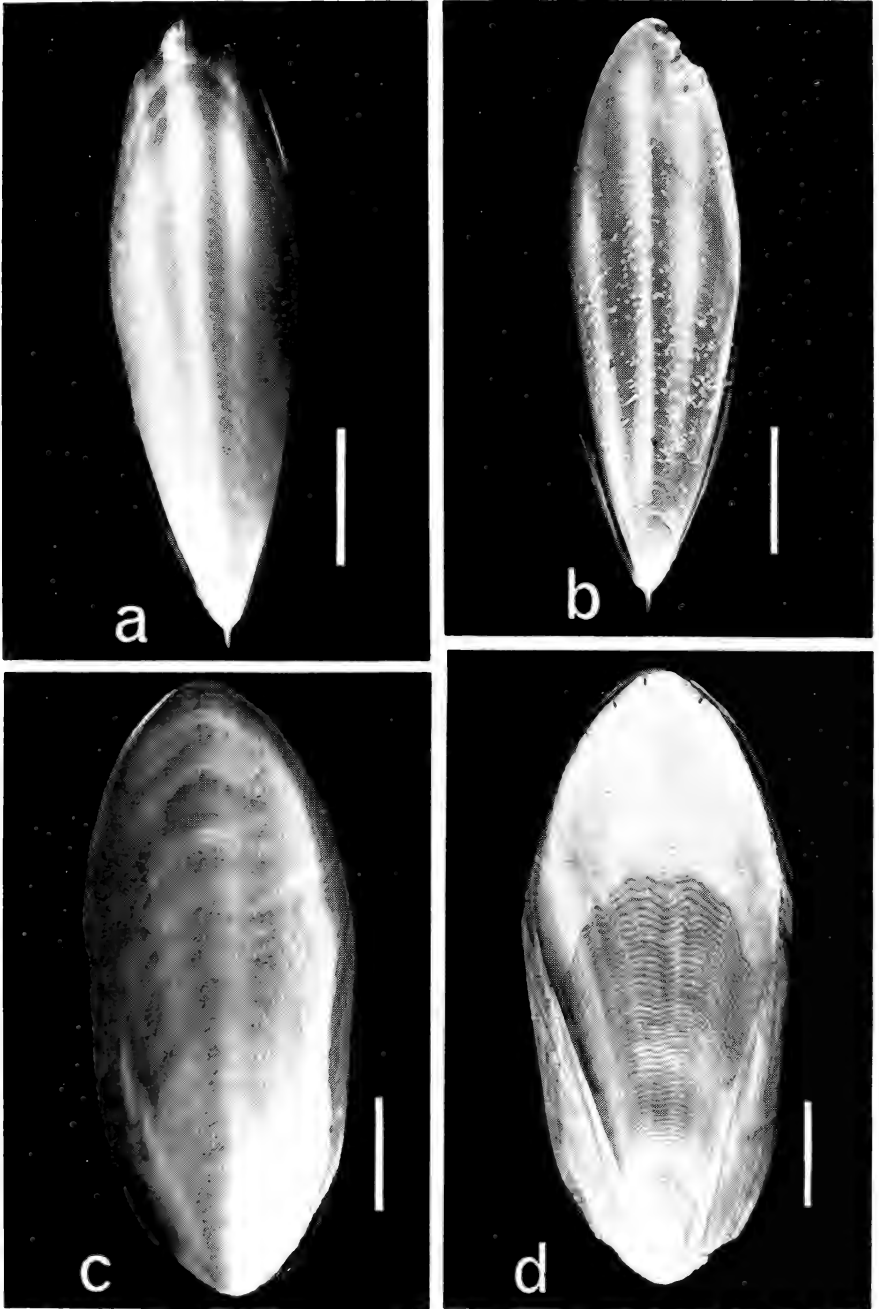
Sepia incerta Smith, N.M.970: a. Ventral view of shells described by Massy (1925: 219) as *S. incerta*.

Sepia incerta Smith, N.M.958: b. Ventral view of shells described by Massy (1925: 215) as *S. burnupi*.

Sepia burnupi Hoyle, A2147: c. Dorsal and d. ventral views of shell (anterior tip broken).
Scale = 10 mm.

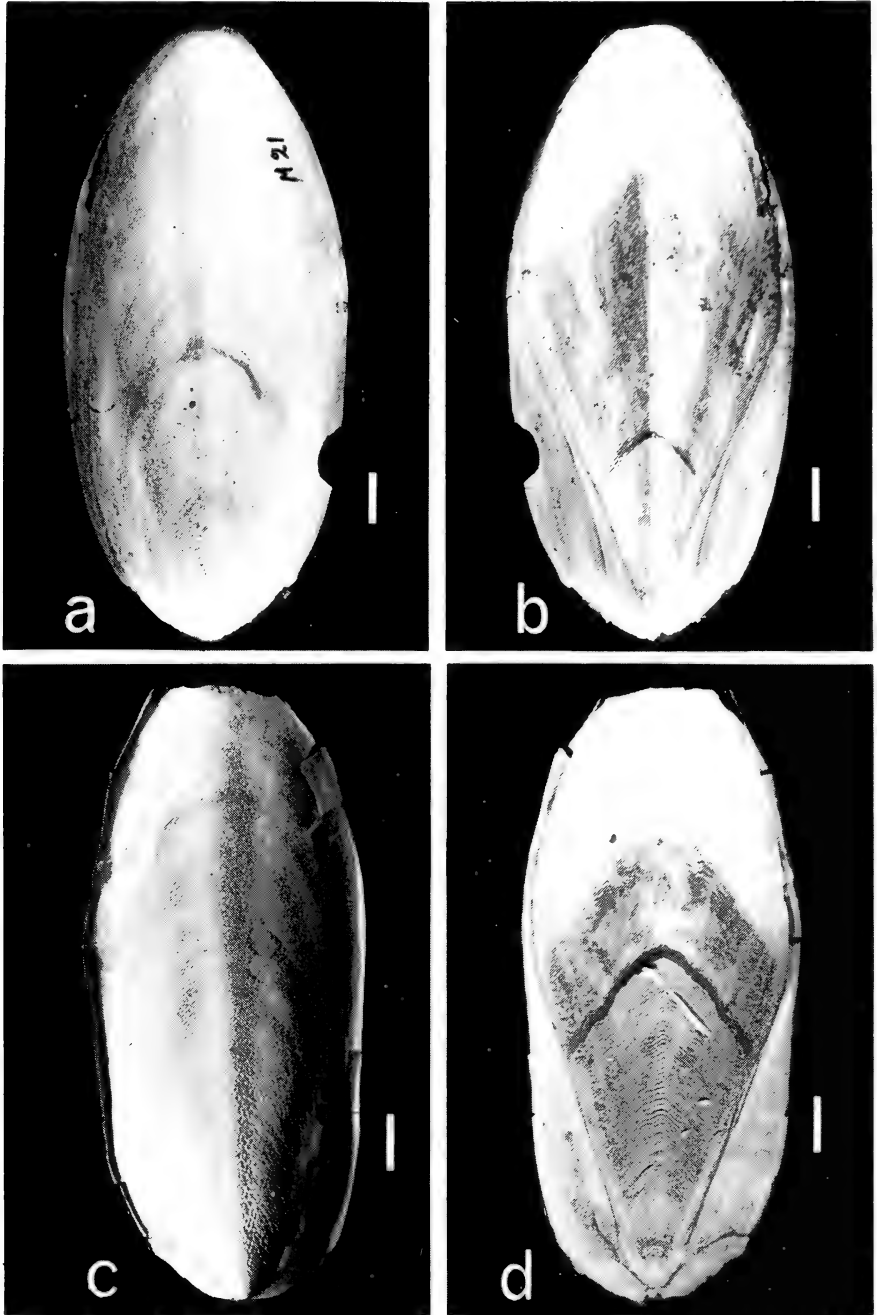


Sepia incerta Smith, from Punta Zavora: a. Dorsal and b. ventral views of shell.
Sepia tuberculata Lamarck, from Cape Agulhas: c. Dorsal and d. ventral views of shell with exceptionally long striated zone.
Scale = 10 mm.



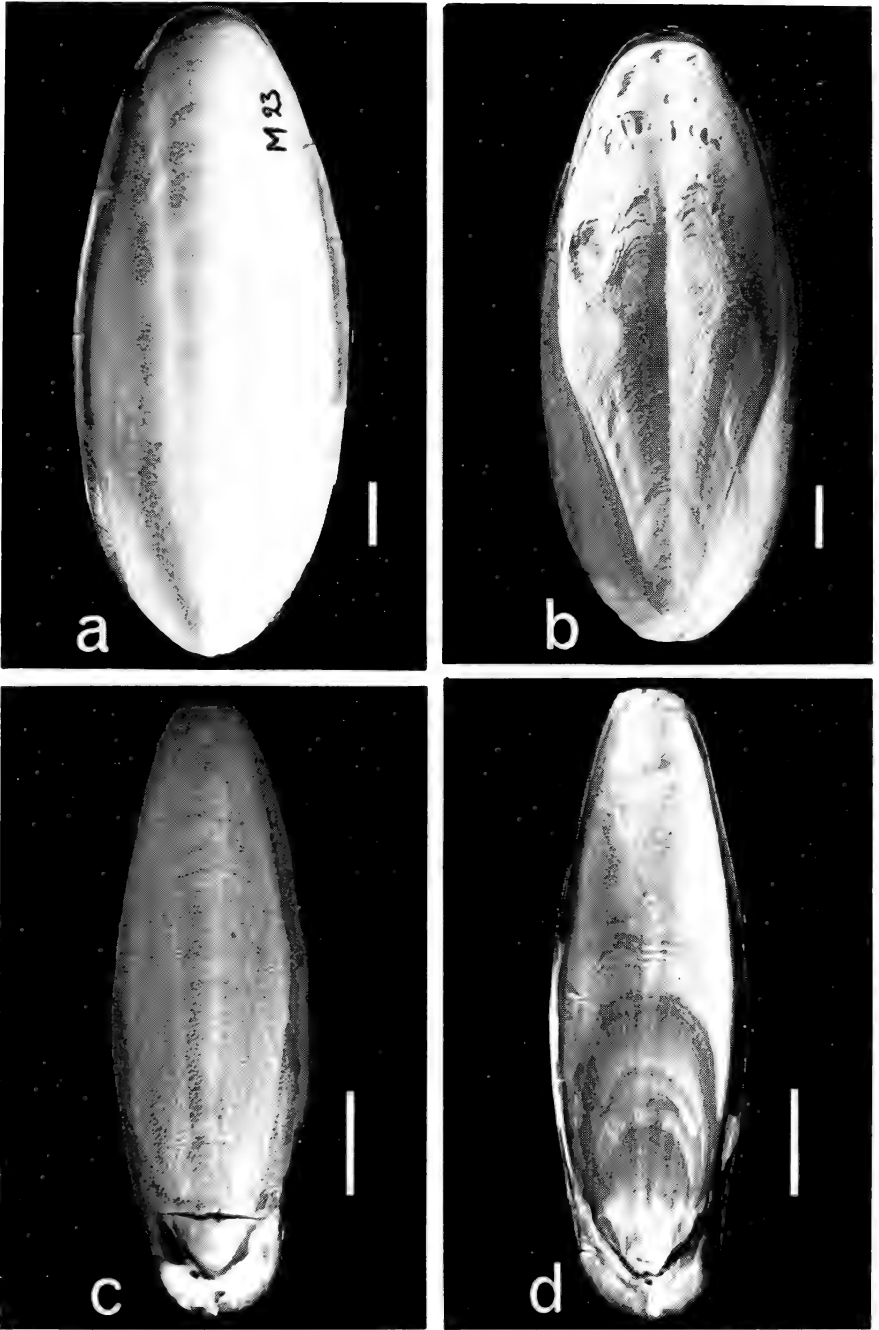
Sepia australis Quoy & Gaimard, from Still Bay: a. Dorsal and b. ventral views of shell.
Sepia tuberculata Lamarck, ♀, A30511: c. Dorsal and d. ventral views of shell with normal striated zone.

Scale = 10 mm.

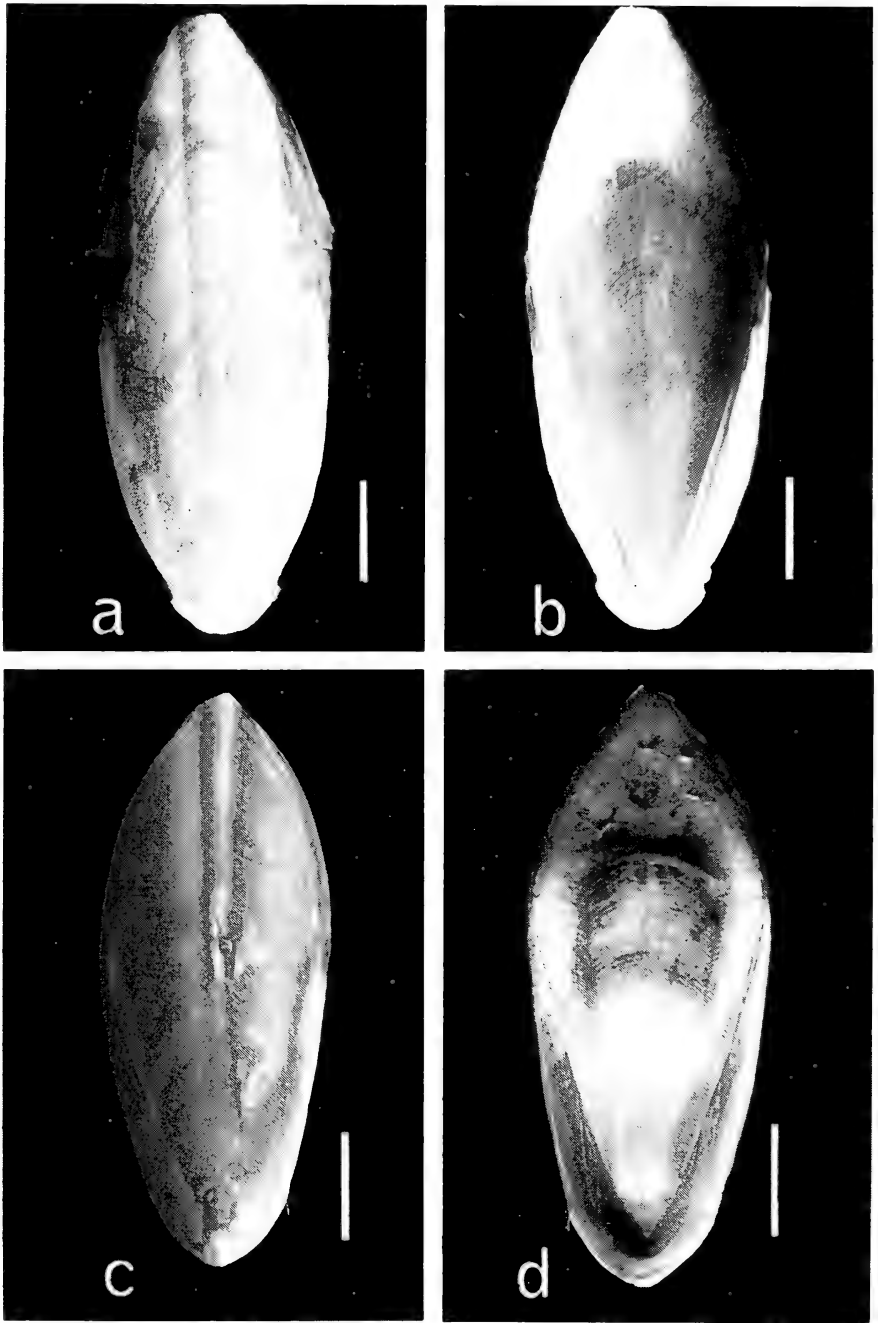


Sepia papillata Quoy & Gaimard, shell form A, from Milnerton beach: a. Dorsal and b. ventral views of shell.

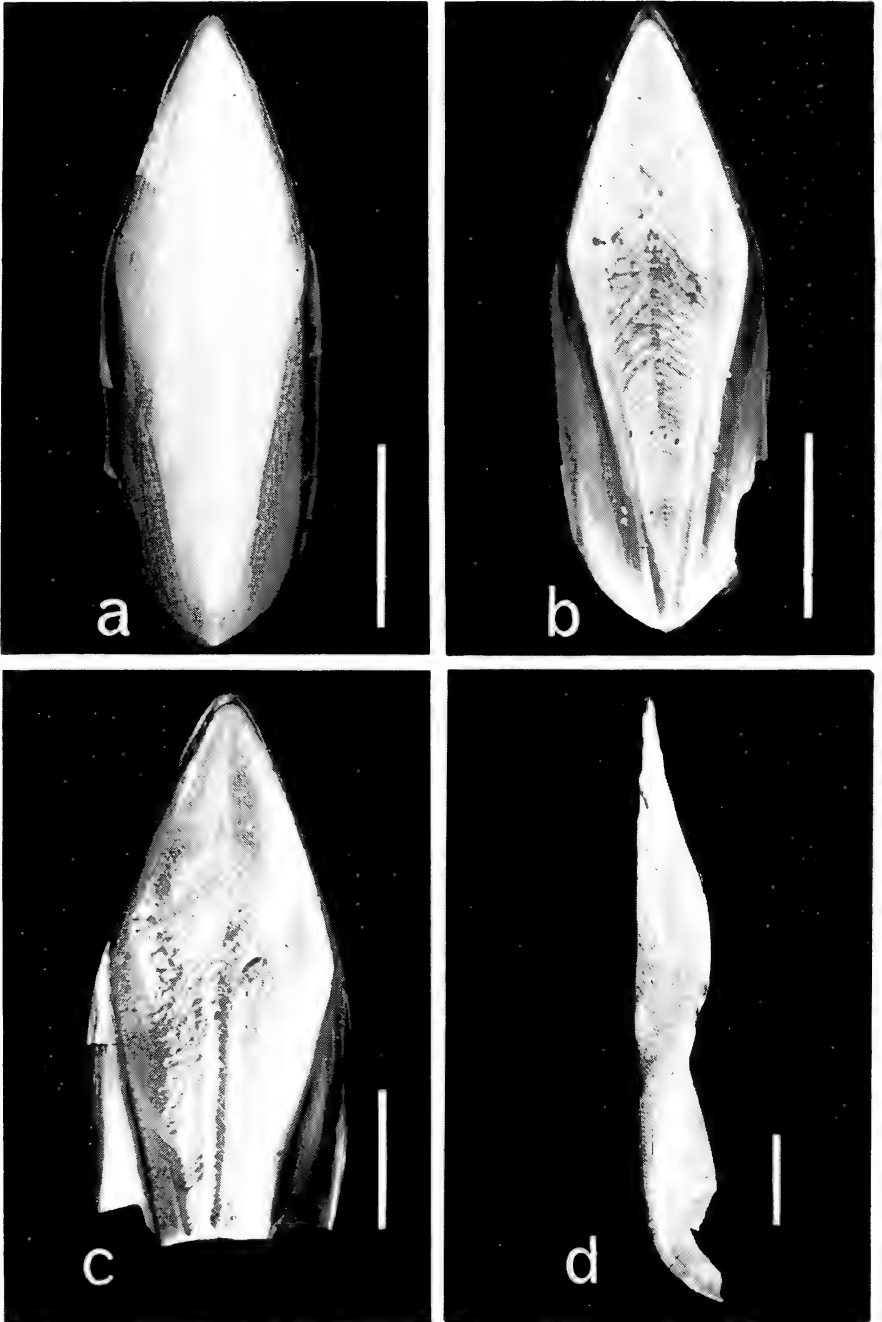
Sepia papillata Quoy & Gaimard, shell form B, ♂, A30120: c. Dorsal and d. ventral views of shell. Scale = 10 mm.



Sepia simoniana Thiele, from Still Bay: a. Dorsal and b. ventral views of shell.
Sepiella cyanea Robson, ♂, A6526: c. Dorsal and d. ventral views of shell.
Scale = 10 mm.



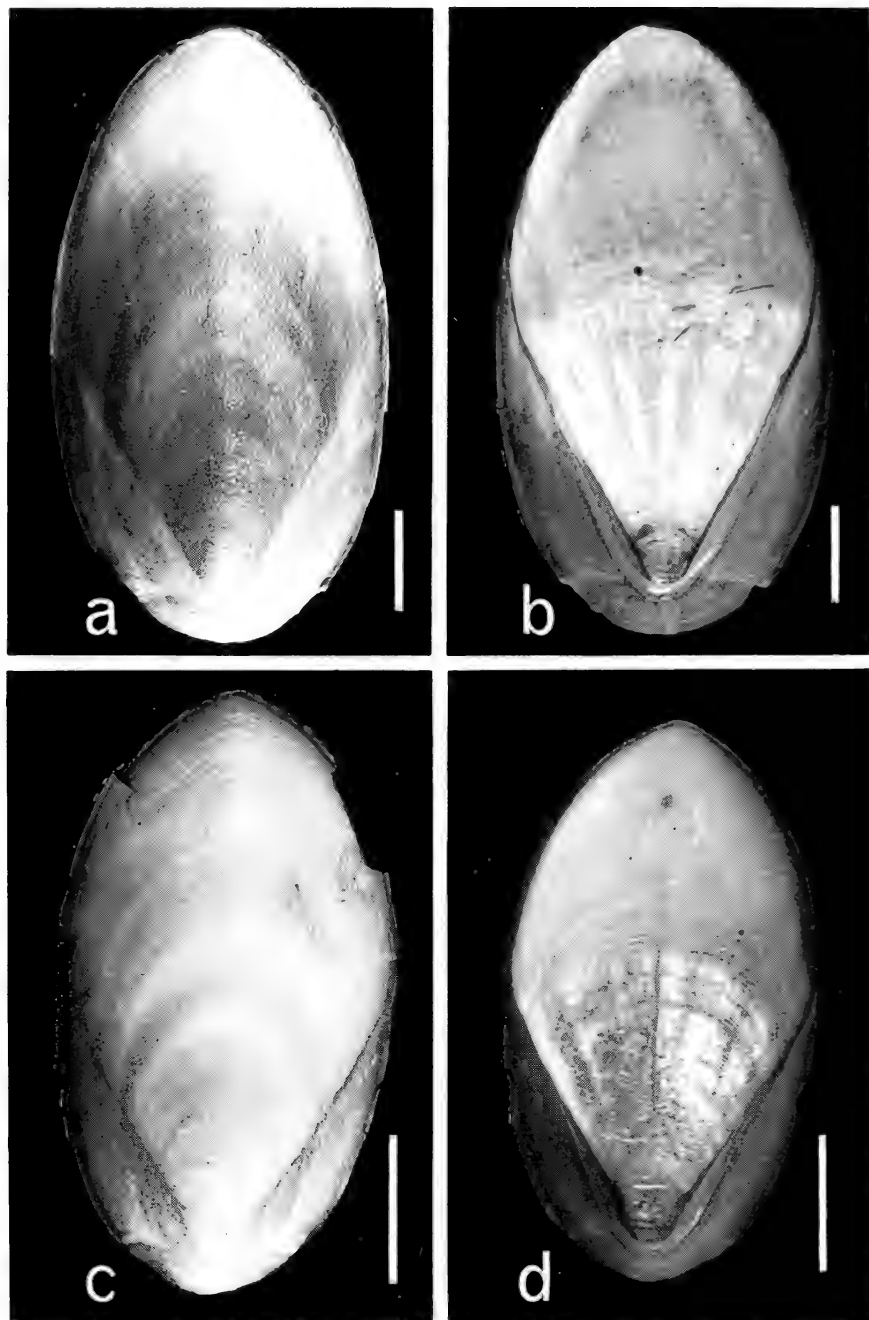
Sepia hieronis (Robson), ♂, A29728 (west coast): a. Dorsal and b. ventral views of shell.
Sepia hieronis (Robson), ♂, A31407 (east coast): c. Dorsal and d. ventral views of shell.
Scale = 10 mm.



Sepia insignis Smith, A31241: a. Dorsal and b. ventral views of shell. c. Ventral view of part of large shell from Bloubergstrand.

Sepia angulata f. sp.: d. Median view of half shell, cut longitudinally to show angle between striated zone and smooth zone.

Scale = 10 mm.



Sepia angulata n. sp., holotype, A31317: a. Dorsal and b. ventral views of shell.
Sepia angulata n. sp., paratype, A31320: c. Dorsal and d. ventral views of shell.
Scale = 10 mm.

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.

Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Examples (note capitalization and punctuation)

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

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

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

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269-270. Jena: Fischer. *Denkschr. med-naturw. Ges. Jena* **16**: 269-270.

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

Example

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

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DISCARD THE NAMES
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A NEW CLASSIFICATION OF THE THERAPSIDA

By
L. D. BOONSTRA

Cape Town Kaapstad

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L. D. BOONSTRA

South African Museum, Cape Town

(With 2 figures)

[MS. accepted 25 January 1972]

CONTENTS

	PAGE
Introduction	315
Diagnoses	318
Diagnoses of the higher taxa	322
Summary	334
References	334

INTRODUCTION

Since the discovery of certain Permian reptiles in Russia and South Africa in the early thirties of the 19th century showing some characters of a mammalian nature and their first descriptions by Kutorga in 1838 and Owen in 1844 numerous attempts have been made by various authors to fit them into the taxonomic system in such a way as to indicate in what manner these reptiles could be considered related and ancestral to the mammals.

I have found the historical study of the various classifications proposed by authors most interesting and illuminating and was tempted to publish a detailed historical review, but on second thoughts have decided that confining myself to the essentials of the ever increasing precision of the phylogenetic views would be more important and valuable and satisfying.

At the present time we know over 300 recorded genera of 'reptiles' which possess to varying degrees characters indicating a development in mosaic pattern in a general mammalian direction.

For this assemblage of 'reptiles' we have the name Therapsida coined by Broom in 1905.

In the present state of our knowledge this group as a whole appears to have evolved from captorhinomorph and sphenacodontid precursors.

The oldest known therapsids, from low down in the Permian, consist of an assemblage in which discrete lines of development are clearly evident.

For these lines of development we have the following denominations available:

1. Anomodontia (Owen 1859)
2. Dicynodontia (Owen 1860)

3. Cynodontia (Owen 1860)
4. Theriodontia (Owen 1876)
5. Dinocephalia (Seeley 1895)
6. Gorgonopsia (Seeley 1895)
7. Therocephalia (Broom 1903)
8. Scaloposauria (Boonstra 1953)
9. Phthinosuchia (Romer 1961)
10. Eotitanosuchia (Boonstra 1963)

There exists strong evidence that the Dinocephalia and Gorgonopsia evolved through the Eotitanosuchia from common sphenacodontid ancestors of the morphological habit such as that of the genus *Haptodus*. Taxonomically there may thus be some reason to coin a higher denomination to include the Eotitanosuchia, Gorgonopsia and Dinocephalia in order to indicate their consanguinity. Both these sublimes of development, each showing the development of certain mammalian characters, became extinct—the Dinocephalia at the end of the Middle Permian and the Gorgonopsia at the end of the Upper Permian.

The dinocephalian line shows certain stages of development. The most primitive stage is represented by a group of animals for which the name Eotitanosuchidae has been used by Tchudinov (1960).

Ascending directly from the Eotitanosuchidae is the group Brithopodidae (Efremov 1954). From the Brithopodidae two higher groups arose dichotomously, viz. the Anteosauridae (Boonstra 1954) and the Titanosuchidae (Broom 1903). From the Titanosuchidae three higher stages diverged, viz. the Tapinocephalidae (Owen 1876), the Styracocephalidae (Haughton 1929) and the Estemmenosuchidae (Tchudinov 1960).

The Gorgonopsia line shows the following stages of development represented by groups with the following denominations:

- Phthinosuchidae (Efremov 1954)
- Hipposauridae (Watson & Romer 1956)
- Gorgonopsidae (Lydekker 1890)
- Burnetiidae (Broom 1923)

The dicynodontian line arising from unknown but probably sphenacodont ancestors has as its oldest known representative the genus *Otsheria* from which I have proposed the group name Otsheriidae (Boonstra 1963). Diverging from this base there are the short-lived groups Venyukoviidae (Efremov 1940) and Galeopsidae (Broom 1912) and the longer lived but also sterile line of the Dicynodontia (Owen 1860) which split up into the Endothiodontidae (Lydekker 1890) and Dicynodontidae (Owen 1876) from which arose the Kistecephalidae (Seeley 1895), Lystrosauridae (Broom 1903) and the Kanmeyeriidae (Von Huene 1948).

The third line, first encountered in the Middle Permian is that of the Therocephalia (Broom 1903). Arising from as yet unknown but probably

sphenacodont ancestors they formed an important group of carnivores during *Tapinocephalus* zone times, when they had already developed diverging branches with the following denominations:

Pristerognathidae (Broom 1906)

Lycosuchidae (Broom 1910)

Alopecodontidae (Broom 1932)

This line, strongly developed in the Middle Permian, became extinct at the end of the Upper Permian with the last off-shoots represented by the Whit-siidae (Haughton 1918) and the Euchambersiidae (Broom 1931).

The last line, also beginning in the Middle Permian, with a few inadequately known forms, is that of the Scaloposauria (Boonstra 1953). This line may have arisen from the therocephalian line during the Lower Permian and is certainly closely related. Both the therocephalian and scaloposaurian lines apparently arose from some earlier sphenacodonts, but we have no certain indication of this as we have in the first line where a *Haptodus*-like form is indicated.

Commencing in the *Cistecephalus* zone and continuing to the top of the *Cynognathus* zone we find the Bauriamorpha (Watson 1917) which are generally considered to have arisen from the earlier ictidosuchian Scaloposauria.

Also commencing in the *Cistecephalus* zone and continuing into the Red Beds we have a final branch—the Cynodontia (Owen 1860) culminating in the near-mammals—the Tritylodontia (Simpson 1925). If the Cynodontia are not a parallel branch to the Scaloposauria, both to be derived from primitive therocephalians, then one must postulate a direct and separate derivation from some earlier sphenacodont.

From the foregoing it is clear that I think that we have three main branches of Therapsida.

An older view was that there were two main branches which have been labelled:

Anomodontia (Owen 1859) and

Theriodontia (Owen 1860)

Anomodontia

Although Owen initially in 1859–60 clearly intended the terms Anomodontia and Dicynodontia to have as type, *Dicynodon*, he later included some theriodonts.

Since then the term Anomodontia has had a chequered career, being used by authors to include a variety of other forms manifestly un-*Dicynodon*-like. The term Anomodontia being thus misused it would be pragmatic to drop it altogether and rather retain the name Dicynodontia solely for those forms showing a *Dicynodon*-like structure as originally intended by Owen.

Theriodontia

In 1860 Owen coined the term Cynodontia with *Galesaurus* as the type and included it as a 'family' of his Anomodontia. In 1876 Owen introduced the

term Theriodontia for the same genera included in his former Cynodontia, apparently to supersede the latter name. As Owen included genera now considered as Gorgonopsia and others as Cynodontia in his Theriodontia, and Watson recently also the Titanosuchia, which three groups are now known to lie on different lines of development, the term Theriodontia unites incompatible groups and should be dropped.

Deciding to discard the names Anomodontia and Theriodontia because they each bracket together lines of development which, as I have indicated, are not nearly related, it appears necessary to coin three new names for the three main branches of the Therapsida, and to include as subdivisions of each of these three new denominations those groups which are in fact closely related.

For the first of these branches I propose the name Alphatherapsida to include the subdivisions Eotitanosuchia, Dinocephalia and Gorgonopsia.

For the second branch—Betatherapsida—to include only those forms related to *Dicynodon*.

For the third branch the name—Gammatherapsida—to include those fertile groups directly related and finally leading to the first mammals, viz. Therocephalia, Scaloposauria and Cynodontia.

DIAGNOSES

ALPHATHERAPSIDA

Dentition primitively carnivorous with pointed incisors, canines and postcanines adapted for snatching and tearing out flesh without cutting or chewing. Short-lived side branches with dentition transformed to herbivorous talon and heel teeth adapted for piercing and crushing without cutting and chewing.

Choanae anteriorly situated with air passage without bony ventral floor to partition it off during feeding.

The temporalis primitively originating from under surface of skull roof and inserted in the adductor fossa and on the upper edge of the dentary.

In the gorgonopsian branch the insertion was improved by the precocious development of a coronoid process on the dentary. Here we thus have a primitive origin coupled with an advanced insertion.

In the dinocephalian branch the origin of the temporalis shifts away from the under surface of the skull roof to the lateral surface of the intertemporal bones, but no coronoid process is developed. Here we thus have an advanced origin coupled with a primitive insertion. The later pachyostosis bedevils this aspect. The postdentary bones of the mandible are persistently well developed due to their retaining the primitive insertion of the adductors which exerted a greater horizontal than vertical pull, with the joint a simple hinge. But in the herbivorous forms a fore-and-aft motion allows for a crushing bite.

Concomitant with the primitive carnivorous jaw-mechanism the locomotory apparatus is of a crawling habit with sprawling limbs and little upraising of the body and only slightly reduced digital segments.

In the braincase the sphenoidal complex is very well ossified, but the prootic is feebly ossified, thus leaving a wide gap in the lateral wall with a loose standing unwidened epipterygoid. In the pachyostotic *Dinocephalia* the gap in the lateral wall is greatly reduced, but the narrow epipterygoid remains uninvolved.

In the *Alphatherapsida* the gorgonopsian branch has its characteristic structures developed early and these are retained, with only insignificant variations, throughout its span of life, notwithstanding that they survived to the end of the Upper Permian.

The dinocephalian branch commencing as a primitive carnivorous group early in its history, develops herbivorous twigs but the whole branch is short lived and unprogressive and is soon cut short by the pathological pachyostosis.

BETATHERAPSIDA

Dentition herbivorous, primitively with a series of marginal teeth, later with marginal teeth in part or wholly replaced by horny sheaths. Choanae shifted moderately posteriorly, with part of air passage with bony partition, separating it from buccal cavity, formed by plates of the premaxilla.

The jaw adductors highly specialized, particularly in their origins, with concomitant great lengthening of the temporal fossa and the development of a unique triradiate squamosal, and everted zygoma accompanied by a lengthened sliding articular facet allowing fore-and-aft sectorial movement of the jaw when feeding, insertions tending to shift on to the outer face of the dentary.

The postdentary bones unreduced.

Feeding on upland plants (except *lytrosaurs* and *Kistecephalidae*) the locomotor apparatus is adapted for a more upright walking gait, with an acromion process, greatly enlarged anterior iliac process, obturator foramen and reduced digital segments. In the braincase the sphenoidal complex is very well developed and situated far anteriorly; the prootic short, thus leaving a very long gap in the lateral wall, with a loose standing slender epipterygoid.

Notwithstanding its long span of life this group remained stationary on its early achieved developmental niveau. What variations arose were quite insignificant, initiating nothing phylogenetically fertile.

GAMMATHERAPSIDA

Dentition primitively carnivorous, but variations commence quite early, viz. reduction of postcanines (in *lycosuchids* and *whaitsiids*); development of additional precanines (in *alopocodontids* and *Scaloposauria*); tricuspid sectorial postcanines arose (in some *Scaloposauria* and some *Cynodontia*); grinding surfaces developed on postcanines (in some *Scaloposauria* and *Cynodontia*); differentiation into 'premolars' and 'molars' (in *Cynodontia*). Thus the primitive snatching and tearing dentition became adapted to cutting and grinding with a process of chewing.

Primitively the choanae were anteriorly situated, but concomitant with

the developing of a chewing habit the choanae shifted backwards with the development of a secondary bony palate partitioning off the air passage from the buccal cavity during the process of mastication.

The temporalis originated from the lateral face of the intertemporal bones and inserted on the coronoid process.

Primitively, where the posterior mandibular bones are still well developed, the superficial masseter inserted on the reflected lamina of the angular and the internal pterygoid wrapped round the ventral edge of the angular. But in the cynodonts part of the superficial masseter inserted on the postero-ventral corner of the dentary and the internal pterygoid also partly moved on to the inner face of the corner of the dentary, which resulted in a reduction of the function and thus the size of the angular.

With the pull of the jaw muscles having strong horizontal components in the early forms the posterior mandibular bones remained strong to withstand the strain on the jaw joint. But with the jaw-closing muscles developing less horizontal and greater vertical pull the strain on the jaw joint decreased with a resulting decrease in size of the posterior mandibular bones.

With the increased strain on the dentary, due to its capturing some of the muscle insertions from the posterior bones, it developed a very large coronoid process and a prominent angle and, extending further and further posteriorly, in the final stages made contact with the squamosal to form a double jaw joint.

In the locomotor apparatus a more upright walking gait is developed with a reduction of the phalanges to 2,3,3,3,3 in all but the early cynodonts where the 4th and 5th digits have 4 segments.

Primitively with pubic foramen, advanced with obturator foramen. Primitively without, advanced forms with, infra-spinatus fossa.

In the braincase the sphenoidal complex is primitively not well ossified, but moderately so in some advanced forms. Primitively the prootic is feebly developed, but in advanced forms extends anteriorly to meet the epipterygoid.

Primitively the epipterygoid is usually slender but broadened in the primitive lycosuchids. In some advanced forms it is greatly broadened and meeting the prootic enters into the sidewall of the braincase (cynodonts).

Postorbital bar primitively well developed as also in some advanced forms but in some others it becomes weak and even incomplete.

Occipital condyle primitively single (tripartite), in advanced forms double and formed by the exoccipitals. Primitively with suborbital fenestra, but sometimes reduced, large in Scaloposauria, absent in Cynodontia.

In contrast to the Alphatherapsida and Betatherapsida the Gamma-therapsida were a very versatile group in which developments, besides leading into a number of early as well as later blind alleys, produced very progressive parallel branches all in a general mammalian direction, with the procynosuchid-galesaurid-tritylodont branch most probably including the actual ancestors of the first mammals.

SYNAPSIDA

The term Synapsida (Osborn 1903) has by all recent students been used with the taxonomic rank of Subclass to include those vertebrates popularly known as the mammal-like reptiles. These animals possess a mosaic of characters some of which pertain to the Class Mammalia and others to the Class Reptilia.

They are thus neither true mammals nor true reptiles and do thus not fit into the Class Mammalia or into the Class Reptilia.

I thus support those recent authors who have proposed that the name Synapsida should have the rank of a separate Class.

The Class Synapsida would then include the two Subclasses Pelycosauria and Therapsida.

For the Subclass Therapsida I propose the following classification:

Subclass	Superorder	Order	Suborder	Family	
Therapsida	Alphatherapsida	Eotitanosuchia		Eotitanosuchidae Phthinosuchidae Rubidginidae	
			Dinocephalia	Brithopia	Brithopodidae Anteosauridae
				Titanosuchia	Titanosuchidae Tapinocephalidae Styracocephalidae Estemmenosuchidae
			Gorgonopsia		Hipposauridae Gorgonopsidae Burnetiidae
		Betatherapsida	Venyukoviidea		Otsheriidae Venyukoviidae ? Dromasauridae
				Dicynodontia	
	Gammatherapsida	Therocephalia		Pristerognathidae Lycosuchidae Whaitsiidae	
			Scaloposauria	Ictidosuchia	Alopecodontidae Ictidosuchidae Scaloposauridae

Subclass	Superorder	Order	Suborder	Family
Therapsida (continued)	Gammatherapsida (continued)	Scaloposauria (continued)	Bauriamorpha	Bauriidae Ericiolacertidae
		Cynodontia	Procynosuchia	Procynosuchidae Galesauridae ? Silphedestidae
			Cynognathia	Cynognathidae Diademodontidae Chiniquodontidae Traversodontidae
			Tritylodontia	Tritylodontidae Trithelodontidae Diarthrognathidae

DIAGNOSES OF THE HIGHER THERAPSID TAXA

SUBCLASS THERAPSIDA

Advanced synapsids of the Permian and Triassic. There is strong evidence that one therapsid superorder, at least, was directly derived from sphenacodont pelycosaur, but the derivation of the other two superorders from sphenacodonts, although very probable, is less certain. The therapsids include the direct ancestors of the mammals.

Further advanced than the pelycosaur in that: the pterygo-basiscranial joint is no longer freely movable; a longitudinal girder is developed, the interpterygoid vacuity is never widely open but partly or completely closed; the squamosal is outflaring with a posterior face; there is no supratemporal; the lacrimal never reaches the nostril and the maxilla is deep.

At the beginning of the Middle Permian the therapsids had already developed in diverse directions each showing a lesser or greater acquisition of certain mammalian characters.

Of the three main branches one became successfully adapted and dominated the scene during the Middle and Upper Permian, comprising herbivores and their predatory carnivores, but proved sterile; a second branch of herbivores became adapted to their special niche, waxed exceedingly and very successfully maintained themselves to near the end of the Triassic when they died out without issue; the third branch, already well established at the beginning of the Middle Permian, firstly as predators and later developing herbivorous side branches, developed more and more in the mammalian direction, with one or more twigs producing the first mammals late in the Triassic.

SUPERORDER ALPHATHERAPSIDA

Permian therapsids a stage further developed than the early Permian sphenacodonts from which they arose, not leading to mammals.

The intertemporal skull table is primitively broad and flat, with the posterior flange of the postorbital lying horizontally in the dorsal skull roof (but modified in some *Dinocephalia*) and reaching the squamosal; the postorbital bar is always complete.

The lower jaw primitively without a prominent coronoid process (but present in *Gorgonopsia*), the dentary always strong, but without a definite postero-ventral angle; the postdentary bones always well developed.

The quadrate is primitively robust with the quadrate ramus of the pterygoid strong (except in *Gorgonopsia*).

Primitively with simple conical incisors, canine and postcanines (but modified in some *Dinocephalia*) and palatal teeth on the pterygoid and palatine.

There is no secondary palate and no suborbital fenestra.

The epipterygoid is slender and does not enter the sidewall of the braincase; the prootic is weakly developed with a free anterior edge; the sphenoidal complex is well ossified.

The postfrontal is well developed; the dorsal premaxillary process is long (but short in *Gorgonopsia*).

A pineal foramen is always present.

The occipital condyle is single.

ORDER EOTITANOSUCHIA

The most primitive therapsids descending from sphenacodonts, with all the primitive characters listed in the diagnosis of the superorder Alphatherapsida of which they are the morphological ancestors.

Family **Eotitanosuchidae**

Eotitanosuchidae with the squamosal not extending into the intertemporal skull roof and the primary palate closed.

Family **Phthinosuchidae**

Eotitanosuchians with the squamosal developing a lappet entering the intertemporal skull roof and the primary palate with a median cleft.

Family **Rubidginidae**

Younger relict eotitanosuchians with a short series of serrated postcanines and a small temporal fenestra.

ORDER GORGONOPSIA

Middle and Upper Permian alphatherapsids descending from eotitanosuchians, which have developed a prominent coronoid process; the quadrate posteriorly situated is reduced in size and the quadrate ramus of the pterygoid is lightly built; the dorsal process of the premaxillary is shortened; a preparietal is developed. Extinct at the end of the Permian leaving no descendants.

Family **Hipposauridae**

Primitive gorgonopsians with a very broad intertemporal skull roof; small temporal fenestra, deep suspensorium, fairly long postcanine series, with the dorsal skull contour strongly curved.

Family **Gorgonopsidae**

Intertemporal skull roof somewhat reduced in both earlier and later forms, but in the latter sometimes secondarily greatly widened; large temporal fenestra, fairly shallow suspensorium, postcanine series reduced, gape of jaws in some Upper Permian forms enormous with very strong canines.

Family **Burnetiidae**

Later aberrant gorgonopsians with very wide intertemporal region, reduced temporal fenestra, dentition reduced with weak teeth; with pachyostotic thickening of roofbones of skull in the form of bosses and ridges.

ORDER DINOCEPHALIA

Early alphatherapsids derivable from an eotitanosuchian niveau and die out without issue at the end of the Middle Permian; with basically primitive structure obscured in some branches by pachyostosis and some abortive specializations.

Width of intertemporal skull table reduced, sometimes greatly so, but secondarily greatly widened where the pachyostosis is great, temporal fenestra moderate to large except where secondarily reduced by the pachyostosis.

No coronoid process on the dentary; primitively with a carnivorous dentition of simple conical teeth, later specialized carnivorous with an early development of a herbivorous branch and intermeshing of some or all the upper and lower batteries.

The quadrate robust, as also the quadrate ramus of the pterygoid; quadrate shifting anteriorly.

Dorsal process of the premaxillary long to very long.

SUBORDER BRITHOPIA

Primitive dinocephalians linked to the eotitanosuchians and morphologically ancestral to the other dinocephalian groups.

The intertemporal skull roof reduced in width with the posterior process of the postorbital lying at a slant down from the horizontal; the temporal fenestra large.

The dentition carnivorous, with the incisors tending to lengthen and the postcanines becoming reduced; the lower and upper incisors and canines intermesh.

Palatal teeth primitively well developed, later practically confined to the palatine.

Quadratojugal never a surface bone.

With no or little general pachyostosis.

Dorsal process of the premaxillary moderately long.

Family **Brithopodidae**

Primitive brithopians with a fairly long postcanine series; incisors not greatly lengthened; postfrontal not bulbously swollen and no other pachyostosis; quadrate with little anterior shift; moderate outflaring of squamosals. Palatal teeth well developed.

Family **Anteosauridae**

A stage further advanced than the brithopids. Postcanine series reduced, incisors greatly lengthened. Postfrontals becoming greatly bulbously swollen and the skull roof moderately pachyostosed. Strong outflaring of squamosals, especially posteriorly.

Palatal teeth reduced, practically confined to the palatine.

SUBORDER TITANOSUCHIA

Advanced dinocephalians derived from a brithopid niveau.

The intertemporal region reduced in width, sometimes to a narrow sagittal crest, but secondarily greatly to enormously widened where the pachyostosis is great; the temporal fenestra large to very large but secondarily greatly reduced.

The dentition is herbivorous, initially with a large conical canine and with only the incisors developing a talon and heel; later the canine is not distinguishable as such and all the marginal teeth develop a talon and heel; the postcanine series always very long. Palatal teeth practically absent.

Quadratojugal sometimes a surface bone.

The pachyostosis is moderate to enormous.

Family **Titanosuchidae**

Primitive titanosuchians developed from a brithopid level and indicating the morphological level from which the tapinocephalids arose.

The intertemporal width reduced with a low thick sagittal crest, posterior process of the postorbital reduced, temporal fenestra fairly large, but squamosals not outflaring.

Strong incisors with piercing talon and crushing heel and large conical canines, a long series of spatulate postcanines, which do not intermesh as do the incisors and canines of the two jaws. No palatal teeth.

Moderate pachyostosis.

Family **Tapinocephalidae**

Specialized titanosuchians derived from a titanosuchid level.

The intertemporal region very variable, mostly of moderate width, sometimes with a sharp sagittal crest, in one subfamily enormously broadened as a result of the excessive pachyostosis; temporal fenestra large to greatly reduced.

All the marginal teeth with talon and heel, upper and lower battery intermeshing.

Pachyostosis light to great.

Family **Styracocephalidae**

Middle Permian aberrant titanosuchians. Intertemporal region very

broad, but temporal fossa roomy with posteriorly flaring squamosal; pachyostosis in the form of 'horns' and bosses.

Weak conical incisors and canine and a long series of postcanines; palatal teeth very well developed, even on the vomer.

Family **Estemmenosuchidae**

The 'horns' situated on the frontals, and directed dorsally, whereas in the Styraucocephalidae the 'horns' are formed by the tabular and directed posteriorly. Otherwise with features very similar to those of the Styraucocephalidae.

SUPERORDER BETATHERAPSIDA

Permian and Triassic therapsids on a developmental niveau far above that of the early Permian sphenacodonts, not leading to mammals.

The intertemporal skull table is primitively reduced in width, but flat, becoming narrow and later developing a sagittal crest, but secondarily widened in the Kistecephalidae; the posterior process of the postorbital inclined downwards from the horizontal and reaching the squamosal, later reduced; the postorbital bar is always complete.

The lower jaw without a coronoid process of the dentary and without a coronoid bone; the dentary always strong without a postero-ventral angle; the postdentary bones well developed. The quadrate is robust lying low down on a pedicel of the uniquely triradiate squamosal, and the quadrate ramus of the pterygoid is weak. Primitively with a modified set of marginal teeth in both jaws, which very early are radically reduced and sometimes wholly lost and replaced by horny sheaths; there are no palatal teeth.

The premaxillaries, primitively paired but later fused, develop plates to form a unique type of secondary palate and the choanae are shifted posteriorly; primitively the maxilla and palatine have no inward palatal growth but later extend palatally but never meet below the air passage. The epipterygoid is slender and does not enter the sidewall of the braincase; the prootic is weakly developed with a free anterior edge; the sphenoidal complex is well ossified and lies far anteriorly.

The postfrontal is primitively well developed but reduced later; the dorsal premaxillary processes are primitively paired and long, later fused and short.

A pineal foramen present; preparietal primitively absent, later present. The occipital condyle is single. There is a fenestra in the mandible between the dentary and angular.

ORDER VENYUKOVIOIDEA

Primitive betatherapsids not directly linked to the sphenacodonts, leading to the higher Dicynodontia.

The width of the intertemporal region is reduced, without sagittal crest and the temporal fenestra is short, the jugal has a large entry into the zygoma which is not strongly everted.

The dentition consists of a well-developed series of bluntly conical marginal teeth on the premaxilla, maxilla and dentary.

No inward growth of palatine and maxilla and the posterior part of the palate is thus primitive, except that the lateral ramus of the pterygoid is somewhat or much reduced.

The premaxillaries are not fused and have a long dorsal process; the septomaxilla is largely superficial, the postfrontal is well developed and there is no preparietal.

Family **Otsheriidae**

The incisors are enlarged, the choana is short, the palatine does not meet the premaxilla; the lateral ramus of the pterygoid is still prominent, the lacrimal is short and there is no pachyostosis.

Family **Venyukoviidae**

The incisors are enlarged, the choana is long; the palatine meets the premaxilla; the lateral ramus of the pterygoid is much reduced; the lacrimal is long; there is some pachyostosis.

Family **Dromasauridae**

The dentition consists of a series of isodont marginal teeth or the jaws are edentulous; the temporal fenestra is very short and deep.

ORDER DICYNODONTIA

Advanced betatherapsids morphologically derivable from *Otsheria*; a long-lived order, rich in species varying in minor characters with a single main theme and phylogenetically sterile.

The intertemporal region reduced in width, sometimes very much so, but is secondarily widened in one aberrant family; the sagittal crest feeble to very high or wholly absent. The temporal fenestra is very long and the jugal is practically ousted from the zygoma by the squamosal which is uniquely everted.

The marginal teeth are greatly modified, there are never any incisors; an upper conical canine present or absent; postcanines present or absent and when present shifted medially and variously disposed.

Palatal flanges of the palatine and maxilla tending to grow inwards to form a variable open trough for the air passage; the lateral ramus of the pterygoid is lost.

The premaxillaries are fused and the dorsal process is short; the septomaxilla tending to shift interiorally; the postfrontal is primitively present but is lost in later forms; a preparietal is developed.

Family **Endothiodontidae**

With postcanine teeth, number and disposition very variable, canines present or absent, with a postfrontal.

Family **Dicynodontidae**

Without postcanine teeth, canines present or absent, the postfrontal is frequently absent.

Family **Kistecephalidae**

The intertemporal region is secondarily greatly widened, without sagittal crest, edentulous, without canines, without pre- and postfrontals and pre-parietal.

Family **Lystrosauridae**

Without postcanines and canines usually present, postfrontal present, nares shifted posteriorly and premaxilla lengthened.

Family **Kannemeyeriidae**

Very high sagittal crest; depression leading into pineal foramen.

SUPERORDER GAMMATHERAPSIDA

Permian and Triassic therapsids probably derived from Early Permian sphenacodonts and including the immediate ancestors of the mammals.

The intertemporal skull table narrow, usually with a sagittal crest, but secondarily widened in one late family; the postorbital is reduced and never reaches the squamosal; the postorbital bar primitively and usually complete, but incomplete and even wholly absent in some advanced forms.

The dentary primitively and usually with a prominent coronoid process, strong and finally greatly enlarged with a strong postero-ventral angle and making contact with the squamosal; the postdentary bones primitively well developed but greatly reduced in some advanced groups.

The quadrate small, with weak to incomplete quadrate ramus of the pterygoid.

Primitively with carnivorous dentition of simple conical teeth, later very variable, often with accessory cusps in the postcanines and in some advanced forms with highly elaborated crowns of a mammalian nature.

Primitively without secondary palate, in later groups incipient in various ways, to incomplete, and finally fully developed in mammalian fashion.

The epipterygoid is primitively slender and remains so in many forms, but is widened in some early forms and in advanced forms very broad and incorporated into the sidewall of the braincase; the prootic is primitively weakly developed, but later growing forwards meets the epipterygoid (alisphenoid) suturally; the sphenoidal complex is usually not well ossified.

The postfrontal small or absent.

The occipital condyle single in earlier forms, later becomes notched and finally with double condyles formed by the exoccipitals.

ORDER THEROCEPHALIA

Middle to Upper Permian gammatherapsids; initially primitive but with a wide gap between them and their sphenacodont precursors; with a degenerate family in the Upper Permian; relation to higher gammatherapsids is uncertain.

The intertemporal region is narrow with a reduced postorbital; the postorbital bar always complete; pineal foramen always present; dentary with a well-developed coronoid process and the postdentary bones well developed; no prominent postero-ventral angle to dentary.

Primitively without secondary palate but aberrantly incipient in the Upper Permian family.

Epipterygoid slender or widened but never incorporated in the sidewall of the braincase.

Dentition primitively carnivorous with a long postcanine series, later greatly reduced to lost, always uncusped. Postfrontal small or absent, suborbital fenestra large in earlier forms but reduced to absent in later forms.

The occipital condyle is always single.

Family **Pristerognathidae**

Middle Permian therocephalians with a well-developed carnivorous dentition with a single canine; no secondary palate, epipterygoid slender, postfrontal small, suborbital fenestra large.

Family **Lycosuchidae**

Middle Permian therocephalians with a well-developed carnivorous dentition, with double canines; no secondary palate, epipterygoid widened; postfrontal small, suborbital fenestra large.

Family **Whaitsiidae** (including **Lycedeopsidae** and **Euchambersiidae** as subfamilies)

Upper Permian therocephalians with reduced dentition, postcanines feeble, few or wholly absent, lower incisors sometimes absent, aberrant development of an incipient secondary palate, epipterygoid widened, suborbital fenestra large to small or absent, dentary scimitar-shaped with postdentary bones not robust.

ORDER SCALOPOSAURIA

Middle Permian to Lower Triassic gammatherapsids, probably independently derived from sphenacodonts with a considerable gap; fairly primitive in the Middle Permian, but advanced in the Upper Permian and Lower Triassic; relations to cynodonts uncertain.

The intertemporal region is usually narrow with a sagittal crest, but widened in one family with loss of crest; the postorbital bar is slender and complete or incomplete; the postorbital is sometimes greatly reduced or even absent; the jugal spur of the postorbital bar is usually present but absent in a few forms; the pineal foramen is sometimes absent.

The coronoid process of the dentary is strong, feeble or absent; there is no prominent postero-ventral angle to the dentary; the postdentary bones are well developed or weakened. A secondary palate is primitively absent, later incipient to well developed. The epipterygoid is mostly slender but sometimes widened and partially included in the sidewall of the braincase in one form.

A prominent canine is usually retained but sometimes not recognizable as such, accessory small canines are usually present, maxillary teeth usually numerous and the postcanines variable, being simple, cusped or with transversely widened crowns.

The suborbital fenestrae are always well developed, the postfrontal is reduced or absent.

The occipital condyle is initially single but later sometimes incipiently double.

SUBORDER ICTIDOSUCHIA

Mostly Permian scaloposaurians just extending into the Triassic; the intertemporal region is usually narrow but later widened in one family, the postdentary bones are weakened and the dentary lightly built; the secondary palate is primitively absent, sometimes incipient but never complete, the epipterygoid is slender but in one case partially enters the sidewall of the braincase.

Family **Alopecodontidae**

Primitive Middle Permian ictidosuchians close to the contemporary therocephalians.

The intertemporal region is narrow with a sagittal crest; the postorbital bar is complete, the coronoid process is strong, the dentary robust and the postdentary bones well developed; there is no secondary palate.

Dentition carnivorous, always with a prominent canine and two small accessories, the postcanines are simple conical teeth, the postfrontal is small and the occipital condyle single.

Family **Ictidosuchidae**

Upper Permian ictidosuchians linked to the alopecodontids.

The intertemporal region is narrow, usually with a sagittal crest and a pineal foramen present; primitively with a complete postorbital bar, but later incomplete; the coronoid process is prominent, the secondary palate absent, incipient to weakly developed; with an enlarged canine behind smaller accessories and the postcanines simple conical teeth, a single occipital condyle.

Family **Scaloposauridae**

Permian to Lower Triassic ictidosuchians.

Primitively with a narrow intertemporal region, but in some later forms this is widened and the pineal foramen is often absent.

Primitively with a complete postorbital bar, but later incomplete and sometimes even without a jugal spur.

The coronoid is weak or absent.

The secondary palate is incipient to weakly developed.

Primitively with an enlarged main canine, but in advanced forms not distinguishable, the postcanines are primitively conical but sometimes cusped.

SUBORDER BAURIAMORPHA

Triassic scaloposaurians further advanced than the ictidosuchians; the intertemporal region is narrow, usually with a sagittal crest and pineal foramen.

Postorbital bar, complete or incomplete.

Dentary with a prominent coronoid process; weak or robust with post-dentary bones well developed or weak; with a well-developed closed secondary palate; epipterygoid moderately widened, lying lateral to braincase.

Incisors and canine conical or peglike, postcanines with cusps and transversely expanded. Occipital condyle notched or double.

Family **Bauriidae**

Intertemporal region narrow with sagittal crest; pineal foramen absent or present; the postorbital bar complete or incomplete, sometimes without jugal spur.

Dentary strong with well-developed postdentary bones. The vomer does not enter the secondary palate. Incisors and prominent canine conical and postcanines expanded.

Family **Ericiolacertidae**

Intertemporal region broadened, without sagittal crest, no pineal foramen; postorbital bar incomplete, without a jugal spur.

Dentary and postdentary bones lightly built.

The vomer enters the secondary palate.

No outstanding canine, incisors modified and postcanines peglike with cusps and expanded transversely.

ORDER CYNODONTIA

Advanced Upper Permian and Triassic gammatherapsids, derived from sphenacodonts probably through an intermediate stage at a morphological level near that of the Middle Permian therocephalians and scaloposaurians; including the ancestors of the mammals.

The intertemporal region is narrow with a sagittal crest, pineal foramen primitively present but later lost; postorbital bar complete in earlier forms but later incomplete. Dentary with weak to very strong coronoid process, the postero-ventral angle to the dentary is primitively weakly developed but very prominent in later forms; primitively without a posterior process but this is developed in later forms and in some forms reaches the squamosal to form an accessory articulation; the postdentary bones well developed in earlier forms but later much reduced. Primitively with a cleft secondary palate, but later closed.

The epipterygoid is widened and enters the sidewall of the braincase and becomes suturally joined to the prootic.

The dentition primitively with conical incisors and canines sometimes with accessory small canines; the postcanines developing cusps and later with widened variously elaborated crowns; primitively polyphyodont later diphyo-

dont with 'premolars' and 'molars' distinguishable.

Postfrontal lost; no suborbital fenestra; occipital condyle notched and later double.

SUBORDER PROCYNOSUCHIA

Primitive Upper Permian and Triassic cynodonts, related to the two older gammatherapsid orders and linked to the first mammals.

Pineal foramen present and postorbital bar complete, zygoma lightly built.

In the dentary the postero-ventral angle is absent or only moderately developed; a masseteric fossa on the coronoid process is incipient to fairly well developed but there is still no masseteric process on the jugal; the posterior process of the dentary is still undeveloped; the postdentary bones are still well developed, but the reflected lamina of the angular is reduced. Initially the secondary palate is still cleft but is later closed.

The incisors and canine conical with accessory small canines sometimes present; accessory cusps on the postcanines.

Family **Procynosuchidae**

Upper Permian primitive procynosuchians still with a cleft palate, fairly weak coronoid process, with accessory precanine maxillary teeth; the occipital condyle is incipiently double.

Family **Galesauridae**

Upper Permian and Lower Triassic procynosuchians with a closed secondary palate, strong coronoid process without precanine maxillary teeth, and a double occipital condyle.

SUBORDER CYNOGNATHIA

Advanced specialized Triassic cynodonts, with a carnivorous and herbivorous branch, derived from Upper Permian procynosuchians, becoming extinct in the Upper Triassic.

Pineal foramen present, postorbital bar complete and a very strong zygoma.

Dentary greatly enlarged, prominent and strong coronoid process with masseteric fossa fairly to very well developed; strong to very strong postero-ventral angle; posterior process of dentary moderately to well developed and in some advanced forms making contact with the squamosal in an accessory articulation; masseteric process on jugal present or absent with a step between maxilla and jugal; postdentary bones greatly reduced with all but loss of reflected lamina of the angular. Secondary palate well developed and closed. Incisors and canines conical, without accessory anterior canines, postcanines with fore and aft accessory cusps or with crowns transversely expanded and further elaborated.

Family **Cynognathidae**

Earlier carnivorous cynognathians with the dentary not making contact

with the squamosal, and with small angular process and jugal process; maxillary teeth divided into premolars with crenulated crowns and molars with a series of sectorial cusps in a longitudinal row.

Family **Chiniquodontidae**

Later carnivorous cynognathians with the dentary making contact with the squamosal in some advanced forms, usually no angular process to the dentary.

Family **Diademodontidae**

Earlier herbivorous cynognathians with very strong masseteric process on the jugal; long series of maxillary teeth with peg-like premolars and transversely widened crushing molars.

Family **Traversodontidae**

Later herbivorous cynognathians with a step between the maxilla and jugal and no masseteric process on the jugal.

SUBORDER TRITYLODONTIA

Advanced Upper Triassic cynodonts, derived from Upper Permian procynosuchians.

Without pineal foramen, postorbital bar incomplete without postorbital and postfrontal; zygoma very strong or fairly weak.

Dentary greatly enlarged with strong coronoid process and well developed masseteric fossa; postero-ventral angle very prominent, posterior process of dentary well developed and making contact with the squamosal in advanced forms; postdentary bones greatly reduced; no jugal process.

Secondary palate closed but greatly reduced in width with median shift of postcanines. Transverse ramus of pterygoid reduced.

Incisors primitively conical or specialized and recumbent, conical canine present or absent, postcanines cusped and further elaborated with crushing crowns.

Mononarial or binarial.

Family **Trithelodontidae**

Zygoma moderately strong; posterior process of the dentary not reaching the squamosal; incisors primitively conical, long diastema, long series of widened molars; mononarial.

Family **Tritylodontidae**

Zygoma strong; posterior process of the dentary not meeting the squamosal; incisors reduced, one enlarged, recumbent in dentary, no canine, long diastema, molars quadrangular with elaborate crushing crowns; mononarial.

Family **Diarthrognathidae**

Zygoma fairly weak; posterior process of the dentary making contact with the squamosal in an accessory articulation; incisors and canine primitively conical, no diastema, molars transversely widened with cusps; binarial.

SUMMARY

The classification of the Therapsida is re-evaluated and the older view of two main branches, Anomodontia and Theriodontia, discarded in favour of three main branches for which the names Alphatherapsida, Betatherapsida and Gammatherapsida are proposed.

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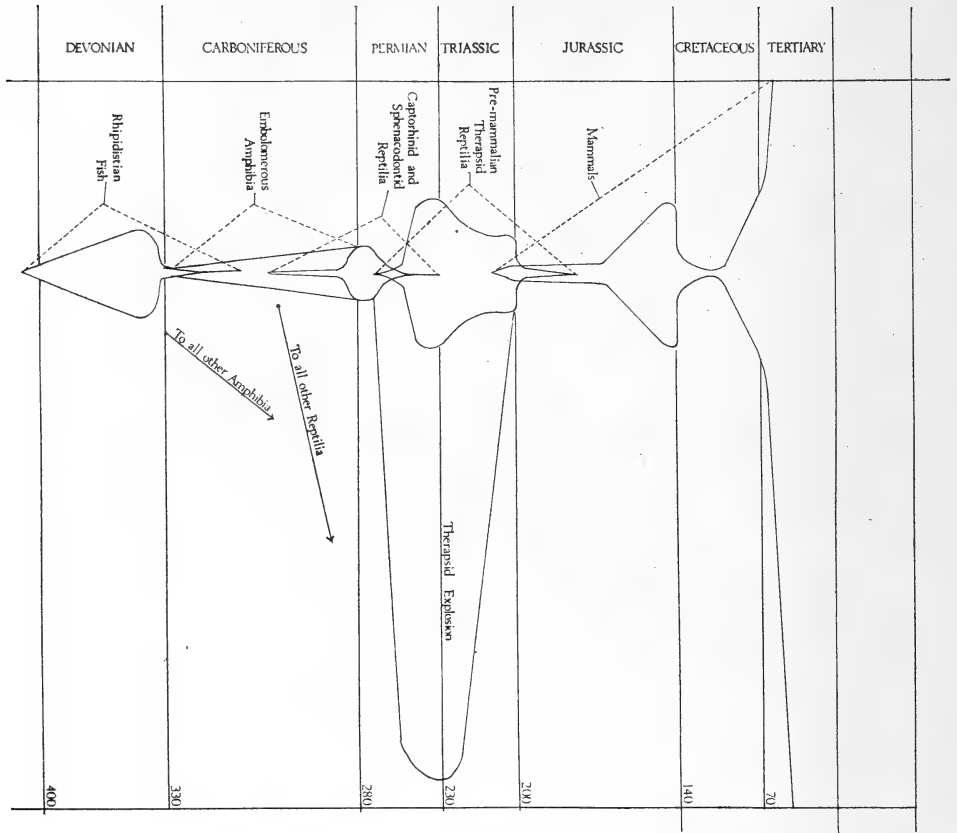


FIG. 1. Schematic representation of the evolutionary story of the mammals. The diagram is based on the number of described genera.

We commence the story nearly 400 million years ago.

At that time (the Devonian) there lived a group of freshwater fish, known as the Rhipidistia, whose paired fins had become adapted to propelling the body forwards with a purchase on the muddy floor of shallow pools.

These rhipidistians were succeeded (during the Carboniferous) by a group of amphibians, known as the Embolomeri, with two pairs of extremities capable of ungainly locomotion on dry land and with the ability of utilizing atmospheric oxygen but returning to the water for reproduction.

Just before the next period (the Permian) we encounter two groups of reptiles that had become completely adapted to life on land. These were the primitive Captorhinidae, with a simple adductor muscular mass for closing the jaw when feeding and the Sphenacodontia, where the adductor muscles had developed into a more efficient mechanism for feeding and able to raise the body from the ground for better locomotion.

Arising from these early reptiles (during the later part of the Permian) we have the Therapsida, which evolved in various directions, but with this in common viz. a great improvement in the jaw mechanism and locomotor ability. The majority of the therapsids, developing along differing but nearly parallel lines, became extinct, some in the Permian and others successfully competing to the end of the Trias.

Of the more successful therapsids we indicate in the scheme a group consisting of the familiar Scaloposauridae, Bauriidae, Tritylodontidae and Diarthrognathidae, brigading them

together as the Premammalian Therapsida. In this group the locomotor ability is greatly improved and the jaw mechanism adapted more and more for chewing their food. For the latter the lower jaw became more and more dominated by a single bone—the dentary—and the teeth developed shearing, cutting and crushing cusps and the respiration during the chewing process was facilitated by the development of a bony secondary palate, separating the air passage from the buccal cavity.

Up to the end of the Triassic period all the vertebrates were poikilothermic or 'cold-blooded', i.e. they had no built in mechanism for temperature control. About this time certain of the higher therapsids, with their higher rate of metabolism, made possible by the improved locomotor and masticatory ability, developed mechanisms to dissipate excess body heat or to conserve it. For the former a skin with glands for sweating and a diaphragm for panting became imperative. To conserve heat the development of an insulating cover of hair or fur took place. These features, together with the dentary-squamosal jaw hinge made these small rat-like creatures mammals.

From their beginning late in the Triassic (about 150 million years ago) these first mammals were small rat-like animals forming a very inconspicuous part of the vertebrate fauna. This continued throughout the Jurassic and Cretaceous, when vertebrate life was dominated by the sauropsid reptiles which included the dinosaurs during their heyday.

But from the Tertiary the mammals waxed exceedingly to fill every possible ecological niche including besides terrestrial conditions varying from arctic to tropical climates, excursions into fresh and salt water and into the air. The culminating event, less than a million years ago, is the emergence of Man.

Since then this single genus has attained a dominant position in the living world, which it is ravaging at an alarming rate.

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.

Style manual for biological journals. Washington: American Institute of Biological Sciences.

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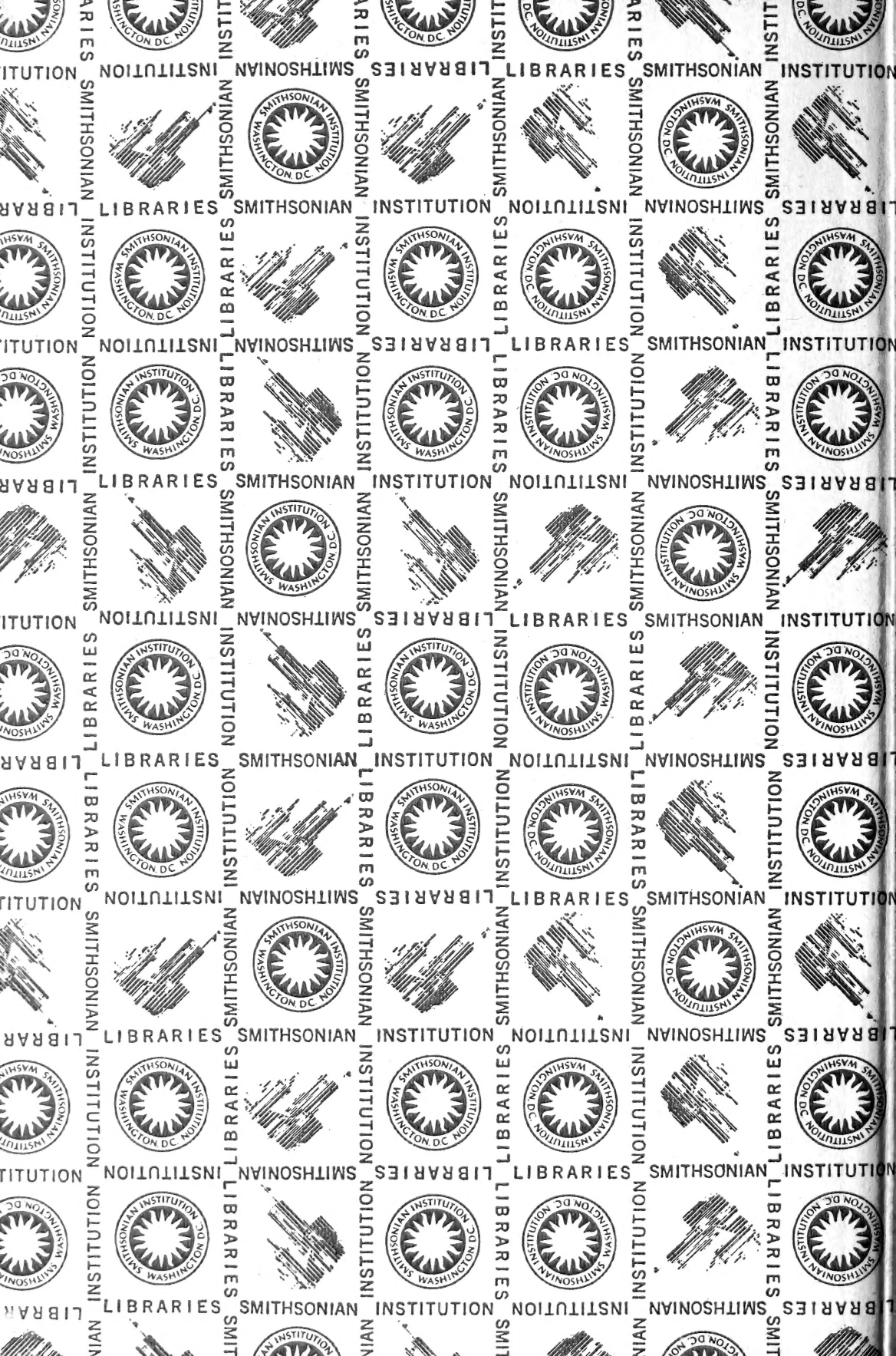
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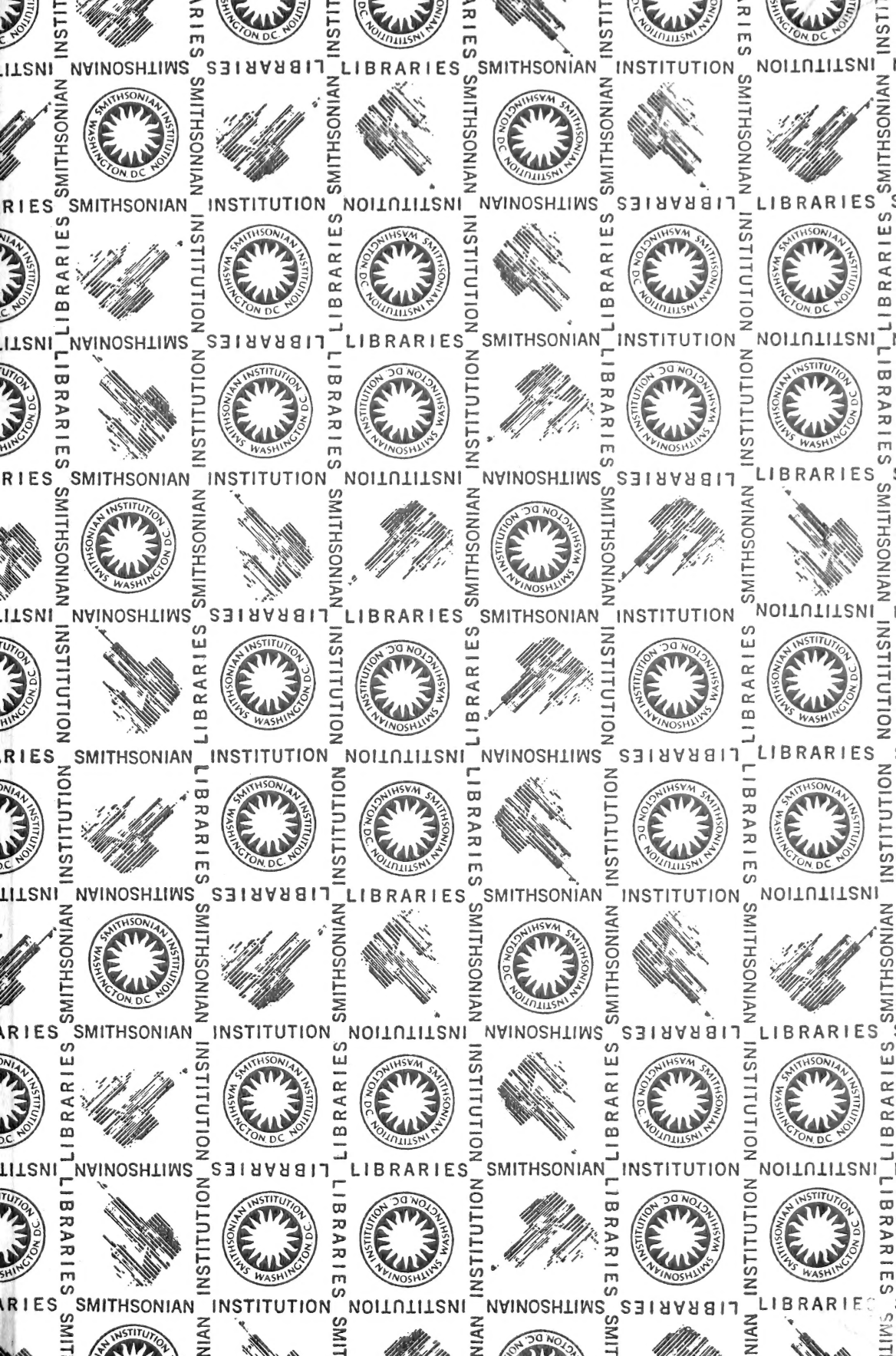
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Example

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