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N. A. H. MILLARD

THE HYDROZOA OF THE SOUTH AND WEST COASTS OF SOUTH AFRICA

PART II. THE LAFOEIDAE, SYNTHECIIDAE AND SERTULARIIDAE

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THE HYDROZOA OF THE SOUTH AND WEST COASTS OF SOUTH AFRICA

PART II. THE LAFOEIDAE, SYNTHECIIDAE AND SERTULARIIDAE

By

N. A. H. MILLARD

Zoology Department, University of Cape Town

(With 16 figures in the text)

CONTENTS

INTRODUCTION

This paper represents the second part of a systematic account of the hydroids of the south and west coasts of South Africa. The first part, dealing with the Plumulariidae, appeared in these *Annals*, vol. 46, 1962. The scope of the work and the source of the material were detailed in the introduction to Part I, and need not be repeated here.

As before the details of the collecting stations are given in the station list which follows, and only the catalogue numbers are quoted in the systematic account. Occasional records which do not come from the south or west coast, but which have been mentioned for some special reason, have been put between brackets.

The author wishes to acknowledge the help of all those bodies or individuals who have helped materially or financially to build up the very extensive collection now present in the University of Cape Town, and also the South African Museum for access to the material dredged by the s.s. *Pieter Faure*. Acknowledgements are also due to the British Museum of Natural History for permission to examine material housed there, and to the Munich Museum for the loan of mounted slides.

Type specimens of new species have been deposited in the South African Museum and have been given a Museum registered number in addition to the University catalogue number.

The Trustees of the South African Museum acknowledge with thanks receipt of grants from the University of Cape Town and the Council for Scientific and Industrial Research towards the cost of publication.

Ann. S. Afr. Mus. **48** (1), 1964: 1–56, 16 figs.

STATION LIST

A. Littoral material from Oudekraal on the west coast of the Cape Peninsula. Position: 33°58·5′S/18°22·2′E.

	Date
A 123	15.3.34
A 381	25.8.34
A 382	13.5.34
A 384	25.8.34

AFR. Material dredged by the government research vessel, R.S. *Africana*.

	Date	*Position*	*Depth (m.)*	*Bottom*
AFR 736	17.8.47	30°42·4′S/15°59·2′E	201	co gn S, Sh
AFR 743	21.8.47	30°2′S/15°2′E	364	gn S
AFR 835	20.11.47	?35°9′S/19°2′E	188	
AFR 866	9.1.48	34°36·8′S/19°16·4′E	38	S, R
AFR 945	19.3.48	36°25′S/21°8′E	177	S, R
AFR 1028.O	15.5.48	28°28′S/32°25·8′E	27	f S, R

B, BB. Littoral material from Lambert's Bay on the west coast. Position: 32°5′S/18°14′E.

	Date
B 105	28.7.38
B 114	29.7.38
B 137	31.7.38
BB 13	18.1.57

BMR. Bushman's River Estuary, on sand and muddy banks. Date: September, 1950. Position: 33°41′S/26°40′E. Depth: 2–4½m.

BRE. Breede River Estuary, littoral. Date: 7.7.51. Position: 34°25′S/20°51·5′E.

CP. Littoral material from various localities on the west coast of the Cape Peninsula.

	Date	*Locality*	*Position*
CP 336	12.5.49	Oudekraal	33°58·5′S/18°22·2′E
CP 379	15.4.53	Sea Point	33°55·2′S/18°22·6′E
CP 650	1.2.61	Bakoven	33°57·6′S/18°22·3′E

CPR. Material from various localities in the Cape Province.

	Date	*Locality*	*Position*	*Depth (m.)*
CPR 7	15.1.50	The Haven	32°15′S/28°57′E	littoral
CPR 9	30.4.50	Glentana Strand	34°4′S/22°20′E	littoral
CPR 46	20.6.59	Umgazi Bay	31°43′S/29°26′E	27

E. Littoral material from Port Elizabeth on the south coast. Date: 9.7.36 Position: 33°56′S/25°36′E.

KNY. Knysna Estuary, on the south coast. Date: July, 1947. Position: 34°5′S/23°4′E (average).

	Depth (m.)	*Bottom*
KNY 22	1–4	M
KNY 30	5–7	S, M
KNY 57	11·5	R
KNY 70	2–6	S
KNY 71	7	Sh, S, M

L. Littoral material from East London, on the south coast. Date: 10.7.37. Position: 33°1′S/27°54′E.

LAM. Dredged in Lambert's Bay, west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
LAM 2	16.1.57	32°4·5′S/18°18·3′E	17	S, R
LAM 7	18.1.57	32°5′S/18°17·9′E	23	R, Sh, S
LAM 9	17.1.57	32°4·7′S/18°17·7′E	23	S, Sh
LAM 13	19.1.57	32°4′S/18°18·1′E	18	R
LAM 14	18.1.57	32°5′S/18°17·7′E	17	S, Sh, R
LAM 18	18.1.57	32°4·8′S/18°17·8′E	17	R
LAM 23	17.1.57	32°4·1′S/18°18·6′E	15	S, Sh
LAM 30	19.1.57	32°5·1′S/18°17·7′E	20	R
LAM 35	19.1.57	32°5·5′S/18°17·7′E	27·5	R, Sh
LAM 40	19.1.57	32°5·5′S/18°17·6′E	28	S, Sh
LAM 41	21.1.57	32°5′S/18°17·7′E	20	S, Sh
LAM 45	21.1.57	32°5′S/18°18·2′E	8	S, R
LAM 46	22.1.57	32°4·4S/18°17·7′ E	23	R
LAM 59	23.1.57	32°9′S/18°18′E	16	S, R

LIZ. Dredged in Algoa Bay, Port Elizabeth, south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
LIZ 2	5·4·54	33°55·7′S/25°37·2′E	9·5	M
LIZ 7	6·4·54	33°58·1′S/25°38·9′E	9	St, R
LIZ 11	6·4·54	33°57·2′S/25°38′E	9·5	R, Clay
LIZ 13	6·4·54	33°58·2′S/25°38·8′E	7·5	S
LIZ 16	7·4·54	33°58·4′S/25°40·5′E	14	St
LIZ 27–40	11·4·54	34°0·8′S/25°42·4′E	6	R

MB. Dredged in Mossel Bay, south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
MB 8–12	12.1.56	34°4·3′S/22°13·9′E	19	R
MB 15	13.1.56	34°11·1′S/22°10·1′E	16	S, R
MB 24	13.1.56	34°11·1′S/22°9·9′E	19	R
MB 26	13.1.56	34°11·1′S/22°10·1′E	21	S
MB 39	16.1.56	34°10·1′S/22°8·0′E	9	R
MB 47	17.1.56	34°11·3′S/22°10·0′E	10	R
MB 52	17.1.56	34°11·0′S/22°9·9′E	14	R, S
MB 58	18.1.56	34°4·3′S/22°13·5′E	12·5	R
MB 59	18.1.56	34°4·1′S/22°13·9′E	11·5	R
MB 64	18.1.56	34°4·8′S/22°13·1′E	26	co S, Sh, R
MB 69	19.1.56	34°8·6′S/22°7·3′E	13·5	S, R
MB 72	19.1.56	34°9·1′S/22°7·2′E	12	R, S, Sh
MB 84	21.1.56	34°11·4′S/22°10·1′E	29	R
MB 88	18.1.56	34°4·8′S/22°13·1′E	26	co S, Sh, R

NAD. Dredged off Natal, east coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
NAD 1	17.5.58	30°47·1′S/30°29·1′E	44	St
NAD 22	12.8.58	29°58′S/31°2′E	49	

PP. Littoral material from Paternoster, west coast. Date: 24.9.57. Position: 32°43′S/17°55′E.

S. Littoral material from Still Bay, south coast. Date: 10.1.32. Position: 34°23′S/21°26′E.

SAMH. Material from the South African Museum. Specimens 146–350 and 374–382 were dredged by the s.s. *Pieter Faure*. Their positions were given in the original records as compass bearings off salient points on the coast, and were probably not very accurate. These have been converted into latitude and longitude and are given to the nearest minute.

	Date	*Position*	*Depth (m.)*	*Bottom*
SAMH 146	23.6.1898	South of Mossel Bay		
SAMH 151–156	15.7.1898	34°8′S/22°16′E		St
SAMH 171–172	11.11.1898	33°49′S/25°56′E		
SAMH 173–178	19.11.1898	33°45′S/26°44′E	73–78·5	M
SAMH 181	22.12.1898	32°52′S/28°12′E		
SAMH 182–192	28.12.1898	33°9′S/28°3′E	86	S, Sh, R
SAMH 204–209	7.3.1899	33°59′S/25°51′E	24–27	
SAMH 213	24.3.1899	33°50′S/26°35′E	91	M
SAMH 216–220	19.6.1899	34°26′S/21°42′E		f S
SAMH 228–232	20.9.1899	34°15′S/22°10·5′E		M
SAMH 234–237	5.7.1900	34°27′S/20°58′E	51	Crl
SAMH 246	11.10.1900	34°8′S/22°59·5′E	73	S, Sh, Crl
SAMH 251–252	15.7.1901	33°13·5′S/27°58′E	89	brk Sh
SAMH 256–272	17.7.1901	33°7′S/27°47·5′E		f S
SAMH 281–282	25.7.1901	32°50′S/28°18·5′E	86	brk Sh
SAMH 288–294	13.8.1901	32°45′S/28°26′E	53	brk Sh, St
SAMH 295	13.8.1901	32°47′S/28°28′E	82	brk Sh
SAMH 301	15.8.1901	32°42′S/28°26′E	31	R
SAMH 310–314	10.9.1901	33°54′S/26°51′E	120	brk Sh, St
SAMH 316–318	23.9.1901	34°5′S/26°34′E	115	S, Sh, bk Spks
SAMH 321	19.2.1902	34°32′S/24°27·5′E	137	S, Sh, R
SAMH 325	22.9.1904	34°12′S/22°15·5′E	51	f S
SAMH 334	4.10.1904	34°12′S/22°15·5′E	51	f S
SAMH 348	19.10.1904	34°15·5′S/22°14′E	64	M
SAMH 350	22.8.1905	33°52′S/26°9′E		M
SAMH 358–359	19.6.1914	33°55′S/18°27′E		
SAMH 374–382	15.3.1899	33°47′S/26°19′E	18–29	S, Sh, St
SAMH 403	–.4.1962	28°37′S/16°25′E	10–20	
SAMH 409	–.10.1962	28°37′S/16°25′E	10–20	

SB. Saldanha Bay, west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
SB 150–168	–.9.57	33°2·5′S/18°2′E	littoral	R
SB 194	1.5.59	33°3·5′S/17°59·2′E	20	R, S
SB 253	22.4.62	33°3′S/17°56·6′E	35	f kh S

SCD. Dredged off the south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
SCD 3	18.4.58	34°30′S/24°40′E	102	R
SCD 5	19.4.58	34°15′S/25°5′E	11	R, Sh
SCD 29	22.6.58	33°38·6′S/26°54·7′E	56	R
SCD 33	21.5.58	35°3′S/27°56·2′E	65	S, Sh
SCD 36–37	19.5.58	32°15·2′S/28°57·7′E	49·5	R
SCD 50	18.5.58	31°38·8′S/29°34·4′E	33	R
SCD 52	20.8.58	34°1′S/25°45·5′E	46	R
SCD 56	19.8.58	33°37′S/26°56·6′E	46	
SCD 60	16.8.58	33°2′S/27°56·2′E	46	
SCD 61	15.8.58	32°17·7′S/28°54·5′E	49	
SCD 75	16.7.59	32°33′S/28°38′E	55	S, M
SCD 79	16.7.59	32°43′S/28°28′E	58	St, Sh

	Date	*Position*	*Depth* (*m.*)	*Bottom*
SCD 82	17.7.59	33°3·7′S/27°54·7′E	51	br S, Sh
SCD 84–85	17.7.59	33°3′S/27°55′E	27	R
SCD 94	20.7.59	33°55·5′S/25°51′E	46	bk M, S
SCD 96	20.7.59	34°21′S/25°41′E	110	Sh
SCD 101	21.7.59	34°33′S/24°1′E	131	R
SCD 103	22.7.59	35°7′S/22°15′E	119	S
SCD 104	23.7.59	34°33′S/21°28′E	67	co S, brk Sh
SCD 106	23.7.59	34°35′S/21°10′E	67	
SCD 108	23.7.59	34°35′S/21°11′E	75	co S, Sh, St
SCD 112	20.7.59	33°55·5′S/25°51′E	46	bk M, S
SCD 113	26.11.59	34°24′S/21°45′E	27	S, f Sh
SCD 114	26.11.59	34°29′S/21°49·5′E	73	gr–gn M
SCD 115	26.11.59	34°54·4′S/22°12·2′E	106	co S, Sh
SCD 117–118	14.2.60	34°24′S/21°46′E	18	R
SCD 119	14.2.60	34°33′S/21°52′E	77	kh S
SCD 122	14.2.60	34°40·5′S/22°0′E	93	kh S
SCD 126	3.6.60	34°26·5′S/21°48′E	67	bk M
SCD 138	28.8.60	34°35′S/21°56′E	77	co & f S
SCD 141	28.8.60	34°46′S/22°5′E	93	kh S
SCD 145	28.8.60	34°46′S/22°5′E	93	kh S
SCD 153–154	25.11.60	34°3′S/25°59′E	84	R
SCD 169	24.11.60	33°58·9′S/25°41·4′E	4–11	R
SCD 175	30.11.60	34°20′S/23°31′E	110	R, kh S
SCD 179	24.11.60	33°58·9′S/25°41·4′E	4–11	R
SCD 184	25.11.60	34°23′S/26°1′E	137	co S, brk Sh
SCD 191	29.11.60	34°4·3′S/23°25·8′E	47	gn M
SCD 206	30.11.60	34°51′S/23°41′E	182	kh S
SCD 219–239	29.11.60	34°2′S/23°28·4′E	49	S, R, M
SCD 250	30.11.60	34°48′S/23°39′E	148	R
SCD 254	16.7.61	33°7·3′S/28°1′E	88	Crl, R
SCD 258	14.7.61	33°53·8′S/25°42·5′E	32	f gr–bl S
SCD 265	14.7.61	33°48′S/25°47′E	27	bl M, R
SCD 276	14.7.61	33°53·8′S/25°42·5′E	32	f gr–bl S
SCD 284	6.2.62	33°1′S/27°55′E	7	f wh S
SCD 290	6.2.62	33°4′S/27°57′E	84	co S, Sh
SCD 296–297	6.2.62	33°9′S/28°2′E	84	
SCD 301	6.2.62	33°39′S/27°15′E	88	S
SCD 304–305	8.2.62	34°0′S/25°53′E	46	R
SCD 320–322	9.2.62	34°15′S/25°50·5′E	108	R, f S
SCD 324	9.2.62	34°27′S/25°57′E	172	M, S
SCD 330	11.2.62	34°3·5′S/23°23′E	11–18	f S
SCD 345	12.2.62	34°16′S/22°17′E	73	kh S, M
SCD 354	11.10.62	32°8′S/29°12′E	210	

TB. Material dredged from Table Bay, Cape Town.

	Date	*Position*	*Depth* (*m.*)	*Bottom*
TB 1	11.2.47	33°47·5′S/18°24·3′E	19–20	S, Sh, St
TB 10	11.2.47	33°50·5′S/18°25·8′E	27	R
TB 11	25.10.46	33°52′S/18°28′E	15·5	S
TB 12	11.2.47	33°47·5′S/18°24′E	19–20	Sh, St
TB 21	15.12.57	33°48·6′S/18°24·6′E	15	St, brk Sh, S

TRA. Material collected by commercial trawlers.

	Date	*Position*	*Depth* (*m.*)	*Bottom*
TRA 23	9.11.47	34°49′S/20°21·5′E	c. 91·5	
TRA 33	20.7.49	34°55′S/21°10′E	c. 90	S, R
TRA 35	21.1.50	34°34′S/20°50′E	70	M, S

	Date	*Position*	*Depth (m.)*	*Bottom*
TRA 37	–.7.50	34°30′S/20°50′E	73	M, S
TRA 38	–.7.50	34°30′S/20°56′E	73	M, S
TRA 42	–.7.51	34°30′S/20°55′E	70	M, St
TRA 56	28.11.52	34°40′S/21°35′E	73	R, S
TRA 59	26.11.52	34°28′S/21°45′E	70	S, St
TRA 92	–.1.54	35°3′S/21°50′E	110	S, R
TRA 151	6.3.58	34°51′S/19°55′E	22	R
TRA 156	15.10.58	34°12′S/18°22′E	18–27	Cable
TRA 159	6.7.58	33°56′S/25°36′E		Turtle

WCD. Dredged off west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
WCD 1	25.2.59	34°9·8′S/18°16·5′E	78	R
WCD 7	24.3.59	34°9·3′S/18°17·5′E	43	R
WCD 12	24.3.59	34°9·4′S/18°16·5′E	75	R
WCD 18	29.4.59	33°5·6′S/17°54·5′E	64	kh M
WCD 30	15.12.59	34°10·5′S/18°14·3′E	126	R
WCD 34	15.12.59	34°11·2′S/18°20·2′E	27	R
WCD 56	21.9.60	32°4·6′S/18°18′E	18	S, R
WCD 81	15.9.49	34°5′S/18°21′E	11	S
WCD 100	2.7.61	32°5·5′S/18°17·3′E	27	S, Sh

List of species

Family **Lafoeidae**

Acryptolaria conferta (Allman, 1877)
Filellum antarcticum (Hartlaub, 1904)
Hebella furax Millard, 1957
Hebella scandens (Bale, 1888)
Hebella urceolata n. sp.
Lafoea fruticosa M. Sars, 1851
Scandia mutabilis (Richie, 1907)
Zygophylax africana Stechow, 1923
Zygophylax armata (Ritchie, 1907)
Zygophylax cornucopia Millard, 1955
Zygophylax enigmatica n. sp.
Zygophylax sibogae Billard, 1918

Family **Syntheciidae**

Hincksella cylindrica (Bale, 1888)
Synthecium dentigerum Jarvis, 1922
Synthecium ?elegans Allman, 1872
Synthecium hians Millard, 1957

Family **Sertulariidae**

Amphisbetia bidens (Bale, 1884)
Amphisbetia minima (Thompson, 1879)
Amphisbetia operculata (Linn., 1758)
Crateritheca acanthostoma (Bale, 1882)
Dictyocladium coactum Stechow, 1923
Diphasia tetraglochina Billard, 1907
Dynamena cornicina McCrady, 1858
Dynamena crisioides Lamx., 1824
Dynamena quadridentata (Ell. & Sol., 1786)
Salacia articulata (Pallas, 1766)
Salacia disjuncta n. sp.
Sertularella africana Stechow, 1919
Sertularella agulhensis n. sp.
Sertularella arbuscula (Lamx., 1816)
Sertularella capensis Millard, 1957
Sertularella congregata n. sp.
Sertularella dubia Billard, 1907
Sertularella falsa Millard, 1957
Sertularella flabellum (Allman, 1886)
Sertularella fusiformis (Hincks, 1861)
Sertularella gilchristi n. sp.
Sertularella goliathus Stechow, 1923
Sertularella mediterranea Hartlaub, 1901
Sertularella megista Stechow, 1923
Sertularella polyzonias (Linn., 1758)

Sertularella pulchra Stechow, 1923
Sertularella striata Stechow, 1923
Sertularella xantha Stechow, 1923
Sertularia distans (Lamx., 1816)
Sertularia marginata (Kirch., 1864)
Sertularia turbinata (Lamx., 1816)
Symplectoscyphus arboriformis (Markt., 1890)
Symplectoscyphus macrogonus (Treb., 1928)
Thyroscyphus aequalis Warren, 1908

Family **Lafoeidae**

Acryptolaria conferta conferta (Allman, 1877)

Fig. 1 A–C, E

Cryptolaria conferta Allman, 1877: 17, pl 12 (figs. 6–10).
Acryptolaria conferta: Totton, 1930: fig. 19a. Leloup, 1937: 29, fig. 19.

Records. West coast: AFR 736Y. South Coast: SCD 101G.

Description. Colonies reaching a maximum height of 3·9 cm. Stem fascicled except for the terminal branches, but slender and flexible; branching in a roughly alternate manner and roughly in one plane, but on the whole very irregular in appearance.

Hydrotheca adnate to stem or branch for over half height; adcauline wall approximately straight and parallel with axis of stem in lower part of adnate section, curving outwards in upper part of adnate section and in free section; abcauline wall usually slightly convex opposite base of adcauline wall, curving evenly outwards beyond this; margin slightly everted. Base of adcauline wall of hydrotheca always above level of top of adnate part of the one below. Diameter at margin approximately $1\frac{1}{2}$ to $2\frac{1}{3}$ times that at base.

Free, solitary hydrothecae also present, arising separately from hydrorhiza or from epizootic stolons creeping over the surface of mature stems. These hydrothecae erect, at right angles to stolon, widening to margin which is slightly everted, quite symmetrical or (more often) somewhat irregular in shape.

No coppiniae.

Measurements. See under subspecies *australis*.

Remarks. Both these colonies are growing on the surface of worm-tubes, and include stems in various stages of development. Certain observations on the method of growth were thus possible.

The hydrorhiza forms a branching reticulum giving off solitary hydrothecae and upright stems. In a young upright stem the first hydrotheca and the hydrocaulus arise separately and side by side from the hydrorhiza (fig. 1C). It appears thus that in the development of the colony a solitary hydrotheca is produced first, and that this is followed by the growth of a separate tube of the hydrorhiza past it, and in contact with it, to become the hydrocaulus of the stem. The development of the rest of the stem proceeds by a method of

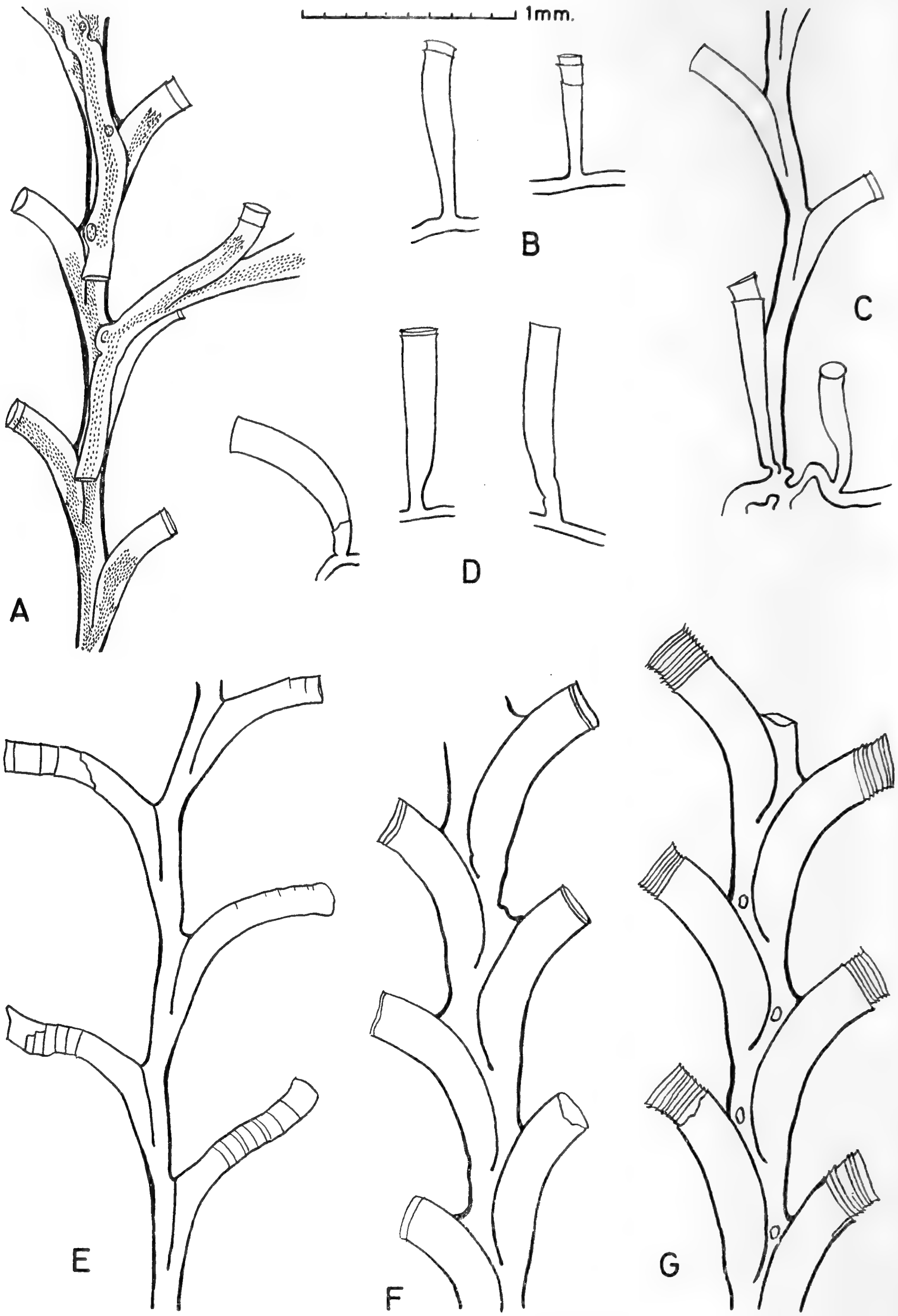

Fig. 1. *Acryptolaria conferta* (Allman).

A. Part of the stem from AFR 736Y, to show branching. Portions of the peripheral tubes in position.
B. Solitary hydrothecae from AFR 736Y.
C. Solitary hydrotheca and young stem from AFR 736Y, to show origin.
D. Subsp. *australis*, solitary hydrothecae from SCD 175N.
E.–G. A few hydrothecae from SCD 101G, SCD 101F and SCD 175N respectively. The last two are included in subsp. *australis*.

sympodial growth. At a later stage the superficial tubes are developed as branches from the hydrocaulus arising opposite the top of the adnate part of the hydrothecae, and remaining in communication with it by a series of connexions in this position. Branches arise in the same position as the accessory tubes and are in cytoplasmic continuity with both the coenosarc of the stem and that of the accessory tube.

The free hydrothecae which are often present on the surface of older stems appear to belong mostly to young epizootic colonies growing on the surface of older ones.

These solitary hydrothecae are similar to those produced by various species of *Lafoea* (e.g. *L. dumosa* (Fleming), *L. gracillima* (Alder) and *L. fruticosa* M. Sars) and are almost identical with them. They also resemble hydrothecae of the creeping *L. tenellula* Allman, which is included by some authorities in *L. dumosa*. It is evident, thus, that extreme care should be taken in assigning such stolonic colonies to a particular species unless the branching form is present as well. For example, the *L. tenellula* described by Stechow in 1925 (p. 453, fig. 23) was growing on a colony of *Acryptolaria humilis* Allman and is probably the creeping form of that species.

The general appearance of the colonies described above resembles Allman's figure (pl. 12, fig. 6), and the shape of the hydrotheca resembles that illustrated by Totton (fig. 19a) from Madeira and by Leloup (fig. 19B) from French Indo-China. The measurements are in range of those quoted by most authors.

This is the first record of the species from South Africa.

Acryptolaria conferta australis Ritchie, 1911

Fig. 1D, F, G

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.

Records. South coast: AFR 835E. SCD 101F, 103F, 175N.

Description. Several colonies, the largest reaching a height of 11 cm. Stem fascicled, stiff and rather woody; branching alternate and always in one plane; branches variable in length, generally arising next to every third hydrotheca of the stem and often rebranching, those on the same side being separated by a distance of 3–4 mm. Branches often anastomosing.

Hydrotheca adnate to stem or branch for over half height; adcauline wall convex throughout; abcauline wall curved gracefully outwards, the curvature being more marked in the distal half. Hydrothecae overlapping, with base of adcauline wall always below level of top of adnate part of the hydrotheca below. Diameter at margin approximately 1½ to 2¼ times that at base.

Free hydrothecae also present in SCD 175N, arising from epizootic stolons.

No coppiniae.

Measurements (mm.)	*A. conferta australis*		*A. conferta conferta*	
	AFR 835E	SCD 175N	AFR 736Y	SCD 101G
Hydrotheca, length adcauline, adnate part	0·75–0·95	0·67–0·85	0·37–0·49	0·33–0·45
*length adcauline, free part	0·20–0·72	0·27–0·55	0·24–0·55	0·12–0·75
diameter at base	0·11–0·13	0·11–0·14	0·065–0·10	0·06–0·09
diameter at margin	0·19–0·23	0·23–0·26	0·135–0·16	0·13–0·15
diameter, margin/base	1·54–1·92	1·64–2·18	1·40–2·29	1·67–2·33
Solitary hydrotheca,† length		0·71–1·27	0·43–0·82	0·57–0·61
diameter at margin		0·16–0·20	0·115–0·15	0·12–0·15

*Including rejuvenated margins.
†Without rejuvenated margins.

Remarks. This material shows the distinctive characters of subspecies *australis*, namely the overlapping hydrothecae and the characteristic thecal shape. It differs markedly from the material which has been assigned to the nominal subspecies in its growth-form, which is stiffer and more regular, and in the measurements of its component parts, which are larger, though the proportions are similar. Neither of the last two characters are necessarily of systematic value, but it is difficult to assess the variability until more material is available.

Filellum antarcticum (Hartlaub, 1904)

Filellum ?antarcticum: Millard, 1958: 175.

Records. South coast: ?AFR 835Z. MB 69C. ?SCD 175R.

Description. The second sample, growing on a polyzoan, bears the remains of a coppinia in a somewhat dilapidated condition. However, the accessory tubes are clearly visible; they are usually forked at the end (in one case twice), occasionally simply truncated, but never curved as in *F. serpens*. The other samples bear no coppiniae.

Measurements (mm., in MB 69C).

Hydrotheca, length of free part, without reduplications	0·18–0·30
diameter at margin	0·10–0·12

Remarks. The structure of the accessory coppinial tubes in MB 69C establishes with certainty the presence of this species in South Africa for the first time. The identity of unfertile samples is doubtful. Stechow (1925, p. 458) has reported the presence of the closely related *F. serpens* in South Africa, but since his specimens were unfertile, these records are also subject to doubt.

Hebella furax Millard, 1957

Fig. 2B–D

Hebella furax Millard, 1957: 200, fig. 8.

Records. South coast: MB 15B, 24T, 26E, 39W, 47K, 72G. SAMH 256, 301. SCD 37U, 84Z, 117R, 179B.

Description. Colonies epizootic on *Lytocarpus filamentosus* (Lamarck), *Thecocarpus* *formosus* (Busk) and *T. flexuosus solidus* Millard. Very few parasitic hydrothecae present among these samples.

Hydrothecae similar to those previously described, though a few are a little shorter and thus the proportion of length/diameter is less.

Gonothecae (described for the first time) borne on hydrorhiza, not sharply demarcated from pedicel, widening towards distal end, often curved towards one side, with smooth or slightly corrugated walls. Pedicel with 2–5 spiral annulations. Containing several medusa-buds in various stages of development. The young gonotheca is closed distally by a slightly convex operculum, which tends to crumple in microscopic preparations, but has no valves. In the ripe gonotheca the operculum is absent and the margin usually everted.

Oldest medusa about 0·4 mm. deep and 0·25 mm. wide, with at least 2 long, spirally coiled, marginal tentacles and a 4-lipped mouth.

Length of gonotheca, including pedicel	1·64–2·52 mm.
maximum diameter	0·50–0·81 mm.

Remarks. The examination of numerous samples of this species shows that the epizootic form is far more common than the parasitic one. It is possible that *H. furax* is conspecific with *H. parasitica* (Ciamician), but the gonophores of the latter have not so far been described.

Hebella scandens (Bale, 1888)

Hebella scandens: Millard, 1957: 202. Millard, 1958: 176. Vervoort, 1959: 237, fig. 12.
Hebella calcarata: Ralph, 1958: 306, fig. 1 a–s.

Records. West coast: WCD 18V, 34K. South coast: MB 8M, 64M. SAMH 183, 229, 237, 289, 382. SCD 37T, 52T, 75F, 79Q, 84Y, 108H, 118L, 154J, 175M, 179A. TRA 92R, 151H.

Hebella urceolata n. sp.

Fig. 2A

Holotype: SCD 154H (South African Museum registered number, SAMH 410).

Description. Colony epizootic on *Halecium beani* (Johnston). Hydrorhiza unsegmented, giving rise to hydrothecal pedicels at irregular intervals.

Hydrotheca about three times as long as wide, distinctly demarcated from pedicel, gibbous below and narrowing above to just below margin. Margin smooth, everted, straight or slightly oblique, sometimes rejuvenated. Pedicel short, not annulated, widening distally. Hydrotheca separated from pedicel by an annular thickening of the wall, to the distal region of which is affixed a delicate diaphragm.

Most hydrothecae show a tendency to be asymmetrical with the margin more strongly everted and the basal region more gibbous on the surface directed towards the distal end of the host colony, while the annular thecal thickening is more strongly developed on the opposite side.

Gonophores absent.

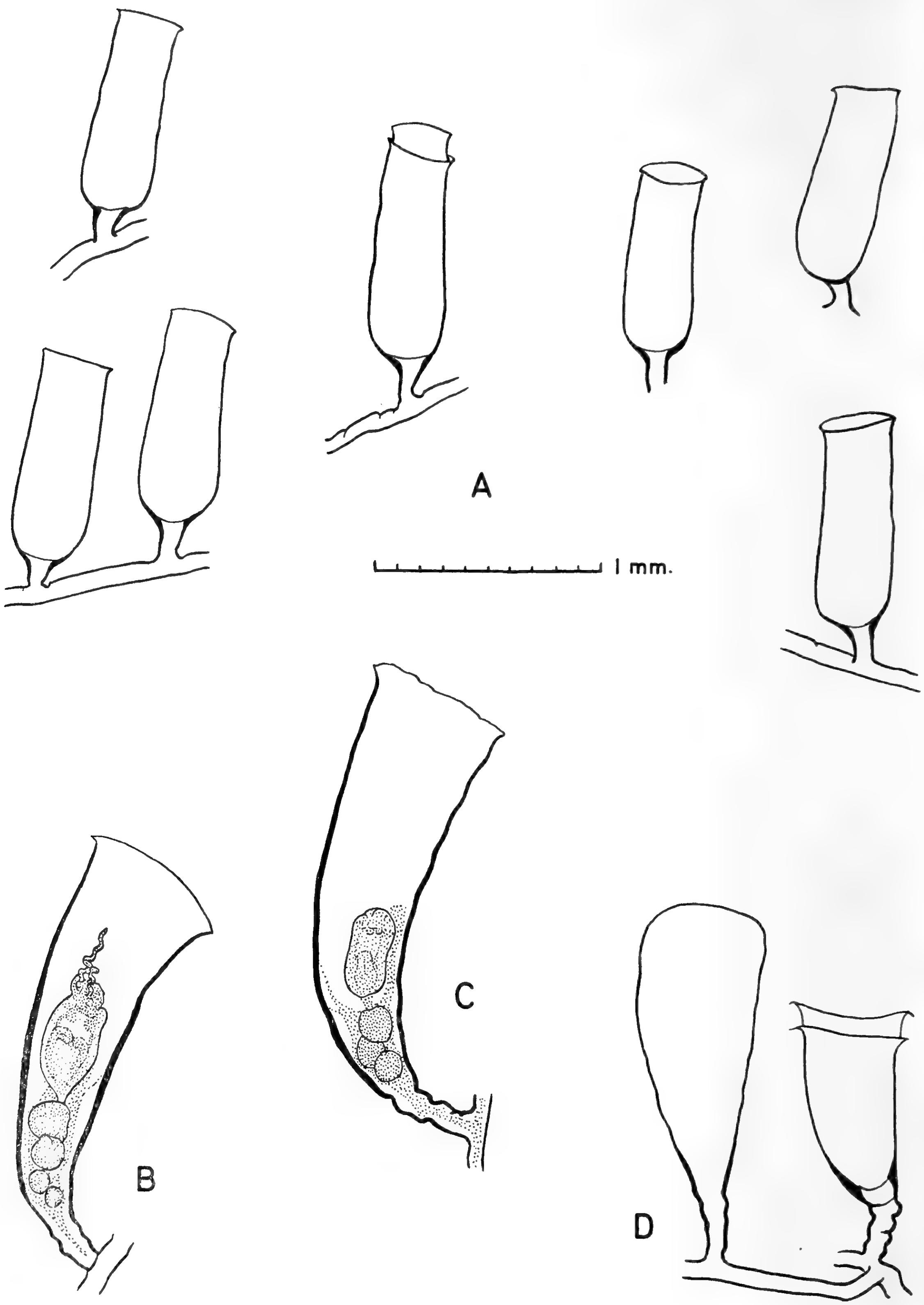

Fig. 2. *Hebella* spp.

A. *Hebella urceolata* n. sp. Various hydrothecae from the holotype.
B.–D. *Hebella furax* Millard. B and C, gonothecae containing young medusae from SCD 84Z. D, a young gonotheca and a hydrotheca from MB 72G.

Measurements (mm.)	
Hydrorhiza, diameter	0·07–0·10
Pedicel, height, to diaphragm	0·11–0·17
Hydrotheca, height, from diaphragm	0·81–0·93
diameter, near base	0·31–0·35
diameter, at margin	0·25–0·33

Lafoea fruticosa M. Sars, 1851

Fig. 3

Lafoea fruticosa: Allman, 1888: 34, pl. 16 (fig. 2, 2a). Broch, 1918: 12. Stechow, 1925: 456, fig. 24B. Totton, 1930: 157, fig. 13. Fraser, 1944: 223, pl. 46 (fig. 206). Vervoort, 1946: 201, fig. 83 c, d.

Records. West coast: WCD 1L. South coast: SCD 175Q.

Description. Branching colonies reaching a maximum height of 9·0 cm. Stems fascicled, branching mainly in one plane but growing together in clusters and anastomosing with each other to produce a shrubby effect.

Hydrothecae arising from all sides of the stem and branches, forming an angle of about 40–60° with branch. Asymmetrical in shape, generally with a double curvature on the adcauline side and a more or less straight abcauline wall. Margin slightly everted. Pedicel short and slightly twisted.

An epizootic colony present on the surface of WCD 1L, giving rise to upright stems and solitary hydrothecae. The latter generally more slender and with thinner perisarc than those borne by upright stems.

Coppinia present in WCD 1L, consisting of closely packed, more-or-less hexagonal gonothecae surmounted by acrocysts, which are loosely attached and come away easily on handling. Gonotheca approximately 0·4 mm. in height and 0·15 mm. in diameter at the shoulder, with a short mouth-funnel of approximately 0·05 mm. in height and 0·05 mm. in diameter at the everted margin. Tubular hydrothecae long (well over 3 mm.) and much coiled.

Measurements (mm.)	WCD 1L	SCD 175Q
Pedicel, height	0·10–0·19	0·14–0·22
Hydrotheca, height	0·42–0·66	0·34–0·59
Pedicel + hydrotheca, height	0·52–0·77	0·46–0·77
Hydrotheca, diameter at margin	0·14–0·19	0·14–0·16
Height of hydrotheca + pedicel / diameter at margin	3·555–5·03	3·29–4·97
Hydrotheca height/pedicel height	2·63–6·00	1·55–3·28
Solitary hydrotheca + pedicel, height	0·41–0·73	
diameter at margin	0·10–0·14	

Remarks. It was difficult to assign this material to a species, as it has features which resemble both *L. fruticosa* and *L. dumosa*. It has been assigned to the former partly because of the appearance of the coppinia, which resembles that illus-

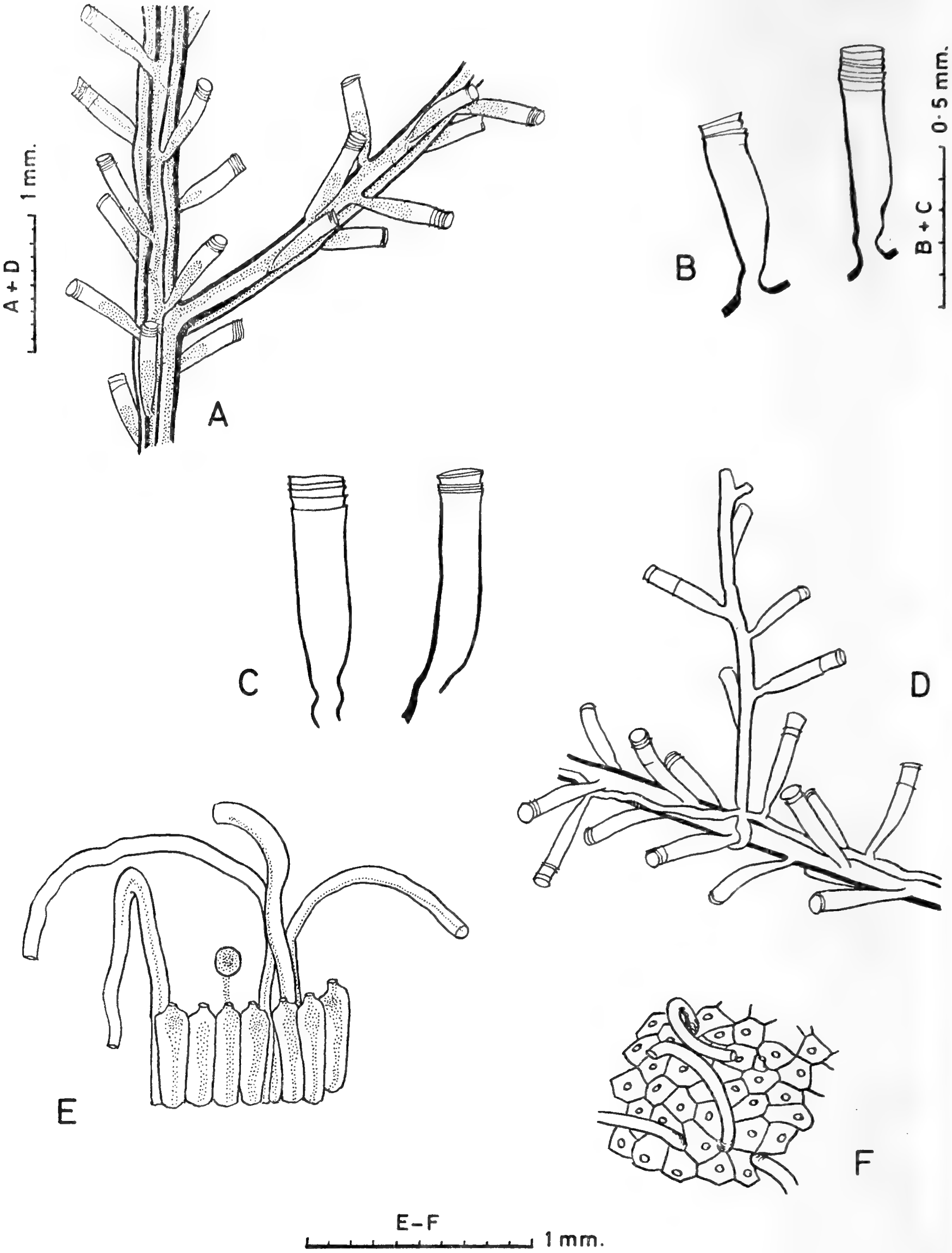

Fig. 3. *Lafoea fruticosa* M. Sars.

A. Part of a fascicled stem, to show branching.
B and C. Hydrothecae.
D. An epizootic colony with solitary hydrothecae and an upright stem growing on the surface of an older colony.
E. Part of a section through a coppinia, showing gonothecae (one with an acrocyst) and tubular hydrothecae.
F. Surface view of part of a coppinia.
(A and B from SCD 175Q, C–F from WCD 1L.)

trated by Fraser and Vervoort, and partly because of the shape of the hydrotheca, which resembles more that illustrated by Stechow, who has described both species from South Africa. The shape and proportions of the hydrotheca are intermediate between those described and illustrated by Totton for *L. dumosa* and *L. fruticosa.*

Since the branches arise from the accessory tubes in this species it is often difficult to distinguish epizootic colonies from the accessory tubes and branches. However, the accessory tubes always run strictly parallel to the axial tube and are in cytoplasmic connexion with the coenosarc of the latter, whereas the epizootic hydrorhiza wanders at will over the surface of the stem, with which it has no communication, and gives off both upright stems and solitary hydrothecae.

Scandia mutabilis (Ritchie, 1907)

Scandia mutabilis: Millard, 1957: 202. Millard, 1958: 176.

Records. South coast: KNY 30U.

Zygophylax africana Stechow, 1923

Fig. 4A–F

Zygophylax africana: Stechow, 1925: 445, fig. 18.

Records. West coast: AFR 743H. South Coast: SAMH 321.

Description. Hydrorhiza growing over the surface of worm-tubes, bearing nematothecae, solitary hydrothecae and upright stems in all stages of development, the latter reaching a maximum height of 9·5 cm. Stem and main branches thickly fascicled with some of the accompanying tubes extending on to the basal part of practically all the smaller branches. Stem bearing alternate hydrothecae and alternate branches given off at the base of every third and fourth hydrotheca. Branches often rebranching in the same manner, or according to a different scheme in which subbranches arise at the base of every third hydrotheca alternately to the right and the left. The hydrotheca at the origin of each branch is not strictly in the axil but shifted slightly onto the branch itself. All branches in one plane, many of the larger ones anastomosing with other parts of the colony.

Smaller branches (Stechow's 'cladia') unsegmented, but often with one or two corrugations close to the base; bearing alternate hydrothecae, of which the two rows are in one plane.

Hydrothecal pedicel short (and covered by the accompanying tubes on the thick part of the stem), sometimes with a distinct indentation on the adcauline side. Hydrotheca long, tubular, curved away from branch, of equal diameter throughout from just above the level of the diaphragm (SAMH 321, fig. 4F), or widening slightly towards margin (AFR 743H, fig. 4E). Margin slightly everted. Hydrotheca set at a varying angle to stem or branch—the angle may be as large as 50° (more common in AFR 743H), or very small so that the adcauline wall is almost in contact with the axial tube (more common in SAMH 321). Diaphragm in form of annular thickening, set obliquely, with adcauline side lower than abcauline.

Nematotheca tubular and of equal diameter throughout, borne on a very short and narrow pedicel, and separated from it by a delicate diaphragm. Nematothecae borne irregularly on the peripheral tubes of the stem, and one on the base of each hydrothecal pedicel. The nematotheca of the first hydrotheca of a branch, however, is situated on the branch itself immediately beyond the hydrotheca instead of on its pedicel. Both hydrothecae and nematothecae often with reduplicated margins.

Coppiniae present around the stem and larger branches, and also borne on the substratum by the hydrorhiza, reaching about 10 mm. in length and 4 mm. in diameter. Consisting of adpressed gonothecae (about 9–12 visible in cross-section), and numerous branching nematophores. Gonotheca pentagonal or hexagonal in surface view; in lateral view widening from base to top of adpressed part, bearing a free tubular neck surmounted by 2 divergent sharply pointed horns. Each with 2 apertures situated on opposite sides of the distal end of the neck immediately below the horns. Male and female gonothecae borne in separate coppiniae, but exactly the same in appearance, female containing a cluster of planula larvae. Nematothecae borne on branching perisarcal tubes which arise from the peripheral tubes of the stem and penetrate between the gonothecae, continuing beyond them to reach a total height of 1½ to 2½ mm.

Solitary hydrothecae borne by hydrorhiza and also by young epizootic colonies growing on the surface of the larger ones. Usually smaller than normal hydrothecae and with longer pedicels. Shape variable; quite symmetrical and straight, irregular, or curved as in the normal type.

Measurements (mm., without reduplications)	AFR 743H	SAMH 321
Final branches, distance between two hydrothecae	0·34–0·48	0·21–0·38
diameter, above hydrotheca	0·05–0·09	0·05–0·07
Pedicel, length adcauline	0·03–0·095	0·02–0·05
Hydrotheca, length adcauline	0·26–0·33	0·24–0·30
length abcauline	0·23–0·28	0·19–0·25
diameter at mouth	0·09–0·10	0·07–0·08
diameter across diaphragm	0·04–0·06	0·05–0·07
Nematotheca, length, including pedicel	0·07–0·12	0·09–0·17
diameter at margin	0·025–0·04	0·02–0·025

Remarks. Although there are slight differences in the appearance of the hydrothecae in these two colonies (e.g. the hydrothecae in SAMH 321 have narrower mouths and shorter pedicels and are more closely set than those in AFR 743H) I can see no reason for specific distinction. Both bear coppiniae (male in SAMH 321, female in AFR 743H) which are exactly alike in construction.

Although the branching in general conforms to the scheme outlined above,

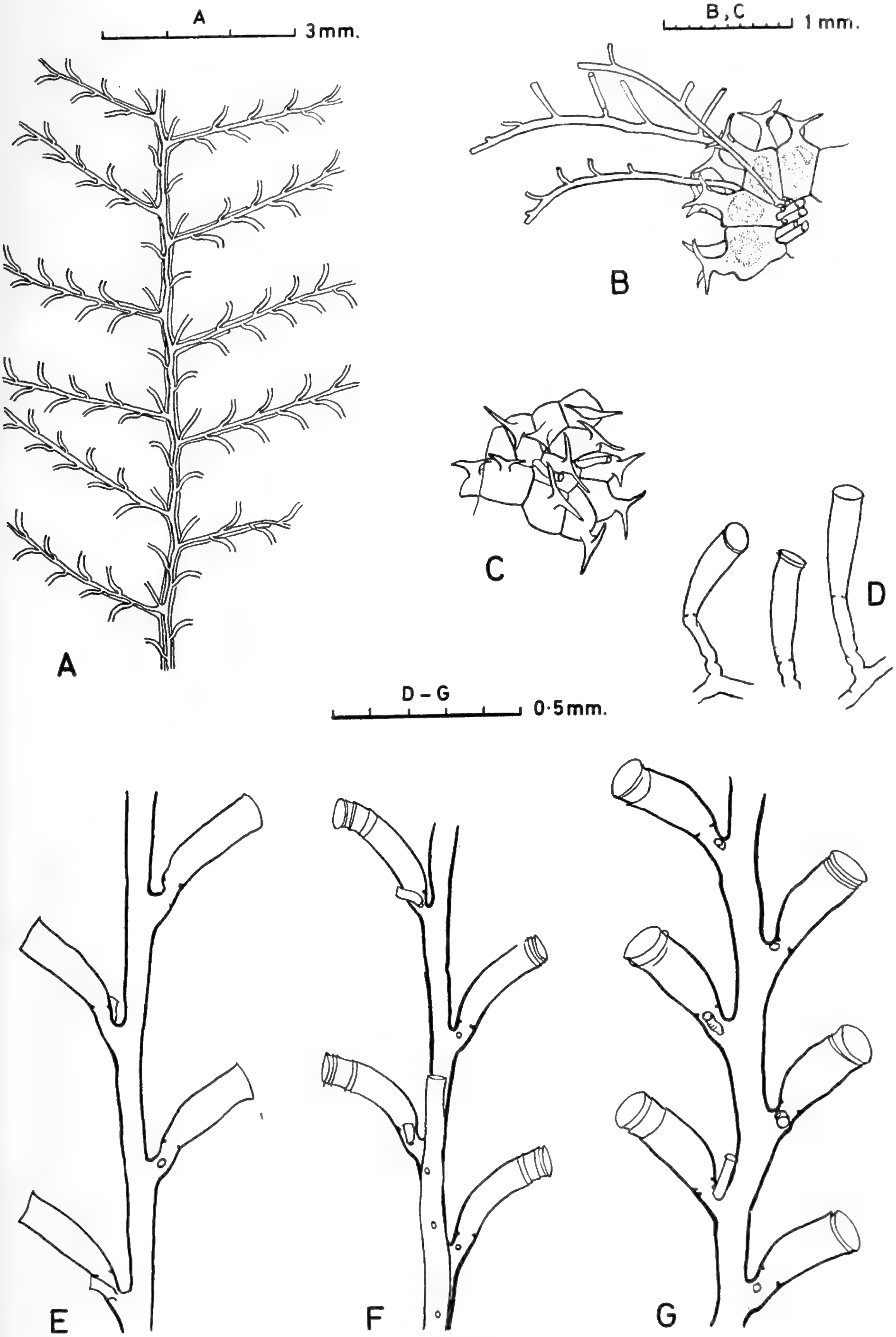

Fig. 4. *Zygophylax* spp.

A.–F. *Zygophylax africana* Stechow. A, part of a fascicled stem to show branching (branches cut off short). B, part of a section through a female coppinia, showing gonothecae and branching nematothecae. C, surface view of part of coppinia (horns of gonothecae displaced by pressure of coverslip). D, solitary hydrothecae from epizootic colony. E and F, portions of branches, to show hydrothecae and nematothecae.

G. *Zygophylax armata* (Ritchie). Part of a branch.

(A and F from SAMH 321, B–E from AFR 743H, G from SCD 254P.)

there are many irregularities, and the branches differ greatly in thickness and in the degree to which they subdivide. The general effect is far from regular.

The species has only once been reported, by Stechow in 1923b, off Cape Town. Stechow described a smaller sterile colony reaching only 1·8 cm. in height, and less heavily fascicled. I have seen a slide of Stechow's material loaned by the Munich Museum, and there is no doubt that it is the same species. The coppiniae are described here for the first time.

The coppiniae of this species are strikingly similar to those of *Cryptolaria pectinata* (Allman) (cf. Stechow, 1925, fig. 20). The latter, however, are dioecious, and the female gonotheca has a relatively shorter neck and horns. The two species are also similar in the general appearance of the colony and in the subopposite method of branching. This emphasizes the close relationship between the genus *Cryptolaria* and certain species of *Zygophylax*. In fact, *Cryptolaria*, by the presence and nature of its diaphragm, its nematothecae, subopposite branching and coppinial structure, is more closely related to certain species of *Zygophylax* than the various species of *Zygophylax* are to one another. *Cryptolaria* differs only in the adherent hydrothecae, which as Stechow has shown (1925, p. 450) is a matter of degree only and does not occur in the young stems. I cannot help but feel that the adherent nature of the hydrotheca is not a character of high systematic value, and that it will be necessary in the future to unite *Cryptolaria* with *Zygophylax*, and possibly *Acryptolaria* with *Lafoea*. I hesitate to do so at this stage as my knowledge of the variability of the species in these genera is insufficient.

Zygophylax armata (Ritchie, 1907)

Fig. 4G

Brucella armata Ritchie, 1907: 533, pl. 2 (fig. 2–2c).

Records. South coast: SCD 254P, 297X.

Description. Two colonies, the larger reaching a height of 3·0 cm., with stem and larger branches fascicled. Branching at the base rather irregular, but larger branches and their subdivisions in one plane. The 2 rows of hydrothecae not always in one plane, but with a tendency to shift on to the anterior surface of a branch. Further details of hydrothecae and nematothecae as described by Ritchie, except that the individual measurements are somewhat smaller.

Solitary hydrothecae present on hydrorhiza and in epizootic colonies, with the same proportions as those on branched stem, but less curved, and sometimes completely symmetrical.

Coppiniae absent.

Measurements (mm., without reduplications).

	SCD 254P
Hydrocladium, diameter above hydrotheca	0·07–0·09
distance between 2 consecutive hydrothecae	0·23–0·35
Hydrothecal pedicel, length adcauline	0·03–0·06

Hydrotheca, length adcauline	0·19–0·26
length abcauline	0·18–0·26
diameter at mouth	0·11–0·13
diameter at level of diaphragm	0·06–0·075
Nematotheca, length, including pedicel	0·05–0·07
diameter at mouth	0·03–0·04

Remarks. This species has only been recorded once before, from off Gough Island in 100 fathoms, and is a new record from South Africa. It can be distinguished from *Z. biarmata* Billard by the nature of the coppinia; and as far as I can determine, the trophosomes of the two species can also be distinguished by the closer approximation of the hydrothecae in *Z. armata* and their more pronounced asymmetry.

Zygophylax cornucopia Millard, 1955

Zygophylax cornucopia Millard, 1955: 219, fig. 3. Millard, 1957: 203.

Records. West coast: TB 1B (reported by Millard, 1955). TRA 156F. South coast: CPR 46K. LIZ 27L, MB 59U. SAMH 192. SCD 36V, 153P.

Description. Colonies epizootic on *Antennella africana* Broch, *A. secundaria* (Gmelin) and *Monostaechas natalensis* Millard.

Zygophylax enigmatica n. sp.

Fig. 5A–F

Holotype: WCD 12E (South African Museum registered number, SAMH 411).

Description. Colony epizootic on *Nemertesia ramosa* Lamx. and reaching a height of 2–3 mm.

Hydrorhiza adherent to stem of host, unsegmented, branching irregularly.

Stem upright and pinnate, divided by straight nodes into long internodes, each of which gives off a hydrocladial apophysis near the distal end. Apophysis with a large mamelon on the upper surface. The first few internodes of the stem sometimes much shorter than the others, and occasionally without hydrocladia. An internodal ridge sometimes present near base of stem internode.

Hydrocladia alternate, the two rows in the same plane. Hydrocladium forming an angle of about 30°–40° with stem. Consisting of one basal internode, followed by a pedicel and hydrotheca which form one unit and are not externally demarcated from one another. Pedicel and hydrotheca expanding evenly towards margin. Thecal margin even, not everted. Pedicel and hydrotheca separated internally by a diaphragm. Diaphragm bilaterally symmetrical, with aperture close to adcauline side, and abcauline section sloping obliquely towards distal end of hydrocladium. Pedicel sometimes with a low internodal ridge near base, and sometimes showing evidence of regeneration.

One nematotheca on each hydrothecal pedicel, seated about midway along adcauline surface, 2-chambered, moveable.

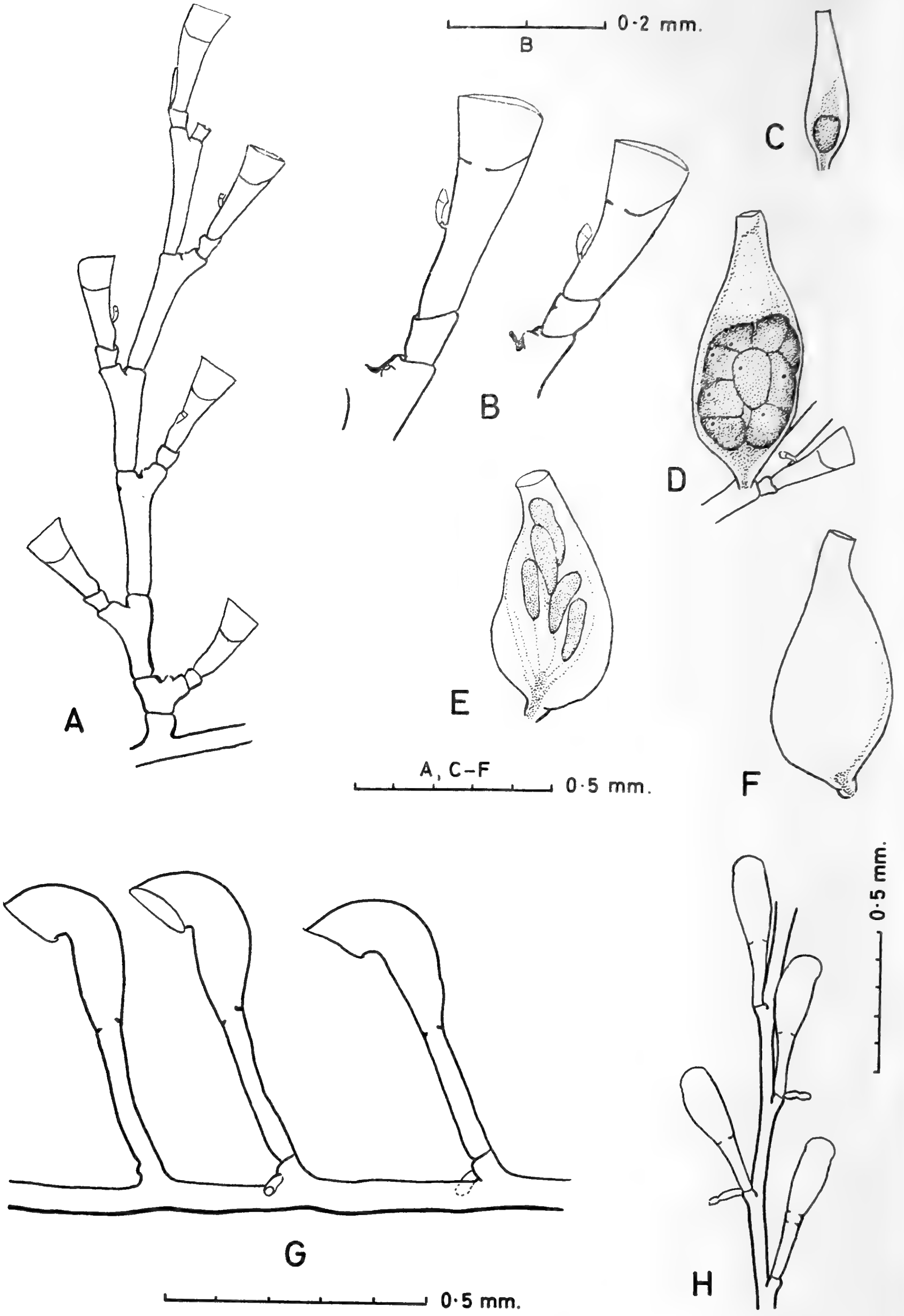

Fig. 5. *Zygophylax* spp.

A.–F. *Zygophylax enigmatica*, n. sp., from the holotype. A, an upright stem. B, two hydrocladia on a larger scale. C–F, gonothecae in various stages of development.

G.–H. *Zygophylax sibogae* Billard, from SCD 301H. G, ventral view of part of a branch. H, anterior view.

Hydranth completely retractable into hydrotheca, hypostome conical when contracted but capable of great distension.

Gonothecae borne on hydrocladial apophyses, very large in comparison with size of hydrothecae. Each gonotheca laterally compressed in a plane at right angles to the axis of the stem, flask-shaped, and tapering to a slender neck. Neck sometimes curved to one side, with margin obliquely set. Containing about 8–10 eggs which develop *in situ* to planula larvae.

Measurements (mm.)

Hydrorhiza, diameter	0·04–0·08
Stem internode, length (not the first 2)	0·20–0·34
diameter	0·04–0·07
Hydrocladium, basal segment, length	0·03–0·07
pedicel, length to diaphragm	0·10–0·20
hydrotheca, height from diaphragm	0·07–0·10
diameter at margin	0·095–0·11
Nematotheca, length	0·035–0·05
Gonotheca, length	0·60–0·71
diameter	0·23–0·33

Remarks. This minute species is obviously closely related to *Z. cornucopia* Millard, particularly in the structure and proportions of the hydrotheca and its pedicel and in the absence of a coppinia, but differs from it in the presence of an upright, pinnate stem.

Both species show tendencies towards the Plumulariidae, but cannot be included in that family since the hydrothecae are not sessile, but borne on a pedicel from which they are separated by a diaphragm. The continuity of pedicel and hydrotheca is characteristic of other species of *Zygophylax*.

Zygophylax sibogae Billard, 1918
Fig. 5G-H

Zygophylax sibogae Billard, 1918: 21, fig. 1. Totton, 1930: 167, fig. 21. Ralph, 1958: 311, fig. 2, e–i.

Records. South coast: SCD 301H.

Description. A number of fascicled stems reaching a maximum height of 3·1 cm., branching pinnately and in one plane. Branches generally arising below every third and fourth hydrotheca, the lower ones fascicled at base and often rebranching in a similar manner.

Hydrothecae borne in two longitudinal rows on the anterior surface of stem and branches, with a sharp angle between the rows, and with the members of one row twisted slightly away from those of the other row. Hydrotheca strongly curved towards distal end of branch, widening to circular aperture which faces towards branch and slightly to one side. Borne on long pedicel of approximately the same length. Diaphragm well developed, often funnel-shaped. Pedicel usually separated from stem apophysis by distinct node.

Nematothecae borne on peripheral tubes and one on the lateral surface of each hydrothecal apophysis, tubular and narrowing slightly to margin, normally about 0·07 mm. in length, but often abnormally lengthened by regeneration.

Gonophores absent.

Measurements (mm.)

Hydrocladium, distance between 2 pedicels	0·28–0·37
diameter	0·05–0·07
Pedicel, length (without apophysis)	0·20–0·26
Hydrotheca, length adcauline	0·16–0·20
maximum length	0·26–0·30
diameter at mouth	0·11–0·13
diameter at diaphragm	0·045–0·05
Nematotheca, length	0·07–0·32
maximum diameter	0·025–0·035
diameter at mouth	0·015–0·03

Remarks. The hydrothecae in this colony have a beautifully regular arrangement, more so than those figured by Ralph, and in appearance are exactly like Billard's diagram. The measurements of hydrothecal length and pedicel length are slightly less than those given by Totton and Ralph, but there is no doubt about the identification of the material.

This species is closely related to *Z. infundibulum* Millard, 1958, differing from it in the greater length of the pedicel and the more marked curvature of the hydrotheca.

Z. sibogae is known from the East Indies and New Zealand. This is the first record from South Africa.

Family **Syntheciidae**

Hincksella cylindrica pusilla Ritchie, 1910

Fig. 6A–D

Sertularella cylindrica var. *pusilla* Ritchie, 1910: 817, pl. 77 (fig. 9).
Hincksella cylindrica var. *pusilla:* Billard, 1925: 124. Vervoort, 1959: 247, fig. 19 b, c.
Synthecium cylindricum var. *pusilla:* Leloup, 1935: 31, fig. 14.

Records. South coast: SCD 297Y.

Description. A single colony of about 6 unfascicled and unbranched stems reaching a maximum height of 0·7 cm. Internodes of irregular length, separated by slightly oblique nodes, and each bearing a hydrotheca near the distal end.

Hydrothecae very delicate, and most of them crumpled, adnate for about ¼ adcauline side, then bent outwards. Margin slightly everted, often regenerated.

Gonothecae absent.

Measurements (mm., without reduplications)

Internode length	0·29–0·54
diameter at node	0·05–0·09

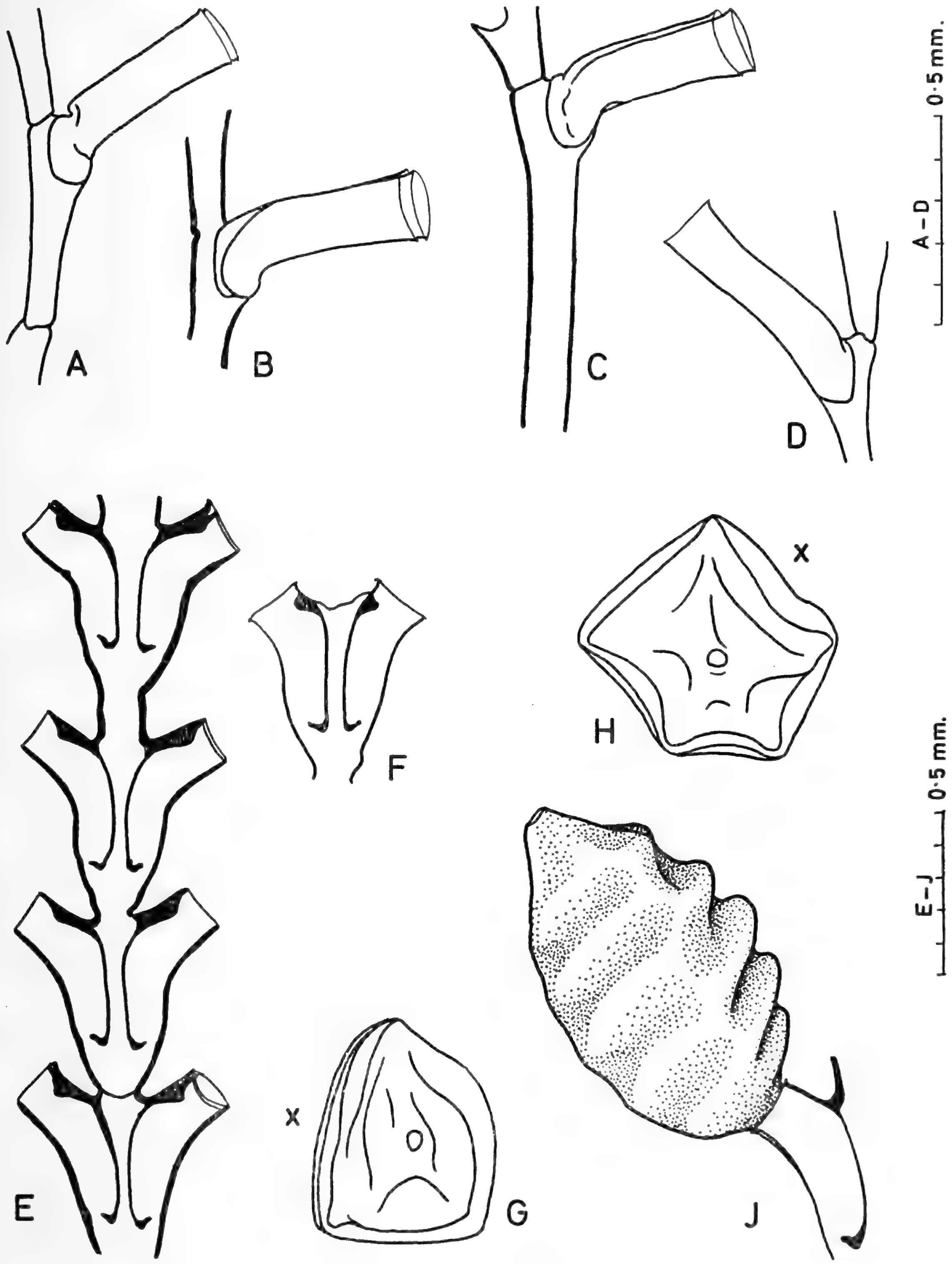

Fig. 6. Syntheciidae.

A.–D. *Hincksella cylindrica pusilla* Ritchie. Hydrothecae from SCD 297Y.

E.–J. *Synthecium dentigerum* Jarvis, from SCD 84G. E and F, portions of hydrocladia. G and H, 2 gonothecae viewed from the distal end (adcauline surface indicated by x). J, gonotheca in side view.

Hydrotheca, total length in centre	0·49–0·60
length adcauline, adnate part	0·15–0·18
length adcauline, free part	0·44–0·47
adnate part/adcauline length	0·24–0·29
diameter at margin	0·14–0·17

Remarks. This is the first record of the species from South Africa. Subspecies *pusilla* has previously been recorded from the Mergui Archipelago, East Indies, Japan, tropical West Africa and the West Indies.

Synthecium dentigerum Jarvis, 1922

Fig. 6E–J

Synthecium dentigerum Jarvis, 1922: 344, pl. 25 (fig. 15 a, b). Totton, 1930: 172.

Records. South coast: SAMH 375. SCD 52G, 84G, 112F. TRA 151G.

Description. A number of colonies reaching a maximum height of 4·0 cm. Stem unfascicled, pinnate, divided into internodes by straight nodes, which are sometimes obscure. Arrangement on internodes variable, common arrangements including 2 pairs of hydrothecae with a pair of opposite hydrocladia arising between them, and one pair of opposite hydrocladia followed by one pair of hydrothecae.

Hydrotheca as described and figured by Jarvis, with one large, adcauline, internal tooth, but the presence of this tooth is by no means constant and is sometimes found on only a few hydrothecae of a colony. Occasional hydrothecae with a small triangular thickening in the centre of the abcauline wall.

Gonothecae (not previously described) borne on stem or hydrocladia, arising within hydrothecae; generally pentagonal when viewed from above, though sometimes two of the angles are smoothed out resulting in a rather flattened triangle; with 5–6 transverse folds on the flat surfaces, which may peter out on the angles or continue over them, but do not produce a definite zigzag line of junction; tapering distally to a small circular opening. Sex not determinable.

Measurements (mm.)

Hydrocladium, internode length	0·58–0·76
Hydrotheca, length abcauline	0·34–0·41
length adcauline, adnate part	0·38–0·48
length adcauline, free part	0·08–0·17
adnate part/adcauline length	0·69–0·85
diameter near base	0·14–0·17
diameter at margin	0·16–0·20
Gonotheca, length	1·01–1·40
maximum diameter	0·56–0·77

Remarks. The dimensions of this material are slightly less than those given by Totton for *S. dentigerum*, but are closer than to *S. carinatum* Totton, a closely related species with internal teeth. The gonotheca of the latter is also different.

S. dentigerum has only been reported once, from Chagos in the Indian Ocean by Jarvis. This is the first record from South Africa.

Synthecium ?elegans Allman, 1872

Synthecium ?elegans: Millard, 1957: 203, fig. 9D. Millard, 1958: 182.

Records. South coast: MB 8U, 64N.

Remarks. As the gonothecae of this species have still not been found in South Africa, the identification must remain uncertain.

Synthecium hians Millard, 1957

Synthecium hians Millard, 1957: 204, fig. 9 A–C.

Records. South coast: MB 12Y, 64L. SAMH 151, 188, 281, 374. SCD 37L, 52F, 84H, 119N, 250K, 254N, 296F. TRA 38G.

Family **Sertulariidae**

Amphisbetia bidens (Bale, 1884)

Thuiaria bidens: Day, Millard & Harrison, 1952: 404 (listed).
Amphisbetia bidens: Millard, 1957: 220. Millard, 1958: 182.

Records. South coast: BMR 23M. KNY 30K, 70D (recorded by Day *et al.* 1952). LIZ 7P, 11H. MB 15F, 24N, 47L, 88M. SAMH 261, 378. SCD 60A, 84K, 153V, 330E.

Amphisbetia minima (Thompson, 1879)

Amphisbetia minima: Millard, 1957: 221. Millard, 1958: 183. Ralph, 1961: 774, figs. 8 a–h.

Records. West coast: B 114F. CP 650A. TRA 156J. WCD 34J, 81F. South coast: MB 24Q.

Description. Stems reaching a maximum height of 0·5 cm., and bearing up to 15 pairs of hydrothecae. Male and female gonothecae present, similar in structure, usually arising below the first pair of hydrothecae, but occasionally below the second or third pair.

Amphisbetia operculata (Linn., 1758)

?Sertularia aperta Allman, 1886: 138, pl. 13 (figs. 1, 2).
Sertularia operculata: Day, Millard & Harrison, 1952: 404 (listed).
Amphisbetia operculata: Millard, 1957: 221. Millard, 1958: 183. Millard, 1961: 204. Ralph, 1961: 775, fig. 8 i–k.

Records. West coast: B 137. LAM 14T, 45Y. SAMH 403. SB 194M. TB 21E. TRA 156H. WCD 34G, 81C. South coast: BMR 9M. CPR 9C. KNY 22G, 30L, 57H, 70A (recorded by Day *et al.* 1952). LIZ 2F, 7Q, 11G. MB 24P, 52A. SAMH 232, 358, 376. SCD 84L, 284A, 304H.

Remarks. Many of these colonies show a form of branching approaching that of *A. fasciculata* (Kirch.), and similar to that figured by Allman, 1886, pl. 14, for *Sertularia crinis* (considered by Billard, 1910, who examined the types, to be conspecific with *A. operculata*), with an elongated 'main stem' and subsidiary branches which may subdivide once or twice. There is sometimes, but not always, a difference in internode length and thickness between the smaller branches and 'main stem' (where the length may be almost twice as great), but the difference is never so marked as described by Ralph, 1961, for *A. fasciculata.* Since this and the normal form may occur in the same colony, it is not possible to distinguish two species. The height of the colony never exceeds about 14 cm.

Sertularia aperta Allman, 1886, from the Cape of Good Hope is almost certainly a growth-form of the same species.

Crateritheca acanthostoma (Bale, 1882)

Fig. 7

?Dynamena pluridentata Kirchenpauer, 1864: 14, fig. 10.

Sertularia acanthostoma: Bale, 1884: 85, pl. 4 (figs. 7–8). Billard, 1907: 352. Warren, 1908: 303, pl. 46 (figs. 23–26), fig. 7. Bale, 1913: 131.

Stereotheca acanthostoma: Millard, 1958: 199.

Crateritheca acanthostoma: Ralph, 1961: 756, fig. 2c.

Records. South coast: SCD 50A.

Description. Several pinnate stems reaching a maximum height of 2·4 cm. Arrangement of hydrocladia, internodes and hydrothecae as in previous descriptions.

Hydrotheca adnate for a little over half adcauline length, with no external ridges or furrows, but with 3 intrathecal septa. These include (fig. 7A, C, D):

(*a*) an adcauline septum about half-way up the hydrotheca in the form of a horizontal shelf bearing 2 or 3 minute denticles on the free inner edge,

(*b*) a lower abcauline septum about a quarter of the way up, in the form of a horizontal shelf behind which is an opening for the passage of a strand of ectoderm, and below which is situated the abcauline blind pouch of the hydranth,

(*c*) an upper abcauline septum about three-quarters of the way up in the form of a narrow horizontal shelf forming the base of a longitudinal trough communicating with the cavity of the hydrotheca and extending to the margin. This trough contains a cluster of large nematocysts embedded in ectoderm which is continuous with the strand passing behind septum b.

Hydropore surrounded by a raised funnel-shaped ridge. Operculum of a single membranous plate filling complete orifice. Marginal teeth and soft parts as described by Warren.

Gonothecae absent.

Remarks. The genus *Crateritheca* is recognized here on the basis of remarks by

Totton, 1930, p. 207, and Ralph, 1961, although the diagnosis of the latter author will need modification to include *C. acanthostoma*.

Stechow in 1919 included Warren's material from Natal and Billard's material from Madagascar in Kirchenpauer's species '*Dynamena*' *pluridentata* from the Cape of Good Hope, although in 1925 he kept them separate. As Kirchenpauer's species is inadequately described and illustrated, and might from the diagrams equally well be *Stereotheca elongata*, no certainty can be reached on this matter.

The South African material of the species differs in certain respects from the Australian material as shown by dissections of hydrothecae made under a high-power dissecting microscope. Thus, the hydrotheca has a smaller propor-

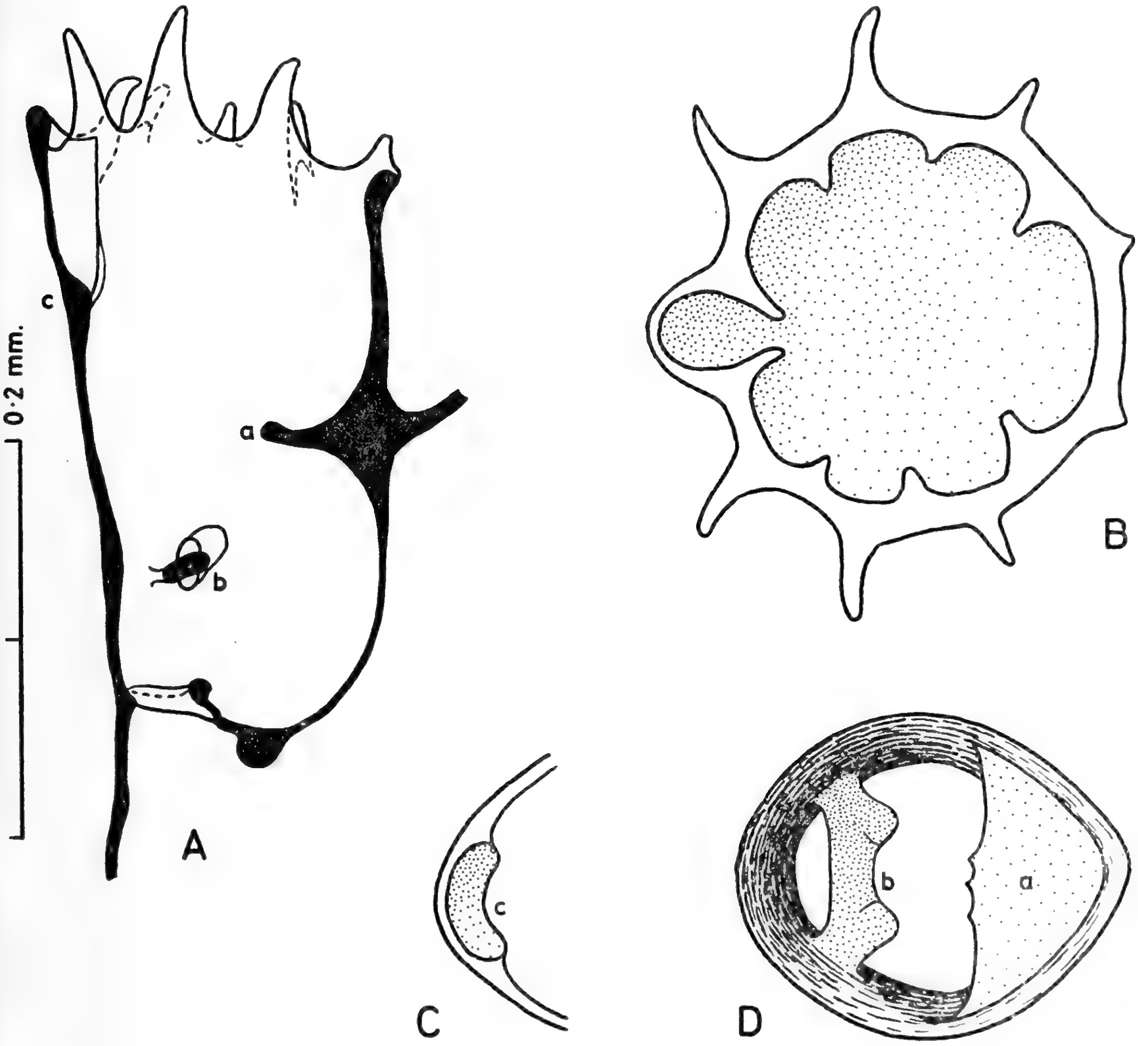

FIG. 7. *Crateritheca acanthostoma* (Bale).
A. A single hydrotheca in side view. Adcauline surface on right.
B.–D. Free-hand diagrams drawn from dissections of hydrothecae. B, distal view of complete hydrotheca with operculum in position. C, distal view of cross-section through abcauline wall taken near distal end. D, distal view of cross-section through hydrotheca at a slightly deeper level.
a, the adcauline septum; b, the lower abcauline septum; c, the upper abcauline septum.

tion of the adcauline wall adnate, the adcauline intrathecal ridge is not continued round the complete diameter of the hydrotheca, and the lower abcauline intrathecal ridge is perforated. These differences, however, are not considered sufficient basis for the separation of another species, although they may prove to be of subspecific value. Further material from both countries is needed to show the degree of variation possible.

Dictyocladium coactum Stechow, 1923.

Dictyocladium coactum: Stechow, 1925: 466, fig. 27. Millard, 1957: 206.

Records. South coast: AFR 866.O.A. SAMH 264, 314. SCD 3C, 36Z, 52P, 85R. TRA 151K.

Diphasia tetraglochina Billard, 1907

Fig. 8

Diphasia tetraglochina Billard, 1907: 358, fig. 7. Billard, 1925: 139.

Records. South coast: SAMH 267.

Description. Small unbranched stems growing on algae and reaching a maximum height of 0·25 cm. Hydrorhiza with internal thickenings of perisarc. Nodes markedly oblique, resembling hinge-joints. Each internode bearing one pair of opposite hydrothecae.

Hydrothecae asymmetrical, with both members of a pair twisted and tilted towards one surface of the stem (here termed the anterior surface), and sometimes contiguous with one another on the opposite surface (in the distal region of some stems only). See figure 8B. Hydrotheca adnate for $\frac{2}{3}$ to $\frac{3}{4}$ of adcauline length, bent outwards, widening towards margin. Perisarc usually thickened in centre part of abcauline wall and often around margin as well. Margin with 4 small, pointed teeth: 2 latero-adcauline and 2 latero-abcauline, but displaced towards the anterior surface of the stem by the twisting of the hydrotheca. Operculum of 1 adcauline valve. Hydranth with no abcauline blind pouch.

Gonotheca (not previously described) borne on anterior surface of stem immediately below first pair of hydrothecae, resembling a prickly pear in appearance, with a variable number of small spines in distal half and a small terminal aperture at the end of a short neck.

Measurements (mm.)

Internode length	0·30–0·54
Hydrotheca, length abcauline	0·27–0·41
length adcauline, contiguous part	0·00–0·17
length adcauline, adnate part	0·24–0·31
length adcauline, free part	0·09–0·15
adnate part/adcauline length	0·65–0·74
diameter at margin	0·19–0·25
Gonotheca, length	0·73–0·77
maximum diameter	0·38–0·45

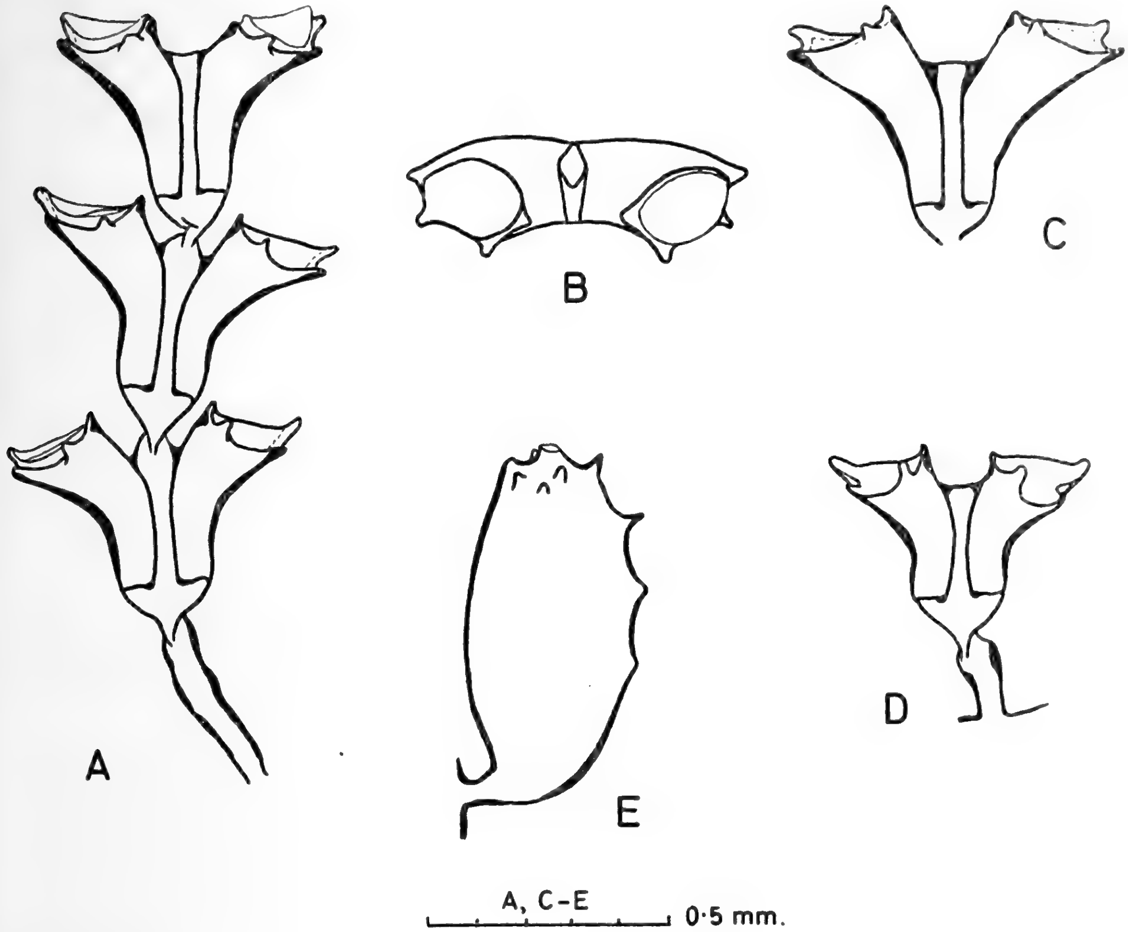

FIG. 8. *Diphasia tetraglochina* Billard.

A. A stem with 3 pairs of hydrothecae.
B. Sketch of distal view of a pair of hydrothecae to show asymmetry. Operculum in place in right hydrotheca.
C. The distal pair of hydrothecae from a stem with 5 pairs.
D. The proximal pair from another stem.
E. The gonotheca.

Remarks. This rare species has only been recorded once before, from Madagascar. It was not possible to determine the sex of the gonothecae.

Dynamena cornicina McCrady, 1858
Fig. 9

Sertularia densa Stechow, 1919: 93, fig. J¹.
Sertularia cornicina: Jarvis, 1922: 338.
Dynamena cornicina: Billard, 1925: 188, pl. 7 (fig. 23), fig. 40. Broch, 1933: 86, fig. 36. Vervoort, 1941: 206, fig. 3.

Records. South coast: LIZ 16C, 40J.

Description. Two colonies, one very rich, growing on coralline algae. Only simple stems present, reaching a maximum height of 0·9 cm. Stem with short, proximal, athecate region terminated by a hinge-joint, and a long thecate region divided into regular internodes by constricted nodes. Each internode bearing a pair of opposite hydrothecae. Consecutive pairs of hydrothecae close, separated by a distance less than the height of a hydrotheca. Members of a pair of hydrothecae contiguous with one another on anterior surface in distal region of stem, but completely separate in proximal region.

Hydrotheca tubular, adnate for over half adcauline length, smoothly bent out in distal half. Margin with two large, but delicate, lateral teeth and a short median adcauline tooth. Abcauline wall thickened just below margin. No internal teeth. Operculum of 2 valves: one large abcauline, and one small adcauline divided into 2 by a median line.

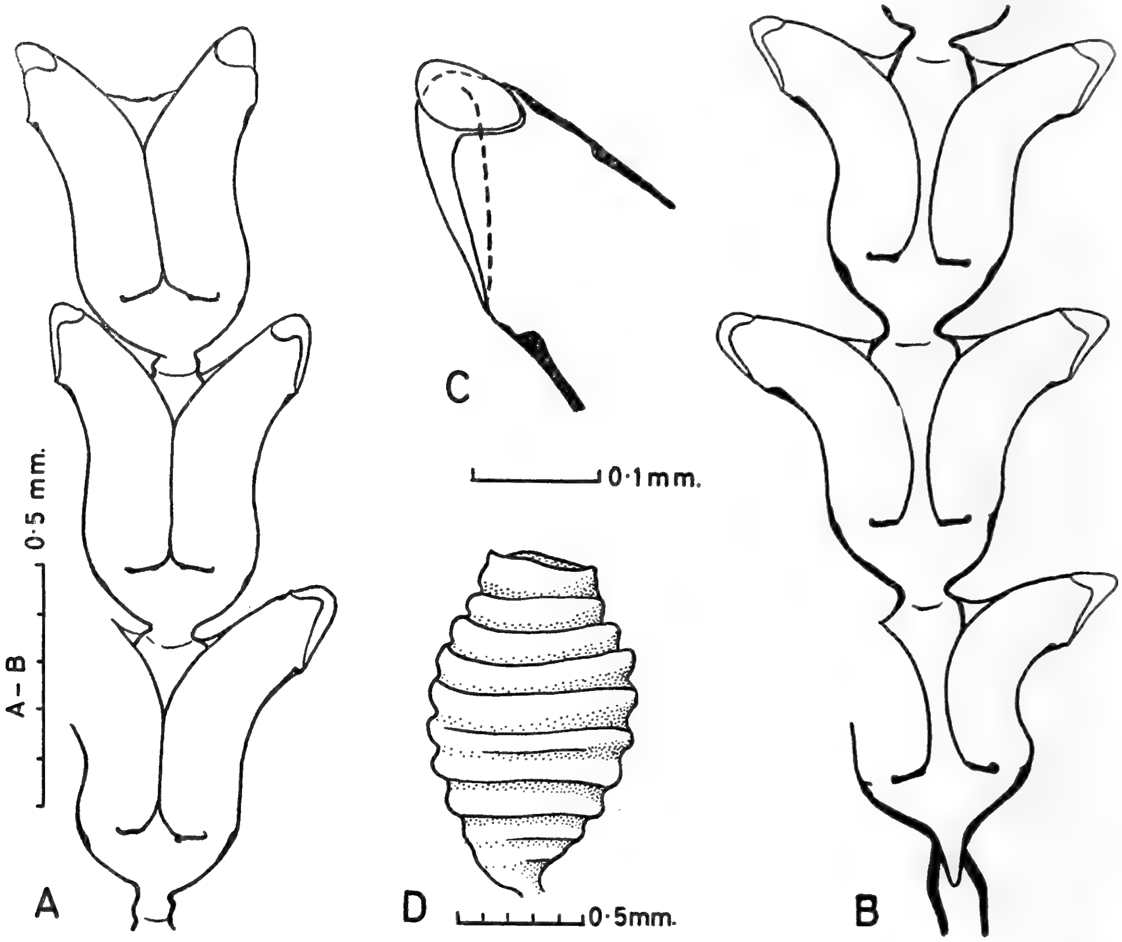

Fig. 9. *Dynamena cornicina* McCrady.
A. and B. The upper 3, and the lower 3, pairs of hydrothecae respectively from a stem bearing 12 pairs in all (anterior view).
C. The margin of a hydrotheca showing the operculum. (Abcauline valve in thick broken line.)
D. The gonotheca.
(All from LIZ 16C.)

Gonothecae abundant, borne on hydrorhiza, ovoid, distinctly annulated throughout, with a broad, operculate aperture.

Measurements (mm.)

Internode length	0·54–0·65
diameter at node	0·07–0·14
Hydrotheca, length abcauline	0·29–0·45
length adcauline, contiguous part	0·00–0·26

length adcauline, adnate part	0·35–0·46
length adcauline, free part	0·14–0·25
adnate part/adcauline length	0·59–0·76
diameter at margin	0·13–0·175
Gonotheca, length	1·06–1·38
maximum diameter	0·76–0·88

Remarks. In this material the pairs of hydrothecae are closely set on the stem, thus resembling that illustrated by Stechow, 1919.

The species has been reported by Jarvis, 1922, from tropical East Africa, but this is the first record from South Africa.

Dynamena crisioides crisioides Lamouroux, 1824

Dynamena crisioides: Millard, 1958: 183. Vervoort, 1959: 260, fig. 27 a, b.

Records. South coast: CPR 7A.

Dynamena quadridentata nodosa Hargitt, 1908

Dynamena quadridentata var. *nodosa:* Billard, 1925: 197, fig. 43D. Millard, 1958: 186, fig. 6B.
Pasythea quadridentata: Warren, 1908: 312, fig. 11.
Dynamena gibbosa Billard, 1925: 199, fig. 45.

Records. South coast: SCD 50P.

Remarks. The South African material of this species appears to be intermediate between *D. quadridentata nodosa* and *D. gibbosa*, which is included here as a synonym.

Salacia articulata (Pallas, 1766)

Fig. 10G

Salacia articulata: Millard, 1957: 208 (synonymy). Millard, 1958: 186. Millard, 1961: 205.

Records. West coast: LAM 7N, 30N. SB 153R, 168E. WCD 12C, 81E. South coast: L 452B. MB 47X, 84B. SAMH 152, 262, 295, 377. SCD 36X, 52N, 56R, 84M, 138J, 153Q, 296G, 330D. TRA 92L.

Salacia disjuncta nov. sp.

Fig. 10A–F

Types. Holotype: SCD 37K (South African Museum registered number, SAMH 412). Paratype: SCD 296H. (Both from South coast.)

Description of Holotype. A single rooted stem 1·4 cm. in height. Stem upright, moderately stiff, not zigzag, pinnate, divided by straight nodes into distinct internodes each of which bears 3 pairs of hydrothecae and 1 pair of opposite hydrocladia arising between the first and second pairs of hydrothecae. First internode of stem with 2 pairs of hydrothecae only. Stem constricted at nodes. Members of a pair of hydrothecae opposite or subopposite, not in contact with one another. The two rows of hydrothecae in 1 plane and on opposite sides of the stem. Consecutive pairs of hydrothecae on an internode separated by a short

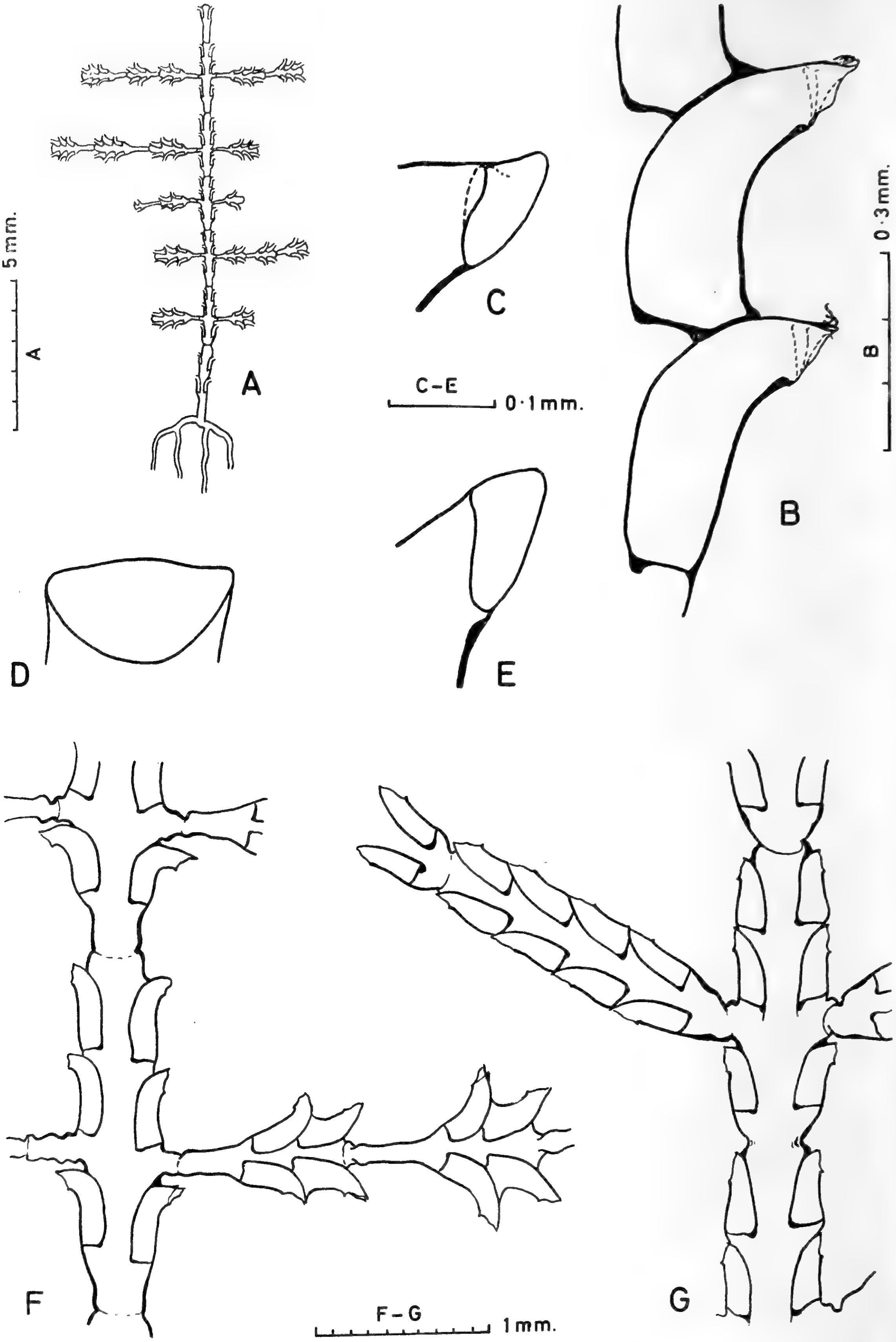

Fig. 10. *Salacia* spp.

A.–F. *Salacia disjuncta* n. sp. A, whole colony. B, 2 hydrothecae of a group. C–E, various views of the margin, C showing the operculum (in broken line). F, part of stem and hydrocladia.

G. *Salacia articulata* (Pallas). Part of stem and hydrocladium as a comparison with *S. disjuncta*. (A–C, F from SCD 37K; D–E from SCD 296H; G from F 254.)

interval or slightly overlapping; the group on one internode well separated from that on the next. Hydrocladia arising from the stem at right angles, the 2 rows in one plane.

Hydrocladium borne on a stem apophysis of variable length, divided into distinct internodes of variable length by constricted nodes. Each internode consisting of a slender proximal region without hydrothecae occupying up to half its length, and a wider distal region bearing 2 or 3 pairs of hydrothecae arranged in a close and overlapping group reminiscent of the genus *Dynamena*. Members of a pair of hydrothecae opposite or subopposite, not in contact with each other; the 2 rows in one plane.

Hydrotheca tubular, narrowing slightly to margin, slightly turbinate in proximal region, smoothly bent outwards in distal region, adnate for most of adcauline length, but with at least 1/10 free. Margin more or less parallel to axis of stem in cauline hydrothecae, but variable in hydrocladial hydrothecae (facing slightly downwards in the proximal pair of a group and slightly upwards in the distal pair). Aperture widened transversely, with no marginal teeth or occasionally with 2 low, rounded, lateral lobes. Operculum of 1 large abcauline valve. Hydranth with no abcauline blind pouch.

Gonothecae absent.

Measurements (mm., exclusive of regenerations).	*Holotype*	*Paratype*
Stem, normal internode, length	1·86–2·16	2·06–2·34
diameter at node	0·22–0·30	0·15–0·25
Hydrocladium, internode length	0·91–1·72	1·20–1·78
diameter at node	0·09–0·12	0·09–0·11
Hydrotheca, length abcauline (cauline only)	0·29–0·36	0·30–0·42
*length adcauline, adnate part	0·30–0·46	0·30–0·47
*length adcauline, free part	0·08–0·25	0·08–0·21
*adnate part/adcauline length	0·55–0·85	0·61–0·85
diameter at margin	0·10–0·14	0·10–0·12

*Including cauline hydrothecae and those on the distal ends of hydrocladial groups.

Remarks. This species is very distinct and easily recognized by its strictly opposite hydrocladia and marked grouping of the hydrothecae on the hydrocladia. Although quite different in appearance from *S. articulata*, it resembles this species in many details of construction and is closely related to it. It can be distinguished by:

(*a*) the position of the hydrocladium which forms a right angle with the stem,

(*b*) the more slender stem internodes,

(*c*) the nature of the hydrocladial internodes, with their slender proximal region and marked bunching of hydrothecae in the distal region,

(*d*) the hydrothecae, which are more bent outwards and are not completely adnate.

The paratype consists of 2 stems, the larger 1·9 cm. in height, in which certain irregularities occur; thus 2 of the stem internodes bear but one hydrotheca each, and there is a tendency towards stolon formation from the tips of the hydrocladia.

Genus SERTULARELLA

Remarks on the diagnosis of species

As has been indicated by Picard (1956) and Millard (1958), the shape of the hydrotheca is sometimes used as a basis for specific differentiation in *Sertularella*. Thus, Picard distinguishes between species in which the margin is tilted towards the distal end of the colony, and those in which the margin is tilted towards the base.

However, it has been found in practice that the category is not always obvious, due to variations in the curvature of the walls and elongation of one or other marginal tooth, and if such categories are to be used it is necessary that they should be more accurately defined. It is proposed, therefore, to distinguish three hydrothecal types, which are defined as follows (fig. 11):

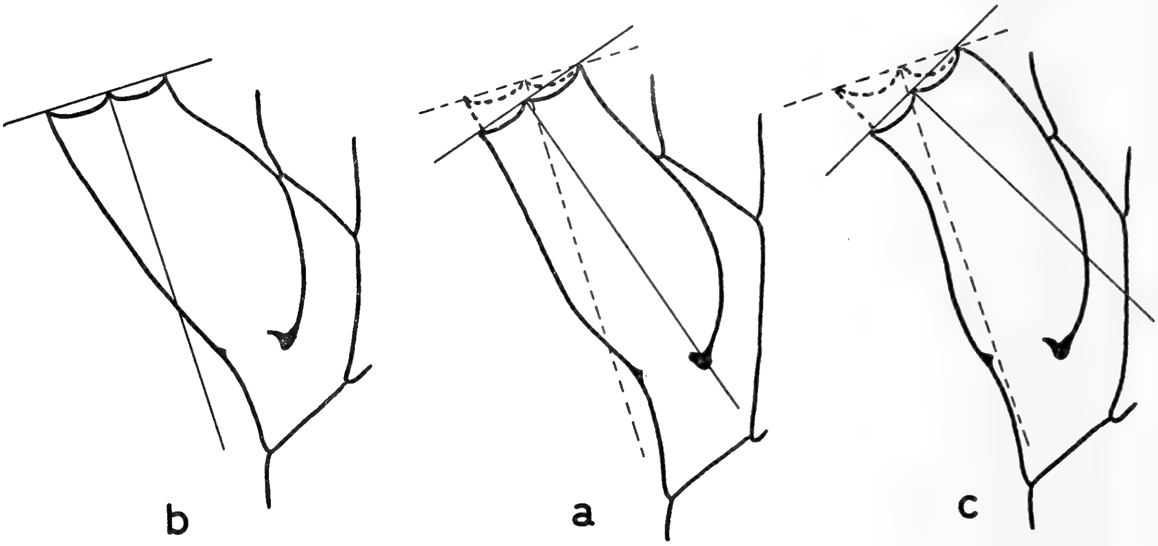

FIG. 11. *Sertularella*.
The three categories of hydrothecal shape. Types a and c could be converted to b by the enlargement of the abcauline marginal tooth (dotted lines). See text for description.

(*a*) *Hydrothecal margin perpendicular to axis.* Forms with a hydrotheca which is obviously symmetrical in lateral view, and in which a line drawn at right angles to the margin and passing through the lateral marginal tooth, will bisect the perisarcal thickening at the base of the adcauline wall, e.g. typical examples of *S. fusiformis* and *S. capensis*.

(*b*) *Hydrothecal margin tilted towards adcauline side.* Forms in which a line drawn at right angles to the margin and passing through the lateral marginal tooth will pass through the abcauline wall outside the base of the hydrotheca (e.g. *S. mediterranea*), or in less extreme examples through the hydropore (e.g. *S. africana*).

(*c*) *Hydrothecal margin tilted towards abcauline side.* Forms in which a line drawn at right angles to the margin and passing through the lateral marginal tooth will pass through the adcauline wall (distal to the perisarcal thickening at its base), e.g. *S. arbuscula*, *S. xantha*.

In the following descriptions the categories will be used in this sense. It will be seen that some species belong strictly to one particular category, but that others can vary from one to another.

Measurements

Measurements of adcauline and abcauline hydrothecal lengths are taken from the base of the hydrotheca to the tip of the respective marginal tooth across any curvature which may be present. Adcauline measurements include the perisarcal thickening at the base of the adcauline wall. All measurements are exclusive of marginal regenerations. The diameter of the internode is measured diagonally across the node.

Sertularella africana Stechow, 1919

Sertularella fusiformis: Warren, 1908: 295, fig. 5C, D.
Sertularella tenella: Stephenson, Stephenson & du Toit, 1937: 374 (listed).
Sertularella africana: Millard, 1957: 207, figs. 10I, 11F.

Records. West coast: A 382. LAM 2H, 9U. PP 1T. SB 168F. South coast: CPR 7B. E 134. S 65D (recorded by Stephenson *et al.* 1937). SAMH 208, 218. TRA 159C.

Remarks. Examination of Warren's material from Park Rynie, Natal, in the British Museum (reg. no. 22.3.6.20) confirms the identity of the above material.

Sertularella agulhensis, nov. sp.

Fig. 12A

Holotype: TRA 151F, from south coast, (South African Museum registered number, SAMH 413).

Description. Stem stiff, fascicled, reaching a maximum height of 3·2 cm., branching (and often rebranching) in a pinnate fashion, normally with 3 hydrothecae between the origins of successive branches. All branches in one plane. Nodes oblique and distinct in terminal regions, often indistinct in older parts of colony. Hydrothecae fairly closely set with the margin of one usually overlapping the base of the next, one to each internode, the two rows in one plane. Perisarc thick.

Hydrotheca adnate for about half adcauline length, distinctly annulated for most of length (about 6 annulations), with convex adcauline wall and straight or slightly concave abcauline wall. Abcauline side of margin produced more than the rest. Margin perpendicular to axis of hydrotheca or tilted slightly

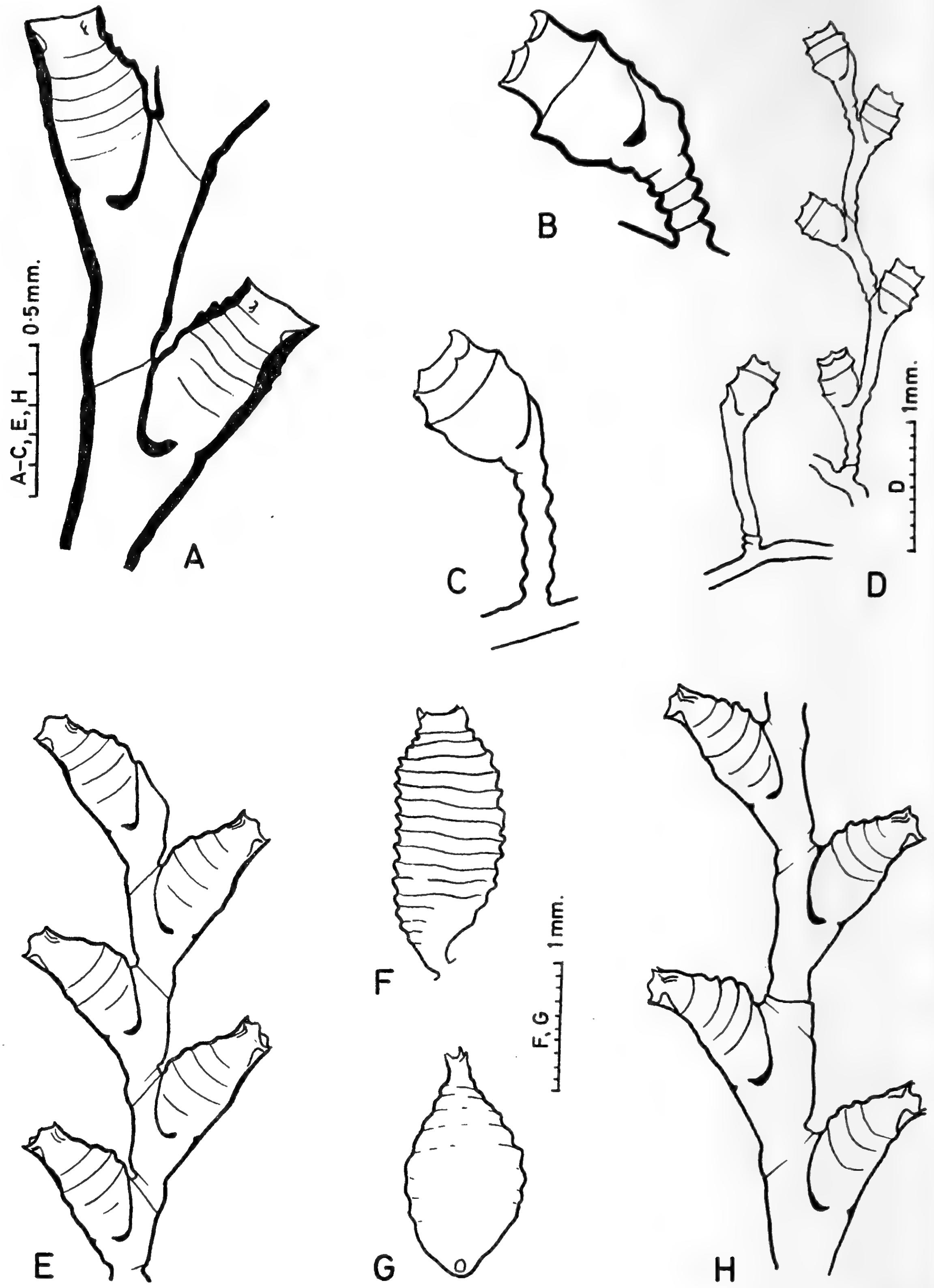

FIG. 12. *Sertularella* spp.

A. *Sertularella agulhensis* n. sp.
B.–D. *Sertularella capensis delicata* n. subsp. B and C, solitary hydrothecae. D, an upright stem and a solitary hydrotheca.
F. *Sertularella capensis capensis* Millard, gonotheca.
E, G, H. *Sertularella gilchristi* n. sp.
(A from TRA 151F, B from SAMH 294, C from SCD 50Q, D from NAD 22F, E and G from the holotype, F from SCD 37G, H from SCD 153X.)

towards adcauline side. 3 internal teeth: 1 abcauline, 2 latero-adcauline, the latter often quite small.

Gonothecae absent.

Measurements (mm.)

Internode length	0·40–0·59
diameter across node	0·24–0·33
Hydrotheca, length abcauline	0·52–0·67
length adcauline, adnate part	0·30–0·37
length adcauline, free part	0·34–0·44
adnate part/adcauline length	0·41–0·51
diameter at mouth	0·23–0·28
maximum diameter	0·31–0·37

Remarks. This species resembles *S. mediterranea* in the shape of the hydrotheca and in the presence of 3 internal teeth, but differs from it in the fascicled stem and annulated hydrotheca.

The structure of the hydrotheca strongly resembles that of *S. richardsoni* Ralph, 1961, but *S. agulhensis* differs from it in the smaller size of the parts and in the fascicled stem.

Sertularella arbuscula (Lamx., 1816)

Sertularia polyzonias: Busk, 1851: 118 (pp.)
Sertularia arbuscula?: Busk, 1851: 118.
Sertularella tumida Warren, 1908: 297, fig. 6A–C. Jarvis, 1922: 342.
Sertularella arbuscula var. *quinquelaminata* Leloup, 1934: 1, figs. 1–3.
Sertularella arbuscula: Millard, 1957: 208, figs. 10B, 11C. Millard, 1958: 188. Millard, 1961: 204.

Records. West coast: A 381. SB 194K. WCD 34H, 81D. South coast: KNY 30N, 71E (reported by Day *et al.* 1952). LIZ 16D. MB 8L, 15C, 64H. SAMH 155, 182, 204, 213, 216, 228, 234, 288, 318. SCD 37C, 61B, 75D, 85D, 117H, 153U, 169Z, 175H, 184P, 354E. TRA 35F, 38F, 42F, 92S, 156G.

Remarks. I have examined specimens of Jarvis's material of *S. tumida* from the Indian Ocean and Warren's material of *S. tumida* from Algoa Bay in the British Museum of Natural History, and can confirm their identity as typical *S. arbuscula.* Unfortunately Warren's material from Park Rynie, Natal, (Warren, 1908, fig. 6B) was not available, but I feel that Stechow (1925, p. 485) was wrong in assigning it to *S. pulchra*, which species is easily distinguished by the adcauline annulations and 4 internal teeth. I have seen unmistakable material of *S. arbuscula* in which some of the hydrothecae are very little bent out as in Warren's diagram, and I have also seen gonothecae which are corrugated in the distal region.

The presence of 2 extra internal teeth (var. *quinquelaminata* of Leloup) is a common variation (found also in *S. mediterranea*), but usually occurs only in some hydrothecae of a colony.

Sertularella capensis capensis Millard, 1957
Fig. 12F

Sertularella capensis Millard, 1957: 210, fig. 10H.

Records. South coast: SAMH 272. SCD 37G, 79K.

Description. Three colonies similar to holotype.

Female gonothecae (not previously described) borne on front of stem, each arising just below the base of a hydrotheca. Spindle-shaped, distinctly annulated throughout, with 4 (or occasionally more) marginal spines. No external marsupium and eggs released within the gonotheca.

Remarks. See under subspecies *delicata*.

Sertularella capensis delicata nov. subsp.
Fig. 12B–D

Sertularella tenella: Hartlaub, 1901: 64, pl. 5 (fig. 24), (material from Algoa Bay).

Types and Records. Holotype: (NAD 22F) (South African Museum registered number, SAMH 414). Other records: SAMH 294, SCD 50Q.

Description of holotype. Stem short, slender and geniculate; unbranched; bearing a small number of hydrothecae (up to 8 observed) and sometimes only one; usually annulated at base and in the region of nodes.

Hydrotheca similar in shape and appearance to the nominate subspecies, but with a smaller proportion of the adcauline wall adnate (less than half); with one or two distinct ridged annulations; mouth rounded in section.

Gonophores absent.

Measurements (mm.)

	Holotype	*SAMH* 294
Internode length	0·49–0·97	
diameter across node	0·10–0·13	
Hydrotheca, length abcauline	0·34–0·45	0·40–0·45
length adcauline, adnate part	0·20–0·24	0·20–0·22
length adcauline, free part	0·25–0·34	0·34–0·35
adnate part/adcauline length	0·37–0·46	0·36–0·39
diameter at mouth	0·25–0·29	0·28–0·30
maximum diameter	0·30–0·37	0·41–0·43

Remarks. The samples other than the holotype consist almost entirely of solitary hydrothecae, and stems bearing more than one hydrotheca are rare. Such specimens are similar to the material from Algoa Bay described and figured by Hartlaub in 1901 and ascribed by him to *S. tenella*. With this diagnosis I do not agree, as the hydrotheca of *S. tenella* has more annulations, a smaller proportion of the adcauline wall adnate to the stem and a narrower, squared mouth. The proportion between the diameter at the mouth and the abcauline length is 0·59–0·79 mm. in the holotype of *S. capensis delicata*, as against 0·39 mm. in typical *S. tenella* (from Stechow's measurements, 1923c, p. 186).

That the solitary hydrotheca is merely a young stage of an upright stem is shown by the presence of both on the same hydrorhiza. Moreover, in the solitary hydrotheca there is an extension of the internode along one wall containing a bud of coenosarc, which will obviously form the continuation of the stem at a later stage. This extension is visible in Hartlaub's diagram, and also in Leloup's diagram of *Thyroscyphus intermedius* f. *peculiaris* (1935, fig. 15) indicating that the latter is merely a young *Sertularella*. *Sertularella campanulata* Warren, 1908, however, has no such extension and can justifiably be included in a separate genus, i.e. *Calamphora*.

The subspecies *delicata* differs from the young stems and branches of the nominate subspecies in the more slender stem with annulations and a hydrotheca which has a smaller proportion adnate to the internode.

S. capensis shows some resemblances to *S. gayi* var. *annulata* Allman, 1888, as revised by Billard, 1910, p. 10, fig. 3, but differs from it in the growth-form.

Sertularella congregata nov. sp.

Fig. 13A–D

Types. Holotype: SCD 254Q (South African Museum registered number, SAMH 415). Paratype: SAMH 185. Both from South coast.

Description. Colonies reaching a maximum height of 6–7 cm. Stem stiff, thick and fascicled, giving off alternate hydrocladia, which are all in one plane. Long, fascicled branches, similar to the stem in structure, often replacing hydrocladia. Segmentation not visible in fascicled part of stem and branches, but oblique nodes usually visible in the distal, unfascicled parts (faint in holotype, distinct in paratype). One hydrotheca to each internode and one hydrocladium normally arising at the base of every third hydrotheca. Hydrothecae on stem moderately closely set, the margin of each just overlapping the base of the next on the opposite side.

Hydrocladia with nodes invisible in distal regions. Hydrothecae crowded, the margin of one often reaching half-way up the length of the next on the opposite side, and sometimes even to the base of the next on the same side. The two rows of hydrothecae in the same plane. The hydrocladium usually starts with several well-spaced hydrothecae separated by oblique nodes, and the crowding and disappearance of nodes becomes more pronounced towards the distal end.

Hydrotheca adnate for half or more of adcauline length, then bent smoothly outwards with margin tilted towards abcauline side. The sides parallel for almost entire length, though usually narrowing very slightly near margin. Marginal teeth low. No internal teeth. A pronounced perisarcal thickening present on abcauline wall below margin, and continued as an annular ridge for about half-way round hydrotheca. Margin often regenerated.

Gonotheca borne on hydrocladium and flattened against its surface, with about 8 low annulations in distal region, and with 5 short, conical, marginal spines.

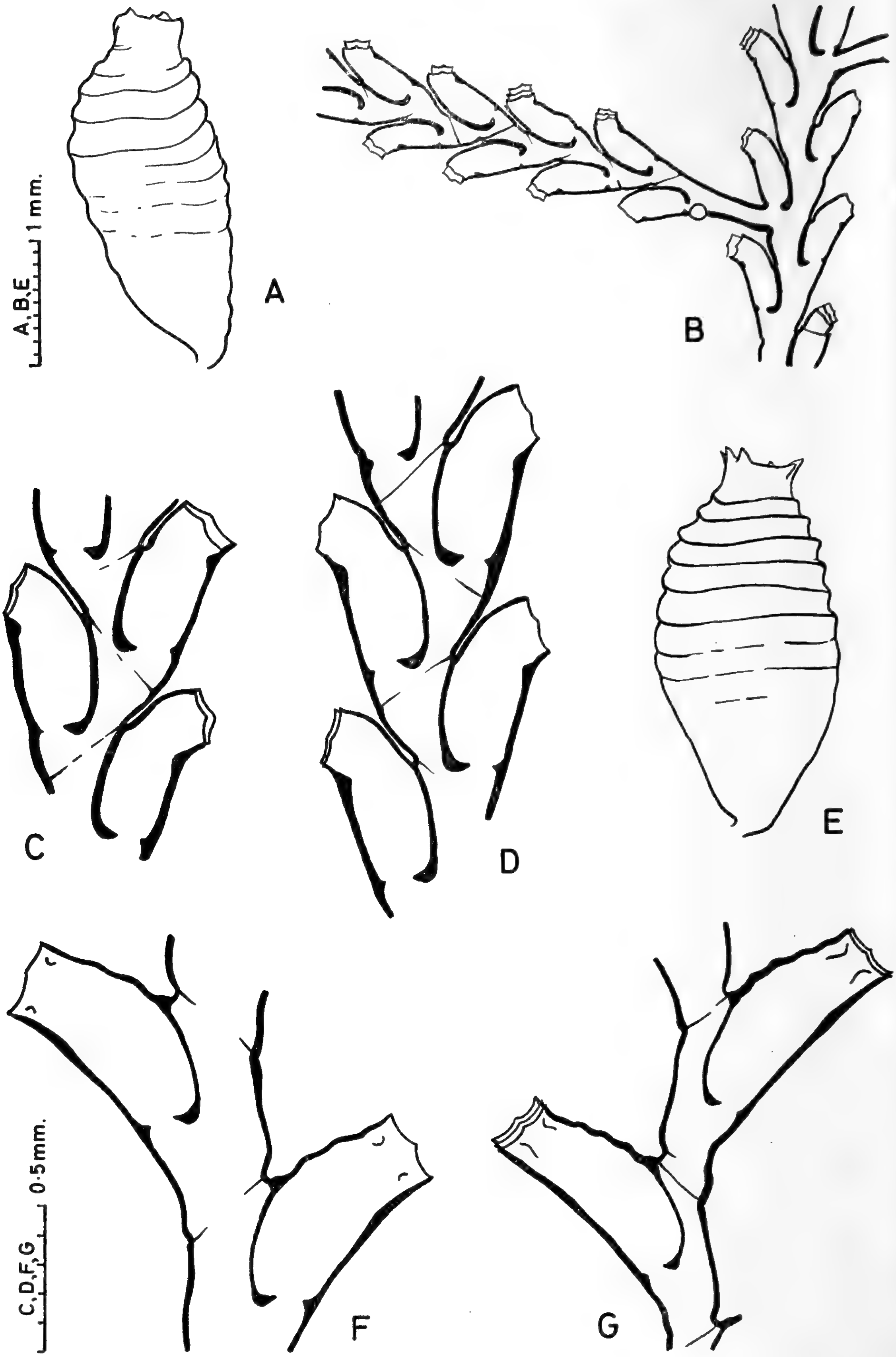

Fig. 13. *Sertularella* spp.

A.–D. *Sertularella congregata* n. sp. A, gonotheca. B, portion of stem and hydrocladium. C and D, a few hydrothecae from hydrocladium.

E.–G. *Sertularella pulchra* Stechow.

(A–C from holotype, D from SAMH 185, E–F from SCD 37H, G from SAMH 219.)

Measurements (mm.)

	Holotype	*Paratype*
Internode length (stem)	0·40–0·42	0·35–0·46
Hydrotheca, length abcauline	0·39–0·46	0·37–0·45
length adcauline, adnate part	0·35–0·41	0·38–0·43
length adcauline, free part	0·28–0·36	0·26–0·33
adnate part/adcauline length	0·49–0·58	0·54–0·62
diameter at mouth	0·19–0·21	0·20–0·22
maximum diameter	0·24–0·27	0·25–0·27
Gonotheca (2 only), length	2·88	
maximum diameter	1·16–1·28	

Remarks. This species shows a superficial resemblance to *S. diaphana*, *S. lata*, *S. quadridens* and others, where the nodes on the hydrocladia occur at irregular intervals, and where the nodes on the stem occur after every third hydrotheca. The fundamental difference in *S. congregata* is that the nodes, when visible, occur after every hydrotheca, both on the stem and hydrocladia, but on the distal parts of the hydrocladia the nodes seem to be eliminated by the crowding of the hydrothecae. *S. congregata* also differs from *S. diaphana* in the nature of the gonotheca.

Sertularella dubia magna Millard, 1958

Fig. 14A–F

Sertularella dubia var. *magna* Millard, 1958: 189, fig. 7A.

Records. West coast: ?LAM 30L (young colony). South coast: SAMH 186, 252, 282. SCD 79J, 82L, 85C, 108G, 112C, 320K.

Description. A number of colonies, all (except LAM 30L, which is unbranched) with stiff, fascicled stems branching in one plane and in a pinnate manner.

Hydrothecae rather variable in structure and appearance—some are comparatively short and fat with well-marked abcauline thickenings as illustrated by Billard, 1907, fig. 3 and Millard, 1958, fig. 7A; others are more slender with distinct corrugations on the adcauline wall and poorly developed abcauline thickenings; and still others show a tendency for an elongation of the abcauline marginal tooth so that the margin becomes tilted towards the adcauline side. Internal hydrothecal teeth never present.

Gonotheca (not previously described) distinctly annulated in distal region, with a short terminal neck bearing 2–7 small spines (usually 5–6). Arising opposite the base of a hydrotheca. All female where the sex could be definitely ascertained. One colony (part of SCD 112C) with practically smooth gonothecae (possibly male).

Measurements (mm., excluding LAM 30L, which is a doubtful record)

Internode length	0·40–0·72
diameter across node	0·20–0·39

Hydrotheca, length abcauline	0·48–0·65
length adcauline, adnate part	0·32–0·53
length adcauline, free part	0·31–0·46
adnate part/adcauline length	0·45–0·58
diameter at mouth	0·22–0·30
maximum diameter	0·31–0·43
Gonotheca, length	2·67–3·94
maximum diameter	1·06–1·48

Remarks. The variability of the shape of the hydrotheca in this species has been the cause of some hesitation in identification, and there appear to be 3 common forms: (i) the short, fat hydrotheca with the margin tilted towards the abcauline side and a well-developed abcauline thickening, as originally described (fig. 14A, B), (ii) a longer hydrotheca with thinner perisarc and distinct adcauline corrugations (fig. 14C), and (iii) a hydrotheca with the margin tilted towards the adcauline side due to elongation of the abcauline marginal tooth (fig. 14F). These forms cannot be separated as distinct species or subspecies, as intergrading forms occur, and specimens in the same sample may vary from form (i) to form (ii), or from form (ii) to form (iii). The macroscopic appearance of the colony and the structure of the gonotheca is identical in all cases.

All the specimens described have greater dimensions than those quoted by Billard, 1907, for the nominate subspecies, and can thus be included in the subspecies *magna*. So far no overlap has been observed.

The form with adcauline thecal corrugations shows resemblances to *S. gayi* var. *robusta* Allman, 1874, but the gonothecae are different (those of *S. gayi* possessing a bilabiate aperture) and the measurements are not so great as those quoted by Billard in 1906 (p. 185) for var. *robusta*.

Some of the specimens also show resemblances to *S. crassicaulis* (Heller), but the latter species has a dichotomously branched stem.

Sertularella falsa Millard, 1957

Sertularella ?tumida: Day, Millard & Harrison, 1952: 404 (listed).
Sertularella falsa Millard, 1957: 211, figs. 10F, 11D.

Records. South coast: KNY 70F (reported by Day *et al.* 1952).

Sertularella flabellum (Allman, 1886)

Sertularella flabellum: Millard, 1957: 212, figs. 10G, 11G. Millard, 1958: 190.

Records. West coast: TB 21D. WCD 12B. South coast: MB 47U. SAMH 171, 178, 205, 217, 263, 312. SCD 5B, 29M, 36Y, 52Q, 56S, 85E, 106P, 112B, 153S, 175J, 206N, 265K, 290S, 320J. TRA 59S, 92P, 151J.

Sertularella fusiformis (Hincks, 1861)

Sertularella ellisii f. *ellisii:* Picard, 1956: 264, fig. 3d, e.
Sertularella fusiformis: Millard, 1957: 213, figs. 10C–D, 11E.

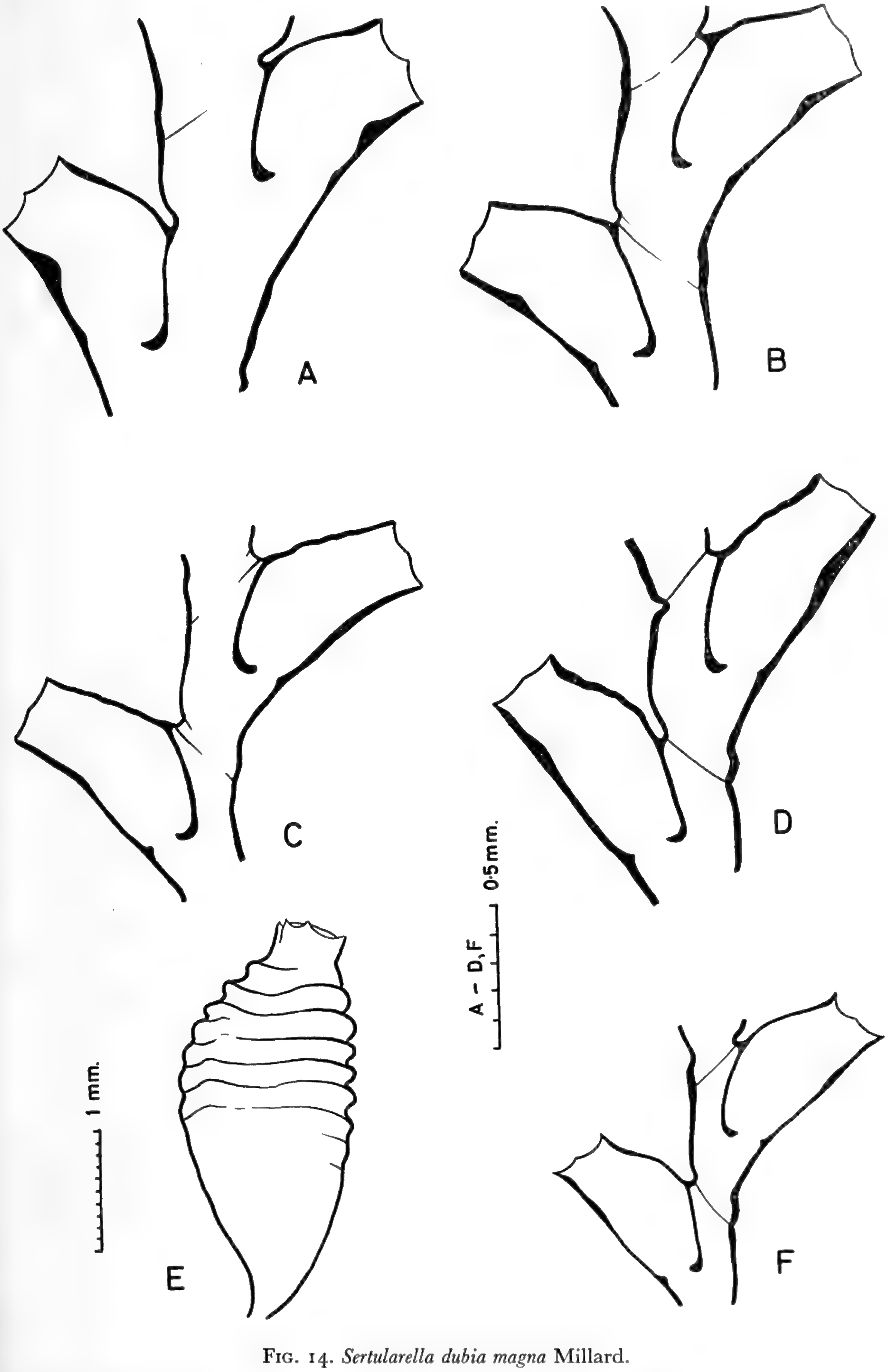

FIG. 14. *Sertularella dubia magna* Millard.
A.–D., F. Hydrothecae from various colonies to show variation in shape.
E. Gonotheca.
(A from PF 12308H (False Bay), B from SAMH 252, C and E from SAMH 282, D from SCD 112C, F from SCD 85C.)

Records. West coast: B 105, 114B. CP 336B. PP 1S, 4M. South coast: MB 24W. SAMH 231, 271. SCD 37F, 61E, 75E.

Remarks. Picard in 1956 has included *S. fusiformis* in *S. ellisii,* but does not seem to have considered the question of the number and position of internal hydrothecal teeth. In his diagrams he shows internal teeth situated immediately below the marginal teeth, which is certainly not the case in South African material allocated to *S. fusiformis,* where internal teeth alternate with the marginal teeth. Stechow, 1923c, described *S. ellisii* as possessing 3 *small* internal teeth (thus differing from *S. mediterranea* where the teeth are large), and until more work has been done on the variability of this character. I prefer to retain *S. fusiformis* as a separate species. The number of internal teeth in the latter is known to be variable, but as has been pointed out before (Millard, 1957, p. 214; 1958, p. 187) the position in South African material at any rate is constant, and differs from that in *S. ellisii.*

Sertularella gilchristi nov. sp.

Fig. 12E, G, H.

Types and Records. Holotype: SCD 85J (South African Museum registered number SAMH 416). Other records: SCD 153X. Both from south coast.

Description of holotype. Stem thick, fascicled, reaching 5·0 cm. in height, branching and rebranching profusely in an irregular pinnate fashion, but not necessarily in one plane. General effect bushy. Terminal branches not geniculate, with distinct oblique nodes and sometimes an annulation above each node. Internodes of variable length, each with one hydrotheca.

Hydrotheca swollen below and narrowing very markedly to margin; adnate for a little less than half adcauline height; symmetrical, or (more commonly) bent outwards with margin tilted towards abcauline side; annulated, with 3 or more annulations passing all round hydrotheca or (less commonly) with annulations indistinct or confined to adcauline surface. Margin with 4 teeth, of which the abcauline one may project slightly more than the others. 3 well-developed internal teeth, 1 abcauline and 2 latero-adcauline.

Gonotheca fusiform, annulated in distal region, with 3 or 4 spines at the distal end of the slender terminal region.

Measurements (mm.)	*Holotype*	*SCD* 153*X*
Internode length	0·28–0·45	0·39–0·53
diameter across node	0·13–0·22	0·15–0·23
Hydrotheca, length abcauline	0·33–0·41	0·36–0·41
length adcauline, adnate part	0·22–0·27	0·23–0·27
length adcauline, free part	0·24–0·34	0·26–0·35
adnate part/adcauline length	0·40–0·48	0·40–0·49
diameter at mouth	0·11–0·14	0·12–0·13
maximum diameter	0·21–0·24	0·22–0·25
Gonotheca, length	1·84–1·86	
maximum diameter	0·97	

Remarks. This species shows strong resemblances to *S. robusta* Coughtrey, 1875 (see Trebilcock, 1928: 16, and Ralph, 1961: 824), but differs from it in the fascicled and freely branching stem, and also to a lesser extent in the shape of the hydrotheca which has a decidedly narrower mouth.

Sertularella goliathus Stechow, 1923

Sertularella goliathus: Millard, 1957: 215, figs. 10A, 11A.

Records. West coast: WCD 7P. South coast: SCD 106Q. TRA 37N.

Sertularella mediterranea mediterranea Hartlaub, 1901

Sertularella mediterranea: Millard, 1957: 215, figs. 10E, 11B. Hamond, 1957: 316, fig. 24. Millard, 1958: 190. Vervoort, 1959: 272, fig. 33a.
Sertularella ?gaudichaudi: Day, Millard & Harrison, 1952: 404 (listed).
Sertularella ellisii f. *mediterranea:* Picard, 1956: 264, fig. 3b.

Records. South coast: A 123, 384B. KNY 57J (recorded by Day *et al.* 1952). SAMH 206.

Sertularella mediterranea asymmetrica Millard, 1958

Sertularella mediterranea Hartlaub var. *asymmetrica* Millard, 1958: 191, fig. 7B.

Records. South coast: CPR 9D. SAMH 270. SCD 60Y.

Sertularella megista Stechow, 1923

Sertularella polyzonias f. *robusta* Kirchenpauer, 1884: 38.
Sertularella polyzonias var. *robusta:* Hartlaub, 1901: 88, pl. 5 (fig. 1). Stechow, 1925: 479.
Sertularella megista: Stechow, 1925: 480, fig. 36. Millard, 1957: 217, figs. 10L, 11J.

Records. West coast: WCD 12A, 56L. South coast: AFR 945M. MB 47V, 52H, 64J. SAMH 181, 246, 310, 316. SCD 5D, 37E, 52R, 85F, 96C, 108E, 153T, 175K, 239C, 254R, 265C, 290R, 320J.

Description. Numerous colonies from all round the coast, the tallest reaching a height of 10·3 cm. Most colonies are unfascicled and sparsely branched, and individual stems may reach a length of over 7 cm. without branching. Only the sturdiest colonies are fascicled, and these only to a small extent and in the basal region. The stems, thus, usually have a flexuous appearance, surprisingly so for a species with so thick a perisarc.

With the abundant material available it is apparent that there is great variation in length of internode and size of hydrotheca. New measurements are thus included to illustrate the range of variation in the species.

The hydrotheca is characterized by a sharp bend in the adcauline wall at the point where it separates from the stem, but the angle of the margin is influenced by the amount of bending and the length of the abcauline marginal tooth, which may be produced. Normally the margin is perpendicular to the axis, but when the bend is marked (and the angle within the hydrotheca lies between 110° and 120°) it is tilted towards the abcauline side, and when the bend is less marked (with the internal angle over 125°) and the abcauline tooth produced it is tilted towards the adcauline side.

Measurements (mm., complete range, including False Bay material described in 1957).

Internode length	0·71–1·52
diameter across node	0·40–0·82
Hydrotheca, length abcauline	0·80–1·28
length adcauline, adnate part	0·67–1·08
length adcauline, free part	0·34–0·72
adnate part/adcauline length	0·55–0·71
diameter at mouth	0·33–0·52
maximum diameter	0·47–0·72
Mature gonotheca, length	3·33–4·03
maximum diameter	0·85–1·90

Remarks. I have included in the synonymy of this species Kirchenpauer's material of *S. polyzonias* f. *robusta* from the Cape of Good Hope. Kirchenpauer's type material unfortunately no longer exists, but was examined and illustrated by Hartlaub in 1901, and I agree with the latter author that it should be removed from *S. polyzonias*. The hydrotheca has the typical angle in the adcauline wall characteristic of *S. megista*, and the size is within range.

Sertularella polyzonias (Linn., 1758)

Sertularella polyzonias: Millard, 1957: 217, figs. 10J, 11H. Millard, 1958: 191. Millard, 1961: 205.

Records. West coast: TB 10, 12A, 21G. South Coast: MB 47W. SAMH 175. SCD 37J, 85G, 112D, 153W, 175L.

Sertularella pulchra Stechow, 1923

Fig. 13E–G

Sertularella pulchra Stechow, 1923b: 113. Stechow, 1925: 485, fig. 39.

Records. South coast: SAMH 219, 313. SCD 37H, 154L, 296J.

Description. Fascicled stems reaching a maximum height of 4·8 cm. and bearing alternate hydrocladia, which are usually very regular in arrangement, one arising below the base of every third hydrotheca. The 2 rows of hydrocladia in one plane.

Hydrothecae generally as described by Stechow, though in most colonies a few of the hydrothecae are bent gently away from the stem, with the adcauline wall slightly convex and the abcauline wall slightly concave (fig. 13 F). As a result the margin is perpendicular to the axis or tilted towards the abcauline side. Adcauline striations very obvious, and only rarely absent. 4 internal teeth, alternating with the marginal teeth, sometimes incomplete in young parts of the colony.

Gonothecae of 2 types. Empty ones, presumably male, as described by

Stechow, with narrow distal end and 4 marginal spines. Female similar, but with wider distal end and 5–6 short marginal spines (fig. 13 E).

Measurements (mm.)		*Stechow's material from Simon's Bay*
Internode length	0·43–0·82	0·49–0·63
diameter across node	0·20–0·42	0·16–0·34
Hydrotheca, length abcauline	0·58–0·78	0·58–0·72
length adcauline, adnate part	0·32–0·46	0·35–0·44
length adcauline, free part	0·36–0·46	0·39–0·56
adnate part/adcauline length	0·44–0·55	0·40–0·53
diameter at mouth	0·21–0·28	0·21–0·28
maximum diameter	0·29–0·38	0·31–0·36
Gonotheca, length	2·95–3·42	2·33–2·84
maximum diameter	0·99–1·63	0·93–1·31

Remarks. I have seen two mounted slides of Stechow's material from Simon's Bay (loaned by the Munich Museum) which confirm the identity of this material. Measurements taken from Stechow's material are included above for comparison.

Stechow includes in *S. pulchra* part of Warren's material described under the name of *S. tumida* (material from Park Rynie, 1908 fig. 6B). With this I do not agree, as Warren shows no striations on the hydrothecae and only 3 internal teeth. His material can probably be included in *S. arbuscula*.

Sertularella striata Stechow, 1923
Fig. 15

Sertularella striata Stechow, 1923: 10. Stechow, 1925: 470, fig. 30.

Records. South coast: LIZ 7Z. MB 64K. SCD 85H.

Description. Stems reaching a maximum height of 1·1 cm., usually unbranched, but occasionally giving off 1 or 2 small branches which arise immediately below a hydrotheca. Details of structure and measurements as described by Stechow.

Gonotheca (not previously described) arising from stem opposite the base of a hydrotheca, annulated throughout, or with annulations becoming indistinct in basal third. Margin with 3 or 4 minute spines. Female with external marsupium.

Measurements (mm.)	*Present material*	*Stechow's material*
Internode length	0·30–0·76	0·45–0·77
diameter across node	0·10–0·16	0·10–0·15
Hydrotheca, length abcauline	0·36–0·48	0·41–0·47
length adcauline, adnate part	0·20–0·26	0·21–0·26

length adcauline, free part	0·18–0·31	0·25–0·34
adnate part/adcauline length	0·39–0·56	0·40–0·49
diameter at mouth	0·15–0·21	0·17–0·23
maximum diameter	0·23–0·30	0·23–0·30
Gonotheca, length	1·35–1·79	
maximum diameter	0·86–0·95	

Remarks. The identity of this material was confirmed by comparison with a mounted slide of Stechow's material from the Agulhas Bank, kindly loaned by the Munich Museum. The measurements of the latter are included above for comparison.

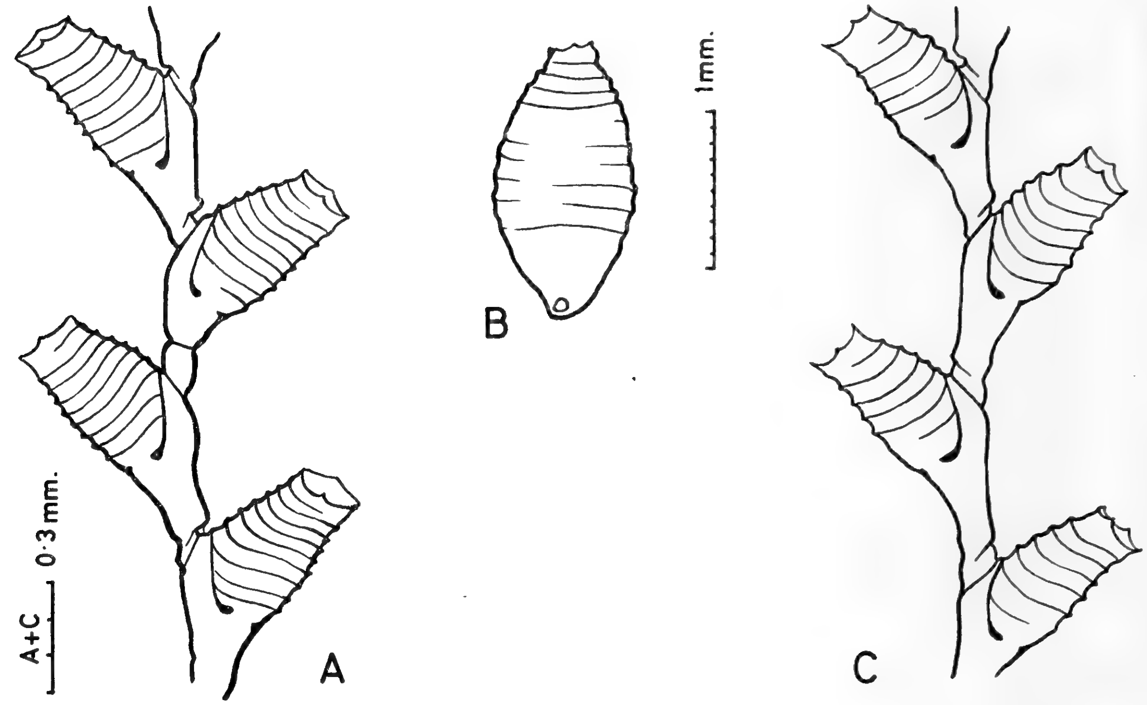

Fig. 15. *Sertularella striata* Stechow.
A. and C. Hydrothecae from different colonies.
B. The gonotheca.
(A and B from SCD 85H, C from LIZ 7Z.)

The species shows variability in the length of internode, which may be shorter or longer than that illustrated by Stechow; in the degree of annulation on the hydrothecal walls, which may be less marked; in the proportion of the adcauline thecal wall adnate to the stem; and in the angle of the thecal margin. The latter may be perpendicular to the axis as illustrated by Stechow, but may also be tilted towards the adcauline side. This is the case in some of the hydrothecae on Stechow's slide, and in most of the hydrothecae in the present material.

This species is closely related to *S. africana*, differing from it in the greater number of more distinct annulations which extend over the full length of the hydrotheca.

Sertularella xantha Stechow, 1923

Sertularella xantha: Millard, 1957: 218, figs. 10K, 11I.

Records. West coast: TB 12B. WCD 30U. South coast: SAMH 146, 154, 220, 325, 334, 348. SCD 33C, 103E, 104E, 108F, 113F, 114F, 115N, 122W, 126K, 141J, 145B, 184Q, 191R, 219W, 239D, 258P, 276T, 290Q, 322G, 324J, 345A. TRA 33L, 35A, 38B, 42E, 56V, 92T.

Sertularia distans gracilis Hassall, 1848

Sertularia heterodonta Ritchie, 1909: 79, fig. 4. Jarvis, 1922: 339.
Sertularia distans var. *gracilis:* Billard, 1925: 175, fig. 33. Leloup, 1935: 47, figs. 28, 29. Millard, 1957: 221, fig. 12. Millard, 1958: 193. Pennycuik, 1959: 197.

Records. South coast: BRE 60R. CPR 7C. LIZ 13E. MB 24R. SAMH 266. SCD 37Y, 50M, 85Q, 112E.

Description. A number of colonies, none taller than 0·8 cm., all with unbranched stems, except in a few instances where side-branches arise from within hydrothecae. Distance between consecutive pairs of hydrothecae very variable, and internodes sometimes very long and slender, as illustrated by Ritchie, 1909, for *S. heterodonta.* Internal pegs of perisarc in lower part of hydrotheca very characteristic, and internal teeth in distal region below margin also common—1 abcauline (fairly common), or 1 abcauline and 2 latero-adcauline (more rare and in occasional hydrothecae only).

Gonothecae present in 2 colonies, as illustrated by Leloup, 1935; female with external marsupium.

Remarks. Examination of Ritchie's type material of *S. heterodonta* (on loan to the British Museum) showed that this species is distinguished from the common form of *S. distans gracilis* only by the presence of 3 internal hydrothecal teeth, longer and more slender internodes, and slightly smaller hydrothecae. The last 2 characters can be attributed to variations in growth-form which are paralleled in the South African material. The presence of a single abcauline internal tooth has been reported in *S. distans gracilis* by a number of authors, and the presence of 2 extra latero-adcauline internal teeth (which were not present in all the hydrothecae of the type material) is here reported in South Africa. I therefore include *S. heterodonta* Ritchie as a synonym for *S. distans gracilis.*

Sertularia marginata (Kirch., 1864)

Sertularia marginata: Millard, 1957: 224, fig. 13. Ralph, 1961: 785, fig. 12a–g (synonymy).

Records. South coast: SCD 305D.

Description. A young colony consisting of 5 stems reaching a maximum height of 0·6 cm., of which one bears 1 branch, another 2, and the rest are simple.

Sertularia turbinata (Lamx., 1816)

Sertularia loculosa: Bale, 1884: pl. 4 (figs. 5, 6), pl. 9 (fig. 12), pl. 19 (fig. 9). Bale, 1913: 121, pl. 12 (figs. 7, 8). Warren, 1908: 306, fig. 8. Jarvis, 1922: 340.

Sertularia brevicyathus: Nutting, 1904: 60, pl. 6 (figs. 1, 2). Jarvis, 1922: 338, pl. 24 (fig. 6).
Tridentata acuta Stechow, 1921: 231. Stechow, 1923c: 207.
Sertularia turbinata: Billard, 1925: 177, fig. 34. Millard, 1958: 197, fig. 8B. Vervoort, 1959: 275, figs. 35, 36.
Sertularia restricta Totton, 1930: 205.
Sertularia acuta: Millard, 1958: 192, figs. 8A, F.

Records. South coast: MB 58E. SCD 85S.

Description. Two small colonies reaching a maximum height of 0·7 cm. One of them (MB 58E) is an old colony with thick perisarc and smoothly worn hydrothecal margins; the whole surface is thickly overgrown with epiphytes. In both colonies the nodes tend to be indistinct, particularly near the proximal end of a stem.

Remarks. Up to the present time *S. acuta* (Stechow) has been held to be separate from *S. turbinata* (Lamx.), although Billard (1925: 178), was dubious about the matter, remarking that the former species differs from the latter only in the shorter internodes, and in the shorter hydrothecae which narrow more abruptly to the margin.

The two samples in this collection are intermediate between the material of *S. acuta* and *S. turbinata* previously described (Millard, 1958) in internode length and abcauline thecal length, and the 4 samples together form a perfect gradation from one extreme to the other. It is thus no longer possible to keep the two species separate, and *S. acuta* must be considered as a somewhat stunted growth-form of *S. turbinata.* Selected measurements (in mm.) of the 4 samples are included for comparison:

	Internode length	*Hydrotheca, length abcauline*	*Hydrotheca, diameter at margin*
RHB 52C	0·39–0·54	0·16–0·21	0·09–0·12
SCD 85S	0·52–0·62	0·19–0·22	0·09–0·11
MB 58E	0·55–0·76	0·22–0·32	0·13–0·16
PZ 13B	0·66–0·85	0·25–0·31	0·12–0·17

In all 4 samples the hydrotheca is very similar in appearance, and grades evenly from the form illustrated for *S. acuta* (Millard, 1958: fig. 8A) to that of *S. turbinata* (Millard, 1958: fig. 8B).

The gonothecae of *S. turbinata* have now been described by Vervoort (1959: fig. 36 b, c) and are exactly similar to those of *S. acuta* (Millard, 1958: fig. 8F; Warren, 1908: fig. 8D), except for the presence of 2 minute distal spines in the former.

It was previously thought (Millard, 1958: 198) that the nature of the nodes was a distinguishing character between *S. acuta* (straight) and *S. turbinata* (oblique). But the new material has shown that this is a variable character and the nodes may be straight, oblique or invisible, and further that both straight and oblique nodes may occur on the same stem. This is discounting the hinge-joints, which always form the termination of an extra athecate internode and which occur quite irregularly.

S. turbinata is closely related to *S. ligulata* Thornely, and the difference between them is largely one of shape, which is obvious to the eye, but which is not shown up at all clearly by the measurements, due mainly to the tendency for variation between the proximal and distal regions of a stem in both species. In *S. ligulata* the members of a pair of hydrothecae are more erect and tend to diverge at a higher level than in *S. turbinata.* As a result the hydrothecae of the former are in general contiguous and adnate for a greater length, and the maximum diameter across a pair tends to be less. *S. ligulata* also has a slightly wider thecal mouth and lower marginal teeth (Millard, 1958: figs. 8B, 9A, B). If these 2 species are to be kept separate, the presence of a ligula in *S. ligulata* cannot be used as a specific character, as it is also clearly evident in a mounted specimen of *S. turbinata* (MB 58E). As a rule specimens are not sufficiently well preserved to determine the presence or absence of this character.

Symplectoscyphus arboriformis (Markt., 1890)

Sertularella arboriformis Marktanner-Turneretscher, 1890: 228, pl. 4 (fig. 5). Stechow, 1912: 358, fig. C.

Records. West coast: SAMH 409. WCD 81L. South coast: SAMH 156, 172, 184, 207, 311, 317. SCD 5C, 37D, 61C, 75C, 138K, 290T. TRA 92Q.

Description. Colonies reaching a maximum height of 11·0 cm., some with gonothecae. Structure agreeing perfectly with Marktanner's description.

Measurements (mm.)		*Stechow's material*
Internode length	0·60–0·80	0·51–0·78
diameter across node	0·17–0·33	0·19–0·42
Hydrotheca, length abcauline	0·34–0·47	0·46–0·63
length adcauline, adnate part	0·31–0·40	0·28–0·43
length adcauline, free part	0·38–0·46	0·35–0·50
adnate part/adcauline length	0·42–0·51	0·36–0·53
diameter at mouth	0·28–0·38	0·25–0·35
Gonotheca, length	1·35–1·92	1·46–1·75
maximum diameter	0·71–0·96	0·81–0·96

Remarks. Two slides of Stechow's material from Algoa Bay were examined by courtesy of the Munich Museum. The measurements are included above for comparison.

Symplectoscyphus macrogonus (Treb., 1928)

Sertularella macrogona Trebilcock, 1928: 11, pl. 1 (fig. 4).
Symplectoscyphus macrogonus: Millard, 1957: 219. Ralph, 1961: 798, fig. 14 a, b.

Records. West coast: BB 13P. CP 379, 650B. LAM 2G, 7M, 9T, 13J, 14S, 18L, 23M, 30K, 35E, 40P, 41G, 46M, 59B. PP 1U. SB 150D, 161Y, 194L, 253D. TB 11, 21F. WCD 81J, 100T. South coast: BMR 23N. SAMH 265. SCD 179C.

Thyroscyphus aequalis Warren, 1908

Fig. 16

Thyroscyphus ramosus: Billard, 1907: 342.
Thyroscyphus aequalis Warren, 1908: 344, pl. 48 (figs. 38–40), fig. 23. Jarvis, 1922: 337. Millard, 1958: 199.
Thyroscyphus regularis: Ritchie, 1910: 811, pl. 77 (fig. 7). Jäderholm, 1923: 5. Stechow, 1925: 463.
Cnidoscyphus aequalis: Splettstösser, 1929: 82, 124, figs. 78–82. Kramp, 1947: 13.

Records. South coast: SAMH 173, 251, 268, 350, 379. SCD 29L, 37A, 61D, 79L, 84J, 94F, 117J, 153R, 169X, 254S, 265D. TRA 23B, 35D, 38D, 56T, 92A.

Description. Numerous samples, some consisting of a few fragments only, the largest reaching 40 cm. in height. Stem weakly fascicled at base in larger colonies only, branching in an irregularly alternate manner. Nodes distinct or only faintly indicated. Hydrotheca-bearing apophysis without basal septum. Hydrothecal pedicel about half width of apophysis, spirally annulated to a varying degree, often regenerated.

Hydrotheca of rather variable shape and size, usually expanding to margin and practically symmetrical, but often with narrower mouth and slightly bulging adcauline wall. Margin with 4 teeth and perisarcal thickening below edge. Diaphragm in form of annular thickening of perisarc, which is better developed on adcauline side and often invisible on abcauline side. An internal ridge of perisarc sometimes present about one-third of height of hydrotheca for attachment of annular fold of hydranth. Two batteries of large rod-shaped nematocysts present in ectodermal lining of hydrotheca in adcauline and abcauline position respectively.

Gonotheca (male) elongated, widening towards distal extremity, which is obliquely truncated, smooth or roughly corrugated. Containing one large gonophore, which is extruded into an external marsupium when mature.

Measurements of hydrothecae (mm.). Samples in which typical nematocyst batteries could be recognized indicated by *.

	Height from diaphragm	*Diameter at mouth*	$\frac{\textit{Diameter}}{\textit{height}}$
TRA 35D*	1·05–1·21	0·90–0·99	0·74–0·92
TRA 38D	1·05–1·21	0·76–0·99	0·72–0·82
(AFR 1028.O.A	0·78–1·01	0·65–0·77	0·69–0·86)
TRA 23B*	1·07–1·28	0·80–1·13	0·68–0·98
SAMH 173*	1·01–1·28	0·83–0·93	0·68–0·92
SAMH 350*	0·92–1·25	0·76–0·90	0·62–0·93
(NAD 1W*	1·00–1·02	0·61–0·74	0·61–0·73)
SCD 29L*	0·79–1·00	0·55–0·75	0·58–0·93
SCD 37B	0·83–1·05	0·44–0·64	0·47–0·64
From Jarvis	0·85–0·9	0·75	0·83–0·88
From Jäderholm	1·1–1·2	0·9	0·75–0·82

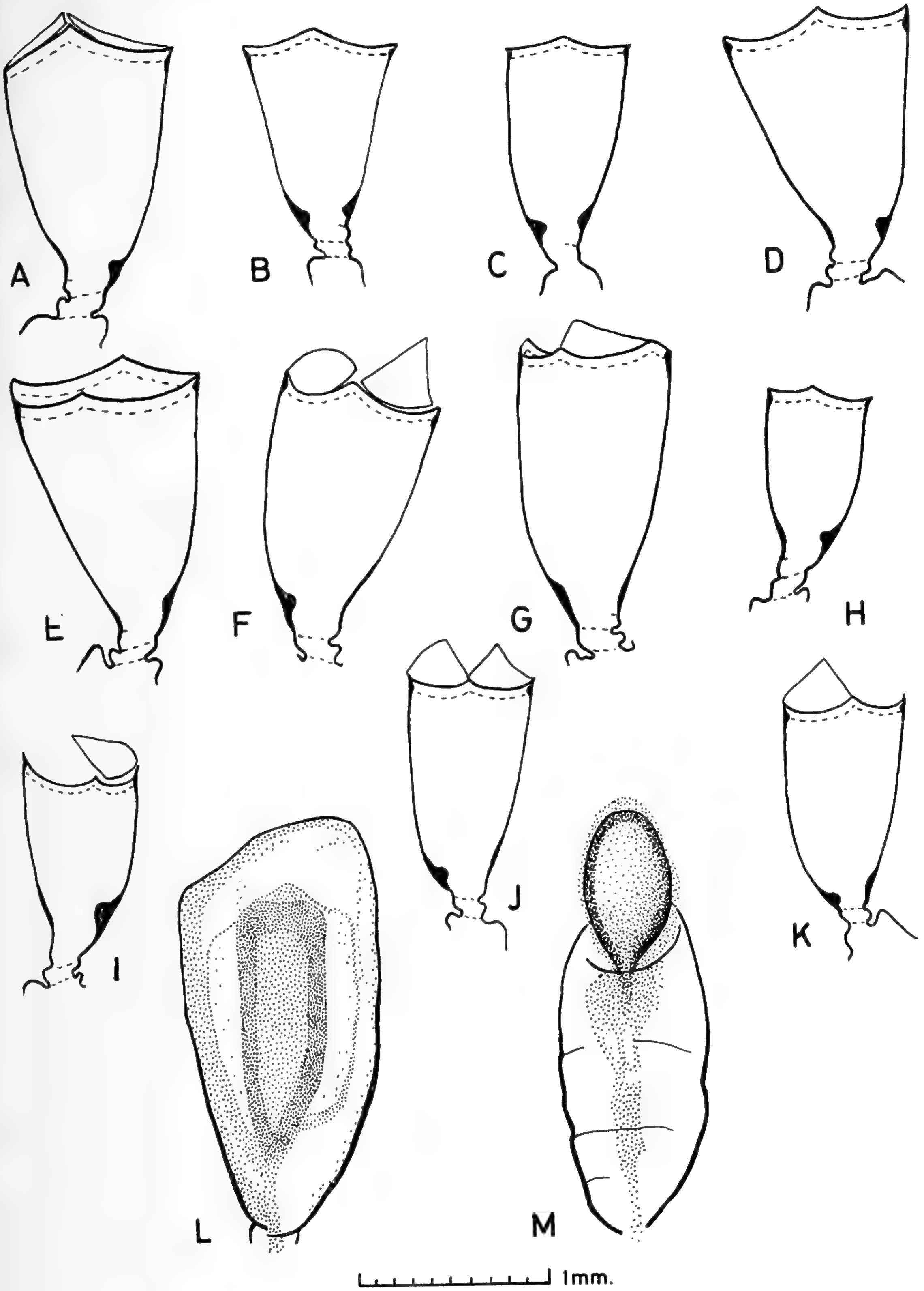

FIG. 16. *Thyroscyphus aequalis* Warren.
A.–K. Hydrothecae and pedicels from various colonies to show variation.
L.–M. Male gonothecae, M with an external marsupium.
(A from TRA 35D; B and C from AFR 1028.O.A (Natal); D and E from TRA 23B; F and L from SAMH 173; G from SAMH 350; H, I and M from SCD 29L; J and K from SCD 37A.)

From Splettstösser	0·8–1·15	0·75–0·92	
From Warren	1·18	0·79	0·67
From Ritchie	0·96	0·63	0·66
From Stechow	0·96	0·60	0·62

Remarks. T. aequalis is closely related to *T. torresi* (Busk) and according to Splettstösser and Kramp the latter is distinguished from the former by (i) the presence of a perisarcal septum at the base of the hydrothecal apophysis, (ii) the presence of a single battery of large nematocysts situated in the 'Deckelplatte' rather than in the ectodermal lining of the hydrotheca, (iii) the shape of the hydrotheca which has a narrower mouth and somewhat protruberant adcauline wall, and (iv) the hydrothecal pedicel which is not annulated.

In none of the South African material is there a septum at the base of the apophysis, and in all specimens where nematocysts are preserved the batteries are arranged as described by Warren, apparently indicating that all the material is conspecific. Yet there is so much variation in the shape and size of the hydrotheca and in the nature of the pedicel that it appears that characters (iii) and (iv) are of less systematic value than previously supposed (see fig. 16).

The shape of the hydrotheca varies from a large form with a wide mouth and practically symmetrical sides to a smaller form with a narrower mouth and protruberant adcauline wall (see diameter/height ratios above), but all intermediate stages are present and nowhere can a definite dividing line be placed between the two forms. Sometimes both forms occur in the same sample. A similar variation is evident in the literature among records assigned by Splettstösser to *Cnidoscyphus aequalis*; thus, the material of Jarvis and Jäderholm belongs near the top of the series and that of Stechow near the bottom.

The hydrothecal pedicel in *T. aequalis* is said to be 'annulated'. This annulation, when well developed, is due to the presence of a groove running spirally around the pedicel and completing a maximum of 2½ turns, usually with half a turn more on the abcauline than on the adcauline side. However, the development of this groove varies considerably (and often within the same colony), and many pedicels would come into the category of 'not annulated' (fig. 16 C). The amount of annulation bears no relation to the size and shape of the hydrotheca, but may possibly be related to the age, as there is a tendency for more distinct annulation in older parts of the colony. In old colonies, however, the spiral grooving is usually obscured by successive regenerations of the pedicel which are marked by deep transverse septa across its width.

The gonotheca, of which only the male has been observed, is similar to that described by Ritchie, and is unique among male hydroids for the extrusion of the sexual products into an external marsupium.

SUMMARY

In the three families of hydroids considered here, a total of 50 species is recorded from the south and west coasts of South Africa. Of these 12 belong to the family Lafoeidae, 4 to the Syntheciidae and 34 to the Sertulariidae.

6 new species are described, namely *Hebella urceolata*, *Zygophylax enigmatica*, *Salacia disjuncta*, *Sertularella agulhensis*, *Sertularella congregata* and *Sertularella gilchristi*, and one new subspecies, namely *Sertularella capensis delicata*. 7 of the other records are new to South Africa.

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

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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).

R. F. LAWRENCE

NEW CAVERNICOLOUS SPIDERS OF SOUTH AFRICA

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NEW CAVERNICOLOUS SPIDERS FROM SOUTH AFRICA

By
R. F. LAWRENCE
Natal Museum, Pietermaritzburg

(With 24 text-figures)

CONTENTS

INTRODUCTION

At the end of the last century only three species of cave arachnids had been described from South Africa, all of them spiders, by E. Simon (1893, 1894, 1896).

The number of Arachnida and Myriopoda known at the present time, including those described in the present paper, is twenty-two, seventeen of them being Araneae. Most of these have been taken from the Table Mountain and Kalk Bay caves in the Cape Peninsula, and the Cango Caves at Oudtshoorn. Specimens have also been collected in: Skeleton Cave, Oudtshoorn; Guano Cave, Hotpot and Onmeetbarediepgat, Bredasdorp; two small caves in Natal, at Champagne Castle in the Drakensberg and at Noodsberg in the New Hanover district. In the Transvaal Simon collected a number of arthropods at a small cave in the suburbs of Pretoria on the banks of the Apies River, and at the Makapan Cave near Potgietersrus. It is worthy of note that in the cave at Pretoria, Simon mentions (1894: 63) finding a number of specimens of an undescribed pseudoscorpion (*Chilifer*, *sic*) which he sent to M. Balzan for identification. In the Makapan Cave he discovered a new species of tenebrionid beetle, *Eurychora simoni*, and observed, but apparently did not collect, Myriapoda. Many of these caves are large, forming long horizontal galleries or extending deep below the surface, and almost all the specimens were collected in totally dark parts of the caves.

It is of interest to compare the numbers of cave Arachnida found in South Africa with those of neighbouring regions of the African continent. In 1931 Fage published a comprehensive list of cave spiders from all parts of the world, omitting however the three South African species already described by Simon.

Ann. S. Afr. Mus. **48** (2), 1964, 57–75, 24 text-figures.

According to this list no less than twenty-six species had been described from East Africa by Berland (1914) and Simon and Fage (1922) as compared with seventeen from South Africa up to 1963 and eight from the (Belgian) Congo (Leleup, 1956). It is possible that collecting in South African caves has not been as extensive as in East Africa.

The Congo has a much larger cavernicolous myriapod fauna than South Africa, Leleup (1956) listing nine species of Diplopoda and three of Chilopoda, while only one diplopod species has been found in the whole South African region and no Chilopoda. On the other hand only eight species of spiders have been recorded from the caves of the (Belgian) Congo.

A number of immature or incomplete specimens, which it has been impossible to describe and include in the South African faunal list, indicate that a fairly large number of South African cave spiders still await description. This would especially apply to the Bredasdorp caves, the Oudtshoorn caves other than the Cango Caves, and various caves in Natal and the Transvaal. It might also be interesting to explore for comparison some of the long tunnels which have recently been excavated for the South African railways, such as the 3-mile-long tunnel between Pietermaritzburg and Howick in Natal.

The large number of specimens placed at my disposal by Mr. J. R. Grindley of the South African Museum were collected by himself and other staff members of this Institution at various times between 1929 and 1961, and by the South African Spelaeological Association.

Descriptions of Species

Family **Dictynidae**

Genus HAEMILLA E. Simon

Haemilla grindleyi n. sp.

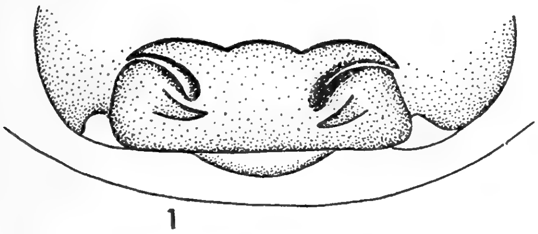
(Fig. 1)

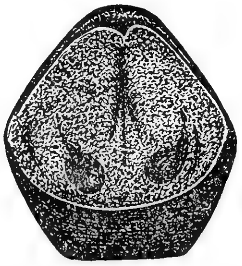
Holotype: 1 ♀ (S.A.M. 10004), Wynberg Caves, Table Mountain, collected J. R. Grindley, August 1956.

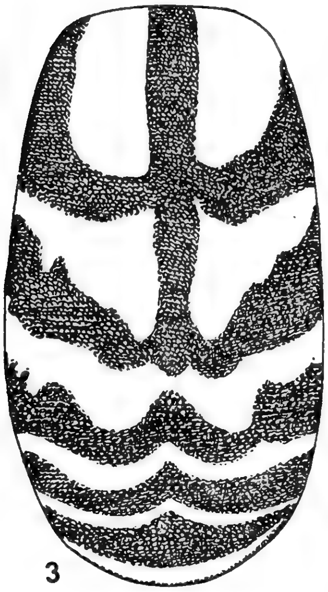
Colour: Carapace light reddish brown, its anterior margin a little darker, sternum reddish brown, mouthparts and chelicerae dark reddish brown; legs (including coxae) yellow brown, the apical segments reddish; pedipalps yellow brown, tibia and tarsus reddish brown. Abdomen dark olive green dorsally, with a series of indistinct lighter chevron markings, some intermixed lighter spots and stripes laterally, ventral surface olive green with a pair of widely separated parallel longitudinal lighter stripes.

Eyes: Anterior row with lower margins forming a straight line, medians less than a diameter apart, their own diameter from the laterals; posterior row distinctly procurved, medians a little more than their diameter apart, two diameters from the laterals; posterior medians distinctly larger than anterior medians, median quadrangle considerably wider behind than in front (by a little less than the diameter of an anterior median), as long as or a very little longer than posteriorly wide; laterals subequal, subcontiguous, anterior medians 3–4 times their diameter from edge of clypeus.

Chelicera with 7–8 teeth on superior margin, 4–6 on inferior margin not much smaller than the superior ones.







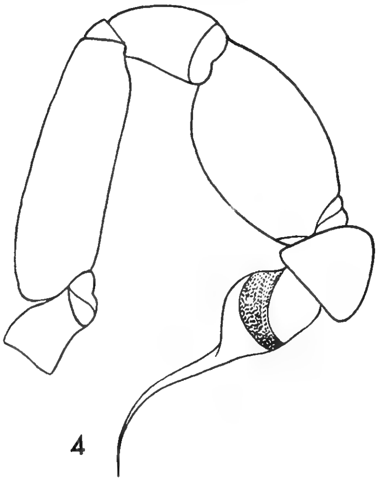


FIG. 1. *Haemilla grindleyi* n. sp. ♀. Vulva.
FIG. 2. *Haemilla profundissima* n. sp. ♀. Vulva.
FIGS. 3, 4. *Loxosceles valida* n. sp. ♂. 3, dorsal pattern of abdomen; 4, pedipalp from inner side.

Vulva as in fig. 1, resembling in its basic pattern those of *tuberculata* Lawr. and *tanganensis* Simon & Fage.

Calamistrum on metatarsus IV with a row of 33 modified hairs occupying only one-eighth of its total length; the segment slightly sinuous in the region of the calamistrum.

Legs: Patellae III and IV with 1 posterior spine, anterior patellae without; tibiae I and II with 2 pairs of inferior spines, 2 lateral pairs; metatarsi I and II with 4 lateral spines on each side, I with 1 small inferior spine at apex, II with 2 pairs of inferior spines. All tarsi with a ventral brush-like scopula, anterior legs with a metatarsal scopula in addition.

Pedipalp: Tibia and tarsus with a dense brush-like scopula, tarsus with 5–6 long spines in addition.

Dimensions: Length of carapace 5·1, abdomen 6 mm.

Further material: 1 immature ♀, Wynberg Caves (S.A.M. B10010), collected R. F. Lawrence, March 1931: 1 ♀, Kalk Bay Caves (S.A.M. B7894), collected R. F. Lawrence, July 1932; 3 ♀♀ (2 fragmentary) from Wynberg Caves (S.A.M. B10007, B10008, B10009), collected J. R. Grindley, August 1956; 1 immature ♀, Bats Cave (S.A.M. B10006), Table Mountain, collected J. R. Grindley, September 1960; 1 juvenile ♀, (S.A.M. B 10006), Oread Halls, Kalk Bay Caves (S.A.M. B10005), collected J. R. Grindley, June 1956.

The species seems to be nearest *tuberculata* Lawrence from Natal. It differs from all other species of the genus in the form of the vulva and in the small extent of the fourth metatarsus occupied by the calamistrum, this being only one-eigth (two-fifths in *tuberculata*) of its length. Only one other species, *cavernicola* Lawrence from Natal, appears to have been recorded from caves.

Haemilla profundissima n. sp.

(Fig. 2)

Holotype: 1 ♀ (S.A.M. B10011), Onmeetbarediepgat, Bredasdorp, Cape Province, collected C. Gow, July 1961.

Colour: Carapace light reddish brown; legs light reddish brown, the basal segments with an olive tinge, the mouthparts all dark reddish brown, sternum reddish brown, chelicerae blackish brown. Abdomen dorsally olive green with very numerous small light dots, a median stripe in anterior two-thirds with chevron markings and a row of ill-defined spots on each side, lighter; lateral surfaces with mixed spots and stripes, venter with two widely separated parallel white stripes.

Eyes: Anterior row from in front slightly procurved, subequal or the laterals a little larger, medians less than their diameter apart and a diameter from the laterals; posterior row from in front distinctly procurved, the medians distinctly smaller than anterior medians, subequal to the laterals, 1½–2 times their own diameter apart, 2–3 diameters from the laterals; laterals on each side the radius of a posterior lateral apart, the posterior distinctly smaller than the anterior; median quadrangle as long as posteriorly wide, wider behind than in front by the diameter of a posterior median eye, anterior medians the length of median quadrangle or 2–3 times their own diameter, from the edge of clypeus.

Mouthparts: Labium a little longer than in *tuberculata* Lawr. (cf. Lawrence 1939: 270, fig. 1*b*), reaching almost to the apices of the maxillae or more than three-fourths of their length.

Chelicerae: Inferior margin with 7–8 teeth, the distal 3 very small, superior margin with 7.

Vulva as in figure 2, differing remarkably from all other species in its basic pattern.

Legs: Tibia I and II with 3 inferior and 3 lateral pairs of spines, metatarsi apparently similar but the spines obscured by a thick brush of hairs on the under side of metatarsi and tarsi, and also on tibia I. Metatarsus IV with a slight sigmoid curve seen from above, the calamistrum very distinct, composed of about 45 stout modified hairs and occupying a little less than a third of its total length.

Dimensions: Length of carapace 5·3, abdomen 5·6 mm.

Family **Sicariidae**

Genus LOXOSCELES Lowe

Loxosceles valida n. sp.

(Figs. 3, 4)

Holotype: 1 ♂ (S.A.M. B10012), Echo Halt Caves, Table Mountain, Cape Town, collected J. R. Grindley, April 1954 (labelled No. 10).

Colour: Carapace in general rich reddish brown, cephalic portion with its lateral margins and 4 narrow parallel stripes behind the median eyes, thoracic portion with some large ill-defined radial markings from the foveal depression outwards, all a little darker than the background; chelicerae reddish brown; sternum light yellow brown, the margins narrowly reddish brown, an irregular cluster of blackish olivaceous spots in the middle; coxae infuscated in apical fourth, remainder yellow; labium reddish brown, maxillae a little lighter, the apices of both with narrow white border. Abdomen dorsally with a brown pattern on light yellow background (fig. 3), ventral surface mostly brown, ventral spinners with a light transverse band in basal half. All legs reddish-brown, femora I and II a little darker, metatarsi and tarsi I–IV a little lighter.

Carapace with a group of fairly coarse black bristles at anterolateral angle and behind the lateral eyes, cephalic portion with 7 distinct longitudinal rows of forwardly directed similar bristles, 3 behind the median, 2 behind the lateral eyes; thoracic portion with 3 weak rows of bristles on each side, the two posterior ones reaching the lateral margin, the anterior row abbreviated; sides of carapace with a regular marginal row of bristles but otherwise smooth, shiny.

Eyes of both the median and lateral pairs contiguous, a line joining the anterior laterals touching the posterior margins of the medians; median pair separated from the laterals by a little more than their combined width, from anterior margin of clypeus by 1½–2 times the long diameter of a median eye.

Chelicerae with a band of black bristles on the lateral half of its anterior surface; apex of chelicera ending in a large black triangular tooth on the inferior margin.

Legs without spines, very long and, as far as patellae, very strong; femora almost entirely smooth but the ventral surfaces of the anterior ones with numerous soft fine hairs in basal half. Tibiae and distal segments with regular rows of large spine-like black bristles increasing in length and slenderness distally, anterior tarsi with a weak scopula ventrally, the posterior ones with a distinctly denser scopula and at the apices of metatarsi in addition. Legs I, II, IV, III, II only a little shorter and not weaker than I.

Pedipalp as in figure 4 seen from inner side; tarsus and tibia with coarse bristles, more numerous on inner than outer surfaces, more dense on tarsus than tibia; tarsus bluntly triangular, tibia much inflated, almost twice as deep as patella seen from the side (its depth two-thirds its greatest length), ovoid, much wider than the remaining segments seen from above.

Dimensions: Length of carapace 5·5, width 4·6; length of abdomen 7·3 mm. Leg I: femur 15, patella-tibia 22, metatarsus 21, tarsus 2·8 mm.

Further material: All the remaining material consists of females as follows: 1 ♀ (S.A.M. B10018), Powder Room Cave, Table Mountain, collected South African Spelaeological Association, March 1956. 1 ♀ (S.A.M. B10016), Wynberg Caves, Table Mountain, collected South African Spelaeological Association, February 1956. 1 ♀ (S.A.M. B10015), Devil's Pit, Kalk Bay, collected J. R. Grindley, June 1954. 1 immature ♀ (S.A.M. B10013), Tartarus Cave, Kalk Bay Mountains, collected J. R. Grindley, July 1961. 1 immature ♀ (S.A.M. B10017), Giant's Workshop, Table Mountain Caves, collected J. R. Grindley, July 1956. 1 immature ♀ (S.A.M. B7892), Wynberg Caves, Table Mountain, collected R. F. Lawrence, March 1931. 1 ♀ (S.A.M. B10014), Bats Cave, Table Mountain, collected J. R. Grindley, September 1960.

These specimens are in general smaller, with shorter legs than the ♂, leg I only about 3 times the body length. The distinctive pattern of the dorsum of abdomen is almost identical with that of the ♂ except that the transverse bars or chevrons are in some cases more numerous, 7–8 in number. Total length of largest ♀ (S.A.M. B10014 from Bats Cave), 14·5, leg I 43 mm.

Remarks: Five other species of *Loxosceles* are known from southern Africa: two from South West Africa, *bergeri* Strand and *simillima* Lawrence, two from the Cape Province, *pilosa* Purcell and *spinulosa* Purcell, and one from the Transvaal, *speluncarum* Simon. All these species are very much smaller, with shorter legs, the first being only 3 times or less the total length of body while in *valida* it is more than 6 times. The only other known cavernicolous species of the genus, *L. speluncarum,* was found in a cave in calcareous deposits of the Apies River valley near Pretoria, while Simon and Fage recorded an unidentified juvenile from Haitajwa Cave on Zanzibar Island (1922: 528). The new species has in all the specimens a strong, very clearly defined colour pattern, without the least sign of the depigmentation characteristic of cave animals.

Family **Leptonetidae**

Subfamily **Ochyroceratinae**

SPELEODERCES new genus

Carapace and abdomen well chitinized, the latter with large oval dorsal scute but no ventral scute. Eyes consisting of three widely separated pairs, two lateral and one median, as in *Cangoderces* Harison, but the median pair situated much farther back. Chelicerae with 4 large teeth on superior margin; labium much wider than long; maxillae wide, fairly short, not meeting distally, their external and internal apices angular. Legs very long and slender, femora subparallel throughout. Patella of male pedipalp much longer than tibia and strongly toothed, remaining segments normal. Type-species of genus: *Speleoderces scutatus* n. sp.

Speleoderces scutatus n. sp.

(Figs. 5–8)

Holotype: 1 ♂, (S.A.M. B10019), Wynberg Caves, Table Mountain, collected South African Spelaeological Association, February 1956.

Colour: Carapace ventrally and dorsally yellow with an orange tinge, abdomen yellow white, dorsal scute a little darker, legs yellow white.

Carapace narrowing a little anteriorly, the anterior margin truncate but rounded at the antero-lateral angles.

Eyes as in figure 5, separated from anterior margin of carapace by an indistinct groove, the laterals on each side occupying a low indistinct rounded tubercle; position of posterior medians unusual in being well back, more or less in a line with the posterior of the two laterals; posterior medians well separated by about their own diameter from each other, far removed from the laterals on each side which are contiguous.

Mouthparts as in figure 6, labium very short, much wider than long, maxillae wide, their inner margins converging, the distal margins quite straight with both the inner and outer angles distinct though rounded.

Chelicerae: Claw very wide at base but narrowing abruptly in distal third, superior margin with 4 teeth, the basal one largest and well separated from the remaining three which are subgeminate; basal half of the claw with minute but very regular and distinct saw teeth (fig. 7).

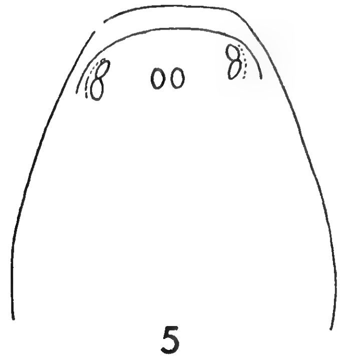
Legs very long and slender, the anterior longer than posterior pair, the femora not incrassate basally; all patellae at dorsal apex with 1, tibiae dorsally with 2 very long erect setae, legs clothed otherwise with series of fairly numerous, much shorter setae as in *Cangoderces lewisi* Harison (1951, p. 83, fig. 1).

Pedipalp as in figure 8 seen from outer side, patella much longer than tibia, subparallel, with a strong hooked tooth at its base directed dorsally and a little to the outer side, another large claw-like tooth at its apex.

Abdomen: Except on the scute, clothed with long slender setae, its dorsal surface with a large oval scute, not strongly chitinized but distinct, covering all except the posterior fifth or sixth of dorsal surface.

Dimensions: Length of carapace 0·65, of abdomen 0·85 mm.

Female: A single ♀ specimen (S.A.M. B10020) from Bats Cave, Table Mountain, collected by the South African Spelaeological Association, February 1956, is undoubtedly the female of this species. It differs from the male only in the somewhat shorter legs, more rounded abdomen and the total absence of a dorsal scute on the latter.



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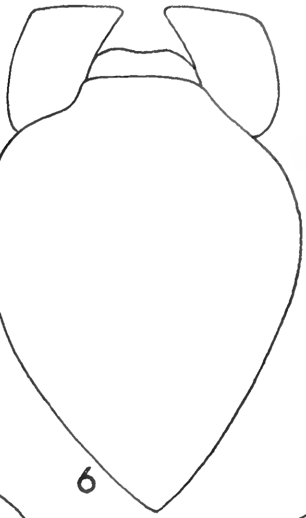

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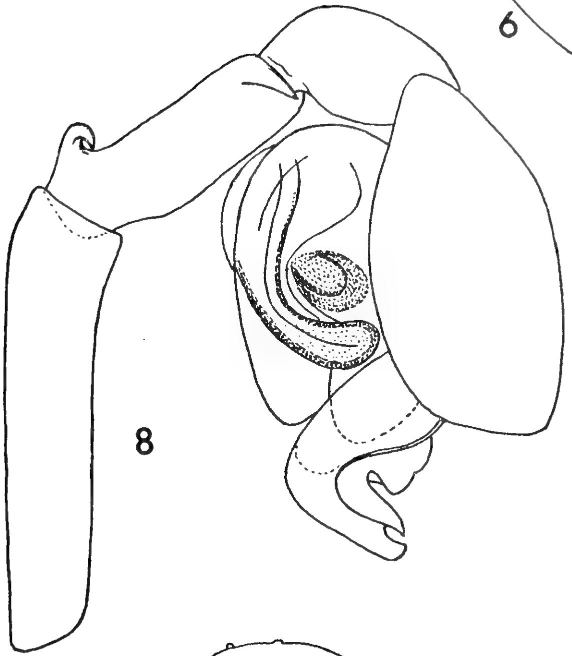

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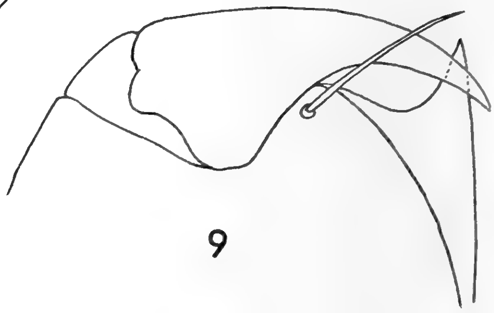

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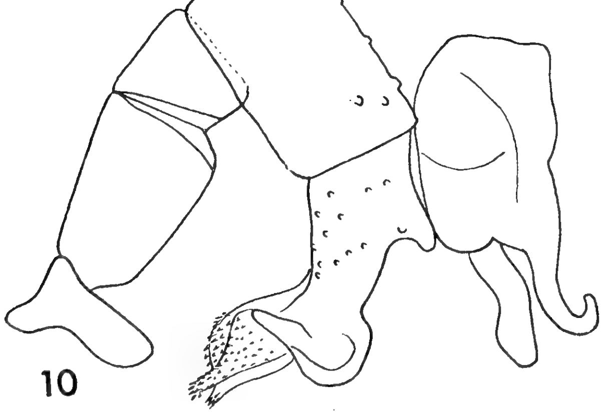

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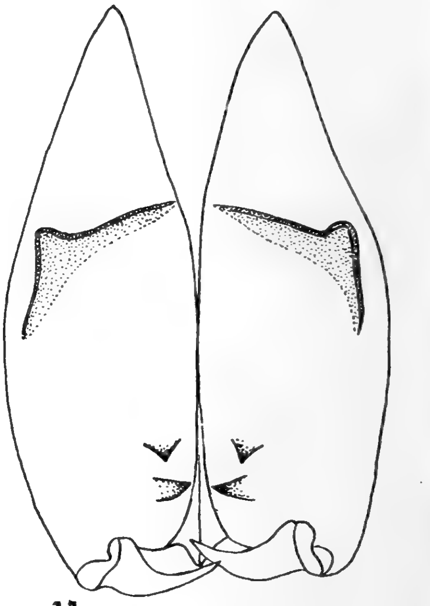

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FIGS. 5–8. *Speleoderces scutatus* n. sp. ♂. 5, eyes from above; 6, sternum and mouthparts; 7, chelicera from below; 8, pedipalp from outer side.

FIGS. 9–11. *Spermophora peninsulae* n. sp. ♂. 9, apex of chelicera; 10, pedipalp from outer side; 11, chelicerae from in front.

Dimensions: Total length 1·1 mm.

Remarks: The new genus appears to differ from all other genera of the family Leptonetidae interpreted in its widest sense to include the Ochyroceratidae. These differences lie in the arrangement of the eyes, the structure of the chelicerae, labium and maxillae, while in possessing a dorsal abdominal scute it seems to approach the Oonopidae. When the male of *Cangoderces* Harison has been discovered it may be found to be most nearly related to this genus.

Family **Pholcidae**

Genus SPERMOPHORA Henz

Spermophora peninsulae n. sp.

(Figs. 9–14)

Holotype, 1 ♂, *paratype*, 1 ♀ (S.A.M. B7897), Kalk Bay Caves, Cape Peninsula, collected R. F. Lawrence, September 1932.

Male (*holotype*)

Colour: The specimen completely bleached, the chitinous structures of the mouthparts and pedipalp a little darker; carapace dorsally and ventrally yellow, a little darker than the abdomen which is quite pale, legs pale.

Chelicerae: The fang stout and short, a very conspicuous triangular tooth on its margin proximal to the fang (fig. 9); anterior surface with two pairs of broad chitinous teeth near its apex (fig. 11), the more distal pair directed inwards, the second pair downwards; base of chelicera near clypeal margin with an oblique projecting ridge behind which is a depression extending almost the whole width of the segment.

Abdomen longish, cylindrical, rounded, considerably longer than that of ♀.

Pedipalp as in figure 10 seen from the outer side, tibia and basal part of tarsus with the sockets of numerous spines which in most cases have been lost.

Legs: I, IV, II, III.

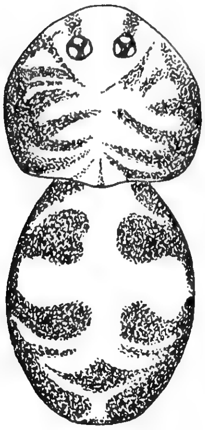
Dimensions: Total length 2·6 mm.

Female (*paratype*)

Colouring similar to that of the ♂; chelicerae unmodified; the chitinized parts of the epigastric area as in figure 14; pedipalp with long, slender, pointed tarsus; legs very long, the femora long and stout, almost twice as wide at base as at apex.

Dimensions: Length of carapace 1·1, length of abdomen 1·9 mm.

Remarks: Another ♂ from the Kalk Bay Cave system (Oread Halls, collected J. R. Grindley, June 1954, S.A.M. B10021) has a jet-black sternum and indistinct markings on the abdomen, but the pedipalp is structurally similar to that of the holotype ♂. Four tubes of female *Spermophora* from the Wynberg and Powder Room caves I assume to be the same species as the types, although in the types all traces of any original colour pattern have been lost after more than 30 years of immersion in alcohol.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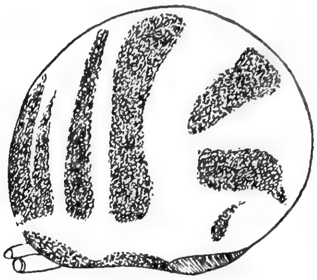
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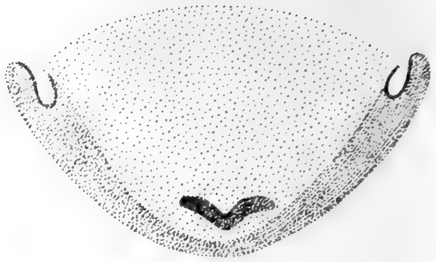
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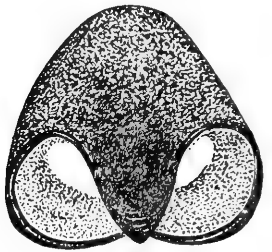
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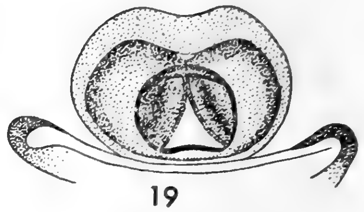
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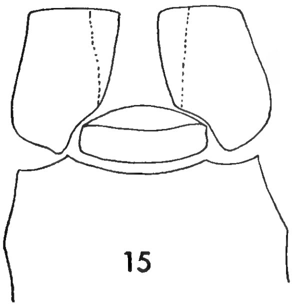
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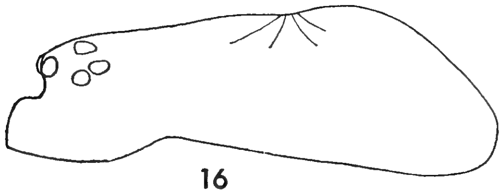
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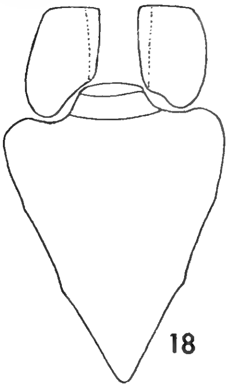
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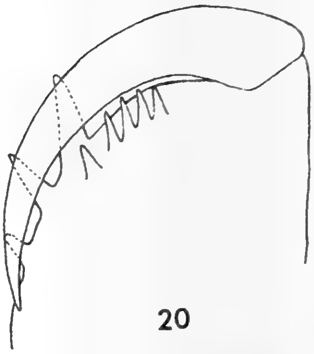
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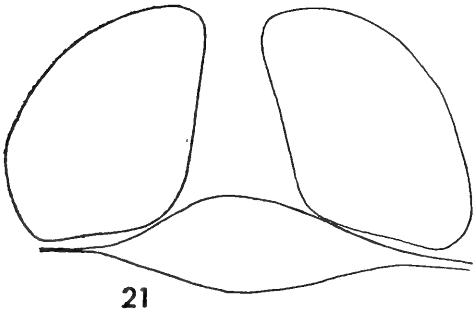
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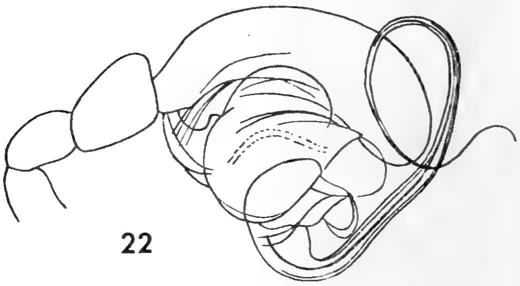
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FIGS. 12–14. *Spermophora peninsulae* n. sp. ♀. 12, dorsal colour pattern; 13, the same of another ♀ from the side; 14, epigastric region.

FIGS. 15–17. *Teutana fagei* n. sp. ♀. 15, mouthparts and anterior margin of sternum; 16, carapace seen in profile; 17, vulva.

FIGS. 18, 19. *Theridion proxima* n. sp. ♀. 18, mouthparts and sternum; 19, vulva.

FIGS. 20–22. *Lephthyphantes rimicola* n. sp. 20, chelicera of ♀; 21, mouthparts of ♀; 22, pedipalp of ♂ seen from the side.

The colouring of the female from Powder Room Cave (S.A.M. B10023) is as follows:

Colour: Carapace with dark but not black markings, as in figure 12, a fairly wide and distinct though slightly crenulated blackish stripe passing forward from each ocular group to edge of clypeus, these diverging slightly anteriorly; chelicerae and mouthparts brown, sternum blackish brown, a little lighter in the middle, contrasting strongly with the yellow coxae. Abdomen with black markings dorsally as in figure 12, a cuneiform white marking at posterior apex just above the spinners, seen from the side as in figure 13 (drawn from another ♀, Wynberg Caves, S.A.M. B10024, collected August 1956); ventral surface with a wide median black band widening to include the epigastric area which is brown and separated on each side by a fairly narrow sinuous white stripe from the blackish sides of the abdomen. Legs yellow with a reddish tinge, tibiae with a narrow, lighter apical annulation.

Further material: 1 ♀ (S.A.M. B10023) with about 24 eggs, Powder Room Cave, collected Spelaeological Association, March 1956; 2 ♀♀ (S.A.M. B10022 and B10024), Wynberg Caves, collected J. R. Grindley, August, 1956; 1 ♂, 2 ♀♀ (S.A.M. B10021), Oread Halls, collected J. R. Grindley, June 1954; 1 ♀ (S.A.M. B10021), Bats Cave, Table Mountain, collected South African Spelaeological Association, February 1956; 4 ♀♀ (S.A.M. B7896), Wynberg Caves, Table Mountain, collected R. F. Lawrence, September 1932; 1 ♂ (S.A.M. B7895), Wynberg Caves, Table Mountain, collected R. F. Lawrence, March 1931.

Simon (1892–1903: 471) writes of two types of colouring, pale species occurring in caves and houses, strongly pigmented ones under stones; all the four East African species, *ensifera*, *globosa*, *minotaura* and *nigrescens*, appear to belong to the latter group. Unfortunately no adult males are present among the Wynberg Caves material and in their absence I have assumed these specimens to be identical with the Kalk Bay Caves species, the absence of pigmentation in the type of the latter being due to prolonged immersion in alcohol.

The only species of this genus hitherto found in caves is *S. minotaura* Berland from the Campbell Cave, Kenya, though it has also been found in the forests of Kenya at high and low altitudes.

Genus SMERINGOPUS Simon

Smeringopus pallidus (Blackwall)

One immature ♀, (S.A.M. B10025), Skeleton Cave, Oudtshoorn, collected J. R. Grindley, September 1961.

Although immature the colouring of the single specimen resembles that of the female of *pallidus* (= *elongatus*) as redescribed by Kraus (1957: 220, fig. 6). No species of the genus appears to have been described from caves but specimens of *Smeringopus* are often found near the entrance of many caves and should be regarded as troglophiles rather than troglobionts.

Family **Theridiidae**

Genus TEUTANA Simon

Teutana fagei n. sp.

(Figs. 15–17)

Holotype: 1 ♀ (S.A.M. B10026), Skeleton Cave, Oudtshoorn, Cape Province, collected by J. R. Grindley, September 1961.

Colour: Carapace, sternum and mouthparts brown with a slight reddish tinge, the radiations from the thoracic fovea a little darker, otherwise without markings. Legs, coxae to tarsi uniform brown with a faint olive tinge; abdomen above reddish violet, a recurved white transverse stripe at anterior apex with a short backwardly projecting stripe in the middle, posterior to this two pairs of ill-defined elongate white markings, above the spinners a short median elongate marking followed by a transverse series of 3–4 very fine white lines; ventral surface with a large comma-shaped white marking laterally to each operculum, posterior to this two elongate, inwardly directed white stripes, the second considerably smaller than the first; between the spinners and epigastric furrow, a large vase-shaped, ill-defined lighter marking (somewhat similar to the well-defined red marking on the venter of *Latrodectus geometricus*), vulva and opercula blackish brown.

Carapace seen from the side level but slightly depressed in the region of the thoracic fovea, which is deep, transversely arcuate and slightly recurved, clypeus strongly rounded and projecting, with a well-marked transverse groove just below the eyes separating them from the rest of the clypeus (fig. 16).

Eyes: Anterior row from above slightly recurved, from in front straight, medians subequal to laterals or a very little smaller, less than their diameter apart and about the same distance from the laterals; posterior row slightly recurved seen from above, medians a little more than their own radius apart, about a diameter from the laterals which are a little larger. Median quadrangle longer than posteriorly wide, a little wider behind than in front; clypeus about 1½ times length of median quadrangle.

Chelicera: Inferior margin with 2 or 3 small, indistinctly geminate teeth.

Mouthparts: Labium at least twice as wide as long, the anterior apex not triquetrous, more or less truncate, straight in the middle, somewhat rounded at the sides, its apex falling well below the middle point of the maxillae (fig. 15).

Vulva as in figure 17, the median septum very strongly chitinized, blackish, ill-defined.

Legs unspined, with rows of weak setae and soft hairs.

Dimensions: Carapace 3·3, length of abdomen 7, width 5·3 mm.

Further material: 1 smaller ♀ (S.A.M. B10027) from Onmeetbarediepgat, Bredasdorp, Cape Province, collected C. Gow, July 1961.

The species differs from the two species of *Teutana* described by O. P. Cambridge from the Cape Peninsula, *lepida* and *connexa*, at least in its larger size and detailed differences in the pattern of the vulva, while agreeing with them in the colouring of the ventral surface. It differs from *T. albovittatus* Lawrence from the Umfolosi River, Zululand, in its considerably larger size, colour pattern of abdomen and structure of the vulva. Only one other species of the genus, *T. grossa*, appears to have been recorded from caves (in Europe only).

Genus THERIDION Walck

Theridion proxima n. sp.

(Figs. 18, 19.)

Holotype: 1 ♀ (S.A.M. B10028), Skeleton Cave, Oudtshoorn, Cape Province, collected J. R. Grindley, September 1961.

Colour: Carapace yellow with a very fine brown margination, cephalic portion and thoracic fovea brown, eyes surrounded by blackish brown rings, chelicerae light olive brown contrasting with the yellow clypeus; sternum yellow brown with narrow blackish brown margin, mouthparts light reddish brown. Legs yellow, the femora with 2 subapical, tibiae with 4 blackish annulations, metatarsi with smaller basal middle and apical annulations, the middle one faint or obsolete. Abdomen dorsally as in Tullgren's description of *kibonotense* and O. P. Cambridge's of *purcellii*, the black area surrounding the light median longitudinal band diffuse, a large white marking on each side in posterior third near the lateral margin; ventral surface with spinners surrounded by a blackish ring which is continuous with the median blackish area of dorsal surface, a medium-sized white spot below the epigastric fold.

Eyes seen from above with anterior row slightly recurved, medians a little larger than laterals, about their diameter apart and a little less from the laterals; posterior row well procurved, medians distinctly larger than the laterals, three-fourths their diameter apart, their diameter or a little more from the laterals; laterals touching on each side, the posterior distinctly smaller than anterior; median quadrangle a little wider in front than behind, a little wider than long; clypeus about 1½ times the length of median quadrangle.

Mouthparts: Labium much wider than long, its anterior margin truncate, almost straight, with a row of 6 long black setae, the segment reaching to about a third the length of the perpendicular maxillae (fig. 18).

Legs: I, IV, II, III; femora with 2 inferior rows of setae mounted on small round tubercles, those of leg II much more regular than the others (the setae of femur I largely missing), each row with 12–15 setae; patella with a long, strong, black seta at dorsal apex; anterior tibiae with 1–3 similar dorsal setae, IV with 4; metatarsi with a ventral row of setae, those of II stronger and more regular than the others; tarsus IV with a row of 6 long, slender modified hairs diminishing progressively in length distally.

Vulva as in figure 19 resembling that of *T. kibonotense* in its general pattern.

Dimensions: Length of carapace 2, length of abdomen 3·6 mm.

Remarks: The species obviously resembles Tullgren's *kibonotense* (1910) and O. P. Cambridge's *purcellii* (1903) both in colouring and the basic pattern of the vulva, but of the two is probably more closely related to *kibonotense*. About 17 species of this large and widespread genus are known from southern Africa, including an almost cosmopolitan form often found in greenhouses, *T. tepidariorum* C. L. Koch; *Theridion rufipes* Lucas has been recorded from caves in Spain.

Family **Linyphiidae**

Genus LEPHTHYPHANTES Menge

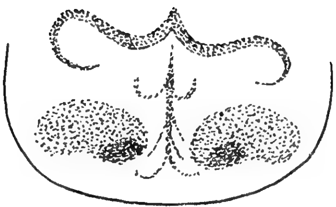
Lephthyphantes rimicola n. sp.

(Figs. 20–23)

Holotype, 1 ♀, *paratypes*, 1 ♂, 2 ♀♀ (S.A.M. B7893), Wynberg Caves, Table Mountain, collected R. F. Lawrence, March 1931.

Female (*holotype*)

Colour: Carapace and legs yellow to white without markings, the eyes surrounded by black rings, posterior medians connected with anterior medians by a subtriangular black marking spanning the space between them; abdomen much faded but darker than remainder of body, light terracotta with a number of large round indistinct blotches.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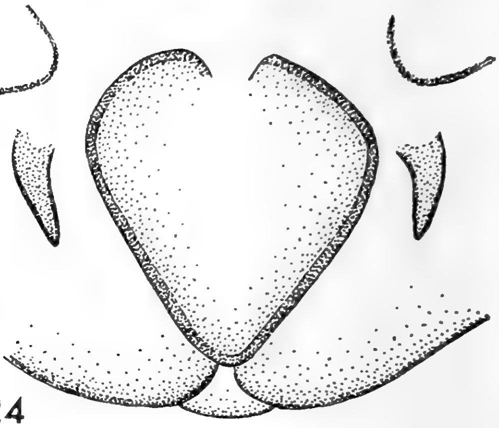
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Fig. 23. *Lephthyphantes rimicola* n. sp. ♀. Vulva.
Fig. 24. *Phanotea gowi* n. sp. ♀. Vulva.

Eyes: Posterior row slightly procurved, the medians distinctly the largest of all the eyes; anterior row straight to very slightly recurved, the medians much the smallest of all the eyes, half the diameter of an anterior lateral and close to each other; laterals contiguous, the anterior a little smaller than the posterior; median quadrangle as long as posteriorly wide, much wider behind than in front; clypeus a little less than the length of median quadrangle.

Mouthparts as in figure 21, maxillae very wide, subparallel, labium semicircular, much wider than long; chelicerae as in figure 20, fang long and robust, superior margin with 3 large teeth, the basal smallest, inferior margin with 5 distinctly smaller sharp teeth, the basal separated from the others which are subcontiguous. Chelicerae subparallel, not narrowing much distally; sternum cordiform, its anterior margin very wide and almost straight.

Vulva as in figure 23.

Legs I–IV long and very slender, the femora ventrally with a more or less regular series of long, fine setae; remaining segments with long, slender, erect dorsal setae as follows (the seta on the patella much longer than any others): patella at apex with 1 almost as long as the segment, tibia with 2 or 3 in distal half, these about a third the length of the segment; metatarsus with 1 subbasal seta, tarsus without; legs otherwise clothed with regular rows of numerous short, weak setae.

Pedipalp tarsus long, slender, longer than tibia, its apex with a long edentate claw, not much thicker than the adjacent setae.

Male (*paratype*)

Not differing from the female except that the chelicerae are somewhat more divergent and more tapered apically, the legs relatively longer and more slender. Carapace not modified, in general similar to that of the ♀.

Pedipalp as in figure 22 seen from the side, very complex, the embolus very long and sinuously curved.

Dimensions: ♀: Length of carapace 0·9, of abdomen 1·2 mm. ♂: Total length 1·9 mm.

Remarks: The material on which the new species is based is very old and fragile but it will be possible to check the description and figures from fresh material which should not be difficult to obtain as the spiders are fairly common, spinning small sheet webs 25–35 mm. in diameter across the fissures in the vertical rock walls of the cave.

The Linyphyiidae are very little known in South Africa and I have considerable doubt as to whether this cave form really is a species of *Lephthyphantes* or whether a new genus is required for it. In some respects it agrees with *Linyphia* (in the appearance of the male pedipalp, with the British species *Linyphia* (*Agyneta*) *cauta* O. P. Cambridge). No members of this genus, however, appear to inhabit caves. In the considerable reduction of the anterior median eyes it agrees with various genera from different parts of the world, such as *Porrhomma*, *Troglohyphantes* and *Asthenargus*, the latter being represented by the species *A. inermis* in East African grottoes; from all of these, however, it also differs in at least one important character.

Family **Agelenidae**

Subfamily **Cybaeinae**

Genus PHANOTEA Simon

Phanotea gowi n. sp.

(Fig. 24)

Holotype: 1 ♀ (S.A.M. B10029), Guano Caves, Bredasdorp, Cape Province, collected C. Gow, July 1961.

Colour: Legs and carapace yellow to orange, carapace becoming progressively more reddish anteriorly; sternum yellow, the margins orange, mouthparts reddish brown, chelicerae dark reddish brown.

Eyes: Anterior row slightly recurved, medians distinctly smaller than the laterals, less than their own diameter apart, about a diameter from the laterals; posterior row a little procurved, medians a little smaller than anterior medians, laterals smaller than anterior laterals, medians their own diameter apart, 2 diameters from the laterals; median quadrangle distinctly longer than posteriorly wide, a little wider behind than in front; anterior medians a little more than their own diameter from the edge of the clypeus.

Chelicerae very strong, inflated and rounded in front, a deep anterior constriction near their bases below the clypeus; lower margin with only 2 small subequal teeth, differing in this respect from all other species of the genus; superior margin with 3 teeth, the middle one large.

Pedipalp with thick scopula ventrally on the distal two-thirds of tarsus.

Vulva as in figure 24, with a large median plano-convex cordiform plate overlying two posterior sclerites which almost meet in the middle line below it.

Legs: Patellae unspined; tibia I and II with 4 inferior pairs of spines, metatarsus I and II with 3 inferior pairs, I with 2 anterior lateral spines in addition, II without lateral spines, tarsus and most of metatarsus I with a distinct scopula, II with a distinct scopula only on tarsus; tibia III and IV with 3 inferior irregularly paired spines, 2 pairs of lateral spines, metatarsus III and IV with 3 inferior pairs, 3 lateral pairs and 1 or 2 superior spines in addition; tarsi III and IV but not metatarsi with distinct scopula.

Dimensions: Length of carapace 6·4, total length 15·3 mm. (including chelicerae).

Further material: One specimen, Hotpot, Bredasdorp, Cape Province, collected South African Spelaeological Association, May 1960.

The genus consists mostly of cave-living species, *natalensis*, *simoni* and *peringueyi;* it appears to be most closely related to *peringueyi* in the eye disposition and spine formula of the legs but can be easily distinguished from it by having only 2 instead of 3 teeth on the inferior margin of chelicera and in the pattern of the vulva.

Subfamily **Hahniinae**

A single, very fragile and much bleached subadult male from the Wynberg Caves (S.A.M. B7896), collected R. F. Lawrence, September 1932, is evidently a member of this subfamily, several species of which have been recorded from caves.

The spinners are long and slender, arranged in a more or less transverse row with the superior pair especially long, the apical segment being subequal to the basal in length. There are, however, only six eyes, all of them large with the anterior medians absent, the general arrangement similar to that of *Bigois* Simon from the Philippine Islands, in which, however, the anterior median eyes, though minute, are present. It does not seem to be closely related to *Scotussa zodarioides* Simon, the only member of the subfamily recorded from the Cape Peninsula, and a new genus may have to be created for its reception.

A LIST OF THE CAVERNICOLOUS ARACHNIDA AND MYRIAPODA OF SOUTH AFRICA

ARANEAE

Species	*Family*	*Locality*
1. *Haemilla cavernicola* Lawrence, 1939	Dictynidae	Noodsberg Caves, Natal.
2. *Haemilla grindleyi* Lawrence, 1964	,,	Wynberg Caves, Table Mt., and Kalk Bay Caves, Cape.
3. *Haemilla profundissima* Lawrence, 1964	,,	Onmeetbarediepgat, Bredasdorp, Cape.
4. *Phyxelia makapanensis* E. Simon, 1894	,,	Makapan Cave, Transvaal.
5. *Loxoscles speluncarum* E. Simon, 1893	Sicariidae	Apies River Cave, Pretoria, Transvaal.
6. *Loxosceles valida* Lawrence, 1964	,,	Wynberg Caves, Table Mt., Cape.
7. *Speleoderces scutatus* Lawrence, 1964	Leptonetidae	Wynberg Caves, Table Mt., Cape.
8. *Cangoderces lewisi* Harison, 1951	,,	Cango Caves, Oudtshoorn, Cape.
9. *Spermophora peninsulae* Lawrence, 1964	Pholcidae	Wynberg Caves, Table Mt., and Kalk Bay Caves, Cape.
10. *Smeringopus pallidus* (Blackwall), 1858	,,	Skeleton Cave, Oudtshoorn, Cape.
11. *Teutana fagei* Lawrence, 1964	Theridiidae	Skeleton Cave, Oudtshoorn, Cape.
12. *Theridion proxima* Lawrence, 1964	,,	Skeleton Cave, Oudtshoorn, Cape.
13. *Lephthyphantes rimicola* Lawrence, 1964	Linyphiidae	Wynberg Caves, Table Mt., Cape.
14. *Phanotea peringueyi* E. Simon, 1896	Agelenidae	Cango Caves, Oudtshoorn, Cape.
15. *Phanotea natalensis* Lawrence, 1951	,,	Noodsberg Caves, Natal.
16. *Phanotea simoni* Lawrence, 1951	,,	Champagne Castle Cave, Drakensberg, Natal.
17. *Phanotea gowi* Lawrence, 1964	,,	Guano Cave, Bredasdorp, Cape.

	Species	*Family*	*Locality*
		OPILIONES	
18.	*Speleosiro argasiformis* Lawrence, 1931	Sironidae	Wynberg Caves, Table Mt., Cape.
19.	*Speleomontia cavernicola* Lawrence, 1931	Triaenonychidae	Wynberg Caves, Table Mt., Cape.
20.	*Larifuga* sp. (1964)	,,	Wynberg Caves, Table Mt., Cape.
		PSEUDOSCORPIONES	
21.	*Chthoniella cavernicola* Lawrence, 1935	Chthoniidae	Wynberg Caves, Table Mt., Cape.
		DIPLOPODA	
22.	*Harpethrix caeca* Lawrence, 1962	Sphaerotrichopidae	Wynberg Caves, Table Mt., Cape.

Summary

Nine new species of cavernicolous spiders from South Africa are described, one of which is included in a new genus. The new species are: *Haemilla grindleyi*, *Haemilla profundissima*, *Loxosceles valida*, *Speleoderces scutatus* (new genus), *Spermophora peninsulae*, *Teutana fagei*, *Theridion proxima*, *Lephthyphantes rimicola* and *Phanotea gowi*. A list is given of the twenty-two species of Arachnida and Myriapoda now known from South Africa.

Acknowledgement

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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.

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So proportioned that when reduced they will occupy not more than 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

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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 (black 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.

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

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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).

J. G. J. KUIPER

CONTRIBUTION TO THE KNOWLEDGE OF THE SOUTH AFRICAN SPECIES OF THE GENUS *PISIDIUM* (LAMELLIBRANCHIATA)

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CONTRIBUTION TO THE KNOWLEDGE OF THE SOUTH AFRICAN SPECIES OF THE GENUS *PISIDIUM* (LAMELLIBRANCHIATA)

By
J. G. J. Kuiper
c.o. Institut Néerlandais, Paris

(With 32 figures in the text)

Contents

Introduction

The fauna of South Africa includes, as far as we know, seven species of the genus *Pisidium*: *pirothi* Jickeli (syn. *lepus* Kuiper), *harrisoni* n.sp., *costulosum* Connolly, *langleyanum* Melvill & Ponsonby, *viridarium* Kuiper, *ovampicum* Ancey, *casertanum* (Poli).

Pisidium langleyanum, *P. costulosum* and *P. harrisoni* seem to be South African endemics. The others are also known from Central Africa, while *P. pirothi* and *P. casertanum* also occur in North Africa. Another species, *P. artifex* Kuiper, which has been described from specimens taken in high mountain tarns in Kenya, has perhaps to be added to the South African fauna.

The *Pisidium* fauna of South Africa is probably richer in species than the present paper suggests. A number of dubious forms are known but not yet described. Publication should wait until their specific identity has been cleared up. To this end, much more collecting has to be done. In the first place large series from each locality, preserved in alcohol (not in formalin which destroys the shell), are needed. This is necessary for a study of their little-known anatomy and in order to establish the subgeneric position of the species.

The identification of the African pisidia is generally difficult, largely because of the high degree of discontinuity in their distribution and the specific poverty of the *Pisidium* associations. Whereas in palearctic regions ten species of *Pisidium* often occur in the same habitat, most of the African localities seem to be inhabited by only one or two species, rarely three. Quantitatively I have the impression that pisidia are not rare in South African inland waters. I have seen many series from widespread localities, a great many more than are

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recorded in this paper, which were, however, all spoiled by formalin and so could not be identified.

The present study is entirely based on material examined by myself. This would not have been possible without the aid of many malacologists who kindly put at my disposal the specimens and documents I needed. I am specially grateful to Dr. A. D. Harrison, at the time principal research officer of the National Institute for Water Research, Pretoria, who has furnished me, during many years, with valuable samples of *Pisidium* collected in South African rivers.

My grateful thanks are also due to the South African Council for Scientific and Industrial Research for its assistance in the publication of this paper.

ABBREVIATIONS

The following abbreviations are employed in the lists of distribution:

BML = British Museum (Natural History), London.
CSIR = Catalogue of the South African Council for Scientific and Industrial Research, Pretoria.
IZRP = Institute for Zoological Research, Potchefstroom University.
KINB = Koninklijk Belgisch Instituut voor Natuurwetenschappen (Institut Royal des Sciences Naturelles de Belgique), Brussels.
LMP = Laboratoire de Malacologie du Museum d'Histoire Naturelle, Paris.
MHNG = Musée d'Histoire Naturelle, Geneva.
MMAT = Koninklijk Museum voor Midden Afrika (Musée Royal de l'Afrique Centrale) (formerly: Congo Museum), Tervuren, Belgium.
NIWR = National Institute for Water Research, Pretoria.
NMP = Natal Museum, Pietermaritzburg.
RML = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.
SAM = South African Museum, Cape Town.
SMF = Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt, Germany.
SSAE = Swedish South Africa Expedition 1950–1.
ZIUL = Zoological Institute, Lund University, Sweden.
ZMA = Zoologisch Museum, Amsterdam University, Netherlands.
ZMB = Zoologisches Museum, Alexander Humboldt University, Berlin.

KEY TO THE SOUTH AFRICAN SPECIES OF *PISIDIUM*

1. Ligament external,* projecting outside shell; ligament-pit long and narrow; shell inequilateral; sculpture regularly and finely striate .. .. *pirothi*
   Ligament internal, not visible externally 2
2. Umbo far back; shell outline oblong ovate, anterior part very prolonged; sculpture rather regularly striate .. .. *harrisoni*
   Umbo median or submedian; shell outline ovate or subtrigonal; equilateral or inequilateral; sculpture costulate or finely striate 3

* Kuiper (1962) distinguishes three positions of the ligament-pit: 1, introverted position (ligament internal); 2, extroverted position (ligament external); 3, enclosed or normal position (ligament internal, may be slightly visible externally, but does not project outside the shell).

3. Sculpture regularly costulate; beaks submedian .. .. *costulosum*
Sculpture regularly and densely striate; nepionic shell often bounded by 4–7 sharp, distinctive striae; shell outline subtrigonal .. .. *langleyanum*
Sculpture regularly and densely striate; shell thin, outline ovate; pIII thickened at the end of its inner slope .. .. *viridarium*
Sculpture irregularly striate, mostly very fine; shell outline ovate or subovate 4
4. Sculpture irregular, very fine; shell swollen, diameter being often more than height; beaks tumid and extremely broad, median .. .. *artifex*
Sculpture irregular, very fine; shell normally swollen, diameter being half height; posterior and anterior end nearly equally rounded; ventral margin of the shell much more curved than the dorsal margin which is nearly straight; beaks median; hinge very narrow .. *ovampicum*
Sculpture irregular, fine; shell normally swollen, anterior end more pointed than posterior end; inequilateral; dorsal margin more curved than ventral margin; beaks submedian; central part of hinge rather broad .. .. *casertanum*

DESCRIPTIONS OF SPECIES

Pisidium pirothi Jickeli

(figs. 1, 9, 30)

Pisidium pirothi Jickeli, 1881: 340.
Pisidium (*Fossarina*) *casertanum* var. *alexandrina* Pallary, 1909: 75, pl. 4, fig. 34.
Pisidium cf. *clarkeanum* Gardner, 1932: 86, pl. 8, figs. 15–18.
Pisidium costulosum Haas, 1936: 43.
Pisidium clarkeanum var. *exile* Stelfox, Favre, 1943: 6–11, figs. 1–3.
Pisidium lepus Kuiper, 1957: 85, figs. 1–4.
Pisidium lepus var. *dampfi* Kuiper, 1957: 88, figs. 5, 6.
Pisidium (*Afropisidium*) *pirothi* Kuiper, 1962.
[*Non*] *Pisidium costulosum* Connolly, 1931.

Remarks

Pisidium pirothi is known from several localities in Egypt, south Sudan and the Central African Republic (formerly French Sudan). It has been collected in South Africa only in the Great Letaba River near Letaba Camp in the Kruger National Park by F. Haas in 1931 (Haas, 1936, p. 43, s.n. *P. costulosum*; Kuiper, 1957, p. 85, s.n. *P. lepus* n.sp.). These specimens are preserved in the Senckenberg Museum, Frankfurt, Germany (holotype SMF 155627, paratypes SMF 152628 and SMF 152886). Paratypes of *P. lepus* have also been deposited in the Zoological Museum, Amsterdam (ZMA/K 4577), the South African Museum, Cape Town (SAM A29771), and the Natural History Museum, Geneva.

For eighty years *P. pirothi* remained an enigmatic species, owing to the fact that the original description was not accompanied by figures and, secondly, that the type-series seemed to be lost. Recently, however, Jickeli's original specimens were found (ZMB 37447, 1 lectotype and 6 paratype valves). This, in addition to the discovery of several other localities in Africa, made it possible to define the range of what I some years ago called *Pisidium lepus* n.sp.

Pisidium pirothi can be easily distinguished from all other South African species of this genus by its prominent external ligament and, consequently, the peculiar situation of its ligament-pit. I drew attention to this fact in my paper on *P. lepus* (Kuiper, 1957, p. 87). Its long, very narrow ligament-pit is bordered

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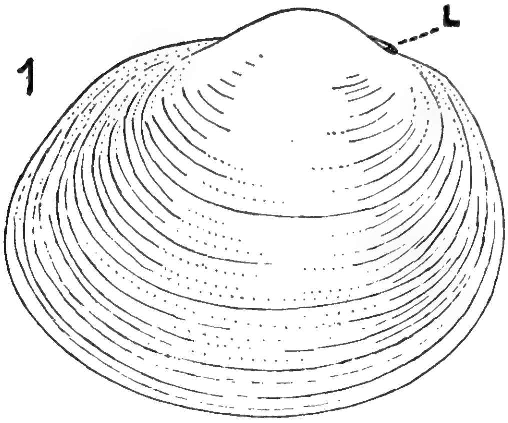

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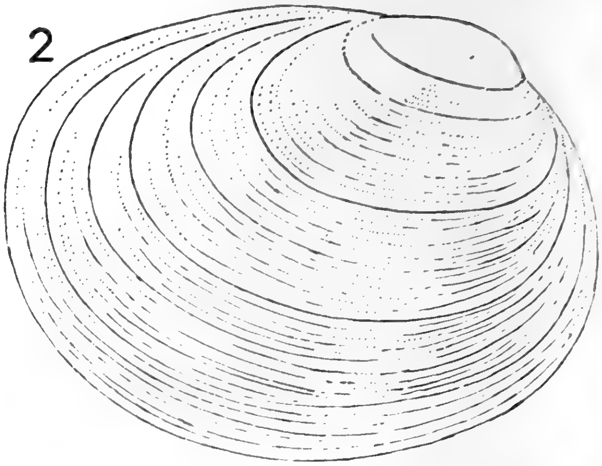

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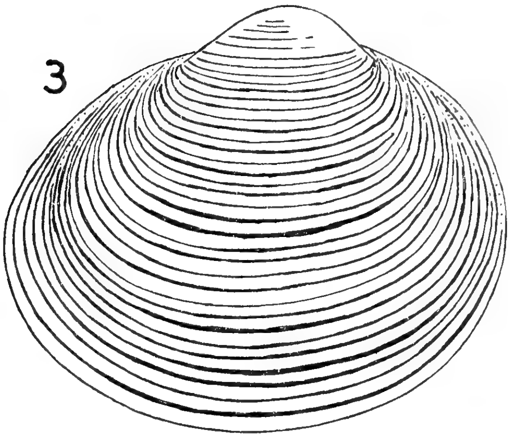

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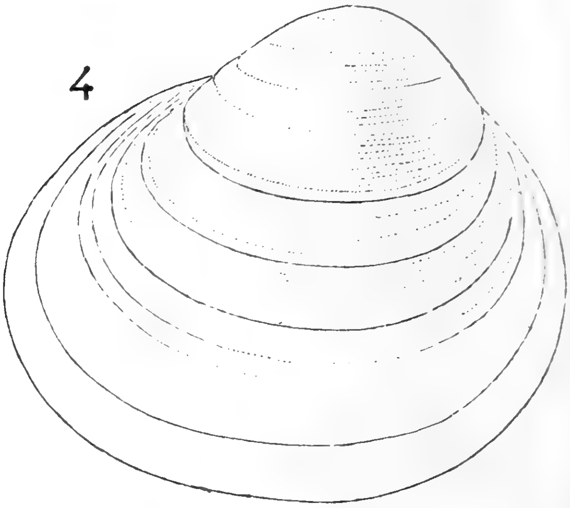

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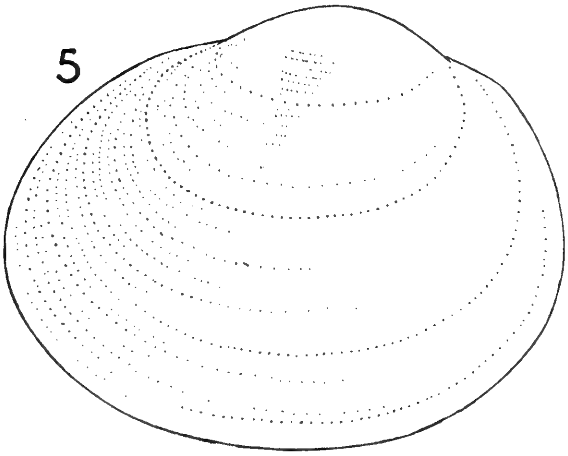

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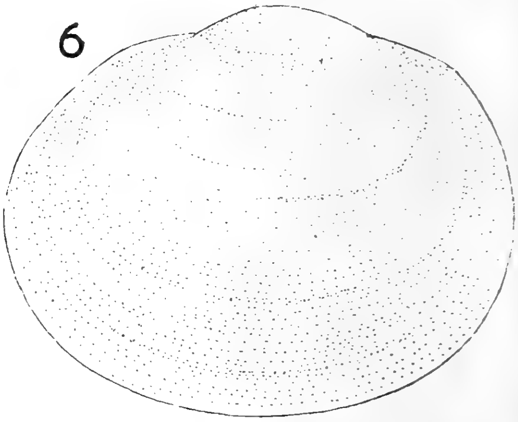

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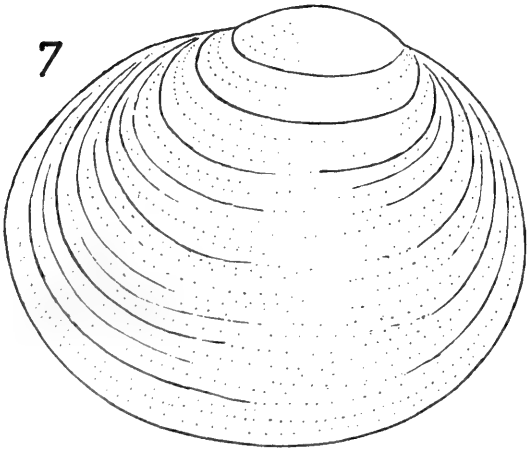

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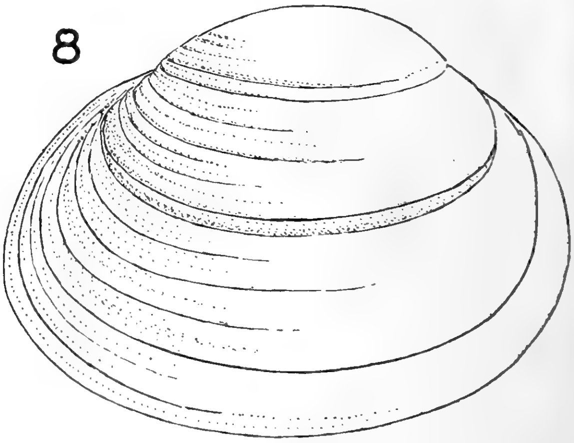

ventrally by a kind of pliciform callosity which has its analogy in the genus *Eupera* (Bourguignat, 1854; Klappenbach, 1960).

A similar ligament has been found in the endemic species of Lake Tanganyika, *Pisidium giraudi* Bourguignat.

The shell of *P. pirothi* is thin, subtransparent, and inequilateral, with a more or less pronounced, rather regular sculpture of concentric fine striae (about 10 striae on ½ mm. in the middle of the shell).

Details of the hinge structure are figured by Kuiper (1957, figs. 1 and 2). See also figure 9 of this paper.

Pisidium pirothi is closely related to the Indian *P. clarkeanum* Nevill, the Javanese *P. javanum* Benthem Jutting and the South American *P. sterkianum* Pilsbry. All these species have an external ligament and belong to the subgenus *Afropisidium* (Kuiper, 1962, p. 55). The Indian species is considerably larger and has a heavier shell than both the African and Indonesian species. J. Favre (1943, p. 11) classified the Egyptian specimens provisionally as a variety of the Indian species. I prefer to consider *P. pirothi* a distinct African species. I shall come back to this matter in a separate paper on the Central African pisidia.

Pisidium lepus is the type of the subgenus *Afropisidium*.

Pisidium harrisoni n.sp.

(figs. 2, 12, 32)

Description

Shell very inequilateral, elongate ovate, thin, beaks low, scarcely prominent, placed far back at one-quarter of the shell length. Dorsal margin short, half the shell length, slightly curved. Ventral margin broadly rounded. Anterior end very prolongate, obtusely pointed, upper side flattened. Posterior end faintly curved, perpendicular. Sculpture consisting of irregular fine concentric striae, 10–15 on ½ mm. in the middle of the shell. Ligament internal. The holotype is a closed shell. Its dimensions are: L. 4·1 mm., H. 3·1 mm., D. 2·1 mm.

Type locality

Vaal River between Morgenzon and Amersfoort, Transvaal (CSIR Val. 443 AA), leg. A. D. Harrison, 15.IX.1958.

←

FIG. 1. *Pisidium pirothi* Jickeli, Kruger National Park, Transvaal; L = ligament visible externally. FIG. 2. *P. harrisoni* n.sp., holotype, Vaal River, Transvaal. FIG. 3. *P. costulosum* Connolly, Klein Berg River, Cape Province. FIG. 4. *P. langleyanum* Melvill & Ponsonby, Lake Chrissie, Transvaal. FIG. 5. *P. viridarium* Kuiper, Maseru, Basutoland. FIG. 6. *P. ovampicum* Ancey (paratype of *P. georgeanum* Kuiper), Gwyang River, Cape Province. FIG. 7. *P. casertanum* (Poli), Mokhotlong, Basutoland. FIG. 8. *P. artifex* Kuiper, paratype, Mt. Kenya. Enlargements: 1–5 and 7, ×15; 6 and 8, ×20.

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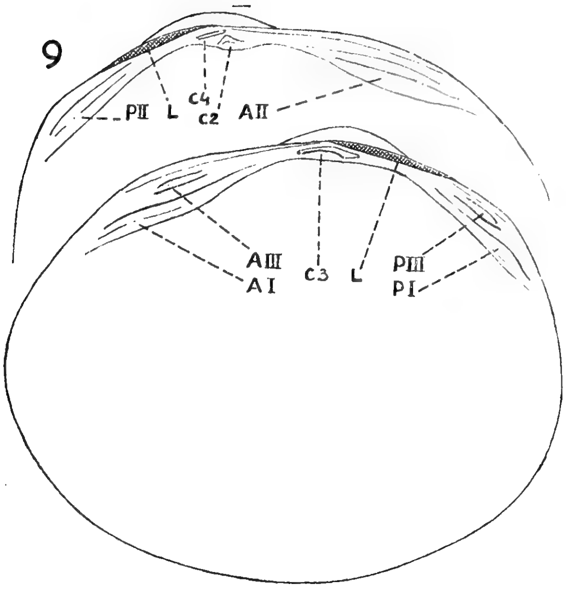

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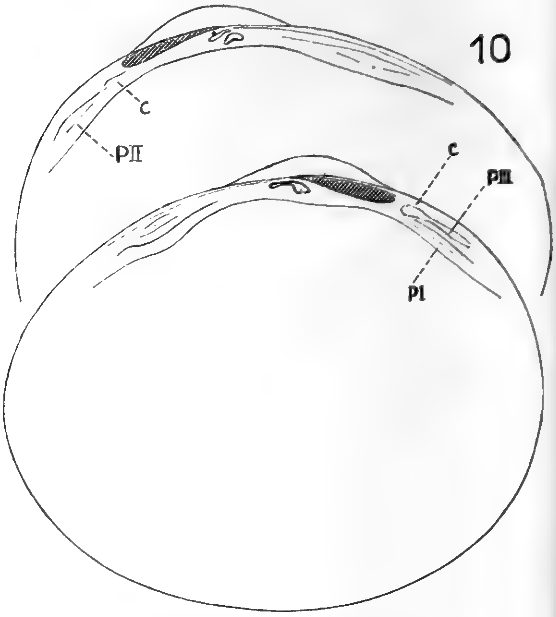

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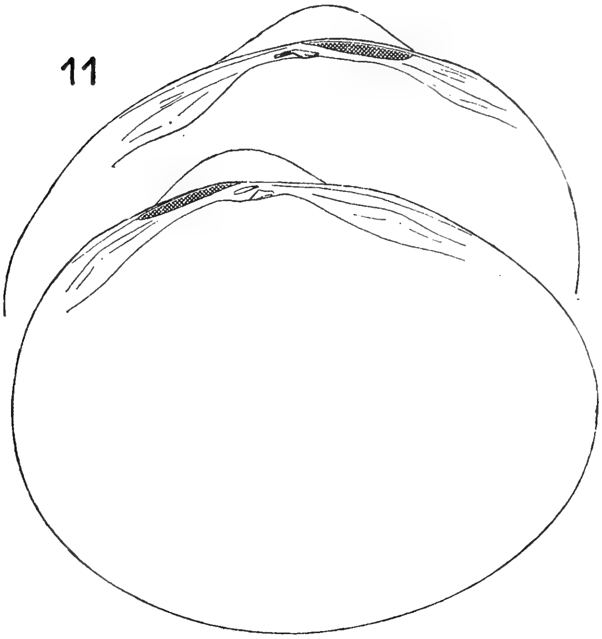

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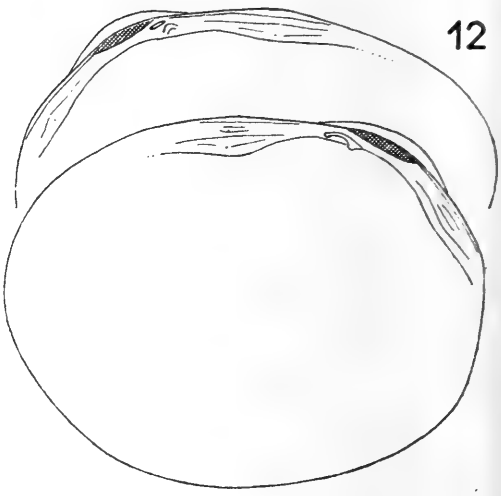

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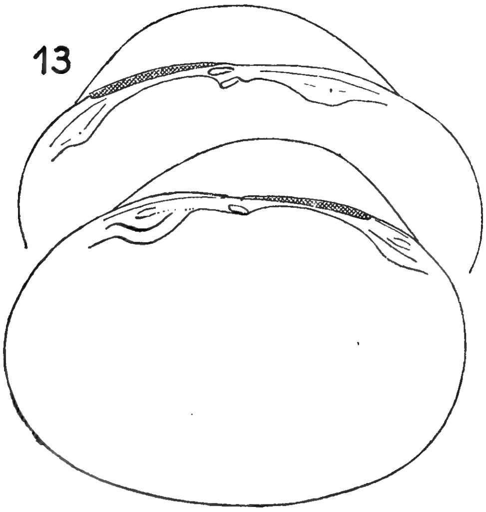

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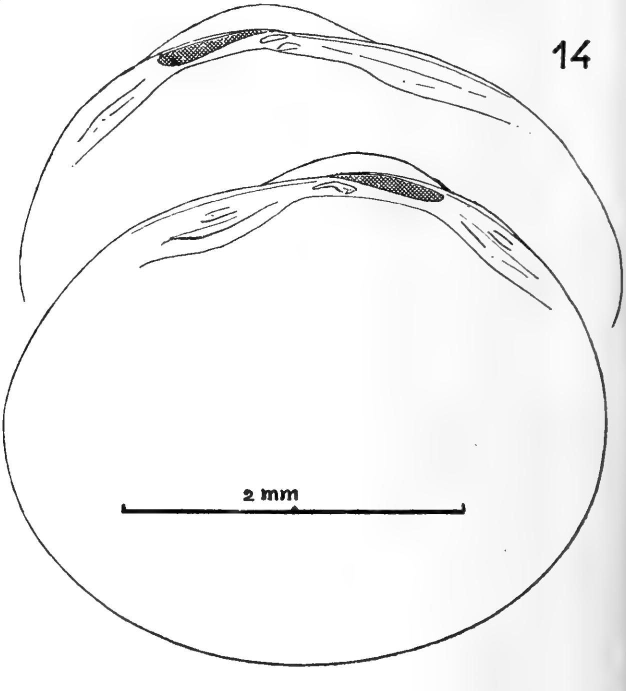


Material

Holotype in the South African Museum, Cape Town (SAM A29773); paratypes in the Zoological Museum of the Amsterdam University (ZMA/K 4979, 4980, 4982, 4983).

Pisidium harrisoni was also collected in the Vaal River near Vereeniging (CSIR Val. 210 B) and at the Barrage (CSIR Val. 141 B), 1956 and 1958, by Dr. A. D. Harrison. These specimens are all smaller than the type. Dimensions of some paratypes:

L. 3·40 mm. H. 2·80 mm. D. 1·90 mm. (CSIR Val. 141 B).
L. 2·80 mm. H. 2·30 mm. D. 1·50 mm. (CSIR Val. 443 AA).
L. 2·35 mm. H. 1·85 mm. D. 1·10 mm. (CSIR Val. 210 B).

Description of the hinge of one of the paratypes (ZMA/K 4983): Hinge plate narrow, in the left valve nearly as broad below the umbo as laterally, in the right valve very narrow under the umbo; length (distance between the cusps of AI and PI) half the shell length. Cardinal teeth C2 and C4 weak and short, C4 slightly posterior; C3 thin, thickened posteriorly. Cardinals nearer to anterior laterals than to posterior laterals. Lateral teeth AI and PI long and narrow, AIII and PIII very short; AII and PII shorter than AI and PI. Ligament-pit interior short, one-sixth of the shell length (fig. 12).

Remarks

I dedicate this species to Dr. A. D. Harrison, presently senior research fellow in the zoological department of the University College of Rhodesia and Nyasaland, Salisbury, Southern Rhodesia.

Pisidium harrisoni may easily be distinguished from all other African species hitherto known by its particular oblique shape. In this respect it somewhat resembles the palearctic species *P. subtruncatum* Malm which extends as far south as Algeria and Tangier.

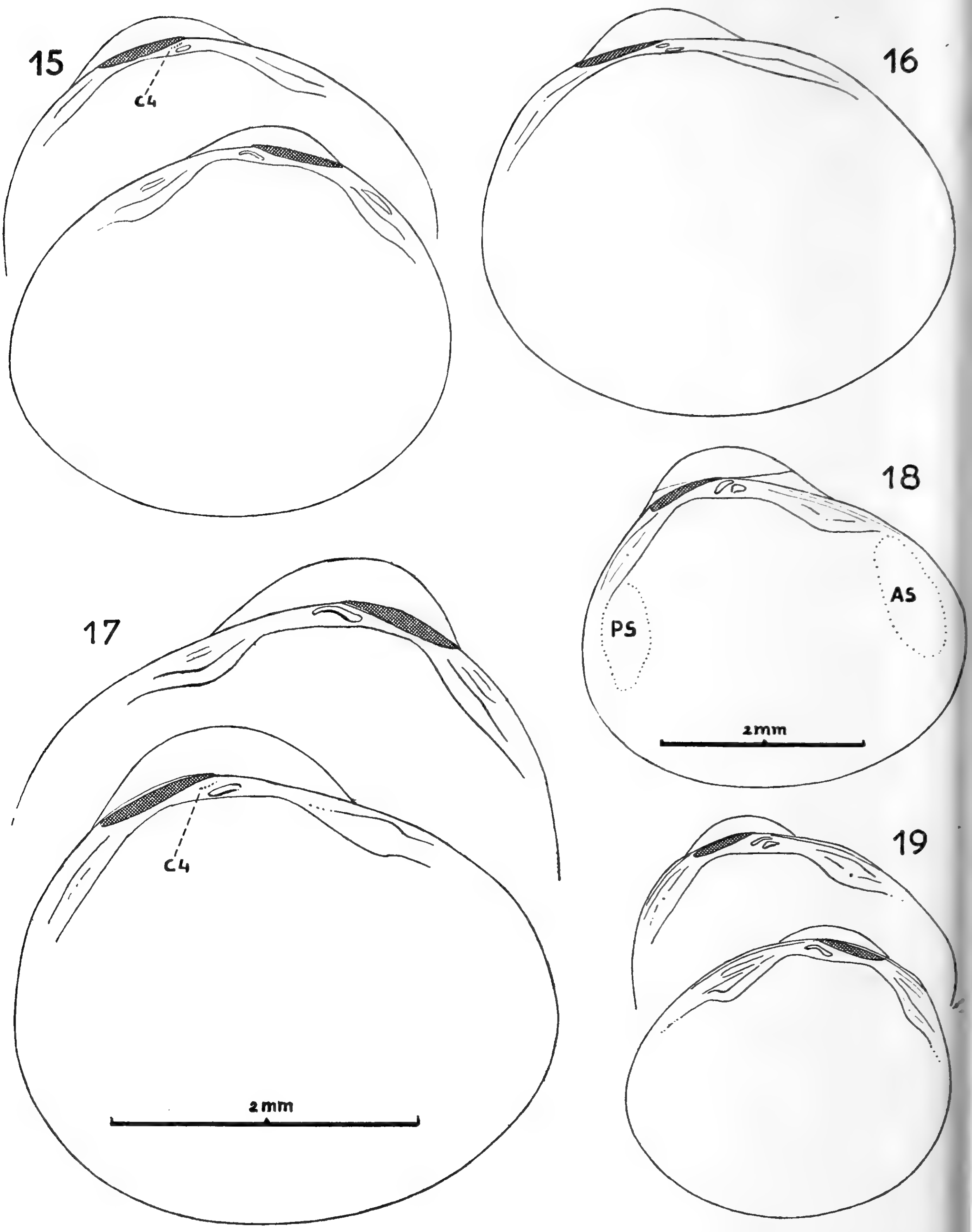
Pisidium costulosum Connolly

(figs. 3, 11, 31)

Pisidium costulosum Connolly, 1931*a*: 310, pl. 13, figs. 24–27; 1939: 626, fig. 57.
[*Non.*] *Pisidium costulosum* Haas, 1936-43.

←

FIGS. 9–14. Hinges of *Pisidium*. FIG. 9. *P. pirothi* Jickeli, Kruger National Park, Transvaal; left valve at the top; AI, AII, AIII, anterior lateral teeth; PI, PII, PIII, posterior lateral teeth; C2, C3, C4, cardinal teeth; L, ligament-pit. FIG. 10. *P. viridarium* Kuiper, Chindamora Reserve near Salisbury, Southern Rhodesia; left valve at the top; PI, PII, PIII, posterior lateral teeth; C, callosity at the inner end of PIII. FIG. 11. *P. costulosum* Connolly, Klein Berg River, Cape Province; right valve at the top. FIG. 12. *P. harrisoni* n.sp., paratype, Vaal River, Transvaal; left valve at the top. FIG. 13. *P. artifex* Kuiper, paratype, Hall Tarns, Mt. Kenya; left valve at the top. FIG. 14. *P. casertanum* (Poli), Mokhotlong, Basutoland, left valve at the top. Enlargement: see scale in fig. 14.



Figs. 15–19. Some forms of *Pisidium langleyanum* Melvill & Ponsonby. Fig. 15. Lectotype, left valve at the top, C4 reduced. Fig. 16. Paratype, left valve, nearly oval. Fig. 17. Trigonal shell with prominent beaks, right valve at the top, C4 reduced; specimen from Jonkershoek near Stellenbosch. Fig. 18. Left valve from Lake Chrissie; AS, anterior adductor scar; PS, posterior adductor scar. Fig. 19. Subtrigonal specimen from Potchefstroom, Transvaal. Enlargements: figs. 15, 16, 17 and 19, see scale in fig. 17; fig. 18, see scale in figure.

Distribution (fig. 31)

Cape Province

Berg River near Cape Town, at three different places (CSIR Gbg. 303 D; Gbg. 400 K; Gbg. 455 N), leg. A. D. Harrison, 1951 (ZMA/K 4189–4191).

Klein Berg River, dam in Tulbagh Kloof (CSIR Gbg. 732 L), leg. A. D. Harrison, 1953 (SAM A29775; ZMA/K 4187, 4188).

Orange Free State

Rustfontein, Rhenoster River (near Bloemfontein), type locality (Connolly) (BML 1937.12.30.9066, lectotype, and 9067–9, three paratypes).

Transvaal

Vaal River, barrage near Vereeniging (CSIR Val. 141 B, Val. 155), leg. A. D. Harrison, 1956 (ZMA/K 4978, 4991, 4994).

Klip River, headwater near Muller's Pass, between Memel and Newcastle (CSIR Val. 620 E), leg. A. D. Harrison, 1959 (ZMA/K 4977).

Klein Jukskei River near Linden, Johannesburg (CSIR Cro. 111 A and 130 E), leg. B. R. Allanson, 1956 (ZMA/K 4972, 4975).

Klein Jukskei River, Johannesburg (CSIR Gen. 44 A), leg. A. D. Harrison, 1954 (ZMA/K 4192).

Braamfontein Stream near Northcliff, Johannesburg (CSIR Cro. 48 B and 118 F), leg. B. R. Allanson, 1956 (ZMA/K 4973, 4976).

Zandfontein Stream, confluence with Jukskei Stream, near Leeukop Prison Farm, Pretoria district (CSIR Cro. 109 A), leg. B. R. Allanson, 1956 (ZMA/K 4974).

Vaal River near Standerton (CSIR Val. 29 J), 7.XII.1955 (ZMA/K 4997).

Description

Pisidium costulosum may easily be distinguished by its regular sculpture of concentric narrow ribs. Its shape does not vary greatly. The characteristic sculpture, however, shows some variability. On the lower part of the shell the ribs are relatively widely spaced (about 5 ribs on ½ mm.), the spaces between the ribs being at least twice as wide as the ribs themselves. Towards the beaks the ribs become narrower and closer (up to 15 ribs on ½ mm.). Sometimes the smooth nepionic shell is surrounded by some strong, more widely spaced ribs.

The shell is regularly porous, the distribution of the pores not being limited to the interstices of the ribs. The ligament is long and internal. The largest known specimen of *P. costulosum* measures: L. 3·4 mm., H. 2·8 mm., D. 2·1 mm. This was collected in the Klein Berg River, Cape Province (ZMA/K 4187).

Remarks

Apart from the Berg River, *P. costulosum* is also known from the Vaal and Orange River systems. It seems to be a typical South African species. It has only been collected in rivers and streams, so far never in brooks. *P. costulosum* is often associated with *P. langleyanum*.

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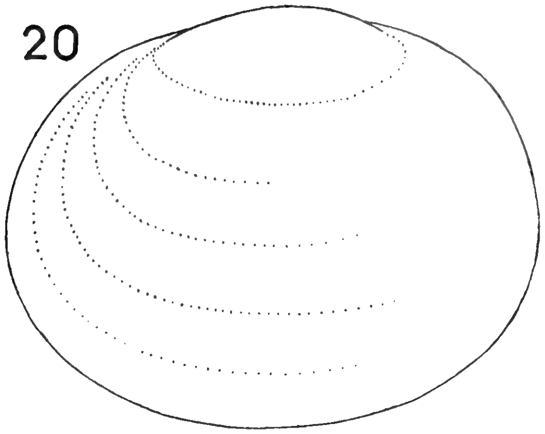

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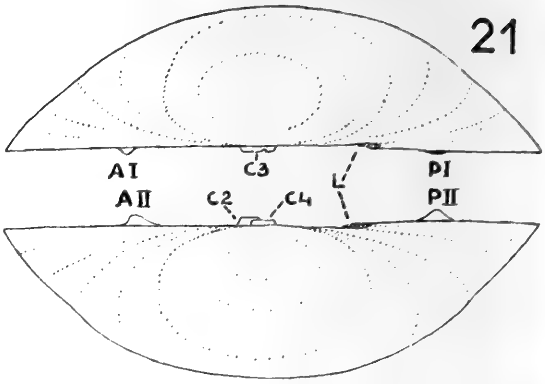

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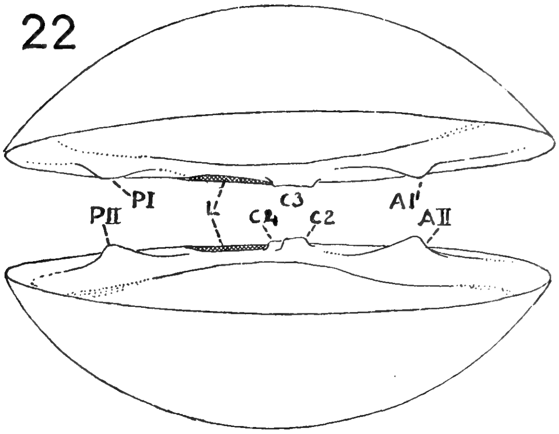

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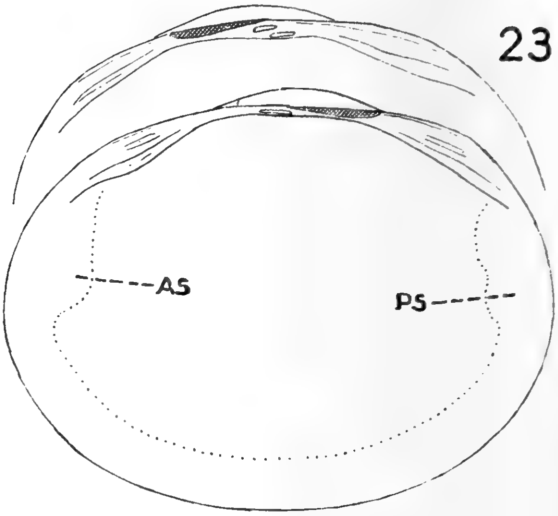

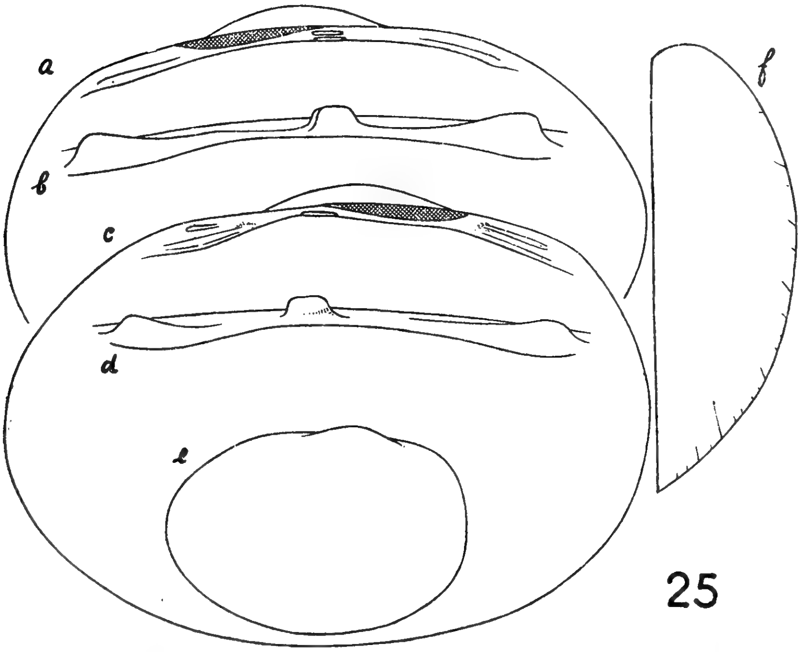

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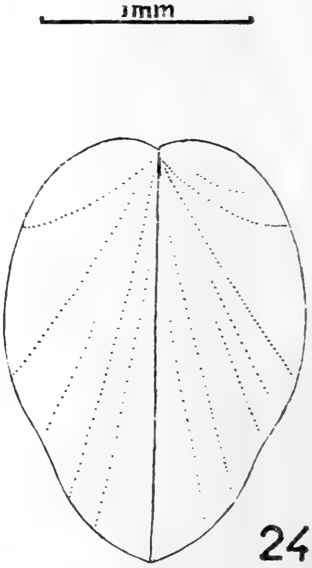

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Figs. 20–24. Lectotype of *Pisidium ovampicum* Ancey. Fig. 20. Right valve. Fig. 21. Dorsal view of both valves, right valve at the top; for abbreviations see explanation to fig. 9. Fig. 22. Ventral view on hinge, right valve at the top; for abbreviations see explanation to fig. 9. Fig. 23. View on hinge, left valve at the top; AS, anterior adductor scar; PS, posterior adductor scar. Fig. 24. Profile view. Fig. 25. *P. georgeanum* (= *P. ovampicum*), paratype as figured by Kuiper, 1952; *a*, left valve; *b*, ventral view on hinge of left valve; *c*, right valve; *d*, ventral view on right valve; *e*, outline of juvenile specimen; *f*, profile view of single valve. Enlargement: figs 20–25, see scale above fig. 24.

The population recorded by Haas (1936, p. 43) in the Kruger National Park, Transvaal, does not belong to *P. costulosum*, but to *P. lepus* (Kuiper 1957), which proved to be a synonym of *P. pirothi* Jickeli.

Pisidium langleyanum Melvill & Ponsonby

(figs. 4, 15–19, 27)

Pisidium langleyanum Melvill & Ponsonby, 1891: 237.
Pilsbry & Bequaert, 1927: 351.
Connolly, 1939: 625.
Kuiper, 1960: 67, figs. 18–23.
[?] *Pisidium* cf. *langleyanum*: Boettger, 1910: 455, pl. 28, fig. 19 *a–b*.
[*Non*] *Pisidium langleyanum*: Melvill & Ponsonby, 1892, pl. 5, fig. 7.

Distribution (fig. 27)

Cape Province

Port Elizabeth, leg. J. H. Ponsonby (Melvill & Ponsonby, 1891, p. 237; BML 1902.7.30.40–42, lectotype and 2 paratypes; SMF 152884, 1 paratype, leg. Ponsonby, 1889, ex coll. O. Boettger; Kuiper, 1960, figs. 18–23).

Jonkershoek near Stellenbosch, fish-ponds (ZMA/K 4185; BML 15 sp.).

Hogsback near Alice, small stream at the edge of the plateau at a height of about 4,000 to 4,500 feet (CSIR Misc. 10 and Misc. 62 B), leg. A. D. Harrison, 1950 and 1953 (ZMA/K 3762, ZMA/K 4177).

Kimberley, leg. J. A. van Eeden, 1.X.1958 (IZRP; ZMA/K 13481).

Grahamstown, leg. J. A. van Eeden, 13.III.1959 (IZRP; ZMA/K 13485).

Uniondale, leg. J. A. van Eeden, 24.III.1959 (IZRP; ZMA/K 13487).

Orange Free State

Rustfontein, Rhenoster River (near Bloemfontein) (Connolly, 1939, p. 625; BML/Mus. Cuming 1937.12.30.9073, 1 specimen).

Natal

Durban, leg. J. A. van Eeden, 30.VII.1959 (IZRP; SAM A29769; ZMA/K 13488).

Transvaal

Klein Vaal (NIWR Val. 733 LL), about 9 miles from its confluence with the Vaal River (ZMA/K 13489).

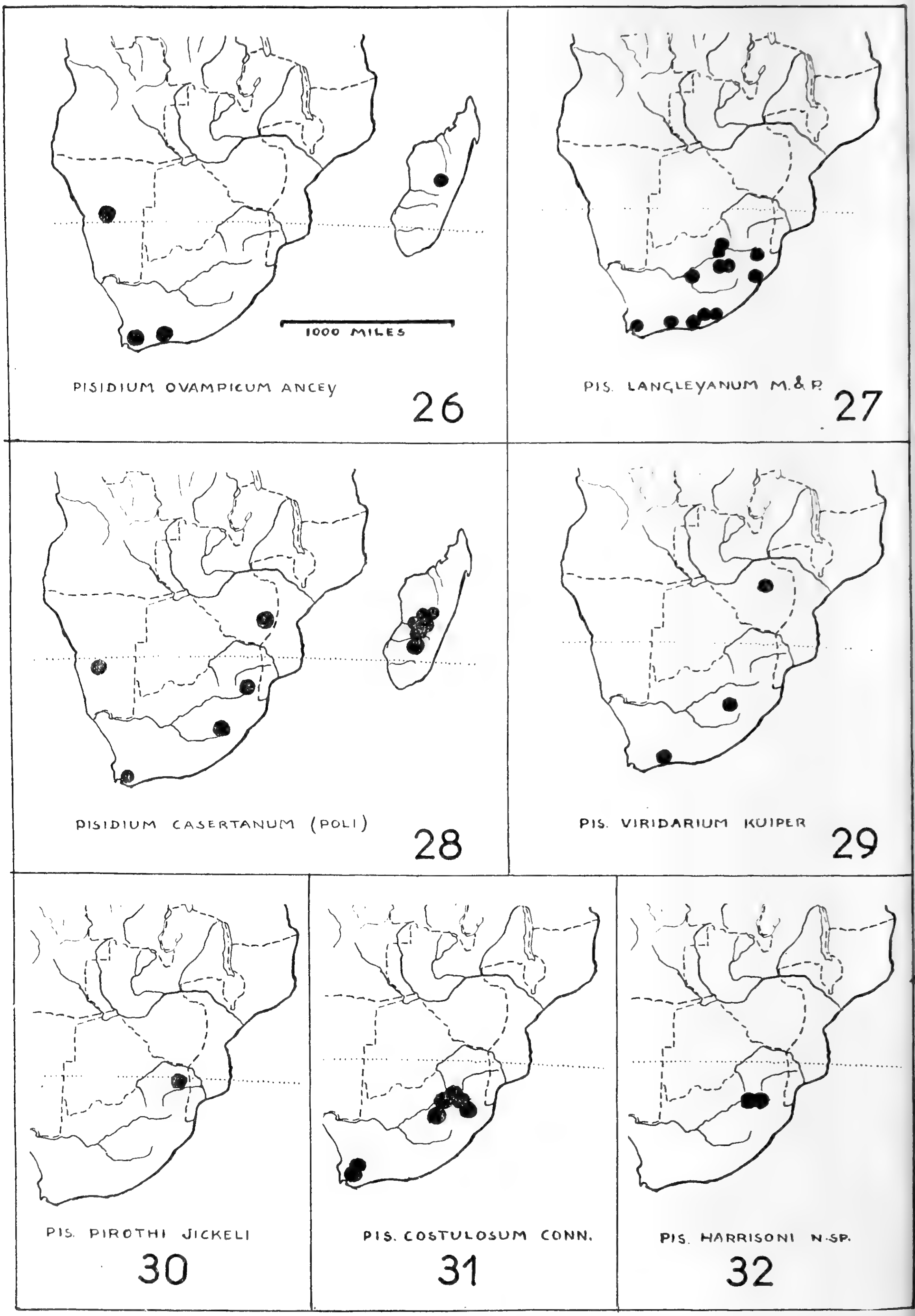
Headwater stream of Vaal River between Breyton and Lake Chrissie (CSIR Val. 743 DD), 22.VII.1959 (ZMA/K 4989).

Lake Chrissie, leg. F. G. Cawston (NMP).

Potchefstroom, leg. M. I. Livingston (NMP).

Description

The shell of *P. langleyanum* is characterized by its subtrigonal shape and its regular sculpture of fine concentric striae. Its nepionic shell is sometimes bordered by some (4–7) sharp striae. The shell is densely porous. Its dorsal margin is more strongly rounded than its ventral one. The shell of the type is



Figs. 26–32. Distribution of Pisidia in South Africa. *Pisidium ovampicum* Ancey and *P. casertanum* (Poli) are also known from Madagascar.

rather thin and has a narrow hinge (figs. 15, 16). The posterior laterals are parallel and do not converge proximally. A detailed description of the type is given by Connolly (1939, p. 625), who calls it 'a somewhat immature shell with hinge system poorly developed' (fig. 15). In heavier shells, such as those from Hogsback, Cape Province, the outer posterior lateral (PIII) bends proximally slightly towards the inner posterior lateral (PI).

The outline of the shell is more or less ovate when the beaks are not prominent, and trigonal when they are prominent. Both forms may occur in the same population (Jonkershoek, Cape Province).

The ligament is internal. It is, however, partially visible externally, resulting from a slight gaping of the valves behind the beaks, a feature which is rather common in the genus *Pisidium*.

Dimensions of the lectotype: L. 2·9 mm., H. 2·5 mm., D. 1·8 mm. Dimensions of a number of other specimens from several localities:

L. 3·9 mm.	H. 3·4 mm.	D. 2·6 mm.	Kimberley.
L. 3·8 mm.	H. 3·3 mm.	D. 2·8 mm.	Lake Chrissie, swollen shell (fig. 18).
L. 3·4 mm.	H. 3·2 mm.	D. 2·4 mm.	Jonkershoek, trigonal shell (fig. 17).
L. 3·2 mm.	H. 2·8 mm.	D. 2·3 mm.	Port Elizabeth.
L. 3·0 mm.	H. 2·6 mm.	D. 2·2 mm.	Hogsback.
L. 2·9 mm.	H. 2·6 mm.	D. 2·0 mm.	Jonkershoek.
L. 2·8 mm.	H. 2·4 mm.	D. 1·9 mm.	Jonkershoek.
L. 2·6 mm.	H. 2·3 mm.	D. 1·8 mm.	Hogsback.
L. 2·4 mm.	H. 2·1 mm.	D. 1·5 mm.	Hogsback.
L. 2·2 mm.	H. 2·0 mm.	D. 1·5 mm.	Potchefstroom (fig. 19).

Details of the hinge structure are figured by Kuiper (1960, figs. 18–20, 23).

Remarks

The specimen figured by Melvill & Ponsonby (1892, pl. V, fig. 7) is not *Pisidium langleyanum*, but another species (Kuiper, 1961, p. 67).

O. Boettger (1910, p. 455) recorded 6 subfossil valves from Witkop, Bechuanaland, under the name '*Pisidium* cf. *langleyanum*'. Connolly (1939, p. 625) has placed this form into the synonymy of *P. ovampicum* Ancey. In my opinion this is not correct. Boettger's figures (1910, pl. 28, fig. 19 *a–b*) prove that it is not the ovate *P. ovampicum*, but a more trigonal species, perhaps indeed *P. langleyanum*. One of these specimens, a very small left valve, which I had the opportunity to examine (SMF 152885), did not allow me to decide with certainty about its specific identity. I have not seen the other valves.

Pisidium langleyanum is known only from southern Africa. It is closely allied to *P. kenianum* which is distributed in Central Africa. Perhaps they will prove to be identical. Both species are related to the Indian *P. nevillianum* Theobald. *P. kenianum* has a trigonal outline and is heavier. It can be considerably larger than *P. langleyanum* (up to 4·6 mm.). The distance between the northernmost known localities of *P. langleyanum* (Transvaal) and the southernmost ones of *P. kenianum* (in Tanganyika) is about 1,500 miles.

Pisidium viridarium Kuiper

(figs. 5, 10, 29)

Pisidium viridarium Kuiper, 1956: 61–63, figs. 1–8.

Distribution (fig. 29)

Cape Province

Gwyang River near George (CSIR Frw. 88), leg. A. D. Harrison, 4.V.1950 (ZMA/K 4178).

Basutoland

Maseru, Roma Mission Station, 5.IV.1958, leg. J. A. van Eeden (IZRP; SAM A29772; ZMA/K 13483).

Remarks

Pisidium viridarium was described from specimens collected in Kenya. This species is also known from Southern Rhodesia, Ethiopia, Uganda, Ruanda and Congo.

Pisidium viridarium has a thin, ovate shell with submedian beaks. Young specimens somewhat resemble *P. ovampicum*. The regular sculpture of fine, equidistant concentric striae is the same as in *P. kenianum* and *P. langleyanum*. Its PIII is proximally thickened (fig. 10) as is often found in *P. kenianum*. The shell is densely porous. The affinities between *P. viridarium*, *P. kenianum* and *P. langleyanum* have not as yet been cleared up. The resemblance to the European *P. personatum* which, incidentally, has been collected in Uganda, is probably phenotypical. *P. viridarium* attains larger dimensions than *P. personatum*, one of the paratypes being nearly 5 mm. long.

Details of the hinge structure are figured by Kuiper (1956, figs. 1, 4, 5, 6).

Ecologically *P. viridarium* seems to prefer marshy biotopes. It also lives in the mud out of the current in rivers where the aquatic vegetation is dense. It has been found associated with *P. kenianum* and *P. ovampicum*.

Pisidium ovampicum Ancey

(figs. 6, 20–26)

Pisidium ovampicum Ancey, 1890: 162.
Pisidium georgeanum Kuiper, 1952: 46–48, figs. *a–f*.
[*Non*] *Pisidium ovampicum* Connolly, 1939: 625.

Distribution (fig. 26)

Cape Province

Gwyang River near George, type locality of *P. georgeanum* Kuiper (CSIR Frw. 88), leg. A. D. Harrison, 4.V.1950 (holotype of *P. georgeanum* in RML, paratypes in LMP, MHNG, SAM A29774, ZMA/K 3604).

Jonkershoek near Stellenbosch, fish-ponds, leg. A. C. Harrison, 1947 (ZMA/K 4184).

South West Africa

Ovamboland (Ancey: Ovampoland = Damaraland), Omanbondè, type locality of *P. ovampicum*, leg. *viatores* Andersson and Chapman (KINB I.G.1059, lectotype of *P. ovampicum*).

Remarks

Pisidium ovampicum has been an enigmatic species for more than half a century. The original description is fairly good, but it is impossible to interpret because details of the hinge structure and figures were not given, and the type material was apparently lost.

Connolly (1931*a*, p. 325), who therefore considered Ancey's species as being 'null and void, a just fate for such a slovenly description',* has tried to give a new identity to *P. ovampicum*. He (1939, p. 626) described the hinge of specimens which he thought specifically identical with *P. ovampicum* Ancey. He too, however, failed to publish illustrations.

P. ovampicum thus remained an obscure species until recently when an authentic specimen of this species was found in the Dautzenberg collection (KIN, Brussels). I now designate this specimen the lectotype of *P. ovampicum* Ancey. It was, as supposed by Connolly (1939, p. 626), 'unopened'. I opened it by soaking the shell in water for some days.

The specimens from Lake Chrissie, on which Connolly based his redescription 'with the purely tentative suggestion that they may represent Ancey's lost species' (Connolly, 1939, p. 625), do not belong to *P. ovampicum* but to *P. casertanum*.

Description

Description of the lectotype *P. ovampicum*. Shell thin, ovate, nearly equilateral, opaque, no pores visible, glossy. Beaks smooth, median, not prominent, scarcely rising above the dorsal shell margin. Sculpture consisting of very fine irregular striae and two slight growth-lines. Greatest shell length in the horizontal median plane, greatest shell height in the vertical median plane. Ventral margin more rounded than dorsal margin. Anterior and posterior margins nearly equally rounded. Ligament internal, dark brown. Hinge plate narrow. In the left valve the lateral parts are scarcely broader than the central part; in the right valve the lateral parts are a little broader than the central part. The lateral teeth, PI, PII, AI and AII are narrow and have pointed, distal cusps. PIII and AIII are short, small teeth. Cardinal teeth thin, short and straight, C3 being the longest of all. C2 is a short tooth on the ventral margin of the hinge-plate; C4 as long as C2 and parallel to it. The distance between the cusps of AII and PII is 1·5 mm.; between those of AII and C2, 0·6 mm.; between PII and C2, 0·9 mm. Ligament-pit 0·5 mm., narrow. Posterior adductor a little larger and situated lower than the anterior adductor. Dimen-

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* It is curious that Connolly (1939, p. 626), quoting Ancey's original description, omitted its beginning: 'Testa fragilis, pallide cornea. . . .'

sions: L. 2·6 mm., H. 1·9 mm., D. 1·5 mm. (in the original description L. $2\frac{2}{3}$ mm., H. $2\frac{1}{7}$ mm., D. $1\frac{1}{2}$ mm.).

The differences between the paratype of *P. georgeanum* and the lectotype of *P. ovampicum* are slight. Shape and sculpture are nearly the same. Equally large specimens of *P. georgeanum* have slightly more prominent beaks and consequently are a little higher. The junction between the dorsal and the anterior as well as the posterior margins of *P. georgeanum* are slightly more angulate. In both forms the hinge-plate is narrow, the laterals are thin and sharp, the cardinals small. In the lectotype of *P. ovampicum*, C4 lies slightly more posteriorly with respect to C2 than in the paratypes of *P. georgeanum*. In both forms the ventral margin is more curved than the dorsal margin. *Pisidium georgeanum* is porous, whereas the lectotype of *P. ovampicum* has no pores at all.

Details of the hinge structure of *P. georgeanum* are figured by Kuiper (1952, figs. *a–d*).

Remarks

The form *georgeanum* is widely distributed in South and Central Africa, as well as on the isle of Madagascar. I have seen series from Uganda, Ethiopia, Congo and Madagascar.

The following records turned out not to be *P. ovampicum*:

(*a*) 'A single weathered valve from Damara or Ovamboland' (Connolly, 1939, p. 625; BML 1937–12.30.9070).

(*b*) Two 'better grown and preserved specimens from Lake Chrissie' (Connolly, 1930, p. 625; BML 1937.13.30.9971–9972), originally published by Hutchinson (1932, p. 49).

(*c*) The subfossil valves from Witkop Bechuanaland (SMF 152885), mentioned by O. Boettger (1910) as *P.* cf. *langleyanum* and placed by Connolly in the synonymy of *P. ovampicum*.

I am not yet certain of the identity of the specimens mentioned under (*a*) and (*c*). I believe that (*b*) belongs to *Pisidium casertanum* (Poli). As to the habitat of these two specimens Hutchinson (1932, p. 49) wrote: '. . . taken on a rock surface under very wet soil at one of the springs bordering the lake.' This agrees well with the ecology of *P. casertanum*.

Dr. A. D. Harrison wrote me the following details on the first-mentioned locality: 'The Gwyang, where these specimens were collected, is a small stream with a muddy bottom covered with *Chara* or *Nitella*; they were not very numerous and I had to sort through three or four sieve-fulls of bottom before we obtained the specimens in the tube. The water is acid with a PH of about 5; it is brown or peat stained.'

As to the second locality, the fish-ponds near Jonkershoek, Dr. Harrison noted: 'The specimens were originally found fastened on to the noses of young trout.' This observation is very interesting in connexion with the passive dispersal of these small clams by means of other animals, a subject about which very little is known.*

Pisidium artifex Kuiper

(figs. 8, 13)

Pisidium langleyanum (*non* M. & P., 1891), Melvill & Ponsonby, 1892: 94, pl. 5, fig. 7.
Pisidium artifex Kuiper, 1960: 68–74, figs. 1–17.

Holotype in BML. Paratypes: SMF 162841–2; SAM A29770 (paratype Nr. 17); Coryndon Museum, Nairobi; ZMA/K 4909–4925, 4927.

Remarks

This species is known only from some high mountain tarns in Kenya. It is easily recognizable by its extraordinary swollen shape, its diameter being the same or even more than the height of the shell, and by its very broad and tumid beaks.

Details of the hinge structure are figured by Kuiper (1960, figs. 1, 2, 3, 6 and 9).

In the original description of *P. artifex*, I drew attention to the fact that the specimen figured by Melvill & Ponsonby (1892, pl. 5, fig. 7) cannot be *P. langleyanum* but probably belongs to *P. artifex*. If this should prove to be true, *P. artifex* has to be added to the South African fauna. Melvill & Ponsonby (1892), however, do not mention any locality.

Pisidium casertanum (Poli)

(figs. 7, 14, 28)

Cardium casertanum Poli, 1791: 65, pl. 16, fig. 1.
Pisidium ruwenzoriense Germain, 1911*a*: 135.
Pisidium ovampicum (*non* Ancey) Connolly, 1939: 625.
Pisidium edouardi Kuiper, 1953: 26–28.

There are several specimens in the South African Museum (A29767 and A29768) from Ethiopia and Cyrenaica.

Distribution (fig. 28)

Cape Province

Krom River, Stellenbosch (CSIR Ers. 6 L), leg. A. D. Harrison, 22.VIII.1952 (ZMA/K 4757).

Transvaal

A spring bordering Lake Chrissie (Hutchinson, 1931, p. 49, s.n. *Pisidium* sp. juv.; Connolly, 1939, p. 625, s.n. *P. ovampicum*; BML 1937.12.30.9971–72).

Basutoland

Makkeka Mountains, 15 miles E.N.E. Mokhotlong, alt. 9,500 ft. In slow-flowing part of the stony high mountain stream, leg. Per Brinck (SSAE), 8.IV.1951 (ZIUL 2931; ZMA/K 4414).

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* See the classic work of H. Wallis Kew: *The dispersal of shells*. London, Kegan Paul & Co., 1893, pp. 61 sqq. [Ed.].

South West Africa

Grootfontein, farm Urupupa, leg. Thomson, 1912 (SMF 152883, one right valve ex coll. O. Boettger).

Remarks

Pisidium casertanum (Poli) is the commonest and most variable species in the holarctic region. In the Southern hemisphere this species is less variable. In northern Africa it lives in the coastal region from Morocco to Cyrenaica. It has not yet been found in Egypt. *P. casertanum* (Poli) var. *alexandrina* Pallary belongs not to this species but to *P. pirothi* Jickeli.

In equatorial Africa it is known from many high mountain localities in Ethiopia, Uganda and Tanganyika. It has also been collected in Rhodesia (Herrington, 1962, p. 34). *P. casertanum* has been described from Madagascar under the name *P. edouardi*. The Austrian Madagascar Expedition 1958 collected this species commonly in central Madagascar. The specimens from the Makkeka Mountains, Basutoland, collected by the Swedish South Africa Expedition 1951, are identical with the types of *P. edouardi* from Madagascar (Kuiper, 1953, pl. 1, figs. 1–5). The dimensions of the five specimens taken in the Makkeka Mountains are:

L 3·8 mm.	H. 3·2 mm.	D. 2·3 mm.
L. 3·6 mm.	H. 3·0 mm.	D. 2·1 mm.
L. 3·4 mm.	H. 2·8 mm.	D. 1·9 mm.
L. 2·9 mm.	H. 2·4 mm.	D. 1·7 mm.
L. 2·8 mm.	H. 2·3 mm.	D. 1·5 mm.

The East African mountain range seems to provide a climatic bridge from the palearctic region to the southern African area for this species. The dispersion involved is perhaps due to the migration of aquatic birds.

The identification of this variable species is often difficult. I have based my conclusions on conchological characters only, as these are more reliable than anatomical characters for specific identification in the genus *Pisidium*.

SUMMARY

The seven, or perhaps eight, species of the fresh-water lamellibranch genus *Pisidium* which are found in South Africa are described, with one new species, *P. harrisoni*. Taxonomic notes and figures and remarks on distribution are included.

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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).

J. H. DAY

A REVIEW OF THE FAMILY AMPHARETIDAE (POLYCHAETA)

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A REVIEW OF THE FAMILY AMPHARETIDAE (POLYCHAETA)

By

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Contents

Introduction

The most complete account of the family Ampharetidae is that of Hessle (1917). He reviews earlier work including that of Malmgren (1865) and Fauvel (1897) on family and generic characters, Nilsson (1912) on the nervous system, Wiren (1885) on the alimentary canal, and Meyers (1887) on the nephridia. After giving further evidence from his own researches on the nephridia and structure of the stomach he goes on to discuss generic characters. While he follows the main lines laid down by Malmgren he finds that the genera were so narrowly defined by the latter worker that they seldom include more than one or two species, so that broader generic definitions are necessary. He criticizes Fauvel's work on the enumeration of the anterior segments and his genera as being based partly on internal anatomical characters. Surprisingly enough Hessle's own generic divisions may be criticized on the same lines. Although he stresses that the number of nephridia may vary from species to species in the same genus he has grouped the genera largely on the relative sizes and arrangement of these internal structures.

Since the publication of Hessle's work many new genera have been erected, particularly by Augener (1918), Chamberlin (1919), Benham (1921), Annenkova (1930), Caullery (1944) and Eliason (1955). In general these later workers focused attention on external features, particularly the development

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of the paleae and the number of thoracic setigers, and they do not describe the nature of the nephridia nor the morphology of the stomach. As a result it is difficult to correlate the genera they describe with those defined in Hessle's monograph. There is also another source of confusion. Nilsson and Hessle recognize only a single two-ringed buccal segment in front of the paleal or first branchiferous segment, so that the latter becomes segment II. This interpretation is followed by Annenkova (1930), Eliason (1955), and Uschakov (1957). On the other hand Malmgren (1865), Fauvel (1897 and 1927) and Caullery (1944) recognize two segments in front of the paleae, so that the latter which also bears the first pair of branchiae becomes segment III. At first sight it would seem of little taxonomic importance whether the first branchiferous segment is labelled segment II or III, but as many workers do not state which system of numbering they are using, statements such as 'setae present on segment III' or 'nephridia absent from segment V' or 'notosetae of segment XIII modified' lead to confusion.

To date about 150 species have been described, distributed through about 49 genera. Fifty-six species are ascribed to the three genera *Amphicteis*, *Amage*, and *Ampharete*, and the remaining 94 are distributed through the remaining 46 genera, many of which are monotypic. The need for revision is obvious.

In the account that follows the various diagnostic characters are discussed, the grouping of genera is considered, and tables and keys are provided for the whole family.

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Discussion of diagnostic characters

The head and buccal tentacles. The Ampharetidae are deposit feeders and the food particles are collected by mobile projections that arise from the roof of the buccal cavity. The most common type are buccal tentacles which are either smooth with a longitudinal groove on one side as in the Terebellidae or papillose; often these papillae are pinnately arranged, but not always, and buccal tentacles of this type are best described under the more general term 'papillose'. Apart from tentacles, folded or probosciform feeding membranes have been described in *Amythas membranifera* Benham and *Pabits deroderus* Chamberlin. An examination of *Isolda whydahensis* Augener showed a long ribbon-shaped structure protruding from the mouth with the distal end split into a number of short tentacles.

As stated, these feeding organs arise from the roof of the buccal cavity and in some cases the mouth cavity leads straight back into the pharynx; in other cases, however, an internal shelf or horizontal septum separates the tentacular cavity above from the pharynx below. According to Hessle this septum corresponds to the dorsal lip of the Terebellidae.

Above the mouth there is a hood-shaped lobe which Hessle refers to as the 'Tentakelmembran' and Fauvel as the prostomium. Since it bears the eyes and nuchal grooves and contains the cerebral ganglia the latter term will be used here. In some genera it also bears a pair of glandular ridges which diverge anteriorly and project from the antero-lateral margins as a pair of blunt processes.

When the buccal tentacles are retracted the prostomium may appear bluntly pointed with obvious lateral grooves, so that the whole prostomium (or tentacular membrane) has been described as trilobed. When the buccal tentacles are fully extended, however, the whole head is stretched, the anterior margin is straightened, and the lateral grooves disappear. This mobility of the head means that the exact shape of the prostomium is of little systematic value. The glandular ridges, however, are always recognizable and the eye-spots can usually be found.

The segmentation of the head region. As described earlier (Day 1961) the region behind the prostomium is telescoped and the segments are distorted. The branchiae are often grouped on a transverse branchial ridge which partially overhangs the segments immediately behind the prostomium. The ventral surface in *Melinna* and related genera is distorted by the formation of a pair of lateral folds which slope back from the mouth region towards the dorsum of segment VI where they unite to form a transverse dorsal crest. On the basis of dissection and examination of external features I have accepted the interpretation of Malmgren, Fauvel, and others that there are two achaetous segments preceding the branchiae in all genera. The first branchiferous segment, which bears the paleae in some genera, thus becomes segment III.

The branchiferous region (segments III–VI). In the more primitive genera, including *Phyllocomus*, *Melinna*, *Isolda*, *Amphicteis* and *Ampharete*, there are four pairs of gills. Dissection of the blood-vessels of *Amphicteis gunneri*, described by Day (1961), showed that the four gills are supplied by four blood-vessels corresponding to segments III, IV, V and VI. With the telescoping of the anterior segments, however, there is a tendency for the four pairs of gills to be grouped on the dorsal surface of segments III and IV. In *Phyllocomus* the first two pairs are on segment III and the last two pairs are segmentally arranged. The same arrangement has been reported in *Amage auriculata* and *Amphicteis posterobranchiata*. In other genera the arrangement may be 2 : 2 or 3 : 1 where three pairs of gills are arranged in a transverse row across segment III with the fourth pair immediately behind.

In many genera the primitive number of four pairs of gills has been reduced to three and in *Auchenoplax* Ehlers and its synonym *Melinnoides* Benham only two pairs have been reported.

The gills may be separate from one another or united by a basal web.

Commonly this web unites only the first three pairs of gills, leaving the fourth posterior pair free. The gills may be smoothly cylindrical in shape or may develop lateral papillae or flanges or even a series of lateral lamellae. Commonly the branchial papillae are arranged in two lateral rows, and such branchiae have been termed bipinnate, but this is not always the case. In *Pterampharete luderitzi*, for example, numerous irregularly arranged papillae arise from the anterior surface of the branchial axis. In generic descriptions such gills are best described by the broader term papillose. Similarly the lateral lamellae of such forms as *Phyllamphicteis collaribranchis* Augener and *Phyllocomus* (*olim Schistocomus*) *hiltoni* (Chamberlin) may be arranged in one or more rows.

The telescoping of the branchiferous region often results in the fusion of segments and the loss of setae. In *Isolda* and *Melinna* of the sub-family *Melinninae* the neurosetae of the four segments III–VI are present though those of segment VI may be lacking in some species. Segment III never has notosetae, and segment IV has notosetae in the form of stout hooks behind the gills, but the notosetae of segments V and VI are either small or absent. In *Melinnopsis* McIntosh the hooks of segment IV are lacking, but notopodial capillaries are present on segments V and VI.

In the sub-family *Ampharetinae* neurosetae are never developed on segments III to VI. In a few cases all four segments may be distinct, but usually segments III and IV are fused and occasionally segments III, IV and V. The notosetae are variously developed. In primitive forms such as *Amphicteis* the notosetae of segment III are enlarged to form stout paleae and those of segments IV–VI are all present as normal capillaries. Often, however, the capillary notosetae of IV and V are small or absent. Similarly the notosetae of segment III may remain small and not form paleae, or may be entirely lacking. In *Sabellides*, for example, the notosetae of segment III are either absent or represented by small capillaries, segment IV is fused to segment III and lacks setae, and the first normal capillaries are on segment V. In *Neosabellides elongatus* there are no setae on segments III and IV, and in *Paramage madurensis* Caullery reports that the first bundle of notosetae appears on segment VI though earlier achaetous notopodia remain. In view of the many variations in the setation of the branchiferous segments III to VI and the difficulty of deciding whether small setae present on the fused third and fourth segments represent small paleae of segment III or small capillaries of segment IV, it would seem undesirable to base generic divisions on the presence or absence of paleae as has been done in the past.

Internal characters: diaphragm, nephridia, stomach. Apart from a few minor details no new researches are reported here under this heading. The information concerning the type-species of each genus has been extracted from Hessle (1917), supplemented by additional information from Annenkova (1930), and has been summarized in tables I and II. In several genera no information is available concerning the internal anatomy.

The coelomic cavity of the first few segments is separated from the rest of the thorax by a relatively stout septum or diaphragm. According to Hessle this always lies between segments IV and V, but according to the enumeration of segments adopted here it lies between segments V and VI. Following Hessle's terminology the nephridium in segment V (Hessle's segment IV) is termed the anterior nephridium, and all later ones are posterior nephridia.

Never more than five pairs of nephridia have been reported; in some cases there are only three and in exceptional cases only two. At first sight the number of nephridia would appear to provide a reasonable basis for classification, but as Hessle himself has pointed out, their distribution is not constant. In some cases four pairs may be present in segments V to VIII, in others the nephridium in VI is missing and the four pairs are in V, VII, VIII and IX; again V may be missing and the four pairs are in segments VI–IX. The same variability occurs in those species in which there are only three pairs of nephridia. They are located in segments V, VI and VII in *Sosanopsis wireni*, *Parhypania brevispina* and *Hypania invalida*, and in segments V, VII and VIII in *Sabellides octocirrata*. Even when the number is reduced to two pairs there are differences in arrangement. In *Phyllocomus crocea* and *Schistocomus* (=*Phyllocomus*) *hiltoni* the nephridia are in segments VII and VIII, and in *Lysippides fragilis* they are in segments V and VII.

Hessle further reports that the number of pairs of nephridia is not constant within the single genus *Ampharete* but may vary from two pairs situated in segments V and VII for *A. acutifrons* and *A. arctica* to four pairs situated in segments V, VII, VIII and IX for *A. lindstromi* and *A. kerguelensis*. The numbering of the segments given here is of course one higher than that given by Hessle.

In view of this variability of the nephridia and the labour involved it would seem undesirable to base generic divisions on these structures as has been done by Hessle. None the less the nephridial papillae of the anterior nephridia in segment V are occasionally visible. In *Sabellides* and *Pterampharete* the ducts are elongated dorsally and two nephridial papillae may be found on the branchial ridge between the two groups of gills. In *Anobothrus*, *Sosane* and *Asabellides* the ducts open on a single nephridial papilla in the same position. These characters, while not in themselves sufficient for generic distinction, provide useful confirmatory evidence.

The alimentary canal is normally a fairly straight tube divided into pharynx, oesophagus, stomach and intestine. At the anterior end of the stomach where it joins the oesophagus a pair of lateral pouches project forward in *Ampharete*, *Microsamytha* and *Anobothrus*, but not in *Melinna* nor fourteen other genera which have been investigated by Wiren (1885), Hessle (1917) or Annenkova (1930). There is also a curious invagination of the ventral wall of the stomach of some genera, which is referred to by Hessle as an 'innere Blindsack' and is here termed an internal diverticulum. It has been found in *Amage*, *Amphicteis*, *Amphisamytha and Hypania*, but not in fourteen other genera which have been examined. Since such characters demand dissection they are of doubtful value in practical classification.

The posterior thorax. As stated earlier, the first branchiferous (or paleal) segment is reckoned here as segment III and the branchiferous region as extending over segments III to VI. The beginning of the posterior thorax on segment VII is marked by the first appearance of uncini in the neuropodia in all genera. It is the most important and most easily recognizable landmark on the body. Segments anterior to it may be distorted or fused and individual segments may lack notosetae or nephridia, but segment VII and the posterior thoracic segments are always well defined and fully developed. The maximum number is 14 and the minimum number is 11 in all genera except *Mugga*, where there are 9. It is suggested therefore that the numbers of such uncigerous thoracic segments provide better generic characters than the total number of thoracic setigers which have led to such confusion.

The notopodia of the posterior thorax are conical projections which in *Amphicteis* and several other genera bear a terminal papilla or 'notopodial cirrus'. The neuropodia are short projecting pinnules and in a few genera such as *Phyllocomus* they bear a superior papilla or cirrus above the row of uncini.

The notosetae are winged capillaries which are very uniform in shape with few exceptions. In *Anobothrus* the 8th uncigerous segment has its notopodium elevated and the tips of the notosetae are minutely spinulose. In *Mugga* the same phenomenon occurs on uncigerous segment 9, and in *Sosane* and *Sosanopsis* it occurs on uncigerous segment 12.

The uncini are flattened tooth plates of various shapes but are all roughly triangular to quadrangular, with one or more series of teeth above the base. In the *Melinninae* there is always a single series of teeth, but in the *Ampharetinae* the teeth of the thoracic uncini may be arranged in 1, 2 or as many as 5 vertical rows. Abdominal uncini often have more rows of teeth. The base of the uncinus may be long and well separated from the tooth rows, or it may be short and curve up towards the lowest tooth to form a bluntly rounded prow. Hessle and others have quoted such differences as generic distinctions, but to me they appear to be no more than specific characters, for the shapes vary very considerably. The number of tooth rows seems to be more important when there are only one or two vertical series, but when there are three or more they lose their value.

The abdomen. There is seldom any abrupt narrowing between thorax and abdomen, merely a change in the parapodia. This, however, is well marked. The notosetae disappear and the notopodia are either reduced or absent. In *Melinna*, *Amphicteis*, *Amage*, *Phyllocomus* and many other genera, rudimentary notopodia persist on abdominal segments, and this is regarded as the more primitive condition. In *Ampharete*, *Sabellides* and others, notopodia are entirely lacking. Where notopodial cirri are present on the thorax they tend to persist on the rudimentary notopodia of the abdomen, as may be seen in *Amphicteis* and *Amage*. Similarly, where neuropodial cirri are present on the thorax these also are continued on the abdomen. Actually the uncigerous pinnules very often have an obscure superior papilla and this tends to become better marked towards the end of the abdomen. This is particularly well shown by *Sabellides octocirrata* where the superior papillae become long cirriform projections.

The whole abdomen consists of a variable number of segments. In the *Melinninae* there is always a large number of segments, the extremes being a minimum of 20 in *Melinnexis antarctica* and a maximum of 90 in *Irana heterobranchia*. In a few primitive genera of the *Ampharetinae* there are also large numbers of abdominal segments. Thus *Phyllocomus crocea* has 45 but in the great majority of genera the number is much less, 12–18 being the usual range. It is doubtful whether the exact number is constant for a species, and certainly it is not of generic importance.

The abdominal uncini are more or less similar to those of the thorax but usually there are more teeth arranged in more vertical rows or transverse arcs.

The *pygidium* is terminal and may be encircled by a number of low indistinct papillae or may bear a reduced number of longer anal cirri.

DIVISION INTO SUB-FAMILIES AND GENERA

Hessle (1917) does not divide the Ampharetidae into sub-families, although his remarks on p. 90 show that he is inclined to separate *Melinna* and *Isolda* from other genera in this way. Chamberlin (1919) proposed three sub-families, namely the *Melinninae* with dorsal hooks behind the gills but no paleae, the *Ampharetinae* with paleae but no hooks, and the *Samythinae* with neither paleae nor hooks.

Since the publication of Chamberlin's monograph many new genera have been described. The diagnostic characters of the various type-species are set out in tables I and II, and it will be immediately obvious that there are several genera related to *Melinna*. Not all of these possess dorsal hooks behind the gills, but they all possess fine acicular neurosetae in segments III, IV, V and often VI. I agree with Hessle in regarding this as an important and primitive feature which links the *Amphaetidae* to *Terebellides* and other genera of the *Trichobranchidae* and through them to the *Terebellidae*. I have therefore enlarged Chamberlin's diagnosis of the *Melinninae* to include all *Ampharetidae* with acicular neurosetae in segments III–VI whether they possess dorsal hooks or not. The amended characters of the sub-family are given later.

Chamberlin's sub-families *Ampharetinae* and *Samythinae* are distinguished by the presence or absence of paleae. The variability of these setae has been described earlier; as the accompanying tables show, the setation of the whole branchial region is not sufficiently reliable for the distinction between genera, let alone sub-families. Several other possible groupings of genera have been tried on the basis of the number of branchiae, the number of uncigerous thoracic segments and the number of tooth rows on the thoracic uncini. None of them were satisfactory in that they distinguished groups of genera with many characters in common. It was concluded that all the *Ampharetidae* apart from the *Melinninae* must be included within the sub-family *Ampharetinae* and that Chamberlin's sub-family *Samythinae* must be sunk.

TABLE I.

CHARACTERS OF GENERA AND TYPE-SPECIES OF SUB-FAMILY MELINNINAE

a = neuropodial acicular setae. *c* = small notopodial capillaries. H = notopodial hooks.
(*a*) or (*c*)—letters in parenthesis indicate setae may be present or absent.

Genus and type-species	Buccal tentacles	Setation of segments III–VI				Uncigerous thoracic segments	Tooth rows of thoracic uncini	Branchiae	Nephridia	Dorsal crest on segment VI	Lateral pouches on stomach	Internal diverticulum to stomach	Abdominal segments	Abdominal notopodia	Remarks
		III	IV	V	VI										
Moyanus Chamberlin 1919 (type *M. explorans* Cham. 1919)	*see remarks*	*a*	H *a*	H *a*	? ?	12	1	4 prs. (all smooth)	?	yes	yes	?	*c.* 65	no	Prostomium probosciform with a tentaculiferous lobe below it.
Melinna Malmgren 1866 (type *Sabellides cristata* Sars 1856)	smooth	*a*	H *a*	*c* *a*	*c* (*a*)	14	1	4 prs. (all smooth)	4 prs. in VI–IX	yes	no	no	30–50	feeble	No anal cirri, merely circle of indistinct papillae.
Isolda Müller 1858 (type *I. pulchella* Mül. 1858)	smooth	*a*	H *a*	*c* *a*	*c* (*a*)	13	1	4 prs. (2 smooth, 2 papillose)	?	yes	?	?	25–36	no	*I. whydahensis* Aug. has a retractile tentaculiferous lobe.
Irana Wesenberg-Lund 1949 (type *I. heterobranchiata* W.-L. 1949)	smooth	*a*	H *a*	*a*	*a*	12	1	3 prs. (1 smooth, 2 papillose)	?	yes	?	?	*c.* 90	no	
Oeorpata Kinberg 1867 (type *O. armata* Kbg. 1867)	?	?	H ?	?	?	?	1	2 prs. (papillose)	?	yes	?	?	many	?	? a synonym of *Isolda*.
Melinnopsis McIntosh 1885 (type *M. atlantica* McI. 1885)	smooth	*a*	*a*	*c* *a*	*c* ?	?10	1	4 prs. (all smooth)	?	no	?	?	25–30	?	
Melinnexis Annenkova 1930 (type *M. arctica* Ann. 1930)	smooth	*a*	*a*	*c* *a*	*c* *a*	14	1	4 prs. (all smooth)	4 prs. in V, VII, VIII, IX	feeble	?	?	20–30	?	1 very large tentacle. 1 pr. long anal cirri. ? synonym of *Melinnopsis*.
Melinnides Wesenberg-Lund (type *M. rostrata* W.-L. 1950)	smooth	*a*	*a*	*c* *a*	*c* *a*	12	1	4 prs. (all smooth)	?	yes	?	?	40–50	feeble	Prostomium a stout rostrum ? a synonym of *Melinnopsis*.
Melinnopsides Day gen. nov. (type *Melinnopsis capensis* Day 1955)	smooth	*a*	*a*	*c* *a*	*c*	10	1	3 prs. (all smooth)	?	no	?	?	28	no	

The reliability of the various characters which may be used to distinguish genera has been discussed earlier. To be of practical value in a taxonomic key such characters must not only be constant within a group of species which are obviously similar in other ways, but they must also be easily seen when sorting a sample. It is suggested that among such characters are the number of gills, and the number of uncigerous thoracic segments, the presence of glandular ridges on the prostomium and the possession of notopodial cirri. These have therefore been used as the main basis for grouping genera with the addition of several other features in specialized cases. It is tempting to use the obvious ornamentation of the gills as well as their number, but after careful consideration this was omitted for it would have increased the number of monotypic genera without breaking up the three large genera *Amphicteis*, *Amage* and *Ampharete*. In any case the gills are often missing so that their ornamentation cannot be decided, and only the scars remain to determine their number.

As stated earlier, 49 genera are currently recognized as valid. In the accompanying key these have been reduced to 33 of which 6 are assigned to the *Melinninae* and 27 to the *Ampharetinae*. This means that 16 genera have been sunk, and reference to the tables will show that 11 of these were monotypic and the other 5 contained 2 species each. One new genus has been erected in the sub-family *Melinninae*.

It is hoped that this revision will make the recognition of genera much simpler, but inevitably it will be found that many species have been assigned to the wrong genus. This is certainly true of two species assigned to *Lysippe* by myself and one referred with hesitation to *Neosabellides*.

Key to sub-families

1. Segments III–V (or III–VI) with fine acicular neurosetae. No paleae. Post-branchial hooks sometimes present .. .. *Melinninae*

Segments III–VI without neurosetae. No post-branchial hooks. Paleae sometimes present .. .. *Ampharetinae*

SUB-FAMILY **Melinninae** Chamberlin 1919 (characters amended)

Buccal tentacles never pennate or papillose, usually smooth with a groove along one side. Paleae absent. One or two pairs of stout notopodial hooks may be present behind the gills. Small acicular neurosetae embedded in segments III, IV and often V and VI. Uncini are from segment VII and always have a single series of teeth. Numerous (20–90) abdominal segments.

Key to genera of Melinninae

1.	Stout notopodial hooks behind the gills	2
	No notopodial hooks	5
2.	Notopodial hooks on two segments. Prostomium elongated	*Moyanus* (doubtful)
	Notopodial hooks on segment IV only. Prostomium short	3
3.	4 pairs of gills	4
	3 pairs of gills, including both smooth and papillose forms	*Irana*
	2 pairs of papillose gills	*Oeorpata* (doubtful)
4.	All gills smooth	*Melinna*
	Some gills smooth, some papillose	*Isolda*
5.	4 pairs of smooth gills	*Melinnopsis*
	3 pairs of smooth gills	*Melinnopsides*

MOYANUS Chamberlin 1919

Prostomium elongated and probosciform. Buccal tentacles mounted on long tongue-shaped projection. Four pairs of smooth gills. A dorsal crest on segment VI. Segments III–VI with notopodial hooks on segments IV and V and fine acicular neurosetae on segments III, IV and V. Twelve uncigerous thoracic segments and about 65 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Moyanus explorans* Chamberlin 1919.

MELINNA Malmgren 1866

Buccal tentacles smooth with a groove on one side. Four pairs of smooth gills. A dorsal crest across segment VI. Segments III–VI with notopodial hooks on segment IV and notopodial capillaries on segments V and VI. Fine acicular neurosetae on segments III–V and sometimes on VI as well. Fourteen uncigerous thoracic segments and 30–50 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Sabellides cristata* Sars 1851.

ISOLDA Müller 1858

Buccal tentacles smooth with a groove on one side. Four pairs of gills of which 2 are smooth and 2 are papillose. A dorsal crest across segment VI. Segments III–VI with notopodial hooks on segment IV and notopodial capillaries on segments V and VI. Fine acicular neurosetae on segments III–V and sometimes on VI as well. Twelve to 13 uncigerous thoracic segments and 25–36 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Isolda pulchella* Müller 1858.

IRANA Wesenberg-Lund 1949

Buccal tentacles smooth. Three pairs of gills of which 1 is smooth and 2 are papillose. A dorsal crest across segment VI. Segments III–IV with notopodial hooks on segment IV and fine acicular neurosetae on segments III–VI. Twelve uncigerous thoracic segments and about 90 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Irana heterobranchia* Wesenberg-Lund 1949.

OEORPATA Kinberg 1867

An incompletely described genus with two pairs of pennate gills; notopodial hooks on segment IV; many abdominal segments; uncini with a single series of teeth.

Type species *Oeorpata armata* Kinberg 1867.

MELINNOPSIS McIntosh 1885

Synonyms *Melinnexis* Annenkova 1930 and *Melinnides* Wesenberg-Lund 1950.

Buccal tentacles smooth with a groove along one side. Four pairs of smooth gills. Dorsal crest on segment VI present or absent. Segments III–VI without notopodial hooks on segment IV but with notopodial capillaries on segments V and VI. Fine acicular neurosetae on segments III–V and sometimes on VI as well. Ten to 14 uncigerous thoracic segments and 25–50 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Melinnopsis atlantica* McIntosh 1885.

MELINNOPSIDES gen. nov.

Buccal tentacles smooth with a groove along one side. Three pairs of smooth gills. No dorsal crest on segment VI. Segments III–VI without notopodial hooks on segment IV but with notopodial capillaries on segments V and VI. Fine acicular neurosetae on segments III–V. Ten uncigerous thoracic segments and about 30 abdominal ones. Thoracic uncini with a single series of teeth.

Type-species *Melinnopsis capensis* Day 1955.

SUB-FAMILY **Ampharetinae** Chamberlin 1919 (characters amended)

(including *Samythinae* Chamberlin 1919)

Buccal tentacles either smooth with a groove along one side or papillose. Paleae present or absent. No notopodial hooks behind the gills. Neurosetae absent from segments III to VI. Neuropodial uncini start on segment VII and may have one or more series of teeth. Few (8) to many (60) abdominal segments.

TABLE II.

CHARACTERS OF GENERA AND TYPE-SPECIES OF SUB-FAMILY AMPHARETINAE

C or *c* = large or small notopodial capillaries. P or *p* = large or small paleae on segment III.
(*c*) or (*p*)—letters in parenthesis indicate setae may be present or absent.

Genus and type-species	Glandular ridges on prostomium	Buccal tentacles	Setation of segments III–VI				Uncigerous thoracic segments	Tooth rows on thoracic uncini	Branchiae	Nephridia	Notopodial cirri	Lateral pouches on stomach	Internal diverticulum to stomach	Abdominal segments	Abdominal notopodia	Remarks
			III	IV	V	VI										
Amphicteis Grube 1851 (type *Amphitrite gunneri* Sars 1835)	yes	smooth	P	C	C	C	14	1	4 prs. (all smooth)	5 prs. in V–IX	yes	?	?	15	yes	1 pair anal cirri.
Paramphicteis Caullery 1944 (type *Sabellides augustifolia* Gr. 1878)	yes	? papillose	–	*c*	*c*	C	14	1	4 prs. (all smooth)	?	yes	?	?	15	small	1 pair anal cirri.
Amage Malmgren 1866 (type *A. auriculata* Malm. 1866)	yes	smooth	–	*c*	C	C	11	1–2	4 prs. (all smooth)	4 prs. in V–VIII	yes	no	yes	8	yes	2 pairs anal cirri.
Parhypania Annenkova 1928 (type *Amphicteis brevispinus* Gr. 1860)	yes	smooth	P	C	C	C	14	1	4 prs. (all smooth)	3 prs. in V–VII	no	no	no	16–20	feeble	
Hypania Ostromoouv 1897 (type *Amphicteis invalida* Gr. 1860)	yes	smooth	P	*c*	C	C	13	?	4 prs. (all smooth)	3 prs. in V–VII	no	no	yes	15–30	yes	
Grubianella McIntosh 1885 (type *G. antarctica* McI. 1885)	yes	smooth	–	*c*	C	C	11	2	4 prs. (all smooth)	?	?	?	?	25	yes	1 pair anal cirri.
Paiwa Chamberlin 1919 (type *P. abyssi* Cham. 1919)	no	smooth	*p*	C	C	C	14	2–3	4 prs. (all smooth)	?	yes	?	?	20	small	? synonym of *Phyllamphicteis*.
Phyllamphicteis Augener 1918 (type *P. collaribranchis* Aug. 1918)	no	smooth	P	*c*	*c*	C	14	1	4 prs. (2 smooth, 2 lamellate)	?	yes	?	?	15	no	1 pair anal cirri.
Lysippides Hessle 1917 (type *Amphicteis fragilis* Wollebaek 1912)	no	smooth	*p*	*c*	C	C	14	3	4 prs. (2 smooth, 2 flanged)	2 prs. in V & VII	no	no	no	8	yes	

Amphisamytha Hessle 1917 (type *A. japonica* Hessle 1917)	no	smooth	–	*c*	C	C	14	1	4 prs. (all smooth)	4 prs. in V–VIII	no	no	yes	14	yes	? synonym of *Lysippides.*
Hypaniola Annenkova 1928 (type *Amphicteis kowalewskii* Grimm 1877)	no	smooth	*p*	C	C	C	14	?	4 prs. (all smooth)	3 prs. in V–VII	no	no	?	23	?	? synonym of *Lysippides.*
Lysippe Malmgren 1866 (type *L. labiata* Malm. 1866)	no	smooth	*p*	*c*	C	C	13	2	4 prs. (all smooth)	4 prs. in V–VIII	no	no	no	14	yes	1 pair anal cirri.
Pterolysippe Augener 1918 (type *P. bipennata* Aug. 1918)	no	smooth	*p*	*c*	*c*	C	13	3	4 prs. (3 smooth, 1 papillose)	?	no	?	?	?12–17	?	? synonym of *Lysippe.*
Ampharete Malmgren 1866 (type *A. acutifrons* Gr. 1860)	no	papillose	P	–	C	C	12	2	4 prs. (all smooth)	2 prs. in V & VII	no	yes	no	12	no	1 pair anal cirri.
Asabellides Annenkova 1929 (type *Sabellides sibirica* Wiren 1883)	no	papillose	–	–	C	C	12	2	4 prs. (all smooth)	?	no	yes	?	21	yes	1 pair anal cirri.
Pseudosabellides Berkeley & Berkeley 1943 (type *P. littoralis* B. & B. 1943)	no	papillose	–	–	C	C	12	2	4 prs. (all smooth)	?	no	?	?	18–20	no	? synonym of *Asabellides.*
Phyllocomus Grube 1878 (type *P. crocea* Gr. 1878)	no	smooth	–	C	C	C	12	1	4 prs. (flanged)	2 prs. in VII & VIII	yes	no	no	45	yes	A circle of anal papillae.
Schistocomus Chamberlin 1919 (type *S. hiltoni* Cham. 1919)	no	smooth	–	C	C	C	12	1	4 prs. (1 smooth, 3 lamellate)	2 prs. in VII & VIII	no	?	?	30–53	yes	2 pairs anal cirri. ? synonym of *Phyllocomus.*
Sosane Malmgren 1866 (type *S. sulcata* Malm. 1866)	no	smooth	P	*c*	C	C	12	1	4 prs. (all smooth)	4 prs. in V, VII, VIII, IX	no	no	no	13	small	1 nephridial papilla between branchiae. Notosetae of last thoracic segment modified.
Anobothrus Levinsen 1883 (type *Ampharete gracilis* Malm. 1866)	no	smooth	P	*c*	C	C	12	2	4 prs. (all smooth)	4 prs. in V, VII, VIII, IX	no	yes	no	13	yes	1 nephridial papilla between branchiae. Notosetae of uncigerous thoracic segment 8 modified. ? synonym of *Sosane.*

TABLE II—*continued.*

Genus and type-species	Glandular ridges on prostomium	Buccal tentacles	Setation of segments III–VI				Uncigerous thoracic segments	Tooth rows on thoracic uncini	Branchiae	Nephridia	Notopodial cirri	Lateral pouches on stomach	Internal diverticulum to stomach	Abdominal segments	Abdominal notopodia	Remarks
			III	IV	V	VI										
Sosanopsis Hessle 1917 (type *S. wireni* Hessle 1917)	no	smooth	–	*c*	C	C	12	3	4 prs. (all smooth)	3 prs. in V, VI, VII	no	no	no	11	yes	Notosetae of uncigerous thoracic segment 12 modified.
Paramage Caullery 1944 (type *P. madurensis* Caul. 1944)	no	smooth	–	–	–	C	11	1	4 prs. (all smooth)	?	no	?	?	11	no	Notopodia but no setae on segments IV and V.
Sabellides M.-Edwards 1838 (type ? *Sabella octocirrata* Sars 1835)	no	papillose	(*p*)	–	C	C	11	1	4 prs. (all smooth)	3 prs. in V, VII, VIII	no	no	no	*c.* 17	no	2 nephridial papillae between branchiae.
Pterampharete Augener 1918 (type *P. luderitzi* Aug. 1918)	no	papillose	P	–	C	C	11	2	4 prs. (all papillose)	3 prs. in V, VII, VIII	no	?	?	11	no	2 nephridial papillae between branchiae. ? synonym of *Sabellides*.
Samythopsis McIntosh 1885 (type *S. grubei* McI. 1885)	yes	smooth	–	*c*	C	C	14	3–5	3 prs. (smooth)	?	?	?	?	22	yes	1 pair anal cirri.
Samytha Malmgren 1866 (type *Sabellides sexcirrata* Sars 1856)	no	smooth	–	C	C	C	14	2–3	3 prs. (smooth)	3 prs. in V–VII	no	no	no	13	yes	1 pair anal cirri.
Amythas Benham 1921 (type *A. membranifera* Ben. 1921)	no	folded membrane	–	*c*	C	C	14	2	3 prs. (smooth and grooved)	?	?	?	?	14+	no	
Aryandes Kinberg 1867 (type *A. gracilis* Kbg. 1867)	?	?	P	*c*	C	C	14	?	3 prs.	?	?	?	?	?	?	
Microsamytha Augener 1928 (type *M. rychiana* Aug. 1928)	no	smooth	–	C	C	C	13	?	3 prs. (all smooth)	?	no	?	?	?15	?	
Alkmaria Horst 1920 (type *A. romijni* Horst 1920)	?	?	–	C	C	C	13	?	3 prs. (all smooth)	?	?	?	?	?13	?	? synonym of *Microsamytha*. Head not known.

Melinnampharete Annenkova 1937 (type *M. eoa* Annen. 1937)	no	papillose	P	C	C	C	12	?	3 prs. (all smooth)	3 prs. in V, VII, VIII	no	yes	?	many	?	A dorsal ridge between segments VI and VII.
Neosabellides Hessle 1917 (type *Sabellides elongatus* Ehl. 1913)	no	papillose	–	–	C	C	12	2	3 prs. (all smooth)	4 prs. in V, VII, VIII, IX	no	yes	no	19	small	1 pair anal cirri.
Pabits Chamberlin 1919 (type *P. deroderus* Cham. 1919)	no	smooth	–	*c*	C	C	12	2	3 prs. (all smooth)	?	?	?	?	?	yes	Tentacular lobe prolonged.
Samythella Verrill 1873 (type *S. elongata* Ver. 1873)	no	smooth	–	C	C	C	12	1	3 prs. (smooth and flanged)	?	no	?	?	29–35	?	A circle of anal papillae.
Eusamytha McIntosh 1885 (type *E. pacifica* McI. 1885)	no	smooth	–	C	C	C	12	?1 ?2	3 prs. (all smooth)	?	no	?	?	31	no	
Eclysippe Eliason 1955 (type *Lysippe vanelli* Fauvel 1936)	no	smooth	P	*c*	*c*	C	12	2	3 prs.* (all smooth)	?	few	?	?	12	no	*Fauvel 1936 gives 4 pairs of gills for *L. vanelli*.
Glyphanostomum Levinsen 1883 (type *Samytha pallescens* Theel 1878)	no	smooth	–	C	C	C	11	2	3 prs. (all smooth)	4 prs. in V–VIII	no	no	no	25	?	1 pair anal cirri.
Amythasides Eliason 1955 (type *A. macroglossus* Eli. 1955)	no	smooth	P	*c*	C	C	11	3–6	3 prs. (unknown)	?	no	?	?	12	no	A very few stout tentacles. ? synonym of *Glyphanostomum*.
Mugga Eliason 1955 (type *M. wahrbergi* Eli. 1955)	no	smooth	P	*c*	C	C	9	4–5	3 prs. (? smooth)	?	no	?	?	8+	?no	Notosetae of uncigerous thoracic segment 9 dorsal and setae modified.
Auchenoplax Ehlers 1887 (type *A. crinita* Ehl. 1887)	no	smooth	–	–	C	C	12	1	2 prs. (smooth)	?	no	?	?	12–15	?	First row of uncini long and ventrally placed.
Melinnoides Benham 1921 (type *M. nelsoni* Ben. 1921)	no	smooth	–	–	C	C	12	2	2 prs. (smooth)	?	?	?	?	12	?	First row of uncini long. ? synonym of *Auchenoplax*.

Key to genera of Ampharetinae

1.	4 pairs of gills	2
	3 pairs of gills	13
	2 pairs of gills; first row of uncini very long	*Auchenoplax*
2.	Glandular ridges on prostomium. Buccal tentacles always smooth and grooved along one side	3
	No glandular ridges on prostomium. Buccal tentacles either smooth or papillose	6
3.	Notopodial cirri present	4
	No notopodial cirri	5
4.	14 uncigerous thoracic segments	*Amphicteis*
	11 uncigerous thoracic segments	*Amage*
5.	14 uncigerous thoracic segments	*Parphypania*
	13 uncigerous thoracic segments	*Hypania*
	11 uncigerous thoracic segments	*Grubianella*
6.	14 uncigerous thoracic segments	7
	13 uncigerous thoracic segments	*Lysippe*
	12 uncigerous thoracic segments	8
	11 uncigerous thoracic segments	12
7.	Notopodial cirri present	*Phyllamphicteis*
	Notopodial cirri absent	*Lysippides*
8.	Tentacles papillose. Abdominal notopodia seldom present	9
	Tentacles smooth and grooved. Abdominal notopodia always present	10
9.	No nephridial papilla on the branchial ridge	*Ampharete*
	One nephridial papilla on the branchial ridge	*Asabellides*
10.	No specialized posterior notosetae or elevated notopodia. Over 30 abdominal segments	*Phyllocomus*
	Specialized notosetae present in some elevated posterior notopodia. Less than 20 abdominal segments	11
11.	One nephridial papilla on the branchial ridge	*Sosane*
	No nephridial papilla on the branchial ridge	*Sosanopsis*
12.	Tentacles smooth with a longitudinal groove. No nephridial papillae on the branchial ridge	*Paramage*
	Tentacles papillose. 2 nephridial papillae on the branchial ridge	*Sabellides*
13.	14 uncigerous thoracic segments	14
	13 uncigerous thoracic segments	*Microsamytha*
	12 uncigerous thoracic segments	16
	11 uncigerous thoracic segments	*Glyphanostomum*
	9 uncigerous thoracic segments. Last notopodium elevated and bears modified notosetae	*Mugga*
14.	Glandular ridges on prostomium	*Samythopsis*
	No glandular ridges on prostomium	15
15.	Abdominal notopodia present. Tentacles numerous and smooth. Paleae usually absent	*Samytha*
	Abdominal notopodia absent. Tentacles represented by a folded membrane. Paleae usually absent	*Amythas*
	(With paleae, other characters unknown)	*Aryandes*
16.	Tentacles papillose	17
	Tentacles smooth	18
17.	A dorsal ridge between segments VI and VII. Paleae present on segment III	*Melinnampharete*
	No dorsal ridge. No setae on segment III	*Neosabellides*
18.	Tentacular lobe prolonged	*Pabits*
	No elongate tentacular lobe	*Samythella*

AMPHICTEIS Grube 1851

Synonyms *Crossostoma* Gosse 1855, *?Rytocephalus* Quatrefages 1865, and *Paramphicteis* Caullery 1944.

Prostomium with a pair of glandular ridges. Buccal tentacles smooth with a groove along one side. Four pairs of gills. Segments III–VI without neurosetae. Segment III often with paleae; segments IV–VI with notopodial capillaries. Fourteen uncigerous thoracic segments. Notopodial cirri present. Thoracic uncini with a single vertical series of teeth. Thirteen to 19 abdominal segments sometimes with rudimentary notopodia as well as uncigerous pinnules.

Type-species *Amphitrite gunneri* Sars 1835.

AMAGE Malmgren 1866

Prostomium with glandular ridges. Buccal tentacles smooth with a groove along one side. Four pairs of gills. Segments III–VI without neurosetae. Segments IV–VI usually with notopodial capillaries. Eleven uncigerous thoracic segments. Notopodial cirri present. Thoracic uncini with 1 or 2 series of teeth. Eight to 15 abdominal segments usually with rudimentary notopodia as well as uncigerous pinnules.

Type-species *Amage auriculata* Malmgren 1866.

PARHYPANIA Annenkova 1928

Prostomium with glandular ridges. Buccal tentacles smooth. Four pairs of gills. Segments III–VI without neurosetae. Segment III often with paleae, segments IV–VI usually with notopodial capillaries. Fourteen uncigerous thoracic segments. Notopodial cirri absent. About 16–20 abdominal segments sometimes with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Amphicteis brevispinus* Grube 1860.

HYPANIA Ostrooumov 1897

Prostomium with glandular ridges. Buccal tentacles smooth. Four pairs of gills. Segments III–VI without neurosetae. Segment III often with paleae, segment IV may have notosetae, segments V and VI always with notopodial capillaries. Thirteen uncigerous thoracic segments. Notopodial cirri absent. About 15–30 abdominal segments sometimes with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Amphicteis invalida* Grube 1860.

GRUBIANELLA McIntosh 1885

Prostomium with glandular ridges. Buccal tentacles smooth. Four pairs of gills. Segments III–VI without neurosetae. Notopodial capillaries present on segments V and VI and sometimes on segment IV. Eleven uncigerous thoracic segments. Thoracic uncini usually with 2 series of teeth. Notopodial cirri doubtful. About 25 abdominal segments; the last few are reported to be swollen in the type but this is probably an abnormality.

Type-species: *Grubianella antarctica* McIntosh 1885.

LYSIPPIDES Hessle 1917

Synonyms *Amphisamytha* Hessle 1917 and *Hypaniola* Annenkova 1928.

Prostomium without glandular ridges. Buccal tentacles smooth with a groove along one side. Four pairs of gills. Segments III–VI without neurosetae. Notosetae present on segments V and VI and usually III and IV as well. Fourteen uncigerous thoracic segments. Notopodial cirri absent. Thoracic uncini with 1–3 series of teeth. Between 8 and 23 abdominal segments usually with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Amphicteis fragilis* Wollebaek 1912.

PHYLLAMPHICTEIS Augener 1918

Synonym *Paiwa* Chamberlin 1919.

Prostomium without glandular ridges. Buccal tentacles smooth. Four pairs of gills. Segments III–VI without neurosetae. Notosetae present on segments V and VI and usually on III and IV as well. Fourteen uncigerous thoracic segments. Notopodial cirri present. Thoracic uncini with 1–3 series of teeth. Between 15 and 20 abdominal segments sometimes with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Phyllamphicteis collaribranchis* Augener 1918.

LYSIPPE Malmgren 1866

Synonym *Pterolysippe* Augener 1918.

Prostomium without glandular ridges. Buccal tentacles smooth. Four pairs of gills. Segments III–VI without neurosetae. Small notosetae often present on segments III and IV and notosetae always present on V and VI. Thirteen uncigerous thoracic segments. Thoracic uncini with 2–3 series of teeth. Notopodial cirri absent. About 12–15 abdominal segments sometimes with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Lysippe labiata* Malmgren 1866.

AMPHARETE Malmgren 1866

Synonym *Branchiosabella* Claparède 1863.

Prostomium without glandular ridges. Buccal tentacles papillose. Four pairs of gills. No nephridial papilla on the branchial ridge. Segments III–VI without neurosetae. Notosetae of segment III usually enlarged to form paleae; notosetae of segment IV usually absent; notosetae of segments V and VI always present. Twelve uncigerous thoracic segments. Notopodial cirri absent. Thoracic uncini usually with 2 series of teeth. About 12–15 abdominal segments which have uncigerous pinnules but usually lack rudimentary notopodia.

Type-species: *Amphicteis acutifrons* Grube 1860.

ASABELLIDES Annenkova 1929

Synonym *Pseudosabellides* Berkely and Berkely 1943.

Prostomium without glandular ridges. Buccal tentacles papillose. Four pairs of gills. One nephridial papilla on the branchial ridge between the two groups of gills. Segments III–VI without neurosetae. Notopodial capillaries present on segments V and VI but usually absent from III and IV. Twelve uncigerous thoracic segments. Notopodial cirri absent. Thoracic uncini usually with 2 series of teeth. About 21 abdominal segments which have uncigerous pinnules but lack rudimentary notopodia.

Type-species: *Sabellides sibirica* Wiren 1883.

PHYLLOCOMUS Grube 1878

Synonym *Schistocomus* Chamberlin 1919.

Prostomium without glandular ridges. Buccal tentacles smooth with a groove along one side. Four pairs of gills. Segments III–VI without neurosetae. Notopodial capillaries present on segments IV, V and VI. Twelve uncigerous thoracic segments. No specialized notosetae. Notopodial cirri present or absent. Thoracic uncini with a single series of teeth. Numerous (over 30) abdominal segments.

Type-species: *Phyllocomus crocea* Grube 1878.

SOSANE Malmgren 1866

Synonym *Anobothrus* Levinsen 1883.

Prostomium without glandular ridges. Buccal tentacles smooth. Four pairs of gills. One nephridial papilla on the branchial ridge between the two groups of gills. Segments III–VI without neurosetae. Notosetae usually present on all four segments III to VI and often enlarged to form paleae on segment III. Twelve uncigerous thoracic segments with one or more of the posterior notopodia elevated and bearing specialized notosetae. Notopodial cirri absent. Thoracic uncini with 1–2 series of teeth. About 13 abdominal segments usually with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Sosane sulcata* Malmgren 1866.

SOSANOPSIS Hessle 1917

Prostomium without glandular ridges. Buccal tentacles smooth. Four pairs of gills. No nephridial papillae on the branchial ridge. Segments III–VI without neurosetae. Segments V and VI with notopodial capillaries and usually segment IV as well. Twelve uncigerous thoracic segments with the last notopodium elevated and bearing specialized notosetae. Notopodial cirri absent. Thoracic uncini with 2–3 series of teeth. About 11 abdominal segments usually with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Sosanopsis wireni* Hessle 1917.

PARAMAGE Caullery 1944

Prostomium without glandular ridges. Buccal tentacles smooth. Four pairs of gills. No nephridial papillae on the branchial ridge. Segments III–VI without neurosetae. Segment VI with notopodial capillaries but notosetae often absent from more anterior segments. Eleven uncigerous thoracic segments. No specialized posterior notosetae. Notopodial cirri absent. Thoracic uncini usually with a single series of teeth. About 11 abdominal segments with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Paramage madurensis* Caullery 1944.

SABELLIDES Milne-Edwards 1838

Synonyms *Heterobranchus* Wagner 1885 and *Pterampharete* Augener 1918.

Prostomium without glandular ridges. Buccal tentacles papillose. Four pairs of gills. A pair of nephridial papillae on the branchial ridge between the two groups of gills. Segments III–VI without neurosetae. Segments V and VI with notopodial capillaries, segment IV usually fused to segment III and without notosetae, but notosetae often present on segment III. Eleven uncigerous thoracic segments. No specialized posterior notosetae. Notopodial cirri absent. Thoracic uncini with 1 or 2 series of teeth. Between 11 and 18 abdominal segments with uncigerous pinnules but no rudimentary notopodia.

Type-species: ? *Sabella octocirrata* Sars 1835.

SAMYTHOPSIS McIntosh 1885

Prostomium with glandular ridges. Buccal tentacles smooth. Three pairs of gills. Segments III–VI without neurosetae. Segments IV–VI with notopodial capillaries. Fourteen uncigerous thoracic segments. Notopodial cirri doubtful. About 22 abdominal segments which may have rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Samythopsis grubei* McIntosh 1885.

SAMYTHA Malmgren 1866

Prostomium without glandular ridges. Buccal tentacles numerous and smooth. Three pairs of gills. Segments III–VI without neurosetae. Segments IV–VI with notopodial capillaries. Fourteen uncigerous thoracic segments. No notopodial cirri. Thoracic uncini with 2–3 series of teeth. About 13 abdominal segments with rudimentary notopodia as well as uncigerous pinnules.

Type-species: *Sabellides sexcirrata* Sars 1856.

AMYTHAS Benham 1921

Prostomium without glandular ridges. Buccal tentacles replaced by a frilly membrane. Three pairs of gills. Segments III–VI without neurosetae. Segments IV–VI with notopodial capillaries. Fourteen uncigerous thoracic segments. No notopodial cirri. Thoracic uncini with 2 series of teeth. Fourteen or more abdominal segments without rudimentary notopodia above the uncigerous pinnules.

Type-species: *Amythas membranifera* Benham 1921.

ARYANDES Kinberg 1867

A questionable and incompletely described genus generally similar to *Samytha* but with paleae.

Type-species: *Aryandes gracilis* Kinberg 1867.

MICROSAMYTHA Augener 1928

Synonym ? *Alkmaria* Horst 1920.

Note: Both genera are incompletely described and may belong to the family Terebellidae. More is known of *Microsamytha* and this name is retained *pro tem.*

Prostomium without glandular ridges and 'of the *Ampharete* type'. Buccal tentacles smooth. Three pairs of gills. Segments III–VI without neurosetae. Segments IV, V and VI with notopodial capillaries. Thirteen uncigerous thoracic segments. Between 13 and 19 abdominal segments.

Type-species *Microsamytha rychiana* Augener 1928.

MELINNAMPHARETE Annenkova 1937

Prostomium without glandular ridges. Buccal tentacles papillose. Three pairs of gills. Segments III–VI without neurosetae. Notosetae usually present on all four segments (III–VI) and often enlarged to form paleae on segment III. A dorsal ridge between segments VI and VII. Twelve uncigerous thoracic segments. No notopodial cirri. ? number of abdominal segments.

Type-species: *Melinnampharete eoa* Annenkova 1937.

Neosabellides Hessle 1917

Prostomium without glandular ridges. Buccal tentacles papillose. Three pairs of gills. Segments III–VI without neurosetae. Notosetae present on segments V and VI but usually absent from III and IV. No dorsal ridge between segments VI and VII. Twelve uncigerous thoracic segments. No notopodial cirri. Thoracic uncini usually with 2 series of teeth. About 19 abdominal segments.

Type-species: *Sabellides elongatus* Ehlers 1913.

PABITS Chamberlin 1919

Prostomium without glandular ridges. Buccal tentacles smooth and borne on a long probosciform organ. Three pairs of gills. Segments III–VI without neurosetae. Notosetae present on segments V and VI and usually on IV as well. Twelve uncigerous thoracic segments. No notopodial cirri. Thoracic uncini with 2 series of teeth. Number of abdominal segments unknown.

Type-species: *Pabits deroderus* Chamberlin 1919.

SAMYTHELLA Verrill 1873

Synonyms *Eusamytha* McIntosh 1885 and ? *Eclysippe* Eliason 1955.

Prostomium without glandular ridges. Buccal tentacles smooth and not borne on an elongate tentacular lobe. Three pairs of gills. Segments III–VI without neurosetae. Notopodial capillaries present on segments IV–VI and sometimes on III as well. Twelve uncigerous thoracic segments. Notopodial cirri may be present on the last few thoracic setigers. Thoracic uncini with 1 or 2 series of teeth. Up to 36 abdominal segments.

Type-species: *Samythella elongata* Verrill 1873.

GLYPHANOSTOMUM Levinsen 1883

Synonym *Amythasides* Eliason 1955.

Prostomium without glandular ridges. Buccal tentacles smooth (? always). Three pairs of gills. Segments III–VI without neurosetae. Segments IV–VI with notopodial capillaries and segment III sometimes with paleae. Eleven uncigerous thoracic segments. Notopodial cirri absent. Thoracic uncini with 2 or more series of teeth. Twelve to 25 abdominal segments without rudimentary notopodia but with uncigerous pinnules.

Type-species *Samytha pallescens* Theel 1878.

MUGGA Eliason 1955

Prostomium without glandular ridges. Buccal tentacles smooth. Three pairs of gills. Segments III–VI without neurosetae but all of them may have notosetae. Nine uncigerous thoracic segments. Notopodium of the last thoracic segment dorsally situated and bearing modified notosetae. Thoracic uncini with more than 2 series of teeth. Number of abdominal segments unknown.

Type-species: *Mugga wahrbergi* Eliason 1955.

AUCHENOPLAX Ehlers 1887

Synonym *Melinnoides* Benham 1921.

Prostomium without glandular ridges. Buccal tentacles smooth with a groove along one side. Two pairs of gills. Segments III–VI without neurosetae. Segments V and VI with notopodial capillaries. Twelve uncigerous thoracic segments and about 12–15 abdominal ones. First row of thoracic uncini on segment VII very long. Thoracic uncini with 1–2 series of teeth. Notopodial cirri absent.

Type-species: *Auchenoplax crinita* Ehlers 1887.

SUMMARY

The characters of existing genera are discussed and it is shown that confusion has arisen because the anterior segments have been telescoped and there are two different systems of numbering them. It is proposed that the separation of genera be based primarily on the number of gills and the number of uncigerous thoracic segments. The main diagnostic characters of 49 type-species have been tabulated and it is suggested that 16 genera which are mostly monotypic be sunk. Keys and definitions of the remaining 33 genera are provided.

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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).

LIEUWE DIRK BOONSTRA

THE GIRDLES AND LIMBS OF THE PRISTEROGNATHID THEROCEPHALIA

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THE GIRDLES AND LIMBS OF THE PRISTEROGNATHID THEROCEPHALIA

By

Lieuwe Dirk Boonstra
South African Museum, Cape Town

(With 50 text-figures and one Plate)

Contents

Introduction

In the *Tapinocephalus* zone of the Karoo the oldest Therocephalia known are well represented. The Therocephalia form the main component of the carnivores, the only other carnivores being the very large anteosaurs represented by five genera and a few small to medium-sized Gorgonopsia represented by 10 genera, of which 30 specimens are known in all.

The Therocephalia are represented in the *Tapinocephalus* zone by the families Pristerognathidae, Lycosuchidae, Scylacosauridae and Scaloposauridae. Of these the pristerognathids are the dominant family and are well represented in numbers of specimens as well as in the number of distinct species. Hitherto 16 genera with 28 species have been described. Most of the specimens consist of partly preserved snouts, with good complete skulls few in number. Of the postcranial skeleton little is known, for only rarely are some of the postcranial

Ann. S. Afr. Mus. **48** (5), 1964: 121–165, 50 figs. and 1 Plate.

bones preserved and then mostly associated with cranial parts difficult to classify.

In this paper I present an account of the girdle and limb material in the South African Museum mostly collected by myself since 1928.

This collection includes material which necessitates the establishment of the following new genus and species.

ZINNOSAURUS new genus

Type-species: Zinnosaurus paucidens.

Diagnosis: A medium-sized pristerognathid with the dental formula i.5, c.1, pc.2; the incisors are fairly weak and well spaced and the postcanines are weak and lie far apart; the postcanines situated on a thin lappet of the maxilla clearly demarcated from the general maxillary surface. Scapula with a well-developed flange-like process on its posterior border immediately above the glenoid for the scapular head of the triceps. The glenoid widely open and facing much laterally. Humerus with greatly expanded epicondyles, thin and sheet-like. Femur with broadly oval caput and strong thickened internal trochanter.

Affinities: Nearest relative *Glanosuchus.*

Zinnosaurus paucidens new species

(Figs. 1, 19, 28, 46*d* and 46*e*)

Holotype. S.A.M. 12185, skull with lower jaw, scapulo-coracoid, humeri, ends of femora.

Locality: Meyerspoort, Beaufort West, South Africa.

Horizon: High *Tapinocephalus* zone, Lower Beaufort Beds, Karoo.

I have great pleasure in naming this new genus after H. Zinn, who has, as techinical assistant, accompanied me on numerous collecting trips in the *Tapinocephalus* zone.

The scapulo-coracoid, humeri and ends of femora of the holotype are described in the appropriate sections of this paper.

MATERIAL

In the South African Museum catalogue 219 specimens of pristerognathids from the *Tapinocephalus* zone are listed. Of these only the following 37 specimens have parts of the girdles and limbs preserved. Taken together one gets a good idea of the family character of these structures.

The material studied consists of the following specimens listed in the order of the date of acquisition by the South African Museum collection.

S.A.M. 4335. *Pristerognathus* sp. Beaufort West. High? *Tapinocephalus* zone. Coll. Whaits 1916? Incomplete coraco-scapulae, distal and proximal ends of a humerus and the proximal halves of an ulna and radius. No skull.

S.A.M. 5018. *Pristerognathus* sp. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Haughton 1916. Two incomplete ilia, proximal and distal halves of two femora and of two humeri, proximal ends of tibiae, radii and ulnae. No skull.

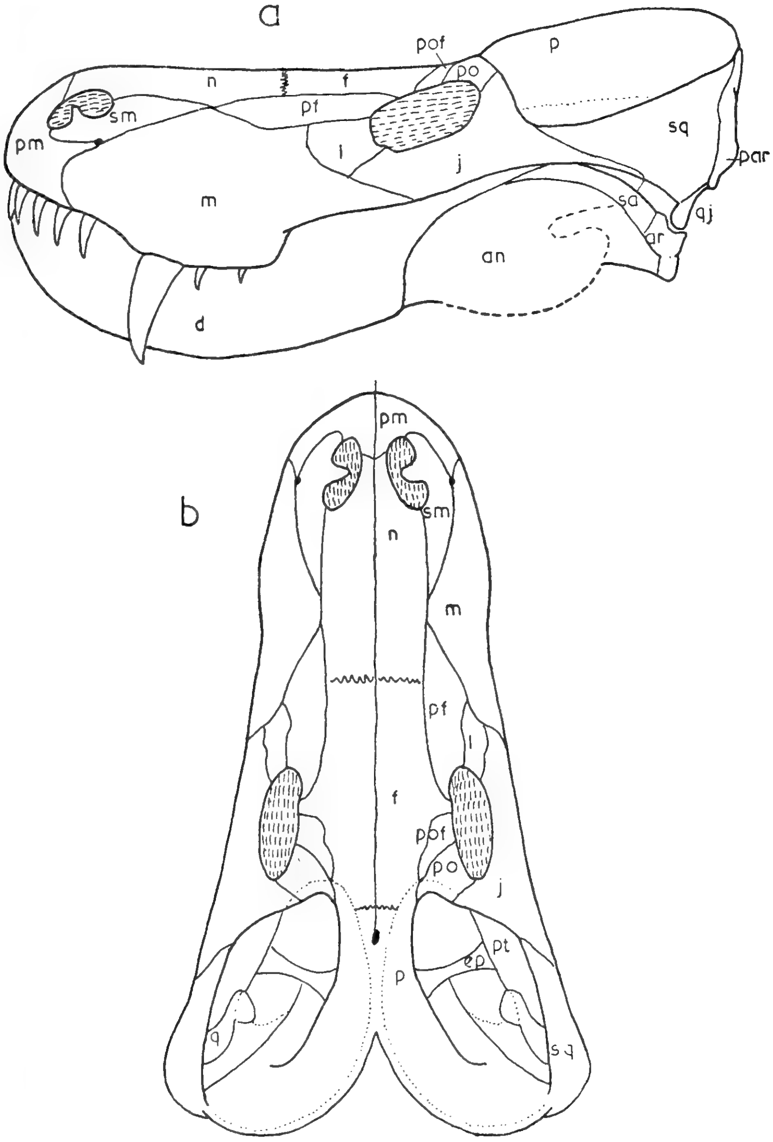

FIG. 1. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. Type × ⅓. Skull. *a*, lateral. *b*, dorsal.

S.A.M. 9005. *Scymnosaurus major*. Holotype. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. Interclavicle with proximal parts of both clavicles, distal ends of both humeri, complete radius and ulna, associated with a good anterior half of the skull.

S.A.M. 9084. *Scymnosaurus ferox*. Rietkuil, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. A coracoid, proximal and distal ends of a humerus and proximal ends of an ulna and radius associated with a good skull.

S.A.M. 11458. *Pristerognathus* sp. Mynhardtskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Avenant 1939. An interclavicle, proximal ends of clavicles, parts of coracoids, poor ends of femur, humerus, radius, ulna. No cranial material.

S.A.M. 11459. *Scymnosaurus* sp. Buffelsvlei, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Marais 1939. Part of carpus and tarsus associated with a poor snout.

S.A.M. 11557. *Scymnosaurus* sp. Die Cypher, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1940. A scapula, humerus, femur, interclavicle, clavicle, radius, and partial manus. Without skull.

S.A.M. 11558A. *Scymnosaurus?* Die Cypher, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1940. A pair of well-preserved ischia.

S.A.M. 11695. *Scymnosaurus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Jooste 1946. A coraco-scapula, interclavicle, clavicles and humerus. With good anterior half of skull.

S.A.M. 11794 *Cynariognathus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Jooste 1947. Imperfect pelvis, femora, humeri, epipodials and manus. With a poor skull.

S.A.M. 11888. *Therioides cyniscus*. Holotype. Vindragersfontein. Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1948. Parts of pectoral girdle, humerus, radius, ulna and part of manus associated with a nearly complete skull.

S.A.M. 11934. *Pristerognathus?* Steenboksfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Distal end of femur and proximal ends of tibia and fibula. Without cranial association.

S.A.M. 11936. *Pristerognathoides* sp. Bosluiskraal, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Proximal and distal end of a femur associated with a snout.

S.A.M. 11942. *Ptomalestes avidus*. Holotype. Steenboksfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1951. Part of pectoral girdle, humeri, ulnae and radii associated with a good skull.

S.A.M. 11957. *Scymnosaurus* sp. Abrahamskraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Le Roux 1923. Acetabular parts of ischium and pubis and proximal end of femur. Without skull.

S.A.M. 12051. *Alopecognathus* sp. Rietfontein, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Fourie 1957. Part of scapula, proximal end of humerus, proximal and distal ends of femur, ends of radii and ulna and part carpus, tibia and fibula and a complete pes associated with a snout.

S.A.M. 12102. *Pristerognathoides* sp. Kalkkraal. Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957. Most of the pectoral girdle, ends of humerus, ulna and radius associated with a complete skull.

S.A.M. 12112. *Pristerognathus?* Skoppelmaaikraal, Laingsburg. Low *Tapinocephalus* zone. Coll. Botes 1957. Part of ilium, proximal end of humerus and other fragments without any skull parts.

S.A.M. 12118. *Scymnosaurus* sp. Palmietfontein of Kruidfontein, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957. Proximal end of femur, part scapula.

S.A.M. 12185. *Zinnosaurus paucidens* gen. et spec. nov. Meyerspoort, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Part coraco-scapula, one complete humerus and one proximal half, proximal and distal end of femur and proximal end of ulna and radius and distal end of radius associated with a good skull.

S.A.M. 12193. *Scymnosaurus* sp. Fortuin of Dalajalon, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Fairly complete pectoral girdle, humerus, ulna and radius associated with piece of jaw containing teeth.

S.A.M. 12204. *Pristerognathoides* sp. Plaatjiesrivier, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Fairly complete pectoral girdle, humerus, ulna and radius associated with the posterior third of a skull.

S.A.M. 12262. *Scymnosaurus* sp. Seleryfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Jooste 1959. Femur, radius, ulna and manus.

S.A.M. K218. *Alopecognathus* sp. Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Weathered pelvis.

S.A.M. K233A and B. *Alopecognathus* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Two incomplete pectoral girdles.

S.A.M. K223C. *Pristerognathoides* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. A nearly complete pelvic girdle associated with a skull.

S.A.M. K227. *Pristerognathus* sp. Louisrus of Dalajalon, Beaufort West. *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. Two ilia found in association with a poor snout.

S.A.M. K231. *Alopecognathus angusticeps* Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra and Gow 1959. The major part of an articulated skeleton articulated to a skull.

S.A.M. K234. *Pristerognathus* sp. Palmietfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. Part of pelvis associated with a snout.

S.A.M. K238A. *Pristerognathus?* Lammerkraal, Prince Albert. High *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959. A pelvis and pes.

S.A.M. K245A. Pristerognathid? Rietfontein of Vlakfontein, Beaufort West. High *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1959. A pelvis and part of the pes.

S.A.M. K306. *Pristerognathus* sp. Kranskraal, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow 1960. Distal and proximal ends of two femora.

S.A.M. K317. *Pristerognathus* sp. Bulwater, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Gow 1960. Proximal and distal ends of femur with parts of skull.

S.A.M. K339. *Alopecognathus* sp. Klipbanksfontein, Beaufort West. *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962. Incomplete pectoral girdle associated with anterior two-thirds of a skull.

S.A.M. K352. *Scymnosaurus* sp. Skoppelmaaikraal, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra 1962. Femur (isolated).

S.A.M. K353. *Scymnosaurus* sp. Klein-Koedoeskop, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1929. Proximal end of a large femur.

Historical

Hitherto little was known of the postcranial skeleton of the Pristerognathidae.

In 1929 Broom published a figure of the shoulder girdle of *Pristerognathus minor* as seen in ventral view. Broom does not state on what specimen this restoration was based and I have not been able to trace the specimen. In the sequel I am reproducing figures (fig. 2) of the pristerognathid pectoral girdle drawn from a model I have carved out of a rectangular block of plaster which has enabled me to be quite sure that the lateral, anterior and ventral views are really at right angles to each other. My ventral view differs considerably from that given by Broom, particularly in the disposition of the scapulo-coracoid.

In 1932 Broom published as a front view of the pelvis of a therocephalian (possibly *Pristerognathus minor*) what is in fact a ventral view, but again I have not been able to trace the specimen on which the drawing was based.

The specimen on which Seeley founded *Theriodesmus phylarcus*, from the *Endothiodon* zone, has by some recent compilators been referred to the Pristerognathidae. Comparison with the pristerognathid material described in this paper shows that *Theriodesmus* is not a therocephalian at all, but really a gorgonopsian.

General Morphology

Pectoral Girdle (fig. 2)

This general account is compiled from facts derived from 18 specimens representing 6 pristerognathid genera described in the systematic part of this paper. The material as a whole is not well preserved and in even the best specimens the constituent bones have been displaced relative to each other and distorted mostly by dorso-ventral compression. The reconstructions presented here in semi-diagrammatic form have been drawn from a composite model carved out in a block of plaster.

As in all primitive reptiles the pectoral girdle is composed of 11 bones—one unpaired and five paired, but in no case is the cleithrum preserved and its presence is only indicated by the facet on the scapula to which it was applied. There is no ossified sternum.

The girdle consists of two sets of bones—replacement and dermal bones. The replacement bones, forming the so-called scapular girdle, form a scapulo-coracoid composed of a dorsal plain blade-like scapula, lying practically vertically but curving slightly round the thorax, and a ventral antero-posteriorly elongated coracoidal plate, composed of a large precoracoid and a smaller posterior coracoid, curving gently inwards towards the middle line. The pair of scapulo-coracoids are held in position relative to each other by their connexion with the clavicular girdle of dermal bones consisting of an unpaired medially disposed interclavicle and a pair of bracing clavicles. Ventrally the coracoidal plate rests on the upper face of the interclavicle. Ventrally the spatulate end of each clavicle curves below around the anterior end of the interclavicle to fit into an oval hollow on the under face of this bone. Dorsally the stem of the clavicle sweeps upwards externally of the anterior end of the precoracoid and the lower part of the scapula and is then applied to the anterior edge of the scapular blade. Here it meets the cleithrum which is in all probability a splint-like bone applied to the upper anterior scapular edge.

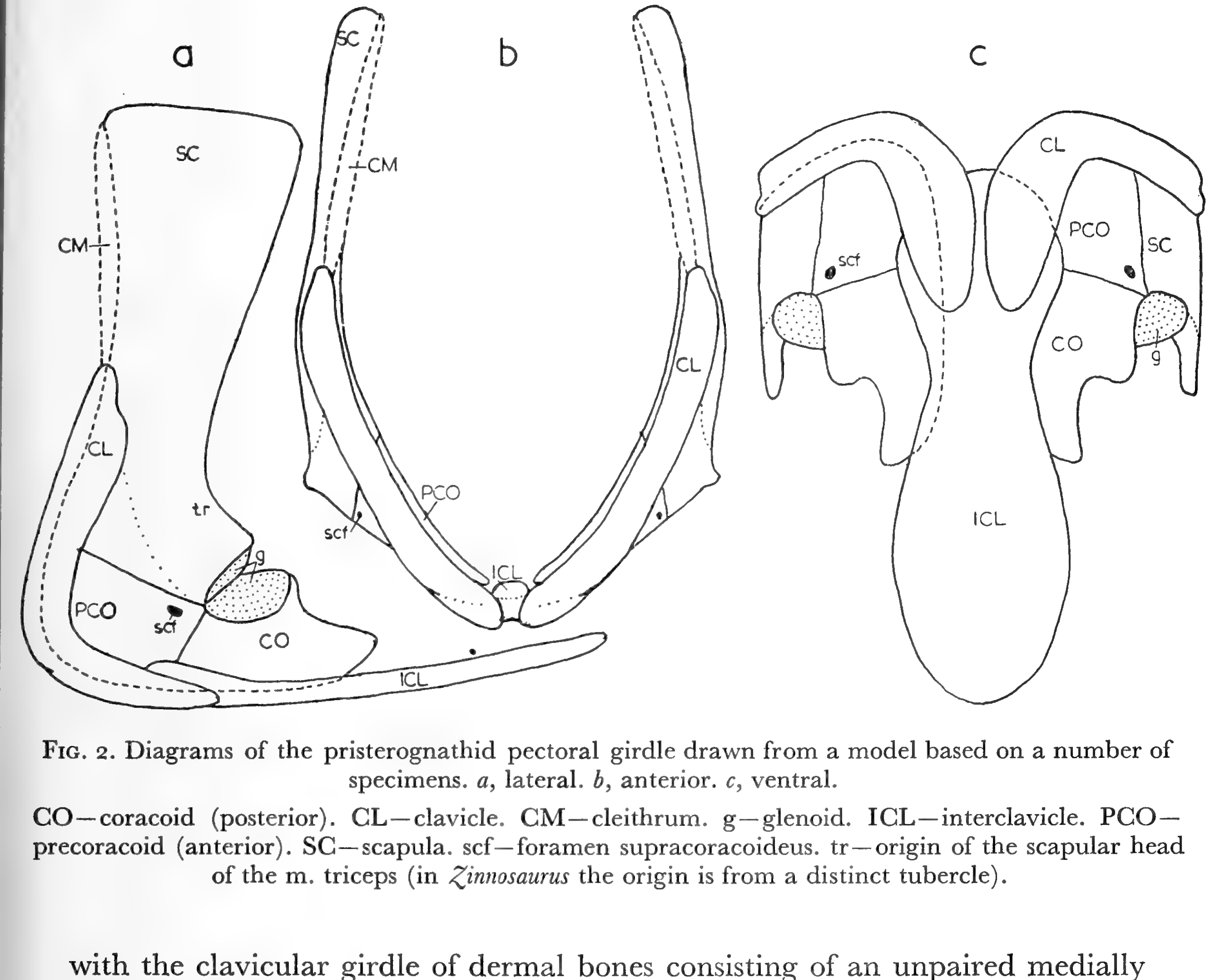

FIG. 2. Diagrams of the pristerognathid pectoral girdle drawn from a model based on a number of specimens. *a*, lateral. *b*, anterior. *c*, ventral.

CO—coracoid (posterior). CL—clavicle. CM—cleithrum. g—glenoid. ICL—interclavicle. PCO—precoracoid (anterior). SC—scapula. scf—foramen supracoracoideus. tr—origin of the scapular head of the m. triceps (in *Zinnosaurus* the origin is from a distinct tubercle).

On the posterior border of the scapulo-coracoid, at the junction of the scapular and the coracoid, lies the simple, antero-posteriorly shortened, glenoid cavity. The glenoid has a dorsal scapular facet which faces ventro-posteriorly and but slightly externally, and a ventral coracoid facet which faces dorso-externally and slightly posteriorly. The nature of the glenoid cavity prevents the humerus from assuming any appreciable downward disposition and also limits an anterior disposition, but it can be freely directed upwards and backwards.

The area of origin of the scapular head of the triceps muscle from the postero-lateral surface of the scapula above the glenoid is very indistinct, except in one specimen, the type of the new genus *Zinnosaurus*, where a prominent tubercle is developed very similar to that present in the anteosaurian dinocephalian genus, *Eccasaurus*. On the anterior edge of the scapula there is no indication of an incipient acromion process. The scapula blade is flat with no indication of any spine.

The precoracoid takes no part in the formation of the glenoid cavity and just enters into its anterior rim. Immediately anterior to this lies the foramen supracoracoideus. The anterior extent of the precoracoid is great, forming a large surface for the origin of the m. supra-coracoideus. Above the precoracoid lies the thin anterior plate of the scapula from whose outer face the m. scapulo-humeralis originates.

The coracoid is a smaller but more heavily built bone than the precoracoid, with a large strong glenoid facet. There is no special process as in the pelycosaurs for the origin of the coracoidal head of the triceps and this head was probably absent.

The clavicle of the pristerognathids is very distinctive, differing greatly from both that of the more primitive pelycosaurs and of the other contemporary therapsids. It is peculiar in that the ventral spatulate end curving round to the under face of the interclavicle is sharply bent backwards and extends far posteriorly along the under face of the interclavicle. The dorsally sweeping stem is also relatively stronger.

The interclavicle is a long, well-developed bone with the anterior spatulate end rounded in outline, not much expanded laterally and curving upwards only very slightly. In these features it differs markedly from the interclavicle in both pelycosaurs and the other therapsid contemporaries.

The cartilaginous sternum presumably lay above the spatulate posterior end of the interclavicle and extending to the coracoids.

Humerus (fig. 3)

A dozen fairly complete humeri and numerous proximal and/or distal ends are available for study, but bad preservation due to both erosion and post-mortem deformation makes it difficult to get a good picture of the nature of the pristerognathid humerus. It is particularly difficult to determine the angle subtended by the proximal and distal ends and thus the rotation on the shaft.

The pristerognathid humerus varies from a fairly light bone with moderately expanded ends and a fairly long and slender shaft to a moderately heavy bone with greatly expanded ends and a short thickened shaft. The rotation of the ends on the shaft apparently varies from 10° to 25°.

The proximal surface has the processus medialis and processus lateralis indistinctly demarcated from the caput which is narrowly oval in outline. The facet of the caput curves a little on to the dorsal surface of the humerus. The delto-pectoral crest is fairly weak and this subsides into the shaft without continuing as an oblique ridge in the direction of the entepicondylar foramen.

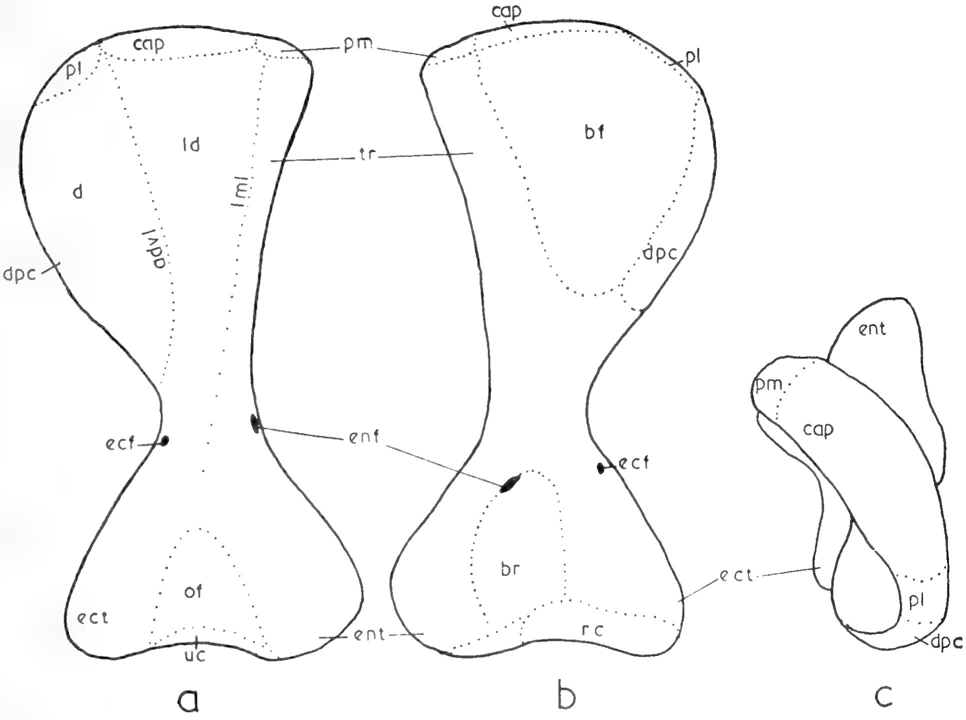

FIG. 3. Diagrams of the pristerognathid humerus. *a*, dorsal. *b*, ventral. *c*, proximal.

advl—anterior dorso-ventral line. bf—bicipital fossa. br—origin of the m. brachialis. cap—caput humeralis. d—insertion of the m. deltoideus. dpc—delto-pectoral crest. ect—ectepicondyle (radial). ecf—ectepicondylar foramen. ent—entepicondyle (ulnar). enf—entepicondylar foramen. ld—insertion of the m. latissimus dorsi. lml—latero-medial line. of—fossa for olecranon (trochlear). pl—processus lateralis. pm—processus medialis. rc—radial condyle or capitellum. tr—origin of the medial head of the triceps. uc—ulnar condyle.

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

The proximo-dorsal surface of the humerus is divided by the anterior dorso-ventral line (ADVL) into two parts. Anteriorly (preaxially) to this line lies the roughly triangular surface for the insertion of the m. deltoideus. On the surface posterior (postaxially) of the ADVL there is a weak oblique latero-median line (LML). Anterior to this line the area of insertion indicates a strong m. latissimus dorsi. Posterior to the LML a well-developed rectangular area indicates the origin of a strong medial head of the m. triceps.

Distally the epicondyles are usually moderately developed, except in *Zinnosaurus*, where the epicondyles have widely expanded thin flanges of bone. In this genus the ectepicondyle, which is fused to a well-developed supinator flange, forms a widely expanded thin sheet of bone. A rounded foramen pierces the supinator-ectepicondylar flange obliquely. The entepicondyle in this form forms an extensive distal sheet of bone indicating well-developed flexors.

Distally the condyles are weakly developed. This is particularly so in the case of the radial condyle whose articulatory face lies practically wholly distally with hardly any ventral surface and no indication of a ventral bulbous swelling (capitellum) as is present in most of the contemporary therapsids. On the dorso-distal surface the trochlear fossa is shallow, which is related to the virtual absence of an olecranon on the ulna.

The elbow joint in the pristerognathids thus differs markedly from that of the other therapsids.

The distal position of the distal humeral condyles makes a more upright dispostion of the limb possible. With the weak development of the olecranon a deep trochlear fossa is not necessary for the extension of the epipodial.

Ulna and Radius (fig. 4)

The pristerognathid ulna has its proximal end greatly expanded. Proximally the lateral corner is developed into a short but thickened olecranon with a rugose surface for the reception of the m. triceps. The sigmoid face for the reception of the humerus is shallow but the coronoid process is well developed. Dorsally the sigmoid rim is concave to receive the head of the radius, and the sigmoid face of the ulna and the proximal face of the radius form a common articulatory facet for the reception of the humerus. This facet is shallow and, the humerus having hardly a capitellum, the elbow joint forms a poor hinge joint.

The sigmoid face of the ulna lies on the proximal end of the bone and the coronoid process on the medial edge is also proximally situated, so that in the elbow joint the propodial and epipodial meet end-on without the ulna curving round the distal end of the humerus.

Carpus and Manus (fig. 4)

The proximal row of carpals consists of three elements—a robust radiale, a lighter elongated ulnare and a small laterally compressed intermedium. A pebble-like pisiforme lies laterally of the ulna-ulnare articulation.

In the middle row there are two centrals—one lying between the radiale and the first and second distals, the central one lying wedged in between the ulnare and radiale and distally articulated with the third distal.

There are four distals—the fourth and fifth are fused and articulate with the fourth and fifth metacarpals.

The metacarpals are well developed—the first is very short and looks very much like the first phalanx, the second is nearly twice as long as the first, the third about 2½ times as long, the fourth 3 times as long and the fifth just over 3 times as long. The phalangeal formula is 2, 3, 3, 3, 3. The proximal phalanges are all fairly short and robust and there is no indication of any further reduction. The ungual phalanges carried talon-like claws and have a ventral thickening proximally.

The first digit is the shortest, then come the second and fifth of equal length, then the third and fourth which are again of equal length.

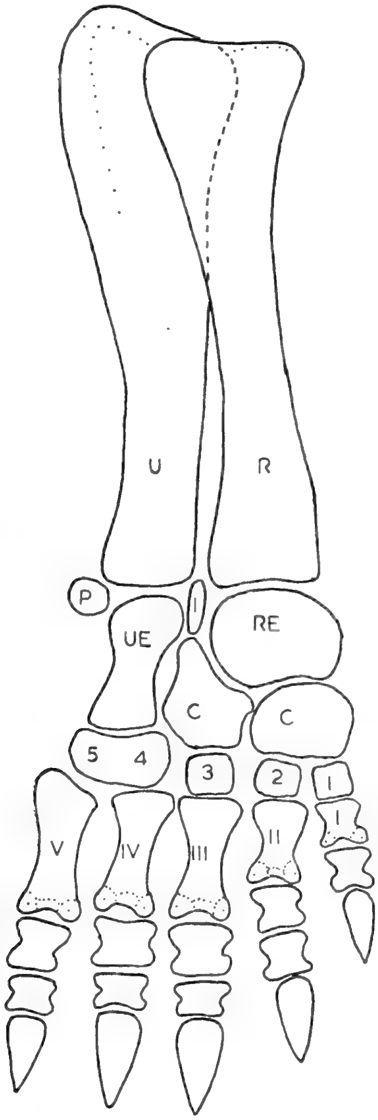

FIG. 4. Diagram of the pristerognathid epipodial and manus in dorsal view.

C_1, C_2—centrals. I—intermedium. P—pisiforme. R—radius. RE—radiale. U—ulna. UE—ulnare. 1–5—distals. I–V metacarpals.

The purchase of the forefoot on the ground is thus more meso-post-axonic than pre-axonic.

The digits as a whole are short and the metacarpals and carpus in comparison long. The manus can be considered semi-digitigrade.

Pelvic Girdle (fig. 5)

Pelves are not well represented and this account is compiled from half a dozen specimens representing four genera.

The pelvis is much lower than the pectoral girdle and the pubo-ischiadic plate shorter than the interclavicle, but longer than the coracoidal plate.

The three bones of each side are not firmly ankylosed and the junction between the two sides is weak between the pubis but stronger at the ischiadic keel.

The acetabulum is large and nearly circular in outline; all three bones take part, with the ilium contributing about half. The acetabulum faces mainly outwards; it is shallow, with strong rims for the attachment of the joint capsule and ligaments. Dorsally lies a strong supra-acetabular buttress formed by the ilium, overhanging the acetabulum and forming the main attachment of the joint capsule. At the dorso-posterior corner of the acetabulum, just posterior to the buttress, lies the supra-acetabular notch.

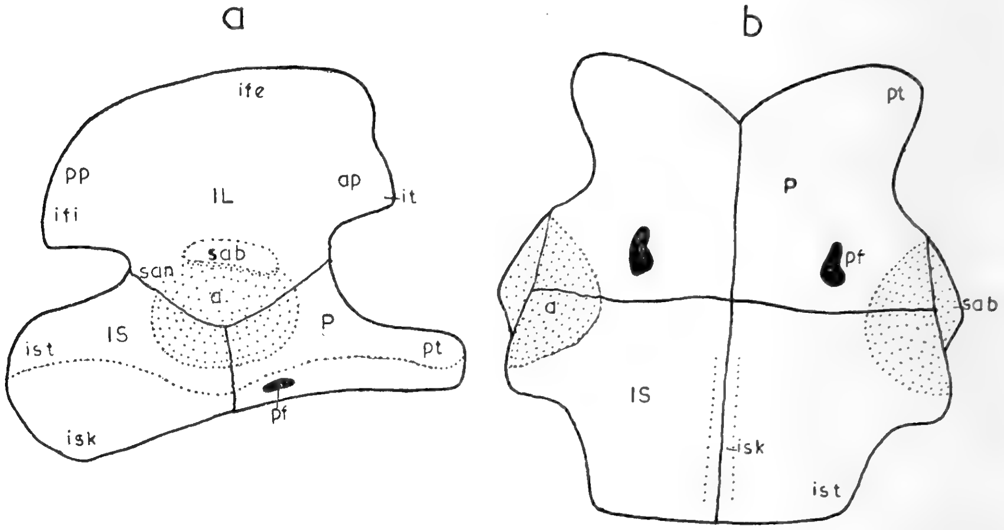

FIG. 5. Diagram of the pristerognathid pelvis. *a*, lateral. *b*, ventral.
a—acetabulum. ap—anterior process of the iliac blade. ife—area of origin of m. ilio-femoralis. ifi—area of origin of m. ilio-fibularis. it—area of origin of m. ilio-tibialis. IL—ilium. IS—ischium. isk—ventral keel of the ischia. ist—ischial tuber. P—pubis. pf—pubic foramen. pp—posterior process of the iliac blade. pt—pubic tuber. sab—supra-acetabular buttress. san—supra-acetabular notch.

At the level of the iliac buttress the iliac blade is antero-posteriorly expanded to form a high anterior and a somewhat lower posterior process. In most specimens the anterior process is much shorter than the posterior process, but in two specimens the lower corner of the anterior process is prolonged to form a long but weak process. In the other specimens there is an indication of this process. More and better-preserved specimens may prove that this elongation is normal for the family. The outer face of the iliac blade is both dorso-ventrally as well as antero-posteriorly convex. In antero-dorsal direction runs a shallow groove and near the dorsal edge in a vertical line with the posterior end of the buttress there is also a slight hollow. One can thus speak of an undulating surface. There is no eversion of either anterior or posterior edges. The areas of origin of the ilio-fibularis, ilio-femoralis and ilio-tibialis are thus indefinitely determinable.

The ischium in its acetabular part is massive and forms here, the strongly thickened postero-ventral segment of the strong acetabular rim. From here it tapers posteriorly and forms a thickened upper edge but without a distinct ischial tuber. Extending medially the ventral surface is flattened anteriorly but just behind the junction with the pubis it carries a strong and prominent ventral keel.

The pubis in its acetabular part is fairly massive and here forms a fairly strong acetabular rim. From here it tapers anteriorly and forms a thickened lateral edge but without a marked pubic tuber. The ventral surface of the pubis is fairly flat. Just medial to the acetabular rim, near its posterior edge, lies a well-developed pubic foramen.

The pubo-ischiadic plate is broad and large as in the pelycosaurs, the antero-posterior dimension of the pubis being relatively larger than in other therapsids and both anterior and posterior pelvic openings broad and not V-shaped as in other therapsids; but the posterior opening is incipiently V-shaped because of the ischial keel.

Femur (fig. 6)

The pristerognathid femur is represented in 20 specimens of 5 separate genera. Ten femora are fairly complete and there are a couple of dozen poor to good distal and proximal ends unconnected and usually lacking a shaft.

The femur, always longer than the humerus, is a fairly light bone with only slightly expanded ends and with a long, fairly slender shaft. There is a considerable twist on the shaft so that the proximal head and the distal condyles subtend an angle of 30°–40°. The distal preaxial condyle lies a little further ventrally than the postaxial distal condyle and a little proximal of its fellow.

The preaxial border is more concave than the postaxial border due to the femoral head being directed somewhat preaxially.

Proximally the caput femoris is terminal but somewhat preaxially directed; it is antero-posteriorly elongated, thick preaxially with a rounded edge; postaxially it tapers and curves gently towards the external trochanter, into which it flows. In its thickened preaxial part the caput is convex and rounded in its postaxial part. The caput femoris is much smaller than the acetabulum.

The external trochanter forms the proximo-postaxial rounded corner of the femur; it flows with a rounded curve into both the caput and the postaxial edge.

On the dorsal proximal surface lies a well-developed ridge near the preaxial border of the femur; it lies parallel to the preaxial border and commencing from the caput runs for a short distance distally and then fades away. This ridge serves as the area of insertion of the m. pubo-ischio femoralis internus. Between this ridge and the external trochanter lies the area of insertion of the m. ilio-femoralis.

On the ventral proximal surface a sharp, prominent longitudinal ridge is developed. Lying in the middle of the bone, it commences a short distance distally of the caput and extends distally for a variable distance to fade away into the general ventral face of the shaft. This ridge is the only part of the primitive Y system of adductor ridges preserved in the pristerognathids and represents an internal trochanter.

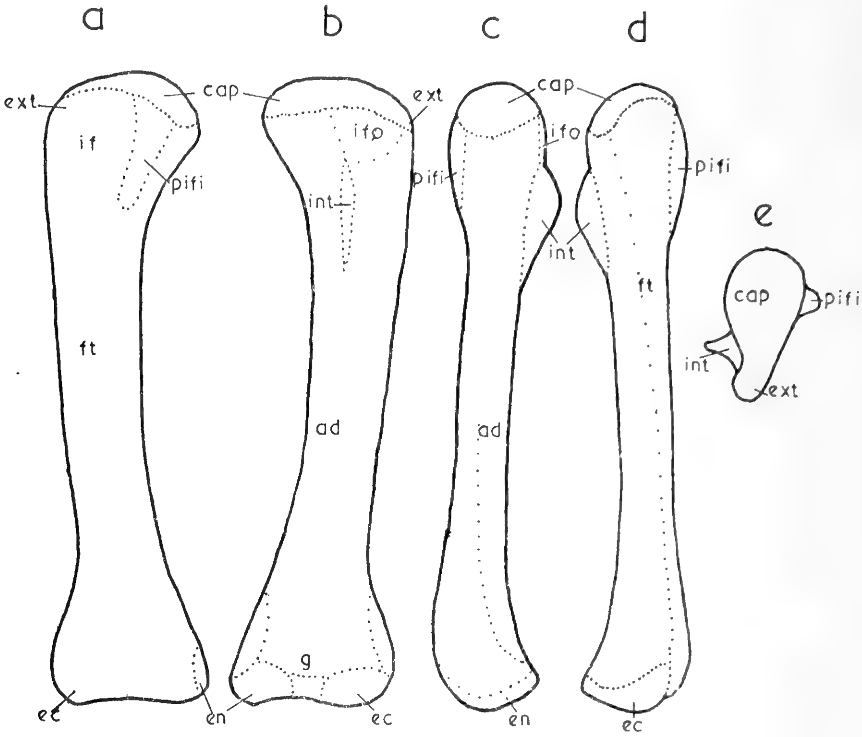

Fig. 6. Diagrams of the pristerognathid femur. *a*, dorsal. *b*, ventral. *c*, anterior. *d*, posterior. *e*, proximal.

ad—insertion of adductor muscle. cap—caput femoris. ec—ectocondyle. en—entocondyle. ext—external trochanter (major). ft——origin of m. femoro-tibialis. g—origin of the gastrocnemius. if—insertion of the m. ilio-femoralis. int—internal trochanter. ifo—intertrochanteric fossa. pifi—ridge on which is inserted the m. pubo-ischio-femoralis internus.

Between the internal and external trochanters lies a relatively small intertrochanteric fossa.

The distal condyles lie terminally facing very slightly ventrally and are well modelled. The intercondylar sulcus is very shallow. Dorsally the intercondylar fossa is very shallow, but ventrally the gastrocnemic fossa is quite well developed.

Tibia, Fibula and Pes (fig. 7)

The posterior epipodial and pes are not as well represented in the material at my disposal as the corresponding structures of the forelimb.

The posterior epipodial is longer than the anterior one, as we have already seen is also the case in regard to the propodial.

Both tibia and fibula are lightly built, slender bones, lighter and slenderer than the radius and ulna. In both epipodials the pairs of bones are approximately of equal length. Proximally the tibia and fibula form a common terminal articular facet to meet the femoral condyles end on. Distally the tibia articulates with a rounded face on the astragalus and the fibula with an elongated facet on the proximal end of the calcaneum.

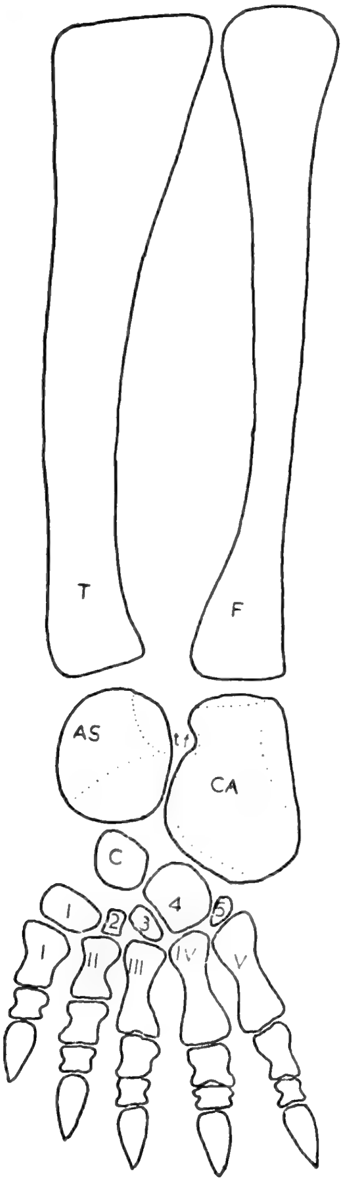

FIG. 7. Diagram of the pristerognathid epipodial and pes in dorsal view. AS—astragulus. CA—calcaneum. C—central. F—fibula. T—tibia. tf—tarsal foramen. 1–5—distals. I–V —metatarsals.

As in pelycosaurs and therapsids generally the pristerognathid tarsus has a pair of proximal elements—an astragalus and a calcaneum.

The astragalus is a robust, roughly ovoid bone with a rounded face for articulation with the tibia; laterally it has an elongated facet articulating with the calcaneum and distally a curved facet facing the centrale.

The calcaneum is a larger but more lightly built bone. It is a sheet of bone, thickened proximally to form an elongated facet for the reception of the fibula and with a thickened medial edge abutting against the astragalus, but notched for the passage of the penetrating tarsal vessels, and thickened distally where it carries a facet to receive the fourth distal carpal. There is no indication of a tuber-like heel.

One fairly small centrale is present. There are five distal tarsals, but in one specimen the small fifth distal is fused to the large fourth distal as is usual in therapsids.

The fourth distal is always large; the third and second distals, when well developed, have flattened upper faces and are roughly squarish in outline; the first distal is usually large, articulating with both first and second metatarsals, but in one specimen it is a small, pebble-like bone.

The first metatarsal is a short, fairly squat bone, the second, also short, has a more constricted shaft; from the third to the fifth the metatarsals become progressively longer with well-expanded ends.

The digits are, as in the manus, short, with the phalangeal formula 2, 3, 3, 3, 3. The first phalanx in all the digits is usually fairly long, but in one specimen that of the first digit and in another that of the fifth digit is greatly shortened, being disc-like without a constricted waist.

The second phalanx of the second to the fifth digits is short with a constricted waist.

The terminal phalanges are long, curving, claw-like. The first digit is short and the other four of about equal length. The purchase of the hind foot thus lies in the postaxial part of the foot.

Systematic Descriptions of Specimens

A. PECTORAL GIRDLE

Alopecognathus (figs. 8–10)

The specimen 12051 includes a scapular blade; K339 has a nearly complete scapula; K223A and K223B each consists of a fairly complete girdle, but both lack the scapular blades and the upper part of the clavicles and have undergone distortion and displacement of the constituent elements; K231 includes a nearly complete girdle, but is distorted by dorso-ventral compression. In the accompanying figures the distortion has been corrected and the symmetry restored. In none of these is the cleithrum preserved.

The girdle is a structure of considerable size; high, broad, with its ventral element—the interclavicle—long. The scapula, as restored, is dorsally directed or is tilted slightly backwards and curved slightly to follow the contour of the thorax. The area of origin of the scapular head of the triceps is indistinct—there is no ridge, mound or tubercle. The coracoidal plate is long, but in two specimens the anterior edge of the procoracoid is concave, whereas in the other it forms an even convex curve. The clavicles have a long, posteriorly directed ventral spatulate end in two specimens, whereas in another this part of the clavicle is quite short. The interclavicle is large, with a rounded anterior

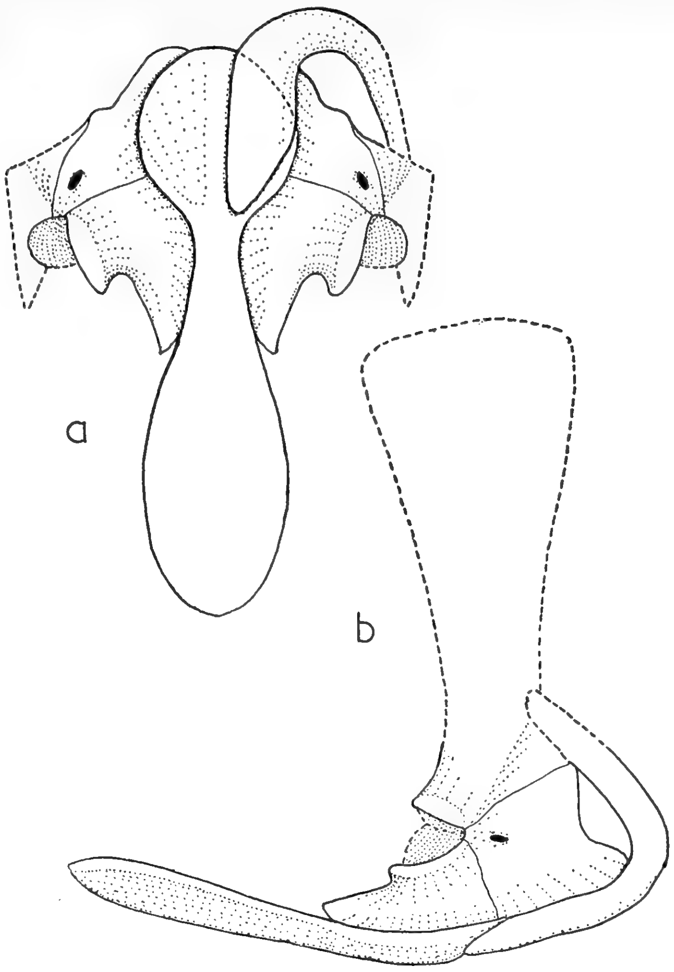

Fig. 8. *Alopecognathus angusticeps* ? S.A.M. K223A. × $\frac{1}{3}$. Pectoral girdle. *a*, ventral. *b*, lateral.

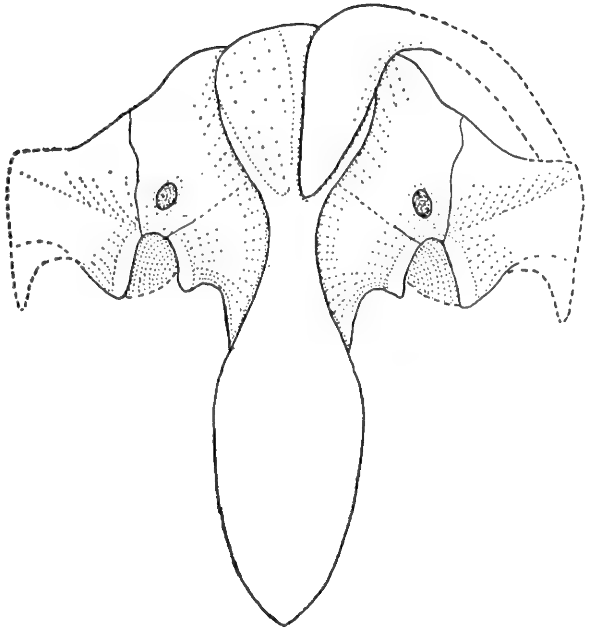

Fig. 9. *Alopecognathus angusticeps* ? S.A.M. K223B. × $\frac{1}{3}$. Pectoral girdle in ventral view.

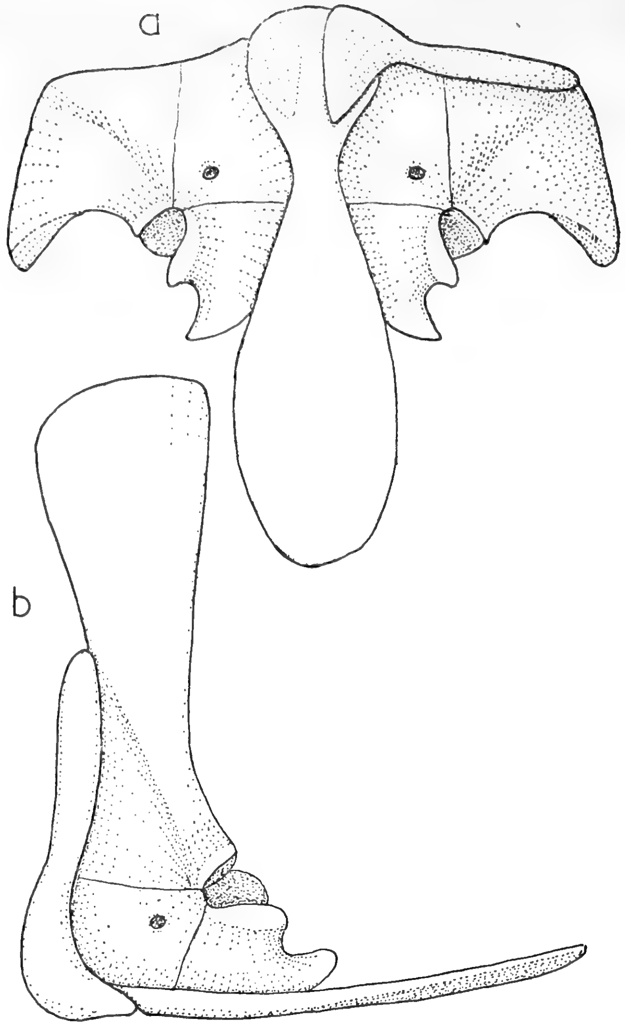

Fig. 10. *Alopecognathus angusticeps*. S.A.M. K231 × $\frac{1}{3}$. Pectoral girdle. *a*, ventral. *b*, lateral.

expansion and a long broad posterior spatula joined by a fairly narrow neck at the level of the posterior coracoids.

Priesterognathoides (figs. 11 and 12*a*)

In 12102 the right half of the pectoral girdle is preserved together with an incomplete interclavicle and parts of the left half of the girdle. The girdle is partially disarticulated but only slightly distorted in its fall backwards when the soft tissues decomposed.

In 12204 a disarticulated girdle has a good scapula, coracoid, procoracoid, interclavicle and the ventral spatulate ends of the clavicles.

The scapula is apparently tilted somewhat backwards and shows a marked curvature around the thorax. No origin of the triceps can be determined and there is definitely no tubercle. The coracoid is short, but the procoracoid well developed. The interclavicle is very similar to that of *Alopecognathus*.

Pristerognathus (fig. 12*b* and *c*)

In 4335 there are a pair of incomplete scapulo-coracoids. The coracoid is short and the procoracoid well developed. No scar or tubercle for the scapular

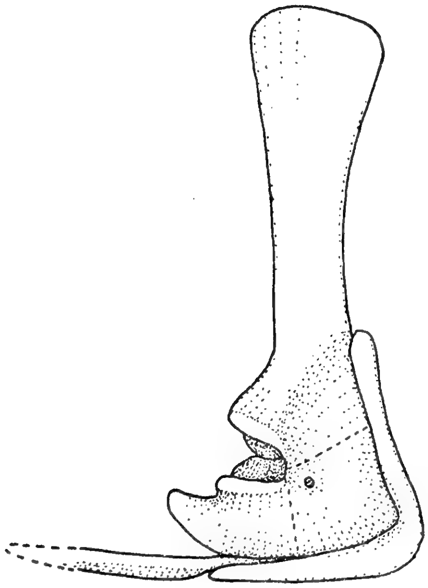

FIG. 11. *Pristerognathoides sp.* S.A.M. 12102. × ⅓. Pectoral girdle in lateral view.

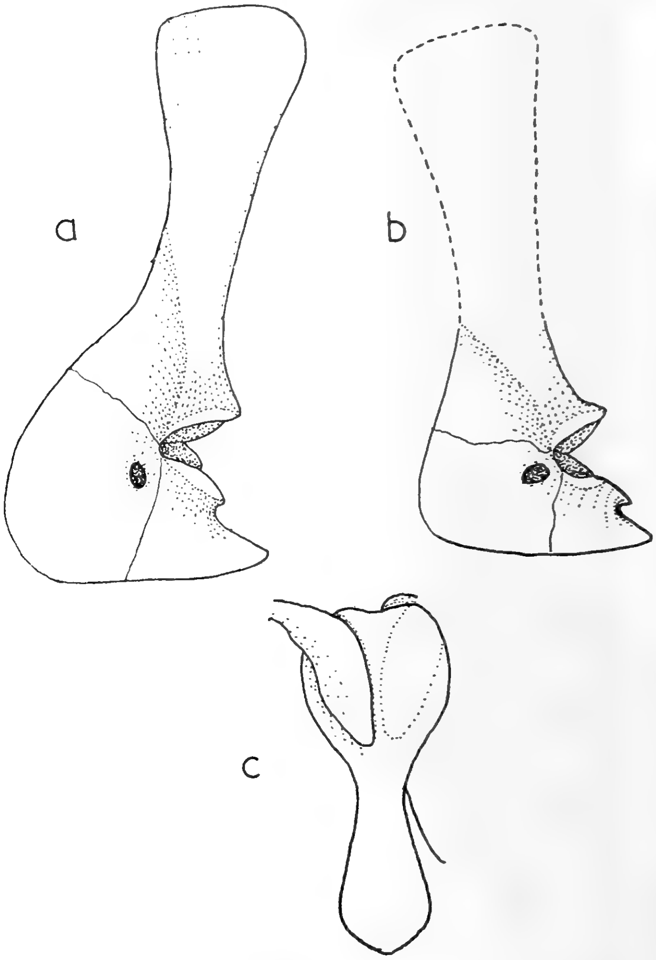

FIG. 12. Pectoral girdles. × ⅓. *a, Pristerognathoides* sp. S.A.M. 12204 in lateral view. *b, Pristerognathus* sp. S.A.M. 4335 in lateral view. *c, Pristerognathus* sp. S.A.M. 11458 in ventral view.

head of the triceps can be traced. In 11458 there is a good interclavicle which has a large anterior expansion, but the posterior spatula is only slightly expanded. The ventral spatulate ends of the clavicles extend well posteriorly. The procoracoid extends anteriorly of the interclavicle.

Scymnosaurus (figs. 13–17)

Five specimens have parts of the pectoral girdle preserved. 8034 and 12193 have a well-preserved coracoid each. Both are massive, and that of 12193 is probably of *S. major*. In the type specimen of *S. major* (9005) there are the anterior two-thirds of a large interclavicle and the ventral spatulate ends of both clavicles, which, though massive, have relatively a short posterior extent. In 11557 there are a disarticulated scapula, interclavicle and clavicle. The scapula is robust but short; the glenoid facet faces much posteriorly and laterally; the facet for the cleithrum is clearly shown, but the origin of the scapula head of the triceps is from the smooth postero-lateral surface just above the glenoid.

A left clavicle is stoutly built; the dorsal end clasping the anterior border of the scapula is expanded and strong. The ventral spatulate end is large and extends far posteriorly along the circular head of the interclavicle. Both the articulating surface of the clavicle as well as the hollowed face on the inter-

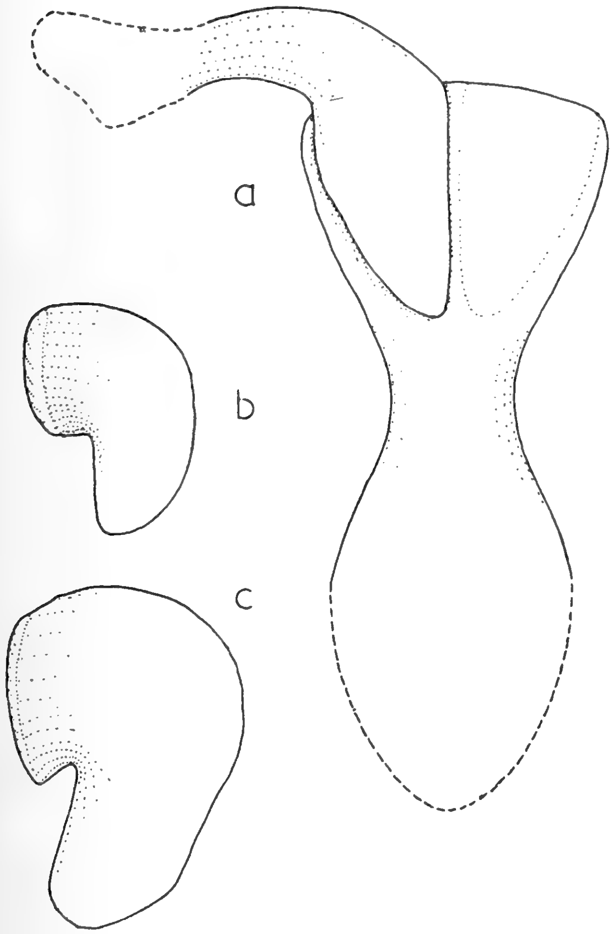

Fig. 13. Bones of pectoral girdles. × $\frac{1}{3}$. *a*, *Scymnosaurus major*. S.A.M. 9005. Type. Ventral view of interclavicle and clavicle. *b*, *Scymnosaurus ferox*. S.A.M. 9084. Right coracoid in ventral view. *c*, *Scymnosaurus* sp. S.A.M. 12193. Right coracoid in ventral view.

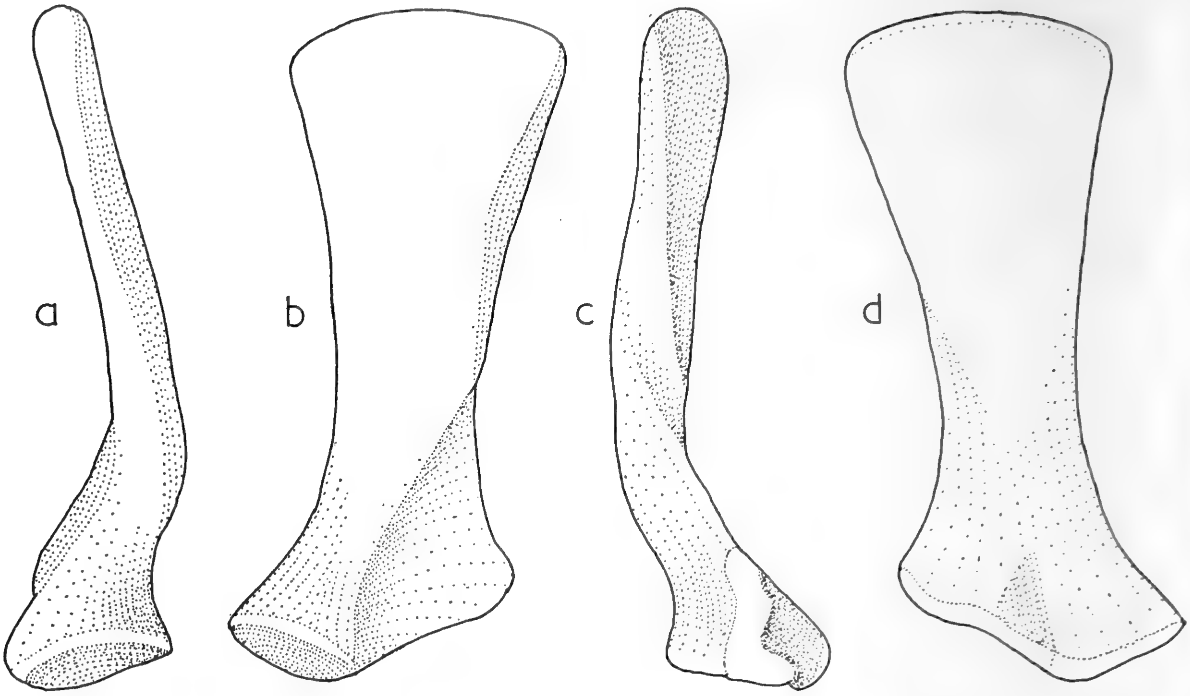

Fig. 14. Right scapula of *Scymnosaurus* sp. S.A.M. 11557. × ⅓. *a*, posterior. *b*, lateral. *c*, anterior. *d*, internal.

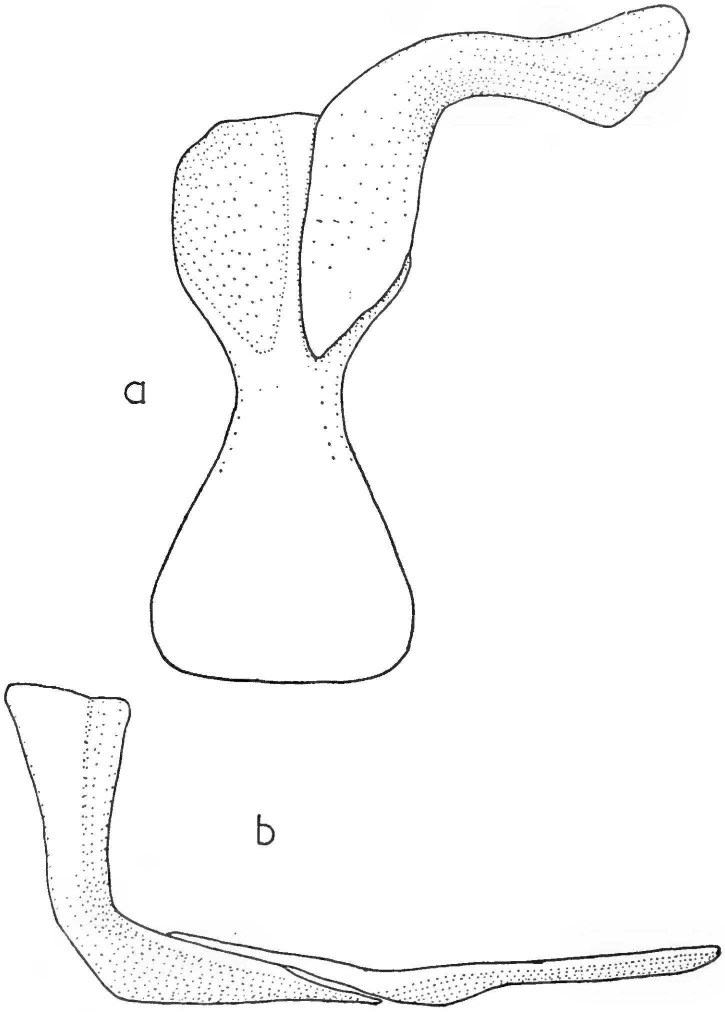

Fig. 15. *Scymnosaurus* sp. S.A.M. 11557. × ⅓. Clavicle and interclavicle. *a*, ventral. *b*, lateral.

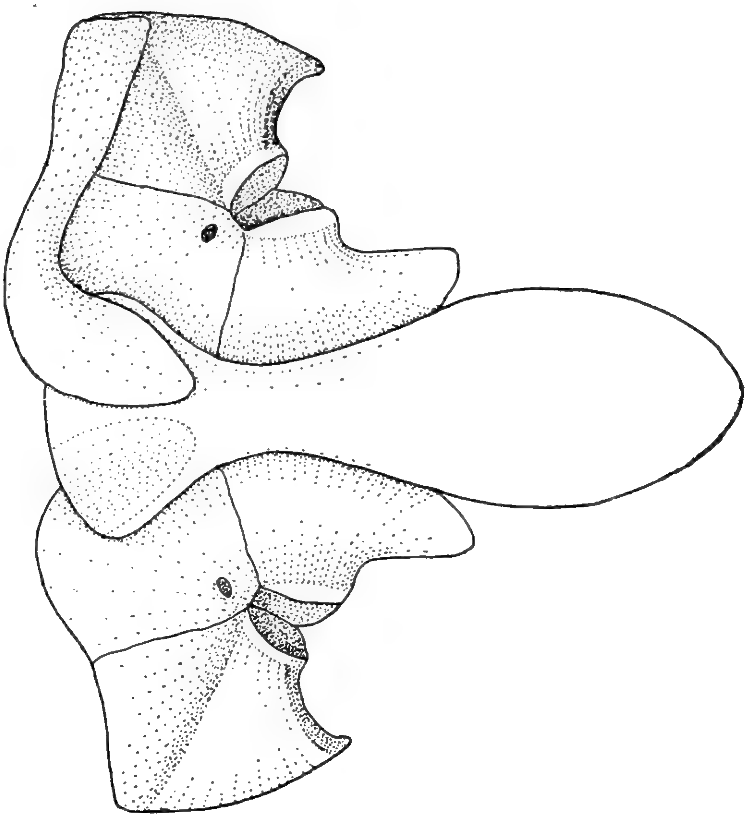

FIG. 16. *Scymnosaurus* sp. S.A.M. 11695. ×⅓. Ventral view of pectoral girdle.

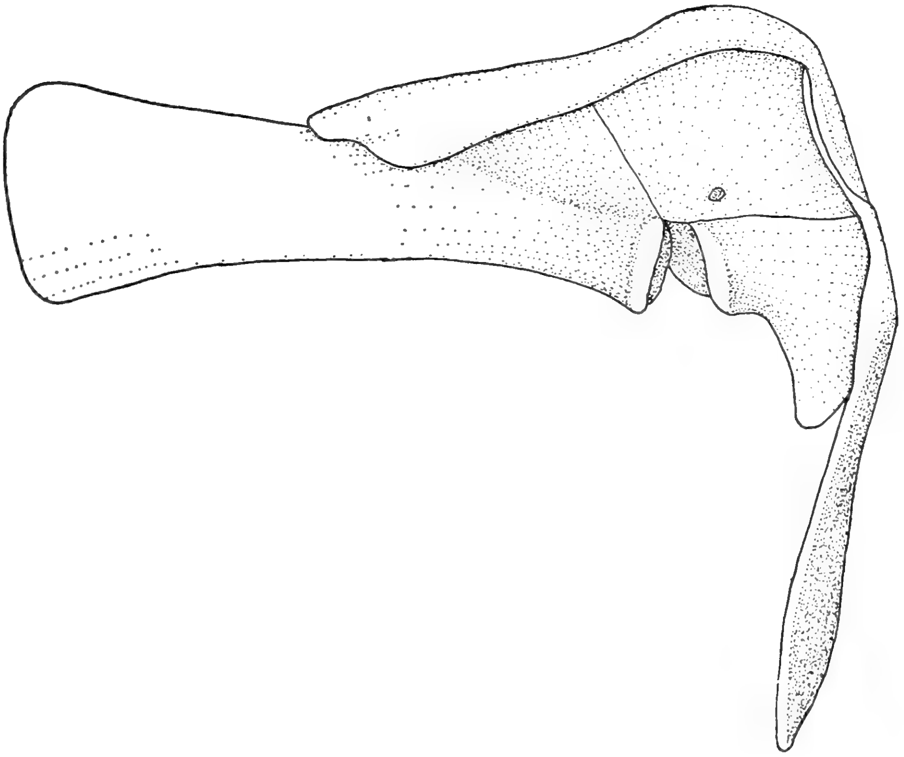

FIG. 17. *Scymnosaurus* sp. S.A.M. 11695. ×⅓. Lateral view of pectoral girdle.

clavicle bear longitudinal striae, and the backward movement of the clavicle is limited by a thickened border on the clavicle which abuts against the anterior edge of the interclavicle. The dorsal stem of the clavicle and its ventral spatulate end subtend what is nearly a right angle.

The anterior end of the interclavicle is large and nearly circular in outline, and a strong median ridge separates the two facets for the clavicles. The posterior end is greatly expanded but short, and is remarkably lightly built.

In 11695 there is a fairly complete shoulder girdle, but with the constituent bones displaced and distorted by dorso-ventral pressure. The anterior head of the interclavicle and ventral spatula of the clavicle are both relatively smaller than in 11557, and the dorsal stem of the clavicle is longer and more slender, with a bifurcated end. The scapular blade is fairly tall but is relatively lightly built.

Therioides (fig. 18)

In 11888, the holotype specimen, much of the pectoral girdle is preserved, but here again disarticulation and distortion have made reassembly and restoration of symmetry, as shown in the figures, difficult. The girdle is very like

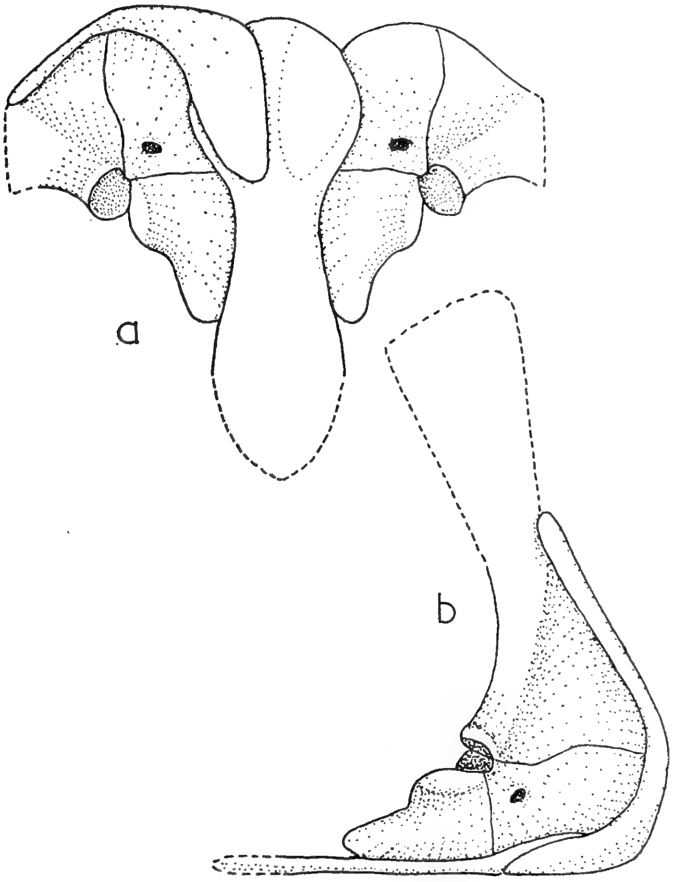

Fig. 18. *Therioides cyniscus*. Pectoral girdle. S.A.M. 11888. Type. × 1/3. *a*, ventral. *b*, lateral.

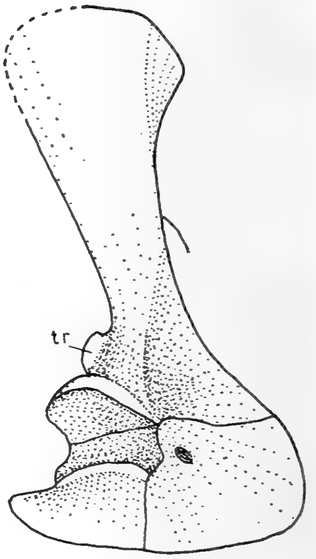

Fig. 19. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. Type. × 1/3. Lateral view of scapulo-coracoid.

that in *Alopecognathus*, but smaller and of a lighter build, with a proportionately large anterior expansion of the interclavicle.

Zinnosaurus paucidens gen. et spec. nov. (fig. 19)

In 12185, the holotype specimen, there is a well-preserved right scapulocoracoid without scapular blade, and a left scapular blade. This scapulocoracoid differs very markedly from all those hitherto considered. The scapular blade has its upper anterior part expanded and on this outer face lies a facet for the upper end of the cleithrum; lower down the cleithrum is applied to the anterior edge of the scapula.

Immediately above the upper rim of the glenoid there lies a process on the posterior face of the scapula for the origin of the scapular head of the triceps. This process forms a strong, prominent flange of bone, laterally compressed and dorso-ventrally elongated.

The glenoid is a widely open cavity facing largely outwards. Both its dorsal scapular rim and ventral coracoidal rim are sharp and prominent. Anteriorly there is no rim on the procoracoidal border of the glenoid so that in its anterior movement the head of the humerus would ride in a broad groove.

The procoracoid extends far anteriorly.

B. HUMERUS

Alopecognathus (fig. 20)

In 12051 there is a good, apparently undistorted, proximal half of a humerus. In K231 both humeri are preserved but both are quite obviously distorted and in the figures I have tried to correct the distortion. The result is not very convincing and the two humeri have quite distinctive outlines.

In 12051 the central part of the caput quite definitely flows over onto the dorsal surface and this would obviously affect the nature of the shoulder joint

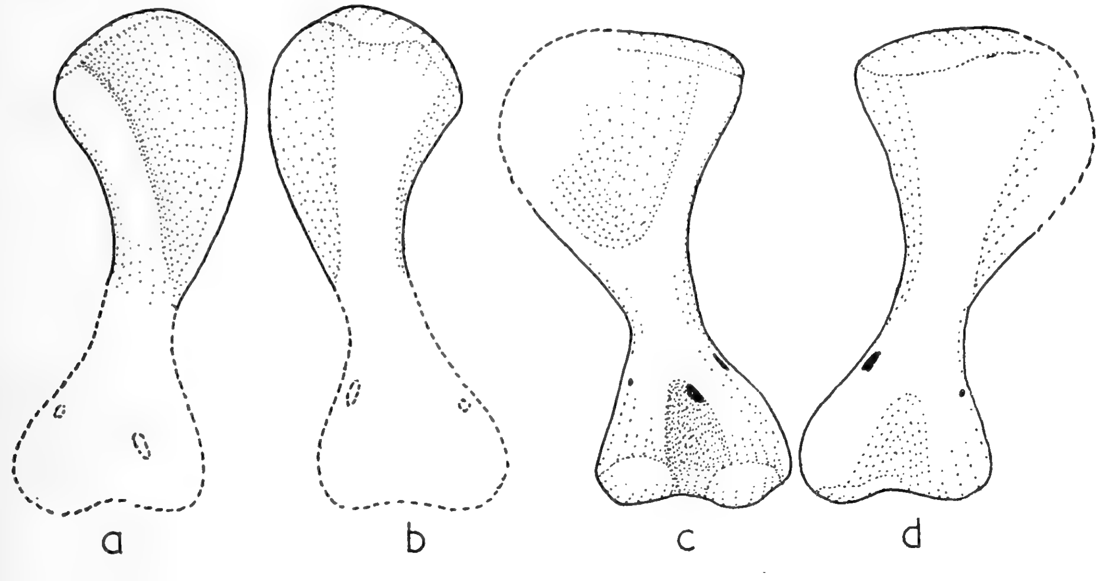

FIG. 20. *Alopecognathus angusticeps*. Humerus. × $\frac{1}{3}$. S.A.M. 12051: *a*, ventral. *b*, dorsal. S.A.M. K231: *c*, ventral. *d*, dorsal.

as the humerus would tend to be directed more horizontally. In K231 the caput is terminal. In 12051 the delto-pectoral crest is weak with little indication of the pectoralis insertion, and the processus medialis, caput and processus lateralis flow into one another.

In K231 the distal condyles are mostly terminal with only a little extension onto the ventral face. Both supra-trochlear fossa and brachialis fossa are deeply excavated. The radial condyle is not developed into a rounded capitellum.

Cynariognathus (fig. 21*a*)

In 11794 both humeri are imperfectly preserved. The bone is lightly built and the distal condyles mostly terminal without a bulbous capitellum.

Pristerognathoides (figs. 21*b*, *c* and *d* and 22)

In 5018 both humeri are incompletely preserved and in 12204 is a fairly good left humerus. In other specimens, e.g. 12102, only poorly preserved humeral ends are present. In 5018 the humerus is long, with both ends well expanded and the shaft slender. The caput, mainly terminal, curves slightly onto the dorsal surface. The distal condyles are a little ventral of terminal, and the capitellum is moderately swollen. I have not been able to locate an ectepicondylar foramen. In 12204 the ulnar condyle is separated from the olecranon fossa by a well-developed ridge which would appear to limit the extension of the epipodial. The delto-pectoral crest is weak and the area for the insertion of the deltoideus small.

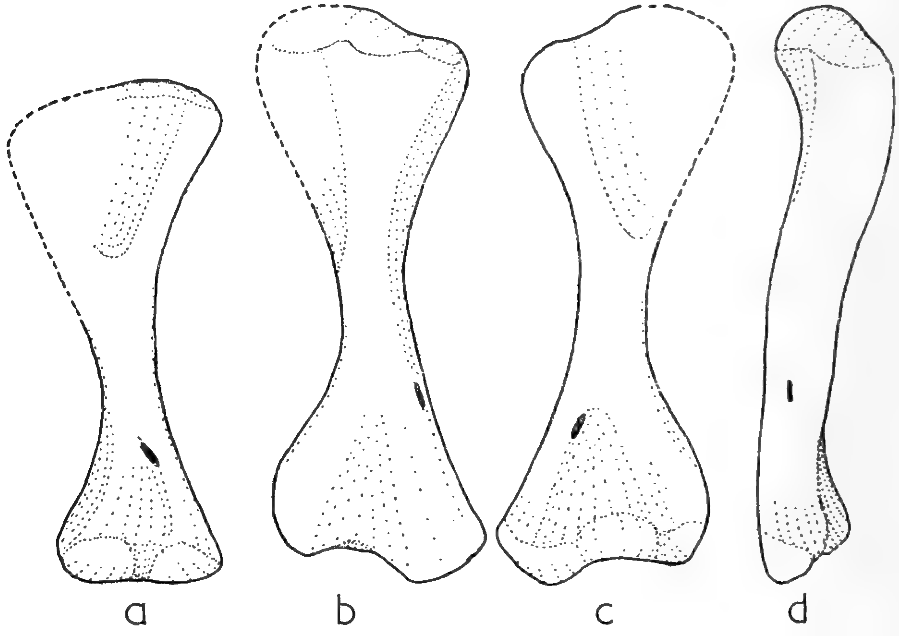

Fig. 21. Humerus. $\times \frac{1}{3}$. *Cynariognathus* sp. S.A.M. 11794. *a*, ventral. *Pristerognathoides* sp. S.A.M. 5018. *b*. dorsal. *c*, ventral. *d*, posterior.

Pristerognathus

A number of humeral ends of *Pristerognathus* are poorly preserved and warrant no description except to state that the humerus is very similar to that of *Pristerognathoides*—but smaller.

Ptomalestes (fig. 23)

In 11942, the holotype, both humeri are preserved. I am including figures of both the right and left humerus which show how much they have suffered from post-mortem distortion. If the distortion is corrected the humerus would be a fairly robust bone, moderately long with well-expanded proximal and

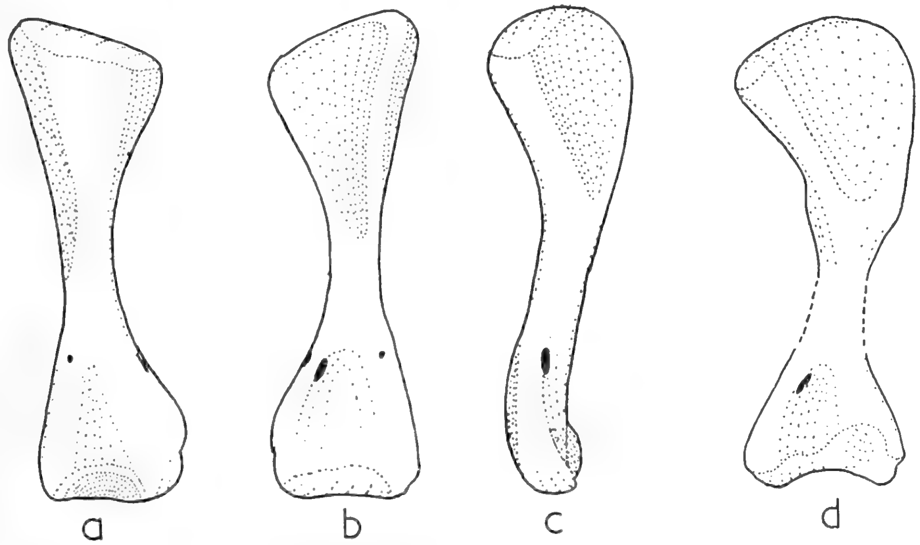

FIG. 22. Humerus. *Pristerognathoides* sp. S.A.M. 12204. × ⅓. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, S.A.M. 12102, ventral.

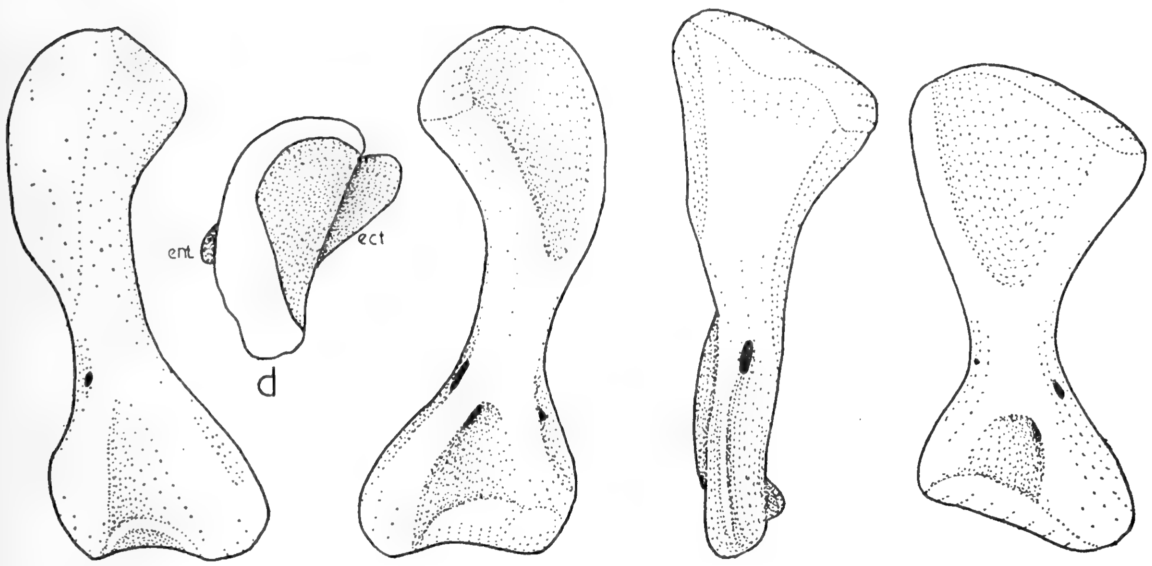

FIG. 23. Humerus. *Ptomalestes avidus*. S.A.M. 11942. Type. × ⅓. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, proximal. *e*, ventral of right humerus.

distal ends and a fairly short shaft; both caput and distal condyles are terminal, with the capitellum weak and little ventrally placed. A ridge separates the ulnar trochlea from the shallow supra-trochlear fossa.

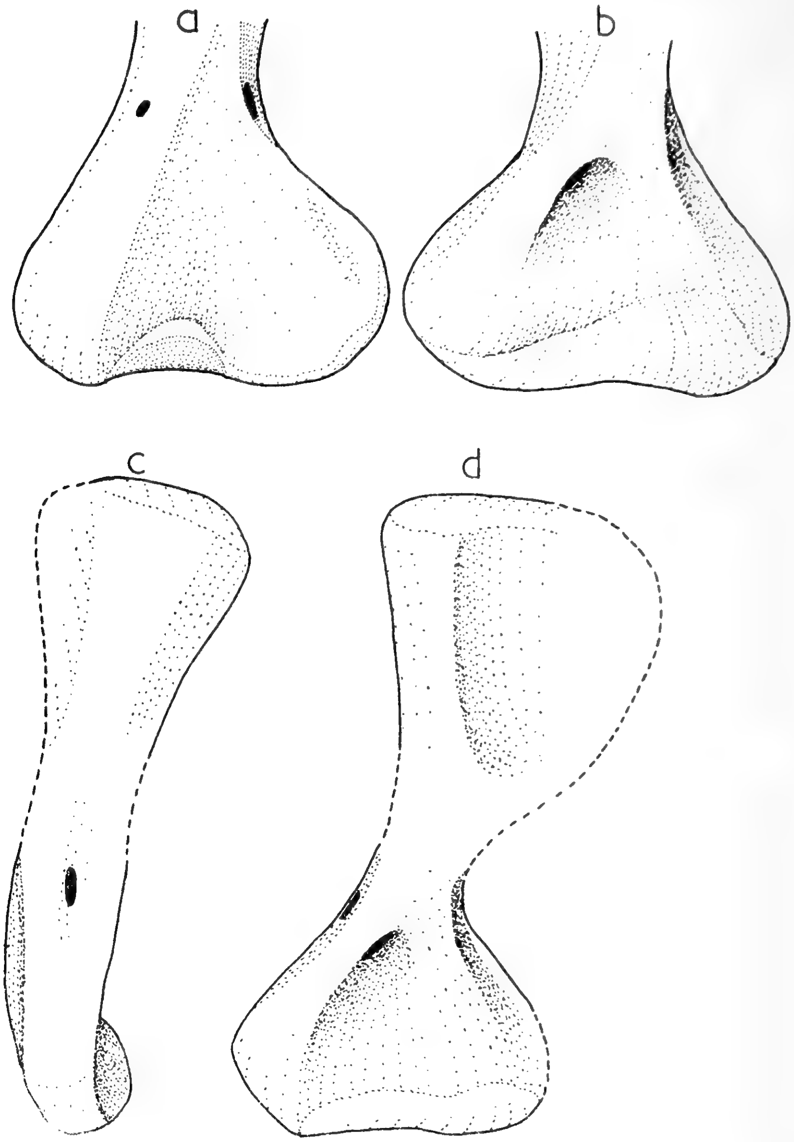

FIG. 24. Humeri. × $\frac{1}{3}$. *Scymnosaurus major.* S.A.M. 9005. Type. *a*, dorsal. *b*, ventral. *Scymnosaurus ferox.* S.A.M. 9084. *c*, posterior. *d*, ventral.

Scymnosaurus (figs. 24–26)

Of this genus I have two very well preserved distal ends, and one good complete humerus, which I believe to be undistorted, and this specimen must be taken to give us the best idea of the pristerognathid humerus as represented by the largest genus of this family of primitive Therocephalia.

In 9005, the type specimen of *Scymnosaurus major*, the good distal humeral end is, considering the bulk of the animal, only moderately robust. The epi-

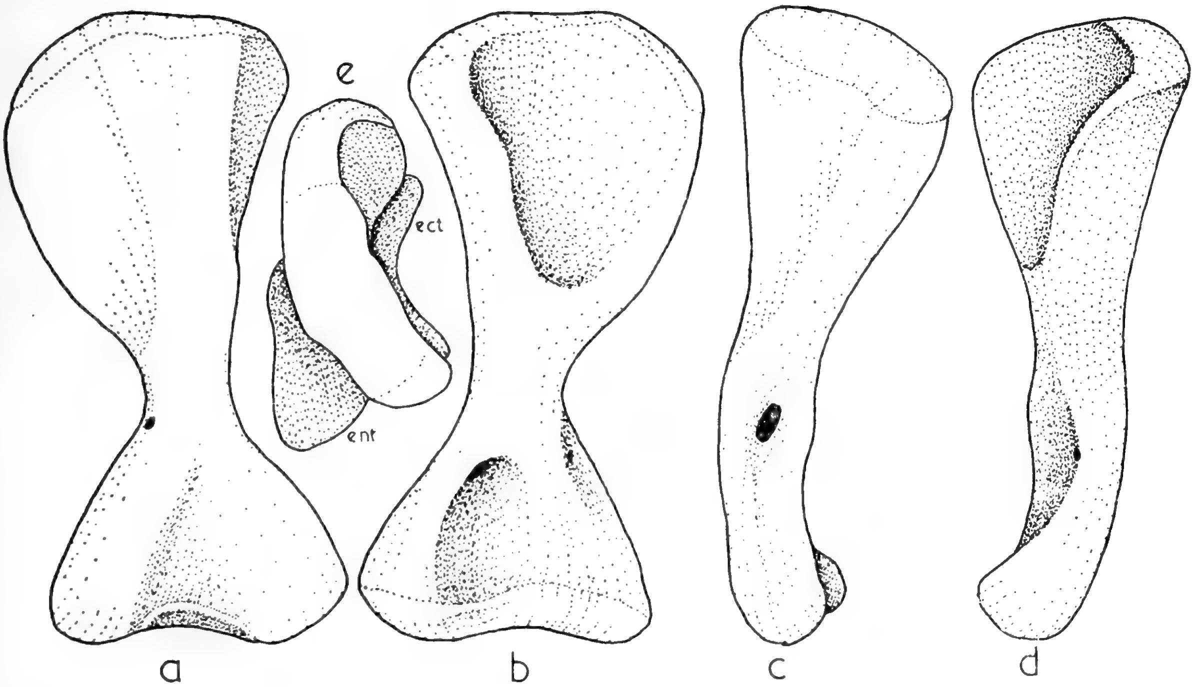

FIG. 25. *Scymnosaurus* sp. S.A.M. 11557. × ⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, anterior. *e*, proximal.

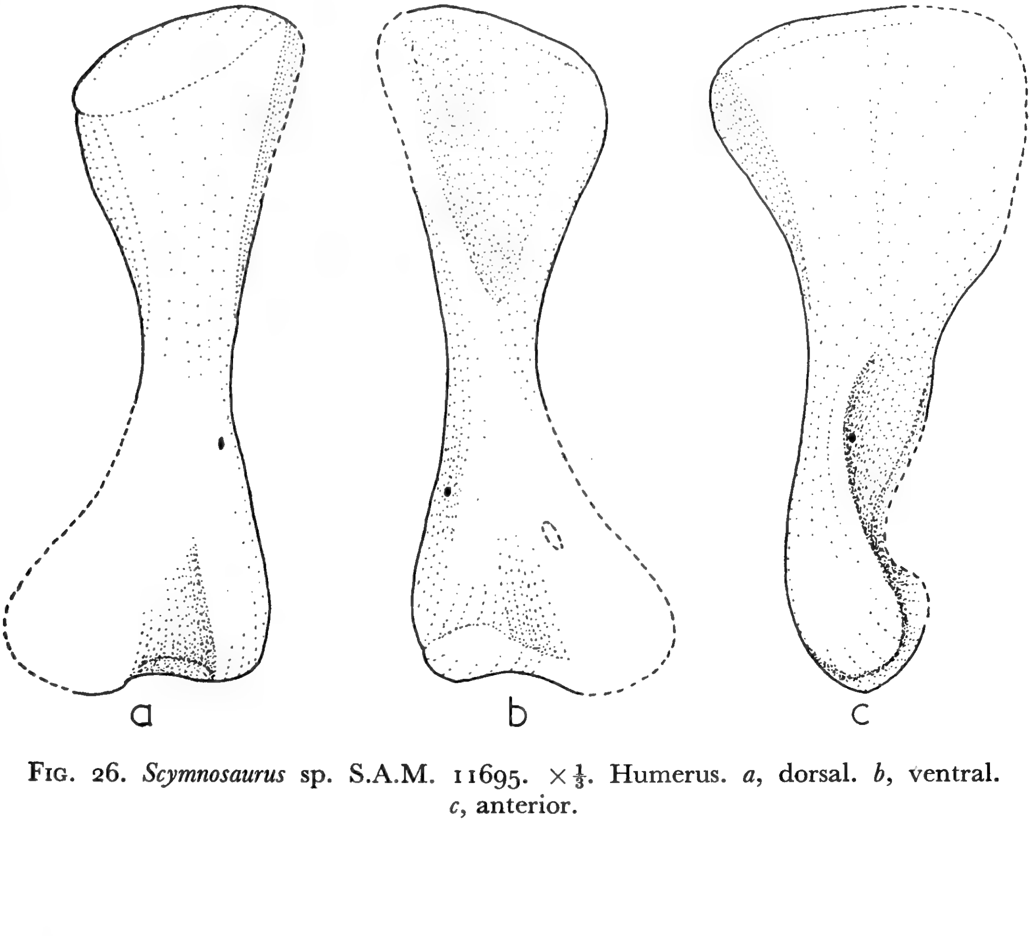

FIG. 26. *Scymnosaurus* sp. S.A.M. 11695. × ⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, anterior.

condylar expansions are modest, with the confluent supinator flange and ectepicondyle slightly more prominent than the entepicondylar edge. The condyles lie chiefly terminal. The radial condyle forms only a weak capitellum, which only slightly enters the ventral surface. The ulnar condyle forms a shallow trochlea, which dorsally has a ridge separating it from the very shallow supra-trochlear fossa hardly functioning as an olecranon fossa. Ventrally there is hardly a coronoid fossa, but the large oval entepicondylar foramen opens into a deep hollow bounded postaxially by a strong rounded ridge. The distal epicondylar edges are strong but not much expanded and their rugose surfaces give a strong origin for the flexors and extensors. In 9084, which is smaller and lighter, being a humerus of the less bulky *Scymnosaurus ferox*, the ectepicondylar flange is more expanded and curves downwards to form a deep groove. In 11557, which is most probably also of *Scymnosaurus ferox*, there is a well-preserved left humerus. Its terminal distal condylar face is less rounded than in 9084 and has no capitellum to speak of, and in its postaxial part it is concave instead of convex, indicating the presence of considerable joint cartilege. Its ectocondyle is without the flange present in 9084. Its supratrochlear fossa is deeper than in 9084 with a strong preaxial border.

11557 is the only *Scymnosaurus* humerus with a good proximal two-thirds preserved. Ventrally the bicipital fossa is deep and well demarcated from the surface of the short shaft. The delto-pectoral crest is fairly strong but the pectoralis insertion is not localized but diffuse. The postaxial border of the bicipital fossa is formed by a robust rounded ridge which on its postaxial face gives a strong face for the origin of the medial humeral head of the triceps. Dorsally both the anterior dorso-ventral line and latero-medial line are moderately developed and the areas of insertion of the deltoideus, latissimus dorsi and both the scapulo-humeralis anterior and posterior are well developed.

Proximally the caput is terminal with only a slight extension onto the dorsal surface; it is a very flat oval and flows evenly into both the processus medialis and lateralis.

The incomplete humerus of 11695 shows a greater twist on the shaft but is otherwise very similar to that of 11557.

Therioides (fig. 27)

The one humerus known in the type, 11888, is fairly short with moderately expanded ends but otherwise shows no special features to distinguish it from those of the other medium-sized pristerognathids so far described.

Zinnosaurus gen. et spec. nov. (fig. 28)

In the type material (12185) there are a practically complete right humerus and the proximal half of the left humerus. Both have suffered from distortion. I am including figures of the right humerus with the distortion corrected.

The caput is strap-shaped but in its middle part tends to overflow slightly onto the dorsal face. The processus medialis and processus lateralis flow gently into the caput. The delto-pectoral crest is long, with its proximal edge thin and its distal end somewhat thickened for the reception of the pectoralis.

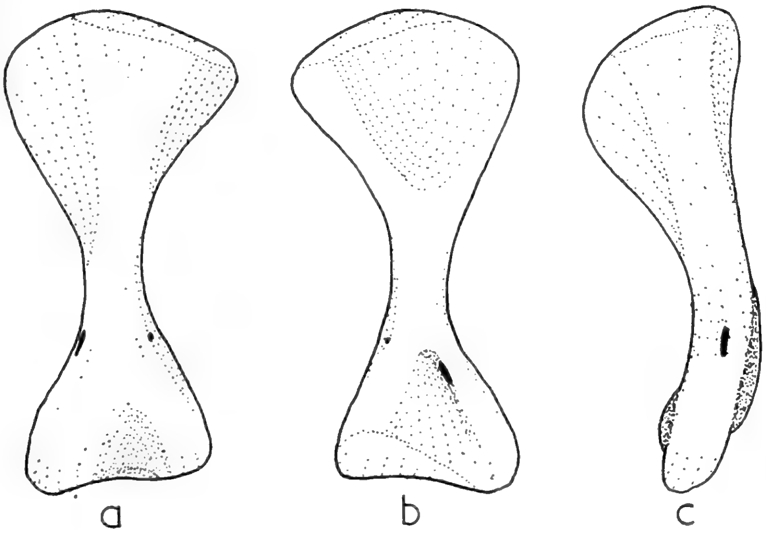

FIG. 27. *Theroides cyniscus*. S.A.M. 11888. Type. × ⅓. Humerus. *a*, dorsal. *b*, ventral. *c*, posterior.

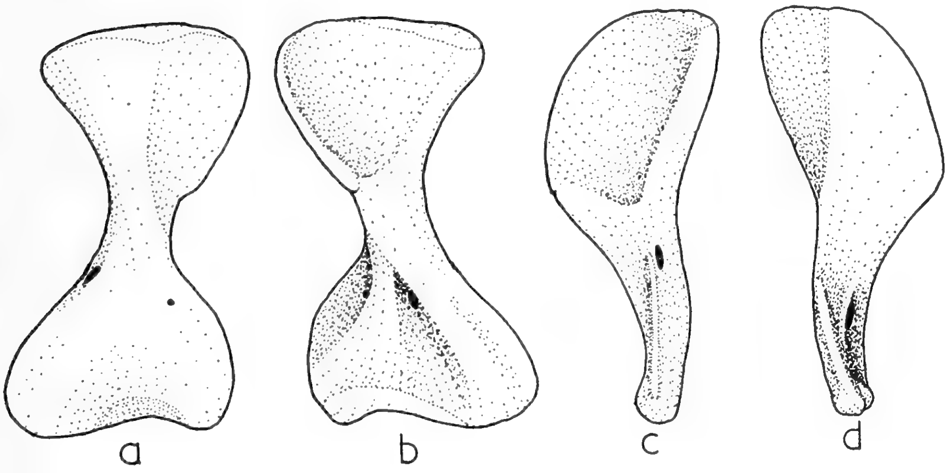

FIG. 28. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. × ⅓. Right humerus with distortion corrected. *a*, dorsal. *b*, ventral. *c*, posterior. *d*, anterior.

The distal end is greatly expanded. This expansion is mainly due to the development in both epicondyles of thin sheets of bone. This is particularly so in the ectepicondyle, where the confluent supinator process and the epicondyle form an extensive antero-ventrally sweeping sheet of bone.

The distal condyles are terminal with very little capitellar development, but the ulnar condyle is quite well developed with a dorsal ridge separating it from the very shallow supra-trochlear depression.

C. THE LOWER FORELIMB AND FOREFOOT

Alopecognathus (fig. 29)

In 12051 proximal and distal ends of both ulnae and radii and one good carpus are preserved.

Proximally the head of the radius fits into the concave sigmoid rim of the ulna so that its facet lies nearly as far proximally as that of the sigmoid facet of the ulna which is also situated terminally. The olecranon is robust but does not extend proximally as a process.

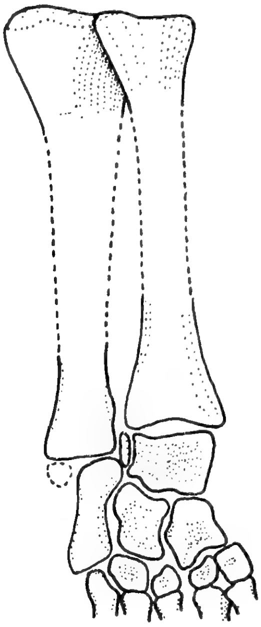

Fig. 29. *Alopecognathus angusticeps.* S.A.M. 12051. ×⅓. Epipodial and carpus.

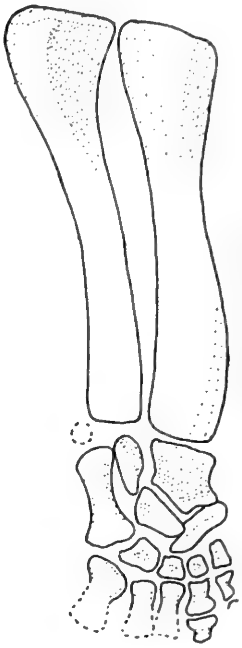

Fig. 30. *Cynariognathus* sp. S.A.M. 11794. ×⅓. Right epipodial and partial manus.

In the carpus the radiale is a stout bone roughly rectangular in outline. A longitudinal ridge separates a larger preaxial dorsal face from a smaller postaxial face. Distally a ridge separates the facets for the two centrals.

The intermedium is a laterally flattened small bone wedged in between radiale and ulna and ulnare.

The ulnare is a long element with expanded ends and a long constricted waist. Its proximal facet is much smaller than the distal ulnar facet.

Both centralia are well-developed bones, each articulating with a pair of distals.

There are four distals—the fused fourth and fifth articulating with the fourth and fifth metacarpals.

Only the proximal ends of the five metacarpals are preserved.

Cynariognathus (fig. 30)

In 11794 both anterior epipodials are preserved but the preservation is not very good. Both the ulna and radius are lightly built and the ulna has no olecranon process. In the figure the proximal ends of the two bones are shown as lying next to each other but in life the proximal head of the radius is applied to the edge of the sigmoid cavity of the ulna so that the two bones have their proximal facets forming a confluent articulating face. The radial facet meets the capitellum and in extension the ulna rides on the trochlear facet of the humerus.

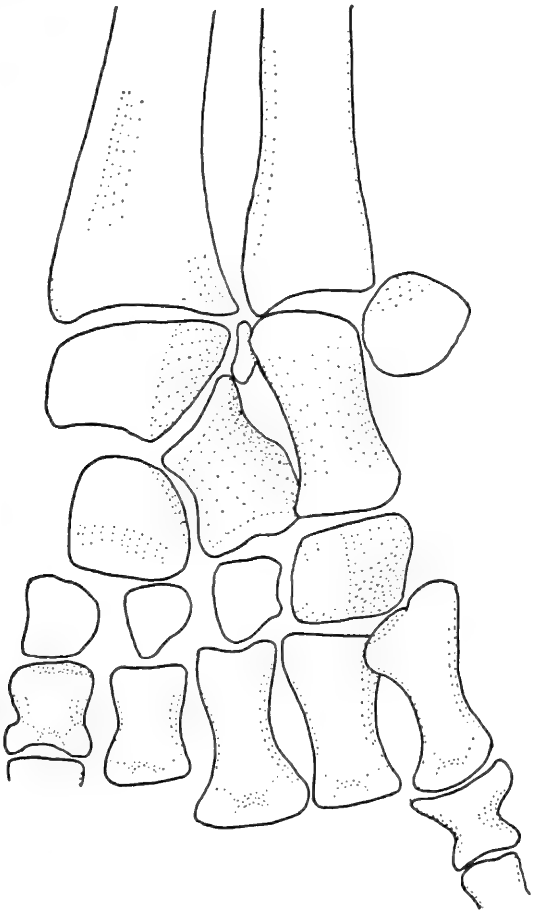

FIG. 31. *Pristerognathoides* ? S.A.M. K357. Nat. size. Partial manus.

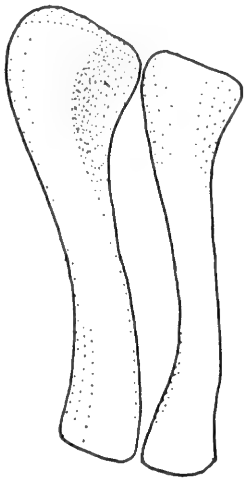

FIG. 32. *Ptomalestes avidus.* S.A.M. 11942. Type. × ⅓. Epipodial.

Only the right manus is in part preserved—the digits are missing.

In the carpus 9 bones are preserved. The proximal row consists of a long slender ulnare shaped somewhat like a metacarpal, a large laterally compressed intermedium and a short, broad radiale with distally two well-developed concave facets for the two centralia.

The two centrals are well-developed bones of irregular shape each with a good facet for articulation with the radiale.

There are four distalia; the first three articulate with the first three metacarpals, whereas the fourth articulates with both the fourth and fifth metacarpals.

Of the five metacarpals the last three have only their proximal ends preserved. They are short, with well-expanded ends. No. 1 is small and light, and from the second to the fifth they increase rapidly in size so that No. 5 is quite a strong element.

Pristerognathoides (fig. 31)

In a number of specimens ulnae and radii are preserved, exceptionally complete but mostly represented by proximal and distal ends. They call for little comment, except that in all these there is no definite olecranon process, and that proximally the two facets form a confluent terminal articulating face for the humeral condyles.

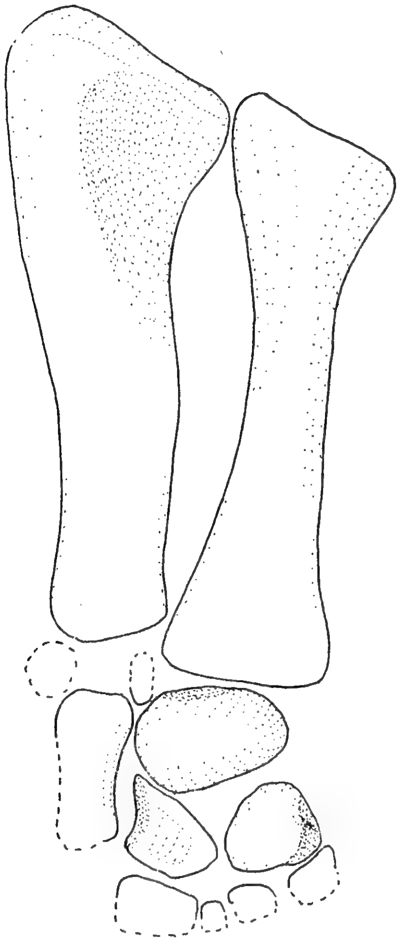

FIG. 33. *Scymnosaurus major* × ⅓. Epipodial of S.A.M. 9005. Type. Carpus of S.A.M. 12193.

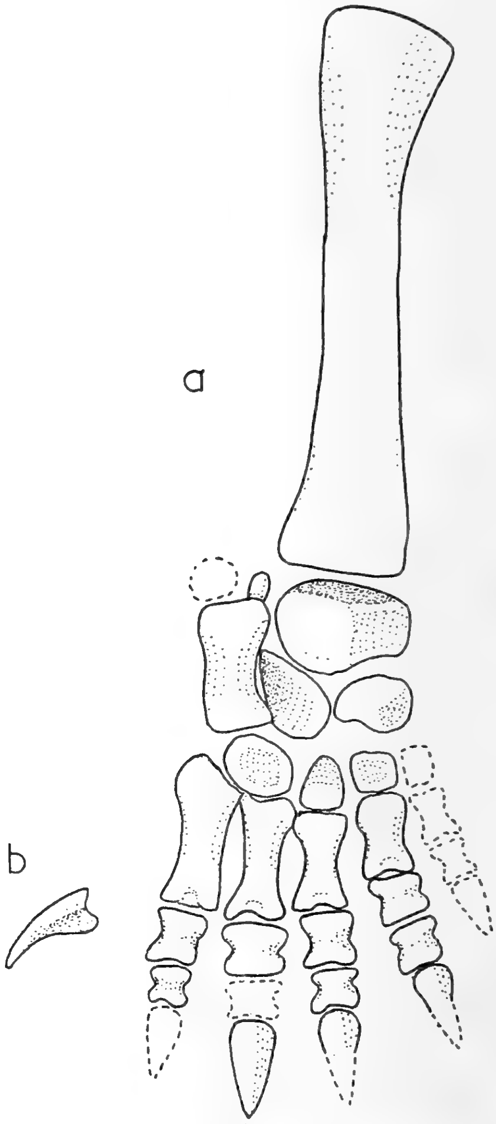

FIG. 34. *Scymnosaurus* sp. S.A.M. 11557. × ⅓. *a*, radius and manus in dorsal view. *b*, lateral view of no. IV terminal phalanx.

In K357 there is a good carpus with all five metacarpals present. Here the intermedium is a weak element and articulating with the ulna and ulnare there is a well-developed pebble-like pisiforme. The ulnare is elongate, the radiale robust, and the two centrals well developed. There are four distals, with the fourth articulating with both the fourth and fifth metacarpal.

The first two metacarpals are short, squat bones and the other three much longer, with the fifth the longest. The proximal phalanx of the fifth digit has its proximal end greatly expanded.

Ptomalestes (fig. 32)

In the type specimen of *Ptomalestes* (11942) both anterior epipodials are preserved. Both the radius and ulna are lightly built and the ulna has no distinct olecranon process. In the figure the proximal head of the radius is shown moved out of its articulation with the proximal end of the ulna.

Scymnosaurus (figs. 33–35)

In this genus the epipodial, carpus and manus are represented by some very good specimens.

The epipodial in the type specimen of *Scymnosaurus major* (9005) is represented by a well-preserved left ulna and radius (a mirror image is shown in the figure). In 9084 there are good proximal ends of the right ulna and radius in articulation. In 11557 there is a good radius, in 12193 proximal and distal ends of both ulna and radius and in 12262 a good complete radius and ulna.

In all these specimens the olecranon process of the ulna extends little proximally of the sigmoid face, and the proximal head of the radius lies anteriorly (morphologically dorsally) of the proximal end of the ulna and fits securely against the sigmoid edge forming a confluent articulating face for the feeble capitellum and the shallow trochlea of the humerus.

The carpus is preserved in part or nearly complete in 12193, 11459, 11557 and in 12262.

In 12193 the radiale is a robust bone; in dorsal view oval in outline with a convex dorsal and proximal face; concave distally for the first centrale and with a convex facet for the second centrale; ventrally it has a deep oblique groove.

The ulnare has its dorsal face with an outline like that of a metacarpal. Ventrally it has a longitudinal groove and its preaxial edge is convex in contrast to the dorsal concave preaxial edge.

The two centrals are robust; the first is nearly circular in outline with a penetrating foramen near its preaxial edge. The proximal central has its postaxial edge deeply concave, facing the concavity of the ulnare, thus forming a passage for the vessels penetrating the carpus.

Of the distal carpals only the proximal parts are preserved with the fourth distal strongly developed.

In 11459 the two centrals, distals together with metacarpals 1, 2 and 3, and the proximal phalanx of the second digit are preserved. The first central has a groove and a penetrating foramen near its preaxial border. The metacarpals increase in length from 1 to 3.

In 11557 there is a nearly complete carpus, but the manus is incomplete with the preserved bones partly displaced and disarticulated. In the figure the constituent bones are shown in natural relation. The radiale is fairly robust, with a flattish face for the radius; its dorsal surface shows two faces—the preaxial face nearly rectangular and the postaxial face more squarish, meeting at an angle of about 130°; the facet for the first central is slightly concave and for the proximal central convex.

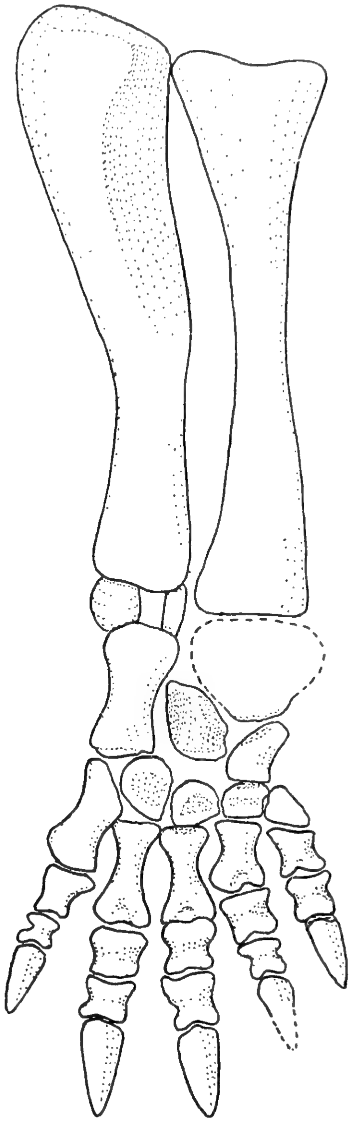

FIG. 35. *Scymnosaurus* sp. S.A.M. 12262. × $\frac{1}{3}$. Epipodial and manus in dorsal view.

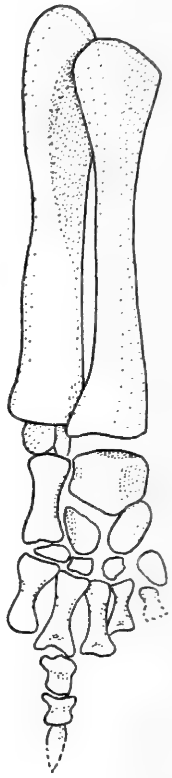

FIG. 36. *Theriodes cyniscus*. S.A.M. 11888. Type. × $\frac{1}{3}$. Dorsal view of epipodial and partial manus.

The ulnare is elongated, with a dorsal outline resembling that of a metacarpal.

The intermedium is a small, laterally compressed bone. The first central has a depression near its preaxial border and the proximal central is hollowed out near its proximal wedge-like end.

The first distale is missing, numbers 2 and 3 lie proximally to their respective metacarpals and the large fourth articulates with both the fourth and fifth metacarpals.

The first metacarpal is missing; from number 2 to 5 the metacarpals increase in length with the fifth about $1\frac{1}{2}$ times the length of number 2.

The phalangeal formula is 2, 3, 3, 3, 3, 3. The ungual phalanges are curved, narrow, pointed and claw-like. The others are short, broad and squat, with well-expanded ends.

In 12262 the forefoot is very well preserved and is complete except that part of the radiale and the tip of the ungual phalanx of the second digit have been lost in transit from the field. The general structure is as in all the pristerognathids described above, viz. carpal formula 3, 2, 4 plus an ulnar pisiforme, and phalangeal formula 2, 3, 3, 3, 3. The fourth and fifth metacarpals articulate with the large fourth distal carpal; the metacarpals increase in length in postaxial direction and the distal ends of the third and fourth are particularly well modelled, with a dorsal trochlear fossa and well-rounded distal corners. The third and fourth digits are the longest and strongest; the first digit is relatively weak and the fifth strong. The weight is thus carried somewhat more postaxially than preaxially.

Therioides (fig. 36)

In the type specimen (11888) much of the right forefoot is preserved. The carpus is complete; the last four metacarpals are present but only the second digit is completely preserved.

The structure is typically pristerognathid but the metacarpals are relatively long and slender.

D. PELVIC GIRDLE

Alopecognathus (fig. 37)

In K218 a fairly large pelvis is preserved. This is, however, badly weathered and all that can be determined is that the pelvic plate is large with a distinct ischial keel and that the outer face of the ilium is convex.

In K231 most of a fairly large pelvis is preserved, but with the edges of the ilia incomplete. The pelvic plate is long and broad with both ischium and pubis strong; just more than half is contributed by the ischium; the ilium is large, with its length nearly as long as the ventral plate (91%). The pelvis is low and long, with the height 79 per cent of the length.

The ilium is not completely preserved on either side, but the two sides are complementary so that the figure could be compiled fairly accurately. The antero-posterior length of the iliac blade is great but its supra-acetabular height moderate; the height is a little more than half the length (52%). The posterior process of the iliac blade is long but fairly low, whereas the anterior process is fairly short but high; although its ventral corner apparently has a long, low elongation.

The outer face of the iliac blade is in general convex both antero-posteriorly as well as dorso-ventrally. The m. ilio femoralis (gluteus) thus originated from a convex area whereas in tetrapods this area is usually concave. The supra-acetabular ridge is strong. The ilium forms more than half of the acetabulum.

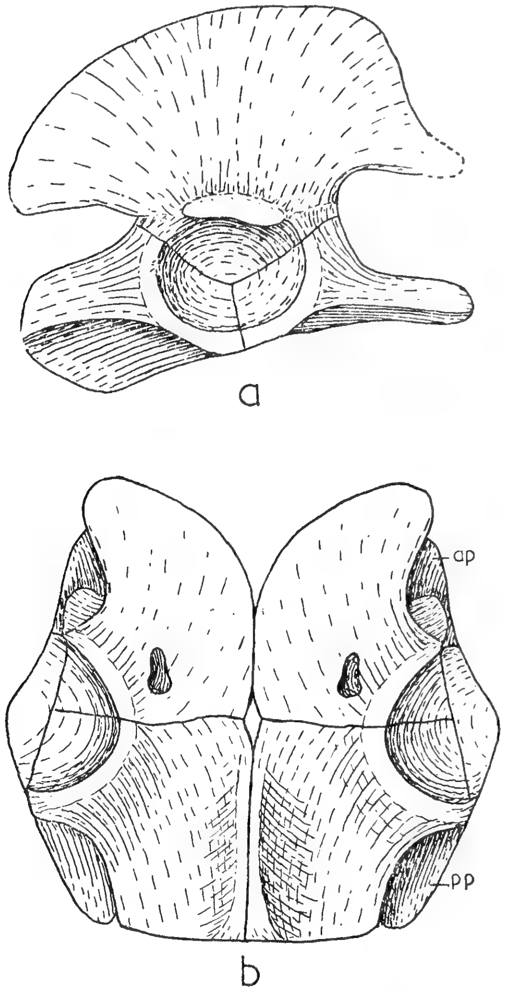

Fig. 37. Pelvis of *Alopecognathus angusticeps*. S.A.M. K231. $\times \frac{1}{3}$. *a*, lateral view. *b*, ventral view.

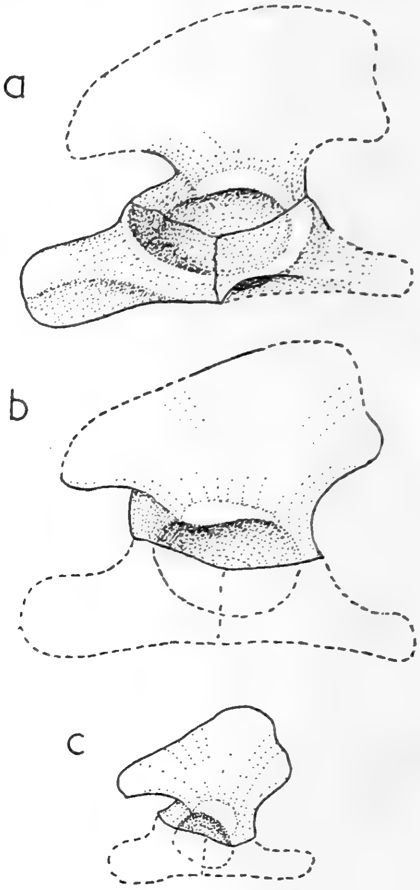

Fig. 38. Lateral views of pelves. $\times \frac{1}{3}$. *a*, *Cynariognathus* sp. S.A.M. 11794. *b*, *Pristerognathoides* ? S.A.M. 5018. *c*, *Pristerognathus*? S.A.M. K227.

The pubis is massive in its acetabular part, with a strong dorso-lateral edge, terminating in a moderate pubic tuber somewhat outwardly directed. The two pubes form a weak symphysis. A fairly large foramen pierces the bone near its posterior edge just medial to the strong acetabular rim. The ischium is longer than the pubis: its acetabular part is strongly developed and its rounded dorso-lateral edge ends in a moderate tuber. The two ischia form a strong symphysis which develops a strong medial keel.

The acetabulum is large and faces mainly outwards.

Cynariognathus (fig. 38*a*)

In 11794 there are preserved, of the right half of the pelvis, the acetabular proximal parts of the three constituent bones, whereas on the left there are a fair ischium and the proximal part of the pubis. The iliac blade is not preserved. Although of lighter build, the pelvis is essentially as in *Alopecognathus*. The pubic foramen is large.

Pristerognathoides (figs. 38*b* and 39)

In 5018 the two ilia are partly preserved and the figure incorporates features of both sides. The ilium is very similar to that of *Alopecognathus*, however its outer face, though also convex, is less so than in *Alopecognathus*.

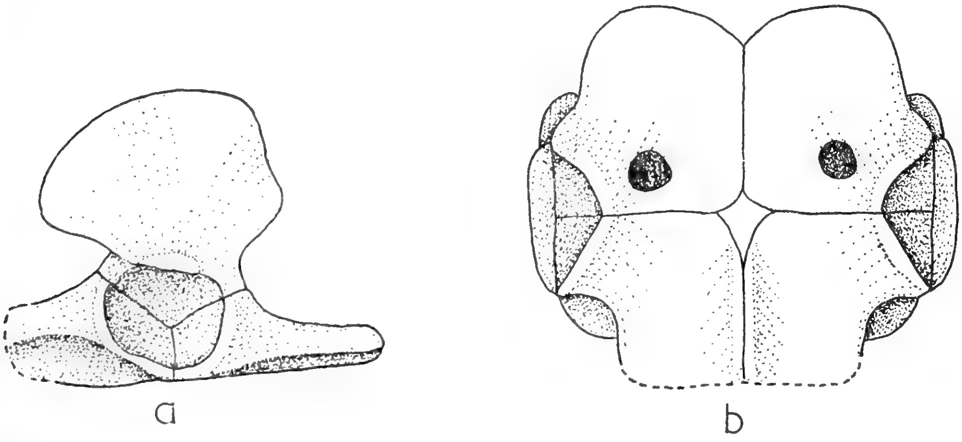

FIG. 39. Pelvis of *Pristerognathoides* sp. S.A.M. K223C. ×⅓. *a*, lateral. *b*, ventral.

In K233C the pelvis lacks only the posterior ends of the ischia. The pelvis is fairly low but quite long, the height being 75 per cent of the length as reconstructed. The blade of the ilium is both low and very short, the height being 74 per cent of the length. The outer face of the iliac blade is peculiar. It is not hollowed out as is usual in all other therapsids, but cannot be described as convex either. Dorso-anteriorly there is a pronounced bulge separating two hollows so that the surface can be described as undulating. The anterior process is short but high, with its anterior edge cut back at the level of the anteriorly hollowed-out area.

The posterior process is also short but much lower than the anterior process.

The supra-acetabular ledge is strong.

Both ischia and pubes are robust in their acetabular parts, with strong circum-acetabular borders. Anteriorly the pubis has a broad, thin anterior edge with the outer corner showing little of a pubic tuber. The pubic foramen is large but the symphysis is weak. The ischia form a fairly strong ventral keel. In its pubic part the pelvis has a flat floor, which in its ischial part becomes shallowly V-shaped.

Pristerognathus (fig. 38*c*)

In K227 there is a pair of beautifully preserved ilia. Much smaller than the ilia in the forms so far described, these ilia are nevertheless very similar. The undulating outer face is clearly shown; the anterior process is high, with its anterior edge notched; the posterior process is relatively longer and lower. The supra-acetabular height of the ilium is about two-thirds of the length of the iliac blade.

In K238A there are a partial ilium and most of a pair of ischia.

Scymnosaurus

Of this genus only the acetabular parts of an ilium and a pubis which indicate a moderately robust pelvis with an acetabulum of moderate size directed outwards are preserved (11957).

In 11558A a pair of good ischia are preserved.

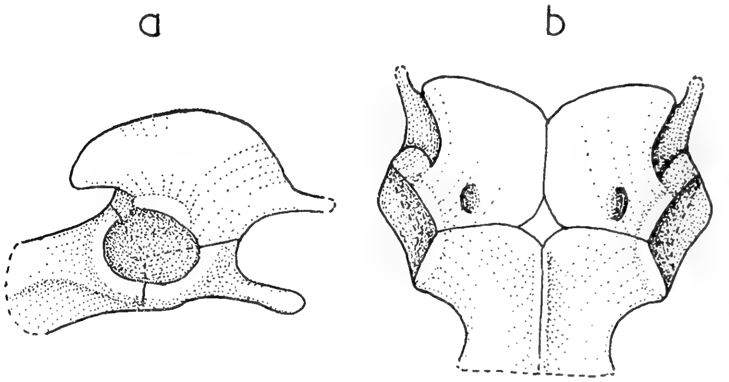

FIG. 40. Pelvis of a pristerognathid. S.A.M. K245A. ×⅓. *a*, lateral. *b*, ventral.

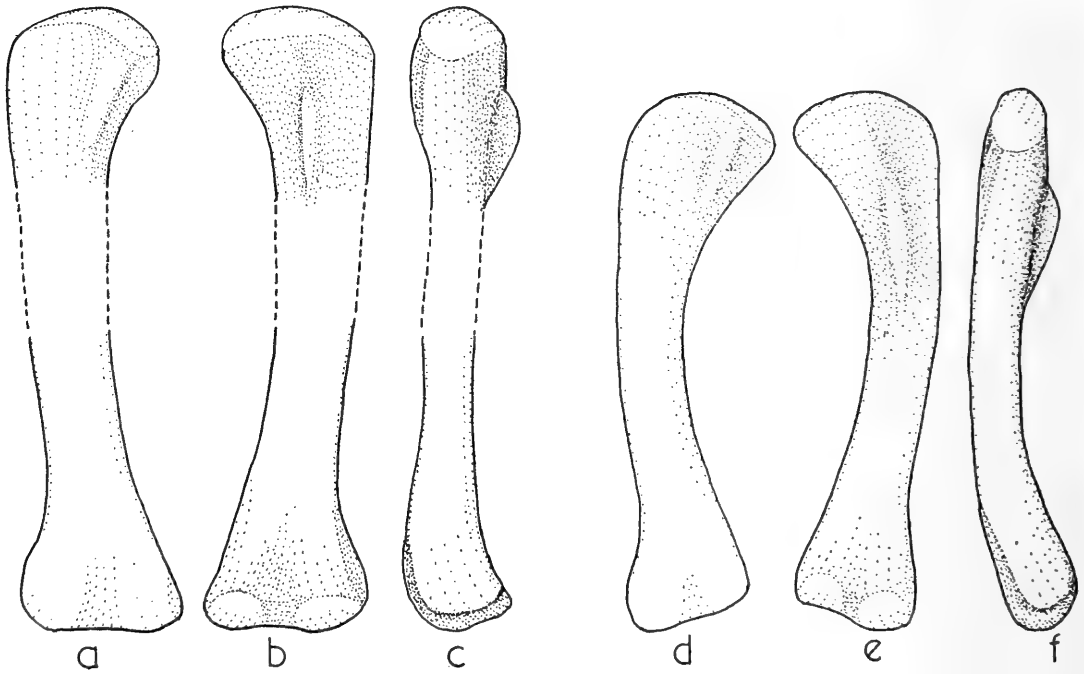

FIG. 41. Femora. ×⅓. *Alopecognathus* sp. S.A.M. 12051. *a*, dorsal. *b*, ventral. *c*, anterior. *Cynariognathus* sp. S.A.M. 11794. *d*, dorsal. *e*, ventral. *f*, anterior.

An unidentified pristerognathid (fig. 40)

In K245A there is a good pelvis, basically as in the above described forms, but the ilium is rather peculiar, with a long, low process directed anteriorly.

E. FEMUR

Alopecognathus (fig. 41*a*, *b* and *c*)

In 12051 a proximal and two distal femoral ends are preserved. The ends are moderately expanded, shaft fairly strong, somewhat dorso-ventrally flattened, and fairly straight.

The well-rounded caput, although terminal, is directed somewhat pre-axially. The external trochanter is not prominent and is situated well proximally. The pubo-ischio femoralis internus ridge is well developed, not near the anterior border. The internal trochanter forms a sharp ridge. The inter-trochanteric fossa is small and shallow.

In K231 both femora are present and, although badly preserved, are essentially similar to that figured here.

Cynariognathus (fig. 41*d*, *e* and *f*)

In 11794 both femora are preserved, but are both somewhat weathered and distorted. The curvatures in the figures on the long axis are thus artificial. The ridge forming the internal trochanter is long and not so far proximally situated.

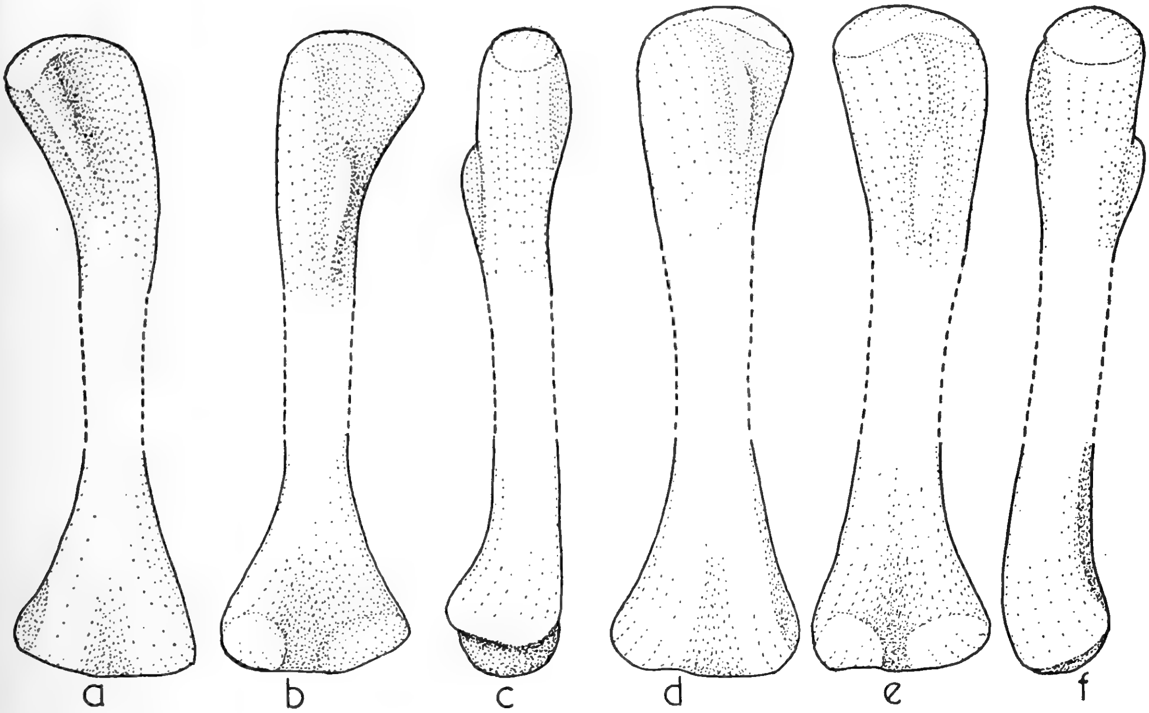

FIG. 42. Femora. × $\frac{1}{3}$. *Pristerognathoides* sp. S.A.M. 5018. *a*, dorsal. *b*, ventral. *c*, anterior. S.A.M. 11936. *d*, dorsal. *e*, ventral. *f*, anterior.

Pristerognathoides (figs. 42 and 43)

The femur in this genus is represented by the distal and proximal ends of both femora in 5018 and K306 and one femur in 11936.

In 5018 the internal trochanter forms a long ridge extending on to the shaft, but it does not extend far proximally, so that the intertrochanteric fossa is long. The pubo-ischio femoralis internus ridge is low. The distal end is well expanded. In 11936 the femur is more robust.

In K306 the right femur is a larger, heavier bone than the left and is certainly not of the same individual and may be of a different species. The distal ends are only moderately expanded.

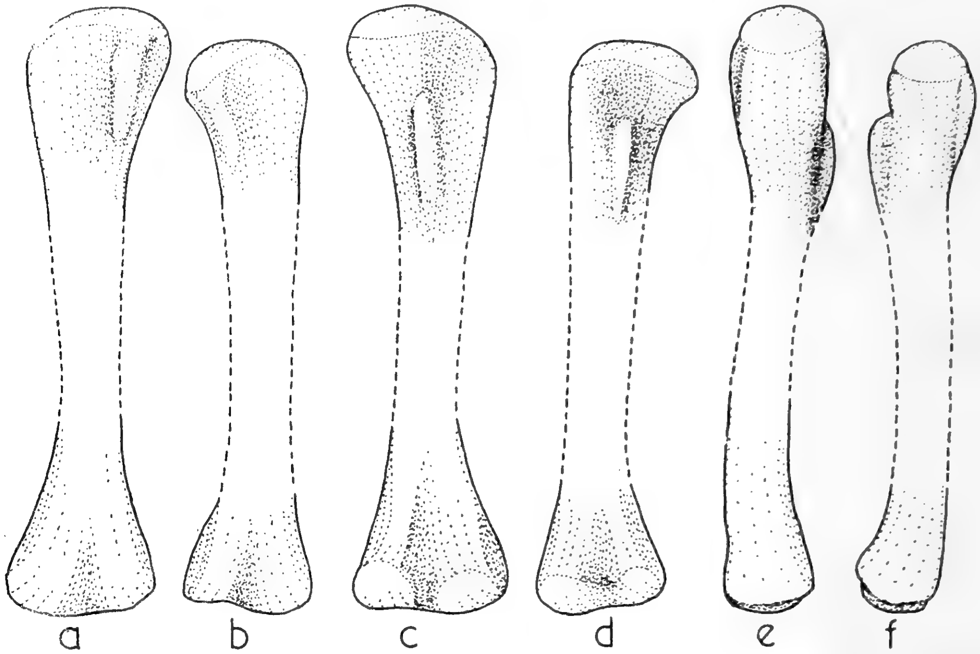

FIG. 43. Femora. × $\frac{1}{3}$. *Pristerognathoides* sp. S.A.M. K306. Right: *a*, dorsal. *c*, ventral. *e*, anterior. Left: *b*, dorsal. *d*, ventral. *f*, anterior.

Pristerognathus

In this genus the femur is represented by poor ends. In K317 the internal trochanter forms a short, thickened ridge proximal to which lies a long, deep inter-trochanteric fossa.

Scymnosaurus (figs. 44, 45, 46*a*, *b* and *c*, 47)

In this genus the femur is fairly well represented. In 11557 there is a good, well-preserved femur, in 11597 a proximal end, in 12118 a proximal end, in 12193 a distal and proximal end, and in 12262 and K352 a poorly preserved but nearly complete femur.

In the three complete femora there is a greater amount of twist or rotation of the two ends on the shaft relative to each other than in the femur of all the other pristerognathids as hitherto described. This twist or rotation is an anticlockwise or postaxial movement of the proximal expansion in relation to the distal end. The result is that the caput, though terminal, is directed somewhat dorsally, whereas in the hitherto described forms this direction runs somewhat anteriorly.

Another difference is that the pubo-ischio femoralis internus ridge in *Scymnosaurus* lies on the morphological anterior edge of the bone and not somewhat away from this edge onto the dorsal surface. The straight, long axis of 11557 is normal whereas the downward curvature of the proximal end in both 12262 and K352 would appear to be due to post-mortem distortion. The internal and external trochanters are as in the already described Pristerognathids.

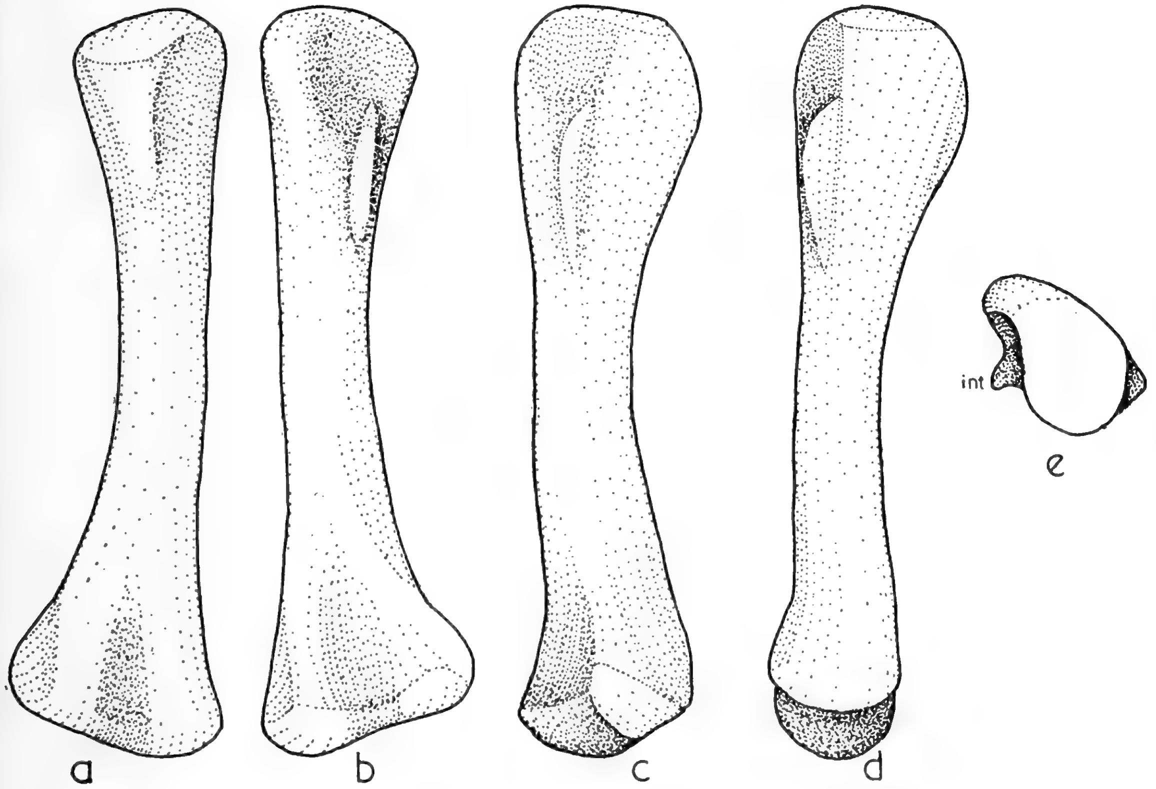

FIG. 44. Left femur of *Scymnosaurus* sp. S.A.M. 11557. ×⅓. *a*, dorsal. *b*, ventral (projection onto plane of distal condyles). *c*, ventral (projection onto the plane of the ventral face of the proximal end). *d*, anterior. *e*, proximal.

K353 consists of an isolated, well-preserved proximal end of a large femur which may be that of *Scymnosaurus major*. Although it has an internal trochanter and pubo-ischio femoralis internus ridge as in the other pristerognathid femora, both these structures are feebly developed and appear to be out of proportion to the size of the bone.

Zinnosaurus (fig. 46*d* and *e*)

In 12185 a proximal and distal femoral end is preserved. The caput is well rounded and somewhat anteriorly directed. The internal trochanter forms a robust ridge. The external trochanter is weak and the inter-trochanteric fossa short but deep.

The pubo-ischio femoralis internus ridge is very weak; it forms the anterior border of the bone and runs into the anterior edge of the caput.

F. THE LOWER HIND LIMB AND PES

Alopecognathus (figs. 48 and 49*a*)

In 12051 the left epipodial and pes are completely preserved and in K231 both epipodials and an incomplete pes.

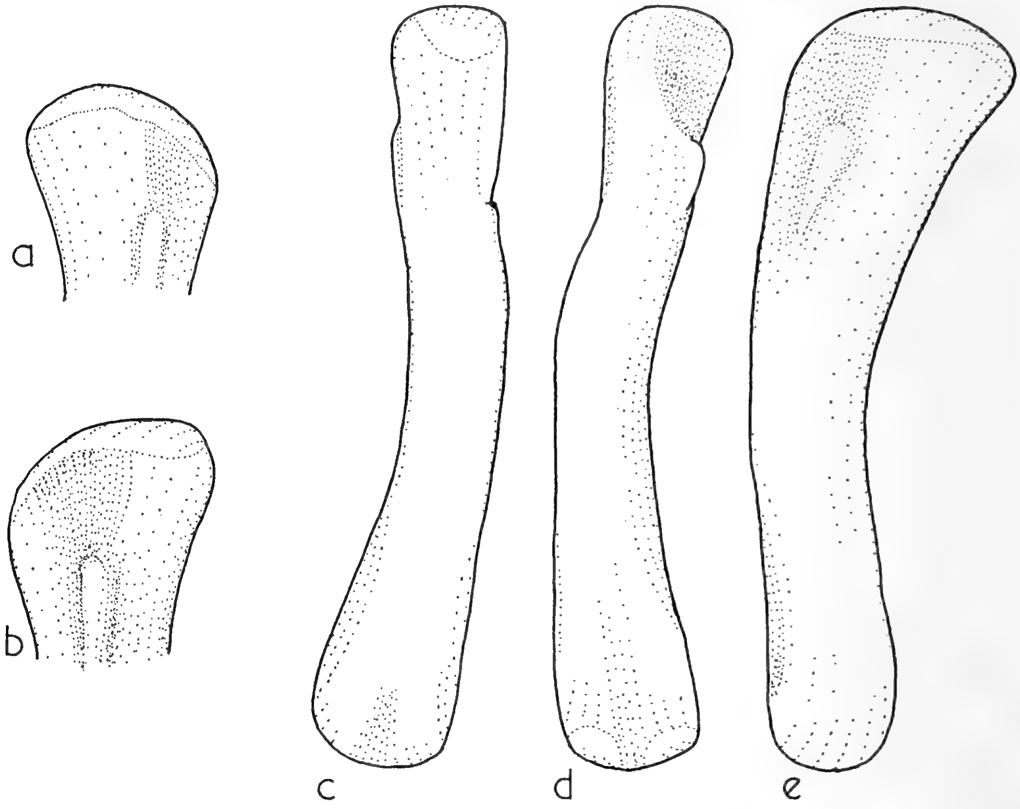

Fig. 45. Femora. × $\frac{1}{3}$. *Scymnosaurus* sp. S.A.M. 11957. *a*, ventral. *Scymnosaurus* sp. S.A.M. 12118. *b*, ventral. *Scymnosaurus major*. S.A.M. 12262. *c*, dorsal. *d*, ventral. *e*, anterior.

The tibia is stout proximally with a well-developed facet for the femur. The fibula is much slenderer and curved to give a wide spatium interosseum. The proximal facet of the fibula is terminal and not applied to the outer corner of the femoral condyle but end-on.

The astragalus is a robust, rounded bone with a convex facet for the tibia.

The calcaneum is a large but lightly-built flat bone thickened proximally at the facet for the fibula. Preaxially it is notched for the passage of the intertarsal vessels.

The central is quite small.

There are five distals. The first is large and articulates with both first and second metatarsals. The fourth is the largest whereas numbers 2, 3 and 5 are small.

The metatarsals increase in length from number 1 to 5.

The digital formula is 2, 3, 3, 3, 3, with the fourth the longest, but due to the short phalanges all the digits are short. The ungual phalanges are curved and carried sharp claws.

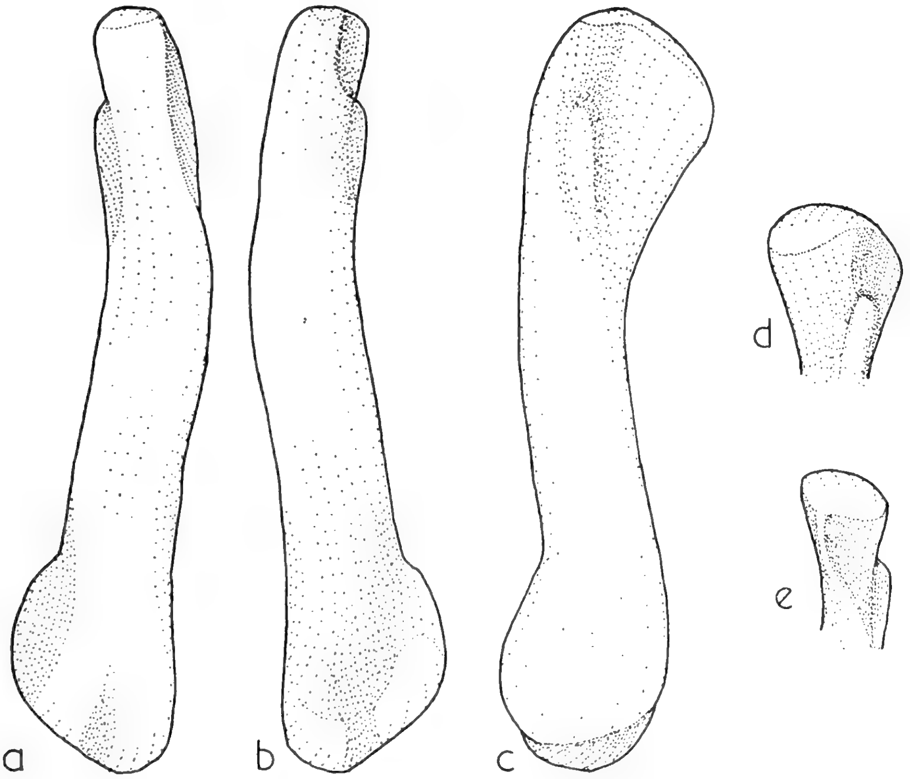

FIG. 46. Femora. ×⅓. *Scymnosaurus major* ? S.A.M. K352. *a*, dorsal. *b*, ventral. *c*, anterior. *Zinnosaurus paucidens* gen. et spec. nov. S.A.M. 12185. *d*, ventral surface of proximal end. *e*, anterior face of proximal end.

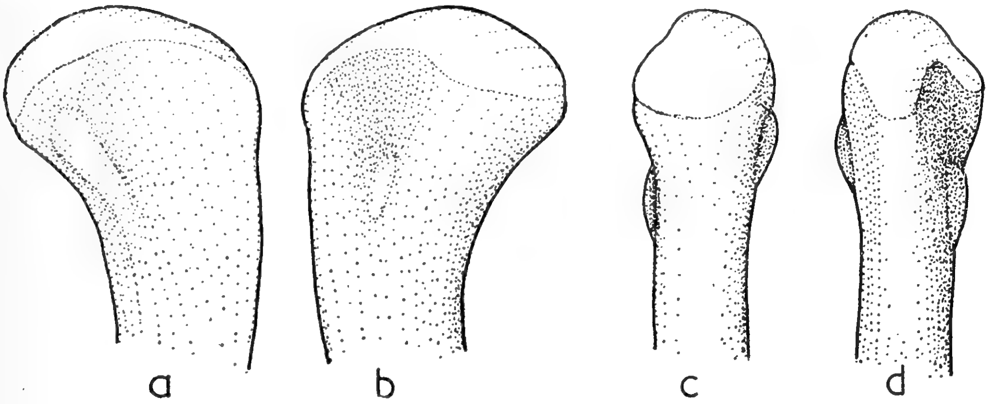

FIG. 47. *Scymnosaurus major* ? S.A.M. K353. ×⅓. Proximal end of femur. *a*, dorsal. *b*, ventral. *c*, anterior. *d*, posterior.

Cynariognathus (fig. 49*b*)

In 11794 a somewhat crushed tibia and fibula are preserved, with features as shown in the figure. Distal to the tibia lies a bony element of quite intricate shape, not at all like the astragalus preserved in *Alopecognathus* and probably is not this bone at all.

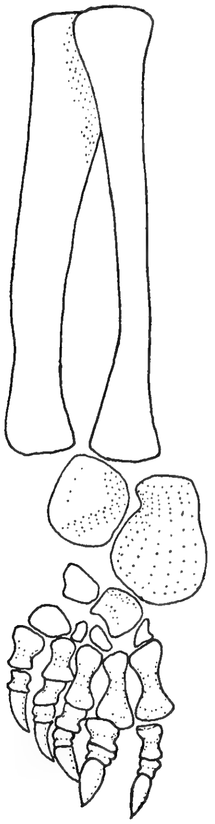

FIG. 48. Epipodial and pes of *Alopecognathus*. S.A.M. 12051. $\times \frac{1}{3}$.

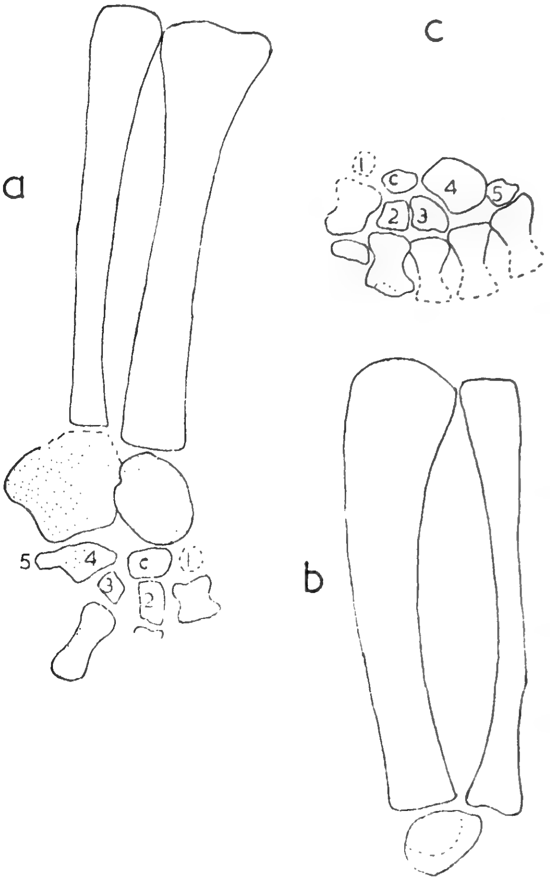

FIG. 49. Epipodials and pes. $\times \frac{1}{3}$. *a*, *Alopecognathus angusticeps*. S.A.M. K231. *b*, *Cynariognathus* sp. S.A.M. 11794. *c*, *Scymnosaurus* sp. S.A.M. 11459.

FIG. 50. Pes of a pristerognathid. S.A.M. 245A. $\times \frac{1}{3}$.

Scymnosaurus (fig. 49*c*)

In 11459 part of a pes is preserved. I have identified a small central. Distals 2 and 3 are small, 4 is much larger, and 5 is still a small, separate element. Parts of all five metatarsals are present. Number 1 digit has a very short first phalanx.

DISCUSSION

It would be of interest to compare the girdles and limbs of the pristerognathid Therocephalia with those of the other therapsids of the *Tapinocephalus* zone. Unfortunately these structures in the contemporary therapsids are inadequately known. Only in the Dinocephalia have they been adequately described, and in the Dromasauria two specimens have these structures preserved. Of the Gorgonopsia, they have been described in one genus. Of the Dicynodontia nothing has as yet been published. Of the other therocephalian families represented in this zone, a shoulder girdle of a lycosuchid has been figured, of the Akidnognathidae a manus, and of the Scaloposauridae a brief account has been given of parts of a hind limb.

I have in recent years collected some gorgonopsians and dicynodonts from the *Tapinocephalus* zone in which parts of the girdles and limbs are preserved.

As soon as these specimens have been prepared a comparative discussion will be presented.

SUMMARY

Descriptions are given of the girdles and limbs of the pristerognathid Therocephalia from the *Tapinocephalus* zone of the Karoo. The descriptions are based on 37 specimens in the South African Museum which have parts of the girdles and limbs preserved. Taken together this material gives a good idea of the family character of these structures. A new genus and species of pristerognathid therocephalian, *Zinnosaurus paucidens*, is described.

ACKNOWLEDGEMENTS

The specimens collected in recent years were obtained on Museum collecting trips, which were in part financed by the C.S.I.R. For these grants we are grateful.

Some of the later specimens have been prepared for study by Mr. C. Gow, to whom our thanks are due.

The Trustees of the South African Museum are grateful to the C.S.I.R. for a grant to publish this paper.

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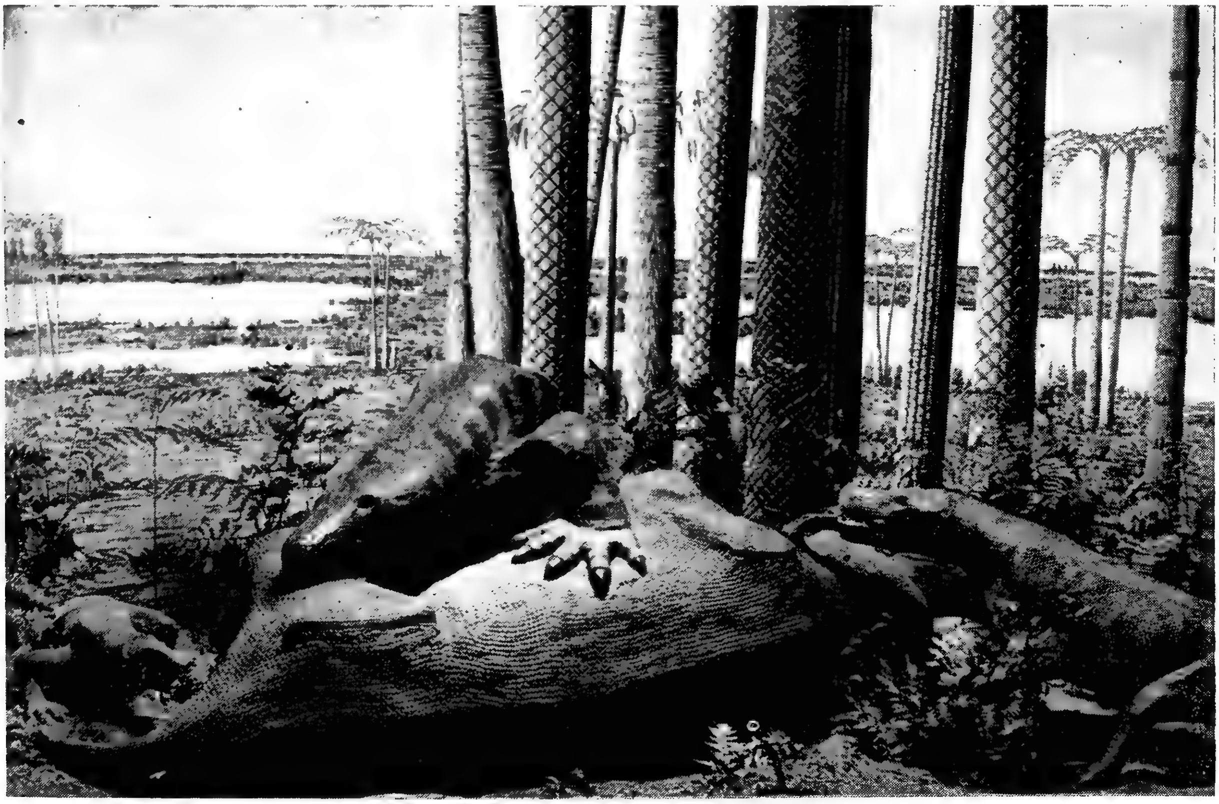
SEELEY, H. G. 1888. Researches on the structure, organization and classification of the fossil Reptilia. III. On parts of the skeleton of a mammal from Triassic rocks of Klipfontein, Fraserberg, South Africa (*Theriodesmus phylarchus*, Seeley), illustrating the reptilian inheritance in the mammalian hand. *Phil. Trans. R. S.* (B) **179**: 141–155.

A. Photograph of a habitat group with life-sized models modelled by the author and exhibited in a diorama in the South African Museum. *Scymnosaurus* feeding on *Brachypareia.*



B. Photograph of life-sized models made by the author and exhibited as a habitat group in the South African Museum. The Therocephalians (l. to r.) *Pristerognathoides, Therioides* and *Alopecognathus* feeding on a cadaver of *Moschops*.

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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).

M.-L. WAPENAAR & F. H. TALBOT

NOTE ON THE RIGIDITY OF THE PECTORAL FIN OF *MAKAIRA INDICA* (CUVIER)

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NOTE ON THE RIGIDITY OF THE PECTORAL FIN OF *MAKAIRA INDICA* (CUVIER)*

By

Mary-Louise Wapenaar & Frank Hamilton Talbot

South African Museum

(With 1 plate and 7 figures in the text)

Abstract

It has been known for a long time that the pectoral fin of the black marlin, *Makaira indica*, cannot be folded flat against the side of the body as it can in all other istiophorid fishes. The anatomy of the pectoral girdle of the black marlin is here compared with that of the striped marlin, *M. audax*, to determine the mechanism of the rigid joint. The osteology and musculature of the pectoral girdle of both species is described and discussed, with particular reference to the articular region. It is concluded that the bony structure of the joint and the strength and disposition of its fibrous connective tissue sheath together ensure the rigidity of the pectoral fin in *M. indica*. It is suggested that the rigid pectoral fin of *M. indica* is used as a plane of elevation.

I. Introduction

Ever since Nakamura (1938) and, more particularly, Gregory & Conrad (1939) showed that the black marlin *Makaira indica* (Cuvier) has a rigid pectoral fin which cannot be folded flat against the body, while all other istiophorids have a folding pectoral fin, the reason for such a difference, and the structural features that prevent the fin from folding in the black marlin, have been a source of speculation among ichthyologists.

The pectoral fin of marlins is in the main an inflexible, sickle-shaped structure with a narrow leading edge formed by the sharp edge of the strong marginal ray, and a small movable posterior lobe formed by the last ten rays or actinosts. In all marlins it is set at an angle of about 35° to the horizontal, so that when extended at right angles to the body it acts as a plane of elevation by presenting a horizontal or oblique surface to the direction of flow of the water rather than a vertical surface as in many teleosts. In all istiophorids other than *M. indica* the fin can be rotated from the extended position to lie flat against the side of the body, but in *M. indica* the fin is permanently extended and cannot be folded against the body without structural damage, for which considerable force must be used.

An anatomical study was undertaken in which the pectoral girdle of *M. indica* was compared with that of the striped marlin, *M. audax* (Philippi), to

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* This paper formed part of the Oceanography Symposium held during the 61st Annual Congress of the South African Association for the Advancement of Science at Durban, July 1963. The association has kindly given permission for publication here.

Ann. S. Afr. Mus. **48** (6), 1964, 167–180, pl. II., 7 figs.

determine the reason for the rigidity of the pectoral fin in *M. indica.* The articular regions of the pectoral girdles of *M. albida* (Poey) and *M. nigricans* (Lacépède) were also examined.

Nakamura (1938), Gregory & Conrad (1939), LaMonte & Marcy (1941), LaMonte (1955), J. L. B. Smith (1956), Robins (1957), Robins & de Sylva (1961), and Talbot & Penrith (1962) and others have referred to the rigidity of the pectoral fin of *M. indica,* but only one attempt to investigate this feature on an anatomical basis has been made (Morrow, 1957).

Morrow states that the rigidity of the fin in *M. indica* is due to three bony pads associated with the articular surface of the marginal ray of the fin, giving it a rigid three-point suspension and thus preventing it from being rotated and folded back as occurs in the other species. In our opinion this explanation is untenable, for reasons which are given below.

II. MATERIAL

Makaira indica (Cuvier)

(*a*) Two loose girdles, fresh, of a 600 lb. fish, length 2,935 mm., taken aboard the fishing vessel *Karimona* by longline west of Slangkop, Cape Peninsula, 30/1/1962. S.A.M. Reg. No. 23194.

(*b*) Anterior half, fresh, of an 800 lb. fish, length 3,210 mm., taken aboard the fishing vessel *Walvis Pioneer* by longline 40 miles west of Cape Point, 28/1/1962. S.A.M. Reg. No. 23193.

(*c*) Anterior half, fresh, of a 462 lb. fish, length 2,540 mm., taken on rod and line 25 miles west-north-west of Cape Point, 25/2/1962. S.A.M. Reg. No. 23244.

(*d*) Prepared girdle of a 1,028 lb. fish taken by longline south-west of Hout Bay, March 1961. S.A.M. Reg. No. 23054.

Makaira audax (Philippi)

(*a*) Anterior half, fresh, of a 130 lb. fish, length 2,120 mm., taken aboard the fishing vessel *Overberg* by longline west of Cape Point, 2/2/1962. S.A.M. Reg. No. 23197.

(*b*) Prepared girdle of small specimen taken west of Hout Bay by longline, March 1961. S.A.M. Reg. No. 23052.

Makaira nigricans (Lacépède)

(*a*) Prepared girdle of large specimen taken aboard the fishing vessel *Cape Point* by longline 45 miles north-west of Dassen Island, 29/6/1961. S.A.M. Reg. No. 23104.

Makaira albida (Poey)

(*a*) Prepared girdle of specimen taken by longline south-west of Hout Bay, March 1961. S.A.M. Reg. No. 23053.

III. Osteology of the pectoral girdle of *M. audax* and *M. indica*

The pectoral girdle of marlins (figs. 1, 2) is suspended from the skull by a three-pronged post-temporal and a long, flat supra-cleithrum, and is typical in consisting of a complex of three bones. There is an anterior cleithrum which has medial and lateral flanges or arms, a rod-like ventral process which meets that of the opposite side in the mid-ventral line, and two dorsal processes, an anterior, rod-like one and a posterior expanded process. The posterior bone of the complex is the coracoid, which is roughly triangular. From its antero-dorsal corner a ridge runs ventro-caudally. Above the ridge is the dorsal process of the coracoid; the ventral process of the coracoid meets the cleithrum just above the ventral process of that bone. Dorso-medially between the cleithrum and the coracoid lies the scapula, a fairly small semicircular bone perforated by the scapular foramen, through which the nerves supplying the abductor musculature of the fin pass. The scapula bears the articular surfaces for the pectoral fin.

No bony pads such as those described by Morrow (1957) were found in any of the South African specimens of *M. indica*. If they are not present in all specimens it seems unlikely that those found by Morrow are of any significance in the mechanism of the rigid joint.

The pectoral complex is very similar in *M. indica* and *M. audax*, with a major difference in the articulation of the fin (described below in section V),

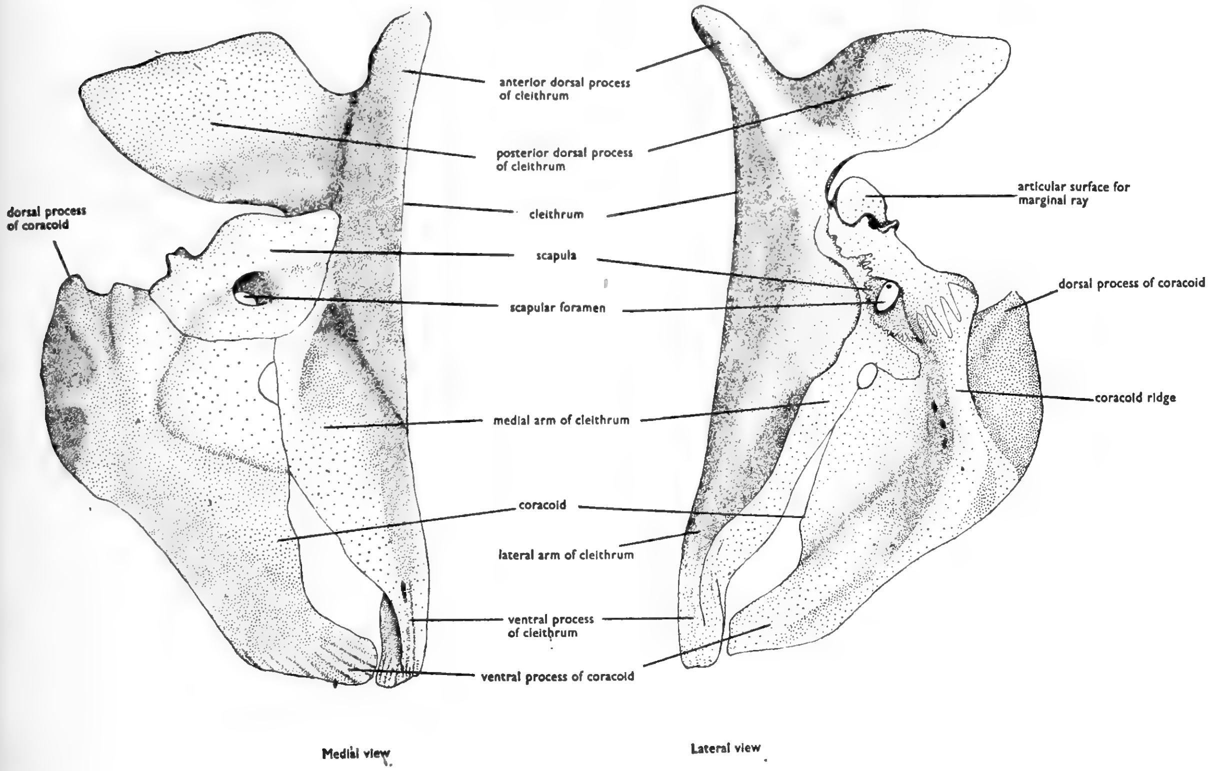


Fig. 1. Pectoral girdle of *Makaira indica*.

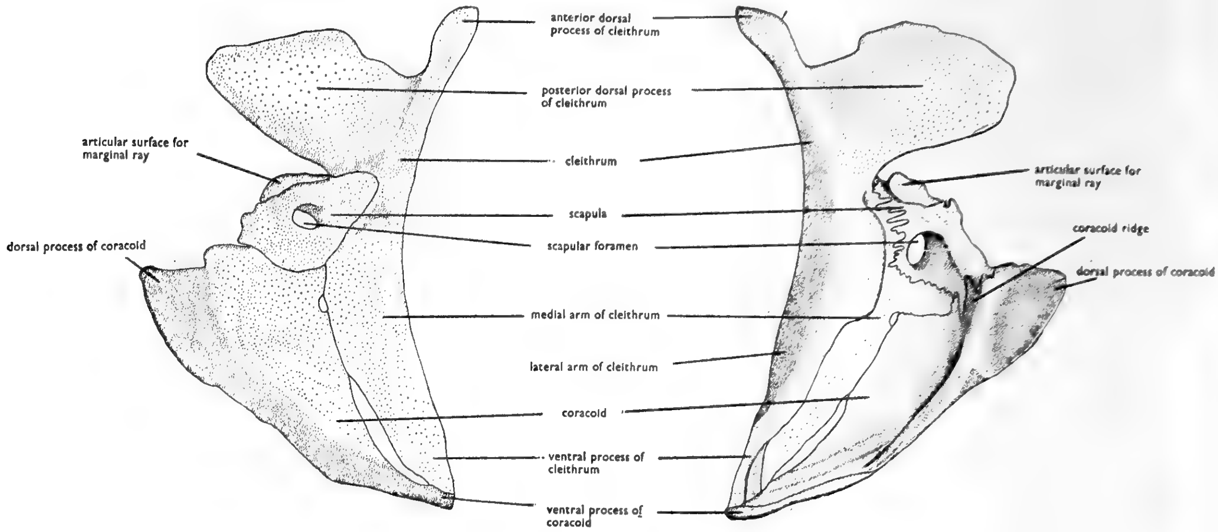


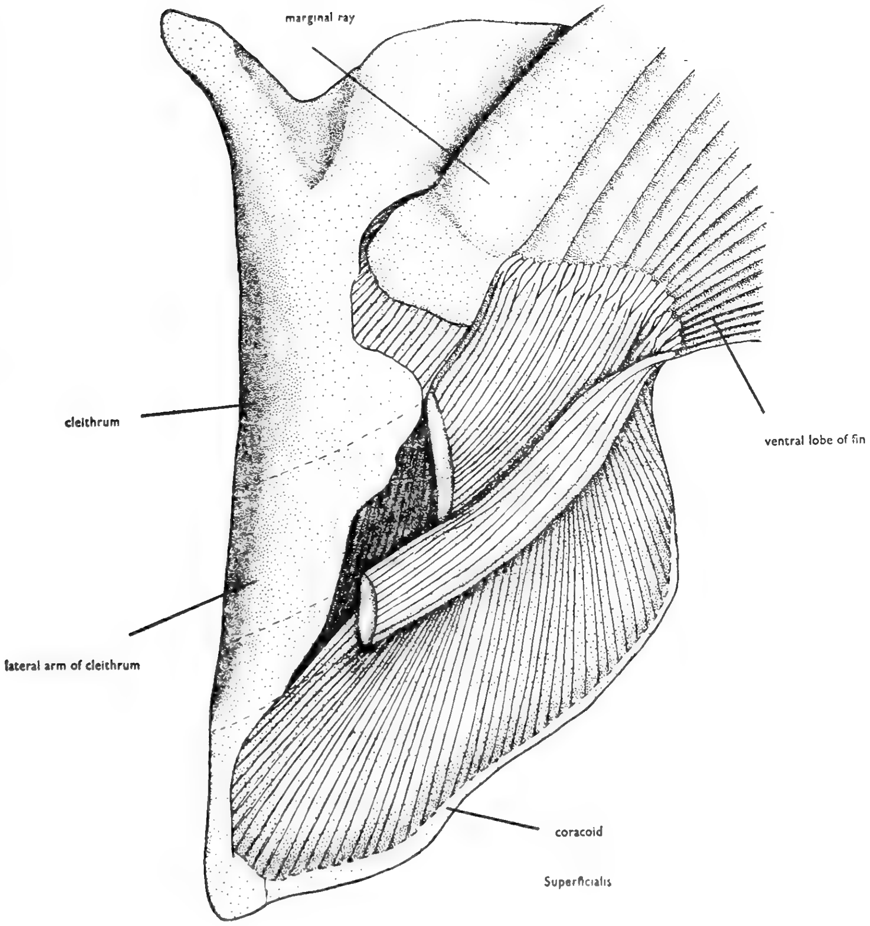
FIG. 2. Pectoral girdle of *Makaira audax*.

and other minor differences. In *M. audax* the anterior edge of the cleithrum is concave, while in *M. indica* this edge is almost straight, with the ventral process of the cleithrum somewhat backwardly directed. The coracoid ridge is shorter and heavier in *M. indica* than in *M. audax*, and the dorsal process of the coracoid is pointed in the former and rounded in the latter. The scapular foramen is relatively larger in *M. audax* than in *M. indica*.

IV. MUSCULATURE OF THE PECTORAL GIRDLE OF *M. indica* AND *M. audax* (figs. 3, 4, 5)

The musculature of the pectoral girdle of *M. indica* and *M. audax* was investigated. The body muscles and the muscles between the pectoral girdle and the head and visceral skeleton were found to be identical in *M. indica* and *M. audax* and will not be included here.

The musculature of the pectoral girdle consists as in all fishes of adductor and abductor portions (Shann, 1919), which draw the fin towards and away from the body respectively. Both portions are more or less divided into superficial and deep parts, although these are often not easily separable. The abductor musculature arises from the lateral surface of the scapula and the coracoid, and the lateral surface of the medial flange of the cleithrum, and inserts on the marginal ray and the bases of the remaining rays of the fin. For most of their length from their fleshy origin the superficial and deep fibres are not clearly separable, but towards their insertion they become more distinct and have a separate tendinous insertion on the bases of the rays, the deep fibres inserting on the ventral extremities of the bases of the rays while the superficial fibres insert on a slight ridge a short distance above the bases of the rays. The last ten rays are movable in relation to the rest of the fin and have a fairly specialized musculature, some of which inserts on the radials supporting them (described below, section V). The adductor musculature arises from the medial surface



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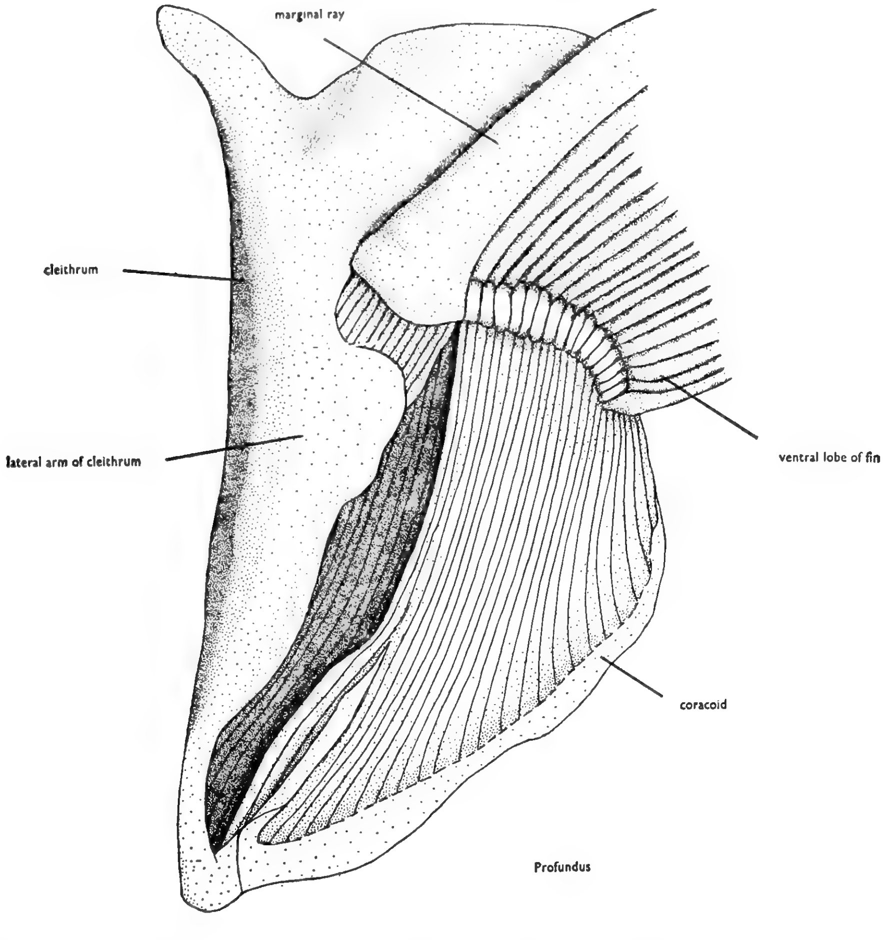
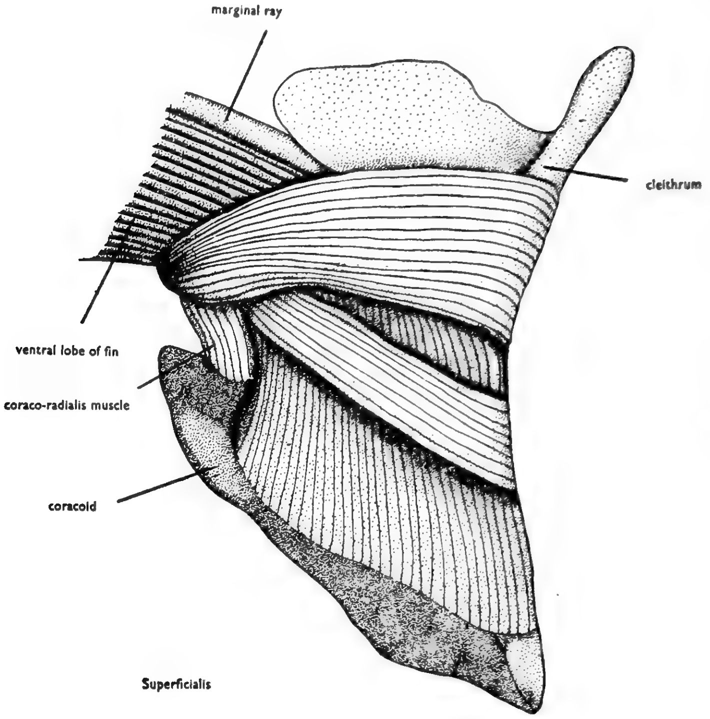


Profundus

FIG. 3. Abductor musculature of *Makaira indica*.

of the cleithrum, scapula, and coracoid, and also has a tendinous insertion on the bases of the rays on the medial side of the fin. As in the case of the abductor musculature, the adductors of the last ten rays are separate and very well developed. An additional adductor, present in many fishes, the coracoradialis



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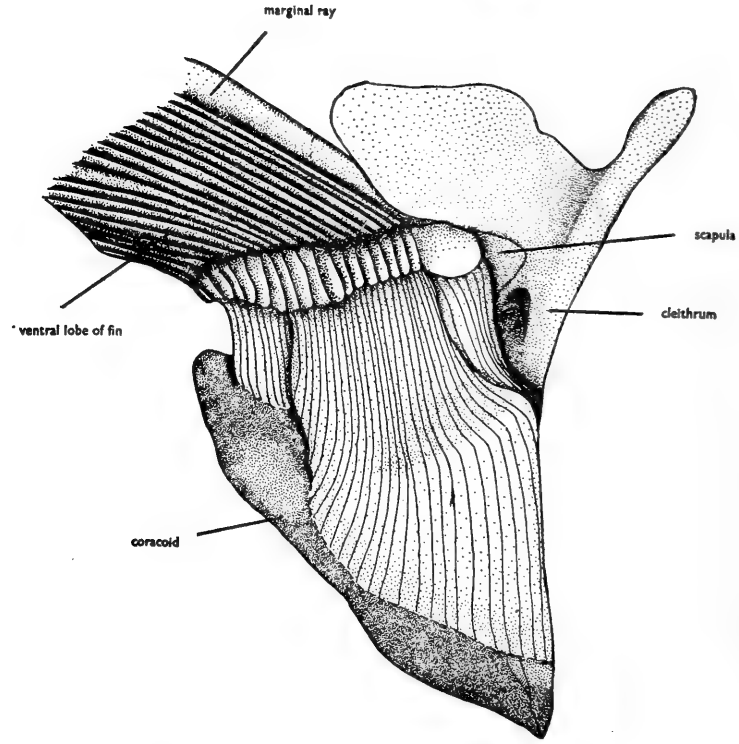

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Fig. 4. Adductor musculature of *Makaira audax*.

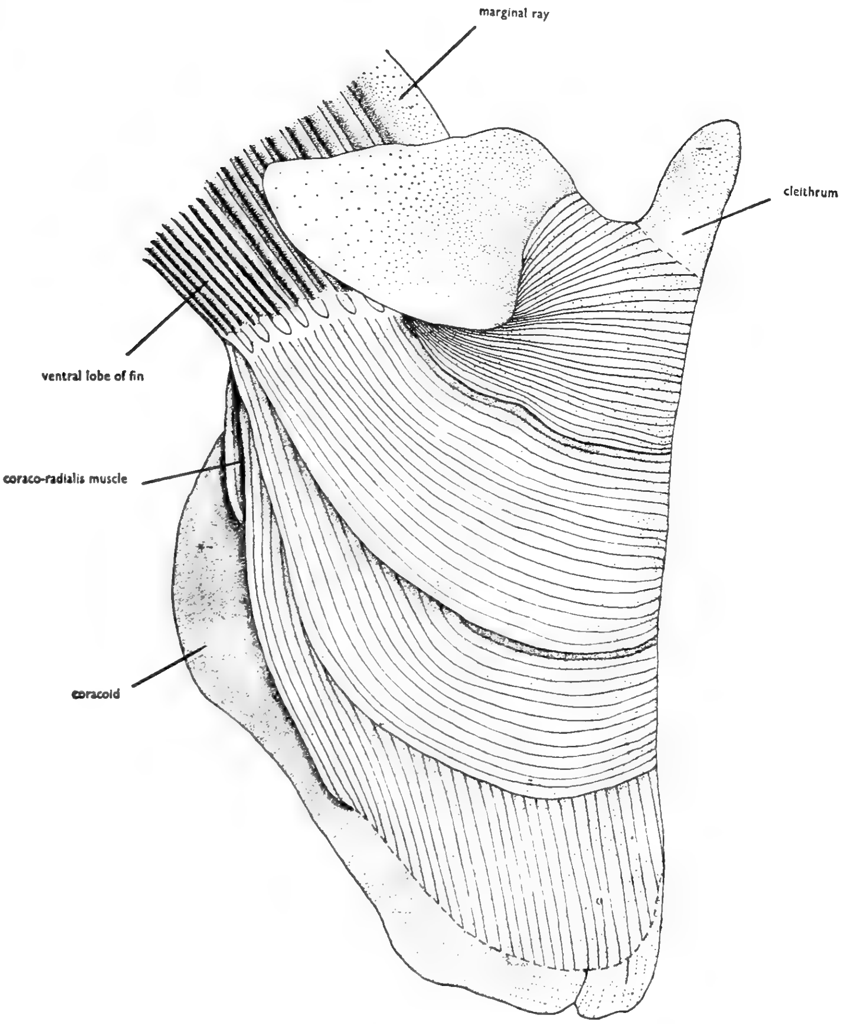

FIG. 5. Adductor superficialis musculature of *Makaira indica*.

muscle, arises from the medial surface of the coracoid and inserts on the last two radials.

In general the abductor and adductor portions are very similar in *M. indica* and *M. audax* (figs. 3, 4, 5). In *M. indica* the superficial and the deep abductor of the marginal ray form a bundle clearly separated from the abductors of the remaining fin rays, while in *M. audax* the abductors for the marginal ray are not distinct. In both species the last ten rays form a distinct lobe with a separate and well-defined musculature; the abductor portions of the musculature of this lobe are identical in the two species.

There are certain differences in the adductor musculature of the two species (figs. 4, 5); again in *M. indica* the adductors of the marginal ray are clearly defined and in addition have a slightly different origin, arising from the posterior dorsal process of the cleithrum rather than from the medial arm of the cleithrum. In general the adductor muscles in *M. audax* are arranged so that the fibres are relatively longer than in *M. indica*. The greatest difference is in the adductor musculature of the ventral lobe, with which the present discussion is not concerned as it has no bearing on the mechanism of the rigid joint. This lobe clearly has important hydrodynamic effects on the fin, however, and one would expect its mode of action to differ in two species in which the action of the fin as a whole differs strongly.

The adductor and abductor muscles then are responsible for the movements of the pectoral fin. By contraction of the abductors other than those of the ventral lobe the antero-ventral tip of the fin-base is pulled forward and downward. In *M. audax* (pl. II) this movement causes the fin to be pulled away from the body into the extended position. This actually involves two movements, the drawing downwards of the antero-ventral tip of the fin base and the drawing forwards of the fin as a whole so that the direction of the fin tip is at right angles to the direction of the body, but both movements occur simultaneously in *M. audax*. In the extended position in *M. audax* either movement can be carried out; by twisting, the plane of the fin to the water can be altered by about 10°, and the leading edge can move through any arc between the fully extended position and the folded position.

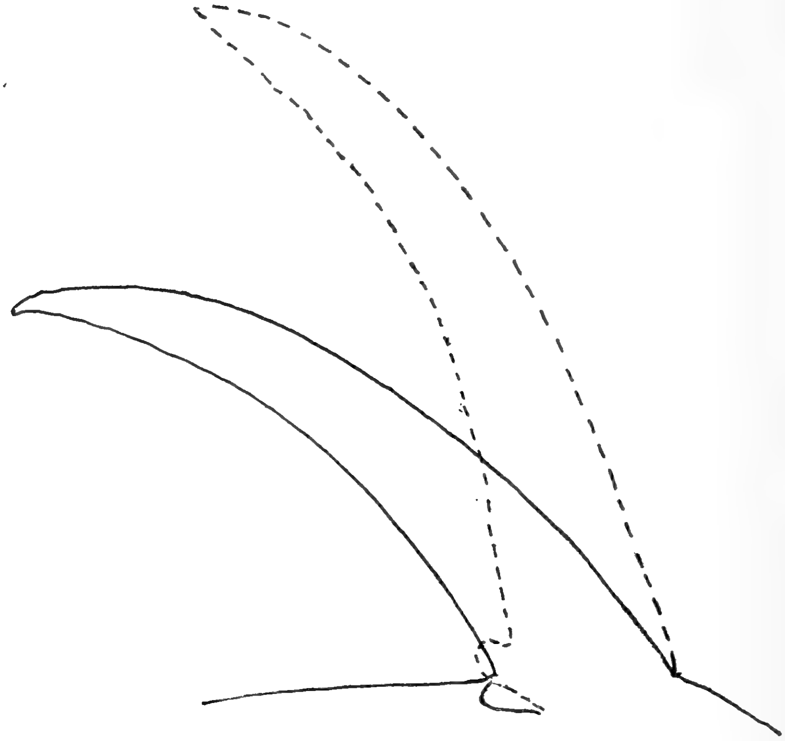

Fig. 6. Range of movement of fin in *Makaira indica*.

In *M. indica* (fig. 6), where the fin is permanently extended, two limited movements are possible, and are also brought about by the abductor and adductor muscles. The angle of incidence of the fin plane to the water can be altered within an arc of about 4°, brought about by the pulling down by the abductors of the antero-ventral tip of the marginal ray base; the fin is also capable of an antero-posterior movement in a horizontal plane through an angle of 12°. It can thus be seen that the range of movement is far more limited in *M. indica* than in *M. audax*.

It would be anatomically unusual if the rigidity of the fin were dependent on the musculature. This would imply continual sustained muscle activity to hold the fin rigid during forward movement of the fish; that is, during most of its life. The total extension of a muscle group is never limited by its own action alone (Professor L. H. Wells, personal communication). The maximum extension is normally limited by the structure (ligament, cartilage and bone) of the joint itself. If they were not limited in this way, the structure of muscle fibres is such that on relaxation they could expand until damaged. If muscles held the fin rigid in the black marlin it would also follow that in a freshly dead specimen the fin should be able to move back against the body, even if the muscle fibres were damaged in so doing. This is not the case. As would be expected, therefore, the structure of the joint itself and not the muscles is the limiting factor to further backward movement. In any joint the arrangement of the muscles will depend on the amount of movement allowed by the arrangement of the bones and ligaments of the joint. Thus in *M. audax*, where the range of possible movement of the fin is more extensive, the muscle fibres are longer than in *M. indica*.

The fin musculature of *M. indica* is very well developed in spite of the small range of movement of the fin. It is suggested that while the fin of *M. audax* encounters little water resistance in the initial stages of its extension, water pressures render considerable muscular effort necessary for moving the fin when it is extended. It is these latter movements with which the muscles of *M. indica* are concerned, so that they must be well developed, as well developed as in *M. audax*, in fact. Short fibres are adequate for these short-range movements, however.

The main point arising from the study of the pectoral musculature is that, if the abductors of *M. audax* are contracted, the pectoral fin can be maintained in the same position as that of *M. indica*, but in *M. indica* the fin is maintained in this position even when the abductor muscles are relaxed and the adductors contracted. The muscles do not assist in rendering the joint rigid; as would be expected, *M. indica* has developed some method of maintaining the rigid position of the fin other than by sustained muscular contraction.

V. Articulation of the pectoral fin (fig. 7)

The most significant difference in the pectoral complex lies in the arrangement and shape of the articular surfaces for the pectoral fin. In *M. audax*, *M. nigricans*, and *M. albida* the articular surface for the base of the marginal ray lies on the dorsal edge of the scapula; its surface is markedly convex and curves smoothly from the lateral to the medial surface of the bone; in other words it is saddle-shaped. The base of the marginal ray in these species is concave to correspond with its articular surface on the girdle. In *M. indica* the articular surface for the marginal ray, although close to the dorsal edge of the scapula, lies entirely on the lateral surface and is flat, so that a limited amount of sliding but no rolling movement is possible. The base of the marginal ray in this species is correspondingly flat. The dorsal edge of the scapula above the articular surface (which surface is occupied by the inner half of the saddle-shaped articular surface in *M. audax*) is here extremely rugose and pitted for the attachment of connective tissue.

In all four species there is at the posterior end of the articular surface for the marginal ray a shallow trough, which receives a downward process of the articular surface of the marginal ray base. This trough lies mainly on the dorsal edge of the scapula.

Posterior to the articular surface for the marginal ray are the articular surfaces for the radials (fig. 7). The radials are very similar in all four species. They are four in number, the first two being short and cubical, and the posterior two rather long and slender and forming the base of the posterior lobe of the fin. Their articulation lies mainly on the dorsal edge of the scapula; that of the

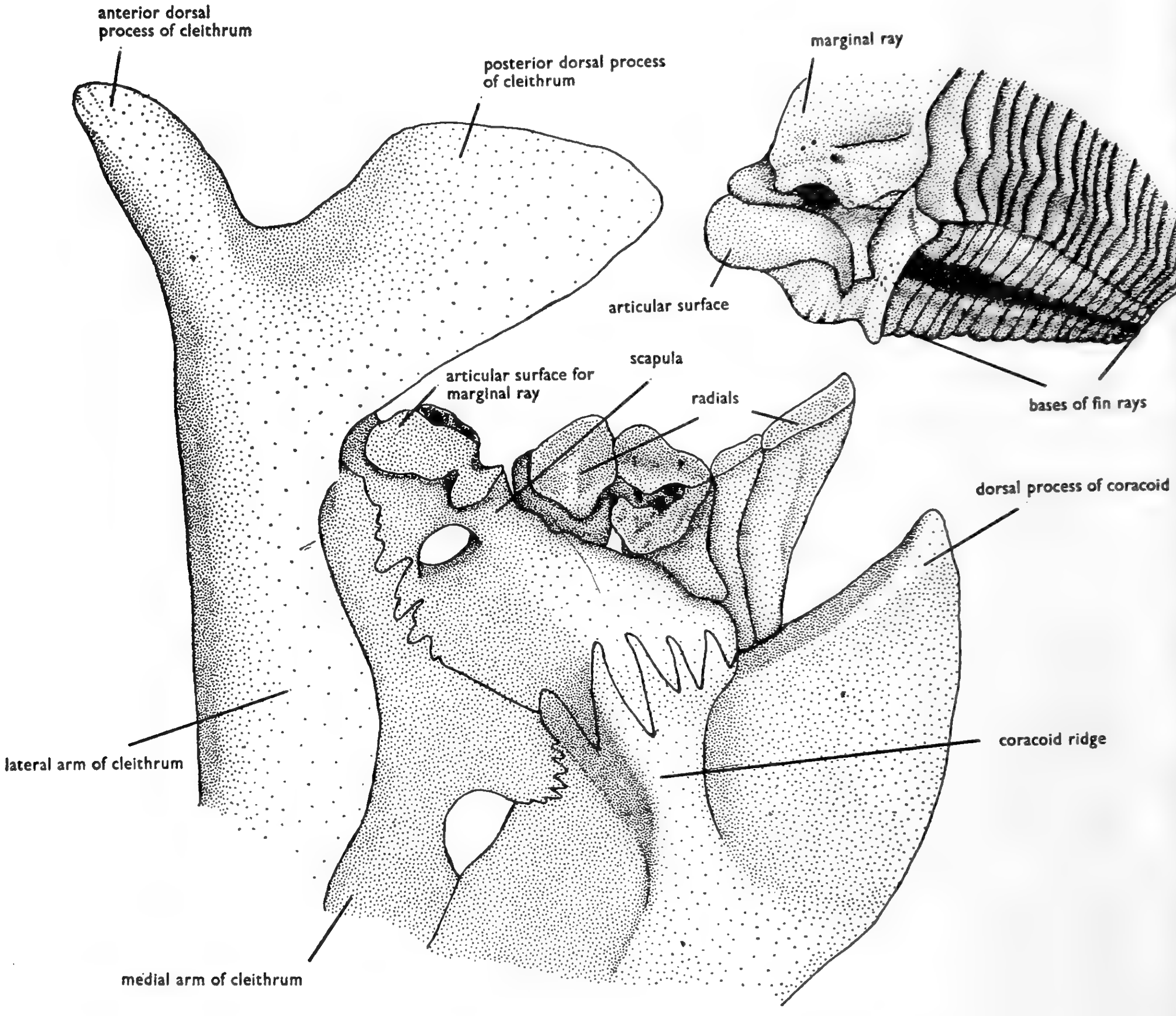

FIG. 7A. Articular region of pectoral girdle of *Makaira indica*.

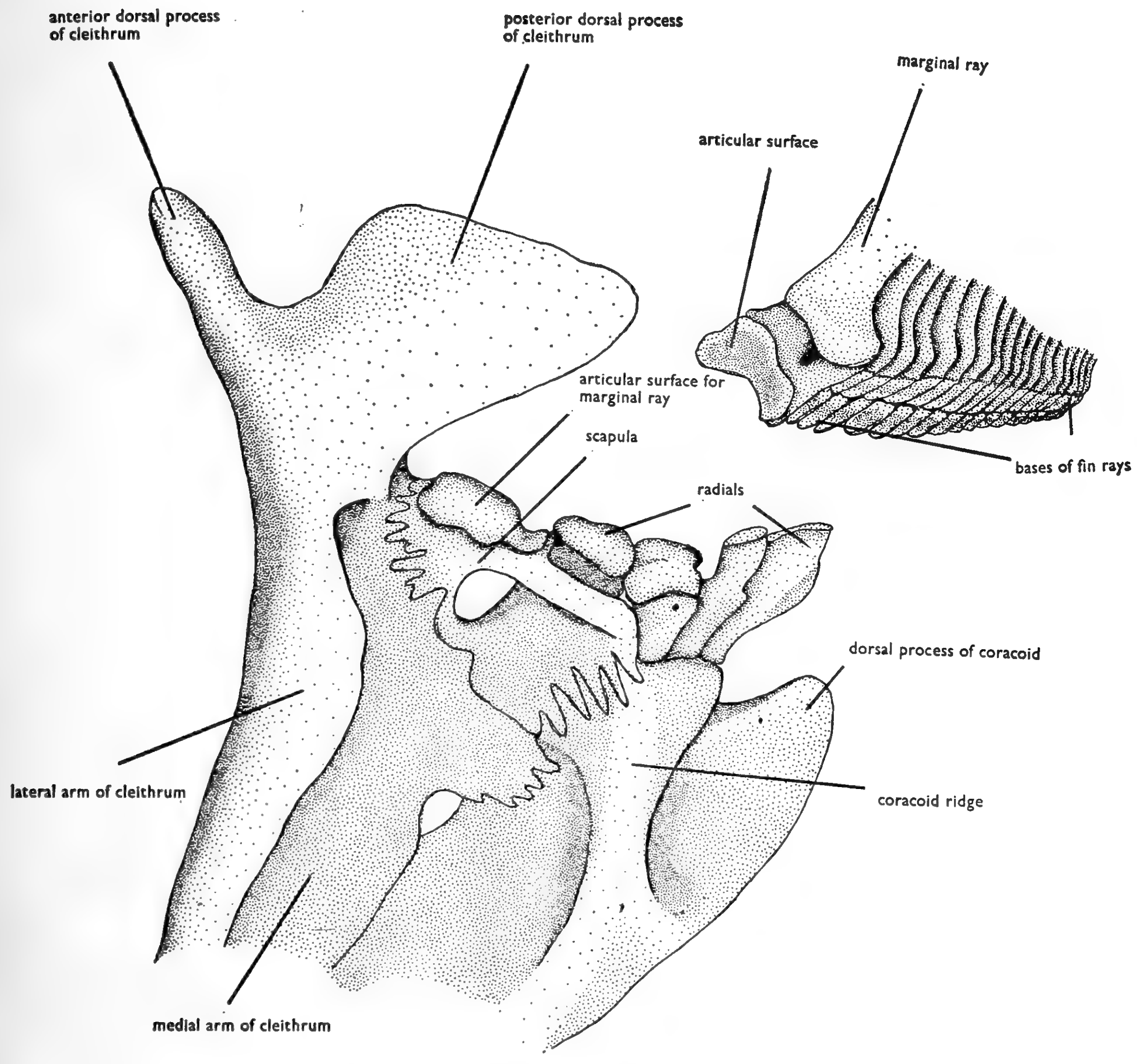

FIG. 7B. Articular region of pectoral girdle of *Makaira audax*.

first two is an area of attachment rather than articulation, most movement taking place between their distal ends and the bases of the rays. The third and fourth radials are slightly more movable, and movement is possible between the second and third radials in all species. The distal ends of the first two radials are smoothly curved in *M. audax*, allowing free movement of the rays over them, but are strongly rugose and pitted in *M. indica* for the attachment of connective tissue. The last ten rays are movably articulated on the distal ends of the third and fourth radials in both species.

In both *M. audax* and *M. indica* the pectoral fin is held to its articular surfaces by a connective tissue sheath, but this sheath shows significant differences in the two species. In *M. audax* the ligaments are elastic and loosely arranged so as to allow maximum movement of the joint, but in *M. indica* a very strong sheath of interwoven fibrous tissue is developed which holds the fin strongly to its articular surfaces; the fibres are short and their area of attachment to the bone is more extensive than in *M. audax*.

VI. DISCUSSION

No features of the osteology of the pectoral girdle other than the articular region suggested a mechanism for maintaining the rigidity of the fin. The muscular system, although showing differences connected with the movements carried out by the fin in the two species compared, is not adapted to hold the fin away from the body in *M. indica.*

It is suggested that the only difference between the pectoral girdles in *M. indica* and the other species studied which is large enough to be of significance in the functioning of the joint of the pectoral fin lies in the position and conformation of the articular surfaces of the fin, in particular that for the marginal ray, and in the development of the connective tissue of the joint.

Owing to the flat, lateral articular surface for the marginal ray base of the fin of *M. indica,* the fin cannot roll back so that its base rests on the dorsal edge of the scapular, without leaving its articular surface; to prevent it from being forced off its articular surface by the pressures it encounters in the extended position, a very strong connective tissue sheath is developed around the joint. This tough connecting sheath prevents the fin from lying back against the body.

If the fin is forced back against the body in a dead specimen, an operation requiring considerable force, the connective tissue sheath is torn. The bones, including the radials, are undamaged, suggesting that there can be no bony locking or strutting device for maintaining the rigidity of the fin.

After the ligaments have been broken the fin can fold back considerably farther than before, but not completely as in the other species; it is stopped by the dorsal expansion of the marginal ray being jammed against the posterior edge of the posterior dorsal process of the cleithrum, which is slightly thickened in this species. Unless the ligamentous sheath is torn this position is not reached, so this is not a mechanism for holding the pectoral fin rigid.

It is suggested that at some time and for some reason in its evolutionary history *M. indica* or its ancestors found it necessary to maintain the fin in a laterally extended position. This was presumably accomplished at first by muscular contraction sustained over long periods, but in time the tension was taken by greatly strengthening the connective tissue sheath attaching the fin to the girdle, and the inner portion of the girdle's articular surface, which is used only when the fin lies against the side, was lost.

The pectoral fin of the black marlin appears to act either as a stabilizer, or as a plane of elevation. The body is very large and deep, and it may be that some stabilizing factor is necessary during forward movement. The broadbill swordfish, *Xiphias gladius,* of similar body shape, also has rigid pectoral fins. However, if this is the reason for the modification, it is surprising that the blue marlin, *Makaira nigricans,* also a large, deep-bodied marlin, does not have rigid pectoral fins.

The other possibility, that the fin acts as a plane of elevation during forward movement, deserves consideration.

It is interesting to speculate on the possible reasons for the necessity of such continuous lifting force. In pelagic surface teleosts very small marine species usually possess a well-developed closed swim bladder, but among many medium and large sized species, particularly in the Scombridae, it is variable or absent (Jones & Marshall, 1953). For example, in many species of the genus *Thunnus*, it is variably reduced or rudimentary; in *Katsuwonus pelamis*, *Sarda lineolata*, *S. chiliensis*, the genus *Auxis*, the genus *Euthynnus* and most species of the genus *Scomberomorus*, it is absent. It is probable that in fast-swimming forms which change depth rapidly a large swim bladder is a liability because of its necessarily slow change of volume. The absence or reduction of the swim bladder would necessitate some upward thrust to counteract the tendency to sink because of increased density. In such powerfully swimming fishes as the tunas and the marlins where forward movement may be continuous this presents little difficulty, and presumably the increased effort has not been too great to offset the advantage gained in vertical manoeuvrability.

Preliminary examination (dissection of one black marlin and one striped marlin) showed that the swim bladder structure is very different between the two species, and that the black marlin seems to have a relatively smaller swim bladder. This work is being continued.

It is therefore tentatively suggested that the black marlin has a reduced swim bladder, and that some upward thrust is supplied by the rigid pectoral fins.

Comparison may be made here with the sharks. In this group the pelagic surface forms are large, and in the absence of a swim bladder upward thrust is obtained by the broad and rigid pectorals.

Acknowledgements

We are indebted to the manager and skippers of the Atlantic Tuna Corporation and to Mr. F. Slack and Mr. W. Gilmore of the South African Marlin & Tuna Club for the specimens; to Dr. N. A. H. Millard of the Zoology Department of the University of Cape Town and Mr. M. J. Penrith of the South African Museum for advice and help; to Professor L. H. Wells of the Department of Anatomy, University of Cape Town, for advice on joints; and to all those who helped with the conveying and handling of the material.

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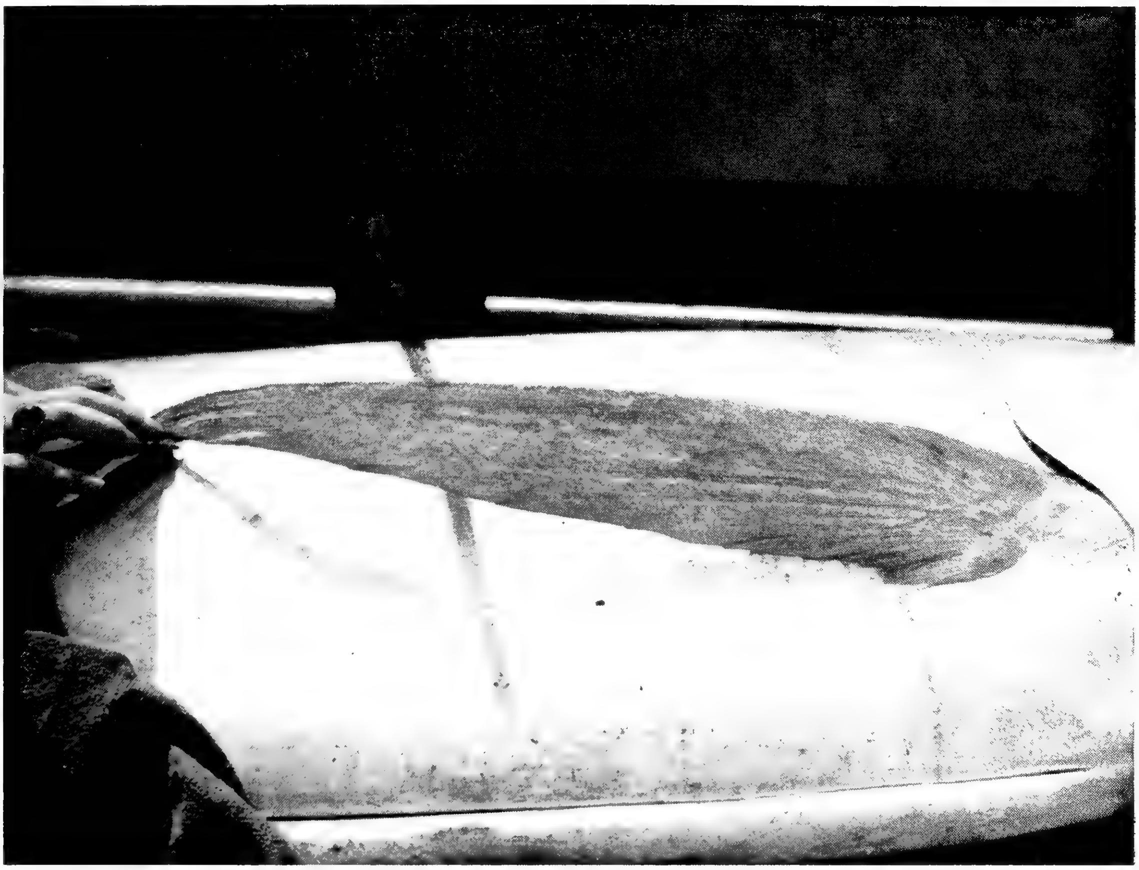
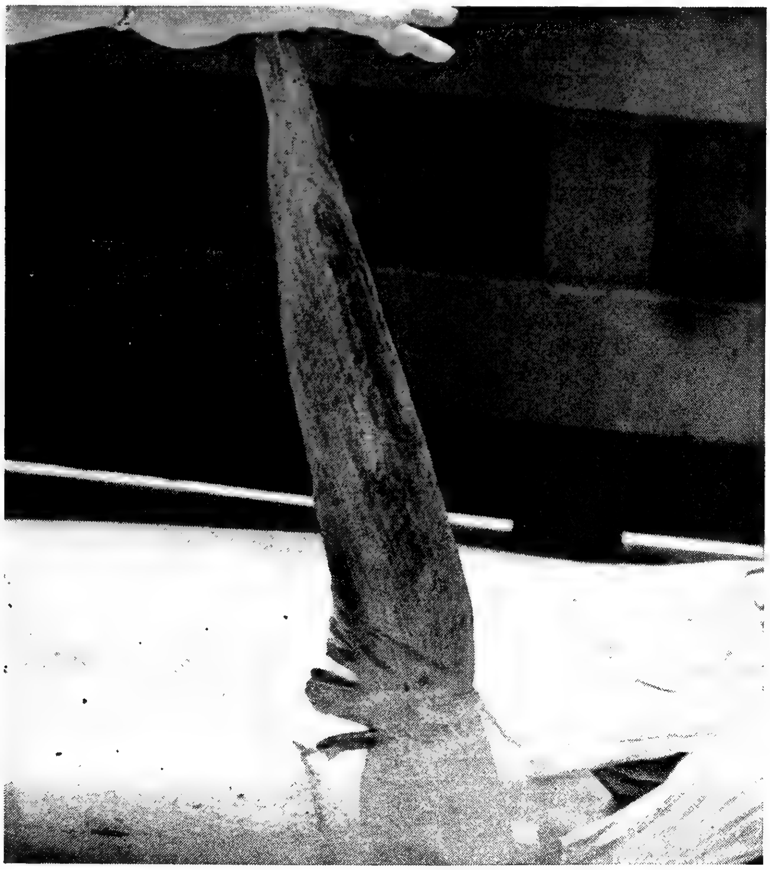


(*a*) Folded position.



(*b*) Extended position.

Range of movement in *Makaira audax*.

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

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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).

M. J. PENRITH

A NEW SPECIES OF FLAT FISH, *MANCOPSETTA MILFORDI*, FROM SOUTH AFRICA, WITH NOTES ON THE GENUS *MANCOPSETTA*

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A NEW SPECIES OF FLATFISH, *MANCOPSETTA MILFORDI*, FROM SOUTH AFRICA, WITH NOTES ON THE GENUS *MANCOPSETTA*

By

M. J. Penrith*

South African Museum, Cape Town

(With 2 figures in the text and 1 plate)

Contents

Introduction

The genus *Mancopsetta* was proposed by Gill (1881) to replace the preoccupied generic name *Lepidopsetta* used by Gunther (1880) when describing *M. maculata*, the first of the bothid fishes found which lacked pectoral fins. This species has until now remained the only species in the genus and has been known from a very few specimens found in the Southern Hemisphere. The related genus *Achiropsetta* (Norman, 1930) was known from two species, both rare and recorded only from the Southern Hemisphere. Recently the South African Museum was presented with two specimens of a bothid fish lacking pectoral fins. These have been assigned to the genus *Mancopsetta*.

Mancopsetta milfordi sp. n.

(fig. 1, pl. III)

Material:

S.A.M. 24041: trawled by a commercial trawler in 300 fathoms west of Cape Town. Standard length 393 mm. (Holotype).

S.A.M. 23767: trawled by a commercial trawler in 370 fathoms west of Cape Town. Standard length 298 mm.

The body is compressed, sinistral and fairly elongate, the maximum depth being about $2\frac{2}{3}$ in body length (excluding the caudal fin). The axial portion of the body is thickened relative to the rest of the body in the smaller specimen,

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* Seconded from the Council for Scientific and Industrial Research Oceanographic Unit, University of Cape Town.

Ann. S. Afr. Mus. **48** (7), 196~~4~~5, 181–188, 2 figs., 1 pl.

but this seems to become less marked with increase in size as it is not noticeable in the larger specimen. The caudal peduncle is very short, being only $\frac{1}{3}$ of the longitudinal diameter of the eye.

There is a single straight lateral line on both sides with about 160 scales on the ocular side. The scales are ctenoid with normally eight to twelve spinules. Towards the edges of the fish, especially on or near the fins, the spinules project at an angle away from the body, but on the main trunk they lie flat. The entire head, including the jaws and part of the eyes, is covered with fine scales. The eyes are separated by a low, scaled, bony ridge. All fin rays, including the caudal, have a row of scales.

The head from the tip of the maxilla to the hindermost edge of the operculum is contained 4 times in standard length, while the greatest diameters of the eyes (both eyes equal) are $\frac{1}{4}$ the length of the head. The snout is slightly shorter than the eye diameter. There is a small fleshy growth over the front of the maxilla. The mouth reaches back to a point almost level with the posterior edge of the lower eye. Teeth are present on both sides of the jaw but are slightly better developed on the ocular side. The mouth has a very wide gape and is protrusible. The membranes on the ocular side are more protrusible than those on the blind side. There are nine small gill-rakers on the lower arch of the first gill.

There is no trace of any pectoral fin on either side. The pelvic fin on the ocular side is larger than that on the blind side. On the eyed side the anterior base of the pelvic fin is median, while posteriorly the base is twisted to the left, i.e. on to the ocular surface of the body (fig. 1).

The body proportions and meristic counts of the two specimens are given in Table I and compared with a specimen of *M. maculata* from the collection of the British Museum (Natural History) (Registered No. 1930.5.6: 41).

The colour, preserved in formalin, is brown-grey with the anal and dorsal fins grey slate/blue. There is no trace of any pattern.

TABLE I

	M. milfordi	*M. milfordi*	*M. maculata*
Total length	456	334	239
Standard length	392	298	199
Greatest depth	143 (364)	99 (332)	88 (442)
Head length	101 (258)	76 (255)	53 (266)
Length of snout	22 (56)	15 (50)	10 (50)
Diameter of eye (horizontal)	24 (61)	20 (67)	17 (85)
Interorbital width	8 (17)	5 (15)	3 (15)
Length of Maxillary	48 (122)	33 (111)	18 (90)
Number of scales in lateral line ..	164	177	119
Dorsal rays	130	133	119
Anal rays	109	110	98
Pelvic rays, blind side	6	6	5
Pelvic rays, ocular side	7	7	7
Gill-rakers, lower arch	9	9	12

Body proportions and meristic counts of *M. milfordi* and *M. maculata*. Body proportions in millimetres and in thousandths of standard length in parentheses.

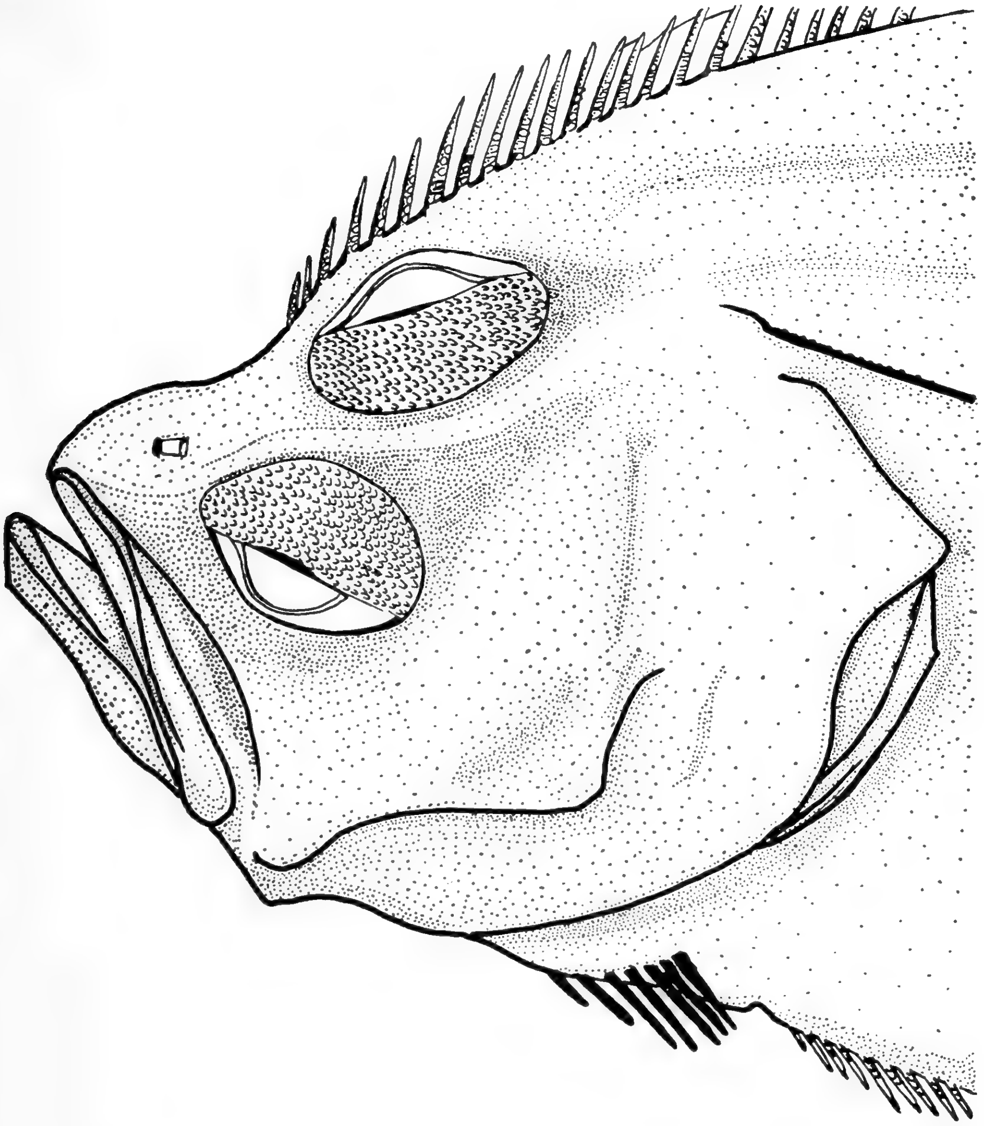

FIGURE 1. Head of *M. milfordi* showing the twisting of the posterior portion of the left pelvic fin onto the ocular surface.

Mancopsetta milfordi differs from *M. maculata* in the number of dorsal and anal rays and lateral line scales, the twisting of the posterior end of the left pelvic fin onto the ocular surface and in certain body proportions. It resembles *M. maculata*, however, in general body shape, especially head shape, and in the type of scales.

The species is named for Mr. C. S. Milford, managing director of the trawling firm, Messrs. Irvin and Johnson (Pty.) Ltd., in recognition of generous support for marine biological research.

GENERIC GROUPING

According to Norman (1934) there are only two genera of bothids (both known only from the Southern Hemisphere) which lack both pectoral fins.

These two genera, *Mancopsetta* and *Achiropsetta* are said to differ in the following characters. . . .

(*a*) *Achiropsetta* is said to have a flat scaled interorbital space, whereas that of *Mancopsetta* is stated to be a naked narrow bony ridge.

(*b*) *Achiropsetta* is said to be more elongate and to have a thickened trunk.

(*c*) In *Mancopsetta* the pelvic fin on the ocular side is not directed to the left posteriorly as is said to be the case in *Achiropsetta.*

(*d*) In both genera the scales are small and ctenoid, but in *Mancopsetta* the 8–14 spinules lie flat, whereas in *Achiropsetta* there are only one or two spinules which are directed away from the body.

These differences would seem to be clear cut, but the finding of a second species of *Achiropsetta*, *A. slavae* (Andriashev, 1960) and the present species have suggested that the differences between the genera are not so marked as was formerly thought. Neither *A. slavae* nor *M. milfordi* fits completely the generic description of the genus in which it has been placed. The distribution of various taxonomic characters among the four species of bothids which lack pectoral fins is shown in Table II below.

TABLE II

	Achiropsetta		*Mancopsetta*	
	tricholepis	*slavae*	*maculata*	*milfordi*
Dorsal rays	132	114–117	116–119	130–133
Anal rays	114	93–96	97–98	109–110
Lateral line scales	?	115	114–120	164–177
Depth in standard length	2·4	2	2·2	2·7
Gill-rakers in lower arch	9–10	12	12	9
Head in standard length	4·5	3·5	3·8	4
Coloration	plain	patterned	patterned	plain
Fleshy lip on maxilla tip	present	present	present	present
Spinules on scales	vertical	vertical	flat	flat
Pelvic fin of eyed side twisted to the left	yes	no	no	yes
Maximum known total length (mm.)	105	63	270	456
Smallest known total length (mm.)	100	48	134	334

Comparison of the four known species of bothid fishes which lack pectoral fins.

From the table it is clear that the only important character that the two species of *Achiropsetta* have in common, and distinct from the two species placed in the genus *Mancopsetta*, is the unusual form of the scales with vertically projecting spinules.

Although *A. tricholepis* is stated to have a flat scaled interorbital space (Norman, 1930, 1934), a specimen examined from the collection in the British Museum (1933.5.8: 1) shows a clear bony ridge. *M. maculata* on the other hand was said (Norman, 1934) to have a bony ridge without scales. In the specimen of *M. maculata* examined however, scale pockets were clearly present on the ridge. It seems likely that the scales were rubbed off in the trawl net. A scaled ridge is therefore present in *M. maculata*, *M. milfordi* and *A. tricholepis*. Nothing is known concerning this feature in *A. slavae*.

Another difference, the thickened trunk in *Achiropsetta*, is most probably a function of size as it is present in *Achiropsetta* (of which only small specimens are known) and the smaller of the two *M. milfordi* but not in the larger nor in *M. maculata*.

From the illustrations in Norman (1934) there is a strong suggestion of marked differences in the shape of the head in *M. maculata* and *A. tricholepis* but this is caused by illustrating the largest available example of the former species and the smallest of the latter. Figure 2 gives some idea of the changes of head shape that may occur in a species with an increase in size.

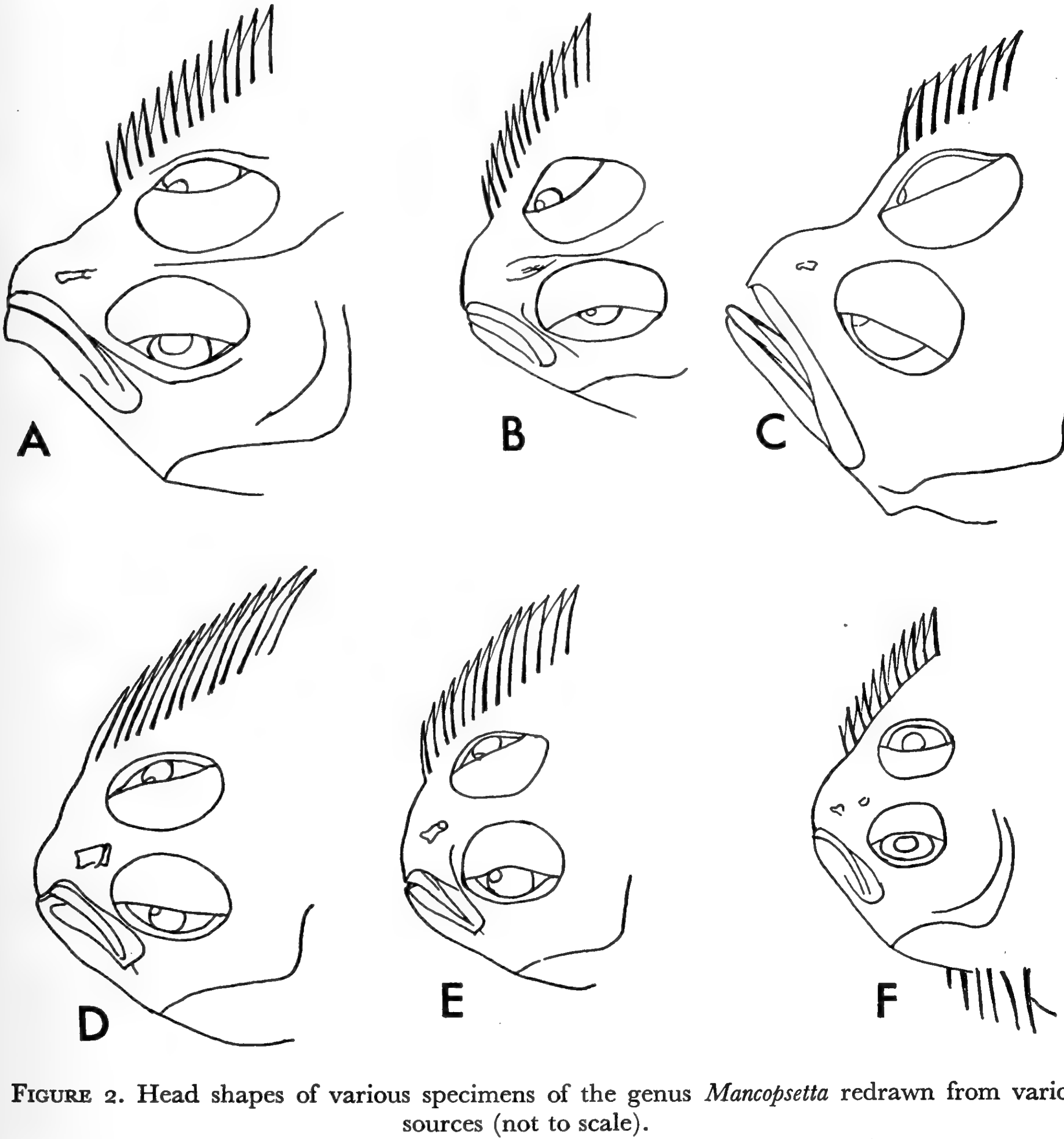

FIGURE 2. Head shapes of various specimens of the genus *Mancopsetta* redrawn from various sources (not to scale).

A. *M. maculata* of 238 mm. total length (After Norman, 1934).
B. *M. maculata* of 134 mm. total length (After Gunther, 1880).
C. *M. milfordi* of 334 mm. total length.
D. *M. slavae* of 63 mm. total length (After Andriashev, 1960).
E. *M. slavae* of 56 mm. total length (After Andriashev, 1960).
F. *M. tricholepis* of 100 mm. total length (After Norman, 1930).

From the above it is evident that there is only one important and constant difference between the two genera *Mancopsetta* and *Achiropsetta*, viz. the type of spinules present on the scales. At the same time, however, there are several clear points of similarity between *A. tricholepis* and *M. milfordi* and again between *A. slavae* and *M. maculata*.

It is extremely probable that the presence of vertically projecting spines in *Achiropsetta* is a larval or juvenile character as similar spines occur in many bothid larvae (Kyle, 1913). Andriashev (1960) holds a similar view and has stated 'It is very probable that the peculiar prickliness of the body of *Achiropsetta* (that is, the strongly developed, vertically projecting spines) can be considered as a larval character of a caenogenetic nature'. He also noted the similarity in fin counts between *A. slavae* and *M. maculata*, as well as the fact that these two species had the most similar distribution. He concluded, however, that the specimens of *A. slavae* could not be assigned to the genus *Mancopsetta* since in the latter genus the body is not transparent and the scales do not have the vertically projecting spinules. Andriashev further states that it is not possible to explain these in terms of development, as the difference in size between the smallest *M. maculata* and the largest *A. tricholepis* is only 29 mm. The greatest similarities are, however, between *M. milfordi* and *A. tricholepis*, where the minimum difference between the two species is 229 mm., and between *A. slavae* and *M. maculata*, where the difference is 71 mm.

While it is not possible at this stage in our knowledge of these fishes to suggest that *A. tricholepis* is actually the juvenile stage of *M. milfordi* or *A. slavae* that of *M. maculata*, it is suggested that for the reasons given above, and bearing in mind that these four species, in lacking pectoral fins, form a unique group within the family Bothidae, the species should not be separated into two genera but should rather be united into one genus, *Mancopsetta*. The differences between the species of the former genus *Achiropsetta* and those of *Mancopsetta* being far more likely due to growth rather than major genetic differences. The generic definition of *Mancopsetta* will, however, have to be modified from that given by Norman (1934), not only to include the species formerly placed in the genus *Achiropsetta*, but also the new species *M. milfordi*.

Genus MANCOPSETTA

Lepidopsetta (*non* Gill, 1864) Gunther, 1880, p. 18.
Mancopsetta Gill, 1881. p. 373.
Achiropsetta Norman, 1930. p. 361.

Body fairly elongate, compressed and sinistral. Eyes large, close together and with the upper parts of each eyeball densely scaled. Lower eye a little in advance of the upper. Mouth of moderate size not reaching farther back than a point level with the posterior edge of the lower eye, maxillary narrow, not expanded behind. Jaws and teeth about equally developed on both sides. A small fleshy growth over the front tip of maxilla. Teeth small, conical and usually uniserial; vomer toothless. Few gill-rakers, those present being short.

Dorsal fin starting far forward on head. All fin rays simple, scaled. Pelvic fin of eyed side may or may not be posteriorly deflected to the left. No true pectoral fins but a fin bud may be present in small specimens. Lateral line on both sides single, straight and well developed.

Type species *Lepidopsetta maculata* Gunther, 1880.

The genus contains four species:

M. maculata (Gunther) 1880.
M. tricholepis (Norman) 1930.
M. slavae (Andriashev) 1960.
M. milfordi sp. n.

DISTRIBUTION

Andriashev (1955) has discussed the distribution of these fishes and has shown that they are known from a few specimens found over a wide area of the Southern ocean. The following are the only published locality records:

M. maculata. This species is known from three specimens, all caught by bottom trawling in deep water—

Marion Island: 46° 43′ S. 38° 5′ E. 580 m. (Gunther, 1880).
Falkland Islands: 45° 45′ S. 59° 35′ W. 311–247 m. (Norman, 1937).
South Georgia: 53° 48′ S. 35° 57′ W. 411–401 m. (Norman, 1938).

M. tricholepis. This species is known from only two examples taken by bottom trawling in shallow water—

Tierra del Fuego: 53° 00′ S. 68° 06′ W. 22–20 m. (Norman, 1930).
Falkland Islands: (No details available) (Norman, 1937).

M. slavae. Four specimens of this species are known and all were caught in midwater using an Isaacs–Kidd midwater trawl—

Wilkes Land: 64° 51′ S. 114° 17′ E. 725 m. cable (Andriashev, 1960).
(Antarctic) 63° 50′ S. 116° 25′ E. 1,100 m. cable (Andriashev, 1960).
64° 22′ S. 121° 08′ E. 1,100 m. cable (Andriashev, 1960).
64° 10′ S. 127° 46′ E. 1,100 m. cable (Andriashev, 1960).

M. milfordi. Known from only two specimens both taken by bottom trawl in deep water—

Cape of Good Hope, west of Cape Town. 550 m.
Cape of Good Hope: 33° 40′ S. 17° 30′ E. 675 m.

Some of these records are very widespread, especially *M. maculata* and suggest that these fishes are more common than the small number of known records would suggest. This is undoubtedly due to the very small amount of trawling that has been undertaken in the Southern ocean. More collecting would be very useful, as a good set of growth stages would certainly show whether *M. slavae* and *M. maculata* are in fact growth stages of the same species, and likewise with *M. milfordi* and *M. tricholepis.*

Acknowledgements

I am grateful to Professor J. L. B. Smith of Grahamstown, Dr. A. P. Andriashev of Leningrad, and Mr. P. R. Sloan of La Jolla for help in obtaining literature; to the Trustees of the British Museum (Natural History) for the loan of valuable material for comparative purposes; to Messrs. Irvin and Johnson (Pty.) Ltd. for presenting these two interesting specimens to the South African Museum; and to Dr. F. H. Talbot and my wife, Mary-Louise Penrith, for reading the manuscript.

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.

Summary

A new species of bothid, *Mancopsetta milfordi* (Pisces: Bothidae), is described from deep water off the Cape of Good Hope. Four species of bothids are known which lack pectoral fins. They have been placed in two genera, *Mancopsetta* and *Achiropsetta*. It is shown that the two genera exhibit a marked overlap in characters and can be divided on only one character, which is probably a juvenile feature. The genus *Mancopsetta* is redefined to include all four species.

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Mancopsetta milfordi Holotype.

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 4¾ in. × 7 in. (7½ 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.

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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).

FRANK HAMILTON TALBOT AND MARY-LOUISE PENRITH

CTENOGOBIUS CLOATUS SMITH, 1960 A SYNONYM OF *CTENOGOBIUS SALDANHA* (BARNARD, 1927)

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CTENOGOBIUS CLOATUS SMITH, 1960, A SYNONYM OF *CTENOGOBIUS SALDANHA* (BARNARD, 1927)

By

Frank Hamilton Talbot and Mary-Louise Penrith

South African Museum, Cape Town

(With 2 figures in the text and 1 plate)

Contents

Introduction

New material in the South African Museum fish collections from Port Elizabeth, False Bay, and Saldanha Bay, has shown clearly that *Ctenogobius cloatus* Smith, described from Knysna, and *Ctenogobius saldanha* (Barnard), described from Saldanha Bay, are synonymous.

The material examined is as follows:

S.A.M. 23277: 1 specimen, 79 mm., tidal swimming pool, St. James, False Bay;
S.A.M. 21488: 1 specimen, 33 mm., shallow water, Langebaan, Saldanha Bay;
S.A.M. 21489: 1 specimen, 30 mm., shallow water, Langebaan, Saldanha Bay;
S.A.M. 21490: 2 specimens, 34–37 mm., shallow water, Langebaan, Saldanha Bay;
S.A.M. 22034: 1 specimen, 40 mm., inter-tidal pool, Sea Point, Table Bay;
S.A.M. 17355: 1 specimen, 85 mm., Saldanha Bay (type of *saldanha* Barnard);
S.A.M. 23832: 6 specimens, 28–34 mm., dredged in 7 m. water, Saldanha Bay;
S.A.M. 23831: 4 specimens, 51–61 mm., inter-tidal pools, Port Elizabeth;
S.A.M. 24047: 4 specimens, 46·5–54 mm., tidal swimming pool, Port Elizabeth;
S.A.M. 24048: 3 specimens, 45·5–50 mm., inter-tidal pools, Port Elizabeth;
S.A.M. 23979: 3 specimens, 53–79 mm., inter-tidal pool, Strandfontein, False Bay;
S.A.M. 24049: 2 specimens, 67 mm., 70 mm., inter-tidal pool, Strandfontein, False Bay;
Rhodes Univ.: 1 specimen, 85 mm., lagoon, Knysna (type of *cloatus* Smith).

Ann. S. Afri. Mus. **48** (8), 196~~4~~5, 189–193, 2 figs., 1 pl.

Ctenogobius saldanha (Barnard)
(pl. IV, figs. 1, 2)

Gobius saldanha Barnard, 1927, p. 823.
Bathygobius saldanha (Barnard), Smith, 1949, p. 331.
Monishia saldanha (Barnard), Smith, 1960, p. 304.
Ctenogobius cloatus Smith, 1960, p. 302.

Fin counts: D. VI + I 10–11; A. I 9–10; P. 19–23; C. 15 (branched rays only). Gill-rakers: 6–7 on lower arch, total 9. Scales 34–38, transverse 11. Depth 4·9–6·8. Head 3·0–3·6 in standard length. Teeth in jaw in several series; outer row markedly enlarged, inner rows viliform, no canines. Tongue truncate or feebly bilobed. Pectoral girdle without flaps, but with a low, indented ridge on the anterior border. Pectoral fin with upper 3–4 rays free, silk-like, markedly bifurcating (fig. 1). Pelvic fraenum (i.e. membrane connecting outer rays across base) strong and well developed (fig. 1). Eye 2·9–3·7 in head. Bony interorbital narrow, less than 5 in eye diameter, eyes adjacent. Pores and papillae of head shown in fig. 2.

Ground colour whitish, with three very broad, irregular, faintly dusky cross-bars on body. Sides irregularly spotted with black. Underparts white. Nape dusky with a lighter transverse bar. Head whitish grey. A few small dark

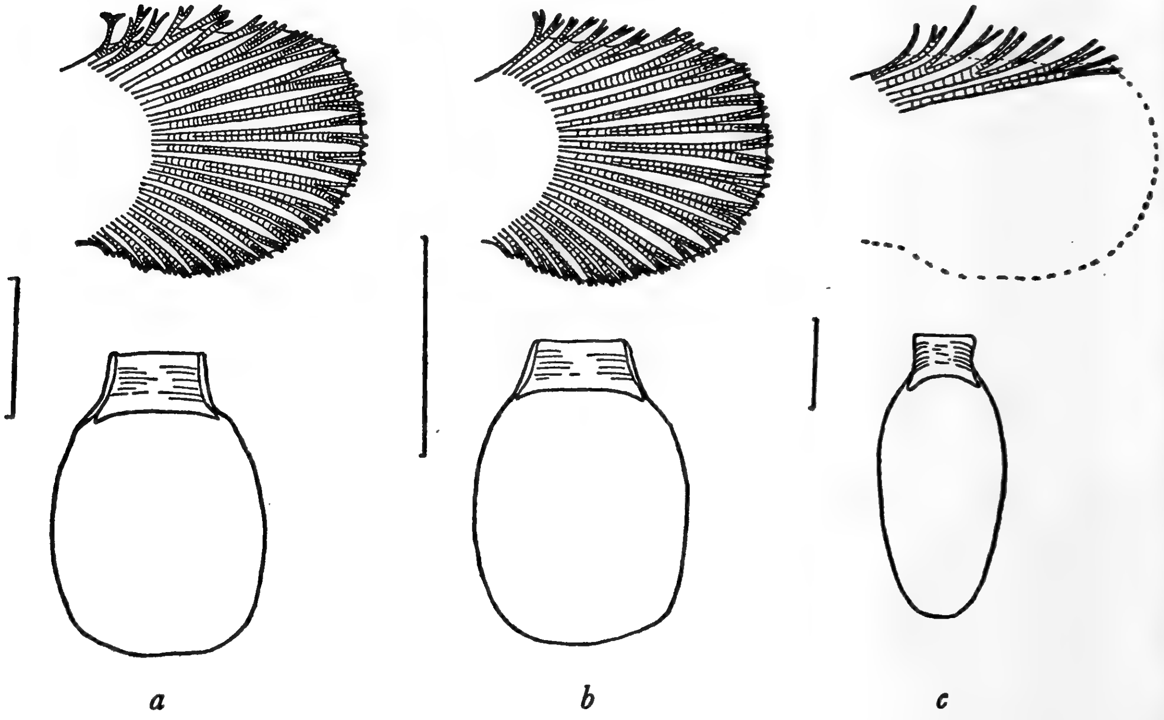

FIGURE 1.

Pectoral fin and pelvic fraenum of *Ctenogobius saldanha* (Barnard) from (*a*) Port Elizabeth; standard length 45.5 mm., (*b*) Saldanha Bay; standard length 35 mm., and (*c*) Knysna (type of *cloatus* Smith); standard length 85 mm. The fin is more contracted in (*c*) than in (*a*) and (*b*).

spots on preopercle, and usually four in a straight line along hind margin of opercle. Pectoral base dusky with several dark spots. Dorsal fins dusky with rows of black dots forming bands. A large black spot on the membrane between the fourth and fifth and the fifth and sixth dorsal spines. Pectoral, pelvic, anal and caudal fins dusky.

Head, nape, preopercle, and opercle naked; pectoral base, prepelvic, and belly with cycloid scales.

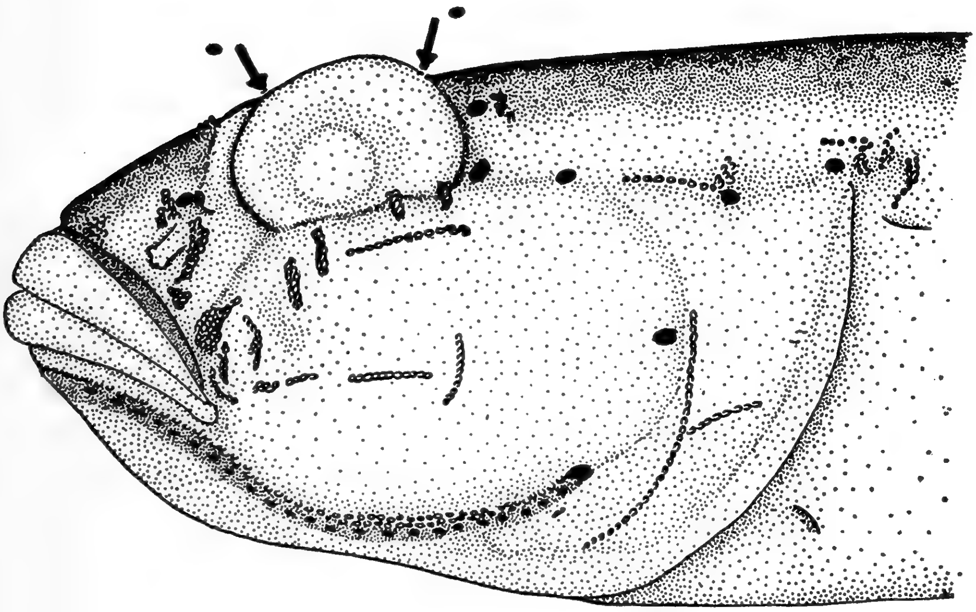

FIGURE 2.

Diagram of pores and papillae on head of *Ctenogobius saldanha* (Barnard).

DISCUSSION

A re-examination of the type of *saldanha* shows certain errors in the original description. The outer row of teeth in each jaw is clearly enlarged (not villiform throughout); there are 11 series of scales between the first anal spine and the dorsal fin base, not 10 as stated in Barnard's description; and the bases of the pectorals are scaled.

Smith's description of *cloatus* indicates the following differences from *saldanha*: strong development of the pelvic fraenum, absence of free upper pectoral rays in his specimens, enlargement of the outer row of teeth, number of transverse scale rows, shape of the tongue, and distribution.

The pelvic fraenum of *saldanha* shows no differences from that of the type of *cloatus* (fig. 1). In both cases the fraenum is well developed.

Smith's type has ragged fins with many rays broken off, and the fin membranes are damaged. Nevertheless, this specimen has the upper pectoral rays very similar to those of *saldanha* (fig. 1) (both the type of *saldanha* and fresh specimens from the type locality). In addition, South African Museum specimens from Port Elizabeth have the upper rays similar to those of the type of *saldanha.*

The apparent differences in teeth and in number of transverse scale rows fall away after re-examination of the type of *saldanha.*

The tongue in both *cloatus* and in specimens of *saldanha* from the type locality is truncate or feebly bilobed. It is not adnate, and Barnard (1927) seems to have been correct in his suggestion that the apparently adnate tongue of the type was due to the fact that the specimen was preserved with the mouth unusually widely opened. Dehydration may also have played a part in this, and in the shrinkage of the tongue, which has obscured its shape.

Böhlke & Robins (1960) have shown that the pore system of the head is important in the classification of gobies. This was found to be identical in all specimens examined, including Smith's type specimen of *Ctenogobius cloatus* (fig. 2).

As has been found in another intertidal group of fishes, the Clinidae, and in gobies such as *Psammogobius knysnaensis* Smith and *Coryphopterus nudiceps* (C. & V.), distribution around the Cape from at least as far west as Saldanha Bay to Algoa Bay or farther occurs commonly.

We can find no difference between east and west coast specimens, and conclude that *cloatus* and *saldanha* are synonymous.

The well-developed fraenum, presence of prepelvic scales, naked head and nape, scale and fin counts, narrow bony interorbital, enlarged outer teeth, tongue shape, and restricted gill openings, place this species within the genus *Ctenogobius* Gill, 1858, as defined by Koumans (1953).

Acknowledgements

Acknowledgement is made to Professor J. L. B. Smith of the Department of Ichthyology, Rhodes University, Grahamstown, for the loan of the type specimen of *cloatus*, and to Miss R. M. Tietz, of the Port Elizabeth Museum, and Mr. M. J. Penrith of the South African Museum, who assisted in the collection of fresh material.

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.

Summary

It is shown that *Ctenogobius cloatus* Smith is synonymous with *Ctenogobius saldanha* (Barnard) (Pisces: Gobiidae). *Ctenogobius saldanha* is redescribed.

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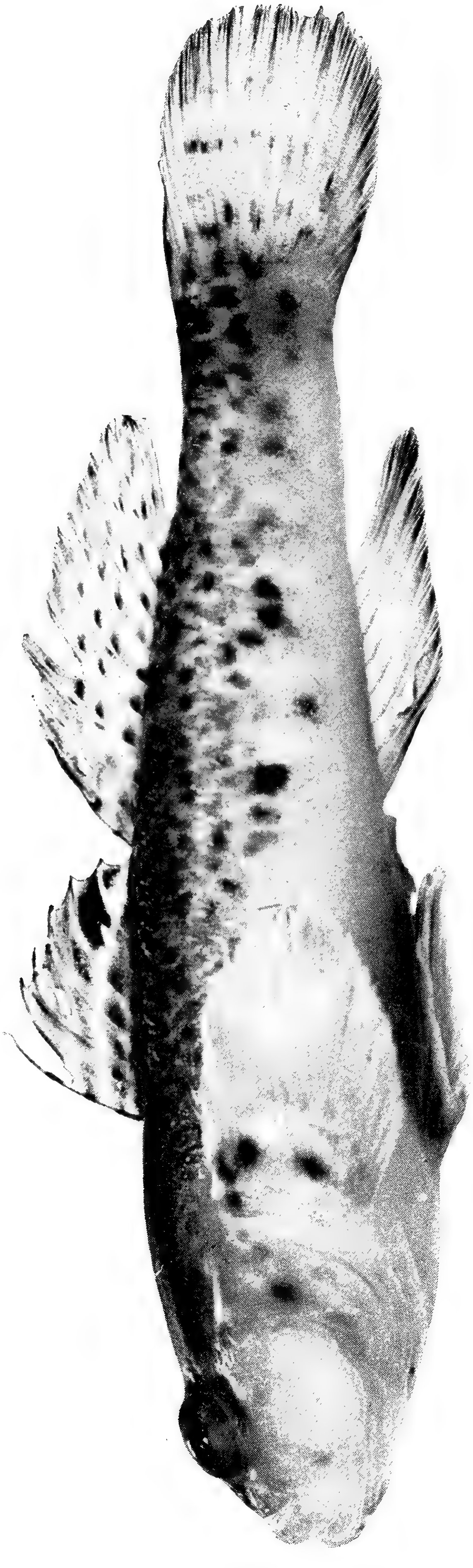

Ctenogobius saldanha (Barnard).

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 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

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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.

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

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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).

K. H. BARNARD

ISOPODA AND AMPHIPODA COLLECTED BY THE GOUGH ISLAND SCIENTIFIC SURVEY

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ISOPODA AND AMPHIPODA COLLECTED BY THE GOUGH ISLAND SCIENTIFIC SURVEY

By

K. H. Barnard[†]
South African Museum, Cape Town

(With 3 figures in the text)

CONTENTS

PREFATORY NOTE

The collection described in this paper was made by the Gough Island Scientific Survey, which worked on Gough Island from 13 November 1955 until 13 May 1956. Attention was largely concentrated on terrestrial biology, and consequently the marine amphipods and isopods described here were all obtained from a small number of collecting stations in the littoral and sub-littoral zones near the mouth of The Glen on the east coast of the island. No dredging was undertaken. The material was submitted to the author soon after the return of the Expedition, and this paper was written in 1957. At that time it was hoped that all the Expedition collections might be described in a comprehensive report, but the unequal progress of work on different taxonomic groups, some of which have yet to receive study, has made this impossible. Rather than delay publication still further it has been decided that all results should be presented as they stand, and the belated appearance of this paper is a direct consequence of this decision.

Martin W. Holdgate

INTRODUCTION

The following collection of Isopoda and Amphipoda from the Gough Island Scientific Survey was entrusted to me by Dr. M. W. Holdgate, to whom I express my thanks for the opportunity of studying specimens from this remote and little known locality (Position: 40° 21′ S., 09° 55′ W.). The Collection is deposited in the British (Natural History), with reference specimens of most species in the South African Museum.

[†] Dr. K. H. Barnard died on 22 September 1964.

Ann. S. Afr. Mus., **48** (9), 1965: 195–210, 3 figs.

The Isopoda were more interesting than the Amphipoda as was to be expected for Stephensen (1949) had already studied the species of Amphipoda found at Tristan d'Acunha by the Norwegian Expedition. No species of amphipod was collected at Gough Island which was not already known from the sister isle; but not all the 32 (littoral and shallow-water) species recorded from the latter have been found at Gough Island.

Much less is known about the Isopoda of these islands. Only three littoral or shallow-water marine species have been recorded from Tristan, two of them also from Gough Island. One introduced cosmopolitan woodlouse has been long known from Tristan, and one endemic species since the visit of H.M.S. *Challenger*. The *Discovery II* collected one of these marine species from Gough Island; the other two, also the two terrestrial woodlice, have been obtained by the present survey party.

In addition six marine species new to the Tristan–Gough Island area were collected, two of which are described as new species. The rediscovery of the New Zealand *Munna neozelanica* is noteworthy.

The isopodan and amphipodan fauna of these islands has relationships, in general, with South Africa, the Magellanic region, Australasia, and the subantarctic islands. Stephensen (1949) gave some zoogeographical remarks on the amphipods. An analysis for the isopods may be premature, but for what it is worth is as follows (excluding the two deep-water species collected by the *Challenger*):

Endemic on Tristan and/or Gough Island: 3 marine species (*Paridotea apposita* n. sp., *Jaeropsis vibicaria* n. sp., and *Isocladus tristensis*), 1 terrestrial (*Styloniscus australis*).
Common to Gough Island and New Zealand: 1 marine species (*Munna neozelandica*).
Common to Gough Island and St. Paul Island: 1 marine species (*Jaeropsis paulensis*).
Common to Tristan and/or Gough Island and South Africa and New Zealand: 2 marine species (*Paridotea ungulata, Dynamenella huttoni*).
Common to Tristan and/or Gough Island and other subantarctic regions: 1 marine species (*Iais pubescens,* commensal on Sphaeromids).
Cosmopolitan, introduced: 1 terrestrial species (*Porcellio scaber*).

Mention may be made of one maritime woodlouse whose absence (seemingly) on Tristan and Gough Island is rather remarkable, namely *Deto*. The species of this genus are known from South Africa, South America, Australia, New Zealand and its subantarctic islands, and St. Paul (southern Indian Ocean) (see Chilton, 1915: 437; and Barnard, 1932a: 220). They are large, conspicuous, and abundant. It is, therefore, a fair presumption that the genus does not occur on these islands.

Dr. Sivertsen and Dr. Holthuis are at present studying the isopods collected on Tristan and neighbouring islands by the Norwegian Expedition.

Their results will give a much clearer picture of the fauna of the whole group than the analysis here given based on Gough Island alone.

The preponderance of amphipods in the present collection may perhaps be due, at least in part, to methods of collecting. Kelp is a favourite haunt of these crustaceans, and numerous specimens can usually be obtained from only a few handfuls of weed. Isopods, however, often present a more difficult problem, varying with the type of beach, rock formation, tide range and other factors, not least Neptune's co-operation in curbing the turbulence of the waves.

ISOPODA

Family **Anthuridae**

Paranthura sp.

A single juvenile specimen, 4·5 mm. in length, with only 6 peraeon segments and 6 pairs of legs. It has styliform mouth-parts, and the 5th joint of peraeopods 5 and 6 does not underride the 6th. It is therefore probably a species of *Paranthura.*

The colour pattern may prove distinctive when more specimens can be obtained, possibly at Tristan if not at Gough Island. Pale yellowish, a dark patch on front of head, and a dark transverse band across pleon, faint speckling on the peraeon segments, eyes black.

Locality: Dell Rocks (A 47. M 54).

Family **Sphaeromidae**

Isocladus tristensis (Leach)

Exosphaeroma tristense (Leach) Tattersall, 1913: 882, pl., fig. 1 (juv. ♂ and ♀).
Isocladus tristensis (Leach) Barnard, 1914: 384, pl. 33, fig. B (adult ♂); 1955: 62 (transverse profile of body mentioned).

Localities: Beach debris, Glen mouth; shore near Base; Dell Rocks; stomach of Soldier fish (A 27. M 1; A 47. M 60; B 5. M 83; B 10. M 88; and B 10. M 90).

A 27. M 1 a lot comprising adult and immature males, ovigerous females, and juveniles. Specimens of the commensal asellid *Iais pubescens* have been removed from some of them.

A 27. M 9 (part) one very juvenile, probably this species.

Previously recorded from Tristan and Gough Island.

A re-examination of *I. magellanensis* Richardson, 1906, is necessary before it can be synonymised with *tristensis.*

Dynamenaella huttoni (Thomson)

Dynamenella huttoni (Thomson) Chilton, 1909: 657. Barnard, 1940: 419 (references).
Dynamenella kraussi Barnard, 1914: 415, pl. 35, fig. B.

These specimens agree with South African specimens in convexity of body, and absence of a raised rim on frontal margin of head. Although the surface is glabrous (Barnard, 1914), it is not polished except in the mid-dorsal line of peraeon segments 2–6; on the head, lateral portions of peraeon, and on pleon and telson it is finely shagreened, and on the dorso-lateral portions of peraeon finely reticulated.

Colour (as preserved) corresponding with that of South African specimens (Barnard, 1914: 417): reddish, with or without a paler stripe (or series of spots) on each side, and indications of paler patches in middle of back.

The size (male 7 mm., female with embryos 5 mm.) is considerably less than the average size of South African specimens.

Localities: Dell Rocks and Seal Rocks (A 40. M 25; B 4. M 81; 1504).

Family **Idoteidae**

Paridotea ungulata (Pallas)

Paridotea ungulata (Pallas) Hale, 1924: 221, fig. 9 *e*, *f*. 1929: 320, fig. 325 *b* (side view of 6th and 7th peraeon segments). Sheppard, 1957: 151, fig. 4 *a–e*.

(Fig. 1 *a*)

Tristan d'Acunha and Gough Island. Not taken by the present Survey.

Paridotea apposita n. sp.

(Fig. 1 *b*)

The parallel-sided body gives this species the appearance of a large form of *fucicola* Barnard (1914: 327, pl. 36, fig. E). In other respects closely resembling *ungulata*.

Side-plates 5 and 6 postero-lateral angle quadrate, 7 a little produced, the angle slightly acute.

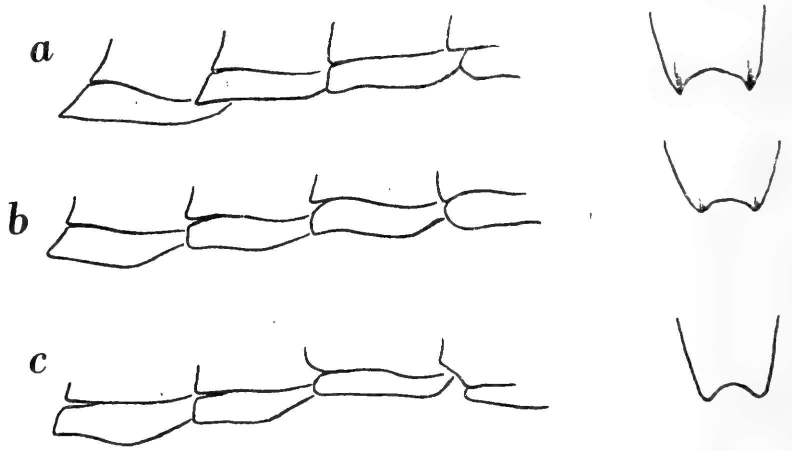

FIGURE 1. *Paridotea*. Side-plates 4–7 and apex of telson of: (*a*) *ungulata* (Pallas). (*b*) *apposita* n. sp. (*c*) *munda* Hale.

Pleo-telson scarcely more than one-third of the total length (*ungulata:* two-fifths), apex shallowly emarginate between the rounded postero-lateral angles, on which a faint keel is traceable. Sternal plates as in *ungulata* (see Barnard, 1914: pl. 36, fig. D, *st. u.*).

Maxilla 1 (of male 30 mm. long) outer plate with 12 spines, with a slender one between the two groups of 6, 4 of the inner group serrulate, but not the innermost shortest one, a seta in middle of plate below bases of spines; inner plate with 4 plumose setae and a simple seta. Maxilliped 7-jointed.

Paraeopods as in *ungulata*; 3 stout serrulate spines on inner margin of 6th joint of peraeopod 1, one in each of peraeopods 2–7; 4th–6th joints of peraeopods 1–6, furry on inner margin in the large male, not furry in females or the smaller specimens.

Uropod peduncle without median keel, a plumose seta at outer (when appendage is folded in) distal corner; length of ramus slightly less than basal width (2: 2·3), outer (when folded) margin more oblique (following the outline of telson) than in *ungulata*, the truncate distal margin relatively narrower.

Pleopod 2 of male, stylet as in *ungulata*.

Colour (as preserved): dull pinkish or reddish.

Localities: Beach debris, Glen mouth; stomach of Soldier fish (A 27. M 2) 1 immature, 18 mm.; B 10. M 86 1 ♂ 30 mm., 2 immature 19 and 22 mm.; B 10. M 89 1 ♀ 31 mm.; B 10. M 90 1 ♀ 27 mm., 1 immature 18 mm. (head missing).

The 31 mm. female shows the brood lamellae beginning to develop as tiny lobes, 0·5 mm. long, on segments 2–5; the 27 mm. female shows only slight pits in the positions where the lobes will appear at the next moult. Neither female shows any sign of the anterior peraeon segments broadening.

Thanks to the kindness of Dr. H. M. Hale, then Director of the South Australian Museum, I was able to examine a specimen of *P. munda* Hale 1924, a species which merits comparison with *ungulata* and the Gough Island species. The accompanying figures (fig. 1) of the posterior side-plates and the telsonic apex will illustrate the differences in the three species. Hale's figures of the side-plates (1924 and 1929) do not seem to show the correct shapes, in comparison with the specimen I have seen. This specimen also has a narrower notch at the telsonic apex. (fig. 1 *c*).

The Cape species *fucicola* Barnard (not figured here) has a narrower telsonic notch than *munda*, side-plates 5 and 6 do not reach as far back as the hind margin of their segments, and the narrowly rounded apex of side-plate 7 extends only slightly beyond its segment.

Family **Jaeridae**

Iais pubescens (Dana)

Iais pubescens (Dana) Chilton, 1909: 649. Barnard, 1914: 435, pl. 37, fig. C (typ. err. fig. of plp. 3 has been inverted and labelled 'mxp'. See corrigendum 1916: 106). Nordenstam, 1933: 178, figs. 41 *a–c* (references). Menzies J. L., Barnard, 1951: 138, pls. 42, 43.

Nordenstam (1933) stated that my figure (Barnard, 1914) of the mandible differed from that given by Stebbing (1900: pl. 38), apparently without noticing that the former was the male, notwithstanding that he himself examined a male. He was also unaware of the corrigendum relating to the 'mxp'.

Paraeopod 1 triunguiculate (or as worded by Menzies & J. L. Barnard (1951), 'biunguiculate, the inferior claw bifid') as in the other peraeopods.

Localities: Stream, at 150 ft. altitude, free-living; Beach debris, Glen mouth, on *Isocladus*; stomach of Soldier fish, on *Isocladus* (A 11. G. 64; A 27. M 1; B 10. M 88).

The occurrence free-living in a stream at 150 ft. altitude is interesting. Chilton (1909: 650) found them free-living at the mouths of fresh water streams in the Sounds on the west coast of New Zealand, often out of range of ordinary high tides. But at 150 ft. altitude the Gough Island individuals would be probably far above even an occasional splash of salt water.

Previously recorded as a commensal on the same Sphaeromid from Tristan.

Note on South African specimens. Menzies & J. L. Barnard (1951: 148) have relegated the specimens recorded from the Cape and Durban to 'species inquirendae', and state that the former are 'possibly not *Iais*'. This latter statement may perhaps have been due to the unfortunate typ. err. regarding the 3rd pleopod mentioned above.

I have re-examined Cape material, and find that the 1st peraeopod is triunguiculate as in the other peraeopods, and therefore these specimens can be assigned to *pubescens* as diagnosed by the collaborating authors. The enlargement of the mandibles in fully adult males, of which I have found two additional specimens, is also confirmed. Males with pleopods developed, and thus presumably functional, are much less common than females, and fully adult males with enlarged mandibles are rare.

A single specimen from Durban was in poor condition, and consequently indecisive. Possibly specimens from Natal and from Inhambane, Portuguese East Africa (University of Cape Town Ecological Survey) and from Ceylon may prove referable to *singaporensis* Menzies & J. L. Barnard.

Genus JAEROPSIS Koehler

Only the austral species are here considered. According to the position and shape of the uropods two groups of species can be separated (fig. 2). In *marionis*, *patagoniensis*, *intermedius* and *palliseri* they are inserted only a short distance apart, project straight backwards, and their inner margins are straight (or nearly so) and fit closely together. In *paulensis* and *curvicornis* (of Stebbing) they are inserted well apart, fold obliquely inwards, and even when fully folded their apices do not touch one another. The shape of the telsonic apex is correlated: triangular and more or less acute in the first, rounded in the second group. Other taxonomic characters seem to be variously distributed. Chilton's descriptions (1892a and 1912) of *neozeylanicus* are inadequate (see also Hurley, 1957: 19).

First group	Lateral margin head	Lateral margin telson	2nd antenna joints of peduncle	Uropod apex of peduncle	Maximilliped 2nd joint of palp
marionis	serrate	serrate	linear	hooked	?
patagoniensis	smooth	1 tooth	enlarged	hooked	linear
intermedius	serrate (anteriorly)	serrate	enlarged	hooked	lobed
vibicaria	smooth	smooth	enlarged	rounded	lobed
palliseri	smooth	smooth	enlarged	rounded	?
Second group					
curvicornis (Ceylon, S. Africa)	smooth	serrate	enlarged	hooked	lobed
paulensis (St. Paul)	smooth	smooth	enlarged	rounded	?lobed*
paulensis (Gough Is.)	smooth	smooth	enlarged	rounded	lobed

* Vanhöffen's fig. 59 *f* shows a linear joint but the palp has been displaced, either in dissection or mounting, and consequently no reliance can be placed on the shape, as drawn, being the true shape.

Jaeropsis paulensis Vanh.
(Fig. 2 *b*)

Jaeropsis paulensis Vanhöffen, 1914: 531, fig. 59 *a–l*.

Anterior half of head grey, forming a transverse bar, posterior half and upper lip creamy-white, peraeon irrorated with grey, paler than the bar on head, pleo-telson faintly dusted with grey, appendages creamy-white, eyes black.

Males 4–4·5 mm., ovigenous females 3–4·5 mm.

Appears to agree very closely with *paulensis* from St. Paul Island (southern Indian Ocean). The discrepancy in the palp of the maxilliped is probably explainable as suggested in the footnote to the table above.

The apex of the uropod is rather broadly rounded and has no hook, but the inner margin appears to be minutely serrulate.

Localities: Dell Rocks; West Point Reef (A 40. M 33; A 47. M 60; B 1. M 69; 1541).

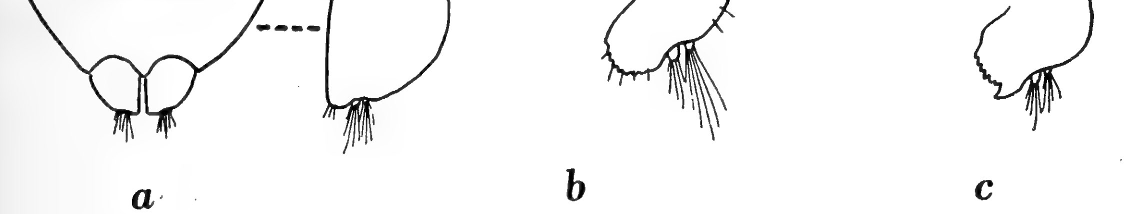

FIGURE 2. *Jaeropsis*. (*a*) *vibicaria* n. sp., pleo-telson, with uropod further enlarged. (*b*) *paulensis* Vanh. apex of telson, with uropod further enlarged. (*c*) 'curvicornis' (South Africa), apex of telson, with uropod further enlarged.

Jaeropsis vibicaria n. sp.
(Fig. 2 *a*)

Although only a single specimen is present, a new species seems unavoidable; its main taxonomic characters are given in the above table. Nordenstam (1933) had both sexes of *patagoniensis* and *intermedius*, consequently the smooth telsonic margin and lack of apical hook on the uropod cannot be attributed to sexual differences.

Antenna 2, left missing, right mutilated; 4th and 5th peduncular joints enlarged, with scarious outer edge which appears to be crenulate. Maxilliped, lobe of 2nd joint of palp extending only one-third length of 3rd joint; 6 coupling hooks.

Peraeopods and pleopods as for genus.

Uropods inserted close together, directed backwards, their inner margins straight and approximate, apex rounded, with 2–3 setae (?plumose); both rami minute, especially the outer ramus, each with a tuft of setae.

A dark grey triangular patch covering head except hind corners, continued as a mid-dorsal somewhat moniliform stripe on peraeon, expanding into a subtriangular patch on pleo-telson, but not covering the anterior corners or the posterior third; rest of body, and appendages creamy-white, eyes black. 5·5 mm.

Locality: Dell Rocks (A 47. M 60). One male.

The colour pattern resembles that figured for *patagoniensis* Richardson (1909: 421, fig.).

Jaeropsis curvicornis Stebb. (?*non* Nicolet)
(Fig. 1 *c*)

Jaeropsis curvicornis (?*non* Nicolet) Stebbing, 1905: 51, pl. xi, fig. C. Barnard, 1914: 224, pl. 20, fig. C.

Since my description of one male from the Cape, I have seen more material: St. James (False Bay) and Sea Point (Cape Town) (coll. K.H.B.), Lambert's Bay and Saldanha Bay (both on west coast) and Mossel Bay (coll. University of Cape Town Ecological Survey).

The lateral margin of head is smooth, that of pleo-telson serrate, both in juveniles and adults.

The uropod has an apical hooked tooth,* and the inner distal margin serrulate; each ramus with a tuft of setae. A better figure than my 1914 one is given here.

The colour resembles that of *paulensis*, and the dark crossbar on head offers a ready means of picking out this asellid from other species.

Presumably Stebbing was able to compare his Ceylonese specimen with Nicolet's description and figure; but it would be much more satisfactory to have a full description of specimens from the original Chilean locality. Until

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* Stebbing mistook this for the inner ramus; as also did Miss Richardson (1909) in her description of *patagoniensis*.

that is available I feel some hesitation in identifying Cape specimens with Nicolet's *curvicornis*, but none in identifying them with the 'curvicornis' of Stebbing.

Family **Munnidae**

Munna neozelanica Chilton

Munna neozelanica Chilton, 1892a: 267. 1892b: 2, pl. 1. figs. 1–8*a*, pl. 2, figs. 8*b*–15, Monod, 1931: 14, figs. 8*c*, 9 *c–e*.
Haliacris neozelanica (Chilton) Chilton, 1909: 650, fig. 14 *a* (prp. 1 ♂). 1912a: 132. Stephensen, 1927: 357.

Largest male 4 mm., smallest, with hammer-shaped 1st peraeopod 2·5 mm.; ovig. females 2·5–2·75 mm.

Peraeopod 1 of male, 'hammer' more strongly calcified than the other joints. The other peraeopods setose in male, especially 4th–6th joints of peraeopods 6 and 7.

Chilton and Monod figured the 1st peraeopod of a juvenile male (Monod's specimen 1·5 mm. in length), closely resembling that of the female figured by Chilton. Chilton figured three stages in the development of the 'hammer' (figs. 8*b*, 8*c*, 8*d*). giving the magnification of the figures but without stating the respective lengths of the specimens from which the appendages were removed. At what size, therefore, the change in shape occurs cannot be stated; in the present smallest male, 2·5 mm. in length, the peraeopod has already assumed its final shape, but of course is smaller than in the 4 mm. male. Chilton's largest specimen was 3 mm. in length.

No other Munnid has been described with the 1st peraeopod of the male shaped as in the New Zealand species, and the present specimens agree with the descriptions and figures of Chilton and Monod. Hitherto recorded only from New Zealand (south island) and the subantarctic Auckland and Campbell Islands.

Localities: Dell Rocks and shore nearer Base (A 40. M 27; A 47. M 33; B 5. M 84).

Family **Trichoniscidae**

Genus STYLONISCUS Dana

Vandel, 1952: 14.

Styloniscus australis (Dollfus)

(Fig. 3)

Trichoniscus (?) *australis* Dollfus, 1890: 6.
Styloniscus (?) *australis* (Dollfus), Vandel, 1952: 17.

Sparsely and minutely granulate, chiefly on posterior margins of head and peraeon segments. Eye composed of 3 ocelli in a triangle, contiguous or almost so.

Antenna 2, 5th joint with a basal and a subapical conical spine sometimes

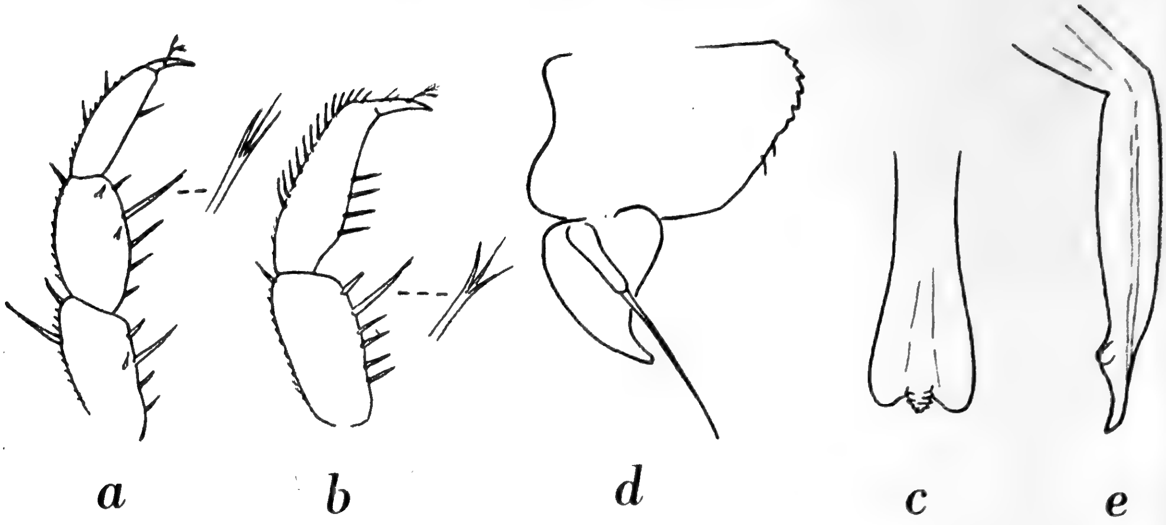

FIGURE 3. *Styloniscus australis* (Dollfus). (*a*) distal joints of peraeopod 1. (*b*) distal joints of peraeopods 6 and 7. (*c*) penial process. (*d*) pleopod 1 ♂. (*e*) pleopod 2 ♂.

1 or 2 smaller intermediate ones, and an apical spine on outer margin; flagellum 3-jointed, with apical tuft of setae, slightly shorter (excluding apical tuft) than 5th joint.

Maxilla 1, outer plate with 9 spines, the inner ones simple, and 2 accessory setae scarcely extending beyond the longest spines and extremely finely setulose, outer margin entire, setose. Maxilliped, basal plate with convex outer margin, apically lobed, palp (outer plate) unjointed, inner plate composed of 1 joint with a small terminal joint, the latter much smaller than in *magellanicus*, cf. *verrucosus* Budde-Lund (1906: pl. 4, figs. 10, 11) and Vandel (1952, fig. 9).

Peraeopod 1, 4th joint with one long and one short spine on outer margin, 4 spines on inner margin, the 3rd longest; 5th joint with 5 spines on inner margin, the 4th longest and apically trifid; 6th joint with 2 small spines on outer margin, one on inner margin. No sexual difference.

Peraeopods 6 and 7, 5th joint with 5 or 6 spines on inner margin, the subapical one longest and apically trifid; 6th joint with 4 spines on inner margin, a series of about 15 close-set spines on outer margin. No sexual difference.

Penial process with short, conical, wrinkled process in the apical emargination. Pleopod 1 of male, outer corner of basal plate serrulate. Pleopod 2 of male, see fig. 3*e*. Pleopod 5 of male, exopod grooved.

3·5–4 mm. × 1·3–2 mm. Mottled grey.

Localities: Gough Island: various, from Beach debris, Glen mouth, to summit of Expedition Peak, alt. 2950 ft.; and Penguin Island (A 1. G 5; A 2. G 13; A 2. G 23; A 8. G 56 [A 9 on label]; A 12. G 194; S [*sic*? =A] G 88; A 14. G 80; A 27. G 149; A 29. G 171; A 29. G 216; A 30. G 184; A 30. G 191; A 32. G 200; A 35. G 211; A 37. G 226; A 39. G 246; A 41. G 252; A 43. G; 268; B 3. G 305; B 3. G 315; B 8. G 338; B 13. G 373).

Tristan d'Acunha: Jenny's Watrin.

Vandel (1952: 99 and chart 76) said in regard to the geographical distribution of *Styloniscus*: South Africa (southern coastal area), Madagascar, Mauritius, Patagonia, Australia, Tasmania, New Zealand and southern islands, Crozet Is., and 'perhaps Tristan d'Acunha and Juan Fernandez'. Chilton's 'Marion Island' (*obiter dictum* 1915: 454), is surely a *laps. cal.* for Crozets, which is correctly listed in his *Subantarctic Islands New Zealand* (1909: 799).

The rediscovery of this species, first taken by H.M.S. *Challenger* on Tristan d'Acunha, is therefore welcome.

Family **Porcellionidae**

Porcellio scaber Latr.

Porcellio tristensis White, 1847: 99.
Porcellio scaber Latr., Barnard, 1932a: 252, fig. 21 *a–c*.

Localities: Gough Island: various, from the Glen up to Michael's Ridge, alt. 1000 ft. (A 1. G 5; A 2. G 13; A 2. G 23; A 4. G 30; A 8. G 53; A 13. G 73; S [*sic* ? = A] 13. G 88; A 14. G 80; A 16. G 84; A 16. G 93; A 21. G 117; A 21. G 119; A 24. G 127; A 27. G 149; A 28. G 164; A 35. G 211; A 37. G 222; A 38. G 236; B 3. G 305; B 11. G 350; B 13. G 365; B 13. G 373; B 14. G 380; B 15/16. G 397).

Tristan d'Acunha: Jenny's Watrin.

Collected on Tristan by Capt. Dugald Carmichael (1816) and described as a new species by White (1847); later recorded from Tristan by Barnard (1932a).

The Gough Island material comprises uniform slaty-grey and variously mottled specimens; some, e.g. from the Open *Phylica* forest by Lower Watersmeet (A 8. G 53) are very sparsely spotted with grey on a yellowish ground colour.

AMPHIPODA

Schellenberg, 1931; Barnard, 1932b; Stephensen, 1949; Macnae, 1953.

Family **Lysianassidae**

Parawaldeckia kidderi (S. I. Smith)

Parawaldeckia kidderi (S. I. Smith) Stephensen, 1927: 300, fig. 2. Schellenberg, 1931: 6 and 22 (contrasted with *Socarnoides kergueleni*). Stephensen 1949: 5.

Stephensen (1927) gave figures of uropod 3 in the two sexes: in the male it carries a brush of long setae.

Locality: Dell Rocks (B 2. M 75).

Recorded from Tristan and neighbouring islands (Nightingale and Inaccessible).

Acontiostoma marionis Stebb.

Acontiostoma marionis Stebbing, 1888: 709, pl. 30. Chilton, 1912b: 462. Barnard, 1932b: 32.
Acontiostoma magellanicum Stebbing, 1888: 714, pl. 31. (= juv.)

Gough Island, 100 fathoms (Chilton: *Scotia*).

Family **Stenothoidae**

Stenothoe sivertseni Steph.

Stenothoe sivertseni Stephensen, 1949: 9, figs. 2, 3. Macnae, 1953: 1026.

Locality: from *Macrocystis* kelp (M 25. Misc.).

Previously recorded from Tristan and neighbouring islands.

Family **Pontogeneiidae**

Pontogeneia tristanensis Brnrd.

Pontogeneia tristanensis Barnard, 1932b: 199, figs. 118 *m*, 120. Stephensen, 1949: 15.

Localities: Midshipman Rock, Dell Rocks, outer fringe kelp, kelp between Reef Point and Dell Rocks (A 42. M 34; A 44. M 34; A 44; B 1. M 65; BM. M 77; M. 25. Misc.).

Previously recorded from Tristan and neighbouring islands.

Paramoera tristanensis Brnrd.

Paramoera tristanensis Barnard, 1932b: 209, figs. 118 *k*, 127. Stephensen, 1949: 16. Macnae, 1953: 1026.

Localities: Dell Rocks and Half-way Cave (A 40. M 26; A 47. M 42; B 4. M 80; B 5. M 82).

Previously recorded from Gough Island, Tristan and neighbouring islands.

Family **Gammaridae**

Melita tristanensis n. sp.

Melita gayi (*non* Nicolet) Stephensen, 1949: 22. Macnae, 1953: 1027.

Agreeing with Stephensen's Tristan material in having no medio-dorsal tooth on pleon segment 4, and thus disagreeing with the South African *orgasmos* Barnard, 1940. Stephensen said pleon segment 5 had 'one pair of small subdorsal teeth'; the Gough Island specimens resemble *orgasmos* in having a pair of denticles with a seta between them *on each side* of the median line. I think one may assume that the two denticles in the Tristan specimens were actually double.

Side-plate 1 strongly expanded forwards as in *orgasmos*, but postero-inferior angle of pleon segment 3 quadrate with a small point (as in *palmata*).

In view of these conflicting characters it is difficult to decide what specific name to attach to the Tristan-Gough Island specimens. Schellenberg (1931: 203) separated *gayi* Nicolet (incl. *inaequistylis* auct.) from the northern *palmata* mainly because of lack of material for comparison; he made no mention of such critical characters as the dorsal dentation of the pleon, or the shape of the hind corner of pleon segment 3.

In 1940 (p. 454) I revised my opinion as to the identity of '*inaequistylis*' and its possible synonyms, and distinguished two species *orgasmos* Barnard and *zeylanica* Stebbing in the South African material previously recorded as *inaequistylis.* I consider it desirable to recognize distinct species in regions which have been separated for a considerable period, until material from each region has been thoroughly examined.

Therefore, because no detailed description has yet been given of the South American *gayi,* I attach a new name to the Tristan-Gough Island specimens.

A further question is: which characters are critical for defining the species? Typically *orgasmos* has a dorsal tooth on pleon segment 4, but sometimes (Barnard, 1940: 455) this is absent!

Colour (as preserved): purplish-brown, eyes black.

Locality: Dell Rocks (A 40. M 26; A 47. M 60).

Previously recorded from Tristan and neighbouring islands.

Family **Talitridae**

Orchestia platensis Kröyer

Orchestia platensis Kröyer, Stephensen, 1944: 57, figs. 15, 16. 1949: 25. Macnae 1953: 1027.
Orchestia tristensis (Leach MS.) White, 1847: 86.

Locality: Beach, opposite Hut (A 13. G 92).

Previously recorded from Tristan and Inaccessible Island.

Orchestia scutigerula (Dana)

Orchestia scutigerula (Dana) Stephensen, 1949: 26, figs. 11, 12; Macnae, 1953: 1027.

Localities: Penguin and Midshipman Islands (A 38. G 232; A 39. G 242; A 39. G 247; A 42. G 261).

Previously recorded from Nightingale and Inaccessible Islands.

Hyale hirtipalma (Dana)

Hyale hirtipalma (Dana), Stephensen, 1949: 30, fig. 13.

Only one Male (in B2. M 75) has the strongly setose flagellum of antenna 2 (cf. Barnard, 1916: 234); *per contra* the hand of gnathopod 2 lacks the characteristic brush of setae.

Localities: Beach debris, Glen mouth; Dell Rocks, Penguin Island, Half-way Cave, West Point Reef (A 27. M 11; A 28. M 18; A 28. M 19; B 2. M 75; B 4. M 79; B 5. M 82; 1541; 1543).

Previously recorded from Tristan and neighbouring islands.

Hyale grandicornis (Kröyer)

Hyale grandicornis (Kröyer), Chilton, 1912b: 508. Stephensen, 1949: 33. figs. 14, 15. Macnae, 1953: 1028.

Localities: Glen mouth and Dell Rocks (A 28. M 19; B 1. M 72; B 2. M 75).

Previously recorded from the shore of Gough Island by Chilton (1912), and by Stephensen (1949) from Tristan and Nightingale Island.

Allorchestes tristanensis Macnae

Allorchestes tristanensis Macnae, 1953: 220.

One immature female in the *Discovery* collection was assigned to this genus, and later collecting has confirmed its occurrence on Tristan. Stephensen (1949) regarded specimens as a variety of *Hyale grandicornis*, but Macnae (1953) has described them as a species of *Allorchestes*, commenting on the slight difference between the two genera.

Family **Aoridae**

Aora typica Kröyer

Aora typica Kröyer, Stephensen, 1949: 41, fig. 18. Macnae, 1953: 1032.

Locality: Dell Rocks (A 40. M 26; B 1. M 69).

Previously recorded from Tristan and neighbouring islands.

Family **Photidae**

Eurystheus remipes Brnrd.

Eurystheus ?afer Stebbing, Chilton, 1912b: 510, pl. 2, figs. 30–34.
Eurystheus remipes Barnard, 1932b: 229, fig. 143.

Gough Island, trawled in 100 fathoms (Chilton: *Scotia*).
Falkland Islands, 105–115 metres (Barnard: *Discovery*).

Family **Ampithoidae**

Ampithoe brevipes (Dana)

Ampithoe brevipes (Dana), Barnard, 1932b: 239, fig. 150. Stephensen, 1949: 44.

Locality: Dell Rocks, from kelp (A 44. M 34; B 1. M 69).

Previously recorded from Tristan and neighbouring islands.

Family **Jassidae**

Ischyrocerus longimanus (Haswell)

Ischyrocerus anguipes var. *longimanus* (Haswell), Barnard, 1932b: 243.
Ischyrocerus longimanus (Haswell), Stephensen, 1949: 45 (references). Macnae, 1953: 1032.

Locality: from kelp (M 25 Misc.; M 27).

Previously recorded from Tristan and neighbouring islands.

Stephensen (1949) considered that the true *anguipes* is confined to the northern hemisphere.

Family **Caprellidae**

Caprella acutifrons Latr.

Caprella acutifrons Latr., Barnard, 1932b: 300. Macnae, 1953: 1032.
Caprella acutifrons var. *natalensis* Mayer, Stephensen, 1949: 53.

Localities: from kelp (A 44. M 35; A 44. M 36; A 44 outer fringe kelp; M 24. Misc.; M 26; M 27).

Previously recorded from Tristan and neighbouring islands.

ACKNOWLEDGEMENT

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SUMMARY

An account is given of the Isopoda and Amphipoda of Gough Island (40° 21′ S., 09° 55′ W.) based on the collections of the Gough Island Scientific Survey, 1955–1956. Eleven species of Isopoda and sixteen species of Amphipoda are recorded, including six marine species of Isopoda new to the Tristan–Gough area. Two new species of Isopoda, *Paridotea apposita* and *Jaeropsis vibicaria*, and one new species of Amphipoda, *Melita tristanensis*, are described.

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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. I. DESCRIPTION OF A NEW SPECIES OF *PAVOCLINUS*, AND REDESCRIPTION OF *GYNUTOCLINUS ROTUNDIFRONS* (BARNARD)

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By

MARY-LOUISE PENRITH
South African Museum, Cape Town

(With 4 figures in the text and 1 plate)

CONTENTS

INTRODUCTION

During the course of a systematic and biological study of the South African fishes of the family Clinidae, extensive collecting has been carried out in the intertidal region of the south-western Cape coast.

In May 1963 two specimens of a clinid which could not be identified with any of the species known at present were collected with hand-nets from the dense beds of the green alga *Caulerpa filiformis* at Strandfontein, in False Bay. Eleven more specimens were subsequently collected from the same area, and recently a single specimen was collected at Onrus River mouth, near Hermanus.

The specimens were placed in the genus *Pavoclinus* Smith, 1945, on account of their lack of a supra-orbital tentacle, possession of a raised crest consisting of the first three dorsal spines, which is not separated from the rest of the fin by a notch in the membrane between the third and fourth dorsal spines, and their toothed vomer.

While collecting was being carried out in kelp-filled pools at the bottom of the intertidal zone at Lambert's Bay in January 1964, a male specimen of *Gynutoclinus rotundifrons* (Barnard, 1937) was caught. This species was previously known only from a single female specimen collected at Oudekraal in 1934 by the University of Cape Town. In March 1964 a juvenile specimen was collected from kelp in a gully at Lambert's Bay. A redescription of the species is desirable, since the holotype was not fresh by the time it was received by Dr. Barnard and the colouring had therefore completely disappeared, the male was unknown, and there are a few errors in the original description.

Ann. S. Afr. Mus. **48** (10), 196~~4~~5: 211–217, 4 figs., 1 pl.

Pavoclinus litorafontis n. sp.
(Pl. V, figs. 1, 2)

(*litorafontis* from *Litus, -oris*: beach; *fons, -ntis*: fountain)

Material: (*a*) From *Caulerpa* beds in the intertidal zone, Strandfontein: S.A.M. 23876, 2 specimens, male and female, 91 mm., 110 mm.; S.A.M. 23877, 2 males, 102 mm., 175 mm.; S.A.M. 23952, 4 specimens, 1 male, 3 juveniles, 46–132 mm.; S.A.M. 23962, two juveniles, 41 mm., 43 mm.; S.A.M. 23972, one male, 136·5 mm.; S.A.M. 24052, one male, 164·5 mm. (holotype); (*b*) from an intertidal pool at Onrus River mouth, in *Bifurcariopsis brassicaeformis*; S.A.M. 24081, one female, 64 mm.

Description: D. XXIX–XXXIII 6–8; A. II 20–23; P. 12; V. I 3; C. 13. Depth 4·5–5·75; Head 3·75–5 in standard length; eye 3·5–4·25 in head. Upper jaw (from angle of jaw to snout tip) 33·5–41·5% of head length (2·4–3 in head). Caudal peduncle length 58·5–75% of head length; caudal peduncle depth 22·5–33·5% of head length.

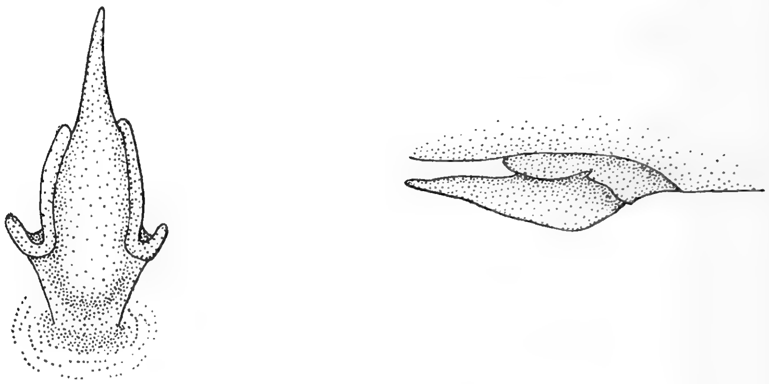
(*a*) Ventral view. (*b*) Lateral view.

Figure 1. Intromittent organ of Pavoclinus litorafontis.

First three spines of dorsal fin elevated to form a crest, decreasing in relative height with increase in size of fish. Not even a shallow notch in membrane between third and fourth spines. Upper pectoral rays short, pectoral fin roughly elongate-ovate. Inner pelvic ray stout, equal to others. Caudal peduncle long. Caudal fin subtruncate.

Body somewhat elongate, compressed, covered with small imbricating scales. Snout bluntly conical. Eye rounded, protuberant, equal to snout. No supra-orbital tentacle. Nasal cirrus a small flap. Lips moderately thick.

Lateral line of minute double and alternating single pores to the post-pectoral curve in the line, thereafter of minute, non-alternating single pores. Intromittent organ of male with a large, conical tip and a very short basal portion; a single pair of fleshy crescentic lips ensheathing the lower part of the tip (fig. 1).

Colour: Mainly green, with darker green, yellow, and iridescent silver longitudinal stripes. Usually a longitudinal silver or yellow stripe across the cheek and operculum. Fins green, dorsal and anal sometimes with translucent patches, always translucent patches in the caudal fin. Underparts green. The colouring is often much like that of the specimen figured in Smith (1949), No. 1001 (middle), as one of the colour variations of *Pavoclinus heterodon* (C. & V.), but the specimen is shown with a short caudal peduncle and a reduced inner pelvic ray. It is common for species of this genus to have silvery or pearly markings, often arranged longitudinally.

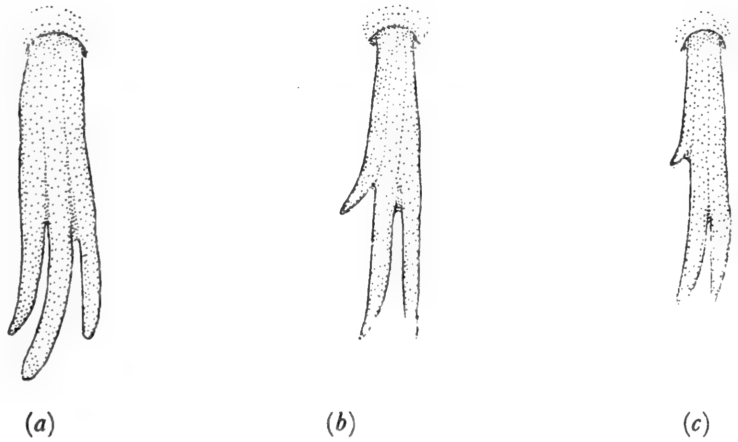

FIGURE 2. Left pelvic fin of (*a*) Pavoclinus litorafontis, (*b*) Pavoclinus heterodon, (*c*) Pavoclinus pavo.

Table 1. Fin counts and body proportions of the four species of *Pavoclinus*.

	litorafontis	*heterodon*	*pavo*	*profundus*
Dorsal spines	29–33	30–35	30–35	30
D. rays	6–8	4–6	2–4	4
A. rays	20–23	21–24	20–23	21
Head in S.L.	3·75–5	3·5–4·75	3·5–4·75	3·9
Depth	4·5–6	3·25–5	3·75–5	4·75
Upper jaw (% of head)	33·5–41·5	30–36	22–36·5	36
Caudal peduncle length (% of head) ..	58·5–75	26·5–38·5	40–46·5	36
1st d. spine (% of std. L.)	9–16·5	6·5–11	5·5–10·5	5·7
Eye in head	2·75–4·5	2·5–3·75	3–4	2·75

DISCUSSION

Only one specimen of *Pavoclinus profundus* was available for comparison, since this species is known only from the single specimen, taken in relatively deep water at Knysna (Smith, 1960). However, the specimen examined differs from *P. litorafontis* in a number of ways: *P. profundus* has a rather even dorsal fin, the first three spines not forming a crest; the inner pelvic ray is reduced; the caudal peduncle is short; there are fewer dorsal soft rays than in *P. litorafontis*.

For a comparison of the fin counts and body proportions of the four species of *Pavoclinus* see table 1.

Pavoclinus litorafontis differs from *P. heterodon* and *P. pavo* in that (i) the inner pelvic ray is not reduced, (ii) the caudal peduncle is very elongate, (iii) the dorsal soft rays are more numerous.

Pavoclinus heterodon and *P. pavo* both have the inner pelvic ray reduced to half or less than half the length and thickness of the other two rays (fig. 2), while in *P. litorafontis* all the specimens had the inner pelvic ray as stout as the other two and equal to them in length.

From table 1 it can be seen that the caudal peduncle of *P. litorafontis* is relatively considerably longer than that of *P. heterodon* or *P. pavo*. The caudal peduncle of *P. heterodon* is not elongate, the average caudal peduncle length for most of the South African Clinidae being about 25–35% of the head length. *P. pavo* has the caudal peduncle somewhat elongate, but in none of the specimens in the South African Museum collection did the caudal peduncle length approach that of *P. litorafontis*.

P. pavo has 2–4 dorsal soft rays, *P. heterodon* 4–6, and *P. litorafontis* 6–8 (see table 1), thus both *P. heterodon* and *P. litorafontis* may have 6 dorsal soft rays. However, by far the majority of the specimens of *P. heterodon* examined had 5 dorsal soft rays, while only one of the specimens of *P. litorafontis* had 6, so that there is little overlap between the two species in this respect.

P. litorafontis most closely resembles *P. heterodon* in that both are relatively large species with a bluntly conical snout, while *P. pavo* is a small species with an acutely pointed snout. *P. litorafontis* is more elongate and compressed than *P. heterodon*, and has a higher dorsal crest. This is particularly noticeable in the juvenile specimens of 40–60 mm., which in *P. litorafontis* have a high crest (12–16·5% of standard length), while the crest is lower in juvenile *P. heterodon* (7·5–10% of standard length). The differences in caudal peduncle length and in the development of the inner pelvic ray between these two species are particularly striking, and the specimens can almost invariably be separated by the soft dorsal ray count as well. Male and female specimens of *P. heterodon* of a similar size to the specimens of *P. litorafontis* were collected from the *Caulerpa* beds at Strandfontein at the same time and were clearly different from them in all the respects mentioned above, so that *P. litorafontis* cannot be regarded as a local or sexual variation or a geographical subspecies of *P. heterodon*.

It is rather unusual to find an undiscovered species of intertidal fish in a well-known area. However, no intensive collecting of Clinidae has been done in this area for many years, and probably none at Strandfontein, and as this species is well camouflaged, evidently fairly rare, and possibly restricted with regard to distribution, it is perhaps not surprising that it has only now come to light. Strandfontein is an extremely interesting area zoologically; during the present study another clinid, *Petraites brevicristatus*, previously known from only a few specimens, was found to occur in quite large numbers at Strandfontein, as well as the brotulid *Bidenichthys capensis*, also previously considered rare.

Gynutoclinus rotundifrons (Barnard, 1937)
(Figs. 3, 4)

Clinus rotundifrons Barnard, 1937: 63.
Gynutoclinus rotundifrons Smith, 1945: 358.

Material: S.A.M. 18587, one female, 83.5 mm., from kelp in an intertidal pool at Oudekraal, W. coast of Cape Peninsula (holotype); S.A.M. 24009, one male, 43·5 mm., from kelp, intertidal pool, Lambert's Bay; S.A.M. 24082, one juvenile male, 26 mm., from kelp, intertidal gully, Lambert's Bay.

Description: D. XXX–XXXII 8; A. II 22–23; P. 12–14; V. I 3; C. 13. Depth 3·8, 3·95 in larger specimens, 5·2 in juvenile. Head 3·7–4·15 in standard length; eye 3·5–4 in head. Upper jaw 42·5–54·5% of head length. Caudal peduncle length 28·6–36·4% of head length; caudal peduncle depth 28·6–32·2% of head length.

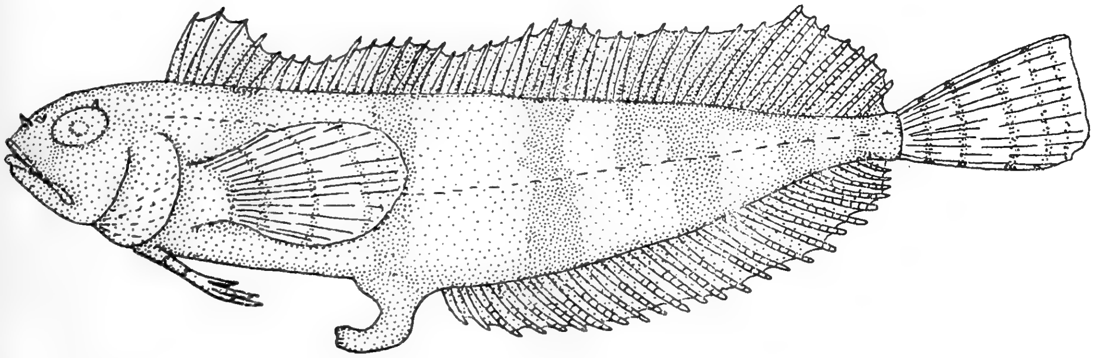

FIGURE 3. Gynutoclinus rotundifrons (Barnard), ♂, 43·5 mm. (Drawn as in life from specimen contorted on preservation).

First four dorsal spines slightly elevated, particularly in the two smaller specimens, to form a low, rounded crest, the second and third spines being the highest. Crest not separated from the rest of the fin by a notch in the membrane. Profile of dorsal fin undulating. Pectoral fin rounded. Inner pelvic ray reduced, not more than half of other two rays. Caudal peduncle short, about as broad as long. Caudal fin subtruncate.

Body compressed, not elongate, more so in the juvenile specimen than in the larger ones; covered with minute cycloid scales, not imbricating. Head spherical, inflated, broad, with mucus pores opening on conspicuous papillae. Eye rounded, somewhat protuberant. A minute, simple papilla over the eye. Anterior nostril tubular, nasal cirrus large, deeply bilobed. Posterior nostril conspicuous, surrounded by short, skinny flaps. Mouth rather large. Vomer toothed. Lips very thin.

Lateral line of single, non-alternating pores throughout, obsolete posteriorly in the holotype, but distinct on the caudal peduncle in the smaller specimens. Intromittent organ of male with a long basal portion and a club-shaped tip, ensheathed at the tip by a pair of thin, crescentic lateral lips and a minute pair of more or less confluent dorsal lips (fig. 4).

Colour: (*a*) Male, 43·5 mm. Ground colour pale brown with about seven darker brown irregular cross-bars, edged with iridescent blue in fine broken lines. A very dark brown narrow vertical line behind and above the pectoral axil, and another at the end of the caudal peduncle. Cross-bars of body continued on to the dorsal fin, with translucent patches between them; translucent areas with fine black dots. Dorsal fin uniformly dark brown posteriorly; a single small translucent patch at the base near beginning of dorsal soft rays. Caudal fin translucent with very faint brown cross-bars, darkening at the margins. Pectoral fin translucent with four very fine dark brown cross-bars, the proximal one curved. Anal fin mainly dark brown, with two translucent patches near the base. Pelvic fins light brown with dark brown cross-bars. Head mainly light brown below. A dark brown stripe from the eye forwards in front of cheek to angle of jaw. Head above and opercular region deep pink. Snout pink with a darker pink bar between the eyes and another above the upper lip, a fine darker pink line down the middle. Eye silvery with golden-brown radii. Chin and lips light brown mottled heavily with darker brown. Branchiostegal membranes and jugular region silvery grey with fine black speckling. Belly silvery with a golden-brown sheen. Intromittent organ of male greyish, with fine black speckling.


(*a*) Ventral view. (*b*) Lateral view.

FIGURE 4. Intromittent organ of Gynutoclinus rotundifrons.

(*b*) Juvenile, 26 mm. Whole body and head yellow, without cross-bars or markings, underparts lighter yellow. Dorsal fin with alternating pink and translucent patches. Anal fin yellow. Caudal and pectoral fins translucent. Pelvic fins yellow with brown cross-bars.

DISCUSSION

Neither Barnard (1937) nor Smith (1945) noticed the supra-orbital papilla. This is not surprising, as it is very small, and in the holotype had shrunk owing to desiccation in the preservative; in life it is erect and quite distinct even to the naked eye. None of the other South African Clinidae described have a simple supra-orbital papilla; either there is a multifid supra-orbital tentacle, or a supra-orbital outgrowth is completely lacking.

Gynutoclinus rotundifrons is apparently a weed-dwelling species, as all three specimens so far found were taken from amongst fronds of kelp. It is the only species which has not been recorded east of Cape Point, but if it is as rare as it appears to be, it is possibly more widely distributed.

ACKNOWLEDGEMENTS

Acknowledgement must be made to Dr. F. H. Talbot of the South African Museum for advice and help; to Professor J. L. B. Smith of the Department of Ichthyology, Rhodes University, for the loan of the unique specimen of *Pavoclinus profundus*; to my husband Mr. M. J. Penrith of the South African Museum, who collected most of the specimens studied, and to Mr. C. Berrisford for the Onrus River mouth specimen.

The Trustees of the South African Museum acknowledge the award of a grant by the Council for Scientific and Industrial Research for the publication of this paper.

SUMMARY

A new species of clinid, *Pavoclinus litorafontis* (Pisces: Clinidae), is described. *Gynutoclinus rotundifrons* (Barnard), previously known only from a unique specimen, is redescribed.

REFERENCES

BARNARD, K. H. 1937. Further notes on South African Marine Fishes. *Ann. S. Afr. Mus.* **32** (2): 41–67.

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.* Central News Agency Ltd., South Africa.

SMITH, J. L. B. 1960. A new species of South African clinid fish. *Ann. Mag. nat. Hist.* (13) **3**: 689–691.

Pavoclinus litorafontis n. sp.

The membrane between the dorsal spines and rays is continuous throughout the length of the fin, although in this plate the unpigmented areas are not visible (photograph: M. J. Penrith).

INSTRUCTIONS TO AUTHORS

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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.

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

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

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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).

F. W. GESS

CONTRIBUTION TO THE KNOWLEDGE OF THE SOUTH AFRICAN SPECIES OF THE GENUS *CERAMIUS* LATREILLE (HYMENOPTERA: MASARIDAE)

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By

F. W. Gess

South African Museum, Cape Town

(With 1 map)

Contents

Introduction

While arranging the Masaridae in the collection of the South African Museum according to the recent revision of the family by Richards (1962), it was found that this material, which was unfortunately not seen by Richards, supplemented his account in several instances, especially in the genus *Ceramius* Latreille.

In the present paper, dealing with the above genus, the hitherto unknown ♀ of *clypeatus* Richards and ♂ of *metanotalis* Richards are described; the ♂ assigned by Richards to *peringueyi* Brauns is removed from that species and together with a matching ♀ is described as a new species, *richardsi*, and lastly, ***rex*** de Saussure is resurrected. The locality records of all the specimens in the collection are given in the hope that these may aid in presenting a more complete picture of the distribution of the various South African species. Finally the distribution of the genus as a whole is discussed in the light of the biology of these wasps.

The sequence of species followed is nearly the same as that adopted by Richards, and this paper closely follows the presentation set by the latter in his revision. South African Museum is here abbreviated to S.A.M.

Descriptions of Species and Distribution Records

Ceramius cerceriformis de Saussure

Ceramius cerceriformis de Saussure, 1853: xxi, ♂; Richards, 1962: 97, ♂, ♀.
Ceramius (*Ceramioides*) *cerceriformis* de Saussure, 1854: pl. 4, fig. 1, ♂; 1855: 72, ♂.
Cerceris vespiformis de Saussure, 1855: 79, ♀.

Ann. S. Afr. Mus. **48** (11), 1965: 219–231, 1 map.

No specimens were found in the South African Museum collection that could be assigned to this species.

Ceramius schulthessi Brauns

Ceramius schulthessi Brauns, 1902: 182, ♀; Brauns, 1913: 196, pl. 2, fig. 6, ♂, ♀; Richards, 1962: 99.

Specimens examined: Cape Province: Willowmore, no date, 3♀♀ (one marked as co-type), 1. xii. 1904, ♀, xi. 1917, 2 ♀♀ (Dr. Brauns); Augusfontein, Calvinia, ix. 1947, 3 ♀♀ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, 3 ♀♀ (S.A.M. Staff); Touws River—Hondewater (18 miles E. of Touws River), xii. 1962, ♀ (S.A.M. Staff); Bloutoring Station (30 miles E. of Touws River), xii. 1962, 4 ♀♀ (S.A.M. Staff).

Namaqualand: Between Kamieskroon and Springbok, x. 1939, 4 ♂♂ 4 ♀♀ (S.A.M. Staff); Wallekraal, x. 1950, ♀ (S.A.M. Staff).

Ceramius peringueyi Brauns

Ceramius peringueyi Brauns, 1913: 194, ♀; Richards, 1962: 100 [♀ only].
[*non*] *Ceramius peringueyi* Brauns, Richards, 1962: 100, ♂ [= *richardsi* sp. n.].

Specimens examined: Cape Province: Stellenbosch, x. 1888, holotype ♀ (L. Peringuey) (Transvaal Museum); Het Kruis, x. 1947, 3 ♀♀ (S.A.M. Staff); Paleisheuwel, xi. 1948, ♀ (S.A.M. Staff).

Ceramius clypeatus Richards

Ceramius clypeatus Richards, 1962: 99, ♂.

♀. Black; raised disk of clypeus to a variable degree, inner orbits at deepest portions of ocular sinus, spot of variable size on tempora, usually a small spot on prepectus, variably sized spot at apex of scutellum, rarely a minute spot on propodeal spine, occasionally a short basal streak along outer side of fore tibiae and rarely indicated basal spots on outer side of mid and hind tibiae, spots at sides of gastral tergites 1–4 and usually also on 5, sometimes produced inwards on 2–5 either forming narrow continuous or interrupted bands, *creamy-white to yellowish.*

Underside of antennal joints 4–12 though sometimes fewer, legs except coxae, trochanters and base of femora, *orange.* Wings light fuscous, veins brown. Length 14–16 mm., length of fore wing 10·5–11·5 mm., hamuli 18–24.

Altogether very similar indeed to the male, the peculiarly modified clypeus, for example, except in its greater width in the female, being virtually identical in the two sexes. The chief secondary sexual structural differences are the following: eyes somewhat smaller, further apart, interocular distance at level of sockets twice length of scape (without radicle); antennal scape less curved and less robust, segment 3 shorter, only half as long as scape (without radicle), 4–10 progressively wider, 10 about 1½ times as wide as long, 11–12 a little narrower; fore trochanter simple.

From the specimens examined it appears that in both sexes the longer spur of the hind tibia is not originally simple but may become so by the loss or wearing away of the fine spines situated near the tip of the spur. While the trifid condition is common, there is a specimen with a 4-spined spur and others with all graduations to the simple condition.

Specimens examined: Cape Province: Clanwilliam, Nardouw, ix. 1941, 11 ♂♂, 2 ♀♀ (S.A.M. Staff); Het Kruis, x. 1947, 7 ♂♂ (S.A.M. Staff); Citrusdal Dist., xi. 1948, 5 ♀♀ (S.A.M. Staff); 4 miles S. of Clanwilliam, ix. 1961, ♀ (S.A.M. Staff).

Ceramius richardsi sp. n.

Ceramius peringueyi (*non* Brauns) Richards, 1962: 100 [*partim*, ♂ only].

The ♂ of this new species, which has been adequately described by Richards, was unfortunately assigned by him to *peringueyi* Brauns to which species it most certainly does not belong. This misidentification was made obvious by the discovery in the collection of the South African Museum of a hitherto undescribed ♀ which closely matches Richards' ♂ in all important characters such as the unusual form of the clypeus. That this latter character is of value in associating the sexes is demonstrated by the discovery, also in the South African Museum collection, of the hitherto undescribed ♀ of *clypeatus* Richards, a closely related species, the ♂ of which was used by Richards as a comparison in describing what he thought was the ♂ of *peringueyi* Brauns. In *clypeatus* Richards the form of the clypeus is common to both sexes. I have pleasure in naming the ♂ under consideration and the here described matching ♀ after the author, Professor Richards. The true ♂ of *peringueyi* Brauns is thus still unknown.

♀. Black; spot on mandibles near base, large discal spot on clypeus, inner orbits to top of ocular sinus, streak at top of tempora, two widely separated streaks on hind margin of pronotum, dot at apex of scutellum, moderately large spot on prepectus, small anterior spots at base of fore tibiae and end of mid femora, narrow lateral spots on gastral tergites 1–5 (tergite 6 hidden) produced inwards and forming narrow incomplete bands on tergites 2–3 and centrally widened ones on 4–5, *creamy-white*.

Antennal segments 4–12 beneath, portions of mandibles, anterior vertical portion of clypeus beneath disk, whole of legs except coxae of all legs and trochanters and bases of femora on mid and hind legs, *reddish*.

Wings fuscous, venation dark brown.

Length 15 mm., length of fore wing 10 mm., hamuli 21.

Head, thorax and gaster with long, rather dense, whitish hairs. Mandibles strongly striate distally, ending in two large blunt teeth with a smaller more dorsal one. Clypeus elongate, strongly raised, anteriorly falling at right angles towards ventral margin; length of vertical part $\frac{3}{5}$ length of disk; from just below point of inflection two small curved teeth project upwards; ventral margin produced, somewhat lamellate, truncate and slightly emarginate; disk narrower at apex than at base; anterior-lateral margins raised and slightly lamellate. Antennal sockets separated by 3½ times their diameter; interocular distance at level of sockets twice the length of scape (without radicle); total length of scape 3½ times greatest width (at apex); segment 2 very short, 3 slightly shorter than 4+5+6, 4–12 all of about same length, 4–10 becoming gradually and progressively wider, 11 slightly narrower than 10, 12 narrower still, rounded at apex. Disk of clypeus and small, roughly triangular area above it and between antennal sockets almost smooth; frons punctured; posterior ocelli a little in front of hind margin of eyes; distance between eye and posterior ocellus: distance between posterior ocelli = 10 : 7; occiput behind eye somewhat wider than interocellar distance; occipital keel present.

Thorax with fairly coarse, separated punctures, the interstices shining, about as wide or wider than the punctures. Mesoscutum shining; prescutal furrows deep over their entire length, especially so behind. Raised disk of scutellum with rounded edges and without a central keel.

Metanotum with a central prominence, lateral depressions fairly deep but open. Tegula smooth and shining, only the base punctured. Propodeum with fairly long blunt spines; posterior surface almost flat; spiracle with anterior margin strongly produced backwards. Fore tibial spur regularly curved, tip somewhat recurved. Mid and hind tibiae with two spurs, longer spur of hind tibia simple. Inner keel of hind coxa present on proximal half only. Claws simple. Gaster shining; tergite 1 constricted posteriorly, more finely punctured than thorax; tergites 2–6 becoming progressively finer punctured, 2 somewhat contracted at base.

Specimens examined: Cape Province: Clanwilliam, ix. 1928 (Dr. Brauns), Holotype ♂ (Transvaal Museum, Pretoria); Paleisheuwel, xi. 1948 (S.A.M. Staff), Allotype ♀ (S.A.M.).

The female has ten mites present on the axillae and lateral depressions of the metanotum.

Ceramius nigripennis de Saussure

Ceramius (*Paraceramius*) *nigripennis* de Saussure, 1854: pl. 3, fig. 4, ♀; 1855: 69.
Ceramius nigripennis de Saussure, Richards, 1962: 100.
Ceramius hessei Turner, 1935: 296, ♂, ♀.
[*non*] *Ceramuis nigripennis* of other authors.

Specimens examined: Namaqualand: Kamieskroon, ix. 1930, ♂ holotype, ♀ allotype of *C. hessei* Turner, 24 ♀♀ (S.A.M. Staff); between Kamieskroon and Springbok, x. 1939, ♂, ♀ (S.A.M. Staff); Bowesdorp, xi. 1931, ♂, ix. 1941, 2 ♂♂ (S.A.M. Staff); Outiep, Garies, ix. 1953, ♂ (J. du Toit).

Ceramius toriger von Schulthess

Ceramius toriger von Schulthess, 1935: 383, ♀; Richards, 1962: 101.

Specimens examined: Cape Province: Augusfontein, Calvinia, ix. 1947, 19 ♀♀ (S.A.M. Staff); Tankwa Karoo, Waterval, xi. 1952, 10 ♀♀ (S.A.M. Staff); 5 miles N. of Nieuwoudtville, ix. 1961, 2 ♀♀ (S.A.M. Staff).

A single female from Namaqualand: Knersvlakte, x. 1950 (S.A.M. Staff), differs from the description of this species and from the above listed specimens in that the light coloured markings are more extensive and are yellow, not ivory. Structurally there are no differences. The distribution of the yellow markings is given below.

Black; large spots on basal half of mandibles, clypeus (except for oblique black streaks arising from bottom of antennal sockets, infuscation between ends of these streaks and lateral margins, and ferruginous lateral and apical margins), a large pentagonal spot enclosing a black triangle on frons above clypeus, inner orbits to centre of ocular sinus, spots behind eyes, uninterrupted pronotal band extending onto sides, large spots on mesopleura, sides of mesonotum next to tegulae, a small median spot in posterior region of mesoscutum, posterior quarter of scutellum and centre of metathorax, streaks on axillae, whole of propodeum behind level of spiracles, broad apical bands widened laterally on tergites 1–5, tergite 6 except for depressed area, whole of sternite 2, wide apical bands on sternites 3 and 4, portions of femora and tibiae, *yellow*.

In addition, the antennae are much lighter in colour, the scape being largely yellow.

Ceramius braunsi Turner

Ceramius braunsi Turner, 1935: 294, ♂, ♀; Richards, 1962: 101.

Specimens examined: Cape Province: Olifants River, between Citrusdal and Clanwilliam, x–xi. 1931, ♂ holotype, ♀ allotype, 3 ♂♂, 32 ♀♀ (S.A.M. Staff); Pakhuis Pass, Clanwilliam, ix. 1942, ♀ (S.A.M. Staff); 4 miles S. of Clanwilliam, ix. 1961, 2 ♂♂, 2 ♀♀ (S.A.M. Staff).

Ceramius jacoti Richards

Ceramius jacoti Richards, 1962: 101, ♂, ♀.
Ceramius nigripennis (*non* de Saussure) Brauns, 1913: 201, pl. 2, fig. 3, ♂.

Specimens examined: Cape Province: Hex River, i. 1884, ♀; Oudtshoorn, Zebra, x. 1951, 17 ♀♀ (S.A.M. Staff); Ouberg Pass, S.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff); Verkeerde Vlei, Touws River–Hottentots Kloof, xii. 1962, 11 ♀♀ (S.A.M. Staff); Constable, xii. 1962, ♀ (S.A.M. Staff); Touws River–Ouberg Pass, xii. 1962, ♀ (S.A.M. Staff); 8 miles N.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 98 ♀♀ (S.A.M. Staff).

Ceramius beyeri Brauns

Ceramius beyeri Brauns, 1903: 69, ♂, ♀; Richards, 1962: 102, figs. 105–9.

Specimens examined: Cape Province: Willowmore, no date, ♀ cotype, 2 ♀♀ (Dr. Brauns); Somerset East, 25–30. xi. 1930, ♂, ♀ (R.E. Turner); Nieuveld

Escarpment, Rietvlei, i. 1949, ♀ (S.A.M. Staff); Tankwa Karroo, Renoster River, xi. 1952, 116 ♀♀ (S.A.M. Staff); Constable, xii. 1962, 3 ♀♀ (S.A.M. Staff); Matroosberg Station, xii. 1962, ♀ (S.A.M. Staff); Touws River–Hondewater (18 miles E. of Touws River), xii. 1962, 2 ♀♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 2 ♀♀ (S.A.M. Staff).

Ceramius damarinus Turner

Ceramius damarinus Turner, 1935: 293, ♂, ♀; Richards, 1962: 102.

Specimens examined: S.W. Africa: Ongandjera, iii. 1923, type ♂, 2 ♂♂ cotypes, ♂, type ♀ (S.A.M. Staff); Kamanyab, iii. 1925, 2 ♂♂ (S.A.M. Staff).

Ceramius lichtensteinii (Klug)

Gnatho lichtensteinii Klug, 1810: 36, 38, pl. 1, fig. 3, e and f.
Ceramius lichtensteinii (Klug), Klug, 1824: 225; de Saussure, 1855: 73, ♀; Brauns, 1913: 193; Bequaert, 1928: 145; Richards, 1962: 102.
Ceramius macrocephalus de Saussure, 1854: pl. 3, fig. 2, ♀; Brauns, 1903: 65, 68, ♂, ♀.
Ceramius rufomaculatus Cameron, 1906: 325, ♀.
[*non*] ?*Ceramius rex* de Saussure, Richards, 1962: 102.

Specimens examined: Cape Province: Willowmore, 15. xii. 1899, ♂, 10. i. 1900, ♀ (Dr. H. Brauns); Dunbrody, 1900, ♂, ♀ (Rev. O'Neil), 1901, ♀ (J. A. O'Neil); Uitenhage, Dunbrody, no date, ♀ (Rev. O'Neil); Pearston, 1905, 2 ♀♀ (Dr. Broom); Aberdeen, xi. 1935, ♀ (S.A.M. Staff); Tankwa Karroo, Waterval, xi. 1952, 21 ♂♂, 9 ♀♀ (S.A.M. Staff); Bloutoring Station, 30 miles E. of Touws River, xii. 1962, 2 ♀♀ (S.A.M. Staff).

South West Africa: Damaraland, 1890, ♀ (R. Lightfoot). It is very doubtful whether this last record is correct.

Ceramius caffer de Saussure

Ceramius caffer de Saussure, 1855: 76, ♀; Richards, 1962: 104, figs. 110–113, 115, ♂, ♀.
Ceramius consobrinus de Saussure, 1855: 77, ♀; Brauns, 1913: 198, ♂, ♀.

Specimens examined: Cape Province: Stellenbosch, x. 1888, 3 ♂♂, 2 ♀♀, no date, ♀ (L. Peringuey), 1908, 26 ♀♀ (C. P. Lounsbury).

All the specimens carry mites in the acarinarium.

Ceramius metanotalis Richards

Ceramius metanotalis Richards, 1962: 106, fig. 114, ♀.

♂. Black; whole disk of mandibles, labrum, clypeus except very narrow margins, roughly rectangular area above and between antennal sockets (separated from clypeus by a narrow black line at suture and produced slightly upwards at inner margins of antennal sockets and with a small black tubercle at centre), narrow orbits up to centre of eye emargination, small occipital spots behind upper portion of eyes, underside of antennal scape, underside of 2nd segment and basal two thirds of 3rd segment, pronotal band (narrowly interrupted at centre and produced on to humerus and to tegula), a minute spot on postero-lateral corner of mesoscutum and inner corner of axilla, sometimes a small spot at tip of scutellum, sometimes a very narrow streak on lower part of axilla, a spot at angles of propodeum, a single dorsal spot on mesopleuron, legs (except dorsal portions of coxae and trochanters, hind surface of middle and hind femora and tips of tarsal segments 3, 4 and 5 of above legs), inner margin of tegula, distal part of humeral plate, large spot on each side of first gastral tergite (not or only narrowly joined at hind margin), bands on tergites 2–5 (strongly widened at sides and plano-convex medially at hind margins), posterior portion of tergite 6 and small spot at sides of tergite 7, almost all of sternites 2–5 and sides of sternites 6 and sometimes 7, *pale yellow*.

Antennal flagellum except some black dorsal suffusion on all segments bar the last, *ferruginous*. Wings faintly brownish, veins brown. Length 17, 18, 19 mm., length of fore wing 12, 13, 13 mm., hamuli (20, 21), 22 (20, 22).

The chief secondary sexual structural differences are the following: Sides of clypeus more converging ventrally; margin narrower and very slightly concave. Eyes larger, a lot closer together; interocular distance at level of sockets = 1·5 times length of scape (without radicle) (2·2 in ♀). Antennal scape strongly widened, curved as in ♀; segment 3 flattened in side view, narrow except at apex, a little shorter than scape (without radicle) and slightly longer than 4+5+6; 4–11 becoming progressively wider; 12 forming a powerful, long, flattened and fairly wide hook, curved at base and at apex; inner surface of hook with a low, off-central, longitudinal carina on distal half; 8–10 with a shining, slightly raised transverse swelling beneath; entire underside of 11 swollen and shining. Fore trochanter with a very large, crescentic lobe, curving outwards, outer edge transparent, somewhat sinuate. Segment 1 of mid tarsus longer, curved; 2–5 strikingly laterally compressed, wide in side view; 3 and 4 almost oval in outline. Gaster with tergite 7 elongate, apically with a wide, shallow, angular emargination; sternite 3 with disk transversely swollen, raised on each side into a mound ending in a blunt tubercle, without raised preapical lateral keels; sternite 4 unmodified in structure; disks of both sternites 3 and 4 covered with dense white pubescence; sternites 7 and 8 very similar to those of *caffer* de Saussure; prominence on 7 more pronounced.

Specimens examined: Cape Province: Bulhoek, Klaver–Clanwilliam, x. 1950, 3 ♂♂, 27 ♀♀ (S.A.M. Staff).

Six of the 27 females have mites in the acarinium. The three males are free of mites, however.

Ceramius rex de Saussure

Ceramius rex de Saussure, 1855: 75, ♀; Turner, 1935: 290.
Ceramius lichtensteinii (*non* Klug), Richards, 1962: 102.

A single female specimen from Namaqualand: Klipvlei, Garies, xi. 1931 (S.A.M. Staff), believed to be this species, bears the label '*Ceramius rex* Sauss. ♀, det. Turner'. Concerning this specimen, Turner (1935: 290–1) correctly stated that it corresponds to the description of *rex* de Saussure, but measures only 19 mm., not 24. His further statement that it is allied to *lichtensteinii* (Klug) is incorrect for the specimen is entirely different from the latter species, being allied to *caffer* de Saussure and *metanotalis* Richards, though distinct from both of these. Richards (1962: 102) treated *rex* de Saussure as a doubtful synonym of *lichtensteinii* (Klug) but did not see the specimen now under consideration which appears to be the true *rex* de Saussure. The following is a description of this specimen.

♀. Black; clypeus, a large, broad pentagonal spot between the antennae and above the clypeus (from which it is separated by a narrow black line at suture), a narrow streak on inner margins of eyes below, streak in ocular sinus, spot on mandibles near base, underside of scape, spots behind eyes (joined along occipital margin), pronotal band produced onto humerus and to tegula (leaving a triangular black area on side), spot at postero-lateral corner of mesoscutum, inner corner and streak on lower part of axilla, posterior part of scutellar disk and flap of posttegula, central area of metanotum and portion below acarinarium, whole of propodeum (except for black region anterior to spiracles on sides, black lateral streaks on posterior surface near junction with metanotum and two black marks just above oriface), a large spot on mesopleuron, spots on anterior surface of coxae 2 and 3, portions of trochanters, greater part of femora and tibiae of all legs, inner margin of tegula, wide posterior bands widening on sides on gastral tergites 1–5, almost whole disk of 6, two small streaks on posterior area of sternite 1, whole of sternites 2–5 except extreme base of 2, *pale yellow.*

Anterior margin of clypeus, distal half of mandibles, antennal flagellum (except some black dorsal suffusion), some suffusion on tibiae and entire tarsi, suffusion on gastral sternite 6, *ferruginous.* Wings faintly brownish, veins brown.

Length 19 mm., length of fore wing 13·8 mm., hamuli 23.

Head, thorax and base of first gastral segment with long whitish hairs, densest on head, dense on pleura, sides and angles of propodeum; rest of gaster with very fine tomentum-like pubescence.

Clypeus one third longer than wide at ventral margin, moderately coarsely punctured; ventral margin truncate, sharply angled, with a fairly wide, smooth border. Antennal sockets separated by 4·1 times their diameter; interocular distance at level of sockets twice the length of scape (without radicle); scape (without radicle) almost 3 times as long as greatest width; segment 2 very short, broader than long; 3 half as long as scape (without radicle), twice as long as greatest width, of same length as 4+5+6; 4–10 progressively wider; 10 about twice as wide as long; 11 and 12 a little narrower. Frons dull, finely punctured; POL : OOL = 1 : 1·7; posterior ocelli about half ocellar diameter in front of hind margin of eyes; occipital keel absent. Pronotum with spiracular lobe well defined by a furrow; lateral furrow partially obscured by legs, apparently rather weak; anterior margin apparently not markedly keel-like; dorsal surface finely and closely punctured. Mesoscutum dull, finely, confluently punctured; prescutal furrows well marked over their entire length, especially behind; parapsidal furrows fairly weak; median notal suture marked anteriorly by a smooth, shining, unpunctured line, posteriorly marked by a furrow. Suture between axilla and scutellum with a pit ventrally. Raised disk of scutellum convex, in profile smoothly arcuate to posterior margin, with a well marked, raised, median keel and moderate lateral keels posteriorly, dull, punctured like mesoscutum; lateral declivities more shining, feebly punctured. Metanotum with central prominence smooth; acarinaria present laterally; entrance to acarinarium large, larger than that of *caffer* de Saussure, about 4 times longer than wide, width nearly constant throughout, only very slightly wider laterally; part of metanotum in front of slit of about same width as latter. Mesopleuron dull, with very close microscopic punctures and sparse coarse ones. Metapleuron dull, with similar but less pronounced puncturation and with some microscopic transverse striae on dorsal half; as in *metanotalis* Richards with a marked bean-shaped depression dorsally in the posterior boundary. Propodeum with angles rounded; posterior surface shallowly concave; spiracle long and narrow with anterior margin produced backwards. Fore tibial spur regularly curved, slightly recurved at apex; mid tibia with two spurs; larger spur of hind tibia bifid. Claws with a small tooth. Gaster dull, with exceedingly minute and close punctures, smaller than those of *metanotalis* Richards, and with very fine tomentum; larger punctures completely absent from all tergites; tergite 1 very transverse, nearly 3½ times wider than long, a little constricted posteriorly, with a hyaline border; tergite 2 constricted anteriorly, maximum width 1¼ times greater than maximum width of tergite 1; tergite 3 of equal width anteriorly as tergite 2 posteriorly; tergites 3–6 becoming progressively narrower; sternites nearly flat, very closely and finely punctured.

Four mites are visible in the acarinaria.

Ceramius bicolor (Thunberg)

Philanthus bicolor Thunberg, 1815: 131, 289 [♂].
Ceramius karooensis Brauns, 1902: 282, ♀, 373, ♂.
Ceramius bicolor (Thunberg), Schulz, 1912: 68–69, 99; Bequaert, 1929: 79; Richards, 1962: 115, figs. 131, 132.

Specimens examined: Cape Province: Aberdeen, xi. 1935, 3 ♂♂, 8 ♀♀ (S.A.M. Staff); Murraysburg Dist., xi. 1935, 6 ♂♂, 2 ♀♀ (S.A.M. Staff); Augusfontein (Calvinia), ix. 1947, ♂, 2 ♀♀ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, ♂ (S.A.M. Staff); Moordenaars Karoo, Lammerfontein, x. 1952, 3 ♀♀ (S.A.M. Staff); Willowmore–Vondeling, x. 1952, ♀ (S.A.M. Staff); Rooinek Pass, x. 1952, ♂ (S.A.M. Staff); Tankwa Karoo, Waterval, xi. 1952, 25 ♂♂, 85 ♀♀ (S.A.M. Staff); Touws River–Hondewater (18 miles E. of Touws River), xii. 1962, 5 ♂♂, 5 ♀♀ (S.A.M. Staff); Bloutoring Station (30 miles E. of Touws River), xii. 1962, 9 ♀♀ (S.A.M. Staff).

Ceramius linearis Klug

Ceramius linearis Klug, 1824: 227, ♂; Richards, 1962: 115, figs. 128–130, 113 (*b*).
Ceramius (*Paraceramius*) *linearis* de Saussure, 1855: 71, ♂.
Ceramius fumipennis Brauns, 1902: 275, ♂, ♀; Bradley, 1922: 397 (correction of Brauns).

Specimens examined: Cape Province: Algoa Bay, 25. xii. 1898, ♂, ♀ (Dr. H. Brauns); Dunbrody, 1900, ♀ (Rev. O'Neil); Aberdeen, xi. 1935, ♀ (S.A.M. Staff).

Ceramius capicola Brauns

Ceramius capicola Brauns, 1902: 278, ♂, ♀; Bradley, 1922: 397; Richards, 1962: 117.

Specimens examined: Cape Province: Willowmore, 1. x. 1899, ♀ (Dr. H. Brauns); Somerset East, 25–30. xi. 1930, 2 ♀♀, ♂ (R. E. Turner); Aberdeen, xi. 1935, 7 ♂♂, 3 ♀♀ (S.A.M. Staff); Murraysburg Dist., xi. 1935, 5 ♂♂, 11 ♀♀ (S.A.M. Staff); Teekloof, Fraserburg Dist., xi. 1935, 5 ♂♂, ♀ (S.A.M. Staff); Oukloof, Fraserburg Road, xi. 1936, 2 ♀♀ (S.A.M. Staff); Richmond Dist., xi. 1939, ♂ (S.A.M. Staff); Oudtshoorn, Zebra, x. 1951, 5 ♂♂, ♀ (S.A.M. Staff).

Ceramius socius Turner

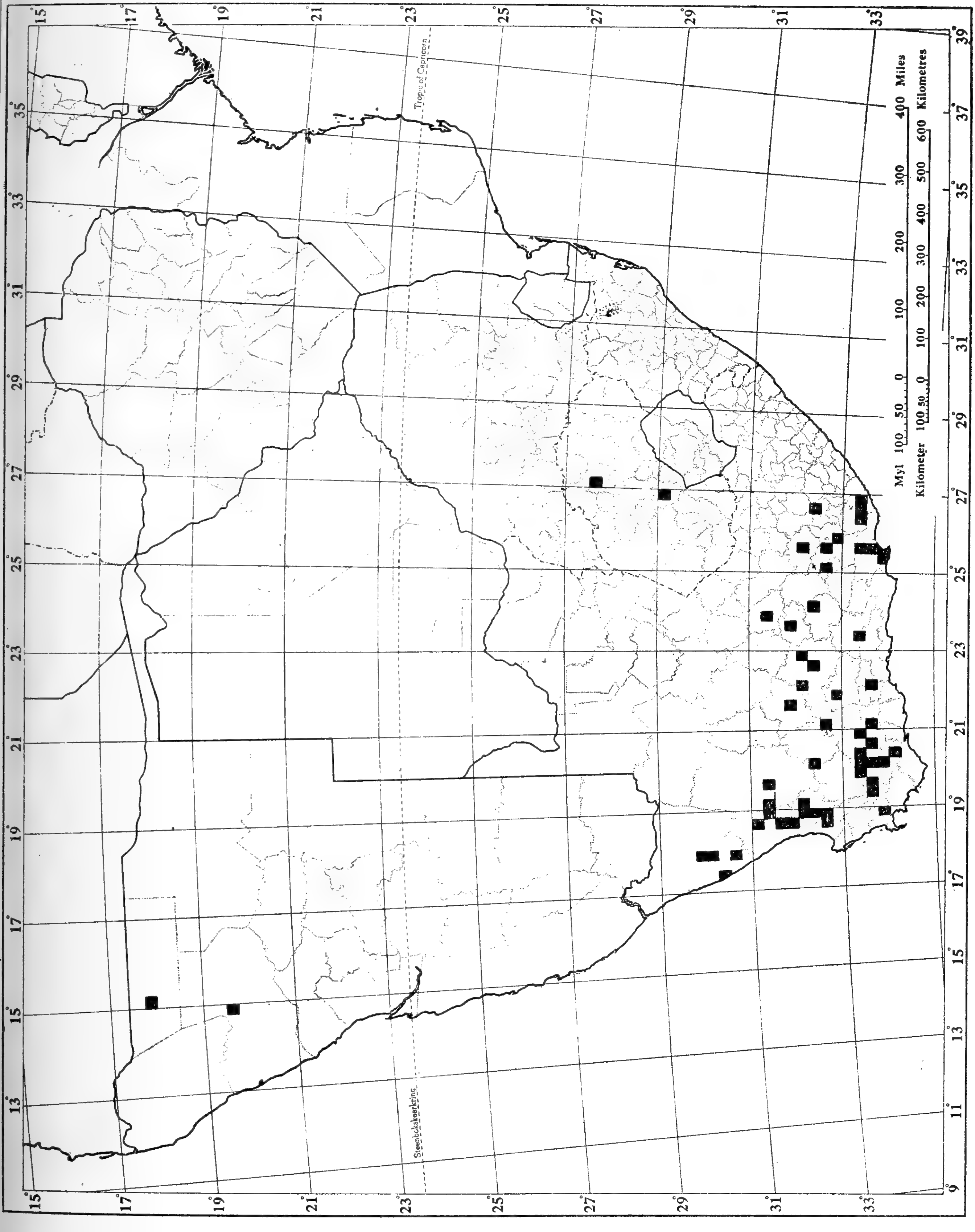
Ceramius socius Turner, 1935: 297, ♂, ♀; Richards, 1962: 117, figs. 113 (*a*), 134–136.

Specimens examined: Cape Province: Montagu, x–xi. 1919, ♀ (Collector's name not recorded); Worcester, ix. 1921, 2 ♂♂, 2 ♀♀ (R. E. Turner); Verkeerde Vlei (Touws River–Hottentots Kloof), xii. 1962, ♂, 13 ♀♀ (S.A.M. Staff); Constable, xii. 1962, 3 ♀♀ (S.A.M. Staff); Matroosberg Station, xii. 1962, ♂, ♀ (S.A.M. Staff); 8 miles N.E. of Touws River, xii. 1962, ♀ (S.A.M. Staff).

Discussion of the Distribution of the Genus *Ceramius*

The genus *Ceramius* occurs in two widely separated geographical regions in the Old World, one being the extreme south-west of the Ethiopian Region and the other that portion of the Palaearctic bordering on the Mediterranean Sea. Thus, in the Ethiopan Region, the genus is in the main restricted to the Cape Province where it is found in Little Namaqualand, the South Western Cape, the Little Karroo and the southern parts of the Great Karroo. It does not extend further east than the Great Fish River. Outside the Cape Province, one species (*damarinus* Turner) is endemic to South West Africa (Kaokoveld and Ovamboland), and one Eastern Cape species (*capicola* Brauns) has been recorded from two localities (Kroonstad and Thaba Nchu) in the Orange Free State. This distribution has been plotted by means of a $\frac{1}{4}$° square grid system on an outline plotting map (Map 1). In the Palaearctic, the genus occurs in Algeria, Morocco, Gibraltar, Portugal, Spain, the south of France, Greece, Turkey, Russian Armenia and probably Israel.

Climatically the above areas are characterised by a predominantly winter rainfall while the vegetation is generally low and semi-desert in nature.



Map 1. Distribution of the genus *Ceramius* in the Ethiopian Region.

In South Africa, *Ceramius* favours those parts of the Karroid and False Karroid areas (as defined by Acocks, 1953) which lie within the winter rainfall region, though two of the nineteen species, *damarinus* Turner and *capicola* Brauns, have been recorded from summer rainfall regions.

A study of the records shows that in the southern hemisphere no species flies earlier than September or later than March, while in the northern hemisphere no species flies earlier than March or later than August. In other words, flight is restricted to the dry spring and summer months succeeding the winter rainy season.

Having ascertained where and when *Ceramius* occurs it seems of interest to examine the reasons. In this connection the biology of the genus has to be taken into account. As stated above, the adults fly during the dry months of the year succeeding the winter rainy season. During this time mating takes place and burrows lined with mud pellets are built in the ground and surmounted by mud chimneys. In these the eggs are deposited and, in the South African species at least, it is recorded by Brauns (1910, cited by Richards, 1962: 29) that the female continues to provision the young with pollen and nectar until these larvae are ready to pupate, when she seals the opening to the nest with a plug of mud. There is only one generation per year.

Two requirements for the successful run of the life-history are immediately apparent: there must be a copious supply of pollen and nectar at the time the young are being reared and there must be an extended dry period, not only to allow the adult to collect this pollen and nectar but also on account of the fact that the burrows in the ground remain unplugged during the larval stage. Despite some possible protection afforded by the chimneys, the larvae would have little chance of survival in case of heavy rain.

The combination of winter rainfall followed by an abundance of suitable flowers rich in pollen and nectar during an extended dry period is obviously the clue to the distribution of the genus *Ceramius*. The only areas fulfilling these requirements are those in which *Ceramius* occurs. In this connection it is likely that the flowers visited by *Ceramius* will prove to be low-growing Compositae and mesembryanthemums (Aizoaceae) which, following the winter rains, are such a striking feature of the semi-desert areas inhabited by *Ceramius* in South Africa.

Summary

The account of the South African species of *Ceramius* included in the revision of the Masaridae by Richards (1962) is supplemented by the study of the material in the South African Museum collection.

One new species, *richardsi*, and the hitherto unknown ♀ of *clypeatus* Richards and ♂ of *metanotalis* Richards are described as is also a specimen thought to be *rex* de Saussure. The locality records of all the specimens in the collection are given and the distribution of the genus in South Africa is mapped. Lastly the distribution of the genus as a whole is discussed with reference to the biology of these wasps.

ACKNOWLEDGEMENTS

I wish to thank Dr. G. van Son of the Transvaal Museum, Pretoria for the loan of type material of *peringueyi* Brauns, *clypeatus* Richards and *metanotalis* Richards. The Trustees of the South African Museum are grateful to the Council for Scientific and Industrial Research for a grant to publish this paper.

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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).

L. D. BOONSTRA

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THE RUSSIAN DINOCEPHALIAN *DEUTEROSAURUS*

By

L. D. Boonstra

South African Museum, Cape Town

Contents

Introduction

In recent compilative publications in English, German, French and Russian the compilers Romer, von Huene, Piveteau and Orlov, in following the latest views of our Russian colleagues Efremov and Orlov, have added the weight of their authority to perpetuate some rather serious mistakes.

I have, during a four weeks' stay in Moscow, had the opportunity of studynig the dinocephalian material housed in the Palaeontological Museum of the Academy of Sciences of the U.S.S.R. and feel that a preliminary note pointing out these errors would be welcomed by those who have not had the opportunity of seeing the material for themselves.

Deuterosaurus

Orlov in 1954 gave a full account of all the material he considered warranted inclusion under the appellation *Deuterosaurus*.

This material consists of parts of two skulls, teeth and many postcranial bones of which there is little evidence of having been found in association. In fact, except in the case of some postcranial bones, there is definite evidence that they were not found in association. These separate finds have on various grounds been considered to belong to one and the same genus.

This lumping together started on its false course seriously when Seeley in 1894 described specimen No. 2 and identified it as a second specimen referable to Eichwald's type (No. 1) of *Deuterosaurus* and produced a composite drawing of a skull in which the type lower jaw, teeth and partial occiput were fitted to the distorted partial skull of No. 2 and associated with this some vertebrae, a femur, a radius, part of a humerus and scapula and parts of the pelvis. Eichwald's type specimen (No. 1) consists of a lower jaw from which the nature of the incisors, canines and postcanines as well as that of the upper incisors and canines can be determined and fitting on to this are the posterior part of the lower jaw, suspensorium, parts of the occiput, braincase and subtemporal and suborbital arches.

Ann. S. Afr. Mus. **48** (12), 1965: 233–236.

This specimen (No. 1) constitutes the type of Eichwald's *Deuterosaurus biarmicus*.

The Diagnostic Characters of the Genus DEUTEROSAURUS:

1. Dental formula: $i\frac{5}{4}\quad c\frac{1}{1}\quad pc\frac{1+?}{6+?}$
2. Incisors and canines of the upper and lower jaws intermesh.
3. Lower canine passes outward of upper jaw margin.
4. Incisors fairly long, with slight lingual step, unequally developed in the different teeth and separated from the talon.
5. Postcanines with bulbous spatulate crown; series short, probably not more than 8.
6. Quadratojugal no longer a bone of the outer lateral surface.
7. Quadrate posteriorly situated and lower jaw long.
8. No boss on the angular.
9. Slight indication of upward sweep of the premaxillaries.
10. Snout probably higher than broad.
11. Infra-temporal bar fairly weak with deep temporal fossa.

Taxonomic Position of DEUTEROSAURUS:

It is evident that the type is poor and important diagnostic features are not preserved.

Of the determinable characters none are typically tapinocephalian, but rather represent a mixture of anteosaurian and titanosuchian features.

The anteosaurian features are:

the short series of bulbously spatulate postcanine teeth;
the fairly long incisors, but the lingual step is more pronounced than is usual in the better known anteosaurians:
the medial shift of the quadratojugal, which is no longer a lateral surface bone;
the slight upward sweep of the alveolar border of the premaxillaries;
the snout probably higher than broad;
the weak infra-temporal bar and deep temporal fossa.

The titanosuchian features are:

the intermeshing of the upper and lower canines with the lower canine passing outside the upper jaw;
the absence of the angular boss and the general little pachyostosis.

I would thus place *Deuterosaurus* in a separate family—Deuterosauridae—in the Infra-order Anteosauria.

Postcranial Bones referred to DEUTEROSAURUS:

The femur is represented by a number of specimens (Nos. 59, 13, 1/1326, 294/20, 72). All indicate a slender curved femur quite distinct from the femur of both Tapinocephalia and Titanosuchia, but strikingly similar to the few known femora of the South African Anteosauria.

If the type jaws of *Deuterosaurus* are, as I am convinced, anteosaurian and the femora also anteosaurian it may very well be that the above specimens are correctly referred to *Deuterosaurus*, but they could equally well be referred to one or other of the other known Russian anteosaurians as e.g. *Titanophoneus*, *Doliosauriscus*, *Syodon*, *Admetophoneus*.

The distal end of a humerus (No. 33) and the tibia (No. 86) also appear to be anteosaurian.

MNEMEIOSAURUS

Specimen No. 2, which Seeley (1894) mistakenly referred to Eichwald's *Deuterosaurus*, consists of an incomplete and distorted skull from which few diagnostic features can be determined.

Diagnostic Characters of the Genus MNEMEIOSAURUS:

1. Dental formula: $i\frac{?}{?}\quad c\frac{1}{?}\quad pc\frac{1+?}{?}$
2. Crown of postcanine tooth spatulate.
3. Intertemporal width small, with high and sharp parietal crest flanked by the postorbital.
4. Anterior to the temporal fossa proper there is a sloping surface, below the level of the dorsal surface proper, which is formed by the postfrontal, frontal and postorbital (cf. *Phthinosuchus*).
5. Pachyostosis moderate.
6. Skull and particularly the snout, high and apparently short.
7. Orbit large.
8. Postorbital bar slender, but forming a wide flange of bone forming the posterior bony face of the orbit (cf. *Phthinosuchus*).
9. Vomers narrow, choanae short.
10. Pineal canal of moderate length.
11. Lacrimal with antero-dorsally directed process as in *Ulemosaurus*.
12. Vomers narrow and vaulted as in primitive gorgonopsians (*Phthinosuchus*), but posteriorly spatulate.

Mnemeiosaurus, on the scanty evidence, is difficult to place taxonomically, but is probably a tapinocephalian as suggested by Nopcsa. The presence of a canine indicates a primitive form but otherwise it appears quite specialised.

Provisionally it may be placed with the moschopids, where a form like *Avenantia* also has a narrow intertemporal region.

Teeth referred to DEUTEROSAURUS:

The teeth numbered No. 3, 4 and 5 and figured by Efremov (figs. 19, 20, 21) were not found in association with either specimens No. 1 or No. 2.

They are quite distinct from the incompletely preserved incisors of the type of *Deuterosaurus* (No. 1) and no comparison is possible with the one incisor root preserved in *Mnemeiosaurus* (No. 2).

The teeth in *Deuterosaurus* (No. 1) are slightly modified anteosaurian teeth.

Tooth No. 4 approaches most nearly to the incisor teeth of the Tapinocephalidae.

Teeth No. 3 and No. 4 may very well be of a form very close to *Ulemosaurus*.

The incisor teeth hitherto considered as deuterosaurian are thus really typical of the Tapinocephalia and the real deuterosaurian incisors are really anteosaurian incisors.

SUMMARY

The Russian dinocephalian *Deuterosaurus*, is discussed after study of the material in Moscow and it is shown that some material has been erroneously included in this genus. It is considered that the type species, *Deuterosaurus biarmicus* Eichwald should be placed in the family Deuterosauridae, in the infra-order Anteosauria. *Mnemeiosaurus*, which was referred to *Deuterosaurus*, appears to be a tapinocephalian which might be placed provisionally with the moschopids. The true affinities of postcranial bones and teeth that had been referred to *Deuterosaurus* are considered.

ACKNOWLEDGEMENTS

The author's visit to Moscow was in part made possible by a special grant from the Department of Education, Arts and Science of the Government of the Republic of South Africa. In Moscow my work was greatly facilitated by the kind helpfulness of my colleagues Orlov, Tchudinov, Shishkin and Tatarinov. To them my sincerest thanks.

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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).

LIEUWE DIRK BOONSTRA

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

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

By

LIEUWE DIRK BOONSTRA

South African Museum, Cape Town

(With 11 figures in the text)

CONTENTS

INTRODUCTION

From the *Tapinocephalus* zone twelve gorgonopsian species have been described, each based on a single specimen, the number of genera being eleven. Of these eleven Watson has put eight into five separate families with the remaining three uncertain as to family. Only six species are based on adequate skulls. Hitherto the postcranial skeleton in only one specimen has been described.

In the South African Museum we have eighteen specimens and of these parts of the girdles and limbs are present in only six specimens.

MATERIAL

Specimens with parts of girdles and limbs preserved are:

S.A.M. 8950. *Hipposaurus boonstrai.* Holotype.
Skull and most of the skeleton much damaged in preparation by a labourer under direction of S.H. Haughton.
Klein-Koedoeskop, Beaufort West, Low *Tapinocephalus* zone. Collected Boonstra 1928.

S.A.M. 9012. Gorgonopsian.
Isolated proximal end of a femur.
Klein-Koedoeskop, Beaufort West.
Low *Tapinocephalus* zone. Collected Boonstra 1929.

Ann. S. Afr. Mus. **48** (13), 1965, 237–249, 11 figs.

S.A.M. 9081. *Hipposaurus major*. Holotype.
Skull, incomplete pectoral and pelvic girdles, distal end of front epipodial and incomplete manus.
Klein-Koedoeskop, Beaufort West.
Low *Tapinocephalus* zone. Collected Boonstra 1929.
S.A.M. 9084A. ?*Hipposaurus major*.
An isolated humerus lacking the proximal head.
Rietkuil, Beaufort West. Low *Tapinocephalus* zone.
Collected Boonstra 1929.
S.A.M. 12010 Galesuchid?
Bloemhof of Voëlfontein, Prince Albert.
Low *Tapinocephalus* zone. Collected Boonstra and Zinn 1956.
S.A.M. 12118A. Galesuchid.
Part of pelvis associated with a snout.
Palmietfontein of Kruidfontein, Prince Albert.
Low *Tapinocephalus* zone. Collected Boonstra and Zinn 1957.

Pectoral Girdle

(Figs. 1 and 2)

In the two species of *Hipposaurus* the two specimens have the pectoral girdle adequately preserved, but in neither is the cleithrum and in only one is the ossified sternum preserved in part.

The coraco-scapula is well developed with the scapular blade lying at right angles to the vertebral axis but curving slightly around the thorax. The coracoidal plate is large and long and rests on the interclavicle. There is no supraglenoidal buttress or foramen. The scapular facet of the glenoid faces downwards and backwards and slightly outwards.

The coracoidal facet faces upwards and slightly outwards. The precoracoid forms the anterior corner of the glenoid. Immediately anterior to the glenoid, but in a slightly higher level, the precoracoid is pierced by a fairly large foramen supracoracoideum.

Above the glenoid on the posterior edge of the scapula is an indistinct scar for the origin of the scapular head of the triceps muscle. The coracoid is without a process or even a scar for the origin of a coracoidal head of the triceps.

The dermal clavicular girdle is well developed, except the cleithrum which was apparently a slender splint-like bone judging by the facet on the anterior edge of the scapular blade.

The interclavicle is well developed with a broad spatulate anterior expansion curving slightly upwards, a constricted waist and a fairly long and broad tongue-like posterior part.

The anterior spatulate end is underlain in its lateral part by the broad ventral end of the clavicula, which ends well away from the middle line and

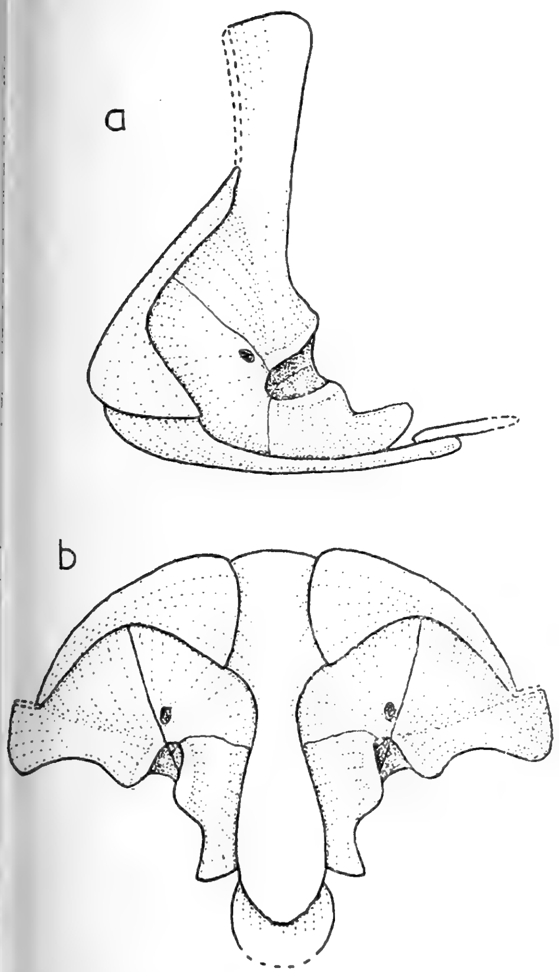

Fig. 1. *Hipposaurus boonstrai. Holotype. S.A.M.* 8950.
Pectoral girdle × ⅓. *a*. Lateral. *b*. Ventral

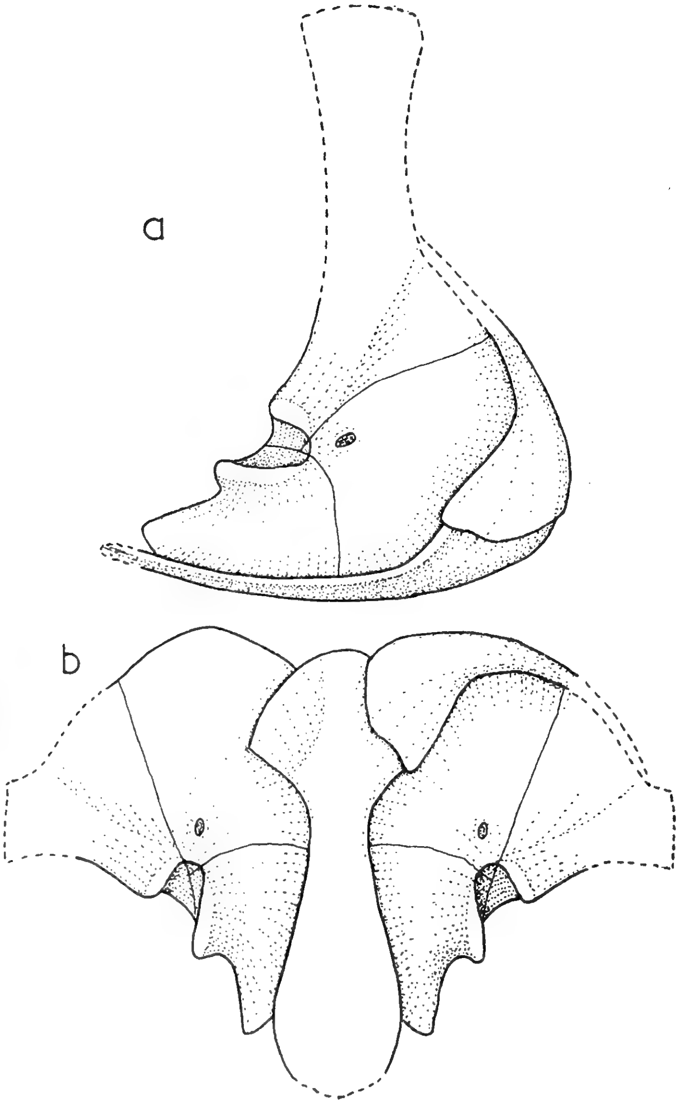

Fig. 2. *Hipposaurus major*. Holotype. S.A.M. 9081.
Pectoral girdle × ⅓. *a*. Lateral. *b*. Ventral.

which has no posteriorly directed process to underlie the interclavicle in posterior direction as is the case in the pristerognathid clavicle.

From its broad, ventral expansion the clavicle sweeps upwards with a rather slender process lying externally and extending slightly anterior to the curved anterior edge of the scapulo-coracoid. Its upper extremity is applied to the anterior scapular edge, where it also meets the ventral end of the cleithrum.

The sternum is ossified as a flattish disc-like element lying above the posterior end of the interclavicle. No facets for the ribs can be seen.

PELVIC GIRDLE

(Figs. 3 and 4)

The two specimens of the two species of *Hipposaurus* have the pelvic girdle preserved in part. In both the iliac blade is poorly preserved, but the

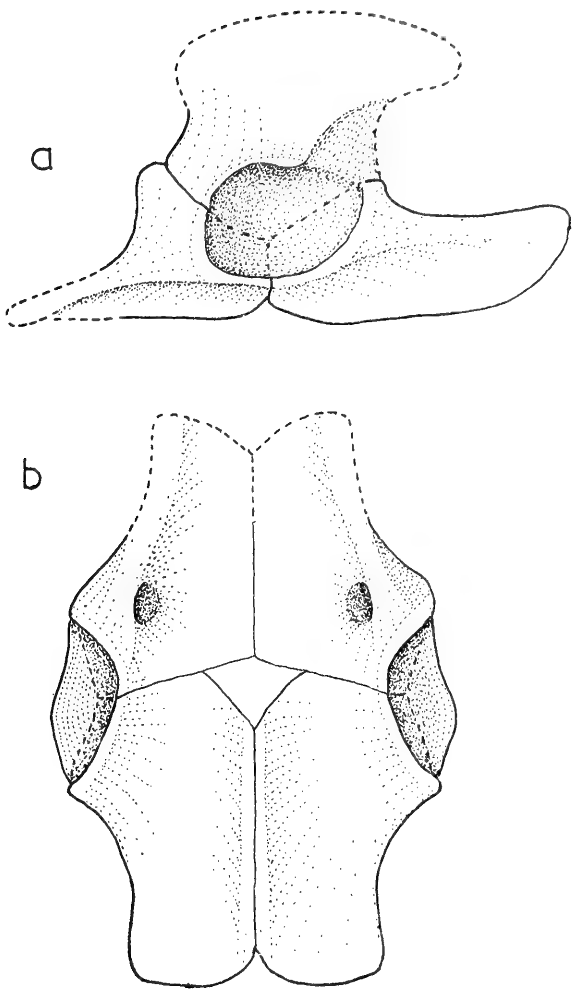

Fig. 3. *Hipposaurus major*. Holotype. S.A.M. 9081.
Pelvic girdle × ⅓. *a*. Lateral. *b*. Ventral

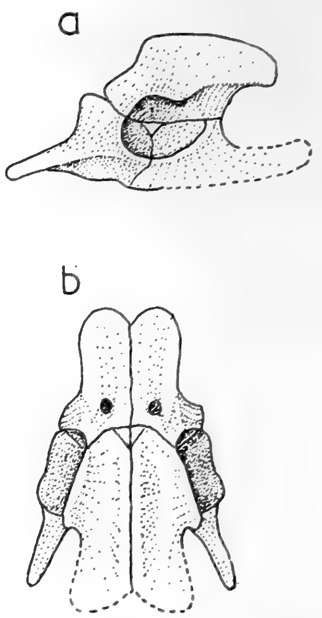

Fig. 4. Galesuchid. S.A.M.
12118 A.
Pelvic girdle × ⅓. *a*. Lateral
b. Ventral.

two ventral elements are adequately represented. Associated with a snout identified as a galesuchid species there is the left half of a pelvis with a damaged iliac blade, a good pubis and an incomplete ischium.

From this inadequate material it would appear that the oldest gorgonopsians of the *Tapinocephalus* zone had a low, long pelvic girdle, flattish in its pubic part and V-shaped in its ischiadic part.

The ilium was apparently low. Its blade has little or no anterior process, but with a well developed long but low posterior process. The supra-acetabular edge is sharp with only a weak supra-acetabular buttress, but with a distinct supra-acetabular notch.

The ilium forms about half of the large outwardly facing acetabulum.

The pubes form a flat pelvic floor, long but not very broad. The pubic tubera are weakly developed, but the lateral edge in *Hipposaurus* is strong and girder-like. Each pubis is pierced by a fairly large foramen lying some distance anterior to the posterior pubic edge, facing ventrally it is obscured in lateral view by the girder-like thickened outer pubic edge. Ventrally the two pubes do not form a keel, where they meet in the median line. In the median line a diamond-shaped lacuna separates the pubes from the ischia.

The ischia meet in the middle line as a strong symphysis forming a well developed ventral keel. Together they are broader than the pubes and also longer. The postero-lateral corners, although thickened, are hardly tuber-like. The ischium forms a strong posterior rim to the acetabulum.

The Humerus
(Figs. 5 and 6)

In the holotype of *Hipposaurus boonstrai* there is a good complete right humerus and the distal end of the left humerus. In addition I have the distal three-quarters of a larger humerus found unassociated with any other part of the skeleton, which I tentatively identify as that of ?*Hipposaurus major*.

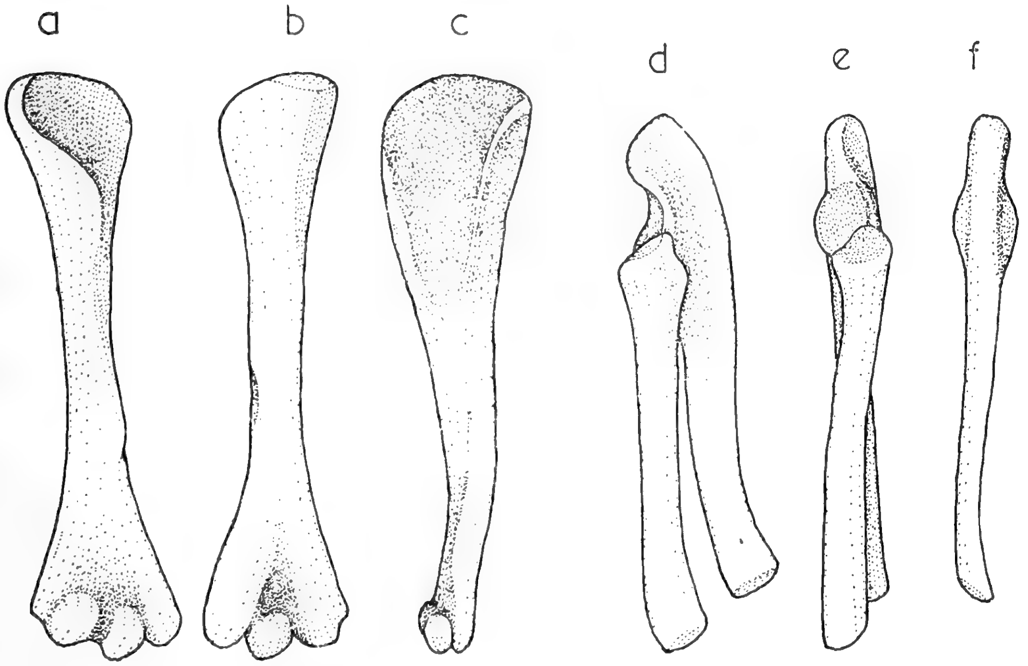

Fig. 5. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950.

Humerus × ⅓. *a*. Ventral in orthoprojection on the distal expansion. *b*. Dorsal in orthoprojection on the distal expansion. *c*. Posterior in orthoprojection on the distal expansion.
Ulna and radius × ⅓. *d*. Anterior. *e*. Median. *f*. Lateral or outer view of the ulna.

The hipposaurid humerus is relatively a long slender bone with a long slender shaft and both the proximal as well as the distal ends moderately expanded. There is a considerable 'twist' on the shaft so that the ends subtend an angle of about 70°.

In the figures the views called dorsal, ventral and posterior are orthoprojections on to the plane in which the distal condyles lie.

The caput is terminal, narrowly oval, flowing into the processus medialis and lateralis, both indistinctly demarcated. The delto-pectoral crest is of moderate size with no distinct pectoralis tuber. The bicipital fossa is deep and long. The surface for the origin of the medial humeral head of the triceps is well developed. Midway on the shaft there is on the ventral surface a strong ridge lying somewhat posteriorly, flanked by a groove on its postaxial side. This would appear to serve for the insertion of the m. coraco-brachialis longus.

The distal end is remarkable in that no epicondylar foramina are present. In ventral view a longitudinal groove can be seen near the postaxial edge, which is sharp and bent backwards, and this entepicondylar groove housed the median vessels usually passing through the entepicondylar foramen. A similar edge and groove, but of much weaker development on the radial side carried the radial vessels which pass through the ectepicondylar foramen when this is present. Distally the entepicondyle is better developed than the ectepicondyle.

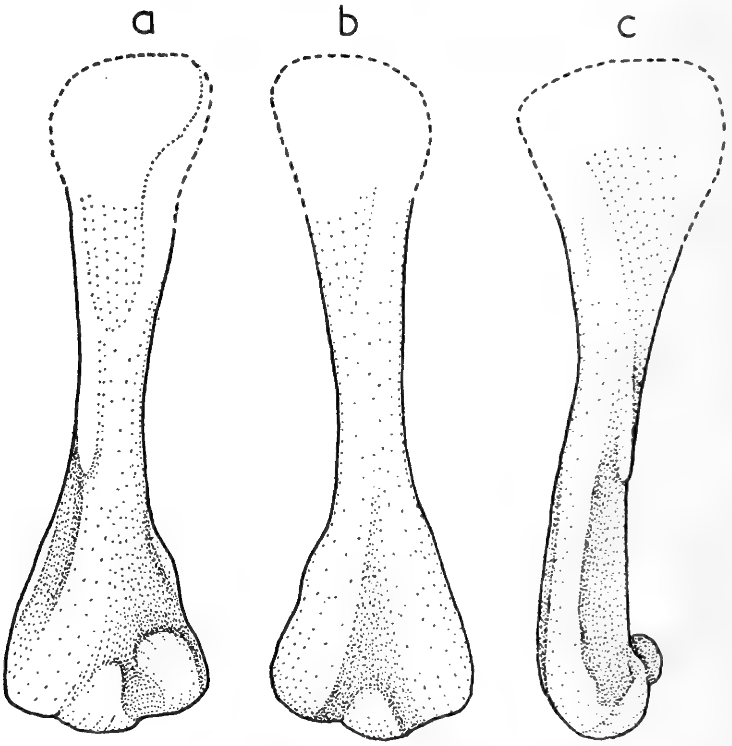

Fig. 6. ?*Hipposaurus major*. S.A.M. 9084A. Humerus × $\frac{1}{3}$. *a*. Ventral. *b*. Dorsal. *c*. Posterior.

Both condyles are well modelled. The radial condyle forms a prominent oval capitellum which faces mostly ventrally. The ulnar condyle lying further distally curves around the end of the bone on to the dorsal surface, where proximally lies a deep, well excavated trochlear fossa. Ventrally the brachialis fossa is very shallow, giving the hipposaurid humerus a quite different appearance from that of the other therapsids where there is a well developed entepicondylar foramen.

The Femur
(Fig. 7)

In the type specimen of *Hipposaurus boonstrai* there are a good right femur and the proximal and distal ends of the left femur. The only additional material at my disposal is a proximal end found as an isolated fragment and thus only subordinately identifiable.

The hipposaurid femur is a long lightly built bone with very moderately expanded proximal and distal ends. It is sigmoidally curved with the ends subtending an angle of about 30°. The caput femoris is terminal, but through the preaxial curvature on the shaft, it is somewhat preaxially directed. The external trochanter is not very clearly demarcated.

In ventral view the proximal end of the femur is most peculiar.

Halfway along the bone the ventral surface of the shaft has a low curvature in section. In proximal direction in the midline a low ridge becomes progressively developed, with the surface both pre- and postaxially becoming only slightly hollowed out in section. This ridge then ends abruptly with a sharp oblique edge. This ridge representing a remnant of the primitive 'Y' system, represents the internal trochanter. Proximal to the internal trochanter the preaxial edge is strongly rounded and postaxially a hollow represents the intertrochanteric fossa. Distally of the internal trochanter there is no indication of a separate fourth trochanteric ridge for the m. coccygeo-femoralis.

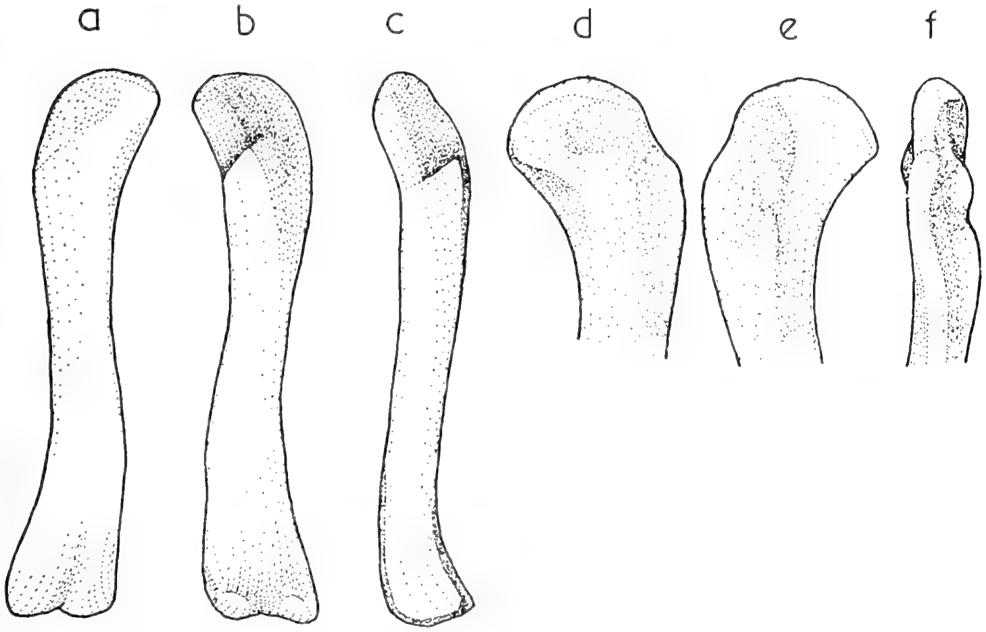

Fig. 7. Femora × ⅓. *Hipposaurus boonstrai.* Holotype. S.A.M. 8950.
a. Dorsal. *b.* Ventral. *c.* Anterior.
Gorgonopsian. S.A.M. 9012A.
d. Dorsal. *e.* Ventral. *f.* Posterior.

On the dorsal proximal surface there is a weak ridge near the preaxial edge for the insertion of the m. pubo-ischio-femoralis internus and externally of this ridge a shallow depression for the insertion of the m. ilio-femoralis. The distal condyles for the reception of the tibia are terminal with the fibula articulating with the outer face of the ectocondyle.

The other gorgonopsian femur available differs considerably from that of the above hipposaurid.

The external trochanter is clearly demarcated and on the dorsal preaxial edge there is a distinct pubo-ischio-femoralis internus ridge flanked by a groove.

On the ventral surface there is a distinct low mound distally of the intertrochanteric fossa constituting a separate internal trochanter. Distally of this lies a long low ridge to which the m. coccygeo-femoralis was attached and this constitutes the fourth trochanter.

The Anterior Epipodial

(Figs. 5d, e, and f and 8)

In *Hipposaurus boonstrai* there is a good left and parts of the right epipodial, whereas in *H. major* only the distal ends of the radius and ulna are preserved.

Both radius and ulna are long slender bones. The radius has a well modelled proximal facet, cup-like to fit closely on to the well modelled capitellum of the humerus. On the postaxial corner of the radius there is a well developed flange for the insertion of the biceps. The proximal postaxial edge of the radius fits against the rim of the sigmoid fossa of the ulna.

The ulna is much longer than the radius, with its sigmoid fossa and olecranon process lying proximally of the proximal radial facet.

The sigmoid fossa is formed by the preaxial surface of the olecranon and the proximal surface of the coronoid process. It fits accurately round the trochlea of the humerus to form an efficient hinge-joint.

Proximally of the sigmoid fossa the olecranon carries a very well developed process, broad but dorso-ventrally compressed. In extension this process passes into the deep olecranon fossa on the dorsal surface of the humerus.

In the type specimen of *Hipposaurus major* the distal end of the radius is seen to have a large oval facet for its articulation with the radiale. A similar facet on the ulna articulates with both intermedium and ulnare.

The Manus

(Fig. 8)

In 1935 I gave a figure and description of the badly damaged carpus of *Hipposaurus boonstrai*. Now I have the carpus of *Hipposaurus major* prepared by myself with the aid of adequate equipment and from this specimen one gets a better picture of the structure of the hipposaurid carpus.

In the proximal row there are three bones, with an additional large disc-like pisiforme postaxially. The radiale is a stout bone with a large oval proximal facet for the radius and distally a smaller facet for the first centrale. On its curved postaxial surface the intermedium and second centrale are articulated.

The intermedium has a well developed dorsal surface as the bone is not compressed from side to side. Proximally a good oval facet faces the inner part of the distal ulnar facet and a similar facet distally meets the second centrale distally.

The ulnare is an elongated fairly flattened bone with expanded ends and a

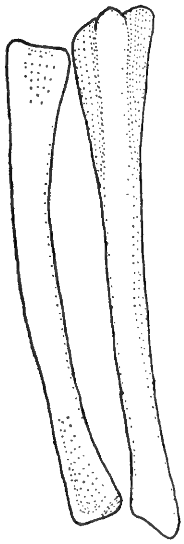

Fig. 9. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950 × ⅓. Hind epipodial.

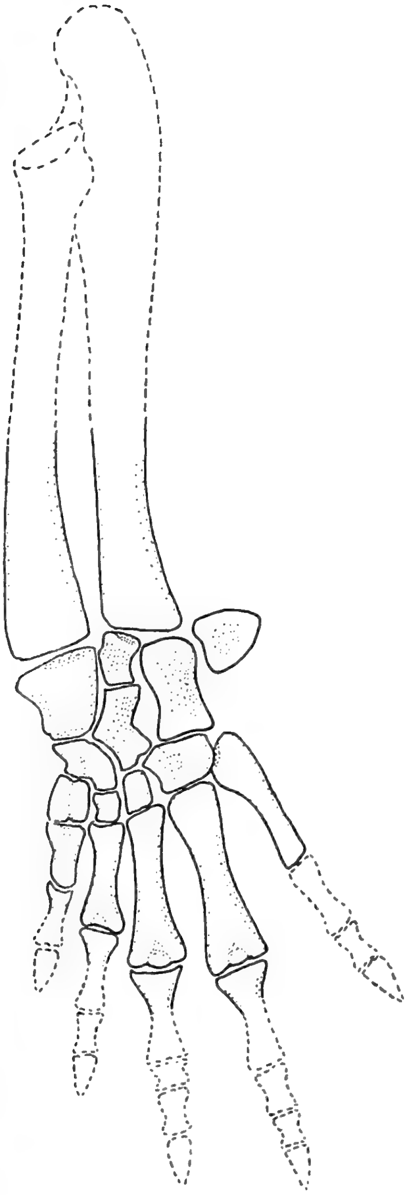

Fig. 8. Epipodial and manus in dorsal view × ⅓. *Hipposaurus major*. Holotype. S.A.M. 9081.

slightly constricted waist. The proximal facet is a long oval and distally a similar facet meets the enlarged fused fourth and fifth distal carpals. The first centrale is a curiously shaped bone, distally it has two facets for the first two distal carpals, a proximal facet for the radiale and postaxially a curved face is applied to the concave face of the second centrale. The second centrale is larger, but also curiously shaped with two distal facets, one for the third distal and the other for that part of the fused element constituting the fourth distal. Proximally it has good contact with the intermedium and preaxially two faces fit against the radiale and first centrale respectively.

There are four distal carpals. The first large, the second and third smaller and the fourth a large element representing a fusion of the fourth and fifth.

All five metacarpals are completely and well preserved.

The first metacarpal is the shortest with an expanded proximal end matching the large first distal; but the distal end is unexpanded.

The second metacarpal is longer with both ends expanded and a long constricted shaft.

The third metacarpal is even longer with a well expanded and well modelled distal end.

The fourth metacarpal is the longest bone of the metapodium, with both ends expanded and the distal well modelled.

The fifth metacarpal is of distinctive shape; its proximal end has its facet for the fused fourth and fifth distal directed preaxially and its distal end is not expanded.

Of the digits only the proximal ends of the first four phalanges are preserved.

POSTERIOR EPIPODIAL
(Fig. 9)

The right epipodial is well and completely preserved and the left incompletely in the type specimen of *Hipposaurus boonstrai*. It is composed of two long bones with the tibia fairly robust and the fibula of lighter build. The tibia is a straight bone, but the fibula is much curved so that there is a good spatium interosseum. In the fibula the two ends are expanded with the proximal end the stronger. In the tibia the distal end is only moderately expanded, whereas the proximal end is quite massive. This meets the femoral condyles end on, whereas the proximal end of the fibula is applied in a sliding joint to the postaxial epicondyle.

On its dorsal face the tibia has proximally a strongly developed cnemial crest, which extends far proximally fitting into the intercondylar sulcus of the femur and gives a good surface for the insertion of the tendon of the femorotibialis and associated muscles.

Distally the tibia is applied to the rounded knob-like facet on the astragulus and the fibula to a similar facet on the calcaneum.

THE PES
(Fig. 10)

In the holotype of *Hipposaurus boonstrai* there are a good right pes and parts of the left foot. Since my original description in 1934 I have been enabled by better equipment to expose the tarsal elements more fully. This applies particularly to the astragulus, which is now also visible from the plantar surface.

The calcaneum is most peculiar, but its structure can be easily derived from the typical disc-like element found in most therapsids. In its distal part the calcaneum is typically therapsid and its distinctive shape is due to the additional development of a strong well modelled tuber proximally. Distally the calcaneum has a slightly domed dorsal surface and a broad distal facet for the large conjoined fourth and fifth distal tarsals. Further proximally the dorsal surface carries a strong rounded facet for the fibula. Proximally of this facet a strong hook-like curved tuber is developed, with postaxially a strong rounded ridge running from the fibular facet to the extremity of the tuber. Between this ridge and the fibular facet there is a saddle-shaped excavation.

Preaxially the calcaneum is applied to the astragulus so that the fibular and tibial facets lie in the same plane as also the distal facets of the two bones. The cruro-tarsal articulation thus lies in one plane. In plantar view it is seen that the calcaneum in its preaxial part is overlain by the astragulus.

The astragulus has on its proximal dorsal surface a strong rounded knob-like facet for the tibia. Distal to this knob there is a deep transverse groove, with distally a shallowly concave upper surface passing distally into the distal facet for the centrale. In my original description I thought that this groove

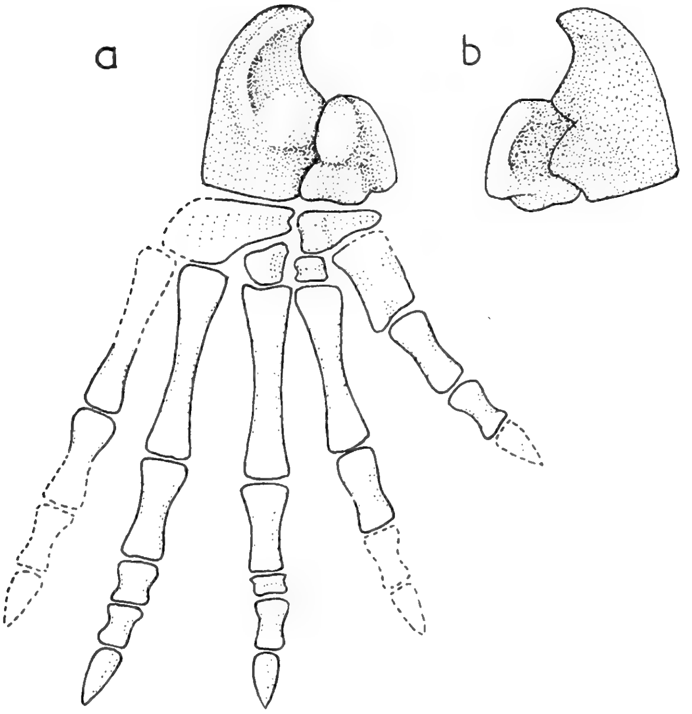

Fig. 10. *Hipposaurus boonstrai*. Holotype. S.A.M. 8950 × ½.
a. Dorsal view of pes as reconstructed. *b*. Plantar view of astragalus and calcaneum.

indicated a line of junction between two formerly separate elements, but the exposure of the plantar surface does not support this view. Preaxially it can now be seen, particularly in plantar view, that the astragalus extends further than shown in my original figure. In plantar view this preaxial extension is seen to form a strong process with a downwardly directed thick rounded edge.

The single centrale is a peculiar wedge-shaped bone lying transversely between the astragalus and the first two distal tarsals.

The greatly enlarged fused fourth and fifth distal tarsal has a very similar wedge shape and lies between the calcaneum and the third distal and articulating with the fourth and fifth metatarsals.

The first distal tarsal is of most unusual shape. It is a large elongated bone looking much more like a shortened metatarsal than a distal tarsal.

The second distal is a small squarish bone articulating with the centrale and the second metatarsal. The third distal is larger and lies between the fused fourth and fifth tarsal and the third metatarsal.

The metatarsals are all long bones with expanded ends and slender shafts, except the first which is quite short.

The phalanges are only completely preserved in the fourth and fifth digits. The phalangeal formula can thus be given as 2, 3, 4, 4, 3.

The second phalanx of the third digit is much reduced and in a near descendant of *Hipposaurus* one can expect a formula of 2, 3, 3, 4, 3 which would later become 2, 3, 3, 3, 3.

In another specimen, S.A.M. 12010, which is in all probability a galesuchid, and prepared for study since the above was written, there are associated with fragments of skull and vertebrae much weathered parts of the limbs, including the proximal part of a tarsus, an ulna and the middle part of a manus. The ulna has its sigmoid face not situated medially, nor does it have the well developed proximal process to the olecranon as in *Hipposaurus*. The ulna thus agrees more with the ulnae as known in later gorgonopsians.

The proximal tarsals merit description (fig. 11).

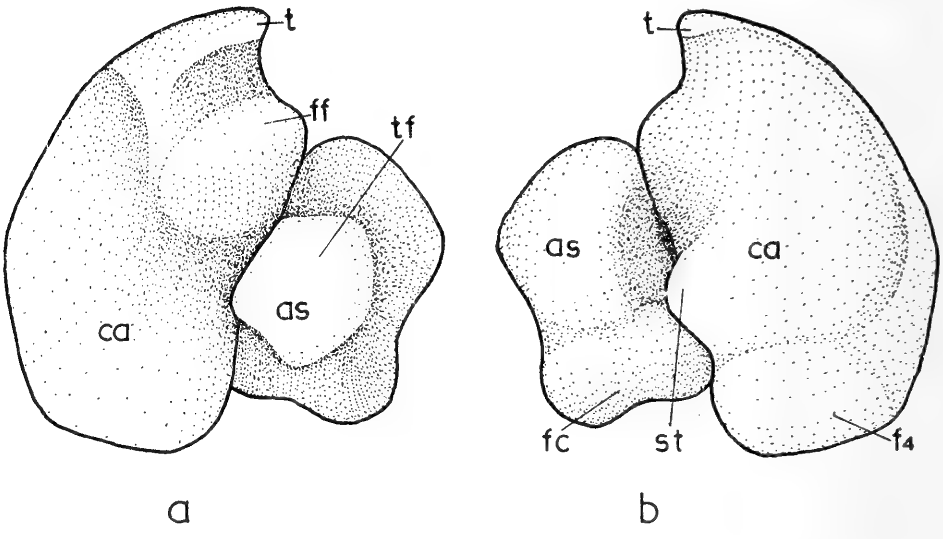

Fig. 11. *Hipposaurid.* S.A.M. 12010 × 1.

The proximal tarsal bones of the left hind foot. *a.* Dorsal. *b.* Ventral.

As—astragalus
Ca —calcaneum
fc — facet for the centrale
ff — facet for the fibula
f4 — facet for the fourth distal
t — tuber calcis
tf — facet for the tibia.

The calcaneum is a large element which still retains some of the characters of the primitive flattened disc-shaped structure, but in its proximal part shows highly advanced characters, viz. the facet for the fibula no longer lies proximally but is shifted on to the dorsal surface and protruding backwards it shows a quite well developed tuber separated from the fibular facet by a deep groove.

In ventral view it is clearly seen that the astragalus overlies the calcaneum medially. Here the calcaneum has a well developed process extending under the astragalus and this process can be considered a sustentaculum tali. The gorgonopsians from so low down as the *Tapinocephalus* zone are thus the first therapsids to show this typical mammalian structure.

The astragalus is a much smaller bone than the calcaneum and has a most remarkable facet for the tibia raised well above the base of the bone as a high eminence.

The distal facets of both the calcaneum and astragalus for the fourth distal and centrale, respectively, are very well modelled.

Discussion

A comparative account will be given in a subsequent paper, when I have completed my study of the other therapsids of the *Tapinocephalus* zone.

Summary

Descriptions are given of the girdles and limbs of the Gorgonopsia of the *Tapinocephalus* zone in South Africa. Of the eighteen specimens in the South African Museum, six have parts of the girdles and limbs present, and this account is based on these specimens.

Acknowledgements

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

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So proportioned that when reduced they will occupy not more than 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

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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).

LIEUWE DIRK BOONSTRA

THE SKULL OF
STRUTHIOCEPHALUS KITCHINGI

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THE SKULL OF *STRUTHIOCEPHALUS KITCHINGI*

By

LIEUWE DIRK BOONSTRA

South African Museum, Cape Town

(with 11 figures in the text)

CONTENTS

INTRODUCTION

Since Brink's description in 1958 of the type skull (B.P.I. 284) found on De Bad, Beaufort West by Kitching, the author with H. Zinn and H. Boonstra had the good fortune to excavate a second skull (S.A.M. K272) on Perdefontein, Beaufort West in 1960.

This skull was found *in situ* lying upside down with parts of the lower jaws exposed and the rest intact in a mudstone matrix. Unfortunately the exposed lower jaws have suffered from weathering which has destroyed the posterior parts of both rami. The palatal surface of the skull was firmly encased in a jacket of reinforced plaster and the massive skull could be lifted in one piece. On preparation the skull proved to be very well preserved and only very slightly distorted.

On study it became apparent that this specimen shows a number of structural features much better than the type specimen does. Certain additions to Brink's description can thus be made and in the sequel it will also become clear that I differ in interpretation on a number of points, even if allowance is made for considerable individual variation.

A correction has also to be made in regard to the type species due to Brink having misread Broom. The species *whaitsi* has as its holotype the skull (S.A.M. 2678) from Vivier, Beaufort West and the second specimen mentioned by Broom consists of a skull and much of the skeleton (S.A.M. 3012) from Abrahamskraal, Prince Albert. Broom rightly thought that the second specimen belonged to the same species as the holotype skull. There are thus two skulls and one skeleton.

Ann. S. Afr. Mus. **48** (14), 1965, 251–265, 11 figs.

Description

Build and carriage of the skull

The fronto-nasal boss in my specimen is very like that of the type, but I do not think that it represents a horn-core. In the collection of the South African Museum there are over two dozen skulls of *Struthiocephalus* and *Keratocephalus*. These all have a fronto-nasal boss developed to a varying degree and in all of them the sculpturing of the boss is very similar to that of the skull in general. If the boss were a horn-core one would have expected its surface to differ from that of the general skull sculpturing. That the boss could have been used as a battering ram is most probable, but then without a special horn covering.

There is no doubt about the hang-dog carriage of the skull in *Struthiocephalus*. As a matter of fact this applies to all the tapinocephalians in general —also to those without a naso-frontal boss. The struthiocephalines, with their long snouts and anteriorly directed upper front teeth, undoubtedly fed on softer vegetable matter than the moschopines. Their limbs have also been shown to be more adapted to marshy conditions and Brink's suggestion that the struthiocephalines may even have fed duck-like under water is quite probable. The surface moulding of the bone around the nostrils—especially of the septomaxilla—suggests the presence of musculature for the closing off of the nostril.

The structure of the skull

Although the present skull is very well preserved and prepared a number of sutures cannot be traced with absolute certainty. This is due to a number of factors such as the rugose nature of the outer surfaces, closure of sutures, fusion of elements and small displacements. When comparing the figures given here with those of the type skull, and also with those of other species of the genus the effects of the pachyostosis should be born in mind. The pachyostosis in the tapinocephalians is to some extent individual with differences often seen between the relations and extent of the two bones of a pair in the same skull. Age is also a factor. Differences that have been given as specific are often due to differences in the tempo of the pachyostosis in adjoining bones. Thus a strong pachyostotic development in, for instance, the postfrontal, causes an overlap or overgrowth over the adjoining bones and affects the relative size and shape of the outer surfaces of these bones. Where, however, authors show a radical difference in the relations of bones errors of observation and/or interpretation must be considered probable.

Lateral and dorsal surfaces. (Figs. 1 and 2)

In comparing my figures with those of Brink it is manifest that the type skull has been subjected to dorso-ventral compression. The effects are especially obvious in the nature and disposition of the lateral pterygoid flange and the quadrate. It should, moreover, be borne in mind that my figures are orthoprojections and not perspective drawings. This would in part account for the fact that in my figures the tabular is visible in dorsal view and in lateral view forms much of the posttemporal bar. But in my specimen the tabular is really much more developed and in its forward growth overlaps much of the lateral

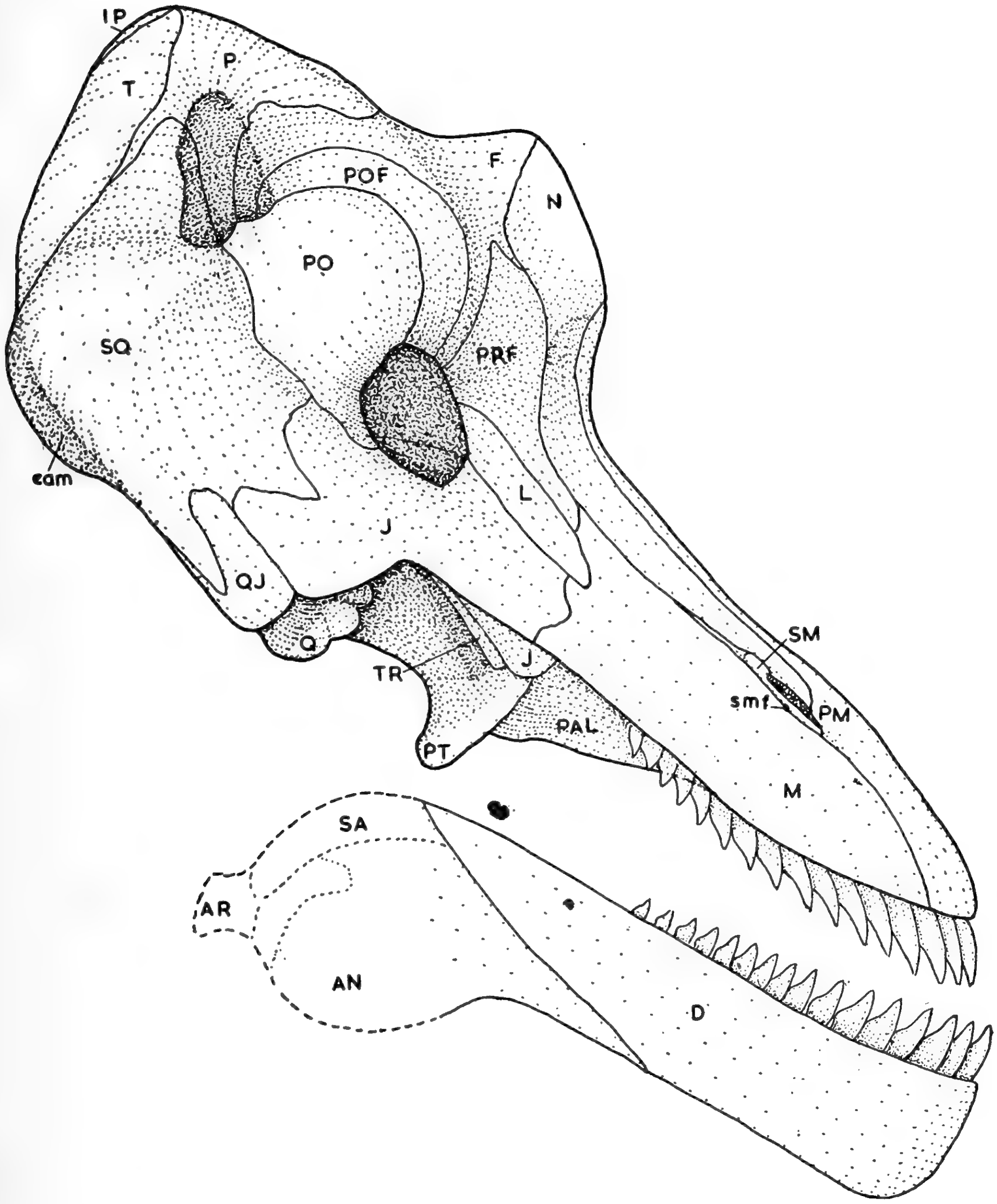

Fig. 1. *Struthiocephalus kitchingi*. S.A.M. K272 × 1/6. Lateral view. Orthoprojection on to the sagittal plane.

AN—angular. AR—articular. D—dentale. eam—external auditory meatus. F—frontal. IP—inter- or postparietal (dermo-supraoccipital). J—jugal. L—lacrimal. M—maxilla. N—nasal. P—parietal. PAL—palatine. PM—premaxilla. PO—postorbital. POF—postfrontal. PRF—prefrontal. PT—pterygoid. Q—quadrate. QJ—quadratojugal. SA—surangular. SM—septomaxilla. smf—septomaxillary foramen. SQ—squamosal. T—tabular. TR—transversum (ectopterygoid).

tongue of the parietal which is wedged in between the tabular and the upsweeping process of the squamosal. In my specimen the postorbital is more developed and this at the expense of the postfrontal. This particularly affects the appearance of the postorbital bar as seen in dorsal view.

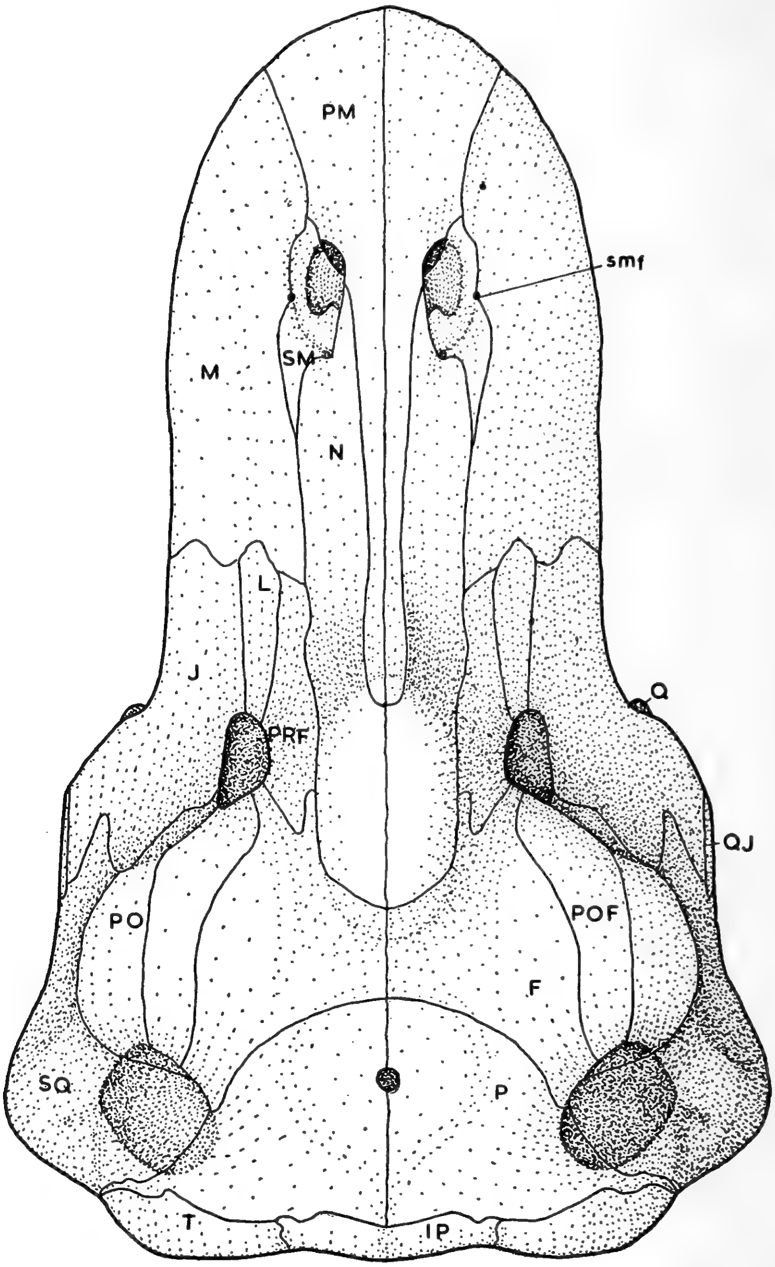

FIG. 2. *Struthiocephalus kitchingi*. S.A.M. K272 × 1/6. Dorsal view. Orthoprojection on to the alveolar plane.

Brink figures the squamosal as entering the ventral orbital border, whereas in my specimen the jugal extends posteriorly, ventral to the postorbital and forms nearly all of the ventral rim of the orbit with a small contribution by the postorbital. This is the normal relation, not only in the tapinocephalids but also in all the other Dinocephalia (anteosaurids, titanosuchids, styracocephalids and the Russian brithopids). Brink's figure indicates an error in observation.

In the present specimen the outer surface of both septomaxillaries is well preserved and this shows a distinctive moulding of the posterior border of the nostril to form a rounded swollen rim set off by the presence of a lateral groove. I suggest that this moulded structure indicates attachments for a valvular closure of the nostril when the animal is feeding with the snout submerged.

Occiput. (Fig. 3)

The occiput is low and broad with the squamosals bulging laterally to form prominent 'cheeks'. A strong rounded thickened upper and lateral border formed by the interparietal and the tabulars prominently demarcates a deep bipartite area of origin for the nuchal muscles. The interparietal and the tabulars have large posterior faces, whereas the supraoccipital is very low. The large face of the paroccipital is directed much more ventrally than posteriorly. The ridge on the squamosal bounding the external auditory meatus medially is very prominent. The posttemporal fossa is all but closed by the downgrowth

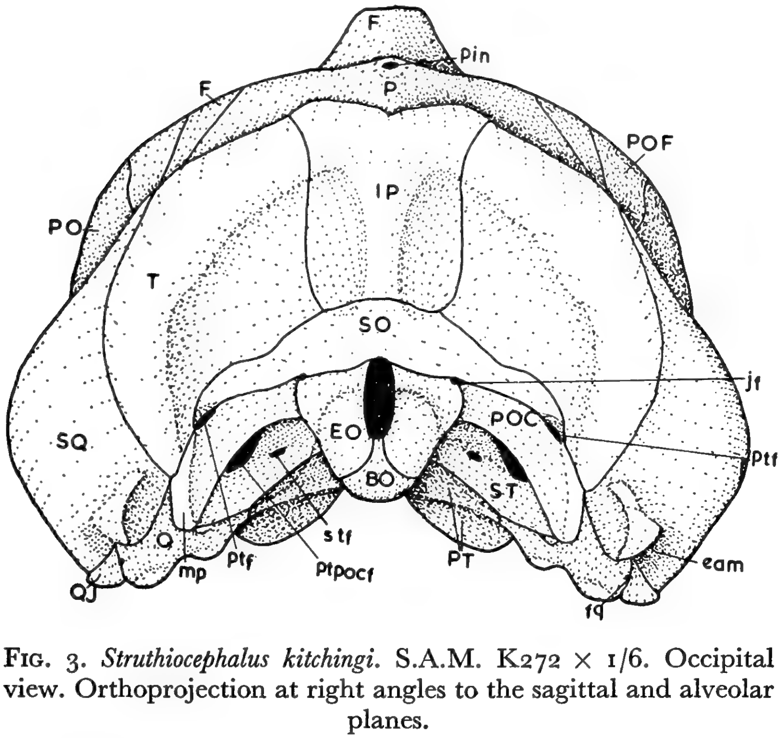

FIG. 3. *Struthiocephalus kitchingi.* S.A.M. K272 × 1/6. Occipital view. Orthoprojection at right angles to the sagittal and alveolar planes.
BO—basioccipital. EO—exoccipital. fq—quadrate foramen. jf—jugular foramen. mp—mastoid process of the paroccipital. pin—pineal (parietal) foramen. POC—paroccipital. ptf—posttemporal fenestra. ptpocf—pterygo-paroccipital fenestra. SO—supraoccipital. ST—stapes. stf—stapedial foramen. Other lettering as for Fig. 1.

of the tabular. The stapes is seen to lie diagonally with the distal end lying low down in the recess on the quadrate. Little is seen of the posterior face of the quadrate in this view because of its horizontal disposition. The occipital condyle is directed much ventrally with the exoccipitals forming most of the posterior face and the basioccipital facing mainly ventrally.

Ventral surface. (Fig. 4)

Comparing my figure of the ventral surface to that given by Brink a number of differences are apparent, apart from the fact that mine is a projection and Brink's a perspective drawing. The differences are in main due to the fact that the present specimen being uneroded is in a much better state of preservation. The regions mainly affected are the transverse processes of the pterygoids, quadrate and stapes, the occipital condyle and the relations of the supraoccipital, interparietal, tabular and squamosal.

In the present specimen the lateral flanges of the pterygoids form well demarcated deep transverse ridges extending far ventrally in their lateral parts, lying far below the level of the quadrate rami.

In its lateral part the quadrate ramus forms a deep vertical flange of bone which meets the quadrate along a large synchrondrotic face. More medially the pterygoid is deeply vaulted and sends a process posteriorly which abuts against the paroccipital at a level higher than the quadrate process of the paroccipital.

The quadrates are well preserved and carry cotyli shaped as shown in the figure. The stapedial recess is well preserved on both sides.

Both stapes are well preserved and are seen to lie diagonally with the distal ends lying well anterior to the plane of the fenestrae ovales. The occipital condyle is a prominent large knob roughly circular in outline with its articular face directed only slightly posterior off the ventral. The exoccipitals form more of the articular face than is shown in Brink's figure.

The paroccipital has a large ventral face. Medio-anteriorly it has a process meeting the proötic above the level of the fenestra ovalis. Latero-anteriorly there is a long quadrate process applies to the quadrate and terminating posterior to the stapedial recess. At a higher level the quadrate process of the paroccipital has a thin flange of bone whose anterior edge meets a process of the quadrate ramus of the pterygoid. Posterolaterally the paroccipital develops an everted thickened edge underlying the squamosal to form a mastoid process. The supraoccipital is wide but low and the posttemporal fossa all but obliterated by the overgrowth of the large paroccipital. The tabular has a large ventral face which, however, does not extend anteriorly between the paroccipital and squamosal as shown by Brink in his figure of the type.

The squamosal carries a prominent ridge, roughly comma-shaped in outline, and this forms the internal limit of the external auditory meatus developed as an antero-posteriorly directed groove.

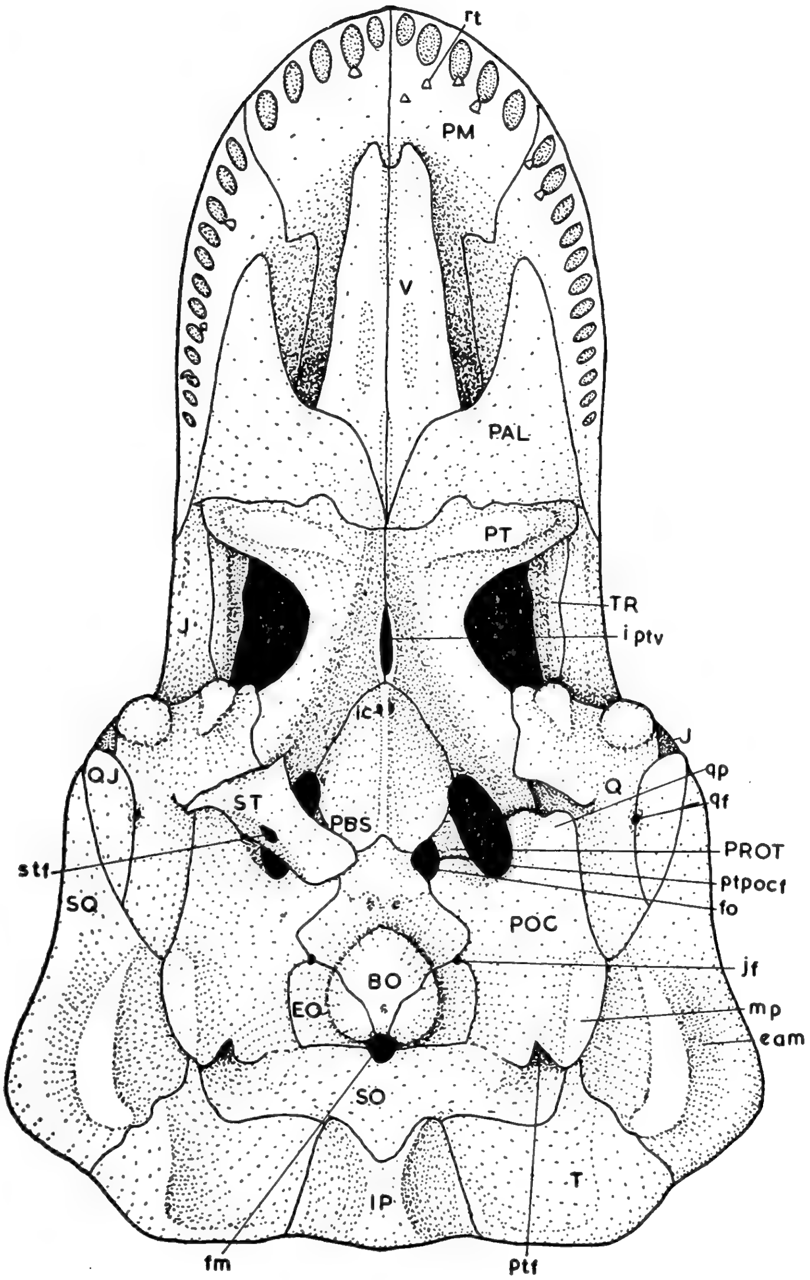

FIG. 4. *Struthiocephalus kitchingi.* S.A.M. K272 × 1/6. Ventral view. Orthoprojection on to the alveolar plane. fm—foramen magnum. fo—fenestra ovalis. ic—internal carotid foramina. iptv—interpterygoid vacuity. PBS—parabasisphenoid. PROT—proötic. qp—quadrate process of the paroccipital. rt—replacing teeth. V—vomer. Other lettering as in previous figures.

The position of the stapes. (Fig. 5)

In order to describe the relations of the stapes to the bones with which it makes contact I have sketched the various bones disarticulated but lying in their relative positions.

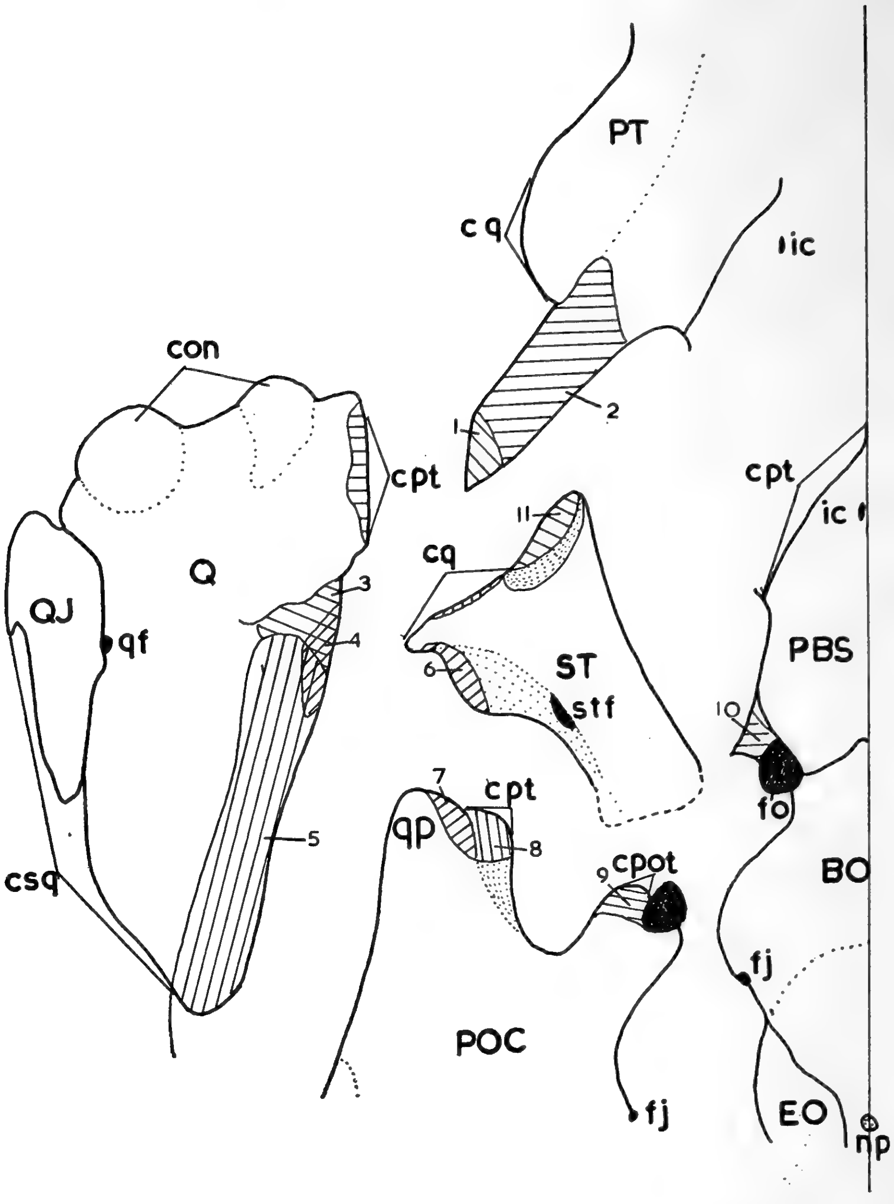

FIG. 5. *Struthiocephalus kitchingi.* S.A.M. K272 × 1/3. The stapes and contiguous bones as disarticulated. Ventral view. Orthoprojection on to the alveolar plane.

con—condyles of the quadrate. cpt—contact of pterygoid (quadrate ramus) with the quadrate, paroccipital and para-basisphenoid. cpot—contact of paroccipital with the proötic. cq—contact of quadrate with the pterygoid and the stapes. csq—contact of the squamosal with the quadrate and the quadratojugal. np—notochordal pit in the basioccipital.

Other lettering as in previous figures.

1—wedge of the pterygoid applied to the medial edge of the quadrate (4).
2—area on the posterior process of the quadrate ramus of the pterygoid overlapping the distal end of the stapes.
3—surface of the quadrate overlapping the stapes dorsal to the stapedial recess proper.
4—area on the medial edge of the quadrate making contact with the posterior process of the quadrate ramus of the pterygoid.
5—surface of the quadrate underlapped by the paroccipital.
6—area on the dorsal process of the stapes in contact with the paroccipital (7).
7—area on the paroccipital in contact with the dorsal process of the stapes (6).
8—area on the paroccipital underlapped by the stapes.
9—area on the paroccipital underlapped by the proximal end of the stapes.
10—area of the proötic underlapped by the stapes.
11—hollow in the distal end of the stapes which receives a process of the quadrate.

The footplate of the stapes lies fitted into the fenestra ovalis on both sides so that its proximal end cannot be seen.

Antero-dorsally the proximal end of the stapes is applied to a face on the proötic and further posteriorly underlies a face on the paroccipital. Both these contacts are not very intimate—definitely not synostotic—but rather syndesmotic or synchondrotic. Ventrally the footplate is in contact with the edges of the fenestra ovalis formed by the paroccipital, basioccipital and the para-basisphenoid.

The distal end of the stapes makes contact with the quadrate and paroccipital.

Postero-laterally the distal end of the stapes has a fairly short truncated process—the tympanic process—whose tip is connected directly or by the intercalation of a cartilaginous extra-stapes to the tympanum.

Antero-medially of this tip the distal end of the stapes fits into an elongated groove-like stapedial recess in the quadrate, lying in a plane nearly parallel to the quadratic cotyli. The fit is not tight and movement in this diagonal plane is possible even with the presence of cartilage or connective tissue.

The anterior part of the distal surface of the stapes has an oval hollowed-out articulatory face which makes contact with a process of the quadrate lying anterior to the elongated stapedial recess and posterior to the surface of contact with the end of the quadrate process of the pterygoid.

On the postero-distal surface of the stapes, posterior and medial to the tympanic process, and at a higher level than the main shaft of the stapes lies the dorsal process of the stapes, which makes contact with the quadrate process of the paroccipital. This contact was apparently synchrondrotic.

Stapes. (Fig. 6)

In ventral view the stapes presents a main portion consisting of a proximal end forming the footplate, a greatly expanded distal end and a shaft with a waist-like constriction. From the posterior edge of this main portion the rest of the bone lies at a higher level. About halfway along the shaft a large oval stapedial foramen pierces this flange. Postero-distally of the foramen there is a process which meets the paroccipital—this is the dorsal process.

The distal end bears a process directed postero-distally—this is the tympanic process. Anterior to the tip of the tympanic process the distal end has an elongated face which fits into the stapedial recess in the quadrate.

Anterior to this the distal end presents a concave oval articulating face, which articulates with a convex process on the quadrate lying immediately posterior to the contact face on the quadrate, which receives the quadrate process of the pterygoid.

In dorsal view the stapes has the surface of its main portion and the surface of the dorsal process lying in the same plane. On the upper face of the dorsal process there rises a conical protuberance with its tip directed medially. This I have labelled the medial dorsal process. The function of this process

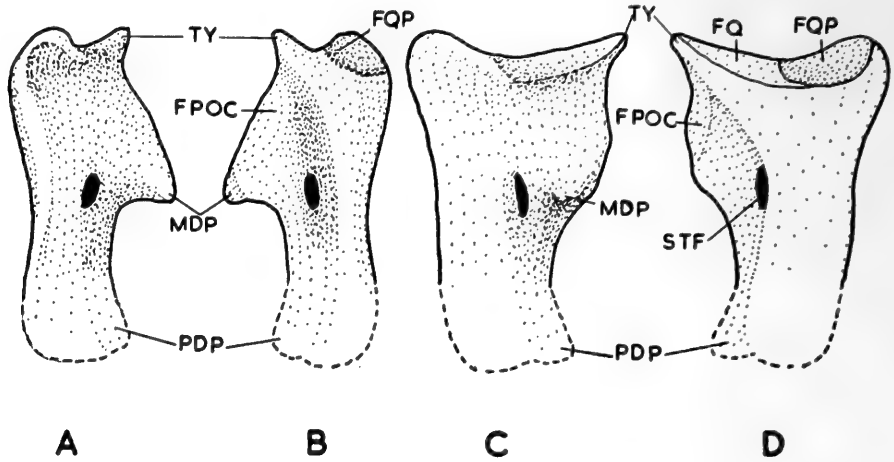

FIG. 6. Right stapes of *Struthiocephalus kitchingi*. S.A.M. K272 × 1/3. A—anterior. B—posterior. C—dorsal. D—ventral. FPOC—facet on the dorsal process which is applied to the quadrate process of the paroccipital. FQ—facet fitting into the elongated stapedial recess in the quadrate. FQP—concave facet applied to a convex process on the quadrate lying medial to the stapedial process proper. MDP—medial dorsal process. PDP—proximal dorsal process. STF—stapedial foramen. TY—tympanic process.

would appear to be to receive a tendon probably attached to the inner edge of the quadrate.

In anterior and posterior view this median dorsal process is seen to be both strong and prominent.

Quadrate. (Fig. 7)

The quadrate is a large bone—robust in its cotylar region and in the parts making contact with the squamosal, quadratojugal and the quadrate ramus of the pterygoid. But its inner portion overlying the paroccipital consists of a thin sheet of bone with a free edge.

Its stout pterygoid process bears a large roughly oval area for the reception of the quadrate ramus of the pterygoid, which at a higher level has an additional process meeting the quadrate in a groove on the lower part of the inner edge of the quadrate. The articulatory area on the pterygoid process is a hollowed out area with, in its middle part, a longitudinal ridge. This is matched on the quadrate ramus of the pterygoid by an articulating face bearing a median groove flanked by two longitudinal ridges.

The nature of this joint is such that it admits of movement between the quadrate and the pterygoid in a parasagittal plane. The roughness of both articulating faces indicates the presence of synchondrotic cartilage.

Just above the quadrate-pterygoid articulation there is a transverse everted flange of bone. The upper edge of this flange carries a transverse groove which thus lies between two lips. This groove is the stapedial recess. The outer end of this everted flange develops a thin free standing process to which the tympanum was probably attached.

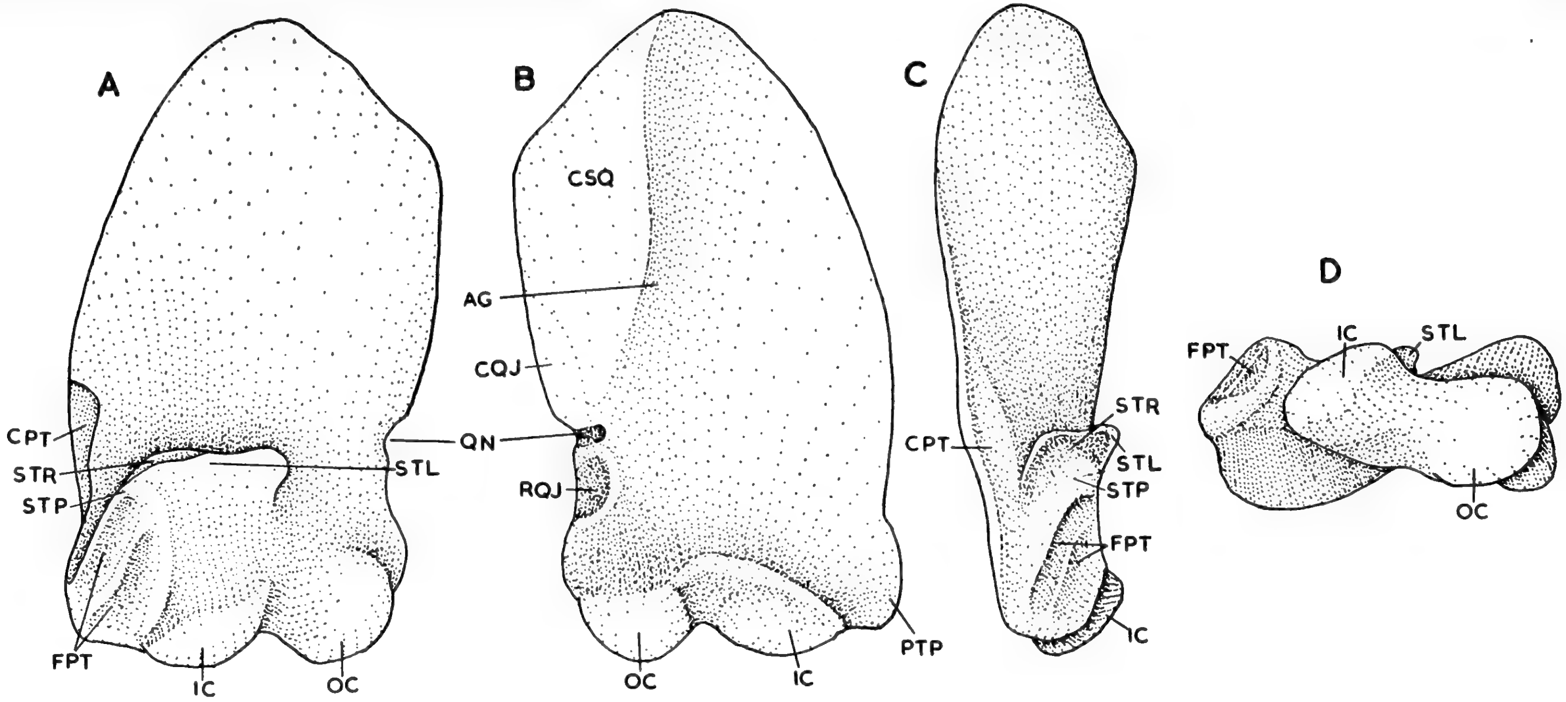

FIG. 7. Right quadrate of *Struthiocephalus kitchingi*. S.A.M. K272 × 1/3.

A—ventral (morphologically posterior). B—dorsal (morphologically anterior). C—inner or medial. D—anterior (morphologically ventral). AG—groove in dorsal (anterior) surface housing part of the m. capiti-mandibularis. CPT—surface on the medial edge of the quadrate receiving the posterior process of the quadrate ramus of the pterygoid. CQJ—surface of contact with the quadratojugal. CSQ—surface for contact with the squamosal. FPT—facet on the pterygoid process of the quadrate receiving the quadrate ramus of the pterygoid. IC—internal condyle. OC—external condyle. PTP—pterygoid process of the quadrate. QN—notch forming the inner border of the quadrate foramen. RQJ—recess receiving the ventral end of the quadratojugal. STL—ledge forming the posterior lip of the stapedial recess. STP—convex process for articulation with the concave facet on the distal end of the stapes. STR—the elongated recess for the reception of the stapes (stapedial recess proper).

In between the quadrate-pterygoid joint and the outer lip the everted flange has a rounded process to which is articulated the hollow face on the distal end of the stapes.

On its posterior face the quadrate is greatly thickened where it is applied to the squamosal and quadratojugal. Medial to this thickened area lies a wide groove with a smooth surface. This housed part of the body of the m. capiti-mandibularis.

A moschopid and jonkeriid quadrate. (Figs. 8 and 9)

I am including comparable figures of a quadrate of a moschopid and a jonkeriid. Essentially these are of the same type as that of *Struthiocephalus*, except that in the jonkeriid quadrate a very definite recess is developed on the posterior face well above the stapedial recess. I can offer no suggestion as to what was received in this recess.

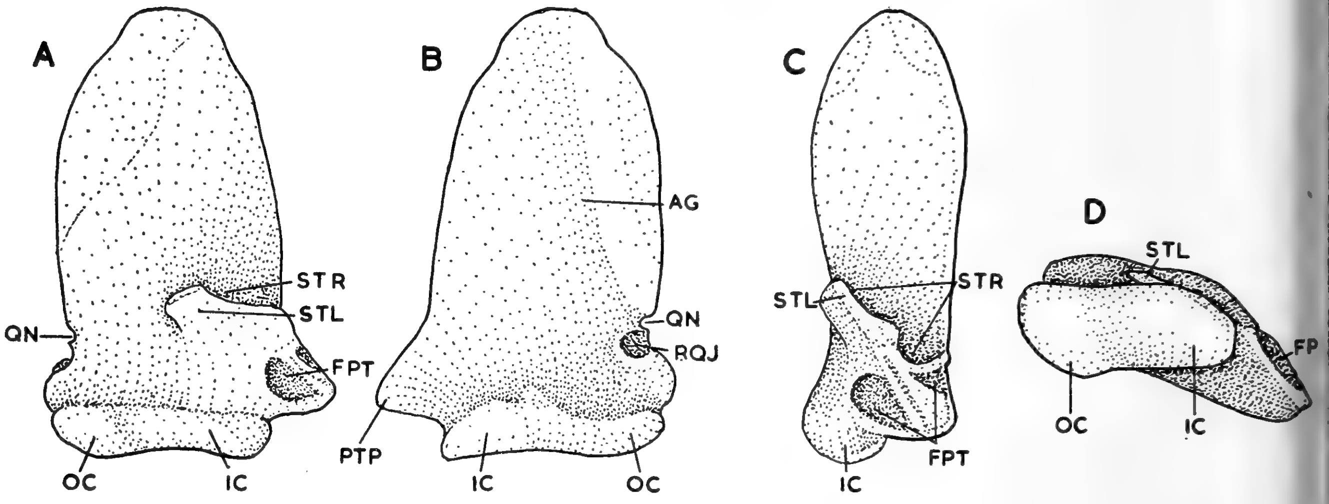

Fig. 8. Left quadrate of *Moschops* sp. S.A.M. 11701 × 1/3.

The Tympanum

A depressor mandibuli muscle originating from the prominent ridge on the squamosal just medial of the groove housing the external auditory meatus and inserted on the process of the articular would allow ample room for a tympanum with a diameter of about 30 mm.

The tympanum having one point of attachment on the free tip of the lip of the ledge bounding the stapedial recess could lie in a parasagittal plane and receive the tympanic process of the stapes meeting it at right angles.

The external auditory meatus extending from the tympanum along the groove in the posterior face of the squamosal could have its opening just above the level of the upper limit of the squamosal ridge.

The nature of the joint of the stapes with the quadrate as described above would allow of movement of sufficient amplitude for the conduction of sound waves.

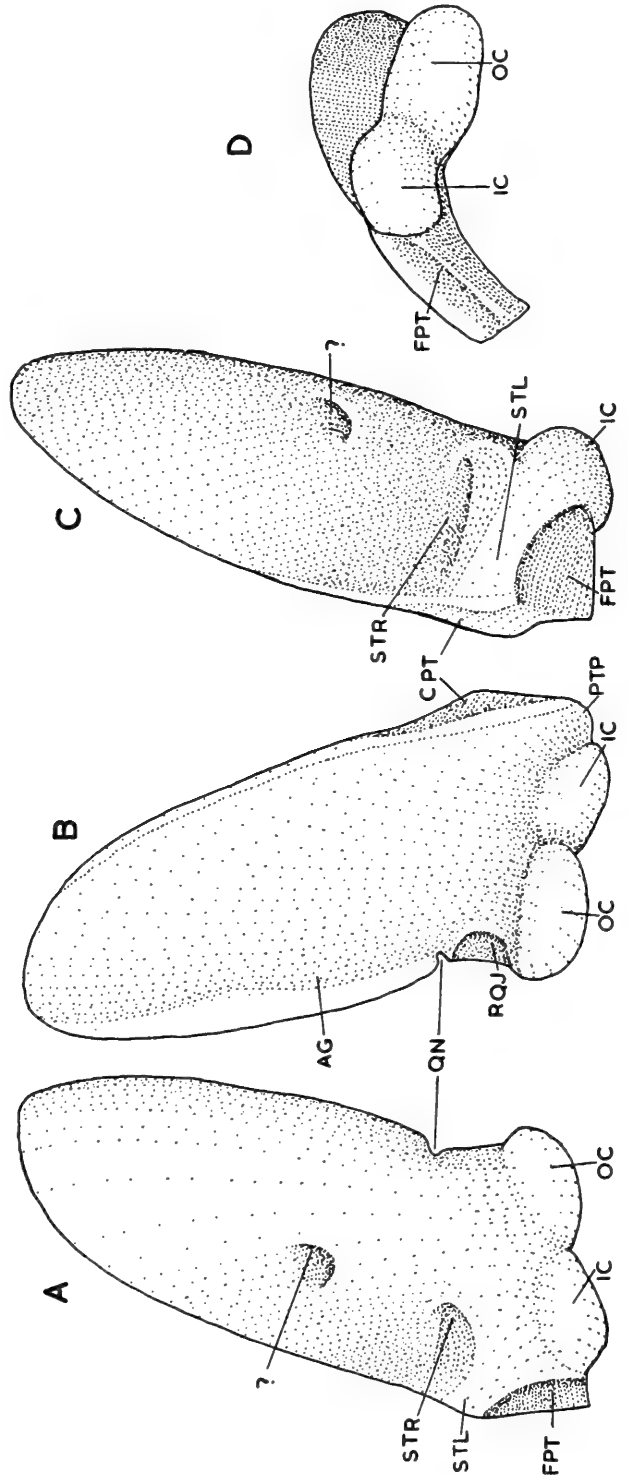

FIG. 9. Right quadrate of *Jonkeria haughtoni*. S.A.M. 4343 × 1/3.

Dentition. (Fig. 10)

Brink maintains that in the type specimen the marginal teeth are disposed in a double row both functional at the same time. This view is manifestly incorrect. The fact is that the replacing teeth arise lingually of those in use and each new tooth is thus a younger member of the same tooth family of

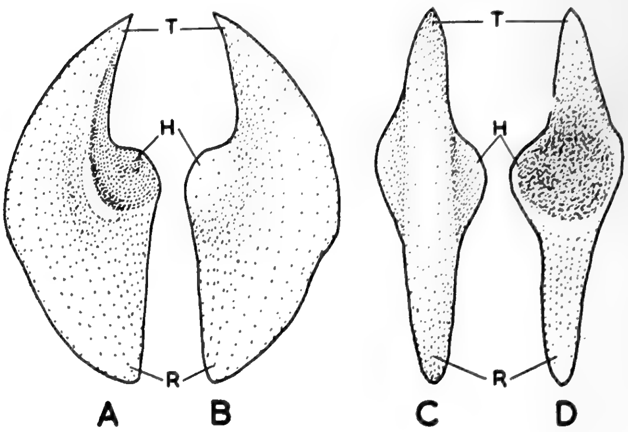

FIG. 10. First left incisor of *Struthiocephalus kitchingi*.
S.A.M. K272 × ½.
A—posterior. B—anterior. C—labial view.
D—lingual view. H—heel. R—root. T—talon.

the tooth it replaces. The position is thus as in the Titanosuchia. The structure of the teeth is of the talon-and-heel type thoughout the series, with decrease in size in posterior direction.

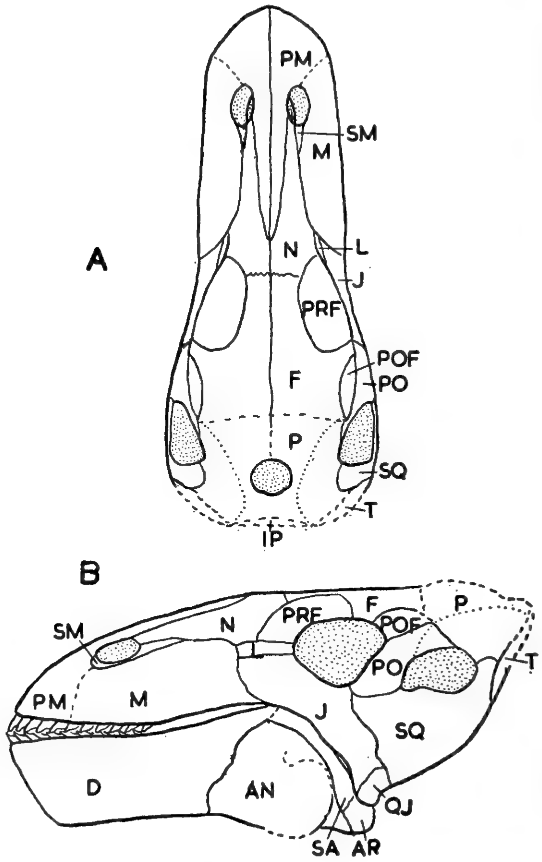

FIG. 11. Skull of *Moschosaurus longiceps*. Type.
S.A.M. 3015 × 1/6.
A—dorsal. B—lateral.

Discussion

In a recent paper I have suggested that all the described species of *Struthiocephalus* could well be considered conspecific and I arranged them in a growth series.

I would now go further and suggest that *Moschosaurus* could very well be the youngest form of such a series. (Fig. 11)

Summary

A detailed description of the skull of *Struthiocephalus kitchingi* is given, based on a second skull from Beaufort West. This specimen shows a number of features much better than the type specimen and leads to some differences in interpretation.

Acknowledgements

The skull here described was obtained on a collecting trip by the South African Museum which was in part financed by a grant from C.S.I.R. to whom we tender our thanks.

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

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Brink, A. S. 1959. *Struthiocephalus kitchingi* sp. nov. *Palaeont. Afr.* **5**: 39–56.

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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).

R. A. JUBB

A NEW PALAEONISCID FISH FROM THE WITTEBERG SERIES (LOWER CARBONIFEROUS) OF SOUTH AFRICA

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A NEW PALAEONISCID FISH FROM THE WITTEBERG SERIES (LOWER CARBONIFEROUS) OF SOUTH AFRICA

By

R. A. Jubb

Albany Museum, Grahamstown.

(With 1 plate and 2 figures in the text)

Contents

Introduction

In May 1963 Mr. G. Walsh, an official of the Sundays River Irrigation Board, discovered a deposit of fossil fishes in the mountains just south of Lake Mentz and close to the entrance of Karroo Poort. Mr. J. J. G. Blignaut, a retired geologist, visited the site immediately and confirmed the importance of its discovery. Since the beds are well exposed, from the upper portion of the Witteberg quartzites through the complete sequence of Upper Witteberg Shales to the Dwyka Tillite, it was possible for Mr. J. A. Marais of the Geological Survey Department to determine the geological horizon on which the fossil fish occur. The fossiliferous bed, which is nearly vertical and from three to six inches thick, occurs 740 feet above the topmost white quartzite of the Witteberg and in the upper shales which were formerly known as the Lower Dwyka Shales. These shales are regarded as of lacustrine origin.

Lithologically, according to Haughton (1963), the Series, as now defined, consists of fine-grained thinly bedded whitish quartzites intercalated with dark green or blue (buff when weathered) micaceous shales and flagstones. Locally lenses of grey sandy limestone or calcareous quartzite, sometimes carrying plant fragments, are present, as well as bands of coarse grit. The uppermost member (formerly Lower Dwyka Shales) consists mainly of greenish and bluish shales and flagstones with some hard sandstone bands.

The most characteristic fossil in the quartzites of the series is the spiral

Ann. S. Afr. Mus. **48** (15), 1965: 267–272, 1 pl., 2 figs.

impression known as *Spirophyton* which is characteristic of the Middle Devonian of America. Other fossils previously discovered, although scanty, include *Bothrodendron*, *Cyclostigma* (characteristic of the Carboniferous of Queensland and New South Wales), *Didymophyllum*, *Halonia*, *Knorria*, *Lepidodendron*, *Lepidostrobus*, *Singularia*, *Selaginites* and *Stigmaria*. Fragments of the body segments of a eurypterid named *Hastimima* have also been discovered, as well as some fish scales. A recent discovery by Mr. J. A. Marais is a species of *Psilophyton*. In age Du Toit (1954) considers these non-marine beds, about 4,000 feet in thickness, to embrace the whole time interval from about the Middle Devonian to the Lower Carboniferous, and it is to this latter period that the Lake Mentz fish fossil bed appears to belong.

An outstanding feature of the exposed section of the fossil bed is the concentration of fish impressions it contains. This concentration spoils what could have been, in many cases, perfect impressions. As stated above, the maximum thickness containing fishes varies from three to six inches but the extent of the bed is unknown as it dips and disappears. Under normal circumstances sediments of this thickness would represent an appreciable interval of time, but, from the great number of fishes overlapping one another, and the disposition of some, it is evident that a mass mortality involving a large concentration of Palaeozoic fishes occurred. Such a mass mortality, followed by perfect preservation, could only have taken place if the primeval pool of lake they were inhabiting was completely frozen over in the first place. Total freezing would have resulted first in the concentration of fish in the bottom layers, then asphyxiation followed by preservation in the bottom muds under freezing conditions before being finally entombed by some major earth or glacial movement. The open mouths of many of the fishes suggest asphyxiation due either to deoxygenation of the water by the fishes themselves, or to their being forced down into a deoxygenated hypolimnion.

Although the Witteberg Series is associated with lacustrine conditions, certainly non-marine, it would be misleading to regard the Lake Mentz fossils as being those of entirely freshwater species. Of the Palaeozoic and Mesozoic fishes described from southern Africa many belong to widely distributed genera and families which are associated with both marine and non-marine formations. Rayner (1958) quoting Gunter points out that, as a general rule, marine fishes are more tolerant of fresh waters than vice versa. There is ample evidence of this today where marine species such as *Carcharinus leucas*, *Pristis microdon*, *Megalops cyprinoides* and *Glossogobius giuris* are all found up to 300 miles by river from the sea in many of the rivers of the east coast of Africa.

The Lake Mentz fossil fishes represent two distinct species and possibly a third. Of the two more complete species one is a platysomid-like fish with very large dorsal ridge scales, and the other a slender stream-lined palaeoniscid which is described below as representing a new genus and species. The generic name refers to the type locality and the specific name is in honour of the discoverer of the fossil bed.

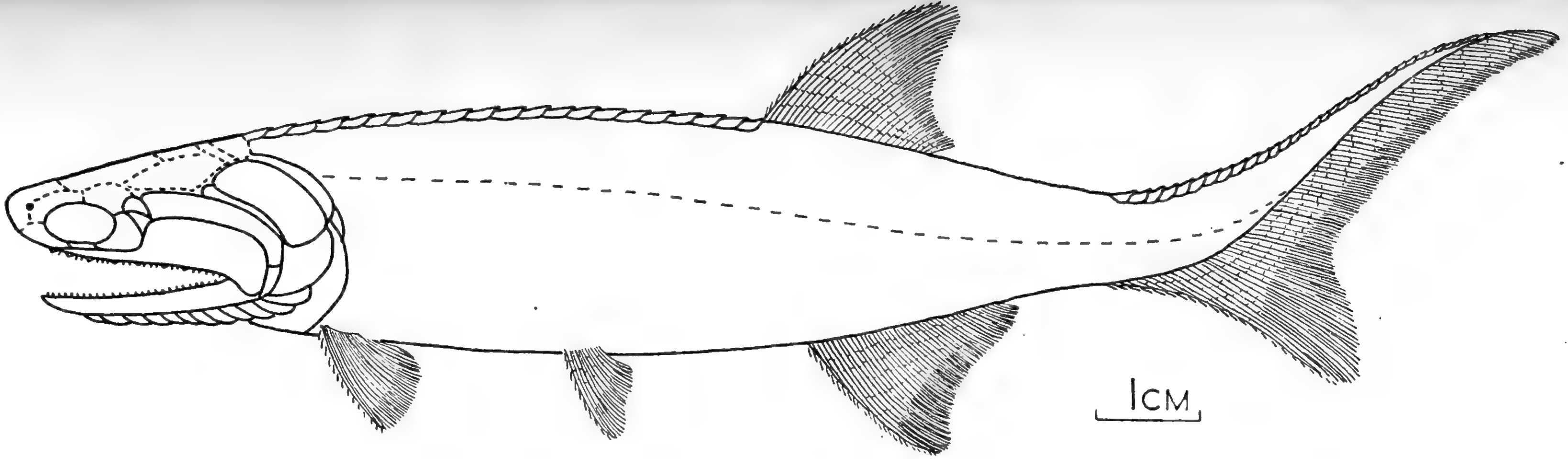

Fig. 1. *Mentzichthys walshi*. Restoration of type, squamation not shown.

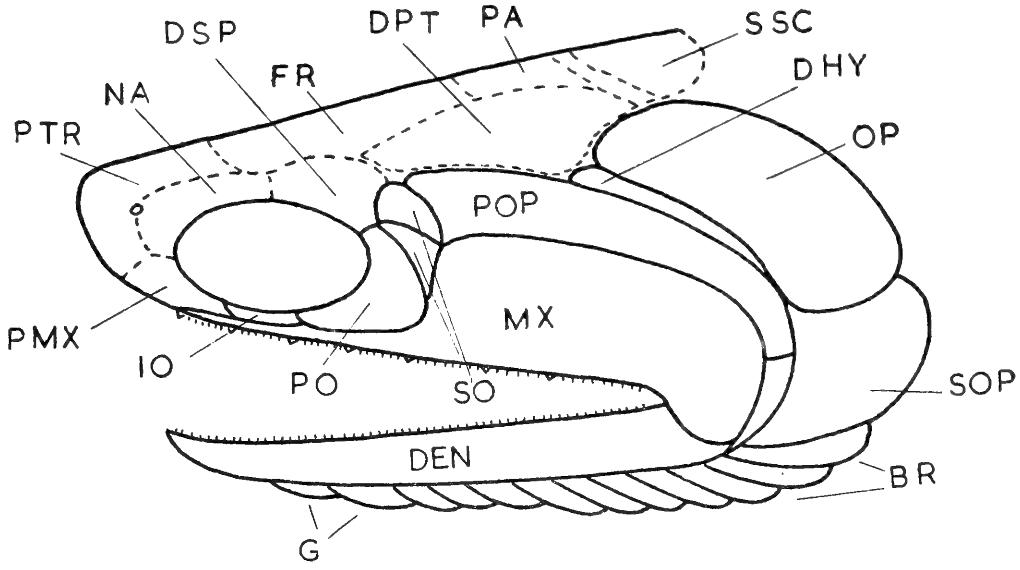

Fig. 2. *Mentzichthys walshi*. Restoration of the skull in lateral view. Dotted lines indicate indistinct sutures.

Key:
BR. branchiostegal rays; DEN. dentary; DHY. dermohyal; DPT. dermopterotic; DSP. dermosphenotic; FR. frontal; G. median gular and gular; IO. infraorbital; MX. maxillary; NA. nasal; OP. opercular; PA. parietal; PMX. premaxillo-antorbital; PO. postorbital; POP. preopercular; PTR. postrostral;. SO. suborbital; SOP. subopercular; SSC. suprascapular.

Family **Palaeoniscidae**

Genus MENTZICHTHYS nov.

Definition: Body fusiform and elongate; principal rays of pectoral fins not articulated till towards their terminations; dorsal and anal fins situated posteriorly, moderate in size, triangular in shape, the former originating slightly ahead of the latter; caudal fin heterocercal, inequilobate and deeply cleft, the axial lobe being well developed; distinct fulcra on all fins; head with prominent rostrum and relatively large anteriorly placed orbit with large postorbital; suspensorium very oblique, gape wide, teeth consisting of short well-spaced cutting teeth and fine conical teeth on the maxillary, and numerous fine conical teeth on dentary; opercular large, larger than subopercular, branchiostegal rays fairly numerous, head bones sculptured with striae and tubercles; scales rhombic, of moderate size, with large peg-and-socket articulation, entire posteriorly, ridge-scales running from the occiput to the origin of the dorsal and along the leading edge of the caudal fin.

Mentzichthys walshi sp. nov.

(Figures 1, 2. Plate VI A, B)

Specific diagnosis: Slender fusiform fishes whose maximum total length appears to be about 18 cm., the length of the head being contained about four and a half times, and the greatest depth six and a half times in the total length of the body.

The Skull

The shape and arrangement of the bones of the skull are shown in Figure 2, which has been prepared, allowing for distortion, from three impressions of heads which were cleaned and then polished with a nylon brush before photographing. Plasticine casts were also used for reconstructing the skull, broken lines being used in the final drawing where sutures could not be determined with confidence.

The ornament of the frontals, supratemporals, parietals and post-temporals consists of striae running more or less antero-posteriorly. The postrostral is ornamented mostly with tubercles which extend down to the nasals (see Plate VI A). The branchiostegal rays are not ornamented but the large and prominent postorbital bone is markedly rugose. Numerous transverse striae ornament the maxillary and particularly the dentary. The suspensorium is very oblique. The opercular and subopercular are also ornamented, the former being much larger than the latter. The teeth showing on the dentary are minute and numerous, similar teeth appear on the maxillary but there are well spaced short cutting teeth as well which are confined to the anterior and middle section.

The Paired Fins

Preservation is not good enough to detect ornamentation of the supracleithrum or cleithrum. The pectoral fin, situated low down ventrally, is medium in size with a base length about one third that of the longest lepidotrichia. The lepidotrichia, which number about 19 are unarticulated and unbranched until their distal ends. The anterior edge of the pectoral fin is covered with small fulcra. The pelvic fin, whose origin is about midway between the origin of the pectoral and the origin of the anal, is relatively small with about 13–15 lepidotrichia which are articulated and distally branched. The anterior edge is covered with small fulcra.

The Unpaired Fins

The dorsal fin, which is situated nearer to the caudal fin than to the head, is one and a quarter times as high as the length of the base. It is triangular in shape with from 28–35 lepidotrichia which are articulated and branched distally. The anal fin, whose origin is posterior to that of the dorsal, has a base longer than its height. It is triangular in shape with 35–45 lepidotrichia which are articulated and branched distally. Small fulcra are present along the anterior edge. One of the outstanding features of this new species is the large axial lobe of the caudal fin. This fin is distinctly heterocercal, deeply cleft and inequilobate, the leading edge being covered with ridge scales.

Squamation

Not many scales are available for examination as, in most of the samples, just the underneath pattern of the squamation appears in the impression. The scales are medium in size and rhombic in shape with pronounced peg-and-socket articulation. The few scales available, mostly immediately posterior of the head, show transverse furrows with pits, the posterior edges being rough but entire. There are from 16–18 rows of scales from the dorsal to the ventral surface at the point of maximum girth, and 52–58 scales along a lateral series. Moderately enlarged ridge-scales, numbering about 21, extend from the occiput to the origin of the dorsal fin. Ridge-scales of a similar size anteriorly extend along the caudal peduncle and up the leading edge of the caudal fin.

Material

The holotype is an impression on a slab No. A.M./64/4562 in the Albany Museum, Grahamstown. A photograph of this is shown in Plate B. This slab, from two to three inches thick, has numerous impressions on both faces. Other samples of importance in constructing the illustrations in Figures 1 and 2 were A.M. 64/4563, A.M. 64/4564 and A.M. 64/4565, in the Albany Museum. Further material, S.A.M. K1169 and S.A.M. K1170 is preserved in the South African Museum, Cape Town.

DISCUSSION

Reasonably entire specimens of *M. walshi* have the following extreme measurements:

Total length: 90 mm. Std. length: 70 mm.
Total length: 145 mm. Std. length: 110 mm.

From these measurements it has been possible to estimate the maximum size of incomplete fossils to be about 180 mm. The type, Figure 1 and Plate B, has a total length of 145 mm.

M. walshi belongs to the group pf palaeoniscids having a very oblique mandibular suspensorium (Woodward, 1891). The remarkable development of the axial caudal lobe, the smaller orbits and the large postorbital bones distinguish this new genus from *Rhadinichthys* Traquair, 1877 as re-defined by Moy-Thomas and Dyne (1938). These features, as well as the larger opercular, distinguish *Mentzichthys* from the genus *Cycloptychius* Young, 1865, as re-defined by the same two authors. Of the known palaeoniscids it would appear that *Mentzichthys* is most closely related to those of the Lower Carboniferous assigned to the genus *Cycloptychius*.

ACKNOWLEDGMENTS

I wish to thank Professor Orvar Nybelins of Stockholm, Sweden, for reading this paper in its draft form and for providing valuable comments. Dr. H. V. Eales of the Department of Geology, Rhodes University, assisted by his team of senior students, provided the material from which the holotype of *M. walshi* was selected. This project, carried out in collaboration with Dr. T. H. Barry, was part of a research programme sponsored by the C.S.I.R., who also granted funds for the publication of this work.

SUMMARY

A new palaeoniscid fish *Mentzichthys walshi* n. gen. *et* sp. is described from the Witteberg Series (Lower Carboniferous) of South Africa, just south of Lake Mentz in the eastern Cape. It is suggested that a mass mortality of these fishes took place in lacustrine conditions under ice.

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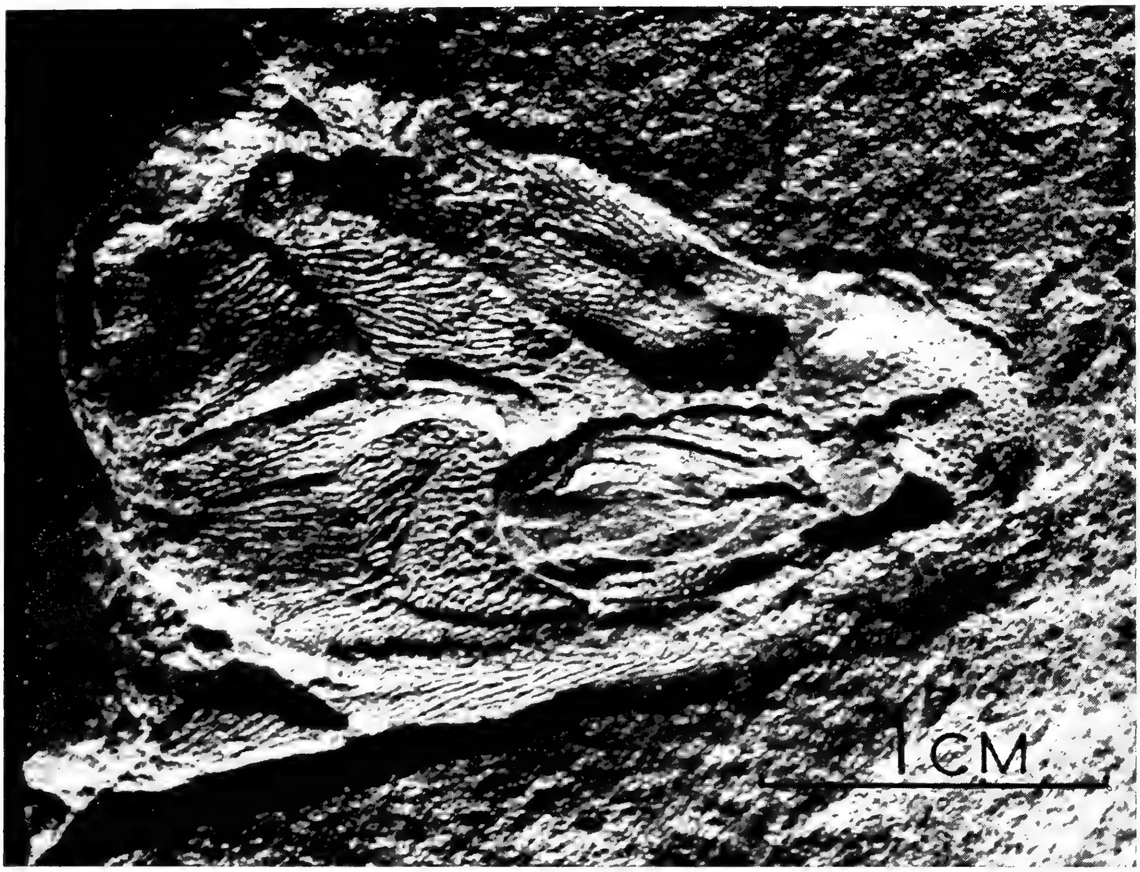
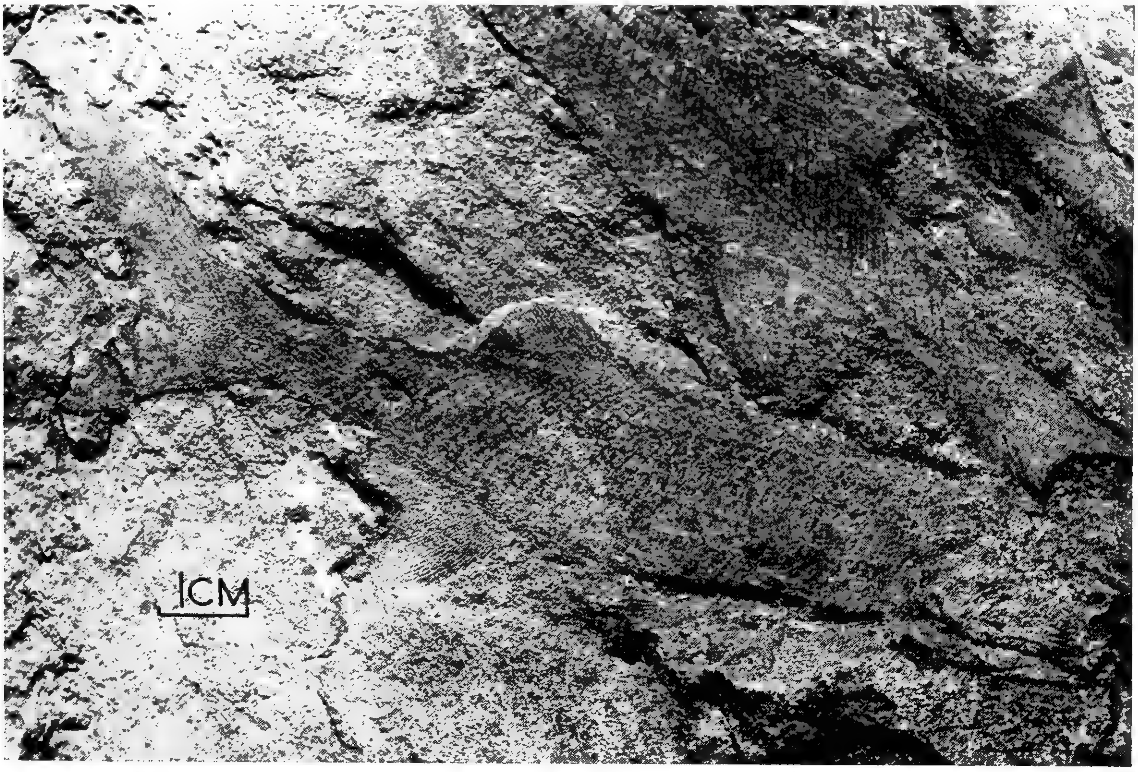


A. Portion of a skull of *Mentzichthys walshi*, partly obliquely crushed, showing pronounced postorbital bone and ornamentation.



B. Holotype of *Mentzichthys walshi*.

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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).

EDUARD L. BONÉ & RONALD SINGER

HIPPARION FROM LANGEBAANWEG, CAPE PROVINCE AND A REVISION OF THE GENUS IN AFRICA

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HIPPARION FROM LANGEBAANWEG, CAPE PROVINCE AND A REVISION OF THE GENUS IN AFRICA[1]

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(With 24 tables, 16 text figures and 13 plates)

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Ann. S. Afr. Mus. **48** (16), 1965: 273–397, 24 tab., 16 figs., 13 pls.

Introduction

GENERAL

The discovery of the genus *Hipparion* de Christol 1832 in Africa was first mentioned as late as 1878 (Pomel) and then again in 1884 (Thomas), but it was not properly described before 1897 (Pomel). These early papers dealt with specimens found in the Maghreb, North Africa. Additional finds were then made in the Oran and Constantine areas, and, somewhat later, specimens were discovered in Tunisia, in the Nile Valley at Wadi Natrun, in Ethiopia, in the Kaiso Beds of Uganda, and at Cornelia (Uitzoek) in South Africa. The scanty stratigraphical data and faunal associations of these discoveries led to an overmultiplication of genera and species, based mostly on isolated single teeth.

Subsequently more complete discoveries and more detailed descriptions were published. In 1937 Hopwood presented some conclusions of the Oldoway Expedition in a monograph on the fossil Equidae. Dietrich (1942) described an important hipparionid[1] series from South Serengeti, to which Arambourg (1947) added important collections from Omo (Ethiopia). The more extensive material gave rise to a more unified knowledge of the African *Hipparion*. It enabled Gromova (1952), in her revision of the genus *Hipparion*, to point out the characteristic features of the African forms, as well as to sketch their general evolutionary and migratory patterns within Africa.

The lack of stratigraphical correlations and insufficient knowledge of conditions of exposure and of faunal associations at the various sites where hipparionids have been discovered, only permitted attempts at relative dating of the various sites and their fossil horizons. Furthermore, these sites belong exclusively to Upper Pliocene and Pleistocene epochs. Therefore, it was generally accepted that *Hipparion* had appeared in America in Pliocene times

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[1] The term 'hipparionid' refers in a general sense to all forms of African tridactyl equidae. Previously Dietrich (1942, p. 94) erected the sub-family 'Hippariinae' for the same purpose but without taxonomic definition. Furthermore he also used (1942, p. 94) '*Hipparion* de Christol, *i.w.S.*' in a non-generic sense.

As the present authors have come to the conclusion that all African forms belong to a single genus *Hipparion*, the general term 'hipparionid' corresponds to the taxonomic one.

and had migrated to Eurasia where the differentiation of the 'Pontian fauna' had taken place, and that only subsequently, as late as Pliocene times, *Hipparion* had reached Africa as a kind of refuge area. This view was still supported less than ten years ago when material was discovered in lacustrine limestone at Mascara (Arambourg, 1956).

Recently *Hipparion* material was discovered in Algeria in undoubted Upper Miocene beds. This led Arambourg (1959) to propose the relationships between the several African hipparionids, and to reduce drastically the former several genera and species to a more sober and unified taxonomy of three different groups, namely *H. africanum*, *H. sitifense* and *Stylohipparion* sp. These formed a chronological succession from the Upper Miocene through the Upper Pliocene to the 'Villafranchian' or early Pleistocene times. This classification was more satisfactory and had definite merits and advantages which will be commented on later in this paper.

THE LANGEBAANWEG DEPOSITS

Recent discoveries (Singer, 1961) of a fairly extensive series of *Hipparion* teeth at the Langebaanweg fossil sites, from which *Stegolophodon* sp. had previously been reported (Singer & Hooijer, 1958), necessitated a thorough study and comparative review of the African hipparionids. The unique and uniform nature of the Langebaanweg material adds materially to our knowledge of the African hipparionids and also provides new evidence for revising the relationships between the several forms already recognized in the literature.

Thus the purpose of this paper is twofold:

(*a*) to record a description and diagnosis of the *Hipparion* remains from Langebaanweg, and

(*b*) to review and revise the taxonomy of the African hipparionids.

Localization of the sites

The Langebaanweg fossil sites are situated, like the 'Elandsfontein' (Hopefield) site, in the vast Sandveld of the Western Cape, and are located about 75 miles (120 km.) northwest of Cape Town (fig. 1) and 12 miles (19 km.) from the late Middle Pleistocene—early Upper Pleistocene site at 'Elandsfontein'. The former are 150–200 feet (46–62 metres) above sea-level, while the latter are situated at 300 feet (Singer, 1961).

The fossils are mainly located in and around two quarries being commercially exploited for phosphates by the African Metals Corporation (AMCOR). The 'Varswater' site is situated on the farm 'Langberg Suid', and the 'Baard's' site is on the farm 'Remainder of Langberg', the two being subdivisions of 'Langberg' (fig. 2).

History of the discoveries

The first hipparionid teeth were recovered from Baard's Quarry in 1958. In 1961, Mr. Robin Warren, an employee of AMCOR, recovered two excel-

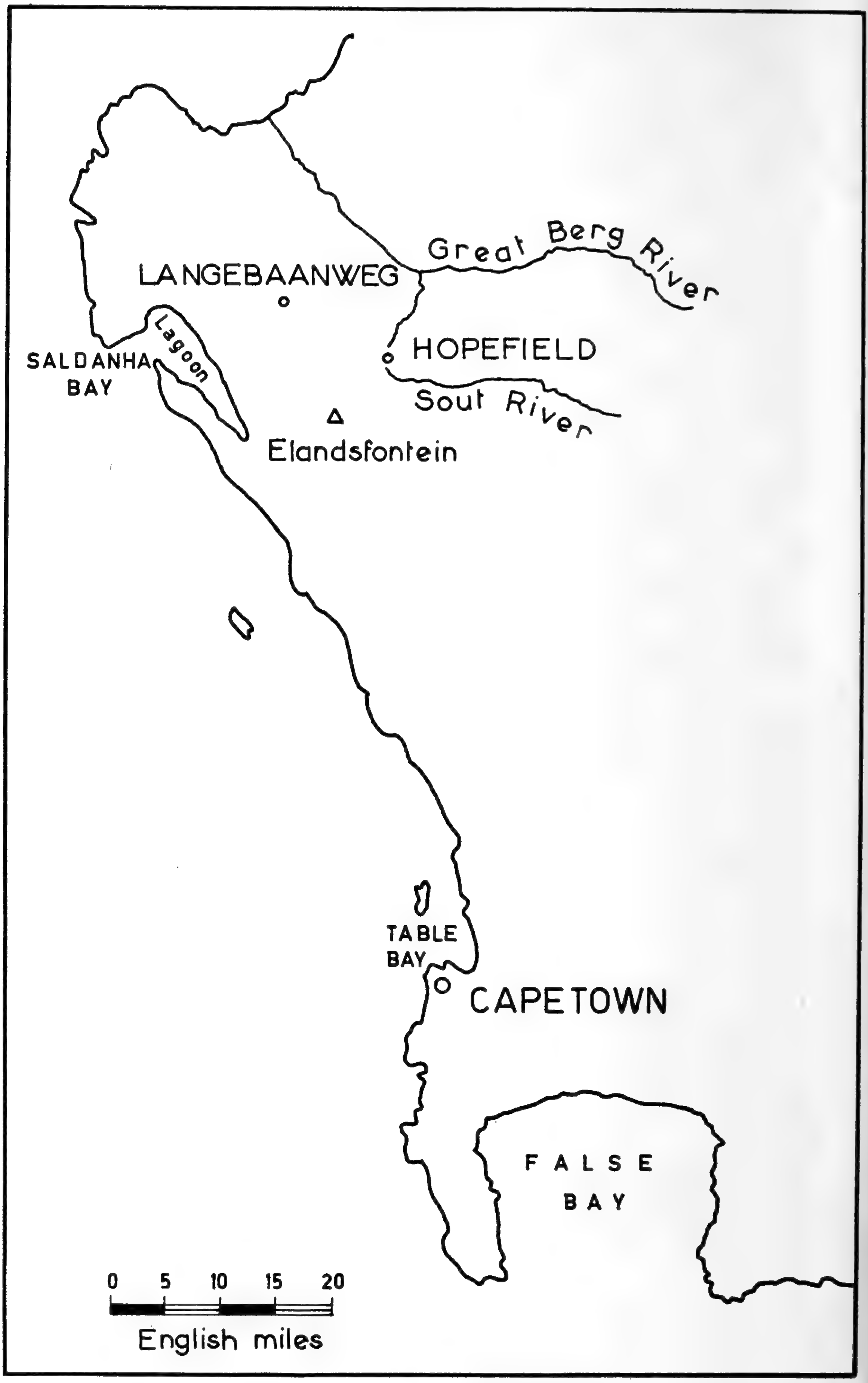

Fig. 1. Map indicating the position of Langebaanweg relative to Cape Town.

lently preserved milk molars at Varswater. Thereafter the remainder of the specimens were found at various sites in the two quarries.

Geology

The geology of the more than 4 square miles of fossiliferous deposits is not easy to interpret. There is little with which to compare it, as virtually nothing is known of the Quaternary geology of the Cape Province.

The surface siliceous sands, possibly aeolian, forms a discontinuous cover of 4 to 5 feet, which may extend to more than 15 feet in a few places. Below this layer, at both quarries, there occurs a *Dorcasia*-type caliche, discontinuous and stratigraphically above the phosphates. There is also ferricrete, younger than the phosphates and intimately associated with them.

The *Dorcasia*-type surface limestone also occurs on the solid calcrete dunes at 'Elandsfontein', at Saldanha Bay, at False Bay (Singer and Fuller, 1962) and elsewhere. The distribution of the caliche is patchy, and is considerably stripped by erosion.

At Varswater the phosphate, a variety of collophane, occurs as the cementing material of the consolidated sand, probably as the result of diagenetic replacement of interstitial limes. There are three main layers which vary laterally in thickness within a range of 3 feet to 6 feet.

At Baards, the phosphate occurs as nodular to bouldery phoscrete (up to 5 feet thick). The phoscrete is a hard, compact mass of phosphatized sand consisting of sand grains which have been cemented and partially corroded by an amorphous calcium phosphate cement. It overlies the phosphatized nodular sands, sandy clays, and clayey sand. The phoscrete and nodular phosphate sands, represent replacement of older shelly sands by phosphate solutions, the phosphate of which is probably derived from guano. A significant feature is that at Varswater the phosphate has remained unaltered as lime phosphate (Singer & Warren, in preparation).

The discovery of shark teeth and other marine forms (*vide infra*) at the same level as and with the land mammals indicates earlier invasion of the area by the sea. Studies on borehole cores and the presence of shelly sands and gravels suggest the formation of sand bars, especially at Varswater, while the clay and clayey sands at Baard's indicates a possible lagoonal stasis. Further studies are being carried out in an attempt to clarify the geological genesis and morphology of the region.

The major portion of the phosphatic deposits is located at both sites at up to 100 feet above sea-level. The archaic fossils are related to or found just above these deposits. The 'rolled' nature of much of the fossil material suggests some transport prior to final deposition. The upper phoscrete and calcrete layers, as well as the clayey deposits, contain the faunal forms represented also at 'Elandsfontein' (*Ceratotherium*, *Equus*, *Sivatherium*, *Homoioceras* and various antelopes), typical of the late Middle Pleistocene—early Upper Pleistocene ('Hopefield Period').

On a comparative basis with other sites, it seems likely that the stegolophodont—stegodont—archidiskodont complex and the hipparionids derive from a period extending from the Lower Pleistocene to the early Middle Pleistocene. The stegolophodont and stegodont specimens together indicate a very early phase of the Lower Pleistocene. Elsewhere (e.g. at Olduvai) archidiskodont material overlaps this phase and extends up to the Middle Pleistocene. It will be demonstrated below that the hipparionids from Langebaanweg belong to the same species as that from the lower layers of South Serengeti, so that their presence is suggestive of the earliest phases of the Pleistocene.

FAUNAL ASSEMBLAGE FROM LANGEBAANWEG

The following identifications have been made thus far:

MOLLUSCA

Trigonephrus sp.

CARNIVORA

cf. *Arctocephalus*
Canis sp.
Hyaena brunnea

PROBOSCIDEA

Stegolophodon sp.
Stegodon sp.
Archidiskodon sp.
Palaeoloxodon sp.

PERISSODACTYLA

cf. *Ceratotherium*
Hipparion (Hipparion) albertense baardi subsp. nov.
Equus helmei

ARTIODACTYLA

Hippopotamus sp.
Sivatherium(1) *olduvaiense*
cf. *Oreotragus* sp.
cf. *Damaliscus* sp.
cf. *Redunca* sp.
Homoioceras sp.

REPTILIA

cf. *Testudo*

AVES

cf. *Struthio*

SELACHII(2)

Isurus cf. *glaucus*
Lamna nasus
Carcharias sp.
C. ferox
Rhinoptera cf. *dubia*
Glopias vulpes

(1) According to Arambourg's recent re-description (1960) of Pomel's type specimen from St. Charles (Oran), *Libytherium maurusium* has precedence (see also Singer and Boné, 1960).

(2) Identified by Dr. B. Schaeffer, American Museum of Natural History, New York.

METHODS AND NOMENCLATURE

For the description of the occlusal surfaces of the teeth, the nomenclatures used by Arambourg (1947, 1959), Cooke (1950), and Sondaar (1961) have been modified (see pp. 325–8) and synthesized (figs. 10, 11).

The measurements of the teeth have been taken according to the method described by Sondaar (1961).

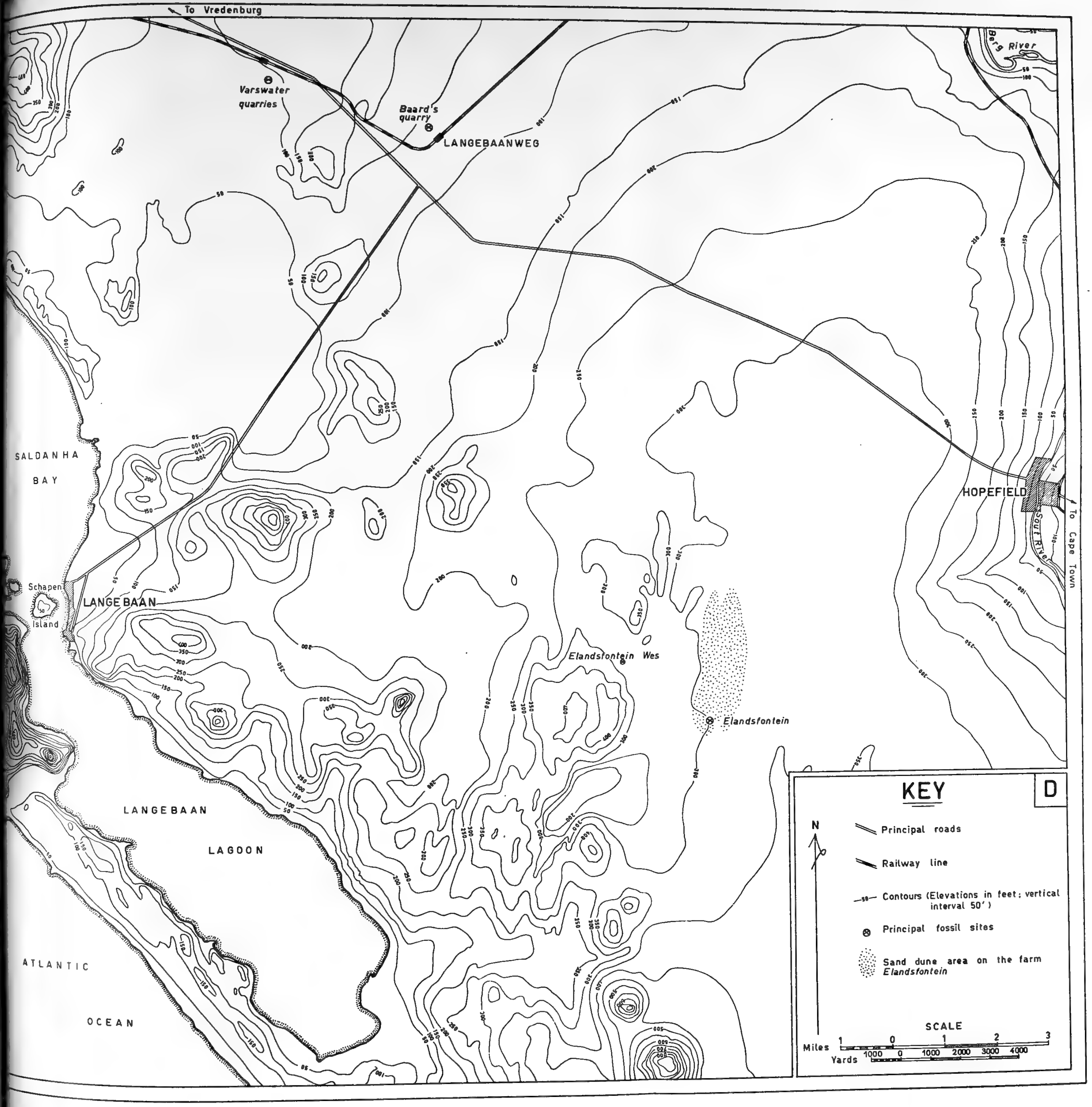

FIG. 2. Contour map showing the location of the quarries at Langebaanweg.

The indices devised by the authors are described at appropriate places in the text.

The following abbreviations refer to the collections and sites of the source material:

Archaeol. Surv. = Archaeological Survey of South Africa, now in the University of the Witwatersrand, Johannesburg, South Africa.
B.M.N.H. = British Museum (Natural History)
C = Cornelia
L = Langebaanweg
M.M.K. = McGregor Memorial Museum, Kimberley
Nas. Mus. = Nasionale Museum, Bloemfontein
Old. = Olduvai
S.A.M. = South African Museum, Cape Town
U.C. = University of California, Berkeley.

GEOGRAPHICAL DISTRIBUTION OF AFRICAN SITES WHERE HIPPARIONIDS HAVE BEEN RECORDED (figs. 3–7)

Site	*Specimen*	*Reference*
MOROCCO		
Camp Berteaux (Gara Ziad)	(*a*) Molar teeth Femur fragment with proximal epiphyses	Bourcart, 1937
	(*b*) Left M^2	Ennouchi & Jeannette, 1954
Oued el Akrech (near Argoub el Hafid)		Ennouchi, 1951
Fouarat (south of Kenitra (Rharb))		Choubert, Ennouchi & Marcais, 1948
ALGERIA		
Tafna (Guiard, Prov. Oran)		Dalloni, 1915
Oued el Hammam	Adult skull no. 141 Adult skull no. 125 Adult skull with dentition no. 116 Juvenile palate with dentition no. 122 Adult mandible no. 143 Adult half mandible no. 89 2 juvenile mandibles with milk teeth nos. 95–96 Several teeth series, juvenile and adult Isolated teeth Humerus, distal fragment no. 159 Radio-ulna no. 123, fragments no. 13, no. 22 and no. 27 Femur: fragment without epiphyses and distal fragment Tibia: distal fragment Pelvic fragment	Arambourg, 1959

Site	*Specimen*	*Reference*
Oued el Hammam (*cont.*)	Astralagus, 2 Calcaneum, 1 Numerous complete metapodials (5 Mc III, 5 Mt III), many (6) of them with lateral digits	
Marceau	P^a and M^a, P_2	Arambourg, 1959
Mascara	Skull fragments of one individual: palate with nearly complete left dental series, and half right dental series; symphysis with incisors	Arambourg, 1956
St. Donat	'Teeth of two jaws'	Joleaud, 1936 Arambourg, 1956
St. Arnaud (Cemetery)	(*a*) upper molars	Pomel, 1897
	(*b*) lower molars	Arambourg, 1956
Aïn el Hadj Baba	Metapodials with developed lateral digits	Thomas, 1884
	Upper teeth: right P^4–M^2 left M^2	
	Lower teeth	
Aïn el Bey		Thomas, 1884
Mansourah		Thomas, 1884
Setif		Thomas, 1884
Beni Foudda (Aïn Boucherit)		Pomel, 1897
Aïn Hanech		Arambourg, 1949
Oran (Puits Kharouby)	M^a, left P_3 or P_4, M_a	Pomel, 1897
Aïn Jourdel	M_3, P	Thomas, 1884
TUNISIA		
Garet Ichkeul		Arambourg, 1949
Tozeur Beds		Roman & Solignac, 1931
Utique		Solignac, 1927
Djebel M'dilla		Solignac, 1927
FAYUM		
Wadi Natrun, Gart el Moluk Hill	Left upper P (P^4 ?)	Andrews, 1902
ETHIOPIA		
Omo Valley	(*a*) 1 incisor, 5 M_a, 1 M^a (brought back by Brumpt from the du Bourg de Bozas Mission, 1903)	Haug, 1911; Joleaud, 1933
	(*b*) right P^2 no. 396 left M^3 no. 395 left M^a fragment no. 370 right M_1 or M_2 no. 3 & no. 4 right humerus fragment	Arambourg, 1947
CENTRAL AFRICA		
Tchad, Koro Toro region		Coppens, 1960
Goz-Kerki		
Koulá		
Bochianga		
Quadi Derdeney		
Koulá Ri Katir		
(It is not clear at which of these five sites *Stylohipparion* has been found)		

Site	*Specimen*	*Reference*
EAST AFRICA		
Uganda: East shore of Lake Albert in Kaiso layers	1 incomplete upper molar BM M12615	Hopwood, 1926
Kenya: Kanam lower beds. Kanjera		
Tanganyika: North-east shore of Lake Eyasi (W. and N. of Mumba Hill)	Teeth	Reck & Kohl-Larsen, 1936
South Serengeti (various localities)	Loose teeth, fragmented mandibles	Dietrich, 1942
Olduvai		Hopwood, 1929, 1937
SOUTH AFRICA		
Cape Province:		
(i) Namaqualand (40 mi. east of Springbok)	Left P_2–M_1 and M_3 Right P_4, M_1, M_2 and part of M_3 (above specimens are S.A.M. 9982)	Haughton, 1932
(ii) (*a*) Sydney-on-Vaal	Left M^3 (MMK 431)	Cooke, 1950
(*b*) Pniel, near Barkly West	Left P_{+} or M_{+} (MMK 5225)	
(*c*) Vaal River at Christiana	Left M^2 or M^3 (Arch. Surv. 113)	
Orange Free State:		
Cornelia (Uitzoek)	(*a*) right M^1 (or M^2) (Nas. Mus. C558) left M^3 (Nas. Mus. C555) left M_1 + M_2 (Nas. Mus. C556)	Van Hoepen, 1930
	(*b*) symphysial fragment and incisors	Van Hoepen, 1930
	(*c*) right M_2 (Nas. Mus. C797) left P_2 (Nas. Mus. C796)	Van Hoepen, 1932
	(*d*) left P_3–M_3 (Nas. Mus. C795)	Van Hoepen, 1932
Transvaal:		
Kromdraai Cave	2 lower teeth (discovered by Broom)	Cooke, 1950
Bolt's Farm		Cooke, 1963
? Makapansgat		Cooke, 1963

NOTE: M^a indicates upper molar; M_a lower molar, etc.

SUMMARY OF PUBLISHED GEOLOGICAL EVIDENCE FROM AFRICAN HIPPARIONID SITES

The present state of our knowledge of the geological evidence from sites in Africa where hipparionids have been discovered indicates that they first appeared in Upper Miocene deposits. A summary of the data is considered useful for the assessment of the status of the Langebaanweg material.

MIOCENE

The continental layers of vertebrate fossils at OUED EL HAMMAM (between Mascara and Mercier Lacombe, upstream from Bou Hanifia,

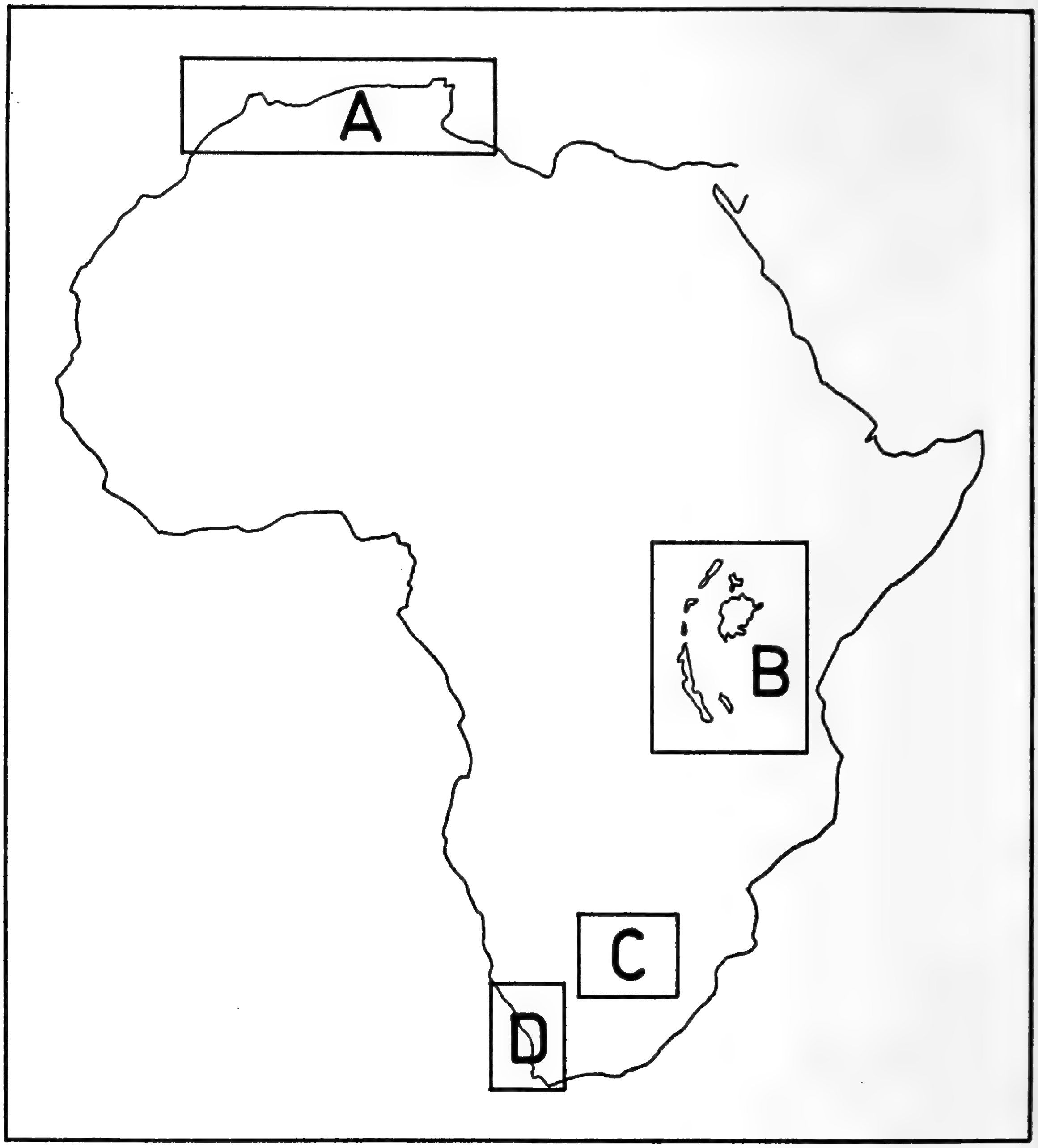

Fig. 3. Map of Africa indicating major areas of discovery of hipparionids. Details of areas A–C are shown in figs. 4–6, while area D is enlarged in fig. 1.

Algeria—figs. 3, 4) occur between two marine horizons, namely, (1) a Burdigalian one, characterized by its mollusc and echinid fauna and (2) an Upper Miocene *Lithotamnium* limestone. On this stratigraphical basis, the *Hipparion* horizon has been dated as Tortonian, i.e. Upper Vindobonian (Late Miocene) immediately antedating the Tortono-Sahelian transgression which occurs at the end of the Miocene marine period in this area (Arambourg, 1959).

The MARCEAU deposit, and especially its lignite and lacustrine clay and limestone which yield the *Hipparion* specimens, are referred to a period anterior to the Pliocene transgression, i.e. they belong to the Upper Miocene and may be equated with Oued el Hammam (Flandrin, 1942).

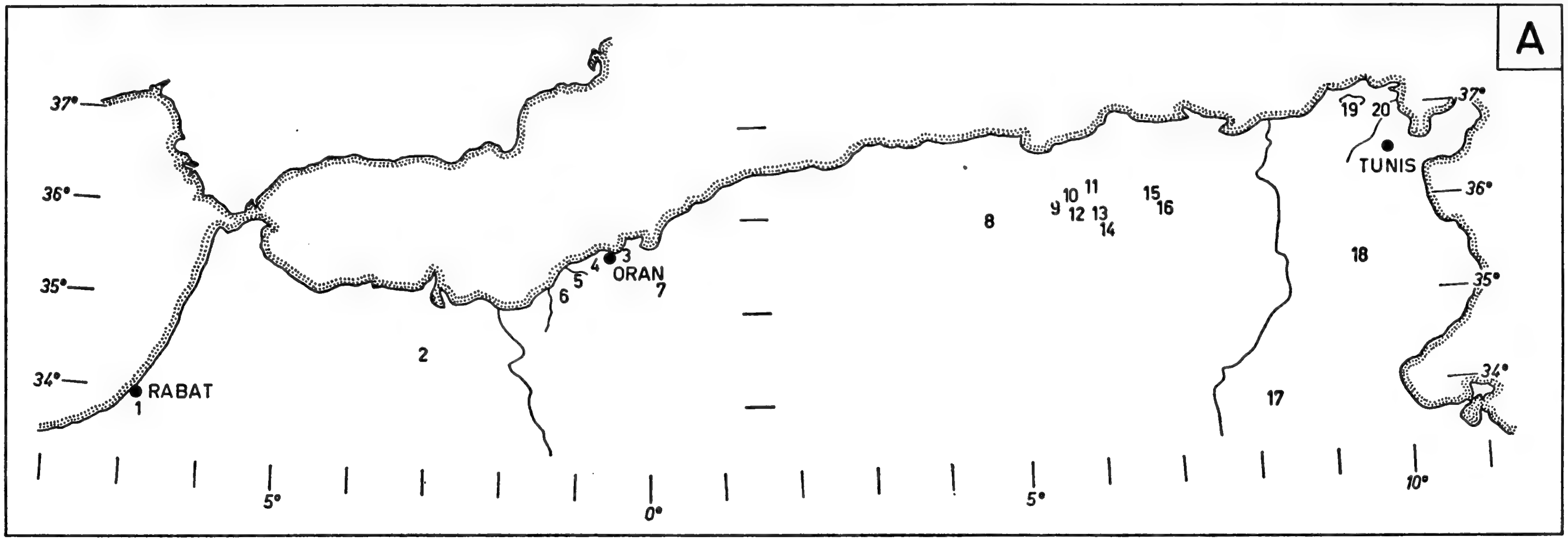

FIG. 4. Map of the Maghreb (A in fig. 3) indicating the localities from which *Hipparion* has been described, namely,

MOROCCO:

1. Rabat; 2. Camp Berteaux.

ALGERIA:

3. St. Charles (Oran); 4. Puits Kharouby (Oran); 5. Oued el Hammam; 6. Tafna; 7. Mascara; 8. Mansourah; 9. Sétif; 10. Aïn Boucherit and Beni Foudda; 11. Aïn Hanech; 12. St. Arnaud; 13. St. Donat; 14. Marceau; 15. Aïn Jourdel and Aïn el Bey; 16. Aïn el Hadj Baba.

TUNISIA:

17. Tozeur; 18. Djebel M'Dilla; 19. Garet Ichkeul; 20. Utique.

There is good evidence that CAMP BERTEAUX (near Taourirt, Eastern Morocco) belongs to this period. The *Hipparion* layers, from which *Mastodon* cf. *angustidens* has been recovered (Bourcart, 1937), form the base of a lacustrine series of 'argiles smectiques' which are lying on marine horizons with Tortonian fauna and are covered with Pontian deposits. Choubert and Ennouchi (1946) have dated the *Hipparion* layers as Upper Tortonian, being a sub-continental phase at the end of the Miocene period. Thus, they are somewhat younger than those from Oued el Hammam (Arambourg, 1959).

The brack water deposits of TAFNA (near Guiard, Province of Oran) show a 'Sarmatian facies' of the Upper Vindobonian. On faunal and lithological grounds, they were first referred to the 'classical Pontian' (Dalloni, 1914), but recently they were re-studied and correlated with the Oued el Hammam horizon (Perrodon and Tempere, 1953). However, the geological evidence is not clear.

PLIOCENE

Pliocene palaeontological sites are rare in the Maghreb. Some fossiliferous lacustrine formations in the SETIF–CONSTANTINE area have been referred to this period (Middle Pliocene). Included are also the limestone deposits of the ST. ARNAUD Cemetery and of the MASCARA region, AÏN EL BEY, AÏN EL HADJ BABA, ST. DONAT, and possibly UTIQUE in Tunisia.

Most of these exposures correspond to the fluviolacustrine filling of a vast depression between the Tellian and Sahara–Atlas. According to Arambourg (1956) the *Hipparion sitifense* layers of St. Arnaud Cemetery, Aïn el Hadj Baba and Mascara are lithologically different (sands and lacustrine limestones) from the *Stylohipparion* and *Equus numidicus* deposits of Aïn Boucherit and Aïn Jourdel (gray marls and red conglomerate). While these represent the base of the 'Villafranchian' (similar to Lac Ichkeul and Fouarat), they are referred to the Middle Pliocene. No satisfactory geological evidence is available for TOZEUR (Tunisia): it was referred by Boule (1910) and Solignac (1931) to the 'Pontian' stage because of the presence of *Merycopotamus* and *Hipparion*. Now that the occurrence of these forms is known in Upper Miocene deposits in India and North Africa, there is a special need for obtaining better stratigraphical evidence for dating this site.

At WADI NATRUN (Gart el Moluk Hill) in the Nile Valley, fluviomarine gypsiferous clays (containing, among other rare vertebrates, *Hipparion albertense*) are interbedded with limestones and shales, and deposited in an arm of the Mediterranean in the Nile Valley. On a stratigraphical basis they are dated as Middle Pliocene.

PLEISTOCENE

North Africa

The *Hipparion* fossiliferous horizons in the Maghreb correspond stratigraphically to the marine regression following the major Pliocene extension.

The most significant exposures are St. Arnaud and Oran in Algeria, and Lac Ichkeul, near Bizerta, in Tunisia (figs. 3, 4). The sequence has been extensively described and discussed (Howell, 1959). The general feature is that of a 300-foot series of marls and lacustrine clays and silts, with interbedded fossiliferous sandstones, gravels and calcareous conglomerates.

At LAC ICHKEUL the base is formed by deep-water Plaisancian and lagoonal Astian marine deposits capped with fresh-water beds from the early Pleistocene, with intercalation of a one-foot thick conglomerate.

At BEL HACEL eroded dune sandstones overlying transgressive Astian marls and sands are bearing the 'Villafranchian' fauna: they are further overlain by the 100-metre high Sicilian beach.

In the ST. ARNAUD area, two distinct fossiliferous horizons are visible. The lower one (Aïn Boucherit, i.e. Beni Foudda) is a coarse calcareous conglomerate; the upper one (Aïn Hanech) is a cracked, rather sandy or gravelly clay, intercalated in the thick marl filling the old marshy or lacustrine depression. Faunal and stratigraphical considerations make the St. Arnaud upper deposit somewhat younger than Lac Ichkeul.

At ORAN (ST. CHARLES), where *Libyhipparion* (?) *libycum* was first recovered and named by Pomel (1897), the consolidated dune sandstones and clays are concordantly overlying the calabrian sandstones, of which they represent the regression facies. The calabrian itself is in direct contact with the *Flabellipecten flabelliformis* sands and sandstones of the marine Pliocene; and at the base, the sequence reaches the Tortono-Sahelian marks and red stone of the Upper Miocene (Arambourg, 1960).

Ligniferous clays of the PUITS KHAROUBY near Oran from which *H. massoesylium* Pomel was recovered, has usually been placed—on the basis of its mollusc fauna—in the Upper Pliocene, but there is little geological evidence for it being older than Lower Pleistocene.

East Africa

Most of the fossiliferous horizons of East Africa (figs. 3, 5) are linked with tuffs, ashes or lapilli projected and deposited by volcanic eruptions. This volcanic activity spans over a long period of time, probably from Lower Miocene up to Upper Pleistocene and even to historical times. Therefore it is difficult, on purely geological grounds, to date the different fossil deposits. Usually it is only by convergence of tectonic, stratigraphical, lithological and chemical methods on the one hand, and by faunal studies on the other that it is possible to propose a satisfactory date.

At KANAM, on the slope of the dissected volcanic centre of Homa Mountain, the lacustrine brown calcareous fossiliferous clays, with their interbedded fine tuffs from intermittent volcanic explosions, are commonly referred to the Lower Pleistocene.

The KAISO series is complex. It has been repeatedly studied (Wayland, 1926; Fuchs, 1934), and recently Lepersonne (1949) subdivided it into three

FIG. 5. Map of Central-East Africa (B in fig. 3) indicating the localities from which *Hipparion* has been described, namely, 1. Lake Albert; 2. Kanjera; 3. Mumba Hills, Lake Eyasi; 4. Olduvai Gorge; 5. South Serengeti, Laetolil beds.

main stages of sedimentation, the middle one being highly fossiliferous. It is a clayey deposit, alternating with thin beds of fine sands and sandstones, and discontinuous ironstone horizons and limonite lenses (Kaiso bone beds), containing silicified wood and a high proportion of vertebrates. It overlies a silty lower deposit with some minor gravel horizons, resting on a basal ironstone layer (laterite) capped by unstratified sands above the down-faulted peneplain surface. This lower part of the Kaiso series, including the fossil horizon, is usually placed in the Lower Pleistocene (Howell, 1959; Bishop, 1963).

The OMO beds are lithographically comparable to the Kaiso deposits. The 'Villafranchian' fauna, and the *Hipparion* material in particular, occur in sandstone horizons between lacustrine volcanic clayey tuffs. In the evolution of the Rudolph depression in its Nilotic or open phase, Arambourg (1943) has distinguished two major extensions of the lake during the Pleistocene: (1) the vertebrate beds occur in a sand and sandstone horizon of the lower Omo Valley, representing a first phase of lacustrine deposition prior to the general tectonic uplift of the end of the Lower Pleistocene. (2) Posterior to the tectonic dislocation, the second phase corresponds to the series of horizontal terraces on the slope of the Rudolph Basin—they are not fossiliferous. This distinction, confirmed by the study of the fauna, permits the fossil beds to be dated as Lower Pleistocene, probably younger than Kaiso and Kanam.

It is more difficult to specify the geological location of the SERENGETI *Hipparion* material. The Laetolil beds in the Vogel River area show a sequence of upfaulted subaerially deposited yellow and gray tuffs (Kent, 1941). Unfortunately the fauna collected by Kohl-Larsen 'in den Schluchten und Wasserrissen' of the South Serengeti was probably recovered from various horizons which were altered and mixed-up by subsequent erosion (Dietrich, 1942). The gray tuffs, about 20 m. thick, which appear to contain the 'older fauna' (Kohl-Larsen, 1939), are dated as Lower Pleistocene, more or less contemporary with Omo and Olduvai I. Efforts have been made to identify this stratigraphically older fauna by such means as the type of mineralization and colour. Conclusions based on this method can only be accepted with reserve because of the fact that possible weathering may have altered the original appearance of the fossils. Nevertheless, Dietrich (1942) believed that all his *Hypsohipparion* material derived from the lower gray tuffs.

The vast sequence of stratified beds exposed in the OLDUVAI GORGE (northern Tanganyika) has been extensively discussed in recent years, and lately by Pickering (1960) and Leakey (1963). Independently of the chemical dating of the beds, which provides evidence of a great duration and antiquity of Bed I, dating has also been attempted on studies of the fauna and on a climatological basis. Little has been added from the strictly geological point of view. It is important to note that the major climatic, geological and apparently faunal 'break' occurs near the base of Bed II and not, as was previously thought, between Beds I and II. Most workers agree that Olduvai I belongs to the Lower Pleistocene, being more or less contemporary with (and probably prior to) Omo and Laetolil, while Beds II, III, IV are considered to belong to the Middle Pleistocene.

The KANJERA exposures, on the low cliffs of the Homa Mountain close to Lake Victoria, consist of a tripartite series of basal greenish ash and tuffs, succeeded by clays with limestone and by upper transgressive beds of brown-greenish clay. Most of the fossils are obtained from and in close association with the lower tuff and ash layer, but it is not possible to be certain whether or not all the material came from this source (Kent, 1942). However, there is sufficient evidence that the *Hipparion* may be considered to be more ancient than the human fossil remains which were recovered from the middle beds. The Kanjera faunal beds are referred to the Middle Pleistocene, roughly contemporary with Olduvai IV.

The LAKE EYASI beds are usually referred to an early Upper Pleistocene period, more on a palaeontological than on a geological basis.

According to Reck and Kohl-Larsen (1936), it is probable that the *Hipparion* teeth recovered west and north of Mumba Hill, in the north-east section of the Eyasi basin (*see* p. 283), do not belong to the original beds. Indeed they are very much rolled, which is not the case for the presumably contemporaneous material, and constitute a secondary deposition. If this interpretation is correct, these teeth are probably more ancient than the typical Eyasi fauna, and should be dated to a period prior to the Upper Pleistocene.

South Africa

The only relatively satisfactory stratigraphical information concerning *Hipparion* in South Africa is obtained at the YOUNGER GRAVELS OF THE

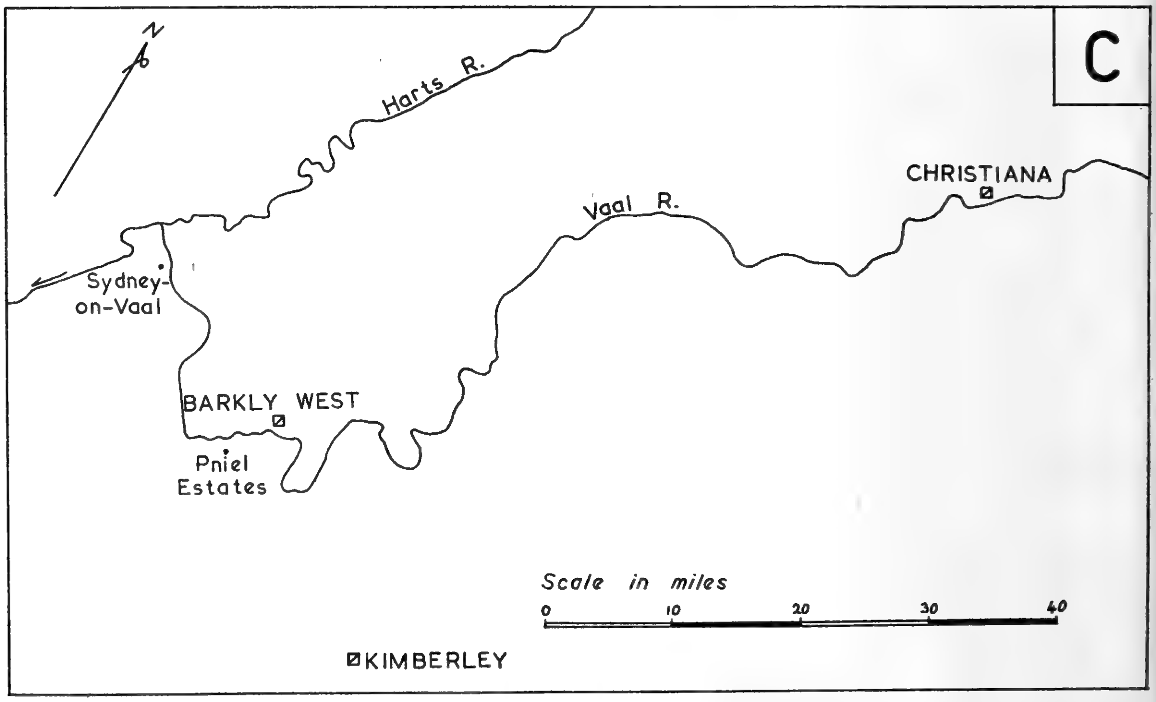

Fig. 6. Map of northern Cape Province, South Africa (C in fig. 3) indicating localities from which *Hipparion* has been described, namely, Sydney-on-Vaal, Pniel and Christiana.

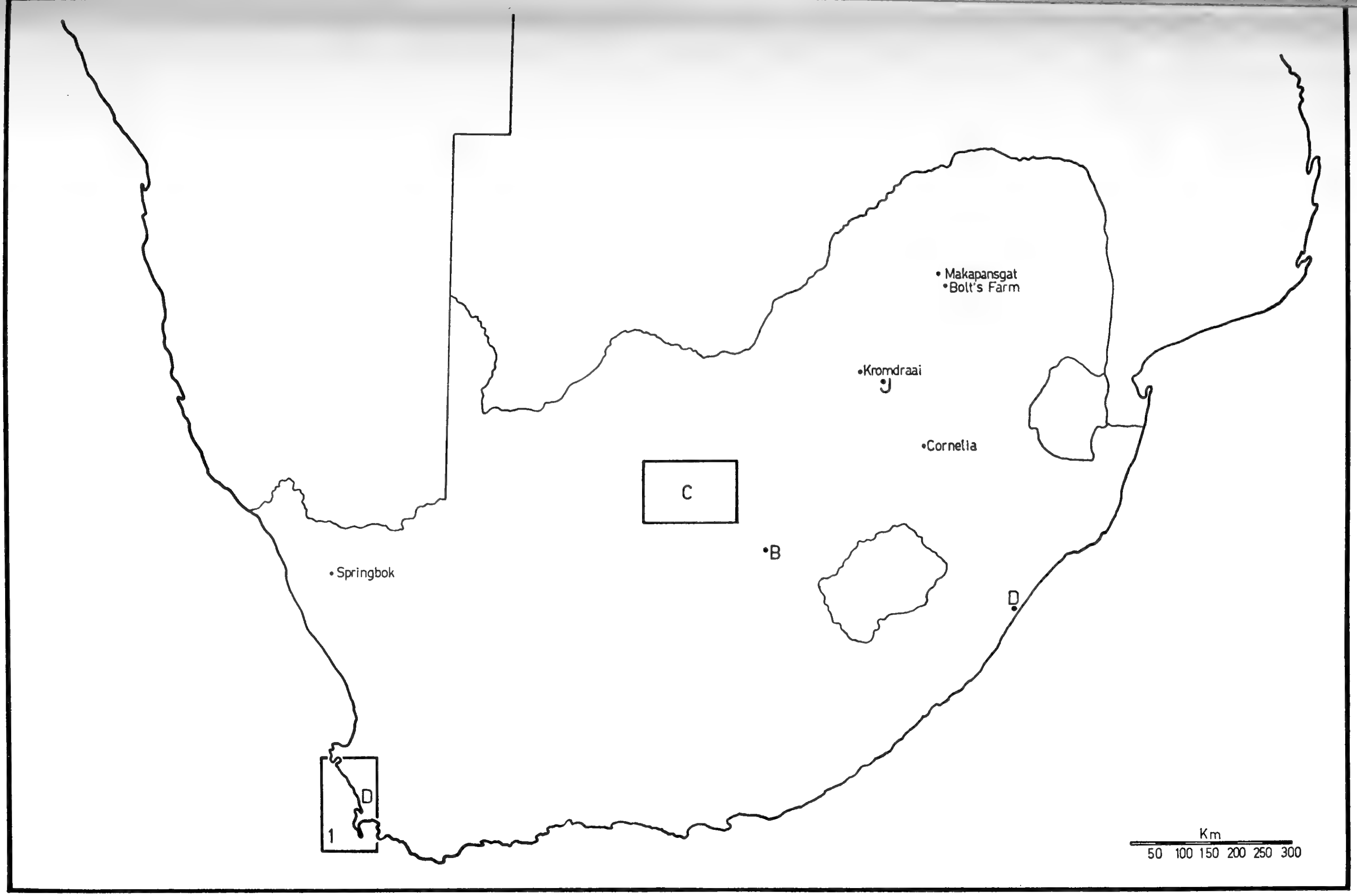

FIG. 7. Map of South Africa indicating certain localities of discovery of hipparionids, in relation to areas C and D of fig. 3. The positions of three cities are shown: B = Bloemfontein; D = Durban; J = Johannesburg.

VAAL RIVER (Christiana; Pniel; Sydney-on-Vaal: fig. 6). In this horizon, which actually presents the first fossil occurrence in the Vaal area (as fossils of the oldest gravels have probably been destroyed), three phases have been recognized from their elevation and their stone artefact associations. However, most of the fossils seem to have derived from Phase II and III, although it is not impossible that the fossils found below Barkly West may have been contained in Phase I of the Younger Gravels (Cooke, 1963). On the basis of a climatological interpretation (Söhnge, Visser and Lowe, 1937; amended by Cooke, 1947, and Lowe, 1952), the Younger Gravels were correlated with the Middle Pleistocene Olduvai Beds II and IV.

The CORNELIA beds, an open site on the farm 'Uitzoek' in the Orange Free State, consists of exposures of clays, gravels and sand, which represent an old 'pan' filling. Oakley (1954) emphasizes the Pleistocene nature of the site by referring to a 'lower Fauresmith industry' from the beds. There is no reliable date based purely on stratigraphy for this site.

At present it is also impossible to make any tentative geological dating for the *Notohipparion* material from NAMAQUALAND. It was recovered from a granite level in a well, 60 feet down in the surface limestone, 40 miles east of Springbok. It is known that the infilling of the valleys with sand has been occurring in Namaqualand from Upper Cretaceous times, with probable breaks in the sedimentation, but there is no information on the actual sequence of gravels and limestone in the well (Haughton, 1932).

The *Hipparion* occurrence in cave fillings at KROMDRAAI, (?) MAKAPANSGAT and BOLT'S FARM has been dated by faunal and climatological methods (Ewer, 1957; Brain, 1958), and nothing further can be added from a purely stratigraphical point of view.

LISTS OF FAUNAL ASSEMBLAGES AT THE AFRICAN HIPPARIONID SITES

It is considered useful to include lists of all the diagnosed, published fauna from the various sites where *Hipparion* has been recovered. Omission of particular sites is due to lack of information, and Hopefield is included because of the richness of fauna and for comparison with contemporaneous sites. The faunal assemblage of Langebaanweg is listed on page 280. The sites are listed according to the order presented on pages 281–3. Wherever possible, generic and specific names are retained as they appear in the publications quoted.

INDIVIDUAL HIPPARIONID SITES

Oued el Akrech (Morocco) (After Arambourg and Choubert, 1957)

PROBOSCIDEA

†*Anancus osiris*
†*Elephas africanavus*

PERISSODACTYLA

†*Stylohipparion* sp.

Oued el Hammam (Oran) and Marceau (Algiers) (After Arambourg, 1963)

PRIMATES

†*Macaca flandrini*

RODENTIA

†*Hystrix* sp.

CARNIVORA

†*Hyaena algeriensis*

TUBULIDENTATA

†*Orycteropus mauritanicus*

PROBOSCIDEA

†*Turicius* sp.
†*Mastodon* sp.

PERISSODACTYLA

†*Dicerorhinus primaevus*
†*Hipparion africanum*

ARTIODACTYLA

†*Palaeotragus germaini*
†*Samotherium* sp.
†*Damalavus boroccoi*
†*Gazella praegaudryi*
†*Tragocerus* sp.
†*Cephalophus* sp.

AVES

†*Struthio* sp.

Aïn Hanech (Algeria) (After Arambourg, 1947; 1949)

CARNIVORA

Hyaena sp.
Canis sp.

PROBOSCIDEA

†*Anancus osiris*
†*Elephas* cf. *planifrons*
†*E.* aff. *meridionalis* or *recki*

PERISSODACTYLA

†*Atelodus* aff. *simus*
†*Stylohipparion libycum*
Equus sp.

ARTIODACTYLA

Hippopotamus amphibius
†*Omochoerus*(1) sp.
Giraffa sp.
†*Libytherium maurusium*
Bos sp.
†*Bubalus* sp.
Oryx sp.
Alcelaphus sp.
†*Gazella sitifensis*

(1) According to Leakey, 1958 = *Mesochoerus*.

Garet Ichkeul (Tunisia) (After Arambourg, 1949)

PROBOSCIDEA

†*Anancus osiris*
†*Elephas* cf. *planifrons*

PERISSODACTYLA

†*Atelodus* aff. *simus*
†*Stylohipparion libycum*
Equus

ARTIODACTYLA

Hippopotamus sp.
†*Libytherium maurusium*
Bos sp.
Oryx sp.
Alcelaphus sp.
†*Gazella* aff. *sitifensis*
Redunca sp.

Tozeur (Tunisia) (After Roman & Solignac, 1934)

PROBOSCIDEA

†*Mastodon* cf. *longirostris*

PERISSODACTYLA

†*Hipparion* sp.

ARTIODACTYLA

†*Merycopotamus* aff. *dissimilis*
†*Capreolus matheroni*
†*Tragocerus amaltheus*
†*Hemitragus perimensis*
Antilopinae

Wadi Natrun (After Studer, 1898; Andrews, 1902; Arambourg, 1947 and 1963)

MAMMALIA

PRIMATES

†*Libypithecus markgrafi*

CARNIVORA

†Machairodontidae gen. sp. indet.
Phocidae gen. sp. indet.
Lutra sp.

LAGOMORPHA

? Leporidae

PROBOSCIDEA

†*Mastodon* sp.

PERISSODACTYLA

†*Hipparion* sp.

ARTIODACTYLA

†*Hippopotamus protamphibius*
†*Sivachoerus giganteus*
Camelidae gen. sp. indet.
†*Libytherium maurusium*
†*Hippotragus* (?) *cordieri*

REPTILIA

Crocodilus
†*Euthecodon nitriae*
†*Sternothaerus dewitzianus*
†*Trionyx pliocaenicus*

PISCES

Protopterus
Synodontis

Omo (After Arambourg, 1947)

PRIMATES

†*Dinopithecus brumpti*

CARNIVORA

†*Homotherium* (?) *ethiopicum*

PROBOSCIDEA

†*Deinotherium bozasi*
†*Elephas* (*Archidiskodon*) *recki*
†*Elephas* (*Archidiskodon*) cf. *planifrons*

PERISSODACTYLA

†*Atelodus* cf. *germano-africanus*
†*Stylohipparion albertense*
Equus cf. *zebra*

ARTIODACTYLA

†*Hippopotamus* (*Tetraprotodon*) *protamphibius*
†*Omochoerus heseloni*(1)
†*Metridiochoerus andrewsi*(2)
†*Notochoerus capensis*(3)
†*Phacochoerus africanus fossilis*(4)
Giraffa camelopardalis
†*Giraffa gracilis*
†*Sivatherium olduvaiense*(5)
†*Menelikia lyrocera*
Kobus (*Kobus*) *sigmoidalis*
Kobus (*Kobus*) sp.
†*Redunca ancystrocera*
Alcelaphus sp.
†*Strepsiceros imberbis*
Aepyceros melampus
Antidorcas sp.
Oryx cf. *gazella*
Tragelaphus nakuae
Taurotragus cf. *procanna*
Gazella praethomsoni
Syncerus aff. *brachyceros*

(1) = *Mesochoerus heseloni* (Leakey, 1958).
(2) = *Pronotochoerus jacksoni* (Leakey, 1958).
(3) = *Notochoerus euilus* (Leakey, 1958).
(4) According to Leakey, 1958 = *Tapinochoerus meadowsi*, but does not belong to the Omo Beds.
(5) See footnote to Langebaanweg fauna (p. 280).

Koro Toro (Tchad) (After Abadie, Barbeau and Coppens, 1949; Coppens, 1960)

MAMMALIA

PRIMATES

†'*Australopithecus*' sp.

CARNIVORA

Hyaena cf. *striata*

PROBOSCIDEA

†*Archidiskodon africanavus*(1)
†*A. recki*(2)
†*Anancus* sp.
†*Stegodon* sp.

PERISSODACTYLA

†*Stylohipparion* sp.
Ceratotherium simum

ARTIODACTYLA

†*Hippopotamus* cf. *protamphibius*
†*Sivatherium*(3) sp.
Giraffa camelopardalis
Alcelaphus sp.

REPTILIA

Crocodilus niloticus

(1) According to Cooke, 1960=*Elephas africanavus*.
(2) According to Cooke, 1960=*Palaeoloxodon recki*.
(3) See footnote to Langebaanweg fauna (p. 280).

Kaiso[1]

CARNIVORA

† ? *Homotherium ethiopicum*

PROBOSCIDEA

†*Stegodon kaisensis*
†*Archidiskodon exoptatus*

PERISSODACTYLA

†*Stylohipparion albertense*
†*Metaschizotherium hennigi*
Ceratotherium simum

ARTIODACTYLA

†*Hippopotamus imaguncula*
†*H. protamphibius*
†*Notochoerus euilus*
†*Mesochoerus limnetes*

Kanam[1]

CARNIVORA

Crocuta crocuta

PROBOSCIDEA

†*Anancus kenyensis*
†*Stegodon kaisensis*
†*Archidiskodon subplanifrons*
†*A. exoptatus*
†*Deinotherium bozasi*

PERISSODACTYLA

†*Stylohipparion albertense*
†*Equus oldowayensis*
Ceratotherium simum
Diceros bicornis

ARTIODACTYLA

†*Hippopotamus imaguncula*
†*Metridiochoerus pygmaeus*
†*Nyanzachoerus kanamensis*
Giraffa camelopardalis
†*Libytherium olduvaiense*

[1] Compiled from Hopwood, Leakey & McInnes *in* Leakey, 1951; Dietrich, 1950; McInnes, 1953; Cooke, 1963; Leakey, 1958.

Eyasi[1]

PRIMATES

Homo sp.

RODENTIA

†*Pedetes surdaster*
Thryonomys swinderianus

CARNIVORA

Crocuta crocuta
Caracal caracal
Panthera leo
Panthera pardus

TUBULIDENTATA

†*Orycteropus aethiopicus*

PERISSODACTYLA

Equus burchelli
†*Stylohipparion* sp.
Diceros bicornis

ARTIODACTYLA

Hippopotamus amphibius
Potamochoerus koiropotamus
Giraffa camelopardalis
Strepsiceros strepsiceros
Taurotragus oryx
Syncerus caffer
†*Homoioceras nilsoni*
Kobus ellipsirymnus
†*Adenota kob*
†*Redunca redunca*
Pelea sp.
†*Oryx beisa*
Aepyceros melampus
†*Gazella granti*

Laetolil (South Serengeti)[1]

PRIMATES

†*Simopithecus oswaldi*

RODENTIA

†*Pedetes surdaster*
†*Hystrix galeata*

CARNIVORA

Canis mesomelas
C. mesomelas latirostris
†*Canis africanus*
Crocuta crocuta
Caracal caracal
? *Panthera pardus*

TUBULIDENTATA

†*Orycteropus aethiopicus*

PROBOSCIDEA

†*Anancus kenyensis*
†*Archidiskodon subplanifrons*
†*A. exoptatus*
†*A. recki*
†*Deinotherium bozasi*

PERISSODACTYLA

†*Stylohipparion albertense*
Equus burchelli
†*Metaschizotherium hennigi*
Ceratotherium simum
†*Serengeticeros efficax*

ARTIODACTYLA

Hippopotamus amphibius
†*Notochoerus euilus*
†*Okapia stillei*
Giraffa camelopardalis
†*Libytherium olduvaiense*
†*Tragelaphus buxtoni*
Taurotragus oryx
Syncerus caffer
? *Kobus ellipsirymnus*
†*Redunca redunca*
†*Hippotragus equinus*
†*Damaliscus angusticornis*
Aepyceros melampus

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[1] See footnote p. 295.

Olduvai (After Leakey, 1958, and Cooke, 1963)
Numbers I, II, III and IV refer to the various beds

PRIMATES

†*Simopithecus oswaldi* (I, II, III, IV)
†*S. jonathani* (II, ? IV)
†*Paranthropus boisei* (I, II)
†*Homo sp.* (I, II)

CARNIVORA

Canis mesomelas (II, IV)
C. mesomelas latirostris (II, IV)
†*Canis africanus* (II, IV)
Aonyx capensis (II)
Crocuta crocuta (I)
Panthera leo (II, III)
P. pardus (? I)

PROBOSCIDEA

†*Anancus kenyensis* (I, II)
†*Archidiskodon exoptatus* (I)
†*A. recki* (I, II, III, IV)
†*Deinotherium bozasi* (I, II)

PERISSODACTYLA

†*Stylohipparion albertense* (I, II, III, IV)
Equus burchelli (II, III, IV)
†*E.* aff. *grevyi* (I, II, III, IV)
†*E. oldowayensis* (I, II, III, IV)
†*Metaschizotherium hennigi* (I, II)
Ceratotherium simum (I, II, III, IV)
†*Serengeticeros efficax* (II)
Diceros bicornis (I, II, III, IV)

ARTIODACTYLA

†*Hippopotamus gorgops* (I, II, III, IV)
†*Notochoerus hopwoodi* (III, IV)
†*N. compactus* (II)
†*Mesochoerus olduvaiensis* (I, II, III, IV)
†*Potamochoerus majus* (I, II, III, IV)
Phacochoerus africanus (II, III, IV)
†*P. altidens altidens* (II, III, IV)
†*P. altidens robustus* (I, II)
†*Tapinochoerus minutus* (IV)
†*T. meadowsi* (I, II, III, IV)
†*Afrochoerus nicoli* (II, III, IV)
†*Metridiochoerus andrewsi* (I)
Orthostyonyx brachiops (II)
†*Okapia stillei* (? I)
Giraffa camelopardalis (II, IV)
†*G. gracilis* (II)
†*Libytherium olduvaiense* (I, II, III, IV)
Strepsiceros strepsiceros (? I, II, IV)
†*Strepsiceros imberbis* (? I, II, IV)
†*Tragelaphus buxtoni* (II)
Taurotragus oryx (I, II, IV)
†*Homoioceras nilssoni* (IV)
†*Bularchus arok* (II, III, IV)
†*Adenota kob* (I, II, III)
†*Hippotragus equinus* (III, IV)
†*H. niro* (II, IV)
†*Oryx beisa* (I)
†*Damaliscus angusticornis* (II, IV)
†*D. teste* (I, II, IV)
†*Alcelaphus kattwinkeli* (II, III, IV)
†*Beatragus hunteri* (I, II, IV)
†*Gorgon taurinus semiticus* (I, II, III, IV)
†*Gazella gazella praecursor* (I, II, IV)
†*G. granti* (I, II, IV)
†*Phenacotragus recki* (IV)
†*Pultiphagonides africanus* (I, II)
†*Pelorovis oldowayensis* (II, IV)

Vaal River Younger Gravels (After Cooke and Wells, 1946; Cooke, 1949, 1963; Wells, 1964)

CARNIVORA

cf. *Crocuta crocuta*

PROBOSCIDEA

†*Gomphotherium* sp.

†*'Archidiskodon' subplanifrons*
†*'Archidiskodon' broomi*
†*'Archidiskodon' transvaalensis*
†*'Palaeoloxodon archidiskodontoides'* (=*P. recki* ?)
†*'Loxodonta'* cf. *atlantica*
cf. *Loxodonta africana*

PERISSODACTYLA

†*Stylohipparion steytleri*
†*Equus helmei*
†*Equus plicatus*
†*'Equus sandwithi'* (=*E. plicatus* ?)
Equus cf. *burchelli*
Equus cf. *quagga*
cf. *Diceros bicornis*

ARTIODACTYLA

†*Mesochoerus paiceae*
†*Notochoerus capensis*
†*Tapinochoerus modestus*
†*'Tapinochoerus' meadowsi*
†*Stylochoerus compactus*
†*Phacochoerus aethiopicus*
Phacochoerus africanus
Hippopotamus cf. *amphibius*
†*Sivatherium* (?) *cingulatum*(1)
†*Sivatherium olduvaiense haughtoni*(1)
cf. *Alcelaphus caama*
†*'Alcelaphus robustus'*
†cf. *Megalotragus eucornutus*
Connochaetes cf. *gnou*
cf. *Connochaetes* sp.
cf. *Damaliscus* sp.
cf. *Sylvicapra grimmia*
cf. *Aepyceros melampus*
cf. *Antidorcas marsupialis*
†*Gazella wellsi*
cf. *Hippotragus* sp.
cf. *Strepsiceros strepsiceros*
Taurotragus cf. *oryx*
Syncerus cf. *caffer*
†*'Homoioceras'* cf. *baini*

(1) See footnote to Langebaanweg fauna (p. 280).

Cornelia (Uitzoek) (After Cooke, 1963)

PERISSODACTYLA

†*Stylohipparion steytleri*
Equus burchelli
†*E. plicatus*
†*Eurygnathohippus cornelianus*

ARTIODACTYLA

†*Hippopotamus gorgops*
†*Notochoerus compactus*
Phacochoerus africanus
†*Orthostonyx* sp.
Giraffa camelopardalis
†*Libytherium olduvaiense*
Strepsiceros strepsiceros
Taurotragus oryx
†*'Homoioceras' baini*
†*Kobus venterae*
Damaliscus cf. *albifrons*
†*Damaliscus* sp.
Alcelaphus caama
† ? *A. helmei*
†*Connochaetes laticornutus*
†*Megalotragus eucornutus*
†*Gazella wellsi*
†*G. helmoedi*
†*Gazella* sp.
†*Antidorcas marsupialis*

Kromdraai (After Cooke, 1963)

INSECTIVORA

†*Proamblysomus antiquus*
†*Elephantulus langi*
Crocidura cf. *bicolor*
Suncus cf. *etruscus*
† ? *Myosorex robinsoni*

PRIMATES

†*Parapapio jonesi*
†*Papio robinsoni*
†*Paranthropus robustus*

LAGOMORPHA

Lepus capensis

RODENTIA

†*Mystromys antiquus*
Tatera cf. *brantsi*
?*Desmodillus auricularis*
Grammomys cf. *dolichurus*
†*Rhabdomys* cf. *pumilio*
Mastomys cf. *natalensis*
Malacothrix cf. *typica*
Steatomys cf. *pratensis*
†*Palaeotomys gracilis*
†*Cryptomys robertsi*

CARNIVORA

Canis mesomelas pappos
†*Canis atrox*
†*Canis terblanchei*
Vulpes pulcher
†*Herpestes mesotes*
†*Crossarchus transvaalensis*
†*Crocuta spelaea*
†*C. ultra*
†*Hyaena bellax*
†*Felix crassidens*
†*Therailurus piveteaui*
†*Panthera* aff. *leo*
†? *P. whitei*
†*P. shawi*
†*Megantereon eurynodon*

HYDRACOIDEA

†*Procavia antiqua*
†*P. transvaalensis*

PERISSODACTYLA

†*Stylohipparion steytleri*
? *Equus burchelli*
†*E. plicatus*
†*E. helmei*

ARTIODACTYLA

†*Potamochoerops antiquus*

Bolt's Farm (After Cooke, 1963)

INSECTIVORA

†*Proamblysomus antiquus*
†*Atelerix major*
†*Elephantulus langi*
†*Elephantulus antiquus*
E. cf. *brachyrhynchus*
Suncus cf. *etruscus*
†*Myosorex robinsoni*

CHIROPTERA

Rhinolophus cf. *capensis*
†cf. *Myotis* sp.

PRIMATES

† ?*Parapapio broomi*
†? *P. whitei*
†*Cercopithecoides williamsi*

RODENTIA

Pedetes cf. *caffer*
†*Mystromys hausleitneri*
Tatera cf. *brantsi*
†*Dasymys bolti*
†*Rhabdomys* cf. *pumilio*
†*Thallomys debruyni*
Leggada cf. *minutoides*
L. cf. *major*
Malacothrix cf. *typica*
†*Palaeotomys gracilis*
Hystrix africae-australis
†*Cryptomys robertsi*

CARNIVORA

Canis mesomelas
C. mesomelas pappos
Aonyx cf. *capensis*
Suricata suricatta
†*Crossarchus transvaalensis*
†*Hyaena bellax*
†*Leptailurus spelaeus*

†*Therailurus barlowi*
†*Panthera* aff. *leo*
†*Machairodus transvaalensis*

PROBOSCIDEA

†*Loxodonta atlantica*

HYDRACOIDEA

Procavia capensis

PERISSODACTYLA

†*Stylohipparion steytleri*
Equus burchelli
†*E. plicatus*

ARTIODACTYLA

†*Tapinochoerus meadowsi*
†*Potamochoeroides shawi*
†*P. antiquus*
Tragelaphus scriptus
Taurotragus oryx
Syncerus caffer
Damaliscus cf. *pyrgatus*
? *D.* cf. *lunatus*
†*Alcelaphus robustus*
†*A. helmei*
Connochaetes taurinus
†*Makapania broomi*
† ? *Raphicerus campestris*
†*Gazella wellsi*
† ? *Phenacotragus vanhoepeni*
† ?*Antidorcas marsupialis*

Makapansgat (After Cooke, 1963)

INSECTIVORA

†*Chrysotricha hamiltoni*
†*Elephantulus langi*
Suncus cf. *etruscus*
†*Myosorex robinsoni*

PRIMATES

†*Simopithecus darti*
†*Parapapio jonesi*
†*P. broomi*
†*P. whitei*
†*Papio robinsoni*
†*Australopithecus africanus*
†*Cercopithecoides williamsi*

LAGOMORPHA

Pronolagus randensis

RODENTIA

†*Mystromys hausleitneri*
†*M. darti*
? *Tatera* cf. *brantsi*
Grammomys cf. *dolichurus*
Pelomys cf. *fallax*
†*Rhabdomys* cf. *pumilio*
Aethomys cf. *namaquensis*
Mastomys cf. *natalensis*
Leggada cf. *minutoides*
Dendromus cf. *mesomelas*
† ?*Malacothrix makapani*
Steatomys cf. *pratensis*
†*Palaeotomys gracilis*
†*Hystrix major*
H. africae-australis
†*Xenohystrix crassidens*
†*Gypsorhychus makapani*
†*Cryptomys robertsi*

CARNIVORA

? *Canis mesomelas pappos*
†*Cynictis penicillata brachyodon*
†*Crocuta* cf. *brevirostris*
†*Hyaena makapani*
†*Therailurus barlowi*
†*Megantereon* sp. nov.

HYRACOIDEA

†*Procavia antiqua*
†*P. transvaalensis*
†*Procavia* sp.

PERISSODACTYLA

† ? *Stylohipparion steytleri*
†*Equus helmei*
†*Metaschizotherium* (?) *transvaalensis*
Ceratotherium simum
Diceros bicornis

ARTIODACTYLA

Hippopotamus amphibius
†*Notochoerus euilus*
†*Potamochoeroides hypsodon*
†*P. shawi*
Giraffa camelopardalis
†*Libytherium* cf. *olduvaiense*
Strepsiceros strepsiceros
Tragelaphus angasi
Taurotragus oryx
Syncerus caffer
†*S.* cf. *makapani*
†*Cephalophus pricei*
C. caerulus
†*Redunca darti*
Redunca arundinum
R. fulvorufula
Oryx gazella
†*Alcelaphus robustus*
†*A. helmei*
Connochaetes taurinus
†*Oreotragus major*
†*Makapania broomi*
Aepyceros melampus
†*Gazella gracilior*
†*Phenacotragus vanhoepeni*

'ELANDSFONTEIN', HOPEFIELD (SOUTH AFRICA)

(Modified from Singer, 1957)

PHOLIDOTA

Manis sp.

PRIMATES

†*Simopithecus oswaldi hopefieldensis*
†*Homo sapiens rhodesiensis* ('Saldanha Man')

LAGOMORPHA

Lepus sp. (cf. *capensis*)

RODENTIA

Bathyergus sp. (cf. *suillus*)
Georychus sp. (cf. *capensis*)
Hystrix sp. (cf. *africae-australis*)
Otomys sp. (cf. *saundersiae*)
Parotomys sp. (cf. *brantsi*)

CARNIVORA

Canis mesomelas
Canis adustus
†*Lycaon pictus magnus*
Mellivora capensis
Herpestes sp. (cf. *ichneumon*)
Herpestes eogale
Hyaena brunnea
†*Crocuta spelaea*
Lynx caracal
Leptailurus serval
†*Panthera leo spelaea*
†*Megantereon gracile*

PROBOSCIDEA

†*Loxodonta* (*Palaeoloxodon*) cf. *antiquus recki*
† ? *Archidiskodon* sp.

PERISSODACTYLA

†*Equus* (*Hippotigris*) *plicatus*
†*E. helmei*
†*E.* cf. *sandwithi*
Ceratotherium simum
Diceros bicornis

ARTIODACTYLA

†*Mesochoerus lategani*
†*M. paiceae*
†*Tapinochoerus meadowsi*
Hippopotamus amphibius
†*Sivatherium olduvaiense*(1)
†*Giraffa* cf. *gracilis*
†*Homoioceras* sp.
Taurotragus oryx
Redunca arundinum
Raphicerus campestris
Antidorcas marsupialis
†*Antidorcas* sp.
Tragelaphus(2) sp.

cf. *Hippotragus niger*
†cf. *H. leucophaeus*
†*Hippotragus* sp.
†*Damaliscus* cf. *dorcas*
†*Damaliscus* sp.
Connochaetes sp.
†*Lunatoceras* sp.
†*Pelea* sp.
†cf. *Gazella wellsi*
†*Gazella* sp. nov.

(1) See footnote to Langebaanweg fauna (p. 280).

(2) In the other faunal lists *Tragelaphus* has not been substituted for the earlier labelling *Strepsiceros*.

Refer now to table 1 on pages 303 to 313.

COMMENTARY ON THE PUBLISHED FAUNAL ASSOCIATIONS AT HIPPARIONID SITES IN AFRICA

MIOCENE

Oued el Hammam and Marceau

Arambourg (1959) has clearly demonstrated that these two sites contain fundamentally the same fauna: both include *Hipparion africanum*, *Samotherium* sp. and *Hyaena algeriensis*, and cannot but be contemporaneous, as is confirmed by their stratigraphy.

It seems clear that these assemblages correspond to a very special and, so far, little-known stage of development of the fauna of Africa, posterior to the Burdigalian and anterior to the 'classical Pontian'. The fauna from these sites are very different from the well-represented assemblage of the Lower Miocene in East Africa (Losodok, west of Lake Rudolph; Rusinga and Moboko Islands in the Kavirondo Gulf of Lake Victoria) and South West Africa. The typical Burdigalian assemblages contain, *inter alia*, *Mastodon* cf. *longirostris*, *Deinotherium hobleyi*, *Aceratherium*, *Teleoceras*, and *Anthracotheriidae*, *Propalaeochoerus*, *Bunolistriodon*, *Dorcatherium*, *Creodonta*, none of which are found at Oued el Hammam, nor are the anthropomorpha which constitute the typical African 'touch' of this Burdigalian fauna. The only similarity between the sites and a Burdigalian fauna is the presence at Oued el Hammam of an orycterope, namely, *Orycteropus mauritanicus* which is comparable with *Myorycteropus* McInnes of East Africa. The separation between Oued el Hammam and the Lower Miocene fauna of East and South West Africa is emphasized by the presence (at Oued el Hammam) of Giraffidae (*Samotherium* and *Palaeotragus*), the development of Bovidae (*Damalavus*, *Gazella*, *Tragocerus*, *Cephalophus*) and the appearance of *Hyaena* and especially of the equids with *Hipparion africanum*.

On the other hand, the assemblages from the two North African localities are at first sight characteristic of the so-called 'classical Pontian' of Eurasia (Eppelsheim, Pikermi, Mont Luberon). However, on detailed study and comparison of the several groups involved, Arambourg has shown that Eurasian 'Pontain' assemblages and the material from Oued el Hammam may belong to the same ensemble, but they are not identical: specific and generic differences exist and there is not even a single species in common (table 2).

TABLE I

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG	Chelmer	Broken Hill	Mumbwa	Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
INSECTIVORA																														
**Proamblysomus antiquus*					X	X																								
**Chrysotricha hamiltoni*			X																											
**Chlorotalpa spelea*		X		X																										
**Atelerix major*						X																								
**Elephantulus langi*		X	X	X	X	X						X																		
**Elephantulus antiquus*						X																								
E. cf. *brachyrhynchus*	X			X		X																								
**Mylomygale spiersi*	X	X																												
**Crocidura taungsensis*	X																													
C. cf. *bicolor*		X			X							X				?														
Suncus cf. *etruscus*		X	X	X	X	X																								
**Myosorex robinsoni*		X	X	X	?	X																								
CHIROPTERA																														
Rhinolophus cf. *capensis*	X		X			X																								
R. cf. *geoffroyi*												X																		
*cf. *Myotis* sp.						X																								
Miniopteris cf. *schreibersi*												X																		
PRIMATES																														
**Simopithecus oswaldi*[a]									X											X	X	X	X	X	X		X			
**S. jonathani*[a]																							X		?					
**S. darti*[a]			X																											
**S. danieli*[a]				X																										
**Simopithecus* sp.																?														

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[a] See also Singer (1962).

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
**Gorgopithecus major*				*X*																												
**Dinopithecus ingens*				*X*																												
**Parapapio antiquus*	*X*																															
**P. jonesi*	*X*	*X*	*X*	*X*	*X*																											
**P. broomi*		*X*	*X*			?																										
**P. whitei*	*X*	*X*	*X*			?																										
**Papio neumanni*																																*X*
**P. izodi*	*X*																															
**P. wellsi*	*X*																															
**P. angusticeps*				*X*																												
**P. robinsoni*			*X*	*X*	*X*																											
P. ursinus												X	X																			
**Paranthropus boisei*																								*X*	*X*							
**P. robustus*				*X*	*X*																											
**Australopithecus africanus*	*X*	*X*	*X*																													
**Telanthropus capensis*				*X*																												
**Homo rhodesiensis*									*X*								*X*															
**H.* cf. *sapiens*										*X*		*X*																				
**Homo* sp.																					*X*			*X*	*X*						*X*	*X*
**Cercopithecoides williamsi*	*X*	*X*	*X*	*X*		*X*																										
LAGOMORPHA																																
Pronolagus randensis			X									X																				
Lepus capensis	X			X	X				X																							
Lepus saxatilis												X																				
PHOLIDOTA																																
Manis sp.									X																							

RODENTIA																															
Xerus capensis										X																					
*Pedetes hagenstadi										X																					
*P. surdaster																							X								X
*P. gracile	X																														
P. cf. caffer						X																									
Mystromys antiquus	X																														
*M. hausleitneri		X	X		X	X																									
*M. darti			X																												
Tatera cf. brantsi	X	X	?		X	X																									
Desmodillus auricularis	X				?																										
Grammomys cf. dolichurus			X		X																										
*Dasymys bolti				X		X																									
Pelomys cf. fallax		?	X																												
*Rhabdomys cf. pumilio	X	X	X		X	X																									
Aethomys cf. namaquensis		X	X																												
Aethomys cf. chrysophilus												X																			
*Thallomys debruyni	X					X																									
T. cf. paedulcus												X																			
Mastomys cf. natalensis	X	X	X		X																										
Leggada cf. minutoides		X	X			X																									
L. cf. major		X				X																									
Saccostomus campestris												X					?														
*Dendromus antiquus	X																														
D. cf. mesomelas		X	X									X																			
Malacothrix cf. typica	X				X	X																									
*? M. makapani			X																												
Steatomys cf. pratensis			X		X							X																			
Otomys cf. irroratus										X							X														
*O. cf. saundersiae									X																						
Myotomis cf. turneri										X																					
M. cf. unisulcatus										X																					
Parotomis cf. brantsi									X																						
*Palaeotomys gracilis	X	X	X	X	X	X						?																			
*Prototomys campbelli	X																														
*Hystrix major			X																												

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG	Chelmer	Broken Hill	Mumbwa	Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	'Olorgesailie'	Eyasi	Gambian
Hystrix cf. *cristata*		X																												
H. africae-australis			X			X			X			X	X			X	X													
**H. galeata*																					X									X
**Xenohystrix crassidens*			X																											
Thryonomys swinderianus												X					X												X	X
**Petromus minor*	X																													
**Gypsorhychus darti*	X																													
**G. minor*	X																													
**G. makapani*			X																											
Georychus cf. *capensis*									X																					
**Cryptomys robertsi*	X	X	X	X	X	X																								
Bathyergus cf. *suillus*									X																					
FISSIPEDA																														
Canis mesomelas	X					X			X			X									X		X		X					
C. mesomelas latirostris																					X		X		X					
C. mesomelas pappos		X	?	X	X	X																								
**C. africanus* (? *Lycaon*)																					X		X		X					
**C. atrox*					X																									
**C. brevirostris*		X																												
**C. terblanchei*					X																									
C. adustus									X							X	X													
Vulpes pulcher				?	X																									
V. chama											X	X																		
Lycaon pictus											X	X																		
**L. pictus magnus*										X																				
Otocyon megalotis												X																		
Mellivora capensis									X				X																	

Aonyx capensis																									X							X
A. cf. *capensis*						X				X																						
Suricata suricatta						X						X																				
**Herpestes mesotes*					X																											
H. cauui										X																						
H. ichneumon									X			X					X															
**Atilax paludinosus*										X																						
**Crossarchus transvaalensis*					X	X																										
Cynictis penicillata				X																												
**C. penicillata brachyodon*			X																													
**Leecyaena forfex*				X																												
**Lycyaena silberbergi*		X		X																												
**L. nitidula*		?		X																												
Crocuta crocuta							X				X	X						X			X		X	X							X	
**C. crocuta angella*				X																												
**C. spelaea*					X				X																							
**C. venustula*				X																												
**C. ultra*					X																											
**C.* cf. *brevirostris*			X																													
Hyaena brunnea				X					X	X			X				X	X														
**H. dispar*				X																												
**H. makapani*			X																													
**H. bellax*					X	X																										
**Felis crassidens*					X																											
Lynx caracal									X																							
Caracal caracal												X											X								X	
**Leptailurus spelaeus*						X																										
**L. hintoni*																	X															
L. serval									X																							
**Therailurus barlowi*		X	X	?		X																										
**T. piveteaui*					X																											
Panthera leo									X								X								X	X					X	X
**P.* aff. *leo*				X	X	X			X																							
P. pardus											X						X						?	?							X	
**P. pardus incurva*				X																												
**P. whitei*				?	?																											
**P. shawi*				?	X																											

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gambian'
**Megantereon gracile*		*X*							*X*																							
**M. eurynodon*				*X*	*X*																											
**M.* sp. nov.			*X*																													
**Machairodus transvaalensis*						*X*																										
**M.* sp.																	*X*															
**Homotherium ethiopicum*																				?		*X*										
PINNIPEDIA																																
cf. *Arctocephalus*														X																		
TUBULIDENTATA																																
**Orycteropus aethiopicus*																							*X*						*X*		*X*	*X*
**O.* sp.																		*X*														
PROBOSCIDEA																																
**Gomphotherium* sp.							*X*																									
**Anancus kenyensis*																					*X*		*X*	*X*	*X*							
**Stegodon* sp.														*X*																		
**Stegodon kaisensis*																				*X*	*X*											
**Stegolophodon* sp.														*X*																		
**Loxodonta atlantica*						*X*	*X*																						*X*			
L. africana																	*X*															*X*
**Archidiskodon subplanifrons*							*X*														*X*		*X*									
**A. exoptatus*																				*X*	*X*	*X*	*X*	*X*								
**A. recki*									*X*													*X*	*X*	*X*	*X*	*X*	*X*		*X*	*X*		
**A. broomi*							*X*																									
**A. transvaalensis*							*X*																									
**A.* sp.									*X*					*X*																		
**Palaeoloxodon*														*X*																		
**Deinotherium bozasi*																					*X*	*X*	*X*	*X*	*X*							

HYRACOIDEA																																
Procavia capensis						X						X						X														
*P. antiqua	X	X	X	X	X																											
*P. transvaalensis	X	X	X	X	X	X																										
*P. sp.			X																													
PERISSODACTYLA																																
*Hippariinae sp.[a]														X																		
*Stylohipparion albertense[a]																				X	X	X	X	X	X	X	X		X	X		
*S. steytleri[a]			?		X	X	X	X																								
Equus burchelli					?	X	X	X		X	X	X	X			X	X						X		X	X	X				X	X
*E. aff. grevyi																						?		X	X	X	X		X			
*E. oldowayensis																					X	X		X	X	X	X		X	X		
*E. plicatus				?	X	X	X	X	X	X	X		X			X		X														
*E. helmei			X		X		X		X	X	X	X	X	X		X																
*E. quagga							?			X			X																			
*E. sandwithi									X																							
*Eurygnathohippus cornelianus[a]								X																								
*Metaschizotherium hennigi																				X			X	X	X							
*M. (?) transvaalensis			X																													
Ceratotherium simum			X						X				X	X			?			X	X	X	X	X	X	X	X	X	X	X		
*Serengeticeros efficax																							X		X							
Diceros bicornis			X				X		X	X		X	X				X				X			X	X	X	X				X	
ANCODONTA																																
*Hippopotamus gorgops								X																?	X	X	X	X	X	X		
*H. imaguncula																				X	X							X				
*H. protamphibius																						X										
H. amphibius			X				X		X	X	X					X				X		X	X						X		X	X
ARTIODACTYLA																																
SUIDAE																																
*Notochoerus capensis							X																									
*N. hopwoodi																										X	X	X				
*Notochoerus euilus			X																	X			X									
*Notochoerus compactus							X	X		X	X														X							
*Notochoerus sp.																						X										

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG	Chelmer	Broken Hill	Mumbwa	Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
**Mesochoerus paiceae*							X		X																					
**M. olduvaiensis*																						X	X	X	X					
**M. heseloni*																				X										
**M. lategani*									X																					
**M. limnetes*																		X												
Potamochoerus koiropotamus																	X												X	
**P. majus*																						X	X	X	X					
Phacochoerus africanus							X	X		X			X										X	X	X					
**P. altidens altidens*							X																X	X	X					
**P. altidens robustus*																						X	X							
**Tapinochoerus minutus*																									X		X			
**T. meadowsi*		X		X		X	X		X													X	X	X	X			X		
**Afrochoerus nicoli*																							X	X	X					
**Metridiochoerus andrewsi*																						X					X			
**M. pygmaeus*..																			X											
**Pronotochoerus nyanzae*																										X				
**P. jacksoni*																				X										
**Hylochoerus meinertzhageni*																														X
**Hylochoerus antiquus*																											X			
**Nyanzachoerus kanamensis*																			X											
**Orthostonyx brachiops*																							X							
**O.* sp.								X																						
**Potamochoeroides hypsodon*			X																											
**P. shawi*	X		X			X																								
**Potamochoerops antiquus*		?		X	X	X																								
GIRAFFIDAE																														
**Okapia stillei*																					X	?								

Giraffa camelopardalis			X					X		X		X					X				X	X	X		X		X	X	X	X	X	
**G. gracilis*									*X*													*X*			*X*							
**Libytherium olduvaiense*							*X*	*X*	*X*								*X*				*X*	*X*	*X*	*X*	*X*	*X*	*X*	*X*		*X*		
**L.* cf. *olduvaiense*			*X*																													
BOVIDAE																																
Strepsiceros strepsiceros			X				?	X	X								X	X						?	X		X				X	
**S. imberbis*																						*X*		*?*	*X*		*X*					
**Tragelaphus buxtoni*																							*X*		*X*							
T. scriptus						X																										
T. angasi	X		X										X				X															
Taurotragus oryx			X			X	X	X	X	X	X	X	X			X	X	X					X	X	X		X				X	
Syncerus caffer			X			X	X					X	X					X				X	X								X	
**S.* cf. *makapani*			*X*																													
**Homoioceras nilssoni*																											*X*				*X*	*X*
*'*Homoioceras' baini*							*X*	*X*	*X*	*X*	*X*	*X*	*X*			*X*	*X*															
**Homoioceras* sp.														*X*																		
**Bularchas arok*																									*X*	*X*	*X*		*X*			
**Cephalophus parvus*	*X*																															
**C. pricei*			*X*																													
C. caerullus			X															?														
Sylvicapra grimmia							X			X	X		X					X														
Kobus ellipsirymnus												X	X									?	?								X	
**K. venterae*								*X*		*X*	*X*																					
**Adenota kob*																								*X*	*X*	*X*					*X*	
Onotragus leche												X																				
**Redunca redunca*																							*X*								*X*	
**R. darti*			*X*																													
R. arundinum			X						X			X						X														
R. fulvorufula			X															?														
R. sp.														X																		
Pelea capreolus												X																				
P. sp.									X																							
Hippotragus equinus													*X*					*X*					*X*			*X*	*X*		*X*		*X*	
**H. niro*																									*X*		*X*					
**H. broomi*		*X*																														
H. niger							X																									

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Vaal River	Cornelia	Hopefield	Florisbad	Vlakkraal	C. of Hearths	Wonderwerk	LANGEBAANWEG		Chelmer	Broken Hill	Mumbwa		Kaiso	Kanam	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Rawi	Kanjera	Olorgesailie	Eyasi	'Gamblian'
*H. sp.									X																							
**Oryx beisa*																								X							X	
O. gazella			X										X				X															
**Damaliscus angusticornis*																							X		X		X					
D. cf. *pygargus*						X	?		X				X																			
**D. teste*																								X	X		X					
D. cf. *lunatus*						?	X					X					X	X														
D. cf. *albifrons*							X	X		X	X						X															
**D.* sp.									X																							
**D.* sp.								X		X	X	X																				
**D.* sp.														X																		
**Alcelaphus kattwinkeli*																									X	X	X		X			
A. caama							X	X				X	X			X		X														
**A. robustus*			X			X	X					X																				
**A. helmei*			X			X	X	?		X	X	X	X			X																
A. lichtensteini																		?														
**Beatragus hunteri* (?)																								X	X		X					
Connochaetes taurinus			X			X	X					X	X			X	X	X														
**C. antiquus*										X																						
C. gnou							X																									
**C. laticornutus*								X		?																						
**C. grandis*																X																
**Gorgon taurinus semiticus*																								X	X	X	X					
Oreotragus oreotragus												X																				
**Oreotragus major*			X																													
**O. longiceps*	X																															
O. sp.														X																		
**Makapania broomi*		X	X			X																										

*_Raphicerus campestris_						?			X			X	X																		
*_Lunatoceras mirum_									X	?																					
*_Megalotragus eucornutus_								X																							
Aepyceros melampus			X				X					X										X	X								X
Litocranius walleri																	X														
*_Gazella gazella praecursor_																								X	X		X				
*_G. granti_																								X	X		X				X
*_G. gracilior_			X																												
*_G. wellsi_		X				X	X	X	X																						
*_G. bondi_										X	X	X				X															
*_G. helmoedi_								X																							
*_G._ sp.								X																							
*_Phenacotragus recki_																											X		X		
*_P. vanhoepeni_			X			?																									
*_Antidorcas marsupialis_		?				?	X	X	X	X	X	X	X																		
*_A._ (?) sp.									X																						
*_Pultiphagonides africanus_																								X	X						
*_Pelorovis oldowayensis_																									X		X				

Table 1. Synopsis of the Pleistocene faunal assemblages at sites in East and South Africa (according to Cooke, 1963, tables 4, 6 and 7, but the list for Hopefield is replaced by Singer, personal data. The Suidae are corrected after Leakey, 1958).
[*=extinct; _X_=extinct]

EURASIA	_OUED EL HAMMAM_
Dicerorhinus schleiermacheri	_D. primaevus_
Dicerorhinus orientalis	
Hipparion gracile	_H. africanum_
H. mediterraneum	
Orycteropus gaudryi	_O. mauritanicus_
Hyaena salonicae	_H. algeriensis_
Palaeotragus roueni	_P. germaini_

Table 2. Comparison between the ‘classical Pontian’ fauna of Eurasia and that from Oued el Hammam.

These differences indicate that the fauna of Oued el Hammam is more primitive than that of the Eurasian 'Pontian', thereby suggesting an ancient biogeographical autonomy of Africa. The presence of a fauna more primitive than the 'classical Pontian' does not necessarily mean that it antedates the Pontian. However, as is indicated in the section on the geological aspects of the sites (*vide supra* p. 283), the Oued el Hammam deposit lies under lacustrine or marine deposits. These contain clearly recognized Upper Miocene fauna of the Sarmatian or of the Tortono-Sahelian age, which were formed by the marine transgression at the end of the Miocene. As indicated by Arambourg, there is no possible correlation between Oued el Hammam and the 'classical Pontian' which is formed posteriorly to the Sarmatian.

PLIOCENE

The Hipparion-bearing sites in North Africa and in the Nile Valley, which are usually considered to be Pliocene, cannot be satisfactorily dated on the basis of the fauna alone. The faunal assemblages at Tozeur, Aïn el Bey and Mascara are rather poor. Their antiquity is suggested by the presence of *Merycopotamus*, *Helladotherium* and *Rhinoceros pachygnathus*. The Pliocene nature of these sites can only be determined from their geology.

At Wadi Natrun, none of the rare fossils recovered is characteristic of a particular period. Determination of stratigraphical relationships is necessary for the assessment of the Pliocene date of the fossiliferous beds.

PLEISTOCENE

The simple comparison of lists of fauna from numerous sites often results in misleading or incorrect conclusions for the following reasons:

1. The assemblages may represent a sampling of fauna from different biotopes, and furthermore, the sampling (i.e. collecting) may have been made by means of different methods and for differing requirements. For example, in the case of small rodents, they may be an incidental part of a general collection recovered during a thorough investigation, or they may have been sought for exclusively from, say, breccia by a specialist. However, they may have been overlooked in the field when the investigator was merely collecting the larger bones. Thus they would be absent from the collected assemblage, but this would not reflect the fact that they may have been present in situ. Thus someone studying or re-studying a particular collection, and being unaware of the conditions of recovery of the material, may accurately record frequencies but these may yet be misleading.

2. Different palaeontologists may use criteria and terminology at variance with others, often because of a familiarity with material from particular areas or countries. In addition the fragmentary nature of certain specimens may be responsible for differing interpretations.

3. Just as different biotopes may express slight differences in similar forms, so climatic differences may influence similar forms even in adjacent

regions. These differences may be interpreted on a specific rather than on a subspecific level, thus influencing statistical analyses.

Consequently, a practical method of comparing sites within a geographical region is by studying the results obtained by either a single palaeontologist or by a particular institute. This requirement is partially met for the 'Villafranchian' sites of North Africa, for the australopithecine breccias in South Africa, for Olduvai Gorge, and possibly for Laetolil and Rawi in East Africa. It is to be remembered that the success of the investigation within each of these three geographical units varies.

The North African 'Villafranchian' fauna is characterized by the association of the latest mastodonts with primitive elephants, of the Sivatheriinae with *Giraffa*, and of the hipparionids with the modern Equidae.

However, there is sufficient evidence available to suggest that such associations, found in several places in Africa, are not necessarily contemporaneous. Unfortunately, the term 'Villafranchian fauna' is loosely used with a different interpretation in different areas, but it may only be applied, sensu stricto, in a chronological sense to the Mediterranean basin.

Arambourg (1947) proposed a relationship between the fossil-bearing sites of Africa according to the presence or absence of archaic elements, such as *Archidiskodon planifrons*, *Anancus*, *Stegodon* and *Chalicotheriidae*. During the Lower Pleistocene some of these forms seem to have disappeared, being replaced by *A. recki*, while other primitive groups with tertiary affinities like *Stylohipparion*, *Deinotherium* and *Libytherium* persisted.

By means of the Proboscidea sequence, a subdivision of the 'Villafranchian' can be formulated:

A. Lower 'Villafranchian'

Characterized by the PRESENCE of *Anancus*, *Stegodon*, *Stegolophodon* (?), and the appearance (in a stratified deposit) of *Archidiskodon* (or *Elephas subplanifrons*, *planifrons*, *africanavus*, and *exoptatus*): Kanam, Kaiso, Garet Ichkeul.

B. Middle 'Villafranchian'

Characterized by the extinction of *Stegodon*, the persistence of *Anancus*, *Mastodon*, *Archidiskodon* (or *Elephas*) *planifrons* or *subplanifrons* and *exoptatus* and the first appearance of *Palaeoloxodon recki* (or *E. meridionalis*): Koro Toro, Laetolil, Aïn Hanech, Olduvai I.

C. Upper 'Villafranchian'

Characterized by the presence of *Anancus*, *Stegodon*, *Mastodon*, and the continued presence of *A. exoptatus*, *E. africanavus* and even *Deinotherium:* Omo.

The post-'Villafranchian' horizon commences when *Anancus*, *Stegodon*, and *Mastodon* as well as primitive forms of *Archidiskodon* (*exoptatus*) and *Elephas* (*planifrons*, *africanavus*) become totally extinct, coincidental with the appearance of *Loxodonta africana* and *atlantica* as well as the further development of *P. recki.*

North Africa

In a comparison of Garet Ichkeul with Aïn Hanech, the fauna of which are substantially the same, Arambourg (1949) concluded that Garet Ichkeul was the more ancient (Lower 'Villafranchian') because of the more abundant *E. planifrons* and *Stylohipparion* at the former site, while the latter had remains of *P. recki.*

There is good evidence that there is close identity between Aïn Hanech (and Bel Hacel) on the one hand, and Garet Ichkeul, Aïn Boucherit (i.e. Beni Foudda of Pomel) and Oued el Akrech (Arambourg and Choubert, 1957), on the other. On the basis of the fauna alone, it does not seem possible to compare these in any great detail with the other North African Pleistocene *Hipparion*-bearing sites.

	Total number of identified species	*Extinct species*	*Extant species*	*Extinct* / *Total*	*Extant* / *Extinct*
				%	%
SOUTH AFRICA					
Taung	34	25	9	73·5	36·0
Sterkfontein	37	26	11	70·4	42·3
Makapansgat	70	43	27	61·4	62·7
Swartkrans	39	32	7	82	21·9
Kromdraai	41	29	12	70·7	41·4
Bolt's Farm	56	35	21	62·6	60·0
Vaal River	35	20	15	57	75·1
Cornelia	23	17	6	74	35·3
Hopefield	45	23	22	51·2	95·6
Florisbad	32	15	17	46·9	113·4
Vlakkraal..	18	9	9	50	100
Cave of Hearths ..	45	10	35	22·2	350·0
Wonderwerk	25	8	17	32	213·0
RHODESIA					
Chelmer	11	6	5	—	—
Broken Hill	31	7	24	22·6	342
Mumbwa	18	3	15	16·6	500
EAST AFRICA					
Kaiso	10	8	2	80	25
Kanam	16	12	4	75·0	33·3
Omo	21	15	6	71·4	40
Laetolil	33	20	13	60·6	65·0
Olduvai I	34	28	6	82·2	21·4
Olduvai II	49	38	11	77·4	29·0
Olduvai III	23	18	5	78·4	27·8
Olduvai IV	39	30	9	76·9	30·0
Rawi	7	4	3	—	—
Kanjera	17	14	3	82·3	21·4
Olorgesailie	9	7	2	—	—
Eyasi	24	9	15	37·5	166·0
'Gamblian'	12	7	5	58·4	71·4

TABLE 3. The relationships between identified extinct and extant fauna from African Pleistocene sites.

East and Central Africa

The OLDUVAI GORGE has been extensively studied. From the four Beds, 55 species have been identified (table 1), Bed II and IV containing respectively 49 and 39 of them (table 3). However, recent discoveries and more detailed analyses will considerably alter these figures. Dietrich (1942), Arambourg (1947), Hopwood (1951) stressed the general Middle Pleistocene character of the Olduvai faunal assemblage. It has been pointed out that no available faunal evidence suggests that the lower part of Olduvai is of Lower Pleistocene age. This view will probably be considerably modified when descriptions and analyses of recent discoveries are published shortly. In this paper, only the available published data are assessed. Leakey (1963) emphasizes the point that 'Bed I covers a very long period of time with a gradual change from a very wet climate at the beginning to savanna conditions and then subdesert ones'. It is no longer possible to speak simply of 'the fauna of Bed I'. He also points out that the fauna from Bed I, although 'Villafranchian' and older than Omo, does not conform with the Lower 'Villafanchian' fauna as represented in East Africa at Kanam East and West. Furthermore, it is no longer certain whether Bed I contains *Hippopotamus gorgops*, *Taurotragus oryx*, *Tragelaphus strepsiceros*, and even *Palaeoloxodon recki* which is super-abundant in Bed II and Bed IV.

Olduvai I	21·4
Swartkrans	21·9
Olduvai III	27·8
Olduvai II	29·0
Olduvai IV	30·0
Cornelia	35·3
Taung	36·0
Omo	40·0
Kromdraai	41·4
Sterkfontein	42·3
Bolt's Farm	60·0
Makapansgat	62·7
Laetolil	65·0
Vaal River	75·1
Hopefield	95·6
Florisbad	113·4
Eyasi	166·0
Wonderwerk	213·0
Broken Hill	342·0
Cave of Hearths	350·0

TABLE 4. List of sites in the order of increasing proportions of extant species. Ratios (extant/extinct) are determined only for those sites where more than 20 species have been identified.

Cave of Hearths	22·2
Broken Hill	22·6
Wonderwerk	32·0
Eyasi	37·5
Florisbad	46·9
Hopefield	51·2
Vaal River	57·0
Laetolil	60·6
Makapansgat	61·4
Bolt's Farm	62·6
Sterkfontein	70·4
Kromdraai	70·7
Omo	71·4
Taung	73·5
Cornelia	74·0
Olduvai IV	76·9
Olduvai II	77·4
Olduvai III	78·4
Swartkrans	82·0
Olduvai I	82·2

TABLE 5. List of sites in the order of increasing proportions of extinct species. Ratios (extinct/total) are determined only for those sites where more than 20 species have been identified.

	Taung	Sterkfontein	Makapansgat	Swartkrans	Kromdraai	Bolt's Farm	Cornelia	Hopefield	Vaal River	Cave of Hearths	Wonderwerk	Broken Hill	Omo	Laetolil	Olduvai I	Olduvai II	Olduvai III	Olduvai IV	Eyasi	Florisbad
Taung		*10* 41	*10* 58 *15*	*6* 51 *14*	*6* 48 *10*	*8* 52 *16*	42 *2*	48 *3*	45 *3*	*1* 34 *3*	33 *1*	32	40	45	53 *1*	63 *1*	43 *1*	55 *1*	34	40 *1*
Sterkfontein	24·4		54	44 *10*	45 *12*	45 *17*	41 *2*	46 *1*	43 *4*	33 *5*	33 *1*	33	41	46 *1*	53	63	43	55	35	40 *2*
Makapansgat	17·2	27·8		65	60 *15*	61 *12*	58 *1*	65 *3*	59 *2*	48 *2*	50	50	58	62	71 *1*	81 *1*	61 *1*	73 *1*	52	56 *1*
Swartkrans	11·8	31·8	15·4		46	55 *13*	48 *2*	52 *4*	50 *3*	40 *1*	40	39	47	52	59	69	49	61	41	46 *2*
Kromdraai	12·5	22·2	20	32·6		51	44 *5*	48 *5*	46 *8*	38 *6*	37 *3*	36	44	49	57 *1*	67 *1*	47 *1*	59 *1*	38	42 *3*
Bolt's Farm	15·4	35·6	27·8	21·8	25·4		47	53 *4*	47 *8*	39 *4*	40 *3*	42 *2*	50 *1*	55 *1*	62 *2*	72 *3*	52 *2*	65 *2*	44	47 *8*
Cornelia		4·9	3·4	2·1	4·5	10·6		36	29 *7*	23 *3*	22 *3*	22 *3*	31 *4*	36 *3*	43 *4*	52 *5*	33 *4*	45 *4*	26	24 *5*
Hopefield		6·5	1·5	5·7	8·3	9·4	11·1		36	30 *4*	28 *3*	27 *2*	34 *1*	40 *2*	47 *3*	56 *4*	37 *3*	49 *3*	32	33 *7*
Vaal River		7·0	6·8	4	6·5	17·0	27·6	19·4		26	25 *4*	25 *1*	34	38	45	54	35	47	29	28 *6*
C. of Hearths	2·9	9·1	10·4	5	2·6	15·4	17·4	10·0	15·4		14	16 *1*	25	30 *1*	38	48	28 *1*	40 *1*	19 *1*	19 *3*
Wonderwerk		3·0	2·0			7·5	13·6	10·7	12·0	28·6		14	23 *1*	27 *1*	36 *1*	46 *1*	25 *1*	37 *1*	16	20 *1*
Broken Hill							9·1	11·1	8·0	6·3	7·1		21	26 *6*	34 *10*	44 *9*	24 *6*	36 *7*	16	21
Omo							3·2	11·8	2·9			4·8		29	33 *9*	44 *11*	27 *5*	38 *7*	24 *4*	30
Laetolil			1·6				3·0	7·5	5·3		3·7	3·9	20·6		39	47 *23*	33 *13*	43 *16*	25 *4*	35
Olduvai I		1·9		1·7		1·6	4·6	8·5	6·7			2·9	30·3	23·1		43	33 *17*	42 *25*	33 *3*	43 *1*
Olduvai II		1·6		1·4		1·4	5·8	8·9	7·4			2·3	20·4	23·4	53·4		39	43 *17*	44 *2*	52
Olduvai III		2·3		2·0		1·9	6·1	10·8	8·6		4·0	4·2	22·2	15·1	39·4	43·5		41	25 *3*	33
Olduvai IV		1·8		1·6		1·5	4·4	8·1	6·4		2·7	2·8	18·4	16·3	38·1	58·0	41·5		36	45 24
Eyasi											6·3			16·0	12·1	6·8	8·0	8·3		
Florisbad		2·5	3·6	2·2	4·8	6·4	33·3	15·1	25·0	3·2	15·0	4·8				1·9				

TABLE 6. Statistical interpretation of the extinct fauna represented at any two Pleistocene sites. Above the oblique line the italicized figures constitute the absolute number of extinct species *common* to two sites, while the non-italicized figures are the total number of different extinct species identified at any two sites.

Below the oblique line the number of extinct species common to two sites are expressed as a percentage of the total number of different extinct species, i.e. $\left(\frac{\text{italicized}}{\text{non-italicized}}\%\right)$

OMO has classically been equated with Olduvai I and II but recently a proposal has been made that it is more similar to the base of Olduvai II (tables 4, 5). The extinct fauna common to Omo and Beds I and II are 30·3% and 20·4% of the total respectively (table 6). There is no substantial difference between the faunal assemblages except for the presence of *Anancus* and hominids at Olduvai. The absence of *Zinjanthropus* and '*Homo habilis*' at Omo, does not *per se* imply that Omo is younger than Bed I, because the Olduvai Lake shores, permitting the possible development of living sites, favoured a concentration of hominids.

The SERENGETI (Laetolil) fauna is closely related to both Olduvai and Omo. The extinct species at Serengeti in common with Olduvai I are 23·1% with Olduvai II are 23·4%; and with Omo are 20·6% (table 6). The essential difference seems to be the presence at Laetolil of *Anancus* and *Archidiskodon subplanifrons*, both of which are absent at Omo, and also the presence of *Metaschizotherium hennigi* (which is also present at Kaiso). Leakey (1958) believes that the differences between the Laetolil and Bed I faunas do not imply a temporal separation but rather illustrate a difference in ecological conditions existing contemporaneously. He indicates that it has not been proved that Laetolil is older than Olduvai I. Furthermore, it should be pointed out that Laetolil probably contains a mixed assemblage of different faunal stages, as was already suggested by Dietrich.

KAISO and KANAM are badly represented from a faunal viewpoint: 10 (8 of which are extinct) and 16 (12 of which are extinct) species respectively have been identified. In spite of the fact that information about their recovery is unsatisfactory, there is no doubt that a real archaic character is attached to these sites, from which *Chalicotherium*, *Stegodon*, *Anancus*, *Stegolophodon* and *Hippopotamus imaguncula* have been recovered. These forms are considered by most authorities to represent the most ancient East African Pleistocene fauna known at present.

KORO TORO consists of five 'apparently equally old' deposits which contain about 30 identified species of mammals. Abadie, Barbeau and Coppens (1959) and Coppens (1960), studying the fauna of the lowest level, conclude that it belongs to the Lower 'Villafranchian' because of the contemporaneity of *Mastodon*, *Stegodon* and *Elephas*. However, the rarity of both stegodont and mastodont (more typical of the base of the Lower Villafranchian and the Pliocene) and of *P. recki* (more typical of the Kamasian), and at the same time the abundance of *E. africanavus* suggest that we are dealing with an intermediate stage between the very base (e.g. as at Kaiso where *africanavus* is present without *recki*) and the top (e.g. as at Omo where *recki* and *africanavus* are abundant but stegodont and mastodont are absent).

Kent (1942) and Arambourg (1943, 1947) emphasized the great similarity between the Olduvai and the Omo faunal assemblages, and indicated that they considered the Omo fauna to be slightly older. Arambourg suggested that the various East African deposits may be considered to correspond to different phases of the transition between the Upper Pliocene and the Lower Pleistocene: the Serengeti, Kaiso and Kanam tuffs being the most ancient and being the equivalent of the 'Villafranchian' horizons in North Africa and Europe, while Omo and Olduvai I should be considered as being younger and corresponding to the first true Pleistocene deposits. This view has been partially modified because of the recent discoveries at Olduvai. Leakey (1963) describes a major climatic, faunal and geological 'break' near the base of Bed II, the lowest part of which (overlying the 'marker bed' at the top of Bed I) he considers to be of Upper 'Villafranchian' age and comparing very closely with that of Omo. According to Howell (1959), 'the faunas (from the Villafranchian sites of Central and East Africa) differ somewhat in composition, that from Laetolil beds being probably the youngest, overlapping basal Olduvai and that from Kaiso being perhaps the oldest. The Omo fauna overlaps both Laetolil and Kaiso and that from Kanam is probably broadly equivalent.'

South Africa

The fauna of the TRANSVAAL cave breccias (Taung, Sterkfontein, Makapansgat, Kromdraai and Swartkrans) has been extensively studied. The fauna of these sites show a very high degree of similarity: 11·8—32·6% of the total number of extinct species are common to the different sites (table 6). A similar range (15·4—35·6%) has been calculated for the BOLT'S FARM faunal assemblage found in the vicinity of Sterkfontein. The six sites show an extinct/total ratio of species of 61–74% (table 4) and an extant/extinct ratio lower than 63% (table 5), which indicates a considerable antiquity. The conditions of accumulation at and the geology of these sites are also similar. On the basis of the fauna (Ewer, 1957), as well as of mineralogical and climatological studies of the breccia (Brain, 1958; Robinson, 1961), a relative age sequence has been derived, namely, Sterkfontein–Taung, Makapansgat, Swartkrans and Kromdraai, extending from the Lower to the early Middle Pleistocene.

HOPEFIELD and FLORISBAD faunas seem to have rather similar frequencies: not only are 15·1% of the total of extinct species common to both sites, but their close faunal relationship is expressed by a similar ratio of extinct/total species (51% and 47% respectively). However, the extant/extinct ratio (viz. 96% and 113% respectively) suggests a greater antiquity for Hopefield. Furthermore, there are considerable differences in the types of hominids and artefacts recovered from these two sites. Although *Hipparion* has not been recovered from these two sites, they are included as important Middle–Upper Pleistocene sites.

From purely a consideration of the fauna, the YOUNGER VAAL RIVER GRAVELS and CORNELIA could fit satisfactorily in the chronological sequence between the Transvaal cave breccias and Hopefield–Florisbad with the following intermediate ratios (tables 4, 5): 57–74% of extinct species; 35–75% of extant/extinct species; and 27·6% of all the extinct species being common to both sites (table 6). According to Cooke and Wells (1946) 'while it is possible that some of the living species may post-date the Younger Gravels phase of deposition, it appears most probable that the bulk of their material forms a fairly coherent whole, representative of the fauna of the later part of the first wet phase'. The fauna from the Younger Vaal River Gravels and Cornelia deposits could be broadly considered as a Middle Pleistocene fauna, especially in the light of the recent reinvestigation by Cooke and Wells who indicated that the Cornelia fauna is comparable with the Younger Vaal River Gravel material (unpublished; quoted by Cooke, 1963, page 96; see also Wells, 1964).

Although the Lower Pleistocene sites of East and of South Africa have ratios of extinct species higher than 60% and an extant/extinct ratio lower than 70%, direct comparisons between East and South Africa have severe limitations. From an analysis of the fauna (table 1), based on the lists drawn up by Cooke (1963), it appears that not a single species as recorded is common to both East and South African Lower Pleistocene sites. We believe that this lack of relationship is really less marked than indicated because different names have been given to the same species in East and in South Africa. This is mainly because the taxonomy in the two regions has been developed by independent investigations, e.g. the species of *Simopithecus* (Freedman, 1957; Leakey and Whitworth, 1958; Singer, 1962). To some extent this shows the poor state of our knowledge of the African fauna as a whole. Furthermore, Pickering (1960) warned that a critical approach will always be required when comparing a plains fauna, such as that found at Olduvai, with an assemblage obtained from a cave deposit which is usually the case in the Lower and early Middle Pleistocene of South Africa.

There is some affinity between the Younger Vaal River Gravels, Cornelia and Hopefield assemblages on the one hand, and the East African early Middle Pleistocene collections on the other, ranging from 2·9–11·8% of the total number of extinct species for any two particular sites among these groups (table 6).

CONCLUSIONS BASED UPON THE FAUNAL AND GEOLOGICAL EVIDENCE IN THE LITERATURE

The large amount of data discussed in previous chapters may be utilized for the construction of a tentative illustration of the relationships between the sites at which *Hipparion* has been discovered in Africa (fig. 8). By and large this supports the views expressed by Cooke (1963) and Bishop (1963).

CHRONOLOGICAL RANGE OF *Hipparion*

Apart from the actual dating of the geological deposits from which *Hipparion* has been recovered in Africa, there is the general question of its first appearance and its ultimate disappearance on the continent.

It seems that Africa was not the area of origin of hipparionids, as the

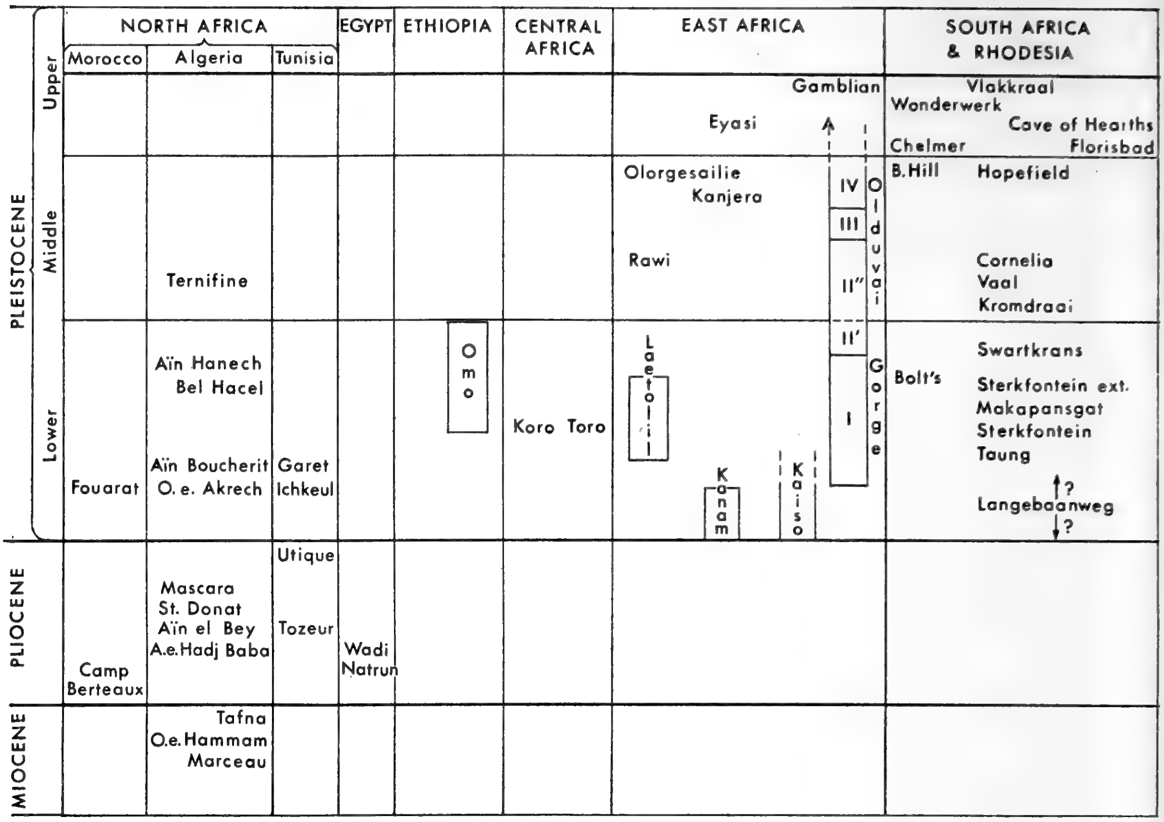


FIG. 8. Tentative correlation between *Hipparion* sites in Africa. A few other sites have been incorporated for reference. B. Hill = Broken Hill; O.e. = Oued el; A.e. = Aïn el; Gamblian = Gamble's Cave; Bolt's = Bolt's Farm.

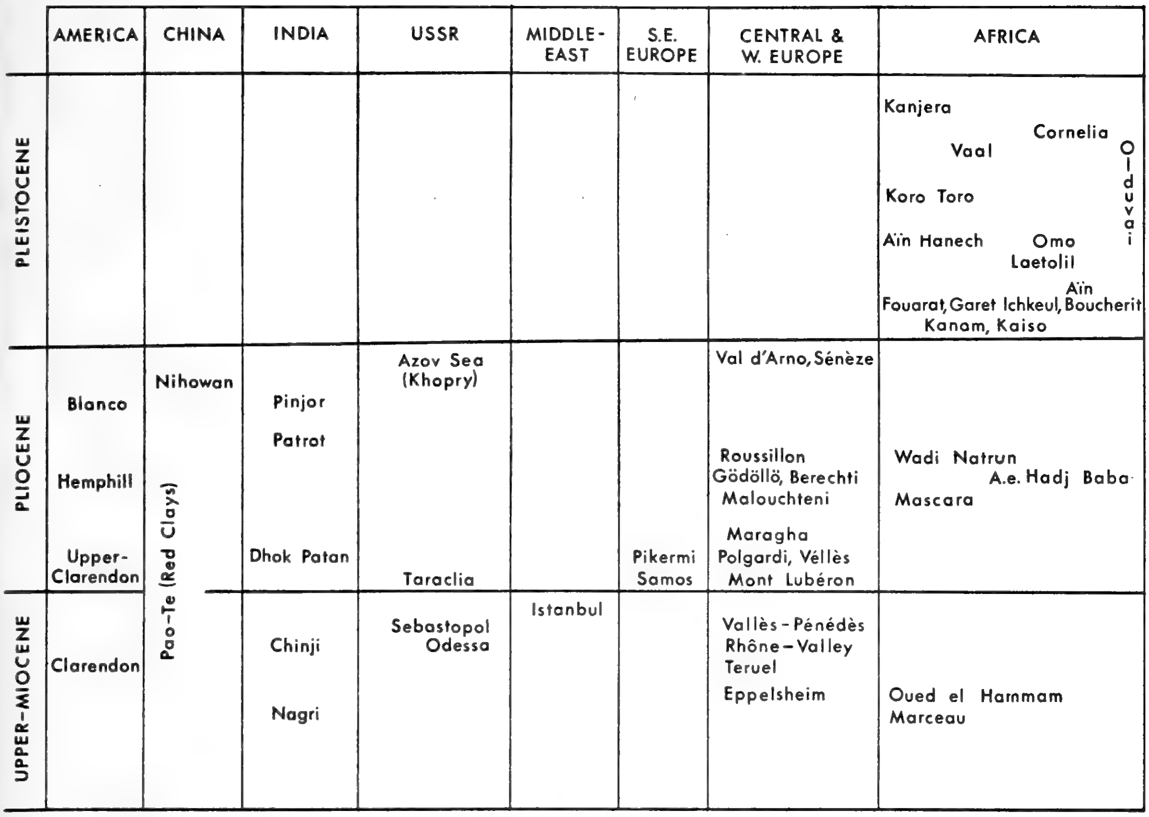
evidence points to probable migrations from Eurasia. Nevertheless, it is sometimes claimed that Africa contains the evidence of the early, if not the earliest, existence of *Hipparion* in the Old World.

At the other end of the chronological range, the hipparionids survived much longer in Africa than in any other area known at present. With very few exceptions, most of the sites where African *Hipparion* have been located are of Pleistocene origin, i.e. a period when they no longer existed in Eurasia and in America.

Consequently it is considered necessary to compare the geological range of occurrence inside with that outside Africa.

UPPER LIMIT

According to available information, the upper limit of *Hipparion* outside Africa seems to correspond roughly to the Upper Pliocene. It is generally accepted that the Villafranchian is defined by the appearance of some modern genera, among which is *Equus*. However, there is no reason to deny, *a priori*, a coexistence of *Hipparion* with modern *Equus* which developed on a parallel line from *Pliohippus*. Such co-existence has actually been demonstrated for Africa. Outside Africa, *Equus* not only heralds the Pleistocene, but it practically replaces the more primitive *Hipparion* in its habitats.



	AMERICA	CHINA	INDIA	USSR	MIDDLE-EAST	S.E. EUROPE	CENTRAL & W. EUROPE	AFRICA
PLEISTOCENE								Kanjera Cornelia Vaal Koro Toro Aïn Hanech Omo Laetolil Aïn Fouarat, Garet Ichkeul, Boucherit Kanam, Kaiso Olduvai
PLIOCENE	Blanco Hemphill Upper-Clarendon	Nihowan Pao-Te (Red Clays)	Pinjor Patrot Dhok Patan	Azov Sea (Khopry) Taraclia		Pikermi Samos	Val d'Arno, Sénèze Roussillon Gödöllö, Berechti Malouchteni Maragha Polgardi, Véllès Mont Lubéron	Wadi Natrun A.e. Hadj Baba Mascara
UPPER-MIOCENE	Clarendon		Chinji Nagri	Sebastopol Odessa	Istanbul		Vallès-Pénédès Rhône-Valley Teruel Eppelsheim	Oued el Hammam Marceau

FIG. 9. A diagrammatic representation of the probable chronological range of *Hipparion* in different continents.

The youngest formation bearing *Hipparion* remains in America is the Blanco formation (Upper Pliocene), where its presence is even questioned by some palaeontologists. Even if accepted, remains are very scarce.

In China, the latest occurrence is in the Nihowan deposits of the Sang Kan Ho Valley, east of Pekin (fig. 9); in India, in the Tatrot and the Pinjor zones of the Siwaliks, while the records are still very insufficient for Mongolia. In the U.S.S.R. (including its Asian portion), the most recent occurrence is to be found in the Azov Sea shore deposit at Khopry; in South and Central Europe at Berechti and Malouchteni in Rumania, and Gödöllö in Hungary. In western Europe, *Hipparion* has not been found in the Villafranchian deposits of the Val d'Arno and Senèze; and it is rather uncommon in the Roussillon, although it is still found in Perrier where it is rather exceptionally associated with *Equus*.

Without going into details which are irrelevant in the framework of this paper, it may be stated that outside Africa, *Hipparion* does not seem to have extended into the Pleistocene. In many instances, it was already becoming rather scarce during the Middle Pliocene and definitely more rare in the Upper Pliocene.

LOWER LIMIT

The lower limit of *Hipparion*, or the time of its first appearance, presents a more difficult problem, as it is not at all easy to correlate the chronological interpretations of all the localities. In addition, a different faunal basis (marine or continental) is applied to various areas, and a direct comparison of the fossil associations is not always possible. Furthermore, some geological terms, like 'Pontian', have been used in a different context and with a different meaning by various authors, e.g. as a facies, or a stratigraphical or a faunal horizon. Consequently it is especially difficult to appreciate the meaning of a particular statement, factual though it may be, without danger of misinterpretation. Therefore, the soundest approach may be, first, to locate the earliest occurrence of *Hipparion*, within a region, and then, to correlate as far as possible the interregional data.

In America, *Hipparion* is not found in the Barstov formation, appearing first in the Clarendon formation (fig. 9). It is also found right at the base of the Mint Canyon formation, and in the Hemphill formation. The upper Clarendon and the Hemphill formations are unanimously considered as 'Lower Pliocene' and correlated with the European 'Pontian'. But for more than thirty years, the Mint Canyon has been a major topic of discussion and argumentation. While most scholars follow Stirton's opinion (1939) and locate the continental basal horizon of Mint Canyon in the Pliocene, Maxson (1930), among others, basing his opinion on the debatable malacological fauna of the overlying marine Cierbo beds, considers it to be middle Upper Miocene age.

In China, *Hipparion* appear in the red clays of Chan-si, Chen-si and Kansou. These Pao-Te formations have not been properly subdivided. At different times, investigators have pushed them back to the Upper Miocene (Teilhard and Young, 1931), or restricted them to the Lower Pliocene (Teilhard and Leroy, 1942).

In India, the first *Hipparion* are recovered in the Chinji zone of the Siwaliks, which is referred either to the Middle (Pilgrim, 1938) or to the Upper (Lewis, 1937) Miocene, or even to the Lower Pliocene (Colbert, 1935).

In the U.S.S.R., the earliest occurrences are those of Moldavia and Odessa and the Sebastopol fauna (Borissiak, 1914). Russian geologists refer the former deposit to the Middle Sarmatian, and the latter two to the Upper Sarmatian, i.e. the Upper Miocene. Similar information was recently obtained from the Upper Sarmatian in the Istanbul vicinity (Chaput and Gillet, 1938; Yalçinlar, 1952).

In central and southern Europe, because of the exceptional associations of *H. primigenium* with the typical Miocene *Anchitherium*, Eppelsheim might be considered as one of the first known areas of occurrence of the genus. But in the Rhone Valley (Denizot, 1939), at Vallès-Pénédès in Catalogne (Villalta and Crusafont-Pairo, 1946, 1947, 1948) and in the Teruel Basin (Sondaar, 1961), abundant remains of *Hipparion* have been recovered in deposits which are dated as Tortonian. Maragha, Pikermi, Samos, Polgardi, Baltavar, Vélès and Mont Luberon, referred to as typical 'Pontian' sites, are probably somewhat younger, and should be placed in the Lower Pliocene.

In spite of many unsolved problems in correlating these sites, it seems difficult to deny that there is in North America, in Asia and in Europe constant and repeated indications of the appearance of *Hipparion* in the Upper Miocene (fig. 9).

GENERAL DESCRIPTION OF *Hipparion* TEETH

UPPER DENTITION

The pattern of horse teeth has been described many times and detailed structures have been extensively discussed in previous publications. The distinctive characters of horse teeth that have been described are based on the original description proposed by Osborn (1907). In 1918, he successfully applied this description in his study of the North American Equidae. Subsequent

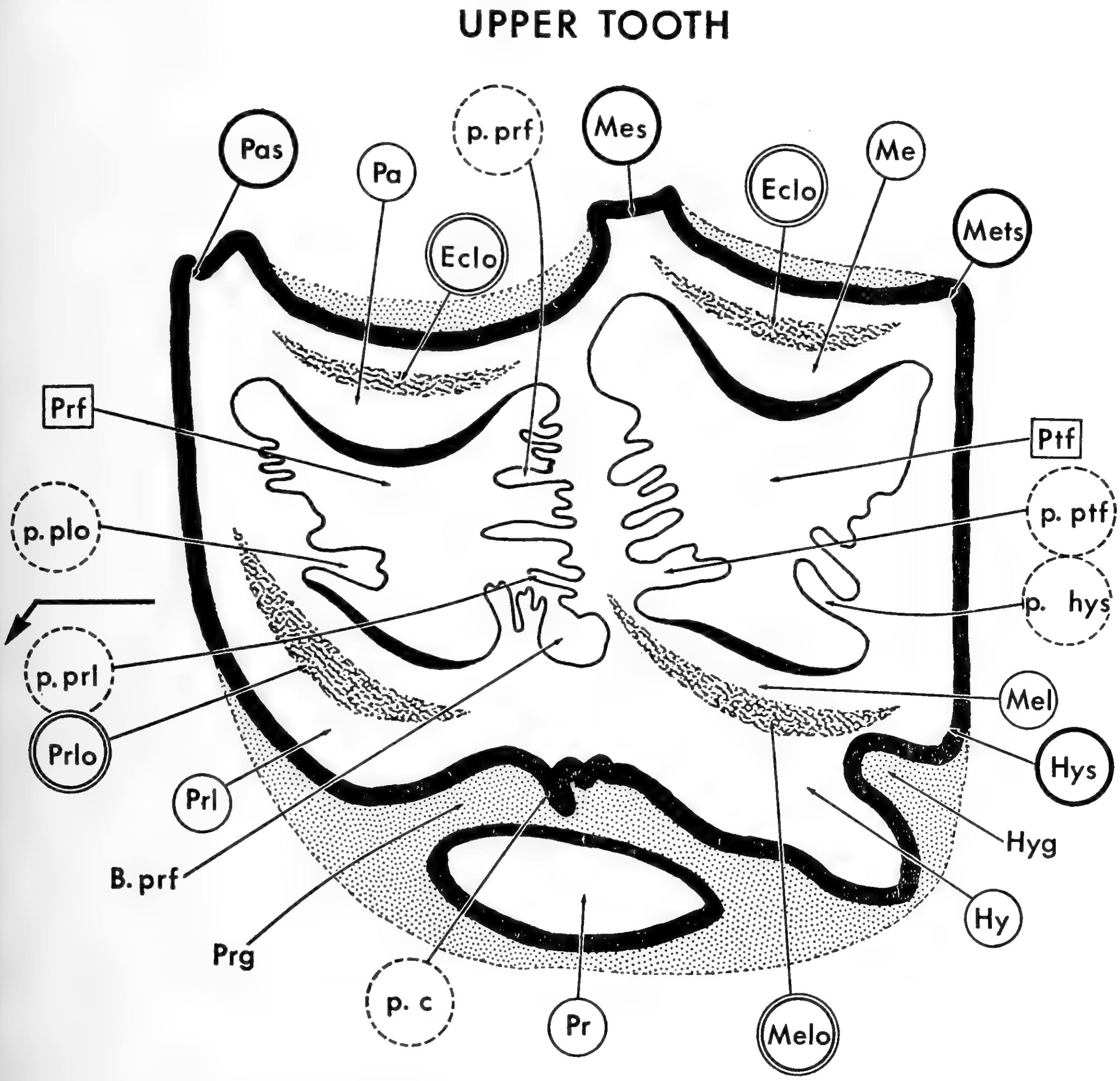


FIG. 10. Features of the occlusal surface of an upper molar tooth of hipparionids. Abbreviations: B. prf—bouclé prefossette; Eclo—ectoloph; Hy—hypocone; Hyg—hypoglyph or hypoconal groove; Hys—hypostyle; Me—metacone; Mel—metaconule; Melo—metaloph; Mes—mesostyle; Mets—metastyle; Pa—paracone; Pas—parastyle; p. c—pli caballin; p. hys—pli hypostyle; p. plo—pli protoloph; p. prf—pli prefossette; p. prl—pli protoconule; p. ptf—pli postpossette; Pr—protocone; Prf—prefossette; Prg—preprotoconal groove; Prl—protoconule; Prlo—protoloph; Ptf—postfossette.

alterations and additions have been proposed by, among others, Stirton (1941), Arambourg (1947, 1959), Gromova (1952), Hopwood (1937) and Cooke (1950). It is not proposed to make any further modifications here, but it is necessary to comment on the dental nomenclature, without any phyletic implications, so as to outline the basis adopted in this monograph.

Typically three crests are recognized. A mesiodistal ectoloph, joining paracone and metacone on the buccal surface, an anterior protoloph and a posterior metaloph. The latter two are more or less transverse in the primitive condition but in advanced Equids they are half-moon-shaped. Being lophodontic specializations of the protoconule and the metaconule, they build the protoselene and the metaselene, and they meet the ectoloph at parastyle and mesostyle, respectively (fig. 10).

Lingually deflected from the main selenic lophs, but more or less attached to them there is a protocone and a hypocone. Their rather deep bordering grooves, filled with cement, tend to isolate them from the crests. These grooves are the pre- and post-protoconal grooves (valleys, sinuses) which lie anteriorly and posteriorly to the protocone, respectively, and the hypoconal groove (sinus) or hypoglyph which is related to the hypocone (the posterior being usually very well marked, and the only one noticeable). Sometimes the protocone shows a 'spur': the 'protoconal spur'.

When the pre- and post-protoconal grooves are maximally deepened, they become confluent in a medivallum or internal depression. Thereby they produce complete isolation of the protocone. This is one of the major and characteristic features of the upper molars of *Hipparion.*

Elevations of the cingulum have also been described: parastyle, mesostyle and metastyle along the ectoloph; hypostyle on the posterior surface which ultimately develops a cusp, seemingly independent of the cingulum.

The protoloph and the metaloph crests enclose, more or less completely, the pre- and postfossettes. The more constant and deeper plications in the enamel wall of the fossettes ('marks') and also isolated 'horns' have been assigned special names: anteriorly, the pli protoloph and the pli postfossette, respectively; posteriorly in the anterior mark, the pli prefossette and the pli protoconule which isolates a 'boucle préfossette' or 'prefossette loop' (Stirton, 1955), while posteriorly in the posterior mark is the pli hypostyle (fig. 10).

Furthermore, a pli caballin appears constantly in the post-protoconal groove or in the internal depression. It is a lingual extension from the outer border of the selene, and eventually, after wear, it displays a two- or threefold division.

LOWER DENTITION

A distinction is commonly drawn between a mesial trigonid, with buccal protoconid and lingual metaconid, and a distal talonid, with hypoconid, entoconid and hypoconulid, separated on the buccal aspect at the level of a fairly constant external depression (fig. 11).

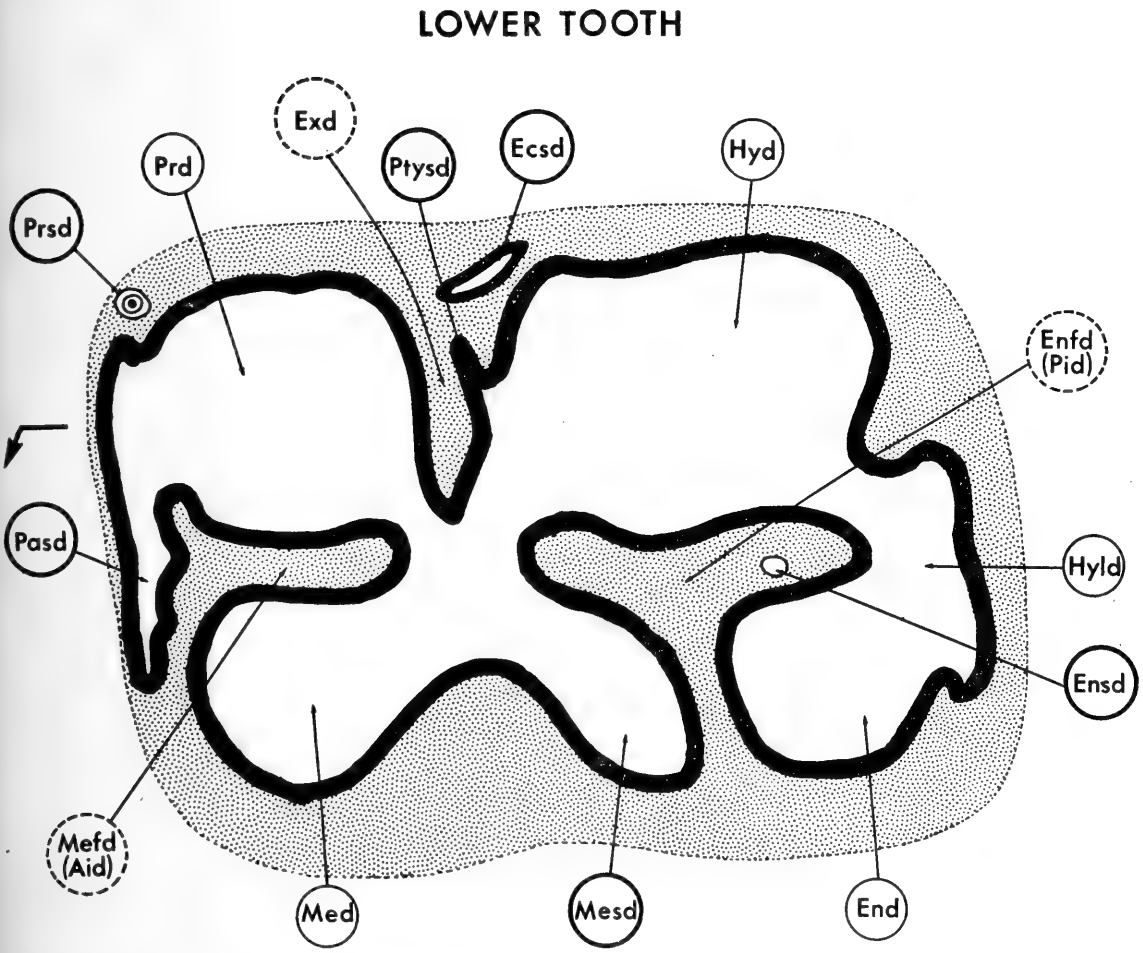


FIG. 11. Features of the occlusal surface of a lower molar tooth of hipparionids. Abbreviations: Ecsd—ectostylid; End—entoconid; Ensd—entostylid; Enfd (Pid)—entoflexid (Post. int. depression); Exd—external depression; Hyd—hypoconid; Hyld—hypoconulid; Med—metaconid; Mefd (Aid)—metaflexid (Anter. int. depression); Mesd—mesostylid; Pasd—parastylid; Prd—protoconid; Prsd—protostylid; Ptysd—ptychostylid.

The stylids on the buccal side are protostylid, an inconstant ectostylid and a ptychostylid, while on the lingual aspect there are the metastylid and the entostylid.

On unworn teeth, a crest, the paralophid, can be distinguished extending from the protoconid to the protostylid in the anterolingual corner.

On the lingual aspect there are two prominent internal depressions or invaginations, the metaflexid anteriorly and the entoflexid posteriorly.

The metastylid and the metaconid are two rounded formations joined by a narrow isthmus, giving the appearance of a bow tie and forming the so-called 'double knot'.

SUMMARY OF THE CHARACTERISTICS OF HIPPARION TEETH

Based on Gromova's detailed description (1952, pp. 70–6), the following characteristic features are noted.

Upper dentition

1. Less hypsodont. But note that the more recent (African and American) *Hipparion* are hypsodont.
2. Pli protocone is present.
3. Enamel plications are usually more developed.
4. There is a rather high percentage of open marks.

Lower dentition

1. Relatively less hypsodont.
2. Double knot:
   (*a*) '*caballus*' type in African *Hipparion.*
   (*b*) '*stenonis*' type in American *Hipparion*, and also in some Chinese.
   (*c*) '*Hipparion*' type in Europe and Asia.
3. External depression: this is rather profound in the Miocene forms.
4. Posterior internal depression: this is elongated, curved anteriorly and lingually. Hence its oblique and 'broken' appearance.
5. Anterior internal depression: not only does this have an antero-external angulation (like in *Equus*), but it also has a postero-external angulation, with long sharp 'horns' directed towards the buccal aspect.
   At the posterior extremity there is a deep invaginated plication.
6. Talonid is bifid on M_3.
7. Anterior depression often shows plications at both extremities.
8. There is a tendency to build stylids (proto-, ecto-, hypostylids) in milk and permanent molars.

REVIEW OF ADDITIONAL ENAMEL ELEMENTS (STYLIDS) OF THE LOWER TEETH

DESCRIPTION

Ectostylid=Ectostylid of Gromova (1952), Arambourg (1959), Hopwood (1937), Sondaar (1961).
=Protostylid of Osborn (1907), Stirton (1941).
=Buitestyltjie of Van Hoepen (1930).
≠Ectostylid of Osborn (1918), Sefve (1912, 1927).

This stylid arises from the basal cingulum. It is an accessory external column or pillar that is always independent and located on the buccal side, close to the mesio-vestibular border of the hypoconid and in the external groove between hypoconid and protoconid, i.e. between talonid and trigonid. In early wear it is seldom apparent on the occlusal surface because it rarely reaches more than a short distance above the crown-root junction and it is usually embedded in very thick cement. It can usually be observed better on the buccal aspect where the cement is thinner.

Ptychostylid =Ptychostylid of Arambourg (1947).
=Pli caballinid of Stirton (1941).
=Ectostylid of Osborn (1918).

This is not an independent pillar, but a fold on the mesial border of the hypoconid, in the interlobar angle on the buccal side. It may be present when the ectostylid is present, but there does not seem to be any relationship between these two formations.

Protostylid =Parastylid of Gromova (1952), Van Hoepen (1932), Stirton (1941).
=Protoconid fold of Cooke (1950).
≠Protostylid of Osborn (1907), Stirton (1941).

This is a broad laminated pillar, compressed mesiodistally, found close to the protocone where it is located on its antero-buccal side. With increasing wear it fuses fairly rapidly with the protocone. This stylid also arises from the cingulum and it may develop into an independent element on the antero-labial angle of a tooth.

Hypostylid

This is a postero-external plication, appearing as a raised element on the talonid. Sometimes it may develop into an independent pillar facing the talonid.

Entostylid

This is a rare and inconstant enamel formation in the entoflexid. It may be completely isolated in the cement (pl. 8, A) or connected to the mesio-lingual corner of the entoconid.

FREQUENCY

Independent of the degree of attrition, which may tend to hide the presence or the development of these formations, the stylids are very differently developed in various genera, species and even in individuals. The stylids may only be observed on some of the teeth of a particular jaw, and occasionally they are found to be present only on one tooth in a complete dentition. Observations have been made by various authors since the time when these stylids were first described by Gaudry (1862) and Weithofer (1888) on the milk and permanent teeth of *Hipparion mediterraneum* from Pikermi.

According to Gromova (1952), these additional elements are usually poorly developed in the non-hipparionid equids. The stylids are best developed in the *Hipparion* group in which they are always present on the milk teeth, but to a varying degree on the permanent teeth. In this respect the African *Hipparion* are the most progressive.

Ectostylid

Statistical analysis of *Hipparion elegans* provides a frequency of 12% ectostylids on the premolars and 1% on the molars, and in *H. moldavicum* frequencies of 7·5% and 6·7% respectively. Sondaar (1961) presents the following data on the presence of ectostylids:

H. periafricanum: 0
H. concudense aguirrei: 0
H. gromovae: 1 in 200 specimens
H. concudense: 5 in 84 specimens
H. koenigswaldi: 20 in 150 specimens
H. primigenium: 23 in 80 specimens

Therefore it can be concluded that the ectostylid is not quite a rarity in Eurasiatic *Hipparion* permanent teeth, especially on the premolars. Nevertheless, the ectostylids appear to be much more frequent in the later forms of *Hipparion*, i.e. in Africa, where it has often been stated to be 'a constant feature' (Arambourg, 1956, 1959). Comments on this will be given below. Furthermore, it can be stated without dubiety that the ectostylids have been commonly observed in most of the specimens from Pleistocene deposits: not only are these stylids very frequent, but they are occasionally strongly developed when they reach along the whole length of the crowns of the teeth.

Ptychostylid

This is the external hypolophid fold which is quite common among all hipparionids, reaching a maximum development in *Neohipparion eurystyle* Cope found in America, in which as many as four may occur. These stylids do not arise from the cingulum and cannot be considered as true stylid cusps. There does not seem to be any direct association between these stylids and ectostylids.

Protostylid

According to Sondaar (1961), this stylid is almost a diagnostic feature of the genus *Hipparion* even though it varies quite considerably in its extent. It is often a fold attached to the protoconid, but it may develop into an isolated pillar. Here again, the African *Hipparion* seem to present the most progressive features: it is found in them as early as the Upper Miocene (i.e. *H. africanum*) and as late as *Notohipparian namaquense*, in which it is a very tall and isolated pillar.

A high frequency is also found in some Eurasiatic forms, namely, in *H. elegans* 75·5% is noted in P_3–P_4 and 80% in M_1–M_2; in *H. moldavicum* 88% is noted in P_3–P_4 and 96% in M_1–M_2

Sondaar (1961) states that it is a common, although not constant, feature in all the Spanish species of *Hipparion*, except *H. truyolsi*. Sometimes a double protostylid has been observed, and this has been especialy noted in *H. koenigswaldi*, in which there is a high frequency of ectostylids (*vide supra*).

In connection with the American material, Stirton (1942), who used 'parastylids' for 'protostylids', points out that 'the statement that the parastylid does not appear in the American *Hipparion* is not supported by the evidence. Though the isolation is not as persistent nor as complete in the New World forms as in some Eurasiatic *Hipparion* (*H. platyodus* Sefve), it does appear in early stages of wear in some teeth. This is true not only in *Neohipparion*, but in *Nannippus* and *Pliohippus*, though extremely rare in the latter.'

Hypostylid

This is very frequently observed in *Equus stenonis* and in *zebra* but it is very rarely seen in *Hipparion*. However, it is sometimes found in the African forms, the most typical example of which is a M_3 from Omo (Joleaud, 1933).

EVOLUTIONARY HISTORY OF THE STYLIDS

The development of these stylids seems to be influenced by a common factor: a higher frequency of ectostylids in a particular group is correlated with a more precocious appearance of the protostylid (i.e. a higher protostylid) in the same population, and vice versa.

In a particular group it is noted that the protostylid seems to be more frequently, more strongly and more permanently developed than the ectostylid.

There seems to be an evolutionary pattern in the tendency to build stylids, from *Merychippus* (possibly from *Parahippus* which already shows a weak protostylid) through Miocene times up to *Hipparion*. Arambourg (1959) notices that this 'tendency to develop cingular formations' is already present in the Upper Miocene *H. africanum* from Oued el Hammam. The tendency seems to have developed further during Pliocene and early Pleistocene times, being most obvious in the African *Hipparion*, in which the most recent forms show the strongest development.

Protostylids and ectostylids appear on the milk teeth of *Merychippus* in which they show slight development. They are constantly present and show a fair degree of development on the milk teeth of all *Hipparion*, and they appear on the permanent dentition of the African Pleistocene *Hipparion*.

Along another evolutionary line of the Equidae, the *Pliohippus–Equus* sequence, it has been shown that protostylids and ectostylids remain weakly developed, the hypostylid being temporarily more developed, as, for example, in *Equus stenonis*. With the appearance of *E. caballus*, all the stylids have practically disappeared.

EVOLUTIONARY SIGNIFICANCE OF THE CONES AND STYLIDS

In a phyletic perspective, it has been established that the additional stylids have originated from enamel buds on the basal cingulum of brachyodont teeth. They developed first on the milk dentition and only later in the evolutionary sequence, and in particular groups, did they become permanent features of the adult dentition, appearing initially on M_1 and M_2 and eventually on the premolars. For example, it is known that the parastylid was present in *Parahippus*, but only on the milk teeth as an ill-developed feature. Later it became a constant and developed characteristic, even of permanent teeth, in *Merychippus* and later equids of the same phylum. The ectostylid is present in *Merychippus*, but only on the milk teeth, and then only occasionally. It becomes an element of the permanent dentition in *Hipparion*, where it appears to be constant in some of the latest representatives of the group, i.e. in the Pleistocene forms of Africa.

The tendency to raise enamel buds and isolate them is thus an early ontogenetic trend, which in evolution has progressively influenced the later (adult) stages of individual development.

Later in this paper it is suggested that this trend was necessitated by the special architecture of the lower dentition with its characteristic development of highly individualized conids.

The same trend, both ontogenetic and phylogenetic, seems to be recognizable in the formation and the isolation of the major cones in the upper dentition. It is really remarkable that the separation of the protocone and the hypocone from the main lophs is a gradual process, both ontogenetic and phylogenetic. The isolation of the protocone is rather ancient, and in the permanent teeth of *Hipparion* it has extended right down to the base of the crown. Contrariwise, the isolation of the hypocone is hardly noticeable on the permanent teeth, but in very early stages of wear it has been observed (*vide infra* p. 373). However in milk teeth the isolation of the hypocone reaches a much more characteristic degree in similar hipparionid groups, e.g. in the South Serengeti *Hypsohipparion* and in the Langebaanweg specimens (see p. 368).

The difference between the expression of cones and stylids in milk and permanent dentitions on the one hand, and the more explicit individualization of these features among later representatives in some phyletic lines, on the other hand, seem to be linked with the increasing hypsodonty of the Equidae teeth in Upper Cenozoic times.

ECOLOGICAL CONSIDERATIONS

Gromova (1952) outlined the ecological significance of the development of the styles (stylids). She promoted the idea that they played a role in strengthening the tooth so as to meet the heavier requirements of coarser food in a dry country where the grass was becoming very tough. The presence of additional pillars and folds probably increases the trituration power of the teeth and their resistance to pressure forces. Thus their appearance on the milk teeth would prevent or decrease rapid wear.

Furthermore, Gromova developed a very suggestive correlation between elongation of the protocone, development of the stylids, thickening of the enamel, reduction of the external groove and higher hypsodonty. These functional features are different methods of improving the efficiency of a tooth with increased power of trituration. Consequently it was suggested that the styles were developed as an adaptation for improving the grinding of coarser food in drier climates.

Sondaar (1961), in turn, described a similar correlation among the Spanish *Hipparion* which have the highest frequency of stylids. In *H. koenigswaldi* the maximal development of plications in the upper molars increased the enamel surface with a double hypoconal groove, while the lower teeth display wavy internal depressions—entoflexid and metaflexid. However, *H. elegans*, with the same functional features, only displayed a very high frequency of protostylids. Most of the African *Hipparion* developed the stylids and a maximal hypsodonty, but not the extreme plications. There seems to be a balanced compensatory effect between stylids, plications and other elements so that, dependent on the specific region, one or other of these elements would develop to a varying degree. In America, *Hipparion* adapted to a hard and tough grass by an increased hypsodonty and a thickening of the enamel. There can be no doubt that numerous plications and deep invaginations of the enamel pattern, as well as elevations of folds and stylids, provide the teeth with a more efficient trituration surface, and are very suitable for herbivorous animals in an area of increasing aridity (Stirton, 1941).

TAXONOMY BASED ON STYLIDS

The observation of the presence of stylids, both proto- and ectostylids, provided a new basis for generically differentiating the various African hipparionids. Haughton (1932) decided to create the genus *Notohipparion* because of the appearance of these stylids. Van Hoepen (1932) followed the same line of reasoning and erected the genus *Stylohipparion*, a distinction supported by Joleaud's publications of *S. libycum* from Omo (1933).

To some extent Dietrich (1942) followed the same tendency and, on the basis of the presence or absence of ectostylids, he divided the Serengeti LOWER cheek teeth into two groups. The group without stylids he termed *Hypsohipparion* and he referred those with stylids to *Stylohipparion*. However, Dietrich did not attach a true taxonomic value to this separation because he found it impossible to distinguish between the UPPER teeth of the two groups. He indicated that the frequency and development of styles (-ids) can be influenced by environment or selective pressure. Consequently he suggested that *Stylohipparion* might not represent a true genus, but only a variety formed under a strong developmental pressure ('Entwicklungswucht').

However, outside Africa, the variation in the development of stylids did not lead to such taxonomic differentiation. Arambourg (1947) questioned the validity of a generic difference (*Stylohipparion*) based upon the presence of a feature which did not seem to separate clearly the Eurasiatic Pliocene forms. Nevertheless, he opined that the very high frequency and the strong development of the ectostylid in African forms supported the validity of the generic differentiation.

Gromova also discussed this matter. She did not consider a true generic differentiation of African hipparionids valid. Ectostylids are not an entirely new characteristic in them exclusively but only represent a further development (either in frequency or structure) of a feature not at all exceptional (albeit irregular and even rare) in Eurasiatic *Hipparion*. Gromova proposed a subgeneric rank *Hipparion* (*Stylohipparion*) for the African group on the basis of obvious peculiarities of this geographical unit. However, she writes of these ectostylids: 'the importance as a diagnostic feature and generic character has been somewhat exaggerated'.

This criticism can be expanded (see pp. 387–92) and even the sub-generic status of *Stylohipparion* can be questioned. In spite of the 'air de famille' (Arambourg, 1959) of all African hipparionids, the major reason for placing the Pleistocene African hipparionids in a special genus or sub-genus is precisely the presence and constancy of a very high frequency (which the present authors doubt) of the ectostylids. Although this is generally accepted, it is a highly debatable basis of separation. As mentioned above, Dietrich (1942) described a very large collection of lower teeth without ectostylids and placed them in the 'genus' *Hypsohipparion*. However, Arambourg (1947) suggested that these teeth had 'erroneously' been attributed to a hipparionid and that, in fact, they belong to *E. zebra*. This suggestion tends to remove *Hypsohipparion* from the hipparionid scene so that the 'frequency' of the ectostylids among African hipparionids still remains artificially high. Arambourg's suggestion and his deletion of this group seem to have been largely accepted. Gromova's monograph does not include the Serengeti material and does not refer to this paper of Dietrich (1942). Arambourg (1956) has maintained his viewpoint and speaks of 'the typically African genus *Stylohipparion* characterized by the presence of a broad ectostylid'. Naturally this does not positively exclude *Hypsohipparion*, but in 1959, in a revision of the 'few' fossil African hipparionids, Arambourg explicitly limits the Pleistocene material to *Stylohipparion*, 'characterized by a *permanent* ectostylid'.

However, it can now be stated that the Serengeti *Hypsohipparion* material can no longer be excluded because of the assumption that it belongs to *zebra*. More than 90% of the small series of Langebaanweg equid upper teeth unquestionably belong to *Hipparion* so that it cannot be asserted that all the lower teeth belong to *zebra* merely because they do not possess an ectostylid. Not only is this statistically highly unlikely but also the morphological features, for example, the division of the talonid in M_3 (on L938, the only M_3 available at Langebaanweg) would definitely exclude this group from belonging to *zebra*. Consequently, as the Langebaanweg material, in which the ectostylid is constantly absent, belongs to *Hipparion*, there are no longer sufficient grounds to exclude *a priori* the Serengeti *Hypsohipparion* teeth from the hipparionid group only on the basis that they do not possess an ectostylid.

Furthermore, it can now also be stated that the concept that African *Hipparion* possess a very high frequency or permanent presence of ectostylid is no longer applicable. Consequently the validity of the generic status of *Stylohipparion* becomes highly questionable. Later in this paper this will be discussed more fully in the light of the evidence presented. At present it suffices to state that in Africa the Pleistocene *Hipparion* may be found with and without ectostylids.

REVIEW OF PUBLISHED AFRICAN *Hipparion* CRANIAL MATERIAL

MIOCENE

Oued el Hammam and Marceau

The presence of *Hipparion* in the Miocene of the Maghreb has been known since 1932 when Suess discovered a mammalian fossiliferous deposit upstream from Bou Hanifia (Oran) during the construction of the Oued el Hammam dam. On several occasions brief comments have been made about this material by, among others, Arambourg (1947, 1951, 1954). A rather rich collection of cranial and postcranial material, with fairly complete milk and permanent dentitions, as well as isolated teeth (table 7), have now been recovered from two Upper Miocene sites in Algeria (figs. 3 & 4): Oued el Hammam (Oran) and Marceau (Algiers). A detailed description was given by Arambourg (1959): he discussed their relationships to and differences from Eurasiatic forms of similar age, and other African forms of the Plio-Pleistocene period. He suggested that this material should constitute a new specific form, namely *Hipparion africanum* for which he proposed the following diagnosis:

> *Hipparion* with a large skull, medium-sized limbs and heavily built extremities. Face and snout are elongated; nasal aparture is long and broad; orbits are situated far back; pre-orbital fossae are long, simple and distant from the orbit. Dentition of medium size: P^2–M^3 = 141—154 mm. Upper molars with strongly plicated enamel; compressed elliptical or lenticular protocone. Cingular formations developed on lower milk teeth but a laminated protostylid sometimes persists on permanent molars. The limbs are rather short, with robust metapodials that have well-developed lateral digits.

Arambourg emphasizes the 'African character' (*vide infra*) of the dentition of this new species: enamel plications and narrow elongated protocone, as well as a tendency to develop cingular formations. Because of these features which distinguish it from all Eurasiatic forms, and because of its stratigraphical location in the Upper Miocene, he suggested that this species should belong to an independent African stock, isolated on the continent of Africa since the end of the Miocene.

Camp Berteaux

Bourcart (1937) mentioned the discovery of *Hipparion* at Camp Berteaux (Taourirt, Eastern Morocco). This material and additional specimens, described by Ennouchi and Jeannette (1954), are now considered to belong to *Hipparion africanum.*

Other sites

It is not possible to comment on the *Hipparion* material that was merely mentioned by Dalloni (1915) and Solignac (1927), which was derived from

UPPER	*Specimen*	P^2	P^3	P^4	M^1	M^2	M^3
A–P length	141	33·0	26·0	25·0	23·0	23·0	20·0
	Mar.*		27·0		24·0		
Transv. breadth	122	22·0	24·0	23·0			16·0
	141	22·5	24·5	25·3	23·0	20·5	18·5
	Mar.*		26·0		25·7		
Height	122	48·0	58·0	60·0			47·0
Protocone length	141	7·8	9·2	10·2	7·3	7·5	7·6
	Mar.*		8·4		8		
Protocone breadth	141	5·0	4·0	3·5	3·7	3·5	2·5
	Mar.*		5·0		4·0		

LOWER	*Specimen*	P_2	P_3	P_4	M_1	M_2	M_3	DM_2	DM_3	DM_4
A–P Length	143	30·0	23·6	25·0	25·3	26·0	23·4			
	89	27·0	27·0	25·0	23·0	23·0	25·0			
	3	29·0	24·0	23·5	20·7	21·0	27·0			
	Mar.*	31·5								
	6							30·5	24·2	26·0
	105							31·6	29·0	30·4
Transv. breadth	Mar.*	18·0								
	6							14·0	14·4	13·5
	105							12·0	12·0	9

* = Marceau: no number given.

TABLE 7. Measurements (mm.) of the teeth of *Hipparion africanum* (from Arambourg, 1959).

the Upper Miocene layers of the lower Tafna Valley (near Guiard, Oran), and the Djebel M'Dilla 'Pontian' horizons (of Tunisia) respectively.

Discussion on the 'African character' of Hipparion africanum Arambourg, 1959

The relationships of *H. africanum*, of the Upper Miocene of the Maghreb, to other African hipparionids have been discussed by Arambourg. He distinguishes three species, stratigraphically separated: *H. africanum* of the Upper Miocene, *H. sitifense* of the Pliocene of the Constantine and Oran area, and *Stylohipparion libycum* of the 'Villafranchian' of North, East and South Africa. Despite the great temporal span, Arambourg believes that there is a 'family air' or unity common to these three forms, which distinguishes them from the Eurasiatic material, and which stresses the common origin of the African hipparionids, isolated since the end of the Miocene.

From the description given of the skeletal material of *H. africanum*, it seems obvious that there is a marked difference between it and the Eurasiatic forms. Until the present, only teeth have been available for comparison, so that the lack of adequate comparative postcranial material has made it impossible to determine to what extent *H. africanum* shares common skeletal features with the African hipparionids of the Pliocene and Pleistocene. Dr. Leakey indicates (personal communication) that considerable postcranial material has now been recovered from Olduvai. These are to be described by Dr. R. H. Stirton of Berkeley, California, who will elucidate the skeletal relationships.*

On the basis of the teeth alone, it is difficult to acknowledge a close resemblance between the three African species. As there is a long span of time separating *H. africanum* from *Stylohipparion libycum*, one expects to find some differences, but it is first necessary to assess and appreciate the importance of the resemblances stressed by Arambourg before it is possible to evaluate the phyletic implications.

Of the 'family air' features linking *H. africanum* and the later African species, Arambourg considers two as most typical: (i) In the upper cheek teeth, the enamel plications and the shape of the protocone of the molars; (ii) In the lower molars, there is a tendency to develop additional cingular stylids. Two other classical features which will be discussed are the hypsodonty of the cheek teeth and the shape of the double knot in the lower molars.

Enamel Plications: It is commonly believed that the enamel plications have little phylogenetic significance. The plications are very variable, being much influenced by functional and ecological conditions. In any event, because of the vast temporal and spatial differences, and especially climatic and biotopical environments, this feature cannot be used as a basis of comparison. This is just an *a priori* consideration.

However, Arambourg writes (p. 93) that *H. africanum* is characterized by the complex pattern of enamel plications, which are more numerous than on most of the European forms. Although there is quite considerable variation in the complexity of the enamel at a particular period and in a particular area (compare *H. crassum* and *concudense;* Greek and Samos Pliocene forms), it cannot be denied that the Eurasiatic forms normally possess a rather plicated enamel mark-wall pattern. Furthermore it is certainly far more developed than that of the African Pliocene and Pleistocene species, which are actually characterized by their small number of plications.

The multiple pli caballin seen in many teeth does not seem to be typically African either: it is observed in many other groups on both sides of the Mediterranean Sea, and also elsewhere—compare *H. sitifense* (Mascara), *H. gracile* (Pikermi), *H. koenigswaldi*, *H. concudense* (South Aragon), *Hypsohipparion albertense* (Serengeti), and even in America in *Neohipparion eurystyle* Cope, in which as many as four may occur on the anterolabial border of the hypoloph.

Protocone: The elongated and narrow protocone is undoubtedly a typical and constant feature of all the African hipparionids so far known from the Pliocene and Pleistocene deposits. It also seems to be a distinct, strongly expressed evolutionary trend in the whole group (see pp. 354–5; table 14;

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* See *Olduvia Gorge 1951–1961*, 1 by L. S. B. Leakey (1965) which was published while this paper was in press.

figs. 12, 13). A satisfactory comparison of individual teeth at different stages of wear is difficult, and published sketches of this feature may be deceptive. Nevertheless, it is obvious that a comparison of the indices of the length and shape of those protocones available for study definitely confirms this 'African feature' of *H. africanum*. For all teeth, it shows a constant greater 'African' index than any of the European species considered (except for the breadth/length index of P^2, which in any event, is a rather atypical tooth). It is important to note that such a progressive feature, characteristic of the African phyletic line, can be traced back as far as the Upper Miocene.

The double knot: Gromova (1952), in a recent review of all the available evidence, indicates that the original type of knot is the '*stenonis*' one: it presents a very different metaconid and metastylid, the latter being strongly angulated, and separated from the metaconid by a narrow deep valley. This original type, found in the *Merychippus* ancestor, has been retained mostly in the American *Hipparion*. However, there seems to be a constant modification amongst Old World *Hipparion:* towards a '*Hipparion*' type of knot in Eurasiatic forms, characterized by a symmetrical and rounded metastylid and metaconid separated by a wide and shallow valley; and towards a more '*caballus*' type in Africa, where the metastylid is sub-triangular. The description and drawings of *H. africanum* indicate clearly that it has a '*Hipparion*' type of knot, more typical of the Eurasiatic form and bearing no resemblance to the African forms. As *H. africanum* is the oldest species of *Hipparion* known in Africa, it needs to be decided whether it has acquired this 'progressive' feature very rapidly or whether the '*Hipparion*' type of knot is not as progressive as was previously considered, having already been present in some Merychippine ancestor, and developed in parallel with the '*stenonis*' type.

Stylids: The tendency to develop stylids is quite marked in many, but not all, African forms. It is said to be expressed in *H. africanum* by a small laminated or rounded, rather isolated protostylid on the permanent P_3–M_2 of specimen no. 2, and by a small ectostylid on the vestibular aspect of most of the milk teeth. The tendency is found to be constant among all *Hipparion*. The stated degree of development of these structures does not seem to be particularly 'African': it is certainly surpassed by some Eurasiatic species, for example, *H. koenigswaldi* from Teruel. Of course, it should not be overlooked that the feature seems to have been expressed rather weakly in *Merychippus* times. The minor development that it shows in the Upper Miocene of Algeria may hardly be considered 'African' when compared with the *Stylohipparion* of the 'Villafranchian'. However, the feature suggests a rather strong and precise evolutionary trend at work.

Hypsodonty: H. africanum is stated to be poorly hypsodont. The indices are by no means comparable to the 'African' specimens of the Pliocene and Pleistocene times, and they are of the same magnitude as the other *Hipparion* groups of the Mediterranean basin. *H. africanum* is even less hypsodont than *H. sitifense* which is stated to have low teeth.

PLIOCENE

Mascara

A palate with an almost complete dentition and a symphysial region with incisors, probably belonging to the same skull, have recently been described by Arambourg (1956).

This Pliocene form is characterized by very small dimensions of the teeth (table 8), which also show few and simple plications and little hypsodonty. The protocone, completely independent of the protoloph right to the base of the crown, is relatively compressed.

The specimens have been referred to *H. sitifense* Pomel with which they are stated to share 'almost identical morphological features and size'.

	P^2	P^3	P^4	M^1	M^2		M^3	P^2–M^3
1. MASCARA								
A–P length	30	20·5	20	19·5	19		18·8	129
Transv. breadth	17 (?)	19	20	19·5	18		18·6	
Crown height	7·4	6·6	10·5	10·7	15		13	
Protocone length	6·6	7	8·3	6·7	7·4		8·8	
Protocone breadth	3·8	4·2	4·4	3·7	3·2		3	
Protocone shape	57	60	55	55	46		34	
Protocone length/Tooth length	22	34	41	33	38		46	
2. ST. ARNAUD CEMETERY								
H. sitifense (type specimen)								
A–P length				23				
Transv. breadth				22·5				
3. AÏN EL HADJ BABA								
					R	L		
A–P length			22·5	20·2	20	20·2		
Transv. breadth			21	20·5	21	20·3		
Protocone length			6·2	6	6·7	6·3		
Protocone breadth			3·2	4	3·5	3		
Protocone shape			51·6	66·6	52·2	47·5		
Protocone length/Tooth length			27·6	29·7	33·5	31·2		

TABLE 8. Summary of measurements (mm.) of teeth of North African Pliocene *Hipparion*.

St. Arnaud Cemetery

The type specimens of *H. sitifensis* (*sic*) Pomel 1897 were recovered from the St. Arnaud Cemetery. These two upper teeth, figured by Pomel (see also Arambourg, 1956) are little hypsodont and rather small (although not quite as small as the Mascara teeth). A broken calcaneum is also mentioned.

Lower teeth of a correspondingly small size and medium hypsodonty, collected by Arambourg but as yet undescribed, have no ectostylid.

Aïn el Hadj Baba

Upper isolated, but partially serial right (?) P^4–M^2, a left M^2, lower teeth, and limb bones were described by Thomas (1884) who referred them to *H. gracile* (Kaup).

However, according to Arambourg (1956), the narrow and small number of plications of the enamel, the double pli caballin, features of the protocone, dimensions of the upper teeth and absence of the ectostylid on the lower teeth, make the Aïn el Hadj Baba specimens very similar to *H. sitifense* types and co-types, as well as to the Mascara specimens. Therefore he considered them to be *H. sitifense*.

From the metapodial, it may be observed that the lateral digits were still very strongly developed.

Utique (Northern Tunisia)

This area also includes the continental sands of the Ferryville region near Bizerta (fig. 4).

Solignac (1927) indicated that the fragmented remains had been assigned by Depéret to *H. crassum* Gervais, but Arambourg (1956) is inclined to refer them to *Stylohipparion*.

St. Donat (Algeria)

Teeth of two maxillae, which Arambourg (1956) interprets as being possibly referable to *H. sitifense*, were found at this site. Joly (1909) recognized further teeth from this site and hastily referred them to *H. gracile*, but they should probably be compared with Arambourg's 1956 material and pooled with *H. sitifense*.

PLEISTOCENE

North Africa

Oran: The teeth recovered by Pomel in the Oran area are among the first discoveries of *Hipparion* in Africa and formed the basis of the first description. Two sites were mentioned:

(i) 'St. Pierre sandstone quarry, on the property of Mr. Brunie, in the St. Charles district, in the east quarter of Oran, which is also the type locality of *Libytherium maurusium*.'

Two lower teeth were described by Pomel (1897) as the type specimens of *Hipparion* (?) *libycum*. The one, a left P_3 or P_4, has an ectostylid while the other is without an ectostylid, but the antero-external region is broken. The specimens were successively referred, first by Van Hoepen (1932) to *Stylohipparion steytleri* because of its similarity to P_3 (Nas. Mus. C795) from Cornelia (*vide infra*, p. 347); then by Joleaud (1933) to *Libyhipparion libycum* because of its fundamental similarity to the du Bourg de Bozas Mission material from Omo, although it is more elongated and somewhat larger; and later by Arambourg (1947, 1956) to *Stylohipparion libycum* (or *albertense*).

A distal portion of a third metatarsal was also recovered from this deposit.

(ii) Puits Kharouby.

Five upper molars were described by Pomel (1897) and referred to *H. massoesylium*. However, Pomel himself was not too sure whether or not these upper teeth belonged to those lower teeth which he had described under the name *Hipparion* (?) *libycum*. Their reciprocal kinship was ascertained by Joleaud (1933) who consequently referred *H. massoesylium* to his *Libyhipparion libycum*, and by Arambourg (1947, 1956), who for the same reason, placed them in *Stylohipparion libycum* (or *albertense*).

Aïn Jourdel (Constantine): The material consists of a M_3 and a lower premolar, the additional stylids of which seem to have been overlooked by Thomas (1884) who referred them to *Hipparion gracile*.

Joleaud (1933) emphasized their similarity to Pomel's Oran specimens and to the material discovered in the Orange Free State of South Africa. He proposed that the Aïn Jourdel material should be placed in a new species *Stylohipparion* (?) *thomasi*.

Arambourg (1947) can see no reason for not pooling Aïn Jourdel (one of the two teeth at least) and '*H. massoesylium*' (= Joleaud's *Libyhipparion libycum*) with *Stylohipparion libycum*.

Beni Foudda (Constantine): This site has been referred to as Aïn Boucherit by Arambourg.

A molar recovered here was attributed by Pomel (1897) to *Hipparion ambiguum* but was referred by Arambourg (1947, 1956) to *Stylohipparion libycum* (or *albertense*).

Wadi Natrun (Gart el Moluk Hill): Andrews (1902) described a left upper premolar (?P^4) of large dimensions (A–P 29 mm.; transv. breadth 28 mm.), but apparently it is little hypsodont (height 38 mm.). However, it is a rather worn specimen.

When the specimen was discovered, very few African *Hipparion* had been recovered, and the typical features of the few that had been recovered were still largely unknown or as such unrecognized. The best comparative material at that time was that from Oran: the enamel pattern of the specimen from Wadi Natrun appeared definitely more complex and it differed in the absence of isolation of its hypostyle. Therefore, in spite of its transversely more compressed protocone, which explicitly suggested some close resemblance to *Hipparion theobaldi* (from the Siwaliks), the specimen was referred to the more widespread *H. gracile*.

After the discovery of further material from Omo and Kaiso, Joleaud (1933) emphasized the difference in the parastyle and mesostyle features from *Libyhipparion ethiopicum*, and he stressed the resemblance with the Kaiso specimen, referring to it the Wadi Natrun premolar, which he called *Hipparion* cf. *albertensis* (*sic*).

Central Africa

Koro Toro: The *Hipparion* material recovered from the 'Villafranchian' horizon of the Tchad has been provisionally referred by Coppens (1960) to *Stylohipparion.* He is preparing a detailed description of these specimens, together with the associated fauna. Therefore, it is not possible to comment on this material at this stage.

East Africa

Omo: The first specimens were recovered by the du Bourg de Bozas Mission (1903) and were described by Joleaud (1933). They consist of a few isolated teeth, namely:

1 incisor;
5 lower cheek teeth (1 right premolar, one left M_3, two left molars and one right molar);
1 fragmented upper right molar.

To this group Arambourg (1947) added a left M^1 or M^2, first interpreted by Joleaud as *Hippotigris.*

A second series of specimens was recovered by Arambourg (1947) during his 1932–33 expedition, and comprises 1 right P^2; 1 left M^3; 1 fragmented right upper molar and 1 right M_1 or M_2.

The first of these groups was described by Joleaud (1933) who erected the new genus and species *Libyhipparion ethiopicum,*[1] generically distinct from the South African specimens from Namaqualand and Cornelia on the one hand, as well as from the Constantine material of Thomas, on the other, and specifically separated from Pomel's St. Charles teeth.

In a later reconsideration of these Omo specimens, to which the second series of teeth from the same area was added, Arambourg (1947) rather emphasized (*a*) the close relationships between all the Ethiopian hipparionids; and (*b*) their profound similarity to the East African (Kaiso, Serengeti *pro parte*, and probably Olduvai) material and the Orange Free State discoveries. Furthermore, Arambourg considered it reasonable to refer most of Pomel's and Thomas' North African (St. Charles, Puits Kharouby and the Constantine) material to *S. albertense* or possibly to *S. libycum.*

The characteristic features common to these specimens are:

(i) pronounced hypsodonty reaching 80 mm. in unworn teeth;
(ii) upper molars with very complicated enamel pattern and laterally compressed and strongly elliptical protocone;
(iii) lower teeth with strongly developed additional stylids, rather large oval or flattened and pointed ectostylid;
(iv) the presence of a ptychostylid; and
(v) ridged or pillar-like protostylid and well-built entostylid.

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(1) With exception of left upper molar, considered by Joleaud as belonging to *Equus* (*Hippotigris*).

Therefore, there are no reasons for proposing any generic or specific distinctions between these Pleistocene African *Hipparion*, which according to the priority rules have been referred to *Stylohipparion albertense.*

Olduvai: Some of the first fossils identified in the Olduvai Gorge, when it was first discovered by Kattwinkel in 1911, were the distal ends of 3 metatarsals of hipparionids, which Hopwood (1937) referred to *Stylohipparion* cf. *albertense* (Hopwood).

The dimensions of the lower articulations of metatarsal III were 40 × 30 mm. The broken metatarsal II and metatarsal IV are stated to have had 'originally' almost the same lengths as metatarsal III, and to have had the appearance of broadening distally.

Further specimens of teeth, recovered by Kattwinkel and Reck in 1913, as well as an upper dental series collected by the British expedition, were referred to the same genus and species. The diagnosis proposed by Hopwood (1937) for this *Stylohipparion* cf. *albertense* is:

> Three-toed equid, with high-crowned molars of the *Hipparion* group. Lower teeth are laterally compressed and display a strong, often laminated ectostylid. Genotype: *Stylohipparion hipkini* Van Hoepen (1932).

Unpublished data

In recent years a large collection of equid material has been recovered from the Olduvai Gorge by Dr. L. S. B. Leakey. All the specimens from Bed II (and a few from Marsabit Road, Olorgesailie and Omo) are now being studied by Dr. R. A. Stirton in California. Dr. Leakey kindly permitted the authors to make a brief survey of this material. In order not to encroach on the final description, only a few features relevant to this paper are mentioned:

(i) In this mixed sample there are 471 *Equus* teeth, of which 224 are from the upper dentition. Of the 186 teeth of hipparionids, 100 are upper. The vast majority of these are from Bed II, only a few deriving from other sites.

(ii) This is then a reasonable sampling to ascertain the expected proportions of upper and lower teeth. It will be indicated below that at Langebaanweg there are approximately equivalent proportions of uppers and lowers, but at the latter site there are almost no *Equus* specimens.

(iii) The data is also useful to assess the situation at South Serengeti (*vide infra*). In this respect it is interesting to note that in the Olduvai collection, among the lower teeth, those of hipparionids have elonggated, strongly marked ectostylids, typical of *Stylohipparion*, while those without ectostylids lack the typical features of *Hipparion* as well as the protostylids of the Langebaanweg specimens. They are typically *Equus* in type.

(iv) There is a great range of variation in the size of these *Hipparion* teeth, and also in the length and shape of the protocone. On the whole, the range seems smaller than that of the Langebaanweg teeth, but the protocone is more elongated. In the *Hipparion* lower (as well as in these *Equus*) teeth, there is a complete absence of protostylids and hypostylids.

South Serengeti: A large collection of *Hipparion* has been made from various localities in the South Serengeti, and was described by Dietrich (1942). A complete list has never been published. However, from the available data, it is possible to ascertain that the collection consists mostly of isolated and fragmented specimens, a few maxillary and mandibular fragments (among which are symphysial portions with incisors), many loose upper and lower teeth, both milk and permanent. There are also some rare postcranial specimens, namely, a proximal fragment of a femur, a distal fragment of a tibia, two third metatarsals, one third metacarpal and tarsals. Dietrich artificially reassembled the isolated teeth into series, and most of the dental series figured in his publication are reconstructed. From the scattered data and illustrations, it is possible to establish an incomplete list of the South Serengeti dental material (table 9).

Description			Origin and Coll. Number	Plate Number in Dietrich (1942)
Milk Dentition				
Upper	r	dP2–dP4	Vo 330	XIII 96
	r	dP2–dP3	Gadj 10	XIII 97
	l	dP2–dP4	Gadj 2.39	XX 162
Lower	r	dP2–dP4	Vo 313	XIII 93b
	r	dP3–dP4	Marambu	XIII 93a
	r	dP4	Gadj 10–13.3.39	XIII 94
Permanent				
Upper	l	P2–M3	Vo, Gar.	XIII 87
	l	M2–M3	Vo 670	XIV 102
	l	P2–M3	Vo 330, Vo 670	XV 107, 108
	l	P2–P4	Vo 670	XX 160
	r	P2–M3	Vo, Gar.	XIII 88
	r	M2–M3	Vo 670 and Marumba	XIV 103
Lower	l	M3–P2	Vo 313, 670	XV 106
	l	P2–M3	Der., Gadj., Gar., Vo	XV 105
	l	P2–M3	Vo, Gar.	XIV 101
	l	P2–M3	Vo 330, Vo 670	XIII 90
	l	M1	Garussi 2.39	XIV 99
	l	M	Gar. River 200	XIII 95
	r	M3–P2	Vo 670, Gar., Olduvai Hill	XVI 109
	r	P2–M3	Vogel River	XIII 89
	r	P2–M3	Vo 670, Gar., Vo	XIII 91
	r	P3–M3	Gadj 10	XIII 92
Symphysial region with incisors			Vogel River 9–10–38	XVI 112

TABLE 9. *Hipparion* material mentioned by Dietrich (1942) and derived from South Serengeti region

In contrast to the relatively unchanged nature of the postcranial skeleton (*vide infra*) since Pliocene times, the advanced and progressive features of the dentition of the South Serengeti hipparionids have been emphasized by Dietrich. The teeth, both upper and lower, are strongly hypsodont (crown length: 9 cm.). The upper molars show numerous enamel plications, and an elongated, ungrooved protocone, completely isolated right down to the base of the crown, and embedded in a thick cement layer. The incisors (see p. 350) are longitudinally grooved on their anterior surface (in one case I_3 is missing).

It does not seem possible to distinguish different forms of hipparionids at Serengeti on the basis of the upper teeth. On the contrary the lower teeth show some constant features whereby it seems possible to distinguish two groups.[1] A large group of teeth, all apparently recovered from the gray tuffs, does not show any additional stylids while another group of some 50 (40 isolated teeth and 2 incomplete dentitions) displays the ectostylids characteristic of most of the African hipparionids then described. In these teeth the ectostylids are sometimes very strongly developed, pillar-shaped or flattened and ridged. Protostylids and hypostylids are also regularly present, and a very peculiar entostylid (see p. 360) may be observed on one tooth (Garussi River 200, fig. 95 of Dietrich, 1942). These teeth derive from deposits that seem to span over a longer period of time than do those from which the teeth without stylids were recovered: some of them probably occur in the gray tuffs, contemporaneously with the first group, while others belong to a probably younger horizon. However, as has been stated previously, the stratigraphy of the South Serengeti is very poorly documented. Other than the presence of the stylids and the average shorter total length of the dental series at a comparable stage of wear (156 mm. *v.* 170 mm.), there seem to be no appreciable differences between the two groups. However, the value that can be attached to the assessment of the total length of the dental series in these specimens is doubtful because (*a*) of the 'reconstruction' of most of Dietrich's series, and (*b*) of the variation of the total length due to wear.

In spite of the above distinction, Dietrich does not consider it necessary to separate generically the South Serengeti material. This attitude is reasonable because

(1) lack of knowledge of a stratigraphical sequence rules out a clear chronological sequence;

(2) too little was known of the skeleton, both cranial and postcranial;

(3) the upper teeth showed no features whereby they could be separated into two groups, and yet it is a statistical probability that, if there were two species at the site, all the uppers could not have belonged only to one of these species; and furthermore,

(4) the development of the ectostylids, ranging from absence through mild formation to strong development, is an expression of dental adaptation to environmental factors (*vide infra*, p. 352).

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[1] See also discussion on Arambourg's concept of the non-validity of *Hypsohipparion*, p. 333.

On the basis of the data available then,[1] Dietrich considered that within the Serengeti material there was an original and conservative African stock of hipparionids for which he erected a new genus *Hypsohipparion* Dietrich, 1942, with *Hipparion albertense* (Hopwood) from the Lake Albert Kaiso bone beds as the type specimen. Into this genus and species he placed the Serengeti material without stylids, as well as all the upper teeth and the postcranial remains. The diagnosis that he proposed was:

> An advanced three-toed, short-snouted *Hipparion* of the dimensions of a small *caballus*, the M^3 of which reaches a crown height of 9 cm. The protocone shows a tendency to become laminated, non-grooved and completely isolated from the protoconule. Teeth show no reduction of the main cusps and styles. Plications are more marked than in all Pliocene species. Lower teeth (deciduous premolars, permanent premolars and molars) are (?)[2] all without ectostylids.

Dietrich believed that the group manifesting the stylids was displaying the developmental trend of a selective pattern. He provisionally placed this group in *Stylohipparion* as a practical measure, partially comparable to *Stylohipparion libycum*, *Stylohipparion ethiopicum*, and *Stylohipparion steytleri*. However, he maintained that the generic labelling had no strict taxonomic value because of the scarcity of the material on which this was based. He did not see the value of assigning his material to a new species.

Arambourg (1947) questioned the validity of the generic status of *Hypsohipparion* on the basis of a possible incorrect determination of what he considered to be lower zebrine teeth (see p. 333). In later publications (especially 1956 and 1959) he seems to have definitely adopted this view permanently. In his opinion the Serengeti material belongs partly to *Stylohipparion* and partly to *E. zebra*. This opinion is discussed and considered unacceptable elsewhere in this paper.

Lake Eyasi: The few isolated teeth recovered from the Lake Eyasi shore (west and north of Mumba Hill) are very much rolled and unsuitable for any detailed study (*vide supra*, p. 287). They were referred to *Hipparion* sp. (Reck and Kohl-Larsen, 1936).

Lake Albert (Uganda): From the east shore of the Lake, one incomplete upper molar (B.M.N.H. M12615) was described by Hopwood (1926) as the holotype of *Hipparion albertensis* (*sic*). The tooth is rather hypsodont, with a complicated enamel pattern. Its antero-posterior diameter is 24·5 mm.

Dietrich (1942) used it as the genotype of his new genus *Hypsohipparion albertense*, the proposed diagnosis of which is noted above.

South Africa

Namaqualand (Cape Province): Nine isolated mandibular teeth of the same jaw, left P_2–M_1 and M_3 and right P_4–M_2 and M_3 (fragmentary) were

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[1] Through the kind collaboration of Dr. K. H. Fischer, Berlin, measurements of some of the '*Hypsohipparion*' teeth were made available to the authors: see table 20.

[2] Dietrich includes this 'query' in his original diagnosis in German (p. 97).

described by Haughton (1932), who erected a new genus and species *Notohipparion namaquense.* The type specimen is S.A.M. 9982. Unfortunately a diagnosis was not provided.

A small ectostylid and a protostylid are occasionally present. It is difficult to comment on the height and relative hypsodonty of these teeth because the crown is rather low, as the specimens are in a very advanced stage of wear (table 10). The teeth possess a thick cement.

Cooke (1950) proposed a diagnosis for the genus *Notohipparion* Haughton: 'rather low-crowned, heavily cemented hypsodont lower cheek teeth with an extra antero-external cingulum fold or column, either isolated or fused with the parastylid, present in all the permanent cheek teeth except the second pre-molar, and a deep groove separating the strongly developed metaconid and metastylid. The upper dentition is unknown'.

Because of the moderate hypsodonty and the weak development of additional stylids, Dietrich (1942) considers *Notohipparion* to be more primitive than *Stylohipparion.* This opinion had also been held by Van Hoepen (1932).

Arambourg (1947) compared these lower molars with the 'single' African Pleistocene genus *Stylohipparion* but, probably because of the poor stratigraphy, he did not revise its taxonomic status. In later comments on the African *Hipparion,* he (1959) makes no further mention of these specimens.

	P_2	P_3	P_4	M_1	M_2	M_3
A–P Length	29·5	27·0	26·0	23·0	24·0	29·0
Transv. breadth	16·0	17·0	17·0	16·0	14·5	12·5
Height	14·5	17·5	25·0	23·0	30·0	34·0
Transv. breadth/A–P length . .	54·2	63	65·4	69·6	60·4	43
Height/A–P length	49·2	64·8	96·1	100	125	117
Hypsodonty Index	110	97	67·9	69·5	48·2	36·8

TABLE 10. Measurements (mm.) of teeth of '*Notohipparion namaquense*' Haughton

Christiana (Cape Province): From this site an upper second (? third) left molar (Archaeol. Surv. 113), considerably worn, undescribed and not illustrated, has been referred to *Stylohipparion steytleri* by Cooke (1950).

Transvaal australopithecine cave breccias: Two lower teeth, recovered by Broom in the breccia filling the Kromdraai Cave, have been referred to *Stylohipparion steytleri* (Cooke, 1950). *Hipparion* teeth recovered from Bolt's Farm and Makapansgat Limeworks have been similarly referred (Cooke, 1963). These specimens have not been described.

Cornelia (Uitzoek): Eleven isolated upper and lower teeth include a group of five and another group of two teeth belonging to single individuals (table 11):

(i) one right M^1 or M^2 (Nas. Mus. C558), one left M^3 (C555), one left M_1–M_2 (C556),[1] described by Van Hoepen (1930) as a new species

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[1] In the original publication (1930), C556 was stated to be composed of lower milk teeth (DM_3 and DM_4), and only in 1932 were they correctly acknowledged as permanent teeth.

Hipparion steytleri, the type being C558 and the paratypes being C555–556.

(ii) A series of five left lower teeth P_3–M_3 (C795), recovered from the type locality, were referred by Van Hoepen (1932) to the same species.

(iii) A right M_2 (C797), in very early wear and therefore displaying a completely uncharacteristic pattern, was used by Van Hoepen (1932) to erect a new genus, namely, *Stylohipparion*, and a new species *hipkini*, to which a left P_2 (C796), recovered from the same locality and formation, was provisionally referred.

Van Hoepen (1932) subsequently referred *steytleri* to the new genus *Stylohipparion*. He considered *Stylohipparion* to be 'obviously the terminal stage of the evolutionary line which originated from *Hipparion* with *Notohipparion*.'

Joleaud (1933), who compared *steytleri*, with *Libyhipparion ethiopicum*, and *hipkini* with the Aïn Jourdel specimen of Thomas, accepted the specific distinction between *steytleri* and *hipkini*. Cooke (1950) considered this distinction to be invalid. This opinion is strongly supported here, for both *a priori* and *a posteriori* reasons: first of all, no upper teeth of *hipkini* have been recovered, and Van Hoepen's species is based on one single lower tooth (C797), which constitutes a very inadequate basis for creating a new taxonomic unit. Furthermore, the tooth is in a very early stage of wear, which is the case of the obviously atypical, peculiar pattern of its occlusal surface. Thus the 'difference' between it and the *Stylohipparion steytleri* is not at a species level.

Van Hoepen provisionally referred specimen C796 to the new species, but it is even less different from the known *steytleri* specimen. In any event, being a P_2, it does not show the typical features of a species.

On the other hand, and quite apart from this question of a specific distinction, the genus *Stylohipparion* Van Hoepen has been generally accepted by all subsequent authors. Hopwood (1932), Dietrich (1942), Arambourg (1947, 1956, 1959), Cooke (1950) and Gromova (1952), among others, have considered *Stylohipparion* as a valid unit (at least at a subgenus level), which expresses the 'African' trend of Pleistocene hipparionids. The following diagnoses have been proposed:

> *Arambourg* (1947): 'Tridactyl equid, with very hypsodont dentition. Upper molars with compressed protocone of very elliptical section, wavy parastyle; especially complicated enamel pattern, particularly around the prefossette. Lower molars with broadly developed ectostylid, laterally compressed, and close to the antero-external hypoconid pillar.' (Direct translation from the French.)
>
> *Cooke* (1950): 'High-crowned rather hypsodont lower cheek teeth with a strongly developed isolated pillar external to the ectostylid, possessing no external groove between hypoconid and hypoconulid, having no protoconid and hypoconid and small rather widely separated metaconid

and metastylid. High-crowned upper cheek teeth with isolated oval protocone and possessing a small flange on the antero-internal side of the parastyle.'

We wish to point out that the 'ectostylid' referred to by Cooke is actually the *ptychostylid*, while the 'strongly developed isolated pillar' is the *ectostylid.*

UPPER TEETH	*St. steytleri* (van Hoepen)	
	M^1 or M^2	M^3
	(C558)	(C555)
A–P length ..	22·0	21·0
Transv. breadth ..	22·0	18·0
Height	54·0	66·0

	St. steytleri				*St. steytleri*		*St. hipkini*	
LOWER TEETH	P_3	P_4	M_1	M_2	M_1	M_2	M_2	P_2
	(C795)				(C556)		(C797)	(C796)
A–P length ..	25·0	28·0	22·0	24·5	—	21·0	28·5	31·0
Transv. breadth	15·0	12·0	12·0	11·5	12·0	12·5	15·0	14·5
Height	64·0	74·0	69·0	73·0	32·0	41·0	81·0	46·0

TABLE 11. Dimensions (mm.) of teeth of '*Stylohipparion*' from the Orange Free State, South Africa.

From Uitzoek also comes an anterior portion of a lower jaw (Nas. Mus. C679), containing four large first and second incisors, which are flattened anteriorly and arranged almost in a straight line. Each incisor shows the 'mark' or the cement-filled depression in the enamel. The third incisor is small and lies behind and in contact with the second incisor.

The above description (Cooke, 1950) is a slightly modified interpretation (also suggested by L. H. Wells) of the original description by Van Hoepen (1930), made, according to Cooke, so as to avoid the 'startling supposition' of the complete absence of the third incisor. However, it should be pointed out that specimen GADJ. 10 from South Serengeti shows complete absence of not only I_3, but also of the canines (Dietrich, 1942).

One of the special features of this specimen C679, besides the reduction (? complete, i.e. absence) of I_3, is that the lingual aspect of I_1 and of I_2 has two surfaces, meeting at an angulated thick ridge. Each surface also has longitudinal parallel 'costae'.

A new genus and species *Eurygnathohippus cornelianus* van Hoepen (1930) was created to include the above material. No measurements were published, but from the illustrations and the cast it is clear that the jaw fragment belongs to a very large skull.

Dietrich (1942)(1) made the suggestion that this mandibular symphysial

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[1] Dietrich incorrectly describes the specimen as belonging to a milk dentition ('Milchvordergebiss', p. 97).

region (for which no cheek teeth are known), should belong to *Stylohipparion*, or at least to the advanced *Hipparion* of the Cornelia layers.

Ewer (1963) refers to *Eurygnathohippus* as a chalicothere. The basis for this opinion is not clear to the authors.

NOTE ON *Hipparion* INCISORS

Hipparion incisors have rarely been discovered in Africa. In a recent, comprehensive study of a large assemblage of *Hipparion* material from South Aragon, Sondaar (1961) indicates a similar shortage there. The small number of recorded specimens from Africa are:

(i) *Upper incisors:* the *H. africanum* type specimen (no. 141) from Oued el Hammam presents a complete snout, and, from the same site, there are also three maxillae with incisors. They have been described by Arambourg (1959) without comment, because there is no comparative material.

(ii) *Lower incisors:*

- (*a*) The *Libyhipparion ethiopicum* (Joleaud, 1933) collection from the Omo Valley contained one incisor (*vide supra*, p. 342).
- (*b*) Dietrich (1942) mentions some incisors from the South Serengeti without going into any detailed description (*vide supra*, p. 344).
- (*c*) *Eurygnathohippus cornelianus* (Van Hoepen, 1930): an anterior portion of a lower jaw. This may belong to an individual of the genus *Hipparion* or *Stylohipparion*, as has been suggested already by Dietrich (1942) and in a personal communication (1964) from Dr. L. S. B. Leakey (who bases his view on material recently discovered at Olduvai).[1]

Each of these specimens raises difficult problems, which cannot be solved until more complete material becomes available. A few of these problems are:

(1) The '*Libyhipparion*' incisor does not show the sub-elliptical section of *Hipparion*. It is completely subdivided into two clearly separated 'marks', no other example of which is known among *Hipparion* in the literature. It has been suggested that this feature is an extreme manifestation of the enamel plications, typical of the African hipparionids. It is impossible to state whether or not the feature is really exceptional. It is not demonstrable in the other few available incisors.

(2) *Eurygnathohippus:* The 'costae' and the blunt ridge on each specimen are unique in this small series. A possible explanation for these features is that they are adaptations to browsing and strengthen the teeth, set practically parallel to the horizontal symphysis.

(3) The occasional reduction (? absence) of the third incisor is referred to above.

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[1] Confirmed while in press. See Leakey, L.S.B.: *Olduvai Gorge 1951–1961*, 1. p. 26.

A SUMMARY OF PUBLISHED POSTCRANIAL REMAINS OF AFRICAN *Hipparion*

The postcranial skeleton of African hipparionids is very poorly known. The only described specimens are:

Camp Berteaux: A femur fragment with the proximal epiphysis.

Oued el Hammam: Distal fragment of humerus (no. 159); radio-ulna (no. 123) and fragments 13, 22 and 27; femur without epiphysis and a distal fragment; distal fragment of tibia; pelvic fragment; two astragali; one calcaneum; five metacarpals and five metatarsals, many with lateral digits.

Aïn el Hadj Baba: Metapodials with lateral digits.

Oran: One fragmentary calcaneum and one third metatarsal.

Omo: Right humerus.

Olduvai: Distal end of three metatarsals. There are also quite a number of undescribed specimens. The authors examined a number of such specimens recently collected at Olduvai Gorge. Data on the metapodials is provided below.

South Serengeti: Proximal fragment of a femur; distal fragment of tibia; two metatarsals III; one metacarpal III; tarsals.

Arambourg (1949) has probably described the largest collection known from one site: it consists mainly of numerous complete metapodials (many of them with lateral digits) which have been referred to *Hipparion africanum*. From the description and the measurements, this North African Upper Miocene *Hipparion* seems to have been about the same size as the smallest *H. mediterraneum* of Pikermi. The extremities indicate that *africanum* was rather short and heavily built. The lateral digits were more robust and strongly developed than those of most other hipparionids, and they certainly were still functional.

From the Pliocene, only a few metapodials with very well developed lateral digits are known from Aïn el Hadj Baba. They have not been adequately studied. It has been assumed that they belong to *H. sitifense*.

From the Pleistocene of East Africa a right humerus is known from Omo, and a few fragmentary long bones and metapodials have been recovered at Olduvai and South Serengeti. The material has not been described. Size and morphology of the metatarsals do not seem to differ noticeably from *H. gracile*. Dietrich (1942, p. 101) states that the South Serengeti metatarsal III 'must

	Breadth, distal end	*A–P diameter, distal end*
Olduvai (Hopwood 1937)	40	30
South Serengeti (Dietrich 1942)	37	35
H. elegans	29·6	25·1
H. moldavicum	33·9	26·8
H. mediterraneum	32·8	

TABLE 12. Dimensions (mm.) of metatarsal III of *Hipparion*

have a length similar to *H. gracile*, i.e. 23–24 cm.' The lower articulating surface is 37 mm. broad and 35 mm. A–P, so that it is only possible to state that the distal end is broader and thicker than in most of the European *Hipparion* (table 12). The lateral metapodials reach almost to the distal articulating facet and are rather strongly developed, but it is not possible to state firmly whether or not they possessed three phalanges. Nothing is known about the front extremities at present.

The only species with similar dimensions of the lower end of metatarsal III is *H. longipes* with 40 and 33 mm. for the breadth and A–P dimensions respectively. *H. africanum* has a distal breadth of 34·7 mm. It is difficult to assess whether these greater dimensions of the East African Pleistocene forms are indicative of larger overall dimensions of the animal, or whether they only refer to more massive metapodials. Although there is no direct correllation between the different structures, it may be mentioned that the larger size of some of the South Serengeti molars may suggest that the first possibility is not excluded. In general, too, Pleistocene mammals tend toward giantism.

On the basis of published material, it was not known whether or not the African Pleistocene hipparionids were three-toed horses. There is some information concerning the existence of metatarsal II and metatarsal IV at Olduvai, of which it is stated that 'they originally had practically the same length as metatarsal III and that they are broadening distally' (Hopwood, 1937). However, no phalanges are mentioned.

Unpublished data

Examination of the *Hipparion* third metapodials from Olduvai Bed II, now in Berkeley, California, reveals conclusively that the lateral digits were robust, reached the distal ends of the metapodials, and were as well developed as those of *Hipparion* from Pikermi. The metapodials II and IV are not represented by complete specimens or by the distal articular end. Measurements of the fragments are considered to be of no value. Despite the lack of complete lateral digits, the evidence of the articular grooves formed by them on the third metapodials convincingly indicates that the East African *Hipparion* were three-toed. Furthermore the data suggests that they possessed slightly longer, but more massive, limbs than the Pikermi *Hipparion* (see also p. 363).

Table 13 indicates the dimensions of the available third metapodials from Bed II, compared with two specimens from Pikermi.

It appears that the African hipparionids have hardly modified their locomotor apparatus since the Pliocene.

THE ECOLOGICAL ADAPTATIONS OF *Hipparion*

Considerable plasticity exists in biological organisms. Factors such as climate (with such variations as in temperature and humidity) considerably affect water supply, food, animal and plant associations and the actual nature of the environment, e.g. savanna, sand dunes, forests. The range of an intra-

Metacarpal III	*Total length*	*Proximal A–P*	*Proximal breadth (max.)*	*Distal A–P*	*Distal breadth (max.)*
1957. SHK II 935*	217	36	46	33	42
F. 345†	206	37	44	34	?45
1955. BK II 45	223	37	>45	36	48
MEAN	215	37	45	34	45
Pikermi UC63402**	206	31	40	29	38
Metatarsal III					
1957. SHK II 557*	253	38	48	35	45
1957. SHK II 729/730	260	37	47	36	45
1955. BK II 68	257	40	46	35	45
1953. BK II	242	37	45	34	44
1957. SHK II 1177	254	—	—	33	>42
1957. BK II 663	—	41	46	—	—
1955. BK II 135	—	—	—	38	48
1941. S I F 797	—	—	—	32	43
MEAN	253	38·6	46·4	36	44·7
Pikermi UC63415**	241	37	45	33	40

* These appear to belong to one individual.

** University of California, Berkeley (Dept. of Paleontology).

† There is a unilateral pathological growth at the distal end.

TABLE 13. Dimensions (mm.) of third metapodials of *Hipparion* from Olduvai Bed II. All the specimens, except the two labelled 'Pikermi', are from Olduvai.

species variation may be considerable and will allow extensive pliability in adaptation to changing environmental conditions. Such modifications may not change the genetic background or consequently, the taxonomic status. In comparing different anatomical patterns, this concept must be borne in mind.

On the other hand, it is also obvious that the environment may favour, either the greater adaptive potential of some individuals in a particular population or mutations, so that selective forces may operate to promote different races and eventually a new species. Therefore, in a survey of a biological group which extends over a vast continent, it is essential to appreciate the plasticity of the organism.

Such a study has been successfully developed for the family Equidae, and the hipparionids in particular, because of the vast amount of available fossil material, both in America and in Eurasia. Following other scholars, Gromova (1952), in her revision of the genus *Hipparion*, has emphasized its variability and evolutionary trends in relation to ecological factors.

The aims of this section are

(*a*) to summarize the main conclusions about the ecological and functional significance of *Hipparion* characteristics;

(*b*) to summarize the available information concerning the African biotopes occupied by *Hipparion* from Upper Miocene to Pleistocene times; and

(*c*) to draw possible conclusions about the migrations and evolution of African *Hipparion* under the influence of these bionomical circumstances, and thereby to contribute to the appreciation of the taxonomic status of the African groups.

ECOLOGICAL AND FUNCTIONAL SIGNIFICANCE OF HIPPARION FEATURES

The *overall dimensions of the Hipparion skeleton* do not allow definite conclusions about the biotope. It is known that the smallest races of extant Equidae are to be found in the driest areas characterized by drier food and, in the northern part of their dispersion, in areas of poor economic conditions. It is probable that similar factors have influenced the *Hipparion*-associated fauna, and that their general dimensions illustrate in some way the nature of the biotope. However, larger and smaller forms (? species) have repeatedly been recovered from the same deposit so that it appears that they co-existed in the same climate, but they may have occupied, within the same area, slightly different ecological niches. On the other hand, this is not a general rule because exceptions have been documented. For example, at Pavlodar (on the right bank of the Yrtych, Moldavia, U.S.S.R.) where it was possible to make independent studies of the nature of the biotope at different ecological stations, a species characterized by longer and more slender extremities and reduced lateral digits, viz. *H. longipes*, lived in a drier habitat than the shorter-limbed *H. elegans* did. Therefore, it is not possible to make any direct inferences about the biotope from a mere consideration of the overall dimensions of the animal. Various factors are probably involved which cannot be adequately isolated.

Relative dimensions of cheek teeth and incisors seem to be largely influenced by the quality of the food: a drier, more steppe-type grass usually develops larger teeth. However, the incisors and the cheek teeth may show differing reactions and adaptability to this ecological feature. This has been demonstrated by comparing species presenting large cheek teeth with species having small cheek teeth, e.g. *H. gratum* and *H. longipes*, which show comparable incisors. The relative size of the teeth in proportion to the overall dimensions of the animal must also be considered, a smaller animal normally having relatively larger teeth.

The development of the preorbital fossa, which has become an important taxonomic consideration, is in the present state of our knowledge not related to any ecological feature. Animals with large and with small preorbital fossae are found together in the same xerophytic (*H. proboscideum* and *H. matthewi*, at Samos) and moist habitats (*H. moldavicum* at Taraklia, or *H. theobaldi* in the Siwaliks). Preorbital fossae may even be missing (*H. platygenys* at Taraklia) without any apparent ecological reason.

The isolated protocone, completely detached from the protoloph and the protoconule right down to the base of the crown, is a constant feature of the hipparionids. It obviously weakens the structure of the tooth. This has to be compensated for, especially in the case of a hard and dry grass diet, by a greater development of the cement in the anterior and the posterior valleys so as to bind and strengthen these individual elements (Stirton, 1931).

Two elements are involved in shaping the protocone: antero-posterior length and transverse breadth. It is known that, relative to the total dimension of the tooth, the A–P length of the protocone is more constant than its transverse breadth. Therefore, a protocone may look elongated, but this is only a reflection of its narrowness. Thus it is advisable to express the functioning structure of the protocone by means of two indices:

(*a*) the protocone length is expressed relative to the general mesiodistal measurement of the tooth, i.e. the 'length index'.

(*b*) The so-called 'shape index' expresses the length of the protocone relative to its breadth (table 14; figs. 12, 13).

These indices highlight the differences in adaptation between the African and Eurasiatic *Hipparion*.

The two indices for the African forms are compared to those for 7 Eurasiatic *Hipparion* species. Available measurements of the total dental series have been utilized. It may be noted from figure 12 that the length index of the African *Hipparion* is constantly higher for each tooth than that of the corresponding tooth of any of the Eurasiatic species. However, in both groups the length index tends to increase in a mesiodistal direction. On the contrary, the shape index (fig. 13) is constantly lower for the African forms, decreasing for both African and Eurasiatic groups in a mesiodistal direction. Thus it may be concluded from the two indices that the protocone of the African *Hipparion* is both relatively longer (elongated) and narrower than in the Eurasiatic forms.

The shape of the protocone varies with progressive wear, the section tending to become more oval and less elongated. But independently of these modifications, for particular locations in the dental series at comparable levels of attrition, there seems to be also an adaptive elongation or broadening of the protocone which is linked with the type of food it has to deal with. It is suggested that the efficiency of the protocone's function in trituration lies in the action of its buccal and lingual enamel crests, developed perpendicularly to the lateral chewing movements of the mandible. It is obvious that the efficiency is maximal for a narrow and elongated protocone, for here the crests are at one and the same time the longest and the most perpendicular. Thus they would favour a dry and harder bunch grass. This suggestion is strengthened by the contemporaneity of the lengthening of the protocone and the development of a typical xerophytic vegetation in America.

Enamel plications

It has been successfully demonstrated that the complexity of the enamel pattern on the occlusal surface of *Hipparion* molars has developed synchronously with the drier environment in Upper Miocene and Pliocene times. Like the elongated protocone, the numerous enamel plications are oriented perpendicularly to the movement of the jaws, and are increasing the triturating power of the teeth for coping with harder grass. Although there seems to be a parallel increase in the degree of plications with increasing toughness of food, there

	H. africanum[b]		*H. sitifense*[c]		*H. elegans*[d]		*H. moldavicum*[d]		*H. platygenys*[d]		*H. periafricanum*[e]		*H. gromovae*[e]		*H. concudense*[e]		*H. koenigswaldi*[e]		*Langebaanweg*	
	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.	L.I.	S.I.
P^2	23·6	64·2	22	57	22·8	59·3	21	65·2	21·9	58·5	20·7	62.6	22·3	60·5	20·1	70	22·9	57·2		
P^3	35·3	43·2	34	60					24·8	64·8										
P^4	40·8	34·3	41	55					28	62·2										
P^3 or P^4					28·4	59·3	25·7	60·6			24·2	68·9	26·2	64·6	26	64·5	30·2	51·1	34·7	49·9
M^1	31·7	50·5	33	55																
M^2	32·6	46·6	38	46					31·6	61.9										
M^1 or M^2					32·3	57	30	60·1			28·2	64·7	27·7	58	28·6	57·2	31·1	47·9	36	47·9
M^3	38	32·9	46	34	35	50·8	34·8	47·1	30·2	53·8	27·7	63·5	31	54·6	29·1	52·4	32·2	47·9		
P^3, P^4 M^1 or M^2:																				
a. range of variation:																			26·5–45·6	36·4–58·9
b. mean for little or moderately worn teeth:																			35·2	48·6
c. General mean:	35·1	43·4	36·5	54	30·3	58·1	27·9	60·3	28·1	62·9	26·2	66·8	26·9	61·3	27·3	60·8	30·7	49·5	35·1	48·9

[a] Length Index (L.I.) = protocone length relative to tooth length.
Shape Index (S.I.) = protocone breadth relative to protocone length.

[b] According to, or calculated from Arambourg, 1959.

[c] According to, or calculated from Arambourg, 1956.

[d] According to, or calculated from Gromova, 1952.

[e] According to, or calculated from Sondaar, 1961, for 'little or moderately worn teeth'.

TABLE 14. Protocone Length Index and Shape Index.[a]

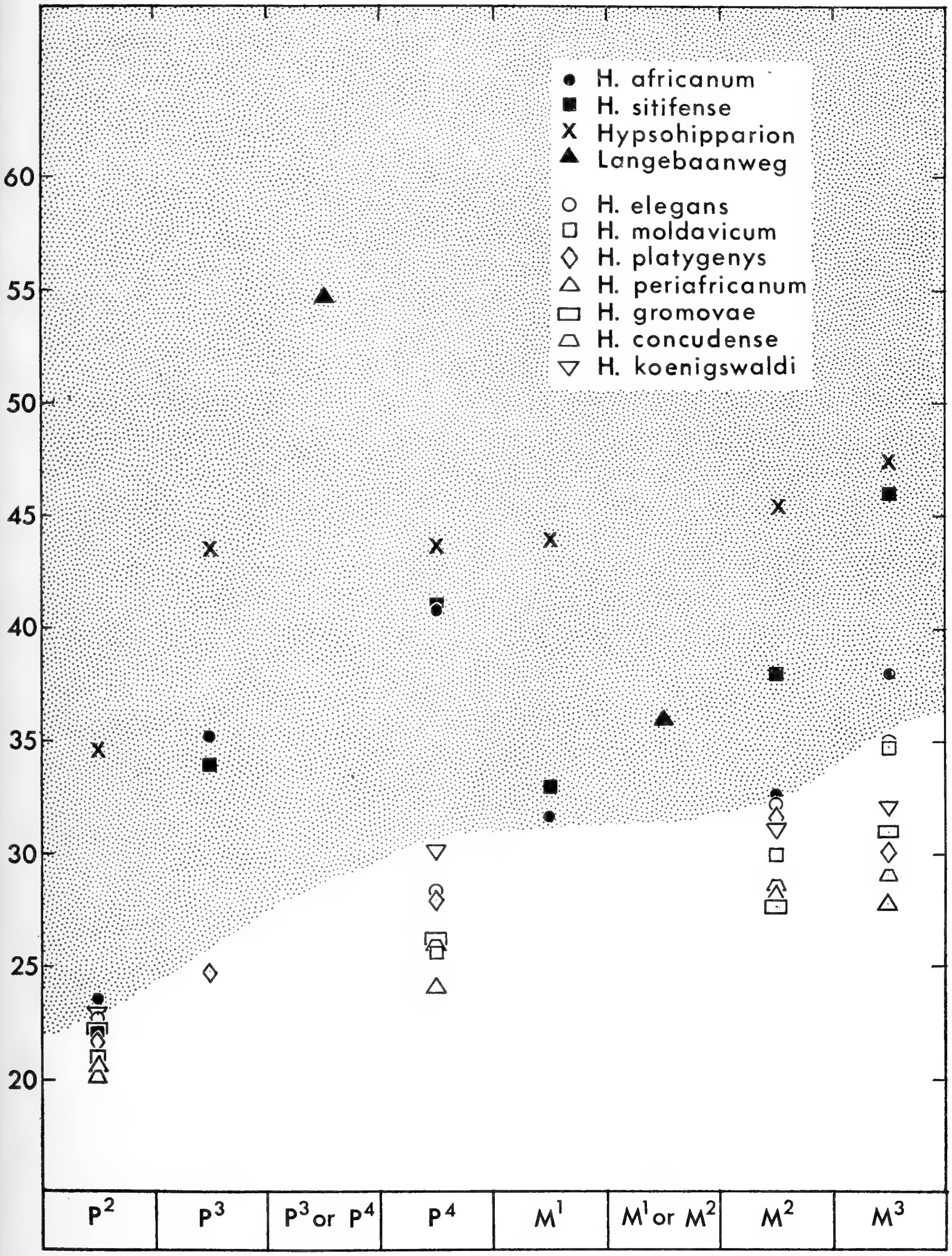

FIG. 12. Protocone length index in the various teeth of African and non-African *Hipparion* species.

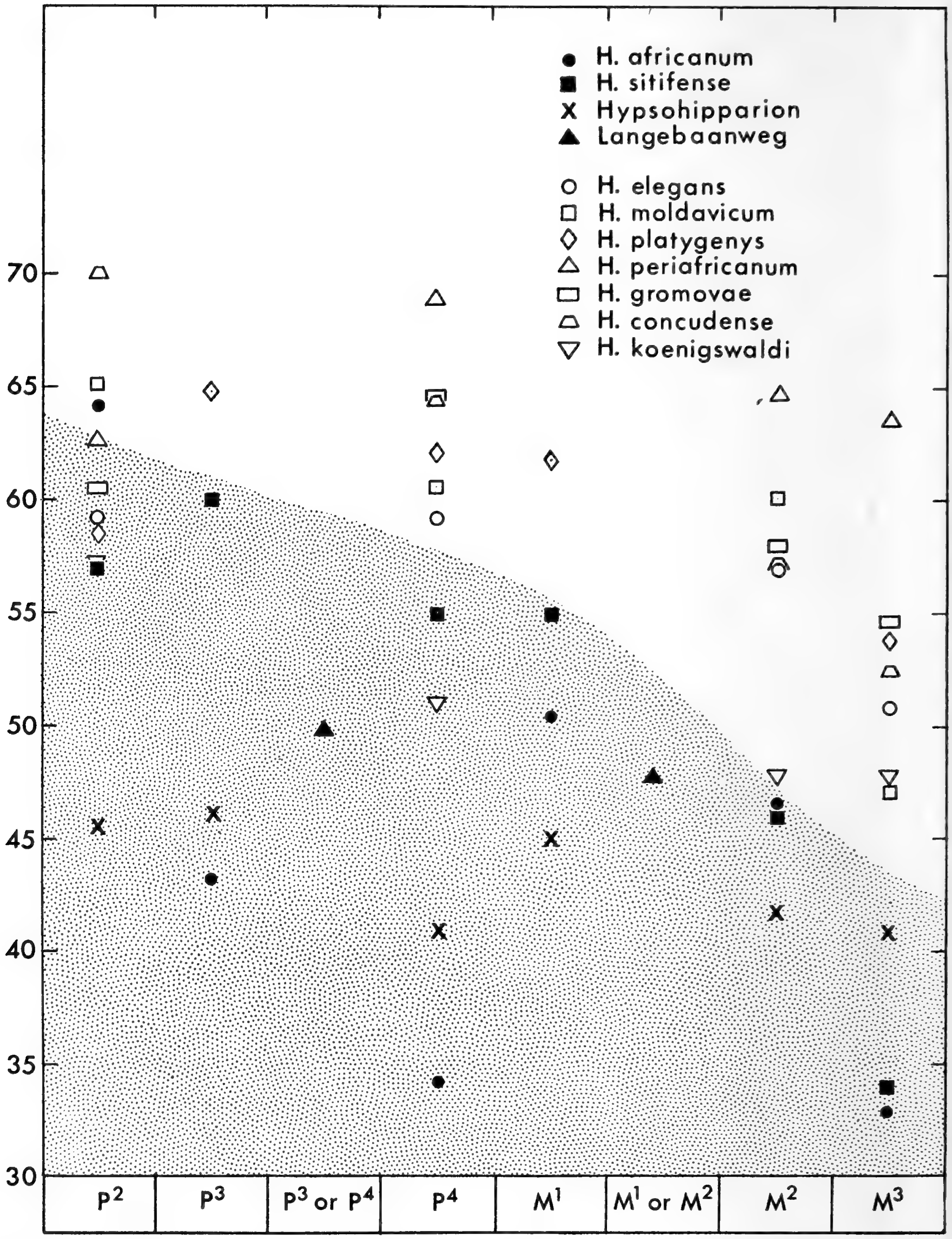

Fig. 13. Protocone shape index in the various teeth of African and non-African *Hipparion* species.

must be a limit to the former. The quantity of available enamel is fairly constant and probably limited, so that an increase in the complex pattern of the enamel will result in a thinning out of the plications. Eventually this would produce too weak a support for the triturating pressure required for hard grass. When this point is reached, the plications again reduce in number and the protocone lengthens as a compensatory mechanism.

Therefore, it is not always possible to ascertain from the small number of plications whether they represent a primitive condition corresponding to a humid environment, or whether they are secondary, resulting from a reduction under the influence of a hard grass food. Then other factors must be considered, e.g. the shape of the protocone, to solve the problem.

A directly comparable situation is encountered in the development of proboscidean teeth. Here an increase in the available grinding surface of the enamel ridges (lamellae) could represent the increasing plications in the teeth of the Equidae, especially as they are also oriented perpendicular to the grinding movement. This parallelism is also demonstrated in the hypsodonty of these two groups.

Hypsodonty

In the evolution of the Equidae most lines show a constant increase in the crown height of the cheek teeth. However, from *Merychippus*, in Miocene times, the progressive hypsodonty has advanced along two phyletic lines (*Hipparion* and *Pliohippus*) at a faster tempo, again under the influence of a general increase in aridity. The same observation has been made among Bovidae. It seems obvious that it is once more an adaptive response of the organism to the xerophytization of the diet.

The dietary changes involved in the evolution of Cenozoic hypsodont horses probably corresponded to a shift from browsing on softer herbaceous plants to grazing on harsh, siliceous grasses, which acted as abrasive agents on the teeth. These changes are, in turn, a consequence of an increasing aridity as has been clearly demonstrated for the Great Plains of America (Stirton, 1947). The association of widespread sandy deposits and of bunch grass of the *Stipidium* type, with the increasing aridity of this area is actually known to be contemporary with the development of hypsodonty from Lower Miocene times onward. This increased height of the crown has played an important role as a protective modification in the dentition. It is supposed, although impossible to prove from the fossil record, that a mutation or other factors, favoured an increase in activity of the odontoblasts and ameloblasts to lay down more dentine and enamel when the tooth was still in the formative stage. The root closure (fusion) may have been considerably retarded as well. Furthermore, it may be suggested that dry climate has influenced the teeth by necessitating some protective mechanism not only because of the harsh conditions of the grass, but also because of the sand mixed with it as a foreign substance. Stirton (1947) states that in the Great Plains area, a close inspection reveals much sand adhering to grass or lodged in between blades and stems, where it is blown by wind or splashed after thunder showers.

The double knot in the lower cheek teeth of the hipparionids displays three typical features:

(*a*) a primitive '*stenonis*' type, inherited from *Merychippus* and generally retained throughout the evolutionary sequence among American species;

(*b*) a more progressive, typical '*Hipparion*' type has been developed by most European forms; and

(*c*) the '*caballus*' type which was lately acquired, particularly in African representatives.

It has been suggested that the double knot of the lower teeth was shaped and typified under the influence of the protocone structure in the upper teeth, with which it is functionally linked in occlusion. There is good reason for developing a long, narrow metastylid parallel to an elongated, elliptical protocone, as is found in most African *Hipparion.* Here, the shape of the metastylid in particular, and consequently of the whole knot, conveys useful information about diet and climate. However, the correlation is probably not a simple one, because American *Hipparion* display an elongated protocone and a rounded '*stenonis*' type of metastylid simultaneously.

Total tooth structure

Upper teeth are rather compact. The outer enamel forms a fairly continuous and parallelipipedic structure, only grooved slightly by a small hypoglyph. The only weak structure which can be broken away from the tooth under excessive strain is the protocone, separated from the rest of the tooth by the internal depression. In the Langebaanweg material, this plane of fracture is noted in L935, L942, L945, L956, S.A.M.11722 and S.A.M.11724 (pls. 1, 7, 8, 9). It has been noted above that, with increasing dryness of the food, this weakness is largely corrected by the development of a narrow protocone closely adherent to the protoloph.

Lower teeth, on the other hand, are built on a very different pattern. The many conids and stylids are much more individualized: they are contiguous but are separated from each other by rather deep depressions right down to the base of the crown. These intervals are filled with cement, but it is softer than the enamel and does not always supply sufficient compensatory protection, as can be seen in many fossil teeth where the cement has disappeared. In drier environments, the hard food influences this structure of the lower teeth, demanding additional strengthening of the enamel-dentine pillars which are embedded in their cement coating to prevent both fracturing and excessive wear of the tooth. Support can be provided in two ways, either

(i) by reducing the depth of the internal and external depressions separating protoconid from hypoconid, metaconid from metastylid, and metastylid from entoconid, or

(ii) by additional stylids.

Reduction of the depth of the depressions is commonly observed. As has been stated previously, this occurs on the lingual surface by the development of a '*caballus*' type of double knot, while on the buccal surface it is secured by a broader connection between the two halves of the ectolophid.

The alternate solution lies in the construction of additional pillars: ectostylid and ptychostylid in particular, just in front of the external depression, and protostylid and hypostylid on the antero- and postero-external corners. Entostylids are occasionally developed in the postero-internal depression. In one particular case (a '*Stylohipparion*' Gar. Fluss no. 200, figured by Dietrich, 1942, pl. XIII, fig. 95), a strong additional pillar is seen between metastylid and metaconid.

The higher frequency of these additional pillars in milk teeth seems to have been necessitated by the lowness of the crown of these teeth and their softer construction. This is the obvious way to prevent too rapid attrition which cannot be compensated as there is no continuous growth of the tooth.

As suggested previously, enamel plications, shape and size of protocone, structure of the double knot, increased hypsodonty and additional pillars are many different methods of meeting the mechanical requirements of a tougher diet. They do not all necessarily develop together at a parallel tempo. Some of them are functionally linked but other elements develop compensatory roles so that all need not be present at one time. Therefore, no single element can give reliable information about climate, biotope and the quality of food, but an assessment of the whole picture and of the reciprocal values of the different features must be considered.

The extremities

Duerst (1926) has successfully demonstrated how a humid climate and a soft grass develop a heavier type of equid with broader extremities (eurysome type), while a leptosome type of a smaller, more slender animal with more gracile extremities tends to be built in drier biotopes characterized by a xerophyte vegetation. This seems to apply especially to metapodials which become relatively longer.

The progressive reduction in size and the disappearance of the lateral digits in equids, with the concentration of the whole body weight on the third metapodial, has always been interpreted as an adaptation to increasing speed in steppe surroundings. It has been repeatedly suggested that the high tempo of evolution of *Pliohippus* towards monodactyly is an expression of its drier habitats, while the lateral digits of African *Hipparion* are kept more or less functional right into the Pleistocene, probably because of a more humid environment.

THE UPPER MIOCENE AND PLEISTOCENE BIOTOPES OCCUPIED BY AFRICAN HIPPARIONIDS

Our knowledge concerning past climates and biotopical conditions in those areas where African hipparionids have been recovered is still inadequate.

The fragmentary information spans over a very long period of time (probably 10–12 million years) and is derived from a large continent where the climates have certainly been variable. Consequently it is not always possible to draw accurate conclusions from the collected data, nor is it possible often to correlate data from one site with those of another.

Furthermore, this information is deduced from fossil assemblages of which some are listed on the basis of debatable fragments, while others are wrongly identified. For example, at Olduvai Gorge, recent and more extensive collections will permit a better analysis.

Even where there is sufficient and accurately identified material, it should be remembered that a fossil specimen is not necessarily found in the typical habitat of the living form. It is well known that in periods of drought or volcanic eruptions (which have played such an important role in the Cenozoic sedimentation of East Africa, from Omo to Eyasi), animals have concentrated around swamps, temporary pools and tuffs, possibly fairly distant from their normal biotope.

This biotope is often less restricted than one imagines, and the adaptation of some organisms is quite fantastic. So, it seems futile to draw definite conclusions from the presence of one or even a few animals. Real associations must be considered to avoid misinterpretation of the presence of a species at a particular site.

(*a*) In the Upper Miocene, the Oued el Hammam faunal assemblage contained *Palaeotragus*, *Samotherium*, *Damalavus*, *Gazella*, *Dicerorhinus*, *Hippopotamus* and *Hyaena*. With slight generic differences, it corresponds very closely to the fauna of the East African plateau of today, and indicates the typical savanna with mimosa biotope of the tropics. According to Arambourg (1959), the presence of *Macaca* and *Cephalophus* in the contemporaneous deposit at Marceau suggests the proximity of forests. This is supported by the location of the deposit in a higher and already tilted portion of the Tellian Atlas, and by the lignite abundant in the deposit.

(*b*) The Lower and Middle Pleistocene faunal assemblages of the East African *Hipparion*-bearing sites clearly indicate the same type of steppe or plain and highland (mimosa) savanna environment, very similar to that of the present day, 'with a marked bias toward somewhat moister conditions in most cases' (Cooke, 1963). The main feature at Omo, Kaiso, Kanam, Olduvai I–IV and Eyasi is undoubtedly that of an open savanna. No true forest association is to be found in these areas, although forest strips and moist woodland occurred occasionally, as is indicated, for example, by the presence of *Nesotragus moschatus*. The cyclical and seasonal variation of the rainfall has provided more humid conditions at times, and consequently the development of swamps and (or) lakes in the lowlands, with very luxurious vegetation, are responsible for the abundant Suidae, Bovidae, Giraffidae, Elephantidae and Equidae. A swampy environment is explicitly suggested at Olduvai by *Aonyx*, and at Omo by *Kobus*. A lake shore or grassland adjacent to water is evident both at

Omo and Olduvai (e.g. *Hippopotamus*, *Omochoerus*) where this is also reflected by the nature of the deposit.

The presence of *Oryx* and *Beatragus hunteri* would suggest arid conditions prevailing in the locality.

Although most of the fauna are suggestive of plains or a plateau, *Tragelaphus nakuae* and *Dinopithecus brumpti* indicate that a mountainous biotope was probably part of the picture at Omo.

(*c*) In South Africa, forest and desert associations are similarly absent, and the prevailing feature remains that of a steppe or a savanna fauna. The Vaal River Gravels suggest a fauna of thornbush and grassland. The cave breccia—probably less representative of a true biocoenose—contains both open plains and dense bush-dwelling forms. It is believed that the rainfall varied considerably during the Pleistocene, with oscillations from 20% to 40% annually (Brain, 1958). The fossil forms represented there would have tolerated such changes. In any case, even in the driest conditions (Taung) well-watered bush valleys could be located at not great distances.

In conclusion, it may be stated in broad terms, that African Upper Miocene and Pleistocene *Hipparion* sites seem to have been areas of (dry to) moist savanna and grass steppe, or of open woodland with mixed savanna. It is not possible to define with any more precision the environment proper to *Hipparion* in this general biotope which extended over half of Africa for several million years. It is probable that local circumstances and features have directed the relationships and balance of the various species in particular areas: but as a whole, and in spite of replacement of species, the African fauna has maintained an essentially constant composition throughout late Cenozoic times, which indicates that the broad ecological pattern did not vary greatly from the Upper Miocene onwards. The main ecological feature, viz., the savanna, may at times have been extensively altered by moister climates producing swampy conditions and even patches of forest. Then later, it would be altered again by a rather low rainfall. Nevertheless, drastic changes probably never occurred. There seems little evidence of a true forest fauna or of conditions too dry to sustain a normal steppe biocoenose (Cooke, 1963).

EFFECTS OF BIONOMICAL CONDITIONS ON THE EVOLUTION AND THE MIGRATION OF AFRICAN HIPPARIONIDS

It has been generally accepted that the three-toed hypsodont *Hipparion* were typical steppe forms. The savanna biotope is commonly emphasized as an important equid environment of the late Tertiary in the Great Basin of the United States, and the vast reduction of this habitat is strongly suggested as a suitable explanation for the extinction of *Hipparion* by the end of the Hemphillian (Shotwell, 1961). The life span of *Hipparion* in North America, namely, Clarendonian-Hemphillian, corresponds rather precisely to the extension of the savanna or steppe biotopes in this area. The recent observations of Sondaar (1961) strengthen this view: at Nombrevilla, in Spain, where *Decennatherium*, *Aceratherium* and *Mastodon* were recovered together with *Hipparion*, there is good evidence for a steppe environment. However, it has become clear that *Hipparion* is not restricted to such narrow ecological conditions. Thenius (1950) interprets *H. gracile* as a forest-dwelling form, and Kurtén (1952), on the basis of the Chinese 'Pontian' fauna, enforced the necessity of a reconsideration of this hypothesis. Because of the almost identical frequency (13%) of *Hipparion* in both the *gaudryi* and *dorcadoides* faunas, characteristic, respectively, of the 'forested' or 'southern', and of the 'steppe' or 'northern' provinces (the classical distinction of Schlosser, 1903), it was suggested that the Chinese *Hipparion* thrived in various surroundings, or at least that the genus as such was not exclusively a steppe form. Furthermore, it is not possible to make a direct correlation between the geographical distribution of a particular species and its biotope. Of the eleven different species recorded by Sefve (1927), some are confined to one locality and others turn up in widely different areas; in some instances, up to four different species have been recorded from the same fossil pocket.

The adaptability of hipparionids explains their extraordinary diffusion both in North America and in the ancient world, from Upper Miocene times onwards. Ecological conditions influenced structural features in different and varying ways, often difficult to explain. A similar geographical distribution and even the simultaneous presence of different fossil forms in one particular pocket are compatible with slightly different ecological niches or habitats in a small vicinity.

Under favourable conditions, observations have often been made of the association of more massive animals (with larger skull, shorter limbs, longer lateral digits and strongly plicated enamel) with open forested areas, characterized by soft and wet ground and tender vegetation. Lighter forms (with slender and elongated limbs, reduced lateral digits and simpler enamel pattern, elongated and narrow protocone and increasing hypsodonty) are found in a more xerophytic environment. Outside Africa, *H. primigenium, theobaldi, crassum* are representatives of the former group; *H. elegans, longipes, moldavicum, proboscideum, matthewi* are typical of the latter.

In general, the various characteristics observed in the African *Hipparion* are clearly indicative of animals adapted to a rather xerophytic steppe environment, although this never seems to have been very severe, and was certainly not constant everywhere. It has been stated above that nowhere in Africa are *Hipparion*-bearing sites located in true desert areas, and none of the forms recovered shows the extreme leptosome type displayed by some North American forms, e.g. *H. whitneyi*.

Hipparion africanum, with its large skull, short and massive limbs with lateral digits well developed, and rather less hypsodont teeth, is probably, from the inadequate data available, the least adapted to a steppe environment. However, the enamel plications and the narrow protocone show an orientation in that direction. It is difficult to assess whether this moderate expression of the steppe features corresponds to the precocity (in time) of *H. africanum* or reflects a humid and even partially forested environment.

The moderate transverse flattening of the protocone, the few and simple plications, the absence of additional stylids, the reduced hypsodonty and the small dimensions of the teeth of *Hipparion sitifense*, as well as the development of the lateral digits, are to be interpreted in the same way, although the absence of skeletal remains does not permit evaluation of the degree of massiveness.

The postcranial skeleton of the African Pleistocene forms is practically unknown. However, quite a few metapodials have been recovered in the Olduvai Gorge (Tanganyika). They are not particularly slender, and the lateral digits are still well developed, but the absolute length of the third metapodial is quite remarkable (metacarpal: 217–223 mm.; metatarsal: 242–260 mm.), being 5–9% longer than the corresponding elements from Pikermi (table 13).

The typical features of the dentition are strongly marked hypsodonty, the fairly complicated enamel pattern of the 'mark' walls, and the elongation of the protocone, which may become very flattened. The extreme flattening corresponds to a spectacular development of the additional stylids. It seems clear that these features must be interpreted as a positive pattern of adaptation to a steppe environment throughout Africa. However, the absence of any extreme slenderness of the metapodials and the complicated enamel pattern seem to strengthen the conclusion drawn from the faunal assemblages, viz. that the xerophytic environments of the African *Hipparion* were never very severe.

In the absence of sufficient cranial and postcranial remains, and because of the vicarious role played by the different tooth structures in their adaptation, it is unnecessary to comment any further on the special features of every single group so as to define more precisely the particular environment of each. Discussion is further limited by the fact that climate and biotope seem to have been rather uniform over a great part of Africa, and have certainly not undergone drastic changes. Throughout the continent, African *Hipparion* reflect in their known morphology the vastly extended steppe or savanna environment with an absence of much aridity.

UNPUBLISHED MATERIAL FROM THE VAAL RIVER DEPOSITS, SOUTH AFRICA

Sydney-on-Vaal and Pniel

The exact location of these two specimens is not known (fig. 6). Cooke (1949) describes other material from these sites which are in the northern Cape Province.

Material:

MMK 431 —left M^3
MMK 5225—left M_1 or M_2

These specimens were diagnosed by the authors as belonging to *Hipparion* in the collection of equid material which was kindly sent on loan by the Director of the McGregor Memorial Museum, Kimberley, South Africa.

MMK 431 (pl. 1)

This is a left M^3 with fairly high crown, in an early stage of wear.

Half of the ectoloph: fairly deep, flattened arc, being angulated at the parastyle and slightly angulated at the mesostyle.

The *parastyle*: the lateral angle is chipped away at the occlusal surface but near the base it is seen to be prominent. It is rounded and projecting, and is separated by a fairly deep groove from the ridged anterior angle. The surface is very oblique, almost in the same plane as the anterior surface.

The *mesostyle* is partly broken. It is fairly large and rounded, and it has a deep groove.

The *metastyle* tends to be broad with a ridged lateral angle, a smaller ridged posterior angle and a slightly concave surface, which is oblique.

The *protocone* is isolated. It is very long, being about half the length of the tooth. Anteriorly and posteriorly, it is sharply angulated. Its inner surface is flattened, and the lateral, outer surface is wavy, presenting an elongated cigar shape.

The *protoconule* is short and has a flattened arc. Posteriorly it becomes markedly angulated and turns laterally to join the base of the pli caballin.

The *hypocone* is elongated and flattened. Its two sides are almost touching.

The *hypoglyph* is deep and circular, demarcating an angulated hypostyle.

The *hypostyle* is joined to the metastyle by a concave arc of enamel.

The *pli caballin* is long, with unequal sides almost touching the protocone.

The *prefossette*: the anterior wall has a small plication and a very deep, narrow pli protoloph which tends to separate the medial part of the prefossette. The posterior wall has shallow plications and a deep narrow pli protoconule which tends to separate the medial part of the fossette.

The *postfossette*: the anterior wall has an irregular shape, with one plication and a very deep and narrow pli postfossette, which tends to separate off a flattened portion of the medial part of the postfossette. The pli hypostyle is duplicated. It is fairly deep, tending to isolate the medial part of the postfossette. The anterolateral angle of the postfossette tends to form a rounded, almost isolated pillar.

MMK 5225 (pl. 1)

A left M_1 or M_2, probably M_1.

The tooth is partly fragmented, especially on its inner aspect.

The *protoconid* is partly broken mesially. It appears that the other wall is flattened. The protoconid is shorter than the hypoconid. The metaflexid is elongated, flattened and biconcave with rounded anterior and posterior ends.

The *metaconid* is broken away. Its outer wall appears to be a flattened arc.

The *parastylid* is partly broken but its posterior wall turns sharply inwards and almost touches the outer wall of the metaconid.

The *metastylid:* the outer wall is flattened in a mesiodistal direction. The entoflexid is elongated, flattened and anvil-shaped.

The *entoconid* is rounded and pillar-like, being almost completely separated.

The *hypoprotonocid groove* is deep and wide, being rounded internally. It has a narrow mouth laterally and a bulge posteriorly.

The *ptychostylid* is finger-like, projecting anterolaterally. The sides are almost parallel and it has a narrow base.

The *ectostylid groove* is a marked indentation, broad and shallow.

The *hypoconid* has a flattened, elongated outer surface with posterior parts tapering sharply inwards.

The *ectostylid* is an isolated triangular pillar, the outer wall being chipped at the occlusal surface, but it can be seen to be flattened near the root. The inner wall is flattened and meets the outer wall at a sharper angle. The two walls are separated anteriorly by a somewhat irregularly concave base. The inner wall of the enamel joins the metaconid.

The *metastylid* forms a distinctive broad arc near the base of the tooth where it is intact.

MMK 5225		MMK 431	
A–P length	*ca* 23·5	A–P length	22·3
Breadth	—	Breadth	21·1
Max. A–P length protoconid	8·1	Breadth/A–P	94·7
Max. A–P length hypoconid	12	Protocone length A–P	12·5
Max. A–P length metastylid	6·2	Prefossette A–P length	10·8
Max. A–P length entoconid	4·6	Prefossette breadth	8·3
Max. A–P length entoflexid	11·8	Postfossette A–P length	10·8
Max. A–P length metaflexid	6·8	Postfossette breadth	7·0
Breadth hypoconid	5·6	Protocone A–P/total A–P length	56·2
Breadth entoconid	4·1	Crown height	*ca* 70
Crown height	*ca* 40		

TABLE 15. Dimensions (mm.) of MMK 431 and MMK 5225 from the Vaal River Deposits.

Taxonomic status

The above two teeth are referred to *Hipparion* (*Stylohipparion*) *libycum* (see p. 387–92 for diagnosis).

MATERIAL FROM LANGEBAANWEG, CAPE PROVINCE, SOUTH AFRICA

DESCRIPTION OF HIPPARION TEETH

Milk dentition

Material:

S.A.M. 11717—right DM^3
S.A.M. 11718—right DM^2

*S.A.M.*11717 (pl. 2)

A right DM^3 in medium stage of wear with a thick layer of cement particularly on the inner side.

Half of the ectoloph: it is shallow and has a slight arc. It is sharply angulated at the mesostyle and slopes up into the parastyle.

Parastyle: the lateral angle is chipped but it is seen to project markedly in a lateral direction near the base of the tooth. The surface is oblique and not quite in the same plane as the anterior surface of the tooth. There is a marked groove. The anterior angle is rounded and forms a ridge.

The *mesostyle* is stumpy, projecting, and flanging at the surface. A fairly marked overlap exists anteriorly. The surface is rounded, not grooved. The sides tend to be parallel.

The *metastyle* is slight and rounded.

The *posterior ectoloph* has a vertical bulge at the centre of its surface.

The *protocone* is oval in a mesiodistal direction, with the medial side slightly more flattened than the other side. It is distinctly separated from the other cones by a thick layer of cement.

The *protoconule* is an elongated, flattened arc with a fringed effect.

The *protoglyph* is deep and wide with an irregular base.

The *hypocone* is elongated, with a rounded medial side and a flattened lateral side, tending to come to a point posteriorly. Anteriorly it is almost completely isolated by a very deep indentation of the hypoglyph. Opposite, there is an indentation tending to separate it from the metaconule. The metaconule also has a fringed appearance.

The *hypoglyph* has a broad mouth. Lateral to the mouth of the hypoglyph, the enamel shows a V-shaped indentation.

The *pli caballin* is long, narrow and arched, tending to touch the protocone. At the base of the pli anteriorly, there is a trace of a duplication of the pli.

The *prefossette:* the anterior wall shows two deep plications and a deeper, narrow pli protoloph which tends to isolate the medial part of the prefossette. The posterior wall of the prefossette shows numerous plications which are markedly complex. One of the plications adjacent to the pli protoconule is large and has become isolated, forming the typical island lateral to the base of the pli caballin, and wedged between the medial portion of the pre- and postfossette. The pli protoconule is deep and narrow, almost touching the medial wall of the paracone. The pli prefossette is deep and complicated with a bifid base, tending to isolate the posterolateral angle of the prefossette.

The *postfossette:* the anterior wall has numerous plications that are not as complicated as the posterior wall of the prefossette. The pli postfossette is deep and narrow, tending to isolate the medial part of the postfossette. The posterior wall of the postfossette shows numerous plications, the most lateral one being rather deep. The pli hypostyle is deep and angulated, tending to isolate the medial wall of the postfossette.

*S.A.M.*11718 (pl. 2)

This is a right DM^2 of the same individual as 11717.

The anterior portion of the tooth is broken away but the remainder of the tooth shows the same features as 11717 with the following differences:

(*a*) Protocone is more elongated and more oval.
(*b*) Hypocone is more oval.
(*c*) Pli caballin is bifid medially.
(*d*) Pli protoconule is more complicated, and is duplicated.

Dimensions	*S.A.M.*11717 (DM^3)	*Hypsohipparion* (DP^3–DP^4)
A–P	31·9	28–34
Transv. breadth . .	26·2	23–26
Height	21	28–34
	(medium wear)	(early wear)

TABLE 16. Dimensions (mm.) of Langebaanweg milk molar compared with '*Hypsohipparion*'.

The features which are observable on the two Langebaanweg milk molars are identical to the description given by Dietrich (1942) for the *Hypsohipparion* material (19 individual teeth and 2 maxillary fragments). The isolation of the hypocone and the shape of the protocone of Dietrich's (1942) specimen illustrated in his figure 162 is typical of the Langebaanweg milk teeth. The dimensions of the latter fall into the range of Dietrich's specimens (table 15).

Lower permanent dentition

Material:

P_2:	Left: L947, L1465D (pl. 6). Right: L939 (pl. 5).
P_3 or P_4:	Left: L937, L943 (pl. 6). Right: L941, L946, L956, L1451A, L1465A (pls. 5, 6, 8, 9).
M_1 or M_2:	Left: L944, L952, L959, L1448 (pls. 6, 8). Right: L948, L954 (pl. 7).
M_3:	Left: L938, L949, L1465B (pls. 8, 9). Right: L1465F (pl. 2).

One specimen, L1465C, a M_1 or M_2, is excluded because of its size and its fragmented appearance which does not permit recognition of any typical hipparionid features.

The following specimens seem to belong to single individuals:

1. L937, L939.
2. L941, L943, L944, L948.
3. L954, L957.
4. L938, L959.

Classification of specimens according to wear:

A. *Unworn or slight wear:* L949.

B. *Early to medium wear:* L947, L1465D, L939, L937, L943, L941, L946, L1451A, L1465A, L944, L952, L959, L1448, L948, L938, L1465B, L1465F.

C. *Late wear:* L954, L957.

General description

All the Langebaanweg specimens obviously belong to one group, viz. *Hipparion (Hipparion) albertense baardi* subsp. nov. The dimensions are presented in table 17. The following features are distinctive:

1. *Entoconid:* Usually in P_2 it is more or less flattened in a bucco-lingual direction. It tends to be more rounded or quadrangular in shape in P_3, P_4, M_1 and M_2. However, in early wear a slight indentation of the enamel produces a ridged effect on its lingual surface mesially.

2. *Metaconid:* It has a slight tendency to a bilobed formation due to a fairly marked indentation on the mesiolingual aspect, which is only recognizable in a very early stage of wear.

3. *Double knot:* This is of the '*caballus*' type which is usually found in African *Hipparion.*

4. *Metastylid:* It has a triangular shape with the right angle found distally on the lingual side of the entoflexid.

5. *Metaflexid:* It constantly shows unique invagination on both its anterior and its posterior walls.

6. *Entoflexid:* The buccal wall shows varying degrees of waviness (plications).

7. *Internal depression:* This valley, lying between the metaconid and metastylid, is very broad, shallow and irregular in P_2, while in P_3–P_4 it is broad but slightly deeper giving it a U-shaped appearance.

8. *Ectostylid:* This is constantly absent, but on L952 there is a small elongated thickening of the enamel at the crown-root junction. However this 'bud' does not arise from the cingulum but extends from the posterior root onto the crown just above the junction (pl. 8).

9. *Ptychostylid:* Present on P_2, and occasionally it is very well-developed. In P_3–P_4 there are irregular indentations on the bucco-distal aspect of the protoconid, i.e. in the valley (external depression) opposite the ptychostylid. Inconstantly, slight indentations are seen on the wall of the hypoconid in the depression.

In M_1–M_2 the ptychostylid and the indentations are not constantly present. In M_3 these features are both absent.

10. *Protostylid:* It may appear as a laminated ridge or as an isolated pillar. Usually, when present, it extends along the whole height of the crown.

Specimens	Crown height	Length	Breadth	Breadth / Length	Length, ant. int. depression	Length, post. int. depression	Length, ant. depression / Length post. depression	Length, post. depression / Tooth length	Max. breadth of entoconid (projection)	Entoconid length (incl. talonid)	Entoconid breadth / Entoconid length	Hypsodonty Index	Height / Length
P_2 L 947	41·1	33·5	17	50·7	9·2	16·2	56·8	48·4	5·4	10·1	53·3	41·3	123
L 939			14·9			16·8							
L 1465D ..	50		18·2			15·8			5·1	10·1	50·5	36·4	
P_3 or P_4: L 937													
L 941	62·3	29·9	16·2	54·2	10·1	12·9	78·5	43·1	6·6	9·7	68·2	26	208
L 943	65	28·3	18·2	64·4	10·5	12	87·5	42·3	4·7	9·6	49	28	230
L 946	53·3	29·1	17·8	61·2	8·9	13·2	67·4	45·3	6·1	9	67·7	33·4	183
L 957			18·7										
L 1451A ..	69	32	18·6	58·2	11·6	13·9	83·4	43·4	5·4	8·5	63·5	26·9	216
L 1465A ..	70	30	16·3	54·3	8·8	14·2	62·1	47	5	9·3	53·7	23·3	233
M_1 or M_2:													
L 944	64·4	28·4	15	52·8	10·1	11·1	91·1	39·1	4·2	10·7	39·2	23·3	226
L 948	62·7	29·3	15·7	53·7	9·9	11·8	84	40·2	4·5	11·2	40·3	25	214
L 952	48·5	26·5	16·7	63·1	7·8	9·7	80·3	36·6	5	9·2	54·3	34·5	183
L 954	47·2	28·6	18·5	64·7	8	11·3	71	39·5	5·7	8·4	68	30·3	165
L 959	50·5	26·5	15·1	56·9	7·3	10·6	68·9	39·9	4·9	8·3	59·2	29·9	190
L 1448	62·6	28·9	16·1	55·7	8·6	11·4	75·6	38·7	4·6	11·4	40·4	25·7	216
M_3 L 938		31·2	11·5	36·9		9·3		29·9	4	14·6	27·4		
L 949	67	24·3	13	53·4								19·3	276
L 1465B ..	53												
L 1465F ..	53	25·3	13·5	52·7	7·7	10·6	72·7	41·8	6	6·8	88	24·5	209
Abs. mean	57·6	28·8	16·4	56·4	9	12·3	76·1	41·0	5·2	9·8	54·8	28·8	236
Mean of indiv. teeth, P_3–M_2	60·7	28·9	17·1	58·9	9·1	11·7	78·0	41·3	5·2	9·5	54·8	28·2	205
Mean of teeth in slight to med. wear: P_3–M_2	65·7	29·6	16·6	56·2	10·1	12·6	81·0	44·1	5·1	9·8	52·3	25·4	221

TABLE 17. Dimensions (mm.) of Langebaanweg lower permanent dentition

It can always be observed as a prominent ridge along the mesio-buccal border of the tooth. It is constantly present on P_3–P_4, and always present on M_1–M_2.

11. *Entostylid:* One entostylid has been observed (L946) *in* the entoflexid on the bucco-mesial aspect of the entoconid. It presents as a distinct flattened enamel island (pl. 8).

12. *Talonid:* Bilobed.

Upper permanent dentition

Material:

P^3 or P^4: Left: L934, L936, L942, L1463, L1467E, S.A.M.11716 (pls. 1, 2, 5, 7).
Right: L955, L1467C, S.A.M.11722, S.A.M.11724 (pls. 1, 3, 7, 9).
M^1 or M^2: Left: L945, L953, L958, L1467B, L1467D, L1467H, S.A.M.11719 (pls. 3, 4, 9).
Right: L940/950, L951, L956, L1459 (pls. 1, 2, 4).
M^3: Right: L935 (pl. 9).
? premolar: Left: S.A.M.11723 (embedded in plaster for sectioning).
Cheek teeth: ?: L1785 (fragment).

The following specimens probably belong to single individuals:

1. L935, S.A.M.11722, S.A.M.11724.
2. L1473, S.A.M.11719.
3. L942, L945, L956.
4. L940/L950, L951.
5. L934, L953, L955, L1459.
6. L1467B, L1467C, L1467D, L1467E.

A completely unworn tooth, L1467A, recovered from the same site as L1467B–E and H (viz. Baard's Quarry), does not present the typical features of hipparionids. It shows the same type of fossilization as the other L1467 specimens, but, because of its exceptional dimensions (*ca.* 32 × 28 mm.), it is provisionally excluded.

The teeth are classified according to their degree of wear as follows:

(*a*) *completely unworn or just erupting:* S.A.M.11716.
(*b*) *early wear:* L1463, S.A.M.11719.
(*c*) *moderate wear:* L935, L940/950, L942, L945, L951, L956, L1467B–E, S.A.M.11722, S.A.M.11724.
(*d*) *advanced wear:* L934, L936, L953, L955, L958, L1459, L1467H.

General dimensions (mm.) of P^3–M^2:

1. A–P length: range of variation: 21·8–30·5
   Mean: 26·6
2. Transverse breadth: range of variation: 23·5–30·3
   Mean: 26·9
3. Breadth/length index: range of variation: 90·7–111·4
   Mean: 99·1
4. Hypsodonty:

Means	*Absolute crown height* (mm)	*Hypsodonty Index** (%)	*Height/length Index* (%)
All P^3–M^2	49·7	49·6	193
Unworn teeth	70	36·4	249
Early wear	63–69·2	42·3	233
Moderate wear	51·8	51·6	201

* The ratio between crown height and breadth.

To indicate the relationships between the Langebaanweg dimensions and those of other African *Hipparion*, the following data has been extracted from table 18 and summarized (table 19):

	H. africanum	*H. sitifense*	'*Hypsohipparion*' *albertense* (South Serengeti)	Langebaanweg
A–P length	23–27	19–23	25–31	26·6
Transv. breadth	20·5–26	18–22·5	24·5–29·5	26·9
Breadth/length	97·2		95·1	99·1
Height (unworn and early wear)	48–60		70	67·4
Hypsodonty index (unworn and early wear)	38·3–41·3			39·3
Height/length index (unworn and early wear) ..	223–240		249	238

TABLE 19. Comparison of dimensions (mm.) of Langebaanweg upper teeth with summary of data of other African *Hipparion*.

From these figures, it is clear that the Langebaanweg *Hipparion* has hypsodont upper teeth, but this hypsodonty has not reached the same degree as it has in the South Serengeti specimens.

Description of selected individual teeth:

Two specimens, an unworn left premolar (S.A.M.11716) and a left M^1 or M^2 (S.A.M.11719) in early wear, have been selected for detailed

	Height	Length	Breadth	Breadth / length	Protocone length	Protocone breadth	Protocone breadth/length (=Shape index)	Protocone length / Tooth length (=Length index)	Hypsodonty Index	Height / Length
L 934	42	27·5	28	102	10·8	5·2	48·2	39·3	66·7	
L 935	40·1	23·6								
L 936	27				7·8	4·6	58·9			
L 940/50	51				8·4	4	47·7			
L 942	54	29·2								
L 945	53	25·7								
L 951	56	25·5	27·2	107	9	4·8	53·3	35·3	48·6	220
L 953	43	24·1	26·8	111·4	11	5·2	47·3	45·6	62·3	
L 955	40	27·8	27·3	98·2	10	5	50	36	68·3	
L 956	45	24·2								186
L 958	23	21·8	23·5	107·8					102	106
L 1459	48·6	24·1	24·3	101	7·6	3·8	50	31·5	50	143
L 1463	69·2	28·9			8·3	4·2	50·5	28·7		239
L 1467B	54·2	24	26·1	108·9	9	4·4	48·9	37·5	48·3	226
L 1467C	56·8	30	28·8	96·1	9	5	55·6	30	50·8	190
L 1467D	54·2	26·5	28·2	106·4	8·3	4·8	57·8	31·3	52·1	204
L 1467E	52	28·9	30·3	104·9	9·4	4·2	44·7	32·5	58·2	180
L 1467H	45·9	30·5			9·3	4·8	51·7	26·5		151
S.A.M. 11716	70	28·1	25·5	90·7	12	5	41·7	42·7	36·4	249
L 11719	63	27·8	26·6	95·7	11	4	36·4	39·6	42·3	227
S.A.M. 11722	54	28·1								
General Mean	49·7	26·6	26·9	99·1	9·3	4·6	48·9	35·1	49·6	193
Mean of Individual Teeth, P_3 to P_4	51·6	28·7	27·9	98·3	9·6	4·7	49·9	34·8	56·0	214
Mean of Individual Teeth, M_1 to M_2	48·8	25·4	26·1	106·2	9·2	4·4	49·1	35·4	57·9	183

TABLE 18. Dimensions (mm.) of Langebaanweg upper permanent teeth.

description. They display the characteristic features of the other Langebaanweg specimens. The typical features of the whole group will be outlined below (see p. 376).

*S.A.M.*11716 (pl. 5)

A left P⁴, unworn.

Occlusal surface: Paracone and metacone are V-shaped and they are curved towards the medial side. The protoconule and metaconule are less angulated than the lateral cone and tend to curve less towards the medial side. The paracone and the metacone tend to overhang the fossettes.

Protocone: The cement is split off near the apex of the tooth. It is lozenge-shaped, completely isolated and the apex tends to curve in a buccal direction.

Shape: The tooth has medium hypsodonty. It has a gentle convexity from root to apex in a lingual direction. The styles stand out as clear costae, forming deep hollows between them. One-third of the distance from the occlusal surface, the hypoglyph becomes increasingly deep so that in the upper half of the tooth the hypocone becomes well demarcated.

Appearance of the tooth, sectioned just above the middle:

The *halves of the ectoloph* are deep and arc-shaped with a slight angularity at the mesostyle.

The *parastyle* is prominent. Most of the prominence is taken up by the lateral angle which is rounded. The surface, flattened but with a slight groove, is markedly oblique and almost in the same plane as the anterior (mesial) surface of the tooth.

The *mesostyle* is prominent, and, because its rounded surface is flanged, it overlaps the buccal depressions on both sides.

The *metastyle* is very slight (almost negligible), its rounded ridge decreasing in prominence from the occlusal surface to the root.

The *protocone* is slightly elongated and oval. Completely separated from the protoconule.

The *protoconule* is a flattened arc, angulating fairly sharply toward the pli caballin.

The *hypocone* is elongated posteriorly, rather flattened. There is no tendency to isolation. There is a deep V-shaped hypoglyph, and the hypostyle is angulated.

The *pli caballin* is bifid, the posterior process just touching the protocone.

The *prefossette:* There are plications which are so deep and complex that the centre of the prefossette is very narrowed and reduced. The anterior wall is plicated and the antero-lateral angle is knob-shaped, tending to be separated from the prefossette. The pli protoloph is deep and narrow, touching the very deep and narrow pli protoconule so that the medial portion of the prefossette is an almost isolated triangle. The plications on the posterior part of the prefossette are very deep and complex. One of the more medial ones tends to flange out to form an almost isolated irregular pillar just lateral to the base of the pli caballin and wedged between the most medial part of the prefossette and postfossette.

The *postfossette:* The plications on the anterior wall are also deep and complicated but not as numerous as on the posterior wall of the prefossette. The pli postfossette is deep and irregular-shaped, almost touching the base of the pli hypostyle, thus tending to isolate an oval portion of the medial part of the postfossette. Just lateral to the pli postfossette, the plications tend to isolate a small rounded pillar.

*S.A.M.*11719 (pl. 3)

A left M^1 or M^2.

It is slightly higher crowned than S.A.M.11716, and slightly less curved.

Half of the ectoloph: The paracone is deep and quadrangular-shaped, angulated at the mesostyle and parastyle.

The *parastyle* is prominent and narrow. The sides tend to be parallel, slightly widening at the base.

The *metastyle* is partly broken. It forms a slight ridge.

The *protocone* is elongated, oval and angulated anteriorly and posteriorly. It is completely isolated.

The *protoconule* forms a broad flattened arc, slightly angulated toward the pli caballin.

The *pli caballin* tends to be duplicated with the anterior tongue longer and almost touching the protocone.

The *hypocone* is rather short, tending to be separated from the metaconule. There is a very deep hypoglyph that is very broad-mouthed.

The *prefossette:* There are a few anterior plications, continuous with a deep narrow pli protoloph which tends to isolate the medial wall of the fossette. The pli protoconule is shallow. The plications tend to be absent. However, the original plications have become isolated to form an irregular circular island (prefossette loop) just lateral to the pli caballin and wedged between medial parts of the pre- and postfossette.

The *postfossette:* The plications tend to be worn away but it can be seen that they were complex anteriorly. The pli postfossette is very deep and touching the medial wall of the metacone. The pli hypostyle is deep, angulated and wide, and it has almost isolated the medial part of the postfossette.

Typical features of the upper teeth:

1. *Protocone:* The characteristic isolated protocone of *Hipparion* is observed in all the complete molars mentioned above. On L935, L942, L945, L956, S.A.M.11722 and S.A.M.11724, as well as on L1785, the lingual portion of the tooth has been broken away along the pre- and postprotoconal grooves and

does not allow any observations of the protocone. However, there is no reason to suppose that the protocone in these teeth displayed different features, and it is as umed that the description proposed for the other teeth applies to these specimens as well.

The protocone is elongated in a mesiodistal direction, and clearly shows angulation in those teeth not worn or in early stages of wear. It becomes more elliptical or oval in the later stages of attrition. Thus the shape index (breadth/length) varies from 36·4 to 58·9, with an absolute mean of 48·9 for all the teeth and an average of 48·3 for those teeth which have not reached an advanced stage of wear (table 14).

The length index ranges from 42·7 to 28·7, with a mean of 35·1 for all the teeth, of 34·7 for teeth in early wear, and of 35·7 for those in advanced wear. This smaller range of variation indicates that the actual length of the protocone does not change as much with wear as does the breadth, and that the apparent elongation of the protocone of the unworn teeth is more due to its narrowness than to its actual length.

Thus it is clear that the Langebaanweg specimens display this typical feature of African hipparionids (see p. 355). In so far as the few available specimens in varying stages of attrition from other African sites permit comparison, there seems to be a great similarity in the shape and dimensions of the protocone between *H. africanum* and the Langebaanweg *Hipparion.* The 'African' character is even more strongly expressed in '*Hypsohipparion*' *albertense* (tables 14, 20; figs. 12, 13).

2. The *hypocone* is commonly angulated, tending to isolate in early wear. Later it becomes more rounded, and the isolation from the metaloph is no longer discernible, the anterior groove tending to disappear. Parallel variations in the shape of the hypoglyph are observed with progressive attrition.

3. The *marks* are constantly closed.

4. The *plications* are numerous, profound and often bifurcated, especially in early or moderate stages of wear (e.g. S.A.M.11716, L940/950, L951). The enamel pattern is most complex on the posterior wall of the prefossette and on the anterior wall of the postfossette. The plications have been counted according to the method suggested by Gromova (1952), and the average plication formula for the Langebaanweg specimens has been established:

$$\frac{(0\text{–}3)-(1{\cdot}5\text{–}6{\cdot}5)-(0{\cdot}5\text{–}5)-(0\text{–}1)}{(1\text{–}2)}$$

There is a constant isolation of a prefossette loop in the lingual-distal angle of the prefossette, being bilobed and large in early stages of wear, and rather triangular and arrow-shaped in advanced wear (e.g. specimens L934, L951, S.A.M.11716; best example is the latter on pl. 5).

The pli caballin is constant, often double, in early and moderate stages of wear. It is not observed in very advanced wear.

In all these features there is not a clear basis of distinction between the

UPPER TEETH	Length	Breadth	$\frac{\text{Breadth}}{\text{Length}}$	Protocone length	Protocone breadth	$\frac{\text{Protocone length}}{\text{Tooth length}}$ (=length index)	$\frac{\text{Protocone breadth}}{\text{Protocone length}}$ (=shape index)
P^2	39	29	74·4	13·6	6·2	34·7	45·5
P^3	31	27·5	88·6	13·2	6·1	43·5	46·2
P^4	31	29·5	95	13·7	5·6	43·6	40·9
M^1	27·3	27	99	12	5·4	43·9	45
M^2	25	24·5	98·1	11·3	4·7	45·4	41·7
M^3	24·2	24	99	11·5	4·7	47·4	40·9
LOWER TEETH							
P_2	33	15·5	47				
P_3	29·5	17·5	59·3				
P_4	28·5	21·5	75·3				
M_1	27	18·5	68·6				
M_2	27	16	59·2				
M_3	26·5	15	56·6				

TABLE 20. Dimensions (mm.) of random teeth of '*Hypsohipparion*' *albertense* Dietrich (1942, table XIII, figs. 88–89) from South Serengeti. Measurements communicated by Dr. K. H. Fischer, 1964.

Langebaanweg material and the '*Hypsohipparion*' upper teeth from Serengeti, the plication formula of which is found to be very similar:

$$\frac{(0\text{–}4{\cdot}5)-(2\text{–}5)-(0{\cdot}3)-(0\text{–}2)}{(0\text{–}3)}$$

POSTCRANIAL EQUID REMAINS

At Langebaanweg seven phalanges have been recovered. Because of their equid structure it could not be excluded *a priori* that they belonged to *Hipparion* represented by the dental remains at the sites. It must be pointed out that a few teeth of *Equus* (to be described in another publication) have been recovered at these sites. However, they only constitute 10% of the total number of equid remains collected thus far. Consequently, because of the lack of comparable *Hipparion* remains from Africa, the Langebaanweg specimens are hesitantly included in this paper, more as a documentation for comparison by others than a positive contribution to the reconstruction of the *Hipparion* limb.

Material:

First phalanges: L1456, L1462A, L1462B, L1462C (pls. 10, 11).
Second phalanges: L1449, L1462D (pl. 12).
Third phalanges: L1444 (pl. 13).

All the absolute dimensions namely, length, diameter of the proximal and distal ends and of the median shaft are usually considerably larger than those (after Gromova, 1952) of the three species of *Hipparion* compared, i.e. *elegans, moldavicum* and *longipes* (table 21). There is virtually no overlap between the two series, although the highest figures for *H. longipes* (the largest of the three species) are sometimes very close to the lowest figures for Langebaanweg (table 22). Sondaar (1961) mentions one first phalanx of the forelimb third digit with an exceptional length of 69·8 mm. In Europe the highest *mean* is known from Eppelsheim, *H. primigenium*, with a length of 64·3 mm. and a proximal extremity breadth of 41·3 mm.

A comparison of the dimensions of the proximal end of the first phalanges from Langebaanweg with the breadth of the distal extremity of metatarsal III from Olduvai and South Serengeti (tables 12, 13) makes it obvious that the Langebaanweg specimens require a much broader metatarsal for articulation. For *H. longipes* the respective breadths of the distal end of metatarsal III and the proximal end of the first phalanx are 40 mm. and 42 mm. The mean distal breadth of the known specimens of metatarsal III from East Africa is 44·7, the maximum being 48 mm., the widths of the proximal end of the first phalanx at Langebaanweg are 50–56 mm. Therefore, either the Langebaanweg specimens belong to a slightly more massive limb of an *Hipparion* or else they belong to *Equus*.

Compared with *Equus zebra* and *burchelli*, the Langebaanweg specimens are larger in a number of dimensions, but there is a greater amount of overlapping

PHALANX I, THIRD DIGIT	Langebaanweg				*H. elegans*[a]		*H. longipes*[a]		*H. moldavicum*[a]		*E. zebra*[b]		*E. burchelli*[b] (ZIN 18411) (female)	
	L1462A	L1462B	L1462C	L1456	Fore	Hind	Fore	Hind	Fore	Hind	Fore	Hind	Fore	Hind
A. Total length	70·2	79·0	77	75·5	58·2	55·5	67·5	69·5	59·6	59·3	74	70	75	70
B. Breadth prox. end	56	55·5	54·0	50	30·6	30·8	41·7	42	32·9	34·6	44	44	48	50
B/A Index	79·8	70·4	70·2	66·2	52·3	55·4	63·2	60·4	55·4	60·1	60	60·5	64	71·3
C. A–P diam. prox. end	44	37·4	36·8	40	24·1	26·2	31·7		25·9	28	31	32	32·5	35
C/A Index	62·7	47·4	47·7	52·9	41·2	47	47·1	48·9	43·5	49·7	41·9	45·7	43·4	50
C/B Index	78·6	67·4	68	80	78·7	85·5	76	80·9	78·6	81·4	70·5	72·7	67·7	70
D. A–P diam. prox. artic. surf.	32	27·3	27	27	20·8	21·7	28·2		22·6	23·8				
E. Breadth distal end	43·3		41·4	41·2	25·9	26·2	34·8	34·5	27·7	28·9	37	37	40	40
E/A Index	61·7		53·7	54·5	44·4	47·4	53·5	49·6	46·4	50·3	49·1	50·8	53·4	57
F. A–P diam. distal end	27·4	25·9	23·2	25·1	15·5	16	21·5	21	17	17·3	22	21	22	22
G. Breadth shaft, median	41·9		34·1	36·6	12·3	22·2	28·7	30·3	22·8	24	27·5	27·5	32	32
G/A Index	59·7		44·3	48·5	35·6	39·1	42·6	43·6	38·2	42·1	37·2	36	42·7	45·7
PHALANX II, THIRD DIGIT														
			L1462D	L1449										
A. Maximum length			48·9	47·2	33·7	34·4	39·9	42	35·7	34·4	37	37	40	40
B. Length ant. surf. (median)			38·1	34·1	27·8	27·8	33·2	34·5	29·8	29·7	29·5	30	32·5	34
C. Breadth prox. end			51·6	47·8	30·2	30·6	39·1	39·5	32·8	33·1	42·5	41	46	46
C/A Index			105·6	101	89·3	89·3	98	94·0	92·2	96·6	114·7	111	115	115
D. A–P diam. prox. end			31·0	31·8	21·5	22·5	28·3		22·8	24·4	25·7	26·5	29	29
E. Breadth distal end				41·7	29·4	27·2	39·4	35	31·2	28·8	38·5	35	43	40
E/A Index				88·3	87·2	70·5	98·5	83·3	87·4	84·4	104	94·6	107	100
F. A–P diam. distal end			25·4	24·1	16·3	16·7	21·5	23	17·7	17·9	27	27	28	29
F/E Index				57·8	53·6	61	54·4	65·7	56·6	62·9	70·2	77·2	65·2	72·5
G. Min. breadth shaft			42	38·4	25·2	24·6	32·9	32·5	26·7	26·6	37	34·5	41·5	39
G/A Index			85·9	81·3	77·5	73·5	82·7	77·4	77·2	76·8	100	93·2	104	97·5

Table 21. Dimensions (mm) of the Langebaanweg limb bones compared with Eurasiatic *Hipparion* (means) and modern African *Equus* (*zebra* and *burchelli*).

[a] According to, or calculated from Gromova (1952).
[b] According to, or calculated from Gromova (1949).

and the dimensions are closer together than in the comparisons with the *Hipparion* above (figs. 14, 15; tables 22, 23, 24). The difference between the Langebaanweg and the *Equus* proximal phalanges average 6%.

The situation is less clear for the relative dimensions. The lowest index for Langebaanweg is constantly smaller than the highest for *burchelli*, and very often even overlaps *H. longipes*. The relatively smaller indices indicate that in the Langebaanweg specimens the length versus the breadth and the breadth versus the A–P diameter are somewhat greater than in *Hipparion* and *burchelli*. In these limited comparisons it seems that, to some extent, the Langebaanweg architecture differs from these groups.

It cannot be denied that the Langebaanweg measurements fit more satisfactorily within the range of *Equus*, but more material and comparisons are needed before this discussion can be taken further.

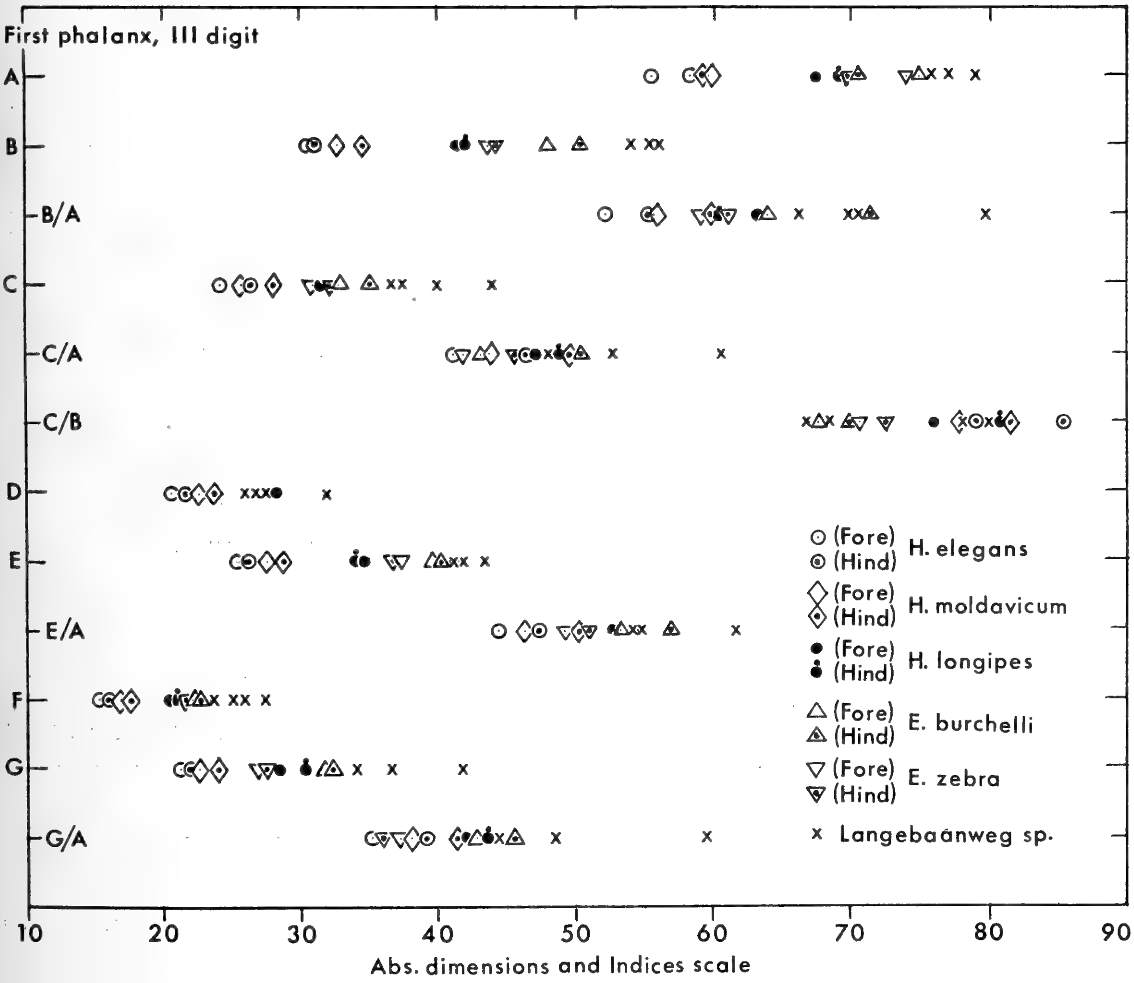

FIG. 14. Absolute dimensions and indices scale for the first phalanx of the third digit in various species of *Hipparion* and *Equus* compared with the Langebaanweg specimens.

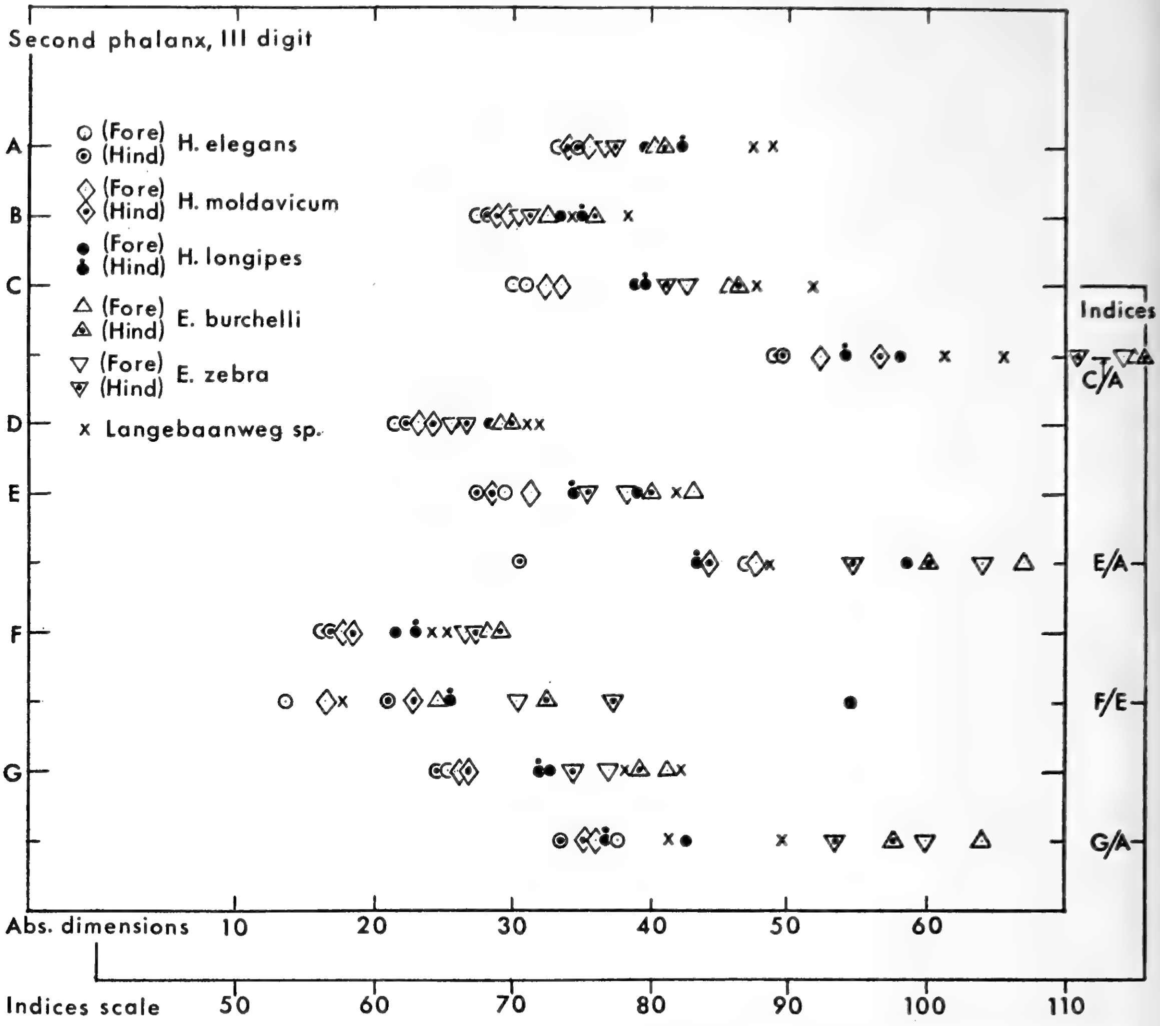

Fig. 15. Absolute dimensions and indices scale for the second phalanx of the third digit in various species of *Hipparion* and *Equus* compared with the Langebaanweg specimens.

ORIGIN AND DIFFERENTIATION OF AFRICAN HIPPARIONIDS

In recent years, it has become evident that Africa was more a true and independent centre of evolution and dispersion than a refuge for 'Pontian' Eurasiatic animal forms. Discoveries at different levels of the history of the mammals and in different regions have supported this concept proposed originally by Pilgrim (1941), and later vindicated by, *inter alios*, Arambourg (1959) and Cooke (1963).

Several independent observations have definitely established the original role played by Africa in the development of late Tertiary mammals in general, and have illustrated its contribution to the establishment of the 'Pontian' fauna in particular:

(i) The endemic evolutionary differentiation of the Proboscidea and Hyracoidea from the Oligocene onwards;

A. ABSOLUTE DIMENSIONS

	H. longipes (largest)	*Equus burchelli* (largest)	Langebaanweg (smallest)
PHALANX I			
Total length	69·5	*75·0*	70·2
Breadth prox. end	42	50	50
Diameter prox. end	31·7	35	36·8
Diameter prox. artic. surf.	*28·2*		27·3
Breadth distal end	34·8	40	41·2
Diameter distal end	21·5	22	23·2
Breadth median shaft	30·3	32	34·1
PHALANX II			
Maximum length	42	40	47·2
Length median ant. surface	*34·5*	34	34·1
Breadth prox. end	39·5	46	47·8
Diameter prox. end	28·3	29	31
Breadth distal end	39·4	*43*	41·7
Diameter distal end	23	*29*	24·1
Minim. breadth shaft	32·9	*41·5*	38·4
PHALANX III	*H. moldavicum*		
Anterior length	54·1	47·5	61
Maximum breadth	54	59	72

B. INDICES

PHALANX I	*H. longipes*		
Prox. breadth/length	63·2	*71·3*	66·2
Prox. diam./length	*48·9*	*50*	47·4
Prox. diam./breadth	*80·9*	*70*	68
Distal breadth/length	53·5	*57*	53·7
Breadth med. shaft/length	43·6	*45·7*	44·3
PHALANX II			
Prox. breadth/length	98	*115*	101
Distal breadth/length	*98·5*	*107*	86·3
Distal diam./breadth	*65·7*	*72·5*	57·8
Minim. breadth shaft/length	*82·7*	*104*	81·3

TABLE 22. Comparison of dimensions (mm.) and indices of Langebaanweg smallest phalanges with the largest of *H. longipes* and *E. burchelli*. The italicized figures indicate those dimensions in which the Langebaanweg specimens are smaller.

PHALANX III	Langebaanweg	*H. medit.* (Pikermi)	*H. elegans*		*H. moldav.*		*E. burchelli*	
			ant	*post*	*ant*	*post*	*ant*	*post*
Length ant. surface	61	50	45·8	47·2	51·8	54·1	46	47·5
Maximal breadth	72	55	46·3	44·2	54	43·4	59	58·5
Index B/L	118	110	101·1	93·6	103	78·9	128	123

TABLE 23. Dimensions (mm.) of phalanx III of Langebaanweg and of some Eurasiatic species and *E. burchelli*.

	Hipparion		*Equus*		Langebaanweg			
	elegans	*moldav.*	*cab* s.l.	*zebra*	L 1444	L 1444		
					L 1449	L1462D		
Index of length Phal. III, 3d digit/Phal. II	ant. 135·9 post. 140·1	145·1 157·3	116·4 118·8	110 116·9	127	123		
Index of length III/I	ant. 78·7	86·9	64·2	57·6	L1444	L1444	L1444	L1444
	post. 85	91·2	66·4	61·3	L1462A	L1462B	L1462E	L1456
					85·3	75·8	77·7	79·3

TABLE 24. Comparison of relative lengths of phalanges.
(In the case of Langebaanweg indices have been calculated from the possible associations.)

(ii) the presence in the Lower Miocene of East Africa and in the Upper Miocene deposits of North Africa of a complete specialized faunal assemblage with typical African characteristics before parallel diversification took place in Europe;

(iii) the constant specific differences between comparable Pontian Eurasiatic and African forms; and

(iv) the African pre-Pleistocene differentiation of Bovidae with the evidence of the local origin of Cephalophini, Neotragini and probably the Alcelaphini (Wells, 1957).

It is suggested that, because of the stability of its climate, its geography and its vegetation, Africa has provided a suitable habitat throughout the Tertiary. Furthermore, groups have evolved and later have developed parallel forms. Elsewhere, these have become extinct, but survival was favoured in Africa. Even in modern times this seems to be the case, e.g. the Proboscidea, Giraffidae, Artiodactyla, and Anthropomorpha. The surviving species, far from being newcomers and refugees from outside, are local representatives of a fauna which has disappeared elsewhere.

Arambourg (1952) and Cooke (1960), *inter alios*, demonstrated that the Plio-Pleistocene forms of elephants may have differentiated within the continent of Africa, paralleling the steps of progress observed elsewhere, but not necessarily linked to Eurasia by periodic invasions as was previously thought.

Analogous circumstances may have influenced the origin and the differentiation of the hipparionids. There is abundant evidence that *Hipparion* evolved in North America from some *Merychippus* stock in Miocene times. Migration probably took place at a rather rapid pace, *Hipparion* being found on both sides of the Mediterranean basin before the end of the Miocene. *Hipparion* has been recovered from brackish water deposits dating from the Sarmatian in the area of Sebastopol (Borissiak, 1914) and Istanbul (Chaput and Nafiz, 1934; Chaput and Gillet, 1938). It is also known from the Upper

Tortonian Beds in the Rhone Valley (Denizot, 1939). Villalta and Crusafont-Pairo (1946a, b, c; 1947; 1948) have described *Hipparion* from the Vallés–Penedès area in Catalonia, in continental and brackish water deposits intercalated in sediments ranging from the Burdigalian to the Tortonian, with *Hipparion* appearing in the Upper horizon (Vallesian, parallel to the Meotian of Eastern Europe, i.e. Upper Sarmatian). In the basin of Teruel, *Hipparion* was recently found to appear in Los Algezares in some gypsum intercalation of the middle light-red clayish deposit overlying the Los Monotos series, dated as the Vindobonian (Sondaar, 1961).

Parallel to these occurrences, and probably very close to the last one in the chronological sequence, hipparionids have been recorded in the Upper Miocene of the Maghreb, i.e. *H. africanum* (Arambourg, 1959) from Oued el Hammam and Marceau.

It is still not known which Atlantic or Pacific bridge the hipparionids used to invade the Old World. The only reasonable assumption which has been proposed is that the migration route probably lay very much to the north. The absence of any important migration of Camelidae and Antilocapridae from America, or of hyaenas, antelopes and giraffes to America, provide good evidence in support of this high latitude of the migratory passage (Simpson, 1947). On the other hand, and as a confirmation, the most ancient Old World *Hipparion* seem to have been much better adapted to a humid and forested biotope of temperate, or even cold, climates than most of the American forms, which evidence a drier and steppe environment. Rather than indulging in some fantasy that a direct connection between America and Africa existed by way of a hypothetical chain of islands across the North Atlantic (Joleaud, 1919a, b), it seems more reasonable to accept the normal Bering route which certainly meets the climatic requirements of the migrants.

Furthermore, in the present state of our knowledge, it is neither possible to formulate any conclusion about those species of *Hipparion* responsible for the origin of the African group, nor to reconstruct the phyletic sequence of African *Hipparion.* The fact that *H. africanum* is found contemporaneous with, or possibly prior to, every other European form and that it already shows typical African differentiation, refutes a European origin of the group from any of the known 'Pontian' species. On the other hand, and for the same reasons, there seems at present to be no possible way of establishing an African origin for the European hipparionids. However, the metapodials of *H. africanum* are rather strong and the lateral digits are well-developed, which must be interpreted as 'primitive' features, less specialized than in most of the early Eurasiatic forms. But other characters, e.g. the articulation of the external cuneiform with the second metatarsal only, a typical mechanical adaptation to tridactyly, show more primitiveness in the relatively contemporaneous *H. catalaunicum* (Pirlot, 1956). It seems that here there is evident some expression of an independent mosiac pattern of evolution in different (Eurasiatic and African) groups. Although they obviously descend from a common ancestral stock, they have been precociously isolated on different continents and have developed their independent stages of evolution.

For several reasons it is not possible to depict accurately the actual evolutionary development of the African *Hipparion*. As has been stated previously, the fossil record is rather poor. At more than thirty sites where Pleistocene hipparionids have been recovered, the available material consists almost exclusively of isolated teeth, and virtually nothing is known of the skeleton. Furthermore, because of the plasticity of the group, and of the fluctuating character of many features, which seem to be highly adaptive to ecological requirements, it would appear hazardous to reconstruct artificially an orthogenetic series. Gromova (1952) states that the diversity among Old World hipparionids usually remains at the level of a particular genus and does not exceed specific differences. On the basis of our present knowledge, this typifies the African representatives of the group: overall dimensions, proportions, size of the teeth, plications of the enamel, development of stylids, elongation of the protocone, preorbital fossae and development of lateral digits. Most of these features are readily adaptive and susceptible to functional interpretation under climatic and ecological circumstances.

On the other hand, it cannot be denied that parallel to the ecological adaptation which has been emphasized previously, some general and fairly continuous trends have characterized the evolution of the hipparionids throughout the world. From *Merychippus* onwards, in late Cenozoic times, the various groups have shown a permanent tendency to

(*a*) increased hypsodont dentition;
(*b*) lengthening and flattening of the protocone;
(*c*) reduction of the external depression in the lower teeth;
(*d*) development of additional stylids; and
(*e*) evolution of the double knot in three different but constant directions, i.e. towards a '*stenonis*' type in America, towards a '*Hipparion*' type in Eurasia, and towards a '*caballus*' type in Pleistocene Africa.

There is insufficient evidence to state that the reduction of lateral digits and the elongation of the third metapodials have obeyed a clearly directed evolutionary trend. The enamel pattern has not been controlled by any constant progressive influence, but it has only responded to the changing ecological conditions.

There is little doubt that these trends have been developing on more or less parallel and independent pathways and at different and varying speeds along the several lines, with the resulting mosaic type of differential radiating evolution.

For the reasons stated earlier in this paper, the degree of relationship between *Hipparion africanum* and the Pleistocene stock of African *Hipparion* is not obvious. There is a great gap in our record, and this is not sufficiently bridged by the fragmentary remains of *H. sitifense*. Therefore it is difficult to appreciate to what extent the distance between *H. africanum*, *H. sitifense* and the Pleistocene forms illustrates the chronological or the phyletic separation.

All Pleistocene African *Hipparion* show a marked progression in the expression of trends (*a*), (*b*) and (*d*) above; and together with the special orientation of trend (*e*), this vindicates their common origin and their genetic homogeneity.

It is suggested that the 'African features' and the more stable biotope are responsible for the prolonged presence of *Hipparion* in Africa during the Pleistocene. However, the differential expression of these trends along various lines of evolution allowed for some differentiation during this period.

A basic group, represented by '*Hypsohipparion*' and the Langebaanweg specimens, is characterized by a greater conservatism in the building of additional stylids: the ectostylid is constantly absent. The flattening of the protocone and the hypsodonty are strongly manifested in '*Hypsohipparion*', but are less marked at Langebaanweg. This basic group seems to be restricted to the Lower Pleistocene (the basal grey tuffs of Serengeti and the archaic forms at Langebaanweg).

'*Stylohipparion*' is more advanced in the expression of additional stylids: the constancy of the ectostylid indicates a group subjected to a particularly clear trend of evolution ('*Entwicklungswucht*' of Dietrich, 1942) in the process of building a new *Hipparion* form. This successful group has rapidly extended throughout the continent, being found in Lower and Middle Pleistocene deposits from the Maghreb to the northern Cape Province, and possibly differentiated on a geographical basis. The oldest record derives from North Africa. It is not impossible that the group migrated eastward and then southward, and, after being widespread throughout Africa, became extinct first in North Africa during the Lower Pleistocene, then in East Africa where it is still found in the Middle Pleistocene deposits.

TAXONOMIC STATUS OF THE AFRICAN HIPPARIONIDS

Family **Equidae** Gray 1821

Sub-family **Equinae** Steinmann & Döderlein 1890

Elongated face with completely closed orbits. Molar teeth, at first moderately, then later strongly hypsodont, with closed valleys, the external portions of which become isolated in the shape of pits, called fossettes or marks. Abundant cement layer on the outer surface and in all the hollows of the tooth. Complete homeodonty, the largest tooth being P_2 of a triangular prismatic shape, pointed forwards. Ulna is first fused with the radius; however, later in the development, it is reduced to its proximal portion (olecranon process), which has the appearance of a mere apophysis of the radius. Limbs are tridactyl in primitive forms, with complete lateral digits although they no longer reach the ground, except during galloping, when they become functional. In advanced forms, however, limbs are monodactyl, and the lateral metapodials are reduced to small splints, eventually only persisting in their proximal portion. Unguligrade.

HIPPARION de Christol 1832

Face is relatively short, with profound lacrimal fossa. Prismatic hypsodont molars, of moderate height, slightly curved, with more strongly plicated enamel pattern than in *Equus*. The protocone pedicle has narrowed, isolating the protocone, giving the appearance of a column which is attached to the protoconule only at its base. On its occlusal surface, the protocone shows an island of dentine, circled with enamel, of a rounded or oval shape. The enamel of the fossettes is rather strongly plicated. Upper and lower incisors show a typical mark. Metapodial moderate to long. Persistent tridactyly; the lateral digits are strongly developed and more closely related to the third metapodial than in *Merychippus*.

Pomel (1897) included in his definition that the lateral metapodials are not very different from those of *Equus*, but they broaden distally into an articular head; there are three phalanges, the most distal not reaching the ground.

Hipparion africanum Arambourg 1959

Hipparion sp. Arambourg, 1951: 2464, Arambourg, 1954: 295.
Hipparion africanum Arambourg, 1959: 75, Pl. 10, 11, 12, 13, 16, fig. 7.

'Hipparion with skull of great dimensions, but with limbs of moderate size and heavy extremities. Face and snout elongated; nasal aperture long and broad; orbits far back; preorbital fossae long, simple, distant from orbit. Dental series of moderate size: P^2–M^3 = 141 to 154 mm. Upper cheek teeth with strongly plicated enamel; compressed protocone, elliptical or lenticular. Cingular formations developed on lower milk teeth. Limbs are relatively short, with strong metapodials, in which the lateral digits are still well-developed.' (Translated from Arambourg, 1959, p. 95.)

Hipparion sitifense Pomel 1897

Hipparion sitifensis (sic.) Pomel, 1897: 14, Pl. 1, figs. 11–15, pl. 2, figs. 9–10.
Hipparion sitifense Pomel, Arambourg, 1956: 817, pl. 26, figs. 1–5a.
Hipparion gracile [*Non*] Kaup, Thomas, 1884: 10, pl. 2, figs. 1–3.
Hipparion crassum [*Non*] Gervais, Thomas, 1884: 10.

Hipparion characterized by its small teeth (A–P and transverse dimensions of P^3–M^2, *ca.* 19 mm.), little hypsodont and markedly curved in the median plane. The upper teeth have a flattened protocone, completely independent from the protoloph right down to the base of the tooth. The enamel plications are few and simple. The lower teeth possess no ectostylid. The lateral digits are well-developed.

Hipparion (*Stylohipparion*) *libycum* Pomel 1897

Hipparion ? libycum Pomel, 1897: 8, pl. I, figs. 1–7, pl. 2, figs. 11–12.
Hipparion massoesylium Pomel, 1897: 11, pl. 1, figs. 8–9.
Hipparium[1] (sic) *ambiguum* Pomel, 1897: 15, pl. 2, figs. 2–4.
Hipparion crassum Gervais, Solignac, 1927: 756.
Hipparion steytleri van Hoepen, 1930: 21, figs. 14–19.
Eurygnathohippus cornelianus van Hoepen,[2] 1930: 23, figs. 20–22.
Stylohipparion hipkini van Hoepen, 1932: 31, figs. 14–20.
Stylohipparion steytleri (van Hoepen), van Hoepen, 1932: 33, figs. 21–23.
Notohipparion namaquense Haughton,[3] 1932: 421, text-fig. 5.
Libyhipparion ethiopicum Joleaud, 1933: 7, pl. 1, figs. 1–4, 6–8, 10–12.
Equus (*Hippotigris*) sp., (*pro parte*)—Joleaud, 1933: 25, pl. 1, figs. 9 and 13.
Libyhipparion steytleri (van Hoepen), Joleaud, 1933: 12.
Stylohipparion cf. *albertense* (Hopwood), Hopwood, 1937: 130.
Stylohipparion, *Notohipparion*, *Libyhipparion*, Dietrich, 1942: 98, pl. 13, figs. 91–95, pl. 14, fig. 99 *pro parte*, pl. 15, fig. 105, pl. 16, fig. 109.
Stylohipparion albertense (Hopwood), Arambourg, 1947: 303, pl. 10, fig. 3, pl. 11, figs. 3–5.

Diagnosis:

Three-toed equid with rather hypsodont cheek teeth with a strongly developed ectostylid, particularly constant on P_4 and M_1. Typically the ectostylid is broad in the centre and narrowed at each end, the greater length being mesiodistally and antero-lingually orientated. The upper teeth show the typical 'African' features, namely, complex enamel plications of the 'mark' walls, and the narrow elongated protocone.

Hipparion (*Hipparion*) *albertense serengetense*, subsp. nov.

Hipparion albertensis (sic) Hopwood, 1926: 17, fig. 4.
Hypsohipparion albertense (Hopwood), Dietrich, 1942: 97, pl. 4, fig. 39, pl. 13, figs. 87–90, 93b, 96, 97; pl. 14, figs. 101–104, pl. 15, figs. 106–108, pl. 16, figs. 110, 112; pl. 20, fig. 160.
Equus (*Hippotigris*), Arambourg, 1947: 306.
Stylohipparion albertense (Hopwood) (*pro parte*) Arambourg, 1947: 306.

Diagnosis:

Three-toed equid with very hypsodont teeth (the M^3 of which reaches a crown height of 80–90 mm.). The lower teeth are characterized by the constant absence of the ectostylid. The protocone is very elongated, the cement is very thick, the enamel plications being complex. The dental series is short, average length being 156 mm.

Hipparion (*Hipparion*) *albertense baardi*, subsp. nov.

Type specimen: L946 (pl. 8) in the S.A. Museum, Cape Town.
Paratypes: L951, S.A.M.11717 (pls. 4, 2) in the S.A. Museum, Cape Town.
Type site: Baard's Quarry, Langebaanweg, C.P.

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[1] It must be a misprint. Everywhere else, except in the title, Pomel writes *Hipparion ambiguum*.

[2] This is tentatively included here on the basis of our belief that this symphysial fragment is referable to other *Stylohipparion* specimens from this area.

[3] This may prove to be a transitional form between the typical *Hipparion* and the more progressive *Hipparion* (*Stylohipparion*).

Diagnosis:

Three-toed equid with rather hypsodont teeth, about 70 mm. crown height. The lower teeth are characterized by the constant absence of the ectostylid and by a tendency to form other additional stylids, especially protostylid extending along the total height of the crown. The protocone is elliptical but less elongated than in *serengetense*, enamel is thin and plications are complex.

DISCUSSION

1. THE AFRICAN NON-PLEISTOCENE HIPPARIONIDS constitute one genus (*Hipparion*) and two species (*africanum* and *sitifense*). The lack of marked affinity to any of the Pleistocene forms which constitute a homogeneous unity precludes any consideration of this group in terms of the subgenera proposed for the Pleistocene forms.

2. THE AFRICAN PLEISTOCENE HIPPARIONIDS constitute a certain unity marked by the characteristics of the genus *Hipparion*. Furthermore they have in common a number of 'African features' which distinguish them from the non-African forms. Nevertheless these different features do not necessitate generic distinction.

Within the group there exist variables of differing degrees of importance.

The most obvious differentiating characteristic is the presence or absence of ectostylids. The evolutionary trend and ecological adaptation of this feature have been discussed (pp. 331, 332, 333) and it is considered that it constitutes a differentiation at the subgeneric but not generic level. The statistical constancy of absence or presence of this feature within groups otherwise identical indicates that consideration must be accorded on both a non-generic and a non-specific basis. Consequently the African Pleistocene *Hipparion* are subdivided into two subgenera, viz.

Hipparion (*Hipparion*) de Christol 1832, and
Hipparion (*Stylohipparion*) van Hoepen 1932.

3. THE CONSIDERATION OF THE SPECIES of *Hipparion* (*Stylohipparion*) is beset with the obvious difficulty of the paucity of the material available. Previous workers, faced with the same problem, have either cautiously avoided speciation or unjustifiably proposed species that are void, e.g. Van Hoepen, 1932—*steytleri*, *hipkini*. Arambourg (1947, 1956, 1959) refers to *libycum* only when he is discussing the North African Pleistocene material; otherwise he generalizes to the extent of using the generic (subgeneric) name *Stylohipparion* without species determination. We concur with this cautious attitude. We recognize that material referable to this subgenus has been recovered from three different geographical areas, namely, the Maghreb, East Africa (incl. Omo) and South Africa. Joleaud (1933), also aware of the geographical distribution, recognized in his new genus *Libyhipparion* three

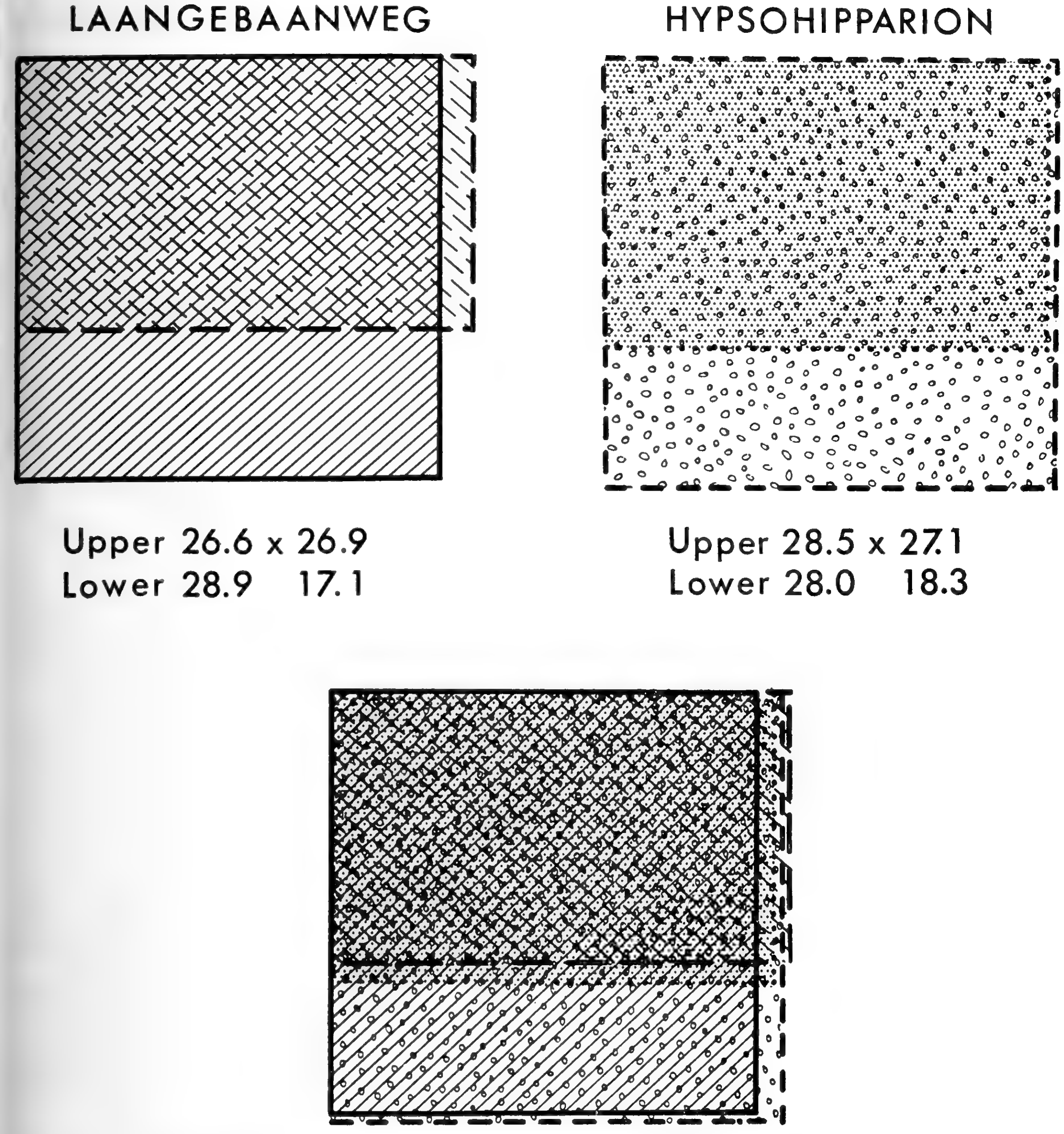

FIG. 16. Diagrammatic superimposition of an upper and a lower molar tooth of the South Serengeti '*Hypsohipparion*', and the Langebaanweg *Hipparion.*

species, viz. *libycum*, *ethiopicum* and *steytleri*. However, despite the differences of the localities, the wide range of variation within the small amount of available material does not provide the evidence for species separation.

Comparison of the various 'diagnoses' provided by Hopwood (1937), Arambourg (1947), and Cooke (1950), and reference to descriptions by Pomel (1897) and Joleaud (1933) indicate quite clearly that no true, clear-cut diagnosis is possible. Therefore, it is proposed to extend Arambourg's generalized usage of *libycum* to cover all the material included in this subgenus, but with the awareness that subsequent discoveries may bring to light information to highlight the differences of locality on a subspecies level.

4. A better situation exists with reference to *Hipparion* (*Hipparion*) which includes a portion of the material from South Serengeti (i.e. '*Hypsohipparion*' Dietrich) and the Langebaanweg specimens.

The dimensions and the main features (fig. 16) of the teeth from both areas are almost identical. However, there are differences in those features which emphasize the 'African' character of the dentition; namely, the hypsodonty, the elongation and narrowing of the protocone (tables, 16, 19, 20; figs. 12, 13). For both of these characters the Serengeti material displays a more progressive stage. Furthermore the latter also exhibits a thicker cement. These differences, although constant, do not constitute sufficient grounds for species separation. Therefore the species *albertense* is retained for both groups. Taking into consideration the ecological adaptation of these features, it is proposed to distinguish these two groups on a subspecies level. The Serengeti '*Hypsohipparion*' group, erected by Dietrich, is now considered to be *Hipparion* (*Hipparion*) *albertense serengetense*, subsp. nov. The reason for dropping the genus *Hypsohipparion* has been discussed above. The Langebaanweg group constitutes the subspecies *Hipparion* (*Hipparion*) *albertense baardi*, subsp. nov. The name *baardi* is chosen because the first specimens were recovered from Baard's Quarry, owned by Mr. J. Baard.

It seems that these two subspecies constitute the earliest Pleistocene forms. The material (to be described by Dr. Stirton) from the base of Olduvai Bed I should confirm or correct this suggestion.

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Dr. K. H. Fischer, Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität zu Berlin kindly took some measurements (at the authors' request) on the original Serengeti material.

Mrs. M. A. Norris patiently typed the manuscript.

SUMMARY

The recent discoveries of hipparionid material at the Langebaanweg fossil sites (Cape Province, South Africa) necessitated a revision and interpretation of similar material recovered elsewhere in Africa. At the same time new data on material from the Vaal River Gravels, Olduvai Gorge and South Serengeti are added. A review of the geological and faunal data described from approximately 40 sites in Africa leads to a tentative chronological correlation. Consideration of the anatomical features (mostly of the dentition) provides opportunity for a discussion of the ecological adaptation and evolutionary trends. The problems of the origins and migrations of African hipparionids are dealt with.

It is concluded that the African hipparionids belong to a single genus, *Hipparion*. The Miocene forms remain limited to *H. africanum*. The Pliocene is represented by *H. sitifense*, while the Pleistocene forms are referable to two subgenera, viz. *Stylohipparion* and *Hipparion*.

The Serengeti '*Hypsohipparion*' group, is referred to *Hipparion* (*Hipparion*) *albertense serengetense* subsp. nov.

The Langebaanweg material forms a unified group and is referred to *Hipparion* (*Hipparion*) *albertense baardi* subsp. nov.

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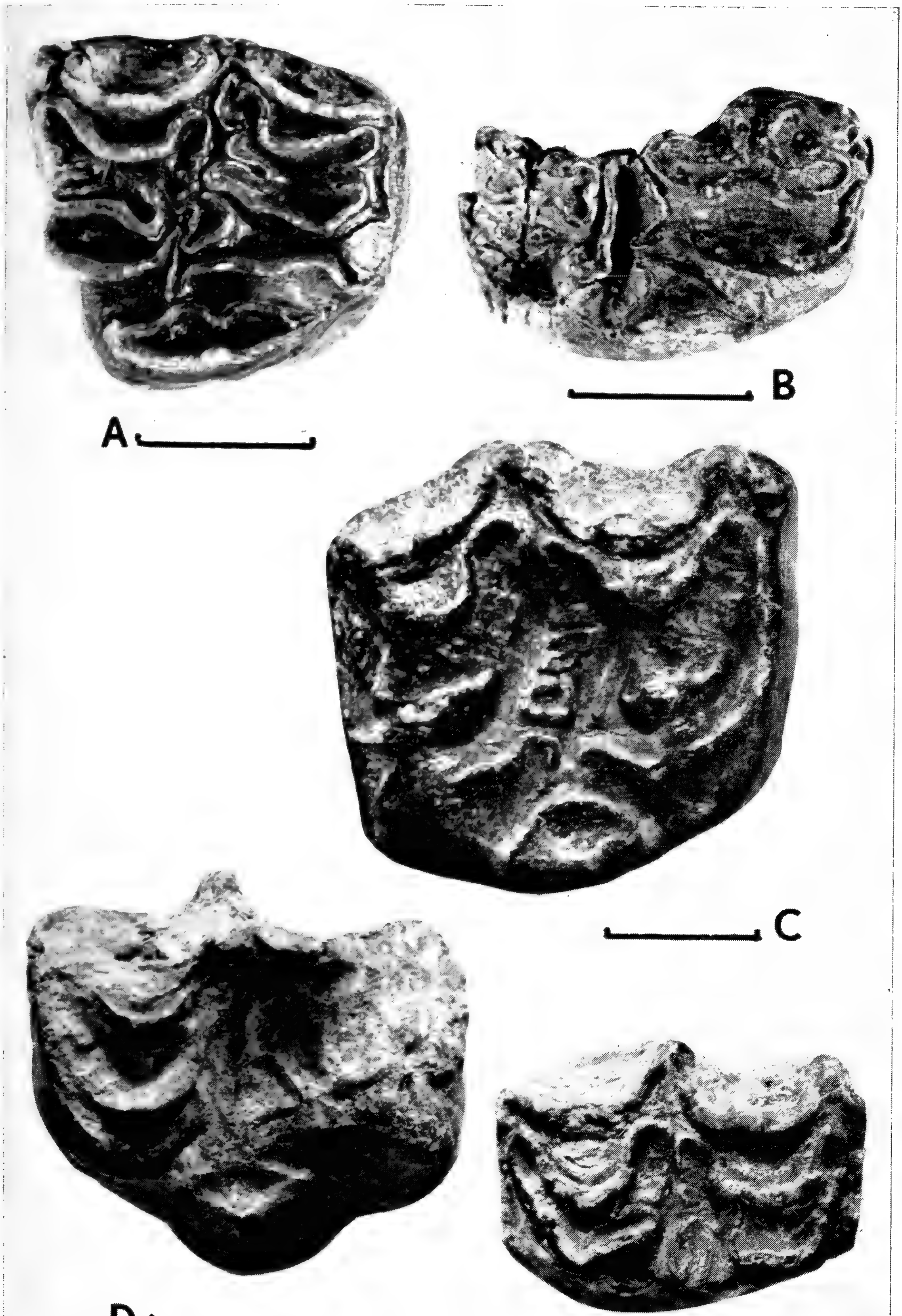


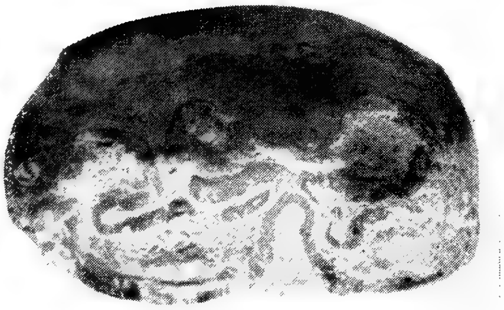
Occlusal aspect. Scale: 1 cm. **A**—MMK 431. **B**—MMK 5225. **C**—L1467c. **D**—L1463. **E**—L956.

A

C

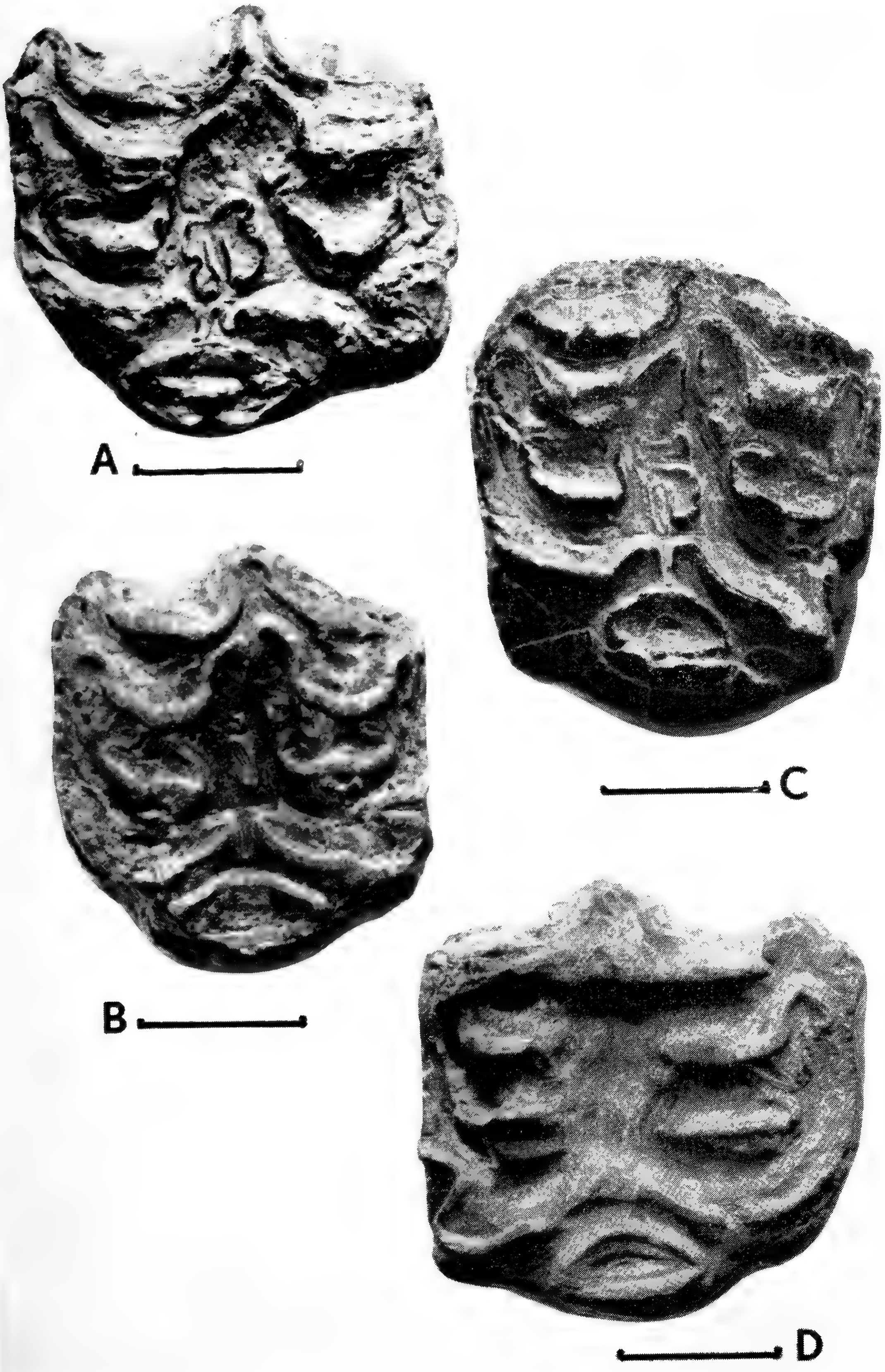
D

B

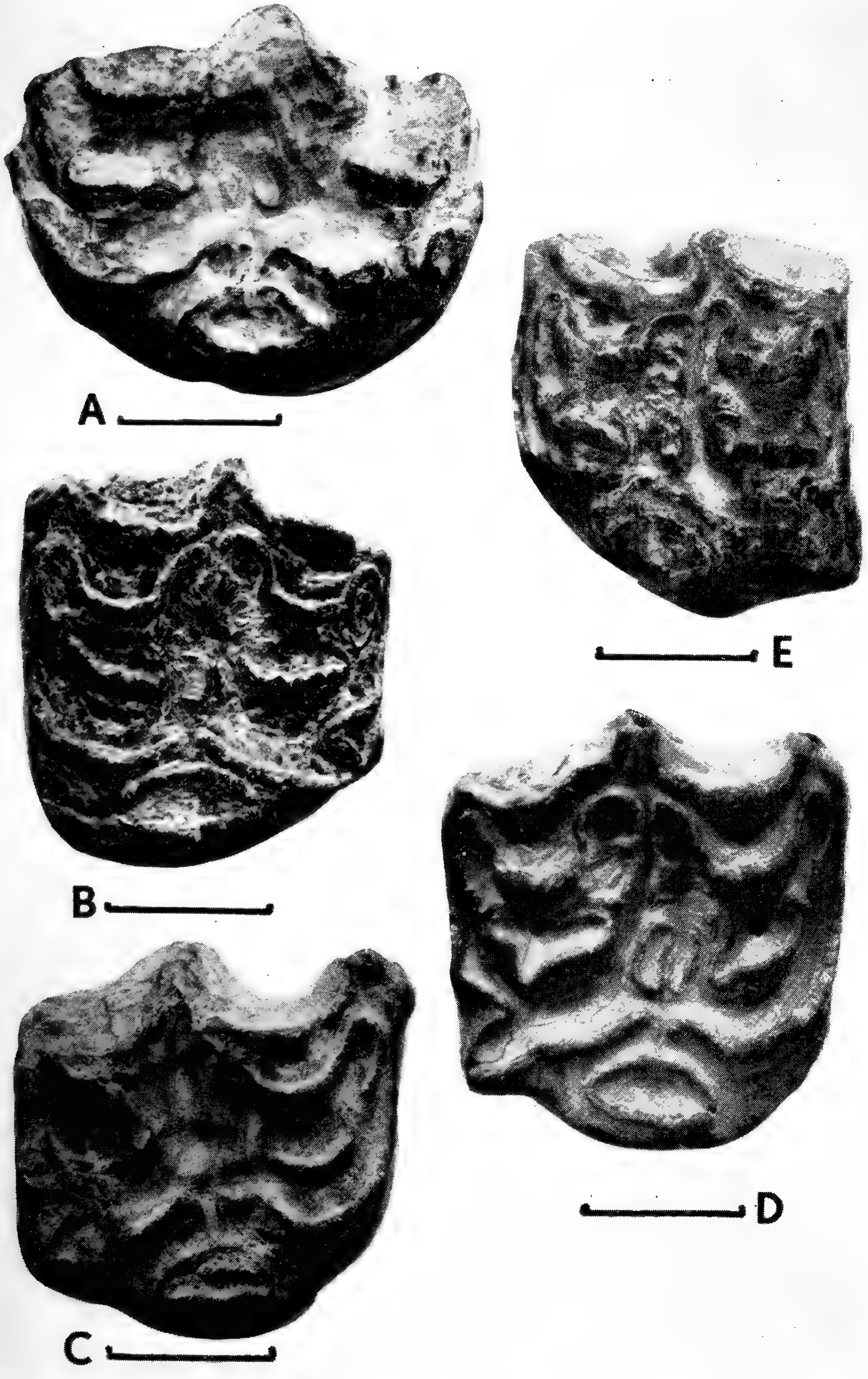


E

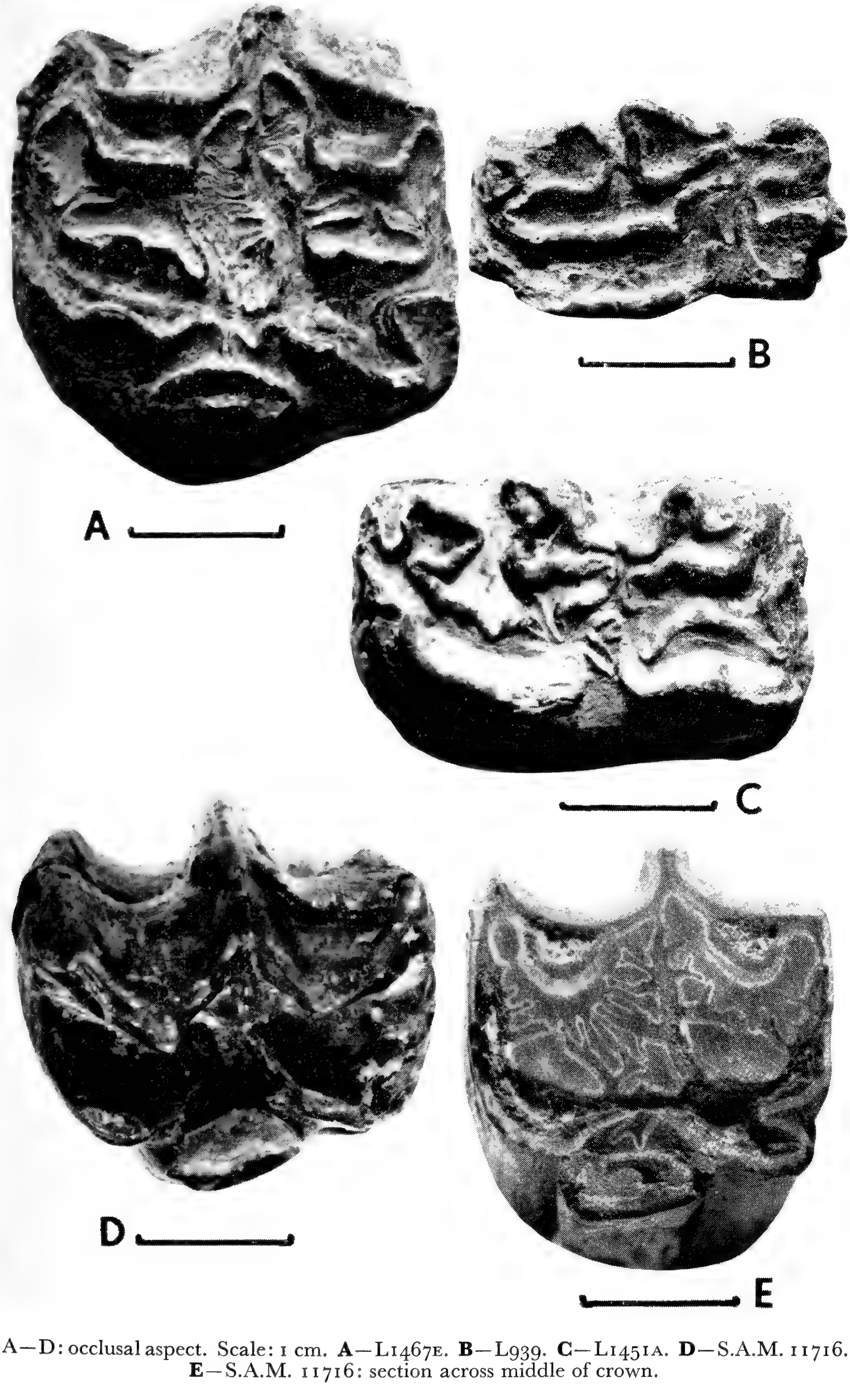
Occlusal aspect. Scale: 1 cm. **A**—S.A.M. 11717. **B**—S.A.M. 11718. **C**—L940 / 950. **D**—L934. **E**—L1465F.



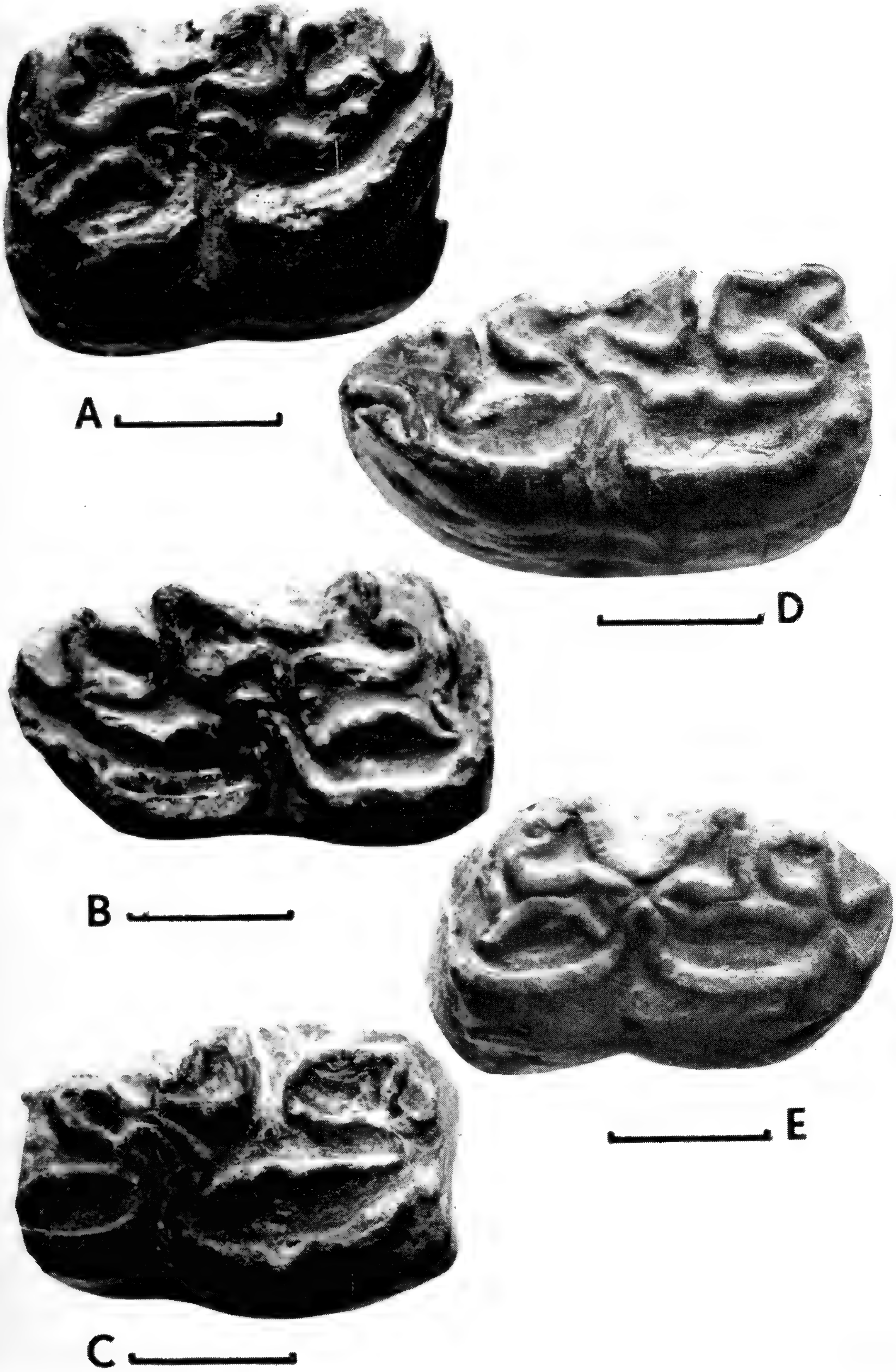
Occlusal aspect. Scale: 1 cm. **A**—S.A.M. 11719. **B**—L953. **C**—L1467D. **D**—L955.



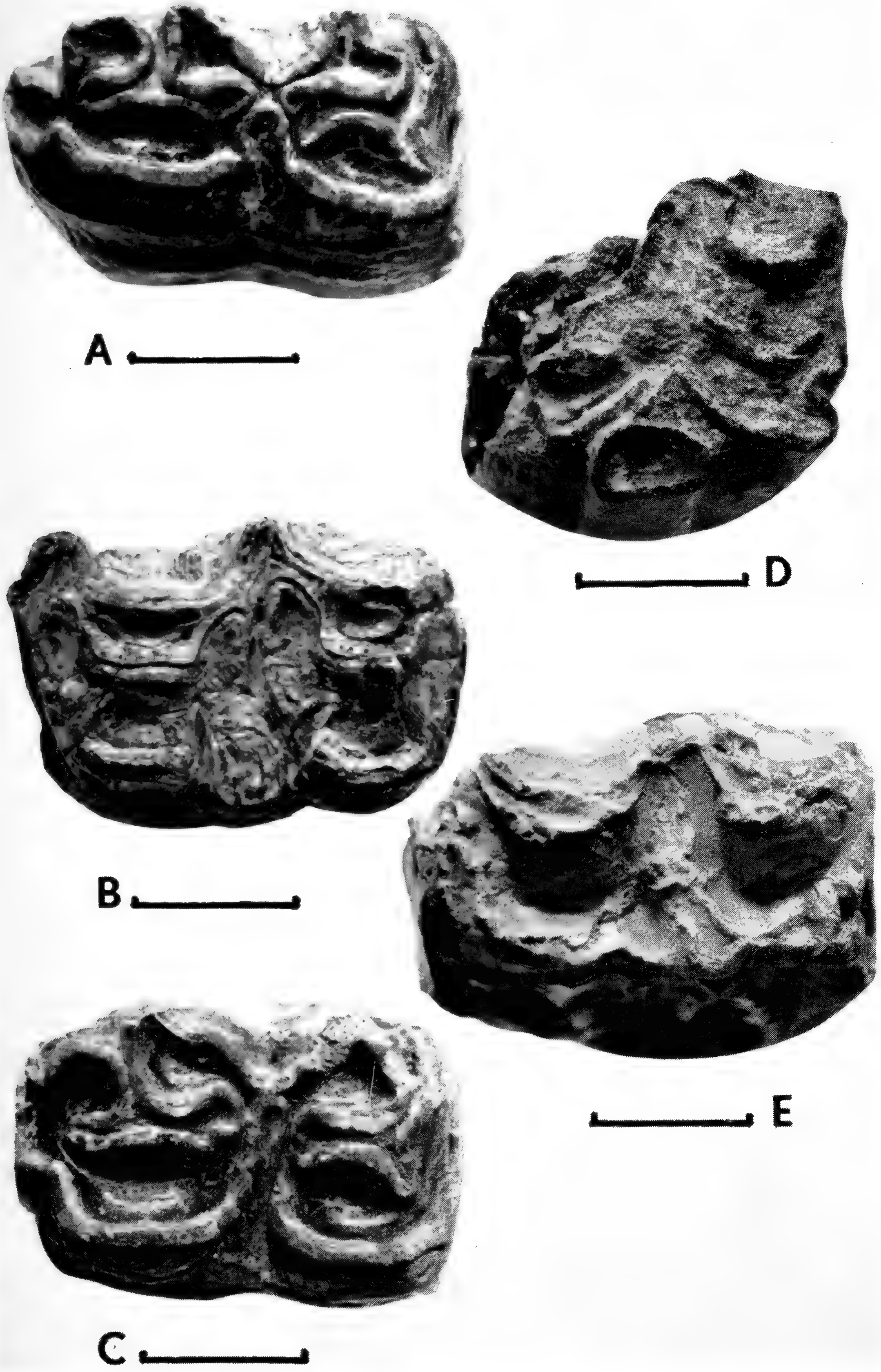
Occlusal aspect. Scale: 1 cm. **A**—L1467H. **B**—L1467B. **C**—L1459. **D**—L951. **E**—L958.



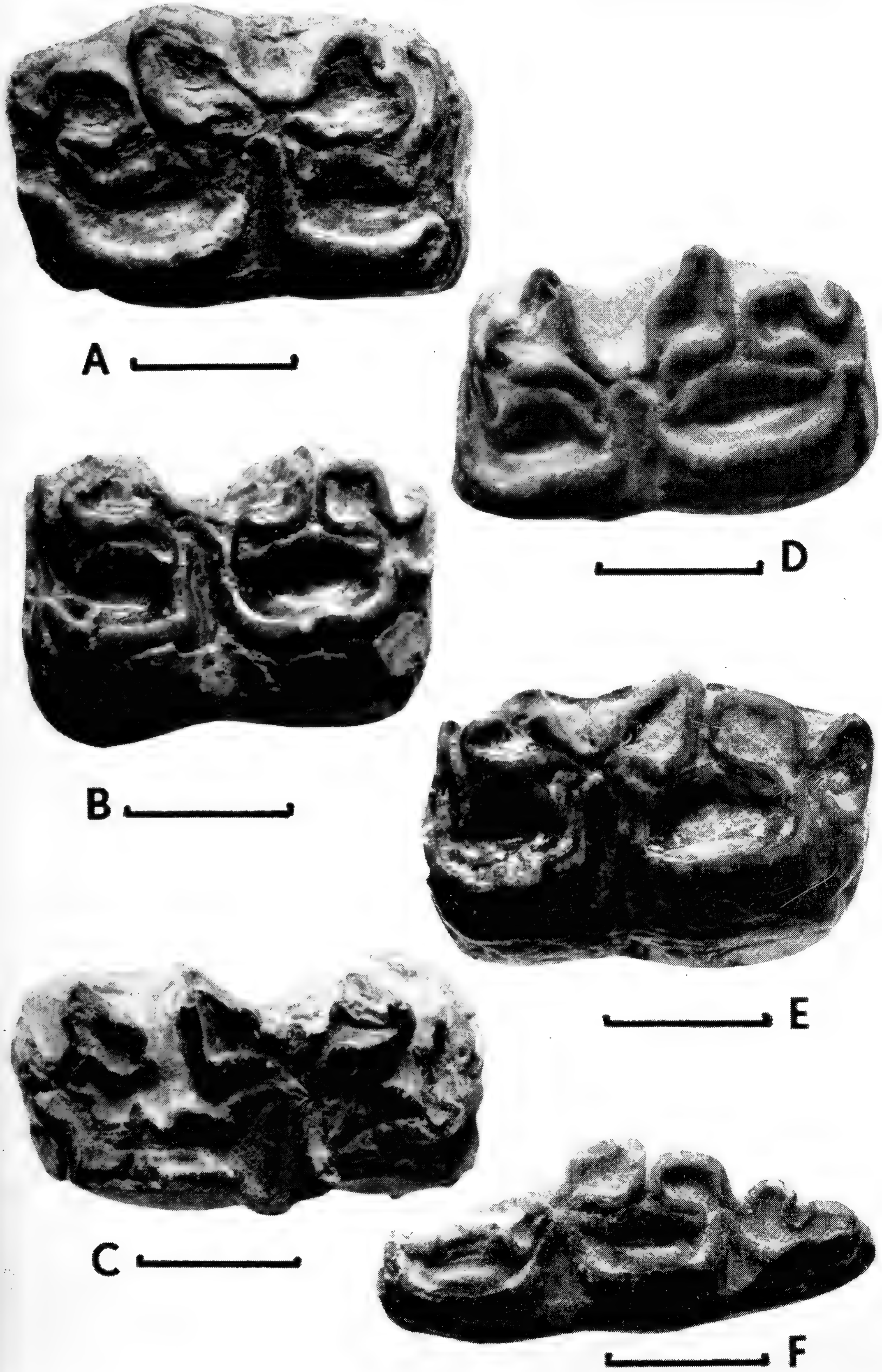
A—D: occlusal aspect. Scale: 1 cm. **A**—L1467E. **B**—L939. **C**—L1451A. **D**—S.A.M. 11716.
E—S.A.M. 11716: section across middle of crown.



Occlusal aspect. Scale: 1 cm. **A**—L943. **B**—L941. **C**—L1465D. **D**—L947. **E**—L944.

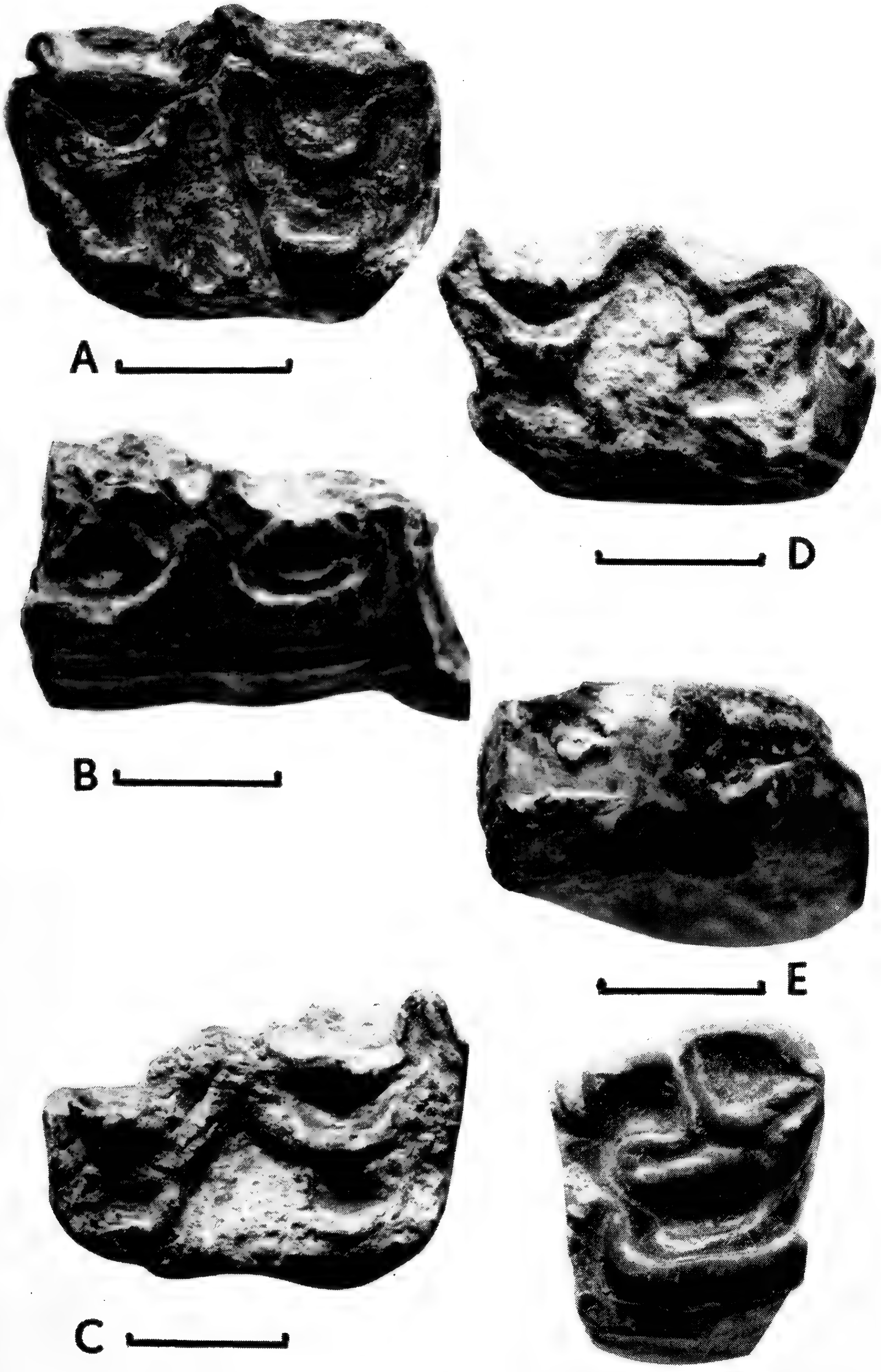


Occlusal aspect. Scale: 1 cm. **A**—L948. **B**—L942. **C**—L954. **D**—L936. **E**—S.A.M. 11724.

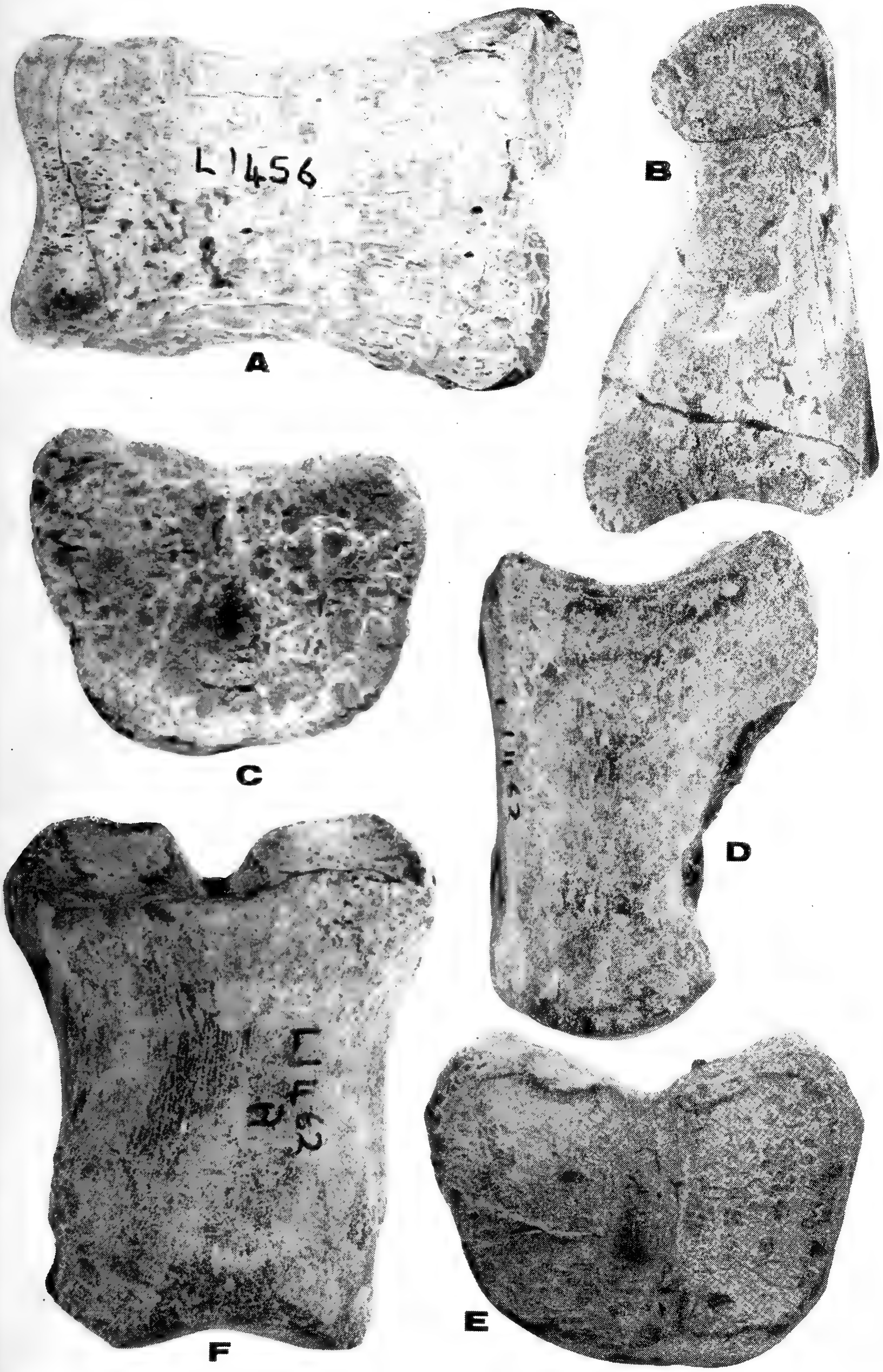


Occlusal aspect. Scale: 1 cm. **A**—L946. **B**—L952. **C**—L1465A. **D**—L959. **E**—L1448. **F**—L938.

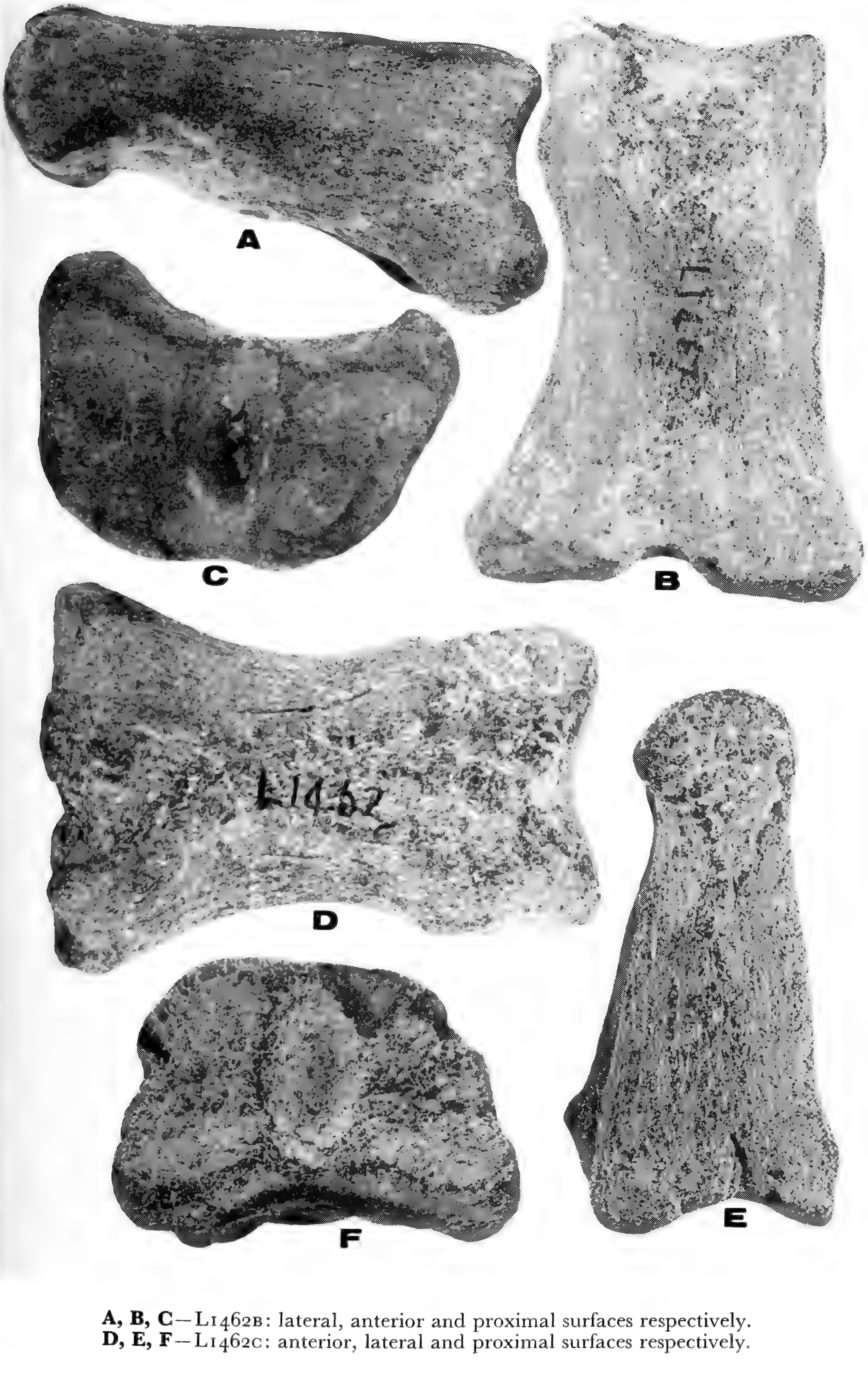
Plate XV



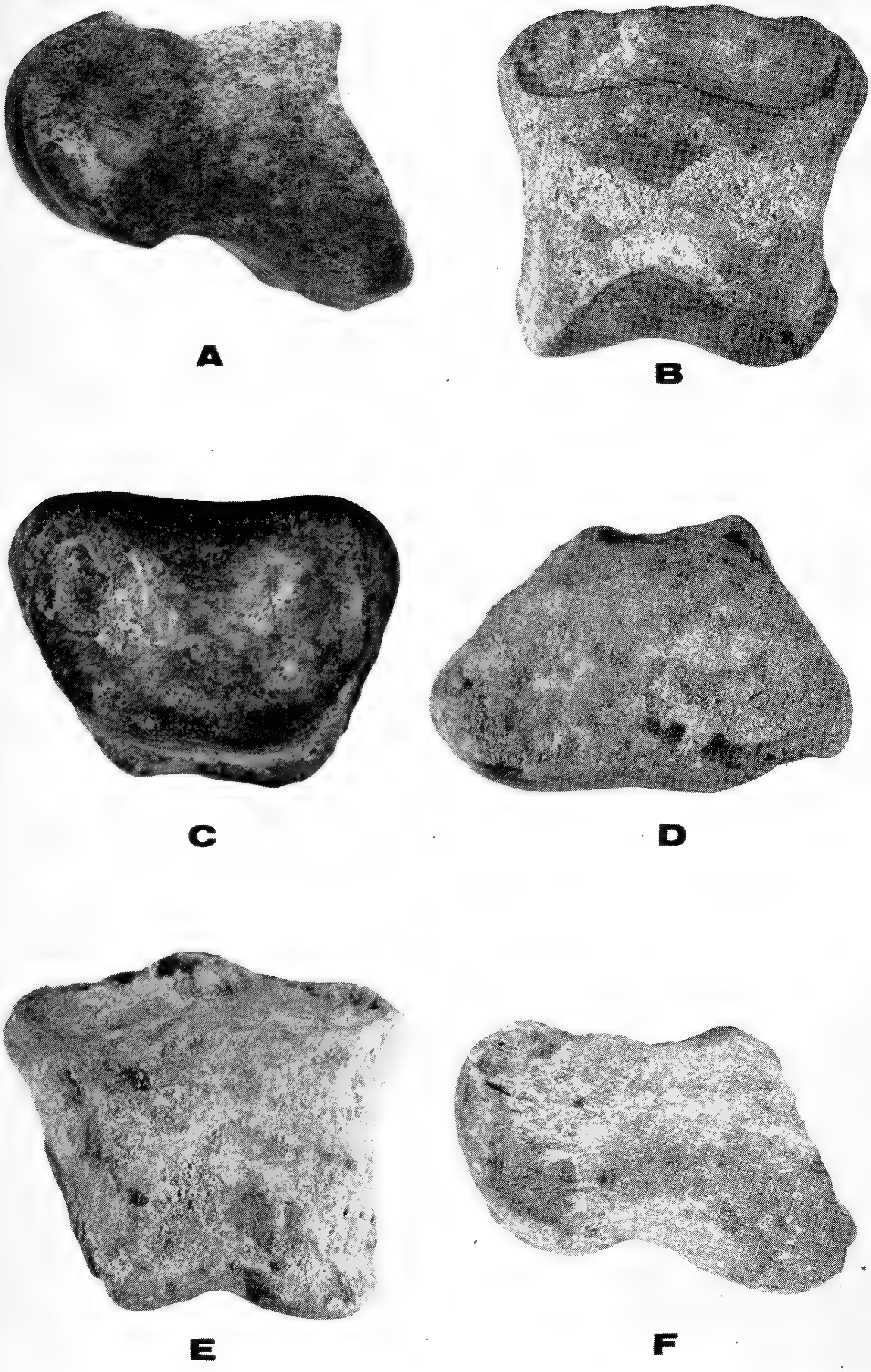
Occlusal aspect. Scale: 1 cm. **A**—L945. **B**—L1465B. **C**—S.A.M. 11722. **D**—L935. **E**—L949. **F**—L957.



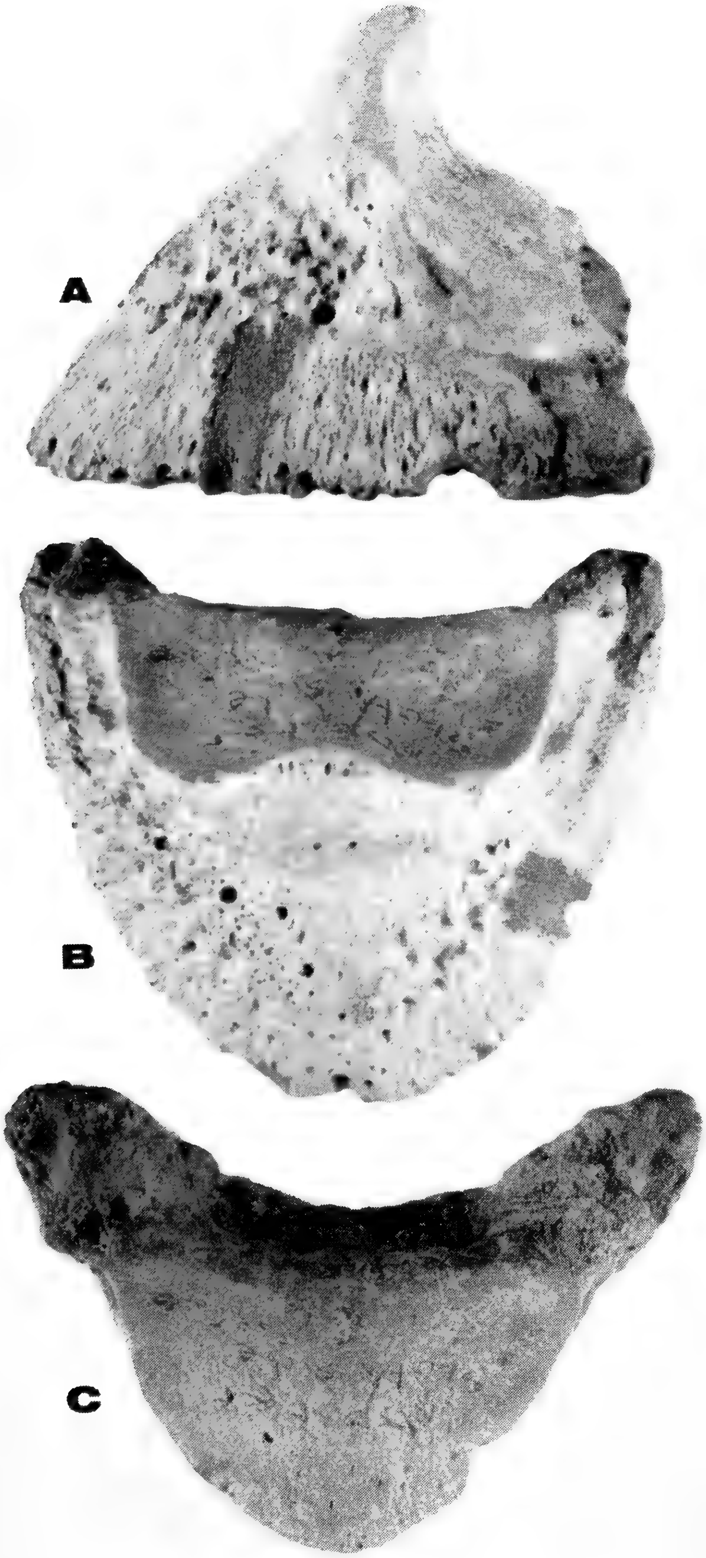
A, B, C—L1456: anterior, lateral and proximal surfaces respectively.
D, E, F—L1462A: lateral, proximal and anterior surfaces respectively.



A, B, C—L1462B: lateral, anterior and proximal surfaces respectively.
D, E, F—L1462C: anterior, lateral and proximal surfaces respectively.



A, B, C—L1449: lateral, anterior and proximal surfaces respectively.
D, E, F—L1462D: proximal, anterior and lateral surfaces respectively.



A, B, C—L1444: lateral, anterior and inferior surfaces respectively.

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ILLUSTRATIONS

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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).

T. H. BARRY

ON THE EPIPTERYGOID–ALISPHENOID TRANSITION IN THERAPSIDA

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ON THE EPIPTERYGOID—ALISPHENOID TRANSITION IN THERAPSIDA

By

T. H. Barry

South African Museum, Cape Town

(With 22 figures in the text)

Contents

Introduction

Mainly as a result of the researches of Gaupp (1902), Allis (1919), Broom (1907, 1909 and 1914), Fuchs (1912) and Gregory and Noble (1924) it is now generally accepted that the reptilian epipterygoid and mammalian alisphenoid, although superficially different in many respects, are homologous structures. The views of these workers have received support from embryologists, comparative anatomists and palaeontologists alike over the last few decades and the theory has now virtually become axiomatic.

In modern reptiles there is a marked degree of variation in the development of the epipterygoid, ranging from the primitive, rather solid, construction of the bone in *Sphenodon*, to the absence or vestigial development of the bone in adult Ophidia and Crocodilia with the Lacertilia displaying a thin columnar structure. The relationship of the branches of the trigeminal nerve to the bone, remains constant throughout the class, the profundus emerging anterior to the epipterygoid and the maxillary and mandibular branches posterior to the bone.

Ann. S. Afr. Mus. **48** (17), 1965, 399–426, 22 figs.

In mammals the development of the alisphenoid as a relatively broad and flattened bone is fairly constant except in *Echidna* where it appears to be absent. In mammals, however, the relationship of the branches of the trigeminal nerve to the alisphenoid varies. This ranges from the 'reptilian' type, where the bone lies between the profundus and maxillary branches, found in *Didelphis*, through stages where first the maxillary and then also the mandibular branches pierce the bone, to where the profundus and maxillary branches both emerge anterior to the alisphenoid.

The palaeontological evidence for the homology of the reptilian epipterygoid and the mammalian alisphenoid presented in the early years (mainly by Broom) naturally reflects the inadequate state of knowledge of the early reptile fossils at the time. Although seldom stated explicitly there was a strong tendency to see in the lacertilian condition the basic type from which the mammalian condition could be derived.

As far back as 1907 Broom stated that palaeontological evidence supported the view that the alisphenoid of mammals had evolved from the reptilian epipterygoid concluding:

> 'In the very primitive reptiles, of which *Procolophon* may be taken as a type, we have a lizard-like columella cranii. In the early types, which have specialized along the mammalian line, such as the Therocephalians, we still have a columella cranii. In the even more mammal-like anomodonts, such as *Dicynodon* and *Oudenodon*, there is a columella cranii, but no alisphenoid. When we come to examine the Cynodonts—those remarkable reptiles, so very nearly related to the Mammals as to be regarded by many as the group ancestral to them—we find a broad flattened bone, which most anatomists would not hesitate to call the alisphenoid, and yet there can be little doubt, it is only the columella cranii of the anomodont flattened out' (p. 114).

In 1914 Broom offered more direct evidence to substantiate his view stating:

> 'A short epipterygoid is known in *Diadectes* and a long lizard-like columella cranii is met with in *Procolophon*. A short epipterygoid occurs in the Pelycosaur *Dimetrodon*. In Anomodonts the epipterygoid is present as a long slender rod—in some species rounded and in others much flattened . . . and its lower end is considerably expanded antero-posteriorly, giving it a long suture with the pterygoid. In Gorgonopsians the epipterygoid is a long, much flattened rod which inferiorly has probably similar relations to the pterygoid as seen in the Anomodonts. In the Therocephalians the epipterygoid is only satisfactorily known in *Scylacosaurus*. Here, . . . it is a relatively short, flattened structure with a very wide base which lies along the pterygoid. In the Cynodonts, at least in the higher forms as exemplified by *Diademodon* and *Cynognathus*, in the region occupied by the epipterygoid in the Therocephalians there is a very much larger bone which there can

> be little doubt is also an epipterygoid development. The upper part is greatly expanded antero-posteriorly and forms much of the cranial wall. The lower portion of the bone is so much more developed than in the Therocephalian that it completely replaces the posterior part of the pterygoid, . . . and extends outwards as far as the quadrate. There can be little doubt that while this bone is homologous with the epipterygoid of the lower forms, it is also the homologue of the mammalian alisphenoid' (p. 30).

In the next thirty years very little advance was made. In 1944 Olson still describes the structural changes undergone by the epipterygoid in the transition from the primitive reptilian condition to that of mammals as follows:

> '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).

In the twenty years that have elapsed since Olson wrote the foregoing descriptions of the palatoquadrate of all the principal groups of reptiles and of the forms ancestral to the reptiles have become available. A restatement of the course of the evolution of the epipterygoid-alisphenoid has therefore become necessary. In the following pages a short review of the present state of our knowledge of this element is given. Although the epipterygoid is a distinct element in the early tetrapod skull its evolution cannot be discussed in isolation since both the number of palatoquadrate ossifications and the extent of these elements vary. An account of the palatoquadrate as a whole will therefore be given and the evolutionary trends evident in its ossifications discussed.

My interest in the transformation of the epipterygoid (and quadrate in so far as it affected the epipterygoid) originated while studying serially ground sections of the skull of the anomodont *Pristerodon buffaloensis*. This technique revealed important features of the palatoquadrate complex which would not have been readily seen in material cleaned in the normal way. As some of these features contradict vital points in the evolutionary sequences as interpreted by Broom and Olson, an account of the *Pristerodon* palatoquadrate will be presented first and will be followed by a general review of the transformation of the palatoquadrate.

MATERIAL

A skull of *Pristerodon buffaloensis* Toerien, No. B.P.I. 339, was made available for sectioning by Dr. A. S. Brink, Assistant Director of the Bernard Price

Institute for Palaeontological Research, Johannesburg. It was discovered in 1956 by Mr. James W. Kitching of the same Institute in *Cistecephalus* Zone strata on the farm Kirkvors, today known as De Hoop, approximately two miles north-west of Murraysburg, Cape Province. *Pristerodon* belongs to the family Endothiodontidae of the Sub-order Anomodontia (Sub-class Synapsida; Order Therapsida).

The Palatoquadrate of *PRISTERODON*

The ossified palatoquadrate of *Pristerodon buffaloensis* is represented by the separated epipterygoid and the quadrate (figs. 1 and 4). Viewed laterally the epipterygoid is L-shaped, with both the vertical and the horizontal limbs well developed. The vertical limb (or columella cranii) is relatively thin and extends upward and slightly forward to meet a ventrally extending ridge originating

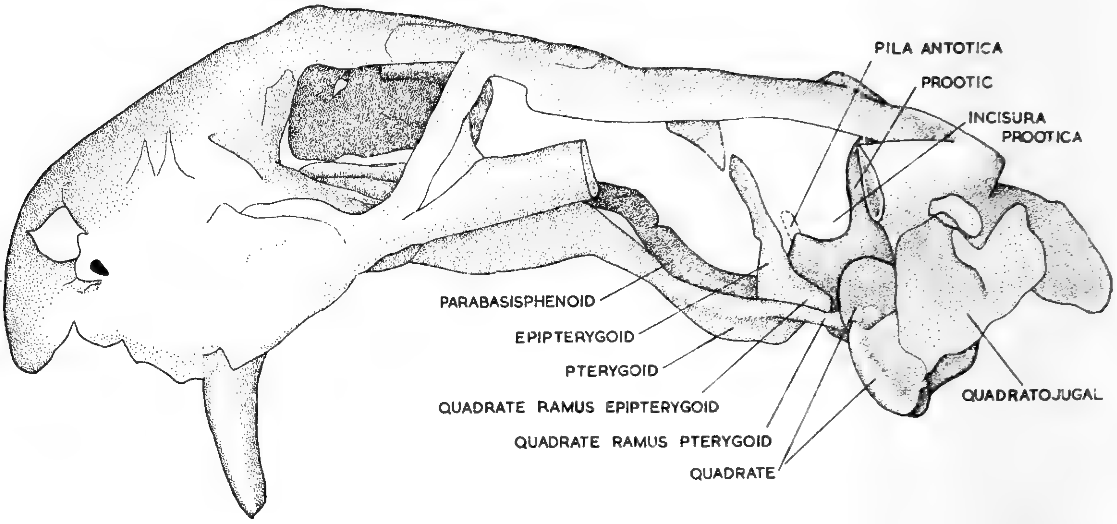

Fig. 1. *Pristerodon buffaloensis*. Lateral view of skull reconstructed from serial sections. Squamosal cut away to show palatoquadrate complex.

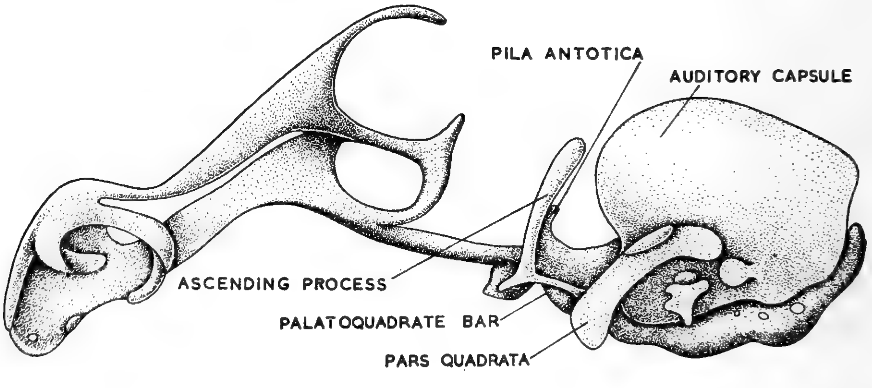

Fig. 2. *Tropiocolotes tripolitanus*. Lateral view of skull of 15·2 mm. embryo. (After Kamal, 1960.)

from the under-surface of the parietal. The posteriorly directed horizontal portion is thickest near the angle of the bone, tapering posteriorly to become rod-shaped (quadrate ramus of the epipterygoid). The entire base of the epipterygoid is applied to the dorsal and/or dorso-lateral surface of the quadrate ramus of the pterygoid. The quadrate rami of both the pterygoid and the epipterygoid are directed postero-laterally, towards the inner surface of the quadrate.

The quadrate is relatively large, has the shape of an inverted Y in cross-section, the upper leg lying in a deep antero-posteriorly directed ventral pocket of the squamosal. It is suturally attached to two other elements only, the quadratojugal on the outside and the stapes to which it is attached through a short horizontal ridge projecting medially from the inner condyle. Antero-dorsally to this ridge there is a longitudinal groove in the vertical face of the quadrate, extending backwards from the anterior border for approximately one-third of the length of the vertical plate (fig. 4). Throughout its length this groove is seen to follow remarkably closely a course parallel to 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, approximately half-way along its length. A distinct rounded bulge terminates the groove in the left quadrate. As the groove follows what could have been the course of a posterior extension of the horizontal limb or quadrate ramus of the epipterygoid it would seem reasonable to assume that the groove housed a cartilaginous rod connecting the quadrate with the epipterygoid.

The occurrence of a solid link between the quadrate and epipterygoid in an adult *Pristerodon*, recalls conditions found in the developmental stages of the skull in many recent reptiles and in developmental stages of *Sphenodon* (fig. 3) as well as in the adult. The complex, as reconstructed in *Pristerodon*,

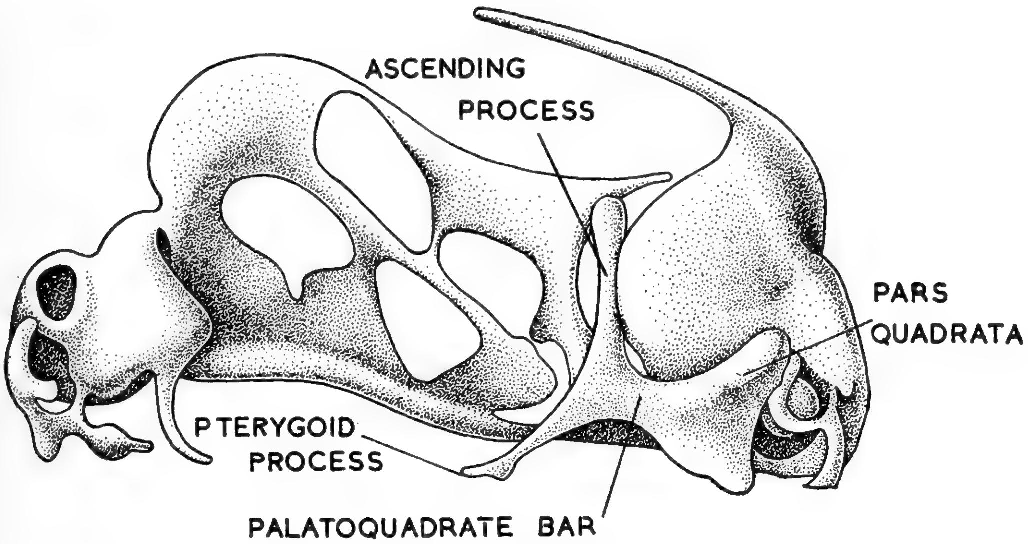

Fig. 3. *Sphenodon punctatus*. Embryo. Lateral view of skull. (After Howes & Swinnerton, 1901.)

shows a remarkable resemblance to the palatoquadrate of *Zonurus* (*Condylus*), as featured by Broom (1925), and of the 15·2 mm. developmental stage of the Egyptian lizard *Tropiocolotes tripolitanus* (fig. 2), described by Kamal (1960). Similarly the relationship between the horizontal limb and the quadrate ramus of the pterygoid in *Pristerodon* is mirrored by conditions found in *Sphenodon*, the base of the palatoquadrate cartilage occupying the dorsal and dorso-lateral surface of the quadrate ramus of the pterygoid in both forms.

In this connection it is important also to consider the relationship of the nerves to the complex, and especially that of the trigeminal nerve to the epipterygoid. In recent reptiles the nerve emerges from the braincase through the incisura prootica. The profundus branch then passes medially to the epipterygoid while the maxillary and mandibular rami pass behind the epipterygoid. In *Pristerodon* there are no indications of the routes followed by the presumed branches of the trigeminal nerve but judging by the nerve foramina and grooves found in some early gnathostomes and tetrapods it would seem indicated that present-day relationships had an early origin.

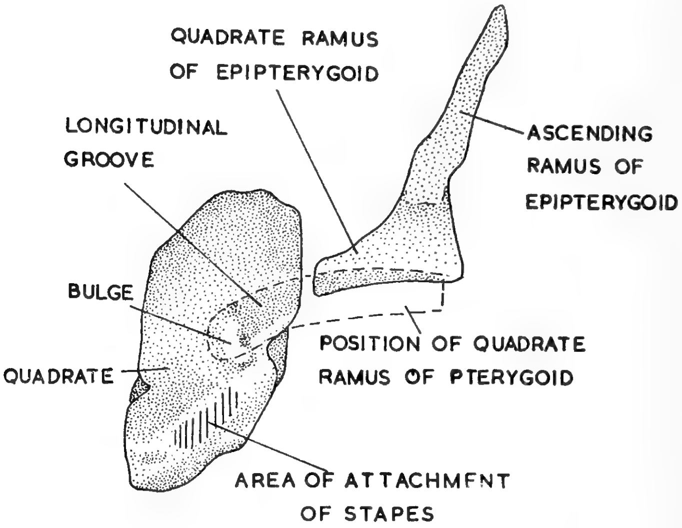

FIG. 4. *Pristerodon buffaloensis*. Medial view of palatoquadrate complex. Left side.

In the phylogenetic review that follows, it will be seen that the basic form of the palatoquadrate is retained from the early gnathostome condition up to the early 'stem reptile' stage. The number of ossifications in the palatoquadrate would seem to vary from stage to stage and even within stages and could possibly be of minor evolutionary importance, especially as cartilaginous inter-connections are indicated. If this is so it might explain the apparent inconsistency of an otic process on the epipterygoid ossification in certain labyrinthodonts while in other labyrinthodonts and later forms it forms part of the quadrate ossification. After the attainment of the basic reptile stage, or possibly even already during the labyrinthodont stage the palatoquadrate begins to undergo evolutionary change which will have far reaching effects. The development is channelled into two main streams; one leading towards the expansion of the epipterygoid and reduction of the quadrate, as exemplified in those trends showing mammalian affinities, and another resulting in the retention of the quadrate and reduction of the epipterygoid in trends showing reptilian affinities.

PHYLOGENY

The first adequately known vertebrates are agnathous forms found in the Late Silurian. Jawed vertebrates have as yet not been discovered in the Silurian but the variety of these forms in the Lower Devonian indicates they must have been undergoing development in the Silurian (Romer, 1955).

PLACODERMI

The early Devonian gnathostomes are predominantly placoderms. Although widely varied in appearance, the jaw apparatus is usually of a relatively primitive type. Amongst them the acanthodians are generally regarded as the earliest and most archaic and their morphology could, therefore, throw light on the problems connected with the formation and evolution of the primitive jaws.

According to Watson (1937) the acanthodian palatoquadrate is large and superficially divisable into two elements, a short horizontal suborbital or palatal portion and a large vertical postorbital or paraotic portion. In the genera *Climatius* and *Cheiracanthus* the palatoquadrate is ossified as a single unit, but in *Mesacanthus* and *Ischnacanthus* the palatal and paraotic portions are ossified independently. In *Acanthodes* (fig. 5), the last surviving member of the group, and therefore possibly specialized, the palatoquadrate is ossified as three separate structures, but it seems certain that these bones, in life, comprised parts of a single palatoquadrate. Anteriorly the paraotic plate ends in a vertical border, which forms the hind margin of the orbit. From the top of this border the bone curves downwards posteriorly to end in the thickened quadrate condyle. Behind the vertical border the paraotic plate is perforated by a foramen, extremely large in *Cheiracanthus*, which could possibly have served for the exit of the maxillary and mandibular branches of the trigeminal. The palatal portion of the palatoquadrate terminates anteriorly at a point in line with the middle of the orbit. This is some distance behind the front end of Meckel's cartilage and would appear to indicate that the palatoquadrate was continued forward as cartilage.

The palatoquadrate does not seem to have contact with the neurocranium in *Climatius*, but in *Mesacanthus*, *Cheiracanthus* and *Acanthodes*, the paraotic flange bears an otic process which articulates with the skull behind the postorbital process. The palatal part of the bone has a basal articulation.

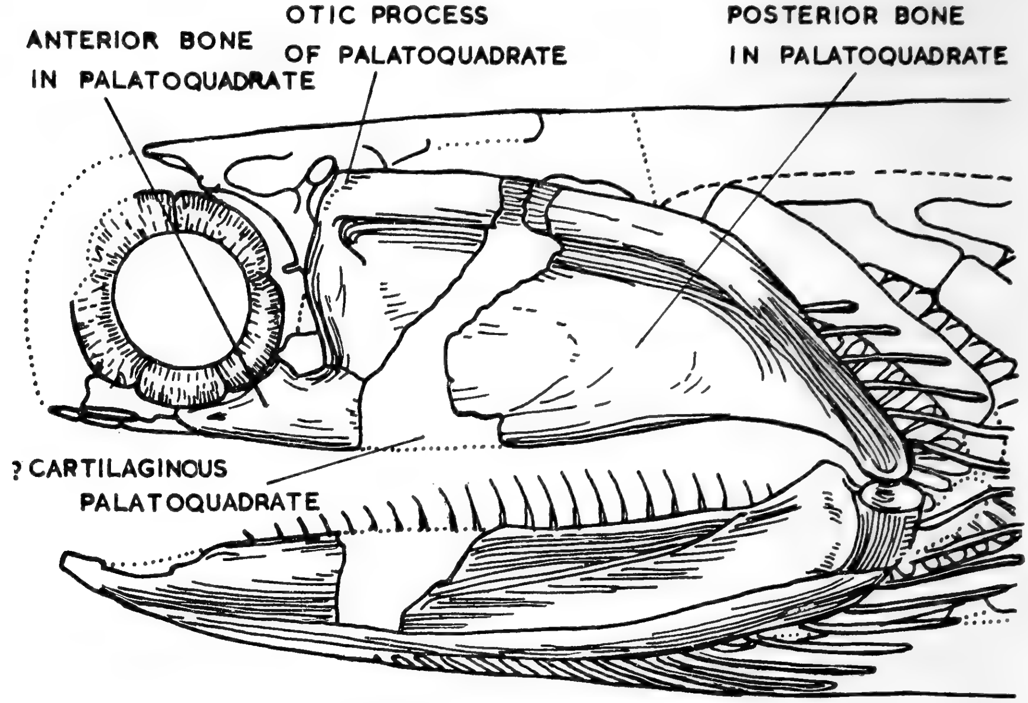

FIG. 5. *Acanthodes* sp. Reconstruction of the skull from specimens from the Lebach ironstones. Complete except for squamation. (After Watson, 1937.)

According to Watson (1937) the palatoquadrate in arthrodires is directly comparable with that occurring in several acanthodians. In *Pholidosteus* the palatoquadrate has two ossifications, an anterior which articulates with the ventral part of the neurocranium just behind the olfactory capsules, and a posterior quadrate.

CROSSOPTERYGII

In the Crossopterygii the processes and future subdivisions of the palatoquadrate become more apparent.

In *Eusthenopteron* the palatoquadrate is a single ossification with, according to Jarvik (1954), five distinguishable parts; an anterior pars autopalatina, articulating with the ethmoidal region and the anterior neural endocranium; a basal process articulating with the basipterygoid process; an antero-dorsally directed ascending process which articulates with the suprapterygoid process of the neural endocranium; a paratemporal process, which articulates with the anterior end of the otic shelf and a thickened pars quadrata posteriorly. A thin film of bone, dotted with large fenestrae, makes up the rest of the palatoquadrate (fig. 6).

Jarvik states that the profundus passed medially to the ascending process while the maxillary and mandibular branches of the trigeminal probably passed through the notch between the ascending and paratemporal processes.

Osteolepis macrolepidotus similarly possesses a completely ossified palato-

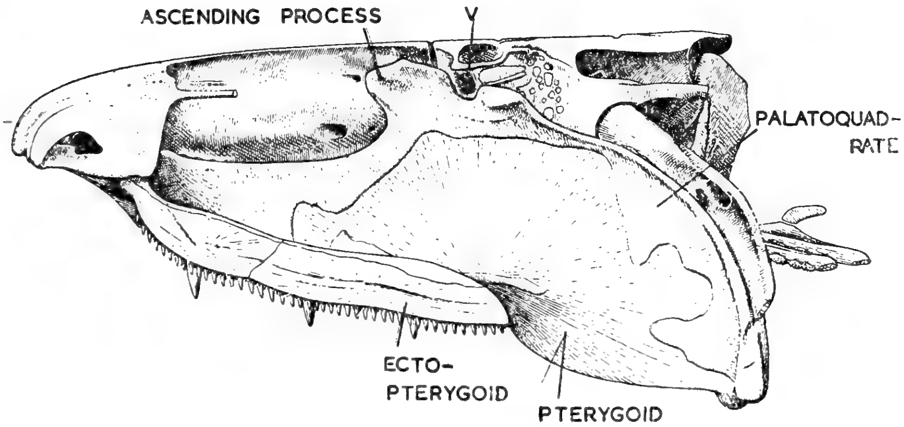

FIG. 6. *Eusthenopteron foordi*. Lateral view of skull with dermal bones removed. (After Jarvik, 1954.)

quadrate (Watson, 1954). But in *Megalichthyes* (Watson, 1925), the palatoquadrate is ossified as a continuous series of bones. Of these the anterior one, which extends into the basal process, represents the epipterygoid, the posterior the quadrate.

LABYRINTHODONTIA

The Coal Measure embolomerous anthracosaurs *Palaeogyrinus decorus* and *Eogyrinus altheyi* (Panchen, 1964) both display well developed palatoquadrates. In *Palaeogyrinus* (fig. 7) a large facet forms the anterior termination of a massive buttress, shaped like the mouth of a horn, which tapers forward as the palatal ramus. The latter appears to have rested on the horizontal palatal ramus of the pterygoid, but its lower edge cannot be made out. In mesial view the columella cranii appears as a slender rod extending dorsally until it expands to form an anteriorly directed process and a second vertical process. Panchen believes that the anteriorly directed process, the dorso-mesial surface of which is grooved, formed the dorsal edge of a notch for the profundus and that the second process probably divided the maxillary and mandibular branches of the trigeminal nerve. In lateral view the columella is continuous with a sheet of bone covering the whole of the upper half of the quadrate ramus of the pterygoid and which runs from the level of the cranial base to the quadrate condyle. A similar expansion is present in *Edops* (Romer and Whittier, 1942). Panchen believes that the epipterygoid may have extended as cartilage further down the quadrate ramus of the pterygoid and there seems also to have been a broad process projecting downward and backward from the level of the basis cranii. There is also a complex articulation for the basipterygoid process of the basisphenoid formed by both epipterygoid and pterygoid.

The quadrate is small in *Palaeogyrinus* but is a much more extensive ossification in *Edops*.

Panchen states that the considerable ossification in the cartilaginous palatoquadrate shown by these forms, and probably by *Eogyrinus* must be

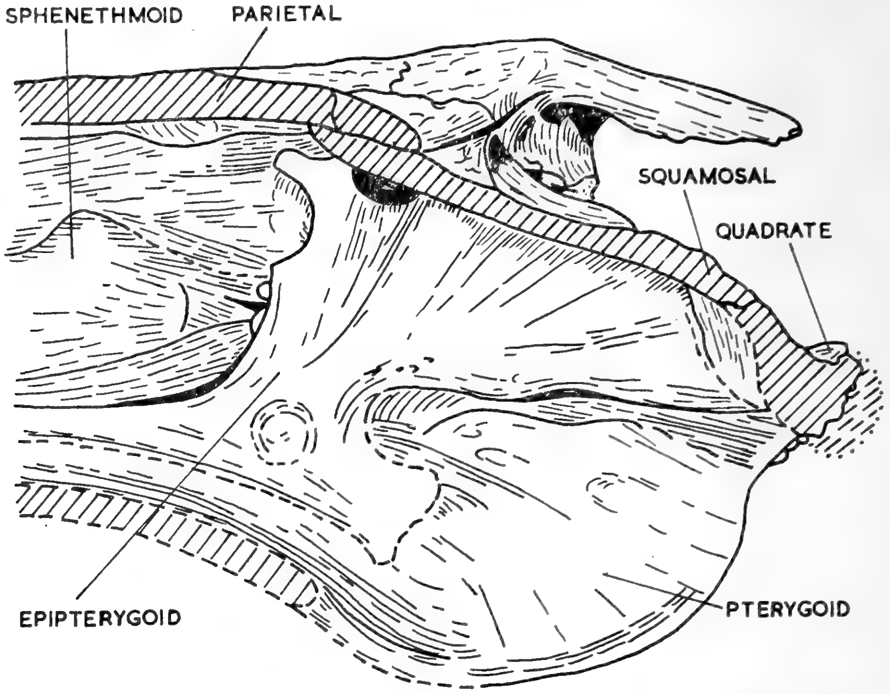

Fig. 7. *Palaeogyrinus*. Lateral view of suspensorial region as though sectioned through a plane parallel to the quadrate ramus. (After Panchen, 1964.)

interpreted as a primitive condition and that a progressive reduction of the epipterygoid ossification is to be seen in later labyrinthodonts.

Although Triassic labyrinthodonts are not on the phylogenetic line leading to reptiles, the structure of the palatoquadrate is nevertheless of interest. It consists of two parts, a horizontal cartilaginous anterior part and a mainly vertical ossified posterior part (Sushkin, 1899; Watson, 1919 and 1926, and Säve-Söderbergh, 1936). The vertical part had, at least in *Lyrocephalus*, basal, ascending and otic processes. Säve-Söderbergh maintains that all these processes were embodied in the epipterygoid in the most completely ossified individuals, but that in *Aphaneramma* and *Platystega* the ascending process only was included in the epipterygoid. The epipterygoid was joined to the quadrate ossification by means of a cartilaginous link which rested in a groove of the ramus of the pterygoid.

We may therefore assume that the palatoquadrate survived in labyrinthodonts complete from the quadrate to at least the front end of the epipterygoid.

Cotylosauria

Whether or not the seymouriamorphs are considered amphibians or reptiles, the skull of primitive forms such as *Seymouria* and *Kollassia* show that they are not far removed from the anthracosaurian amphibians from which the seymouriamorphs and more advanced reptiles have been derived (Romer, 1956). The epipterygoid, which is not well known and seems to be slow to ossify, extends as a rod-like structure to the skull roof. The primitive quadrate, when well ossified, ran forward to meet the epipterygoid. When the quadrate is less fully ossified, a cartilaginous area may have bridged the gap between the quadrate and the epipterygoid (fig. 8). It is presumed that the tendency for the epipterygoid to remain unossified is a degenerate feature (Romer, 1956).

The earliest known reptiles date from the Carboniferous but knowledge of their anatomy is fragmentary. Abundant forms appear in the Upper Carboniferous and Lower Permian but as these include not only primitive forms but also more advanced types, it is certain that a very important section of the early history of the reptiles is still unknown.

In diadectids both epipterygoid and quadrate are greatly developed. *Diadectes* itself features a quadrate of considerable height and width but little length (Romer, 1956). In the South African pareiasaurs both epipterygoid and quadrate are plate-like. The epipterygoid, which has a slender ascending process, furthermore stands transversely on the quadrate ramus of the pterygoid near its articulation with the basipterygoid process (Boonstra, 1934). According to Romer (1956) the margins of the base of the epipterygoid in pareiasaurians are unfinished, indicating a cartilaginous connection with the quadrate which has a similarly unfinished surface facing towards the epipterygoid.

The captorhinomorphs *Limnosceles*, *Captorhinus* and *Labidosaurus* from the Lower Permian of the American Southwest are among the oldest cotylosaurs

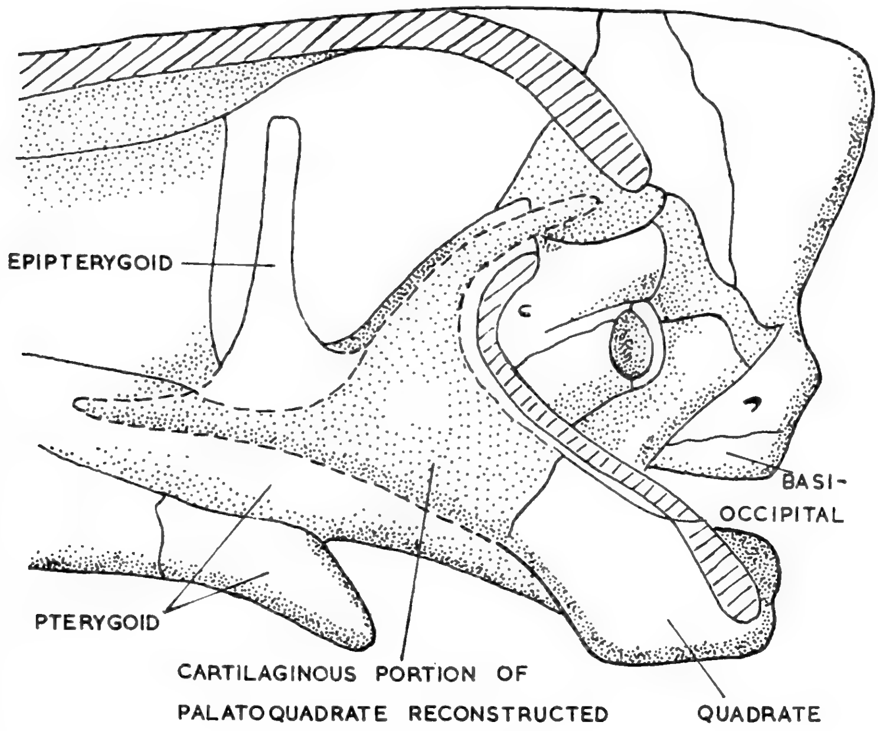

Fig. 8. *Seymouria.* Lateral view of the skull with dermal bones removed. Cartilaginous portion of palatoquadrate reconstructed. (After Romer, 1956.)

of which we have detailed knowledge. Here the quadrate also consists of a vertical sheet of bone with an essentially flat outer surface and an epipterygoid, separated from the quadrate but presumably attached to it in life by cartilage, with a rod-like ascending process (fig. 9).

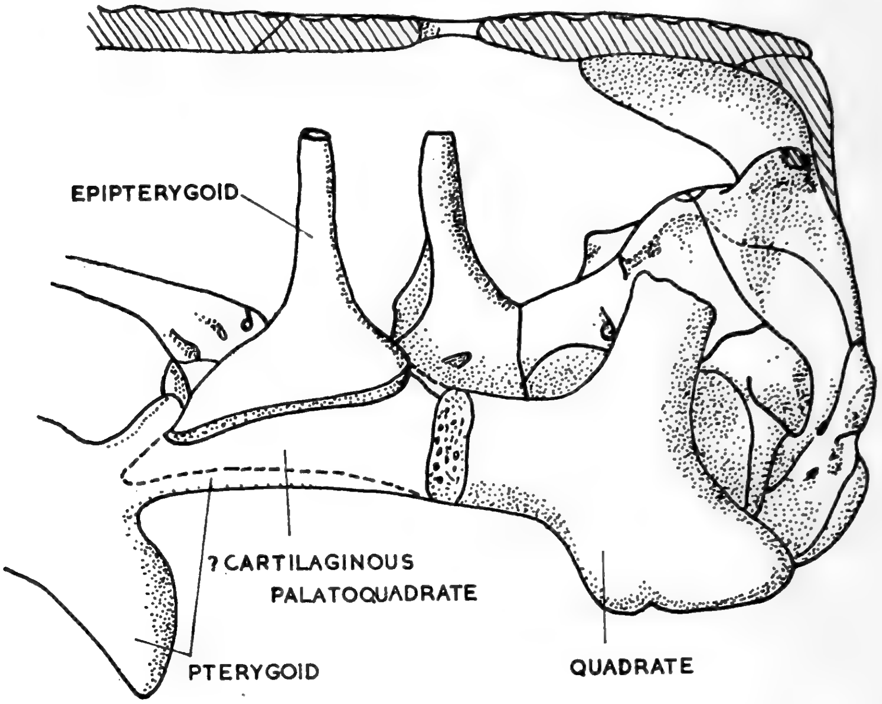

Fig. 9. *Captorhinus.* Lateral view of the skull with dermal bones removed. Cartilaginous portion of palatoquadrate tentatively indicated. (After Romer, 1956.)

Although we have no knowledge of the epipterygoid in the aberrant early Permian form *Bolosaurus* (Watson, 1954), the fact that the inner part of the quadrate continues forward as a ramus, on the outer surface of the pterygoid, would seem to indicate that the palatoquadrate was basically the same as the general cotylosaurian type.

The Lower Triassic form *Procolophon* belongs to the last group of survivors of the cotylosaurs. In this form the epipterygoid has an expanded footplate, the anterior extension of which is more fully developed than the posterior portion. From the posterior portion of the footplate a slender ascending ramus extends dorsally. The quadrate is large and has a process extending forward which partially replaces the quadrate ramus of the pterygoid. In *Procolophon* the latter is reduced in length as well as in height.

Pelycosauria

If, as is generally accepted, the Pelycosauria represent an early stage in mammalian history and that they possess '. . . many archaic features which illustrate the structure of the primitive reptilian stock' (Romer & Price, 1940: 1), then it should not be surprising to find that this group still displays a palatoquadrate complex in which the epipterygoid and quadrate portions are linked. This condition would merely represent the retention in this group of the basic gnathostome condition of a unified palatoquadrate as exemplified in the placoderms, and retained, with modifications, in the crossopterygians, labyrinthodonts and probably also the early stem reptiles.

The epipterygoid has a wide base closely applied to the lateral surface of the anterior portion of the quadrate ramus of the pterygoid (fig. 10). Anteriorly a slender extension curves down along a groove on the dorsal surface of the palatal ramus of the pterygoid. A continuation of this groove in some cases beyond the anterior end of the bone suggests a further cartilaginous extension of the palatoquadrate. The slender rod-like portion of the epipterygoid gains contact, in *Dimetrodon*, with the anterior surface of the paroccipital process.

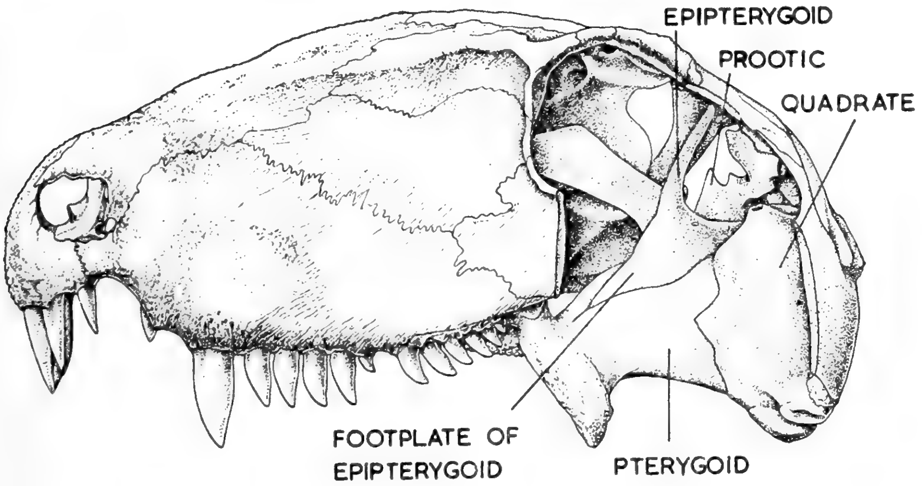

FIG. 10. *Dimetrodon limbatus*. Lateral view of skull with dermal bones cut off to show palatoquadrate. (After Romer & Price, 1940.)

The quadrate is essentially a triangular plate varying greatly in extent in the few forms where it is adequately known. In some cases in which it is well developed it appears to gain contact with the epipterygoid along the dorsal margin of the internal surface of the pterygoid (fig. 10), while in others in which the bone is more restricted in size, it appears to have been continued forward as cartilage.

THERAPSIDA

Dinocephalia

Of the slightly more advanced mammal-like reptiles, the therapsids, the Dinocephalia are generally regarded as the oldest and in many respects the most primitive suborder. In them, according to Boonstra (personal communication), the epipterygoid is small or reduced except in the titanosuchid genus

Anteosaurus. In the latter the bone extends right up to the skull roof, has an expanded waist and a relatively long anterior footplate. In *Jonkeria* (titanosuchid) the footplate is also extended anteriorly but dorsally the epipterygoid only reaches halfway to the roofing bones while the footplate as well as the dorsal ramus are reduced in the tapinocephalid *Struthiocephalus*. In none of the Dinocephalia do we find evidence of a posterior extension to the footplate which could have formed a link between the epipterygoid and the quadrate. According to Watson (1914) the Dinocephalia, as a group, has a very special importance because alone amongst the therapsids it retained a large quadrate. This feature as well as the absence of the quadrate ramus of the epipterygoid indicates affinities with the reptilian rather than the mammalian lines of evolution.

Anomodontia

The anomodonts are generally regarded to be an aberrant group of mammal-like reptiles with but weak mammalian affinities. This is borne out by the structure of the palatoquadrate complex in this group. As in the Dinocephalia the anomodonts *Kannemeyeria erithrea* (Case, 1934), *Dicynodon kolbei* (Broom, 1932), *D. sollasi* (Watson, 1948), *Lystrosaurus murrayi* (Broom, 1932), *Daptocephalus leoniceps* (Ewer, 1961), *Kingoria nowacki* (Cox, 1959), *Dicynodon grimbeeki* and *Pristerodon buffaloensis*, all display an epipterygoid with a long, thin dorsally projecting columellar portion, reminiscent of recent reptiles (see later). However, in contrast to the latter the base of the epipterygoid is expanded, to varying degrees, in all of the above, extending for some distance along the upper edge of the quadrate ramus of the pterygoid. In *Kannemeyeria* the base extends from a point close to the quadrate to beyond the front of the interpterygoid space.

In the anomodonts investigated, there is no direct contact between the epipterygoid and the quadrate (fig. 11), but there is a distinct probability that a cartilaginous link existed in life in some of these forms, as has been shown

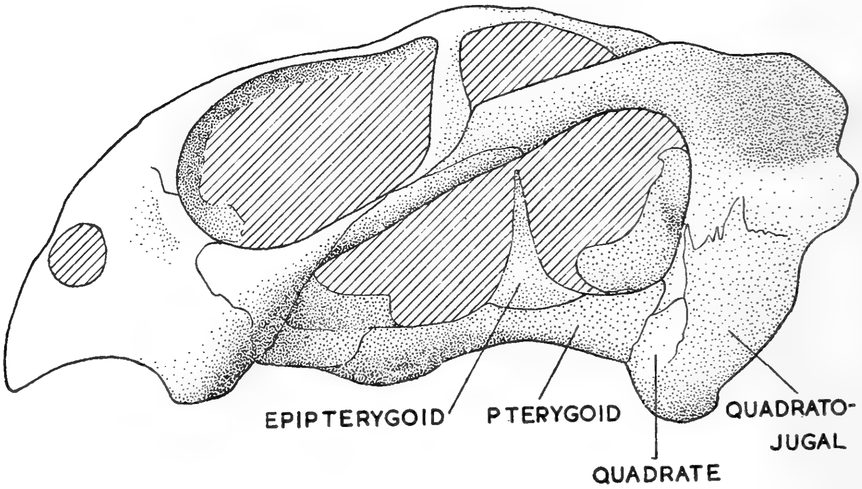

Fig. 11. *Dicynodon* sp. Lateral view of skull.

for *Pristerodon.* However, the general tendency within the group is for the bar, linking the epipterygoid to the quadrate portion, to become reduced; an evolutionary trend, as will be shown later, that was present also in the line that culminated in modern reptiles.

Gorgonopsia

In all known Gorgonopsia the epipterygoid is high and relatively narrow, with a well-developed footplate. In '*Lycaenodon*' (fig. 12), *Scymnognathus*, *Leptotrachelus*, *Cynariops* (Boonstra, 1934a) and *Aelurognathus* (Haughton, 1924), the footplate has a long tapering anterior extension, with a short posterior extension ending some distance away from the quadrate. Boonstra found no evidence in this group of a widening of the vertical portion of the epipterygoid.

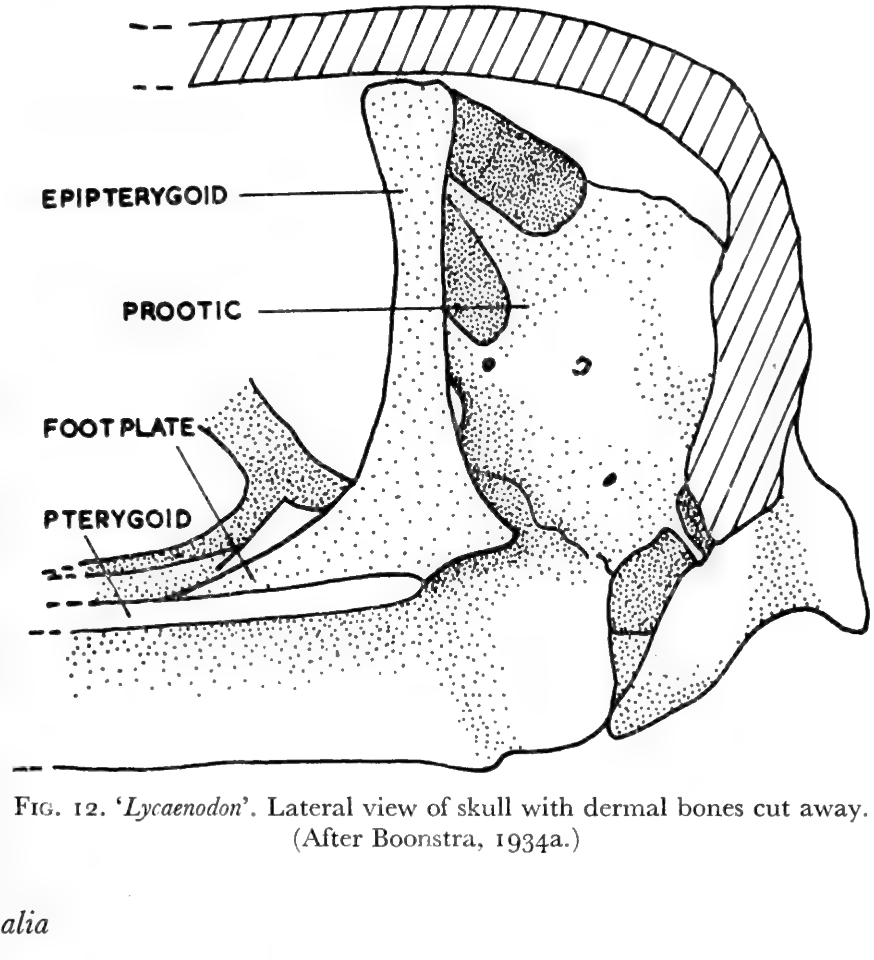

FIG. 12. '*Lycaenodon*'. Lateral view of skull with dermal bones cut away. (After Boonstra, 1934a.)

Therocephalia

In the early *Tapinocephalus* Zone forms such as the pristerognathids *Scylacosaurus* and *Scymnosaurus* (Boonstra, 1934b, 1954), and most of the primitive therocephalians, the vertical portion of the epipterygoid is still relatively narrow, but in *Glanosuchus macrops* (Boonstra, 1954) the epipterygoid has become dumb-bell-shaped, although still not much widened. The base has no noteworthy posterior process. However, in the lycosuchid *Trochosaurus major* (Boonstra, 1934b) occurring in the same zone, the epipterygoid has developed into a large, broad plate which obscures the lateral opening into the pituitary fossa and the foramina for the Vth and VIth nerves. The epipterygoid here is more than twice as broad as in any known gorgonopsian and has the appearance of a cynodont epipterygoid. It differs from that known in *Scymnosaurus* and *Scylacosaurus* in having an expanded upper end in addition to a wide footplate, a condition reaching its greatest development in the later whaitsids (Boonstra, 1934).

Of the *Cistecephalus* Zone Therocephalia, *Euchambersia mirabilis* (Boonstra, 1936) also shows the dorsally and ventrally expanded condition (fig. 13) but the shaft of the bone does not show much expansion. In the scaloposaurid *Ictidosuchops intermedius* (Crompton, 1955), however, the shaft is a broad one, and ends in a slightly more expanded dorsal portion which fits into a shallow depression in the antero-dorsal wall of the prootic, consequently forming part of the true lateral wall of the braincase. The anterior extension of the footplate is long, but the posterior one is short. At the juncture of the posterior extension and the ascending ramus there is a shallow notch which most probably housed the maxillary or both the maxillary and mandibular branches of the trigeminal nerve (Crompton, 1955).

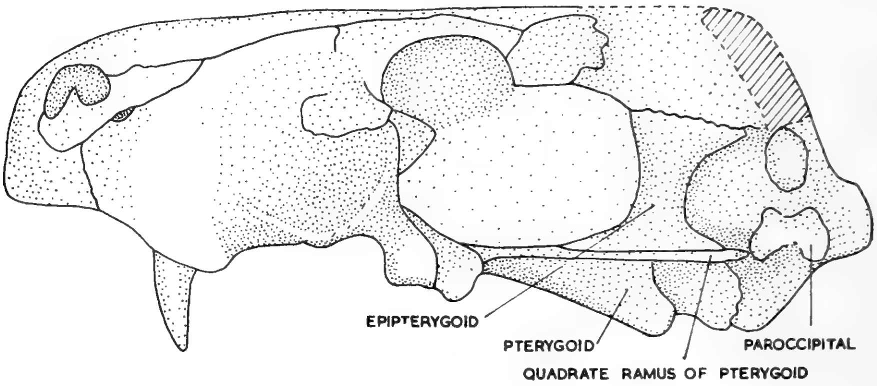

Fig. 13. *Euchambersia mirabilis*. Lateral view of skull with dermal bones cut away. (After Boonstra, 1936.)

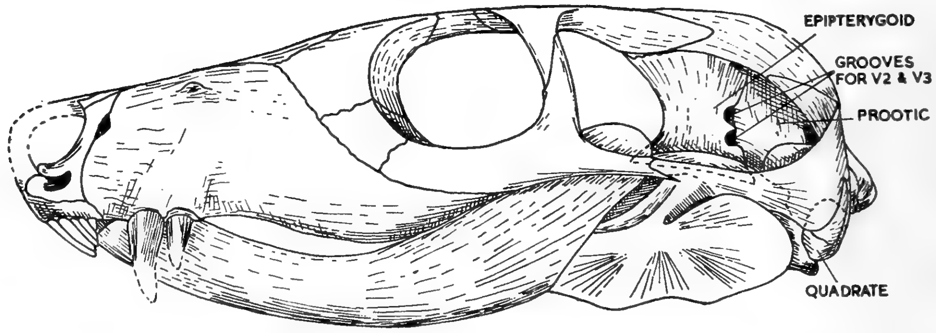

Fig. 14. *Aneugomphius ictidoceps*. Lateral view of skull with outlines of palatoquadrate bones indicated. (After Brink, 1956.)

In *Theriognathus microps* (Boonstra, 1934), *Notosollasia laticeps* (Boonstra, 1934) and *Aneugomphius ictidoceps* (Brink, 1956), as in all known whaitsids, the epipterygoid is broad and flat with greatly expanded dorsal and ventral ends (fig. 14). The base is long and in most forms posteriorly overlaps the prootic obscuring the incisura prootica. The hind wall of the epipterygoid in *Aneugomphius* shows two deep notches, probably for the exit of the maxillary and mandibular branches of the trigeminal nerve.

Cynodontia

Brink (1960) states that the epipterygoids of the primitive cynodont *Scalopocynodon gracilis* are '. . . Cynodont-like in being broadly expanded, but Therocephalian-like in their feeble overlap of the prootics' (p. 145). The anterior extension of the footplate is long and broad while the remainder of the ventral margin follows the dorsal margin of the quadrate ramus of the pterygoid (fig. 15). Brink made the interesting observation that the anterior margin of the epipterygoid is very thick. This may well support the view that this portion of the vertical limb is the more stable and is older phylogenetically than the thinner, posterior section of the limb. The quadrate is in the shape of a wedge lodged loosely in a cavity anteriorly in the squamosal. The anterior margin is straight, blunt and vertical, while the posterior margin is sharp and broadly curved. The quadrate is a much smaller bone than the epipterygoid and is well separated from the latter.

In *Thrinaxodon liorhinus* (Parrington, 1946) the epipterygoid is greatly expanded and dorsally is broadly in contact with the prootic. The quadrate ramus of the epipterygoid joins the prootic, but does not reach the quadrate, leaving a large foramen between the epipterygoid and prootic for the maxillary and mandibular rami. The quadrate, which is about one-third the size of the epipterygoid, has a wide, dumb-bell-shaped articulating surface and a thin, slightly curved dorsal process which medially is greatly strengthened by a pillar-like development which continues to the apex of the bone.

In an unidentified cynodont, which compares closely with *Trirachodon*, Parrington (1946) found two foramina between the epipterygoid and prootic. A groove comparable with that leading into the single foramen in *Thrinaxodon*, leads into the lower, larger foramen from below and behind. The dorsal smaller foramen is probably new. Parrington states that the significance of this development lies in the possibility that the maxillary left the skull by the upper foramen, which is apparently mainly enclosed by the epipterygoid, and is equivalent to the foramen rotundum, and the mandibular by the lower, larger foramen, the equivalent of the foramen ovale. The size of both foramina indicates that blood vessels accompanied the nerves.

In *Diademodon mastacus* (Brink, 1955) the foramen for the trigeminal is also divided into two, although incompletely in this species (fig. 16). The foramen lies slightly above and behind the pituitary fossa. The epipterygoid itself covers the anterior half of the prootic. The footplate is extensive and extends forward as a very thin tapering process while it reaches the quadrate with its posterior extension.

In the cynognathids, the thin plate-like epipterygoid overlaps the anterior superior process of the prootic. The footplate of the base is extensive. It sends back a posterior extension which occupies the position of the quadrate ramus of the pterygoid and which reaches the relatively reduced quadrate.

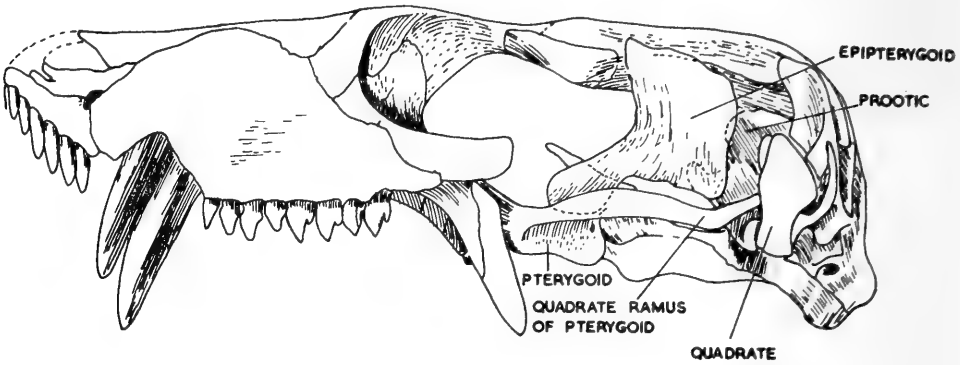

FIG. 15. *Scalopocynodon gracilis*. Lateral view of skull with dermal bones cut away. (After Brink, 1960.)

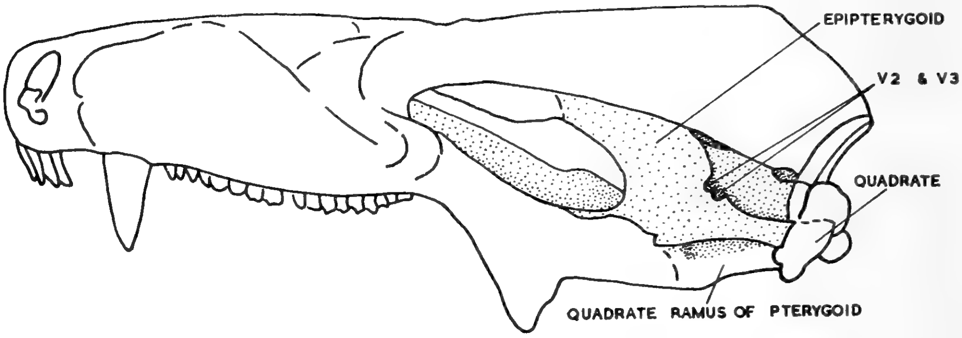

FIG. 16. *Diademodon mastacus*. Lateral view of skull with dermal bones cut away. (After Brink, 1955.)

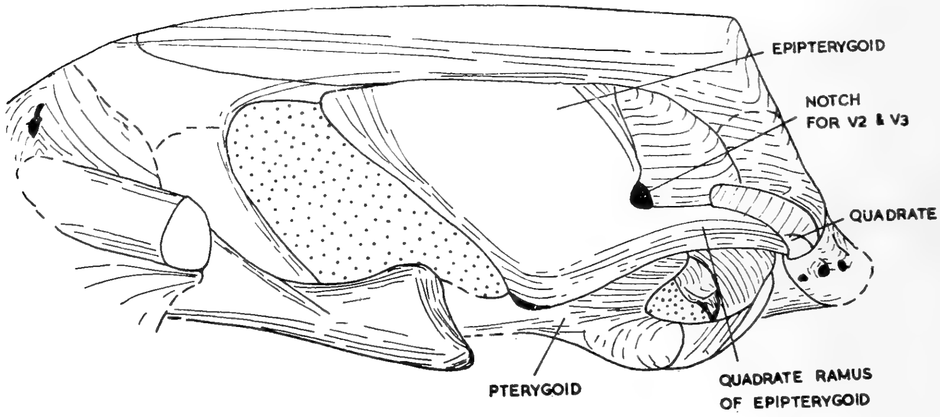

FIG. 17. *Diarthrognathus broomi*. Lateral view of skull. (After Crompton, 1958.)

Ictidosauria

In *Diarthrognathus broomi* the dorsal portion of the epipterygoid is extremely broad and overlaps the prootic above the prootic incisure. Here the posterior edge of the epipterygoid is slightly indented for the maxillary and mandibular branches of the trigeminal nerve (fig. 17). Crompton (1958) states that although it is difficult to ascertain, it would appear that the quadrate ramus of the epipterygoid meets the antero-medial edge of the quadrate. The quadrate is much reduced, S-shaped in occipital view, and the articular surface is markedly concave. This latter feature, according to Crompton, is of great significance as in all known therapsids, including *Bienotherium* and *Oligokyphus*, the articular face of the quadrate is either flat or convex, but never concave. It is also significant that the mammalian malleus (articular) possesses a convex articular surface which meets a convex articular face in the incus (quadrate).

In *Bienotherium* (Hopson, 1964) the epipterygoid and the anterior part of the prootic together form the side wall of the brain case (fig. 18). The quadrate ramus of the epipterygoid is more vertically orientated and deeper than in

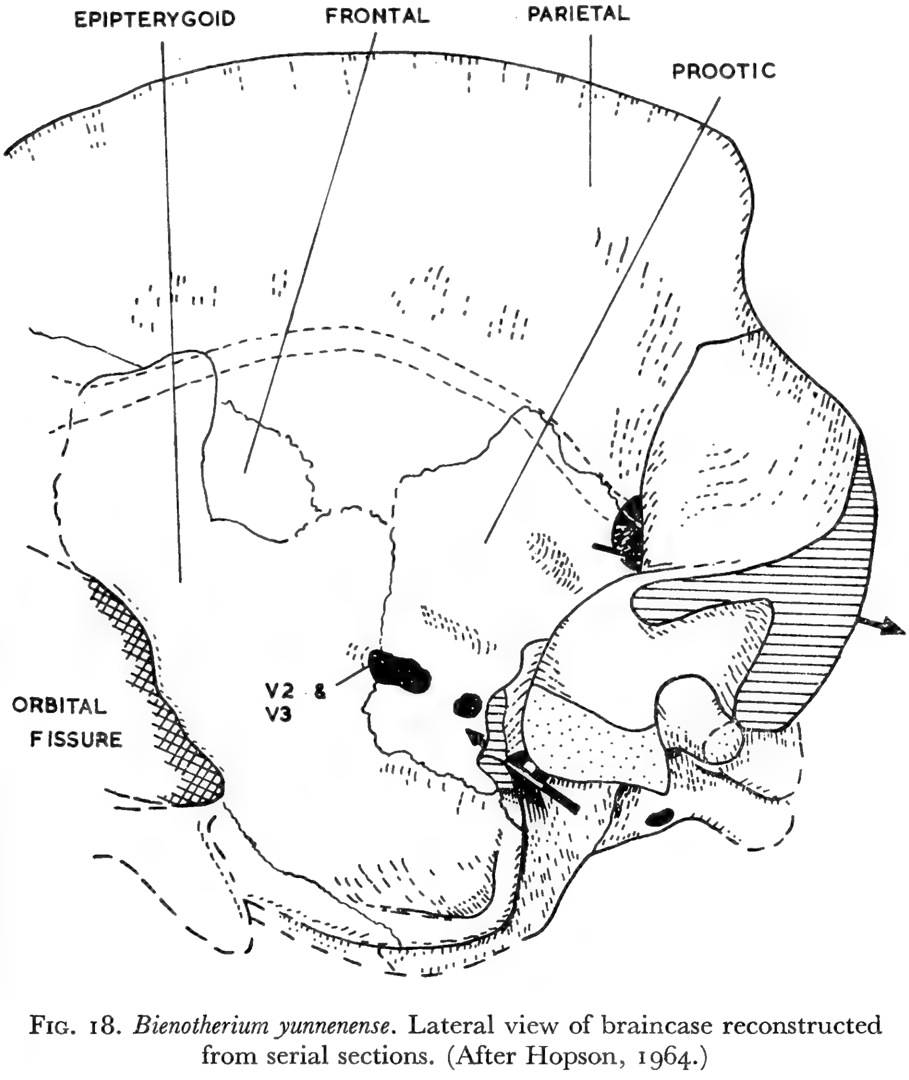

FIG. 18. *Bienotherium yunnenense*. Lateral view of braincase reconstructed from serial sections. (After Hopson, 1964.)

the cynodonts and could have reached the quadrate. The ascending ramus is broad and high with a posterior border which is overlapped laterally, above the trigeminal foramen, by the prootic. This latter is the reverse of the usual reptilian condition in which the prootic lies medial to the epipterygoid, and is ascribed by Hopson to the development of a forward extension of the anterior portion of the prootic in such a way that it lies lateral to the cavum epiptericum. In *Bienotherium* both this extension—the ventro-lateral flange—and the antero-dorsal border of the prootic extend well forward of the prootic incisure, an observation which has led Hopson to conclude that the prootic component of the trigeminal foramen in this form is not strictly homologous with the prootic incisure in cynodonts, because the former is merely a notch in the anterior border of the ventro-lateral flange. This conclusion seems to be supported by the fact that the trigeminal foramen pierces the side wall of the skull anterior to the depression of the semilunar ganglion. It also indicates that the maxillary and mandibular branches extend in an anterior direction through the cavum epiptericum in *Bienotherium*, whereas normally, in those forms with broadened epipterygoids, they pass in a posterior direction.

The trigeminal foramen is slightly constricted at mid-length presumably indicating the incipient subdivision of the single trigeminal foramen into the separate foramina rotundum and ovale of mammals.

TRICONODONTA

In a group of Mesozoic mammals, the Triconodonta, the brain case has an essentially reptilian structure. According to Kermack (1963) *Triconodon mordax* and *Trioracodon ferox* still possessed a cavum epiptericum lying outside the ossified lateral wall of the braincase (formed by the petrosal) and as in *Morganucodon* and possibly all pre-Cretaceous mammals, the alisphenoid formed the lateral boundary of the cavum. The ramus profundus passed out through the anterior end of the cavum epiptericum while the maxillary and mandibular nerves passed out through two foramina formed in the posterior edge of the alisphenoid.

According to Kermack, the semilunar ganglion in *Morganucodon* lay inside the primary wall of the braincase and the mandibular branch of the trigeminal nerve passed though the foramen pseudovale in the anterior lamina of the petrosal. The lamina extends much further forward in *Morganucodon* than it does in cynodonts. The maxillary branch of the fifth nerve presumably left the braincase, passing through the notch at the front end of the anterior lamina. After crossing the cavum epiptericum both branches would have left it by passing behind or through the alisphenoid in some way reminiscent of cynodonts.

In basic construction the braincase of the triconodonts differs from that of an advanced therapsid only in the narrower cavum epiptericum in the former, a difference due to the relatively larger size of the brain in mammals.

Living Reptiles and Mammals

Amongst recent reptiles *Sphenodon* has virtually retained its larval palatoquadrate in the adult (compare figs 3 and 19) but in the lizards *Lacerta* (Gaupp, 1906), *Cordylus*, *Eremias* and *Mabuia* (Broom, 1903), *Tropiocolotes* (Kamal, 1960), *Varanus* (Frazetta, 1962), *Tupinambis* (Jollie, 1960) and many others, and in the chelonians *Emys* (Kunkel, 1912) and *Chrysemys* (Shaner, 1926), the palatoquadrate complex undergoes considerable changes during ontogeny. Ossifications within the complex culminate in the formation of widely separated epipterygoid and quadrate portions, while the rest of the palatoquadrate is resorbed. The quadrate is retained as a comparatively strong element while the epipterygoid is whittled down to a narrow rod-like structure (fig. 20). The base of the bone is not expanded. It has, however, a cartilaginous epiphysis, fitting into the fossa pterygoidei which may be linked with the quadrate through a strand of connective tissue, both epiphysis and connecting strand probably representing remnants of the palatoquadrate cartilage.

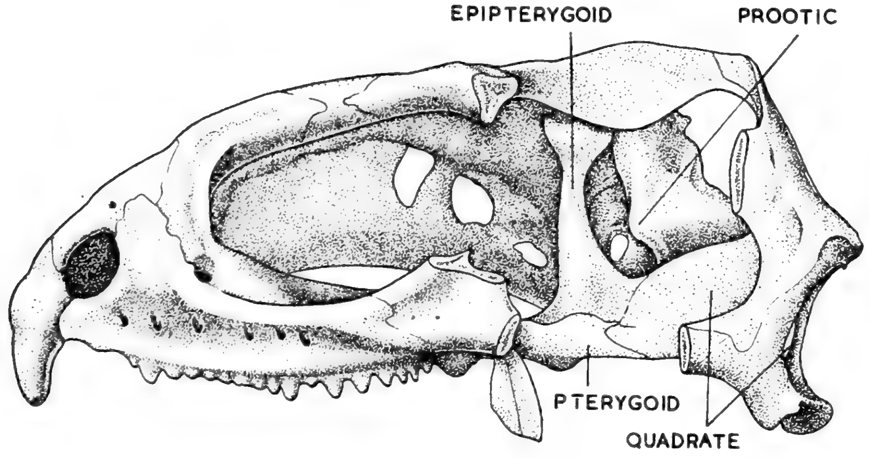

Fig. 19. *Sphenodon punctatus.* Lateral view of the skull with dermal bones cut off to show palatoquadrate.

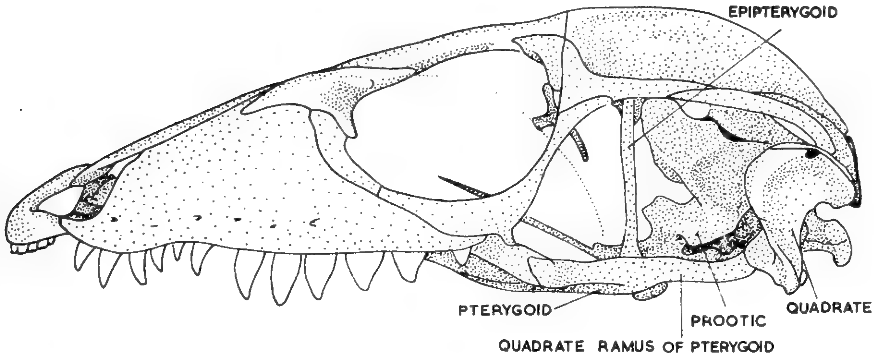

Fig. 20. *Tupinambis nigropunctatus.* Lateral view of skull. (After Jollie, 1960.)

Further reduction of the epipterygoid has taken place in the lizards *Agama*, *Lyriocephalus* and *Calotes* (Ramaswami, 1946), *Ophioceps* and *Anniella* (Jollie, 1960), *Phrynocephalus* (Siebenrock, 1895), *Physignatus*, *Chlamydosaurus* and *Amphibolurus* (Beddard, 1905), where the epipterygoid is very short. However, in the Chamaeleontidae, Dibamidae (Boulenger, 1887) and apparently most Amphisbaenidae (known only in *Trogonophis*, Bellairs, 1950), the epipterygoid is absent. In the Chelonia the epipterygoid is still present but very small (Parker, 1880) while it is much reduced or vestigial in Ophidia and Crocodilia, although the embryos of crocodiles still show the ascending process (Parker, 1883; Shiino, 1914). In birds it appears to be absent (Goodrich 1930), the quadrate being the only part of the palatoquadrate to be retained in the adult.

Where present the epipterygoid lies lateral to the lateral head vein, postero-lateral to the profundus and antero-medial to the maxillary and mandibular branches and the orbital artery.

In mammals the alisphenoid appears to be lost in *Echidna*. In this feature, as will be seen later, *Echidna* probably shows reptilian affinities. In *Dasyurus* the dorsal end of the ala temporalis fuses with the orbital cartilage, but in all other mammals, as far as is known, the ala temporalis ends freely (De Beer, 1937). In *Didelphis* the alisphenoid lies between the profundus and maxillary rami, as in reptiles. In *Trichosurus*, *Mus*, *Mustela* and many others (De Beer, 1937) the alisphenoid is pierced by the maxillary ramus (foramen rotundum), while in *Felis* (fig. 21), and the majority of mammals the mandibular ramus too may pass through it (foramen ovale). In the fourth group the maxillary emerges freely in front of the alisphenoid (De Beer, 1937).

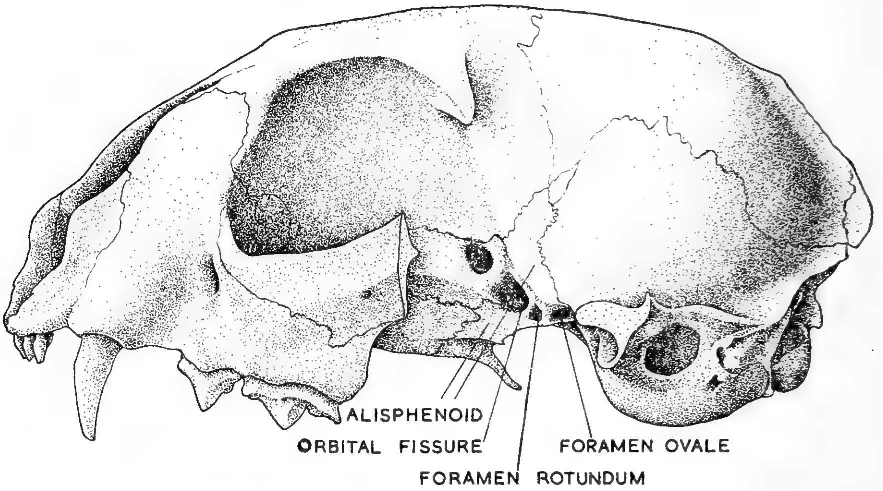

Fig. 21. *Felis domestica*. Lateral view of skull with jugal arch cut away.

Edinger and Kitts (1954) state that the mandibular branch of the trigeminal appears to have been variable in its relations to the alisphenoid in living mammals as the foramen ovale is absent in some of them. Several genera of extant Perissodactyla and Artiodactyla lack the foramen but in both these orders a separate foramen ovale was the usual condition in the early Tertiary. Comparison of fossil and recent material suggests a similar trend in certain families of the Rodentia and Insectivora. They relate the formation of the foramen ovale with an earlier palaeoneurological development when the mandibular nerve came to branch off the trigeminal stem intracranially, during or near the origin of mammals. It is only in some later forms that the nerve used the foramen lacerum for its passage from the braincase. This probably indicates that its absence is a secondary condition and possibly reveals an evolutionary trend within the mammals to abolish the separate exit of the mandibular nerve.

CONCLUSIONS

The evolutionary history of the palatoquadrate has been followed, as far as the availability of information on fossil material permits, from the early gnathostome condition to that in recent reptiles and mammals. It has been shown that the primitive palatoquadrate was a solid structure, consisting mostly of several ossifications, with four main processes for its attachment to the neurocranium. These are the otic, ascending, basal and pterygoid processes. In tetrapods the ossifications are reduced to two.

During its evolutionary history the palatoquadrate shows a tendency to become reduced in size, the pterygoid process shortens considerably while the area between the otic and ascending processes becomes deeply excavated thereby accentuating and demarcating the epipterygoid and quadrate portions. The demarcation of these two elements becomes more pronounced as evolution progresses.

Conditions in recent and fossil forms show that the palatoquadrate of both recent reptiles and mammals are deducable from the early gnathostome condition and that they evolved through the placoderm, crossopterygian, labyrinthodont and early stem reptile stages. In the groups leading to or showing affinities with the lines leading to modern reptiles, the trend is towards the progressive reduction of that part of the palatoquadrate anterior to the quadrate. In most reptiles the epipterygoid is the only part of this area to be retained but in some recent forms even this too disappears. In those lines leading towards mammals the opposite occurred and regression of the quadrate took place while the epipterygoid expanded (fig. 22).

From the foregoing it is clear that the phylogenetic and ontogenetic evidence do not support the view that the epipterygoid in the primitive reptile possessed a restricted base. The latter condition is a specialized reptilian one as is proved by conditions obtaining in adult forms of many recent reptiles. It is a stage in the gradual reduction of the epipterygoid in this group. Olson's (1944) views on the evolutionary development of the epipterygoid, must then differ from those given here.

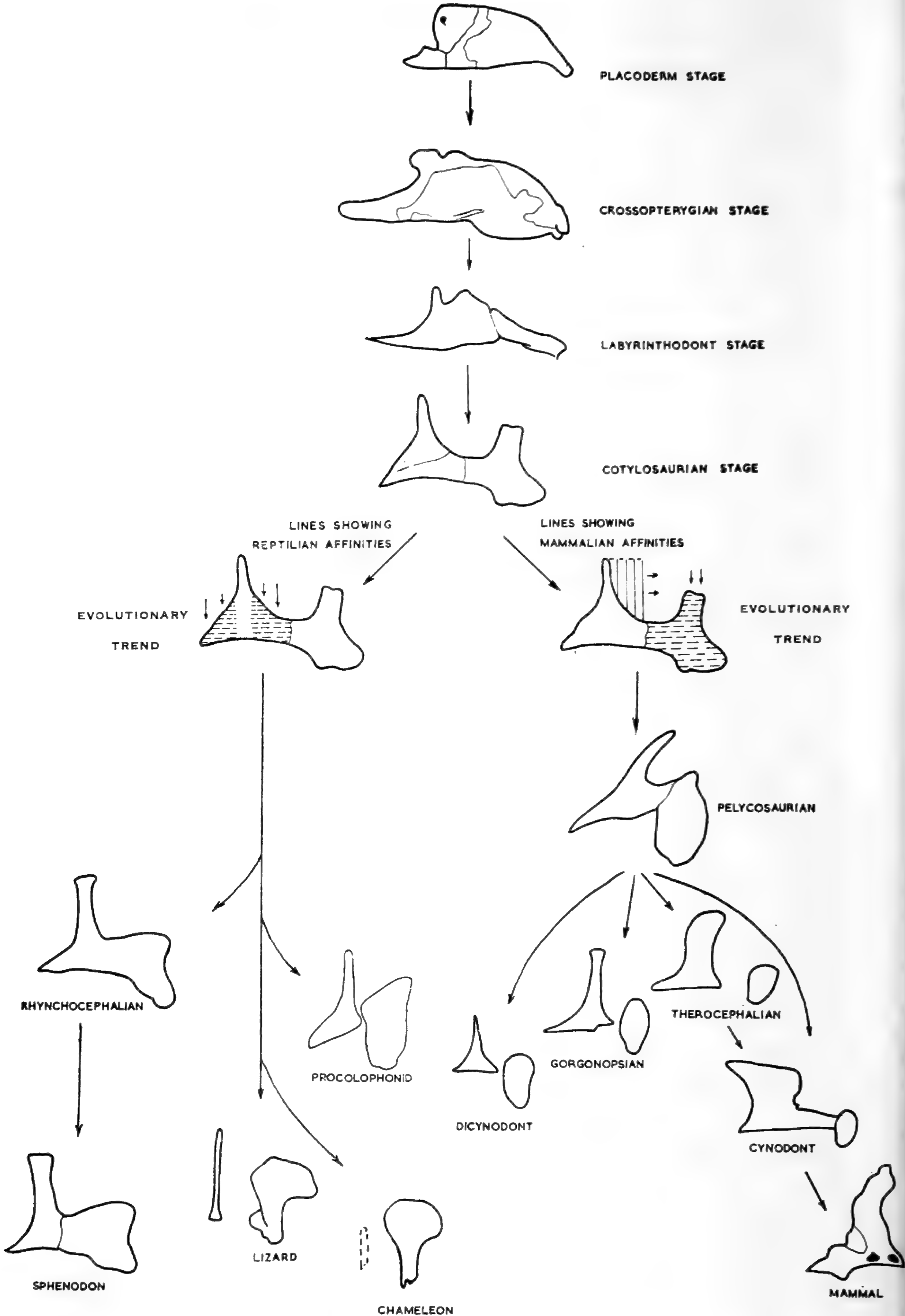

Fig. 22. Schematic presentation of probable evolutionary trend in development of palatoquadrate leading towards recent reptiles and mammals.

Although the therapsids show a marked degree of variability in the structure of the epipterygoid, we find that the groups which show mammalian affinities have also retained certain basic features of the early tetrapod palatoquadrate complex. The most noticeable of these is the retention of the extensive base of the epipterygoid, indicating that a considerable portion of the base of the palatoquadrate anterior to the quadrate, of the early labyrinthodont and stem reptile, had been retained.

Two further features are closely linked with the development of the alisphenoid in mammals. Firstly the expansion posteriorly of the rod-like ascending process of the epipterygoid and secondly, the increase in size of the brain in forms approaching the transitional stage.

Backward extension of the ascending process would result in the maxillary and mandibular branches of the trigeminal nerve being pushed backward by the epipterygoid as the latter progresses past the incisura prootica through which the trigeminal emerges.

The increase in size of the brain in mammals and the consequent lateral expansion of the braincase, could conceivably result in the nerves becoming trapped between the posteriorly extending epipterygoid and the expanding braincase. Close contact between the epipterygoid and braincase could force the nerves to seek an exit through the epipterygoid. Whether this results in the formation of a notch only, a foramen or two foramina depends largely on the separate development of the epipterygoid and prootic, the way these bones make contact and where this contact is made. In this way the maxillary ramus can emerge through the foramen rotundum while the mandibular emerges farther back through its own foramen ovale or merely through a notch in the posterior portion.

If the expansion of the braincase is continued anteriorly the cavum epiptericum would be obliterated, as it has been in mammals. This could mean that the pila antotica, which forms the inner wall of the cavum in reptiles, could have been pushed against the alisphenoid and as the pila will then virtually have become redundant, there is no need for it to develop in mammals. The possibility that this could have happened is strengthened by the fact that isolated cartilaginous fragments of the pila antotica have been found in many higher mammals, e.g. *Lepus* (Voit, 1909), *Homo* (Macklin, 1914), *Felis* (Terry, 1917), *Didelphys* (Töplitz, 1920), *Halicore* (Matthes, 1921) and *Tarsius* (Henckel, 1927).

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SUMMARY

The serial sectioning of the skull of the anomodont *Pristerodon buffaloensis* has produced valuable evidence regarding the structure of the palatoquadrate complex and the evolution of the therapsid epipterygoid. A short review is given of the structure of the palatoquadrate in the most important known fossil vertebrate groups.

It is emphasized that the mammalian alisphenoid should not be looked upon as a transformation of the rod-like epipterygoid, as found in more specialized true reptiles as Broom and others implied, but that both conditions are derived from a common ancestral type.

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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).

N. A. H. MILLARD

THE HYDROZOA OF THE SOUTH AND WEST COASTS OF SOUTH AFRICA. PART III. THE GYMNOBLASTEA AND SMALL FAMILIES OF CALYPTOBLASTEA

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THE HYDROZOA OF THE SOUTH AND WEST COASTS OF SOUTH AFRICA. PART III. THE GYMNOBLASTEA AND SMALL FAMILIES OF CALYPTOBLASTEA

BY

N. A. H. Millard

Zoology Department, University of Cape Town

(With 15 text-figures and 1 plate)

Contents

Introduction

This paper represents the third and final part of a systematic account of the hydroids from that part of the South African coast stretching from South West Africa on the west to the southern border of Natal on the east. For details on the origin of the collections the reader is referred to the introduction to part I of the series (Millard, 1962).

When examining Gymnoblast hydroids one must bear in mind that a considerable quantity of the more delicate material brought up by dredging becomes destroyed by rough handling or is so badly damaged that identification beyond the genus level is impossible. Moreover most genera require the presence of gonophores, usually female, for identification to species level. This applies particularly to such genera as *Eudendrium* and *Tubularia*. It is felt that no useful

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purpose would be served by including dubious records and, at the risk of giving a false impression of the abundance, poorly preserved material and sterile material of doubtful specific identification has generally been omitted.

The author wishes to express thanks to the following: the South African Museum for permission to examine the collection of the s.s. *Pieter Faure*, the Zoology Department of the British Museum of Natural History for accommodation and permission to examine their collection in 1960, Dr. W. Engelhardt of the Munich Museum and Dr. J. S. Pringle of the Natal Museum for the loan of type material, Dr. M. E. Thiel of the Hamburg Museum for identification of certain medusae and finally all past and present members of the Zoology and Oceanography Departments of the University of Cape Town who have helped to accumulate material in the now very extensive University collection.

Type specimens of new species have been deposited in the South African Museum and have been given a Museum registered number in addition to the University catalogue number.

STATION LIST

A. Littoral material from Oudekraal on the west coast of the Cape Peninsula. Position: 33°58·5′S/18°22·2′E.

	Date
A 40	16.1.34
A 116–122	15.3.34
A 139	17.3.34
A 353	
A 383	13.5.34
A 384	25.8.34
A 405	18.10.34

AFR. Material dredged by the government research vessel, R.S. *Africana.*

	Date	*Position*	*Depth (m.)*	*Bottom*
AFR 736	17.8.47	30°42·4′S/15°59·2′E	201	co gn S, Sh
AFR 801	7.10.47	32°34·4′S/17°52·2′E	71	gn M, R
AFR 866	9.1.48	34°36·8′S/19°16·4′E	38	R, S
AFR 967	23.3.48	35°07′S/20°49′E	91	f S
AFR 985	5.4.48	34°47·4′S/20°19′E	80	gn M
AFR 994	19 4.48	34°34·5′S/21°22·5′E	68	co S, Sh
AFR 0002	6.6.49	33°10′S/17°57′E	73	

B. Littoral material from Lambert's Bay on the west coast. Date: July 1938. Position: 32°05′S/18°18′E.

BMR. Bushman's River Estuary, south coast, on sand and muddy banks. Date: 14.9.50. Position: 33°41′S/26°40′E. Depth: 2–4·5 m.

BRE. Breede River Estuary, south coast, littoral. Date: 3.2.52. Position: 34°25′S/20°51·5′E.

CP. Littoral material from various localities on the west coast of the Cape Peninsula.

	Date	*Locality*	*Position*
CP 325	20.9.48	Sea Point	33°55·2′S/18°22·6′E
CP 327	16.12.48	Blaauwberg Strand	33°48′S/18°27·5′E
CP 331	8.8.49	Kommetje	34°08·5′S/18°19·4′E
CP 336	12.5.49	Oudekraal	33°58·5′S/18°22·2′E
CP 378	3.6.52	Cape Town docks (on *Squalus fernandinus*)	33°54·5′S/18°25·5′E
CP 646	5.12.60	Oudekraal	33°58·5′S/18°22·2′E

CPR. Material from various localities in the Cape Province.

	Date	*Locality*	*Position*	*Depth* (m.)
CPR 9	30.4.50	Glentana Strand	34°04′S/22°20′E	littoral
CPR 46	20.6.59	Umgazi Bay	31°43′S/29°26′E	27

HAM. Keiskama River Estuary, Hamburg, on the south coast. Date: 9.1.50. Position: 33°17′S/27°32′E.

HB. Littoral material from Hondeklip Bay on the west coast. Date: 8.2.40. Position: 30°19′S/17°16′E.

KNY. Knysna Estuary on the south coast. Position: 34°05′S/23°04′E (average).

	Date	*Depth (m.)*	*Bottom*
KNY 30	16.7.47	5–7	M, S
KNY 70	15.7.47	2–6	S
KNY 164	9.7.50	0–3	M
KNY 165	9.7.50	1–13	S
KNY 176	11.7.50		Floating buoy
KNY 212	7.7.60	0–1	S
KNY 270	14.2.64	0–1	M

L. Littoral material from East London on the south coast. Position: 33°01′S/27°54′E.

	Date
L 44	6.3.37
L 56–177	–.7.37

LAM. Dredged in Lambert's Bay, west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
LAM 24	16.1.57	32°04·6′S/18°18·15′E	17	R
LAM 30	19.1.57	32°05·1′S/18°17·7′E	20	R
LAM 35	19.1.57	32°05·5′S/18°17·7′E	27	R, Sh
LAM 46	22.1.57	32°04·4′S/18°17·7′E	23	R
LAM 50	23.1.57	32°08·5′S/18°17·7′E	16	R, S
LAM 52	21.1.57	32°04·7′S/18°18·2′E	17	S
LAM 59	23.1.57	32°09′S/18°18′E	16	R, S

LB. Langebaan Lagoon, west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
LB 127	26.4.48	33°05·6′S/18°01·6′E	Littoral	R
LB 166	15.7.46	33°09·0′S/18°03·4′E	7	
LB 266	3.5.51	33°07·4′S/18°02·1′E	Littoral	S

	Date	*Position*	*Depth (m.)*	*Bottom*
LB 296	5.5.51	33°04′S/18°00′E		Ship's hull
LB 314	4.5.51	33°05·7′S/18°01·5′E	Littoral	R
LB 371	7.5.53	33°05·7′S/18°01·5′E	Littoral	R
LB 378	7.5.53	33°05·9′S/18°01·9′E	0–1	Wooden piling
LB 380	7.5.53	33°06·7′S/18°01·0′E	4	S, Sh
LB 386	8.5.53	33°06·5′S/18°02′E		Ship's hull
LB 398	24.7.53	33°07·1′S/18°02·9′E	0–1	S
LB 403	5.12.53	33°10′S/18°03·5′E	Littoral	M
LB 542	4.5.60		Littoral	
LB 556	22.7.63	33°07·3′S/18°03·0′E	Littoral	Wooden piling

LIZ. Dredged in Algoa Bay, Port Elizabeth, south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
LIZ 2	5.4.54	33°55·7′S/24°37·2′E	9	M
LIZ 3	5.4.54	33°56·1′S/25°40′E	17	S
LIZ 7	6.4.54	33°58·1′S/25°38·9′E	9	R, St
LIZ 11	6.4.54	33°57·2′S/25°38·0′E	9	Clay, R
LIZ 13	6.4.54	33°58·2′S/25°38·8′E	7	S
LIZ 16	7.4.54	33°58·4′S/25°40·5′E	14	St
LIZ 24–25	11.4.54	34°00·4′S/25°44·5′E	39	co S, Sh
LIZ 40	11.4.54	34°00·8′S/25°42·4′E	6	R

LU. Littoral material from Luderitz Bay, South West Africa.

	Date	*Position*
LU 59	24.2.63	26°38′S/15°05·5′E
LU 113–118	22.2.63	26°38′S/15°09·3′E

MB. Dredged in Mossel Bay, south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
MB 8–12	12.1.56	34°04·3′S/22°13·9′E	19	R
MB 19	13.1.56	34°08·7′S/22°07·2′E	13	R, S, Sh
MB 25	13.1.56	34°09·3′S/22°10·1′E	29	S
MB 37	16.1.56	34°09·3′S/22°10·0′E	31	S
MB 47	17.1.56	34°11·3′S/22°10·0′E	10	R
MB 52	17.1.56	34°11·0′S/22°09·9′E	14	R, S
MB 55	17.1.56	34°10·7′S/22°09·6′E	9	R
MB 60	18.1.56	34°04·3′S/22°14·2′E	18	R, co S, Sh
MB 64	18.1.56	34°04·8′S/22°13·1′E	26	R, co S, Sh
MB 69	19.1.56	34°08·6′S/22°07·3′E	13	R, S
MB 70	19.1.56	34°08·9′S/22°07·9′E	18	S
MB 81	20.1.56	34°06·2′S/22°10·9′E	27	M
MB 84	21.1.56	34°11·4′S/22°10·1′E	29	R
MB 88	18.1.56	34°04·8′S/22°13·1′E	26	R, co S, Sh

OLF. Olifant's River Estuary, west coast. Date: 23.1.55. Position: 31°42′S/18°15′E.

PP. Littoral material from Paternoster, west coast. Date: 24.9.57. Position: 32°43′S/17°55′E.

SAMH. Material from the collection of the South African Museum. Specimens 147–352 and 361–383 were dredged by the s.s. *Pieter Faure*. Their positions were given in the original records as compass bearings off salient points on the coast, and were probably not very accurate. These have been converted into latitude and longitude and are given to the nearest minute.

	Date	*Position*	*Depth (m.)*	*Bottom*
SAMH 147	23.6.1898	South of Mossel Bay		
SAMH 157–162	15.7.1898	34°08′S/22°16′E		St
SAMH 166–170	11.11.1898	33°49′S/25°56′E		
SAMH 174–177	19.11.1898	33°45′S/26°44′E	73–78·5	M
SAMH 179–180	22.12.1898	32°52′S/28°12′E		
SAMH 189	28.12.1898	33°09′S/28°03′E	86	R, S, Sh
SAMH 202–203	7.3.1899	33°59′S/25°51′E	24–27	
SAMH 214	24.3.1899	33°50′S/26°35′E	91	M
SAMH 221–227	19.6.1899	34°26′S/21°42′E		f S
SAMH 230–233	20.9.1899	34°15′S/22°10·5′E		M
SAMH 235	5.7.1900	34°27′S/20°58′E	51	Crl
SAMH 239–247	11.10.1900	34°08′S/22°59·5′E	73	Crl, S, Sh
SAMH 250–253	15.7.1901	33°13·5′S/27°58′E	89	brk Sh
SAMH 269–274	17.7.1901	33°07′S/27°47·5′E		f S
SAMH 283	25.7.1901	32°50′S/28°18·5′E	86	brk Sh
SAMH 296	13.8.1901	32°47′S/28°28′E	82	brk Sh
SAMH 315	10.9.1901	33°54′S/26°51′E	120	brk Sh, St
SAMH 327–328	22.9.1904	34°12′S/22°15·5′E	51	f S
SAMH 335–338	4.10.1904	34°12′S/22°15·5′E	51	f S
SAMH 341–343	19.10.1904	34°15·5′S/22°14′E	64	M
SAMH 351–352	22.8.1905	33°52′S/26°09′E		M
SAMH 357	19.6.1914	33°55′S/18°27′E		
SAMH 361	11.11.1898	33°49′S/25°56′E		
SAMH 380–383	15.3.1899	33°47′S/26°19′E	23	S, Sh, St
SAMH 404	–.4.1962	28°30′S/16°10′E	15	
SAMH 405–408	–.7.1962	28°30′S/16°10′E	15	

SB. Saldanha Bay, west coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
SB 132	26.3.53	33°04′S/17°59·3′E	8	
SB 153–168	–.9.57	33°02·5′S/18°02′E	Littoral	R
SB 174	27.4.59	33°02·8′S/18°00·6′E	15	S, Sh
SB 178	28.4.59	33°03·6′S/18°00·4′E	15	R, kh S, Sh
SB 196	1.5.59	33°04·4′S/17°56·4′E	35	R
SB 231	4.5.60	33°00·6′S/17°59·6′E	8	R, kh S
SB 235	4.5.60	33°04·1′S/17°59·7′E	9	kh S
SB 267	25.4.62	33°02′S/17°57·2′E	22	kh S
SB 269	25.4.62	33°02·1′S/17°58′E	20	kh S, Sh

SCD. Dredged off the south coast.

	Date	*Position*	*Depth (m.)*	*Bottom*
SCD 5	19.4.58	34°15′S/25°05′E	11	R, Sh
SCD 20	26.5.58	34°07·3′S/23°23·8′E	46	R
SCD 22	26.5.58	34°26·7′S/23°26·0′E	114	Sh
SCD 26	23.5.58	33°47′S/26°04′E	47	M, Sh
SCD 29	22.6.58	33°38·6′S/26°54·7′E	56	R
SCD 37	19.5.58	32°15·2′S/28°57·7′E	49	R
SCD 50	18.5.58	31°38·8′S/29°34·4′E	33	R
SCD 52	20.8.58	34°01′S/25°45·5′E	46	R
SCD 56	19.8.58	33°37′S/26°56·6′E	46	
SCD 60	16.8.58	33°02′S/27°56·2′E	46	
SCD 61	15.8.58	32°17·7′S/28°54·5′E	49	
SCD 75	16.7.59	32°33′S/28°38′E	55	M, S
SCD 79–81	16.7.59	32°43′S/28°28′E	58	Sh, St

	Date	*Position*	*Depth (m.)*	*Bottom*
SCD 84–85	17.7.59	33°03′S/27°55′E	27	R
SCD 94	20.7.59	33°55·5′S/25°51′E	46	bk M, S
SCD 111	23.7.59	34°35′S/21°11′E	75	co S, Sh, St
SCD 112	20.7.59	33°55·5′S/25°51′E	46	bk M, S
SCD 113	26.11.59	34°24′S/21°45′E	27	S, f Sh
SCD 114	26.11.59	34°29′S/21°49·5′E	73	M
SCD 117–118	14.2.60	34°24′S/21°46′E	18	R
SCD 119	14.2.60	34°33′S/21°52′E	77	kh S
SCD 126	3.6.60	34°26·5′S/21°48′E	67	bk M
SCD 129–133	3.6.60	34°48′S/22°06′E	100	kh S
SCD 154	25.11.60	34°03′S/25°59′E	84	R
SCD 169	24.11.60	33°58·9′S/25°41·4′E	7	R
SCD 175	30.11.60	34°20′S/23°31′E	110	R, kh S
SCD 179	24.11.60	33°58·9′S/25°41·4′E	7	R
SCD 188	30.11.60	34°10′S/23°32′E	97	gn M
SCD 190	29.11.60	34°05·8′S/23°23·2′E	10	f S
SCD 206	30.11.60	34°51′S/23°41′E	182	kh S
SCD 215	25.11.60	34°03′S/25°58′E	78	S, Sh
SCD 239	29.11.60	34°02·0′S/23°28·4′E	49	M, R, S
SCD 258	14.7.61	33°53·8′S/25°42·5′E	32	f S
SCD 265	14.7.61	33°48′S/25°47′E	27	bl M, R
SCD 276	14.7.61	33°53·8′S/25°42·5′E	32	f S
SCD 281–283	11.2.62	34°04′S/23°23′E	22	f S, Sh
SCD 284	6.2.62	33°01′S/27°55′E	7	f S
SCD 312	9.2.62	33°58′S/25°47′E	48	f S
SCD 314	9.2.62	33°58′S/25°43′E	36	f M
SCD 328	10.2.62	34°43′S/25°40′E		Floating buoy
SCD 330	11.2.62	34°03·5′S/23°23′E	15	f S
SCD 333	11.2.62	34°02′S/23°27′E	42	M
SCD 347	12.2.62	34°10′S/22°15′E	54	M
SCD 354	11.10.62	32°08′S/29°12′E	210	
SCD 387	8.12.62	34°04·4′S/23°25·6′E	46	R
SCD 394	2.12.62	33°50·7′S/25°47·5′E	36	R, S

SH. Cape Town docks, from pylons and cable below tug jetty.

	Date
SH 433	14.4.61
SH 436	3.4.62

STJ. St. John's River Estuary, eastern coast of Cape Province. Date: 20.1.50 Position: 31°37′S/29°37′E.

SUN. Sunday's River Estuary, south coast. Date: 7.1.50. Position: 33°42′S/25°53′E.

SWD. Dredged off the coast of South West Africa.

	Date	*Position*	*Depth (m.)*	*Bottom*
SWD 12	10.2.63	26°35′S/15°01′E	71	R
SWD 39	12.2.63	26°37·5′S/15°04·5′E	40	R
SWD 42	13.2.63	26°38·0′S/15°00·2′E	71	R

TB. Dredged from Table Bay, Cape Town.

	Date	*Position*	*Depth (m.)*	*Bottom*
TB 6	4.8.46	33°49·5′S/18°27·5′E	13	S, Sh
TB 7–8	25.10.46	33°52·5′S/18°27·5′E	17	S Sh

	Date	*Position*	*Depth (m.)*	*Bottom*
TB 9	25.10.46	33°52′S/18°28′E	15	S
TB 13	4.8.46	33°49·5′S/18°27·5′E	13	S, Sh
TB 14	25.10.46	33°52·5′S/18°27·5′E	17	S, Sh
TB 15	11.2.47	33°47·5′S/18°24·3′E	19	S, Sh, St
TB 16	25.10.46	33°52′S/18°28′E	15	S
TB 17	26.6.47	33°52·7′S/18°28·7′E	9	S, St
TB 19	3.7.47	33°51·2′S/18°27·3′E	23	R, S
TB 21	15.12.57	33°48·6′S/18°24·6′E	15	S, Sh, St.

TRA. Material collected by commercial trawlers.

	Date	*Position*	*Depth (m.)*	*Bottom*
TRA 32	9.11.47	34°49′S/20°21·5′E	*c.* 91	
TRA 33	20.7.49	34°55′S/21°10′E	*c.* 90	R, S
TRA 35	21.1.50	34°34′S/20°50′E	70	M, S
TRA 38	–.7.50	34°30′S/20°56′E	73	M, S
TRA 42	–.7.51	34°30′S/20°55′E	*c.* 70	M, St
TRA 56	28.11.52	34°40′S/21°35′E	73	R, S
TRA 57	27.11.52	34°24′S/21°55′E	59	
TRA 59	26.11.52	34°28′S/21°45′E	70	S, St
TRA 86	23.3.53	32°41·7′S/17°58·5′E	9	S
TRA 92	–.1.54	35°03′S/21°50′E	110	R, S
TRA 99	18.1.56	34°25·5′S/21°50·2′E	60	S
TRA 150	6.3.58	34°42·2′S/20°25·0′E	91	M
TRA 156	15.10.58	34°12′S/18°22′E	22	Cable
TRA 159	6.7.58	33°56′S/25°36′E		Turtle

WCD. Dredged off the west coast of the Cape Province.

	Date	*Position*	*Depth (m.)*	*Bottom*
WCD 7	24.3.59	34°09·3′S/18°17·5′E	43	R
WCD 12	24.3.59	34°09·4′S/18°16·5′E	75	R
WCD 18	29.4.59	33°05·6′S/17°54·5′E	64	kh M
WCD 20	30.4.59	33°07·5′S/17°52·5′E	86	R
WCD 25	1.5.59	33°06·5′S/17°55·4′E	86	gn M
WCD 81	15.9.49	34°05′S/18°21′E	11	S
WCD 125	23.4.62	33°08′S/17°46′E	157	gn M
WCD 134	25.4.62	33°07·3′S/17°57·5′E	26	S
WCD 145	29.8.63	33°50·3′S/18°23·2′E	15	R
WCD 156	22.10.63	34°01·7′S/18°14·7′E	100	R
WCD 158–160	21.10.63	33°55·8′S/18°21·3′E	37	R
WCD 164	7.10.63	32°52′S/18°25′E	29	R

LIST OF SPECIES

Family **Tubulariidae**

Tubularia solitaria Warren, 1906.

Tubularia warreni Ewer, 1953.

Family **Myriothelidae**

Monocoryne minor n. sp.

Myriothela tentaculata n. sp.

Myriothela capensis Manton, 1940.

Family **Corynidae**

Bicorona elegans, n.g., n.sp.

Staurocladia vallentini (Browne, 1902).

Sarsia eximia (Allman, 1859).

Family **Solanderiidae**

Solanderia procumbens (Carter, 1873).

Family **Bougainvilliidae**

Bimeria vestita Wright, 1859.
Bougainvillia macloviana (Lesson, 1836).
Bougainvillia sp.
Dicoryne conferta (Alder, 1856).
Rhizorhagium robustum (Warren, 1907).

Family **Clavidae**

Clava sp.
Merona cornucopiae (Norman, 1864).

Family **Eudendriidae**

Eudendrium ?capillare Alder, 1856.
Eudendrium ?carneum Clarke, 1882.
Eudendrium deciduum Millard, 1957.
Eudendrium ramosum (Linn., 1758).

Family **Hydractiniidae**

Hydractinia altispina Millard, 1955.
Hydractinia kaffraria Millard, 1955.
Hydrocorella africana Stechow, 1921.
Podocoryne carnea M. Sars, 1846.

Family **Pandeidae**

Leuckartiara octona (Fleming, 1823).

Family **Aequoreidae**

Aequorea africana n. sp.

Family **Lovenellidae**

Lovenella chiquitita Millard, 1957.

Family **Haleciidae**

Halecium beanii (Johnston, 1838).
Halecium delicatulum Coughtrey, 1876.
Halecium dichotomum Allman, 1888.
Halecium halecinum (Linn., 1758).
Halecium ?muricatum (Ellis & Sol., 1786).
Halecium tenellum Hincks, 1861.

Family **Campanulariidae**

Campanularia hincksii Alder, 1856.
Campanularia integra MacGill., 1842.
Campanularia laminacarpa n. sp.
Campanularia ?mollis (Stechow, 1919).
Campanularia morgansi Millard, 1957.
Clytia hemisphaerica (Linn , 1767).
Clytia hummelincki (Leloup, 1935).
Clytia paulensis (Vanhöffen, 1910).
Obelia dichotoma (Linn., 1758).
Obelia geniculata (Linn., 1758).

Family **Tubulariidae**

Tubularia solitaria Warren, 1906.

Tubularia solitaria Warren, 1906: 83, pl. 10, 11. Millard, 1957: 179.

Records. West coast: A 122. LB 166 (recorded by Day, 1959). SB 153U. South coast: L 172.

Tubularia warreni Ewer, 1953

Tubularia warreni Ewer, 1953: 351, fig. 1–4. Millard, 1959*a*: 299. Millard, 1959*b*: 240.

Records. West coast: LB 296A, 386A (reported by Day, 1959). South coast: CPR 9G. KNY 176A (reported by Day, Millard and Harrison, 1952, as *T. ?betheris*).

Description. This material conforms to previous descriptions of the species with the exception of the CPR sample which differs in its paler coloration. The general effect, when alive, was a creamy colour, with pink tinges in the manubrium and gonophores. It is obviously a young colony, reaching a maximum height of 1·75 cm., and the largest hydranths measuring only about 2·5 mm. in length and 1 mm. in basal diameter. The blastostyles are unbranched and few in number (5–9) though fully mature gonophores are present. Apart from the colour there is nothing to distinguish it from *T. warreni.*

Family **Myriothelidae**

Monocoryne minor n. sp.

Fig. 1

Material. The holotype, SCD 215C, is a single specimen detached from its substratum and the only specimen known. Most of the colour has gone, though signs of a dark-red pigmentation are visible on the gonophores. South African Museum registered number: SAMH 410.

Description. Polyp measuring approximately 5 mm. in length, though somewhat contracted and curled up. Basal part of body (1 mm.) covered in transparent perisarc which is continued proximally in a number of threads and filaments, some of which appear to be filled with living coenosarc. Remainder of body cylindrical, bearing about 110 capitate tentacles. Tentacles solitary or arranged in groups of 2, 3, or 4 united at their bases. Length of tentacles variable: sometimes the middle one of a group of three is the largest as in *M. gigantea*, but sometimes all members of the group are equal in length and sometimes the first of a group of four is longest.

Eleven gonophores, apparently male, borne irregularly on the body of the polyp, the largest about 0·3 mm. in diameter. Gonophores pear-shaped, not distinctly demarcated from pedicel.

Nematocysts. At least three kinds visible in smears of preserved material:

(i) Desmonemes, the most abundant type. Capsule oval, thread with about 2 complete coils, on which a spiral ridging is visible. Size variable: 9·0–13·5 × 6·3–10·8 μ.

(ii) Stenoteles, fairly common. Capsule egg-shaped, with shaft occupying about half length. 15·3–18·0 × 13·0–15·3 μ.

(iii) Undetermined heteronemes, rare. Capsule elongated, with shaft occupying about $\frac{3}{5}$ length. 16·2–18·9 × 6·3–7·6 μ.

Remarks. As there is only one specimen available no sections were cut and accurate measurements could not be made without damage. A few detached

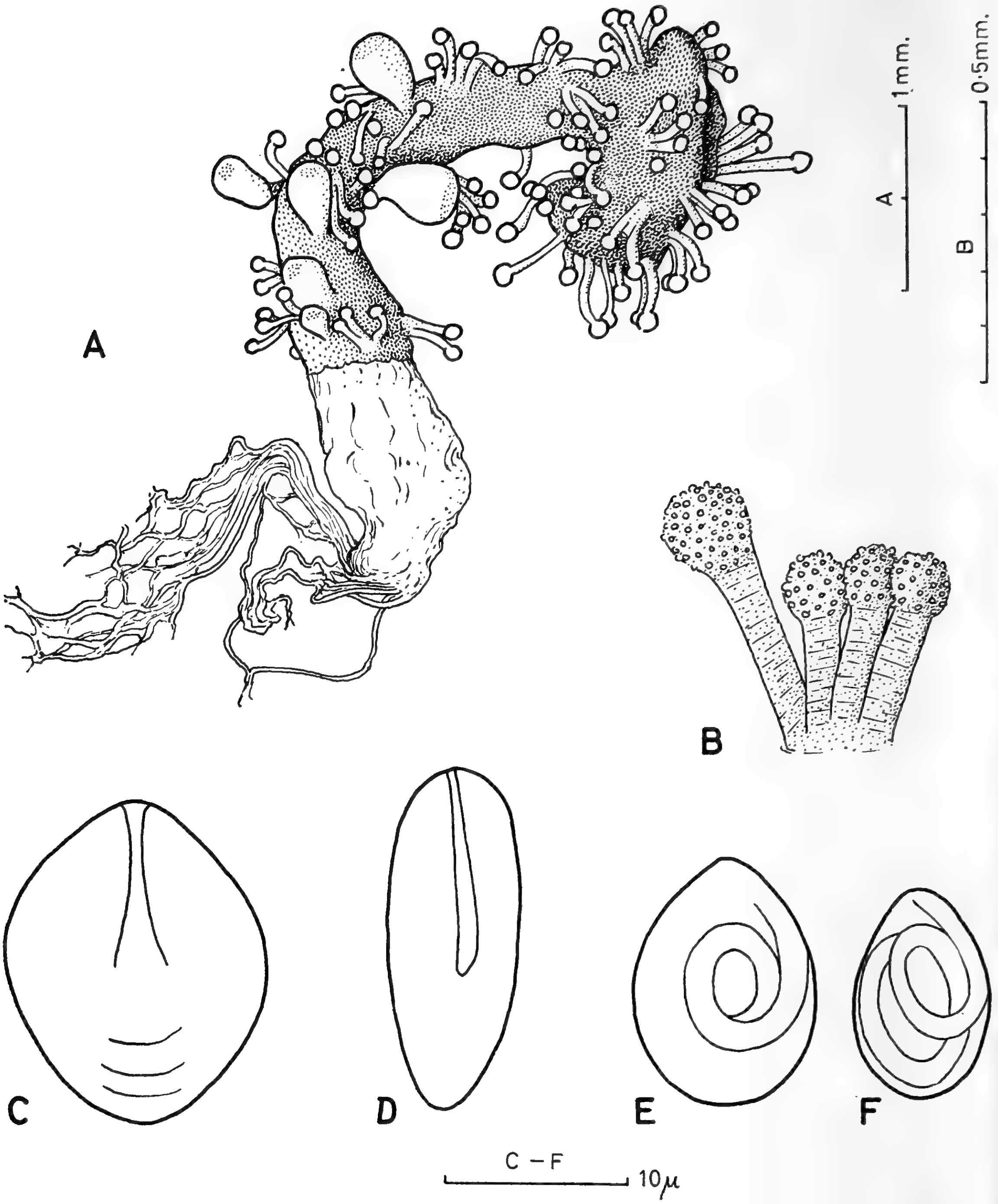

Fig. 1. *Monocoryne minor* n. sp.

A. The whole animal (holotype).
B. A typical group of 4 tentacles.
C–F. Nematocysts. (C, stenotele. D, undetermined heteroneme. E–F, desmonemes).

tentacles were used for examination of nematocysts. The specimen is fairly well preserved, but there is no knowing how many tentacles may have been broken off during handling, or whether the base was originally attached to a firm substratum. Since the tip of the body is curled over, the mouth could not be observed.

The arrangement of the tentacles differs from that in the only two known species of *Monocoryne*, namely *M. gigantea* (Bonnevie, 1898) and *M. bracteata* (Fraser, 1941), in both of which the middle one of a group is the largest. It is also much smaller than either of them. The gonophores are not seated in the axils of the tentacles but distributed at random over the body.

Myriothela capensis Manton, 1940

Myriothela capensis Manton, 1940: 276, pl. 1 (figs. 12, 13), pl. 3 (fig. 27), figs. 7, 8*b*, 9. Millard, 1957: 186.

Records. West coast: CP 331 (one almost mature male specimen attached to weed). LAM 52F (one mature female specimen attached to weed). LU 118Y (two mature male specimens torn from their base and two young specimens on crustacean appendage).

Description. The material from Luderitz Bay (LU 118Y) had retained its colour after about four months in spirit. The whole distal end of the body was a vivid splash of colour—the capita of the body tentacles and tips of the gonophores bright magenta, shading to pink on the stalks and colourless on the base of the polyp. Specimens preserved for a longer period are pale pink or completely colourless.

Largest specimen 1·6 cm. in length. Structure and nematocysts as described by Manton. One mature female specimen with actinulae larvae (one gonophore on opening contained three larvae). Female gonophores reaching 0·9 × 1·0 mm.

Myriothela tentaculata n. sp.

Fig. 2.

Material. WCD 7Q: 5 specimens from west coast attached to encrusting polyzoan, two of them rather badly damaged and the others in various states of preservation. The best preserved was selected as the holotype and another was used for sectioning. South African Museum registered number of holotype: SAMH 411.

Description of holotype. Total length 2·5 cm. No colour left in specimen except for a circle of dark-red spots round the distal end of each gonophore.

Basal region of hydranth (8 mm.) naked and drawn out into an irregular shape, bearing about 9 chitinoid, flattened, adhesive discs attached to the substratum.

Above this a single whorl of 17 long, tapering blastostyles reaching a maximum length of about 2 cm. These are generally somewhat coiled and bear a superficial resemblance to the tentacles of an octopus. They are the most distinctive feature of the species. Blastostyle unbranched, bearing 4–6 gonophores in the proximal 5 mm., of which the most distal is the oldest and the others in various stages of development. Capitate tentacles present amongst the gonophores and others (about 25) scattered irregularly over the distal region of the blastostyle. Tentacles rather poorly developed and resembling boot-buttons. Gonophores male, spherical, reaching a diameter of about

2 mm., each with a very short pedicel and 8–10 pigmented spots around distal end.

Distal region of hydranth (about $\frac{3}{5}$ of length) covered with densely packed capitate tentacles and bearing a terminal mouth. Tentacles well-developed, with slender stalks and large capituli, but more poorly developed in the region of the blastostyles.

Nematocysts. Four types distinguishable from smears and sections:

(i) 'Heteronemes' (fig. 2D), elongated and banana-shaped, with an axial body which stains red in Mallory's stain and a fine much-coiled thread. 44·1–45·9 × 8·1 μ.

(ii) Desmonemes of two sizes (fig. 2E–H), the larger 17·1–18·0 × 12·6–14·4 μ, the smaller 10·2–10·8 × 7·2–7·7 μ. In both, part of the thread stains red in Mallory's stain, the rest remains unstained. It bears a distinct spiral marking which may indicate the presence of barbs. The larger form contains a thread in 3 complete longitudinal coils and the smaller a thread in 2 coils.

(iii) Steroteles (fig. 2C). Oval capsules containing a butt which stains red in Mallory's stain and increases in diameter towards the base. The thread is coiled transversely in the lower half of the capsule and forms an opaque mass in this region. A few were found exploded and showed a characteristic butt, though the thread and spines had been broken off. 14·4 × 10·8 μ.

(iv) Atrichous isorhizas (fig. 2B). Elongated capsules with the contents difficult to discern, but apparently containing a long tangled thread which stains faintly blue in Mallory's stain. 15·3–19·8 × 4·0–7·2 μ.

Histology. The hydranth body wall (fig. 2M) is very similar in structure to that of *M. capensis*. It is 110–180 μ thick, with a fairly thin layer of mesogloea 10–20 μ thick from which slender lamellae bearing muscle fibres project into the ectoderm. The lamellae arise at intervals of approximately 14 μ and are 40–80 μ deep. From the endoderm arise villi anything up to 1 mm. in depth, each containing a very thin supporting lamella of mesogloea. The apical cells of the villi contain dark-staining granules, but the remainder are clear and vacuolated. 85 villi were counted in one section. In the region of the mouth the granular cells are more numerous and many cells contain droplets of a yellowish material.

The body tentacles (fig. 2K) are exactly like those of *M. capensis* as described by Manton (1940), with an apical pad of mesogloea fibrils about 50 μ in thickness and a central cavity which passes into the stalk without constriction. The endoderm of the stalk is separated from that of the hydranth body by a thin layer of mesogloea. The capita of the tentacles are richly armed with nematocysts of all 4 types, of which desmonemes are the most numerous.

The blastostyle is the most distinctive structure in the species. In the proximal region where the gonophores arise the endoderm bears villi which

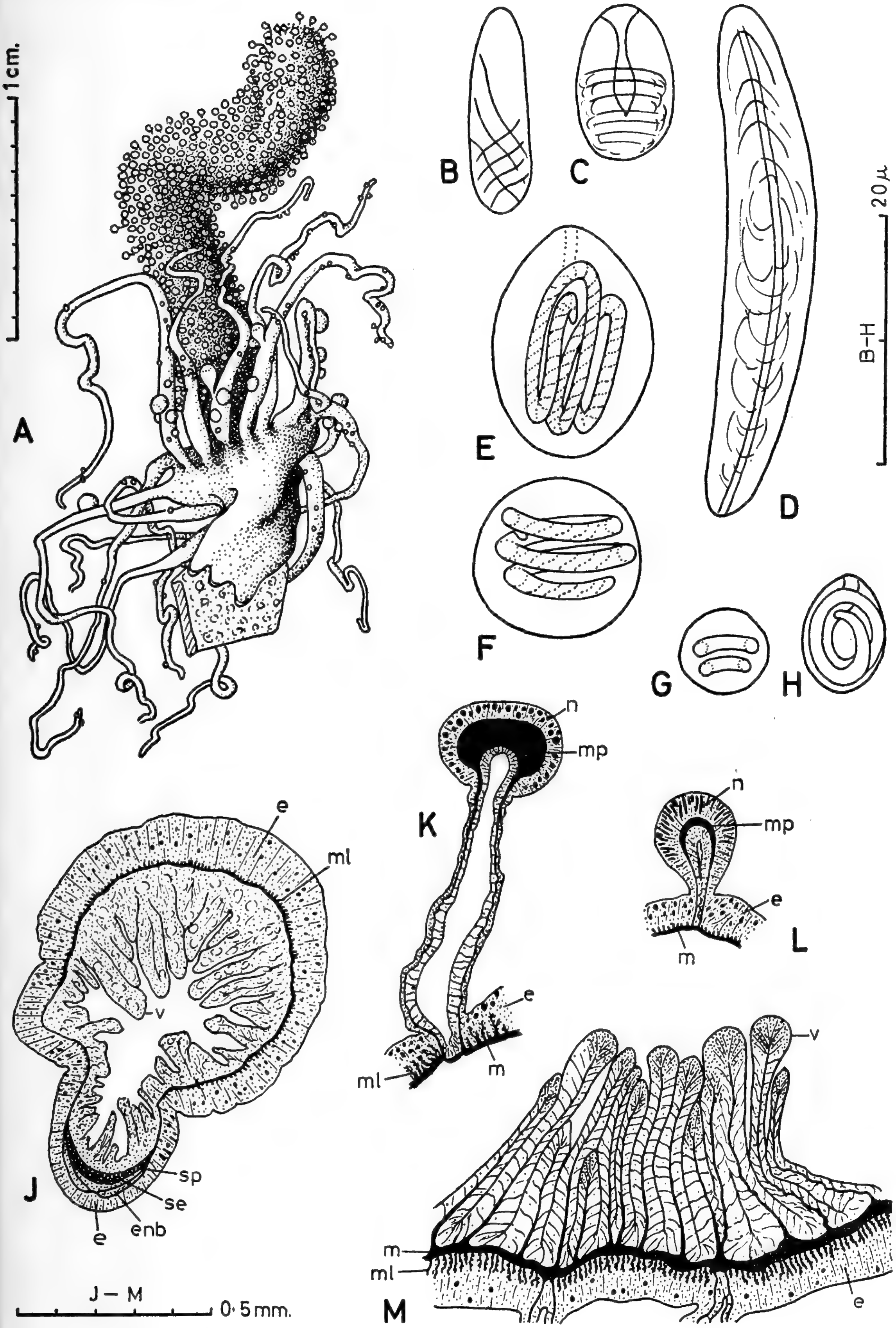

FIG. 2. *Myriothela tentaculata* n. sp.

A. The whole animal (holotype).

B–H. Nematocysts. (B, atrichous isorhiza. C, stenotele. D, 'heteroneme'. E and F, large desmoneme in side view and end-on view. G and H, small desmoneme in end-on view and side view.)

J. t.s. blastostyle in proximal region with young male gonophore arising from it.

K. l.s. body tentacle.

L. l.s. blastostyle tentacle.

M. t.s. through body-wall of hydranth in distal region including the origin of 2 tentacles.

(*e*, ectoderm. *enb*, endoderm of bell. *m*, mesogloea. *ml*, mesogloeal lamella. *mp*, apical pad of mesogloeal fibrils. *n*, nematocysts. *se*, subumbrella ectoderm. *sp*, spermatogenic cells. *v*, endodermal villi).

project into the central cavity and fill it almost completely (fig. 2J). The cells of the villi are densely packed with granules which stain red in Mallory's stain, and many of the granules float freely in the interstices between the villi. The mesogloea bears lamellae about 20 μ deep on its ectodermal surface. The ectoderm contains many developing nematocysts which are particularly abundant around the origins of the tentacles. In the slender distal part of the blastostyle ectoderm and mesoderm are normal and well-preserved, but the endoderm appears to be largely senile. Although remains of villi and their mesogloeal lamellae can be recognised, most of the internal cavity is filled with dead cells and fragments of cells most of which have an opaque yellowish coloration.

The blastostyle tentacles (fig. 2L) are similar to those of the body, but each has a much shorter stalk and a thinner pad of mesogloeal fibrils (about 20 μ thick in maximum). The lumen is very narrow and the endoderm separated from that of the blastostyle by a basal lamella of mesogloea. The superficial layer of the capitum is densely packed with nematocysts, including 'heteronemes' and atrichs, while desmonemes and stenoteles appear to be entirely absent.

The structure and development of the gonophore is similar to that in other species (Briggs, 1929, 1931; Manton, 1940). Only male gonophores are present and the largest one sectioned is 1·24 mm. in diameter with a layer of spermatogenic cells 0·24 mm. thick around the spadix. It is apparently almost mature, for a velar invagination is present in the exumbrella ectoderm though not yet perforate. The endoderm of the spadix bears rounded villi which project into the central cavity which is continuous with that of the blastostyle.

Remarks. Of the six southern hemisphere species listed by Manton, (p. 288) this species is most closely related to *M. capensis*. It differs from it in its larger size, its adhesive structures, which are less obviously tentacular, and its long and tendril-like blastostyles.

The nature of the nematocysts supports the establishment of a new species. All are larger than the corresponding types in *M. capensis*, the banana-shaped 'heteronemes' being enormous, about 4 times those of *M. capensis* and over twice those of *M. penola* and *M. cocksi*. The presence of atrichs in the hydranth is unusual since in other species this type is confined to the actinula. The term 'heteroneme' has been used following Manton, although the only evidence that this type possesses a distinct butt is that of Allman (1876), and needs confirmation. No haplonemes could be identified in this material, and if present cannot be distinguished from stenoteles.

Family **Corynidae**

Genus *Bicorona* nov. gen.

Diagnosis. Corynidae with firm perisarc and upright, monopodially branched stems. Hydranths with two whorls of capitate tentacles. Gonophores in the form of fixed sporosacs borne on the body of the hydranth.

Bicorona elegans nov. sp.

Fig. 3

Types and records. Holotype: SB 161X (South African Museum registered number: SAMH 412), from Saldanha Bay on the west coast. Other records: A 116, 139, 353 (west coast); L 44, 56 (south coast).

Description of holotype. A luxuriant colony of upright branching stems reaching a maximum height of 5·8 cm., growing in the lower intertidal region of the shore.

Hydrorhiza embedded in sponge, branching and giving rise to upright stems. Stem unfascicled, with monopodial growth and terminal hydranths. Branches arising alternately, either bearing one terminal hydranth, or rebranching in a manner similar to the stem. Stem and branches covered with firm perisarc which is closely annulated throughout except for a smooth area on the origin of each branch. Hard part of perisarc terminating just below hydranth, but continued as a gelatinous layer onto the base of the hydranth.

Hydranth *Tubularia*-like, with two whorls of capitate tentacles. Aboral tentacles 10–21 in number in mature hydranths, usually with long and short tentacles alternating. Oral tentacles short, 4–7 in number. 'Neck' region of hydranth (below aboral tentacles) with indistinct longitudinal striations.

Gonophores in form of fixed sporosacs, borne on approximately 7 short blastostyles which form a whorl just distal to the aboral tentacles. Gonophores oval to spherical, 2–4 to a blastostyle, the oldest one terminal.

Histology (fig. 3K). Stem normal, with no endodermal canals, terminating in a swollen region in the last perisarcal segment.

'Neck' region of hydranth with longitudinally ridged ectoderm, surrounded by thick gelatinous sheath continuous with the perisarc of the stem.

Hydranth expanding at level of aboral tentacles, with spacious enteron. Ectoderm of hydranth normal. Endoderm specialized: immediately below aboral tentacles thickened and granular but with no indication of parenchyma, in the region between the two whorls of tentacles folded inward around supporting strands of mesogloea in the nature of endodermal villi, in region of hypostome thickened.

Tentacles solid, with central core of 'chordal' endoderm. Aboral tentacles with no 'supporting lamella' of mesogloea, and endoderm continuous with that of hydranth. Oral tentacles attached obliquely to hydranth body, with a 'supporting lamella' of mesogloea which may be incomplete in its aboral region.

Blastostyle hollow and tubular. Gonophores with a hollow spadix, without subumbrella cavity or radial canals. Female gonophore containing many small eggs arranged in a single series around the spadix (counts give numbers varying from 29 to 84). Eggs 0·05–0·10 mm. in diameter. Male gonophore containing a thick mass of spermatogenic cells.

Nematocysts (fig. 3H, J) all stenoteles, of 2 sizes: large ones reaching

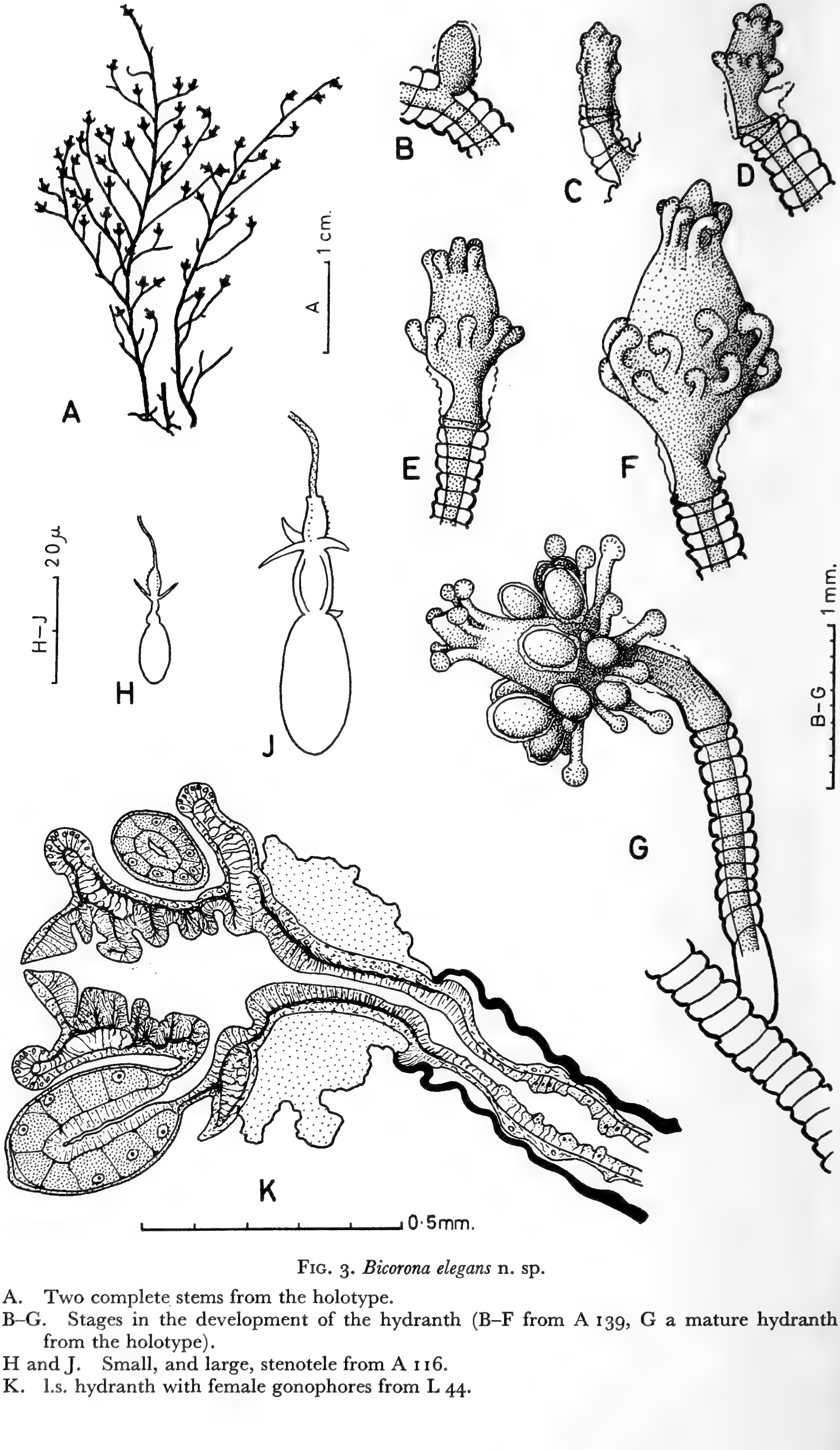

FIG. 3. *Bicorona elegans* n. sp.

A. Two complete stems from the holotype.

B–G. Stages in the development of the hydranth (B–F from A 139, G a mature hydranth from the holotype).

H and J. Small, and large, stenotele from A 116.

K. l.s. hydranth with female gonophores from L 44.

26 × 17 μ, small ones reaching 13·5 × 7 μ (measurements from preserved material, undischarged).

Measurements (mm., preserved).
(*N.B.* the holotype material is well expanded, A 116 less so.)

	holotype	*A* 116
Stem, diameter	0·21–0·35	0·26–0·43
Hydranth, length from end of 'hard' perisarc to hypostome	0·96–1·95	1·29–1·73
Gonophores, length reaching	0·47	0·50
maximum diameter reaching	0·44	0·36

Remarks. The material chosen as the holotype is a well-developed, mature colony, with presumably the maximum number of tentacles on the polyps. One of the other samples (A 139) contains shorter stems with younger, well-relaxed polyps, permitting observations on the origin of the tentacles (fig. 3B–F).

In the young polyp bud, two whorls of capitate tentacles appear simultaneously, 4–7 oral and approximately 7 aboral. These are at first short and knob-like, but they lengthen as development proceeds, especially the aboral ones. The number of oral tentacles is not increased, but before long a new series of aboral tentacles appears, about 7 in number, alternating with those of the first series and at a slightly lower level on the polyp. Polyps at this stage of development (fig. 3F) thus appear to have three whorls of tentacles, one oral and two closely alternating aboral. When the second series of aboral tentacles is about half the length of the first, young blastostyles make their appearance, one in the axil of each aboral tentacle of the first series. The oldest polyps in this particular sample have reached this stage, but the appearance of a third series of aboral tentacles would bring the number up to about 21 (the maximum number observed in the holotype). In the fully mature polyps of the holotype and other samples, however, the aboral tentacles are arranged in a single whorl and at one level (fig. 3G). Whether this is due to further growth in circumference of the polyp or to differences in the state of contraction can only be determined from living material.

Annandale (1915) established a new genus *Dicyclocoryne* for a species previously described in 1907 as *Syncoryne filamentata*, in which the generic diagnosis is the presence of two whorls of capitate tentacles. But *D. filamentata* bears free medusae and thus, following the practice adopted in these papers, cannot be included in the same genus as forms with fixed sporosacs. There are also other differences from the present species (e.g. unbranched stems, smooth perisarc, different position of gonophores) which make the establishment of a new genus for this material desirable, viz. *Bicorona*.

Dicyclocoryne and *Bicorona* appear to be more closely related to the Corynidae than to any other family of Capitata, and this is supported by the presence of only one category of nematocyst. Although stenoteles and desmonemes have been reported from medusae of this family, only stenoteles (large and small) are known from the hydroids (Russell, 1938, and Millard, 1959b, for *Sarsia eximia*). In the Pennariidae on the other hand, with which *Bicorona* also has certain affinities, 3 or 4 different categories of nematocyst occur (Weill, 1934, and Millard, 1959a).

Sarsia eximia (Allman, 1859)

Coryne sp.: Millard, 1957: 179.
Sarsia eximia. Russell, 1953: 50, pl. 2 (fig. 3), figs. 17*a*, 18A, B. Millard, 1959*b*: 241. Kramp, 1959: 79, fig. 15. Kramp, 1961: 27.

Records. West coast: LB 556A. LU 113D. SH 433D, 436A. South coast: CPR 9F. KNY 165E (recorded by Day, Millard and Harrison, 1952, as *Syncoryne ?eximia*).

Remarks. Living material from Table Bay docks (SH 436A) and Langebaan (LB 556A) was kept in the laboratory where it released medusae. At liberation these measured 0·9 mm. in depth and 0·8 mm. in diameter, with a hypostome of 0·3 mm. in length. After 3 days the size had increased to 1·1 mm. depth and 1·2 mm. diameter, with a hypostome of 0·4 mm. At this stage the tentacles reached a length of about 1·8 mm. when extended and bore about 12 clusters of nematocysts. The structure was similar in every way to that of *S. eximia*. The medusa of *S. eximia* has not previously been recorded from South Africa.

Staurocladia vallentini (Browne, 1902)

Cnidonema capensis Gilchrist, 1919: 509, pl. 30.
Staurocladia vallentini: Browne and Kramp, 1939: 274, pl. 14 (figs. 3–4), pl. 15 (fig. 4), pl. 19 (fig. 2).
Cnidonema vallentini: Ralph, 1947: 414, pl. 35 (figs. 1–6).

Records. West coast: LB 266A, 398A (recorded by Day, 1959, as *Cnidonema vallentini*). A 40 (recorded by Bright, 1938, as *Eleutheria vallentini*).

Description. Material from Langebaan (LB) consists of numerous young medusae found crawling on weed (*Gracilaria confervoides*), most of them undergoing asexual reproduction. Medusae reaching a maximum diameter of about 1 mm., and bearing 20–30 tentacles. Aboral branch of tentacle with 4–5 nematocyst batteries, of which one is terminal and the rest dorsal. No gonads present.

Material from Oudekraal (A) includes two larger medusae, reaching a diameter of 3 mm. and bearing gonads. Specimens rather damaged, but apparently bearing over 40 tentacles. Nematocyst batteries as in LB material.

Hydranths not as yet found.

Family: **Solanderiidae**

Solanderia procumbens (Carter, 1873)

Fig. 4 and Plate I

Ceratella procumbens Carter, 1873: 10.
Ceratella spinosa Carter, 1873: 12.
Solanderia atrorubens: Marshall, 1892: 12, pl. 5, pl. 7 (figs. 2–4).

Solanderia procumbens: Vervoort, 1962: 535.
Solanderia spinosa: Vervoort, 1962: 535.
Non Dehitella atrorubens Gray, 1868.

General. The material of this species is divisible into two forms on general appearance (here designated as form A and form B), which do not seem to be specifically distinct, but are kept separate in case they should later prove to be so. In the description which follows the skeleton of the largest specimen of each (WCD 158F and E respectively) is described and the soft parts of the best preserved (SAMH 247).

Records

Form A: West coast: WCD 158F. South coast: SAMH 247. TRA 59A.
Form B: West coast: WCD 158E. South coast: SCD 154A.

Description, form A. The largest colony (Plate IA, left) a magnificent fan-shaped specimen 33 cm. high with a spread of 38 cm. Hydrorhiza 5 cm. broad, and flattened below for attachment. Main stem flattened in the plane of branching and expanding from a base 2·4 cm. wide and 1·2 cm. thick to a broad leather-like blade 5 cm. wide and 0·5 cm. thick; beyond this giving rise to a number of large branches, which in their turn branch and rebranch. Branching in one plane, with a tendency for the branches to bend to one side and give off more sub-branches on this side, suggesting the influence of a strong current during growth. Method of branching variable, often dichotomous, sometimes alternate and sometimes unilateral. Smaller branches quite round in section, comparatively thick and stumpy (about 2 mm. in diameter), with rounded tips.

Fibrous meshwork of main stem reticulate, with rounded, rectangular, or hexagonal apertures between the trabeculae, but no marked longitudinal arrangement. Trabeculae of unworn areas bearing numerous spiny structures 0·3–0·4 mm. in height, some of them flattened and spatulate and resembling abortive hydrophores with one or two supporting ribs (fig. 4D).

Fibrous meshwork of branches arranged in a more definite fashion, in which the longitudinal trabeculae predominate. Groups of trabeculae often raised up into prominent longitudinal ridges surmounted by blade-like crests parallel to the long axis of the branch (Plate IB, lower right corner). Spines reduced to tubercles on the branches and absent on the smallest subdivisions.

Hydrophores numerous and scattered irregularly over surface of branches. A typical one consisting of a scoop-shaped bracket supported on its lower surface by longitudinal ribs continuous with the trabeculae of the branch (fig. 4B). Ribs normally not reaching margin, which is smooth and rounded. Hydrophores, however, subject to much variation, some being bilobed (fig. 4C), some divided into two halves (one on each side of the hydranth) and some represented by a laterally seated hemihydrophore only. Badly eroded hydrophores with margin worn down between the supporting ribs (fig. 4H). Normal hydrophores approximately 0·5 mm. in length, and 0·5 mm. in basal width tapering to 0·3 mm. at margin.

Hydranths arising from coenosarc above hydrophores and, rarely, directly from the stem with no protective supports whatever; bearing approximately 15 capitate tentacles (but difficult to count due to poor preservation).

Gonophores arising directly from coenosarc of stem, spherical, shortly stalked. Immature male gonophores present on two specimens, the largest measuring 0·34 mm. in diameter and 0·32 mm. in length; containing several layers of spermatogenic cells around a central spadix, and 4 distinct radial canals.

Colour: stem and larger branches dark brown, occasionally with a purplish tinge, shading to yellowish-brown on the smaller branches.

Form B. Colonies smaller than form A, the largest reaching 19·5 cm. in height and 15·5 cm. in spread, with more slender branches and lighter coloration (Plate 1A, right). Main stem rounded in section. Hydrophores on smaller branches restricted to two sides, but irregularly scattered on larger ones. The 'double' type of hydrophore predominant (fig. 4E, G), bilobed or single ones rare (fig. 4F).

Nematocysts. Three types present in smears of preserved material:

(i) Large oval stenoteles (fig. 4R, S). Fairly common. Undischarged capsules with a broad, central shaft and a long thread coiled transversely in the lower half. Discharged capsules with a broad, slightly tapering butt armed with 3 large spines and several spiral rows of smaller spines. Thread broken off in all examples seen. 15·3–24·3 × 11·7–18·0 μ

(ii) Small oval heteronemes (fig. 4P). Abundant. Undischarged capsules with a central shaft and a thread which appears to be irregularly coiled. A single discharged and rather distorted capsule bore a short, swollen butt and a number of spines. 8·1–8·7 × 6·3 μ

(iii) Elongate-oval capsules of unknown category (fig. 4Q). Rare. Only discharged capsules seen with no sign of butt or thread. 15·3 × 5·4 μ

Remarks. It is felt that form A and form B represent different growth-forms of the same species, form B including younger colonies which have possibly grown more rapidly. Their main claim to distinction is the nature of the hydrophores which are predominantly 'single' in form A and 'double' in form B, although both types can be found in all colonies. There is no difference in the nematocysts. The 'double' hydrophore is in some ways similar to the 'spines' which flank the hydranth in *S. secunda* (Inaba). However, diagrams by Stechow (1909, pl. 4, fig. 7) and Vervoort (1962, figs. 2*b*, 7) show that the latter are little larger than the area of one mesh of the skeleton, whereas in the present material they approximate to the area of 4 meshes.

Carter's dried type material of *Ceratella procumbens* was available for comparison in the British Museum. It includes one specimen from the Cape of Good Hope (reg. no. 1867.3.22.1) and three from Natal (reg. no. 1872.8.1.1). The largest is one of the latter and measures 26·5 cm. in height with a spread

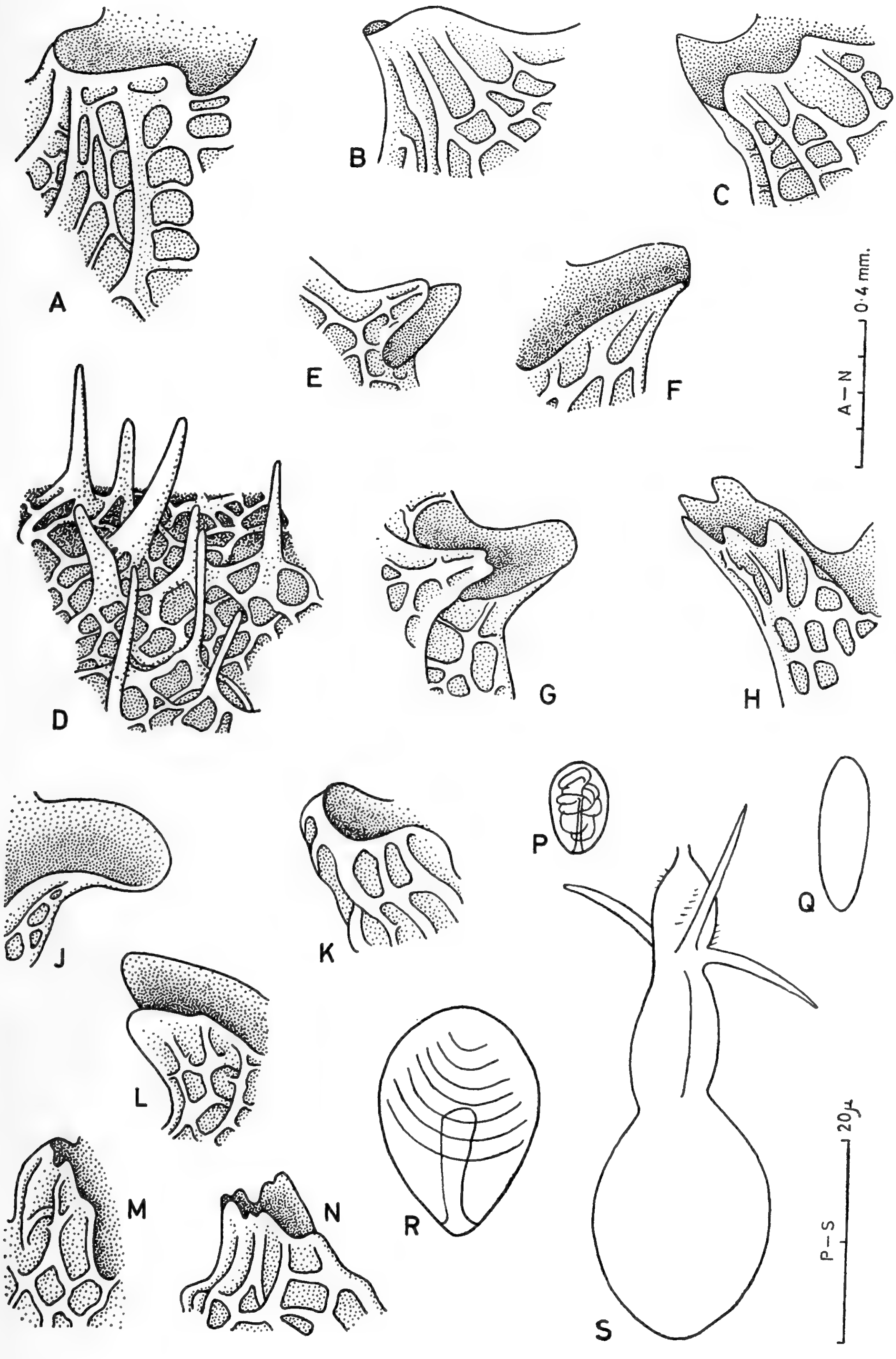

FIG. 4. *Solanderia procumbens* (Carter).

A–C. Hydrophores from form A, WCD 158F (A and B single, C bilobed).
D. A portion of the older part of the stem in WCD 158F showing spines.
E–G. Hydrophores from form B, SCD 154A (F single, E and G double).
H. A typical eroded hydrophore from False Bay.
J–N. Hydrophores from Carter's type material (J and K single, L double, M and N eroded).
P–S. Nematocysts (P, a small heteroneme. Q, undetermined type. R and S, large stenotele).

of 11 cm. The main stem is 1·8 cm. wide and 0·6 cm. thick. This is evidently the specimen whose measurements were quoted by Carter in 1873. I select it as the lectotype.

In spite of the fact that the type material is battered and obviously beach-worn the resemblance to form A described above is unmistakable. Here too the hydrophores are predominantly single (fig. 4J, K) though bilobed and double ones also occur (fig. 4L). In the older and badly worn parts the hydrophores are eroded so that the supporting ribs project and give a spinous appearance to the margin resembling that in *S. fusca* (Gray) (fig. 4M, N).

S. spinosa (Carter, 1873), is here considered to be a synonym for *S. procumbens*. The dried holotype of this species from Port Natal is also present in the British Museum (reg. no. 1872.8.1.17). It is less beach-worn than the type material of *S. procumbens* and this would account for the minor differences said to distinguish the species. Its general appearance is similar to form A described above though most of the hydrophores are of the 'bilobed' type. The 'spines', which are the main specific character, are present only on the older part of the colony as in the present material, and are comparatively delicate structures which would easily be rubbed off by sand erosion. This would account for their absence in the type material of *S. procumbens*.

Another species which possesses well-developed hydrophores is *S. fusca* (Gray, 1868), from Australia, described and figured by Spencer (1892). Gray's type material is present in the British Museum (reg. no. 1884.12.6.15–16; the first of these designated as lectotype by Vervoort (1962: 533). The most obvious characteristic of this species is the nature of the hydrophores which have spiny margins due to the projection of the supporting ribs beyond the edge. That this effect is not in this case the result of wear is evident from the fact that spiny hydrophores are present in the youngest and thinnest branches and, according to Spencer, also in the living animal.

S. atrorubens (Gray, 1868), is closely related to *S. fusca* and possibly a synonym, although Vervoort, 1962, considers that it can be distinguished by its method of growth. An examination of the type material in the British Museum, probably from Australia (of which no. 1962.4.14.1 has since been designated as lectotype by Vervoort, 1962, p. 535), showed that it has the same spiny hydrophores.

The fact that hydrophores of *S. procumbens* may acquire a spiny appearance as the result of erosion has probably led to confusion between this species and *S. fusca* and *S. atrorubens*. Marshall's record of *S. atrorubens* from Port Natal can be included in the synonymy of *S. procumbens* as his figures show that the edges of the hydrophores are smooth. Other species recorded from South Africa, including *S. labyrinthica* (Hyatt, 1877), and *S. rugosa* Marshall, 1892, and also Brazier's record (1887) of *S. atrorubens* are insufficiently described but are possibly all synonyms of *S. procumbens*.

Family **Bougainvilliidae**

Bimeria vestita Wright, 1859

Fig. 5 A–F

Bimeria vestita: Hincks, 1868: 103, pl. 15 (fig. 2). Allman, 1872: 297, pl. 12 (fig. 1–3). Hamond, 1957: 297, figs. 3–4.
Leuckartiara vestita forma *nana*: Vervoort, 1946*a*: 294.

Records. South coast: MB 88L. SAMH 158, 177, 233, 235, 327, 337, 343, 361. SCD 85T, 118M, 347F.

Description. Colonies epizootic on other hydroids, and reaching a height of 3–8 mm. Stem upright, bearing from 1 to 6 or 7 alternately arranged hydranth pedicels. Pedicels occasionally rebranching. Perisarc annulated at base of stem, on origin of pedicels and at other irregular intervals, covered throughout with adherent particles. Stem and pedicels narrower at base than at distal end. Perisarc continued over the hydranth, sheathing the tentacles for part of their length and covering the greater part of the hypostome. Tentacles varying in number from about 10 to 16.

Gonophores borne on the stem and hydranth pedicels, each on a short annulated pedicel, completely covered by a thick coat of gelatinous perisarc male and female on separate colonies. Male sporosac elongated-oval, with branching spadix. Female sporosac oval to spherical, bearing a single terminal ovum, which develops *in situ* into a planula larva (fig. 5 B–D).

Measurements (mm., preserved).

Stem, diameter		0·04–0·09
Pseudohydrotheca, length		0·21–0·49
diameter		0·12–0·30
Gonophore, female, length (without perisarc)	reaching	0·16
diameter	reaching	0·16
male, length (without perisarc)	reaching	0·33
diameter	reaching	0·12

Remarks. These colonies are very similar to those described by Hincks, Allman and Hamond, although they are not so richly branched as some of Allman's specimens. The size of the hydranths and the thickness of the stem appears to be less than in most descriptions, though it corresponds well with Hamond's material.

The only previous record of this species from southern Africa is that of Vervoort, 1946*a*, from Inhaca in Portuguese East Africa. Female gonophores are apparently described here for the first time.

Bougainvillia macloviana (Lesson, 1836)

Perigonimus maclovianus: Vanhöffen, 1910: 284, fig. 10.
Bougainvillia macloviana: Jäderholm, 1923: 3. Millard, 1959*b*: 242, fig. 1 A–C. Vannucci & Rees, 1961: 69.

Records. West coast: SB 178D.

Description. Colony epizootic on other hydroids. Stems only 2 mm. in

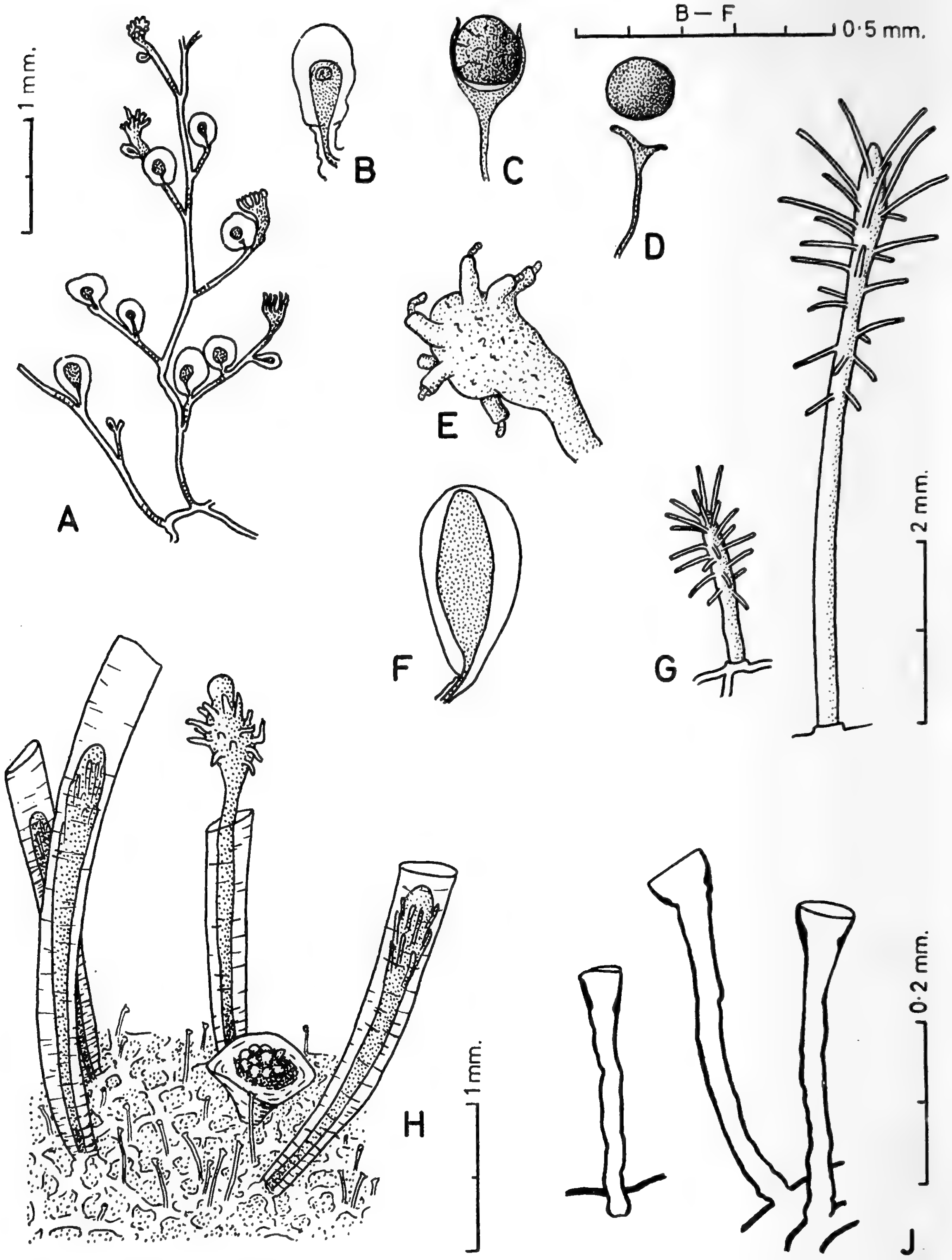

Fig. 5.

A–F. *Bimeria vestita* Wright. A, a typical stem. B–D, stages in the development of the female gonophore (C and D drawn without the perisarcal covering). E, a contracted hydranth. F, a male gonophore. (A–E from SAMH 361, F from SAMH 177).

G. *Clava* sp. Two hydranths sketched from living material (CP 646A).

H–J. *Merona cornucopiae* (Norman) from SCD 119R. H, part of the colony showing hydranths, a single blastostyle and nematothecae. J, three nematothecae on a larger scale.

height, slender, flexuous, branching irregularly, bearing medusa buds, of which the oldest has its tentacles unfurled.

Remarks. In its general appearance this colony strongly resembles Vanhöffen's description of the species and also the material previously described (Millard, 1959*b*). The identification is strongly supported by the discovery of abundant mature medusae of this species from the same area in Saldanha Bay (identification by M. E. Thiel of the Zoologisches Museum, Hamburg). It is interesting also that the two ships on whose hulls this species was recorded in 1959*b* both came from Saldanha Bay.

Bougainvillia sp.

Records. West coast: LB 542A. South coast: KNY 165D (reported by Day, Millard and Harrison, 1952, as *B. ramosa*). SAMH 170, 245. SCD 190A, 281G. TRA 33Z, 150F.

Description. Stems slender, upright, weakly fascicled at the base in the larger colonies and branching profusely in a more-or-less alternate fashion. Maximum height 5·3 cm. Larger stems generally smooth, smaller branches wrinkled or corrugated, particularly over the origins. Smaller colonies unfascicled and less profusely branched. Medusa buds with 4 unbranched oral tentacles and 4 marginal bulbs, each with 2 black ocelli and 2 marginal tentacles.

Remarks. It is felt that this material could not be assigned to a species with any certainty. The general growth-form is very similar in all the colonies, though some are obviously older than others. Well-developed medusa buds may be present on stems of only 3 mm. in height.

The stems are stiffer and more profusely branched than those of *B. macloviana*, yet not so sturdy as those described as *B. ramosa* (Millard, 1959*b*) from ships' hulls.

The material might well be included in *B. ramosa* forma *musca* Allman, 1864, yet no mature medusae of *B. ramosa* have so far been recorded from this country, whereas medusae of *B. macloviana* do occur on the west coast (see above).

Dicoryne conferta (Alder, 1856).

Eudendrium confertum Alder, 1856: 354, pl. 12 (figs. 5–8)
Dicoryne conferta: Allman, 1872: 226, 293, pl. 8. Jäderholm, 1909: 47, pl. 3 (fig. 6).

Records. South coast: SCD 133C.

Description. A dense colony growing on a gastropod shell occupied by a hermit, reaching a maximum height of 2·5 cm. Hydrorhiza reticulate. Stem unfascicled, branching irregularly, increasing slightly in diameter towards distal end. Perisarc roughly corrugated throughout, but more definitely annulated on origin of stem, terminating below hydranth when the latter is expanded and covering the base of the body as a 'pseudohydrotheca' when contracted. Hydranth long, with a single whorl of tentacles near distal end.

'Blastostyles' in the form of tentacle-less hydranths borne on stem and hydrorhiza. Male gonophores present, borne on lower region of blastostyle either as a tight cluster or distributed along its length. The two tentacles of the swimming sporosac clearly visible within the perisarcal covering of the gonophore.

Nematocysts all small, 5·4 × 2·7 μ

Remarks. This appears to be the first record of the species from the southern hemisphere. The appearance of the colony is very characteristic and closely resembles that illustrated by Jäderholm in 1909.

Rhizorhagium robustum (Warren, 1907)

Parawrightia robusta Warren, 1907: 187, pl. 33 (figs. 1–5), figs. 1–4.

Records. South coast: L 177.

Description. A sterile colony growing on a coralline alga. Most stems bear a single terminal hydranth, but many 2 or 3. In some cases a number of stolons or stems (it is impossible to determine which) are twisted together simulating a fascicled stem which is quite free from the substratum and reaches a maximum height of 17 mm. Perisarc well developed and forming a very distinct 'pseudohydrotheca' over the base of the hydranth. Tentacles 18–22.

Family **Clavidae**

Clava sp.

Fig. 5G.

Records. West coast: CP 646A.

Description. Colony growing on a stone just below low tide level. Hydrorhiza reticulate, penetrating into calcareous matter on stone, covered with a thin layer of perisarc which forms a very low collar round the base of each hydranth.

Hydranths reaching a maximum height of 7 mm., creamy pink in colour when alive, with 22 to 30 scattered filiform tentacles which reach a maximum length of 1 mm. when fully extended.

Gonophores absent.

Nematocysts of two kinds:

(i) Microbasic euryteles, 0·67–0·72 × 0·22 μ.
(ii) Desmonemes, 0·45 × 0·32 μ

Remarks. This species cannot be definitely identified in the absence of gonophores. The trophosome is similar in size and all other characters to *C. multicornis* (Forskål, 1775), forma *genuina* Broch, 1916. The sizes of the two categories of nematocyst are also close to those given by Weill, (1934) for *C. squamata* (= *C. multicornis*).

Merona cornucopiae (Norman, 1864)

Fig. 5 H, J.

Merona cornucopiae: Rees, 1956: 499, figs. 1–3.

Records. South coast: LIZ 25P. SCD 119R.

Description. Colonies growing on the bivalve *Crassatella capensis Lamy.* Of the two samples recorded above the first consists of a single bivalve bearing a male colony of about 160 hydranths. The second consists of three bivalves bearing colonies of between 30 and 50 hydranths each, two of these colonies bearing female gonophores. In each case the colony is restricted to one corner of the shell.

Hydrorhiza in the form of an open reticulum at the margins of the colony, but consolidated into a mat in the denser regions.

Hydranths with 16 to 20 scattered filiform tentacles, surrounded by sturdy perisarcal tubes into which they can be completely retracted. Tubes slender at base, expanding distally, often regenerated.

Gonophores borne in clusters on blastostyles which arise separately from hydrorhiza, male and female on separate colonies. Blastostyle surrounded at base by short collar of perisarc.

The hydrorhiza of one colony only (SCD 119R, male) bearing numerous minute nematothecae. Nematotheca in the form of an asymmetrical perisarcal funnel borne on a long and slender pedicel. Containing a cluster of large nematocysts.

Measurements (mm.)

	SCD 119R	LIZ 25P
Perisarcal tube, height	1·83–4·25	2·15–2·72
maximum diameter	0·30–0·38	0·32–0·35
Blastostyle, total height	1·27–1·41	0·63
Gonophore, length	0·17–0·25	0·19–0·35
maximum diameter	0·12–0·20	0·12–0·21
Nematotheca, height	0·03–0·06	
maximum diameter	0·07–0·09	
length of pedicel	0·22–0·54	

Nematocysts. At least two types present:

(i) Microbasic euryteles. Elongated capsules measuring 16·2 × 4·5 μ undischarged. Abundant in nematophores, scarce on hydranth tentacles. A single discharged and rather damaged capsule observed.

(ii) ?Desmonemes. Ovoid capsules measuring 7·2 × 2·7–3·6 μ undischarged. Abundant on hydranth tentacles, scarce in nematophores.

Remarks. This species has so far been reported only from northern seas. It is a new record for South Africa and its presence here is surprising. Even more so is the discovery of nematophores on the hydrorhiza There can be no doubt about the identification of the species thanks to the detailed description of living material by Rees and the characteristic habitat of the animal.

The nematophores, when first noticed, were thought to be the hydrothecae of an epizootic species, but the microscope showed that they arose from the same hydrorhiza as the clavid 'host', a fact which was convincingly proved when the same nematocysts of identical measurements were found in both. A noteworthy point is that nematophores occurred in only one colony (male) out of four which were similar in every way other than sex.

Family **Eudendriidae**

Eudendrium annulatum Norman, 1864.

Remarks. The only record of this species from South Africa is that of Ritchie (1909) from the entrance to Saldanha Bay, and that a doubtful one. In 1960 the opportunity offered to examine two slides of Ritchie's material from Saldanha Bay and to compare them with Norman's preserved type material of *E. annulatum.* In Ritchie's material the stem is not so densely annulated as in the usual conception of *E. annulatum,* although in the type material of the latter smooth areas do occur in some parts of the larger branches. More important is the fact that in Ritchie's material bifurcating spadices could be distinctly seen on some of the female gonophores, whereas in *E. annulatum* the spadices are unbranched (Broch, 1916, p. 62). Ritchie's record of *E. annulatum* from South Africa should thus be discarded, and the material is provisionally placed in *E. carneum* (see p. 455).

Eudendrium ?capillare Alder, 1856.

Eudendrium capillare Alder, 1856: 355, pl. 12 (figs. 9–12). Broch, 1916: 62. Stechow, 1925*a*: 202. Leloup, 1952: 124, fig. 63. Picard, 1955: 183.
Eudendrium parvum Warren, 1908: 272, pl. 45 (figs. 1–4), fig. 1.
Eudendrium ?parvum: Millard, 1959*a*: 305, fig. 1G, H.

Records. South coast: SCD 154K. SH 433A.

Description. SCD 154K: Stems unbranched or sparsely branched. Perisarc annulated at origin of stem and branches and often at other irregular intervals. Old female gonophores present on 'blastostyles' which arise from stem or hydrorhiza. Pedicel of blastostyle corrugated, bearing 3–5 gonophores or their empty capsules irregularly distributed near distal end. Gonophores covered by transparent capsule which has a warty appearance possibly due to shrinkage. Soft parts too badly preserved for nematocyst examination or tentacle counts.

SH 433A: Living material kept in laboratory for several weeks. Stems unfascicled, but profusely branched and reaching a maximum height of 1·7 cm. Perisarc annulated on origins of stems and branches and at other irregular intervals. Hydranths orange-pink in colour with white tentacles and hypostome; with 23–28 tentacles held alternately elevated and depressed. Various stages of female gonophores present on 'blastostyles' which arise from the stem or its branches. Pedicel of blastostyle corrugated. Young blastostyle with fully-formed hydranth and a ring of gonophores around its base; each gonophore with an unbranched spadix arching over a single egg. Older blastostyles with the hydranth showing signs of reduction and the gonophores more irregularly distributed, each gonophore without a spadix and bearing a single embryo surrounded by a transparent capsule. Nematocysts of two types: large isorhizas, 27 × 11·5 μ, and small heteronemes, 8 × 2·4 μ (undischarged).

Remarks. Warren's *E. parvum* is now considered to be a synonym for the cosmopolitan *E. capillare.* This conclusion is based on examination of—

(i) material of *E. capillare* from Marseilles bearing female gonophores and kindly supplied by J. Picard in 1958.

(ii) material of *E. parvum* from Knysna deposited by Warren in the British Museum (slides 22.3.6.104–107). This is obviously not the holotype, which came from Park Rynie, but is labelled co-type. Both male and female gonophores present.

Warren in 1908 summarised the differences between the two species. One of these was the presence of 3-chambered male gonophores in *E. parvum* as against two in *E. capillare.* But the basal chamber in *E. parvum* is very small indeed and its development may well be a matter of degree. Moreover, Alder in his original description of *E. capillare* mentions 2- or 3-chambered gonophores ('two or three capsules in linear series on each pedicle').

Another difference was the presence of a terminal tubercle on the male gonophore in *E. parvum.* This appears to be a variable character. It is present in only some of the gonophores in Warren's material from Knysna, and is apparently present or absent in *E. capillare* (Stechow, 1925*a*).

Further, Warren mentioned the extension of the perisarc over the base of the hydranth in *E. parvum.* This perisarc is very delicate and may well have been missed in earlier descriptions of *E. capillare.* It is visible in Picard's material of the latter from Marseilles.

Although Warren did not describe female gonophores in the holotype of *E. parvum,* they are present in his material from Knysna and are exactly like those of *E. capillare.*

Finally, the mention of small nematocysts only in *E. parvum* by Warren, 1908, and Millard, 1959*a*, is in agreement with Picard's statement (1955) that only small microbasic euryteles occur in *E. capillare.*

The presence of both large and small nematocysts in the present material (SH 433A) is the only reason for the query in the identification. One is loath to create a new species on the basis of nematocysts only, but one is forced to the conclusion that either there are two species with exactly similar female gonophores or that *E. capillare* has the potentiality of producing two kinds of nematocysts, which is not always realised.

Eudendrium ?carneum Clarke, 1882

?Eudendrium annulatum: Ritchie, 1909: 70.
Eudendrium carneum: Vannucci, 1954: 101, pl. 1 (figs. 1–9), pl. 2 (fig. 8), pl. 4 (figs. 2–5). Millard 1959*a*: 302, fig. 1A–F.

Records. West coast: A 118. CP 336A.

Description. Fascicled, branching stems reaching a maximum height of about 5 cm. Colonies more heavily annulated than is usual for the species, the groups of annulations on the main stem more common and more extensive, often with about 15 rings; hydranth pedicels usually completely annulated, though some with smooth areas. Hydranths with 15 to 24 tentacles.

Young female gonophores with bifurcating spadices. Male gonophores 2-chambered.

Nematocysts of two types: large isorhizas, 20 × 9 μ, and small heteronemes, 7 × 4 μ.

Remarks. This material appears to be a smaller and more closely annulated form of *E. carneum.* The young female gonophores are exactly the same, though completely mature ones with basket-shaped capsules were not present. The male gonophores are 2-chambered, whereas material from the east coast had a minimum of 3 chambers (Millard, 1959*a*). However, Vannucci (1954) has described 2-chambered male gonophores in the same species.

The nematocysts are similar to those of *E. carneum,* though both types are slightly smaller. The presence of large nematocysts excludes the material from *E. racemosum* which also has a forked spadix in the female gonophore.

This material is very similar to that reported from Saldanha Bay by Ritchie (1909) as *E. annulatum(?).* Ritchie's material also has bifurcating spadices. (See also p. 454.)

Eudendrium deciduum Millard, 1957

Eudendrium deciduum Millard, 1957: 184, fig. 2.

Records. South coast: LIZ 7R. MB 19R, 47N.

Description. No large nematocysts have been observed in this species. Small heteronemes (probably microbasic euryteles) similar to those of *E. carneum* (Millard, 1959*a*, fig. 1B) present, measuring 6·3–8·1 × 2·7–3·6 μ undischarged.

Eudendrium ramosum (Linn., 1758)

Eudendrium ramosum: Hincks, 1868: 82, pl. 13. Stechow, 1923*a*: 83. Weill, 1934: 388, fig. 237. Leloup, 1952: 127, fig. 64.

Records. West coast: AFR 0002E. South coast: SCD 37R (dubious identification).

Description. The first specimen (AFR 0002E) has long, graceful stems reaching 17·5 cm. Main stem fascicled, branches unfascicled and given off in a pinnate fashion either in one plane or twisted into a spiral. Female gonophores present, with unbranched spadix. Gonophore-bearing hydranths with reduced tentacles.

The second sample (SCD 37R) includes portions of a colony with a more bushy and stiff appearance and with both main stem and principle branches fascicled. Female gonophores present, with unbranched spadix.

Nematocysts (from AFR 0002E)

(i) Small heteronemes, 7·2 × 2·7 μ, present on both body and tentacles.
(ii) Large isorhizas, 18·0–18·9 × 7·2–7·6 μ present on body only.

Remarks. The first of these specimens agrees well with published descriptions of *E. ramosum* and there can be little doubt as to the identification. The appearance and measurements of the two categories of nematocyst in the undischarged state are also close enough to those given for the species by Weill (1934), the small heteronemes probably being microbasic euryteles.

The identification of the second specimen is more doubtful due to the different appearance of the colony and the fact that the hydranths were too poorly preserved for nematocyst examination.

This is the first record of the species from South Africa.

Family **Hydractiniidae**

Hydractinia altispina Millard, 1955

Hydractinia altispina Millard, 1955: 215, fig. 1. Millard, 1957: 179.

Records. West coast: B 62, 92 (reported by Millard, 1955). LAM 50W, 59C. LU 59Z. SAMH 407. SB 153T.

Hydractinia kaffraria Millard, 1955

Fig. 6

Hydractinia kaffraria Millard, 1955: 217, fig. 2. Millard, 1959*a*: 307.

Records. South coast: BMR 23L. BRE 111A. HAM 3Q. KNY 30P, 70E, 164, 270J. SUN 3N. (All reported by Millard, 1955.)

Remarks on living material. Specimens from Knysna Estuary were kept alive on their host snails for a period of two weeks in the laboratory in January, 1956, when the release of the sexual products from mature sporosacs was observed.

The ripe male and female sporosacs have the structure of degenerate medusae, with radial and circular canals and rudimentary marginal tentacles, but the sexual products are discharged while still attached to the gonozooids and there is no active medusoid generation.

The male sporosacs when mature are practically spherical and measure approximately 0·65 mm. in length and 0·63 mm. in diameter. The four radial canals are distinctly visible and around the opening are 4–6 rudimentary but distinct marginal tentacles. The cavity is filled with spermatogenic cells attached to the central spadix. While still attached to the gonozooid irregular powerful contractions of the whole bell expel the active spermatozoa through the aperture. A cloud of massed spermatozoa surrounds the sporosac for some time until finally dispersed by the movements of the hydroids and their host. Once the sporosacs are empty they fall off and lie loose on the bottom, but show no further activity. At this stage they are more oval than spherical, the length being greater than the diameter.

The mature female sporosacs are larger than the male, measuring approximately 0·90 mm. in length and 0·86 mm. in diameter. Radial canals are visible but the marginal tentacles are very indistinct and not so well developed as in the male. The ripe eggs separate from the spadix and lie loose the cavity of the bell. Fertilization apparently occurs inside the bell, since eggs contain either one or two nuclei immediately after discharge. The area

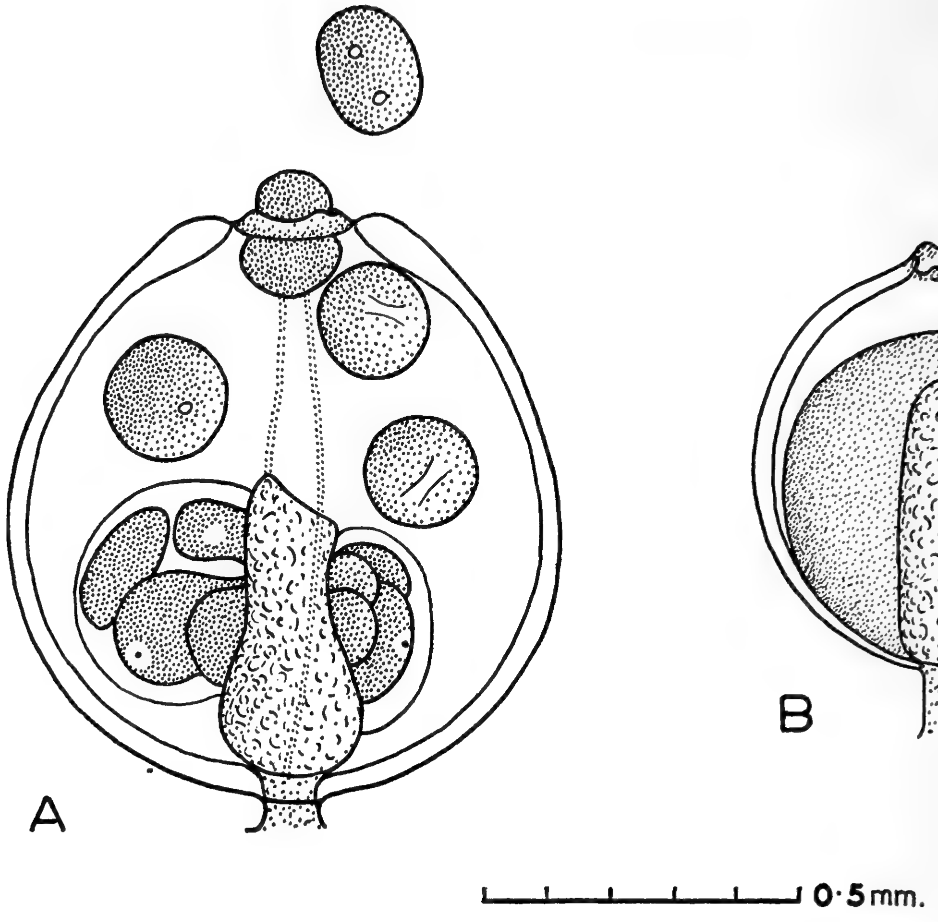

FIG. 6. *Hydractinia kaffraria* Millard.

A. A female sporosac in the process of releasing eggs.
B. A male sporosac.

(Both from living material.)

around the aperture of the sporosac performs irregular contractions which constrict the opening, but no complete contractions of the bell have been observed. These may possibly occur sporadically in the natural condition. Under the microscope the pressure of the coverslip is sufficient to squeeze out the eggs one by one, and the final fillip is provided by the contraction of the margin. The diameter of the eggs is greater than that of the aperture, but their elasticity allows them to be ejected with ease. Occasionally the sporosacs fall off the gonozooids before all the eggs are discharged and continue to perform gentle contractions of the margin, though no swimming movements have been observed.

Hydrocorella africana Stechow, 1921

Fig. 7

Hydrocorella africana Stechow, 1925*b*: 409. Millard, 1957: 183.

Records. West coast: A 405. AFR 801Q. CP 646B. HB 4D. SAMH 408. WCD 12J, 25C. South coast: AFR 866R, 967.O.V, 985E, 994M. SCD 114Q, 133B, 175U, 206R. TRA 33.00.D, 42K, 56C, 99E.

Description. Common on shells of gastropods and hermits. Has been observed on *Turbo sarmaticus* Linn., *Argobuccinum argus* (Gmelin), *Fusus verruculatus* Lam., *Nassa speciosa* A. Adams, and on shells occupied by the hermits *Clibanarius* sp., *Pagurus arrosor* (Herbst), *Diogenes costatus* Hend. and *Eupagurus placens* Stebb.

Skeleton as described by Stechow (1925*b*) with two grades of calcareous ridged processes; the larger 5 mm. or more in height and covered with naked coenosarc bearing gastrozooids and gonozooids; the smaller about 0·5–1 mm. in height, scattered amongst the hydranths. Young colonies with smaller processes only.

Living gastrozooids reaching 3 mm. in length when extended, with 5–12 extensile tentacles, of which 1 or 2 are usually much longer than the others.

Gonozooids reduced, reaching about 0·5 mm. in length in living material, with about 6 rudimentary, knob-like tentacles, and each bearing 3 or 4 spherical sporosacs in various stages of development. Male and female sporosacs on separate colonies. Male sporosacs bearing the spermatogenic cells around a central, hollow spadix, reaching 0·33 mm. in length and 0·33 mm. in maximum diameter. Female sporosacs containing a single central egg surrounded by a number of blind, hollow outgrowths from the basal spadix, reaching 0·36 mm. in length and 0·56 mm. in maximum diameter. Developing gonozooid often enclosed by curved laminar outgrowths of the skeleton, which form a sort of basket-work imprisoning it.

Colour: skeleton and spines white, hydranths creamy white, female sporosacs orange.

Nematocysts of two kinds: microbasic euryteles, 0·72 × 0·27 μ, and desmonemes, 0·45 × 0·27 μ.

Details of female sporosacs. Sections were cut to elucidate the rather unusual structure of the female reproductive bodies.

Female gonozooids are normal in structure with the exception of the tentacles which are reduced to knobs. In each gonozooid a number of young ova are present in the endoderm of the central region of the body. The youngest sporosac is nothing more than a bulge in the ectoderm into which one of the enlarging ova has been pushed together with a few endoderm cells. In one case such a bulge contains two ova, one large and one small. At a slightly later stage the sporosac is well-defined and contains a single large ovum seated on a low evagination of the gonozooid endoderm, which presumably represents a reduced spadix. A few endoderm cells are flattened against the periphery of the egg. There is no entocodon development and the ectoderm is single-layered.

After this the ovum enlarges enormously and becomes packed with yolky material. At the same time from the basal spadix several (usually 4) hollow, finger-shaped processes grow out around the ovum until they partially surround it. These may represent radial canals, but they do not communicate distally and there is no sign of a circular canal or any other medusoid structure. This is the oldest stage seen in sections, but presumably fertilization occurs *in situ*,

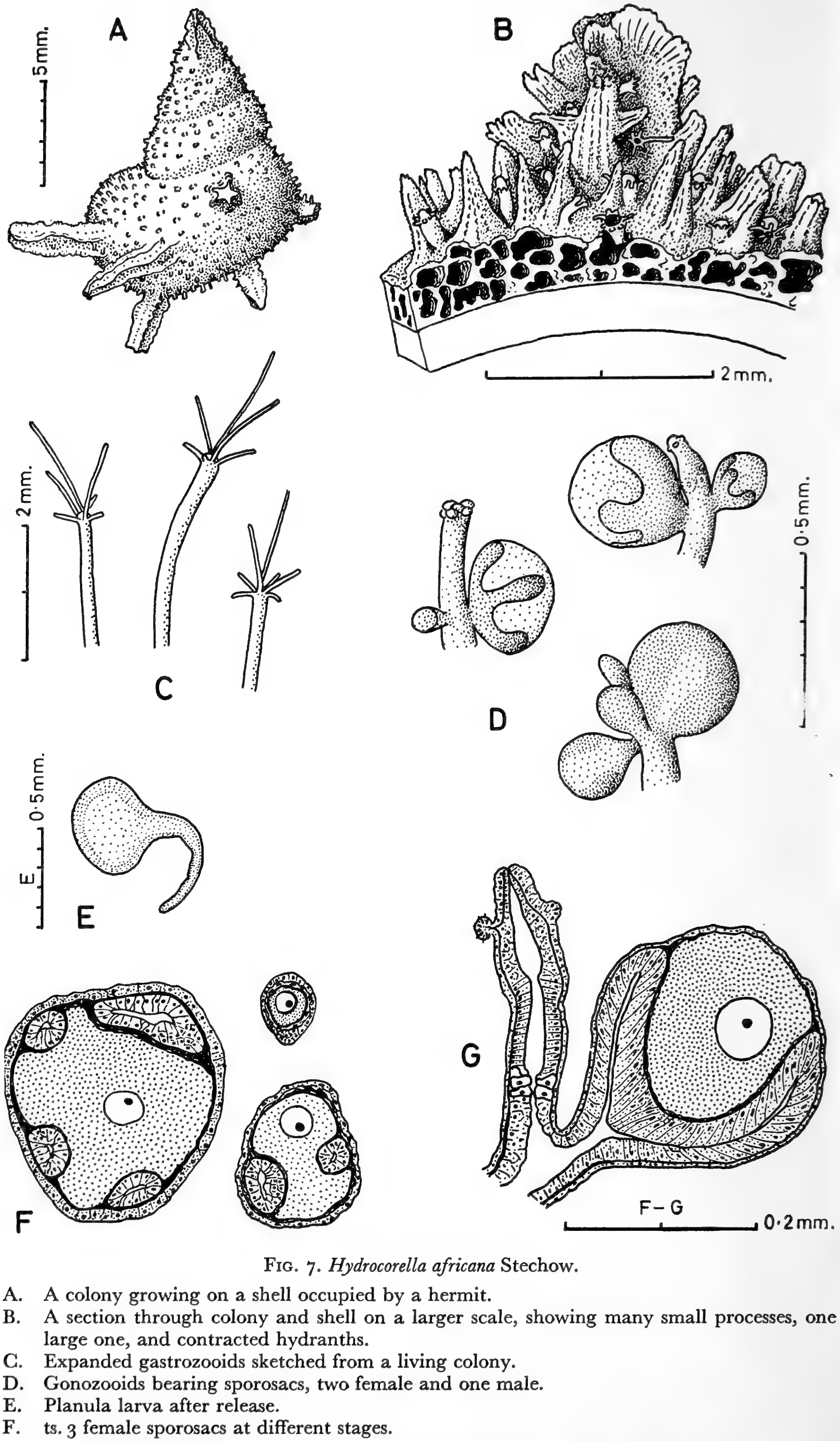

Fig. 7. *Hydrocorella africana* Stechow.

A. A colony growing on a shell occupied by a hermit.
B. A section through colony and shell on a larger scale, showing many small processes, one large one, and contracted hydranths.
C. Expanded gastrozooids sketched from a living colony.
D. Gonozooids bearing sporosacs, two female and one male.
E. Planula larva after release.
F. ts. 3 female sporosacs at different stages.
G. l.s. female gonozooid and sporosac. Young eggs visible in endoderm of gonozooid.

for on several occasions gourd-shaped planulae have been found imprisoned by the over-arching extensions of the skeleton.

Remarks. This species was described by Stechow (1925*b*) with particular emphasis on the skeleton, but it has never been illustrated. Stechow mentioned male sporosacs only and failed to observe the gonozooids.

Podocoryne carnea M. Sars, 1846

Podocoryne inermis Allman, 1876: 255, pl. 10 (figs. 4–5).
Hydractinia carnea: Vervoort, 1946*b*: 126, fig. 49. Millard, 1957: 181.

Records. West coast: LB 380C, 403C. SB 132N, 174M, 231Y, 267V, 269B. TB 13, 14, 15, 21K. WCD 134C. South coast: KNY 212G. LIZ 3B, 24X. MB 25D. SCD 26E, 111C, 113E, 126L, 239G, 258S, 281E, 330F, 333F. All on shells of the gastropod *Nassa* (*Hinia*) *speciosa* A. Adams.

Remarks. One of these colonies (SCD 26E) is without spines and would correspond to the spineless form found in Europe ('*Podocoryne inermis*' of Allman).

Family **Pandeidae**

Leuckartiara octona (Fleming, 1823)

Leuckartiara octona: Rees, 1938: 12, figs. 3–5. Millard, 1957: 182.

Records. South coast: LIZ 3A. SCD 20J, 26D, 94B, 258T, 281F, 314C, 333G.

Remarks. To avoid misidentification, only those specimens with medusa buds are included in the above records. SCD 281F was growing on the shell of *Nassa speciosa* A. Adams, SCD 314C on *Nassa analogica* Sow. and all others on *Bullia annulata* (Lam.).

Family **Aequoreidae**

Aequorea africana n. sp.

Fig. 8

Holotype: MB 70G from Mossel Bay on the south coast. South African Museum catalogue number: SAMH 413.

Description. A colony with well-extended hydranths growing on an empty snail-shell.

Stem unbranched or branching sympodially up to three times, reaching a maximum height of 0·2 cm. Stem and branches annulated or corrugated, increasing in diameter from base to distal end, bearing terminal hydrothecae. Shorter stems closely and distinctly annulated throughout, longer ones closely annulated in basal region, irregularly corrugated in more distal part.

Hydrotheca thin and membranous except for base which is somewhat stouter and remains as a saucer-shaped *Halecium*-like structure in damaged or regenerated specimens (fig. 8A), with distal region irregularly creased and folded longitudinally to form an operculum below which the hydranth can be

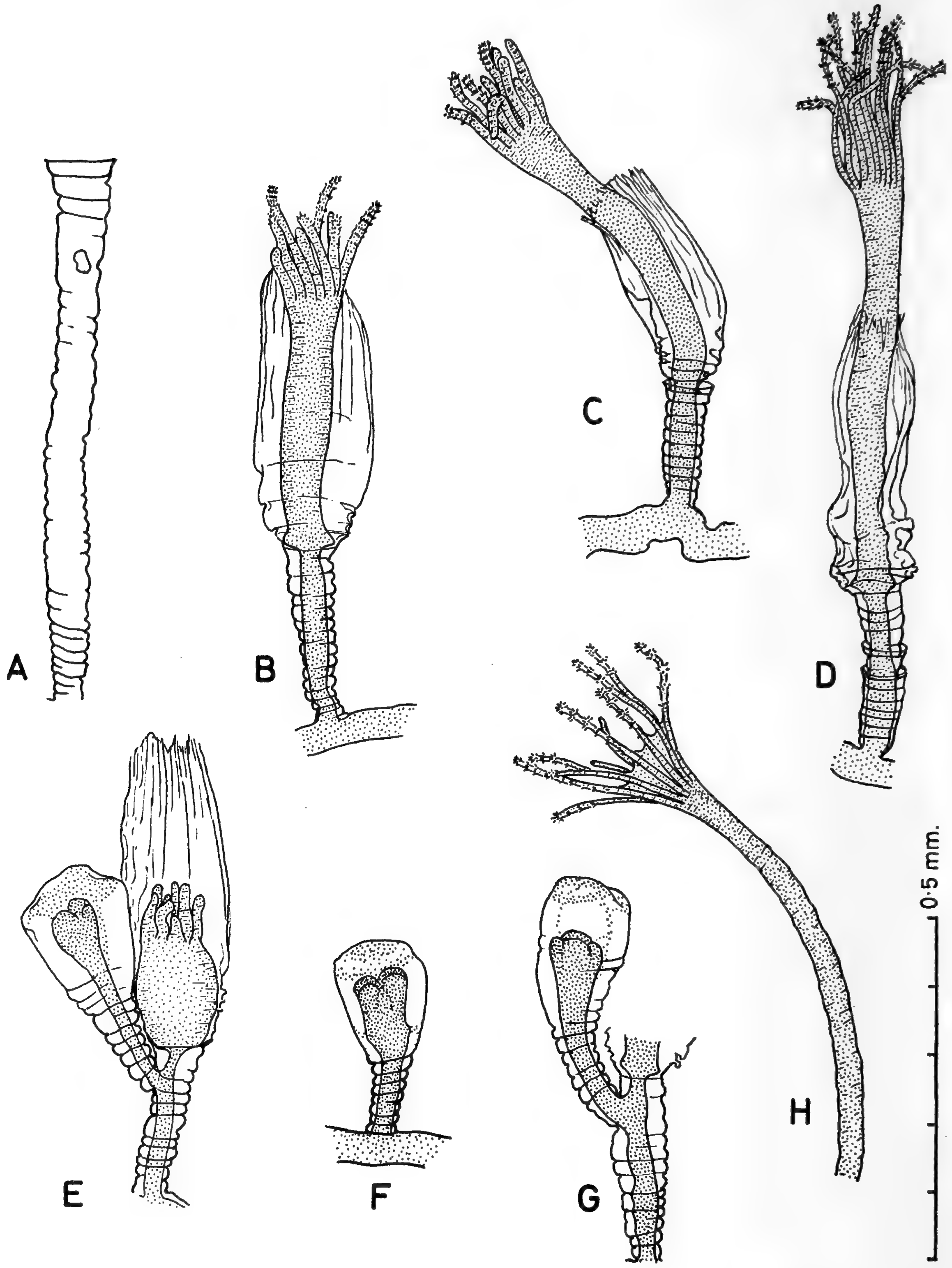

Fig. 8. *Aequorea africana* n. sp.

A. An empty stem surmounted by a saucer-shaped structure (the remains of the hydrotheca). B–E. Hydrothecae containing hydranths in various stages of expansion, E with a gonotheca. F and G. Gonothecae containing medusa buds, F arising from hydrorhiza, G from the stem. H. An expanded hydranth showing the web between the tentacle-bases.

withdrawn. Hydranth long and extensile, with conical hypostome and 11–17 tentacles united by a web at their bases (fig. 8H). Tentacles often moniliform in appearance.

Gonophores borne on stem or hydrorhiza, each on an annulated pedicel which increases in diameter towards the distal end. Gonotheca not sharply demarcated from pedicel, pear-shaped, containing one young medusa-bud.

Measurements (mm.)

Stem, length	0·18–2·05
maximum diameter	0·045–0·07
Hydrotheca, length	0·32–0·55
maximum diameter	0·11.0·18
Hydranth, length to hypostome (preserved)	reaching 0·72
Gonotheca, length, with pedicel	0·29–0·40
maximum diameter	0·12–0·15

Remarks. This species is closely related to several members of the 'Campanulinid' group of hydroids, in particular to the following:

(i) *Campomma hincksi* (Hartlaub, 1897). This species was linked by Hartlaub with the medusa *Eucheilota maculata* Hartlaub, 1894, probably erroneously according to Rees (1939, p. 442) and Russell (1953, p. 313). *Campomma hincksi* is the sole representative of its genus, which is retained provisionally only until such time as the medusa can be definitely placed. Both *C. hincksi* and *E. maculata* are known only from Europe. *Aequorea africana* strongly resembles Leloup's material of *C. hincksi* from Belgium (1952, fig. 70).

(ii) *Campanulina paracuminata* Rees, 1938. This is almost certainly the hydroid of *Aequorea aequorea* (Forskål, 1775) (= *Aequorea forskalea* Péron and Lesueur, 1809; see Russell, 1953, p. 350, and Huvé, 1952, p. 36). The medusa is known from Atlantic coasts including South Africa (Kramp, 1961).

(iii) *Campanulina acuminata* (Alder, 1857). This is probably the hydroid of *Aequorea vitrina* Gosse, 1853 (see Russell, 1953, p. 354) or of *Aequorea pensilis* (Haeckel, 1879) (see Huvé, 1952, p. 37). *A. vitrina* occurs in N.W. Europe and *A. pensilis* in the English Channel and in the Pacific and Indian Oceans including South Africa (Kramp, 1961).

The present material may well be *Campanulina paracuminata*, whose medusa is known from South Africa and material of which was examined in the British Museum in 1960; but as there are slight structural differences (e.g. in the nature of the operculum and the number of tentacles) and as there are other South African species of *Aequorea* with unknown hydroids (e.g. *A. coerulescens* (Brandt, 1838) and *A. macrodactyla* (Brandt, 1838)), a separate species has been established as a temporary measure.

Family **Lovenellidae**

Lovenella chiquitita Millard, 1957

Lovenella chiquitita Millard, 1957: 198, fig. 7. Millard, 1959*b*: 250, fig. 3.

Records. West coast: A 384D. SWD 39G. TRA 156C.

Remarks. The placing of this species in the genus *Lovenella* is a temporary measure only and is based on the morphology of the hydroid generation, which shows close affinity to *Lovenella clausa* (Lovén, 1836).

The medusa, in its absence of cirri at the time of liberation, is more closely related to *Phialella.* That it is not *P. quadrata* (Forbes, 1848) was established by comparison with material of the hydroid generation of the latter in the British Museum in 1960, for which privilege the author is indebted to Dr. W. J. Rees. It might well be *P. falklandica* Browne, 1902, the medusa of which has been found in South Africa at Saldanha Bay (identification by Dr. M. E. Thiel, Zoologisches Museum, Hamburg), yet the youngest known medusae of this species (0·8–1·0 mm. diameter) have 'four perradial tentacles, and the four interradial tentacles are just beginning to develop and are visible as four minute bulbs' (Brown and Kramp, 1939: 298), suggesting that they are liberated with only 4 tentacles and not 8 as in the present species.

Family **Haleciidae**

Halecium beanii (Johnston, 1838)

Fig. 9 A–F

Halecium beanii: Hincks, 1868: 224, pl. 43 (fig. 2). Broch, 1918: 38, fig. 13. Millard, 1957: 188. Millard, 1958: 168. Ralph, 1958: 332, fig. 10 *a*, *b*, *e–k*. Vervoort, 1959: 224, fig. 6.

Records. West coast: CP 336C. SB 196M. SWD 12D, 42F. TB 17A, 21B. WCD 125U, 145V. South coast: CPR 46L. LIZ 7S. MB 47T, 60Q. SAMH 157, 214, 273, 328, 335, 341. SCD 37M, 85M, 154C, 387G, 394B.

Description. Stiff, shrubby colonies, many of them epizootic on other hydroids, the largest reaching a height of 7·4 cm.

Remarks. Since no criterion can be found for distinguishing between sterile colonies of *H. beanii* and *H. halecinum*, only samples containing female gonophores have been included above. The species is certainly more common than is indicated by the records, as a further 26 sterile samples are present in the collection, all, or most of which, probably belong to the same species.

Attempts have been made by various authors to distinguish *H. beanii* from *H. halecinum* on the basis of the angle of the hydrothecal margin and the shape of the basal part of the hydrophore, but, as the accompanying diagrams (fig. 9 A–E, all chosen from fertile specimens) will show, both characters are so variable that no reliability can be placed upon them.

Halecium delicatulum Coughtrey, 1876

Fig. 10L

Halecium parvulum: Millard, 1957: 189, fig. 4A. Vervoort, 1959: 227, fig. 7.
Halecium parvulum, var. *magnum* Millard, 1957: 190, fig. 4 B–O.
Halecium delicatulum: Ralph, 1958: 334 (synonymy), figs. 11*e*, *h–n*, 12 *a–p*.

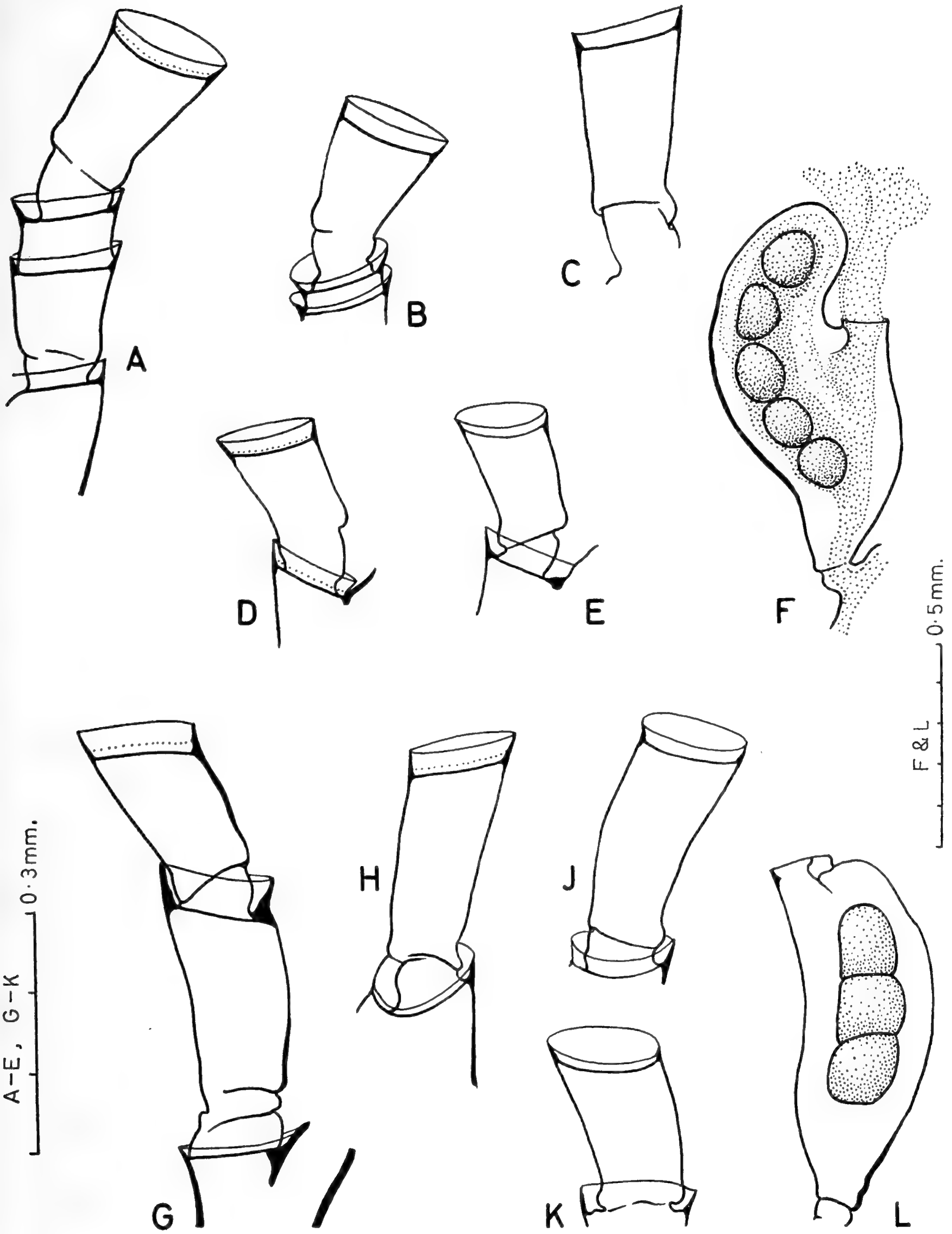

Fig. 9. *Halecium beanii* (Johnston) (A–F), and *H. halecinum* (Linn.) (G–L).
A–E and G–K, hydrophores from various colonies.
F and L, gonothecae.

Records. West coast: AFR 736Z. CP 327C. LAM 30P, 35A. TB 9, 17C, 21C. WCD 18T, 156A, 160P. South coast: LIZ 16F. MB 19Q, 84E, 88J. SAMH 179, 189, 242, 250, 381. SCD 5F, 22A, 29H, 37N, 52J, 85K, 154B, 179H. TRA 92M.

Remarks. It has been pointed out by Ralph (1958) that the large variety (var. *magnum* Millard) described in 1957 has similar dimensions to the type material of *H. flexile* Allman, 1888, which is now recognized as a synonym for *H. parvulum* and *H. delicatulum.* Since so great a variation of size is possible it is not justifiable to retain a subspecies on this character alone.

Halecium dichotomum Allman, 1888.

Fig. 10 A–K

Halecium dichotomum Allman, 1888: 13, pl. 6. Billard, 1910: 4. Stechow, 1925*b*: 419. Millard, 1957: 188 (excluding the male gonophores).

Records. West coast: WCD 20G, 164C. South coast: LIZ 7W. MB 8V, 12W. SAMH 162, 227, 243, 274, 352. SCD 5G, 29J, 37P, 81P, 85N, 154D, 175T, 188S, 239F, 265G, 333C, 387F, 394A. TRA 38J, 92N.

Description. Colonies very variable in appearance and growth-form. Stem fascicled, branching with the typical dichotomy described by Allman and generally in all planes, usually geniculate, with a tendency for annulation in the region of the nodes. Primary hydrophores usually sessile, secondary hydrophores usually symmetrical and annulated in the basal region. Hydrotheca low and wide, with walls flared outwards, over 0·17 mm. in diameter at the margin.

Among the variety of colonies examined two extremes of growth-form occur:

(i) Large upright colonies reaching 11–12 cm. in height, with strongly fascicled stems and branching mainly in one plane. Main stem more or less straight and dichotomy not obvious. Larger stems and branches stiff in appearance and up to 2 mm. thick, though unable to support themselves out of fluid. Smaller branches graceful and flexuous. Stem and branches with long internodes with no annulation other than a shallow constriction near the base. Secondary hydrophores scarce. Closer examination shows that the typical dichotomy is in fact present in this form, but that one limb is always short (the branch) and the other long, contributing to the axis of the stem. The latter limb is enveloped by peripheral tubes in fascicled regions, so obscuring the dichotomy (fig. 10 A, B).

(ii) Low, scrubby colonies, often epizootic, reaching a height of 1–2 cm. Stem usually weakly fascicled and strongly geniculate. Branching profuse and in all planes, and stolonisation common, resulting in a tangled mat which may cover large areas of the substratum and is very easily recognised. The typical dichotomy is common in this form and very obvious (fig. 10 C). The internodes of the stem and branches tend to be shorter and more annulated, and secondary hydrophores are abundant and often closely annulated in their basal regions.

In two specimens (MB 12W and WCD 164C) of the low, scrubby form, the colony is epizootic on a dead polyzoan and the hydrorhiza is provided with

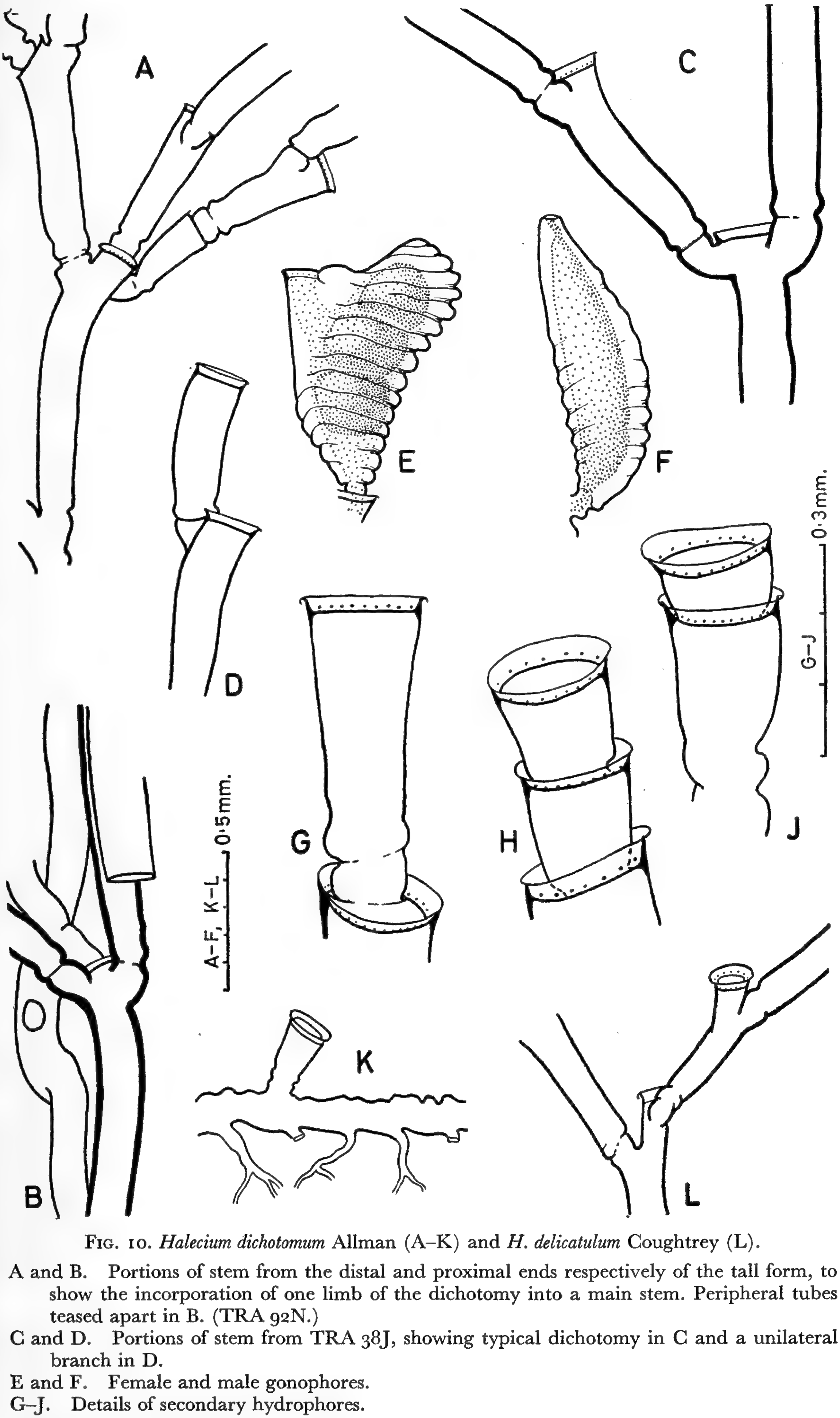

Fig. 10. *Halecium dichotomum* Allman (A–K) and *H. delicatulum* Coughtrey (L).

A and B. Portions of stem from the distal and proximal ends respectively of the tall form, to show the incorporation of one limb of the dichotomy into a main stem. Peripheral tubes teased apart in B. (TRA 92N.)

C and D. Portions of stem from TRA 38J, showing typical dichotomy in C and a unilateral branch in D.

E and F. Female and male gonophores.

G–J. Details of secondary hydrophores.

K. Part of the hydrorhiza to show root-like structures (MB 12W).

L. Part of a branching stem in *H. delicatulum* for comparison.

unusual rootlike projections which enter the pores of the host and anchor the colony (fig. 10 K). Similar 'roots' have been observed on other mounted specimens.

Female gonophores as described by Allman. Male gonophores on separate colonies, slender, elongated and often curved, tapering distally to a small rounded aperture, closely annulated throughout or smooth in distal region (fig. 10 F). Reaching 1·24 mm. in height and 0·36 mm. in maximum diameter.

Remarks. The variation in the growth-form of this species is remarkable, and at first glance the two extremes might be taken for different species. However, female gonophores have been found in both, and intermediate types exist. Comparison with Allman's type material in the British Museum (slide no. 88.11.13.9) confirms the identification, and shows that the hydrophores are similarly variable. Primary hydrophores, though usually sessile, may be quite long. The hydrotheca may be strongly flared out, weakly flared at the extreme distal edge only (the commonest type), or the everted part may be quite worn off.

This variation may introduce difficulties in the identification of sterile colonies and possible confusion with species such as *H. delicatulum*, though to one familiar with the species no difficulty arises. Useful diagnostic characters are the normally sessile primary hydrophores, the typical dichotomy in which 2 or even 3 internodes arise from a previous one at the same level, and the characteristic curved apophysis by which each internode arises from its predecessor. Dichotomy may also occur in *H. delicatulum*, but the two limbs usually arise at different levels and the apophyses are not curved (fig. 10 L). *H. dichotomum* may be distinguished from *H. tenellum* by its fascicled stem and larger hydrothecae.

With the abundant material available, it was possible to clear up the confusion which previously existed over the nature of the male gonophores of this species. A re-examination of the material described from False Bay (Millard, 1957: 188) showed that the smooth gonophores from sample FAL 78Z belonged in fact to an epizootic male colony of *H. beanii* inextricably tangled with a female colony of *H. dichotomum*. The annulated gonophores without lateral openings from sample FAL 64N and thought to be female, were in fact male.

Halecium halecinum (Linn., 1758)

Fig. 9 G–L

Halecium halecinum: Hincks, 1868: 221, pl. 42. Broch, 1918: 36, fig. 11. Vervoort, 1946*b*: 158, figs. 63–64. Vervoort, 1959: 225.

Records. South coast: SCD 85P.

Description. A small epizootic, yet fertile, colony, reaching a maximum height of 0·6 cm. Stems stunted and branching irregularly, but fascicled at base. Internode length about twice width at distal end.

Secondary hydrophores very variable, most are asymmetrical, curving towards abcauline side and with an obliquely set aperture. Some are quite symmetrical in the basal region, though asymmetrical more distally. In only a few is the aperture perpendicular to the axis.

Female gonothecae banana-shaped with concave adcauline side and terminal aperture. Containing a single row of 3–4 large eggs.

Remarks. This species is possibly more abundant than is indicated by this single record, as without gonophores it is impossible to distinguish from *H. beanii*. This is the only fertile colony observed and the first fertile, and therefore unquestionable, record from South Africa.

Halecium ?muricatum (Ell. & Sol., 1786)

Fig. 11 A, B

Halecium muricatum: Hincks, 1868: 223, pl. 13 (fig. 1). Broch, 1918: 43, fig. 17. Vervoort, 1946*b*: 163, fig. 67.

Records. West coast: TB 19A. South coast: SCD 56U.

Description. Fascicled stems reaching a maximum height of 4·7 cm., branching in an irregularly pinnate fashion, straight for most of length though sometimes weakly geniculate in distal regions, fairly rigid and able to support themselves out of fluid, though more graceful in appearance than in *H. beanii*. Nodes oblique and sloping alternately to left and right.

Primary hydrophore long; borne on broad apophysis at distal end of each internode, from which it is separated by a distinct groove; usually asymmetrical with adcauline side more convex than abcauline; with a well-marked pseudodiaphragm in distal region below hydrotheca and usually a second one in proximal region. Pseudodiaphragm better developed on adcauline side. Secondary hydrophores similar, though not so long and usually with only one pseudodiaphragm. Hydrotheca relatively deep, margin everted, more so on adcauline side.

Gonophores absent.

Measurements (mm.)

	TB 19A	SCD 56U
Stem, internode length	0·70–0·86	0·61–0·77
diameter across node	0·19–0·24	0·12–0·28
Hydrotheca, diameter at margin	0·24–0·31	0·24–0·29
depth (diaphragm to margin)	0·09–0·14	0·08–0·12

Remarks. The identification of this species must remain dubious until the gonophores have been discovered. The stem and hydrophores are remarkably similar to those illustrated by Broch (1918) for *H. muricatum*, yet *H. muricatum* is an arctic species and has not been reported from the Southern Hemisphere.

Another closely related species is *H. filicula* Allman, 1877, from the Gulf Stream and N. Atlantic Ocean. This species has smaller dimensions (cf. Billard, 1906: 163) and differs in the presence of 2 annulations at the base of the hydrophore and in the absence of a pseudodiaphragm. The gonothecae

(Billard, 1906, fig. 2) appear to be similar to those of *H. muricatum*, and the two species may prove to be conspecific.

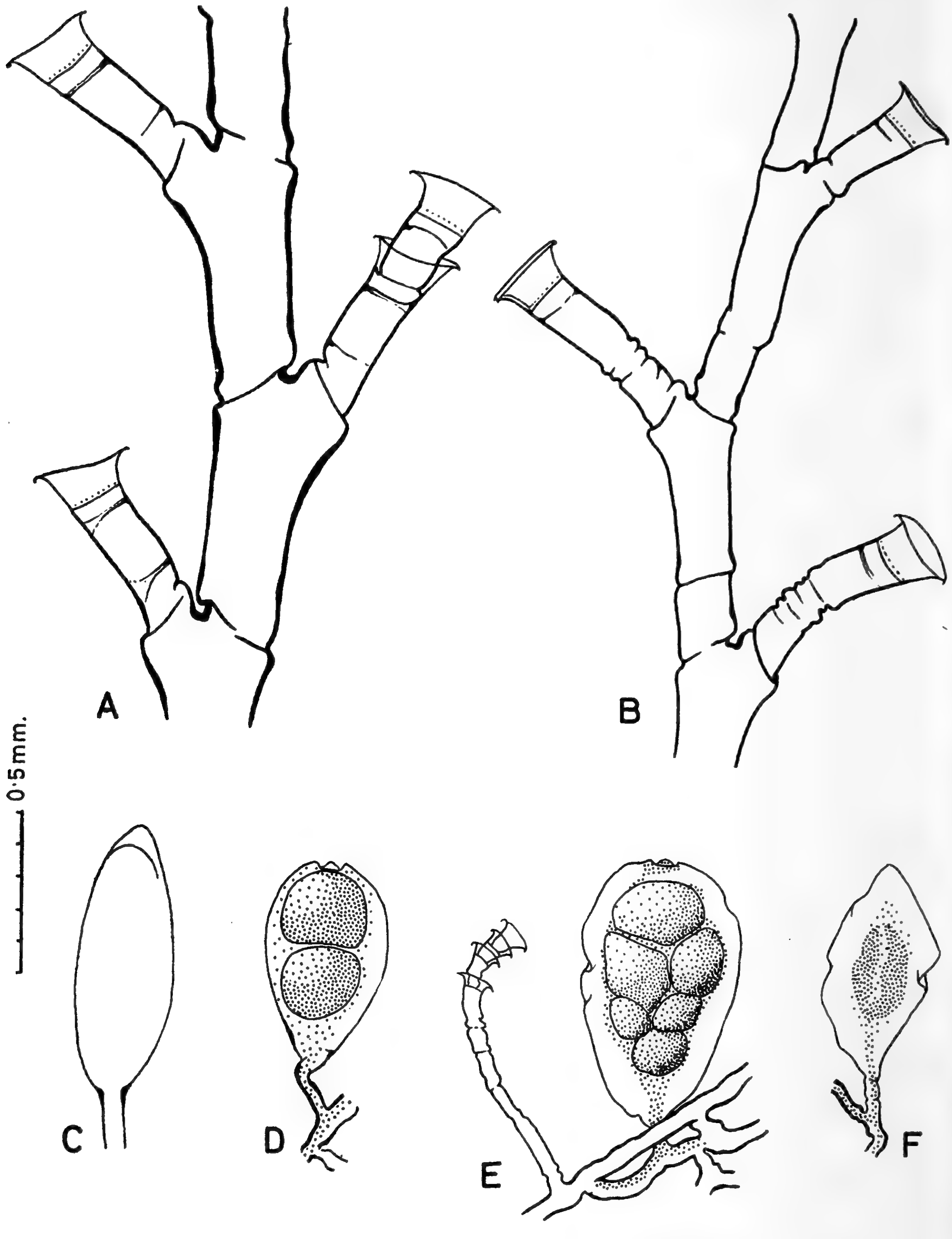

Fig. 11. *Halecium ?muricatum* (Ell. & Sol.) (A–B) and *H. tenellum* Hincks (C–F).

A and B. Portions of stem from TB 19A and SCD 56U respectively.
C and D. Female gonothecae in side and front views respectively, D with 2 larvae (SCD 37Q).
E. Part of colony and female gonotheca with several larvae (SCD 60B).
F. Male gonotheca from SAMH 315.

Halecium tenellum Hincks, 1861
Fig. 11 C–F

Halecium tenellum: Millard, 1957: 193, fig. 5. Hamond, 1957: 307, fig. 14. Ralph, 1958: 340. Vervoort, 1959: 229, fig. 8. Naumov, 1960: 454, fig. 344.

Records. South coast: MB 8X. SAMH 315. SCD 37Q, 60B, 394C.

Description. A number of colonies, mostly epizootic, with unfascicled stems reaching a maximum height of 0·4 cm. Stems geniculate and often branching in a dichotomous manner, usually with many athecate internodes as previously figured (Millard, 1957), but often of more normal appearance as figured by Vervoort (1959) and Hamond (1957).

Male and female gonophores present, on separate colonies. Male gonothecae compressed, broad and bluntly rounded at distal end when young, pointed at distal end when mature, reaching a maximum of 1·07 mm. in length and 0·60 mm. in diameter. Female gonothecae borne on stem or hydrorhiza, compressed, pear-shaped in anterior view with bluntly rounded distal end, and a circular, terminal aperture blocked by a small papilla which is shed on the escape of the contents, reaching a maximum of 1·07 mm. in length, 0·51 mm. in diameter and 0·30 mm. in thickness; with no hydranths; containing 2–7 eggs on a branching blastostyle, which develop into planulae *in situ.*

Remarks. Vervoort was correct in assuming that the male gonophores previously described (Millard, 1957) were young ones, as larger mature ones in the process of shedding their contents have now come to light.

Family **Campanulariidae**

Campanularia hincksii Alder, 1856
Fig. 12 A–D

Campanularia Hincksii Alder, 1856: 360, pl. 13 (fig. 9). Hincks, 1868: 162, pl. 24 (fig. 3), fig. 18 Billard, 1906: 172, figs. 4–5 (incl. var. *grandis*).
Campanularia hincksii: Vervoort, 1959: 311, fig. 55*a*.

Records. South coast: SAMH 283. SCD 354G.

Description. Pedicels unbranched and smooth, except for occasional regeneration lines, with a single spherule at distal end.

Hydrotheca inverted cone-shaped, with 8–12 broad, marginal teeth in which the distal end is either hollowed out to form two points or (more rarely) truncated. Hydrotheca polygonal in end-on view, the angles between the teeth forming longitudinal striations visible in side view, which may continue to the base or peter out half-way down. Diaphragm in form of annular thecal thickening.

Female gonotheca with very short stalk, elongated, broad near base and narrowing slightly to truncated distal end, with about 8 low, rounded annulations. Only 2 gonothecae seen, one empty and one almost spent yet still containing 2 eggs.

Measurements (mm.)	SAMH 283	SCD 354G
Pedicel length	2·26–4·19	3·70–6·81
maximum diameter	0·08.0·13	0·12–0·15
Hydrotheca, length	0·85–1·24	1·20–1·55
maximum diameter	0·47–0·77	0·60–0·88
length/diameter	1·36–1·97	1·48–2·27
Gonotheca, length	1·52	
maximum diameter	0·64	

Remarks. This is the first record of the species from South Africa. The measurements correspond well with Billard's var. *grandis*, but the material resembles the typical form more in the double nature of the marginal teeth. These teeth appear to become truncated as they wear down with age.

Campanularia integra MacGillivray, 1842

Fig. 13 A–D

Campanularia caliculata: Warren, 1908: 338, fig. 19.
Campanularia integra: Billard, 1907: 340. Jäderholm, 1917: 4. Broch, 1918: 159 (synonymy). Millard, 1957: 193. Millard, 1958: 171.
Clytia compressa: Vanhöffen, 1910: 303, fig. 24.
?Campanularia gracilis: Stechow, 1925*b*: 423, fig. 6.
Orthopyxis caliculata: Ralph, 1957: 838, fig. 6 *a–f*.

Records. South coast: CPR 9E. LIZ 7U, 13C. MB 52L, 55J. SCD 84X, 179E.

Description. Colonies creeping on weeds and other hydroids, particularly *Lytocarpus filamentosus*.

Remarks. In the identification of this species I have followed Broch (1918) who considers *C. integra*, *C. caliculata* and *C. compressa* as synonymous, although this opinion is not accepted by all recent authors. The difference between these species is supposed to lie in the gonotheca, which is said to be spirally annulated in *C. integra*, smooth and round in section in *C. caliculata*, and smooth and compressed in *C. compressa*. Broch claims to have found intergrading forms between *C. integra* and *C. caliculata*, while the South African material shows intergrading forms between *C. caliculata* and *C. compressa*. Here the gonotheca is usually compressed and smooth, but may also be round in section, and is sometimes roughly corrugated, though not distinctly annulated.

Medusa systematists distinguish the 'medusa' of *C. caliculata* (*Agastra mira* Hartlaub, 1897) from that of *C. compressa* (*Agastra rubra* Behner, 1914) on minor points such as the arrangement of eggs. Of the two, the South African material resembles more *Agastra rubra*, as the eggs are large and comparatively few in number.

Campanularia laminacarpa n.sp.

Fig. 12 E–K

?Campanularia tincta: Jäderholm, 1923: 6
?Campanularia africana: Stechow, 1925*b*: 420, 421 (material from Agulhas Bank, station 105).
Non Campanularia tincta: Warren, 1908: 337, fig. 18.
Non Campanularia africana Stechow, 1923*b*: 104.

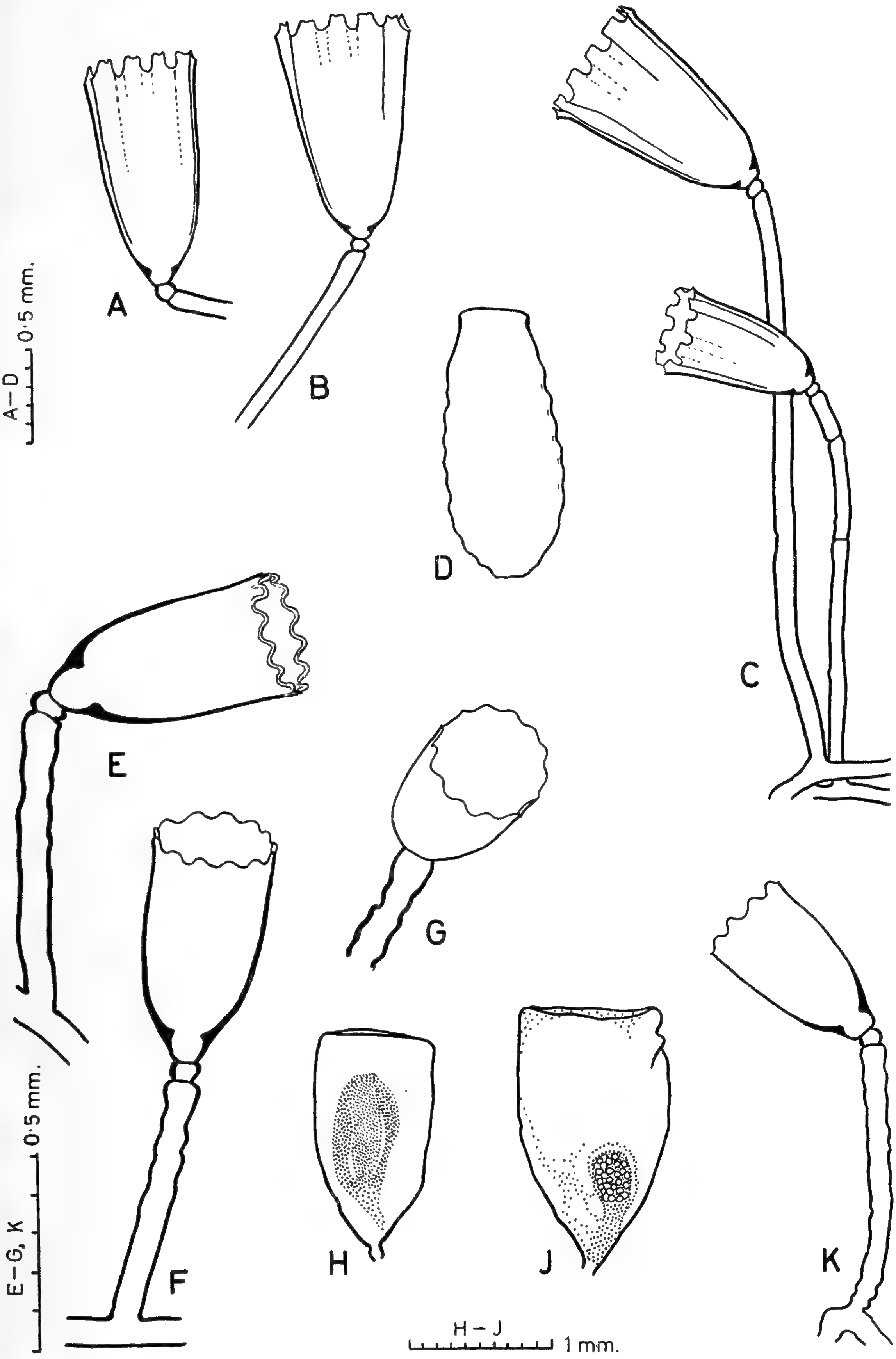

FIG. 12. *Campanularia hincksii* Alder (A–D) and *C. laminacarpa* n. sp. (E–K).

A–C, hydrothecae, and D, gonotheca, from SAMH 283.
E–G, hydrothecae from TRA 38P, and K, from SCD 84U.
H. Male gonophore from SCD 84U.
J. Female gonophore from the holotype, TRA 32A.

Holotype: TRA 32A, a female colony from the Agulhas Bank growing on *Thyroscyphus aequalis* Warren. South African Museum registered number: SAMH 414.

Other records: South coast: SAMH 174, 269, 351. SCD 37V, 61F, 79M, 84U, 112A, 117L, 154E, 169Y, 265E, 394F. TRA 35Z, 38P, 56U, 92B.

Description. Colony stolonic and epizootic on the Sertulariid *Thyroscyphus aequalis*. Hydrothecal pedicel upright, unbranched, smooth or corrugated, with a spherule of smaller diameter at the distal end.

Hydrotheca tubular or slightly expanding to margin, smooth, with length about twice diameter at margin, with a diaphragm in the form of a well-developed annular thickening of the perisarc, with 10–14 rounded marginal teeth.

Gonotheca erect, flat, smooth, generally held in a plane at right angles to the stem of the host, broadening to distal end which is abruptly truncated, with a wide, operculate aperture. Male and female similar. Female containing a single sporosac bearing numerous small eggs. Male with a single sporosac with the structure of a degenerate medusa, spermatogenic cells arranged in 4 longitudinal bands with indications of 4 radial canals.

Measurements (mm.)

Hydrothecal pedicel, length	0·31–1·34
maximum diameter	0·06–0·11
Hydrotheca, height	0·36–0·71
diameter at margin	0·225–0·34
diameter/height	0·46–0·74
Gonotheca, height	1·53–2·01
maximum diameter	0·81–1·20

Remarks. This species has previously been confused with *Campanularia africana* Stechow, 1923*b*. The discovery of gonothecae, which are larger and quite different in appearance from those of the latter species, necessitates the establishment of a new species. Unfortunately the two species have identical trophosomes and there is no method of distinguishing sterile material.

Campanularia africana was originally described from Park Rynie, Natal, as *C. tincta* by Warren in 1908 (p. 337, fig. 18). It has cylindrical to ovate gonothecae, narrowing towards the distal end and then everted to form a short, circular collar around the aperture. Although there are variations in shape the gonothecae are never flattened, but always round or nearly so in section. I have examined Warren's material, which was kindly loaned to me by the Director of the Natal Museum, and found his diagrams to be a faithful representation of the structure. The gonothecae contain a number of large planulae. It was to this material that Stechow (1923*b*) gave the new name of *Campanularia africana*. The species presumably also includes Pennycuik's material from Australia (1959: 169), which possessed male gonothecae, one with '5 shallow annulations'.

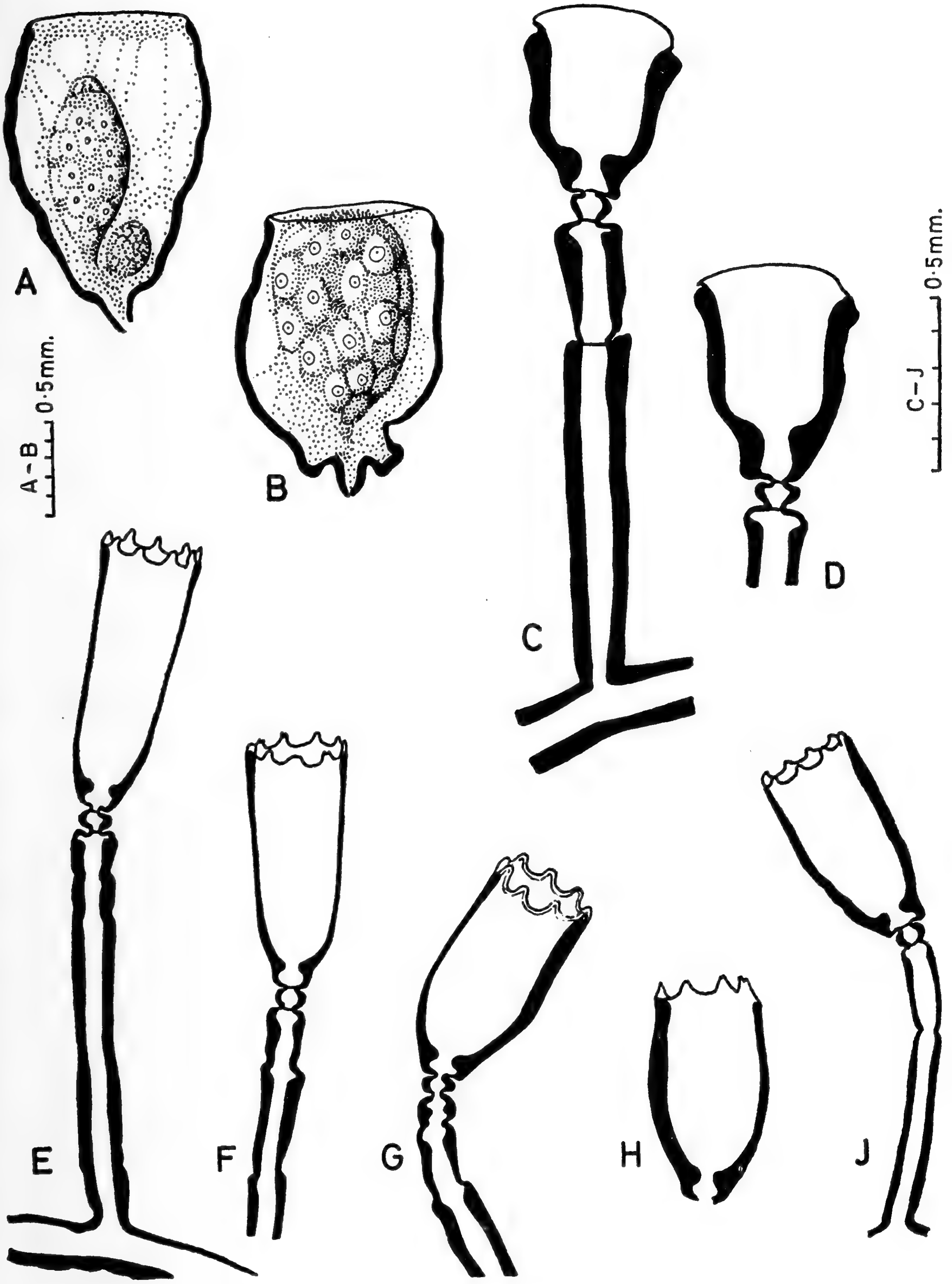

FIG. 13. *Campanularia integra* MacGill. (A–D) and *C. ?mollis* (Stechow) (E–J).
A and B, Gonothecae, and C and D, hydrothecae from CP 258.
E–J, various hydrothecae from CP 646C showing variation in thickness of walls.

Stechow (1925*b*) stated that he had examined material loaned to him by Warren. This was obviously not the type material, and was not recorded by Warren, for it came from Algoa Bay, and it was growing on *Thyroscyphus regularis* (= *T. aequalis*) and presumably unfertile. This material was probably *C. laminacarpa*, as was Stechow's Valdivia material (unfertile) reported in the same paper, at any rate that growing on *T. aequalis*. *C. laminacarpa* possibly only occurs on *T. aequalis* as I could only identify gonothecae in material growing on this host, and I have only quoted records (above) of material growing on *Thyroscyphus*. Of these, 7 have gonothecae of the flattened type.

Several other sterile colonies present in this collection, and growing on other species of hydroids, cannot be identified with certainty, nor can unfertile material in the literature.

Campanularia ?mollis (Stechow, 1919)

Fig. 13 E–J

Clytia mollis Stechow, 1919: 44, fig. L.
Campanularia mollis: Picard, 1951: 344, fig. 3.
Orthopyxis mollis: Ralph, 1957: 840, fig. 7*e–k*.

Records. West coast: CP 646C.

Description. A flourishing colony growing on weed. Pedicel generally smooth, with a single small spherule at distal end, often with regeneration nodes. Hydrotheca cylindrical, with length 2–3 times height, with 7–9 clearly defined marginal teeth separated by broad and shallow bays, diaphragm in form of annular thecal thickening. Marginal teeth sometimes bifurcated at the tip. Margin often reduplicated.

Perisarc of pedicels very thick, that of hydrothecae variable, sometimes thick throughout, sometimes thin for the most part though always thickened at margin and near base.

Gonothecae absent.

Measurements (mm., without reduplications).

Pedicel, length	0·58–1·87
maximum diameter	0·10–0·17
Hydrotheca, length	0·57–0·80
diameter at margin	0·26–0·33
length/diameter	1·94–2·93

Remarks. The identification of this species must remain doubtful in the absence of gonothecae, as there are several closely related species with similar trophosomes. It is close to *C. mollis* though differing from previous descriptions of the species in the larger hydrothecae, better defined marginal teeth and smooth pedicels. A few specimens do, however, show indications of a spiral twisting at the base of the pedicel. The species has not been recorded from South Africa before.

Campanularia morgansi Millard, 1957

Campanularia morgansi Millard, 1957: 195, fig. 6. Millard, 1958: 171.

Records. South coast: LAM 30M. MB 47Y. SAMH 202, 221, 230, 296. SCD 37W, 84W, 117K, 354F. West coast: WCD 12H.

Genus *Clytia* Lamouroux, 1812

Remarks on type species. The genus *Clytia* was established by Lamouroux in 1812 (p. 184) for 3 species, namely:

Sertularia volubilis
Sertularia syringa Linn., 1767
Sertularia verticillata Linn., 1758

Of these, *S. syringa* has been transferred to *Calicella* Hincks, 1859, and *S. verticillata* is generally considered as a species of *Campanularia* but has recently been declared the type species of a new genus *Verticillina* by Naumov (1960).

In the literature 2 species have been confused under the specific name of *volubilis*:

(i) The name *Sertularia volubilis* was originally established by Linnaeus in 1758 (p. 811) for Ellis's 'small climbing Coralline with bell-shaped cups' described and figured by the latter in 1755 (p. 24, pl. 14, fig. *a*, A). But Ellis's description was very inadequate and the material might be either *Campanularia* or *Clytia*. However, the name has been retained for a well-known species of *Campanularia* with fixed sporosacs and a smooth gonotheca which has been declared by Naumov in 1960 to be the type species of this genus (i.e. *Campanularia volubilis* (Linn., 1758)).

(ii) In 1786 Ellis and Solander (p. 51, pl. 4, fig. *e*, *f*, E, F) described and figured under the name of *Sertularia volubilis* material with an annulated gonotheca which is unmistakably recognisable as the species later described by Alder in 1856 as *Campanularia johnstoni*. Ellis and Solander added the corollary that 'there are different varieties and sizes of this twining bell-shaped Coralline'. It is to this description that Lamouroux referred when he created the genus *Clytia*.

So far as I can determine no type species has been established for the genus *Clytia* and I therefore select *Sertularia volubilis* Ellis & Solander, 1786, *non Sertularia volubilis* Linn., 1758.

However, the specific name *volubilis* is obviously untenable. The name *johnstoni* Alder, 1856, is antedated by the name of the medusa of the same species, namely *Medusa hemisphaerica* bestowed by Linnaeus in 1767 on the '*Medusa hemisphaerica*' of Gronovius, 1760 (the latter name being part of a Latin description and thus not valid). The same medusa was later placed in the genus *Phialidium* Leuckart, 1856, by which name it is now generally known, but which is antedated by *Clytia* Lamouroux, 1812.

To sum up, the name of the type species of the genus *Clytia* becomes *Clytia hemisphaerica* (Linn., 1767).

Synonyms: *Medusa hemisphaerica* Linn., 1767
Phialidium hemisphaericum (Linn., 1767)
Sertularia volubilis Ellis & Solander, 1786, *non* Linnaeus, 1758.
Campanularia johnstoni Alder, 1856

Clytia hemisphaerica (Linn., 1767)
Fig. 14 A–F

Laomedea gracilis: M. Sars, 1857: 160, pl. 2 (figs. 1–3, 5).
Campanularia johnstoni Alder, 1856: 359, pl. 13 (fig. 8). Vervoort, 1959: 312.
Clytia raridentata: Vanhöffen, 1910: 301, fig. 22. Fraser, 1944: 145, pl. 26 (fig 118). Millard, 1957: 197.
Campanularia raridentata: Stechow, 1919: 58, fig. Q.
Thaumantias raridentata: Stechow, 1923*a*: 107, fig. M. Stechow, 1925*b*: 426.
Clytia gracilis: Stechow, 1925*b*: 431, figs. 9–10. Millard, 1957: 196. Millard, 1958: 172, fig. 3B, E, G.
Clytia johnstoni: Ralph, 1957: 820, 823, figs. 1*h–u*, 2, 3*a–f*. Millard, 1958: 172, fig. 3A, D, F.
Laomedea (*Phialidium*) *pelagica*: Vervoort, 1959: 313, fig. 55*b*, *c*.

Records. West coast: SB 178C. TB 7, 16. South coast: LIZ 7T, 11K, 40K. MB 8N, 52K, 60N, 64P, 69B, 81W. SAMH 161, 166, 176, 180, 203, 239, 253, 383. SCD 5L, 37X, 50N, 52U, 56V, 61G, 75H, 79P, 84V, 129E, 179D, 265J, 283T, 284E, 330C, 387L, 394G. STJ 31M. TRA 57D, 92W, 159B.

Description. Numerous colonies growing on weeds and other hydroids. Stems solitary or occasionally sparsely branched, annulated at top and bottom and occasionally throughout.

Hydrotheca variable in size, with 8–15 marginal teeth. Teeth acute, sharp or rounded, but always covering a smaller area than the bays between them, often asymmetrical and leaning towards one side. Diaphragm distinct, variable in thickness, but always clearly demarcated from the hydrothecal wall.

Gonotheca generally smooth, with truncated distal end, but sometimes with 1 or 2 irregular corrugations; none of these specimens with distinct annulations.

Remarks. Ralph has demonstrated for *Clytia johnstoni* in New Zealand a variation in size, shape of marginal teeth and degree of annulation on the gonotheca which can be correlated with latitude. While specimens from the southern region correspond to the classical conception of *C. johnstoni*, with annulated gonothecae and broad marginal teeth, those from the northern region have smooth gonothecae and acute marginal teeth and thus cover the form known as *C. gracilis*. We thus have no alternative but to combine the two species. So far as is known there is no difference between the medusae. The range of variation also covers material from South Africa recorded as *C. raridentata*, which is here considered a synonym. See also remarks on p. 477.

Since the latitude on the south coast of Africa is the same as that of the north end of New Zealand, it might be expected that the material in these

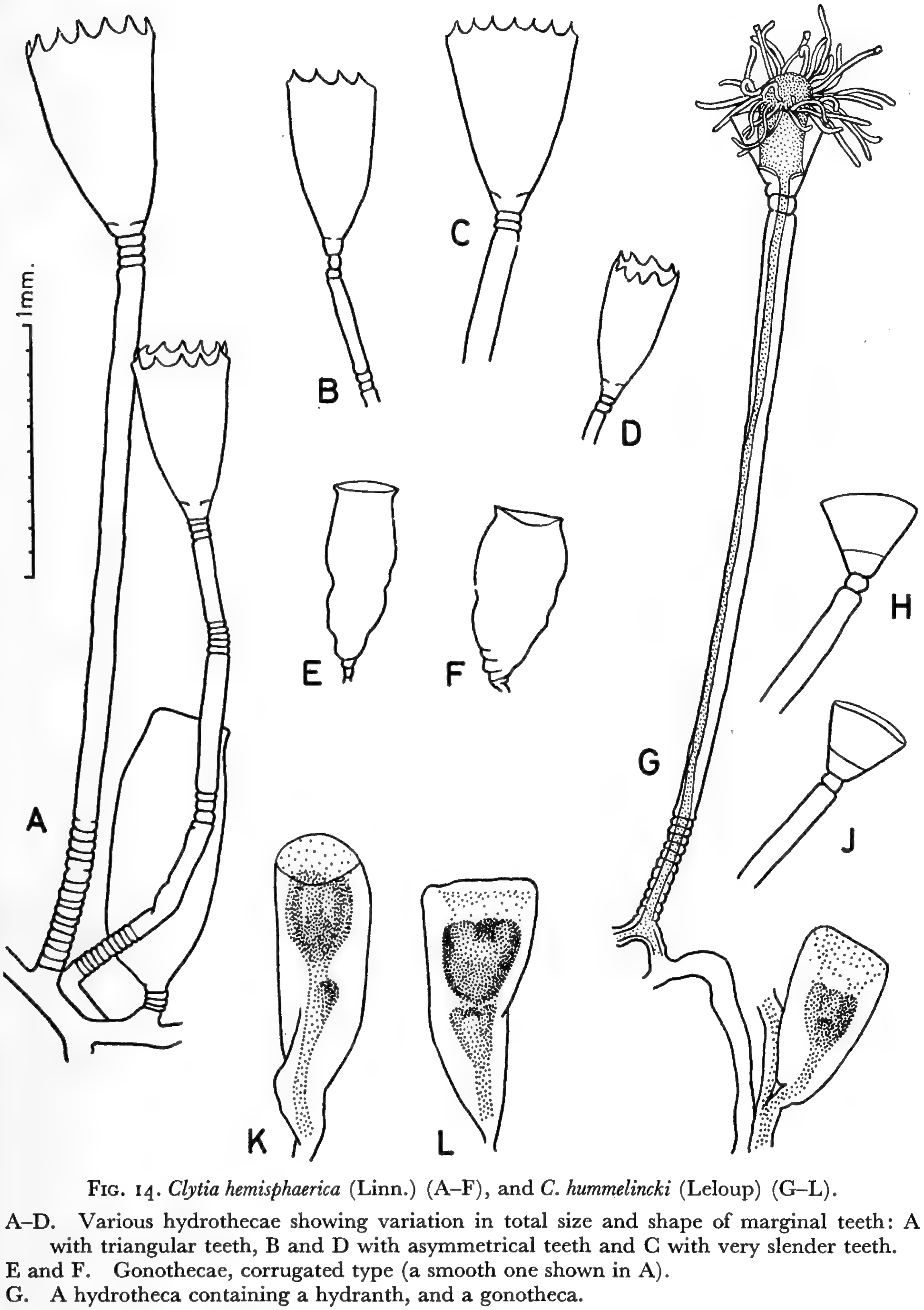

FIG. 14. *Clytia hemisphaerica* (Linn.) (A–F), and *C. hummelincki* (Leloup) (G–L).

A–D. Various hydrothecae showing variation in total size and shape of marginal teeth: A with triangular teeth, B and D with asymmetrical teeth and C with very slender teeth.

E and F. Gonothecae, corrugated type (a smooth one shown in A).

G. A hydrotheca containing a hydranth, and a gonotheca.

H and J. Empty hydrothecae.

K and L. Gonothecae containing young medusae.

(A from TB 16, B from TRA 57D, C from Natal, D–F from False Bay, G–L from SCD 328H.)

two regions would be similar, and that the variation in South Africa would continue from where it left off in New Zealand as one moves up the east coast into warmer waters. This was tested out in the material available and measurements of hydrothecal size and pedicel length are given below.

	Hydrotheca: height (mm.)		*Pedicel: length (mm.)*	
	Range	Mean	Range	Mean
West coast (32–34° S)	0·6–1·0	0·8 (16)	0·7–3·4	2·4 (16)
South coast (34–35° S)	0·4–0·9	0·6 (40)	0·5–5·7	1·9 (39)
East coast (32–28° S)	0·4–0·8	0·6 (32)	1·6–3·8	2·5 (20)
Portuguese East Africa (27–23° S)	0·3–0·6	0·5 (23)	0·4–1·6	1·0 (18)

These figures show that the hydrothecal height from the south coast corresponds well with that from a similar latitude in New Zealand (Ralph gives measurements of 0·40–0·81 mm. between 40° S and 34° S) and that there is a clear decrease in size from the west coast (where the water is colder than the south coast) round the south and up the east coast. A similar trend in pedicel length is not so clear, although pedicels from Portuguese East Africa are certainly shorter than elsewhere. No tendency for a change in the proportions of the hydrotheca was seen.

The marginal teeth are always acute in South African material as in northern New Zealand, and on the east coast there is a tendency for the bays between them to become larger and the teeth narrower (fig. 14C).

With one exception the gonothecae are quite smooth or with a few irregular corrugations, as in those illustrated by Ralph from northern New Zealand. This is as might be expected, and it is difficult to account for the single sample where all gonothecae are distinctly annulated (6–8 rings) described from Portuguese East Africa as *C. johnstoni* (Millard, 1958, fig. 3D).

The variable nature of the gonotheca explains the discrepancy which exists in the literature over the nature of the gonotheca of *Clytia* (*Thaumantias*) *raridentata* (cp. Fraser, 1944, and Stechow, 1923*a*).

The nature of the diaphragm allows for no differentiation between species, and, although variable in thickness, it is always distinct from the hydrothecal wall and thus different from the type characteristic of the genus *Campanularia*.

Clytia hummelincki (Leloup, 1935)

Fig. 14 G–L

Laomedea hummelincki Leloup, 1935: 19, fig. 7.

Records. South coast: SCD 328H.

Description. A rich colony growing on the surface of *Lepas* sp. taken from a buoy. Colony stolonic, stem unbranched, long, closely annulated in basal region and often for short areas at other irregular intervals, otherwise smooth, with a single, rather flattened 'spherule' at distal end.

Hydrotheca in the shape of an inverted cone and usually with straight sides, expanding evenly to margin, with height approximately equal to maximum diameter. Margin untoothed. Diaphragm very delicate, usually oblique. Hydranth with 15–29 tentacles, completely retractable into hydrotheca.

Gonotheca arising separately from hydrorhiza on a short pedicel of 2–4 segments, elongated and expanding to distal end which is truncated, containing 1 or 2 medusa buds. Oldest medusa deep, with manubrium, 4 radial canals and 4 tentacle bulbs visible.

Measurements (mm.)

Pedicel, length	1·92–4·73
maximum diameter	0·09–0·15
Hydrotheca, length	0·25–0·38
diameter at margin	0·22–0·42
length/diameter	0·70–1·36
Gonotheca, length	0·73–1·26
maximum diameter	0·28–0·45

Remarks. This material agrees entirely with Leloup's description of *Laomedea hummelincki* from the West Indies, except that these pedicels are somewhat longer and stouter. The nature of the diaphragm and the presence of medusa buds in the gonotheca (observed here for the first time) shows the species to be a *Clytia.* This is only the second record of this rare species, and a new record for South Africa.

Clytia paulensis (Vanhöffen, 1910)

Fig. 15

Campanularia paulensis Vanhöffen, 1910: 298, fig. 19 *a*, *b*.
Clytia paulensis: Stechow, 1919: 45, 155. Stechow, 1923*a*: 110, fig. N. Stechow, 1925*b*: 428, fig. 7. Stechow, 1925*a*: 211.
?*Clytia ulvae* Stechow, 1919: 47, fig. N. Stechow, 1925*b*: 428.

Records. South coast: LIZ 11M. SAMH 336. SCD 79N, 154G, 258W, 276U, 333D, 387M. TRA 38K.

Description. Several colonies growing on the stems of other hydroids. Stem unbranched, or giving rise to 1 or 2 secondary pedicels in a sympodial manner, closely annulated at base, in distal region and at irregular intervals between.

Hydrotheca very thin and fragile, with 7–10 double marginal teeth. Margin bowed out between teeth giving an undulating outline in end-on view and sometimes the effect of longitudinal striations in the upper part of the hydrotheca. Depth of hydrotheca 1¾ to 3¼ times diameter at margin.

Gonotheca as described by Stechow: smooth and fragile, with annulated pedicel and truncated distal end, containing 1–3 medusa buds.

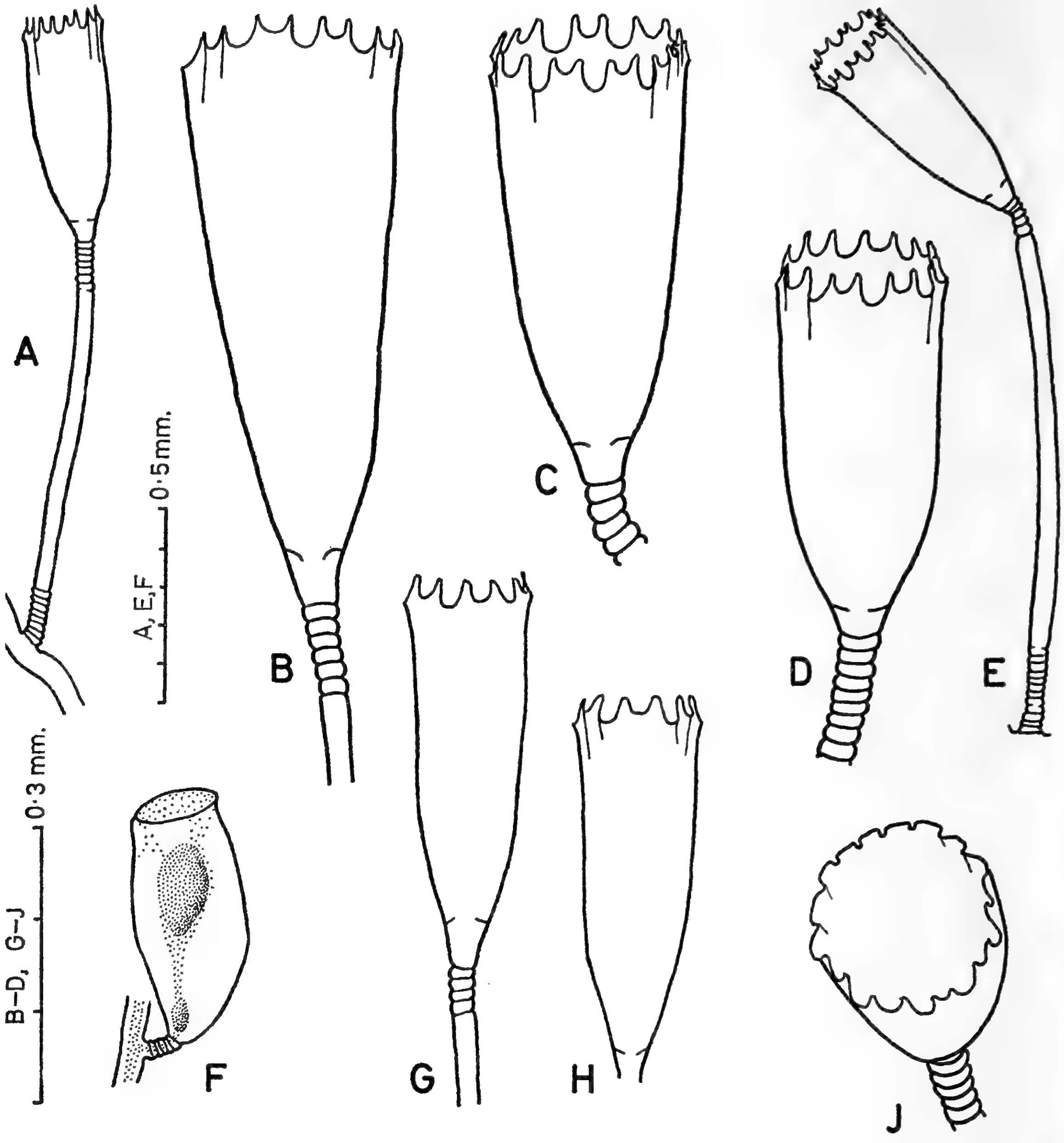

Fig. 15. *Clytia paulensis* (Vanhöffen).

A–E and J. Hydrothecae.
F. Gonotheca.
G and H. Hydrothecae drawn from Stechow's slide of *Clytia ulvae* from Marseilles, 1910.

Measurements (mm.)

	SAMH 336	TRA 38K	SCD 258W	SCD 333D	SCD 154G	*Clytia ulvae* (Marseilles)
Pedicel length	0·57–1·14	0·48–1·82	0·52–0·94	0·91–1·13	0·85–1·00	0·22–0·90
maximum diameter	0·04–0·06	0·04–0·06	0·04–0·05	0·045–0·05	0·035	0·03–0·035
Hydrotheca, length	0·35–0·58	0·41–0·72	0·45–0·69	0·53–0·68	0·42–0·50	0·35–0·44
diameter at margin	0·16–0·33	0·19–0·31	0·15–0·28	0·21–0·25	0·15–0·16	0·12–0·14
length/diameter	1·76–2·47	1·90–2·68	2·17–3·07	2·20–3·10	2·80–3·13	2·71–3·23
Gonotheca, length	—	0·715	0·66–1·00	—	—	—
maximum diameter	—	0·385	0·30–0·36	—	—	—

Remarks. Measurements taken from different localities show that the size and proportions of the hydrotheca are very variable. Vanhöffen's material from the Antarctic is well within range, while some of Stechow's material from South Africa (1925*b*) and Australia (1925*a*) is a little smaller, though the proportions are similar.

It is highly probable that *Clytia ulvae* Stechow, 1919, is a synonym for *C. paulensis*. I have been able to examine a prepared slide of Stechow's material of *C. ulvae* from Marseilles kindly loaned by the Munich Museum and find that the marginal teeth are in fact double (fig. 15G, H), though the bays between members of a pair are almost as large as those between pairs. However, the depth of the former bays is variable within a single colony of *C. paulensis* so that the small teeth may be ⅓ to ⅔ the size of the large double teeth. I have included measurements of Stechow's material (taken by myself) for comparison. These show that the hydrothecae are slightly narrower and the proportion of length/diameter in consequence slightly greater, though the material might well fit near the end of a series of changing proportions arranged as above.

Obelia dichotoma (Linn., 1758)

Obelia dichotoma: Millard, 1952: 420, 426, 433, fig. 3. Millard, 1957: 198. Millard, 1958: 174. Millard, 1959*b*: 250.

Obelia dubia: Vanhöffen, 1910: 307, fig. 27. Nutting, 1915: 77, pl. 19 (fig. 1). Stechow, 1925*b*: 435. Fraser, 1937: 86, pl. 17 (fig. 87).

Campanularia obtusidens Jäderholm, 1904: 2, pl. 1 (fig. 1).

Records. West coast: CP 378. LAM 46P. LB 378F. OLF 21C. SAMH 404, 405. TB 8. South coast: KNY 165C (recorded by Day, Millard and Harrison, 1952). LIZ 2G, 11J. MB 37D, 81V. SAMH 147, 160, 223, 338, 342. SCD 112G, 258V, 281D, 312C. TRA 38L, 42W.

Remarks. Obelia dubia is considered to be a synonym for *O. dichotoma*. The South African material shows all grades of hydrothecal types from the typical *O. dichotoma* form where the marginal teeth are usually not distinct to that of *O. dubia* as illustrated by Jäderholm (1904) and Vanhöffen (1910), where there are distinct marginal teeth and indications of longitudinal striations. It is impossible to draw a dividing line between them. The hydrothecal pedicel is extremely variable in length and the diaphragm may be straight or oblique within the same colony.

The gonothecae of *O. dubia* were illustrated by Fraser (1937) and are said to be 'almost smooth, or provided with broad, shallow undulations'. In the South African material the gonothecae are usually smooth, but examples are also present (with the typical *dichotoma* hydrothecae) where the gonothecae are corrugated, approaching very closely the type illustrated by Fraser.

Obelia geniculata (Linn., 1758)

Obelia geniculata: Millard, 1957: 198. Millard, 1959*b*: 250.

Records. West coast: A 383 (reported by Bright, 1938). CP 325. LAM 24H. LB 127, 314G, 371B. PP 1V. SAMH 357. SB 168G, 235J. TB 6A. TRA 86P. WCD 81G. South coast: TRA 42V.

SUMMARY

A total of 43 species of hydroids is recorded, including 25 Gymnoblasts and 18 Calyptoblasts. Of these 5 are new species, namely *Monocoryne minor*, *Myriothela tentaculata*, *Bicorona elegans*, *Aequorea africana* and *Campanularia laminacarpa*, and 8 are new records for the Republic of South Africa.

The new genus *Bicorona* is established for a Corynid species with 2 whorls of tentacles and fixed sporosacs.

The status of the Campanularian genus *Clytia* is discussed and a type species selected.

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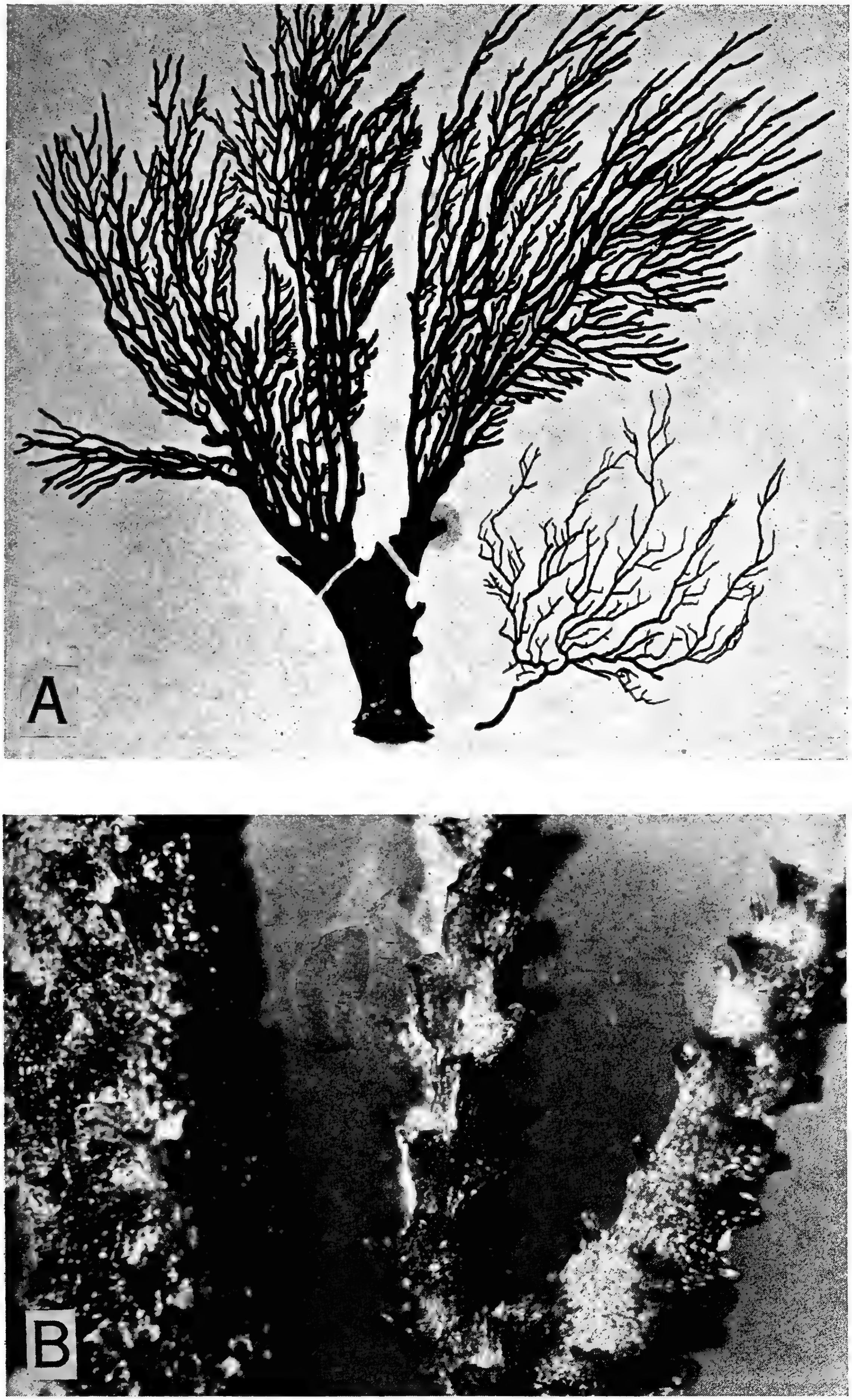

Solanderia procumbens (Carter).

A. Whole colony of form A on left (WCD 158F) and form B on right (WCD 158E).

B. Details of the skeleton in form A (WCD 158F). An old stem shown on left with reticulate meshwork, and a younger stem on right with more marked longitudinal trabeculae and many hydrophores.

(*Photos: Dr. G. J. Broekhuysen*)

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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 4¾ in. × 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

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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).

N. A. H. MILLARD

HYDROIDS OF THE VEMA SEAMOUNT

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HYDROIDS OF THE VEMA SEAMOUNT

By

N. A. H. MILLARD,

Zoology Department, University of Cape Town

(With 1 figure in the text)

CONTENTS

INTRODUCTION

The material recorded in this paper is part of a collection of benthic fauna made by the Department of Oceanography of the University of Cape Town and the Division of Sea Fisheries, Cape Town, in November, 1964. The Vema Seamount is situated in 31° 38′ South Latitude and 08° 20′ East Longitude, approximately 550 miles off the west coast of South Africa, and is surmounted by a plateau of about five square miles with a mean depth of 73 m. The hydroid material was obtained from a rocky bottom in depths varying from 42 to 61 m. and was part of a mixed community containing also sea-weeds, sponges, ascidians and holothurians. Further details of the expedition are reported by Simpson and Heydorn (1965). It is of interest that from a cursory examination of the fauna these authors remark on an apparent affinity with Tristan da Cunha. This was particularly evident in the fish, and the common rock-lobster (*Jasus tristani*), which is now being exploited commercially, is similar to that occurring in the Tristan area.

The hydroid collection is the property of the South African Museum and will be lodged there.

Family Haleciidae

Halecium beanii (Johnston, 1838)

Three infertile samples, two from 54 m. and one from 61 m. Stems reaching a maximum height of 8·6 cm.

Ann. S. Afr. Mus. **48** (19), 1966: 489–496, 1 fig.

Hydrodendron caciniformis (Ritchie, 1907)
Fig. 1

Ophiodes caciniformis Ritchie, 1907: 500, pl. 23 (fig. 11, 12), pl. 24 (fig. 1).
Hydrodendron caciniformis: Millard, 1957: 186, fig. 3. Ralph, 1958: 342, fig. 13b, c, 14a.
Phylactotheca caciniformis: Pennycuik, 1959: 174.
Ophiodissa caciniformis: Vervoort, 1959: 218, fig. 1, 2.

One sample from 54 m. Stems reaching a maximum height of 0·9 cm., most of them unfascicled, though a few weakly fascicled at base. Structure of stem and hydrophore similar to the South African material, though dimensions on the whole slightly smaller.

Gonophores borne in numbers on hydrorhiza. Elongated barrel-shaped, with short pedicel and truncated distal end, lightly annulated. Reaching 1·35 mm. in length and 0·58 mm. in maximum diameter. Male and female similar in appearance and distinguishable only under the microscope. Male

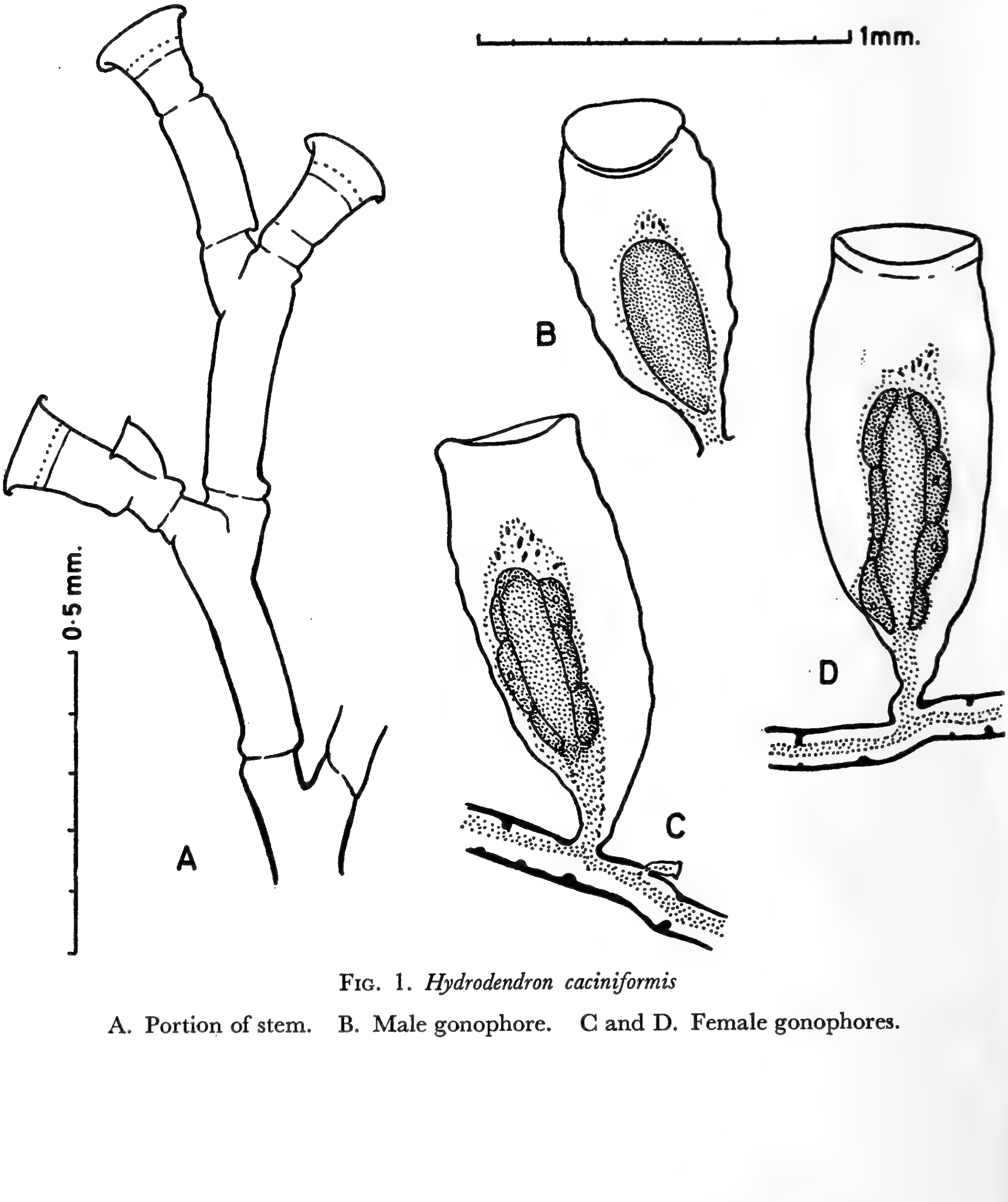

Fig. 1. *Hydrodendron caciniformis*

A. Portion of stem. B. Male gonophore. C and D. Female gonophores.

generally slightly smaller than female. Blastostyle consisting of an elongated spadix bearing a single layer of rather flattened eggs in the female and a mass of spermatogenic cells in the male, the whole enveloped by a diffuse layer of tissue rich in large stenotele nematocysts. No hydranths present.

Although gonothecae were described by Bale (1919), for *Ophiodes australis*, which Ralph suspects to be a synonym, they were not illustrated, and this is the first certain record of gonophores for *H. caciniformis*.

I cannot agree with Pennycuik that *Ophiodissa expansa* Fraser, 1948, from the Pacific coast of North America is a synonym. Not only does Fraser illustrate the nematotheca of this species without the everted rim which is so typical of *H. caciniformis*, but the gonophore is different. In *O. expansa* it is borne on the stem, is much more strongly annulated ('very strongly crested rugosities': Fraser, 1948: 227) and has a narrower aperture.

Family Campanulariidae

Obelia geniculata (Linnaeus, 1758)

One young infertile colony growing on weed from 54 m. Maximum height of stem 0·5 cm.

Family Lafoeidae

Lafoea fruticosa M. Sars, 1851

One small infertile colony from 54 m. Maximum height of stem 1·0 cm.

Family Sertulariidae

Amphisbetia bidens (Bale, 1884)

One infertile colony from 54 m. Maximum height of stem 3·4 cm.

Amphisbetia minima (d'Arcy Thompson, 1879)

One colony, with gonophores, from 54 m. Maximum height of stem 0·6 cm.

Dynamena quadridentata nodosa Hargitt, 1908

Two infertile samples growing on weed, both from 61 m. Maximum height of stem 0·6 cm.

Parascyphus simplex (Lamouroux, 1816)

Thyroscyphus tridentatus: Ritchie, 1909: 74, fig. 1.
Parascyphus simplex: Splettstösser, 1929: 126. Totton, 1930: 179, fig. 29. Ralph, 1961: 755, fig. 1b.

Two small infertile colonies from 42–50 and 54 m. Stems reaching a maximum height of 1·0 and 0·8 cm. respectively. Stem usually unbranched, but in some cases giving off one, or even two, lateral branches. Structure of stem and hydrothecae as in previous descriptions.

This species has not been recorded from South Africa, but has been reported from Gough Island by Ritchie. Apart from this there are several records from Australasia and one from Great Britain.

Salacia articulata (Pallas, 1766)

One colony, with gonophores, from 54 m. Maximum height of stem 2·3 cm.

Sertularella arbuscula (Lamouroux, 1816)

Two very typical, though infertile, colonies from 54 and 61 m. Maximum height of stem 6·8 cm.

Sertularella flabellum (Allman, 1886)

Two infertile colonies from 61 and 54 m. Maximum height of stem 2·0 cm.

Sertularella mediterranea Hartlaub, 1901

One infertile colony from 42–50 m., consisting of stems reaching a maximum height of 2·3 cm., most of them with one lateral branch. Also a fragment from 54 m.

Sertularella megista Stechow, 1923

One infertile colony from 54 m. Maximum height of stem 3·9 cm.

Sertularia distans gracilis Hassall, 1848

Four infertile colonies growing on weed, two from 54 m. and two from 61 m. Maximum height of stem 0·4 cm.

Also a colony with rather larger dimensions and of more doubtful identification from 61 m. The stems in this sample reach a maximum height of 1·0 cm. The hydrothecae are larger than the normal material found on the South African coast (Millard, 1957, 1958, 1964), the internodes longer, and the typical basal hinge-joints are absent. One of the stems has a branch arising from the posterior surface.

Sertularia marginata (Kirchenpauer, 1864)

One infertile colony growing on weed from 54 m. Both simple and branched forms present. Maximum height of branching stem 1·7 cm.

Family Plumulariidae (subfamily Halopterinae)

Antennella quadriaurita Ritchie, 1909

Antenella quadriaurita Ritchie, 1909: 92, fig. 9.
Antennella quadriaurita: Stechow, 1919: 113.

Three infertile samples from 42–50, 54 and 61 m. and one fertile sample from 42–50 m.

Stems reaching a maximum height of 2·2 cm., normally solitary, but sometimes clustered together at base, and sometimes giving off up to four subsidiary branches. These branches arise quite irregularly, usually from the posterior surface of the basal athecate region, and successive branches never form the main axis of the stem as in *Monostaechas faurei* Millard, 1958. Stem with alternate thecate and athecate internodes, of which the athecate ones are longer in the basal region and the thecate in the distal region. Athecate internodes generally bearing two nematothecae each, but sometimes one, and only rarely three. Hydrotheca with depth and marginal diameter approximately equal. Other details as described by Ritchie.

Gonothecae (not previously described) borne on thecate internodes just below hydrothecae, pear-shaped, with truncated distal end and wide spherical aperture, with two nematothecae on basal region (probably female). Pedicel of two segments.

A. quadriaurita is known only from Gough Island and Havana. There is little to distinguish this species from *A. africana* Broch, 1914, other than the number of nematothecae borne on the athecate internodes. For the type material of *A. quadriaurita* from Gough Island Ritchie gives two to four, but generally three, and for the Havana material Stechow gives two. In *A. africana* there is normally only one, but occasionally two, and very rarely three. As shown in the following table, material from the Vema Seamount is intermediate between that from Gough Island and *A. africana* from South Africa. *A. quadriaurita* is retained as a separate species solely on the fact that *most* of the athecate internodes have more than one nematotheca, though it is likely that more material from the Atlantic will show a completely intergrading series, in which case it will be necessary to sink *A. africana* in the synonymy of *A. quadriaurita.* The gonophores of the two species are identical.

Number of nematothecae per athecate internode	1	2	3	4	*Number of internodes examined*
Gough Island (from Ritchie) ..	—	40%	55%	5%	20
Vema Seamount ..	23%	74%	2%	—	90
South Africa	94·3%	5·5%	0·2%	—	506

Halopteris constricta Totton, 1930

Two samples, both from 54 m., one bearing gonophores. Maximum height of stem 0·8 cm.

Family Plumulariidae (subfamily Plumulariinae)

Plumularia pulchella Bale, 1882

Three samples, all from 54 m. The most luxurious colony has stems reaching a maximum height of 1·0 cm. and bears gonophores. Some of its stems bear one to three irregular lateral branches.

Plumularia setacea (Linnaeus, 1758)

Six samples, none of them luxurious, two from 42–50 m., three from 54 m.

and one from 61 m. Two samples bear gonophores, and the maximum height of the stem is 1·7 cm.

Plumularia spinulosa Bale, 1882

Three samples, one from 42–50 m. and two from 54 m. Maximum height of stem 0·5 cm. Young gonophores present in one sample.

Family Plumulariidae (subfamily Kirchenpauerinae)

Pycnotheca mirabilis (Allman, 1883)

One infertile sample from 42–50 m. Maximum height of stem 3·1 cm.

Family Plumulariidae (subfamily Aglaopheniinae)

Aglaophenia pluma pluma (Linnaeus, 1758)

Six samples, one from 42–50 m., three from 54 m. and two from 61 m. Four of these colonies fertile and both male and female corbulae present. Stems reaching a maximum height of 2·4 cm. This material is of more delicate build than that found in South Africa, and in many cases the internodal septa and intrathecal septum are poorly developed or absent. The median nematotheca is always short as shown by Broch (1933, fig. 18a).

Lytocarpus filamentosus (Lamarck, 1816)

Five samples, all infertile, one from 42–50 m., three from 54 m. and one from 61 m. Maximum height of stem 9·0 cm.

Discussion

Of the 23 hydroid species here recorded, 21 also occur in South Africa and it appears that in the case of the hydroid fauna at any rate the two areas have close affinities with one another. Of the remaining two (*Parascyphus simplex* and *Antennella quadriaurita*) both have been reported from Gough Island in the South Atlantic by Ritchie, 1909. The hydroid fauna of the Tristan group of islands is, however, very poorly known, and it is probable that further investigation would show more species in common with the Vema Seamount.

Further analysis shows that of the total 23 species 10 are cosmopolitan, namely:

Halecium beanii
Obelia geniculata
Lafoea fruticosa
Amphisbetia minima (south of the Mediterranean)
Dynamena quadridentata
Sertularella mediterranea
Sertularia distans gracilis
Sertularia marginata

Plumularia setacea
Aglaophenia pluma pluma

With these should probably be included *Parascyphus simplex* and *Hydrodendron caciniformis*, which have a peculiar scattered distribution, the former being known from Australasia, Gough Island and the west coast of Scotland, and the latter from the Cape Verde Islands, Mediterranean, West Indies, tropical West Africa, Australasia and South Africa.

Seven species have an Indo-Pacific distribution, namely:

Amphisbetia bidens: Australia, Madagascar, South Africa.
Sertularella arbuscula: Indian Ocean, Australia, South Africa.
Halopteris constricta: New Zealand, South Africa.
Plumularia pulchella: Australasia, South Africa.
Plumularia spinulosa: Australasia, Japan, South Africa.
Pycnotheca mirabilis: Australasia, Japan, west coast of North America, South Africa.
Lytocarpus filamentosus: Australia, Madagascar, South Africa.

Three species are so far known only from South Africa, namely:

Salacia articulata
Sertularella flabellum
Sertularella megista

One species has an Atlantic distribution, namely:

Antennella quadriaurita: Gough Island, Havana.

Summary

A total of 23 species of hydroids is recorded from the Vema Seamount. Of these the gonophores of *Hydrodendron caciniformis* and *Antennella quadriaurita* are described for the first time.

The distribution of the species in the rest of the world is discussed. It is concluded that the affinities of the hydroid fauna are mainly with South Africa.

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

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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).

P. A. HULLEY

THE VALIDITY OF *RAJA RHIZACANTHUS* REGAN AND *RAJA PULLOPUNCTATA* SMITH, BASED ON A STUDY OF THE CLASPER

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By

P. A. Hulley

South African Museum, Cape Town

(With 8 figures in the text)

Contents

Introduction

The present classification of South African skates is more or less tentative, for this difficult genus shows great variability in its morphological characters, which vary with age and/or sex in the individuals within the species. This high intraspecific variability probably accounts for the present inclusion of 95–100 species in the genus *Raja*. Several South African species have, as yet, proved to be indistinguishable from European species from the corresponding latitudinal belt in the northern hemisphere (Bigelow & Schroeder, 1953), and it would appear that these pairs represent cases of '*masked bipolarity*' (Ekman, 1953). But in very few cases have actual comparisons of the specimens from the two regions been made, although Norman (1935) has given some brief references.

Raja alba, Lacépède, from the N.E. Atlantic is reported here under the same name, but it appears to be cosmopolitan in distribution, being recorded from Morocco (Pietschmann, 1906), West Africa (Fowler, 1936) and Angola (da Franca, 1959).

Ann. S. Afr. Mus. **48** (20), 1966: 497–514, 8 figs.

Norman expressed some doubt about the identification of *R. batis* from South Africa but the material he examined included a single stuffed specimen, on which accurate measurements were impossible. This South African species is now thought to be distinct from *R. batis* Linnaeus, and Smith (1964), on the basis of the shape, the presence of a single median spine and the general markings, has reclassified this skate as *R. pullopunctata*, although he points out that only juvenile material was examined.

Raja rhizacanthus Regan, has been thought to be identical with the European thorn-back skate *R. clavata* Linné, but this has been a matter of speculation. Barnard (1925) and Fowler (1940) have included *R. rhizacanthus* as a synonym of *R. clavata*, but Norman regarded the two as distinct species on the basis of spination and the position of the vent. This has been followed by Smith (1961).

It is the purpose of this paper to compare and contrast certain morphological characters, in the hope that the validity of these latter two South African species may be determined with greater certainty.

Since skates show such great variations in external features, a more critical method of examination needs to be employed. Leigh-Sharpe (1920–1926) has pointed out that in the genus *Raja*, individual species can be recognized by the morphological structures of their claspers. He has extended this further and has postulated the existence of pseudogenera (termed *Alpha-*, *Beta-* and *Gamma-raia*, etc.), recognizable by the similar presence or absence of the clasper elements. Ishiyama (1958) has shown that in Japanese rajids, although intraspecific variations in the clasper can be recognized, the 'external and internal structures of the clasper are species specific without exception' (p. 224). On this basis he has also been able to postulate phyletic, generic and inter-specific relationships, and has concluded that 'the characters in the male external organ (claspers) of the Japanese rajids seem to give the most reliable basis for the systematics of this group of fish'. (p. 243.)

Hence it would appear that since the anatomy of the clasper is valid for the purposes of identification, it should also be valid for the purposes of comparison of geographically separated species. However, 'genitalic differences must be evaluated just like other characters' (Mayr *et al.*, 1953, p. 109), and so differences in the external and measurable characters of the specimens must also be taken into account.

The Claspers or Myxopterygia

Comprehensive anatomical studies have been carried out on the claspers of European elasmobranchs by Petri (1878), Jungersen (1899) and Huber (1901). Two points of view were held as to the function of the claspers: that they were 'holders' (analogous to hands) was originally postulated, but they were later recognized as organs of intromission. Extensive study on the external anatomy and the function of the clasper in the various elasmobranch groups has been made by Leigh-Sharpe, and further work on the function of the organ has been performed by Friedman (1935).

The nomenclature used in this paper is mainly in accordance with that of Leigh-Sharpe and Ishiyama, together with that of the above-mentioned authors.

THE CLASPER OF *R. RHIZACANTHUS* REGAN

The claspers from seven adult specimens of *R. rhizacanthus*, trawled off Cape Columbine and in False Bay, were examined.

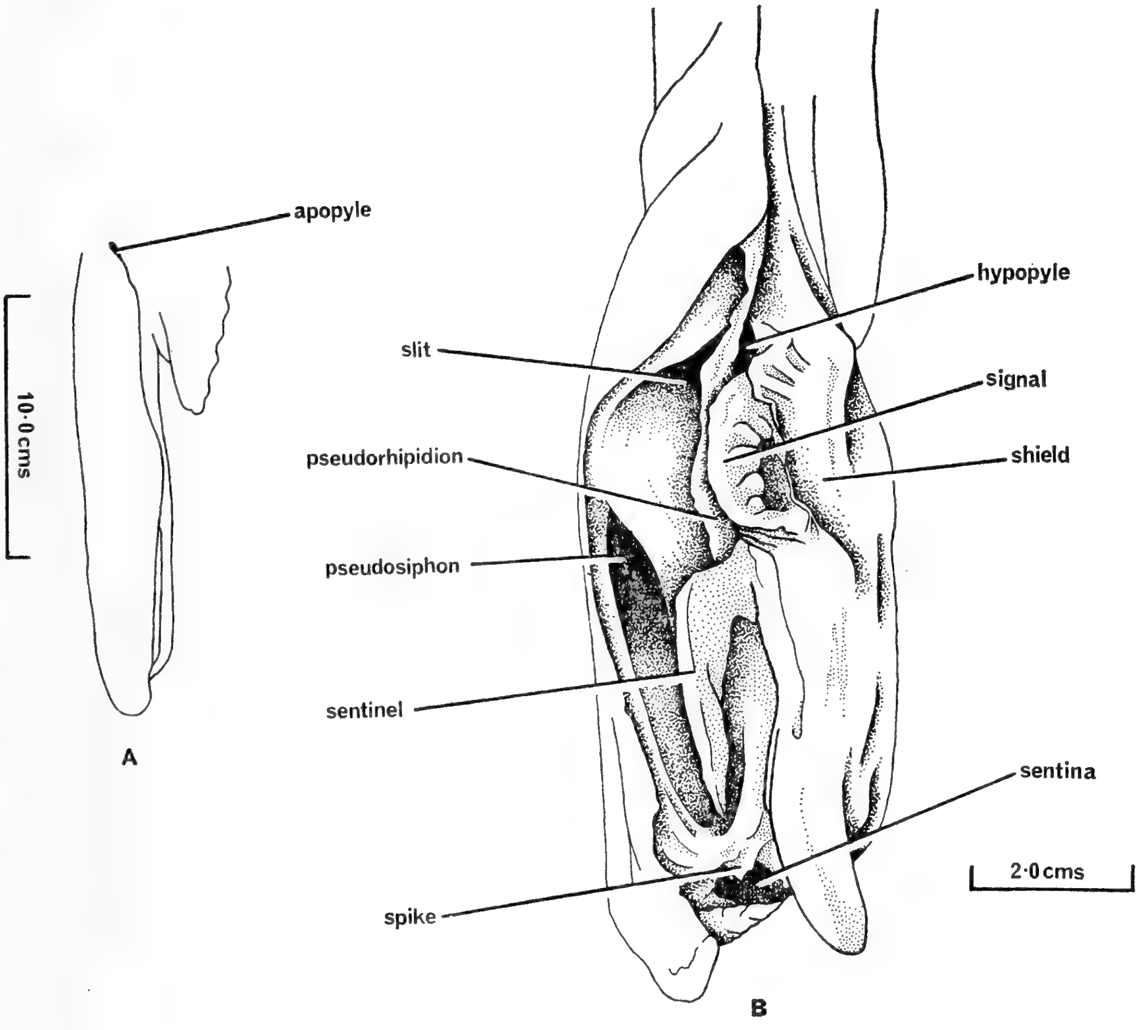

FIG. 1. *Raja rhizacanthus*

A, external view of right clasper from dorsal side; B, lateral view of right clasper, opened to show structural features of glans.

(i) *The external anatomy of the clasper* (fig. 1 A, B)

The clasper of *R. rhizacanthus* is a moderately long, strongly built structure, the outer surface of which is entirely naked. Proximally the clasper is cylindrical, but from about 1/3 its length from the distal end, it becomes broader and dorso-ventrally flattened, especially on its ventral surface. It tapers gradually towards its distal end and terminates in a broadly rounded, spatulate tip. The ventral surface is pale and the dorsal surface tones with the general coloration of the body.

The apopyle (fig. 1 A) is situated dorsally, some little distance behind the vent, and the appendix groove, arising from this point, runs across to the outer margin of the organ, and continues along the distal two-thirds of the lateral edge almost to the tip of the clasper. In some cases, due to the skin stretching across the dorsal terminal 1 cartilage, the groove may be seen from the dorsal side. Proximally the groove is bordered on by the two 'scroll-like' dorsal and ventral marginal cartilages, so that the edges of the groove closely approximate to form a tube, running from the apopyle to the hypopyle. Distally, from about half the clasper length, fleshy lips border the groove, and during erection, brought about by the powerful adductor muscles, and by vascular dilation (Friedman), these lips are opened and the structures of the clasper glans protrude (fig. 1 B).

Two pouches are present on the dorsal surface of the concavity of the clasper glans (fig. 1 B), the smaller, more proximal *slit* and the larger, distal *pseudosiphon*. The median *hypopyle* is bordered dorsally by the pseudorhipidion, a plate-like structure employed as a splash-plate for ejaculating spermatozoa and distinguished from the *rhipidion* of Leigh-Sharpe in not being fan-shaped or pitted. Posterior to the hypopyle, and at about the same level as the pseudorhipidion, is a fleshy pad, the *signal*, which is capable of rotation about the longitudinal axis of the clasper. The *sentinel* is strongly developed and in older specimens its knife-like edge is exposed. There is a deep *sentina* situated distally, its inner border raised into a curved spike. The ventral *shield* is narrow and not well developed. The lining of the concavity is naked, *scale* and *spine* being absent.

All these above-mentioned structures are associated with the cartilages of the terminal group.

(ii) *The internal anatomy of the clasper* (figs. 2, 3)

The skeleton of the clasper is a continuation, in the median axis, of the basipterygium of the fin, and is composed of two groups of cartilages, the basal group (including the basipterygium) and the terminal group.

(*a*) *The basal group* (fig. 2)

Ishiyama has pointed out, that in Japanese rajids, the basal group is not species specific, and, although White (1937) has proved that the number of proximal segments and other cartilages in the basal group tend to vary in large groups of the elasmobranchs, the basal group may only be used in phyletic considerations among the batoid fishes. Examination of the basal group of *R. rhizacanthus* seems to support this view, since the same seven cartilages are present as in the Japanese rajids (see Ishiyama, fig. 7).

The basal group in *R. rhizacanthus* consists of the basipterygium, and b_1 and b_2 cartilages, the Beta-cartilage, and the axial cartilage, which extends

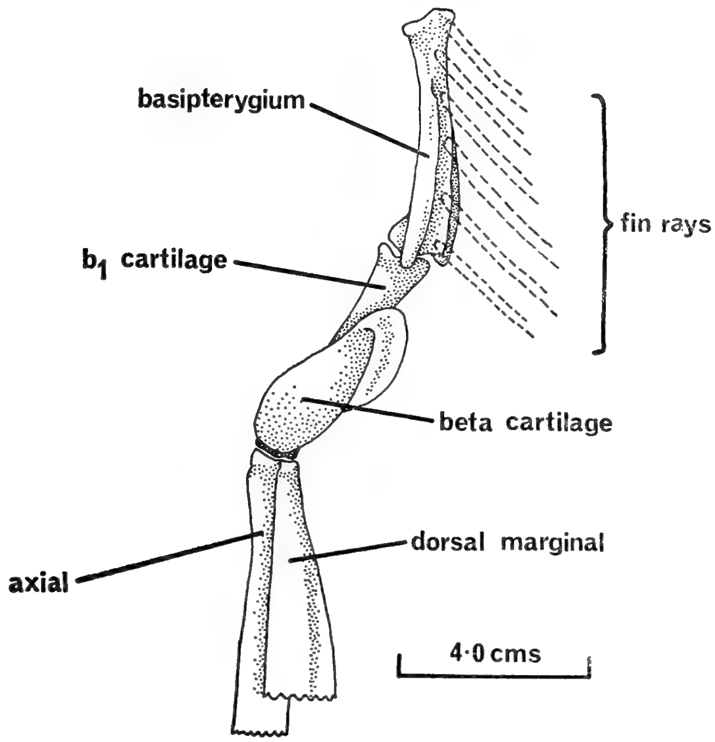

FIG. 2. *Raja rhizacanthus*. Cartilages of the basal group of the clasper.

to the terminal part of the clasper, and is covered by the dorsal and ventral marginal cartilages (fig. 2). The basipterygium is a short, stout structure, to which are attached in a groove on its lateral margin, the last 6 fin rays of the pelvic fin. Distally, the basipterygium is elongated on its dorsal surface to form a protuberance which overlaps the b_1 cartilage. The proximal end of the b_1 cartilage is visible from the dorsal side, but the Beta-cartilage, situated dorsally to the b_1 and b_2 cartilages, completely obscures the b_2 cartilage and the distal end of b_1. The Beta-cartilage is more or less flat, serving as a region of attachment for the *m. flexor internus*, but is slightly thickened and upraised at its proximal end, forming a shelf.

The distal ends of the b_2 and Beta-cartilage are superimposed so that both of these elements play a part in the joint with the axial and marginal cartilages.

The long axial cartilage is cyclindrical at its proximal end, but it becomes dorso-ventrally flattened distally and assumes a spatulate appearance. It is tightly enclosed by the calcified dorsal and ventral marginal cartilages and is only free at its spatulate tip, although it is visible dorsally. The dorsal marginal cartilage attaches tightly to the axial, starting where the axial is connected to the b_2/Beta joint, and runs along the outer lateral margin of the axial for about half its length. The dorsal marginal cartilage is somewhat broadly pointed anteriorly but it becomes expanded distally, its outer lateral edge forming the dorsal edge of the 'scrolled' groove of the clasper. The ventral marginal cartilage, unlike the dorsal marginal, starts posteriorly to the axial and is a flat, tongue-like structure. Its outer lateral margin forms the ventral lip of the 'scroll' and medially it is attached to the axial, overlying it distally. The ventral marginal cartilage extends farther down the length of the clasper than the dorsal marginal cartilage. Attached distally to the axial and to the marginal cartilages, are the elements which comprise the terminal group of cartilages.

(*b*) *The terminal group*

The elements which comprise the terminal group of cartilages are associated with the structures of the glans, and may be divided into three types: ventral terminal, dorsal terminal and accessory cartilages.

1. *Ventral terminal* (figs. 3 A, B, G)

The ventral terminal cartilage is attached to a groove in the distal end of the ventral marginal cartilage. It has a J-like shape, being by far the largest cartilage of the terminal group. It is strongly curved medially, and runs around the axial cartilage, so that it can be seen from the dorsal side. The upright portion of the ventral terminal cartilage is fairly well developed and there is a small shelf on its dorsal side, which is seen as the shield of the clasper glans. Distally, the ventral terminal is thick and somewhat pointed.

2. *Dorsal terminal* 1 (figs. 3 C, G)

The dorsal terminal 1 cartilage ('cover-piece' of Jungersen) is situated on the dorsal side of the clasper, partially covering the dorsal terminal 2 cartilage, to which it is attached along the length of its longest margin. It is flatly rounded and curved proximally, so that it is elongated on its outer lateral margin. From this point, there is a shelf, running in a curve along the anterior margin, which serves as a point of insertion for the aponeurosis of the *m. dilatator*, which consequently covers the whole area of the cartilage. Distally, the cartilage is flat and its distal end is attached, together with the dorsal terminal 2 cartilage, to the axial cartilage. The dorsal terminal 1 cartilage is associated with the development of the pseudosiphon.

3. *Dorsal terminal* 2 (figs. 3 D, G)

This curved element is inserted between the dorsal terminal 1 and the dorsal marginal/axial cartilages. It is firmly attached to the distal region of the dorsal marginal cartilage, and by means of a ligament (which forms the shelf between the slit and pseudosiphon) it is attached at its distal end to the outer lateral margin of the axial cartilage, at about 2/3 the length of that cartilage from its anterior end. The dorsal terminal 2 cartilage is strongly curved, and raised along the side of longest curvature, to form a flat surface 'articulating' with the dorsal terminal 1 cartilage. The dorsal terminal 2 cartilage is associated with the slit.

4. *Accessory cartilages* 1 *and* 2 (figs. 3 E, G)

These two cartilages are strongly united and are attached to the distal end of the ventral marginal cartilage. The accessory cartilage 1 is the S-shaped

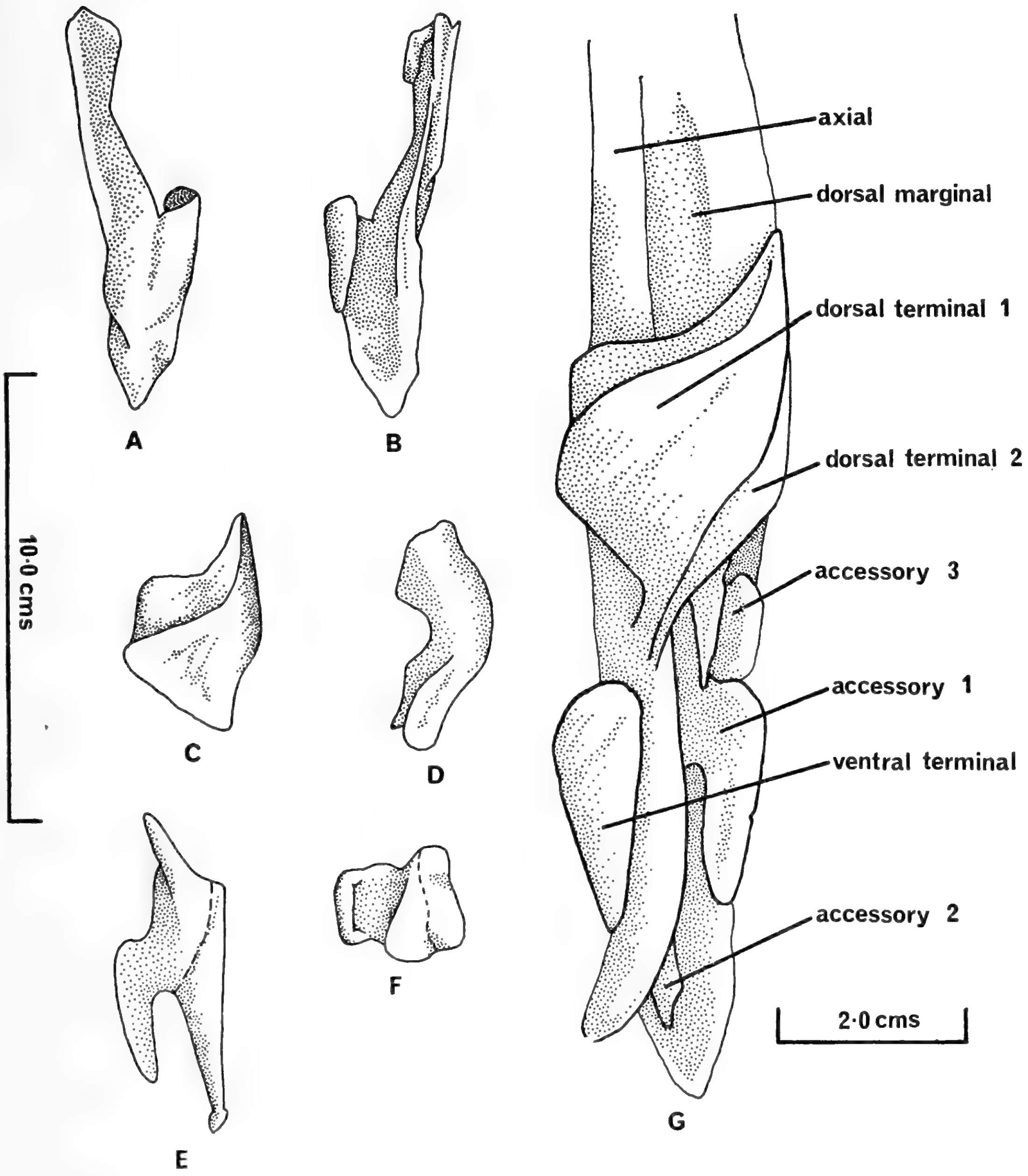

FIG. 3. *Raja rhizacanthus.* Cartilages of the terminal group of the clasper. A, ventral terminal (ventral view); B, ventral terminal (dorsal view); C, dorsal terminal 1 (dorsal view); D, dorsal terminal 2 (dorsal view); E, accessory cartilages 1 and 2 (dorsal (view); F, accessory cartilages 3 and 4 (ventral view); G, terminal cartilages *in situ* from dorsal side.

element, and its knife-edged protruberance is the sentinel. Accessory cartilage 2 is elongate in the longitudinal axis of the clasper, and its distal end is recurved and hook-like, forming the spike of the clasper glans.

5. *Accessory cartilages* 3 *and* 4 (fig. 3 F, G)

Accessory cartilages 3 and 4 form the signal of the glans and are situated on the ventral side of the clasper, between the upright portion of the ventral terminal cartilage and the accessories 1 and 2. The smaller proximal cartilage, accessory 4 is attached in a groove formed between the accessory cartilages 1 and 2 and the ventral marginal cartilage; accessory 3 is movable on accessory 4 and its distal end is bluntly rounded.

Musculature

Only a brief mention of the musculature of *R. rhizacanthus* needs be made for it is identical with that of *R. clavata* as given by Jungersen.

M. dilatator

Proximally this consists of a single muscle mass, but distally it seems to be split into dorsal and ventral muscles. Its origin is on the axial, b_1 and b_2 cartilages, and it inserts as an aponeurosis on the shelf of the dorsal terminal 1 cartilage.

The *m. compressor sacci, m. adductor, m. flexor* (not *extensor* as given in Jungersen), and muscles of the fin are the same as for *R. clavata.*

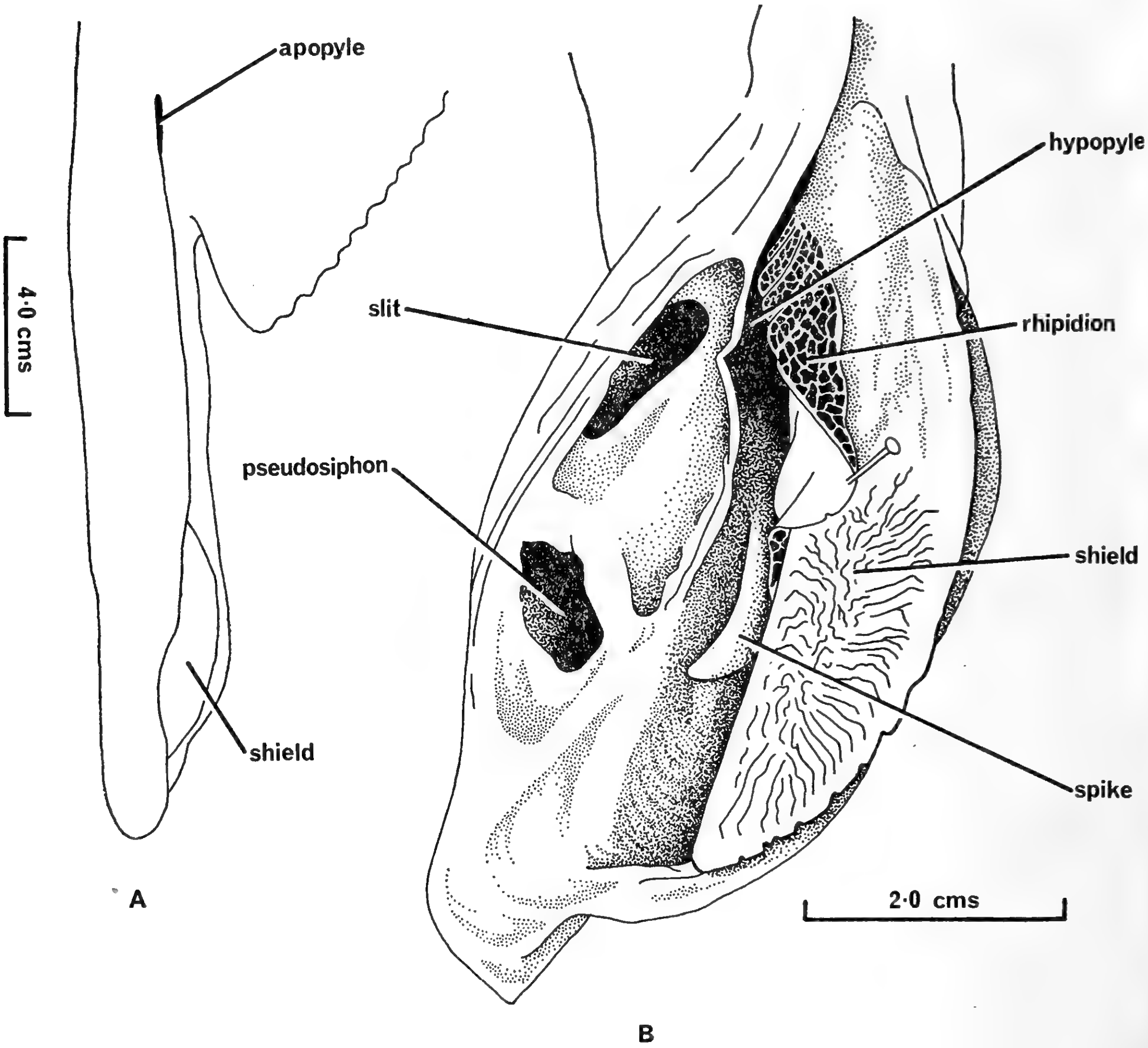

FIG. 4. *Raja pullopunctata*

A, external view of right clasper from dorsal side; B, lateral view of right clasper, opened to show structural features of the glans.

THE CLASPER OF *R. PULLOPUNCTATA* SMITH

The claspers from three adult specimens of *R. pullopunctata*, trawled West of Cape Town and in Algoa Bay were examined.

(i) *The external anatomy of the clasper* (fig. 4 A, B)

The clasper of *R. pullopunctata* is long and stout; its cylindrical body is dorso-ventrally flattened distally, and slightly truncate, giving a spatulate appearance. The glans is much broader than the rest of the clasper, due to the strong development of the shield, which can be clearly seen from the dorsal side. The claspers are entirely naked, scale and spine being absent. The apopyle (fig. 4 A) opens some distance away from the vent, on the dorsal side.

The rhipidion (fig. 4 B) is well developed and fan-shaped and it is attached along the inner ventral wall of the clasper, from the region of the hypopyle to about half-way along the length of the glans. Its lower surface is pitted with cavities of irregular outline, and this spongy tissue is said by Leigh-Sharpe to be erectile and to act as a splash-plate for the ejaculating spermatozoa.

R. pullopunctata may be placed in the pseudogenus *Gamma-raia*, for there is a reduction and crowding of the structural features of the glans. As in all *Gamma-raia*, the signal is absent, while the shield is very well developed and extends along the whole ventral surface of the glans, from the level of the hypopyle almost to the distal extremity of the clasper. The distal region of the shield is covered by pleated epithelia, but this is so thin at the outer lateral edge, that the knife-like appearance of the shield is not unlike the sentinel of *R. rhizacanthus*.

Both the slit and the pseudosiphon are present in the dorsal wall of the concavity of the glans. In *R. pullopunctata* the pseudosiphon is larger and more distally placed than the slit, and these two cavities are separated by a prominent cartilaginous shelf. The pseudosiphon is well separated from the hypopyle by the elongated dorsal marginal cartilage.

Medially placed is a large, single, tongue-like structure, which examination of the terminal cartilages reveals as the spike (cf. Leigh-Sharpe). Although covered by a thick layer of epithelial tissue, the calcified cartilage can be easily felt. The small accessory 1 cartilage is not greatly developed, and the sentinel is not a recognizable element in the external appearance of the clasper.

(ii) *The internal anatomy of the clasper* (fig. 5)

The basipterygium, b_1 and b_2 cartilages and the Beta-cartilage are the same as in *R. rhizacanthus*. The axial cartilage is long, cylindrical at its proximal end, but narrower and dorso-ventrally flattened distally. The distal end of the axial is more heavily calcified than the proximal region, and is slightly curved outwards, terminating in a bluntly rounded point. The dorsal marginal cartilage starts more proximally than the ventral marginal cartilage, and runs for about 2/3 the length of the axial, to which it is tightly bonded for its entire length. The dorsal marginal cartilage is convex at its proximal end, but becomes

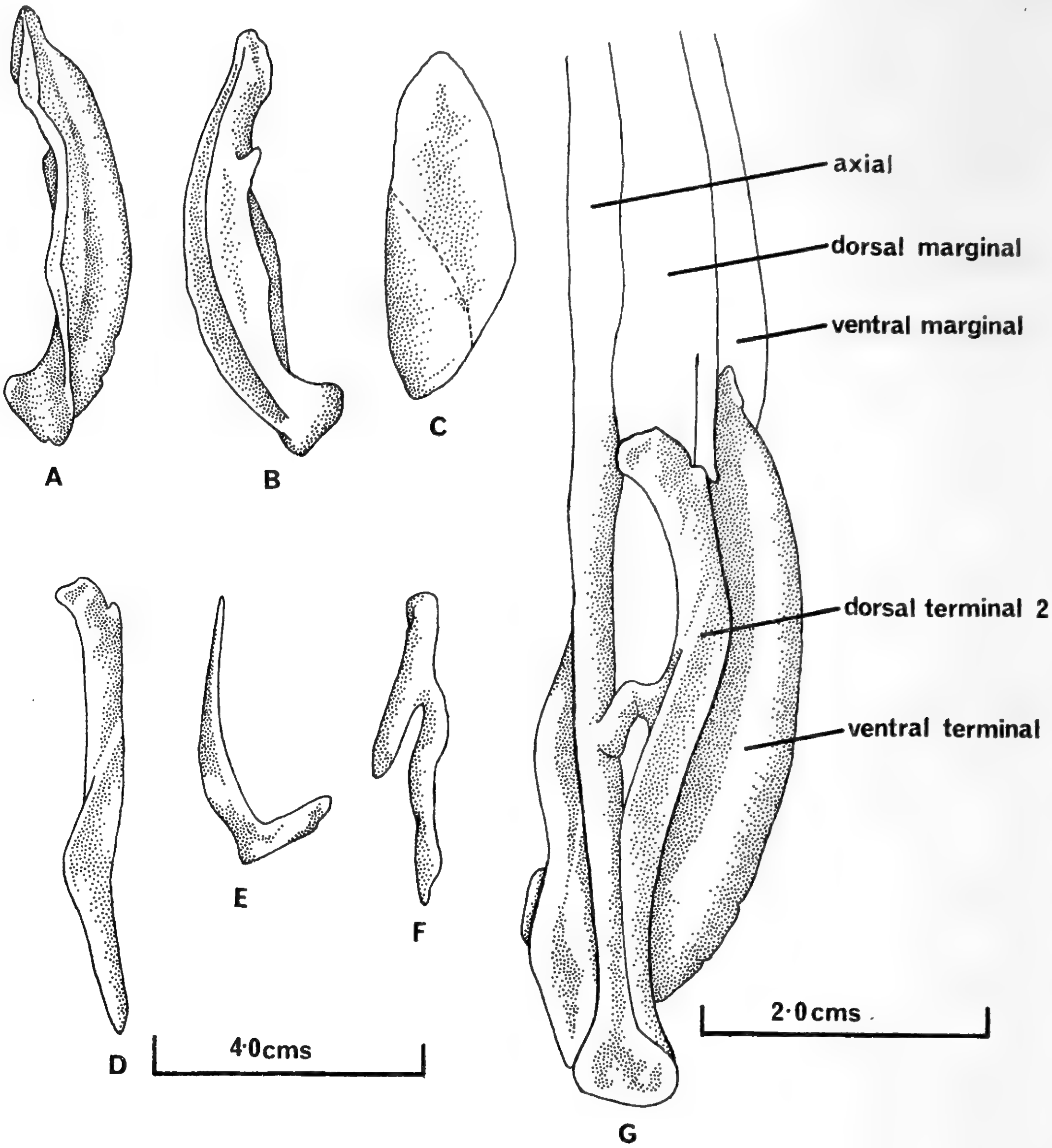

Fig. 5. *Raja pullopunctata*. Cartilages of the terminal group of the clasper. A, ventral terminal (dorsal view); B, ventral terminal (ventral view); C, dorsal terminal 1 (dorsal view); D, dorsal terminal 2 (dorsal view); E, accessory 1 (ventral view); F, accessory 2 (dorsal view); G, terminal cartilages *in situ* from dorsal side, but with dorsal terminal 1 removed.

flatter distally and is extended in a small point, forming the shelf between the pseudosiphon and the hypopyle. The ventral marginal cartilage is flat and slightly expanded distally, so that it more or less overlaps the axial cartilage, to which it is united. Its distal end is truncate.

1. *Ventral terminal cartilage* (figs. 5 A, B, G)

As in *R. rhizacanthus*, the ventral terminal is J-shaped, but its distal end is not so strongly developed. The cartilage is attached to the inner surface of the 'scroll-like' ventral marginal cartilage. It is locked to this cartilage by means of a protuberance, situated ventrally about 1/3 of the length of the ventral terminal from its proximal end. The protuberance engages with a corresponding point (the minute 'sentinel') of the accessory cartilage 1, hooking the two elements together. The ventral terminal cartilage does not extend to the tip of the clasper. The outer lateral edge of this cartilage is well developed and calcified, forming a convex lamina, the shield of the clasper glans. Distally, the apex of the ventral terminal is grooved, through which the distal regions of the axial and dorsal terminal 2 cartilages pass, before becoming dorso-ventrally flattened. The upright limb of the J-like ventral terminal is raised into a ridge on its dorsal surface.

2. *Dorsal terminal* 1 (fig. 5 C)

This cartilage is situated on the dorsal surface of the clasper, and is attached along its outer edge to the dorsal terminal 2 cartilage. The dorsal terminal 1 cartilage is 'shield-like' in appearance and its proximal end is elongated into an obtuse point, to which the dorsal bundle of the *m. dilatator* attaches. The inner distal region of this cartilage is so curved that it wraps around the axial stem and can be seen on the ventral side, where it slightly overlaps the upright limb of the ventral terminal cartilage. Distally, the dorsal terminal 1 is attached by connective tissue to the axial, dorsal terminal 2 and accessory cartilages.

3. *Dorsal terminal* 2 (fig. 5 D)

The dorsal terminal 2 cartilage is attached to the inner distal end of the dorsal marginal cartilage, so that the point and connective tissue, which forms the shelf between the pseudosiphon and hypopyle, lie behind the dorsal terminal 1. The dorsal terminal 2 cartilage is a long, thin, single cartilaginous element, curving and then re-curving, so that its pointed distal end is attached to the axial cartilage (fig. 5 G). Proximally, the dorsal terminal 2 is strongly calcified and has a short blunt protuberance on its outer lateral margin, while distally calcification is not so marked, the soft cartilage becoming dorso-ventrally flattened. About half-way along its length, on the inner edge, there is a ligament (forming the shelf between the pseudosiphon and the slit), which arches and inserts on the axial cartilage about 1/5 the length of this cartilage from its distal end (fig. 5 G).

4. *Accessory cartilage* 1 (fig. 5 E)

This minute V-shaped cartilage is attached to the distal end of the ventral marginal cartilage. The longer of its two arms runs forward along the outer lateral edge of the ventral marginal, while the shorter traverses the distal end of the ventral marginal cartilage. The base of the V is slightly pointed (the minute 'sentinel') and is curved inwards, forming the point on which the ventral terminal engages. It must be noted that this cartilage does not manifest itself as an external structural element in the glans.

5. *Accessory cartilage* 2 (fig. 5 F)

The accessory cartilage 2 resembles an inverted Y. Its cyclindrical proximal end is attached to the inner distal end of the ventral marginal cartilage. The longer limb of the accessory is tightly bonded to the axial, so that distally these two cartilages resemble a single element. The shorter arm of the cartilage is simple in shape and projects laterally outwards. Its terminal end is slightly upturned and forms the spike of the clasper glans.

Musculature

The musculature of *R. pullopunctata* was found to be identical with the description of the musculature of *R. clavata* given by Jungersen, and like *R. batis*, the *m. dilatator* is in two bundles.

(*a*) *Dorsal m. dilatator*

This muscle has its origin on the proximal region of the axial cartilage and its insertion on the dorsal and lateral regions of the dorsal terminal 1 cartilage. The muscle is not strictly dorsal in position but more medio-dorsal, and is much larger than the ventral *m. dilatator*.

(*b*) *Ventral m. dilatator*

The muscle is entirely separate from its dorsal counterpart and has its origin on the ventral proximal region of the axial cartilage and the distal end of the b_2 cartilage. It inserts as connective tissue across the surface of the ventral terminal cartilage, although some fibres attach to the tip of the axial cartilage.

The *m. compressor sacci*, *m. adductor*, *m. flexer* and the muscles of the fin are the same as for *R. clavata*.

Discussion

Two pairs of claspers from specimens of *R. batis* Linnaeus, caught S.W. of Ireland, and a pair of claspers from *R. clavata* Linnaeus, caught at Lowestoft, were examined for purposes of comparison.

Although there is a marked difference in the size of the claspers of *R. pullopunctata* and *R. batis*, the general external appearance of the claspers is similar. In both, the clasper is long, stout and naked, becoming dorso-ventrally flattened and spatulate at its terminal end. The outer lateral edge of the shield can be seen from the dorsal side in both species, but in *R. batis* it is more prominent. This may be due to differences in the size of the claspers. However, examination of the clasper glans reveals that the structural features in *R. pullopunctata* and *R. batis* are different (figs. 4 B, 6).

The pseudosiphon and slit are present on the inner dorsal surface of the glans in both species, but their formation is somewhat different, although they are associated with the degree of development of the dorsal terminal cartilages in both cases. In *R. pullopunctata* there is a marked shelf-like ridge separating

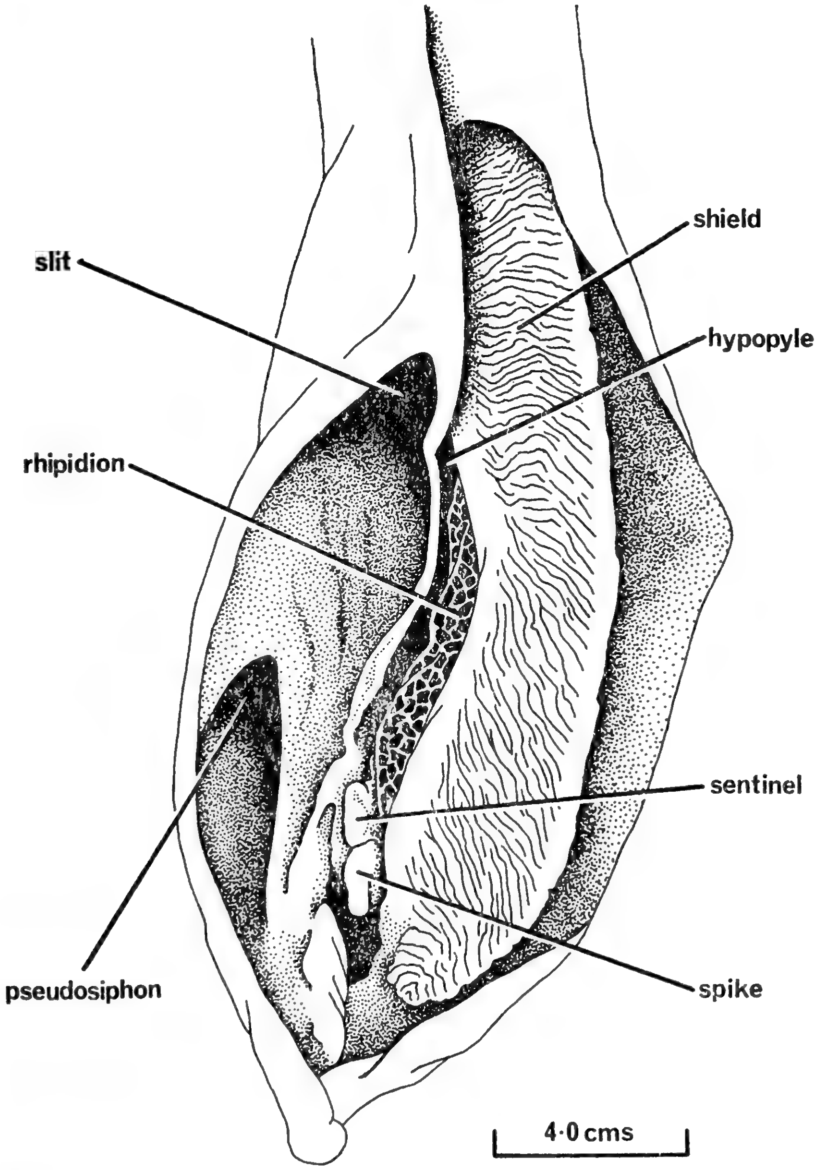

FIG. 6. *Raja batis.* Lateral view of right clasper, opened to show structural features of the glans.

the pseudosiphon from the slit; this shelf is found to be wanting in *R. batis.* The pseudosiphon is similarly situated in the two species, but in *R. pullopunctata* the pseudosiphon resembles a concavity rather than the simple pouch found in *R. batis.* The slit is more proximally situated in *R. pullopunctata,* occurring about half-way along the length of the glans (about one-third the length in *R. batis*). The hypopyle seems to be more distally placed in *R. batis,* but this may be due to the heavier development of the shield. The rhipidion is pitted and fan-shaped in both species, occurring along the inner ventral wall of the hypopyle, and extending about half-way along the length of the glans in *R. pullopunctata* and about two-thirds the length in *R. batis.* The rhipidion is more compact in *R. batis.* The prominent shield extends along the whole inner ventral surface of the glans in both species, but it is thinner and covered with pleated epithelia along its entire length in *R. batis*, while in *R. pullopunctata* the broader shield is only pleated at its distal region.

The most noticeable difference in the structure of the claspers is in the presence of the enlarged sentinel in *R. batis*, which extends distally and fits together with the spike. In *R. pullopunctata*, the sentinel is reduced and lies under the rhipidion, so that it is not seen when the glans is opened, and these two elements are not expanded terminally as they are in *R. batis*.

As has been pointed out, the visible external characters of the clasper are

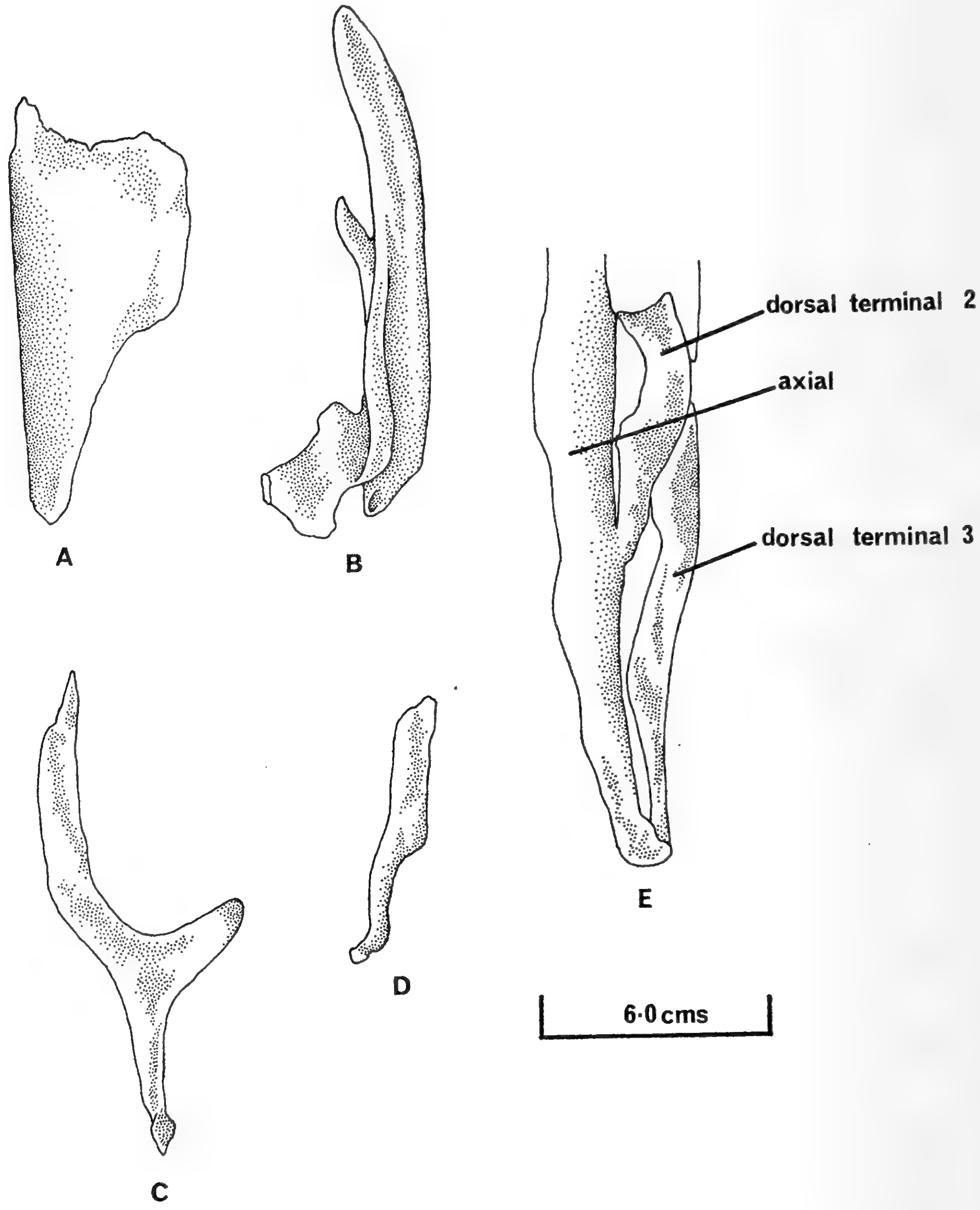

Fig. 7. *Raja batis*. Cartilages of the terminal group.

A, dorsal terminal 1 (dorsal view); B, ventral terminal (dorsal view); C, accessory 1 (dorsal view); D, accessory 2 (dorsal view); E, dorsal terminal 2 and 3 in position.

closely associated with the structure and number of the internal cartilages, and therefore differences in the structure of the glans will be shown by differences in the terminal cartilages. In *R. pullopunctata* there are a total of five cartilages in the terminal group (2 dorsal terminals, 1 ventral terminal and 2 accessory terminals), while in *R. batis* six terminal cartilages are present (3 dorsal terminals, 1 ventral terminal and 2 accessory terminals) (figs. 5, 7).

Although there is a great difference in the size of these elements, their differences in shape and their position may be examined. The dorsal terminal 1 cartilage is similarly situated in both *R. batis* and *R. pullopunctata*, occurring on the dorsal side of the clasper, and it is flat and plate-like, being slightly convex distally. In both species, the median edge is bent in such a manner, that the cartilage wraps round the axial stem and may be seen on the ventral side. Distally, the cartilage is pointed in the two species, but in *R. pullopunctata*, the proximal edge is elongated into a point for the attachment of the aponeurosis of the *m. dilatator*, while in *R. batis* (fig. 7), the proximal edge is almost straight and somewhat more convex. The dorsal terminal 2 cartilage is attached to the distal end of the dorsal marginal cartilage in both species, and it is interesting to note that in *R. pullopunctata*, the dorsal terminal 2 extends to the tip of the axial cartilage, while in *R. batis*, the crescent-shaped dorsal terminal 2 (fig. 7 D, E) is attached to about half way along the axial and that the dorsal terminal 3 extends to the tip of the clasper, i.e. these two cartilages in *R. batis* have been reduced to a single cartilage in *R. pullopunctata*, although there is linking between the dorsal terminal 2 and the axial in both cases. The terminal end of the axial cartilage is similarly curved (laterally outwards) in the two species, and the attachment of the dorsal terminal 2 of *R. pullopunctata* and the dorsal terminal 3 of *R. batis* (fig. 7 E) is similar.

Although both *R. pullopunctata* and *R. batis* possess two accessory cartilages, the accessory cartilage 1 (forming the sentinel) is reduced to a small point in *R. pullopunctata*. In *R. batis* this cartilage (fig. 7 C) is well developed and extends down towards the spike, and fits closely to it. The ventral terminal cartilages are similarly situated in both *R. batis* and *R. pullopunctata* and these elements are similar in shape. Both possess the 'hooking' protuberance on the inner ventral margin, the enlarged convex outer lateral edge and the raised dorsal ridge. However in *R. batis* (fig. 7 B) the distal end of the convex edge projects slightly from the main body of the limb, and the distal end of the ventral terminal is not so markedly grooved as in *R. pullopunctata*.

It may therefore be concluded that, in the structure of the glans and in the number and arrangement of the internal cartilaginous elements, the claspers of *R. pullopunctata* and *R. batis* are different.

Besides differences noted in the structure of the claspers of the two species, some differences can also be seen in the external characters. Smith (1964) points out that there is a difference in shape between the two, but examination of later and adult stages of *R. pullopunctata* reveals that the shape of the disc varies and that the pectorals and anterior margins of the disc become more concave, as they do in *R. batis*. The author is unable to detect any appreciable difference in shape.

Examination of specimens of comparable size indicates that the interorbital is narrower in *R. pullopunctata* than in *R. batis*, and that there is little difference in the comparative size of the eye.

The most noticeable difference is the presence of the large, single, median, nuchal spine in *R. pullopunctata*, which is found both in juveniles and adults (although sometimes worn down). Except about the eyes, the upper surface of the disc is entirely devoid of other large spines, as it is in *R. batis*.

Therefore Smith's proposal that *R. pullopunctata* and *R. batis* are distinct species as based on the general external morphology, is confirmed on the basis of the clasper structure. Recently, two large 'black-bellied' skates, lacking signs of a median nuchal spine, were obtained in trawls off Cape Columbine in 250 fathoms. The external characters of the clasper of the mature male were seen to be identical with those of *R. batis* from European waters. Therefore *R. batis* Linnaeus also may occur off South Africa; however, further investigation on these specimens is necessary.

It is interesting to note that a 'black-bellied' skate from the Falkland Islands, *R. flavirostris* Philippi 1892, greatly resembles the South African *R. pullopunctata* in possessing a single, large, median, nuchal spine. But as yet, clasper material is unavailable for the purposes of comparison.

The author was unable to find a single difference, both in the external structure of the glans and in the number and arrangement of the internal cartilaginous elements, between the claspers of *R. clavata* and *R. rhizacanthus*. The claspers in these two species are identical.

Although Norman points out that the South African species is closely related to the European species, he considers that the two are distinct on the basis of the degree of spination in adults, the position of the vent and the shape of the snout. Preliminary examination of some two hundred specimens of *R. rhizacanthus* has shown that the shape of the snout varies considerably in local populations, as does the degree of spination, and the position of the vent.

Therefore bearing this in mind, and in view of the fact that the claspers are identical, the author agrees with Barnard and Fowler that *R. rhizacanthus* specimens should be referred to *R. clavata* and that *R. rhizacanthus* therefore becomes a synonym of *R. clavata*. This is further supported by the fact that masked bipolarity is already acknowledged in *R. alba*, so that it is not unlikely that distribution of this type also occurs in *R. clavata*.

It may be seen from fig. 8 that the distribution of *R. clavata* ranges from Arctic waters to the tropical waters of the Indian Ocean, having been recorded from greater extremes than *R. alba*. However, through most of their recorded range both species occur in the same waters. As yet, these two species have never been recorded from the equatorial waters of West Africa, but equatorial submergence probably occurs, allowing gene flow from northern hemisphere to southern hemisphere and vice versa.

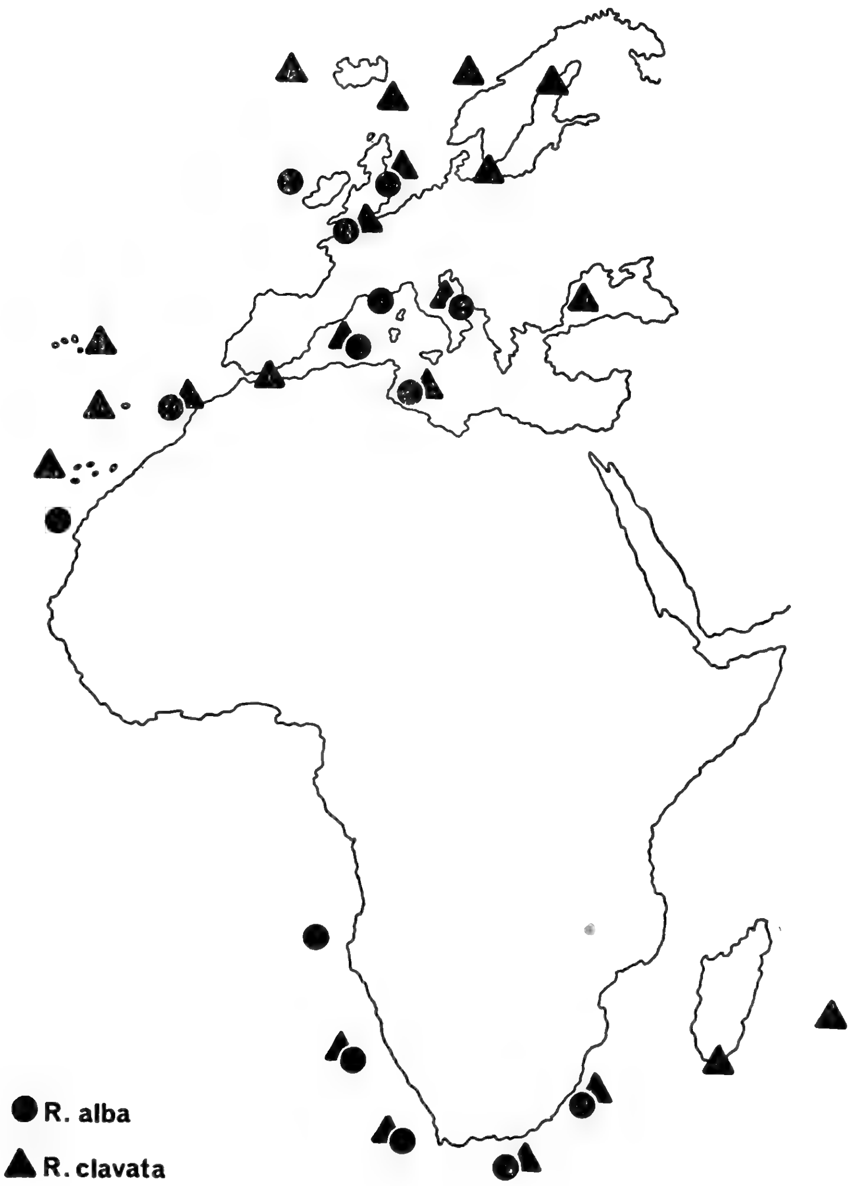

FIG. 8. Map showing the masked bipolar distribution of *R. alba* and *R. clavata*.

ACKNOWLEDGEMENTS

I am grateful to Messrs. M. J. Holden and C. H. Humphries of the Fisheries Laboratory at Lowestoft for the *R. clavata* and *R. batis* material and to Mr. S. X. Kannemeyer for assistance in collection of the South African skates. My thanks are due to Dr. N. F. Paterson for checking the manuscript and for many helpful recommendations.

The Trustees of the South African Museum acknowledge gratefully the receipt of a grant from the Council for Scientific and Industrial Research towards the cost of publication.

Summary

After detailed studies of the anatomy of the claspers of the males, it is considered that *Raja rhizacanthus* Regan is synonymous with *R. clavata* Linnaeus and that *R. pullopunctata* Smith is distinct from *R. batis* Linnaeus, but that *R. batis* Linnaeus may also occur in South African waters.

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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).

HARDING & SMITH

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SOME SOUTH AFRICAN FRESH WATER COPEPODA

By

J. P. Harding and W. A. Smith

British Museum (Natural History), London

(With 9 figures in the text)

Contents

Introduction

The material consisted of 26 tubes from the western Cape Province, 45 tubes from the Jukskei–Crocodile system, 39 tubes from the Vaal River, and 32 tubes from other parts of the Transvaal. The material was collected by Dr. A. D. Harrison and his colleagues.

The collection comprised 9 species of Diaptomidae and 11 species of Cyclopoida. Unidentified Harpacticoida were also present in some of the samples. The following species were identified:

CYCLOPOIDA

1. *Macrocyclops albidus* (Jurine) sub.-sp. *oligolasius* Kiefer
2. *Eucyclops serrulatus* (Fischer)
3. *Eucyclops gibsoni* (Brady)
4. *Tropocyclops prasinus* Fischer
5. *Paracyclops fimbriatus* (Fischer)
6. *Paracyclops finitimus* Kiefer
7. *Acanthocyclops vernalis* (Fischer)
8. *Microcyclops varicans* (Sars)
9. *Mesocyclops leuckarti* (Claus)
10. *Thermocyclops oblongatus* (Sars)
11. *Thermocyclops emini* (Mrázek)

Ann. S. Afr. Mus. **48** (21), 1967: 515–521, 9 figs.

DIAPTOMIDAE

12. *Lovenula barnardi* Sars
13. *Lovenula falcifera* (Lovén)
14. *Paradiaptomus lamellatus* Sars
15. *Metadiaptomus transvaalensis* Methuen
16. *Metadiaptomus capensis* (Sars)
17. *Metadiaptomus colonialis* (Douwe)
18. *Metadiaptomus purcelli* (Sars)
19. *Tropodiaptomus spectabilis* (Kiefer)
20. *Eudiaptomus* sp.

The names used for the Cyclopoida are in accordance with Kiefer's monograph (Kiefer, 1929a). This gives a full synonymy and here we give synonyms only with reference to other works on South African copepods.

Macrocyclops albidus (Jurine) sub.-sp. *oligolasius* Kiefer

The species *M. albidus* is a cosmopolitan one but specimens in Africa south of the Sahara if examined sufficiently closely are usually found to belong to the subspecies *oligolasius* which was first described (Kiefer, 1928a) from the Linjanti River where it flows into the Zambezi. Hutchinson *et al.* (1932) record it from the south-eastern Transvaal. Sars (1927) did not find any representatives of the genus *Macrocyclops* in his survey of the Entomostraca of the Cape Province but two of the present samples from the western Cape Province contained *M. albidus oligolasius*, both from a vlei at Betty's Bay in brown and acid water. It was also present in the Vaal River, the Olifants Vlei near Johannesburg, the Klein Jukskei River and from the Great Usutu River in the eastern Transvaal.

Eucyclops serrulatus (S. Fischer)

This cosmopolitan species was found in all regions sampled in the present survey. It is rather surprising that so common a species was not found in the Cape Province by Sars (1927). Several of the present samples contained it. Hutchinson *et al.* (1932) record it from south-eastern Transvaal and it was present in many of the present samples from the Transvaal.

Eucyclops gibsoni (Brady)

Cyclops gibsoni Brady 1904: 123, pl. 6, figs. 1–10.
Cyclops longistylis Brady 1910: 242. (Nigeria.)
Afrocyclops gibsoni (Brady), Sars 1927: 121, pl. 13, figs. 1–18.
Eucyclops gibsoni (Brady), Hutchinson *et al.* 1932.

This is a species widely distributed in Africa south of the Sahara.

Found in the western Cape Province in the Krom River, Stellenbosch, and under the Blouberg road bridge, Milnerton, and in the Transvaal at the Amato Dam, Benoni, and at the Pretoria sewage works.

Brady's type of *longistylis* from Nigeria is in the BM(NH) on a slide and appears to be this species as Sars suggested.

Tropocyclops prasinus Fischer

Leptocyclops prasinus (Fischer) Sars 1927: 119, pl. 12, figs. 11–20.
Eucyclops prasinus (Fischer) Hutchinson *et al.* 1932.

This is a very widely distributed probably cosmopolitan species, but was represented in the present collections only by a single male from the Crocodile–Jukskei system. It is a very small species and may have passed through the nets. It is recorded from the Cape (Sars, 1927) and the Transvaal (Hutchinson *et al.*, 1932).

Paracyclops fimbriatus (Fischer)

This species is reported from the whole of the Palaearctic and Nearctic regions and most parts of Africa. It was found in four of the samples from the Vaal River, two of which contained the related form *Paracyclops finitimus* as well.

Paracyclops finitimus Kiefer

Platycyclops poppei (*non* Rehberg) Sars 1927: 127, pl. 14, figs. 5–17.

This species was first described from Morocco (Kiefer, 1928b: 99) and has been found in New Zealand. Sars had already recorded it under the synonym given above from the Cape Peninsula.

It was found in three samples from the Cape Province: the Krom River at Stellenbosch and the Berg River and in nineteen from the Transvaal: at Benoni, in the Crocodile–Jukskei System, in the Klipspruit near Johannesburg, in the oxidation pond of the Pretoria sewage works and in the Vaal.

Acanthocyclops vernalis (Fischer)

This species is widely distributed in the Northern Hemisphere and has been recorded from South America and Kerguelen. In the present collection it is represented by a single adult female from the Berg River.

Microcyclops varicans (Sars)

Owing to uncertainties of identification the precise distribution of this species is not known; but there are records from all principal land masses. I know of no record for South Africa south of the Vaal River; but Hutchinson *et al.* (1932) record it from the Transvaal. It was present in three tubes from the Crocodile–Jukskei System in marginal vegetation and from two stations on the Vaal River.

Mesocyclops leuckarti (Claus)

This cosmopolitan species was found in twenty-four of the samples: from the western Cape Province, from the Vaal River and from the Transvaal.

Thermocyclops oblongatus (Sars)

(Figs. 1–9)

Mesocyclops oblongatus Sars 1927: 114, pl. 11, figs. 1–15.
(*Thermocyclops*) *infrequens* Kiefer 1929b: 315, fig. 10.

Sars (1927) described *T. oblongatus* from the Cape Province. Unfortunately his figures are not very accurate, in particular showing a peculiarly shaped receptaculum and a fifth leg with the outer terminal seta less than half the length of the inner. Kiefer (1929b) described *T. infrequens* and many specimens of the present collection from both the Transvaal and the Cape agree with Kiefer's description and figures, but none with Sars. We have examined Sars's original material and find that the receptaculum and fifth leg are the same as in Kiefer's species and as these were the only features by which the two species were thought to be distinguishable we conclude that *oblongatus* and *infrequens* are two names for a single species. There are two tubes of Sars's material, one which had at some time been allowed to dry up was from a small pond at Salt River, collected by Dr. Purcell and referred to in Sars's paper, and the other of specimens in good condition from an unspecified locality. Both tubes appeared to contain the same species and figs. 1–4 are from a specimen from the second tube. Figs. 5–9 are of corresponding parts of specimens from the Transvaal in the present collection. The species is very close to *T. schuurmanae* Kiefer, the main difference being that the rounded prominence on the lamella of leg 4 (figs. 2 and 6) are larger, closer together and bear more spinules. Kiefer's original specimens of *T. schuurmanae* were from the Transvaal (Kiefer, 1928a: 15) and Hutchinson *et al.* (1932) also record it from several Transvaal localities and from a Cape Vlei. However, apart from a few *T. emini*, all the *Thermocyclops* in the present collection are *T. oblongatus*, not *T. schuurmanae*. The localities are: the Zeekoe Vlei on the Cape Flats, various dams at Benoni, Transvaal, five stations in the Crocodile–Jukskei System and the Apies River, Pretoria.

Thermocyclops emini (Mrázek)

Originally found in East Africa (Mrázek, 1896: 4; Sars, 1909: 50) it has since been found in the Sudan and in Egypt (Gurney, 1911: 32) and in the Transvaal and Portuguese East Africa (Hutchinson *et al.*, 1932). The present samples were both from the Vaal Barrage.

Lovenula barnardi Sars

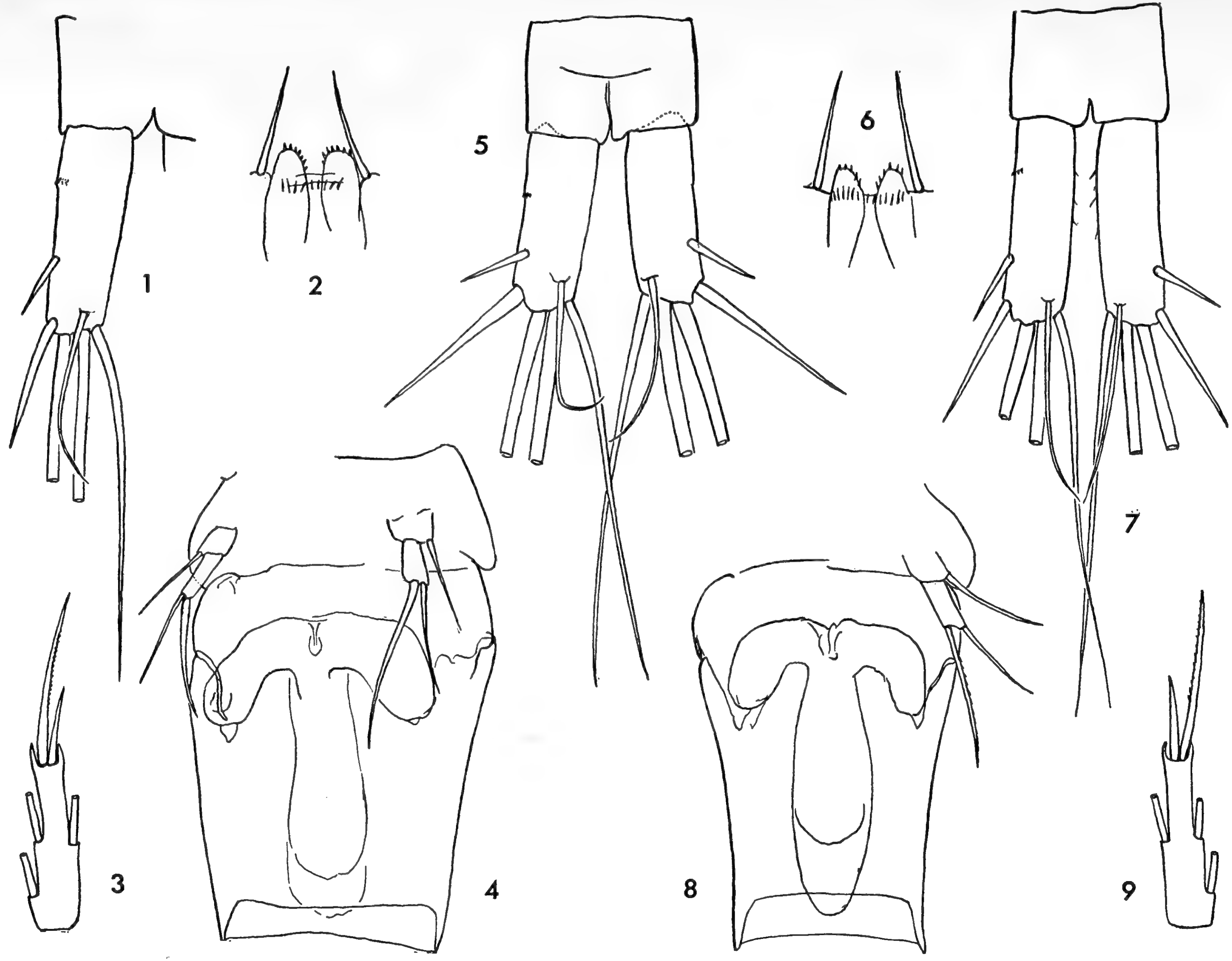
Originally described from Ovamboland, South West Africa (Sars, 1927: 92) this species was present in a number of the samples collected along the Vaal River.

Lovenula falcifera (Lovén)

First described from Natal and later found near Cape Town (Sars, 1927: 86) and in a number of places in the Transvaal (Hutchinson *et al.*, 1932). This species was found only in the Cape Province in the present collections: in temporary waters on the Cape Flats, Berg River localities and the Riet Vlei, Milnerton.

Paradiaptomus lamellatus Sars

The type locality is Knysna, Cape Province (Sars, 1895: 46) and this species is recorded by Sars (1927: 94) also from near Cape Town. Brady (1907: 183) records it from Natal and Rühe (1914: 27) from the Cape. The species was found in three of the present samples, all from the Cape.



Figs. 1–9. *Thermocyclops oblongatus* (Sars). Figs 1–4, Type material from the Cape. Figs. 5–9, Transvaal material. Figs. 1, 5, 7, furcal rami. Figs. 2, 6, uniting lamella of fourth legs. Figs. 3, 9, terminal segment of endopod of fourth leg. Figs. 4, 8, last thoracic segment of genital segment showing receptaculum seminis and fifth legs.

Metadiaptomus transvaalensis Methuen

Metadiaptomus transvaalensis Methuen 1910: 160, pl. 16, figs. 46a–c, pls. 17–18.
Diaptomus meridianus Douwe 1912: 24.
Paradiaptomus transvaalensis (Methuen) Hutchinson *et al.* 1932.
Diaptomus rigidus Sars 1927: 101, pl. 8, figs. 13–18.

This is the type species of the genus and was first described (Methuen, 1910) from Lake Chrissie and other parts in the eastern Transvaal. Hutchinson *et al.* (1932) also record it from this area and other parts of the Transvaal. Van Douwe's 1912 specimens from Great Nama Land are probably the same species and the present samples were mostly from the Vaal River, and also from one station in the western Cape Province at Piquetberg on the Berg River. Only two battered females were present in the last sample.

Metadiaptomus capensis (Sars)

Diaptomus capensis Sars 1907, Rühe 1914: 26, fig. 8a, b. Sars 1927: 98, pl. 8, figs. 1–12.
Paradiaptomus capensis (Sars) Hutchinson *et al.* 1932.

This species as far as I know has only been recorded from the Cape Province, it was present in three of the samples, the Zeekoe Vlei and a temporary pool on the Cape Flats and Sirkel's Vlei near Cape Point.

Metadiaptomus colonialis (Douwe)

Diaptomus colonialis Douwe, 1914.
Paradiaptomus colonialis (Douwe) Hutchinson *et al.* 1932.

The specimens described by Van Douwe were from South West Africa and those collected by Hutchinson *et al.*, from various parts of the Transvaal. Eight of the present samples were from inside the Transvaal and three from its southern border.

Metadiaptomus purcelli (Sars)

Diaptomus purcelli Sars 1907: 12, pl. 2, figs. 3–10. Sars 1927: 103, pl. 9, figs. 1–8.
Paradiaptomus purcelli (Sars) Hutchinson *et al.* 1932.

All records of this species seem to be from the south-western Cape Province and it is characteristic of temporary pools on the Cape Flats.

Tropodiaptomus spectabilis (Kiefer)

Diaptomus spectabilis Kiefer 1929b: 311, figs. 5, 6. Hutchinson *et al.* 1932.
Tropodiaptomus spectabilis (Kiefer) Kiefer 1932.

This is a Transvaal species and was collected from two Transvaal localities.

Eudiaptomus sp.

Three females and one male of an undetermined species of *Eudiaptomus* were present in a sample from the Hartebeespoort Dam.

SUMMARY

Eleven species of Cyclopoida and eight species of Diaptomidae are recorded from inland waters of the Cape Province and Transvaal. Figures of *Thermocyclops oblongatus* (Sars) are given and it is shown that *T. infrequens* Kiefer is a synonym of this species.

ACKNOWLEDGEMENTS

We are indebted to Dr. A. D. Harrison and the National Institute for Water Research of the South African Council for Scientific and Industrial Research for the opportunity of examining this material. We are grateful to Dr. J. R. Grindley for letting us examine specimens described by G. O. Sars in the collections of the South African Museum.

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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 4¾ in. = 7 in. (7½ in. including the caption). A scale (metric) must appear with all photographs.

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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:

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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).

M. J. PENRITH

THE FISHES OF TRISTAN DA CUNHA, GOUGH ISLAND AND THE VEMA SEAMOUNT

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THE FISHES OF TRISTAN DA CUNHA, GOUGH ISLAND AND THE VEMA SEAMOUNT

By

M. J. Penrith*

South African Museum, Cape Town

(With 2 text-figures and 1 plate)

Contents

Introduction

In the south-east Atlantic Ocean there are three known areas of very shallow water (not counting the African coast). Two of these are around the shores of islands, the Tristan da Cunha group and Gough Island, while the third is the Vema Seamount.

Tristan da Cunha

The island of Tristan da Cunha, together with the two smaller islands of Inaccessible and Nightingale, lies almost midway between South Africa and South America (37° 05′ S., 17° 40′ W.). It is permanently inhabited and has been the subject of several scientific expeditions and reports.

Capt. Dugal Carmichael, F.L.S. (army surgeon to the garrison in the island, 1816–17) was the first to publish a report on the flora and fauna of Tristan. In this paper (1818) he described four species of fishes from the island and listed five others as being common to both Tristan and the Cape. Carmichael's work was referred to by Regan (1913*a*) but no further fishes were added to the nine already known from the island until Barnard (1923, 1925) listed two more species which he considered to be conspecific with South African species. Norman (1935*a*) described a further species believed by him to be endemic to the island group. After the Norwegian expedition of 1937–8, Sivertsen (1945) could add a further seven species to the fish fauna of the island, two of them being new species and believed by him to be endemic to Tristan da Cunha. Finally, Rowan & Rowan (1955) added three more records of oceanic fishes from the island.

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* Seconded from the Council for Scientific and Industrial Research Oceanographic Unit, University of Cape Town.

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At present the known fish fauna of Tristan consists of 19 species which Sivertsen (1945) divided into an oceanic component and a coastal component. (In the list below, the first reference to the species occurring at Tristan is given in parenthesis after the author of the species.) The islanders' common name for the species is also given where known.

(*a*) *Oceanic species*

Prionace glauca (Linn.) (Sivertsen, 1945)	Blue shark
Maurolicus muelleri (Gmelin) (Barnard, 1925)	—
Myctophum humboldti (Risso) (Sivertsen, 1945)	—
Scomberesox saurus (Walbaum) (Sivertsen, 1945)	—
Exocoetus exiliens Bloch (Carmichael, 1818)	—
Alepisaurus ferox Lowe (Rowan & Rowan, 1955)	—
Notopogon lilliei Regan (Sivertsen, 1945)	—
Seriola lalandi Valenc. (Rowan & Rowan, 1955)	Yellowtail
Polyprion americanus (Bloch) (Rowan & Rowan, 1955)	Steambrass
Thyrsites atun (Euphrasen) (Carmichael, 1818)	Snoek

(*b*) *Coastal species*

Ariosoma australis (Barnard) (Barnard, 1923)	—
[1]*Gaidropsarus insularum* Sivertsen (Sivertsen, 1945)	—
Acantholatris monodactylus (Carmichael) (Carmichael, 1818)	Fivefinger
Bovichthys diacanthus (Carmichael) (Carmichael, 1818)	Klipfish
[2]*Decapterus longimanus* Norman (Norman, 1935*a*)	Mackerel
Labrichthys ornatus (Carmichael) (Carmichael, 1818)	Concha or Conger
[3]*Helicolenus tristanensis* Sivertsen (Sivertsen, 1945)	Soldier
Sebastichthys capensis (Gmelin) (Carmichael, 1818)	Soldier
Seriolella antarctica (Carmichael) (Carmichael, 1818)	Bluefish
Seriolella christopherseni Sivertsen (Sivertsen, 1945)	Stumpnose

The identity of the fish recorded by Carmichael as the 'Roman fish' *Sparus* ———, is not known. The South African 'Roman' is a Sparid (*Chrysoblephus laticeps*) but has not been recorded from Tristan.

Gough Island

Gough Island lies slightly farther south than Tristan (40° 20′ S., 9° 55′ W.), and is not permanently inhabited, although the South African Government has maintained a weather station on the island for several years.

Although several expeditions have called at the island, it has not been subject to the same degree of collecting as has Tristan. Only one expedition, the Gough Island Scientific Survey 1955–6, has spent much time on the island, but they have not published any data on the fishes obtained.

---

[1] As *G. capensis* (Kaup) by Barnard (1925).

[2] Probably the fish recorded by Carmichael as *Scomber trachurus*.

[3] Recorded by Carmichael as *Sebastichthys maculata*.

Accounts of fish collected by the *Scotia,* which called on the way back from the Antarctic (Regan, 1913*b*) and by the R.V. *William Scoresby* (Norman, 1935*b*), have been published.

The fishes recorded are:

[1]*Helicolenus tristanensis* Sivertsen (Regan, 1935*b*)
Sebastichthys capensis (Gmelin) (Regan, 1913*b*)
Bovichthys diacanthus (Carmichael) (Regan, 1913*b*)
Caesioperca coatsi Regan (Regan, 1913*b*)
Acantholatris monodactylus (Carmichael) (Norman, 1935*b*)

Holdgate (1958), in a popular account of the Gough Island Scientific Survey, listed the following species of fish under their Tristan common names: five-fingers, soldiers, klipfish, congers.

Vema Seamount

This exceptionally shallow seamount was discovered in 1957 by the R.V. *Vema,* and traverses were made then as well as in 1959 by the *Vema* and in 1963 by the R.V. *Robert D. Conrad.* In November 1964 a detailed survey of the peak was undertaken by the South African National Committee for Oceanographic Research, using the diamond prospecting tug, *Emerson K* (Simpson & Heydorn, 1965). The peak was found to have a position 31° 38′ S., 8° 20′ E. and a least depth of only 14 fathoms, with a well-defined plateau about five square miles in extent and of approximately 35 fathoms depth. Subsequent to the visit by the *Emerson K* there have been many visits by commercial fishing vessels from Cape Town as well as a short visit by the R.V. *Africana II* in April 1965.

MATERIAL

The material used for the present paper was obtained from several sources. The South African Museum has been slowly building up a collection of Tristan fish for many years, mainly obtained as donations from Mr. Keytel (1907), the rock-lobster survey of 1949, and small but valuable donations from Tristan and Gough Islands by the Division of Sea Fisheries and Capt. M. T. Scott, master of the rock-lobster fishing vessel, *Tristania.*

Specimens of fishes from the Vema Seamount were obtained from the Division of Sea Fisheries (those from the *Emerson K* collection, and commercial fishing vessels, and a collection made from R.V. *Africana II* by Mr. A. C. Paterson), as well as directly from the fishing companies.

These collections have resulted in several further species being added to the fish fauna of Tristan da Cunha and Gough Island as well as adding to our knowledge of the species already recorded from the islands, and in addition have enabled their fauna to be compared with that from the Vema Seamount.

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[1] Recorded as *Sebastes maculatus* C. & V.

Systematic Account

Exocoetidae

Cypsilurus lineatus (Cuvier & Valenciennes)

Cypsilurus lineatus (Cuvier & Valenciennes) Bruun, 1935: 47.

Only one specimen, of 382 mm standard length, was examined. The fish was found in a drum of unsorted material from Tristan in the Department of Ichthyology, Rhodes University.

The body proportions as thousandths of standard length are as follows: pectoral fin 675, pelvic fin 309, dorsal height 111, depth 157, head 199, predorsal distance 728, preventral distance 560, preanal distance 754, snout 50, eye 65. Fin counts are dorsal 12, anal 10 and pectoral 15.

This is an extremely large specimen of the species.

Gadidae

Gaidropsarus Rafinesque

Kaup (1858) described a small gadid as *Motella capensis* but gave only a brief description and no locality, although on the basis of the trivial name it is believed to be South Africa.

Small rocklings were described from St. Paul Island as *M. capensis* by Kner (1868) and Sauvage (1879), while Barnard (1925) published a description of material in the South African Museum which he also assigned to Kaup's species.

Sivertsen described specimens from Tristan and showed that while they were very similar to those described from St. Paul Island, they showed marked differences from the South African specimens as described by Barnard. Since South Africa was believed to be the type locality of *capensis*, Sivertsen proposed a new name, *G. insularum* for the Tristan and St. Paul Island specimens.

On re-examining the material used by Barnard, I find that only one of the two fish he examined exactly fits the description he published, and that the two fish he examined appear to belong to two distinct species. This view is shared by Mr. A. Wheeler of the British Museum (Natural History), who has also examined the South African Museum material, and Professor J. L. B. Smith, who informs me that he has reached a similar opinion from examination of material in his collection (Table 1).

Table 1

Comparison of *Gaidropsarus*

Table 1*a* gives body proportions of two species of *Gaidropsarus* in millimetres and as thousandths of standard length in parenthesis.

Table 1*b* compares body proportions of *Gaidropsarus* from various sources.

12719	*G. insularum* from False Bay
12528	*G. capensis*. Port Elizabeth
7858	*G. capensis*. East London
A	*G. insularum* from Tristan da Cunha (from Sivertsen, 1945)
B	*G. capensis* from South Africa (Barnard, 1925)

TABLE 1*a*

	12719	12528	7858
Standard length	153	91	156
Depth	22·5 (147)	15 (165)	27 (173)
Head	29 (190)	20·5 (226)	33 (212)
Eye	4·6 (30)	3·8 (42)	5·3 (34)
Snout	8 (52)	6·8 (75)	9·3 (60)
Interorbital	6 (39)	4 (44)	4·5 (29)
Maxilla	13 (85)	10 (110)	17·2 (110)
Base of first dorsal	13 (85)	12 (132)	19 (122)
Base of anal	77 (500)	44 (485)	76·5 (490)

TABLE 1*b*

	A	12719	B	12528	7858
Depth/length	$6\frac{1}{2}-7$	$6\frac{3}{4}$	6	6	6
Head/length	$4\frac{4}{5}-5$	$5\frac{1}{4}$	$4\frac{1}{2}$	$4\frac{1}{2}$	$4\frac{2}{3}$
Eye/head	$6\frac{2}{3}-7$	$6\frac{1}{3}$	5	$5\frac{4}{5}$	$6\frac{1}{4}$
Eye/interorbital	$1-1\frac{1}{5}$	$1\frac{1}{3}$	±1	±1	$1\frac{1}{5}$
2nd Pelvic ray/Origin ray to vent	$\frac{2}{3}$	$\frac{2}{3}$	$\frac{3}{4}$	$\frac{3}{4}$	$\frac{3}{4}$
Caudal peduncle/head	$2\frac{2}{3}-2\frac{4}{5}$	$2\frac{7}{8}$	—	$3\frac{1}{2}$	$3\frac{1}{2}$
Rays, first dorsal	47 – 49	±45	55	65	56
Rays, second dorsal	62 – 64	62	45	44	43
Rays, anal fin	52 – 54	50	40	37	39

One specimen from Kalk Bay in the Cape Peninsula as well as some juveniles from Table Bay and Lambert's Bay fitted the description of the Tristan fishes as given by Sivertsen and the St. Paul Island fishes as described by Kner and Sauvage, while the specimens from East London and Port Elizabeth are clearly different, and are assumed to be *G. capensis.*

Gaidropsarus insularum Sivertsen

Motella capensis (*non* Kaup) Kner, 1868: 279. Sauvage, 1879: 42.
Gaidropsarus capensis (*non* Kaup) Barnard, 1925: 323 (*partim*). Blanc, 1961: 145. Blanc & Paulian, 1957: 327.
Gaidropsarus insularum Sivertsen, 1945: 8.

Recorded from Tristan da Cunha, St. Paul Island, the Cape Peninsula and west coast of South Africa.

Body proportions and fin counts given in Table 1.

Gaidropsarus capensis (Kaup)

Motella capensis Kaup, 1858: 90.
Gaidropsarus capensis (Kaup) Barnard, 1925: 323 (*partim*).

Depth 6 in standard length, head about $4\frac{1}{2}$. Eye equal to interorbital about 6 in head. Second pelvic ray $\frac{3}{4}$ distance origin pelvic to vent. Caudal peduncle $3\frac{1}{2}$ in head. Fin counts: Free dorsal rays 55–65, Dorsal rays 42–45, Anal rays 36–40.

Description based on two specimens, one of 91 mm standard length deposited in the South African Museum (Reg. No. SAM 12528), collected in Algoa Bay at a depth of 25 fathoms by the *Pieter Faure*, and a second of 156 mm standard length in the collection of the Department of Ichthyology, Rhodes University, Grahamstown (Reg. No. 7858), collected at East London.

Body proportions and fin counts are given in Table 1.

G. capensis differs from *insularum* in having a relatively longer first dorsal base (12—13·5% of body length as opposed to about 8·5%), a longer head, larger eye, slimmer caudal peduncle and rather marked differences in fin counts.

Berycidae

Beryx decadactylus Cuvier

Beryx decadactylus Cuvier. Fowler, 1936: 542.

One specimen obtained from Captain Scott, caught in 'Tristan waters'. Tears in the mouth suggest that the fish was caught with hook and line but depth of capture is unknown.

The fish is 362 mm standard length and has the following body proportions (expressed as thousandths of standard length): head 359, depth 472, eye 152, maxilla 185, base of anal fin 348, base of dorsal fin 290. Fin counts are dorsal IV 19, anal IV 27, pectoral 15, pelvic I 10.

B. decadactylus has not been recorded from South Africa although the related *B. splendens* is trawled quite regularly. In the course of this work an unrecorded specimen of *B. decadactylus* was found in the collection of the South African Museum, trawled off Table Bay in 1948. It was 345 mm in standard length and had the following body proportions (in thousandths of Ls): head 322, depth 446, eye 125, maxilla 174, base of anal fin 359, base of dorsal fin 293. Fin counts are dorsal IV 20, anal IV 27, pectoral 15, pelvic I 10.

Macrorhamphosidae

Notopogon lilliei Regan

Notopogon lilliei Regan, 1914: 14. Mohr, 1937: 50.

Sivertsen (1945) records two specimens of *Notopogon* which were found washed up dead on Tristan. He assigned them to *N. lilliei*, a species known from South Africa, Australia and New Zealand. It should be noted, however, that his published figure (fig. 5) resembles *N. macrosolen* Barnard rather than *N. lilliei*, especially as neither the figure nor the text makes any reference to the dorsal brush which is a conspicuous feature of *N. lilliei* but is absent in *N. macrosolen.*

Chilodactylidae

Sivertsen (1945) recorded only one species of fish belonging to the family Chilodactylidae, *Acantholatris monodactylus* (Carmichael); called by the islanders the 'Fivefinger'.

He claimed that the islanders spoke of a second fish very like the fivefinger which they were said to call the 'yellowtail'. Rowan & Rowan (1955) have shown that the fish called yellowtail is *Seriola lalandi.* No additional species of chilodactylids have been received from Tristan but a species which appears to be new has been obtained from Vema Seamount.

An additional species which appears to be undescribed has been obtained from Gough Island, but is not described here as only one specimen was obtained. It is known to fishermen as the 'funny fish'.

Acantholatris monodactylus (Carmichael)

(Plate XXIB)

Chaetodon monodactylus Carmichael, 1818: 500.
Cheilodactylus carmichaelis Cuvier & Valenciennes, 1830: 360. Kner, 1868: 90.
Chilodactylus monodactylus (Carmichael) Sauvage, 1879: 23; Regan, 1913*a*: 466. Norman, 1935*b*: 57.
Acantholatris monodactylus (Carmichael) Gill, 1863: 119. Sivertsen, 1945: 10.

This species is known from Tristan and Gough Islands and has also been found to be common at the Vema Seamount. Gunther (1860) recorded this species from Chile but Norman (1935*b*) has shown this to be a misidentification, the Chilean species being the related *A. gayi* (Kner). In Table 2 below are given body proportions and counts of several examples of the species from Tristan da Cunha, Gough Island and the Vema Seamount.

TABLE 2

Body proportions and fin counts of *Acantholatris monodactylus* in thousandths of standard length.

Origin of the specimen is:

Cat. No. SAM	10500	Tristan da Cunha
	10501	Tristan da Cunha
	11764	No history, but register says 'Very likely Tristan'
	21284	Tristan (perhaps!!)
	22890	Gough
	24288	Vema Seamount
	24291	Vema Seamount

Cat. No. SAM	11764	11784	11764	10500	10501	10501	21284	10501	24291	24288	22890
Standard length	131	153	153	175	227	238	301	353	338	443	444
Head	314	320	316	309	321	336	355	351	325	329	336
Depth	405	385	405	389	379	391	396	391	370	381	405
Eye	84	78	82	75	75	76	67	62	62	59	56
Interorbital	69	78	76	75	84	92	93	88	74	79	88
Base of dorsal	656	620	634	657	625	630	638	636	636	663	605
Base of anal	183	163	177	172	154	160	153	147	148	153	169
Length of pectoral	351	340	336	349	365	353	349	306	328	309	320
Snout to dorsal origin	351	334	329	315	339	344	379	360	343	350	334
Snout to anal origin	679	700	715	680	693	705	687	673	674	665	736
Snout to pectoral origin	313	308	323	303	334	332	342	340	332	332	356
Dorsal spines	17	16	17	17	16	17	17	17	17	17	17
Dorsal rays	25	25	25	25	26	25	26	25	25	25	22
Anal spines	3	3	3	3	3	3	3	3	3	3	3
Anal rays	12	11	12	11	11	11	11	11	11	11	10
Gillrakers	7+14	8+15	8+15	8+14	8+15	7+15	7+15		7+15		

One specimen (SAM 22890) obtained by Captain Scott at Gough Island has been assigned to *A. monodactylus* although the fin counts are lower than normal for the species. The body proportions fit within the range for *A. monodactylus* however and coloration in formalin is identical.

Acantholatris vemae sp.n.

(Plate XXIa, Table 3)

MATERIAL

Two specimens from the Vema Seamount collected by the *Emerson K*, November 1964, donated by the Division of Sea Fisheries, Sea Point (SAM 24290, 24292).

Five specimens (all gutted) from the Vema Seamount collected by commercial fishing vessels and donated by Messrs. Friedman & Rabinowitz (Pty.) Ltd. (SAM 24289, 24293, 24296–8).

Two specimens from the Vema Seamount collected by Mr. A. C. Paterson, April 1965, and donated by the Division of Sea Fisheries (SAM 24525, 24527).

Depth of body about 3, length of head about $3\frac{3}{4}$ in standard length. Eye diameter 5 in length of head, 2 in snout and $1\frac{1}{3}$ in interorbital width.

Dorsal fin XVII 24–26, the eighth spine longest, about equal to snout, 4 in body depth. Last spine $2\frac{1}{2}$ in first ray. Base of dorsal a little over $1\frac{1}{2}$ in body length, distance snout to origin dorsal $3\frac{1}{2}$ in body, about equal to length of pectoral.

Anal fin III 10–11, base short only $\frac{1}{4}$ of dorsal base. Second spine very stout, only a little longer than third, shorter than first ray.

Pectoral having 9 branched, 6 simple rays, first simple ray elongate, $\frac{1}{3}$ body length, free portion $3\frac{1}{3}$ in length of ray.

Forehead scaled to level of posterior nostril, both nostrils of similar size, round.

Scales fairly large, very thin, lateral line 55–58, transverse $\frac{7}{13}$, cheeks scaled. Gill rakers, upper 6–7, lower 14–16, total 21–23.

Colour: in formalin, dark blue-black dorsally; fading to silver below.

Edge of fins dark, caudal with a few dark bands.

In life said to be bright blue.

Detailed body proportions of the seven specimens are given in Table 3.

TABLE 3

Catalogue No.:	24289	24290	24292	24293	24296	24297	24298	24525	24527
Standard length	327	320	385	249	372	338	392	384	383
Head	288	271	260	277	255	264	263	266	253
Depth	345	347	343	333	352	329	349	359	350
Eye	58	57	52	56	54	53	51	50	55
Interorbital	80	75	75	76	75	71	79	78	78
Base of dorsal	624	660	673	650	683	663	666	690	682
Base of anal	165	161	174	169	172	178	168	174	175

TABLE 3 (continued)

Catalogue No.:	24289	24290	24292	24293	24296	24297	24298	24525	24527
Length of pectoral	327	328	294	321	328	340	319	354	329
Snout to dorsal origin	306	306	288	297	272	278	283	294	287
Snout to anal origin	686	627	607	650	650	642	654		
Snout to pectoral	303	278	299	273	253	255	268	263	264
Dorsal spines	17	17	17	17	17	17	17		
Dorsal rays	24	25	26	24	25	24	25		
Anal spines	3	3	3	3	3	3	3		
Anal rays	10	10	11	11	11	11	11		

Body proportions (in thousandths of standard length) of *Acantholatris vemae* sp.n. from the Vema Seamount.

Dates of collection of the various specimens given in the text.

SAM 24527 the Holotype.

The specimen deposited in the South African Museum (Reg. No. SAM 24527) is designated as the type.

A. vemae is very close to *A. monodactylus* (both having 9 branched and 6 simple pectoral rays) which is also found on the Vema Seamount. It differs, however, in colour and colour pattern, lacking the six dark vertical bars found in *monodactylus*; also it has a markedly shorter head and slightly less deep body when compared to *monodactylus*. As a result of the shorter head, the distances of the snout to the origin of dorsal fin, the origin of anal fin and the origin of pectoral fin are proportionately less. The slope of the forehead in *vemae* too is steeper, and whereas it has the upper corner of the pectoral fin angular it is rounded in *monodactylus*. Finally it has much thinner lips than *monodactylus*.

It differs from *A. gayi* and *A. aspersus* in the pectoral not reaching the soft anal.

Latris lineata (Bloch & Schneider)

Cichla lineata Bloch & Schneider 1801: 342.

Latris hecateia Richardson, 1839: 99. Richardson, 1842: 106. Gunther, 1860: 86. Kner, 1868: 95. Sauvage, 1879: 17. Angot, 1951: 19. Blanc & Paulian, 1957: 331. Blanc, 1961: 152.

Two specimens, SAM 22623, 22891, both collected by Captain Scott at Gough Island. The former is a skin with standard length of about 900 mm and the latter a complete specimen of 904 mm.

The body proportions of the 904 mm specimen (as thousandths of L's) are as follows: head 324, depth 303, pectoral fin 192, snout 149, base of dorsal fin 638, base of anal fin 207.

Fin counts are dorsal XVIII 35, anal III 26, pectoral 9 + 9.

Counts of the skin are dorsal XVIII 36, anal III 26, pectoral 9 + 9, gill rakers 8 + 16.

L. lineata was originally described from Australia and New Zealand, but has been recorded from St. Paul Island by Kner (1868), Sauvage (1879) and Angot (1951). This is the only species that is without doubt common to the Atlantic islands and Australasia.

Serranidae

Polyprion americanus (Bloch & Schneider)

Amphiprion americanus Bloch & Schneider, 1801: 205.
Polyprion americanus (Bloch & Schneider) Barnard, 1925: 488. Smith, 1949*a*: 199. Blanc, 1961: 147.
Polyprion cernium Gunther, 1859: 169. Angot, 1951: 15.

As noted above, Sivertsen listed two species of fish known to the Tristan islanders by common names that he was unable to identify due to lack of specimens. The fish called by the islanders the steambrass was said to be a very large fish, nearly as large as a shark (± 2 metres) 'but much broader and with soft rays in the fin'. Rowan & Rowan (1955) record an 8-foot long specimen of *Polyprion americanus* from Tristan and state that it is the species the islanders refer to as the steambrass.

Specimens were received from the Vema Seamount. Two examples from the Seamount of 465 and 602 mm standard length were found to have the length $2\frac{3}{4}-3$ times depth and $2\frac{2}{5}-2\frac{2}{3}$ of head length. In both the pectoral fin was slightly greater than half the head, while the longest dorsal spine went $2\frac{1}{3}-2\frac{4}{5}$ into head. The species occurring at Vema is thus clearly *P. americanus* rather than the related *P. prognathus*.

Ephinephelus aeneus (Geoffroy St. Hilaire)

Serranus aeneus Geoffroy St. Hilaire, 1809: 317. Fowler, 1936: 756.
Epinephelus aeneus (Geoffroy St. Hilaire) Norman, 1935*b*: 9.

One specimen (SAM 24299) presented by Messrs. Friedman & Rabinowitz, Ltd., one of several landed by commercial fishing vessels from the Vema Seamount.

Body proportions as thousandths of the standard length of 465 mm are as follows: head 402, depth 331, length pectoral fin 219, height longest (fifth) dorsal spine 123, eye 62, interorbital 64, snout 114, pelvis 172.

The cheeks are scaled with cycloid scales, as is body above lateral line; scales ctenoid below lateral line. Caudal slightly rounded. Bottom opercular spine posterior to top spine. Pre-operculum serrated, angle produced with very long serrations, operculum acutely pointed.

Mandible with two rows of teeth.

Colour in formalin: Dark brown above shading to lighter below. Sparse scattered very dark brown spots. Unpaired fins dark edged, paired fins light grey-brown. Three dark stripes on face; one from posterior of eye to lowest opercular spine, one from below eye to edge of operculum opposite base of pectoral fin and the third above maxilla to pre-operculum below the angle.

Carangidae

Seriola lalandi Cuvier & Valenciennes

Seriola lalandi Cuvier & Valenciennes, 1833: 208. Barnard, 1925: 555. Smith, 1949*a*: 221. Rowan & Rowan, 1955: 129.
Seriola pappei (Castelnau) Smith, 1959: 256.

One specimen was donated by the Division of Sea Fisheries, caught at the Vema Seamount. It appears to be a very common fish there, as one commercial fishing vessel returned with over a thousand large specimens.

It has also been recorded from Tristan da Cunha (Rowan & Rowan, 1955).

Decapterus longimanus Norman

Decapterus longimanus Norman, 1935*a*: 255.

Two specimens from the Vema Seamount (SAM 24294) presented by the Division of Sea Fisheries. The species was formerly considered endemic to Tristan da Cunha.

The two specimens are the smallest yet recorded being 215 and 225 mm in standard length. Body proportions of the 215 mm specimen in thousandths of standard length are: head 288, depth 204, pectoral fin 260, base of soft dorsal 400, base of anal 335, gillrakers 44, scutes 42.

Measurements could not be made on the other specimen as it was rather damaged, having been obtained from the gut of a larger fish.

Emmelichthyidae

Plagiogeneion rubiginosus (Hutton)

Therapon rubiginosus (Hutton) 1876.
Plagiogeneion rubiginosus (Hutton) McCulloch, 1914. Barnard, 1927. Smith, 1949*a*.

A single specimen was donated by Messrs. Friedman & Rabinowitz (Pty.) Ltd. The fish was about 330 mm in standard length and was caught by handline on the Vema Seamount. Unfortunately the fish had been cleaned and somewhat distorted in freezing so that accurate measurements were not possible. It could readily be distinguished from the related *P. macrolepis* by its lateral line count of 68 as opposed to about 50 in *macrolepis.*

P. rubiginosus is recorded from Australasia and St. Paul Island, is not uncommon off the east coast of South Africa (Smith, 1949) and a single specimen has been recorded off Table Bay (Barnard, 1927).

Pentacerotidae

Pentaceros richardsoni Smith

Pentaceros richardsoni A. Smith, 1844 (Plate XXI and 2 pages unnumbered text). Follett & Dempster, 1963: 315. Smith, 1964: 572.
Pentaceros kneri Steindachner, 1866: 208.
Pseudopentaceros richardsoni (Smith) Barnard, 1927: 621. Smith, 1949*a*: 242.
Griffinetta nelsonensis, Whitley & Phillips, 1939: 233.

Only a partial bibliography is given here; a more complete one is given by Follett & Dempster (1963). It should be pointed out, however, that in Follett & Dempster the references to Andrew Smith's original description are incorrect. The plates each with a page or more of unnumbered text were published separately between 1838 and 1847 but were not dated while only the index and title page were dated and published in 1849. (See Waterhouse, 1880, and Barnard, 1956.)

Pentaceros richardsoni was for long thought to be an extremely rare species of fish, being known from the type, an adult caught off Cape Point, South Africa, on a deep handline, and a few juveniles from Australia and New Zealand. Recently, however, many medium-sized fish have been obtained from the North Pacific (Follett & Dempster, 1963, give a complete set of published records) while Smith (1964) has described in detail a second adult fish from the Cape of Good Hope, and pointed out that the fish described from Cape Horn by Steindachner as *P. kneri* is clearly a juvenile of *P. richardsoni.*

A juvenile of *P. richardsoni* obtained at Tristan was presented to the Museum by Captain Scott. Unfortunately there are no data as to its method or depth of capture. Measurements and counts of this juvenile are given in Table 4, and compared with published measurements and with those of two specimens in the South African Museum; a large adult specimen trawled off Cape Town in 300 fathoms during March 1961 (SAM 23076) and a slightly smaller specimen trawled off Cape Columbine in April 1965 (SAM 24541) both presented to the Museum by Messrs. Irvin & Johnson, Ltd.

TABLE 4

Standard length	286[1]	240[2]	254[2]	80[3]	451[4]	358[5]
Head	325	325	319	338	321	319
Depth	413	433	422	425	418	422
Eye	87	79	83	100	91	76
Interorbital distance	115	117	118	135	109	106
Least depth caudal peduncle	93	100	102	112	106	109
Dorsal spines	14	14	14	14	14	14
Dorsal rays	8–9	9	9	10	9	10
Anal spines	4	4	4	4	4	4
Anal rays	7	7	7	8	8	7
Pectoral	17–18	17	17	18	17	18
Gillrakers total	25	22–25	22–24	—	—	—
Lateral line scales	68–69	71	76	—	86	—

Body proportions (in thousandths of standard length) and counts of *Pentaceros richardsoni* from various localities.

[1] Japan (Abe, 1957).
[2] North Pacific (Welander *et al.*, 1957).
[3] Tristan da Cunha (Reg. No. SAM 21791).
[4] Cape of Good Hope (Reg. No. SAM 23076).
[5] Cape of Good Hope (Reg. No. SAM 24541).

P. richardsoni is probably found throughout the world in the warm temperate waters, but the published records of its occurrence are confined to a few scattered localities. At most of these places it has been found more than once. Both Follett & Dempster (1963) and Smith (1964) suggested reasons for this, but it seems likely that the known distribution of the species bears no relation to the true distribution but is due mainly to the widely scattered areas of intensive fishing and the introduction of new fishing techniques in various areas.

Thunnidae

Thunnus spp.

Several species of the genus *Thunnus* have been landed by commercial fishing vessels from the Vema Seamount. Unfortunately all specimens have been brought ashore gutted and without heads or fins. Many small tuna (about 50—75 lb. whole weight) had bright yellow peduncle keels which is characteristic of the southern bluefin (*T. maccoyi* Castelnau) (known from South Africa and Australia), while others were stated by the fishermen to be yellowfins (*T. albacares* (Bonaterre)) and bigeyes (*T. obesus* (Lowe)). Mr. A. Heydorn (Division of Sea Fisheries) (*pers. comm.*) informs me that he saw a yellowfin while diving on the Vema Seamount.

Until whole examples are obtained nothing definite can be stated concerning the species of tuna congregating about the Seamount.

Stromateidae

Palinurichthys antarcticus (Carmichael)

Perca antarctica Carmichael, 1818: 501.
Seriollella antarctica (Carmichael) Regan, 1913*a*: 467.
Seriolella antarctica (Carmichael) Sivertsen, 1945: 21.
Palinurichthys porosus (Carmichael) Barnard, 1948: 395. Smith, 1949*a*: 304.
Mupus perciformis (Mitchill, 1818: 244). Smith, 1949*b*: 843.

The Tristan bluefish was first described and figured by Carmichael (1818). It was not discussed by Regan in his review of the Stromateidae (1902), but in a later paper Regan (1913) reviewed the fishes described by Carmichael and suggested, but without giving reasons, that *antarctica* was 'rather closely related to Sauvage's *Seriollella velaini* from the Island of St. Paul'.

Sivertsen (1945) placed *antarctica* in the genus *Seriolella*, but again no reasons for doing so were given; nor was the generic definition modified. According to Regan (1902) the genus *Seriolella* had *inter alia* the following characters: a fin formula of VIII 27–40; anal III 19–24, and a lateral line concurrent with the dorsal profile. The fin formula of *antarctica* on the other hand is dorsal IX 18–20, anal III 14–15, and the lateral line becomes straight before the caudal peduncle.

The correct genus for *antarctica* would thus appear to be *Palinurichthys* Bleeker 1859.

A specimen of *P. antarcticus* was donated to the Museum by the Director, Division of Sea Fisheries, after it had died while on display in the Sea Point Aquarium. The fish was unquestionably a Tristan bluefish although actually obtained from Gough Island. When compared with other *Palinurichthys* material in the Museum collection it showed a marked resemblance to two similar sized fish in the collection recorded by Barnard (1948) as *P. porosus* (Richardson).

Table 5

	24532	19573	19557	23311	[1]	[1]
Standard length	884	436	453	432	35	34
Head	339	351	356	358	370	380
Depth	347	344	335	358	400	380
Length anal fin base	191	222	212	226	230	235
Diameter eye	75	66	75	72	103	103
Length pectoral fin	—	266	274	306	260	265
Length pelvic fin	152	160	166	158	245	235
Snout	105	88	95	102	86	88
Maxilla	153	138	150	150	145	147
Pectoral rays	21	21	21	20	—	—
Dorsal spines	8 + 1	8 + 1	8 + 1	8 + 1	8 + 1	8 + 1
Dorsal rays	19	19	18	20	19	19
Anal spines	3	3	3	3	3	3
Anal rays	14	15	14	14	14	14

Body proportions in thousandths of standard length and counts of *P. antarcticus* from the Cape and Gough Island and *P. porosa* from the Kermadac Islands.

SAM 19573 NW. of Cape Town
19557 NW. of Cape Town
23311 Gough Island
24532 Vema Seamount

[1] Kermadec Islands. Collection of the British Museum (Natural History).

Body proportions and counts are given (Table 5) for the Gough Island fish, the two Cape fish and a larger specimen caught at the Vema Seamount by Mr. A. C. Paterson and presented by the Division of Sea Fisheries. As far as proportions and fin counts are concerned it is clear that there are no significant differences between the fish that could be construed as being of a specific nature.

In all four examples the pectoral fin is long and falcate, reaching the anal origin. The preoperculum has a curved scaled patch and the operculum is completely scaled. There is also a small patch of scales on the head above the preoperculum, as shown in Barnard (1948, fig. 14). The mouth is large, reaching the posterior edge of the pupil. The origin of the dorsal fin is posterior to the pectoral fin base.

P. porosus is known from the coast of Australia and the Kermadec Islands. Seven juveniles from the latter locality, kindly lent by the British Museum (Natural History), were compared with *P. antarcticus.* Several differences in body proportions were apparent (Table 5), as well as the shape of the pectoral fin. Regan (1902), however, mentioned that the stromatid fishes changed considerably in body shape during growth, especially in that the pelvic fin becomes shorter and the pectoral fin becomes falcate in shape.

Although there are marked differences in the size of the fishes examined (over 430 mm as opposed to about 35 mm in total length), the similarity in pattern of the scales of the head suggest that *P. porosus* is at least very closely related to *P. antarcticus.*

In recent years large numbers of stromatid fishes assigned to the species

P. porosus have been reported from Australian waters (Cowper, 1960) but no redescription or figure of a specimen larger than the type of 140 mm has been published.

Two stromatids have been recorded from St. Paul Island, *Seriolella velaini* which has a fin formula of dorsal VIII 27 and anal III 20 (Sauvage, 1879), and *P. porosus*, which was recorded and briefly described by Angot (1951). His brief description could apply equally to *porosus* or *antarcticus*, but the sketch shows a fish with a long falcate pectoral fin characteristic of *antarcticus* rather than the short rounded fin as shown in Richardson's figures of the type of *porosus*.

In the North Atlantic there is another related species, *P. perciformis* (Mitchill) which Smith (1949*b*) recorded from the west coast of South Africa.

This species appears to be generally smaller than *antarcticus*; it is said to be dark green in colour (Jordan & Evermann, 1896) whereas *antarcticus* is blue; the dorsal spines after the fourth are subequal (Regan, 1902) whereas in *antarcticus* and *porosus* they decrease in size and, finally, the pectoral fin in *perciformis* (as figured by Merriman, 1945) is markedly shorter and less falcate than in *antarcticus*, even at the largest recorded size (284 mm L's).

It would appear therefore that there are two closely related species of *Palinurichthys* in the Atlantic Ocean, a northern species *P. perciformis* (Mitchill, 1818) and a southern species *P. antarcticus* (Carmichael, 1818). *P. antarcticus* has been found in South Africa, at Tristan and Gough Islands, the Vema Seamount and also appears to be present at St. Paul Island in the southern Indian Ocean. If adult specimens of *porosus* and *antarcticus* are compared and found to be conspecific *P. porosus* (Richardson, 1845) must be relegated to the synonomy of *antarcticus*.

Mupus imperialis Cocco

Mupus imperialis Cocco 1833: 20. Smith, 1949*b*: 843.
Mupus ovalis Smith, 1949*a*: 303.
Lirius ovalis Barnard, 1948: 392.

This species seems very common on the Seamount and grows to a large size, probably at least to 1 metre in length. In view of its rounded head it is called 'stumpnose' or 'biskop' by South African fishermen visiting Vema. Two specimens have been examined. In thousandths of standard lengths of 590 mm and 762 mm the present specimens have the following respective body proportions: head 289–297, depth at pelvic origin 334–343, max. depth 393–370, snout 76–79, eye 68–66, pectoral fin 263–244, base of dorsal fin 728. Counts were dorsal VI–VII 28, –28, anal III 20–21.

M. imperialis has been recorded from wide areas of the Atlantic and the Mediterranean and appears to grow to a large size. Sivertsen (1945) described as new a stromatid fish collected at Tristan which he named *Seriolella christophérseni*. From the description I can find no significant characters whereby this species differs from *M. imperialis*. Both have similar body proportions, especially the large eye and rounded head, rather small mouth and a body which is deepest posterior to the pelvic fin origin. The counts for the unique specimen of *christopherseni* are all within the range for *M. imperialis.*

Coryphaenidae

Coryphaena hippurus Linnaeus

Coryphaena hippurus Linnaeus, 1758: 261. Fowler, 1936: 649. Gibbs & Collette, 1959: 117.

Two small specimens of this species were collected at the Vema Seamount by Mr. Paterson of the Division of Sea Fisheries. Both specimens (SAM 24531) are immature, being only 352 and 375 mm in standard length, but are clearly *hippurus* rather than the related *equiselis,* having total gillraker counts of 9–10 and 62–63 dorsal rays.

Scorpaenidae

Scorpaena scrofa Linnaeus

Scorpaena scrofa Linnaeus, 1758: 266. Smith, 1957: 51
Scorpaena natalensis Regan, 1906: 5. Barnard, 1927: 902. Smith, 1949*a*: 371.

One specimen from a commercial fishing vessel at the Vema Seamount. Body proportions as thousandths of standard length (313 mm) are as follows: head 418, depth 313, eye 80, interorbital 73, snout 130, dorsal base 534, anal base 125, pectoral 265.

Congridae

Ariosoma australis (Barnard)

Congermuraena australis Barnard, 1923: 442. Barnard, 1925: 190. Sivertsen, 1945: 4.
Arissoma balearica (*non* de la Roche) Smith, 1949*a*: 393 *partim.*
Congermuraena ?habenata (Richardson, 1845: 109). Sivertsen, 1945: 4.

Barnard (1923) described two species of congrid eels as *Congermuraena australis* and *C. albescens,* the former from shallow water at the Cape of Good Hope and Tristan da Cunha and the latter from deep water at the Cape. Sivertsen (1945) obtained one specimen at Tristan, and, although he assigned it to *C. australis,* he stated that there were minor differences between his specimen and Barnard's description, and suggested that the Tristan species may be *C. habanata* Richardson, known from New Zealand and St. Paul Island.

Smith (1949*a*) reduced both *australis* and *albescens* to the synonymy of the Mediterranean species *Ariosoma balearica* (de la Roche) but gave no reasons for doing so.

A careful examination of *A. australis* from shallow water at the Cape and Tristan and *A. albescens* (from deep water off the Cape) has shown the two eels to have clear differences. Body proportions are given in Table 6. There is little difference between the fish in so far as the body proportions are concerned except that the eye in *albescens* is proportionally smaller and the interorbital width greater than in *australis* from the Cape and with the Tristan fish having an intermediate eye size but a narrow interorbital width.

In general appearance, however, the fish from Tristan are very similar to *australis*, which differs from *albescens* in the following characters: in *australis* the rays in the vertical fins are clearly visible, the fin has a dark edge, the lateral line has one tiny pore to each myotome, the upper dentition has a rather elongate, slender pattern (fig. 1*a*), the body is well formed and firm, and I can find no trace of the epidermal processes stated by Castle (1960) to occur on the body of *A. balearica*. In *albescens* the vertical fins are enclosed in a thick gelatinous envelope, the fins are pale edged, the lateral line is a distinct ridge and has a

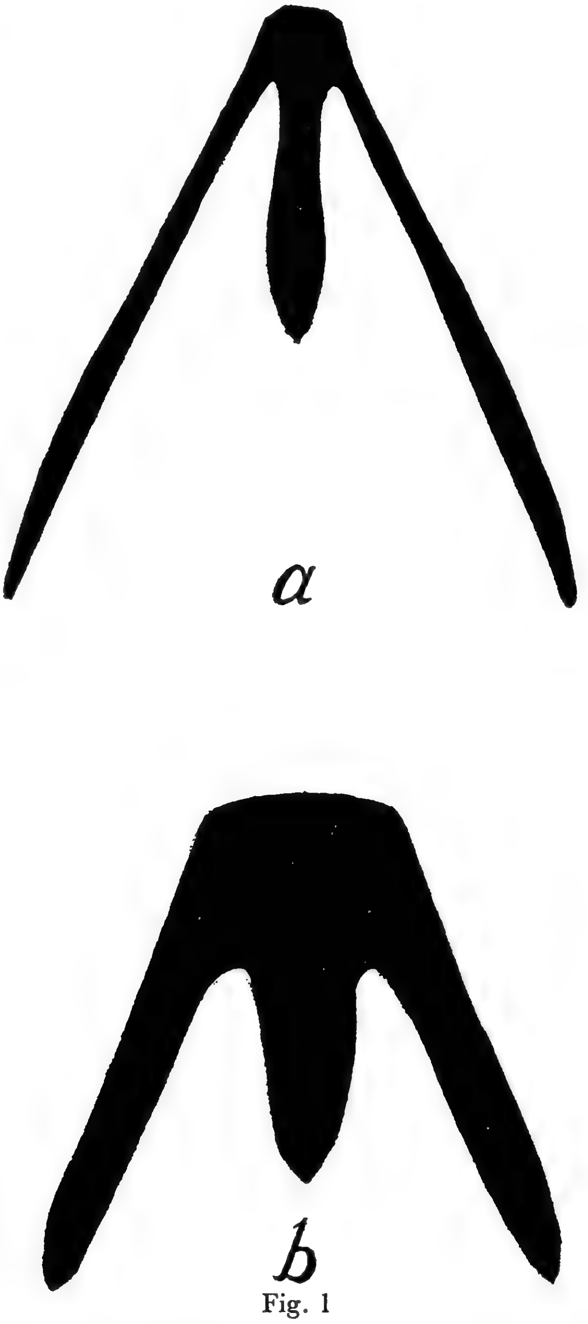

Fig. 1
Upper tooth patterns of *a*, *Ariosoma australis* syntype; *b*, *Ariosoma albescens* holotype. (Diagrammatic and not to scale.)

large lower pore and a small upper one to each myotome, the pattern of the upper dentition is shorter and heavier (fig. 1*b*), there are distinct epidermal processes present and, finally, the body is soft and flabby. It is unlikely that the differences are due to changes taking place during growth, as a specimen of *australis* at 280 mm was found to be fully mature and to have ripe ovaries containing large eggs.

Smith's (1949*a*) combining of *australis* and *albescens* is therefore considered to be incorrect.

A. balearica is known from the tropical Atlantic and the Mediterranean (Fowler, 1936) and is very similar to *A. australis*. It, too, has a very indistinct lateral line which will separate it from *A. albescens*. There is also very little difference between *australis* and *A. habenata* from New Zealand and St. Paul Island as pointed out by Sivertsen (1945) and between the New Zealand deep-water species *Pseudoxenomystax hirsutus* Castle (1960) and the South African deepwater species *A. albescens*. Castle divides the two species by the position of the origin of the dorsal fin, stating that it lies over the gill slit in *hirsutus* and at a level half-way along the pectoral in Smith's specimens of '*balerica*'. In the type of *albescens* (designated in the museum catalogue as SAM 12775) the origin of the dorsal is above the pectoral origin.

TABLE 6

Catalogue No. SAM:	12781	12781	12780	12781	18097	12782	24551	12775	18097	18097
Standard length . . .	206	225	238	274	281	186	368	668	737	879
Depth	53	67	51	55	47	56	65	88	73	74
Head	160	160	160	150	160	161	160	157	151	147
Head to vent . . .	398	391	406	392	403	376	405	454	400	409
Vent to tail	606	608	592	607	597	635	595	550	596	587
Eye	39	38	38	40	32	37	33	25	26	23
Interorbital	14	16	13	16	11	16	18	37	26	26
Snout to origin dorsal .	180	182	189	172	182	178	188	178	162	174
Snout to origin anal .	417	405	420	405	—	403	—	481	—	—
Height, gill slit . . .	17	18	17	18	18	21	19	25	—	—

Body proportions (in thousandths of standard length) of *Ariosoma australis* from South Africa and Tristan da Cunha and *A. albescens* from South Africa.

SAM 12780 *A. australis* paratype, collected Kalk Bay
12781 *A. australis*, Kalk Bay
18097 *A. australis*, Kalk Bay
12782 *A. australis*, Tristan
24551 *A. australis*, Tristan
12775 *A. albescens*, holotype, deep water off Cape Town
23189 *A. albescens*, deep water off Cape Town

The systematics of this group of eels is in a very confused state, there being little agreement even at the generic level, and until such time as a careful revision of the family is made on a world-wide basis it will be impossible to decide whether *A. habenata*, *A. australis* from the Cape, *A. australis* from Tristan and several other species are in fact distinct species or are only geographical variants. It is considered advisable therefore that the existing species be retained in the meantime. It would be surprising, however, if the Tristan and St. Paul Island eels are specifically different.

Lagocephalidae

Sphaeroides cutaneus (Gunther)

Tetrodon cutaneus Gunther, 1870: 287. Barnard, 1927: 971.
Sphaeroides dubius von Bonde, 1923: 40.
Sphaeroides cutaneus (Gunther) Smith, 1949*a*: 417.

This large species of puffer fish is found throughout the warm, temperate and tropical seas. It is known from the Cape and St. Helena Island.

Three specimens from Vema were collected and presented by Mr. Paterson (SAM 24524). All three were a dirty grey-green dorsally with a white belly. Dorsal, anal and pectoral fins were pale yellow. The pectoral fin has a characteristic shape, being broad, rounded on the lower distal corner, and pointed at the upper. The species is capable of very extensive inflation and all three examples examined were much distorted due to this.

ZOOGEOGRAPHY

The relative geographical positions of the islands of Tristan da Cunha, Gough, St. Paul, Marion and Crozet, the Vema Seamount and South Africa are shown in figure 2. Tristan, Gough and St. Paul islands lie on very similar latitudes, whereas the Vema Seamount is roughly as far north of Tristan as the Marion and Crozet groups are south. The Vema Seamount, however, has several fish in common with Tristan whereas the Marion and Crozet groups have no fish in common with Tristan or St. Paul. This, as was suggested by Sivertsen (1945), is almost certainly due to hydrographic conditions, mainly water temperatures.

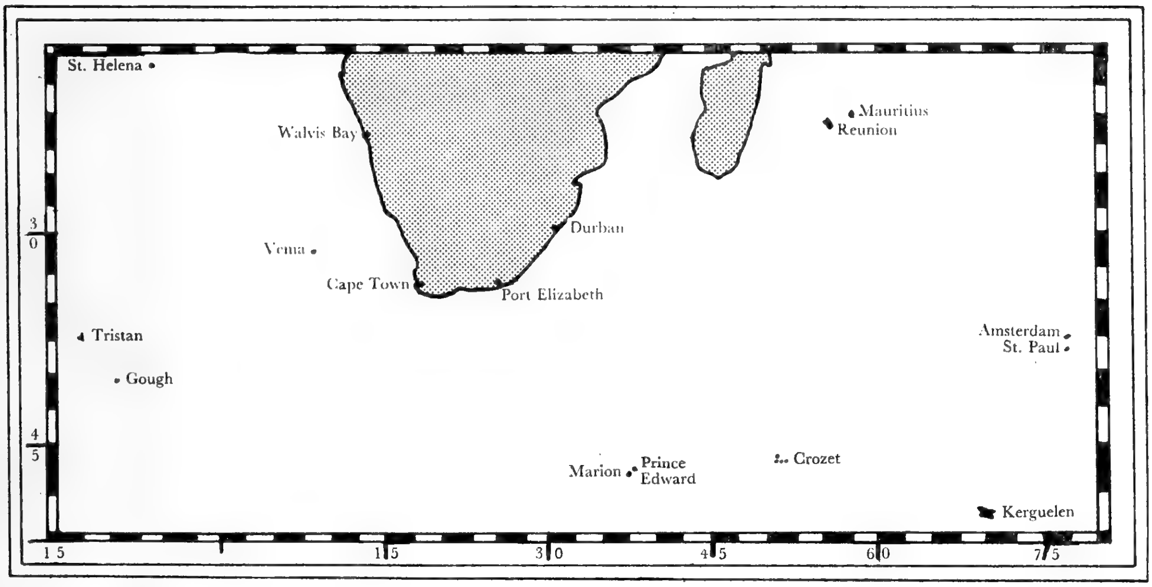

Fig. 2
Shallow-water areas in the southern Atlantic and Indian Oceans.

There are two areas of sudden temperature change in the Southern Ocean, the Sub-Tropical Convergence, where the surface temperature rapidly changes from about 13°C to about 9°C and a more southerly line, the Antarctic Convergence, where the surface temperature again drops, from 6°C to about 2°C. The Antarctic Convergence is quite narrow but the Sub-Tropical Convergence is much broader and Sverdrup *et al.* (1942) refer to it as a Region of Convergence. The Sub-Tropical Convergence fluctuates in latitude, at times the whole zone is 5–6° South of the Island and at other times Deacon (1937) suggests that it may be north of Tristan. Temperatures taken at Gough Island at a time when he suggested this do not support it, however.

Gough Island is approximately 3° 20′ south of Tristan, thus it may lie north or south of the Convergence according to the conditions prevailing in the ocean. Both, however, probably normally lie north of or within the Convergence zone, while Vema always lies well to the north and the Marion and Crozet group well to the south.

There is little published data available giving water temperatures at Tristan and even less for Vema or Gough. Christophersen & Schon (1942) published detailed sea surface temperature records taken during the Norwegian expedition to Tristan. The main features were:

	Temperatures in °C		
Month	*Average*	*Lowest*	*Highest*
December 1937	15·7	15·0	16·4
January 1938	16·7	14·8	17·9
February 1938	18·4	17·6	19·8
March 1938	18·9	18·0	20·0

The above are all surface temperatures taken from the shore. Two stations worked by R.V. *Discovery* gave surface temperatures of 14·59°C (Station 4) in January and 12·95°C (Station 397) in May. Station 4 was taken close inshore where the bottom was only 37 metres. A subsurface sample at 35 m gave a temperature of 13·64°C.

Gough Island too appears to have a very deep thermocline, stations worked by the R.V. *William Scoresby* in June 1927 showed the following:

		Temperatures in °C at Sample Depth		
Station	*Date*	0 *m*	100 *m*	150 *m*
W/s 122	7–8/6/27	11·59	11·69	9·89
125	9/6/27	11·63	11·49	10·99
126	10/6/27	11·79	11·70	9·69
130	12/6/27	12·09	12·09	10·71

In April 1965, the supply ship *R.S.A.* recorded surface temperatures at Gough Island ranging from 11·8°C to 13·7°C over two days (Crawford, *pers. comm.*).

The main fishing areas at Tristan and Gough are in shallow (under 50 metres) water. At this depth it would seem that there is normally but little difference between surface and ambient temperature of the bottom living species.

The surface temperatures at Vema are significantly higher, the *Emerson K* found surface temperatures of between 18·3°C and 18·8°C in November 1964 (Simpson & Heydorn, 1965) and in April 1965 the R.V. *Africana II* obtained the following temperatures on and about the Seamount:

Station	*Sounding (metres)*	*Sampling depth (metres)*	*Temperature °C*
A.3617	90	0	20·44
		50	20·13
		80	18·50
A.3620	900	0	20·37
		50	20·35
		100	16·15
A.3624	480	0	20·40
		50	20·38
		100	16·63
A.3625	73	0	20·36
		50	20·33
A.3626	900	0	20·35
		50	20·28
		100	15·51

There is a more rapid decrease in water temperature in the first hundred metres at Vema than at the two southern islands, but the ambient temperature of the bottom living species (main fishing areas are 70–80 metres deep) is still several degrees higher than at Tristan or Gough.

It is probable that this bottom temperature is close to the maximum for the fish at Vema which are more normally associated with cooler water (*Acantholatris* spp. and *Palinurichthys antarctica*) and yet still suitable for subtropical species (*Seriola lalandii* and *Epinephalus aeneus*).

The surface water temperature at Vema throughout the year, and at Tristan occasionally in the summer is suitable for tropical and subtropical surface pelagic species (*Coryphaena hippurus*, *Sphaeroides cutaneus* and Exocoetidae). Cool water surface species, however, such as *Thyrsites atun*, common at Tristan, appear to avoid the warm water and have not been found at Vema.

TABLE 7

	Tristan	*Gough*	*Vema*	*South Africa*	*St. Paul*
(*a*) Coast fishes					
Gaidropsarus insularum	+			+	+
Acantholatris monodactylus	+	+	+		
Acantholatris vemae			+		
Latris lineata		+			+
Bovichthys diacanthus	+	+			
Decapterus longimanus	+		+		
Labrichthys ornatus	+	?+	?+		+
Helicolenus tristanensis	+	+			
Sebastichthys capensis	+	+		+	
Scorpaena scrofa			+	+	
Epinephalus aeneus			+		
Caesioperca coatsi		+			
Ariosoma australis	+			+	

	Tristan	*Gough*	*Vema*	*South Africa*	*St. Paul*
(*b*) Oceanic fishes					
Prionace glauca	+			+	
Alepisaurus ferox	+			+	
Maurolicus muelleri . . .	+			+	
Myctophum humboldti . .	+			+	
Scomberesox saurus . . .	+			+	
Exocoetus exsiliens. . . .	+			+	
Cypsilurus lineatus . . .	+			+	
Beryx decadactylus. . . .	+			+	
Seriola lalandi	+		+	+	
Plagiogeneion rubiginosus .			+	+	+
Pentaceros richardsoni . .	+			+	
Polyprion americanus . .	+		+	+	+
Notopogon ?macrosolen . .	+			+	
Thunnus spp.			+	+	
Thyrsites atun	+			+	+
Mupus imperialis	+		+	+	
Palinurichthys antarcticus .	+	+	+	+	?
Coryphaena hippurus . . .			+	+	+
Sphaeroides cutaneus . . .			+	+	

Distribution of fishes, known from the Islands of Tristan da Cunha and Gough and the Vema Seamount.

Sivertsen felt that there was a large number of fish endemic to Tristan (33% of the known fish) and a greater similarity with St. Paul Island than South Africa.

Table 7, which lists all the fish known from Tristan, Vema and Gough, is divided into oceanic and coastal species in much the same manner as arranged by Sivertsen. It is never easy, however, to distinguish between oceanic and coastal species and some, considered to be coastal by Sivertsen, are here listed as oceanic. Thirteen species are considered coastal, of these eight are found at Tristan, seven at Gough and six at Vema. Three of these species also occur definitely at St. Paul Island and four in South Africa. None of the species definitely occur at all five localities and only one at Tristan, Gough and Vema.

It is not agreed with Sivertsen that Tristan has a large proportion of endemic fish, in fact it is a surprising conclusion that this isolated island has no endemic fish species. Vema, however, appears to have one, as does Gough. It is also surprising that such an apparently successful species as *A. monodactylus* has reached Vema but not South Africa.

Almost all the oceanic species listed in Table 7 are known from Tristan, only the tropical species being absent. All species recorded from Tristan are also known from South Africa, a few from Vema and almost none from Gough. This pattern is almost certainly due more to the varying intensities to which the various areas have been fished than to any real differences.

Some of the species recorded from Tristan are deep-living bathypelagic species that have either been caught on the surface at night or have come into shallow water due to the abrupt elevation of the ocean floor. Such species are *Maurolicus muelleri*, *Myctophum humboldti*, *Alepisaurus ferox*, and *Pentaceros rich-*

ardsoni. All are species which have been found in widely scattered parts of the world.

Other fish again are surface-living pelagic forms not normally found close to land but presumably attracted by the rich food available at the edges of the oceanic islands and in the shallow water over the Vema Seamount. Fish of this type recorded are *Coryphaena hippurus* and *Thunnus* spp. from Vema, and *Scomberesox saurus*, *Prionace glauca* and *Exocoetus exsiliens* from Tristan.

Another group of pelagic fishes are also wide ranging but normally congregate close to land. *Seriola lalandi*, *Thyrsites atun* and *Sphaeroides cutaneus* are of this type. The first has been taken at both Vema and Tristan, the second only at Tristan and the third only at Vema. All three, however, are known from South Africa and the east coast of America. *Palinurichthys antarcticus* is possibly a similar fish but has a deep pelagic habitat rather than occurring close to the surface. It appears to have a very wide distribution, being known from all three areas discussed, South Africa, probably St. Paul Island and possibly Australia and New Zealand.

Some of the species which have a wide geographic distribution are small, weakly swimming, species, e.g. *Labrichthys ornatus* which is known from Tristan and St. Paul islands, and probably also Gough (Holdgate 1948) and Vema (Heydorn, *pers. comm.*, underwater sighting). Other widely distributed, but weakly swimming species are *Ariosoma australis* which occurs in South Africa and Tristan, and possibly St. Paul as well and *Gaidropsarus insularum* known from South Africa, Tristan and St. Paul. Both the latter two species have pelagic larval stages.

Rowan & Rowan (1955) mention large fish seen jumping in the vicinity of Tristan. At times, in summer, the surface water temperature at Tristan reaches a temperature quite suitable for Tuna, Blue and White Marlin and Broadbill Swordfish. *Isurus glaucus* has been recorded from St. Paul (Blanc, 1961).

It is interesting that no elasmobranchs other than *Prionace glauca* have been recorded from the areas discussed, although 'spiny dog fish' *Squalus fernandinus*, are common at St. Paul (Blanc & Paulian, 1957).

None of the gadids, thought by Rowan & Rowan (1955) to belong to at least two species, have been obtained. They thought that one belonged to the genus *Haloporphyrus* but as they obtained only damaged specimens washed ashore by storms, identification was not possible.

SUMMARY

The fishes known from the newly discovered Vema Seamount are described and compared with those found off Tristan da Cunha and Gough Island. A new species of chilodactylid, *Acantholatris vemae*, is described from Vema. The genus *Gaidropsarus* from Tristan and South Africa is discussed and the South African material shown to belong to two species, *G. insularum*, also known from

Tristan and St. Paul Island, and *G. capensis* from the south-east coast of South Africa.

An attempt is made to relate the fish fauna to what is known of the hydrographic conditions around the islands.

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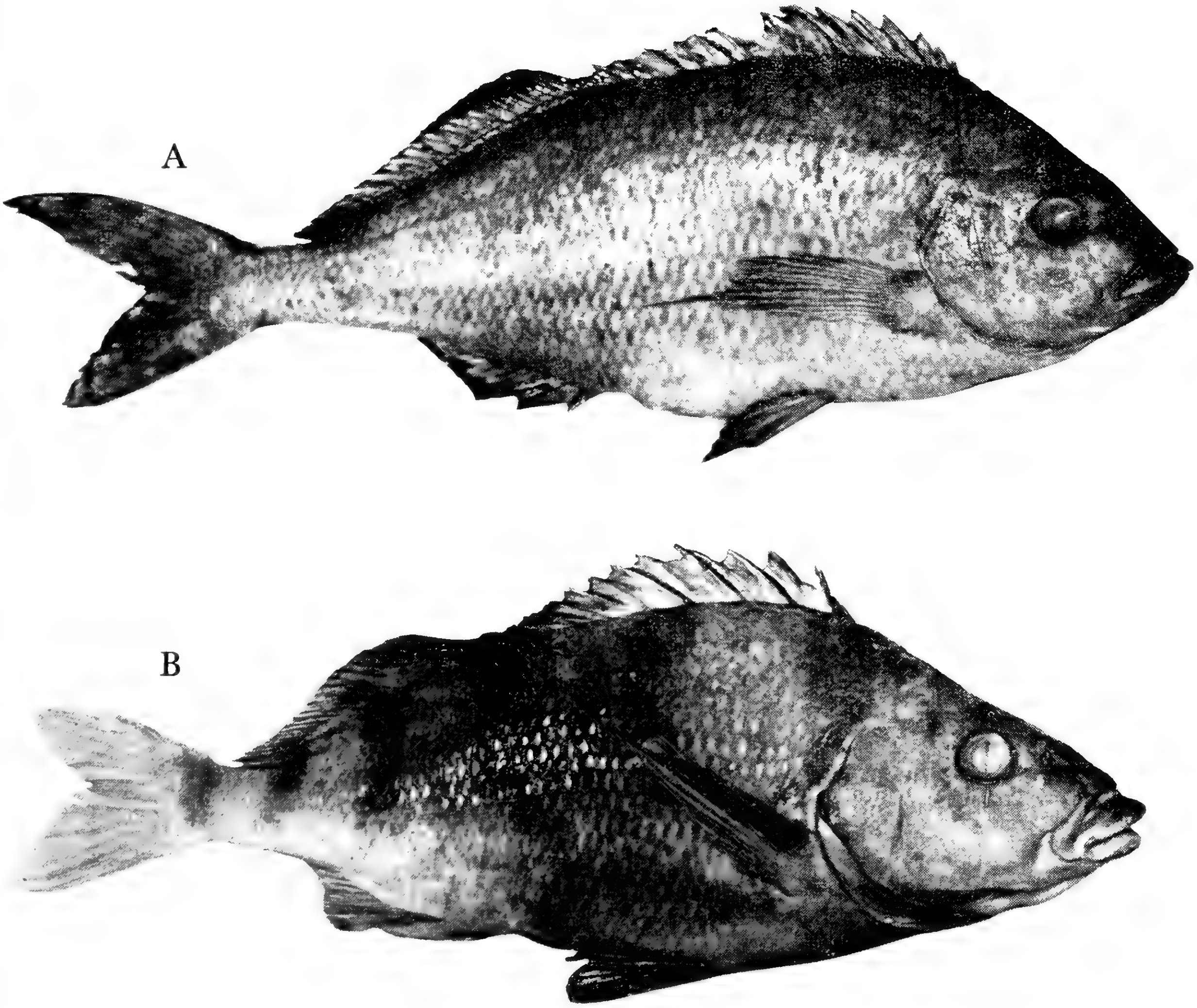

A. *Acantholatris vemae* sp.n. Type of 383 mm. standard length.
B. *Acantholatris monodactylus*. Specimen of similar size from Vema seamount.

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 4¾ in. = 7 in. (7½ 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.

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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).

INDEX TO GENERA AND SUBGENERA

(SYNONYMS IN ITALICS)

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