

17.68

ANNALS OF THE
SOUTH AFRICAN MUSEUM

VOLUME 50

SMITHSONIAN
MAR 20 1969
LIBRARIES

ANNALS
OF THE
SOUTH AFRICAN MUSEUM

VOLUME 50



PRINTED FOR THE
TRUSTEES OF THE SOUTH AFRICAN MUSEUM
1966-1968

SMITHSONIAN INSTITUTION
LIBRARY
SOUTH AFRICAN MUSEUM

ANNALS
OF THE
SOUTH AFRICAN MUSEUM
VOLUME 10



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

LIST OF CONTENTS

	<i>Page</i>
BARRY, T. H. The cranial morphology of the Permo-Triassic anomodont <i>Pristerodon buffaloensis</i> with special reference to the neural endocranium and visceral arch skeleton (published December 1967)	131
BARRY, T. H. Sound conduction in the fossil anomodont <i>Lystrosaurus</i> (published June 1968)	275
BOONSTRA, L. D. The girdles and limbs of the Dicynodontia of the <i>Tapinocephalus</i> zone (published November 1966)	1
BOONSTRA, L. D. The dinocephalian manus and pes (published November 1966)	13
BOONSTRA, L. D. An early stage in the evolution of the mammalian quadrupedal walking gait (published March 1967)	27
BOONSTRA, L. D. The braincase, basicranial axis and median septum in the Dinocephalia (published May 1968)	195
HESSE, A. J. Additions to the Cyrtosiinae (Bombyliidae) of South Africa (published December 1967)	89
JOHN, H. Neue Spezies von <i>Notiophygus</i> Gory nebst Ergänzungen (Discolomidae Col.) (published December 1967)	163
KENSLEY, B. F. Deep sea decapod Crustacea from west of Cape Point, South Africa (published June 1968)	283
MILLARD, N. A. H. Hydroids from the south-west Indian ocean (published December 1967)	169
PENRITH, M.-L. Studies on the South African Clinidae. II. Two new species of <i>Clinus</i> from the western Cape (published October 1967)	43
VOSS, G. L. Some bathypelagic cephalopods from South African waters (published November 1967)	61

SMITHSONIAN INSTITUTION LIBRARIES

NEW GENERIC NAMES PROPOSED IN THIS VOLUME

Pseudoglabellula Hesse, 1967 (Bombyliidae), 118

Psiloderoides Hesse, 1967 (Bombyliidae), 121

NEW SUBGENERIC NAME PROPOSED IN THIS VOLUME

Aetheoptilus Hesse, 1967 (Bombyliidae), 112

INDEX TO GENERA AND SUBGENERA

(SYNONYMS IN ITALICS)

A

Abralia, 66
Abraliopsis, 62, 66
Acanthephyra, 284, 285, 310
Acryptolaria, 171, 172, 192
Aetheoptilus, 92, 108, 112
Agama, 153
Alepisaurus, 61, 72, 73, 76, 79, 82, 86
Alopecognathus, 41
Amalopenaeus, 301, 302
Amphisbaena, 155
Amphitretus, 63, 85
Anniella, 140, 141, 153, 280
Anomaloptilus, 93, 108, 113
Anteosaurus, 198, 230, 260
Aphaniotes, 280
Aprasia, 280
Austrorossia, 62, 65

B

Blennius, 43
Brachyuraniscus, 1
Broilius, 1
Brucella, 176

C

Calliteuthis, 74
Calotes, 153
Ceratolaemus, 91, 96, 99, 100, 119
Ceratophora, 280
Chalydra, 155
Chelone, 147
Chiroteuthis, 63, 76, 87
Chrysemys, 278
Cistecephalus, 132
Cladocarpus, 172, 188, 192, 193
Clinus, 43
Cophotis, 280
Cordylus, 140
Cranchia, 63, 82
Criocephalus, 196, 197, 229
Crocodylus, 278
Cryptolaria, 172, 174
Ctenopteryx, 63, 73
Cyrtisiopsis, 92, 93, 98, 100, 119
Cyrtoides, 107
Cyrtosia, 91, 93, 96, 100, 104, 107, 116, 119,
 122

D

Daptocephalus, 138, 142, 145, 156
Dasypus, 140
Desmoteuthis, 84

Dicynodon, 1, 2, 131, 135, 137, 139, 141,
 198, 260, 270
Dimetrodon, 31, 139, 268, 271, 272
Doliopteryx, 92, 112

E

Eledonella, 63, 85
Empidideicus, 92, 93, 105, 107, 116, 119
Emydochampsia, 155
Emydura, 155
Endothiodon, 151
Enoplateuthis, 70
Ephyra, 310
Eryoneicus, 284, 297
Euanthobates, 89, 93, 106, 116, 118

F

Filellum, 171, 175, 192

G

Galacantha, 284, 292
Galiteuthis, 63, 85
Gennadas, 284, 285, 301
Glabellula, 92, 105, 107, 112, 118
Glabbellula, 107
Glyphocrangon, 286, 318

H

Halicornaria, 172, 184, 191, 192
Haliporus, 284, 285, 299
Hemisepius, 62, 64
Heteroteuthis, 62, 65
Hincksella, 171, 176, 192, 193
Hipposaurus, 34
Histioteuthis, 63, 74, 75
Hymenodora, 285, 309
Hymenodora, 312
Hymenopenaeus, 299

I

Iguana, 149
Inioteuthis, 62, 65

J

Jonkeria, 13, 22, 197, 198, 238, 258, 260

K

Kannemeyeria, 155
Keratocephalus, 196, 197, 219
Kingoria, 145, 155, 156
Kirchenpaueria, 172, 184, 192
Koupia, 1

L

Labidosaurus, 155
 Lacerta, 153, 278
 Lacertilia, 149
 Lafoea, 171, 175, 192
Lafoëa, 175
 Leachia, 81
 Leptodontoteuthis, 66
 Locustana, 121
 Lycoteuthis, 62, 66
 Lyriocephalus, 153, 280
 Lystrosaurus, 142, 146, 156, 158, 275
Lytocarpus, 191

M

Maraisaurus, 198, 264
 Megalocranchia, 63, 82, 87
Meleagroteuthis, 75
 Micrabralia, 70
 Micranteosaurus, 13, 14, 17, 23, 25
 Monopeltis, 140, 149, 280
 Mormosaurus, 196, 211
 Moschoides, 13, 15, 19
 Moschops, 13, 14, 196, 223, 260
 Munida, 284, 287
 Munidopsis, 284, 288

N

Nematocarcinus, 283, 284, 285, 286, 317
 Nemertesia, 172, 175, 185, 192
 Neolithodes, 284, 286
 Notiophygus, 163
 Notostomus, 285, 310
Notostomus, 314

O

Octopodoteuthopsis, 63, 73
 Octopus, 63, 86
 Ocythoe, 63, 86
 Onchopelma, 91, 104, 121, 123
 Onychoteuthis, 62, 72
 Onykia, 62, 72
 Ophioceps, 153, 155
Ophthalmolophus, 43
 Ornithoteuthis, 63, 76
 Otsheria, 272
 Oudenodon, 138, 146, 156

P

Palaeogyrinus, 267
 Parascapanodon, 15, 23
 Pelomedusa, 144
 Peltosaurus, 155
Pentacheles, 293
 Phrynops, 145, 156

Placerias, 145
 Platypygus, 91, 93, 96, 98, 100, 119
 Plesioopenaeus, 284, 285, 298
 Plumularia, 172, 175, 185, 192, 193
Plumularia, 184
 Polycheles, 284, 292
Polycheles, 293
 Pontophilus, 283, 284, 286, 319
 Pristerodon, 1, 131
 Pristerognathoides, 198
 Pseudoglabbellula, 92, 106, 112, 118
 Psilodera, 90, 121
 Psiloderoides, 90, 121
 Pterygioteuthis, 62, 71
 Pyrgopsis, 63, 79
 Pyroteuthis, 62, 70

R

Reticularia, 175
Rhachocaris, 318
 Rhineura, 280
Rhombosepion, 64
 Robertia, 1, 3
 Rossia, 62, 65

S

Salacia, 171, 179, 192
 Scelotes, 141, 280
 Sclerocrangon, 284, 286, 318
 Scymnosaurus, 40
Semirossia, 65
 Sepia, 62, 64
 Sergestes, 284, 285, 302
 Sergia, 303, 308
 Sertularella, 171, 180, 192
Sertularella, 182
Sertularia, 176, 179
 Sphenodon, 140, 146, 152, 156, 278, 279
 Spirula, 62, 63
 Stahleckeria, 155
 Stegopoma, 171, 172, 192
 Stephanoteuthis, 65
 Stereomastis, 284, 293
Stigmatoteuthis, 74
 Struthiocephalus, 14, 15, 195, 196, 197, 199,
 256, 260
 Symplectoscyphus, 171, 182, 192
 Synostocephalus, 158
 Systellaspis, 284, 285, 309
 Systoechus, 124

T

Tapinocephalus, 1, 13, 22, 27, 255, 264, 266
 270, 271, 272, 273
 Terphis, 121
 Testudo, 278

Tetronychoteuthis, 62, 72
Teuthowenia, 84
Thyllis, 121
Titanophoneus, 13, 18, 24, 25
Todaropsis, 63, 76
Tremoctopus, 63, 86
Tripteris, 98
Trogonophis, 153
Tropicolotes, 152

Tympanocryptis, 280
Typhlosaurus, 280

V
Venjukovia, 137

W
Willemoesia, 284, 294
`
Z
Zygophylax, 171, 172, 176, 192

LIEUWE DIRK BOONSTRA

THE GIRDLES AND LIMBS
OF THE DICYNODONTIA OF THE
TAPINOCEPHALUS ZONE

November 1966 November

Volume 50 Band

Part 1 Deel



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

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

25c

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

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

THE GIRDLES AND LIMBS
OF THE
DICYNODONTIA OF THE *TAPINOCEPHALUS* ZONE

By

LIEUWE DIRK BOONSTRA

(With 6 Text-figures)

CONTENTS

	PAGE
Introduction	1
Material	2
Pectoral Girdle	3
Pelvic Girdle	5
The Humerus	6
The Femur	7
The Anterior Epipodial, Carpus and Manus	8
The Pes	10
Discussion	11
Summary	11
Acknowledgement	11

INTRODUCTION

The oldest specimens of the Dicynodontia as yet recovered from the Karroo are from the *Tapinocephalus* Zone of the Lower Beaufort Beds. These are of both the families Endothiodontidae and Dicynodontidae. Hitherto six genera and sixteen species have been described—all based on cranial material alone, viz.

Endothiodontidae

- Brachyuraniscus broomi*
- Brachyuraniscus merwevillensis*
- Brachyuraniscus reuningi*
- Broilius antjiesfonteinensis*
- Koupia koupensis*
- Pristerodon brachyops*
- Robertia broomiana*

Dicynodontidae

- Dicynodon antjiesfonteinensis*
- Dicynodon gamkaensis*

Dicynodon haughtoniscus
Dicynodon huenei
Dicynodon jouberti
Dicynodon megalorhinus
Dicynodon pseudojouberti
Dicynodon schroederi
Dicynodon vanderhorsti.

The Dicynodont fauna at this time consisted of an assemblage of small reptiles, with skull lengths varying from 40 to 130 mm. These small reptiles occur abundantly in the *Tapinocephalus* Zone. The South African Museum Collection alone contains 705 specimens. By far the greater number of specimens have been found as eroded fossils lying loose on the surface. Although a number have been found as isolated specimens—some still *in situ*—they mostly occur concentrated in small patches of loose lying rubble. These have been weathered out of thin layers of about 3–5 inches thickness in the mudstone. In the upper part of the zone these layers tend to be arenaceous. In a number of places in the Koup I have collected over a hundred specimens still *in situ* in such thin layers. These specimens are mostly of skulls and parts of skulls with postcranial parts very rare. This material has obviously been washed into shallow pans or depressions, where they were covered up by the inflowing silt. The paucity of postcranial material is in all probability due to the activities of the contemporary carnivores and carrion eaters.

In one locality only—on the farm Michau's Request—have I found a number of skeletons entombed together in a fairly complete state in a purplish layer of fine mudstone of about 12 inches thickness. This find is of a number of these reptiles which had been overwhelmed by some catastrophe and rapidly imbedded.

These small Dicynodontia must have been present in large numbers (flocks?) and formed the diet of the numerous contemporary Therocephalia.

Although occurring throughout the zone the patches where concentrated assemblages have been encountered are mostly in the upper part of the zone. Often these patches include remains—also mostly skulls—of medium-sized Therocephalia.

Hitherto no part of the postcranial skeleton of any Dicynodont from the *Tapinocephalus* Zone has been described.

MATERIAL

In this contribution an account will be given of the girdles and limbs of these specimens from the *Tapinocephalus* Zone in the collection of the South African Museum in which parts of these structures are preserved. From the following table of the available material it is evident that much more collecting will have to be done before a really adequate picture of this early stage in the development of the girdles and limbs of the Dicynodontia can be given.

- SAM 11588 Endothiodontid. Skull, partial pectoral girdle and humerus.
Cypher, Beaufort West, Low *Tapinocephalus* Zone. Collected
Boonstra 1940.
- SAM 11760 *Robertia broomiana*. Skull, humerus and epipodial.
Klein-Koedoeskop, Beaufort West, Low *Tapinocephalus* Zone.
Collected Boonstra 1929.
- SAM 11825 ? Partial pelvis.
Dubbelefontein, Beaufort West, High *Tapinocephalus* Zone.
Collected Boonstra 1947.
- SAM 11883 ? Vertebral column and ribs with partial girdles and a femur.
Steenbokfontein, Laingsburg, Middle *Tapinocephalus* Zone.
Collected Boonstra 1948.
- SAM 11885 Endothiodontid. A number of fairly complete skeletons.
Michau's Request, Beaufort West. Low *Tapinocephalus* Zone.
Collected Boonstra and Jooste 1948.
- SAM 12255 ? Part of pectoral girdle, humerus and epipodial.
Beukesplaas, Fraserburg. Low? *Tapinocephalus* Zone. Collected
Boonstra and Zinn 1959.
- SAM K259 ? Partial pectoral girdle.
Plaatdorings, Beaufort West. High *Tapinocephalus* Zone. Collected
Boonstra and Zinn 1960.
- SAM K1134 ? Skull and pectoral girdle.
Lammerkraal, Prince Albert. High *Tapinocephalus* Zone. Collected
Boonstra and Zinn 1959.

PECTORAL GIRDLE

(Fig. 1)

The following description of the pectoral girdle is based on SAM 11588 consisting of a left scapulo-coracoid and cleithrum, SAM 11885 in which there are a number of girdles partially preserved, SAM 12255, with most of the left half of a girdle, SAM K259, with an incomplete left scapula and an interclavicle and SAM K1134 with a complete girdle preserved.

Of the last specimen I have made a plaster model enlarged three times and checked with the others, and this forms the basis of the accompanying figures (fig. 1).

The coraco-scapula is well developed with the scapular blade lying at right angles to the vertebral axis, with only a slight curving around the thorax; the coracoidal plate is fairly large, moderately long but low, with the greater part of its ventral edge resting on the stem of the interclavicle. There is no supra-glenoid buttress or foramen. The scapular facet of the glenoid faces mostly backwards and the coracoidal facet upwards and outwards. The precoracoid does not enter the glenoid.

The scapular blade is high with its dorsal part expanded and its outer face flattened. Along the inside of its anterior face it receives the splint-like cleithrum. Lower down the anterior edge of the scapula is everted and forms a well-developed and prominent antero-laterally directed acromion process. The Dicynodontia are thus the earliest Therapsids in which the acromion process is developed and when encountered as low down as the *Tapinocephalus* Zone it is already as well developed as in any later Dicynodont. None of the other contemporary Therapsids have even an incipient acromion process. The upper end of the clavicle is applied to the inner face of the acromion process. No scar for the scapular head of the triceps can be seen on the posterior face of the scapula above the glenoid.

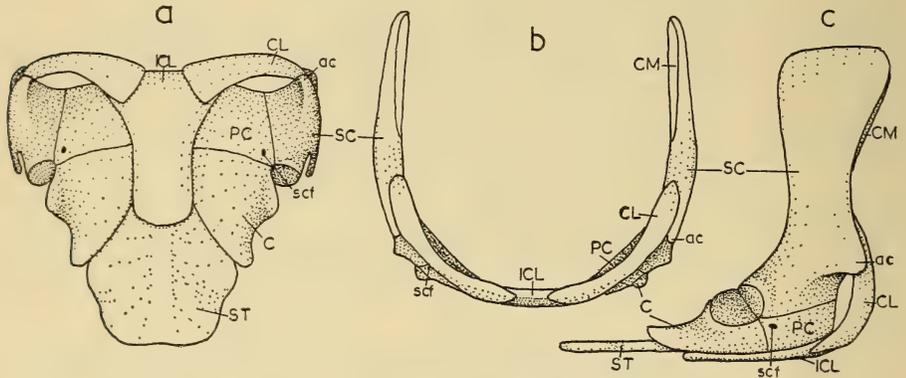


FIG. 1. *Dicynodon jouberti* SAM K1134. Pectoral Girdle $\times 1$.

- a. Ventral. b. Anterior. c. Lateral. All figures are orthoprojections.
 ac—acromion process
 C—coracoid (posterior)
 CL—clavicle
 CM—cleithrum
 ICL—interclavicle
 PC—precoracoid (anterior coracoid)
 SC—scapula
 scf—supracoracoid foramen
 ST—sternum

The precoracoid is relatively small; this is mainly due to the lack of development in its anterior part. Its anterior edge does not reach the plane of the clavicle as it does in all the other contemporary Therapsids. The precoracoid is pierced by a moderate foramen supracoracoideum lying in the acute angle formed by the precoracoid anterior to and below the lower edge of the glenoid.

The coracoid is a robust bone with a fairly long upturned posterior process, but there is no special protuberance or scar for the coracoidal head of the triceps.

The dermal clavicular girdle is moderately well developed but the cleithrum is a weak splint-like element lying applied to the inner anterior edge of the scapular blade.

The interclavicle is fairly short; its anterior end, which is expanded, curves slightly upwards and its lateral corners are underlain by the truncated lower ends of the clavicles; the median stem is broad but short without a definite waist or expanded posterior end. The function of an expanded posterior end is apparently exercised by the well-developed ossified sternum.

The clavicle is a well-developed bone, with its expanded ventral end truncated and underlying the antero-lateral corner of the spatulate anterior end of the interclavicle. It ends well away from the median line and does not extend posteriorly under the interclavicle. This relation is thus much as in the contemporary Gorgonopsians and Dinocephalians and quite different from that obtaining in the pristerognathid Therocephalians. From its ventral expanded end the clavicle narrows and curving upwards has its upper end applied to the inner face of the acromion process. The lower part of the scapula and the precoracoid, having little anterior extent, do not lie applied to the inner face of the clavicle, but lie free of it with their anterior edges in a more posterior plane.

The sternum is ossified as a large broad and squarish plate, with its anterior end overlying the posterior end of the stem of the interclavicle, and its antero-lateral edges are underlain by the inner edge of the coracoids. There are no ossified ribs articulating with the sternum.

PELVIC GIRDLE

(Fig. 2)

Little and poorly preserved pelvic material is available for study. The accompanying figure is a reconstruction based mainly on the specimens SAM 11825 and 11885.

Notwithstanding the inadequate material it is possible to give, in general terms, a statement on the overall nature of the pelvis in these oldest known Dicynodontia, viz. the pelvic girdle is high, short, the pubo-ischium not plate-like, but V-shaped, symphysis absent, pubo-ischiadic fenestra developed; the acetabulum situated above the pubis with its anterior rim on the anterior border of the pelvis. The Dicynodonts of the *Tapinocephalus* Zone are thus the first Therapsids to accomplish the rotation of the pelvis in relation to the acetabulum. This is a *fait accompli* and we know no older forms showing the steps by which this was achieved.

The ilium is high; the iliac blade is large and lies diagonally with the large anterior process directed upwards; the posterior process is weaker, but well developed; the supra-acetabular buttress is strong; about half the acetabulum is formed by the ilium.

The pubis is very short, with its anterior border in a plane posterior to the anterior rim of the acetabulum; its anterior edge carried a well developed tuber which is strongly everted; there is no pubic foramen, but the pubis forms the anterior border of the large pubo-ischiadic fenestra. Ventrally the two pubes

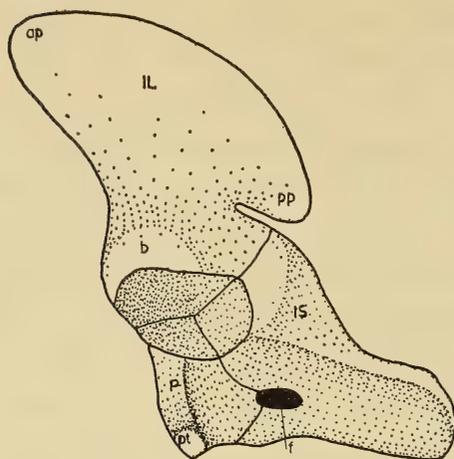


FIG. 2. Dicynodont. Pelvic Girdle $\times 1$. Lateral view.

ap—anterior process of the iliac blade
 b—supra-acetabular buttress
 f—pubo-ischiadic fenestra
 IL—ilium

IS—ischium
 P—pubis
 pt—everted pubic tuber

meet at an acute angle, but there is no symphysis and no median keel is developed.

The ischium is long; the pair lie at an acute angle, with each other and no median keel is developed. The ischiadic tubera are moderately well-developed. Anteriorly the ischium is pierced by a well-developed pubo-ischiadic fenestra. Here again these early Dicynodonts are the first known Therapsids where the old pubic foramen is superseded by a pubo-ischiadic fenestra.

THE HUMERUS

(Fig. 3)

An indifferently preserved humerus is present in SAM 11760 and in SAM 11885 there are seven humeri and SAM 11588 and 12255 have each a well-preserved humerus.

The humerus is a robust bone with greatly expanded ends, a very strong delto-pectoral crest and a short stout shaft. The rotation of the ends on the shaft varies from 30° – 56° .

The proximal surface has the processus medialis and processus lateralis indistinctly demarcated from the caput, which is flattened and narrowly oval in outline.

The delto-pectoral crest is very strongly developed and extends far distally with a thickened bulbous corner for the insertion of the strong m. pectoralis; from here it subsides abruptly into the shaft from where a rounded ridge extends obliquely on to the entepicondyle.

The bicipital fossa is large and fairly deep with a rounded posterior rim, whose posterior face forms a strong and long rectangular area for the origin of the medial head of the m. triceps.

The proximo-dorsal face of the humerus is divided by the anterior dorso-ventral line (ADV L) into two parts. Preaxially to this line lies a triangular area for the insertion of the strong m. deltoideus. Posterior of this line lies the area of insertion for the strong m. latissimus dorsi, whose main insertion is into a hollow extending up to the processus medialis.

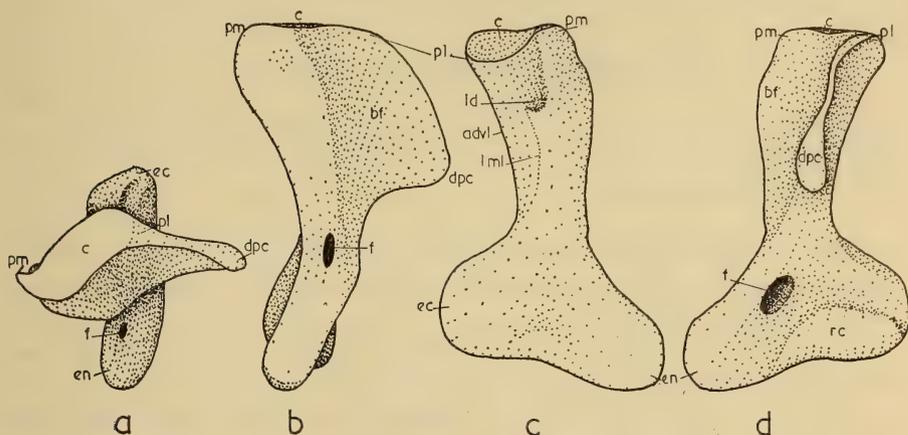


FIG. 3. *Dicynodont*. SAM 11588. Humerus $\times \frac{2}{3}$

a. Proximal. b. Posterior. c. Dorsal. d. Ventral.

advl— anterior dorso-ventral line

bf— bicipital fossa

c— caput humeralis

dpc— delto-pectoral crest

ec— ectepicondyle

en— entepicondyle

f— entepicondylar foramen

ld— insertion of m. latissimus dorsi

lml— latero-medial line

pl— processus lateralis

pm— processus medialis

rc— radial condyle (capitellum)

Distally the epicondyles are both well developed and robust indicating strong flexors and extensors. The entepicondylar foramen is large and oval in outline. There is no ectepicondylar foramen.

The distal condyles are not strongly developed or well moulded. The radial condyle is directed much ventrally and the epipodial capable of full extension. On the dorso-distal surface the trochlear fossa is very shallow, which feature is related to the absence of an olecranon process to the ulna.

THE FEMUR

(Fig. 4)

In SAM 11855 there are six femora, all small and with the various features not very well shown. The accompanying figure is composite with the features shown only diagrammatically correct.

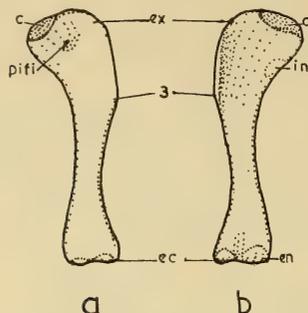


FIG. 4. *Dicynodont*. SAM 11885. Femur $\times 1$.

a. Dorsal. b. Ventral.

c—caput femoris

ec—ectocondyle

en—entocondyle

ex—external trochanter (major)

in—internal trochanter (minor)

pifi—insertion of m. pubo-ischio-femoralis
internus

3—? third trochanter

The femur, longer than the humerus, is a fairly light bone with only slightly expanded ends and a long fairly slender shaft; the preaxial border is concave longitudinally.

The distal condyles lie in the same plane, not well moulded, terminal but facing somewhat ventrally.

Proximally the caput femoris is terminal, but directed appreciably pre-axially and dorsally; widely oval and curving towards the external trochanter into which it flows. From the not prominent external trochanter the postaxial edge is thickened rugosely and is turned slightly ventrally; the distal end of this edge forms a slight protuberance and this muscular scar apparently represents a third trochanter.

On the dorso-proximal surface, near the caput femoris, there is an indication of a muscle-scar for the m. pubo-ischio femoralis internus.

On the ventro-proximal surface there is a slight, low mound near the preaxial border of the bone and this represents an internal trochanter for the insertion of the m. pubo-ischio femoralis externus.

THE ANTERIOR EPIPODIAL, CARPUS AND MANUS

(Fig. 5)

A good epipodial is preserved in SAM 12255 and in SAM 11760 and in SAM 11885 there are six fairly complete radii and ulnae preserved in natural relation. Under this number there are also eight more or less complete carpi and manus. All are small and not very well preserved so that few details of the structure of the individual bones can be given. The figure given is composite incorporating features from the various specimens.

The olecranon process of the ulna is feebly developed. Proximally the radius abuts against a facet on the ulna and thus forms a continuous articulatory

face sliding round the distal humeral end in extension and flexion. Both the ulna and radius have expanded distal ends.

The proximal row of carpals consists of three elements—a radiale of moderate size, rounded in outline, an ulnare, well developed and elongated, and a laterally compressed intermedium. A disc-like pisiforme lies laterally of the ulna-ulnare articulation.

In the middle row there are two centrals—one, elongated lies between the radiale and the last three distals; the central one, squarish in outline, lies flanked by the ulnare and the first central, with the intermedium proximal to it and the enlarged fourth distal distal to it.

There are four distals; the first three small and the fourth, with the fifth incorporated, large.

The metacarpals are moderately well developed—all elongated and fairly slender; they increase in robustness from one to four and the fifth about the size of the third.

The phalangeal formula is 2, 3, 3, 3, 3.

The proximal phalanges are all elongated, with a long shaft or waist. The first is the smallest and is lightly built and fairly short; the second is longer and the third is quite a long and robust bone; the fourth of the same length but of lighter build and the fifth much shorter.

The middle phalanges, smaller than the proximal ones, follow the same pattern of size as the proximal phalanges.

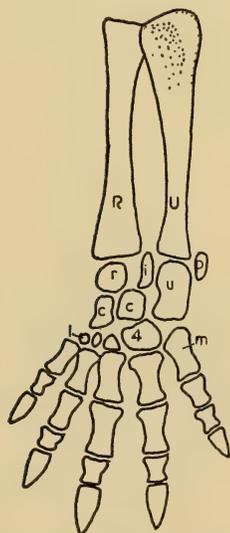


FIG. 5. Dicynodont. SAM 11885. Epipodial and forefoot $\times \frac{3}{4}$.

c—centrals
i—intermedium
p—pisiforme

R—radius
r—radiale
U—ulna

u—ulnare
1-4—distal carpals
m—fifth metacarpal

The ungual phalanges are quite broad and apparently carried broad and long nails adapted to digging.

The third digit is the longest and the purchase of the foot mesaxonic.

THE PES

(Fig. 6)

In SAM 11885 I have a nearly complete hindfoot. The preserved mineralized bone has been dissolved with dilute formic acid to leave a good impression of the dorsal surface.

In the proximal row of the tarsus there is a robust astragalus broader than long and a large disc-like calcaneum. The tibia and the fibula articulate with the distal surfaces of the astragalus and calcaneum respectively.

In the middle row there are two centrals. The preaxial one is the larger and lies distally of the astragalus; the smaller central lies lateral of the first and it articulates with the inner edge of the calcaneum.

There are five distal tarsals, all pebble-like except the first, of which the impression in the mould shows only a crescent-shaped ridge. The fifth distal lies far proximally to abut against the outer edge of the calcaneum.

The five metatarsals are of moderate length, but the first is squat.

The phalangeal formula is 2, 3, 3, 3, 3.

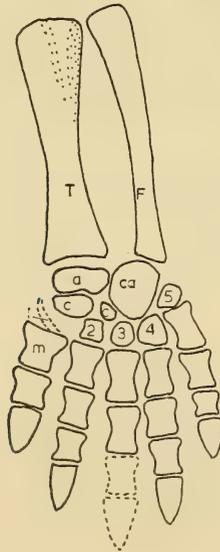


FIG. 6. *Dicynodont*. SAM 11885. Epipodial and hindfoot $\times \frac{3}{2}$.

a—astragalus
ca—calcaneum
c—centrals

F—fibula
T—tibia

1-5—distal tarsals
m—first metatarsal

The phalanges are all fairly long with a good shaft. The proximal one of the third digit is the longest. The ungual phalanges are broad as in the forefoot and probably also carried broad and long nails.

The third digit is the longest and the purchase of the foot was mesaxonic.

DISCUSSION

As I have now completed my study of all the available material of the girdles and limbs of all the Therapsids of the *Tapinocephalus* Zone, I am engaged on a comparative account which will form the concluding paper of this series.

SUMMARY

Descriptions are given of the girdles and limbs of the Dicynodontia of the *Tapinocephalus* Zone in South Africa. Postcranial parts are rarely found and of the 705 specimens in the South African Museum eight have parts of the girdles and limbs present and this account is based on these specimens.

ACKNOWLEDGEMENT

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

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'). with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) 9: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. 2. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. 3: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

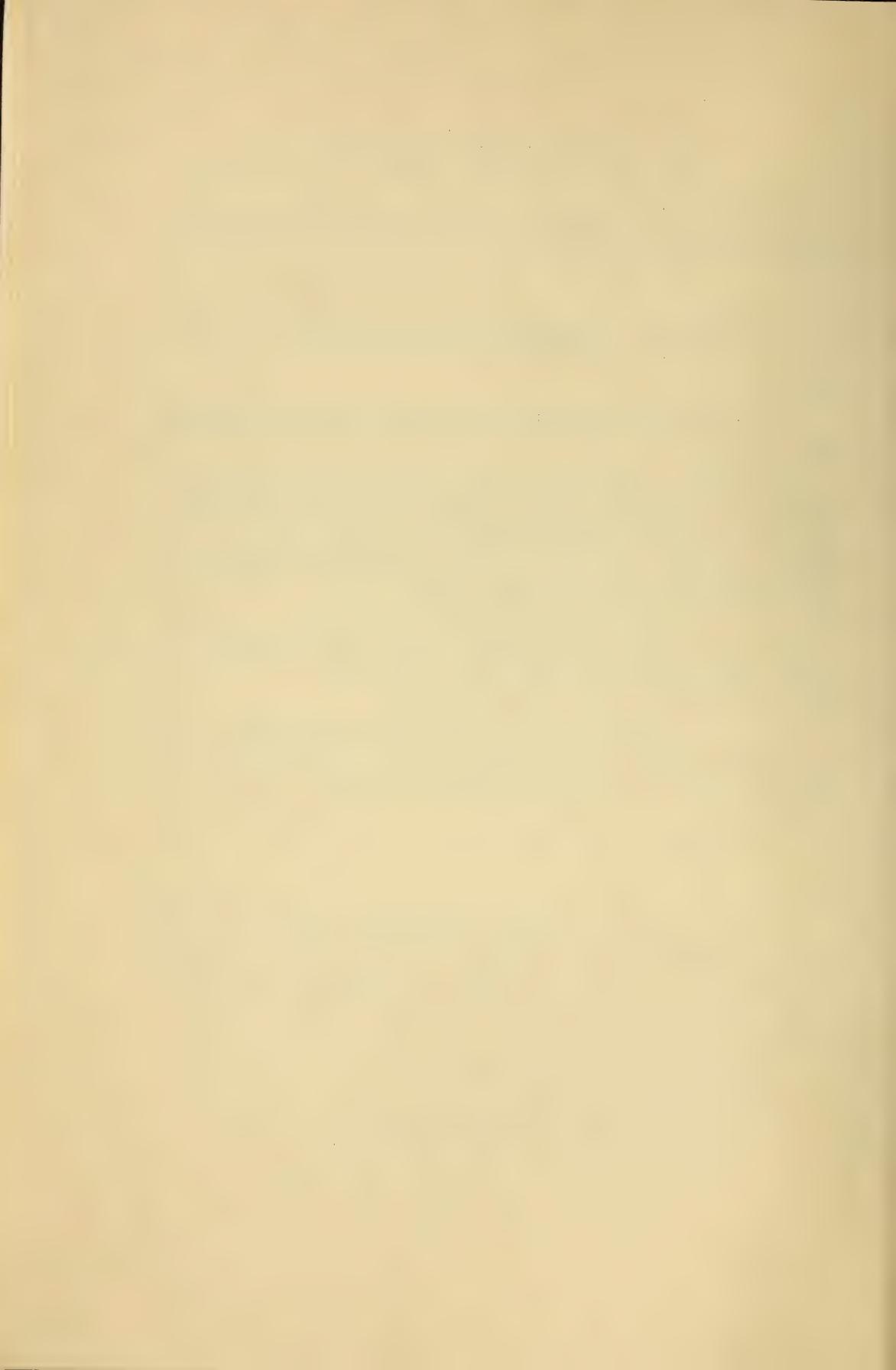
Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



37-38
LIEUWE DIRK BOONSTRA

THE DINOCEPHALIAN MANUS AND PES

November **1966** November
Volume **50** Band
Part **2** Deel



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

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

35c

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

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

THE DINOCEPHALIAN MANUS AND PES

By

LIEUWE DIRK BOONSTRA

(With 10 Text-figures)

CONTENTS

	PAGE
Introduction	13
Material	13
Forefoot	
Tapinocephalia	15
Titanosuchia	16
Anteosauria	17
Hindfoot	
Tapinocephalia	19
Titanosuchia	22
Anteosauria	23
Discussion	25
Summary	26
Acknowledgement	26
References	26

INTRODUCTION

Very little is known of the feet of the South African Dinocephalia.

From a mixed lot of disarticulated elements Gregory produced the mount of *Moschops*, which includes the reconstructed feet, but in his description of 1926 admits his inability to assemble either foot.

In 1929 Broom described the two proximal tarsal elements of *Jonkeria*.

In 1940 Byrne very briefly described both the fore- and hindfeet of *Moschooides*.

In 1954 I described a partial Moschopid carpus and gave descriptions and figures of the fore- and hindfoot of *Micranteosaurus*, which I at the time completely misinterpreted.

From the Russian deposits Orlov in 1958 described and gave beautiful figures of both fore- and hindfeet of *Titanophoneus*.

MATERIAL

After 35 years of collecting in the *Tapinocephalus* zone, during which period I have excavated two hundred and fifty-one specimens of the Dinocephalia, I

have a poor collection of foot material. This is due to the nature of the preservation of the Dinocephalian material in this zone. I know of only one case where a skeleton more or less articulated has been found. In all other cases the bones of the skeleton are disarticulated and scattered with the loss of most of the smaller elements composing the feet.

- SAM 4323 *Micranteosaurus parvus*. An incomplete fore- and hindfoot associated with a good snout.
Merweville Commonage, Low *Tapinocephalus* zone. Coll. Haughton 1917.
- SAM 9157 *Moschops?* An incomplete carpus associated with a humerus, ulna and radius.
Wolwefontein, Prince Albert, Low *Tapinocephalus* zone. Coll. Boonstra 1929.
- SAM 12011 *Struthiocephalus?* Tibia and astragalus.
Rietfontein, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.
- SAM 12017 Tapinocephalian. A calcaneum and fibula with a piece of skull.
Spitskop, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.
- SAM 12033 Tapinocephalian. Radiale.
Worsteling, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.
- SAM 12065 *Struthiocephalus?* Two calcanei found on a small slope which yielded a lot of bones together with some cranial material of *Struthiocephalus*.
Skoenmaker, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1957.
- SAM 12104 Titanosuchian. An isolated astragalus.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.
- SAM 12105 Titanosuchian. An isolated astragalus.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.
- SAM 12109 Titanosuchian. An isolated radiale.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.
- SAM 12110 Titanosuchian? Radius and intermedium.
Kalkkraal, Prince Albert, Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.
- SAM 12210 Titanosuchian. An isolated astragalus.
Kroonplaas, Beaufort West. High? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959.

- SAM 12226 *Struthiocephalus* sp. Hindfoot and manus associated with some teeth.
Knoffelfontein, Beaufort West. Coll. Boonstra and Zinn 1959.
- SAM K201 *Struthiocephalus* sp. Isolated astragalus.
Paradys of Rietfontein, Prince Albert. Middle *Tapinocephalus* zone. Coll. Boonstra 1959.
- SAM K249 *Parascapanodon* sp. Disarticulated skeleton without skull, including two calcanei, one astragalus and other carpal, tarsal and digital bones.
Steynskraal, Beaufort West. Middle *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959.
- SAM K271 Tapinocephalian. Isolated calcaneum and astragalus.
Wonderboom of Plaatdorings, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Boonstra, 1960.
- SAM K323 Tapinocephalian. Scattered foot bones associated with teeth.
Die Bad, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow, 1960.
- SAM K362 Tapinocephalian. Disarticulated carpals, tarsals and phalanges associated with cranial and dental material.
Twee Susters of Grootfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962.
- SAM K366 Moschopid? Isolated Calcaneum.
Moutonsfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962.

FOREFOOT

Tapinocephalia (Fig. 1)

With so little and such poor material available only a tentative description can be given of the Tapinocephalian manus. Of the seven specimens in which elements of the forefoot are preserved four have only disarticulated carpal and digital bones preserved. In SAM 9157 parts of four proximal carpals are present in articulation; in Romer's Chicago specimen of *Moschooides* (which I have not seen) an articulated manus is preserved and in SAM 12226 an incomplete and partially disarticulated manus of a species of *Struthiocephalus* is available for study.

The Tapinocephalian manus is broad and very short with little difference in the length of the toes, but the fourth is the longest digit. The purchase of the foot is thus mainly mesaxonic but somewhat more post- than preaxial. The body weight is mainly transmitted through the radius on to the robust ovoid radiale. The extension and twist of the foot during the stride is executed through the ulna articulating with a flattish plate-like ulnare supported postaxially by the pisiforme and preaxially by a laterally uncompressed intermedium.

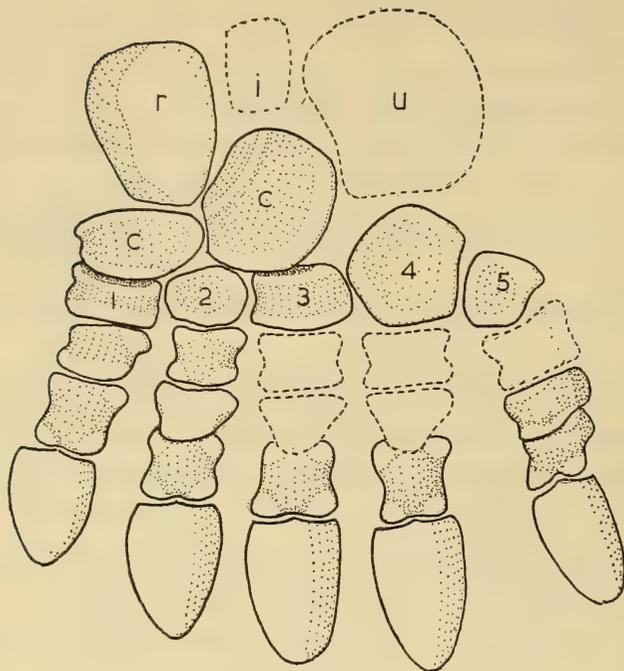


FIG. 1. *Struthiocephalus* sp. SAM 12226 $\times \frac{1}{3}$
Dorsal view of left manus as restored.

In the middle of the foot there are two centralia, of which the proximal one is the larger, circular in outline; the distal or inner centrale is oval in outline.

There are five distalia of which the fourth is the largest; the first three are broader than long and the other two approximately as long as broad.

The first four metacarpals are very short, but the fifth is quite a large bone.

The digital formula is 2, 3, 3, 3, 3. In each digit the proximal phalanx is very short; in the last four digits the second phalanx is slightly longer.

The terminal or ungual phalanges are broad and carried broad, slightly convex nails.

Titanosuchia (Fig. 2)

In the *Titanosuchia* even less material of the manus is available. In SAM K249 a number of disarticulated foot-bones are preserved in very good condition but reassembly as in the figure is an act of faith. As reassembled there are three proximal, two central and five distals in the carpus and the digital formula 2, 3, 3, 3, 3.

The radiale is a strong bone oval in outline and both the intermedium and proximal central are laterally compressed elements. A pair of beautifully preserved ulnaria are preserved. The ulnare is a robust bone with large, well-

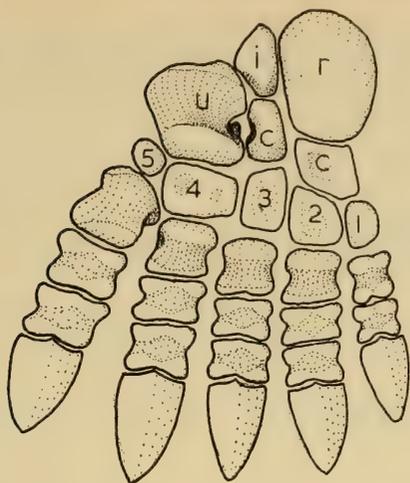


FIG. 2. *Parascapanodon* sp. SAM K249 $\times \frac{1}{4}$
Dorsal view of right manus as restored.

developed convex distal as well as proximal articular faces; dorsally the surface is shallowly concave and ventrally deeply concave; medially the face is deeply excavated and with a similarly excavated lateral face of the contiguous centrale a long tube is formed to house the penetrating carpal nutritive and innervating vessels.

The fourth distal is the largest of the distalia. The metacarpals are very short and have well modelled convex faces both proximally and distally. The fifth metacarpal is large and broad.

Anteosauria (Fig. 3)

From the *Tapinocephalus* zone I have only one specimen of the Anteosaurs—the type of *Micranteosaurus parvus*—in which the forefoot is preserved. With better technical equipment now available I have prepared the specimen further and with increased knowledge of the structure in related forms I wish to correct the misinterpretation I made in my account of 1954.

In the proximal row of the carpus there were three bones. The ulnare is a flattened element with oval proximal and distal articular facets; the outer edge is thin but the inner thickened and rounded, lying preaxially of the ulnare is the intermedium; as preserved it is a thin bone showing a large, flat upper face, but it is possible that it has fallen out of position and would then actually be a laterally compressed bone. Preaxially lies what appears to be a pear-shaped element. I interpret this as a proximal rounded radiale with the distal part actually a central. The lateral central is not preserved.

There are five distals of which the fourth is a large bone with a roughly rectangular upper face. The other distals are pebble-like.

All five metacarpals are preserved; they are all elongated bones with expanded ends and a constricted shaft. They increase in size from 1 to 5, with the fifth a robust bone and the first quite feeble.

The phalanges of only four digits are preserved. The phalangeal formula is 2, 3?, 4, 3, 3, with the third digit the longest and the fourth and fifth only slightly shorter. The first digit is short and feeble. The purchase of the foot thus lies mostly in the postaxial part of the foot.

The proximal phalanges of the last three digits have greatly expanded proximal ends.

The third phalanx of the third digit, although smaller than the first and second phalanges, is not much reduced and apparently not in the process of being lost.

The terminal phalanges are narrow and pointed and would have carried sharp curved claws.

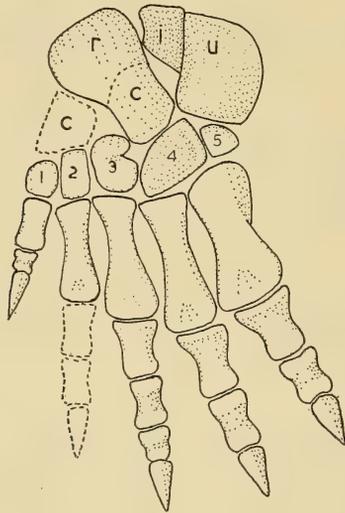


FIG. 3. *Micranteosaurus parvus*. Type. SAM 4323 $\times \frac{1}{2}$
Dorsal view of left manus as restored.

In *Titanophoneus*, Orlov found the carpal formula to be 3, 2, 5, with the intermedium laterally compressed and the fourth distal enlarged. The first metacarpal is small and short and from the second to the fifth became progressively longer with the fifth a quite stout bone with expanded ends. Orlov gives the digital formula as 2, 3, 3, 3, 3, with the second phalanx of the fourth digit showing proximally what looks like an epiphysis, which may represent an additional phalanx fused to it. No such structure is shown in the third digit.

The reduction in the number of phalanges in the third and fourth digits has thus followed a different course in *Titanophoneus* and *Micranteosaurus*, with

the condition in the latter more primitive than in the former.

The purchase of the foot lies more postaxially in *Titanophoneus* than in *Micranteosaurus*.

HINDFOOT

Tapinocephalia (Figs. 4-6)

I have 5 calcanei, 3 astraguli, a number of disarticulated metatarsals and phalanges and one nearly complete pes available for study. In Romer's Chicago specimen of *Moschoides* there is a complete left pes.

In SAM 12226 (fig. 4) it is seen that the proximal bones of the tarsus are very well developed, but the central and distal tarsals fairly weak. The metacarpals and digits are short with the fourth digit slightly the longest and the purchase of the foot mostly postaxial. The digits of the hindfoot are weaker than those of the forefoot.

The proximal row of the tarsus is formed by a robust astragalus and a large flattened disc-like calcaneum.

The astragalus is a strong element of peculiar shape; it is thick, a little longer than broad. In its anterior part the dorsal surface is convex postaxially

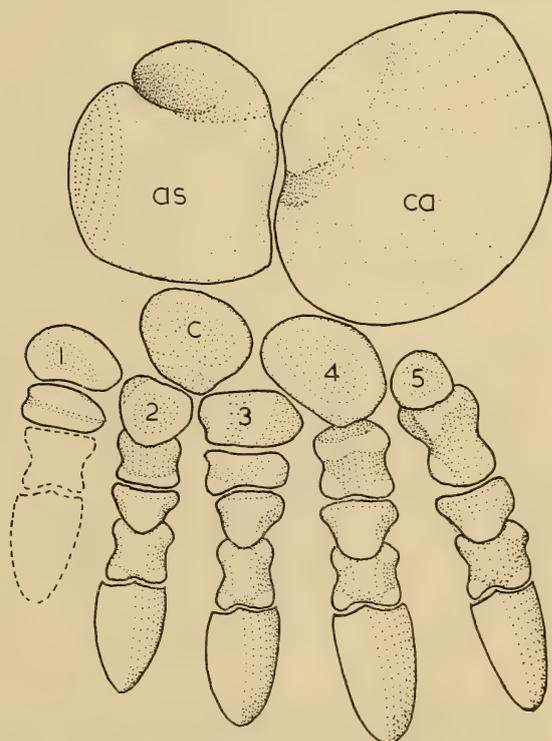


FIG. 4. *Struthiocephalus* sp. SAM 12226 $\times \frac{1}{3}$
Dorsal view of left pes as restored.

and hollowed out towards its preaxial edge. The convex surface covered with a thick cartilage is for the reception of the tibia. Proximal of the tibial facet lies an obliquely directed deep groove, which forms a deep proximal incisure extending round the bone and continuing across the ventral surface as a deep groove connecting with the groove on the postaxial surface of the bone. Proximal to this groove the astragalus carries a strong facet for the fibula facing proximo-postaxially.

The concave postaxial face of the astragalus faces an incisure on the calcaneum thus forming a passage for the vessels passing through the tarsus. Distally the surface of the astragalus is convex and this facet for the central tarsal carried a thick cartilage.

The calcaneum is a large flattened bone oval in outline. Its outer and distal edges are rounded and fairly thin. Proximo-preaxially this disc-like element is thickened and here carries an oval facet which receives a part of the distal facet of the fibula. Distally of this thickening there is a shallow groove, which, extending to the preaxial face, lies opposite to the concavity on the astragalar opposing face.

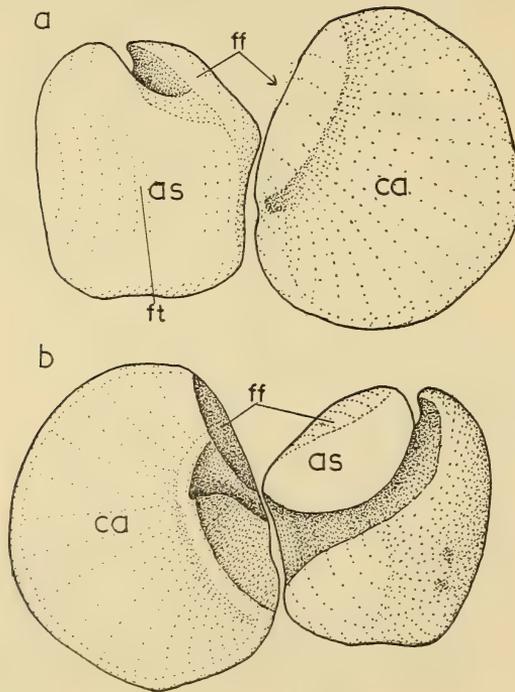


FIG. 5. Tapinocephalid proximal row of tarsals $\times \frac{1}{2}$

a—dorsal view

b—ventral view

As—astragalus of SAM K201

ff—facet for the fibula

Ca—calcaneum of SAM 12065

ft—facet for the tibia

The single centrale is a fairly large rounded bone lying between the astragalus and the second and third distalia.

There are five distal tarsals of which the fourth is the largest.

The first three metatarsals are very short, but the fourth and especially the fifth are larger and look more like normal metacarpals.

The first phalanges are small bones roughly triangular in shape with the apices distally articulated with the second phalanges. The second phalanges are somewhat larger and have expanded ends and a waist.

The terminal phalanges are broad, slightly curving bones carrying a flat nail.

The digital formula is 2, 3, 3, 3, 3, with the toes of nearly equal length, but the first is the shortest with the fourth only slightly longer than the other three.

In figure 5 the system of grooves in both astragalus and calcaneum are well shown in ventral view. These grooves probably housed tendons associated with the tarsal joint which apparently functioned in a most peculiar manner and difficult to understand. I have attempted in figure 6 to show the peculiar action of the ankle joint.

In a. the leg is shown at the completion of the swing forwards with the toes just about to make contact with the ground. In this position it is evident that the fibula has its bipartite distal facet in contact with the facet on the astragalus

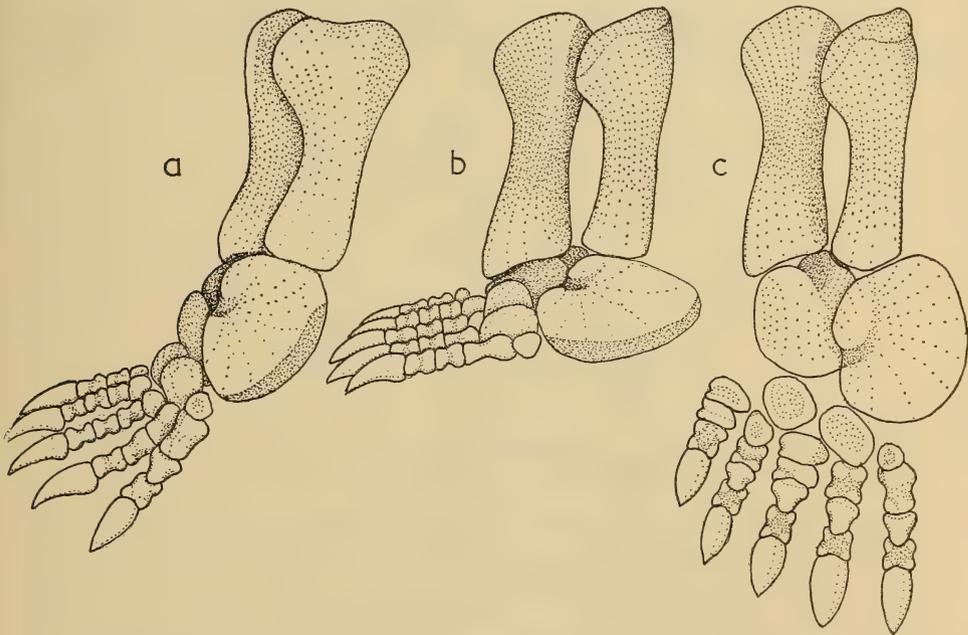


FIG. 6. Tapinocephalid lower hind-limb showing ankle joint in three positions.

a—at completion of the forward swing
b—standing and carrying body weight

c—at completion of the stride

and the facet on the calcaneum, whereas the distal tibial facet is not making contact with the facet on the dorsal face of the astragalus and is in fact out of articulation but held by tendons.

In b. the foot is in the standing position with the body weight transmitted along the long axis of the tibia on to the dorsal facet of the astragalus. In this position it is evident that the distal facets of the fibula are not making contact with the facet on the astragalus nor with the facet on the calcaneum and are in fact out of articulation, but held by tendons only.

In c. the foot is lifted off the ground at the completion of the backward swing of the foot. The body weight is taken off the foot and the astragalus moved away from its contact with the distal facet of the tibia. But the fibula is in contact with the facet on the astragalus and the facet on the calcaneum. Everything is now ready for the forward stride with the foot in position to be swung forwards and twisted by rotation of the fibula on its long axis to assume its contact with the ground position.

If the above representation of the action of the ankle joint is anywhere near being correct, the presence of strong tendons is necessary and these could be housed in the grooves present on both astragalus and calcaneum. I am not so rash as to attempt any description of the mechanism involved.

Titanosuchia (Figs. 7-9)

In addition to the proximal tarsal elements of *Jonkeria* described by Broom and the calcaneum erroneously labelled *Tapinocephalus* by Gregory, I have half

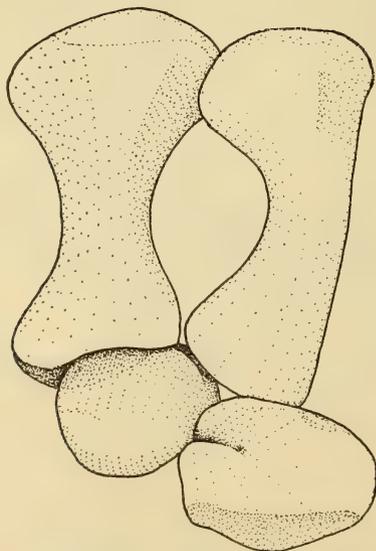


FIG. 7. *Parascapanodon* sp. K249 $\times \frac{1}{2}$
Dorsal view with tibia in and fibula out of articulation.

a dozen good astragali and a couple of good calcanei of *Parascapanodon*.

Both the astragalus and calcaneum in Titanosuchians are very similar in essential structure to the corresponding elements as described above in the case of the Tapinocephalians. They can be distinguished from the latter in that the astragalus is a large and heavier bone and the calcaneum is larger, and in the details of the ventral and penetrating grooves.

In figure 7 the tibia is shown in articulation, in figure 8 the fibula is articulated to both astragalus and calcaneum and in figure 9 the bones are shown in ventral view with the fibula articulated.

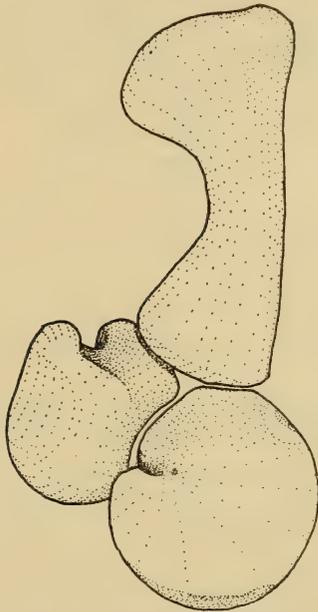


FIG. 8. *Parascapanodon* sp. K249 $\times \frac{1}{3}$
Dorsal view with fibula in articulation.

Anteosauria (Fig. 10)

In the type specimen of *Micranteosaurus parvus* there is an incomplete foot preserved.

The calcaneum is a typical Therapsid flattened disc-like bone—thin in its middle part and with a thin postaxial edge. Both the dorsal and ventral surfaces are concave centrally with a thickened proximal and distal end where good convex facets are developed for the fibula and centrale and second distal. Its preaxial edge facing the astragalus is excavated to form a passage for the penetrating vessels. The system of grooves so typical of the Tapinocephalia and Titanosuchia are not developed.

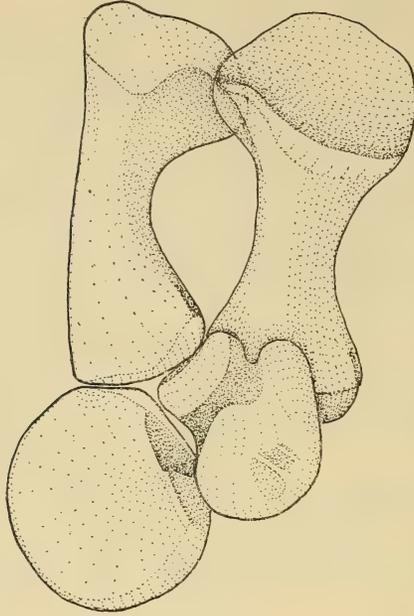


FIG. 9. *Parasapanodon* sp. K249 $\times \frac{1}{8}$
Ventral view with fibula in articulation.

The astragalus is a stout bone and is quite different to the specialized bone seen in the *Tapinocephalia* and *Titanosuchia*. The major part of its dorsal surface is formed by a well-developed rounded articular facet for the tibia. Anterior to this facet lies a groove which flows into the incisure on the postaxial face lying opposite to that on the calcaneum. Anterior to this groove an oval knoblike thickening apparently articulates with the central and the second distal. The ventral surface of the astragalus appears to be convex without grooves.

There probably were five distals and also probably a central, but none are preserved, in their position lie two displaced phalangeal elements.

The five metatarsals are elongated bones with a waist and expanded ends. The first is quite small and the others progressively increase in size, with the fifth a strong element.

The first digit is complete and the first phalanx short with expanded ends and a waist; the terminal phalanx is sharp and narrow and carried a claw. Only the proximal ends of the first phalanx of the second and third digits are preserved. I presume that the digital formula was 2, 3[?]; 4[?]; 3[?]; 3[?], as in the forefoot.

The foot was apparently weak preaxially and strong postaxially.

The pes of *Micranteosaurus* is very similar to that of the Russian *Titanophoneus*, but there Orlov found no centrale and a digital formula 2, 3, 3, 3, 3.

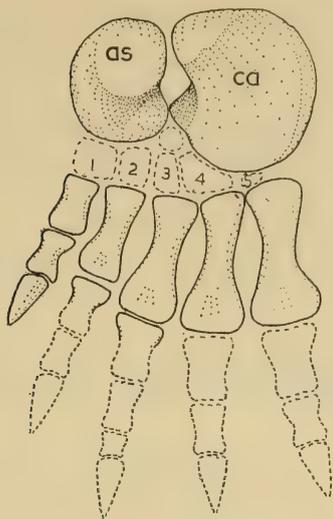


FIG. 10. *Micranteosaurus parvus*. Type. SAM 4323 $\times \frac{1}{2}$
Dorsal view of left pes as restored.

DISCUSSION

The Dinocephalian feet are more primitive than those of the Sphenacodonts in that the first carpal is not elongated, but otherwise they are definitely more advanced.

The digital formula in Sphenacodonts is 2, 3, 4, 5, 3—with a well-developed first digit, a great increase in length from second to fourth digit and a comparatively short fifth digit.

In the Dinocephalia the phalanges of the three middle toes are reduced in number, the first digit is weaker, the three middle digits are shortened and tend to become equal in length and the fifth digit becomes relatively stronger.

Micranteosaurus, with a digital formula 2, 3, 4, 3, 3, has the most primitive feet; then comes *Titanophoneus* in which the fourth digit in the forefoot shows a fusion of two phalanges to produce the formula 2, 3, 3, 3, 3, which also obtains in the Titanosuchia and Tapinocephalia.

Proximally the tarsus is still fairly primitive in the Anteosaurs and becomes more specialized in the Titanosuchians and Tapinocephalians.

The distal phalanges in Anteosaurs still carried a claw as one would expect in carnivores, whereas in the Titanosuchians and Tapinocephalians, which were herbivores, the nails are flattened.

The direction of development in the Dinocephalia seems to have been away from a crawling habit with sprawling feet to a more walking habit with the feet drawn in closer to the median line of the body.

SUMMARY

Descriptions and figures are given of the manus and pes of the Dinocephalia of the *Tapinocephalus* zone in South Africa. Owing to the nature of the preservation of the dinocephalian material in this zone only eighteen of more than two hundred specimens included bones of the feet, and this account is based on these specimens. There are indications that the Dinocephalia show a development from a crawling to a walking habit.

ACKNOWLEDGEMENT

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

REFERENCES

- BOONSTRA, L. D. 1954. The smallest Titanosuchid yet recovered from the Karoo. *Ann. S. Afr. Mus.* **42**: 149-156.
- BROOM, R. 1929. On the carnivorous mammal-like reptiles of the family Titanosuchidae. *Ann. Transv. Mus.* **13**: 9-36.
- BYRNE, F. 1937. A preliminary report on a new mammal-like reptile from the Permian of South Africa. *Trans. Kans. Acad. Sci.* **40**: 221-229.
- GREGORY, W. K. 1926. The skeleton of *Moschops capensis* Broom, a Dinocephalian from the Permian of South Africa. *Bull. Amer. Mus. nat. Hist.* **56**: 179-251.
- ORLOV, J. A. 1958. The carnivorous Deinocephalia (Titanosuchia) from the Upper Permian deposits of the Middle Volga. *Trud. paleont. Inst. Acad. Sci.* **72**: 1-114 (in Russian).
- ROMER, A. S. & PRICE, L. W. 1940. Review of the Pelycosauria. *Spec. Pap. Geol. Soc. Amer.* **28**: 1-538.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

507.68

LIEUWE DIRK BOONSTRA

AN EARLY STAGE IN THE EVOLUTION
OF THE MAMMALIAN
QUADRUPEDAL WALKING GAIT

March 1967 Maart
Volume 50 Band
Part 3 Deel



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

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

45c

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

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

AN EARLY STAGE IN THE EVOLUTION OF THE MAMMALIAN QUADRUPEDAL WALKING GAIT

By

LIEUWE DIRK BOONSTRA

South African Museum, Cape Town

(With 11 figures in the text)

CONTENTS

	PAGE
Introduction	27
Proto-therapsid stage	29
Therapsid stage	30
Pectoral girdle	30
Humerus	32
Forefoot	34
Pelvis	35
Femur	38
Hindfoot	38
Conclusions	40
Summary	42
Acknowledgement	42
References	42
Abbreviations	42

INTRODUCTION

In 1927 I commenced a study of the fauna of the *Tapinocephalus* zone. During this work I paid much attention to the structure of the girdles and limbs. The work on the pareiasaurs was completed many years ago (1932), but it is only recently that I have been able to round off the study of these structures in the oldest known therapsids (1966a & b).

Most workers are now agreed that the therapsids represent a stage in development following on that attained by the pelycosaurs. Hitherto our knowledge of the structure of the girdles and limbs of the early therapsids of the *Tapinocephalus* zone was not as good as it could have been. Now that we know somewhat more, the first steps beyond the pelycosaur stage can be pictured more clearly. Moreover, the first steps of the subordinate groups comprising the order can be considered separately instead of compositely.

The taxonomic arrangement of the available material I intend using is as follows:

Order Therapsida

1. Sub-order Anomodontia
 - a. Infra-order Dinocephalia
 - Family Anteosauridae
 - Family Titanosuchidae
 - Family Tapinocephalidae
 - b. Infra-order Dicynodontia
 - Family Endothiodontidae
 - Family Dicynodontidae
 - c. Infra-order Dromasauria
 - Family Dromasauridae
2. Sub-order Theriodontia
 - a. Infra-order Gorgonopsia
 - Family Hipposauridae
 - b. Infra-order Therocephalia
 - Family Pristerognathidae.

The above formal classification emphasizes the fact that the oldest known therapsids show clear differentiations in their development from a pelycosaur stock. The taxonomy, although largely based on cranial characters, does to some extent also take into account features of the limbs and girdles. On the latter we can now elaborate.

The advances seen in the structure of the girdles and limbs of the early therapsids differ in kind as well as in degree. Some parallelism is evident. The fact that in the pareiasaurs many of these advances are also shown seems to indicate that the achievement of a more upright walking gait does not need a pelycosaur stage as a prerequisite. Manifestly the advances in the girdle and limb structure of the pareiasaurs, although also manifested in *Tapinocephalus* zone times, arose independently from those seen in the therapsids. The pareiasaurs have skipped a stage as far as locomotion is concerned. Although many of the results achieved by the pareiasaurs appear similar to those achieved by the early therapsids, some features show that the course has been different. This is most clearly shown by the difference in the nature of the glenoid which, although shortened in the pareiasaurs does not become a posteriorly situated notch in the scapulo-coracoid as it is in all the early therapsids.

The general nature of the advances in the structure of the girdles and limbs in the early therapsids indicates an origin from a common stock. A common branch appears to have sprouted from a pelycosaur stem, but this soon split into a number of separate twigs.

In a recent publication (1963) I tried to show the nature of these early dichotomies in the therapsids, basing my views on the differentiations in the lower jaw mechanism. I tried to show that differences in the working of the masseter mass lay at the root of these dichotomous splittings.

Changes in the action of the locomotor muscles, without doubt, produced the differences we can observe in the skeleton of the girdles and limbs of the early therapsids. It will be interesting to see whether the divergencies seen in the locomotor apparatus of the different groups of these early therapsids follow the same lines as the dichotomies produced by the different action in the jaw mechanism. This would, of course, not of necessity have to be the case. The tempo of change in the various parts of the body varies.

In the long process of the development of the paired limbs from fish to quadrupedal mammal the condition in the pelycosaurs and the therapsids present two consecutive stages. The condition presented by the therapsids of the *Tapinocephalus* zone is the first step known in this development from the pelycosaurs. The change is quite abrupt.

Most pelycosaurs have been found in North America and most of the early therapsids are from South Africa. Not only is there this geographical gap but there also appears to be a considerable time gap geologically.

In the pre-*Tapinocephalus* zone rocks no intermediate forms have as yet been found.

PROTO-THERAPSID STAGE

The morphological advance in the locomotor apparatus, from pelycosaur to therapsid constitutes a step of considerable dimensions. The size of this step differs in the different groups of the early therapsids, but by combining the common features of the different groups, we could postulate a proto-therapsid stage.

Having no pelycosaur material available I rely for the evaluation of the morphological stage achieved by these reptiles on the excellent work of Romer (1940).

The advance from pelycosaur to proto-therapsid can be formulated as follows:

Pectoral Girdle (fig 1)

The supra-glenoid buttress and foramen are lost; the glenoid has shifted to a position ventral to the origin of the scapular head of the triceps; the length of the glenoid has decreased, and it has lost its screw shape, and has become a notch situated on the posterior scapulo-coracoid border, facing mainly backwards; the facet receiving the propulsive thrust of the humerus has shifted from an anterior to a dorsal position; originally facing backwards it now faces downwards as well as backwards and lies on the scapula only; the participation of the procoracoid in the glenoid is reduced; the procoracoid has increased in height; the process on the coracoid for the origin of the coracoidal head of the triceps has been lost.

Humerus (figs 2 and 3)

The caput is still terminal, but its 'strap shape' is shortened to form a long oval; the ends are still expanded but a slight 'untwisting' has reduced the

angle they subtend; this means that with the proximal end remaining in a horizontal plane, in the distal end the preaxial border moves downwards and the postaxial border moves upwards to bring the distal end into a more horizontal plane; the epicondyles are slightly reduced in size.

Pelvis (fig 5)

The axial muscles no longer attach to the upper outer face of the ilium and the acetabulum has become nearly circular in outline.

Femur (figs 6 and 7)

The Y system of ridges has commenced to break up with the internal trochanter prominent on the preaxial edge and the fourth trochanteric ridge weakened.

THERAPSID STAGE

If we postulate that the limb musculature developed a tendency to pull the propodials inwards and into a more vertical position and the epipodials more in line with the propodials, with the elbow tending backwards and the knee forwards, what would be the effects on the limb skeleton?

Pectoral Girdle (fig 1)

Firstly, the changed position of the humerus would change the direction of the thrust of the humerus at the glenoid from inwards and forward to upwards and forward. The effect of this is the change we have already noted in the glenoid of the postulated proto-therapsid. All the early therapsids have undergone this change, but to a different degree.

In the hipposaurids this advance has been least, as in them the procoracoid has not been ousted from the glenoid, whereas in all the other early therapsids this has taken place. The effect of the upward thrust of the humerus has been greatest in the Dinocephalia, as here the scapular facet faces very little outwards. The great body weight of the Dinocephalia was an additional factor.

The increase in the upward pull of the supracoracoideus has been least in the pristerognathids so that its area of origin has not moved much upwards and the procoracoid to which it is attached has not grown upwards. In the dicynodontids the lack of upward growth of the procoracoid is probably associated with the development of the acromial process and the supracoracoideus has shifted its origin dorsally on to the scapula and this resulted in a backward retreat of the anterior procoracoidal border. In hipposaurids and dinocephalians there has been a great growth of the anterior part of the procoracoid. Contraction of the trapezius tends to pull one half of the pectoral girdle in an anti-clockwise direction pivoting on its long axis, with the result that the glenoid is made to face more outwards and the humerus could then assume a slightly more forward direction and thus increase the length of the stride. Its insertion on the cleithrum and clavicle has caused these bones to remain quite strong in the theriodonts and Dinocephalia. In the dicynodontids the trapezius

has acquired a more localized insertion. This has led to a reduction of the cleithrum and an inward shift of this bone away from the anterior scapular border. With its main insertion on a localized area of the scapula the pull of the trapezius has caused the development of the prominent acromion, so distinctive a structure in the dicynodontids.

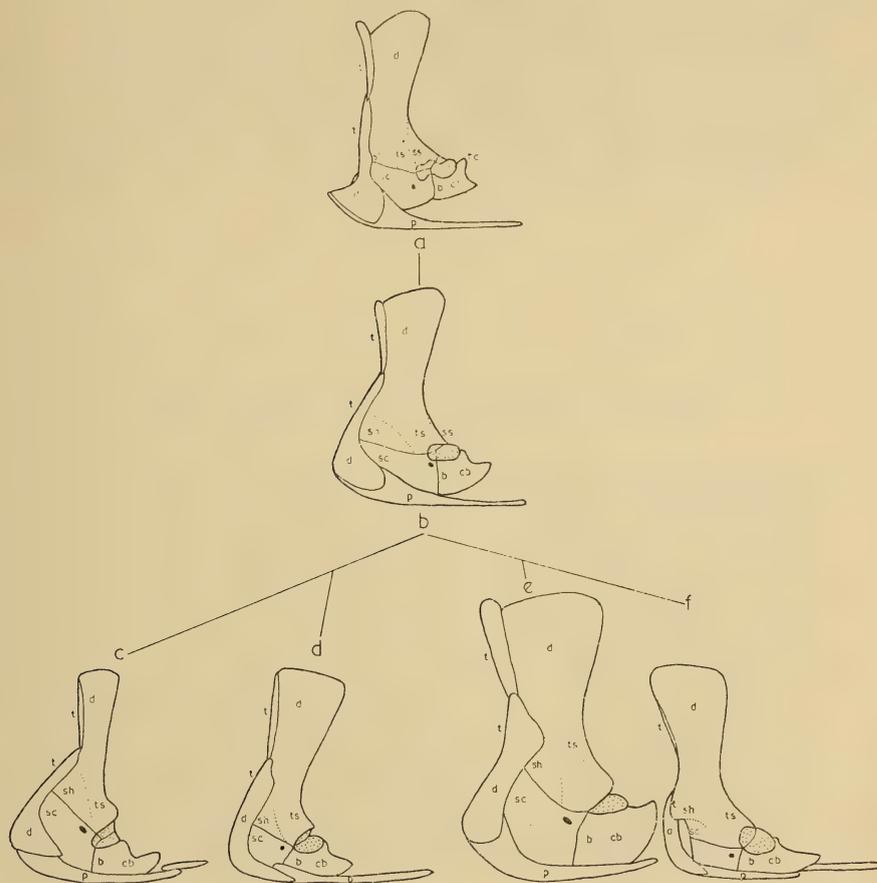


FIG. 1. Pectoral girdles in lateral view, brought to the same basal length.

a. *Dimetrodon* (after Romer). b. Eo-therapsid. c. Hipposaurid. d. Pristerognathid. e. Titanosuchid. f. Dicynodontid.

The development of the mound for the origin of the scapular head of the triceps in the Dinocephalia was probably associated with the great weight in these forms. For the forward swing of the limb a strong extensor action by the triceps would be required.

Although there are considerable differences in the clavicle and interclavicle, which admits of ready distinction infra-ordinally, their function of

affording areas of origin for the deltoid and pectoralis has remained pretty much the same and their structure is basically unchanged.

Humerus (figs 2 and 3)

In assuming a more upright position and in being pulled closer into the body during its backward movement, the humerus has been considerably modified and infra-ordinal differences are clearly marked.

All the early therapsids have lost the strap-shaped proximal caput, which has become a long oval. In all of them the caput is still terminal, but in the hipposaurids and dicynodonts it has become directed more postaxially. This is a decided advance, as with a caput in this position the humerus could swing farther backwards and thus increase the backward reach of the limb. If it is

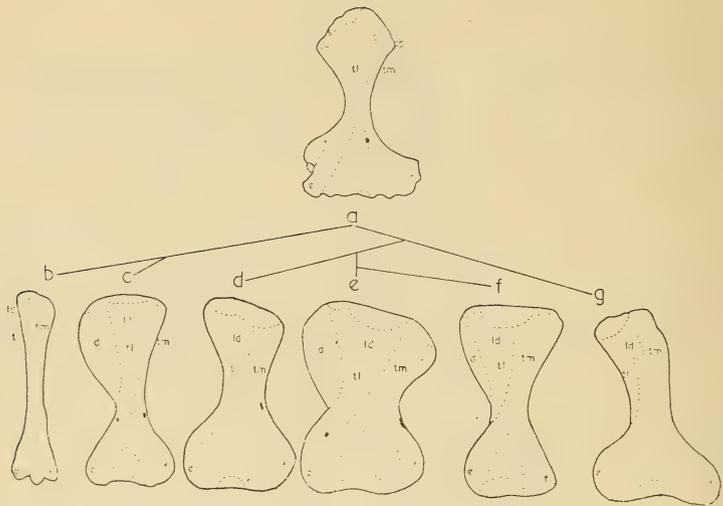


FIG. 2. Humeri, with the distal end in dorsal view, brought to the same length.

a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Pristerognathid. d. Anteosaurid. e. Titanosuchid. f. Tapinocephalid. g. Dicynodontid.

true that the trapezius pull turned the glenoid more outwards in the dicynodontids then the possible forward direction of the humerus would be greater in this group than in any of its contemporaries.

In the infra-orders considerable differences in this process are manifest.

With a more postaxially directed caput the hipposaurids and dicynodontids could rotate the humerus on its long axis in an anti-clockwise direction (seen from the left) and this would bring the capitellum into a position facing downward and lying above the radius which would then be standing vertically to take the weight of the body. In the other therapsids the greater amount of untwisting of the humerus produced the same effect.

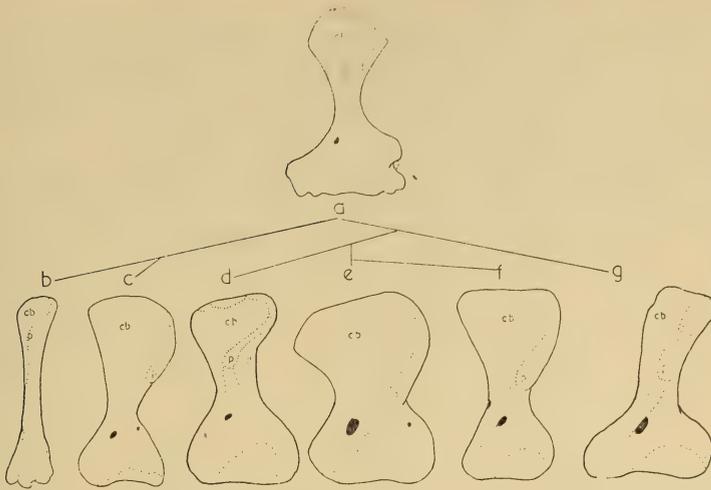


FIG. 3. Humeri with the distal end in ventral view, brought to the same length.

a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Pristerognathid. d. Anteosaurid. e. Titanosuchid. f. Tapinocephalid. g. Dicynodontid.

In hipposaurids and dicynodontids, when the distal end of the humerus lies in a horizontal plane, the proximal end would lie in a plane inclined from the vertical. In this position the areas of insertion of the dorsal muscles on the upper face of the proximal end of the humerus would have rotated in an anti-clockwise direction (as seen from the left). The pull of the deltoid would then be in an anterior direction. The insertion of the latissimus dorsi is still in the primitive position in hipposaurids and dicynodontids but shifted to a more preaxial position in the other therapsids.

On the other hand the untwisting in the other therapsids caused the capitellum to be directed downwards with the proximal end lying horizontally. In these forms the pull of the deltoid would thus be more in a dorsal direction.

On the ventral surface of the humerus it is seen that the untwisting has shifted the delto-pectoral crest to a more preaxial position in the pristerognathids and the herbivorous dinocephalians. The pull exerted by the pectoralis would thus be in a more backward direction than in the hipposaurids and dicynodontids; where it is inwards. This may explain the presence of an ossified sternum in these forms.

In all the early therapsids, except the pristerognathids, the radial condyle (capitellum) is well modelled and faces mostly ventrally. The thrust received is thus from a radius standing vertically with the propodial and epipodial forming a right angle at the elbow joint. To prevent a side slip strong flexors are needed so that we find the entepicondyle well developed and strong antagonistic extensors similarly have a well-developed ectepicondyle for their attachment.

In the pristerognathids the radial condyle is more terminally situated and weakly modelled. Here the epipodial met the propodial at a more obtuse angle. With a vertically disposed radius transmitting the thrust the humerus would have to be more vertical than in the other early therapsids. We thus find in the pristerognathids that the epicondyles are not very strong.

Only in the hipposaurids is there a well-modelled ulnar condyle. In these forms the elbow joint differs greatly from that of all their contemporaries. In addition to the good ulnar condyle there is a deep trochlear fossa. To match

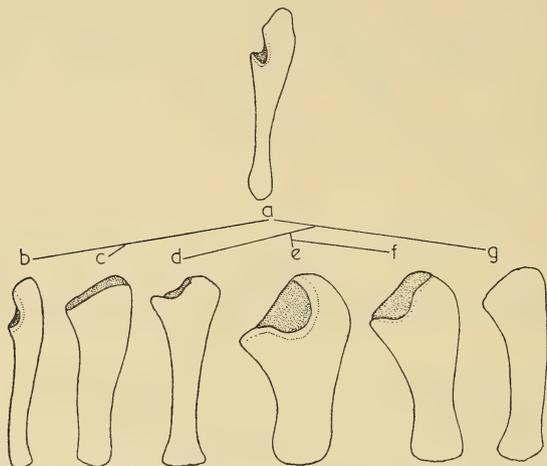


FIG. 4. Ulnae in dorsal view, brought to the same length. a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Pristerognathid. d. Anteosaurid (after Orlov). e. Titanosuchid. f. Tapinocephalid. g. Dicyodontid.

this, only *Hipposaurus* of all the early therapsids, has a well modelled sigmoid fossa to its ulna situated preaxially and with a well-developed olecranon process. The elbow in *Hipposaurus* forms a very efficient close fitting, hinge joint in contrast to the rather loosely fitting joint in all its contemporaries. The whole limb in *Hipposaurus* consists of long slender bones which is in strong contrast to all the other early therapsids. No epicondylar foramina were present in the humerus of *Hipposaurus*.

Except for its slenderness the hipposaurid fore-limb appears to be primitive and there is no evidence of a tendency to a more upright walking gait.

Forefoot (fig 5)

In all the early therapsids the carpus has retained in all essentials the ancestral pelycosaur structure, but in the Dinocephalia and dromasaurs the ulnae has become widened so that it is no longer a long bone.

In the theriodonts the fifth carpal fuses with the fourth.

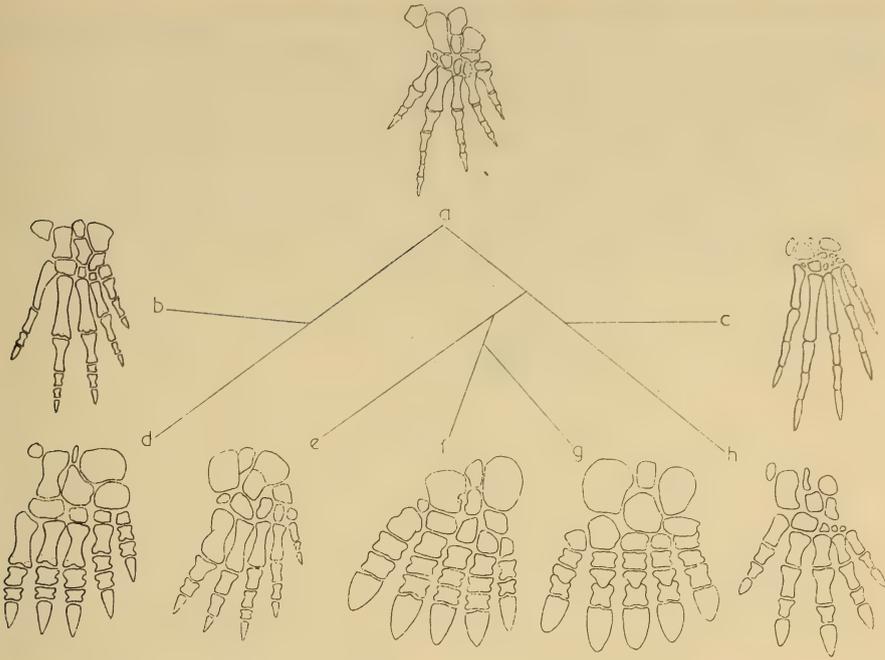


FIG. 5. Manus in dorsal view, brought to the same length.

a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Dromosaur. d. Pristerognathid. e. Anteosaurid. f. Titanosuchid. g. Tapinocephalid. h. Dicynodontid.

The metacarpals remain long and slender in the carnivorous theriodonts and anteosaurs and also in the dromasaurs, but shortened in the herbivorous dicynodonts and very shortened in the heavy herbivorous dinocephalians.

The digits remain long and slender in the hipposaurids and dromasaurs, with the fourth digit the longest; in the former the phalanges are only slightly reduced, to 2, 3, 4, 4, 3 but in the latter they are further reduced to 2, 3, 3, 3, 3; in the anteosaurs to 2, 3, 4, 3, 3. All the others have the primitive mammalian formula 2, 3, 3, 3, 3.

In dicynodonts the third digit is the longest and the fifth still weak, whereas in pristerognathids and the Dinocephalia the fifth digit has become long and strong, with the last four digits tending to be of the same length. The axis of the foot has thus moved postaxially and the foot as a whole is anteriorly directed.

Pelvis (fig 6)

The leg musculature developing a tendency to pull the femur inwards and into a more vertical position, with the knee directed forwards at the beginning of the stroke, would have the following effect on the bones of the girdle and limb: the acetabulum would become more circular in outline with the develop-

ment of a strong iliac buttress dorsally, and shifted to a more anterior position; the head of the femur would tend to become more preaxially directed and shortened and the distal condyles would shift to a more terminal position.

An increase in propulsive thrust by the femur could be obtained by increasing the strength of the ilio-femoralis and the direction of its pull. Increasing

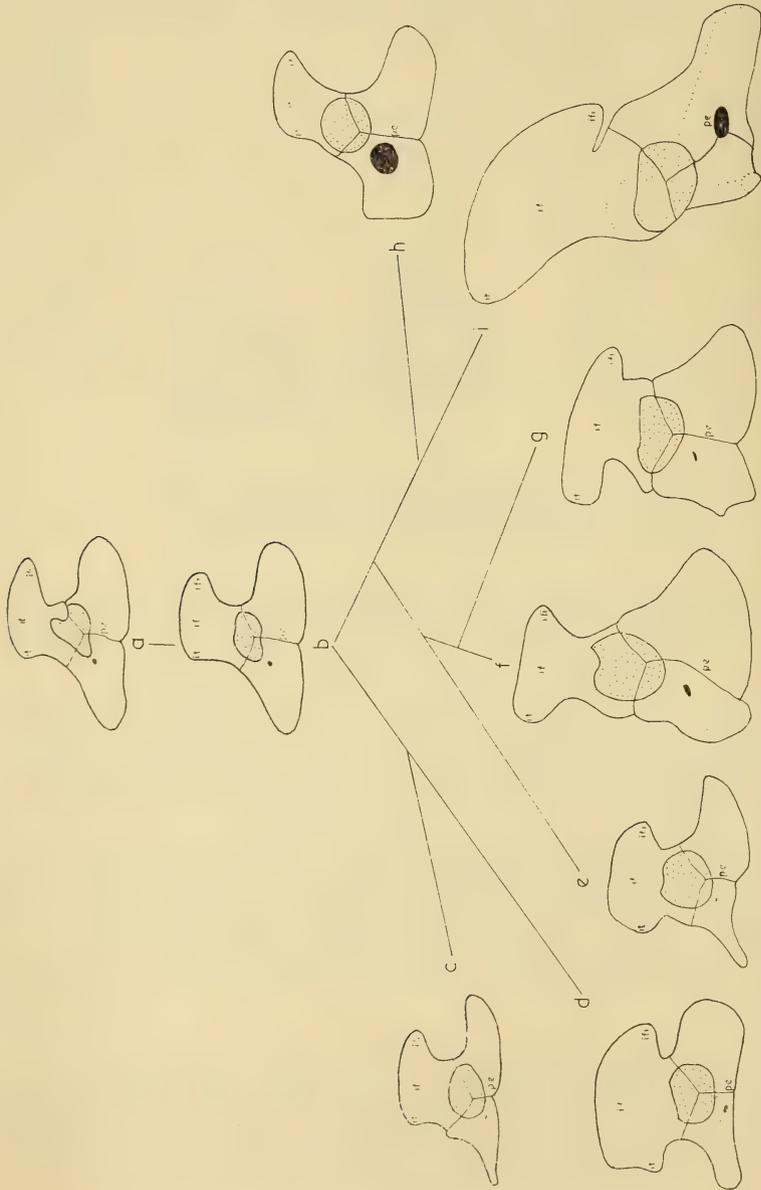


FIG. 6. Pelves in lateral view brought to the same basal length.

a. *Dimetrodon*. b. Eo-Therapsid. c. Hipposaurid. d. Pristerognathid. e. Anteosaurid. f. Titanosuchid. g. Tapinocephalid. h. Dromasaur (after Broom). i. Dicynodontid.

strength would require an improved area of origin on the ilium and a forward development of the ilium relative to the acetabulum would enhance the pull moving the body forwards, with the hip joint as fulcrum. With the ventral adductors requiring less inward pull their area of origin in the pubo-ischiadic plate would be reduced and if shifted backwards in relation to the acetabulum contraction would have a greater propulsive component. In the various groups of early therapsids these changes are apparent in varying degrees.

Upward growth of the ilio-femoralis has pushed the axial muscles off the outer iliac surface and caused an increase in iliac height.

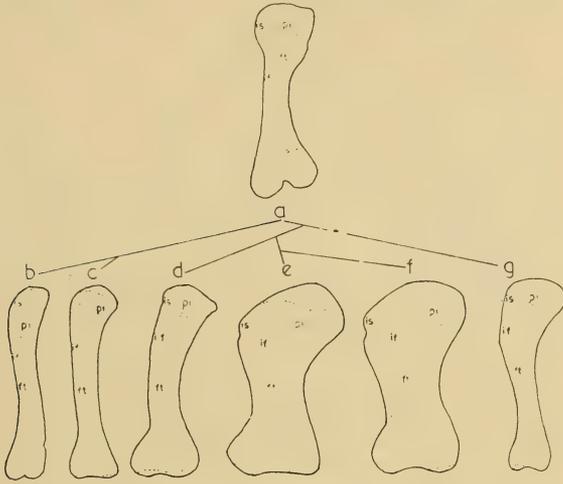


FIG. 7. Femora in dorsal view, brought to the same length.
 a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Pristerognathid. d. Anteosaurid. e. Titanosuchid. f. Tapinocephalid.
 g. Dicynodontid.

In dromasaurids the forward growth of the ilium has been least, with the hipposaurids showing the beginning of an anterior iliac process. In the pristerognathids and the anteosaurs this development is only moderate, but in titanosuchids and tapinocephalids the anterior process is very well developed and in dicynodontids greatly so.

In all the early therapsids the acetabulum has become rounded in outline with a strong iliac buttress, but only in dicynodontids has it moved to the anterior border.

The pubo-ischiadic plate retains its great primitive length in hipposaurids, pristerognathids and anteosaurs, but in contrast to earlier forms the symphysis is strongly ossified in these groups. In titanosuchids, tapinocephalids and especially in dicynodontids the plate is greatly reduced, particularly its pubic part, and the two halves have no ossified symphysis. In these forms the backward

pull by the pubo-ischio femoralis externus and ischio-trochanticus would be much increased.

Femur (figs 7 and 8)

The preaxial shift of the caput femoris has been greatest in the dicynodontids, moderate in titanosuchids and tapinocephalids, but hardly evident in hipposaurids, anteosaurs and pristerognathids where the caput is, however, much shortened.

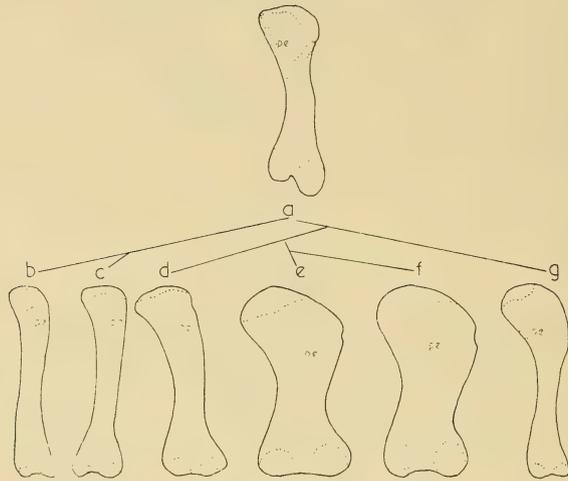


FIG. 8. Femora in ventral view, brought to the same length.
a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Pristerognathid. d. Anteosaurid. e. Titanosuchid. f. Tapinocephalid. g. Dicynodontid.

In all the early therapsids the distal condyles have shifted from the ventral surface to the distal end, but most pronouncedly so in dicynodontids, and in all the two condyles lie in the same plane. The knee joint is thus a simple hinge joint well adapted to a more upright disposition of the limb.

Hindfoot (fig 9)

In the therapsids of the *Tapinocephalus* zone the development in the hind-foot beyond the structural stage achieved by the pelycosaurs is not very radical. The loss of the median central and the reduction of phalanges in the last three digits are two important structural changes.

Within the therapsid stem the first dichotomy was of greater significance. In this parting of the ways the theriodonts took a definite step away from the common proto-therapsid structure. The common pattern of the proximal section of the tarsus was a structure in which the two proximal bones, both wide, lay side by side so that the tarsus was wide proximally. In the pristerognathids

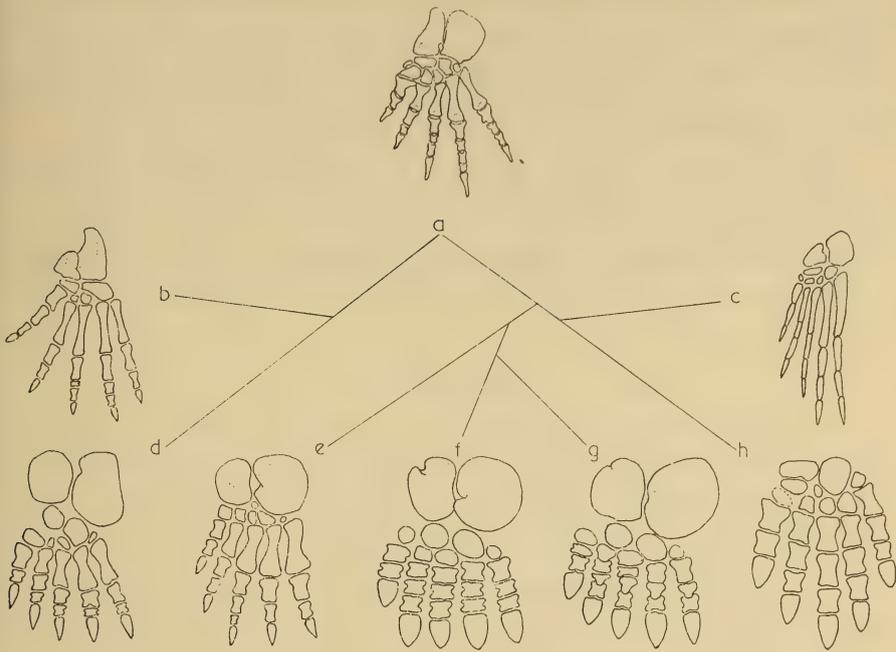


FIG. 9. Pedes in dorsal view, brought to the same length.

a. *Dimetrodon* (after Romer). b. Hipposaurid. c. Dromasaur (after Broom). d. Pristerognathid.
e. Anteosaurid. f. Titanosuchid. g. Tapinocephalid. h. Dicynodontid.

and hipposaurids—the only theriodonts of the *Tapinocephalus* zone in which the tarsus is known, both bones are somewhat reduced in width. But of still greater importance is the fact that in the pristerognathids there is evidence that the astragalus tends to overlies the preaxial edge of the calcaneum and in the hipposaurids the calcaneum developed a pre-axially directed process which passed under the astragalus and is homologous with the mammalian sustentaculum tali.

In the other therapsid groups the proximal part of the tarsus remained wide, with the calcaneum becoming even wider in the Dinocephalia, and the two bones continued to lie side by side without any tendency of overriding.

Before the beginning of *Tapinocephalus* zone times the theriodonts had already experienced a further split. At this stage the hipposaurids developed a tuber calcis, whereas in the pristerognathids the facet for the fibula continued to form the most proximal part of the calcaneum.

Unfortunately we do not know the tarsus in the other *Tapinocephalus* zone families of either the Gorgonopsia or of the Therocephalia and at present this split can only be considered to apply to the hipposaurids, which in other respects are also a rather aberrant family.

In the anomodont stem also, when first encountered in the *Tapinocephalus* zone, a split had already taken place.

In the dinocephalian branch the facet on the astragalus for the tibia has moved on to the dorsal surface, whereas in the dicynodont branch this facet still lies proximally.

In the dicynodont branch the digits are greatly lengthened with curved claws in the Dromasauria, whereas in the dicynodonts the foot is shortened and carried flat nails.

In the Dinocephalia the L-shape of the astragalus is retained in the titanosaurs and tapinocephalians but is lost in the anteosaurs where the navicular is also lost.

CONCLUSIONS

In my previous attempt to show how in pre-*Tapinocephalus* zone times the therapsid stem split up dichotomously, I based my views on the cranial features (1963). Here I suggested that the first split was into theriodonts and anomodonts with a later split by the former into Gorgonopsia and Therocephalia and by the latter into Dicynodontia and Dinocephalia.

No such clear-cut dichotomies are evident in the divergent developments seen in the different parts of the girdles and limbs. The rates of development in the various structures are so different that no general pattern of divergence is apparent. But this does not necessarily invalidate the conclusions drawn from the cranial structures.



FIG. 10. *Scymnosaurus*. Fore limb, nearing the end of the propulsive thrust.

The advances shown by the titanosuchids, tapinocephalids and dicynodontids towards acquiring an upright quadrupedal walking gait are, seen as a whole, of the same order as those known in the pareiasaurs and were as sterile. It is of interest to note that all these groups are herbivores.

The carnivorous anteosaurs retained a crawling habit which also proved to be a dead end.

The early carnivorous theriodonts developed in a more fertile direction, but the hipposaurids, precocious in some of these advances, notably in the proximal part of the tarsus, never showed signs of really fully developing their potentialities towards an upright gait.

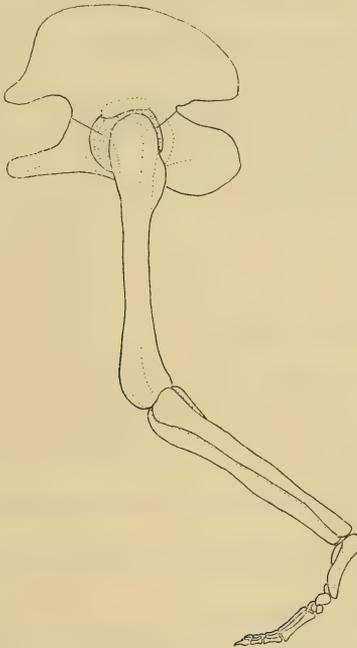


FIG. 11. *Alopepecognathus*. Hind limb, nearing the end of the propulsive thrust.

It is within the therocephalian stem that the starting point towards a mammalian quadrupedal walking gait was most probably located (figs 10 and 11).

Although the pristerognathids of the *Tapinocephalus* zone are a primitive family of early therapsids, I am more inclined to think that the line eventually leading to the mammals had its origin in some such group as the scaloposaurids, which also lived during *Tapinocephalus* zone times. It is a pity, therefore, that its girdles and limbs are still unknown.

SUMMARY

A study of the girdles and limbs of the early therapsids of the *Tapinocephalus* zone reveal early stages in the evolution of the mammalian quadrupedal walking gait. The dichotomy of this group into the theriodonts and the anomodonts and their later subdivisions are not clearly revealed by the developments in their girdles and limbs.

ACKNOWLEDGEMENT

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

REFERENCES

- BOONSTRA, L. D. 1929a. Pareiasaurian studies. Part III. On the pareiasaurian manus. *Ann. S. Afr. Mus.* **28**: 97-112.
- BOONSTRA, L. D. 1929b. Pareiasaurian studies. Part IV. On the pareiasaurian pes. *Ann. S. Afr. Mus.* **28**: 113-122.
- BOONSTRA, 1930. Pareiasaurian studies. Part VI. The osteology and myology of the locomotor apparatus. A. Hind limb. *Ann. S. Afr. Mus.* **28**: 297-366.
- BOONSTRA, L. D. 1932a. Pareiasaurian studies. Part VII. On the hind limb of two little-known pareiasaurian genera: *Anthodon* and *Pareiasaurus*. *Ann. S. Afr. Mus.* **28**: 429-435.
- BOONSTRA, L. D. 1932b. Pareiasaurian studies. Part VIII. The osteology and myology of the locomotor apparatus. B. Fore limb. *Ann. S. Afr. Mus.* **28**: 437-503.
- BOONSTRA, L. D. 1934. A contribution to the morphology of the Gorgonopsia. *Ann. S. Afr. Mus.* **31**: 137-174.
- BOONSTRA, L. D. 1954. The smallest titanosuchid yet recovered from the Karoo. *Ann. S. Afr. Mus.* **42**: 149-157.
- BOONSTRA, L. D. 1955. The girdles and limbs of the South African Dinocephalia. *Ann. S. Afr. Mus.* **42**: 185-306.
- BOONSTRA, L. D. 1963. Early dichotomies in the therapsids. *S. Afr. J. Sci.* **59**: 176-195.
- BOONSTRA, L. D. 1964. The girdles and limbs of the pristerognathid Therocephalia. *Ann. S. Afr. Mus.* **48**: 121-165.
- BOONSTRA, L. D. 1965. The girdles and limbs of the Gorgonopsia of the *Tapinocephalus* zone. *Ann. S. Afr. Mus.* **48**: 237-249.
- BOONSTRA, L. D. 1966a. The girdles and limbs of the Dicynodontia of the *Tapinocephalus* zone. *Ann. S. Afr. Mus.* **50**: 1-11.
- BOONSTRA, L. D. 1966b. The dinocephalian manus and pes. *Ann. S. Afr. Mus.* **50**: 13-26.
- BOONSTRA, L. D. 1967. Langs verskillende weë (Pareiasauria en Dicynodontia). *S. Afr. J. Sci.* (*In press.*)
- BROOM, R. 1932. *The mammal-like reptiles of South Africa*. London: Witherby.
- ORLOV, J. A. 1958. [The carnivorous Deinocephalia (Titanosuchia) from the Upper Permian deposits of the Middle Volga.] *Trudy paleont. Inst.* **72**: 1-114. (*In Russian.*)
- ROMER, A. S. and PRICE, L. W. 1940. Review of the Pelycosauria. *Spec. Pap. geol. Soc. Am.* **28**: i-x, 1-528.

ABBREVIATIONS

advl - anterior dorso-ventral line	p - pectoralis
b - biceps	pe - pubo-ischio-femoralis externus
cb - coraco-brachialis	pi - pubo-ischio-femoralis internus
d - deltoid	pt - pubo-tibialis
e - extensors	sc - supracoracoideus
f - flexors	ss - sub-coraco-scapularis
ft - femoro-tibialis	sh - scapulo-humeralis
if - ilio-femoralis	t - trapezius
ifi - ilio-fibularis	tc - coracoidal head of the triceps
is - ischio-trochantericus	tl - lateral head of the triceps
it - ilio-tibialis	tm - medial head of the triceps
ld - latissimus dorsi	ts - scapular head of the triceps
lml - latero-median line	

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'). with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

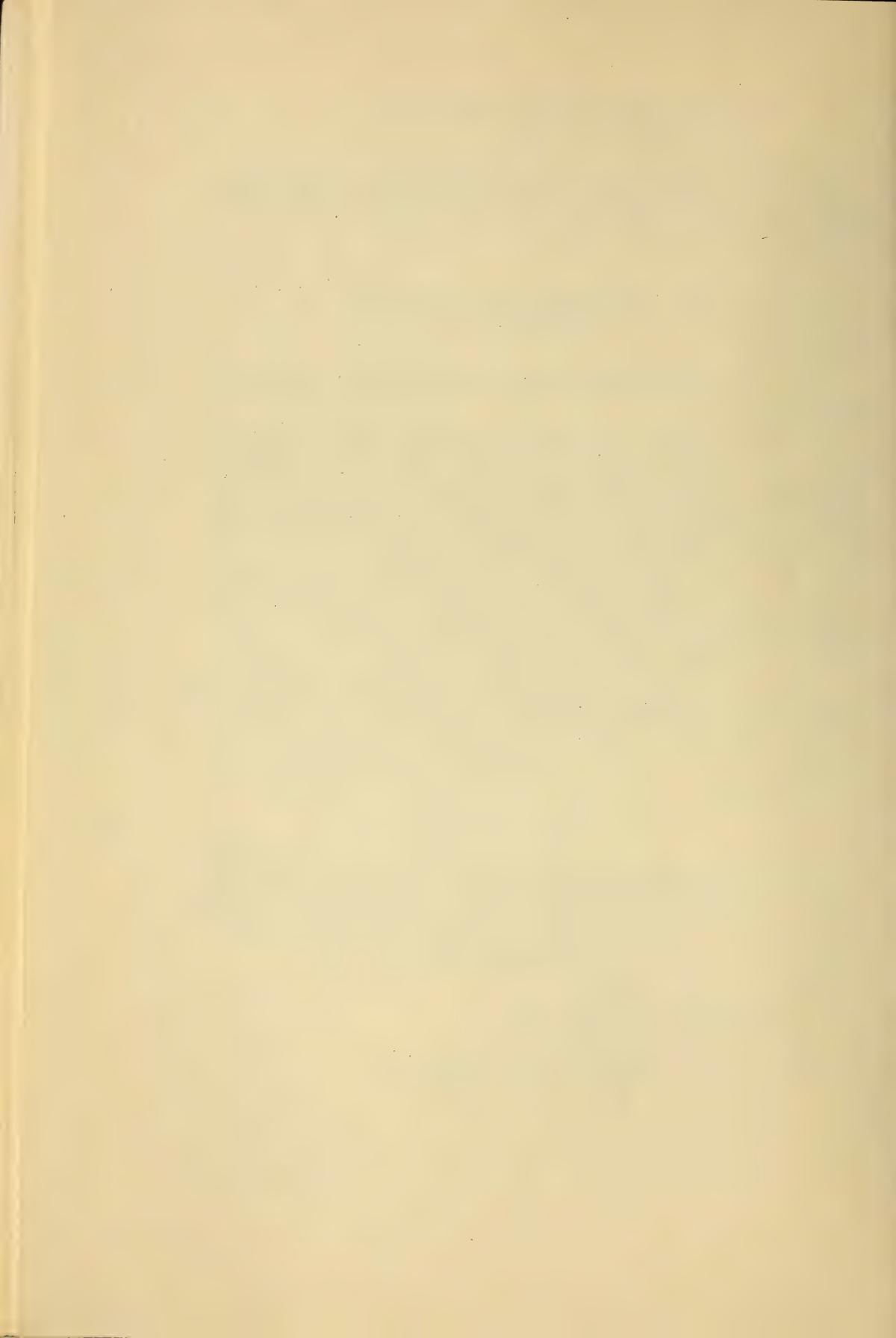
Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



MARY-LOUISE PENRITH

STUDIES ON THE SOUTH AFRICAN CLINIDAE.
II. TWO NEW SPECIES OF *CLINUS* FROM
THE WESTERN CAPE

October 1967 Oktober
Volume 50 Band
Part 4 Deel



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

Cape Town Kaapstad



THE ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

DIE ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

50c

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

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

STUDIES ON THE SOUTH AFRICAN CLINIDAE. II. TWO NEW SPECIES OF *CLINUS* FROM THE WESTERN CAPE

By

MARY-LOUISE PENRITH

South African Museum, Cape Town

(With 18 text-figures)

CONTENTS

	PAGE
Introduction	43
Descriptions	43
Fin ray counts and body proportions	52
Discussion	57
Summary	58
Acknowledgements	58
References	58

INTRODUCTION

During 1963-4 a number of specimens of two clinids were obtained which, although they agree sufficiently in superficial appearance and fin counts with *Clinus acuminatus* (Bloch & Schneider) to have been identified provisionally as that species, have been found on closer examination to differ constantly in several characters from *Clinus acuminatus* and from each other. They are therefore described as new species. A redescription of *Clinus acuminatus* is included for comparative purposes.

DESCRIPTIONS

Clinus acuminatus (Bloch & Schneider, 1801)
(figs. 1, 4(a))

Blennius acuminatus Bloch & Schneider, 1801: 169.

Clinus acuminatus: Cuvier, 1817: 173; Cuvier & Valenciennes, 1836: 370; Swainson, 1839: 75; Gilchrist & Thompson, 1908: 124; Thompson, 1918: 146; Barnard, 1927: 859; Hubbs, 1952: 106.

Ophthalmolophus acuminatus: Smith, 1945: 542; Smith, 1949: 355.

Material: 1 specimen, 59 mm., Angra Pequena (Lüderitzbucht, South West Africa), S.A.M. 10544; 16 specimens, 24-90 mm., Lüderitzbucht, South West Africa, rock pools near top of shore, S.A.M. 24206; 38 specimens, 51-100

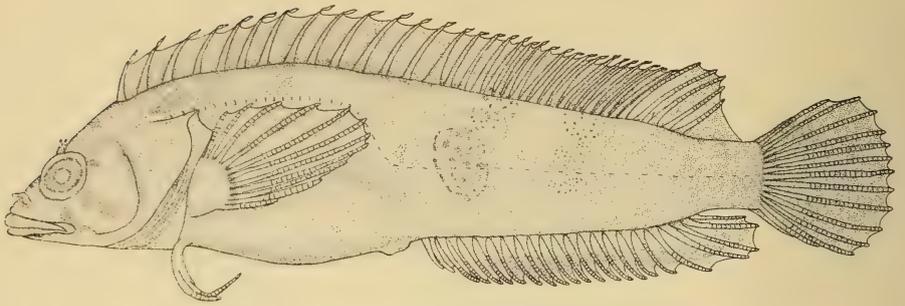


FIG. 1(a). *Clinus acuminatus* (Bloch & Schneider).

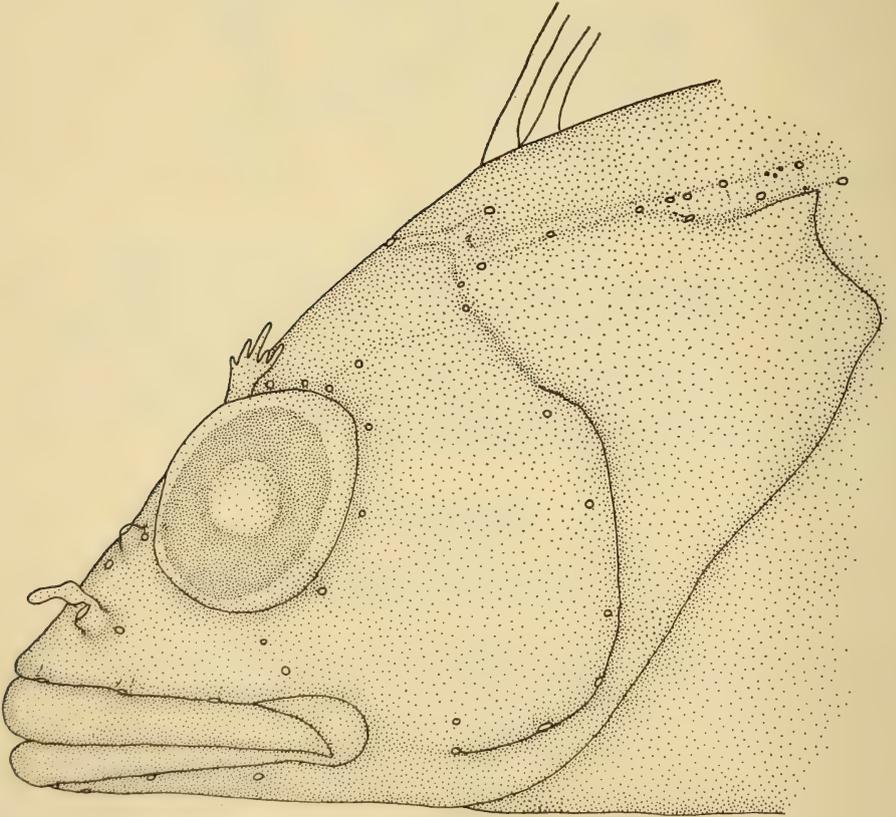


FIG. 1(b). Head pore system, *Clinus acuminatus*.

mm., Port Nolloth, rock pools near top of shore, S.A.M. 24220; 12 specimens, 65–113 mm., Lambert's Bay, rock pools near top of shore, S.A.M. 23922; 2 specimens, 37 & 38 mm., Langebaan, Saldanha Bay, rock pool near top of shore, S.A.M. 23925; 7 specimens, 41–73.5 mm., Sea Point, rock pool near top of shore, S.A.M. 22840; 3 specimens, 66–88 mm., Kommetjie, S.A.M. 10541; 3 specimens, 47–55 mm., Froggy Pond, False Bay, rock pool near top of shore, S.A.M. 23924; 1 specimen, 97 mm., St. James, False Bay, S.A.M. 12023; 27 specimens, 43.3–103 mm., St. James, False Bay, rock pools near top of shore; 21 specimens, 35–86 mm., False Bay, S.A.M. 10542; 4 specimens, 73–88 mm., Hermanus, rock pool near top of shore.

Description

Fin counts: D. XXXI–XXXIV (XXXII–XXXIII) 5–7; A. II 20–24 (21–22); P. 12–13 (12); V. I 2–3; C. 13.

Dorsal fin low, even, first spine shortest, 14.5–25% of head length. Clusters of 2–3 cirri at tips of dorsal spines for about half length of fin. No notch in membrane between third and fourth dorsal spines. Pectoral fin rounded, of twelve rays, exceptionally thirteen. Inner pelvic ray greatly reduced or absent. Caudal peduncle short, 20.5–33.5% of head length, depth of caudal peduncle 20–35% of head length. Caudal fin subtruncate.

Body covered with small scales extending on to dorsal fin base, anal and caudal fin bases and head naked. Depth at anal origin 4.5–5.75 in standard length. Head 3.2–4.25 in standard length. Interorbital flat, 12.5–20.8% of head length. Snout wedge-shaped, angle of profile acute. Eye 2.75–5 in head. Supra-orbital tentacle with a short, flattened stalk, terminating in a number of short, simple branches. Cirrus on anterior nostril short, flattened, trilobed. Upper jaw 34.5–50% of head length, mouth increasing with size of fish. Vomer toothed. Lips moderate to fairly thin.

Pores on head few, large (fig. 1(b)), mostly simple, opening flush with skin.

Lateral line of 2–4 double pores in front above operculum, then of mainly alternating single pores above and below line to post-pectoral curve; after that of short separate horizontal tubes with a pore at either end. Intromittent organ of male large and spade-shaped, with a moderately long, thick basal portion, a small pair of dorsal lips, and a large pair of broad ventral lips ensheathing the tip (fig. 4(a)).

Colouring: Green with brown and cream cross-bars, or green with black speckling forming large sparse spots with a mosaic-like pattern. Tips of all fins and supra-orbital tentacles orange red. Belly whitish. Two dark radiating bands across cheek.

Distribution

Lüderitzbucht (South West Africa) to Cape Agulhas, under stones in shallow pools near the top of the shore.

Clinus obtusifrons n.sp.

(fig. 2, 4(b))

Material: 2 specimens, 24 and 36 mm., Lüderitzbucht, South West Africa, rock pools from mid-tidal level down, S.A.M. 24211; 11 specimens, 56–93 mm., Port Nolloth, rock pools from mid-tidal level down, S.A.M. 24216; 1 specimen, 20 mm., 26 miles north of Swakopmund, South West Africa, rock pool at mid-tidal level, S.A.M. 24201; 5 specimens, 56–80 mm., Sea Point, rock pool at mid-tidal level, S.A.M. 23923; 3 specimens, 56–80 mm., Gert du Toit Bay, southern Namaqualand, S.A.M. 24253; 12 specimens, 32–76 mm., Lambert's Bay, S.A.M. 24254; 3 specimens, 66–115 mm., Hondeklip Bay, rock pools from mid-tidal level down, S.A.M. 24670 (paratypes); 1 specimen, 116 mm., Hondeklip Bay, rock pool at mid-tidal level, S.A.M. 24671 (holotype).

Description

Fin counts: D. XXX–XXXII (XXX–XXXI) 6–7; A. II 20–22 (20–21); P. 13; V. I 2–3; C. 13.

First three dorsal spines not forming a crest, but equal to or longer than fourth and succeeding spines, second spine longest. First spine 27–34% of head length. No notch in membrane between third and fourth dorsal spines. Dorsal spines each with a single cirrus at tip. Pectoral fin rounded, invariably of thirteen rays. Inner pelvic ray minute or absent. Caudal peduncle short, 20–35% of head length, depth of caudal peduncle 20–35% of head length.

Body covered with small scales, extending on to dorsal and caudal fin bases but not on to anal fin base or head. Depth at anal origin 4–5. Head heavy, 3.2–4.25 in standard length. Snout bluntly rounded, angle of profile obtuse. Interorbital flat in small specimens, concave in larger specimens (over 100 mm.), with marked bony ridges over the eye, 16.7–27.3% of head length. Eye 3–4.5 in head. Supra-orbital tentacle with a flattened stalk terminating in several short, simple branches. Some mucus pores on head opening on small papillae. Nasal cirrus flattened, expanded, and roughly triangular at tip. Upper jaw 36.4–50%

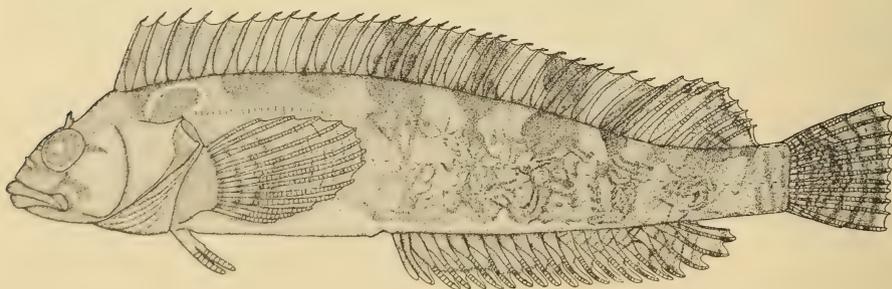


FIG. 2(a). *Clinus obtusifrons* n.sp.

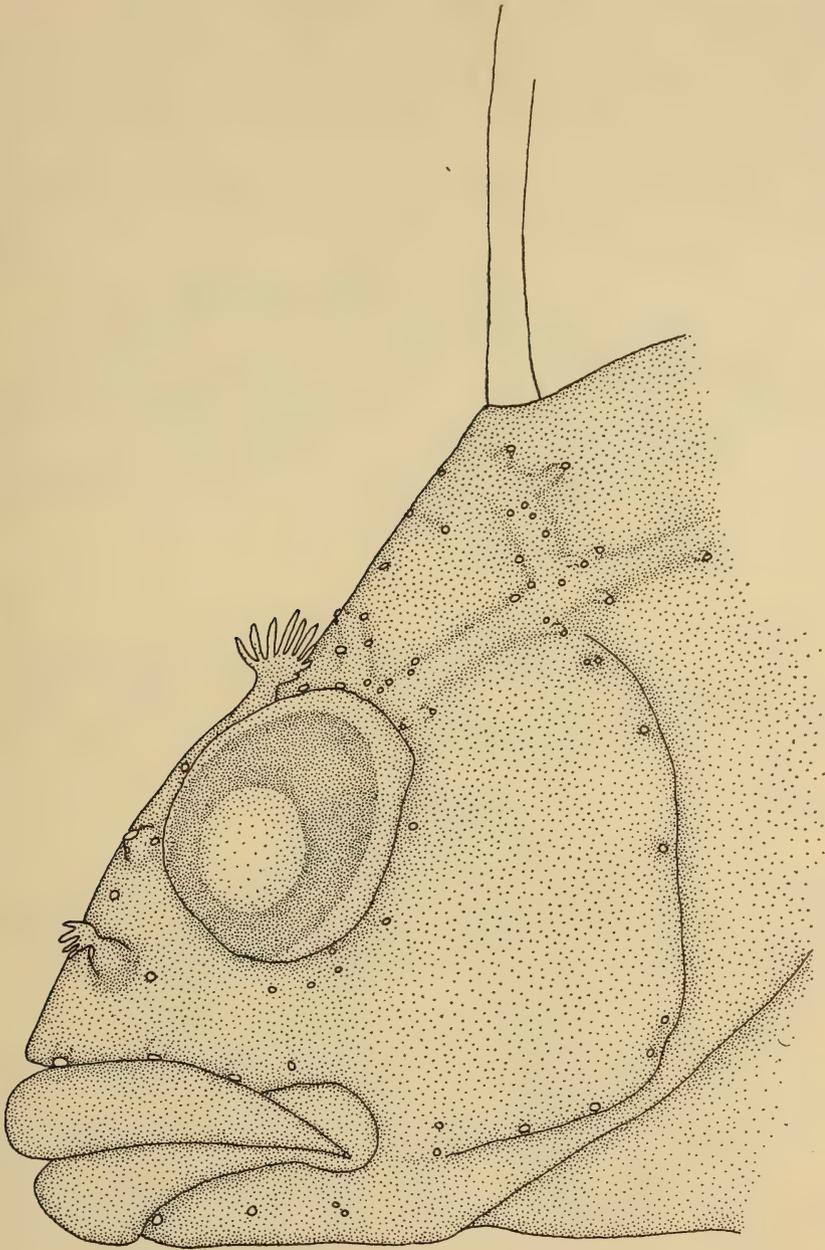


FIG. 2(b). Head pore system, *Clinus obtusifrons*.

of head length, mouth increasing with size of fish. Vomer toothed. Lips moderate to thick.

Pores of head few, most single; several of postocular region double. Most opening flush with skin surface. Some, especially postocular region, opening on papillae (fig. 2(b)).

Lateral line of single pores opening above and below line, interspersed with a few double pores, to post-pectoral curve, then of short separate horizontal tubes with a pore at either end. Intromittent organ of male with a long basal portion and a slender, upwardly hooked tip. A pair of small, rounded lateral lips (fig. 4(b)) and a pair of smaller rounded dorsal lips.

Colouring: Dusky or slaty with darker cross-bars, speckled or mottled with blue or white when fresh. Tips of anal and pelvic rays red. A prominent bluish ocellate spot on shoulder. Two dark radiating bars across cheek. Tips of dorsal fin and supra-orbital tentacles white.

Distribution

Swakopmund (South West Africa) to False Bay, under stones in pools from mid-tidal level to bottom of shore.

Remarks

This species can be distinguished from *Clinus acuminatus* by the shape of the snout, the number of pectoral rays, the form of the intromittent organ, the height of the first dorsal spine, the width of the interorbital and its shape in large specimens. It also occupies a different habitat on the shore.

Clinus berrisfordi n.sp. (fig. 3, 4(c))

Material: 15 specimens, 37.5–96 mm., Onrust River mouth, rock pool near bottom of shore, S.A.M. 24221 (paratypes); 1 specimen, 106 mm., Onrust River mouth, rock pool near bottom of shore, S.A.M. 24601 (holotype).

Description

Fin counts: D. XXXIII–XXXVI (XXXIV–XXXV) 5–6; A. II 23–25 (23–24); P. 11–12 (12); V. I 3; C. 13.

First three dorsal spines not elevated to form a crest, but equal to or longer than fourth and succeeding spines, first spine 25–33.3% of head length. No notch in membrane between third and fourth dorsal spines. Dorsal spines with clusters of 3 fine cirri at tips for about half length of fin. Pectoral fin rounded, of twelve, exceptionally eleven, rays. Inner pelvic ray minute but developed in all specimens examined. Caudal peduncle short, length 20–35% of head length. Caudal fin subtruncate.

Body covered with small scales extending on to dorsal and caudal fin bases; anal fin base and head naked. Depth at anal origin 4.5–5.1 in standard length.

Interorbital flat, 12.5–16.7% of head length. Snout wedge-shaped, angle of profile acute. Eye 3.4–2 in head. Supra-orbital tentacle with a flattened stalk terminating in numerous long, slender filaments. Cirrus on anterior nostril with a narrow stalk and a flattened, bilobed tip. Upper jaw 36.4–50% of head length. Vomer toothed. Lips moderate to thin.

Pores of head more numerous than in preceding species, most double, on more or less raised papillae, sensory canals clearly visible, raised (fig. 3(b)).

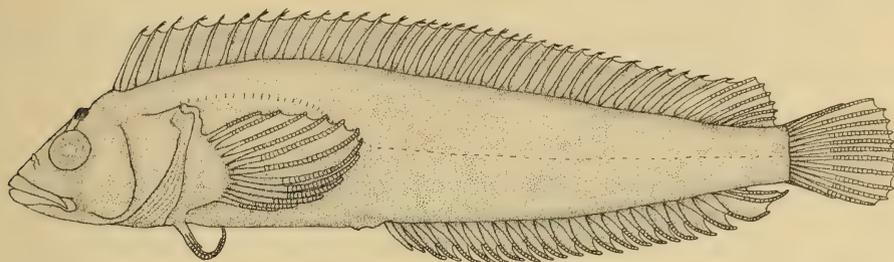


FIG. 3(a). *Clinus berrisfordi* n.sp.

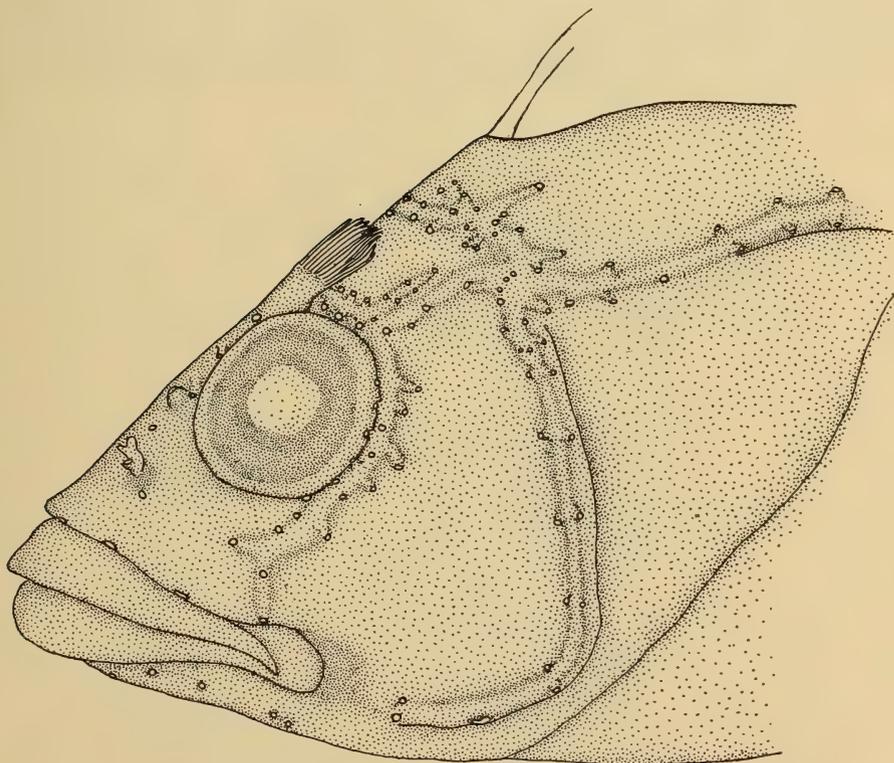


FIG. 3(b). Head pore system, *Clinus berrisfordi*.

Lateral line usually of about 27 double pores in front to post-pectoral curve, then of short, separate horizontal tubes with a pore at each end. Intromittent organ of male with a long basal portion and a slender, upturned tip; a pair of bilobed ventro-lateral lips and a small pair of rounded dorsal lips (fig. 4(c)).

Colouring: Reddish orange with faint darker cross-bars. Two dark radiating lines from eye across cheek.

Distribution

So far recorded from the single type locality, Onrust River mouth, near Hermanus.

Remarks

This species differs from *Clinus acuminatus* in the dorsal and anal ray counts, the form of the male intromittent organ, the height of the first dorsal spine, the form of the supra-orbital tentacle, the anterior part of the lateral line and the head pores and the habitat. It differs from *Clinus obtusifrons* in the dorsal, anal, and pectoral fin counts, the shape of the snout, the form of the supra-orbital tentacle, the form of the intromittent organ, the anterior part of the lateral line, the head pores, the width of the interorbital, the shape of the interorbital in large specimens, and the clusters of cirri at the tips of the dorsal spines.

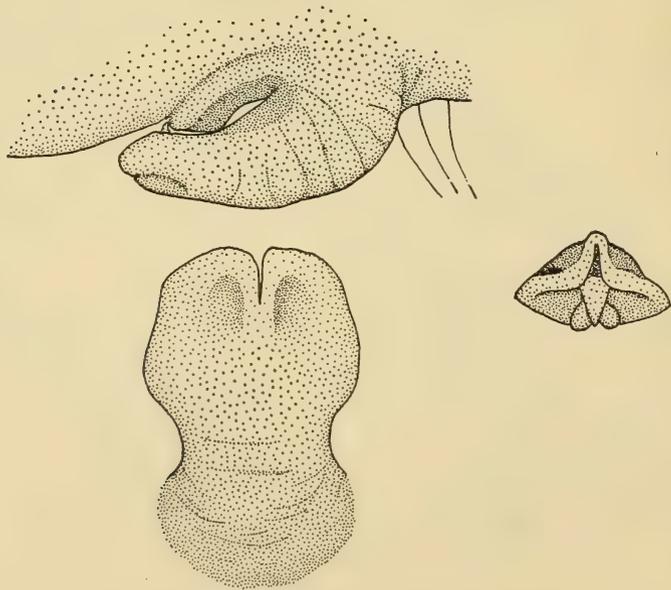


FIG. 4. Intromittent organs of (a) *Clinus acuminatus*.

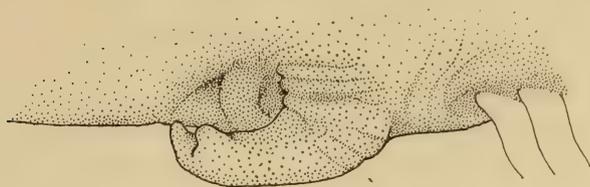


FIG. 4(b). *Clinus obtusifrons*.

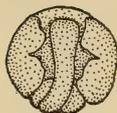
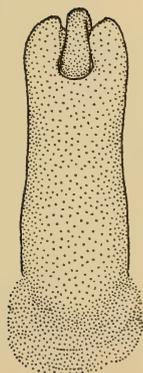
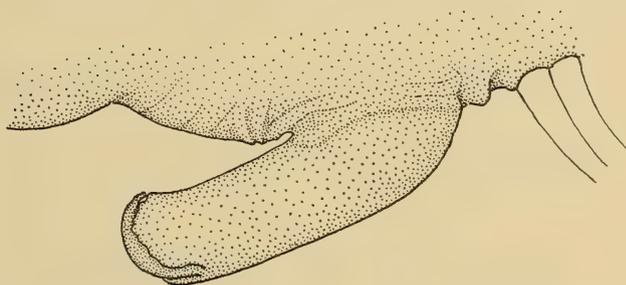


FIG. 4(c). *Clinus berrisfordi*.

FIN RAY COUNTS AND BODY PROPORTIONS

During the examination of the three species described above it was found that for certain characters, such as some of the fin ray counts and body proportions, although the ranges for the different species overlapped considerably or were identical, the means differed widely. It was decided that this could best be demonstrated by a statistical method used by Hubbs (1952) to show statistical differences between populations of American clinids. The method demonstrates graphically the range, mean, and one standard deviation and two standard errors on either side of the mean. Thus, in fig. 5, the base line represents the range, the upright line the mean, and the shaded areas the limits of two standard errors on either side of the mean. The unshaded areas represent the limits of one standard deviation on either side of the mean.

The samples were not divided into different size groups, as allometric growth in the South African Clinidae has been found to be similar and slight for most species. Measurements showing a very wide range, such as orbit diameter and upper jaw length, can be considered to exhibit allometric growth, but those characters show no clear differences between these and many other related species, so are not considered important at the specific level.

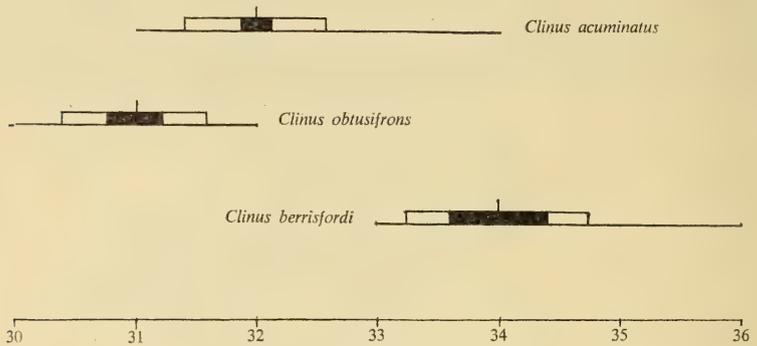


FIG. 5. Number of dorsal spines.

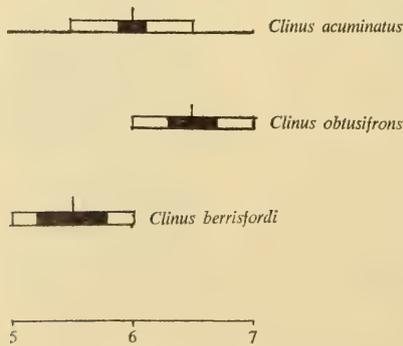


FIG. 6. Number of dorsal soft rays.

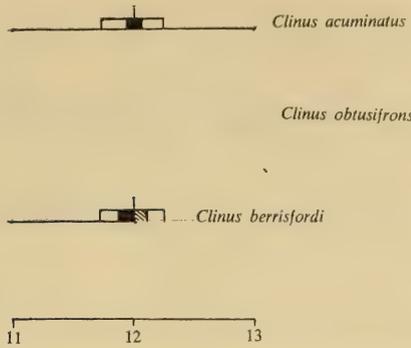


FIG. 7. Number of pectoral rays.

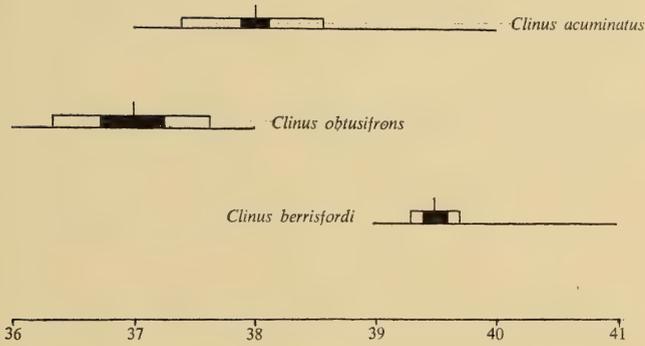


FIG. 8. Total number of dorsal elements.

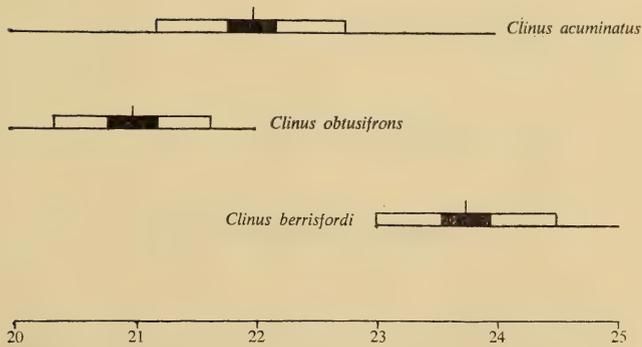


FIG. 9. Number of anal rays.

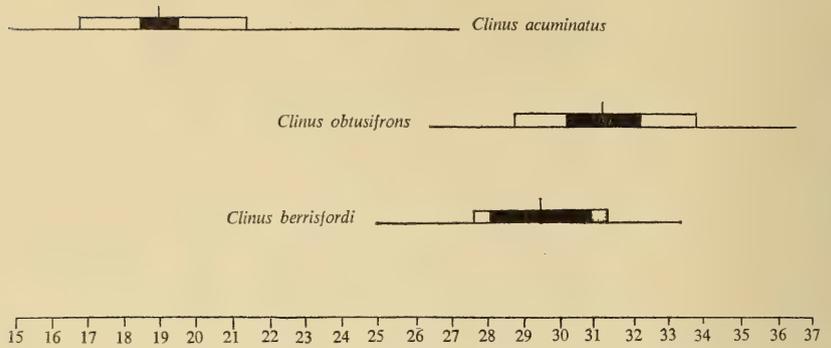


FIG. 10. Height of first dorsal spine as percentage of head length.

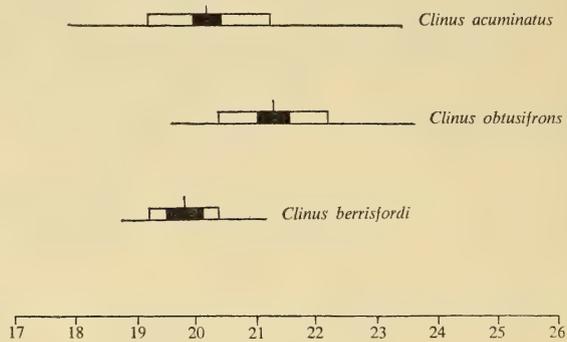


FIG. 11. Depth at dorsal origin as percentage of standard length.

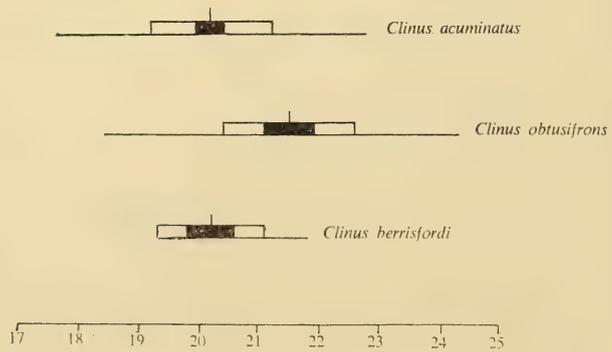


FIG. 12. Depth at anal origin as percentage of standard length.

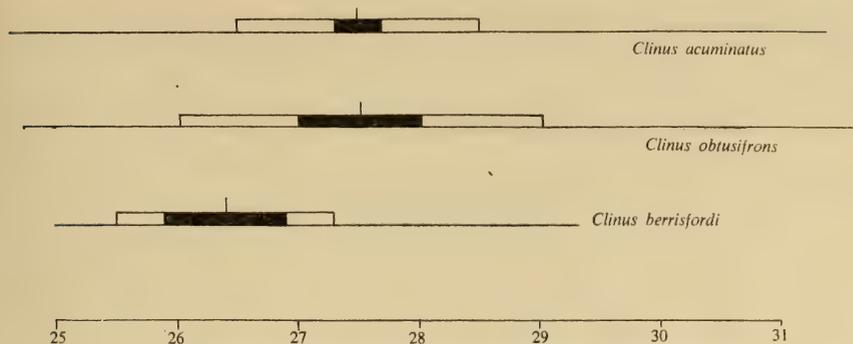


FIG. 13. Head length as percentage of standard length.

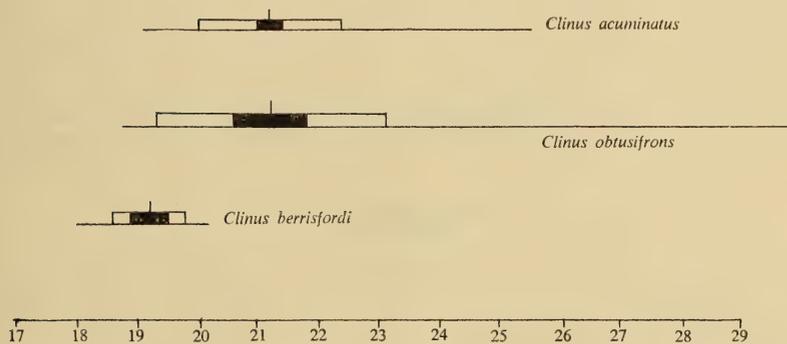


FIG. 14. Dorsal origin to snout as percentage of standard length.

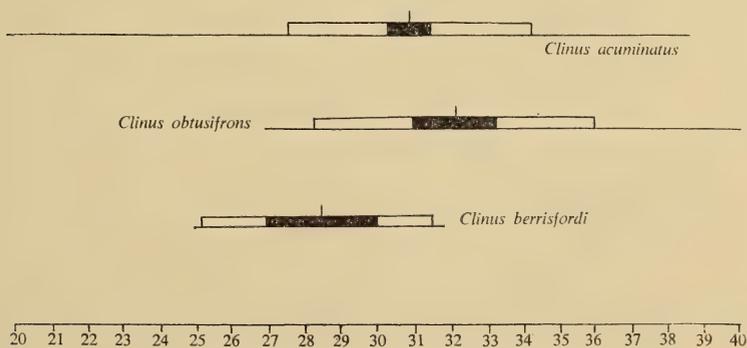


FIG. 15. Snout length as percentage of head length.

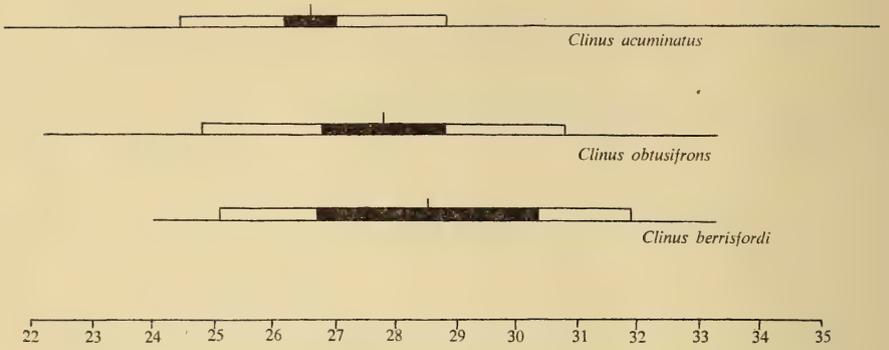


FIG. 16. Orbit diameter as percentage of head length.

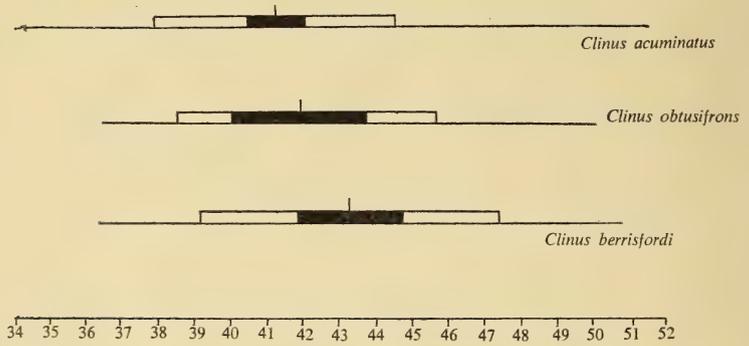


FIG. 17. Upper jaw length as percentage of head length.

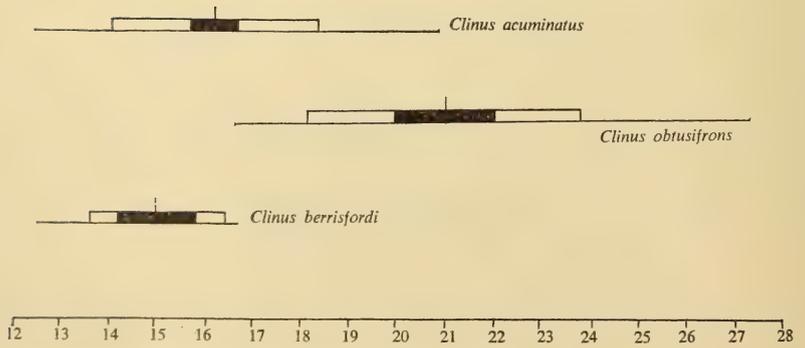


FIG. 18. Interorbital width as percentage of head length.

The results are shown in figs. 5-18. The formulae used for determining the standard error and standard deviation were those given by G. M. Smith (1958). The differences are considered to be significant if there is no overlap between the limits of two standard errors on either side of the mean for two different species.

Fig. 5 shows that *Clinus berrisfordi* has a considerably higher dorsal spine count than the other two species, and also that *Clinus obtusifrons* has a statistically lower count than *Clinis acuminatus*, although owing to the overlap of the normal ranges the dorsal spine count cannot be used as a distinguishing character for these two species. Conversely, *Clinus obtusifrons* has a statistically higher number of dorsal soft rays than the other two species (fig. 6). However, the range of the dorsal soft ray count is so small for all three species that the dorsal total shows little difference from the dorsal spine count (fig. 8). *Clinus obtusifrons* has statistically the lowest anal ray count (fig. 9). It would be expected that an increased number of median fin elements would be associated with elongation of the body, and in this connection it is interesting to note that *Clinus obtusifrons*, with the lowest number of median fin elements, is statistically deeper-bodied, i.e. less elongate, than the other two species (figs. 11, 12). The marked shortness of the first dorsal spine of *Clinus acuminatus* is demonstrated in fig. 10. Figs. 13-15 show *Clinus berrisfordi* to have a statistically shorter head and snout than the other two species. The interorbital is shown to be significantly wider in *Clinus obtusifrons* than in *C. acuminatus* and *C. berrisfordi* (fig. 18).

DISCUSSION

It is evident both from the differences in measurable characters and from differences such as the form of the intromittent organ, supraorbital tentacle, lateral line, cirral clusters on spines, and snout shape that the three clinids discussed cannot be placed together in a single species. The three clinids are therefore treated as separate species. In many groups it might be felt that the differences indicate subspecific rather than specific separation, but among the South African Clinidae there are so many pairs or groups of species that closely resemble one another and can be separated only on minor characters, that to introduce subspecies into the group would necessitate the use of a complex trinomial classification, and this is considered undesirable where the different species are clearly distinguishable, although closely related. The three species in question are sufficiently distinct from one another to render confusion unlikely if specimens are properly examined, and for this reason it is considered justifiable to treat them as separate species. The ecological separation of the species is not decisive, since there is considerable overlap in the ecological ranges of most of them. Although *Clinus acuminatus* has its maximum occurrence in pools at the top of the shore while the other two species are found at mid-tidal level or below, at Port Nolloth a single specimen of *Clinus acuminatus* was collected in a mid-tidal pool together with several specimens of *Clinus obtusifrons*, and presumably this occurs not infrequently, yet the two populations have remained distinct.

SUMMARY

Two new species of fish of the genus *Clinus*, *C. obtusifrons* and *C. berrisfordi*, are described and figured, and compared with *C. acuminatus* (Bloch & Schneider). Differences in the fin ray counts and body proportions of the species are shown by means of statistical diagrams.

ACKNOWLEDGEMENTS

I am indebted to Professor J. L. B. Smith of the Department of Ichthyology, Rhodes University, Grahamstown, for helpful discussions, and to Mr. C. D. Berrisford and my husband, Mr. M. J. Penrith, for collecting the specimens.

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

REFERENCES

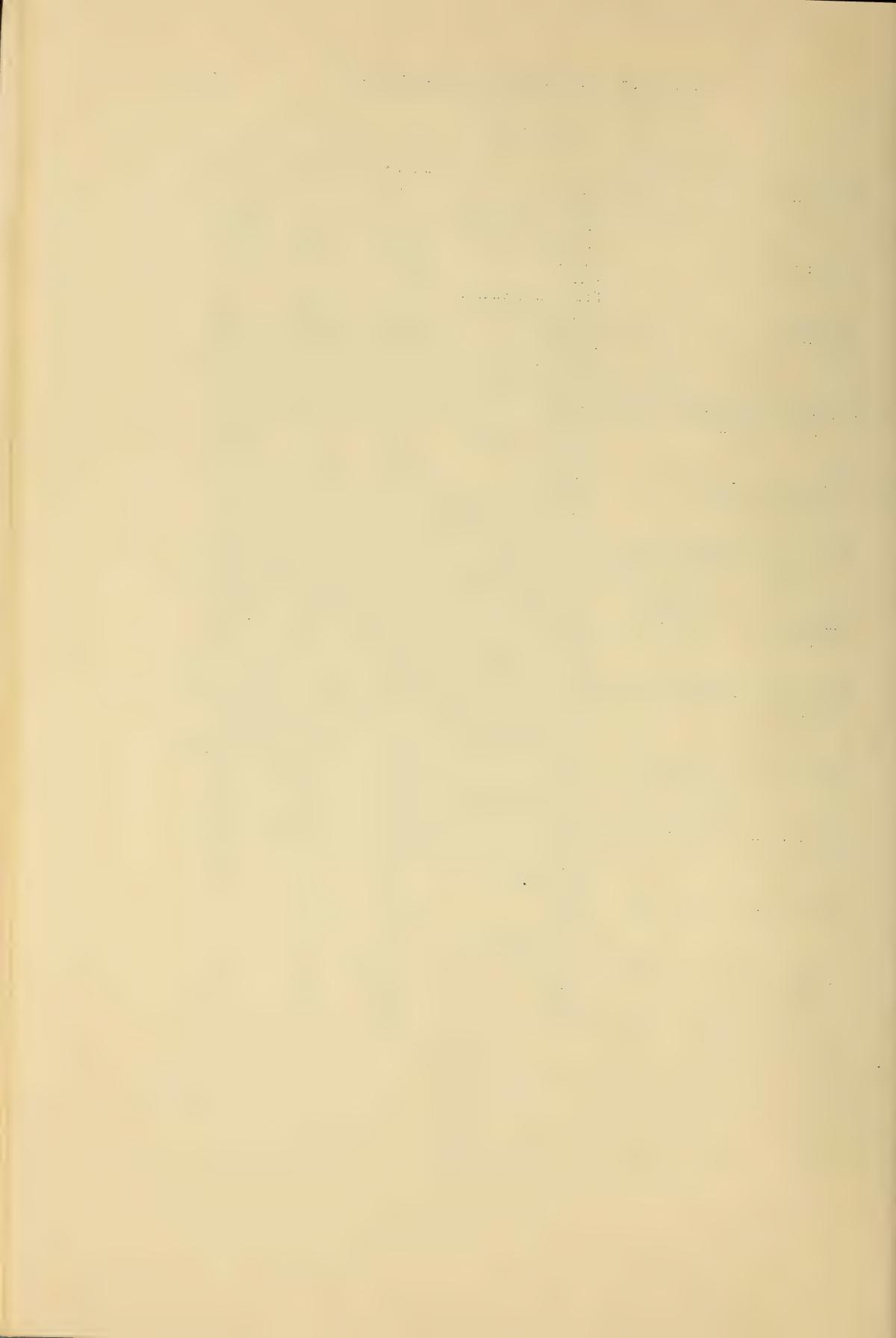
- BARNARD, K. H. 1927. A monograph of the marine fishes of South Africa. *Ann. S. Afr. Mus.* **21**: 419-1065.
- BLOCH, M. E. & SCHNEIDER, J. G. 1801. *Systema ichthyologie inconibus ex illustratum. Post obitum opus inchoatum absolvit, correxit, interpolavit Johann Gottlob Schneider*. Berolini.
- CUVIER, G. L. C. F. D. 1817. *Le règne animal distribué d'après son organisation . . . 2*. Paris.
- CUVIER, G. L. C. F. D. & VALENCIENNES, A. 1836. *Histoire naturelle des poissons*. **11**. Paris: F. G. Levrault.
- GILCHRIST, J. D. F. & THOMPSON, W. W. 1908. The Blenniidae of South Africa. *Ann. S. Afr. Mus.* **6**: 97-142.
- HUBBS, C. 1952. A contribution to the classification of the blennioid fishes of the family Clinidae, with a partial revision of the eastern Pacific forms. *Stanford ichthyol. Bull.* **4**: 41-165.
- SMITH, G. M. 1958. *A simplified guide to statistics for psychology and education*. 3rd ed., revised. New York: Rinehart.
- SMITH, J. L. B. 1945. The fishes of the family Clinidae in South Africa. *Ann. Mag. nat. Hist.* (11) **12**: 535-546.
- SMITH, J. L. B. 1949. *The sea fishes of southern Africa*. Cape Town: Central News Agency.
- SWAINSON, W. 1839. The natural history and classification of fishes, amphibians, and reptiles, or monocardian animals. In *The Cabinet Encyclopedia*. **2**. London: Longman, Orme, Brown, Green & Longman.
- THOMPSON, W. W. 1918. Catalogue of the fishes of the Cape Province. *Mar. biol. Rep., Cape Tn.* 75-177.

TABLE I. Data on which figs. 5-18 are based

Characters		<i>Clinus acuminatus</i>	<i>Clinus obtusifrons</i>	<i>Clinus berrisfordi</i>
Dorsal spines	Range	31-34	30-32	33-36
	Mean	32	31	34
	Standard deviation	0.60	0.60	0.74
	Standard error	0.05	0.10	0.20
Dorsal soft rays	Range	5-7	6-7	5-6
	Mean	6	6.5	5.5
	Standard deviation	0.50	0.50	0.50
	Standard error	0.05	0.09	0.15

TABLE I. (continued)

Characters		<i>Clinus acuminatus</i>	<i>Clinus obtusifrons</i>	<i>Clinus berrisfordi</i>
Pectoral rays	Range	11-13	13	11-12
	Mean	12	13	12
	Standard deviation	0.25	0.00	0.25
	Standard error	0.025	0.00	0.05
Dorsal total	Range	37-40	36-38	39-41
	Mean	38	37	39.5
	Standard deviation	0.60	0.66	0.22
	Standard error	0.05	0.12	0.06
Anal rays	Range	20-24	20-22	23-25
	Mean	22	21	23.75
	Standard deviation	0.80	0.65	0.75
	Standard error	0.10	0.10	0.10
Height of first dorsal spine % of head length	Range	14.6-27.2	26.5-36.4	25.0-33.3
	Mean	19.0	31.3	29.5
	Standard deviation	2.40	2.70	2.80
	Standard error	0.20	0.50	0.70
Depth of body at dorsal origin as % of standard length	Range	17.9-23.4	19.6-23.6	18.8-21.2
	Mean	20.2	21.3	19.8
	Standard deviation	1.00	0.90	0.60
	Standard error	0.10	0.15	0.15
Depth of body at anal origin as % of standard length	Range	17.7-22.8	18.5-24.3	19.7-21.8
	Mean	20.2	21.5	20.2
	Standard deviation	1.00	1.50	0.90
	Standard error	0.09	0.20	0.20
Head length as % of standard length	Range	24.6-31.4	24.7-31.6	25.0-29.3
	Mean	27.5	27.5	26.4
	Standard deviation	1.00	1.50	0.90
	Standard error	0.10	0.25	0.25
Dorsal origin to snout as % of stan- dard length	Range	19.1-25.5	18.8-29.8	18.0-20.2
	Mean	21.2	21.2	19.2
	Standard deviation	1.20	1.90	0.60
	Standard error	0.10	0.30	0.15
Snout length as % of head length	Range	20.0-38.5	26.8-40.0	25.0-31.8
	Mean	30.8	32.2	28.5
	Standard deviation	3.00	3.50	2.70
	Standard error	0.25	0.60	0.80
Orbit diameter as % of head length	Range	21.6-36.3	22.2-33.3	24.0-33.3
	Mean	26.7	27.8	28.5
	Standard deviation	2.20	3.00	3.40
	Standard error	0.02	0.50	0.90
Upper jaw as % of head length	Range	34.3-51.5	36.4-50.0	36.4-50.0
	Mean	41.2	41.9	43.3
	Standard deviation	3.30	3.70	4.10
	Standard error	0.30	0.95	0.70
Interorbital width as % of head length	Range	12.5-20.8	16.7-27.3	12.5-16.7
	Mean	16.2	21.0	15.0
	Standard deviation	2.10	2.80	1.10
	Standard error	0.20	0.50	0.32



INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'). with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

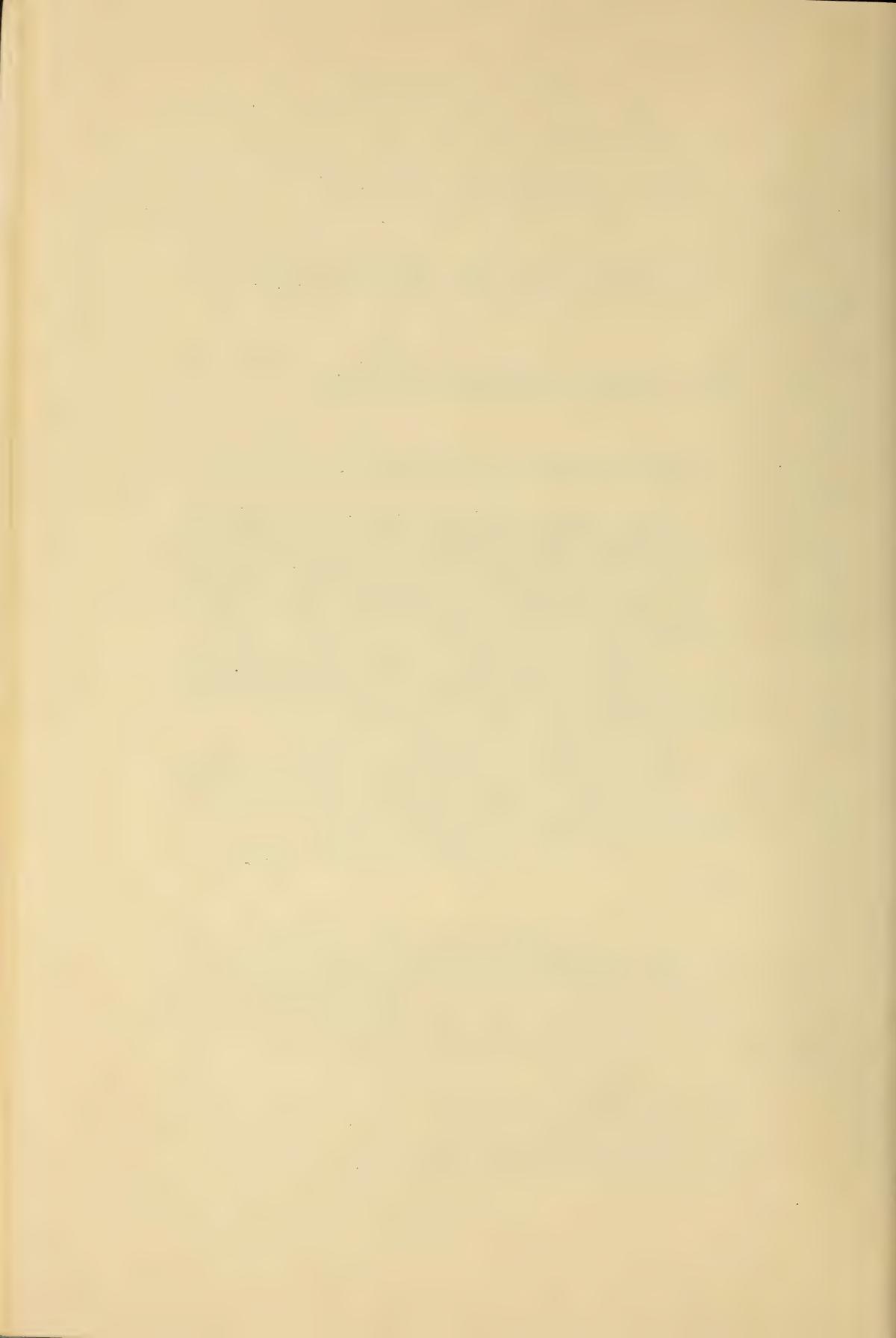
Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



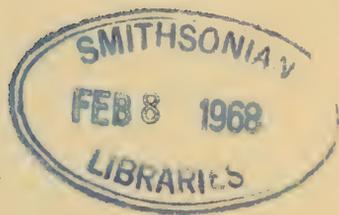
8
GILBERT L. VOSS

SOME BATHYPELAGIC CEPHALOPODS
FROM SOUTH AFRICAN WATERS

November 1967 November

Volume 50 Band

Part 5 Deel



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

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

85c

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

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

SOME BATHYPELAGIC CEPHALOPODS
FROM SOUTH AFRICAN WATERS¹

By

GILBERT L. VOSS

Institute of Marine Science, University of Miami

(With 9 plates)

CONTENTS

	PAGE
Introduction . . .	61
Systematic List . . .	62
Systematic Section . . .	63
Summary . . .	87
Acknowledgements . . .	87
References . . .	87

INTRODUCTION

Through the kindness of Mr. M. J. Penrith and Dr. J. R. Grindley of the South African Museum the writer received in 1963 a small collection of cephalopods taken during the course of midwater trawling (Grindley and Penrith, 1965) in South African waters, mostly off the coast of Natal. The collections consisted of 112 specimens belonging to 17 families, 28 genera and 32 species of which 13 species were unrecorded in the list of South African cephalopods given by the writer in 1962 (Voss, 1962).

Although only one new species and one new subspecies were found, several of the other species are poorly known or confused in the literature and these are treated in some detail in the present paper. One new species is named on the basis of a description by another author. The remainder are listed for the record with a reference to pertinent literature treating with the individual species and with an indication of their general distribution. The collections were obtained by the use of an Isaacs-Kidd midwater trawl (IKMT). A few were from stomach contents of the predatory bathypelagic fish *Alepisaurus ferox*, which were taken by long-line at IKMT stations. All of the specimens are deposited in the South African Museum (SAM).

¹ Contribution No. 789 from the Institute of Marine Science, University of Miami. This study was partially supported by National Science Foundation grants G-17940 and GB 1090.

SYSTEMATIC LIST

In the paper 'South African Cephalopods', the writer (Voss, 1962) reviewed the cephalopod literature treating with the South African region and gave a list of 66 species reported as of that date from South African waters. The present list increases this number to 79 if some localities as much as 600 miles off shore may be referred to as South African. This increase was to be expected when sampling gear such as the Isaacs-Kidd trawl was introduced in addition to more customary fishing gear and undoubtedly its continued use will sensibly increase the number of species so far recorded, especially among those weird inhabitants of the deep cold waters so difficult to obtain with conventional nets.

The list given below includes only those species which were taken in the above-mentioned survey. The species preceded by an asterisk are new records to the South African cephalopod fauna.

Order SEPIOIDEA

Family **Spirulidae**

1. *Spirula spirula* (Linnaeus)

Family **Sepiidae**

2. *Sepia australis* Quoy and Gaimard
3. *S. hieronis* (Robson)
4. *Hemisepius typicus* Steenstrup

Family **Sepiolidae**

5. *Rossia (Austrorossia) enigmatica* Robson
6. *Heteroteuthis hawaiiensis dagamensis* Robson
7. *Inioteuthis capensis* Voss

Order TEUTHOIDEA

Suborder OEGOPSIDA

Family **Lycoteuthidae**

8. *Lycoteuthis diadema* (Chun)

Family **Enoploteuthidae**

9. *Abraliopsis gilchristi* (Robson)
- *10. *A. pfefferi* Joubin
- *11. *Pyroteuthis margaritifera* (Rüppell)
- *12. *Pterygioteuthis gemmata* Chun

Family **Onychoteuthidae**

13. *Onychoteuthis banksi* (Leach)
14. *Onykia* sp.
15. *Tetronychoteuthis dussumierii* (Orbigny)

Family **Bathyteuthidae**

- *16.
- Ctenopteryx sicula*
- (Verany)

Family **Veranyidae**

- 17.
- Octopodoteuthopsis*
- sp.

Family **Histioteuthidae**

- *18.
- Histioteuthis dofleinii*
- (Pfeffer)

- *19.
- H. bonnellii*
- (Férussac)

- 20.
- H.*
- sp.

- *21.
- H. meleagroteuthis*
- (Chun)

Family **Ommastrephidae**

- *22.
- Todaropsis eblanae*
- (Ball)

- *23.
- Ornithoteuthis*
- sp.

Family **Chiroteuthidae**

- *24.
- Chiroteuthis capensis*
- , n. sp.

Family **Cranchiidae**

- 25.
- Cranchia scabra*
- Leach

- 26.
- Galiteuthis*
- sp.

- 27.
- Pyrgopsis pacifica*
- Issel

- *28.
- Megalocranchia megalops australis*
- , n. subsp.

Order OCTOPODA

Family **Bolitaenidae**

- 29.
- Eledonella pygmaea*
- Verrill

Family **Amphitretidae**

- 30.
- Amphitretus pelagicus*
- Hoyle

Family **Tremoctopodidae**

- *31.
- Tremoctopus violaceus*
- (Della Chiaje)

Family **Ocythoideae**

- *32.
- Ocythoe tuberculata*
- Rafinesque

- 33.
- Octopus*
- sp.

SYSTEMATIC SECTION

Order SEPIOIDEA

Family **Spirulidae***Spirula spirula* (Linnaeus, 1758)*Spirula spirula*, Bruun, 1943 (biology).*Material*: 1 ♂, mantle length 43.7 mm, in 500 m, from 32°30'S, 35°08'E, IKMT No. 31, August 12, 1962, SAM A29725.—1 ♀, mantle length 38.8 mm, in

200 m, from 30°31'S, 31°45'E, IKMT No. 37, August 23, 1962, SAM A29701.— 1 juvenile, mantle length 24.0 mm, in 500 m, from 29°55'S, 39°30'E, IKMT No. 35, August 19, 1962, SAM A29695.

This species was reported from off the Cape by Bruun (1943) taken by the Dana. Its general biology is well treated in the paper. The species is apparently circumtropical and warm temperate living at depths from 200 to about 1700 metres.

Distribution: Circumtropical and warm temperate in 200 to 1700 metres.

Family **Sepiidae**

Sepia australis Quoy and Gaimard, 1832

Sepia australis, Voss, 1962 (full synonymy).

Material: 1 ♂, mantle length 34.0 mm, 1 ♀, mantle length 35.0 mm, in 40 m, from west of Slangkop, IKMT No. 12, September 7–8, 1961, SAM A29627.— 2 ♀♀, mantle lengths 39.0–53.0 mm, in 100 m, from west of Slangkop, IKMT No. 19, September 11–12, 1961, SAM A29734.

This species has been discussed and pertinent literature listed in Voss (1962).

Distribution: Known only from southern Africa. See Adam (1941) for complete distribution records.

Sepia hieronis (Robson, 1924)

Sepia sp. A. Robson, 1924: 13.

Rhombosepion hieronis Robson, 1924b: 645, pl. 2, figs. 9, 11; Massy, 1927: 158.

Sepia hieronis, Voss, 1962: 254.

Material: 1 ♂, mantle length 61.3 mm, in 250 m, from west of Slangkop, IKMT No. 23, November 14–15, 1961, SAM A29728.

The sole specimen, a male, was in good condition. Typically for the species, the dorsal arms had only two rows of suckers while both pairs of lateral arms have a patch of enlarged suckers near the tips.

Distribution: Cape Town, 112–150 fathoms (Robson); off Lion's Head, 175–230 fathoms (Massy); 34°09.8'S, 18°16.5'E in 79 metres and 34°09'S, 18°17.5'E in 43 metres (Voss).

Hemisepius typicus Steenstrup, 1875

Hemisepius typicus Steenstrup, 1875: 468; Chun, 1912: 411; Massy, 1927: 164; Thore, 1945: 50; Voss, 1962: 252.

Material: 7 ♂♂, mantle length 8.0–16.0 mm, 6 ♀♀, mantle length 7.8–13.0 mm, from SSE. of Yzervark Point, IKMT No. 2a, SAM A29717.

The present specimens were in very good condition. Their presence in a midwater trawl catch introduces some interesting questions as to their natural

habitat. This species deserves more attention from biologists than it has received in the past.

Distribution: South Africa.

Family **Sepiolidae**

Rossia (Austrossia) enigmatica Robson, 1924

Semirossia sp. A. Robson, 1924a: 10.

Rossia enigmatica Robson, 1924b: 635; Massy, 1927: 153.

Rossia sp. A. Robson, 1925: 450

Rossia (Austrossia) enigmatica, Voss, 1955: 89; 1962: 253.

Material: 1 ♀, mantle length 20.0 mm, from north-west of Cape Town in 400 m, IKMT No. 26, November 15–16, 1961, SAM A29696. — 1 ♀, 5 ♂, badly distorted from the trawl, from 33°10'S, 17°20'E in 120 m, IKMT No. 51, September 18–19, 1963, SAM A29808. — 2 ♂, badly distorted from the trawl, from 33°10'S, 17°20'E in 280 m, September 17–18, 1963, SAM A29806.

For a full discussion of this species see Voss (1962). The present specimens conform well to the description.

Distribution: South Africa.

Heteroteuthis (Stephanoteuthis) hawaiiensis dagamensis Robson, 1924

Heteroteuthis hawaiiensis var. *dagamensis* Robson, 1924a: 11; 1924b: 632.

Heteroteuthis (Stephanoteuthis) hawaiiensis dagamensis, Voss, 1955: 93; 1962: 253

Material: 1 ♀, mantle length 20.5 mm, 28°07'S, 33°28'E in 500 m, IKMT No. 47, SAS Natal, February 24, 1963, SAM A29747. — 5 badly mangled specimens from IKMT No. 51, SAM A29808. — 5 badly mangled specimens from IKMT No. 50, SAM A29806.

A single large female of this species was taken in the hauls. It conforms well with Robson's description.

Distribution: Known only from off South Africa.

Iniotheuthis capensis Voss, 1962

Iniotheuthis capensis Voss, 1962: 255, fig. 1 a–c.

Material: 1 ♀, mantle length 10.0 mm, from SSE. of Yzervark Point, IKMT No. 2a, SAM A29718.

This beautifully preserved small female seems referable with little doubt to this species. Because of its small size little can be added to the original description. The fins are larger than in the type material and there is a papilla-like pore, not seen before, on each side of the light organ on the liver.

Distribution: This species is known only from South Africa from the vicinity of Saldanha Bay and Mossel Bay.

Sepiolid indet.

Material: 1 badly mangled juvenile from west of Slangkop in 100 m, IKMT No. 19, September 9, 1961, SAM A29736.

No identification of this mangled specimen was attempted.

Order TEUTHOIDEA

Suborder OEGOPSIDA

Family **Lycoteuthidae***Lycoteuthis diadema* (Chun, 1900)

Lycoteuthis diadema, Voss, 1962: 262 (South African references); 1962a: 275 (revision of the family).

Material: 1 ♀, mantle length 38.6 mm, from west of Slangkop in 350 m, IKMT No. 16, September 9, 1961, SAM A29732. — 1 juvenile, mantle length 12.3 mm, from west by south of Slangkop in 250 m, IKMT No. 7, May 25, 1961, SAM A29709.

Examination of the present specimens confirms my opinion that *Leptodontoteuthis inermis* Robson, 1926 from South Africa is conspecific. This is an uncommon species living in the mesopelagic zone. Its photophores have been well studied, described and illustrated by Chun (1910) from *Valdivia* specimens.

Distribution: Gulf of Mexico and Straits of Florida (Voss); west coast of South America; Indian Ocean in 46°S, 120°E, Atlantic Ocean (all Pfeffer); Benguela Current in 31°21'S, 15°58'E, West Wind Drift in 40°31'S, 15°06'E (all Chun); South Africa, Cape Marine Province (Robson).

Family **Enoploteuthidae***Abraliopsis gilchristi* (Robson, 1924)

Pl. I, a-d; Pl. II, a-e; Pl. III, a-h

Abralia gilchristi Robson, 1924a: 3; 1924b: 601, pl. 1, text-figs. 6-7.

Abraliopsis gilchristi, Voss, 1962: 264.

Material: Cotypes, 2 ♂♂ (only one measurable), mantle length 37.0 mm, Sta. 81, Cape Town, 280 fathoms, Sta. 84, Cape Town, 240 fathoms, presented by Committee on Fisheries and Marine Biological Survey, Union of South Africa, by Dr. J. Gilchrist. BM 1924.9.9.41-2. — 2 ♂♂, mantle length 35.5-38.9 mm, 1♀, mantle length 37.0 mm, IKMT No. 15, in 15 m west of Slangkop, South Africa, September 8, 1961, SAM A29729. — 1 ♂, mantle length 34.0 mm, 1 juvenile, mantle length 16.5 mm, IKMT No. 16, in 350 m west of Slangkop, South Africa, September 8, 1961, SAM A29732. — 1 juvenile, mantle length 18.0 mm, IKMT No. 15, in 15 m west of Slangkop, South Africa, September 8, 1961, SAM A29706. — 1 juvenile, mantle length 8.0 mm, IKMT No. 5, in 10 m west of Slangkop, October 1, 1961, SAM A29710.

This species was discussed in my 1962 paper on the basis of an examination of the cotypes in the British Museum, and certain discrepancies between the specimens and Robson's description were pointed out. With the new material listed above, it has been possible to redescribe this species and figure it in sufficient detail that its future recognition should hold no difficulties.

Description: The mantle is long, conical and slender, tapering to a sharp point posteriorly. The anterior margin is broadly triangularly produced in the dorso-median area but ventrally is shallowly excavated beneath the funnel with small lateral lappets. The fins are large, occupying over four-fifths of the mantle length. They have conspicuous free anterior lobes. The anterior margin is convex with rounded lateral angles and the posterior margins are concave, with the fins drawn out into a long tail and united posteriorly by a low ridge.

The funnel is of medium size, barely reaching the posterior level of the eyes, and is joined to the head by a single V-bridle. The funnel-mantle locking apparatus is simple, the funnel member a broad, short groove, the mantle member a long, straight, narrow ridge. The funnel valve is very broad and only slightly curved. The dorsal member of the funnel organ is A-shaped. The anterior end is pointed and pressed together laterally forming a small, ventrally turned, grooved papilla. Slightly posteriorly there originates a low ridge which becomes stronger posteriorly forming a low lappet in the centre of each limb. The ventral pads are compactly oval.

The head is large, squarish, with conspicuous eyes. The eyelids are transversely oval with a distinct sinus anteriorly. There are four nuchal folds on each side. The first is blunt and inconspicuous, little more than the rounded corner of the funnel groove. The second is immediately adjacent to the first, small but distinct, and terminates in a small, tongue-shaped, olfactory organ. The third and fourth are distinct folds united posteriorly by a thin, raised, concentric-shaped fold. The buccal membrane is coloured a dark purple with numerous small papillae on the oral surface. It is eight-lobed with eight supports which are attached dorsally on I, II and IV, ventrally on III.

The arms are nearly round in cross-section, slightly laterally compressed, with an approximate formula of 4.2.3.1. Arms I and II are keeled on their distal half or one-third, III is keeled for its entire length, the keel deepest about two-thirds of the length from the base and IV bears only the tentacular sheath on the outer border. All of the arms in both the males and females have two rows of very sharp, slender, strongly curved hooks which become extremely minute distally and are followed immediately by minute, apparently non-ringed suckers in two rows.

In the females, all of the arms are bordered by trabeculate protective membranes which are almost vestigial on the dorsal side of arms I, II and III and on both sides of IV but are well developed on the ventral sides of I, II and III, being rather deep on the latter. In the females both membranes and the lappets are smooth.

In the males, the right ventral arm is hectocotylized as is shown in the figure. Basally, the hooks are of about equal size but in the middle of the arm those of the ventral row suddenly are reduced in size continuing thus to the end of the arm while those of the dorsal row retain their normal size. Along the basal and midportion of the arm the protective membrane is lost and only the broad, flat, somewhat truncate trabeculae remain. In the distal third a broad fleshy flap is found on the ventral border. Near the end of the arm it nearly disappears but immediately expands again and extends to the base of the first of the terminal light organs. On the dorsal side another flap appears at about the middle of the large ventral flap and tapers gradually to the base of the light organ; distally the two form a deep, narrow groove.

The left ventral arm is not modified but the protective membrane is either low or absent and the trabeculae are enlarged to form long, square-tipped, flat flaps.

The protective membranes are also modified on I, II, and III in the males. On I the dorsal border has only small lappets but the ventral border has a membrane between the trabeculae. The latter are often somewhat dentate on their free borders and terminal flaps and there are some slight rugosities on the basal part of the arm proximal of the suckers. On II the basal oral surface of the arm has numerous minute papillae followed by low flap-like trabeculae with few papillae on them on each side of the arm. In the middle third of the arm the ventral trabeculae and membrane become wide, having papillae both on the membrane and the trabeculae. Dorsally only flaps are developed which also bear papillae. In the distal third the flaps and membranes decrease and finally disappear. On III there are flaps dorsally, narrow trabeculae, and full deep membranes ventrally but neither show any trace of papillae.

The tentacles are long and laterally compressed. The clubs are not expanded. The carpal cluster is well separated from the manus and consists of four or five small suckers and about the same number of pads. The manus bears four small hooks on the dorsal side and four large, slender hooks on the ventral side. The dactylus is very short and has about twelve transverse rows of suckers in four longitudinal rows. There is a large somewhat semicircular flap on the ventral border of the club originating at about the middle of the carpus and terminating at about the base of the first ventral hook. Beyond this there is a low membrane bordering the manus but terminating at the dactylus. There is no membrane dorsally. On the aboral surface of the club is a swimming keel which originates about in the middle of the manus and extends to the tip of the dactylus.

The gladius is typically enoploteuthid in shape.

The male genitalia are on the left side and are extremely large for an enoploteuthid. The females have two large nidamental glands and a pair of slender, highly arched supplementary ones.

The light organs on the skin are of the two types: large ones with clear

bead-like centres with dark rings deeply set into the mantle but projecting upward under the epithelium and smaller ones about half the size with darker, smaller centres with broad darker rings, which are not set as deeply into the mantle.

On the mantle these organs are numerous and closely but irregularly distributed on the ventral surface, much sparser on the dorsal surface anterior to the fins. Occasionally there is a clear ventral midstripe. On the funnel there are four symmetrical ventral patches, two on each side of the midline and a band of photophores dorsally on each side of the bridle.

On the ventral side of the head are the characteristic four distinct rows of photophores which so easily distinguish the species. There is a double row of light organs on the midline, slightly separated and with a few scattered small organs between. These two rows originate just within the funnel groove and extend in a straight line out the ventral arms as the inner row of IV. The lateral row on each side is widely separated from the inner row on both the head and ventral arms with no intervening photophores. This row forms the median row of IV but actually is located near the outer border. Between the lateral rows on each side and the circlet of organs around each eyelid are rather numerous scattered photophores not interrupted by a ventral window and of which some form the single widely separated organs along the tentacular sheath of IV. There are no organs on the dorsum of the head.

On IV the light organs are as described above but only those of the dorso-median row extend to the tip of the arm, the others stopping somewhat below the terminal organs. There is a conspicuous, rather closely set row of photophores on III, originating from the eyelid circlet just dorsal of the anterior sinus and extending along the base of the swimming keel on the ventral surface almost to the tip of the arm.

Two other sets of light organs, on the eyeball and on the tips of the ventral

TABLE I. Measurements (in mm) of six specimens of
Abraliopsis gilchristi (Robson, 1924) from South African waters

Trawl number	. . .	16	16	15	15	15	15
Sex	. . .	juv.	♂	juv.	♂	♂	♀
Mantle length	. . .	16.5	34.0	18.0	37.5	34.0	38.0
Mantle width	. . .	—	13.5	—	14.0	—	16.0
Head width	. . .	—	10.0	—	12.1	—	—
Fin length	. . .	—	28.0	14.0	31.0	—	31.0
Fin width	. . .	—	31.0	18.0	33.6	—	31.0
Arm length I	. . .	—	21.0	—	20.0	—	16.5
II	. . .	—	17.0	—	20.0	—	19.0
III	. . .	—	20.5	—	20.0	—	20.0
IV	. . .	—	26.0	—	28.0	—	29.0
Tentacle length	. . .	—	—	—	—	—	57.5
Club length	. . .	—	—	—	—	—	10.0
Arm hooks I	. . .	—	17	—	17	—	17
II	. . .	—	17	—	19	—	20
III	. . .	—	21	—	20	—	19
IV	. . .	—	23	—	28	—	23+

arm, are found in this species. The five photophores on the eyeball are located on the ventral periphery, are round and reddish-brown in colour. The terminal organs are about twice the size of the medians and are set apart from them.

On the tips of the ventral arms are found the characteristic large terminal photophores. These organs are very large in this species, ovoid to round, and set deeply into the aboral surface of the arm tip. Apparently there are three organs in complete specimens but, as these are often missing, no average could be determined. In some they were missing entirely and, when the skin is peeled off by net action, there may be no indication of their former presence.

Discussion: The relationship of this species with the other related forms will be discussed in a revision of the subfamily Abraliinae now being drawn to completion.

Distribution: Known only from South African waters.

Abraliopsis pfefferi Joubin, 1896

Abraliopsis pfefferi Joubin, 1896: 19; Pfeffer, 1912: 156.

Material: 1 ♂, mantle length 20.5 mm, 500 m from 27°00'S, 43°39'E, SSE. of Natal, IKMT No. 45, February 21, 1963, SAM A29755.

Considerable confusion has existed in the literature concerning the identification of *Abraliopsis pfefferi* and its relationship to the other species of the genus. From the members of the subgenus *Micrabralia* (*affinis*, *lineata*, *gilchristi*) it can be distinguished by the diffuse distribution of the photophores on the ventral surface of the head, while from its closest relative *A. (Abraliopsis) hoylei* (Pfeffer, 1884) it can readily be separated by the presence of a semicircular flap or membrane in the carpal region of the tentacular club and by the absence of minute, ringed suckers on the tips of the arms between the terminal hooks and the terminal minute fleshy suckers.

Distribution: This species appears to be confined to the Atlantic Ocean and the Mediterranean Sea, being replaced in the Indo-Pacific by *A. hoylei*. This is the only record from the Indian Ocean.

Abraliopsis sp.

Material: 1 spec., mantle length 20.0 mm, in 500 m from 26°42'S, 40°07'E, SSE. of Natal, IKMT No. 46, February 22, 1963, SAM A29749.

This specimen is in such poor condition that definite identification is nearly impossible. It may be a young, mutilated specimen of *Abraliopsis gilchristi*.

Subfamily **Pyroteuthinae**

Pyroteuthis margaritifera (Rüppell, 1844)

Enoploteuthis margaritifera Rüppell, 1844: 129.

Pyroteuthis margaritifera, Hoyle, 1904: 42; Chun, 1910: 136, pl. 11, figs. 1-4 (full description and figures); Pfeffer, 1912: 196, pl. 19, figs. 17-30 (detailed description, distribution).

Material: 1 ♀, mantle length 43.0 mm, in 500 m from 32°30'S, 35°08'E, IKMT No. 31, August 12, 1962, SAM A29727. — 1 ♀, mantle length 21.0 mm, in 500 m

from 25°30'S, 40°40'E, IKMT No. 34, August 19, 1962, SAM A29697.—1 ♀, mantle length 17.0 mm, in 200 m from 30°30'S, 31°45'E, IKMT No. 37, August 23, 1962, SAM A29699.—1 ♂, mantle length 29.0 mm, in 500 m 27°00'S, 43°39'E, SSE. of Natal, IKMT No. 45, February 21, 1963, SAM A29754.—1 ♀, mantle length 27.0 mm, in 500 m from 28°07'S, 33°28'E, IKMT No. 47, SAS Natal, February 24, 1963, SAM A29746.—1 indet., mantle length 12.0 mm, in 500 m from 27°00'S, 43°39'E, IKMT No. 45, SAS Natal, February 21, 1963, SAM A29753.

This is a common mesopelagic species living in the upper 600 metres of water. It is somewhat similar in appearance to *Pterygioteuthis* but may immediately be distinguished from it by the presence of hooks on the tentacular club and hectocotylization of the right ventral arm. The eyeball bears 12 light organs and the oviduct is on the left side.

Distribution: Widely distributed in the Mediterranean and Atlantic from the surface to about 600 metres. This appears to be the first record from the Indian Ocean of the typical form.

Pterygioteuthis gemmata Chun, 1910

Pterygioteuthis gemmata Chun, 1910: 108, pl. 13, fig. 3, pl. 14, figs. 4, 5, 9, pl. 15, figs. 2-3, 6-12, pl. 16, figs. 1-2, 5, 7-19; Thiele, 1920: 447, pl. 54, figs. 10-12.

Material: 1 ♂, mantle length 22.0 mm, in 500 m from 30°49'S, 45°47'E, SSE. of Natal, IKMT No. 44, February 19, 1963, SAM A29744.—2 ♂♂, mantle length 18.2, 17.9, in 200 m from 30°30'S, 31°45'E, IKMT No. 37, August 23, 1962, SAM A29699.—? 1 ♀, mantle length 20.0 mm (badly damaged), in 100 m from west of Slangkop, IKMT No. 19, November 11-12, 1961, SAM A29735.

This species, closely related to the preceding, is distinguished by the characters stated previously. From its closest relative, *Pterygioteuthis giardi* Fischer, 1895, it may be separated by means of the following table.

<i>gemma</i>	<i>giardi</i>
1. I-III arms with 3-5 hooks in midpart of ventral row.	1. I-III arms with a pair of hooks in midpart.
2. Hectocotylus with a comb-like series of teeth.	2. Hectocotylus with two hooklike teeth.
3. 14 light organs on eyeball.	3. 15 light organs on eyeball.
4. Ventral arms with minute paired suckers on left, with a single row on right arm of male.	4. Ventral arms without hooks and suckers.

This is a common mesopelagic species.

Distribution: This has been reported from the South Atlantic by Chun and from the tropical Atlantic by Thiele. It is probably widely distributed in the oceans.

Family **Onychoteuthidae***Onychoteuthis banksi* (Leach, 1817)

Onychoteuthis banksi, Pfeffer, 1912: 70, pl. 3, figs. 13-25, pls. 4, 5, 6.

Material: 1 ♀, mantle length 66.0 mm, in 15 m from west of Slangkop, IKMT No. 15, September 8-9, 1961, SAM A29731.—3 ♀♀, mantle lengths 56.0-76.0 mm, surface from 3°30'S, 35°08'E, dipnetted at night, SAM A29739.—1 juvenile, mantle length 22.2 mm, in 500 m from 31°44'S, 44°35'E, from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29715.—1 juvenile, mantle length 24.0 mm, in 500 m from 31°44'S, 44°35'E from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29720.—1 juvenile, mantle length 24.0 mm, in 500 m from 31°44'S, 44°35'E, from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29713.

This is one of the commonest oceanic cephalopods, the young often caught in plankton nets. I have noted elsewhere (Voss, 1960): 'The young may easily be identified from all other squids by the sleek, compact appearance with partially withdrawn head, nearly terminal fins, beyond which projects the sharp, tapered, slightly curving and transparent conus of the gladius, and the dark streak along the dorsal midline of the mantle composed of the visible rib of the gladius with a streak of closely set brown chromatophores over it.' The adults are readily identifiable by the large hooks on the clubs and the dark dorsal midline.

Distribution: Cosmopolitan in all seas from the North Cape to Cape Horn.

? *Onykia* sp.

Material: 1 juvenile, somewhat damaged, in 500 m from 26°38'S, 44°28'E, IKMT No. 33, August 17, 1962, SAM A29703.

This specimen is flaccid and in poor condition. From the available characters it seems to belong to the genus *Onykia* but specific determination is doubtful.

Tetronychoteuthis dussumieri (Orbigny, 1839)

Tetronychoteuthis dussumieri, Pfeffer, 1912: 98, pl. 13, pl. 14, figs. 10-14.

Tetronychoteuthis massyae Pfeffer, 1912: 102, pl. 14, figs. 15-19.

?*Tetronychoteuthis* sp. Robson, 1926: 4.

Material: 1 juvenile, mantle length 25.0 mm, in 500 m 31°44'S, 44°35'E, from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29716.

This species has only been recorded a few times in the literature and is considered rather rare. However, the writer now has at his disposal a small series of specimens from the Gulf of Mexico and the south-eastern Pacific which indicate that it may be fairly common. A careful study of all of the specimens available is yet to be made, but a cursory examination indicates that the differences in the surface tubercles between *dussumieri* and *massyae* is due to age differences as Pfeffer had suggested.

This species can be easily recognized under the microscope or with a hand

lens by the presence of small stalked tubercles covering the mantle, like paving. The stalks bear discs distally which in the young (*massyae* stage) are star-shaped with numerous points but in adults are round and smooth-edged. There are numerous dorsal nuchal folds.

Distribution: Gulf of Mexico, south-eastern Pacific (Voss), Mauritius (Orbigny), 46°S, 120°E (Pfeffer), off South Africa!

Family **Bathyteuthidae**

Ctenopteryx sicula (Verany, 1851)

Ctenopteryx sicula, Pfeffer, 1912: 332.

Material: 1 juvenile, mantle length 13.1 mm, in 500 m from 31°44'S, 44°35'E from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29711.

This is a small specimen in poor condition due to the digestive juices of the fish from which it was taken. This species is easily distinguished from all other known species by the presence of lateral fins extending from near the anterior mantle margin to the posterior end. The fin is composed of numerous strong, finely tapered supports or trabeculae united by a delicate, thin membrane. In all except perfect specimens the membrane is partially torn between the supports so that the animal appears to be surrounded by a fringe, hence the generic name—comb fin.

Although not often reported in the literature, this is a common species, occupying the surface layer.

Distribution: Probably world wide in distribution and recorded from the Mediterranean Sea, South Atlantic and Pacific, off South Africa!

Family **Veranyidae**

?*Octopodoteuthopsis* sp.

Octopodoteuthopsis sp. Robson, 1924b: 606, text-fig. 8.

Material: 1 juvenile, mantle length 19.0 mm, in 100 m from west of Slangkop, IKMT No. 24, November 15, 1961, SAM A29707.

This specimen, unfortunately, is in very poor condition and little can be added to Robson's description. Its condition does not permit specific identification. There is no trace of tentacles or their bases. The hooks on the arms are very slender and curved to form no less than a 90° angle and usually more. The mantle projects only slightly beyond the fins which are much wider than long.

The funnel organ is much as described and figured by Robson but the anterior angles are more rounded and the central slit shown in his figure is the result of the slender terminal papilla having been broken off as occurred in the present specimen.

As this is only the second specimen no assumption is warranted as to their vertical distribution.

Distribution: Off Cape Town (Robson).

Family **Histioteuthidae****Histioteuthis dofleini* (Pfeffer, 1912)

Calliteuthis ocellata, Chun, 1910: 147-170 (in part: only references to *C. ocellata*), text-figs. 22, 23, text-pl. 1, figs. 1, 2, pl. 20, figs. 7-9.

Stigmatoteuthis dofleini, Sasaki, 1929: 258, text-figs. 126, 127, pl. 22, figs. 1-3.

Material: 1 ♀, mantle length 15.0 mm, in 500 m from 25°30'S, 40°40'E, IKMT No. 34, August 18, 1962, SAM A29698.—1 ♀, mantle length 13.3 mm, in 500 m from 26°42'S, 40°07'E, IKMT No. 46, S. of Natal, Indian Ocean, February 22, 1963, SAM A29750.

These two juveniles are the first specimens of this species recorded from African waters. They are distinguished by certain details in their photophore pattern and by the sculpture on the surface of the dorsal pad of the funnel organ. On the dorsal pad, a strong ridge originating at the anterior apical papilla runs medially down each limb expanding into a broad flap on the posterior half. On the base of arms IV, the photophores are arranged in three to four longitudinal rows; on the ventral surface of the mantle, the photophores are rather widely set, with a diagonal row commencing at the lateral angle containing about nine organs; seventeen large photophores form a circle around the margin of the right eyelid. The male of this species is unique in the family in possessing a double set of functional genitalia.

Despite the sparsity of literature on this species, it appears from collections made principally by the *Dana* and U.S. Fish and Wildlife vessels to be one of the commonest and most widespread of the histioteuthids. A full study of *H. dofleini* will appear in a forthcoming monograph of the family by N. Voss.

Distribution: From the literature and unpublished material, *H. dofleini* occurs widespread in the North Atlantic and the North Pacific, and, on the basis of the present specimens, occurs in the Indian Ocean. It is found from the surface to about 1500 metres.

Histioteuthis bonnellii (Férussac, 1835)

Histioteuthis bonnelliana, Pfeffer, 1912: 297, pls. 23, 24, 25.

Material: 1 ♀, mantle length, 17.3 mm, in 500 m from 32°30'S, 35°08'E, IKMT No. 31, August 12, 1962, SAM A29724.

This species is known from waters off the north and north-western coasts of Africa but the present small female is the first record from off the south-eastern coast.

H. bonnellii is easily recognized by the deep inner web connecting the arms for approximately 50 per cent or more of their length, the presence of a single enlarged elongate photophore on the tip of arms I, II and III, and a six-membered buccal membrane.

* The information and descriptions on the family Histioteuthidae given here are by N. Voss. A full monographic treatment of the family is now in press.

Distribution: *H. bonnellii* is known from throughout the North Atlantic, the Mediterranean, the Indian Ocean off South Africa (present specimen), and possibly off the south-west coast of Australia. It has been collected at depths down to approximately 3000 metres.

Histioteuthis sp.

Histioteuthis bonelliana, Robson, 1924b: 608, text-figs. 9-12.

Material: 1 ♀, mantle length approx. 55 mm, in 400 m from west of Slangkop, IKMT No. 18, September 9, 1961, SAM A29637.

This specimen, in very poor condition, is identical with two specimens collected by the s.s. *Pickle* from an area just a few degrees north of the location of the present specimen. Robson identified these specimens as *H. bonelliana* but noted a number of differences between his material and that described by Pfeffer, Chun, etc., for *bonelliana*.

A study of Robson's material, which is deposited in the British Museum, and the present specimen reveals important differences between these individuals and members of the species *H. bonnellii* (= *H. Bonelliana*). Like *bonnellii*, this new material has the deep inner web between the arms and the single enlarged elongate photophore on the tip of arms I, II and III, but differs most strikingly in having a seven-parted buccal membrane rather than a six-parted one.

The identity of this specimen together with those of Robson must await a complete study and description in the afore-mentioned monograph.

Distribution: Known at present from off the west coast and southern tip of South Africa from depths of +720 to 1755 metres.

Histioteuthis meleagroteuthis (Chun, 1910)

Meleagroteuthis hoylei, Pfeffer, 1912: 291, pl. 22, figs. 1-8.

Material: 1 ♂, mantle length 38.0 mm, in 500 m from 35°42'S, 24°10'E, IKMT No. 42, November 17-18, 1962, SAM A29738.

This specimen, in very good condition, is the first record of this species from African waters. The species has been seldom recorded in the literature, but is commoner than is supposed, being represented in the yet undescribed *Dana* collections by a number of specimens.

The species is easily distinguished by the densely set small photophores, particularly on the ventral surface of the mantle and head; a median line of tubercles on the dorsal surface of the mantle and on the basal half to two-thirds of arms I, II and III; and a seven-membered buccal membrane. On the ventral surface of the mantle, a diagonal row of photophores commencing near the lateral angle on the anterior margin contains approximately 25 photophores; on the base of arms IV, the photophores are set in nine longitudinal rows.

Distribution: *H. meleagroteuthis* is known from throughout the North Atlantic (Joubin, unreported *Dana* material); the South Atlantic off the tip of South Africa (present specimen); and throughout the North Pacific (Pfeffer, Joubin, Adam, Sasaki, Akimushkin, and Voss) from depths of 494 to 730 metres.

Family **Ommastrephidae**

Todaropsis eblanae (Ball, 1841)

Todaropsis eblanae (Ball), Voss, 1962: 264.

Material: 1 ♂, mantle length 42.0 mm, in 100 m from west of Slangkop, IKMT No. 19, November 11–12, 1961, SAM A29737.—1 juvenile, badly damaged, in 200 m from north-west of Cape Town, IKMT No. 27, November 16, 1961, SAM A29691.

Two specimens in poor condition were represented in the collections. This is a common species in the eastern Atlantic and has been well described by various authors. For sources for distributional records see Voss, 1962.

Ornithoteuthis sp.

Material: 1 ♀, mantle length 66.0 mm, in 500 m from 26°38'S, 44°28'E, from stomach of *Alepisaurus ferox*, IKMT No. 33, August 17, 1962, SAM A29721.

A single half-grown female of *Ornithoteuthis* in fair condition was found in the collections from *Alepisaurus* stomachs. It is unfortunate that the specimen is not an adult and in good shape in order to determine whether it belongs to the oriental *O. volatilis* Sasaki, 1915 or to the Atlantic *O. antillarum* Adam, 1957.

This specimen shows adequately the generic characters: long slender tail-like mantle tip and fins, a light organ on the ventral surface of the eyeball and two light organs on the ventral side of the visceral mass, the anterior one oval, the other a long slender luminous stripe down the midline. There is a distinct foveola in the funnel groove.

Family **Chiroteuthidae**

Chiroteuthis capensis, n. sp.

Pl. IV, a–g; Pl. V, a–h

Material: Holotype.—1 ♀, mantle length 100.0 mm, in 400 m west of Slangkop, IKMT No. 18, September 9, 1961, SAM A29730.

The mantle is long and slender, squarely truncate ventrally but produced dorsally in the midline in a triangular lappet. It is widest near the anterior margin and tapers gradually to the level of the insertion of the fins. Anteriorly the mantle wall is thin and muscular; at the level of the fins it becomes thick, choroidal and tubular and tapers only very slightly posteriorly. It is broken off just posterior to the end of the fins, with the end of the broken gladius somewhat projecting.

The fins are nearly circular in outline but taper slightly both anteriorly and posteriorly. There are no free anterior lobes. The fins are rather thick and fleshy.

The funnel is small, with a small tubular opening, and is free for only a few millimetres. The sides of the soft neck tissue appear to be fused to the funnel but are free in the present specimen with the funnel attachment muscles only being securely fused to the funnel in a large area near the opening. The funnel-mantle locking apparatus is simple. The mantle member is a small raised ridge, set obliquely on the mantle and tapering anteriorly so that in side view it resembles the outline of a human nose. The funnel member is slightly oval with the groove forming an \perp shaped structure. The funnel organ is large. The dorsal member is shaped like a broad inverted heart but blunt anteriorly. On its inner surface it bears a narrow median ridge terminating in a small papilla. Laterally there is a broad ridge on each side, narrow anteriorly, but broadening posteriorly. The ventral pads are large, elliptical, with a thickened inner ridge.

The head is long and tubular but squarish in the area of the eyes. Typically chiroteuthid, the eyes are situated about midway between the arm bases and the end of the funnel. The long neck region has collapsed but in life it would probably be about as wide as the head proper. Only one eye is present. It is large and bears traces of an inner and outer solid row of photogenic material each end terminating in a roundish patch. There is an olfactory organ postero-ventrally on either side of the head. It consists of a long slender tube broadened at the end but the shape of the terminal lobe cannot be accurately determined.

The arms are long, round in cross-section, but flattened aborally. The bases are rather stout but taper to slender attenuate tips. They are in the order $4:3=2:1$. Arms I noticeably shorter than the others while IV are very long and stout. The skin is rubbed off almost all the arms so that little can be determined concerning keels, protective membranes, etc. Only the right third arm bears a distinct swimming keel in its present condition. All of the arms bear two rows of suckers born on slender pedicels set on broad pad-like bases. The suckers of the midportion of the arms bear about 8-10 long, slender, sharp teeth on the distal edge and about twenty, low, blunt teeth on the rest of the circumference. The teeth of the distal suckers are slender and sharp while those of the basal suckers are short and broad.

The tentacles are exceedingly long. The stalks are very slender and in their present skinless condition lack suckers over the greater length. The club is slightly larger than the stalk and is about one-fifth the total length. Basally there is a solid fringe of lappets originating in the carpal region and covering a very small area. Beyond this the fringe separates into single broad pointed lappets united by a thin transparent membrane. These individual lappets border the club on each side to the tip of the club which ends in a long oval light organ. The suckers are in four rows arranged in groups of two at the base of each lappet. The outer suckers have a stalk about twice as long as the inner ones. Both the inner and outer stalks bear an outer raised keel which terminates

distally in a lappet-like crest. Each sucker is hood-shaped, open on its inner surface. The inner ring is toothed and bears a single large hooked tooth on the distal margin with about 7-8 teeth on each side. Of these latter, the ones close to the median tooth are larger and slender while the proximal ones are shorter and broader. The proximal base is slightly irregular but not toothed.

The buccal membrane was badly torn and in very poor condition so that its structure could not be made out. However, the attachments were visible and were dorsally inserted on I, and II, and ventrally on III, and IV.

An examination of the viscera showed little detail. The specimen was a female indicated by the presence of small nidamental glands. The posterior section of the mantle contained a considerable concentration of large fatty cells.

Of possible considerable importance is the lack of any trace of a light organ on the ventral surface of the liver. The most careful examination failed to reveal a trace of present or former organs.

The mantle, funnel, head and arms still retain some skin which bears reddish violet chromatophores, more particularly on the dorsal aspect.

There are no indications of light organs on the body and head. There is a row of possible photophores along the base of the swimming keel of the third arms. These are rather small and regularly spaced. On the ventral arms the skin is missing except in two or three small patches but in these the typical large photophores are interspersed between the suckers of the ventral row.

TABLE 2. Measurements (in mm) of the holotype of *Chiroteuthis capensis*, n. sp. from South African waters.

Trawl number	. . .	18	Arm length I	. . .	48.5
Sex	. . .	♀	II	. . .	58.0
Mantle length	. . .	100.0	III	. . .	60.0
Mantle width	. . .	14.2	IV	. . .	204.0
Head width	. . .	22.0	Tentacle length	. . .	500.0
Fin length	. . .	50.5	Club length	. . .	146.0
Fin width	. . .	45.5			
Sucker diameter I6			
II8			
III96			
IV	. . .	1.12			
Tentacular sucker	. . .	1.12			

Type. South African Museum SAM A29730.

Type locality. West of Slangkop, South Africa.

Discussion. At this time five large species of *Chiroteuthis* are known: *veranyi*, *lacertosa*, *imperator*, *picteti*, and *macrosoma*. All of the other species, belonging to various genera and subgenera, are in my opinion larval stages of these or other adult forms and are not referable to identified adults. Their names should be dropped from consideration (see also Joubin, 1924, p. 79). *C. veranyi* and *lacertosa* are closely related forms and it may be that *lacertosa* is a subspecies of *veranyi* as Pfeffer (1910) has proposed. They are easily separated from the other

species by the prominent strongly striped skirt around the pedicels of the tentacular suckers just below the suckers. In *veranyi* the light organs on the ink sac are round, in *lacertosa* they are oblong, tapered at the ends. In 1933 Joubin, under the name *C. lacertosa*, described and figured a specimen taken by the *Dana* at station 1171 II at 8°19'N, 44°35'W. He misidentified this as *lacertosa*, and, drawing attention to the single light organ on the ink sac and the multiple light organs on the eyeball, he stated that *lacertosa* was not a subspecies of *veranyi*. Unfortunately, for Joubin, the type of *lacertosa* in the U.S. National Museum has, as mentioned above, two light organs on the ink sac and two strip organs on the eyeball. The specimen described in his 1933 paper is actually a new species and I here name it *Chiroteuthis joubini* n. sp. The original description is Joubin, 1933, pp. 26-30, figs. 23-29.

The remaining three species of *Chiroteuthis* are closely related and very similar. *C. picteti* and *C. imperator* were both well described and illustrated, the latter profusely so. While many features are similar to the present species, they are easily separable on the basis of the three rows of light organs on the eyeball, differences in the tentacular club, and the presence of double light organs on the ink sac. *C. macrosoma* was insufficiently described by Goodrich (1896); it has no tentacles and the light organs were not mentioned. On the basis of the radula which was figured and the differences in the suckers, I consider the present species to be distinct from *macrosoma*. It is unique among known chiroteuthids by the lack of light organs on the ink sac.

Family **Cranchiidae**

Subfamily **Cranchiinae**

?*Pyrgopsis pacifica* (Issel, 1908)

Pl. VI, a-e; Pl. VII, a-i

Pyrgopsis pacifica, Robson, 1924b: 619; Sasaki, 1929: 338.

Material: 1 ♀, mantle length 63.0 mm, west of Slangkop, from *Alepisaurus ferox* stomach, IKMT No. 14 in 500 m, September 8, 1961, SAM A29705.— 3 ♂♂, 3 ♀♀, mantle lengths 40.0-52.0 mm, in 15 m west of Slangkop, IKMT No. 15, September 8-9, 1961, SAM A29722.— 1 ♀, mantle length 61.0 mm, in 100 m north-west of Cape Town, IKMT No. 27, November 16, 1961, SAM A29692.

The eight specimens grouped here under the name *Pyrgopsis pacifica* are placed here only tentatively since the status of the various species in the genus, and the genus itself, is in dispute. In addition, there are certain inexplicable differences between the specimens which may, or may not, be of specific nature.

All of the specimens have the mantle considerably contracted and wrinkled so that detailed descriptions of the shape cannot be given. However, the body is long and slender, somewhat spindle-shaped. The anterior margin seems to be

slightly produced in the mid-dorsal region and slightly excavated beneath the funnel. The anterior margin is fused to the head in the neck region and on each side of the funnel. The mantle is widest just posterior to the anterior margin and thence tapers gradually to the anterior insertions of the fins where it becomes slender and attenuate. On each side of the mantle, originating at the point of fusion to the funnel, is a line of tubercles. All but the last three on each side are united in a narrow basal cartilaginous strip. There are 10–12 multifid tubercles on each side. Those on the strip are separated by one or more small unicuspid tubercles.

The fins are large, terminal and transversely elliptical in outline. The conus of the gladius extends to the posterior edge.

The funnel is rather large and reaches to about the middle of the base of the ocular peduncles. The funnel organ varies somewhat in the specimens. The 63.0 mm specimen, probably a female, has a V-shaped dorsal funnel organ with a single foliate flap on each lower limb. The dorsal pads seem to be elliptical but indented on the inner posterior margin. In the remaining specimens whose funnel organs were observable, the lower limbs each bore a single long narrow flattened papilla.

In the three males from trawl No. 15, the right ventral arm is hectocotylized. It is longer than the left ventral arm, is turned dorsad on the outer portion, and the distal part of the arm is expanded on the ventral side by the enlargement and palisading of the sucker pedicels. The first six pairs of suckers are normal. From the seventh pair the ventral suckers remain comparatively large to the end of the arm. The dorsal suckers diverge from those of the ventral row to leave a large clear area in the oral face of the arm. The dorsal suckers become minute, on minute pedicels, and extend to the tip of the arm finally converging upon the ventral row at the tip.

The head is narrow and stalked as is characteristic of the genus and squarish in cross-section with sharp angles. The eyes are small, ovoid, on stout, fat ocular peduncles in the large specimens but in the smaller ones the stalks are slender. The eyes bear a rostrum on the ventral side and on the outer surface are two or more small photophores. The exact number could not be made out due to the poor condition of the specimens.

The arms are in the order 3.2.4.1. They are rounded and in the present specimens seem to lack any vestige of a protective membrane on any of the arms nor is any swimming keel noticeable. The arm suckers are small, largest on III in the distal three-fourths of the arm and bear chitinous rings equipped with about 10–12 small teeth on the distal portion but are smooth basally. The third arms are much longer and stouter than the others. In the large female from Slangkop the tip of each of the third arms is broadened, devoid of suckers and is bordered by a ruffled membrane exactly as shown in the figure. In the remaining males and females, which are smaller, there is no such expanded portion but instead the ends of the third arms are normal and bear numerous small suckers to the tip.

The buccal membrane is 7-lobed with seven supports united to the arms dorsally on I and II, ventrally on III and IV.

The tentacles are a little larger than the third arms. The stalks are slender, round, flattened on the oral surface and bear short, slightly expanded clubs bordered by a protective membrane and with an aboral swimming keel. The suckers are in four rows, the median suckers large, three to four times the size of the marginal suckers. The median sucker rings are formed by a smooth inner ring surrounded by a broad papillated collar whose innermost papillae form a row of small, blunt teeth. There is no distinct carpal cluster but suckers and buttons extend down the stalk nearly to the base of the tentacle.

The liver is prominent and shaped like a stout cigar. It is suspended obliquely in the mantle cavity.

The mandibles each bear a tooth on their inner corners as shown in the illustration. The radula is as figured; there are lateral cusps on the rhachidian and a prominent inner cusp with a smaller outer cusp on the admedians. The lateral plates are small and ovoid.

TABLE 3. Measurements (in mm) of the largest specimen of *Pyrgopsis pacifica* (Issel, 1908) from off South Africa

Sex	?	Arm Length I	4.1
Mantle length	63.0	II	12.0
Head width	12.0	III	26.5
Fin length	19.0	IV	9.8
Fin width	29.5	Tentacle length	37.0
Length tubercular ridge	19.2	Club length	6.4

Discussion: The specimens before me have been placed in *pacifica* for lack of a better identification and because they most closely resemble this species. I cannot account for the variation in the structure of the dorsal funnel organ member. This may be due to poor condition and be partly an artifact in the specimen from Sta. No. 14. Sasaki (1929) describes the flaps in his *pacifica* from the Japanese islands as being a triangular flap. Too much reliance cannot be placed on this character here.

The spoon-shaped organ on the end of the third arms on the female from Sta. No. 14 is not found on the other females. This may be due to the animal's somewhat larger size. It is not described in Sasaki's monograph.

Specimens of *Pyrgopsis* are very common in plankton tows. Most have been considered to be larval forms but Sasaki believed his large males to be adult and figured the male genitalia of a specimen of 52.0 mm mantle length. It corresponds well with the somewhat mangled largest male from Sta. No. 15. Two of the present females bore rudimentary nidamental glands but there were no signs of developing eggs.

It has been a commonly held opinion that *Pyrgopsis* might represent a larval stage of *Leachia*. This position seems doubtful. Two adult female *Leachia cyclura* listed by me from Bermuda (Voss, 1960) were both smaller than most of

the present material and were markedly different in appearance and general characters. The final word on *Pyrgopsis* must await a detailed study of a great deal of well-preserved material from the major oceans.

Cranchia scabra (Leach, 1817)

Cranchia scabra, Robson, 1924: 624, figs. 14-16.

Material: 1 ♀, mantle length 70.0 mm, in 500 m from 32°30'S, 35°08'E, IKMT No. 31, August 12, 1962, SAM A29726. — 1 ♀?, mantle length 40.0 mm, in 15 m from 60 miles west of Slangkop, IKMT No. 15, September 8-9, 1961, SAM A29626. — 1 ♀?, mantle length 35.0 mm, in 100 m from west of Slangkop, IKMT No. 20, November 12, 1961, SAM A29630. — 1 juvenile, length indet., in 500 m from 29°50'S, 31°29'E, IKMT No. 48, SAS Natal, February 25, 1963, SAM A29745. — 1 ♀, mantle length 35.0 mm, in 500 m from 27°00'S, 43°39'E, IKMT No. 45, SAS Natal, February 21, 1963, SAM A29752.

Apparently this is only the second record from South African waters of this very common cranchiid squid. Pfeffer (1912) has considered that the species may be divisible into several forms or subspecies for which he proposed names. However, the species appears to exhibit considerable individual variation and until a large series of specimens is available from all oceans and subjected to searching analysis, it seems preferable to retain all forms in the present species. It is easily recognized by the presence of numerous tubercles distributed over the entire surface of the mantle and much of the fins.

The young of this species are often found in the plankton catches from the epipelagic zone. Larger individuals inhabit the meso- and bathypelagic zones.

Distribution: Worldwide in tropical and temperate regions.

Subfamily **Taoniinae**

Megalocranchia megalops australis, new subspecies

Pl. VIII, a-e, Pl. IX, a-f

Material: Holotype. — 1 ♀?, mantle length 89.0 mm, in 500 m 38°52'S, 33°10'E, IKMT No. 40, November 13-14, 1962, SAM A29733. *Paratypes*. — 2 specimens, mantle lengths 39.0 and 29.0 mm, and damaged, in 500 m from 31°44'S, 44°35'E, from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29714. — 1 juvenile, mantle length 24.0 mm, in 500 m from 32°30'S, 35°08'E, IKMT No. 31, August 12, 1962, SAM A29723.

Description: The mantle is oval, truncated anteriorly and tapering to a slender point posteriorly. It is widest at about the anterior third. It is fused to the head dorsally in the neck region without a lappet and marked only by a slender oval clear strip indicating the anterior end of the gladius. The point of fusion on each side of the funnel is marked by a small three or four pointed tubercle. The mantle is thin, muscular and liberally covered with large reddish brown separate spots which are arranged in a narrow but distinct row down the dorsal midline.

Posteriorly, the gladius widens in a generally slender diamond shape, widest just posterior to the anterior fin insertion. Posteriorly it tapers to a slender point.

The fins together are oval in outline, broadest in about the posterior third and border the posterior expanded part of the gladius but anteriorly are attached to the mantle wall. The fins overreach the end of the mantle only slightly.

The funnel is large, prominent, and reaches to the base of the ventral arms just anterior of the eyes. There is no funnel valve. The dorsal member of the funnel organ is U-shaped with slightly rounded posterior limbs. There is a long round papilla at the end of each limb and another in the posterior edge of the anterior central portion. The paired ventral members are ovoid, directed transversely with the narrow end pointed laterally.

The head is small with large projecting eyes. In the type, the skin is missing over the eyes. The olfactory organ is located posterior to the eyes immediately adjacent to the funnel on either side. It is cylindrical, slightly expanded distally and supported on a long slender pedicel. The eyes bear at least two large semicircular light organs ventrally and there are indications of another small one at the inner end of the small half moon organ. However, both eyes are badly damaged and the details cannot be discerned.

The arms are rather short, in the order 3.2.4.1, the third arms longer and stouter. The arms are rounded in cross-section and bear two rows of suckers bordered on each side by a prominent strongly trabeculate protective membrane of which the ventral one is usually slightly deeper. The basal arm suckers are all smooth ringed with no true teeth although under the highest power the larger distal suckers are toothed on the distal borders. The dorsal arms have normal suckers along their entire length, the distalmost only slightly larger than those of the midsection. Beyond the normal suckers the tip of the arm is slender and has about 3-4 rows of minute suckers visible only under high power. The dorso-lateral arms bear about 7-8 pairs of small suckers followed by about 3-4 pairs of slightly enlarged suckers. Beyond the distal suckers the tip of the arm is slender and has about 2-4 rows of minute suckers. The ventro-lateral or third arms bear about seven pairs of normal suckers increasing gradually in size distally, followed by about 4 pairs of noticeably enlarged suckers beyond which the suckers are again small. The tips of the third arms are not slender and do not have microscopic suckers. All of the suckers on the ventral arms are small with no differentiation in size.

The buccal membrane is 7-pointed with 7 supports. The supports are dorsally attached on arms I and II, ventrally attached on III and IV.

The tentacles are short, rather stout, with only slightly expanded clubs. The oral surface of the stalks are slightly flattened and with a slight median groove. On each side of the groove there is a pair of minute suckers arranged so that a line drawn through both pairs will form an angle to each other. The club is bordered on each side by a broad trabeculate membrane originating in the carpal region and extending to the tip of the club ventrally but not dorsally.

There is a short dorsal swimming keel.

The suckers of the manus are arranged in four rows, those of the hand large in comparison to the others, and mounted on rather long pedicels. The suckers bear chitinous rings with about 24–26 slender sharp teeth only slightly larger on the dorsal border. The suckers of the dactylus are small and have very small teeth.

The viscera were partially damaged but the liver is short, thick, cigar-shaped, supported transversely in the mantle cavity with the intestine attached to the posterior border and the rectum opening at the ventral tip of the liver.

The radula is as figured. The beaks are also figured.

TABLE 4. Measurements (in mm) of the holotype of *Megalocranchia megalops australis*, new subspecies, from off South Africa

Sex	♀?	Arm length I	15.0
Mantle length	89.0	II	18.5
Mantle width	30.0	III	25.0
Head width	26.0	IV	19.5
Fin length	20±	Diameter of tentacular sucker8
Tentacle length	29.5	Diameter of arm sucker	1.3
Club length	9.0		

Type: South African Museum No. A29733.

Type locality: 28°52'S, 33°10'E.

Discussion: The entire problem of the affinities of the various species of the *Megalocranchia*—*Desmoteuthis*—*Teuthowenia* complex is a confusing one. It is not the purpose of this discussion to contribute further to the problem of the identity of the genus to which the species *megalops* belongs. This must wait for a detailed report upon the question now in preparation by the present writer. However, it must be stated that the problem really was created by the habit of numerous authors of creating genera and species on the basis of larval forms in which, by definition, adult characters are either not present or insufficiently developed. And despite some efforts to the contrary, it is almost impossible to trace out developmental sequences from long preserved larvae.

The problem has been considerably compounded in the Antarctic region by the work of Pfeffer and Chun. Unfortunately, the types and unique material upon which their specimens were based are now lost, probably due to the ravages of World War II, and we have only inadequate pictures and texts to rely upon. It is my opinion that these larval stages should be disregarded and future work based upon new material attaining at least juvenile stages.

The present specimens have been placed with reservation as a subspecies of *Megalocranchia megalops* because, in the stages available, they compare very favourably with this species. They differ from *M. megalops* consistently in the tuberculation of the mantle-funnel fusion area, the structure of the beaks, and the details of the radula. Since this form is a Southern Ocean form, as presently known, it seems safer to retain this as a subspecies rather than to identify it

with *megalops* or separate it as a new species. It differs from *Teuthowenia antarctica* Chun (1910) in a number of ways but, on the basis of the radula, is similar to Massy's *Teuthowenia antarctica* (Massy, 1916) whose identity is unknown. Similarly, it is distinct from Chun's *Desmotheuthis pellucida* in numerous characters.

Remarks: The name *australis* refers to its habitat in the southern hemisphere.

Galiteuthis sp.

Material: 1 juvenile, mantle length *ca.* 25 mm, in 100 m from west of Cape Town, IKMT No. 24, November 15, 1961, SAM A29708.

This small specimen is most closely referable to *Galiteuthis armata* Joubin but specific identification is not possible. Under high power with the dissecting microscope a few of the median suckers of the tentacular club appear to be in the transitional stage between normal toothed suckers and hooks. *Galiteuthis armata* has been previously reported from South African waters and it may prove that this is the young of this species.

Cranchiid

Material: 1 badly damaged specimen from 26°30'S, 33°40'E in 500 m, IKMT No. 36, August 21, 1962, SAM A29693.

This specimen is in such a poor condition that identification was not attempted.

OCTOPODA

Family **Bolitaenidae**

Eledonella pygmaea Verrill, 1884

Eledonella massyae, Robson, 1924, p. 672.

Eledonella pygmaea, Thore, 1949: 39, figs. 30-41.

Material: 1 head and attached viscera of a male from 26°38'S, 44°28'E in 500 m, IKMT No. 33, August 17, 1962, SAM A29702.

The single specimen in the collections is in poor condition and no further comments can be made concerning its identity or whether Thore (1949) was correct in synonymizing Robson's species under the older *pygmaea*, although the evidence presented by him is convincing to the present writer. For a detailed analysis of this species and considerations of its biology and habits see Thore's monograph. This is a bathypelagic species.

Distribution: Worldwide in tropical and temperate seas between about 50°N and 40°S (see Thore, 1949).

Family **Amphitretidae**

Amphitretus pelagicus Hoyle, 1885

Amphitretus pelagicus, Thiele, 1914: 532; Thore, 1949: 51, figs. 42-51.

Material: 1 specimen, badly damaged, from 30°30'S, 31°45'E in 200 m, IKMT No. 37, August 23, 1962, SAM A29700.

These delicate little octopods have twice before been reported from South African waters (Thiele, 1914, and Robson, 1930). The species is only known from the Indo-Pacific region, its closest approach to the Atlantic being the South African records. Few specimens of the species have been obtained and it is a pity that the present example is in such poor condition. For further information see Thore, 1949.

Distribution: Bathypelagic, known only from the Indo-Pacific region.

Family **Octopodidae**

Octopus sp.

Material: 10 juveniles, mantle length 10.5–17.0 mm, in 500 m from 31°44'S, 44°35'E from gut of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29719.

The ten specimens listed above are very young juveniles of a species of the genus *Octopus*. Since, however, the adult characters are lacking it is impossible at the present stage of our knowledge of the life histories of the southern hemisphere octopods to venture upon an identification.

Family **Tremoctopodidae**

Tremoctopus violaceus Delle Chiaje, 1830

Tremoctopus violaceus, Robson, 1931: 206.

Material: 1 ♀, mantle length 24.0 mm, in 500 m from 31°44'S, 44°35'E, from stomach of *Alepisaurus ferox*, IKMT No. 32, August 15, 1962, SAM A29712. — 1 ♀, mantle length 16.0 mm, in 500 m from 26°42'S, 40°07'E SAS Natal, February 22, 1962, IKMT No. 46, SAM A29751.

This is apparently the first record of this species from South African waters, which are probably south of its normal range. The larger specimen is in excellent condition, having suffered little ill effects as a consequence of having been engulfed by its enemy, but the smaller one is somewhat damaged. This is another species which is sadly in need of a complete revision based upon large series of specimens. It is probably a tropical species infrequently entering cold temperate seas. For the only general discussion in the literature see Robson (1931).

Distribution: Epipelagic in all tropical and temperate seas.

Family **Ocythoidae**

Ocythoe tuberculata Rafinesque, 1814

Ocythoe tuberculata, Robson, 1931: 201.

Material: 1 ♀, mantle length 21.0 mm, in 15 m from west of Slangkop, IKMT No. 15, September 8–9, 1961, SAM A29704.

This is the first record from South African waters of this rather uncommon species. It is unfortunate that the present example is of such a small size that the distinctive adult characters are undeveloped. It is easily recognized by the absence of an interbrachial web, presence of ventral water pores only, and the complicated mantle-funnel locking apparatus unique among the octopods. The characteristic papillae found on the ventrum of the mantle in the females are just visible. This is an epipelagic species.

Distribution: Worldwide in tropical and temperate seas (Robson, 1931).

SUMMARY

An account is given of 112 specimens of bathypelagic cephalopods, belonging to 32 species, taken by midwater trawling in the seas around South Africa. Thirteen of these species were not previously known from this area. One new species, *Chiroteuthis capensis*, and one new subspecies, *Megalocranchia megalops australis*, are described.

ACKNOWLEDGEMENTS

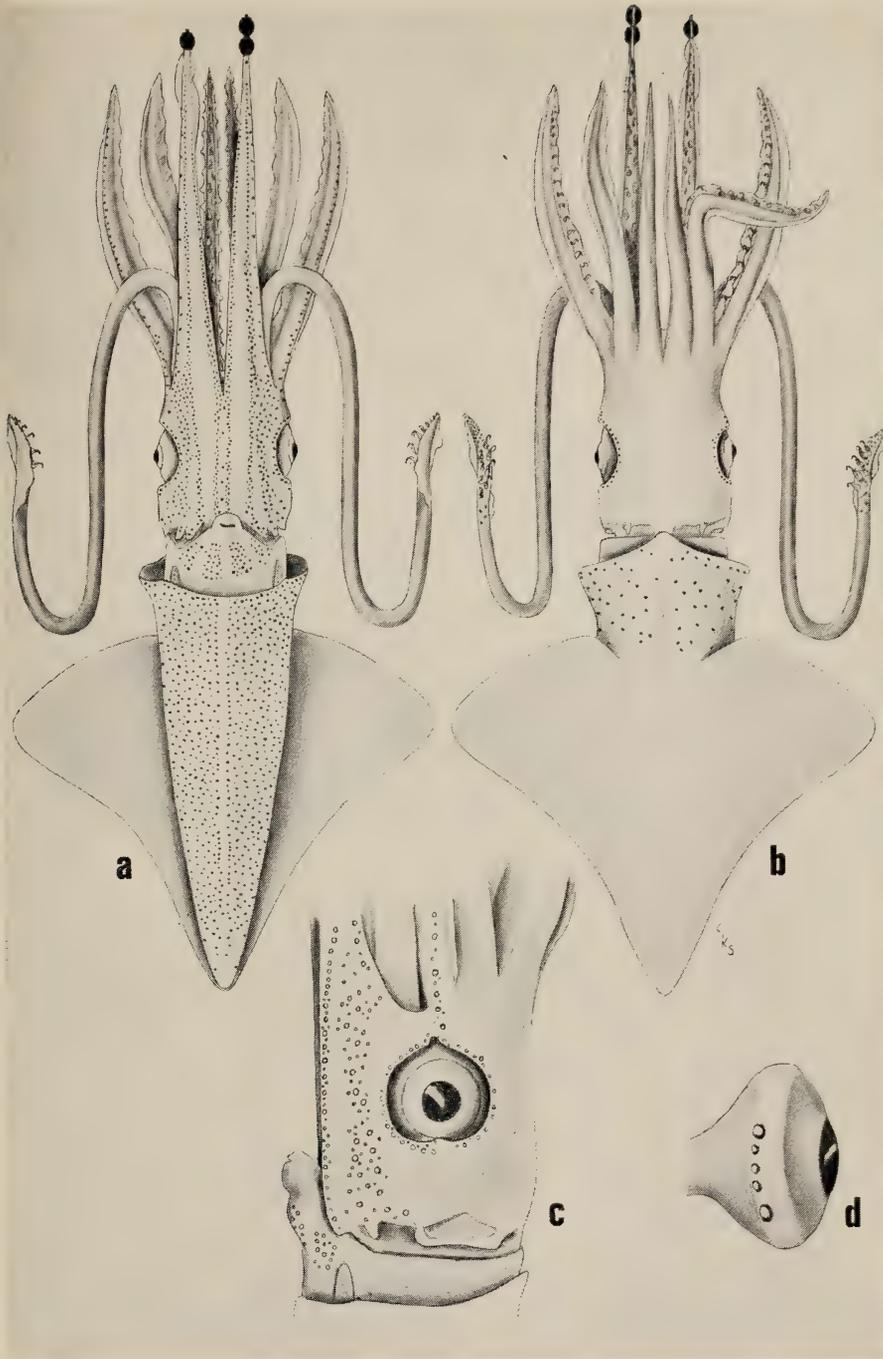
The writer wishes to express his thanks to the Director of the South African Museum, Cape Town, for the opportunity to examine the collections and to the National Science Foundation for a grant-in-aid (NSF G-17940 and GB 1090) under which this study was partially accomplished. The illustrations were executed by Constance Stolen to whom grateful thanks are extended.

The Trustees of the South African Museum wish to thank the Council for Scientific and Industrial Research for a grant towards trawling costs.

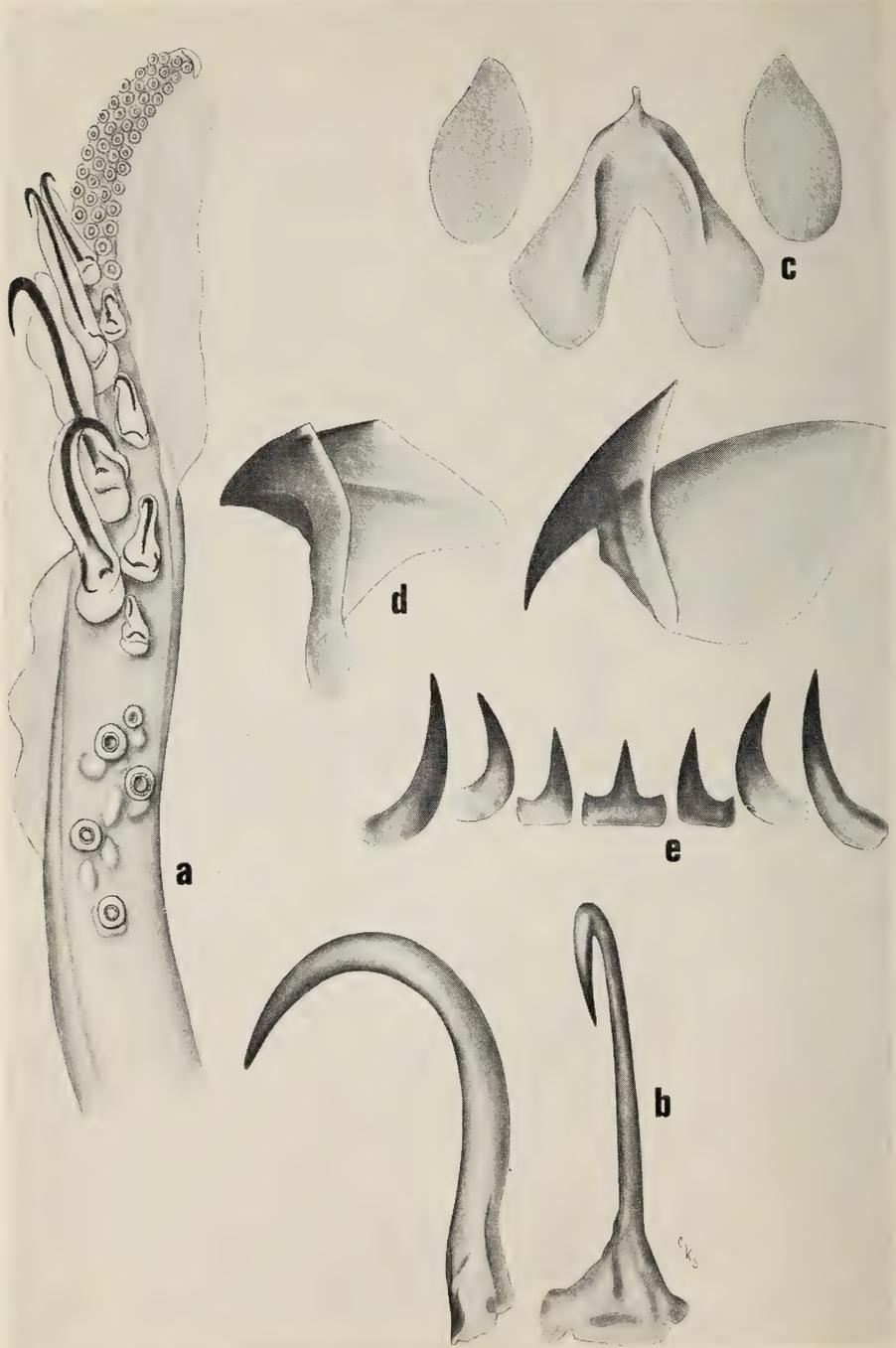
REFERENCES

- ADAM, W. 1941. Résultats scientifiques des croisières du navire-école belge 'Mercator'. III (4). Cephalopoda. *Mém. Mus. r. Hist. nat. Belg.* **21**: 83-161.
- BALL, R. 1841. On a species of *Loligo* found on the shore of Dublin Bay. *Proc. R. Ir. Acad.* **1**: 362-364.
- BRUUN, A. F. 1943. The biology of *Spirula spirula* (L.). *Dana Rep.* **24**: 1-42.
- CHIAJE, S. DELLE. 1830. *Memorie . . . animali senza vertebre del Regno di Napoli.* **4**. Naples.
- CHUN, C. 1900. *Aus den Tiefen des Weltmeeres.* Jena: Fischer.
- CHUN, C. 1910. Die Cephalopoden. 1. Teil: Oegopsida. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **18**: 1-401.
- CHUN, C. 1914. Die Cephalopoden. 2. Teil: Myopsida, Octopoda. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **18**: 405-552.
- FERUSSAC, A. E. 1835. Note sur des céphalopodes nouveaux. *Annl. Sci. nat.* **3**(2): 339-390.
- GOODRICH, E. S. 1896. Report on a collection of Cephalopoda from the Calcutta museum. *Trans. Linn. Soc. Lond.* **7**: 1-24.
- GRINDLEY, J. R. & PENRITH, M. J. 1965. Notes on the bathypelagic fauna of the seas around South Africa. *Zool. afr.* **1**: 275-295.
- HOYLE, W. 1885. Diagnoses of new species of Cephalopoda. *Ann. Mag. nat. Hist.* (5) **15**: 222-236.
- HOYLE, W. 1904. Reports on the scientific results of the expedition to the tropical Pacific . . . on the . . . 'Albatross' . . . VI. Reports on the Cephalopoda. *Bull. Mus. comp. Zool. Harv.* **43**: 1-71.
- ISSEL, R. 1908. Raccolte planctoniche fatte dalla R. Nave 'Liguria' . . . Vol. I, fasc. IV. Mol-luschi. Parte 1. Cefalopodi planctonici. *Pubbl. Ist. Studi sup. prat. Firenze* **1908**: 201-243.

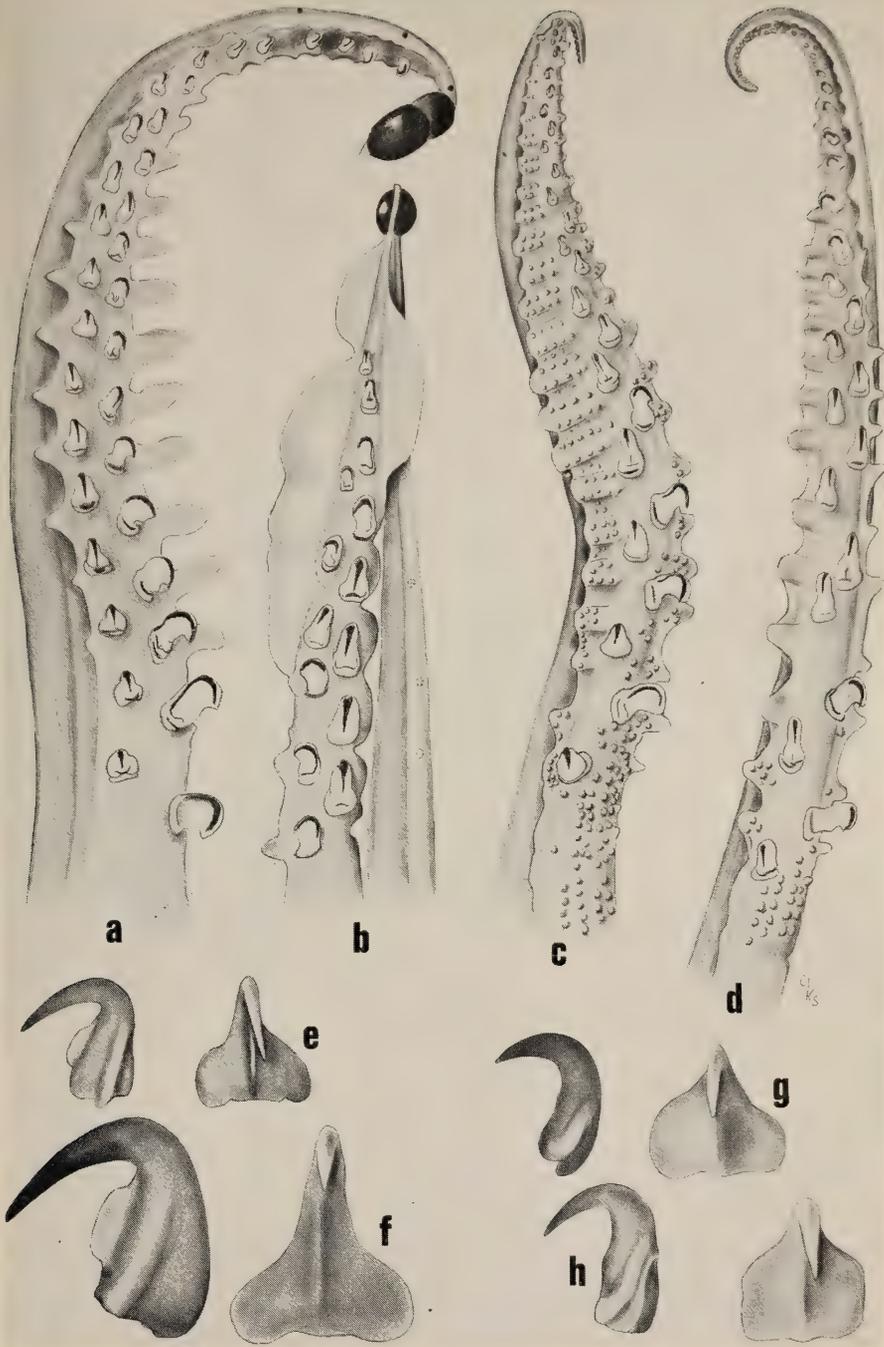
- JOUBIN, L. 1896. Observations sur divers céphalopodes. Première note: *Abraliopsis Pfefferi* (nov. gen. et spec.). *Bull. Soc. scient. med. Ouest* **5**: 19-35.
- JOUBIN, L. 1924. Contribution à l'étude des céphalopodes de l'Atlantique nord. *Résult. Camp. scient. Prince Albert I* **67**: 1-113.
- JOUBIN, L. 1933. Notes préliminaires sur les céphalopodes des croisières du 'Dana' (1921-1922), 4^e partie. *Annls. Inst. océanogr., Monaco* **13**: 1-49.
- LEACH, W. E. 1817. Synopsis of the orders, families, and genera of the class Cephalopoda. *Zool. Misc.* **3**: 137-141.
- LINNAEUS, C. 1758. *Systema naturae*. Ed. 10 **1**.
- MASSY, A. L. 1916. Mollusca. Part II. Cephalopoda. *Nat. Hist. Rep. Br. Antarct. Terra Nova Exped.* **2**: 141-175.
- MASSY, A. L. 1927. The Cephalopoda of the South African Museum. *Ann. S. Afr. Mus.* **25**: 151-167.
- ORBIGNY, A. d'. 1834/48. In Ferussac & Orbigny. *Histoire naturelle générale et particulière des céphalopodes acétabulifères vivants et fossiles*. Paris: Baillière.
- PFEFFER, G. 1912. Die Cephalopoden der Plankton Expedition. *Ergebn. Atlant. Ozean Plankton-expd. Humboldt-Stift.* **2** (F.a.): 1-815.
- QUOY, J. R. & GAIMARD, J. P. 1832. Mollusques. In *Voyage de . . . l' Astrolabe . . .* 1826-29. Zoologie, **2**. Paris.
- RAFINESQUE-SCHMALTZ, C. S. 1814. *Précis des découvertes et travaux somiologiques . . .* Palermo.
- ROBSON, G. C. 1924a. Preliminary report on the Cephalopoda (Decapoda) procured by the S.S. 'Pickle'. *Rep. Fish. mar. biol. Surv. Un. S. Afr.* **3**(9): 1-14.
- ROBSON, G. C. 1924b. On the Cephalopoda obtained in South African waters by Dr. J. D. F. Gilchrist in 1920-21. *Proc. zool. Soc. Lond.* **1924**: 589-686.
- ROBSON, G. C. 1925. On a new species of *Rossia* from South Africa. *Ann. Mag. nat. Hist.* (9) **15**: 450-454.
- ROBSON, G. C. 1926. The Cephalopoda obtained by the S.S. 'Pickle'. Supplementary report. *Rep. Fish. mar. biol. Surv. Un. S. Afr.* **4**(8): 1-6.
- ROBSON, G. C. 1930. Cephalopoda, I. Octopoda. 'Discovery' *Rep.* **2**: 373-402.
- ROBSON, G. C. 1931. *A monograph of the recent Cephalopoda*. Part II. The Octopoda. London: British Museum (Nat. Hist.).
- RÜPPEL, W. P. E. 1844. *Intorno ad alcuni cefalopodi del mare di Messina lettera . . .* Messina.
- SASAKI, M. 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *J. Coll. Agric. Hokkaido imp. Univ.* **20** (suppl.): 1-357.
- STEENSTRUP, J. 1875. *Hemisepius*, en ny slaegt af *Sepia*-blæksprutternes familie med bemærkninger om *Sepia*-formerne i almindelighed. *K. danske Vidensk. Selsk. Skr.* (5) **10**: 465-482.
- THIELE, J. 1920. Die Cephalopoden der deutschen Südpolar-Expedition 1901-1905. *Dt. Südpol. Exped.* (16) *Zool.* **8**: 433-465.
- THORE, S. 1945. On the Cephalopoda of Professor O. Carlgren's expedition to South Africa in 1935. *K. fysiogr. Sällsk. Lund Förh.* **15**(7): 49-57.
- THORE, S. 1949. Investigations on the 'Dana' Octopoda. *Dana Rep.* **33**: 1-85.
- VERANY, J. B. 1851. *Céphalopodes de la Méditerranée*. Gènes.
- VERRILL, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England coast, etc. *Trans. Conn. Acad. Arts Sci.* **6**: 139-294.
- VOSS, G. L. 1955. The Cephalopoda obtained by the Harvard-Havana expedition off the coast of Cuba in 1938-39. *Bull. mar. Sci. Gulf Caribb.* **5**: 81-115.
- VOSS, G. L. 1960. Bermudan cephalopods. *Fieldiana, Zool.* **39**: 419-446.
- VOSS, G. L. 1962. South African cephalopods. *Trans. R. Soc. S. Afr.* **36**: 245-272.
- VOSS, G. L. 1962a. A monograph of the Cephalopoda of the North Atlantic. I. The family Lycoteuthidae. *Bull. mar. Sci. Gulf Caribb.* **12**: 264-305.



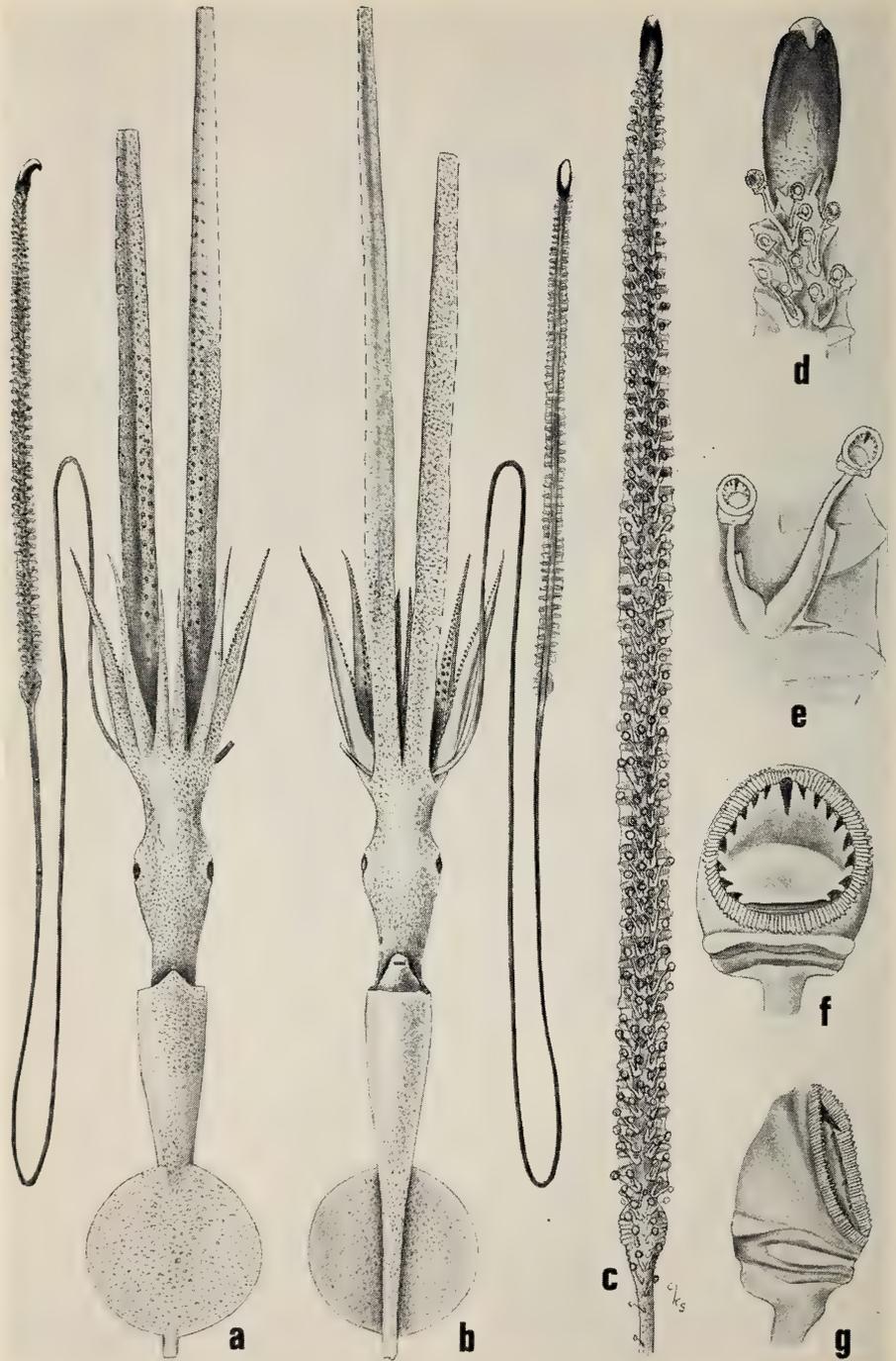
Abraliopsis gilchristi (Robson, 1924). Male, mantle length 38.9 mm. SAM A29729. *a*. Ventral view; *b*. Dorsal view; *c*. Side view of head and eye; *d*. Light organs of ventral side of left eye.



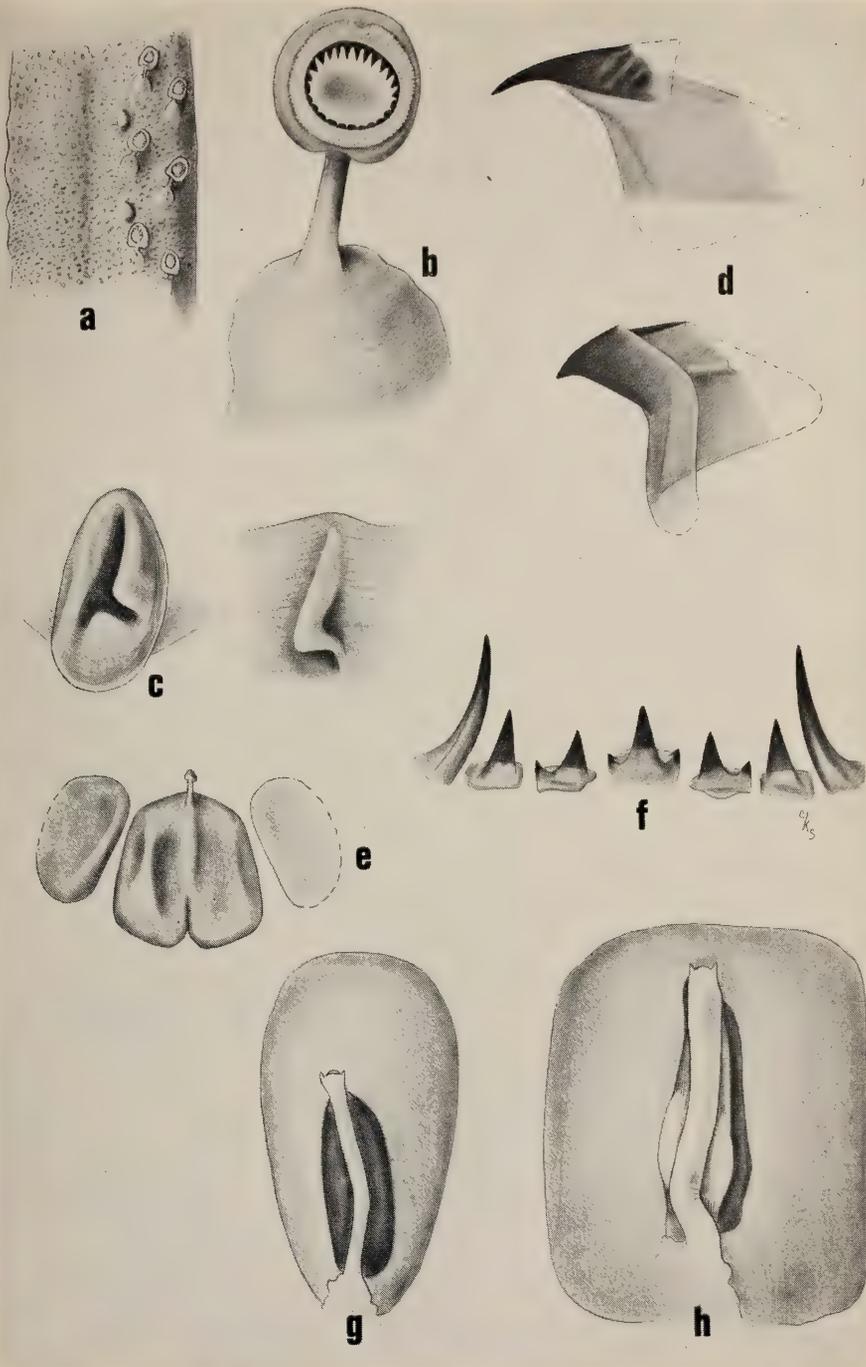
Abraliopsis gilchristi. a. Left tentacular club; b. Large hook from left tentacular club; c. Funnel organ; d. Mandibles; e. Radula.



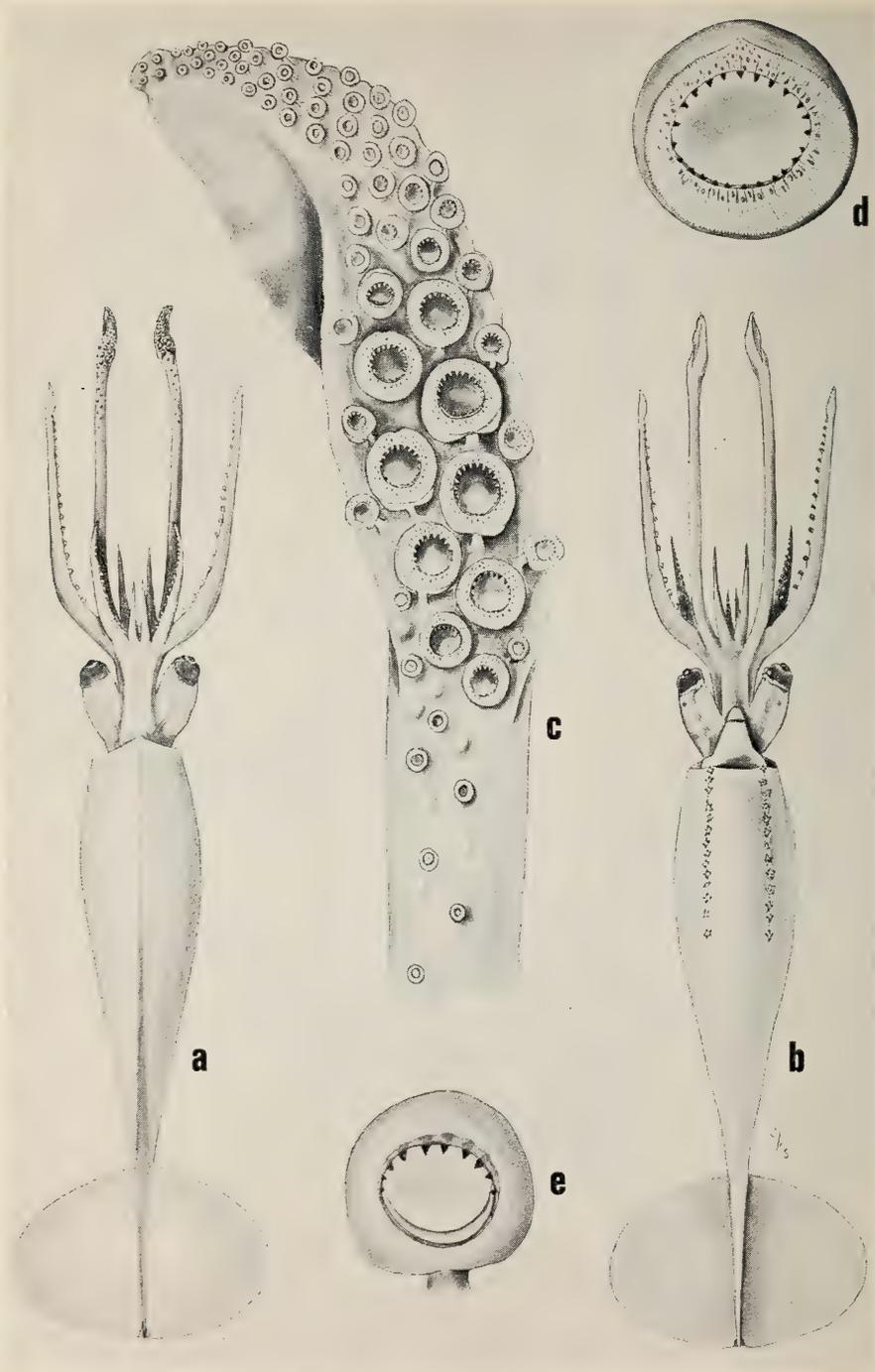
Abraliopsis gilchristi. a. Left fourth arm of male; b. Right fourth arm of male; c. Right second arm of male; d. Right dorsal arm of male; e. Hooks of fourth left arm; f. Hooks of right hectocotylized arm; g. Hooks of left third arm; h. Hooks of left second arm.



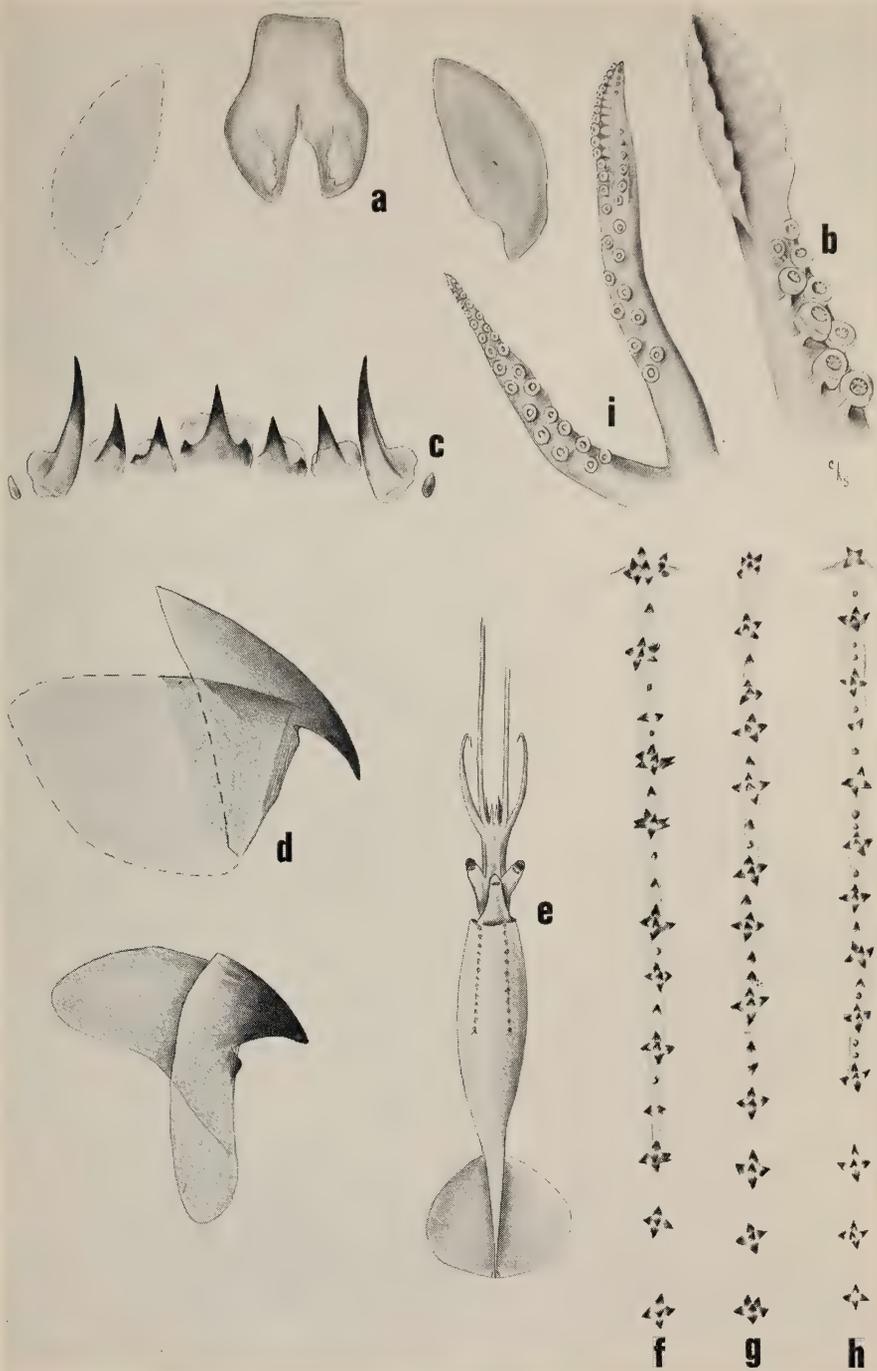
Holotype of *Chiroteuthis capensis*, n. sp. *a*. Dorsal view; *b*. Ventral view; *c*. Left tentacular club; *d*. Tip of tentacular club showing light organ; *e*. Enlargement of suckers and pedicels of tentacular club; *f*.-*g*. Oral and lateral views of sucker from inner row of second pair from base of tentacular club.



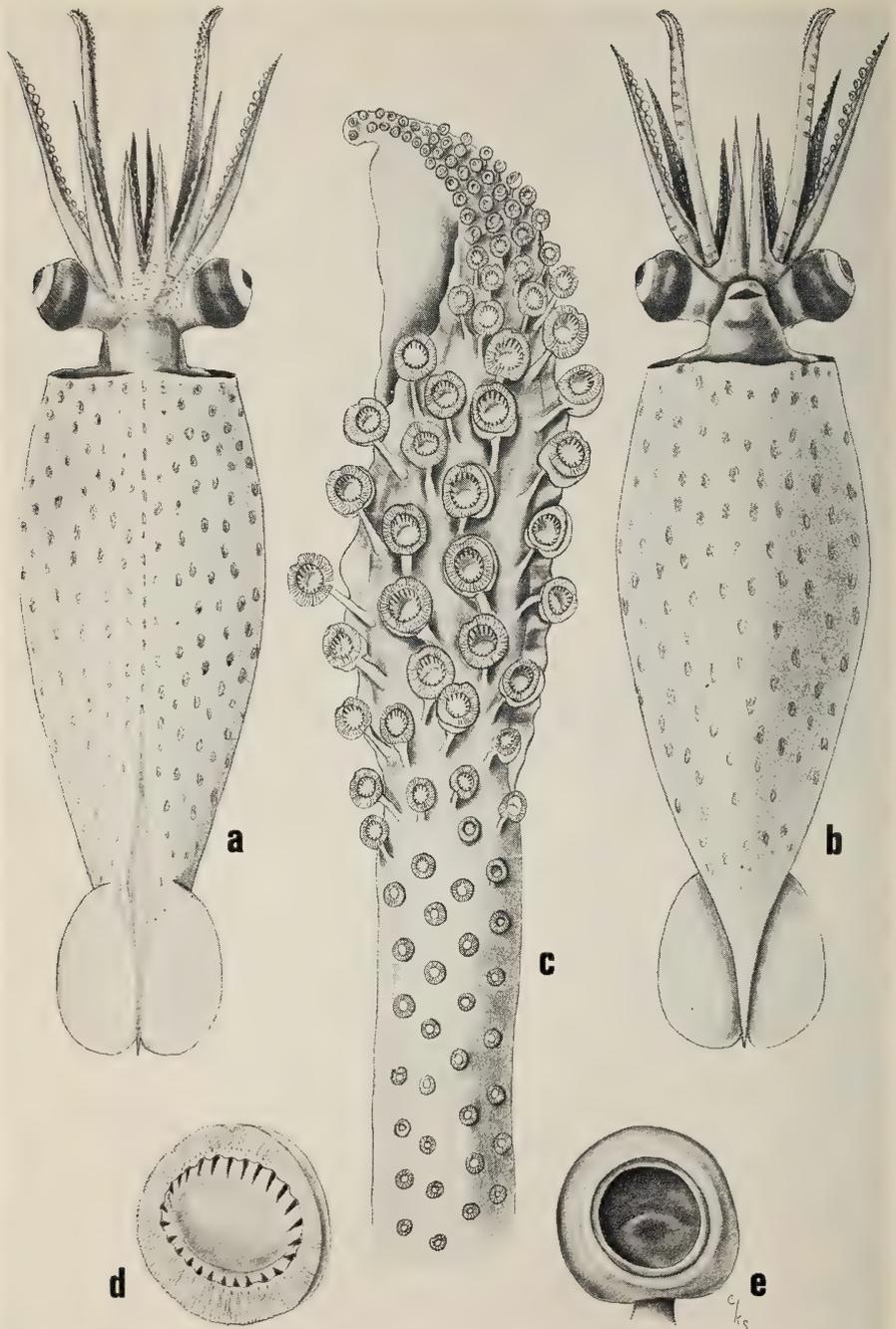
Chiroteuthis capensis, n. sp. *a.* Details of oral surface of fourth arm; *b.* Papilla, pedicel and sucker from left third arm; *c.* Funnel (left) and mantle (right) components of locking apparatus; *d.* Mandibles; *e.* Funnel organ; *f.* Radula; *g.* Liver and ink sac of *C. capensis*; *h.* Liver, ink sac and light organs of holotype of *Chiroteuthis lacertosa* Verrill.



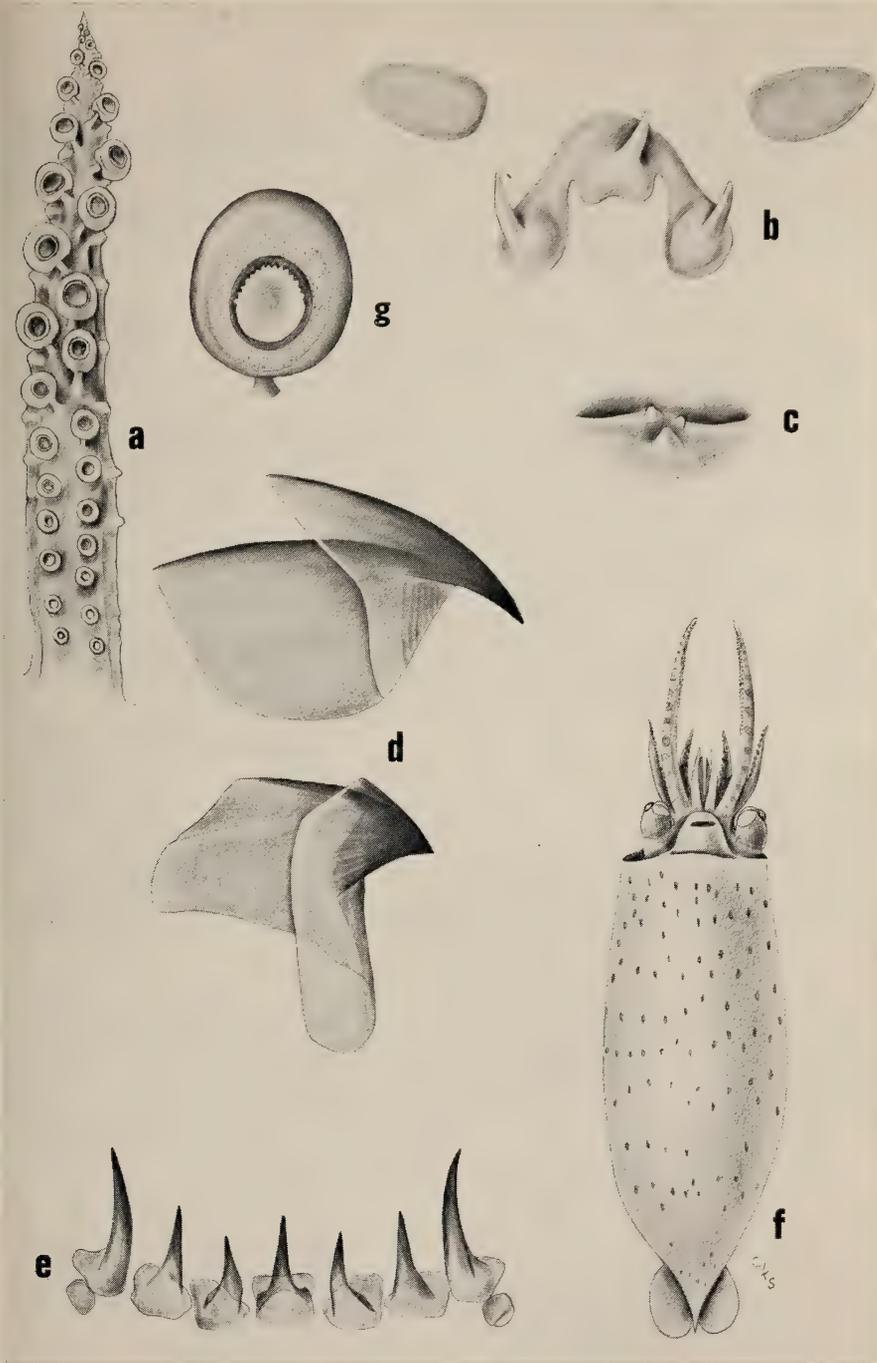
Pyrgopsis pacifica (Issel), female, SAM A29705. *a*. Dorsal view; *b*. Ventral view; *c*. Left tentacular club; *d*. Large sucker from club; *e*. Large sucker from left third arm.



Pyrgopsis pacifica (Issel). *a.* Funnel organ of SAM A29705; *b.* Tip of left third arm of same; *c.* Radula of same; *d.* Mandibles of same; *e.* Ventral view of smallest specimen of SAM A29722; *f.* Tubercular row of smallest specimen; *g.* Tubercular row of intermediate specimen of SAM A29722; *h.* Tubercular row of specimen SAM A29705; *i.* Ventral arms showing hectocotylyzation of right arm of largest male SAM A29722.



Megalocranchia megalops australis, n. subsp. Holotype, SAM A29733. a. Dorsal view; b. Ventral view; c. Left tentacular club; d. Large sucker from tentacular club; e. Large sucker from left third arm.



Megalocranchia megalops australis. a. Left third arm; b. Funnel organ; c. Tubercles at fusion of mantle and funnel; d. Mandibles; e. Radula; f. Ventral view of specimen of 45.0 mm mantle length; g. Distal sucker of left third arm tip.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol. '), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

7.68

A. J. HESSE

ADDITIONS TO THE CYRTOSIINAE
(BOMBYLIIDAE) OF SOUTH AFRICA

December 1967 December
Volume 50 Band
Part 6 Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R1.20

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

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

ADDITIONS TO THE CYRTOSIINAE (BOMBYLIIDAE) OF
SOUTH AFRICA

By

A. J. HESSE

South African Museum, Cape Town

(With 8 figures in the text)

CONTENTS

	PAGE
Introduction	89
Revised key to the known African genera	90
Notes on the genera and descriptions of new genera and species	93
Summary	129
Acknowledgement	130
References	130

INTRODUCTION

Since the publication of my revision of the Cyrtosiinae as a constituent section of my revision of the Bombyliidae of Southern Africa in 1938, members of the South African Museum staff have collected some new species of this subfamily. In addition Mr. and Mrs. B. Stuckenberg of the Natal Museum have recently submitted certain new forms obtained by them in Natal, Zululand, Lesotho, in the eastern Cape, and in the western Cape. Of more biological importance is the interesting cyrtosiine predator or parasite in egg-packets of the brown swarm locust, represented by a remarkable new genus submitted by Mr. R. J. Mansfield of the Department of Agriculture at Pretoria, and which probably plays some role in the biological control of this pest. To this must be added the interesting new genus collected in South West Africa by Professor Per Brinck of the Zoological Institute of Lund, which I described as a new genus *Euanthobates* in *South African Animal Life* in 1965, and of which genus another new South African representative was subsequently discovered in the collections of the South African Museum.

As a supplementary contribution to my original revision of this subfamily a revised key to the known African genera is given below, the new forms are described, and the taxonomic position of others is commented upon.

Representatives of this subfamily, of which most of the forms are small,

often minute, usually with characteristic dark and yellow markings, and in most cases adapted to flower feeding, are mainly characterized by a reduction of the wing-venation; presence of only one submarginal cell; absence or reduction of the marginal cell in many forms; the quadri-articulate antennae; the presence of a slight indentation in the inner margin of the eyes opposite antennae in many of the forms; the markedly convex, humped or arched thorax; the more or less poorly developed vestiture and the absence of bristly elements or macrochaetae on the body; absence of spines and distinct spicules on the legs; the spine-like, or sometimes clasper-like, process on each side of the last sternite in ♂♂ of some genera; and the tendency for the telomeres of the paramere in the hypopygium to be flattened and to be leaf-shaped in quite a number of forms.

REVISED KEY TO ALL THE KNOWN AFRICAN GENERA

1. (a) Proboscis well developed, stoutish, often long; ocellar area more triangular, not separated from frons by a distinct depressed line, and lateral ocelli much nearer together; thorax, though humped, not so globular, not punctured or sculptured above, usually with a distinct lateral depression on sides above wing-base; abdomen more normally ovate or cylindrical, tergite 1 not or only slightly depressed discally, and dorsum of abdomen not relatively coarsely punctured or sculptured; venter not, or scarcely, depressed; wings either with a normal marginal cell or, if with a reduced marginal cell, the latter is smaller or even absent, its posterior vein joining costal cell, not costal margin; discoidal cell present or absent and, if present, distinctly more elongate; mostly very small or small forms, not exceeding 3·4 mm., the body not resembling that of acrocerid genera; flower-feeding forms 2
- (b) Proboscis very much reduced, rudimentary, minute, vestigial, or almost absent; ocellar area more transverse, broader, distinctly separated from frons by a depressed line, and lateral ocelli very widely separated; thorax more globular, more markedly humped, punctured or sculptured above, without any distinct lateral depression on each side above wing-base; abdomen much arched or convex above, very much broader, at broadest part, than thorax, markedly depressed discally on tergite 1 and dorsum of abdomen comparatively coarsely punctured or sculptured; venter markedly hollowed or excavate; wings with a reduced more scalene-triangular or irregularly rhomboidal marginal cell, its posterior vein ending in costal margin near or a little beyond apex of costal cell; discoidal cell present, shorter, hexagon-like; slightly larger forms, 2·6-4·4 mm., the body resembling that of the acrocerid genus *Psilodera*; non-feeding forms *Psiloderooides* n. gen.
2. (a) Wings with a distinct and normal marginal cell, its bounding vein ending in anterior margin of wings; hairs on body and legs, even if sparse, usually longer, more conspicuous; integument of body, especially of dark or black parts, tending to be more shining or sometimes even brilliantly so; slightly larger forms, usually more than 2 mm. in length 3
- (b) Wings either without a marginal cell, or with a much reduced, abnormal and small, triangular one, of which the bounding vein ends in lower vein of costal cell, not in anterior margin; hairs on body and legs very short or minute, almost imperceptible; integument of body usually duller; very small forms, usually not more or much more than 2 mm. in length 7
3. (a) Head usually more elongated, the eyes situated more forwards and postocular part longer, more convex, not flattened; head below longer, either produced behind to a variable extent, or it is sulcate, depressed, or grooved below, ending in a process or spine behind, or on each side behind in a blunt prominence or even subangular prominence; frons usually depressed to a variable extent; buccal cavity usually much

narrower or smaller; antennal joint 3 broader, more conical, elongate-ovate or leaf-shaped; body narrower, more laterally compressed, the thorax more conspicuously roundly convex or humped; first basal cell in wings usually longer than, or at least subequal in length to, second; anal cell narrowly or broadly open apically; axillary lobe narrower, not or scarcely much broader than anal cell; hind tarsi in ♂♂ normal 4

(b) Head more globular, the eyes normally situated, and postocular part short, flattened; head below broad, shorter, not sulcate, not produced behind below; frons, if slightly depressed, then so only anteriorly; buccal cavity much broader, more gap-like or normally broad; antennal joint 3 more cylindrical or rod-like, even if broadened basally; body more plump, the thorax less roundly and conspicuously humped; first basal cell distinctly shorter and narrower than second; anal cell acute and stalked apically; axillary lobe more broadly lobe-like, broader than anal cell; base of basal joint of hind tarsi in ♂♂ sometimes produced into a curved, hook-like process *Onchopelma* Hesse

4. (a) Head below broader, not distinctly longitudinally depressed or sulcate, sometimes even slightly ridged or ending medially behind in a slight or blunt prominence; postocular part usually shorter or much shorter, the head less elongate; inner margins of eyes opposite antennal insertions without even an indication of an indentation; thorax usually more highly convexly humped; wings without a discoidal cell *Cyrtosia* Perris

(b) Head below, especially anteriorly, very much narrower, distinctly more longitudinally depressed or sulcate, either slightly heel-like prominent behind (side view), or ending medially behind in a spine-like process or in a subangular prominence on each side behind; postocular part usually longer, the head appearing more elongate and the eyes usually situated more forwards; inner margins of eyes usually with a distinct indentation or an indication of one opposite antennae; thorax slightly less convexly humped; wings with or without a discoidal cell 5

5. (a) Head below more broadly depressed or grooved longitudinally, ending behind in a heel-like prominence (side view), or in a blunt or subangular prominence on each side behind; occipital part comparatively shorter, either shorter than, as long as or not longer than frons, more rounded or convex, less sloping to neck, and there distinctly broader; wings with a discoidal cell; body usually less, or less extensively, shining; hypopygium of ♂♂ armed with more strongly developed, or at least more visibly protruding, clasper organs (process on each side of last sternite) 6

(b) Head below narrowly sulcate, at least anteriorly, produced posteriorly, ending behind in a longish, median, spine-like process; occipital part relatively longer, longer than frons, usually more sloping to neck and there more narrowed; wings without a discoidal cell; body more extensively shining or polished in appearance; hypopygium of ♂♂ armed with much feebler, smaller, not so visibly protruding and only shortly spine-like clasper organs (processes of last sternite) *Ceratolaemus* Hesse

6. (a) Head more subglobular, less elongate, the postocular part more convex or rounded, usually relatively shorter, the distance between hind margin of eye and posterior angle below head being much shorter, at most only about half, or a little more than half, length of eye; head below less produced posteriorly, in side view appearing only heel-like; proboscis comparatively shorter, less stout, usually not much longer, often shorter, than head; antennal segment 4 comparatively longer relative to length of 3; vestiture more strongly developed, and microtrichial fringe, and microscopic hairs on membrane, of wings usually also more developed; wings relatively longer, usually much longer than head and body; last sternite in ♀♀ distinctly larger, more elongate; clasper organs of last sternite of ♂♂ less strongly developed, only their apices visibly protruding *Platypygus* Lw.

(b) Head distinctly more elongate, the postocular part less rounded, more sloping to neck, relatively longer, the distance between hind margin of eye and posterior angle below head longer, usually more or much more than half length of eye; head below more conspicuously produced behind, in side view ending in a more conspicuous prominence on each side posteriorly below; proboscis relatively longer, stouter, usually distinctly longer than head; antennal joint 4 relatively much shorter relative to length of 3; vestiture much shorter, sparser, and with much finer or without any microtrichial

- fringe and membranal microscopic hairs on wings; wings relatively shorter, not very much longer than head and body; last sternite in ♀♀ shorter or much shorter; clasper organs (processes of last sternite) of ♂♂ usually more strongly developed, more conspicuously visible and protruding *Cyrtisioptis* Séguéy
7. (a) Marginal cell in wings much reduced, represented as a small triangular cell, the bounding vein of which ends directly, sometimes at right angles, in costal cell . . 8
 (b) Marginal cell entirely absent, its place being occupied by the submarginal cell . . 11
8. (a) Wings with the veins and cells less reduced, two basal cells normally present, and four posterior cells normally delimited by longitudinal veins, the fourth vein entire, either joining directly on to enlarged second basal cell, or its basal half forming the division between basal cells; fourth posterior cell very much shorter, its base forming apical cross vein of second basal cell; coxae sometimes rather strongly developed, stout and thick 9
 (b) Wings with the veins and cells much reduced, only one basal cell (first) being normally developed, the second being entirely absent or only indicated as a vestige below apex of first, with the four posterior cells not all normally delimited by continuous longitudinal veins, the normal fourth vein of other Bombyliidae being only represented in apical part of wings, the basal parts of normal first and second (or third) posterior cells being confluent and undivided; fourth posterior cell very much longer, its base forming lower vein of first basal cell; coxae normally developed *Doliopteryx* Hesse (1956: 936)
9. (a) Discoidal cell in wings absent; submarginal cell much shorter or very short, ending much before apex of wing; first posterior cell also very much shorter, very much less than twice length of first basal cell; third posterior cell longer, not parallelogram-shaped; anal cell usually more gradually narrowed apically, either fairly broadly open or roundly sessile on hind margin; terminal element (joint 4) of antennae much shorter, not more than $\frac{1}{2}$ length of 3 or even minute; head below only shallowly, or scarcely, or not deeply, grooved below 10
 (b) A distinct discoidal cell present; submarginal cell long, extending round to near apex of wings; first posterior cell long, nearly or quite twice length of first basal cell; third posterior cell shorter, quite or very nearly a parallelogram; anal cell rapidly and acutangularly narrowed apically, very shortly stalked; terminal element (joint 4) of antennae much longer, much more than $\frac{1}{2}$ length of 3; head below more distinctly and very deeply grooved *Aetheoptilus* n. subgen. of *Empidideicus*
10. (a) First basal cell in wings shorter or much shorter than second, the latter evidently formed by the fusion of a discoidal and a second basal cell, and from it radiate 4 longitudinal veins delimiting the four posterior cells; first posterior cell much broader, opening very broadly on apical margin; thorax distinctly more convexly humped; face much longer; antennal joint 3 ending in a distinct longish terminal element or joint *Glbellula* Bezzi s. str.
 (b) First basal cell much longer than second, the latter not formed by fusion of a discoidal and second basal cells, a discoidal cell being entirely absent, and from the second basal cell radiate only 3 longitudinal veins, the fourth vein forking to form the triangular second posterior cell; first posterior cell distinctly very much narrower, narrowed and curving anteriorly apically, and only narrowly opening on anterior margin, not at apex; thorax distinctly less humped; face markedly short; antennal joint 3 ending apically in a minute, almost imperceptible, terminal element *Pseudoglbellula* n. gen.
11. (a) Face much longer; antennal joint 3 proportionally shorter, ending in a conspicuous, longish, slender fourth joint; head below without any downwardly-projecting processes in the groove; proboscis, if extruded, usually shorter; thorax more convexly humped; first posterior cell in wings much broader, widely or broadly divergent apically, its lower or posterior vein ending much behind apex of wings; first basal cell only a little longer than second; part of fourth vein between first basal and second posterior cells long; anal cell narrower 12
 (b) Face markedly short; antennal joint 3 proportionally longer, more spear-blade- or leaf-shaped, ending in a minute, scarcely perceptible, fourth joint; head below sometimes with conspicuous, downwardly-projecting, finger- or caeca-like processes from the

groove; proboscis, if fully extruded, sometimes very long, or even longer than head and body; thorax less convex, not so humped; first posterior cell much narrowed, much narrowed apically, its posterior vein ending before apex of wings; first basal cell distinctly much longer than second; part of fourth vein between apex of first basal and the second posterior cells markedly short, very much shorter than latter cell; anal cell much broader, sometimes very acute apically *Euanthobates* Hesse

12. (a) Discoidal cell in wings absent; fourth vein forking to form second posterior cell; process or spine-like process on each side of last sternite in ♂♂ shorter, less developed.

Empidideicus Beck. s. str.

(b) Discoidal cell present; fifth vein forking, its anterior (upper) branch, together with basal part of fourth and base of second posterior cells, forming the discoidal cell; process on each side of last sternite in ♂♂ more triangularly spine-like, larger, more developed *Anomaloptilus* Hesse subgen. of *Empidideicus* Beck.

DESCRIPTIVE

Genus CYRTOSIA Perr.

Cyrtosia Perris, 1839: 55. Bezzi, 1925: 256. Séguy, 1930: 79. Engel, 1933: 103.

This Palaearctic genus, described by Perris in 1839 and more comprehensively redescribed by Engel in 1933, is represented by quite a number of known species, at least 16, in Europe, the Mediterranean, Asia Minor and north Africa, but has not been recorded from Africa south of the Sahara. Two representatives of it, belonging to two distinct species, have now been collected in South Africa since my revision of the Cyrtosiinae. The discovery of representatives of this genus in South Africa extends the geographical range of the genus and, together with representatives of the other Palaearctic genera *Platypygus* Lw. and *Cyrtisiopsis* Séguy which have also been found in South Africa in the interim, completes the list of Palaearctic cyrtosiine genera extending so far south in the African continent.

The characters distinguishing this genus from nearly related genera have been listed by Engel in his revision (1933). From *Platypygus*, which also has a distinct and normal marginal cell in the wings, representatives of *Cyrtosia* may at once be distinguished by the head which is broader below, not distinctly grooved or sulcate below, not prominently projecting posteriorly below; by the postocular part which is shorter, the head being less elongate; by the entire absence of a slight indentation in inner margins of eyes opposite antennal insertions; by the distinctly more convexly humped thorax; and by the absence of a discoidal cell in the wings.

From the genus *Cyrtisiopsis* Séguy, which is very near *Platypygus*, it differs, apart from the absence of a discoidal cell, by the more globular or subglobular head which is not sulcate or grooved below and which is not angularly or subangularly conspicuously produced on each side of the groove behind and below; by the absence of indentations in inner margins of eyes; by the shorter proboscis; and by the usually less prominent, less sharply hook-like clasper organs (processes on last sternite). The two new South African species are:

Cyrtosia namaquensis n.sp.

Unfortunately represented in the collections by a single ♀ specimen only which is characterized as follows:

Body mainly black, the following parts pale yellowish: face, buccal rim, anterior part of frons, a large humeral spot, extending down anteriorly on each side to transverse suture between mesonotum and pronotum, and also includes anterior spiracle and is confluent with the yellow propleural sclerite, notopleural connection and area just in front of wing-bases, postallar calli and a broadish fascia extending forwards from it to opposite level of wing-base, a prosternal spot above front coxae, area below wing-bases, sutural part between pteropleuron and sternopleuron, posterior part of hypopleuron, hind margin of metapleural part, halteres and their knobs, narrow hind margins of tergites, becoming slightly broader posteriorly and on sides, hind margins of sternites, a spot at base of hind femora below, apical parts of femora, greater part of tibiae (excepting a brownish infusion before middle on inner hinder faces of front and middle ones and the apical parts of hind ones), and basal joint of tarsi; integument subshining, covered with a faint greyish whitish bloom.

Vestiture with the hairs on body and legs fine, very short, slightly longer on abdomen posteriorly, entirely pale, gleaming slightly sericeous yellowish, especially on thorax above.

Head with the frons centrally and longitudinally deeply depressed, as wide anteriorly at level of antennae as ocellar tubercle on head behind; face shorter than frons, about as long as wide at level of antennae, narrowed anteriorly; part of buccal cavity in head in front narrow, vertical, sulcus-like; antennal joint 1 longer than 2, quite 1.5 times as long; joint 3 elongate, about 1.6 times as long as joints 1 and 2 combined and about 2.3 times as long as broad and also about 2.3 times as long as the rather stoutish joint 4 which itself is about as long as joint 1; proboscis relatively stout, much longer than head, about 0.88 mm. long; palps very short, inconspicuous; head below not produced posteriorly, medially appearing slightly, but distinctly, ridged, with a distinct, conspicuous, pore-like puncture on each side of ridge a little beyond middle.

Wings hyaline, but with a very feeble whitish subopacity, more perceptible basally; veins yellowish brownish, becoming more yellowish at base of wing and darker brownish in apical half of costal vein and in basal veins of the cells; veins between basal cells and anal and axillary cells very pale, almost whitish; second posterior cell a little more than twice as long as distance between it and first basal cell, and this latter distance distinctly less than twice distance of the same vein to base of third posterior cell; first basal cell much longer than second; squamae pallid; halteres yellowish whitish, their knobs relatively large.

The ♀ holotype in the South African Museum.

Length of body: about 2.24 mm.

Length of wing: about 2.4 mm.

Locality: Bushmanland: Aggenys between Springbok and Pella (Mus. Staff, Oct. 1939).

This species resembles the Palaearctic (Mediterranean) species *obscuripes* Lw. in coloration. From the latter it may however at once be distinguished by the very much longer proboscis which is much longer than the head, the more extensively yellow tibiae, and the much longer basal part of fourth vein (between base of third posterior cell and apical cross vein of first basal cell) relative to the rest of it to base of second posterior cell.

Cyrtosia stuckenbergi n.sp.

Another specimen of *Cyrtosia*, a single ♂, which, though resembling the ♀ *namaquensis* in colour-pattern and notwithstanding the similarity of colour-patterns among species of *Cyrtosia*, I think belongs to a different species which is characterized as follows:

Body mainly black, the integument dulled by fine greyish whitish tomentum; the following parts yellowish whitish: extreme apex of frons, greater part of face, extending down along upper half of buccal rims on each side, anterior margin of head below, a narrowish streak on mesonotum anteriorly on each side from humeral angle down to pronotal part and also extending spot-like down anterior margin of mesopleuron to include a propleural vertical streak, a triangular dorso-lateral thoracic spot, just above and in front of wing-bases, a streak on each side of thorax above to scutellum, the notopleural fold and area in front of and just below wing-bases, to a certain extent pleural sutures, an infusion above middle and hind coxae, to a slight extent posterior metapleural margin, hind margins of tergites and sternites, to a certain extent apices of coxae, bases and apical parts of femora, to a variable extent inner faces of front tibiae, the outer exterior faces of middle ones, to a feebler extent bases and distal halves of hind tibiae, and basal parts or halves of tarsi.

Vestiture with the hairs on body and legs fine, very short, fairly dense, entirely pale, those on disc of thorax appearing slightly more yellowish, and those on abdomen slightly longer, more whitish, and longest (tuft-like) on each side of last tergite above hypopygium; hairs on tibiae very fine, short, dense and whitish.

Head with the frons slightly depressed, slightly narrowed anteriorly, there narrower than space between two posterior ocelli; face shorter than frons, also slightly narrowed anteriorly; part of buccal cavity in head in front vertical as in *namaquensis*; antennal joint 1 (as far as can be seen) as long as 2; joint 3 ovate, slightly longer than broad, broadest before middle, about as long as 1 and 2 combined, about a fourth longer than terminal joint; proboscis about 0.56 mm. long; palps not perceptible; head below slightly longitudinally raised ridge-like, and also with a minute pore on each side posteriorly.

Wings hyaline, with a very feeble whitish subopacity; veins brownish; costal margin slightly sagging downwards opposite level of base of submarginal cell; second posterior cell a little more than twice as long (along upper vein) as distance between it and first basal cell; vein between apex of second basal cell and base of second posterior cell equal or subequal in length to lower vein

of second posterior cell; first basal cell much longer than second; alula narrowish; squamae whitish; halteres yellowish, their knobs white.

Hypopygium with the claspers or processes of last sternite (text-fig. 1) fairly large, broad, rather sharply bent inwards to apical part, bluntly pointed.

The ♂ holotype in the Natal Museum.

Length of body: about 1.52 mm.

Length of wing: about 1.6 mm.

Locality: Karoo at junction of Calvinia and Sutherland roads near Inverdoorn, Ceres Div. (B. and P. Stuckenberg, 2-3 Oct. 1959).

Apart from its smaller size, the ♂ of this species differs from the ♀ of *namaquensis* in the much smaller and less extensive yellowish whitish markings on body, presence of a distinct triangular yellowish whitish spot on sides of thorax above (just above wing-bases) which is absent in *namaquensis*; narrower yellowish whitish hind margins of tergites; narrower yellowish apical parts of femora; more darkened tibiae and basal joints of tarsi; much darker and entirely dark veins in wings; different proportions of antennal joints 3 and 4, the former being proportionally distinctly much shorter, more ovate and only a fourth longer than 4 (in *namaquensis* it is quite 2.3 times length of 4); and more slender proboscis, its labella nearly $\frac{1}{3}$ length of entire proboscis (in *namaquensis* proportionally longer, nearly $\frac{1}{3}$ this length).



FIG. 1. Dorso-posterior view of abdomen of ♂ *Cyrtosia stuckenbergi* n. sp. showing the processes (one on each side) of last sternite.

Genus PLATYPYGUS Lw.

Platypygus Loew, 1844: 127. Bezzi, 1925: 259. Paramonow, 1929: 197 (135). Engel, 1933: 120.

At the time of my revision of the Cyrtosiinae of southern Africa in 1938 no species of *Platypygus* s. str. had been recorded from this part of Africa. The only representative of what at the time I took to be a *Platypygus* was the species *xanthogrammus* which I then referred to a new subgenus *Ceratolaemus* of the latter genus. As stated below there are now sufficient reasons for raising my subgenus to the status of a distinct and separate genus. Recently Mr. and Mrs. B. Stuckenberg of the Natal Museum submitted a single ♀ specimen from Natal which obviously belongs to the genus *Platypygus* s. str. This is apparently the first record of a true *Platypygus* species from southern Africa. As in the case of *Cyrtosia*, this genus is well represented in southern Europe, the Mediterranean, North Africa and Asia Minor.

In his revision of the Palaearctic forms Engel has given an adequate redescription of this genus which is chiefly characterized by the presence of a distinct discoidal cell in the wings; the rather longish wings, usually much longer than head and body; a conspicuous groove on head below of which the

rims posteriorly project backwards rather heel-like; the relatively longish antennal joint 4; relatively shortish proboscis which is usually not much longer than the head, often shorter; the rather long and conspicuous, more scoop-like, last sternite in ♀♀; and the distinctly visible, or slightly protruding, claspers (processes on sides of last sternite) of the hypopygium of the ♂♂. The new species from South Africa is:

Platypygus natalensis n.sp.

The ♀ of this species is characterized as follows:

Body mainly yellowish, the anterior part of frons, the face and legs paler yellowish; postvertical and occipital part, antennal joints 3 and 4, apical halves of tarsi and the claws black; eyes blackish brownish; proboscis darkened laterally to a variable extent; disc of thorax above with 3 broadish, longitudinal, brownish streaks, narrowed posteriorly, and with the lateral ones extending only from just before middle on each side, and the lateral ones also flanked on each side above level of wing-bases by a roundish brownish spot; dorsum of abdomen also brownish, especially discally on tergites 1-3, fading out more posteriorly; hind margins of tergites paler, more pale yellowish, becoming slightly broader posteriorly and on sides.

Integument of head, especially occiput, body above and to a certain extent pleurae, especially mesopleural part, more or less shining.

Vestiture rather well developed and dense, though shortish, fairly dense on abdomen above, mainly dark or blackish brownish; dark hairs on dark apical halves of tarsi more blackish.

Head subglobular; frons gradually, but slightly, narrowed anteriorly, medially longitudinally depressed; face above subequal in length to frons; occipital part rounded, slightly less than half axial length of eyes along sides; head below broadly grooved, hind margin of the sulcus distinctly projecting heel-like behind; antennae with joint 1 scarcely longer than 2, with 3 about $1\frac{1}{4}$ longer than 1 and 2 combined, ovate, somewhat flattened, and with 4 rather long, quite as long as 1 and 2 combined or $\frac{3}{4}$ length of 3, cylindrical; proboscis subequal in length to that of head, about 0.72 mm. long, its labral part about 0.48 mm. long.

Wings much longer than body, very faintly, but distinctly, infuscated; veins dark brownish; membrane with distinct, microscopic hairs, and hind margin with a distinct microtrichial fringe, longer along alular and axillary margins; first posterior cell parallel-sided; middle cross vein a little before middle of discoidal cell; knobs of halteres yellowish, but darkened above along base.

The ♀ holotype in the Natal Museum.

Length of body: about 2.48 mm.

Length of wing: about 3.28 mm.

Locality: Natal: Lilani, Ahrens Dist. (B. and P. Stuckenberg, Apr. 1962).

Genus *CYRTISIOPSIS* Séguy

Cyrtisiopsis Séguy, 1930: 80, fig. 1.

Cyrtisiopsis subgen. of *Platyppygus* Lw. Engel, 1933: 120, 125, fig. 58.

This is another Palaearctic genus very near *Platyppygus* which Séguy established to accommodate the new species *singularis* he described from north west Africa and Spain. Subsequently Engel however maintained that the species *Platyppygus melleus*, described by Loew from Egypt in 1856, was specifically identical with *singularis*, and at the same time relegated *Cyrtisiopsis* to the status of a subgenus only of *Platyppygus*. From the descriptions and illustrations of species of *Platyppygus* it is however quite evident that the latter genus differs from *Cyrtisiopsis*, as defined and figured by Séguy, in certain important respects. These distinguishing characters appear to me to be of sufficient importance to merit the retention of *Cyrtisiopsis* as a separate and distinct genus as maintained by Séguy. Moreover a series of both ♂♂ and ♀♀ of a South African cyrtisiine species, collected by me in the Koup Karroo in 1945, agree with Séguy's description and figure of *Cyrtisiopsis* in most of these distinguishing features. It not only supplements the validity of this genus, but at the same time extends the geographical distribution of this genus to the far South.

Both the north African and the South African representatives of *Cyrtisiopsis* appear to differ from *Platyppygus* s.str. in the distinctly more elongated head, with the occipital part relatively longer, less convexly rounded, more sloping to neck; the deeper, more distinct and longer sulcus below the head, which ends behind in a distinctly longer, more conspicuous, blunt, subangular prominence on each side; the distinctly longer, stouter or even incrassate proboscis, which is much longer than the head and longer than in known species of *Platyppygus*; the relatively shorter antennal joint 4 (relative to length of joint 3); the much shorter and sparser vestiture on head, body and legs; the apparently shorter wings, without or with much finer microtrichial fringe and also without or with very much finer microscopic hairs on the membrane; the comparatively shorter and smaller last sternite in ♀♀; and the distinctly more strongly developed and more conspicuously protruding clasper organs (or hook-like processes of last sternite) of the hypopygium of the ♂♂. The new species from South Africa is:

Cyrtisiopsis crassirostris n.sp.

The series of both ♂♂ and ♀♀ of this species (text-fig. 2) was collected on the yellowish flowers of a Composite *Tripteris sinuata* growing in the Koup Karroo. This species is characterized as follows:

Body and legs mainly black; the following parts however very pale yellowish, ivory yellowish, or pallid: antennal sockets, narrow notopleural ridge from shoulder to a broader area surrounding wing-bases, postalar calli, a small propleural spot below shoulders, a spot above front coxae, another prosternal one on each side anterior to front coxae, a narrow sutural line below meso- and pteropleurae, a spot on pleurae just above middle coxae joining on with a larger spot posterior to it astride hind margin of pteropleuron

and anterior margin of hypopleuron, a spot just anterior to base of halteres, narrow hind margin of metapleural part, narrow hind margins of tergites and usually slightly broader hind margins of sternites, and in ♀ often also the visible integumentary membranes between tergites and sternites on sides below.

Integument of head behind ocellar tubercle, thorax and scutellum above scarcely or only shining a little, duller, and with very fine microsculpture; integument of frons, pleurae, and abdomen however smooth, polished in appearance, brilliantly shining; legs also shining; head below on each side of sulcus and on sides of head behind eyes finely, transversely striolate and shining.

Vestiture with the hairs, where present, very minute, not perceptible, the body and legs being mainly smooth and shining, and only very minute hairs perceptible on tibiae.

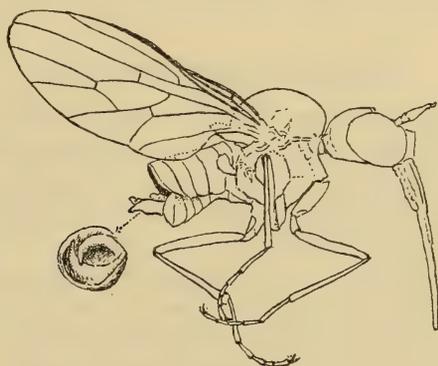


FIG 2. Side view of ♂ *Cyrtisiopsis crassirostris* n. sp., showing processes of last sternite in side view and separately below in posterior view.

Head with the sulcus below fairly deep, not produced medially behind as in next genus *Ceratolaemus*, but the sides of head bluntly and tumidly produced posteriorly into a rounded, slightly knob-like prominence, the hind margin below and posterior to sulcus being fairly deeply emarginate; eyes above slightly more broadly separated in ♀ than in ♂; frons foveately depressed; face narrow, convex, smooth and shining, about as long as frons from anterior ocellus to antennae; antennal joint 1 a little longer than 2, even quite 1.5 times length of 2; joint 3 elongate, slightly flattened, about twice (or a little more) length of 1 and 2 combined, about or nearly, or even a little more than, 3 times as long as broad, its terminal element cylindrical, subequal in length to, or a little longer than, transverse joint 2; proboscis comparatively stout and long, stouter in ♀, much longer than head, about 1.12–1.68 mm. (to 2.2 mm. when extended); palps not discernible.

Pronotum not much developed, not so prominent and lobe-like as portrayed in the Palearctic species.

Wings vitreous hyaline, highly iridescent; veins dark reddish brownish; first basal cell distinctly much longer than second; middle cross vein a little beyond middle of discoidal cell; latter subspindle-shaped, markedly narrowed apically, its apical cross vein very much shorter than base of third posterior cell, usually shorter or much shorter than middle cross vein; anal cell fairly broadly open apically; knobs of halteres usually entirely pallid or whitish in both sexes, but sometimes with the outer edge slightly infuscated basally.

Hypopygium of ♂ (text-fig. 2) with the inwardly curved forceps-like processes of last sternite very conspicuous, markedly and strongly developed, very stout, entirely black, gripping over each other like the jaws of a pair of pliers.

From 32 ♂♂ and 15 ♀♀, including the types, in the South African Museum.

Length of body: about 1.76–3 mm.

Length of wing: about 2–3 mm.

Locality: Koup Karoo: Prince Albert Road Station (A. J. Hesse, July–Aug. 1945).

Subgenus CERATOLAEMUS Hesse

Ceratolaemus Hesse, subgen. of *Platypygus*, 1938: 969. Hesse, 1960: 316.

The generic identity of the species *xanthogrammus* Hesse (1938) has now become confused. Originally I described it as a subgenus of *Platypygus*. Since then Mr. and Mrs. Stuckenberg of Pietermaritzburg have submitted 3 other new species of this same subgenus. A comparison of these species with the South African representative of what I take to be a true *Platypygus* and with the descriptions of the Palaearctic forms referred to the latter genus however makes it evident that my subgenus differs consistently in certain characters from *Platypygus* s.str. and to such an extent that *Ceratolaemus* can no longer be retained as a subgenus of *Platypygus*.

It appears to represent a distinct and separate taxon which differs from *Platypygus* s.str. chiefly in the absence of a discoidal cell; rather elongated head of which the groove or narrow sulcation below ends in a distinct, single, median spine or spine-like process and not in only a heel-like prominence or, as in *Cyrtisiopsis*, in two prominences; the the more brilliantly shining or polished head and body; the much longer and stouter proboscis; and in the much smaller, more reduced and hidden claspers of the hypopygium of the ♂♂.

To make matters worse Bowden recently (1965: 203–4) relegated the subgenus provisionally as a synonym of *Cyrtosia* Perris, referring it to the Palaearctic *Cyrtosia nitens* group, a group which appears to differ much from the generotypical or *marginata* group and to which the two South African representatives, described in this paper, appear to belong.

From the latter and from descriptions of other Palaearctic forms of *Cyrtosia*, not belonging to the *nitens* group, the *Ceratolaemus* forms differ consistently in certain cephalic characters such as the head below, especially anteriorly, which is very much narrower, distinctly more longitudinally sulcate, ending medially behind in a more spine-like or subangular prominence; the distinctly

longer postocular part, the head appearing more elongate and the eyes usually situated farther forward; the inner margins of the eyes have a distinct indentation opposite the antennae; and the thorax is less convexly humped.

From all this it appears that the genus *Cyrtosia* in the Palaearctic region, as at present constituted, is by no means homogeneous and that a comprehensive revision would necessitate its subdivision. Until the true generic identity of *Cyrtosia* is established I provisionally retain the South African forms of *Ceratolaemus* as belonging to a separate genus.

From *Cyrtisiopsis*, as redefined in this paper and which it resembles superficially even more than species of *Platypygus*, it differs, apart from the single angular spine on head below already mentioned, in the longer occipital part, absence of a discoidal cell, more shining body, and the very much smaller, more reduced telomeres of the ♂♂.

The other species of *Ceratolaemus* are:

Ceratolaemus longirostris n.sp.

A unique ♀ specimen from Natal which resembles ♀♀ of the other Natal species *xanthogrammus* Hesse superficially, but agrees and differs from the latter in the following respects:

Body paler, paler yellowish brownish or more yellowish, the head mainly very pale yellowish or yellowish brownish, not mainly dark castaneous- or blackish brownish, the apex of face and buccal rims however not pale yellowish; thorax above discally, apart from anterior and lateral yellowish markings, not mainly uniformly very dark or blackish, but more dark reddish brownish, replaced discally by two submedial yellowish streaks, becoming broader in hinder half, and anteriorly medially by a faint narrow central yellowish line; sides of thorax above also more broadly yellowish; scutellum also entirely yellowish as in typical *xanthogrammus*; pleurae and legs more extensively and mainly yellowish, the lower pleural parts not darkened to a variable extent; abdomen above paler, paler reddish brownish, not dark castaneous or blackish brownish, and yellowish hind margins of tergites comparatively broader yellowish, not so contrasting with the darker rest as in *xanthogrammus*; entire body similarly shining.

Vestiture with the fine and shortish hairs very similar, as dense, also dark or brownish, but those towards end of abdomen above also dark, not tending to be paler, and distinctly slightly shorter.

Head with the antennae very similar, but with joint 4 proportionally shorter; proboscis distinctly very much longer (even if much extruded in specimen), its labral part slightly more slender, smoother, quite 1.32 mm. long, and entire proboscis from theca to apex about 1.88 mm. (in *xanthogrammus* only about 0.76–0.8 mm. and 0.92–1.008 mm. respectively, and labral part distinctly finely punctured), the proboscis, unlike that of *xanthogrammus*, without any perceptible hairs, especially on sides.

Wings very similar; halteres however more uniformly yellowish, the knobs not tending to be entirely or mainly whitish.

Holotype in the Natal Museum.

Length of body: about 2.6 mm. (excl. proboscis).

Length of wing: about 2.68 mm.

Locality: Natal: Tugela Valley, Kranskop Dist. (B. and P. Stuckenberg, May 1960).

Ceratolaemus bilineatus n.sp.

A single ♂ specimen from the Cape in the collections before me resembles both *xanthogrammus* and *longirostris* from Natal, more especially the latter, but may be distinguished as follows:

Body with the head, thorax above and abdomen above mainly very dark castaneous brownish or blackish brownish as in *xanthogrammus*; narrow sides of frons and face yellowish whitish; sides of thorax above broadly yellowish as in *longirostris*, but with a more distinct and conspicuous blackish spot above opposite wing-bases; disc of thorax as in *longirostris*, with two submedial yellowish streaks which broaden in posterior half, but without an indication of a narrow central yellowish line; pleurae with the lower sternal parts also darkened as in *xanthogrammus*; scutellum entirely yellowish; hind margins of tergites narrowly yellowish discally, broadish on sides; legs also mainly yellowish as in the other two species, but at least apical halves of basitarsi (as in some forms of *xanthogrammus*) and rest of tarsal joints darkened.

Vestiture very similar, also darkish; hairs towards apex of abdomen appearing slightly paler as in *xanthogrammus*.

Head with the antennae very similar, but joint 4 comparatively longer, appearing more slender, quite $\frac{2}{3}$ length of 3 (in the other two forms distinctly less than this); proboscis about 1.2 mm. long, slightly longer than in *xanthogrammus*, but much shorter than in *longirostris*, without any perceptible hairs as in the former species, the labral part also dullish due to very fine microscopic puncturation as in *xanthogrammus*, about 1 mm. long, shorter than in *longirostris*.

Wings as in the other two species, also slightly greyish yellowish, but relatively slightly broader; second posterior cell distinctly much longer, more parallel-sided than in the other two species, its lower vein nearly twice as long as part of vein between base of this cell and apex of first basal cell (in the other two forms these lengths are subequal or lower vein of the cell only a little longer); halteres and knobs yellowish whitish.

Holotype in the Natal Museum.

Length of body: about 2.8 mm. (excl. proboscis).

Length of wing: about 2.88 mm.

Locality: Southern Koup Karoo: Sevenweekspoort, Laingsburg Dist. (B. and P. Stuckenberg, 19-22 Sept. 1959).

Ceratolaemus montanus n.sp.

Still another smaller Cape species which resembles *xanthogrammus* more than *bilineatus*. Apart from being comparatively smaller, it agrees and differs from the three described species in the following respects:

Body with the head, thorax above and abdomen above mainly very dark or blackish as in *xanthogrammus*; thorax above with the same pattern of yellowish markings as in latter species, but with the anterior yellowish shoulder spot larger; disc of thorax entirely black, without submedial yellowish streaks as in *longirostris* and *bilineatus*; pleurae with more blackish or dark parts than in even *xanthogrammus*, not only the sternal parts being dark but also parts of meso- and pteropleurae, especially in ♂, where even the greater parts of these are sometimes darkened; scutellum mainly yellowish in ♀, darkened basally, in ♂ more extensively so; hind margins of tergites yellowish whitish, broader posteriorly, discally narrower than in *xanthogrammus*, broadened on sides, especially in ♀, the hind margins in ♂ narrowish, narrower than in ♀; venter darkened more than in the other species, especially in ♂, and yellowish hind margins of sternites more contrastingly evident; legs, excepting yellowish coxae, bases and apical parts of femora and, in ♀, to an obscure extent bases of tibiae, more darkened, especially in ♂, than in the other three forms, being either more infused with brownish, or in ♂, almost darker brownish.

Vestiture with the hairs on head and thorax distinctly very much shorter and sparser than in the other species, scarcely perceptible, also dark; those on abdomen also sparser, but scarcely shorter, appearing slightly paler, even towards base; those on legs also palish, but apparently even shorter than in the other forms.

Head with the antennae similar to those of the other species, but joint 4 relatively longish and slender as in *bilineatus*, also quite $\frac{2}{3}$ length of 3, in ♂ apparently even a little longer; proboscis comparatively shorter than in any of the other forms, shorter in ♂ than in ♀, the labral part about 0.32–0.68 mm. and entire proboscis from theca to apex about 0.4–0.88 mm., the labral part also minutely microscopically punctured, and sides of proboscis appearing hairless, not conspicuously hairy as in *xanthogrammus*.

Wings as in the other species, also appearing very faintly greyish yellowish; veins dark brownish; second posterior cell distinctly more divergent and broader apically than in the other forms, comparatively shorter, its lower vein usually longer than vein between base of the cell and apex of first basal cell: knobs of halteres white.

From 2 ♂♂ and 2 ♀♀ (♂ holotype and ♀ paratype in the Natal Museum, and ♀ allotype and ♂ paratype in the South African Museum).

Length of body: about 1.4–2.72 mm.

Length of wing: about 1.72–2.84 mm.

Locality: Southern Koup Karroo: Sevenweekspoort, Laingsburg Dist. (B. and P. Stuckenberg, 19–22 Sept. 1959).

The four known species of *Ceratolaemus* may be separated as follows:

1. (a) Disc of thorax above, apart from yellowish markings anteriorly and on sides, entirely uniformly dark castaneous brownish, blackish brownish or black, and sides less extensively or not continuously, yellowish; abdomen above darker, more dark castaneous brownish to blackish brown or even black 2
- (b) Disc of thorax above, apart from yellowish markings anteriorly and on sides, with two submedial yellowish lines or streaks which broaden posteriorly, and sides more extensively continuously yellowish; abdomen above paler brownish 3
2. (a) Proboscis slightly longer, usually 0.88 mm. and more, with longer, more conspicuous fine hairs perceptible on sides, and with longer labral part, longer than 0.68 mm.; antennal joint 4, relative to 3, much shorter and stouter, distinctly less than $\frac{2}{3}$ length of 3; hairs on head and thorax distinctly longer; second posterior cell in wings relatively longer, appearing less divergent apically; yellowish spot anteriorly on thorax above humeral angles smaller, linear or even wanting; pleurae and legs with more yellowish, the meso- and pteropleurae being usually entirely yellowish or pale, and femora and tibiae either entirely yellowish or very pale yellowish brownish ♂ ♀ *xanthogrammus* Hesse (and forms of it)
- (b) Proboscis shorter, only about 0.4–0.88 mm., with only very fine, not very perceptible, hairs on sides, and with a shorter labral part, only about 0.32–0.68 mm.; antennal joint 4 distinctly longer, more slender, about or scarcely less than $\frac{2}{3}$ length of 3; hairs on head and thorax minute and sparser; second posterior cell appearing shorter, more broadly divergent apically; yellowish spot above humeral angles larger, more triangular; pleurae and legs more darkened, the meso- and pteropleurae also darkened to a variable extent, and femora and tibiae appearing darker, the paler base and apex of femora and base of tibiae contrasting more with the darker rest ♂ ♀ *montanus* n. sp.
3. (a) Proboscis longer, quite 1.88 mm. long, with longer labral part, quite 1.32 mm., the latter more shining above, without or with scarcely perceptible microscopic puncturation; antennal joint 4, relative to 3, much shorter, stouter, distinctly less than $\frac{2}{3}$ length of 3; second posterior cell in wings broader, more divergent apically; head mainly pale yellowish brownish; sternal part of pleurae pale like rest of pleurae; abdomen above paler brownish, and tarsi darkened only from joint 2 ♀ *longirostris* n. sp.
- (b) Proboscis shorter, only about 1.2 mm., with a relative shorter labral part, about 1 mm. long, the latter duller above, due to minute more perceptible puncturation; antennal joint 4 distinctly longer, more slender, quite $\frac{2}{3}$ length of 3; second posterior cell more subparallel-sided, appearing narrower and longer; head mainly dark castaneous or reddish brownish; sternal parts of pleurae darkened; abdomen above darker brownish, and tarsi darkened from near or about middle of joint 1 ♂ *bilineatus* n. sp.

Genus ONCHOPELMA Hesse

Onchopelma Hesse, 1938: 973.

This genus which I described for the first time in 1938, and based on two South West African species, *pulchella* and *trilineata* (pp. 976 and 978), has since been enriched by still another species, a new one from South Africa, which is described below. This genus is chiefly characterized and different from the other South African cyrtosiine genera in having a distinct and normal marginal cell in the wings, a condition found only in *Cyrtosia*; the first basal cell distinctly shorter and narrower than the second; the acute and stalked anal cell; relatively broad, more lobe-like, axillary lobe which is broader than anal cell; more globular head, with the eyes more normally situated, and occipital part short and flattened, and with the head below broad, short, not grooved, or ridged, or produced posteriorly into a process or processes; more cylindrical or rod-like antennal joint 3, even if broadened basally; longer and denser vestiture,

even in ♀♀; and the presence of a hook-like, curved process at base of basal joint of hind tarsi in some ♂♂.

The new species is:

Onchopelma karooana n.sp.

This species, based on a single ♀ specimen from the Koup Karoo in the South African Museum, is apparently nearer to *pulchella* Hesse than *trilineata* Hesse.

From *pulchella* it differs in having the greater part of pleurae, excepting only black or dark sternal part and very pale yellowish band above it, yellowish and sides of thorax (excepting only three black bands on disc and oblique spot above wing-bases) broadly yellowish, without a notopleural black stripe; entire pale yellowish scutellum; abdomen above with broad yellowish to ivory yellowish hind margins, broad black transverse basal bands across tergites 1-6, narrow on 5 and 6, with central black spots on 7 and 8, and a row of black segmental spots decreasing in size on sides of 3-8; the entirely yellowish tarsi, with only claws dark; and the more sericeous yellowish hairs on body, especially the abdomen above.

From *trilineata* it may be distinguished by the more extensively darkened head, the three black streaks on thorax above confluent posteriorly, not entirely yellowish pleurae, broader frons, longer face, longer antennal joint 3 which is much longer than 1 and 2 combined, shorter labella of proboscis, longer and denser hairs on body and legs, etc.

Length of body about 3.4 mm.

Length of wing: about 3.4 mm.

Length of proboscis: about 0.8 mm.

Locality: Koup Karoo: Laingsburg Div. (Mus. Staff, Feb. 1938).

Genus *GLABELLULA* Bezz.

Glbellula Bezzi, 1902: 191. Bezzi, 1925: 255. Engel, 1933: 116.

The genus *Glbellula* Bezzi s.str., as redescribed and defined by Engel (1933), has up to now apparently never been recorded from South Africa. One specimen from Natal, in a collection of Cyrtosiinae submitted by Mr. B. Stuckenberg and described below, is however referable to this genus and constitutes the first authentic record of this genus from southern Africa.

The species *Glbellula mellea*, described by Bezzi (1908: 180) from Namaqualand and referred to by me (1938: 985), is not a *Glbellula* but an *Empidideicus* (see Bezzi, 1925: 254).

Representatives of this genus cannot be confused with other cyrtosiines and may be easily recognized by the presence of a distinct, small, rudimentary, triangular, marginal cell in the wings; by the relatively large second basal cell which suggests the fusion of a discoidal and a normal second basal cell, and from which there radiate 4 longitudinal veins to demarcate the four posterior cells; and by the rather narrowish, almost parallel-sided anal cell. Other dis-

tinguishing features are the rather convexly humped thorax, the relatively long face, absence of a projecting pronotal lobe, and the longish antennal joint 4.

The only other South African genera which may be confused with it are the two new ones *Euanthobates* and *Pseudoglbellula*, described below. They however differ in the markedly narrow first posterior cell which is much narrowed apically and which opens before apex of wings, by the much longer first basal cell, the much broader anal cell, the markedly short face, and the very minute, scarcely perceptible joint 4 or terminal element of antennal joint 3.

Glbellula natalensis n.sp.

As stated above a single ♀ specimen submitted by Mr. Stuckenberg is referable to the genus *Glbellula* and it is characterized as follows:

Body mainly dark blackish brownish, with the following parts pale yellowish or yellowish: rim of buccal cavity, a spot on humeral angles of thorax, a streak on each side above wing-base, extending to and including postalar calli, sides and narrow hind margin of scutellum, narrow upper margin of mesopleuron along notopleural suture, a subtriangular spot on posterior half of mesopleuron, propleurae above front coxae, upper margin of sternopleuron, a spot above middle coxae and to a certain extent posterior part of metapleurae, narrow hind margin of tergite 1 discally, narrow hind margin of tergite 2 (broader on sides), hind margins of 3 and 4 (broader on sides below), broader hind margins of 5 and 7 (broader on sides below), sides of 8, upper parts of genital segments, hind margins of sternites, apical margins of coxae, greater basal part of trochanters, extreme base of femora, quite apical third of femora, greater part of tibiae (though the middle part along outer and inner faces slightly darkened), and greater part of tarsi, excepting their blackish or dark apical segments and claws; thorax above with 2 faint, palish, submedial streaks.

Integument of entire head and body dull, only that of venter slightly shining.

Vestiture very short and rather dense, especially on thorax above, greyish yellowish; hairs across hind margins of tergites, especially posteriorly, longer; face and frons and to a certain extent thorax above, especially along the slightly paler submedial discal streaks and to a certain extent pleurae with slight greyish tomentum; hairs on legs also very short, minute, appearing more whitish or sericeous in certain lights.

Head subglobular; eyes large, distinctly, though slightly, indented on inner margin opposite antennae; face about as long as frons, narrower than latter and slightly narrower apically than basally; frons also narrowed apically, medially depressed; buccal cavity longer than face; antennae with the two basal joints together about subequal in length to terminal joint, the first being very short, small, not distinctly perceptible, the second much longer, more cup-shaped, quite as broad as joint 3, the latter oval, the terminal element or joint 4 slender, rod-like, very much narrower than 3, nearly half (about $\frac{2}{3}$) length of 3 (the proportions of 1+2, 3 and 4 being about 3:8:3); proboscis relatively stoutish, slightly upcurved, about 0.24 mm. long.

Wings distinctly longer than body, greyish hyaline, the costal cell and triangular marginal cell appearing slightly darker, the extreme base yellowish; veins with the more thickened ones in anterior part and upper one of anal cell dark reddish brownish, the rest paler; first posterior cell subequal in width across apical margin to that of third; alula almost wanting, narrow, linear; knobs of halteres yellowish whitish, the upper basal two-thirds and inner face however brownish.

Abdomen (in this specimen) depressed above up to apical margin of tergite 3; tergites 1-3 each longer than posterior ones and 3 the longest, about as long as 4-6 together.

Legs rather stoutish, the front and middle tibiae slightly longer than femora, but hind ones subequal in length to hind femora.

From 1 ♀ (holotype) in the Natal Museum.

Length of body: about 1.6 mm.

Length of wing: about 1.48 mm.

Locality: Natal: From grassland (1,500 m. alt.), Royal Natal National Park, Drakensberg Mts. (B. and P. Stuckenberg, 15/9/1963).

Genus EMPIDIDEICUS Bezz.

Empidideicus Becker, 1907: 97. Bezzi, 1908: 180. Bezzi, 1925: 254. Engel, 1933: 100. Hesse, 1938: 979.

Glbellula Bezzi (nec Becker) in part (*mellea*), 1908: 180. Bezzi, 1925: 254.

This is one of the genera of the subfamily which, according to the various authors, is chiefly characterized and distinguished by the entire absence of a marginal cell in the wings, its place being occupied by the submarginal cell. Much confusion however appears to exist as to the true identity of the genus, which is probably due to the paucity of material on which to base a proper comparison of the various species referred to it. At present the genus seems to be very unstable, not only in other wing-characters, but in certain cephalic and body peculiarities. As pointed out by Engel (1933), who revised the genus, some Palaerctic species placed in it belong to *Cyrtosia*, a genus which however has a distinct normal and unreduced marginal cell in the wings, non-grooved head below, and a rather prominent pronotal lobe. Engel referred only three Palaearctic forms to *Empidideicus* and one (*efflatouni*) he placed in a distinct subgenus *Cyrtoides* which has a distinct indentation in the inner eye margins opposite the antennae.

The South African species which constitute this genus appear to have a similar generic instability. The single species *beckeri* assigned to it by Bezzi (1908: 180) is not represented in the collections before me, but judging from the description it is doubtfully an *Empidideicus*; in fact Engel himself maintained that it does not belong to *Empidideicus* s.str. The other species *mellea* which Bezzi described at the same time and in the same publication he at first referred to *Glbellula*, but subsequently (1925: 254) transferred it to *Empidideicus*. This latter species too I have not seen and can only attempt to deduce its generic

identity from the description. The short terminal element of antennal joint 3, the markedly long palps, and certain wing characters however appear to exclude it from *Empidideicus* s.str. Of the other two South African species *turneri* and *celluliferus*, described by me (1938: 982, 983), the second one, which has a distinct discoidal cell present in the wings and the last sternite in the ♂ produced on each side into a larger spine-like process (directed inwards behind and slightly below the telomeres), is also anomalous. To accommodate it I erected the subgenus *Anomaloptilus*, to which the Egyptian species *completus* Bezzi (1925: 254), of which I was unaware at the time, should probably also be assigned.

The number of South African representatives of *Empidideicus* s.str. is thus reduced to two species, *melleus* (Bezzi) and *turneri* Hesse, if the doubtful former be included in the genus. In the interim three other new species of the subgenus *Anomaloptilus* have however been collected in the Republic and Lesotho. In addition another specimen from Zululand has been discovered which agrees with both *Empidideicus* s.str. and the subgenus *Anomaloptilus* in essential generic characters, but differs from both in having a distinct, though much reduced, marginal cell. In this respect it upsets the definition of *Empidideicus* as based on wing-venation. To accommodate it a new subgenus *Aetheoptilus* is proposed. This new subgenus as well as the three new forms of *Anomaloptilus* are described below.

Empidideicus turneri Hesse

Empidideicus turneri Hesse, 1938, p. 982.

This species which was described from Mossel Bay is apparently more widely distributed. A ♀ specimen from Ndumu Reserve in the Ingwavuma District of Zululand, collected by B. and P. Stuckenberg (1-10 Dec. 1963), obviously belongs to it even though the pale or yellowish whitish hind margins of the tergites are comparatively narrower. No other specific differences are apparent.

Empidideicus (Anomaloptilus) notatus n.sp.

A species very similar if not merely an aberrant variety of *celluliferus* and from the same locality, but as it appears to show certain consistent differences and in view of the fact that species of Cyrtosiinae show a remarkable similarity in colour-patterns, it is considered to be a separate and distinct species which is characterized as follows:

Body, apart from the dark, dark reddish brownish or dark blackish brown on body above, distinctly very much paler than in *celluliferus*, more pale yellowish whitish; facial and buccal parts anteriorly and groove below head distinctly more extensively pale yellowish whitish; thorax discally above dark reddish brownish or blackish brown, in ♂ almost black, this dark in both sexes, but more so in ♂, however resolved more in three broadish longitudinal streaks of which the lateral ones have a more conspicuous spot-like extension above wing-bases, and the pale yellowish on sides of the thorax above broader than

in *celluliferus*; anterior humeral yellowish spots comparatively larger (in *celluliferus* the disc of thorax is more uniformly dark reddish- or blackish brownish and in addition with 5 more conspicuous dark longitudinal lines); pleurae paler, more extensively very pale yellowish or even yellowish whitish (not mainly reddish yellowish or reddish brownish), the dark along lower part of sclerites and sternal parts less extensive; hind margins of tergites paler, more yellowish whitish, distinctly more broadened on sides and, in ♂, more so in posterior half of abdomen, with a distinct and rather conspicuous shining blackish spiracle-like spot on each side of the tergites (not evident in *celluliferus*); legs on the whole paler, more yellowish whitish or very pale yellowish, the femora not with much reddish brownish or reddish, and, if slightly darkened along middle, this is much less than in *celluliferus*, and more blackish than reddish.

Vestiture very similar, also pale, but apparently slightly less dense, especially on abdomen above.

Head very similar; terminal element of antennal joint 3 also longish and slender, but comparatively a little longer, distinctly much more than half length of joint 3.

Wings very similar, but fourth posterior cell distinctly much broader apically than third, as 7:5 (in *celluliferus* as 6:5).

Last sternite in ♂ with a larger spine-like inwardly-directed process on each side (cf. text-fig. 3, left).

From 1♂ and 5♀♀, including types, in the South African Museum.

Length of body: about 1.08–1.6 mm.

Length of wing: about 1.08–1.56 mm.

Locality: Southern Cape: Mossel Bay (R. Turner, Nov. 1938).

Empidideicus (Anomaloptilus) basutoensis n.sp.

This is a highland species which is characterized as follows:

Body mainly blackish; eyes dark reddish brownish; anterior part of frons, face, buccal part to a variable extent, and to a variable extent also groove below head and base of proboscis below pallid or pale yellowish whitish; following parts pale yellowish to yellowish whitish: large triangular humeral spot and down anterior thoracic declivity, a triangular spot on each side of thorax anteriorly, mainly down declivity (slightly larger in ♂ and in ♀ more linear down the declivity), a broadish streak on each side of thorax above notopleural groove, interrupted just above wing-base and extending posteriorly

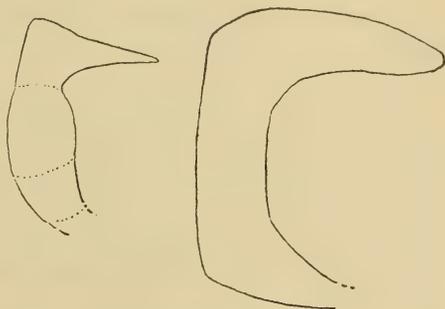


FIG. 3. Left: Posterior view of left process on left side of last sternite of ♂ *Empidideicus (Anomaloptilus) notatus* n. sp. Right (same proportions): Posterior view of left process on left side of last sternite of ♂ *Empidideicus (Anomaloptilus) basutoensis* n. sp.

to occupy postalar calli and to a duller (more variable and more brownish yellowish) extent apex or hind margin of scutellum, propleural tubercles, anterior, upper and greater hinder part of mesopleuron, upper half or greater part of pteropleuron, upper parts of sterno- and hypopleurae, metapleurae, apical half or greater part of front coxae, narrow anterior margin of tergite 1, hind margins of tergites, becoming broader posteriorly and very much so on sides (the entire extreme sides beyond a blackish shining longitudinal linear impression being yellowish whitish and tergites 5-7 in ♂ and 6 and 7 in ♀ being also very broadly or almost entirely yellowish), processes of last sternite in ♂, broad hind margins of sternites or even greater part of venter, trochanters of legs, and greater part of latter, excepting variable dark or blackish infusions on femora above and a smaller infusion on their anterior basal part and across the middle, to a fainter extent across basal part of tibiae and more than blackened apical half of tarsi; telomeres of ♂ blackish.

Integument mainly dull, the extreme base of tergites (under the overlapping hind margin of the preceding one) and some scattered smallish spots sometimes visible across some of the tergites however shining; telomeres of ♂ also shining black.

Vestiture very short, though slightly longer in ♂, fairly dense on thorax above and on abdomen, being longest across hind margin of tergites, appearing darker on thorax above (though paler in ♂), paler, more sericeous yellowish on abdomen and legs and even paler or more whitish in ♂; face in front in ♂ with some relatively longish whitish hairs; head, thorax above, pleurae and abdomen above also with slight, dull, but not very dense, greyish tomentum.

Head with the face shorter and narrower than frons; latter distinctly depressed, more so towards anterior part, the margins appearing almost rim-like, especially in ♀; antennae with the combined joints 1 and 2 short, joint 3 oval and its terminal element (or joint 4) slender, rod-like, longish, only a little shorter than 3 and tending to be slightly curved; head below rather deeply grooved; proboscis relatively stoutish, more slender in ♂, narrowed apically, about 0.36-0.6 mm. (extruded about 0.48-0.72 mm.), ending in the two rather pointed labellar lobes.

Wings longer than the head and body, greyish hyaline, appearing very slightly darker in ♀ than in ♂; veins dark reddish brownish, the lower one of anal cell and vein between basal cells transparent (in ♂ holotype the upper vein of discal cell also transparent); microtrichial fringe along hind margin distinct, appearing dark; first basal cell slightly, but distinctly, longer than second; upper vein of second posterior cell distinctly longer than part of it above discal cell; fourth posterior cell apically much broader than any of the other cells; apex of discal cell either truncate (with cross vein) or sharply acutangular (without a cross vein); halteres, including knobs, yellowish whitish to almost white.

Abdomen with the process on each side of last sternite in ♂, as shown in posterior view in text-fig. 3 (right), relatively broadish, directed inwardly and

in its apical part bent anteriorly (or towards apex of abdomen).

From 2 ♂♂ and 7 ♀♀ (♂ holotype, ♀ allotype and 5 ♀ paratypes in Natal Museum, and a ♂ and ♀ paratype in the South African Museum).

Length of body about 0.92–1.56 mm. (in natural humped condition).

Length of wing: about 1–1.8 mm.

Locality: Lesotho (Basutoland): Roma Mission, Maseru Dist., upper Cave Sandstone level (6,000 ft.) (B. and P. Stuckenberg, 4–13 Jan. 1913).

This species resembles *notatus* superficially, but differs in not having a yellowish infusion basally on thorax above, only the apex discally of the scutellum yellowish or yellowish brownish, the pleurae less extensively and not so uniformly yellowish, with more dark infusions on femora, darker wing-veins, and in the ♂ the much larger, broader, less sharply spine-like processes of last sternite (cf. text-fig. 3, right and left).

Empidideicus (Anomaloptilus) brevistilus n.sp.

This species from Zululand, with relatively shortish terminal element of third antennal joint, is characterized as follows:

Body mainly dark above; head above, proboscis and abdomen above blackish; basal colour of thorax above dull yellowish brownish, with 4 blackish longitudinal lines, the lateral ones broader; the following parts pale yellowish to yellowish whitish: face anteriorly and to a certain extent its sides, to a variable extent sides of head below and rims of gular groove, rim of buccal cavity below, anterior part of thorax in declivity, extending upwards on each side to include humeral angles and an anterior, submedial, triangular spot on each side, contiguous with humeral spot, sides of thorax above, continuous to include postalar calli and broken only in notopleural part in front of wing-base, greater part of scutellum (excepting a variable, medial, basal, dark infusion), greater upper part or half of pleurae (lower part being very dark or almost black), basal and hind margins of tergite 1 and hind margins and sides of rest of tergites (the sides more extensively so in ♀, isolating the lateral shining black spot on each from tergites 2–5, which in ♂ is still in the blackish part), hind margins of sternites, more broadly so in ♀ or even entire venter in ♀, apical parts of upper and lower parts of genitalia in ♀, lower part of process of last sternite in ♂, halteres (excepting the dark brownish upper surface of knobs), anterior and antero-lateral parts of front coxae and sides of rest of coxae, and greater part of legs (excepting the obscure darkish or brownish infusions along upper surface and across base and a little beyond middle of femora, to a feebler extent upper surface and subbasal part of tibiae and the little less than apical half of the blackish tarsi).

Integument of body mainly dull, only the dark spots on sides of tergites 2–6 and the less distinct ones (more evident in ♀) in a row across the tergites shining graphite-like; hypopygial parts of ♂ also more shining.

Vestiture with the hairs very short as in the two preceding species, fairly dense on thorax above and on abdomen above, being longest across hind

margins of tergites, appearing pale or pale sericeous yellowish in certain lights, though appearing dark on thorax above, without any longish ones discernible on face in front in ♂; hairs on legs pale, minute, scarcely perceptible, less so than in the preceding two forms.

Head with the frons and face relatively narrow, even allowing for post-mortem shrinkage, slightly depressed, subequal in length; antennae with joint 3 rather longish, distinctly longer than in preceding two species, more elongate-conical, relatively narrower, more gradually narrowed apically, its terminal element (or joint 4), relative to 3, distinctly very much shorter than in other two species, scarcely $\frac{1}{3}$ length of 3; head below shallowly grooved; proboscis relatively short, stoutish, shorter than, or as long as, head, about 0.24–0.4 mm. long, pointed apically.

Wings much longer than head and body, greyish hyaline; veins brownish to dark brownish or slightly reddish brownish; microtrichial fringe along hind margin minute, but distinct, appearing dark; first basal cell distinctly longer than second and vein between them transparent; anterior vein of second posterior cell longer than anterior vein of discoidal cell; fourth posterior cell broader apically than any of the others.

Abdomen in ♂ with the hypopygial structures withdrawn in both ♂ specimens and difficult to make out without dissecting and damaging the abdomen, but last sternite apparently like that of *notatus*, but the projecting process shorter and blunter.

From 2 ♂♂ and 2 ♀♀ (♂ holotype and ♀ allotype in the Natal Museum and a ♂ and ♀ paratypes in the South African Museum).

Length of body: about 0.92–1.32 mm.

Length of wing: about 1.12–1.48 mm.

Locality: Zululand: Ndumu Reserve, Ingwavuma Dist. (B. and P. Stuckenberg, 1–10 Dec. 1963).

This species may at once be distinguished from the other three known South African species of the subgenus *Anomaloptilus* by the distinctly more elongate-conical antennal joint 3 and, relative to length of latter, the proportionally much shorter terminal element (which in this case is about $\frac{1}{3}$ length of 3, whereas in the others it is quite, or nearly, half length of 3); the relatively narrower frons and face; proportionally shorter proboscis, which is not longer than head; and the knobs of halteres which are dark or blackish above.

AETHEOPTILUS n.subgen. of EMPIDIDEICUS Becker

The deviation from the normal wing-venation of *Empidideicus* s.str., as described by Becker (1907) and Engel (1933) and as is present in the South African species *Empidideicus turneri* Hesse, has gone a step further in a single ♀ specimen from Zululand in which, in addition to the presence of a discoidal cell as in the subgen. *Anomaloptilus* Hesse there is also present a reduced or vestigial marginal cell (cf. text-fig. 4) as in species of *Glbellula* Bezzi, *Doliopteryx* Hesse and the new genus *Pseudoglbellula* described below.

To accommodate it a new subgenus *Aetheoptilus* of *Empidideicus* is proposed provisionally, pending the discovery of more material of both sexes.

This new subgenus, as typified by this single ♀ specimen, agrees with *Empidideicus* s.str. in most of its generic characters, but differs, apart from the presence of a distinct discoidal cell and a narrowish reduced marginal cell, in having the anal cell angularly acute apically and very shortly stalked, and in its broader frons, face and groove in head below.

From the subgenus *Anomaloptilus*, which also has a discoidal cell, it differs in the presence of a vestigial marginal cell, the apically acute and very shortly stalked anal cell, the more S-curved anterior vein of second posterior cell, more parallelogram-shaped third posterior cell, and in the cephalic characters mentioned above. As far as the wing-venation is concerned this subgenus appears to be even more primitive than *Anomaloptilus*. If the type of wing-venation of *Empidideicus* s.str. be considered as a specialization on an ancestral type in which reduction has taken place, a step nearer this ancestral condition is represented by *Anomaloptilus* where a discoidal cell still persists. On this assumption *Aetheoptilus* represents an even more primitive condition in which not only the discoidal cell is still found, but in addition there is also a vestige of the normal marginal cell of the ancestral type.

The type-species of this new subgenus is the new species *zuluensis* described below.

Empidideicus (*Aetheoptilus*) *zuluensis* n.sp.

This species is characterized as follows:

Body, including legs, mainly yellowish; medial occipital part blackish, the sides of occiput behind eyes more reddish yellowish than yellow; proboscis and eyes blackish; antennae dark reddish brownish; the following spots and markings on body very dark reddish brownish or dark chocolate brownish: a broad central streak on thorax above, not reaching base, a large submedial subquadrate spot on each side almost midway between shoulder and wing-base, extending laterally as a narrow line to notopleural fold, an ovate spot on each side above wing-base and of which the inner anterior part is continuous (or in juxtaposition) with a broadish, shortish, submedial, outwardly dilated streak, not reaching base, but extending more posteriorly than broad middle streak, a narrow central streak on scutellum, broadening posteriorly, an elongated vertical spot or streak on sternopleuron and above middle and hind coxae respectively, a broadish subbasal transverse band across tergite 1, indented

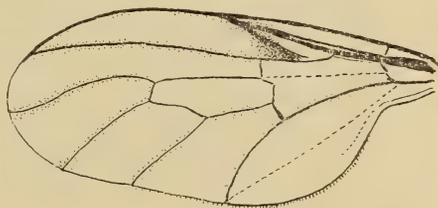


FIG 4. Wing of *Empidideicus* (n. subgen. *Aetheoptilus*) *zuluensis* n. sp.

medially and slightly less so submedially along its hind margin, a large Γ -shaped mark submedially on each side basally of rest of visible tergites 2-6 (the inner limb of each mark being broader than outer one and the mark on tergite 2 basally also extending down to sides), a small shiny spot on each side of tergites 2-4, greater part of venter, front and hinder parts of middle and hind coxae, trochanters to a variable extent, a variable infusion subapically and subbasally on front and middle femora (more distinct on hind surface), a more distinct and less faint, subbasal and subapical infusion on hind femora and also to a certain extent along upper and lower surfaces of the same femora, a faintish subbasal infusion on tibiae, and apex and claws of tarsi (which are more blackish).

Integument of head and body dull, only the dark spots on sides of tergites shining graphite-like.

Vestiture very short, fairly dense, especially on thorax above, longer across hind margins of tergites and posterior sternites, pale yellowish, appearing dark on disc of thorax in certain lights, and gleaming yellowish on abdomen, with some distinct longish dark hairs in a row on each side of thorax above wing-base and shorter ones anteriorly above notopleural fold; hairs on legs very short, gleaming yellowish whitish to yellowish in certain lights.

Head subglobular; occiput somewhat flattened; frons rather broad, quadrate, about as broad as long, deeply depressed, its sides and base raised rim-like, not longer than face; the latter also relatively broad, but narrower than frons, depressed at base, but more convex apically where the apical margin is even raised; buccal cavity vertical; head below rather broadly and deeply grooved, with relatively sharp edges; proboscis as long as head, about 0.8 mm. long, stoutish at base (labral part), more slender in apical $\frac{2}{3}$, the labrum itself rather short, not longer than frons; palps minute; antennae with joints 1 and 2 very short, joint 3 somewhat conical, narrowed apically, more so below, its terminal element (or joint 4) comparatively long, only $\frac{1}{4}$ shorter than 3 (proportions being 3:4), slender, rod-like.

Wings (text-fig. 4) longer than head and body, faintly tinted smoky greyish, the base of submarginal cell distinctly infuscated brownish and the posterior veins with very faint fuscous borders; veins dark reddish brownish, but lower vein of anal cell and vein between basal cells transparent; microtrichial fringe along hind margin very short and scarcely perceptible; reduced marginal cell represented at base of submarginal cell as a narrowish, elongated, triangular, clearish area; first basal cell slightly longer than second; anterior vein of second posterior cell slightly S-curved; third posterior cell parallelogram-shaped; anal cell acutely angular and very shortly stalked apically; axillary lobe broadish, about as broad as broadest part of anal cell; halteres dirty yellowish, the knobs slightly brownish on sides basally, extreme base above and on base below.

From a single ♀ in the Natal Museum.

Length of body: about 1.2 mm. (in natural humped condition).

Length of wing: about 1.72 mm.

Locality: Zululand: Ndumu Reserve, Ingwavuma Dist. (B. and P. Stuckenberg, 1-10 Dec. 1963).

The known South African species of *Empidideicus* may be separated as follows:

1. (a) First basal cell in wings only a little or scarcely longer than second, and vein between it and second posterior cell much longer or very long, the base of third posterior cell or discoidal cell (if present) not deeply and sharply angularly projecting in between basal cells, and anal cell narrower, more gradually narrowed apically and more broadly open (if acutely angular and stalked or sessile the other venational characters conform); terminal element of antennal joint 3 usually much longer, slender, rod-like, conspicuous, quite half as long as 3; palps inconspicuous, very short, minute or not perceptible; body not mainly yellowish, the thorax above and abdomen above extensively dark or with dark markings 2
- (b) First basal cell distinctly or much longer than second and vein between it and second posterior cell markedly short, the base of third posterior cell distinctly deeply and sharply angularly projecting in between basal cells, and anal cell relatively broad, rapidly angularly narrowed apically, almost sessile on hind margin; terminal element of antennal joint 3 much shorter, much less than half length of 3; palps very long, conspicuous, as long as proboscis; body mainly yellow, only 3 obscure darkish lines on thorax above and abdomen mainly yellow ex descr. ♂ *melleus* (Bezzi), Namaqualand
2. (a) Wings without a discoidal cell 3 (*Empidideicus* s.str.)
- (b) Wings with a distinct discoidal cell 4
3. (a) Terminal element of antennal joint 3 long, slender, rod-like, quite or more than half length of 3; thorax above black and yellow, the black in form of more or less three broadish, conspicuous, longitudinal bands and an oblique black spot above wing-base; yellowish whitish to yellowish hind margins of tergites broader; wings, relative to body, shorter, 1.2-1.6 mm. ♂ ♀ *turneri* Hesse, E. Cape, Zululand
- (b) Terminal element short and thick; thorax above mainly black, with only a triangular yellowish spot anteriorly on each side, confluent with the yellow humeral angle, and an oblique yellow spot posteriorly near posterior angles, without a conspicuous black spot above wing-base; whitish hind margins of tergites apparently narrower; wings, relative to body, longer, quite 2 mm. ex descr. ♀ *beckeri* Bezzi, Namaqualand
4. (a) A marginal cell in wings entirely absent; base of submarginal cell without any infuscation; anterior vein of second posterior cell not S-curved; anal cell more gradually and only slightly narrowed apically, opening on hind margin, not acutely angular apically and shortly stalked; frons and face narrower; the former longer than broad; labral part of proboscis longer, longer than frons; thorax above, if with dark streaks, these not in form of a broadish middle one and three spots submedially more or less in line; scutellum without a central dark streak; abdomen with only the hind margins yellowish, without dark \square -shaped markings 5 (*Empidideicus* subgen. *Anomaloptilus*)
- (b) A distinct, narrow, triangular, reduced marginal cell present above base of submarginal cell; base of submarginal cell distinctly infuscated spot-like; anterior vein of second posterior cell S-curved; anal cell sharply acute apically, very shortly stalked; frons and face relatively broader, the former about, or nearly, as broad as long; labral part of proboscis shorter, not much longer than frons; thorax above with a broad central dark band and three broadish spots on each side arranged longitudinally, the second more to the side; scutellum with a central dark band; abdomen above with conspicuous dark \square -shaped markings submedially on each side
 ♀ *Empidideicus* (n. subgen. *Aetheoptilus*) *zuluensis* n. sp., Zululand
5. (a) Antennal joint 3 more oval or ovate, its terminal element distinctly longer, quite or nearly half, or even slightly more than half, length of 3; proboscis longer, usually distinctly longer than head; frons and face relatively broader; knobs of halteres paler or entirely pale above and below 6

- (b) Antennal joint 3 more elongate, more elongate-conical, its terminal element distinctly shorter, distinctly less than half, or only about $\frac{1}{3}$ length of 3; proboscis relatively shorter, less than, or as long as or scarcely longer than head; frons and face more compressed, relatively narrower; knobs of halteres conspicuously darkened or blackened above
 $\delta \text{ } \eta$ *brevistilus* n.sp., Zululand
6. (a) Scutellum entirely and extensively yellowish; base of thorax also distinctly extensively yellowish; disc of thorax paler, more reddish brownish to dark reddish brownish, with the pale and dark submedial longitudinal lines more distinct, in $\eta \eta$ at least; dark infusions on femora scarcely evident or less distinct; veins in wings paler, more yellowish brownish or paler reddish brownish; process on each side of last sternite in $\delta \delta$ narrower, more spine-like 7
- (b) Scutellum pale, yellowish, or yellowish reddish only at apex medially; base of thorax dark like rest of disc; disc of thorax much darker, very dark blackish brownish to black, without, or with scarcely evident, dark longitudinal lines; dark infusions on femora darker, distinctly more conspicuous; veins in wings darker, blackish brown; process on each side of last sternite in δ distinctly broader, larger, less spine-like
 $\delta \text{ } \eta$ *basutoensis* n.sp., Lesotho
7. (a) Facial part anteriorly less extensively yellowish; thorax above darker, more dark reddish brownish, with four narrowish dark lines and even a fifth central one, its sides above less extensively yellowish; pleurae darker, the yellowish less extensive; tergites with the yellowish hind margins less broadened on sides, without conspicuous spiracle-like marks; middle parts of femora or even greater part of latter darker, more reddish brownish; fourth posterior cell in wings only a little or scarcely much broader apically than third (as 6 : 5); halteres more reddish or yellowish reddish, with more yellowish knobs; hairs on body, especially on abdomen, slightly denser, longer $\delta \text{ } \eta$ *celluliferus* Hesse, S. Cape
- (b) Facial and buccal parts, as well as groove on head below, more extensively pale yellowish; thorax above mainly reddish brownish to dark reddish brownish (δ), this dark however more resolved into 3 broadish, longitudinal streaks, the lateral ones extending more spot-like above wing-base, the sides of thorax above more broadly yellowish; pleurae more extensively very pale yellowish whitish, the dark sternal parts less extensive; tergites with the very pale yellowish whitish hind margins more broadened on sides and there with conspicuous shiny black spiracle-like markings; legs much paler, the femora less extensively darkened medially; fourth posterior cell distinctly much broader apically than third (as 7 : 5); halteres very pale yellowish whitish, their whitish knobs only slightly darkened above across base; hairs, especially on abdomen, apparently slightly less dense and shorter $\delta \text{ } \eta$ *notatus* n.sp., S. Cape

Genus EUANTHOBATES Hesse

Euanthobates Hesse, 1965: 482.

This genus was erected to accommodate a new species of a peculiar flower-feeding cyrtosiine collected by the Swedish Expedition in the arid western part of South West Africa in 1951.

It resembles the genera *Empidideicus* and *Cyrtosia*, especially the former, differing from it in the markedly short face; the more elongate, leaf-shaped third antennal joint which ends in a minute, scarcely perceptible, terminal element or joint; more protrusible proboscis; the presence (in the type-species at least) of remarkable, downwardly-projecting, finger-like or strap-like processes arranged irregularly comb-like along the sulcus on head below (cf. text-fig. 5, top); the longer first basal cell (longer than second) in wings (cf. text-fig. 5, bottom); the markedly narrow first posterior cell which is also narrowed apically and which opens on apical margin of wing (not posterior

to it); the markedly short part of vein between first basal and second posterior cells and which is considerably shorter than in *Empidideicus*; comparatively broader anal cell; and the apparently denser and shorter vestiture, especially on abdomen.

Since the description of this new genus and its type-species *pectinigulus* (1965: 483) two ♀ specimens of still another species, obviously belonging to the same genus, but without the gular structures, have been discovered among some other insects in the South African Museum caught on flowers in the Koup Karoo. This Cape species is described below.

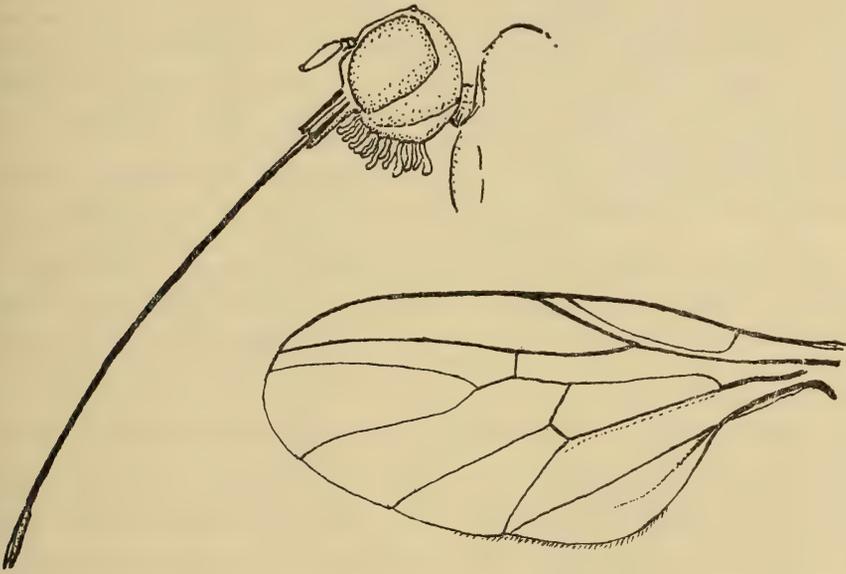


FIG. 5. Top: Composite drawing of the head of *Euanthobates pectinigulus* Hesse. (Head of ♀ paratype + extruded proboscis of ♀ holotype.)
Bottom: Left wing of ♀ of *Euanthobates mellivorus* n. sp.

Euanthobates mellivorus n.sp.

This other, rather larger, species from the Koup Karoo, also represented by the ♀ only, and which may at once be distinguished from *pectinigulus* by the entire absence of any processes in the gular groove, is characterized as follows:

Body mainly black above; narrow sides of frons, face, lower half of broadish occipital part behind eyes, a broadish humeral spot confluent with anterior spiracular area just below it, notopleural ridge and sides of thorax along it, sides of abdomen from tergite 2, upper parts of pleurae to a variable extent, prosternal part above front coxae, front coxae, apical parts and narrowish sides of middle and hind coxae to a variable extent, front femora (or their anterior lower parts), bases and apices of middle and hind femora, front and

middle tibiae, basal halves of front and middle tarsi, and to a variable extent venter reddish brownish to reddish yellowish, sometimes inclining to more yellowish; more distinctly yellowish to pale yellowish are: a small spot on each side of frons basally at level of front ocellus, buccal rim, upper anterior part of mesopleuron, area in front of and below wing-bases, ridge on sides of thorax above wing-bases and postalar calli, scutellum, a large subelongate spot on each side at base of thorax (sometimes more whitish or lemon yellowish), a propleural spot, a streak along middle of pleurae, metapleural part below and around base of halteres, hind margin of metapleural part, hind margins of tergites (broader on sides where they merge into the yellowish reddish or sometimes also yellowish sides and on last two or three segments), broad connecting part between tergites and sternites below, broadish hind margins of latter, front and middle tibiae (if not pale reddish yellowish), hind tibiae, and basal halves of front and middle tarsi; integument of body dull, with slight greyish whitish bloom on head and thorax above.

Vestiture with the hairs on body and legs very fine, minute, gleaming slightly sericeous yellowish to golden on abdomen above, more whitish on legs.

Head with the face narrowish, short, only about a third length of frons; antennal joints 1 and 2 subequal in length; joint 3 leaf- or subspindle-shaped, narrowed and pointed apically, about twice as long as broad, proportionally broader than in *pectinigulus*; proboscis about 0.44 mm., its labral part about 0.32 mm.; sulcus or groove on head below without any trace of downwardly-projecting processes.

Wings (text-fig. 5, bottom) slightly dusky, tinted slightly greyish brownish, iridescent; veins dark brownish; first posterior cell also characteristically narrow, narrowed apically, but slightly more broadly open than in *pectinigulus*; anal cell also very broad, more rapidly narrowed and more sharply acute apically than in *pectinigulus*, and almost sessile on hind margin; knobs of halteres entirely pale yellowish.

From 2 ♀♀ in the South African Museum (the paratype with the head unfortunately missing).

Length of body: about 2.32-2.5 mm.

Length of wing: about 1.56-1.68 mm.

Locality: Koup Karoo: Laingsburg Div. (Mus. Staff, Feb. 1938). Collected together with other insects by sweeping flowering shrubs.

PSEUDOGLABELLULA n.gen.

A ♀ specimen from the Koup Karoo in the collections before me and which was obtained together with other insects by sweeping flowering shrubs, cannot be allocated to any of the known genera of Cyrtosiinae. It appears to represent a new and as yet undescribed genus. Certain wing-characters seem to suggest a relationship to the genus *Glbellula*, but in most of the other venational characters it shows even closer affinity with the preceding genus *Euanthobates*. If the presence of a distinct, though much reduced, marginal cell be taken as

a group character, it is referable to the group of cyrtosiine genera, such as *Cyrtosia*, *Platygygus*, *Cyrtisiopsis*, *Ceratolaemus* and *Glabellula*, in which a marginal cell is present in the wings, even though sometimes much reduced. On the other hand the rest of its wing-characters, as well as certain antennal and cephalic characters, place it in close proximity to *Euanthobates*.

By comparing it with the descriptions and illustrations of species of the Palaearctic *Glabellula*, which also has a similarly reduced marginal cell, its wings (text-fig. 6), like those of *Euanthobates*, differ in having the first basal cell distinctly very much longer than the second, and this second basal cell is apparently not formed by the fusion of a discoidal and a second basal cell as is suggested in the case of *Glabellula*; only 3 longitudinal veins, not 4, radiate out from this second basal cell; the 4 posterior cells not formed directly by these delimiting longitudinal veins, but the fourth vein bifurcates into two branches, forming the elongate triangular second posterior cell; first posterior cell, unlike that of *Glabellula*, distinctly very much and markedly narrower and narrowed apically, as in *Euanthobates*, to open on anterior or costal margin and not on apical part of it or very near apex of wing as in *Glabellula*; triangular marginal cell comparatively larger than in *Glabellula*.

Other characters which also distinguish it from *Glabellula* are the markedly short face, the great reduction of antennal joint 4, which is minute, scarcely perceptible as in *Euanthobates*, and not elongate, slender or even rod-like, and the distinctly less convexly humped thorax.

From *Euanthobates*, to which it is generically very closely related and with which it shares such wing-characters as the much narrowed first posterior cell, the very short part of fourth vein before base of second posterior cell, and cephalic characters such as the very short face, and much reduced antennal joint 4, it however differs in having a distinct, reduced, triangular marginal cell present, a very much shorter first posterior cell which curves anteriorly, opening on anterior costal margin at a much longer distance before apex of wings, thus reducing the length of the combined marginal and submarginal cells; a much narrower, more parallel-sided anal cell, more like that of *Glabellula*; a very much broader frons, and even shorter face; much larger antennal sockets; comparatively shorter and broader, truncated, vertical, anterior part of head, with the buccal cavity directed more obliquely forwards; and the head below broadly hollowed out or excavated, without a well-defined or delimited, central sulcus.

In other characters, such as the absence of a projecting pronotal lobe, it agrees with *Glabellula*, *Empidideicus* and *Euanthobates*, and differs from *Cyrtosia*, *Platygygus*, and *Ceratolaemus* where this lobe is present. The type-species of the genus is *Pseudoglabellula meridionalis* n.sp. described below.

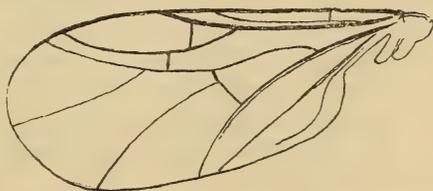


FIG. 6. Wing of *Pseudoglabellula meridionalis* n. gen. et n. sp.

Pseudoglabellula meridionalis n.sp.

The ♀ of this species is characterized as follows:

Body mainly black above and on venter; antennae, proboscis, dark parts of pleurae, coxae, femora, apical halves of front tarsi, entire middle and hind tarsi, and more or less apical parts of hind tibiae dark castaneous brownish; the following parts yellowish or pale yellowish: a broadish streak on each side of frons from level of front ocellus to antennal sockets, narrow rims of these sockets, a quadrate spot behind each eye at level of humeral tubercles, humeral tubercles and anterior spiracular prominences, notopleural ridge and less definitely sides of thorax above it, area anterior to wing-bases and that just below these bases, postalar calli and faint streak extending from them forwards above wing-base, discal part and central hind border of scutellum, connection between squamae and posterior basal part of scutellum, infusions on upper parts of meso- and pteropleurae, propleural spot above front coxae, prosternal part in front of front coxae, a broadish streak across upper part of sternopleuron, metapleural part below halteres, hind margin of metapleural part, narrowish hind margins of tergites, passing into the broader sides of abdomen, becoming broader across tergites 6 and 7, hind margins of sternites obscurely, apical margins of front coxae, to a fainter extent those of middle and hind coxae, and also anterior trochanters, extreme bases of hind femora, apices of all the femora, the tibiae (excl. the slightly darkened apical parts of hind ones), and bases of front tarsi; integument of body mainly dull.

Vestiture with the hairs on body and legs very fine, sparse, almost imperceptible, and, where perceptible, apparently dark on dark parts above and pale on yellowish parts.

Head about as long as broad, but distinctly longer than high; frons slightly longitudinally and centrally depressed, slightly narrower anteriorly than basally at level of front ocellus; face perpendicular in front, much shorter than frons; antennal sockets rather conspicuous, relatively large; antennal joints 1 and 2 very short, transverse, subequal in length, the first sunk in the socket; joint 3 almost ovate, but more pointed apically, about $\frac{2}{3}$ of its length at broadest part (at about middle), its apical or terminal joint minute; proboscis short, markedly stoutish, about 0.4 mm. long; palps not detectable.

Wings (text-fig. 6) distinctly somewhat dusky, infused brownish; veins dark brownish in costal region, more yellowish in rest of wings; triangular marginal cell rather large; long first basal cell about as long as narrow first posterior cell; knobs of halteres entirely pallid.

Holotype in the South African Museum.

Length of body: about 1.8 mm.

Length of wing: about 1.68 mm.

Locality: Koup Karoo: Laingsburg Dist. (Mus. Staff, Feb. 1938).

PSILODEROIDES n.gen.

This new genus, of which the known representatives have a striking resemblance to species of the genus *Psilodera* of the spider parasites (dipterous family Acroceridae), is established to accommodate a remarkable bombyliid submitted by Mr. R. J. Mansfield and of which the adults were reared in a laboratory of the Department of Agriculture in Pretoria from a batch of bombyliid larvae found both in egg-packets of the brown trek locust (*Locustana pardalina*) and in loose soil in association with such egg-packets.

This bombyliid cannot be referred to any other subfamily of the Bombyliidae but to the Cyrtosiinae. With the latter it agrees in certain characters, such as the reduction of the wing-venation, the presence of only one submarginal cell, the peculiar reduced and somewhat triangular marginal cell, the characteristic quadri-articulate antennae, the slight indentation in the inner margin of the eyes opposite the antennae, the absence of distinct spines and spicules on the legs, absence of macrochaetae on body, the arched or humped and convex thorax, broad and arched abdomen, and rows of small shiny depressed black spots on abdomen (present in some cyrtosiines).

In certain other characters, such as the very much reduced, rudimentary or vestigial proboscis, the widely separated ocelli of which the middle, slightly anterior, one is remarkably large, the less developed occiput, the sculptured or punctured thorax and abdomen, the excavate venter, and even more convexly humped or arched thorax and abdomen, it however differs from other known genera of the Cyrtosiinae to such an extent that at least a distinct section or tribe of the latter is indicated to include it.

As the life histories of all the other known South African cyrtosiine bombyliids (if not of the world) are unknown, the discovery of this genus and its host is of great importance.

The genus is characterized as follows:

Body (text-fig. 7) arched and humped, with a striking and marked resemblance to that of the genera *Psilodera*, *Terphis* and *Thyllis* of the spider parasites (fam. Acroceridae), its widest part across between tergites 2 and 3.

Head (text-fig. 7, upper left) almost spherical; occiput more flattened, not very prominent, more like that of *Onchopelma*, medially not depressed behind ocellar prominence; eyes large, not tending to be situated far forwards, separated on vertex in both sexes, apparently more widely so in ♀♀, their inner margin slightly indented opposite antennae, in ♀♀ somewhat uneven, not uniformly convex, but slightly shallowly depressed groove-like from ocellar corner obliquely down to near middle; ocellar prominence relatively broad, slightly more raised in ♂♂, transverse, delimited from frons by a distinct, forwardly-curved, depressed line or suture, not evident in other cyrtosiine genera, the lateral ocellar part higher than middle, the ocelli widely separated, more so than in the other genera, in a slightly forwardly-curved line, the lateral ones very near or at upper corner of eyes and thus very broadly separated, the ocelli relatively large, especially the middle one which is also more elongated trans-

versely; frons with a slight central depressed line, slightly raised on each side basally in front of each lateral ocellus, broader in ♀♀, broader basally than at antennae, and slightly broader than long; face in side view curving down to buccal cavity to the same extent as eyes, longer and narrower than frons, basally separated from antennal insertions by a transverse depression or depressed line, slightly narrowing from base to apex (beginning of buccal cavity); buccal cavity gradually widening to head below, the interocular space on head below being as wide as, or slightly wider than, base of face, the buccal depression not very deep, as long as, or slightly longer than, face; proboscis much reduced, minute or vestigial, represented by a small finger-like lobe or minute nipple; antennae (cf. text-fig. 7, extreme left) situated close together, quadri-articulate, joint 4 elongate, slender, rod-like, narrower than rest, armed with a terminal style or short bristle, joint 2 cup-shaped; head below and behind broadish, slightly depressed, not sulcate.

Thorax almost globular, very convex above, in side view semicircularly arched or humped above and high above level of vertex, almost or about as high above latter as depth of head itself; anterior sloping part behind head very steep, slightly hollowed and prothoracic part not distinctly separately discernible or prominent as in genus *Cyrtosia*; prothoracic humeral lobes broad, rounded, reminiscent of those of the Acroceridae; sides of thorax above notopleural fold a little anterior to wings not distinctly transversely depressed as in the other genera; postalar calli, owing to convexity of thorax, not so prominently ridge-like; dorsum or discal part of thorax above areolately punctured, more rugulose posteriorly; scutellum relatively broad, with a slight, but distinct, arcuate depression across basal part; pleurae slightly more convex or bulging than in the other genera, the mesopleuron more triangular and with some setiferous puncturation.

Wings (text-fig. 7, left) either clear as in ♂♂ or slightly infuscated as in ♀♀; marginal cell reduced, the posterior vein of which joins the costal margin much before apex of wing; one submarginal, a discoidal and four posterior cells present; first basal cell longer than second; anal cell open apically; axillary lobe narrowish, not lobe-like; alula much reduced, narrowish and linear; knobs of halteres tetrahedral in shape.

Abdomen (text-fig. 7, left and right) broad, ovate, at broadest part (between tergites 2 and 3), much broader than thorax, arched or humped in appearance; discal part of tergite 1 flattened, slightly depressed, areolately punctured; rest of tergites above in ♀♀ also areolately punctured or sculptured, but only discal basal three-quarters of tergite 2 and to a certain extent narrow discal basal part of 3 (under apical margin of 2) in ♂♂, in addition to flattened discal part of 1, areolately sculptured; rest of tergites in ♂♂ very finely transversely rugulose sculptured; dorsum of abdomen in both sexes with two rows of segmental, slightly depressed, shiny, dark or blackish spots on each side from tergite 2 to apex as in some other *Cyrtosiinae*, each spot nearer base of the tergite, and in some ♂♂ often also with an extra central pair on tergite 2; venter

markedly and characteristically hollowed or excavated, the sides of tergites and plate-like hinder part of metapleurae much inflexed and overhanging venter, and middle of venter with two longitudinal ridge-like elevations.

Legs relatively stoutish and shortish, without any spines on hind femora and without distinct spicules on tibiae; apex of tibiae without distinct spurs, but apparently ending in a minute spine-like point on each side of tarsal insertion.

Vestiture without any macrochaetal elements, the hairs distinctly more developed than in other genera, excepting *Onchopelma*, even the hairs in ♀♀, though much shorter than in ♂♂, still denser and more evident than in most cyrtosiine genera; hairs on thorax above, scutellum and mesopleuron situated in the areolar crater-like punctures, comparatively dense, longer in ♂♂ than in ♀♀, in latter however apparently equally dense; those on abdomen, sides of tergite 1, greater part of 2 and on rest of tergites in ♂♂, though shorter than on thorax, markedly dense, shining silvery whitish, arranged transversely and directed towards centre along the middorsal line of which they form a sort of ridge composed of hairs; hairs on abdomen above in ♀♀ situated in the crater-like punctures, very much shorter than in ♂♂, minute, but also directed towards midline; posterior and lower parts of pleurae bare; hairs on legs relatively longer and denser than in the other genera, slightly longer and finer in ♂♂ than in ♀♀.

Hypopygium of ♂♂ (text-fig. 8, right, drawn upside down, the upper part being ventral in position in the specimens) with the last sternite (LS) not spined or very sharply produced at its posterior apical angle as in most other cyrtosiine genera; the basimere (B) of the paramere rather broadish, more saddle-shaped, not shell-like as in the other genera; the telomeres (T) of paramere leaf-shaped, flattened, without any hook or hook-like structure; aedeagal apparatus with the aedeagus proper (Ae) appearing double at its

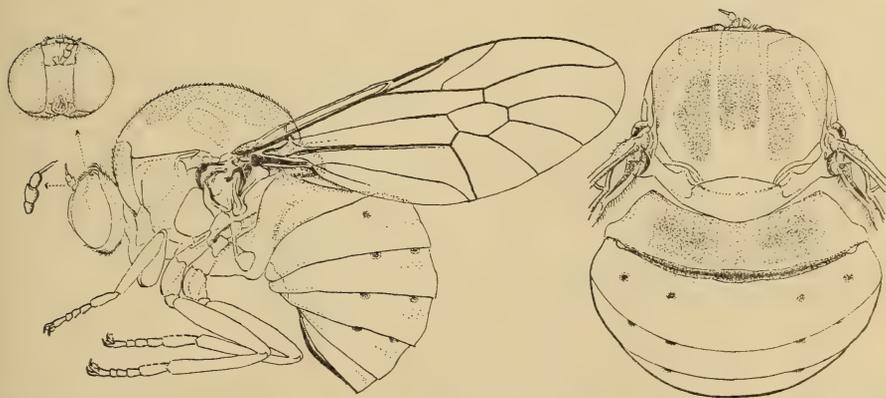


FIG. 7. Side view (left) and dorsal view (right) of ♀ *Psiloderoides mansfieldi* n. gen. et n. sp., and also front view of head and enlarged left antenna.

end, reversed in position, bending towards dorsum instead of towards venter or downwards as in most bombyliids; posterior end of the apodeme of the aedeagal apparatus bulb-like or vesicular, not flattened as in most bombyliid genera; and the paraphyses of the apparatus in form of a ventral hood-like extension of which the hind margin is slightly emarginate medially.

Biology: According to Mr. Mansfield of the Agricultural Department, bombyliid larvae were collected by field staff at a farm 'Sidi Berani' in the Kenhardt District during May 1964 (10th-15th instant). The larvae were already in an advanced state of development and some were found in the egg-packets of the brown trek locust. Others however were collected in loose soil in association with egg-packets. Representatives of such bombyliid larvae, from this batch collected at Kenhardt, were however also submitted to me; at first some preserved in spirit by Mr. J. E. van Someren Gréve and subsequently some other dead and live specimens by Mr. Mansfield.

From all these specimens it is quite obvious that at least three different species of Bombyliidae are represented. It is therefore impossible to state which of these three kinds of larvae represent those of this new genus. The specimens forwarded by Mr. Mansfield and stated by him to have been found in loose soil in association with egg-packets of the locust and from representatives of which adults of the new genus were supposed to have been bred, however appear to me to represent those of some other bombyliid genus, possibly those of some *Systoechus* species. Pending the result of a breeding experiment conducted at the South African Museum with the three live larvae among those submitted by Mr. Mansfield, the supposition that they represent larvae of this new genus cannot be corroborated*. It is however quite evident that the larvae of this new genus are in fact parasites or predators in egg-packets of the brown trek locust even if they were represented among those found loose in egg-packet infested soil samples.

In support of this the investigations of Potgieter (1929: 32-3) may be mentioned during which he also found larvae of another bombyliid parasite, *Systoechus xerophilus* Hesse (syn. *albidus* Munro nec Loew), both in the egg-packets of the brown trek locust and in loose soil in association with these. The larvae of such bombyliid predators apparently crawl away from destroyed egg-packets to change into pupae somewhere else in the same environment.

Pupa: The empty pupal skins from which the adult specimens of the new genus were hatched, and which have been pinned under the specimens by Mr. Mansfield, are therefore the only stage in the life history which could be reliably described and figured. The pupal skin shows some external structures typical of bombyliid pupae and it is characterized as follows:

Body (cf. text-fig. 8, left) semicircularly curved or humped, composed of a cephalic part with cephalic armature, thoracic part with wing and leg sheaths, a scutellar part and an arched abdomen with 8 segments, the last with caudal armature.

* These have since died without developing any further.

Cephalic part with anterior armature (see also separate drawing below) on each side consisting of a slightly obliquely situated basal part, ending apically in a forwardly-projecting, slightly dorso-ventrally flattened, slightly upcurved, blunt, chitinous spine, the inner basal part of which is carinately prominent step-like; outer part of the spine-bearing basal part ending in a chitinous half cup-like or scoop-like process; ventral part of head showing sheath knob of vestigial proboscis.

Thorax with sheath lobes of wings and sheaths of legs below, but without any bristles or spines; scutellar part with 3 long, flagellar bristles on each side.

Abdomen humped or arched in side view, with segment 1 the shortest dorsally, its hind margin medially dorsally slightly emarginate, with 2 bristles on extreme side below, one above and the other below ridge-like side below; segment 2 with a row of 3 bristles on each side in upper half across more or less the middle and 2 on extreme side (above and below lateral ridge); segments 3-6 each with a row of 3 bristles in upper half and 2 below on each side of lateral ridge, but beyond the middle, the bristles decreasing in size posteriorly and those across segment 6 the shortest; segment 7 with a row of 6 (3 on each side of midline) posteriorly-directed, curved, embedded, chitinous hooks on upper part beyond middle (see separate drawing of caudal part) as well as the usual 2 bristles below on each side of lateral ridge; segment 8 larger in ♀♀ than in ♂♂, armed on each side of middle with a strong, upwardly-curved, chitinous hook which arises from a vertically-embedded sole- or slipper-shaped basal part, the dorsal part of which projects freely as a flattened, lobe- or

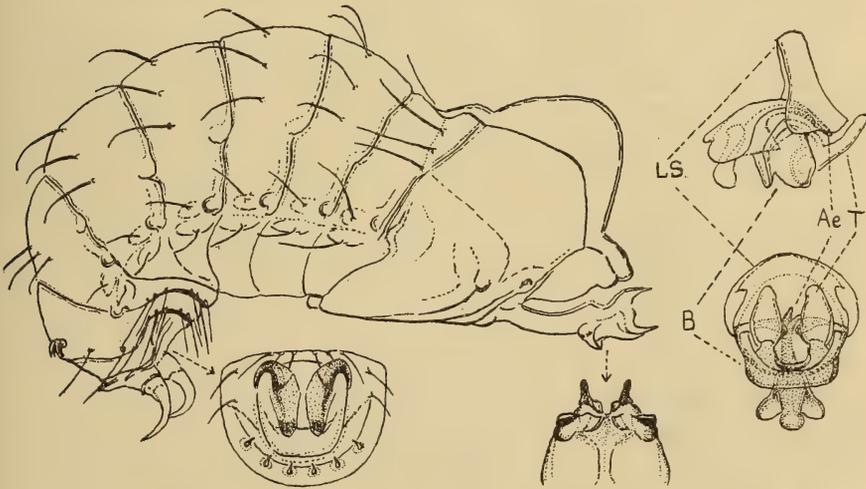


FIG. 8. Left: Side view of empty pupal skin of a ♂ *Psiloderoides mansfieldi* n. gen. et n. sp., also showing separately ventral view of cephalic armature and posterior view of caudal armature. Right: Side and posterior (dorsal) views (drawn upside down) of hypopygium of ♂ of the same species. Ae = aedeagus proper; B = basimere; LS = last sternite; and T = Telomeres.

tongue-shaped, chitinous process on each side of midline; sides of segments above the lateral ridge each also with a small semicircular, backwardly-projecting lobe; venter with sternites 1-5 without any bristles, but 6 and 7 each with a row of 6 slender, whip-like bristles (3 on each side of midline) beyond middle, with sternite 6 narrow, almost ridge-like medially, the part between it and 5 being deeply sunk in, causing the posterior part of abdomen to be characteristically bent or curved downwards and which, in conjunction with the strong upwardly-curved caudal hooks, probably acts as a strong fulcrum in the living pupa with which to facilitate forward and upward progression through soil or sand to enable the adult to escape.

The duration of both the larval and pupal stages has not been recorded.

Length of pupal skin in the natural humped state: about 4-5.75 mm.

Deepest part in side view, between tergite 3 (or part of 3) and venter: 47-74 mm. (53-74 mm. in case of ♀♀).

Only one, and apparently slightly variable, species of this new genus is represented in the material submitted by Mr. Mansfield which I wish to name *Psiloderoides mansfieldi* in appreciation of this investigator's contribution, and which is to be considered as the type-species of this new genus.

Psiloderoides mansfieldi n.sp.

This type-species is represented by 4 ♂♂ and 2 ♀♀ of which 2 ♂ paratypes and the ♀ allotype are in the South African Museum and the ♂ holotype, and a ♂ and ♀ paratypes in the Department of Agriculture in Pretoria.

The ♂ differs markedly from the ♀ in size, colour, integumental sculpture and in vestiture. It is characterized as follows:

Body and legs mainly ivory whitish or ivory yellowish, with the following parts black: occipital part, vertex including basal part or half of frons, to a certain extent middle of buccal depression, hollowed anterior declivous part of thorax, extending slightly laterally on to pronotal or shoulder lobes and continued medially along anterior part of thorax as a broad central band confluent with the greater discal black part of thorax which extends slightly peninsula-like on each side towards shoulder and leaving only a very narrow part above wing-base and the lateral and hinder part of postalar calli pale, greater part of scutellum (excepting the pale central part in hinder half or sometimes most of pale hinder border), greater depressed discal part of tergite 1, discal basal part or half of tergite 2, extending centrally to near its apex, extreme base of tergite 3, two rows of slightly depressed segmental spots on each side of abdomen above (the spots at base of tergites) from 2-6, a spot on extreme sides of tergite 1 and basally on extreme sides of 2-6 as well as two spots on mesopleuron, greater part of pteropleuron, excepting its posterior border, a large spot on sternopleuron, excepting its upper and anterior borders, a spot on hypopleuron, two spots on metapleural parts, hinder part of front coxae, rest of coxae, a subbasal infusion and spot beyond middle on anterior

lower aspect of front femora as well as their posterior face from near base, upper surface, upper anterior surface and a streak from near base to middle on anterior face of middle femora, upper and posterior surfaces from near base, a lateral anterior streak from near base to beyond middle and a subapical spot on hind femora, sometimes inner lower face of tibiae to a variable extent, and apices of claws; antennae reddish brownish; eyes reddish brownish to blackish brown; front ocellus yellowish or brownish, the lateral ones darker, more brownish.

Integument of head dull; that of thorax above punctured in anterior and antero-discal part, more rugulosely so discally and posteriorly, more or less shining anteriorly, especially on ivory yellowish parts, but dull discally and posteriorly; scutellum more distinctly punctured across base, somewhat shiny there; mesopleuron punctured and somewhat shining; pteropleuron and sternopleuron sometimes duller on black parts and former finely longitudinally striate, the pale borders more shining; metapleural part also somewhat shining; abdomen mainly dull, the discal depressed part of tergite 1 and blackened discal basal part of 2 areolarly punctured; integument of rest of abdomen above very finely, more or less transversely, rugulosely sculptured.

Vestiture with the hairs on head, the dense and longish ones on thorax above, scutellum and mesopleurae gleaming sericeous snow whitish, those on thorax above directed towards the middorsal part and those on sides of scutellum also directed upwards and forwards; hairs in crater-like areolar puncturation on depressed discal part of tergite 1 and on basal sculptured discal part of 2 minute, scarcely perceptible, appearing yellowish or yellowish brownish in certain lights; those on sides of latter tergites silvery whitish; those on rest of abdomen above longer, very much denser than discally on 1 and 2, but much shorter and denser than those on thorax, shining silvery whitish, brilliant in certain lights, decumbent, fur-like, directed towards midline where they form a carina-like raised central line or mane; those on genital segment also whitish; venter without any discernible hairs; hairs on legs gleaming sericeous or silvery whitish, those on coxae and femora longer than on abdomen, but shorter than on thorax above.

Head with the two more posterior ocelli separated by a space about 3 times distance between each of them and the more anterior central ocellus; frons broader basally than long, anteriorly with a slight pit-like central depression just behind antennae, the length of frons to face about as 5:9 (or 8); proboscis entirely vestigial, minute, nipple-like, sometimes scarcely detectable, its position evident by some shortish hairs; antennae with segments 1 and 2 almost subequal in length, segment 2 however a little longer, but much broader, more cup-shaped, with 3 subequal to or scarcely longer than 2, slightly narrower apically than basally and basally narrower than 2, with segment 4 slender, rod-shaped, about as long as or only very little longer than 3, ending in a short more or less clear seta-like style.

Wings transparent, tinted slightly milky whitish; veins brownish or

yellowish brownish, but greater part of costal vein to beyond level of base of triangular marginal cell, greater part of vein between basal cells and entire posterior vein of anal cell whitish transparent; microtrichial fringe minute, more evident along axillary lobe and alula; marginal cell rather elongate, scalene-triangular; first posterior cell rather rapidly broadened divergently near apex; discoidal cell more or less 2 times as long as broad, the middle cross vein at about, or a little beyond, middle of the cell; squamae opaquely whitish; knobs of halteres white.

Hypopygium as shown in text-fig. 8 (right) and as described for genus.

The ♀ (text-fig. 7) differs considerably from the ♂ and, apart from being distinctly much larger, it differs in the following respects:

Body and legs mainly yellowish; occipital part, including ocellar part, blackish or black; entire frons yellowish like face and buccal part, head below and behind eyes; antennae reddish brownish; thorax mainly yellowish, with the following parts brownish or reddish brownish (cf. text-fig. 7, right): a broad longitudinal, central streak (separated by a yellowish line) extending to near base (darker in last part), an irregular quadrate spot on each side discally near middle, an oblique oblong spot on each side just above wing-base, extending towards quadrate spot, a large oblong and darker (more blackish brownish) spot on each side beyond middle, beginning at (or narrowly confluent with) posterior narrow part of quadrate spot and extending to near postalar calli and separated from broad central streak on each side by a yellowish longitudinal line; prescutellar basal part in one ♀ also tending to be slightly darkened; scutellum mainly yellowish, its transverse depression across base partly brownish; pleurae mainly yellowish, the margins of the sclerites more yellowish whitish, the anterior part of mesopleuron infused slightly yellowish brownish and pteropleuron, sternopleuron and hypopleuron infused with reddish brownish to a variable extent, especially towards anterior part; abdomen, unlike the almost entirely yellowish white abdomen of ♂, more or less dirty yellowish to greyish yellowish brownish, variegated with irregular dark infusions or streaks more or less across middle of tergites and on extreme sides, the depressed discal part of tergite 1 and some basal discal parts of 2 blackish brown and, as in ♂, with two rows of blackish shiny depressed spots on each side above and a row of fainter, more indistinct, ones on extreme sides; venter mainly yellowish, the two medial ridge-like elevations more yellowish whitish and space between them more pale yellowish brownish like the genital parts; legs mainly yellowish, with more or less the same parts as in ♂ darkened, but much fainter, more yellowish brownish than black, the entire tibiae however yellowish, not darkened along inner lower face as in some ♂♂.

Integument also mainly dull, only the apex of shoulder lobes, pleurae, especially darkened parts, metapleural parts and legs, especially coxae, and apical part of femora somewhat shining; integument of thorax above, scutellum and mesopleuron sculptured as in ♂, but more coarsely so; that of entire abdomen above, unlike that of ♂, fairly coarsely areolarly punctured (crater-

like punctures) throughout, only slightly more coarsely so in depressed discal part of tergite 1, the suture between tergites 1 and 2 rather deep, furrow-like, especially across middle part.

Vestiture, unlike that of ♂, very much shorter; hairs on ocellar part appearing dark, those on pale parts (frons and face) more yellowish or golden yellowish, not whitish as in ♂, though apparently not much shorter and sparser; those on thorax above, though arranged in same way and more or less equally dense, distinctly very much shorter, gleaming more yellowish or golden yellowish discally, not silvery whitish; hairs on abdomen above, located in the crater-like punctures, minute, appearing less dense, yellowish, not silvery, but also directed obliquely towards the midline; those on legs longer than on body, but relatively shorter than in ♂, distinctly gleaming more golden yellowish.

Head (text-fig. 7, left and upper left) with the fronto-facial part distinctly much broader than in ♂, the frons across base also much broader than long, length of frons to face about as 6 : 8; face about as broad across base as long (to beginning of buccal cavity) which in ♂ is distinctly much narrower across base than long; proboscis, though also vestigial or rudimentary, very slightly longer than in ♂, slightly more finger- or lobe-like; posterior ocelli separated by a space a little more than 3 times distance between them than between each and middle ocellus, the latter distinctly larger than in ♂; eyes in the two specimens not equally convex as in ♂, but uneven as described under the genus; antennae with segments 1-3 proportionally similar to those of ♂, but slender segment 4 distinctly longer than 3.

Wings (text-fig. 7, left) distinctly infuscated, somewhat opaquely brownish; veins darker than in ♂; middle cross vein distinctly beyond middle of discoidal cell; knobs of halteres yellowish brownish, not whitish as in ♂.

Length of body: about 2.6-3.2 mm. (♂♂) and 4.2-4.4 mm. (♀♀) (in natural condition).

Length of wing: about 3.2-3.88 mm. (♂♂) and 4.36-4.96 mm. (♀♀).

Width of widest part of abdomen: about 1.92-2.52 mm. (♂♂), 3.2-3.6 mm. (♀♀).

Locality: North-western Cape: Farm 'Sidi Berani' in Kenhardt District (Dept. of Agriculture, Pretoria, from larvae collected 10-15 May 1964 and hatched out during Sept.-Oct. 1964).

SUMMARY

Following an introductory note a revised key to all the known African genera, both old and new, of the Cyrtosiinae is given. Six genera not previously recorded from South Africa, of which two are new, are dealt with, a new subgenus and 16 new species are described. Keys to the known species of genera, which contain several species, are also given. To supplement the descriptions 8 text-figures are given.

ACKNOWLEDGEMENT

Apart from the various collectors mentioned in the introduction and to whom I am indebted for material, it should be recorded that the Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research of South Africa for the award of a grant towards the cost of publishing this paper.

REFERENCES

- BECKER, T. 1907. Die Ergebnisse meiner dipterologischen Frühjahrsreise nach Algier und Tunis, 1906. *Z. syst. Hym. Dipt.* **7**: 97-128.
- BEZZI, M. 1902. Neue Namen für einige Dipteren-Gattungen. *Z. syst. Hym. Dipt.* **2**: 191.
- BEZZI, M. 1908. Simuliidae, Bombyliidae, . . . *Denkschr. med.-naturw. Ges. Jena* **13**: 179-201.
- BEZZI, M. 1925. Notes additionnelles sur les bombyliides (Dipt.) d'Égypte. *Bull. Soc. ent. Égypte* **9**: 244-273.
- BOWDEN, J. 1965. Diptera of Nepal: Bombyliidae. *Bull. Brit. Mus. (nat. Hist.) Entom.* **17**: 203-208.
- ENGEL, E. O. 1933. Bombyliidae. *Flieg. pal. Reg.* **69**: 97-192.
- HESSE, A. J. 1938. A revision of the Bombyliidae (Diptera) of southern Africa. *Ann. S. Afr. Mus.* **34**: 1-1053.
- HESSE, A. J. 1955. Diptera: Bombyliidae. In Hanström, B., Brinck, P. & Rudebeck, G., eds. *South African animal life*. **2**: 382-401. Stockholm: Almqvist & Wiksell.
- HESSE, A. J. 1956. A revision of the Bombyliidae (Diptera) of southern Africa. Part III. *Ann. S. Afr. Mus.* **35**: 465-972.
- HESSE, A. J. 1960. Diptera, Bombyliidae. Mission zoologique de l'I.R.S.A.C. en Afrique centrale (P. Basilewsky et N. Leloup, 1957). *Ann. Mus. Congo belge* 8vo (Sci. zool.) **88**: 315-317.
- HESSE, A. J. 1965. Diptera (Brachycera): Bombyliidae, Cyrtosiinae, *Euanthobates*, a remarkable new genus. In Hanström, B., Brinck, P. & Rudebeck, G., eds. *South African animal life*. **11**: 482-484. Stockholm: Swedish natural science research council.
- LOEW, H. 1844. Beschreibung einiger neuen Gattungen der europäischen Dipterenfauna. *Stettin. ent. Ztg.* **5**: 114-130.
- PARAMONOW, S. J. 1929. Beiträge zur Monographie einiger Bombyliiden-Gattungen. *Trav. Mus. zool. Acad. Sci. Ukr.* **6**: 1-161, I-V.
- PERRIS, E. 1839. Notice sur quelques diptères nouveaux. *Ann. Soc. ent. Fr.* **7**: 45-57.
- POTGIETER, J. T. 1929. A contribution to the biology of the brown swarm locust *Locustana pardalina* (Wlk.) and its natural enemies. *Sci. Bull. Dep. Agric. S. Afr.* **82**: 1-48.
- SÉGUY, E. 1930. Risultati zoologici della missione inviata dalla R. Società geografica italiana per l'esplorazione dell'oasi di Giarabub (1926-1927). Insectes diptères. *Ann. Mus. Stor. nat. Genova* **55**: 75-93.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{1}{2}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) 9: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. 2. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. 3: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



7.68

T. H. BARRY

THE CRANIAL MORPHOLOGY OF THE
PERMO-TRIASSIC ANOMODONT *PRISTERODON*
BUFFALOENSIS WITH SPECIAL REFERENCE TO
THE NEURAL ENDOCRANIUM AND
VISCERAL ARCH SKELETON

December 1967 December
Volume 50 Band
Part 7 Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R1.50

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

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

THE CRANIAL MORPHOLOGY OF THE PERMO-TRIASSIC
ANOMODONT *PRISTERODON BUFFALOENSIS*
WITH SPECIAL REFERENCE TO THE NEURAL
ENDOCRANIUM AND VISCERAL ARCH SKELETON

By

T. H. BARRY

South African Museum, Cape Town

(With Plates X–XI and 14 figures in the text)

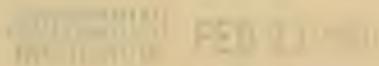
CONTENTS

Summary	131
Introduction	132
Material and technique	132
Cranial morphology	135
Dermal bones	
<i>The Maxillary</i>	138
<i>The Septomaxillary</i>	139
<i>The Nasal</i>	141
<i>The Lachrymal</i>	141
<i>The Squamosal</i>	141
The neurocranium	
<i>The Occiput</i>	142
<i>The Internal Ear</i>	144
<i>The Stapes</i>	144
The visceral arch skeleton	
<i>The Palatoquadrate</i>	150
<i>Meckel's Cartilage</i>	153
<i>Hyobranchial Skeleton</i>	156
Dermal bones of the lower jaw	157
Acknowledgements	159
References	159
Abbreviations	160

SUMMARY

The skull of the fossil mammal-like reptile *Pristerodon buffaloensis* has been sectioned and reconstructed to show the external and internal features of the skull. The skull is compared with the type and other specimens as well as with a sectioned specimen of *Dicynodon grimbeeki*.

Special emphasis has been laid on the structure of the neurocranium and visceral arch skeleton. It is suggested that ossified trabeculae are definable in the basicranial axis and that the quadrate and epipterygoid were synchondro-
tically attached in life to form a palato-quadrate complex.



The stapes is suturally attached to the quadrate, ruling out any movement of the stapes without movement of the quadrate. It is maintained that conditions in *Pristerodon* do not support the theory that anomodonts possessed a tympanum.

Deductions are also made regarding the neck musculature and processes developed on the occiput.

INTRODUCTION

Comparative anatomists and palaeontologists have been studying the origin of mammals for more than a hundred years now. At this stage of our knowledge it seems reasonably established that mammals arose from the Therapsids, which in turn arose from the Captorhinomorpha via the Pelycosauria. Most of the research has, quite naturally, been directed at finding the structural links between the mammal-like reptile and the primitive mammal and the tendency has been to study those animals falling within the accepted lines which lead to the mammal.

Side branches are not thought to hold the same fascination as those leading towards the mammals and are often neglected, in spite of the fact that they too can supply a wealth of information regarding evolutionary processes. The Sub-order Anomodontia (Class Reptilia; Sub-class Synapsida; Order Therapsida) is of especial interest not only because it shows a marked degree of parallel evolution of certain mammalian characteristics, but also because the abundance of its species and the availability of specimens make this group ideal for comparative anatomical studies.

According to Houghton and Brink (1954) the characteristics of the genus *Pristerodon* are the following:

'Small. Molars situated in a row on the alveolar ridge on the maxilla, postero-medial to the canine or caniniform process. Palatine not in contact with the premaxilla. Parietal bar broad' (p. 65).

The genus is divided into the following species: *Pristerodon agilis*, *P. brachiops*, *P. buffaloensis*, *P. mackayi*, *P. raniceps* and *P. whaitsi*.

MATERIAL AND TECHNIQUE

The specimen sectioned, No. B.P.I. 339, was found in 1956 by Mr. J. W. Kitching of the Bernard Price Institute for Palaeontological Research, Johannesburg, on the farm Kirkvors, (today known as De Hoop) approximately 2 miles north-north-west of Murraysburg, South Africa. The horizon is *Cistecephalus*.

The type specimen, No. B.P.I. 241, used in this investigation, is a well-preserved skull (pl. X A, B, C, and XI A, D). It belongs to the Bernard Price Institute for Palaeontological Research. It was found on the farm Swartbos, in the Murraysburg district. The horizon was Lower *Cistecephalus*.

Three other specimens, Nos. B.P.I. 242, B.P.I. 243 and B.P.I. 244, were also used for comparison.

Skull No. B.P.I. 339 was serially sectioned by means of the parallel grinding method, leaving exposed transverse sections at intervals of 200 micron. As it was possible to determine the general outline of the skull the specimen could be orientated for sectioning without removal of the matrix. This had the advantage that clear definition was obtained between matrix and bones and obviated the possibility of accidental grooving or pitting of the bones through mechanical cleaning. Three thin metal rods, fixed parallel to the cranial axis, served as base-lines for the transverse orientation of the skull before imbedding in 'Callistone' plaster of Paris.

In this investigation use was made of a Croft Parallel Grinder. Under normal circumstances the grinding method offers an accurate and satisfactory picture of the relationships of the bones, and supplies information about the internal structures which are not readily available from other methods of

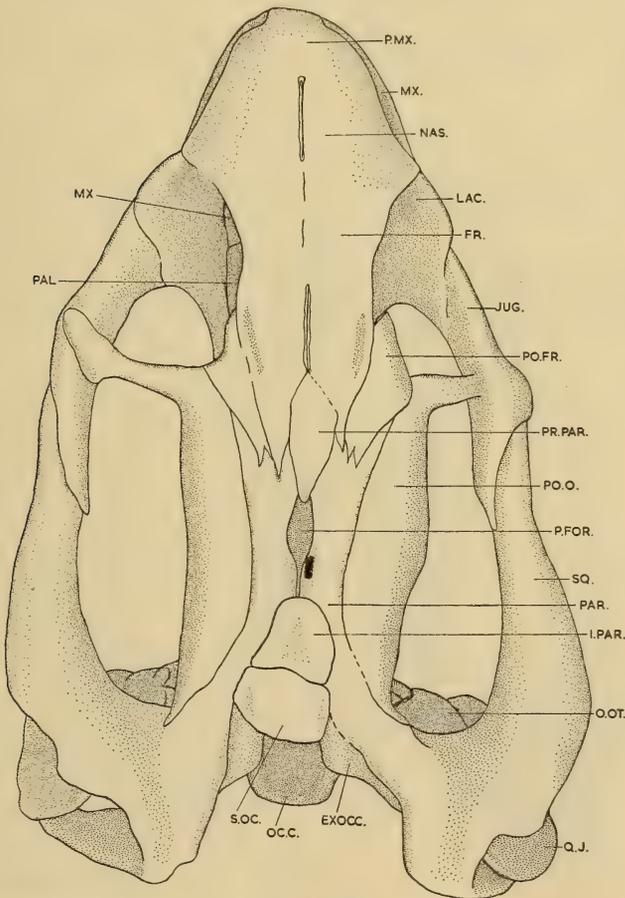


Fig. 1. *Pristerodon buffaloensis*. Dorsal view of skull reconstructed from serial sections. Abbreviations on p. 160.

preparation. The disadvantage of the serial grinding method is the complete loss of the specimen, thus necessitating the use of the more common species in this type of investigation. However, specimens of less common species are sometimes sectioned when the additional information procurable warrants it. Less common specimens are known, however, to have been sectioned in error, in the belief, resulting from the superficial method of fossil identification often employed, that a more common species is being investigated.

To counteract the loss of the fossil, photographs are taken and enlarged drawings made of each exposed surface and these are used later in making the reconstructions. The method used in making the reconstructions is that described by Pusey (1939) for drawings made from microtome sections.

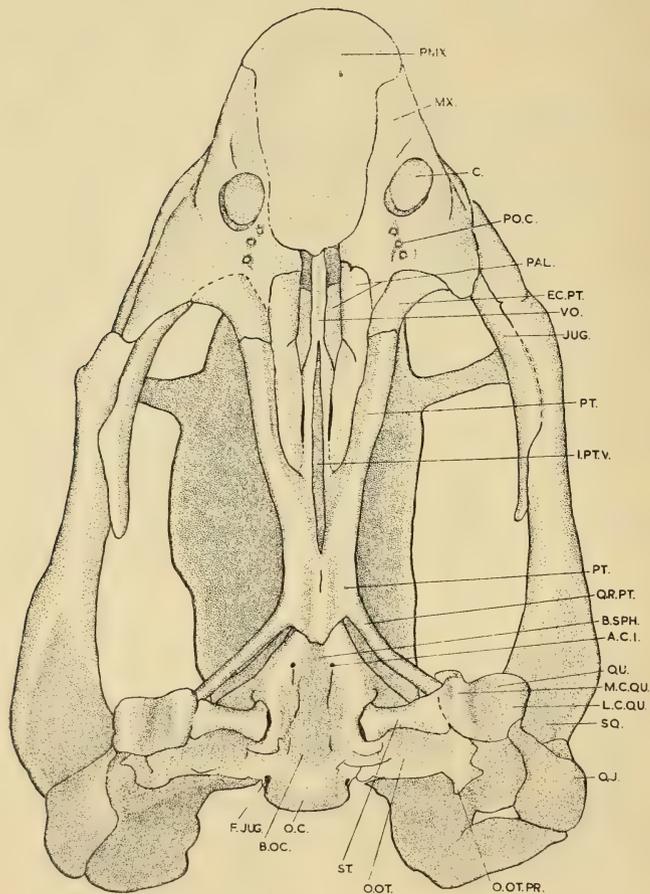


Fig. 2. *Pristerodon buffaloensis*. Ventral view of skull with lower jaw removed. Reconstructed from serial sections. Abbreviations on p. 160.

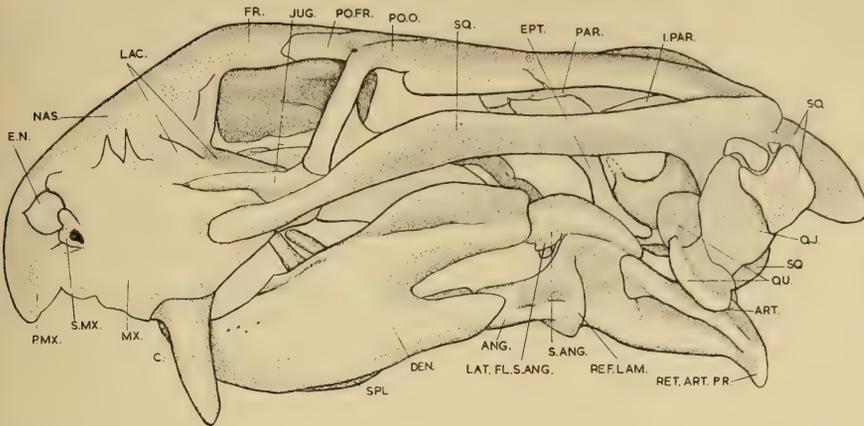


Fig. 3. *Pristerodon buffaloensis*. Lateral view of skull with lower jaw in original position. Reconstructed from serial sections. Abbreviations on p. 160.

CRANIAL MORPHOLOGY

Toerien (1953) selected fifteen measurements and indices for a comparative study of skull variation in *Dicynodon grimbeeki* and *D. sollasi*. The same method has been adopted for *Pristerodon buffaloensis*.

The following is a table of the measurements and indices of the sectioned skull and includes a comparison with the type specimen of *P. buffaloensis*.

		<i>Value in mm.</i>	
<i>Measurement or index</i>		<i>No. 339</i>	<i>Type</i>
1.	Skull length	64.8	83
2.	Basal length	58.4	76
3.	Skull width	44.8	60
4.	Interorbital width	9.8	13
5.	Intertemporal width	16.2	20
6.	Snout length	16.6	20
7.	Snout length plus orbital length	26.6	40
8.	Tip of snout to pineal length	36.2	49
9.	$\frac{\text{Skull width} \times 100}{\text{Skull length}}$	67.9	72
10.	$\frac{\text{Interorbital width} \times 100}{\text{Intertemporal width}}$	60.5	65
11.	$\frac{\text{Interorbital width} \times 100}{\text{Skull width}}$	21.8	21.7
12.	$\frac{\text{Intertemporal width} \times 100}{\text{Skull width}}$	36.2	33.3

		<i>Value in mm.</i>	
<i>Measurement or index</i>		<i>No. 339-</i>	<i>Type</i>
13.	$\frac{\text{Snout length} \times 100}{\text{Skull length}}$	18.4	24
14.	$\frac{\text{Snout length plus orbital} \times 100}{\text{Skull length}}$	41.0	48.2
15.	$\frac{\text{Tip of snout to pineal length} \times 100}{\text{Skull length}}$	55.9	59

In Fig. 4 these measurements and indices are plotted against the corresponding ranges of five specimens of *Pristerodon buffaloensis*.

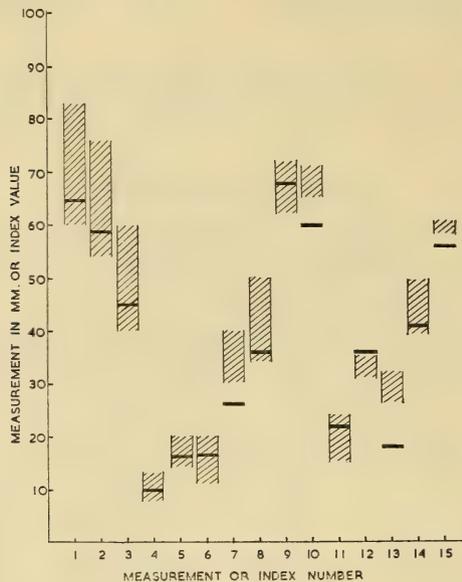


Fig. 4. Range in measurements and index values for five specimens of *Pristerodon buffaloensis*. Ranges indicated by shaded blocks. Values for sectioned specimen by black lines.

DERMAL BONES

A feature of the snout region of the sectioned skull is the absence of sutures between the premaxillary, nasal and the frontal bones (see figs. 1 and 3). Transverse sutures are often difficult to distinguish in transverse sections but none of the sutures here should have presented this problem. Of the three specimens of *Pristerodon buffaloensis* figured by Toerien (1953), two do not show sutures between these bones, while in the type specimen the outline of the prefrontal, internasal and nasopremaxillary sutures only are visible. It is possible that the variability of sutures in this region could be the result of suture closure which develops with age, a phenomenon which is not unknown in

extant mammals where various degrees of suture closure have been recorded in older animals. The size of the canine tusks seem to underline the fact that the skull is that of an adult.

The facial portion of the premaxillo-maxillary border is indistinguishable. The palatal portion of the premaxillary is concave and extends to the point in line with the second post-canine tooth, where it forms the anterior border of the internal choanae. Peripherally the bone terminates in a sharp cutting edge. A median ridge developed on the posterior third of the premaxillary projects into the oral cavity. The contact posteriorly between the premaxillary and the median vomer is a deep one involving not only the ventral ridge but also the dorsal ridge which projects into the snout (fig. 5). There is no indication of the pair of shallow palatal ridges found at the anterior end of the premaxillary of *Dicynodon grimbeeki* and many other dicynodonts. Near the midline, in this area the bone is pierced by a small foramen which leads into the nasal passage. Sollas & Sollas (1914) found two pairs of foramina in this vicinity and suggested that these naso-palatine foramina served for the passage of blood-vessels. From the dorsal surface of the palatal portion of the bone, a median plate-like inter-nasal process extends upwards for about one-third of the distance to the roof of the snout. The height of the plate increases posteriorly with the increase in height of the dome of the snout. A shallow groove in the dorsal edge of the posterior half of the plate probably accommodated a cartilaginous nasal septum (see fig. 7A).

No evidence was found that the premaxillaries were paired as reported for *Venjukovia* by Watson (1948). In its front half the bone is pierced by a small foramen.

The degree of progress towards the development of a secondary palate in *Pristerodon* is probably indicated by the increase in relative length of the palatal portion of the premaxillary and the fact that it overlaps a third of the vomer

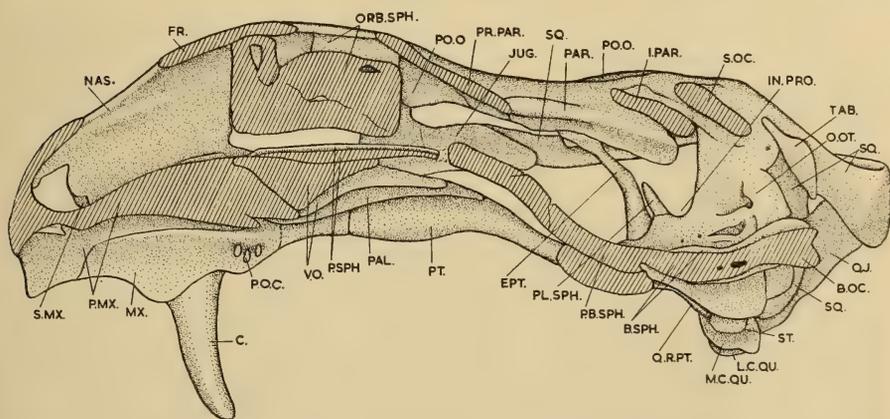


Fig. 5. *Pristerodon buffaloensis*. Medial view of skull of sectioned specimen. Median bones hatched. Abbreviations on p. 160.

behind it. As the median ridge of the premaxillary occupies a position corresponding to that of the anterior part of the vomer in lizards, it is not unreasonable to assume that the ridge on the premaxillary has taken over whatever function was previously performed by the vomer in this area.

The Maxillary

The maxillary forms the major portion of the side wall of the snout projecting ventrally to well below the level of the palate. The sharp peripheral ridge of the premaxillary is continued on to the anterior third of the maxillary before it flattens out on reaching the canine tusk (fig. 2).

Posteromedially the palatal portion of the maxillary participates in the formation of the lateral walls of the choanae through the formation of a wedge which inserts between the premaxillary and the palatine. Toerien (1953) used the relationships between these three bones as basis for the classification of the Anomodontia but this has not been generally accepted.

In addition to the large canine, the maxillary has three small post-canine teeth situated in a row, posteromedially to the canine, and at a slight angle to the longitudinal axis of the skull (fig. 2). The teeth show a slight variation in size, the anterior one being slightly bigger than the other two. The sections do not show whether the teeth were serrated, a feature regarded by Broom as being significant in classification and identification. Toerien (1953), however, claims that serrations only occur on erupting or newly erupted teeth and that the older teeth were completely devoid of denticulations. Nor can the number of post-canine teeth be used as a basis for generic or specific distinction as the number can vary not only within the same species but also on the two sides of the upper jaw. Specimen No. B.P.I. 243, like the sectioned skull, has three post-canine teeth in each half of the upper jaw. The type, however, has four. There are no replacement teeth in the upper jaw of the sectioned skull but the type and B.P.I. 243 show at least one each.

The maxillary antrum is not an intra-osseal maxillary space, as Broom claimed for *Oudenodon*, but inter-osseal, with the maxillary, jugal and lachrymal participating in its formation (fig. 7A). This is also the case in *Daptocephalus* (Sollas & Sollas, 1914), but in this form the transpalatine also contributes to the walls of the cavity.

The median vomer is attached to the premaxillary in front of it over a narrow but extremely deep, posteriorly slanting vertical area. Transverse sections show that the premaxillary is actually continued further posteriorly than is seen from the outside because a thin postero-ventrally directed sliver of the premaxillary is wedged into the vertical vomer so that the latter virtually clasps the posterior part of the premaxillary between two thin laminae. At approximately two-thirds of its length measured from the front, the vomer splits into two flanges, each of which attaches laterally to the palatine and posteriorly to the pterygoid. The flanges demarcate the anterior part of the interpterygoidal vacuity. In median section the vomer shows as a triangular bone with the apex

of the triangle pointing ventrally (fig. 5). From the apex to the point where the vomer splits, the ventral surface is deeply grooved as if it housed a cartilaginous structure (fig. 7c).

The dorsal surface of the plate-like median portion of the vomer is also grooved, housing the anterior portion of the parasphenoid rostrum in a close fit.

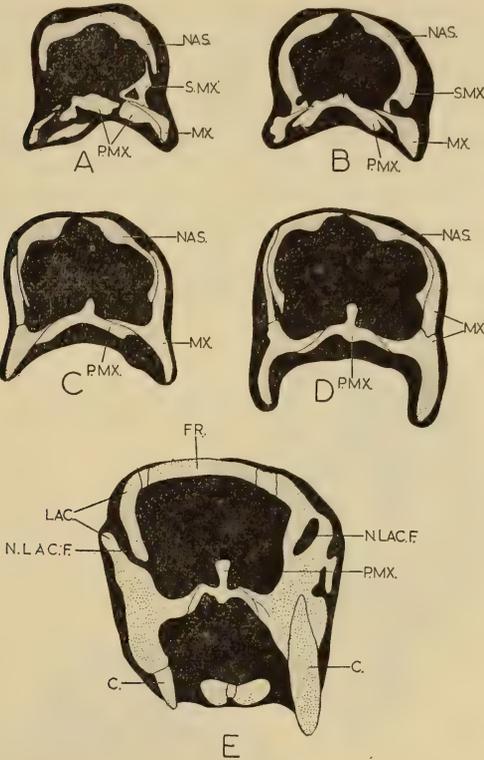


Fig. 6. *Pristerodon buffaloensis*. A-D: transverse sections through the snout of the sectioned specimen. Abbreviations on p. 160.

The Septomaxillary

The septomaxillary, a typically reptilian membrane bone represented in only two orders of mammals, the Monotremata and the Edentata (De Beer, 1937), occupies the postero-ventral border of the external nostril in *Pristerodon*. It is roughly triangular in cross-section with the base resting mainly on the palatal process of the maxillary. As in *Dicynodon grimbeeki*, an obliquely running longitudinal canal pierces the bone. In *Dimetrodon*, the only pelycosaurian species in which the septomaxillary is fully known, a foramen of moderate size pierces the base of the bone near its external border (Romer and Price, 1940). It is possible that the canal served to transmit blood-vessels and

nerves into the nostril, as it still does in the lizards *Cordylus polyzonus* (Van Pletzen, 1946) and *Monopeltis capensis* (Kritzing, 1946). In these two species the ramus medialis nasi V, accompanied by a small artery, passes through a foramen in the anterior tip of the septomaxillary. In *Anniella pulchra*, however, the blood-vessel and nerve are accommodated in a deep groove on the dorsal surface of the bone (Toerien, 1950).

Williston (1925) claims that the primitive position of the septomaxillary is on the postero-lateral rim of the external naris, a position corresponding to that occupied by the bone in *Pristerodon buffaloensis*. In *Sphenodon* where the septomaxillary occupies a corresponding position, it is solely concerned with the support of the floor of the Organ of Jacobson and with the formation of the side wall of the vestibule (Fuchs, 1911). According to Fuchs the same conditions obtain in *Dasybus*. Whether *Pristerodon* possessed a vomero-nasal organ, which, as in *Sphenodon*, opened into the choana, or whether like adult Chelonians, crocodylians and birds, it lacked one (Romer, 1949) is difficult to say, but there are no separate openings in the palate anterior to the choanae which could be associated with their ducts.

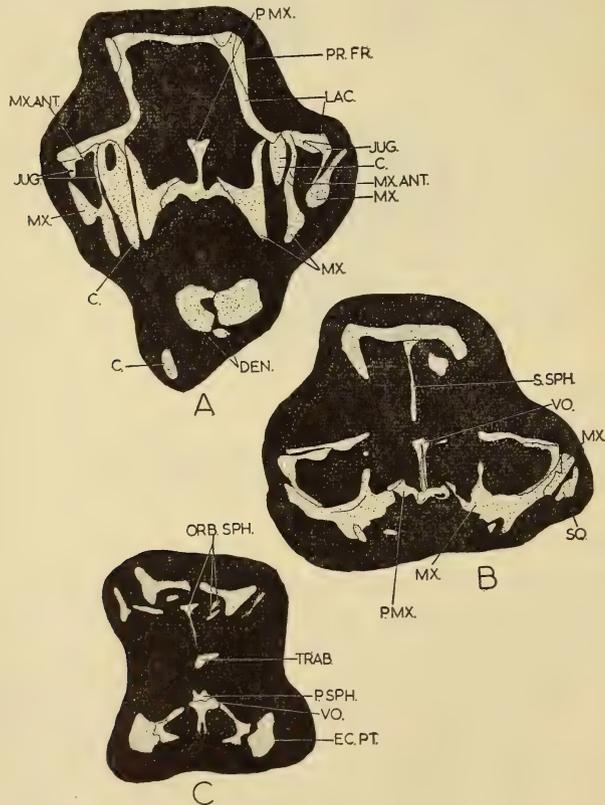


Fig. 7. *Pristerodon buffaloensis*. Transverse sections through A: the maxillary antrum; B: anterior part, and C: posterior part of the orbit of the sectioned specimen. Abbreviations on p. 160.

The Nasal

The anterolateral tip of the nasal contributes to the formation of the rim of the external naris. The nasal also forms the major portion of the internal dome-shaped nasal cavity, contributing the lateral and dorsal walls. One-third to one-half of the lateral surface of the bone is overlapped by the facial portion of the maxillary (figs. 6c & d).

Cross-sections show a shallow, rounded ridge, high up on the inner surface of the nasal cavity, which extends from the external naris to a point in line with the naso-lachrymal foramen (figs. 5, 6c & d). The ridge is mostly evenly rounded but it may also jut out in the form of a ledge. It is possible that the ridge represents the area of a lateral attachment of a membranous or cartilaginous structure which extended across the dorsal part of the nostril and probably formed the floor of the olfactory lobes. A seemingly comparable ridge on the inner surface of the snout in the lizards *Scelotes* and *Anniella* (Malan, 1946) albeit on the frontal, serves as attachment for the membrane supporting the anterior part of the olfactory lobes.

The Lachrymal

The lachrymal forms the major portion of the anterior rim and floor of the orbit. Anteriorly it expands into the side of the face (fig. 3) but it ends well behind the naris.

Individually, the frontal, postfrontal, preparietal, parietal, interparietal and postorbital show little structural deviation from conditions as seen in *Dicynodon grimbeeki*, but collectively they form a pattern which distinguishes *Pristerodon* from other small-skull anomodonts. Here the relative widths of the interorbital and intertemporal bars, seen within the outline of the skull, are of importance especially as they simplify superficial identification.

A feature which has possibly more significance than would normally be attributed to it, is the rounded depression in the fronto-parietal region. A similar type of depression is seen in the type specimen (pl. XA & c). Although such a condition would normally be attributed to post-mortem damage, the fact that the depression occurs in a small specific area and that it is so neatly excavated makes it difficult to accept, without reservation, that it was caused by pressure from above. It is believed that this area of the skull in *Pristerodon* was either normally depressed or otherwise the flatness of the skull makes it less resistant to pressure than the slightly convex skull of many *Dicynodon* species.

The Squamosal

The squamosal is tetra-radiate. Its antero-ventrally directed flange, which with the jugal on its inside, forms the temporal arch, extends forward to contact the maxillary, ventral to the anterior rim of the orbit. Its antero-dorsal process is short and runs medially to the postorbital. The third prong is extended ventrally and gains contact with the quadrato-jugal, quadrate, tabular, exoccipital and opisthotic, while the fourth process is posteriorly directed. It is

probable that the shallowly grooved dorsal surface of this flange, as well as the dorso-medially flattened surface of the squamosal in the temporal arch, are associated with the attachment of the adductor muscles.

THE NEUROCRANIUM

The Occiput

The interparietal and tabular, both of which are dermal roofing bones, and the squamosal appear on the hind wall of the skull. For the rest the occiput is formed by cartilage bones.

The posterior surface of the supraoccipital is in contact laterally with the tabular and ventro-laterally with the exoccipital. It is the roofing bone of the foramen magnum, and the posterior portion of the brain (pl. XIA & c). The body of the supraoccipital extends forward along the midline to a point in line with the pro-otic incisure. Its ridge-like ventro-lateral border forms a sutural contact with the dorsal portions of the exoccipital and pro-otic.

The exoccipital extends plate-like across the posterior surface of the skull to form the lateral border of the foramen magnum, the medial and ventral borders of the post-temporal fossa and the dorsal half of the rim of the jugular foramen (for nerves IX, X and XI). Dorso-laterally it is bordered by the tabular, laterally by the squamosal, ventro-laterally by the opisthotic and ventro-medially by the basioccipital. Exoccipital participation in the formation of the occipital condyle seems restricted to the lateral bulges of the condyle although the sutures are not very well defined. The exoccipitals do not exclude the basioccipital from the foramen magnum as in *Daptocephalus* (Ewer, 1961) and *Lystrosaurus* (Van Hoepen, 1913).

The post-temporal fossa is small. According to Versluijs (1936) the fossa tends to become smaller in those groups where the surrounding bones become more robust. In *Pristerodon* the dorsal expansion of the opisthotic and the enlargement of the tabular have narrowed the opening and consequently the area of attachment of the temporalis muscle on the occiput has also been decreased. Versluijs (1936) has found that the neck muscles play an important part in the determination of the shape of the hind wall of the skull, while Pointner (1931) maintains that traction not only exerts its influence on the construction of a bone but that the relative length of the functionally important neck muscles can be ascertained from the bones forming the hind part of the skull.

The occiput in *Pristerodon* indicates the origin of at least three groups of neck muscles and two jaw muscles. The rectus capitis posterior group shows signs of subdivision into a large dorsal muscle, the rectus capitis posterior major, having an area of origin occupying the supraoccipital, tabular and the dorsal half of the exoccipital, and the rectus capitis posterior lateralis et medialis occupying most of the ventral and lateral portions of the exoccipital and the dorsal half of the opisthotic (pl. XIc). Contraction of the r.c.p. lateralis et medialis would pull the skull back while the lateralis portion would have some

influence in swinging the snout sideways. The r.c.p. major would also pull the skull back but the forward slant of the hind wall of the skull dorsal to the foramen magnum suggests that its contraction would also lever the snout upwards. This action would allow the animal to tear off portions from its food source which are small enough to be handled by the jaws.

The ventral half of the distal portion of the opisthotic served as origin for the obliquus capitis. Contraction of this muscle which in living reptiles is inserted on the neural arch of the axis and atlas, would cause a lateral swing of the skull. Between this muscle and the lateral portion of the one above it (r.c.p. lateralis et medialis) the opisthotic is drawn out into a pointed posteriorly projecting process, which may be called the opisthotic process for lack of a more suitable name.

Stresses caused by the contraction of these two functionally important but differently directed muscles would seem to be the main reason for the development of the opisthotic process. Cox (1959) contends that this process, which he called the 'tympanic process', was not concerned with the occipital musculature. Comparison of *Pristerodon* with living chelonians gives strong indications that the two muscle groups mentioned not only flanked the process dorso-medially and ventro-medially respectively, but were also attached along part of the process. It is of interest to note that some of the recent turtles show an analagous

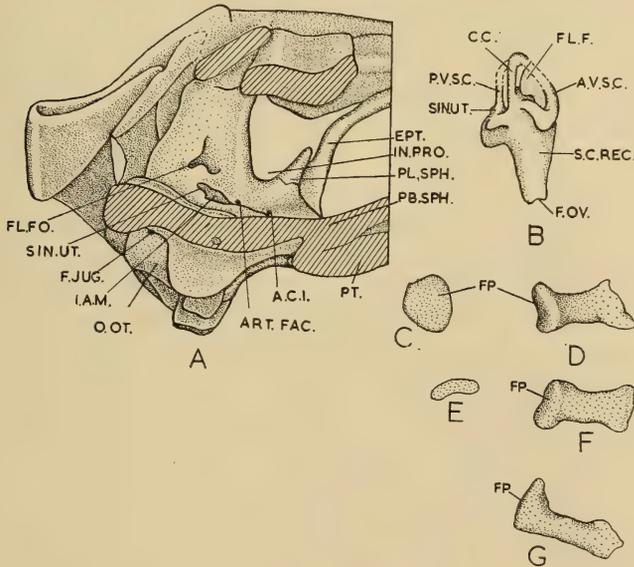


Fig. 8. *Pristerodon buffaloensis*. Sectioned specimen. Reconstructions of A: medial view of posterior third of the skull; B: lateral view of impression of left membranous labyrinth; C: medial view of stapes footplate; D: dorsal view of right stapes; E: lateral view of quadrate face of the right stapes; F: ventral view of right stapes; G: posterior view of right stapes. Abbreviations on p. 160.

process on the opisthotic, more prominently developed in some than in others (pl. XI_B). The muscle attachments on one of them, *Pelomedusa subrufa* show the muscles extending along nearly the entire length of the process.

A scar on the inside of the basioccipital-basisphenoid tuber probably indicates the area of attachment of the rectus capitis anterior. In living reptiles this muscle is inserted on the ventral surface of the axis and atlas. Contraction in *Pristerodon* would, therefore, pull the snout down.

The depressor mandibulae is the more prominent of the two jaw muscles associated with the hind wall of the skull in *Pristerodon* and covers the entire surface of the occipital face of the squamosal. A transverse ridge half-way down, similar to that found in most recent turtles, probably demarcates the border between the area of origin of a dorsal longer group, from a ventral, shorter, group of muscle fibres. The depressor is inserted on the ventral posterior part of the lower jaw.

The small post-temporal fossa allows only a small portion of the second jaw muscle, the temporal, to enter the hind wall.

The internal ear

The features of the internal ear are distinct except for small portions of the semi-circular canals which have become obliterated (fig. 8_B). The structure of the ear does not seem to differ radically from the anomodonts described by Sollas & Sollas (1914) and Olson (1944). There is no sign of an endolymphatic duct, and only one ampulla, that of the posterior vertical semicircular canal, can be made out. The sacculus ends distally in the fenestra ovalis. The perilymphatic duct would seem to have entered directly into the jugular canal at the level of the sacculo-utricular junction.

The Stapes

In most anomodonts the prominent postero-ventral tubers, which form the bony casing for the fenestra ovalis, are described as being formed by the basioccipitals, but this could not be confirmed in *Pristerodon* because of the lack of well-defined sutures in this area. Between the tuber, proximally and the quadrate, distally the stapes lies at right angles to the cranial axis with a slight ventral inclination laterally. Viewed from the ventral side it is broad and dumbbell-shaped; in posterior view it is flat and L-shaped with the footplate forming the dorsal expansion (see figs. 8_{C-G}). The diameter of the footplate is greater than that of the fenestra ovalis with the result that it overlaps it considerably, especially ventrally. The plate presses against the rim of the tuber but is nowhere fused to it. Halfway along the length of the stapes the shank exhibits a slightly raised dorsal edge which might have been the point of attachment of a ligament. There is no stapedia foramen.

The anterior one-fifth of the quadrate facet of the stapes is free from the quadrate but the rest of the bone is suturally attached to the quadrate. This facet is compressed dorso-ventrally to give it a slightly raised, semicircular out-

line. The postero-lateral part of the facet is extended backward as a process and lies against the downwardly directed paroccipital process. The extent of the fusion of the distal end of the stapes and the quadrate rules out lateral movement of the stapes without concomitant movement of the quadrate. This is a point worth considering for, as will be seen later, the quadrate lies free in the groove between the quadratojugal and paroccipital process except for its attachment to the stapes and a short sutural attachment to the base of the quadratojugal.

The presence or absence of a tympanum in Anomodonts is still a subject of controversy with Camp and Welles (1956), Cox (1959) and Ewer (1961) disclaiming Watson's (1953) view that the Anomodonts did not possess a tympanum. The arguments in favour of a tympanum largely hinge around facets and processes on the stapes and grooves on the quadrate which, according to these authors, could indicate the presence in life of an extrastapedial process and, therefore, also a tympanum.

Camp and Welles (1956) believe that a cartilaginous extrastapes was present in the Anomodont *Placerias* and that it extended from the ventro-lateral extremity of the stapes along a groove sometimes found at the back of the quadrate. Suffice it to say here that *Pristerodon* shows no such groove.

In support of his view that *Kingoria* possessed an extrastapes, a tympanum and an external auditory meatus, Cox (1959) points to the presence of a small facet on the postero-lateral corner of the stapes as possibly marking the point of attachment of an extra-stapedial cartilage, and a backwardly directed process on the opisthotic (his 'tympanic process') which according to him could have served as dorsal attachment for the tympanum.

Cox's argument that the opisthotic process (which also occurs in *Pristerodon* and has been described earlier in this paper) was associated with a tympanum and not with muscle attachments must be rejected on the ground that a process similar to it occurs in *Phrynosops* and several other recent turtles, where it is surrounded by neck muscles and where its sides are utilized for the attachment of these muscles. The significance of the postero-laterally directed facet on the distal end of the stapes, which he suggests might be for the base of a cartilaginous extrastapes can be discussed in conjunction with Ewer's (1961) claim.

Ewer found a small shaft-like bone lying loose against the right ramus of the lower jaw of *Daptocephalus* of which she states: 'At one end it expands to form a little facet slightly inclined to the axis of the shaft. If this facet is placed against the facet on the distal end of the stapes a good fit is obtained and I believe the little bone to be an ossified extrastapes. If this is correct then its only possible function is to connect the stapes with the tympanum' (p. 391).

Personal examination of Ewer's material provides conclusive evidence that the shaft-like bone she identified as the extrastapes is, in fact, the posterior part of the shorter of the two hyoid bones she found in the same skull. The shaft-like bone and the hyoid fit perfectly and even the colour variations which occur within the core of the two broken ends match perfectly. When the two bones are joined in this way they form a structure which, if placed in the position sug-

gested by Ewer, would extend well past the lateral limits of the quadrate. This feature and the fact that the joined structure is a mirror image of the longer bone which she identified as a hyoid bone, and with which I am in agreement, disclaim her suggestion that the small shaft-like bone represents an extrastapes. If the hyoid bone is fitted to the facet on the stapedia process it shows that it curved backward and downward, resembling to some degree the curvature of the ceratohyal in *Sphenodon*. The claim that the shaft-like bone represents part of a hyoid cornu is strengthened by the discovery that in two species of *Lystrosaurus* the ends of the hyoid bones (identified as the ceratohyals) are fused to the postero-ventro-lateral border of the stapes (Barry, 1967). In an *Oudenodon* investigated by Mr. M. A. Cluver of the South African Museum the posterior process is developed as a medio-laterally compressed process which shows indications of a shallow facet. However in *Pristerodon* and most of the smaller dicynodonts investigated, the facet is only weakly developed. It is clear, therefore, that the different degrees of development of the posterior process on the stapes in Anomodonts are associated, not with an extrastapedial process, but must be credited to a variable association with the hyoid apparatus.

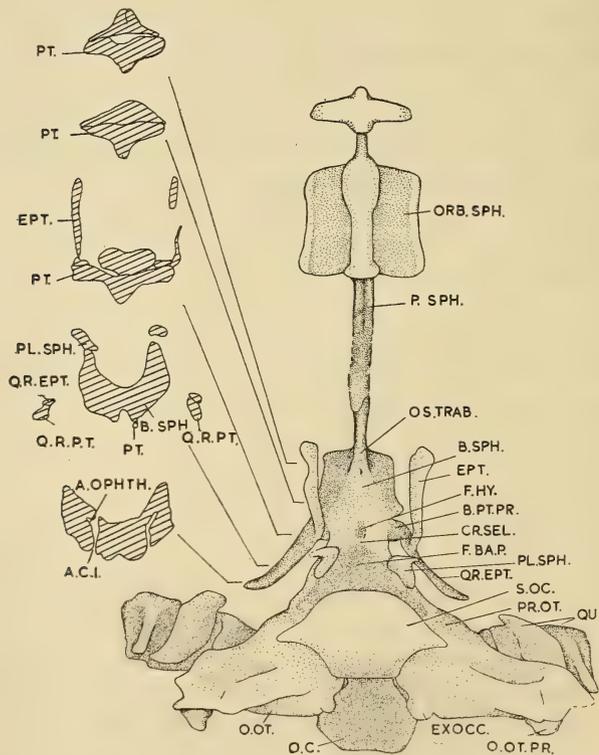


Fig. 9. *Pristerodon buffaloensis*. Reconstruction of dorsal view of neurocranium of sectioned specimen with insets of transverse sections through the areas indicated. Abbreviations on p. 160.

The tubera also form a bony casing for part of the cochlear recess of the internal ear. Two converging ridges extend anteriorly from the tubera to form a deeply excavated area between them. In the type specimen the art.^e carotis internae pierce the skull at the confluence of these ridges (pl. XB) but in the sectioned specimen they pierce the ridges much further back. Within the bone each artery gives off a branch possibly representing the art. ophthalmica (fig. 9).

Immediately in front of the confluence, the floor of the brain case widens to form a flat, roughly rectangular structure (figs. 9, 10). Near its posterior border the sides of this rectangle are notched, thereby separating it from the two posterior processes. It is suggested that the rectangular base represents the lateral wings of the parasphenoid and the two processes, the pterygoid processes. The identification of the latter are based on the fact that the antero-ventral borders of the epipterygoids are in sutural contact with the processes.

On top of the parasphenoid wings there is a dorsally rounded to flattened triangular raised area which, it is suggested, represents the ossified trabeculae. The apex of the triangle, which points anteriorly, represents the trabeculae communis, the posteriorly widening area of the triangle representing the diverging trabeculae cranii (fig. 9). Between the separated trabeculae there is a shallow depression which probably represents the hypophysial plate. The depression is terminated posteriorly by a rounded transverse ridge which probably represents the ossified dorsum sellae. Behind the latter the base is again depressed. This area probably represents the filled in fenestra basicranialis posterior. A median basicranial fontanella is found further back.

Anterior to the parasphenoid wings, the parabasisphenoid complex is continued as a narrow, relatively high, rostrum which gradually curves upwards towards the interorbital septum where it becomes shallower and straightens out horizontally. It is probable that the trabecula communis extends anteriorly beyond the apex of the triangle and forms at least the dorsal part of this rostrum. There are questionable indications of a suture dividing the rostrum horizontally along its length and the shape of the posterior part of the rostrum lends support to the conclusion that it consists of two fused elements; the rostrum parasphenoidale ventrally and either a rostrum basisphenoidale or a rostrum praesphenoidale dorsally (see fig. 5). The latter depends upon whether the ossification in the trabecula communis represents an extension anteriorly into the trabeculae of the ossification of the basisphenoid or whether it is a separate ossification in the trabecula communis.

Among recent reptiles, lizards display a rostrum parasphenoidale while *Chelone* has a rostrum basisphenoidale (Fuchs, 1910; Nick, 1912: quoted Versluijs 1936). In crocodiles the basisphenoid ossification extends forward into the trabecula communis to just behind the optic chiasma (Bellairs, 1949).

At the point where the upwardly curved rostrum straightens horizontally, there is a short break in the bone and it is assumed that participation of the

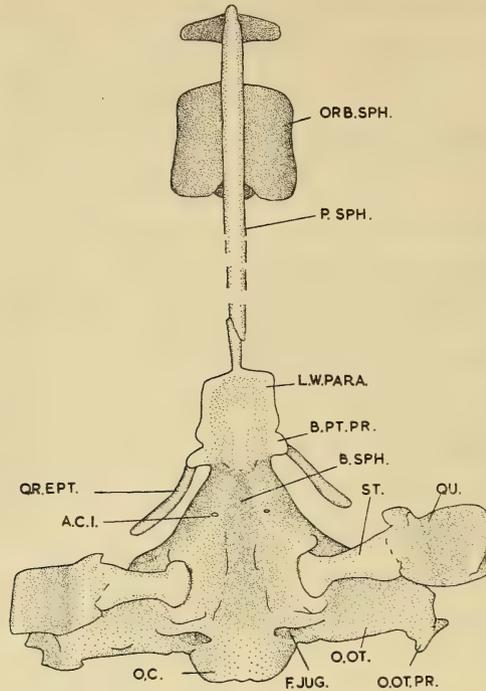


Fig. 10. *Pristerodon buffaloensis*. Reconstruction of ventral view of neurocranium of sectioned specimen. Abbreviations on p. 160.

presphenoid in the formation of the rostrum must have ended in this region, as the structure of the rostrum anterior to the break is distinctly different. It is reduced to about half its previous height and a longitudinal dorsal groove now runs along its length (fig. 5). This section of the rostrum is probably of parasphenoid origin, an extension anteriorly of the ventral portion of the parasphenoid-presphenoid rostrum. The front half of the rostrum lies in a shallow groove in the dorsal edge of the vomer. Anterior to the front end of the rostrum the dorsal groove is continued forward in the vomer and premaxilla. As this portion of the groove and that in the rostrum parasphenoidale behind it lie in a straight line and on a horizontal plane, it would seem to indicate a sliding action which was either used by the living animal or merely represents the retention of an ancestrally functional apparatus. Contact between the rostraparasphenoid and vomer is such that movement between these bones would not be possible—a point of importance in the evaluation of kinesis in *Pristerodon*.

The anterior part of the neurocranium is of especial interest in anomodonts as the '... principal problems of evolution of the sphenethmoid complex are to be found in the transition from therapsids to mammals'. (Olson, 1944: 77.) Unfortunately the derivation of the structures forming the bony complex in

anomodonts has not been fully agreed upon with the result that a terminology has arisen which instead of clarifying the position, has complicated it. Seeley (1898) considered the entire complex to be the orbitosphenoid; Sollas & Sollas (1914, 1916) called it the mesethmoid; Broom (1926) stated that it was the presphenoid; Olson (1944) subdivided the complex into a dorsal orbitosphenoid with a possible mesethmoid component, and a ventral presphenoid, while Camp (1956) used the term septosphenoid and frontosphenoids where separate lateral wings occur.

In *Pristerodon* the complex consists of a median bony interorbital plate roughly rectangular in shape and extending from the anterior rim of the orbit to the postorbital bar; paired, trough-shaped projections from the dorsal ridge of this plate and paired rod-shaped projections on the antero-ventral borders of the pro-otics. A study of the sections shows a break in the interorbital plate which runs from antero-dorsal to postero-postero-ventral. The two triangular bones thus formed may well represent anterior and posterior ossifications within the cartilaginous septum of the living animal.

As the posterior ossification includes the dorso-lateral expansions of the interorbital septum, representing the planum suprasedale of recent reptiles, and the planum and most of the interorbital septum in gnathostomes develop from the orbital cartilages (De Beer, 1926; Shaner, 1926), it is reasonable to assume that the posterior triangle represents an orbitosphenoid. In *Lacertilia* the orbitosphenoid is normally limited to the pila metoptica but in *Iguana* Bellairs (1949b) and *Monopeltis* (Malan, 1946) the orbitosphenoid ossification extends into the planum suprasedale and the dorsal part of the interorbital septum. In *Monopeltis* it invades even the posterodorsal part of the nasal septum.

The anterior ossification is definitely a separate ossification but it is difficult to ascertain to what extent the trabeculae contributed to its formation. If the ventral rim of the anterior ossification is divided into quarters it will be seen that the anterior quarter shows no thickening of the rim, the second quarter shows a concave ventral rim, while the third and fourth quarters display a ridge which becomes progressively thicker and even round in cross-section. There would, therefore, seem to be some justification for the assumption that the trabeculae are incorporated into the posterior half of the ventral periphery but that it remained cartilaginous farther forward and fitted into the concave ventral groove mentioned earlier. The gap between the interorbital plate and the rostrum parasphenoidale below it, is probably due to a displacement dorsally of the former. In the older literature any ossification in the interorbital septum of lizards was called a presphenoid (Huxley, 1863; Parker, 1880, etc.) but as Camp (1942) and Bellairs (1949a) have pointed out this is undesirable since the term has been more generally used for the trabecular ossification which develops in contact with the basisphenoid. The term septosphenoid, suggested by Camp (1942) would, therefore, be more suitable. The anterior portion of the septosphenoid reaches the roof of the orbit where it expands laterally to form two narrow, slightly convex, wings (figs. 5, 9, 10).

These projections probably covered the olfactory lobes from above and could conceivably represent the commissurae sphenethmoidalis of recent reptiles. Slightly farther back the wings of the orbitosphenoid project outward and upward from the dorsal rim of the septum. They occupy the position of the planum suprasetale of recent reptiles and should probably be regarded as such. The continuation of the parasphenoidal groove beyond the anterior limit of the septosphenoid indicates that the interorbital septum was probably extended farther forward in cartilage. It would also seem probable that the nasal cavity had some form of median division, as the floor of the premaxillary in this region displays a remarkably well-developed dorsally directed longitudinal ridge, which occupies a position in line with the parasphenoid rostrum behind it (figs. 6B, C, D & E). The grooved dorsal aspect of this ridge, shown in many sections, and the low, longitudinal ridges high up on the inner surface of the nasal cavity, described earlier as possibly representing dorso-lateral projections of a median nasal septum would seem to strengthen this view.

The pleurosphenoid forms the hindmost element of the side wall. It is an antero-dorsally directed, rod-shaped process, internally attached to the basisphenoid (figs. 5, 8, 9 & 12A).

THE VISCERAL ARCH SKELETON

The Palatoquadrate

The palatoquadrate of *Pristerodon* is represented by two separated bones, the epipterygoid and the quadrate. Viewed laterally the epipterygoid is L-shaped with both the vertical limb and the posteriorly directed horizontal limb well developed. The vertical limb is relatively thin and extends upwards and slightly forwards towards a ventrally directed lamina extending from the ventral surface of the parietal.

The epipterygoid is widest near the angle of the bone and here it is connected to the basisphenoid by a short basiptyergoid process (figs. 11, 12A & B). The entire base is applied to the dorsal and/or dorso-lateral surface of the quadrate ramus of the pterygoid which is directed towards the inner surface of the quadrate.

The quadrate lies in a deep concave groove between the squamosal and the paroccipital. Except for short sutural attachments to the base of the quadratojugal postero-laterally and the distal head of the stapes medially, the quadrate lies free in the groove. In life it probably had a cartilaginous head.

In cross-section the quadrate is shaped like an inverted Y, the two ventrally directed limbs representing the medial and lateral condyles. These are separated by a deep groove, which is also utilized as an articular surface. The condyles, which extend the entire length of the ventral face of the quadrates, show that only very limited sideways movement of the lower jaw is possible, a feature also borne out by the close fit of the lower jaw between the upper jaw canines when the jaws are closed. In *Pristerodon*, as in all known Anomodonts,

the lower jaw slides forwards and backwards during mastication. During maximum gape the posterior portion of the articular surface of the articular is involved, but with the close of the mouth and backward traction by the jaw-closing muscles, the jaw slides backwards so that the anterior portion of the articular surface is involved when the jaw is closed. This action allows the animal to chop the food. It is interesting to note that in *Endothiodon*, a genus characterized by the loss of canine teeth, Watson (1948) found '... the very remarkable condition of a convex articular surface of the quadrate articulating with a convex surface of the articular' (p. 848). Watson maintains that this arrangement permits very free movements as the lower jaw cannot only move forwards and backwards but it is even probable that the jaw can be slewed round on the palate.

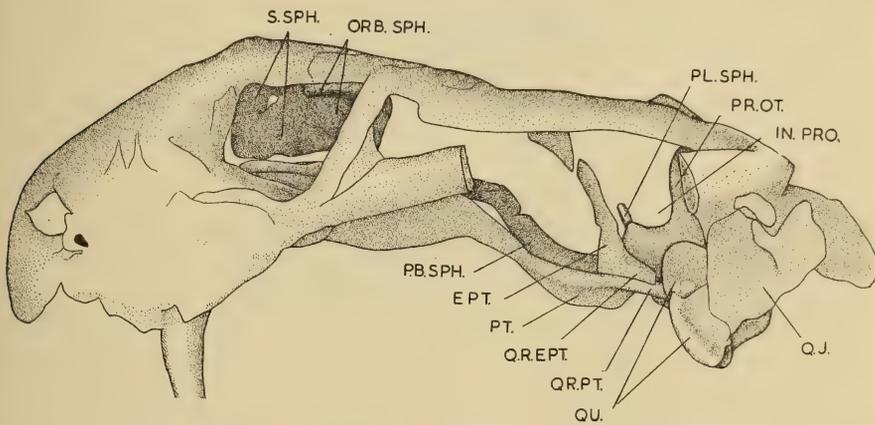


Fig. 11. *Pristerodon buffaloensis*. Reconstruction of lateral view of skull with squamosal cut away to show palatoquadrate complex. Abbreviations on p. 160.

The inner condyle bears a short medially projecting ridge, the stapelial process of the quadrate, to which the distal portion of the stapes is suturally attached. Dorso-medially to this ridge there is a shallow longitudinal groove in the vertical face of the quadrate, extending from the anterior border backwards for approximately one-third of the length of the vertical plate (fig. 12B). Throughout its length this groove is seen to follow remarkably closely a course dorso-laterally and parallel to that of the posterior portion of the quadrate ramus of the pterygoid, the latter bone terminating close to, but free from the inner surface of the quadrate (fig. 12C-E). As the groove follows what could have been the course of a posterior extension of the base of the epipterygoid, it would seem reasonable to assume that the groove contained a rod-like cartilaginous structure connecting the quadrate with the epipterygoid. In the left quadrate a distinct rounded bulge terminates the groove.

As thus reconstructed the palatoquadrate complex of *Pristerodon*, not only shows a remarkable resemblance to the palatoquadrate complex of a 15.2 mm

developmental stage of the Egyptian lizard *Tropicolotes tripolitanus*, described by Kamal (1960), but the possible occurrence of a solid link between the quadrate and epipterygoid in what is most definitely an adult *Pristerodon*, recalls conditions found in the developmental stages of most recent reptiles and also in the adult *Sphenodon*. The relationship of the base of the complex and the quadrate ramus of the pterygoid in *Pristerodon* and *Sphenodon* fully support these conclusions as the base of the palatoquadrate cartilage always seems to occupy a position on the dorsal and dorso-lateral surface of the quadrate ramus of the pterygoid. The retention of a palatoquadrate complex displaying a link between the epipterygoid and quadrate portions of the complex must then, according to the foregoing remarks, reflect a primary condition. This view is contrary to that expressed by Olson (1944).

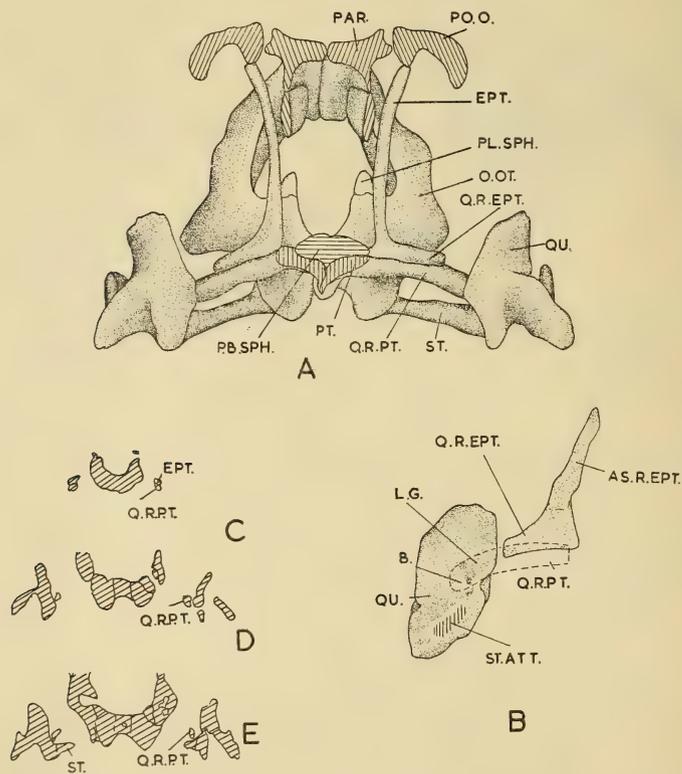


Fig. 12. *Pristerodon buffaloensis*. A: reconstruction of anterior view of palatoquadrate complex; B: reconstruction of medial view of left palatoquadrate complex; C-E: transverse sections through palatoquadrate complex. Abbreviations on p. 160.

In his discussion of the principal changes undergone by the epipterygoid from the primitive reptilian condition to that of mammals, Olson states: 'In primitive reptiles the bone is composed of a restricted basal portion and a

slender ascending ramus, the columella cranii. In somewhat more advanced forms, the basal portion is expanded into a posterior quadrate ramus and an anterior pterygoid process. At this stage the ascending ramus remains a thin rod. In the advanced mammal-like reptiles the ascending ramus is much expanded and has attained intimate association with the periotic behind and the parietal above. The quadrate and pterygoid processes are somewhat elongated' (p. 110).

Phylogenetic and ontogenetic evidence do not lend support to the view that the epipterygoid in the primitive forms possessed a restricted base and the adult forms of recent reptiles bear this out.

As has been shown previously (Barry, 1965) conditions found in recent and fossil forms indicate that the palatoquadrate undergoes divergence in the development of its component parts after the early crossopterygian stage. Those groups leading to or showing affinities with recent reptiles show progressive reduction of that part of the palatoquadrate anterior to the quadrate, while groups with mammalian affinities show reduction of the quadrate. In recent reptiles the quadrate has remained as a fairly strong element but anterior to it only a thin rod-like epipterygoid is left of this part of the palatoquadrate. This is the position in adult forms of many lizards. In others such as *Agama*, *Lyriocephalus* and *Calotes* (Ramiswami, 1966). *Ophioceps* and *Anniella* (Jollie, 1960) further reduction of the epipterygoid has taken place resulting in an epipterygoid which is very short. The epipterygoid is still present but very small in *Chelonia* (Parker, 1880) while it is much reduced or vestigial in *Ophidia* and *Crocodylia*. In *Chamaeleontidae*, *Dibamidae* (Boulenger, 1887) and most *Amphisbaenidae* (known only in *Trogonophis*, Bellairs, 1950) reduction has been taken further and the epipterygoid has disappeared.

In groups showing mammalian affinities the vertical limb and the base were retained and the former probably expanded while the quadrate has been much reduced and is generally believed to have developed into the incus of the middle ear.

Although the therapsids, as a group, show a marked degree of variability in the structure of the epipterygoid we find that those species which show mammalian affinities invariably show that certain basic features of the complex, represented already in the early gnathostomes and tetrapods, have been retained, with but slight changes, right through to the mammal stage. The most noticeable of these features is the retention of an extensive base to the epipterygoid.

Meckel's Cartilage

In recent reptiles the articular is the only ossification in Meckel's cartilage. Gaupp (1906) mentions that he found a calcification in the anterior end of Meckel's cartilage in an adult *Lacerta vivipara* and that because of this it could not be excluded 'dasz auch bei Sauriern das vorderste Ende des M. Knorpels verknöchern kann' (p. 775). The articular is, however, also the only ossification

in Meckel's cartilage in *Pristerodon*. It displays an articular area which covers more than half of its dorsal length and shows three distinct articular surfaces; a high central articular ridge flanked on each side by a more ventrally situated articular groove (fig. 13A). The medial groove is deeper and shorter than the lateral groove and is situated in a dorso-medially directed flange extending from the centre of the medial surface of the posterior portion of the articular. This flange flares out anteriorly, simultaneously becoming thinner to form a concave plate-like bone. The lateral groove lies in a well-developed lateral projection of the dorsal portion of the articular. This projection extends virtually the entire length of the articular. Anteriorly it is fused to the lateral surface of the surangular, just below the dorsal ridge of the latter. The medial and lateral quadrate condyles fit into these grooves while the articular ridge fits into a corresponding but shorter groove in the quadrate. Among recent reptiles conditions approximating these are only found in the Chelonia.

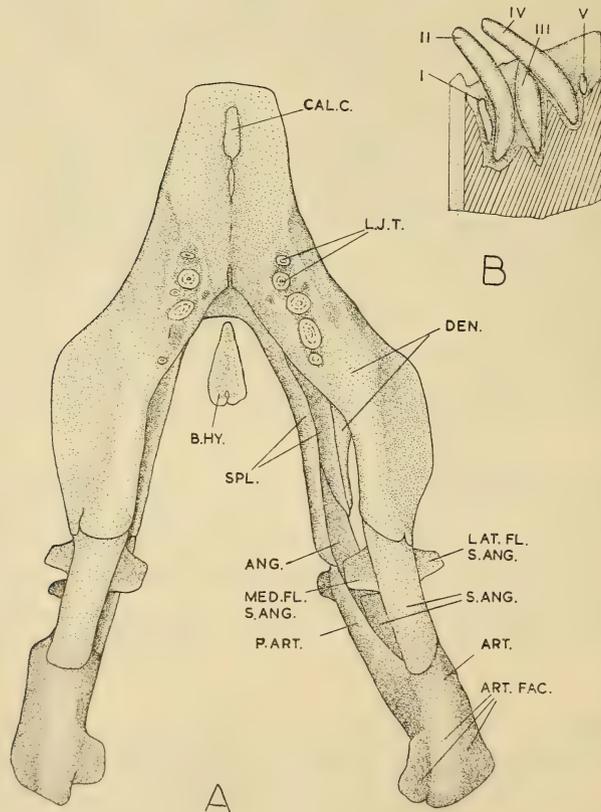


Fig. 13. *Pristerodon buffaloensis*. Sectioned specimen. A: reconstruction of dorsal view of lower jaw with protruding teeth cut off; B: reconstruction of section through right half of lower jaw to show teeth. Abbreviations on p. 160.

The ventral portion of the articular is continued forward as a blunt process covered laterally and ventrally by the angular and medially by the prearticular (fig. 14A). The blunt front end is directed into the meckelian groove. For virtually its entire length Meckel's cartilage lay in a U-shaped groove formed by the prearticular, angular, splenial and dentary (fig. 14B). At the symphysis of the dentaries the groove is continued forward as a canal which pierces the dentary for a short distance before turning medially to meet its mate of the other side. In all recent reptiles investigated Meckel's cartilage lie ventral and ventromedial to the dentary and never pierces it.

There is only a short retroarticular process in *Pristerodon* which is formed as a posterior extension of the central stem of the articular and not, as in *Kingoria*, by the lateral condyle (Cox, 1959). It is not curved ventrally to the same extent as in *Kannemeyeria*, *Stahleckeria* (Camp & Welles, 1956), *Kingoria* (Cox, 1959) or *Emydochampsia* (Broili & Schreuder, 1936, after Jannensch). In *Stahleckeria* and *Emydochampsia* the process actually points downwards and forwards.

Jannensch (1952) states that a horizontally directed retroarticular process is never developed in the anomodonts and that the ventrally directed process found in this group is not morphologically identical with a true retroarticular process. He states, furthermore, that the two processes do not have the same function for, whereas the horizontally directed retroarticular serves for the insertion of the M. depressor mandibulae, the anomodont process could not have had this function, '... da von ihm aus eine einigermaßen geradlinige, für Hinterhauptfläche, an der Gelenkkapsel des Kiefergelenks vorbei nicht möglich war' (p. 238).

In reptiles the retroarticular process is absent or only weakly developed in certain Cotylosauria (*Labidosaurus* Versluijs, 1936) some Chelonia (*Emydura*, *Chalydra*, Versluijs, 1936) some Chamaeleontidae (*Peltosaurus*, *Ophioseps* McDowell & Bogert, 1954) and *Amphisbaena* (Versluijs, 1936; Jollie, 1962) but in the majority it is a strong, horizontally developed process serving mainly for the insertion of the M. depressor mandibulae, the main jaw opener in reptiles. The development, or reduction, of the retroarticular process could, therefore, have an effect not only on the insertion of the muscle but possibly also on its development and relationship to neighbouring structures.

In *Pristerodon* structural conditions in the jaws and occiput strongly suggest that the feeding mechanism of this animal resembled that of some recent chelonians. As function plays an important role in muscle arrangement and expression, it would seem logical, therefore, to compare the muscle impressions in the *Pristerodon* skull with the muscular arrangements in those Chelonia which show similarities in the structure of the jaws and occiput. In the latter the M. depressor mandibulae arises from the occipital region of the skull and passes downward to insert on the retroarticular process. The fact that the M. depressor mandibulae is present and functions effectively whether the retroarticular process is large, small or stunted, leaves little doubt that *Pristero-*

don possessed a well-developed and functional depressor mandibulae in spite of the weak development of its retroarticular process (see fig. 14A & B). It is also significant that in spite of the strong development of the M. depressor mandibulae in *Phrynops* and some other Chelonians, the retroarticular process is hardly developed at all. This would seem to weaken Jannensch's (1952) theory.

Hyobranchial Skeleton

In the sectioned skull an independent bone was found lying in the angle of the jaw. Viewed from dorsally the bone is roughly triangular, the apex pointing towards the symphysis of the lower jaw (fig. 13A). There is a shallow medial groove on the dorsal surface which widens posteriorly and then splits when two short rod-like extensions develop.

It is probable that the median element represents the basihyal. If this is so the two short posterior extensions could represent processes for the attachment of cartilaginous ceratobranchials II and the apex, the processus lingualis. In *Sphenodon* ceratobranchials II are fused to the cartilaginous processus lingualis while perichondral ossification can apparently occur in the processus lingualis (De Beer, 1937).

The only known records of ossified parts of the hyoid skeleton in Anomodonts are *Ondenodon*, in which Owen (1859) found a 'uro-hyal', a 'basibranchial' and two 'hypobranchials'; in *Kingoria* where Cox (1959) found a pair of slender rods lying between the rami of the lower jaw and which he believes to be preserved portions of the hyoid skeleton; in *Daptocephalus* in which Ewer (1961) found two branchial horns and a median plate; and in three specimens of *Lystrosaurus* in which the author (Barry, 1967) found ossified ceratohyals.

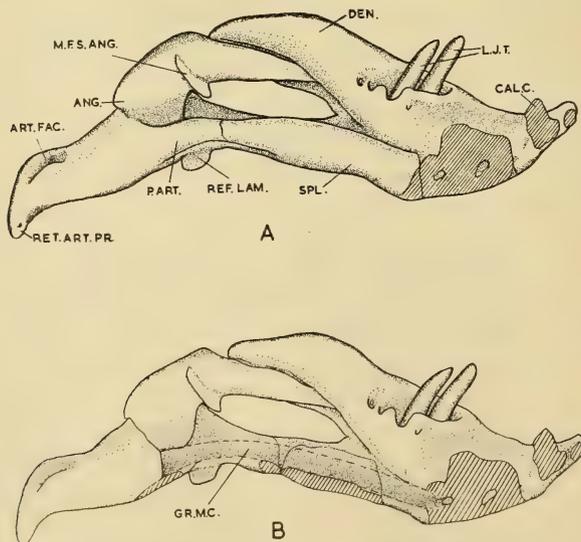


Fig. 14. *Pristerodon buffaloensis*. A: reconstruction of medial view of left half of lower jaw; B: same with bones cut away to show groove for Meckel's cartilage. Abbreviations on p. 160.

DERMAL BONES OF THE LOWER JAW

The lower jaw consists of one cartilage bone, the articular, and five dermal bones, the dentary, angular, surangular, splenial and prearticular. The prearticular, which is indistinguishably fused with the articular, and the splenial form the inner surface of the jaw, while the others are primarily associated with the outer surface (see fig. 14A).

The dentary forms more than half of the lower jaw. The mandibular teeth are arranged in a groove in the dentary which shows indentations corresponding to the roots of the teeth. Viewed superficially the sectioned specimen shows two functional teeth and two empty sockets in each mandibular tooth row (see fig. 13A). In addition two teeth are not in line with the others, but occupy separate sockets medial and lateral to the tooth row in the area of the second and third tooth. In the right half of the jaw both these teeth are missing; in the left half the small lateral tooth is in position. However, as will be seen in figure 13B representing a longitudinal section through the tooth row of the right half, there are unreputed teeth in the groove.

The first tooth is thin and relatively long and in time would have probably replaced the tooth behind it. The latter, which is the first functional tooth but second in the row, is extremely large for the lower jaw. In fact, both functional teeth in the lower jaw are more like lower jaw tusks, being nearly half the size of upper jaw tusks (fig. 3). The third tooth in the right half of the lower jaw is again an unerupted replacement tooth and pushes against the second functional tooth (no. 4 in the row) behind. The fifth tooth in the row is appreciably smaller than any of the preceding ones and it is difficult, therefore, to say whether it will develop into a tusk-sized tooth or whether it will be smaller as is often found in anomodont tooth rows. The medial and lateral teeth behind tooth no. 2 must of necessity remain small and insignificant as there is no room for development. In the left half of the jaw the socket for tooth no. 4 is empty and tooth no. 3 has attained the size of no. 2 in that row and has become functional. There is no tooth bud in the empty socket of no. 4 and we do not, therefore, know if the teeth were replaced more than once.

In the type skull, of which only the left lower jaw was available for study, it was not possible to see the small lateral and medial teeth but the tooth row, apart from showing two additional teeth well back in the row, resembles that of the sectioned specimen. Here, nos. 2 and 4 are long and stout, while nos. 1, 3 and 5 are still developing. Behind tooth no. 5, which is appreciably longer than nos. 1 and 3, there is an empty socket where tooth no. 6 has probably been replaced. Behind position 6 there are three further tooth buds in the row lying in an upward sweep of the jaw. These teeth point forward at an angle of approximately 45° to the horizontal instead of upwards. These teeth probably move forward and rotate upward during life otherwise they would be of little use to the animal. Judging by the size and positioning of the replacement teeth in *Pristerodon* it is almost certain that the teeth were replaced alternately, nos. 1, 3 and 5 replacing 2, 4 and 6.

It is generally accepted that Anomodonts possessed a horny beak. From a functional point of view it would seem reasonable, therefore, to assume that functional teeth would be a limiting factor in the extent to which the boney beak is allowed to overgrow the jaws. If this is the case the horny beak of the upper jaw could not have progressed beyond the canine tusk as the latter as well as the four post-canine teeth situated postero-medially to it would have been the limiting factors. The same considerations would limit the horny beak of the lower jaw to the area anterior to the tooth row. There is a possibility that horn could have progressed farther backwards laterally to the tooth row and on to a shallow longitudinal groove situated here, but this is uncertain.

The longitudinal groove is terminated laterally to the 4th tooth when the dentary arches upward in the form of a crest (see fig. 3). Lateral to this crest the dentary is expanded into a flat-topped ledge probably associated with the insertion of the *M. adductor mandibulae externus* (possibly the *M. add. mand. ext. superficialis*). Contraction of this muscle would probably result in retraction of the jaw as the muscle most likely originated on the postero-dorsal flange of the squamosal.

Posteriorly the dentary is bifurcate. The dorsal process overlaps and covers the dorsal and lateral surfaces of most of the anterior half of the surangular while the ventral process overlaps the anterior portion of the angular laterally. The dorsal and ventral arms of the dentary and the angular and the surangular form between them the borders of a relatively large fossa in the lower jaw. This fossa seems to be confined to the anomodonts within the Therapsida but even in this group its development is varied. In *Pristerodon* (see figs. 3, 14A & B) as in *Synostocephalus* (Watson, 1948) the fossa is extremely long, being approximately one-quarter of the length of the lower jaw, while in *Lystrosaurus* it is much smaller. This suggests that soft tissue filling the cavity restricted the dorso-ventral expansion of the dentary flanges but allowed them to continue posteriorly above and below it. If this is the case, it would seem probable that the structure has its origin on the inside of the lower jaw and expanded outwards to a varying degree, depending on its size.

Viewed laterally, the surangular is seen to follow the dorsal arm of the dentary, dipping ventrally towards its end. However, when viewed medially, it is seen that the bone also has a long anterior projection lying in a notch on the medial surface of the dorsal arm of the dentary, while a wide, flat flange lying against and on the inside of the dorsal projection of the angular projects ventrally from the dorsal ridge. Immediately posterior to the dentary the dorsal ridge of the surangular displays two flat ledges, one projecting from the medial (figs. 13A, 14A & B) and the other from the lateral side of the bone (figs. 3, 13A). Both ledges are directed postero-dorsally, the ledge on the inside of the surangular being longer and extending upwards nearly to the top of the surangular. The ledges seem either to have protected some underlying structure in the posterior portion of the mandibular fossa or to have separated it from overlying structures, or both.

The angular which forms a continuation of the ventral arm of the dentary is trough-shaped forming the medial and lateral wall of the groove which housed Meckel's cartilage. The reflected lamina of the angular is funnel-shaped with the opening facing posteriorly (fig. 3).

ACKNOWLEDGEMENTS

I wish to record my indebtedness to the South African Council for Scientific and Industrial Research for the allocation of research and capital grants to conduct this investigation. My thanks are also due to Dr. A. S. Brink of the Bernard Price Institute for Palaeontological Research, Johannesburg, for permission to section the specimen used in this investigation, and for the loan of the type and other specimens. To Dr. M. E. Malan of the Zoology Department of the University of Stellenbosch my thanks for her critical reading of the manuscript of this paper.

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

REFERENCES

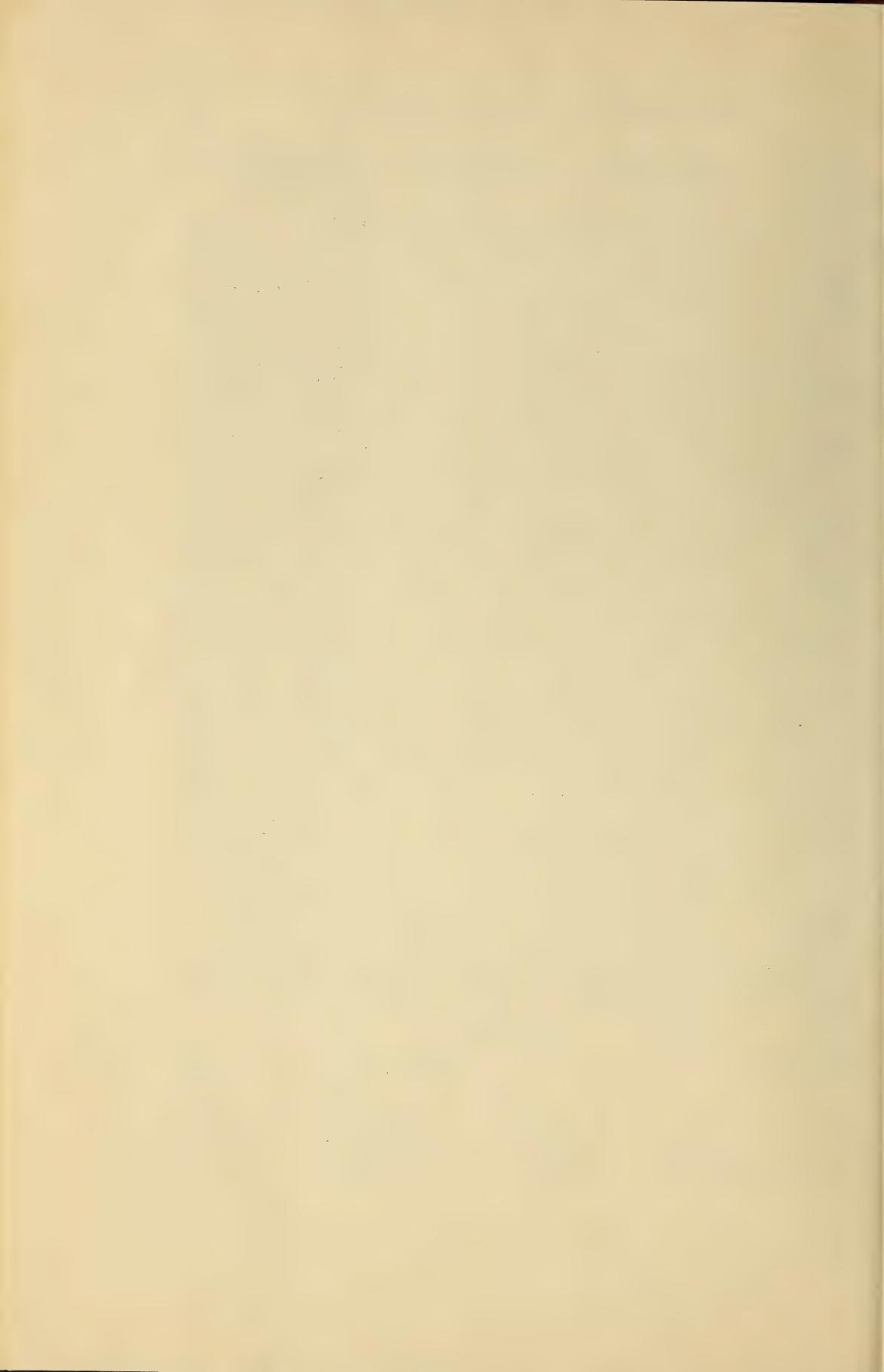
- BARRY, T. H. 1965. On the epipterygoid-alisphenoid transition in Therapsida. *Ann. S. Afr. Mus.* **48**: 399-426.
- BARRY, T. H. 1967. Sound conduction in the fossil anomodont *Lystrosaurus*. *Ann. S. Afr. Mus.* (In press.)
- BELLAIRS, A. D'A. 1949a. Orbital cartilages in snakes. *Nature, Lond.* **163**: 106-107.
- BELLAIRS, A. D'A. 1949b. Observations on the snout of *Varanus* and a comparison with that of other lizards and snakes. *J. Anat. Lond.* **83**: 116-146.
- BELLAIRS, A. D'A. 1950. Observations on the cranial anatomy of *Anniella*, and a comparison with that of other burrowing lizards. *Proc. zool. Soc. Lond.* **119**: 887-904.
- BOULENGER, G. A. 1887. *Catalogue of the lizards in the British Museum (Natural History)*. 2nd ed. **3**. London: British Museum.
- BROILI, F. & SCHRÖDER, J. 1936. Beobachtungen an Wirbeltieren der Karrooformation. XVI. Beobachtungen am Schädel von *Emydochamps* Broom. *Sber. bayer. Akad. Wiss.* **1936**: 21-44.
- BROOM, R. 1926. On the mammalian presphenoid and mesethmoid bones. *Proc. zool. Soc. Lond.* **1926**: 257-264.
- CAMP, C. L. & WELLES, S. P. 1956. Triassic dicynodont reptiles. Part 1. The North American genus *Placerias*. *Mem. Univ. Calif.* **13**: 255-304.
- COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 321-367.
- DE BEER, G. R. 1926. Studies on the vertebrate head. Pt. II. The orbito-temporal region of the skull. *Q. Jl. microsc. Sci.* **70**: 263-370.
- DE BEER, G. R. 1937. *The development of the vertebrate skull*. London: Oxford University Press.
- FUCHS, H. 1910. Über das Pterygoid, Palatinum und Parasphenoid der Quadrupeden, insbesondere der Reptilien und Säugetiere, nebst einigen Betrachtungen über die Beziehungen zwischen Nerven und Skeletteilen. *Anat. Anz.* **36**: 33-95.
- FUCHS, H. 1911a. Bemerkungen über das Munddach der Amnioten, insbesondere der Schildkröten und Schlangen. *Anat. Anz. Jena* **38**: 609-637.
- FUCHS, H. 1911b. Über die Beziehungen zwischen den Theromorphen Cope's, bzw. den Therapsiden Broom's und den Säugetieren, erörtert auf Grund der Schädelverhältnisse (nebst einem weiteren Beitrag zur Frage der Homologie des Kiefergelenkes und der Morphologischen Bedeutung des Squamosums). *Z. Morph. Anthrop.* **14**: 367-438.
- FUCHS, H. 1911c. Über das Septomaxillare eines rezenten Säugethieres (*Dasybus*) nebst einigen vergleichend-anatomischen Bemerkungen . . . *Anat. Anz.* **38**: 33-55.

- GAUPP, E. 1906. Die Entwicklung des Kopfskelettes. In HERTWIG, W. A. O., ed. *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere*. 3: 573. Jena.
- HAUGHTON, S. H. & BRINK, A. S. 1954. A bibliographical list of Reptilia from the Karroo Beds of Africa. *Palaeont. afr.* 2: 1-187.
- HUXLEY, T. H. 1863. *Lectures on the elements of comparative anatomy*. London: Churchill.
- JANENSCH, W. 1952. Über den Unterkiefer der Therapsiden *Paläont. Z.* 26: 229-247.
- JOLLIE, M. T. 1960. The head skeleton of the lizard. *Acta. zool., Stockh.* 41: 1-64.
- KAMAL, A. M. 1960. The chondrocranium of *Tropicolotes tripolitanus*. *Acta zool. Stockh.* 41: 297-312.
- KRITZINGER, C. C. 1945. The cranial anatomy and kinesis of the South African amphibia *Monopeltis capensis* Smith. *S. Afr. J. Sci.* 42: 175-204.
- MALAN, M. E. 1946. Contributions to the comparative anatomy of the nasal capsule and the organ of Jacobson of the Lacertilia. *Univ. Stellenbosch Annale (A)* 24: 69-137.
- MCDOWALL, S. B. & BOGERT, C. M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguimorph lizard. *Bull. Am. Mus. nat. Hist.* 105: 1-142.
- NICK, L. 1912. Das Kopfskelet von *Dermochelys coriocea* L. *Zool. Jb.* 33: 1-238.
- OLSON, E. C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. *Spec. Pap. geol. Soc. Am.* 55: i-xi, 1-136.
- PARKER, W. K. 1880. Development of the green turtle (*Chelone viridis*, Schneider). *Rep. Voy. Challenger 1873-76 Zool.* 1 (5): 1-58.
- POINTER, R. 1931. *Nackermuskulatur des Reptilien*. Dis. Wien. (Quoted from Versluys, 1936.)
- RAMASWAMI, L. S. 1946. The chondrocranium of *Calotes versicolor* (Daud.) with a description of the osteocranium of a just hatched young. *Q. Jl. microsc. Sci.* 87: 237-297.
- ROMER, A. S. 1949. *The vertebrate body*. Philadelphia & London: Saunders Co.
- ROMER, A. S. & PRICE, L. W. 1940. Review of the Pelycosauris. *Spec. Pap. geol. Soc. Am.* 28: i-x, 1-538.
- SEELEY, H. G. 1898. On the skull of *Mochlorhinus platiceps* from Bethulie, Orange Free State, preserved in the Albany Museum, Grahamstown. *Ann. Mag. nat. Hist.* (7) 1: 164-176.
- SEELEY, H. G. 1898. On *Oudenodon (Aulacocephalus) pithecopis* from the Dicynodon beds of East London, Cape Colony. *Geol. mag.* (4) 5: 107-110.
- SHANER, R. F. 1926. The development of the skull of the turtle with remarks on fossil reptile skulls. *Anat. Rec.* 32: 343-367.
- SOLLAS, I. B. J. & SOLLAS, W. J. 1914. A study of the skull of *Dicynodon* by means of serial sections. *Phil. Trans. R. Soc. (B)* 204: 201-225.
- SOLLAS, I. B. J. & SOLLAS, W. J. 1916. On the structure of the dicynodont skull. *Phil. Trans. R. Soc. (B)* 207: 531-539.
- TOERIEN, M. J. 1950. The cranial morphology of the Californian lizard—*Anniella pulchra* Gray. *S. Afr. J. Sci.* 46: 321-342.
- TOERIEN, M. J. 1953. The evolution of the palate in South African Anomodontia and its classificatory significance. *Palaeont. afr.* 1: 49-177.
- VAN HOEPEN, E. C. R. 1913. Bijdragen tot kennis der reptielen van Karrooformatie. I. De schedel van *Lystrosaurus latirostris* Owen sp. *Ann. Transv. Mus.* 4: 1-46.
- VAN PLETZEN, R. 1946. The cranial morphology of *Cordylus* with special reference to the cranial kinesis. *Univ. Stellenbosch Annale (A)* 24: 41-68.
- VERSLUYS, J. 1936. Kraniaum und Visceralskelett der Sauropsiden. I. Reptilien. In BOLK, L. et al. *Handbuch der vergleichenden Anatomie der Wirbeltiere*. 4: 699-805. Berlin & Vienna.
- WATSON, D. M. S. 1948. *Dicynodon* and its allies. *Proc. zool. Soc. Lond.* 118: 823-877.
- WILLISTON, S. W. 1925. *The osteology of the reptiles*. Cambridge: Harvard University Press.

ABBREVIATIONS

A.C.I.	Arteria carotis interna.	A.V.S.C.	Antero-ventral semicircular canal.
ANG.	Angular.		
ART.	Articular.	B.	Bulge.
ART. FAC.	Arteria facialis.	B.HY.	Basihyal.
A. OPTH.	Arteria ophthalmica.	B. OC.	Basioccipital.
AS. R. EPT.	Ascending ramus of the epipterygoid.	B. PT. PR.	Basipterygoid process.
		B. SPH.	Basisphenoid.

C.	Canine tusk.	O. OT. PR.	Opisthotic process.
CAL. C.	Calcified cartilage.	ORB. SPH.	Orbitosphenoid.
C.C.	Crus commune.	OS. TRAB.	Ossified trabeculae.
CR. SEL.	Crista sellaris.		
DEN.	Dentary.	P. ART.	Prearticular.
		PAL.	Palatine.
EC. PT.	Ectopterygoid.	PAR.	Parietal.
E.N.	External naris.	PAR. OC. PR.	Paroccipital process of the opisthotic.
EPT.	Epipterygoid.		
Exocc.	Exoccipital.	P.B. SPH.	Parabasisphenoid.
		P. FOR.	Pineal foramen.
F.BA.P.	Fenestra basicranialis posterior.	PL. SPH.	Pleurospenoid.
		P. MX.	Premaxillary.
F. HY.	Fenestra hypophyseos.	PO. C.	Postcanines.
F. JUG.	Foramen jugulare.	PO. FR.	Postfrontal.
FL. FO.	Floccular fossa.	PO. O.	Postorbital.
F. OV.	Fenestra ovalis.	PR. FR.	Prefrontal.
F. PL.	Footplate of the stapes.	PR. OT.	Prootic.
		PR. PAR.	Preparietal.
G.R.M.C.	Groove for Meckel's cartilage.	P. SPH.	Parasphenoid.
		PT.	Pterygoid.
I.A.M.	Internal auditory meatus.	P.T.FO.	Posttemporal fossa.
IN. PRO.	Incisura prootica.	P.V.S.C.	Postero-ventral semicircular canal.
I. PAR.	Interparietal.		
I. PT. V.	Interpterygoidal vacuity.	Q.J.	Quadratojugal.
JUG.	Jugular.	Q.R. EPT.	Quadrate ramus of the epipterygoid.
LAC.	Lachrymal.	Q.R. PT.	Quadrate ramus of the pterygoid.
LAT. FL. ANG.	Lateral flange of the surangular.	QU.	Quadrate.
L.C.QU.	Lateral condyle of the quadrate.		
L.G.	Longitudinal groove on the quadrate.	REF. LAM.	Reflected lamina of the angular.
		RET. ART. PR.	Retro-articular process.
L.J.T.	Lower jaw teeth.	S. ANG.	Surangular.
L.W. PARA.	Lateral wing of the parasphenoid.	S.C. REC.	Sacculo-cochlear recess.
		SIN. UT.	Sinus utricularis.
M.C.QU.	Median condyle of the quadrate.	S. MX.	Septomaxillary.
		S. OC.	Supra-occipital.
M.F.S. ANG.	Medial flange of the surangular.	SPL.	Splénial.
		S.Q.	Squamosal.
MX.	Maxillary.	S. SPH.	Septosphenoid.
MX. ANT.	Maxillary antrum.	ST.	Stapes.
		ST. ATT.	Stapes attachment.
NAS.	Nasal.		
N. LAC. F.	Naso-lachrymal foramen.	TAB.	Tabular.
		TRAB.	Trabeculae.
O.C.	Occipital condyle.		
O. OT.	Opisthotic.	VO.	Vomer.

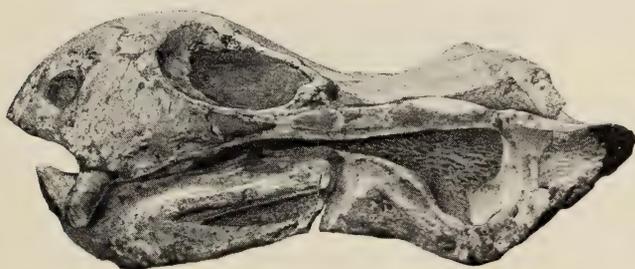




A

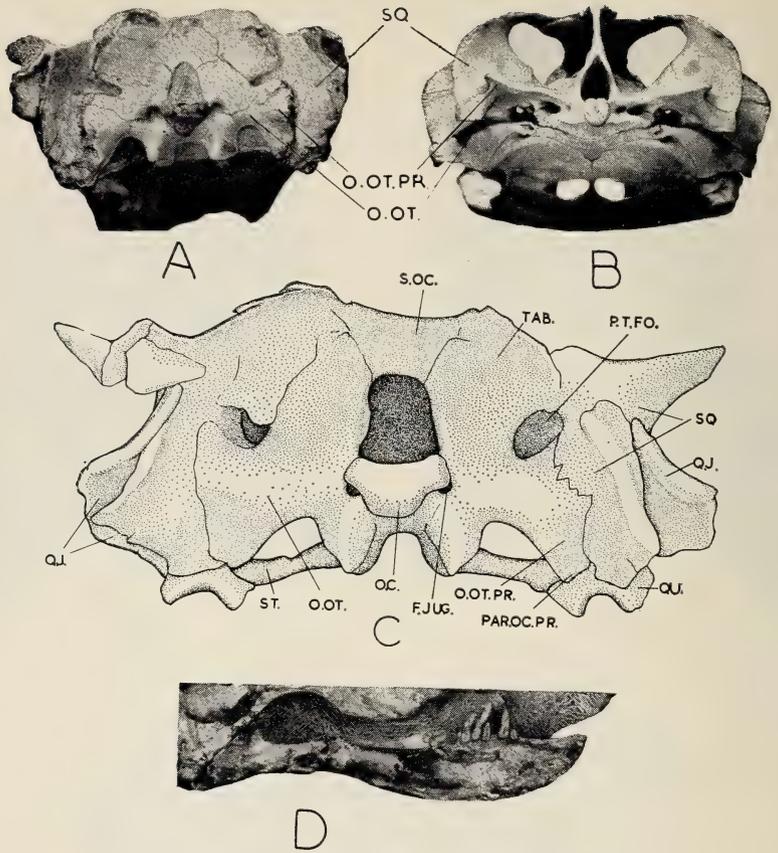


B



C

Pristerodon buffaloensis. Type specimen. A: dorsal; B: ventral, and C: lateral view of skull.



A: occipital view of type specimen of *Pristerodon buffaloensis*; B: occipital view of *Phrynops* sp.; C: occipital view of sectioned specimen of *Pristerodon buffaloensis*; D: medial view of left half of lower jaw of type specimen of *Pristerodon buffaloensis*. Abbreviations on p. 160.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol. '), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



7.68

HANS JOHN

NEUE SPEZIES VON *NOTIOPHYGUS* GORY
NEBST ERGÄNZUNGEN
(DISCOLOMIDAE COL.)

December 1967 December

Volume 50 Band

Part 8 Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

60c

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

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

NEUE SPEZIES VON *NOTIOPHYGUS* GORY
NEBST ERGÄNZUNGEN
(DISCOLOMIDAE COL.)

Von

HANS JOHN

Bad Nauheim

(Mit 3 Tafeln)

Aus dem South African Museum, Cape Town, erhielt ich einige Exemplare von *Notiophygus*, die zum Teil von Dr. H. Andreae determiniert waren. Meine erste zusammenfassende Arbeit über diese Gattung ist in den Suppl. Ent. Berlin-Dahlem, 17, 1929 erschienen. Sie berichtete über 69 Spezies (Gory 5, Fairm. 1, Grouv. 20, John 43) und 3 Subspezies. Da fast jeder neu besammelte Ort auch eine neue Spezies bringt, ist die Zahl der bis jetzt publizierten Spezies auf über 200 angewachsen. Die nach Grouvelles Vorschlag Notiophygidae benannte Familie musste später in Discolomidae umbenannt werden. Ein Überblick über die inzwischen auf 16 Gattungen angewachsene Familie erschien in den Genera Insectorum, Fasc. 213^E, 1959. Der Versuch eine Bestimmungstabelle zu geben (Grouvelle-Lesne: Encycl. Ent. B, 97, 1927) und mein eigener Versuch (l. c., 1929) konnten nicht befriedigen, da bei der wachsenden Zahl der einander sehr ähnlichen Spezies sich diese durch derartige kurze Angaben nicht sicher trennen liessen. Ich habe daher bereits damals (l. c., 1929) jede Spezies nebst Details gezeichnet, und dieses Verfahren in Verbindung mit der Beschreibung auch für alle 16 Gattungen angewendet. Neben 5 neuen Spezies bringt die vorliegende Arbeit Ergänzungen zu einigen bisher nur als ♀ bekannten Spezies.

Notiophygus acutus spec.n.

Die Spezies zeichnet sich durch ein breites Pronotum und einen spitz zusammenlaufenden Umriss der Elytren aus. Die Farbe ist düster grau, sie entsteht durch das dunkle Chitin und eine fast gleichmässig verstreute helle Behaarung. Die Haare gehören zum Typ 4 (Gen. Ins. Taf. 3). In wagerechter Lage hat das Pronotum einen breiten Kopfausschnitt und gut abgesetzte breite Randstücke, welche die Krümmung des Discus zum Rand hin fortsetzen. Die gerade geschnittene Basis dieser Randstücke bildet einen scharfen Winkel zu der stark konvexen Basis des Discus. Die am Rande befindlichen Poren sind etwas erhöht und ihre Umgebung ist teilweise mit schwarzen Haaren fleckartig

besetzt. Die Oberfläche ist dicht gerunzelt und die leicht eingedrückten Haarpunkte tragen in ihrer Mitte ein Körnchen, aus dem das Haar der 2. Form entspringt. Die kleinen Haare 1. Form sind nur spärlich dazwischen gestreut. Bei den Elytren schmiegt sich die Basis dem Pronotum an, die Basaltuberkel sitzen dicht am Winkel, den die Basis des Pronotums bildet. Von dort aus fällt die Schulter schräg nach aussen ab und ist ein wenig breiter als die grösste Breite des Pronotums. Zur Mitte erweitert sich der Umriss nur wenig, um dann mit deutlicher Spitze zusammen zu fliessen. Von der Schulter her ist eine schmale Randpartie etwas aufgebogen, die sich zur Spitze hin verliert. Auf ihrem Rand sind jederseits 5 erhöhte Poren, zwischen denen der Umriss jedesmal fast gerade verläuft (Dies ist bei *Notiophygus* der 2. Fall, dass die Porenzahl der Elytren geringer ist als die Familien- und Gattungsgebundene Zahl 6). Auch diese Poren sitzen in kleinen schwarzen Flecken. Leider ist die Behaarung des Tieres nicht unverletzt, daher sind schwarze Stellen vorhanden, bei denen nicht festzustellen ist welche Farbe die dort stehenden Haare hatten. Bei genauer Prüfung sind aber schwarze Flecke hinter den Basaltuberkeln und jederseits der Spitze sowie neben den Randtuberkeln 3 und 4 festzustellen. Weitere schwarze Haare stehen vereinzelt neben dem Scutellum und auf dem Discus ohne Flecke zu bilden (in der Zeichnung sind die verletzten Stellen durch feine Punktierung angegeben). Die Farbe der Unterseite gleicht der Oberseite, doch ist die Behaarung der Sternite etwas länger haarförmig, nur an den Seiten der Sternite verbreitert. Die Sternite sind analseitig gegeneinander abgesetzt, das "1". Sternit ist median etwas gewölbt, das 5. Sternit zeigt eine halbrunde Erhebung, deren Mitte etwas eingedrückt ist. Die Tibien der 3 Beinpaare haben kurz hinter ihrer Einlenkung in den Femur einen schwarzen Fleck. Die Fühler sind schlank, schwarz, ihr Basalglied ist dick behaart, die Geissel und die schlanke Keule sind dünn, transparent behaart.

Grösse: 4.2 × 3.3 mm.

Material: 1 ♀ Expl. (Holotypus) im South African Museum, Cape Town.

Fundort: Doringbaai, Nov. 1956.

Abbildung: Taf. XII, fig. 1a-f.

Notiophygus fungivorus spec.n.

(*parvulus*-Gruppe) Als *parvulus* determiniert, ist die Spezies etwas robuster im Körper und unterscheidet sich zuerst durch dunklere Farbe, die hervorgerufen wird durch kleinere nicht ganz so dicht stehende Behaarung der Oberfläche. Die Haare sind glasig-transparent im Gegensatz zu den hellgrauen Haaren bei *parvulus*. Daher sind die eingedrückten Punkte der Oberfläche des Pronotums deutlich zu sehen. Bei *parvulus* müssen diese Punkte erst unter den Haaren gesucht werden (bei beiden Spezies entspringt die 2. Haarform aus kleinen Körnchen innerhalb der Punkte). Die breiten Randstücke sind gut gegen den Discus abgesetzt und haben entlang ihrer Innenseite eine Schwellung, die sich zu den beiden Poren verlängert. Das Pronotum ist im ganzen etwas grösser

zum Körper und die Randstücke liegen mit ihren Rändern etwas flacher als bei *parvulus*. Bei den Elytren ist der Umriss, seitlich gesehen, vor der abfallenden Spitze etwas rückläufig, bei *parvulus* fällt er senkrecht ab. Die Basaltuberkel sind nach innen kräftig abgesetzt, die Pseudoporen sind so gross wie die Punkte des Pronotums aber viel tiefer eingedrückt und gegenüber *parvulus* vermehrt. Am Rande sitzen jederseits 6 aufgesetzte Poren. Das Scutellum berührt das Pronotum nicht und ist rundlich aufgeblasen. Die Sternite des ♀ gleichen denen von *parvulus*.

Grösse: 3.05×2.3 mm.

Material: 1 ♀ Expl. (Holotypus) im South African Museum, Cape Town.

Fundort: Somerset West, on mushrooms, 2.6.1953, A. J. Hesse.

Abbildung: Taf. XII, fig. 2a-g.

Notiophygus tritus spec.n.

(*parvulus*-Gruppe) Die Spezies besitzt im Vergleich mit *parvulus* und *fungivorus* spec.n. das kleinste Pronotum im Verhältnis zur Körpergrösse. Haartyp 1b. Die Randstücke sind gegen den Discus nur schwach abgesetzt und ihre Fläche liegt im Verlauf der Abflachung des Discus. Die vorderen Ecken erscheinen durch die dicht daneben stehenden Tuberkel der 1. Pore etwas stumpf, die Basalecken sind manchmal zu einer nach unten gerichteten Spitze ausgezogen. Die Oberfläche ist mit kleinen eingedrückten Punkten besetzt, aus denen die gekrümmten Haare 2. Form aufsteigen. In wagerechter Lage ist der Kopfausschnitt gerade, die vorderen Abschnitte der Randstücke erheben sich daraus in leichter Krümmung. Die Fläche zwischen den Haarpunkten ist runzelig und in ihr sind die Ansätze der kleinen 1. Haarform zu finden. Die Elytren überragen mit ihrer abgerundeten Schulter die Breite des Pronotums stärker als bei den anderen Mitgliedern der Gruppe. Die Seiten sind bis über die Mitte parallel und runden sich zur Spitze halbkreisförmig. An der Schulter ist die Randpartie verlaufend etwas aufgebogen. Die Basaltuberkel sind etwas kleiner als bei *parvulus* und *fungivorus*. Die Oberfläche des Discus ist durch die empor quellende Fläche zwischen den weich und tief eingelassenen Pseudoporen etwas gewellt. Ihre Zahl ist etwas geringer als bei *fungivorus*. Die Randleiste trägt jederseits 7 Tuberkel, zwischen denen der Rand gelegentlich etwas eingezogen ist. Bei den ♂♂ zeigt das "1". Sternit die ursprüngliche 3-Teilung sehr deutlich, bei den ♀♀ ist sie nur angedeutet, aber das 5. Sternit hat einen rundlichen Zapfen mit einer scharfen Spitze. Leider waren beide Exemplare so stark und fest verschmutzt mit festgeklebten Fäden und kleinem Abfall, dass es nur mit Mühe gelang, zur Oberfläche vorzudringen. Auch der Penis wurde nicht gefunden.

Grösse: 3×2.3 mm.

Material: 2 Expl. (Typus ♂♀) im South African Museum, Cape Town.

Fundort: Jonkershoek, 13.7.1965, H. Geertsema.

Abbildung: Taf. XIV, fig. 3a-f.

Notiophygus globulus spec.n.

Die Spezies gehört zur *parvulus*-Gruppe und wurde als *crassipilus* J. determiniert. Die Schwierigkeit die Käfer dieser Gruppe richtig zu trennen beruht z.Teil auf den Zeichnungen in den Suppl. Ent. 17, 1929, wo ich die unterschiedliche Grösse der Tiere wiedergegeben hatte, wobei die kleinen Spezies zu kurz kamen. Herr Dr. Andreae hatte mich brieflich bereits darauf hingewiesen. Leider sind diese Spezies bisher nur vereinzelt wieder gefunden worden aber neue Spezies sind hinzugekommen. Ich habe daher nach den Typen im Deutschen Entomologischen Institut, Eberswalde, DDR, neue Zeichnungen angefertigt welche die wünschenswerte Klarheit bringen. Die Publikation dieser Ergänzungen erfolgt in den Opusc. Zool., München, in Verbindung mit einer Neubeschreibung.

Globulus ist stark konvex und hat breite aber spitzoval zusammen laufende Elytren. Haartyp 1b. Seitlich gesehen fällt der Discus schräg zur Elytrenspitze hin ab (*crassipilus*: der Discus hängt vor der Spitze etwas über). In wagerechter Lage hat das Pronotum einen breiten Kopfausschnitt, die Vorderecke der Randstücke ist etwas stumpf, die Basalecken sind verschwunden, da der Seitenrand ohne Unterbrechung rund in die Basis hinein läuft. (*crassipilus*: Basalecken vorhanden, basaler Abschnitt der Randstücke geht in die Richtung der konvexen Basis über). Die Oberfläche des Discus ist stumpf, fein genarbt und die Punkte liegen z.Teil offen, z.Teil sind sie mit Haaren 2. Form besetzt, die nicht sehr dicht stehen und undurchsichtig weiss sind (*crassipilus*: die Oberfläche ist rau genarbt, glitzernd, die Punkte sind verschwommen eingesetzt. Die Haare sind in der Form wie bei *globulus*, sind aber transparent). Bei beiden Spezies ist der Kiel dieser Haare kräftig, bei *globulus* oft verlängert. Die Unterseite ist mit Beinen und Mundteilen schwarz, beim ♂ hat das 5. Sternit einen basalen Eindruck, vordem 2 kleine Erhöhungen liegen die miteinander verbunden sind. Beim ♀ ist das 5. Sternit leicht gezipfelt. Die Fühlerkeule hat eine distale Abschnürung.

Grösse: 3.1 × 2.5 mm.

Material: 2 Expl. (Typus ♂♀) im South African Museum, Cape Town.

Fundort: Leipoldtville C.P., XI. 1956, Museum Expedition.

Abbildung: Taf. XIII, fig. 1a-g, Penis Taf. XIV, fig. 5.

Notiophygus inops spec.n.

Parvulus-Gruppe, Haartyp 1b. Die kleine Spezies unterscheidet sich von den anderen durch den Besitz von 7-9 Tuberkelporen an den Rändern der Elytren und ist—seitlich betrachtet—niedriger im Körper als *globulus* sp. n. Das Pronotum hat in wagerechter Lage einen geraden Kopfausschnitt, die Vorderecke der Randstücke ist nicht sehr scharf, hinter dem 2. Randtuberkel ist der Umriss bis zur Basalecke konkav. Die Oberfläche glänzt matt, die Punktierung ist gut sichtbar, aus ihr entspringen die Haare 2. Form, welche Kiel und Randadern haben. Die Basis der Elytren schmiegt sich dem Pronotum

an, sie ist zwischen den Basaltuberkeln konkav und läuft von der Schwellung um die Tuberkel zur abgerundeten Schulterecke. Zur Mitte ist der Umriss sanft erweitert und läuft halbkreisförmig zur Spitze zusammen. Eine Randpartie oder Leiste fehlt, die Tuberkel überragen den Rand. Auf dem Discus sind die Pseudoporen grösser als die Punkte des Pronotums, sie sind weich eingelassen und über den ganzen Discus verteilt. Auf der Unterseite sind die Hüften braun die Tibien distal und die Tarsen sind braun behaart. Beim ♂ ist das 5. Sternit analseitig gerade, das Ventralstück des 7. Tergits trägt einen schwachen Knopf. Der Penis wurde nicht gefunden. Beim ♀ ist das 5. Sternit leicht gezipfelt.

Grösse: 3.15 × 2.5 mm.

Material: 2 Expl. (Typhus ♂♀) im South African Museum, Cape Town.

Fundort: Papiessfontein, Gamtoos River, E. Cape, VII. 1960, F. W. Gess.

Abbildung: Taf. XIII, fig. 2a-g.

BEREITS BEKANNTE SPEZIES

Notiophygus fulvipes John

(*South Afr. An. Life* II, 1955, p. 313)

Typen in Lunds Entom. Inst. Lund, Schweden, 1 Expl. im South African Museum, Cape Town.

Fundort: Matroosberg, Hex River Mts. 6500 ft. ix. 1923, K. H. Barnard.

Abbildung: Penis Taf. XIV, fig. 4.

Notiophygus cuspidatus John

(*Suppl. Ent.* 17, 1929, p. 55)

Holotypus ♀ im South African Museum, Cape Town, 2 Expl. ebenda.

Fundort: Oudebosch, Riviersonderend, x. 1933, Museum Staff; Montagu, xi. 1919, R. Lightfoot.

Notiophygus dentipennis Gory

(*Suppl. Ent.* 17, 1929, p. 53)

Typen im South African Museum, Cape Town, 1 Expl. ebenda.

Fundort: Kapstadt, 2.11.41.

Notiophygus funestus Grouv.

(*Suppl. Ent.* 17, 1929, p. 57)

Typus im Museum Paris, 2 Expl. im South African Museum, Cape Town.

Fundort: Potchefstroom, Transvaal, i. 1930, J. Joubert, und Bothaville, Oranje Fr. St., ii. 1938, Dr. Brauns.

Notiophygus humeralis simulatus John

(*Arb. morph. tax. Ent.* 2, 1, 1935, p. 23)

Typus im Museum Paris, 1 Expl. im South African Museum, Cape Town.

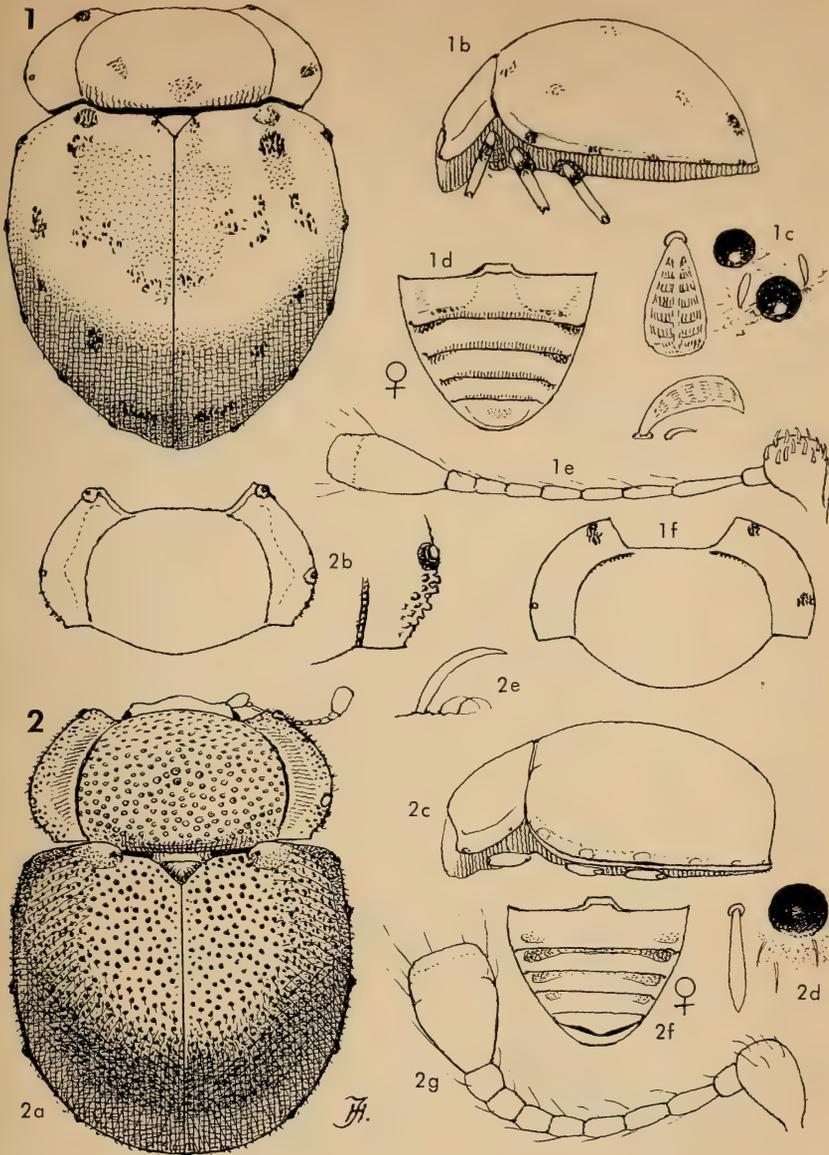
Fundort: Montagu Pass, i. 1940, Museum Staff.

SUMMARY

Descriptions are given of 5 new species of *Notiophygus* (Discolomidae): *N. acutus*, *N. fungivorus*, *N. tritus*, *N. globulus* and *N. inops*. A list of 5 other species, described previously, but also represented among the material submitted, is appended. Three plates illustrating the new species and important structures, such as shape of the pronotum, the antennae, ventral sternites, hairs and the male genitalia of one species, are also given.

ACKNOWLEDGEMENT

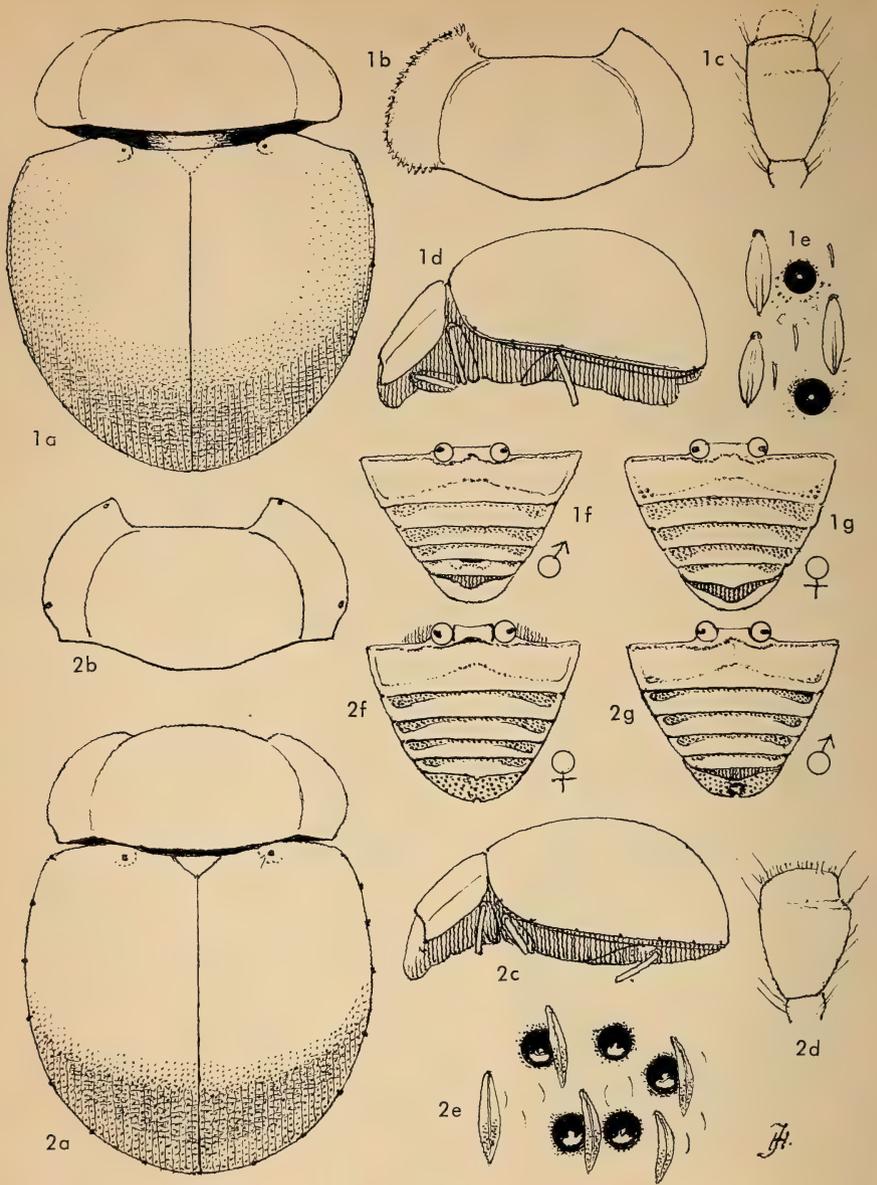
The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research of South Africa for the award of a grant towards the cost of publishing this paper.



Taf. xii

FIG. 1. *Notiophygus actus* spec.n. a, Ansicht von oben. b, Seitenansicht. c, Haartyp 4 (2. Form gegittert) dazu die Grösse der Pseudoporen. d, Sternite des ♀. e, Fühler. f, Pronotum wagerecht.

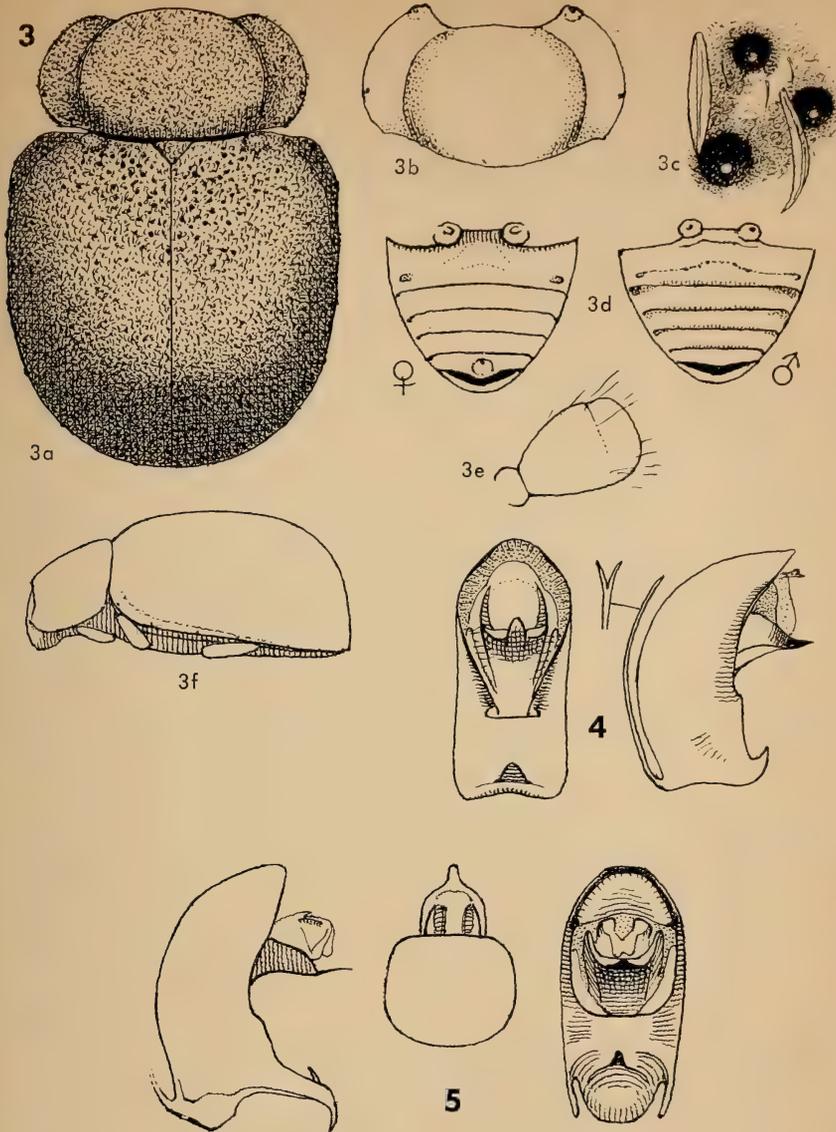
FIG. 2. *Notiophygus fungivorus* spec.n. a, Ansicht von oben. b, Pronotum wagerecht, daneben Basalecke vergrössert. c, Seitenansicht. d, Haartyp 1, dazu die Pseudoporen. e, Haare seitlich. f, Sternite ♀. g, Fühler.



Taf. XIII

FIG. 1. *Notiophygus globulus* spec.n. a, Ansicht von oben. b, Pronotum wagerecht. c, Fühlerkeule (punktiert) mit Riechkegel. d, Seitenansicht. e, Haare (Typ 1b) und Pseudoporen. f, Sternite ♀. g, Sternite ♂.

FIG. 2. *Notiophygus inops* spec.n. a, Ansicht von oben. b, Pronotum wagerecht. c, Seitenansicht. d, Fühlerkeule. e, Haare (Typ 1b) und Pseudoporen. f, Sternite ♀. g, Sternite ♂.



Taf. xiv

FIG. 3. *Notiophygus tritus* spec.n. a, Ansicht von oben. b. Pronotum wagerecht. c, Haare (Typ 1b) und Pseudoporen. d, links Sternite ♀, rechts Sternite ♂. e, Fühlerkeule. f, Seitenansicht.

FIG. 4. *Notiophygus fulvipes* John, Penis, ventral und lateral.

FIG. 5. *Notiophygus globulus* spec.n., Penis, lateral, von oben, ventral.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

7.68

N. A. H. MILLARD

HYDROIDS FROM THE SOUTH-WEST INDIAN OCEAN

December **1967** December
Volume **50** Band
Part **9** Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R1.00

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

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

HYDROIDS FROM THE SOUTH-WEST INDIAN OCEAN

By

N. A. H. MILLARD

Zoology Department, University of Cape Town

(With 6 figures in the text)

CONTENTS

	PAGE
Introduction	169
Station list	171
List of species	171
Systematic account	172
Discussion	192
Summary	192
Acknowledgements	193
References	193

INTRODUCTION

This paper deals with an assortment of Indian Ocean hydroids from the area east of South Africa and south of Madagascar. With the exception of a small collection from Walter's Shoal all are from depths greater than 300 m. and are thus over the edge of the Continental Shelf, the margin of which is located at 150–300 m. Thus, although some of the stations are situated less than 30 nautical miles off the coast where it shelves steeply, the fauna cannot strictly be included in that of South Africa.

The material from Walter's Shoal is a shallow-water fauna dredged from 38 to 46 m., but, since Walter's Shoal is situated over 420 nautical miles from Madagascar and over 600 nautical miles from Africa, its fauna cannot be included in that of either country.

It was felt that the material from the whole of this area might conveniently be described together.

The material comes from two sources. Those samples bearing the prefixes ABD and WSS were collected by the R/V *Anton Bruun* during her seventh cruise in the International Indian Ocean Expedition in 1964. A final cruise report of the expedition was published by the U.S. Program in Biology, I.I.O.E., in 1965, to which body I am indebted for the opportunity of examining the material.

UNIVERSITY OF CAPE TOWN
LIBRARY

Material bearing the prefix AFR is part of a collection in the Zoology Department, University of Cape Town, and was collected in 1961 by the government research vessel *Africana II* belonging to the Division of Sea Fisheries, Department of Commerce and Industries.

The position of the collecting stations is roughly indicated on the accompanying sketch-map (fig. 1), and the complete data given in the station list which follows.

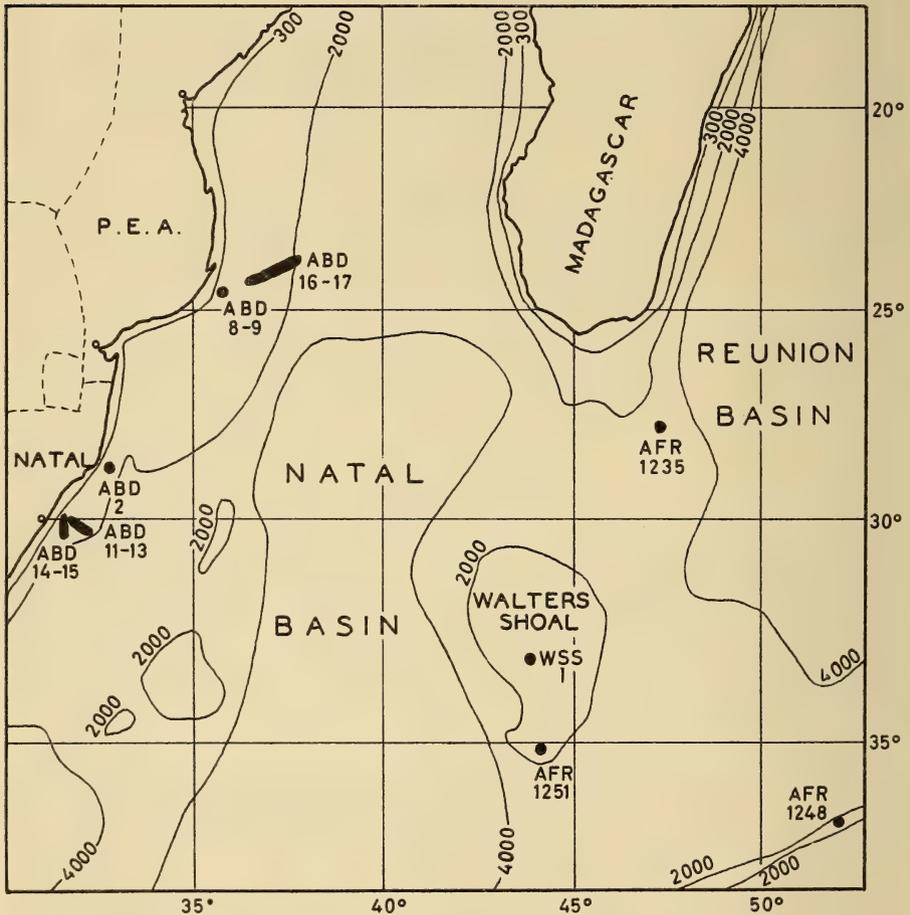


Fig. 1

Sketch-map of the area under consideration showing the approximate positions of the different collecting stations. The reference numbers are the same as those used in the station list. Depths in metres.

In the systematic section the full synonymy is not quoted in every case, but instead a number of references from which such can be obtained.

STATION LIST

U.C.T. cat. no.	Date	Position	Depth (m.)	Bottom	<i>Anton Bruun</i> stat. no.
ABD 2	31/7/64	28°43'S/32°38'E	1207	R	359C
ABD 8-9	18/8/64	24°40'S/35°28'E	347	sh. S.	370G
ABD 11	7/9/64	30°12'S/32°01'E	1360	Gl. Oz.	389C
ABD 12	7/9/64	30°09'S/31°37'E	930	s. M. Cl.	389E
ABD 13	8/9/64	29°57'S/31°31'E	700	Gl. Oz.	389G
ABD 14	8/9/64	29°45'S/31°40'E	440	h. S.	390C
ABD 15	8/9/64	29°42'S/31°38'E	350	s. M.	390E
ABD 16	17/8/64	23°48'S/37°45'E	2200	Gl. Oz.	369C
ABD 17	17/8/64	24°04'S/36°15'E	1610	Gl. Oz.	369F
WSS 1	30/8/64	33°13'S/43°51'E	38-46	Calc. Algae	381A-C
AFR 1235	22/6/61	27°48'S/47°19'E	875		
AFR 1248	9/7/61	36°48'S/52°08'E	400		
AFR 1251	11/7/61	35°03'S/44°12'E	600		

LIST OF SPECIES

Family **Campanulinidae***Stegopoma fastigiatum* (Alder)Family **Lafoeidae***Acryptolaria conferta australis* (Ritchie)*Acryptolaria crassicaulis* (Allman)*Acryptolaria rectangularis* (Jarvis)*Filellum serratum* (Clarke)*Lafoea fruticosa* (M. Sars)*Zygophylax armata* (Ritchie)Family **Syntheciidae***Hincksella echinocarpa* (Allman)*Hincksella indiana* n.sp.Family **Sertulariidae***Salacia ?desmoides* (Torrey)*Sertularella arbuscula* (Lamouroux)*Sertularella mediterranea* Hartlaub*Sertularella megista* Stechow*Sertularella polyzonias* (Linnaeus)*Sertularella xantha* Stechow*Symplectoscyphus ?amphoriferus* (Allman)*Symplectoscyphus paulensis* Stechow

Family **Plumulariidae**

- Kirchenpaueria triangulata* Totton
Nemertesia ramosa Lamouroux
Plumularia antonbruuni n.sp.
Plumularia setacea (Linnaeus)
Cladocarpus distomus Clarke
Halicornaria gracilicaulis (Jäderholm)

SYSTEMATIC ACCOUNT

Family **Campanulinidae***Stegopoma fastigiatum* (Alder, 1860)

Stegopoma fastigiata: Millard, 1958: 175.

Stegopoma fastigiatum: Ralph, 1957: 850, fig. 8 n-o. Vervoort, 1959: 234, fig. 10.

Records. ABD 9F (epizootic on *Zygophylax armata*).

Remarks. This species has already been reported from the area, from 333 m. off the coast of Natal (Millard, 1958).

Family **Lafoeidae***Acryptolaria conferta australis* (Ritchie, 1911)

Cryptolaria conferta var. *australis* Ritchie, 1911: 826, pl. 84 (fig. 2), pl. 87 (fig. 1).

Acryptolaria conferta var. *australis*: Totton, 1930: 163, fig. 19 c-e. Ralph, 1958: 315, fig. 4 a-g.

Acryptolaria conferta australis: Millard, 1964: 9, fig. 1 D, F, G.

Records. ABD 9G, 15B.

Description. One colony (ABD 9G) reaching a height of 3.7 cm. and fairly regularly branched, a branch arising next to every third hydrotheca. Hydrothecae with a rather greater proportion of their height adnate than usual (0.59 to 0.88), especially on the thicker parts of the stem and branches. Margins practically parallel to axis of stem.

The other colony (ABD 15B) a single, little-branched stem 5.3 cm. high, with hydrothecae similar to those previously described (Millard, 1964).

Acryptolaria crassicaulis (Allman, 1888)

Fig. 2A

Cryptolaria crassicaulis Allman, 1888: 41, pl. 19 (figs. 3, 3a). Ritchie, 1911: 828-830, pl. 87 (fig. 4).

Stechow, 1913: 113, figs. 86, 87.

Cryptolaria crassicaulis, var. *dimorpha* Ritchie, 1911: 830, pl. 87 (figs. 5, 6). Jarvis, 1922: 335.

Records. AFR 1248A.

Description. A single fascicled stem 4.7 cm. in height, giving off a number of branches in a roughly alternate manner.

Hydrotheca adnate for about half height, with base very slightly above top of adnate part of preceding one, with diameter at margin approximately three times that at base. Margin very slightly everted.

Coppiniae absent.

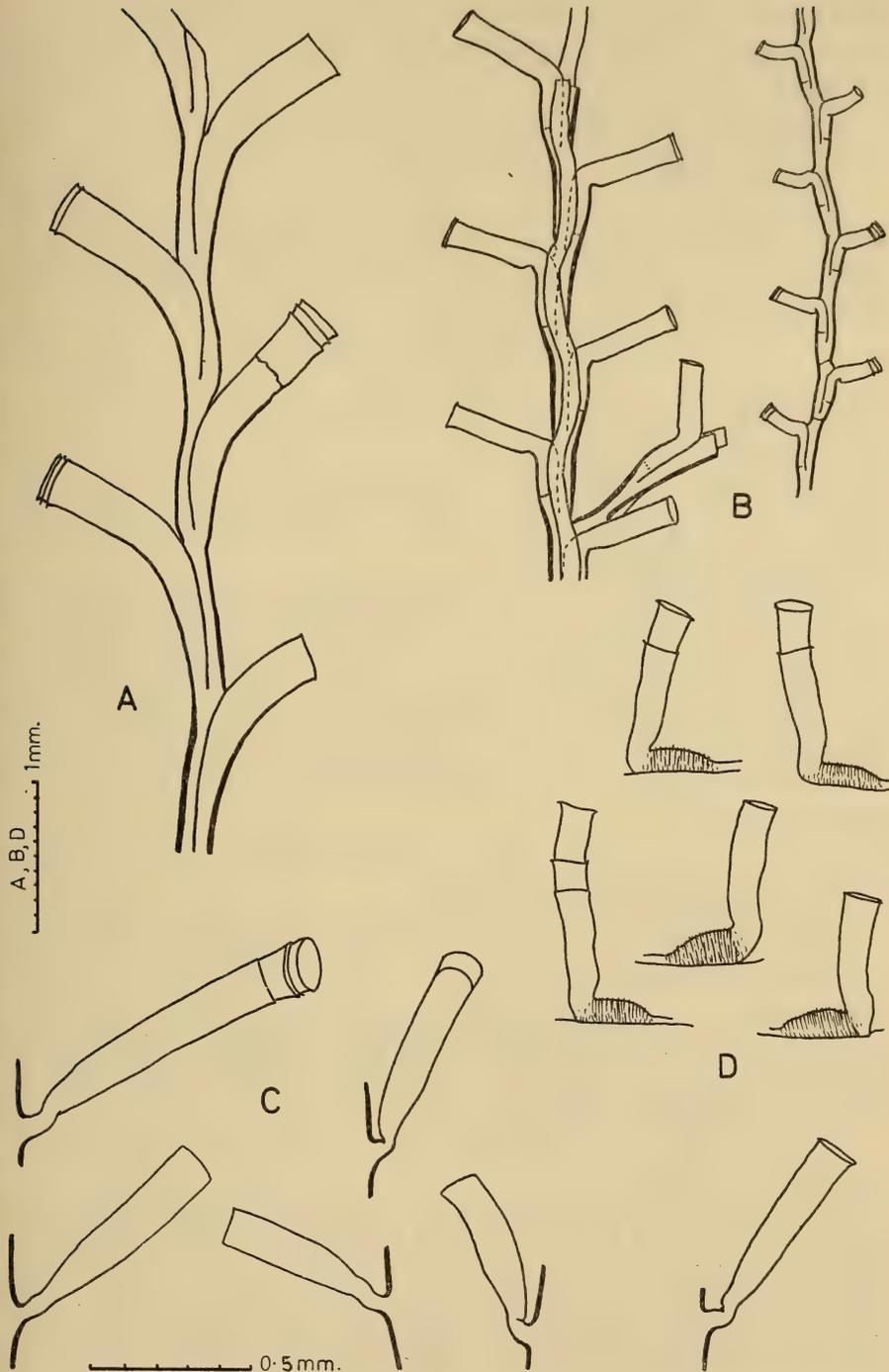


Fig. 2. Lafoeidae.

- A. *Acryptolaria crassicaulis* (Allman).
 B. *Acryptolaria rectangularis* (Jarvis) from ABD 15P (left) and AFR 1251D (right).
 C. Various hydrothecae of *Lafoea fruticosa* (M. Sars).
 D. *Fillellum serratum* (Clarke) from ABD 9E.

Measurements (mm.)

Hydrotheca, length of adnate part	0.79-1.01
length of free part	0.69-1.18
adnate part/total length	0.40-0.59
diameter at base	0.09-0.13
diameter at margin	0.31-0.39
base/margin	0.29-0.38

Remarks. As the ability to produce solitary hydrothecae is a feature common to many, and possibly all, Lafoeidae, it is not necessary to retain Ritchie's variety *dimorpha*.

Acryptolaria rectangularis (Jarvis, 1922)

Fig. 2B

Cryptolaria rectangularis Jarvis, 1922: 335, pl. 24 (fig. 3).

Records. ABD 15P. AFR 1251D.

Description. Two small and probably young colonies reaching a maximum height of 1.1 cm. Stems unbranched or giving off a few irregular branches. Proximal parts of stem and branches fascicled.

Hydrotheca tubular, adnate for about $\frac{1}{2}$ to $\frac{2}{3}$ height, then free and directed sharply outwards. Free part forming an angle of 70-75° with stem, with free part of adcauline wall straight, or slightly concave and recurved towards distal end of stem, with a distinct notch on abcauline wall at point of divergence from stem. Diaphragm present or absent. Margin even and often regenerated. No nematophores.

Gonophores absent.

Measurements (mm.)

	AFR 1251D	ABD 15P
Hydrotheca, adnate part (adcauline)	0.24-0.40	0.52-0.59
free part (adcauline)	0.15-0.29	0.52-0.72
adnate part/total length	0.48-0.71	0.43-0.52
diameter at margin	0.10-0.12	0.18-0.23

Remarks. This material strongly resembles *Cryptolaria angulata* Bale, 1914, except for the absence of a 'boss' or perisarcal thickening on the adcauline wall of the hydrotheca just below the bend. It was mainly on the absence of this boss that Jarvis established the species *rectangularis*.

The two samples have hydrothecae of very different sizes, though the proportions are similar.

In the nature of the diaphragm the species is intermediate between the genera *Acryptolaria* and *Cryptolaria*. In the youngest parts of the colony the diaphragm is either completely absent or is represented by a ring of raised tubercles where the base of the hydranth is attached, but in older parts the tubercles become thickened processes which are attached to one another around the circumference by a thin chitinous shelf, thus forming a definite diaphragm.

This is not visible as a joint on the outer surface of the hydrotheca. The species has been included in the genus *Acryptolaria* mainly on the absence of nematophores.

Filellum serratum (Clarke, 1879)

Fig. 2D

Lafösa serrata Clarke, 1879: 242, pl. 4 (fig. 25).

Reticularia serrata: Ralph, 1958: 312, fig. 2j, 3a.

Records. ABD 9E. WSS 1R.

Description. Two colonies differing in dimensions and proportions, though both with the adherent part of the hydrotheca sculptured externally by 30-40 delicate perisarcal ridges.

ABD 9E (from 347 m.) epizootic on *Nemertesia ramosa*; hydrothecae large, adnate for about $\frac{1}{3}$ - $\frac{1}{2}$ length, free part bent out at right angles.

WSS 1R (from shallower water: 38-46 m.) epizootic on *Plumularia setacea*; hydrotheca small, adnate for $\frac{1}{2}$ - $\frac{3}{4}$ length, free part bent out at angle of 60-70°.

Measurements (mm.)

	ABD 9E	WSS 1R
Hydrotheca, length of adnate part	0.48-0.67	0.22-0.47
length of free part (without reduplications)	0.60-1.32	0.12-0.26
adnate part/total length	0.29-0.50	0.52-0.76
diameter at margin	0.22-0.30	0.11-0.14

Remarks. Although these two samples differ greatly in dimensions, they have been included in the same species. The measurements of the smaller form agree with those given by Ralph from New Zealand.

Lafösa fruticosa (M. Sars, 1851)

Fig. 2C

Lafösa fruticosa: Stechow, 1925: 456, fig. 24B. Totton, 1930: 157, fig. 13. Naumov, 1960: 275, fig. 164. Millard, 1964: 14, fig. 3.

Records. ABD 9H.

Description. A young colony with solitary hydrothecae and unbranched stems reaching 0.8 cm. Stems weakly fascicled in basal region.

Hydrothecae long and slender, forming an angle of 40-60° with stem, with adcauline wall very slightly convex. Pedicel with double twist.

Coppinia absent.

Measurements (mm.)

Hydrotheca + pedicel, height	0.52-0.91
Hydrotheca, diameter at margin	0.11-0.17
Hydrotheca + pedicel/diameter	3.71-6.07

Remarks. In general appearance this material differs from that recorded from South Africa (Millard, 1964) in its longer and more slender hydrothecae which

show no sign of a double curvature. In most cases the total length of the hydrotheca plus pedicel is over five times the diameter at the margin. Yet on the same stem are shorter hydrothecae resembling some of those figured in 1964.

The colony strongly resembles Alder's figure of *Lafoea gracillima* (1856, pl. 14, fig. 6), except that the pedicels are not quite so long. However, from the literature I can find no satisfactory means of distinguishing *L. gracillima* from *L. fruticosa*. Totton, who figures both, is himself in doubt and Naumov has united the two species.

Zygophylax armata (Ritchie, 1907)

Brucella armata Ritchie, 1907: 533, pl. 2 (fig. 2-2c).

Zygophylax armata: Millard, 1964: 18, fig. 4G.

Records. ABD 8D, 14V.

Description. Two rather straggling, sterile colonies reaching 4.2 and 3.1 cm. in height respectively.

Family **Syntheceiidae**

Hincksella echinocarpa (Allman, 1888)

Fig. 3 A-C

Sertularia echinocarpa Allman, 1888: 57, pl. 28 (figs. 1, 1a).

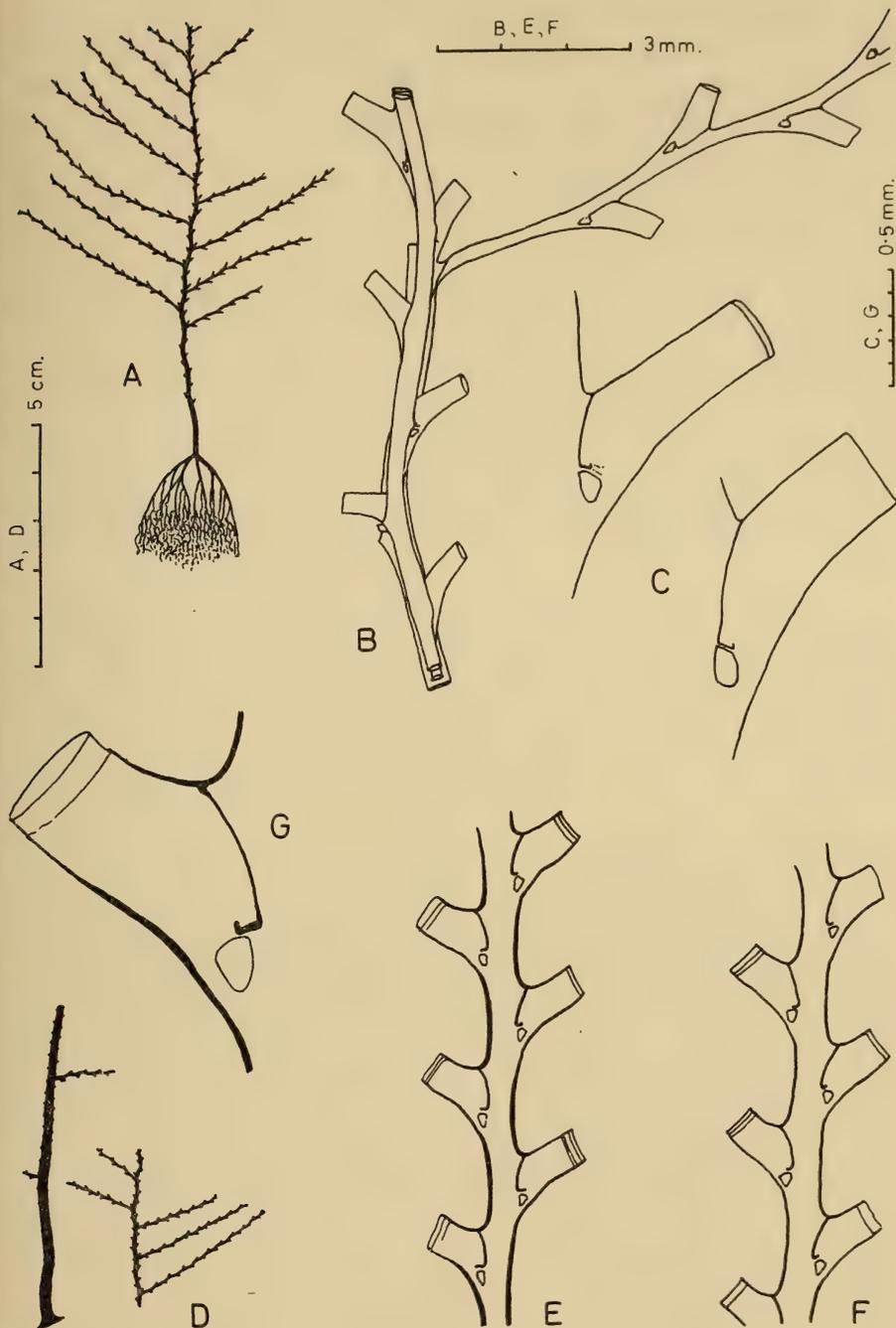
Records. ABD 16A, 17A.

Description. Altogether six rooted stems, of which the longest is 9.0 cm., and many incomplete stems and fragments.

Rootstock in the form of a branching system for penetration of a soft substratum; consisting of a number of fascicled 'roots' arising at the same level from the base of the stem, these subdividing a number of times and finally producing very delicate unfascicled 'rootlets'.

Stem comparatively flexuous and unable to support itself out of fluid; slightly geniculate; unsegmented; fascicled for most of its length but unfascicled in distal region; the central axial tube giving rise to alternate hydrothecae and alternate hydrocladia. Hydrocladia normally arising immediately below every third hydrotheca; long (reaching 4 cm.); flexuous; the two rows in one plane at origin, but due to flexibility producing an irregular effect; rarely rebranching. Each hydrocladium separated from stem by a distinct oblique joint and thereafter unsegmented except for an occasional transverse node immediately above a hydrotheca; bearing alternate hydrothecae.

Hydrotheca tubular, adnate for less than half adcauline height; then straight or curved very slightly outwards. Free part of adcauline wall straight or slightly convex. Margin untoothed, not everted, facing outwards and upwards, forming an angle of 30-40° with hydrocladium. Two distinct oval areas closed over by thin perisarc present in the perisarc immediately below the base of each hydrotheca.

Fig. 3. *Hincksella*.

A-C. *Hincksella echinocarpa* (Allman) from ABD 16A. A, a whole stem; B, a portion of a fascicled stem showing origin of hydrocladium; C, two hydrothecae from different stems.

D-G. *Hincksella indiana*, n.sp., from the holotype. D, two portions of the stem; E and F, old and young portions of hydrocladia respectively; G, a hydrotheca.

Gonophores absent, but presumably emerging through the oval areas mentioned above.

Measurements (mm.)

Hydrotheca, length abcauline (approximate only)	0.85-1.05
length adcauline, adnate part	0.36-0.57
length adcauline, free part	0.60-0.83
adnate part/adcauline length	0.30-0.48
diameter at mouth	0.31-0.45

Remarks. This species is known only from Allman's original material from Kerguelen Island in the southern Indian Ocean. Unfortunately it was not redescribed by Billard in his revision of the British Museum hydroids in 1910. The form of the colony in the present material bears a striking resemblance to Allman's diagram though the individual dimensions are a little less. Other resemblances include the absence of regular segmentation, the shape of the hydrotheca and the presence of the oval areas below the hydrothecae. Allman did not mention nodes at the origins of the hydrocladia, nor did he describe the rootstock. Gonothecae are necessary for final confirmation of the identification.

Closely related is *H. cylindrica* (Bale, 1888), which is a smaller species with an unfascicled stem and without the characteristic oval areas. Possible synonyms of the latter are *H. alternans* (Allman, 1888) and *H. halecina* (Torrey, 1902), both of which bear gonophores from within the hydrothecae. *H. formosa* (Fewkes, 1881) is unfascicled and has hydrothecae of quite different proportions.

Hincksella indiana n. sp.

Fig. 3 D-G

Types and records. Holotype: AFR 1235A (South African Museum registered number SAMH 1646). Other records: AFR 1248C.

Description of holotype. A stiff fascicled stem in three separate portions, together reaching about 13.5 cm., and a number of separated hydrocladia. Rootstock disc-shaped and flattened below, presumably attached to a hard substratum. Stem unsegmented; strongly fascicled at base and consisting of a central hydrotheca- and hydrocladia-bearing tube covered by 8-9 peripheral tubes, the latter gradually decreasing in number towards the distal end, which is unfascicled.

Hydrocladia stiff, alternate, with the two rows in one plane (though most are detached); arising below every third hydrotheca; reaching a maximum length of 4.8 cm.; unfascicled; separated from stem by a partial or complete oblique joint and thereafter unsegmented; with only very rarely a faint oblique or transverse node (probably the result of regeneration).

Hydrothecae alternate on stem and hydrocladia, with the two rows in one plane; large; adnate for over half adcauline length; tubular, with the free part curved towards the adcauline side and with concave adcauline wall. Margin

circular and untoothed, often regenerated. Two distinct oval windows present in the perisarc below the base of each hydrotheca; these are closed by thin membrane only and not by perisarc as in *H. echinocarpa*.

Gonophores absent, but presumably emerging through the oval windows mentioned above.

Measurements (mm., without regenerations) `

Hydrotheca, length abcauline (approximate only)	0.66-0.80
length adcauline, adnate part	0.60-0.73
length adcauline, free part	0.30-0.48
adnate part/adcauline length	0.56-0.70
diameter at margin	0.48-0.57

Remarks. This species has certain resemblances to *H. echinocarpa* (Allman, 1888) and *H. formosa* (Fewkes, 1881). It differs from the former in its thicker perisarc and more rigid hydrocladia, in the greater length of the adnate part of the hydrotheca and in the concave adcauline wall; from the latter it differs in the absence of segmentation and in the plane of the hydropore, which is at right angles to the stem or hydrocladial axis rather than approximately parallel to it (cp. Vervoort, 1959, fig. 29).

Family **Sertulariidae**

Salacia ?desmoides (Torrey, 1902)

Fig. 4 A-C

Sertularia desmoides: Nutting, 1904: 56, pl. 3 (figs. 1-3). Fraser, 1937: 161, pl. 37 (fig. 194).

Salacia desmoides: Billard, 1924: 66. Billard, 1925: 207.

Records. WSS 1S.

Description. A small colony of ten unbranched stems reaching a maximum height of 0.6 cm. Hydrorhiza creeping, unsegmented. Stem bearing up to nine pairs of hydrothecae, which are generally, but not always, separated by strongly oblique nodes resembling hinge-joints. Thecal pairs well spaced and always separated by a distance greater than their length. Members of a pair of hydrothecae in contact with one another on anterior surface of stem, free behind.

Hydrotheca adnate to stem for over half adcauline length, widening from base to top of adnate part, then curved outwards and narrowing again to margin. Margin facing outwards and downwards, untoothed. Orifice roughly in the shape of an inverted triangle. Operculum of one large abcauline valve.

Gonophores absent.

Measurements (mm.)

Internode length (where nodes are present)	0.55-0.75
diameter	0.06-0.08
Hydrotheca, length abcauline	0.17-0.21
length adcauline, contiguous part	0.14-0.18

length adcauline, adnate part	0.22-0.26
length adcauline, free part	0.13-0.18
adnate part/total length	0.56-0.65
diameter (vertical) at margin	0.10-0.12

Remarks. There is nothing in the published descriptions to exclude this material from being a young colony of *S. desmoides*, a species known from the Pacific coast of North America. Fraser's material, reported from a number of localities, appears to have somewhat larger dimensions. A greater variety of material and gonophores are necessary for final identification.

Sertularella arbuscula (Lamouroux, 1816)

Sertularella arbuscula: Millard, 1957: 208, fig. 10B, 11C. Millard, 1958: 188. Millard, 1964: 37.

Records. WSS 1N.

Description. A richly branched colony with a strongly fascicled stem 4.8 cm. in length. Hydrothecae closely set and smaller than is normal for the species (abcauline length 0.34-0.40 mm.), but typical in shape. Internal teeth five in number: one large abcauline, two slightly smaller latero-adcauline and two minute latero-abcauline.

Gonothecae abundant, male, smaller than normal (length, mature, 1.54-1.90 mm.), annulated in distal half.

Remarks. This material resembles the common form of *S. arbuscula*, as it is known from South Africa, in the form of the colony and shape of the hydrotheca, but differs in the smaller dimensions of the hydrotheca and gonotheca and in the annulations present on the latter. However, since annulated gonothecae are known to occur in the species (Millard, 1958 and 1964) it is not possible to differentiate the material on these grounds. The gonotheca is similar in appearance to that illustrated by Warren (1908, fig. 6B).

Sertularella mediterranea Hartlaub, 1901

Sertularella mediterranea: Millard, 1957: 215, figs. 10E, 11B.

Records. WSS 1Q.

Description. A small infertile colony reaching a maximum height of 1.6 cm.

Sertularella megista Stechow, 1923

Fig. 4D

Sertularella megista: Millard, 1957: 217, figs. 10L, 11J. Millard, 1964: 45 (synonymy).

Sertularella sp.: Millard, 1958: 192 (PF 12456E).

Records. ABD 8B.

Description. A single unfascicled, unbranched stem 9.8 cm. in height.

Hydrotheca similar to that previously described for this common species, except that the free part is much elongated and exceeds the adnate part in length. Free part of both adcauline and abcauline walls straight or nearly so.

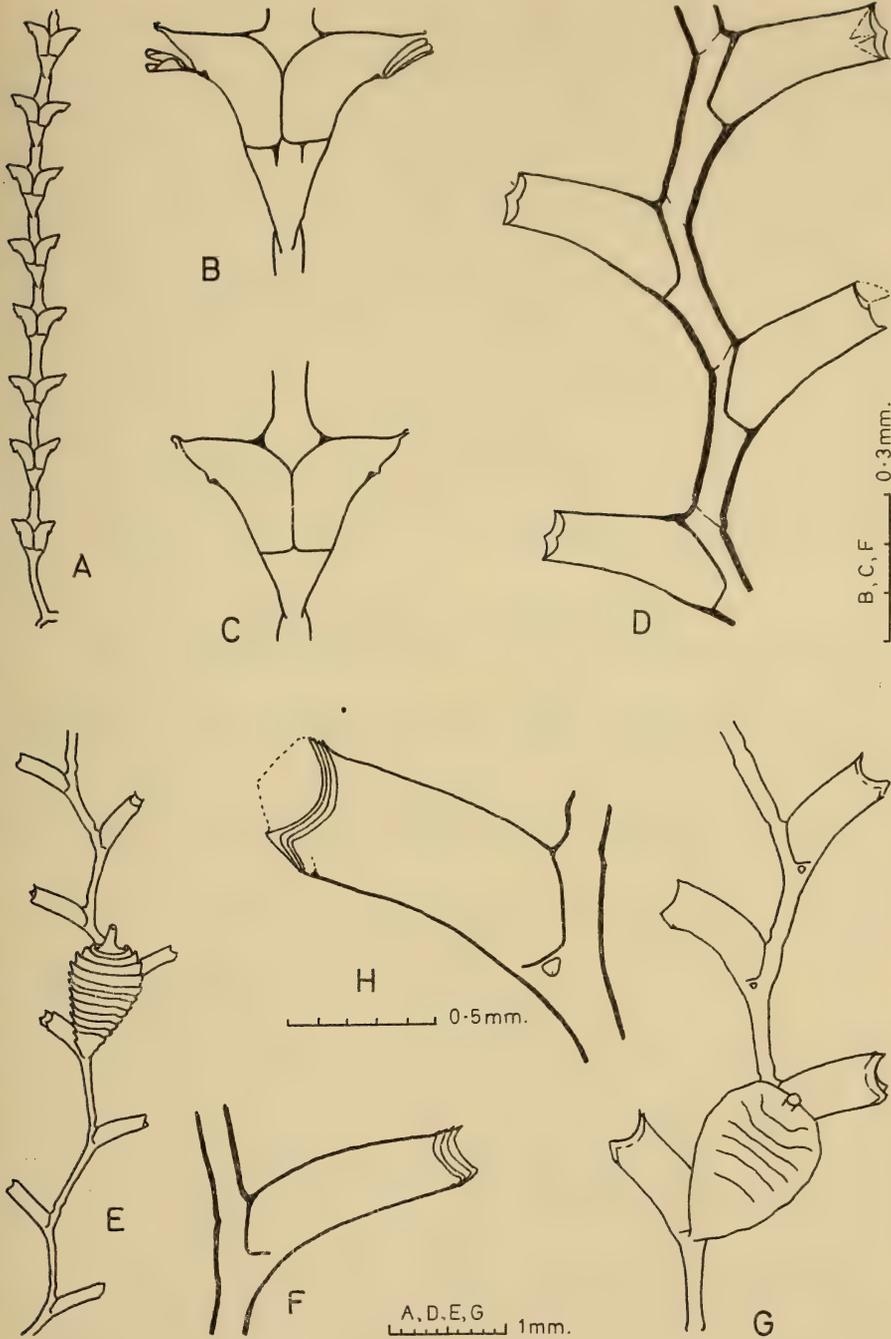


Fig. 4. Sertulariidae.

A-C. *Salacia ?desmoides* (Torrey).D. *Sertularella megista* Stechow.E-F. *Symplectoscyphus ?amphoriferus* (Allman).G-H. *Symplectoscyphus paulensis* Stechow, from ABD 8C.

Measurements (mm.)

Internode length	1·21-1·61
diameter across node	0·42-0·50
Hydrotheca, length abcauline	1·39-1·58
length adcauline, adnate part	0·65-0·75
length adcauline, free part	1·03-1·28
adnate part/adcauline length	0·34-0·42
diameter at mouth	0·48-0·56

Remarks. This material cannot be considered as specifically distinct from *S. megista* since intermediate colonies have been found (chiefly from the Natal coast) with all intergradations in measurements. It should rather be regarded as a form with especially produced hydrothecae. It is similar to the material recorded as *Sertularella* sp. (Millard, 1958), which is now included as a synonym.

The specimen bears a superficial resemblance to *S. polyzonias* var. *gigantea* Hincks, 1874, reported by Stechow (1925, fig. 6) from Plettenberg Bay, which may eventually prove to be a synonym. At present *S. megista* can be readily distinguished by the marked angle in the adcauline thecal wall and the less turgid hydrothecae.

Sertularella polyzonias (Linnaeus, 1758)

Sertularella polyzonias: Millard, 1957: 217, figs. 10J, 11H. Millard, 1958: 191.

Records. WSS 1P.

Description. Colony bearing gonophores and reaching a maximum height of 1·6 cm.

Sertularella xantha Stechow, 1923

Sertularella xantha: Stechow, 1925: 472, fig. 32. Millard, 1957: 218, figs. 10K, 11I.

Records. ABD 15A.

Description. A typical, though sterile, stem 8·5 cm. in length. Rootstock branching and fibrous for penetration of a soft substratum.

Symplectoscyphus ?amphoriferus (Allman, 1877)

Fig. 4 E, F

Sertularella amphorifera Allman, 1877: 22, pl. 15 (figs. 8-10). Nutting, 1904: 88, pl. 20 (figs. 1-2).
Billard, 1906: 183.

Records. AFR 1248 IIQ.

Description. A small colony of about ten unbranched and unfascicled stems reaching a maximum height of 1·1 cm. Stem distinctly geniculate in distal part, more or less straight in proximal part, with very slender internodes and indistinct nodes.

Hydrotheca deep and slender, standing well away from stem, adnate for about $\frac{1}{4}$ adcauline length, then curved gently outwards and narrowing very slightly to margin. Margin with three teeth (one adcauline and two lateral), often regenerated.

Gonotheca arising below hydrotheca, pear-shaped, tapering evenly to base, with a terminal aperture at the end of a slender neck, with 13 well-marked, crested, transverse annulations. One gonotheca present (sex not determinable) and scars of two others.

Measurements (mm., without regenerations)

Internode length	0.60-0.84
Hydrotheca, length abcauline (approximate)	0.35-0.45
length adcauline, adnate part	0.12-0.14
length adcauline, free part	0.34-0.46
adnate part/adcauline length	0.21-0.28
diameter at margin	0.12-0.15
Gonotheca, length	1.19
maximum diameter	0.65

Remarks. This material is assigned to *S. amphoriferus* mainly on the gonotheca, which Billard states may be less elongated and with a shorter neck than that figured by Allman. However, since the species is known only from the North Atlantic, there is some doubt as to the identification. There are also some minor differences in the trophosome, namely

- (i) The lack of any sign of branching, though this may be a juvenile character.
- (ii) A smaller proportion of the hydrotheca adnate to the stem than generally indicated.
- (iii) The detailed measurements, which are all less than those given by Billard.

The shape of the hydrotheca is most like that figured by Nutting, though the internodes are longer and more slender.

The material also shows resemblances to *S. plectilis* (Hickson and Gravely, 1907) from the Antarctic, but the gonothecae are very different.

Symplectoscyphus paulensis Stechow, 1923

Fig. 4 G, H

Symplectoscyphus paulensis: Stechow, 1925: 467, fig. 28.

Records. ABD 8C, 14B. AFR 1248 IIN.

Description. Small, and probably young, colonies reaching a maximum height of 4.7 cm. Hydrorhiza creeping. Most stems unfascicled and unbranched, though two are lightly fascicled at base and several have one or two branches or stumps thereof. Branches arising below hydrothecae and forming a wide angle with stem. The two rows of hydrothecae and branches in one plane. Stem and branches markedly geniculate in younger parts, practically straight in older parts. Nodes only faintly indicated. Internodes slender.

Hydrotheca large, tubular and not narrowing towards margin, curved slightly outwards, adnate for a third or less of adcauline length. Margin sometimes with thickened rim, with three well-marked teeth, one adcauline and two lateral. Consecutive hydrothecae separated by a distance approximately equal to abcauline thecal length. Below each hydrotheca a pair of oval fenestrae

closed by thin perisarc, through which the gonophores emerge and through which the tubes of the fascicled stem communicate.

A single gonotheca present (on ABD 8C), with about five light corrugations around distal half, with a slender terminal neck which is slightly everted at margin.

Measurements (mm.)

	ABD 8C	AFR 1248 IIN
Internode length	0.96-1.48	1.16-1.36
Hydrotheca, length abcauline (approximate)	0.71-0.91	0.64-0.87
length adcauline, adnate part	0.34-0.39	0.22-0.28
length adcauline, free part	0.76-0.92	0.72-1.00
adnate part/adcauline length	0.27-0.34	0.19-0.27
diameter at margin	0.38-0.44	0.34-0.42
Gonotheca, length	1.47	
maximum diameter	1.05	

Remarks. *S. paulensis* has been reported only once, by Stechow from St. Paul in the southern Indian Ocean. His material was sterile.

Stechow states that the discovery of intermediate forms may prove that *S. paulensis* is a form of *S. columnarius* (Briggs, 1914). However, instead of bridging the gap, the present material emphasizes the differences between the two. *S. paulensis* differs from *S. columnarius* in the following features:

- (i) The well-separated hydrothecae.
- (ii) The narrower hydrothecae (diameter at margin in present material 0.34-0.44 mm., Stechow's material 0.46, *S. columnarius* (from Ralph, 1961a) 0.40-0.60 mm.).
- (iii) The smaller proportion of the adnate part of the adcauline thecal wall (adnate part/adcauline length 0.19-0.34 in present material, 0.34-0.40 in Stechow's material, 0.43-0.5+ in *S. columnarius*).
- (iv) The smaller gonotheca with less definite annulations.

This material is also very close to *S. tropica* (Hartlaub, 1900) from the Pacific.

S. paulensis differs from *S. amphoriferus* in the larger size, different appearance of the gonotheca and different shape of the hydrotheca.

Family Plumulariidae

Kirchenpaueria triangulata (Totton, 1930)

Plumularia triangulata Totton, 1930: 225, fig. 61. Ralph, 1961b: 41, fig. 5 f-g.

Kirchenpaueria triangulata: Millard, 1962: 292, fig. 6 E-J.

Records. ABD 2C, 15S.

Description. The first sample with pinnate stems without rootstock, reaching a maximum height of 1.6 cm. Male gonophores present.

The second sample epizootic on *Halicornaria gracilicaulis* and including

both simple and pinnate stems, the latter reaching a maximum height of 2.2 cm. No gonophores present.

Structural details as in previous descriptions. In the second sample (ABD 15S) stem nodes visible only in the extreme distal region and in many hydrocladia the node between the apophysis and the first thecate internode missing.

Nemertesia ramosa Lamouroux, 1816

Nemertesia ramosa: Millard, 1962: 299, fig. 7 A-D.

Records. ABD 8A, 13F, 15Q.

Description. Colonies provided with branching rootstock for penetration of a soft substratum. Stems reaching a maximum height of 21.7 cm., some with gonophores.

Plumularia antonbruuni n. sp.

Fig. 5

Holotype. ABD 14C (South African Museum registered number: SAMH 1647).

Description. Four stems, reaching a maximum height of 5.1 cm. Hydrorhiza of branching, filamentous rootlets for penetration of a soft substratum.

Stem unfascicled, unbranched, bearing alternate hydrocladia, the two rows in one plane. Segmentation not present in lower region, indistinct in upper region. Where demarcated each internode bears one hydrocladium from an apophysis at the distal end. No internodal septa. Apophysis with a distinct mamelon on upper surface. Cauline nematothecae: one on each internode, midway along its length, on opposite side to apophysis; two on each apophysis, one on each side of, and slightly proximal to, the mamelon.

Hydrocladium with one athecate internode, sometimes followed by long thecate internodes only, but often with intermediate athecate internodes present, especially towards the distal end. First internode very short, without nematotheca, with one internodal septum in central region. Thecate internode with two internodal septa, one near proximal end and one near distal end, with 0-3 median inferior nematothecae, one pair of laterals overtopping the thecal margin and sometimes one median superior. Athecate intermediate internode, when present, with two internodal septa, one proximal and one distal, and 0-2 median nematothecae. When no athecate internodes occur the hydrotheca is seated in the distal half of the thecate internode and there are generally two median inferior nematothecae. Athecate internodes, when they occur, appear to be formed by cutting off the proximal end of a thecate internode together with one or more of the median inferior nematothecae. The following thecate internode is shorter, with the hydrotheca seated more or less in the centre and and there is generally only one median inferior nematotheca. However, many variations occur.

Hydrotheca completely adnate, with more or less straight abcauline wall and distinctly convex adcauline wall. Width at margin slightly exceeding depth.

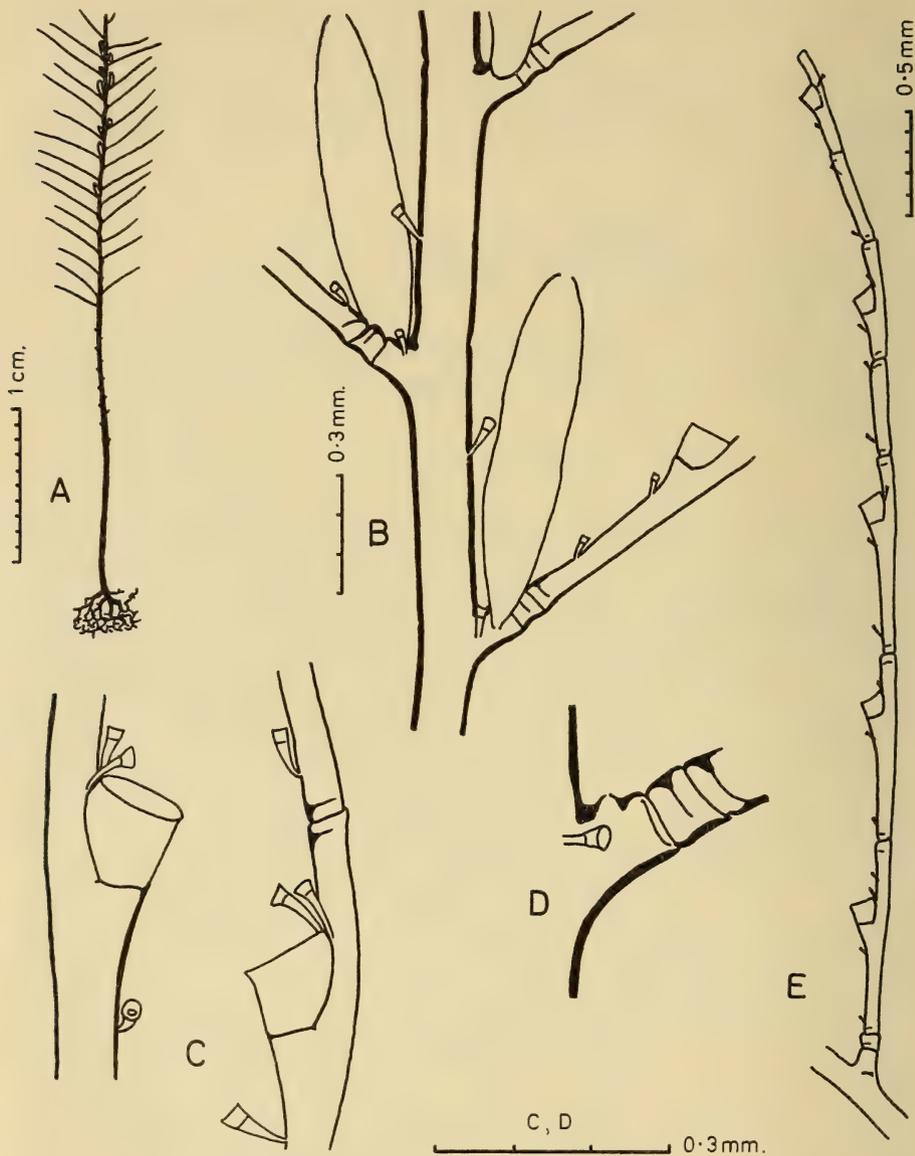


Fig. 5. *Plumularia antonbruuni* n.sp.

- A. A whole stem.
 B. A portion of the stem showing cauline nematothecae and gonothecae.
 C. Portions of hydrocladia with hydrothecae.
 D. The origin of a hydrocladium.
 E. A single complete hydrocladium.

Nematothecae all two-chambered and movable, laterals slightly shorter than hydrothecae.

Gonothecae (male) borne on hydrocladial apophyses, one or two to each, smooth, elongated, with terminal aperture, held at a small angle ($10-15^\circ$) to stem.

Measurements (mm.)

Stem internode, length	0.63-0.70
diameter at node	0.13-0.17
Hydrocladium, first athecate internode, length	0.06-0.11
normal thecate internode, length	0.85-0.95
diameter near centre	0.06-0.08
athecate internode, other than first, length	0.38-0.66
Hydrotheca, depth abcauline	0.08-0.10
diameter at margin	0.11-0.12
Gonotheca, length	0.82-0.92
maximum diameter	0.20-0.27
Lateral nematotheca, length	0.07-0.09

Remarks. Although I am reluctant to create a new species in a genus which is already so richly represented there is no other species with quite the same assortment of characters. *P. antonbruuni* is close to *P. diploptera* Totton, 1930, differing from it in the fact that athecate intermediate internodes are normally absent, in its much longer internodes and in the absence of a subthecal inter-nodal septum.

It is also close to *P. ventriculiformis* Marktanner, 1890, differing from it in the presence of a short athecate internode at the base of the hydrocladium and in the presence of only one hydrocladium to a stem internode. It resembles it in the sporadic occurrence of athecate intermediate internodes in the distal parts of the hydrocladium, but in *P. ventriculiformis* these seem to be cut off from the distal ends of the internodes. The two species differ in the shape of the gonotheca.

It is closest of all to *P. orientalis* Billard, 1913, differing only in its larger size, in the usual absence of intermediate athecate internodes and in the presence of cauline nematothecae on the main axis of the stem. The hydrothecae are also a little deeper. The gonothecae of *P. orientalis* are unknown.

Closely related to *P. orientalis* are *P. delicata* Nutting, 1905, and *P. milleri* Nutting, 1905. In these the gonothecae of the former are relatively short and fat while those of the latter are held at right angles to the stem.

Plumularia setacea (Linnaeus, 1758)

Plumularia setacea: Hincks, 1868: 296, pl. 66 (fig. 1). Millard, 1962: 301.

Records. WSS 1L.

Description. A rich colony of numerous fertile stems reaching a maximum height of 6.8 cm.

Cladocarpus distomus Clarke, 1907

Fig. 6

- Cladocarpus distomus* Clarke, 1907: 17, pl. 14. Stechow, 1925: 506, fig. 47.
Cladocarpus sibogae: Billard, 1913: 71, fig. 57, 58, pl. 4 (fig. 39). Billard, 1918: 25.
Cladocarpella multiseptata Bale, 1915: 304, pl. 47 (figs. 1-5). Bale, 1919: 356.
 ?*Cladocarpus bathyzonatus* Ritchie, 1911: 861, pl. 89 (figs. 2, 6-11).
 ?*Cladocarpus multiapertus*: Billard, 1913: 73, fig. 59.
 ?*Cladocarpus alatus* Jarvis, 1922: 351, fig. 2, pl. 26 (fig. 25).
 ?*Cladocarpus plumularioides* Jarvis, 1922: 352, fig. 3.

Records. ABD 11A, 12F, 13E, 16B, 17B.

Description of typical form. Hydrorhiza forming a branching and filamentous rootstock penetrating up to 2.5 cm. into the bottom ooze. The first rootlets arise from the peripheral tubes of what would normally be considered stem and from here on the tubes continue to separate and subdivide until the final ramifications are only 0.15 mm. in diameter.

Stem reaching a maximum height of 9.7 cm., weakly fascicled in basal region; the principal tube always exposed on anterior surface and divided very irregularly by distinct oblique nodes, sometimes with a group of three or four of the latter close together below the level of the first hydrocladium and thereafter isolated ones at more distant, but irregular, intervals. Principal tube giving rise to alternate hydrocladia in its distal part and bearing a row of fairly regularly spaced cauline nematothecae on anterior surface. Of the latter there are 2-12 between the origins of two consecutive hydrocladia, of which one is always axillary.

Hydrocladium bearing up to 23 thecate internodes separated by oblique nodes. Internodal septa variable in number: one below level of median inferior nematotheca, 1-11 behind the hydrotheca and 0-7 above it. Each internode bearing, in addition to the hydrotheca, one median inferior nematotheca which is quite free from the hydrotheca, one pair of laterals and one to three (usually one) median superior nematothecae.

Hydrotheca deep, expanding towards margin, which is perpendicular to hydrocladium. Those hydrothecae at distal end of hydrocladium deeper than those at proximal end. A delicate shelf arising from adcauline side near base and overarching the hydropore. Margin with one median abcauline tooth.

Median nematotheca with a terminal aperture in the form of a narrow transverse slit, which may be subdivided into two parts, and a rounded opening on upper surface near base.

Lateral nematotheca applied to margin of hydrotheca and extending round it usually as far as the median tooth, though sometimes terminating before this; with numerous distal apertures, of which the first is generally raised slightly above the level of the others.

Phylactocarps arising from bases of thecate internodes, as many as six to a hydrocladium, each consisting of 3-6 internodes bearing two nematothecae each. Gonotheca borne on basal phylactocarpal internode, elongate, with a broad distal aperture.

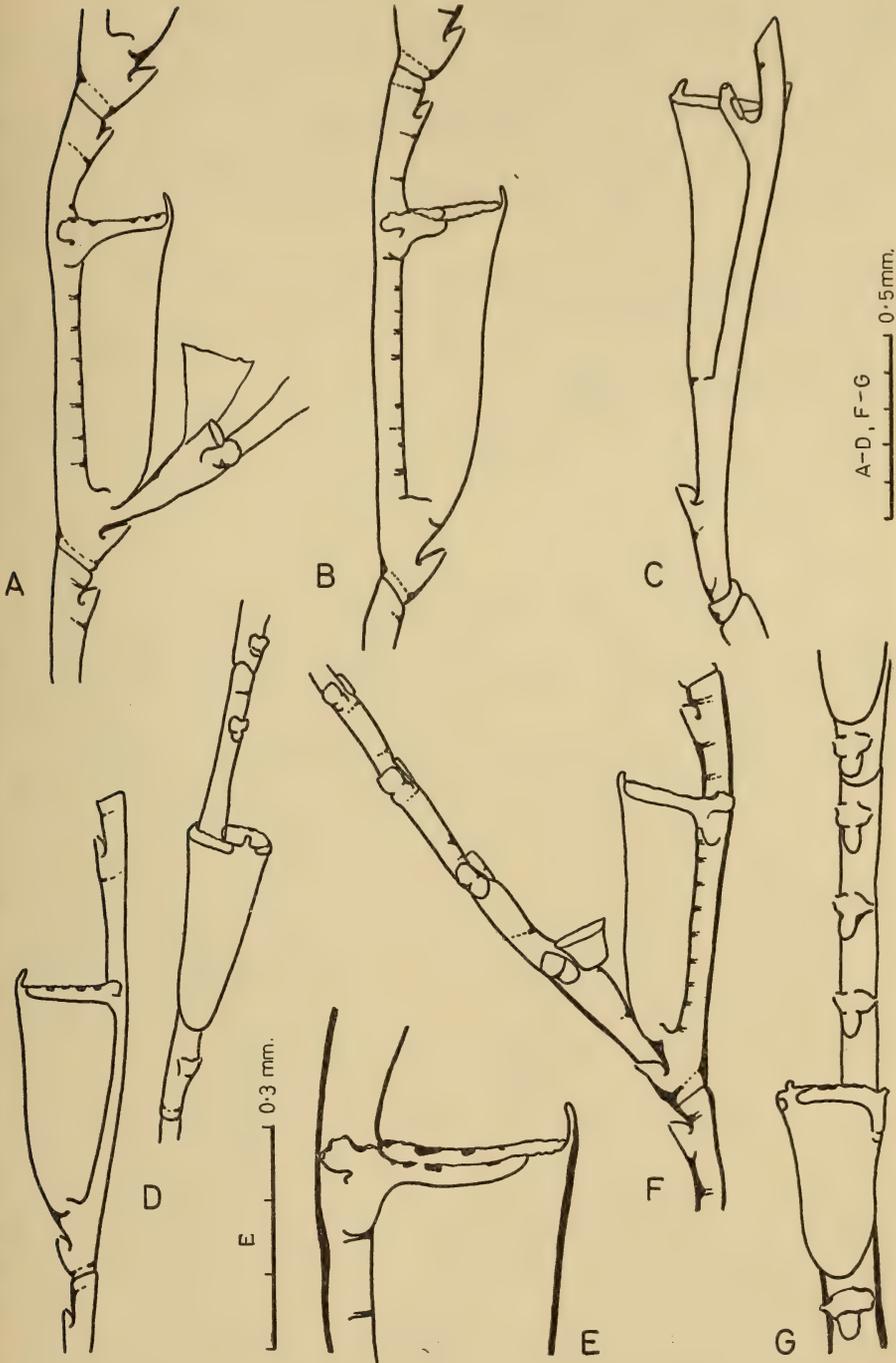


Fig. 6. *Cladocarpus distomus* Clarke.

A-D. Hydrothecae from different colonies. A and B from ABD 13E, C from ABD 16B, D from ABD 11A.

E. Part of a hydrotheca showing the lateral nematotheca from ABD 13E.

F-G. Diagrams from Stechow's slides from Valdivia stations 258 and 264 respectively. (A and F show portions of phylactocarps)

Measurements (mm.)

	ABD 16B	ABD (rest)	Stechow's material	
			Vald. 258	Vald. 264
Distance between 2 consecutive hydrocladia	1.69-2.87	0.81-1.19		
Hydrocladium, internode length	1.55-1.60	1.14-1.52	1.11-1.38	1.08-1.17
Hydrotheca, depth including median tooth	0.83-1.01	0.51-0.92	0.53-0.83	0.65-0.79
diameter at margin	0.26	0.21-0.29	0.20-0.27	0.24-0.26
Gonotheca, height		1.40-1.50	1.08-1.12	
maximum diameter		0.32-0.36	0.34-0.38	

Remarks. One of the samples, ABD 16B, shows certain divergences from the above description. It consists of a single stem 3.5 cm. in height, with rootstock, but with only two imperfect hydrocladia remaining. The stem has no oblique joints, but a few irregular and indistinct transverse nodes in the distal region. The hydrocladial internodes are long, especially in their proximal regions, so that the median inferior nematotheca is well separated from the hydrotheca. The superior median nematotheca is missing on those hydrocladia which remain and the lateral nematothecae have only one terminal aperture each and do not extend round the lateral margin of the hydrotheca.

The remaining samples are identical with Stechow's material from East Africa described in 1925 and attributed to *C. distomus*. This was established by comparison with Stechow's slides from Valdivia stations 258 and 264 kindly loaned to me by the Munich Museum. The 'Verdoppelung des Thekenrandes' described and figured by Stechow is none other than the extension of the lateral nematotheca as in the present material. Measurements of Stechow's specimens, taken by myself, are included above for comparison.

Stechow has included two other species under the synonymy of *C. distomus*, namely *C. sibogae* Billard, 1911, and *C. multiseptatus* (Bale, 1915). Also closely related are *C. bathyzonatus* Ritchie, 1911, *C. multiapertus* Billard, 1911, *C. alatus* Jarvis, 1922 and *C. plumularioides* Jarvis, 1922. These species appear to differ in certain features such as the number of internodal septa, number of cauline nematothecae, presence or absence of superior median nematothecae, the structure of the lateral nematothecae, etc.

The number of internodal septa has been recognised as being of little systematic value and has been shown to be variable in *C. multiseptatus* by Bale in 1919, in *C. sibogae* by Billard in 1913 and in the Valdivia material by Stechow

in 1925. The number of cauline nematothecae between two consecutive hydrocladia is equally unreliable as it can vary within a single colony.

A superior median nematotheca is present in the type material of *C. distomus*, in Stechow's Valdivia material and in *C. plumularioides*, but absent in all other species. In this collection it is absent in ABD 16B but present in the other samples. In Stechow's material the number varies from one to three depending on the length of the internode. It is probable that this also is a variable character.

The nematothecae of all the species listed are similar in that they possess a circular lateral aperture and a narrow slit-like terminal aperture which has a tendency for subdivision. The latter tendency is particularly marked in the lateral nematothecae where, of the species listed above, one terminal aperture is described for *C. distomus* (type material), *C. sibogae*, *C. multiseptatus* and *C. plumularioides*, two for *C. multiapertus*, one to three in *C. bathyzonatus* and many in *C. alatus*. Stechow's Valdivia material was shown by examination to have many, as does the present material, excepting ABD 16B where there is only one. In the most extreme examples the lateral nematotheca extends right round the margin of the hydrotheca to the median abcauline tooth. Ritchie has shown that the number of terminal apertures may vary from one to three in *C. bathyzonatus*, and Jarvis has remarked on variation in the number in *C. alatus*. In the present material and in Stechow's material a similar variation occurs within a colony, so that some nematothecae are like those of *C. bathyzonatus* and some like those of *C. alatus*.

Apparently the number of terminal apertures in the median nematothecae is also variable in *C. bathyzonatus* where Ritchie describes one or two, and in *C. multiapertus* where Billard describes one, two, or three.

It is probable, therefore, that all these records should be included in one very variable species, namely *C. distomus* Clarke, occurring in deepish tropical or subtropical waters all round the globe. As such, the recorded distribution would include the Eastern Pacific, East Africa, the East Indies and Australia. The rootstock appears to be similar in those records where it is described and is adapted for obtaining a foothold in a muddy or sandy bottom.

Halicornaria gracilicaulis (Jäderholm, 1903)

Lytocarpus gracilicaulis Jäderholm, 1903: 299, pl. 14 (figs. 3-4).

Halicornaria gracilicaulis: Billard, 1907: 364, fig. 12, pl. 25 (fig. 7). Billard, 1913: 63. Millard, 1958: 219, fig. 15 I, J.

Records. ABD 15R.

Description. A single young stem, 3.9 cm. in total height. About 1.5 cm. of this represents a rootstock and apparently penetrates into mud. It consists of numerous and sometimes branching rootlets arising from the central fascicled axis at irregular levels. Stem fascicled except for the distal region, unbranched, bearing no pinnae but alternate hydrocladia with a maximum of six hydrothecae each.

Hydrocladia with internodal septa poorly developed and internodes rather long and slender.

Hydrothecae very similar to those illustrated by Billard, 1907, and differing from those previously illustrated (Millard, 1958) in their greater length.

Gonophores absent.

DISCUSSION

The hydroid fauna of the deeper waters of the Indian Ocean is at present very poorly known. A total of 18 species is recorded here from depths of over 300 m., of which two are new: *Hincksella indiana* and *Plumularia antonbruuni*. Of the remainder, 6 are cosmopolitan (*Stegopoma fastigiatum*, *Acryptolaria conferta*, *A. crassicaulis*, *Filellum serratum*, *Lafaea fruticosa* and *Nemertesia ramosa*), 6 have affinities in the southern oceans (*Zygophylax armata*: Gough Island, South Africa; *Hincksella echinocarpa*: Kerguelen Island; *Sertularella megista*: South Africa, possibly Antarctic; *S. xantha*: South Africa; *Symplectoscyphus paulensis*: St. Paul; *Kirchenpaueria triangulata*: New Zealand, South Africa), 3 have tropical or subtropical affinities (*Acryptolaria rectangularis*: tropical East Africa; *Cladocarpus distomus*: Eastern Pacific, East Indies, North Australia, East Africa; *Halicornaria gracilicaulis*: Eastern Pacific, East Indies, Indian Ocean, Natal) and one is known only from the North Atlantic (*Symplectoscyphus amphoriferus*).

Seven species are recorded from the shallower water of Walter's Shoal, of which four are cosmopolitan (*Filellum serratum*, *Sertularella mediterranea*, *S. polyzonias* and *Plumularia setacea*), one occurs in South Africa (*Sertularella megista*), one in the southern oceans extending into the tropics (*Sertularella arbuscula*: Australia, tropical East Africa, South Africa, South Atlantic) and one is known only from the North Pacific (*Salacia desmoides*).

It is interesting that a number of species can adapt themselves to life in deeper waters by the development of a fibrous, branching rootstock suitable for penetrating and supporting the colony in the soft substratum which is normally encountered. Six species show this characteristic, namely *Hincksella echinocarpa*, *Sertularella xantha*, *Nemertesia ramosa*, *Plumularia antonbruuni*, *Cladocarpus distomus* and *Halicornaria gracilicaulis*. Some of these at least can also produce the normal flattened hydrorhiza on a hard substratum.

SUMMARY

A total of 23 species of hydroids is recorded from the Indian Ocean in the area east of South Africa and south of Madagascar. Some of these were collected by the R/V *Anton Bruun* during the International Indian Ocean Expedition in 1964 and some by the R/V *Africana II* in 1961. Descriptions and diagrams are included for the lesser known species. Two new species are described

and illustrated, namely *Hincksella indiana* and *Plumularia antonbruuni*. The geographical distribution of the species is briefly discussed.

ACKNOWLEDGEMENTS

The Author wishes to acknowledge with thanks the loan of Stechow's slides of *Cladocarpus distomus* from the Zoologische Sammlung des bayerischen Staates, Munich. Acknowledgements are also due to the Editorial Board of the University of Cape Town and to the Council for Scientific and Industrial Research for financial aid in publication. The holotypes of the new species will be deposited in the South African Museum.

REFERENCES

- ALDER, J. 1856. A notice of some new genera and species of British hydroid zoophytes. *Ann. Mag. nat. Hist.* (2) **18**: 353-362.
- ALLMAN, G. J. 1877. Report on the Hydroida collected during the exploration of the Gulf Stream by L. F. de Pourtalès, assistant United States Coast Survey. *Mem. Mus. comp. Zool. Harv.* **5**: 1-66.
- ALLMAN, G. J. 1888. Report on the Hydroida dredged by H.M.S. *Challenger* during the years 1873-76. Part II. The Tubularinae, Corymorphinae, Campanularinae, Sertularinae and Thalamophora. *Rep. Voy. Challenger 1873-76* **23** (70): 1-90.
- BALE, W. M. 1888. On some new and rare Hydroida in the Australian Museum collection. *Proc. Linn. Soc. N.S.W.* (2) **3**: 745-799.
- BALE, W. M. 1914. Report on the Hydroida collected in the Great Australian Bight and other localities. Part II. *Zool. Res. Fish. Exp. 'Endeavour'* **2**: 166-188.
- BALE, W. M. 1915. Report on the Hydroida collected in the Great Australian Bight and other localities. III. *Zool. Res. Fish. Exp. 'Endeavour'* **3**: 241-336.
- BALE, W. M. 1919. Further notes on Australian hydroids. IV. *Proc. roy. Soc. Vict.* **31**: 327-361.
- BILLARD, A. 1906. Hydroïdes. *Expéd. sci. 'Travailleur' et du 'Talisman'* **8**: 153-244.
- BILLARD, A. 1907. Hydroïdes de Madagascar et du Sud-Est de l'Afrique. *Arch. Zool. exp. gén.* (4) **7**: 335-396.
- BILLARD, A. 1910. Revision d'une partie de la collection des Hydroïdes du British Museum. *Ann. Sci. nat. zool.* (9) **11**: 1-67.
- BILLARD, A. 1913. Les Hydroïdes de l'expédition du Siboga. I. Plumulariidae. *Siboga Exped.*, no. VIIa: 1-115.
- BILLARD, A. 1918. Notes sur quelques espèces d'hydroïdes de l'expédition du 'Siboga'. *Arch. Zool. exp. gén.* **57**: 21-27.
- BILLARD, A. 1924. Note critique sur divers genres et espèces d'Hydroïdes avec la description de trois espèces nouvelles. *Rev. suisse Zool.*, **31**: 53-74.
- BILLARD, A. 1925. Les Hydroïdes de l'expédition du Siboga. II. Synthecidae et Sertularidae. *Siboga Exped.*, no. VIIb: 117-232.
- CLARKE, S. F. 1879. Report on the Hydroida collected during the exploration of the Gulf Stream and Gulf of Mexico by Alexander Agassiz, 1877-78. *Bull. Mus. comp. Zool. Harv.* **5**: 239-252.
- CLARKE, S. F. 1907. The Hydroids. In: Reports on the scientific results of the expedition to the Eastern Tropical Pacific, etc. *Mem. Mus. comp. Zool. Harv.* **35**: 1-18.
- FRASER, C. McL. 1937. *Hydroids of the Pacific coast of Canada and the United States*. Toronto.
- JÄDERHOLM, E. 1903. Ausereuropäische Hydroiden im schwedischen Reichsmuseum. *Ark. Zool.* **1**: 259-312.
- JARVIS, F. E. 1922. The hydroids from the Chagos, Seychelles and other islands and from the coasts of British East Africa and Zanzibar. *Trans. Linn. Soc. Lond. Zool.* **18**: 331-360.
- MARKTANNER-TURNERETSCHER, G. 1890. Die Hydroiden des k. k. naturhistorischen Hofmuseums. *Ann. naturh. Mus. Wien* **5**: 195-286.

- MILLARD, N. A. H. 1957. The Hydrozoa of False Bay, South Africa. *Ann. S. Afr. Mus.* **43**: 173-243.
- MILLARD, N. A. H. 1958. Hydrozoa from the coasts of Natal and Portuguese East Africa. Part I. Calyptoblastea. *Ann. S. Afr. Mus.* **44**: 165-226.
- MILLARD, N. A. H. 1962. The Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae. *Ann. S. Afr. Mus.* **46**: 261-319.
- MILLARD, N. A. H. 1964. The Hydrozoa of the south and west coasts of South Africa. Part II. The Lafoeidae, Syntheciidae and Sertulariidae. *Ann. S. Afr. Mus.* **48**: 1-56.
- NAUMOV, D. V. 1960. Hydroids and hydromedusae of the marine, brackish and freshwater basins of the U.S.S.R. (In Russian). *Opred. Faune SSSR* **70**: 1-585.
- NUTTING, C. C. 1904. American hydroids. Part II. The Sertulariidae. *Spec. Bull. U.S. nat. Mus.* **4** (2): 1-151.
- NUTTING, C. C. 1905. Hydroids of the Hawaiian islands collected by the steamer 'Albatross' in 1902. *Bull. U.S. Fish Comm.* **23**: 931-959.
- RALPH, P. M. 1957. New Zealand thecate hydroids. Part I. Campanulariidae and Campanulinidae. *Trans. roy. Soc. N.Z.* **84**: 811-854.
- RALPH, P. M. 1958. New Zealand thecate hydroids. Part II. Families Lafoeidae, Lineolariidae, Haleciidae and Syntheciidae. *Trans. roy. Soc. N.Z.* **85**: 301-356.
- RALPH, P. M. 1961a. New Zealand thecate hydroids. Part III. Family Sertulariidae. *Trans. roy. Soc. N.Z.* **88**: 749-838.
- RALPH, P. M. 1961b. New Zealand thecate hydroids. Part IV. The family Plumulariidae. *Trans. roy. Soc. N.Z. Zool.* **1**: 19-74.
- RITCHIE, J. 1907. The hydroids of the Scottish National Antarctic Expedition. *Trans. roy. Soc. Edinb.* **45**: 519-545.
- RITCHIE, J. 1911. Hydrozoa (hydroid zoophytes and Stylasterina). In: Scientific results of the trawling expedition of H.M.C.S. 'Thetis'. *Mem. Aust. Mus.* (4) **2**: 807-869.
- STECHOW, E. 1913. Hydroidpolyphen der japanischen Ostküste. II. Campanulariidae, Haleciidae, Lafoeidae, Campanulinidae und Sertulariidae, nebst Ergänzungen zu den Athecata und Plumulariidae. *Abh. bay. Akad. Wiss. math.-phys.* **3** (2): 1-162.
- STECHOW, E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. 'Valdivia'* **17**: 383-546.
- TOTTON, A. K. 1930. Coelenterata. Part V. Hydroida. *Nat. Hist. Rep. Terra Nova Exped.* **5**: 131-252.
- U.S. Program in Biology, International Indian Ocean Expedition. 1965. Final Cruise Report, Anton Bruun Cruises 7, 8, 9, **1**: Woods Hole Oceanographic Inst.
- VERVOORT, W. 1959. The Hydroida of the tropical west coast of Africa. *Atlantide Rep.* **5**: 211-325.
- WARREN, E. 1908. On a collection of hydroids, mostly from the Natal coast. *Ann. Natal Mus.* **1**: 269-355.

INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) 9: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. 2. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. 3: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1953*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).

7.68

L. D. BOONSTRA

THE BRAINCASE, BASICRANIAL AXIS AND
MEDIAN SEPTUM IN THE
DINOCEPHALIA

May 1968 Mei
Volume 50 Band
Part 10 Deel



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

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R3.00

THE BRAINCASE, BASICRANIAL AXIS AND MEDIAN SEPTUM IN THE DINOCEPHALIA

By

L. D. BOONSTRA

(With 58 figures)

CONTENTS

Introduction	195
Material	195
Technique	198
Descriptions of specimens systematically	199
Tapinocephalia	199
Anteosauria	230
Titanosuchia	238
The Dinocephalian Braincase	255
Contemporary Therapsids	259
Dicynodontia	260
Therocephalia	264
Comparative	266
References	273

INTRODUCTION

During the past few years I have been able to collect some interesting cranial material of three of the infra-orders of the suborder Dinocephalia. Part of this material has been collected with financial aid from the South African Council for Scientific and Industrial Research. To this Council I am moreover indebted for funds which made the acquisition of diamond-studded circular saws for cutting serial sections possible. This method has revealed important points of structure which would have been wellnigh impossible to ascertain at all accurately by the hammer-and-chisel technique on which I have had to rely hitherto.

MATERIAL

All previously described specimens have been re-examined and the following new material has been studied:

TAPINOCEPHALIA

S.A.M. 5584 *Struthiocephalus* sp., Abrahamskraal, Prince Albert. Pres. W. van der Byl 1919.

This specimen consists of a partially disarticulated skull. Through the posterior part of the skull a number of longitudinal sections have been cut to show the posterior part of the braincase and the parietal tube in sagittal section.

S.A.M. 9129 *Struthiocephalus* sp., Voëlfontein, Prince Albert. Collected L. D. Boonstra 1929.

This consists of an isolated lower half of an occiput beautifully preserved. It has been cut through sagittally and the left half of the posterior part of the braincase has been exposed internally.

S.A.M. 12294 *Keratocephalus moloch*, Boesmansrivier, Beaufort West. Collected L. D. Boonstra 1937.

This specimen consists of the posterior half of a skull. Both sides of the braincase have been well exposed and a sagittal cut has enabled me to clear the left half of the endocranial cavity.

S.A.M. 11701 *Criocephalus* sp., Elandsberg, Sutherland. Collected L. D. Boonstra 1946.

This specimen consists mainly of an incomplete occiput and skull-cap through which a sagittal cut has been made to show the parietal tube and adjacent bones.

S.A.M. 11972 *Moschops capensis*, Kruisvlei, Beaufort West. Collected L. D. Boonstra 1929.

The specimen consists of a good posterior half of a skull figured in 1957. A block has now been cut out of the middle portion and this has been serially sectioned in the transverse plane to study the internal structure of the braincase and adjacent structures.

S.A.M. 11985 *Moschops* sp., Dikbome, Laingsburg. Collected L. D. Boonstra 1951.

This is a beautifully preserved lower half of an occiput in which the posterior part of the braincase has been exposed internally.

S.A.M. 12046 *Criocephalus* sp., Skoppelmaaikraal, Laingsburg. Collected L. D. Boonstra and H. Zinn 1956.

A skull-cap in which most of the surface bone has been weathered away, but a longitudinal cut has exposed the parietal tube in sagittal section.

S.A.M. 12049 *Struthiocephalus whaitsi*, Dwarsrivier, Laingsburg. Collected L. D. Boonstra and A. Bothma 1957.

This is a good skull, which on exposure has fortuitously cracked through in a more or less longitudinal plane, so that I have been able to clean the whole of the braincase internally and take a direct cast of the endocranial cavity.

S.A.M. 12060 *Mormosaurus* sp., Aasvoëlbos, Beaufort West. Collected L. D. Boonstra and G. S. Victor 1957.

This specimen located by Mr. Victor consists of a very good skull fractured longitudinally, so that I could study the left half in the conventional manner and of the right half I have cut a consecutive series of 76 transverse sections.

S.A.M. 12062 *Struthiocephalus* sp., Skoenmaker, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A skull-cap through which some longitudinal sections have exposed the parietal tube in sagittal section.

S.A.M. 12066 *Criocephalus* sp., Skoenmaker; Beaufort West. Collected L. D. Boonstra 1957.

This is a well preserved skull cap showing much of the outer surface and a sagittal cut has exposed the whole parietal tube.

S.A.M. 12091 *Struthiocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A skull-cap in which a number of transverse sections have shown the nature of the olfactory tracts and the pineal tube.

S.A.M. 12092 *Struthiocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

A fair skull in which a series of longitudinal sections have revealed much of the structure of the braincase.

S.A.M. 12093 and 12094 *Keratocephalus* sp., Kalkkraal, Beaufort West. Collected L. D. Boonstra and H. Zinn 1957.

These two skulls have by natural weathering exposed much of the internal structure of the braincase.

S.A.M. K268. *Criocephalus gunyankaensis*, Gunyankás Kraal, Busi Valley, Southern Rhodesia. Pres. A. M. MacGregor 1945.

Posterior parts of crania showing little of the structure but with most interesting evidence of the parietal organ.

TITANOSUCHIA

S.A.M. 11486 *Jonkeria* sp., Mynhardtskraal, Beaufort West. Collected L. D. Boonstra 1940.

A good snout of which the one half has been serially sectioned transversely to show the structure of the anterior part of the median septum.

S.A.M. 11556 *Jonkeria* sp., Mynhardtskraal, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A skull of which the outer surface has mostly been weathered away. I have cut a block out of the middle part of the back of the skull and this has been serially sectioned in the transverse plane to study the braincase.

S.A.M. 11574 *Jonkeria* sp., Klein-Koedoeskop, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A fairly good skull of which 144 consecutive transverse sections have been cut and from which much of the internal cranial structure can be determined.

S.A.M. 11575 *Jonkeria* sp., Klein-Koedoeskop, Beaufort West. Collected L. D. Boonstra and C. J. Avenant 1940.

A snout serially sectioned in the transverse plane.

S.A.M. 11884 *Jonkeria vanderbyli*, Skroefpaal, Prince Albert. Collected L. D. Boonstra and P. J. Rossouw 1948.

A good skull in which the braincase has been exposed laterally by conventional preparation.

ANTEOSAURIA

S.A.M. 9085 *Anteosaurus* sp., Boesmansrivier, Beaufort West. Collected L. D. Boonstra 1929.

A snout from which a number of transverse slabs have been cut.

S.A.M. 12082 *Anteosaurus* sp., Boesmanskop, Beaufort West. Collected L. D. Boonstra, H. Zinn and A. Viviers 1957.

An imperfect skull contained in blocks of sandstone. Serial transverse sections have revealed some interesting internal structures.

ANOMODONTIA

S.A.M. 12217 *Dicynodon* sp., Buffelsvlei, Beaufort West, Collected L. D. Boonstra and J. Marais 1959.

Serially sectioned.

THEROCEPHALIA

S.A.M. K210 *Maraisaurus parvus*, Lammerkraal, Prince Albert. Collected L. D. Boonstra 1959.

Serially sectioned.

S.A.M. K253 *Pristerognathoides* sp., Rietfontein, Prince Albert. Collected L. D. Boonstra 1960.

Serially sectioned.

TECHNIQUE

A number of specimens have been prepared conventionally by mechanical means to expose the surface features of the cranial base from the ventral side and the braincase and interorbital, septum and anterior dermal septum in lateral view using hammer and chisel, vibro-needles and abrasive burrs.

In a few cases fortuitous natural fractures have enabled me to expose the internal faces of the endocranial cavity mechanically. In some others I have cut posterior parts of skulls longitudinally and was thus enabled to remove the infilling matrix in the endocranial cavity mechanically.

Certain pieces of the posterior parts of fragmentary skulls were cut by circular diamond-studded saws into slabs longitudinally. If luckily cut in the right plane quick results were obtained especially for sections in the sagittal plane. But in general longitudinal serial sectioning is unsatisfactory.

The best results were obtained when cutting thin slabs serially in a transverse plane. Although the thickness of the blade caused some loss, the fact that neither the skulls themselves were symmetrical nor the cut truly transverse usually resulted in a loss on one side only. I first used a large diameter saw to cut through the whole skull, but later got better results by first cutting a rectangular block out of the middle of the skull and then serially sectioning the smaller block with a smaller and thinner blade.

The sections were lightly etched with hydrochloric acid, which also caused a differential bleaching action in many cases.

By making sure that one always has a base line, it is easy to obtain graphical reconstructions in planes at right angles to the sections.

Although I have not done so it will be quite easy to prepare reconstructions in three dimensions in wax or any other suitable material.

In those cases where the endocranial cavity was cleaned mechanically I have made casts in a pliable material (Minimould and Revultex).

I may add here that when contemplating cutting serial sections with a diamond-studded circular saw only suitable material should be selected. In any case, only saws which polish as well as cut should be used.

Sound skulls, unweathered and with little fracturing or cracks, should be selected.

Specimens in an arenaceous matrix are better than those in a more argillaceous matrix because in the latter the differentiation between bone and matrix is difficult to obtain by the etching process I have used.

DESCRIPTIONS OF THE SPECIMENS SYSTEMATICALLY

TAPINOCEPHALIA

S.A.M. 5584 *Struthiocephalus* sp. (Fig. 1)

A number of longitudinal sections have been cut through the posterior third of a skull and the posterior part of the braincase and the parietal tube is

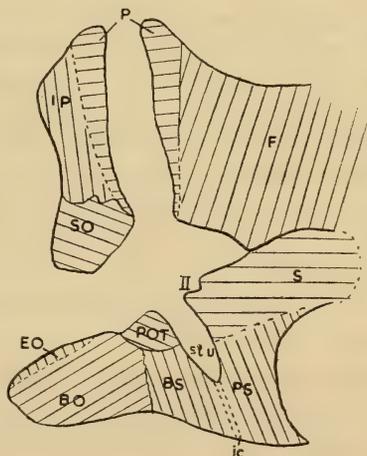


FIG. 1. *Struthiocephalus* sp. S.A.M. 5584 $\times \frac{1}{4}$.
Sagittal section of the posterior part of the skull.

See overleaf for key to this and the other figures in this paper

KEY TO THE FIGURES

abnp	— anterior border of the nasal passage	PBS	— parabasisphenoid
ac	— accessory carotid foramen	pc	— postcanine
bol	— olfactory bulb	pin	— pineal (parietal) foramen or tube
BS	— basisphenoid	PM	— premaxilla
bpp	— basipterygoid process	POC	— paroccipital
C	— canine	PO	— postorbital
ch	— choana	PF	— postfrontal
ds	— dorsum sellae	PP	— postparietal
E.O.	— exoccipital	PRF	— prefrontal
E.P.	— epipterygoid	POT	— proötic
F	— frontal	PRS	— presphenoid
fj	— jugular foramen	PS	— parasphenoid
fl	— flocculus	PT	— pterygoid
fo	— fenestra ovalis	ptf	— posttemporal fossa
fob	— foramen for ophthalmic branches of V and VII	pts	— septum of the pterygoid
FS	— frontosphenoid	qr	— quadrate ramus of the pterygoid
fvc	— foramen entering vomerine canal for the branch of the naso-palatine nerve	S	— sphenoid-complex
hy	— hypophysis	seo	— sutural face for the exoccipital
iam	— internal auditory meatus	sep	— sutural face for the epipterygoid
ic	— internal carotid foramen	sip	— sutural face for the interparietal
I.P.	— interparietal (postparietal, dermo-supraoccipital)	sp	— sutural face for the parietal
ipv	— interpterygoid vacuity	spbs	— sutural face for the parabasisphenoid
L	— lacrimal	spt	— sutural face for the pterygoid
lob	— lobus olfactorius	sq	— sutural face for the quadrate
lrp	— lateral ramus of the pterygoid	ssq	— sutural face for the squamosal
mcv	— medial cerebral vein	st	— sutural face for the tabular
med	— medulla	SM	— septomaxilla
N	— nasal	smf	— septomaxillary foramen
nob	— notch for the ophthalmic branch of V and VII	sml	— ledge of septomaxillary
np	— notochordal pit in the basioccipital	sms	— spur of septomaxilla
obg	— groove for the olfactory bulb	SO	— supraoccipital
OO	— opisthotic	SS	— septosphenoid
OS	— orbitosphenoid	ST	— stapes
P	— parietal	stu	— sella turcica
PA	— palatine	tol	— tractus olfactorius
		uz	— unossified zone
		V	— vomer
		VC	— vomer canal for naso-palatine nerve
		VS	— median septum of the vomer

here figured in sagittal section. Noteworthy features ascertained are: the proötics meet in the median line to form the upper part of the dorsum sellae; the lower half of the sella turcica lies in the basisphenoid and the internal carotids enter at the bottom of the sella; the frontals form part of the roof of the braincase above the olfactory lobes. This specimen also shows that the ascending process of the proötic meets a descending process of the supraoccipital in the lateral wall of the braincase so that the proötic incisure is closed anteriorly to form a large trigeminal fenestra. The parasphenoid and the sphenoidal complex form a median septum.

The constituent parts of the sphenoidal complex are not recognizable as separate ossifications.

S.A.M. 9129 *Struthiocephalus* sp. (Figs 2-4)

This beautifully preserved disarticulated piece of the occiput found as an isolated piece shows a number of features very clearly. In occipital view (fig. 2)

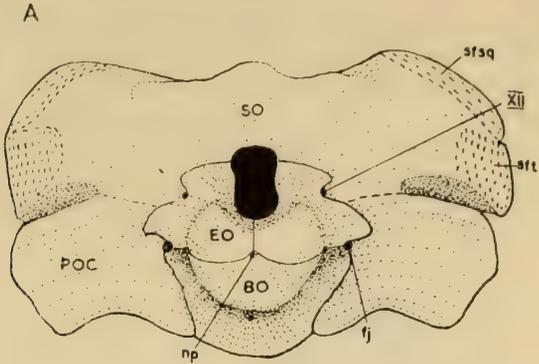


FIG. 2. *Struthiocephalus* sp. S.A.M. 9129 $\times \frac{1}{4}$.
 A. Posterior view of an isolated occiput. B. Anterior view of an isolated occiput.

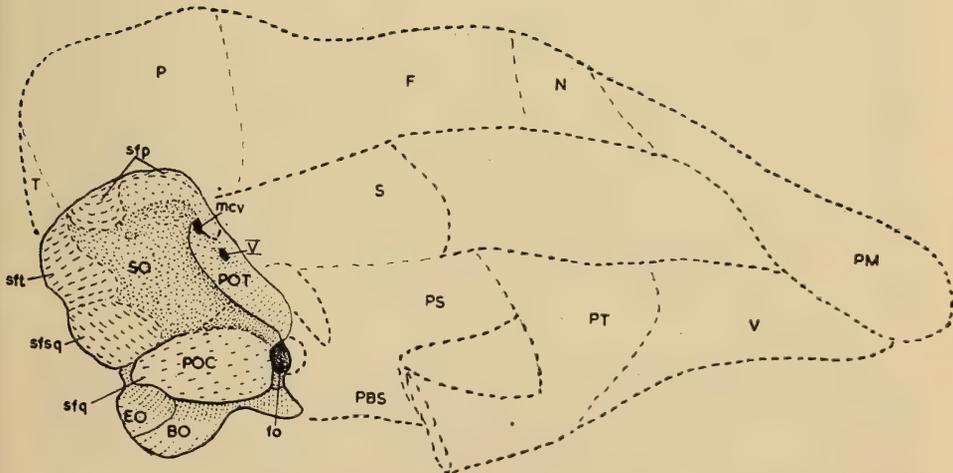
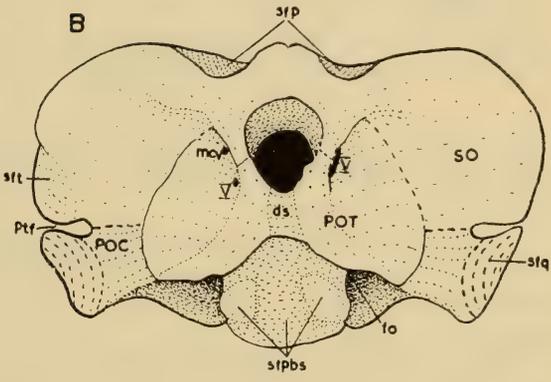


FIG. 3. *Struthiocephalus* sp. S.A.M. 9129 $\times \frac{1}{4}$. Parasagittal view of occipital segment in relation to the rest of the skull (shown in broken lines).

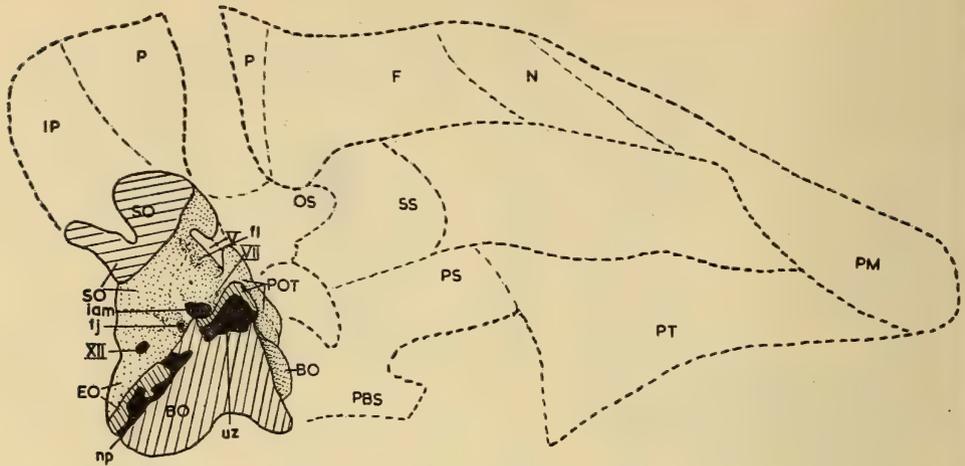


FIG. 4. *Struthiocephalus* sp. S.A.M. 9129 $\times \frac{1}{4}$.
Sagittal view of the occiput cut through in this plane in relation to the rest of the skull shown in broken lines.

the exoccipitals are seen as well-developed bones forming the upper and dorso-lateral part of the condyle, the lower and most of the lateral rim of the pinched-in oval foramen magnum.

The hypoglossal foramen is separate from the jugular foramen; the latter is bounded by the basioccipital, exoccipital and opisthotic. The supraoccipital and opisthotic are fused except laterally where they are separated by the slit-like posttemporal fenestra.

The anterior aspect of the occiput is interesting (fig. 2B). The parabasisphenoid is not preserved, having become disarticulated at the suture with the basioccipital to leave the sutural face perfectly preserved. Two rounded knobs of basioccipital fit into depressions in the basisphenoid medial to the fenestra ovalis. The rim of the fenestra ovalis is formed by basioccipital, basisphenoid, opisthotic and proötic. The proötic is clearly shown to be ankylosed to the anterior faces of the supraoccipital and opisthotic. The proötics have a median anterior face forming the upper part of the dorsum sellae. Laterally a process of the proötic ascends to meet a descending process of the supraoccipital to form a pillar, which closes the proötic incisure anteriorly. On the left side there is a large trigeminal fenestra but on the right there are two separate foramina—the upper for the median cerebral vein and the lower for the trigeminalis.

In figure 3 the occiput is shown in lateral view. The extremity of the paroccipital process shows the sutural face with which it abuts against the quadrate. The greatest part of the outer lateral surface of the posterior part of the brain-case is seen to be formed by the supraoccipital. Its lateral ends bear sutural faces for the squamosal and the tabular and its dorsal edge sutural faces for the parietal and interparietal. The proötic shows a small lateral face with a closed

proötic incisure divided into two separate foramina of which the lower one is for the Vth nerve and the upper for the median cerebral vein. The foramen for the VIIth nerve has not been located with certainty but may emerge lateral to the dorsum sellae through the ascending proötic pillar.

In figure 4 the occiput is shown cut through sagittally and with the inner face of the braincase exposed by mechanical removal of the infilling matrix.

The rounded boss on the anterior sutural face of the basioccipital fitting into the basisphenoid is clearly shown.

Dorsally the basioccipital is separated from both the exoccipital and the proötic in the median line by an unossified zone. Between the exoccipital and the proötic a hump of the basioccipital enters the floor of the braincase.

The hypoglossal nerve leaves the braincase by a large foramen passing through the exoccipital well above the level of the medullary floor. But both the jugular foramen and the internal auditory meatus leave the braincase through openings situated at floor level and both passages are directed downwards and outwards. A sharp ridge separates these two openings. The jugular foramen itself is of moderate size but lies in a deep recess in the sidewall.

The vestibule has a large opening through the sidewall.

A shallow depression in the inner face of the proötic dorso-anteriorly of the vestibule is for the flocculus.

The foramen for the facialis lies anterior to the vestibule and enters the proötic pillar lateral to the dorsum sellae.

S.A.M. 12049 *Struthiocephalus whaitsi* (Figs 5-8)

The outer surface of the braincase (fig. 5) has been prepared by hammer and chisel. Lateral to the braincase proper the supraoccipital and the paroccipital process are seen in section. The posterior part of the sidewall of the braincase is seen to be formed by the supraoccipital, exoccipital and opisthotic. No foramen for the hypoglossal opens externally and there is evidence pointing to its confluence with the jugular tube. The jugular foramen opens at the point where the ex-, basi- and paroccipital meets. The jugular passage has been cleared and is seen to form a long roomy tube 25 mm in length with diameters 4×6 mm.

Dorsally the supraoccipital sends a flange anteriorly to form the middle dorsal part of the sidewall. A process descends anteriorly to the trigeminal fenestra and this meets the ascending process from the proötic. Anteriorly the supraoccipital flange meets the posterior edge of the orbitosphenoid.

The proötic is ankylosed to the anterior face of the opisthotic and has in lateral view a small outer face. An ascending process meets the supraoccipital to enclose a dumbbell-shaped trigeminal fenestra. Ventrally it rests on the ascending part of the basisphenoid to form the anterolateral edge of the dorsum sellae. No external opening for the facialis has been seen.

The opisthotic sends a process towards the fenestra ovalis of which it forms the posterior edge. The rest of the rim is formed by the basisphenoid.

The sphenoid complex rests with its ventral edge on the median septum

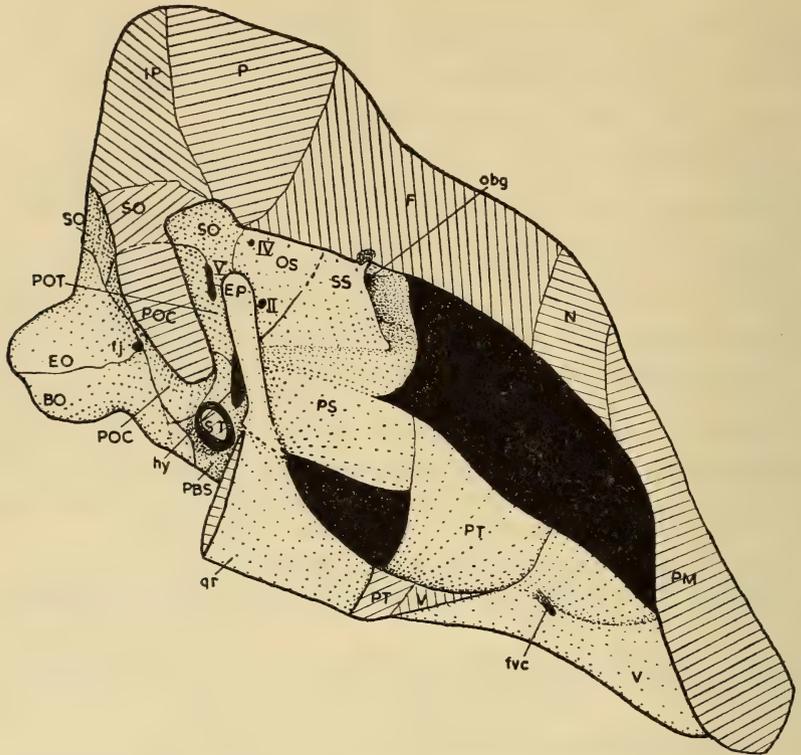


FIG. 5. *Struthiocephalus whaitsi* S.A.M. 12049 $\times \frac{1}{4}$. Parasagittal view of the skull. Drawn directly from the exposed surface of the internal bones. The occiput, roof-bones and quadrate and lateral ramus of the pterygoid seen in section.

formed by the parasphenoidal rostrum. A step is formed at this contact and a little higher up there is another step running nearly parallel. This recessed strip of bone may represent a distinct ossification—a presphenoid?—and it continues the median septum ventrally composed of the parasphenoid. Higher up the sphenoid complex begins an outward convexity but this still forms part of the median septum. Still further up the convexity curves round the olfactory tract. Anteriorly this outward bulge forms a sharp edge which dorsally bounds the opening from which the olfactory tract emerges and ventrally forms the limit of the recess in which the posterior part of the olfactory bulb is housed. Here a median septum separates the two olfactory bulbs.

In the posterior half of the sphenoid complex there appears to be a suture. Posterior to this suture the sphenoidal complex is pierced by two foramina. The lower one I believe to be for the optic nerve (II) and the upper one for the trochlearis (IV). This part of the complex I have labelled as the orbitosphenoid and the rest is a septosphenoid.

Above the opening from which the olfactory tract emerges there is a small recess in the frontal bone which may have housed an accessory olfactory bulb.

The parasphenoid is fused to the basisphenoid, but the lower part of the sella turcica apparently lies in the basisphenoid, which also appears to form the anterior and dorsal rim of the fenestra ovalis. The anterior rim of the sella appears to be formed by the parasphenoid but as remarked above the ossification here may represent a separate presphenoid. The parasphenoidal rostrum forms a strong but not greatly thickened median septum, which is anteriorly clasped by the ascending septum formed by the pair of pterygoids.

The epipterygoid

Lateral to the braincase and covering much of the open lateral sella lies the epipterygoid. The footplate of the epipterygoid rests on the quadrate ramus of the pterygoid and appears to enter the now immovable basipterygoid joint. The epipterygoid extends obliquely dorsally as a pillar of bone flattened from side to side with fairly straight anterior and posterior edges. Dorsally it has a free rounded edge which does not reach the parietal.

The pterygoid and vomer

Of the palatal complex only the pterygoid and vomer need to be considered here. The pterygoids develop a high and strong septum lying in the median line. Posteriorly they clasp the anterior extremity of the median septum formed by the parasphenoid. Anteriorly the pterygoids are in turn clasped by the well-developed median septal sheets developed by the vomers. On the lateral surface of the vomer at the transition between the vomerine interchoanal bar and the vomerine septum there is a foramen entering the vomer from behind and traversing the bone in anterior direction as a roomy canal or tube, which probably housed the naso-palatine nerve.

The inner surface of the braincase (Fig. 6)

A fortuitous natural longitudinal fracture through the skull has enabled me to clear the endocranium of the infilling matrix. This was accomplished by a laborious process of grinding with corundum burrs. If used with care a good surface can be obtained with a grinding tool, notwithstanding the contrary opinion expressed by a well-known colleague. When nearing the surface of the bone a flicking action with the burr causes the remaining film of matrix to flick cleanly away leaving an unground face less marked than when a metal point is used as a chisel even in the form of a vibro-needle.

Posterior to the plane of the dorsum sellae the floor of the braincase is formed by the proötics, basioccipital and exoccipital and the sidewall by the exoccipital, supraoccipital, opisthotic and the proötic. The hypoglossal nerve leaves through a small foramen through the exoccipital just above the floor level. The foramen jugulare is large and bounded by the opisthotic, and exoccipital and lies at floor level. Its canal is directed latero-ventrally. The vestibule is widely open and extends to below floor level. The opening is bounded by the opisthotic, basioccipital and proötic. Anterior to the vestibule lies the transverse ridge formed by the proötics whose anterior faces form the upper part of the

The endocranial cast (Fig. 7)

From the cleaned endocranial cavity I have made an endocranial cast using a pliable rubber compound (revultex). Of this cast I am including here outline drawings as projected from the side and from above.

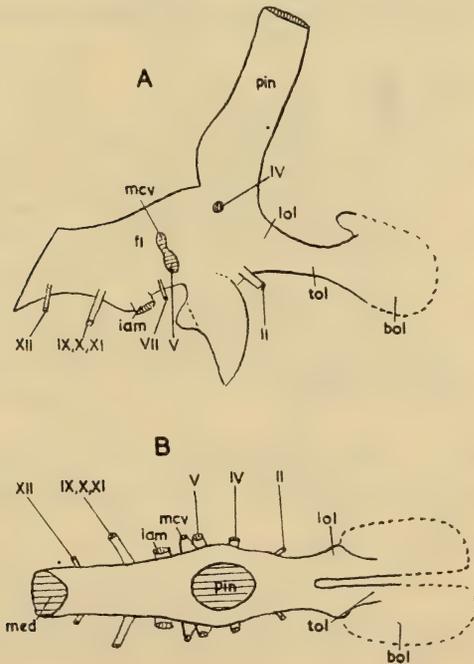
It is obvious that such a cast is of the endocranial cavity and not of the brain, which did not fill the cavity, with the result that the various divisions of the brain are but vaguely indicated.

Of the forebrain (prosencephalon) the shape of the olfactory bulbs cannot be determined as they were for the greater part not enclosed in bone. The olfactory tracts, lying as they do in tubes formed by the septosphenoid, can be distinguished. The tract was short and oval in cross-section. The olfactory lobe is indicated by a small laterally directed bulge. The position of the thalamus is indicated by the position of the optic stalk and the pituitary cavity. The hypophysial or pituitary cavity is enormous. How much of the cavity was filled by infundibulum, pituitary and accessory structures cannot be determined, but the tendency to gigantism and the pachyostosis would indicate the presence of a large pituitary gland.

Above the thalamus lies the truly enormous parietal canal or tube. If the soft structures completely fill this space their mass would be considerable. The volume in this specimen is ± 65 cc and the total volume of the endocranial cast (with allowance made for the olfactory bulbs) is ± 270 cc.

In vertebrates a number of structures are known arising from the brain

FIG. 7. *Struthiocephalus whaitsi*
S.A.M. 12049 $\times \frac{1}{4}$.
A plastic cast taken from the cleaned endocranial cavity drawn in: A. Lateral view. B. Dorsal view with the root of the pineal mass seen in section.



the braincase to immobility.

In figure 8B the basioccipital-parabasisphenoidal complex is shown disarticulated. In figure 8C the disarticulated complex is shown in lateral view. Points of interest are: the large sella turcica is a pit in the basisphenoid, with the anterior face probably formed by the presphenoid; the parasphenoidal rostrum forms a septum directed antero-dorsally; the original basipterygoid process is indicated in broken lines forming an immovable sutural face for both the epipterygoid and the pterygoid.

The position of the fenestra ovalis is shown in black. This fenestra leads into the opisthotic in which the inner ear lies.

S.A.M. 12062 *Struthiocephalus* sp. (Fig. 9)

From a number of longitudinal sections cut through the posterior part of a poor skull I have reconstructed a section in a plane just lateral of the median plane to show, in particular, the olfactory tract in longitudinal section and the canal for the internal carotid. An unossified zone is present in the anterior part of the basioccipital.

The parietal tube is 97 mm in length with average diameters 23 × 26 mm.

S.A.M. 12091 *Struthiocephalus* sp. (Fig. 10)

Cross-sections of the olfactory and pineal regions

1. The anterior end of the sphenoidal complex consisting of a septosphenoid is seen to be wedged in between the frontals. Laterally there is a deep groove in the under surface of the frontal which apparently housed a large olfactory bulb.
2. A sharp wedge of the septosphenoid is dorsally intercalated between the frontals. Laterally the septosphenoid develops a lateral flange forming a groove to hold the olfactory bulb.
3. Further back the wings composed of the orbitosphenoids enclose the olfactory tracts which are dumbbell-shaped in cross-section.
4. Still further back the upper part of the median septum is lost and the two separate olfactory tracts fuse and house the unpaired olfactory lobes.
5. This section shows the parietal tube in cross-section in the plane of the emergence of the IVth cranial nerve. Note the irregular outline of the tube.
6. Further back the parietal canal presents an elongated pear-shaped out-

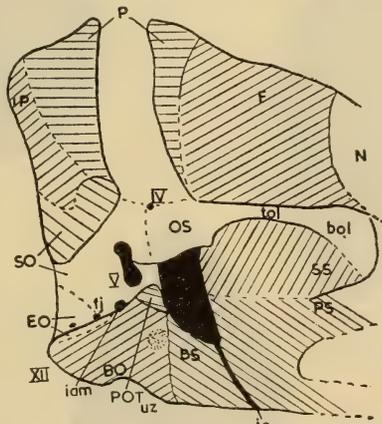


FIG. 9. *Struthiocephalus* sp.
S.A.M. 12062 × ¼.
A longitudinal section of the posterior part of the skull just lateral to the median line.

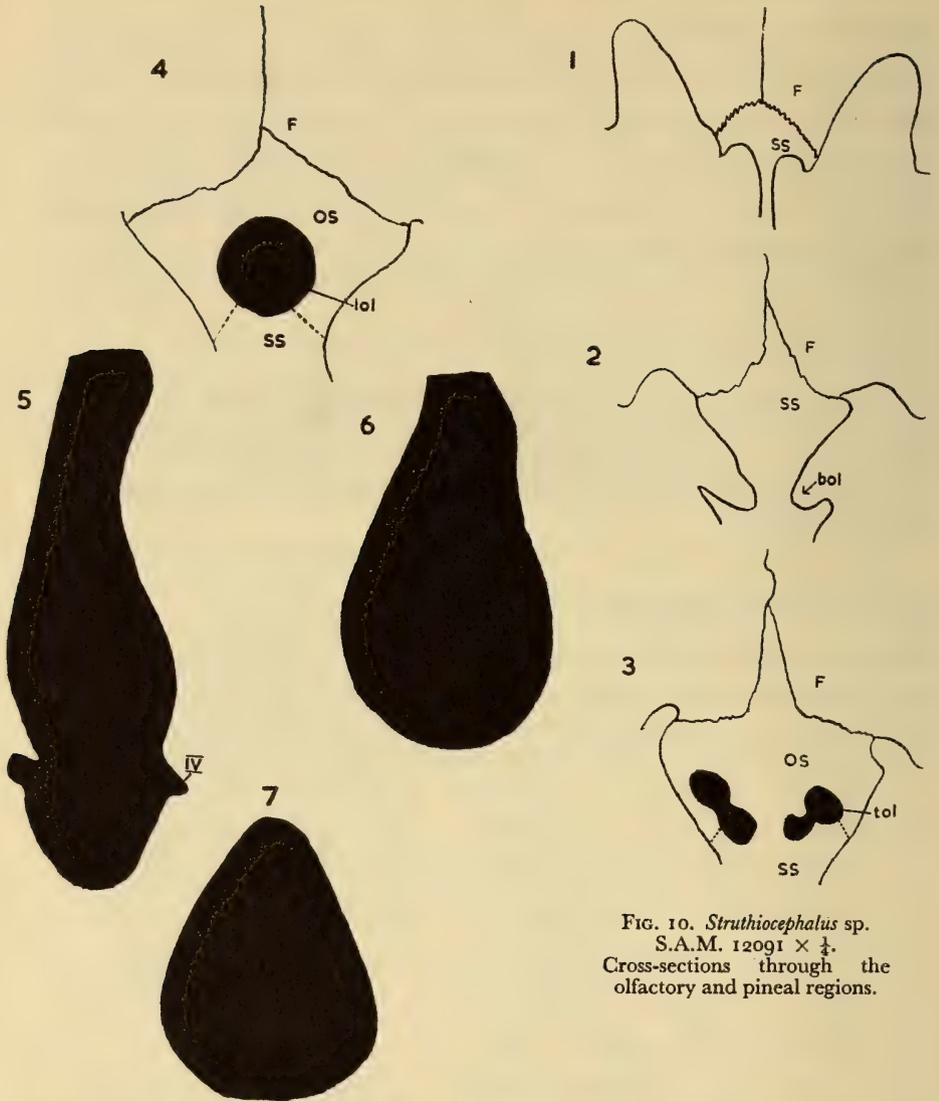


FIG. 10. *Struthiocephalus* sp.
S.A.M. 12091 $\times \frac{1}{4}$.
Cross-sections through the
olfactory and pineal regions.

line in cross-section.

7. And a cross-section through the posterior bulge of the parietal tube presents a squat pear-shaped outline.

S.A.M. 12092 *Struthiocephalus* sp. (Fig. 11)

From a longitudinal fracture and a number of longitudinal sections I have been able to reconstruct and figure the braincase in sagittal section and in lateral view. The structural relations determined corroborates the findings arrived at from other specimens of *Struthiocephalus*. In addition this specimen shows that anterior to the sella turcica the bone fibres in the parasphenoidal part of the median septum diverge and this I take to indicate that the lower

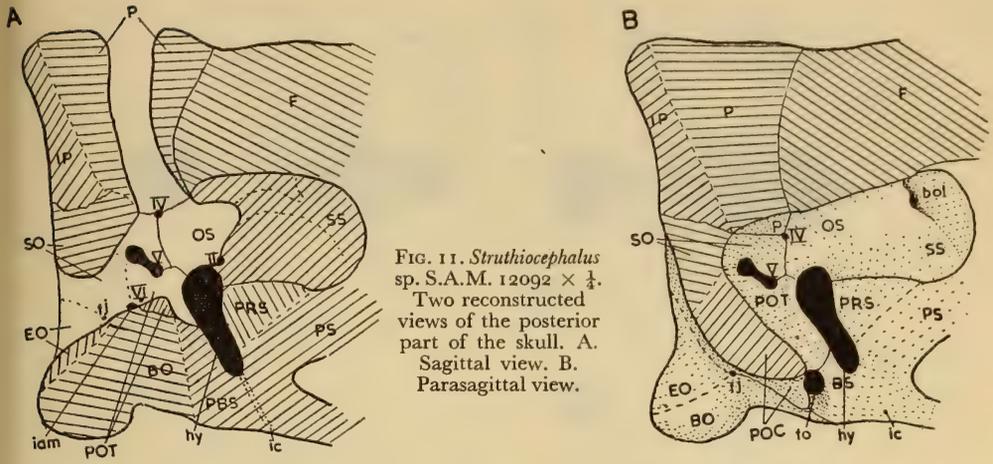


FIG. 11. *Struthiocephalus* sp. S.A.M. 12092 $\times \frac{1}{4}$. Two reconstructed views of the posterior part of the skull. A. Sagittal view. B. Parasagittal view.

part is composed of the parasphenoid, and that the upper part, forming most of the anterior border of the sella turcica, may represent a distinct presphenoid.

S.A.M. 12060 *Mormosaurus* sp. (Figs 12-16)

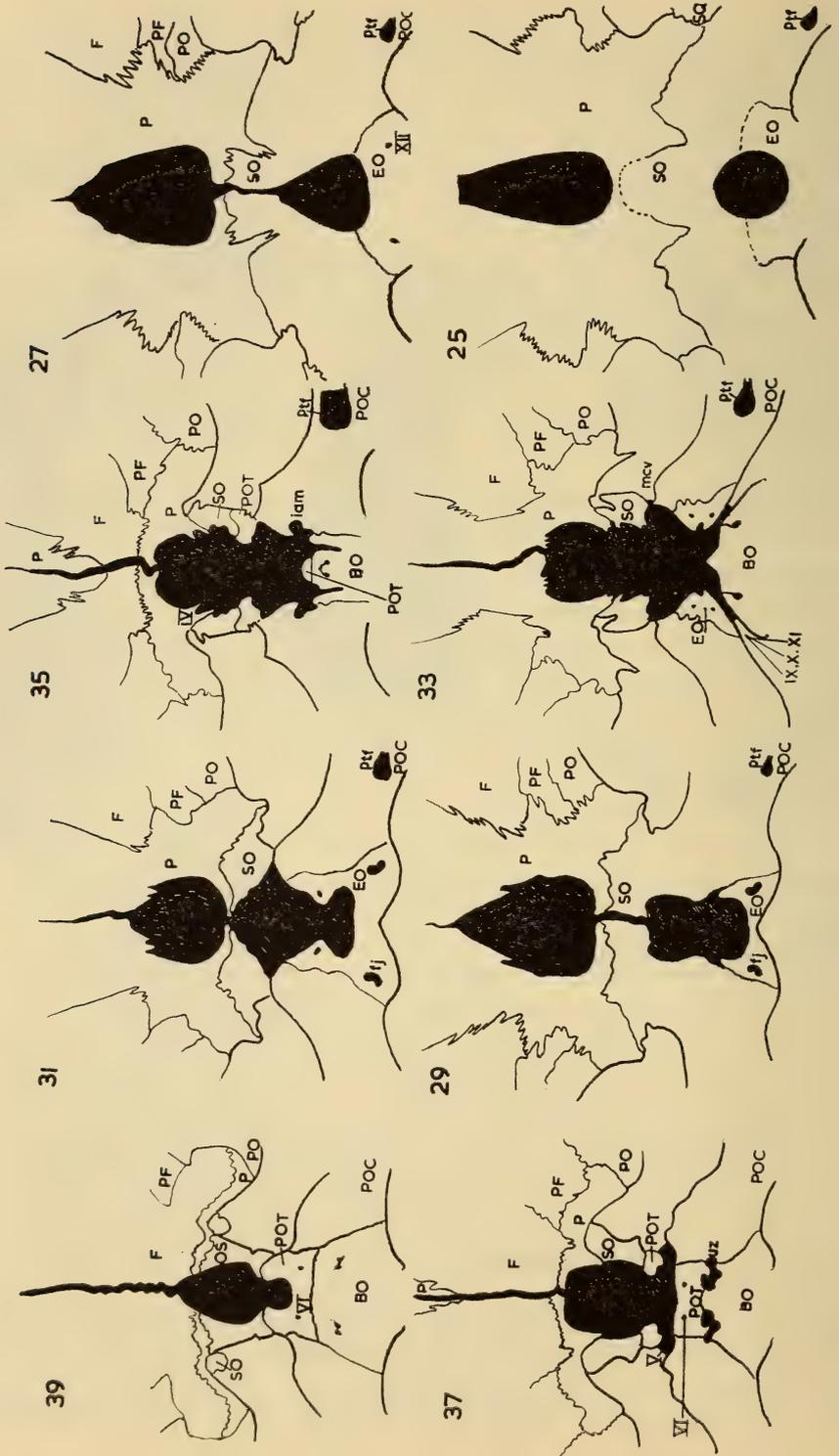
This specimen consists of a good skull of which the snout has been weathered away. A longitudinal fracture has made it possible to study the left half of the skull conventionally and to make a series of cross-sections of the posterior part of the right half of the skull. I have combined the results so obtained to produce reconstructed figures showing the skull in sagittal and in parasagittal view.

A series of cross-sections (Fig. 12)

To show the nature of the endocranial cavity and the structure of the bony braincase I am reproducing here a series of cross-sections. This series of sixteen sections consists of the consecutive odd numbers, commencing anteriorly in the plane of the olfactory bulbs. The sections are at intervals of 9 mm.

55. This section passes through the anterior end of the sphenoidal complex and shows this complex forming a median septum with its upper end intercalated between the two frontals and its lower end resting on the rostral part of the parasphenoid. In the upper part of its lateral face the recess for housing the olfactory bulb is well developed. Below this recess the bone forms a stout septum whose inner part consists of cancellous bone, lateral of which is an unossified zone which in turn is flanked by a strip of compact bone. The septum then abruptly narrows and rests on the fairly thin upper edge of the parasphenoid. The section passes through the parabasisphenoid just posterior to the original basi-ptyergoidal joint.

The pair of foramina for the internal carotids are seen in their passage through the bone. The parasphenoid is completely fused with



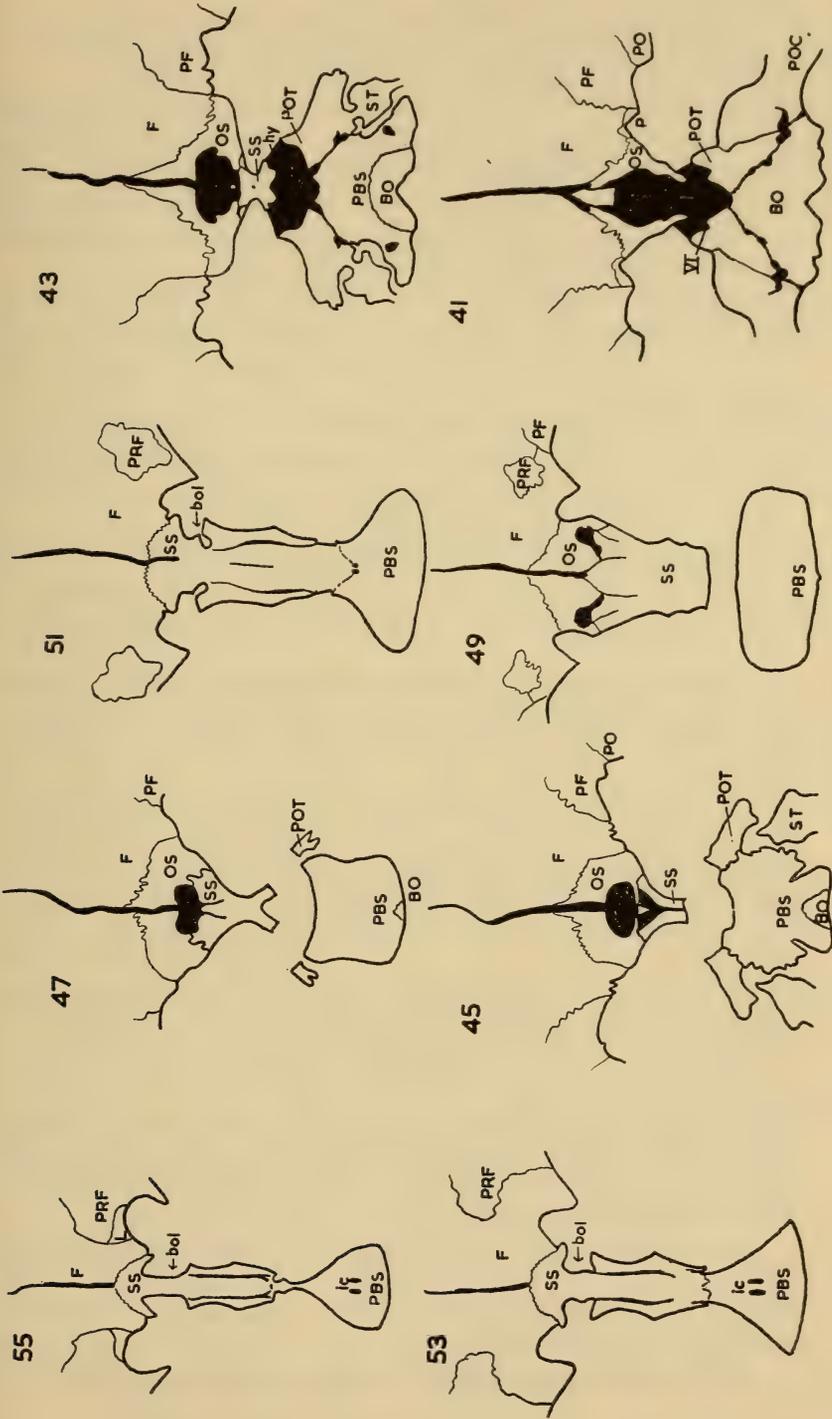


FIG. 12. *Mormosaurus* sp. S.A.M. 12060 $\times \frac{1}{2}$.
A consecutive series of cross-sections through the braincase from back to front.

the basisphenoid with no indication of their relative contribution.

Lateral to the recess in the septosphenoid the under surface of the roof-bones is also excavated to house the olfactory bulb.

53. The olfactory recess in the septosphenoid is deeper, the septosphenoidal part of the septum is thickened as is also the parasphenoidal part on which it rests. The lateral compact face of the septosphenoid is still separated from the internal cancellous part by a strip of matrix. It would appear that this separation is a postmortem feature and that it does not indicate the presence of two separate bones.
51. The olfactory recess develops a deeper pocket which is nearly closed off laterally. The septum becomes greatly thickened and rests on the wide upper edge of the stout parasphenoid. In the upper part there is a wide median suture in the septosphenoid.
49. The olfactory tracts are enclosed in tubes formed by the orbitosphenoid. The septosphenoid no longer rests on the parasphenoid, because of the presence of the sella turcica developed in the parabasisphenoid. Dorsally there is a median suture which bifurcates ventrally.
47. The pair of separate tubes for the olfactory tracts have in this plane coalesced to form a single kidney-shaped tube which now houses the olfactory lobes. Ventrally the septosphenoid is forked to form a domed roof to the sella turcica.

Laterally the anterior edge of the proötic begins to form a lateral wall to the sella turcica in its lower part. Above the olfactory lobes there is a persistent open median suture, and below the brain this suture bifurcates.

45. The forebrain is housed in a single tube bounded by the orbitosphenoids. Below the forebrain a median suture in the ventral part of the septum bifurcates dorsally to form a pair of widely open spaces. Lateral to these fissures there is a suture separating the upper orbitosphenoidal part from the lower paired septum. This septal part is formed by a septosphenoid.

Ventrally the parabasisphenoid still forms the floor and part of the dorsum sellae. The proötic is extending dorsally into the sidewall.

The proötic and parabasisphenoid are seen to form an irregular rim of the fenestra ovalis.

43. The forebrain is still enclosed in the orbitosphenoid, which is dorsally deeply intercalated between the frontals in the median plane, except for the floor which is now formed by the septosphenoid. The median septum is now low but broad.

A spur of the proötic is seen to extend well dorsally and is extending medially to enter the dorsum sellae which is, however, still mainly formed by the basisphenoid. The proötic is separated from the parabasisphenoid by an unossified zone.

Within the fenestra ovalis the proötic is connected to the stapes by

a neck of bone, with no indication of any suture in between.

41. The median septum below the brain ends in this plane. The ventral edge of the orbitosphenoid nearly meets the ascending proötic to close up the sidewall.

The proötics nearly meet in the middle line, where the basioccipital still forms the middle part of the dorsum sellae. A notch in the proötic is for the VIth nerve.

39. The orbitosphenoid has met the ascending proötic to close off the sidewall of the braincase which has been open laterally of the sella turcica.

The proötics meet in the median line to form the upper part of the dorsum sellae. The foramen for the VIth nerve passes through the proötic part of the dorsum sellae.

37. In this plane the anterior end of the supraoccipital flange has taken over the formation of the sidewall of the braincase from the orbitosphenoid.

The anterior border of the parietal canal is formed by the parietals and the floor of the braincase by the proötics. Note the unossified zone between the proötics and the basioccipital.

There is an opening in the sidewall through the proötic for the Vth nerve.

35. The sidewall is here formed by the supraoccipital, proötic and the opisthotic.

The vestibule lies in the opisthotic and basioccipital.

33. An opening laterally between the supraoccipital and the opisthotic is for the exit of the middle cerebral vein. Just posterior to the vestibule there is a foramen low down at floor level for the exit of the IXth, Xth, and XIth nerves.

31. Here the exoccipital forms the floor on which the medulla rests.

29. The medulla is encased in the supraoccipital and the exoccipital.

- 27 & 25. Shows sections through the parietal canal and the medulla.

Lateral view of the braincase (Fig. 13)

Laterally the brain is seen to be enclosed in bone, except for the absence of a lateral wall to the sella turcica and the olfactory bulbs.

The anterior part of the braincase is formed by the sphenoid complex composed of orbito- and septosphenoid.

The posterior part is enclosed by the bones of the otic capsule—proötic and opisthotic—and the occipital bones—supraoccipital and exoccipital.

The sphenoidal septum rests on the parasphenoid.

The anterior median septum is formed by septal upgrowths of the pterygoid flanked by sheets from the vomers.

The pterygoidal septum clasps the anterior end of the parasphenoidal septum.

Epipterygoid

The epipterygoid has a short footplate without posterior process, standing

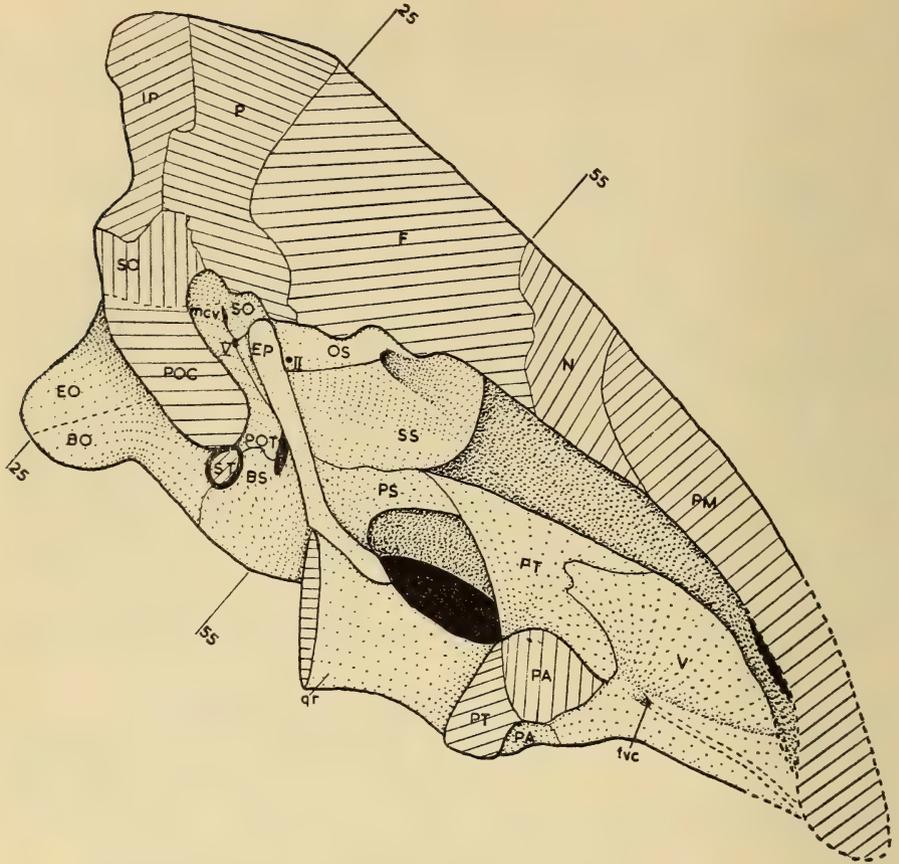


FIG. 13. *Mormosaurus* sp. S.A.M. 12060 $\times \frac{1}{4}$.
A parasagittal view of the skull drawn partly from cross-sections and partly directly from a fracture surface 25-25, 55-55 indicates location of cross-sections.

on the quadrate ramus of the pterygoid. From here it rises obliquely in the skull as a fairly slender rod to reach the anterior lateral flange of the supraoccipital just below the ventral surface of the parietal.

Sagittal view (Fig. 14)

In sagittal section it is seen that the floor of the braincase is formed by the exoccipitals, basioccipital, proötics, basisphenoid, orbito- and septosphenoids.

The inner lateral face of the endocranial cavity is formed by the exoccipital, supraoccipital, opisthotic, proötic and orbitosphenoid.

The vestibule, and the foramina for the vagus complex and the XIIth nerve lie low down at floor level.

The trigeminal fenestra lies half-way up and is bounded by the supraoccipital and proötic.

The optic nerve leaves the endocranium low down through the

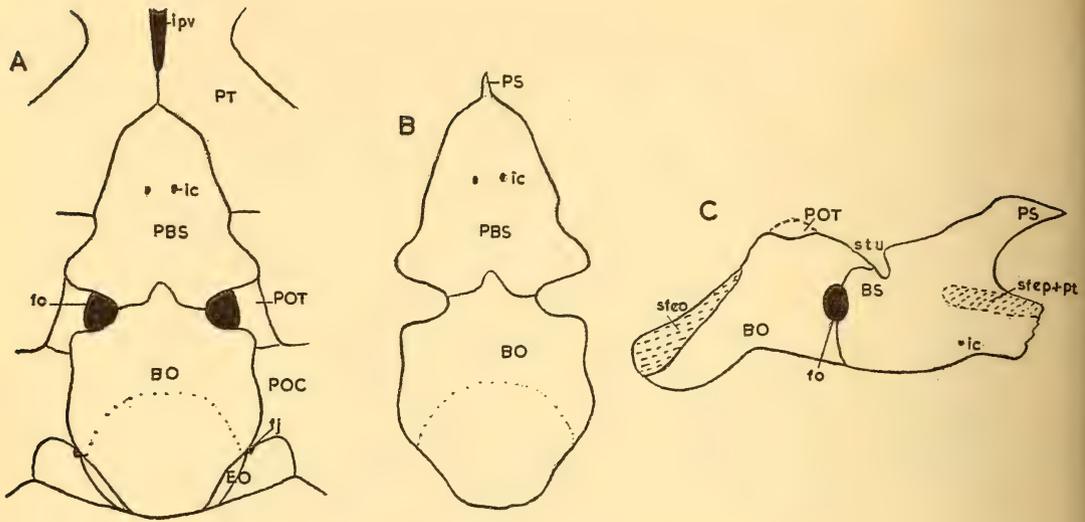


FIG. 15. *Mormosaurus* sp. S.A.M. 12060 $\times \frac{1}{4}$.

The basicranial axis reconstructed from cross-sections and direct observation. A. Ventral view in relation to the supporting bones. B. Ventral view. C. Lateral view.

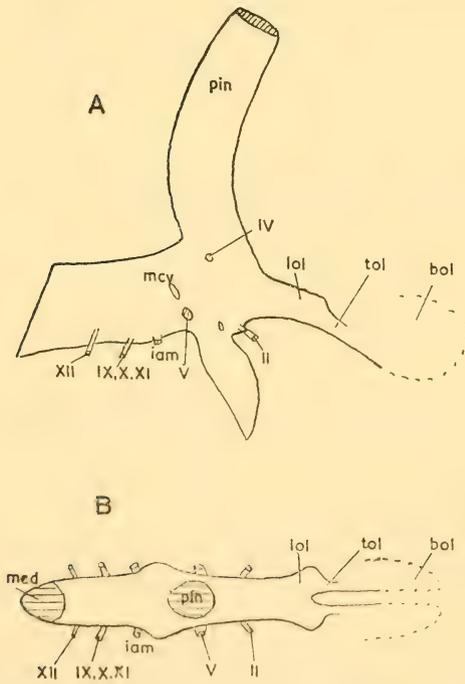


FIG. 16. *Mormosaurus* sp. S.A.M. 12060 $\times \frac{1}{4}$.

Outline drawings of the endocranial cavity reconstructed from sections. A. Lateral view. B. Dorsal view with the root of the pineal mass seen in section.

and a process of the paroccipital forms the postero-lateral border and the proötic the upper border.

The rostrum is short and low.

The endocranial cavity (Fig. 16)

From the cross-sections I have graphically reconstructed two outline drawings of the endocranial cavity in lateral and dorsal views and on them indicated the exits of the cranial nerves.

The parietal canal is 125 mm in length and the antero-posterior diameter averages 15 mm. Due to its pear-shape the lateral diameter varies greatly—16–55 mm.

The sella turcica is deep, extending downwards for half the height of the parabasisphenoid.

The brain is long, narrow and fairly high.

S.A.M. 11294 *Keratocephalus moloch* (Figs 17–20)

This weathered and incomplete posterior part of a skull was described by me in 1956. My interpretation of the nature of the epipterygoid and proötic have proved to be at fault and will now be corrected. In addition I have now cut a median sagittal section through the specimen which has enabled me to clean the left half of the braincase of matrix and to take an endocranial cast.

Outer view of the braincase (Fig. 17)

Both the left and right sides of the braincase have been adequately exposed. The occipital, otic and sphenoidal regions are fully ossified so that the only opening, in addition to the nerve foramina, is in the lateral wall of the sella turcica. As usual the olfactory bulbs have no ossified lateral wall.

The bones forming the lateral wall are: opisthotic, supraoccipital, proötic and the two sphenoidal bones (orbitosphenoid and septosphenoid). The sphenoidal region rests on a median septum formed by the parasphenoid to which a presphenoid is probably indistinguishably fused.

The supraoccipital has dorsally a well-developed flange extending well anteriorly to meet the orbitosphenoid in a plane well anterior of the trigeminal fenestra. Curving down to form the anterior border of the trigeminal fenestra the supraoccipital meets the ascending pillar of the proötic so that the proötic incisure is closed anteriorly.

In lateral view the proötic is seen to be intimately fused to the anterior face of the paroccipital and supraoccipital. Ventrally the proötic enters the margin of the fenestra ovalis and meets the ascending process of the basisphenoid and together they form the dorsum of the sella turcica. Above the pituitary fossa the proötic meets the orbitosphenoid and here we find the outer opening for the facial nerve (VII). Further dorsally the ascending pillar of the proötic meets the descending process of the supraoccipital.

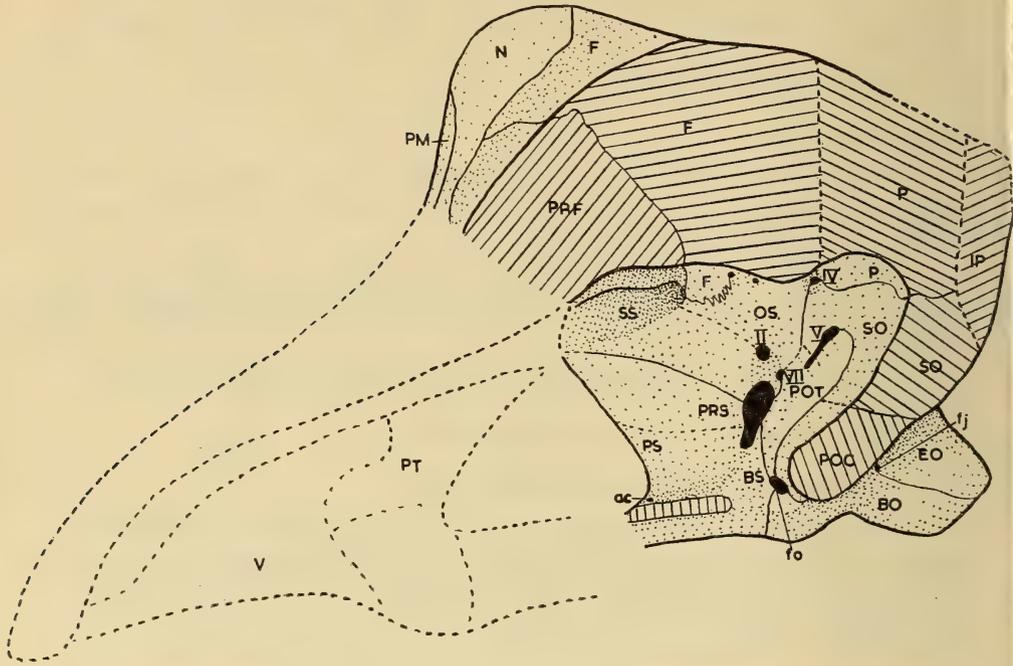


FIG. 17. *Keratocephalus moloch* S.A.M. 11294 $\times \frac{1}{4}$.
Lateral view of the braincase based on the exposed surfaces of both sides, with the occipital and roof-bones shown in reconstructed section.

Orbitosphenoid

The orbitosphenoid has a large lateral face. Its lower part forms a median septum resting on the septosphenoid. Its upper part encloses the diencephalon. Above the pituitary fossa there is a depression to house the Gasserian ganglion. In the upper part of this hollow lies a large rounded foramen for the optic nerve (II).

The orbitosphenoid is applied to the under surface of the frontal. Here lie two fairly small foramina. At the junction of orbitosphenoid, supraoccipital, frontal and parietal there is another foramen. This is probably for the trochlearis (IV) and one of the anterior foramina for the oculomotorius (III).

Septosphenoid

The septosphenoid forming the upper part of the median unpaired interorbital septum rests on the presphenoidal and parasphenoidal part of the interorbital septum.

Dorsally it meets the lower edges of the orbitosphenoidal wings and is applied to and intercalated between the frontals.

Its lateral face carries a longitudinal groove in which the olfactory bulb is housed.

Further back it also forms the floor of the tubes housing the olfactory tracts.

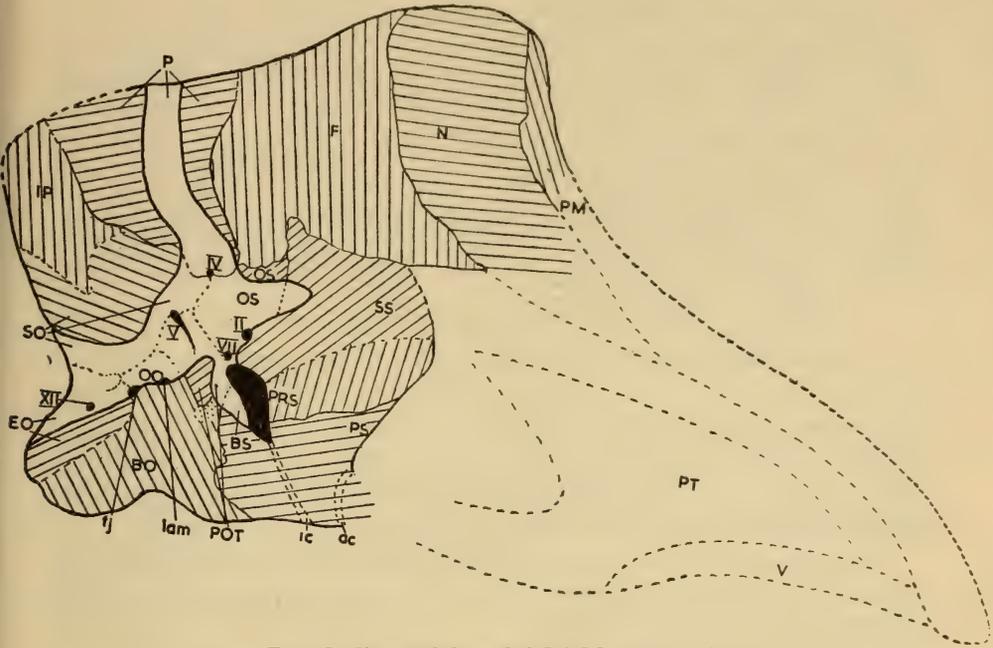


FIG. 18. *Keratocephalus moloch* S.A.M. 11294 $\times \frac{1}{4}$.

The sagittal view of the braincase drawn directly from a sagittal section and the left half of the cleaned endocranial cavity.

Inner view of braincase (Fig. 18)

After cutting through the skull in the sagittal plane I have removed the matrix filling the left half of the endocranial cavity.

The floor of the braincase is formed by the exoccipital, basioccipital, proötic, basisphenoid, presphenoid, orbitosphenoid and septosphenoid.

The lateral wall is formed by the exoccipital, supraoccipital, opisthotic, proötic, orbitosphenoid and septosphenoid. The parietal organ lies wholly in the parietals.

The roof is formed by the supraoccipital, orbitosphenoid and septosphenoid. The hypoglossal foramen through the exoccipital, the jugular foramen bounded by the exoccipital and opisthotic, the internal auditory meatus into the opisthotic, the facialis foramen through the proötic and the optic foramen through the orbitosphenoid all lie low down, mostly at floor level. The trigeminal fenestra bounded by the proötic and supraoccipital lies well up in the side wall and the trochlear foramen bounded by the supraoccipital, parietal and orbitosphenoid lies near the root of the parietal organ.

The dorsum sellae has its lower half formed by the basisphenoid and its upper half by the proötic. The frons sellae is formed by the presphenoid and septosphenoid.

The parietal tube is 108 mm high, with maximum diameters 30×60 mm.

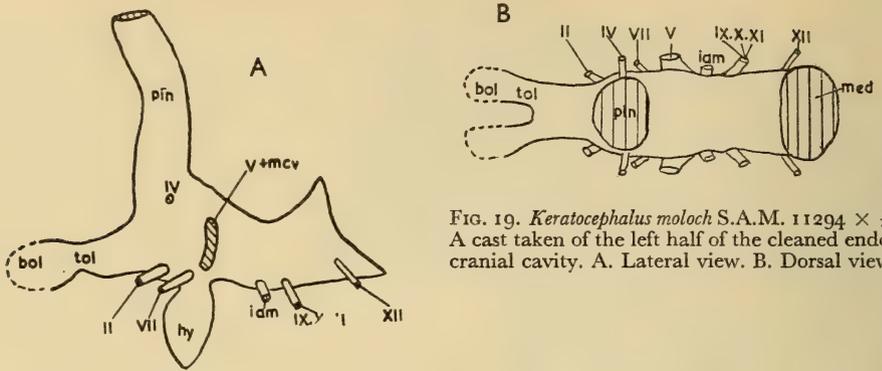


FIG. 19. *Keratocephalus moloch* S.A.M. 11294 $\times \frac{1}{4}$.
A cast taken of the left half of the cleaned endocranial cavity. A. Lateral view. B. Dorsal view.

Cast of the endocranial cavity (Fig. 19)

The cavity is short and as high as it is wide. The exits for nerves II, VII, VIII, IX, X and XI and XII are at floor level. The trigeminal fenestra lies well up the side and that of the trochlearis very high up.

The olfactory tract was short, the olfactory lobes and cerebral hemispheres were small: the chiasma is faintly indicated as a cross swelling at the level of the emergence of the optic nerves.

The presence of a flocculus is faintly indicated.

S.A.M. 12093 *Keratocephalus* sp. (Fig. 20)

This skull lacks the basicranial axis, but dorsally of this it is quite well preserved. After cutting it through in the sagittal plane I have been able to clean both halves of the endocranial cavity of matrix.

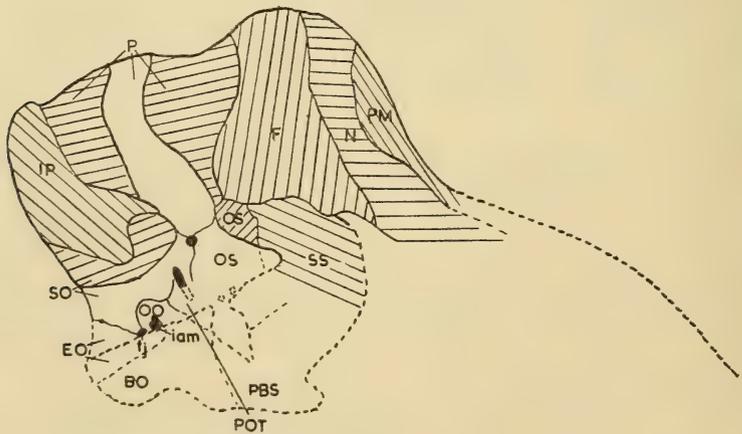


FIG. 20. *Keratocephalus* sp. S.A.M. 12093 $\times \frac{1}{4}$.
Sagittal view of the dorso-posterior part of a skull sectioned in the median plane and after cleaning the endocranial cavity.

The sutures between the constituent bones of the braincase as shown in the accompanying figure are clearly shown. It is quite definite that the septo-sphenoid forms a median septum lying dorsally between the olfactory tracts and the olfactory bulbs.

The orbitosphenoid forms the roof and sides of that part of the braincase enclosing the thalamus and cerebral hemispheres.

The parietal canal is curiously curved; its height is 100 mm: the greatest antero-posterior diameter is 32 mm but it is greatly expanded from side to side with the greatest diameter 48 mm.

S.A.M. 11972 *Moschops capensis* (Figs 21-26)

This specimen, consisting of a good posterior two-thirds of a skull, was described and figured by me in 1957.

I have now cut out the median part of the skull as a rectangular block and of this block I have cut a series of 120 cross-sections in order to study the detailed structure of the braincase and the supporting bones.

I am publishing here some of the cross-sections and a number of figures reconstructed from these serial sections.

Outer view of braincase (Fig. 21)

In the figure the right side of the braincase is seen in lateral view and the bones of the occipital plate and the dermal bones of the skull-cap are seen in

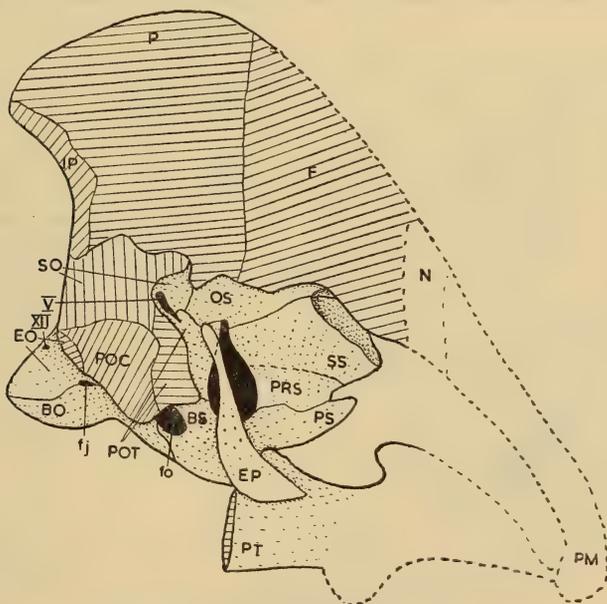


FIG. 21. *Moschops capensis* S.A.M. 11972 $\times \frac{1}{4}$. Parasagittal view of the braincase reconstructed graphically from a series of cross-sections.

parasagittal section.

It is clear that the lateral wall is well ossified; anteriorly the olfactory region has no lateral bony wall; in the middle the metoptic fissure is still widely patent, except dorsally where it is closed through the junction of the ossifications of the otic and sphenoidal regions. Noteworthy is the great anterior extent of the lateral flange of the supraoccipital. This, together with the great forward growth of the proötic, closes the trigeminal incisure with a wide sheet of bone ossified in the pila antotica, but the trigeminal fenestra, through which passes the median cerebral vein and the trigeminal nerve is still large.

Laterally to the persistent metoptic fissure lies the slender upper part of the epipterygoid, forming above a roomy cavum epiptericum. There is no posterior process to the footplate of the epipterygoid. When fully developed the epipterygoid would dorsally extend to meet the downwardly directed flange of the parietal.

The median septum of the pterygoid is not fully developed in this specimen; but in the American Museum of Natural History there is a specimen figured by me in which the pterygoid septum makes contact with the tip of the parasphenoidal rostrum.

The fenestra ovalis lies low down in the skull with its rim formed by the basioccipital, parabasisphenoid, opisthotic and proötic.

The braincase in sagittal view (Fig. 22)

In sagittal section it is evident that the brain rests on the exoccipitals, basioccipital, proötics, basisphenoid and the sphenoids. Laterally the brain is

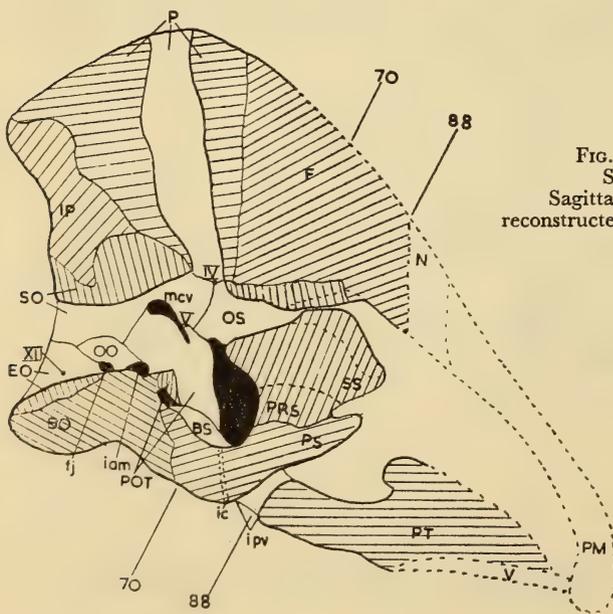


FIG. 22. *Moschops capensis*
S.A.M. 11972 $\times \frac{1}{4}$.
Sagittal view of the braincase
reconstructed graphically from a series
of cross-sections.

bounded by the following bones: exoccipital, supraoccipital, opisthototic, proötic and orbitosphenoid. The roof to the brain is formed by the supraoccipital, frontal, and orbitosphenoid.

Internally the openings for the hypoglossal, the foramen jugulare and the internal auditory meatus lie low down on the sidewall at floor level.

The upper part of the dorsum sellae is formed by the proötics meeting each other in the median line. The lower part of the dorsum sellae is formed by the basisphenoid.

The IVth nerve lies high—at the root of the parietal organ.

The orbitosphenoid is a small bone intercalated between the frontals in the median line and forms part of the roof of the rhienecphalon.

In its upper part the orbitosphenoid posteriorly encloses the olfactory lobes, and further forward forms a pair of tubes to house the tracti olfactorii and anteriorly the septosphenoid forms grooves opening laterally to house the olfactory bulbs.

The lower part of the sphenoid complex forms a median septum and this part would appear to be composed of a septosphenoid and a presphenoid resting on the upper edge of the parasphenoidal rostrum.

The parietal tube is large with a height of 130 mm. Its sides are irregular with diameters varying from 16 to 34 mm.

The basicranial axis (Fig. 23)

The basicranial axis is formed by the firmly united exoccipitals, basioccipital and the fused parabasisphenoid.

In ventral view it is evident that the fenestrae ovales lie very close to the median line. Only the posterior part of the interpterygoid vacuity is patent with the result that the parasphenoidal rostrum is obscured by the pterygoids meeting in the median line. The parabasisphenoid is firmly joined to the epipterygoid and the footplate of the epipterygoid but, though immovable, the old basiptery-

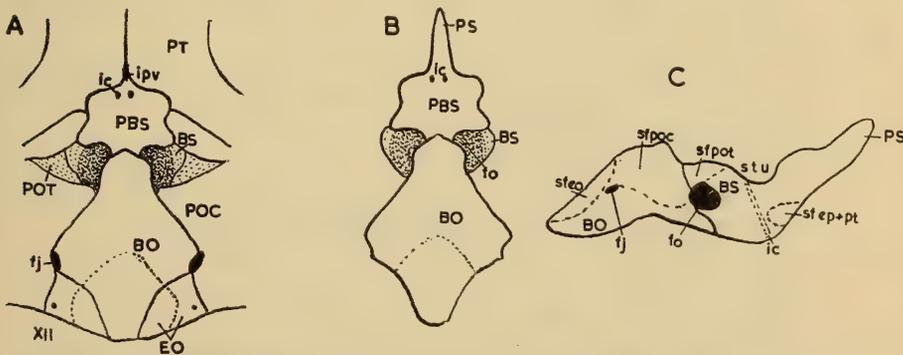


FIG. 23. *Moschops capensis* S.A.M. 11972 $\times \frac{1}{4}$.

The basicranial axis reconstructed from cross-sections. A. Ventral view in relation to supporting bones. B. Ventral view. C. Lateral view.

goidal process of the basisphenoid is still defined.

In lateral view it is seen that the parasphenoidal rostrum is directed upwards at an angle of 45° to the cranial base.

The endocranial cavity (Fig. 24).

From the series of cross-sections I have graphically reconstructed outline drawings of the endocranial cavity in lateral and dorsal views.

The parietal organ is enormous, but the large size indicated for the hypophysis is due to the fact that the ossification of both the dorsum and frons of the sella turcica is incomplete.

The telencephalon appears to have been weakly developed.

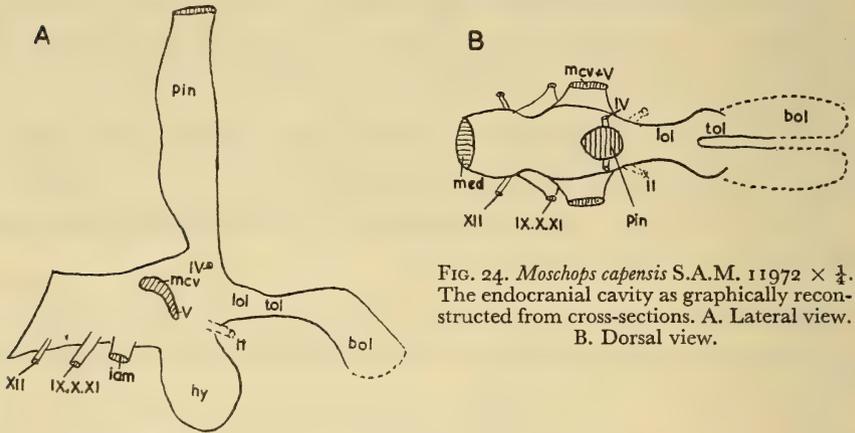


FIG. 24. *Moschops capensis* S.A.M. 11972 $\times \frac{1}{4}$. The endocranial cavity as graphically reconstructed from cross-sections. A. Lateral view. B. Dorsal view.

The sphenoidal complex (Fig. 25)

In the accompanying figure some cross-sections through the sphenoidal region show the relations of the constituent elements.

70. At the level of the olfactory lobe the orbitosphenoids in section present a Y enclosing the brain from below, above and from the sides. Dorsally they abut against the lower face of the frontals.
74. 10 mm anteriorly the septosphenoid is Y-shaped and dorsally abuts against the orbitosphenoid, which is a small elongated median bone intercalated between the two frontals.
80. 14 mm anteriorly the brain forms a pair of olfactory tracts separated by a median pillar formed of the septosphenoid. Above this there is still an orbitosphenoid which has become narrower and shallower.
82. 5 mm further forward there is still a narrow orbitosphenoid and the olfactory bulbs are exposed laterally. The septum formed by the septosphenoid is greatly thickened.
88. The orbitosphenoid has terminated and the upper part of the septum is still wide, whereas the lower part is narrow and may represent a pre-sphenoid. This rests on the parasphenoidal rostrum.

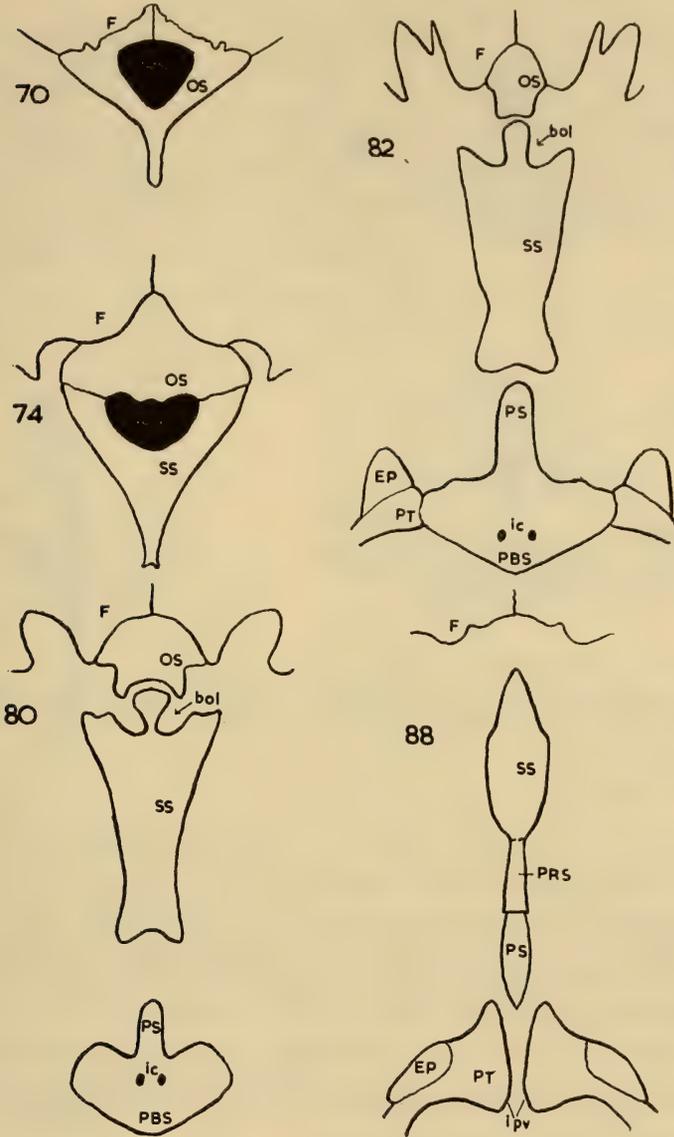


FIG. 25. *Moschops capensis* S.A.M. 11972 $\times \frac{1}{2}$
 A series of sections through the sphenoidal region from back to front.

S.A.M. 11985 *Moschops* sp. (Fig. 26)

This specimen consists of a very well-preserved isolated occipital plate.

In posterior view (A) the tripartite nature of the condyle is well shown, with the basioccipital lower third forming the articular face so that the skull

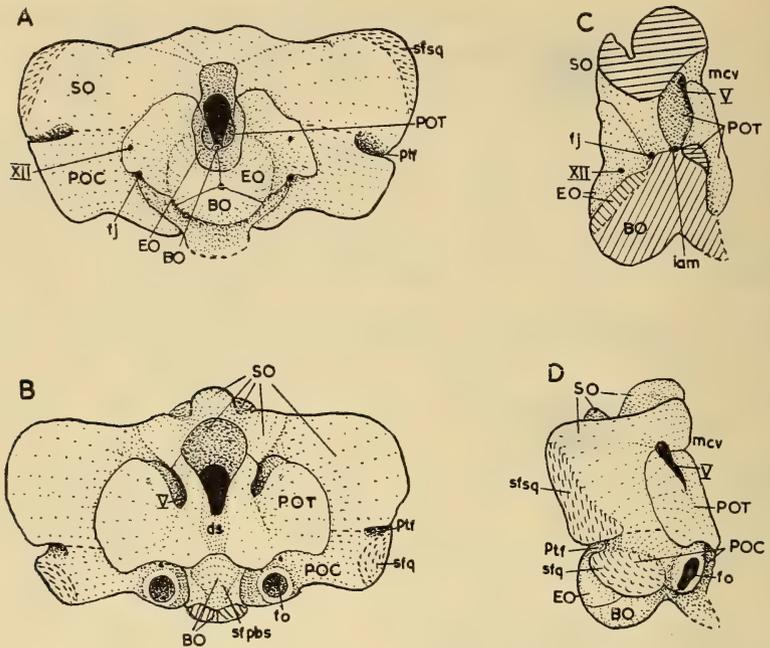


FIG. 26. *Moschops* sp. S.A.M. 11985 $\times \frac{1}{4}$.
An isolated occipital plate. A. Posterior view. B. Anterior view. C. Sagittal view.
drawn after the endocranial cavity had been cleaned. D. Parasagittal view.

would hang down at a sharp angle. The exoccipitals meet in the median line to form the floor for the medulla. Anterior to the exoccipitals a hump in the floor is formed by the basioccipital lying between the internal auditory meati.

In anterior view (B) the proötics are seen lying intimately applied to the anterior face of both supraoccipital and opisthotic. They meet in the median line, where they are hollowed out and form the upper part of the dorsum sellae. Dorsally the proötic has an ascending pillar, which meets a descending process of the supraoccipital. These are ossifications in the pila antotica and enclose the trigeminal fenestra anteriorly. Lateral to the trigeminal fenestra lies the foramen for the VIth cranial nerve.

Below each proötic lies the circular fenestra ovalis, which forms a cup-shaped depression in the opisthotic pierced by two foramina leading into the internal auditory meatus.

The hollow is bounded by a sharp raised rim formed by the opisthotic. The parabasisphenoid has fallen away, but when present the basisphenoid together with the basioccipital and proötic form an outer rim to the fenestra ovalis which partly obscures the inner rim formed solely by the opisthotic.

Between the lower edge of the proötic and the fenestra ovalis lies the opening of the VIIth cranial nerve.

In sagittal section (C) it can be seen that the braincase floor is formed by the exoccipital, basioccipital and proötic, with the foramen for the XIIth, the jugular foramen and the internal auditory meatus lying at floor level.

Piercing the ascending process of the proötic is the foramen for the VIth nerve. Behind the proötic-supraoccipital bar lies the slit-like trigeminal fenestra. Behind this the sidewall of the braincase, here formed by the proötic, is hollowed out and in this hollow the flocculus was housed.

In (D) the occipital plate is seen in lateral view and shows the slit-like trigeminal fenestra bounded anteriorly by the proötic and supraoccipital and the fenestra ovalis bounded by a rim formed by the opisthotic.

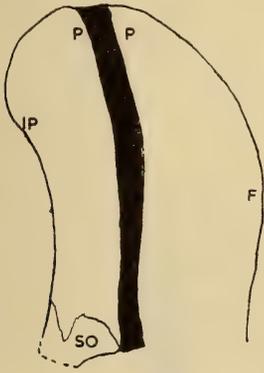


FIG. 27. *Criocephalus* sp.
S.A.M. 11701 $\times \frac{1}{4}$.
Sagittal section through the skull cap
showing the pineal tube.

S.A.M. 11701 *Criocephalus* sp. (Fig. 27)

A sagittal cut through this skull-cap shows the constituent bones to be of cancellous nature and the fusion of these spongy bones has obliterated nearly all traces of the original sutures between them.

The parietal tube is curved and lies parallel to the midline of the occiput and the curvature of the dorsal surface of parietal and frontal. It is very long—185 mm, the antero-posterior diameter varies from 9 to 14 mm.

S.A.M. 12046 *Criocephalus* sp. (Fig. 28)

A sagittal section cut through a badly weathered skull-cap shows the great thickness of the parietal bone with the parietal tube penetrating this bone. The tube measures 240 mm in height and the diameters vary from 15 to 20 mm.

S.A.M. 12066 *Criocephalus* sp. (Fig. 29)

A sagittal section through this skull-cap shows the limits of the constituent bones, although they are spongy.

The parietal tube runs nearly parallel to the midline of the occiput. Its length is 198 mm and the antero posterior diameter varies from 16 to 23 mm.

S.A.M. K268 *Criocephalus gunyankaensis* (Fig. 30)

Four of the skull-caps, described in 1946, are here figured.

A. In this specimen most of a natural cast of the parietal tube is preserved as well as the tube itself. The length of the tube is 310 mm. At its dorsal

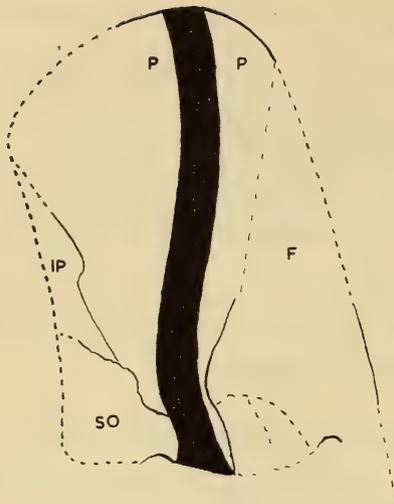


FIG. 28. *Crioecephalus* sp.
S.A.M. 12046 $\times \frac{1}{4}$
Sagittal section through the pineal tube.

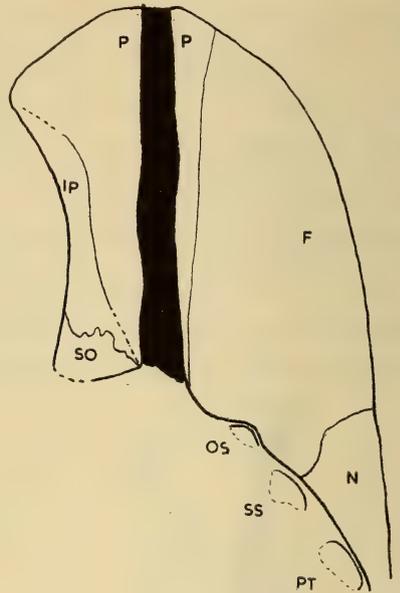


FIG. 29. *Crioecephalus* sp.
S.A.M. 12066 $\times \frac{1}{4}$
Sagittal section through the skull cap.

extremity the cast is oval in cross-section with diameters 22×27 mm. The skull bones are very spongy, but the face of the tube is very smooth and is formed of dense and compact tissue.

- B. I have cut a frontal section through the parietal tube of this specimen. The tube is 306 mm in length and the side to side diameter varies from 17 to 26 mm. No sutures in the surrounding cancellous bone can be determined.
- E. A natural longitudinal fracture passes through the parietal tube, whose length as reconstructed is 308 mm with antero-posterior diameters varying from 16 to 25 mm.
- F. A longitudinal cut has been made through the skull to give a sagittal section of the parietal tube which has a length as reconstructed of 170 mm and antero-posterior diameters varying from 17 to 26 mm.

ANTEOSAURIA

S.A.M. 9085 } *Anteosaurus* sp. (Figs 31-37)
S.A.M. 12082 }

As S.A.M. 12082 lacks the anterior end of the snout I have sectioned a snout S.A.M. 9085 and from these combined I have graphically reconstructed the skull from two views.

S.A.M. 12082 was contained in a sandstone bed of about 24 inches. Much of the upper surface of the skull was weathered away and the rest contained in a

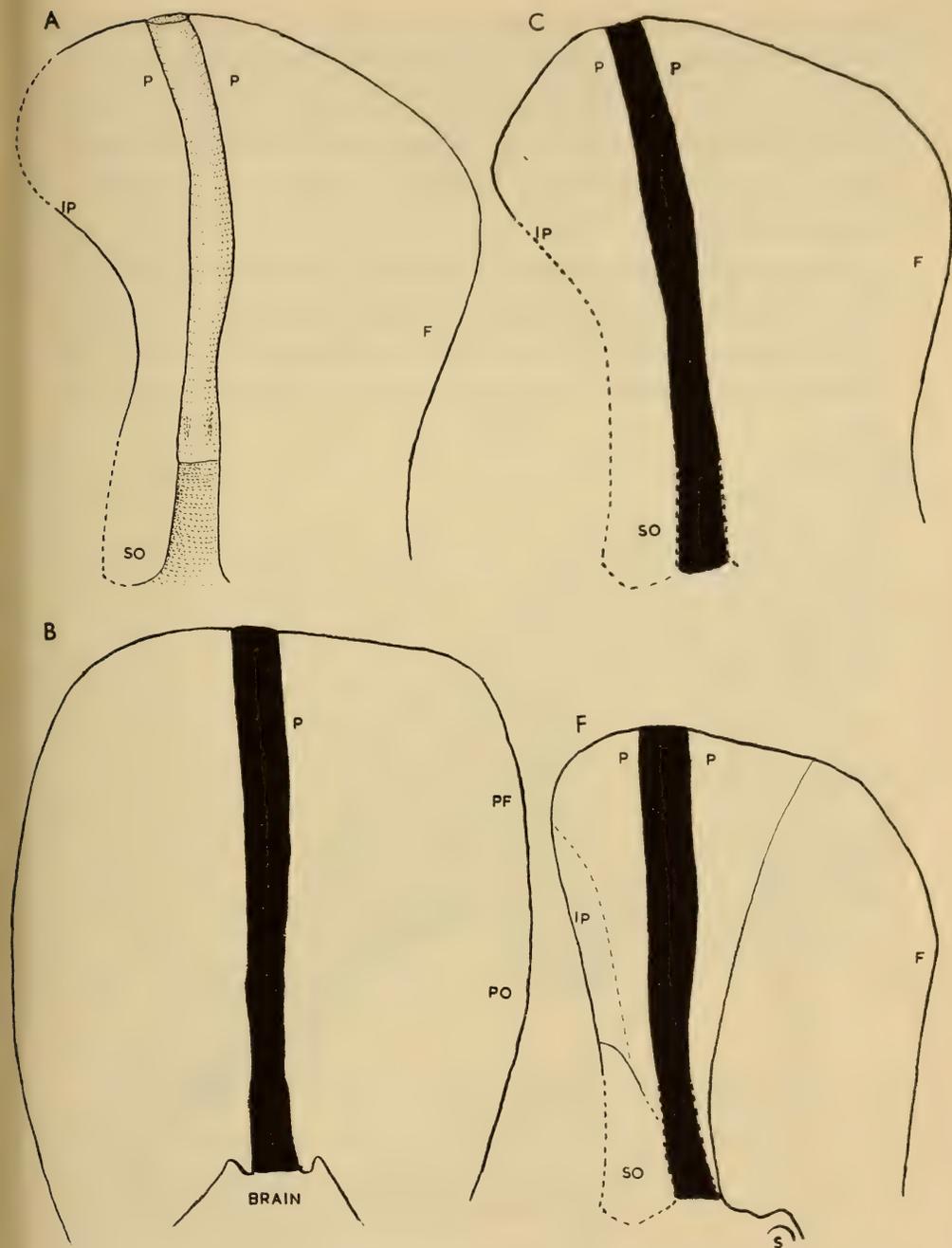


FIG. 30. *Criocephalus gwyankaensis* $\times \frac{1}{4}$. S.A.M. K268.

A. A cast of the pineal tube lying loosely in its tube shown in sagittal view. B. A frontal section through the skull showing the pineal tube. C. A sagittal section through the pineal tube. F. Sagittal section through another skull-cap.

number of blocks weathered at the fracture faces. Unfortunately these fractures have passed through vital regions of the skull. So that, although the well-preserved parts have given excellent sections, a number of structural features are indeterminable and some doubtful. However, the reconstructions give a fair picture of the internal structures of the anteosaur skull and profitable comparisons can be made with the other Dinocephalia.

Parasagittal view (Fig. 31)

The outer surface of the braincase is formed by the bones found here in all Dinocephalia. Posteriorly the bones of the occipital plate are seen in section. The exoccipital has a large outer face and is pierced by a large jugular foramen.

The supraoccipital sends the usual flange anteriorly to meet the sphenoid complex and a downwardly directed process curving down in front of the

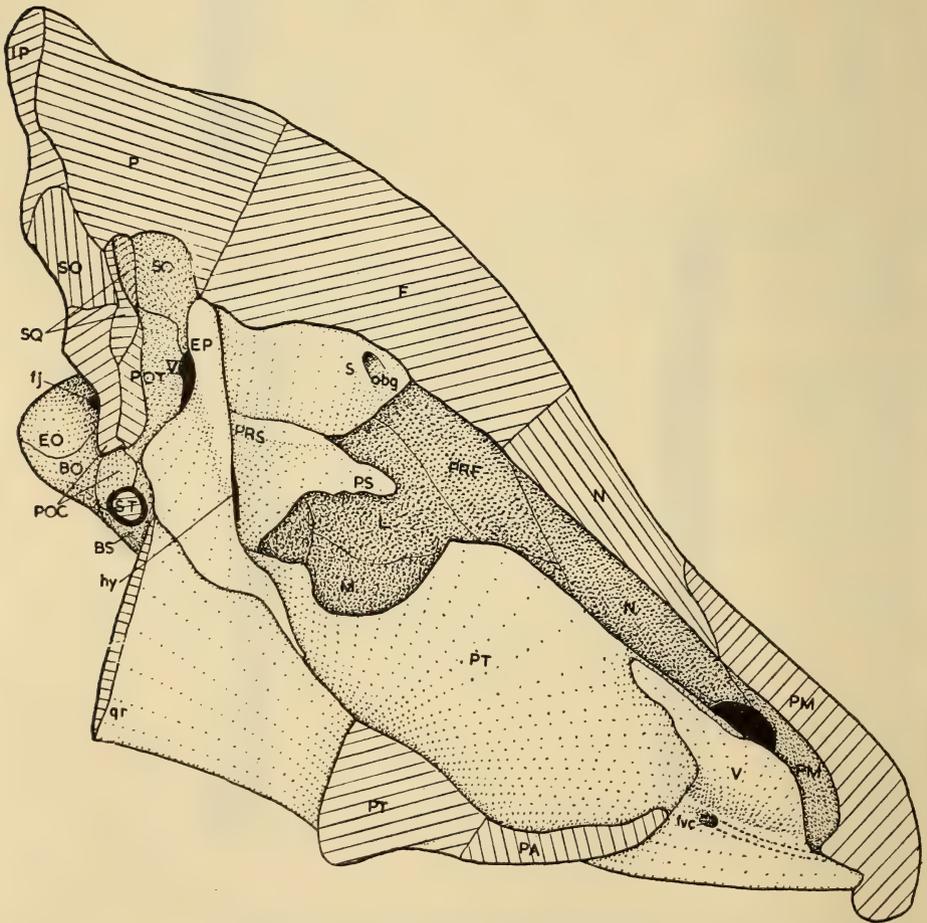


FIG. 31. *Anteosaurus* sp. S.A.M. 12082 $\times \frac{1}{4}$. Parasagittal view reconstructed from cross-sections. The snout is from S.A.M. 9085.

trigeminal fossa.

The proötic, as ossified, is of small postero-anterior extent. Its anterior margin carries a trigeminal notch. In maturity, I believe, that the antotic pila, here cartilaginous, would be ossified.

Of the foramina for the cranial nerves I have only been able to determine the position of the trigeminal nerve and the jugular foramen.

The fenestra ovalis is large and lies low down, with its borders formed by the opisthotic, basisphenoid and the proötic.

The sphenoid complex is of the usual dinocephalian nature, but the limits of the orbitosphenoid and septosphenoid cannot be wholly determined. The open groove in the septosphenoid for the olfactory bulb is small.

Below the sphenoid complex lies the median septum formed chiefly by the parasphenoid. A distinct presphenoid cannot be determined but would form the postero dorsal corner above the parasphenoid.

As preserved the lateral wall has a large fenestra due to the fact that the trigeminal fenestra is not closed anteriorly and is thus confluent with the hypophyseal fenestra.

Lying lateral to this is the very well-developed epipterygoid. The footplate resting on and wedged in the pterygoid and the basisphenoid is very well developed and of great antero-posterior extent, but without a posterior process. The ascending process is only moderately expanded, but is very strong. Its upper part and the upper anterior border are greatly thickened. In section this thickening presents a strong bulbous knob (fig. 36).

The median septum of the snout is strongly developed but the ossification fails to reach the interorbital septum dorso-posteriorly.

It is mainly composed of well-developed sheets of the pterygoids and only anteriorly is the pterygoidal septum flanked by sheets from the vomers.

Posteriorly the pterygoids, in the region of the inter-pterygoidal vacuity, have the septal sheets widely separated to enclose a roomy trough. Further anteriorly the pair of sheets approach one another and finally coalesce (fig. 35).

Where the interchoanal vomerine bar curves inwards to the median septum there is the usual groove leading into the vomerine tunnel which carries a branch of the naso-palatine nerve.

Sagittal view (Fig. 32)

Due to poor preservation the details of the internal structure of the endocranial cavity could not be determined. The general structure is, however, in essentials very similar to that of the other Dinocephalia. The endocranial cavity is relatively small and short. The proötic is not ossified anterior to the trigeminal notch; it, however, meets its fellow in the median line and forms the upper part of the dorsum sellae.

Above the interpterygoid vacuity the two pterygoidal median sheets arise well lateral to the median line and form a deep trough.

The parasphenoidal septum is fairly weak.

The basicranial axis (Fig. 33)

Except that it is rather broad the axis has the same structural plan as the other *Dinocephalia*. The fenestra ovalis is situated very low down and the parasphenoidal septum stands practically vertically to the long axis, with its posterodorsal corner probably formed by the presphenoid.

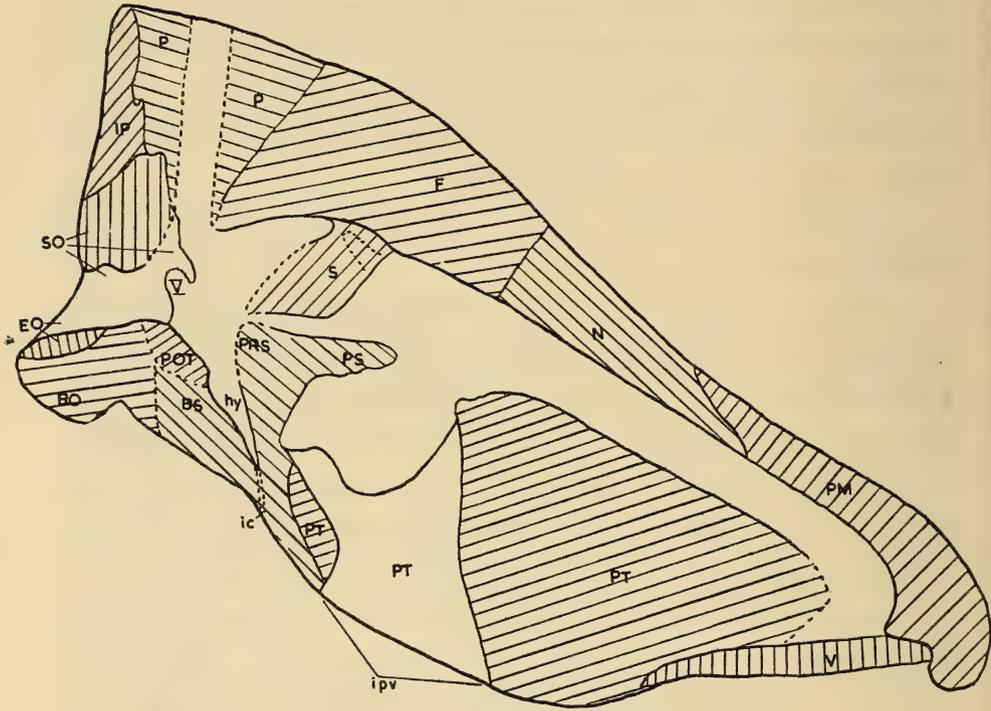


FIG. 32. *Anteosaurus* sp. S.A.M. 12082 and S.A.M. 9085 $\times \frac{1}{4}$.
Sagittal view reconstructed from cross-sections.

Cross-sections through septum of the snout (Fig. 34)

1. This section across the anterior end of the choanae shows the premaxillary processes overlying the anterior end of the vomers. The tunnel for the naso-palatine nerve branch lies between the vomer and premaxillary process. The pterygoid does not meet the premaxilla.
2. Shows the groove on the lateral surface of the vomer for the entry of a branch of the naso-palatine nerve.
3. Near the posterior end of the choanae the fused pterygoidal septum is

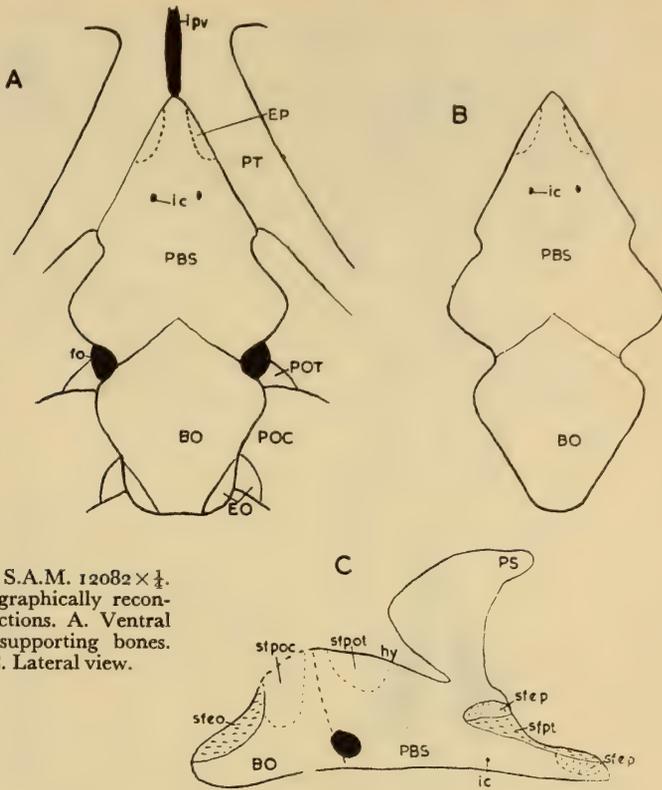


FIG. 33. *Anteosaurus* sp. S.A.M. 12082 $\times \frac{1}{4}$. The basicranial axis graphically reconstructed from cross-sections. A. Ventral view in relation to supporting bones. B. Ventral view. C. Lateral view.

seen flanked by the vomerine septa. A cavity separates the middle portions of the pterygoidal and vomerine septa.

4. Just posterior to the choanae the postero-dorsal part of the vomerine septa still flank the pterygoidal septum. The palatine is seen to overlie the vomer.
5. The fused pterygoids form a high median septum with the posterior ends of the vomerine septa still flanking it dorsally.

Cross-section through the footplate of the epipterygoid (Figs 35-36).

Part of the ventral region has been destroyed by weathering but enough is preserved to show most of the relations of the epipterygoid to the pterygoid and parabasisphenoid.

42. Near the posterior end of the interpterygoidal vacuity the pterygoids are seen to carry two dorsally directed sheets of bone lying well lateral of the median line.
43. Immediately posteriorly a tongue of the epipterygoid is seen lying in the substance of the pterygoid.

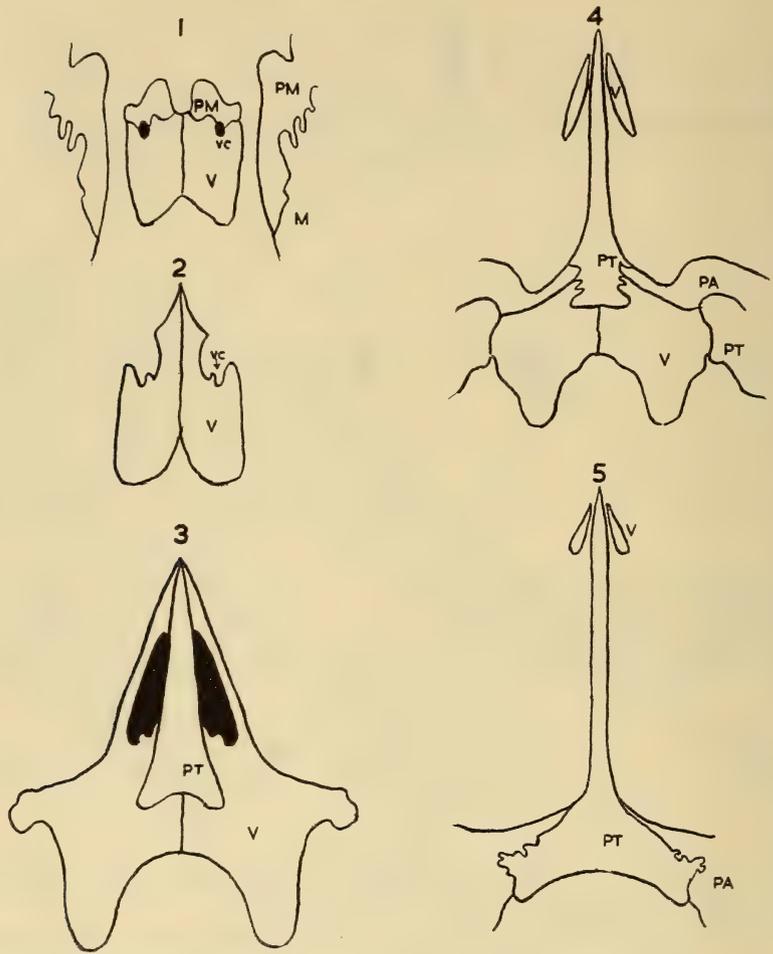
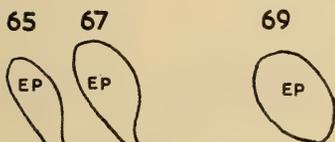
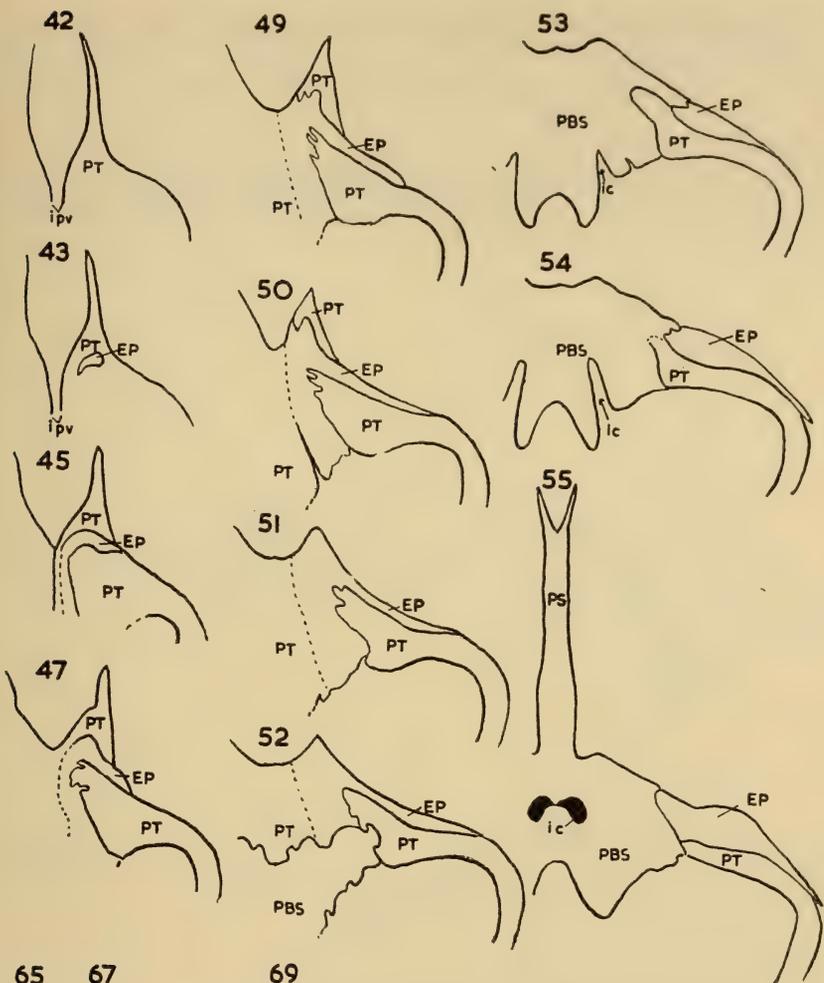


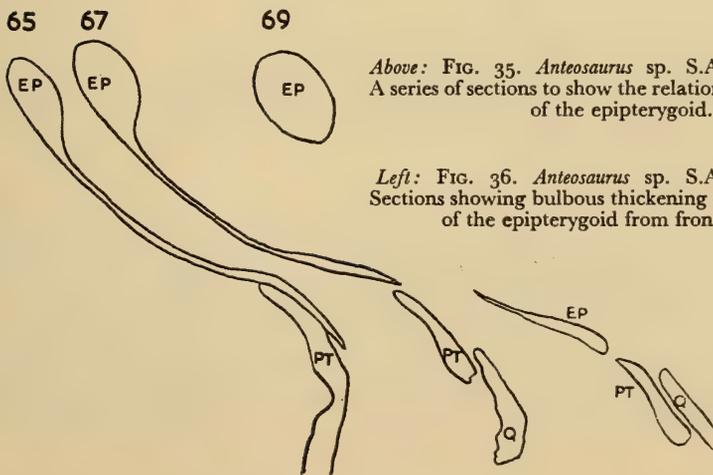
FIG. 34. *Anteosaurus* sp. $\times \frac{1}{2}$.
1 and 2 from S.A.M. 9085; 3 to 5 from S.A.M. 12082. Sections across the snout to show the median septum.

- 45 & 47. Just posterior to the interpterygoidal vacuity the epityergoid is seen to extend medially and also ventrally.
- 49, 50 & 51. The epipterygoid forms part of the floor of the median trough and apparently also enters the ventral surface.
52. The epityergoid apparently overlies the anterior part of the basiptyergoid process against which the pterygoid is also applied.
- 53, 54 & 55. The footplate has moved laterally and is applied to the basiptyergoid process together with the pterygoid.
65. The footplate of the epipterygoid lies on and over the dorsal edge of the



Above: FIG. 35. *Anteosaurus* sp. S.A.M. 12082 $\times \frac{1}{2}$. A series of sections to show the relations of the footplate of the epipterygoid.

Left: FIG. 36. *Anteosaurus* sp. S.A.M. 12082 $\times \frac{1}{2}$. Sections showing bulbous thickening of the upper edge of the epipterygoid from front to back.



quadrate ramus of the pterygoid. Note the thickening of the upper edge of the epipterygoid.

67 & 69. The footplate ends without reaching the quadrate.

The endocranial cavity (Fig. 37)

From the cross-sections in this area which has suffered much from weathering along fracture faces I have attempted graphically to reconstruct the endocranial cavity.

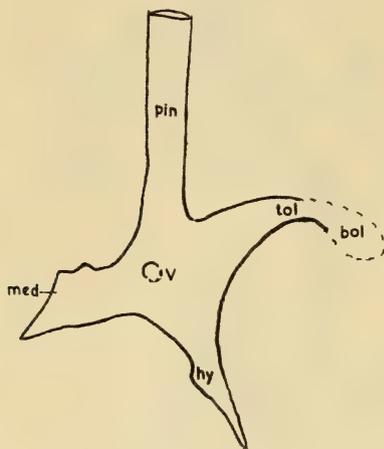


FIG. 37. *Anteosaurus* sp.
S.A.M. 12082 $\times \frac{1}{4}$.
Lateral view of the endocranial cavity
in outline.

Few details can be determined but we get some idea of the proportions.

The parietal tube was long—110 mm. The brain could have only been fairly short and low with a small cerebral region.

TITANOSUCHIA

S.A.M. 11486 *Jonkeria* sp. (Figs 38-52)

From a snout a series of 64 cross-sections have been cut and from these reconstructions have been made to show the anterior part of the median septum in sagittal and parasagittal view.

Lateral view (Fig. 38)

The median septum is seen to be formed by the pterygoids rising fairly high in the skull and extending very far anteriorly. The vomer has no dorsal septal development but flanks the pterygoid as a stout interchoanal bar.

The vomerine bar is pierced by a long tunnel. This enters the bone by a foramen from a groove situated fairly high up in the side of the vomer in a plane at the level of the posterior choanal border. It opens anteriorly at the junction of the vomer and the premaxilla.

This tunnel is connected with a shorter tunnel with a separate dorsal entry and a ventral exit foramen. These probably housed branches of the nasopalatine nerve.

Median view (Fig. 38)

The median pterygoid septum is seen to be deeply intercalated between the two vomera and meets the premaxilla.

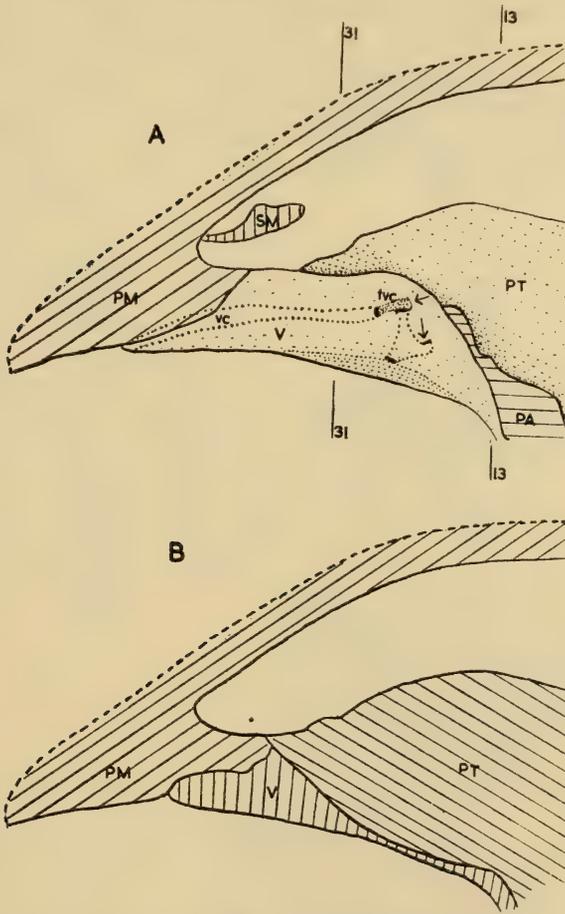


FIG. 38. *Jonkeria* sp. S.A.M. 11486 $\times \frac{1}{4}$.
 A. Parasagittal view of the snout reconstructed from cross-sections. B. Sagittal view. 13-13 and 31-31. Region through which the sections, given in the following figure, pass.

Sections (Fig. 39)

Seven sections from front to back show the interesting relations of the component bones.

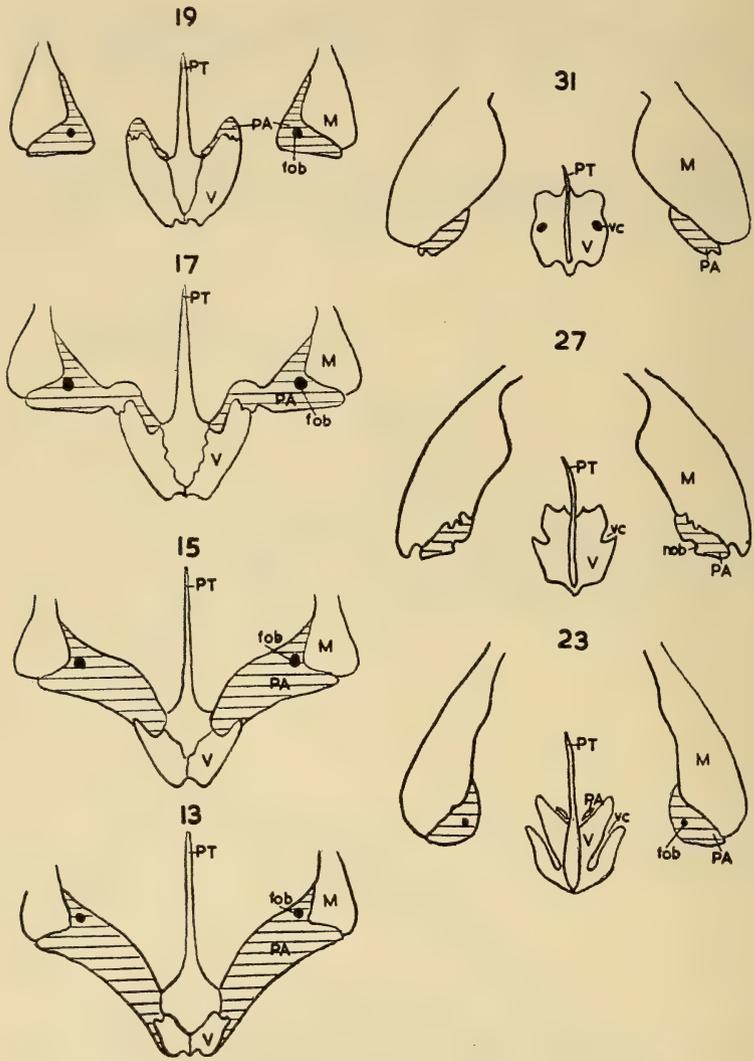


FIG. 39. *Jonkeria* sp. S.A.M. 11486 $\times \frac{1}{4}$.
A series of sections through the median septum of the snout from front to back.

31. Shows the pterygoids as a thin sheet of bone deeply intercalated between the vomers. The tunnel (vc) for the naso-palatine nerve is seen in section.
27. The tunnel opens into a lateral groove. A notch (nob) in the palatine is where the ophthalmic branches of V and VII emerge.
23. Shows the vertical connection between the two tunnels in the vomer. The tunnel for the branches of V and VII is seen penetrating the palatine.

- 19. The palatine caps the vomer.
- 17. The palatine overlies the vomer.
- 15. The palatine meets the pterygoid.
- 13. The palatine commences to underlie the vomer.

S.A.M. 11556 *Jonkeria* sp. (Figs 40-44)

A poorly preserved skull with most of the outer bones missing has been used to cut a series of cross-sections to reveal the internal structure. The braincase was cut out of the skull in the form of a rectangular block which was then cut across in a consecutive series of 100 sections.

Drawings of some of the sections are here reproduced as also graphically reconstructed sagittal and parasagittal views of the posterior part of the skull and the two outline figures of the endocranial cavity.

The lower surface of the parabasisphenoidal and pterygoidal region has unfortunately suffered from weathering.

Parasagittal view (Fig. 40)

The occiput and dorsal roof-bones are seen in section and the braincase and related bones in lateral aspect.

The trigeminal foramen is anteriorly not closed as the anterior process of the supraoccipital and proötic fail to meet each other. Dorsally it has no border and anteriorly lies the posterior edge of the orbitosphenoid.

Otherwise the proötic is well developed with the foramen for the VIth and VIIth cranial nerves well back from its anterior border.

The sphenoid complex is well developed in its anterior part which is formed

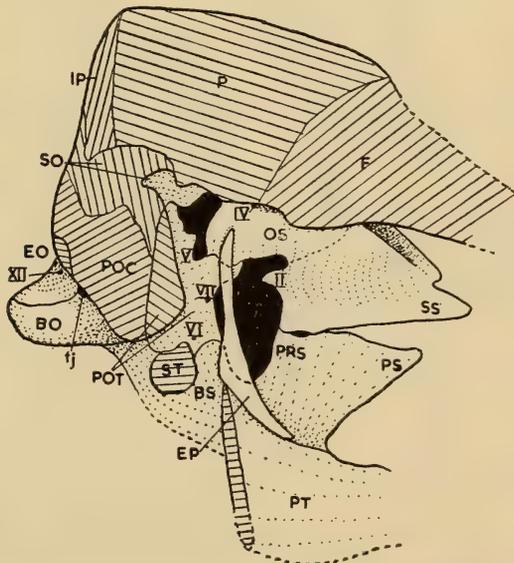


FIG. 40. *Jonkeria* sp. S.A.M. 11556 $\times \frac{1}{4}$. Lateral view of the braincase graphically reconstructed from a series of cross-sections.

by the septosphenoid; its posterior part is less well ossified and it does not meet the supraoccipital and ventrally the orbitosphenoid does not extend so far as to include the optic foramen which therefore pierces cartilage.

Ventrally the septosphenoid has its posterior part supported by the presphenoid. With fuller ossification it would also rest on the parasphenoidal rostrum.

The parasphenoid is directed sharply upwards and forwards making with its anterior edge an angle of $\pm 70^\circ$ with the basis cranii.

The postero-dorsal part of the parasphenoidal septum is formed by the presphenoid indistinguishably fused to it.

The epipterygoid has a well-developed footplate, but the ascending process, although nearly reaching the parietal, is slender so that the large lateral fenestra is well exposed.

Sagittal view (Fig. 41)

A sagittal section clearly shows that the present specimen is of an immature reptile. Incomplete ossification is seen in the exoccipital, which only forms part of the posterior floor of the braincase, the incompletely formed dorsum sellae and the large unossified zone in the parabasisphenoid and thirdly the unossified lower part of the orbitosphenoid which does not enclose the optic foramen.

In addition the internal auditory meatus is widely open and the orbitosphenoid is not met by the supraoccipital.

This is the only specimen where there is some indication of the line of

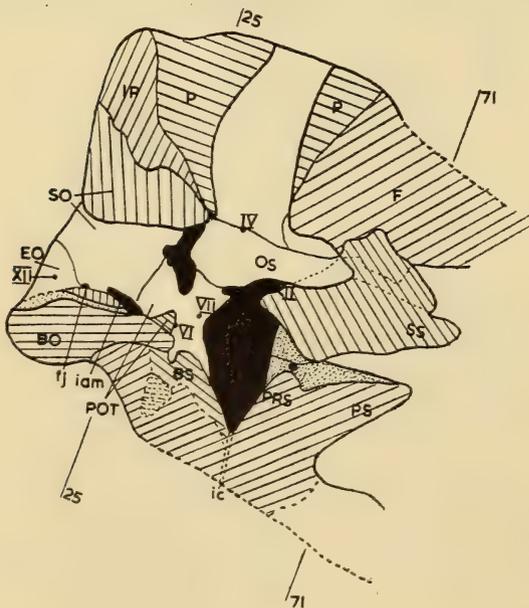


FIG. 41. *Jonkeria* sp. S.A.M.
11556 $\times \frac{1}{4}$.
Sagittal view of the braincase as reconstructed. Numbered lines show the plane of the cross-section of the correspondingly numbered sections.

fusion of the basisphenoid to the underlying parasphenoid; but there is no line of junction indicated between the presphenoid and the parasphenoid.

Sections through the posterior part of the braincase (Fig. 42)

- 25. A section through the plane in which the vestibules lie shows the roof and sides of the braincase formed by the supraoccipital and the floor by the basioccipital.
- 31. A section through the plane in which the trigeminal foramina lie shows the pair of proötics meeting in the floor of the braincase. Note the imperfect ossification in the parabasisphenoid.

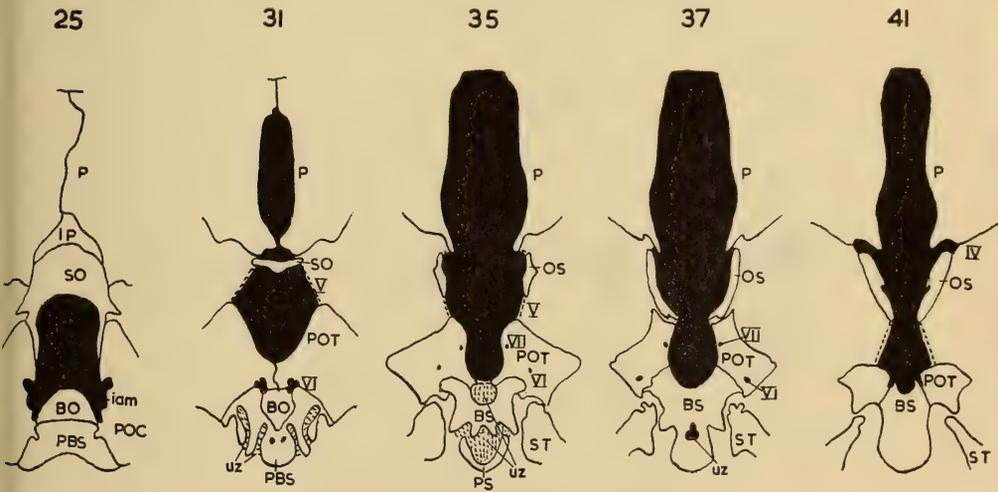


FIG. 42. *Jonkeria* sp. S.A.M. 11556 $\times \frac{1}{4}$.

A selected series of cross-sections through the posterior part of the braincase. Each section bears its number in the consecutive series.

- 35. This section shows the imperfectly ossified dorsum sellae and an unossified zone between the basisphenoid and the parasphenoid.
- 37. Here the sidewalls of the braincase are seen to be formed by the orbitosphenoids and the proötics.
- 41. Lateral to the root of the pineal tube lies the foramen from the IVth cranial nerve and below the orbitosphenoid the sidewall is membranous.

Sections through the sphenoid-complex (Fig. 43)

These cross-sections are from front to back and the line of sections is indicated in figure 41 under the section numbers.

- 71. In the anterior part of the sphenoid complex the septosphenoid is seen to carry lateral of a median septum grooves which house the paired

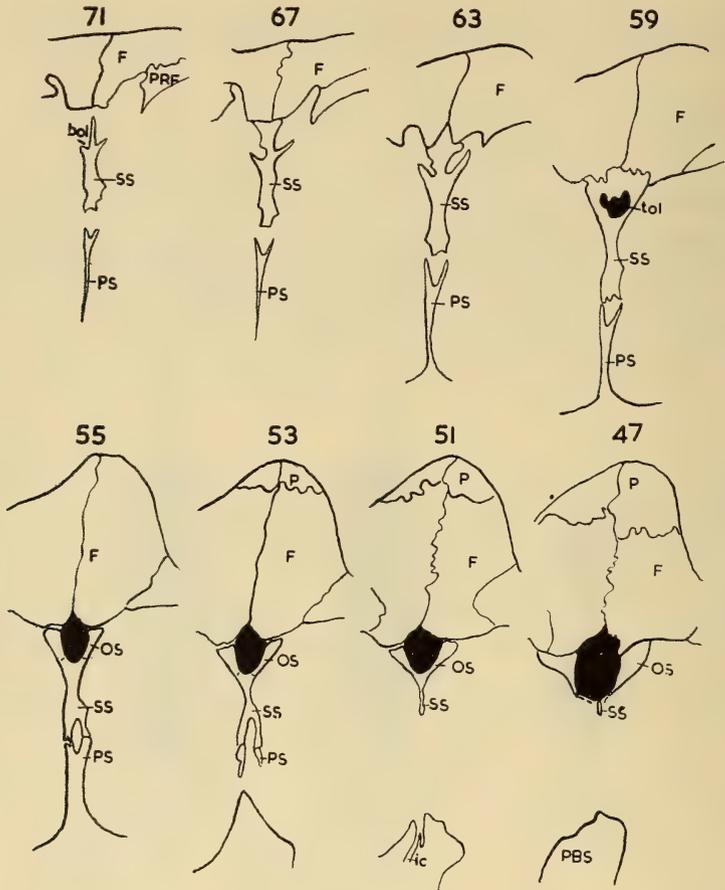


FIG. 43. *Jonkeria* sp. S.A.M. 11556 $\times \frac{1}{4}$.
Sections numbered from front to back through the sphenoidal region.

olfactory bulbs. The forked upper edge of the parasphenoid does not extend to the thickened lower edge of the septosphenoid.

- 67 & 63. The wings of the septosphenoid curve round the olfactory grooves.
59. The unpaired olfactory tract is enclosed by bone, which may be orbitosphenoid but no break between the wings and the lower septal part can be determined.
55. The lower thickened edge of the sphenoidal septum is forked and meets the upwardly directed fork of the parasphenoid (?presphenoid) to enclose a canal (trabecular canal). The wings enclosing the olfactory lobes appear to be orbitosphenoid.
53. The sphenoidal fork is well developed.
51. In the plane of the perforations for the internal carotids the sphenoidal septum becomes reduced.

47. The sphenoidal septum ends and laterally lie the wings of the orbito-sphenoids.

The endocranial cavity (Fig. 44)

In lateral and dorsal outline views of the endocranial cavity the exit points of the various openings and foramina in the braincase are indicated. Of the subdivisions of the brain only the olfactory bulbs, tracts and lobes are clearly demarcated.

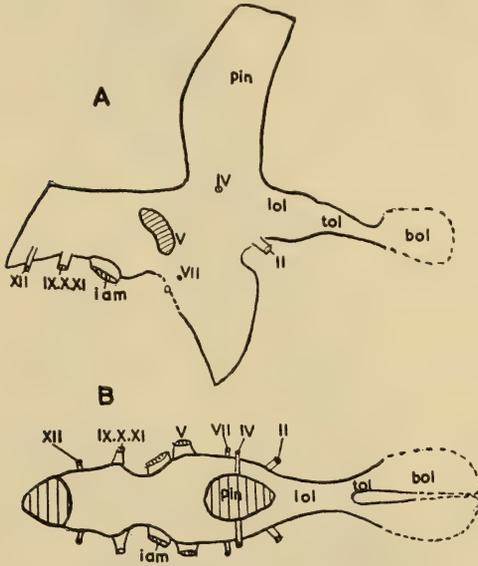


FIG. 44. *Jonkeria* sp. S.A.M. 11556 $\times \frac{1}{4}$.
Outline figures of the endocranial cavity:
a. Lateral view; b. Dorsal view.

S.A.M. 11574 *Jonkeria*

Of this fairly good skull I have cut 144 cross-sections. From these I have graphically reconstructed the skull in parasagittal and sagittal section, the basicranial axis in two views and made outline drawings of the endocranial cavity in lateral and dorsal views.

Parasagittal view (Fig. 45)

The lateral wall of the braincase is well ossified and is closed except for a large fenestra in the hypophyseal area and small openings for some of the cranial nerves. Lateral to the olfactory bulbs there is also no bony wall.

Below the anterior part of the braincase there is a fairly well-ossified inter-orbital septum.

In the snout there is a fairly well-developed septum formed by the pterygoids.

Lateral to the hypophyseal fenestra lies an epipterygoid of small dorsal extent.

The large hypophyseal fenestra, the moderately developed interorbital septum, the posteriorly truncated pterygoidal septum and the weakly developed epipterygoid, all indicate that the skull is in all probability not fully mature.

The constituent bones of the lateral wall of the braincase are: exoccipital, supraoccipital, opisthotic, proötic, orbitosphenoid and septosphenoid.

The proötic is well developed; posteriorly firmly applied to the opisthotic, dorsally meeting the anteriorly directed flange of the supraoccipital, ventrally resting on the basisphenoid, anteriorly, its lower half has a free edge forming the posterior border of the hypophyseal fenestra, whereas its upper half abuts against the orbitosphenoid. Near its anterior edge there are two foramina; the upper is a relatively small trigeminal foramen and the lower the small foramen for the facialis (VII).

The orbitosphenoid is an elongated bone dorsally, applied to the under surface of the parietal and frontal; ventrally it has a free edge which forms the upper border of the large hypophyseal fenestra; antero-ventrally it rests on the septosphenoid along an oblique suture.

At the junction of orbitosphenoid, proötic and supraoccipital lies a slit-like foramen probably for the IVth nerve.

The septosphenoid presents a large lateral surface. Dorsally it meets the orbitosphenoid and the under surface of the frontal. Ventrally it rests on the parasphenoidal and presphenoidal median septum.

Dorso-anteriorly the outer face of the septosphenoid is hollowed out and in this groove the olfactory tract opens and in it lies the olfactory bulb. Behind the groove the septosphenoid meeting the orbitosphenoid forms the lateral wall of the olfactory tract. Below this level the septosphenoid forms a median septum which ventrally fits into a groove of the parasphenoid and ?presphenoid.

The parasphenoid indistinguishably fused with the presphenoid forms a rather weak median septum which is dorsally forked to receive the septosphenoid.

The median septum of the snout is mainly formed by the pterygoids but anteriorly it is flanked by weak septal flanges of the vomers.

The epipterygoid is weakly developed in this specimen which appears to be immature. The footplate is elongated and quite strong but the ascending columella is but feebly developed. In the mature skull the epipterygoid probably meets the parietal and would thus largely cover the fenestra laterally of the cavum epiptericum.

Sagittal view (Fig. 46)

It is apparent that the floor of the braincase is incompletely ossified. Dorso-anteriorly of the basioccipital the two proötics have not met in the median line

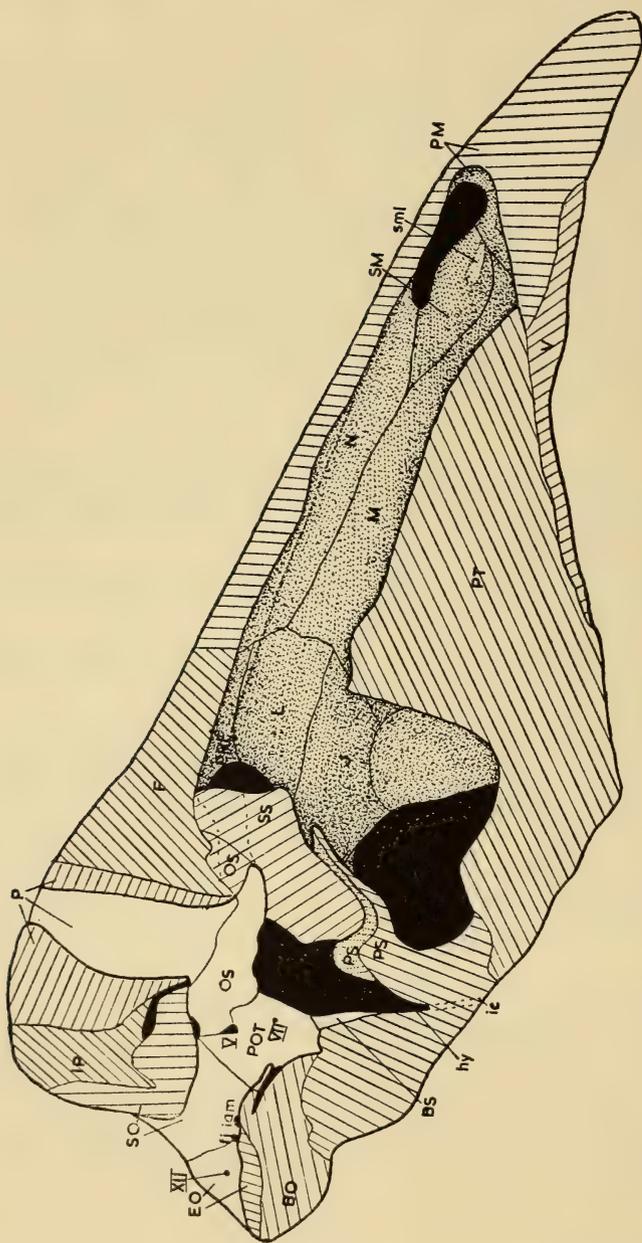


FIG. 46. *Jonkeria* sp. S.A.M. 11574 $\times 4$.
Sagittal view drawn from cross-sections.

so that the upper part of the dorsum sellae is unossified.

The presphenoid cannot be identified as a separate element, but is probably represented by the weakly and incompletely ossified area lying postero-dorsally of the parasphenoidal septum.

The orbitosphenoid has its ventral part unossified. The exit of the optic nerve (II) is thus through the upper part of the large lateral fenestra.

The septosphenoid is seen to form a well-developed median septum which in its dorsal part separates the paired olfactory tracts and the olfactory bulbs.

The median septum of the snout is seen to be formed of an extensive vertical sheet formed by the pterygoids extending right up to the premaxilla

Cross-sections through the sphenoidal region (Fig. 47)

This series of sections, from front to back, show the relations of the orbito- and septosphenoids.

49. The septosphenoid is a simple median septum with a ridge indicating the ventral limit of the groove housing the olfactory bulb. Dorsally there is a pocket in the frontal and prefrontal for the posterior end of the nasal sac.
51. The olfactory groove becomes deeper and the tip of the parasphenoid is seen bifurcating.
53. The groove becomes pinched in before entering the tube for the olfactory tract.
54. The olfactory tracts lie in tubes enclosed above by the orbitosphenoids and below by the septosphenoid.
55. The pair of olfactory tracts coalesce to house the olfactory lobes in a kidney-shaped tube.
57. The parasphenoid diverging dorsally clasps the septosphenoidal septum.
- 59 & 61. Show the orbitosphenoids only forming the lateral walls and no longer roofing the cerebral hemispheres. The parasphenoid forms a thin septum.

The basicranial axis (Fig. 48)

The accompanying figure shows the basicranial axis and its relations to the adjacent bones.

The primitive basiptyergoidal processes are not distinguishable. Their original situation is indicated by the sutural faces for the epiptyergoid and ptyergoid.

The parabasisphenoidal tubera are quite prominent and the outer borders of the fenestra ovalis is seen to be formed by the basioccipital, parabasisphenoid, proötic and opisthotic.

Two pairs of foramina pierce the parabasisphenoid, the posterior are the internal carotid foramina and the anterior pair the accessory carotid foramina.

The parasphenoidal rostrum is weak and is directed sharply upwards at an

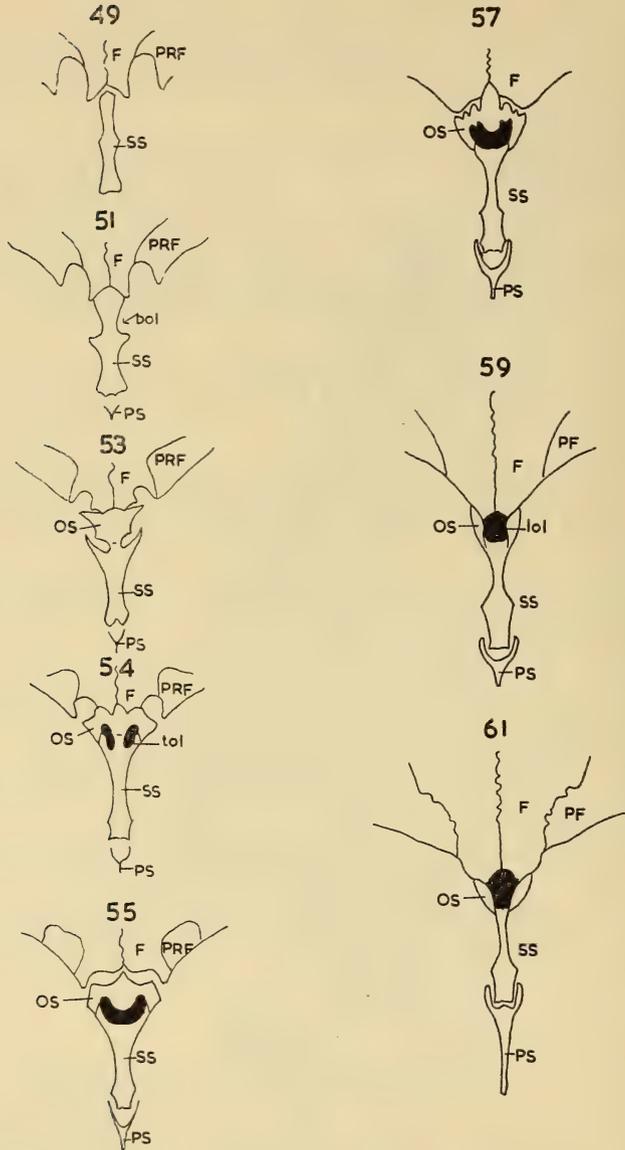


FIG. 47. *Jonkeria* sp. S.A.M. 15574 $\times \frac{1}{4}$.
A series of sections, from front to back, through the sphenoidal region.

angle of about 100° to the lower edge of the axis.

The postero-dorsal bulge in the septum may be formed by a presphenoid.

The endocranial cavity (Fig. 49)

The incomplete ossification in the proötic and sphenoidal regions of the

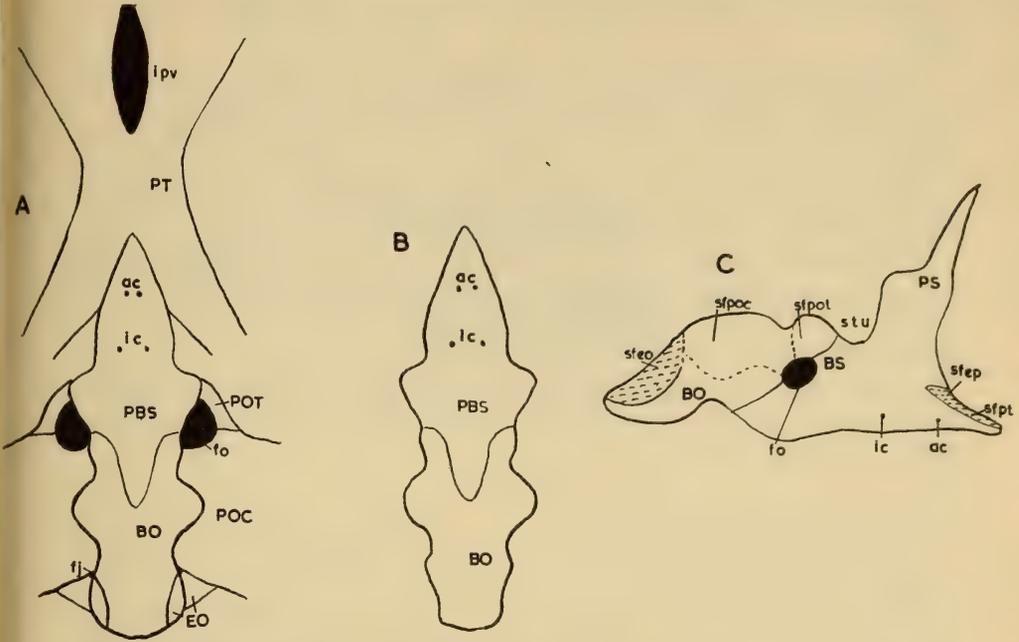


FIG. 48. *Jonkeria* sp. S.A.M. 11574 $\times \frac{1}{4}$.
 The basicranial axis reconstructed from serial cross-sections. A. Ventral view, with contiguous bones. B. Ventral view. C. Lateral view.

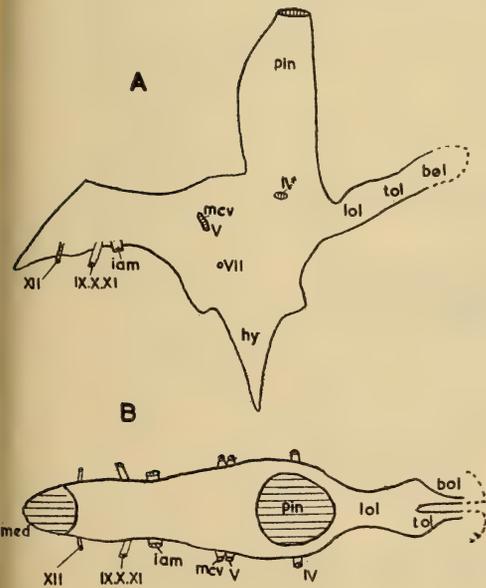


FIG. 49. *Jonkeria* sp. S.A.M. 11574 $\times \frac{1}{4}$.
 The endocranial cavity reconstructed from serial sections. A. Lateral view. B. Dorsal view.

endocranial floor prevents us from determining the lower border of the mid-brain.

The roots of the posterior cranial nerves lie near the ventral edge; the trigeminal exit lies well up the side and the IVth nerve emerged high up.

The olfactory lobes must have been very poorly developed. The tractus olfactorius was short.

The parietal canal is of moderate height—about 90 mm and the maximum antero-posterior and side to side diameter 40 mm.

The parietal foramen is much smaller than the diameters of the parietal tube, due to a forward growth of the upper part of the posterior wall.

S.A.M. 11575 *Jonkeria* sp.

I have cut a series of cross-sections of this specimen, which consisted of a snout found in association with S.A.M. 11574. From these I have prepared three graphic reconstructions.

The snout in parasagittal view (Fig. 50)

The interchoanal bar formed by the vomers is pierced by a pair of tunnels running through the vomers from back to front.

Each tunnel enters the bone from a longitudinal groove high up the side of the bar and has its exit between the anterior end of the vomer and the premaxilla. They housed a branch of the naso-palatine nerve.

Dorsally the vomer is pinched in and here forms a sheet of bone flanking the sagittal septum composed of the pterygoid. The pinched-in hollow in the vomer housed the lower part of the nasal capsule. Anterior to this lies the direct air passage (abnp) between external and internal nares.

In this figure the inner surface of the septomaxilla is shown. At the posterior

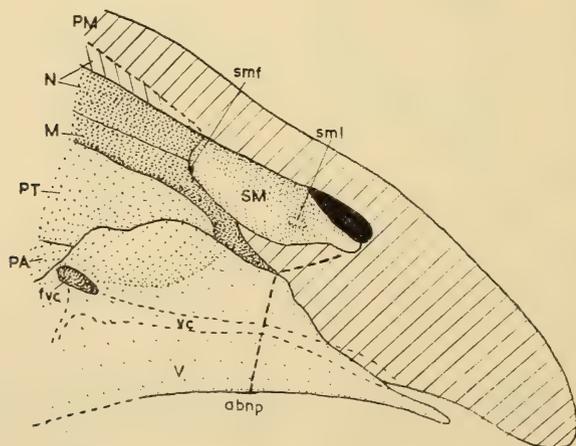


FIG. 50. *Jonkeria* sp. S.A.M. 11575 $\times 4$. Parasagittal view of the snout reconstructed from sections.

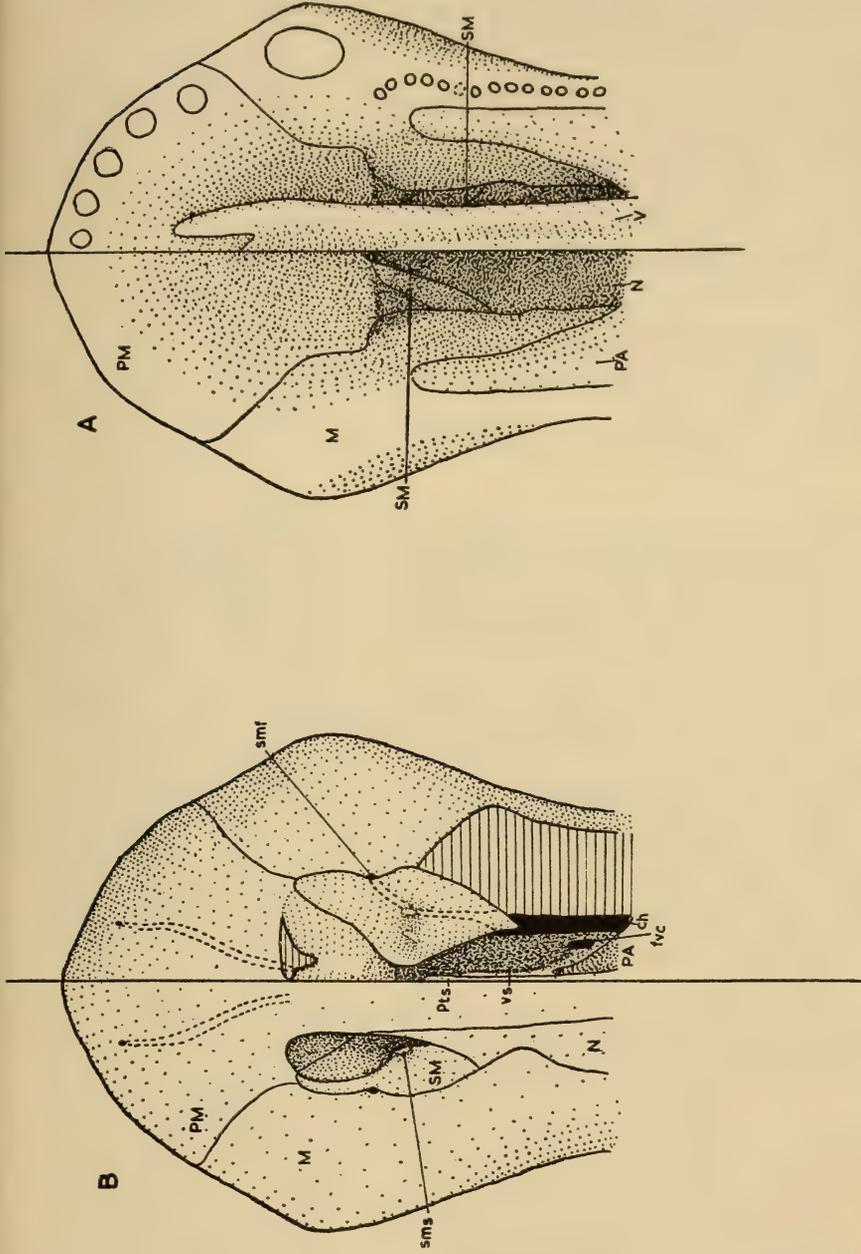


FIG. 51. *Jonkeria* sp. S.A.M. 11575 $\times \frac{1}{4}$.
 A. Ventral view of snout with right vomer removed. B. Dorsal view of snout with the roof-bones of the right half cut away.

edge of the septomaxilla lies the inner opening of the septomaxillary foramen. In its anterior half it carries a horizontal ledge which forms the floor of the nares.

The interior border of the air passage leading from the external naris to the choana is shown by a thick broken line (abnp).

Ventral view (Fig. 51)

A reconstructed ventral view shows the choanae in relation to the nares. From the anteriorly situated naris the direct air passage to the choana runs backwards below the horizontal ledge of the septomaxilla, whereas the passage to the olfactory sac runs above this ledge.

Dorsal view (Fig. 51B)

On the right side part of the premaxilla and maxilla and the whole nasal bone are shown cut away to expose the floor of the nares, the choana and the dorsal surface of the interchoanal bar.

The anterior and lateral part of the floor of the nostril is formed by the premaxilla and the septomaxilla.

Medially lies the direct air passage passing below the ledge of the septomaxilla to the choana. The passage above the ledge leads to the olfactory sac.

The course of the septomaxillary tunnel from the internal to the external opening is shown in broken lines.

In the median line the median septum formed by the pterygoids and vomers is shown to form a partial wall between the two olfactory cavities.

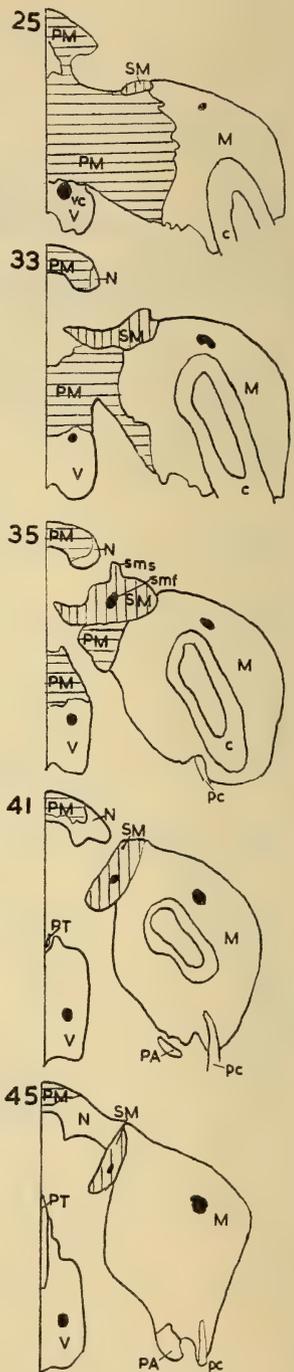


FIG. 52. *Jonkeria* sp.
S.A.M. 11575 $\times \frac{1}{4}$.
A series of sections from front
to back, through the septo-
maxilla.

The foramen (fvc) leading into the longitudinal tunnel through the vomer lies lateral to the choana in the dorso-lateral surface of the vomer.

Sections (Fig. 52)

Five cross-sections are here reproduced to show the relations of the septomaxilla.

25. A section through the anterior part of the nostril which shows the nostril floor to be formed chiefly by the premaxilla. Note the forward extension of the nasal cavity into the premaxilla.
33. The septomaxilla now forms the outer part of the floor, whereas the premaxilla forms the median part of the floor over which passes the direct air passage to the choana.
35. The median and lower direct air passage is seen connecting with the choana; whereas the septomaxilla forms the floor for the higher olfactory passage.
- 41 & 45. Show the median septum formed by the pterygoids and vomers.

The Dinocephalian Braincase

From the foregoing detailed descriptions of the specimens studied it has become clear that the three groups of the Dinocephalia studied (unfortunately I have no suitable specimen of the Styraocephalia), viz. the Anteosauria, Tapinocephalia and the Titanosuchia, have much in common as far as the structures here examined are concerned. A general account for the Dinocephalia as a group can now be presented and this can be followed by a comparative consideration of the constituent sub-groups.

In lateral view very little of the ossifications of the original chondrocranium can be seen. Ventrally only the lower face of the basioccipital and of the exoccipitals and opisthotic are exposed—the rest being sheathed by the parasphenoid. Posteriorly the basioccipital, exoccipitals and the supraoccipital are seen enclosing the foramen magnum, with the opisthotic extending laterally to form the stout paroccipital process. Laterally the stout postorbital bar obscures most of the lateral face of the braincase and through the orbit little of the interorbital septum can be seen.

Dorsally of course the dermal bones of the roof overlie the endochondral bones. A parasagittal cut removes the lateral dermal bones and the bones of the palatoquadrate so that the braincase can be seen in lateral view with the opisthotic and supraoccipital showing a sectioned lateral face.

In contrast to their pelycosaur ancestors and also to all contemporary therapsids of the *Tapinocephalus* zone, the dinocephalian brain is well enclosed in a practically complete bony box of strongly ossified bones. Except for the openings for the cranial nerves, blood vessels and otic ducts (endo- and perilymphatic) there is one large lateral opening representing the original metoptic fissure situated between the pila antotica and the pila metoptica. Anteriorly the nasal capsule is of course unossified so that the bulbus olfactorius is not

covered laterally by bone.

The closure of the lateral wall above the pituitary fossa is effected by the meeting of the ossifications of the otic and sphenoidal regions. This is in part due to the posterior location of the sphenoidal ossifications, but also to the well-developed condition of the otic ossifications which have extended well forwards. The proötic and supraoccipital both extend well anterior to the plane of the original proötic incisure.

The bones enclosing the brain are: the exoccipitals, basioccipital, basi-sphenoid, supraoccipital, opisthotics, proötics and the sphenoids with the parasphenoid sheathing the basisphenoid ventrally and the sphenoid complex clasped and supported ventrally by the presphenoid and the parasphenoidal rostrum.

The exoccipital

In posterior view the exoccipitals form the upper and latero-dorsal part of the stout condyle. Laterally they overlap on to the posterior face of the opisthotic and dorsally on to the posterior face of the supraoccipital.

The two exoccipitals meet each other in the median line and thus form the surface on which the medulla and hindbrain rest. The exoccipital part of the floor ends just posterior to the plane in which the internal auditory meati lie. Anterior to this lies a hump formed by the basioccipital. Laterally each exoccipital curves upwards to form most of the lateral rim of the foramen magnum. Dorsally it meets the supraoccipital and thus forms the lower posterior part of the sidewall. The inner face of the exoccipital is pierced by two foramina situated low down on the sidewall, practically at floor level. The smaller and posterior foramen gives exit to the hypoglossal nerve (XII). The larger and anterior foramen, the so-called jugular or vagus foramen, forms the inner opening of a long tube (25 mm in length in a specimen of *Struthiocephalus*) which in addition to nutritive vessels housed the glossopharyngeal (IX), vagus (X) and the accessory (XI) nerves. The exoccipital is really notched not pierced by this foramen as it forms only the posterior half of the border—the anterior half being formed by the opisthotic. In some cases these two tubes merge and open into a single external foramen.

The basioccipital

The basioccipital forms the ventral part of the condyle. Posteriorly a notochordal pit is evident. This unossified part sometimes extends anteriorly under the exoccipitals and may even join an unossified space lying between the basioccipital and the proötic.

Ventrally the basioccipital overlaps the lower face of the opisthotic, where it is notched to form the inner edge of the jugular foramen.

The basioccipital makes only a very small contribution to the floor of the braincase. Just posterior to the plane in which the internal auditory meati lie, the ends of the exoccipitals diverge and here there lies a low hump in the floor

composed of basioccipital. Anterior to the vestibules the basioccipital meets the proötics above in an unossified zone.

Anteriorly the basioccipital abuts against the basisphenoid and internally forms part of the inner face of the foramen ovale.

The proötics

In lateral and anterior views the proötic is seen to have an extensive outer face as it lies firmly ankylosed against the inner face of that part of the occipital plate formed by the supraoccipital and the opisthotic and its paroccipital process. Anteriorly an edge of the proötic forms the posterior border of a large fenestra—the trigeminal foramen. This is in some cases transformed to two separate openings—the upper one for the median cerebral vein and the lower for the trigeminal nerve. Anterior to the fenestra a pillar of the proötic ascends and this in some cases meets a descending pillar of the supraoccipital to enclose the trigeminal fenestra anteriorly.

The two proötics meet each other in the median line to form the floor of the braincase anterior to the plane in which the internal auditory meati lie. The proötics form a transverse ridge across the brain floor and the anterior face of this ridge forms the upper part of the dorsum sellae. The lower part of the posterior wall of the sella turcica is formed by the basisphenoid. Laterally, just behind the transverse proötic ridge, the proötic forms the anterior border of the internal auditory meatus, whose posterior border appears to be formed by the opisthotic. From the floor the proötic laterally curves upwards to form part of the side wall, where it posteriorly and dorsally meets the downwardly extending inner face of the supraoccipital.

The most lateral anterior edge of the proötic forms the posterior border of the large trigeminal fenestra. More medially and anteriorly the proötic forms a dorsally directed stout process developed in the pila antotica and this pillar forms the lower half of the anterior border of the trigeminal fenestra. Here it often meets the downwardly directed process of the supraoccipital. The original proötic incisure is thus closed anteriorly and a proötic fenestra is thus formed and this is directed much anteriorly.

The median ventral face of the proötic abuts against the ascending process of the basisphenoid and these two together form the dorsum sellae. Higher up the anterior edge of the proötic meets the orbitosphenoid.

Just behind this edge and below the trigeminal fenestra the proötic is pierced by a foramen for the facial nerve (VII).

The supraoccipital

In the internal face of the braincase the supraoccipital forms the upper smaller part of the lateral rim of the foramen magnum above the exoccipital. Extending dorsally it forms the dorsal edge of the foramen magnum and from here anteriorly it forms the whole domed roof of the brain up to the root of the parietal organ.

In the lateral wall the supraoccipital descends to meet the anterior edge of the exoccipital and the dorso-posterior edge of the proötic and the opisthotic.

Anterior to the plane in which the trigeminal fenestra lies, a process of the supraoccipital descends to meet the ascending proötic process formed in the pila antotica to form the upper part of the anterior border of the trigeminal fenestra. The anterior edge of this process meets the posterior edge of the orbito-sphenoid. Antero-dorsally the supraoccipital meets the parietal where the parietal organ emerges from the brain.

Postero-dorsally of the internal auditory meatus is an outward directed bulge for the flocculus.

The basisphenoid

The basisphenoid houses the pituitary fossa of which it forms the anterior and most of the posterior face. At the bottom of the pit a pair of foramina enter carrying the internal carotids. No demarcation between the basisphenoid and the sheathing parasphenoid is usually evident, cf. *Jonkeria*.

There being no sidewalls to the sella turcica the metoptic fissure is patent and the pituitary vein has no special foramen but it would appear that both the oculomotorius (III) and the trochlearis (IV) emerging higher up pierce the posterior part of the sphenethmoid complex.

The opisthotic

In its median part the opisthotic is firmly ankylosed to the supraoccipital above and the proötic anteriorly. Laterally it is produced as a very strong paroccipital process and forms most of the rim of the foramen ovale—posteriorly, anteriorly and laterally.

In the inner face of the endocranial cavity the opisthotic has no great face and appears only to enter into the rim of the internal auditory meatus. Lateral to this it of course houses the internal ear.

The parietal

Above and between the foramina for the exit of the pair of trochlear nerves the braincase has a large dorsal foramen whose rim is wholly formed by the parietals. This is the lower end of the parietal tube which pierces the greatly thickened skull roof.

Laterally the ventral edge of the parietals rest on the upper edges of the supraoccipital and the sphenoid complex. Here the parietal tube is somewhat constricted—but immediately widens again with a decided posterior bulge—then narrows again with the tube during the whole length presenting in section an irregular oval outline. Dorsally at its opening on to the outer surface the tube is again somewhat constricted and the outer parietal or pineal foramen usually opens in the middle of a mound.

The parietal tube varies in length from 100–320 mm. Its walls are smooth and formed of compact bony tissue.

The sphenoidal region

Anterior to the otic region lies the sphenoidal complex usually in maturity well ossified. Ventrally it rests in the form of a median septum on the septum formed by the parasphenoid. Dorsally it is intercalated between the frontals. Posteriorly it meets the parietal, supraoccipital and proötic, but postero-ventrally the sidewall is fenestrated as here the metoptic fissure is still patent and the hypophysis laterally not enclosed with bone.

The sphenoidal complex is composite and the limits of the component parts difficult to determine as the sutures are in maturity usually closed, but from the sections it is manifest that three discrete elements are present, viz. a presphenoid, an orbitosphenoid and a septosphenoid.

The presphenoid is a sheet of bone lying in the median plane and ventrally resting on the parasphenoidal septum to which it is usually intimately fused, and dorsally supports the septum formed by the septosphenoid. Its posterior edge forms the anterior border of the pituitary fossa.

The septosphenoid is also a vertically orientated sheet of bone which rests ventrally on the upper edges of the presphenoid and the parasphenoid. Its posterior edge is free and forms the upper part of the anterior border of the hypophysal fenestra. Dorsally it is clasped by the frontals.

In its dorso-anterior part a pair of lateral grooves are developed separated by a median septum. The posterior part of the olfactory bulbs are housed in these grooves. The olfactory bulbs thus have no lateral bony wall. Posterior to these grooves the olfactory tracts are housed in a pair of tubes.

The orbitosphenoids form the postero-dorsal part of the sphenoidal complex. They form the postero-dorsal part of the median septum. From this median stem the pair of orbitosphenoids curve round the thalamus and the cerebral hemispheres. Just above the median stem each orbitosphenoid is pierced by a large rounded foramen for the optic nerve (II).

Dorsally the orbitosphenoids abut against the under surface of the parietals and frontals and under the frontals the two orbitosphenoids meet each other in the median line to form a roof for the cerebral hemispheres.

Posteriorly each orbitosphenoid meets the supraoccipital high up in the sidewall and lower down the proötic to form a bony lateral wall enclosing the brain.

The ethmoidal region

Anterior to the sphenoidal region there are in the Dinocephalia no ossifications in the ethmoidal region nor in the nasal capsules.

Anterior to the parasphenoid the median septum is formed by a high sheet of the pterygoids flanked by upgrowths of the vomers.

Contemporary therapsids

In order to enable me to compare the nature of the braincase, basicranial axis and median septum in the Dinocephalia to that developed in their con-

temporary fellow therapsids I present here descriptions of these structures as determined in one specimen of a dicynodont and in two pristerognathid therocephalians. Unfortunately I have as yet not been able to collect a suitable specimen of a gorgonopsian.

(a) DICYNODONTIA

S.A.M. 12217 *Dicynodon* sp.

I have cut a series of 62 cross-sections of a fair-sized *Dicynodon* skull from the lower part of the *Tapinocephalus* zone.

For comparison with the foregoing Dinocephalia I have graphically reconstructed views of the skull in the same way as for the Dinocephalia.

Parasagittal view (Fig. 53A)

The braincase occupies a great part of the length of the skull—74% (*Moschops* 59%, *Struthiocephalus* 44%, *Jonkeria* 34%, *Anteosaurus* 32%) and also of the height of the skull (excluding the thickness of the roof-bones) viz. 61% (*Moschops* 41%, *Struthiocephalus* 41%, *Anteosaurus* 40%, *Jonkeria* 36%). The braincase is high relative to its length—79% (*Anteosaurus* 31%, *Moschops* 26%, *Struthiocephalus* 25% and *Jonkeria* 21%).

But its sides are widely open. There is a large gap between the sphenoidal region and the otic region.

The anterior extent of the proötic is not great and the trigeminal emerges through a notch at the junction of the proötic and the supraoccipital.

The sphenoidal complex situated far forward is very well developed. Dorsally it is applied to and intercalated between the frontals. Its median septal part extends far ventrally where it rests on the tip of the parasphenoidal rostrum.

On its dorso-anterior face there is a groove which housed the olfactory bulbs. Posteriorly this groove pierces the bone and connects with the trough which houses the unpaired olfactory lobes.

The sides of this trough may be formed by a separate bone. A notch posteriorly indicates its limits.

The complex would then be composed of a median septal part—the septosphenoid—and a pair of wings—the frontosphenoid or orbitosphenoid.

The parasphenoidal rostrum, which lies horizontally stretches far forward to make contact with the palatal sheets of the premaxillae. On its dorsal edge it carries a sheet of bone directed antero-dorsally towards the postero-ventral edge of the septosphenoid. This is the presphenoid.

Anteriorly the lower edge of the parasphenoidal rostrum rests on the upper surface of the vomers, which lie far posteriorly in the middle third of the skull. The choanae lie posterior to the anterior third of the skull.

Anterior to the vomers the premaxillae form a well-developed median septum in the snout.

The fenestra ovalis pierces the basioccipital well above the lower edge, here formed by the strong basioccipital tubera.

The epipterygoid has a fairly short footplate resting on the pterygoid and meeting the basisphenoid at the basiptyergoidal process. Its ascending process which is fairly slender is directed somewhat anteriorly and meets the under surface of the parietal.

The quadrate ramus of the pterygoid is low and weak.

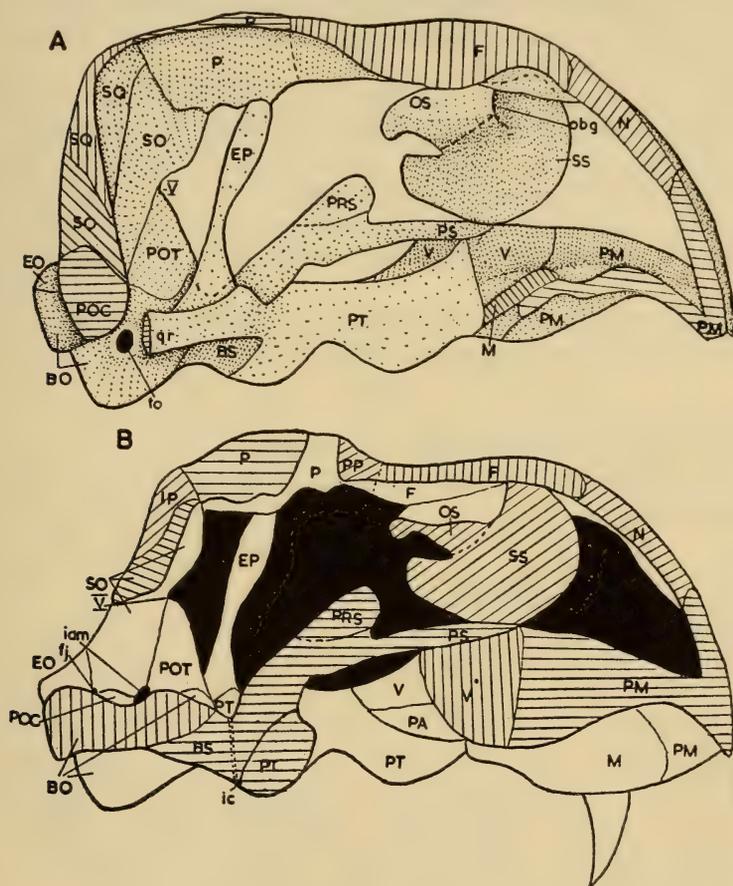


FIG. 53. *Dicomodons* sp. S.A.M. 12217 \times 1.
A. Parasagittal view of the skull as reconstructed graphically from a series of cross-sections. B. Sagittal view.

Sagittal view (Fig. 53B)

The posterior part of the braincase is seen to have its lateral wall formed by the exoccipital, supraoccipital, opisthotic and proötic; the floor is formed by the basioccipital which is anteriorly not overlain by the proötics. The proötics fail to meet each other in the middle line so that the upper part of the sella

turcica has no ossified dorsum. The lower part of the dorsum sellae is as usual formed by the basisphenoid. The sella turcica also has only a short ossified frons formed by the basisphenoid. The hypophysis was thus apparently small.

The jugular foramen and internal auditory meatus lie at floor level, but the notch for the exit of the trigeminal nerve lies very high in the sidewall. The roof is formed by the supraoccipital and parietal. There is also a downwardly directed flange of the parietal into the sidewall.

The large middle part of the braincase wall is unossified, but in a more lateral plane lies the slender epipterygoid. The floor is here formed by the basisphenoid and presphenoid.

In the sphenoidal region the sidewall is formed by flanges of the frontal meeting the curved wings of the orbitosphenoid, which also forms the floor for the olfactory tract. Further anteriorly the median septum of the septosphenoid separates the grooves housing the paired olfactory bulbs. The parasphenoidal rostrum lying horizontally is seen to overlie the vomers which lying far back form a deep median keel. Anteriorly the premaxillae carry a fairly high dorsal septum.

Anteriorly the pterygoids do not enter the median plane and neither do they develop any dorsal parasagittal septa.

The basicranial axis (Fig. 54)

I have reconstructed three figures of the cranial base.

In A the basicranial structures are shown in ventral view in relation to the contiguous bones.

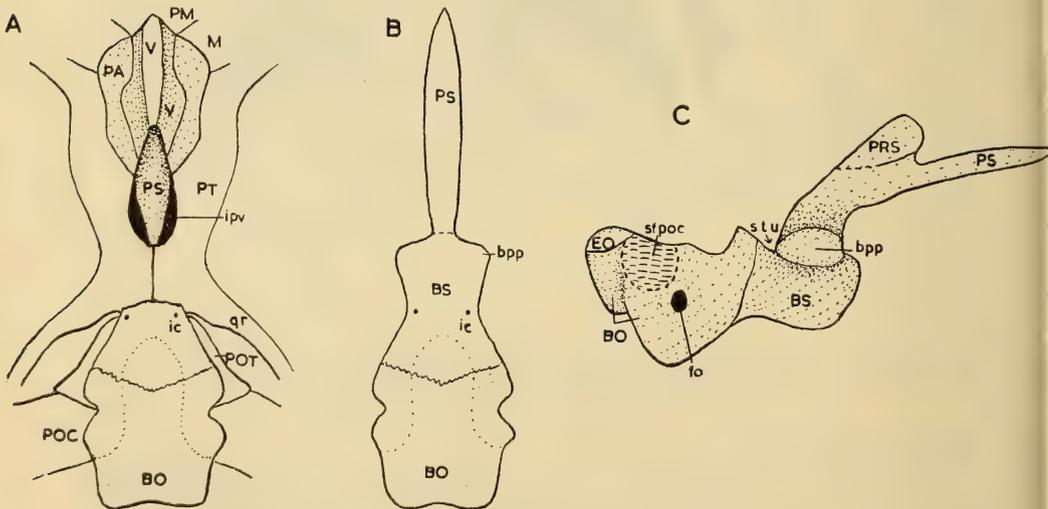


FIG. 54. *Dicynodon* sp. S.A.M. 12217 \times 1
Basicranial axis reconstructed from serial sections. A. Ventral view in relation to the surrounding bones. B. Ventral view. C. Lateral view.

The parasphenoidal rostrum is seen lying above the interpterygoid vacuity with its anterior end underlain by the vomers, which here carry a well-developed ventral keel.

The choanae are seen to open posteriorly to the edge of the premaxilla into longitudinal grooves roofed by the vomers and flanked by the palatines.

In B the adjacent bones have been removed to show the basicranial bones in ventral view. The basipterygoid processes are still quite prominent. In C the above is seen from the side and the dorsum sellae appears to have its upper part formed by the basioccipital.

The endocranial cavity (Fig. 55)

In the accompanying figures the endocranial cavity is shown in outline in lateral and dorsal view.

The brain cavity is long; wide and high posteriorly and low and narrow elsewhere.

The parietal tube is short (6 mm) and its diameters small (4.5 mm) and the sella turcica shallow.

The mes- and metencephala could have been well developed but the fore-brain could have had but a small volume.

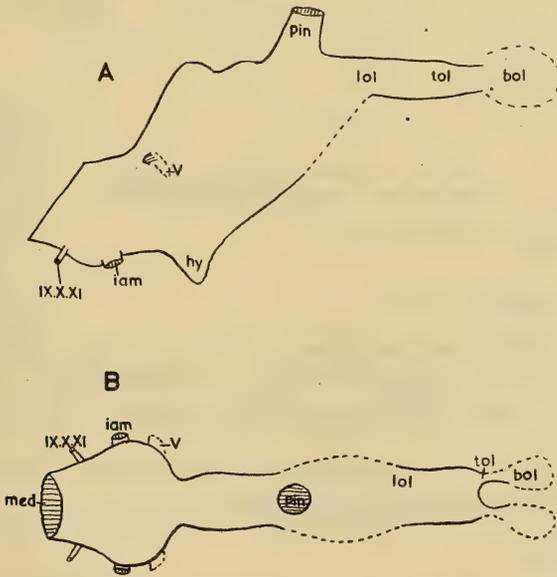


FIG. 55. *Dicynodon* sp. S.A.M. 12217 $\times 1$.
The endocranial cavity reconstructed in outline from sections.
A. Lateral view. B. Dorsal view.

Sections (Fig. 56)

I am reproducing here four sections from front to back to show the structure of the sphenoidal region.

16. The septosphenoid forms a thin median septum and the median premaxillary septum is flanked by the anterior ends of the paired vomerine septum.
20. The sides of the septosphenoid are excavated for the olfactory bulbs. The posterior end of the premaxillary septum is clasped by the vomers. The tip of the parasphenoidal rostrum rests on the vomers.
24. The olfactory lobes are housed by the orbitosphenoids resting on a septum formed by the septosphenoid. The parasphenoidal rostrum is clasped by the vomers.
28. The orbitosphenoids lose contact with the median septum and the parasphenoidal rostrum rests on the vomers.

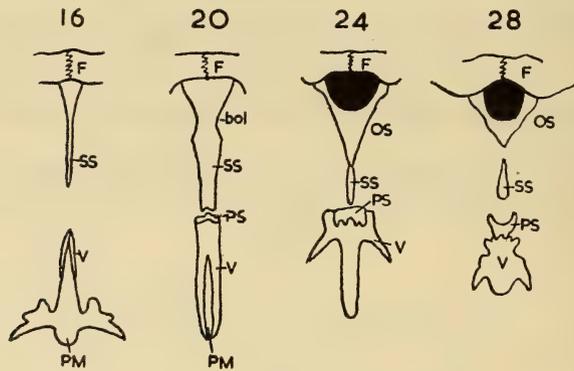


FIG. 56. *Dicynodon* sp. S.A.M. 12217 \times 1.
Cross-sections through the sphenoidal region.

(b) THEROCEPHALIA

S.A.M. K210 *Maraisaurus parvus*

I have cut 82 cross-sections through the skull of this small pristerognathid from low down in the *Tapinocephalus* zone. From these I have reconstructed drawings on the same basis as for all the preceding specimens to facilitate direct comparisons.

Unfortunately, however, the sphenoidal region was unossified which leads one to conclude that the skull was immature.

Parasagittal view (Fig. 57)

In the posterior part the lateral wall of the braincase is formed by the exoccipital, paroccipital, supraoccipital and proötic.

The proötic has a large outer face. Its anterior edge is notched for the trigeminal nerve and above this there is a gap between the proötic and the supraoccipital. This lack of ossification also denotes that we are dealing with an immature skull.

The anterior part of the proötic is pierced by two small foramina for the VIth and VIIth cranial nerves.

The fenestra ovalis is bounded by the opisthotic, basioccipital, basisphenoid and proötic and is situated quite high up in the skull.

The epipterygoid has a long footplate and a fairly broad ascending columella.

It lies lateral to the sella turcica and to the anterior edges of the proötic and supraoccipital and meets the parietal.

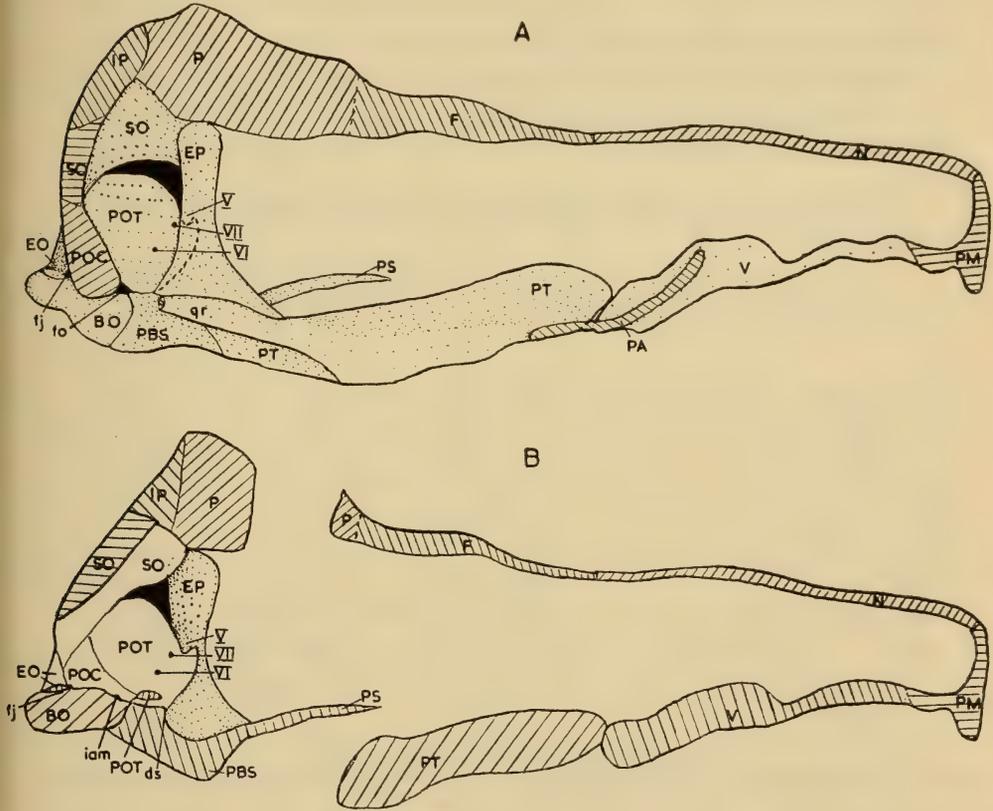


FIG. 57. *Maraisaurus parvus* S.A.M. K210 \times 1.
 A. Parasagittal view reconstructed from serial sections. B. Sagittal view.

The pterygoid dorsally bears a low septum. Posteriorly, above the interpterygoid vacuity, the paired parasagittally situated septa enclose a trough, but anteriorly these meet in the median line to form a single median septum. For a short distance the upper edge of this septum is forked and these would apparently clasp the lower edge of the septosphenoid when ossified.

Anteriorly the pterygoids do not extend in between the vomers.

Sagittal view (Fig. 57B)

The exoccipital forms the posterior part of the braincase floor. Most of the floor is formed by the basioccipital. Anterior to this the two proötics meet in the middle line above the basisphenoids with an unossified gap between them.

The upper part of the dorsum sella is thus formed by the proötics and the lower part by the basisphenoid.

The sella turcica is shallow with no frons.

The parasphenoidal rostrum lies horizontally and no presphenoid is ossified above it.

The basicranial axis (Fig. 58)

Three reconstructed views of the bones of the basicranium are given.

In A a ventral view shows the basal bones in relation to the supporting bones, with the parasphenoidal rostrum lying above the interpterygoidal vacuity.

In B the contiguous bones have been removed. The basispterygoid process is just evident.

In C a lateral view shows the horizontal disposition of the parasphenoidal rostrum, and the shallow sella turcica without an ossified frons.

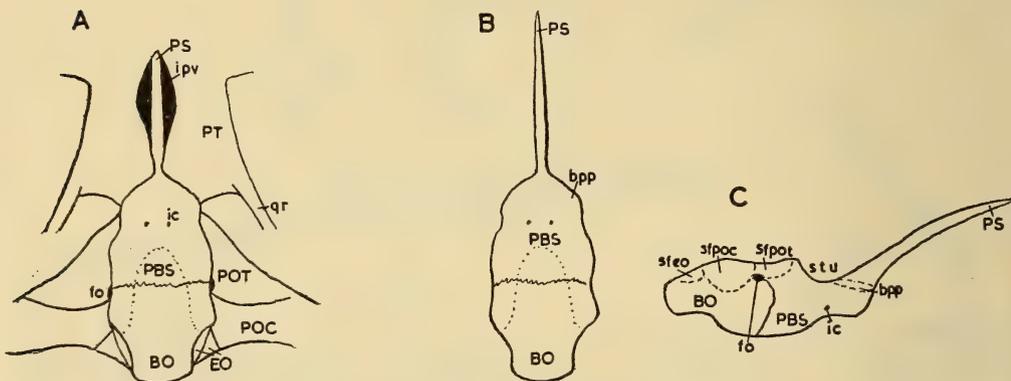


FIG. 58. *Maraisaurus parvus* S.A.M. K210 \times 1.
Basicranial axis as reconstructed from serial sections. A. Ventral view in relation to contiguous bones. B. Ventral view. C. Lateral view.

COMPARATIVE

In a recent publication I attempted to show how the families of the therapsids diverged in pre-*Tapinocephalus* zone times, basing my views on the effects of the differential developments of the jaw mechanism.

Here I found that, as far as the South African therapsids were concerned, from a first divergence emerged the two suborders Anomodontia and Theriodontia. Two later splits produced from the former the two infra-orders Dicyno-

dontia and Dinocephalia and from the latter the two infra-orders Gorgonopsia and Therocephalia.

To what conclusions does the above study of the braincase, basicranial axis and median septum bring us?

A review of the nature of these structures in the morphological series—primitive labyrinthodonts—captorhinomorphs to sphenacodont pelycosaurs may help to indicate the developmental trends towards the pre-*Tapinocephalus* zone eotherapsids and their immediate descendants.

The primitive labyrinthodonts (e.g. Palaeogyrinus)

In these forms in the sagittal plane, the occiput makes an angle of 90° with the basicranial axis (and the general level of the palate and alveolar border of the upper jaw).

The long parasphenoidal rostrum thus lies horizontally and there is no downturn of the face.

The sphenethmoid resting on the parasphenoid and stretching dorsally to the frontals houses the anterior part of the brain which thus with the olfactory bulbs as a whole lies horizontally.

The exoccipital does not enter the brainfloor.

The sidewall of the braincase is well ossified with the exception of the ethmoidal region and nasal capsules.

The proötic is well developed, extending well forward to enclose the foramen for the Vth nerve, but it does not meet the sphenoidal bones above the metoptic fenestra. Below this fenestra the basisphenoid is intercalated between the proötic and the sphenethmoid and forms the floor of the shallow *sella turcica*, whose *dorsum* is formed by the proötic and the *frons* by the sphenethmoid.

In the sphenoidal region there is a single bone pierced by the foramen for the IIInd nerve. The bone has two dorsal wings standing on a median septum, which is supported below on the parasphenoidal rostrum, which is long and lies horizontally. The bone does not form a roof for the braincase.

Both the *fenestra ovalis* and the *sella turcica* lie high up in the skull.

In the median line the ventral surface of the cranial base, formed by the basioccipital and the long parasphenoid, lies horizontally with the rostrum exposed through the long widely open interpterygoidal vacuity. Anteriorly the long processes of the pterygoids meet in the median line, but form no dorsal septum. Further anteriorly lie the short vomers in the same plane. There is no median dorsal septum in the ethmoidal region.

The captorhinomorphs

The occiput is slightly inclined forwards to make an angle of about 80° with the cranial base. The shortened parasphenoidal rostrum is slightly inclined upwards to make an angle of about 30° with the cranial base.

The sphenethmoid resting on the dorsally inclined parasphenoid houses the rhinencephalon, which is thus carried upwards away from a horizontal

plane. The exoccipital does not enter the brainfloor.

The sidewall of the braincase is poorly ossified with a wide gap between the otic and sphenethmoidal regions.

The proötic is poorly developed, not extending forwards to enclose a foramen for the Vth nerve. It does not meet the sphenoidal bones. Below the metoptic fenestra it meets the basisphenoid, which forms the floor of the deep *sella turcica* and the very high *dorsum sellae*.

The single sphenethmoidal ossification is Y-shaped in section with the stem forming an interorbital septum.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the shortened upturned parasphenoidal rostrum is exposed through the long widely open interpterygoidal vacuity. Anteriorly the long anterior processes of the pterygoids meet in the median line but form no dorsal septum. Further anteriorly lie the elongated vomers in the same plane.

The pelycosaurs

In *Dimetrodon* the occiput is inclined further forwards to make an angle of about 60° with the cranial base.

The long parasphenoidal rostrum is inclined upwards with its tip lying on the upper edge of the high pterygoidal septum, well posterior to the vomer. There is thus a strong downturn of the face. The exoccipital forms the posterior part of the brainfloor.

The sidewall of the braincase is poorly ossified with a wide gap between the otic and sphenoidal regions.

The proötic is weakly developed; it does not extend far anteriorly and does not enclose a foramen for the Vth nerve; it does not meet the sphenoidal complex above the pituitary fenestra. Ventrally the two proötics meet in the middle line to form a high *dorsum sellae* of a fairly deep *sella turcica* whose *frons* as well as its floor is formed by the basisphenoid.

A median ossification is present in the interorbital region; it is essentially a vertical plate lying in the midline of the skull and split above so that it is Y-shaped in section. Its ventral septal part is clasped by the parasphenoid; its dorsal part encloses a tube in its posterior part, which is anteriorly divided into two for the olfactory tracts. It seems probable that this ossification is tripartite: the septal part being a septosphenoid and the wings orbitosphenoids with a foramen for the passage of the IIInd nerve.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the long parasphenoidal rostrum is exposed through the fairly long and widely open interpterygoidal vacuity.

Anteriorly the very long anterior pterygoidal processes meet in the median line and form a high median dorsal septum. Further anteriorly the long vomers lie with their medio-ventral edges in nearly the same plane as the pterygoids. The vomerine septum is fairly low.

The early therapsids of the Tapinocephalus zone

The study of the structural features used in the above comparisons in the case of the early therapsids reveals such a great degree of variation that it is difficult to treat the infra-orders together as a group representing a single morphological stage beyond the pelycosaur stage.

Intermediate stages appear imperative in order to link up the pelycosaur and therapsid stages of development.

I will thus treat the 4 infra-orders separately and then indicate what intermediate proto-Therapsid stages could be postulated.

The Dinocephalia

In the three families Anteosauridae, Titanosuchidae and Tapinocephalidae the occiput is inclined *backwards* at an angle of 110° – 170° to the cranial base. The median ventral edge of the fairly short parasphenoidal rostrum is inclined upwards to make an angle with the cranial base varying from 5° to 80° . There is thus little to very great downturn of the face. The parasphenoid meets or does not meet the high pterygoid septum and always ends far posterior to the vomer.

The exoccipital forms the posterior part of the brainfloor.

The sidewall of the braincase is always well ossified and the small fenestra between the otic and sphenoidal regions is dorsally closed through the meeting of the sphenoidal, otic and occipital bones. The braincase, however, lies far posteriorly with a large area between the sphenoidal region and the nostril without bony sides

The proötic is well developed, extending anteriorly and, together with a flange from the supraoccipital, meets the orbitosphenoid to close the dorsal part of the metoptic fenestra. The Vth nerve thus passes through a foramen enclosed by bone. Ventrally the two proötics meet in the median line and thus form the upper part of the *dorsum sellae*. The *sella turcica* is very deep with the lower part of the *dorsum sellae* and the floor formed by the basisphenoid. The *frons* is formed by the presphenoid which forms a vertical septum standing on the parasphenoid.

In the interorbital region there is a well-ossified sphenoidal complex consisting of a median septum formed by a septosphenoid resting on the para- and presphenoid. Above the septosphenoid the orbitosphenoids, pierced by a foramen for the IIInd nerve, form wings posteriorly enclosing a single tube for the olfactory lobes and anteriorly a pair of tubes for the olfactory tracts.

Both the *fenestra ovalis* and the *sella turcica* lie low down in the skull.

In the median line the short parasphenoidal rostrum is mostly invisible in palatal view through the reduction of the length and width of the interpterygoidal vacuity.

Anteriorly the anterior pterygoidal processes meet in the median line and form a very high and long dorsal septum extending anteriorly in between dorsal flanges of the vomers.

Further anteriorly the vomers, with strong dorsal septa, are inclined upwards at an angle of 5° – 40° to the cranial base.

The Dicynodontia

In a *Dicynodon* from the *Tapinocephalus* zone the occiput is inclined forwards at an angle of 80° to the cranial base.

The long parasphenoidal rostrum is inclined upwards at an angle of 25° to the cranial base.

There is thus considerable downturning of the face.

The parasphenoid anteriorly rests on the vomer since the pterygoids do not meet in the median line anterior to the interpterygoidal vacuity.

The exoccipital does not form the posterior part of the brainfloor.

The sidewall of the braincase is widely open, due to the poor development of the proötic and the extreme forward position of the sphenoidal complex. The brain is thus very long in relation to the total skull length.

The proötic is weakly developed and does not even extend so far anteriorly as to form a notch for the Vth nerve. Ventrally the two proötics do not meet in the median line and have no part in the formation of a *dorsum sellae*, this being formed by basisphenoid and basioccipital.

The *sella turcica* is shallow, with its *frons* formed by the parasphenoid.

The presphenoid is a vertical sheet of bone in the median line standing on the parasphenoidal rostrum and it makes no contact with the anteriorly situated interorbital sphenoidal complex.

The sphenoidal complex is well ossified and consists of a ventral septal sheet resting on anterior tip of the parasphenoidal rostrum. This is the septosphenoid. Above rests two wings enclosing the forebrain. These are the orbitosphenoids. A posterior notch serves for the passage of the IIInd nerve.

The *fenestra ovalis* appears to lie high up in the skull but this is due to the development of the strong basioccipital tubera.

In the median line the long parasphenoidal rostrum is well exposed through the long and wide interpterygoidal vacuity.

With the radical change in the nature of the anterior pterygoidal processes the pterygoids do not meet each other in the median line anterior to the interpterygoidal vacuity.

Anterior to the interpterygoidal vacuity the vomer lies in the median line and supports the anterior end of the parasphenoidal rostrum.

Further anteriorly lie the palatal sheets of the premaxilla forming a secondary palate.

The Therocephalia

In the Pristerognathidae the occiput is inclined forwards at an angle of 80° to the cranial base.

The long parasphenoidal rostrum is inclined upwards at an angle of 30° . Its anterior end lies free, unsupported by the pterygoid.

The exoccipital forms a small part of the posterior part of the brainfloor.

The sidewall of the braincase is widely open since the sphenoidal complex is usually not ossified.

The proötic is weakly developed, but forms a notch for the Vth nerve. The pair just meet in the middle line to form the upper part of the *dorsum sellae* with the basisphenoid lying lower down and also forming the floor of the *sella turcica*, which is very shallow.

The sphenoidal complex is only present in a specimen sectioned by Broom where it is feebly ossified.

In the median line the parasphenoidal rostrum is visible through the narrow interpterygoidal vacuity. Anteriorly the long anterior pterygoidal processes meet in the median line and carry only a low median septum.

Further anteriorly the long vomers lie in a nearly horizontal plane and form no dorsal septum.

The Gorgonopsia

Not having a gorgonopsian from the *Tapinocephalus* zone that could be sectioned I have to rely on a single specimen of a hipposaurid in which parts of the structures under consideration are visible.

The occiput is about at right angles to the cranial base.

The short parasphenoidal rostrum is inclined upwards at an angle of about 50° to the cranial base.

The exoccipital does not form part of the brainfloor.

The sidewall of the braincase is widely open between the otic and sphenoidal regions.

The proötic is weakly developed and apparently would not enclose the foramen for the Vth nerve.

The sphenoidal complex appears to be well developed with apparently a septal part formed by a septosphenoid and dorsal wings composed of the orbitosphenoids.

The interpterygoid vacuity is reduced and the short anterior pterygoidal processes meeting in the middle line anterior to the vacuity forms a high dorsal septum supporting the parasphenoid. Further anteriorly the long vomers carry a well-developed dorsal septum.

Derivation of the therapsids

If all the therapsids of the *Tapinocephalus* zone developed from a common ancestral group then that group must have been more primitive than the sphenacodont pelycosaurs (e.g. *Dimetrodon*).

Considering only the nature of the structures studied in this report it is clear that the ancestral group would have to be without the following characters developed by *Dimetrodon*:

1. The occiput would not be sloping forwards.
2. The proötic would not be present in the *dorsum sellae*.
3. The exoccipital would not form the posterior part of the brainfloor and the basioccipital would not be excluded from the brainfloor.

4. There would be no strongly developed dorsal median septa on the pterygoid or vomer.
5. The face would not be so downturned.

Even the ophiacodonts appear to be too advanced as far as the characters we are here considering are concerned.

Dinocephalia

If, however, the four therapsid groups of the *Tapinocephalus* zone arose from different groups of the pelycosaur one could reasonably derive the Dinocephalia from a group very near to *Dimetrodon*. The developments shown by the Dinocephalia are: a backward sloping of the occiput for mechanical reasons associated with a changed function of the nuchal muscles and with a concomitant posterior shift of the braincase and greater strength in the sidewall of the braincase and an abnormal development of both the parietal organ and hypophyseal mass. The latter is related to the pathological pachyostosis which caused the extinction of the Dinocephalia before the end of *Tapinocephalus* zone times.

Dicynodontia

The morphological gap between the Dicynodontia of the *Tapinocephalus* zone and the Pelycosauria is so great that no known pelycosaur group can be envisaged as being directly ancestral. Even the Russian *Otsheria*, of which the relevant structures are mostly undetermined, does not provide pointers to an ancestral pelycosaur.

A forerunner of the Dicynodontia would have to be a form in which the proötic does not enter the *dorsum sellae*, the exoccipital is excluded from the brainfloor, no or weak dorsal pterygoidal septum, intermediately situated sphenoid complex and with the premaxilla just commencing to push the vomer posteriorly.

Such a form could not also be an ancestor of the Dinocephalia and Theriodontia.

Many other features of the dicynodont skeleton also point to a separate origin for these remarkable reptiles, which in their further development right up to *Kannemeyeria* in the Trias maintain their basically unique structure.

Therocephalia

The early pristerognathid Therocephalia are, in the features under discussion, more primitive than the sphenacodont pelycosaur. The proötic is just entering the *dorsum sellae*, the exoccipital is just entering the posterior brainfloor, the anterior pterygoidal processes and vomers, although long, have as yet not developed dorsal median septa and lie horizontally in a plane just ventral to the cranial base and the sphenoidal complex has just started to ossify.

It would thus appear that the pristerognathids have advanced from a common ancestor with the sphenacodonts and ophiacodonts at a tempo of development somewhat less than the higher pelycosaur.

This slower tempo in development makes the pristerognathids a group well suited for further advances in the direction of the mammals, which their descendants have in fact realized.

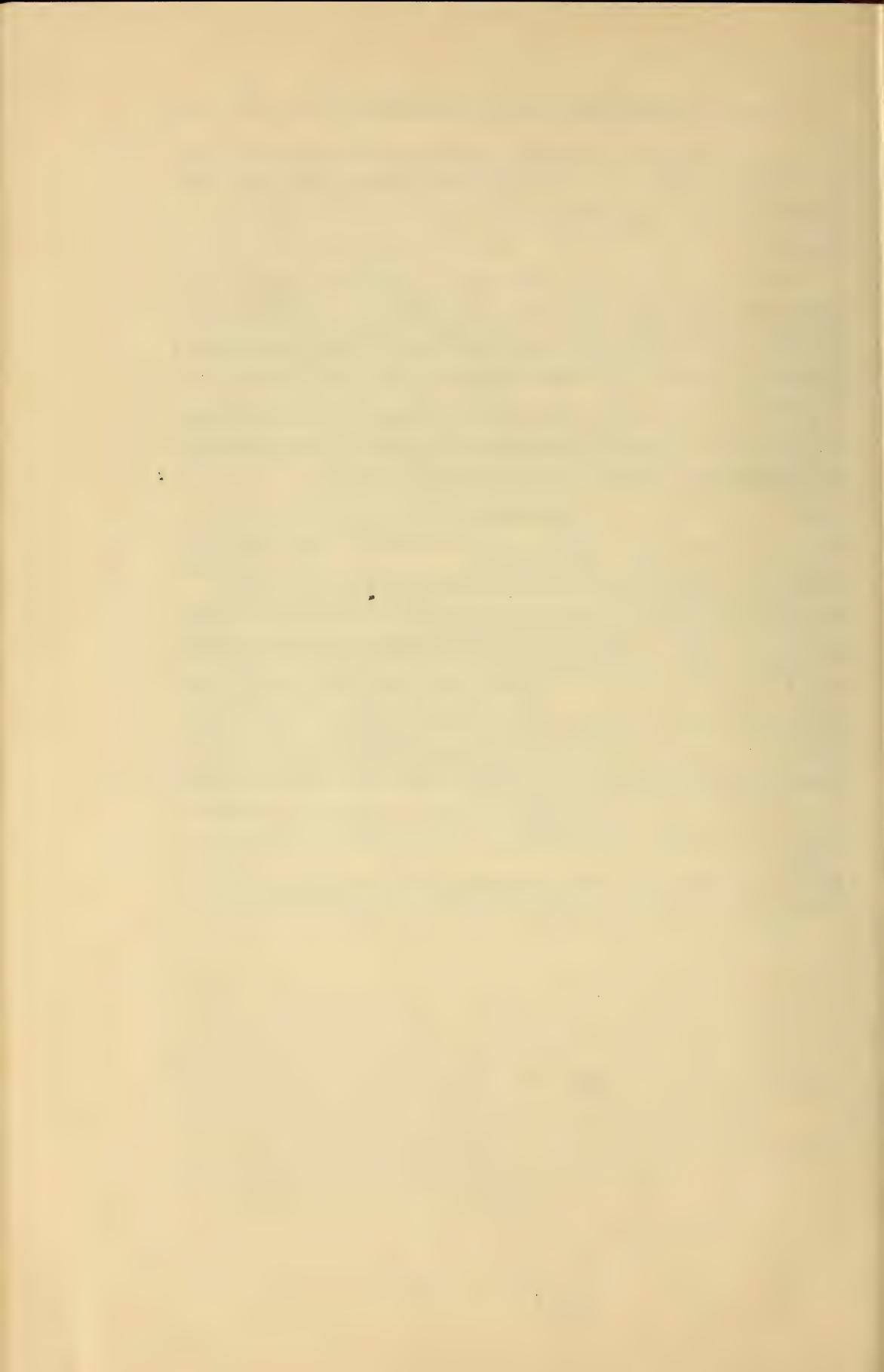
Gorgonopsia

Although the features under discussion are inadequately known in the Gorgonopsia of the *Tapinocephalus* zone it would appear that in them the tempo of development was rapid and the morphological stages reached further than that reached by the pelycosaur. Knowledge of these structures in the Russian phtinosuchids may very well help to bridge the gap between Gorgonopsia and Pelycosauria.

In contrast to the Therocephalia the Gorgonopsia with their more rapid tempo achieved a higher stage of development quicker but their descendants thus committed were off the line leading to the mammals.

REFERENCES

- BOONSTRA, L. D. 1936a. Some features of the cranial morphology of the tapinocephalid deinocephalians. *Bull. Am. Mus. nat. Hist.* **42**: 75-98.
- BOONSTRA, L. D. 1936b. The cranial morphology of some titanosuchid deinocephalians. *Bull. Am. Mus. nat. Hist.* **42**: 99-116.
- BOONSTRA, L. D. 1951. Kurze Notiz über den Schädel der Dinocephalen-Gattung *Keratocephalus* F. v. Huene. *Neues Jb. Geol. Paläont. Mh.* **11**: 341-344.
- BOONSTRA, L. D. 1953. The cranial morphology and taxonomy of the tapinocephalid genus *Struthiocephalus*. *Ann. S. Afr. Mus.* **42**: 32-53.
- BOONSTRA, L. D. 1956. The skull of *Tapinocephalus* and its near relatives. *Ann. S. Afr. Mus.* **43**: 137-169.
- BOONSTRA, L. D. 1957. The moschopid skulls in the South African Museum. *Ann. S. Afr. Mus.* **44**: 15-38.
- BOONSTRA, L. D. 1963. Early dichotomies in the therapsids. *S. Afr. J. Sci.* **59**: 176-195.
- BROOM, R. 1936. On the structure of the skull in the mammal-like reptiles of the suborder Therocephalia. *Phil. Trans. R. Soc. (B)* **226**: 1-42.
- OLSEN, E. C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. *Spec. Pap. geol. Soc. Am.* **55**: 1-131.
- ORLOV, Y. A. 1964. *Basis of palaeontology*. Moscow: State Science-Technological Publ. (In Russian).
- PRICE, L. 1935. Notes on the brain case of *Captorhinus*. *Proc. Boston Soc. nat. Hist.* **40**: 377-385.
- ROMER, A. S. & PRICE, L. W. 1940. Review of the Pelycosauria. *Spec. Pap. geol. Soc. Am.* **28**: 1-538.



INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol. '), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

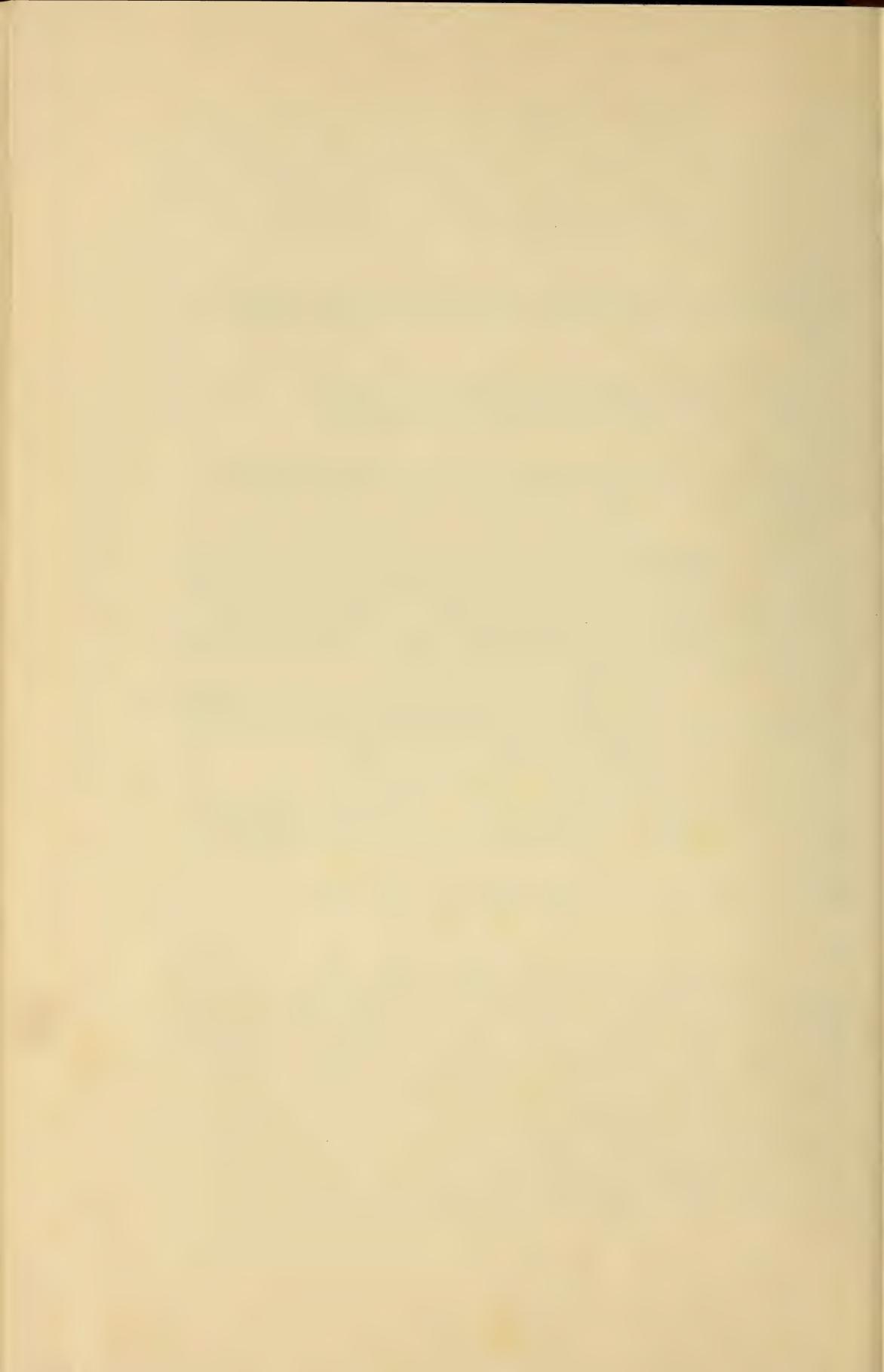
Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



6.68
7

T. H. BARRY

SOUND CONDUCTION IN THE FOSSIL
ANOMODONT *LYSTROSAURUS*

June 1968 Junie
Volume 50 Band
Part II Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R1.00

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1968

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

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

SOUND CONDUCTION IN THE FOSSIL ANOMODONT
LYSTROSAURUS

By

T. H. BARRY

South African Museum, Cape Town

(With 1 plate and 3 text-figures)

CONTENTS

	PAGE
Introduction	275
Description	275
Discussion	277
Summary	280
Acknowledgements	281
References	281

INTRODUCTION

In a paper published in 1963, the author drew attention to the marked degree of variation that exists in the structure of the sound-conducting apparatus of many closely related genera of living reptiles and expressed the view that the structure of the middle ear region in many fossil forms supplied circumstantial evidence to substantiate the view that a marked degree of variation could also have existed in fossil mammal-like reptiles, not only between sub-orders but also within some of them. The evidence presented in this paper would seem to lend support to this view.

DESCRIPTION

In 1964 Mr. Chris Gow of the South African Museum drew my attention to a thin rod-like bone attached to the ventro-lateral surface of the right stapes of a specimen of *Lystrosaurus murrayi* (Huxley) which he had prepared with acid (fig. 1, plate XV, B). From its base the rod extends antero-medially at an angle of approximately 45° to the long axis of the stapes, following a course roughly parallel to the quadrate ramus of the pterygoid. In lateral view it can be seen that the rod curves downward and then upward to end free (plate XV, A). On the left side both the stapes and the rod are absent.

As a stapedia process of this nature has not been reported for any Anomodont it was essential to ascertain whether this attachment represented a chance fusion during life or afterwards, or whether this association actually existed during life.

UNIVERSITY OF CAPE TOWN
LIBRARY
AUG 13 1968

By careful removal of the matrix surrounding the base of the rod it was found that the rod could be lifted off the stapes. The area of attachment on the stapes proved to be smooth, indicating that the attachment of the rod to this area of the stapes represents a postmortem association. However, further examination revealed the existence of a triangular, flattened, slightly rugose area on the ventro-medial surface of the stapes not previously recorded for *Anomodonts*. As will be shown later this depression probably represents the original area of attachment of the rod to the stapes.

This discovery led to the preparation of a second skull, that of *Lystrosaurus natalensis* (specimen No. K.1165 of the South African Museum collection). In this specimen both stapes are present, but they are displaced anteriorly to lie between the lower jaw rami. A long, curved, rod-shaped process, slightly expanded distally, extends from the ventro-lateral border of the left stapes (plate XV, D). The right stapes is without this rod-like process but a slender bone, conforming to its general configuration, lies slightly in front of it. A roughly triangular, flattened area on the ventro-medial surface of the right stapes shows where this rod had probably been attached.

Removal of the matrix covering the area of contact between the rod and the stapes on the left side revealed that the two bones were not actually fused but had become cemented together by the matrix. Of interest, however, is that the area of contact partly overlaps an indented area similar to that found on the right stapes. The anterior ends of both rods are unfinished and slightly expanded indicating that the bones were probably continued in cartilage.

Conditions very similar to these were found in two specimens of *Lystrosaurus verticalis*. In the first the right stapes only was still in position, the left stapes and two rods lying grouped together a short distance forward. Both stapes show the triangular flattened area found in *L. natalensis*. After cleaning it was found that the proximal part of each rod followed the outline of and could be perfectly fitted on to the triangular area of the corresponding stapes. In this position the distal ends of the rods do not meet in the midline.

The second specimen of *L. verticalis* had both stapes in position but no rods were found. However, the triangular areas on the stapes are well developed and very similar to those found in the specimen previously mentioned.

In another fossil specimen investigated, the type of *Lystrosaurus oviceps* (specimen No. 641 of the South African Museum collection) both stapes are present and in position. Two curved rods, outwardly similar to those described for the other *Lystrosaurus* specimens, lie in front of but at a deeper dorsal level than the two stapes (plate XV, C). Unfortunately part of the ventral surface of the skull, including the ventral surface of the stapes, had been scoured away, obliterating any evidence of a possible attachment to the stapes.

In *Lystrosaurus declivis* in which the stapes is well preserved, there is no indication of the ventro-medial flattened areas found in *L. murrayi*, *L. natalensis* and *L. verticalis*. This suggests that there was a variable relationship between the rod-like process and the stapes within the genus. In *L. murrayi*, *L. natalensis*

and *L. verticalis* the connection was probably synovial, in *L. declivis* it could have been weakly synchondrotic, but without leaving a mark on the stapes, or it could have been syndesmotic or free.

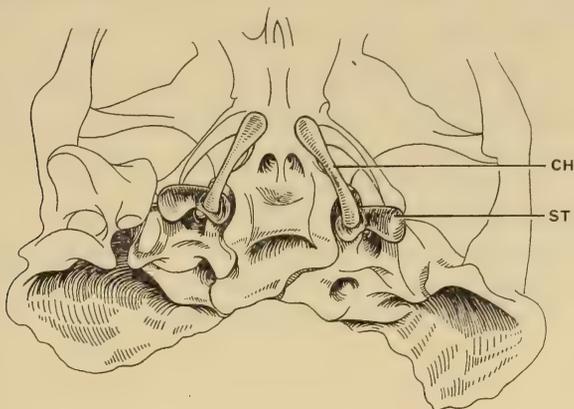


FIG. 1. *Lystrosaurus murrayi*, reconstruction of ventral view of the middle ear region with ceratohyals in position.
C.H., ceratohyal; S.T., stapes.

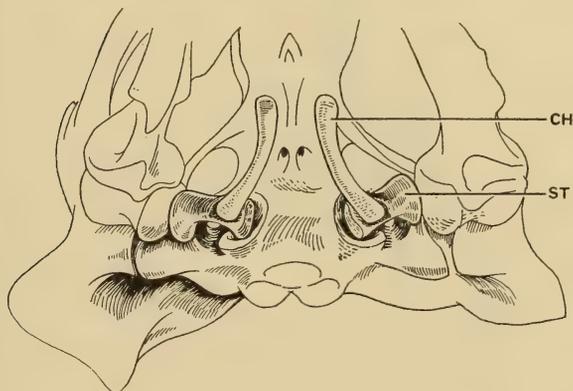


FIG. 2. *Lystrosaurus verticalis*, reconstruction of ventral view of the middle ear region with ceratohyals in position.
C.H., ceratohyal; S.T., stapes.

DISCUSSION

Reconstruction of the missing stapelial attachment of the first specimen, *L. murrayi*, shows that, as in the case of *L. verticalis*, the rods occupy a position normally associated in recent reptiles with the ceratohyals or ceratobranchials I or II of the hyobranchial skeleton. The fact that the distal ends of the rods do not meet in the mid-line would seem to strengthen this view as this area is normally occupied by the median basihyal. The absence of any evidence of the latter would seem to indicate that it was cartilaginous.

Conditions in living reptiles and mammals favour the assumption that the rods represent fossilized ceratohyals, for in both living groups an embryonic connexion exists between the ceratohyal and parts of the sound-conducting apparatus; in reptiles with the extra-columella and in mammals with the stapes.

In *Lacerta* and many other lacertilians the ventrally projecting pars accessorius posterior (processus interhyalis) represents the stump of the ligament which connected the ceratohyal with the extra-columella in earlier developmental stages. This is also the case in early developmental stages of the chelonians *Chrysemys* (Smith, 1914) and *Testudo* (Bender, 1911). In the adult stages the ceratohyal can be free or it can become attached to the skull.

In *Sphenodon* and *Crocodylus*, however, a direct connexion is retained throughout life between the ceratohyal and the columella. In the adult the connexion is cartilaginous, resulting, in *Sphenodon*, in the entire hyobranchial skeleton being suspended from the columella (fig. 3).

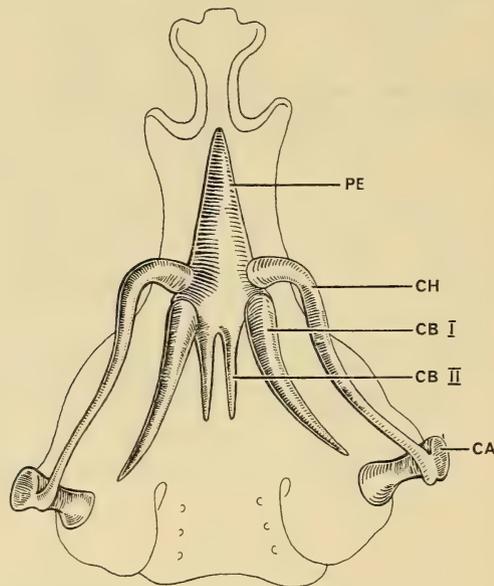


FIG. 3. *Sphenodon punctatus*, ventral view of hyobranchial skeleton (after Schauinsland).

C.A., columella auris; CB I-II, ceratobranchial I-II; C.H., ceratohyal; P.E., processus lingualis.

The condition found in *L. murrayi* would seem to resemble most closely that found in *Sphenodon*. This similarity, together with the phylogenetic relationship which exists between the ceratohyal and the columella auris and stapes in recent reptiles and mammals, respectively, and the fact that the processus interhyalis is the most consistent process of the reptilian columella auris, are the bases on which the assumption is made that the stapedia processes found in *Lystrosaurus* represent ossified ceratohyals.

The question arises whether the stapedia attachment in *L. murrayi*, *L. natalensis* and *L. verticalis*, represents the primitive condition or whether it represents a neotenic condition. The same question has been debated regarding the conditions found in the adult *Sphenodon* and the answers have been divergent; Schauinsland (1900), Wyeth (1924) and Goodrich (1930) declaring that it represented the primitive condition, while De Beer (1937) maintained that the condition must be 'associated with the degeneration of the tympanic membrane and therefore constitutes a secondary condition brought about by the arrest of development' (p. 241).

In many features of the skull *Sphenodon* shows that it is a relict of the past. It may be argued, therefore, that it retained also the primitive connexion between the ceratohyal and the sound-conducting apparatus and that this assumption is now borne out by the evidence uncovered in the fossil *Lystrosaurus* forms. However, the latter are highly specialized forms and as the condition found here is, to date, unique among anomodonts and is representative of some species of *Lystrosaurus* only, it may well represent a neotonic condition. Unfortunately we lack further information.

The further question arises as to whether *Sphenodon* uses the avenue provided by the hyoid-columella connexion for the transmission of sound to the internal ear, as it is known that full tympanic expansion of the cavum tympani does not occur during the ontogeny of *Sphenodon* and that a thick layer of tissue is left between the cavum tympani and the skin (Simonetta, 1963).

Although tests have frequently been conducted on the sensitivity of the ear in various reptiles no one has as yet attempted to find out whether the ceratohyal in *Sphenodon* acts as a sound-transmitting agent. This knowledge would be invaluable for any theory regarding sound perception and the presence or absence of the tympanum in *Lystrosaurus* for we cannot exclude the possibility that the persistence in *Sphenodon* of the embryonic connexion, whether it be the cause or effect of the non-development of the tympanum, may also be an indication of the existence of similar conditions in the fossil form.

Regarding his observations on *Sphenodon* Newman (1877) writes: 'When the tuatara inspires it greatly depresses the hyoid and trachea, thereby enlarging the pharyngeal cavity. By this means the tuatara inhales a large quantity of air, filling the lungs, mouth, trachea and the large pharyngeal cavity. This particular mode of respiring by depressing the hyoid bone (which with its cornua is very large) enables the tuatara to inhale sufficient air to remain under water for hours without coming to the surface to breathe' (p. 225).

It is not impossible, therefore, that the air contained in the expanded trachea could act as resonator for sound travelling through the water and as the hyoid apparatus is tense, such movement could be transmitted on to it and to the columella. When on land, where it frequents burrows, the lack of a tympanum would seem to indicate that sound waves are picked up directly from the substrate. Thus sound could be transmitted directly not only via the lower jaw and quadrate to the stapes but also via the hyoid apparatus.

Bone conduction is not uncommon in living burrowing and non-burrowing reptiles which lack a tympanum or have a reduced tympanic membrane. This has led to various changes in the composition of the middle ear structures in order to facilitate sound perception. In the non-burrowing lizards *Tympanocryptis*, *Aphaniotes*, *Cophotis*, *Lyriocephalus* and *Ceratophora* (Smith, 1938), loss of the tympanum is accompanied by reduction of the extracolumella to a vestige projecting from the stapes, but compensation is made through the attachment of the columella by the ossified dorsal and internal processes to the quadrate. In burrowing lizards, where loss of the tympanum is mostly accompanied by a reduction of the middle ear and Eustachian tube, the columella can be attached direct to the quadrate by means of the cartilaginous extra-columella (*Anniella*, Toerien, 1950) or by a ligament to the quadrate, supratemporal and otic capsule (*Scelotes*, Toerien, 1963) or by a ligament to the retroarticular process of the lower jaw (*Typhlosaurus*, Toerien, 1963). In others the columella itself is expanded and continued anteriorly to end either in the upper lip (*Typhlosaurus*, Toerien, 1963) or in the skin over the lower jaw (*Monopeltis*, Kritzing, 1945, *Rhineura*, Toerien 1963).

It is important to note too that none of the burrowing forms investigated by Toerien showed a reduction of the papilla basilaris (the actual organ of hearing in the inner ear) or of the stapes. The stapes, on the contrary, is often greatly increased in size. Although there are exceptions (the Australian burrowing lizard *Aprasia pulchella*, in which the middle ear is almost completely absent, has according to Underwood, 1957, only a tiny nodule which is presumably a vestige of the footplate of the stapes) it is nevertheless a significant observation. The tympanum is not essential for sound perception via the columella auris and Toerien's observation adds the possibility that the absence of the tympanum, whether caused by or contributing to, the reduction of the extra-columella does not affect the stapes and could even have a compensating effect on the development of the footplate. This is worth noting for the stapes seems unaccountably large in some anomodonts.

The connexion of the hyobranchial skeleton to the stapes in *Lystrosaurus* would seem to point to a system of sound transmission not based on sound perception via the tympanum. Sound waves were probably picked up by placing the head against the ground and transmission effected by bone conduction either via the lower jaw, the hyobranchial skeleton, or both.

There is reason to believe that a variable association between the stapes and ceratohyal could also have existed in some of the other anomodont genera but at this stage it would seem that a definite association was far more common in the genus *Lystrosaurus*.

SUMMARY

A description is given of a rod-like process on the stapes of *Lystrosaurus*, an extinct mammal-like reptile from the Beaufort Beds of the Karoo of South Africa. It is suggested that the bone represents the ossified ceratohyal. This

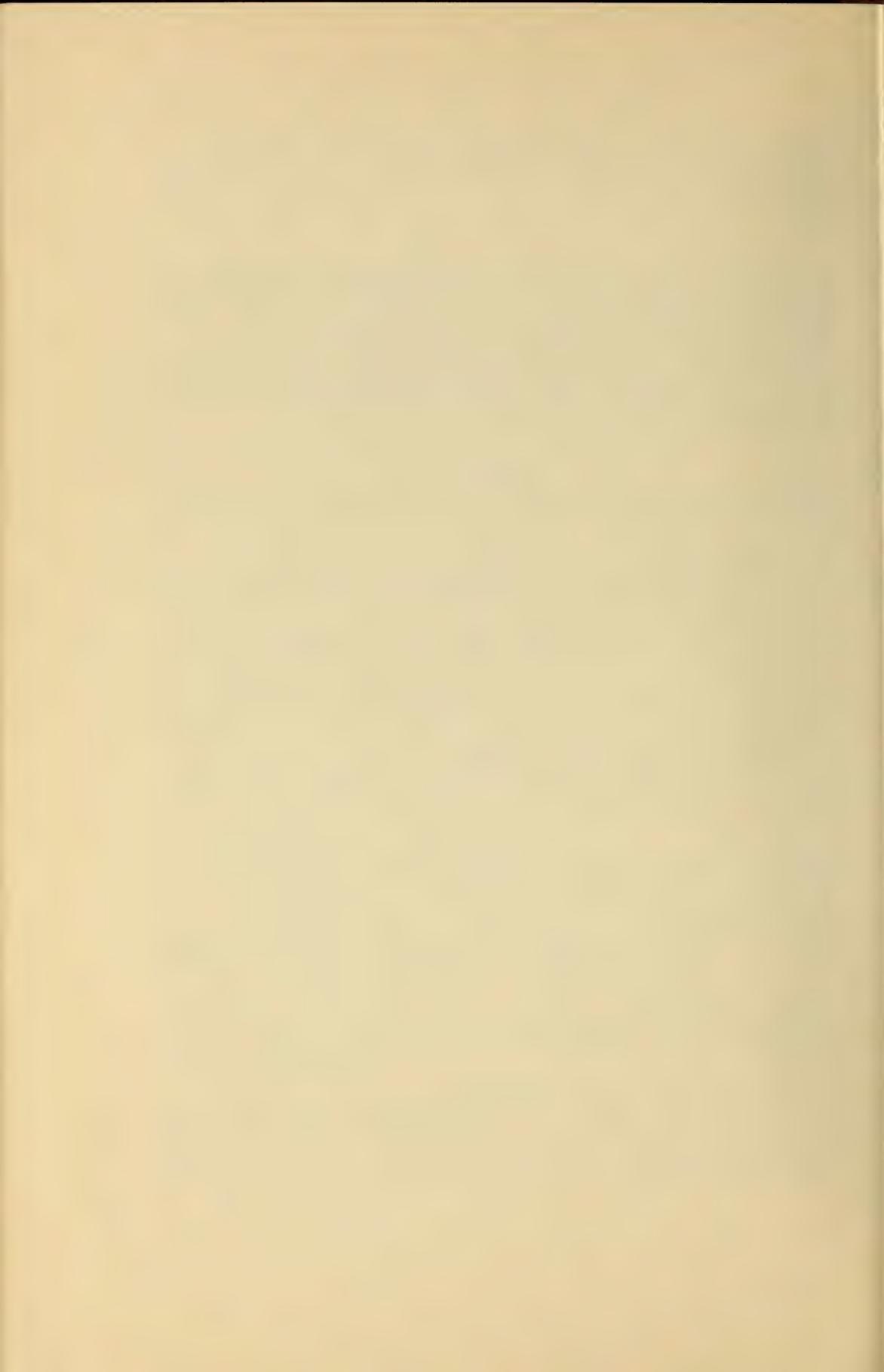
stapedial process is regarded as highly significant and it is claimed that it throws new light on the method of sound transmission in this genus of Anomodont Therapsids.

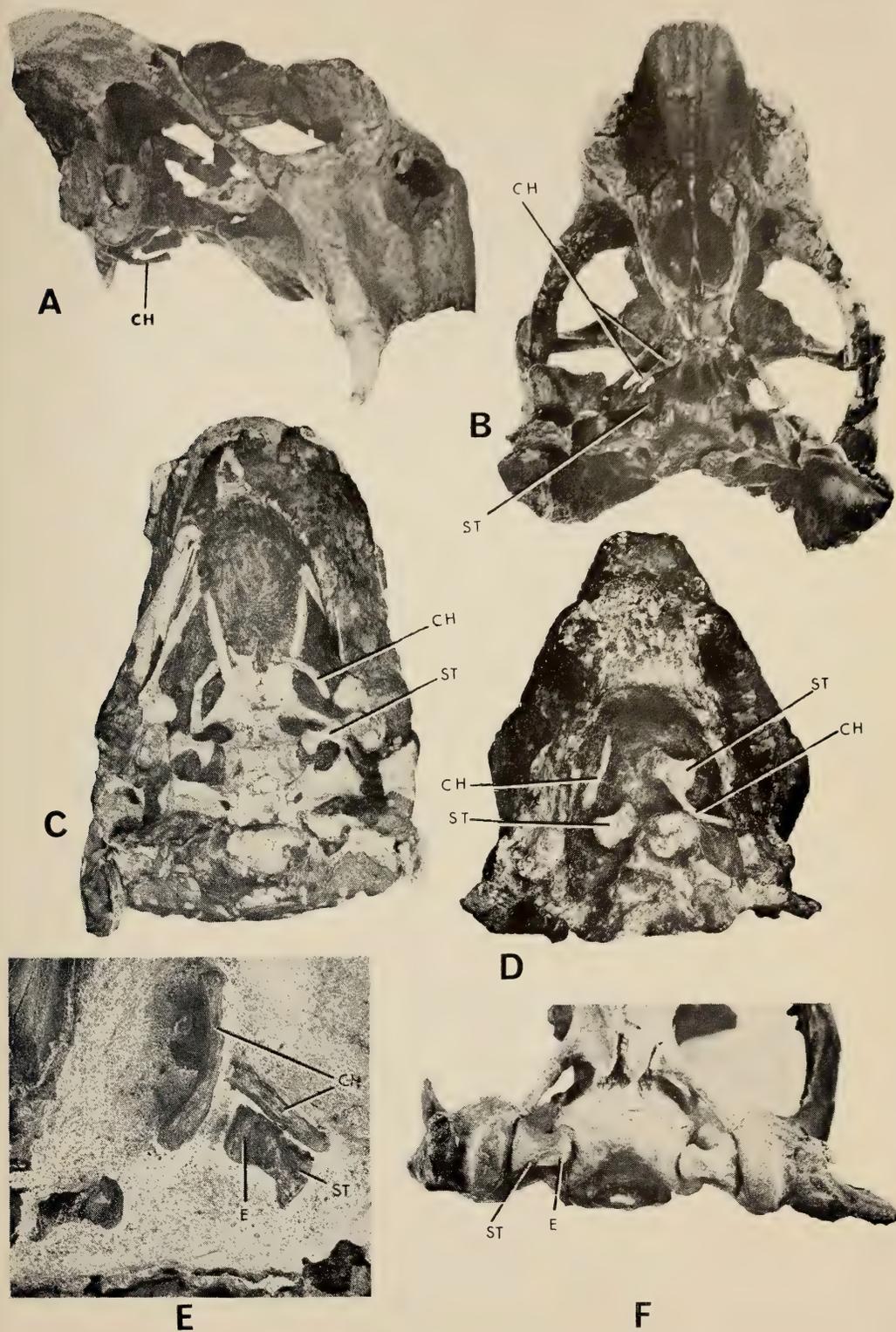
ACKNOWLEDGEMENTS

This project and the publication of these results were in part financed by a grant received from the South African Council for Scientific and Industrial Research. For this I wish to thank the Council. I also wish to thank Dr. M. E. Malan of the Department of Zoology, University of Stellenbosch for criticism of the manuscript and for helpful suggestions and Mrs. I. Rudner and Mr. C. Gow of the South African Museum for preparation of the fossils used in this investigation.

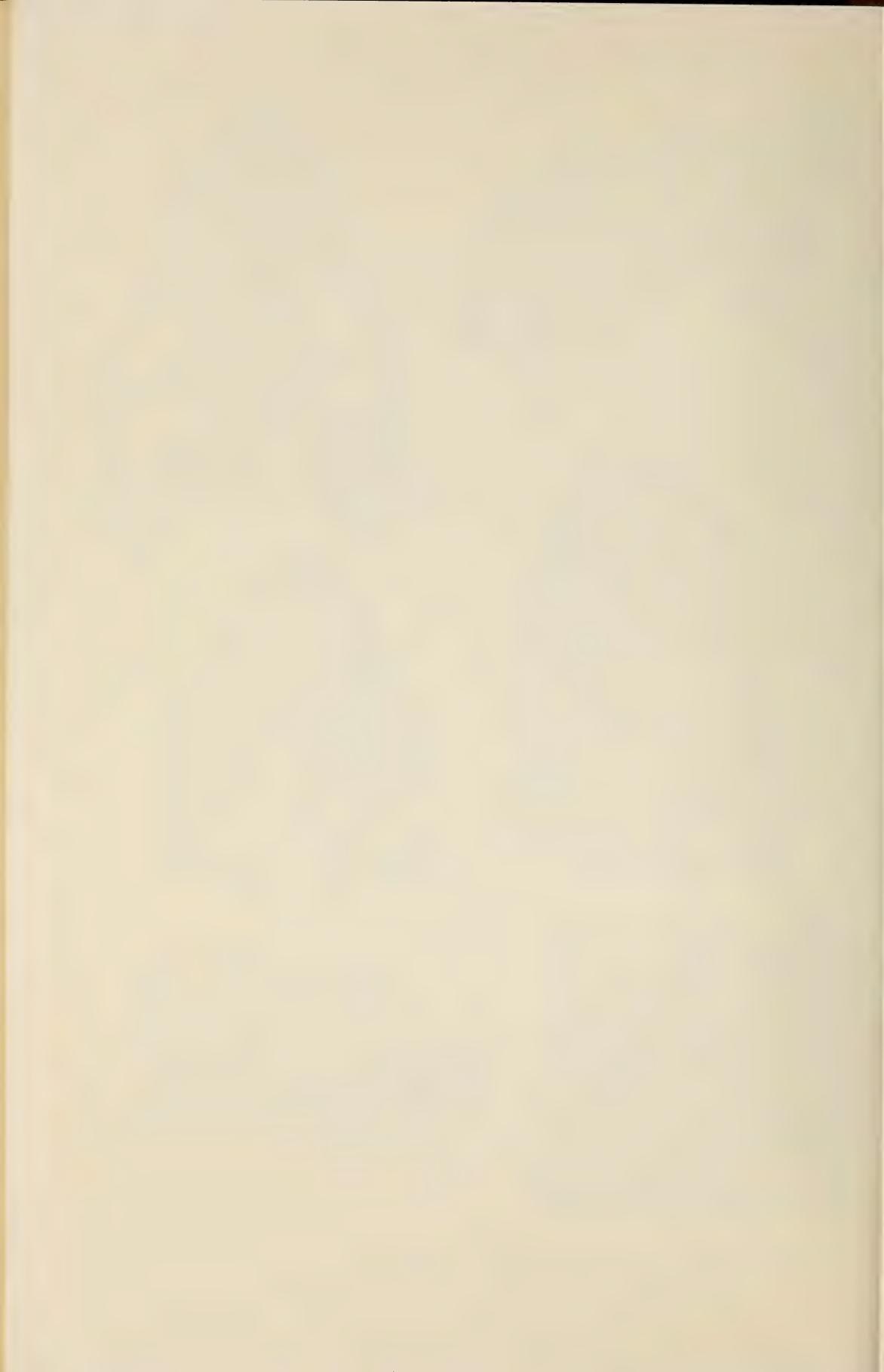
REFERENCES

- BARRY, T. H. 1963. On the variable occurrence of the tympanum in recent and fossil tetrapods. *S. Afr. J. Sci.* **59**: 160-175.
- BENDER, O. 1911. Über Herkunft und Entwicklung der Columella auris bei *Testudo gracilis*. *Anat. Anz.* **40**: 161-177.
- COX, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 321.
- DE BEER, G. R. 1937. *The development of the vertebrate skull*. Oxford University Press, London.
- EWER, R. F. 1961. The anatomy of the Anomodont *Daptocephalus leoniceps* (Owen). *Proc. zool. Soc. Lond.* **136**: 375.
- GOODRICH, E. S. 1930. *Studies on the structure and development of vertebrates*. Constable & Co., London.
- KRITZINGER, C. C. 1945. The cranial anatomy and kinesis of the South African amphisbaenid *Monopeltis capensis* Smith. *S. Afr. J. Sci.* **42**: 175.
- NEWMANN, A. K. 1877. Notes on the physiology and anatomy of the Tuatara (*Sphenodon guntheri*). *Trans. N. Zealand Int.* **10**: 222-239.
- SCHAUINSLAND, H. 1900. Beiträge zur Entwicklungsgeschichte der Hatteria. *Arch. Mikr. Anat. u. Entw.* vol. **57**.
- SIMONETTA, A. 1963. Cranial kinesis and morphology of the middle ear: two possibly related features. *Evolution* **17**: 580-587.
- SMITH, L. W. 1914. The origin and development of the columella auris in *Chrysemys marginata*. *Anat. Anz.* **46**: 457-560.
- SMITH, M. A. 1938. Evolutionary changes in the middle ear of certain agamid and iquanid lizards. *Proc. zool. Soc. Lond.* **108**: 543.
- TOERIEN, M. J. 1950. The cranial morphology of the Californian lizard—*Anniella pulchra* Gray. *S. Afr. J. Sci.* **46**: 321.
- TOERIEN, M. J. 1963. The sound-conducting systems of lizards without tympanic membranes. *Evolution* **17**: 540-547.
- UNDERWOOD, G. 1957. On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the squamata. *Morph.* **100**: 207.
- WYETH, F. J. 1924. The development of the auditory apparatus in *Sphenodon punctatus*; with an account of the visceral pouches, aortic arches, and other accessory structures. *Phil. Trans. roy. Soc. Lond.* **212**: 259-368.





A. *Lystrosaurus murrayi*, lateral view; B. *Lystrosaurus murrayi*, ventral view; C. *Lystrosaurus oviceps*, ventral view; D. *Lystrosaurus natalensis*, ventral view; E. & F. *Lystrosaurus verticalis*.
 CH., ceratophyal; E., excavated area on stapes; ST., stapes.



INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol. '), with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

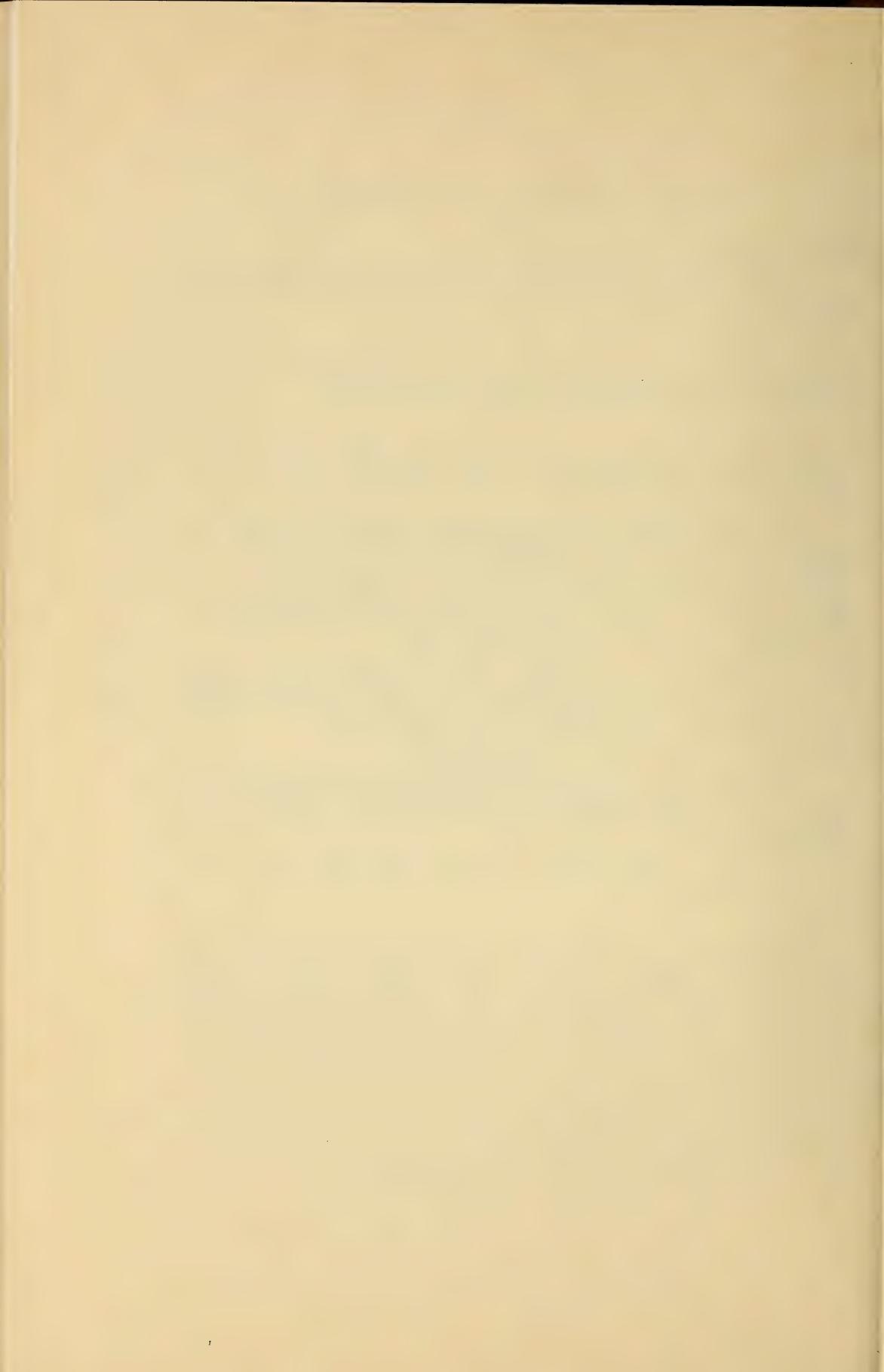
Euplonia capensis (Smith) Brown, 1955: 259.

When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).



6.68
7

B. F. KENSLEY

DEEP SEA DECAPOD CRUSTACEA FROM
WEST OF CAPE POINT, SOUTH AFRICA

June 1968 Junie
Volume 50 Band
Part 12 Deel



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

Cape Town Kaapstad



The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town
(Cash with order, post free)

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid
van stof

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

OUT OF PRINT/UIT DRUK

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

Price of this part/Prys van hierdie deel

R1.75

Trustees of the South African Museum © Trustees van die Suid-Afrikaanse Museum
1968

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

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

DEEP SEA DECAPOD CRUSTACEA FROM WEST OF
CAPE POINT, SOUTH AFRICA

By

B. F. KENSLEY

South African Museum, Cape Town

(With 19 figures in the text)

CONTENTS

	PAGE
Introduction	283
List of species and stations	284
Description and notes ..	286
Summary	321
Acknowledgements ..	321
References	322

INTRODUCTION

In 1959 the research ship *Africana II* of the Division of Sea Fisheries carried out trawls at twelve stations off the west coast of the Cape Peninsula and off Cape Point, under the supervision of Dr. F. H. Talbot, then of the South African Museum. The trawls were done with a 15' beam trawl, between depths of 1098 and 3440 metres. The exact positions of the stations may be obtained from the Annual Report for the Division of Sea Fisheries for the period 1st April, 1959, to 31st March, 1960, published by the Government Printer, Pretoria. The fish, Crustacea, Mollusca, and other invertebrates obtained are of particular interest, as very little fishing has been done at these depths in South African waters. Also included in this paper are references to material obtained with an Isaacs-Kidd mid-water trawl in 1960-1.

Approximately 480 decapod Crustacea belonging to 35 species were obtained (excluding fragments and specimens damaged beyond identification, and the hermit crabs, which were sent to Mme Dechancé of the Paris Museum). These include anomurans, palinurans, penaeideans, and carideans. Of these, twelve are new records for the South African region and three are previously undescribed species. The two species of *Nematocarcinus* appear to be the most plentiful decapods at these depths, followed by *Pontophilus occidentalis* var. *indica*. Many more carideans than penaeideans were collected.

From such a small collection it is obviously impossible to draw any conclusions regarding the distribution of the species involved, but in very general terms they can be classified into those which appear to be endemic to the region, those which are cosmopolitan in distribution, and those which have Indo-

UNIVERSITY OF CAPE TOWN
LIBRARY

Pacific affinities. Eight species appear to be endemic to the South African region, viz. *Neolithodes capensis*, *N. asperrimus*, *Munidopsis chacei*, *M. barnardi*, *Willemoesia bona-spei*, *Gennadas gilchristi*, *G. kemp* and *Sclerocrangon bellmarleyi*. The following species are distributed throughout the Atlantic, Indian and Pacific Oceans: *Galacantha rostrata*, *Stereomastis sculpta*, *Gennadas bouvieri*, *Sergestes atlanticus*, *S. armatus*, *Systellaspis debilis*, *Acantheephyra haekelii*, *A. brevisrostris*, while the following have affinities with the Indo-Pacific fauna: *Polycheles demani*, *Plesiopenaeus nitidus*, *Haliporus villosus*, *Sergestes regalis*, *S. prehensilis*, *Acantheephyra quadrispinosa*, *A. coralina*, *Nematocarcinus longirostris*, *N. parvidentatus*, *Pontophilus occidentalis* var. *indica*.

The whole collection is now in the South African Museum and catalogued with South African Museum catalogue numbers.

LIST OF SPECIES AND STATIONS

SAM = South African Museum catalogue numbers.

* = new record

IK = Isaacs-Kidd trawl specimens

Species	SAM	Station	Specimens	Depth (metres)
ANOMURA				
<i>Neolithodes capensis</i> Stebbing	A10542	A193	1	2745
	A10447	A190	1	2269
	A10469	A193	1	2745
	A10541	A319	1	2690-2727
<i>Neolithodes asperrimus</i> Barnard	A10445	A189	2	1098
* <i>Munida</i> sp.	A10525	A318	1	2525-2782
* <i>Munidopsis chacei</i> n.sp.	A10470	A193	3	2745
* <i>Munidopsis barnardi</i> n.sp.	A10465	A193	2	2745
	A10497	A317	1	2708-3038
	A10508	A317	3	2708-3038
	A10485	A315	3	2891-2965
	A10546	A322	2	2745
<i>Galacantha rostrata</i> A. Milne-Edwards	A10449	A190	1	2260
	A10518	A318	1	2525-2782
	A10547	A193	14	2745
	A10519	A318	3	2525-2782
	PALINURIDA			
<i>Polycheles demani</i> Stebbing	A10520	A318	1	2525-2782
	A10501	A317	2	2708-3038
	A10460	A192	3	2708
	A10568	A322	1	2745
	A10522	A318	3	2525-2782
	A10569	A193	2	2745
	A10453	A191	2	2745
	A10570	A317	2	2708-3038
	A10487	A315	3	2891-2965
	A10533	A319	4	2690-2727
	A10475	A315	5	2891-2965
<i>Stereomastis sculpta</i> (Smith)	A10443	A189	3	1098
<i>Stereomastis nana</i> (Smith)	A10559	A189	2	1098
* <i>Willemoesia bona-spei</i> n. sp.	A10509	A317	3	2708-3038
	A10473	A193	2	2745
	A10543	A322	3	2745
	A10448	A190	1	2269
<i>Eryoneicus spinoculatus</i> Bouvier				

Species	SAM	Station	Specimens	Depth (metres)
PENAEIDEA				
<i>Plesiopenaeus nitidus</i> Barnard	A10441 A189	1	1098
		A10442 A189	5	1098
* <i>Haliporus villosus</i> Alcock & Anderson	A10461 A192	1	2708
<i>Gennadas gilchristi</i> Calman	A10577 A321	2	3239-3440
<i>Gennadas kemp</i> Stebbing	A10575 A321	3	3239-3440
		A10576 A190	2	2269
* <i>Gennadas bouvieri</i> Kemp	A10578 A321	1	3239-3440
* <i>Sergestes atlanticus</i> A. Milne-Edwards	A12529 IK6	1	183 (west of C.T.)
<i>Sergestes armatus</i> Kröyer	A10528 A318	1	2525-2782
		A10532 A319	1	2690-2727
* <i>Sergestes sargassi</i> Ortman	A12528 IK6	1	183 (west of C.T.)
* <i>Sergestes corniculum</i> Kröyer	A10502 A317	1	2708-3038
		A10556 A321	1	3239-3440
		A10571 A321	1	3239-3440
* <i>Sergestes regalis</i> Gordon	A10574 A192	2	2708
<i>Sergestes prehensilis</i> Bate	A10572 A321	1	3239-3440
		A10573 A317	1	2708-3038
		A10516 A318	1	2525-2782
		A10483 A315	1	2891-2965
CARIDEA				
<i>Systellaspis debilis</i> (A. Milne-Edwards)	A10444 A189	1	1098
		A10494 A316	1	3148-3257
		A10544 A322	1	2745
		A10455 A191	1	2745
		A10495 A316	1	3148-3257
<i>Hymenodora glacialis</i> (Buchholz)	A10566 A192	1	2708
		A10563 A190	1	2269
		A10562 A192	1	2708
		A10513 A317	2	2708-3038
<i>Notostomus westergreni</i> Faxon	A10517 A318	1	2525-2782
<i>Acanthephyra haeckelii</i> (Von Martens)	A10536 A319	1	2690-2727
		A10439 A189	1	1098
		A10553 A321	1	3239-3440
		A10452 A190	1	2269
<i>Acanthephyra quadrispinosa</i> Kemp	A10561 A321	2	3239-3440
		A10458 A192	2	2708
		A10560 A319	2	2690-2727
* <i>Acanthephyra gracilipes</i> Chace	A10565 A190	1	2269
* <i>Acanthephyra brevirostris</i> Smith	A10564 A192	1	2269
* <i>Acanthephyra corallina</i> (A. Milne-Edwards)	A12531 A319	1	2708
		A12532 A319	1	2690-2727
		A12533 A190	1	2690-2727
		A10523 A318	4	2269
<i>Nematocarcinus longirostris</i> Bate	A12541 A316	2	2525-2782
		A12542 A317	1	3148-3257
		A12543 A193	2	2708-3038
		A12544 A317	3	2745
		A12545 A315	3	2708-3038
		A12546 A192	2	2891-2965
		A12547 A189	1	2708
		A12548 A189	10	1098
		A12549 A190	8	2269
		A10471 A193	16	2745

Species	SAM	Station	Specimens	Depth (metres)	
<i>Nematocarcinus longirostris</i> Bate A12551	A191	4	2745	
	A12552	A317	14	2708-3038	
	<i>Nematocarcinus parvidentatus</i> Bate A12553	A190	9	2269
		A12554	A316	6	3148-3257
		A12555	A192	1	2708
		A10474	A193	7	2745
		A10551	A322	4	2745
		A12556	A318	3	2525-2782
		A12557	A317	3	2708-3038
		A12558	A318	14	2525-2782
		A12559	A317	12	2708-3038
		A12560	A319	7	2690-2727
		A12561	A316	20	3148-3257
		A12562	A193	10	2745
		A12563	A315	10	2891-2965
<i>Glyphocrangon sculptus</i> (Smith)	 A12534	A193	1	2745
	A10459	A192	2	2708	
	A10547	A322	5	2745	
	A10462	A193	2	2745	
	A10464	A193	1	2745	
<i>Glyphocrangon sculptus</i> (Smith) A10549	A322	1	2745	
	A10539	A319	4	2690-2727	
	A10535	A319	4	2690-2782	
	A10521	A318	7	2525-2782	
	A10451	A190	Sev.	2269	
<i>Sclerocrangon bellmarleyi</i> Stebbing A10446	A189	1	1098	
* <i>Pontophilus occidentalis</i> var. <i>indica</i> de Man A12535	A318	2	2525-2782	
	A10512	A317	2	2708-3038	
	A12536	A318	7	2525-2782	
	A12537	A191	2	2745	
	A12538	A318	5	2525-2782	
	A10457	A192	10	2708	
	A10476	A315	2	2891-2965	
	A10503	A317	5	2908-3038	
	A12539	A322	2	2745	
	A12540	A316	7	3148-3257	
	A10480	A315	Many	2891-2965	
	A10482	A315	6	2891-2965	
	A10524	A318	1	2525-2782	
	A10489	A316	1	3148-3257	
	A10500	A317	1	2708-3038	
A10468	A193	Many	2745		

ANOMURA

Family **Lithodidae***Neolithodes capensis* Stebbing, 1905

Neolithodes capensis Stebbing, 1905: 70. Barnard, 1950: 410, fig. 77 a-c.

Previous records and distribution

Off Cape Point, 800 fathoms, (1570 m).

Material

- SAM.A10542, carapace length 13 mm. St. A193, 2745 m.
SAM.A10447, carapace length 10 mm. St. A190, 2269 m.
SAM.A10469, carapace length 15 mm. St. A193, 2745 m.
SAM.A10541, carapace length 14 mm. St. A319, 2690-2727 m.

Remarks

All four specimens are juveniles, yet all have the finger of the right chela equal to the upper margin of the hand. In all, the dactyls are smooth and terete; these specimens can therefore tentatively be assigned to *capensis*.

Neolithodes asperrimus Barnard, 1947

Neolithodes asperrimus Barnard, 1947: 374. 1950: 411, fig. 77 d-f.

Previous records and distribution

Off Saldanha Bay, 500 fms (980 m); off Cape Point, 550 fms (1080 m).

Material

- SAM.A10445, ♀, carapace length 55 mm. St. A189, 1098 m.
♀, carapace length 45 mm. St. A189, 1098 m.

Remarks

The specimens agree with the original description in having the finger of the right chela one and a half times the length of the upper margin of the hand, distally flattened denticulate dactyls and more spines than *capensis*.

Family **Galatheidae***Munida* sp.*Description*

Eyes not wider than the eyestalks. Rostrum tridentate, with a row of six small spines at its base. Well-marked cervical and branchial grooves present. Whole carapace covered with transverse setiferous ridges. Two or three spines on lateral border of carapace anterior to the cervical groove, five spines posterior to it. Posterior margin of carapace a raised crenulated ridge. Second and third abdominal terga with a smooth transverse groove.

Distribution

M. subcaeca Bouvier: (Bouvier, 1922: 46. Chace, 1942: 43). Cuba, West Indies, Madeira, Canary Islands.

M. microphthalmalma M. Edw.: (Benedict, 1903: 310. Bouvier, 1922: 45. Doflein & Balss, 1926: 172. Chace, 1942: 40). Atlantic coast of Europe, West Indies, Ceylon, Polynesia, tropical west coast of America, Cuba.

Material

- SAM.A10525, ♀ ovigerous, carapace length 13 mm. St. A318, 2525-2782.

Remarks

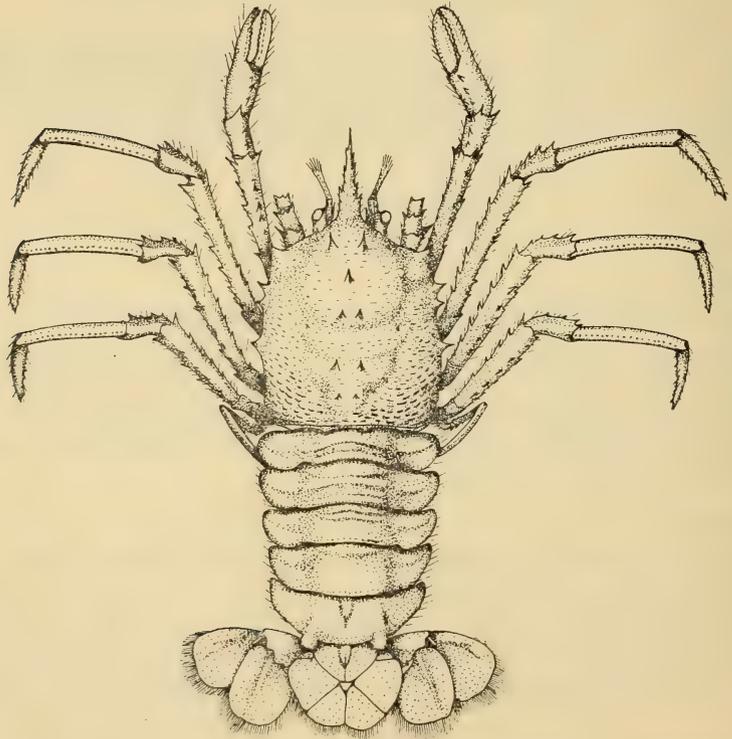
This specimen is unfortunately rather damaged, having the rostrum and accompanying spines broken and all the walking legs missing. The antennules and the third maxillipeds are present and agree exactly with Chace's figures of *M. microphthalmalma* (1942). The merus of the third maxilliped has two spines and not three as in *subcaeca*. The characteristic spinal armature of the second abdominal segment of *microphthalmalma* is lacking in this specimen, the second abdominal segment being smooth as in *subcaeca*. This, together with the poor state of the material, makes it difficult to give the specimen specific status.

Munidopsis chacei n.sp.

Figs 1, 3 a, b

Description

Carapace one and a quarter times longer than wide. Lateral margins slightly convex, front slightly narrower than posterior part of carapace. Rostrum half length of carapace, moderately slender, laterally armed with three or four spines. Distal portion of rostrum dorsally carinate, upcurved, ventrally flattened. No antennal spines. Antero-lateral angle formed by outwardly

FIG. 1. *Munidopsis chacei* n.sp.

directed conical spine. Three other conical spines along lateral branchial margin. Gastric region fairly well defined by smooth cervical groove. At base of rostrum a pair of prominent conical spines, followed by single median spine in mid-gastric region, and pair of spines in post-gastric region. Cardiac region armed with two pairs of spines. Posterior carapace margin thickened, armed with four short spines. Whole carapace covered with scattered short hairs, surface rough, lateral branchial regions with elongate transverse rugae. Eyestalk short, fairly mobile, produced on inner side into slender spine, slightly longer than diameter of eye. Latter unpigmented, spherical. Rest of eyestalk unarmed. Basal joint of antennular peduncle armed with four prominent spines, ventral one having denticulate margin, externo-lateral and dorsal spines longest, interno-lateral spine shortest. Second and third joints of equal length, unarmed. Basal joint of antenna with prominent outwardly directed spines, second joint with four spines on distal margin, lateral ones largest. Ischium of third maxilliped triangular in cross-section, innermost angle finely denticulate. Inner margin of merus with three or four small denticles. Chelipeds shorter than ambulatory pereiopods. Ischia, meri, and carpi armed with prominent spines. Dactyl of chela equal to palm in length. Finger and thumb denticulate, teeth becoming obsolete proximally. Ischia, meri and carpi of ambulatory pereiopods also armed with rows of prominent spines. Dactyls slender, two-thirds length of propodus, ventrally armed with short spines. Abdomen equal in width to carapace, dorsally rounded, unarmed. Second and third segments with smooth dorsal groove formed by two raised transverse ridges. Pleurae all ventrally rounded, that of second segment widest. Sixth segment with two prominent lateral lobes. Exo- and endopods of uropods equal in length, fringed with setae. Endopods with median ridge just off-centre. Telson slightly wider than long, distally broadly bilobed. Eggs 2 mm in diameter.

Material

SAM.A10470, ♀ ovigerous, carapace length 36 mm, overall length (including rostrum) 100 mm. (Holotype).

♀, carapace length 25 mm, overall length 62.5 mm.

♂, carapace length 25.9 mm, overall length 72 mm. St. A193, 2745 m.

Remarks

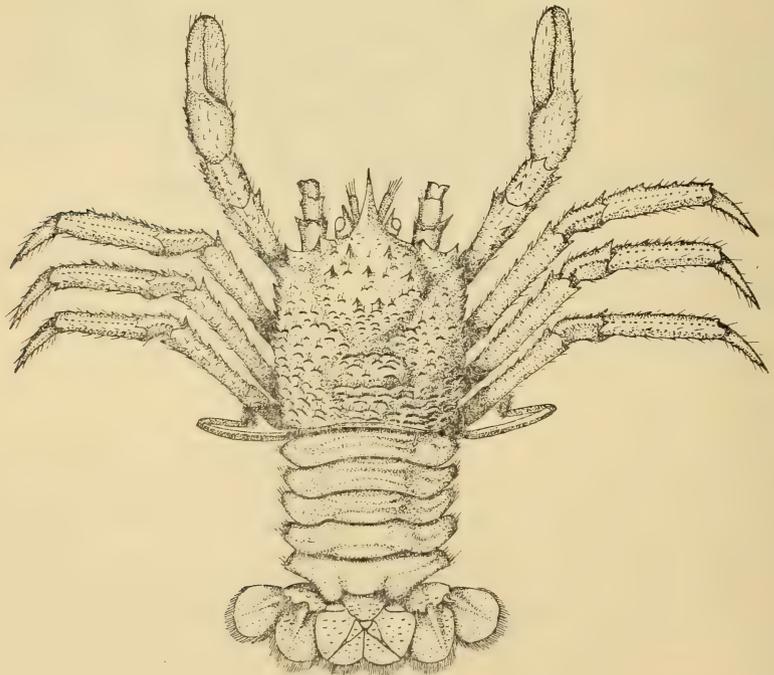
The present species most closely resembles *M. bairdii* (Smith, 1884) but differs in the following respects: there are three pairs of spines in the gastric region of *bairdii*, whereas the present species has an anterior and a posterior pair and a single median spine. In the cardiac region, *bairdii* has a pair of median spines followed by a single median spine, while in the present species there are two pairs of spines. The posterior carapace margin in *bairdii* is armed with ten spines, while there are only four in the present species. In *bairdii*, the dactyls are about three-quarters the propodus length (taken from Benedict's 1903 paper) while in this the dactyls are just over half the propodus length

Munidopsis barnardi n.sp.

Figs 2, 3 c, d

Description

Carapace slightly longer than broad. Lateral margins very slightly convex, more or less parallel. Frontal margin between hepatic spines not narrower than rest of carapace. Rostrum triangular, about half length of carapace, curving distally upward, dorsally carinate, with minute tubercles. Base broad. Small broadly triangular antennal spine, followed by outwardly directed conical spine in hepatic region. Antero-lateral angle formed by prominent conical spine, followed by three or four smaller spines to weakly demarcated mid-branchial groove. Latter followed by one large spine, and several flattened rugae. Gastric region well defined by cervical groove. Two well-developed spines at base of rostrum. Posterior to these, transverse row of three spines. Posterior gastric region with pair of spines, and several transverse flattened setiferous rugae. Rest of carapace especially posterior portion covered with rugae. Posterior margin separated by narrow smooth groove. Posterior margin a double raised ridge, minutely crenulated. Eystalks short, only slightly movable, eyes unpigmented, almost embedded in stalk. Inner angle of latter produced into slender spine, longer than diameter of eye. Slight tubercle just below eye, exterior to eyestalk spine. First antennular peduncle joint armed with two long spines on

FIG. 2. *Munidopsis barnardi* n.sp.

outer side, inner side with short spooned denticulate process. Merus of second maxilliped smooth. Chelipeds slightly longer than carapace (including rostrum). Merus equal to chela in length, with four prominent distal spines. Three pairs of ambulatory pereiopods slightly longer than chelipeds; propodi, carpi, and meri with tubercles along angles. Dactyls not very stout, longer than carpi, spinous on lower edge, spines becoming obsolete proximally. Abdomen equal in width to carapace, dorsally rounded and unarmed. Second and third segments with two

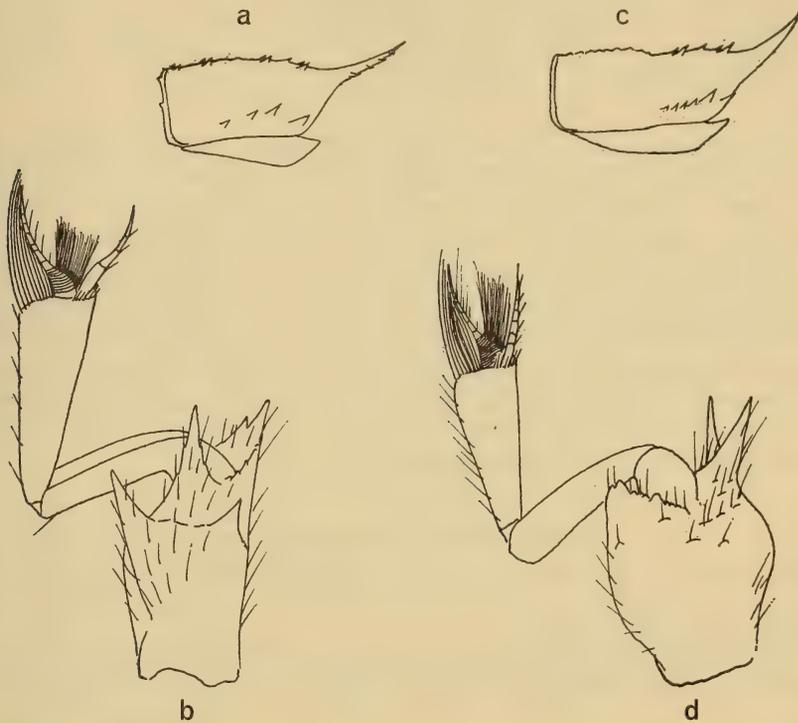


FIG. 3.

a. *Munidopsis chacei* n.sp. Lateral view of carapace. b. *Munidopsis chacei* n.sp. Ventral view of left antennule. c. *Munidopsis barnardi* n.sp. Lateral view of carapace. d. *Munidopsis barnardi* n.sp. Ventral view of left antennule.

raised dorsal ridges, separated by smooth transverse groove. Fourth and fifth segments merely with smooth transverse groove. Sixth segment posteriorly trilobed, median lobe wider than lateral lobes, latter longer than former. Pleurae all ventrally rounded, second broadest. Anterior three pleurae slightly tuberculate, with median curved ridge. Exo- and endopods of uropods sub-circular, fringed with setae, each having slight raised ridge. Telson equal in length to exopod of uropod.

Material

		♂	♀	♂	♀	Station	Depth (m)
		Carapace length	Carapace length	Overall length	Overall length		
SAM.A10497	..	15.5 mm		35 mm (including rostrum)		A317	2708-3038
SAM.A10465	..	14.0 mm		34.0 mm		A193	2745
SAM.A10508	..	14.5 mm		36.4 mm		A317	2708-3038
		17.0 mm		41.2 mm			
		17.0 mm		42.0 mm			
SAM.A10485	..	17.5 mm		43.0 mm		A315	2891-2965
		11.0 mm		26.0 mm			
SAM.A 12636 (Holotype)			15.5 mm		25.5 mm		
			15.0 mm		41.0 mm		

Remarks

This species is very similar to *M. crassa* Smith, 1884, but differs in the following respects: The rostrum, which in *crassa* is very nearly horizontal, is in the present species sharply upcurved; the frontal margin appears to be proportionally wider than in *crassa*, the telson differs in shape (see Chace in correspondence); the infero-mesial edge of the merus of the second maxilliped in *crassa* is armed with three conical spines, which are lacking in the present species; *crassa* also lacks the two extra rows of spines in the gastric region, found in the present species. The holotype female of *crassa* has an overall length of 125 mm, whereas the largest female in the present series is 41 mm long, several of the males also being of comparable size. There is thus a considerable difference in size between the two species.

Galacantha rostrata Milne-Edwards, 1880

Galacantha rostrata M. Edw. 1880: 52. Benedict, 1903: 304. Barnard, 1950: 494, fig. 92 e, f.

Previous records and distribution

Off Cape Point, Atlantic and Pacific coasts of North America, East Indies, Bay of Bengal, Arabian Sea.

Material

Twenty-one specimens of this species were taken from stations A190, A193, A318, A322, in depths varying from 2269-2782 m.

PALINURA

Family **Eryonidae***Polycheles demani* Stebbing, 1917

(?) *Polycheles beaumontii* (Alcock), Stebbing, 1908: 25. Stebbing, 1910: 377.

Polycheles demani Stebbing, 1917: 28. Barnard, 1950: 570, fig. 105 a-c.

Previous records and distribution

Off Cape Point, 500-1400 fms (980-2760 m).

Material

					♀ Overall length	♂ Overall length	Station	Depth (m)
SAM.A10453	50 mm		A191	2745
					41 mm			
SAM.A10460	78 mm		A192	2708
					51 mm			
					41 mm			
SAM.A10569	43 mm		A193	2745
					36 mm			
SAM.A10487	64 mm		A315	2891-2965
					62 mm			
					53 mm			
SAM.A10475	65 mm	82 mm	A315	2745
					54 mm			
					41 mm			
					39 mm			
SAM.A10570	71 mm		A317	2708-3038
					67 mm			
SAM.A10501	52 mm		A317	2708-3038
					41 mm			
SAM.A10522	100 mm		A318	2525-2782
					38 mm			
SAM.A10520	94 mm		A318	2525-2782
SAM.A10533	101 mm		A319	2690-2727
					99 mm			
					85 mm			
SAM.A10568	75 mm		A322	2745

Stereomastis sculpta (Smith, 1882)

Pentacheles sculpta Smith, 1882: 23.

Polycheles sculpta: Stebbing, 1910: 377.

Stereomastis sculpta: Barnard, 1950: 572, fig. 105 d.

Previous records and distribution

Off Cape Point, 600 fms (1180 m), off Durban, 440 fms (865 m), Gibraltar, Canary Islands, East African coast, Mediterranean, East Indies, west coast of North America.

Material

SAM.A10443, ♀♀, overall length 92 mm, 87 mm, ♂, 69 mm. St. A189, 1098 fms.

Stereomastis nana (Smith, 1884)

Pentacheles nanus Smith, 1884: 359.

Polycheles nana: Stebbing, 1910: 377.

Stereomastis nana: Barnard, 1950: 573, fig. 105 e.

Previous records

Off Cape Point, 800 fms (1570 m), 1200 fms (2360 m), east and west coasts of North America, Gulf of Panama.

Material

SAM.A10559, ♀♀, overall length 55 mm, 47 mm. St.A189, 1098 fms.

Remarks

This species is very similar to the preceding one, the main differences being in the median carapace spines (2, 1, 2, 1—2, 2, 2 in *sculpta*, 2, 1, 1, 2, 1—2, 2, 2, in *nana*), the spinous structure of the sixth abdominal keel in *nana* and the slightly more spinous condition of the posterior portion of the carapace in *nana*. With reference to this, it is interesting to note that in two of the three specimens of *sculpta* in this collection there are traces of spines on the raised keel of abdominal segment six. The possibility exists that *nana* is a juvenile form of *sculpta* and that some of the spines are lost with development.

Willemoesia bona-spei n.sp.

Figs 4, 5

Description

Carapace one and a half times longer than broad, lateral margins of posterior carapace parallel, anterior margins converging. Antero-lateral angle formed by large spine (largest on carapace). Frontal margin emarginate. Two prominent spines above antennules, between which a prominent median spine (latter not marginal but just posterior to margin) projecting almost vertically from carapace. Medio-dorsal carina spine formula variable, three to five single spines, one pair and final single spine anterior to cervical groove. (1.1.1.1.2.1.C.2, . . .). Prominent posterior median carina in some specimens with pair of small spines just posterior to cervical groove. No regular arrangement posterior to this. Lateral branchial spine formula variable (6—9, 5—8, 18—30). Whole carapace covered with close-set tiny spinules. Latter scattered over orbito-gastric and post-median ridges. Supra-branchial ridge with about eight tiny spines. Anterior carapace margin and antero-lateral margins fringed with short hairs. Basal joints of antennules produced mesially into two wing-like processes, furnished with eight to ten small spines. Second and third antennular joints together equal in length to 1st joint. Antennal peduncle slightly longer than antennular peduncle. Mandible with thirteen to fourteen heavily chitinized teeth. Chelipeds almost three times longer than carapace. Finger of chela with spine at right angles to it, situated in distal half of finger. Latter and thumb equal in length to or slightly longer than palm. Latter with spines along both edges, and along outer edge of finger. Carpus two-thirds length of chela with spines along outer edge. Merus equal in length to chela, with inner margin spined.

Abdomen (excluding telson) three quarters carapace length. First five segments dorsally carinate, first four each with single small forwardly-directed tooth. Sixth segment dorsally smooth. Postero-lateral angle of sixth segment with small lobe. Telson triangular, apically acute, equal in length to posterior three and a half segments. Exopod of uropod subcircular, endopod elongate-

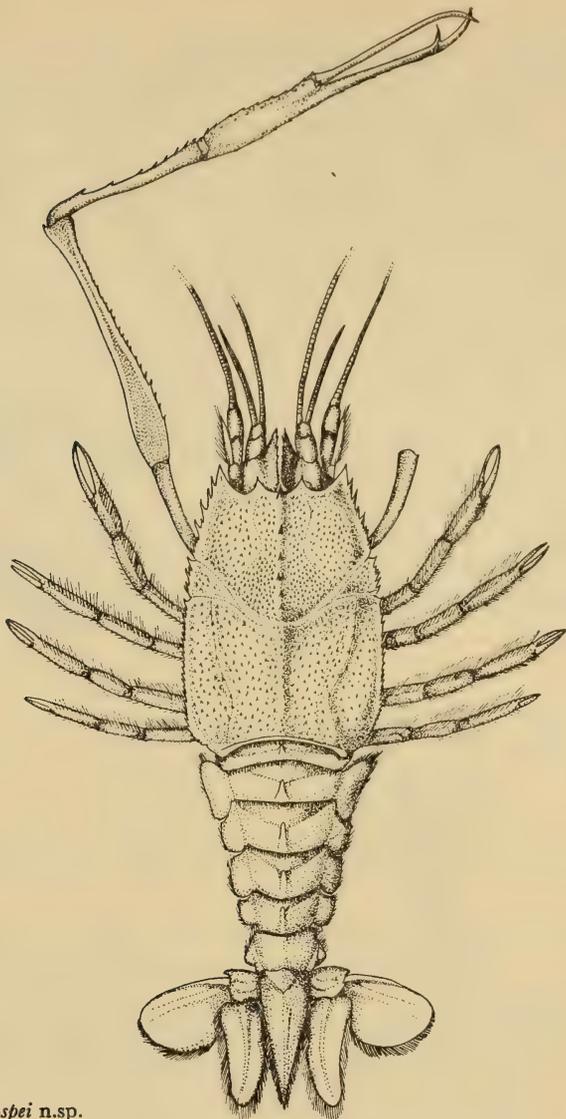


FIG. 4.
Willemoesia bona-spei n.sp.

oval, both fringed with setae. Pleuron of second segment almost circular, twice as broad as that of third. Pleurae of fifth and sixth segments ventrally pointed, anterior three ventrally rounded.

Material

	♀ Overall length	♂ Overall length	Station	Depth (m)	Spine formulae	
					Median	Lateral
SAM.A10473 ..		108 mm 74 mm	A193	2745	11121/2..	9/7/27 9/6/27

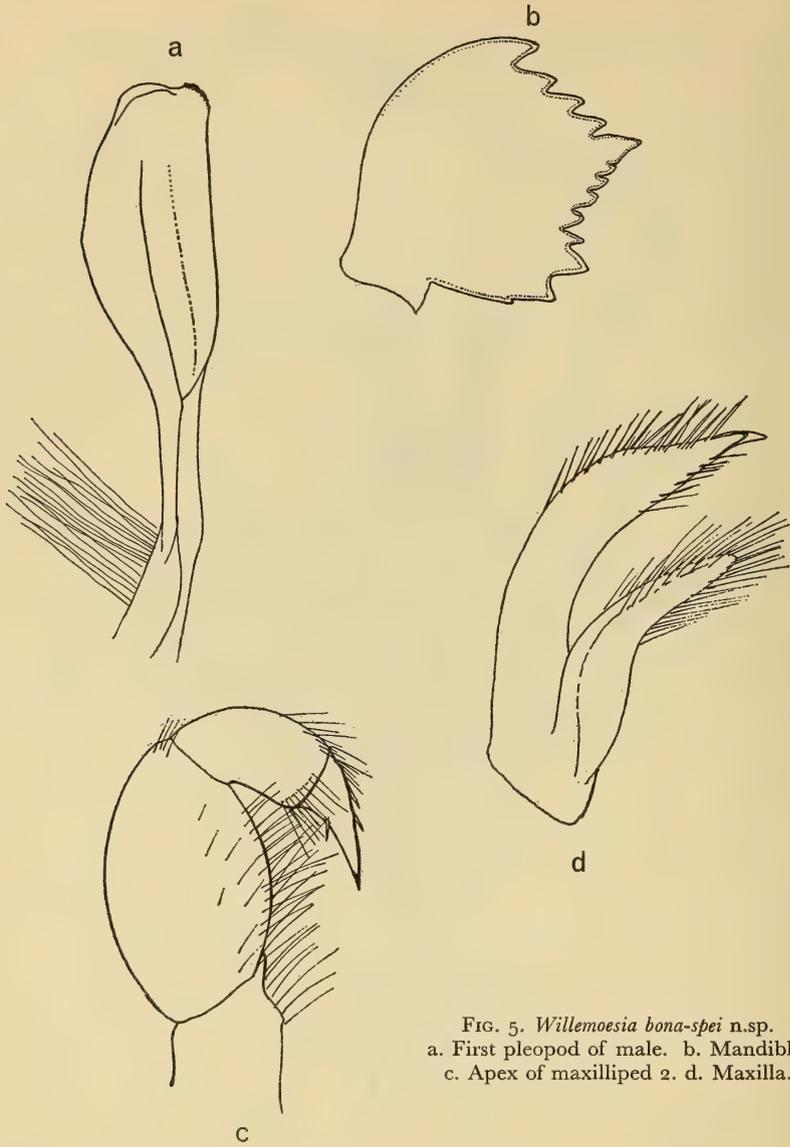


FIG. 5. *Willemoesia bona-spei* n.sp.
 a. First pleopod of male. b. Mandible.
 c. Apex of maxilliped 2. d. Maxilla.

	♀ Overall length	♂ Overall length	Station	Depth (m)	Spine Median	formulae Lateral
SAM.A10509	.. 87 mm	113 mm	A317	2708-3038	111121/2..	8/7/30
		108 mm			11121/2...	7/5/27
SAM.A10543 (Holotype)	.. 109 mm (ovig.)		A322	2745	111211/...	9/7/21
SAM.A12637	..	107 mm			11121/....	6/8/30
		94 mm			11121/2...	9/7/18
					1111121/2.	9/5/25

Remarks

From an assessment of the spine formulae of the present species, it would seem that it is closely related to several described species, such as *leptodactyla* (Willemoes-Suhm), *pacifica* Sund, or *challengeri* Sund. Specific delimitation in this genus is very difficult, particularly as the number of specimens available is very low. Both *leptodactyla* and *challengeri* have a thick 'fur', unlike the present species, the carapace of which is covered with tiny spines. The present species resembles Bate's 1888 plate 19 C (a specimen captured off the coast of Chile and named *pacificus* by Sund in 1920) both in the shape of the frontal margin, and in the presence of teeth on the supra-branchial ridge. This species differs from *pacificus* and indeed from all the described species in that the posterior portion of the median dorsal carina does not have any regular spine formula, but simply has a scattering of the tiny spines as found on the rest of the carapace.

Sund's *pacificus* has the orbital sinus more angular than the present species and the most anterior median spine is not marginal. In lateral view, the present species is only feebly arched, while in *pacificus* 'the carapace, when seen in profile, is strongly arched' (Sund, 1920). The present specimens are thus described as a new species, but every likelihood exists that with more material becoming available, it will be found to be synonymous with an already described species.

Eryoneicus spinoculatus Bouvier, 1905

Fig. 6

Eryoneicus spinoculatus Bouvier, 1905: 480. Bernard, 1953: 34. Belloc & Lorillou, 1961: 10.

Description

Carapace longer than wide, unarmed except for carinal spines. Rostrum a pair of small spines. Median dorsal carina spine formula — 1, 1, 2, '1, 1, C, 2, 2, '1, 2, ('1 indicates a blunt spine). Lateral carina spine formula 6, 3, 7. Posterior carapace ridge, between median and lateral carinae, with ten or eleven spines. Orbito-cervical line with three small spines. Frontal margin rounded. First abdominal segment with two medio-dorsal spines, segments two to five with three medio-dorsal spines. Sixth with single posterior spine, anterior portion smooth. Single lateral spine on each abdominal tergum. Single spine on pleurae two to five. Pleuron of second segment twice as wide as that of third. Ventral margins of pleurae denticulate. Telson with two median spines, seven or eight lateral spines. First pleopods relatively undeveloped.

Material

SAM.A10448, one specimen, carapace length 24 mm, width 20 mm, overall length 44 mm. St. A190, 2269 m.

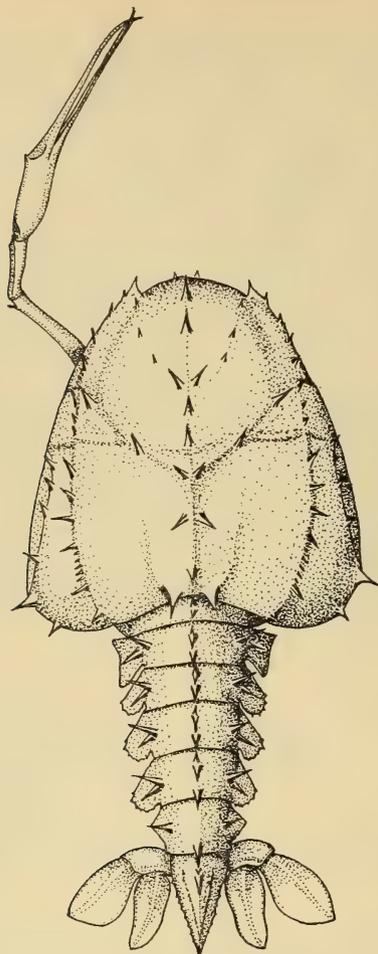


FIG. 6.
Eryoneicus spinoculatus Bouvier.

Remarks

From the median dorsal spine formula, it would seem that this specimen belongs to the *spinoculatus* group (Bernard, 1953). Using his key to the group, one arrives at *E. spinoculatus* var. *hibernicus* (Selbie), distinguished from *spinoculatus* s.s. by the lack of anterior spines on the sixth abdominal tergum. This variety has been recorded from 2100 metres off the coast of Ireland, from the north Atlantic and from the waters of Greenland.

PENAEIDEA

Family **Penaeidae**

Plesiopenaeus nitidus Barnard, 1947

Plesiopenaeus nitidus Barnard, 1947: 383. 1950: 622, fig. 116. Grindley & Penrith, 1965: 280.

Previous records

Off Cape Point, 475-630 fms (930-1240 m), south-west Indian Ocean.

Material

				♀ Carapace length	♂ Carapace length	Station	Depth (m)
SAM.A10441	17.2 mm		A189	1098
SAM.A10442	27.2 mm		A189	1098
				31.0 mm			
				31.6 mm			
					27.5 mm		
					22.7 mm		

Haliporus villosus Alcock & Anderson, 1874

Figs 7, 8

Haliporus villosus Alcock & Anderson, 1894: 146. Alcock, 1900: pl. 26, fig. 1.

Hymenopenaeus villosus: Burkenroad, 1936: 105.

Description

Integument soft and glabrous; carapace torn in places, rostrum missing. Carapace dorsally carinate, strongly arched, with distinct notch one third of carapace length from base of rostrum, formed by cervical groove. Mid-dorsal carina flattened for three millimetres just posterior to cervical notch. Eight dorsal teeth between cervical notch and rostral base. Strong post-antennal carinate spine present. Post-antennal carina meets obliquely descending cervical

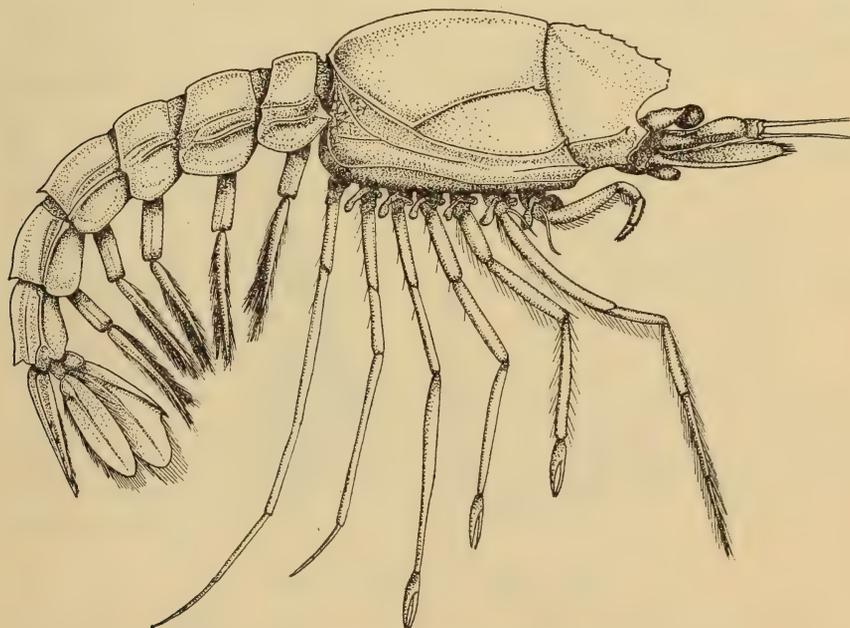


FIG. 7. *Haliporus villosus* Alcock & Anderson.

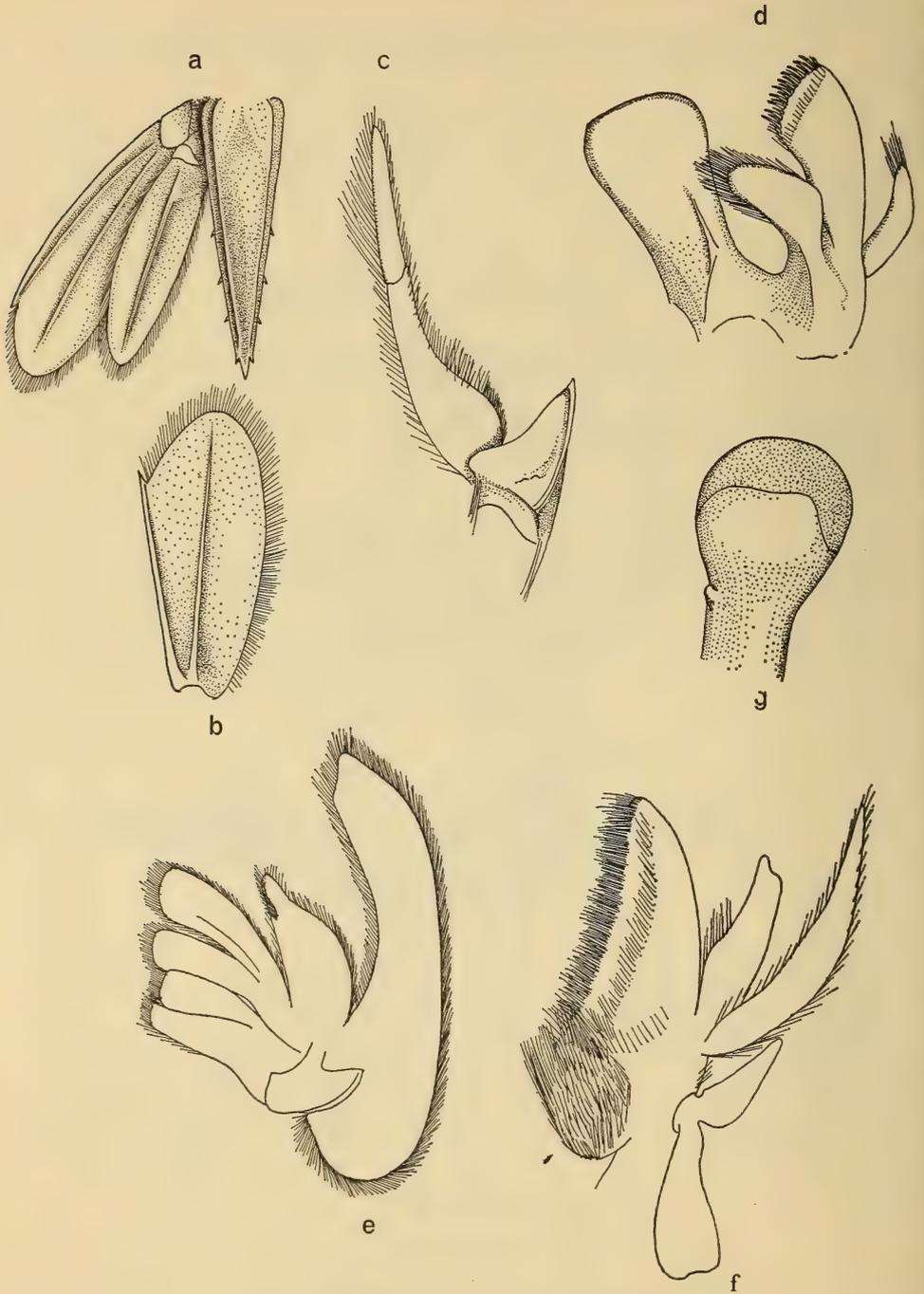


FIG. 8. *Haliporus villosus* Alcock & Anderson.
 a. Telson and left uropod. b. Antennal scale. c. Mandible. d. Maxilla 1. e. Maxilla 2.
 f. Maxilliped 1. g. Eyestalk.

groove at hepatic spine, then runs posteriorly upward to posterior midline of carapace. A carina, anteriorly with two spines, stretches from the lateral midpoint of cervical groove, to lateral midpoint of post-antennal carina. No antennal spine but a blunt projection on carapace margin. Branchiostegal spine minute. Pterygostomial spine much larger. Pterygostomial carina stretches to below cervical groove. Another keel, ventral to pterygostomial carina, extends length of carapace to posterior margin. Several smaller branching keels in posterior region of carapace, meeting in posterior midline. Eyes slightly wider than eyestalks, reaching to end of first antennular peduncle joint. Antennular peduncle two and a half times length of eyestalk, basal joint with small spine on outer distal angle. Tiny tubercle on inner margin of eyestalk. Second joint of antennal peduncle with strong outwardly flared spine, just anterior to pterygostomial spine. Antennal scale broad, flexible, almost foliaceous, fringed with setae, tiny spine on outer margin. All mouthparts fringed with setae. Exopod of maxilliped 2 twice length of exopod of maxilliped 3. Maxillipeds 2 and 3, and pereopods 1-4 with leaf-like epipods. Epipod of maxilliped 2 also has podobranch, maxilliped 3 with rudimentary podobranch. Epipods of pereopods without podobranchs. Maxilliped 3 and pereopod 4 reaching equally far forward, former with slender dactyl, propodus and carpus of almost equal length. Pereopods long, fairly stout, 1 to 3 chelate. Fifth pereopod longest, ending in very slender dactyl. All abdominal segments dorsally carinate, fourth, fifth, and sixth ending in slight raised spines. Each abdominal segment with two lateral ridges, latter meeting on posterior margin of each segment. Pleopods large, with long setiferous endo- and exopods. Telson apically acute, armed with four small lateral spines. Uropods almost foliaceous, setiferous, endopod slightly shorter than exopod. Latter with marginal tooth some distance from apex.

Previous records

Presumably from the Indian region (the paper containing the original description is not available in South Africa).

Material

SAM.A10461, ♀, carapace length 58.5 mm, overall length 168 mm. St. A192, 2798 m.

Remarks

This is a new record for the South African region. The species has apparently not been collected since it was recorded by the *Investigator* in 1894. The only difference between the present specimen and the holotype is that in the latter the integument is covered with short fine hairs, while the former has a glabrous integument.

Gennadas gilchristi Calman, 1925

Gennadas gilchristi Calman, 1925: 6. Barnard, 1950: 633, fig. 118 g, h.
Amalopenaeus elegans (non Smith) Stebbing, 1917: 31.

Previous record

Off Cape Point, 360–1014 fms (700–1990 m).

Material

SAM.A10577, ♂, carapace length 8.3 mm; ♀, carapace length 11.2 mm.
St. A.321, 3239–3440 m.

Gennadas kempi Stebbing, 1914

Gennadas kempi Stebbing, 1914: 283. Calman, 1925: 4. Balss, 1927: 260. Barnard, 1950: 630, fig. 118 a–d.

Previous records

Off Cape Point, 1000 fms (1970 m), south Atlantic.

Material

SAM.A10575, ♂, carapace length 8.5 mm. St. A321, 3239–3440 m.
SAM.A10576, ♂♂, carapace length 9 mm, 9 mm. St. A190, 1240 fms.

Gennadas bouvieri Kemp, 1909

Gennadas bouvieri Kemp, 1909: 727. Burkenroad, 1936: 80. Tirmizi, 1960: 360.
Amalopenaeus alcocki (non Kemp) Balss, 1935: 266.
Amalopenaeus bouvieri: Balss, 1925: 267.

Description

Rostrum of typical *Gennadas* type. Carapace carinate throughout its length. Thelycum of female with eighth thoracic sternite bearing a pair of slightly elongate antero-lateral projections, with setose tips.

Previous records and distribution

Arabian Sea, Zanzibar, eastern Pacific, Bahamas, Bermuda, Caribbean, south Atlantic (Ascension).

Material

SAM.A10578, ♀, carapace length 8.3 mm. St. A321, 3239–3440 m.

Remarks

On lifting the thelycal plate between the bases of the third and fourth pereopods, a pair of brown spermatophores could be seen. Each spermatophore has a rounded swollen base and a curved neck ending in a hook which is inserted into the spermatheca and makes removal difficult.

Apart from Balss's record of a male from the Ascension Island region, this species has not been found in the south Atlantic. This is thus a new record for the South African region.

Family **Sergestidae**Genus **SERGESTES** Milne Edwards

Up to and including 1950, the following species of *Sergestes* had been recorded from South African waters: *articus* Kröyer, *potens* Burkenroad (= *phorcus*

Faxon), *prehensilis* Bate (= *gloriosus* Stebbing), *armatus* Kröyer, *splendens* Sund.

The 1960 midwater collection of Decapoda yielded the following species: *potens* Burkenroad, *prehensilis* Bate, *regalis* Gordon, *armatus* Kröyer, *atlanticus* Milne Edwards, *sargassi* Ortmann, *corniculum* Kröyer, *splendens* Sund.

The present deep-water collection has yielded *regalis* Gordon, *armatus* Kröyer, *prehensilis* Bate, *corniculum* Kröyer.

Burkenroad (1937), in describing the Sergestidae of the Templeton Crocker Expedition to California, noted that only some species of *Sergestes* had specialized organs in the gastrohepatic region, first noted by Pesta in 1918. It is thought that these 'organs of Pesta' have a luminescent function. Burkenroad also noted that those species of *Sergestes* which lacked organs of Pesta invariably possessed dermal photophores, and went further to suggest that possibly the genus could be split into two natural groups. This has been done by Yaldwyn (1957). Those species possessing organs of Pesta fall into the subgenus *Sergestes*, while those possessing photophores fall into the subgenus *Sergia*. This classification has been followed in this work. In life, the organs of Pesta have a conspicuous colouring of red and blue, but in preserved material these organs, which are internal and difficult to see without damage to the specimen, become opaque-white.

Further division of the subgenus *Sergia* can be based on the type of photophore, whether it posses a translucent lens-like structure or whether merely an opaque-white dermal spot.

Sergestes (*Sergestes*) *atlanticus* Milne Edwards, 1830

Figs 9 d, 10 c, 11 d

Sergestes atlanticus Milne Edwards, 1830: 346. Bate, 1888: 389. Hansen, 1896: 951. 1903: 58. 1922: 41.

Sergestes (*Sergestes*) *atlanticus*: Yaldwyn, 1957: 8.

Description

Rostrum an apically acute spine. Prominent supra-orbital spine; well-developed hepatic spine. Feeble cervical groove midway along carapace. Slight gastrohepatic groove and suprabranchial ridge. Eyes wider than the eyestalk. Eyestalk half length of first antennular segment. Maxilliped 3 equals pereopod 3 in length. Two distal segments of pereopod 5 setose on only one margin. No dermal photophores.

Petasma of male short and stumpy. Processus uncifer not apically hooked. Processus ventralis apically acute, broadly triangular in shape. The lobus terminalis a short lobe below the oblong-oval lobus inermis. Lobus connectens and lobus armatus short; apically blunt lobes.

Previous records and distribution

North Atlantic, off South American coast, off Japan, Fiji, south of Australia.

Material

SAM.A12529, ♂ carapace length 27.9 mm. IK. St. 6, west of Cape Town; caught 200 metres in a depth of water 1600 metres.

Remarks

This appears to be the first record from South African waters of this species.

Sergestes (Sergestes) armatus Kröyer, 1855

Sergestes armatus: Hansen, 1922: 174. Calman, 1925: 26. Barnard, 1950: 643, fig. 120 m-p.
Sergestes (Sergestes) armatus: Yaldwyn, 1957: 8.

Material

SAM.A10528, ♀ carapace length \pm 17 mm. St. A318, 2525-2782 m.

SAM.A10532, ♀ carapace length 11.6 mm. St. A.319, 2690-2727 m.

Remarks

The most useful diagnostic feature of this species is the very obvious and well-developed third maxilliped, which is longer and stouter than the longest pereopod. This feature is also found in *Sergestes sargassi* to some extent, but that species can easily be distinguished by the two distal segments of the fifth pereopod which have setae on only one margin in *armatus*.

Previous records and distribution

Table Bay, 300 fms (590 m), Cape Point, 310 fms (600 m), north and south Atlantic, off Agulhas, off Natal coast, south-west Indian Ocean, South Australia, Mediterranean.

Sergestes (Sergestes) sargassi Ortmann, 1893

Figs 9 c, 10 d, 11 c

Sergestes sargassi Ortmann, 1893: 34. Hansen, 1922: 148.

Sergestes (Sergestes) sargassi: Yaldwyn, 1957: 8.

Description

Rostrum short, anterior margin almost vertical, topped by a short, sharp, horizontal spine. Carapace with well-defined cervical groove, prominent supra-branchial ridge, distinct gastrohepatic groove, minute supra-orbital and hepatic spines. Eyestalk twice as long as eye, latter slightly wider than the stalk. Eyestalk reaching half-way along first joint of antennular peduncle. Maxilliped 3 stouter and longer than the pereopods, two distal segments with internal margins having comb-like rows of bristles. Pereiopod 3 longest, reaching slightly beyond the antennular peduncle. Pereiopod 4 flattened with long setae on distal segments. Pereiopod 5 about half length of fourth, two distal segments setose on both margins. No dermal photophores. Petasma lobes generally elongate, possessing lobus inermis (a small lobe on the lobus terminalis), stout processus ventralis, and smaller, thinner lobus armatus. Inner surface of processus ventralis armed with five stellate spines, followed by a marginal row of hooks, ending in two slightly larger apical hooks.

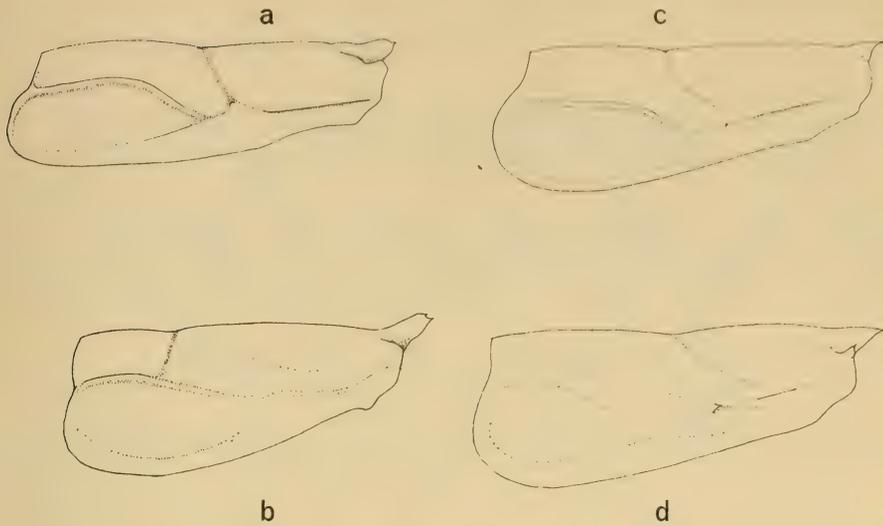


FIG. 9.

a. *Sergestes corniculum* Kröyer. Carapace. b. *Sergestes regalis* Gordon. Carapace.
c. *Sergestes sargassi* Ortmann. Carapace. d. *Sergestes atlanticus* Milne Edwards. Carapace.

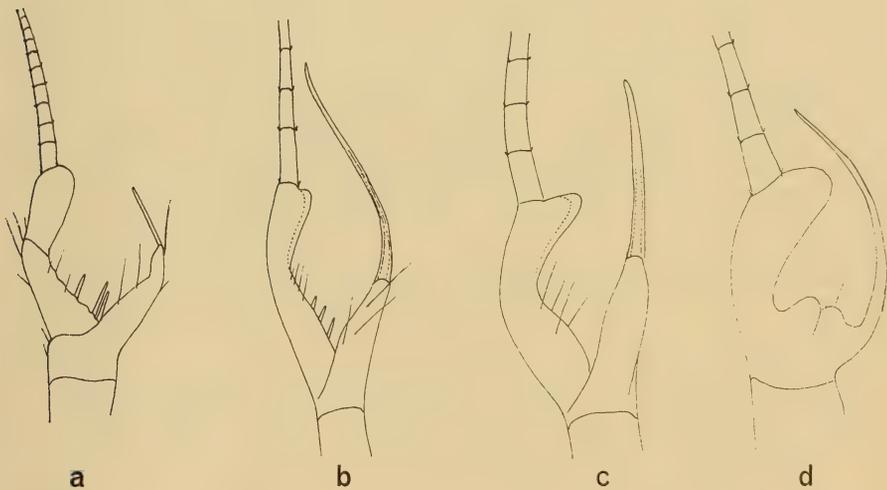


FIG. 10.

a. *Sergestes regalis* Gordon. Second ramus of antennule of male. b. *Sergestes corniculum* Kröyer. Second ramus of antennule of male. c. *Sergestes atlanticus* Milne Edwards. Second ramus of antennule of male. d. *Sergestes sargassi* Ortmann. Second ramus of antennule of male.

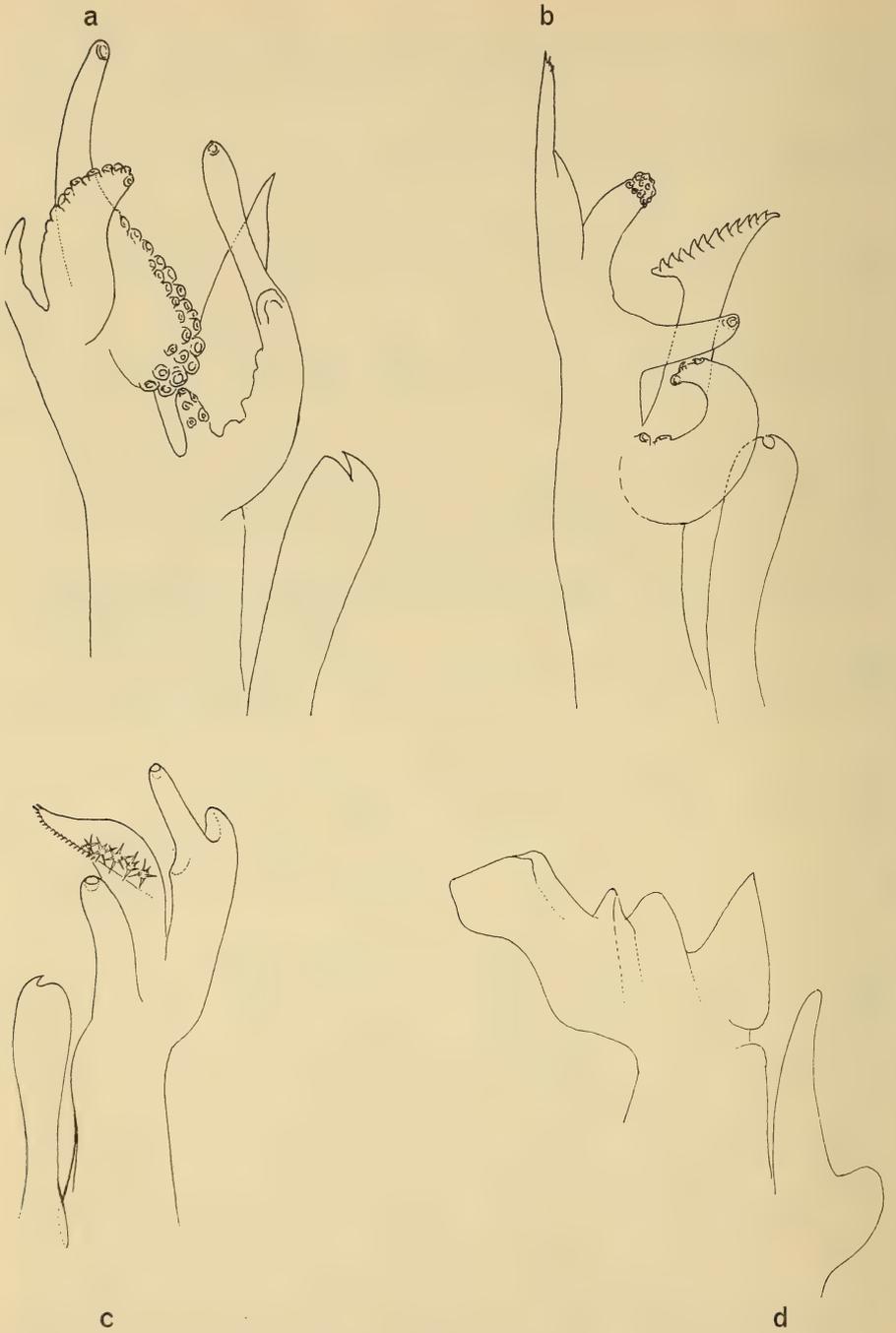


FIG. 11.

a. *Sergestes regalis* Gordon. Petasma. b. *Sergestes corniculum* Kröyer. Petasma. c. *Sergestes sargassi* Ortman. Petasma. d. *Sergestes atlanticus* Milne Edwards. Petasma.

Distribution

Off Madeira, Azores, Sargassum Sea.

Material

SAM.A12528, ♂, carapace length 8 mm, overall length 27 mm, IK St. 6, west of Cape Town caught at 200 metres in a depth of water of 1600 metres.

Remarks

It is remarkable that, like *Sergestes atlanticus*, only one specimen of this species was taken from all the hauls containing sergestids. This is the first record of this species from the South African region.

Sergestes (Sergestes) corniculum Kröyer, 1855

Figs 9 a, 10 b, 11 b

Sergestes corniculum Kröyer, 1855: 22. Pesta, 1918. Burkenroad, 1937: 316. Hansen, 1922: 126.
Sergestes (Sergestes) corniculum: Yaldwyn, 1957: 7.

Description

Rostrum with single acute apical spine, flanked by well-developed supra-orbital ridges, very seldom having a minute spine. Well-defined cervical groove about half-way along carapace. At base of cervical groove, a prominent ridge runs anteriorly to eye. Two well-defined ridges in the branchial region. A minute hepatic spine is sometimes present, more usually a blunt knob-like protuberance. Eye prominent, black, wider than the eye-stalk. Tiny tubercle on inner side of stalk, just posterior to eye. Eyestalk reaching half-way along first antennular peduncle segment. All pereopods laterally compressed. Second and third pereopods equally long and slender. Fifth pair about half the length of fourth. Two distal segments of pereopod 5 setose on both margins. No dermal photophores. Petasma of male with processus ventralis distally expanded, having eight to ten papilla-like protuberances. Lobus armatus stout, curved. Lobus connectens small, lobus terminalis apically blunt; lobus inermis longest, reaching furthest distally, apically acute, ending in two or three spines.

Previous records and distribution

Mediterranean, north Atlantic, off Durban, Agulhas, south-west Indian Ocean, off Cape Point.

Material

SAM.A10502, ♂, carapace length 15 mm. St. A317, 2708–3038 m.

SAM.A10556, ♀, carapace length 13 mm. St. A321, 3239–3440 m.

SAM.A10571, ♀, carapace length 14 mm. St. A321, 3239–3440 m.

Remarks

This appears to be the first record of this species from South African waters. It appears to be plentiful, occurring at most of the Isaacs-Kidd midwater stations in addition to the 1959 collection, in depths ranging from 200 metres to about 3700 metres.

Sergestes (Sergia) regalis Gordon, 1939

Figs 9 b, 10 a, 11 a

Sergestes regalis Gordon, 1939: 498.*Sergestes (Sergia) regalis*: Yaldwyn, 1957: 9.*Description*

Rostrum apically bifid. Carapace with well-defined supra-branchial ridge, with a less well-defined ridge ventral to the former. Cervical groove in posterior third of the carapace. Slight groove in antero-lateral third of carapace. Eye prominent, eyestalk two-thirds the length of first antennular peduncle segment. Pereiopods 1-3 slender, third longest, second and third chelate, with stiff red bristles. Pereiopods 4 and 5 shorter, flattened, fringed with long setae. Sixth abdominal segment ends in a spinule, telson medially grooved. Photophores of the 'opaque spot' type, difficult to detect. A variable number of photophores on the merus of the third pereopod, usually about ten. Petasma of male with lobus connectens longer than lobus terminalis; lobus armatus and lobus connectens ending in retracted hooks, lobus armatus longer than processus ventralis.

Previous records and distribution

Mid south Atlantic, off Durban, south-west Indian Ocean.

Material

SAM.A10574, ♀, carapace length 26 mm, abdominal length 44 mm. St. A192, 2708 m.

Remarks

Only one large female was taken in this collection, but several more specimens were obtained from the Isaacs-Kidd midwater collection. This is the first record of the species from the South African region.

Sergestes (Sergia) prehensilis Bate, 1888*Sergestes prehensilis* Bate, 1888: 193. Gordon, 1935: 314.*Sergestes (Sergia) prehensilis*: Yaldwyn, 1957: 9.*Sergestes gloriosus* Stebbing, 1905: 84. 1910: 38. Barnard, 1950: 642, fig. 120 h-j.*Description*

Rostrum apically acute, sometimes a small denticle on the upper margin; indistinct supra-orbital ridge present, no supra-orbital spine. No hepatic spine but a blunt knob-like protuberance. Dermal photophores of the lens-like type.

Previous records and distribution

Off Sandy Point, 800 fms (1570 m), off Durban, 260 fms (510 m), East London region, Agulhas, south-west Indian Ocean, Japan.

Material

					♂	♀	Station	Depth (m)
					Carapace length	Carapace length		
SAM.A10483	12 mm		A315	2891-2965
SAM.A10513		12.4 mm	A317	2708-3038
SAM.A10516		11.0 mm	A318	2525-2782
SAM.A10553		11.8 mm	A321	3239-3440

Remarks

This species appears to be the most plentiful sergestid in South African waters. It was obtained at all the Isaacs-Kidd midwater stations in large quantities. It does not appear to be very plentiful in the hauls from the greater depths of the 1959 collection.

CARIDEA

Family **Oplophoridae***Systellaspis debilis* (Milne Edwards, 1881)

Systellaspis debilis: Chace, 1940: 181. Barnard, 1950: 663, fig. 124 a. Grindley & Penrith, 1965: 281.

Previous records and distribution

Off Cape Point, 1500 fms (2950 m), off Natal, north and west Atlantic, Indo-Pacific.

Material

					♀	♂	Station	Depth (m)
					Carapace length	Carapace length		
SAM.A10444		10.2 mm	A189	1098
SAM.A10455	12 mm		A191	2745
SAM.A10494		11.0 mm	A316	3148-3257
SAM.A10495	13 mm (ovig.)		A316	3148-3257
SAM.A10544	12 mm		A322	2745

Remarks

The carapace length of ovigerous females varies from 12 mm to 14 mm in the Isaacs-Kidd material as well as the present collection. Egg size is 3.3-3.5 mm.

Hymenodora glacialis (Buchholz, 1874)

Hymenodora glacialis: Kemp, 1910: 72. Calman, 1925: 15. Barnard, 1950: 665, fig. 124 b.

Description

Number of rostral spines varying from three to six. Eyes very feebly pigmented, narrower than eyestalk. Telson broken in all the specimens.

Previous records and distribution

Off Cape Point, 1500 fms (2950 m), north Atlantic, west coast of Ireland, 1150 fms (2260 m), north and east Pacific.

Material

					♀	♂	Station	Depth (m)
					Carapace length	Carapace length		
SAM.A10563	11.0 mm		A190	2269
SAM.A10562		13.5 mm	A190	2708
SAM.A10566		15.0 mm	A192	2708
SAM.A10513	9.6 mm 12.0 mm		A317	2708-3038

Notostomus westergreni Faxon, 1893

Notostomus westergreni Faxon, 1893: 208. 1895: 171. Stebbing, 1905: 110. 1910: 395. Chace, 1940: 171.

Notostomus auriculatus Kemp (in MS) Barnard, 1950: 670, fig. 124 b, i.

Previous records and distribution

Off Cape Point, 800 fms (1570 m), off coast of Ecuador, off Bermuda, 900 fms (1770 m) off Keeling Islands, Indian Ocean.

Material

SAM.A10517, ♀, carapace length 38.6 mm, overall length (excluding rostrum), 97.5 mm. St. A318, 2525-2782 m (rostrum missing).

SAM.A12563, ♂, carapace length 42 mm, overall length (excluding rostrum), 90 mm, IK. St. 14, caught at 500 metres in a depth of 2000 metres.

Remarks

Stebbing (1905) noted that the specimen from Cape Point was perhaps a species other than *westergreni*, as it had a strong posterior tooth on the sixth abdominal segment. According to Barnard (1950), Kemp saw this specimen and named it *auriculatus* in MS.; this MS. could not be traced. Comparison of the present specimens and Stebbing's specimen with the original description of *westergreni* make it seem probable that all three specimens belong to this species. Although Faxon does not mention a spine on the sixth abdominal segment, the colour plate illustration (pl. F) shows one. Chace, 1940, also notes that the specimen of *westergreni* in the U.S. National Museum possesses a tooth on the sixth segment. There are minor variations in all the specimens. The lateral carina of the rostrum curves downward in Stebbing's specimen, while the above specimens are as in Faxon's plate, ending horizontally in the gastric region. The asymmetry of the antennal scales in Stebbing's specimen is almost certainly abnormal. The present specimens agree with Faxon's sketch; the outer apical spine extends some way past the apex of the scale and there is no asymmetry. The length of the rostral spines also seems to vary, but as these are very brittle, this variation may have no specific importance. Until further specimens are available for comparison the extent of variation of the species will remain unknown, and the name *westergreni* should be retained.

Acanthephyra haeckelii (Von Martens, 1868)

Ephyra haeckelii Von Martens, 1868: 54.

Acanthephyra haeckelii: Kemp, 1939: 575. Chace, 1940: 140. Barnard, 1950: 668. Grindley & Penrith, 1965: 280.

Previous records and distribution

Off Cape Point, 900 fms (1770 m), south-west Indian Ocean, north Atlantic, south Atlantic, Mediterranean, south Pacific.

Material				Station	Depth (m)	Telson spines
	♀ Carapace length	♂ Carapace length				
SAM.A10536	20.0 mm			A319	2690-2727	10
SAM.A10553		15.0 mm		A321	3239-3440	10
SAM.A10452	16.5 mm			A190	2269	9
SAM.A10439	11.5 mm			A189	1098	9

AcanthePHYra quadrispinosa Kemp, 1939

AcanthePHYra quadrispinosa Kemp, 1939: 576. Barnard, 1950: 668, fig. 124 g. Grindley & Penrith, 1965: 280.

AcanthePHYra batei (non Faxon) Stebbing, 1905: 107.

Previous records and distribution

Off Cape Point, 700-1800 fms (1380-3540 m), off Natal, 820 fms (1610 m), south-east of Agulhas, south-west Indian Ocean, Indo-Pacific.

Material				Station	Depth (m)
	♀ Carapace length	♂ Carapace length			
SAM.A10561	15.5 mm			A321	3239-3440
	9.5 mm				
SAM.A10560	14.0 mm	17.0 mm		A319	2690-2727
SAM.A10458	15.0 mm	11.0 mm		A192	2708
	(ovig.)				

Carapace lengths of ovigerous ♀♀ (from IK material): 14.0 mm, 14.3 mm, 15.0 mm, 15.5 mm, 17.6 mm, 18.4 mm, 19.3 mm.

AcanthePHYra gracilipes Chace, 1940

Figs 12, 14 a

AcanthePHYra gracilipes Chace, 1940: 149. Sivertsen & Holthuis, 1956: 6.

Description

Integument soft, thin; the specimen somewhat damaged. Eyestalk shorter than rostrum, widest at distal end. Small blunt tubercle on inner angle of stalk, just behind eye. Rostrum acutely triangular, with six dorsal teeth and no ventral teeth, reaching end of second joint of antennular peduncle. Dorsal carina ends before reaching the cervical groove. Tiny antennal spine present, also a slightly larger branchiostegal spine, unsupported by a keel. Distinct ridge-like keel above branchial region, stretching from hepatic region almost to the posterior margin. First two abdominal segments dorsally smooth, last four segments dorsally carinate, ending in short spines (spines of fifth segment broken). Distal portion of telson missing. Endopod of uropod equal in length to the sixth abdominal segment. Pereiopods long and slender.

Previous record

Off Bermuda.

Material

SAM.A10565, ♂, carapace length 16 mm, overall length \pm 50 mm. St. A190, 2269 m.

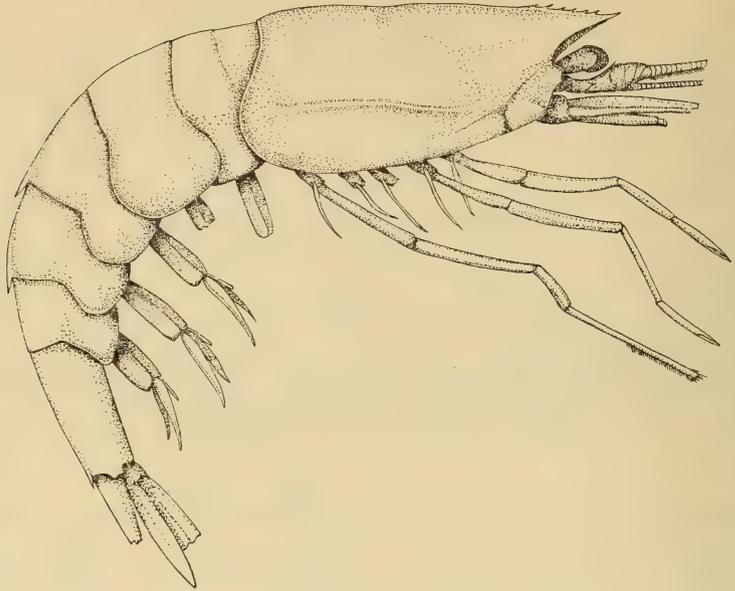


FIG. 12. *AcanthePHYRA gracilipes* Chace.

Remarks

This specimen agrees almost exactly with the original description of Chace (1940). The mandible is toothed over its entire length, confirming the genus. This is the first record of this species from South African waters and possibly from the southern hemisphere.

AcanthePHYRA breviostris Smith, 1885

Figs 13, 14 b

AcanthePHYRA breviostris Smith, 1885: 504. Balss, 1925: 252. Chace, 1940: 148. Sivertsen & Holthuis, 1956: 5.
Hymenodora duplex Bate, 1888: 843.

Description

Integument thin. Eye wider than eyestalk. Rostrum acutely triangular, reaching to end of second joint of antennular peduncle, with eight dorsal teeth; no ventral teeth. Posterior portion of carapace not carinate. Tiny antennal spine present, also a slightly larger branchiostegal spine, the anterior portion of which is supported by a slight keel. A slightly keeled ridge in the branchial region, reaching almost to posterior margin of the carapace. First two abdominal segments dorsally smooth, third to sixth segments dorsally carinate, each ending in a tooth; that of the third segment a large fleshy leaf-like structure, giving the species a distinctive appearance. Teeth of segments four to six small and sharp. Tip of telson missing.

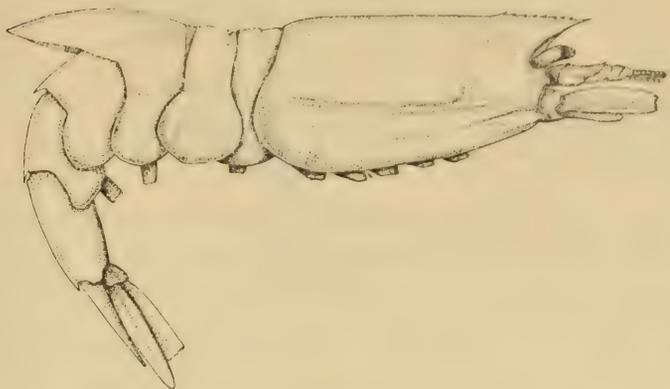


FIG. 13. *Acanthephyra brevirostris* Smith.

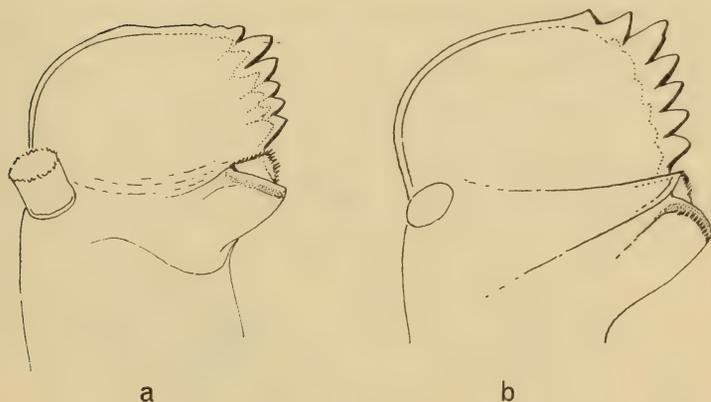


FIG. 14.

a. *Acanthephyra gracilipes* Chace. Mandible. b. *Acanthephyra brevirostris* Smith. Mandible.

Previous records and distribution

North-east coast of U.S.A., Bermuda, Bahamas, off Portugal, West Africa, south-west Indian Ocean, off Pacific coast of Ecuador, off Marion Island.

Material

SAM.A10564, carapace length 19 mm, overall length 54 mm. St. A192, 2708 m.

Remarks

The mandible is almost identical to that of *A. gracilipes* and is dentate throughout its length. This is the first record of the specimens from South African waters. The closest record to South Africa was that of a specimen taken by the *Challenger*, off Marion Island.

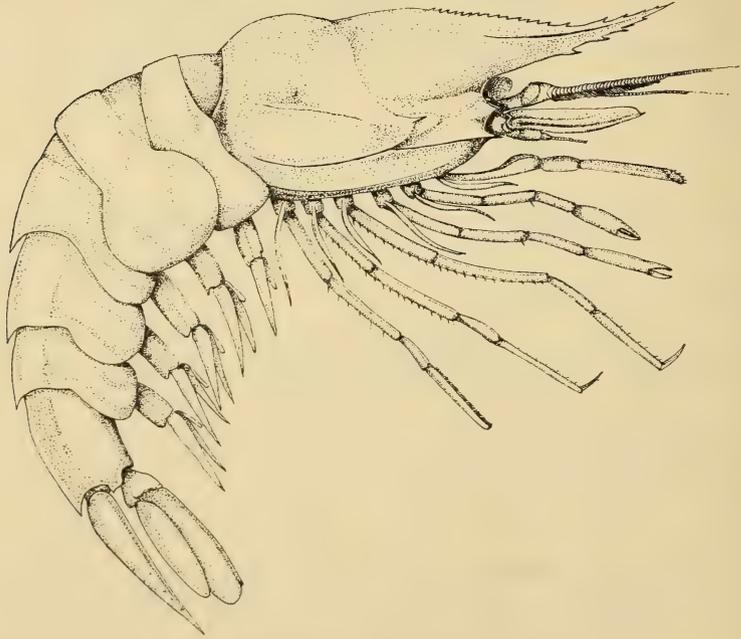
Acanthephyra corallina (Milne Edwards, 1883)

Figs 15, 16, 17

Notostomus corallina Milne Edwards, 1883.*Acanthephyra valdiviae* Balss, 1914: 595. 1925: 260.*Acanthephyra corallina*: Chace, 1936: 27.*Description*

Integument firm. Carapace carinate throughout its length. A notch present in the dorsal carina, about two-thirds down the carapace. Rostrum stout, extending a little way past the antennal scales, curving slightly upward, supported by lateral keels which end some distance posterior to the orbits.

Rostral teeth: 18/3, 18/4, 17/3, 20/3, 22/3, 19/4, seven or eight teeth posterior to the orbit. The distance between the orbital groove and the dorsal carina equal to the distance between the orbital groove and the branchiostegal spine. Latter stout, outwardly flared, supported by a prominent keel. Antennal spine small. Strong hepatic spine at base of cervical groove, which is not well defined. Cervical groove joined by orbital groove. Branchiostegal keel joins with a well-developed keel in mid-branchial region. In the posterior portion of the carapace, this keel curves upwards and joins with a ridge which marks the upper border of the branchial region. Ventral branchial keel stretches from below branchiostegal keel to posterior margin of carapace, curving upward in this region. All abdominal segments dorsally keeled; segments 3-6 each ending

FIG. 15. *Acanthephyra corallina* (Milne Edwards).

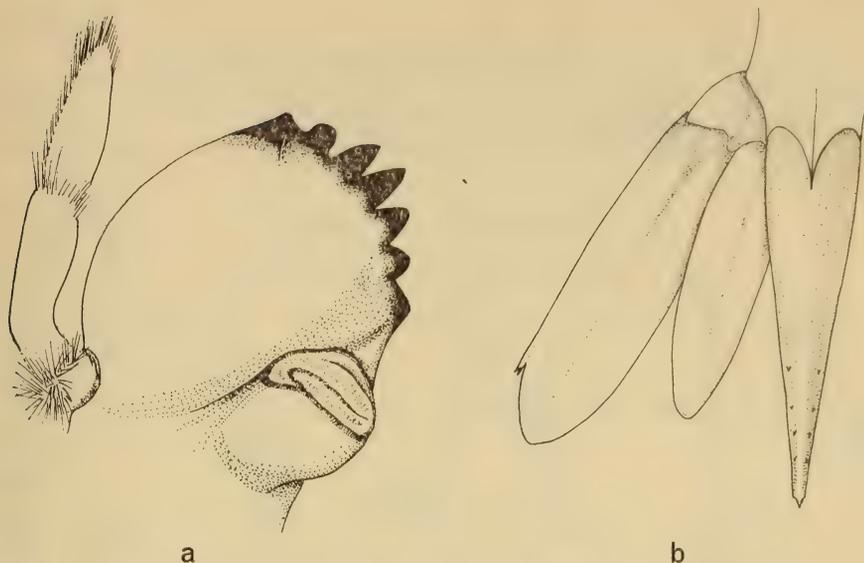


FIG. 16. *Acantheephyra corallina* (Milne Edwards).
a. Mandible. b. Telson and left uropod.

in a strong tooth. Dorso-ventral length of second abdominal segment equals the greatest dorso-ventral length of the carapace. Eyes slightly wider than eyestalks. Antennal scales narrow. Mandibular palp short, three-jointed; seven teeth on cutting edge. Maxilliped 3 as stout as the pereopods, reaching almost to the end of the antennal scale. Pereiopod 4 the longest, but only slightly longer than the other pereopods. Meri of pereopods 3, 4, 5 armed on posterior border with a single row of spinules. Dactyls of pereopods 3 and 4 short, slender; that of pereopod 5 reduced. Propodus of latter has a series of short stiff bristles at its distal end. Slender exopods on maxillipeds 2 and 3 and on all the pereopods. Pleopods stout with well-developed endo- and exopods. Telson with four pairs of dorso-lateral spinules in distal half and pair of terminal spines flanking acute apex. The apex appears to be worn down with age, as some of the larger specimens do not have the sub-apical pair of spines. Exopod of uropod almost equal in length to telson, with two spines next to one another on the outer margin, some distance from the apex. Endopod slightly shorter than exopod.

Material

		♀	♂		
		Carapace length	Carapace length	Overall length	Station Depth (m)
SAM.A12531		39.5 mm	149 mm	A319 2690-2727
SAM.A12532 (ovig.)	34.0 mm		138 mm	A319 2690-2727
SAM.A12533	27.0 mm		111 mm	A190 2269
SAM.A10523 (ovig.)	37.0 mm		134 mm	A318 2525-2782
		33.5 mm		132 mm	A318 2525-2782
			33.5 mm	129 mm	A318 2525-2782
			26.0 mm	99 mm	A318 2525-2782

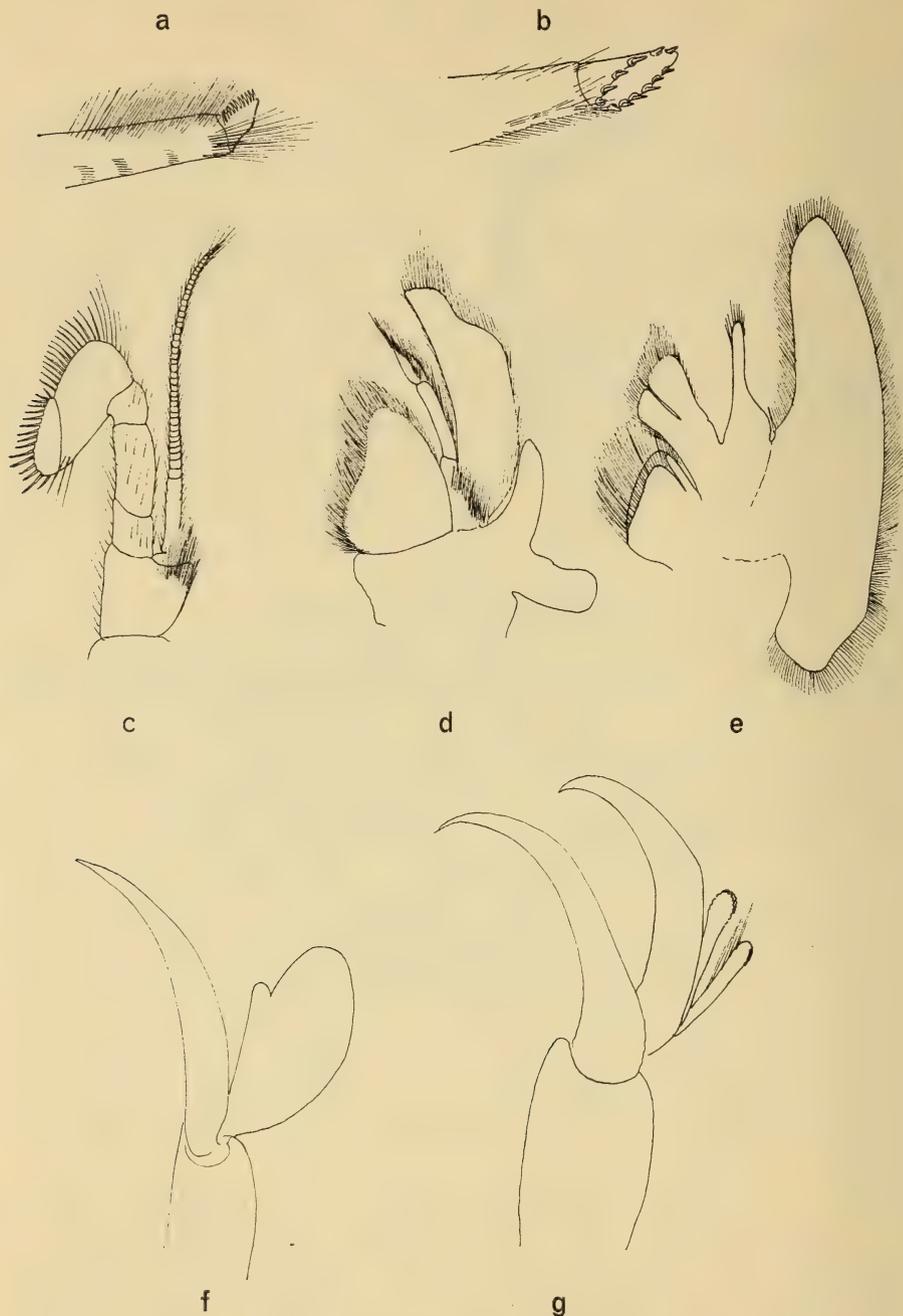


FIG. 17. *Acanthephyra corallina* (Milne Edwards).
 a. Tip of pereopod 5. b. Tip of maxilliped 3. c. Maxilliped 2. d. Maxilliped 1.
 e. Maxilla 2. f. Pleopod 1 of male. g. Pleopod 2 of male.

Remarks

This is a new record for the South African region. The species was previously recorded from the mid-Indian Ocean, where a single male was caught by the *Valdivia*. The presence of a hepatic spine on the carapace together with the deep rostral base serves to distinguish this uncommon species.

Family **Nematocarcinidae***Nematocarcinus longirostris* Bate, 1888

Nematocarcinus longirostris Bate, 1888: 806. Stebbing, 1914: 44. Calman, 1925: 15. Barnard, 1950: 671, fig. 125 a-k.

Previous records and distribution

Off Cape Point, 1200 fms (2360 m), Marion Island, Japan, East Indies, west coast of South America.

Material

A total of 78 specimens of this species was obtained from the following stations: A189, A190, A191, A192, A193, A315, A316, A317, A318, A319. Of the 78, 10 were ovigerous females, with a carapace length varying from 28–34 mm, while 15 were mature males, with a carapace length varying from 23 to 29 mm.

Nematocarcinus parvidentatus Bate, 1888

Nematocarcinus parvidentatus Bate, 1888: 814. Stebbing, 1915: 99. Barnard, 1950: 674, fig. 125 l-o.

Previous records and distribution

Off Durban, 440 fms (865 m), off East London, 400 fms (780 m), off Cape Point, 900 fms (1770 m), Japan.

Material

A total of 108 specimens of this species was obtained from the following stations: A190, A192, A193, A315, A316, A317, A318, A319, A322. Of the 108, 15 were ovigerous females with a carapace length varying from 19–26 mm, while 20 were mature males with a carapace length varying from 17 to 22 mm.

Remarks

Several specimens of either *parvidentatus* or *longirostris* from most of the stations were so damaged that specific identification was impossible. As can be expected from two species so closely related, the mouthparts are almost identical and are of no use in distinguishing the species. The most useful characters are the lengths of the carapace at which the males and females become mature, as well as the rostral shape. In *parvidentatus* the minimum carapace length of mature males and females is usually less than that of *longirostris*. The rostrum is variable, relative length being unsatisfactory for specific separation. In general, *parvidentatus* has a rostrum broader in the vertical plane compared with its length than *longirostris*. The ventral sinuosity at the base of the rostrum in

parvidentatus noted by Barnard (1950) is also a useful character. A bopyrid isopod was found on a specimen of *longirostris* but is neither of the two bopyrids previously recorded on *Nematocarcinus* from South Africa.

Family **Glyphocrangonidae**

Glyphocrangon sculptus (S. I. Smith, 1883)

Rhachocaris sculpta Smith, 1883: 49.

Glyphocrangon sculptus: Smith, 1884: 365. Stebbing, 1908: 37. Barnard, 1950: 719, fig. 134 a-d.

Previous records and distribution

Off Cape Point, 1000 fms (1970 m), east coast of North America.

Material	♀		♂	Juveniles	Station	Depth (m)
	Carapace length	Carapace length	Carapace length			
SAM.A10521			20.5 mm 21.0 mm 22.8 mm	4	A318	2525-2782
SAM.A10515			22.8 mm	2	A318	2525-2782
SAM.A10535	21.0 mm		22.1 mm 22.5 mm		A319	2690-2727
SAM.A10451	26.0 mm (ovig.) 25.5 mm (ovig.) 25.0 mm (ovig.) 25.0 mm (ovig.) 24.0 mm (ovig.) 21.5 mm 22.0 mm 19.3 mm 22.8 mm 21.0 mm		21.1 mm 19.5 mm 19.0 mm 21.3 mm 21.0 mm 17.5 mm 18.9 mm 17.5 mm 18.9 mm 15.6 mm 15.6 mm		A190	2269
SAM.A12534				1	A193	2745
SAM.A10459				2	A192	2708
SAM.A10547				5	A322	2745
SAM.A10462				2	A193	2745
SAM.A10464				1	A193	2745
SAM.A10549				1	A322	2745
SAM.A10539				4	A319	2745

Family **Crangonidae**

Sclerocrangon bellmarleyi Stebbing, 1914

Sclerocrangon bellmarleyi Stebbing, 1914: 29. Barnard, 1950: 804, fig. 152.

Previous records and distribution

Off Durban, 440 fms (865 m), Natal coast, 400 fms (780 m).

Material

SAM.A10446, ♀ ovigerous, carapace length 13 mm, overall length 52 mm.
St. A189, 1098 m.

Remarks

This ovigerous female is the largest specimen of this species yet obtained. The eggs, of which only four remain, measure 2.5 mm in length and are in an advanced state of development, the shape of the larvae being clearly visible. This is the most southerly record of this apparently endemic species.

Pontophilus occidentalis Faxon var. *indica* de Man, 1918

Figs 18, 19

Pontophilus occidentalis var. *indica* de Man, 1918: 161. 1920: 264.

Description

Carapace with median dorsal keel bearing one cardiac and two gastric spines, the more anterior of which always the smaller. Two lateral carapace spines, one hepatic, one epibranchial, lying in an oblique plane. Well-developed antennal and branchiostegal spines, latter supported by a blunt keel. Minute post-orbital spinule above the post-orbital fissure. Antero-lateral angle of carapace with a minute spine. Rostrum varies in length in relation to eyes and in general shape; usually with one or two pairs of minute denticles at its base. Eyes large and rounded, tending to obscure the stalks. Pereiopod 1 stout, armed with the characteristic crangonid chela. Pereiopod 2 about half the

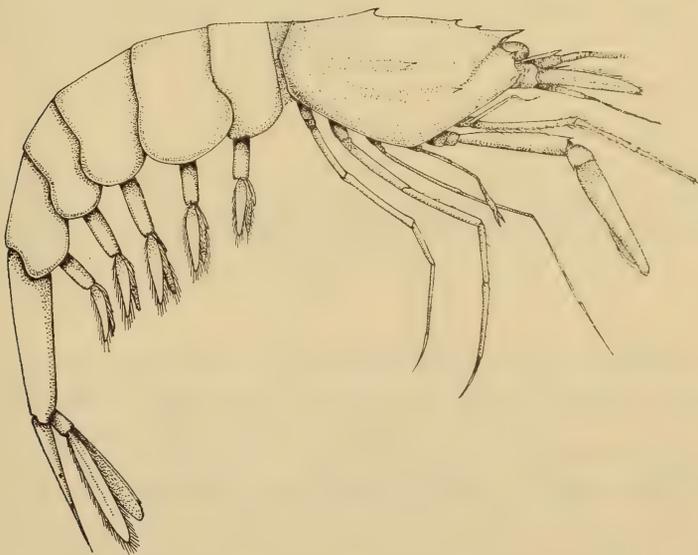


FIG. 18. *Pontophilus occidentalis* var. *indica* de Man.

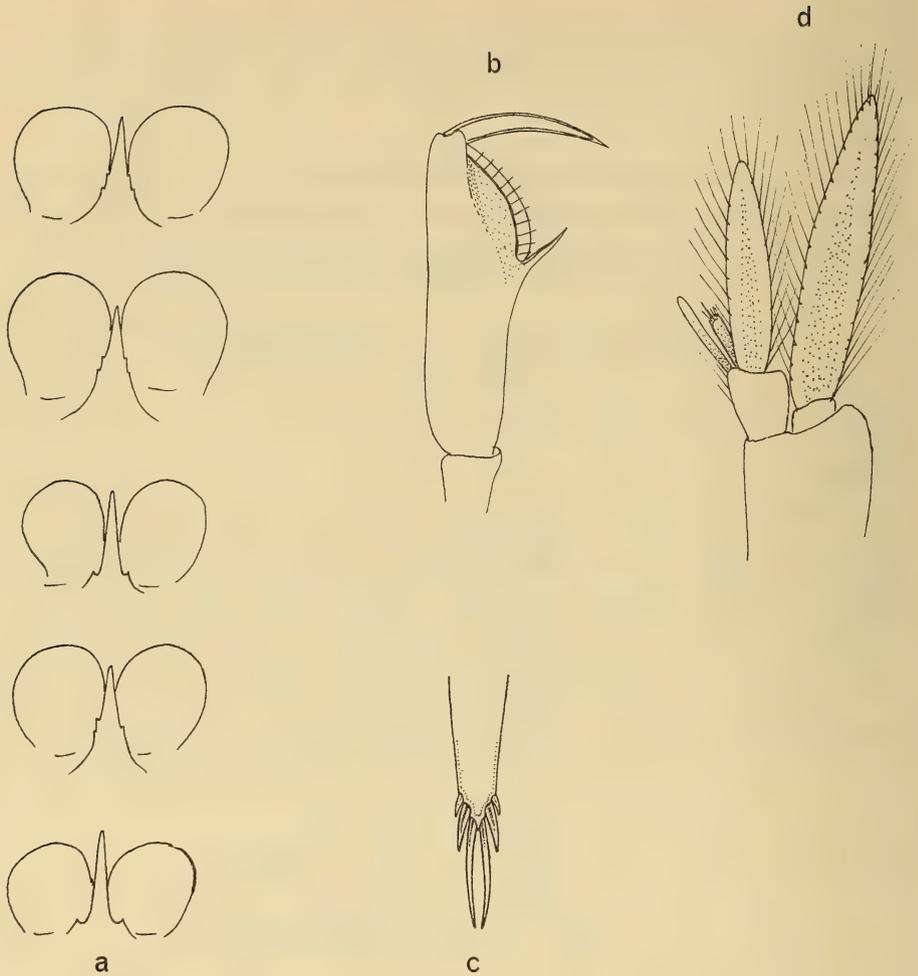


FIG. 19. *Pontophilus occidentalis* var. *indica* de Man.
 a. Rostrum and eyes, showing variations. b. Chela of pereopod 1. c. Tip of telson. d. Pleopod 2 of male.

length of pereopod 1; chelate, very slender. A rounded knob ending in a tiny spine present between bases of second pair of pereopods. Pereopod 3 longer than pereopod 1, very slender. Pereopods 4 and 5 almost equal in length to pereopod 3, but slightly stouter. Abdomen dorsally smooth, the sixth segment at least twice the length of the fifth. Appendix masculina of pleopod 2 of the male shorter and stouter than the appendix interna. Telson with two pairs of minute lateral spines ending in three pairs of spines, the submedian pair being the longest.

Previous records and distribution

East Indies, in region of Makassar Straits.

Material

A total of about 90 specimens from the following stations was obtained: A191, A192, A193, A315, A316, A317, A318, A319, A321, A322.

The carapace lengths of ovigerous females varied between 11 and 12.5 mm.

Remarks

De Man (1920) distinguishes *Pontophilus occidentalis* Faxon from its variety *indica* by its smaller size (48 mm as against 73 mm), the almost microscopical size of the anterior gastric spine and the length of the abdomen. In *occidentalis* the abdomen is two and a half times the length of the carapace, while in *occidentalis* var. *indica* it is three times the carapace length. De Man (1920) noted that the closely related species *gracilis* Smith, *abyssi* Smith, *challengeri* Ortmann, *junceus* Bate, *profundus* Bate, *occidentalis* Faxon, and *occidentalis* var. *indica* de Man, might prove to be geographical races of a widely distributed species. It certainly is difficult to distinguish between the species and its variety. In all the present specimens, the first gastric spine is always smaller than the second (characteristic of the variety). The ratio between carapace length and abdominal length is very variable, being anything from 2.2 to 3. This criterion is thus not reliable in distinguishing the variety from the species. The largest specimen had an overall length of 53.1 mm, only slightly larger than de Man's limit of 48 mm. This is the first record of the species from the South African region. *Pontophilus gracilis* Smith, known from off the Cape Peninsula, has been recorded from depths of 190, 250, 470 fms (370, 490, 925 m), while the present species has been taken from depths of 2525-3440 m.

SUMMARY

A collection of deep-sea decapod Crustacea from west of Cape Point, South Africa, in depths between 1098 and 3440 metres, is described. The collection includes approximately 480 specimens of 35 species, of which 3 are new species and 12 are new records.

ACKNOWLEDGEMENTS

The trawling was done by courtesy of the Director, Division of Sea Fisheries, Cape Town, to whom we are very grateful.

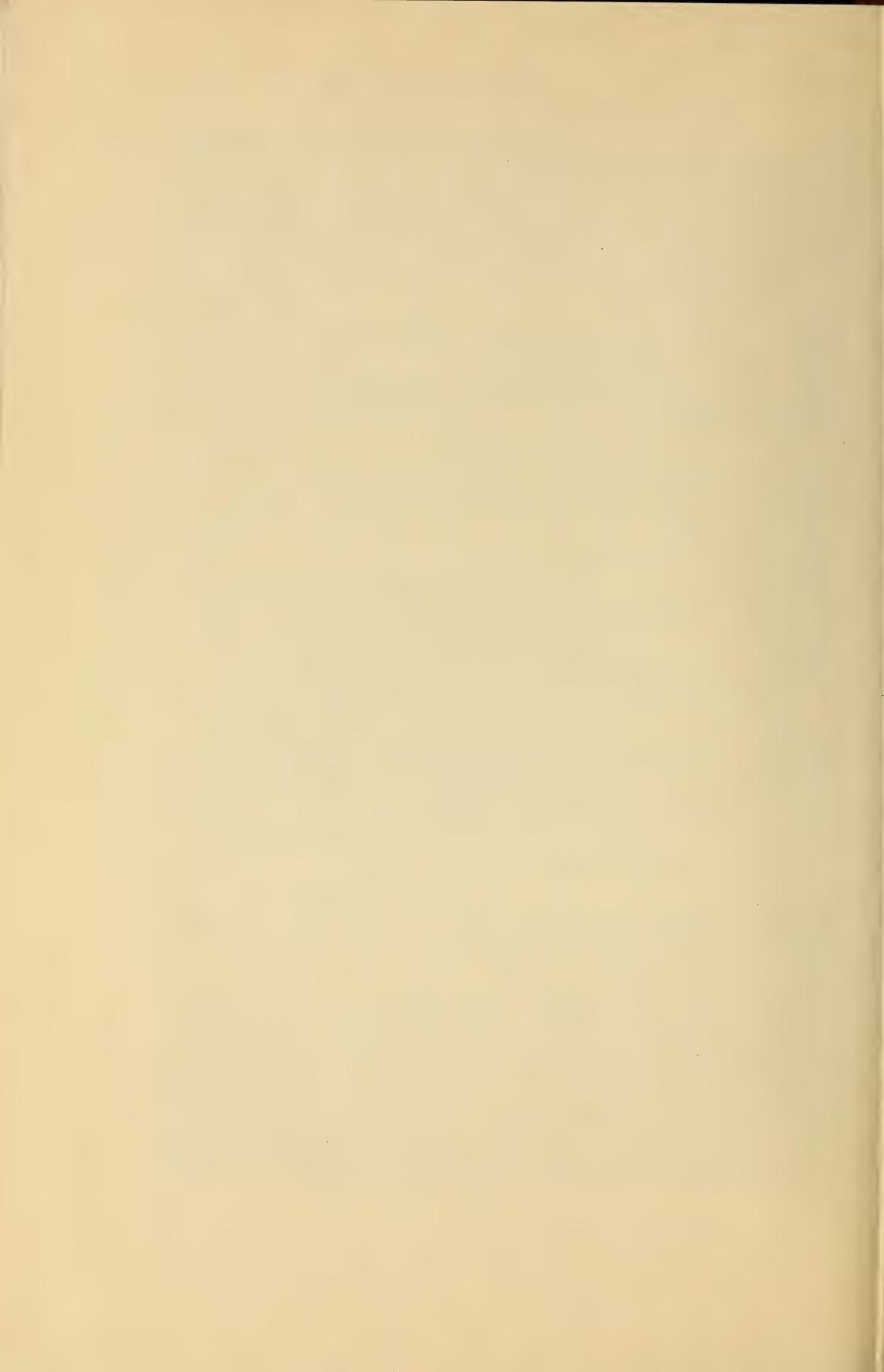
I am indebted to Dr. M.-L. Penrith of the South African Museum for reading the manuscript and for making constructive criticisms and suggestions throughout the preparation of this work.

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

REFERENCES

- BALSS, H. 1925. Macrura der Deutschen Tiefsee-Expedition. 2. Natantia, Teil A. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **20**: 217-315.
- BALSS, H. 1927. Macrura der Deutschen Tiefsee-Expedition. 3. Natantia, Teil B. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **23**: 247-275.
- BARNARD, K. H. 1947. Descriptions of new species of South African decapod Crustacea, with notes on synonymy and new records. *Ann. Mag. nat. Hist.* (11) **13**: 361-392.
- BARNARD, K. H. 1950. Descriptive catalogue of South African decapod Crustacea. *Ann. S. Afr. Mus.* **38**: 1-837.
- BATE, C. S. 1881. On the Penaeidae. *Ann. Mag. nat. Hist.* (5) **8**: 169-196.
- BATE, C. S. 1888. Report on the Crustacea Macrura collected by H.M.S. *Challenger* during the years 1873-1876. *Rep. Voy. Challenger*, 1873-1876 **24**: 1-942.
- BELLOC, G. & LORILLOU, C. 1961. Catalogue des types de décapodes du Musée océanographique de Monaco. *Bull. Inst. oceanogr. Monaco* no. 1212: 1-19.
- BENEDICT, J. E. 1903. Descriptions of a new genus and forty-six new species of crustaceans of the family Galatheididae with a list of the known marine species. *Proc. U.S. natn. Mus.* **26**: 243-334.
- BERNARD, F. 1953. Decapoda Eryonidae (*Eryoneicus* et *Willemoesia*). *Dana Rep.* **6** (37): 1-93.
- BOUVIER, E. L. 1905. Sur les palinurides et la eryonides recueillies dans l'Atlantique oriental par les expéditions françaises et monagasques. *C.r. hebdom. Séanc. Acad. Sci., Paris* **140**: 479-482.
- BOUVIER, E. L. 1917. Crustacés décapodes (macroures marcheurs). *Résult. Camp. scient. Prince Albert I* **50**: 1-140.
- BOUVIER, E. L. 1922. Observations complémentaires sur les crustacés décapodes (abstraction faite des carides), provenant des campagnes de S.A.S. le Prince de Monaco. *Résult. Camp. scient. Prince Albert I* **62**: 1-103.
- BURKENROAD, M. D. 1936. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. *Bull. Bingham oceanogr. Coll.* **5** (2): 1-51.
- BURKENROAD, M. D. 1937. The Templeton Crocker Expedition. 12. Sergestidae (Crustacea decapoda) from the lower Californian region, with descriptions of the two new species and some remarks on the organs of Pesta in *Sergestes*. *Zoologica, N.Y.* **22**: 315-329.
- CALMAN, W. T. 1925. On the macrurous decapod Crustacea collected in South African waters by the s.s. 'Pickle'. *Rep. Fish. mar. biol. Surv. Un. S. Afr.* 4 Spec. Report 3: 1-26.
- CHACE, F. A. 1936. Revision of the bathypelagic prawns of the family Acanthephyridae with notes on a new family Gomphonotidae. *J. Wash. Acad. Sci.* **26**: 24-31.
- CHACE, F. A. 1940. The plankton of the Bermuda Oceanographic Expedition. 9. The bathypelagic caridean Crustacea. *Zoologica, N.Y.* **25**: 117-209.
- CHACE, F. A. 1942. Report on the scientific results of the Atlantis Expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. *Torreia* **11**: 1-106.
- DOFLEIN, F. & BALSS, H. 1926. Die Galatheiden der Deutschen Tiefsee-Expedition. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'* **20**: 1-184.
- FAXON, W. 1893. Reports on the dredging operations off the west coast of central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer 'Albatross' during 1891, Lieut. Commander Z. L. Tanner, U.S.N. commanding. *Bull. Mus. comp. Zool. Harv.* **24**: 149-220.
- FAXON, W. 1895. Reports on an exploration of the west coasts of Mexico, central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer 'Albatross' during 1891, Lieut. Commander Z. L. Tanner, U.S.N. commanding. The stalk-eyed Crustacea. *Mem. Mus. comp. Zool. Harv.* **18**: 1-292.
- GORDON, I. 1935. New or imperfectly known species of Crustacea Macrura. *J. Linn. Soc. Zool.* **39**: 307-351.
- GORDON, I. 1939. A new species of *Sergestes* (Crustacea, Decapoda) from the South Atlantic. *Ann. Mag. nat. Hist.* (11) **4**: 498-509.
- GRINDLEY, J. R. & PENRITH, M. J. 1965. Notes on the bathypelagic fauna of the seas around South Africa. *Zool. afr.* **1**: 275-295.
- HANSEN, H. J. 1896. On the development and the species of the crustaceans of the genus *Sergestes*. *Proc. zool. Soc. Lond.* **1896**: 936-970.

- HANSEN, H. J. 1903. On the Crustacea of the genera *Petalidium* and *Sergestes* from the 'Challenger' with an account of luminous organs in *Sergestes challengeri* n.sp. *Proc. zool. Soc. Lond.* **1903**: 52-79.
- HANSEN, H. J. 1922. Crustacés décapodes (Sergestides) provenant des campagnes des yacht *Hirondelle* et *Princesse-Alice* (1885-1915). *Résult. Camp. scient. Prince Albert* **1** **64**: 1-232.
- HOLTHUIS, L. B. 1955. The recent genera of the caridean and stenopodidean shrimps (class Crustacea, order Decapoda, supersection Natantia) with keys for their determination. *Zool. Verh., Leiden* **26**: 1-157.
- KEMP, S. 1909. The decapods of the genus *Gennadas* collected by H.M.S. 'Challenger'. *Proc. zool. Soc. Lond.* **11**: 718-730.
- KEMP, S. 1910. The decapod Natantia of the coasts of Ireland. *Scient. Invest. Fish. Brch Ire.* 1908 (1): 1-190.
- KEMP, S. 1939. On *Acanthephyra purpurea* and its allies (Crustacea, Decapoda, Hoplophoridae). *Ann. Mag. nat. Hist. (11)* **4**: 568-579.
- KRÖYER, H. 1855. Bidrag til kundskab om brebsdyrslaegten *Sergestes*. *Over. K. danske Vidensk. Selsk. Forh.* **1855**: 22-23.
- MAN, J. G. de. 1918. Diagnoses of new species of macrurous decapod Crustacea from the Siboga Expedition. *Zool. Meded. Leiden* **4**: 159-166.
- MAN, J. G. de. 1920. The Decapoda of the Siboga Expedition. *Siboga Exped. monogr.* 39 a³: 1-320.
- MARTENS, E. von. 1868. Ueber einige ostasiatischen Süsswasserthiere. II. Crustacea. *Arch. Naturgesch.* **34**: 1-64.
- MILNE-EDWARDS, A. 1880. Études préliminaires sur les crustacés. I. *Bull. Mus. comp. Zool. Harv.* **8**: 1-67.
- MILNE-EDWARDS, A. 1930 after 1883. *Recueil de figures de Crustacés nouveau ou peu connus*. Paris.
- MILNE-EDWARDS, A. 1930. Description des genres *Glaucothoe*, *Sicyonie*, *Sergeste* et *Acète* de l'ordre des crustacés décapodes. *Annl. Sci. nat. Zool.* **19**: 333-352.
- MILNE-EDWARDS, A. & BOUVIER, E. L. 1894. Considerations générales sur la famille des Galatheides. *Annl. Sci. nat. Zool.* (7) **16**: 191-327.
- ORTMANN, A. 1893. Decapoden und Schizopoden der Plankton-Expedition. *Ergeb. Atlant. Ozean Planktonexped. Humboldt-Stift.* **2**: 1-210.
- PESTA, O. 1918. *Die Decapodenfauna der Adria. Versuch einer Monographie*. Leipzig & Wien. (not seen).
- PESTA, O. 1918. *Die Decapodenfauna der Adria. Versuch einer Monographie*. Leipzig & Wien.
- SIVERTSEN, E. & HOLTHUIS, L. G. 1956. Crustacea Decapoda (the Penaeidae and Stenopodidae excepted). *Rep. scient. Results Michael Sars. N. Atlant. deep Sea Exped.* **5** (12): 1-54.
- SMITH, S. I. 1882. Reports on the results of dredgings, under the supervision of Alexander Agassiz, on the east coast of the United States, during the summer of 1880, by the U.S. Coast Survey Steamer 'Blake', Commander J. R. Bartlett, U.S.N. commanding. Report on the Crustacea. Part I. Decapoda. *Bull. Mus. comp. Zool. Harv.* **10**: 1-108.
- SMITH, S. I. 1884. Crustacea of the 'Albatross' dredgings in 1883. *Rep. U.S. Commr. Fish.* **1882**: 356.
- SMITH, S. I. 1885. On some new or little known Decapoda Crustacea from recent fish commission dredgings off the east coast of the United States. *Proc. U.S. natn. Mus.* **7**: 493-511.
- STEBBING, T. R. R. 1905. South African Crustacea, part 3. *Mar. Invest. S. Afr.* **3**: 21-120.
- STEBBING, T. R. R. 1908. South African Crustacea, part 4. *Ann. S. Afr. Mus.* **6**: 1-96.
- STEBBING, T. R. R. 1910. General catalogue of the South African Crustacea (part 5). *Ann. S. Afr. Mus.* **6**: 281-293.
- STEBBING, T. R. R. 1914. South African Crustacea (part 7). *Ann. S. Afr. Mus.* **15**: 1-55.
- STEBBING, T. R. R. 1915. South African Crustacea (part 8). *Ann. S. Afr. Mus.* **15**: 57-104.
- STEBBING, T. R. R. 1917. South African Crustacea (part 9). *Ann. S. Afr. Mus.* **17**: 23-46.
- SUND, O. 1920. The 'Challenger' Eryonidae (Crustacea). *Ann. Mag. nat. Hist.* (9) **6**: 220.
- TIRMIZI, N. M. 1960. Crustacea, Penaeidae, part 2. Series Benthescymae. *Scient. Rep. John Murray Exped.* **10**: 319-383.
- WILLEMOES-SUHM, R. von. 1873. In Thomson, C. W. Notes from the 'Challenger'. *Nature, Lond.* **8**: 51.
- YALDWYN, J. C. 1957. Deep water Crustacea of the genus *Sergestes* (Decapoda Natantia) from Cook Strait, New Zealand. *Zoology Publs. Vict. Univ. Wellington* **22**: 1-27.



INSTRUCTIONS TO AUTHORS

MANUSCRIPTS

In duplicate (one set of illustrations), type-written, double spaced with good margins, including TABLE OF CONTENTS and SUMMARY. Position of text-figures and tables must be indicated.

ILLUSTRATIONS

So proportioned that when reduced they will occupy not more than $4\frac{3}{4}$ in. = 7 in. ($7\frac{1}{2}$ in. including the caption). A scale (metric) must appear with all photographs.

REFERENCES

Authors' names and dates of publication given in text; full references at end of paper in alphabetical order of authors' names (Harvard system). References at end of paper must be given in this order:

Name of author, in capitals, followed by initials; names of joint authors connected by &, not 'and'. Year of publication; several papers by the same author in one year designated by suffixes a, b, etc. Full title of paper; initial capital letters only for first word and for proper names (except in German). Title of journal, abbreviated according to *World list of scientific periodicals* and underlined (italics). Series number, if any, in parenthesis, e.g. (3), (n.s.), (B.). Volume number in arabic numerals (without prefix 'vol.'). with wavy underlining (bold type). Part number, only if separate parts of one volume are independently numbered. Page numbers, first and last, preceded by a colon (without prefix 'p'). Thus:

SMITH, A. B. 1956. New *Plonia* species from South Africa. *Ann. Mag. nat. Hist.* (12) **9**: 937-945.

When reference is made to a separate book, give in this order: Author's name; his initials; date of publication; title, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; place of publication; name of publisher. Thus:

BROWN, X. Y. 1953. *Marine faunas*. 2nd ed. **2**. London: Green.

When reference is made to a paper forming a distinct part of another book, give: Name of author of paper, his initials; date of publication; title of paper; 'In', underlined; name of author of book; his initials; title of book, underlined; edition, if any; volume number, if any, in arabic numerals, with wavy underlining; pagination of paper; place of publication; name of publisher. Thus:

SMITH, C. D. 1954. South African *Plonias*. In Brown, X. Y. *Marine faunas*. 2nd ed. **3**: 63-95. London: Green.

SYNONYMY

Arranged according to chronology of names. Published scientific names by which a species has been previously designated (subsequent to 1758) are listed in chronological order, with abbreviated bibliographic references to descriptions or citations following in chronological order after each name. Full references must be given at the end of the paper. Articles and recommendations of the *International code of zoological nomenclature adopted by the XV International congress of zoology, London, July 1958*, are to be observed (particularly articles 22 and 51).

Examples: *Plonia capensis* Smith, 1954: 86, pl. 27, fig. 3. Green, 1955: 23, fig. 2.

When transferred to another genus:

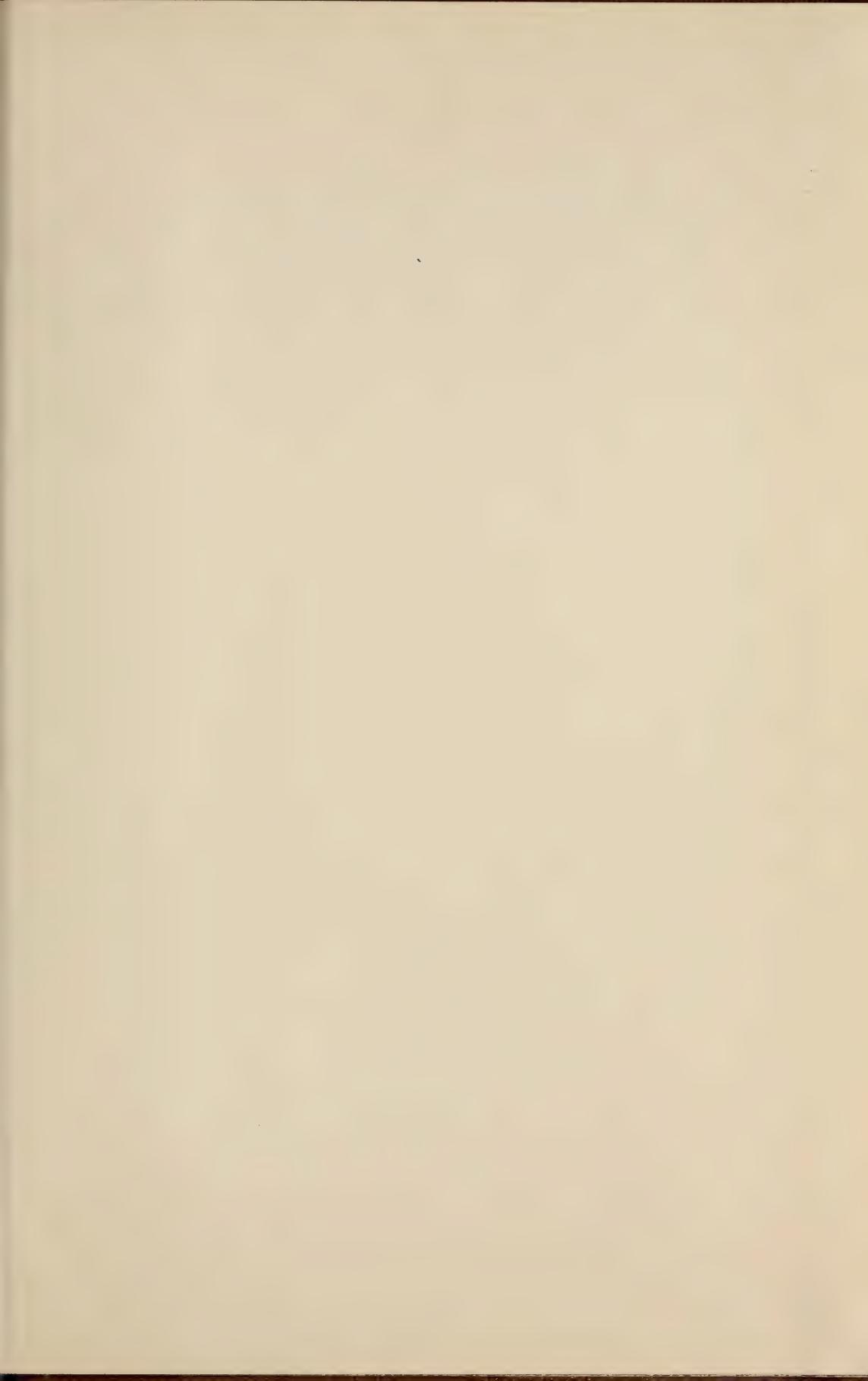
Euplonia capensis (Smith) Brown, 1955: 259.

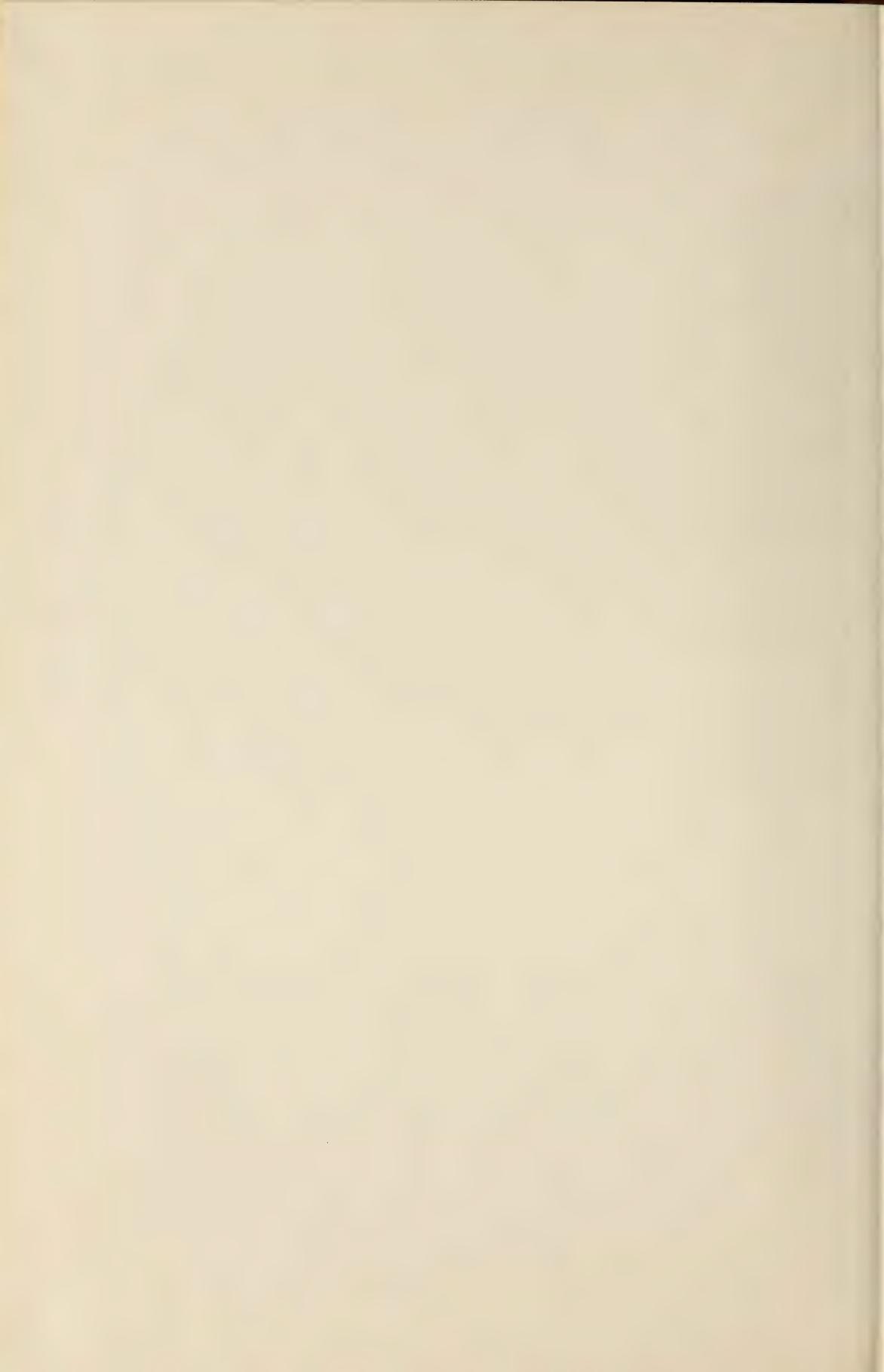
When misidentified as another species:

Plonia natalensis (non West), Jones, 1956: 18.

When another species has been called by the same name:

[non] *Plonia capensis*: Jones, 1957: 27 (= *natalensis* West).









SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01206 6031