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BY

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EARTHWORMS (ACANTHODRILIDAE AND EUDRILIDAE : OLIGOCHAETA) FROM GAMBIA

by R. W. SIMS

CONTENTS

SYNOPSIS

Earthworms are reported from the coastal and central areas of Gambia. Seven species of Acanthodrilidae and two of Eudrilidae are recognized; two species of the former have previously been recorded from the savannas of western Africa while one species of the latter has a wider distribution from the Congo to Senegal; the remaining species are regarded as being endemic. One new genus and five new species of Acanthodrilidae (Octochaetinae) and one new species of Eudrilidae (Pareudrilinae) are described. With the exception of one species of *Benhamia*, all of the other species are new records for Gambia. A brief Appendix contains a new record for Senegal.

INTRODUCTION

Although the savannas of the northern tropical region of western Africa form a discrete area of special faunal interest, the terrestrial oligochaetes are poorly known. There are few records of earthworms from the territories north of Sierra Leone and our total knowledge of Gambian Oligochaeta rests on the first descriptions of three new species of *Benhamia* (Beddard, 1900 : 653 and 1901 : 210). The lack of information on the terrestrial Oligochaeta of the savannes of western Africa although important in itself, prevents an understanding of the structure of the oligochaete fauna of the western Aethiopean region generally. Knowledge of the earthworms of this northern area permits the recognition of a lowland savanna component in faunae in other areas especially where vegetational zones are complicated by altitude.

The climate of the region may be largely the cause of our poor knowledge of the earthworms. The weather is dry for most of the year, the soil is parched and earthworms are difficult to find; then there are heavy rains during the height of the northern summer when travelling becomes difficult and collecting is not attempted. There are localities where these generalizations do not strictly apply and one is the strip of land along both sides of the River Gambia. Here the soil is less arid in the dry season, or at least during the earlier part, than in most places in the region. One result is that collecting is possible here at a time when earthworms are seldom found elsewhere. To increase our knowledge of the terrestrial Oligochaeta of the savanna of western Africa, I visited the area in 1964 and took advantage of the more favourable conditions along the River Gambia to collect at several localities in Gambia. An account of the visit and of the material obtained is presented in this report together with details of a small collection of earthworms from Senegal.

ACKNOWLEDGEMENTS

I must record my gratitude to the Trustees of the Godman Fund for their generosity in contributing towards the expenses incurred in visiting Gambia. To Mr. Hector Davidson, Director of Agriculture, and to other members of the Department of Agriculture, Gambia, go my grateful thanks for the willing assistance they gave to me without which the field programme could not have been completed. My thanks are also due to Professor A. Chabaud, Museum National d'Historie Naturelle, Paris, and Dr. P. L. G. Benoit, Koninklijk Museum Voor Midden Africa, Tervuren, for their courtesy in permitting me access to the collections in their charge. Finally, I must acknowledge the assistance given to me by Mr. E. G. Easton during the preliminary laboratory studies on the material reported here and by Mr. P. Green who is responsible for the excellent photographs reproduced below.

COLLECTING LOCALITIES

The material listed in this report was collected at the end of the rainy season in September and October when the more favourable conditions begin. Field work was carried out from two centres in Gambia, the first near to the coast around Yundum and the second in central Gambia near to Sapu. Samples were collected in a number of habitats in the localities listed in Table 1.

TABLE 1

Abuko	10 miles south of Bathurst
Bakau	7 miles west of Bathurst
Brikama	20 miles south of Bathurst
Brikama Ba	10 miles west of Georgetown
Nyambai	16 miles south of Bathurst
Sapu	12 miles west of Georgetown
Willigara	13 miles west of Georgetown
Yundum	14 miles south of Bathurst

The numbers of earthworms present in each sample varied considerably and in many places no specimens were obtained, for example, collecting was frequently attempted in the bush, i.e. forested savanna, but earthworms were never found there. It is possible, however, that where negative results were obtained they may be largely attributed to the collecting methods employed (see below). The paucity of earthworms led to a wide search for favourable sampling plots but few were found. The few that were satisfactory, were confined to soil under mulch near cultivation, at the sides of fields where weeds and the unwanted tops of ground crops had been discarded, or, near to water. In these situations earthworms were often present in large numbers.

ECOLOGY: CLIMATE AND SOIL

The two main collecting areas are similar in consisting of lightly wooded grassland with scattered villages surrounded by cultivated land. In the coastal region, however, the climate is slightly more humid and the temperature a little lower than inland. The soils of the two areas also differ slightly although in both localities they are essentially sandy loams.

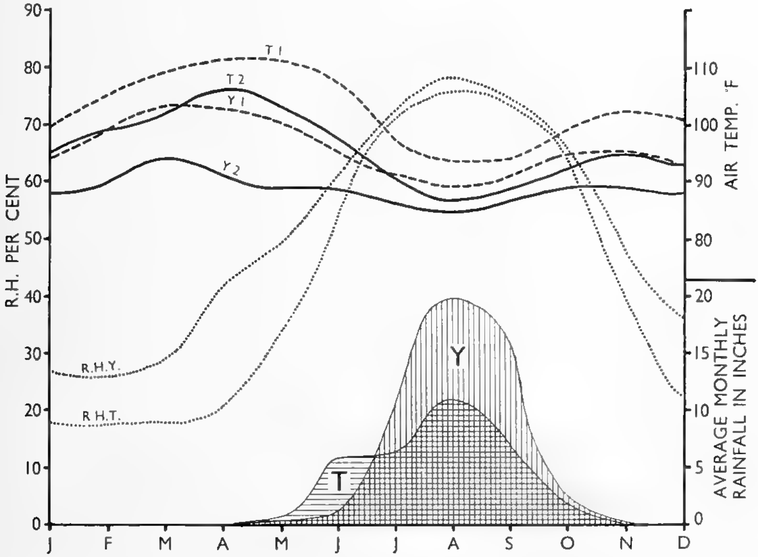

Fig. 1. Climate of the basin of the R. Gambia. Temperature (Fahrenheit), *Broken line:* average highest temperature each month, *T.*1.–Tambacounda; *Y.*1.–Yundum. *Continuous line:* average daily temperature, *T.*2.–Tambacounda; *Y.*2.–Yundum. Humidity, *Dotted line:* relative humidity, *R.H.T.*–Tambacounda, daily average R.H. at 11.00 hrs.; *R.H.Y.*–Yundum, daily average R.H. at 14.00 hrs. Rainfall (Inches) Average monthly precipitation. *Horizontal lines: T.*–Tambacounda (average total annual rainfall 39·5 inches); *vertical lines: Y.*–Yundum (average annual rainfall 51·0 inches).

The only meteorological station in Gambia is situated at Yundum in the coastal region but meteorological information of inland areas can be obtained from data collected at Tambacounda in Senegal, near to the eastern extremity of Gambia. The meteorological data available (Meteorological Office, London, 1958) were obtained by standard apparatus so the temperature and humidities at ground level, or indeed the soil itself, which influence earthworm ecology and behaviour, are unknown. Nevertheless, the data recorded (Text-fig. 1) provide a useful guide to the general conditions experienced and it can be readily seen that Tambacounda is hotter and drier than Yundum. Clearly the rainfall pattern largely governs the climate of the region with the rate of precipitation being a more important factor than the duration of the rainy season in affecting the humidities and temperatures of the two areas.

The air temperatures at Yundum and Tambacounda are of especial interest because they straddle the temperature ranges which contain critical thresholds in earthworm physiology. El-Duweini & Ghabbour (1965*a*) investigated the effect of temperature on the behaviour of Egyptian material of the tropical earthworm *Pheretima californica* and of the northern temperate species *Allolobophora caliginosa*, their results are summarized in Text-fig. 2 in relation to the air temperature data derived from Text-fig. 1. It can be seen that the average daily temperatures recorded at Yundum are similar to the temperature preferences of *Pheretima californica* and near to the upper limit of that of *Allolobophora caliginosa* whereas the average daily temperatures at Tambacounda (also the monthly maxima at Yundum) not only exceed the temperature preferences of both of these worms but also the onset of thermal death.

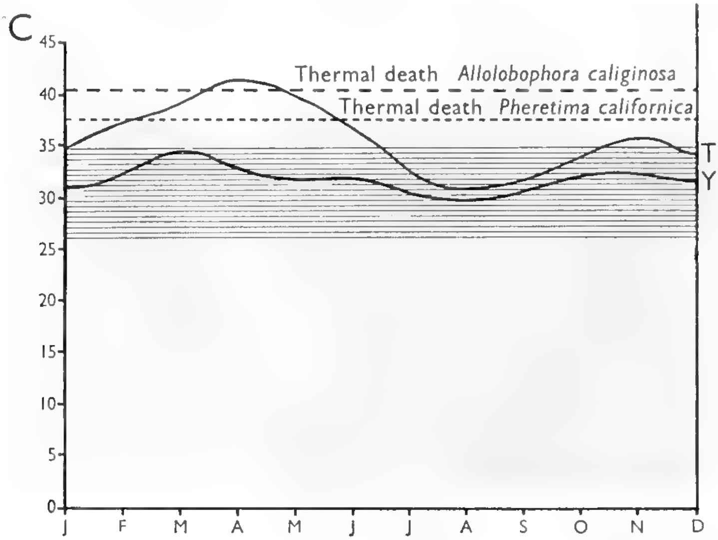

FIG. 2. Comparison of the average daily air temperatures at *T.* (Tambacounda) and *Y.* (Yundum) with earthworm thermal thresholds showing lethal temperatures (dry heat) and thermal preferences, (based on data from El-Duweini & Ghabbour). *Stipple:* thermal preference range of *Allolobophora caliginosa*. *Shading* (horizontal lines): thermal preference range of *Pheretima californica*.

The physiology of Gambian earthworms has not yet been invsetigated but it is reasonable to assume that it will not prove to be dissimilar from that of the Egyptian worms. Although there is no information available about soil temperatures in Gambia, it is almost certain that the temperatures of the soil near to the surface will often be in excess of the shade temperatures of the air. Hence, the temperatures of the surface layers of the soil in western Gambia will be unsuitable for earthworms and species normally dwelling just below the surface will be unable to survive there.

Evelyn & Thornton (1964) sampled soils at Yundum and at Yoroberikunda which is in central Gambia between Sapu and Georgetown. They concluded that the upland soils of Gambia are very sandy with a low humus content and low fertility status. At Yundum the soil is loose and sandy and is representative of the soils of the coastal region but the soil at Yoroberikunda is more compact being a leached ferruginous soil which is typical of most inland soils. An indication of the similarities and characteristics of the two main soil types of Gambia, is provided by the data in Table 2. From the aspects of earthworm ecology and distribution, it is particularly interesting to note that there is a marked resemblance between the soil at a depth of 14–30 inches at Yundum and in the top 8 inches at Yoroberikunda.

The aridity of soil is an important factor governing earthworm distribution. El-Duweini & Ghabbour (1965*b*) showed that in soils with a low water content the degree of aridity is more important than the pH value in limiting both species and numbers of earthworms. Although the water content of a soil is dependent on a number of factors, comparisons are possible between the aridity of the soils in the two collecting areas in Gambia despite the fact that no comparative data are available of the water contents of the soils throughout the year. An indication of the differences can be obtained since the soil types and the drainage patterns are so similar that any differences in the water content may be directly correlated with the climate. The lower rainfall and the ensuing lower humidities and higher temperatures in the interior provide the clue to the greater aridity of the soil in the inland localities. Here the hazard of desiccation is greater and exists only a short distance from the River Gambia, where cocoons and the newly emerged young with limited burrowing ability which dwell near the surface are particularly vulnerable.

Attention is drawn to these dissimilarities between the temperature and the soils of the coastal and central areas because not all species of earthworms are uniformly distributed throughout the country (see below). It is probable that either the temperatures or the characteristics of the soil, or both of these factors acting in conjunction and affecting the aridity of the areas, are responsible for the restriction in the ranges of some of the species so far recorded. They could well operate in the same way that the combined effects of soil type, water content and soil temperatures influence the distribution of the European Lumbricidae (Atlavinyté, 1965).

COLLECTING TECHNIQUES AND PRESERVATION

Earthworms were collected by methods seldom employed in a tropical region. They were driven from the ground by the direct application of a dilute solution of formalin following the recommendations of Raw (1959) who found that 25 ml. of concentrated formalin added to 1 Imperial gallon (approximately 1·5 litres) of water and applied to a 4 foot quadrat (about 1·5 square metres) of soil led to the collection

TABLE 2

Soil profiles and analyses (Evelyn & Thornton, 1964)

			Mechanical Analysis				*Chemical Analysis*					
Site	*Depth in inches*	*Type and structure*	*Course sand* %	*Fine sand* %	*Silt* %	*Clay* %	*pH*	*C* %	*N* %	*C/N ratio*	*Total P p.p.m.*	*Ca/K ratio*
Yundum	0–6	Light brown loose sandy loam of single-grain to weak subangular blocky structure.	46·0	50·7	0·0	3·3	6·0	0·41	0·035	11·7	38	7·3
	6–14	Reddish-yellow structureless sandy loam.	43·8	44·2	4·7	7·3	5·9	0·29	0·044	6·6	52	3·8
	14–30	Reddish-yellow compact sandy loam of massive to weak subangular blocky structure, and slightly hard consistence.	39·8	44·5	1·4	14·3	5·7	0·25	0·037	6·8	71	2·7
	30–62	Reddish-yellow compact sandy loam, as in the 14–30 in. horizon	35·4	41·3	3·6	19·7	. .	0·21	0·035	6·0	83	13·2
Yoroberi-kunda	0–8	Light brown compact sandy loam of massive to weak subangular blocky structure and slightly hard consistence	43·8	46·5	1·6	8·1	5·7	0·21	0·033	6·4	52	9·8
	8–25	Reddish-yellow very compact sandy loam of very weak polyhedral structure and hard consistence.	38·2	45·0	5·6	11·2	5·5	0·12	0·033	3·6	68	10·2
	25–35	Reddish-yellow clay of massive structure and hard consistence.	1·5	17·5	12·4	68·6	5·6	0·12	0·031	3·9	107	15·0

of a large percentage of the earthworms present in the plot. The formalin extraction method proved suitable for collecting in many localities in Gambia; on two occasions samples were obtained by digging near to plots subsequently sampled by the formalin method but the results from hand-sorting proved inferior. The disadvantage of using the formalin method in a region where water is scarce is the need to carry large water containers when collecting some distance from wells and rivers.

When the earthworms were expelled from the ground they were narcotized by being placed in a 1% solution of Propylene Phenoxetol. Usually 5–10 minutes immersion was sufficient for complete relaxation and narcosis, depending on the size of the specimen. The worms were then transferred to a 4% solution of formalin for killing and fixing. After 24 hours they were removed from the fixative and preserved in a 1% solution of Propylene Phenoxetol.

The 1% solution of " Phenoxetol " was prepared following the procedure recommended by Owen & Steedman (1956). A " stock " solution, i.e. a 20% solution in alcohol, was prepared in advance and the " Phenoxetol " was taken into the field in this dilution, thereafter, the 1% solution of " Phenoxetol " was prepared when required. It was found when travelling that the chief advantages of " Phenoxetol " over alcohol are that loss by evaporation is negligible and that " Phenoxetol " is not subject to the same rigorous fire or customs and excise regulations.

The specimens reported below were later transferred to a 1% solution of preserving " Phenoxetol " (β-phenoxyethylalcohol) and they are currently in a better condition than specimens which have been preserved in 80% alcohol for the same period. The septa, for example, have remained supple and other delicate structures are not brittle which so often happens to tissues in other preservatives. Moreover, the animals are still in a relaxed state and can be manipulated. The body pigments at first retained their colours but after the first year, although stored in the dark, the colours faded and the specimens became the usual grey-straw colour of alcohol preserved specimens. (" Phenoxetol " is manufactured by NIPA Laboratories Ltd, Treforest Trading Estate, Pontypridd, Glamorgan, Great Britain.)

RESULTS

Nearly 2,500 earthworms were collected in Gambia but only 698 were subsequently studied taxonomically and added to the collections of the British Museum (Natural History), London, S.W.7. Details of the latter provide the basis of this report. The remainder of the specimens were found to be immature and unsuitable for taxonomic study. One result of the collection containing a high proportion of indeterminate, juvenile specimens has been that it has not proved possible to analyse the earthworm populations in the localities investigated.

A summary of the identified specimens and the localities from where they were obtained is given in Table 3. It is evident that half of the species collected have restricted distributions, *Hyperiodrilus africanus* was collected only in the coastal areas while *Omodeona proboscoides* is apparently confined to Abuko where it occurs in large numbers in the banks of the reservoir. Similarly, *Benhamia mandinka*, *B. fula*, *B. reducta* and *Chuniodrilus fragilis* were collected only in central Gambia.

TABLE 3

Numbers of identified earthworms (adults and sub-adults) from Gambia

	Coastal region					Central Gambia		
	Abuko	*Bakau*	*Brikama*	*Nyambai*	*Yundum*	*Brikama Ba*	*Sapu*	*Willigara*
Benhamia budgetti species-group*	—	—	—	2	2	23	9	87
Benhamia mandika sp. nov.	—	—	—	—	—	22	—	3
Benhamia fula sp. nov.	—	—	—	—	—	35	10	8
Benhamia reducta sp. nov.	—	—	—	—	—	—	3	—
Dichogaster ehrhardti (Michaelsen)	4	1	1	—	—	3	2	15
Dichogaster titillata sp. nov.	—	—	1	—	—	52	1	187
Omodeona proboscoides gen. et sp. nov.	30	—	—	—	—	—	—	—
Chuniodrilus fragilis sp. nov.	—	—	—	—	—	1	6	—
Hyperiodrilus africanus Beddard	42	27	14	18	78	—	—	—
TOTAL	76	28	16	20	80	136	31	300

* This species complex comprises: *Benhamia budgetti* Beddard, *B. gambiana* Beddard and *B. michaelseni* Beddard, known only from McCarthy Island which is situated in the River Gambia near to Sapu.

Although *Hyperiodrilus africanus* seems to be confined to coastal areas in Gambia and nearby Senegal where it is the common earthworm of Dakar (see Appendix), in the Congo it has also been recorded from inland localities (Omodeo, 1958 : 100). The reason for the differences in the local distributions between the two areas, may lie in the dissimilarities between the climate of the regions. The temperatures recorded in Leopoldville are closer to those at Yundum, Dakar and Lagos (the type locality) than at Tambacounda where the climate is hotter and drier. These factors could be of the greatest importance in governing the distribution of *Hyperiodrilus africanus* which dwells in the surface layers of the soil where air temperature and humidity play a major part in determining the physical environment of the worms living there. From the literature, the genus *Benhamia* would also appear to consist of coastal species (Omodeo, 1958 : 104) but the three new species described below from Gambia were recorded only from inland localities. The explanation, in this case, may be that collecting in other territories was confined in the past to the coastal regions so that collections made inland in the future will reveal the presence of several more species, some of them new, as in Gambia.

DISCUSSION

Only a small number of genera and species of earthworms were collected in Gambia and in comparison with areas further south where greater numbers have been recorded, it is evident that the terrestrial oligochaete fauna of Gambia is reduced. Few of these Gambian species have been reported from outside the territory and most appear to be endemic, many being confined to inland localities near to the River Gambia. Here they are separated by compartively arid country from those areas further to the south with the richer earthworm faunae. Under these conditions of isolation and reduced interspecific competition, speciation is favoured and the extent of the differentiation detected in the Gambian species indicates that this process has been taking place. The new genus and species *Omodeona proboscoides* shows an unusual degree of specialization among western African Octochaetinae, particularly in the reduction in the number of caliciferous glands, while *Dichogaster titillata* sp. nov. has highly developed prostatic glands. In both of these species, the amount of modification would appear to be in accord with the specializations which tend to occur in reduced, isolated populations.

The species of *Benhamia* recorded here are of especial interest not only because of evidence of their plasticity but also since among them are two species groups whose members differ morphologically only slightly from others in the same complex. The first group consists of the three taxa described by Beddard, *B. budgetti*, *B. gambiana* and *B. michaelseni* and the second comprises the two new species *B. mandinka* and *B. fula*. The restricted distributions of the members of these two groups, together with the absence of related forms of most from elsewhere, permit us to regard many of them as emergent species. The taxonomic status of the three taxa in the *budgetti-gambiana-michaelseni* group is uncertain (see p. 16) but clearly the present confused situation is indicative that speciation and change are currently taking place. Evidence that the *budgetti* element in the complex may be the stem form is largely distributional and is provided by the presence in Liberia of *B.*

robertsiana (Michaelsen) which shares sufficient characters with *budgetti* for the two taxa to be regarded as possibly synonymous (see p. 17), whereas no earthworms have so far been described from outside of Gambia with *gambiana* or *michaelseni* attributes. This being so, *budgetti* (inc. *robertsiana*) which it is morphologically stable throughout its wide range, can be regarded as undergoing a minor radiation in the basin of the River Gambia.

Only three species of earthworms with wide distributions have so far been collected in Gambia, there are the two species previously discussed, *Hyperiodrilus africanus* and *Benhamia budgetti*, and a third, *Dichogaster ehrhardti* which was originally described from Portuguese Guinea. As already mentioned, *H. africanus* is widely distributed from the interior of the Congo northwestwards along the western African coastal regions at least as far north as Dakar. Throughout its range it lives in a variety of soil and floral types which experience fairly equable temperatures. As *H. africanus* is the only species of earthworm from Gambia with such a wide distribution, it can be regarded as forming a separate element in the oligochaete fauna of the country. The other two widely distributed species, *B. budgetti* and *D. ehrhardti*, form a second element. Both are species of the grasslands of western Africa but their distributions are wider than those of the remaining species collected. This last group of species forms a third element in the earthworm fauna of Gambia, it comprises those species which have been recorded only from in the basin of the River Gambia where they are apparently endemic.

CLASSIFICATION

It is necessary to comment on the classification of the non-Eudrilid earthworms recorded below. The generic criteria which are adopted were proposed by Omodeo (1955) and later employed by him in his report on the Oligochaeta from Mount Nimba (1958). One result of following this author has been the necessity to describe a new genus, *Omodeona* (see below). However, the suprageneric categories proposed by Omodeo are not accepted and instead the higher classification follows the system proposed by Gates (1959). The decision to accept Omodeo's generic criteria yet follow Gate's classification, rests on the results of a re-appraisal of 29 Megascolecoid genera (Megascolecidae *sensu* Stephenson, 1930) by using taxonometric techniques (Sims, 1966). It was found, for example, that the genera *Benhamia* and *Millsonia* were sufficiently dissimilar from *Dichogaster* that all three should be regarded as distinct, which is in agreement with Omodeo. Whereas the genera in the families as defined by Gates, occurred together in a vector diagram while those included in Omodeo's higher catagories were apart (as were many of those in the classification proposed by Lee (1959) arising from studies on New Zealand earthworms).

One interesting aspect of the results of the computer investigation was that in the vector diagram the genera of the Megascolecidae *sensu* Gates (1959), were somewhat isolated from all of the other genera assessed. In reporting this comparative isolation no conclusions were reached about the status of each group of genera, that is, the hierarchical categories to which the groups could be assigned. However, in view of the isolation of the Megascolecidae *s.s.* and the undoubted similarity of both of the other groups of genera investigated, I am now of the opinion that the latter cannot be divided into separate families as Gates proposed. Accordingly, their status is now modified although Gates's criteria of classification are accepted.

KEY CHARACTERS TO THE CLASSIFICATION OF THE MEGASCOLECOID EARTHWORMS (MODIFIED AFTER GATES, 1959)

Family **MEGASCOLECIDAE**	Prostatic glands racemose in structure, usually in segment *xviii*.
Family **ACANTHODRILIDAE**	Prostatic glands tubular in structure, situated in either or both segments *xvii* and *xix*.
Subfamily **OCNERODRILINAE**	Calciferous glands in segment *ix*, or, *ix* and *x*.
Subfamily **ACANTHODRILINAE**	Calciferous glands, arrangement non-Ocnerodriline. Execretory system holonephridial.
Subfamily **OCTOCHAETINAE**	Calciferous glands, arrangement non-Ocnerodriline. Excretory system meronephridial.

All of the non-Eudrilidae so far collected in Gambia have tubular prostatic glands, paired caliciferous glands situated between segments *xiv* and *xvii* and meronephridial excretory systems; they are, therefore, assigned to the family Acanthodrilidae, subfamily Octochaetinae. (The non-Eudrilids in a collection of earthworms from Ghana were similarly classified (Sims, 1965) although no explanation was provided in that report of the criteria for recognizing the higher groups).

TAXONOMY

Family **ACANTHODRILIDAE**

Subfamily **OCTOCHAETINAE**

Benhamia budgetti species-group

(Plates I & II)

Benhamia budgetti Beddard, 1900, *Proc. zool. Soc. Lond.*, **1900** : 653.—McCarthy Island, central Gambia.
Benhamia gambiana Beddard, 1901, *Proc. zool. Soc. Lond.*, **1901** (2) : 210.—McCarthy Island, central Gambia.
Benhamia michaelseni Beddard, 1901, *Proc. zool. Soc. Lond.*, **1901** (2) : 213.—McCarthy Island, central Gambia.
? *Dichogaster robertsiana* Michaelsen, 1922, *Cap. zool.*, **1** : 18.—Robertsport, Liberia.

Forest floor, Nyambai Forest Reserve, 23 Sept. 1964; 1 clitellate, 1 aclitellate specimens.

Under groundnut mulch, nursery plots, Forestry Department, Yundum, 28 Sept. 1964; 2 clitellate specimens.

Semi-flooded forest, edge of Jahkali Swamp, Sapu, 3 Oct. 1964; 3 clitellate, 6 aclitellate specimens.

Sides of paths through groundnut fields, Brikama Ba, 5–7 Oct. 1964; 8 clitellate, 15 aclitellate specimens.

Sides of paths through groundnut fields, Willigara, 7 Oct. 1964; 21 clitellate, 66 aclitellate specimens.

DESCRIPTION. *External characters.* Non-regenerating worms measure between 192 and 286 mm. in length and 4–5 mm. in diameter anteriorly and 3 mm. posteriorly. The number of segments varies between 166 and 218. In life the worms are a cream-flesh colour ventrally, a more brownish-flesh dorsally in the pre-clitellar region and a very dark green dorsally in the intestinal region; the clitellum is almost black with a greenish hue. Preserved specimens are medium brown above in the intestinal region, the clitellum is dark brown, while the remainder of the body is a pale straw colour. (In regenerating individuals, the regenerating portion is paler than elsewhere). The cuticle has a slight rose-green iridescence which gives a copper-like lustre, there are additional violet reflections around each dorsal pore. The first dorsal pore is usually situated in furrow 13/14, occasionally in furrow 14/15 or even in 19/20 or 20/21 when the dorsal pores are occluded in the clitellar region. The prostomium is prolobous and somewhat inclined to the pro-epilobic condition. There is some feeble triannulation in the pre-clitellar region where the setal rings are sometimes slightly raised. The clitellum is saddle-shaped, dorsally it extends from segment $\frac{1}{2}$*xiii* to *xx* ($7\frac{1}{2}$ segments) and ventrally from segment *xiv* to $\frac{1}{2}$*xx* ($6\frac{1}{2}$ segments). The ventral border is in setal line *b* except in the segments containing the genital field where it is edged by the seminal grooves.

The setae are closely paired on the ventral surface. The setal formula at segment *ix* is $aa : ab : bc : cd = 2{\cdot}5 : 1 : 2{\cdot}5 : 1$ and $dd = \frac{2}{3}$ circumference, at segment *xxv* it is $3{\cdot}5 : 1 : 3 : 1$ and $dd = \frac{3}{4}$ circumference.

The male pores are paired on segment *xviii* midway between the setal lines *b* and *c* where they discharge into slightly convex, paired seminal grooves which join the prostatic pores of their respective sides. The prostatic pores are paired in segments *xvii* and *xix* and lie midway between setal lines *a* and *b*. Paired penial setae are present on segments *xvii* and *xix* in setal line *a*. The penial setae of most specimens are 2·8 mm. long and taper from $80\,\mu$ in diameter proximally $40\,\mu$ in diameter distally (Text-fig. 3a (1)). These penial seta have a simple outline, the only ornamentation being the presence of small pits in the region of the distal end. (Unless examined under very high-power, the pits may be mistaken for small spines). Penial setae of a few specimens are smaller with a digitiform tip to a slightly swollen distal end (Text-fig. 3a (2)).

Paired female pores are present on $\frac{1}{3}$*xiv* within setal lines *aa*, each pore is situated approximately $\frac{1}{2}$*ab* medially to setal line *a*.

The spermathecal pores are paired in furrows 7/8 and 8/9 and lie in setal line *b*.

The genital field is sunken only in the more fully mature individuals. It consists of six, low transverse ridges bounded laterally by the seminal grooves, the anterior ridge is developed from the posterior region of segment *xvii* while the posterior ridge is formed from the anterior region of segment *xix*. Genital papillae are indistinct; single, median ventral papillae are present in varying combinations in furrows 13/14, 14/15, 21/22 and 22/23, sometimes these hinder papillae are situated slightly anteriorly to the furrow near to the posterior borders of segments *xxi* and *xxii*. Occasionally a broad, median ventral papilla, or two closely paired papillae, may be present on segment *xx*. Paired papillae are present in furrows 16/17 (sometimes), 17/18 and 18/19 where they are situated in setal line *a*, there is also a pair on segment *xviii* in setal line *b*.

Internal characters. The first septum is 4/5 and all of the anterior septa to 12/13 are thickened, 13/14 being only slightly less so. The first four septa, 4/5–7/8, are strongly conical, septa 8/9 to 12/13 are moderately conical while septum 13/14 is only slightly so.

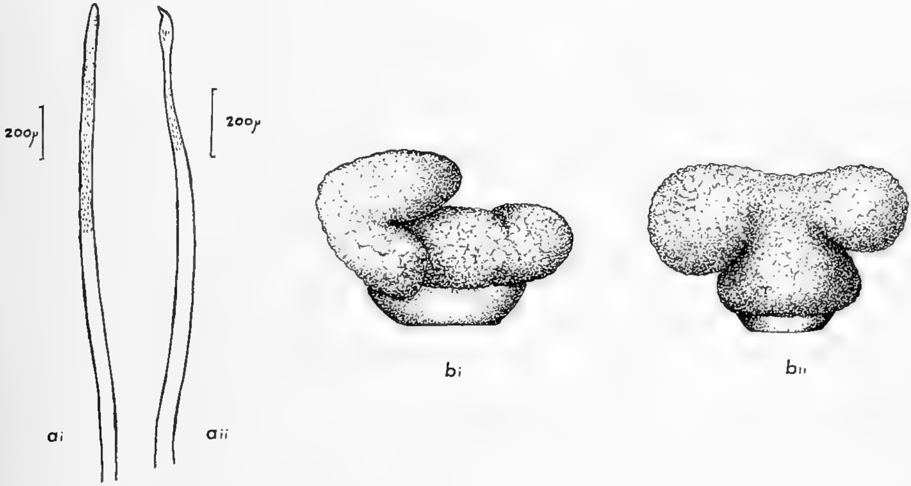

Fig. 3. *Benhamia budgetti* species-group. (a) Distal ends of penial setae: (1) *michaelseni*-type; (2) *budgetti*-type. (b) Spermathecae (medio-dorsal view): (1) *michaelseni*-type; (2) *budgetti*-type.

The pharynx extends posteriorly to septum 4/5. There are two gizzards, the anterior gizzard in segment *v* is slightly smaller than the posterior gizzard in segment *vi*. Each gizzard superficially resembles a mammalian heart, anteriorly there is a double, thin-walled " auricular " region and posteriorly a double, highly muscular " ventricular " region. In contracted individuals, the thin-walled anterior half lies partly dorsal to the muscular, posterior half which is inclined antero-dorsally. Numerous tendinous strands pass posterolaterally from the gizzards to the body wall throughout the oesophageal region. The oesophagus extends to segment *xvii* and the intestine begins in segment *xviii*. The anterior region of the intestine is swollen and its bulk displaces septum 17/18 anteriorly so that superficially the contents of segment *xvii* appear to have been suppressed. The swollen region is thickened inter-segmentally to septa 25/26–28/29. The two hindermost intersegmental thickenings tend to coalesce to form the posterior limit of a crop-like region. The typhlosole arises as a low ridge in segment *xviii* but it increases in height until by segment *xxiv* it is equal to about half the internal diameter of the intestine.

Calciferous glands are paired in segments *xiv*, *xv* and *xvi*. The anterior pair is slightly smaller and paler than the others, the posterior pair being the darkest in colour.

The dorsal blood vessel is well-developed between the posterior gizzard and segment *xxx*. A pair of commissural vessels are present in each segment from *vi* to *xii*. The anterior pair is small but each successive pair is larger than the preceding pair until segment *x*. In segments *x*, *xi* and *xii* they are functional as contractile, lateral hearts.

There is a holandric arrangement of the testes which are apparently free. The funnels are large. The seminal vesicles are poorly developed in segments *xi* and *xii*, the anterior pair being particularly small The vasa deferentia were not seen. The prostatic glands are paired in segments *vxii* and *xix* and although they are moderately sized, their bulk slightly displaces the adjacent septa posteriorly. Each gland is regularly convoluted but not coiled; an ectal muscular portion, equal in length to about one half of the length of the glandular portion of the prostate, passes into the ventral parietes postero-ventrally to the muscular sheath of a penial setal bundle.

The ovaries which are paired in segment *xiii*, are small. They are pendent from the posterior surface of septum 12/13 almost ventrad to the oesophagus. The funnels were not seen.

The spermathecae are paired in segments *viii* and *ix*. Each spermatheca consists of a squat, muscular ectal portion (the " duct ") and a large, irregular, ampulla (Text-fig. 3b). The ampulla is divided into a central portion with a lateral lobe on each side. The lobes may be low, or one or both of them may be developed into flexed digitiform processes.

The excretory system is meronephridial A few nephridia can be seen in the anterior region of the body where they are thinly scattered around the posterior region of each segment near to where the septa join the parietal wall. In segments *x* to *xvi* they are more numerous and throughout the intestinal segments they are large and completely cover at least the posterior half of the parietal wall in each segment.

REMARKS. The specimens listed above are only tentively identified due to an uncertainty which became apparent as work progressed, about the validity of the characters which Beddard employed to separate *budgetti*, *gambiana* and *michaelseni*. The three taxa were named on a series from McCarthy Island which Beddard at at first described as *budgetti*, but split in the following year when he separated the other two species. They cannot, however, be recognised from the original descriptions of their internal characters but apparently only on their external morphology. Unfortunately even these differences prove to be of little value when examining worms in series. The specimens reported here increase the problem of identification as their external characters are present in various combinations and do not always coincide with the patterns which are diagnostic of any of the three taxa, in addition these characters are mainly imperfectly developed. Generally, however, most of the specimens tend towards the condition described for *michaelseni*, twelve tend towards *budgetti* and only two have some resemblance to *gambiana*. Even so, the differences are slender and incomplete.

Difficulty of identification is increased by the fact that out of the three type series, only one complete, but dissected, specimen and a few fragments of a second have survived and do not help fix the identity of the taxon which they represent. The specimens are labelled as the types of *Benhamia budgetti* but in the pattern and the number of the genital papillae, the complete specimen approaches the description of *gambiana*, while a penial seta examined matches the illustration of a penial seta of *michaelseni*; the specimen, however, does agree with the description of *budgetti* in size and in the number of segments. In view of the discrepancies between the surviving type specimen of *budgetti* and the description and especially the variation present in the series reported here, it seems advisable not to merge the three taxa but to regard them as a closely related species group until further collecting provides evidence for elucidating the problem.

In all of the specimens reported here there is a basic *gambiana*-like pattern of the genital papillae in the genital field although most specimens have additional papillae arranged in a *michaelseni*-like manner. Beddard did not record the presence of genital papillae within the genital fields of *budgetti* or *michaelseni* but only mentioned the presence of swellings. This omission suggests that his types were not fully mature. Unfortunately the same would appear to be true of the present specimens because the genital fields are poorly developed and the genital papillae are difficult to see.

The possibility that Beddard's material was not fully adult may account for the discrepancy between the form of the penial seta removed from the type and that originally figured. Replacement penial setae commonly become successively more ornate as a worm matures and so it could be with *budgetti*, the *michaelseni*-type of penial seta preceding the *budgetti*-type. The alternative condition with more than one kind of penial seta present at the same time, is unlikely as this condition has not so far been recorded in *Benhamia*; only one kind of seta, the *michaelseni*-type, was found in all of the new specimens examined.

The problem of establishing the characters by which *budgetti* can be distinguished prevents the easy recognition of other taxa which may be synonymous. Nevertheless, the general characters of *budgetti* agree sufficiently with the description of *Dichogaster robertsiana* Michaelsen from Liberia that it seems reasonable to suggest that these two taxa may be synonymous. The illustrations of the penial setae in particular, are almost identical There are a few discrepancies and the most readily evident is the absence of genital papillae from *robertsiana* but the difficulty experienced in seeing the papillae of *budgetti* indicates that too much importance cannot be attached to their reported absence in the former.

Omodeo (1958 : 41) recorded four specimens from the Ivory Coast which he identified as *Benhamia robertsiana* var. These specimens differ on description from the worms listed above mainly in the presence of an annular clitellum, the number of genital papillae and the shape of both the spermathecae and the penial setae. These differences indicate that the Ivory Coast specimens may possibly represent a different, probably un-named, species. However, as the identity of *robertsiana* Michaelsen is not entirely certain. I do not propose to separate this Ivory Coast material. Clearly the solution to this problem must await the collection of further specimens from the Ivory Coast, Liberia and Gambia, particularly the last from where more fully mature, topotypical material is required.

Benhamia mandinka sp. nov.

(Plate III)

Sides of paths through fields of maize and groundnut, Brikama Ba, 5–7 Oct. 1964; Syntypes: 6 clitellate, 16 aclitellate specimens. B.M.(N.H.) Reg. No. 1966.30.129/150. [Schizosyntype (slide) 1966.30.151].

OTHER MATERIAL: Sides of paths through groundnut fields, Willigara, 7 Oct. 1964; 3 aclitellate specimens.

DIAGNOSIS. *External characters.* Length 102–122 mm., diameter 2–3 mm. Segments 148–160. Colour: in life, anterior region pink, clitellum yellow pink, unpigmented posteriorly. First dorsal pore 18/19. Prolobous. Setae ventral, closely paired. Clitellum saddle-shaped. Genital setae absent from region of spermathecal pores, penial setae present. Male and prostatic pores combined *xvii*, paired midway between *b* and *c*. Female pores closely paired *xiv* within ***aa***. Spermathecal pores paired in furrow 8/9 near to *a* within *aa*. Genital papillae as single, transverse ridges *ix–xvi* and *xviii*, *xix* mainly extending to *cc*, paired genital papillae *xvii* bearing penial setae.

Internal characters. Septa 4/5–8/9 conical, 5/6–12/13 thickened. Gizzards *v*, *vi*. Calciferous glands paired *xiv*, *xv*, *xvi*. Intestine begins *xvii*, anterior region slightly dilated *xix–ixl* terminated by thickened rings 39/40 and 40/41. Typhlosole *xx–xl* width equal to internal diameter of intestine, more posteriorly width equal to $\frac{1}{4}$ diameter of intestine. Lateral hearts *x–xii*. Holandric, testes paired in testes sacs *x*, *xi*; seminal vesicles small, granular *xi*, *xii*. Prostatic glands paired *xvii*, extending into *xviii*, *xix*. Ovaries paired *xiii*. Spermathecae paired *ix*; ampullae thin-walled, duct thick -walledand spherical with two long digitiform, ental diverticula. Meronephridial.

DESCRIPTION. *External characters.* The length of the worms in the series varies between 102 and 122 mm., and the diameter between 2 and 3 mm. (3–4 mm. in the clitellar region). There are 148–160 segments in the clitellate specimens. The anal region, comprising the last 15 or so segments, is slightly swollen in most specimens. In life the colour of the intestinal region is brownish flesh, the anterior region a bright pink and the clitellum is yellow pink; in presperved specimens the intestinal region is a pale greyish flesh, the anterior region whitish flesh and the clitellum is purple brown. The cuticle has a slight green-pink iridescence. The prostomium is broad and prolobous. The first dorsal pore occurs in furrow 18/19. The ventral surfaces of the anterior segments are moderately trianulate; segments in the intestinal region are faintly pentannulate. The ventral surface between setal lines *cc* of the third annulus of segments *ix* to *xix* is raised and forms a genital ridge (see below). The body is often swollen in the anterior intestinal region, circa *xx* to *xxxiv*.

Setae are situated ventrally and are closely paired. The setal formula (*aa* : *ab* : *bc* : *cd*) at segment *ix* is 5 : 1 : 3 : 1 and $dd = \frac{3}{4}$ circumference; at segment *xxv* it is 4 : 1 : 4 : 1 and $dd = \frac{2}{3}$ circumference while at segment *c* the formula is 4 : 1 : 3 : 1, $dd = \frac{3}{4}$ circumference. The setae *cd* are absent from the clitellar region.

Setae in the region of the spermathecal pores are unspecialized. Paired penial setal bundles are present on segment *xvii* with each bundle usually comprising two slender setae about 1·3 mm. in length (Text-fig. 4a). Each seta tapers distally, about 0·2 mm. from the distal end it becomes slightly swollen and serrated, it is tipped with a small tooth-like process. The laterally directed surface of the swollen distal portion of each seta is ornamented with a large number of very small, distally directed ridges.

The clitellum is saddle-shaped and extends ventrally to setal line *c* on segments ½*xiii* to *xviii* (5½ segments).

The male terminalia have a microscolecine reduction with combined paired male and prostatic pores on segment *xvii*. The pores are situated near to furrow 17/18 midway between setal lines *b* and *c* where they are partly obscured anteromedially by paired genital papillae which bear the penial setae.

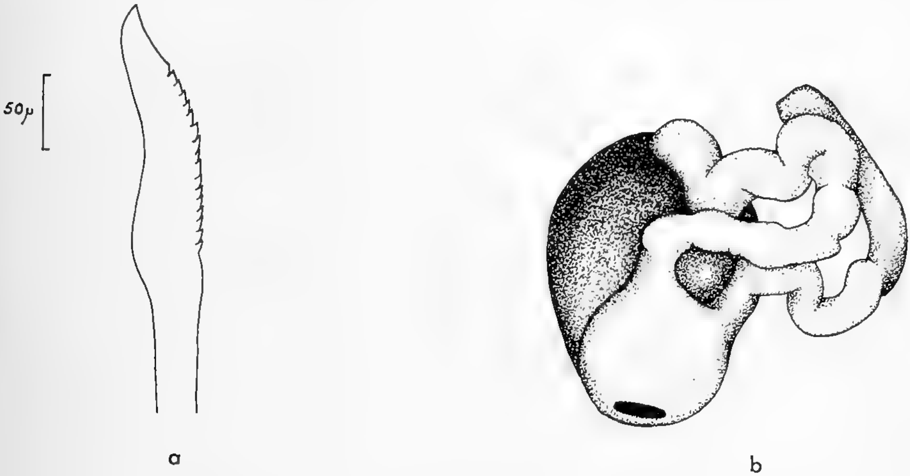

FIG. 4. *Benhamia mandinka* sp. nov. (a) Distal end of penial seta. (b) Spermatheca (ventral view).

The female pores are paired on segment *xiv* and are seen on the ventral surface as two, short longitudinal slits situated on the anterior part of the second annulus only a short distance (½*ab*) within the setal lines *aa*.

The spermathecal pores are large, they are paired and lie in furrow 8/9 slightly within the setal lines *aa*. Each pore is situated within a lateral slit extending across setal lines *ab*. In fully adult specimens, the body wall in the region of the slits is raised and the two slits join medially so that superficially there appears to be a single, median ventral pore. The raised, swollen region is formed by the median-ventral portion of the body wall being raised in both the posterior half of segment *viii* and the anterior half of segment *ix*.

Genital papillae are present as single, median-ventral transverse ridges on segments *ix* to *xvi* and on *xviii* and *xix* (Plate III); the paired papillae in segment *xvii* each bear the penial setae. The majority of the papillae, or ridges, are confined between setal lines *cc* but those in segments *xvi* and *xviii* extend further laterally.

Internal characters. The first septum is 4/5, septa 5/6 to 8/9 are moderately thickened while septa 9/10 to 12/13 are only slightly thickened. Septa 4/5 to 8/9 are strongly conical.

The pharynx is long and slender. Two gizzards are present, one in each of segments *v* and *vi*. The anterior gizzard is highly muscular and campanulate in shape with the broader end leading from the pharynx and the narrower end passing into the posterior gizzard. The hinder gizzard is more oval in shape and only the posterior half is strongly muscularized.

Paired calciferous glands are present on the oesophagus in segments *xiv*, *xv*, and *xvi*, the anterior pair is the smallest and the posterior pair the largest.

The intestine begins in segment *xvii* and gradually increases in diameter in the first three or four segments. There is a dilated anterior region between segments (*xix*) *xx* to *ixl* with slightly thickened intersegmental rings. A strongly thickened ring, with a reduced diameter occurs at both intersegments 39/40 and 40/41, these rings mark the posterior end of the dilated, crop-like, region; thereafter the intestine has a smaller diameter and is undifferentiated. The typhlosole arises from the mid-dorsal line of the intestine in segment *xx*. It is large, single and ribbon-like. In the dilated anterior region of the intestine its width is nearly equal to the internal diameter of the intestine and it causes the lumen of the gut of this region to be divided into two longitudinal chambers. More posteriorly, after segment *xl*, the typhlosole is narrower and its width is equal to only one-quarter of the diameter of the undifferentiated intestine.

The condition of the testes is holandric. Each pair of testes is enclosed by a thin, membraneous, median-ventral, suboesophageal sac which lies against the posterior face of the anterior septum of the segment. The seminal vesicles are paired in segments *xi* and *xii*, they are small and granular in appearance. The vasa deferentia which are slender and semi-transparent, are paired on each side. They pass posteriorly to segment *xvii* where each pair forms a loop on the parietal wall. There the vasa deferentia pass laterally then medially over the antero-dorsal surface of the ectal portion of the prostatic duct of their side and with it enter into the parietes.

Only one pair of prostatic glands is present, they are tubular in structure and enter the parietes in segment *xvii*. The glandular, ental portions of the glands are coiled, usually in segments *xvii* to *xix* or even as far posteriorly as segment *xxi*. The muscular, ectal duct of each gland is confined to segment *xvii* where it enters the parietes near to septum 16/17. A penial setal follicle is associated with the ectal end of each prostatic duct. The follicles are small and lie transversely on the ventral parietes, they pass into the body wall immediately anteriorly to the adjacent prostatic duct.

The ovaries are paired in segment *xiii* where they are freely pendent from the posterior surface of septum 12/13 laterally to the oesophagus. The funnels are paired and small on the posterior septum of the ovarian segment. The paired oviducts in segment *xiv* pass medio-ventrally from septum 13/14 and converge towards the median ventral parietes.

One pair of spermathecae is present in segment *ix*. Each spermatheca has a short, spherical, thick-walled duct and a somewhat larger but thinner-walled ampulla. Two long, digitiform, transulcent diverticula arise from the latero-ventral surface of the ental end of the spermathecal duct. The diverticula are loosely coiled but when they are unravelled they are found to be about three times longer than the length of the duct although their diameter is only about one-fifth (Text-fig. 4b).

The excretory system is meronephridial. The nephridia are comparatively large but are thinly distributed. They are absent from the parietal wall in the pre-clitellar region, two to four are present in segments *xiv* to *xviii* thereafter, throughout the intestinal region, six to eight are present on the parietes of each segment.

REMARKS. See the " Remarks " on p. 22 following the description of the next species.

Benhamia fula sp. nov.

(Plate IV)

Sides of paths through fields of maize and groundnut, Brikama Ba, 5–7 Oct. 1964; Syntypes: 8 clitellate, 27 aclitellate specimens. B.M.(N.H.) Reg. No. 1966.30.155/189 [Schizosyntype (slide) 1966.30.190].

Sides of paths through fields of groundnut, Willigara, 7 Oct. 1964; 2 clitellate, 6 aclitellate specimens.

Semi-flooded light woodland at edge of Jahkali Swamp, Sapu, 3–5 Oct. 1964; 6 clitellate, 4 aclitellate specimens.

DIAGNOSIS. *External characters.* Length 98–133 mm., diameter 2 mm. (3 mm. at clitellum). Segments 158–183. Unpigmented posteriorly, in life anterior region bright pink, clitellum yellow pink. First dorsal pore 18/19. Prolobous. Setae ventral, closely paired. Clitellum saddle-shaped. Genital setae absent from region of spermathecal pores, penial setae present. Male and prostatic pores combined *xvii*, paired midway between *b* and *c*. Female pores closely paired *xiv* within *aa*. Spermathecal pores paired in furrow 8/9 within *aa* but near to *a*. Genital papillae as single transverse ridges *xii–xvi* and *xviii–xx* mainly between *cc*, paired genital papillae *xvii* bearing penial setae.

Internal characters. Septa 4/5–8/9 conical, 5/6–12/13 thickened. Gizzards *v*, *vi*. Calciferous glands paired *xiv*, *xv*, *xvi*. Intestine begins *xvii*; anterior region, *xix–xxxiv*, slightly dilated extending to thickened rings 34/35 and 35/36. Typhlosole *xx–xxxv* width equal to internal diameter of intestine, more posteriorly width equal to ¼ diameter of intestine. Lateral hearts *x–xii*. Holandric, testes paired in testes sacs in *x*, *xi*; seminal vesicles small, granular *xi*, *xii*. Prostatic glands paired *xvii*, extending posteriorly through four or more segments (*xvii–xx*). Overies paired *xiv*. Spermathecae paired *ix*; ampullae thin-walled, duct thick-walled and spherical with two long, digitiform, entral diverticula. Meronephridial.

DESCRIPTION. A full description of this species is not provided as it is similar to *mandinka* from which it may be distinguished by the following attributes (the corresponding characters of *mandinka* are given for comparison in parenthesis): *External characters.* Length 98–133 mm. (102–122 mm.). Segments 158–183 (148–160).

Genital papillae present as single, median ventral, transverse ridges on segments *xii–xvi* and *xviii–xx* (*ix–xvi* and *xviii*, *xix*).

Internal characters. The anterior region of the intestine is slightly dilated, this specialized region is terminated by thickened intersegmental rings at intersegments 34/35 and 35/36 (39/40 and 40/41).

REMARKS. Only two species of *Benhamia* (sensu Omodeo) have previously been described with a single pair of prostatic pores discharging on segment *xvii*. The first, *hupferi* (Michaelsen, 1891), which is a larger worm than either *mandinka* or *fula*, has the male and spermathecal pores situated in different positions relative to the setae and has specialized setae in the region of the spermathecal pores. The second, *stockhauseni* (Michaelsen, 1913), is also a larger worm but, among other differences, it has an annular clitellum and no genital ridges on the ventral surface, however, the prostatic glands are similar to those of *mandinka* (Omodeo, 1958 : 43). Generally the Gambian worms differ externally from these other species by the pattern of the genital ridges and internally by the characteristic spermathecae with their long diverticula* and the broad typhlosole in the expanded anterior region of the intestine. In turn, they can be distinguished from each other by the characters given above.

The two earthworms, *mandinka* and *fula*, are regarded as representing separate species because although individuals of both come from the same samples none with intermediate features or a combination of the characters of both, has been found. There is, however, the possibility that the two taxa may represent a single dimorphic species but I believe that it is better to regard the two taxa as distinct species.

It is possible that the worms of both species are protandrous as there is a seemingly precocious development of the male organs. Most individuals collected are aclitellate and have small ovaries and spermathecae yet the genital ridges, or papillae, and prostatic glands are fully developed and the seminal vesicles full of developing sperm.

Benhamia reducta sp. nov.

(Plate V)

Semi-flooded forestland, edge of Jahkali Swamp, Sapu, 5 Oct. 1964. Syntypes: 3 clitellate specimens. B.M.(N.H.) Reg. No. 1966.30.209/211 [Schizosyntype (slide) 1966.30.212].

DIAGNOSIS. *External characters.* Length 42–60 mm., diameter 1–1·5 mm. Segments 116–137. Clitellum bright orange in life, pale orange in preserved specimen; body unpigmented., Epilobous. First dorsal pore 20/21. Clitellum annular, *xiii–xix* (7 segments). Setae ventral closely paired. Male and prostatic pores combined, single, median ventral *xvii*. Penial setae present. Female pores small *xiv*, closely paired within *aa*. Spermathecal pore single, median ventral 8/9. Genital papillae absent.

Internal characters. Septa 5/6–10/11 conical, thin; 12/13 and 13/14 join laterally. Gizzards *vii*, *viii*. Calciferous glands paired *xiv*. *xv*, *xvi*. Intestine begins *xviii*, typhlosole arises *xix*. Paired lateral hearts *xi*, *xii*. Metandric. Prostatic glands tubular, paired *xvii* (ental portions in *xviii*). Ovaries paired *xiii*. Spermatheca single *ix*; duct squat with paired lateral ental diverticula; ampulla large, simple. Meronephridial.

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* It is interesting to note that in *braunsi* (Michaelsen, 1895 : 27) from Sierra Leone, the spermathecae resemble those of *mandinka* and *fula*. However, *braunsi* differs from these two new species in having among other characters, a balantine reduction of the male terminalia.

DESCRIPTION. *External characters.* The lengths of the syntypes vary between 42 and 60 mm., the anterior diameters between 1–1·5 mm. and the posterior diameters 0·75–1 mm. In one specimen there are 116 segments (last 6 segments regenerating) in another 125 (last 10 segments regenerating) and in the third, 137 segments. The cuticle has a slight yellow-green iridescence. The clitellum is bright orange in life but pale orange in preserved specimens, otherwise the body is unpigmented. The prostomium is broad and epilobous; the peristomium is slightly cleft dorsally. The first dorsal pore occurs in the first post-clitellar, furrow i.e. 20/21. The clitellum is annular, *xiii–xix* (7 segments) and the body wall of segment *xiii* not so intensively pigmented as the remainder of the clitellum. At both ends of the clitellum the body wall is constricted and the external segmentation is difficult to determine especially anteriorly where much of segment *xiii* has been suppressed.

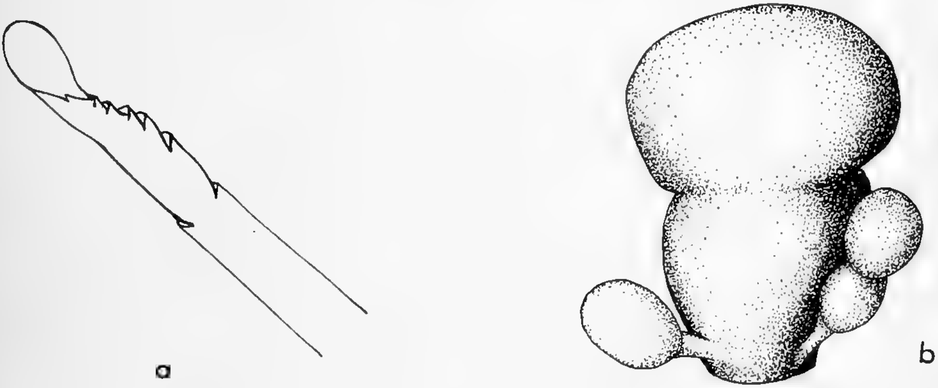

FIG. 5. *Benhamia reducta* sp. nov. (a) Distal end of penial seta. (b) Spermatheca (dorsal view).

The setae are very small, ventrally situated and closely paired; they are absent from the clitellar region. The setal formula is *aa* : *ab* : *bc* : *cd*, 6 : 1 : 4 : 1; *dd* $= \frac{2}{3}$ circumference.

There is a microscolecine reduction of the male terminalia and the male and prostatic ducts discharge on *xvii* through a common, single, median ventral pore situated on a papilla. Paired penial setae are present; they are mostly smooth but serrated distally with a spatulate tip (Text-fig. 5a). One penial seta measured 540 μ in length and 15 μ in diameter. Genital papillae are absent.

The female pores are very small and inconspicuous; they are paired in setal lines *aa* on segment *xiv*. In one individual there is a slight depression in the region of the female pores with two crescentic grooves extending a short distance postero-laterally to within setal line *cd*.

The spermathecal pore is single, median ventral in furrow 8/9.

Internal characters. The first septum is 4/5. Septa 5/6–8/9 are strongly conical and septa 9/10 and 10/11 are slightly less so. The anterior septa are thickened.

A small pharynx extends posteriorly to segment *iv*. The oesophagus is undifferentiated in segments *v* and *vi* but in segment *vii* it is developed into the anterior gizzard which is separated from the posterior gizzard in the hinder half of segment *viii* by a short portion of soft-walled oesophagus in the anterior half of the segment. The gizzards are comparatively large and their bulk has led to a posterior displacement of the coelomic contents so that the posterior gizzard in *viii* lies within the parietes of segment *ix*. Three pairs of calciferous glands are present on the oesophagus, one pair occurring in each of segments *xiv*, *xv* and *xvi*. The intestine begins in segment *xviii* and the typhlosole arises in segment *xix*. The typhlosole is lamellate for the first 3 to 5 segments but for most of its length it is a simple ribbon with a width approximately equal to half of the diameter of the intestinal lumen.

Paired lateral hearts are present only in segments *xi* and *xii*.

There is a metandric reduction of the testes; the testes and funnels are paired and free in segment *ix*. There is a small pair of seminal vesicles in segment *xii*. The prostatic glands are tubular in structure and are seen as a pair of simple loops in segment *xviii*. A slender duct passes anteriorly over the lateral parietes from the ectal end of each prostate into segment *xvii* where the duct is sharply flexed and passes medially into the parietes by the ventral nerve cord. Paired penial setal bundles lie transversely on the ventral parietes in the hinder part of segment *xvii* near to septum 17/18.

A pair of ovaries are present in segment *xiii* and can be seen pendent from the posterior surface of septum 12/13 laterally to the oesophagus. Medially septa 12/13 and 13/14 are the same distance apart as other nearby septa but laterally they join together at the parietes so that when this region is dissected the ovaries are to be found within a small compartment formed by the septa. One result of this curious structure is that the paired funnels on the anterior face of septum 13/14 are so close to the ovaries that each funnel almost envelopes the ovary of its side.

A single, median ventral spermatheca is situated in segment *ix* either to the right or to the left side of the ventral nerve cord. It is a simple structure with a short wide duct and large ampulla. A pair of small lateral diverticula are present near to the ectal end of the duct, each terminates in one or two spherical chambers (Text-fig. 5b).

The excretory system is meronephridial and four pairs of nephridia are present in each segment throughout the intestinal region.

REMARKS. This is a fragile little worm which may be mistaken in the field for an Ocnerodriline species, especially as it appears to have a limnetic habitat. However, it clearly possesses all of the attributes characteristic of the genus *Benhamia* as emended by Omodeo (1958). It is readily distinguishable from all other Benhamias by the presence of a single, median ventral, combined prostatic and male pore on segment *xvii* and a single, median ventral spermathecal pore in furrow 8/9. Internally it has features which resemble those of *Dichogaster titillata* (see below), in particular, the gizzards occur in segments *vii* and *viii* also the blood vessel leading from the prostatic gland can be clearly seen passing forward to segment *xiii* where it enters the dorsal vessel.

Dichogaster ehrhardti (Michaelson, 1898)

(Plate VI)

Balanta Ehrhardti Michaelsen, 1898, J. Hamburg wiss. Anst., **15** : 1.—Bissau, Portuguese Guinea.

Side of rice field, Brikama, 25 Sept. 1964; 21 clitellate specimens.

Grass banks, Abuko Reservoir, 29 Sept. 1964; 4 aclitellate specimens.

Semi-flooded light forest, edge of Jakhali Swamp, Sapu, 5 Oct. 1964; 2 aclitellate specimens.

Sides of path through groundnut field, Brikama Ba, 7 Oct. 1964; 1 clitellate, 2 aclitellate specimens.

Sides of paths through groundnut fields, Willigara, 7 Oct. 1964; 15 aclitellate specimens.

Under Rheum palms, edge of rice field, Bakau, 10 Oct. 1964; 1 aclitellate specimen.

DESCRIPTION. *External characters.* The worms are 79–112 mm. in length and 2–2·5 mm. in diameter having 126–166 segments (one specimen is regenerating from segment *xciv*). The body wall is unpigmented but the clitellum is a vinous brown. The cuticle is iridescent being mainly pink and green but a deep blue on the dorsal surface of the clitellum and on the anterior region of the body. The first dorsal pore occurs in a few individuals in furrow 11/12 otherwise it is to be found in furrow 12/13; in the more mature of the clitellate specimens the dorsal pores appear to be occluded in the clitellar region. The form of the prostomium is epilobous with a single, mid-dorsal, longitudinal furrow running from the posterior end of the prostomium to furrow 1/2 which is represented by only a slight transverse groove in the mid-dorsal region with the result that the peristomium appears to merge into segment *ii* (Text-fig. 6a). The peristomium is withdrawn in contracted individuals and segment *ii* may be mistaken for the first segment.

The setal formula appears to be fairly constant throughout the entire length of each worm and may be expressed as $aa : ab : bc : cd = 4 : 1{\cdot}25 : 3{\cdot}5 : 1$ and $dd = \frac{2}{3}$ circumference. The ventral setal pairs are missing from segment *xix*.

The clitellum is saddle-shaped between segments *xiv–xix* (occupying 6 segments) ventrally and ½*xii–xx* (7½ segments) dorsally. It extends towards the ventral surface as far as setal lines *ab* where there is only a diffuse region on each side to mark its borders.

There is a balantine reduction of the male terminalia. The male pores cannot be seen but they presumably discharge, together with the prostatic pores, into a short, lateral furrow passing between each penial setae and setal line *b* on segment *xix*.

Paired penial setae are present on segment *xix*, midway between setal lines *a* and *b*. Usually there are 4 to 5 penial setae at different stages of development in each bundle. The largest vary in size between 1–2 mm. in length, they are hooked with a hooded, almost gouge-like, distal end and with a series of shallow, distally directed, irregular serrations on the inner surface of the distal one-fifth of the shaft.

The serrations do not extend to the hooked end-portion of the setae (Text-fig. 6b).

There is a single female pore on segment *xiv* situated midway between setae *aa*.

The spermathecal pores are paired in furrow 7/8 and lie between setal lines *ab*.

Numerous genital papillae are present on segments *vi–viii* and *xvii–xxii*. Closely paired anterior genital papillae occur in furrow 6/7 within setal lines *aa*, while on segment *viii* there are two pairs situated in setal lines *bb*, the first is in furrow 7/8 laterally to the spermathecal pores and the second in furrow 8/9; there is a single, median ventral papilla near to the posterior border of segment *vii*. Paired posterior genital papillae occur on segments *xvii–xxii* in setal lines *bb* (in some specimens one member of a pair may be missnig); there is a single, median ventral papilla in the posterior half of both segments *xviii* and *xix*.

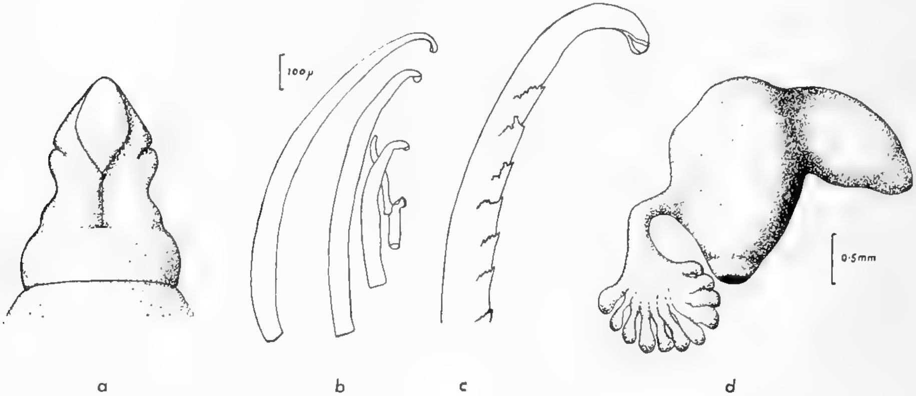

FIG. 6. *Dichogaster ehrhardti* (Mich.). (a) Anterior region showing the prostomium and the relationship between the peristomium and segment *ii*. (b) Penial setal bundle. (c) Distal end of a well-developed penial seta (very high-power). (d) Right spermatheca (dorsal view).

Internal characters. The first septum is 4/5 and septa 4/5–9/10 are conical and and thickened, septa 10/11–12/13 are moderately thickened and 13/14–17/18 only slightly thickened.

The pharynx is long but extends posteriorly only to segment *iv*. The oesophagus leads from segment *v* into the anterior half of *vi* then begins to dilate as it passes into the anterior gizzard in segment *vii*, there is a posterior gizzard in segment *viii*; both gizzards are alike. The oesophagus continues posteriorly to $\frac{1}{2}$*xix* where the intestine begins. Three pairs of calciferous glands are present in segments *xv*, *xvi* and *xvii*, the anterior pair is the smallest and the posterior pair the largest. The anterior region of the intestine is dilated in segments *xix–xxiv* to produce a series of six crop-like pouches each separated from the next by an intersegmental thickening. The internal surface of the intestine is convoluted in this region and is apparently strongly glandular. The typhlosole arises in segment *xx* and gradually increases in size until it reaches its fullest development in segment *xxiv* where its height is nearly equal to the internal diameter of the intestine thus dividing the instestine longitudinally into two chambers. The free, distal edge of the typhlosole is thickened and there is a series of thickened vertical ridges on each side, with five ridges extending to halfway up the typhlosole in each segment. There is also a pair of longitudinal ridges along the dorsal surface of the intestine lying one to each side of the typhlosole, the ridges arise in segment *xxiv* where the typhlosole first reaches its full size.

Paired lateral hearts are present in segments *x*, *xi* and *xii*.

There is a holandric condition of the anterior male organs with free testes and funnels in segments *x* and *xi*. The testes are situated on the ventral parietes on each side of the ventral nerve cord by the anterior septum of segment *x* and *xi*; the funnels are seen as large, paired rosettes on the anterior surface of the posterior septum of each testis segment and, like the testes, they are situated near to the ventral parietes by the ventral nerve cord. The seminal vesicles are paired in segments *xi* and *xii* and are glanular in appearance.

One pair of tubular prostatic glands is present. Each gland is loosely coiled in segment *xxii* and perhaps in segment *xxiii*, it passes forward into segment *xxi* becoming more muscular to form the ectal duct which continues through segment *xx* and enters into the parietes in segment *xix*. The penial setal bundles are paired in segment *xix*, each enters the parietes medially to the muscular ectal region of the prostatic duct of its side.

The ovaries are very closely paired in segment *xiii* and appear almost to be single. They are pendent from the posterior surface of septum 12/13 between the ventral surface of the oesophagus and the ventral parietes. There is no funnel on the anterior surface of septum 13/14, instead a large, single, simple, slit-like aperture ventrad to the oesophagus leads into the oviduct. The oviduct is single and median in segment *xiv*, it passes down the posterior surface of septum 13/14 to the ventral parietes where it is slightly flexed posteriorly before entering the ventral parietes.

One pair of spermathecae is present in segment *viii*. The duct of each spermatheca passes medially from the ventral parietes by septum 7/8, it is stout and has a greater diameter than the ampulla which is flexed posteriorly. A diverticulum arises from the anterior surface of the ectal end of the duct, it is short and slender and develops distally into a number of diffuse seminal chambers (Text-fig. 6d).

The excretory system is meronephridial. Twelve meronephridia are present in all segments except *x*, *xi*, *xii* where apparently there is none. In the oesophageal region they are small but in the intestinal region they are larger and form a continuous covering to the parietes.

REMARKS. The distinctive pattern of the genital papillae and the balantine reduction of the male terminalia are easily recognisable characters by which *ehrhardti* can be separated from all other species of *Dichogaster*. Internally, the form of the spermathecae and the penial setae serve as useful confirmatory features.

The worms listed above represent only the second record for this species in addition to being a new record for Gambia.

Dichogaster titillata sp. nov.

(Plate VII)

Sides of paths through groundnut fields, Willigara, 7–9. Oct. 1964. Syntypes: 128 clitellate, 59 aclitellate specimens. B.M.(N.H.) Reg. No. 1966.30.240/426 [Schizosyntype (slide) 1966.30.427].

OTHER MATERIAL: Pasture and sides of paths through groundnut fields, Brikama Ba, 5–7 Oct. 1964; 44 clitellate, 8 aclitellate specimens.

Side of rice field, Brikama, 28 Sept. 1964; 1 clitellate specimen.

Semi-flooded light forest, edge of Jahkali Swamp, Sapu, 4 Oct. 1964; 1 clitellate specimen.

DIAGNOSIS. *External characters.* Length 90–158 mm., diameter 2·5–3 mm. (clitellar diameter 3–5 mm.). Segments 129–168. Colour above green-brown in life, grey-brown preserved; below unpigmented. First dorsal pore 12/13. Epilobous. Setae small, ventral, closely paired. Clitellum *xiii–xxi* (9 segments), saddle-shaped. Male pores paired *xviii* in setal line *a*. Prostatic pores paired *xvii*, *xix*. Penial setae present *xviii*, *xix*, 11 mm. long. Female pore single, midventral *xiv*. Spermathecal pores paired 7/8, 8/9 in setal line *b*. Genital papillae present, single or very closely paired (14/15) 15/16, 19/20 (sometimes widely paired), 20/21; also one often adjacent to each spermathecal pore.

Internal characters. First septum 4/5, 4/5–8/9 conical, 9/10–12/13 less so; 8/9–16/17 thickened. Septa 17/18–29/30 conical but with apex of cone directed anteriorly. Gizzards *vii*, *viii*, partly fused. Calciferous glands paired *xv–xvii*. Intestine begins *xviii*, anterior region pouched; typhlosole arises *xix*. Lateral hearts paired *x–xii*. Holandric, testes paired in anteriorly directed septal pouches. Seminal vesicles paired *xi*, *xii*. Prostates tubular, paired *xvii*, *xix*, extending posteriorly (with penial setal sheaths) to *xxxv ixl*; convoluted. Ovaries very closely paired *xiii*. Spermathecae paired *viii*, *ix*; duct stout with long, coiled diverticulum, ampullae simple. Meronephridial.

DESCRIPTION. *External characters.* Worms in the type series are 90–158 mm. in length and 2·5–3 mm. in diameter in the intestinal region and 3–5 mm. in diameter in the clitellar region. There are 129–168 segments present in undamaged individuals. The worms are mainly triannulate but occasionally the groove separating the first from the second annulus is not clearly seen in the anterior segments and these segments may appear to be biannulate; more frequently there is a tendency for individuals to become pentannulate in the post-clitellar region and even anteriorly to this region where locally this process may be imperfectly developed to produce a tetrannulate condition. The prostomium is epilobous and the first dorsal pore occurs in furrow 12/13.

The colour of the dorsal surface is in life green-brown and in preserved specimens grey brown, the ventral surface is unpigmented. The cuticle has a green-red iridescence.

The setae are small and are closely paired on the ventral surface. The setal formula at segment *xx* is $aa : ab : bc : cd = 3{\cdot}5 : 1 : 3 : 1$ and $dd = \frac{3}{4}$ circumference.

The clitellum is saddle-shaped extending over segments *xiii–xxi* (9 segments) with the ventral borders passing down to setal lines *bb*.

The male pores are paired on segment *xviii*, they are inconspicuous and situated in setal lines *aa*. Small glandular folds join each pore with the slightly more laterally situated seminal grooves. The prostatic pores are paired on segments *xvii* and *xix*; the pair on segment *xvii* discharge on the posterior surfaces of the papillae from which the anterior pair of penial setae protrude and the pair on segment *xix* discharge on the anterior surfaces of the papillae bearing the posterior pair of penial setae. The prostatic pores of each side are joined by an inconspicuous, convex, seminal groove which in segment *xviii* almost touches the ventral border of the clitellum.

The penial setae are paired on segments *xvii* and *xix* and arise from paired papillae each in setal line *a*. The setae measure up to 11 mm. in length and are very slender and flexible. There is little ornamentation apart from a tooth-like tip and a slight moniliform appearance of the distal half (Text-fig. 7a).

The genital field is small covering the ventral surface only on segments *xvii* and *xix* where it is smooth and uniformly concave.

The female pore is single on segment *xiv* being situated mid-ventrally in the setal ring.

Two pairs of spermathecal pores are present in furrows 7/8 and 8/9 in setal lines *bb*. They are conspicuous and each may have an adjacent papilla situated slightly latero-posteriorly which superficially gives the appearance of the pore being double.

Genital papillae are present. In the region of the genital field most are single but they may be very closely paired instead. Paired papillae occur occasionally in furrow 14/15 but always in furrows 15/16, 19/20 and 20/21; sometimes the papillae in furrow 19/20 may be widely paired when they may be as far apart as setal lines *aa*.

Internal characters. The first septum is 4/5 and all of the anterior septa to 8/9 are strongly conical while septa 9/10–12/13 are only moderately conical. Septa 17/18–24/25 are also conical but with the " apex " pointing anteriorly, septa 25/26 29/30 become progressively flatter. Septa 10/11–12/13 are thickened and septa 8/9 and 13/14–16/17 are slightly thickened.

A large pharynx extends posteriorly into segment *iv*. In segment *v* the oesophagus is undifferentiated although it begins to dilate posteriorly and continues enlarging in segment *vi* until it is the same diameter as the oesophageal gizzards in segments *vii* and *viii*. Throughout segments *v* and *vi* the oesophageal wall becomes progressively thicker. The gizzards are fused with only a slight intersegmental constriction at septum 7/8. The calciferous glands are lamellate and paired in segments *xv, xvi* and *xvii*. The intestine begins in segment *xviii* and is dilated until segment *xxiii*, or *xxiv*, to form a crop-like region. Here the intestine is divided internally by a series of intersegmental thickened rings to form a series of pouches. The typhlosole arises in segment *xix* as a low slender ridge, it gradually forms into a thick, lamellate structure which by segments *xxiv–xxvi* is fully developed, extending nearly half-way across the lumen of the intestine.

The dorsal blood vessel is seen anteriorly as a slender vessel passing posteriorly from the pharynx and over the gizzards. It increases in diameter in segments *x*, *xi* and *xii* where it is apparently contractile. Paired lateral hearts are present in segments *x*, *xi* and *xii* where they join the dorsal and ventral vessels. A supra-oesophageal vessel can be traced between the posterior region of the dorsal surface of the first gizzard in segment *vii* and the calciferous glands. Paired circumoesophageal vessels are present in segments *vii–xii* joining the supra-oesophageal vessel with a pair of longitudinal latero-ventral oesophageal vessels. The latero-ventral oesophageal vessels arise in segment *xii* and pass anteriorly to the ventral surface of the pharynx, they are dilated in segments *vii* and *viii* where they receive blood from the spermathecae. In segment *xiii* paired vessels pass ventrally from the supraoesophageal vessel then each flexes posteriorly and passes to the prostatic gland of its side.

The testes arrangement is holandric with both the testes and the funnels paired in segments *x* and *xi*. The testes are situated in paired pouches formed by anteriorly directed extensions of the anterior septa of the testes segments. Depending on the length of the pouch, the testes may be seen lying on the parietes one or two segments in front of the testes segments, the posterior pouches are usually smaller than the anterior pair. The testes are contained in testes sacs which are continuous with the funnels and the seminal vesicles. The seminal vesicles are paired in segments *xi* and *xii* and are deeply incised with a granular texture. The anterior pair is large, the posterior pair small.

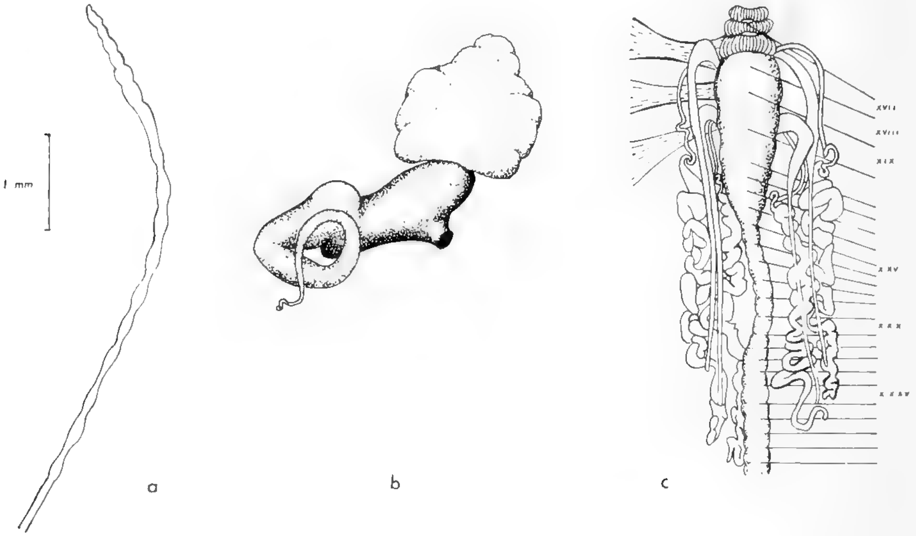

FIG. 7. *Dichogaster titillata* sp. nov. (a) Distal end of penial seta. (b) Spermatheca (antero-ventral view). (c) Dorsal dissection showing the prostatic glands and the muscular sheaths of the penial setae. The septa of the left-half of the body are omitted and the muscles of the right-halves of segments *xvii*, *xviii* and *xix* are not shown.

Two pairs of tubular prostatic glands are present as elongate, convoluted masses in the anterior intestinal region, with a muscular duct entering the parietes in segments *xvii* and *xix*. (Text-fig. 7c). Each prostatic duct is slender and slightly convoluted, as it leads posteriorly through about three segments into the tubular prostatic gland.

Each gland is loosely coiled and lies alongside the intestine, extending posteriorly to segments *xxxv-ixl.* There are two pairs of penial setae whose muscular sheaths enter the parietes medially to the ectal ends of the muscular prostatic ducts. The penial setal sheaths are exceptionally long and flexed posteriorly, the anterior pair extend from segment *xvii* to *xxxii* and the posterior pair from segment *xix* to *xxxiv.*

The ovaries are very closely paired in segment *xiii*; they may be seen as a single, median ovary pendent from the posterior surface of septum 12/13 ventrally to the oseophagus. The funnel is single being a simple, vertical, slit-like aperture in the anterior face of septum 13/14 below the oesophagus close to the ventral parietes. The oviduct is thin-walled, it passes down the posterior surface of septum 13/14 then is flexed a short distance posteriorly over the ventral parietes before entering the body wall.

The spermathecae are large and are paired in segments *viii* and *ix.* Due to the posterior displacement of the foregut they are situated ventrally to the pre-gizzard portion of the oesophagus. The duct of each spermatheca is about half of the diameter of the ampulla which is very large; a long, coiled, unilocular diverticulum arises from the duct (Text-fig. 7b). In well-developed, mature individuals, torsion has resulted in each spermatheca appearing as a long, tapering coil joined to an ampulla by a stout duct from which a smaller, shorter duct leads into the parietes.

The excretory system is meronephridial. Anteriorly there are a few diffuse nephridia situated on the septa near to the parietal wall but posteriorly from segment *xv* the nephridia are slightly more numerous. They lie on the parietes in the line of the setal ring and more posteriorly they form four longitudinal rows along the body on each side of the intestine. The nephridia are small throughout the region containing the prostatic glands and do not reach their full size until segment *xxxvi.*

REMARKS. Although this species may be recognized externally by the presence of papillae both adjacent to the spermathecal pores and in the region of the genital field, it can be more readily identified by internal features. The shape of the spermathecae, the great length of the prostatic glands and the muscular sheaths surrounding the penial setae are unusual specializations. The function of the penial setae is obscure. These setae are very long, extremely slender and bend easily so that they would seem unlikely to be able to pierce another individual during copulation. When uncoiled, the spermathecal diverticula are also found to be long and it may be that their size is correlated with the great length of the penial setae. If each seta enters into the lumen of a partner's spermatheca during copulation, it is necessary for the seta to be flexible for it to follow round the coils of the diverticulum.

D. titillata resembles *D. ehrhardti* in that the oesophageal gizzards are situated in segment *vii* and *viii* but differs, among other characters, in that the oesophagus is slightly thickened and dilated in segment *vi* but the same diameter as the gizzard in the following segment. The modification of the oesophagus in segment *vi* could almost be regarded as a rudimentary gizzard, if so then *titillata* would have to be placed, by definition, in the genus *Eutrigaster* Cognetti which differs from *Dichogaster* only in the presence of a third oesophageal gizzard. However, the degree of muscularization provides insufficient evidence for arriving at this conclusion. The oesophageal muscularization may represent the penultimate stage either in the posterior migration of the gizzards from *vi* and *vii* to *vii* and *viii* or, more likely, the loss of the anterior gizzard from a condition in which gizzards were present in the three segments *vi*, *vii* and *viii*. Whatever the explanation, it would seem that generic criteria of this nature may need re-assessment.

The paired blood vessel passing between the supra-oesophageal blood vessel in segment *xiii* and the prostatic glands is of especial interest although it is not unique to this species, for example it can be traced in *Benhamia reducta*, but it is more easily seen in *D. titillata*. The prostatic blood supply is of interest because although the glands lie in segments *xvii* and *xix* the paired vessel passes from a more anterior segment. There may well be a functional necessity for the prostatic blood vessels to arise from the supra-oesophageal blood vessels which terminate posteriorly at the calciferous glands. On the other hand, it could indicate the original, ancestral, position of one of the pairs of the prostatic glands. During the evolution of this group of earthworms, the prostatic glands (and the ectal ends of the vasa deferentia) may have moved posteriorly while the blood vessels still rise in the primitive position. If this were so then the male pores would have been originally situated on segment *xiv*, an unknown condition in present-day worms. A more probable explanation could be that the blood supply to the anterior prostatic glands from the supraoesophageal vessel was lost and that both pairs of prostates came to be supplied by the vessel which originally passed only to the posterior prostatic glands. This condition would result in the prostatic glands being originally situated in segments *xi* and *xiii* and the male pores in segment *xii*. This arrangement of the male terminalia is similar to the condition present in the less highly specialized worms, both freshwater and terrestrial, in the families Syngenodrilidae and Alluroididae which have many features not found in the Octochaetinae (Gates, 1945; Brinkhurst, 1964). This single factor, the origin of the prostatic blood vessels, cannot be taken to indicate phylogenetic affinity but it can serve to indicate the grade of structure of an ancestor which may have been similar to that now found among species of more primitive families. It may be significant that currently the Syngenodrilidae and, with the exception of one species, the Alluroididae are solely African in distribution.

Omodeona gen. nov.*

Diagnosis. Octochaetinae (Acanthodrilidae) with a lumbricine arrangement of the setae. Two gizzards present, an anterior gizzard in segment *v* and a posterior gizzard in segment *vi*. Two pairs of calciferous glands present as stalked, lamellate, oesophageal diverticula; the first pair in segment *xv* and the second pair in segment *xvi*. Intestine simple throughout, typhlosole λ-shaped. Anterior male organs holandric; prostatic glands tubular in structure. Penial setae present. Excretory system meronephridial.

Type species. *Omodeona proboscoides* sp. nov.

Remarks. *Omodeona* is distinguished from other genera sharing a large number of common attributes by the situation and the number of the calciferous glands. Species of the genera *Pickfordia* Omodeo, *Neogaster* Cernosvitov (sensu Omodeo) and

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* Named in honour of Dr. Pietro Omodeo.

Wegeneriella Michaelsen resemble *Omodeona* in having two pairs of calciferous glands but they differ in that the glands are situated more anteriorly, the first pair occurring in segment *xiv* and the second pair in segment *xv*. On the other hand, *Omodeona* is readily separable from the genera *Benhamia* Beddard (sensu Omodeo) and *Dichogaster* Beddard (sensu Omodeo) because of the presence of three pairs of calciferous glands in segments *xiv–xvi* and *xv–xvii* respectively in species of these genera. Yet, it is possible to regard *proboscoides* as an aberrant member of either of these genera which has lost one pair of calciferous glands, the anterior pair in the case of *Benhamia* or the posterior pair in the case of *Dichogaster*. Generally, *proboscoides* has greater affinity with species of *Benhamia* than with species of other genera (*see* Remarks, p. 36) nevertheless it is necessary to erect a new genus to accommodate it in view of the validity of the separation of *Benhamia* and related genera (Sims, 1966) on the positions and number of their calciferous glands (Omodeo, 1955).

Omodeona proboscoides sp. nov.

(Plate VIII)

Beside Pumping House, grass banks of the reservoir, Abuko, 24–28 Sept. 1964.

Syntypes: 22 clitellate, 8 aclitellate specimens. B.M.(N.H.) Reg. No. 1966. 30. 483/512 [Schizosyntypes (slides) 1966.30.513/514].

GUT CONTENTS. Small particles of vegetable matter (fibres and seeds) with a quantity of very fine soil.

DIAGNOSIS. *External characters.* Length 59–83 mm., diameter 1·5–2·5 mm. (clitellum diameter 2·5–3·5 mm.). Segments 132–173. Unpigmented. First dorsal pore 20/21. Epilobous; proboscis present, when fully everted equal in length to first three segments. Setae small, ventral, closely paired. Clitellum *xiii–xx* (8 segments), annular. Male and prostatic pores combined, paired *xvii* in setal line *b*. Penial setae present. Female pores closely paired *xiv* within setal lines *aa*. Spermathecal pores paired in furrow 7/8 in setal line *b*. Genital papillae absent.

Internal characters. First septum 4/5–8/9 conical, 9/10 less so; 5/6–11/12 thickened. Gizzards *v, vi*. Calciferous glands paired *xv, xvi*. Intestine begins *xviii*; typhlosole arises *xx*. Lateral hearts paired *x–xii*. Testes holandric in testes sacs. Seminal vesicles paired *ix, xii*. Prostates tubular paired *xvii*. Ovaries paired *xiii*. Spermathecae paired *viii*, duct short and stout with two short, convoluted, ental diverticula each terminated by three digitiform processes; ampulla simple. Meronephridial.

DESCRIPTION. *External characters.* The worms are 59–83 mm. in length, 1·5–2·5 mm. in diameter in the intestinal region and 2·5–3·5 mm. in diameter at the clitellum. There are 132–173 segments present in undamaged individuals. The prostomium is very broad and epilobic but there are longitudinal striations on the peristomium which superficially give the appearance of being tanylobic. An obvious feature of this species is the presence of a small, eversible, digitiform proboscis which is strongly reminiscent of the proboscis of some species of *Alma*. It arises from the postero-ventral surface of the prostomium and when fully everted is equal in length to the first three body segments. Secondary annulation is weak and may be seen only on the ventral surface of the posterior end of the intestinal region where the middle, i.e. setal, annulus of each segment may be slightly raised. The clitellum is annular and extends from segments *xiii to xx* (eight segments), sometimes segments *xiii* and *xx* may be reduced when the clitellum may seem to extend over only segments *xiv* to *xix*. The first dorsal pore occurs in the first postclitellar furrow, i.e. in furrow 20/21.

The body wall is unpigmented and the preclitellar region is a bright pink colour in life but a whitish grey in preserved specimens; in the intestinal region the gut contents can be seen through the body wall which is a reddish brown in life but otherwise a greyish brown. The clitellum is a bright orange when the animal is alive but fades to a greyish brown when the specimens are preserved. The cuticle is not strongly iridescent and it has only weak pink and pale green reflections to which blue is added in the clitellar region.

The setae are small, closely paired and situated ventrally. The setal formula is the same throughout the body, $aa : ab : bc : cd = 3 : 1 : 4 : 1$ and $dd = \frac{3}{4}$ circumference.

The male and prostatic pores are paired and apparently combined on the surface of segment *xvii*. They discharge from a pair of mammalate papillae in setal lines *bb*. The papillae are situated in an oval, glandular area sunken into the clitellum. Each papilla carries a penial seta. The penial setae are slender, being 1·9 mm. long but only 15 μ in diameter. They are smooth and rounded for most of their length but towards the distal end they become crenulated then flattened immediately before a hook-line tip (Text-fig. 8a).

The female pores are inconspicuous and closely paired on segment *xiv*; they are situated in the setal ring about $\frac{3}{4}ab$ within setal lines *aa*.

The spermathecal pores are paired in furrow 7/8 and situated in setal line *b*. Each pore opens into a deep transverse slit extending from setal line *a* to within *bc*.

Genital papillae are absent but between setal lines *bb* on segment *xv*, the ventral surfaces of the more mature individuals have an unpigmented, oval area.

Internal characters. The first septum is 4/5, all of the anterior septa to septum 8/9 are strongly conical and septum 9/10 is slightly less so; septa 5/6 to 11/12 are thickened. A large pharynx extends posteriorly to septum 4/5. Two gizzards are present, they are large and of equal size being situated in segments *v* and *vi* where they are joined by a short portion of dilated but otherwise undifferentiated oesophagus in the anterior region of segment *vi*. Two pairs of calciferous glands are present, occurring in segments *xv* and *xvi* as stalked, lamellate diverticula arising from the dorso-lateral surface of the oesophagus. The intestine begins in segment *xviii*, it is undifferentiated throughout. A typhlosole arises in segment *xx*; it is λ shaped in cross section and its height is little more than half of the internal diameter of the intestine.

The dorsal blood vessel is slender except in the region of the calciferous glands where it is somewhat dilated. Paired lateral hearts are present in segments *x*, *xi* and *xii*, the posterior pair is slightly smaller than the other two pairs. A peri-oesophageal blood sinus is present in segments *xiv*, *xv* and *xvi* serving the calciferous glands in segments *xv* and *xvi*, anteriorly it is supplied by a slender supra-oesophageal blood vessel which is difficult to trace because of its small size.

There is a holandric condition of the testes which are paired and situated within testes sacs in segments *x* and *xi*, the sacs being continuous with the funnels. The arrangement of the seminal vesicles is unusual among the Octohaetinae in that the vesicles are paired in segments *ix* and *xii*. The seminal vesicles in segment *ix* are developed from the anterior surface of septum 9/10 but the seminal vesicles in segment *xii* are developed in the more usual manner from the posterior surface of septum 11/12. The prostatic glands are paired in segment *xvii*. They are tubular in structure, small and do not extend into the adjacent segments. Entally each gland is slightly convoluted with three or four flexures, ectally a straight portion leads into a slender, muscular duct, about one quarter of the total length of the gland which passes into the ventral parietes anteriorly to the muscular sheaths of the penial setae.

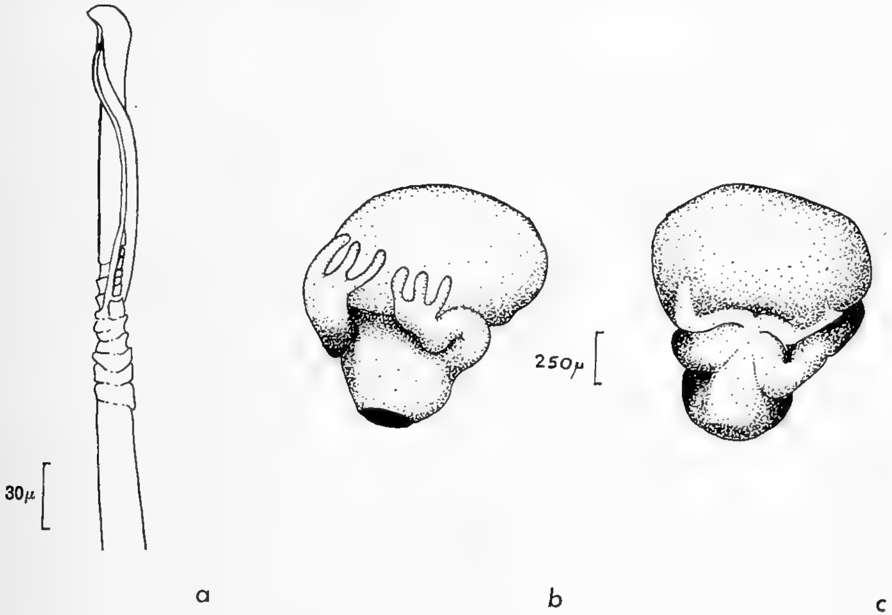

FIG. 8. *Omodeona proboscoides* gen. et sp. nov. (a) Distal end of penial seta. (b) Spermatheca (ventral view). (c) Spermatheca (dorsal view).

The ovaries are paired in segment *xiii* where they are situated pendent from the posterior face of septum 12/13 laterally to the oesophagus. The funnels are paired on the anterior face of septum 13/14 near to the ventral parietes.

The spermathecae are paired in segment *viii*. Each has a wide, stout duct with ampullae of almost the same length and only a slightly greater diameter. Two diverticula arise from the ental end of the dorsal surface of the duct, they are slightly convoluted and pass around each side of the ampulla, terminally each is tripartite (Text-figs. 8b, c).

The excretory system is meronephridial. There are few nephridia in the preclitellar region of the body but up to twenty-five in each segment in the intestinal region, here they form a continuous band around the parietes completely filling the central third of each segment.

REMARKS. Externally *proboscoides* may be readily recognized by the presence of a proboscis similar to that of some species of *Alma* also by the microscolecine reduced male terminalia discharging in a small genital field surrounded by a smooth annular clitellum. Its affinity with other species is mainly with those of the genus *Benhamia*. The prostomium is broad and the testes are enclosed within testes sacs, moreover, unlike western African species of *Dichogaster*, the anterior region of the intestine is unspecialized.

Family **EUDRILIDAE**

Subfamily **PAREUDRILINAE**

Chuniodrilus fragilis sp. nov.

(Plate IX)

Semi-flooded, lightly wooded land at edge of Jahkali Swamp, Sapu. Syntypes: 5 clitellate, 1 aclitellate specimens, 3 Oct. 1964; B.M.(N.H.) Reg. No. 1966.30.555 560 [Schizosyntypes (slides) 1966.30.561/563].

Other material: Side of path through groundnut field, Brikama Ba., 5 Oct. 1964. 1 aclitellate specimen.

DIAGNOSIS. *External characters.* Length 86–125 mm., diameter 1·5 mm. Segments 137–217. Dorsal pores absent. Proepilobous. Clitellum annular. Setae *ab* = *cd*, *aa* = 5*ab*, *bc* = 2·5*ab*. Penial setae present. Male pore single, median ventral *xvii*. Female pores paired 14/15 in setal line *d*. Spermathecal pore single, median ventral *xiii*. Nephridiopores paired in setal line *d*. Genital pad *xviii–xx* extending to setal lines *aa*.

Internal characters. First septum 4/5, 5/6–8/9 slightly thickened, 4/5–12/13 conical. Oesophageal gizzard *v*, intestinal gizzards absent. Oseophagus dilated and modified *xiv–xvi*, calciferous glands and oesophageal fat-bodies absent. Paired, commissural blood vessels *v–xii*. Holandric, testes free. Seminal vesicles paired *xi*, *xii*. Euprostates extending posteriorly to *xxi–xxiii*. Female and spermathecal systems separate. Ovaries paired *xiii* associated with a complex ovarian apparatus within an interconnecting coelomic sac. Spermathecal atrium single, median ventral *xiii* leading into a small receptaculum. Meganephridial.

DESCRIPTION. *External characters.* The body length varies between 86 and 125 mm., averaging 106 mm., the diameter is 1·5 mm. There are 137–217 segments present, the average number being 162. The body wall is unpigmented, in life the preclitellar region is pink in colour and the clitellum slightly paler while the intestinal region is a pinkish brown due to the gut contents being seen through the transparent body wall; in preserved specimens the preclitellar and clitellar regions are white and the intestinal region yellowish brown in colour. The cuticle is only slightly iridescent with pale green and bronze-pink reflections. Dorsal pores are absent. The prostomium has a proepilobic condition. Apart from some slight signs of triannulation in the preclitellar region, there is no secondary annulation.

The clitellum is annular and extends from segment *xiii* to *xviii* (six segments) dorsally but only from segment *xiv* to *xvii* (four segments) ventrally. The clitellar segments are approximately twice the length of the intestinal segments.

The setae are lumbricine in arrangement, the setal formula at segment *xxx* is $aa : ab : bc : cd = 5 : 1 : 2{\cdot}5 : 1$, the dorsal distance between *dd* being $\frac{3}{5}$ of the circumference. In the clitellar region, setae *cd* may be absent while setae *ab* are slightly larger than elsewhere.

The male pore is single on segment *xvii* and is accommodated on a small, median ventral papilla. The orifices of the euprostatic ducts are situated within the male pore and can be seen below a pair of lateral lips as a pair of short, slender longitudinal slits. Penial setae are present also within the male pore; the paired sheaths open immediately anteriorly to the orifices of the prostatic ducts. The penial setae are 1·5 mm. long, sigmoidal in shape and lack ornamentation (Text-fig. 9a). One or two are present in each bundle.

The female pores are paired in furrow 14/15, they are situated in the anterior wall of the furrow opposite to the nephridiopores in setal line *d*.

The spermathecal pore is single, it opens on a small raised, median ventral papilla on segment *xiii*.

The nephridiopores are paired and discharge in the posterior wall of each furrow in setal line *d*.

Internal characters. The first septum is 4/5, most septa are thin and delicate but 5/6 and 8/9 are slightly thickened. Septa 4/5 to 12/13 are strongly conical, 13/14 less so and partly applied to septum 12/13.

The pharynx extends posteriorly to septum 4/5, followed in segment *v* by a large gizzard. The latter is cup-shaped with a thickened muscular ring anteriorly which forms the rim to the " cup ". The oesophagus is slender and undifferentiated throughout segments *vi* to *xii* but it begins to dilate in segment *xiii*, throughout segments *xiv* and *xvi* it is the same diameter as the intestine but decreases in size to half of this diameter in segments *xvii* and *xviii*. A peri-oesophageal blood plexus is well-developed over the dilated portion of the oesophagus in segments *xiv* to *xvi* while calciferous glands and fat-bodies are absent from its entire length. The intestine begins in segment *xix* with a diameter equal to the oesophagus in the preceding segment, but immediately increases to its full size in segment *xx*. A typhlosole does not appear to be present.

The dorsal blood vessel passes forward to the dorsal surface of the pharynx, it is dilated in segments *xii* to *xix* as it passes through the region where the oesophagus is modified. A pair of commissural blood vessels is present in each segment from *vi* to *xii*, all are apparently contractile. Each successive pair is slightly stouter than the preceding pair, the vessels in segment *vi* being slender while those in segment *xii* are comparatively large. They convey the blood from the dorsal vessel to the ventral vessel which extends posteriorly from a pair of branches supplying the pharynx. A supra-oesophageal blood vessel lies on the oesophagus beneath the dorsal vessel with which it is interconnected by the commissural vessels. It can be traced posteriorly from the hinder end of the gizzard to segment *xii* where it passes ventrally to the right of the oesophagus and the main trunks to become the subneural vessel. A small sub-oesophageal blood vessel extends posteriorly from the gizzard. It gradually decreases in diameter as it passes along the oesophagus and by segments *xi* or *xii* the sub-oesophageal blood vessel becomes too small to trace further with a dissecting microscope. Due to its small size I was unable to observe whether there were any branches or interconnections with other vessels.

The testes are holandric being paired in segments *x* and *xi*. They are not enclosed within sacs but may be attached to posterior face of the anterior septum or embedded in a sperm mass. The funnels are small. The seminal vesicles are paired in segments *xi* and *xii*, the posterior pair may be as much as twice the length of the anterior pair. The vasa deferentia were not seen. Paired euprostatic glands are present in segment *xvii*, they are comparatively small and extend posteriorly to segments *xxi* to *xxiii*. A short duct leads from the ectal end of each euprostate and passes into the parietes by the ventral nerve cord. The penial setal sheaths are also paired in segment *xvii*. They lie transversely with their ectal ends entering the parietes immediately anteriorly to the euprostatic duct of the side.

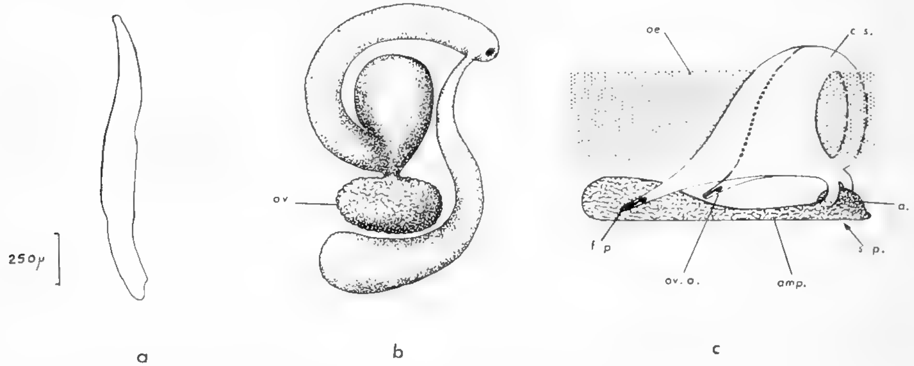

FIG. 9. *Chuniodrilus fragilis* sp. nov. (a) Penial seta. (b) Ovarian apparatus; *ov.*, ovary. (c) Schematic diagram of the coelomic sac in the posterior region of the oesophagus showing its relationship with the female and spermathecal systems; *a.*, atrium; *amp.*, ampulla; *c.s.*, coelomic sac; *f.p.*, (right) female pore; *oe.*, oesophagus; *ov.a.*, (left) ovarian apparatus; *s.p.*, spermathecal pore.

The ovaries are paired in segment *xiii* where they are situated near to the lateral parietes in the posterior region of the segment. Septum 13/14 is slightly conical and the ovaries lie within the parietes of the hinder part of segment *xiv*. Each ovary is contained within a small sac, it discharges into an ovisac at the ental end of a short oviduct which passes postero-laterally and opens into furrow 14/15; a digitiform diverticulum arises near the ectal end of the oviduct and extends forwards and partly curls around the ovary (Text-fig. 9b). The female organs lie within a continuous coelomic sac formed by a delicate membrane. The sac passes anteriorly from the region of the ovaries to the dorsal surface of the spermathecal atrium and dorsally around the oesophagus (Text-fig. 9c).

The spermathecal system is single and is situated median ventrally in segments *xiii* to *xv* ventral to the ventral nerve cord. It consists of two parts, anteriorly there is a dome-like atrium which is confined to segment *xiii* which lead posteriorly into a slender, membraneous sac-like ampulla or receptaculum in segments *xiv* and *xv*.

The excretory system is meganephridial. The nephridia in the clitellar region are somewhat larger than others elsewhere.

Morphological notes. Attention is drawn above to the dilation of the oesophagus in segments *xiii–xviii* where the oesophagel wall is also modified in having a granular appearance and reflects light as if small crystals were present. Under high-power a large number of granules can be seen lying mainly immediately within the cell boundaries in the cytoplasm of the cells. All of the granules are of similar size, irregular in shape and translucent. The results of immersing a portion of the oesophageal wall in a dilute solution of hydrocholoric acid are inconclusive, a small number of the granules apparently dissolve but most seemed to remain unaltered. The same region of the oesophagus is further specialized in that the internal surface is thrown up into a large number of low, slender, longitudinal folds which substantially increase the surface area.

Other structures in the segments containing the posterior region of the oesophagus are also modified. The dorsal blood vessel has a greater diameter than elsewhere and the nephridia, like those in the clitellar region of Eudriline species (Sims, 1964 : 600), are larger. These two latter modifications indicate an increased metabolism in these segments although the segments may each contain only a portion of the oesophagus and a pair of nephridia. Functionally there is no readily evident reason for the specializations, particularly as the body wall in the clitellar region apparently plays a small part in locomotion. However, the physiology of the epidermis of this region is unknown during periods of clitellar activity and these modifications may well have arisen in response to breeding requirements.

The combinations of specializations could, nevertheless, be significant when they are considered in relation to the absence of calciferous glands and fat-bodies from elsewhere along the oesophagus. Laverack (1963) summarized the function and physiological requirements of the calciferous glands in the Lumbricidae and, in the case of this Pareudriline species, the enriched blood supply, enlarged nephridial vesicles, modified oesophagus with longitudinal ridges and cytoplasmic includions in the cells, provide evidence for suggesting that the posterior oesophageal region in this species may carry out the functions of the calciferous glands of other earthworms. Wasawo & Omodeo (1963) reported the presence of some of these specializations in the hinder oesophagus of *C. vuattouxi* and reached the same conclusion about the function of the specialized oesophageal wall in this region.

The absence of oesophageal glands and oesophageal fat-bodies, however, could be correlated with the ecology of this species. Among earthworms there is a tendency for calciferous glands to be reduced in size or absent in aquatic species (Stephenson, 1930 : 106) and to be larger in species living in soils with a high pH (Laverack, 1963 : 34). In the case of this new worm, the type series was collected in a swampy area adjacent to the River Gambia where the soil PH may be slightly depressed by the decay of vegetable matter although salts would tend to be leached out by the water. (The specimen from Brikama Ba is damaged and aclitellate so it can be only provisionally assigned to this species. The conditions at Brikama Ba are dissimilar to those in the swampy, type locality).

REMARKS. Although *fragilis* lacks intestinal gizzards, it clearly belongs to the genus *Chuniodrilus* Michaelsen (*sensu* Wasawo & Omodeo, 1963 : 217). The female and spermathecal systems are functionally separate and comparatively simple, the hinder oesophageal wall is specialized and calciferous glands and oesophageal fat-bodies are absent. It resembles *Chuniodrilus compositus* in having the spermathecal pore on segment *xiii* instead of in the more usual position of furrow 12/13. It differs, however, in that the female pores and nephridiopores are situated in setal line *d* compared with setal lines *a* and *b* respectively in *compositus* and the large, smooth area extending over the ventral region of segments *xviii* and *xx* of *fragilis* is replaced in *compositus* by a number of small papilliform genital pads near by the male pore.

The comparatively simple morphology of the species of this genus could well represent the grade of struction of an ancestral Eudrilid from which existing forms were derived. If the function of the modified portion of the hinder oesophageal wall is concerned with acid-base balance then further modification in this region leading to the localization and development of calciferous glands would produce a Eudriline condition. Similarly, two, divergent lines of evolution of the female and spermathecal systems of the *Chuniodrilus*-grade could result in the appearance of either an *Eudrilus*-like or *Hyperiodrilus*-like condition. The paired female system of *C. fragilis* consists of an ovary and a small ovisac from which a short oviduct passes to the exterior, in addition there is a short digitiform diverticulum near to the ectal end of each oviduct. The female systems are contained within an interconnecting coelomic sac which encircles the oesophagus. The loss of the coelomic sac, the spermathecal atrium and the receptaculum would produce a condition similar to that present in species of *Eudrilus*. In this genus, the spermathecal atrium and pore have disappeared and the ectal, oviducal diverticulum of each paired ovarian apparatus has taken over the function of the spermatheca. On the other hand, the further development of the coelomic sac and the loss of the spermathecal recepaculum so that the spermathecal atrium discharged directly into the coelomic sac, would produce a complex female-spermathecal system similar to that present in species of *Hyperiodrilus* and *Legonea* which also includes a small oviducal diverticulum of unknown function (Sims, 1964).

Subfamily **EUDRILINAE**

Hyperiodrilus africanus Beddard, 1891

Hyperiodrilus africanus Beddard, 1891, *Quart. J. micr. Sci., n. set.*, **32**.236.—Lagos.

Bungalow garden, Agricultural Experimental Station, Yundum, 25 Sept. 1964; 4 clitellate, 6 aclitellate specimens.

Nursery plots, Forestry Department, Agricultural Experimental Station, Yundum, 28 Sept. 1964; 26 clitellate, 42 aclitellate specimens.

Plantation, Nyambai Forest Reserve, 23 Sept. 1964; 11 clitellate, 7 aclitellate specimens.

Grass banks, edge of reservoir, Abuko, 27 Sept. 1964; 13 clitellate, 8 aciitellate specimens.

Sandy soil forming bank to stream flowing from reservoir, Abuko, 27 Sept. 1964; 3 clitellate, 1 aclitellate specimen.

Edge of rice field, Abuko, 27 Sept. 1964; 4 clitellate, 13 aclitellate specimens.

Under Rheum palms, edge of rice field, near Bakau, 10 Oct. 1964; 12 clitellate, 15 aclitellate specimens.

Edge of rice fields, Brikama, 25 Oct. 1964; 9 clitellat: specimens.

REMARKS. New record for Gambia.

APPENDIX

Monsieur R. Roy, Départment de Zoologie Invertébrés Terrestres, Institut Fondamental d'Afrique Noire, Université de Dakar, kindly sent me a small collection of earthworms from Senegal which are listed below. I am most grateful for the opportunity of examining the specimens particularly as I have been unable to find any reference to a previous collection of earthworms from that country.

Family **ACANTHODRILIDAE**

Subfamily **OCTOCHAETINAE**

Benhamia sp.

Mission I.F.A.N., Parc National du Niokolo-Koba. Aug.–Sept. 1955; 4 aclitellate specimens.

REMARKS. All of the specimens are juveniles, their prostatic glands and penial setae are hardly discernible. Due to their extreme youth specific identification is not possible. There is a wide range of variation present among the specimens from which I conclude that the series consists of more than one species.

Family **EUDRILIDAE**

Subfamily **EUDRILINAE**

Hyperiodrilus africanus Beddard, 1891

Hyperiodrilus africanus Beddard, 1891, *Quart. J. micr. Sci.*, n.ser. **32** : 236.—Lagos.

Villa garden, Dakar, Apl. 1966; 8 clitellate, 3 aclitellate specimens.

REMARKS. This series provides the first record of this species in Senegal and further extends the northern limit of the known range of *H. africanus*. The species is distributed throughout the coastal regions of western Africa from Senegal southwards to the Congo where it has also been recorded from inland localities.

Family **LUMBRICIDAE**

Bimastos sp.

Villa garden, Dakar, Apl. 1966; 1 clitellate specimen.

NOTES. The setae are closely paired and the paired male pores on segment *xv* are surrounded by a swollen area which overlaps onto the adjacent segments, *xiv* and *xvi*; additional internal characters observed permit the specimen to be placed in the genus *Bimastos* (Omodeo, 1956 : 178). The condition of the prostomium is epilobic. Tuberculae pubertates are absent but certain specific identification is impossible due to damage to the anterior region of the clitellum. It seems, however, that the clitellum extends over segments *xxiv* to *xxviii* ventrally and segments *xxiii* to *xxix* dorsally. Although the evidence is slender, it is possible that the specimen represents the species *parvus* (Eisen).

REMARKS. The genus *Bimastos* has a fairly restricted range in Europe and does not extend to Africa (Omodeo, 1956). As this single specimen was collected in a town garden, it seems likely that the genus has been introduced into the Dakar region.

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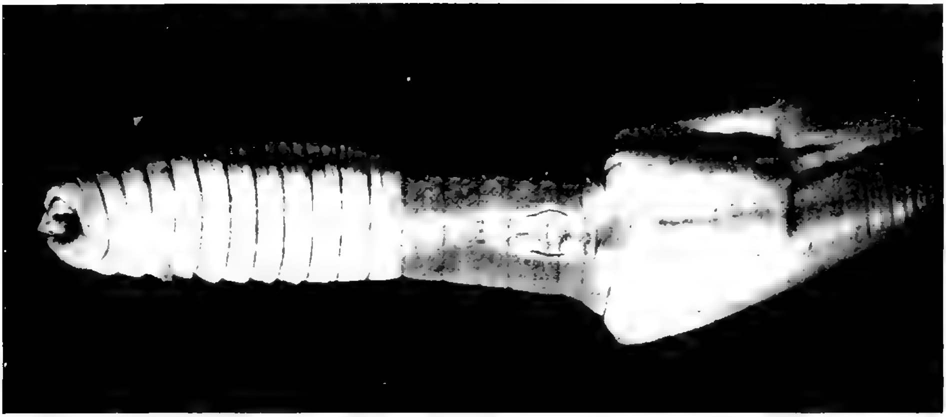
PLATES 1–3

1. *Benhamia budgetti* Beddard. Anterior region (ventral view) of the surviving whole syntype.

2. *Benhamia budgetti* species-group. Anterior region (ventral view) of a specimen with some *michaelseni*-like attributes.

3. *Benhamia mandinka* sp. nov. Anterior region (ventral view).



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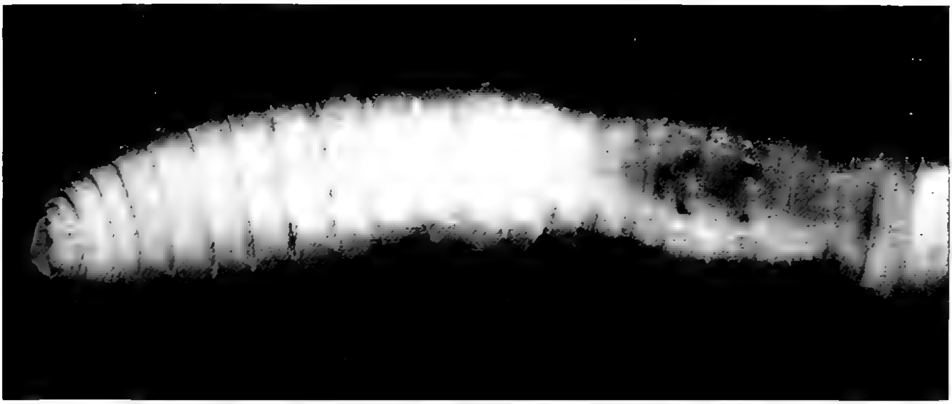

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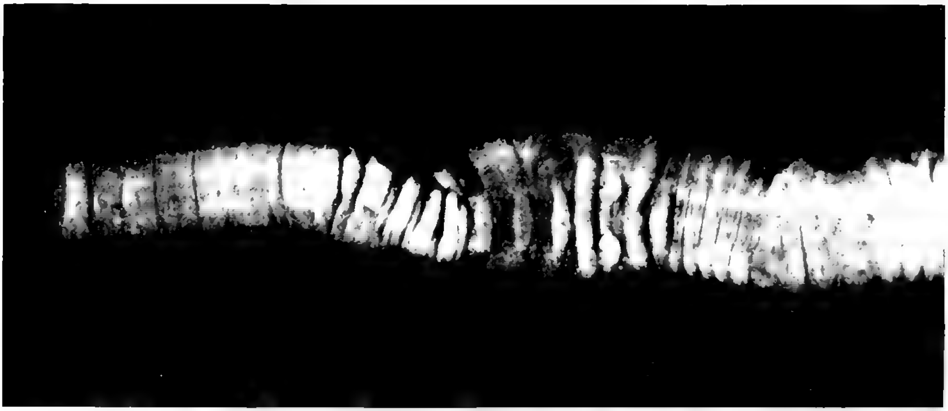

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PLATES 4–6

4. *Benhamia fula* sp. nov. Anterior region (ventral view).

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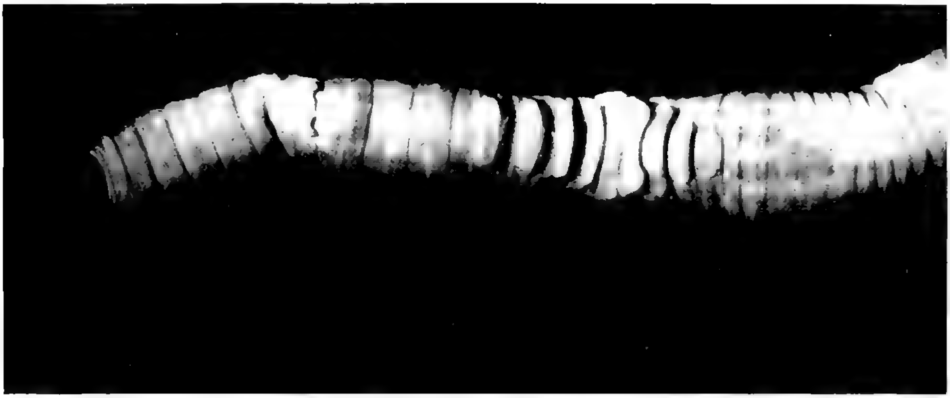

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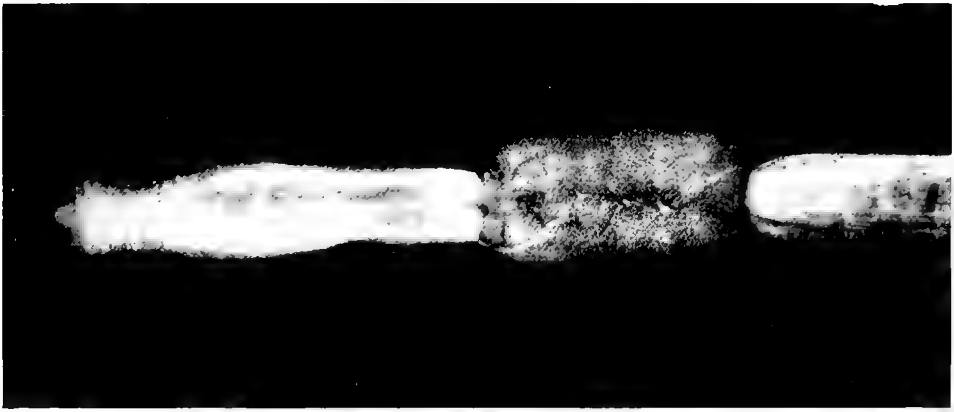

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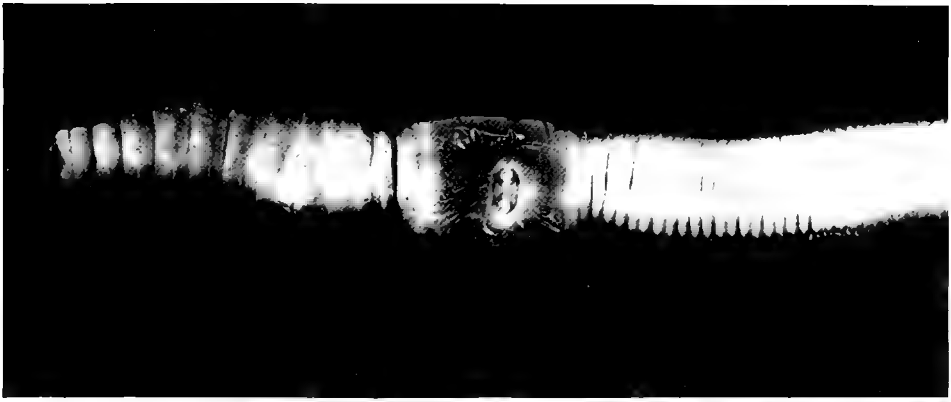

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A REVISION OF THE ELEPHANT-SHREWS, FAMILY MACROSCELIDIDAE

G. B. CORBET & J. HANKS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 16 No. 2
LONDON : 1968

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Pp. 45–111 ; 1 *Plate* ; 18 *Text-figures*

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A REVISION OF THE ELEPHANT-SHREWS, FAMILY MACROSCELIDIDAE

By G. B. Corbet & J. Hanks

CONTENTS

SYNOPSIS

Fourteen species are recognized in the family Macroscelididae. The subfamily Rhynchocyoninae contains one genus, *Rhynchocyon*, with three species. The form *melanurus* Neumann, hitherto considered a race of *R. petersi*, is believed to be a synonym of *R. cirnei macrurus*. One new subspecies of *R. cirnei* is described from southern Malawi. On the basis of an assessment involving thirty-one characters, three genera are recognized in the subfamily Macroscelidinae, *Nasilio* being considered a synonym of *Elephantulus*. *Petrodromus* and *Macroscelides* are considered to be monospecific; nine species are recognized in *Elephantulus*. Distribution maps are presented for each species, and the ecological relationships amongst the species are discussed.

INTRODUCTION

THE Macroscelididae are one of the most clearly defined groups of mammals and there has been general agreement that they are a monophyletic group not very closely related to any other group of mammals. The controversial question of their degree of affinity with the Insectivora and Primates does not therefore affect classification within the family and is not considered here. Recently strong arguments have been put forward for placing the family as the sole member of an order Macroscelidea (Butler, 1956; Patterson, 1965).

The family is confined to Africa. No comprehensive revision has previously been made and the only comprehensive list is that of Allen (1939) who grouped eighty-two named forms in forty species and six genera. Subsequently the southern African forms have been revised by Roberts (1951) and by Ellerman *et al.* (1953). The single North African species was listed, with comments on the classification of the family, by Ellerman & Morrison-Scott (1951) and the genus *Petrodromus* was revised in its entirety by Corbet & Neal (1965).

In the present study the primary object has been to delimit the species. The generic classification of the fourteen species recognized has been reviewed, and the subspecific variation described in general terms. The chance of additional species being discovered is rather slight and the specific classification can be considered to be nearly definitive, although there are one or two cases of apparently isolated pairs of forms where it is at present difficult to apply any objective criteria of conspecificity.

It is considered that formal trinominal nomenclature is frequently more misleading than useful as a method of describing subspecific variation. Subspecific names are only useful to designate completely isolated segments of a species (and only if most individuals can be recognized by their characters as belonging to one segment); or to designate contiguous segments when the zone of intergradation is so narrow as to suggest that the contiguity is secondary. In practice many forms already bearing trinomina must be considered provisionally valid until the distribution and variation are better known, but the policy has been followed of refraining from naming groups whose apparent isolation and homogeneity are probably due to absence of material from intervening areas.

The study was based on the entire collection of the British Museum, amounting to about a thousand specimens, along with smaller numbers received on loan or examined in other institutions (detailed under each species).

GENERIC CLASSIFICATION

The differences between *Rhynchocyon* (including *Rhinonax*) and the other, smaller, elephant-shrews are sufficiently numerous and great (Table 3) to leave no question about its generic distinctness, and there seems to be full justification for treating the two groups as subfamilies. Amongst the eleven species of the subfamily Macroscelidinae the genera have hitherto been based precariously on very few characters and the classification is correspondingly unstable. *Petrodromus* is the most distinct and its validity and content have never been disputed. It is characterized especially by large size and the absence of a hallux. The remaining,

Table 1

Specific characters in the subfamily Macroscelidinae. 2 : character fully present ; 1 : character slightly developed ; 0 : character absent.

	P. tetradactylus	*M. proboscideus*	*E. fuscipes*	*E. brachyrhynchus*	*E. rozeti*	*E. rufescens*	*E. revoili*	*E. intufi*	*E. rupestris*	*E. myurus*	*E. edwardi*
Large size	2	0	0	0	0	0	0	0	0	0	0
Pelage soft and silky	0	2	0	0	1	0	0	0	0	0	0
Rhinarium hairy below	0	0	0	0	0	2	2	0	0	0	0
Pale ring round eye	2	0	1	1	0	2	2	2	1	1	1
Dark spots behind eye	2	0	0	0	0	2	2	0	0	0	0
Buff behind ears	0	0	1	2	2	2	2	2	2	1	2
Supratragus large	0	2	0	0	0	0	0	0	0	0	1
Supratragus twisted	0	0	2	0	0	0	0	0	0	0	0
Tragus large	0	2	0	0	2	0	0	0	0	0	1
Pectoral gland	1	0	2	0	0	2	2	0	0	0	0
Abdominal (third) teats	0	2	2	2	2	2	2	2	2	2	2
Hallux	0	2	2	2	2	2	2	2	2	2	2
Interdigital pads very rugose	0	2	0	0	2	0	0	0	0	0	0
Tail tufted	0	2	0	0	2	0	2	1	2	0	1
Subcaudal gland	0	2	1	2	2	2	2	2	2	2	2
Post. edge of palate highly perforate	0	2	2	2	2	2	2	2	2	2	2
Foramen between parietal and squamosal	2	2	0	0	2	2	2	2	2	2	2
Ventral elements of bullae hypertrophied	0	2	0	0	0	0	0	0	0	0	0
Mastoids grossly inflated	0	2	0	0	0	0	0	0	0	0	0
Ectotympanic part of bulla level with entotympanic part	0	0	0	0	0	0	0	0	0	2	2
Suture between premaxilla and maxilla sinuous	1	0	1	1	0	1	1	2	2	1	0
I^2 : posterior cusp	0	2	1	1	1	0	0	1	1	1	1
I^3 : posterior cusp	2	2	1	1	0	0	0	1	1	1	1
I^3 : double root	2	0	0	0	1	0	0	0	0	0	0
C^1 : double root	2	0	1	1	2	1	1	2	2	2	2
P^1 : lingual cusp	0	0	0	0	0	0	0	2	2	0	0
P^2 : anterior lingual cusp	0	2	2	2	0	1	1	2	2	1	0
P^2 : posterior lingual cusp	0	2	2	2	0	2	2	2	2	2	0
P^3 : postero-external cusps as large as antero-external	0	2	2	2	1	1	1	2	2	1	0
P_1 : double root	0	0	2	2	0	0	0	2	2	2	0
M_3	0	0	2	2	0	0	0	0	0	0	0
Xiphisternum bifid	0	2	2	2	2	0		2		2	2
Superovulation	0*	2*		1†	0†	0†		0*	0*	2*	2*
No. of peculiar characters	4	2	1	0	0	0	0	0	0	0	0

* Data from Horst (1944).

† Observations made by Mr. H. Tripp, Zoological Society of London.

smaller species, originally in the genus *Macroscelides*, were dispersed into three genera by Thomas & Schwann (1906), namely *Macroscelides*, characterized by enormously enlarged auditory bullae and two lower molars; *Elephantulus*, characterized by normal bullae and two lower molars; and *Nasilio*, similar to *Elephantulus* but with three lower molars. Except for Winge (1941), who did not recognize *Nasilio*, these three genera were recognized by all subsequent workers until Ellerman *et al.* (1953) listed *Nasilio* as a subgenus of *Elephantulus*.

In order to assess affinity amongst the eleven species of Macroscelidinae attention was paid to all variable characters that seemed sufficiently clear-cut to be scored " present " or " absent " with only a minority of species requiring an " intermediate " scoring. Thirty-one such characters are listed in Table 1, along with two others that could not be observed on some species because of lack of suitable material. Characters were scored " 2 " if fully present, " 0 " if absent and " 1 " if intermediate. The number of characters could have been greatly increased, but only by choosing characters whose variation is less clear-cut, involving mensuration, e.g. relative length of tail. To arrive at a three-level assessment of such characters one would have to calculate a mean value for each species, and test for significance the differences between these means. The validity of such mean values would depend heavily upon the assumption that the specimens measured constituted a random sample of the species, adequately representing the variability present in nature. The available collections so obviously fall short of this ideal (being far from random with respect to locality, season, age, etc.) that it was felt that such characters would add little to the analysis.

TABLE 2

Magnitude of the difference between each pair of species of Macroscelidinae, based on Table 1. Each figure is the sum of the differences between the two species in each of the thirty-one characters, the maximum difference in one character being 2 units.

	tetradactylus	*proboscideus*	*fuscipes*	*brachyrhynchus*	*rozeti*	*rufescens*	*revoili*	*intufi*	*rupestris*	*myurus*	*edwardi*
tetradactylus	0										
proboscideus	42	0									
fuscipes	33	31	0								
brachyrhynchus	33	27	6	0							
rozeti	30	20	29	23	0						
rufescens	24	32	19	17	22	0					
revoili	26	30	21	19	20	2	0				
intufi	31	27	16	10	21	17	17	0			
rupestris	33	25	16	10	19	19	17	2	0		
myurus	27	27	14	10	19	15	17	8	10	0	
edwardi	26	26	25	19	12	20	20	17	17	11	0

In such a study one cannot assess the number of characters necessary to achieve a stable classification without considering the number of species involved and the

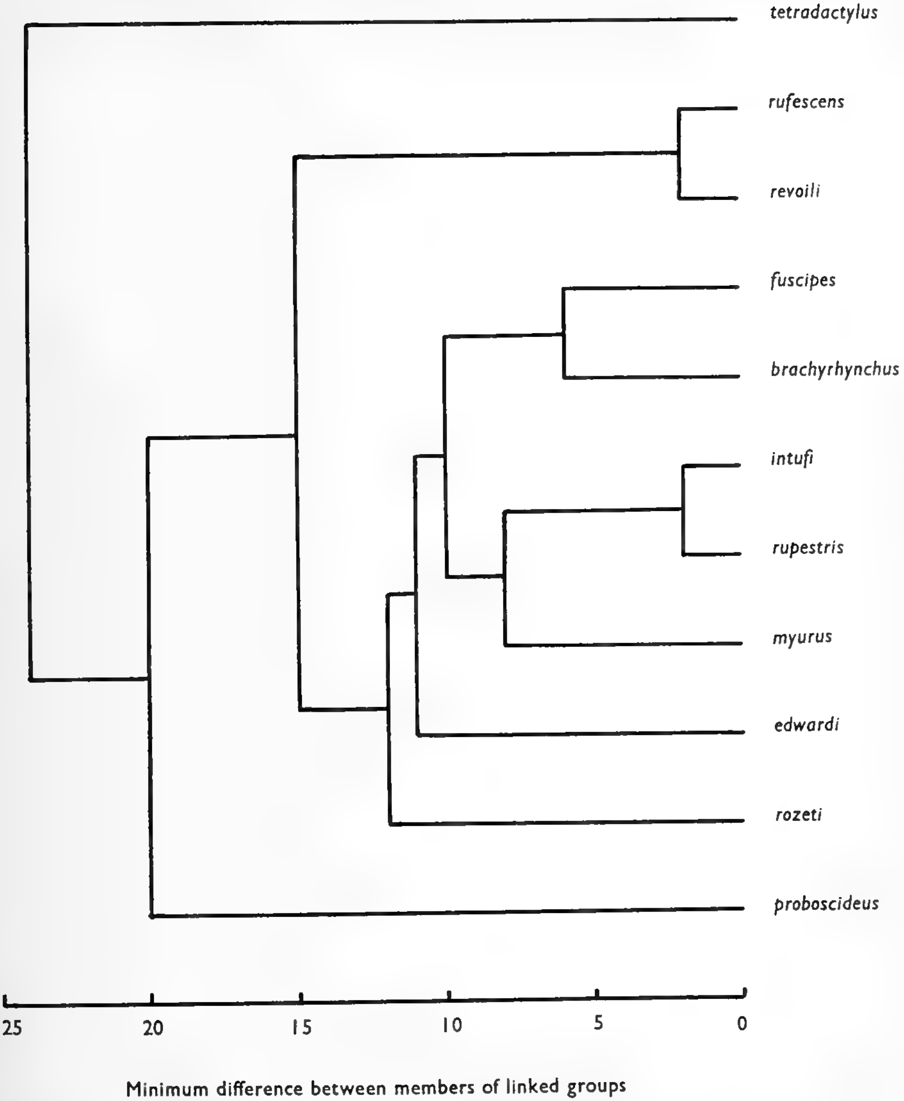

FIG. 1. Dendrogram showing the phenetic relationship between members of the subfamily Macroscelidinae, based on the data in Table 2. The scale is in " units of difference " as in Table 2.

overall variability. For example by including the species of *Rhynchocyon* the number of characters would immediately be increased to about seventy, but it was so obvious that thirty of these serve to separate the species of *Rhynchocyon* from all the others (Table 3) that it was considered quite unnecessarily cumbersome to enlarge the scope of the analysis to include *Rhynchocyon*.

Table 2 shows, for each pair of species, the sum of the differences in score for each of the thirty-one characters (the maximum possible difference being sixty-two). These are presented in the form of a dendrogram in Text-fig. 1, in which the clusters have been formed by single linkage, the position of the link between two clusters representing the minimum difference between any members of the two clusters.

Considering these results at first without weighting any characters, we see that *tetradactylus* differs by never less than twenty-four units (equivalent to twelve characters) from any other species. Two other groups that show only slightly less distinctiveness are *proboscideus* by itself and *rufescens* and *revoili* together. Any division amongst the remainder would be quite arbitrary, although two other closely similar pairs are apparent within this large group, namely *rupestris* with *intufi*, and *brachyrhynchus* with *fuscipes*.

The " traditional " classification and diagnostic characters can now be considered in the light of these unweighted measures of difference. The distinctiveness of *tetradactylus* shown by the unweighted assessment is reinforced by its possession of five characters not present in any other species. These are (1) the absence of a hallux ; (2) very large size ; (3) the absence of four large regular perforations at the posterior edge of the bony palate ; (4) the absence of abdominal mammae ; and (5) the presence (but only in some areas) of knobbed bristles under the tail. In the other species the hallux, although small, is not rudimentary, and therefore its absence in *tetradactylus* can be considered a major, clear-cut difference. The knobbed bristles are only present in certain parts of the range of *tetradactylus* (and are therefore excluded from the numerical analysis), but this character is so peculiar, being apparently unknown in any other mammal, that it must be considered of some importance. This species can therefore be considered the sole species of the genus *Petrodromus*.

Of the small species, *proboscideus* is almost as distinct as *tetradactylus* and can therefore be retained as the sole member of the genus *Macroscelides*. This is reinforced by the presence of one unique, specialized feature, namely the grossly enlarged bullae. This has been treated as only two characters in the analysis but in fact it involves many parts of the auditory region that show no such enlargement in other species.

On the basis of Text-fig. 1 the pair of East African species, *rufescens* and *revoili*, form the most distinct group within the central block. However, these species have no single character that is unique to them (although the post-ocular spots are shared only by *Petrodromus tetradactylus*), they are less distinct from the group as a whole than are either *proboscideus* or *tetradactylus*, and therefore there seems no good reason to create a new genus to contain them.

The remaining seven species are interlinked by many characters and there is no justification for dividing the group on the basis of an unweighted assessment of variation. The two species that have been separated are *brachyrhynchus* and *fuscipes* (genus *Nasilio*) on the basis of an extra posterior lower molar (which is small but not rudimentary). But *brachyrhynchus* shows very close overall resemblance to *intufi*, differing by only five characters (Table 2) and therefore the only justification for upholding the genus *Nasilio* would be by giving overwhelming weight to this difference in dentition. The possession of third lower molars can almost certainly be considered as the retention of an ancestral character that has been lost in the other members of the family. The fact that they have been lost by such a remote relative as *Rhynchocyon* suggests that the loss of these teeth may not be a monophyletic character. There therefore seems little reason for considering this character sufficiently important to segregate *brachyrhynchus* and *fuscipes* from the remaining species with which they show many other affinities. These nine species then form the genus *Elephantulus*.

The only other grouping of species that has been made was the creation of a genus *Elephantomys* by Broom (1937) for a Pleistocene form, *langi*, along with *intufi*. This was based on a single character, the molariform P^2, which is in fact shared by several other species and is present in a lesser degree in yet others. Later Broom (1938) concluded that *Elephantomys* was a synonym of *Elephantulus*, not because he considered the division invalid, but because he realized that *E. rupestris*, the type species of *Elephantulus*, also belonged to the group with molariform P^2. He therefore considered that the group with P^2 sectorial should be named as a subgenus but did not in fact do so. Ellerman *et al.* (1953) gave *Elephantomys* subgeneric rank but again did not take into account those species that are intermediate in this respect, e.g. *rufescens*, *revoili*, and *myurus*. The present study supports Broom's later view that *Elephantomys* is a synonym of *Elephantulus* and rejects the validity of a subgeneric division on the basis of this character.

The fossil members of the family have recently been reviewed by Patterson (1965) who recognized eight extinct species as detailed below.

Myohyrax oswaldi Andrews, 1914 and *Protypotheroides beetzi* Stromer, 1922. These are placed in an extinct subfamily, Myohyracinae, formerly considered to be Hyracoidea. They have somewhat hypsodont molars with third molars present above and below.

Mylomygale spiersi Broom, 1946. This Pleistocene species from South Africa, represented only by an imperfect mandible, has very hypsodont molars. Broom (1948) considered it to be a very aberrant member of the Macroscelididae and Patterson (1965) agreed, placing it in a separate subfamily, Mylomygalinae. However, it is clear from Broom's account that he did not compare it with the most hypsodont of the recent species, namely *Macroscelides proboscideus*, and in fact it shows a considerable resemblance to that species, although the teeth are undoubtedly more extremely hypsodont, with a deep third lingual re-entrant angle that is not present in recent species. The overall shape of the mandible and the crowded toothrow are closely matched by *M. proboscideus*. Its separation from *Macroscelides* in a separate subfamily seems scarcely justifiable.

Rhynchocyon clarki Butler & Hopwood, 1957. A small species of *Rhynchocyon* from the Miocene of Kenya.

Metoldobotes stromeri Schlosser, 1910. A mandible from the Oligocene of Egypt, lacking M_3 and not greatly dissimilar from *Petrodromus* or *Rhynchocyon*. Placed tentatively in the Macroscelidinae by Patterson (1965).

Palaeothentoides africanus Stromer, 1932. Mandibles from the early Pleistocene of Little Namaqualand. This species has a small M_3 and appears very close to *Elephantulus brachyrhynchus* in every respect, although Patterson (1965) considered that it comes between " *Nasilio* " and *Macroscelides* and upheld its generic distinctness.

Elephantulus broomi nom. nov. We propose this name to replace *E. langi* (Broom, 1937) which name is preoccupied by *langi* Roberts, 1929, a form of *E. brachyrhynchus.* This species, from the Pleistocene of South Africa, is very close to *E. rupestris* and *E. intufi*, differing perhaps in the absence of a lingual cusp on P^1.

Elephantulus antiquus Broom, 1948. Also from the Pleistocene of South Africa, this species appears to be very close to *E. myurus* and *E. edwardi.*

Two further fossil genera that have been allocated to the Macroscelididae (and the only ones from outside Africa) can be rejected. These are *Pseudorhynchocyon* Filhol, 1892 and *Cayluxotherium* Filhol, 1880, both from the Oligocene of France. The former has been excluded from the family by Butler & Hopwood (1957) and by Patterson (1965). *Cayluxotherium* was considered by Winge (1941) to belong to the Macroscelididae, but Butler (1948) referred it, as did Filhol, to the Erinaceidae.

These fossil species do not greatly assist in the classification of the living species. It is, however, of interest to note that species lacking the third molars were present as early as the Oligocene. The available Pleistocene species referable to, or similar to, *Elephantulus* are not sufficient to throw much light on the antiquity of the loss of third molars in this group.

To summarize the generic classification of the recent species, the eleven species of Macroscelidinae can be distributed in three genera as follows: *Petrodromus tetradactylus* ; *Macroscelides proboscideus* ; *Elephantulus fuscipes, E. brachyrhynchus, E. intufi, E. rupestris, E. myurus, E. edwardi, E. rozeti, E. rufescens, E. revoili.*

Family **MACROSCELIDIDAE**

DIAGNOSIS. Size rather small (head and body *c.* 100–300 mm.) ; snout long, slender and flexible ; ears of moderate length, reaching usually to the eye when laid forwards ; fore legs rather shorter than hind ; legs plantigrade or semi-digitigrade ; manus with four or five digits ; pes very elongate, with four or five digits ; tail *c.* 80–120% of head and body, shortly haired ; prepuce far forward on abdomen ; vulva elongate ; nine transverse palatal ridges ; dental formula $\frac{0\text{–}3 \,.\, 1 \,.\, 4 \,.\, 2}{3 \,.\, 1 \,.\, 4 \,.\, 2\text{–}3}$; no diastema ; cheek teeth forming progressive series from simple P^1 to complex molars, P^4 being largest or subequal with M^1 ; molariform teeth brachyodont or slightly hypsodont (more hypsodont in some fossil species), dilambdodont ; deciduous dentition well developed, not replaced until growth of body is almost complete ; zygomata complete, with large jugals ; auditory bullae with prominent ectotympanic, entotympanic and sphenoidal elements ; lachrymals very large; sagittal crest confined to posterior half of parietals ; vertebral formula 7, 13, 7, 3, *c.* 20–28 ; clavicles large ; pubic symphysis long ; tibia and fibula fused throughout distal half ; testes dorsal ; litter normally 2 or 1 ; caecum present.

RANGE. The Mediterranean zone of North West Africa and the whole of Africa south of the Sahara, except for the region northwest of the rivers Congo and Ubangi and west of about 27° E. (Text-fig. 18).

TABLE 3

The diagnostic characters of the two subfamilies of Macroscelididae.

	Rhynchocyoninae	Macroscelidinae
Size	Large (head and body *c.* 250 mm.)	Medium or small (head and body 200 mm. or less)
Pelage	Sparse; coarse; no long black proximal zone	Dense; fine; long black proximal zone dorsally
Mystacial vibrissae	Short, sparse	Long, abundant
Rump	Completely haired	Partly naked
Pollex	Absent	Present
Fifth digit of manus	Very short	Long
Carpal pad	Absent	Present
Proximal half of pes	Hairy below	Naked below
Mammae	Abdominal only	Nuchal, pectoral, ± abdominal
Post-anal gland	Present	Absent
Subterminal white zone of tail	Present	Absent
Skeleton of proboscis	Partly ossified	Wholly cartilaginous
Nasal cavity	Very wide	Narrow
Frontals	Very wide, overhanging orbits and surrounding posterior end of nasals	Narrow, scarcely overhanging orbits, not surrounding end of nasals
Anterior limit of orbit	Behind M^2	Over P^4/M^1
Post-orbital processes	Present	Absent
Bony palate	Entire	Perforated
Lateral pterygoid fossae	Short and shallow	Very long and deep
Sphenoid component of bullae	Medial parts inflated	Lateral parts inflated
Paraoccipital processes	Well developed	Rudimentary
Occiput	Concave	Highly convex
Upper incisors	Absent or rudimentary	Present, functional
Upper canines	Very large	Small
Angle between ramus and coronoid process of mandible	*c.* 140°	*c.* 115°
Ulna	Thick throughout	Distal half rudimentary*
Ilio-sacral fusion	With first sacral vertebra	With first and second sacral vertebrae*
Neural spines of sacrum	Second largest	First largest*
Pubic symphysis	Not keeled	Keeled*
Uterus	Slightly bicornuate	Deeply bicornuate*
Pupil	Circular	Vertically elongate*

* Not confirmed in *E. revoili* and *E. rupestris*.

Subfamily **RHYNCHOCYONINAE**

Diagnosis. See Table 3. Of the thirty characters listed in Table 3 the following seem especially important : the absence or rudimentary nature of the upper incisors ; the very large upper canines ; the extremely wide nasal and frontal region of the skull ; the large ulna ; and the more digitigrade feet, involving reduction of the lateral digits of the manus, absence of the carpal pad and the presence of hair on the proximal part of the metatarsal sole.

Contents. A single genus, *Rhynchocyon*. The recognition of an additional genus, *Rhinonax*, was based on the retention or loss of rudimentary upper incisors and the difference in pattern of the pelage. The retention of upper incisors is now known to be variable within each species (Table 4).

Genus ***RHYNCHOCYON***

Rhynchocyon Peters, 1847. Type-species *Rhynchocyon cirnei* Peters.
Rhinonax Thomas, 1918. Type-species *Rhynchocyon chrysopygus* Gunther.

Diagnosis, As for the subfamily (Table 3).

Range. See map (Text-fig. 2). Confined to forest (lowland and montane) and thick riverine bush, rarely in woodland without a closed canopy. The range appears to be limited by the Zambezi in the south, and between the Congo and Ubangi in the northwest. Elsewhere the distribution is probably limited only by habitat. The degree of fragmentation of the range is probably increasing due to deforestation.

Contents. Treated here as three species which are completely allopatric with one very dubious exception, namely the possible sympatry of *R. cirnei reichardi* and *R. petersi* in the Nbuka Forest, South West Tanzania (Allen & Loveridge, 1933). This must be considered a rather provisional arrangement until the nature of the discontinuities are better known. Since they have never been kept, far less bred, successfully in captivity, the probability of directly studying reproductive compatibility is slight.

Key to the species of *RHYNCHOCYON*

1 Rump straw-coloured, contrasting sharply with surrounding rufous pelage (Plate 1a) **R. chrysopygus**
Rump not straw-coloured 2
2 Rump and posterior half of back with a pattern of dark lines or spots on a yellowish-brown or rufous ground ; top of head without a rufous tinge (Plate 1d–m) . **R. cirnei**
– Rump and posterior half of back black ; top of head with a rufous tinge (Plate 1b–c) **R. petersi**

Rhynchocyon cirnei

Rhynchocyon cirnei Peters, 1847. Quelimane, Bororo district, Mozambique. Syntype examined : Leiden Museum, mounted skin, ♂.

Synonymy. Under subspecies.

Taxonomic status. The inclusion of the isolated northwestern form (*stuhlmanni*) in this species is open to question, but this course is not new, having been taken by Ellerman *et al.* (1953). The form *melanurus* is here transferred from *R. petersi* to this species, since it is now known to intergrade completely with *R. c. macrurus* (but not with *R. petersi*).

DESCRIPTION (Plate 1d–m). Dorsal pelage with a pattern of three longitudinal dark lines on either side, extending from near the base of the tail forwards to about one-half or two-thirds of the distance to the ears ; the central lines continuous but indented, black or chestnut ; the second and third lines continuous or broken into individual spots, fainter and less extensive ; the ground colour grizzled yellow or cream and black, with or without an orange-rufous wash which may almost, but never completely, obliterate the pattern ; top of head grizzled cream or yellow and black.

RANGE. See Text-fig. 2. The entire range of the genus except for the coastal zones of Kenya and northern Tanzania (and Zanzibar). In southeastern Tanzania at least as far north as Kilwa (*c.* 8° 50′ S.).

REGIONAL VARIATION. Six races can be recognized, but further collecting may well demonstrate clinal variation linking some of these or discover yet others. Of the four races that are known by specimens from a considerable number of localities two (*R. c. macrurus* and *R. c. stuhlmanni*) show internal clinal variation whilst the other two are very uniform. The overall pattern of variation cannot be assessed until more data are available from Mozambique.

R. c. cirnei

SPECIMENS EXAMINED. The type (a mounted skin, received on loan from the Leiden Museum).

DESCRIPTION. Dorsal ground colour grizzled black and yellow, becoming quite *rufous* on the rump and thighs ; many contour hairs of back yellow with a dark tip but *no* grey base ; dorsal spots *chestnut*, central rows reaching a little more than half-way from base of tail to ears, rather irregular, the spots of each row united by a thin medial line ; second rows of spots rather faint but *discrete* ; third rows just discernable ; *no pale spots* between the dark ones ; feet and ears as rump ; ventral pelage yellowish brown, only slightly paler on throat ; proximal three-quarters of tail dark brown above, paler below ; distal quarter white.

RANGE. Known only from the type locality, i.e. Quelimane, north of the mouth of the Zambezi.

REMARKS. A single specimen in the British Museum from Mirrote on the Lurio River, Mozambique, i.e. much further north at 13° 50′ S., 39° 35′ E., has a very similar pelage, but the tail, except for the distal white zone, is totally black above and very dark brown below (Plate 1j). This specimen is in some respects intermediate between *R. c. cirnei* and *R. c. macrurus*.

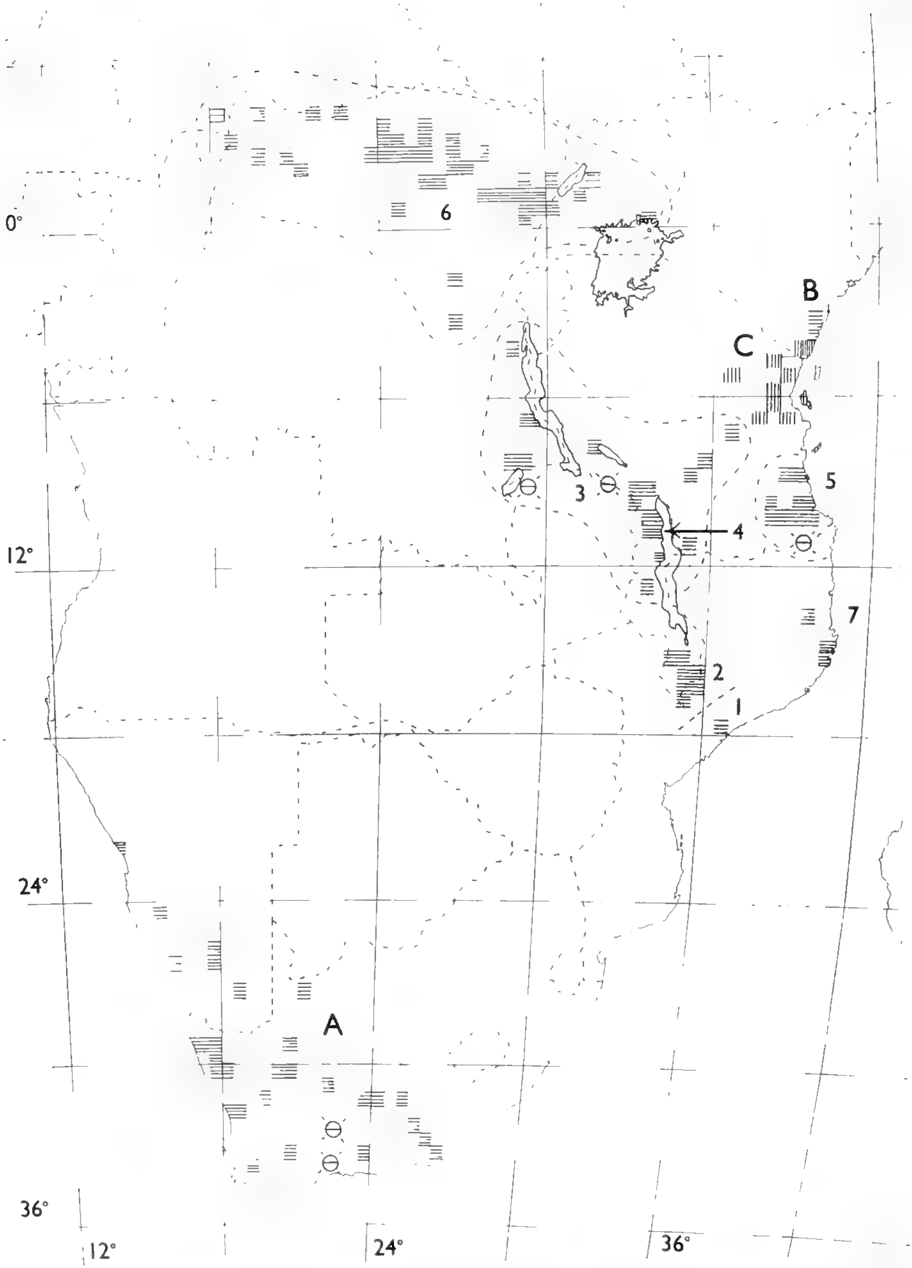

FIG. 2. Recorded distribution of A: *Macroscelides proboscideus*; B: *Rhynchocyon chrysopygus*; C: *Rhynchocyon petersi*; remainder: *Rhynchocyon cirnei*. 1: *R. c. cirnei*; 2: *R. c. shirensis*; 3: *R. c. reichardi*; 4: *R. c. hendersoni*; 5: *R. c. macrurus*; 6: *R. c. stuhlmanni*; 7: *R. c.* subsp. Circle: locality not precisely known; square: record unconfirmed.

Rhynchocyon cirnei shirensis subsp. n.

HOLOTYPE. B.M.(N.H.) number 34.1.11.8, skin, with skull, of an adult female from Lichenja Plateau, Mlanje Mountain, Malawi, 16° 00′ S., 35° 33′ E., altitude 1,900 m., collected by Mr. J. Vincent, 3rd January, 1932.

SPECIMENS EXAMINED. Seventeen skins and skulls from the following localities in southern Malawi: Mlanje Mt., Zomba Mt., Cholo, Chiradzulu, Chiromo, Dzonze (670–1,900 m.). The one from Dzonze was kindly shown to G.B.C. by Mr W. F. H. Ansell while he had it on loan from the Transvaal Museum; one from Mlanje was received on loan from the Leiden Museum.

DESCRIPTION (Plate 1i). Dorsal ground colour grizzled black and cream, much *less yellow* than that of *R. c. cirnei*; contour hairs *all grey-based*; a very slight tinge of rufous brown on the thighs but *not* on the rump; pattern of dorsal spots as in *R. c. cirnei* but colour *darker*, a very dark blackish brown, lighter at the edge of each spot; pale spots alternating with dark ones, very slightly paler than the ground colour (including a few all-pale hairs); feet and ears slightly browner than rest of pelage; ventral pelage dull greyish buff, slightly paler on throat; proximal two-thirds of tail sharply bicoloured, the dorsal black stripe varying in width from about one-fifth to one-half the circumference; distal third white with or without a small black tip; deciduous upper canines usually with a small anterior cusp (six out of seven examined) (Text-fig. 4a and b).

VARIATION. Variation in pelage is slight. A juvenile 156 mm. long (head and body) has both the dark and light elements of the second and third rows of the pattern more distinct than the adults. One specimen from Zomba has DP^3 and DP^4 of both sides connate. The lingual aspect is normal but of the labial roots the posterior one of DP^3 and the anterior one of DP^4 are represented by a single, large root. The variation in the upper incisors is shown in Table 4.

TABLE 4

Incidence of upper incisors in *Rhynchocyon* spp.

	Animals with permanent dentition			Animals with deciduous dentition (Incisors present in all)
	Present both sides	Present one side	Absent both sides	
R. cirnei shirensis	7	2	2	6
R. c. reichardi	3	3	9	5
R. c. hendersoni	0	0	1	1
R. c. macrurus	16*	2	11	3
R. c. stuhlmanni	12	7	34	12
R. petersi petersi	5	2†	1	1
R. p. adersi	3	0	2	1
R. chrysopygus	18	1	2	1

* Two with 1/2; one with 2/2.
† One with 0/2.

RANGE. Known only from the Shire Valley of southern Malawi. The uniformity of pelage within the group suggests that the discontinuity with *R. c. cirnei* to the south and *R. c. reichardi* to the north may be real.

R. c. reichardi

Rhynchocyon reichardi Reichenow, 1886. Marungu, South East Congo. Syntype examined. Leiden Museum, skin and skull, ♀.
Rhynchocyon swynnertoni Kershaw 1923*a*. Kipera, Kilosa, Tanzania.

SPECIMENS EXAMINED. The female syntype (in the Leiden Museum); thirty-three skins and twenty-three skulls, from the following localities. Malawi: Nyika Plateau, Vipya Plateau, Chinteche (three from Transvaal Museum), Fort Hill; Zambia: Kayomba (Mweru Wantipa); Tanzania: Ufipa Plateau, Songea district, Kipera (type of *swynnertoni*); Congo: Fizi,[1] Mpala,[1] Lambwe[2] (all Tanganika district), L. Moero.[2]

DESCRIPTION (Plate 1h). Dorsal ground colour as in *R. c. shirensis*, grizzled black and cream, *no* rufous on rump; all contour hairs grey-based (except those of the white spots); central stripes *black* except round the edges, extending *further forwards* than in *R. c. shirensis*, to about two-thirds of the distance from tail to ears; second row of spots *confluent*, reaching as far forwards as the central pair; third rows faint but confluent and usually joining with the second to form a broad chestnut band obliterating the ground colour between the second and third rows; pale spots alternating with dark ones *white*, at least in the outer rows, least distinct in the anterior part of the central rows; feet and ears as rest of dorsal ground colour; ventral pelage paler than in *R. c. shirensis*, especially in mid-line and on the throat; proximal two-thirds of tail bicoloured, black dorsally; deciduous upper canines *lacking* an anterior cusp (twelve specimens) (Text-fig. 4c).

VARIATION. The form *swynnertoni* (only the type examined) from the north-eastern extremity shows the least development of white spots but is very closely approached in this respect by other, far distant, specimens. The southernmost locality, the Vipya Plateau (*c.* 12° 50′ S. in Malawi), is probably also an isolated habitat and is represented by one specimen which is quite typical, showing no approach to *R. c. shirensis*. Three specimens from Chinteche (11° 50′ S.) were considered by Ansell (1964) to be intermediate between *reichardi* and *cirnei* (meaning specimens from southern Malawi). These same specimens were examined by G.B.C. They are slightly deeper brown on the flanks and feet than most *reichardi* but appear very much closer to *reichardi* than to *shirensis* or *cirnei*.

RANGE. The mountains in, and flanking, the rift valley from at least 13° S. on Lake Nyasa to the northern end of Lake Tanganyika; west to Lake Mweru; much of southwestern Tanzania reaching to Kilosa in the northeast. It is probable that the extreme northeastern part of the range is fragmented.

REMARKS. Many specimens of this race have been erroneously recorded as *R. c. hendersoni* (see Ansell, 1964).

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[1] In the Institut Royal des Sciences Naturelles, Brussels.

[2] In the Musée royal de l'Afrique Centrale, Tervuren.

R. c. hendersoni

Rhynchocyon hendersoni Thomas, 1902. Near Livingstonia, west of Lake Nyasa, Malawi. Holotype: B.M. (N.H.) 2.9.8.1, skin, ♂.

Specimens examined. The type (skin only) and two entire specimens in phenoxytol from near the type locality.

Description (Plate 1g). Ground colour grizzled black and yellow but with the yellow subterminal bands very short, making the overall tone *very dark*, closely similar to some *R. c. stuhlmanni* from Uganda and quite different from the closely adjacent *R. c. reichardi*; pattern exactly as in *R. c. reichardi*, the resemblance enhanced by the broad, anterior part of the central black stripes and the rufous ground colour between the second and third stripes; pale spots noticeable but yellow instead of white and without pale-based hairs; proximal part of tail bicoloured, black above; white zone subterminal and very short, beginning 40–45 mm. from tip.

Range. Known only from the neighbourhood of Livingstonia, Malawi. The only precise locality available is the summit of Mount Nyamkhowa (= Mt. Laws), north of Livingstonia, 2,050 m., 10° 34′ S., 34° 04′ E. (B.M. 36.2.20.3 and 4).

Remarks. The presence of two other specimens virtually identical with the type confirms that this is indeed a local race and is not based on an aberrant individual as had been suspected. The close proximity of this locality to the Nyika Plateau where only *R. c. reichardi* has been collected emphasizes the highly fragmented range of this species, living in isolated patches of forest.

The name *hendersoni* has been widely and erroneously used for *R. c. reichardi* as has been pointed out and documented by Ansell (1964).

R. c. macrurus

Rhynchocyon macrurus Günther, 1881: 163. Rovuma River, east of 38° 20′ E (limited by Moreau *et al.*, 1946). Holotype: B.M. (N.H.) 63.10.12.1, skin and skull.

Rhynchocyon petersi melanurus Neumann, 1900: 542. Lindi, South East Tanzania. (*Not* Uluguru Mountains: see Moreau *et al.*, 1946.)

Specimens examined. The type (skin and skull); thirty-two skins and twenty-three skulls from the Liwale district, South East Tanzania (five of these in the National Museum, Nairobi); five skins and four skulls from the Lindi district (i.e. topotypical *melanurus*); ten skins and nine skulls from the Kilwa district.

Description (Plate 1k–m). A variable race showing a cline in the extent of a rufous wash which is minimum at Liwale (and in the type) and maximum at the coast (Lindi and Kilwa). The inland form: dorsal ground colour as in *R. c. cirnei*, much yellower than in *R. c. reichardi* and *R. c. shirensis*; rump and flanks *conspicuously rufous*, almost or quite obliterating the third row of spots; central stripes prominent, chestnut, with little or no black; second rows consisting of *isolated spots* but more prominent than in *R. c. cirnei*; pale spots absent in central rows but faintly present in second rows, creamy white; feet and ears slightly rufous ; ventral pelage rufous, except for throat and centre of chest which are pale ; tail bicoloured proximally, white zone usually subterminal.

In the coastal form the rufous wash is much brighter and extends over the entire dorsal surface to just in front of the ears (but *not* the rest of the head), almost, but not quite, obliterating the pattern of stripes. These rufous hairs are all grey-based. Ventrally the rufous colour is present forward to the angle of the mouth, leaving only the inter-ramal region pale fawn. The hairs of the tail are longer and the black extends onto the ventral surface towards the end of the proximal zone.

The two extreme forms are linked by intermediates along the Mbemkuru River. At one locality (Mbemba, 10° 02′ S., 38° 37′ E.) two specimens have the yellow ground colour completely obliterated above, although the pattern is more conspicuous than in the coastal population ; whilst one has the pattern obliterated only on the rump, with some yellow remaining between the anterior ends of the central stripes (Nat. Mus. Kenya, 4233–5). One from Mahendera, also on the Mbemkuru River (co-ordinates ?), is similar to the last (B.M. 62.400–Plate 1l).

RANGE. The coastal forests of Tanzania at least from Kilwa to Lindi ; the Mbemkuru Valley as far as Liwale ; and the Rovuma Valley.

REMARKS. The presence of these animals in the dense riverine thicket suggest that there may be a fair degree of continuity from the coast inland to Liwale, but might suggest discontinuity from one river system to another, except through the rufous coastal populations. This rufous pigmentation is, therefore, likely to be a recently acquired character in the coastal population.

This race shows rather more affinity with *R. c. cirnei* than with *R. c. reichardi* although it is clearly separable from both. The transfer of the form *melanurus* from *R. petersi* to *R. cirnei* is fully justified by the cline in variation linking the two extremes of this race and involving only a single character, namely the extent of the rufous wash. The former allocation of *melanurus* to *R. petersi* was due to a superficial resemblance, but there are in fact three quite clear-cut differences : *melanurus* lacks the pale tail, black back and rufous head of *R. petersi*.

R. c. stuhlmanni

Rhynchocyon stuhlmanni Matschie, 1893. Andunde (Bundundi), Semliki River, Congo. (See Moreau *et al.*, 1946.)

Rhynchocyon stuhlmanni nudicaudata Lydekker, 1906. Mawambi, Ituri Forest, Congo.

Rhynchocyon claudi Thomas & Wroughton, 1907*a*. Beritio, Uele River, Congo.

SPECIMENS EXAMINED. Five skins and skulls from Uganda ; eighty-three skins, seventy-nine skulls and one entire in spirit from the Congo (most of the latter in the museums at Brussels and Tervuren, but including the types of *nudicaudata* and *claudi* in the British Museum).

DESCRIPTION (Plate 1 d–f). Considerable clinal variation. Ground colour grizzled black and cream or yellow, the overall colour yellowish brown in the west, very dark blackish brown in the Ituri Forest, and rather lighter greyish brown in Uganda ; head concolorous with nape ; central dark stripes deeply indented, anterior ends much shorter and narrower than in *R. c. reichardi* ; second row disjointed, short ; third row obscure but with a continuous chestnut band on the medial side as in *R. c. reichardi* ; feet very dark brown ; ventral pelage pale creamy buff in mid-line, in the darker forms limited to a narrow line (or eliminated on the thorax) by encroachment of the dorsal colour ; tail either completely pallid (in west) or with the proximal two-thirds pale brown above, *never black* ; white zone very variable, usually detectable and usually subterminal ; *nasals short* (extension behind maxillae less than 13 % of condylobasal length).

RANGE. The lowland rain forest of the Congo between the rivers Congo and Ubangi, south at least to 3° 10′ S., north to the River Uele (both banks) and east to the foot of the volcanic highlands of Kivu ; also isolated populations in at least four areas of lowland forest in Uganda, namely Bwamba, Bugoma, Budongo and Mabira. A single juvenile in Paris Museum is reputed to have been collected in 1966 between Bangui and M'Baiki, Central African Republic, i.e. on the right bank of the Ubangi River.

VARIATION. The ground colour shows a cline from yellowish brown in the west, with which the pattern contrasts clearly, to very dark brown in Ituri where the pattern may be almost completely obscured. The western form differs clearly from *R. c. reichardi* in the yellow-brown wash, especially on the shoulders and neck, and in the all-white tail. The Uganda specimens have the base of the tail more clearly bicoloured. Although the pattern is obscure the pale spots are always visible. Too few specimens are available from the Uganda forests to show whether there are any constant differences between these widely isolated populations. The two specimens available from the Budongo Forest have the throat yellowish buff, darker than at all the other eastern localities. The deciduous upper canine has an anterior cusp in six out of sixteen skulls. The single specimen reputedly from the Central African Republic is indistinguishable from specimens from the western part of the range in the Congo.

REMARKS. Of all the races of *R. cirnei* this one is the most distinct and could with some justification be treated as a species. The short nasals distinguish it, although with a slight overlap, from the other two species of *Rhynchocyon* as well as from the other races of *R. cirnei*.

Rhynchocyon petersi

Rhynchocyon petersi Bocage, 1880. Mainland opposite Zanzibar (see Dollman, 1912).

SYNONYMY. Under subspecies.

TAXONOMIC STATUS. This species appears to continue the clinal variation shown within *R. cirnei macrurus*. However, the major discontinuity (geographical and morphological) is between *petersi* and "*melanurus*", not between "*melanurus*" and *macrurus* as suggested by the current classification. Further collecting in the area between Kilwa and the Uluguru Mountains may serve to confirm or reject the specific separation of *cirnei* and *petersi*. On the other hand it is possible that extinction, perhaps recent due to deforestation, may have destroyed the evidence.

DESCRIPTION (Plate 1b–c). Rump and centre of back black (extending forwards almost to scapular region); rest of upper surface and flanks orange-rufous or dull maroon without grey bases to the hairs; head tinged with rufous but somewhat grizzled; pattern of *R. cirnei* obliterated except that the central dark stripes can be seen with difficulty in good light; ventral pelage, including whole of throat, orange-rufous or maroon; feet and ears orange-brown; tail very pale orange-brown, the long black hairs of the rump extending onto the tail in the form of a wedge; subterminal white zone usually visible but obscure.

RANGE (Text-fig. 2). Forests of the coastal region of Tanzania and Kenya from at least 6° 45′ S. (near Dar-es-Salaam) to the Rabai Hills, Kenya (4° 00′ S.); the islands of Zanzibar and Mafia. The westernmost locality is Kibaya (Swynnerton & Hayman, 1951). This is far into the steppe zone and is presumably an isolated forest habitat.

Allen & Loveridge (1933) accepted a sight record of this species made by Loveridge's local assistant in the Nkuka Forest, Rungwe Mountains, where a series of *R. cirnei reichardi* was obtained (erroneously reported as *R. c. hendersoni*). This seems so unlikely that it cannot be accepted (nor rejected) without confirmation. There is also the possibility that it was an abnormal rufous individual of *R. cirnei* similar to the coastal form of *R. c. macrurus* (i.e. "*R. petersi melanurus*") rather than a true black-backed *R. petersi*.

VARIATION. Two subspecies can be recognized, the form on the islands being distinct from that on the mainland. There is no clinal variation within the mainland race showing any approach to either *R. cirnei* or to *R. chrysopygus*.

R. p. petersi

Rhynchocyon petersi usambarae Neumann, 1900: 542. Usambara, Tanzania.
Rhynchocyon petersi fischeri Neumann, 1900: 543. Uzigua, Tanzania: "between 5° 20′ and 5° 30′ S, 37° 50′ and 38° 40′ E." (Moreau *et al.*, 1946.)

SPECIMENS EXAMINED. Thirteen skins, ten skulls and one entire from the following localities. Tanzania: Makindo, Mandera, Vihinga, Amani; Kenya: Shimba Hills, Rabai Hills. Of these one skin and skull were in the National Museum, Kenya, and four skins and five skulls were in the Paris Museum.

DESCRIPTION (Plate 1b). Pelage of shoulders, flanks and ventral surface *orange-rufous*, head showing more yellow; feet orange-brown, lacking black-zoned hairs; tail very pale orange at base becoming cream-coloured distally, white subterminal zone faintly or not visible.

RANGE. The mainland part of the species' range.

REMARKS. There is a gap of about 200 km. between the nearest known localities of *R. c. macrurus* and this race, and of about 30 km. between *petersi* and *chrysopygus* to the north. But there is no hint of clinal variation *within* this race tending towards either of these neighbouring species. Moreover, in each case the difference involves several characters. Neumann's form *usambarae* was distinguished by the absence of a white zone on the tail (compared with specimens from Zanzibar Island, not *R. p. petersi*). The distinctness of the white zone is variable, even at one locality, e.g. the Shimba Hills, and therefore cannot be used to validate a race *usambarae*. An approximately topotypical specimen of *usambarae* from Amani has been examined in the National Museum, Nairobi. Newmann's *fischeri* was based on a specimen with the underparts pale, but this again was in comparison with material from Zanzibar (*R. p. adersi*). No topotypical specimens have been examined but it seems unlikely that this name is valid.

R. p. adersi

Rhynchocyon adersi Dollman, 1912. Zanzibar Island. Holotype: B.M. (N.H.) 12.1.6.1, skin and skull.

Specimens examined. Six skins and five skulls (including the type) from Zanzibar Island; one skin and skull from Mafia Island.

Description (Plate 1c). Pelage of shoulders, flanks and ventral surface *dull maroon*, head paler but rufous rather than yellow; feet dark reddish-brown, the hind feet especially with many black-banded hairs; tail brighter orange-brown than that of *R. p. petersi*, contrasting more sharply with the white zone which is usually terminal.

Range. Zanzibar and Mafia Islands.

Rhynchocyon chrysopygus

Rhynchocyon chrysopygus Günther, 1881 : 164. "River Mombaça", corrected by Moreau *et al.* (1946) to "Mombasa, Kenya Colony". This must be interpreted rather vaguely as Mombasa district, since there is no evidence of the presence of this form closer to Mombasa than Takaunga, 40 km. to the north. Lectotype (Thomas, 1918): B.M. (N.H.) 80.11.30.7, skin and skull.

Specimens examined. Twenty-nine skins and twenty-two skulls, including the type, from the following localities in Kenya (neglecting the type locality): Takaunga; Sokoke Forest; Arbagundi, Galana River; Gede; Malindi. Of these twenty-one skins and seventeen skulls are in the National Museum, Kenya.

Description (Plate 1a). Pelage of flanks, thighs and back (except rump and head) maroon, similar to that of *R. petersi adersi* but with an admixture of black hairs; rump straw-coloured; central dark stripes of the *R. cirnei* pattern represented by black anterior parts (on maroon ground) and by two rufous marks near the anterior edge of the straw patch, but absent from the posterior part of the rump; second rows faint but visible, third rows obscure; pale spots of the *R. c. reichardi* pattern faintly visible in the second rows, more obscurely in the central rows; top of head grizzled cream, brown and black, closer to *R. cirnei* than to *R. petersi*; ventral pelage only a little paler than dorsal except on throat; feet and ears almost black; proximal part of tail bicoloured, black above, shortly haired except for a tuft of long black hair about 50 mm. from the root; white zone long and subterminal.

Variation. Pelage very constant, but one animal shows partial albinism, having white on the nape, in front of the ears and slightly on the flanks.

Range. The coastal forests of Kenya from at least 3° 40′ S. north to the Galana River (Text-fig. 2).

Remarks. Without knowing what form of *Rhynchocyon*, if any, occurs in the small area between the known ranges of *R. petersi* and *R. chrysopygus*, three alternative situations can be postulated : (1) there is a continuous population with a cline linking the two forms (indicating conspecificity) ; (2) there is a continuous population with an abrupt boundary (indicating a *specific* difference) ; or (3) there are no representatives of the genus in the intervening area. The absence of clinal variation *within* either of the known forms makes the first alternative unlikely. The last alternative seems the most probable but one must postulate an isolation of rather long standing to account for the very considerable differences involved.

Subfamily **MACROSCELIDINAE**

Diagnosis. See Table 3.

Contents. Three genera, two monospecific, the other with nine species.

Range. That of the family except for the lowland rain forest of the Congo north of the Congo River.

Key to the genera of Macroscelidinae

1 Hallux absent ; size large (head and body of adult over 160 mm., condylobasal length over 45 mm., upper tooth-row over 25 mm.) ; two pairs of mammae (antebrachial and pectoral) . . . . ***PETRODROMUS***

– Hallux present ; size smaller (head and body under 160 mm., condylobasal length under 40 mm., upper tooth-row under 22 mm.) ; three pairs of mammae (including abdominal) 2

2 Auditory bullae grossly inflated (Text-fig. 6a) (they can be felt through the skin as a pair of prominent swellings on the *dorsal* surface of the skull on either side of the occiput) ; teeth very crowded, posterior ones rather hypsodont (Text-fig. 9a) ***MACROSCELIDES***

– Auditory bullae not grossly inflated (Text-fig. 6b and c) ; teeth less crowded and less hypsodont (Text-fig. 9b–j) . . . . ***ELEPHANTULUS***

Genus ***PETRODROMUS***

Petrodromus Peters, 1846. Type-species *Petrodromus tetradactylus* Peters.
Cercoctenus Hollister, 1916. Type-species *Petrodromus sultan* Thomas.
Mesoctenus Thomas, 1918. Type-species *Petrodromus rovumae* Thomas.

Diagnosis. Hallux absent ; size large (head and body of adult over 160 mm.) ; two pairs of mammae ; palate relatively entire, lacking very large perforations between M^1–M^1 ; I^1 prominent, more than twice as long as I^2 ; I^3 double-rooted.

Contents. A single, variable species, with one or two marginal forms that may prove to justify specific rank.

Petrodromus tetradactylus

Petrodromus tetradactylus Peters, 1846. Tette, Mozambique.

Synonymy. Under subspecies.

Taxonomic status. The form *tordayi* (Congo), here included in this species, could with some justification be treated as a distinct allopatric species. The other races are either very little differentiated, or highly differentiated but connected by extensive intergradation.

Description. See diagnosis of genus above, and the characters listed in Table 1.

Range. See map (Text-fig. 3). Forest, thicket and the denser types of savanna woodland from Natal north to the Galana River in Kenya, and northwest to the Congo River.

Regional variation. Extensive and complex. It has been described and discussed in detail by Corbet & Neal (1965) and only an outline is presented here. The range is much more continuous than that of *Rhynchocyon* spp. and some of the races listed below must be considered provisional since it is probable that further collecting will confirm the widespread existence of clinal variation.

P. t. tetradactylus

Petrodromus matschiei Neumann, 1900 : 541. Barungi, Tanzania (*c.* 5° 10′ S., 36° 00′ E. according to Moreau *et al.*, 1946).
Petrodromus venustus Thomas, 1903. Namwiwe, Zambia, *c.* 10° 05′ S., 33° 20′ E., according to Ansell *et al.* (1962).
Petrodromus occidentalis Roberts, 1913 : 69. " Northwestern Rhodesia ".
Petrodromus robustus Thomas, 1918 : 367. Upper Lufua River, Katanga, Congo.

Description. A variable race. Dorsal pelage without a clearly defined central stripe ; ventral pelage white ; mid-ventral hairs of the tail unspecialized or with a few slightly enlarged ; sutures between premaxillae and maxillae sinuous ; posterior palatal vacuities large (Text-fig. 5a).

Variation. There is a cline from southeast to northwest across Zambia, the northwestern form " *robustus* " being very large with almost no buff on the flanks.

Range. From the Zambezi through Zambia and Malawi to Katanga, and through western Tanzania as far as Ruanda and Kondoa.

P. t. rovumae

Petrodromus rovumae Thomas, 1897 : 434. Rovuma River, 100 miles inland. Holotype : B.M. (N.H.) 63.10.12.2, in phenoxytol with skull extracted, ♀.
Petrodromus nigriseta Neumann, 1900 : 541. (Nomen nudum).
Petrodromus (*Mesoctenus*) *mossambicus* Thomas, 1918 : 369. Cabaceira, Mozambique.

Description. Dorsal pelage without a clearly defined dorsal stripe ; ventral pelage usually white, occasionally tinged buff ; mid-ventral hairs of tail usually large and club-shaped, occasionally with a terminal knob ; sutures between premaxillae and maxillae sinuous ; posterior palatal vacuities usually small (Text-fig. 5b).

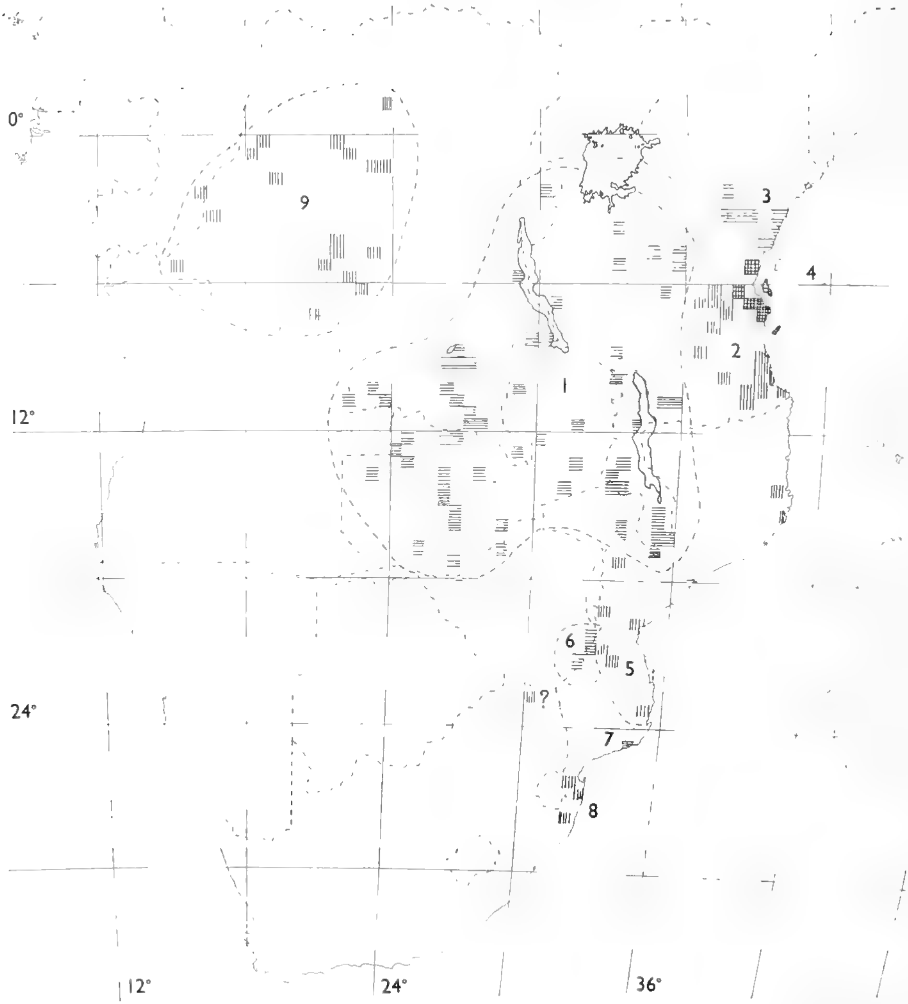

FIG. 3. Recorded distribution of *Petrodromus tetradactylus*. 1: *P. t. tetradactylus*; 2: *P. t. rovumae*; 3: *P. t. sultan* (incl. *sangi*); 4: *P. t. zanzibaricus*; 5: *P. t. beirae*; 6: *P. t. swynnertoni*; 7: *P. t. schwanni*; 8: *P. t. warreni*; 9: *P. t. tordayi*.

VARIATION. There is very great individual variation in the mid-ventral bristles of the tail. The southern form "*mossambicus*" tends towards *P. t. tetradactylus* in that the caudal bristles are less developed and the palatal vacuities are rather larger (*not* smaller as stated by Thomas (1918)). The complex variation in north-eastern Tanzania is described below under *P. t. sultan*.

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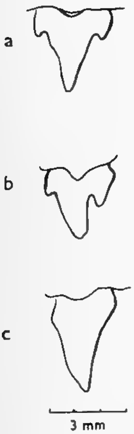

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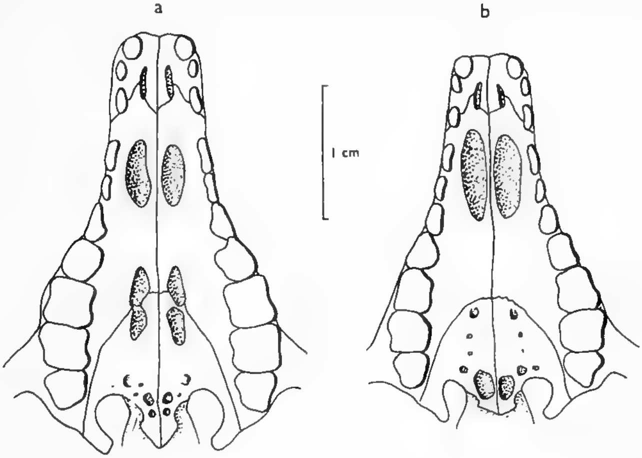

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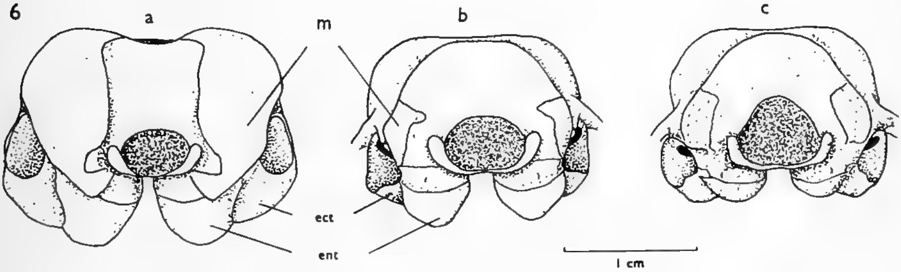

FIG. 4. Left DC^1 of *Rhynchocyon cirnei*. (a) *R. c. shirensis* (B.M. 11.7.3.1); (b) ditto (B.M. 10.9.21.1); (c) *R. c. reichardi* (B.M. 11.1.29.4). Anterior edge to the left.

FIG. 5. Palate of *Petrodromus tetradactylus*. (a) *P. t. tetradactylus*, South West Tanzania (B.M. 33.8.19.1); (b) *P. t. rovumae*, eastern Tanzania (B.M. 22.7.17.105).

FIG. 6. Occipital views of skull. (a) *Macroscelides proboscideus* (B.M. 4.2.3.12); (b) *Elephantulus rupestris* (B.M. 25.1.2.33); (c) *Elephantulus myurus* (B.M. 1.7.9.5). *ect:* ectotympanic component of bulla; *ent:* entotympanic component of bulla; *m:* mastoid.

RANGE. Eastern Tanzania and northeastern Mozambique.

REMARKS. This race may prove to intergrade with *P. t. tetradactylus* in the south (in Mozambique), but there is no indication of intergradation with the typical race in western Tanzania, from which *P. t. rovumae* can be distinguished by the knobbed bristles and relatively entire palate (Text-fig. 5).

P. t. sultan

Petrodromus sultani Thomas, 1897 : 435 (corrected to *sultan* by Thomas (1898)). Mombasa, Kenya. Holotype : B.M. (N.H.) 80.11.30.10, skin and skull, ♂.

Description. Dorsal pelage with median reddish brown zone narrow and discrete, flanked by zones of pure grey ; mid ventral bristles of tail very long, and expanded at the tip to form a clearly defined knob, tail almost naked above ; ventral pelage usually buff ; skull large (upper tooth row over 28 mm.) ; rostrum narrow ; sutures between premaxillae and maxillae not sinuous ; posterior palatal vacuities absent or almost so ; nasals short (less than 130% of frontals).

Variation. Very slight except in the region of contact with *P. t. rovumae* (see below).

Range. The coastal area of Kenya and Tanzania from the Galana River south to the Pangani River, with a zone of hybridization with *P. t. rovumae* extending further south at least to Dar-es-Salaam.

Remarks. In the region where this race overlaps with *P. t. rovumae* animals occur with all combinations of "*rovumae*" and "*sultan*" characters—there is no cline with uniformly intermediate characters.

P. t. sangi

Petrodromus sultani sangi Heller, 1912. Mount Mbololo, Taita Hills, Kenya Holotype : U.S. Nat. Mus. 181822, ♂.

Description. Differs from *P. t. sultan* only by the pale, rather yellowish, colour of the dorsal stripe.

Range. Only known from the type locality. This may be an isolated population ; a specimen from Taveta is typical of *P. t. sultan*.

P. t. zanzibaricus

Petrodromus tetradactylus zanzibaricus Corbet & Neal, 1965. Makunduchi, Zanzibar Island. Holotype : B.M. (N.H.) 19.6.9.10, skin and skull, ♀.

Description. Dorsal pelage with the central zone discrete and separated from the buffy flanks by zones of pure grey, as in *P. t. sultan*, but rather less red ; caudal bristles knobbed ; smaller than *P. t. sultan* (upper tooth-row under 28 mm.) ; rostrum relatively wide, tooth-rows convergent anteriorly as in *P. t. rovumae* ; sutures between premaxillae and maxillae sinuous as in *P. t. rovumae*.

Range. Zanzibar Island.

Remarks. This is a fairly uniform population showing a mixture of the characters of *sultan* and *rovumae*.

P. t. beirae

Petrodromus beirae Roberts, 1913 : 69. Zimbiti, Beira, Mozambique. Holotype : Transvaal Museum, skin and skull, ad. ♂.

Description. Dorsal stripe diffuse ; flanks bright buff, sharply demarcated from the white ventral pelage ; tail lacking specialized bristles and almost naked above ; skull as in *P. t. tetradactylus* but P^3 commonly with an anterior cusp.

Range. Known from the Beira and Gorongoza districts of Mozambique, i.e. south of the Zambezi, and from the south bank of the Save River (Dalquest, 1965).

P. t. swynnertoni

Petrodromus tetradactylus swynnertoni Thomas, 1918 : 368. Chirinda Forest, Melsetter, Rhodesia. Holotype : B.M. (N.H.) 8.7.19.10, skin and skull, ♂.

Description. Dorsal pelage duller than that of *P. t. beirae* and the nominate race ; tail thinly haired above so that the scales are obscured.

Range. Montane forest of the Melsetter district, Rhodesia.

Remarks. This form is doubtfully distinguishable from the nominate race but may prove to intergrade with *P. t. beirae*.

P. t. schwanni

Petrodromus schwanni Thomas & Wroughton, 1907*b*. Coguno, Inhambane, Mozambique. Holotype : B.M. (N.H.) 6.11.8.32, skin and skull, ♂.

Description. Dorsal stripe diffuse but rather grey ; flanks grey, with very little buff, not sharply demarcated from belly ; ventral pelage usually buff ; caudal bristles knobbed as in *P. t. sultan* ; skull as in *P. t. tetradactylus* except that the posterior palatal vacuities are small or absent, as in *P. t. sultan*.

Range. Known only from the type locality. Corbet & Neal (1965) postulated that this form might be isolated between the Limpopo and Save Rivers, but Dalquest (1965) has since recorded *P. t. beirae* from the Save river and has confirmed (*in litt.*) that his specimens did indeed lack knobbed bristles and did come from the south side of the river.

Remarks. This race resembles *P. t. sultan* in two characters, the knobbed caudal bristles and the entire palate, but more closely resembles the nominate race in all other respects.

P. t. warreni

Petrodromus tetradactylus warreni Thomas, 1918 : 364. Mangazi, Zululand, Natal. Holotype : B.M. (N.H.) 18.4.9.1, skin and skull, ♂.

Description (based only on the type). Similar to the nominate race but flanks grey with very little buff ; tail very scantily haired, ventral hairs normal.

Range. Coastal region of northern Natal and adjacent part of Mozambique.

P. t. tordayi

Petrodromus tordayi Thomas, 1910. Misumba, Sankuru River, Congo. Holotype: B.M. (N.H.) 9.12.12.5, skin and skull.
Petrodromus tordayi tumbanus Kershaw, 1923*b*. Bikoro, Lake Tumba, Congo.

Description. Dorsal pelage darker than in any other race, not forming a discrete stripe; buff stripe on flanks very prominent; ventral pelage cream, often washed with buff; tail nearly naked; size considerably smaller than in the adjacent Katangan form of *P. t. tetradactylus* (condylo-basal length usually under 50 mm.); skull as in the nominate race.

Variation. The ventral pelage is variable and in some individuals the orange-buff of the flanks extends over the entire under-parts without interruption.

Remarks. There is an apparent gap between the range of this race and the very large form of the nominate race in Katanga. The morphological differences are sufficiently sharp and numerous to suggest that there is no intergradation between the two forms. This must be considered a potential species, although there is no character that distinguishes it from *all* other races.

Genus *MACROSCELIDES*

Macroscelides Smith, 1829. Type-species *M. typus* Smith = *Sorex proboscideus* Shaw.
Eumerus I. Geoffroy, 1829.
Macroscelis Fischer, 1830.
Rhinomys Lichtenstein, 1831. Type-species *R. jaculus* Lichtenstein = *Sorex proboscideus* Shaw.

Diagnosis. Auditory bullae enormously enlarged, involving the mastoids and parts of the occipital, squamosal and parietal bones; two lower molars; posterior teeth rather hypsodont; hallux present; three pairs of mammae (antebrachial, pectoral and abdominal).

Contents. A single species.

Remarks. The osteological description of this genus by Evans (1942) is invalid since he mistakenly used *Elephantulus rozeti* to represent the genus *Macroscelides* in contrast to *E. rufescens* representing *Elephantulus*.

Macroscelides proboscideus

Sorex proboscideus Shaw, 1800 : 536. "Cape of Good Hope", limited by Roberts (1951) to Roodeval, Oudtshoorn division, southwestern Cape Province.
Macroscelides typus Smith, 1829. "Interior of South Africa".
Rhinomys jaculus Lichtenstein, 1831. "East coast of South Africa".
Macroscelides typicus Smith, 1838.
Macroscelides melanotis Ogilby, 1838 : 5. Between Cape Town and Damaraland.
Macroscelides proboscideus hewetti Roberts, 1929. Cradock, Cape Province.
Macroscelides proboscideus chiversi Roberts, 1933 : 265. 76 miles north of Upington, Cape Province.
Macroscelides proboscideus langi Roberts, 1933 : 265. Vlermuisklip, Van Rhynsdorp Dist., Cape Province.
Macroscelides typicus isabellinus Shortridge & Carter, 1938. Port Nolloth, Cape Province.

Macroscelides typicus ausensis Roberts, 1938 : 231. 20 miles north of Aus, S.W. Africa.
Macroscelides typicus harei Roberts, 1938 : 232. Brospan, midway between Brandvlei and Van Wyk's Vlei, Cape Province.
Macroscelides typicus brandvleiensis Roberts, 1938 : 232. Brandvlei, Cape Province.
Macroscelides typicus calvinensis Roberts, 1938 : 232. 15 miles east of Calvinia, Cape Province.
Macroscelides proboscideus flavicaudatus Lundholm, 1955 : 285. 6 miles from the mouth of the Omaruru River, South West Africa.

Specimens examined. Ten skins and seven skulls from South West Africa (Berseba) ; eight skins and four skulls from Cape Province (Deelfontein and Klipfontein) ; the type of *M. melanotis* (skin and skull) ; two in spirit (and one of these skeletonized) from " Bushmanland ".

Description (in amplification of the generic characters given above and the characters listed in Table 1). Length of head and body about 110 mm. (104–115) ; length of tail about 120 mm. (115–130 ; mean 108 % of head and body) ; length of hind feet 32–35 mm. ; length of ear 19–22 mm. ; length of snout, from incisors, about 12 mm. Pelage very long, about 17 mm. long dorsally, softer than in any other species, scarcely distinguishable in colour from that of *Elephantulus edwardi* and *E. rupestris* ; light greyish brown dorsally becoming a purer yellowish-brown on the flanks and changing fairly abruptly to white ventrally ; all hairs black for proximal three-quarters or more. Distinguished from *Elephantulus* spp. by absence of any strong tinge of buff behind the ears. Tail bicoloured proximally, black tips of hairs increasing in length distally so that distal half is uniformly black above and below, with the hairs completely obscuring the scales. Ear with the supratragus and tragus large, thin and almost naked (Text-fig. 8a). Claw of hallux reaching half-way to margin of distal pads. Inflation of auditory region of skull extending dorsally to leave a sagittal gap of about 4 mm., and forwards in the pterygoid region as far as the posterior edge of the palate. Rostrum very short, teeth crowded (Text-fig. 9a). I^1 unicuspid ; I^2 to P^1 about equal in size, clearly bicuspid, incisors with one, canine with two roots ; P^2 molariform with two prominent lingual cusps ; P^4 and M^1 equal and largest. Mandible short and deep with the teeth closely crowded. I_2 to P_1 subequal, obscurely two- or three-lobed ; P_2 and P_3 narrow, sectorial ; P_4 largest.

Range (Text-fig. 2). The subdesert steppes of Cape Province and South West Africa, extending northwestwards at least to the Omaruru River (22° S.) and southeastwards to Grahamstown, apparently avoiding the coastal macchia zone. Probably not extending north of the upper Orange River. Sympatric throughout its range with *Elephantulus edwardi* and/or *E. rupestris*, but probably not overlapping extensively with *E. myurus* in the northeast, nor with *E. intufi* in the northwest.

The range is divided into two by the Orange River, but in each of the two parts it is likely to be continuous.

Claims that this species extends further north are based on two pieces of evidence : (1) the type specimen of *M. melanotis* which is labelled " Damaraland ", and (2) the record of this species having been collected at Benguella, Angola by Monteiro, quoted by Sclater (1900) and Roberts (1951). This latter claim can be immediately dismissed : the specimen (in spirit in the British Museum) has been labelled *M.*

proboscideus but is in fact an *Elephantulus intufi*. The type of *melanotis* has been examined and is undoubtedly a *Macroscelides proboscideus*. Allowing for the poor condition (the skin, now dry, was probably in alcohol originally and the skull is represented only by the rostrum and mandibles, with very worn teeth), it is not distinguishable from the series from Namaqualand and from Deelfontein. (There is no indication of the " pale reddish brown chest " of the original description, but that part of the skin is very tattered and dirty). There is no reason for assuming that this specimen came from Damaraland. It was described by Ogilby (1838) as having been " procured by Captain Alexander during his recent journey into the country of the Damaras ". But Alexander's journey started and finished at Capetown !

Subspecific variation. Roberts (1951) recognized nine subspecies in addition to the enigmatic *melanotis*. These were all diagnosed by trivial differences in the shade of the pelage and in average size and there was no implication that any of them represent objective subspecies or anything more than arbitrary samples from a system of continuous variation. Shortridge used the name *melanotis* for all the animals from South West Africa, i.e. from north of the Orange River, and claimed that they differed from true *proboscideus* in having black ears, as opposed to brown, and longer, darker tails. Series examined from Berseba (South West Africa—nine specimens), Klipfontein (Little Namaqualand—five specimens) and Deelfontein (central Cape Province—three specimens), the last two being south of the Orange River, show no differences in size, length and pelage of tail, nor in the colour of the ears (in dry skins). There is a very slight difference in colour, the specimens from Deelfontein being rather more yellow and less grey than the others, but judging from Roberts' description of the other forms this character shows no consistent pattern of variation.

M. p. flavicaudatus is known from two specimens from the Omaruru River, about 500 km. north of the nearest known locality. It is characterized by the very pale dorsal pelage and tail : " The tail of the male is whitish, with the end pale yellowish and covered with long hairs. In the female the tail is yellowish brown and only the very base is whitish. " (Lundholm, 1955). It is therefore a distinctive race on the basis of present knowledge and it seems probable that it may represent an isolated northern segment of the species.

Genus ***ELEPHANTULUS***

Macroscelides Smith, 1829 (in part).
Elephantulus Thomas & Schwann, 1906 : 577. Type-species *Macroscelides rupestris* Smith.
Elephantomys Broom, 1937. Type-species *E. langi* Broom.

Diagnosis. Auditory bullae not grossly inflated ; hallux present ; three pairs of mammae.

Contents. Nine species.

Delimitation of the species. *E. rozeti* of northwestern Africa is an isolated and clearly defined species. The suggestion of Ellerman & Morrison-Scott (1951) that it is conspecific with *E. rufescens* of East Africa was quite unjustified.

Amongst the group with three lower molars, previously placed in a genus or subgenus *Nasilio*, the only discontinuity of variation suggesting specific rank is between *E. fuscipes* of western Uganda and adjacent regions and the remainder, which can be considered a single species, *E. brachyrhynchus*. The latter includes the forms *brachyurus* and *molosae* which were given specific rank by Allen (1939).

Allen (1939) listed eight other species from East Africa. Of these all but one (*E. revoili* of Somalia) appear to represent a single species showing considerable regional variation, mostly clinal, the earliest name being *E. rufescens*.

The remaining forms in southern Africa have caused a great deal of confusion. Smith (1836, 1838) described and illustrated three species of this group, namely *edwardi*, *intufi* and *rupestris*, with type localities, " Oliphant's River ", " Flats beyond Kurrichane " (i.e. Marico district, W. Transvaal), and " mountains near the mouth of the Orange River ". Specimens bearing these names, but all labelled simply " South Africa ", came to the British Museum. The two labelled " *Macroscelides rupestris* " were subsequently marked " cotype " by Thomas. Allen (1939) listed five species, namely *capensis*, *edwardsii*, *intufi*, *rupestris* and *vandami* (*capensis* and *vandami* having been described by Roberts in 1924). Roberts (1951) recognized nine species, namely *barlowi*, *capensis*, *edwardi*, *intufi*, *kobosensis*, *myurus*, *namibensis*, *rupestris* and *vandami*. This differed from Allen's list in the addition of *barlowi*, *kobosensis* and *namibensis*, all described by Roberts in 1938, and by the recognition of *myurus* as a distinct species (listed as a race of *E. rupestris* by Allen). Ellerman *et al.* (1953) reduced the entire group to two species, *intufi* and *rupestris*, which bear almost no relation to the species of previous authors. These were described as a more western species, *intufi*, with P^2 molariform, and a more eastern species, *rupestris*, with P^2 sectorial. This drastic change from Robert's classification was due to the realization that the so-called cotypes of *rupestris* in the British Museum had P^2 sectorial and therefore did not correspond to Robert's conception of *rupestris*. This is indeed the case, but there is no evidence that these specimens came from the type locality of *rupestris* and they do in fact agree perfectly with *E. myurus*, a species not recognized by Smith, and which has not subsequently been found anywhere near the mouth of the Orange River. The name *rupestris* can therefore be retained for the species with molariform P^2 found in that region. *E. intufi* also has P^2 molariform but differs from *E. rupestris* in size and pelage. Two other species can be recognized, differing from *rupestris* and *intufi* in having P^2 sectorial and the ectotympanics greatly swollen. These are a northern one, which is *E. myurus*, and a southern one, which we consider to be *E. edwardi* of Smith and *E. capensis* of Roberts. Roberts (1951) has disputed this synonymy and there are in fact some discrepancies between Robert's *capensis* and Smith's description and figure of *edwardi*. But topotypical specimens of *capensis* do agree closely with the type of *edwardi* and with a considerable number of specimens labelled *edwardi* received by the British Museum from Edward Verreaux after whom the species was named. All these, including the type, are only labelled " South Africa ". The lack of close agreement with Smith's figures can probably be explained by the confusion in obtaining specimens for illustration, reported by Smith himself (1838 : text to Plate 15).

KEY TO THE SPECIES OF *ELEPHANTULUS*

1 Pectoral gland present (naked or short-haired patch in centre of thorax) 2

– Pectoral gland absent 4

2 Prominent brown mark behind eye ; two lower molars (i.e. ten lower teeth) 3

– No brown mark behind eye ; three lower molars **E. fuscipes** (p. 102)

3 Hair of tail becoming long towards the tip, forming a brush ; tail about 120 per cent of head and body ; I^2 equal in size to I^1 and I^3 **E. revoili** (p. 88)

– Hair of tail not forming a brush ; tail about equal to head and body , I^2 much smaller than I^1 **E. rufescens** (p. 82)

4 Tail usually shorter than head and body ; three lower molars (i.e. eleven lower teeth) **E. brachyrhynchus** (p. 97)

– Tail not shorter than head and body ; two lower molars 5

5 P^1 with a lingual cusp ; P^2 molariform, with *two* well developed lingual cusps (Text-figs. 7a and b) ; ventral pelage superficially white 6

– P^1 lacking a lingual cusp ; P^2 sectorial with or without *small* lingual cusps (Text-figs. 7c and d) ; ventral pelage showing grey (except in the North African *E. rozeti*) 7

6 Size larger (upper tooth row usually over 18·7 mm.) ; tail about 115% of head and body, distinctly tufted towards the tip, predominantly black above ; white eye-ring narrow, broken above and below the eye ; P_2 and P_3 with three cusps, arranged in a triangle, behind the principal cusp **E. rupestris** (p. 90)

– Size smaller (upper tooth-row usually under 18·7) ; tail about 105% of head and body, not distinctly tufted, speckled above ; white eye-ring conspicuous and unbroken ; P_2 and P_3 with only two cusps, arranged transversely, behind the principal cusp **E. intufi** (p. 89)

7 Ectotympanic parts of bullae inflated to same level as entotympanic parts (Text-fig. 6c) ; I_2 equal to I_1 and I_3 (southern Africa) 8

– Ectotympanic parts of bullae much less inflated than entotympanic parts (cf. Text-fig. 6b) ; I_2 larger than I_1 and I_3 (North Africa) **E. rozeti** (p. 76)

8 P^2 with one, occasionally two, lingual cusps (Text-fig. 7c) , P_1 with two roots ; supratragus small and fairly thick ; premaxillary suture slightly sinuous (Text-fig. 9h) ; tail bicoloured throughout its length, yellow-brown above, entirely short-haired **E. myurus** (p. 93)

– P^2 without a lingual cusp (Text-fig. 7d) ; P_1 with a single root ; supratragus large and thin (Text-fig. 8c) ; premaxillary suture straight (Text-fig. 9i) ; tail black above, distal half black all round and slightly tufted **E. edwardi** (p. 96)

Elephantulus rozeti

Macroscelides rozeti Duvernoy, 1833. Near Oran, Algeria.

SYNONYMY. Under subspecies.

DESCRIPTION. See Table 1 for diagnostic characters. This species shows no very close resemblance to any other. It differs from the nearest East African species (*E. rufescens* and *E. revoili*) in lacking a pectoral gland and a distinctive facial pattern, in having the rhinarium naked, P^2 narrower and in the auditory bullae in which the anterior (alisphenoid) part is almost as large as the posterior (tympanic) part.

The length of head and body is about 110 mm. (90–130) ; tail about 120 mm. (about 110% of head and body) ; hind feet about 33 mm. (29–37) ; ear about 26 mm. (23–30) ; snout (from incisors) about 15 mm. The pelage is about 14 mm. long dorsally, the proximal three-quarters black, the overall colour varying from

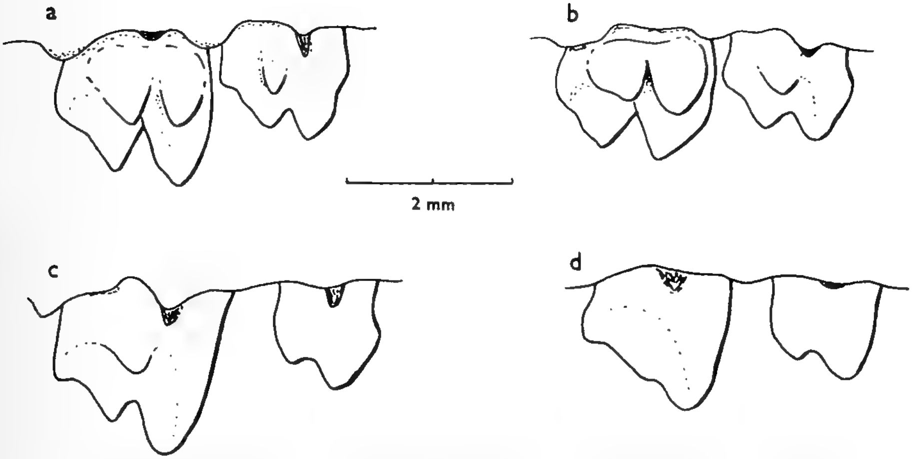

FIG. 7. Lingual aspect of P^1 (right) and P^2 (left) of *Elephantulus spp.*, viewed from a little below the horizontal. (a) *E. rupestris* (B.M. 25.1.2.33); (b) *E. intufi* (B.M. 28.9.11.72); (c) *E. myurus* (B.M. 9.1.20.11); (d) *E. edwardi* (B.M. 1417a).

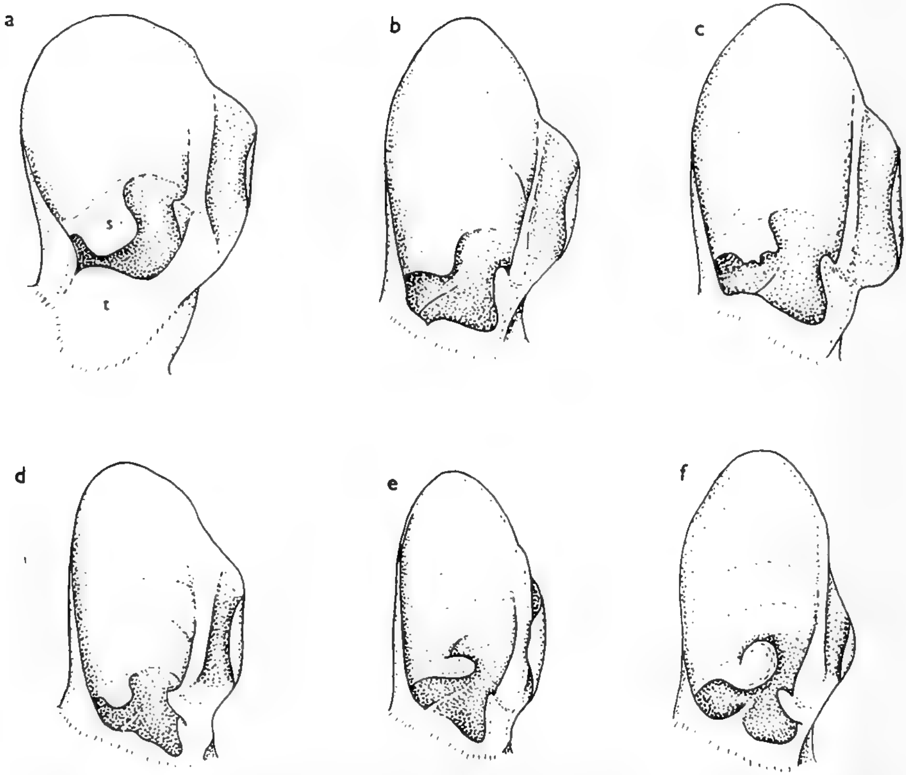

Fig. 8. Left ear of (a) *Macroscelides proboscideus* (B.M. 12.4.25.18); (b) *Elephantulus rufescens* (B.M. 36.11.4.67); (c) *E. edwardi* (B.M. 66.3565); (d) *E. brachyrhynchus* (B.M. 63.1009 from Angola—supratragus typical); (e) *E. brachyrhynchus* (B.M. 58.6.18.16 from Mozambique—supratragus atypical); (f) *E. fuscipes* (B.M. 84.5.1.6, the type). Hair is not shown except to indicate the limit of the body pelage. *s*: supratragus; *t*: tragus.

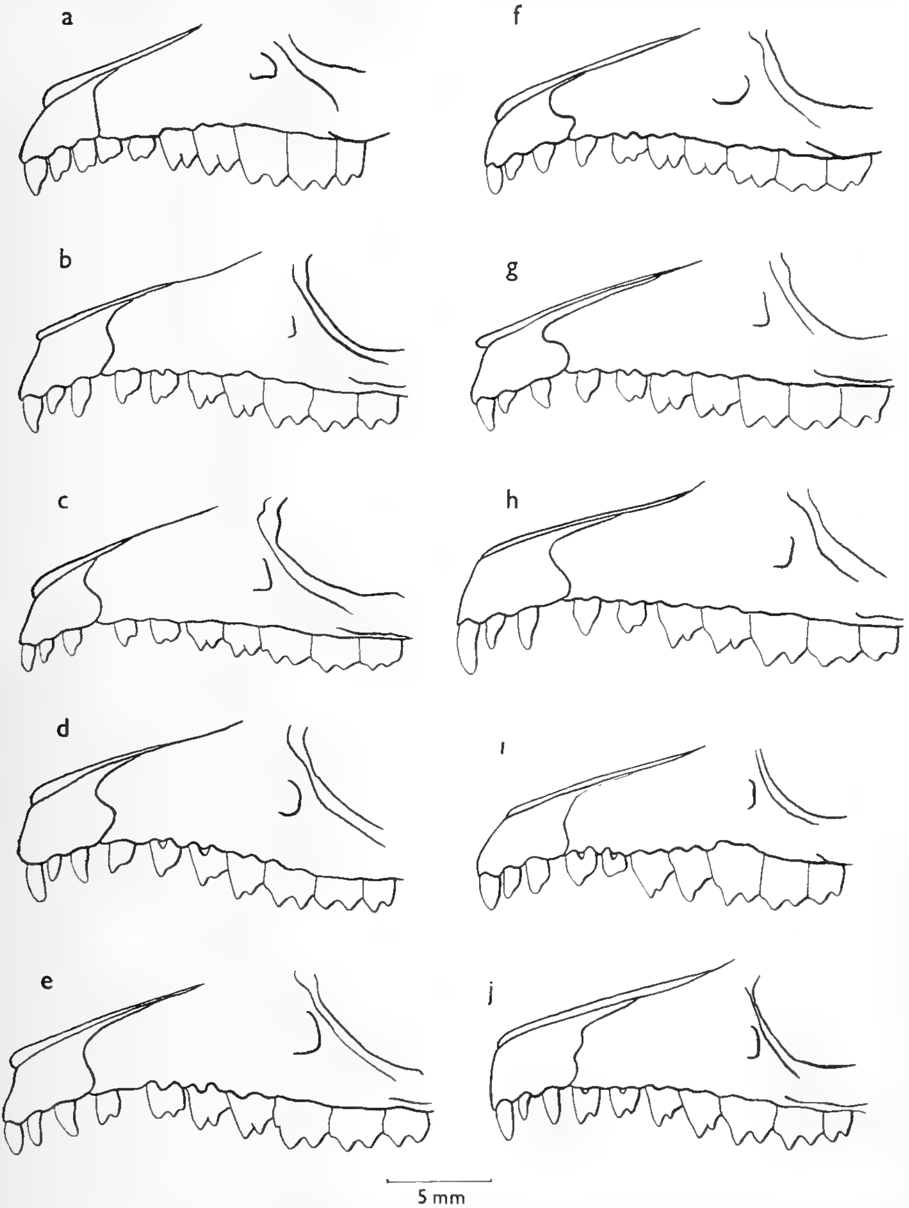

FIG. 9. Left profile of rostrum with permanent dentition. (a) *Macroscelides proboscideus* (B.M. 4.2.3.14); (b) *Elephantulus brachyrhynchus* (B.M. 13.10.18.19); (c) *E. fuscipes* (Tervuren 8957); (d) *E. rufescens* (B.M. 51.406); (e) *E. revoili* (B.M. 5.3.2.3); (f) *E. intufi* (B.M. 28.9.11.72); (g) *E. rupestris* (B.M. 25.1.2.55); (h) *E. myurus* (B.M. 9.1.20.11); (i) *E. edwardi* (B.M. 1.7.9.3); (j) *E. rozeti* (B.M. 27.3.9.1).

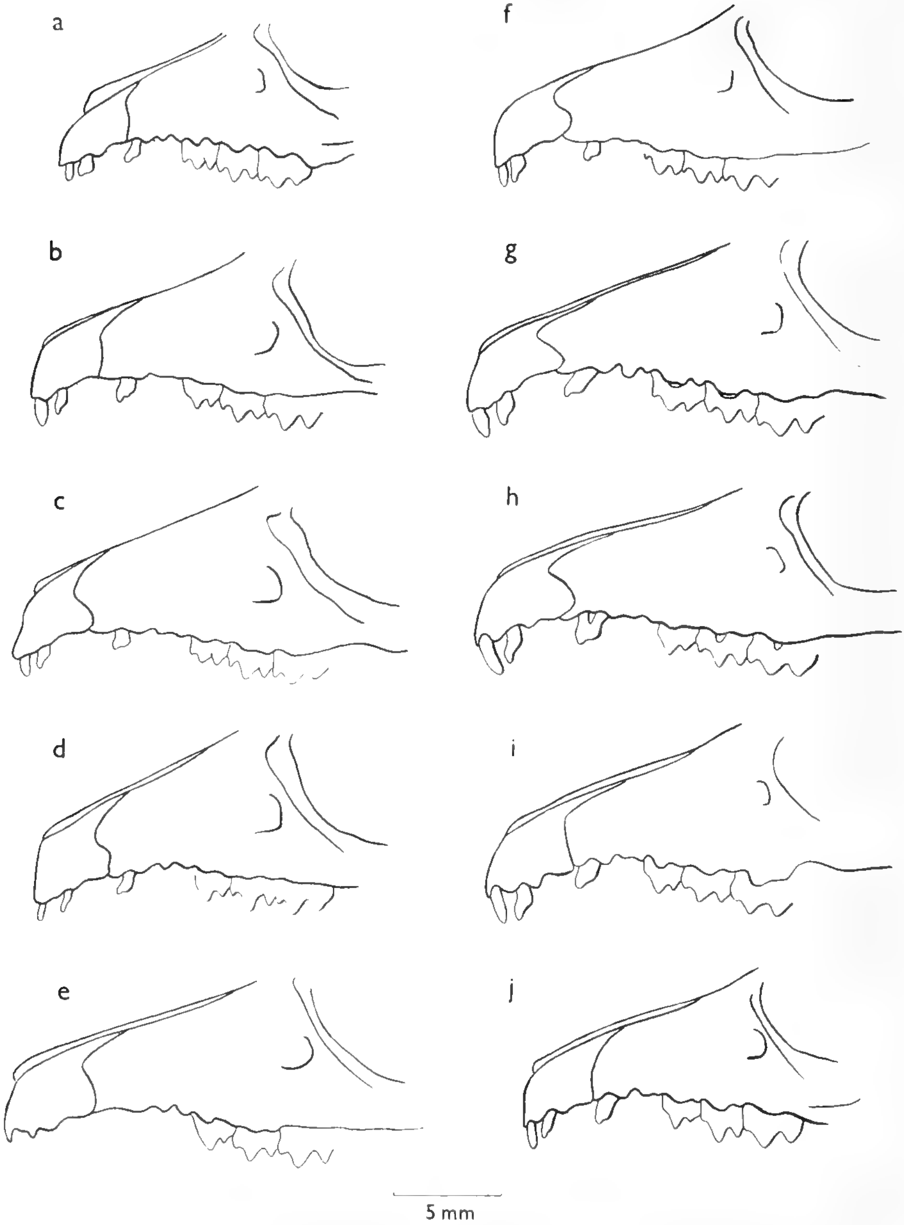

FIG. 10. Left profile of rostrum with deciduous dentition. Deciduous teeth are shown by continuous lines, permanent teeth by dotted lines. (a) *Macroscelides proboscideus* (B.M. 2.9.1.18); (b) *Elephantulus brachyrhynchus* (B.M. 26.5.12.24); (c) *E. fuscipes* (B.M. 84.5.1.6, the holotype); (d) *E. rufescens* (B.M. 64.514); (e) *E. revoili* (B.M. 97.8.9.5); (f) *E. intufi* (B.M. 28.9.11.62); (g) *E. rupestris* (B.M. 1.7.9.2); (h) *E. myurus* (B.M. 1.7.9.5); (i) *E. edwardi* (B.M. 7.1.1.3); (j) *E. rozeti* (B.M. 67.187).

yellowish brown to pale pinkish buff, yellower on the flanks above the fairly sharp transition to the white ventral pelage. The proximal zone of the ventral pelage is black giving a slight greyness to the surface appearance. The subcaudal gland is especially well developed. The diploid chromosome number is 28 (Matthey, 1954).

RANGE (Text-fig. 12). The Mediterranean and subdesert zones of northwestern Africa from southwestern Morocco to Tunisia and Tripolitania. It has been recorded from sea-level up to 1,100 m. *E. rozeti* is unique amongst the Macroscelididae in having no contact with any other species of the family, which may allow a wider range of habitats to be occupied. The Atlas Mountains divide the western part of the range into a coastal region with typical Mediterranean climate, and a drier southern region continuous with the desert. In northeastern Algeria and Tunisia the range is more likely to be continuous from the coast to the edge of the desert.

REGIONAL VARIATION. From western Morocco twelve specimens are available from nine localities, including the types of *atlantis* and *moratus*. These names were based on slight differences of size and colour, but the group as a whole cannot be divided on this basis. Six skins from Oran (topotypical *rozeti*) could not be clearly separated from the Moroccan series although they were inclined to be rather darker. There is therefore no reason to recognize more than one race in the coastal part of the range. From the southern slopes of the Algerian Atlas twenty-two specimens are available from the area north and south of Biskra (including the type of *deserti*) and six from Guelt-es-Stel (including the type of *clivorum*). These cannot be clearly separated into two groups, but together they are distinguishable from the coastal form by their smaller size and pale, sandy colour. The size difference can be most accurately assessed by the length of the upper tooth-row. Taking 17·45 mm. as the dividing line, this separates 86% of the *E. r. rozeti* (n = 14) from 87% of the *E. r. deserti* (n = 23). It is unlikely that the two groups are completely isolated, but provisionally they can be treated as distinct subspecies dignosed as follows, all measurements referring to individuals with complete permanent dentition.

E. r. rozeti

Elephantulus rozeti moratus Thomas, 1913 : 587. Jebel Chedar, about 80 km. southeast of Mazagan, S.W. Morocco.

Elephantulus rozeti atlantis Thomas, 1913 : 587. North slope of Great Atlas, south of Seskawa, Ain Moussa, Morocco.

DESCRIPTION. Head and body 113–130, mean 121 ; tail 127–140, mean 132 ; hind foot 33–37, mean 34·4 ; upper tooth-row 17·0–18·8, mean 17·8 ; dorsal pelage darker, brown tips of hairs about 2 mm. long.

RANGE. Morocco and Algeria north of the Atlas.

E. r. deserti

Macroscelides rozeti deserti Thomas, 1901*b*. Near Jebel Bourzel, Biskra, Algeria.

Elephantulus deserti clivorum Thomas, 1913 : 588. Guelt-es-Stel, E. Algeria.

DESCRIPTION. Head and body 90–120, mean 105; tail 95–128, mean 117; hind foot 29–33, mean 31·7; upper tooth-row 16·5–17·6, mean 16·9; dorsal pelage pale greyish buff, brown tips 3–4 mm. long.

RANGE. Tunisia and Algeria south of the Atlas.

Elephantulus rufescens

Macroscelides rufescens Peters, 1878. Ndi, Taita, Kenya.
Macroscelides pulcher Thomas, 1894 : 69. Usambiro, south of Lake Victoria, Tanzania.
Macroscelides boranus Thomas, 1901*a*. Mega, Ethiopia (4° S.). Not Kenya (Moreau *et al.*, 1946).
Macroscelides peasei Thomas, 1901*b*. Hoolul, 30 miles northwest of Harar, Ethiopia.
Macroscelides somalicus Thomas, 1901*c*. Arabsiyo, 25 miles northwest of Hargeisa, Somalia.
Elephantulus dundasi Dollman, 1910. Harich, near Lake Baringo, Kenya.
Elephantulus phaeus Heller, 1910. Sotik dist., Kenya (0° 52′ S., 35° 25′ E.).
Elephantulus delicatus Dollman, 1911. Mt Nyiro, Orr Valley, Kenya.
Elephantulus pulcher rendilis Lönnberg, 1912. Near Chanler Falls, Kenya.
Elephantulus rufescens mariakanae Heller, 1912. Mariakani, Kenya (3° 52′ S., 39° 29′ E.)
Elephantulus ocularis Kershaw, 1921. Dodoma, Tanzania.
Elephantulus renatus Kershaw, 1923*a*. Gwao's, near Itiga, Singida, Tanzania.
Elephantulus rufescens hoogstraali Setzer, 1956. Ikote, Sudan (4° 05′ N., 33° 04′ E.).

TAXONOMIC STATUS. A clearly defined species, not closely resembling any other except *E. revoili*.

SPECIMENS EXAMINED. Ethiopia ten (including five received on loan from Oklahoma State University); Kenya 102 (including nine in the National Museum, Kenya); Somalia eighteen (including seven received on loan from the University of Florence); Sudan five; Tanzania thirty-four (including two received on loan from Berlin Museum, and six in the museum of the College of Wildlife Management, Mweka, Tanzania); Uganda ten.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8b, 9d and 10d for structural details. *E. rufescens* is closely similar to *E. revoili* with which species alone it shares the presence of a hairy rhinarium and distinctive facial pattern. The last feature gives these species a very close resemblance to the much larger *Petrodromus tetradactylus* which meets *E. rufescens* in parts of Tanzania and Kenya, and it is also of interest to note that in *Petrodromus* there is often a naked or shortly haired area apparently representing a vestigial pectoral gland. *E. rufescens* differs from *E. revoili* in its smaller size (see Text-fig. 13), shorter and less hairy tail, small I^2, and in the dorsal pelage which everywhere shows considerably more yellow than does that of *E. revoili*. The subcaudal gland is rather rudimentary being represented by a slight ridge in the mid-ventral line of the proximal part of the tail. The pectoral gland is fringed by short, wholly white hairs, quite different from the surrounding pelage.

RANGE (Text-fig. 11). The dry woodland and steppe zones of East Africa from Tanzania (south at least to the River Ruaha) northeastwards through Kenya to Somalia and eastern Ethiopia; and northwestwards as far as eastern Uganda and the extreme southern region of Sudan. In Tanzania there is one record from the

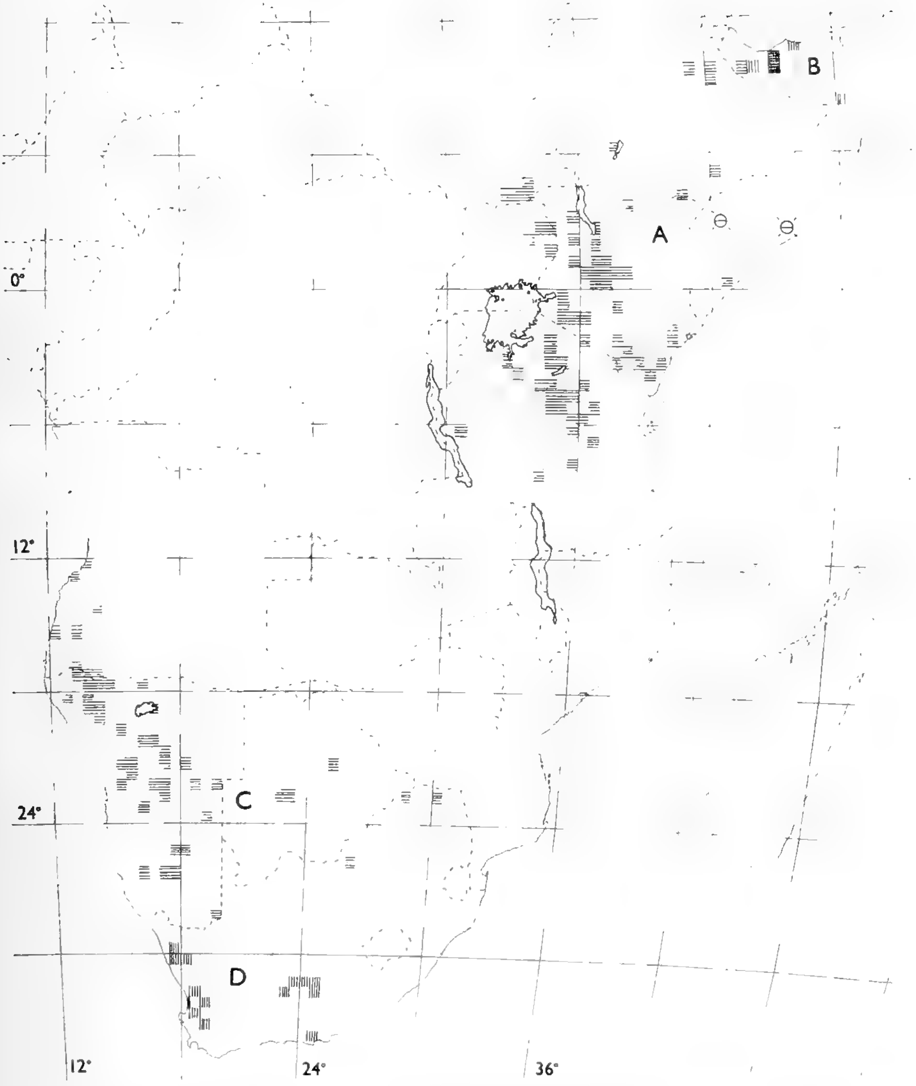

FIG. 11. Recorded distribution of A: *Elephantulus rufescens*; B: *E. revoili*; C: *E. intufi*; D: *E. edwardi*. The circles indicate approximate localities of *E. rufescens*.

extreme west from Katavi Mbuga (*c.* 6° 45′ S., 30° 50′ E.), given, without details, by Swynnerton and Hayman (1951). Comparison with a vegetation map suggests that this may be an isolated population. In Tanzania the range of *E. rufescens* abuts that of *Petrodromus tetradactylus* but there may well be a clear difference in

FIG. 12. Recorded distribution of A: *Elephantulus rozeti*; B: *E. rupestris*; C: *E. myurus.*

habitat, the *Elephantulus* being in the more open grassland and the *Petrodromus* in woodland. In Kenya the range overlaps that of *E. brachyrhynchus*, but here also there is probably a difference in habitat, *E. brachyrhynchus* being confined to the wetter woodland. In Uganda there is no evidence of precise overlap with *E. brachyrhynchus* and *E. fuscipes*, which replace *E. rufescens* entirely in the wetter western parts of the country. In Somalia *E. rufescens* is probably replaced by *E. revoili* in the drier parts of the north and east.

Judging by the distribution of the wooded steppe zone occupied by *E. rufescens*

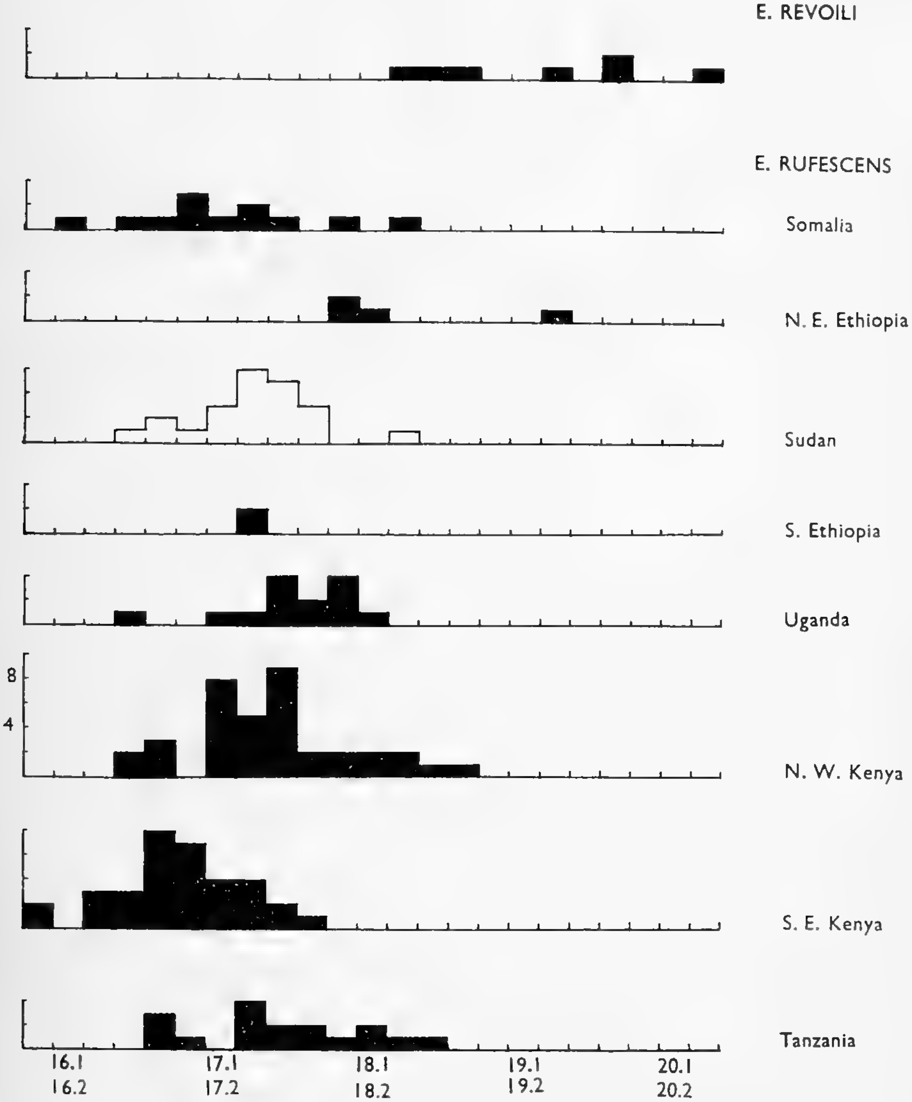

FIG. 13. Variation in length of the upper tooth-row of *Elephantulus revoili* and *E. rufescens*. The data for the Sudan were supplied by Dr. H. Setzer from specimens in the U.S. National Museum.

there is no reason to suspect the presence of any gross discontinuities in the range except in the southwest and perhaps in the mountains of Ethiopia. However, it is narrowly constricted by the subdesert of northern Kenya which, along with the Tana River, may effectively isolate the northern and southern populations.

REGIONAL VARIATION (Text-fig. 13). In view of the probable continuity of distribution it is unlikely that any objective subspecific boundaries can usefully be recognized. No significant variation can be detected in cranial characters nor in external measurements except that the available specimens from Ethiopia are rather large. All previous subspecific descriptions have been based almost entirely on colour. This undoubtedly varies considerably throughout the range, but the existing collections are sufficient to suggest that most of this variation is clinal.

In Tanzania no specimen has been examined from the presumably isolated southwestern population, but samples are available from four other widely spaced regions. Comparing the samples from the southernmost locality, Dodoma (thirteen skins including the type of *ocularis*) and from Mwanza, south of Lake Victoria (six skins, including the type of *pulcher*) the difference in colour is fairly clear-cut, *ocularis* being rather yellowish above and on the flanks whilst *pulcher* is much greyer. Ventrally *ocularis* has the dark basal zone of the hairs very short or completely absent whilst in *pulcher* it is prominent. However, four skins from intermediate localities, including the type of *renatus*, are rather variable and, on the whole, intermediate between *ocularis* and *pulcher*. A single specimen from Kibaya (5° 17′ S., 36° 34′ E.), northeast of Dodoma, is a deeper yellowish brown, linking *ocularis* with *rufescens s.s.* of southeastern Kenya. All the skins from Tanzania are characterized by a more prominent white eye-ring than is found in Kenya, especially the white streak between the eye and the ear.

Within Kenya the twelve skins from the vicinity of Voi, i.e. nearly topotypical *rufescens*, are noticeably more rufous than any others (except the Ethiopian *boranus* —see below). This can probably be considered as an adaptation to the colour of the local soil, which is very dark red. All the other available specimens from Kenya are less rufous and show very little variation amongst themselves. These include series from Taveta (eight skins) and from near Archer's Post on the northern Uaso Nyiro (nineteen skins). All these have hitherto been referred to *dundasi*. Specimens from further north (in the Northern Frontier District) are noticeably paler, being very similar in colour to *ocularis* of Tanzania, which they also resemble in the prominence of the eye-ring and in the tendency to lack the dark bases in the ventral pelage. The type of *delicatus* represents this form and is further characterized by the very long tail.

North of the subdesert zone of northern Kenya, from which *E. rufescens* is probably absent, specimens are available from three main regions; the extreme southern (coastal) area of Somalia; several montane areas in southern Ethiopia; and northeastern Ethiopia and the adjacent parts of Somalia. In eastern Kenya a single specimen from the Tana River is considerably greyer than all the other Kenya specimens and this greyness is even more marked in a series from southern

Somalia (0° 26′ N., 42° 48′ E.). The five specimens available from southern Ethiopia fall into three groups. The type of *boranus* from Mega on the southern border (1,370 m.) is a very rufous form almost indistinguishable from topotypical *rufescens*, but even deeper in colour. The other three from further east (Farda Robo and Murri) are less bright and are virtually indistinguishable from the *dundasi* of Kenya, being darker than those from the N.F.D. A single skin from Lake Abaya (1,300 m.) is much greyer than these, with a more clearly defined dorsal stripe and almost black post-ocular spots and upper surface of the tail. These characters are unique in the species.

Specimens from northern Somalia (*somalicus*) are again very yellow dorsally, a little more so than those from northwestern Kenya. The form *peasei* from northeastern Ethiopia, only about 200 km. from the *somalicus* group, is represented by the type and by five other skins and skulls borrowed from the Oklahoma State University. It is distinctly different from *somalicus*, being very grey above and showing very little yellow even on the flanks. (In fact the types of *peasei* and of *renatus* from Tanzania are scarcely distinguishable). They are also rather large and one of the four measurable skulls is exceptionally large (condylobasal length 37·3, upper tooth-row 19·3 mm.). The buff patches behind the ears, present in all *E. rufescens*, are especially noticeable in contrast to the grey back. Since there is no obvious barrier separating these two forms they are likely to be connected by intermediates. The types of *peasei* and *somalicus* were both collected at 2,400 m.

The only described forms of *E. rufescens* that have not been examined are *phaeus*, *rendilis*, *mariakanae* and *hoogstraali*. *Phaeus*, from southwestern Kenya, was described as being " closely allied to *pulcher* from which it differs in the darker umber-brown colour, being ' grey-fawn ' only on the sides ". This is consistent with the view that it is intermediate in colour, as well as geographically, between *pulcher* and *dundasi* of central Kenya. *Rendilis*, from the Uaso Nyiro, was described entirely on the basis of colour, the ventral hair being white to the roots and the post-ocular streak pale by comparison with *pulcher*. This form is therefore represented by a nearly topotypical series available from Archer's Post, which are scarcely separable from *dundasi*. *Mariakanae*, from near Mombasa, was compared with *pulcher* and *rufescens* and described as intermediate between these forms in colour, no other characters being described. *Hoogstraali* was described, compared with *dundasi* of northwest Kenya, as having the belly white, tail and hind feet long, dorsal colour dark and post-ocular spot more prominent. One specimen available from the Didinga Mountains, about 70 km. east of the type locality of *hoogstraali*, fits this description but at the same time is only marginally separable from the type of *dundasi* and from a series from Karamoja, Uganda. *Hoogstraali* represents the northwestern extremity of the range, but there is no reason to suppose that it is geographically isolated.

None of these descriptions is inconsistent with the overall pattern of regional variation outlined above. Few are likely to represent isolated populations and no abrupt discontinuities of variation have been demonstrated. The difference between *peasei* and *somalicus* is the nearest approach to such a discontinuity.

Elephantulus revoili

Macroscelides revoilii Huet, 1881. Medjourtine, i.e. northeastern Somalia Holotype: Paris Museum, 1881–11, mounted skin.

TAXONOMIC STATUS. A clearly defined species, closely related only to *E. rufescens*.

SPECIMENS EXAMINED. Fifteen, including two received on loan from the University of Florence.

DESCRIPTION. See Table 1 for diagnostic characters. Head and body 122–148, mean of six 132; tail 144–167, mean of six 157 (119% of head and body); hind foot 34–39, mean of six 37·3; ear 24–26; upper tooth-row 18·4–20·4, mean of eight 19·1 (Text-fig. 13).

E. revoili differs from *E. rufescens* only in its long hairy tail, large size, pale pelage and large I^2. Two small juveniles have the dorsal pelage paler than that of the adults, with more yellow and less grey. The pectoral gland is present in every individual and is marked by dense fringes of short white hair, but in all but one skin no secretion is visible on the surrounding hair, whereas in *E. rufescens* most specimens show extensive staining in the vicinity of the gland. This may have led Heller (1912) to state that the pectoral gland is absent in *E. revoili*.

The caudal hairs are white with brown tips which become longer towards the tip of the tail, forming a dark brush; the dorsal pelage is pale brownish or pinkish grey, when compared with *E. rufescens* rather paler than the form *peasei* but less yellow than *somalicus*, most similar to *E. rozeti deserti*.

RANGE (Text-fig. 11). Specimens in the British Museum are from seven localities, all on or near the north coast of Somalia between 44° and 48° 20′ E. The only reliable record away from this area is from Run, Garoe (8° 17′ N., 48° 20′ E.) (two specimens in the Zoological Museum of the University of Florence). Peel (1900) recorded seeing a specimen at Sinnadogho, Marehan country. This is much further south (5° 15′ N., 46° 15′ E.), but since *E. rufescens somalicus* had not yet been described and *E. revoili* was thought to be the only species in Somalia, this cannot be treated as a positive record of *E. revoili*.

E. revoili appears to be sympatric with *E. rufescens* at Wagar (10° 01′ N., 45° 26′ E.) and at Upper Sheikh (9° 56′ N., 45° 12′ E.), but field notes suggest that the two differ in habitat, *E. revoili* occurring on stony ground and *E. rufescens* being found amongst bushes on sandy soil. The information available is insufficient to determine whether *E. revoili* is confined to the rocky, montane habitats of northern Somalia or whether it is more widespread, replacing *E. rufescens* throughout the drier parts of the country.

REGIONAL VARIATION. No subspecies have been described. The two available skins from Gabadir (10° 24′ N., 45° 02′ E., 240 m.), one of adult size, the other juvenile, have the dorsal pelage very pale and yellowish. The remaining eight adult skins from the northern part of the range are uniform in colour, and of these five are from localities of known altitude, all over 1,300 m. The two southernmost specimens (Garoe) are a very pale, pinkish buff, the proximal zone of the dorsal hairs being short (rather less than half the length of the hair) and grey, not black as in the northern specimens. Also the black-tipped guard hairs are much fewer.

Elephantulus intufi

Macroscelides intufi Smith, 1836 : 42. Flats beyond Kurrichaine, Marico district, western Transvaal. Holotype : B.M. (N.H.) 59.5.7.13 (= 41.799 = 1314a), skin and skull.

Macroscelides alexandri Ogilby, 1838 : 5. Damaraland, South West Africa.

Macroscelides brachyrhynchus schinzi Noack, 1889. Ondongastamm, Ovamboland, South West Africa.

Elephantulus intufi kalaharicus Roberts, 1932 : 17. Damara Pan, central Kalahari, Botswana.

Elephantulus intufi mossamedensis Hill & Carter, 1937. 101 km. east of Mossamedes, Angola.

Elephantulus namibensis Roberts, 1938 : 233. 45 miles north of Aus, South West Africa.

Elephantulus intufi campbelli Roberts, 1938 : 234. Barby Farm, 25 miles west of Helmeringshausen, South West Africa.

Elephantulus intufi mchughi Roberts, 1946 : 309. Okombahe, Omaruru, South West Africa.

Elephantulus intufi omahekensis Lehmann, 1955. Klein Okaputa, south of Okavango, South West Africa.

Elephantulus intufi canescens Lundholm, 1955 : 283. Ohopoho, Kaokoveld, South West Africa.

SPECIMENS EXAMINED. Angola eleven ; Botswana one (received on loan from the National Museums of Rhodesia) ; South West Africa fifty-six (including the type of *alexandri*) ; Transvaal one (type of *intufi*).

TAXONOMIC STATUS. As understood here, this species agrees with *E. intufi* of Roberts (1951) with the addition of his *E. namibensis*. Ellerman *et al.* (1953) included in *E. intufi* all the forms included by us, but also all those that we include in *E. rupestris*.

DESCRIPTION. See Table 1 for the diagnostic characters and Text-figs. 7b, 9f and 10f for cranial details. *E. intufi* resembles *E. rupestris*, and differs from the other two southern species, in having P^2 molariform, with two well-developed lingual cusps ; P^1 with a lingual cusp ; the ectotympanic less swollen than the entotympanic parts of the bullae ; and the ventral pelage white, showing little grey at the surface. It differs from *E. rupestris* in its smaller size (upper tooth-row under 18·7 mm.) ; relatively shorter, untufted tail (*c.* 105% of head and body) ; generally paler and more yellow dorsal pelage ; conspicuous and unbroken white eye-ring ; and by the absence of an additional cusp on P_2 and P_3 between the principal cusp and the two posterior cusps (indeterminable if the teeth are heavily worn). The bullae are also rather larger and less angular than those of *E. rupestris* ; this varies somewhat from region to region but is a useful confirmatory character if both species are available from the same region.

The dorsal pelage is usually yellowish buff with the very long, black-tipped guard hairs contrasting strongly, especially on the rump. The brighter buff patches behind the ears are especially conspicuous. The hairs of the tail are white, only those on the dorsal surface having black tips, giving a speckled appearance. Although they increase in length towards the tip there are very few wholly black as in *E. rupestris*. The ventral pelage shows even less grey at the surface than that of *E. rupestris*.

RANGE (Text-fig. 11). Dry savanna woodland, steppe and subdesert of south-western Angola, the whole of South West Africa except the coastal desert, probably most of Botswana, and the extreme northeastern region of Transvaal. The northernmost locality is Catumbella, Angola (12° 25′ S.) (specimen in British Museum), the easternmost the Zoutpansberg, North Transvaal (Roberts, 1917), and the southernmost Ariamsvlei near the Orange River (Roberts, 1951).

Through most of South West Africa *E. intufi* is sympatric with *E. rupestris*. The range overlaps slightly with that of *Macroscelides proboscideus* in southern South West Africa and touches that of *E. myurus* in the east. Roberts (1917) records a specimen of *E. intufi* from the Zoutpansberg, collected " not far from a place " where the type of *E. myurus mapogonensis* was collected. It also touches upon the range of *E. brachyrhynchus* in the north and probably in the east, both species having been recorded from Quillingues, Angola (14° 05′ S., 14° 04′ E.) and from adjacent areas in western Transvaal.

Regional variation (Text-fig. 14). No specimens from southern South West Africa have been examined and only the type and one other from the eastern part of the range. All the races that have been described have been based on slight variation in colour. It is unlikely that there is any gross discontinuity of range or variation in the central part of the range.

Four skins from Catumbella, Angola are almost identical to the large series examined from the Kaokoveld in northern South West Africa. Lundholm's name *canescens* is available for this group. The type locality of *mossamedensis*, described as being paler than adjacent forms, lies between these areas. Four skins from Ovamboland (east of Kaokoveld) are less grey and more yellow than the Kaokoveld series. Noack's name *schinzi* is available for this form if required. It is clear from his description (Noack, 1889) that this is a form of *E. intufi* rather than of *E. brachyrhynchus* in which it was originally placed (see p. 98). Three from Karabib (*c.* 22° S.) are paler and yellower than the Kaokoveld specimens. These agree well with the type of *alexandri* (from " Damaraland ", but in fact it could have come from anywhere in South West Africa) and this form is probably also represented by Roberts' *mchughi*. (A fourth specimen from Karabib, reported by Thomas & Hinton (1925) as *E. intufi*, is in fact *E. rupestris*. These authors described it as being greyer than the others but said nevertheless " there is no doubt that they are really referable to this species " (*E. intufi*). This specimen was again commented upon by Thomas (1926) when he noted that the bullae differed from those of the rest of the series.) If, as seems probable, all these represent one race distinct from the nominate form (which may represent an isolated eastern population), the earliest name is *alexandri*.

Specimens from southern South West Africa (forms *namibensis* and *campbelli* of Roberts) are, according to Roberts, also pale, as is his *kalaharicus* from central Botswana. A single specimen examined from eastern Botswana (near Lethaking) is slightly more pink and less yellow than most western specimens.

Elephantulus rupestris

Macroscelides rupestris Smith, 1831. Mountains near the mouth of the Orange River. Neotype: B.M. (N.H.) 4.2.3.7, skin and skull (see below under " Nomenclature ").

Elephantulus vandami Roberts, 1924 : 62. Cradock, Cape Province.

Elephantulus barlowi Roberts, 1938 : 233. Aus, South West Africa.

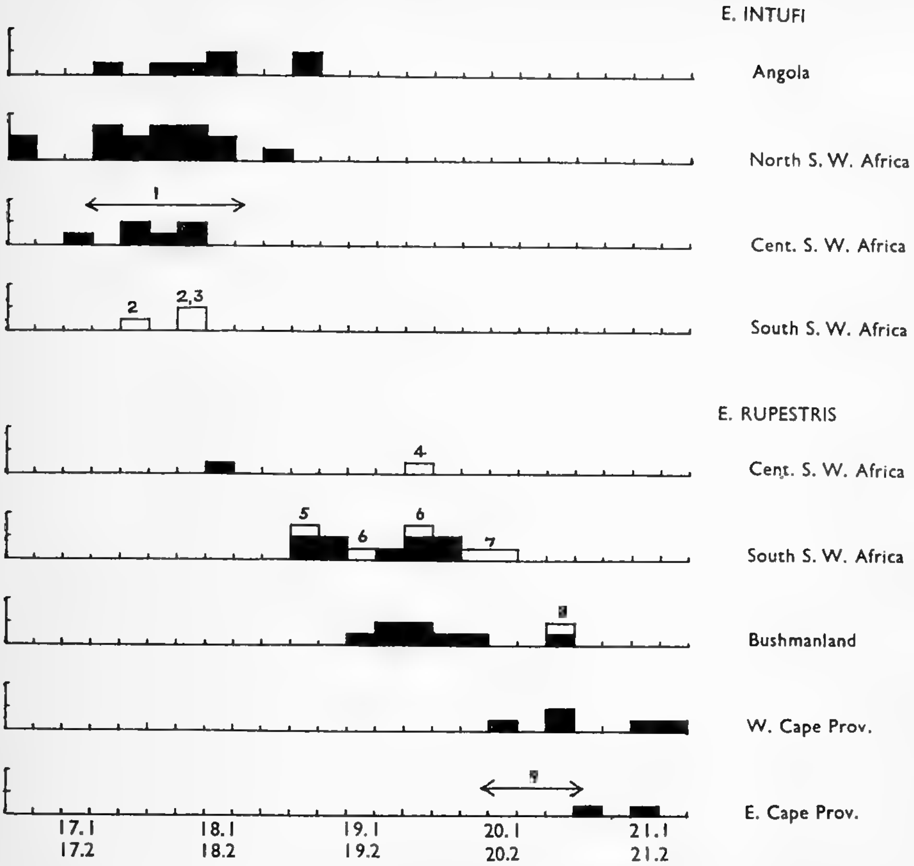

FIG. 14. Variation in length of the upper tooth-row of *Elephantulus intufi* and *E. rupestris*. The open blocks and lines represent data taken from Roberts (1951) as follows: 1: range of 22 *mchughi*; 2: *campbelli* (incl. type); 3: type of *namibensis*; 4: type of *okombahensis*; 5: type of *kobosensis*; 6: *tarri*; 7: type and topotype of *barlowi*; 8: *vandami*; 9: *vandami* (incl. type).

Elephantulus kobosensis Roberts, 1938 : 233. Kobos, 30 miles southwest of Rehoboth, South West Africa.

Elephantulus rupestris tarri, Roberts, 1938 : 234. Barby Farm, 25 miles west of Helmeringshausen, South West Africa.

Elephantulus barlowi okombahensis Roberts, 1946 : 309. Okombahe, Omaruru, South West Africa.

Elephantulus barlowi gordoniensis Roberts, 1946 : 309, Upington, Cape Province.

Elephantulus intufi [part] : Ellerman *et al.* (1953).

Elephantulus vandami montanus Lundholm, 1955 : 282. Oropembe, Kaokoveld, South West Africa.

Specimens examined. Cape Province twenty-four (including four from the U.S. National Museum); South West Africa sixteen.

Nomenclature. Ellerman *et al.* (1953) included this species in *E. intufi* and used the name *rupestris* for the species that we call *E. myurus* and *E. edwardi*. This error was caused by their acceptance as the type of *rupestris* of one of Smith's specimens in the British Museum labelled " *Macroscelides rupestris*—South Africa " (no. 59.5.7.12). This specimen agrees in every way with *E. myurus*. Since *E. myurus* has not been found anywhere near the mouth of the Orange River (in spite of extensive collecting) and since there is nothing to indicate that the specimen in question came from there, it has no claim to be the type of *rupestris*. In fact none of Smith's specimens in the British Museum is *E. rupestris*, i.e. the species subsequently collected, to the exclusion of all others except *E. edwardi* (of which good type material exists), near the mouth of the Orange River.

In fact none of Smith's specimens of this species, agreeing with subsequent topotypical material, have ever been reported. Most of his original material was lost (Smith, 1838: text to plate 15), and it is probable that topotypical *rupestris* did not survive. In view of the confusion that has been caused by the absence of a genuine type specimen, it would seem wise to designate a neotype. For this we choose number 4.2.3.7 in the British Museum, a skin and skull of an adult male collected at Klipfontein, Namaqualand, Cape Province (29° 13′ S., 17° 39′ E., 3,100 ft.) on 29th April, 1903 by C. H. B. Grant. This locality is consistent with the original type region.

Description. See Table 1 for diagnostic characters and Text-figs. 6b, 7a, 9g and 10g for cranial details. Head and body about 130 mm.; tail about 140–150 mm., about 115% of head and body; hind feet about 35 mm.; ear about 25 mm. Dorsal pelage greyish brown becoming almost pure grey on the flanks. Buff patches behind ears prominent. Ventral pelage showing more grey on the surface than in *E. intufi* but considerably less than in *E. myurus* and *E. edwardi*. Dorsal surface of the tail including many wholly black hairs which reach 6 mm. long at the tip.

E. rupestris can be distinguished from *E. intufi* by the longer, darker and more tufted tail; slightly greyer ventral pelage; darker, greyer dorsal pelage; less distinct eye-ring; smaller, more angular bullae; and by the presence of an additional cusp on P_2 and P_3, behind the principal cusp (only visible in unworn teeth).

Range. See Text-fig. 12. The subdesert steppe of South West Africa, north at least to 18° S.; and of Cape Province, in Little Namaqualand and from Upington to Grahamstown. The northernmost localities are Oropembe and Sanitatas from where Lundholm (1955) described *montanus*. The fact that only four specimens have been obtained in the Kaokoveld, compared with large numbers of *E. intufi*, suggests that it is local, and the same applies to the central area of South West Africa. In the south of South West Africa the opposite is true, *E. intufi* having been collected rarely amongst large numbers of *E. rupestris*. It seems probable that the population in the mountains of Little Namaqualand is isolated from the rest of the species, whilst the southeastern localities are also likely to represent isolated populations.

E. rupestris overlaps with *E. intufi* extensively in South West Africa. It overlaps with *Macroscelides proboscideus* in southern South West Africa (Shortridge (1934) records that the two species live in close contact on the same ground), and in most of its range in Cape Province. It is probably only marginally sympatric with *E. edwardi* and *E. myurus*, the range of *E. rupestris* forming a narrow strip in Cape Province between these other two species. It has been recorded with *E. edwardi* at Witwater, Little Namaqualand (Shortridge, 1942) and with both *E. edwardi* and *E. myurus* at Deelfontein, 31° 00′ S., 23° 48′ E. (specimens in British Museum). In the latter collection (which also includes *Macroscelides proboscideus*) the single specimen of *E. rupestris* is labelled " Karroo, Deelfontein ".

REGIONAL VARIATION. See Text-fig. 14. Insufficient material has been examined from the extremities of the range to assess the validity of the marginal races. All the named forms are based on slight variation in pelage and in size and it seems unlikely that any genuinely discontinuous races exist. Series examined from Little Namaqualand, the Upington district, and Berseba in South West Africa (nearly topotypical *rupestris*, *gordoniensis* and *tarri* respectively) show no variation justifying the recognition of subspecies. Animals from western and northern South West Africa are reported to be pale. This includes the forms *barlowi*, *kobosensis*, *okombahensis* and *montanus*. Only one such specimen is available in the British Museum, from Karabib (about 22° S., 16° E.). Its tail is as tufted as in other *E. rupestris*, but very few of the hairs are wholly black. The dorsal pelage is very pale, but lacks the yellow colour of *E. intufi*.

The southeastern form, *vandami*, is described by Roberts, comparing it with typical *rupestris*, as being browner above, darker grey on the flanks, and having the tail wholly dark at the tip. The five specimens examined, from Deelfontein, and near Beaufort West, do not confirm this and cannot justify subspecific rank. Mr. C. G. Coetzee of the Transvaal Museum has kindly reported on the type of *vandami* and confirmed that it does indeed have the auditory region and P^2 of *rupestris* as here defined.

Elephantulus myurus

Elephantulus rupestris myurus Thomas & Schwann, 1906. Woodbush, Northeastern Transvaal. Holotype : B.M. (N.H.) 6.4.3.2, skin and fragment of skull, ♀.

Macroscelides rupestris Smith, 1831 (in part).

Elephantulus rupestris jamesoni Chubb, 1909. Johannesburg, Transvaal.

Elephantulus rupestris mapogonensis Roberts, 1917. Njelele River, north of Zoutpansberg, Transvaal.

Elephantulus rupestris centralis Roberts, 1946 : 310. Fauresmith, Orange Free State.

Elephantulus rupestris : Ellerman *et al.*, 1953.

Elephantulus rupestris fitzsimonsi Lundholm, 1955 : 184. Nyamaziwa Falls, Inyanga area, Rhodesia.

SPECIMENS EXAMINED. Botswana four ; Cape Province nine ; Orange Free State six ; Natal one ; Transvaal thirty-five (including the types of *myurus* and *jamesoni*) ; Rhodesia six (including five in the National Museums, Rhodesia). Eight of the South African specimens were from the U.S. National Museum.

TAXONOMIC STATUS. This species was only recognized as specifically distinct from *E. rupestris* in 1935 (Roberts, 1935), and the species as defined by Roberts (1951) is recognized here. However, Ellerman *et al.* (1953) treated it as conspecific with *E. edwardi* and used for this enlarged species the name *rupestris* because of the reputed type specimen in the British Museum (see p. 92 above). The differences between this species and *E. edwardi* are small but clear-cut and the two species are sympatric in at least one locality (Deelfontein).

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 6c, 7c, 9h and 10h for cranial details. Head and body about 120 mm.; tail about 140 mm.; hind foot about 35 mm.; ear about 24 mm. Dorsal pelage dull greyish brown, rather more yellow on the flanks. Ventral pelage with the white tips short, making the overall colour pale grey, much greyer than in *E. rupestris*. Pelage behind ears only faintly differentiated from rest of dorsal pelage by scarcity of black-tipped hairs (but more strongly differentiated in the north of the range). Tail shortly haired throughout, variable in colour.

Externally *E. myurus* can be distinguished from *E. rupestris* by the very much less hairy tail, by the less conspicuous buff patches behind the ears (at least in the south) and by the darker ventral pelage. From *E. edwardi* it can be distinguished by the slightly less hairy tail which is never wholly black above and at the tip (this may *not* apply in some northern parts of the range where *E. edwardi* is absent), and by the slightly lesser contrast between brown back and grey flanks.

The skull of *E. myurus* is easily separated from that of *E. rupestris* and *E. intufi* by the greatly swollen ectotympanics which are level with the entotympanics or nearly so (Text-fig. 6c), by the absence of a lingual cusp on P^1, and by P^2 which is narrower, usually with only a single small lingual cusp (Text-fig. 7c). Occasionally two small lingual cusps are present but these are always less than half the height of the labial cusps and are usually very close together. The discrepancy in size between the labial cusps of P^2 is also greater than in *E. rupestris* (cf. Text-figs. 7a and c). From *E. edwardi* it is distinguished by the sinuous suture between premaxilla and maxilla, by the double-rooted P_1, by the larger size (Text-fig. 15), and, less certainly perhaps, by the presence of a lingual cusp on P^2.

RANGE. See Text-fig. 12. The high grasslands from Deelfontein and Burghersdorp (Cape Province) through Orange Free State and western Natal to northern Transvaal, Rhodesia and eastern Botswana. In northern Transvaal and Rhodesia the range is probably fragmented, being confined to areas of drier grassland or more open montane habitats. Everywhere this species is found especially where outcrops of rock provide cover.

In the southwest the range touches that of *E. rupestris*, *E. edwardi* and *Macroscelides proboscideus*, all four species being either sympatric or closely adjacent in the Deelfontein area. In northwestern Transvaal *E. myurus* meets *E. intufi* whilst in northern Transvaal and Rhodesia there is a wider overlap with *E. brachyrhynchus* although there is probably a habitat difference, *E. brachyrhynchus* being on the more wooded ground.

REGIONAL VARIATION. There appears to be no significant variation in pelage throughout the range. The form *jamesoni* (Johannesburg) was described in comparison with *E. rupestris* rather than *myurus*. Roberts (1951) rejected any difference in pelage between *jamesoni* and *myurus* (with which we agree) but retained *jamesoni* as a race on the basis of its large size. He likewise diagnosed *mapogonensis* (North Transvaal) solely on the basis of its small size. He described *centralis* (from the south of the range) by comparison only with *E. edwardi*. In fact it cannot be distinguished from more northern samples. The only accurate available comparison of size, using upper tooth-row (Text-fig. 15), suggests that size decreases towards the north but provides no grounds for the recognition of discrete subspecies.

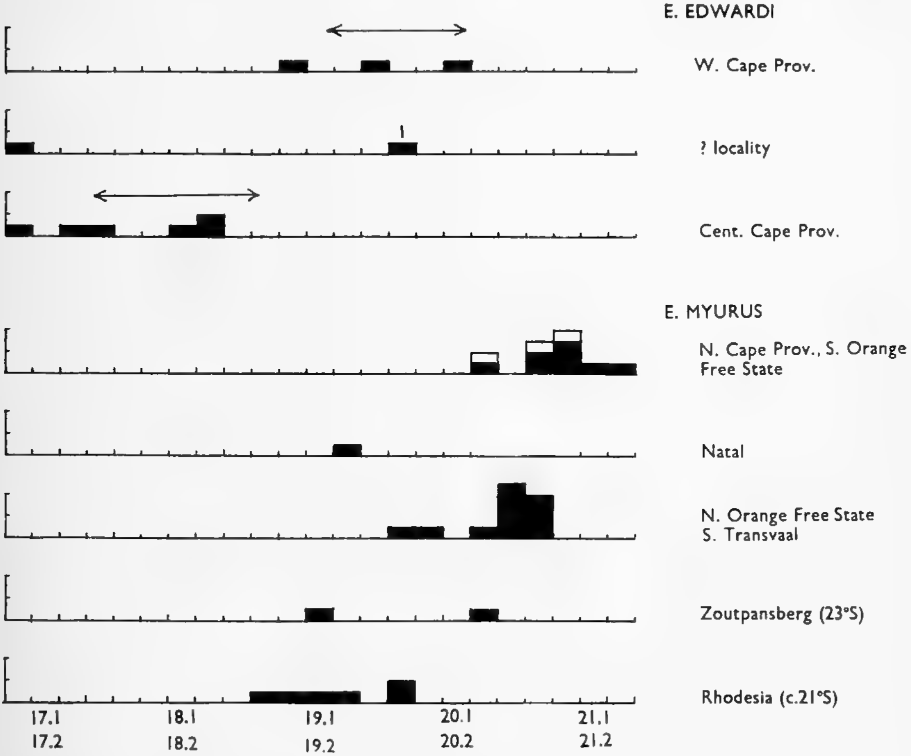

Fig. 15. Variation in length of the upper tooth-row of *Elephantulus edwardi* and *E. myurus*. The lines represent the ranges given by Roberts (1951). I : type of *edwardi*.

The form *fitzsimonsi* (Inyanga area, Rhodesia) is based on a single specimen with greyish back, pale post-auricular patch and black dorsal surface of the tail. It is probably an isolated form and may be a valid race. The only specimens examined from Rhodesia, one from Matopos and five from the Lundi River, do not show these characters and are scarcely distinguishable from Transvaal specimens although the post-auricular patch is brighter.

Elephantulus edwardi

Macroscelides edwardii Smith, 1839. Oliphants River, Cape Province. (Probably the one flowing into the Atlantic, since it has subsequently been found in many parts of that district but not near the other Oliphants River in the Oudtshoorn district). Lectotype: B.M. (N.H.) 41.796, skin and skull (specimen labelled, but apparently never published, by Thomas).
Macroscelides edwardsii Sclater, 1901.
Elephantulus capensis Roberts, 1924. Klaver, Cape Province.
Elephantulus karoensis Roberts, 1938 : 234. Deelfontein, north of Richmond, Cape Province.
Elephantulus rupestris : Ellerman *et al.*, 1953.

SPECIMENS EXAMINED. Southwestern Cape Province four (including one from the U.S. National Museum and one from the Kaffrarian Museum, King William's Town, both of these from Pakhuis Pass, Clanwilliam ; and one from Klaver district, i.e. topotypical *capensis*) ; Little Namaqualand one (U.S. National Museum) ; central Cape Province seven (including topotypical *karoensis*) ; " S. Africa " five (including the type of *edwardi*).

TAXONOMIC STATUS. Roberts (1951) did not equate his *capensis* with *edwardi* because it did not appear to agree closely with Smith's description. But the type of *edwardi*, along with four specimens bearing this name received from Mr. Edward Verreaux (who collected the type material and after whom it was named) is in the British Museum. All these specimens agree closely with topotypes of *capensis* and of *karoensis*, which Roberts (1951) subsequently treated as a race of *capensis*. Ellerman *et al.* (1953) treated *edwardi* as conspecific with *E. myurus* (which they called *E. rupestris*). However, *edwardi* and *myurus* differ with respect to several apparently independent characters and a series of each is available from Deelfontein.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 7d, 8c, 9i and 10i for structural details. Head and body about 110–120 mm. ; tail 130–140 mm. ; hind feet about 32–35 mm. ; ear about 25 mm. Dorsal pelage greyer than in the other southern species, tinged with yellow rather than with reddish brown, and more sharply separated from the grey flanks. The post-auricular region is tinged with yellowish brown, less conspicuously than in *E. rupestris* but more so than in southern *E. myurus* since there is a greater contrast with the greyish back. Ventral pelage grey. Tail black above, pale below at the base but completely black distally. Hairs very short at the base, increasing in length distally but not exceeding about 4 mm., i.e. considerably less tufted than that of *E. rupestris*.

Externally *E. edwardi* very closely resembles *E. rupestris* and *E. myurus*. From *E. rupestris* it can be distinguished by the darker ventral pelage, by the yellow-rather than orange-buff behind the ears and by the shorter, less hairy tail. From *E. myurus* it can be distinguished less easily by the dark, slightly more tufted tail and the larger, more truncate, supratragus.

Skulls of *E. edwardi* can be readily distinguished from those of *E. rupestris* by the inflated ectotympanic and less inflated entotympanic bullae, and from both *E. rupestris* and *E. myurus* by the reduction of all but one principal cusp on P^1, the absence of any lingual cusps on P^2, the single-rooted P_1, and the non-sinuous vertical suture between premaxilla and maxilla. In the region of overlap it can also be distinguished from *E. myurus* by its small size (Text-fig. 15). (One skull, from Clanwilliam, has what appears to be a small lingual cusp on P^2, but the teeth are heavily worn and this may be an effect of wear).

RANGE. See Text-fig. 11. Apparently in at least two segments: western Cape Province from Little Namaqualand south to Tulbagh district; and in the Upper Karroo from Richmond district to the coast at Port Elizabeth (the latter may be an isolated locality). The habitat appears to be the same as for the other southern species, i.e. rocky outcrops on grassland.

E. edwardi is marginally sympatric with *E. rupestris* in the north, with *E. myurus* in the northeast, and is more extensively sympatric with *Macroscelides proboscideus.*

REGIONAL VARIATION. The four dry specimens examined from the western part of the range differ slightly from the series from Deelfontein and one from near Graaf Reinet in the darker, more shortly haired tail (completely black above) and the purer grey flanks. The type of *edwardi* has a similarly dark tail, and the pelage appears to resemble the western rather than the eastern form, although its age makes such a comparison of doubtful validity. There is also a difference in size, the western sample, and the type of *edwardi*, being larger (Text-fig. 15). If these differences prove to be constant, the western form may be taken as the typical race (synonym *capensis*) and the eastern one as *E. e. karoensis.*

Elephantulus brachyrhynchus

Macroscelides brachyrhynchus Smith, 1836: 42. Between Kuruman (northern Cape Province) and the tropic in Bechuanaland. Lectotype (selected here from two syntypes): B.M. (N.H.) 39.10.5.5, skin labelled " S. Africa, Dr. Smith ", associated with skull no. 59.5.7.17.
Macroscelides brevirostris Schintz, 1844: 284.
Macroscelides fuscus Peters, 1852. Boror, near Quelimane, Mozambique.
Macroscelides brachyurus Bocage, 1882. Caconda, southeast of Benguela, Angola.
Macroscelides brachyrhynchus malosae Thomas, 1898. Mount Molosa, 5,500 ft., Malawi.
Macroscelides delamerei Thomas, 1901*b*: 155. Athi R., Kenya.
Nasilio brachyrhynchus albiventer Osgood, 1910. Lake Elmenteita, Kenya.
Nasilio brachyrhynchus luluae Matschie, 1926. Near Luluaburg, Congo.
Nasilio brachyrhyncha tzaneenensis Roberts, 1929: 85. Tzaneen, East Transvaal.
Nasilio brachyrhyncha langi Roberts, 1929: 85. Mazambo, lower Limpopo River, Mozambique.
Nasilio brachyrhyncha shortridgei Roberts, 1929: 86, Ndola, Zambia.
Nasilio brachyrhynchus mababiensis Roberts, 1932: 18. Tsotsoroga Pan, Ngamiland, Botswana.
Nasilio brachyrhyncha selindensis Roberts, 1937. Mount Selinda, Melsetter dist., Rhodesia.

SPECIMENS EXAMINED. The type and a paratype; Transvaal seven; South West Africa fourteen; Angola seventeen; Rhodesia fifteen; Zambia fifty-four, including strictly topotypical *shortridgei*; Mozambique eleven (including eight from the U.S. National Museum); Malawi seventeen (including the type of *malosae*); Congo twenty-one; Tanzania three (including one in the museum of the College of Wildlife Management, Mweka, Tanzania); Kenya thirty-two (including the type of *delamerei* and including twenty-three in the National Museum, Nairobi); Uganda three.

TAXONOMIC STATUS. Clearly defined from all other species except *E. fuscipes.* This species includes all forms that have hitherto been placed in the genus *Nasilio* except *fuscipes*, which is considered a distinct species, and *schinzi*, which is believed to belong to *E. intufi*. Noack (1889) described *Macroscelides brachyrhynchus schinzi* on the basis of a single skin from "Ondongastamm, Ovamboland". The type was said by Shortridge (1934) to be in the Senckenberg Museum, Frankfurt, but it is no longer there. Several features of Noack's description point to *E. intufi*, rather than *E. brachyrhynchus*: pelage 15 mm. long, thick and fine; dorsal colour "ein lebhaftes bräunlich gemischtes Gelbroth"; tail well-haired, obscuring scales, yellow-grey above, lighter below, hairs black-tipped towards the end but no brush. *E. intufi* has subsequently been found in this area, but not *E. brachyrhynchus*.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8d, 8e, 9b and 10b for structural details. Head and body variable, most often about 110–120 mm.; tail variable but usually shorter than head and body, 65 to 105%; hind feet usually 25–32 mm.; ear usually about 19 to 22 mm.

Dorsal pelage reddish or yellowish brown, about 10 mm. long, with emergent dark-tipped guard hairs, rather similar to some forms of *E. rufescens*. White eye-ring fairly prominent. Ventral pelage white-tipped but the white not quite obscuring the grey bases. Tail bicoloured, very shortly haired, the hairs uniform in length throughout.

E. brachyrhynchus is superficially most similar to *E. fuscipes*, *E. rufescens* and *E. intufi*. From *E. fuscipes* it can be distinguished by the absence of a pectoral gland and by the untwisted supratragus; from *E. rufescens* by the absence of a pectoral gland, absence of a post-ocular mark and shorter tail; and from *E. intufi* by the shorter, uniformly haired tail, and shorter hind feet (usually under 31 mm.). From *E. myurus* in the Transvaal it is readily distinguished by the predominantly brown rather than grey pelage and the short tail.

The adult skull can be distinguished from all but *E. fuscipes* by the presence of small, third lower molars. The cranial differences between it and *E. fuscipes* are discussed under that species.

RANGE. See Text-fig. 16. Steppe and savanna woodland zones from Transvaal, northern Botswana and northeastern South West Africa north to Kasai in the Congo and through Tanzania to Kenya and Uganda. In Tanzania comparison with the data available for other species suggests that it is genuinely absent from large areas, e.g. in the north.

E. brachyrhynchus is sympatric with *E. intufi* and *E. myurus* in the south and with *E. rufescens* in Kenya, but it is probable that it occurs in more wooded areas than these species (including riverside scrub in otherwise dry country). It overlaps more extensively with *Petrodromus tetradactylus* in Zambia, Malawi, Mozambique and the southern Congo. Records from Uganda are too few to show its geographical relationship with *E. fuscipes*.

REGIONAL VARIATION. See Text-fig. 17. Colour of pelage, relative length of tail and overall size show some regional variation. Wherever material is available from a number of scattered localities there are indications of clinal variation. It is possible that the major rivers may introduce some genuinely discontinuous variation, but in no case are sufficient specimens available from either side of a river to demonstrate this. It is probable that more complete collections will in time render most, if not all, subspecific names invalid.

The collection from Zambia (including topotypical *shortridgei*) can be taken as a base for reference, since they are centrally placed in the range and are numerous enough to demonstrate the extent of individual and seasonal variation. Most of

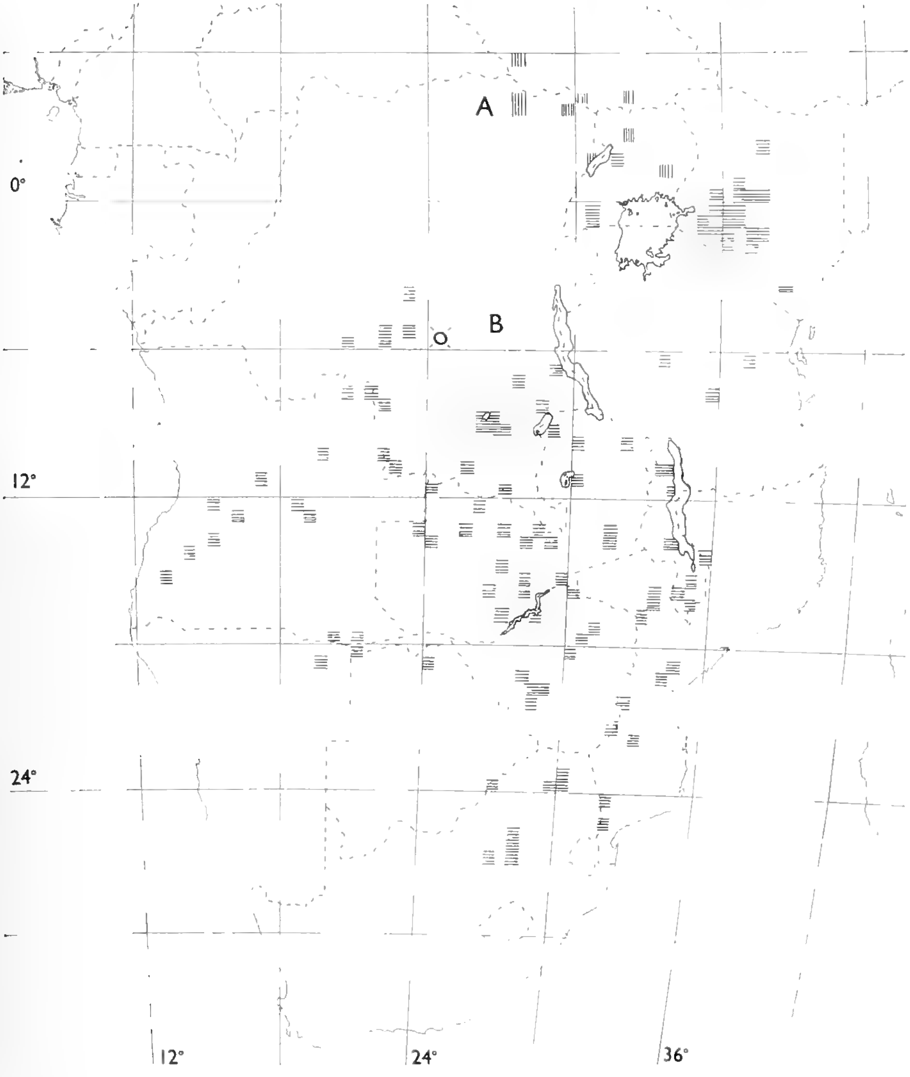

FIG. 16. The recorded distribution of A: *Elephantulus fuscipes*; B: *E. brachyrhynchus* Circle: locality uncertain.

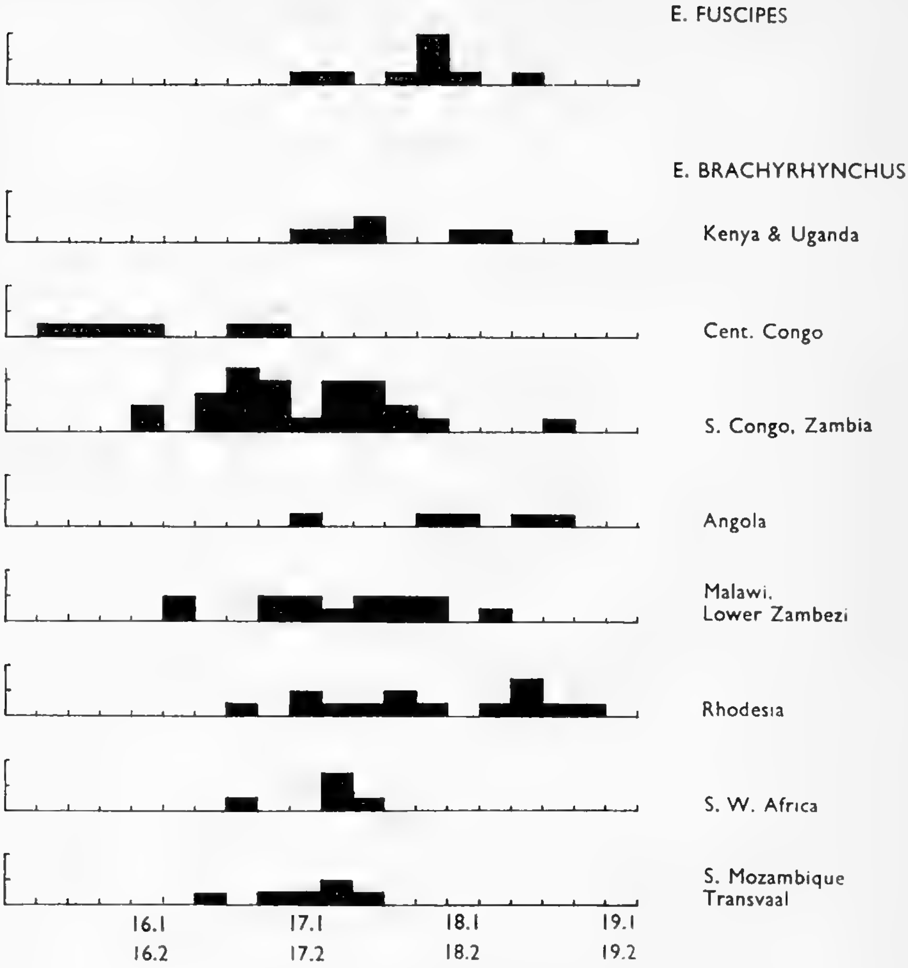

Fig. 17. Variation in length of upper tooth-row of *Elephantulus fuscipes* and *E. brachyrhynchus*.

the specimens were collected in the dry season and are distinctly yellowish brown above with much clearer buff on the flanks, the buff being demarcated rather sharply from the white ventral pelage. They are of medium size for the species (upper tooth-row 16·1–18·0) and the tail is of medium length (70–90% of head and body). Only two wet-season skins are available (from Solwezi) and they are distinctly darker. Five skins from Mwinilunga (extreme northwest) are more rufous than typical *shortridgei* from Ndola.

From Malawi the six available skins of *malosae* including the type, from high altitude in southern Malawi, July to December, are dark greyish brown with very little yellow on the flanks. They are therefore very distinct from specimens from Zambia, but others from low altitude in southern Malawi are much less grey suggesting that there is no discontinuity between the two extremes. Skins from northern Malawi are very similar to those from Zambia but are slightly more rufous.

From Rhodesia eleven skins are available. All are similar to the two wet-season skins from Zambia although five were taken in the wet season (November and December: Essexvale) and the other six in the dry season (July to September: Mazoe, 1,200 m.). No topotypical material of *selindensis* (Melsetter district) has been seen, but this form was described mainly on the basis of its large size. In fact it does not differ in size from the available material from elsewhere in Rhodesia; there is wide overlap between these and Zambian specimens and therefore it is unlikely that *selindensis* has any validity. The relative tail-length in Rhodesia is high, about 85–105% of head and body.

From Transvaal six skins have been examined (July to September, Zoutpansberg, i.e. nearly topotypical *tzaneenensis*). They are rather grey but very similar to those from Rhodesia. They are smaller than the two *tzaneenensis* listed by Roberts (1951) (upper tooth-row 16·9–17·6). The tail is 88–96% of head and body. Roberts diagnosed *tzaneenensis* by its large size (upper tooth-row 18·3 and 18·5) and darker dorsal pelage, compared with specimens from western Transvaal which he called *N. b. brachyrhynchus*, although the type locality of *brachyrhynchus* is indeterminate, between Kuruman in northern Cape Province and the tropic in Botswana. No material is available from Botswana nor Cape Province except the two cotypes which cannot be used for comparison of colour since they have been in spirit and exposed to light.

From South West Africa a series of fourteen is available from the extreme north-east (April to July). They show little variation in colour, being a very pale buffy grey, lacking the darker brown tones of Zambian skins. The white eye-ring is large and unbroken (the last feature being unique in the species). These are called *N. b. schinzi* by Shortridge (1934), but this name is applicable to *E. intufi*, not *E. brachyrhynchus* (see under " Taxonomic status " above).

From Angola, specimens are available from several localities indicating a transition from the grey montane form in the west (*brachyurus*) to the Zambian form already described. Three January skins from Fort Quilenges (14° 14′ E.) are grey with a slight tinge of olive dorsally. Four topotypical *brachyurus* (Caconda, 15° 13′ E., 1,740 m., September to December) are also very grey but lack the olive tinge. They are in fact very similar to the series from South West Africa but are darker. Two skins from Mount Moko (15° 18′ E., 1,800 m., March) are similar but a little browner. Four from Munhango (18° 42′ E., 1,300 m.) are much browner, but are still not so lacking in grey as dry-season Zambian skins. A further four from Lunda (19° 14′ E., July to August) are similar.

In the Congo, skins from Katanga (two February, two July) are identical with corresponding skins from Zambia, showing the same seasonal difference. From Kasai a series of fourteen (June to November, topotypical of *luluae*) are darker and more rufous than Zambian ones and they are also small (upper tooth-row 15·6–

17·0, mean of six 16·2), and short-tailed (65–83% of head and body) although both of these measurements show a wide overlap with series from Katanga and Zambia. The contrast in colour between the samples from Kasai and from Katanga is paralleled (in a more extreme degree) in *Petrodromus tetradactylus* in which there is also an absence of material from the intervening region.

Specimens from Kenya and Uganda (referable to *delamerei*) are again greyer than those from Zambia, being only slightly less dark than *malosae* of southern Malawi, and scarcely distinguishable from *brachyurus* of western Angola. In spite of their apparent isolation from the southern forms it seems impossible to apply a subspecific name, since no diagnosis can be made that excludes the greyer forms from southern Africa. Within East Africa variation is very slight.

ABNORMAL VARIATION. Of 102 adult skulls examined three have a small, unicuspid third upper molar on one side of the mouth (two from Zambia, one from Mozambique). Two wet-preserved animals (from Malawi and Mozambique) have the supratragus twisted backwards on a slightly constricted stalk, resembling that of *E. fuscipes* although less extreme (Text-fig. 8e). This condition appears to be present also in a dry skin from the lower Zambezi, and is clearly shown in the original figure of *fuscus* (Peters, 1852 : pl. 19b). Tail-length also seems to be very variable in this region, and the situation clearly requires further investigation.

Elephantulus fuscipes

Macroscelides fuscipes Thomas, 1894 : 68. N'doruma, Niam-Niam country, North East Congo. Holotype : B.M. (N.H.) 84.5.1.6, in phenoxytol with skull extracted, juv. ♀.

SPECIMENS EXAMINED. Congo eight (including the type, and six borrowed from the Musée Royal de l'Afrique Centrale, Tervuren) ; Sudan one ; Uganda five.

TAXONOMIC STATUS. Closely similar to *E. brachyrhynchus* with which it probably forms an allopatric pair.

DESCRIPTION. See Table 1 for diagnostic characters and Text-figs. 8f, 9c and 10c for structural details. No reliable external measurements are available but the following estimate can be made from dry skins : head and body about 120 mm. ; tail 80–90 mm., always considerably shorter than the head and body ; hind foot *c.* 25 mm. Specimens from Uganda appear rather larger than *E. brachyrhynchus* from Uganda.

Dorsal pelage dark brown, less red than most skins of *E. brachyrhynchus*. Ventral pelage with white tips which do not completely obscure the grey bases. Tail bicoloured, almost black above.

E. fuscipes is very similar to *E. brachyrhynchus* but can be distinguished externally from that species by the presence of a pectoral gland, by the peculiar, twisted supratragus, by the darker dorsal surface of the tail and by the absence of an interdigital pad at the base of the hallux. When not apparent, the pectoral gland can be detected by parting the hair transversely across the chest, when the hairs in the mid-ventral line will be seen to be short and white, contrasting with the long slaty bases of the adjacent hairs. The difference in the supratragus holds for all the specimens of *E. brachyrhynchus* examined from Uganda and Kenya but several specimens from Malawi and Mozambique have the supratragus approaching the condition characteristic of *E. fuscipes*.

The skull of *E. fuscipes* is very similar to that of *E. brachyrhynchus*, being narrower than in most other species. The most nearly constant difference appears to be the greater spacing of the anterior teeth in *E. fuscipes*. In particular the gap between I^3 and C^1 is longer than the alveolar length of C^1 in all the skulls of *E. fuscipes* examined. In *E. brachyrhynchus* the gap is shorter than C^1 in all but two East African skulls, the two exceptions being from the Laikipia Plateau, Kenya.

RANGE. See Text-fig. 16. Savanna of the extreme southwestern Sudan, northeastern Congo and parts of Uganda. It is not known to be precisely sympatric with either *E. brachyrhynchus* or *E. rufescens*, but it is likely to be in some form of contact with these species.

DISCUSSION

Gross distribution

The distribution of the family and of the genera is shown in Text-fig. 18. The family as a whole is unique amongst exclusively African taxa of mammals in its absence from the whole of West Africa north and west of the Congo and Ubangi Rivers, in spite of its presence in the Atlas region. Although it is a distinct species, the northwestern *E. rozeti* is sufficiently similar to the other members of the genus *Elephantulus* to preclude the view that its isolation is very ancient. It therefore seems probable that this genus has become extinct in an intervening region in relatively recent times, e.g. during or since the Pleistocene. If Horst (1946) is correct in identifying the representations of the ancient Egyptian god Set as an elephant-shrew, which seems reasonable, this would suggest the Nile Valley as the link between the two segments of the range. It may be, therefore, that the family has never been present in the west African savanna in recent geological time, but there does not appear to be any other group of insectivorous mammals replacing the elephant-shrews in that region.

Ecological relationships of the species

In discussing this topic it will be convenient to reserve the word *sympatric* for gross overlap of the ranges of two species and to employ the term *syntopic*, as used by Rivas (1964), to denote species that " occur together in the same locality, are observably in close proximity, and could possibly interbreed ". However, it seems that a further division of this concept is necessary to distinguish between species that occupy *different* habitats, meeting only on the boundaries of the habitats, and which we shall call *marginally syntopic* ; and species that occupy the *same* habitat so that most individuals are liable to meet members of the other species, and which we shall call *widely syntopic* species. In fact it is probably very rare in mammals to find a pair of congeneric species that are sympatric without being at least marginally syntopic, but by using the word syntopic for such intimate contact, the terms *marginally sympatric* and *widely sympatric* can be used to denote the extent of gross overlap of the ranges.

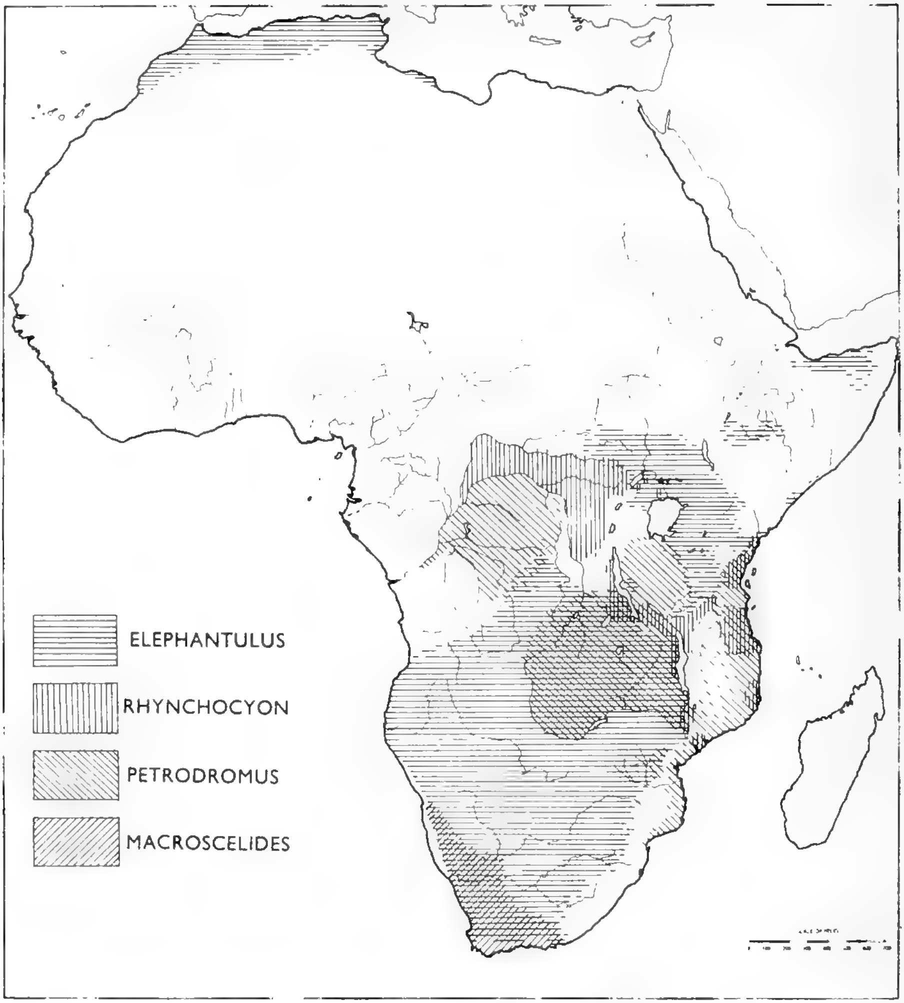

FIG. 18. Distribution of the genera of Macroscelididae.

It is rare for more than two species of elephant-shrew to be syntopic in either sense. The species of *Rhynchocyon*, themselves allopatric, are confined to forest or very thick bush with a closed canopy. They come into contact chiefly with *Petrodromus tetradactylus*, which extends also into the denser savanna woodlands. The latter has been seen within a few yards of *R. petersi* in the Shimba Hills in Kenya. *Rhynchocyon cirnei* might be expected to have marginal contact also with *E. fuscipes* in the northeastern region of the Congo, and in Uganda ; and with *E. brachyrhynchus* in Malawi and southeastern Congo. *P. tetradactylus* is widely sympatric with *E.*

brachyrhynchus, e.g. throughout Zambia. In the Luangwa Valley *P. tetradactylus* has been observed in mopane woodland adjacent to areas of tall grass in which *E. brachyrhynchus* was trapped. A similar situation may obtain in southern Tanzania but records of *E. brachyrhynchus* in Tanzania are peculiarly scarce. *E. rufescens* also abuts with *P. tetradactylus* in Tanzania but since the former is especially characteristic of the short-grass plains any overlap is likely to be slight.

E. rufescens and *E. brachyrhynchus* are sympatric in the Central Highlands of Kenya but they are probably only marginally syntopic. None of the available records are sufficiently precise to throw light on the ecological relationship of the two species. Elsewhere in East Africa any overlap of species is only marginal, e.g. between *E. rufescens* and *E. revoili* in Somalia and perhaps between *E. brachyrhynchus* and *E. fuscipes* in Uganda.

South of the Zambezi sympatry of two or more species is more frequent, although good evidence of syntopy is scarce. *E. brachyrhynchus* overlaps extensively with *E. intufi* and *E. myurus* but these latter form an east–west pair only marginally in contact. Further south, *E. intufi* overlaps very extensively with *E. rupestris* in South West Africa, but they are probably only marginally syntopic since Shortridge (1934) did not find them in precisely the same locality. Further south yet, both *E. rupestris* and *E. myurus* are replaced by *E. edwardi*. A report by Shortridge (1942) suggests that *E. rupestris* and *E. edwardi* are syntopic in rocky habitats in Little Namaqualand. All three of these species approach each other closely at Deelfontein in Cape Province but there is no information on habitats in that area.

M. proboscideus is widely sympatric with both *E. rupestris* and *E. edwardi* and at least comes close to *E. myurus* at Deelfontein. According to Shortridge (1934) it is widely syntopic with *E. rupestris* in parts of South West Africa where they " often occur side by side in about equal numbers, the two species being indistinguishable from a distance ".

There is therefore no good evidence of even two species of *Elephantulus* being widely syntopic over any large area and in most cases of gross sympatry the species are likely to be separated by habitat preference rather than by differential exploitation of the same habitat. By contrast *M. proboscideus* seems likely to be widely syntopic with *E. rupestris* and in this connection it would be interesting to have details of food especially in view of the much greater degree of hypsodonty in *M. proboscideus*.

Uncertainties

Taxonomic uncertainty at the specific level concerns chiefly two situations. In *Rhynchocyon* there may be found grounds for treating the form *stuhlmanni* as specifically distinct from *R. cirnei*. In *Petrodromus* the same may be said for the form *tordayi* in the Congo in relation to *P. tetradactylus*. However, in the case of *Petrodromus* there is less certainty that the two forms are spatially isolated than in the case of *Rhynchocyon*. Further areas requiring investigation of *Petrodromus* are northeastern Tanzania where the complex interaction of *P. t. sultan* and *P. t. rovumae* would repay study ; and in southern Mozambique to determine the spatial and morphological relationship of *P. t. schwanni* to the adjacent forms.

Within the genus *Elephantulus* a question of particular interest is the nature of the relationship between the members of the two species-pairs, namely *E. brachyrhynchus*/*E. fuscipes* in Uganda, and *E. rufescens*/*E. revoili* in Somalia. Any case of syntopy would repay study, but an area of especial interest would seem to be the Richmond district of Cape Province where three species of *Elephantulus* and *Macroscelides proboscideus* all approach each other closely. Specimens of all four species from Deelfontein are in the British Museum (collected in 1901 and 1902). That these did indeed come from a limited area is suggested by the fact that both *E. myurus* and *E. rupestris* were collected on one day; and *E. myurus* and *E. edwardi* on one day with *M. proboscideus* the previous day.

The subspecific taxonomy can only be clarified by a great deal of further collecting to determine especially the detailed range of each species. Areas from which data is especially scanty are Angola, Mozambique and Somalia.

NEW NAMES

The name *Rhynchocyon cirnei shirensis* subsp. n. is proposed (p. 59), type locality Lichenja Plateau, Mlanje Mountain, Malawi.

The name *Elephantulus broomi* nom. nov. is proposed (p. 54) to replace *E. langi* (Broom, 1937), preoccupied by *langi* Roberts, 1929.

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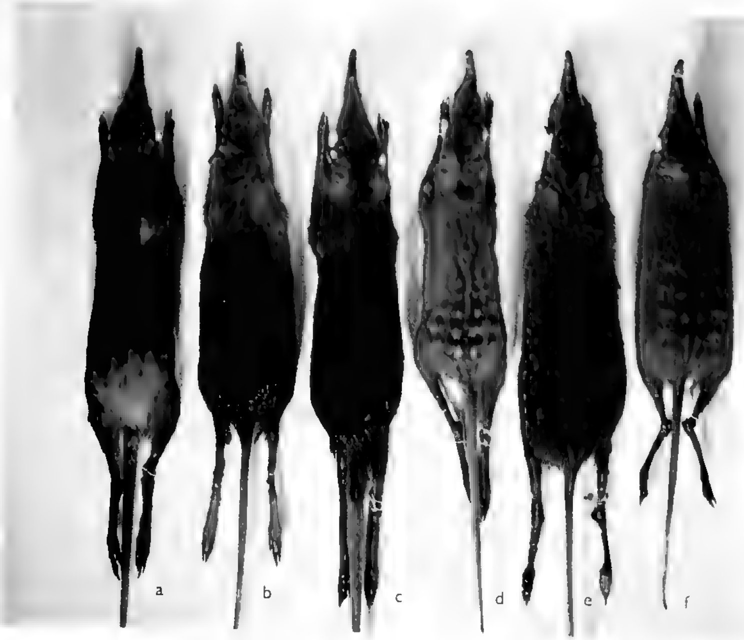
PLATE 1

- FIG. a. *Rhynchocyon chrysopygus* Günther ; Kenya. Lectotype, B.M. 80.11.30.7.
- FIGS. b–c. *Rhynchocyon petersi.*
  - b *R. p. petersi* Bocage ; Shimba Hills, Kenya. B.M. 8.3.21.1.
  - c *R. p. adersi* Dollman ; Zanzibar. Holotype, B.M. 12.1.6.1.
- FIGS. d–m. *Rhynchocyon cirnei.*
  - d *R. c. stuhlmanni* Matschie ; Beritio, Congo. Holotype of *claudi* Thomas & Wroughton, B.M. 7.7.8.53.
  - e *R. c. stuhlmanni* Matschie ; Ituri Forest, Congo. Holotype of *nudicaudatus* Lydekker, B.M. 6.12.22.1.
  - f *R. c. stuhlmanni* Matschie ; Bugoma Forest, Uganda. B.M. 19.4.17.2.
  - g *R. c. hendersoni* Thomas ; Livingstonia, Malawi. Holotype, B.M. 2.9.8.1.
  - h *R. c. reichardi* Reichenow ; Nyika Plateau, Zambia. B.M. 62.326.
  - i *R. c. shirensis* subsp. n. ; Mlanje Mt., Malawi. Holotype, B.M. 34.1.11.8.
  - j *R. cirnei* subsp. ; Lurio River, Mozambique. B.M. 34.1.11.6.
  - k *R. c. macrurus* Günther ; Liwale, South East Tanzania. B.M. 1938.10.13.3.
  - l *R. c. macrurus* Günther ; Mahendera, Mbwemkuru River, South East Tanzania. B.M. 62.400.
  - m *R. c. macrurus* Günther ; Kilwa, South East Tanzania. B.M. 62.419.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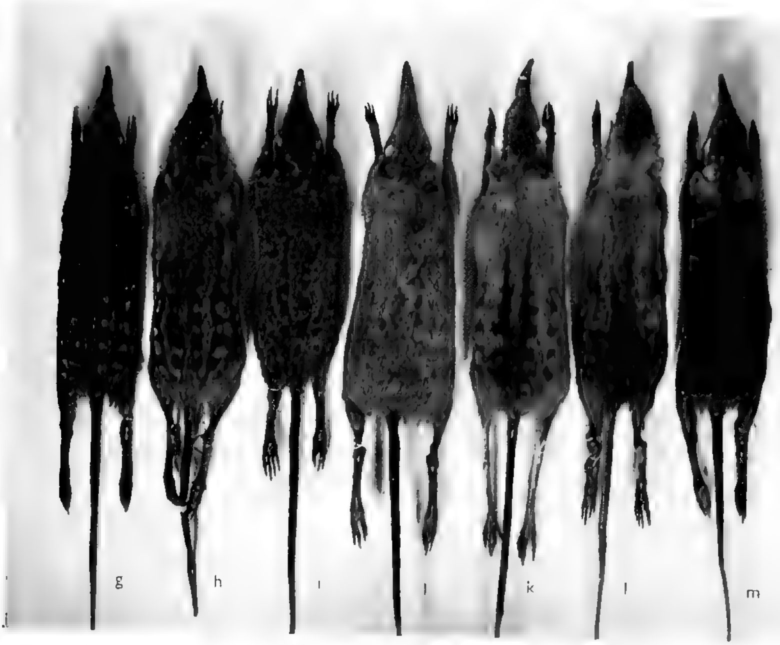
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POLYZOA FROM WEST AFRICA
THE MALACOSTEGA
PART I

PATRICIA L. COOK

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 16 No. 3
LONDON: 1968

POLYZOA FROM WEST AFRICA
THE MALACOSTEGA
PART I

BY

PATRICIA L. COOK
British Museum (Natural History)

Pp. 113–160 ; 3 *Plates* ; 20 *Text-figures*

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POLYZOA FROM WEST AFRICA
THE MALACOSTEGA
PART 1

By PATRICIA L. COOK

CONTENTS

INTRODUCTION

THE Collections studied have been described by Cook (1964*a* : 44). They include the " Calypso " Collection I, from Senegal and the Bay of Biafra, and Collection II, from the Cape Verde Islands; the Marche-Marchad Collections from Senegal; and the Achimota Collection, from the coast of Ghana. In addition, records are included of species from the "Atlantide " and " Galathea " Expeditions to western Africa; the Mortensen Java–S. Africa Expedition (west African Stations); and other Collections stored at the Universitetets Zoologisk Museum, Copenhagen. Some records of species from the Collections of the Musée Royal de l'Afrique Centrale, Tervuren, Belgium, are also included. Material was treated with eau de javel for examination of calcareous parts, and decalcified and stained to show chitinous parts. The following measurements (in mm.) were made where possible:

Length of zooid	Lz	Width of zooid	lz
Length of operculum	Lop	Width of operculum	lop
Length of opesia	Lopes	Width of opesia	lopes
Length of avicularium	Lav	Width of avicularium	lav
Length of mandible	Lm	Width of mandible	lm
Length of ovicell	Lov	Width of ovicell	lov
Length of kenozooid	Lkz	Width of kenozooid	lkz

Specimens in the Collection of the British Museum are referred to by their registered numbers, thus: 1966.10.12.1.

Malacostega Levinsen

Malacostega Levinsen, Harmer, 1926 : 187, Bassler, 1953 : G 155.

The genera have been grouped into families, usually following Bassler (1953) or Osburn (1950). Waters (1898), reviewing the characters of the Membraniporidae, considered that " generic division is at present somewhat risky ", and study of these species has shown that today there are still no criteria which may be used exclusively to define many families and genera. In some cases, it has been extremely difficult to define species, as the characters hitherto considered diagnostic have been found to intergrade, particularly under certain conditions of growth (see pp. 123, and 153).

The generic groupings below have therefore been based upon the highest correlation of common characters; where there is great variation of characters within a genus or a species, this is discussed briefly.

MEMBRANIPORIDAE Busk

Membraniporidae Busk, Osburn, 1950 : 18.

MEMBRANIPORA de Blainville

Membranipora de Blainville, Osburn, 1950 : 19.

TYPE-SPECIES. *Flustra membranacea* Linnaeus.

Osburn (1950 : 19) reviewed the characters and history of the genus. He concluded that the genera *Biflustra*, *Nitscheina* and *Acanthodesia* were all synonymous with *Membranipora* s.s. Lagaaij (1952 : 18) also clarified the definition of *Biflustra*, of which he considered *Acanthodesia* to be a synonym. Lagaaij included *Flustra savartii* Audouin in *Biflustra*. This species is known to develop from a twinned ancestrula, as do all the species considered to belong to *Membranipora* s.s. Whatever the status of *Biflustra*, *F. savartii* is so similar in character to the other species described here under *Membranipora*, that it is included with them.

The amount of material available for study in the west African, the British Museum and the Copenhagen Museum Collections is very large, and exhibits a great range of variation. Considerable difficulty has been found in defining some of the forms described below satisfactorily; at the means of their ranges of variation they are easily distinguishable, but at the ends of these ranges their characters seem to merge. Several of the features hitherto considered to be diagnostic of certain species have been found in all of them, under certain conditions of growth. The type of substrate has also been found to affect the zoarial and zooidal characters of some of the species. The synonymies given below are therefore restricted, as it is possible that many previous records may, in fact, include more than one " species ". Much further work is needed, both on the larval form and early astogeny, and on the correlation of zoarial and zooidal variation with ecological conditions, particularly with regard to the effects of substrate and salinity.

The characters showing particularly wide variation are as follows:

Gymnocystal tubercles. These occur in specimens of all the species of *Membranipora* described below, but they may be absent, especially at the growing edges of the colony.

Cryptocyst. In all species where they have been observed, the periancestrular zooids have a well-developed proximal cryptocyst. Unless the colony also includes later-developed zooids, it is virtually impossible to distinguish young colonies specifically. The extent of the cryptocyst also varies in fully developed colonies. In *M. arborescens* it is not usually developed proximally, but zooids with a well-developed proximal cryptocyst do occur, and are very similar to some of the variants found in *M. commensale* and *M. tenuis*, which, conversely, frequently shows zooids with hardly any proximal cryptocyst at all. The variation in extent of the proximal cryptocyst in *M. tuberculata* is very large, and is correlated with the occurrence of internal cryptocystal denticles (see below). The variation in *M. tenuis* has been particularly studied by Osburn (1940, see p. 128).

Cryptocystal denticles. With the exception of *M. commensale* s.s., all the species described below may show denticles arising from the cryptocyst. In large numbers of zooids, these may, however, be completely absent.

Chitinous spinules. These small spinules occur on the frontal membrane, and have been considered diagnostic of *M. commensale.* In fact, they are rare, and often absent in this species, but have been found in profusion in the encrusting phase of *M. arborescens,* and are present in some colonies of *M. tenuis.*

Septulae. The range of intraspecific and interspecific variation in the position and nature (whether uniporous or multiporous) of the septulae has been found to be random and continuous in all species. There seems to be no correlation of the type of septulae with locality, substrate or zoarial form.

Commensalism. One species, *M. commensale,* is here defined as being consistently and exclusively commensal on gastropod shells, whether they are inhabited by the mollusc or by pagurid crabs. Two other species, *M. arborescens* and *A. tincta* (see pp. 121, 140) may be associated with gastropod shells, and seem to have a commensal relationship with the occupants, but this appears to be accidental, and these species also occur on other substrates. Certain modifications of zoarial and zooidal form occur in *M. arborescens,* which are dependent upon the type of substrate; but the form found on inhabited gastropod shells is the same as that found, for example, on dead lamellibranch shells. This form is specifically distinct from *M. commensale* s.s. (see p. 125).

The specimens described below have been assigned to species somewhat arbitrarily, pending further investigations of the relationships of the complex. The correlation of characters used as specific criteria for the west African specimens is as follows:

M. tuberculata. Zoarium encrusting algae and wood, occasionally on stone, worm tubes, etc. Cryptocyst well-developed distally, forming a shelf, little developed laterally, variable proximally. Branched denticles growing from the edge of, and from below, the cryptocyst. Large gymnocystal tubercles usually present.

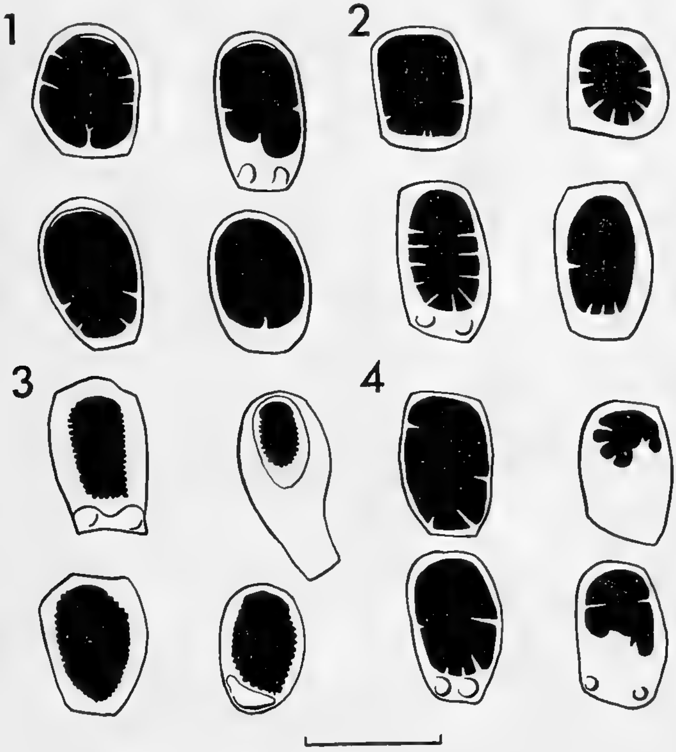
M. arborescens. Zoarium erect, tubular or bilaminar and foliaceous, on hydroids and algae, or encrusting, plurilaminar, on shell, worm tubes, or other Polyzoa. Cryptocyst slightly developed proximally, with a series of simple denticles developed laterally and proximally. Small gymnocystal tubercles sometimes developed. *Erect phase:* zooids nearly as wide as long, cryptocystal denticles numerous, chitinous spinules rare or absent. *Encrusting phase:* zooids more elongated, cryptocystal denticles reduced or absent, chitinous spinules and brown line outlining zooids present.

M. commensale. Zoarium encrusting gastropod shells, commensal with mollusc or pagurid crab, plurilaminar, never erect. Cryptocyst sometimes well-developed proximally, becoming much thicker in older zooids. No denticles on cryptocyst. Chitinous spinules and brown line outlining the zooids occasionally present. Large gymnocystal tubercles present.

M. tenuis. Zoarium encrusting shell. Cryptocyst well-developed proximally, finely tuberculate. Simple or branched cryptocystal denticles present in nearly all zooids. Gymnocystal tubercles rare.

M. annae. Zoarium encrusting wood and barnacle plates. Zooids with cryptocyst well developed proximally and laterally, with regularly spaced, long, simple denticles extending to the distal end of the opesia. Large vicarious avicularian individuals occasionally present. Found in waters of reduced salinity.

Although no specimens of *M. savartii* have been found so far from west Africa, it is included here in order that the variation in characters found may be compared with those seen in the other species of *Membranipora*. Zoarium encrusting, or erect, tubular. Cryptocyst often well-developed proximally, with a central proximal serrate denticle. Gymnocystal tubercles sometimes present.



Figs. 1–4. Intra- and interspecific variation in *Membranipora*. Scale = 0·5 mm. 1. *M. tuberculata* (Bosc). 4 "non-typical" zooids, showing simple, reduced denticles and variation in the development of the proximal cryptocyst. 2. *M. arborescens* (Canu & Bassler). 4 zooids, some showing reduced denticles, and 1 (bottom left) with denticles similar to those of *M. annae*. 3. *M. commensale* (Kirkpatrick & Metzelaar). 4 zooids showing the variation in development of the cryptocyst and of the gymnocystal tubercles. 4. *M. tenuis* Desor. 4 zooids showing variation in the development of the cryptocyst, the denticles, and the gymnocystal tubercles.

Membranipora tuberculata (Bosc)

(Pl. 2, figs. C, D, text-fig. 1)

Nichtina tuberculata (Bosc) Harmer, 1926 : 208, pl. 13, fig. 10, East Indies.
Membranipora tuberculata (Bosc) Marcus, 1937: 33, pl. 5, fig. 12; 1939 : 125, pl. 6, figs. 4A–B, Brazil. Osburn, 1950: 23, pl. 2, figs. 4, 5, 6. Maturo, 1957: 33, fig. 27, N. Carolina. Shier, 1964 : 609, N.W. Florida.

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 104, W. Annobon, B. de Santa Cruz, 4.vii.56, 8–12 m., C7A, C30A.

Achimota Coll. Stn. A, bottom net off Accra, 27.iv.51, 14 m., 1B; Stn. B, Winneba shore, 15.xi.49, 10B; Stn. D, as above, 30A; Stn. E, Christiansborg shore, 15.1.49, 34B; Stn. F, as above, 14.ii.49, 13D; Stn. G, as above, 19.xi.49, 38B; Stn. M, on antipatharian, 3 miles offshore, 2 miles W. of Densu River, 15 fath., 2.ii.49, 52A; Shore, no locality, A, B. Coll. II. Winneba, 22.xi.49, 20A, on worm tubes.

Zoologisk Museum, Copenhagen. " Galathea " Stn. 37, Rockpool, Christiansborg, Accra, 4.xi.50, rock and sand, with *Electra verticillata*, 50B. Stn. 38, Teshi, Accra, 24.xi.50, with *E. verticillata*, 34B.

Clausen Coll., Lagos, on algae, 16D, 95F.

Musée royal de l'Afrique Centrale, Tervuren, Belgium. Entre Banane et Moanda, Congo, on wood, No. 265A.

British Museum. A large number of specimens have been examined, including the following: San Pedro, west Africa, 1877.3.16.16; Angola, 1877.3.16.13; near Dixcove, Ghana, 1942.5.8.2; Algoa Bay, S. Africa, 1899.7.1.360; Aden, 1928.9.13.2. Labelled " *Membranipora denticulata* " Adriatic, 1899.5.1.431, Hincks Coll.

" John Murray Coll.", Stn. 44, N. of Khorya Morya Is, S. Arabian coast, at the surface, 29.x.33, Z172B.

DIMENSIONS. Lz 0·41–0·57 mm., lz 0·17–0·38 mm., Lopes 0·26–0·43 mm.

Zoarium almost exclusively encrusting algae, especially *Sargassum*. Zooids with a pair of large tubercles on the gymnocyst, which may coalesce. Cryptocyst with a distinct distal shelf, narrow laterally, variably developed proximally. Branched denticles protruding into the opesia from the edge of, and from below, the cryptocyst.

The great majority of the specimens encrust algae, and are also associated on this substrate with colonies of *Electra verticillata* (see p. 132). The " Calypso " specimen encrusts stones and barnacle plates.

The specimens exhibit a large range of variation. The proximal tubercles are little developed in one of the specimens from San Pedro, but large in another slide from the same locality. Achimota 10B has little development of the proximal cryptocyst, which is extensive in specimen 1B and in 1899.5.1.431 (see below). The specimen from the Arabian coast is similar to that from Aden, which was described by Harmer (1926 : 210), in which the gymnocystal tubercles were not calcified distally, but covered by a membrane. Some scattered zooids from west Africa show a similar form of tubercle.

The paired, comb-like denticles, which protrude into the zooidal cavity from beneath the proximal cryptocyst, are well-developed in some of the west African specimens, but apparently completely absent in others. They were first described by Waters (1898 : 675, pl. 48, figs. 6–8), and further discussed by Marcus (1939 : 125, pl. 6, figs. 4A, B). The occurrence of these structures seems to be postively correlated with a well-developed proximal cryptocyst, and they occur in the zooids of 1899.5.1.431, and Achimota Coll. 1 B.

The twinned ancestrula of *M. tuberculata* has been described by Hastings (1930 : 706, pl. 3, figs. 9, 10) and by Maturo (1957 : 35, text-figs. 25).

The specimen Achimota 1B, which encrusts algae, resembles that labelled as " *M. denticulata* " from the Adriatic. The zooids of both specimens have a greatly developed, irregularly denticulate, proximal cryptocyst (see pl. 2, fig. D). Paired, comb-like denticles are present beneath the cryptocyst, and the specimens are certainly referable to *M. tuberculata,* although greatly resembling *M. tenuis* in appearance. The specimens, Achimota II, 20A, encrusting worm-tubes, include zooids which show an unusually large range of variation. Comb-like denticles are present in a few zooids only, but branched denticles occur in many zooids both beneath and on the edge of the cryptocyst. As this type of branched denticle does not occur in any of the other species, their presence must be considered characteristic of *M. tuberculata.* In some parts of the colony the denticles are, however, simple and reduced in number to one or two per zooid. In other parts they are frequent and regularly spaced, and resemble those found in *M. arborescens.* The cryptocyst is well-developed proximally in some zooids, resembling *M. tenuis,* in others it is completely deficient. Gymnocyst tubercles vary from being absent to large and paired.

The cryptocyst in the majority of specimens forms a distinct shelf distally, a character which seems to distinguish *M. tuberculata* from the other species described here. It is not invariably present, however, and in its absence, together with the absence of comb-like denticles beneath the cryptocyst, it would be impossible to distinguish isolated zooids from some of those of *M. arborescens, M. tenuis* or *M. savartii.*

Membranipora arborescens (Canu & Bassler)

(Pl. 1, figs. B, C, D, pl. 2, fig. E, text-fig. 2)

Biflustra savartii (Audouin), Smitt, 1873 : 20, pl. 4, figs. 92–95, Florida; not *Flustra savartii* Audouin, see p. 129.

Acanthodesia arborescens Canu & Bassler, 1928*a* : 15, pl. 1, figs. 2–5, Cap Blanc, Mauritania, 20–40 m. Redier, 1965 : 381.

? *Conopeum commensale* Kirkpatrick & Metzelaar, Marcus, 1937 : 37, pl. 5, fig. 13, Brazil-1939 : 126, pl. 6, figs. 5A, B, C, Brazil; 1941 : 16, fig. 5. Osburn, 1950 : 30, pl. 2, figs. 12–15, N. Mexico to Ecuador. Maturo, 1957 : 37, text-fig. 29, N. Carolina. Soule, 1959 : 7, W. Mexico. Lagaaij, 1963 : 166, pl. 8, fig. 2, Gulf of Mexico. Not *C. commensale*, see p. 125.

Acanthodesia (*Biflustra*) *mogadori* Gantès & Balavoine, 1961 : 187, pl. 7, figs. 1–4.

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 7, 9° 40′ N, 13° 53′ 5″ W, 17.v.56, 18 m., C4C; Stn. 8 entre I. Tamara & I. Cassa, 18.v.56, 7–8 m., C24A, tubular. Stn. 17, 5° N, 5° 28′ 30″ W, 21.v.56, 27 m., C34A, tubular. Stn. 18, 5° 2′ 5″ N, 5° 24′ 4″, 21.v.56, 20–25 m., C5A, tubular, anastomosing. Stn. 19, 5° 2′ 30″ N, 5° 24′ 40″ W, 21.v.56, 21–27 m., C57B, tubular arising from algae. Stn. 49, 4° 03′ N, 6° 12′ E, 26.v.56, 32 m., C49D, tubular. Stn. 56, 0° 38′ 25″ S, 8° 46′ E, 16.vi.56, 5 m., C22B, tubular. Stn. 104, B. de Santa Cruz, Annonbon, 4.vii.56, 8–12 m., C30A, encrusting.

Marche-Marchad Coll. I. 2C, Konakrey, Guinée Ise, tubular. 4B, C, Cap Matakong, Guinée Ise, encrusting and erect on *Pecten* shell with *Cleidochasma oranense*, *C. porcellanum*, and many other species. 26K, S.W. Madeleines, 9.i.54, 45–46 m., tubular. 41A, S.W. Cap de Bald, 31.iii.54, 18 m., encrusting and erect, foliaceous. 48A, Pointe de Fomone, 13.iv.54, 10 m., foliaceous and tubular.

Coll. II, 12D, Large de Gorée, 5.vii.55, 50 m., foliaceous. 18A, M'Bour, 19.v.49, 25 m., tubular. 32B, Pointe de Formone, 13.iv.54, 10 m., foliaceous. 38A, Est de Gorée, 24.xi.53, 48 m. tubular. 43E, Sud de Gorée, 13.xi.53, 34–37 m., tubular. 44A, Par de travers de Joal, 11.v.55, 18–32 m., foliaceous. 45A, Bourée de Persée, S. Gorée, 10.xi.55, 15 m., foliaceous. Coll. III, 2A, Sud de presque l'île du Cap Vert, 18.2.54, 46–50 m., encrusting.

Achimota Coll. Stn. E, Christiansborg shore, 15.i.49, 34G, foliaceous. Stn. F as above, 14.ii.49, 13E, encrusting. Stn. G, as above, 19.xi.49, 38A, encrusting worm tubes. Christiansborg, 13.x.50 on *Eucidaris*, 94D (see p. 141). Stn. K, on trawl debris, 1 mile offshore, 2 miles W. of Densu River, 8 fath., 2.iii.49, 36A, on *Pecten* shell, and 44A on shell inhabited by Acrothoracid Cirripede. Stn. S, shore seine, Chorkor, March 1949, on shell, 39A. Stn. W, Apam shore, 16.ii.49, 66G, foliaceous. Stn. 56, 15.i.51, 16 m, 90 II C, encrusting shell. Stn. 117, 5.iv.51, 64 m., 32 R + S, foliaceous. Stn. 123, 11.iv.51, 9 m., 89 I C, on Pecten shell. Stn. 126, 12.iv.51, 20 m., 37A, on Pecten, with many other species. [? Stn. 89.7.ii.51, 16 m., 76A, Stn. 93, 12.iii.51, 12 m., 2A, and Stn. 103, 29.iii.51, 85. I B, see below.]

Zoologisk Museum, Copenhagen " Atlantide " Coll. Stn. 44, 10° 22′ N, 16° 22′ W, 17.xii.45, 41 m., 63 G + L, encrusting and tubular. Stn. 45, 9° 23′ N, 15° 07′ W, 18.xii.45, 34 m., 14B, tubular, 14C, encrusting shell. Stn. 55, 6° 03′ N, 10° 25′ W, 8.i.46, 44 m., 31A, tubular. Stn. 85, 5° 37′ N, 0° 38′ E, 30.i.46, 50 m., 29E, 108a, tubular. Stn. 96, off Lagos, 14.ii.46, 40–51 m., 104A, tubular. Stn. 109, Dowes Island, Niger Delta, 21.ii.46, 59A, worm, encrusting stone. Stn. 133, 7° 19′ S, 12° 40′ E, 16.iii.46, 47 m., 43B, tubular. Stn. 136, 8° 30′ S, 13° 14′ E, 18.iii.46, 45 m., 3A, foliaceous. Stn. 145, 9° 20′ N, 14° 15′ W, 13.iv.46, 32 m., 44K and 110F tubular on hydroids and *Jullienella*, and 110G encrusting Polyzoa and worm tubes. Stn. 146, 9° 27′ N, 14° 48′ W, 13.iv.46, 51 m., 72 I, tubular and 107E tubular and encrusting. Stn. 147, 9° 28′ N, 14° 58′ W, 14.iv.46, 45 m., 77B, tubular. Stn.1 48, 9° 57′ N, 15° 22′ W, 14.iv.46, 25 m., 10C, tubular and encrusting, shell inhabited by Pagurid crab.

Naturhistoriska Riksmuseet, Stockholm, Lå 19, 283, 1860, Florida, 29 fath., figured specimen of *Biflustra savartii* Smitt, not Audouin, Smitt 1873, pl. 4, figs. 92, 93.

British Museum. As *Conopeum commensale*, 1947.3.28.1, Hancock Stn. 136, Clarion Is., Osburn Coll.

DIMENSIONS. Lz 0·34–0·55 mm., lz 0·23–0·47 mm., Lopes 0·26–0·43 mm.

Zoarium with zooids very regularly shaped. Cryptocyst slightly developed proximally, with small simple denticles growing laterally and proximally round the opesia. Occurring in two phases:

1. Zoarium erect, arising from a small, unilaminar base surrounding hydroids or algae; foliaceous and bilaminar, or tubular, branching and anastomosing. Zooids almost square, opesiae regularly oval or almost circular. Simple denticles arising from the edge of the cryptocyst, proximally and laterally, not extending beyond the distal third.

2. Zoarium encrusting, on shell, other Polyzoa, etc., occasionally accidentally commensal with gastropod molluscs, or with pagurids inhabiting gastropod shells, plurilaminar. Zooids regularly rectangular, opesiae elongated oval. Small cryptocystal denticles usually present proximally, and laterally. The denticles may be absent over large areas of the colony, but are always present in a few zooids. Zooids outlined by a dark brown line, frontal membrane covered by small chitinous spinules, which are occasionally rare or absent.

The occurrence of two distinct phases in this species which are superficially quite unlike each other (see pl. 2, figs. A and E), seems to be positively correlated with the type of substrate settled upon by the larvae. The two forms may occur from the same Station, but generally the preponderance of specimens of the erect type is found where the available stable substrate is reduced by the muddy or sandy sea-bottoms of the Gulf of Guinea to algal and hydroid stems. The zooidal characters of the two forms also differ, but their ranges of variation overlap considerably, and they are therefore assigned to the same species.

The encrusting phase has been confused in the past with *M. commensale.* It differs in the presence of cryptocystal denticles, which never occur in *M. commensale* s.s. (see below), and in the abundance of chitinous spinules on the frontal membrane, which are rare in *M. commensale.* The brown line outlining the zooids is usually present in the encrusting phase of *M. arborescens*, but is frequently absent in *M. commensale.*

The two species also differ in their form of growth on shell. *M. arborescens* grows in large, regular sheets. Where two growing edges meet there is little distortion of the zooids, and few kenozooids are produced. The zoarium usually continues to grow as a bilaminar expansion at right angles to the original directions of growth. In *M. commensale* the zooids are budded in fan-shaped groups, and seem incapable of producing erect expansions where two growing edges meet. The zooids of the plurilaminar colonies are therefore irregular in shape and arrangement, and large groups of kenozooids are present at points of pressure.

Many American records of *M. commensale* are almost certainly referable to the encrusting phase of *M. arborescens*, which may be commensal with gastropods shells. *M. commensale* is not found on any other substrate, and thus records listing gorgonid stems, stones and algae, etc., may perhaps be referred to *M. arborescens.* Many descriptions and figures by American authors also show cryptocystal denticles and large numbers of chitinous spinules, both characters typically found in encrusting *M. arborescens.* Without examination of all the described material, it is not possible to be certain of the identity of previous records, but the material from American waters which has been seen, has proved to be assignable to species other than *M.*

commensale s.s. For example, a specimen from Brazil labelled "*C. commensale*", from the Marcus Collection (1942.2.16.36), appears to belong to *M. savartii*, and another from Western Mexico, from the Osburn Collection (1947.3.28.1, Hancock Stn. 136, Clarion Is.), is referable to *M. arborescens.*

Recent specimens from N. Carolina and Louisiana, and fossil material from Jackson Bluff sent by Dr. R. Scolaro have shown there may be intergradation between the American forms here associated with *M. arborescens* and *M. tenuis* (see p. 127). Dr. Scolaro's specimens are here discussed under *M. tenuis*, but it must be noted that large areas of zooids in the colonies are indistinguishable from encrusting *M. arborescens*, and, if they had been isolated, would have been assigned to that species. Smitt's figured specimen of *B. savartii* has been re-examined. It consists of an erect tubular, branching fragment. The cryptocyst has simple denticles, and a brown line outlines the zooids. The specimen would appear to be typical erect *M. arborescens* (see pl. 1, fig. E).

A. mogadori is certainly the same species as *M. arborescens.* Gantés & Balavoine described the zoarium as very large, 5 cm. wide and 3·5 cm. high. One of the zoaria from the Marche-Marchad Collection (Coll. I 48A) measures 11 cm. × 6 cm., as does one from the "Atlantide" Collection (45A). The zoaria are foliaceous and arise from gorgonid stems. Superficially, the tubular zoaria of *M. arborescens* resemble the erect parts of the colonies of *Crassimarginatella falcata* (see p. 153), and the two species occur together in samples from Senegal.

The specimens in the "Atlantide" Collection best show the dual nature of *M. arborescens* (see pl. 1, figs. C, D). The encrusting form of zoarium occurs on shells (fully commensal from Stn. 148, 10C), and on other Polyzoa, particularly *Cleidochasma oranense* and *Triporula stellata.* These last 2 species themselves encrust hydroid stems, often forming large plurilaminar masses. The form of *M. arborescens* associated with them is not, however, the erect, tubular type which grows directly from hydroid stems (pl. 1, fig. D), but is exactly the same as that found encrusting shell. All these 3 types of substrate, and both forms of *M. arborescens*, occur at Stn. 145. Specimen 63L, from Stn. 44, combines both forms of growth; it is encrusting, with unilaminar expansions.

The specimen from the "Atlantide" Coll., 10C, is fully commensal, with a pagurid crab, inhabiting a small gastropod shell. The zooids are thickly covered with chitinous spinules and outlined by a brown line. The cryptocyst is thick and the opesiae almost circular, like those of the specimen from Clarion Island. Cryptocystal denticles are present proximally and occasionally laterally, and paired gymnocystal tubercles occur on most of the zooids.

The specimens from the Achimota Collection, 85 I B and 2A encrust small pieces of wood. The colonies are very young, and all have twinned ancestrulae and periancestrular zooids with well-developed proximal cryptocysts. Small but distinct gymnocystal tubercles are present in some zooids, as are single series of chitinous spinules on the frontal membranes. The proximal cryptocyst is symmetrical and not denticulate (cf. *M. tenuis*, p. 127). The specimen 76A includes another young colony with a twinned ancestrula. The periancestrular zooids have symmetrical proximal cryptocyst, with no trace of a denticle, and the later developed zooids greatly resemble those of encrusting *M. arborescens*. Small chitinous spinules are present on the frontal membranes of the zooids. Although these specimens cannot be identified with certainty, it seems possible that they may belong to *M. arborescens*.

Membranipora commensale (Kirkpatrick & Metzelaar)

(Pl. 1, fig. A, text-fig. 3)

Conopeum commensale Kirkpatrick & Metzelaar, 1922 : 985, pl. 1, fig. 2, Capo Blanco, West Africa. Not *C. commensale* auctt., see *M. arborescens*.
not *C. commensale* Kirkpatrick & Metzelaar, Marcus, 1938 : 16, pl. 3, fig. 6A, B, C = *M. tuberculata*.
Membranipora fusca Canu & Bassler, 1925 : 11, pl. 2, figs. 6–8, Mauritania. Buge & Lecointre, 1962*a* : 555, pl. 18, figs. 3, 4, 6–8, pl. 19, figs. 1–4, 6, 7, Quarternary and Recent, Mauritania. 1962*b* : 244–5, Rio de Oro, Spanish Sahara. Lecointre, 1963 : 30, Quaternary, Spanish Sahara.
not *Membranipora fusca* Osburn, 1950 : 25, pl. 1, fig. 14, an independent introduction of the name.

MATERIAL EXAMINED. Holotype, B.M. 1922.9.9.1, Capo Blanco, 5–10 fath., Metzelaar Coll.

Achimota Coll. The great majority of the specimens encrusts *Turritella* shells. Stn. A, off Accra, 14 m., 27.iv.51, 1A. Stn. G. Christiansborg, 19.xi.49, 38A, on *Thais haemostoma*, inhabited by the Mollusc. Stn. 5, 9.xi.50, 13 m., 88A. Stn. 10, 19.xi.50, 14 m., 47A, ancestrula present (B.M. 1965.8.10.4). Stn. 11, as above, 13 m., 23A. Stn. 12, as above, 16 m., 74A, ancestrula present. Stn. 14, 26.xi.50, 26 m., 25A. Stn. 15, 28.xi.50, 20 m., 9A, 16A. Stn. 20, 30.xi.50, 20 m., 72A. Stn. 21, as above, 11 m., 78A. Stn. 23, 7.xii.50, 14 m., 35A. Stn. 26, 90 I A, II A, IV A. Stn. 29, 20.xii.50, 13 m., 82 I A. Stn. 47, 4.i.51, 44 m., 14c. Stn. 58, as above, 20 m., 4A. Stn. 59, as above, 24 m., 55A, 92A. Stn. 83, 26.ii.51, 15 m., 29A. Stn. 84, 26.ii.51, 77A. Stn. 85, as above, 21 m., 17A. Stn. 86, 28.ii.51, 8A. Stn. 90, as above, 21 m., 71A. Stn. 93, 12.iii.51, 12 m., 2A. Stn. 94, as above, 17 m., 56A. Stn. 95, 12.iii.51, 17 m., 86A. Stn. 97, 14.iii.51, 20 m., 6A, 83 I A. Stn. 98, as above, 25 m., 3A, 83 II A. Stn. 99, as above, 28 m., 69A, 83 III A. Stn. 106, as above, 19 m., 5 A. Stn. 107, 30.iii.51 m., 23 m., 91A. Stn. 121, 11.iv.51, 8 m., 93A. Stn. 123, as above, 9 m., 89 I A. Stn. 124, 12.iv.51, 11 m., 18A. Stn. 125, as above, 16 m., 24A. Stn. 127, 14.iv.51, 17 m., 12A. Stn. 130, 26.iv.51, 32 m., 70A. Stn. 131, 2.v.51, 37 m., 43B. Coll. II 3A, on shell fragments, near petrol barge, off Accra, 9.i.52.

Zoologisk Museum, Copenhagen. " Atlantide " Coll. Stn. 85. 5° 37′ N, 0° 38′ E, 29.i.46, 50 m., 108I. Brinkmann Coll., Dakar 82A.

British Museum. Paratypes, 1922.9.9.2.3; 1922.9.9.9 and 15, 1922.9.9.4–6, Archimedes Bay, 18 fath. Metzelaar Coll. Faux Cap, west Africa, 1967.7.11.1, and Malacostraca Section registration, 1954.6.20.42, Rio de Oro, Marche-Marchad Coll., with *Pseudopagurus granulimanus* (Miers).

Zoarium encrusting, plurilaminar, sometimes massive, growing on gastropod shells, commensal either with the mollusc or pagurid crab. Zooids rectangular, frequently distorted. Gymnocyst with paired, occasionally coalescent tubercles. Cryptocyst granular, often well-developed proximally, variable in extent but regularly serrate.

Cryptocystal denticles absent. Chitinous spinules rarely present on the frontal membrane, zooids more frequently outlined by a brown line.

DIMENSIONS. Lz 0·32–0·45 mm., lz 0·26–0·38 mm., Lopes 0·26–0·35 mm.

Kirkpatrick & Metzelaar first described the association between *M. commensale* and shells inhabited by pagurid crabs from west Africa (Cf. Buge & Lecointre, 1962b: 557). The pagurid most commonly present was *Pseudopagurus granulimanus* (Miers), a species also frequently found associated with the Polyzoan genus *Hippoporidra* (see Cook, 1964*b* : 22). Kirkpatrick & Metzelaar found that small shells were encrusted by the Polyzoan " A few layers thick near the orifice ". Larger shells were encrusted by so many layers that the specimens were 6 cm. in diameter, and globular (see below). Canu & Bassler (1925) described *Membranipora fusca* as symbiotic with " grands gastropodes ", and mentioned that the zoarium was plurilaminar. Their specimens frequently had one gymnocystal tubercle extending across the zooids, but paired tubercles were also present. Marcus (1937 : 35) placed *M. fusca* in the synonymy of *C. commensale*. Canu & Bassler distinguished their species from *M. tuberculata*, which, they stated, had " deux tubercles distants ". The tubercles in *M. tuberculata* are, in fact, proximal in origin. *M. commensale* differs from *M. tuberculata* in the form and extent of the cryptocyst, and in the absence of cryptocystal denticles. The specimen figured as *C. commensale* by Marcus (1938, pl. 3, fig. 6) shows internal cryptocystal denticles and is referable to *M. tuberculata*.

Buge & Lecointre (1962*a*) redescribed Canu & Bassler's specimen of *M. fusca* together with Quaternary specimens from the Spanish Sahara. The majority of the specimens was massive and plurilaminar, like the type specimens of *M. commensale* and the Malacostraca Section specimen listed above. One Recent specimen (Port Étienne, pl. 18, fig. 8) resembles the majority of the Achimota Collection specimens from the Gulf of Guinea, in having only a few layers of zooids.

As stated above, material described by American authors as " *Conopeum commensale* " is almost certainly all referable to *M. arborescens* or *M. tenuis*. *M. commensale* s.s. would appear to be confined in distribution to the west African coast.

The range of variation in zooidal characters is large, and may frequently be found either within a single specimen, or within a population from one locality.

The operculum has a thickened rim, and is often dark brown. A brown line may outline the zooids, in some cases also outlining the opesiae. The small brown, chitinous spinules do not occur profusely in any of the specimens examined, and they are rare in the type material, being restricted to a pair situated at the base of the operculum.

The gymnocystal tubercles are large, and coalescent in some specimens, notably 1922.9.9.9, and Achimota Collection 1A. Large areas of the same specimens have, however, no trace of tubercles. The cryptocyst is granular, and finely serrate, particularly in young zooids, but is never denticulate. In older zooids it becomes massive and ridged.

M. commensale does not produce erect " arms " as does *Antropora tincta* (see Osburn, 1950 : 54), *Hippoporidra senegambiense* and *H. picardi*, all species which are commensal with gastropods or hermit-crabs (see Cook, 1964*b* : 23). There is, however, as in *Hippoporidra*, a difference in colonial form, which is apparently correlated with the type of shell encrusted by the Polyzoan. The thick, massive, plurilaminar colonies appear to be most frequently associated with short-spired shells; the single, or few-layered colonies with long-spired, *Turritella* shells.

The type-specimens are large (the diameter of the colonies ranges from 55–68 mm.), and plurilaminar. More than 50 layers of zooids may be seen in a section of specimen 1922.9.9.8B. Most of the Achimota Collection material encrusts *Turritella* shells, and is only 1–3 layers thick. The zooidal characters of the two forms are very similar. The growing edge of laminae in both forms have zooids with finely serrate cryptocysts, and the gymnocystal tubercles are very small or absent. In older zooids there is progressively greater calcification of the cryptocyst and gymnocyst.

The plurilaminar type-specimens are each associated with a hermit-crab. The layers of Polyzoan are encrusted by sessile barnacles, and inhabited by large numbers of boring bivalve mollusca. Kirkpatrick & Metzelaar (1922 : 983–4) described the associated sessile fauna. The specimens from Rio de Oro are also plurilaminar, and associated with the crab, *Pseudopagurus granulimanus*. Specimen 38A (on *Thais haemostoma*, with a short-spired shell) has plurilaminar colonies. In this case, the shells are occupied by the Mollusc. Specimen 70A has similar colonies which encrust empty shells.

The specimen from Archimedes Bay has only 1–3 layers and encrust a *Turritella* shell, which is occupied by *P. granulimanus*. Most of the remaining west African specimens encrust *Turritella* shells, and have few layers of zooids.

M. commensale is one of the dominant species of Polyzoan from the Gulf of Guinea. Many of the Stations in the Achimota Collection especially those from the " silty sand " and " sandy silt " communities described by Buchanan (1958) had no other Polyzoan present. Several hundred *Turritella* shells have been examined, and the great majority are inhabited by pagurid crabs or are empty. Although *M. commensale* is found associated with the mollusc, it would appear that it is principally commensal with hermit-crabs.

Membranipora tenuis Desor

(Pl. 2, fig. B, text-fig. 4)

?Hemiseptella africana Canu & Bassler, 1930*b* : 29, pl. 1, fig. 7, Tunisia.

Acanthodesia tenuis (Desor), Osburn, 1940 : 353, pl. 3, figs. 22–30, Porto Rico. Marcus, 1941 : 17, fig. 7, Brazil. Maturo, 1957 : 35, text-fig. 28, North Carolina.

Material examined. Achimota Coll. Stn. X, Hospital Reef, Axim, 7.i.51, on worm-tubes and shell, 68 G + H.

Scolaro Coll. Upper Miocene, Jackson Bluff, Florida, *Ecphora* facies. Recent, Rivers Island, Beaufort, North Carolina, and between Creole and Cameron, Louisiana.

Zoologisk Museum, Copenhagen. " Atlantide " Coll. Stn. 148, 9° 57′ N, 15° 22′ W, 14.iv.46, 25 m., 10D, on shell, ancestrula present.

Zoarium encrusting, with unilaminar expansions. Zooids with well-developed, often asymmetrical proximal cryptocyst. Denticles present on cryptocyst, one lateral pair being frequently elongated. Gymnocystal tubercles occasionally present.

DIMENSIONS. Lz 0·44–0·60 mm., lz 0·23–0·50 mm., Lopes 0·24–0·37 mm.

The range of variation in the form of the cryptocyst of *M. tenuis* is very large, and was illustrated by Osburn (1940). Some zooids of Achimota Coll. 68 G + H have very little proximal cryptocyst, and a few simple denticles; they are outlined by a brown line, and are indistinguishable from those of *M. arborescens* (see pl. 2, fig. B). Other zooids in the same colony, have a well-developed proximal cryptocyst with a serrate proximal denticle, and greatly resemble *M. savartii*. Generally, the proximal cryptocyst is asymmetrically developed, and one pair of lateral denticles is longer than the rest, as figured by Osburn (1940, pl. 3, fig. 22). The " Atlantide " specimens have the majority of the zooids of this type. *Hemiseptella africana* Canu & Bassler (1930*b*) appears to be referable to *M. tenuis*. The figured zooids have a well-developed proximal cryptocyst, with proximal and lateral denticles, which resemble some of those on pl. 2, fig. B.

The specimens from Dr. R. Scolaro show complete intergradation between " typical " *M. tenuis* and the type of zooids here associated with *M. arborescens* from American localities. The zooids have no chitinous parts, but some show traces of a brown line. The proximal cryptocyst is frequently fairly well-developed, with an asymmetrical proximal denticle, and a few lateral denticles. In large areas of these colonies, however, the cryptocyst is small, and only simple lateral denticles are present. These zooids are indistinguishable from those of *M. arborescens*.

It must be stressed, that were any one of the groups of zooids from both the west African or American colonies isolated, it could be confidently referred to *M. arborescens*, *M. savartii* or *M. tenuis*, depending upon the degree of variation displayed. Further, zooids from adjacent groups in the same colony could be referred to different species.

The periancestrular zooids of *M. tenuis* (" Atlantide " 10D), differ from those of *M. arborescens* only in their asymmetrical proximal cryptocysts, which may be denticulate. The periancestrular zooids of *M. savartii* are so similar to those of *M. tenuis*, that the two forms are indistinguishable in the absence of later-developed zooids (see below).

Membranipora annae (Osburn)

Acanthodesia serrata (Hincks) Hastings, 1930 : 707, pl. 4, figs. 13–15. Balbao, Panama (not *M. membranacea* form *serrata* Hincks).

Membranipora hastingsae Osburn, 1950 : 29, pl. 2, fig. 1, Balbao and Perlas Is., Gulf of Panama (preoccupied by *M.* (*Electra*) *hastingsae Marcus*, 1940).

Membranipora annae Osburn, 1953 : 774.

MATERIAL EXAMINED. Zoologisk Museum, Copenhagen. " Galathea " Stn. 54, bouy off Victoria 1.xii.50.

Museum royal de l'Afrique Centrale, Tervuren, Moanda, Congo, on wood, Nos. 163A, 164A. Entre Banane et Moanda, on wood, No. 264A. Cotonou, Dahomey, Nos. 278A, 279A, 280A, with *Hippoporina americana*.

British Museum. From S.T. " Harpula ", docked in Bonny River for 6 weeks, on Cirripedes and Mollusca, 1960.5.12.1.

Bonny river, Nigeria, 25 ft., 28.1.58, 1959.2.20.2, Stubbings Coll.

Balboa, Panama, St. George Coll., 1929.4.26.61, 62, 64.

M. annae is not present in the "Calypso", "Atlantide", Marche-Marchad or Achimota Collections.

Zoarium encrusting. Zooids with well-developed cryptocyst, with long, regularly spaced denticles and spinules. Large vicarious avicularia, sometimes present, with rounded mandibles and polypides.

DIMENSIONS. Lz 0·42–0·60 mm., lz 0·20–0·34 mm., Lopes 0·24–0·42 mm., Lav 0·50–0·70 mm., Lm 0·27–0·31 mm.

The remarkable avicularia were described by Hastings (1930); they are present in specimens 278A, 279A and 280A from Moanda, and in the specimens from the Bonny River. The species is here retained in *Membranipora* pending the discovery of its ancestrula and form of early budding.

The variability of development of the cryptocyst is considerable, the zooids of some specimens, notably No. 264A, Moanda, approaching those of the young, encrusting phase of *M. arborescens*. Some consistent differences are apparent in well-preserved material, but it would be virtually impossible to distinguish some forms of the two species in a fragmentary or worn condition. The distal rim of the zooids in *M. annae* are raised, and the small proximal gymnocyst has two areas of thin calcification (lacunae), which later develop small tubercles. These lacunae are not present in young *M. arborescens*, but they may occur in some young zooids of *M. tuberculata*, also before the gymnocystal tubercles develop. The proximal cryptocyst of specimen No. 264A is only slightly developed, and the opesia is surrounded by a series of numerous, long spinules. These are present in the distal half of the opesia and the median lateral pair are longer than the others, resembling zooids of some specimens of *M. tenuis*. The zooids are narrower than those of *M. tenuis*, and differ from those of *M. arborescens* in that the spinules reach the distal part of the opesia. They may, however, be as long as, and nearly as numerous in some specimens of *M. arborescens* (see 110F, on *Jullienella*).

M. annae is found in warm shallow waters, where the salinity is reduced or variable.

Membranipora savartii (Audouin)

Flustra savartii Audouin, 1826 : 240, pl. 10, figs. 10^1, 10^2, ? Red Sea.
Acanthodesia savartii (Audouin), Harmer, 1926 : 213, pl. 13, figs. 8, 13, 14, 16, East Indies. Marcus, 1937 : 40, pl. 7, figs. 16 A–C; 1938 : 66, pl. 14, fig. 36, Brazil.
Membranipora savartii (Audouin), Maturo, 1957 : 35, text-fig. 27. Shier. 1964 : 607, Florida.
not *Biflustra savartii* (Audouin), Smitt, 1873=*M. arborescens*, see p. 121.

MATERIAL EXAMINED. British Museum. Aden, on shell, 1966.1.2.1, 2, Sgt. Cambridge Coll. 1966.7.2.1, Kor Dongola, Red Sea, specimen from Waters, O'Donoghue Coll. N. Straits of Malacca, 30–34 fath, 1877.5.21.108.

Zoarium encrusting on weed or shell, or erect, tubular. Zooids with a variously developed proximal cryptocyst, with a median serrate denticle, or small tooth.

M. savartii has not been found in the west African Collections. A description is included here for comparison with those of *M. arborescens* and *M. tenuis* some characters of which may be extremely similar to those of *M. savartii*.

The zoarium occurs in two forms, like that of *M. arborescens*. In most erect zoaria, the median proximal cryptocystal denticle is reduced, or is directed downward into the zooidal cavity, as the cryptocyst descends steeply. The denticle is therefore often difficult to see, and zooids of *M. savartii* in this form would be indistinguishable from those of an erect colony of *M. arborescens* in which the cryptocystal denticles were deficient. In this connection, it is important to note that the fauna of Recent west Africa has much in common with that of Pliocene southern Europe, and that it is possible that some Pliocene records of erect *M. savartii* may be referable to *M. arborescens*. In worn specimens, where the finer structure of the cryptocyst was no longer present, it would be impossible to distinguish between the two forms.

Encrusting specimens of *M. savartii* usually have a well-developed median proximal serrate denticle, as figured by Marcus (1937, 1938). Savigny did not figure the denticle, and it is often reduced even in encrusting specimens from the Red Sea, which is presumed to be the type locality. Savigny's figure shows confused, plurilaminar growth on lamellibranch shell. The specimen from Aden has exactly this form, and its zooids are very similar to those of Savigny's magnified figure. This specimen also has a twinned ancestrula, as has that from Malacca Straits. The periancestrular zooids have well-developed proximal cryptocysts with median denticles, which may, however, tend to be asymmetrical. The zooids thus greatly resemble the periancestrular zooids of *M. tenuis* (see above), and, in the absence of later-developed zooids, would be difficult to assign with certainty to either species.

CONOPEUM Gray

Conopeum Gray, Harmer, 1926: 210. Bobin & Prenant, 1962.

TYPE-SPECIES. *Millepora reticulum* Linnaeus.

Conopeum tenuissimum (Canu)

(Pl. 1, fig. F)

Membranipora tenuissima Canu, 1908 : 253, pl. 2, figs. 9, 10. Holocene, Bahia Blanca, Argentine. Lagaaij, 1963 i 165, pl. 1, fig. 2. Pleistocene, Gulf of Mexico, Recent, Texas coast, Louisiana coast and Sabine Bank (4–74 ft.).

MATERIAL EXAMINED. Achimota Coll. Stn. N, Densu Estuary, ½ mile from the sea, on mangrove " stems ", 19A.

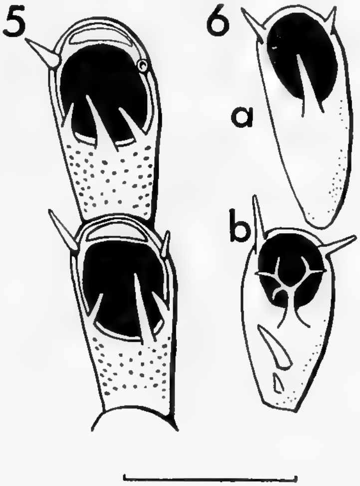
British Museum. Pt. Harcourt, Nigeria, 5.xi.57, in dead oyster shells. Stubbings Coll. 1959.2.20.7.

DIMENSIONS. Lz 0·42–0·51 mm., lz 0·23–0·34 mm., Lopes 0·28–0·35 mm., lopes 0·15–0·20 mm.

Zoarium encrusting. Zooids with a finely granular cryptocyst. Gymnocyst small. One pair of small distal spines occasionally present. Some zooids with a calcareous lamina closing the opesia beneath the thickened frontal membrane.

C. tenuissimum is found in waters of reduced salinity. The west African specimens encrust the rooting " stems " of mangroves collected half a mile up the Densu river estuary, and oyster shells from Port Harcourt, about 20 miles up-river in the Niger Delta. Lagaaij's material from the Gulf of Mexico was almost all from " very shallow brackish inshore and offshore waters".

The fully closed zooids described by Lagaaij, in which the opesia is reduced by a calcified lamina to a small central pore, and where the former position of the operculum is marked by a cresentic scar in the lamina, do not occur in the west African specimens.[1] The early stages of the development of the calcareous lamina as an extension of the cryptocyst, and the thickening of the frontal membrane, have been seen. These phenomena are exactly the same as those found in *Conopeum seurati* (Canu) and *Conopeum laciniosum* (Shier) which are also species inhabiting waters of reduced salinity (see Cook & Hayward 1966).



FIGS. 5–6. *Electra* Scale = 0·5 mm. 5. *E. verticillata* (Ellis & Solander). 2 zooids, showing the elongated, porous gymnocyst, Achimota Collection, 10A. 6. *E. bellula* (Hincks). a. 1 zooid with a simple proximal spine, 1959.2.12.6, b. 1 zooid with a branched proximal spine and subsidiary spines, 1963.2.12.60.

The distal spines are minute and infrequent, unlike those of *C. seurati* which are long. *C. seurati* may have lateral spines (see Bobin & Prenant 1962*b* and Sacchi, 1961 : 31, fig. D (as *Membranipora spiculata*)). *C. seurati* and *C. laciniosum* have been referred to *Conopeum* because of the form of their early astogeny (see Cook & Hayward, 1966). No young colonies with ancestrulae have yet been described in *C. tenuissimum*, and none have been found in this material.

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[1] A large number of closed zooids, at a slightly later stage of development, are present on mangrove stems and the barnacle, *Balanus pallidus* Darwin, from Stn. N, B.M. Entomostraca Collection. No ancestrulae are present.

ELECTRIDAE Stach

Electridae Stach, Lagaaij, 1952.

ELECTRA Lamouroux, 1816

Electra Lamouroux, Harmer, 1926 : 206.

TYPE-SPECIES, *Flustra verticillata* Ellis & Solander.

Electra verticillata (Ellis & Solander)

(Text-fig. 5)

Electra verticillata (Ellis & Solander), Canu & Bassler, 1925 : 12, pl. 2, figs. 1–3, Fedhala, Atlantic coast of Morocco. Bobin & Prenant, 1960 : 121–156, figs. 2, II; 3, IV–IX; 4; 5; 6; 7; 8, II; 9; 10; 11, Roscoff.

MATERIAL EXAMINED. Marche-Marchad Coll. I. 44A. Presque l'île du Cap Vert, 15.v.53. Coll. II, 46A, M'Bour, Senegal.

Achimota Coll. I. Stn. B, Winneba Shore, 15.xi.49, 10A. Stn. D, as above, 22.xi.49, 30C. Stn. E, Christiansborg shore, 15.i.49, 34E. Stn. F, as above, 14.ii.49, 13C. Stn. G, as above, 19.xi.49, 38C. Achimota, 1947 specimen A, A. Coll. II, Chorkor, seine net, 8A.

Zoologisk Museum, Copenhagen, " Galathea " Coll. Stn. 37, Rockpool, Christiansborg, Accra, 4.xi.50, 50C. Stn. 38, Teshi, Accra, 24.xi.50, 34A.

Clausen Coll., Lagos, 16C and 95A.

British Museum. West Africa, 1952.5.8.1. Senegambia, 1899.7.1.1297, Busk Coll. Algiers, 1899.5.1.696, Hincks Coll. Morra des Lagostas, Angola, 1877.3.7 15, and many other specimens.

Zoarium erect, arising from an encrusting base, or from a complex of kenozooidal stolons. Zooids arranged round an imaginary axis in whorls. Zooids with from 4–7 spines, usually 5, the most proximal frequently greatly enlarged. Gymnocyst very long, porous.

DIMENSIONS. Lz 0·43–0·55 mm., lz 0·18–0·30 mm., Lopes 0·20–0·23 mm.

The complex of forms which have in the past been assigned to *Electra pilosa* requires further investigation. Bobin & Prenant (1960) studied *E. pilosa* and *E. verticillata* from the Roscoff area, and concluded that the two forms were specifically distinct. *E. pilosa* is capable of a great range of variation, which appears to be continuous. It is normally encrusting, but Norman (1894 : 114–122) described several forms with free, erect zoaria. His specimens show that the varieties he named merge, varying from colonies where the preponderance of zooids is in single chains, to others where the greater part of the growth of the colony is cellariiform. Colonies of *E. verticillata* also vary from sheets of zooids encrusting algae, to erect, free, strap-shaped bilamellar lobes and cellariiform branches.

The encrusting parts of *E. verticillata* either consist of irregular kenozooidal stoloniferous growth, or regular rows of zooids, which are not arranged in quincunx. The network of stolons which apparently anchor the erect parts of the colony in sandy conditions may be purely an ecological adaptation, characteristic of certain areas and conditions. *E. pilosa* may produce similar stolons, and they are present in Norman's variety *eucrateiformis*, but they do not appear to give rise to cellariiform erect branches.

Encrusting colonies of *E. pilosa* have the zooids arranged in quincunx, and apparently erect branches have in fact been found to encrust algal and hydroid stems in all the many specimens examined. Some of these " erect " zoaria, notably those from Australia labelled " var. *flagellum* " (1897.5.1.482, 483, 484, and 1899.5.1.701) greatly resemble *E. verticillata*. The zooids do not, however, have elongated gymnocysts, and are arranged in a spiral pattern around the algal stem they encrust. Spirally arranged, encrusting colonies of *E. verticillata*, however, do occur in specimens from South Africa (1923.7.26.8, O'Donoghue Collection).

Bobin & Prenant found that the number of spines in their material of *E. verticillata* was invariably 5. Specimens from South Africa in the British Museum show that the number may vary from 4–7, but that in the great majority of zooids it is 5. The range of variation in *E. pilosa* is larger, but a count of spines from 650 zooids from 16 specimens each, of both *E. verticillata* and *E. pilosa*, gave an average of 5·2, range 4–7, in *E. verticillata*, and 5·6, range 3–11, in *E. pilosa*.

The number of spines on the ancestrula of *E. pilosa* and *E. verticillata* is also not a consistently differing character between the two forms, and both their ancestrulae and early astogeny are similar. In this respect, the otherwise closely similar species *E. posidoniae* Gautier differs completely from both *E. pilosa* and *E. verticillata* (see Cook & Hayward, 1966 : 440).

When a large amount of material from widely different localities and substrates is examined, the other characters considered by Bobin & Prenant, such as the form of the opercular sclerites, the size of the pores on the gymnocyst, and the absolute size and proportions of the zooids, show a continuous range of variation between the two species. However, using the correlation of characters given above, *E. verticillata* does appear to be specifically distinct.

The distribution of *E. verticillata* is interesting. Bobin & Prenant (1960) found it associated with the alga, *Gracilaria verrucosa* and with sandy sea-bottoms off Roscoff. Bobin & Prenant concluded (p. 154), that " Sa bionomie est très spéciale, car elle vit en des stations peu nombreuses et précises, liées à quelques algues définis et au sable fin nécessaire au réseau stolonial." Gautier (1962 : 34) had already emphasized the association of the alga, *Posidonia* and *E. posidoniae* in the Mediterranean.

In the British Museum Collections *E. verticillata* occurs from Algiers, from West and South Africa, New Zealand, and the Atlantic coasts of France and Portugal. The encrusting parts of the colonies are all associated with algae. With one exception (Manorbeer, Tenby, 1899.7.1.1286 Busk Coll.), there is no record of *E. verticillata* from the British coast (see also Norman, 1894 : 116).

The specimen from Lagos (Clausen Coll.) arises from a base encrusting Rhodophyceae. The fronds measure 75 mm. in length. The specimen from Senegal (Marche-Marchad Coll. II, 46A) arises from an accretion of calcareous fragments, and shows stolons at its base. The specimen labelled " Senegambia ", from the Busk Collection, has encrusting zooids, whereas that from Algiers, from the Hincks Collection, has narrow erect fronds like those described by Bobin & Prenant. The specimen from Angola has wide, strap-like fronds.

Electra bellula (Hincks)

(Text-figs. 6*a*, *b*)

Electra bellula var. *bicornis* (Hincks) Hastings, 1930 : 706, pl. 2, fig. 8; Galapagos and Panama.
Electra bellula (Hincks) Marcus, 1937 : 37, pl. 6, figs. 14A–F (synonymy); 1955 : 280, Brazil-Lagaaij, 1963 : 170, Gulf of Mexico; Shier, 1964 : 611 (synonymy) Florida.

MATERIAL EXAMINED. Marche-Marchad Coll. II 26C, 20–25 milles au large de Saloum, 8.3.55, 35–37 m.

Zoologisk Museum, Copenhagen. Lagos, Clausen Coll., 16B, 73B and 95B.

British Museum. Lagos, University College Coll. 1, 1959.2.12.6; Cape Verde Islands, 1899.7.1.1277, Busk Coll., 1926.12.9.2, 2a, and 1963.2.12.60.

E. bellula is not present in the " Calypso " or Achimota Collections.

DIMENSIONS. Lz 0·32–0·53 mm., lz 0·17–0·22 mm.; Lopes 0·19–0·32 mm., L proximal spine 0·26–0·50 mm.

Zoarium encrusting and erect, branching dichotomously. Zooids with a well-developed gymnocyst. One pair of lateral oral spines, one large proximal spine, and subsidiary spines arising from the gymnocyst.

Marcus (1937) included both of Hincks's varieties (var. a, *bicornis*, and var. b, *multicornis*) in the species. Specimens from the Cape Verde Islands encrust algae and have the majority of their proximal spines branched; those from Senegal and Lagos are erect and have unbranched proximal spines like those figured by Marcus (1937, pl. 6, fig. 14F) in specimens from Brazil.

The colonies from Senegal arise from calcareous worm-tubes and sponges, they measure up to 20 mm. high and 18 mm. across.

ASPIDELECTRA Levinsen

Aspidelectra Levinsen, 1909 : 160.

TYPE-SPECIES. *Lepralia melolontha*, Landsborough.

Zooids with the frontal membrane covered by flattened spines arising round the opesia. No avicularia, no ovicells.

Marcus (1940 : 199), placed *Aspidelectra* in the Cribrilinidae. It was included, with *Tendra* Nordman and *Heterooecium* Hincks, in the Electridae by Bassler (1953 : G157–158). The type species, *Lepralia melolontha* Landsborough is found from localities of reduced salinity bordering the North Sea, see Hastings (1966 : 63).

A. melolontha has a well-developed gymnocyst, 13–17 lateral spines, and one pair of oral spines. Dimensions of British specimens are : Lz 0·35–0·55 mm., lz 0·25–0·30 mm., Lopes 0·30–0·41 mm., L "orifice" 0·07–0·08 mm., l "orifice " 0·10–0·11 mm., cf. *A. densuense* below.

Aspidelectra densuense n. sp.[1]

(Text-fig. 12)

MATERIAL EXAMINED. Holotype. 89B,[1] Stn. 123, Achimota Coll. Trawl 3, 11.4.51, 8 m., off Densu R. on shell. (British Museum.)

Paratypes. As above, remaining material from Stn. 123.

Achimota Coll. Stn. K on trawl debris 1 mile offshore, 2 miles beyond Densu River, 4 fath., 2.iii.49, 36L, 44N. Stn. 121, 11.4.51, 8 m., off Densu River, 93B. Stn. 126, 12.4.51, 20 m., 37J.

DIMENSIONS. Lz 0·30–0·43 mm., lz 0·18–0·24 mm., L opes 0·26–0·30 mm., L " orifice " 0·05–0·07 mm., l " orifice " 0·05–0·07 mm.

Zoarium encrusting shells, colonies fan-shaped. Gymnocyst very small or absent. Frontal membrane covered by 11–14 over-arching, flattened spines, fused centrally. 2–3 pairs of oral spines.

A. densuense is very similar in character to *A. melolontha*, but shows the following consistent differences. The zooids are shorter, but proportionately broader, and the opesiae are proportionately longer, than those of *A. melolontha*. The gymnocyst is vestigial in the majority of zooids. The number of spines covering the frontal membrane is smaller than in *A. melolontha*, and the spines are flatter and definitely fused at the tips. The most proximal spine is not enlarged and erect, as it is frequently in *A. melolontha*. The oral spines differ in that there are always 2, and occasionally 3 pairs present. The spines have stout, swollen, hollow bases, and curved, dark brown chitinous tips. An ancestrula is present in the holotype; it is broken, but was apparently membraniporan, as is that of *A. melolontha*, which, however, has a more distinct gymnocyst. The ancestrula gives rise to 2 distal zooids which later bud 2 series of zooecia, forming the characteristic fan-shaped colony in both species.

A. melolontha has been found only in waters of reduced salinity, bordering the North Sea (see Hastings, 1966 : 63). The waters in which *A. densuense* has been found may be fully marine, but Stns. K, 121, and 123 are off or near the mouth of the Densu River, in shallow water, and the area may be subject to some seasonal reduction in salinity of the water. Both *A. melolontha* and *A. densuense* are found encrusting the inner side of shells.

FLUSTRIDAE Smitt

Flustridae Smitt, Silén, 1941 : 49.

CHARTELLA Gray

Chartella Gray, Harmer, 1923 : 304.

TYPE-SPECIES, *Flustra papyracea* Ellis & Solander.

Chartella and *Terminoflustra* Silén have similar characters, and *C. elongata* (see below) could be referable to *Terminoflustra*. The nature of its ovicells is, however, unknown, and it is here included in *Chartella* due to its affinity with *C. tenella* Hincks.

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[1] Named after the River Densu, Ghana.

Flustrine species are rare in these Collections, and the 2 species described below are from the same station, off Cap Blanc, Mauritania. Canu & Bassler (1925) recorded only 2 species from the Moroccan coast, *C. papyracea* and *Spiralaria strictocella*, which last has not been found in these Collections.

Chartella papyracea (Ellis & Solander)

Flustra papyracea Ellis & Solander, Hincks, 1880*a* : 118, pl. 16, figs. 2, 2*a*, southern coasts of Britain and Ireland.

Flustra (*Chartella*) *papyracea* Ellis & Solander, Canu & Bassler, 1925 : 14, Morocco.

Carbasea papyracea (Solander), Prenant & Bobin, 1966 : 183, text-figs. 48, VIII; 55.

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 1, 21° 05′ N, 17° 14′ W, 10.v.56, 43–45 m. C51E. *C. papyracea* is not present in the Marche-Marchad, Achimota or " Atlantide " Collections.

Zoarium erect, bilamellar, lobes dividing dichotomously. Zooids with a pair of oral spines. Edges of lobes bordered by kenozooids. Ovicells endozooecial. Avicularia absent.

DIMENSIONS. Lz 0·41–0·50 mm., lz 0·17–0·24 mm., L marginal Kz 0·80 mm., Lov 0·14–0·16 mm., lov 0.12–0·17 mm.

The 6 specimens arise as small, undivided lobes, from bases encrusting hydroid stems. The lobes average 8 mm. in height and 2·5 mm. in width. Embryos are present in the ovicells, average diameter 0·12 mm.

C. papyracea occurs in the eastern Atlantic. The British Museum possesses specimens from the south-western British coasts, from western France and from Spain. Canu & Bassler (1925) recorded it as common at Fedhala (Fédala, south of Rabat), Morocco. These specimens from northern Mauritania appear to the most southerly so far recorded.

Chartella elongata n. sp.[1]

(Text-fig. 7)

MATERIAL EXAMINED. Holotype, 31A,[1] see below, rest of material paratypes. (Museum National d'Histoire Naturelle, Paris). " Calypso " Coll. I, Stn. 1, 21° 05′ N, 17° 14′ W, 10.v.56, 43–45 m., C 31A.

C. elongata is not present in the Marche-Marchad, Achimota or " Atlantide " Collections.

Zoarium erect, bilamellar, lobes dividing dichotomously. Spines absent. Edges of lobes bordered by kenozooids. Avicularia within kenozooids, occupying the position of the distal bud of a pair where the zooidal rows bifurcate. Mandible semicircular, directed distally. Ovicells not seen. Tentacle number 12–14.

DIMENSIONS. Lz 0·90–1·15 mm., lz 0·15–0·20 mm., L marginal kz 2·5 mm., L av kz 0·17–0·20 mm., Lm 0·06 mm., lm 0·10 mm.

The 6 colonies have an average height is 70 mm., the lobes being 2–2·3 mm. in width. The colour (preserved in spirit) is brown, with light yellow growing tips.

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[1] Latin, *elongatus*, prolonged; referring to the long zooids of this species.

The tentacles are extremely long, and, even when completely retracted, are curled round each other at the tip (see Text-fig. 7). Each colony arises as a narrow frond composed of kenozooids with thickened walls which bifurcates several times, forming about 8 lobes. One colony is entire, the part proximal to the kenozooids being composed of rootlets, to which adhere sand grains, small fragments of shell and Foraminifera. It seems possible that *C. elongata* is capable of growing directly from sandy substrates.

C. elongata differs from *C. tenella* (Hincks, 1887 : 313, pl. 9, fig. 1, from the Mediterranean and Adriatic), in its more elongated, narrower zooecia. Those of *C. tenella* average 0·68 mm. in length, and have a pair of oral spines. The mandibles of *C. tenella* are acute, triangular, and directed obliquely (see Gautier, 1962 : 48).

HINCKSINIDAE Canu & Bassler

Hincksinidae Canu & Bassler, Bassler, 1953 : G159.

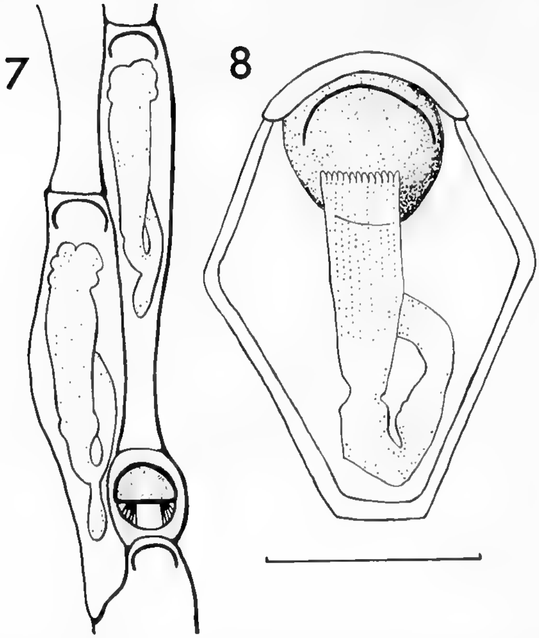
ANTROPORA Norman

Antropora Norman, 1903 : 87. Osburn, 1950 : 51.

TYPE-SPECIES, *Membranipora granulifera* Hincks.

The diagnosis given by Norman specified the presence of dietellae and of a well-developed proximal cryptocyst. *A. granulifera*, the type species, *A. papillata* and *A. minus* (which last have in the past been referred to *Membrendoecium*), have these characters. *A. nigra* (Hincks) does not have dietellae, and has large vicarious avicularia, like those of *A. marginella* (Hincks), which otherwise do not appear to be present in other species of *Antropora* s.s. Canu & Bassler (1929: 93) expressed doubts that *M. nigra* was congeneric with *A. granulifera*. Harmer (1926 : 233) described large vicarious avicularia in *A. granulifera*, but two of the specimens in which they occurred (Skikoku Is., Japan, 1928.9.13.17, and Sumbawa, E. 1928.3.6.49) differ from the rest of the material available for examination in the British Museum, in some important respects. These specimens have no dietellae, and the avicularian chambers reach the basal lamina between the zooids. The proximal cryptocyst is is not well-developed. Another specimen with similar characters in the British Museum is from Mauritius (1934.10.8.9). Most of Harmer's specimens of *A. marginella* also differ considerably from Hincks's type material. The slides from Siboga Stn. 164 (New Guinea, 1928.3.6.51), Stn. 81 (Borneo Bank, 1928.3.6.50) and Torres Straits (1928.9.13.18) are not the same species as that from Torres Straits (1928.9.13.19), which alone appears to be referable to *A. marginella* s.s. (see Powell, 1967 : 164). The zooids of the aberrant specimens also have no dietellae, and it is possible that all of them, and those mentioned above under *A. granulifera*, should be referred to species of *Crassimarginatella*. It is hoped to revise all these records fully in the near future.

Osburn (1950 : 51), considered that there was no distinction between *Antropora*, *Membrendoecium*, *Dacryonella* and *Canua*. Certainly the type-specimen of *Membranipora papillata*, which is the type-species of *Membrendoecium*, is congeneric



FIGS. 7–8. *Chartella* and *Aplousina*. Scale = 0·5 mm. 7. *Chartella elongata* n. sp. 2 zooids and an avicularium, " Calypso " Collection, C 31A. 8. *Aplousina major* (Calvet). 1 zooid with embryo beneath the retracted tentacles, " Calypso " Collection, C10C.

with *Antropora minus* (see below). Both species have very small zooids, vestigial ovicells, and avicularia whose chambers reach the basal layers of the colony between the zooids. The principal difference between them and *A. granulifera* is that the avicularian chambers are not in series with the dietellae (see below). *Amphiblestrum papillatum*, as described by Canu & Bassler (1929 : 104, pl. 7, fig. 8, specimen examined from Stn. 5179, " Albatross ", Philippines, 1931.12.30.25) is not Busk's species. The gymnocyst is elongated, the opesial rim is greatly raised, the ovicells are hyperstomial, and spines are present.

Antropora granulifera (Hincks)

(Text-fig. 9)

Membranipora granulifera Hincks, 1880*b* : 72, pl. 9, fig. 4, Madeira.
Antropora granulifera (Hincks), Osburn, 1950 : 52, pl. 4, fig. 5.

MATERIAL EXAMINED. " Calypso " Coll. I. Entre Pta da Mina & Pta Novo Destino, 26.vi.56, 6 m. (worn), C47B. Coll. II. Stn. 16, an N.W. Pta Geneanes, 17.xi.59, 235–400 m., C70H, Stn. 31, 14° 53′ 35″ N, 23° 29′ 58″ W, 19.xi.59, 70–170 mm., C66Q, Stn. 35, 45–55 m., C105E, C112E. Stn. 50, ile Brava, Porto dos Ferreiros, 21.i.59, 30–50 m.,

Zoologisk Museum, Copenhagen. Mortensen Coll., La Luz, Canary Is. 28.iii.30, 50 m., 90H.

British Museum. Madeira, 1879.5.28.6, and 1919.6.25. 23 and 24. Norman Coll.

Zoarium encrusting. Zooids with paired distal avicularia, their chambers in series with, and replacing, two dietellae. Rostrum acute, directed inwardly. Ovicells vestigial or very small, closed by the operculum.

Dimensions. Lz 0.40–0·58 mm., lz 0·27–0·40 mm., Lopes 0·20–0·32 mm., Lav 0·11–0·15 mm., Lm 0·07–0·10 mm.

This species was originally described from Madeira, and these specimens agree well with those from the Norman collection listed above. Each of the avicularian chambers replaces a dietella and the avicularia are thus interzooecial in the sense used by Hastings (1963 : 181). Harmer's (1926) and Osburn's (1950) description of the avicularia as " belonging to the succeeding zooecium ", and not belonging " to either zooecium ", respectively, are thus not strictly accurate. Lacunae in the basal wall were described by Norman (1903 : 88), they are present in all these specimens. The ovicells are vestigial in some zooids, slightly more developed in others. The avicularia in fertile zooids are directed distally, and the tips of their rostra do not tend to approach each other as they do in the other zooids.

Specimens from the Indo-Pacific region have larger zooids than those from Panama, Madeira and west Africa (Lz 0·05–0·08 mm.), but are similar in all other characters. The opercula of their fertile zooids show slight dimorphism, being wider and darker in colour than those of the other zooids.

Antropora minus (Hincks)

(Text-fig. 10)

Membranipora trifolium var. *minor* Hincks, 1880*c* : 87, pl. 11, fig. 6, Bahia.
Membrendoecium minus (Hincks), Marcus, 1937 : 50, pl. 19, figs. 22A, B, Brazil.

Material examined. " Calypso " Coll. I, Stn. 108, Ise Tortuga, face N.W., Annobon, N.E. 4.vii.56, 15–40 m., C6B, on echinoderm spine. Achimota Coll. Stn. X, Atim, Hospital Reef, 68A, on *J. foetida*, shell and stones.

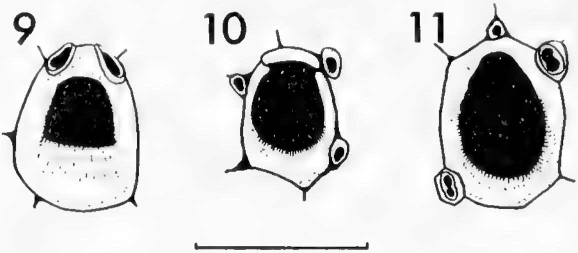
British Museum. Bahia, 1899.5.1.654, Hincks Coll., Type. Fernando Noronha, 1888.4.16.9.

A. minus is not present in the Marche-Marchad or " Atlantide " Collections.

Zoarium encrusting. Zooids very small. Ovicells vestigial. Avicularia small, subrostral chambers reaching the basal lamina between the zooids.

Dimensions. Lz 0·25–0·33 mm., lz 0·17–0·20 mm., Lopes 0·15–0·23 mm., Lav 0·04–0·07 mm.

A. minus differs from *A. granulifera* principally in its smaller zooids, and in that the avicularia are less regular in position, being situated between the zooids, and not replacing dietellae. *A. minus* greatly resembles *A. papillata* (Busk), differing only in having smaller zooids and avicularia, and a less well-developed proximal cryptocyst. Measurements on the type specimen of *A. papillata* (Stn. 208, 1887.12.9.327, Challenger Coll.), may be compared with those for *A. minus* given above. Lz 0·30–0·42 mm., lz 0·15–0·23 mm., Lopes 0·12–0·15 mm., Lav 0·05–0·09 mm. *A. papillatum* Canu & Bassler is not referable to *Antropora*, see above.



FIGS. 9–11. *Antropora*. Scale = 0·5 mm. 9. *A. granulifera* (Hincks). 1 zooid with paired distal avicularia, "Calypso" Collection, C 105E. 10. *A. minus* (Hincks). 1 zooid with an ovicell, and 3 avicularia, Achimota Collection, 68A. 11. *A. tincta* (Hastings). 1 zooid with 2 avicularia and a distal kenozooid, "Atlantide" Collection, 107B.

Antropora tincta (Hastings)

(Text-fig. 11)

Crassimarginatella tincta Hastings, 1930 : 708, pl. 5, figs. 16–19, pl. 17, fig. 120, Balboa, Panama. Galapagos, Mexico.

Antropora tincta (Hastings) Osburn, 1950 : 54, pl. 4, fig. 7, pl. 29, figs. 7, 8. California to Peru and Galapagos.

MATERIAL EXAMINED. "Calypso" Coll. I. Stn. 25, 4° 36′ 5″ N, 1° 31′ W, 24.v.56, 50 m., C10M, Coll. II, Stn. 75, 16° 04′ 20″ N, 22° 58′ 10″ W, 25.xi.59, 45 m., C106C.

Achimota Coll. I. Stn. K, on trawl debris, 1 mile offshore, 2 miles beyond Densu R., 2.iii.49, 36J. Stn. 126, 12.iv.51, 20 m., 37C. Christiansborg, 13.x.50 on spines of *Eucidaris tribuloides* var *africana* Mortensen, 94C.

Zoologisk Museum, Copenhagen. "Atlantide Coll. Stn. 49, 7° 29′ N, 13° 38′ W, 30.xii.45, 74–79 m., 41B and 114C, on shell. Stn. 70, 4° 50′ N, 2° 49′ W, 15.i.46, 65 m., 76H on shell. Stn. 75, 4° 43′ N, 1° 41′ W, 23.i.46, 46 m., 51N on coral. Stn. 123, 2° 03′ S, 9° 05′ E, 5.iii.46, 50 m., 20B, on coral. Stn. 145, 9° 20′ N, 14° 15′ W, 13.iv.46, 32 m., 7F, 110T, on shell. Stn. 146, 9° 27′ N, 14° 48′ W, 13.iv.46, 51 m., 45I, 107B, on shell.

British Museum. Gorgona and Balboa, Panama, 1929.4.26.68–72, 74, "St. George" Coll.

Zoarium encrusting, plurilaminar, arising into irregular branches when in association with gastropod shells inhabited by Pagurid crabs. Dietellae present. Kenozooids and avicularia frequent between the zooids.

DIMENSIONS. Lz 0·35–0·52 mm., lz 0·29–0·36 mm., Lopes 0·19–0·34 mm., Lav 0·06–0·13 mm., Lm 0·03–0·07 mm.

Small dietellae are present in the type and in the west African material. They were not described by Marcus (1937 : 46, pl. 8, fig. 20A, pl. 9, figs. 20B, C), for *C. leucocypha*, but specimens of that species from Brazil in the Marcus Collection sent to the British Museum have small dietellae present. The ovicells of *A. tincta* are vestigial (see Hastings, 1930), as are those of *C. leucocypha* (see Marcus, 1937), and the two forms appear only to be separated by the frequency of occurrence of kenozooids, the size of the avicularia, and the shape of the avicularian mandible. The zooids show great variation in size, the primary individuals of a new lamina being large, and the succeeding zooids considerably smaller. The occurrence of kenozooids and avicularia is variable and sporadic. In some colonies, or parts of colonies, each zooid is surrounded by small kenozooids, and avicularia are frequent, in others, both are completely absent from areas of the zoarium.

The specimen encrusting the sea-urchin *E. tribuloides* var *africana*, was accompanied by *M. arborescens*, the zooids of which had the frontal membrane covered in small chitinous spinules. The colonies encrusted the large club-shaped spines of the sea-urchin to a depth of 3 layers, and covered even the spines surrounding the mouth. Associated Polyzoa were *Bowerbankia gracilis* Leidy and *Alcyonidium* sp. These four forms covered nearly every spine, and their diameter was increased by the Ctenostomes to nearly ¾ in. in some cases. The spines remained capable of movement, and the sea-urchin appears to have been alive when collected. *A. tincta* appears to be a frequent commensal of molluscs, but none of these specimens has shown any tendency to produce erect " arms ", as described by Osburn (1950).

A. tincta may thus appear superficially very similar when living commensally in shells, to both *Membranipora commensale* and *M. arborescens*. In areas of the colony where avicularia are absent, only the presence of diatellae distinguish *A. tincta*.

APLOUSINA Canu & Bassler

Aplousina Canu & Bassler, 1927 : 2.

TYPE-SPECIES. *A. gigantea*, Canu & Bassler.

Zoarium encrusting. Zooids very large. Gymnocyst and cryptocyst generally narrow. Ovicells endozooecial. Avicularia absent.

There are few criteria available for specific distinction in *Aplousina*, and some of these have now been found to show a hitherto unsuspected range of variation. The development of the proximal cryptocyst varies with the shape of the zooids, which are frequently very irregular in outline. The presence of a raised mural rim and of a lateral cryptocyst, may have specific value, but have been found to be very variable within a single colony. A pair of distal spines has been described in some forms but these seem to be variable in occurrence, even in those species in which they are known. The large range in size of the zooids within a colony has been noted by several authors (see Osburn, 1950, and Canu & Bassler, 1930), and although the species considered here fall roughly into two groups, one with larger zooids, on average, than the other, this does not seem to constitute a useful specific character. The ovicells are of 3 main types. The first is a fully-developed, endozooecial form. The distal wall of the ovicell protrudes beneath the proximal cryptocyst of the next succeeding zooid (see Soule, 1959 : 11). The ovicell is closed by a special membrane, or by an extension of the frontal membrane distal to the operculum. The second form does not protrude into the cavity of the next zooid, but may produce a distinct swelling frontally. This type of ovicell is closed by the zooidal operculum. The third form intergrades with the second, and at one end of its range of variation is completely vestigial. The distal wall of the zooid is slightly concave, and the distal rim slightly raised and thickened. The embryos are seen beneath the retracted tentacles, at the distal end of the zooid, below the operculum (see Text-fig. 8).

The synonymies of the various described forms of *Aplousina* are in a confused state, and a large amount of material from many localities might show that these could be ascribed to at most 2 or 3 species. Until this can be studied, it is only possible to summarize the characters of some of the known species, and to indicate their possible range of variation.

Aplousina filum (Jullien & Calvet)

Membranipora filum Jullien & Calvet, 1903 : 41, pl. 5, fig. 4. Azores. Calvet, 1907, part : 386 (not var. *major*, see below).

A. filum was first described with paired distal spines and figured with a raised mural rim and narrow, but distinct crenulated lateral cryptocyst. Later records from the Azores and the Cape Verde Islands confirmed the presence of spines and described the ovicells, which were of the first type (see above) and were closed by a separate operculum.

A. capriensis (Waters 1898 : 690, pl. 47, fig. 6), appears to be distinguished from *A. filum* s.s. by the absence of spines and by its vestigial smooth lateral cryptocyst. The type of ovicell (see pl. 3, fig. D) and range in size of the zooids (specimen 1960.11.2.1, Mediterranean, Gautier Coll., Lz 0·50–0·90 mm.), is very similar to that of *A. filum* described by Jullien & Calvet (dimensions calculated from their figure, Lz 0·71–0·81 mm.). " *A. filum* " Gautier (1962) has a vestigial ovicell and is not referable to *A. filum* Jullien & Calvet (see below).

" *A. filum* " Canu & Bassler (1930*a* : 5, pl. 1, figs. 1, 2, Galapagos Islands), was described without distal spines, and the ovicell figured (pl. 1, fig. 2) is apparently vestigial. The material described as *A. filum* by Osburn (1950 : 47, pl. 4, fig. 7, from the Gulf of California to the Galapagos) may not be homogenous. His figure shows a vestigial ovicell, but he described it as " prominent, lunate, the aperture wide and closed by a special operculum ". His figured specimen is almost certainly " *A. filum* " Canu & Bassler, and it seems possible that there may be more than one species of *Aplousina* in the eastern Pacific. Neither the form with well-developed ovicells, nor the form with vestigial ovicells, is referable to *A. filum* s.s.

" *A. filum* " Gautier (1962 : 38) had been discussed by Bobin & Prenant (1961 : 165), as *Aplousina* sp., a specimen from the Mediterranean (1960.11.2.2, on shell and stone, Gautier Coll.) shows vestigial ovicells, and agrees with the figures given by Bobin & Prenant (see Pl. 3, fig. F). The zooids are very large, although not consistently as large as those of *A. major*, see below (Lz 0·70–0·85 mm., lz 0·47–0·60 mm., Lopes 0·55–0·72 mm., lop 0·21–0·25 mm., Lov 0·05–0·07 mm., lov 0·20–0·26 mm.). It is possible that this, so far unnamed, species of *Aplousina* may be found to intergrade with *A. major*, but the present specimens differ in their wider lateral cryptocyst, larger ovicell, and in the more proximal position of the operculum, as well as their slightly smaller dimensions.

Aplousina gigantea Canu & Bassler

(Pl. 3, fig. A, B, C)

Biflustra lacroixii Smitt, 1873, part : 18, pl. 4, figs. 85–87 (not fig. 88, ?=*Crassimarginatella tuberosa* q.v.).
Aplousina gigantea Canu & Bassler, 1927 : 2, pl. 1, fig. 1, 1928*b*, 20, pl. 2 fig. 6, text-fig. 3, S.W. Florida. Osburn, 1940 : 357, pl. 3, fig. 3, fig. 31, Porto Rico, 5 fath. Maturo, 1957 : 38, text-fig. 32, North Carolina.

MATERIAL EXAMINED. Naturhistoriska Riksmuseet, Stockholm. Smitt's figured material of *B. lacroixii*, Lå 19, 195, 1781, S.W. Tortugas, 60 fath.

British Museum, 1931.12.19.13, S. of Tortugas, 4.vii.31, 40 fath., Colman-Tandy Coll. 1932.3.7.94, " Albatross " Stn. 2405, 28° 45′ N, 85° 2′ W, Gulf of Mexico, 30 fath., Canu & Bassler Coll.

Zoarium encrusting. Zooids very large. Spines absent. Ovicells raised frontally, variable, not protruding into the cavity of the succeeding zooid, closed by the zooidal operculum.

A. giganteum	Lz (mm.)	lz (mm.)	lop (mm.)	Lov (mm.)	lov (mm.)
Canu & Bassler, 1927	1·10	—	—	0·15	0·35
Canu & Bassler, 1928*b*	0·84–0·90	0·60–0·64	0·18	—	—
Osburn, 1940	0·84–0·90	0·60–0·65	0·20	0·16	0·30
Maturo, 1957	0·77–1·10	0·44–0·66	0·20	—	—
Smitt specimen	0·70–1·3	0·60–0·80	0·21–0·28	0·10–0·18	0·35–0·42
B.M. Tortugas specimen	0·70–1·3	0·60–0·75	0·21–0·28	0·07–0·18	0·35–0·42

The specimens in the British Museum agree well with Canu & Bassler's description and figures of their species. The material shows a large amount of variation in the width of the mural rim and lateral cryptocyst. In some zooids the rim is smooth, and the cryptocyst descends steeply. In others both rim and cryptocyst are finely tuberculate, and the cryptocyst descends more gently, like that figured by Osburn (1940, pl. 3, fig. 31). The proximal cryptocyst is frequently well-developed in some zooids. The ovicell is well-developed frontally in Canu & Bassler's and Osburn's descriptions, and some of the ovicells in the specimen from Tortugas (1931.12.19.13), resemble their figures. Other ovicells in the same colony are, however, almost vestigial. Smitt's figured material has been examined; it belongs to *A. gigantea*. It shows the same range in cryptocyst and ovicell development. The ovicells tend to be less well-developed than in the other Tortugas specimen, but the ranges of variation are almost identical. The identity of Smitt's specimens has been discussed by Jullien & Calvet (1903),[1] and Hastings (1945), see also p. 151.

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[1] *B. lacroixii* Smitt not Audouin, was considered to be a synonym of *M. filum* by Jullien & Calvet (1903), but the ovicells are entirely different. Another synonym included (1903 : 41, footnote, and Calvet, 1907 : 386), was *Membranipora reticulum* (L.), from Corsica. This record is referable to *Conopeum seurati* (Canu), see Gautier, 1962 : 39.

Generally the zooids of *A. gigantea* are larger than those of *A. filum* and of *A. capriensis*, but their range of variation overlaps the dimensions of both those two species, and those of *Aplousina* sp. and *A. major* (see below).

Aplousina errans Canu & Bassler (1928*c* : 60, pl. 1, figs. 3, 4, from Brazil), had a well-developed gymnocyst, thick, raised mural rims, and two distal tuberosities on ovicelled zooids. The ovicells figured were very small and vestigial.

Aplousina major (Calvert)

(Pl. 3, fig. E, text-fig. 8)

Membranipora filum var. *major* Calvet, 1907 : 386, Morocco.

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 25, 4° 36′ 5″ N, 1° 31′ W, 24.v.56, 50 m., C10C, on stone.

A. major is not present in the Marche-Marchad, Achimota or " Atlantide " Collections.

Zoarium encrusting. Zooids extremely large. Cryptocyst and gymnocyst vestigial laterally and proximally. Spines absent. Ovicells vestigial.

DIMENSIONS. Lz 0·65–1·2 mm., lz 0·43–0·68 mm., lop 0·22–0·30 mm., lop (fertile) 0·25–0·40 mm.

Calvet noted that his specimens from N.W. Morocco from (717 m.) had zooids distinctly larger than those of typical *A. filum*. The zooidal walls were less robust than those of *A. capriensis*, the zooids larger, and spines and ovicells absent.

It appears that the specimen from the " Calypso " Collection belongs to this form, which is certainly specifically distinct from *A. filum*. The ovicells are so little apparent that unless the embryo is present, they are difficult to distinguish. The cryptocyst, too, is vestigial laterally and proximally. The large embryos (average diameter 0·30 mm.), can be seen beneath the retracted tentacles, just below the operculum, which is placed at the extreme distal edge of the zooid (see Text-fig. 8).

Aplousina major Osburn (1950 : 47, pl. 4, fig. 2), from California to Galapagos, was an independent introduction. The characters of the species show it to be very similar to *A. major* (Calvet). The zooids were very large (Lz 0·80–1·20 mm.), and the operculum wide (0·25 mm.). The ovicells were vestigial. It is possible that the species are identical although Osburn mentioned the presence of dietellae, which are specifically excluded in his diagnosis of *Aplousina*.

ALDERINIDAE Canu & Bassler

Alderinidae Canu & Bassler 1927 : 13.

CALLOPORA Gray

Callopora, Gray, Osburn 1950 : 63.

Type-species, *Membranipora lineata* Linnaeus.

Zooids with marginal spines. Dietellae present. Ovicells hyperstomial, not closed by the operculum.

The characters listed above limit a genus the species of which show a great diversity of character. One of the two species described below, *C. confluens*, shows close similarity with *Membraniporella*, from which it is only separated by the type of closure of the ovicell. A similar example of convergent characters in *Membraniporella* and *Callopora* has recently been described and discussed by Bobin & Prenant (1965), for *Membraniporella nitida* and *Callopora rylandi*.

Callopora depressa n. sp.[1]

(Text-fig. 15)

MATERIAL EXAMINED. Holotype, 45D,[1] Achimota Coll., Stn. 133, see below (British Museum).

Achimota Coll. St. 72, 24.i.51, 38 m., 61C. Stn. 110, 4.iv.51, 40 m., 48D. Stn. 111, as above, 43 m., 49M. Stn. 112, as above, 43 m., 60E. Stn. 131, 2.v.51, 37 m., 41E and 43Z. Stn. 133, 2.v.51, 51 m., 45D, all on *Jullienella foetida*.

Zoologisk Museum, Copenhagen. " Atlantide " Coll. Stn. 163, 13° 43′ N, 17° 23′ W, 25.iv.46, 65 m., 71B, on *J. foetida*.

" Galathea " Stn. 4, 22° 19′ 18″ N, 17° 05′ W, 2.xi.50, 62 m., 69E, on *J. foetida*.

Zooids with a raised mural rim, gymnocyst short but distinct, depressed. Cryptocyst absent. 10–14 short, slightly curved, flattened marginal spines, curving above the frontal membrane. Ovicells hyperstomial, raised, smooth or very finely tuberculate, imperforate. One distal and 2–3 lateral dietellae present. Avicularia absent.

DIMENSIONS. Lz 0·45–0·56 mm., lz 0·30–0·37 mm., Lopes 0·37–0·46 mm., L spines 0·08–0·10 mm., Lov 0·13–0·16 mm., lov 0·20–0·22 mm.

C. depressa is not present in the " Calypso " or Marche-Marchad Collections.

The zooids are distinct, and the raised mural rims are separated by a smooth, depressed channel. The gymnocyst is variably developed, but when present, is at a lower level than the slightly raised rim of the next proximal zooid, and is concave. The spines are not present on all zooids, and frequently only the distal pair are present. The operculum opens at the extreme distal end of the frontal membrane. The ovicell is closed by a special membrane, distal to the operculum.

The species which most closely resembles *C. depressa* is *C. whiteavesi* Norman, an Arctic form, see Osburn (1950 : 70, pl. 6, fig. 6).

Very few of the colonies of this delicate species have escaped damage. Entire spines are rarely present, and the ovicells are frequently broken. It is easily recognized, however, even when worn, by the prominent dietellae, and the depressed, concave gymnocyst. Colonies of *C. depressa* have some similarity to those of *Parellisina curvirostris* (see p. 156), which, however, has characteristic avicularia.

All the specimens of *C. depressa* and many of *P. curvirostris* have been found growing on *Jullienella foetida* Schlumberger, a large, foliaceous Foraminiferan with an arenaceous test which is typically associated with sandy and muddy sea-bottoms off the west African coast (see Nørvang, 1961).

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[1] Latin, *depressus*, flat; referring to the depressed gymnocyst of this species.

Callopora confluens n. sp.[1]

(Text-fig. 13)

Material examined. Holotype, C57E pt, see below (Museum National d'Histoire Naturelle, Paris).

" Calypso " Coll. Stn. 19, 5° 2′ 30″ N, 5° 24′ 40″ W, 21.v.56, 21–27 m., C57E, on *Jullienella foetida*, with *Parellisina curvirostris.*

C. confluens is not present in the Marche-Marchad, Achimota, or " Atlantide " Collections.

Zoarium encrusting. Zooids with one pair of distal spines and 5–7 pairs of thick, flattened, lateral and proximal spines, curved over the frontal membrane and fused at the tips, forming a frontal shield. One distal, and 1–2 lateral dietellae present. Ovicells globular, minutely porous and tuberculate. Avicularia between the zooids, the subrostral chambers reaching the basal lamina, rostra acute, linear, raised, directed distally. Mandibles long, setiform.

Dimensions. Lz 0·45–0·56 mm., Lz 0·22–0·29 mm., L spine 0·12–0·19 mm., Lov 0·15–0·18 mm., lov 0·15–0·19 mm., Lav 0·12–0·17 mm., Lm 0·16–0·25 mm.

The spines forming the frontal shield are wide, and the lacunae between them slit-like, unlike those of *C. rylandi*, which has fewer spines and correspondingly wider lacunae. The oral spines are also stout, and are directed upwards, but in some zooids they curve terminally and meet above the orifice. The operculum has a marginal sclerite. The ovicells are minutely porous, unlike those of *C. rylandi*, and resemble those of *Copidozoum tenuirostre* (see below). The avicularia are large, with a raised rostrum, the distal part of which is linear, with a narrow channel into which the setiform mandible fits. The avicularia have a pair of condyles, but no bar. The mandibles are hooked terminally.

C. confluens, like *C. rylandi*, resembles *Membraniporella nitida*, differing in the form of the avicularia, and in the closure of the ovicell. (See Bobin & Prenant, 1965, and Cook, 1967 : 330). *C. confluens* also shows superficial similarities with *Copidozoum tenuirostre*, the globose porous ovicells, the prominent oral spines, and the setiform avicularia being almost exactly the same in appearance in the two species.

C. confluens differs from *C. rylandi* in the number and form of its spines, and in its porous ovicell. The occurrence of two species of *Callopora*, both of which greatly resemble *Membraniporella*, suggests that the characters defining these genera, and indeed, their position in the classification, require further investigation. *M. nitida*, the type species of *Membraniporella*, possesses dietellae, like *Callopora*, but many of the other species referred to *Membraniporella* do not (see Cook, 1967 : 329). The ovicell in *Membraniporella* is closed by the zooidal operculum, unlike that of *Callopora* but the significance of this as a generic character has yet to be assessed. *Membraniporella* is usually considered to belong to the Division Cribrimorpha, but the similarities in structure of the frontal shield in *M. nitida*, *Callopora confluens* and *C. rylandi* suggest that there is no real division between the Divisions Cribrimorpha and

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[1] Latin, *confluus*, place where two streams unite, referring to the convergence in character between *Callopora* and *Membraniporella* shown in this species.

Anasca. The development of such genera as *Tremogasterina*, *Triporula* and *Exechonella* indicate a similar intergradation in character between the Cribrimorpha and the Ascophora Imperfecta (see Powell & Cook, 1967 : 8, and Cook, 1967 : 334).

COPIDOZOUM Harmer

Copidozoum Harmer, 1926 : 226. Cheetham & Sandberg, 1964 : 1019.

Type-species, *Membranipora plana* Hincks.

Copidozoum tenuirostre (Hincks)

(Text-fig. 14)

Membranipora tenuirostris Hincks, 1880c : 70, pl. 9, fig. 3, Madeira.
Copidozoum tenuirostre (Hincks), Osburn, 1950 : 72, pl. 7, fig. 4, California to Peru & Galapagos Is. Cheetham, 1964 : 1019, text-figs. 10, 12, Louisiana. Bobin & Prenant, 1962*a* : 23, text-fig. 5.

Material examined. " Calypso " Coll. I. Stn. 19, 5° 2′ 30″ N, 5° 24′ 4″ W, 31.v.56, 21–27 m., C57J. Stn. 3, 13° 1′ N, 17° 24′ W, 15.v.56, C54B, on *J. foetida*. Coll. II. 15° 16′ 28″ N, 23° 47′ 24″ N, 18.xi.59, 40–45 m., on shells and Bryozoa, C61G. Marche-Marchad Coll. II, on shell with other spp, Boa Vista (Ile du C. Vert), 23.x.48, 30 m., 24D; Coll. III, Gérard Fréca, dr. 5, 18.ii.54, 27F. Achimota Coll. Stn. 35, 21.xii.50, 37 m., 59I. Stn. 45, 31.12.50, 32 m., 62B. Stn. 47, 4.i.51, 44m. ,14M. Stn. 72, 24.i.51, 38 m., 61B. Stn. 110, 4.iv.51, 37 m., 48C. Stn. 112, 4.iv.51, 48 m., 60E. Stn. 131, 2.v.51, 37 m., 41D and 43C. Stn. 132, 2.5.51, 44 m., 40O and 42C. Stn. 133, 2.5.51, 51 m., 45C, all on *J. foetida*.

Zoologisk Museum, Copenhagen, " Atlantide " Coll. Stn. 39, San Pedro Bay, St. Vincent, 10.xii.45, 41–50 m., 30A, on *Cupuladria*. Stn. 43, Bay of Praia, 13.xii.45, 8–25 m., 47K, on stone. Stn. 49, 7° 29′ N, 13° 38′ W, 30.xii.45, 74–79 m., 25I, on stone. Stn. 145, 9° 20′ N, 14° 15′ W, 13.iv.46, 32 m., 7J, 110d, on *J. foetida*. Stn. 146, 9° 27′ N, 14° 48′ W, 13.iv.46, 51 m., 107 g. Stn. 163, 13° 43′ N, 17° 23′ W, 25.iv.46, 65 m., 60F, 71A.

" Galathea " Coll. Stn. 4, 22° 19′ 18″ N, 17° 05′ W, 2.xi.50, 62 m., 69A, on *J. foetida*.

Brinkmann Coll., Dakar, 68C, on shell.

Zoarium encrusting. Zooids with a very small or vestigial gymnocyst, cryptocyst narrow, serrated. One distal and 2 lateral dietellae present. Operculum with a marginal sclerite. One pair of stout distal oral spines, and from 1 -3 delicate lateral and proximal spines. Ovicells raised, globular, minutely porous and finely tuberculate. Avicularia between the zooids, the subrostral chambers reaching the basal lamina. Rostra with a linear distal channel, condyles spinous, occasionally meeting to form a bar, directed distally. Mandibles long, setiform.

Dimensions. Lz 0·35–0·49 mm., lz 0·25–0·49 mm., Lov 0·15–0·17 mm., lov 0·16–0·20 mm., Lav 0·18–0·25 mm., Lm 0·17–0·23 mm.

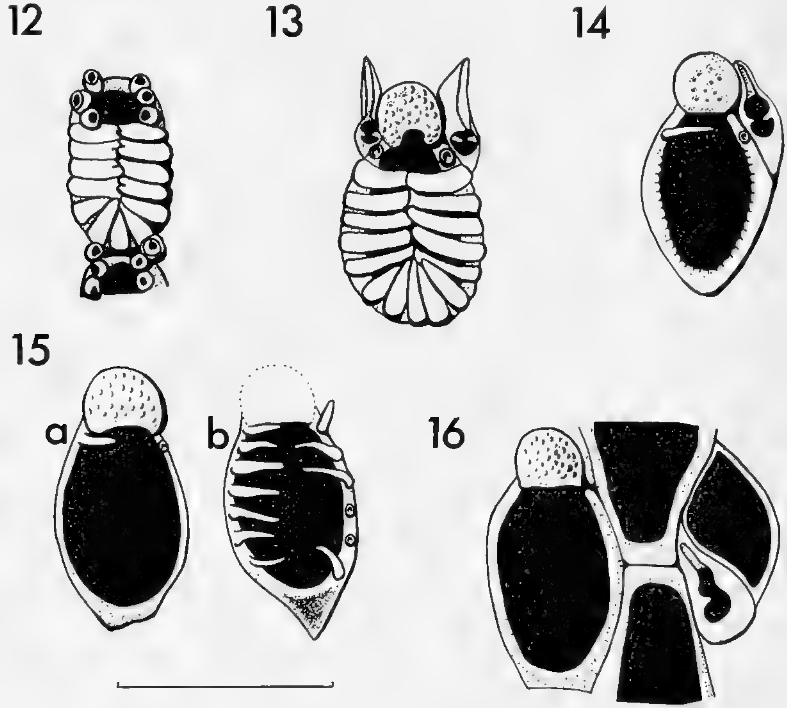
C. tenuirostre, and the closely related *C. planum*, have been defined and distinguished by Bobin & Prenant (1962*a*). *C. tenuirostre* has smaller zooids than

C. planum, which has no spines. Both species occur in the Mediterranean, but *C. tenuirostre* alone occurs from Madeira and west Africa.

The remarkable convergence of characters already noted between *Membraniporella nitida*, and *Callopora rylandi* and *C. confluens*, is repeated, to a lesser extent, between *C. confluens* and *Copidozoum tenuirostre*. The ovicells are very similar, and the hooked, setiform mandibles are almost identical in the two species.

The delicate lateral spines are not often present in the west African material, but the oral spines are large, and may be directed distally, upward, or occasionally curved proximally over the opesia, in a similar manner to those of *Crassimarginatella falcata*, see p. 153.

In the west African Collections *C. tenuirostre* is almost exclusively found encrusting *Jullienella foetida*.



Figs. 12–16. *Aspidelectra*, *Callopora*, *Copidozoum* and *Parellisina*. Scale = 0·5 mm. 12. *Aspidelectra densuense* n. sp. 1 zooid showing oral and frontal spines, Achimota Collection, 89B. 13. *Callopora confluens* n. sp. 1 zooid with an ovicell and paired avicularia, "Calypso" Collection, C57E. 14. *Copidozoum tenuirostre* (Hincks). 1 zooid with ovicell and avicularium, Marche-Marched Collection, II, 14M². 15. *Callopora depressa* n. sp. a. 1 zooid with an ovicell and a pair of distal spines, b. 1 zooid with marginal spines. Note the concave gymnocyst (ovicell damaged), Achimota Collection, 45D. 16. *Parellisina curvirostris* (Hincks). 1 zooid with an ovicell, and an avicularium with large distal chamber, "Calypso" Collection, C 57J.

CRASSIMARGINATELLA Canu

Crassimarginatella (Canu), Hastings, 1945.

TYPE-SPECIES, *Membranipora crassimarginata* Hincks.

Zooecia with septulae, dietellae absent. Avicularian chambers reaching the basal lamina between the zooecia. Ovicells hyperstomial.

The characters given above are common to all species, and although there is great variability in other details, they appear to constitute a natural group. The avicularia, which vary considerably in size from species to species, all reach the basal lamina. The possession of a complete bar in the avicularia of *C. crassimarginatella* alone, does not seem to be of generic importance; some species have well developed avicularian condyles, other none (see below). Spines may be present or absent, and are also not of generic significance (see Hastings, 1945 : 70). The ovicells may be well-developed, or vestigial, great variation being found within a species, and occasionally within a specimen. For detailed notes on the occurrence of reduced and vestigial ovicells, including those of *Crassimarginatella* (see Hastings, 1964 : 250–252).

Of the 7 species of *Crassimarginatella* described here, 3 have been reported from the Cape Verde Islands. *C. crassimarginata* and *C. maderiensis* have a more northerly distribution, and do not seem to occur south of the Canary Islands.

The species described here show a range in variation in the development of the avicularium, extending from species in which it may be small in comparison with the the zooids, to those in which it may be hardly differentiated from them.

KEY TO SPECIES DESCRIBED HERE

1 Avicularia apparently absent, distal spines forked, ovicells well-developed ***C. latens*** (p. 155)
– Avicularia present 2
2 Avicularia with a bar . . . . ***C. crassimarginata*** (p. 149)
– Avicularia without a bar 3
3 Avicularian rostrum and manible acute 4
– Avicularian rostrum rounded, mandible rounded or spathulate 5
4 Avicularia frequent, smaller than the zooids, rostrum curved, polypide absent ***C. falcata*** (p. 153)
– Avicularia rare, as large as the zooids, manible triangular, polypide present ***C. similis*** (p. 154)
5 Zooids with lateral spines 6
– Zooids with a pair of distal spines only. Avicularia spathulate, ovicells vestigial ***C. tuberosa*** (p. 151)
6 Zooids and avicularia with distinct gymnocyst. Lateral spines simple ***C. maderensis*** (p. 150)
– Zooids and avicularia with vestigial gymnocyst. Lateral spines branched ***C. quadricornuta*** (p. 151)

Crassimarginatella crassimarginata (Hincks)

Crassimarginatella crassimarginata (Hincks) Norman, 1909 : 287, Madeira. Hastings, 1945 : 73, text-fig. 1A, not Calvet, 1931, see *C. tuberosa*.

Grammella crassimarginata (Hincks) Gautier (part), 1956 : 194, figs. 3, 4, 7–11 (not figs. 5, 6, see *C. maderensis*), west Mediterranean.

MATERIAL EXAMINED. Zoologisk Museum, Copenhagen. Mortensen Coll. La Luz, Canary Islands, 24.iii.30. 30–40 m., 88H.

British Museum. Teneriffe, 70 fath., 1967.7.11.3. Madeira, 1911.10.1.616, Norman Coll.; 1966.1.4.5 and 1964.7.28.1, Watson Coll. and 1967.7.11.2, Kirkpatrick Coll.

Zoarium encrusting. Zooids with well-developed, ridged cryptocyst. Gymnocyst small. 2 distal spines rarely present. Avicularia large, with a gymnocyst and ridged cryptocyst. Mandible variable in shape, hinged on a complete bar. Ovicells small, well-developed, smooth.

DIMENSIONS. Lz 0·40–0·60 mm., lz 0·25–0·33 mm., Lopes 0·26–0·33 mm., Lov 0·15–0·20 mm., lov 0·21–0·26 mm., Lav 0·29–0·37 mm., Lav opes 0·14–0·19 mm.

C. crassimarginata does not occur in the " Calypso ", Marche-Marchad, Achimota or " Atlantide " Collections. It has not been found so far further south than the Canary Islands. The most distinctive character is that of the avicularia, which have a complete, robust bar across the opesia, against which the mandible is hinged.

Crassimarginatella maderensis (Waters)

Membranipora maderensis Waters, 1898 : 677, pl. 48, fig. 19, Madeira.

Hincksina maderensis (Waters) Norman, 1909 : 286, Madeira 40–70 fath. (note that the reference to Water's figure in the synonymy should read as above).

Grammella crassimarginata (Hincks) Gautier (part), 1956 : 192, text-figs. 5, 6, west Mediterranean.

MATERIAL EXAMINED. British Museum. Madeira, 1911.10.1.345, Norman Coll.; photographs of type material 1964.2.10.11; Adriatic, 1911.10.1.521, specimen received from Heller as *Membranipora lineata*.

C. maderensis is not present in the west African Collections.

Zoarium encrusting. Zooids with well-developed cryptocyst. Gymnocyst distinct, frequently long. Six straight distal spines, and 8–12 slightly curved lateral and proximal spines present. 2–3 lateral and 1 distal septula. Avicularia large, rostrum rounded and raised distally, small condyles present. Ovicells well-developed, wide, with a ridge across the front.

DIMENSIONS. Lz 0·40–0·60 mm., lz 0·29–0·35 mm., Lopes 0·32–0·35 mm., Lav 0·60–0·70 mm., Lav opes 0·29–0·33 mm., Lov 0·12–0·15 mm., lov 0·23–0·26 mm.

The specimen from the Adriatic, sent by Heller to Norman as " *Membranipora lineata* " is certainly *C. maderensis*. Ovicells, spines and avicularia are present. Heller's description (1867 : 96) of *M. lineata* does not seem to refer to this specimen.

The specimens with distal spines and raised rostra, figured by Gautier from Grand Congloué, are referable to *C. maderensis*. Gautier later (1962 : 47) mentioned that his material consisted of a mixture *C. maderensis* and *C. crassimarginata*.

C. maderensis is very similar to *Membranipora tenuis* Jullien (1883 : 522, pl. 17, fig. 67, N.W. Spain, 1,000 m., see also Calvet 1907 : 390). *M. tenuis* had 6 distal spines only, but the lateral spines of *C. maderensis* are often absent. Jullien's specimen had no ovicells and avicularia, and the gymnocyst was generally less developed than in specimens of *C. maderensis*; the zooids were also larger (Lz 0·625 mm., lz 0·438 mm.).

C. maderensis resembles *C. spatulifera* Harmer (1926 : 223, pl. 14, figs. 2, 3, Nightingale Island and the East Indies), differing in the possession of spines and well-developed ovicells.

Crassimarginatella quadricornuta (Waters)

Membranipora quadricornuta Waters, 1918 : 9, pl. 1, fig. 8, Cape Verde Islands.

MATERIAL EXAMINED. British Museum. Cape Verde Islands, on clinker, 1926.10.1.11, Waters Coll. Porto Grande, St. Vincent, Cape Verde Islands, on coal, 10 fath., 1935.3.6.370–372, with *C. tenuirostre*, Vallentin Coll.

Zoarium encrusting. Zooids with narrow cryptocyst, small gymnocyst. One pair of branched oral spines, and from 2–4 branched lateral and proximal spines. Large vicarious avicularia present, with an elongated spathulate mandible. Ovicells not seen.

DIMENSIONS. Lz 0·50–0·65 mm., lz 0·25–0·32 mm., Lav 0·50–0·55 mm., Lm 0·33–0·38 mm. *C. quadricornuta* is not present in the west African Collections.

It is possible that the material listed above is part of the type-material. 1926.10.1.11, has a label in Waters's hand, and the details of locality for 1935.3.6.370–372 are almost the same as those given by Waters for his specimens.

The frontal spines are all stout, and the lateral spines are branched terminally, and arched over the frontal membrane. They may fuse at the tips forming a partial frontal shield very similar to that of *Membraniporella marcusi* Cook (1967 : 331).

Waters noted that there were " a considerable number of vicarious avicularia ". They are rare in these specimens, occurring with a frequency of approximately 1 av : 100 zooids. The avicularia are large, and have no spines. The proximal cryptocyst is thick and crenulated, and distally it forms a narrow shelf. The distal part of the rostrum is not as expanded as that of *C. tuberosa*. The specimens examined are all dried, but it does not appear that the avicularia possessed polypides, as in *C. similis*. The mandible is far more differentiated than in that species, being elongated and spathulate.

Crassimarginatella tuberosa (Canu & Bassler)

(Text-fig. 17)

? *Biflustra lacroixii* (Audouin) Smitt, 1873 (part), fig. 88, Tortugas.
Aplousina tuberosa Canu & Bassler, 1928*b* : 21, pl. 2, figs. 4, 5, Gulf of Mexico.
? *Crassimarginatella crassimarginata* (Hincks), Calvet, 1931 : 59, Cape Verde Islands, 875 m.
Crassimarginatella tuberosa (Canu & Bassler) Hastings, 1945 : 85 (not synonymy). Cheetham & Sandberg, 1964 : 1017, text-fig. 5, Louisiana.

MATERIAL EXAMINED. " Calypso " Coll. I, Stn. 45, 0° 25′ N, 9° 0′ E, 8.vi.56, 73 m., C55A.

Zoologisk Museum, Copenhagen. " Atlantide " Coll. Stn. 123, 2° 03′ S, 9° 05′ E, 5.iii.46, 50 m., 57I.

Naturhistoriska Riksmuseet. Lå 19, 282, Smitt's figured specimen of *B. lacroixii*, fig. 88, W. of Tortugas, Florida, 35 fath. on *Steganoporella magnilabris*.

British Museum. Gulf of Mexico, "Albatross" Stn. D2387, on *Steganoporella magnilabris*, 1932.3.7.95, Canu & Bassler Coll. Campeche Bank, Gulf of Mexico, 1961.11.2.54, Cheetham Coll.

C. tuberosa is not present in the Marche-Marchad or Achimota Collections. Zoarium encrusting. Zooids large, cryptocyst narrow, finely serrated. Gymnocyst small. Mural rim raised distally, with one pair of distal spines which may curve proximally. One distal and 2–3 lateralse ptulae. Avicularia spathulate, vicarious, nearly as large as the zooids. Avicularian cryptocyst well-developed proximally, and forming a wide shelf distally, opesia oval or pear-shaped. Ovicells vestigial.

DIMENSIONS. Lz 0·55–0·75 mm., lz 0·35–0·51 mm., Lopes 0·47–0·64 mm., Lav 0·40–0·70 mm., lav 0·30–0·35 mm., Lav opes 0·25–0·34 mm.

Smitt's specimen consists of a young colony without either ovicells or avicularia, growing on *S. magnilabris*. The zooids greatly resemble those of Canu & Bassler's specimen of *C. tuberosa*, and have minute paired, distal spines bases, which were not mentioned by Smitt.

Calvet considered that his specimen from the Cape Verde Islands was perhaps *Membranipora crassimarginata* var. *erecta* Busk (1884 : 63, pl. 14, fig. 3, from Bass's Straits). This species has large, spatulate avicularia, but is referable to *Acanthodesia perfragilis* (see Hastings, 1966 : 65). Calvet particularly mentioned "Les avicularies avec leur mandibule largement spatulée", and it seems probable that his specimen was *C. tuberosa*.

The avicularia of the west African colonies differ slightly from those from the Gulf of Mexico in being proportionately smaller, and less expanded distally. The condyles, which are formed from an ingrowth of the lateral walls (see Text-fig. 17) are also less well-developed in the west African material.

Cheetham discussed the similarities between *C. tuberosa* and *Aplousina*. The ovicells show similar ranges in variation in both genera, and those of *C. tuberosa* resemble those of "*A. filum*" Gautier (see p. 142). The paired distal spines are developed as two small tubercles flanking the ovicell, which consists of the raised distal rim of the zooids. Some of the ovicells in the material from the Gulf of Mexico are slightly more developed, with a frontal tubercle.

The specimens from west Africa are without chitinous parts. The colony from the "Calypso" Collection encrusts a bivalve shell ; that from the "Atlantide" Collection is plurilaminar, surrounding a fragment of *Schizammina reticulata* (see Nørvang, 1961). Both Canu & Bassler, and Osburn (1940 : 357), commented on the association of *C. tuberosa* with *Steganoporella*, but it has not been found on any specimens of *S. magnilabris* from west Africa, which is however frequently associated with *C. falcata*, see below.

C. tuberosa shows the smallest development of ovicells in the west African members of the genus. It most resembles *C. falcata*, differing in the development of the spines and the form of the avicularia. In *C. tuberosa*, the avicularia are found at the bifurcation of series of zooids; they are fairly common, occurring in the proportion of approximately 1 av: 10 zooids (cf. *C. falcata* and *C. similis*).

Crassimarginatella falcata n. sp.[1]

(Text-figs. 19*a*, *b*)

MATERIAL EXAMINED. Holotype. 40P,[1] Achimota Coll., see below (British Museum). Marche-Marchad Coll. I. Konakrey, Guinée Ise., 1J. Sud de Gorée, 27.x.53, 38–42 m., 9E, and 24.xi.53, 40–41 m., 11 I. S.W. Madeleines, 15.ix.53, 48 m., 18A and 9.i.54, 45–46 m., 26L. Sud de presque l'île de Cap Vert, 18.ii.54, 95 m., 33F. Coll. II. Au large de Gorée, 5.vii.55, 50 m., 8C, 27D. S.W. Madeleines, 15.ix.53, 48 m., 40D. Baie de Gorée, 50–100 m., 7J. Coll. III. Au large de Gorée, Stn. 55, 50 m., 18E. Drag 1, 18.ii.54, 23E. No information, 21E, 24E.

Achimota Coll. Stn. 132, 2.v.51, 51 m., 40P. Stn. 133, 2.v.51, 44 m., 20F. Jar C, specimen C, Achimota, on *Steganoporella magnilabris*.

Zoologisk Museum, Copenhagen. "Atlantide" Coll. Stn. 60, 5° 06′ N, 9° 34′ W, 9.i.46, 78 m., 54I. Stn. 85, 5° 37′ N, 0° 38′ E, 30.i.46, 40 m., 108P, on *Steganoporella magnilabris*. Stn. 163, 13° 43′ N, 17° 23′ W, 25.iv.46, 65 m., 60G.

C. falcata is not present in the "Calypso" Collection.

Zoarium encrusting, or erect, tubular, branching. Zooids with finely tuberculate, denticulate cryptocyst, occasionally well-developed proximally. Gymnocyst vestigial. One pair of large distal spines, arising from the raised distal rim of the zooecia, long, curved, directed proximally. One distal, and 1–2 large, lateral septulae. Avicularia at the bifurcations of series of zooecia. Avicularian cryptocyst well-developed, opesiae elongated. Rostrum acute, curved toward the sister zooid. Ovicells vestigial, sometimes with a small distal tubercle.

DIMENSIONS. Erect zooids. Lz 0·50–0·70 mm., lz 0·35–0·45 mm., Lopes 0·35–0·50 mm., Lav 0·38–0·60 mm., Lav opes 0·23–0·30 mm., Lm 0·21–0·34 mm. Encrusting zooids. Lz 0·45–0·55 mm., lz 0·25–0·40 mm., Lopes 0·34–0·42 mm., Lav 0·45–0·55 mm., Lav opes 0·25–0·32 mm., Lm 0·20–0·35 mm., Lov 0·04–0·07 mm., lov 0·10–0·13 mm.

The specimens from Senegal are all fragments of erect, tubular zoaria; those from Ghana are all encrusting (on *Steganoporella magnilabris* in the majority of cases). The zooidal dimensions of the erect zoaria are, on average, slightly larger than those of the encrusting zoaria. The mandibles are dark brown and strongly curved. The avicularia are more numerous (1 : 4 zooids) in the encrusting, than in the erect (1 : 20 zooids) zoaria, and occur at the bifurcation of zooidal rows.

The distal spines of *C. falcata* are remarkable both for their length and for their recurved direction of growth. When fully developed, they extend proximally over the entire length of the opesia.

The erect tubular specimen (Marche-Marchad I 18A) has one ovicell, it has a small distal tubercle. The ovicells of the encrusting zooids have no tubercles.

C. falcata somewhat resembles *Hincksina velata* (Hincks), see Osburn (1950 : 44, pl. 5, figs. 3, 4), which, however, has dietellae and endozooecial ovicells, and lacks the remarkable spines of *C. falcata*.

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[1] Latin, *falcatus*, sickle-shaped; referring to the distal spines in this species.

The tubular zoaria of *C. falcata* are superficially similar to the erect, tubular colonies of *Membranipora arborescens* (see p. 123), and they are frequently found together. *C. falcata* differs in the presence of distal spines and avicularia, and in the absence of denticles on the cryptocyst.

Crassimarginatella similis n. sp.[1]

(Text-figs. 18*a*, *b*)

MATERIAL EXAMINED. Holotype. 15B,[1] " Atlantide " Coll., see below (Zoologisk Museum, Copenhagen). " Atlantide " Coll., Stn. 44, 10° 22′ N, 16° 22′ W, 17.xii.45, 41 m., 63M. Stn. 145, 9° 20′ N, 14° 15′ W, 13.iv.46, 32 m., 7K, 15B, 110H. Stn. 146, 9° 27′ N, 14° 48′ W, 13.iv.46, 51 m., 107A.

C. similis does not occur in the " Calypso ", Marche-Marchad or Achimota Collections.

Zoarium encrusting, plurilaminar. Zooids distinct, cryptocyst descending steeply, finely serrate. Gymnocyst small. One pair of long distal, and 2 pairs of lateral spines, curved very slightly over the opesia. One distal, 2 lateral septulae. Operculum dark brown, without proximal sclerite. Avicularia hardly differentiated, mandible slightly elongated, triangular, dark brown, with a proximal sclerite. Rostrum raised and pointed. Polypide present. Ovicells vestigial.

DIMENSIONS. Lz 0·50–0·71 mm., lz 0·35–0·52 mm., Lopes 0·30–0·53 mm., Lav 0·53–0·72 mm., lav 0·33–0·40 mm., Lm 0·15–0·22 mm.

The specimens encrust *Jullienella foetida*, *Steganoporella magnilabris* and fragments of echinoderm test. The mural rims of the zooids and avicularia are raised and finely beaded. The spines are stout, and directed upwards, the lateral pair showing only a slight tendency to curve over the opesia (cf. *C. quadricornuta*). The ovicells are slightly more developed than in *C. tuberosa*, but are very shallow, consisting only of the raised, distal rim of the zooids.

The avicularian individuals are not common (approximately 1 av : 100 zooids) They are as large as the zooids, and have a polypide but no spines. The rostrum varies in shape, being pointed in some individuals, more rounded distally in others (cf. *C. latens*, below). The rostrum is slightly raised distally, but it has no distal cryptocystal shelf as in *C. tuberosa*. There are no condyles. The mandible is triangular, with a well-developed proximal sclerite.

The avicularia in *Crassimarginatella* may be very large, but none have so far been observed with polypides.

These avicularian individuals are particularly interesting in view of the occurrence in *C. latens* of hardly differentiated zooids which may be avicularian in nature (see below).

C. similis greatly resembles *C. quadricornuta*, from which it differs in the form of the avicularia and lateral spines.

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[1] Latin, *similis*, like; referring to the similarity between autozooids and avicularia in this species.

Crassimarginatella latens n. sp.[1]

(Text-figs. 20*a*, *b*)

MATERIAL EXAMINED. Holotype. 76F part, Cape Verde Islands. (Museum d'Histoire Naturelle, Paris.) " Calypso " Coll. II. Cape Verde Islands, ile Brava. Porto dos Ferrieros, 21.i.59, 30–50 m., C76F.

C. latens does not occur in the Marche-Marchad, Achimota or " Atlantide " Collections.

Zoarium encrusting. Zooids distinct, with a raised mural rim. Gymnocyst distinct, cryptocyst thin, smooth. One pair of distal spines, recurved as in *C. falcata*, but shorter, and forked at the end. One proximal and from 1–2 pairs of curved lateral spines. Ovicells large, raised, finely tuberculate, with a frontal area, or tubercle, and an everted proximal lip. Avicularia apparently absent, but some zooids with a raised, everted distal rim, curved round the operculum, spineless.

DIMENSIONS. Lz 0·45–0·50 mm., lz 0·25–0·36 mm., Lopes 0·25–0·32 mm., Lov 0·15–0·22 mm., lov 0·20–0·27 mm., L spine 0·14–0·17 mm.

This small colony (of approximately 500 zooids), although similar in some characters to *C. falcata*, differs in presence of well-developed gymnocyst, ovicells and lateral spines, and in the apparent absence of avicularia.

The zooids have a distinct gymnocyst, and the opesiae have a raised rim. The distal spines are robust, and when undamaged, curve proximally over the opesiae and fork terminally. The remaining spines are finer and rarely present, but may be long and curved. The ovicells are rounded, well-raised, smooth at first, becoming finely tuberculate. A small frontal area, very variable in shape, and bounded by a raised ridge, may be present. Later, a frontal tubercle may develop, almost obscuring the frontal area. The distal spines are fused with the walls of the ovicell, and, where they are well-developed, a prominent everted lip is formed between them. The majority of the ovicells is consistently of this form, but 5 have been seen, containing embryos, which are vestigial, consisting only of a raised distal rim of the zooid, with the basal part of the distal spines forming the lateral walls of a shallow chamber. It is therefore possible that the " potential avicularia " described below, may be zooids with vestigial ovicells but without embryos. They differ, however, in the absence of distal and lateral spines, and in the curvature of the mural rim around the operculum, which is more distally placed than in the other zooids.

Only 4 zooids have been seen with these characteristics. The distal mural rim is raised, slightly elongated, and curved round the operculum. The operculum is not differentiated from those of other zooids to form a mandible, as it is in *C. similis*. Until plentiful material is available, so that the variation of this, and other species of *Crassimarginatella* may be studied, it is tentatively inferred that these zooids in *C. latens* may represent the end in a series of avicularian development in the west African species belonging to the genus.

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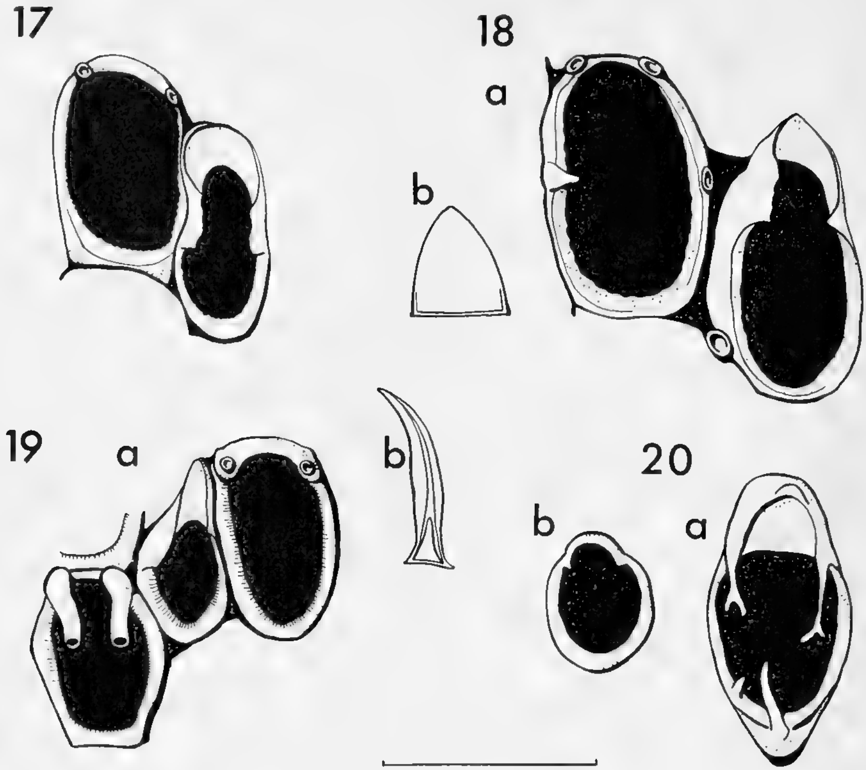
[1] Latin, *latens*, hidden, latent; referring to the occurrence of " potential avicularia " in this species.



FIGS. 17–20. *Crassimarginatella.* Scale = 0·5 mm. 17. *C. tuberosa,* (Canu & Bassler). 1 zooid and 1 avicularium, "Atlantide" Collection, 67 I. 18. *C. similis* n. sp. a. 1 zooid and 1 avicularium. b. mandible, "Atlantide" Collection. 63N. 19. *C. falcata* n. sp. a. 2 zooids, one with long (broken) spines, with an avicularium and an ovicell, b. mandible, Achimota Collection, 20F. 20. *C. latens* n. sp. a. 1 zooid with spines and an ovicell, b. potential avicularium, "Calypso" Collection, C 76F.

PARELLISINA Osburn

Parellisina Osburn, 1940 : 360; 1949; 1950 : 75.

TYPE-SPECIES, *Membranipora curvirostris* Hincks.

Parellisina curvirostris (Hincks)

(Text-fig. 16)

Ellisina curvirostris (Hincks) Harmer, 1926 : 228, pl. 14, fig. 7, East Indies. Hastings, 1930 : 711, pl. 7, figs. 28–31, Galapagos.

Parellisina curvirostris (Hincks) Osburn, 1940 : 361, pl. 4, fig. 32, Porto Rico; 1950 : 75, pl. 8, fig. 8, Mexico to Galapagos Is. (synonymy). Cheetham & Sandberg, 1964 : 1020, text-fig. 6, Louisiana.

MATERIAL EXAMINED. " Calypso " Coll. I. Stn. 19, 5° 2′ 30″ N, 5° 24′ 40″ W, 21.v.56, 21–27 mm., C57J, on *J. foetida*. Stn. 110, Grand Frère, N.E., 1° 20′ 45″ N, 7° 17′ 37″ E, 7.vii.56, 25–40 m. (Ise Hermano Grande off Principe), C9H, on shell.

Zoologisk Museum, Copenhagen. " Atlantide " Coll. Stn. 85, 5° 37′ N, 0° 38′ E, 30.i.46, 50 m., 108L on *Steganoporella buskii*. Stn. 145, 9° 20′ N, 14° 15′ W, 13.iv.46, 32 m., 110u, on *S. magnilabris*. Stn. 146, 9° 27′ N, 14° 48′ W, 13.iv.46, 51 m., 72F, on sponge, and 107I, on *J. foetida*. Stn. 147, 9° 28′ N, 14° 58′ W, 14.iv.46, 45 m., 77L, on *J. foetida*.

British Museum. Type. Cornwall, 1899.5.1.564, Hincks Coll., 1911.10.1.548, Norman Coll.; Galapagos 1929.4.26.240, " St. George " Coll.; N. of Cuba, Albatross Stn. 2320, 1932.3.7.49, Canu & Bassler Coll.; New Harbour, Singapore, 1928.9.13.10, Hanitsch Coll.; Adelaide, 20–35 fath., 1928.9.13.12 Verco Coll.

P. curvirostris is not present in either the Marche-Marchad or the Achimota Collections.

Zoarium encrusting. Zooids with a very small gymnocyst and narrow cryptocyst. Septulae and dietellae present. Avicularia large, reaching the basal lamina of the colony, rostrum and mandible curved, acute. A large chamber, formed by a kenozooid, distal to each avicularium. Ovicell small, hyperstomial, finely tuberculate.

DIMENSIONS. Lz 0·40–0·60 mm., lz 0·30–0·45 mm., Lav + kenoz 0·30–0·40 mm., Lm 0·20–0·25 mm., Lov 0·13–0·15 mm., lov 0·15–0·20 mm.

Parellisina was fully discussed by Osburn (1940 and 1949). The genus is easily recognized by the presence of the kenozooidal chamber distal to each avicularium (see Text-fig. 16).

Hastings has described the presence of both septulae and dietellae in this species. Several small septulae communicate between the avicularian chamber and the distal kenozooid (see also Waters, 1898, pl. 47, fig. 2); and lateral septulae communicate between the kenozooid and neighbouring zooids.

There is a great deal of variation in the size of the zooids. Those of the west African specimens are similar to those of the type specimen (Lz 0·45–0·60 mm., Lav + kenoz 0·40–0·50 mm.). Those from Singapore and Adelaide are smaller (Lz 0·30–0·45 mm., Lav + kenoz 0·28–0·33 mm.) as were those described by Cheetham & Sandberg (1964). The avicularian rostra of the type specimen are raised distally, those from west Africa are not.

P. centetica Marcus (1955 : 28, pl. 2, fig. 22, Brazil) differs from *P. curvirostris* in having lateral spines and larger ovicells.

SUMMARY

The fauna of " membraniporine " species in the " Calypso ", Marche-Marchad, Achimota, " Atlantide " and other west African Collections is extensive. Twenty-nine species of Malacostega are here described, 26 from west African waters, 24 of which have been found in the present collections.

The species here referred to *Membranipora* have shown considerable inter- and intra-specific variation, and the specimens have been classified somewhat arbitrarily,

following the highest correlation of certain variable characters, which are briefly discussed.

New species of *Aspidelectra* and *Chartella* are described, and the characters of the genera *Antropora* and *Aplousina* discussed. Two new species of *Callopora* are described, one of which, *C. confluens*, shows a striking convergence of characters with the genus *Membraniporella*. Seven species of *Crassimarginatella* have been found to occur from the west African area, of which 3 are considered to be new. An interesting series of avicularian development has been found in the species of this genus.

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PLATE 1

Membranipora commensale, M. arborescens and *Conopeum tenuissimum*

FIG. A. *Membranipora commensale* (Kirkpatrick & Metzelaar). Achimota Coll., Ghana, 1A. Zooids showing serrated cryptocysts. Note the irregular growth of the zooids, and the kenozooids at the junction of the growing edges. × 18.

FIG. B. *M. arborescens* (Canu & Bassler). Marche-Marchad Coll. I, Senegal, 48A. Part of an erect foliaceous zoarium. Note the numerous cryptocystal denticles and the small lacunae proximal to the opesiae in some zooids. × 18.

FIG. C. *M. arborescens.* " Atlantide " Coll., French Guinea, 110G. Encrusting form, covering a Polyzoan colony, which originally grew over a hydroid stem. The colony is plurilaminar, with erect, bilaminar expansions. × 2·4.

FIG. D. *M. arborescens.* " Atlantide " Coll., French Guinea, 110F. Erect, tubular anastomosing form. This form arose directly from a hydroid stem. × 2·4.

FIG. E. *M. arborescens.* " *Biflustra savartii* ", part of the specimen figured Smitt, 1873, figs. 92, 93. Florida, 29 fath., Naturhistoriska Riksmuseet, No. 283, 1860. Note the brown line outlining the zooids, and the lateral and proximal cryptocystal denticles. × 42.

FIG. F. *Conopeum tenuissimum* (Canu). Achimota Coll., Densu estuary, Ghana, 19A. × 24.

Figures C and D photographed by Mr. H. V. Christensen, Zoologisk Museum, Copenhagen; figures A and B by Mr. P. Green, and E. and F by Mr. J. V. Brown, British Musuem (Natural History).

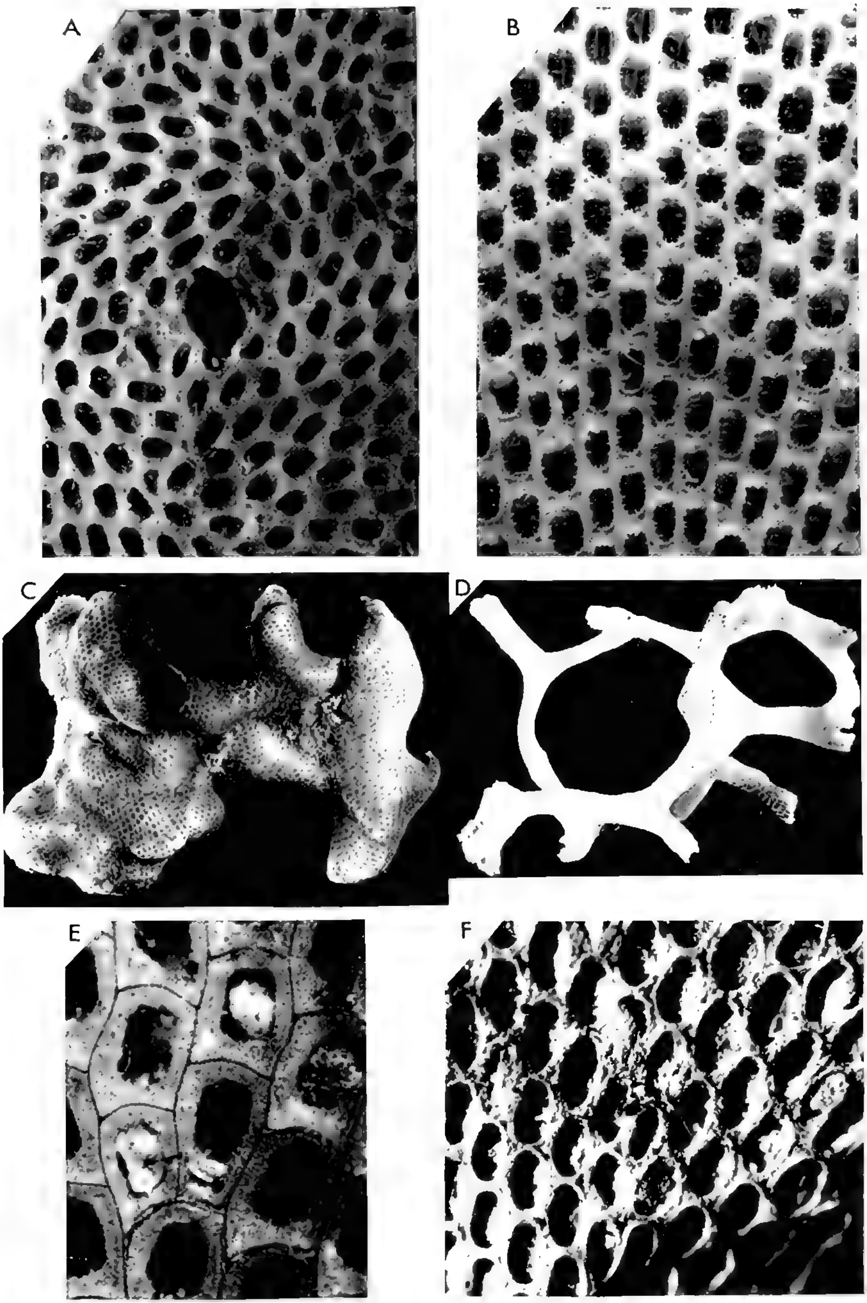
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PLATE 2

Membranipora arborescens, M. tenuis and *M. tuberculata*

FIG. A. *Membranipora arborescens* (Canu & Bassler). Achimota Coll., Ghana, 44A. Encrusting specimen, partially cleaned, showing the chitinous spinules and some zooids (marked x) with lateral and proximal cryptocystal denticles. × 24.

FIG. B. *M. tenuis* Desor. Achimota Coll., Ghana, 68G. Specimen showing zooids similar in character to those of *M. arborescens* in the proximal part of the fragment, and those of " typical " *M. tenuis* in the distal part. × 20.

FIG. C. *M. tuberculata* (Bosc). Achimota Coll., Ghana, 52A. Part of a " typical " specimen, showing the branched cryptocystal denticles, and large gymnocystal tubercles. Compare the development of the proximal cryptocyst in this specimen with that in figure D. × 28.

FIG. D. *M. tuberculata*. Achimota Coll., Ghana, 1B. Specimen encrusting algae, with a greatly developed proximal cryptocyst, and no gymnocystal tubercles. Compare the zooids with those in the distal part of the fragment in figure B, of *M. tenuis*. × 28.

FIG. E. *M. arborescens*. Marche-Marchad Coll. I, 48A. Part of an erect tubular branch. Note the large number of cryptocystal denticles, and the gymnocystal tubercles visible in profile on the left-hand side of the fragment. × 24.

Photographs by Mr. P. Green, British Museum (Natural History).

PLATE 2

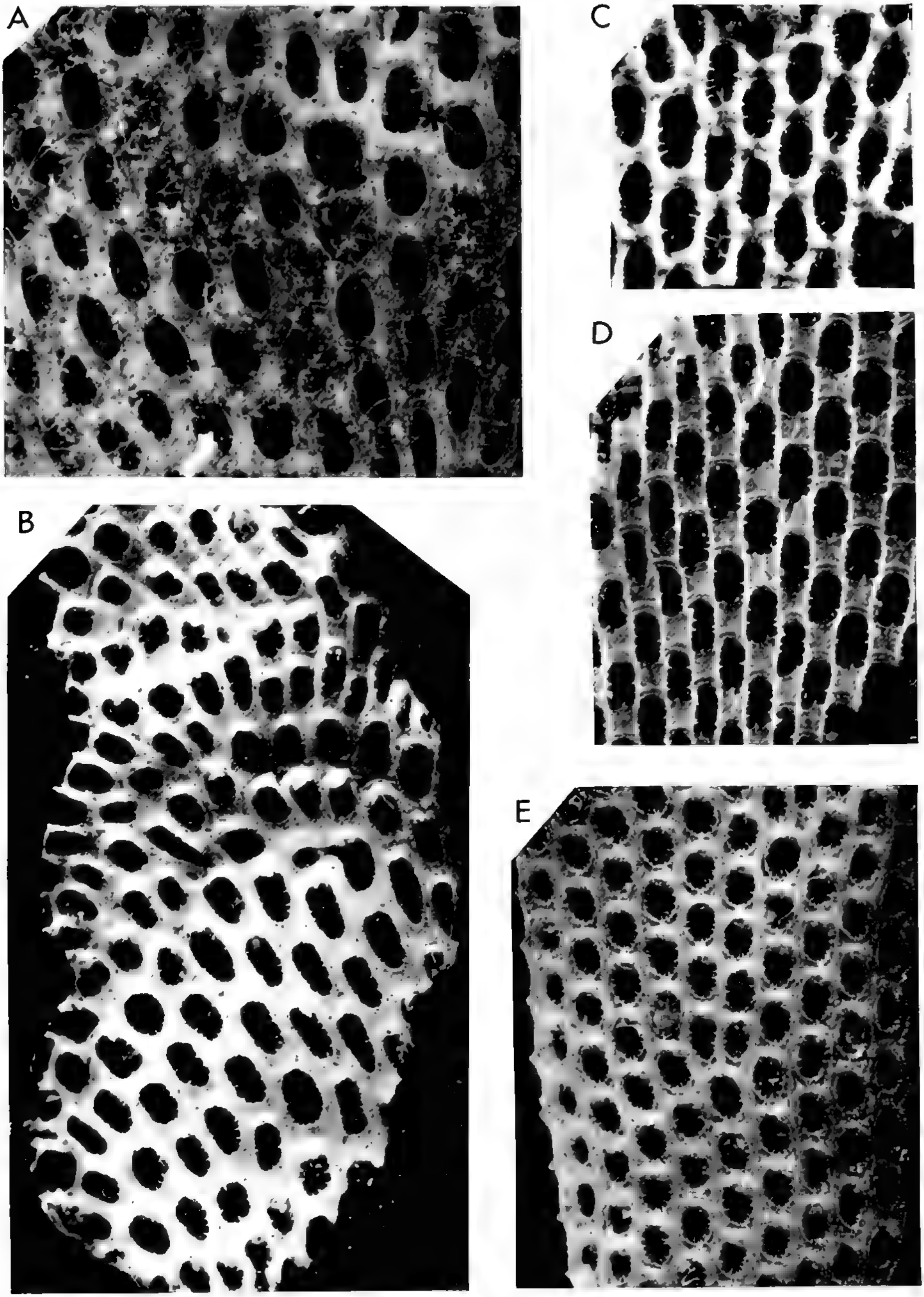


PLATE 3

Aplousina

Fig. A. *A. gigantea* Canu & Bassler. "*Biflustra lacroixii*", Naturhistoriska Riksmuseet, No. 188, 1901, Tortugas, 13 fath. Specimen with ovicells (marked o). × 28.

Fig. B. *A. gigantea*. As above, No. 195, 1781, S.W. Tortugas, 60 fath., specimen figured by Smitt, 1873, fig. 87. Specimen without ovicells, showing the dried polpyides adherent beneath the frontal membrane, as figured by Smitt, compare with figures E and F. × 28.

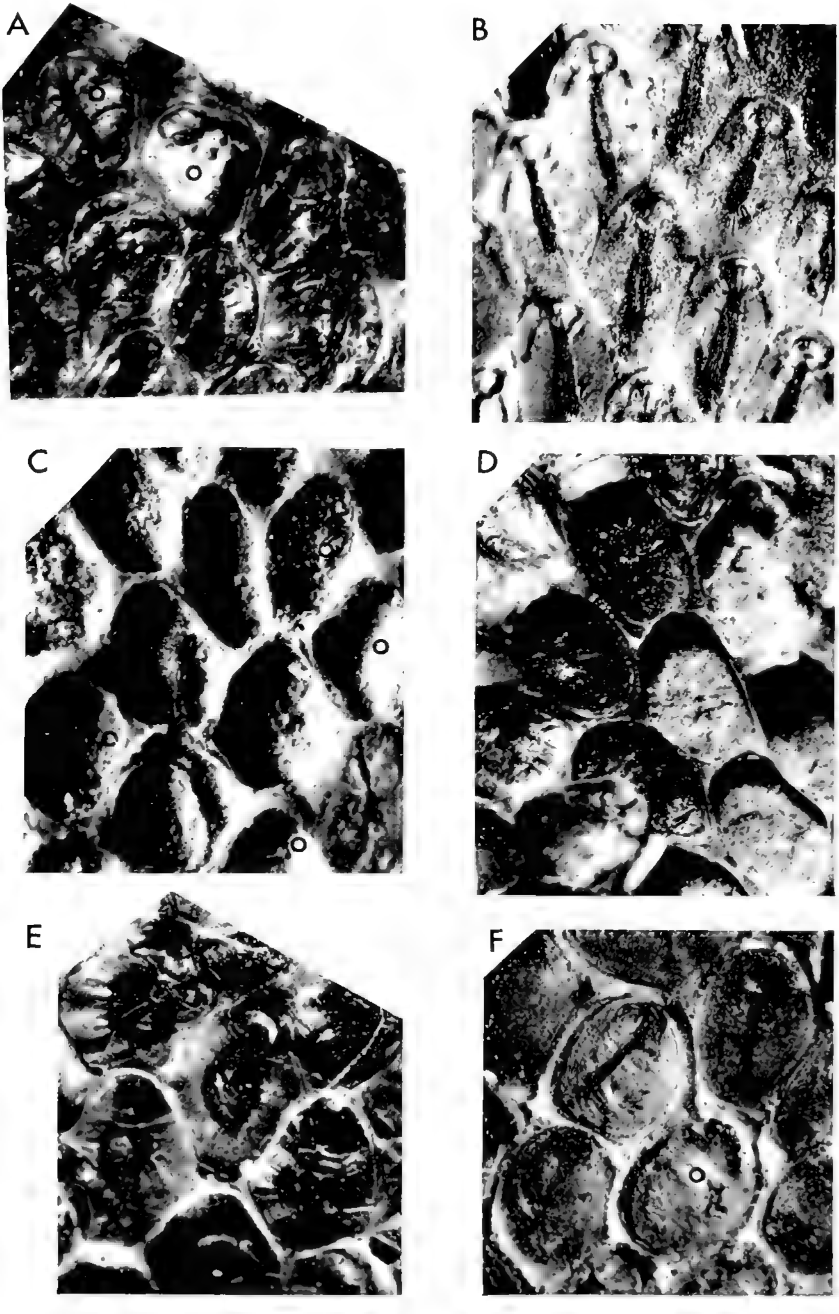
Fig. C. *A. gigantea*. Gulf of Mexico, 1932.3.7.94, Canu & Bassler Coll. Showing zooids with ovicells (marked o). × 28.

Fig. D. *A. capriensis* (Waters). Mediterranean, 1960.11.2.1, Gautier Coll. Showing the thin zooidal walls, with extremely narrow, smooth lateral cryptocyst, and the prominent ovicells, which protrude into the cavity of the next distal zooid. × 28.

Fig. E. *A. major* (Calvet). "Calypso" Coll., Stn. 25, C 10C. Showing the thin zooidal walls, see also Text-figure 8. × 28.

Fig. F. *Aplousina* sp., "*A. filum*" Gautier not Jullien & Calvet. Showing the thick zooidal walls and two ovicells (marked o). × 28.

Photographs by Mr. P. Green, British Museum (Natural History).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NEMATODES PARASITIC IN WESTERN AUSTRALIAN FROGS

W. GRANT INGLIS

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NEMATODES PARASITIC IN WESTERN AUSTRALIAN FROGS

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Pp. 161–183; 33 *Text-figures*

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NEMATODES PARASITIC IN WESTERN AUSTRALIAN FROGS

By W. GRANT INGLIS

SYNOPSIS

Five species of nematodes are reported from the rectum of frogs in southern Western Australia. Of these species *Aplectana flindersi* Johnston & Mawson, 1941 (which is referred to a new genus *Austracerca*) and *Raillietnema kartanum* Johnston & Mawson, 1941 were previously known from South Australia. The remaining three species are all new and referable to the genus *Parathelandros*. As a consequence the genus *Parathelandros* is reassessed and is here considered to contain seven species six of which are described, thus: *P. mastigurus* Baylis, 1930 (type species); *P. australiensis* (Johnston & Simpson, 1942) comb. nov.; *P. limnodynastes* (Johnston & Mawson, 1942) comb. nov.; *P. propinqua* (Johnston & Simpson, 1942) comb. nov.; *P. johnstoni* sp. nov.; *P. carinae* sp. nov.; *P. maini* sp. nov. This regrouping of the genus *Parathelandros* has necessitated the introduction of a new genus, *Skrjabinodon*, for seven species previously referred to the former genus, thus: *S. mabuyae* (Sandground, 1936) (type species); *S. anolis* (Chitwood, 1934); *S. apapillosus* (Koo, 1938); *S. mabuiensis* (Malan, 1939); *S. megalocerca* (Skrjabin, 1916); *S. oedurae* (Johnston & Mawson, 1947); *S. scelopori* (Caballero, 1938).

CONTENTS

INTRODUCTION

THE parasites on which this report is based were collected in Western Australia from newly trapped frogs; from frogs collected by Professor A. R. Main, Western Australia University; and from some frogs in the collections of the Western Australian

Museum. This combination of sources has enabled me to delimit the species of parasites on the basis of very good material so that it was then possible to recognize the same species fairly easily when they were obtained from long preserved host specimens. In this way it was possible to cover a wider host and geographical range (Text-fig. 1) than would otherwise have been possible.

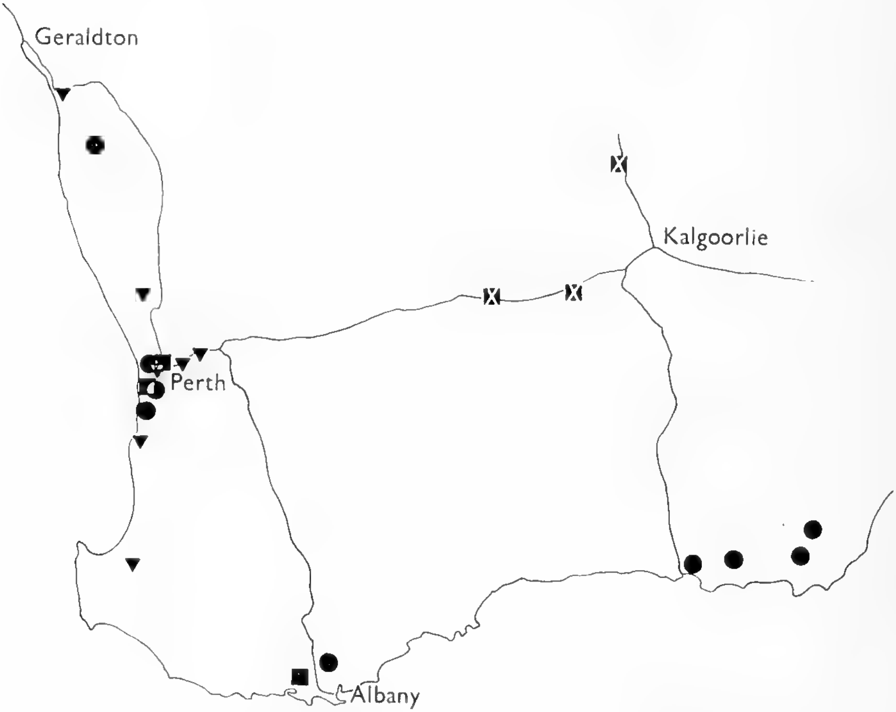


FIG. 1. Outline map of southwest corner of Western Australia from about Geraldton in the north to Esperance in the east, showing distribution of *Parathelandros* species. *P. johnstoni*—squares; *P. maini*—circles; *P. carinae*—triangles. The crossed squares represent the records of *P.*(?) *johnstoni* from Yellowdine, Moorine Rock and Comet Vale reading from left to right on the map. The lines indicate some of the major roads of the area

A total of 197 frogs was examined, of which 84 were parasitized by rectal nematodes. In addition a few were parasitized by a cestode in the intestine, more often by lung flukes and in a very few cases an acanthocephalan was recovered from the intestine. There was no observable relationship between the occurrence of any of these parasites and the rectal parasites. The remainder of this paper is based on the rectal parasites alone.

In addition to the Western Australian parasites, similar parasites from hosts in the eastern part of Australia were studied from the collections of the University of Adelaide. Holotypes and some paratypes of all new species are deposited in the collections of the Western Australian Museum, Perth. Other paratypes and specimens are in the collections of the British Museum (Natural History).

TAXONOMIC RESULTS

The majority of the 2,000 (approximately) parasite specimens collected in Western Australia are referable to the oxyurid genus *Parathelandros*, but two cosmocercoid species, previously known from South Australian hosts, were also found and are described first.

COSMOCERCIDAE Railliet, 1916

Austracerca flindersi (Johnston & Mawson, 1941) comb. nov.

(Text-figs. 2-4)

Material studied. 1 ♂, Holotype ex *Hyla jervisiensis*, Kangaroo Island, South Australia. Specimen in South Australian Museum.

1 ♂, 1 ♀. ex rectum of Hyla *cyclorhyncha*, 14 miles east of Esperance, Western Australia. From host collected by Dr. G. M. Storr on 9th December, 1959.

1 ♂, 1 ♀ ex rectum of *Helioporus australiacus*, Boya, Western Australia. From host collected by Prof. A. R. Main on 22nd April, 1954.

2 ♀, 1 larva. ex rectum of *Helioporus psammophilus*, Dongara, Western Australia.

Measurements (mm.).

Males. Body length: 2·0; 2·6. Body breadth: 0·16; 0·17. Oesophagus length: 0·38; 0·41. Distance of excretory pore from anterior end of body: 0·24; 0·27. Length of tail: 0·23; 0·26. Length of spicules: 0·12; 0·12. Length of gubernaculum: 0·13; 0·16.

Females. Body length: 2·9; 4·9. Body breadth: 0·21; 0·24. Oesophagus length: 0·66; 0·67. Distance of excretory pore from anterior end of body: 0·28; 0·31. Length of tail: 0·61; 1·12. Distance of vulva from anterior end of body: 0·29; 0·36. Eggs: 0·098–0·100 (spherical).

There are narrow lateral alae on the body on both sexes and there are no papillae on the general surface of the body. The oesophagus has the usual tri-valvulate posterior oesophageal bulb. The excretory pore lies well anterior to the posterior end of the oesophagus.

The mouth opening is bounded by three, shallow lips of which the dorsal carries two stout, double outer papillae and each ventro-lateral lip carries a similar papilla ventrally and a smaller papilla laterally associated with the lateral amphids. There appear to be two small papillae on the inner edge of each lip, but it is impossible to be sure although two nerve tracts are certainly present (Text-fig. 4). The anterior end of the oesophagus is modified as a chamber with very thick, sclerotized walls, into which project three distinct onchia (Text-fig. 4).

The male tail is simple, without alae, and all the papillae are sessile, although some are well developed. There are two pairs of ventro-lateral pre-cloacal papillae; three pairs arranged in a triangle lying at the level of the cloacal opening; five papillae on the anterior lip of the cloacal opening, one of which is median (Text-fig. 3); and there are six pairs of post cloacal papillae of which three pairs are almost wholly ventral, one pair is lateral about half way along the tail, and two pairs lie just anterior to the terminal spike (Text-fig. 2).

The spicules are very slim and needle-like while the gubernaculum is very prominent with lateral processes near its anterior end so that it is dagger-shaped in ventral view (Text-figs. 2, 3).

The female tail is long and stout, and the reproductive system is doubled.

DISCUSSION. The specimens described above are indistinguishable from those described by Johnston & Mawson (1941) as *Aplectana flindersi* and are referred to that species. This species is however very different from the more typical *Aplectana* Railliet & Henry, 1916 species particularly in the presence of the oesophastome with three well developed onchia and in the small spicules associated with the very large gubernaculum. I therefore propose to refer the species to a new genus which may be diagnosed thus:

Austracerca gen. nov.

Cosmocercidae: Cosmocercinae: no papillae on body surface; lateral alae present; mouth bounded by three distinct lips; oesophastome distinct cavity into which project three onchia. Male: spicules slim; gubernaculum large and massive; no caudal alae; caudal papillae simple and sessile. Female: vulva anterior to posterior end of oesophagus.

TYPE SPECIES: *Aplectana flindersi* Johnston & Mawson, 1941.

HOSTS AND GEOGRAPHICAL DISTRIBUTION: *Hyla jervisiensis*, Nr. Esperance, Western Australia; *Helioporus australiacus*, Boya, Western Australia; *Helioporus psammophilus*, Dongara, Western Australia.

Raillietnema kartanum Johnston & Mawson, 1941

(Text-figs. 5-8)

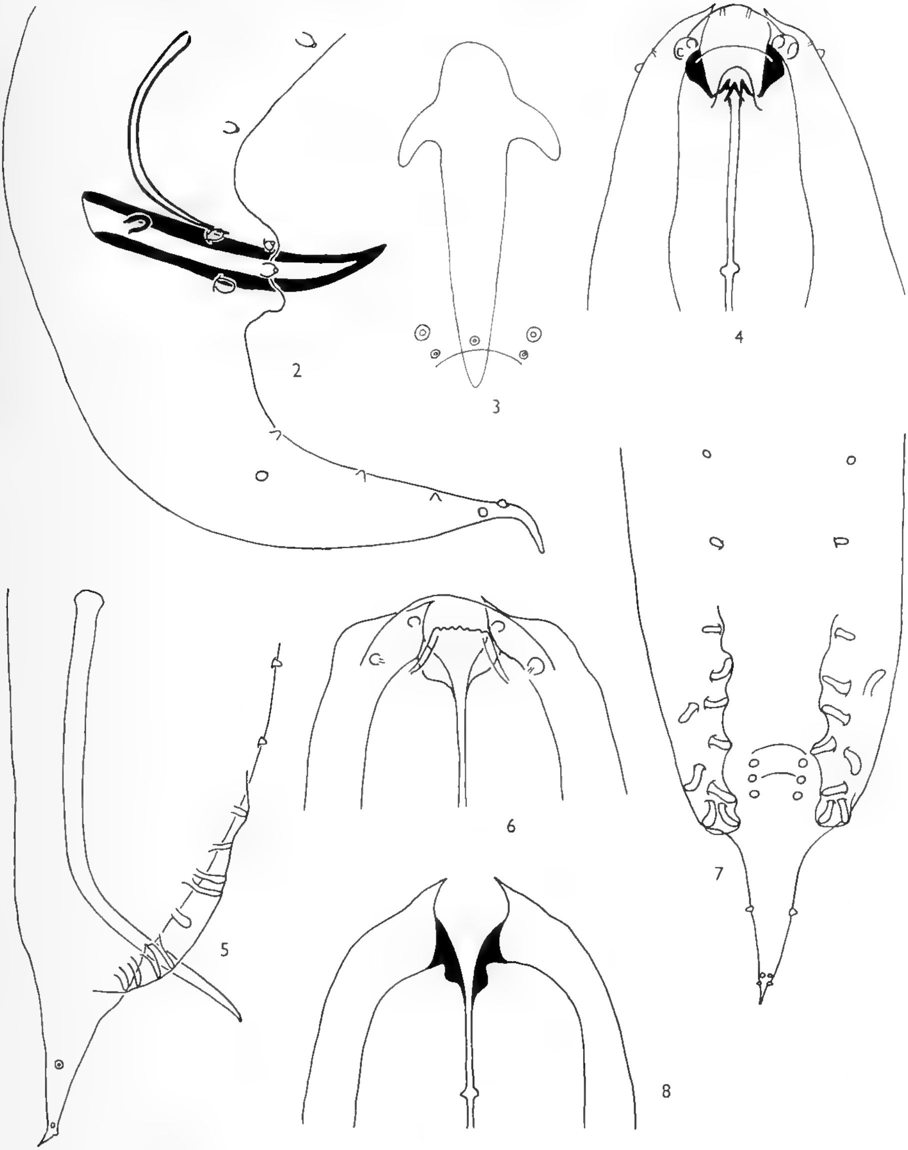
MATERIAL STUDIED. 1 ♂, Holotype. ex *Hyla jervisiensis*, Kangaroo Island, South Australia. Specimens in South Australian Museum.

1 ♂, 1 ♀ ex rectum of *Hyla moorei*, Bolganup Dam, Porongorup Range, Western Australia. Host collected by Dr. G. M. Storr on 14th December, 1959.

2 ♀. ex rectum of *Helioporus eyrei*, Chidlows, Western Australia.

Measurements (mm.).

MALE. Body length: 4·0; Body breadth: 0·23; Oesophagus length: 0·57; Distance of excretory pore from anterior end of body: 0·36; Length of tail: 0·13; Length of spicules: 0·23.



FIGS. 2–8. *Austracerca flindersi.* 2. Lateral view of male tail. 3. Ventral view of gubernaculum and papillae on anterior lip of cloacal opening. 4. Dorsal view of head showing detail of buccal cavity. 5–8. *Raillietnema kartanum.* 5. Lateral view of male tail. 6. Dorsal view of head. 7. Ventral view of male tail showing distribution of caudal papillae. 8. Head in optical section showing shape of cuticular thickening at anterior end of oesophagus.

FEMALE. Body length: 6·1; Body breadth: 0·40; Oesophagus length: 0·66; Distance of excretory pore from anterior end of body: 0·41; Length of tail: 0·33; Distance of vulva from anterior end of body: 3·4; Size of eggs: 0·062–0·066 (spherical).

There are narrow lateral alae in both sexes and there are no papillae on the general surface of the body. The oesophagus is typical with the usual tri-valvulate posterior bulb. The excretory pore lies about the middle of the oesophagus length in both sexes.

The mouth opening is bounded by three lips of which the dorsal bears two single outer papillae while each ventro-lateral lip carries a single ventro-lateral papilla and a small papilla associated with the lateral amphids. There are six prominent papillae arranged in pairs on the inner edge of each lip (Text-fig. 6). The anterior end of the oesophagus bears a region of thickened cuticle which projects anteriorly to line each lip (Text-fig. 8). There are no tooth-like structures at the anterior end of the oesophagus.

The posterior end of the male bears thick, ventro-lateral alae supported by nine pairs of pedunculate papillae arranged roughly in two rows; an inner more ventral row of four and an outer of three. The remaining two pairs occur side by side at the posterior end of the alae (Text-fig. 7). Anterior to the alae are two pairs of ventral sessile papillae while there are three pairs of similar, but less prominent, papillae flanking the cloacal opening. The tail bears three pairs of small, sessile papillae of which two lie close together just anterior to the small terminal spike, while the third pair is lateral in position about two thirds of the length of the tail posterior to the cloacal opening.

The spicules are stout, equal in length, non-alate, identical in structure and taper evenly posteriorly (Text-fig. 5). There is no gubernaculum.

The female tail is relatively long and stout and the reproductive system is doubled.

DISCUSSION. The specimens described here are morphologically indistinguishable from *Raillietnema kartanum* Johnston & Mawson, 1941 from *Hyla jervisiensis* in South Australia of which I have studied the holotype. Any apparent differences can be attributed to differences in the fixation of the specimens or can be looked on as falling well within the normally expected range of variation.

Johnston and Mawson (*loc. cit.*) comment on the fact that their specimens are not wholly typical of the genus *Raillietnema* while Skrjabin, Schikhobalova & Lagodovskaya (1961) refer the species to *Oxysomatium* (S.L.) because of this uncertainty. However the only apparently marked difference between the Australian specimens and typical *Raillietnema* species is the absence of a gubernaculum. But the genus *Raillietnema* is relatively poorly known and, while later study may demonstrate other differences between *R. kartanum* and other species of the genus, I treat this Australian species as a member of *Raillietnema*, at least provisionally.

OXYURIDAE Cobbold, 1864

Parathelandros Baylis, 1930

Since 1930 when Baylis erected the genus *Parathelandros* for *P. mastigurus* three further species have been referred to the genus, thus: *P. anolis* Chitwood, 1934;

P. oedurae Johnston & Mawson, 1947 and *P. scelopori* Caballero, 1938. In addition Skrjabin, Schikhobalova & Lagodovskaya (1960) refer a further four species, previously referred to other genera, to *Parathelandros*, thus: *Pharyngodon bassii* Walton, 1940; *Ph. mabuiensis* Malan, 1939; *Ph. mabuyae* Sandground, 1936 and *Oxyuris megalocerca* Skrjabin, 1916; while Read & Amrein (1953) refer *Ph. apappillosus* Koo, 1938 and *Ph. medinae* Calvente, 1948 to the genus.

The genus itself has been accepted as distinct by most authors except Yamaguti (1961) who treats it as indistinguishable from *Pharyngodon* Diesing, 1861. It can be said immediately, in anticipation of the descriptions which follow, that *Parathelandros* warrants recognition as a distinct genus. The species described below all occur in Australian hosts and because of their morphological uniformity it is doubtful if the species referred to the genus by authors other than Baylis can be considered con-generic with *P. mastigurus.* This is discussed in detail later and I shall first describe the anatomy of the six species which appear to be definitely congeneric with *P. mastigurus*, of which three are here described as new and two have not previously been recognized as members of the genus. A seventh species, of which I have not seen specimens, is referred to the genus on the basis of a published description.

Morphology. The heads bear four large, single, dorso- and ventro-lateral papillae and a pair of small, slightly finger-like lateral amphids (Text-figs. 10–12, 16). There may be six small papillae of the inner circle present (see particularly Text-fig. 16) but I cannot be certain. The mouth opening is bounded by three major lip lobes each of which is divided into two, largely cuticular, subsidiary lobes. The extent of this division into lobes and the degree to which the lips are set-off from the head varies somewhat but the differences are not constant from species to species, as recognized on other characters, and appear to reflect the extent to which the mouth is open or shut (Text-figs. 11, 12, 16). The mouth leads in to a shallow cheilostome which is triangular in transverse section. The lumen at the anterior end of the oesophagus is expanded to form a cup-like cavity into which project three apparently wholly cuticular onchia (Text-figs. 10, 11; see Inglis, 1962). The degree of development of the onchia, as with the lip lobes, varies from specimen to specimen but this also appears to reflect muscular contraction rather than a constant difference between the species.

The oesophagus is typically oxyurid with a prominent, tri-valvulate posterior bulb (Text-figs. 14, 15, 17). Single lateral alae which are present on both sexes, start anteriorly about the middle of the oesophagus length as stout swellings (Text-fig. 17) which narrow tangentially and widen laterally more posteriorly. The width of the alae varies considerably from species to species, particularly when male specimens are compared. The tail in both sexes ends posteriorly in a very long, slim spike (Text-fig. 13).

Male. The male tail narrows rapidly, posterior to the cloacal opening, to form a terminal spike (Text-figs. 13, 20, 21, 26). The lateral alae stop slightly posterior to the cloacal opening after constricting sharply (Text-figs. 18, 20, 21, 26). The region round the cloacal opening is raised as a genital cone on which there are two pairs of papillae, one pair anterior to the cloacal opening and one pair posterior. The relative sizes of these papillae vary from species to species. In some species there is a median post-cloacal spherical swelling or posteriorly directed process which lies between the more posterior pair of papillae (Text-figs. 19, 23–25). A third pair of papillae lie on the ventral surface of the tail about the posterior limit of the lateral alae. These papillae frequently arise from a common basal platform, or swelling, and are usually of a rosette type, as are some of the cloacal papillae. A single, frequently poorly sclerotized spicule is present and a small, insignificant gubernaculum supports the posterior lip of the cloacal opening in most specimens. Phasmids have been seen on some specimens lying roughly mid-way between the genital cone and the pair of tail papillae.

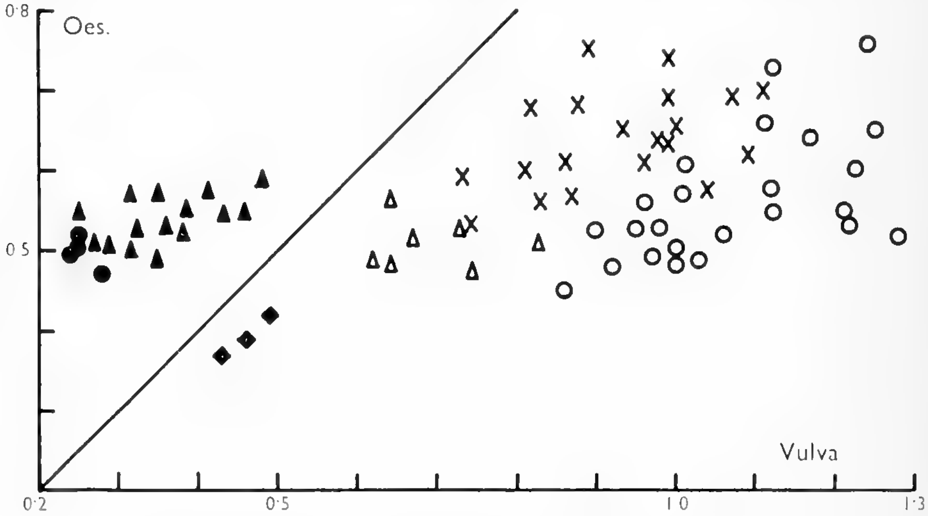


FIG. 9. Scatter diagram plotting distance (in mm.) of vulva from anterior end of body against length of oesophagus, in species of *Parathelandros*. *P. mastigurus*—solid circles; *P. maini*—solid triangles; *P. australiensis*—solid diamonds; *P. limnodynastes*—empty triangles; *P. johnstoni*—crosses; *P. carinae*—empty circles. Note particularly the extent to which the longer specimens of *P. johnstoni* and shorter specimens of *P. carinae* overlap and the separation of *P. limnodynastes* and *P. johnstoni* which may simply reflect the difference in size of the specimens studied (see text). Note that this scatter diagram includes some specimens not listed in the measurements given at the end of the taxonomic section of this paper.

In some male specimens there is a swollen region on the ventral surface of the body anterior to the cloacal opening (Text-fig. 32). This feature is not constant in occurrence and, as it occurs most commonly in specimens recovered from host specimens which had been stored for some time, it is almost certainly a fixation artefact.

FEMALE. The vulva, which can open anterior to, on a level with the posterior end of, or posterior to the oesophagus, is very prominent and leads into a stout, muscular vagina (Text-figs. 14, 15, 17). The vagina in turn leads to a somewhat clubbed chamber from which two uteri arise. One uterus runs posteriorly and the other almost immediately runs anteriorly. The eggs are elongate, spindle-shaped with a latero-terminal operculum and are segmented *in utero*. There is a small, ovoid swollen region just posterior to the anus.

DELIMINATION OF SPECIES. The specimens, particularly the males, are small but the species from Western Australian hosts, at least, can be distinguished fairly readily by the width of the lateral alae and the position of the vulva. It is not, however, possible to identify specimens from other areas with certainty on these criteria if their geographical origins are unknown and even with Western Australian specimens it is advisable to study the cloacal region of the males in ventral view.

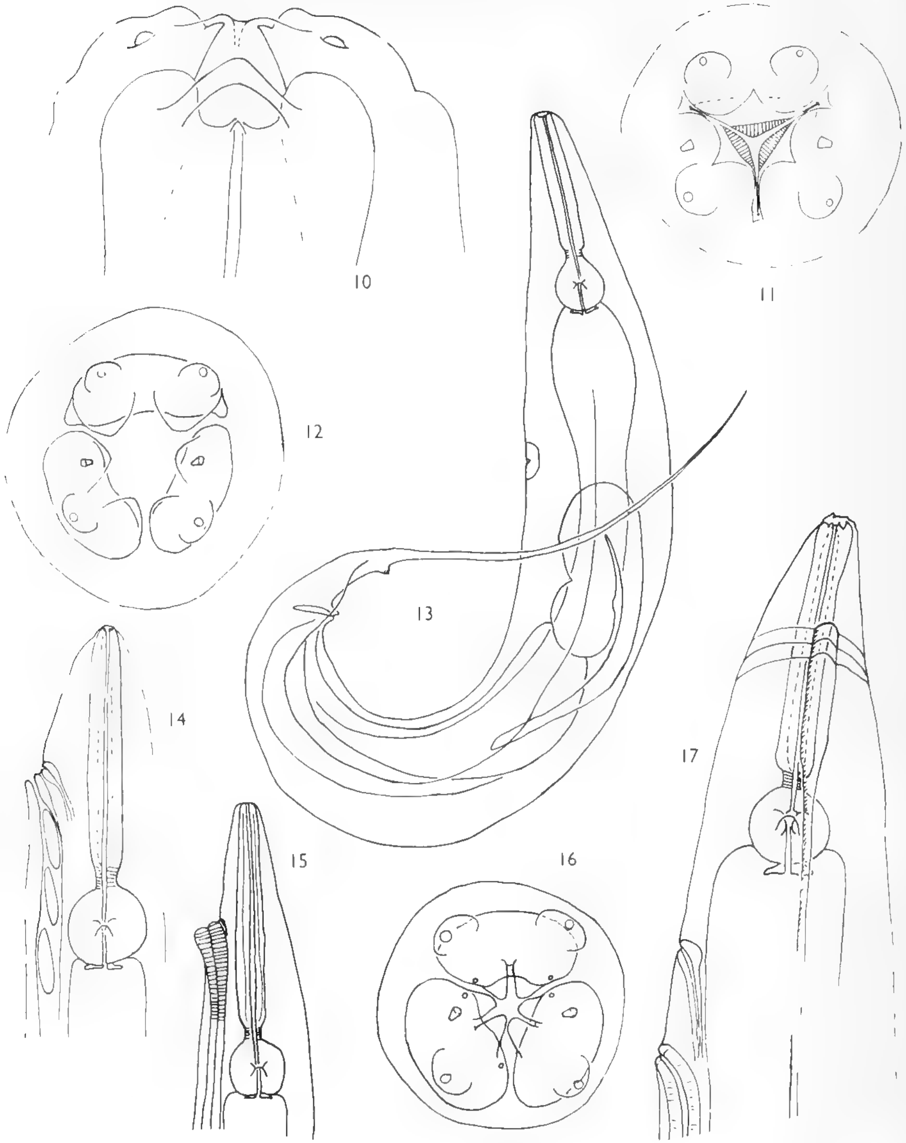
All the species recognized here can be distinguished by some combination of the characters discussed below.

1. The position of the excretory pore relative to the posterior end of the oesophagus enables three groups to be distinguished, one in which the excretory pore lies about the middle of the oesophagus length, one in which it lies close to the posterior end of the oesophagus and one in which the excretory pore is relatively far posterior to the posterior end of the oesophagus.

2. The position of the vulva relative to the posterior end of the oesophagus falls into three groups corresponding to the groups formed on the basis of the excretory pore. In general the excretory pore and the vulva lie close together with the former slightly anterior to the latter, and the vulva is easily seen because it projects slightly above the surrounding body surface (Text-figs. 14–15). The possibility of confusing these three divisions occurs with immature or small specimens of the groups in which the adult vulva is posterior to the posterior end of the oesophagus. In such specimens the vulva lies relatively more anterior than it does in adult or large specimens (Text-fig. 9).

3. The breadth of the lateral alae in both sexes forms two groups in one of which the alae are narrow while in the other they are very wide. This character is much more easily used than it may appear at first sight because the wide alae particularly on the males are very prominent being together equal in width to the width of the body (Text-figs. 18, 21, 26), and this difference can be easily seen even under a fairly low power stereoscopic microscope. In male specimens the alae can cause great difficulty in rolling specimens to obtain a ventral view of the cloacal region.

4. The size of the genital cone and associated papillae on the males is particularly useful and forms the most characteristic feature of the various species. Two major groups can be recognized, one in which the papillae are prominent and there is no post-cloacal process and one in which such a process is present and the papillae are small. In addition the relative sizes of the cloacal papillae vary from species to species and some of the papillae may be of a rosette-type (Text-figs. 18, 20, 26). The post-cloacal lobe itself may be of two major forms, one in which it is a spherical ball-like structure which may be smooth or may be covered by small cuticular



FIGS. 10–17. 10. *P. maini*: dorsal view of head. 11. *P. carinae: en face* view of head; cross-hatched regions are teeth at anterior end of oesophagus. 12. *P. carinae: en face* view of head to illustrate difference in appearance caused by contraction of musculature. 13. *P. limnodynastes:* lateral view of whole male to show general facies of the genus. 14. *P. maini:* anterior end of body. 15. *P. mastigurus:* anterior end of body, compare with *P. maini*. 16. *P. carinae*: *en face* view of head showing further variation in appearance. 17. *P. johnstoni:* anterior end of body. Note how the alae start as broad low swellings and then narrow about the anterior limit of the posterior oesophageal bulb

granulations, and one in which it is a posteriorly directed triangular process (Text-figs. 19, 23–25).

On the basis of these characters the following six species can be distinguished: *P. mastigurus* (Type species); *P. australiensis* and *P. limnodynastes* (new combinations); *P. maini*, *P. carinae* and *P. johnstoni* (new species).

Unless qualified all host and locality records are new. Numbers refer to material in collection of the University of Adelaide.

Parathelandros mastigurus Baylis, 1930

(Text-figs. 15, 18, 19, 27, 28).

Hosts and localities. *Hyla caerulea:* Neighbourhood of Townsville, Queensland (Here selected as type host and locality; recorded by Baylis, 1930). Burnett River, Queensland (U.A. 1/1911; U.A. HC2341); Sydney, New South Wales (U.A. HC2336; U.A. HC2344; U.A. HC8).

Hyla gracilis: Neighbourhood of Townsville, Queensland (recorded by Baylis, 1930).

Bufo marinus: Brisbane, Queensland (from class material: U.A. HC9/56).

This species is well described by Baylis (1930) and the head is described by Inglis (1963).

This species is characterized by the excretory pore and vulva opening about the middle of the oesophagus length and by the possession of very wide alae. The cloacal cone is small with small papillae of which the more posterior pair is very small while the anterior pair is prominent, pedunculate and rosette-type. A post-cloacal lobe is present which is long, smooth, triangular in outline and posteriorly directed. The caudal papillae do not arise from a distinct common base.

Parathelandros australiensis (Johnston & Simpson, 1942) comb. nov.

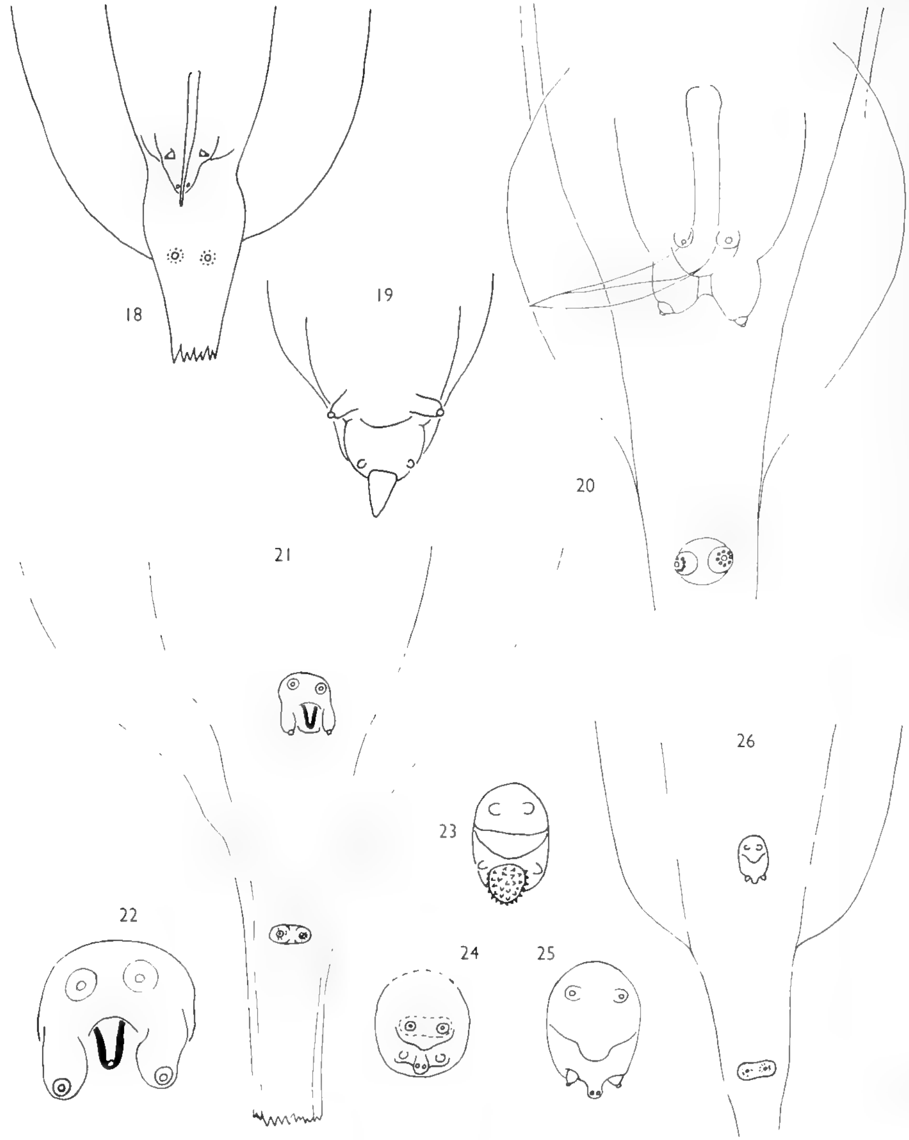
(Text-figs. 23, 33).

Cosmocerca australiensis Johnston & Simpson, 1942.

Hosts and localities. *Limnodynastes dorsalis:* from vicinity of Adelaide, South Australia. (Type host and locality; recorded by Johnston & Simpson, 1942);

Limnodynastes fletcheri: Chowilla Station, on River Murray, S.A. (U.A. A1401; U.A. A1402).

This species was described and named on the basis of females which, as Johnston & Simpson (1942) point out, made classification difficult. The specimens I have seen agree with the published description. Although the very broad lateral alae were not mentioned, they are frequently not prominent on females. In spite of the difficulty mentioned above in identifying females in the absence of males, my experience with Western Australian species suggests that it is unlikely that there will be another South Australian species with very broad alae and a vulva opening slightly posterior to the posterior end of the oesophagus.



FIGS. 18–26. Ventral views of cloacal regions of *Parathelandros* males. 18, 19. *P. mastigurus:* general view showing breadth of alae and detail of cloacal cone respectively. 20. *P. carinae:* showing particularly the bursa-like modification of the alae in the cloacal region and the very large size of the more posterior pair of cloacal papillae relative to the anterior pair. 21, 22. *P. johnstoni:* general view of the cloacal region showing

This species is, therefore, distinguished by the excretory pore and vulva opening slightly posterior to the posterior end of the oesophagus and in possessing very broad lateral alae particularly in the male. The cloacal cone is small with small cloacal papillae of equal size. A post-cloacal lobe is present which is spherical and bears cuticular granulations. No gubernaculum has been seen in any of the specimens examined. The caudal papillae rise from a common base.

Parathelandros limnodynastes (Johnston & Mawson, 1942) comb. nov.

(Text-figs. 13, 31).

Pharyngodon limnodynastes Johnston & Mawson, 1942.

HOSTS AND LOCALITIES. *Limnodynastes dorsalis:* Tailem Bend, South Australia (Type host and locality; recorded by Johnston & Mawson, 1942; host recovered from a tiger snake, *Notechis scutatus*); Coromandel Valley, Mt. Lofty Range, South Australia (from class material: U.A. HC2366); Magill, Adelaide, South Australia (class material: U.A. HC3176).

The original description of this species was based on female specimens so that, as with *P. australiensis*, its allocation is difficult. Nevertheless the description given by Johnston & Mawson (1942) agrees well with the specimens I have seen. I have also studied the type specimen, a female, and there is nothing to distinguish it from the other female specimens I have seen.

In this species the excretory pore and vulva open fairly close to the posterior end of the oesophagus and the lateral alae are broad. The cloacal cone is large with large pedunculate papillae which are equal in size. There is no post-cloacal lobe and the caudal papillae arise from a common base. No gubernaculum has been seen.

Parathelandros johnstoni sp. nov.

(Text-figs. 21, 22, 30)

HOSTS AND LOCALITIES (all in Western Australia). *Helioporus eyrei:* Bibra Lake, (Type host and locality). Sheepwash Creek (17 miles north east from Denmark on the Mt. Barker road); Butlers Swamp, Lake Claremont, Perth; Beechina; Swanview.

Neobatrachus pelobatoides: Caversham.

Lymnodynastes dorsalis: Bibra Lake; Bayswater Road, Nr. Garratt Road Bridge, Perth.

Neobatrachus centralis: Yellowdine; Moorine Rock; Comet Vale (all records slightly doubtful, see discussion below).

This species is characterized by the excretory pore and vulva opening relatively close to the posterior end of the oesophagus and by the possession of wide lateral

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wide lateral alae and the smaller cloacal papillae relative to *P. carinae*, and detail of the cloacal cone. 23. *P. australiensis:* detail of cloacal cone showing, slightly diagrammatically, the denticulate spherical post-cloacal lobe. 24–26. *P. maini:* 24, 25 Detail of cloacal cone showing variation in appearance. Note the double(?) papilla on the post-cloacal lobe. 26. General view showing wide lateral alae.

alae. The cloacal cone is small with medium sized cloacal papillae which do not arise as distinct structures. There is no post-cloacal lobe and the caudal rosette papillae arise from a common platform. The spicule and gubernaculum tend to be poorly developed and may even be absent in some specimens.

This species is very similar to *P. limnodynastes*. The differences between them are slight but consist of the smaller and slimmer spicule; the cloacal papillae, which never appear to stand out distinctly from the smallish cloacal cone; and the vulva which lies relatively further posterior to the oesophagus (Text-fig. 9). The similarities to *P. limnodynastes* are very marked but the slight differences are very consistent so I will treat this species as distinct, at least until more specimens of *P. limnodynastes* are available for study.

The specimens from *Neobatrachus centralis* are in very poor condition and it is difficult to decide, in view of what I say above, whether they are *P. maini* or *P. limnodynastes*.

Parathelandros carinae sp. nov.

(Text-figs. 11, 12, 16, 20, 29, 32)

Hosts and Localities (all in Western Australia). *Helioporus albopunctatus:* Bakers Hill, Northam (Type host and locality) Beechina (31 miles from Perth on road to Northam).

Helioporus australiacus: Middle Swan.

Helioporus psammophilus: Near Geraldton (257 miles from Perth); Beechina; 161 mile peg on Augusta Road from Perth.

Helioporus eyrei: Beechina; Bushmead.

Neobatrachus pelobatoides: Wannamal.

This species is characterized by the excretory pore and vulva opening far posterior to the posterior end of the oesophagus and by the possession of very narrow lateral alae.

The alae expand in the cloacal region of the male to form a bursa. The cloacal cone and papillae, particularly the more posterior pair, are very large. The spicule and gubernaculum are very distinct in all the specimens studied.

This species is the largest of all those studied and is easily recognized by the bursa-like modification of the caudal alae (Text-fig. 20).

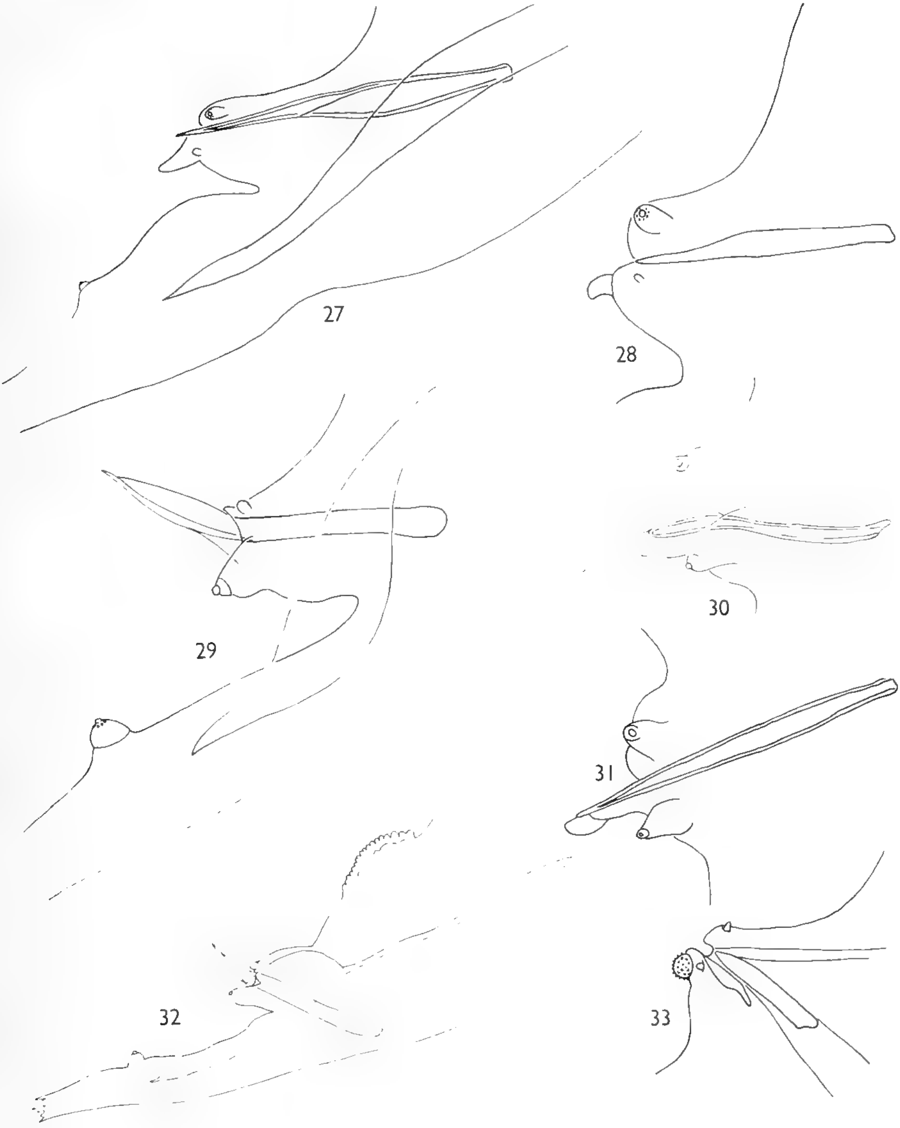
Parathelandros maini sp. nov.

(Text-figs. 10, 14, 24, 25, 26)

Host and Localities (all in Western Australia). *Hyla moorei:* swamp in Hardy Road, Cloverdale (Type host and locality); swamp in Hardy Road, Cannington; Nr. Garratt Road Bridge, Bayswater; Bolgonup Dam, Porongorup Range; Diannela, Perth; 21 mile peg on Mandurah Road, East Rockingham; 25 miles south west of Eneaba.

Hyla cyclorhyncha: Pine Hill, 13 miles north west from Mt. Ragged; Lake Condingup, 14 miles east of Esperance; Scadden.

Hyla adelaidensis: Pine Hill, 13 miles north west from Mt. Ragged.



FIGS. 27–33. 27, 28. *P. mastigurus:* 27. General lateral view of male tail. 28. Detail of cloacal cone from the lateral aspect. Note the small posterior pair of papillae and the flange-like post-cloacal lobe. 29. *P. carinae:* general lateral view of cloacal region. Note the large posterior pair of cloacal papillae. 30. *P. johnstoni:* detail of cloacal cone from lateral aspect. 31. *P. limnodynastes:* detail of cloacal cone from lateral aspect. Note the stouter spicule and the freestanding papillae in contrast to the condition shown in Fig. 30. 32. *P. carinae:* general view of posterior end of body showing the bursa-like modification of the alae and the pre-cloacal male swelling found on some specimens. 33. *P. australiensis:* detail of cloacal cone from lateral aspect.

This species is characterized by the excretory pore and vulva opening anterior to the posterior end of the oesophagus and by the possession of very wide lateral alae. The cloacal cone and papillae are small, with a smooth, rounded, ball-like post-cloacal lobe on which there appear to be two very small papillae. The post-cloacal papillae are rosette and arise from a common platform.

This species is most similar to *P. australiensis* from which it differs most markedly in the smooth post-cloacal lobe and the anterior position of the vulva.

Parathelandros propinqua (Johnston & Simpson, 1942) comb. nov.

Cosmocerca propinqua Johnston & Simpson, 1942.

HOST AND LOCALITY. *Limnodynastes dorsalis*, Adelaide, South Australia (Type host and locality).

This species, in which the vulva opens anterior to the posterior end of the oesophagus, is known from females only. It is clearly referable to *Parathelandros* in which it could only be confused with *P. mastiguris* or *P. johnstoni*. No decision on its status can be taken until male specimens are collected from hosts in South Australia.

OTHER SPECIES REFERRED TO *PARATHELANDROS*

The following nine species have been referred to the genus *Parathelandros* at various times by various authors, thus: *Parathelandros anolis* Chitwood, 1934; *P. oedurae* Johnston & Mawson, 1947; *P. scelopori* Caballero, 1938 were all originally described as members of the genus. The following species have been referred secondarily to the genus: *Pharyngodon apappillosus* Koo, 1938 and *Ph. medina* Calvente, 1948 were referred to *Parathelandros* by Read & Amrein (1953) while Skrjabin *et al.* (1960) referred the following four species to the genus: *Ph. bassii* Walton, 1940; *Ph. mabuiensis* Malan, 1939; *Ph. mabuyae* Sandground, 1936 and *Oxyuris megalocerca* Skrjabin, 1916. None of these species possess the combination of characters considered diagnostic of *Parathelandros*, as restricted here.

Although it is easy to conclude that these species are not congeneric with the Australian species referred to *Parathelandros* it is difficult to know how to treat them, other than to leave them floating in limbo as species *incertae sedis*. This difficulty is a reflection of the general need for a revision of the subfamily Pharyngodoninae. Some attempt is made to carry out such a revision by Skrjabin *et al.* (1960) but they are hampered by their forced reliance on published descriptions many of which leave much to be desired. These authors regrouped some species previously referred to *Pharyngodon* in the genera *Spauligodon* and *Parathelandros*. The species they left in *Pharyngodon* have all the caudal papillae of the males surrounded by caudal alae; those referred to *Spauligodon* have the most posterior pair of papillae free of the caudal alae and those referred to *Parathelandros* have none of the caudal papillae surrounded by caudal alae.

This simple grouping breaks down with the discovery of so many morphological very similar species in Australian frogs in which the cloacal papillae arise from the cloacal cone. In the species grouped in *Parathelandros* by Skrjabin *et al.* (1960), with the exception of *P. mastiguris*, the cloacal papillae do not lie on such a cone, when present, but are grouped on the body surface around it. I shall, therefore, refer these latter species to a new genus *Skrjabinodon*. This is done mainly on grounds of expediency because the species concerned fall into two groups, and some of the species left in *Pharyngodon* by Skrjabin *et al.* do not appear to belong in that genus. In fact the delimitation of the groups represented by the genera *Pharyngodon*, *Spauligodon* and *Skrjabinodon* needs to be revised before any final judgement can be reached.

The genera may be diagnosed thus:

PARATHELANDROS Baylis, 1930

Oxyuridae: Pharyngodoninae: mouth opening bounded by three bilobed lips; small onchia in cavity at anterior end of oesophagus; lateral alae on both sexes; excretory pore and vulva variable in position from anterior to posterior end of oesophagus to posterior to oesophagus; tail terminates in long spike in both sexes. Male: spicule and poorly developed gubernaculum present; cloacal region raised as distinct cone; two pairs of papillae borne on cloacal cone; no caudal alae; pair of rosette papillae on tail, frequently arising from a common base.

TYPE SPECIES: *Parathelandros mastigurus* Baylis, 1930.

OTHER SPECIES: *P. australiensis* (Johnston & Simpson, 1942); *P. limnodynastes* (Johnston & Mawson, 1942); *P. maini* sp. nov.; *P. carinae* sp. nov.; *P. johnstoni* sp. nov.; *P. propinqua* (Johnston & Simpson, 1942).

HOSTS AND GEOGRAPHICAL DISTRIBUTION: Amphibia in Australia.

SKRJABINODON gen. nov.

Oxyuridae : Pharyngodoninae: mouth opening bounded by three (?) bilobed lips; no onchia at anterior end of oesophagus (?); lateral alae on both sexes frequently very narrow particularly in females; excretory pore and vulva generally about level of posterior end of oesophagus; tail terminates in long spike, in both sexes, frequently with barbs on female terminal spike; Male: spicule sometimes lacking; cloacal region raised as narrow elongate cone; two pairs of cloacal papillae which do not lie on cone; no caudal alae; one pair of post-cloacal papillae which frequently lie close to cloacal papillae; post-cloacal papillae not rosette and very prominent.

TYPE SPECIES: *Pharyngodon mabuyae* Sandground, 1936.

OTHER SPECIES: *S. anolis* (Chitwood, 1934); *S. apapillosus* (Koo, 1938); *S. mabuiensis* (Malan, 1939); *S. megalocerca* (Skrjabin, 1916); *S. oedurae* (Johnston & Mawson, 1947); *S. scelopori* (Caballero, 1938).

HOSTS AND GEOGRAPHICAL DISTRIBUTION: Reptiles in most regions of the world.

MEASUREMENTS FOR *PARATHELANDROS* SPECIES

These measurements are only intended to be indicative of the general range of size encountered. Many of the specimens were contracted, as is only natural with animals which depend upon an internal hydrostatic pressure to retain their shape, and most identification was carried out on morphological characters. All measurements are in mm., and in females the distance of the vulva only from the anterior end of the body is listed in some species where this is virtually the same as the distance of the excretory pore.

Parathelandros mastigurus

MALES. Body length: 1·36; 1·41; 1·43; 1·56. Body breadth: 0·094; 0·100; 0·098; 0·103. Oesophagus length: 0·26; 0·22; 0·26; 0·19. Distance of excretory pore from anterior end of body: 0·24; 0·19; 0·25; 0·16. Length of tail: 0·35; 0·33; 0·27 (broken at tip); 0·34. Length of spicule: 0·070; 0·069; 0·066; 0·070.

FEMALES. Body length: 3·38; 3·63; 3·67; 3·79. Body breadth: 0·32; 0·29; 0·30; 0·33. Oesophagus length: 0·51; 0·47; 0·50; 0·52. Distance of vulva from anterior end of body: 0·25; 0·21; 0·24; 0·25. Length of tail: 1·09; 0·91; 1·11; 1·12. Size of eggs: 0·139 × 0·043 and 0·132 × 0·041 (representative).

Parathelandros australiensis

MALES. Body length: 1·46; 1·76; 1·76. Body breadth: 0·15; 0·17; 0·18. Oesophagus length: 0·21; 0·22; 0·21. Distance of excretory pore from anterior end of body: 0·26; 0·30; 0·29. Length of tail: 0·53; 0·57; 0·59. Length of spicule: 0·031; 0·033; 0·030. Breadth of lateral alae: 0·046; 0·040; 0·046.

FEMALES. Body length: 5·12; 5·24; 5·33. Body breadth: 0·33, 0·34; 0·34. Oesophagus length: 0·37; 0·39; 0·42. Distance of vulva from anterior end of body: 0·43; 0·46; 0·49. Length of tail: 1·19; 1·26; 1·26. Size of eggs: 0·139 × 0·040 and 0·133 × 0·038 (representative).

Parathelandros limnodynastes

MALES. Body length: 2·04; 2·16; 2·19; 2·31; 2·38; 2·40. Body breadth: 0·23; 0·21; 0·23; 0·26; 0·27; 0·22. Oesophagus length: 0·35; 0·33; 0·33; 0·33; 0·34; 0·31. Distance of excretory pore from anterior end of body: 0·57; 0·43; 0·49; 0·55; 0·56; 0·61. Length of tail: 0·78; 0·62; 0·73; 0·82; 0·69; 0·66. Length of spicule: 0·084; 0·081; 0·074; 0·073; 0·083; 0·082.

FEMALES. Body length: 3·20; 3·32; 3·39; 3·42; 3·51; 4·29; 4·31. Body breadth: 0·31; 0·27; 0·31; 0·30; 0·31; 0·46; 0·42. Oesphagus length: 0·49; 0·53; 0·49; 0·52; 0·51; 0·57; 0·56. Distance of vulva from anterior end of body: 0·62; 0·73; 0·64; 0·67; 0·83; 0·63; 0·67. Length of tail: 0·53; 0·65; 0·57; 0·56; 0·59; 0·69; 0·78. Size of eggs: 0·102 × 0·036, 0·104 × 0·041 and 0·079 × 0·030 (representative).

Parathelandros johnstoni

MALES. Body length: 1·21; 1·67; 1·94; 1·99; 2·20; 3·13; 3·17. Body breadth: 0·22; 0·21; 0·19; 0·24; 0·23; 0·23; 0·31; 0·35. Oesophagus length: 0·39; 0·37; 0·36; 0·38; 0·40; 0·43; 0·44; 0·44. Distance of excretory pore from anterior end of body: 0·43; 0·43; 0·45; 0·46; 0·48; 0·51; 0·66; 0·63. Length of tail: 0·72; 0·66; 0·67; 0·65; 0·69; 0·74; 0·82; 0·83. Length of spicule: 0·063; 0·064; 0·064; 0·065; 0·068; 0·068; 0·078; 0·073. Breadth of lateral alae: 0·039–0·047.

Females. (first four specimens are either immature or early gravid). Body length: 3·91; 3·98; 4·38; 4·47; 4·72; 6·36; 7·20; 7·54; 8·56; 8·97. Body breadth: 0·31; 0·29; 0·35; 0·33; 0·33; 0·38; 0·34; 0·39; 0·46; 0·44. Oesophagus length: 0·64; 0·64; 0·74; 0·62; 0·60; 0·69; 0·66; 0·69; 0·64. Distance of vulva from anterior end of body: 0·99; 0·98; 0·99; 1·09; 0·91; 1·00; 0·93; 1·04; 0·99; 1·17. Length of tail: 0·52; 0·60; 0·62; 0·71; 0·98; 1·24; 1·14; 1·19; 1·34; 1·31. Size of eggs: 0·112 × 0·033 and 0·116 × 0·036 (representative). Breadth of lateral alae: 0·025–0·028.

Parathelandros carinae (N.B. vulva and excretory pore measurements differ)

Males. Body length: 0·91; 1·14; 1·26; 1·38; 1·48; 1·64; 1·92. Body breadth: 0·078; 0·12; 0·13; 0·14; 0·11; 0·12; 0·18. Oesophagus length: 0·25; 0·28; 0·44; 0·33; 0·39; 0·40; 0·45. Distance of excretory pore from anterior end of body: 0·28; 0·35; 0·52; 0·39; 0·49; 0·52; 0·43. Length of tail: 0·22; 0·28; 0·27; 0·26; 0·34; 0·34; 0·33. Length of spicule: 0·073; 0·096; 0·094; 0·095; 0·072; 0·073; 0·089.

Females. Body length: 2·17; 2·22; 3·89; 4·51; 4·94; 7·66; 7·92. Body breadth: 0·21; 0·18; 0·25; 0·29; 0·26; 0·46; 0·43. Oesophagus length: 0·46; 0·42; 0·55; 0·55; 0·53; 0·70; 0·73. Distance of vulva from anterior end of body: 0·85; 0·87; 1·21; 1·12; 1·22; 1·24; 1·12. Distance of excretory pore from anterior end of body: 0·54; 0·54; 0·81; 0·81; 0·94; 0·80; 0·97. Length of tail: 0·55; 0·53; 1·00; 0·97; 1·04; 1·24; 1·48. Size of eggs: 0·152 × 0·046.

Parathelandros maini

Males. Body length: 1·20; 1·52; 1·67; 1·95; 2·07; 2·07. Body breadth: 0·092; 0·13; 0·12; 0·22; 0·24; 0·23. Oesophagus length: 0·26; 0·30; 0·28; 0·30; 0·30; 0·32. Distance of excretory pore from anterior end of body: 0·21; 0·27; 0·24; 0·28; 0·29; 0·26. Length of tail: 0·43; 0·45; 0·49; 0·59; 0·53; 0·55. Length of spicule: none seen; 0·039; none seen; 0·042; 0·054.

Females. Body length: 4·21; 4·41; 4·50; 5·12; 6·63; 7·48. Body breadth: 0·25; 0·29; 0·26; 0·29; 0·44; 0·38. Oesophagus length: 0·52; 0·55; 0·49; 0·55; 0·55; 0·59. Distance of excretory pore from anterior end of body: 0·35; 0·22; 0·31; 0·42; 0·40; 0·45. Distance of vulva from anterior end of body: 0·38; 0·25; 0·35; 0·46; 0·44; 0·48. Length of tail: 0·96; 1·16; 0·98; 0·96; 0·98; 1·07. Size of eggs: 0·135 × 0·046 and 0·122 × 0·040 (representative).

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Thanks are also due to Professor A. R. Main of the Department of Zoology, University of Western Australia for making available to me many of the specimens he had collected during his studies on the frogs of Western Australia; to Mr. Barry Muir of the same Department who collected so many live frogs during my period in Perth; to Professor H. G. Andrewartha, Department of Zoology, University of Adelaide who allowed me to work in his Department on two occasions; and finally I would express my particular appreciation to Mrs. P. M. Thomas of the University of Adelaide who not only looked after me so very well while in Adelaide, but also sent me specimens to study in London after my return from Western Australia.

Parathelandros maini is named in appreciation of the help received from Professor Main; *P. johnstoni* is named for the late Professor T. Harvey Johnston at whose instigation and upon whose encouragement so much of our knowledge of Australian helminths has depended; finally *P. carinae* is named for Miss Carina Wilson, whose father is Curator of Molluscs in the Western Australian Museum, as it was first recognized on the occasion of her sixth birthday.

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ON THE NEOTYPE OF *RADIICEPHALUS ELONGATUS* OSÓRIO WITH REMARKS ON ITS BIOLOGY

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ZOOLOGY Vol. 16 No. 5
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BY

C. M. H. HARRISSON

(National Institute of Oceanography)

AND

G. PALMER

(British Museum, Natural History)

Pp. 185–208: 6 *Text-figures*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 *May,* 1968 *Price Twelve Shillings*

ON THE NEOTYPE OF *RADIICEPHALUS ELONGATUS* OSÓRIO WITH REMARKS ON ITS BIOLOGY

By C. M. H. HARRISSON & G. PALMER

SYNOPSIS

The demonstration that *Radiicephalus elongatus* Osório 1917 does not belong to the Trachipteridae, (to which family it has recently been relegated as *incertae sedis*), is offered in completion of a review of the dealfishes of the Eastern Atlantic and Mediterranean. A need is shown for selecting a neotype for *R. elongatus*, and a male specimen from the same locality as the lost holotype is so designated. (No full description of an adult female exists). Two further specimens, smaller in size, are considered, and notes on the biology and development of the species are offered. *R. elongatus* is tentatively reinstated in Osório's family Radiicephalidae, and the position of this family with reference to the other families of taeniosome allotriognaths is discussed. A full translation of the species description (originally published in Portuguese) is given in an appendix.

INTRODUCTION

A SHIP'S engineer, Senor José da Glória, on his return from a voyage with the Portuguese distant water fleet to the Moroccan shelf, went in Lisbon to the Bocage Museum, taking with him a strange fish 760 mm. long, caught off Salé at 200 m. (110 braças). A published account of the specimen was subsequently produced by Osório (1917) who described it as the only known representative of a wholly new family of dealfishes, the Radiicephalidae, with a single genus and species *Radiicephalus elongatus*. The description appears to have remained without further notice until 46 years later brief reference was made to it as an anomaly " incertae sedis " (Walters 1963*b*), but during a cruise of R.R.S. " Discovery " in 1966, three new specimens were caught: one of 304 mm. S.L. off São Miguel in the Azores, an even smaller example of 154 mm. S.L. close to Fuerteventura, and a third, the largest, of 597 mm. S.L. (692 mm. total length) off Morocco, close to Osório's type locality.

OSÓRIO'S TYPE

In order to understand any apparent discrepancies between Osório's type and the material to be described here, a critical analysis of the case-history of José da Glória's specimen is essential. First, it must be stressed that this specimen has disappeared without trace. We take this opportunity of thanking Professor Saccarão and Senor Luiz Saldanha for their thorough but fruitless searches for it in the Bocage Museum. All the required information must therefore be drawn from the rather brief description which Osório published in Portuguese. Secondly, when Osório first saw it, his specimen was already badly damaged. He thought that the fact that most of the body was quite devoid of scales was " by virtue of the mischances the specimen underwent before it entered the museum " (Osório, p. 113, lines 14, 15). The tail appears to have been incomplete, (as the caudal seemed to have been destroyed), (p. 113, line 24) and ended in " a length of vertebrae almost completely stripped of soft parts " (p. 114, lines 2, 3) with two long rays remaining a certain distance from the tip. The anal fin was represented by only a small " remainder of spines " (p. 113, line 35) which nevertheless seemed to Osório to represent what had been a long fin. The ventrals " should have been thoracic " (p. 113, line 27), but were missing (p. 113, line 35–p. 114, line 1). Even the first ray of the dorsal fin was broken (p. 114 line 24) while the rest of the dorsal lacked any connecting membrane as it had " disappeared, naturally decomposed whilst the specimen was exposed to the air, and perhaps to the sun " (p. 114, lines 26–28).

The impression given is that José da Glória put the specimen carefully aside, but left it dry, and either lying on decking smeared with blood, scales and scraps of offal, or else wrapped in a piece of the sacking used to wipe gutted fishes from the catch prior to salting. Osório's figure shows a rather shrivelled dealfish with a sunken eye, yet considering how difficult it is to keep such material in good condition even with all the facilities of a modern research vessel, the specimen was in a remarkably good state, and must have been well tended aboard the small fishing vessel on its journey back to Lisbon. As will be shown subsequently, the characters of Osório's specimen agree in almost every respect with the new material, but a primary difference we ascribe to handling prior to its arrival in Portugal. Osório believed that his specimen " must have been covered with scales " (p. 144, line 11) even though " in our example it is almost completely devoid of them " (p. 113, line 16), because there were some " though in very small numbers, in the dorsal region near the dorsal fin ". It seems likely, for reasons adduced later (p. 201 this paper), that these scales belonged to other fishes, and having stuck to the specimen as it dried, became inseparably attached to the dessicated fish finally deposited in the Bocage Museum. Alternatively, it is quite possible that the scales in *Radiicephalus* are very delicate and dissolve in formalin, in which case they might have disappeared in the neotype.

DESCRIPTION OF THE 1917 HOLOTYPE

Stripped of such evident reservations, what Osório described (c.f. Appendix) was a long, laterally compressed fish of 760 mm. total length, with a gently curved dorsum. The height of the body contained c.8½ times, the greatest thickness 38 times, in the total length. The head with an oblique profile and a long snout, the mouth a little protracted to lie sub-obliquely, and bearing small, strong, pointed teeth in both jaws. These teeth directed inwards and arranged in two rows with those of the inner row larger than those of the outer in either jaw. The broad inferior maxillary was striated. Eyes were rather large, their diameter 3 times in the length of the head. There were 4 gill arches, and pseudobranchs were present. The operculum, suboperculum and interoperculum were striated (like the maxilla). The lateral line began above the orbit at more than ⅔ the maximum body height, and sloped gradually towards the ventral profile which it reached " just beyond the anus, without having shown any curvature along its length. The anus was situated at about ⅔ of the total length measured from the snout ". The skin was covered with rounded silvery bodies resembling pinheads, the silvering confined to linear areas and forming a pattern, like bricks in a wall, especially visible in the abdominal region. A long dorsal fin commencing just behind a vertical drawn through the anterior border of the orbit ended well before the tail. The first few rays were the longest and were very long and thin, shorter rays followed and the rays numbered about 159 in total. The pectorals were small, set close to the angle of the opercular flap and contained c.9 rays. The ventrals were absent or missing, but a thoracic base was present. The anal fin was represented by a few rays. The tail ended in a filament borne by two rays originating on a preterminal vertebra.

From this critical appraisal and condensed summary of Osório's original diagnosis one may turn to the new material which shows virtually all but one of the features listed in the above paragraph, and allows, in addition, observation of details not visible in the damaged specimen which is now lost. It is therefore considered necessary to select a neotype of *Radiicephalus elongatus* Osório. The specimen chosen is the largest individual taken by " Discovery " and a description of it is followed by an amplified definition of the family Radiicephalidae and the genus *Radiicephalus*, using the two smaller " Discovery " specimens as evidence for such variation, (in meristic and other characters), as occurs within the species and during the course of development.

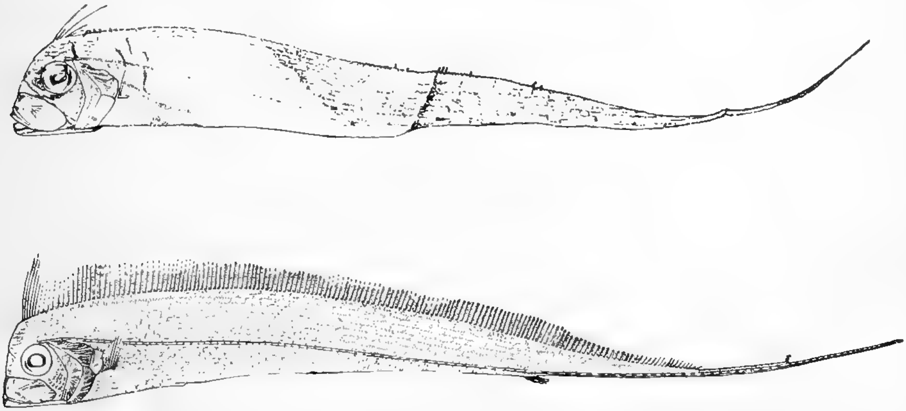

FIG. 1. The holotype of *Radiicephalus elongatus* (above) 760 mm. T.L. (after Osório, 1917) compared with the 1966 " Discovery " neotype (below) 692 mm. T.L. The course of the postcleithra in the holotype is held to be shown by the curved shadow bending towards the ventral profile (c.f. with the neotype, Fig. 2).

THE NEOTYPE OF *RADIICEPHALUS ELONGATUS* OSÓRIO

In accordance with the International Code of Zoological Nomenclature 74–75 (1964), adopted by the XV International Congress of Zoology, a neotype may be designated only if the holotype is lost or destroyed, and no lectotypes or syntypes exist. This is the case with *R. elongatus*. The present paper is offered in completion of revisionary work (Palmer, 1961) on the dealfishes of the Mediterranean and Northeast Atlantic, and the proposition of a neotype is considered necessary in the interests of stability of nomenclature, as it will avoid the proliferation of names for material demonstrably belonging to a single species, and prevent future confusion involving the identity of any other members of the same family that may subsequently be discovered. The neotype of *R. elongatus* has been deposited in the British Museum (Natural History) London, registration number: 1967.10.2.1.

The specimen of 692 mm. T.L. (597 mm. S.L.) was taken off the Moroccan coast with an Engel's trawl (Harrisson 1967) fished between 570 and 0 m. on November 17th, 1966 at a position, 34° 17·3′ N, 8° 00′ W, (Table 2) very close to where the holotype was caught. Its general shape (Text-fig. 1) is a tapered triangle broad at the head and narrowing to a thin caudal filament. The dorsum is gently curved, and the body is laterally compressed. The maximum dorsoventral " height " (depth) of the body is contained 8·9 times in the total length, and its maximum thickness nearly 41 times.

The head and the body closely resemble Osório's specimen (see Text-fig. 1.) The dentition consists of a single row of retrorse premaxillary teeth, and in the lower jaw a symphysial tooth is followed on either side by two rows of teeth bordering the mouth, each formed of four small pointed teeth, those of the inner row being slightly larger than those of the outer in either jaw. There is a large striated maxilla, and the premaxilla has an anterior process reaching more than $\frac{4}{5}$ the way up the frontal profile. The jaws are protrusile. The eye is contained 3·4 times in the head length, with an orbital diameter of 26 mm. The lens fully fills and slightly protrudes from the pupillary aperture. The iris is silvered presumably with guanine. X-radiographs taken at 20 KV with an exposure of some 1,200 m.a.s. show a faint streak running obliquely across the orbit towards a pale semilunar patch at the posteroventral margin of the orbit (see Text-fig. 2.). These streaks are assumed to be the 4 rectus muscles of the eye running down towards the posterior myodome, represented by the pale patch, and the bar dividing this from the main area of the orbit would then constitute the basisphenoid bar separating the apertures of the muscle canals of the two sides of the head. The nasal capsule lying anterior to the orbit appears to have a single round aperture.

There are four gill arches, and pseudobranchs are present. The gill rakers are longish, tooth-bearing papillae, those of the first arch numbering $2+0+7-8$. The lower part of the hyoid arch consists of a reflexed interhyal nearly as long as the following rather short epihyal, which bears 4 branchiostegal rays. The ceratohyal is elongate, with a narrow anterior shank carrying two more branchiostegals. The preoperculum, operculum, suboperculum and interoperculum are striated (like the maxilla). The suboperculum has a pectinate postero-dorsal border. An elongate, pallid, cylindrical body marked with brown protrudes from beneath the opercular flap of the left side, and probably represents a copepod parasite (possibly related to *Cardiodectes*) with its anterior head processes in, or close to, the ventral aorta.

The pectoral girdle is seen in the x-radiographs to consist of flattened cleithra, like tilted hockey sticks, bearing posteriorly a pair of very long slender postcleithra (running above and just beyond the pelvics) and the ventrally directed pistol-shaped scapulocoracoids, with the horizontally set pectoral fins borne on the upper borders of the scapulae.

The lateral line canal of the body begins above the operculum and slopes down towards the ventral profile which it closely approaches in the region of the anal fin. It continues beyond the vertebral column, where the canals of either side are closely joined, flattened, and form the major part of a long caudal filament supported by some 7 very elongate dermotrichia of the lower caudal lobe and receiving additional strength basally from some of the long haemal spines of the first few preural vertebrae anterior to the fifth (using the terminology of Nybelin, 1963). One hundred and twelve tubular scale elements were counted in the canal wall of the left flank, 92 along the body and 20 in the caudal filament. The posterior elements are longer than the anterior ones, but become shorter again in the caudal filament as one approaches the smoothly rounded tip. The canal scales are smooth but more posteriorly they bear spots of dark pigment. The lateral line canals of the head are not visible superficially. Traces in radiographs with the diameter of the body canal suggest supra- and suborbital systems extending respectively to just above and below the nasal capsule. Scales, other than the tube elements of the lateral line, are absent.

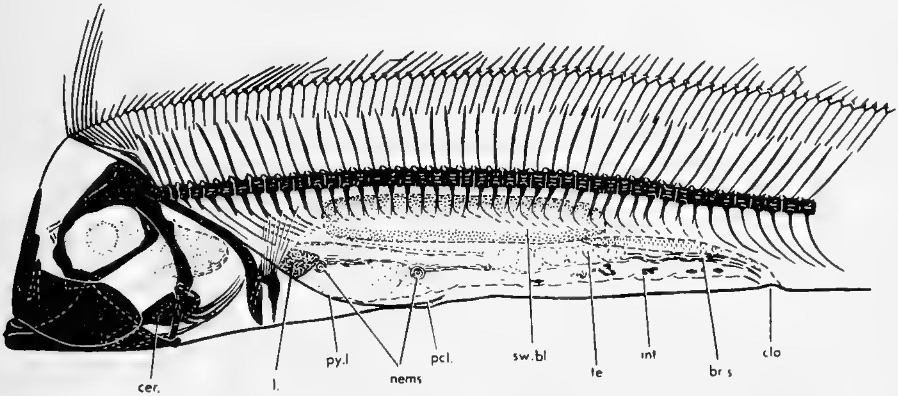

FIG. 2. Internal anatomy of the neotype of *R. elongatus* Osorio. Details visible from x-radiographs are shown in solid black, those seen externally or in dissection are stippled or shaded. The figure is semi-diagrammatic, particularly in the details of the hyomandibular arch. The posterior ribs are represented as truncated to avoid obscuring the soft anatomy of the body cavity. *cer.* = ceratohyal; l. = liver; *p. cl.* = postcleithrum; *nems.* = nematode cysts in gut mesentery; *py.* l. = pyloric loop; *sw. bl.* = swim bladder; *te.* = testis; *int.* = intestine with faecal material visible in x-radiographs; *br. s.* = brown sac; *clo.* = cloaca.

The anus is situated at the level of the 44th vertebra, opposite dorsal ray no. 70, 2·8 head lengths along the body from the snout, and opens into a cloaca that receives the urinogenital ducts and the opening of a brown sac. This sac appears to be an unpaired median structure. Dissection of the left side of the neotype showed that the sac extended forward, between the gonads, and was suspended by a mesentary below presumed kidney tissue, to the level of the 31st vertebra. The gonads were

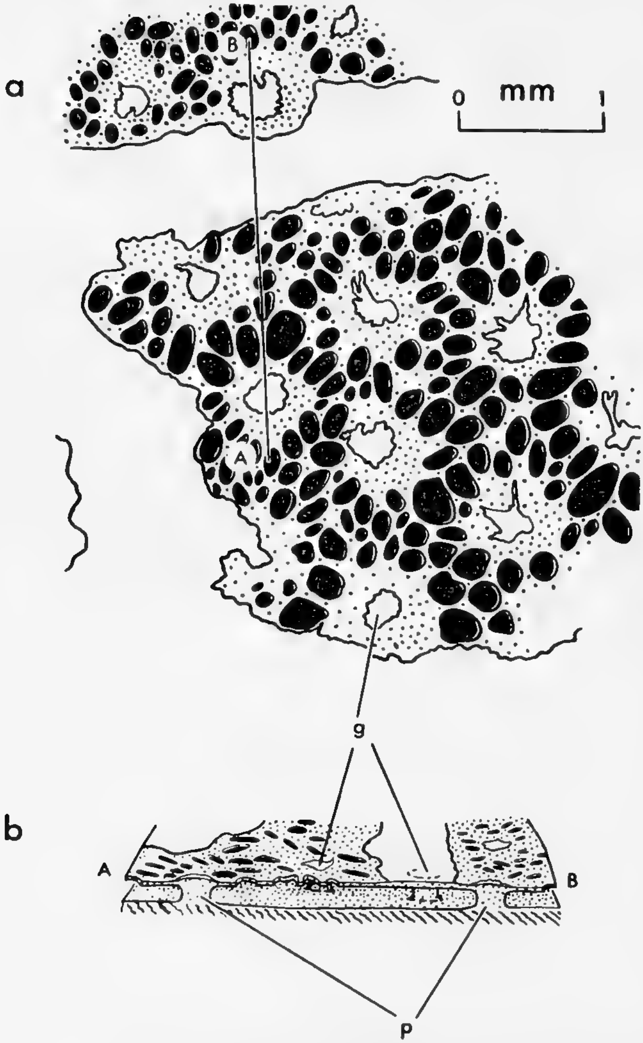

FIG. 3. Skin from the flank of the neotype, in an area just below the lateral line and behind the pectoral fin. a. Surface view with pores shown in black, skin stippled and areas with guanine silvering left white. b. Diagrammatic section along the line A–B (in fig. 3a). *g.* = guanine patches; *p.* = papillae.

well developed, showing the neotype to be a male, and suspensory filaments reached forward to the anterior end of an elongate and well developed swim-bladder with a silvery wall, probably invested with guanophores. This bladder extends from the level of the 14th vertebra to the end of the 33rd centrum (see Text-fig. 2). It is closely appressed to the broad parapophyses and limited laterally by the fine pleural ribs in the wall of the peritoneum. An orange lobe of liver extends beyond the level of the postcleithrum to near the vertical from the anterior margin of the swimbladder. The gut consists of a sac-like stomach with a reflexed pyloric section without caeca.

The skin has a guanine layer with, beneath it, a mesh punctured with elliptical pores radiating from mushroom shaped papillae which support the poreweb from the basal dermis (Text-fig. 3). As the guanine is developed along lines forming a parallelogram brickwork-pattern, in the unsilvered " brick areas " the pores are exposed, and appear to connect the exterior with a dermal space interrupted only by the bases of the papillae. Drops of aniline blue dye passed freely from one area to those around it. (It must be remembered that if in the fresh animal this space was filled with a mucopolysaccharide jelly, this could be lost during fixation in formalin). The heads of the papillae bear a guanine spot which makes them look like silver pinheads in the skin. Where the silvered lines on the skin are damaged, the tops of the underlying papillae remain, and resemble further pinheads.

The fins include a long dorsal of 156 rays, pectoral fins with a short upper splint and 9 rays, ventrals with (only the bases of) c.9 rays, an anal fin with 7 rays, and a caudal with 4 short rays in an upper section (see Text-fig. 4) and a lower filament bearing the continuation of the body lateral-line canals, containing 7 rays (as far as could be ascertained from radiographs). The dorsal fin commences at a vertical drawn through the anterior border of the orbit. Eight rays articulate with pterygiophores associated with a Y-shaped bone connected with the forwardly directed neural spine of the 1st vertebra. The Y-bone itself seems formed by the fused two first interneurals and bears 2 rays distally. These 10 anterior rays are slender and form a nuchal crest. Rags of epithelium borne terminally on the posterior borders of some of them, suggest that in life they may be "flagged" (like the pennant rays of the nuchal crest in *Regalecus*). The neural spines of vertebrae 1 to 101 have pterygiophores associated with them, some spines (apart from the first) carry one (posteriorly), others have two interneurals, before and behind them. The pectorals are set close below the angle of the operculum, just above the juncture between the suboperculum and the interoperculum. The ventrals appear to lie directly below the tips of the postcleithra, at the level of the 21st vertebra, and are thus more nearly abdominal than thoracic. The anal fin is borne by interhaemals associated with the haemal spines of vertebrae 72–75, a considerable distance (0·7 of a head's length) caudad from the external opening of the cloaca. It is difficult to interpret the structure of the caudal (Text-fig. 4). The neotype is the only specimen with all the tail present. It is already very slender at the caudal peduncle, and tapers further into the caudal filament. The caudal cockade appears to be borne on a terminal plate (c.f. *Stylephorus*). It is assumed that the ural vertebrae have fused together in a terminal complex. The preceding centrum bears a neural arch and is therefore presumed to be a preural element. As it bears two rays ventrally it may represent the fusion of preurals 1 and 2. The preceding element may likewise be equivalent to preurals 3 and 4. The element bearing the last well developed haemal spine would then be designated the fifth preural.

The axial skeleton is composed of 118 vertebrae and the terminal element, discussed above. The centra composing it consist of 4 short discs behind the skull followed by a series remarkably constant in length. The 6th vertebra is 4·8 mm. long anteroposteriorly, and the antepenultimate vertebra is longer (5·5 mm.) by just less than one millimetre.

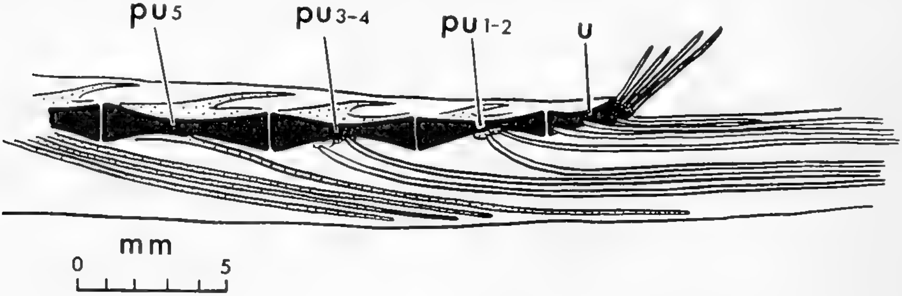

Fig. 4. Diagram of the caudal structure in the neotype of *R. elongatus*, drawn from soft x-radiographs. Paired caudal rays white, unpaired median structures black. The overlying lateral line canals are omitted. Standard lengths quoted in the text are taken to the insertion of the posteriormost ray of the upper part of the caudal. Total lengths are taken to the tip of the lower filament. *PU* 1–5 = pre-ural centra; *U* = ural complex.

The first 25 centra bear neural arches inclined anteriorly, the 27th neural arch and all the arches on the more posterior centra are directed backwards. There are well developed pre- and postzygapophyses on vertebrae 4–95 though the prezygapophyses are stronger in the more posterior part of the caudal region. There are well developed blade-like parapophyses which appear to be fused to the centra, and are present on the 3rd–39th vertebrae. The parapophyses on centra 4–16 point backwards and down, those on centra 21–39 forwards and down. There are long slender pleural ribs borne by the parapophyses of vertebrae 4–39. The first haemal spine is carried on the 40th centrum, the last on centrum 116.

Having presented an extract of the characters visible in the type and the new specimen one may now weigh the evidence for their conspecific identity. Much of the matter may be best displayed in tabular form. Further information about development and biology can then be drawn from an examination of the two smaller " Discovery " specimens. Finally the position of the family may be examined in relation to the other taeniosome fishes known to science, and distinguishing characters can then be set out in the manner of a formal diagnosis.

THE CONSPECIFICITY OF THE LARGEST "DISCOVERY" SPECIMEN WITH OSÓRIO'S TYPE

Both from the descriptions and from the figures (Text-fig. 1) it will be clear that the " Discovery " specimen is very like Osório's fish. A summary of similarities is drawn up in Table 1. Further marked resemblances will be seen between even the minute details of bone sculpture of the maxilla and opercular bones as figured by Osório and the pattern seen in the present individual. The shape, the colour pattern, the " pinheads " of the skin, the teeth, gill arches and such meristic details as are available all correspond closely. Although Osório believed he could make out truly thoracic bases for the ventrals, his figure (Text-fig. 1, above) shows the course of the postcleithra to have been identical with that in the neotype. There remains but one difficulty, as stated above.

Osório, (on his p. 114, line 22) says " the anus is situated at approximately two thirds of the total length measured from the head ". In the " Discovery " specimen the anus lies at about $\frac{1}{3}$ the total length from the head.

Osório's specimen was the larger, and one might imagine an allometric shift back of the anus, were there not good evidence to the contrary (see p. 196). If, though, one takes into account Osório's remarks about the damaged caudal region, and the fact that the anal fin was so battered that it was impossible, from what remained, to tell whether it had been a long or a short fin (p. 113), then it seems more likely that either partial evisceration had made it hard to judge just where the anus came or that, dried and wrinkled, the position of the anus was as hard to determine as in Günther's *Lophotes fiski* (Günther 1890, p. 246). In such an event it might have been reasonable to suppose it lay just in front of the anal fin.

If one assumes that this is indeed what Osório supposed, then the proportions for the position of the anal fin are in good accord for both specimens (Column 10, Table 1). In fact the anus of the original type specimen, before it was damaged, probably lay well in advance of the anal fin just as in the " Discovery " specimen. In that case one should read " anal fin ", not " anus " in the appropriate passage cited from Osório's description. As all the other characters ot the two fish agree so well, this seems a reasonable assumption to make and it may then be allowed that the second specimen, caught after a lapse of nearly half a century, is in fact conspecific with the first one taken off Salé.

THE DEVELOPMENT, DISTRIBUTION AND BIOLOGY OF *RADIICEPHALUS ELONGATUS* OSÓRIO

One may now turn to the two smaller specimens collected by R.R.S. " Discovery " in 1966. The position of their capture is shown in Text-fig. 6, and details for comparison with the features seen in the neotype are summarized in Table 2. Like the larger neotype, both of the smaller individuals had a well developed gas-filled swimbladder identifiable in radiographs. Dissection of the medium sized specimen was expertly done by Dr. N. B. Marshall who found a ventral blood supply passing to 7 unipolar retia on either side, each rete c.2 mm. long being associated with a separate pad of the gas gland (Text-fig. 5). These specimens, too, possessed ribs. Where the skin was undamaged the colour pattern was similar, the dentition agreed, so did the structure of the cloaca, while the uniformity of the meristic features detailed in Table 2 is, likewise, most apparent. Some minor differences and supplementary observations from both the additional individuals allow one to construct a fuller picture of the biology and development of the species, while further suggestions are offered about its geographical distribution together with its vertical range in the Atlantic Ocean.

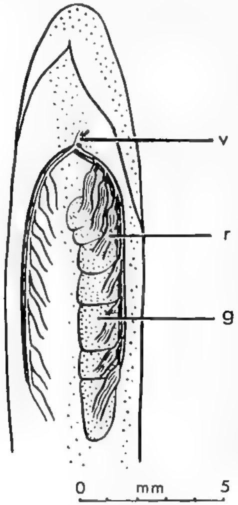

FIG. 5. Diagram of the inside of the swimbladder in the medium-sized " Discovery " specimen of *R. elongatus*, after a drawing by N. B. Marshall. Only the retia and gas-gland pads of the right side are shown in detail. *r.* = retia; *g.* = gas gland; *v.* = vascular system.

The figures for body proportions, Table 2 (Column 3), suggest a decrease in body depth relative to standard length, a common feature in fishes where the myotomes become folded progressively from the originally flat sheets in the larva. The same table (Column 9) shows that the position of the cloaca remains unchanged during growth from a small postlarva to a relatively large and mature fish: in the smallest specimen it was located beneath the 44th vertebra (counted from the head) just as in the large neotype, while in both the neotype and the medium sized specimen the cloaca lay beneath the 5th vertebra that bore a haemal arch.

There is no evidence for a significant alteration in the size of the eye relative to the head during growth, but the available figures suggest a reduction in head size relative to the body length in the transition from post-larva to juvenile. A marked change which may also be assumed to occur at this time involves the ventral fins. In the smallest specimen they are composed of long slender rays nearly a quarter of the fish's standard length, yet in the juvenile and the neotype there are only rudimentary skin-covered stubs, so there seems to be an almost total loss of the ventral fins during development. The position of the pelvic bases on the body appears to remain constant, abdominal, and close to the tips of the postcleithra.

Round blobs visible in the x-radiographs of the medium sized individual from São Miguel were juxtaposed to incomplete, lightly ossified lengths of fish vertebral columns. Dissection yielded the remains of at least three small fishes, and the otoliths with round borders carrying a single notch (for the point where the saccular nerve supplies the macula) resemble those of either a species of sternoptychid or some lantern fish. For fishes of comparable sizes the sagittal otoliths are generally larger in lantern fishes, so that from the size of those in the *Radiicephalus* stomach and from the other bones in the stomach contents, it seems most likely that the blob-shaped otoliths belong to a lantern fish of the genus *Lampanyctus*. The advanced state of digestion strongly suggests these myctophids are natural prey, and not chance specimens swallowed in the trawl-bag as the catch was brought in. The damaged state of the specimen when brought aboard also reduces the likelihood that feeding occurred subsequent to capture.

It may, then, be assumed that small lantern fishes form part of the natural diet of *Radiicephalus elongatus*. The large eyes suggest that it hunts by sight, aided also by the well-developed lateral line, and as the captures were made at depths of less than 700 m., that is, shallower than the daytime occurrence of *Lampanyctus* species in the area (Harrisson 1967 and in press), then it seems probable that predation either occurs by night, possibly when the lantern fishes produce bioluminescent display, or during dusk and dawn vertical migrations of the myctophids through the layer which *R. elongatus* normally inhabits.

Text-figure 6, which shows the sites of capture of the *Radiicephalus* specimens, also includes, tentatively, data for some taeniosomes taken on a cruise of the S.S. " Walther Herwig " which Dr. G. Krefft (in litt.) suggests may represent six further individuals of *R. elongatus*. If this surmise is correct, then the depth distribution would appear to be centred on the upper mesopelagic zone. Five out of six specimens from night time hauls came from depths less than 400 m. and three of these were taken in depths of less than 330 m. The sixth was from somewhere between 600 m. and the surface. The geographical range of the species stretches nearly the full length of the eastern basin of the North Atlantic.

Having thus considered what information is currently available on the anatomy and biology of *Radiicephalus*, the data can be compared with features of the structure and behaviour of the other taeniosomes in an attempt to assess the status of Osório's family Radiicephalidae.

THE STATUS OF THE FAMILY RADIICEPHALIDAE

The rediscovery of material of *Radiicephalus* poses almost as many problems as it provides hints about the relationships within the taeniosome allotriognaths (Regan, 1907). Currently, Regan's group may be said to include the Trachipteridae with three genera and of the order of ten species, (most of them in *Trachipterus*), the Lophotidae with two genera and three species, the Regalecidae with two genera and two or more species, and the Stylephoridae with at least two species in a single genus. The question to be answered is whether the genus *Radiicephalus* shows a sufficient number of unique features to be retained in the separate family erected by Osório. A proper appraisal can only be made by taking into consideration such features as development, biology, feeding, digestive physiology and swimming behaviour if

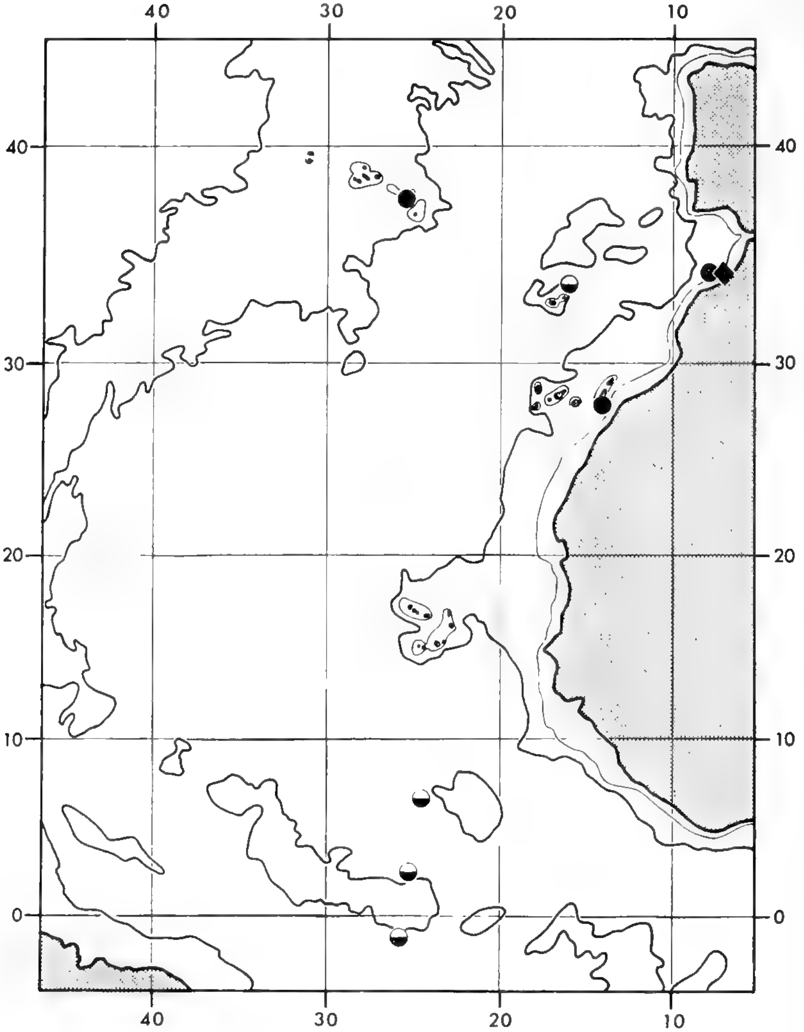

Fig. 6. Map of the central region of the eastern basin of the North Atlantic, showing stations at which specimens of *R. elongatus* are supposed to have been taken.

◆ = 1917 holotype which coincides with the solid disc indicating the collection position of the " Discovery " neotype.

● = the two smaller " Discovery " specimens.

◒ = " Walter Herwig " stations for unsorted taeniosome material believed to be *R. elongatus* (Krefft in litt.).

Shaded areas indicate land. 100 and 2,000 fm. contours are shown.

structural features are to be given their appropriate relative importance. As comparatively little is known about any one family of taeniosomes, such conclusions as are drawn at present must remain but partially satisfactory guesses. Dealfishes have seldom been caught by past oceanographic expeditions, and only the use of giant trawls appears to be accelerating the rate at which new species are being found. The material in older collections largely represents specimens washed ashore, or else taken accidentally in large commercial set-nets or by line-fishing.

Regan's Allotriognathi includes a range of brightly coloured fishes with many features oddly intermediate between " berycoids " and percomorphs. The Opah is blue and red with white spots, *Velifer hypselopterus* is green, and many taeniosomes have silver bodies with red fins. Oddities in structure and colour may be used together in the light of recent work to orientate features noted in *Radiicephalus*.

Walters (1963*b*) decided that there was no criterion to distinguish the Radiicephalidae from the Trachipteridae. A closer reading of Osório's paper shows that *Radiicephalus* has an anal fin. The additional information offered above indicates that other differences are to be found in the presence of a well developed gas-filled swimbladder, ribs, the possession of a sac filled with a brown fluid, and a higher number of vertebrae in *Radiicephalus* as compared with *Trachipterus*, *Zu*, or *Desmodema*.

Further clarification may be obtained from a developmental feature noted by Parker (1886); Meek (1890). In regalecids and trachipterids, the posterior caudal centra became 2–5 times longer than anterior centra, altering greatly the body proportions and the relative positions of skeletal and soft parts. In the Lophotidae and the Stylephoridae the vertebrae are of nearly identical length along the axial skeleton, throughout the life history. *Radiicephalus* resembles the latter group, all its vertebrae are of almost the same length. Like *Stylephorus* it has a caudal filament carrying back the lateral line canals beyond the vertebral column, but unlike *Stylephorus* the eyes are directed laterally, and the anterior crest borne by a Y-shaped bone connected to the 1st neural arch prevents the head being thrown back. Also, the neural spines in *Radiicephalus* are strong, the body shape flattened, rather than sub-cylindrical.

From this it is clear that *Stylephorus* has diverged from most taeniosomes. *Radiicephalus* would appear to share more features in common with the Lophotidae, as it has a " brown sac ", an anal fin, a cloaca, smooth lateral line plates, a large swimbladder, strong ribs, and the body pattern an exaggerated form of that seen in *Lophotes*. However, lophotids have an exceptionally long gut with the anus only just anterior to the caudal fin in both *Eumecichthys* and *Lophotes*, while the few haemal spines that are left, crowded in the short caudal zone, are expanded hockey stick like laminae that stiffen the caudal fan to which the anal fin contributes. In *Radiicephalus* the gut is short, with the cloaca only $\frac{1}{3}$ along the total length of the body (Table 1), and there is a large number of normal unexpanded haemal spines. Further, the crest formed by an exaggerated development of the Y-bone, carries the dorsal fin well anterior to the eye in *Lophotes* and by hypertrophy forms an unicorn-like spike in *Eumecichthys*, but is not pronounced in *Radiicephalus* where the dorsal fin begins behind the anterior border of the eye.

Structure thus suggests that *Radiicephalus* lies outside the limits of the other taeniosome families as currently defined. As an interim measure, pending a full review of all the allotriognath fishes, (which is much needed), it seems justifiable to reestablish Osório's family for the single genus and species known at present. The Radiicephalidae could then be defined as laterally compressed taeniosomes with vertebrae of equal length, a gas filled swimbladder, ribs, smooth lateral-line scales, laterally directed eyes, no body-scales, a cloaca (enclosing genital, renal, intestinal and brown-sac apertures) at about $\frac{1}{3}$ along the total length from the snout, and with lateral line canals borne back on a long slender lower caudal filament supported by 7 rays.

One may turn to such conjectures as can reasonably be made about distribution, behaviour and physiology to try to ratify this position. It seems necessary to try to interpret the functional significance of a confusing array of both structures and colours. It is possible, however, that the taeniosomes may be regarded as a series progressively adapting to a deep-sea mode of life. Were this so, one would expect plain silver shallow living species with well ossified skeletons and large swimbladders passing into dusky chocolate forms with reduced skeletons and poorly developed swimbladders, and finally violet or black species with slightly ossified skeletons and, perhaps, telescopic eyes. Such a series could be compared to sequences of genera and species in the gonostomatids, sternoptychids and their relatives among the stomiatoids, or the lantern fishes among iniomes.

This scheme at first sight appears to fit the families of taeniosomes supremely well. *Radiicephalus* is silver with a pale dorsal fin, *Lophotes* (among Lophotids) is also silver but resembles *Regalecus* and certain *Trachipterus* species in having a red dorsal fin. *Radiicephalus* has a large swimbladder in which the 14 short retia resemble those of an upper mesopelagic species, while in *Lophotes*, which also has a well developed swimbladder, the rather longer retia resemble those of a deeper living form, (Marshall, pers. comm.). Some authors (Starks, 1908) report the absence of a swimbladder in *Stylephorus*. The small specimen examined by Marshall (1960, p. 44) had a regressed bladder with one unipolar rete. In at least one large individual of a *Trachipterus* species that has been properly examined, the swimbladder was minute (Palmer, 1961), while dissection of other individuals and several other species showed the swimbladder was further reduced, and absent. In the genus *Regalecus* there is apparently no swimbladder (Gunther, 1891). Apart from predominantly silver-bodied forms, there are *Trachipterus* species which have brown pigment, silvering, and crimson fins (*T. trachyurus* Leapley, 1953), or are black headed (*T. nigrifrons* Smith, 1956). *Desmodema* is chocolate brown, while *Stylephorus* is violet and silver with large telescopic eyes, which have three superimposed layers of retinal rods giving great visual sensitivity combined with binocular acuity of sight (Munk, 1966, p. 32), and reduced ossification, though a small swimbladder is retained in one species at least. The presence or absence of ribs and swimbladder seem correlated. Their absence may be regarded as an economy feature fitting deep-sea existence (cf. Denton and Marshall, 1958).

Probably all taeniosomes live in the mesopelagic zone as defined by Hedgepeth (1957, p. 18) or above it. If *Desmodema*, which is dark-coloured, is in fact a deeper living form by day, then it probably performs considerable vertical migrations. It has been taken by night at depths of less than 50 m. (Krefft in litt.). Fitch (1964, p. 238) suggests vertical migration by *T. fukuzakii* while Sardou (1966, p. 199) reports migration by other *Trachipterus* species without providing the evidence. Smitt (1893, p. 318) and Palmer (1961, p. 342) both cite near surface observations of *Trachipterus*, while Fitch (1964) suggests a broad depth range for *T. altivelis*.

As in other mesopelagic fishes scale reduction appears to have gone hand in hand with a lightening of ossification. *Zu* retains modified cycloid scales. Histological sections of skin from material lent by Dr. G. Krefft showed a thin layer of silvering above and below each scale pocket. This makes it improbable that Osório's dried specimen could have lost its scales yet retained its silvering intact. However, there are reasons for caution in reporting the presence or absence of scales. *Zu cristatus* is possibly the most epipelagic of the family Trachipteridae. Few other taeniosomes appear to have retained scales. Fitch (1964) describes thin scales with two divergent keels in *Desmodema*, but Walters (1963*a*, fig. 1) assumes modified scales which cannot occur in their normal taeniosome position, or the hydrodynamic system he elegantly describes would have the pore apertures inconveniently blocked. Nishimura (1964, p. 127) reports that the scales of *Trachipterus ishikawai* disappear after preservation in formalin. It has been pointed out above (p. 193) that polysaccharide slime may also dissolve during preservation. It then becomes clear that any observations on pores, scales and hydrodynamics, need to be made on very fresh fish. As regards pores, genera of taeniosomes usually assumed to be scaleless, like *Trachipterus* and *Regalecus*, do have the intra-dermal canal system, but the pores are either partially exposed or lie wholly covered by a layer of epidermis with guanine. When this is removed the pores come to lie at the surface. Existence of an exposed pore system thus depends on the whole or partial failure of the guanine layer to develop (see Text-fig. 3), or else upon skin abrasion. The question of pores and swimming dynamics, together with scale formation and degeneration, thus needs further study.

The fact that severe storms coincide with strandings of *Regalecus* (Gunther, 1887, p. 73) suggests that these fishes swim in the upper layers of the ocean. Further, they must frequently approach the surface. During a cruise of R.V. " Atlantis II " in 1964, Mr. P. J. Herring saw two specimens by day off Mozambique, swimming round a water-bottle which was being hauled to the surface. *Regalecus* sp. is apparently commonly taken during trawling operations off the Cape of S. Africa (M. J. Penrith, in litt.). If the ink produced by *Lophotes* (Griffin, 1934, p. 243; Kershaw, 1909, p. 79) really acts as a blind to would-be predators, then fishes of this genus probably live in the photic zone too. The ink's chemical composition is that of a melanin compound, resembling squid ink (Fox, 1957, p. 371), and it seems likely that it serves the same function. The brown sac of *Radiicephalus elongatus* liberated into the preserving alcohol a yellow tint with a maximal light absorption in the ultraviolet. This may probably be compared with Fox's yellow extract from *Lophotes*. Again, King and Ikehara (1956) report that their specimen of *Eumecichthys* was taken at the surface by day. What is intriguing about taeniosome swimming, with reference too to depth distribution, is that Nishimura (1964) has

TABLE I

OSÓRIO'S HOLOTYPE OF *RADIICEPHALUS ELONGATUS*

	1 Shape	2 Colour markings	3 T.L. in mm.	4 Depth in T.L.	5 Head in T.L.	6 Eye in head	7 Teeth
Osório's specimen	Laterally compressed with a gently curved dorsum	Silvery lines forming a brickwork pattern	760	8·5 times	7·6 times	3 times	Sharp in 2 rows, the inner being the larger
" Discovery " specimen	as above	as above	692	8·9 times	7·7 times	3·4 times	as above

COMPARED WITH THE "DISCOVERY" NEOTYPE

8	9	10	11				
Gill arches and pseudobranch	Position of " anus "	No. head lengths from snout of anal fin	Fin Ray counts				
			D.	P.	V.	A.	C.
4 gill arches and a pseudo-branch	at about $\frac{2}{3}$ of total length from snout (5 head lengths)	ca. 5	159	9	bases only	Present. Few rays	Only lower lobe remaining, this forming a slender caudal filament
as above	at about $\frac{1}{3}$ of total length from snout (2·8 head lengths)	4·8	156	9	bases of c. 9 rays	Present. 7 rays	Small upper lobe of 4 rays + lower lobe with ca. 7 rays forming a slender filament

Table II.

MERISTIC AND OTHER CHARACTERS AND PROPORTIONS OF THE THREE

	S.L.	Depth in S.L.	Head length	Head in S.L.	Eye in head	Position of cloaca	No. of vert.	Position of anal fin	Branch. rays	Gill rakers
Neotype	597 mm	8·9 times	90 mm	6·7 times	3·4 times	In approx 1st $\frac{1}{3}$ of body beneath 44th (= 5th caudal) vert. 2·8 head lengths from snout	118 (39+ 79)	407 mm from front of orbit 4·8 head lengths from snout	6	2+ 0+ 7–8 large
Juvenile	304 mm	8·4 times	44 mm	6·8 times	3·5 times	c.f. above. below 41st (= 5th caudal) vert. 2·8 head lengths from snout.	114 (36+ 78)	182 mm from front of orbit 4·13 head lengths from snout	6	2+ 0+ 7 large
Postlarva	154 mm	6·7 times	28 mm	5·5 times	3·4 times	c.f. above. below 44th (= 7th caudal) vert. 2·5 head lengths from snout	114 (37+ 77)	85 mm from front of orbit 3·04 head lengths from snout	6	2+ 0+ 7 large

"DISCOVERY" SPECIMENS OF *RADIICEPHALUS ELONGATUS* OSÓRIO

P.	V.	D.	A.	C.	Discovery Station	Position	Date	Depth m.	Net
9	9 bases only of rays left	156 (ends above the 99th vert.)	7	4+7	6187	34° 17′ N 8° 00′ W (off Morocco)	17 XI 1966	570 –0	EMT
11–12	9 bases of rays only	157	7	4+? (broken)	6117	37° 36′ N 25° 13′ W off São Miguel, Azores	17 X 1966	400 –0	EMT
10	9 rays very long ca. 60 mm long	152	7	?4 with a very long filament	6173	28° 04′ N 14° 04′ W (off Fuerteventura, Canary Islands)	10 XI 1966	725 –0	N113(H)

observed live *Trachipterus* propel themselves by passing ripples along the dorsal fin, in the manner of a *Notopterus* using its anal fin. If those taeniosomes with red fins live chiefly in the zone where blue light predominates, then the red pigment, by blacking out the fin, will eliminate the flicker of scattered light as waves shimmer back and forth along the dorsal during swimming, and so give these species the advantage of concealment both from prey and predators alike.

Information on feeding behaviour in the taeniosomes might yield much of interest. A radiograph of *Zu cristatus* showed it had eaten fish, as did others of *Trachipterus* species (see also Palmer, 1961, p. 348). The type of *Lophotes cristatus* was reported by Johnson (1863) to contain fish and squid remains. Further probing of this specimen has now produced an additional small trichiuroid from the stomach, while in the intestine (which has a backwardly directed valve flap about half way along it) was the beak of a small squid (possibly a small *Architeuthis*). *Radiicephalus elongatus* is, at least in part, piscivorous (see p. 197). For the present the differences in digestive physiology (implied by strongly contrasting differences in gut length) between lophotids and radiicephalids, must remain obscure. *Regalecus* like *Lophotes* has a long gut laid down in the embryo. In *Regalecus*, though, it is the stomach which stretches back, and by far overreaches the anal aperture (Vayssière, 1917). In a small *Regalecus* caught from R.R.S. " Discovery " off Fuerteventura (Canary Isl.) the anus opened at 29% of the standard length measured from the snout, yet the stomach tapered back to a point at 53% along the same length. The short intestine was bent forwards in a pyloric loop bearing very large numbers of caeca, and the greatly elongate stomach was packed along its entire length with small shrimp-like euphausiids.

From this sketchy survey of additional data, *Radiicephalus elongatus*, which has pale fins, appears the least specialized of all the taeniosomes. It does seem to have lost its scales, yet it shares features in common with each of the other families. The axial skeleton, fin structure and colour pattern, show various similarities with stylephorids or lophotids; the body form and the structure of the haemal spines, together with the anterior insertion of the dorsal fin, are of the type seen in trachipterids. The number of pterygiophores forming the nuchal crest, and perhaps, too, the pennanted nature of the first few dorsal rays, are most like these features in regalecids. *Radiicephalus elongatus* likewise appears to be least adapted among the taeniosomes to a fully mesopelagic existence, and has retained a large swimbladder of a type common among epipelagic fishes. Further collection combined with observations on live animals, and a better examination of its histology and anatomy must show whether or not these conclusions are substantially correct.

ACKNOWLEDGMENTS

We should like to thank Dr. Luiz Saldanha for a photocopy of Osório's paper (in addition to his searches for the holotype of *R. elongatus* see p. 187). Mr. G. E. Maul kindly checked the accuracy of our translation of Osório's description (see appendix). Mr. K. Twinn and Miss Joy Smith at Guys Hospital provided a fine series of x-radiographs taken with soft x-rays, and Mr. Arnold Madgwick skilfully made prints and enlargements from these negatives. Miss Pam Verity of the

Nuffield Institute of Comparative Medicine at Regent's Park provided additional x-radiographs of the neotype and of a specimen of *Regalecus*. Dr. G. Krefft supplied us with information about a cruise of the " Walter Herwig " and with material of *Zu cristatus* for an investigation of skin structure. Dr. Bruce Collette, Dr. J. King, Mr. R. Lavenberg, Dr. M. Cohen, Mr. M. Penrith and Dr. J. Fitch either lent material, answered queries by letter, or offered helpful suggestions, as did Dr. V. Walters. We are grateful to all these people who contributed in their different ways to the construction of a difficult paper. Dr. P. H. Greenwood, Dr. N. B. Marshall and Mr. P. M. David have all offered constructive criticism of the text. Dr. N. A. Mackintosh sheltered both authors for varying periods, and we should like to thank him and the other members of the Whale Research Unit of the National Institute of Oceanography for their warmly appreciated hospitality.

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APPENDIX

Translation of Osório's description of Radiicephalidae et. seq.

Family **RADIICEPHALIDAE** Osório

This family, which we propose here, is designed to include a fish whose characters do not allow it to be placed in any of those which until now have been mentioned and proposed by naturalists, past or present.

It is certain that it is close to some which are known, but the fish to which we are going to refer cannot be put into any of those at present accepted.

The families which are close to the one that we have proposed are as follows:–

Lophotidae, Trachipteridae, Stylephoridae, Regalecidae.

The family Trachipteridae is distinguished from ours because the fishes representing it have a strongly compressed body, are almost leaf-like, have no anal, the body is moderately elongated and they have ventral fins.

The family Stylephoridae. The fishes which belong to it have a caudal terminated by an excessively long appendage. They have no anal. The mouth is toothless, etc.

In the family Regalecidae each ventral is represented only by a very long ray, the head is oblong, etc.

In the family Lepidopidae there are no rays on the head, the fishes have a distinct, bifurcate caudal; a spine or scute, or a pair of scutes behind the anal pore; the teeth are lanceolate.

The family Lophotidae, that which our example most resembles, is characterized by the following: the head is produced into a triangular crest above which is a strong and very elongate spine.

The characters that we mention, and which belong to each of the families cited, do not exist in the representative of the family Radiicephalidae which we propose and for that reason distinguish them from ours.

Characters: Body long, compressed, covered with scales, having a definitely triangular shape, the lower side corresponding to abdominal region, being rectilinear and the upper or dorsal surface being slightly curved. Though the body is almost completely destitute of scales (by virtue of the mischances which the specimen underwent before it entered the museum) there exist nevertheless some, though in very small numbers, in the dorsal region near the dorsal fin, and which lead us to affirm that the body was covered with scales.

The head does not show any projecting triangular crest, nor above it is there a strong spine, but there are a certain number of very long rays, thin and flexible which are continuous with other shorter ones which make up the dorsal fin, which stretches the whole length of the back. These spines, however, end before the final portion of the tail.

The tail, which in our example appears to be incomplete, ends in two rays similar to, though thinner than those found on the head. In our example there is no caudal (destroyed?). Ventrals thoracic. Snout long. Teeth strong, pointed, in upper jaw as well as in lower, inwardly directed, in two rows, those of the inner row larger than those of the outer. Branchial arches four, pseudobranchs present.

Genus ***RADIICEPHALUS***

The head slopes obliquely from the frontal region, being furnished on the upper part with several rays. of which the first are the biggest and which are followed by a very long spinous dorsal. Anal long as far as can be judged from the remainder of the spines which can be seen. The ventrals are not present and the pectorals are small. There appears to be no caudal fin. The end our example (rather damaged) is a length of vertebrae almost completely stripped of soft parts; at a certain distance from the tip of the part remaining there are two long rays similar to those to be seen on the head, but more slender. Mouth a little protractile, sub-oblique. Teeth strong and pointed, though small, in both jaws. Four gill arches.

Radiicephalus elongatus n. sp.

(Plate 2, figs. 2, 3, & 4)

The height of the body is contained about 8½ times in the total length and its greatest thickness 38 times in the same length. The skin should be covered with scales, (but in our example it is almost completely destitute of them), especially in the region which remains directly beneath the dorsal fin. They are, however, represented by rounded, silvery, hemi-spherical bodies in the skin comparable to pin-heads, which the scales probably cover. The substance which silvers the bodies to which we allude, appears generally to be arranged in the various regions of the body in lines which form parallelograms built up one on the other reminiscent in their arrangement of bricks in a wall, when seen narrow end on and superimposed; this character is most marked in the abdominal region. The anus is situated at approximately two thirds along the total length measured from the tip of the snout. The profile of the head is oblique and above the brow there begins a series of thin rays of different lengths, (the first which we judge to be the largest is broken in our example), which continue with other smaller rays and form the dorsal. The connecting membrane of these rays has disappeared, naturally decomposed whilst the specimen was exposed to the air and perhaps to the sun. The snout is long, the mouth not very large, horizontal, slightly protractile. Teeth sharp, in two rows, the larger are those of the inner row. The eyes are rather large, their diameter is ⅓ of the length of the head. The operculum, suboperculum and interoperculum are striated. Likewise striated is the lower maxillary which is very broad. The lateral line which begins on the upper part of the orbit at more than ⅔ of the maximum [body] height descends gradually, approaching more and more closely to the ventral surface which it reaches a little beyond the anus, without showing any curvature along its length. The dorsal commences on the frontal region a little behind a vertical drawn from anterior border of the orbit and ends well before the end of the tail; we count about 159 rays in it. We do not know for the reasons already mentioned whether there is a caudal fin. The pectorals are small and set at a short distance from the tip of the angle of the suboperculum. There are no ventrals. The cheeks, like the rest of the body, should be covered with scales.

Total length	760 mm.
Height of body	90 mm.
Breadth	20 mm.
Length of head	110 mm.

D 159—A?—C? P 9 (?).

Caught at Salé on the Morocco coast, at a depth of 110 braças [= 200 m.]. It is probably a fish of not very great depths, like the *Lophotes* species, which according to Günther do not live in the great depths.

A specimen offered to the Bocage Museum by Sr. José da Glória, engineer, distant water fleet.

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LONDON: 1968

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BY

P. H. GREENWOOD

Department of Zoology, British Museum (Natural History)

Pp. 213–273 ; 34 *Text-figures*

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THE OSTEOLOGY AND RELATIONSHIPS OF THE DENTICIPITIDAE, A FAMILY OF CLUPEOMORPH FISHES

By P. H. GREENWOOD

CONTENTS

INTRODUCTION

THE family Denticipitidae was erected by Clausen (1959) for *Denticeps clupeoides*, a a peculiar little herring-like fish which he collected in a few streams in southwest Nigeria. As the name implies, the fishes have small, denticle-like structures on the dermal skull bones, an unusual feature in teleosts. But, the denticipitids show many other peculiar characteristics besides the dermal denticles, and Clausen suggested a number of possible affinities for the family; of these a clupeoid relationship seemed the most probable (Clausen, *op. cit.*).

While Clausen was working on Nigerian material I was puzzling over an unusual fossil fish from presumed Tertiary deposits at Singida, Tanzania (East Africa). With the publication of Clausen's paper, it was immediately apparent that the fossils should be referred to the Denticipitidae. Indeed, the fossils differed only slightly from the extant west african form (Greenwood, 1960).

The fossil denticipitid (*Palaeodenticeps*) did not throw any more light on the phyletic relationships of the family. This question was considered by Rosen, Weitzman, Myers and myself (Greenwood *et al.*, 1966). At that time it became obvious that a detailed study of the Denticipitidae would be necessary to establish its inter- and intragroup relationships. However, from the evidence before us we concluded that the Denticipitidae constitutes a group of subordinal status within the superorder Clupeomorpha.

The present paper is an elaboration of the osteological and some other anatomical studies made in connection with our phyletic review. It is based on a greater number of specimens than were then available, and includes observations on skeletal systems which we could not then examine.

I feel incapable of adequately expressing my gratitude to Dr. Stenholt Clausen who so graciously allowed me to carry out this work on a family in which he has a very great personal interest. The information and specimens he so freely provided have been of inestimable value.

Material and methods. Most of the work is based on three alizarin transparencies prepared from the following specimens:

(i) B.M. (N.H.) reg. no. 1963. 12.11.6., 33 mm. standard length
(ii) B.M. (N.H.) reg. no. 1962. 5.17.7., 35 mm. S.L.
(iii) B.M. (N.H.) reg. no. 1962. 5.17.8., 34 mm. S.L.

Supplementary information was obtained by dissection and from radiographs. All drawings were made with the aid of a camera lucida.

ABBREVIATIONS USED IN FIGURES

A_1; A_2	posterior openings to *recessus lateralis*
AF	articular facet for first vertebra
Aob	antorbital
ART	articular
ASBoc	articular surface on basioccipital
ASEo	articular surface on exoccipital
ASV	articular surface on first vertebra
af	auditory fenestra
ahf	anterior facet for hyomandibula
ang	retroarticular
as	articular surface on the palatine (contacting ethmoid)
B1–3	first to third basibranchials
BH	basihyal
Boc	basioccipital
Bs	basisphenoid
b1–5	branchiostegal rays
C1–4	first to fourth ceratobranchials
C5	fifth ceratobranchial (lower pharyngeal bone)
CH	ceratohyal
Cl	cleithrum
COR	coracoid
cart	cartilage
D	dentary
DIM	dorsal intermuscular bone
DR	distal pectoral radials
Dsp	dermosphenotic
dHH	dorsal hypohyal
dopc	dorsal opening of main preopercular laterosensory canal
E	median ethmoid bloc
E1–4	First to fourth epibranchials
ECT	ectopterygoid
EH	epihyal
ENT	entopterygoid
Ep	epural
Epi	epiotic

EX	extrascapular
Exo	exoccipital
Fbo	oblique frontal bridge
Fbs	parasagittal frontal bridge
FM	*foramen magnum*
FR	" floating " ribs
Fr	frontal
Fri	ridge on frontal
Fro	supraorbital ledge of frontal
Frs	pectoral fin rays
Frt	temporal flange of frontal
f	foramen for internal carotid artery
Gr	groove leading to supraorbital laterosensory area
gasc	groove for anterior semicircular canal
H1–3	first to third hypobranchials
H_1–H_3	first to third hypurals
Hmd	hyomandibula
HS	haemal spine
hsc	horizontal semicircular canal
INF	infundibular foramen
IOP	interoperculum
ihy	interhyal
ioc	opening for infraorbital laterosensory canal into *recessus lateralis*
LE	Lateral ethmoid
LJ	lateral wall of the *pars jugularis*
lopoc	lower opening of the preopercular laterosensory canal
MC	mesocoracoid
ME	mesethmoid
MET	metapterygoid
MS	median septum of basioccipital
Mx	maxilla
mc	Meckel's cartilage
N	nasal
NaU	reduced neural arch of 1st ural vertebra
Nlm	nasal lamina
Obs	orbitosphenoid
OP	operculum
ORL	opening into *recessus lateralis* for preopercular and infraorbital laterosensory canals

OSB	foramen for swimbladder diverticulum
OSBD	opening for swimbladder duct
O and ö	anterior and posterior openings respectively for the horizontal semicircular canal
P	parietal
P1–4	first to fourth infrapharyngobranchials
Pa	parasphenoid
PAL	palatine
PE	*planum ethmoidale*
PF	facet for articulation with the palatine
PG	pelvic girdle
Pmx	premaxilla
POP	preoperculum
POPs	preopercular spine
Pp	pelvic plate
PR	proximal pectoral radials
Pro	prootic
PROB	prootic bulla
Psp	procurrent " spines "
Pter; Ptr	pterotic
Ptm	posttemporal
Pts	pterosphenoid
phf	posterior facet for hyomandibula
poc	opening for preopercular laterosensory canal into *recessus lateralis*
popg	groove on preoperculum leading to main laterosensory canal
Q	quadrate
rFr	pelvic radials
rPp	radial for pelvic plate
SBD	bony eminence surrounding the opening for the swimbladder duct
SC	scapula
So	supraorbital
Soc	supraoccipital
SOP	suboperculum
Sph	autosphenotic
SR	saccular recess
SYM	symplectic
sa	sesamoid articular
tf	temporal foramen

U1–U2	first and second ural vertebrae	vHH	ventral hypohyal
UF	utricular foramen	X	anterior ridge on prootic
UN	uroneural		
uopoc	upper opening to the main preopercular laterosensory canal	1–5	first to fifth infraorbital bones
		1st C	first principal caudal ray
		1st PR	first pleural rib
V	vomer	III	passage for oculomotor nerve
V_1	first vertebra	IX+X	foramen for glossopharyngeal and vagus nerves
VIM	ventral intermuscular bone		

THE OSTEOLOGY OF *DENTICEPS CLUPEOIDES* CLAUSEN, 1959

The Syncranium

An outstanding feature of the skull in denticipitids is the occurrence of odontodes (Ørvig, 1967) on at least part of the exposed surfaces of all dermal bones (see Text-fig. 1; also Clausen, 1959, fig. 1, and Greenwood, 1960, fig. 1, and pl. 2). The odontodes are of different form, varying from long and slender to short and stout variants of a basically conical shape. Their distribution patterns on the bones, and their density, appear to be constant in all the specimens examined. Since most of the frontals lie below and well separated from the skin (see below), the dorsicranium shows a relative absence of odontodes, which are confined to a patch on the temporal region and a prominent line above the eye. The jaws, cheeks and opercular region are densely " toothed " and give the ventral half of the head a decidedly " furred " appearance.

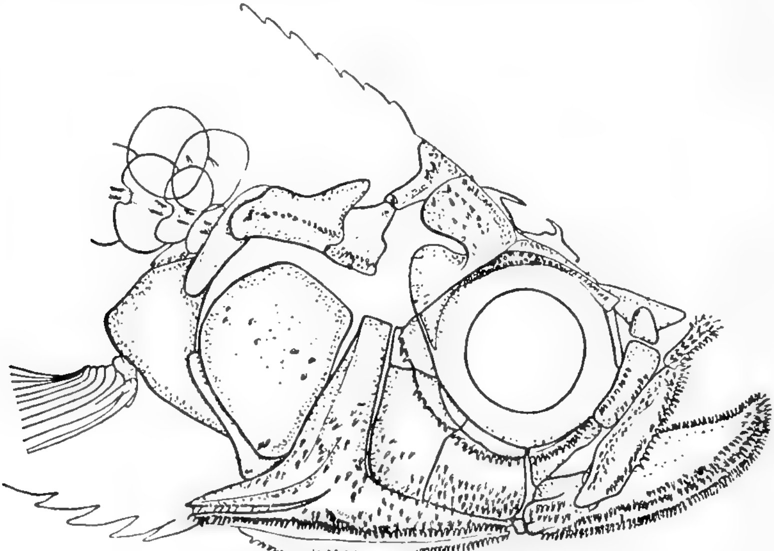

FIG. 1. *Denticeps clupeoides;* syncranium in lateral view to show distribution of odontodes. Modified after Clausen(1959).

Odontodes occur on the extrascapular and posttemporal bones, but are restricted to a single row following the course of the laterosensory tubes. A similar condition is found on the parietal.

The neurocranium of *Denticeps clupeoides* (Text-fig. 6) also has a characteristic appearance, smoothly contoured, and markedly inflated in the otico-occipital region. In dorsal view it has an almost rectangular outline, with a slight narrowing of the anterior half (see Text-fig. 3). The dorsal surface is entire since neither frontal fontanelles nor pre-epiotic fossae are present. The large, gutter-like nasals, together forming a U-shaped structure, lie above the level of the skull roof. The dorsal surface is further broken by the two bony bridges crossing the orbital region of each frontal (Text-figs. 3 and 5). In the transverse plane, the neurocranium is almost circular, its contours broken ventrally by the prominent bulge of the prootic bullae, and the small auditory fenestrae.

Olfactory region. (Text-figs. 2, 3, 5 and 6.) The ethmoid bloc is short, and dominated by its large lateral wings (Text-figs. 2 and 3). Judging from the pattern

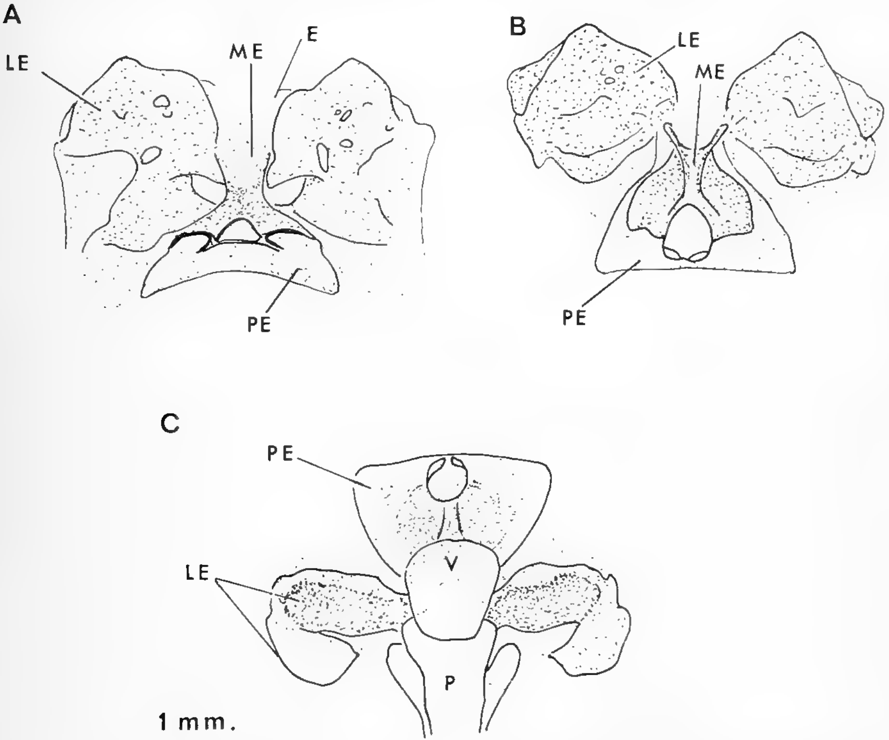

FIG. 2. Ethmoid bloc. (A) Anterior view. (B) Dorsal view, long axis aligned horizontally. (C) Ventral view, the long axis aligned horizontally. The density of alizarin uptake is indicated by the intensity of stippling. For abbreviations, see p. 216.

and intensity of alizarin uptake, the whole region is poorly calcified, and much remains cartilaginous.

The expansive, shield-shaped **lateral ethmoids** (Text-figs. 2 and 3) are probably the most heavily ossified elements, but even here the ventral, wing-like projection on each side is mostly cartilage, as is a large part of the lateral margin of each shield. The lateral ethmoids do not meet in the midline but are separated by a median ethmoid bloc which, in this region, is cartilaginous. There is a deep excavation for the olfactory nerve in the inner margin of each lateral ethmoid.

The **median ethmoid** (Text-fig. 2) is shaped like a broad-based and somewhat waisted pyramid. Anteriorly it is penetrated by a large cardiform foramen which is occluded by the underlying *planum ethmoidale*. This broad, thin sheet of cartilage forms a floor to the nasal capsules, and unites the ventral face of the lateral ethmoids with the median ethmoid bloc. Part of this bloc (especially in the midline) stains deeply and should presumably be identified as the mesethmoid (*sensu* Weitzman, 1967). Dorsally, this ossified region has a small area of contact with the anteromedial part of each lateral ethmoid. The anteromedial face of the palatine barely touches the lateral border of the median ethmoid bloc, which it overlies slightly. At the anterior angle of the bloc, there is a poorly defined facet with which the tip of the maxillary head is in articulation.

The toothless **vomer** (Text-fig. 3) is a very thin sheet of bone, almost circular in outline, and lying well–back from the anterior margin of the ethmoid bloc; thus it is only visible from the ventral side. Its anterior margin barely overlaps the posterior margin of the mesethmoid; posteriorly it overlaps the anterior tip of the parasphenoid.

The **nasals** (Text-figs. 3 and 5) are hook-shaped, gutter-like bones posteriorly contiguous in the midline, but widely separated anteriorly so as to form a U-shaped structure lying above the dorsal skull roof. At their medial point of contact each nasal is weakly attached to the underlying frontal near its anterior margin.

The posterior wall of the nasal, near its point of maximum curvature, is continued posterolaterally as a narrow, curved lamina. The lamina runs backwards at an angle of about 45° to the nasal, curving somewhat laterally to meet the anterior margin of the main frontal bridge (see below). After contacting the bridge and giving off a broad tongue of bone which overlaps it, the lamina curves along the anterior margin of the bridge. In this way the lamina almost completely occludes the anterior opening of the supraorbital laterosensory canal; however, a small open area remains laterally. The broad tongue extends across the width of the bridge, but is completely free from the underlying bone. Likewise, the entire ventral margin of the lamina is free from the underlying frontal. In an alizarin specimen the lamina is readily moveable and spring-like, always returning to its position against the anterior edge of the frontal bridge.

Orbital region. The **frontals** are large bones of rather complex form (see Text-figs. 3, 4, 5, 6 and 7). Above most of the orbit each frontal forms a flat shelf, but medial to this the bone is slightly arched towards the midline. The lateral margin of the supraorbital ledge carries a single row of stout odontodes anteriorly, but a double row posteriorly.

Behind the orbit, and extending ventrally to about the level of the eye's centre, the frontal forms an extensive temporal shield covering a large part of the anterior otic region. This temporal shield is divided horizontally by a deep but narrow indentation extending inwards from the posterior margin (Text-figs. 5 and 6). The upper flange so formed lies in a more superficial plane than the lower one, and overlaps it somewhat. The flanges together delimit the greater part of the temporal foramen; posteriorly, the foramen is without a definite superficial bony margin because the posteroventral tip of the parietal is directed away from this region.

The upper temporal flange carries a fairly dense patch of short and stout odontodes on its lateral face. This area of the frontal was mis-identified as the parietal in Clausen's original description of the species (see Greenwood, 1965).

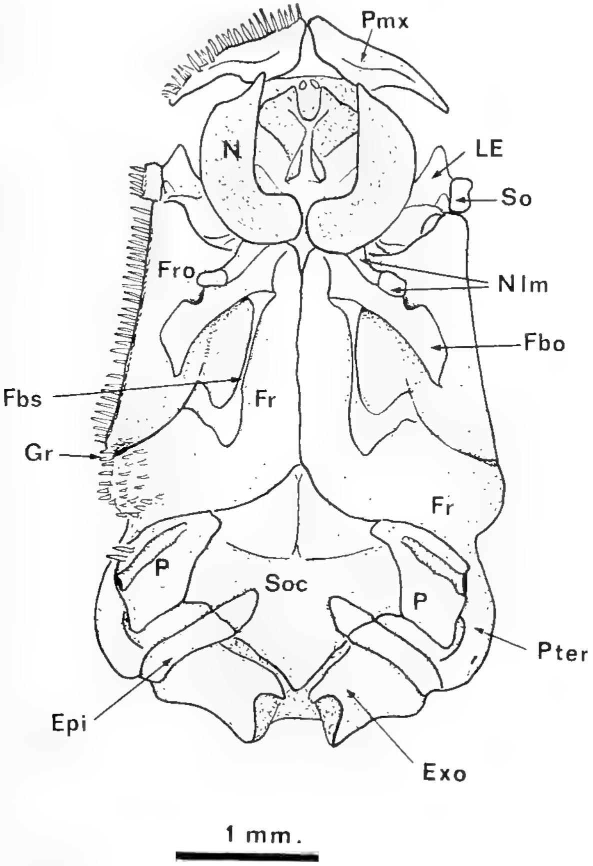

FIG. 3. Neurocranium, dorsal view. Drawn from a different specimen than that used for Figs. 6 and 9.

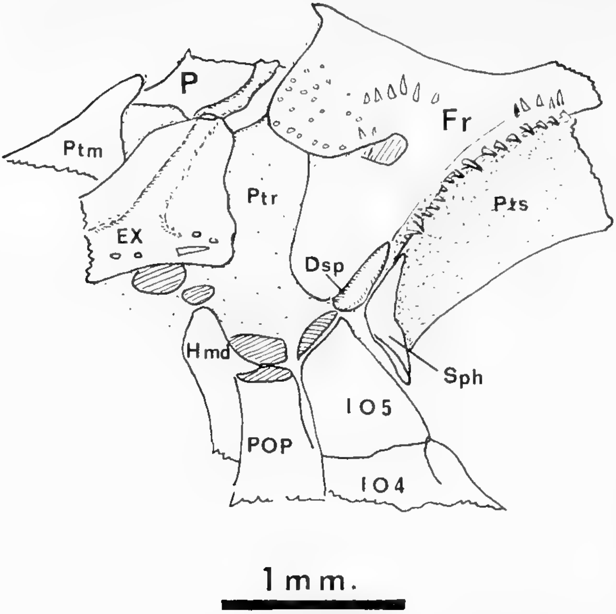

FIG. 4. Temporal region of skull to show dermosphenotic (Dsp) and openings to *recessus lateralis*. IO 4 and IO 5 : fourth and fifth infraorbital bones.

The lower temporal flange (together with the base of the upper flange) is continuous laterally with the ventrally curved postorbital extension of the supraorbital frontal ledge. However, the transition is abrupt and gives rise to a deep but narrow, furrow-like groove, the base of which is slightly expanded. This furrow follows the posterior outline of the orbit, and serves to link (*via* the short tubular dermosphenotic) the supraorbital lateral-line channel with the infraorbital canal and the *recessus lateralis* (see Text-fig. 5 and below).

At its upper end the furrow is bridged by a narrow strip of bone; thereafter it continues anteriorly in the slight groove formed in the angle between the supraorbital ledge and the curved medial part of the frontal.

The supraorbital lateral-line (including its temporal branch) is not enclosed in a bony tube. Instead, the neuromasts lie superficially on the frontal and are contained in a cavernous space formed below two bony bridges over which the skin is stretched. One bridge, a broad, flat arch of bone spans obliquely across the supraorbital area from about the midpoint of the shelf to near the anterior margin of the arched medial part of the frontal (Text-figs. 3 and 5). The second bridge is aligned parasagittally. It is an extremely narrow length of bone arising from a fairly broad base situated posteriorly near the opening of the nerve tube for the temporal neuromast.

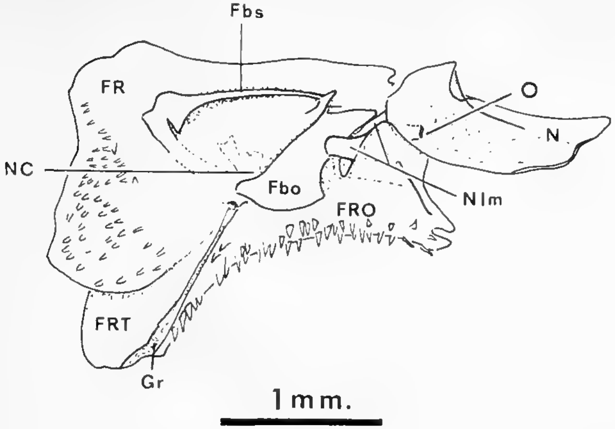

FIG. 5. Right frontal and nasal seen somewhat obliquely from above, to show supraorbital laterosensory region bridges (Fbs and Fbo), the nasal lamina (Nlm) and the groove (Gr) leading from the dermosphenotic to the supraorbital laterosensory chamber.

Anteriorly, this bridge ends near the medial end of the transverse one (Text-figs 3 and 5).

Further support for the skin roof of the supraorbital cavern is provided anteriorly by the process derived from each nasal (see above, p. 220). Besides providing support for the roof, these laminae serve as a lateral wall for the anterior part of the cavern, and in this way connect the supraorbital and nasal laterosensory canals. Further connection between these parts of the system is provided by a short bony tube opening anteriorly into the floor of the nasal, and posteriorly into the groove formed between the supraorbital and medial parts of the frontal.

On the ventral face of each frontal there is a narrow but prominent ridge following the course of the postorbital groove for the lateral-line (see above). The ridge is directed somewhat medially. Along most of its length it contacts the pterosphenoid, while ventrally it articulates with the sphenotic.

Nerves supplying the posterior frontal neuromasts are carried in bony tubes on the ventral face of the bone. Two short tubes open close together into the posterior part of the supraorbital groove; a third, much longer tube runs back to the temporal region. The latter canal opens at the posterior base of the parasagittal bridge. Its origin, on the ventral face of the frontal, lies behind the ridge described above, whereas the two supraorbital tubes originate in front of the ridge.

Nerves supplying the anterior frontal neuromasts of the supraorbital line are not enclosed in tubes, but gain access to the cavern through two foramina lying in the anterior parts of the supraorbital groove.

The frontals contact one another along a barely sinuous median suture. Their anterior tips diverge slightly and each is intimately articulated with the dorsal margin of a lateral ethmoid (Text-fig. 3). The median ethmoid cartilage barely touches the two frontals in the midline.

There is a single, small cuboid and densely "toothed" **supraorbital** bone on each side. Medially the supraorbital is attached to the lateral ethmoid, and posteriorly it articulates with the frontal. Clausen (1959) apparently interpreted the entire odontode-bearing margin of the frontal as a supraorbital bone (see his figure 1). Since there is no indication of fusion between the supraorbital ledge and the main body of the frontal, and because the element here identified as a supraorbital bone is readily separated from the frontal, I would dispute Clausen's identification.

The large unpaired **orbitosphenoid** (Text-figs. 6 and 9) is broadly U-shaped in cross-section, with a distinct median keel, low posteriorly but greatly expanded and ventrally produced anteriorly. Neither the main body of the bone nor its anteriorly directed keel contacts the ethmoid region.

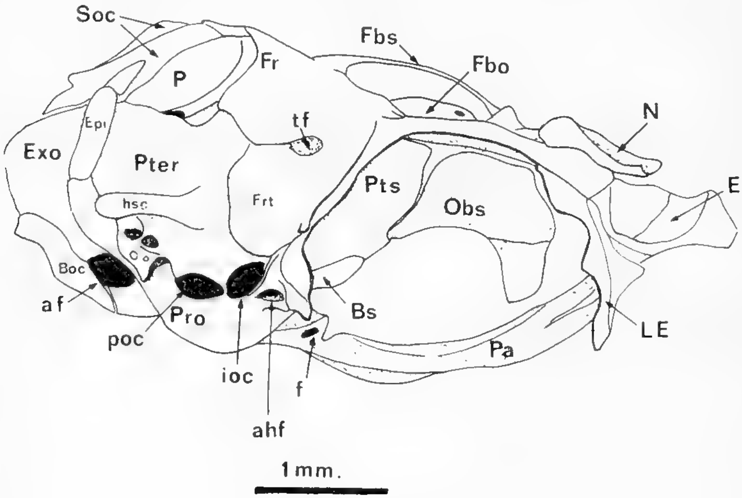

FIG. 6. Neurocranium in lateral view.

The paired **pterosphenoids** (Text-figs. 6 and 9) are in contact with the posterior margin of the orbitosphenoid anteriorly, with the frontals dorsally, and with the prootics and basisphenoid posteriorly and posterolaterally. At no point are the two pterosphenoids in contact with each other. Each is a large, broadly concave bone almost square in outline. Near the posterolateral angle is a notch which contributes to the medial margin of the large foramen opening into the *pars jugularis*. Posterodorsally the bone is pierced by a foramen for the trochlear nerve (IV).

Articulating with the ventromedial margin of each pterosphenoid is the unpaired, hexagonal and concavo-convex **basisphenoid**, its convex face directed anteroventrally. No ventral limb is present. The ventrolateral margins of the basisphenoid articulate with a ledge on the face of each prootic; except for these points, the ventral margin has no other contact with the prootics. At these points of contact the basisphenoid is notched by a foramen for the oculomotor nerve (III), and there is a deep infundibular notch at about the middle of its ventral margin. The dorsal margin, in conjunction with the medial margin of each pterosphenoid, delimits a large foramen for the optic nerve (II).

Each of the paired **autosphenotics** is a short, stout and near conical bone, intimately connected dorsally with the descending postorbital wing of the frontal. Medially, the autosphenotic articulates with the pterosphenoid. The ventral face of the autosphenotic is deeply recessed and forms part of the articular facet for the anterior hyomandibular head. Its posterior face abuts against the pterotic to form the anterior wall of the *recessus lateralis*. Medially, the autosphenotic contributes to the margin of the anterior foramen of the *pars jugularis*.

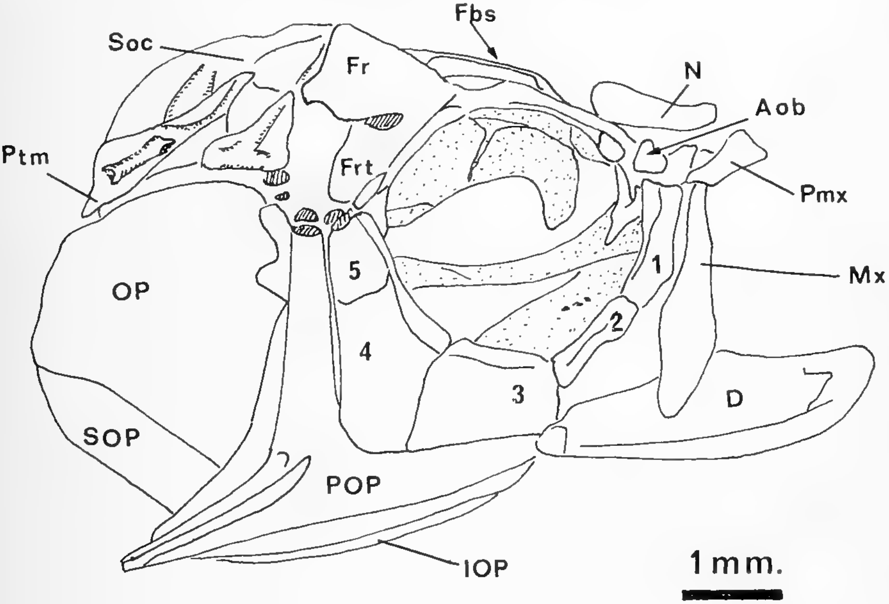

FIG. 7. Syncranium; odontodes not shown.

Excluding the antorbital, there are six bones in the **infraorbital series** (Text-fig. 7). The small antorbital is a thin, poorly ossified triangular bone. It is free from the supraorbital above and is broadly connected below with the elongate and rather slender *lachrymal*. The infraorbital lateral-line canal is carried in a tube on the anterior half of the lachrymal, but beneath a flange from its upper margin on the posterior half. *Infraorbital 2* is also elongate and slender, but with a distinct notch at about the middle of its ventral margin; the lateral-line lies below a flange from the upper border. *Infraorbital 3* is a deeper bone; the flange housing the sensory canal lies a little below its upper margin. Anteriorly, the flange appears to be formed entirely from odontodes, but posteriorly these are less dense and clearly arise from a shelf of bone. *Infraorbital 4* is the largest element in the series; as on the third infraorbital, the flange arises a little below the upper margin. *Infraorbital 5* is reduced to the flange, albeit a deep flange. In outline the bone is a truncated cone, U-shaped in section with the opening directed posteriorly.

The *dermosphenotic* (infraorbital 6) is the smallest element of the series and is reduced to a simple, slightly curved tube closely applied to the posterior face of the supraorbital flange of the frontal (Text-figs. 3–5). Dorsally it opens into the furrow formed between this part of the frontal and the lower temporal flange of that bone (see above, p. 222). Ventrally, its opening is directed towards the infraorbital foramen of the *recessus lateralis*, whose anterior border the dermosphenotic just contacts. The dermosphenotic is discussed further on p. 263.

Excepting the antorbital and dermosphenotic, all elements of the infraorbital series carry odontodes. On the lachrymal and on infraorbital 2 the odontodes are virtually confined to single rows bordering the upper and lower margins, and the upper margin of the bones respectively. Infraorbitals 3 and 4, however, are almost completely covered; only a narrow area above and below the lateral flange is naked. The anterior half of infraorbital 5 is naked, but the remainder has a fairly dense covering of odontodes.

The toothless **parasphenoid** (Text-figs. 2, 8 and 9) is so short that it barely extends beyond the confines of the orbit. In lateral view the parasphenoid is curved, with the anterior three-quarters sharply inclined. This ascending part has, at first, an inverted V cross-section but it broadens anteriorly into an inverted U. Just

FIG. 8. Parasphenoid (dorsal view), anterior end upwards.

behind its junction with the ethmoid, the parasphenoid flattens and divides into a broad, spatulate median region and two narrow, divergent lateral arms. The central part contacts both the vomer and the median ethmoid bloc, while the side arms articulate with the lateral ethmoids alone.

The posterior quarter of the parasphenoid is a narrow, compressed strut which slopes gently upwards towards the prootics. Before contacting the latter, it is produced into two short ascending arms which articulate with the anterior face of each prootic. There is a well-defined foramen for the internal carotid artery situated posterior to the base of each arm. The anterior face of each arm is deeply notched for the passage of the efferent pseudobranchial artery.

Except for a short medial tongue, the parasphenoid does not extend any further

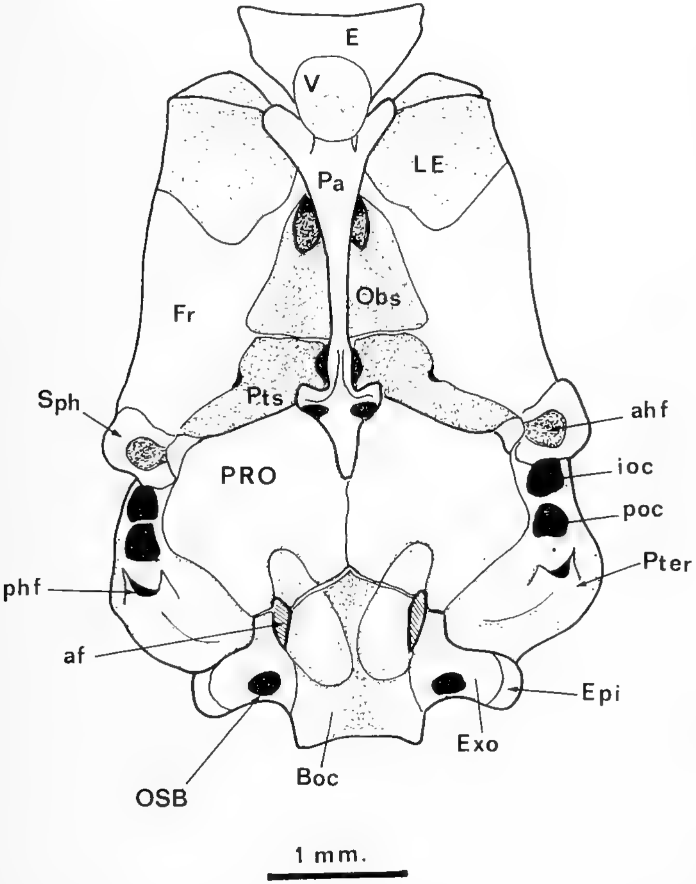

FIG. 9. Neurocranium, ventral view.

posteriorly than the anterior face of the prootics, a most unusual feature (see page 265). Since the prootics meet ventro-medially behind the posterior tip of the parasphenoid, the **myodome** is a very small affair. It is floored by the parasphenoid, has its lateral walls formed by the prootics and, except anteriorly where the basisphenoid arches over the interprootic gap, is without a bony roof. There is no obvious posterior opening to the myodome; but, the posterior tip of the parasphenoid stands slightly away from the ventral face of the prootics to leave a minute aperture.

Otic and occipital regions. (Text-figs. 9–15). The otic region has a decidedly inflated appearance due to the presence of especially large bullae surrounding the two paired intracranial swimbladder vesicles. The bullae are associated with the prootic and pterotic bones, which in consequence are the largest elements in the otico-occipital region of the skull.

When compared with the bullae of clupeoid fishes, those of *Denticeps* appear to be relatively much larger, and to have exerted a far greater influence in moulding the contours of the skull. To give some indication of relative bulla size, a comparison was made between a 6·5 mm. long neurocranium of *Denticeps* and a 40·0 mm. long

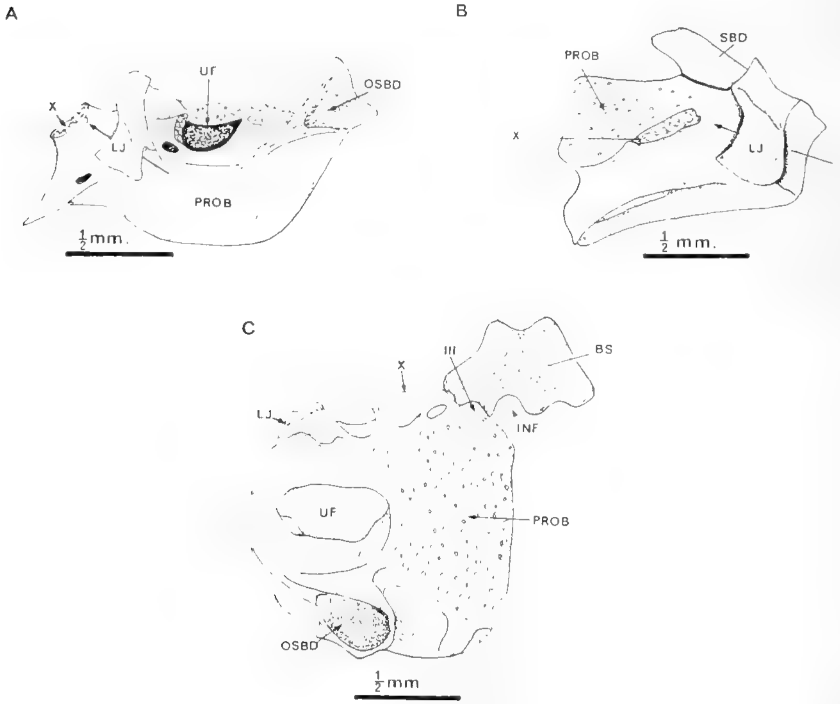

FIG. 10. Prootic (left) and its bulla. (A) Lateral view. (B) Anterior view. (C) Dorsal view (with basisphenoid, BS.). The arrow indicates the *pars jugularis*.

neurocranium of *Clupea harengus*. The results are tabulated below; all measurements are in millimetres, and represent maxima for the character:

	Prootic bulla		Pterotic bulla	
	Denticeps	*Clupea*	*Denticeps*	*Clupea*
Length	1·8	3·0	2·0	3·0
Depth	1·0	3·0	2·0	3·0
Breadth	1·0	3·5	1·0	3·0

Since it is difficult to differentiate between the **prootic** (Text-figs. 6, 9 and 10) and its associated bulla, the combined structure will be described.

The bulla is in the form of a somewhat compressed and truncate ovoid with the long axis transversely aligned, and the truncated face directed medially. As far as I can determine, the prootic proper sheathes the anterior, ventral and a greater part of the medial aspects of the bulla.

On the anterior face are two ridges. The upper and shorter ridge provides articular surfaces for the basisphenoid and pterosphenoid bones. It is pierced near its medial margin by a tunnel-like foramen. The lower ridge is longer and lies near the ventral edge of the bone. Its medial margin is drawn out into an anteriorly directed spur which contacts the short ascending limb of the parasphenoid. The ridge runs laterally and somewhat dorsally to unite with the base of the broad lateral commissure of the *pars jugularis*. The commissure slopes upwards and forwards to reach the upper margin of the prootic. It is so orientated that its face is directed almost anteriorly. From the upper, posterior corner of the commissure there is a narrow ledge of bone which follows the outline of the upper lateral margin of the prootic to its termination. This ledge provides an articular surface for the pterotic, and also serves as the floor for the *recessus lateralis*.

The ventral face of the prootic is smooth except for a short spatulate depression extending forwards from about the middle of its posterior margin; this depression floors the anterior part of the saccular cavity.

The prootic bulla has two openings. One is situated dorsally and opens at the base of the utricular recess. The other, and smaller, opening is funnel-shaped and lies at the posterolateral edge of the bulla. It is the entrance for the swimbladder diverticulum, and is continuous with a similar shaped dilatation of the exoccipital base. (The swimbladder diverticulum enters the skull through the exoccipital.) Below and medial to this funnel, the bulla is invaginated for almost its entire width and for about a third of its length. The concavity so formed is the anterior part of the saccular recess.

The prootics of each side are in contact medially over most of their apposed faces. Anteriorly they curve slightly away from one another to form a shallow cleft which serves as the posterior myodome (see above, p. 228).

Since the *pars jugularis* of the *trigemino-facialis* chamber lies almost entirely in the prootic it can be described here. It is of a simple type with a single *trigemino-facialis* foramen opening into its anterior part. Most of the foramen margin is derived from the prootic, but it is completed dorsally by the pterosphenoid (see p. 224); the lateral commissure is described above. The orbital artery does not have a separate foramen but passes into the *pars jugularis* through its posterior opening (as in clupeoids). However, unlike the condition found in clupeoids, there is no distinct foramen for the hyomandibular branch of VII. This branch shares the posterior opening with the head vein and the orbital artery. In this respect the *pars jugularis* of *Denticeps clupeoides* resembles that of perciform fishes (see Patterson, 1964).

The *pars ganglionaris* of the chamber is a narrow shelf projecting from the inner prootic face immediately medial to the *pars jugularis*.

Like the prootic, the **pterotic** is intimately associated with its bulla, and the two bones cannot be separated readily (Text-figs. 6 and 11). The pterotic, however, sheathes only the lateral and posterolateral aspects of the bulla. In adult animals it is impossible to distinguish between dermal and endochondral pterotic elements since only a single sheet of bone is present. The situation is further complicated when, as in this case, a *recessus lateralis* is developed and in consequence the laterosensory canal lies medial to the bone and not superficially on any part of it.

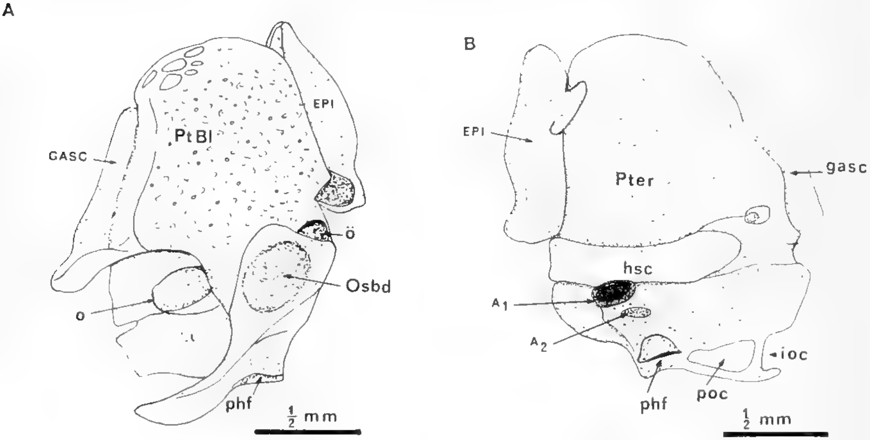

FIG. 11. Pterotic (right), pterotic bulla, and the epiotic. (A) Median view. (B) Lateral view.

The pterotic is approximately ovoid in lateral outline, the narrower pole directed upwards; slightly below the equator, the bone bulges a little around the horizontal semicircular canal. Over its ventral third the bone is slightly bowed in the vertical plane, with the concavity facing inwards. The anteroventral angle is deeply notched, the notch being separated by a narrow vertical pillar from a large foramen immediately behind it. In an entire neurocranium the notch is closed anteriorly by the sphenotic, and forms the first of four foramina opening into the *recessus lateralis*. Through it the infraorbital and supraorbital laterosensory canals open into the *recessus*; the succeeding foramen receives the opening of the preopercular sensory canal (Text-fig. 11B).

Just behind the preopercular foramen there is a projecting, cup-like eminence, the articular facet for the posterior hyomandibular head. Above this facet lie the third and fourth openings into the *recessus*. Of these foramina, the upper (and larger) is surrounded by a prominent margin so that it projects well beyond the general level of the bone. This opening receives the laterosensory canal from the extrascapular bone. The lower and smaller foramen has no obvious connection with a superficial canal. By analogy with the typical clupeoid condition (see Wohlfahrt, 1936, 1937) it should connect with an extratemporal canal, but I was unable to verify this point.

The **pterotic bulla** has a slightly greater volume than its prootic counterpart. It is best seen from the medial aspect. It is a compressed ovoid with a broad posteroventral stalk, opening medially, through which the duct of the swimbladder vesicle passes. The stalk is delimited from the main body by two indentations; one accommodates the utricular sac, the other the horizontal semicircular canal. It is separated from the pterotic laterally by the chamber of the *recessus lateralis*. A short but broad horizontal wing arises from the anterior face of the bulla immediately above the horizontal semicircular canal groove. This wing is continued laterally and dorsally to a point near the dorsal pole of the capsule. Its outer face is deeply concave and surrounds the anterior semicircular canal medially. The anterodorsal surface of the bulla is finely fenestrated, and is crossed by the anterior semicircular canal.

The **intercalar** (opisthotic) is absent.

The **recessus lateralis,** mentioned in connection with both the prootic and pterotic bones, is a peculiar feature of clupeomorph fishes (see Greenwood *et al.*, 1966). Essentially it is a chamber, developed in the otic region, into which all the major cephalic laterosensory canals open (see Wohlfahrt, 1936, for a detailed anatomical description). The lateral wall is provided by the pterotic and, in *Denticeps*, it has four openings. The first is shared by both the supra- and infraorbital laterosensory canals, the former being led in through the dermosphenotic (see Text-fig. 4). In this respect the *recessus* of *Denticeps* differs from all other clupeomorph fishes I have examined or which have been described. A typical clupeoid *recessus* has a separate opening (from the medial side) for the supraorbital canal, and often a small part of the frontal bone contributing to its roof. (A possible exception to this generalization is found in the engraulid genus *Coilia*, where the *recessus* is invaded by the prootic bulla and consequently is considerably modified; nevertheless, it is certainly not of the *Denticeps* type.)

In *Denticeps*, as in the clupeoids, the floor of the *recessus* cavity is provided by the prootic, and there is no bony medial wall, the cavity being separated from the perilymph cavity by a membrane. Its roof is entirely of pterotic origin (other clupeoids have a small frontal contribution), but part of the anterior wall is provided by the autosphenotic.

The elongate, semitubular and slightly arched **epiotic** (Text-fig. 11) is firmly attached to the posterodorsal surface of the pterotic and the underlying portion of the bulla. It is little more than a bony cover intimately applied to the semicircular canal. On its anterior face, however, there is a narrow tab which is closely applied to the pterotic (Text-fig. 11B).

No trace of a preepiotic fossa could be found; possibly it has been obliterated by the expansion of the pterotic bulla.

The otic region is floored by the paired prootics anteriorly, and the median basioccipital posteriorly. As will be recalled (p. 226) the parasphenoid does not extend much further posteriorly than the forward margin of the prootics (Text-fig. 9). The **basioccipital** (Text-fig. 14) is about as long as the prootics, and almost rectangular in dorsal outline. Its floor is deeply recessed on either side of a broad-based median ridge running the entire length of the bone. Arising from the ridge are two wing-like flanges which curve gently outwards to provide part of the median wall and roof of the saccular recess lying in the basioccipital floor.

The anterior face of the basioccipital is firmly articulated with the prootics, and the posterior face contributes to the tripartite occipital condyle for the first vertebra (see below).

An **auditory fenestra** (bounded by the prootic, exoccipital and basioccipital) is present on each side of the skull posterior to the prootics and below the ventral edge of the pterotics (Text-figs. 6 and 9). At least in an alizarin preparation, part of the saccular otolith can be seen through the fenestra.

The posterior face of the skull is formed partly from the paired exoccipitals and partly by the supraoccipital. Each **exoccipital** (Text-fig. 12) is a vertically elongate, relatively narrow bone with a bulbous basal region in which is lodged the posterior wall of the saccular recess and part of the posterior semicircular canal. Below and posterior to the bulge of the semicircular canal is a single large foramen for the glossopharyngeal (IX) and vagus (X) nerves. Also opening into this region is a

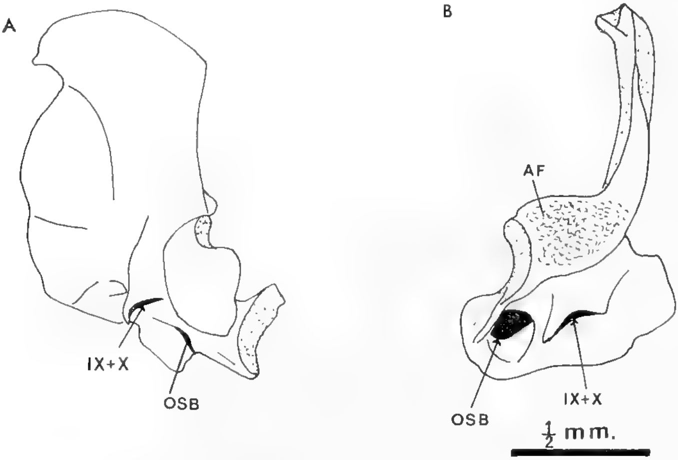

FIG. 12. Exoccipital (right). (A) Lateral aspect. (B) Posterior aspect.

funnel-shaped tube through which the anterior prolongation of the swimbladder enters the neurocranium. This passage connects with its mirror image in the prootic, and with the ventral opening of the pterotic bulla.

The anterior margin of the exoccipital is firmly articulated with the pterotic, the basal part with the basioccipital behind the auditory fenestra, while the anterodorsal tip contacts the supraoccipital above. The dorsoposterior tips of the exoccipitals do not quite meet above the *foramen magnum* but are apparently connected by a small wedge of cartilage.

Internal to the *foramen magnum*, a short median shelf from the inner face of each exoccipital contacts the corresponding wing of the median basioccipital lamina, thus roofing the posterior part of the saccular recess.

On the posterior face of the exoccipital bone there is a rough-surfaced facet directed medially and ventrally (Text-fig. 13). The facets on each exoccipital, together with the median basioccipital facet, form a tripartite condyle for the first vertebra. The rough anterior face of this vertebra is bevelled to fit closely with the facet, and can only be prised from it with some difficulty.

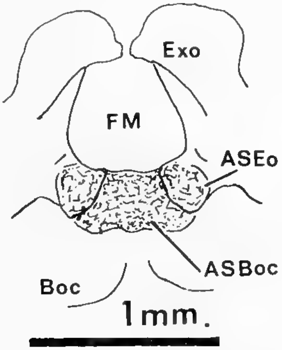

FIG. 13. Condylar surfaces for the first vertebra.

A condyle of this type is not present in any of the clupeoids I have examined. There is a certain resemblance, however, to the condition found in the osteoglossid *Heterotis niloticus*, the hiodontid *Hiodon alosoides*, and in the elopoid *Megalops cyprinoides*. In the latter, the union of vertebra and skull is more complete than in *Denticeps*, and the centrum of the first vertebra is short. Furthermore, the neural arch associated with this centrum is lost in *Megalops* but is present in *Denticeps*.

Ridewood (1904), commenting on the occipital condyle in various lower teleosts (including six clupeoid genera) concluded that in all, the remnants of a half-centrum was incorporated in the condyle. Thus, *Denticeps* would seem to preserve an early stage in the evolution of a condyle type found in most lower teleosts. The condition found in *Heterotis* (where a complete neural arch, pleural rib and epicentral bones are associated with the centrum), however, appears to be at an even more primitive stage.

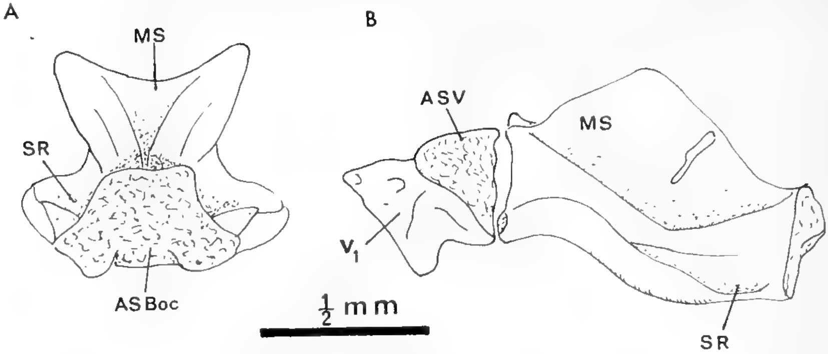

FIG. 14. Basioccipital and first vertebra. (A) Posterior view of basioccipital. (B) Lateral view (right) of basioccipital and first vertebra.

The **supraoccipital** (Text-figs. 3 and 15) is a large and expansive bone bent transversely about its midpoint through almost 45°. The dorsal (i.e. horizontal) part is largely covered by the posterior part of the frontals, and laterally by the parietal tips. A few weak odontodes occur on the exposed part of the horizontal surface. At the point of flexure there is a transverse groove interrupted in the midline by a lateral expansion of the low sagittal crest which extends slightly forward from the posterior (i.e. sloping) part of the bone. The dorsomedial tip of each

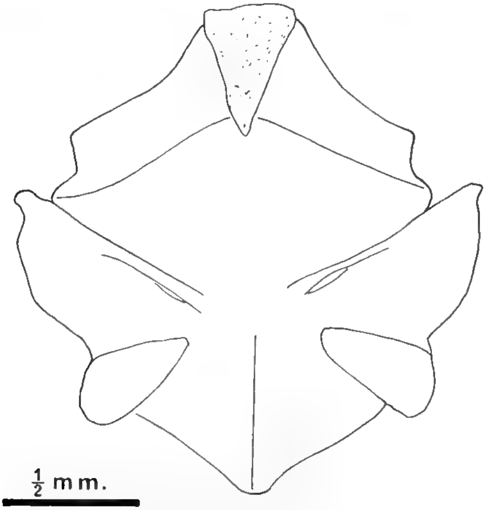

FIG. 15. Supraoccipital (dorsal aspect), the anteroposterior axis aligned horizontally.

parietal fits into the respective lateral limits of the groove. Thus, the groove continues the course of the parietal laterosensory canal.

The sloping posterior face of the supraoccipital has a low, broad-based sagittal ridge; laterally it is marked by well-defined protuberances indicating the position of the uppermost portion of the posterior semicircular canals.

Anteriorly and anterolaterally the otic region is roofed by the frontals whose temporal flanges cover the anterolateral parts of the pterotics. The latter bones are also partly roofed by the parietals.

Each **parietal** (Text-figs. 3 and 6) is a flat, scale-like bone approximately rectangular in outline but with the anteromedian angle somewhat produced. A laterosensory canal crosses the parietal slightly anterior to the middle of its lateral margin. This canal opens into the transverse groove of the supraoccipital (see above). Except for a narrow area, all that part of the parietal lying in front of the tube is overlain by the frontal. The remainder of the parietal overlies the dorsolateral surface of the pterotic bulla, to which it is firmly joined. A single line of odontodes runs along the laterosensory tube, and there is a small patch on the narrow exposed area between the frontal margin and the tube.

In his original description of *Denticeps clupeoides*, Clausen (1959) misidentified the upper temporal flange of the frontal as a parietal. Thus he was led to think that the parietals meet in the midline. The true parietals, however, do not meet since they are separated by the broad sagittal ridge of the supraoccipitals. Also as a result of this misidentification, Clausen described the temporal foramen (his " postemporal foramen ") as being " roofed over mainly by the parietal ". It is in fact contained entirely within the frontal (but with an open posterior margin, see page 221).

Much of the dorsolateral pterotic face is covered by the **extrascapular** (Text-fig. 4) which is loosely joined along its anterior margin to that bone. The posterior margin stands slightly away from the pterotic, and is articulated with the posttemporal (see below). The thin plate-like extrascapulars are broadly triangular in outline, the apex pointing posteriorly. The extrascapular laterosensory canal is triradiate; the upper arm passes to the parietal canal, while the much shorter lower arm passes to the upper of the posterior two *recessus* foramina in the pterotic. The only odontodes present lie in a single line partly along the lower laterosensory tube and partly on the median tube.

Oromandibular region. The **premaxillae** (Text-figs. 3 and 7) are short bones (about half the length of the maxillae), with a fairly marked curvature in the horizontal plane, and moveably apposed to one another in the midline. As seen through the dense pile of odontodes covering the lateral surface of the premaxilla, the bone appears loosely cancellous. The odontodes are reduced to a single row of relatively spaced teeth on the ventral margin.

Along the posterior half of the medial face and near the ventral margin there is a narrow shelf of bone. Anteriorly this shelf widens considerably, and its inner margin curls inwards to form a broad groove. Part of the maxillary head slips under the posterior shelf and the inner wall of the anterior groove lies on the ethmoid, over which it has a restricted area of sliding movement.

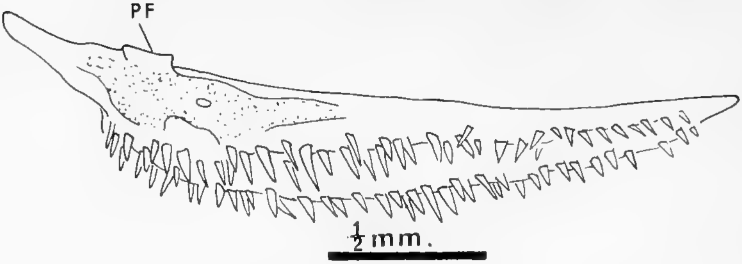

FIG. 16. Maxilla (left) seen somewhat obliquely from above.

Each **maxilla** (Text-fig. 16) is an elongate, flattened, lanceolate bone abruptly narrowing anteriorly to form a distinct head, cylindrical basally but flattened distally. At the point where the head joins the blade there is a dorsally directed elongate facet for articulation with a similar facet on the palatine. The dorsal margin of the maxillary blade is thickened over its anterior half; a shallow, barely discernible groove runs almost the complete length of the blade.

The maxilla is less densely " toothed " than the premaxilla. A double row of odontodes extends along the upper lateral margin of the blade above the groove and is continued posteriorly beyond the groove almost to the tip of the bone. Another double row runs along the lateral face of the lower maxillary margin, and there is a single row along the margin itself (that is, in the usual position of the maxillary teeth). The area between the upper and lateral odontode rows is bare, and noticeably so.

The maxilla articulates with the palatine through a distinct flat facet. It has a second articulation (through the anterior tip of its head) with the anterolateral corner of the ethmoid, but here no distinct facets are developed. A third articulation point may be present between the maxillary head and the anterolateral face of the palatine. All these joints are simple sliding surfaces and only in the case of the palato-maxillary articulation are definite facets developed on the apposed surfaces. In preserved specimens very little upper jaw movement can be achieved by manipulation.

When the mouth is closed, only a small area near the maxillary head slips under an infraorbital bone, the rest of the maxilla lying ventral to the infraorbital series.

No supramaxillae are present. Like Clausen (*op. cit.*), I can find no trace of a supramaxilla-maxilla suture. But, the conspicuous longitudinal area free from odontodes is not readily explained, and should be carefully examined from the ontogenetic viewpoint if embryos become available.

Lower jaw (Text-figs. 7 and 17). The **dentary** is a long, slender bone, somewhat thickened in the mental region, and with only a slight coronoid eminence. The mandibular laterosensory canal runs along the ventral third of the dentary. Over the posterior half of its course it is an open groove, but anteriorly it is enclosed in a tube. The tube opens anteriorly into a short groove and is perforated along its length by at least four small openings.

Most of the lateral face of the dentary is without odontodes. There are, however, dense patches of elongate odontodes covering the anterior and posterior quarters of the lateral face. These two areas are connected by a linear patch (two rows deep posteriorly, becoming multilinear anteriorly) situated along the ventral margin of the lateral face. On the ventral face (which slopes medially at a gentle angle) odontodes occur in a single line on the tubular part of the laterosensory canal, and in several rows along the ventromedial margin.

An initially double but posteriorly single row of odontodes extends along what would normally be the alveolar surface of the dentary. It reaches posteriorly to beyond the hinder level of the posterior lateral odontode patch, thus extending along about the anterior third of the coronoid eminence. There is complete spatial continuity between the anterior lateral odontode patch and the odontodes forming the mandibular " tooth-row ", and no difference in the external appearance of the odontodes and the teeth.

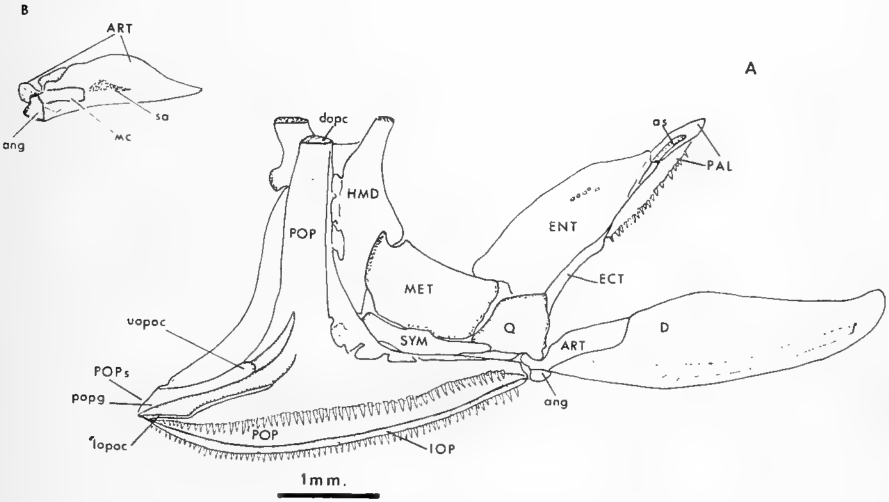

FIG. 17. (A) Lower jaw, palatoquadrate arch, preoperculum and hyomandibula (right), in lateral view. (B) Articular (left) in medial view. The bases of the entopterygoid teeth are shown as circles.

The **articular** (angular of authors) is an elongate, rather shallow bone that penetrates deeply into a narrow longitudinal recess of the dentary (Text-fig. 17). Posteriorly it is thickened, the dorsal surface provided with a deep, hook-like notch for articulation with the quadrate; the posteroventral margin is excavated to receive the retroarticular. Medially there is a well-developed and ossified portion of Meckel's cartilage (the articular of authors), preceded by a slender, spicule-like sesamoid articular. On the lateral face there is a sensory canal crossing obliquely downwards below a dense patch of elongate odontodes; it links the preopercular and dentary laterosensory canals.

The **retroarticular** is a fairly large bone, with about its ventral half exposed, the remainder lying medial to the articular. No odontodes are developed on this bone.

Palatoquadrate arch (Text-fig. 17). The **palatine**, in dorsal view, has the appearance of an arrow head. The slender posterior arm is capped anteriorly by a broad flat head, bearing on its lateral face a well-defined articular facet for the maxilla. Although the anterior tip of the head touches the ethmoid (see above, p. 220), no facet is developed. An irregular double row of teeth runs along the entire ventral length of the palatine arm. The medial face of this arm is firmly united with the anterior half of the lateral face of the entopterygoid.

The **entopterygoid** (Text-figs. 17 and 33) itself is a thin, poorly ossified and gently curved sheet of bone with, at about its middle, a row of five tiny teeth. Anteriorly, the medial entopterygoid margin slightly overlaps the lateral part of the parasphenoid, but posteriorly it is quite free from that bone.

The **ectopterygoid** is a slender bone, slightly curved near its posterior end. For most of its length, the ectopterygoid is in firm contact with the posterior half of the lateral entopterygoid margin; its tip is firmly united with the palatine, and the curved posterior part lies in a corresponding indentation of the quadrate. The union between ectopterygoid and quadrate seems a very loose one.

Each **metapterygoid** (Text-fig. 17) is an expansive, well-ossified and nearly rectangular bone. Anteriorly, the metapterygoid has a firm but flexible junction with the posterior face of the quadrate. Posteriorly there is a deep, flap-like projection which slightly overlaps, and is firmly joined to the underlying part of the outer hyomandibular face.

The main body of the **quadrate** (Text-fig. 17) has the typical quadrant outline of this bone; its ventral margin is produced posteriorly into a narrow, handle-like projection underlying the metapterygoid and symplectic for some distance. There is a narrow but deep notch between this handle and the quadrate body into which the symplectic is inserted. At its anteroventral angle, the quadrate bears a simple condyle for articulation with the notch of the articular, and its anterodorsal angle is recessed to receive the curved posterior end of the ectopterygoid.

Opercular series (Text-figs. 17 and 18). The **preoperculum** has a very characteristic outline, and a decidedly inflated appearance resulting from the enlarged laterosensory canals which occupy most of the bone.

Its anterior outline has a typical crescentic curvature, but the posterior margin is drawn out into a substantial spine-like process. At first sight, the posterior spine appears to be double; however, the " division " is actually a narrow groove of poorly ossified bone.

Immediately above the groove are two openings to the laterosensory canal. The ventrally directed lower opening is a long slit. It is connected with the main canal by an elongate tube which runs parallel to a shallow groove leading away from the upper opening. The latter is semicircular and narrow; it is linked to the main canal by a short tube.

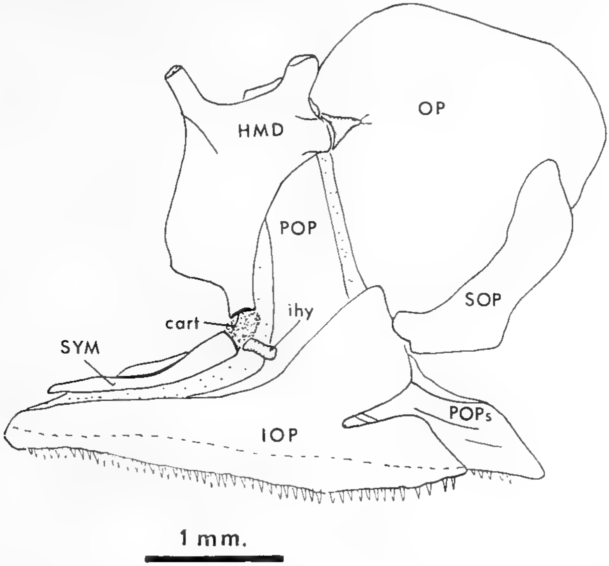

FIG. 18. Hyomandibular and opercular series (right) in medial view.

The main part of the laterosensory canal occupies most of the ascending limb of the preoperculum, and expands ventrally to fill almost the entire horizontal limb except for a small area anteriorly. The ventral wall of this canal is perforated by four extensive openings separated by narrow struts of bone. The ventral margin of the preoperculum is therefore, double. Its smooth inner margin projects further ventrally than the outer margin, which is fringed with odontodes (Text-fig. 17). Odontodes also border the margin of the upper laterosensory canal in the posterior spine, and occur irregularly over the entire exposed lateral face of the preoperculum.

The anterior preopercular angle is filled by the third and fourth infraorbital bones. The distal margins of these bones fit into a flange formed by the junction of the inflated, canal-bearing part of the preoperculum and a narrow ledge of bone which outlines the anterior margin. A similar narrow flange delimits the posterior preopercular margin.

The **interoperculum** (Text-figs. 17 and 18), although flimsy and poorly ossified, is an expansive bone (*pace* Clausen, 1959), whose outline and area is almost equal to that of the anterior and posterior horizontal part of the preoperculum, so that in lateral view little more than its toothed ventral margin protrudes. The odontodes fringing the interoperculum are arranged in a double row anteriorly but a single one along about the posterior half.

The **suboperculum** (Text-fig. 18) is also a flimsy bone, and is much narrower and more linear in outline than the interoperculum. It underlies the entire ventral margin of the operculum which overlies its upper third. A few scattered odontodes occur over the exposed surface (apparently absent in the specimens examined by Clausen [*op. cit.*]). Clausen compared the suboperculum of *Denticeps* to that in osteoglossids, on the grounds that it is " partly hidden under operculum ". However, the bone is relatively larger and more exposed in *Denticeps* than in the osteoglossids; it is, I think, more readily comparable with the clupeoid condition.

The only outstanding characteristics of the **operculum** (Text-figs. 1 and 18) is its odontode distribution pattern. The odontodes are arranged in six or seven, somewhat curvilinear rows separated by distinct interspaces. Each row may be double in places, and none except the last row extends over the upper two-fifths of the operculum. Even the last row (which lies along the posterior margin of the operculum) does not extend beyond the dorsoposterior angle of the bone.

Odontode distribution is clearly influenced by the development of dermal laterosensory canals on the operculum (see p. 266, and Clausen, *op. cit.*); the rows are confined to the interspaces between the canals. The absence of odontodes dorsally is due to the contiguity of the dermal canals in that area.

Hyoid arch. The **hyomandibula** (Text-figs. 17 and 18) has a broad main body, whose distal end narrows abruptly into a short vertical limb distally tipped with cartilage. There are two prominent articular heads, the anterior somewhat narrower than the posterior one. A prominent perforated ridge runs across the lateral face from the base of the anterior head to the posterior margin of the bone; it ends near the tip of the narrow distal limb. The preoperculum fits into the posterior face of this ridge. A large oval foramen for the hyomandibular branch of the facial nerve penetrates the hyomandibula near its centre.

The anterior hyomandibular head articulates with a deep, conical socket formed mainly in the sphenotic, but also partly from the prootic. The posterior head fits into a horizontally aligned conical projection from the pterotic.

The short **interhyal** (Text-fig. 18) is barrel-shaped, and is attached to the cartilaginous area between the hyomandibula tip and the symplectic.

The **symplectic** (Text-fig. 18) is an elongate, slightly angled bone. Its anterior tip inserts deeply into the quadrate, and its entire posterior ventral surface is closely bound to the preoperculum. The posterodorsal surface is intimately associated with the ventral margin of the metapterygoid. Proximally, the symplectic articulates with the hyomandibula through an extensive synchondrosis.

The **epihyals** (Text-figs. 20 and 21) are fairly stout, shield-shaped bones each bearing laterally a single branchiostegal ray (see below). Union between the epihyal and the ceratohyal of its side is through a flexible syndesmotic joint.

Each **ceratohyal** (Text-figs. 20 and 21) is axe-shaped, the forward pointing " handle " expanded anteriorly to form a double articular surface, the smaller facet of which contacts the dorsal hypohyal, and the larger ventral surface contacts the ventral hypohyal. Four branchiostegal rays articulate laterally with the ventral margin of the expanded " axe-head " of the bone. This margin is slightly sinuous but the contours cannot be correlated with the position of individual branchiostegal rays.

Both the epi- and ceratohyals of each side are traversed by a tubular canal housing the hyal artery. The tube opens anteriorly on the dorsal aspect of the ceratohyal and posteriorly it opens on the lateral face of the epihyal.

The paired **dorsal hypohyals** (Text-figs. 22 and 23) are small, ovoid bodies closely applied to the posterior tip of the basihyal on its ventral surface. The ventroanterior tips of the dorsal hypohyals articulate with the underlying postero-dorsal tips of the ventral hypohyals through a very small point of contact. Posteriorly they approach closely the anterior tip of the first basibranchial but do not actually contact that bone.

The **ventral hypohyals** (Text-figs. 22 and 23) are much larger, pyramidal bones, also separated narrowly in the midline. They articulate with the dorsal hypohyals and more extensively, with the head of the ceratohyals.

The unpaired, median **basihyal** is a poorly ossified elongate bone (Text-fig. 22), hemicylindrical in section and somewhat broader anteriorly than posteriorly. It articulates with the dorsal hypohyals, and with the anterior tip of the first basibranchial. Continuous with its cartilaginous anterior tip is a small hemispherical nubbin of cartilage (Dr. G. Nelson, who has examined the material, interprets this as a case of secondary segmentation of the basihyal, in his experience an unusual occurrence).

No teeth are present on any part of the hyal skeleton.

The **urohyal** is a poorly ossified, elongate and rather slender bone; except for a short distance anteriorly it has a double ventral margin, the bone being an inverted " V " in cross-section.

The **branchiostegal rays** (Text-figs. 19 and 20) have been mentioned briefly above. In all specimens examined by Dr. Clausen and me there are five pairs of rays. Of these, four articulate with the ceratohyal, and one with the epihyal. The branchiostegals show an anteroposteriorly progressive expansion, although the first ray has the broadest proximal articular surface. The third to fifth branchiostegals also show an increasingly marked indentation of the anterior face which, on the fourth and fifth rays, could be described as notched.

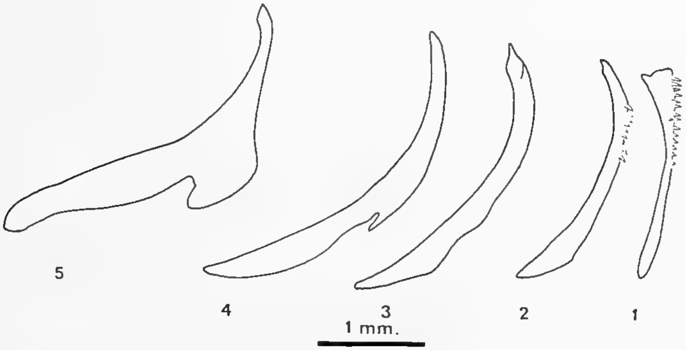

FIG. 19. Branchiostegal rays (right) in lateral view.

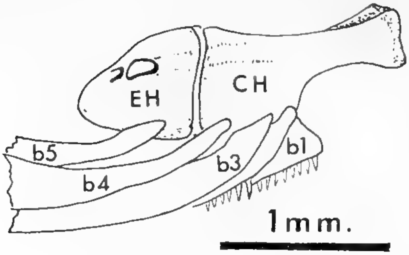

Fig. 20. Part of hyal arch (right), and branchiostegal rays *in situ*; lateral view.

Odontodes are present on the anterior margin of the first and second rays only (Clausen reports them present on the first ray only).

Branchial skeleton (Text-figs. 21 and 22). An outstanding feature of the branchial skeleton in *Denticeps* (especially as compared to most clupeoids, all elopomorphs and all osteoglossoids) is the marked reduction in the number of dermal tooth-bearing plates associated with the gill-arches. *Denticeps* also stands apart from all clupeoids in the relative proportions of the various arch elements (particularly the hypo- and ceratobranchials of arches I and II). These and other characters will be discussed elsewhere (p. 269).

Each of the first four gill-arches has an **infrapharyngobranchial,** that of arch IV being very poorly ossified or even cartilaginous.

Infrapharyngobranchial I (I.P.H. I): is short, slender and cylindrical, and is directed anteromedially.

I.P.H. II. is elongate, flattened-cylindrical in cross-section, slightly angled a little anterior to its midpoint, the dorsolateral face with a low swelling at the point of inflection; anterior tip parallel with that of I.P.H. I.

I.P.H. III: is about as long as I.P.H. II, but is flatter and has its posterior tip expanded and foot-like; its anterior tip is orientated sagittally.

I.P.H. IV: is small, roughly rectangular (narrowed anteriorly), and poorly ossified or cartilaginous.

The infrapharyngobranchials do not come together in the mid-line (as they do in most clupeoids, see Nelson, 1967) but are separated by a fairly wide gap.

Epibranchials (E.B.) are present on the first four arches.

E.B. I and E.B. II: are similar in shape (elongate rectangular), the second slightly smaller.

E.B. III: is noticeably more slender than the preceding epibranchials. It bifurcates at about its midpoint; the dorsally directed posterior arm is slightly shorter and more slender than the medially directed anterior arm.

E.B. IV: has the posterior part triradiate and more heavily ossified than the anterior portion. The arms of the triradiate part meet in a Y junction. The space between the short posterodorsally directed arm and the tail of the Y is filled by a thin sheet of bone so that the posterolateral part of the epibranchial is triangular in outline.

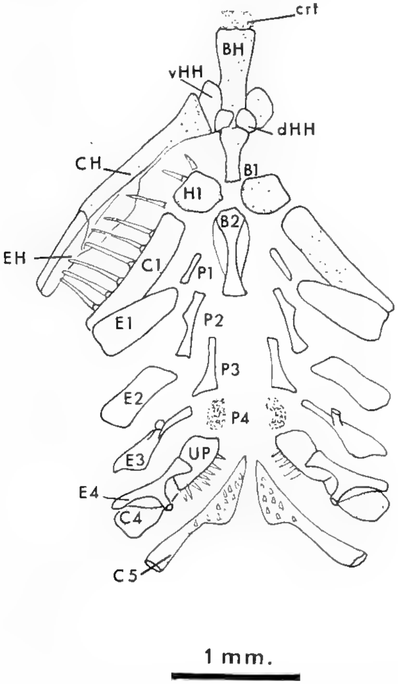

FIG. 21. Branchial skeleton and left hyal arch, seen from above. Gill rakers are shown only on the lower part of the first gill arch. crt : cartilage.

The **ceratobranchials** (C.B.) of gill-arches I to IV are similar, that is, elongate, rather flattened cylinders; the proximal (ventral) tips of ceratobranchials III and IV are slightly expanded. The ceratobranchial of arch V is narrow but has on its posterior face, near the proximal end of the bone, a tooth-bearing expansion.

Hypobranchials (H.B.) are present in the first three gill-arches.

H.B. I: is short and square.

H.B. II: is also short, but is roughly diamond-shaped in outline, the bones of each side apparently linked by an ill-defined cartilaginous plate.

H.B. III: is a slender, roughly T-shaped bone, the crosspiece short and obliquely aligned to the longer shaft; from the medial tip of the cross-piece a ventrally directed bar forms, with its partner of the opposite side, an aortic canal. The posterior tip of the main shaft is cartilaginous and contacts the cartilage plate between the bases of ceratobranchials IV and V.

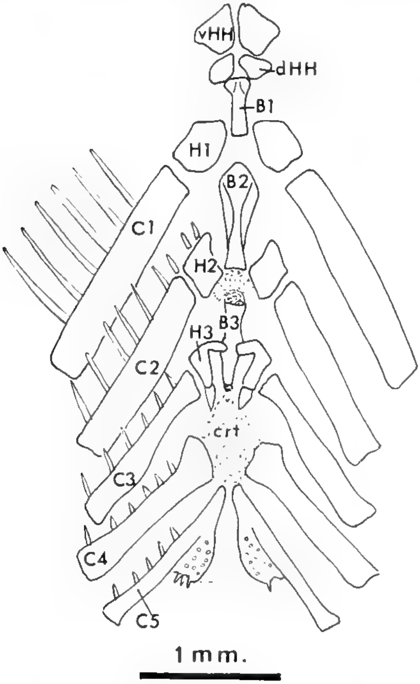

FIG. 22. Branchial skeleton and hypohyals, ventral view. crt : cartilage.

Ossified, median, unpaired **basibranchials** (B.B.) occur between the first three gill-arches only. At the base of arch IV there is a thin cartilaginous plate which, at least in part, represents an unossified fourth basibranchial.

The three ossified basibranchials are long, slender bones, each with an expanded anterior tip. Basibranchial II is the longest and broadest element of the series; viewed ventrally, the body of the bone is constricted into an elongate hour-glass continuous with a flat plate lying above it. No dermal tooth-bearing bones are associated with any of the basibranchials.

In addition to the toothed fifth ceratobranchials (the lower pharyngeal bones), there is a pair of toothed **upper pharyngeal bones**. The ventral faces of these flat, approximately square bones are densely covered with long teeth. Each bone lies partly below the anterior tip of epibranchial IV of its side (Text-fig. 21), with which it articulates freely. In life, much of the toothed area is apposed to the tooth-patch on the fifth ceratobranchial.

Dr. Nelson (personal communication) is of the opinion that the upper pharyngeal bones of *Denticeps* correspond to the fifth upper pharyngeal tooth plates of clupeoid fishes (U.P. 5 of Nelson, 1967).

Gill rakers are carried on the anterior and posterior faces of all gill-arches except the fifth, where they are found on the anterior face only.

Gill raker counts and distribution in one fish (35 mm. S.L.) are tabulated below; where a raker is situated between two elements of an arch it is shown in that position in the table. 0 = gill rakers absent; — = skeletal element absent.

	I		II		III		IV		V	
	Ant.	Post	Ant.	Post	Ant.	Post	Ant.	Post	Ant.	Post
I.P.B.	0	0	0	0	0	0	0	0	—	—
E.B.	4	5	4	4	4	4	0	0	—	—
	1		1							
C.B.	7	4	6	5	7	7	7	9	7	0
	1									
H.B.	1	0	3	1	1	0	—	—	—	—

All gill rakers are poorly ossified except near their basal articulation. Those on the anterior face of ceratobranchial I are long and slender (but well-spaced), while those on succeeding arches are progressively shorter and stouter until, on arch V, they are reduced to low knobs. Gill rakers on the posterior face of an arch are shorter than those on the anterior face. Shortest posterior rakers occur on arch I. On this arch the posterior ceratobranchial rakers are almost vertically aligned; on other arches the rakers have a dorsomedial orientation.

PECTORAL GIRDLE

The pectoral girdle of *Denticeps clupeoides* is a substantial structure with expansive cleithra and coracoids. The pectoral fins, however, are in no way exceptional in size or shape for a fish of this size.

The horizontal part of the *cleithrum* (Text-fig. 23) is longer than the vertical arm, is fairly expanded, and deeply concave in transverse section (the concavity facing inwards). The vertical limb is short and stout, with the ascending arm produced posteriorly into a thin but expansive shield whose anterior margin extends up about three-quarters of the arm.

The **coracoid** (Text-fig. 23) is also an expansive bone, plate-like and approximately ovoid in outline. It meets the cleithrum of its side along the entire medial edge of the latter's horizontal arm. Anterodorsally, the coracoid margin is irregularly serrate, the serrae forming a deeply interdigitating suture with those of the opposite coracoid. Near the posterior margin there is a thin but broad-based projection which meets the basal expansion of the mesocoracoid.

The **mesocoracoid** (Text-fig. 23) is shaped rather like a fish-hook, the " barb " being directed anteriorly. It is a flattened but slightly twisted bone, broadest over the area of curvature. Near the head of the " hook " (where the mesocoracoid articulates with the cleithrum) there is a moderately prominent posterior projection.

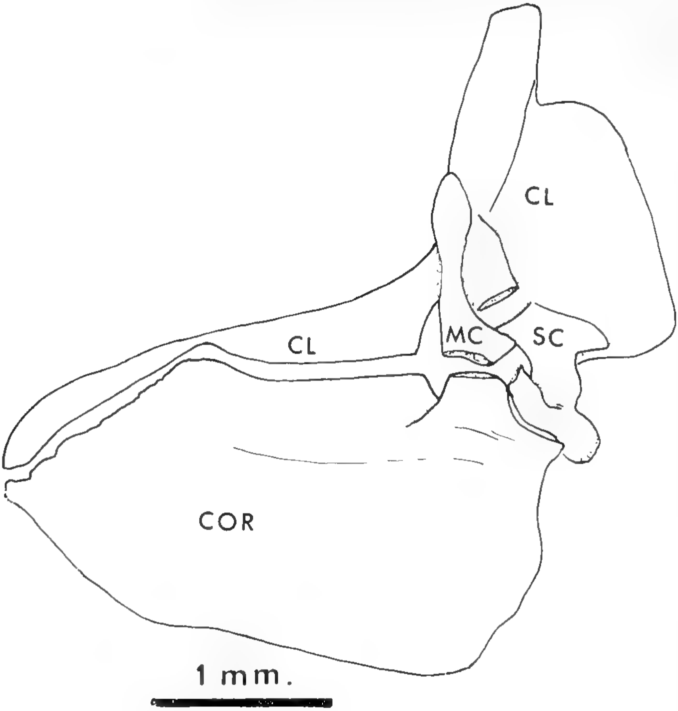

FIG. 23. Pectoral girdle (right half), medial aspect seen from slightly above. The various elements have separated during treatment and are shown in that position.

The scapula articulates with a broad ridge on the medial face of the cleithrum, near the junction of its ascending and horizontal arms.

The scapular foramen is very large, with only its posterior margin provided by the scapula itself. Its lateral margin is formed from the cleithrum, its anterior margin from the cleithrum and coracoid, while the inner margin is provided by the coracoid alone. No intercalated cartilage was found between the scapula and the other bones contributing to the boundary of the foramen.

Articulation of the pectoral fin rays (Text-fig. 24). The pectoral fin is unusual in having a double row of radials supporting the ventral (i.e. posterior) third of the fin. In all, there are two distal and three proximal radials supporting the eleven (rarely twelve) rays of the fin.

The first ray articulates directly with the scapula over a slight, elongate eminence between the posterior scapular projection and the more pronounced posteroventral prominence with which the small second and third rays articulate.

The fourth and fifth rays also articulate (but through a common radial) with the scapula. The sixth to eighth rays also share a large, single distal radial which in

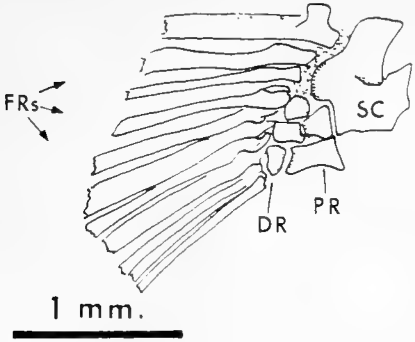

FIG. 24. Articulation of the pectoral fin rays (left side), seen from above with the anteroposterior axis of the fin aligned horizontally.

turn articulates with a capstan-shaped proximal element associated with the mid-ventral area of the scapular margin.

The ninth to the eleventh pectoral rays share a common distal radial which, in turn, articulates with an elongate, rectangular proximal element meeting the coracoid immediately below the scapulo-coracoid junction.

In one specimen examined, there is a twelth ray, very short and fine; it too shares the same radial as the ninth to eleventh rays.

Dorsal elements of the pectoral girdle. The **extrascapular**, which should be included here, has already been discussed (p. 235) in connection with skull roofing bones. Of the two remaining bones, the **supracleithrum** is firmly attached to the cleithrum. It is a large, flat bone, kidney-shaped in outline with the concave side directed forward. The tube carrying the laterosensory canal from the body passes obliquely across the supracleithrum. It opens into the laterosensory tube of the posttemporal where the latter overlaps the anterodorsal half of the supracleithrum.

The **posttemporal** (Text-fig. 25) has a large, nearly rectangular and flat body, but with the anterodorsal angle greatly produced into a substantial, flattened spine. The tip of this spine is firmly attached to the pterotic and the epiotic. The medial limb of the posttemporal is partly ligamentous; only about the proximal half is ossified. Distally, the ligamentous section is firmly associated with the pterotic at a point slightly below the horizontal semicircular canal, just anterior to the pterotic-exoccipital junction.

The laterosensory tube runs near the ventral margin of the bone, and joins with the lower limb of the extrascapular laterosensory tube. A single row of odontodes runs along at least part of the posttemporal tube.

Postcleithrum. The postcleithrum is probably represented by two small, scale-like bones associated with the upper part of the cleithrum. The superior, and larger, element is nearly circular and is pierced by a tubule of the somatic lateral-line. It lies immediately behind and in contact with the uppermost part of the vertical

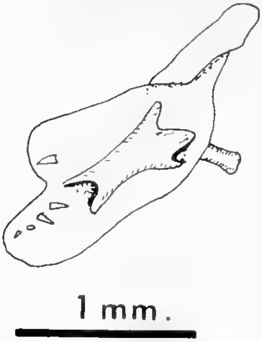

FIG. 25. Right posttemporal, in dorsolateral view.

cleithrum limb; its ventral tip barely overlaps the dorsal margin of the lower postcleithrum.

The latter is bean-shaped and relatively elongate; about half of the bone is covered by the posterior, flange-like extension of the cleithrum.

As Clausen (1959) observed, the postcleithra have a striking resemblance to body scales, the upper even showing traces of what appear to be annuli.

AXIAL SKELETON

Vertebral column (Text-figs. 26–29). There are forty vertebrae (including the small second ural centrum) in the column of the three specimens examined, and in three others that were radiographed.

All the vertebrae are well-ossified; excepting the first abdominal and the second ural centra, all have the neural and haemal arches firmly fused to the centra, and are amphicoelous. Again excepting the first abdominal centrum, all centra are pierced by a narrow but distinct notochordal foramen.

Intermuscular bones are present (save for the first vertebra) along the entire length of the column. Over about its anterior half only epipleurals or epicentrals are present, but over the posterior half both dorsal and ventral intermusculars are developed; for a short section all three types of intermuscular bones are present.

The **first abdominal vertebra** (Fig. 14) is reduced and very firmly attached to the skull. The anterior face of the centrum is rough and clearly divided into three facets corresponding to the occipital condyle of the skull (see p. 233). The long, slender neural arches are autogenous; their somewhat expanded distal ends do not meet in the midline. No intermuscular bone is associated with this vertebra.

The **second vertebra** is slightly shorter than the third (Text-fig. 26). It has a fully developed neural spine and arches. Immediately above the spinal cord, the arches curve medially and almost meet, thus roofing the cord at this point. Because the proximal ends of the neural spine are widely separated, a space is formed above the spinal cord roof.

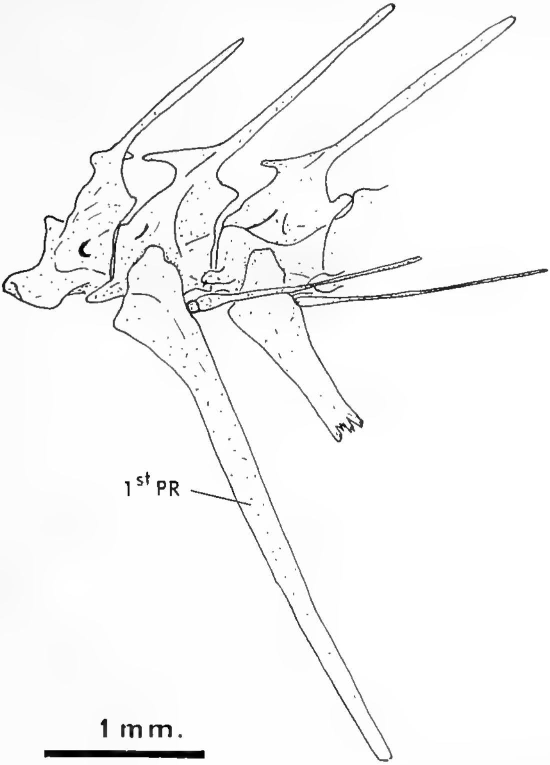

FIG. 26. Second to fourth abdominal vertebrae, left lateral view.

A broad, anteriorly directed process arises ventrolaterally from each side of the centrum, and projects slightly beyond its anterior face. As the tips of these processes are turned inwards, they effectively embrace the posterolateral aspect of the first centrum.

I am uncertain as to the identity of these processes, but because the intermuscular bone (which in the more posterior and rib-bearing vertebrae articulates with a rib) is joined to the process, it could be an enlarged parapophysis fused with the centrum.

No pleural rib is associated with this vertebra, but an epicentral intermuscular bone is present.

Abdominal vertebrae 3–14: all carry well-developed pleural ribs which articulate directly with the centrum except on the fourteenth vertebra. Here there is an autogenous parapophysis-like structure which closely resembles the head of the rib on other vertebrae; it also bears the intermuscular bone.

All vertebrae in this section of the column are similar in form. The long-based neural arches almost meet medially above the spinal cord, and are capped by the bifurcate base of the neural spine. On the third and fourth vertebrae the medial shelf is produced anteriorly so as almost to meet the preceding vertebra. This anterior projection is much shorter in the other vertebrae, and is barely recognizable on the fourteenth vertebra.

Short dorsal pre- and postzygapophyses are present. Ventrally there is a prezygapophysis-like projection curved medially and contacting the posterior face of the preceding centrum. The process increases in size anteroposteriorly and becomes increasingly involved in the articulation of the pleural ribs. From the tenth vertebra backwards, the greater part of the rib head is in contact with this process, although the rib still has a distinct articulation with the centrum. Because of this relationship with the rib, I would identify these projections as parapophyses fused with the centra.

The **pleural ribs** (of which there are twelve articulating pairs, and two floating pairs) are long and substantial bones with deep, somewhat concave heads merging indistinguishably with the broad proximal part of the rib (Text-fig. 26). Each rib articulates directly with the centrum; a well-defined articular boss on the upper part of the head fits into a deep pit in the centrum. The articulation with the presumed parapophysis mentioned above is effected through the anteriorly curved ventral margin of the head.

The fine, slender and unbranched **epipleurals** are attached to the ribs near their articulation with the centrum.

Ventrally, the distal tips of the ribs contact the medial line of scutes. Clausen (1959) states that the ends of the ribs join the scutes " . . . causing the ribs to form a complete hoop exactly as the similar scutes in many Clupeidae ". I have been been unable to confirm this in the specimens I examined. In these the scutes are free and merely touch (but to not join) the ribs. The scutes are without a distinct ascending arm.

The **fifteenth vertebra** has a short haemal arch which arises from the base of what appears to be a short parapophysis fused with the centrum (and with which the epicentral intermuscular bone articulates).

Immediately below this vertebra are a pair of short but otherwise fully-developed ribs, closely resembling their anterior congeners except for having attenuated and not truncated ends. In an alizarin transparency this rib pair seems to " float " in the hypaxial musculature (see Text-fig. 27).

The **sixteenth vertebra** is similar to the fifteenth but has a more expansive, plate-like haemal spine. It too has a pair of " floating ribs " and an epicentral articulating with the parapophysis.

The **seventeenth vertebra** (or using Nybelin's [1963] nomenclature, the twenty-second preural) is the first true caudal vertebra. From this point until the first ural vertebra all vertebrae are of a generally similar form, with long, slender haemal spines.

The neural arch of all preural vertebrae is long-based, a transverse supraneural shelf is present (as in the abdominal vertebrae) but the aperture above it, formed between the bases of the neural spine, becomes progressively smaller caudad. From

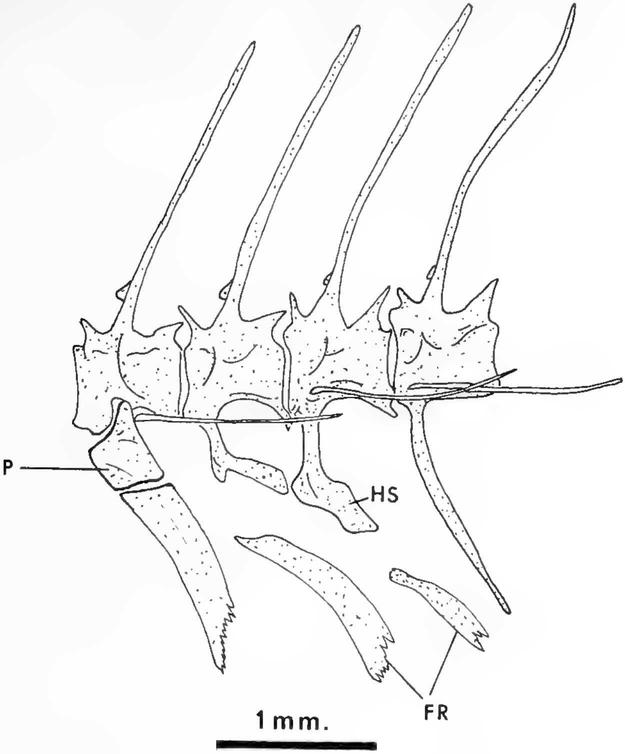

FIG. 27. Transition between abdominal and caudal vertebrae, showing the last pleural rib, its parapophysis-like process (P), and the two " floating " ribs (FR); left lateral view.

the fifth to the first preural, the shelf is absent and consequently there is only one aperture between the centrum and the neural spine.

Preural vertebrae 3 to 5 have a longer haemal arch base than do the preceding elements, and a foramen is present in it. The neural spines of preural vertebrae 2–5 are expanded anteroposteriorly, but that of preural 1 is greatly reduced. Haemal spines of preural vertebrae 1–6 are also expanded, that of preural 6 only slightly so, and that of preural 2 greatly expanded (more so even than the haemal spine of preural 1; see Text-fig. 29).

Equally developed dorsal pre- and postzygapophyses are present on the more anterior preural vertebrae, with the prezygapophysis becoming slightly larger on the posterior vertebrae.

Ventral postzygapophyses are developed on the anterior preural vertebrae, but in the posterior elements a prezygapophysis-like process is developed from the base of the haemal arch as well. This process does not, however, directly contact the ventral postzygapophyses of the preceding vertebra.

Fig. 28. Caudal vertebrae (preurals 14 and 15), left lateral view.

Epicentral intermuscular bones are associated with preural vertebrae 22 to 15. **Dorsal intermuscular bones** (Text-fig. 28) first appear above the eighteenth preural vertebra. The first few dorsal intermusculars are fine, short and branched; they become progressively larger and longer but the short upper limb is not developed in about the posterior half of the series (Text-fig. 28). The last dorsal intermuscular bone lies above the second preural vertebra. **Ventral intermuscular bones** first appear below the twentieth preural vertebra, and are stouter than their dorsal counterparts which they otherwise resemble. The lower limb is absent in bones from the posterior half of the series. The last ventral intermuscular bone is associated with the fourth preural vertebra.

CAUDAL FIN SKELETON

The caudal skeleton (Text-fig. 29) is one of the most characteristic features of the Denticipitidae. Although undoubtedly of the clupeomorph type (see Gosline, 1960, 1961; Greenwood *et al.*, 1966) it differs from all known living and fossil clupeomorphs (including *Diplomystus* and *Knightia*). Like several other features of the denticipitids, the caudal skeleton is a mosaic of primitive and specialized features.

Five vertebrae are involved, namely: two urals (U1 and U2) and the first three preurals (PU1–3). Five hypurals are present, and there are two epural bones. A single uroneural is present on each side. The axis of the skeleton curves gently and evenly upwards through four vertebrae (PU1–2, U1–2).

In addition to the eighteen principal caudal rays (comprising one unbranched and eight branched rays in each lobe) there is an upper and two lower procurrent rays

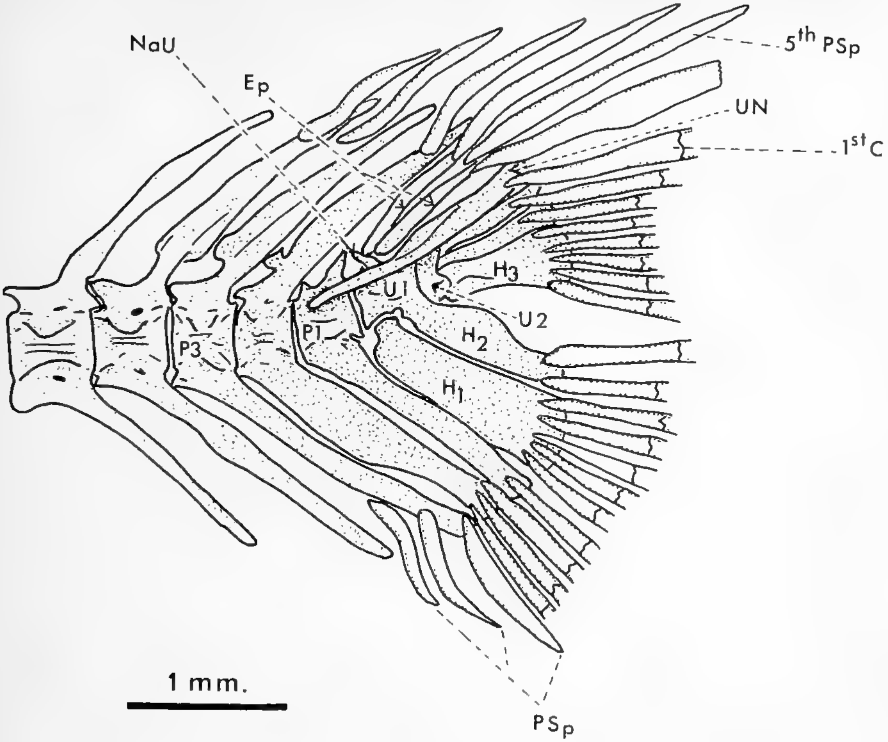

FIG. 29. Caudal fin skeleton. Intermuscular bones removed for clarity. Left lateral view. P1–3 : first to third preural vertebrae.

(short, but segmented distally) and a series of procurrent " spines ", five dorsally and three ventrally (Text-figs. 29). These " spines " have a deeply divided base, but cannot be separated into left and right halves. Each dorsal procurrent " spine " is articulated with a single vertebral element (the first with the neural spine of PU4 the second with PU3, the third with PU2, and the remaining two with the two epurals), The three ventral spines, however, all articulate with the expanded haemal spine of the third preural vertebra.

Both dorsally and ventrally, the procurrent " spines " increase in length towards the fin, thereby forming a graded series with the segmented procurrent ray preceding the first and last (unbranched) principal caudal rays. These three procurrent rays are segmented distally, but the proximal portion resembles that of a " spine ". Thus, it seems certain that the spines are merely modified procurrent rays.

The **first preural centrum** (PU1) is slightly longer than the second (Fig. 29). Its neural arch is complete but very narrow-based and short, the neural spine showing a correspondingly great reduction in length to little more than a slight spur. The haemal spine is expanded but less so than that of the second preural vertebra. There is a well-developed but low hypurapophysis near the base of the spine.

The **first ural vertebra** (U1) has a well-developed centrum, slightly longer than that of PU1 (see Text-fig. 29). The neural arches, however, are greatly reduced spurs which do not meet in the midline. In one specimen the arches of each side are of a different size and shape, one directed anteriorly, the other posteriorly.

The **first hypural** has a broad articulation with the anterior half of PU1, but it is clearly autogenous (Text-fig. 29). **Hypural 2**, however is indistinguishably ankylosed with the centrum over almost its entire posterior half. Both these hypurals are broad, the first somewhat more so than the second, and also slightly longer. The posterior margin of hypural 2 is deeply excavated over the distal half in some specimens, but less markedly so in others.

The **second ural vertebra** (U2) is reduced to a short, rather wedge-shaped centrum. Like the other centra, it is penetrated by a distinct notochordal foramen which in this centrum leaves near the posterodorsal margin.

Hypurals 3 to 5 articulate with the posterior face of the second ural centrum (Text-fig. 29). Hypural 3 is relatively broad, and its dorsal margin is closely applied to the ventral margin of hypural 4; in one specimen these two hypurals appear to be fused, but with the line of fusion still evident. Hypural 5 is narrow and clearly separated from Hypural 4; it is partly obscured proximally by the uroneural.

Each of the paired **uroneurals** (Text-fig. 29) is a long, strap-like and thin bone, firmly articulated with the first preural vertebra through a pit on its anterodorsal surface; although the articulation is firm, the bones are not fused. Above the second ural centrum, the dorsal margin of the uroneural is slightly expanded. Beyond this point, the uroneurals meet medially and are closely apposed but not fused for the remainder of their length.

The two **epurals** (Text-fig. 29) are slender and elongate. The first epural contacts the aborted neural arch of the first ural centrum, while the second epural touches the base of the first a little above its point of articulation with the neural arch. The fourth and fifth procurrent " spines " articulate with the two epurals respectively, and the proximal tip of the upper procurrent ray articulates with the second epural.

SKELETON OF THE MEDIAN FINS

The short **dorsal fin** is supported by seven pterygiophores. The first has a broad distal base and carries two rays. The remaining pterygiophores have a similar shape but decrease in size posteriorly. Each supports only one ray. The first dorsal ray articulates directly with the pterygiophore head but all other rays have a small radial (presumably the distal) interposed.

The relationship of pterygiophores to vertebrae is rather irregular and shows some individual variability, but with at least one instance in each fish of two pterygiophores situated between a pair of vertebrae.

The long **anal fin** is carried by twenty-two pterygiophores. The first has three rays (two unbranched and unsegmented) and a relatively long head. Its two unbranched rays lack an intermediate radial, but a radial is present at the base of all other anal rays. The first pterygiophore articulates proximally with the posterior face of the broad but short haemal spine carried by the twenty-second preural vertebra. The remaining twenty-one pterygiophores are of similar shape, and each supports one branched ray, except the last, which carries two (but both sharing one radial).

In the anal fin, as in the dorsal, there is a variable relationship between the pterygiophores and the vertebrae. However, in this fin there is a higher incidence of two pterygiophores per vertebral pair. For example, two specimens each have seven cases of such pterygiophore pairs, but different pairs of vertebrae are involved.

Interneurals are present between the tips of neural spines 2 to 11 (i.e. between the third to twelfth vertebrae). The first five interneurals are fairly broad and somewhat boomerang-shaped bones which contact the neural spine a short distance from its tip. The remaining interneurals are more slender and splint-like; all are poorly calcified.

PELVIC GIRDLE

The two halves of the girdle lie below the sixth to seventh pairs of ribs, which are shorter than those preceding and following them.

Each half of the girdle is a long, slender, and poorly ossified bone; in outline they are triangular, in cross-section somewhat curved. The two halves are closely apposed medially, at an angle of about 45° to the vertical, but only in contact at the ischial region. Lateral to the point of contact, the girdle is rather bulbous in section.

Two cuboid radials of approximately equal size articulate with the posterior, face of the bulbous section. The inner radial may represent two fused elements, a small inner and a larger outer one, if a densely staining vertical bar represents a line of fusion. The innermost pelvic fin ray is moveably articulated with this radial (see Gosline, 1961).

On the upper surface of the ischial swelling there is a stout L-shaped ossicle, lying with one arm closely but moveably applied to the bone. The tip of the upper half of the first pelvic ray articulates with the posterior face of this ossicle. Articulating with its dorsal face is a small plate of slightly calcified bone lying parallel to the long axis of the girdle (Text-fig. 30). In life this plate is embedded (albeit super-

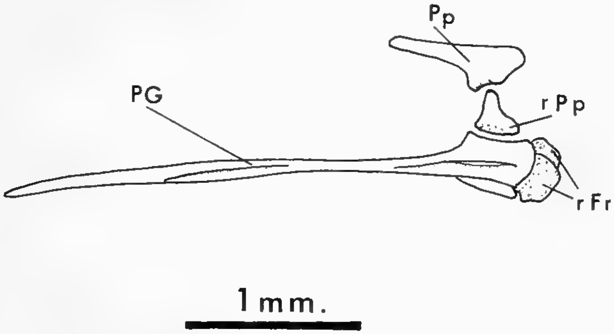

FIG. 30. Pelvic girdle and associated pelvic plate of the right side in medial view.

ficially) in the body muscle; I have been unable to trace any ligamentous connection between the plate and any part of the pelvic girdle or fin.

The plate is variable in outline, and can even be of a different shape on either side of one fish. Basically, however, it is anvil-shaped, with the foot directed ventrally and always clearly formed into an articulatory surface.

Whitehead (1963*a*) identified this enigmatic bone as a pelvic scute, and suggested that it represented an early stage in the evolution of a typical clupeoid pelvic scute from a pelvic splint bone. He did not realize at that time that the bone was articulated, through a radial-like element, with the pelvic girdle.

I find difficulty in accepting Whitehead's interpretation (see below), partly because of the articulation, and partly because the pelvic scutes in other clupeomorphs are so similar to abdominal scutes. Admittedly, the presence of the pelvic scutes in otherwise scuteless forms requires explanation, and at present such an explanation is not readily forthcoming. It seems, however, that the answer will only be found when more is known about the phyletic history of the Clupeomorpha. An aspect of this history particularly relevant to the scute problem is whether or not the earliest clupeoids were scuted, and if they were, what was the nature of the scutes.

The abdominal midline in *Denticeps* is covered by a single row of transversely V-shaped and deeply keeled scales which can certainly be considered scute-like (Text-fig. 31). The scales do, however, differ from typical clupeoid scutes in lacking a protracted ascending arm. But, could not the *Denticeps* abdominal scute-scale represent an early stage in scute evolution? The arm could develop through differential growth of the upper margin.

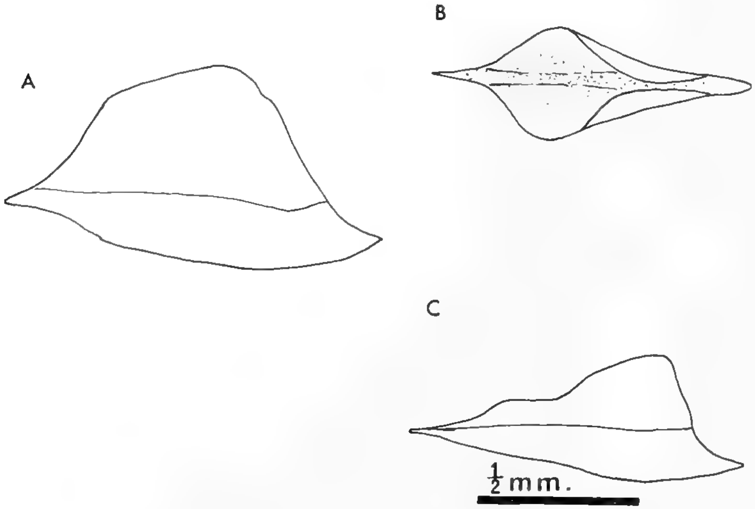

Fig. 31. Ventral scutes. (A) Abdominal (prepelvic) scute in left lateral view (B) Pelvic scute from above, anterior to the left. (C) Pelvic scute in left lateral view.

In *Denticeps* there is no break in the continuity of abdominal scute-scales at the pelvic fin base. However, the scale between the fins is shorter, and of a different form. Whereas the others are of a simple U or V cross-section with the arms diverging, the pelvic scale is dorsally constricted over its posterior half. As a result, the arms almost meet medially. The anterior half also differs since the arms do not rise steeply but lie almost horizontally. (Text-fig. 31B). The constricted part of the scale fits closely behind the conjoined halves of the pelvic girdle, while the nearly horizontal forward section lies immediately anterior to the base of the innermost fin rays. Indeed, seen *in situ*, this scale closely resembles the medial part of the pelvic scute in *Spratelloides delicatulus* figured by Whitehead (*op. cit.*, fig. *2b.*). Lateral and dorsal growth of the anterior part of the *Denticeps* scale would produce a *Spatelloides* type of scute.

Thus, I would suggest that the pelvic scute in clupeoids is derived from an abdominal scute (through perhaps, a stage of scute-scale) and not from a pelvic splint bone as Whitehead (1963*a*) argues. It this is so, then the bony pelvic plate of *Denticeps* is another structure altogether, and one not directly connected with the evolution of pelvic scutes in the template-model fashion that Whitehead postulates.

No other clupeomorph fish appears to have a pelvic plate like that of *Denticeps*, and its identity and homology are not obvious. A lateral pelvic plate, possibly articulating with the girdle, occurs in an atheriniform fish identified by Sewertzoff (1934) as *Belone acus*. I have dissected a specimen of *Belone belone* (probably the species actually seen by Sewertzoff) and find that although there is a vertical plate associated with the ischial region of the girdle, it appears to be continuous with the girdle and not moveably articulated, (which is what I take Sewertzoff to mean when he describes it as " gelenkig verbunden "). Sewertzoff (*op. cit.*) was unable to identify the plate in *Belone* with any other structure in the teleostean pelvic girdle, and concluded that " Es ist eine Neubildung ". But, if it is not a separate ossification, then it would seem to be merely a localized hypertrophy of the girdle. Similar plates are found in species of *Scomberesox* (personal observation), and a flattened or stylar process occurs posterolaterally from the girdle in many exocoetids, scomberesocoids and adrianichthyoids (Rosen, 1964).In all these fishes, the process is continuous with the girdle.

The situation in *Denticeps*, where there is a distinct articulation (through a radial-like ossicle) between plate and girdle, does not seem to be comparable with the atheriniform condition described above. Rather it invites comparison with the radial and the proximal end of a pelvic fin ray.

Could it perhaps be, as Whitehead suggested, homologous with the pelvic splint bone found in a number of lower teleostean fishes (Gosline, 1961; Patterson, 1964) but not in the Clupeoidei (Whitehead, 1963*a*)? Pelvic splints are usually unpaired bones (*Albula* is apparently exceptional, see Whitehead, *op. cit.*), lying asymmetrically to the fin axis, and not having direct contact with the girdle. Patterson (*op. cit.*) believes splint bones to be derived from fulcral scales, and is the only author to express views on their origin. If Patterson's interpretation is correct (but he admits it is only speculative) then the pelvic plate in *Denticeps* is unlikely to represent the remnants of a pelvic splint. Unless, of course, it is a fulcral scale that has sunk further into the body than is the case with typical splint bones, and developed a sesamoid radial articulation with the girdle.

On the other hand, if pelvic splints are reduced fin rays which have lost their basal articulation with the girdle, *Denticeps* could represent another trend. That is, one in which the basal articulation is retained but the distal portion of the ray, and most of its head, is lost (see below).

Without more fossil and comparative histological evidence it is impossible to develop either suggestion further. Whatever the outcome, the pelvic plate in *Denticeps* remains an unusual and highly characteristic structure.

Another unusual feature of the pelvic fin is its branched outer (i.e. first) ray, distinguishable from the other four rays only by its slightly greater length. Branched first pelvic rays are of rare occurrence amongst teleosts, but are recorded from two distantly related families, the Astronesthidae (Stomiatoidei) and Aphredoderidae (Percopsiformes). The absence of an unbranched and relatively enlarged first ray in *Denticeps* (together with the low pelvic ray count), coupled with presence of the pelvic plate, might suggest that the plate represents an aborted first ray.

ADDITIONAL NOTES ON THE OSTEOLOGY OF *PALAEODENTICEPS TANGANIKAE* GREENWOOD 1960

Since the original description was published (Greenwood 1960) I have been able to examine four more specimens from the same deposits (at Singida, Tanzania). This material, together with the better knowledge I now have of the living genus, enables me to reinterpret certain features of the fossils. In turn, this has led to a rediagnosis of the genus *Palaeodenticeps*.

Recent work on other fossil fishes from the same beds as *Palaeodenticeps tanganikae* also suggests that the genus may be somewhat older (possibly Oligocene) than the Miocene date at first supposed (see Greenwood & Patterson, 1967).

Thus, the original description of *P. tanganikae* can be amplified and amended as follows:

Syncranium. In the holotype of *P. tanganikae* (B.M. [N.H.], reg. no. P. 42610), part of the pterotic can be recognized (see pl. 2 in Greenwood, *op. cit.*). It shows the two large, contiguous openings for the infraorbital and preopercular laterosensory canals just as in *Denticeps clupeoides*. Immediately behind the pterotic fragment there is an almost entire extrascapular, which differs little from that of *Denticeps*.

An elongate fragment of bone lying in the orbit of the holotype is almost certainly not the supraorbital (see fig. 2, p. 7, Greenwood, *op. cit.*). The supraorbital of *Denticeps clupeoides* is a small, cuboid bone situated anteriorly in the orbit (see above, p. 224). There is the possibility that the bone is the supraorbital ledge of the frontal, which Clausen originally identified as the supraorbital (see p. 224). However, the ledge carries a row of strong odontodes; these are not visible in the fossil, and the bone does not have the pitted appearance of a surface which has lost its odontodes. I am, therefore, now inclined to identify the bone as part of the orbitosphenoid, probably its ventral margin. Certainly its position relative to the skull roof and to the parasphenoid does not negate this new interpretation.

That the posteroventral preopercular " spine " is shorter in *Palaeodenticeps* than in *Denticeps* is confirmed by the additional material. The large depression situated near the base of the vertical arm of the preoperculum in *Palaeodenticeps* (Greenwood, *op. cit.*, p. 7) is apparently equivalent to the upper posterior opening in *Denticeps* (see p. 238 above). Its greater prominence in *Palaeodenticeps* may be correlated with the shorter " spine " in that genus.

Palaeodenticeps was thought to differ from *Denticeps* in having a " toothed " suboperculum but it is now known that odontodes also occur on this bone in *Denticeps* (see p. 240).

Jaw structure in both genera appears to be remarkably similar, although there are fewer maxillary odontodes in *Palaeodenticeps*. My earlier remarks about fewer odontodes on the dentary of the fossil are not confirmed by the new material.

The bone tentatively identified as a urohyal in the holotype now seems more likely to be the dentary of the left side protruding from under the right dentary (Greenwood, *op. cit.*, fig. 2 and pl. 2). If it is the urohyal, then it is a much stouter bone than in *Denticeps*.

Axial skeleton. The marked difference in the number of vertebrae characterizing the genera (thirty-one or thirty-two in *Palaeodenticeps*, cf. forty in *Denticeps*) is confirmed by the additional fossils, all of which have thirty-two vertebrae. Undoubtedly correlated with these differences is the fact that there are ten pairs of attached pleural ribs in *Palaeodenticeps*, and twelve pairs in *Denticeps*. Both genera have two pairs of " floating ribs " associated with the ultimate and penultimate abdominal vertebrae (and not three pairs as I indicated in the original description of *Palaeodenticeps*).

There is close similarity in the caudal fin skeleton of both genera. The difference in the number of upturned vertebrae, which I noted in 1960, is probably of no significance since in *Denticeps* there are only two vertebrae showing distinct inclination (ural I and II), as is the case in *Palaeodenticeps*.

The size, shape and relationships of the single uroneural are identical in both genera. In my description of *Palaeodenticeps*, I implied, by using the words " ultimate uroneural ", that another was present. It is now clear that only one uroneural is present in *Palaeodenticeps*, and that it extends further posterodorsally than I described.

Unfortunately, it is still not possible to determine the number of epurals present in the fossils. In the holotype there appear to be two epurals, but in another specimen (from Sheffield University) three seem to be present.

This Sheffield University specimen clearly shows that the first hypural is free from the ural centrum, and that there are three hypurals in the upper lobe of the caudal fin skeleton (that is, just as in *Denticeps*).

Contrary to my original counts, the number of principal caudal fin rays in both *Denticeps* and *Palaeodenticeps* is identical, i.e. eight branched and one unbranched ray in each lobe of the fin. Both genera also have the same number of spinous procurrent rays.

Pectoral girdle. No further information is available on the postcleithrum of *Palaeodenticeps* (see Greenwood, 1960, p. 6), and the possible generic differences in this structure must remain an open question.

Discussion. When this new information is taken into account it is necessary to redefine the genus *Palaeodenticeps* as follows: a member of the family Denticipitidae, differing from the extant genus *Denticeps* in having fewer vertebrae (thirty-one or thirty-two cf. forty), lateral line scales (thirty-two or thirty-three cf. thirty-seven to forty) and pleural ribs (ten pairs cf. twelve), and in having the origin of the dorsal fin above or slightly anterior to the first anal fin ray.

The resemblances between *Denticeps* and *Palaeodenticeps* are now seen to be closer than was previously realized. Possibly the two genera should not be maintained. However, as judged by the criteria employed in the systematics of extant clupeoids, generic status is justified. From the evolutionary viewpoint the morphological differentiation that took place in the family between Palaeogene (probably Oligocene) times and the present is of a fairly low order.

RELATIONSHIPS AND CLASSIFICATION OF THE DENTICIPITIDAE

Neither Clausen (1959) nor Greenwood (1960) paid more than passing attention to the systematic position of the Denticipitidae. Clausen, at least implicitly considered that the family has decided clupeoid affinities. He also stated that it had many features in common with the Elopidae, Albulidae and Osteoglossidae.

I can find no grounds for maintaining the suggested affinity with the Elopidae and Albulidae (or for that matter with the Megalopidae). Clausen (*op. cit.*) probably thought that the supposed medioparietal condition of *Denticeps clupeoides* was elopoid; but, as is now known, the parietals are not in contact (see p. 235). Greenwood *et al.* (1966) stated that the caudal fin skeleton of *Denticeps* " . . . approaches the condition of the elopiforms . . .". This view too must now be abandoned since it was based on insufficient detailed knowledge of the skeleton. As will be discussed later, the denticipitid caudal skeleton is definitely clupeomorph, albeit somewhat different from the typical condition seen in extant clupeoids.

In both general and detailed skull morphology, the denticipitids are far removed from the elopoids. Likewise there are no significant points of resemblance in the branchial skeleton. The specializations of the denticipitids in both these systems make it impossible even to suggest any close relationships with the more primitive elopoids. The articulation of the upper jaw elements is similar in both groups, but since the condition is a primitive one, it is of little value as a phyletic indicator.

Possible denticipitid--osteoglossid relationships are difficult to substantiate, but relationships with the Osteoglossomorpha as a whole are possible.

At first sight, the enlarged, partially contiguous nasals of the denticipitids resemble the osteoglossid condition. But, there are differences in detail which considerably reduce the resemblance (for instance, their suprafrontal situation, medial contact confined to the hind limits, and their flimsiness). In fact, it is difficult to visualize how the denticipitid condition could be related to any evolutionary stage leading to or from the osteoglossid condition.

There is, however, a greater resemblance between the nasals of *Denticeps* and those of certain notopteroid fishes (currently classified in the Osteoglossomorpha), a resemblance probably correlated with the existence of open, gutter-like supraorbital laterosensory canals in both groups (Greenwood, 1963). The phyletic significance of this similarity in the cephalic laterosensory system is not fully apparent, especially since the denticipitids and notopterids both differ from and resemble one another in several other cranial characters. If these resemblances have any phyletic significance, they must be of great antiquity because both lines have now evolved away from one another to a considerable degree.

The relationships of upper jaw elements (including the palatine) to each other and to the skull, are rather similar in the denticipitids and osteoglossids. But, since this arrangement is a very simple one (especially in *Denticeps*) and presumably is primitive, no phyletic importance can be attached to it. In other orobranchial characters the two families are very dissimilar, and the dissimilarity can be extended to include all osteoglossomorphs (see Greenwood *et al.*, 1966; too little is known about the orobranchial region in the recently discovered fossil, *Singida jacksonoides*, to include it in this generalization [see Greenwood & Patterson, 1967]).

Similarly, there are very few resemblances in neurocranial architecture; the Osteoglossidae retain a primitive structure including a well-developed basipterygoid process. Other Osteoglossomorpha (Notopteroidei and Mormyriformes) show a more specialized level of neurocranial organization, but these specializations are not of the type found in the Denticipitidae (excepting, perhaps, the cephalic laterosensory canal system in certain Notopteroidei).

There is a noticeable resemblance between the preoperculum in denticipitids, especially *Palaeodenticeps*, and certain osteoglossids (especially *Scleropages* and *Osteoglossum*, to a lesser extent *Arapaima* and *Heterotis*), the Singididae and the Notopteridae. In all these fishes the entire ventral limb of the preoperculum is virtually an enlarged laterosensory canal with several ventral openings arranged in a straight line, and with the inner face of the bone projecting beyond this line. Often there is a large opening near the junction of the horizontal and vertical preopercular arms, and the posteroventral margin may be protracted.

This type of preoperculum cannot be considered truly primitive. Rather, it is a derivative of the primitive type found in *Thrissops* and its allies (Nybelin, 1964, 1967). That it occurs in such otherwise dissimilar groups as the Denticipitidae and certain Osteoglossomorpha may be significant as an indicator of distant relationships between the groups. It would be on a par, phyletically speaking, with the notopterid-denticipitid similarities in cephalic lateral-line arrangements (see above).

The short parasphenoid of *Denticeps* is another osteoglossid-like feature (but a short parasphenoid also occurs in the Engraulidae among the clupeoids), as is the direct articulation between rib head and centrum (Greenwood, 1963). Neither of these characters has been sufficiently studied amongst teleosts to assess their significance.

The types of caudal fin found in the known Osteoglossomorpha are characteristic (see Greenwood, 1967, Greenwood & Patterson, 1967, Greenwood *et al.*, 1966), and do not appear to be closely linked with the clupeomorph type to which the denticipitid caudal clearly belongs. However, all could be derived from the *Thrissops-Allothrissops* type (see Patterson, 1967).

Other osteoglossid-like characters of *Denticeps* which Clausen (1959) noted are the loss of supramaxillae, and the position of the median fins. The relative position of the dorsal and anal fins is unlikely to be of value in determining phylogenies. Although loss of the supramaxillae is certainly a specialized feature in both groups, I do not know what value to attach to it.

To summarize: there are certain characters, all of a specialized or derived nature, common to the Denticipitidae and the osteoglossomorph fishes. The nature of these characters, taken in concert with those in which the two taxa differ, strongly suggests that if any phyletic connection exists between them it is a distant one, possibly from as far back as the level represented by the Jurassic genus *Thrissops*.

The clupeomorph affinities of the Denticipitidae, in contrast, are clear, although the relationships of the family with the Clupeoidei are somewhat obscure.

The living Clupeomorpha are trenchantly defined on the basis of three character complexes (Greenwood *et al.*, 1966), namely: (i) The presence of intracranial swimbladder diverticula encased in bony bullae developed in association with either the prootic and pterotic bones, or the prootic alone; the prootic bulla is intimately associated with the utricular recess. (ii) An intracranial space, the *recessus lateralis*, into which open the major cephalic laterosensory canals as well as the temporal canal; the *recessus* is separated by a membranous fenestra from the perilymphatic spaces of the ear (see Wohlfahrt, 1936). (iii) The caudal fin skeleton (see below; also Hollister, 1936; Gosline, 1960, 1961; Greenwood *et al.*, 1966, and Cavender, 1966).

To the best of my knowledge, none of these characters (either singly or in combination) has been found in any other teleostean group (see also Greenwood *et al.*, *op. cit.*).

The intracranial swimbladder diverticula of *Denticeps clupeoides* are typically clupeomorph in their basic morphology and interconnections with each other and with the inner ear. What differences there are between *Denticeps* and other clupeomorphs are concerned with the relative sizes of the bullae.

The *recessus lateralis* in *Denticeps* is particularly interesting because, compared with the typical clupeoid condition, it is incomplete in not having a separate opening for the supraorbital laterosensory canal (see p. 231).

In clupeoid fishes a posterior extension of the frontal carries this canal backwards to open into the *recessus* (which is bounded by the pterotic and sphenotic, and partly roofed by the frontal) in an anteromedial position. In *Denticeps* the frontal canal ends short of the *recessus*, and external to it. It is, however, connected to a *recessus* opening (that for the infraorbital canal) through the tubular dermosphenotic (see Text-fig. 4). The dermosphenotic (i.e. the uppermost infraorbital bone) in cluepeoids carries the infraorbital canal and opens into the *recessus* through a separate foramen. Thus, *Denticeps* cannot be said to have a typical clupeoid *recessus lateralis*. But, apart from the shared supra- and infraorbital openings (and the correlated difference in frontal morphology) the *recessus* is like that of the clupeoids, and includes a fenestral connection with the perilymphatic system.

Nothing is yet known about the evolution of the clupeoid *recessus*. It is apparently not developed in *Diplomystus*, at least in those species which have been studied in detail (see Patterson, 1967). The Cretaceous species *D. brevissimus* figured by Patterson (*op. cit.*) seems to have a superficial temporal lateral-line canal, and the infraorbital and preopercular canals are well-separated from one another proximally. By analogy with living clupeoids these details suggest that the *recessus* was not developed. Also significant is the well-developed, large and flat dermosphenotic in *Diplomystus brevissimus.* Its relationships with other canal-bearing bones of the postorbital region are quite unlike those of the dermosphenotic in extant clupeoids or *Denticeps*, again suggesting the absence of a *recessus.*

Possibly *Denticeps* (and *Palaeodenticeps*, see above, p. 258) represent an advanced stage in *recessus* evolution but one differing in detail from the clupeoid evolutionary pattern. That is, it has reached a point at which the *recessus* has developed and, as it were, captured the cephalic canals save for the supraorbital one. The dermosphenotic, primitively linking both the supraorbital and infraorbital canals with the temporal canal (Gosline, 1965), still serves this function, albeit somewhat indirectly. In fact, it is more closely associated with the supraorbital than with the infraorbital canal. The clupeoid pattern, on the other hand, could have developed through essentially this stage, but diverged as a result of the dermosphenotic becoming more closely associated with the infraorbital canal, the supraorbital canal developing an independent opening into the *recessus.* The dermosphenotic continued to link the infraorbital and temporal canals but via the *recessus.*

The caudal fin skeleton of extant clupeoid fishes (at least when adult) is a very characteristic structure, in itself diagnostic for the group. Its principal features are as follows: (i) Hypural 1 is completely separate from the first ural centrum, and is usually separated from it by a distinct gap. (ii) The first ural centrum is greatly reduced in size, sometimes to little more than an enlargement at the base of hypural 2, which is always indistinguishably fused with it. (iii) The second ural centrum is always present (probably fused in with the posterior ural centra if these are present). (iv) The first uroneural extends anteriorly to the first preural centrum, and fuses with it (two other uroneurals are present). (v) The neural spine of the second preural centrum is elongate, its tip reaching to the same level dorsally as that of the third preural vertebra; a procurrent ray articulates with its tip.

In most clupeoids the parhypural (haemal spine of the first preural vertebra, equivalent to the first hypural in Gosline's [1960, 1961] terminology, and Hollister [1936]) is autogenous but closely articulated with the centrum. It may, however, be fused with the centrum in some Dussumieridae (Gosline, 1960). Certain dussumierids may also provide another exceptional condition, namely the fusion of the first ural and preural centra (see Hollister's [1936] figs. 42–44. of *Jenkinsia*).

The denticipitid caudal skeleton differs somewhat from the clupeoid type but is clearly related to it in general plan and in detail (Text-fig. 29, p. 253). Hypural 1 is autogenous but still articulates with the first ural centrum. The articular head is, however, markedly narrower than the proximal part of the hypural body. Hypural 2, like that of the clupeoids, is fused indistinguishably with the centrum. Compared to clupeoids, the centrum of the first ural vertebra in denticipitids is large, in fact only a little smaller than the first preural centrum. As in the clupeoids, a second ural centrum is present as a reduced structure. The first (and only) uroneural extends forward to the first preural centrum. Unlike the first uroneural of clupeoids, the uroneural in denticipitids does not fuse with the centrum, but fits into a pit on its dorsolateral face. No trace of more than one uroneural could be found in *Denticeps* or *Palaeodenticeps*. Like the clupeoids, the neural spine of the second preural vertebra reaches the dorsal body outline, and has a procurrent ray (in this case, a " spine ") articulating with it. The parhypural is completely fused with the first preural centrum in *Denticeps*, but is usually autogenous in clupeoids; the condition in *Palaeodenticeps* cannot be determined.

The differences are, in my opinion, relatively slight, and in most respects are variants of the clupeoid type, variants which could be considered representative of a primitive condition. On the other hand, the loss of two uroneurals, and the presence of only five hypurals and two epurals seem to be specializations.

In most of those caudal characters in which it departs from the clupeoid condition, the denticipitid skeleton resembles that of the fossil clupeomorph genus *Diplomystus* which has a time range from Cretaceous to Eocene (Cavender, 1966; Patterson, 1967).

For example, the relationships of hypurals 1 and 2 to the first ural centrum are identical; in both taxa the first uroneural reaches the first preural centrum but is not fused with it, and the parhypural is fused with its centrum (Text-fig. 32).

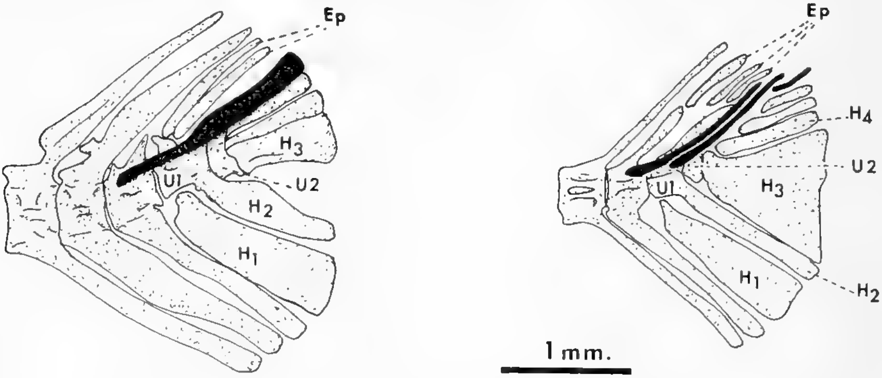

FIG. 32. The caudal fin skeletons of : (left). *Denticeps clupeoides* and (right) *Diplomystus dentatus* (compounded from several specimens in the B.M. [N.H.)].

Differences between the denticipitid and *Diplomystus* caudal skeleton also differentiate the denticipitids from the clupeoids. Thus, the caudal skeleton of the Denticipitidae can be considered a specialized variant of the *Diplomystus* type.

Greenwood *et al.* (1966) expressed the view that the caudal skeleton of *Denticeps* ". . . approaches the condition of the elopiforms ". This view is no longer tenable. Our opinion that it is one of the most primitive types shown in living teleosts also requires some modification.

Like the *recessus lateralis*, the caudal skeleton of the Denticipitidae appears to represent, in its basic morphology, a relatively primitive state, but one still manifestly of the clupeomorph level. Cavender (1966) seems to imply that the *Diplomystus* caudal skeleton is not of a clupeomorph type (i.e. Clupeomorpha *sensu* Greenwood *et. al.*). That there are differences will be apparent from the foregoing discussion, but that these differences can still be contained within a distinctively clupeomorph pattern should also be apparent[1].

Although the Denticipitidae possess the three major diagnostic features of the Clupeomorpha, in two of these they show a more primitive level of organization than do other living members of the superorder.

Nor are these the only characters in which the family departs from the generality of clupeomorphs. The deeply embedded scales contrast with the cauducous, flimsy scales of the clupeoid fishes, as does the complete lateral-line of the body. Both are " primitive " relative to the clupeoid condition. The simple scutes (without elongate ascending arms) appearing as folded, keeled scales and the but slightly differentiated pelvic scute (see p. 257), are not readily interpreted since both could be interpreted either as " primitive " or " derived, through reduction ". *A priori*, one is inclined to consider the condition as primitive (especially for the pelvic scute which is enlarged in the otherwise scuteless Dussumieridae; but, see Whitehead [1963*b*]. Yet " typical " clupeoid scutes occur in the Cretaceous *Diplomystus* species (Schaeffer, 1947).

The absence of supramaxillae in Denticipitidae is an advanced character, and one that sets the family apart from all known Clupeomorpha except the monotypic family Congothrissidae (Poll, 1964). The poorly developed coronoid process of the lower jaw is also an atypical clupeomorph condition, but one which is less easily classified in terms of specialization or primitiveness; however, a high coronoid occurs in *Diplomystus*.

The neurocranium provides several interesting problems, many of which cannot be investigated in depth because of insufficient information about the Cretaceous clupeomorphs. The extremely short parasphenoid of *Denticeps* (p. 228) is approached only by certain engraulids (*Coilia* species) amongst the living Clupeomorpha. But even in *Coilia* the parasphenoid reaches the anterior part of the basioccipital (just contacting the prootics in *Denticeps*). In other clupeoids the parasphenoid extends to below the posterior part of the basioccipital, and often to beyond the posterior margin of that bone (see Ridewood, 1905).

Denticeps also differs from all known extant clupeoids in having a tripartite occipital condyle (see p. 233). A rather similar condyle exists in *Megalops* (see p. 233) and a very similar one is found in the Jurassic elopoid *Anaethalion angustissimus* (Nybelin, 1967, pl. VIII, fig. 6). In this respect *Denticeps* must be considered primitive, but the short parasphenoid is less easily evaluated. Probably it should be considered a specialization, as should the posteriorly produced parasphenoid in those clupeoids where it extends beyond the condyle. In *Denticeps* the great enlargement of the prootic bullae (see p. 229) may be correlated with the posterior

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[1] Schaeffer (1947) places *Diplomystus*, and the related *Knightia*, in the family Clupeidae, a placement accepted by Cavender (1966). From what is known about the caudal and cranial osteology of *Diplomystus* and the Clupeidae (Cavender, *op. cit.*; Patterson, 1967; Gosline, 1960; Hollister, 1936; Greenwood *et al.*, 1966) this relationship is no longer acceptable. *Diplomystus*, at least, should be accorded familial rank (less is known about *Knightia* but it should probably be kept with *Diplomystus*).

shortening of the parasphenoid; it may also be significant that in *Coilia* too the bullae are hypertrophied.

The largely cartilaginous ethmoid region of *Denticeps* is distinctive, even when compared with that region in clupeoids which also only reach a small adult size. The small size and posterior position of the vomer in *Denticeps* is approached by the Engraulidae alone amongst clupeomorphs (Ridewood, 1905; Whitehead, 1963*a*). But, even when compared to the engraulid condition, the vomer of *Denticeps* is much smaller, and little more than a flat disc of bone.

It is with the Engraulidae too that the Denticipitidae show most resemblance in cephalic lateral-line canal morphology. Among clupeomorphs (both fossil and living) only the engraulids and denticipitids have open, gutter-like supraorbital canals, bridged by bony struts, and closed by skin. In details of strut pattern, and of course in relation to the nasals anteriorly and the *recessus lateralis* posteriorly, the two families differ. This type of supraorbital canal can only be considered a specialization. Its functional significance is unknown.

The enlarged, superficially placed and complex nasals (p. 220) of the denticipitids are not encountered among any other clupeomorphs. Again, the only interpretation possible is one of specialization, possibly correlated with the open supraorbital canal system (*vide* the Notopteroidei; Greenwood, 1963).

Clausen (1959) thought that the extension of the cephalic lateral-line tubules onto operculum was "... an important characteristic of the family Denticipitidae ...", and that the arrangement in *Denticeps* might be "... unique among teleosts, although it bears a certain resemblance to that found in Clupea (personal observation) and possibly also to that seen in some other clupeids (Berg, 1940)". Actually, the resemblance is extremely close, differing only in minor details like the fewer ramifications of the canals in *Denticeps*. This opercular radiation of canal branches occurs, with slight variations, in all living clupeomorphs (see Whitehead, 1963*a*, and Wohlfahrt, 1937). As in the clupeoids, the canals in *Denticeps* do not house neuromasts (personal observations) but merely provide additional openings to the laterosensory system.

The hyopalatine series show a few peculiarly denticipitid characters. One of these is the spatial relationship of the metapterygoid and the hyomandibula. In all clupeoids I have examined (at least one representative of all families and subfamilies) the posterior part of the metapterygoid distinctly overlaps the hyomandibula for an appreciable distance, thereby forming a clearly circumscribed vertical pocket between the bones. The anterior margin of the pocket is closed since the metapterygoid is slightly concave in that region, and curves inwards to contact the anterior, flange-like projection of the hyomandibula.

No such pocket is formed in *Denticeps*, although there is a slight posterior overlap of the metapterygoid and hyomandibula.

These osteological differences are correlated with differences in the jaw musculature of denticipitids and clupeoids. In clupeoids (dissections were made of *Clupea harengus*, *Engraulis encrasicholus* and a species of *Coilia*) the *levator arcus palatini* is in two distinct parts (Text-fig. 34). The upper, and larger, originates mainly on the frontal but partly on the sphenotic (posteriorly in *Clupea* and *Engraulis*, more anteriorly in *Coilia*); it has a narrow insertion onto the head of the hyomandibular ridge. The lower (and smaller) division has a narrower origin on the ventral face of the sphenotic. It soon broadens to insert partially on the anterior face of the hyomandibular ridge, partly around the metapterygoid lip of the pocket mentioned above, but mainly into the pocket (Text-fig. 34). Within the pocket, the muscle attaches to both the hyomandibula and the metaptergyoid. This condition was found in all the clupeoids examined.

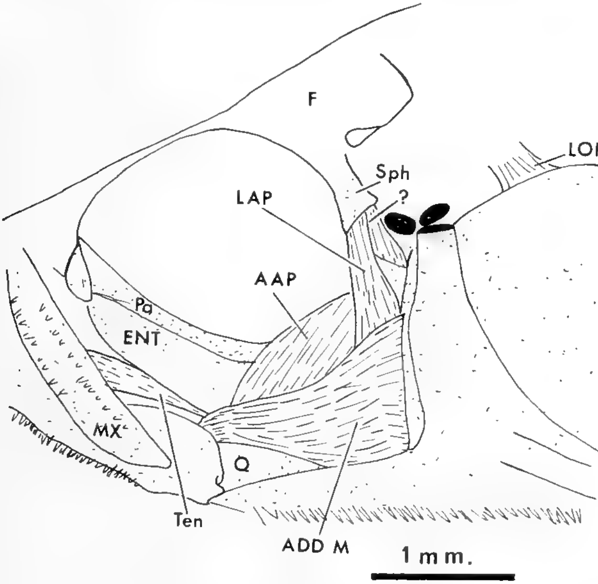

Fig. 33. *Denticeps clupeoides.* Jaw muscles. Abbreviations for muscles: AAP: adductor arcus palatini; ADDM: adductor mandibulae series; DILOP: dilatator operculae; LAP: levator arcus palatini; LAP L: lower division of levator arcus palatini; LAPU: upper division of levator arcus palatini; LOP: levator operculae; ?: possible remnant of dilatator operculae muscles. Ten: tendon. For other abbreviations see p. 216.

Denticeps shows a much simpler arrangement. There is but a single division of the *levator* muscle. It originates on the ventral face of the sphenotic, is columnar in shape, and inserts on the hyomandibula (Text-fig. 33). No trace of the large upper division seen in clupeoids could be found; presumably the *levator* in *Denticeps* is homologous with the lower *levator* division in clupeoids.

Other myological differences (Text-figs. 33 and 34) are the presence of a large *adductor arcus palatini* in *Denticeps* (where it occupies almost the posterior third of the orbit floor) and the apparent absence of this muscle in the clupeoids examined. Also apparently absent, this time in *Denticeps*, is a *dilatator operculi*; this contrasts with the extensive *dilatator* in clupeoids. *Denticeps* has, originating from the sphenotic and pterotic, a small tendinous muscle which inserts on the preoperculum

(Text-fig. 33). Since part of the *dilatator operculi* in clupeoids originates in this area, the muscle in *Denticeps* may be its homologue.

The absence (or great reduction) of the *dilatator operculi* in *Denticeps* may be correlated with the shape of the greatly enlarged pterotic and the resulting position of the lateral-line openings into the *recessus lateralis*. If a *dilatator* was present it could only lie across these openings (Text-fig. 33). In the clupeoids examined (Text-fig. 34), despite their varied skull forms, the *recessus* openings are so situated as to lie above the muscle, whose upper margin skirts the lower lip of the foramina. (Parenthetically it may be noted that a *dilatator* fossa is present in the clupeoids, but not in *Denticeps*.)

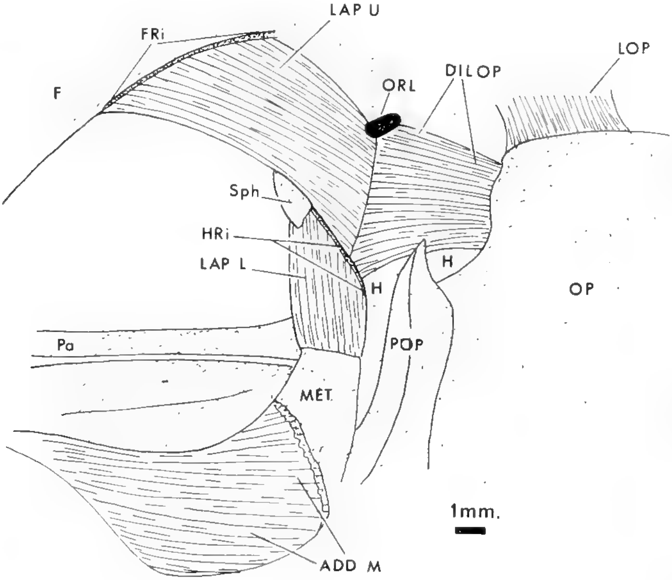

Fig. 34. *Clupea harengus.* Jaw musculature (for abbreviations see Fig. 33). The head of the adductor mandibulae series has been dissected away to show the superficial insertion of the levator arcus palatini muscle. H: Hyomandibula; HRi: ridge on hyomandibula.

There are other myological differences, but these will not be discussed here. They do, however, reinforce the impression gained from those differences discussed above, namely, that compared with clupeoids, the orobranchial musculature of *Denticeps* is in part highly specialized, and in part much more primitive. Thus, for the moment it is impossible to classify the system in *Denticeps* as more or less primitive than the clupeoid condition.

A similar conclusion is reached when the hyobranchial skeleton is considered. In its gross morphology, the branchial skeleton lacks the typical elongation of individual parts which characterizes most extant clupeomorphs, and the few gill-rakers are relatively short and widely spaced. *Denticeps* also differs from most (but not all) clupeoids in having the infrapharyngobranchials well-separated in the midline (Nelson, 1967). In all these respects *Denticeps* does not show the specializations of the clupeoids.

However, *Denticeps* does show other branchial specializations seldom found in the clupeoids, namely the almost complete reduction of dermal tooth-plates associated with the hyobranchial skeleton (see Nelson, 1967; and Text-figs. 21 and 22). Only the fifth upper pharyngeal tooth-plate is present as a separate element, and there are a few teeth fused to the fifth ceratobranchial. The Pellonulinae alone among the clupeoids show a reduction approaching that of *Denticeps*, but in the pellonulines a basihyal tooth-plate is present as well (Nelson, *op. cit.*)

A reduction in the number of branchiostegal rays is considered to be a derived condition among clupeoids (Whitehead, 1963*b*.). In this respect the Denticipitidae show greater specialization than most clupeoids (p. 241). Since the number of branchiostegal rays in some *Diplomystus* species is probably about seven to ten (personal observation), the denticipitid condition is specialized in that context also.

The relatively short and simple intermuscular bones (p. 252) of the Denticipitidae, coupled with the absence of epineurals, stand in strong contrast to the situation found in extant clupeoids. On the basis of the simplicity of these bones, and especially the absence of epineurals, the denticipitid condition should be considered primitive.

Little information is available on the pectoral girdle of clupeomorph fishes, so the girdle in *Denticeps* (p. 245) cannot be evaluated fully. The scale-like postcleithra, however, seem to be outstanding and probably unique characters representing a primitive level of organization. Also at a primitive level is the double row of pectoral radials, which are otherwise only recorded in *Chirocentrus* among the extant clupeomorphs.

The pelvic plate is a baffling structure (see p. 255). I have examined the pelvic girdle in representatives of all clupeoid families, and have failed to find anything resembling a pelvic plate (*pace* Whitehead, 1963*a*). Not can I find any reference to a similar structure occurring in any other teleosts (see p. 257).

The distinctive preoperculum of the Denticipitidae is discussed above in relation to the Osteoglossomorpha (p. 261). It should probably be considered a specialized development of the *Thrissops* type, and is certainly distinctive among the Clupeomorpha.

Finally, consideration must be given to one of the most outstanding features of the Denticipitidae, the occurrence of odontodes on the roofing bones of the skull, and extraorally on the jaws (for a detailed discussion of odontodes, see Ørvig, 1967).

Clausen (1959) argues that the shape, structure and distribution of the " denticles " in *Denticeps*, together with the fact that they are attached to " . . . normal skeletal elements of the skull and pectoral girdle . . ." is indicative of a " . . . truly primitive condition . . .". As a corollary to this argument he believes that the " dermal denticles " in other teleosts (especially on the scales of siluroids and the rostrum of the swordfish *Xiphias*) are specializations, a view generally held. Clausen's argument regarding *Denticeps* is certainly not upheld by the fossil record, and I cannot find any other evidence to support his premises.

Consequently, I would add the occurrence of such extensive odontode patches in *Denticeps* as a specialization. We have, at present, no idea of the functional significance (if any) of the odontodes in the Denticipitidae. The proliferation of toothlike elements outside the orobranchial cavity contrasts strongly with the great reduction of dermal tooth-plates within the cavity (see above).

Taking into account the characters discussed, the Denticipitidae clearly stand apart from all other living Clupeomorpha (i.e. the Clupeidae, Engraulidae, Dussumieridae, Congothrissidae, Pristigasteridae and Chirocentridae of authors), and as far as can be told, from the fossil forms as well. Yet, in a number of fundamental characters, the family is a clupeomorph.

This departure from living forms led Greenwood *et al.* (1966) to give the Denticipitidae subordinal status (Denticipitoidei) within the Clupeomorpha. The remaining extant families were grouped together in another suborder, the Clupeoidei. Nothing has come to light in the present study that would invalidate our earlier conclusion.

When considering the phyletic relationships of the Denticipitoidei, I have been impressed by the relatively primitive condition of fundamental clupeomorph characters in the suborder. The caudal skeleton has, of course, certain specialized attributes (see p. 264) but it is still much less generally specialized than the clupeoid type. The *recessus lateralis*, by contrast, is more primitive than the clupeoid type and does not show any peculiarly denticipitoid specialization.

On this basis I would conclude that the Denticipitoidei represent a distinct trend, conservative in these and other characters, which split off from the clupeoid ancestral line well back in the history of the group. Presumably the dichotomy occurred after the evolution of a clupeomorph type of ear-swimbladder connection (since this is developed comparably in the two lines), and after the preliminary stages of *recessus lateralis* development had taken place. But, without a lot more detailed information from the known fossil clupeomorphs (especially the *Diplomystus–Knightia* complex), the possibility of parallel evolution of these characters cannot be eliminated.

The presence of unique specializations in the Denticipitoidei seems to confirm their independent trend, and perhaps reinforces the idea of a temporally distant separation from the clupeoid stem.

Other specialized characters are shared by the Denticipitoidei and the Clupeoidei. For instance, there is similarity in the ethmoid region of the Denticipitidae and the Engraulidae, particularly with regard to the position and size of the vomer; again, the two families show similarities in the organization of the supraorbital lateral-line canal. The short parasphenoid of *Coilia* is the nearest approach, among the clupeoids, to the denticipitoid condition of that bone. Loss of supramaxillae, and a marked reduction in the number of branchiostegal rays are prominent (and restricted) characters shared by the Denticipitoidei and the clupeoid family Congothrissidae. These intergroup similarities in specialized characters would appear to be instances of parallel evolution, because both the engraulids and the congothrissids show the unifying specializations of their suborder.

The overall relationships of the Denticipitoidei to the Clupeoidei are probably best expressed by Hennig's concept of " sister groups " (see Brundin, 1966; Hennig, 1966). Following this scheme the Denticipitoidei would be the plesiomorph (i.e. unspecialized) sister group of all other extant Clupeomorpha, which would form the apomorph (i.e. derived) sister group.

The resemblances between Denticipitoidei and Osteoglossomorpha (see p. 260) are more difficult to assess on a phyletic basis. That the characters involved are apparently derived ones, and do not, for example, appear among the living Elopoidei, is probably significant. For the moment, however, the possibility of convergence cannot be overruled. Greenwood *et al.* (1966) suggested that the fossil so-called Chirocentridae (the *Spathodactylus–Xiphactinus*, and *Thrissops–Chirocentrus* line of Bardack [1965]) might be allied to the Osteoglossomorpha. If the Clupeomorpha can be derived from a *Thrissops*-like stem, then the osteoglossomorph characters of the Denticipitidae could be explained as parallelism rather than convergence. Again, following Hennig's reasoning, the Osteoglossomorpha would be the plesiomorph sister group of the Clupeomorpha.

The idea of an osteoglossomorph–clupeomorph relationship is at the moment extremely speculative, and I mention it here simply in the hope that it may provoke further discussion. Patterson (1967) has also suggested a possible relationship between these groups, and has included the Elopomorpha in the relationship. The Denticipitoidei do not provide any evidence to support the inclusion of the Elopomorpha.

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NOTES ON SOME TROPICAL INDO-PACIFIC OPHIOTRICHIDS AND OPHIODERMATIDS (OPHIUROIDEA)

AILSA M. CLARK

BULLETIN OF
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Pp. 275–322; 1 *Plate,* 10 *Text-figures.*

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NOTES ON SOME TROPICAL INDO-PACIFIC OPHIOTRICHIDS AND OPHIODERMATIDS (OPHIUROIDEA)

By AILSA M. CLARK

In the course of studies on the shallow-water species of ophiuroids of the tropical Indo-West Pacific, I have sought to clarify the systematic positions of some of the less well-known species, especially of the family Ophiotrichidae. Valuable type-material has been borrowed from Dr. K. K. Günther of the Institut für Spezielle Zoologie und Zoologisches Museum, Berlin, Dr. H. B. Fell of the Museum of Comparative Zoology, Harvard and Dr. F. Jensenius Madsen of the Universitetet Zoologiske Museum, Copenhagen, to all of whom I am much indebted. This material forms the basis for the major part of this paper but in addition a new Ophiotrichid species from the collections of the Zoologisk Museum, Oslo, is included, for the opportunity of studying which my thanks go to Dr. T. Soot-Ryen and Mr. K. Knaben. Two new species of *Macrophiothrix* are also described from the British Museum collections. As for the Ophiodermatidae, the holotype of one new species is from the collections of the Smithsonian Institution, where I was able to examine it some years ago; that of the other is in the British Museum. In addition the genus *Ophiopsammus* is revived here from the synonymy of *Pectinura.*

Under the distribution headings for each species the first locality mentioned is the type-locality. The species themselves are dealt with in alphabetical order.

Ophiothrix* (*Acanthophiothrix*) *vigelandi sp. nov.

fig. 1

Ophiothrix koreana: Koehler, 1922 : 242–246, pl. 45, figs, 1–6, pl. 99, fig. 4; 1930 : 142–143. [Non *O. koreana* Duncan, 1879.]

Material. Oslo Museum, New Caledonia, Johnson and Seeberg, 18/10/1887, one specimen. Oslo Museum, Noumea Harbour, New Caledonia, Vigeland, 13/8/1959, four paratypes. B.M. No. 1967.10.23.36–38, same locality and source, the holotype and three paratypes.

Description of holotype. D.d. (disc diameter) 4·75 mm. All the arms have the tips broken; their length was probably *c.* 30 mm.

The disc is sparsely covered with predominantly trifid stumps, though the number of points ranges from one to four. In addition there are about twenty thorny spines, up to 0·8 mm. long. The radial shields are about 1·3 mm. long, or just over half the disc radius; they are almost completely naked but for three to nine, usually about six stumps similar to those on the disc scales, placed mostly towards the proximal end.

On the ventral side the stumps are a little more sparse proximally though fairly numerous near the periphery. The adoral shields meet broadly interradially proximal to the broad pentagonal oral shields.

The arms are fairly narrow; at the fifth free segment the minimum breadth is 1·1 mm. The dorsal arm plates are rhombic, about as long as broad near the arm bases but becoming relatively longer distally by attenuation of the proximal end. The distal angle is slightly truncated but for a faint median " beak " emphasized by the median carination which it continues. The consecutive plates are only narrowly contiguous. The first two ventral arm plates have the distal edge convex but on all the rest it is distinctly concave. On the proximal half of the arm the breadth of the plates just exceeds their length but the distal ones become narrower.

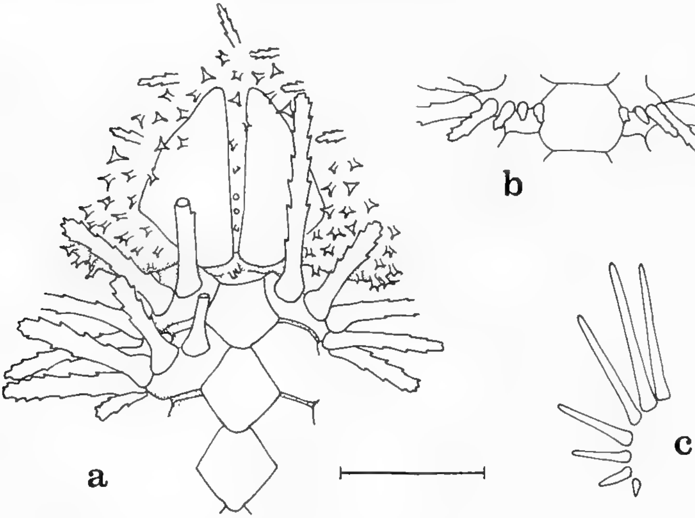

FIG. 1. *Ophiothrix (Acanthophiothrix) vigelandi* sp. nov. Holotype. a. Dorsal view of part of disc and arm base; b. ventral view of fourth free segment; c. arm spines of second free segment. The scale equals 1 mm. for a and b and 2 mm. for c.

The arm spines number seven for one or two basal segments, the two uppermost being the longest and measuring up to 2·1 mm. compared with a segment length of 0·65 mm., a ratio of 3·2 : 1. The third spine from the top measures *c.* 1·75 mm. and the lower ones are progressively shorter. The number of spines soon falls to five and their length, especially that of the uppermost ones, tends to increase so that the distal upper spines are up to 2·6 mm. long. The spines are markedly flattened dorsoventrally and so appear smooth and fairly slender when viewed along the plane of the arm. Conversely, seen from above or below, they appear strongly thorny and moderately stout, the uppermost one or two slightly tapering but the lower ones bushy at the tip or even somewhat clavate (Text-fig. 1a, b). Distally the lowest spine becomes hooked with three or four sharp teeth.

There is no tentacle scale on the first segment; on the remaining pores the scale is somewhat rugose.

The colour of the disc in spirit is pinkish and the arms are almost white except for some reddish-brown spots on some of the dorsal arm plates but more particularly on the upper side of the lateral plates.

VARIATIONS. Of the eight paratypes in the British Museum and Oslo collections, four have a conspicuous double dark line along the arms while two others show the same pattern more faintly, the lines tending to resolve into spots. The largest specimen, d.d. 5·5 mm., has the dorsal arm plates more obviously beaked at the distal end than the holotype but its disc armament is equally sparse, whereas the other specimens may have more numerous stumps than the holotype, often with very long points, as shown by Koehler (1922, pl. 99, fig. 4), presumably from one of his Philippine specimens. One specimen lacks disc spines.

REMARKS. As I pointed out in 1965 (p. 61), *Ophiothrix koreana*: H. L. Clark, 1911, is not the same as *koreana* Duncan, 1879, which belongs to *Ophiothrix* sensu stricto. It is therefore necessary to find a new name for the tropical Pacific specimens which Koehler (1922 and 1930) referred to *O. koreana* following Clark's misinterpretation.

AFFINITIES. *Ophiothrix vigelandi* is referable to the subgenus *Acanthophiothrix* on account of the relatively elongated dorsal arm plates and the position of the largest arm spines on the upper end of the series, as well as by the almost bare radial shields. More precisely it can be related to *Ophiothrix* (*Acanthophiothrix*) *scotiosa* Murakami, 1943, *armata* Koehler, 1905, *exhibita* Koehler, 1905, *diligens* Koehler, 1898 and *eusteira* H. L. Clark, 1911. All these belong to the group of species intermediate between *Acanthophiothrix purpurea* and its relatives and *Ophiothrix* sensu stricto, since they have the radial shields less conspicuously naked, the arm spines relatively shorter and not needle-like and the arms not so attenuated, though the dorsal arm plates are at least as long as broad.

Of these nominal species, *O.* (*A.*) *scotiosa* from the Caroline Islands differs from *vigelandi* in having short points on the disc stumps (judging from the figure), the disc completely naked on the under side, the radial shields completely naked and as much as two-thirds as long as the disc radius, though this may not be significant, while the figure shows as many as nine arm spines, though the lowest might be the tentacle scale and only six or seven are mentioned in the description; finally the colour is black above.

O. (*A.*) *armata* again differs in having the disc naked below although on the radial shields some disc stumps do occur proximally. According to Koehler's description the ventral arm plates differ in being longer than broad but in the figure the reverse proportions are shown. There are only five arm spines at d.d. 5 mm., rather than seven. However, like *vigelandi* there may be a light midline to the arms bordered by two dark lines.

O. (*A.*) *exhibita* only appears to differ in having the ventral arm plates with the distal side " rounded " (though they appear straight in Koehler's diagrammatic drawing), besides lacking any disc spines, though this last is true in one of the paratypes of *vigelandi*. However, O. *exhibita* has only been taken at a depth of 180 or more metres.

O. (*A.*) *diligens* also has trifid disc stumps with very long points, as well as a few disc spines, six or seven very thorny arm spines and a colour pattern very like that of *vigelandi* with pink or grey disc and a light midline along the arms defined by dark markings, though these are evidently discontinuous. It differs in having the arm spines all pointed and the ventral arm plates, as well as the dorsal ones, longer than broad, though this could be correlated with the small size, d.d. only 3 mm. The type locality is the Andaman Islands at a depth of 75 metres.

None of these species are described as having the dorsal arm plates carinate, unlike *vigelandi* but keeled arms are found in *O.* (*A.*) *custeira* from Japan. However, the arm spines in *custeira* are described and figured as acute and the radial shields are completely naked.

Were it not for the fact that Koehler in 1922 recorded *O.* (*A.*) *armata* from the East Indies simultaneously with *koreana* and in 1930 likewise *O.* (*A.*) *diligens* and *exhibita*, I would have been inclined to refer these specimens from New Caledonia to one of the three, most likely *diligens*. As it is, it seems best to propose a new name for *koreana*: Koehler though I am reluctant to overburden *Ophiothrix* with yet another specific name.

DISTRIBUTION. Known from New Caledonia, probably between tidemarks; also from the Philippine Islands, Amboina and the Kei Islands in 7–618 metres; doubtfully from Port Hacking, N.S.W. in 3–5 metres (Koehler, 1930).

***Ophiothrix* (*Acanthophiothrix*) *viridialba* von Martens**

Text-fig. 2a–d

Ophiothrix viridialba von Martens, 1867 : 347, 1870 : 256–257; Lyman, 1882 : 218; Koehler, 1922 : 265–266; 1930 : 159–160.

MATERIAL. Zoologisches Museum, Berlin, no. 1499; China Sea; 73 metres; one syntype.

DESCRIPTION. D.d. 10 mm. Those arms which are not broken appear to have regenerated and this has exaggerated the degree to which they taper. The longest remaining is less than 40 mm. long.

The disc is almost completely covered by the huge radial shields, up to 4·0 mm. long, or three-quarters to four-fifths of the disc radius, leaving only narrow areas of scales between them. The scales mostly bear very short rugose stumps but a few of them are markedly enlarged and carry single, slightly tapering, but blunt-tipped thorny spines *c.* 1·5–2·0 mm. long. There are about seven of these spines in each interradial area. The ventral side of the disc bears short rugose stumps all over. The adoral shields are broadly contiguous interradially.

The arms are constricted basally and the lateral arm plates of the first free segment are reduced in comparison with the much enlarged ones of the second segment, which almost meet mid-radially above. The proximal dorsal arm plates are rhombic, with marked distal median angles, as long as or slightly longer than broad and only narrowly contiguous but becoming somewhat truncated medially on the following segments and more widely in contact. They are raised into a marked median keel.

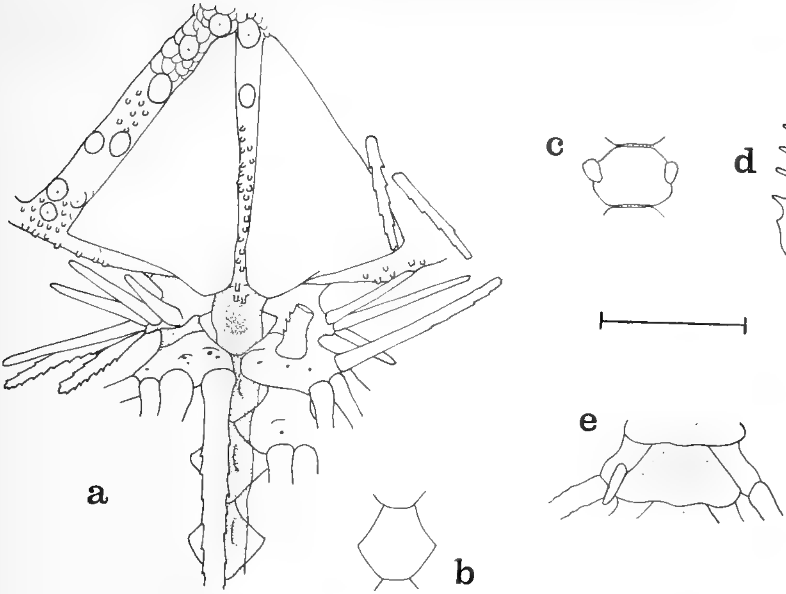

FIG. 2. *Ophiothrix* (*Acanthophiothrix*) *viridialba* von Martens. Holotype. a. Dorsal view of part of disc and arm base; b. the sixth dorsal arm plate; c. ventral view of fourth free segment; d. lowest arm spine from distal segment. e. *Ophiothrix* (*Keystonea*) *propinqua* Lyman (syntype of *O. triloba* von Martens), dorsal view of ninth free segment. The scale equals 2 mm. for a, b, c and e and 0·5 mm. for d. In (a) the upper arm spines are displaced.

Contrary to von Martens' description, only the first three ventral arm plates have strongly convex distal edges, the following ones (on the broadest part of the arm) having a distinct distal concavity, while their shape is octagonal and broader than long, the plate of the fourth free segment (the eighth actual plate) having length : breadth = 0·85 : 1·05 mm.

There are eight glassy arm spines on the second free segment but the number soon falls to the four or five counted by von Martens. The uppermost one or two spines of the proximal segments are extremely long, 7 or 8 mm., or seven or eight times the segment length, with fine rugosities along their length and ending in a blunt tip. The lowest spine on the more distal segments is hook-like with three to five strong curved teeth, usually four.

The tentacle scale is elongated, blunt-tipped and, in the specimen as preserved, inclined obliquely over the ventral arm plate rather than projecting across the pore.

The colour after a hundred years or more in spirit is mainly white but the arms have a broad coloured mid-line which is now khaki but was vivid green in von Martens' day. This band has very well-defined lateral edges and tends to intensify in colour mid-radially, so that the central keel is certainly no lighter than the rest, in contrast to that of *O.* (*A.*) *proteus* Koehler, 1905 and *accedens* Koehler, 1930. The sides of the arms are dappled with small brown spots.

AFFINITIES. I had anticipated that this species might be synonymous with *Ophiothrix proteus* Koehler, of which there are numerous specimens in the British Museum collections from Macclesfield Bank in the South China Sea. However, although there is considerable resemblance between them in many characters, *O. proteus* rarely has the radial shields completely naked, while its ventral arm plates—a valuable source of differential characters in this family—are quite a different shape, all of them longer than broad at d.d. 10 mm. and with the distal edge slightly *convex*. Also *O. proteus* invariably has the midline of the arms pale. *O. accedens* Koehler does have relatively broad and distally concave ventral arm plates, even more markedly than in *viridialba*, but differs again in having the midline of the arms pale; also its arm spines are not so over-developed and the arms are relatively broader.

The species closest to *O.* (*A.*) *viridialba* are *O.* (*A.*) *signata* Koehler, 1922, *vetusta* Koehler, 1930, *vexator* Koehler, 1930 and *purpurea* von Martens, 1867. Not only do these have a median dark more or less broad band along the arms but also the radial shields are completely naked.

O. (*A.*) *vetusta* has the ventral arm plates concave distally but they are not broader than long, though the holotype has d.d. only 6 mm., which could account for this difference. Also the lowest spine modifies into a hook with only two teeth. *O. vetusta* has a conspicuous light ventral midline bordered by two dark lines, of which there is no trace in *viridialba*.

As for *O.* (*A.*) *vexator*, I doubt whether it can be maintained distinct from *O. purpurea*, which is rather variable. Koehler distinguished it by the greater number of arm spines basally, eight or nine in the holotype with d.d. 10 mm., compared with up to seven in larger specimens of *purpurea*, and by the more uniform red colour of the disc, which seems to me to be of very doubtful importance, judging from the colour variation of so many Ophiotrichids.

The holotype of *O.* (*A.*) *signata* from nearly 140 metres in the Philippines appears very similar to that of *viridialba* in the proportions of the arm spines. The disc armament differs in having intermediates between the stumps and the spines, though I doubt if this is significant, also the radial shields have a row of small stumps near the radial border, but this again may not be significant since the occurrence of such stumps is variable in *O.* (*A.*) *proteus*. The dorsal arm plates are " strongly carinate " in *signata* but slightly broader than long (at d.d. 11 mm.). The ventral arm plates have the distal edge slightly convex, though on the proximal part of the arm they are broader than long. Basally there are ten arm spines. The colour of the disc of *O. signata* is pinkish grey with some brownish-purple spots but the arms have a broad dark green band along the upper side covering the entire dorsal arm plates and the uppermost ends of the lateral arm plates. A narrow median part of the keel, however, is lighter in colour. This being the case, it is possible that the affinities of *signata* are with *proteus*. Koehler noted that *signata* appears to be very close to *viridialba* but he was hampered by von Martens' very brief description. Both have strongly keeled arms and distinctive green colouration on the arms but differ again in the shape of the ventral arm plates and possibly in the breadth of the dorsal arm plates and number of arm spines.

Since green-patterned specimens have been recognized by Koehler (1922) as conspecific with examples of *O. proteus* of the more usual red or purple colour, the green tint may not be a barrier to synonymy of *viridialba* with *purpurea*. However, here again there appears to be a difference in the ventral arm plates which are relatively longer in *purpurea* and with the distal edge usually straight or only slightly notched, while their whole surface is slightly convex in contrast to the very slightly keeled contours of the ventral arm plates of the type of *viridialba*. Also *O. purpurea* usually has the radial shields with their broadest part near the middle of their length or even proximal to this, though they are rather variable in shape.

DISTRIBUTION. Known only from the China Sea in 73 metres.

Ophiothrix **(*Keystonea*)** ***propinqua*** Lyman

fig. 2e

Ophiothrix propinqua Lyman, 1861 : 83; 1865 : 174–175; Koehler, 1898 : 98–100, pl. 3, figs. 20–22; 1922 : 256–257, pl. 38, figs. 1, 2, pl. 101, fig. 4.

Ophiothrix triloba von Martens, 1870 : 260–261; Brock, 1888 : 509; de Loriol, 1893 : 41–43, pl. 24, fig. 4; Döderlein, 1896 : 293, pl. 16, fig. 15; Koehler, 1898 : 97.

Ophiotrichoides propinqua: H. L. Clark, 1939 : 90–91; Balinsky, 1957 : 21–22.

MATERIAL. Zoologisches Museum Berlin No. 1750, Red Sea, one syntype of *Ophiothrix triloba*. Also about fifty specimens in the British Museum collections ranging from the Gulf of Suez south to Mauritius and east to Tonga.

SYNONYMY. After studying the syntype of *O. triloba* von Martens, I believe that it is not specifically distinct from *O. propinqua*. Comparison with the "Challenger" specimens from Tongatabu, identified as *O. propinqua* by Lyman, shows no significant difference. The shape of the dorsal arm plates, supposedly characteristically trilobed in *triloba*, is very variable in *propinqua*, being most often more or less flattened fan-shaped but sometimes the median part of the distal side instead of being straight (rarely even slightly concave) has a small lobe. (See Text-fig. 2e.) Koehler (1898 and 1922) has commented on the occurrence of trilobed plates in *propinqua* and his earlier figure shows a form very similar to that of the syntype of *triloba*. Contrary to von Martens' description, the syntype has the longest arm spines little more than twice the segment length; in shape these spines are slightly expanded and rounded at the tips, as usual in *O. propinqua*. Proximally there are up to nine spines in the syntype. This specimen also has single tentacle scales (von Martens thought these were absent), which distally at least have a single point, as Koehler (1922) showed is the case in *propinqua*. The comblike form of the lowest arm spine distally is also as Koehler showed it (pl. 101, fig. 4.) There is just one character shown by the syntype of *O. triloba* which is worthy of comment; this is the relatively elongated form of the stumps on the ventral side of the disc. These are up to 0·45 mm. long, or more than four times as long as broad. The shape of the stumps is, however, very variable in *O. propinqua*.

AFFINITIES. *Ophiothrix propinqua* occupies an intermediate position between *Ophiothrix* subgenus *Keystonea* as defined by me in 1967 (a) and *Macrophiothrix*, since the disc scales of the upper side in many specimens have a sparse armament of almost granuliform stumps. However, large specimens of *O.* (*Keystonea*) *nereidina* may also have some stumps centrally.

DISTRIBUTION. Known from the Gilbert and other south Pacific islands (but not from the Hawaiian Islands) westwards to the Red Sea, Mauritius and Mozambique.

MACROPHIOTHRIX

This genus was established by H. L. Clark in 1938 with type-species *Ophiura longipeda* Lamarck, 1816 and with twenty-one further species included, of which ten were new to science. In 1957 Balinsky referred another new species to *Macrophiothrix* and in 1967(a) I included six further previously-described species removed from *Ophiothrix* as well as five more provisionally. As a result of the present study I would also include now:

Macrophiothrix demessa (Lyman), 1861—now regarded as distinct from *M. hirsuta.*
M. coronata (Koehler), 1905—though this is possibly a synonym of *demessa* also
M. picturata (de Loriol), 1893—though this is possibly a synonym of *M. hirsuta cheneyi.*

Thanks to Drs. Günther, Fell and Madsen I have been able to examine type-material of the following:

Ophiothrix galateae Lütken, 1872. Copenhagen Museum.
Ophiothrix aspidota Müller & Troschel, 1842. Berlin Museum.
Ophiothrix hirsuta Müller & Troschel, 1842. Berlin Museum.
Ophiothrix punctolimbata von Martens, 1870. Berlin Museum.
Ophiothrix cheneyi Lyman, 1861. Harvard Museum.
Ophiothrix demessa Lyman, 1861 (a " topotype " only) Harvard Museum.
Ophiothrix rhabdota H. L. Clark, 1951. Harvard Museum.
Macrophiothrix callizona H. L. Clark, 1938. Harvard Museum.
Macrophiothrix calyptaspis H. L. Clark, 1938. Harvard Museum.
Macrophiothrix rugosa H. L. Clark, 1938. Harvard Museum.
Macrophiothrix scotia H. L. Clark, 1938. Harvard Museum.
Macrophiothrix spinifera H. L. Clark, 1938. Harvard Museum.
Macrophiothrix sticta H. L. Clark, 1938. Harvard Museum.

Supplementary descriptions of these are given in the following pages.

Apart from that of H. L. Clark himself, the greatest contribution to our knowledge of the species currently included in *Macrophiothrix* is that of Koehler. However, my examination of type-material convinces me that he was mistaken in his identifications of *M. galateae* and *punctolimbata* as well as of the Pacific specimens which he referred to *hirsuta*. This results in the establishment here of two new nominal species and the restoration of *Ophiothrix variabilis* Duncan as distinct from *M. hirsuta*. In addition I believe that *O. cheneyi* Lyman can be subspecifically distinguished from *M. hirsuta*. I also find now that my identification in 1952 of specimens from the Gulf of Aqaba as *M. hirsuta* coupled with reference to *hirsuta* of the Murray Expedition's specimens named *demessa* by H. L. Clark, were incorrect, further comparison between *hirsuta* and a specimen of *demessa* from the type-locality having revealed several differences. Recognition of *demessa* brings *Amphiophiothrix* H. L. Clark, 1946, of which it is the type and only species, within the synonymy of *Macrophiothrix*.

The characters which I have found most useful in distinguishing between the species of *Macrophiothrix* include the shape of the dorsal and ventral arm plates, the shape and distribution of the disc stumps, the modification of the lowest arm spine distally, the shape of the longest arm spines, the relative arm length, the occurrence of stumps or spinelets on the distal edge of the oral shields and the colour pattern. I do not think that other differences in the oral structure are significant in this genus, nor do differences in the shape and size of the radial shields provide reliable distinctions.

Macrophiothrix aspidota (Müller & Troschel)

Text-figs. 3a, 4a, 5a, b, c, 7a

Ophiothrix aspidota Müller & Troschel, 1842 : 115; Lyman, 1874 : 234; Bell, 1889 : 7; Koehler, 1904 : 87–90, figs. 50–54; 1922 (pt.) : 209–211, pl. 32, figs. 1, 2, pl. 33, fig. 8 [non pl. 32, figs. 3–5, nec pl. 33, fig. 7, nec pl. 97, fig. 3]; 1930 : 134.
Macrophiothrix aspidota: H. L. Clark, 1938 : 284; Balinsky, 1957 : 18 [? = *M. robillardi*].

Material. Berlin Museum no. 1008; "Ostindien"; Schöenlein; holotype. British Museum No. 88.11.15.1–2; Ramesvaram, Gulf of Manaar; Thurston collection; three specimens. 1958.11.5.3 and 1961.8.23.11–14; Bombay; Sane collection; seven specimens. 81.4.1.21 and 82.1.5.11–12; Karachi; from Karachi Museum; four specimens.

Description of holotype. Disc diameter (d.d.) 11·5 mm.; the arms are all broken within 50 mm. of the disc. [It may be noted here that Koehler (1904) estimates the disc diameter as only 10·5 mm.]

The radial shields are conspicuous, *c.* 3·8 mm. long and abruptly naked in contrast to the superficially granuliform armament of stumps on the disc scales. No special preparation of these stumps was made because of the relatively small size and imperfect condition of the specimen but the peripheral stumps appear to be cylindrical or slightly tapering and the dorsal ones are multifid with usually five or six points and relatively short.

The dorsal arm plates (Text-fig. 5a) are fan-shaped, widest just distal to the middle, the lateral angles being about 90° since the distal edge curves back a little more abruptly at its extremities. However, some of the plates have the distal edge divided into three parts by a pair of angles, although these are very obtuse, so that the shape of the plate may be somewhat hexagonal. The arms are slightly carinate and some of the dorsal arm plates are divided into two longitudinally, as sometimes occurs in other species of the genus. The fifteenth dorsal arm plate has length : breadth = 0·68 : 1·58 mm., a ratio of 1 : 2·3.

The ventral arm plates (Text-fig. 7a) are broad hexagonal with the widest part at about the middle; the consecutive ones are slightly separated. The plate of the fifteenth free segment has length : breadth = 0·60 : 1·00 mm. or 1 : 1·7. The distal edge of each plate is straight or slightly concave.

Basally there are eight arm spines on one or two segments only but the number soon falls to six. [Müller & Troschel give the number as eight or nine but I cannot find the larger number.] The flattened spines when viewed from above or below are moderately rugose for most of their length with the sides almost parallel but some of the longest are slightly clavate. These long spines measure about 2·6 mm. Many of the lowest spines are damaged but some are clearly modified into a hook with about four teeth but the very tips may be rugose (Text-fig. 4a).

No colour remains.

Variations. Of the British Museum specimens, five from Bombay have most of the arms complete. There appears to be some variation in length even within a single individual, one having d.d. : a.l = 1 : 5·3–7·8, while in the four others the ratio is 1 : 5·3–6·2, 1 : 6·3–7·4, 1 : 7·2–7·5 and 1 : 8·0. A specimen from Ramesvaram has an almost complete arm *c.* 120 mm. long, d.d. being 14 mm., giving a ratio of 1 : 8·6, while two larger specimens from Karachi with d.d. 19 and 22 mm. have ratios of 1 : 8·2 and 1 : 8·0. Koehler (1904) estimated the holotype to have arms *c.* 90 mm. long giving a ratio of 1 : 7·8 using my measurement of 11·5 mm. for the disc diameter. Koehler also had a specimen from Trincomalee, Ceylon, for which he gave a ratio of 1 : 9. It therefore appears that *M. aspidota* habitually has relatively short arms, less than ten times the disc diameter, unlike most species of the genus.

The radial shields of the British Museum specimens appear to be a little smaller relatively than those of the holotype, with ratios to the disc radius of 1 : 1·7–2·0, compared with 1 : 1·5, but this may be due to an underestimate of their length in these better-preserved specimens, all of which have some tapering stumps or grains along the abradial margins which tend to conceal the proximal end of the shields. There are also a few scattered grains over the rest of the surface of the shields, more in some specimens than others but the general impression is that the shields are naked in comparison with the rest of the disc.

The shape of the dorsal arm plates is rather variable. In the two large specimens from Karachi they are broad fan-shaped with the broadest part hardly at all distal to the middle and the lateral angles acute; in the Bombay specimens (Text-fig. 5c) they are more often distinctly hexagonal, while the Ramesvaram material (Text-fig. 5b) shows both shapes or intermediates between them, even on different parts of the same arm. The fifteenth plate in one of the last specimens has a length : breadth ratio of 1 : 2·4.

The arms may be distinctly carinate, at least basally.

The ventral arm plates have the distal edge more or less distinctly concave.

The longest arm spines measure four to five times the corresponding segment length and are slightly expanded and bushy at the tip, sometimes sufficiently so to be termed clavate, this being particularly true of some of the Bombay specimens.

The lowest arm spines are modified into a well-developed transparent hook, though the number of teeth varies, even in a single specimen; most often there are two subterminal teeth within the enlarged end tooth but there may be up to five teeth altogether. The outside of the end of the hook may be smooth or slightly rugose.

The disc stumps studied in one of the Karachi specimens are cylindrical and multifid (Text-fig. 3a).

The colour is purple, often with very dark spots on the abradial sides of the radial shields and with the arms predominantly purple above, usually deeper on every fourth segment to give a banded effect. The edges of the dorsal arm plates are rimmed with white and on some specimens the distal white rim is broad, especially on the distal plates. Often there is also a median white mark, which occasionally is large enough to give the impression of a discontinuous longitudinal light line. The purple colour over most of the dorsal plates may be even or mottled. The ventral arm plates have a more or less broad light area extending on both sides of the suture between consecutive plates.

REMARKS. The specimen from Ibugos Island, north of the Philippines, which Koehler (1922) referred to *aspidota* is clearly not conspecific with the holotype and the present material, or with Koehler's earlier examined specimen from Trincomalee. Not only does it have the dorsal arm plates trapezoidal with the distal edges almost straight (as in *M. galateae* and *longipeda*) but the arms were evidently more than ten times the d.d., the disc stumps are mainly trifid and the lowest arm spines are comblike with numerous closely-placed teeth. I think the specimen should be referred to true *M. galateae* Lütken, which Koehler confused with another species, (see below).

DISTRIBUTION. Known to the east and west of India and Pakistan.

Macrophiothrix belli (Döderlein)

Text-figs. 3b, 4b–e, 5d, 7b

Ophiothrix belli Döderlein, 1896 : 292–293, pl. 14, fig. 5, pl. 16, fig. 14.
Macrophiothrix belli: H. L. Clark, 1938 : 287–288; 1946 : 221.

MATERIAL. Fourteen specimens in the British Museum collections, from Thursday Island (the type-locality), Great Barrier Reef Expedition station XIX, Port Essington, Northern Territory, the N. side of Holothuria Bank, N.W. Australia, Cape Boileau, N.W. Australia and the Monte Bello Islands.

DISTRIBUTION. Known from the northern coasts of Australia.

Macrophiothrix callizona H. L. Clark

Text-figs. 3c, 4f, 5e, f, 7c

Macrophiothrix callizona H. L. Clark, 1938 : 293–294, pl. 24, fig. 1; 1946 : 221.

MATERIAL. Museum of Comparative Zoology, Harvard, No. 5113; Broome, N.W. Australia, one paratype.

DESCRIPTION. The d.d. is 10·0–10·5 mm. All the arms appear to have regenerated from close to the base.

The disc stumps (Text-fig. 3c) are probably mostly trifid, as described by H. L. Clark but many of those in the preparation made have been badly rubbed and blunted at the tips. The armament of the radial shields also consists of stumps, not rugose granules; these are slightly spaced in comparison with the stumps on the scales.

The original basal dorsal arm plates (Text-fig. 5e) are slightly carinate, overlapping, rounded fan-shaped and with a few small peripheral rugosities. The regenerated dorsal arm plates (Text-fig. 5f) in contrast are elliptical, almost flat and fairly smooth, the consecutive ones slightly spaced. The plates of the widest part of the arm have length : breadth = *c.* 0·7 : 1·6 mm. = 1 : 2·3 and the longest spines of these segments are *c.* 2·4 mm. long, or 3·4 times the segment length. The spines are moderately thorny for at least the outer two-thirds of their length, the longer ones with parallel sides and truncated tips. Basally there are eleven spines. The lowest one on the more distal segments becomes hook-like with usually three teeth, the outermost the largest (Text-fig. 4f).

The ventral arm plates (Text-fig. 7c) are relatively broad rectangular, the proximal ones *c.* 0·4 : 0·75 mm. with the distal edge concave and the consecutive plates widely separate. The tentacle scales have one to three sharp points.

REMARKS. See under *M. calyptaspis*.

DISTRIBUTION. Known only from Broome, N.W. Australia.

Macrophiothrix calyptaspis H. L. Clark

Text-figs. 3d, 4g, 5g, 7d

Macrophiothrix calyptaspis H. L. Clark, 1938 : 294–295, pl. 25, fig. 3; 1946 : 222.

MATERIAL. Museum of Comparative Zoology, Harvard, No. 5115; Broome, N.W. Australia; one paratype.

DESCRIPTION. The d.d. is 11 mm.

The disc stumps (Text-fig. 3d) are of moderate length with three to six points, most often three. The radial shields are more sparsely covered with stumps than the disc scales.

The arms appear faintly carinate but this may be illusory since the suture between consecutive dorsal arm plates is abruptly finer midradially. The dorsal arm plates (Text-fig. 5g) are hexagonal and widest just distal to the middle of their length ; the distal edge is slightly concave in the middle. The twelfth plate has length : breadth = 0·7 : 1·7 mm. = 1 : 2·4. The corresponding longest arm spines are *c.* 2·6 mm. long, or 3·7 times the segment length. Basally there are eleven arm spines. The longer ones are moderately thorny except for the basal quarter of their length and are slightly broadened at the tip. The lowest spine distally is hook-like with three or four teeth (Text-fig. 4g).

The ventral arm plates (Text-fig. 7d) are widely separated, concave both proximally and distally and relatively broad, that on the twelfth free segment having length : breadth = 0·55 : 0·8 mm.

AFFINITIES. *M. calyptaspis* seems to me to be very closely related to the sympatric *M. callizona,* the main difference being in the relative length of the arms, which are ten to twelve times the d.d. in *callizona* but only seven to eight times in *calyptaspis.* However, the paratype of *M. calyptaspis* which I have seen has clearly regenerated all its arms and, judging from the elliptical shape of the dorsal arm plates described for the holotype, the same may be true of that specimen. It is possible that regeneration has resulted in abnormal arm lengths. Only two specimens of each nominal species have been recorded. Both species have stumps rather than granules on the radial shields, broad rectangular widely spaced ventral arm plates with proximal and distal sides concave, similar arm spines, the longer ones slightly expanded at the tips and similar hook-like lowest arm spines. There are small differences in the shape of the disc stumps and possibly in the dorsal arm plates but I suspect that further material from Broome will prove that only a single species can be recognized.

Otherwise the affinities of the two are with *M. hirsuta* and *variabilis,* the differences lying in the elongated armament of the radial shields and the smaller disc stumps with fewer points.

DISTRIBUTION. Known only from Broome, N.W. Australia.

Macrophiothrix demessa (Lyman)

Text-figs. 3e, f, 4h, 5h, 7e

Ophiothrix demessa Lyman, 1861 : 82; 1865 : 172–173; Marktanner-Turneretscher, 1887 : 310; Brock, 1888 : 513; Koehler, 1905 : 91–92, pl. 9, figs. 5, 6; H. L. Clark, 1921 : 109; 1939 : 83; Ely, 1942 : 44–45, fig. 11; A. H. Clark, 1949 : 39–40.

Ophiothrix mauritiensis de Loriol, 1893 : 38–39, pl. 24, fig. 5.

Macrophiothrix hirsuta: A. M. Clark, 1952 : 209–210; Tortonese, 1953 : 33–34 (?). [Non *M. hirsuta* (Müller & Troschel, 1842) nec A. M. Clark, 1967.]

Macrophiothrix mossambica Balinsky, 1957 : 18–20, fig. 7, pl. 3, figs. 11, 12.

Amphiophiothrix demessa: H. L. Clark, 1946 : 217.

MATERIAL. Museum of Comparative Zoology, Harvard, No. 4491; off Lahaina, Maui, Hawaiian Islands. Also twenty-three specimens in the British Museum collections, from the Gulf of Aqaba, the Sudanese Red Sea, the Gulf of Aden, Zanzibar, the Seychelles, Amirante, Maldive and Ellice Islands.

DESCRIPTION. The Hawaiian specimen approximates to Lyman's type-locality. It has the d.d. only 8·5 mm.; the arms are all broken. [Lyman gives the ratio of d.d. : a.l. as *c.* 1 : 9, H. L. Clark (1946) as 1 : 9–12, de Loriol (for *mauritiensis*) as *c.* 1 : 10, Balinsky (for *mossambica*) as " a little under " 1 : 10 and Ely as 1 : 4, which last must surely be a mistake.]

The superficial appearance is very like that of *M. hirsuta.*

The disc is covered with slightly waisted stumps with three to six terminal points (Text-fig. 3e). [Lyman gives the number of points as commonly four to six but certainly in this specimen three is the usual number.] There are similar but slightly smaller stumps on the radial shields; on the under side of the disc the stumps do not extend far below the ambitus but as the disc is dry and shrunken some could have been lost.

The dorsal arm plates (Text-fig. 5h) are fan-shaped with the distal edge evenly convex except at the lateral extremes where it sweeps back abruptly so as slightly to round off the lateral angles. The plates bear scattered stumps but these are much shorter than those on the disc and usually have only two or three points. The plate of the tenth free segment has length : breadth = 0·55 : 0·85 mm., a ratio of 1 : 1·6.

The ventral arm plates after the first few are relatively narrow with length and breadth approximately equal but soon become distinctly longer than broad (Text-fig. 7e). They are octagonal with the proximal and distal sides longer than the rest. The distal edge is straight or, more often, slightly concave and on the more distal parts of the arms the concavity is more marked. The plate of the tenth free segment has length : breadth = 0·55 : 0·50 mm.

Basally there are eleven arm spines, all of which are slightly tapering and bear strong thorns, much more prominent than those of *M. hirsuta*, for their whole length. The longest spine of the tenth free segment is *c.* 1·15 mm. long, or just over twice the segment length. The lowest spine beyond the basal segments is modified into a comb with five to nine teeth (Text-fig. 4h).

VARIATIONS. A specimen from Sherm Sheik, Gulf of Aqaba, has d.d. : a.l. = 21 : *c.* 240 mm., a ratio of 1 : 11·5, while in another from the Sudanese Red Sea it is 19 : *c.* 280 — 1 : 15, an unusually high value, though possibly correlated with the much larger size in comparison with the Hawaiian specimen. The largest of nine specimens from the Seychelles (the closest to the type-locality of *mauritiensis*) has d.d. : a.l = 18 : 170–*c.* 200 mm., a ratio of probably just over 1 : 10, as in de Loriol's holotype. It also has thirteen or rarely even fourteen arm spines on the basal segments. The disc stumps in these Seychelles specimens are variable in length, sometimes as long as in specimens from the Red Sea or somewhat shorter but the stumps on the dorsal arm plates are granuliform and more or less densely crowded so as to obscure the limits of the plates. When denuded the plates are seen to have approximately 90° latero-distal angles; the tenth has length : breadth = 0·90 : 1·85 mm., a ratio of *c.* 1 : 2; a number of the plates are split longitudinally. The armament of the radial shields in the Seychelles specimens is also unusually granuliform. Ventrally the disc stumps extend almost to the oral shields, while in the large specimen from the Gulf of Aqaba all the scales of the ventral side bear stumps.

The Aqaba specimen has a median white area across the distal end of each dorsal arm plate extending on to the next plate, this area being generally devoid of stumps, which are restricted to the sides of the plates. A similar colour pattern and restriction of the armament are evident in de Loriol's figure of these plates in the type of *mauritiensis*, while the colour pattern of the ventral plates with a curved dark mark on each side is also found in the Seychelles specimens, though the one from Aqaba has instead a coloured rim along both sides and across the distal edge of each ventral arm plate.

REMARKS. My confusion of *M. demessa* with *hirsuta* in 1952, owing to inadequate knowledge of the latter has probably misled Tortonese (1953). Judging from his description of the dorsal arm plates as armed with grains or short stumps, his specimen from Nocra, Eritrea, was more likely to have been *demessa* than *hirsuta*. Apart from the superficial nature of this armament, the two species can most easily be distinguished by the shape of the ventral arm plates, those of *demessa* being longer than broad.

AFFINITIES. Except for the unusually high number of arm spines and the relatively inconspicuous radial shields—neither of which do I consider are characters of more than specific weight –*Ophiothrix demessa* Lyman seems to me to agree very well with H. L. Clark's diagnosis of *Macrophiothrix* (1938), notably in the puffy disc with uniform covering of stumps, the relatively long arms and the broadly contiguous dorsal arm plates. Balinsky did not hesitate to refer his new nominal species, *mossambica*, to *Macrophiothrix*, evidently regarding the presence of thorny granules on the dorsal arm plates as less than a generic character—as I also do. Accordingly *Amphiophiothrix*, which H. L. Clark subsequently established (1946) to accommodate *demessa*, is here referred to the synonymy of *Macrophiothrix*.

As for the specific limits of *M. demessa*, I do not think that either *mauritiensis* or *mossambica* can be maintained as separate species. De Loriol noted that *mauritiensis* is very close to *demessa* but he distinguished it on several characters to do with the oral structure, such as the number of tooth papillae, which I do not consider are of taxonomic importance, as well as on the shape of the ventral arm plates, which look to me to be very similar, while the lateral angularity and the density of armament of the dorsal arm plates are somewhat variable in the specimens now studied; nor can I see a significant difference in the arm spines. *M. mossambica* was based on a single specimen with d.d. only 8 mm. Balinsky compared it with *M. obtusa* and *callizona*, neither *demessa* nor *mauritiensis* having been mentioned in connection with the genus up to that time. The only difference which might be of some significance is that the arm spines are said to number only eight. Even at this small size, one would expect to find ten or more spines basally in *M. demessa*. If I am correct in synonymizing these two with *M. demessa*, then we have a single species of wide range, from Mauritius and S.E. Africa to the Hawaiian Islands.

In relation to the other species of *Macrophiothrix*, *M. demessa* occupies a fairly isolated position. *M. callizona, hirsuta, cheneyi* and *rugosa* approximate to it though they have a rugose texture to the fan-shaped dorsal arm plates, as opposed to having separate superimposed stumps or grains, but they differ in having broad ventral arm plates and hook-like rather than comb-like lowest arm spines with only about four teeth.

DISTRIBUTION. Known from the Hawaiian Islands to northern Australia and westwards to the Red Sea and S.E. Africa.

Macrophiothrix elongata H. L. Clark

Text-figs. 3g, 4i, 5i, 7f

Macrophiothrix elongata H. L. Clark, 1938 : 292–293, pl. 24, fig. 4.

MATERIAL. Two specimens in the British Museum collection from Hor Kawi and Tarub Island, Persian Gulf and one from Muscat, Gulf of Oman.

Remarks. Although close to *M. hirsuta* both geographically and morphologically, *M. elongata* is easily distinguished by the relatively much longer arms, about twenty times the d.d. rather than ten times or less, also by the relatively narrow ventral arm plates and the smaller disc stumps with fewer points. Both have the distal lowest spines hooked and *M. hirsuta cheneyi* also has median light stripes on the arms like *elongata*.

Distribution. Known only from the Persian Gulf and Gulf of Oman.

Macrophiothrix expedita (Koehler)

Text-figs. 3h, 4j, 5j, 7g

Ophiothrix expedita Koehler, 1905 : 96–98, pl. 9, figs. 10–14, pl. 15, fig. 5; 1922 : 229–230, pl. 31, fig. 6, pl. 33, fig. 5, pl. 98, fig. 5; 1930 : 140.
Macrophiothrix expedita: H. L. Clark, 1938 : 284–285.

Material. One specimen in the British Museum collections from Zamboanga, Philippines, "Challenger" Expedition; named *O. longipeda* by Lyman (1882).

Remarks. See under *M. rhabdota*.

Distribution. Known from the East Indies, Philippines and the Palao (Pelew) Islands.

Macrophiothrix galateae (Lütken)

Text-figs. 3i, 4k, l, 5k, 7h, pl. 1, fig. 1

Ophiothrix galateae Lütken, 1872 : 90–92, 108. [Non *O. galateae*: Marktanner-Turneretscher, 1887 : 309; Brock, 1888 : 517; de Loriol, 1893a(?) : 420; H. L. Clark, 1915 : 272; nec *O. galatheae*: Koehler, 1905 : 84–85; 1922 : 233–234; 1930 : 141; Tortonese, 1936 : 219; nec *Macrophiothrix galateae*: H. L. Clark, 1938 : 285; nec *M. galatheae*: Tortonese, 1953 : 34; see *M. koehleri*.]

Material. Universitetets Zoologiske Museum, Copenhagen, Nicobar Islands, the holotype. Also one specimen in the British Museum collections from Tongatabu, "Challenger" Expedition; named *O. longipeda* by Lyman (1882).

The identity of this species has generally been mistaken since Brock stated that it is characterized by the opacity of the arm spines; consequently the name has been used for quite another species, possibly more than one, in which this character holds good in combination with the development of naked radial shields. Re-examination of the holotype reveals the fact that *M. galateae* is a species of the *longipeda*-group with dorsal arm plates of trapezoidal form, having very sharp latero-distal angles.

Description. The holotype has the disc somewhat shrunken; it now measures 14 × 15 mm. The arms are broken and their length is difficult to estimate; Lütken puts it at 250 mm., which is about eighteen times the disc diameter.

Superficially the disc appears smooth due to the bare radial shields and the very fine armament on the scales, which looks granuliform in spirit, the skin covering the stumps not being shrunken. The radial shields are completely naked except for a very few granuliform stumps on the distal projection. The ratio of length : breadth of a shield is 4·0 : 1·75 mm., the broadest part being near the middle. The form of the disc stumps is shown in Text-fig. 3i. On the ventral side the stumps are reduced to fine thorns, often with single points; these extend up to the genital slits but stop short of the oral shields. The oral shields are as usual broad rhombic and the rather transparent adoral shields do not meet proximal to them.

The dorsal arm plates are of the *longipeda*-type, trapezoidal in shape, with very sharp latero–distal corners (fig. 5k). The plate of the twelfth free arm segment has length : breadth = 0·8 : 1·9 mm.; the arm breadth at this point is 2·0 mm. and the longest spine of the corresponding segment measures 1·9 mm. Further out on the arm the spines become longer, up to *c.* 2·25 mm.

The ventral arm plates (Text-fig. 7h) after the first few are slightly broader than long; length : breadth of the twentieth (i.e. the plate of the twelfth free segment) = 0·8 : 0·9 mm. The distal edge of each plate is straight or very slightly concave.

There are ten arm spines on about two basal segments, then the number falls to nine; the longer ones have parallel or slightly divergent sides and are blunt at the tip, so that they appear spatulate rather than clavate. The longest spines of the twelfth free segment are *c.* 1·9 mm. They are light brown in colour and translucent, without the opaque distal core described by Koehler. The proximal halves of the longer spines are almost completely smooth but the distal halves are finely thorny. On the distal part of the arm some of the lowest spines become rather comb-shaped (Text-fig. 4k), but many are somewhat irregular.

The colour is very distinctive and most unusual for a member of this genus. The radial shields are marked with three, sometimes four, discontinuous undulating dark-brown to black lines running parallel close to the proximal interradial side, with a single brownish line just inside the edge of the radial and distal sides, together making an inset replica of the shape of the shield. Similarly the dorsal arm plates are emphasized by a dark blue or purple band close to the lateral and distal edges. The ventral arm plates also have light edges but are centrally darker. On about two consecutive plates out of every four or five the darker colour is deeper, giving a banded effect.

VARIATIONS. The " Challenger " specimen from Tongatabu has d.d. 20 mm. and arm length over 300 mm., giving a ratio of more than 1 : 15. The disc armament is like that of the holotype, the stumps being very short, not more than twice as long as wide and superficially appearing granuliform. Some extremely short stumps or granules extend on to the radial shields both at their proximal and distal ends but the main part of the shield is again naked. Length : breadth of one pair of shields measured is 5·5 : 2·0–2·3 mm., the widest part being at about the middle of the length.

The dorsal arm plates are as in the holotype, trapezoidal with acute latero-distal angles. The twelfth plate has length : breadth = 0·9 : 1·7 mm. = 1 : 1·9. The spines are again light brownish but a little more opaque than in the holotype; the distal half of the longer spines is somewhat expanded but again they can hardly be called clavate; the texture of the spines is more extensively rugose, even on the basal parts, which are only smooth on the side facing the disc.

The distal lowest arm spines are hardly at all modified and none were seen to be comb-like (Text-fig. 4l).

The colour pattern is somewhat similar to that of the holotype, with the radial shields outlined in darker colour and the dorsal arm plates with pale edges all round but darker markings within. However, in this case all the coloured markings are reddish-brown. Also the dark patches on the dorsal arm plates are mainly lateral, there being no strong transverse band near the distal border.

REMARKS. *Macrophiothrix galateae* is most easily distinguished from the species which Koehler confused with it by the trapeziform dorsal arm plates and the absence of stumps from the distal edge of the oral shields. In addition the disc stumps are much shorter and the arm spines less opaque and less clavate.

DISTRIBUTION. Owing to the uncertainty hitherto about the identity of this species, the only two positive records are from the Nicobar and Tonga Islands.

Macrophiothrix hirsuta hirsuta (Müller & Troschel)

Text-figs. 3j, 4m, 5l, m, 7i

Ophiothrix hirsuta Müller & Troschel, 1842 : 111; Lyman, 1865 : 176; 1882 : 226; Marktanner-Turneretscher, 1887 : 311–312 (part); Tortonese, 1936 : 218; 1949 : 37–38 (?). [Non *O. hirsuta*: Koehler, 1898 : 96; Ludwig, 1899 : 549; Koehler, 1905 : 93; M'Intosh, 1910 : 164; Matsumoto, 1917 : 225–226, fig. 63; Koehler, 1922 : 234–235; Gravely, 1927 : 8; Koehler, 1930 : 141; Mortensen, 1942 : 67–68(?); A. H. Clark, 1948 : 4(?).]

Macrophiothrix hirsuta: H. L. Clark, 1938 : 285 (part); Tortonese, 1953 : 33–34(?); 1954 : 70; A. M. Clark, 1967 : 47. [Non *M. hirsuta*: Murakami, 1943 : 209; A. M. Clark, 1952 : 209–210; Balinsky, 1957 : 17–18.]

MATERIAL. Zoologisches Museum, Berlin, No. 1000, Red Sea, the holotype. Also ten specimens in the British Museum collections from the "Red Sea" (no details), the Dahlak Archipelago, Eritrea and from Aden.

REMARKS. Contrary to widespread opinion, I believe that *M. hirsuta* has a restricted geographical range, confined to the Red Sea and the immediate vicinity. I consider that Lyman's second thoughts (1882) about the separate identity of his *Ophiothrix cheneyi* with *hirsuta* and Koehler's (1905) similar synonymizing of *O. variabilis* Duncan are incorrect, though the former does merit a subspecific distinction. Koehler's concept of *hirsuta* is, I think, based on a misidentified specimen of *cheneyi*, as his description of the dorsal arm plates as laterally rounded is at variance with that of Müller and Troschel. Fortunately it is now possible to give a full description and figures of the holotype of *hirsuta*.

DESCRIPTION. The holotype has d.d. 22 mm. and arm length 170 + mm., probably when complete more than 200 mm., since Müller & Troschel estimate the ratio as 1 : 10. The disc is covered with fairly short multifid stumps (Text-fig 3j), markedly flared from the base or from the middle, up to *c.* 0·4 mm. long and usually with five or six points. The radial shields are covered with coarse granules. They are *c.* 6 mm. long.

The fan-shaped dorsal arm plates (Text-fig 5l) have a fine rugose texture proximally and laterally; they are slightly carinate and the proximal ones have a more or less well developed median distal angle, though the following plates become more flattened medially. The latero-distal corners on most plates are distinctly acute, or else right-angled. The widest part of each plate is just distal to the middle of its length. The plate of the twelfth free arm segment has length : breadth = 0·9 : 2·1 mm. The longest spines of this segment are *c.* 4·0 mm. Except for the basal few, the ventral arm plates (Text-fig. 7i) are markedly broader than long, that of the twelfth free segment having length : breadth = 0·9 : 1·5 mm.; they are broadest in the middle of the length and distinctly concave distally. I cannot count more than nine arm spines proximally, though Müller & Troschel give the number as ten. The spines have their sides parallel or else are slightly tapering, the ends blunt but not very thorny and the sides moderately thorny for most of the length; they are somewhat opaque at the tip. Distally the lowest spine becomes a well-developed hook with three or four teeth, the outermost the largest (Text-fig. 4m). The single tentacle scale is small and rounded.

The colour is lost.

VARIATIONS. The specimens from the " Red Sea " have d.d. 12–20 mm. The three larger ones have the dorsal arm plates (Text-fig. 5m) laterally angular like the holotype but in the smallest there is some rounding of the angles. The ventral arm plates are not so broad, especially in the smallest one where the plates proximally are about as broad as long. This specimen has up to only eight spines, whereas the larger ones have nine or ten basally. The colour pattern is dappled or spotted dark greyish-blue but the middle of the distal edge of most of the dorsal plates is paler, though this is not sufficiently extensive as to give the effect of a light longitudinal line. Similar light markings are shown on the specimens from the Dahlak Archipelago, the colour being otherwise dappled. Three of these have some arms more or less complete so that an estimate can be made; the ratios of d.d. : a.l. are: 13/120 mm. = 1/9·2; 20/200 mm. = 1/10; 17/155 or 195 + mm. (the arms being obviously very variable in length since the shorter one is complete and does not show any sign of having regenerated) = 1/9 or 1/c. 12. Finally the specimen from Aden has d.d. : a.l. = 15/190 mm. = 1/12·5. Its dorsal arm plates are rather variable in shape, some laterally angular, others somewhat rounded; they are finely rugose all over. The ventral arm plates are broad and the longest arm spines are slightly clavate. The disc stumps are a little smaller than those of the specimens previously mentioned, some of them having only three points. There is no sign of median light markings on the upper side of the arms, which are dappled all over.

The specimen from Mogadishu, Somalia, described as *M. hirsuta* by Tortonese (1949) had d.d. only 6 mm. and the arms but seven to eight times as long. The radial shields are almost naked. The dorsal arm plates are fan-shaped with well-marked lateral angles. The colour is grey-blue with darker markings on the radial shields and dorsal arm plates but no sign of median light areas. In spite of the relatively short arms, these last two characters suggest that the specimen could be a true *hirsuta*, the arm length being attributable to the small size; smaller specimens of subspecies *cheneyi* from Zanzibar often having the ratio only *c.* 1 : 5.

Clearly there is some variation in the relative arm length, the shape of the dorsal arm plates and the development of median light markings on the arms in specimens of *hirsuta* from the vicinity of the southern end of the Red Sea. Although the material available is small, the difference in all three characters taken together justifies, in my opinion, at least a subspecific difference from *cheneyi* Lyman, the large sample of which from Zanzibar mentioned below shows consistent and correlated differences in these same characters.

Distribution. Known only from the Red Sea and the immediately adjacent Indian Ocean.

Macrophiothrix hirsuta cheneyi (Lyman)

Text-figs. 3k, 4n, 5n, 7j

Ophiothrix cheneyi Lyman, 1861 : 84: 1865 : 175–176.
Ophiothrix hirsuta: Ludwig, 1899 : 549; Koehler, 1905 : 95 (part); 1922 : 234–235, pl. 31, fig. 1 [non fig. 2], ?pl. 99, fig. 2. [Non *O. hirsuta* Müller & Troschel, 1842.]
Macrophiothrix brevipeda H. L. Clark, 1938 : 290–292, fig. 20; 1939 : 91.
Macrophiothrix hirsuta: Balinsky, 1957 : 17–18.

Material. Museum of Comparative Zoology, Harvard, No. 4097; Zanzibar; one paratype. Also *c.* 170 specimens in the British Museum collections from Zanzibar (*c.* 120), Mossel Bay, S. Africa and several stations of the John Murray Expedition off S. Arabia.

History. In 1865 Lyman redescribed *Ophiothrix cheneyi* and noted that it is closely related to *O. hirsuta* Müller & Troschel, of which he had studied the holotype in the Berlin Museum. However, he said then that two other specimens from the Red Sea " agree well with *O. cheneyi*; but are not clearly the same species as the original " (i.e. of *hirsuta*). Nevertheless, in 1882 (p. 226) Lyman included *cheneyi* in the synonymy of *hirsuta*, a disposition which has been followed by subsequent authors.

Notwithstanding Müller & Troschel's description of the dorsal arm plates of *O. hirsuta* as angular laterally (see Text-fig. 5l) Koehler described them as rounded, never keen and the specimen from the Red Sea of which he published photographs in 1922 appears to be an example of *cheneyi*, having not only laterally rounded dorsal arm plates but also a median light line along the proximal part of the arms, though this is not very strongly defined.

When he established *Macrophiothrix* in 1938, H. L. Clark seems to have had a rather confused impression of the identity of *hirsuta*, based largely on the type-material of *cheneyi* from Zanzibar, which he says is " typical ". It is remarkable that at the same time he described some specimens from Natal as a new species, *M. brevipeda*, which is clearly indistinguishable from *cheneyi*, having the same obtuse lateral angles to the dorsal arm plates, median light lines and relatively short arms, less than ten times the d.d. (Lyman gives nine times under the heading "special marks " but in his description the ratio of 21 : 170 mm. works out at eight times; the paratype lent to me has all the arms broken in the middle.) The John Murray Expedition specimens determined as *M. brevipeda* by H. L. Clark are in the British Museum and show no significant differences from the Zanzibar material.

DESCRIPTION. The following remarks may be added to Lyman's description. D.d. of the paratype studied is 18 mm.; the arms are all broken. The disc is densely covered with multifid stumps (Text-fig. 3k) but the radial shields with much lower rugose grains. The ventral armament is more nearly spiniform with fewer points on the individual stumps.

The dorsal arm plates (Text-fig. 5n) are hexagonal with the distal edge often slightly concave in the middle and with the widest part at about the middle of the length or just distal to this and the lateral angles 90° or more, often more or less continuously curving. Laterally the plates are somewhat rugose in surface texture. Some of them are also split longitudinally. The twelfth free segment has the dorsal arm plate with length : breadth = 0·95 : 2·1 mm., the corresponding longest arm spines measuring 3·4 mm. The spines are relatively long, moderately thorny especially in the distal half and more or less clavate at the tip, especially the longer ones. Basally they number ten.

The ventral arm plates (Text-fig. 7j) have the distal edge distinctly concave; the consecutive ones are separated and they are relatively broad, that of the twelfth free segment measuring 0·7 : 1·3 mm.

The longest remaining arm stump extends only to the forty-fifth segment and the lowest arm spine is only partially modified into a hook.

The arms are marked with a double dark blue line defining a median light line on the upper side.

VARIATIONS. Eighty-seven specimens from Zanzibar have the d.d. ranging from 4 to 20 mm.; in twenty-eight with one or more arms near enough to being complete, the ratio of d.d. : a.l. is 1 : 5·0–10·0, with a mean of 1 : 7·35. Only a single individual has the top value of 10·0 and but two others have it over 9·0.

The specimens consistently have the dorsal arm plates without sharp lateral angles, though their shape is somewhat variable; the widest part is usually at or just distal to the middle; they are more or less distinctly carinate, at least proximally and those of the distal part of the arm, if not of the entire arm, show the pair of dark longitudinal lines bordering the light line. The ventral arm plates always have the distal edge distinctly concave and, except for the smallest specimen, are broader than long. The lowest arm spine distally is hooked with three or four teeth (Text-fig. 4n). The longitudinal ventral stripe is not always distinct. The general colour is variable, being most often greyish-purple but occasional specimens are khaki-coloured, greenish or brownish.

AFFINITIES. Certainly *M. cheneyi* is very closely related to *M. hirsuta*, agreeing in the armament of the disc, the disc stumps being almost identical, in the shape of the ventral arm plates, the proportions of the arm spines (though the longer ones tend to be more clavate than those of *hirsuta*) and the hooked shape of the distal lowest arm spines (though this last is shared by several other species). However, the consistently more rounded dorsal arm plates, arms nearly always shorter than ten times the disc diameter and the longitudinal lines on the arms convince me that it is worthwhile distinguishing *cheneyi*, at least at an infra-specific level. Judging from the present evidence, *M. hirsuta* is restricted to the Red Sea with *cheneyi* coming in at the southern end. It is unfortunate that Koehler did not give a more precise locality for the specimen figured in 1922 which I believe is referable to *cheneyi*. As noted under the heading of *M. hirsuta hirsuta*, specimens from the islands off Eritrea and from Aden show some intermediate characters.

Distribution. Known from Zanzibar south to Mossel Bay, S. Africa and north to southern Arabia and the southern part (at least) of the Red Sea.

Macrophiothrix koehleri sp. nov.

Text-figs. 3l, 4o, 5o, 7k, pl. 1 fig. 2

?*Ophiothrix longipeda*: Müller and Troschel, 1842 : 113. *O. longipeda* (part): H. L. Clark, 1932 : 204. [Non *O. longipeda* (Lamarck), 1816.]

?*Ophiothrix galateae*: Marktanner-Turneretscher, 1887 : 309; Brock, 1888 : 517; de Loriol, 1893a : 420; H. L. Clark, 1915 : 272. [Non *O. galateae* Lütken, 1872.]

Ophiothrix galatheae: Koehler, 1905 : 84–85; 1922 : 233–234 (part), pl. 33, fig. 11, pl. 34, figs. 1, 3 (non ?2, 4), pl. 99, fig. 1 (part); 1930 : 141.

Material. British Museum No. 1967.12.13.3, Matui Island, Marovo Lagoon, New Georgia Islands, Solomon Islands, Dr. H. G. Vevers, Royal Society Expedition, 1965, the holotype; reef platform, Graham Point, Maran Sound, E. Guadalcanal, Solomon Islands, Dr. P. E. Gibbs, same expedition, six specimens. No. 82.12.23.191, Ternate, Mollucca Islands, "Challenger" Expedition, one specimen. No. 40.11.30.–, Mindoro, Philippines, Hugh Cuming, two specimens. No. 1932.4.28.46–47, Low Islands, Queensland, Great Barrier Reef Expedition, two specimens.

Description. D.d. is 20 mm. and the arm length 280 + at least another 50 mm., the ratio being well over 1 : 15.

The disc is densely covered with small multifid stumps (Text-fig. 3l) about 0·3 mm. long, flared from just below the middle of their length, with transparent flanges ending in usually four to six points. The radial shields are about 6 mm. long and bear a few scattered very low granules, mainly around the edge, though there are some widely-spaced ones centrally. On the lower side of the disc the stumps extend on to the distal side of the oral shields, which are very broad rhombic in shape.

The dorsal arm plates (Text-fig. 5o) are trapezoidal with sharp and often slightly prolonged lateral angles. Their distal edge is usually divided into three sectors by two extremely obtuse angles but sometimes the entire distal edge is slightly convex. The twelfth plate has length : breadth = 0·9 : 1·9 mm. = 1 : 2·1.

The ventral arm plates (Text-fig. 7k) are hexagonal but distinctly broader than long on the widest part of the arm, though the distal ones become as broad as long. The plate of the twelfth free segment has length : breadth = 0·9 : 1·05 mm. The median part of the distal edge is usually quite straight, occasionally slightly concave.

There are up to ten arm spines basally. The longest ones of the twelfth free segment are up to 2·35 mm. long, or 2·6 times the segment length. The longer spines are flared from just beyond the base to a broad tip and can be described as clavate, though they are neither so bushy nor so thick distally as those of *M. belli*.

Their shafts are smooth until just short of the tip. Beyond the arm base the lowest spine (Text-fig. 40) transforms into a comb with about eight teeth but with a slightly irregular tip as a rule.

The tentacle scale is small and rounded or may have an indented free edge.

The colour consists of very dark bluish-purple spots or blotches on a lighter ground with the arm spines evenly light purple except for their tips which are abruptly white.

Variations. A paratype from the Solomon Islands has d.d. 23–24 mm. and arm length 580 + *c.* 10 mm., a ratio of *c.* 1 : 25 and in a third specimen from the same locality the proportions appear to about the same. The Ternate specimen has d.d. : a.l. = 16/260 + *c.* 20 mm. = 1 : 17·5. The Philippine and Low Islands specimens are dried and their arms are broken or coiled up and difficult to estimate but again appear to be extremely long. Most of these have the granulation of the radial shields restricted to the periphery. In the largest specimens the armament of the oral shields is reduced to a few spaced pointed thorns or even lost altogether on some shields and the shields themselves become extremely short and broad. On at least one specimen many of the dorsal arm plates are split longitudinally. There may also be a white midline along the arms.

As for Koehler's specimens, one from Dumurug Point, Philippines shown in pl. 33, fig. 11 and pl. 34, fig. 1 and the one from Billiton shown in pl. 34, fig. 3, agree well with the present material of *M. koehleri* in the appearance of the disc including the nearly naked radial shields, the shape of the dorsal arm plates and spines. The one in pl. 34, fig. 3, may possibly also be conspecific with *koehleri* but the other Billiton specimen in fig. 4 is very doubtful. Unfortunately, except for part *b*, which is definitely of this last specimen, Koehler does not make it clear from which specimens the various parts of pl. 99, fig. 1 are taken. The disc stumps, *a*, certainly agree with those of *koehleri*, unlike those in *b*, while the clavate, thorny-tipped longer arm spines are also similar. However, fig. 1*f* of the distal lowest arm spines show only four teeth and Koehler rightly says that they contrast with the comparable spines of *longipeda*, whereas the comblike form in *koehleri* does agree with *longipeda*. I suspect that the spines shown by Koehler are from this same specimen of pl. 34, fig. 4.

The specimen described under the name of *O. longipeda* by Müller & Troschel (1842) has stumps on the distal part of the oral shields and so could well belong to this species rather than to *longipeda*. Although they also describe the oral shields as being as long as wide—an unusual condition for *Macrophiothrix*—it is possible that the shields were obscured by opaque skin and they were misled by the contours of the adoral shields.

Affinities. *M. koehleri* is certainly related to *M. longipeda* in its trapezoidal dorsal arm plates and comblike lowest arm spines but the species to which it comes the closest is *M. expedita* Koehler, 1905. They agree especially in the arm structure, the arms of both being immensely long, more than fifteen times the d.d., while the dorsal and ventral arm plates are almost identical in shape and the clavate, thorny-tipped but smooth-shafted longer arm spines are indistinguishable. Also the disc stumps are very similar, although in none of the specimens of *koehleri* which I have seen are any of the stumps elongated into spinelets, as often happens in *expedita.* However, there are notable differences, particularly the reduction of the armament of the radial shields to scattered low granules in *koehleri*, in contrast to the covering of elongated stumps in *expedita*, besides the development of spinelets or stumps along the distal edge of the oral shields in *koehleri*, which are evidently lacking in *expedita* (at least in the two specimens seen by me, while they are not mentioned in Koehler's descriptions not shown in his figures). In addition the colour pattern is different, there being no more than a single light line along the arms, if any, compared with the triple line said by Koehler to be a constant feature of *M. expedita.*

Another close relative is *M. belli* Döderlein, 1896, so far recorded only from the northern coasts of Australia. Like *M. koehleri* this has the radial shields superficially appearing almost naked, the dorsal arm plates trapezoidal and the arm spines clavate. However, the clavate form is carried to a much greater degree, especially on the distal halves of the arms in *M. belli*, which also differs in having more slender disc stumps not flared distally and with fewer points, the lowest arm spines not becoming comblike, but irregular, though variable in form judging from the present material and in addition the oral shields completely naked. The arms appear to be a little shorter in *M. belli*, Döderlein gives a measurement of fourteen times the d.d., but this may not be a significant difference. H. L. Clark (1938) stresses the development of stumps on the oral shields as a specific character of importance but it is possible that it may prove to be variable; some of the present specimens, especially the largest ones, lack stumps on one or more of the shields. If this does prove to be unreliable, then there may be insufficient grounds for maintaining *koehleri* and *belli* as distinct species.

DISTRIBUTION. Known from the Solomon Islands, the Low Islands in the Great Barrier Reef, the Philippines and Moluccas.

Macrophiothrix longipeda (Lamarck)

Text-figs. 3m–o, 4p–r, 5p–r, 7l, m

Ophiura longipeda Lamarck, 1816 : 544.

Ophiothrix longipeda: Lyman, 1865 : 176–177; de Loriol, 1893 : 36–37; Döderlein, 1896 : 293, pl. 14, fig. 6, pl. 16, fig. 17; Koehler, 1922 : 235–238, pl. 31, figs. 3, 4, pl. 33, figs. 9, 10, pl. 100, fig. 2. [?Non *O. longipeda*: Müller & Troschel, 1842; see *M. koehleri*.]

Ophiothrix punctolimbata von Martens, 1870 : 257. [Non *O. punctolimbata*: de Loriol, 1893a : 416–419, pl. 15, fig. 2; nec Döderlein, 1896 : 294, pl. 14, fig. 7, pl. 16, fig. 18; nec Koehler; 1905 : 93–95; nec Matsumoto, 1917 : 226; see *M. lorioli*.]

Macrophiothrix longipeda: H. L. Clark, 1938 : 288–290; 1946 : 221.

MATERIAL. Zoologisches Museum, Berlin, No. 1749, Java, Jagor, the holotype of *Ophiothrix punctolimbata* von Martens. Also thirty-five specimens in the British Museum collections from Mauritius (one), S.E. Africa (one), Zanzibar (nine), the Seychelles (ten), Maldive Islands (three), Christmas Island, Indian Ocean (two), Timorlaut (one), Loyalty Islands (one), Tahiti (one), Fiji Islands (one), northern Australia (five).

Remarks. Although von Martens ranged *O. punctolimbata* among the species of *Ophiothrix* with granuliform disc armament, Brock (1888) described it as having multifid granulation on the radial shields and disc scales alike, which was interpreted by de Loriol and others as meaning that the armament consists of similar and somewhat elongated stumps all over. This is not the case in the holotype of *punctolimbata*, described below and consequently I cannot find any way of distinguishing this from *M. longipeda*.

Description. The holotype of *O. punctolimbata* has d.d. 13 mm. and arm length 180 + *c.* 20 mm., giving a ratio of *c.* 1 : 15.

The disc has a dense covering of short stumps (Text-fig. 3o), some of which are almost granuliform, though others are more than twice as long as wide; the longer ones are less than 0·2 mm. long. The radial shields have a dense covering of granules no higher than broad. The oral shields are broad rhombic and completely bare.

The dorsal arm plates are trapezoidal (Text-fig. 5r) with sharp latero-distal angles; that of the tenth free arm segment has length : breadth 0·95 : 2·0 mm. = 1 : 2·1. Occasional plates are split longitudinally.

The ventral arm plates on the basal half of the arm (Text-fig. 7m) are very little broader than long, that of the tenth free segment having length : breadth = 0·95 : 1·05 mm. Their shape is octagonal and the distal edge straight.

Basally there are ten arm spines on one or two segments. The longest ones measure *c.* 2·3 mm. They are finely thorny for the distal half of their length at least, sometimes also on the basal half to some extent. The lowest spine distally (Text-fig. 4r) becomes comb-like with multiple teeth.

The colour is now white with greenish-black spots along the distal and often also the proximal edges of the dorsal arm plates, while about every fourth plate is more extensively coloured so as to give a banded appearance. There are also spots on the disc.

Variations. Unfortunately the only available specimen from Mauritius, the type-locality of *M. longipeda*, is dried and not in very good condition. It is unusual in having many of the dorsal arm plates with the distal edge convex (Text-fig. 5q), although the lateral angles are still acute. In the other specimens the distal edge is usually divided into three straight sectors by two very obtuse angles, though occasional plates are somewhat convex. The length : breadth ratio of the plates is usually 1 : just over 2.

The armament of the disc scales (Text-fig. 3m) in the Mascarene specimen is fairly elongated, the stumps being mostly 2·5–3·5 times as long as broad; also the more pheripheral granules of the radial shields are often slightly longer than broad. The same is true of the specimen from the Loyalty Islands, near the opposite end of the range of *M. longipeda*, but usually the armament of the radial shields is simply granuliform. In most of the other specimens where the disc armament was examined microscopically, the stumps on the scales were usually 2·5–3·0 times as long as broad but in one of the specimens from the Seychelles they are particularly short, many of them almost granuliform (Text-fig. 3n). Koehler notes (1922) that in specimens from the Philippines the disc stumps are " three to four times as long as broad ", but it is clear that throughout the range there is some variation in the relative length. However, the shape is otherwise fairly constant in being cylindrical, very few stumps being at all flaring, and there are usually three to five points at the tip.

The arm spines do not normally exceed the arm breadth in length, as Lamarck commented, and indeed are often somewhat shorter, the longer ones usually just exceeding twice the segment length. Most of them are finely rugose for almost their entire length but the second and third spines from above may be smooth on the basal half, at least on the side facing the disc. These longer spines have their sides parallel or slightly tapering and the ends truncated so they cannot be described as at all clavate. The lowest spine distally (Text-fig. 4p) is always more or less comb-like with multiple teeth but in the specimen from the Seychelles the terminal tooth may be unusually enlarged (Text-fig. 4q).

The colour pattern normally consists of the well-defined dark intersegmental spots on the arms said to be characteristic of *punctolimbata*.

DISTRIBUTION. Known from Mauritius, E. Africa, the islands of the western Indian Ocean, the Maldive Islands, Ceylon, the East Indies, Philippines, southern Japan, the S. Pacific islands (but not the Hawaiian Islands) and northern Australia. Records from the Red Sea and Persian Gulf need confirmation, being possibly based on material of *M. hirsuta*, *demessa* or *elongata*.

Macrophiothrix lorioli sp. nov.

Text-figs. 3p, 4s, 5s, 7n, pl. 1, fig. 4

Ophiothrix punctolimbata: de Loriol, 1893a : 416–419, pl. 15, fig. 2; Koehler, 1905 : 93–95; 1922 : 237, pl. 32, fig. 6, pl. 101, fig. 7. [Non *O. punctolimbata* von Martens, 1870.]

MATERIAL. British Museum No. 1967.12.13.1, north side, Gaskell Island, (Florida Islands), Solomon Islands, Dr. H. G. Vevers, Royal Society Expedition, 1965, the holotype; No. 1967.12.13.2, north-west side, Gaskell Island, same source, one paratype; reef platform, Graham Point, Maran Sound, Guadalcanal, Solomon Islands, Dr. P. E. Gibbs, same expedition, one specimen. No. 92.8.22.49, Macclesfield Bank, S. China Sea, 24 metres, Admiralty, one specimen. No. 82.12.23.200 (part), Tongatabu, "Challenger", one specimen. No. 94.5.18.1, coral reef, Tongatabu, R. B. Leafe, one specimen.

DESCRIPTION. The holotype has d.d. 16 mm. and arm length *c.* 300 mm. and *c.* 225 mm. on two arms measured, giving ratios of 1 : 19 and 1 : 14.

The disc is closely covered with elongated stumps (Text-fig. 3p) having two to five points, most often three; most of them are flared from close to the base with transparent flanges ending in the points. The longer stumps are *c.* 0·4 mm. long. The radial shields are about 6 mm. in length and closely covered with stumps similar to but smaller than those on the disc scales; again these are mostly trifid. On the ventral side of the disc the stumps tend to have fewer points, especially the proximal ones, which may consist of a single tapering thorn. These stop short of the genital slits and the oral shields, which are broad rhombic, with length : breadth 1·25 : 1·9 mm.

The dorsal arm plates (Text-fig. 5s) are approximately fan-shaped, though the median part of the distal edge tends to be flattened. Some are angular laterally, the angle usually measuring just over 90°, but others are somewhat rounded. The widest part is distal to the middle of the length of the plate. The twelfth plate has length : breadth = 0·8 : 1·75 mm. = 1 : 2·2. The corresponding longest spines measure 2·35 mm. Further out the arms are slightly broader, the thirty-fifth plate measuring 0·9 : 2·05 mm. and the longest spines are *c.* 2·9 mm. long. Some of the basal dorsal arm plates are slightly arched but for most of the arm they are flattened.

The ventral arm plates (Text-fig. 7n) are approximately hexagonal with the three distal sides curving into one another, the distal edge being slightly convex. The plate of the twelfth free segment has length : breadth = 0·8 : 1·1 mm.

The arm spines number up to eight proximally. The longer ones have parallel sides and truncated tips and are finely rugose for most of their lengths. Distally the lowest spines become comb-like but with rugose tips (Text-fig. 4s).

The colour in spirit is purple on white. There are dark spots on the radial shields and on the dorsal arm plates leaving a light transverse bar towards the distal edge of each plate. The colour is intensified at regular intervals giving a banded effect. The ventral side of the arms is marked only with about four dark spots between each segment; there is no trace of a median ventral light line.

VARIATIONS. A second specimen from the Solomon Islands has numerous bifid as well as trifid disc stumps. Its disc appears to have regenerated as well as the distal parts of the arms. It has many of the proximal dorsal arm plates split longitudinally and also differs from the holotype in having opaque cores in the distal parts of the arm spines. The white markings on the arm plates are more T-shaped and suggest a median white line, though this is discontinuous. A more definite white midline is shown in the specimen from Macclesfield Bank and the same is true in one of the specimens from Tongatabu.

REMARKS. The discovery that the holotype of *Ophiothrix punctolimbata* has trapeziform dorsal arm plates and granular armament on the radial shields and is a synonym of *M. longipeda* leaves nameless the specimens which de Loriol and Koehler referred to von Martens' species, necessitating the introduction of the name *lorioli*.

I am uncertain as to the identity of the specimen from Thursday Island, Torres Strait, which Döderlein (1896) referred to *O. punctolimbata*. Superficially it resembles the present species but its disc stumps are evidently multifid.

AFFINITIES. The species most closely related to *M. lorioli* is *M. rhabdota* H. L. Clark, which shares the combination of fan-shaped dorsal arm plates (though in the paratype of *rhabdota* seen by me these are more consistently angular laterally), predominantly trifid elongated stumps on the radial shields as well as the disc scales, naked oral shields and distal lowest arm spines which are irregularly comb-like in form. The main difference is the presence of triple light lines along the upper side of the arms and a single light line on the lower side in *M. rhabdota*. Koehler (1915) finds that such lines are a consistent feature of *M. expedita*, though in that case the dark intervening lines are reddish and not blue. Accordingly there seems to be some justification for ranking *lorioli* as specifically distinct on the basis of the present material at least.

DISTRIBUTION. Known from the Solomon Islands, the East Indies and the Philippines.

Macrophiothrix megapoma H. L. Clark

Text-figs. 3q, 4t–v, 6a, 7o

Ophiothrix longipeda (part): H. L. Clark, 1932 : 204.
Macrophiothrix megapoma H. L. Clark, 1938 : 297–299, fig. 22; 1946 : 219–220; Endean, 1957 : 243.

MATERIAL. British Museum No. 1936.6.2.1, station IX, 22-27 metres, Great Barrier Reef Expedition, the holotype. Also twenty other specimens in the British Museum collections ranging from the Dampier Archipelago near the north-west corner of Australia to Port Curtis, Queensland in depths down to 68 metres.

REMARKS. As shown in Text-fig. 6a, the shape of the dorsal arm plates in the holotype is rather different from the trilobed form drawn by H. L. Clark, presumably from the paratype in the Harvard Museum's collection from near Cape York. The contours of the plates are also less markedly carinate. There is some variation in the shape of the plates in the other specimens; in one with d.d. only 10 mm. from Torres Strait they are almost flat but usually there is some degree of carination.

The longest arm spines on the broadest part of the arm are long and slender; on the twenty-fifth free segment in the holotype they are up to 3·6 mm. long or four times the segment length. The arms are broken within 60 mm. of the base in the holotype and the more distal lowest arm spines are little modified; however, the tip of one arm has regenerated and the lowest spines on that have teeth on one side only (Text-fig. 4t); in one there are as many as seven teeth but more often the shape is hook-like with only about four teeth. In some of the other specimens from which preparations of lowest distal spines were made there are similarly about four teeth and the tip is slightly irregular (Text-fig. 4u, v).

The arms may be spotted above, as in *M. sticta*.

DISTRIBUTION. See under material.

Macrophiothrix rhabdota (H. L. Clark)

Text-figs. 3r, 4w, 6b, 7p

Ophiothrix rhabdota H. L. Clark, 1915 : 278, pl. 13, fig. 4; 1921 : 113, pl. 15, figs. 6, 7.
?*Ophiothrix expedita* var. *rhabdota*: Koehler, 1922 : 230–233, pl. 31, fig. 5, pl. 33, fig. 6.
Macrophiothrix rhabdota: H. L. Clark, 1938 : 286–287; 1946 : 220–221; Endean, 1957 : 243.

MATERIAL. Museum of Comparative Zoology, Harvard, No. 3817, Mer, Torres Strait, one paratype.

REMARKS. The paratype has d.d. 9·5 mm.; the arms are all incomplete. The dorsal arm plates (Text-fig. 6b) have the distal edge curved back at the sides to form an angle of usually about 90° with the divergent sides. This contrasts with the more acute angles in the specimen of *M. expedita* in the British Museum collections, which give the plates a trapeziform-shape rather than a fan-shape. In this respect *M. rhabdota* is intermediate between the *longipeda*-group of species with trapeziform plates and the *hirsuta*-group with fan-shaped plates. Although there is some variation in the shape of the plates in any one species of *Macrophiothrix*, and indeed of different plates of any one specimen, the shape normally provides a useful character for distinguishing the groups of species. Accordingly I am inclined to support H. L. Clark in retaining *rhabdota* as a species distinct from *expedita*, though better samples may show that Koehler was correct in ranking *rhabdota* infraspecifically. He did this on the basis of three specimens from the Philippines which agree with the type-material of *M. expedita* (but not with that of *rhabdota*) in having spinelets among the disc stumps. Koehler's reason for referring these specimens to *rhabdota* is that the colour pattern is greyish-blue rather than the red usual in *expedita*. Having seen reddish specimens of both *M. demessa* and *M. galateae* which are morphologically indistinguishable from type-material of the more usual colour, I doubt whether this provides a valid distinction, although I think that the colour *pattern* is more important.

As mentioned under the heading of *M. lorioli*, that species is closely related to *M. rhabdota*, the main difference being the absence in *lorioli* of triple light lines on the arms, besides rather rounded lateral angles on many of the dorsal arm plates.

DISTRIBUTION. Known with certainty only from Torres Strait, the records of H. L. Clark and Koehler from the Philippines needing a critical comparison.

Macrophiothrix robillardi (de Loriol)

Text-figs. 3s, 4x, 6c, 7q

Ophiothrix Robillardi de Loriol, 1893 : 39–41, pl. 24, fig. 3.
Macrophiothrix robillardi: A. M. Clark, 1967 : 649.

MATERIAL. British Museum No. 1949.10.21.1, Mauritius, one specimen. [This is an old specimen of which the original registration number (if any) has been lost; it is quite possible that it came from de Robillard like the holotype, since much of our old mascarene material was purchased from him.]

REMARKS. There is a faint suggestion of a median longitudinal light line, what little colour remains elsewhere being blue.

DISTRIBUTION. Known only from Mauritius.

Macrophiothrix rugosa H. L. Clark

Text-figs. 4y, 6d, 7r

Macrophiothrix rugosa H. L. Clark, 1938 : 229–230, fig. 23; Endean, 1957 : 243.

MATERIAL. Museum of Comparative Zoology, Harvard, No. 3799A, Mer, Thursday Island, Torres Strait, one arm of the holotype.

Description. The dorsal arm plates (Text-fig. 6d) are broad fan-shaped except that the median part of the distal edge is slightly concave; there appears to be an additional suture at the proximal end of each plate so that the successive plates do not overlap. Many of the plates are split longitudinally, a feature not mentioned by H. L. Clark. He also describes the surface of the plates as uniformly covered with prickly granules, implying that these are superimposed, whereas in fact the surface of the plate itself has a markedly rugose texture. One of the proximal dorsal arm plates on the detached arm has length : breadth = 0·75 : 1·9 mm. = 1 : 2·6. The longest corresponding spine is 2·75 mm. The longer spines are slightly tapering and finely thorny. The lowest spines distally (Text-fig. 4y) become very short, with a few short transparent points on the outer part or a slightly curved tooth but they cannot really be described as hook-like. There are only seven spines on the proximal-most segment remaining.

The ventral arm plates (Text-fig. 7r) are broad rectangular and widely separated, though the proximal edge is very indistinct; the distal edge is slightly convex in contrast to that of *M. callizona* and *calyptaspis*. A proximal plate measured has length : breadth = 0·55 : 1·0 mm.

Distribution. Known only from Torres Strait.

Macrophiothrix scotia H. L. Clark

Text-figs. 3t, 4z, 6e, 7s

Macrophiothrix scotia H. L. Clark, 1938 : 300–302, pl. 24, fig. 2; 1946 : 220.

Material. British Museum No. 1967.11.14.7, Broome, N.W. Australia, one paratype.

Affinities. The differences detailed by H. L. Clark in his key between *M. megapoma* and *scotia* appear to me very slight. The disc armament of multifid stumps (Text-fig. 3t) and the shapes of the arm plates and spines, with the lowest one distally (Text-fig. 4z) only half-way modified into a hook, are very similar, allowing for the difference in size of the specimens illustrated (d.d. 19 mm. in the holotype of *megapoma* or 18 mm. according to H. L. Clark and 13 mm. in the paratype of *scotia*). The tentacle scales of *scotia* are not significantly smaller and although the colour is particularly dull, this may also be true in *megapoma*; both have a broad light longitudinal band along the under side of the arms.

Distribution. Known from Lagrange Bay (west of Broome), N.W. Australia, eastwards only to Darwin.

Macrophiothrix spinifera H. L. Clark

Text-figs. 3u, 6f, 7t

Macrophiothrix spinifera H. L. Clark, 1938 : 302–304, pl. 24, fig. 3; 1946 : 220.

Material. British Museum No. 1967.11.14.8, Broome, N.W. Australia, one paratype.

Affinities. Judging again from only single preserved specimens I cannot see any significant difference in the flatness or shape of the arms and arm spines between *M. spinifera* and *scotia*, as postulated by H. L. Clark in his key. The disc stumps of *spinifera* are rather smaller as Dr. Clark notes but this alone does not provide a specific distinction. He comments that the young of *spinifera* and *scotia* are indistinguishable but the adults are very different.

Distribution. Known only from the Broome area of N.W. Australia, from Lagrange Bay to Cape Leveque.

Macrophiothrix sticta H. L. Clark

figs. 4a′, 6g, 7u

Macrophiothrix sticta H. L. Clark, 1938 : 304–305, fig. 24; 1946 : 219.

Material. Museum of Comparative Zoology, Harvard, No. 2345A, Shark Bay, W. Australia, part of one arm of the holotype.

Description. The piece of arm measures 95 mm. and is probably about half or less of the whole arm, judging from the very slight degree of tapering distally; H. L. Clark's estimate of their probable total length is *c.* 200 mm.; he also gives the d.d. as 15 mm.

The dorsal arm plates (Text-fig. 6g) are flat broad and hexagonal or elliptical, widest at about the middle of their length. A proximal one has length : breadth = 0·85 : 2·2 mm. = 1 : 2·6. The longest corresponding spine is 3·8 mm. long or 4·5 times the segment length but the spines on the more distal remaining segments are even longer, up to *c.* 5·25 mm. The longer spines have almost parallel finely thorny sides and some of them are slightly expanded at their truncated tips. The lowest spine on the more distal remaining segments (Text-fig. 4a′) is not very much modified; possibly those on the lost distal part of the arm were more hook-like.

The ventral arm plates (Text-fig. 7u) are contiguous and rounded pentagonal in shape with the proximal angle slightly truncated. The distal side is straight or very slightly concave.

The dorsal arm plates are marked with large spots, as described by H. L. Clark, or with poorly defined transverse lines.

Affinities. Of the three other Australian nominal species besides *M. megapoma* with the oral shields armed with stumps and included by H. L. Clark, *M. sticta* seems to me to be the only one significantly different from *megapoma*, judging from the arm structure. The dorsal arm plates are broad hexagonal, as opposed to fan-shaped and the arm spines are relatively longer, 4·5 times the segment length compared with 3·3 to 3·7 times the segment length in the material of *megapoma*, *scotia* and *spinifera* measured. In these three also the longer spines are not at all broadened at the tip.

Distribution. Known only from Shark Bay, W. Australia.

Macrophiothrix variabilis (Duncan)

Text-figs. 3v, w, 4b′, c′, 6h, i, 7v, pl. fig. 3

Ophiothrix variabilis Duncan, 1887 : 99–101, pl. 9, figs. 18, 19, pl. 11, figs. 32–36.
Ophiothrix hirsuta: Koehler, 1905 : 93; 1922 : 234–235 (part), pl. 31, fig. 2 (non fig. 1), pl. 33, fig. 13 (?non pl. 99, fig. 2). [Non *O. hirsuta* Müller and Troschel, 1842.]

MATERIAL. Oslo Museum, off Pasir Panjang Power Station, Singapore, and specimen. Also six specimens in the British Museum collections from Tuticorin one Ramesvaram, Gulf of Manaar.

REMARKS. I disagree with Koehler (1905) that *O. variabilis* is conspecific with *O. hirsuta* although the two are certainly closely related. In all the specimens of

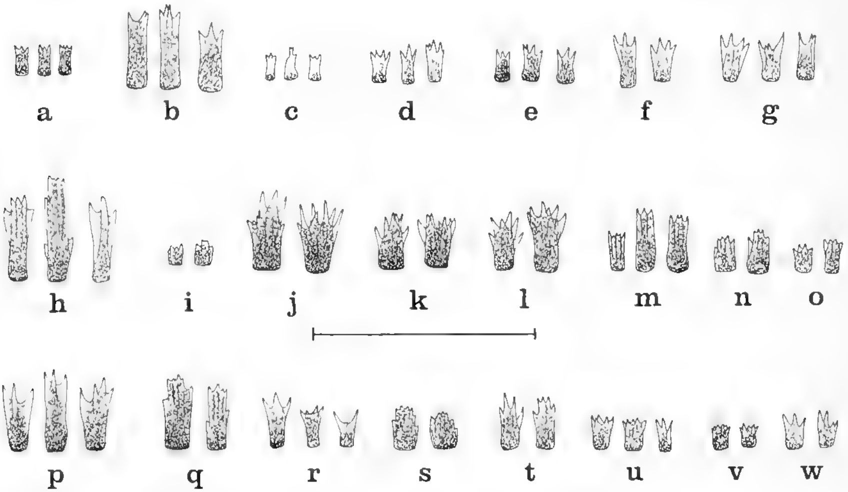

FIG. 3. *Macrophiothrix* spp. Disc stumps. a. *M. aspidota*, 82.1.5.11, Karachi, d.d. 22 mm.; b. *M. belli*, 42.2.24.1, Port Essington, N. Australia, d.d. 25 mm.; c. *M. callizona*, paratype, M.C.Z. 5113, Broome, d.d. 10·5 mm.; d. *M. calyptaspis*, paratype, M.C.Z. 5115, d.d. 11 mm.; e. *M. demessa*, M.C.Z. 4491, Hawaiian Islands, d.d. 8·5 mm.; f. *M. demessa*, 1949.10.20.1, Gulf of Aqaba, d.d. 19 mm.; g. *M. elongata*, 1922.3.1.11, Persian Gulf, d.d. 16 mm.; h. *M. expedita*, 82.12.23.62, Philippines, d.d. 15 mm.; i. *M. galateae*, holotype, Copenhagen Museum, Nicobar Islands, d.d. 14·5 mm.; j. *M. hirsuta hirsuta*, holotype, Berlin Museum 1000, Red Sea, d.d. *c.* 22 mm.; k. *M. hirsuta cheneyi*, paratype, M.C.Z. 4097, Zanzibar, d.d. 17 mm.; l. *M. koehleri*, holotype, 1967.12.13.3, Solomon Islands, d.d. 20 mm.; m. *M. longipeda*, 42.12.26.60, Mauritius, d.d. 25 mm.; n. *M. longipeda*, 82.10.16.85, Seychelles, d.d. 20 mm.; o. *M. longipeda* (holotype of *Ophiothrix punctolimbata*), Berlin Museum 1749, Java, d.d. 13 mm.; p. *M. lorioli*, holotype, 1967.12.13.1, Solomon Islands, d.d. 16 mm.; q. *M. megapoma*, holotype, 1936.6.2.1, Great Barrier Reef, d.d. 18 mm.; r. *M. rhabdota*, paratype, M.C.Z. 3817, Torres Strait, d.d. 9·5 mm.; s. *M. robillardi*, 1949.10.21.1, Mauritius, d.d. 15 mm.; t. *M. scotia*, paratype, 1967.11.14.7, Broome, d.d. 13 mm.; u. *M. spinifera*, paratype, M.C.Z. 5126, Broome, d.d. 11 mm.; v. *M. variabilis*, Oslo Museum, Singapore, d.d. 22 mm.; w. *M. variabilis*, 88.11.15.1, Ramesvaram, d.d. 25 mm.

variabilis I have seen many of the dorsal arm plates (Text-fig. 6h, i) are distinctly trilobed, a form not found in *hirsuta* and in addition the lateral angles are much more rounded, as in *hirsuta cheneyi* but not in *hirsuta hirsuta*. The arms are very smooth dorsally and covered with thick skin which tends to obscure the limits of the plates in spirit specimens. There is no sign of the rugosities on the surface of the plate which are regularly found in *M. hirsuta*. The disc stumps (Text-fig. 3v, w) are consistently only half as long as those of *M. hirsuta* and usually have only three or four points instead of about six, although in the specimen from Singapore they are

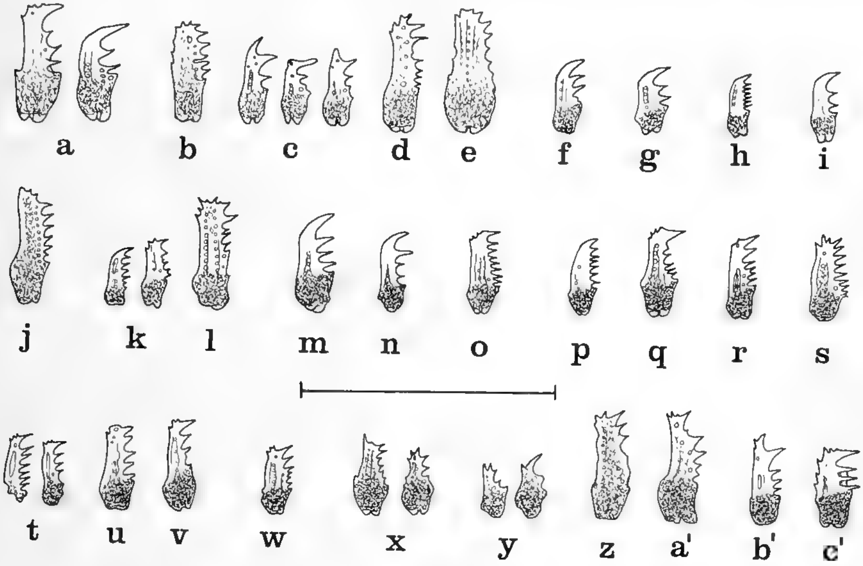

FIG. 4. *Macrophiothrix* spp. Lowest arm spines, from distal part of arm unless otherwise stated. a. *M. aspidota*, 88.11.15.2, Ramesvaram; b. *M. belli*, 83.12.9.55, Torres Strait; c. *M. belli*, 82.2.22.133, Torres Strait; d. *M. belli*, 42.2.24.1, Port Essington; e. *M. belli*, 1953.1.24.13, Monte Bello Islands (? middle segment); f. *M. callizona*, paratype, M.C.Z. 5113, Broome; g. *M. calyptaspis*, paratype, M.C.Z. 5115, Broome; h. *M. demessa*, M.C.Z. 4491, Hawaiian Islands; i. *M. elongata*, 1922.3.1.11, Persian Gulf; j. *M. expedita*, 82.12.23.62, Philippines (? middle segment); k. *M. galateae*, holotype, Copenhagen Museum, Nicobar Islands; l. *M. galateae*, 82.12.23.200(pt.), Tonga Islands. (? middle segment); m. *M. hirsuta hirsuta*, holotype, Berlin Museum 1000, Red Sea; n. *M. hirsuta cheneyi*, paratype, M.C.Z. 4097, Zanzibar; o. *M. koehleri*, holotype, 1967.12.13.3, Solomon Islands; p. *M. longipeda*, 42.12.26.60, Mauritius; q. *M. longipeda*, 82.10.16.85, Seychelles; r. *M. longipeda* (holotype of *Ophiothrix punctolimbata*), Berlin Museum 1749, Java; s. *M. lorioli*, holotype, 1967.12.13.1, Solomon Islands; t. *M. megapoma*, holotype, 1936.6 2.1, Great Barrier Reef (from regenerated arm tip); u. *M. megapoma*, 82.12 23.179, Torres Strait; v. *M. megapoma*, 81.10.26.95, Port Curtis; w. *M. rhabdota*, paratype, M.C.Z. 3817, Torres Strait; x. *M. robillardi*, 1949.10.21.1, Mauritius; y. *M. rugosa*, holotype, M.C.Z. 3799A, Torres Strait; z. *M. scotia*, paratype, 1967.11.14.7, Broome; a'. *M. sticta*, holotype, M.C.Z. 2345A, Sharks Bay (middle segment);); b'. *M. variabilis*, Oslo Museum, Singapore; c'. *M. variabilis*, 88.1.2.60, Tuticorin.

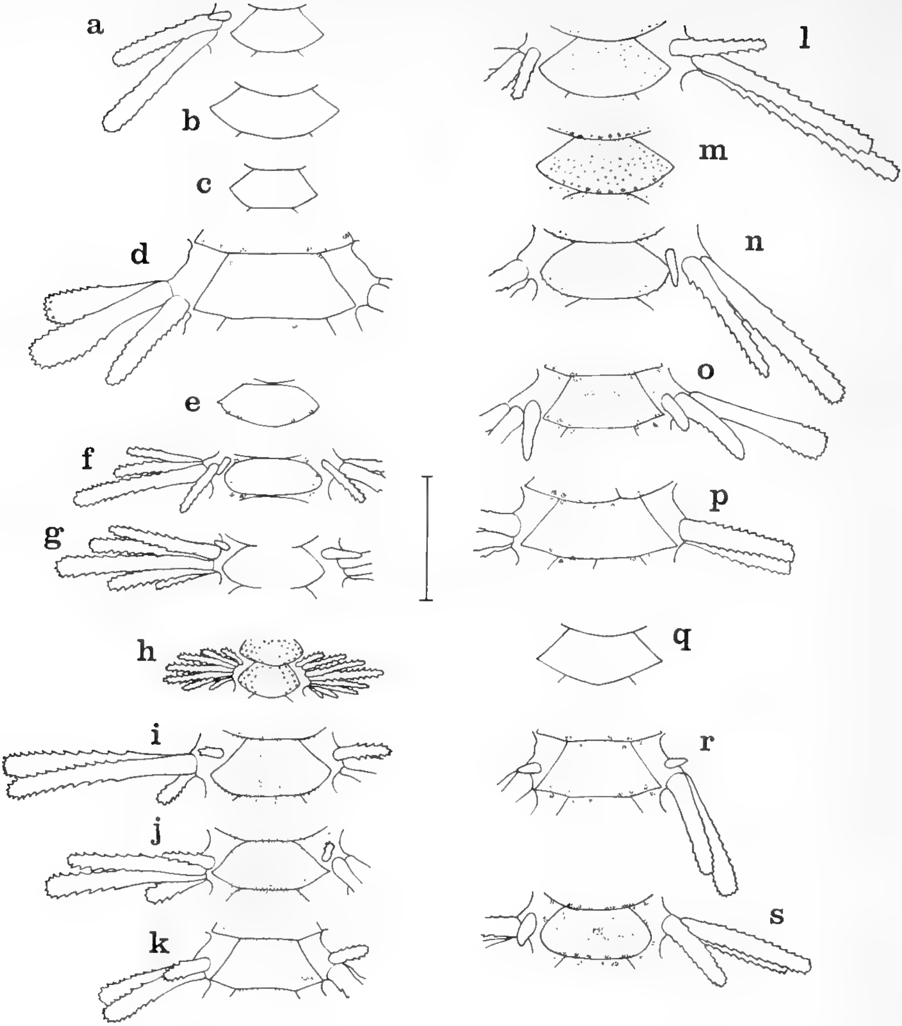

FIG. 5. *Macrophiothrix* spp. Proximal arm segments from about twelfth to twentieth free ones), in dorsal view. a. *M. aspidota*, holotype, Berlin Museum 1008, E. India; b. *M. aspidota*, 88.11.15.2, Ramesvaram, d.d. 14 mm.; c. *M. aspidota*, 1961.8.23.11, Bombay, d.d. 15 m.m; d. *M. belli*, 1953.1.24.13, Monte Bello Islands, d.d. 22 mm.; e. & f. fourth dorsal arm plate and twentieth free segment of *M. callizona*, paratype, M.C.Z. 5113, Broome, d.d. 10·5 mm.; g. *M. calyptaspis*, paratype, M.C.Z. 5115, Broome, d.d. 11 mm.; h. *M. demessa*, M.C.Z. 4491, Hawaiian Islands, d.d. 8·5 mm.; i. *M. elongata*, 1922.3.1.11, Persian Gulf, d.d. 16 mm.; j. *M. expedita*, 82.12.23.62, Philippines, d.d. 15 mm.; k. *M. galateae*, holotype, Copenhagen Museum, Nicobar Islands, d.d. 14·5 mm.; l. *M. hirsuta hirsuta*, holotype, Berlin Museum 1000, Red Sea, d.d. *c.* 22 mm.; m. *M. hirsuta hirsuta*, 49.8.24.118, Red Sea, d.d. 18 mm.; n. *M. hirsuta cheneyi*, paratype, M.C.Z. 4097, Zanzibar, d.d. 17 mm.; o. *M. koehleri*, holotype, 1967.12.13.3, Solomon Islands, d.d. 20 mm.; p. *M. longipeda*, 82.10.16.85, Seychelles, d.d. 20 mm.; q. *M. longipeda*, 42.12.26.60, Mauritius, d.d. *c.* 25 mm.; r. *M. longipeda* (holotype of *Ophiothrix punctolimbata*), Berlin Museum 1749, Java, d.d. 13 mm.; s. *M. lorioli*, holotype, 1967.12.13.1, Solomon Islands, d.d. 16 mm. The colour pattern is shown in d, f, i, j, k, m-p, r and s only.

multifid, though extremely small (Text-fig. 3v). The arm spines are relatively much longer in *hirsuta*, the longest ones over four times the corresponding segment length in the holotype of *hirsuta* compared with less than 3·5 times the segment length in *variabilis*. This is also shown up in a comparison of figs. 1 and 2 in Koehler's pl. 31, 1922, fig. 1 being of a specimen from the Red Sea, probably of *M. hirsuta cheneyi*, while I believe that fig. 2 is of *variabilis*. The lowest arm spine distally is somewhat different; in *M. hirsuta* it usually forms a perfect hook (Text-fig. 4m) but in *variabilis* (Text-fig. 4b′, c′) the tip of the hook is more or less irregular. Finally, Duncan gives the arm length of *variabilis* as twelve to fourteen times the d.d., whereas in *M. hirsuta hirsuta* although in one specimen from Aden the arms are about 12·5 times the d.d. the usual proportion is probably about ten times and in *hirsuta cheneyi* even less.

DISTRIBUTION. Known from the Mergui Archipelago, Singapore and the southern tip of India. It remains to be seen whether the specimens from the East Indies which have been referred to *hirsuta* are in fact *variabilis*; I suspect that many of them are.

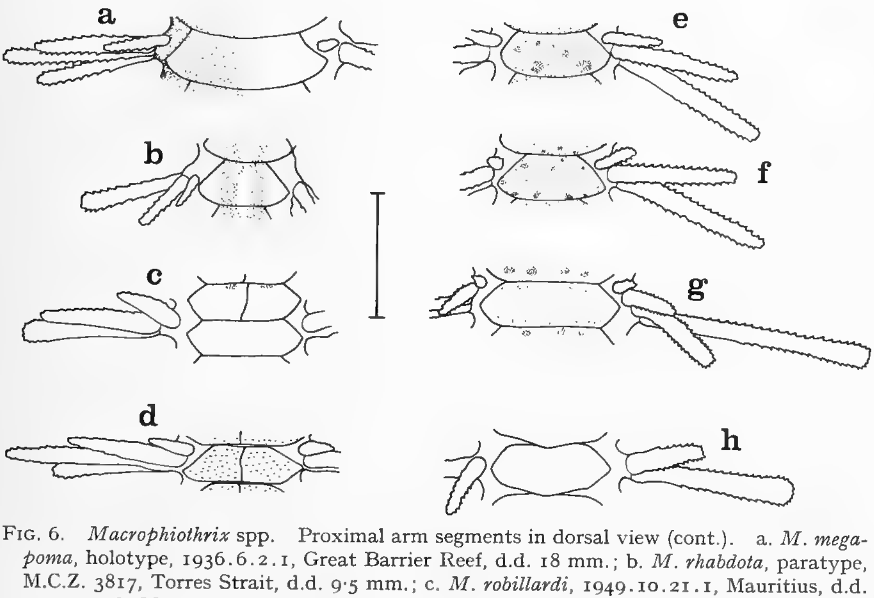

FIG. 6. *Macrophiothrix* spp. Proximal arm segments in dorsal view (cont.). a. *M. megapoma*, holotype, 1936.6.2.1, Great Barrier Reef, d.d. 18 mm.; b. *M. rhabdota*, paratype, M.C.Z. 3817, Torres Strait, d.d. 9·5 mm.; c. *M. robillardi*, 1949.10.21.1, Mauritius, d.d. 15 mm.; d. *M. rugosa*, holotype, M.C.Z. 3799A, Torres Strait, d.d. 16 mm.; e. *M. scotia*, paratype, 1967.11.14.7, Broome, d.d. 13 mm.; f. *M. spinifera* paratype, 1967.11.14.8, Broome, d.d. 11 mm.; g. *M. sticta*, holotype, M.C.Z. 2345A, Shark's Bay, d.d. 15 mm.; h. *M. variabilis*, Oslo Museum, Singapore, d.d. *c.* 22 mm. The carination is shown by shading in (a) and the colour pattern in b, c, e, f & g only.

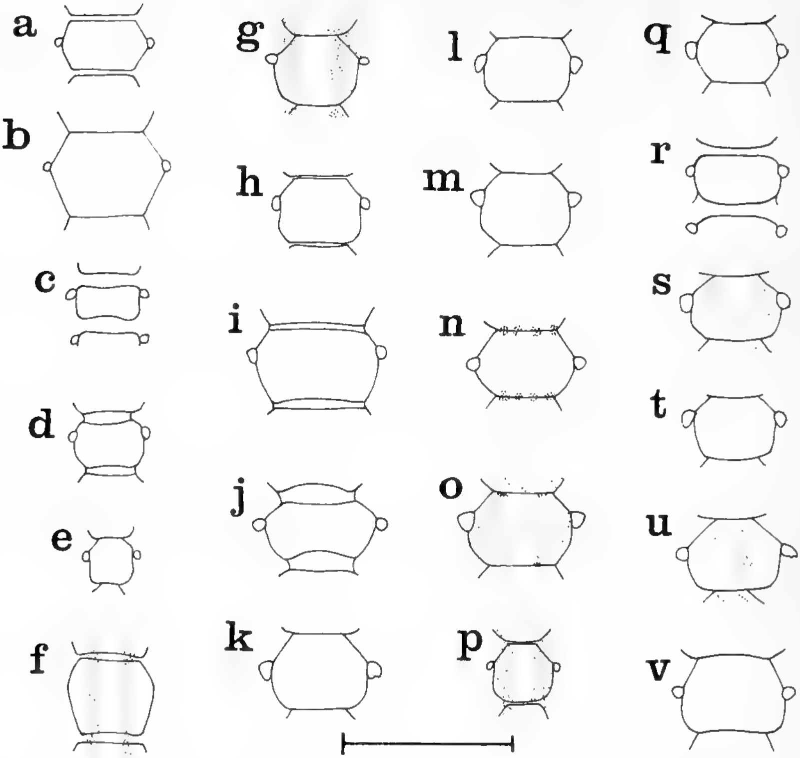

FIG. 7. *Macrophiothrix* spp. Proximal arm segments in ventral view. Details as for figs. 5 and 6, unless otherwise stated. a. *M. aspidota*, holotype; b. *M. belli*, 1953.1.24.13; c. *M. callizona*, paratype; d. *M. calyptaspis*, paratype; e. *M. demessa*, M.C.Z. 4491; f. *M. elongata*, 1922.3.1.11; g. *M. expedita*, 82.12.23.62; h. *M. galateae*, holotype; i. *M. hirsuta hirsuta*, holotype; j. *M. hirsuta cheneyi*, paratype; k. *M. koehleri*, holotype; l. *M. longipeda*, 42.12.26.60; m. *M. longipeda* (holotype of *Ophiothrix punctolimbata*); n. *M. lorioli*, holotype; o. *M. megapoma*, holotype; p. *M. rhabdota*, paratype; q. *M. robillardi*, 1949.10.21.1; r. *M. rugosa*, holotype; s. *M. scotia*, paratype; t. *M. spinifera*, paratype; u. *M. sticta*, holotype; v. *M. variabilis*, 88.1.2.1, Tuticorin, d.d. 20 mm. The colour pattern is shown in f, g, n, o, p, s and u only.

Family ***OPHIODERMATIDAE***

Ophiopeza fallax fallax Peters

Text-fig. 9c

Ophiopeza fallax Peters, 1851 : 465; Lyman, 1874 : 221.
Pectinura fallax: H. L. Clark, 1909 : 119; 1915 : 303, pl. 18, figs. 9, 10.

MATERIAL. About forty specimens in the British Museum collections from Zanzibar.

Nomenclature. The use of the combination *Ophiopeza fallax* by Mortensen (1940), when dealing with what I am now calling *O. fallax arabica*, is preferable to that used by H. L. Clark. As Mortensen commented, the synonymizing of *Ophiopeza* Peters, 1851 with *Pectinura* Forbes, 1843 was premature in view of the very little which is known about the type-species of *Pectinura*, *P. vestita* Forbes, the genus being originally monotypic. The holotype is the only recorded specimen and its whereabouts are unknown. It had d.d. only 2 or 3 mm. (one-tenth of an inch). Judging from the description and figures each oral shield (ovarian plate of Forbes) is accompanied by a broad supplementary shield. No such supplementary shields are exposed as a rule in *Ophiopeza fallax* (although they may be present concealed under the granulation) but H. L. Clark discarded their occurrence as a character of generic weight, a conclusion with which I concur in view of the variable occurrence of such shields in several species of Ophiodermatidae. I think it quite possible that the holotype of *P. vestita* could have been a specimen of *Ophioconis forbesi* (Heller) with the granule-covering rubbed off the oral shields. *O. forbesi* has been recorded from the Adriatic and further west in the Mediterranean. The type-locality of *P. vestita* is off southern Turkey, from which part little collecting has been done; until this omission is rectified and more Ophiodermatids are taken from that area of the Mediterranean, no further assumptions about the nature of *Pectinura* should be made.

In 1949 A. H. Clark referred *fallax* to *Ophiopezella*, again dealing with the subspecies described below, on account of the prominence of the series of plates just above the margin of the disc interradially. This same character was used by H. L. Clark as diagnostic of *Ophiopezella* Ljungman, 1872, type-species *Ophiarachna spinosa* Ljungman, 1867, regardless of its occurrence, though less conspicuously, in *Ophiopeza fallax* (Text-fig. 9a, p. 318). Since *Ophiopeza* antedates *Ophiopezella* the latter becomes a synonym and the two species included, *O. spinosa* and *O. dubiosa* de Loriol, are referable to *Ophiopeza*. A third nominal species, *Ophiopezella decorata* Mortensen (1933, Vidensk. Meddr dansk naturh. Foren. **93** : 379) from Durban, South Africa, I think is probably a synonym of *Ophiopeza fallax*; it has no exposed supplementary oral shields and the relatively broad oral shields provide a dubious distinction since the shape of these is somewhat variable in most Ophiodermatids. The remaining species which have been referred to *Pectinura* (namely *aequalis* Lyman, *anchista* H. L. Clark, *arenosa* Lyman, *assimilis* (Bell), *cylindrica* (Hutton), *dyscrita* H. L. Clark, *exilis* (Koehler), *gracilis* Mortensen, *maculata* (Verrill) and *nigra* H. L. Clark) with the exception of *P. yoldii* dealt with below, are all congeneric with *Ophiopeza fallax* in my view.

Distribution. Known from Mozambique (? south to Natal) to Zanzibar; Brock's record from Amboina (1888) and Koehler's from the Sulu Archipelago, Philippines, need re-investigation in view of the subspecies described below.

Ophiopeza fallax arabica subsp. nov.

fig. 8, pl. 1, figs. 5, 6

Ophiopeza fallax: Mortensen, 1940 : 100 [Non *O. fallax* Peters, 1851.]
Ophiopezella fallax: A. H. Clark *in* Clark & Bowen, 1949 : 5.

MATERIAL. U.S.N.M. No. E.7734, Tarut Bay, Persian Gulf, under stones, the holotype. B.M. No. 1962.8.16.5, north of Jazirat al Yas Island, Trucial Oman, Persian Gulf, one specimen. Pakistan Marine Biological Laboratory No. 836 and B.M. No. 1967.11.1.14, Bulejee Village, Karachi, two specimens.

DESCRIPTION. The holotype has the d.d. 14 mm. and arm length *c.* 45 mm. The disc is covered with fine granules which under high magnification can be seen to be polygonal and often centrally indented. There are *c.* 28 granules to the linear mm. near the centre. The peripheral interradial plates on the upper side are distinctly convex and their contours are emphasized by a slight increase in the size of the granules covering them. The major parts of the radial shields, a broad plate in the middle of each interradius and a triad of plates opposite the base of each arm are abruptly bare of granules. The bare areas stand out slightly from the surface of the plates bringing them level with the top of the granules to give a smooth finish. A few other smaller bare areas also occur on the peripheral plates. On the ventral side of the disc the granulation is continuous up to the oral shields.

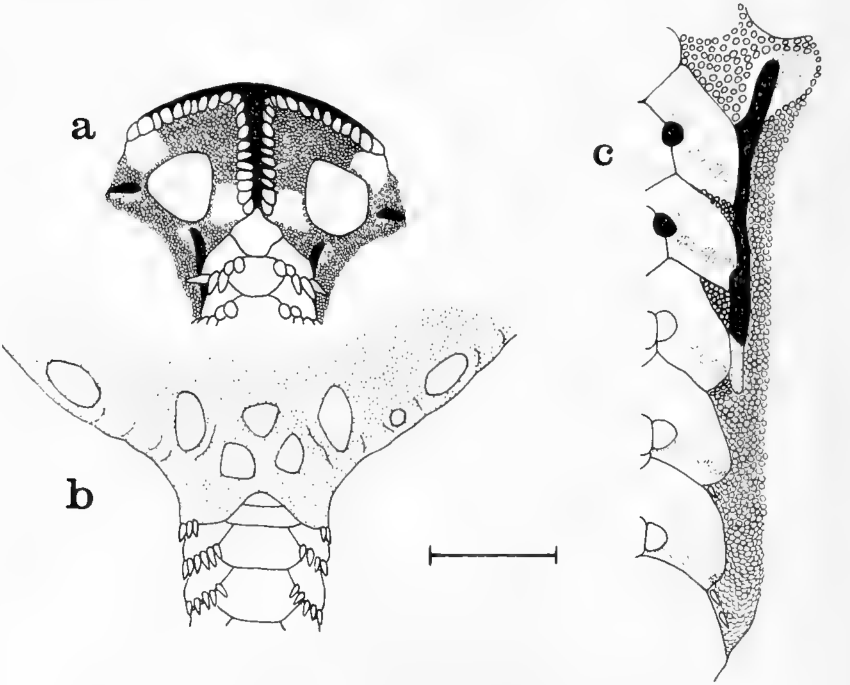

FIG. 8. *Ophiopeza fallax arabica* subsp. nov. Holotype, U.S.N.M. No. E.7734, Tarut Bay, Saudi Arabia (Persian Gulf). a. Two jaws; b. part of disc and arm base in dorsal view, the very fine granulation is indicated by stippling; c. detail of the side of an arm base in ventral view showing a few fine spinelets on the adjacent disc scales; the arm spines and the tentacle scales of the first two pores lacking. The scale measures 2 mm. for a and b and 0·67 mm. for c.

The oral shields are pentagonal or could be described as triangular with the latero-distal angles truncated; their length is about equal to or just exceeds the breadth. The proximal granules were removed from two interradii (pl. 1, fig. 5); one of these shows a well-developed supplementary oral shield previously concealed but otherwise resembling the corresponding shield of species such as *Ophiarachnella infernalis*. In the second area, however, there are two enlarged scales in this position adjacent to the oral shield. The distal parts of the adoral shields are naked but the rest of the jaw angle is covered with granules which are coarser than those on the disc. There are about ten oral papillae each side, including the second oral tentacle scale at the distal end of the series.

The arms become squarish in cross section distally with the dorsal side slightly concave; proximally they are somewhat more rounded. The dorsal arm plates are proximally hexagonal with the middle of the distal side straight or slightly concave. The plates are thickened and bevelled at the edges but flat above. The ventral arm plates are mostly octagonal, the proximal ones slightly broader than long. Basically there are eleven arm spines, each tapering to a blunt point, the lowest one no longer than the rest and none of them exceeding half the segment length. There are two tentacle scales, the smaller outer one overlapping the base of the lowest spine, as usual in the family.

The arms are marked with sharply defined dark brown bands.

[I am much indebted to Miss M. Downey of the U.S. National Museum for estimating the density of the disc granulation and the occurrence of the supplementary oral shields for me, these being features which I omitted to examine when visiting the U.S. National Museum in 1953. Miss Downey also tells me that the two other specimens from the same locality as the holotype mentioned by A. H. Clark must be in the American Museum in New York.]

VARIATIONS. The three other specimens studied have d.d. : a.l. respectively 11·5 : 40 mm. = 1 : 3·5; 14 : 45 mm. = 1 : 3·2 and 11 : 40 mm. = 1 : 3·6. They also appear to have rather coarser disc granulation than the holotype, the larger Karachi specimen having about nineteen granules per linear mm. in the centre of the disc while the one from Trucial Oman has only about seventeen. None of the specimens has so many bare disc plates as the holotype and only the Oman specimen has any of the radial shields bare; in this case three and a half pairs of the shields are partially naked. In all three specimens a rounded bare patch occurs in most of the interradii just above the margin and there are one to three bare areas opposite the base of each arm on the triad of slightly swollen plates. The Oman specimen has unusually elongated oral shields with length : breadth = 1·35 : 1·0 mm. Only in the larger Karachi specimen is even one supplementary oral shield partly naked but wherever the granulation was removed in all the specimens one or sometimes two distinctly enlarged scales, more or less semicircular in shape, were revealed. The specimens have up to eleven (rarely twelve), thirteen and twelve arm spines basally respectively, the corresponding disc diameters being 11·5 mm., 14 mm. and 11 mm. The extent of the dark bands on the arms is variable; in the Oman specimen they extend for only one and a half to two segments, in the larger Karachi specimen for three to six segments and in the smaller one for about three segments. The discs are mid-brown, dappled with small darker spots.

Affinities. These specimens from the Persian Gulf and Arabian Sea are very similar to *Ophiopeza fallax* from E. Africa, differing mainly in the consistent occurrence of some bare plates on the disc. I had thought that the disc granulation was also coarser in the northern specimens, since examples of *fallax* from Zanzibar examined have twenty-five to thirty granules per mm. and those from Oman and Karachi less than twenty. However, the number in the holotype of *arabica* comes within the range for *fallax fallax*. Accordingly I do not believe that the difference between them can be rated as a specific one, the distribution of the disc granulation being somewhat variable.

Ophiopeza fallax arabica serves to bridge the gap not only between *Ophiopeza* without exposed supplementary oral shields and *Ophiopezella* in which such plates are present (and incidentally serves to confirm the doubtful worth of this character as already expressed, notably by H. L. Clark in 1909), but also between *Ophiopeza* with granule-covered radial shields and *Ophiarachnella* with naked ones (as well as with naked supplementary oral shields). Thus it tends to minimize the extent of the granulation as a character of generic weight in this family.

OPHIOPSAMMUS Lütken, 1869

Ophiopsammus Lütken, 1869 : 37(19), 88(70), 98(80). Type-species *Ophiopeza Yoldii* Lütken, 1856.
Ophiopeza (part): Lyman, 1874 : 221; Bell, 1884 : 137; Koehler, 1905 : 12.
Pectinura (part): H. L. Clark, 1909 : 119; Koehler, 1922 : 338.

Diagnosis. A genus of Ophiodermatidae in which the disc is wholly covered with granules, concealing the radial shields; there is a horizontal series of enlarged scales interradially between the radial shields just above the periphery but these are not in the least convex, their existence and positions being revealed only by removal of the granules; the oral shields are naked and are normally unaccompanied by supplementary shields; the arms are markedly carinate above with relatively broad dorsal arm plates, the proximal ones more than twice as broad as long and with straight distal edges; the arm spines are relatively few, up to only nine in large specimens (very rarely ten) with d.d. *c.* 15 mm. or seven or eight when d.d. is 10–12 mm., they are not closely appressed to the side of the arm and the longer ones are about equal in length to the segment; the tentacle scales number two basally, the outer one overlying the base of the lowest arm spine, but give way to one further out on the arm; there are only two genital slits in each interradial area.

Remarks. I have been unable to trace any justification by Lyman for his inclusion in 1874 of *Ophiopsammus* in the synonymy of *Ophiopeza*, a move which was followed by other specialists until 1909 when H. L. Clark revised the generic limits within this part of the family and referred *Ophiopeza* to the synonymy of *Pectinura*, from which he simultaneously removed *Ophiarachnella* Ljungman, 1872, *Ophiochasma* Grube, 1868, *Ophiopezella* Ljungman, 1872, *Bathypectinura* and *Cryptopelta*, the last two being new genera. As mentioned above, I agree with Mortensen (1940) that the synonymizing of *Ophiopeza* is premature and it should be retained as a genus separate from *Pectinura* until more is known about the type-species of the latter. Nor do I consider that *Ophiopeza yoldii* is congeneric with *O. fallax*. One of the main characters which has been used for distinction of the genera of Ophiodermatidae is the extent of the granulation, whether or not it covers the adoral, oral, supplementary oral (if present) and radial shields and arm bases. In view of the variation in granulation shown by some Ophiodermatidae including *Ophiarachnella infernalis* and *Ophiopeza fallax fallax* as opposed to *fallax arabica* I do not regard this character as having any great weight. A number of species such as *Ophiopeza fallax*, *Ophiarachnella infernalis*, *Ophiostegastus instratus* and *Cryptopelta granulifera* among others show considerable morphological resemblance, notably in the structure of the arms which are flattened above while the dorsal arm plates are not particularly broad and have continuously rounded distal edges. However, these are placed in different genera on account of differences in the distribution of the granules. The markedly carinate arms with very broad rectangular dorsal arm plates in *Ophiopeza yoldii* are such a conspicuous departure from this form that I am convinced it should be kept in a distinct genus as treated by Lütken.

Apart from the difference in arm structure, the smooth periphery of the disc also serves to differentiate it from the species of *Ophiopeza*, mature specimens of which have the interradial plates above the margin markedly convex. A comparable series of enlarged plates is developed in *Ophiopsammus yoldii* but they are not at all convex (Text-fig. 9b).

Ophiopsammus yoldii (Lütken)

fig. 9a, b

Ophiopeza Yoldii Lütken, 1856 : 9; Lyman, 1874 : 221.
Ophiopsammus Yoldii: Lütken, 1869 : 37.
Ophiopeza conjugens Bell: 1884 : 137–138; Döderlein, 1896 : 281–282, pl. 15, fig. 1.
Pectinura yoldii: H. L. Clark, 1909 : 119; Koehler, 1922 : 338; 1930 : 270.

MATERIAL. About thirty-five specimens in the British Museum collections of which twelve are from the Indian Ocean, the rest from northern Australia.

NOMENCLATURE. The revival of the generic name *Ophiopsammus* for this species is dealt with above.

DISTRIBUTION. The type-locality is unknown, "possibly the West Indies" according to Lütken but probably rather the East Indies. The species is very common in northern Australia and extends westwards to the Bay of Bengal.

Ophiostegastus compsus* sp. nov.

Text-fig. 10

MATERIAL. B.M. No. 1967.11.9.1–3, Qudhaibiya Bay, Bahrein, Persian Gulf, on stones on mud flats, intertidal, Capt. England, the holotype and three paratypes.

DESCRIPTION OF THE HOLOTYPE. D.d. 10·5 mm. All the arms are broken within 27 mm. of the disc, the complete length may have been about 35 mm.

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*From the greek compsos—elegant.

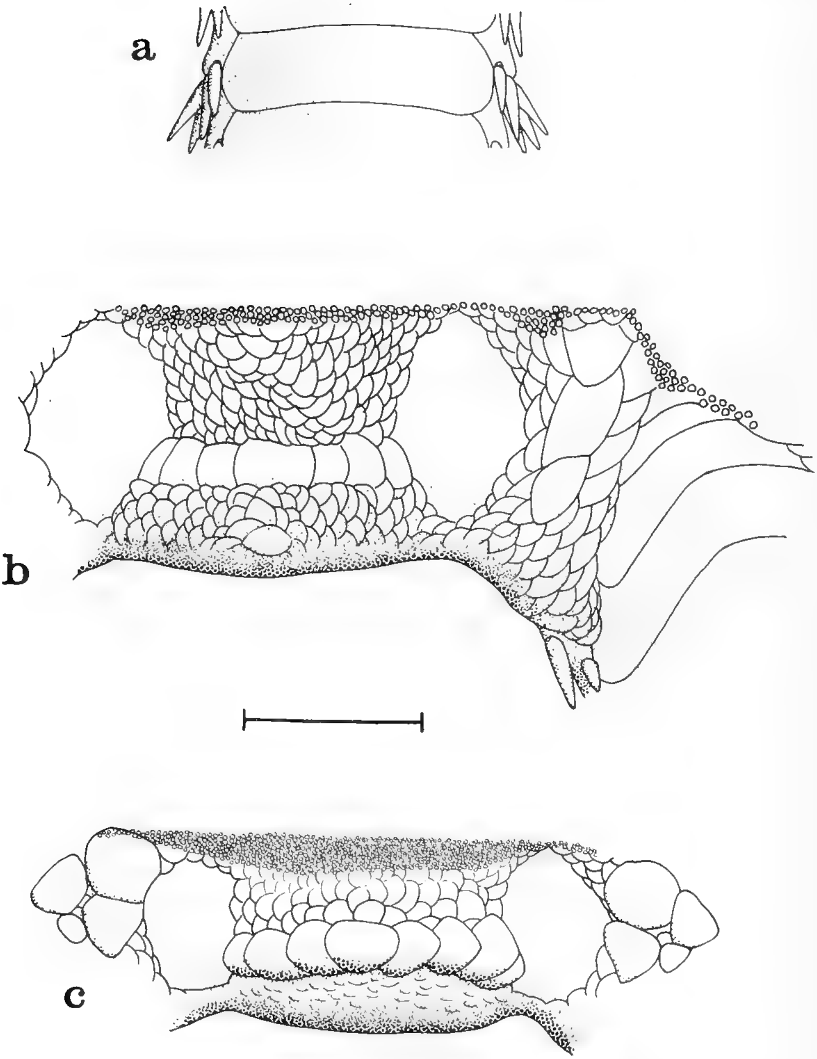

FIG. 9. *Ophiopsammus yoldii* (Lütken). B.M. No. 1949.1.14.19, " Indian Ocean ", d.d. 15 mm. a. Fifth free arm segment in dorsal view; b. a denuded interradius and one adjacent arm base in side view. c. *Ophiopeza fallax fallax* Peters, 1965.6.1.501, Zanzibar, d.d. 11 mm., a denuded interradius in side view. The scale measures 2 mm.

The disc is covered uniformly with fine granules, which also conceal the radial shields; there are about 20 in a linear mm. near the centre of the disc. Most of the granules are rounded but some are slightly polygonal. The marginal plates are slightly convex, their contours visible through the granulation and the enlarged mid-interradial plate has been partially rubbed clean of granules in three interradii. On the ventral side the granulation continues up to and around the oral shields, separating them more or less completely from the adoral shields.

The oral shields are bare and approximately triangular in shape though the latero-distal angles are slightly truncated. Their length and breadth are approximately equal. Proximal to the oral shields the jaws are covered with granules which are coarser than those on the disc. There are about ten oral papillae in each series, counting the superficial second oral tentacle scale at the distal end of the series. The second to fifth papillae are conical but the distal ones more nearly rectangular.

The arms are square in cross-section, especially distally where the dorsal surface becomes slightly concave. The disc granulation continues on to the arm bases dorsally, completely encircling the first four to six dorsal arm plates but it becomes reduced at the proximal median part of the segment so that there is only a single row of granules between the lateral plate each side and the dorsal plate from about the twelfth free segment. The naked parts of the proximal dorsal arm plates are broad heart-shaped, the fourth plate with length : breadth = 0·8 : 1·25 mm. with a slightly concave median sector to the distal edge. The following plates become more nearly triangular, widest near the distal end and the median part becomes first straight and then shortens until it is lost and the whole distal edge is slightly convex. When the granulation is removed from the proximal plates the cleared areas are seen to be slightly sunken. The ventral arm plates have the common octagonal form found in many species of this family, with the three distal edges tending to form a continuous curve and the lateral edges notched for the tentacle pore and partially overlain by the inner of the two tentacle scales. The ninth ventral arm plate, corresponding to the fourth free segment, has length : breadth = 0·8 : 1·05 mm. The arm spines number up to nine basally; all are short, less than half the segment length and taper to blunt tips; the lowest is no longer than the rest.

The disc in alcohol is now light brown in colour, dappled with small lighter areas and finely dotted with individual dark brown granules. The oral shields have a median brown spot. The arms are each marked with about five dark brown bands, extending for from one to four segments and separated by longer lighter areas.

Paratypes. None of these have the arms complete. The largest has d.d. 10·5 mm. like the type but it differs in having less granulation on the arms and the median distal edges of the dorsal arm plates are mostly straight rather than concave; also opposite the base of four of the arms there is a small bare patch on the disc with a brown spot in the middle of it. Both these features add to the resemblance to *Ophiopeza fallax arabica*. The two smaller specimens have d.d. 8 mm. and show no sign of bare areas on the disc. Conversely their arm granulation is more extensive than in either of the larger specimens, the granules running right across the proximal end of each segment as far out as about the twentieth free segment. They also have some dorsal arm plates with a median concavity in the distal edge. Their

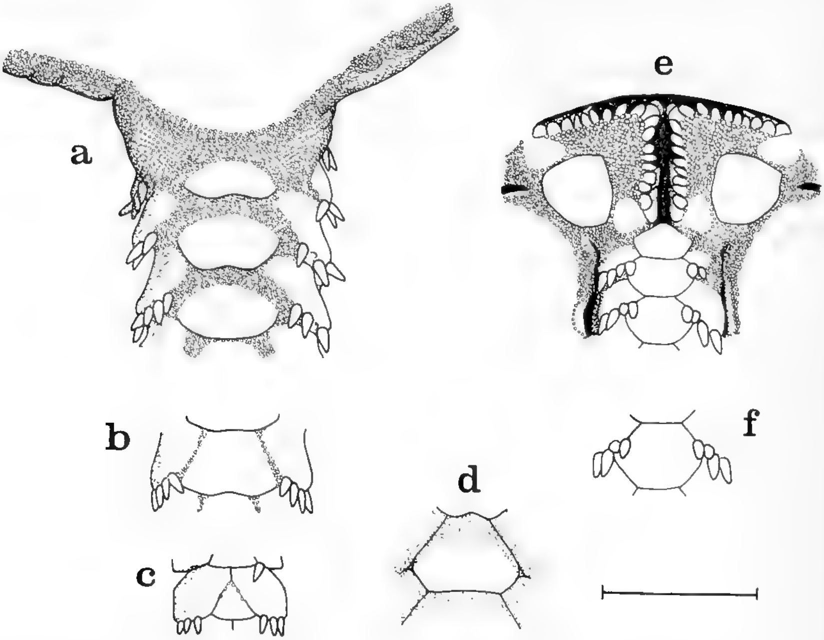

FIG. 10. *Ophiostegastus compsus* sp. nov. Holotype, B.M. No. 1967.11.9.1, Bahrein, Persian Gulf. a. Part of disc and arm base in dorsal view; b. the tenth free segment and c. the thirtieth free segment, also in dorsal view; d. the second dorsal arm plate denuded showing the recesses to house the granules; e. two jaws and the adjacent arm base; f. the eighth ventral arm plate. The scale measures 2 mm.

arm spines number up to eight. None of the three have any bare supplementary oral shields present and cleaning the proximal parts of two interradii of one of the smaller specimens did not reveal any such plates under the granulation, though in one case the two scales bordering the oral shields were somewhat enlarged.

AFFINITIES. At first I thought that these specimens were referable to *Ophiopeza* since they have squared arms, slightly convex marginal disc plates and disc granulation of much the same extent as *Ophiopeza fallax*. However, since other Ophiodermatids with the granulation extending on to the arms have been generically distinguished, it seems best to ally the present species with *Ophiostegastus* Murakami, 1944, type-species *O. instratus* Murakami from Japan, from which it differs in having the supplementary oral shields undeveloped and the dorsal arm plates with a tendency to become concave at the distal edge. *Ophiostegastus* has similar granulation around the proximal dorsal arm plates and leaving bare the oral and adoral shields, unlike *Ophiodyscrita* H. L. Clark, 1938, although the latter too has granulation on the arms. I must admit to considerable doubt about the distinctness of these two nominal genera, especially in view of the progressive reduction in the extent of the granulation with size shown by the present material, even though their size range is only 2·5 mm. The types of *Ophiodyscrita acosmeta* and *pacifica* have d.d. only 5 and 4 mm. respectively, which could well explain the extension of the granulation over the oral and adoral shields. A good series of specimens should give a better appreciation of the interrelationships of these species.

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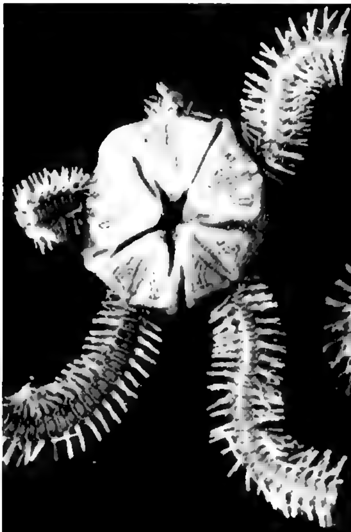
PLATE 1

Fig. 1. *Macrophiothrix galateae* (Lütken), holotype, Nicobar Islands.
Fig. 2. *Macrophiothrix koehleri* sp. nov., holotype, Solomon Islands.
Fig. 3. *Macrophiothrix variabilis* (Duncan), 88.1.2.1, Tuticorin.
Fig. 4. *Macrophiothrix lorioli* sp. nov., holotype, Solomon Islands.
Fig. 5. *Ophiopeza fallax arabica* subsp. nov., holotype, Persian Gulf, part of disc in ventral view, × 4.
Fig. 6. The same in dorsal view. [Both by courtesy of Miss M. Downey, Smithsonian Institution.]

(all × 2, except for fig. 5)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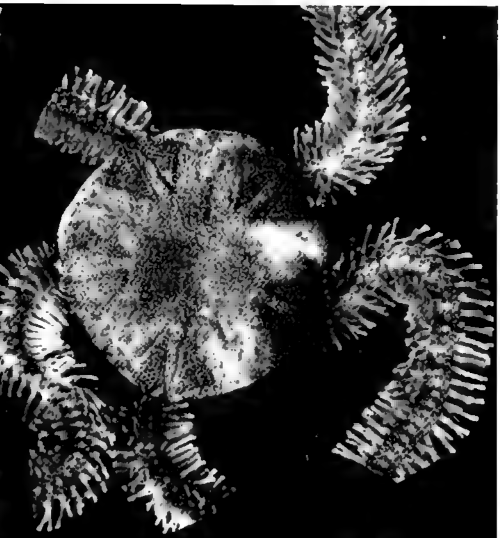
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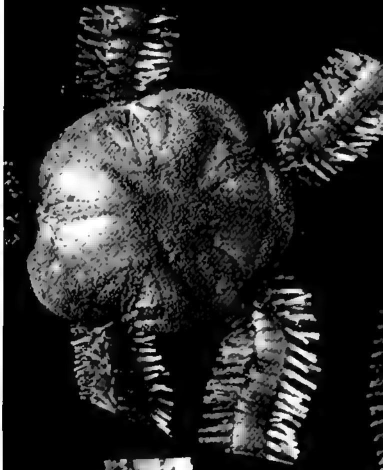
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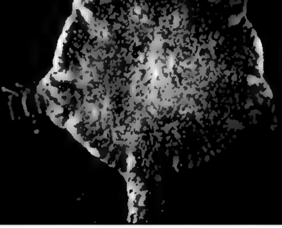
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AN ACCOUNT OF A PATHOLOGIC STRUCTURE IN THE FAVIIDAE (ANTHOZOA): A REVISION OF *FAVIA VALENCIENNESII* (EDWARDS & HAIME) AND ITS ALLIES

BRIAN R. ROSEN

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CONTENTS

SYNOPSIS

The current concept of the coral *Favia valenciennesii* (Edwards & Haime) is reviewed and shown to include two groups of forms, the first similar to the type specimen, the second to the type of *Favia bertholleti* Edwards & Haime; these species have previously been regarded as synonymous. An important feature of the *F. valenciennesii* group is the unusual mode of corallite junction, taken in the past to be diagnostic of this species. This structure is seen in a number of dried (museum) specimens and is described here in detail for the first time. Evidence is presented for its occurrence in four different species and its diagnostic significance is accordingly doubted. Reasons are given for believing this structure to be pathologic. Specimens of the *F. bertholleti* group are regarded here as a growth-form of *Favia favus* (Forskål) and three principal intergradational facies are defined for this species.

I. INTRODUCTION

The necessity for a revised systematic status for *Favia valenciennesii* was suggested in the first instance by Matthai's occasional difficulty in distinguishing each of the thin-walled facies he had described for *F. bertholleti* (= *valenciennesii* of later authors) and *F. favus*. One of his captions (1914, pl. 22, fig. 7) for instance, which shows one of Forskål's types of *Madrepora favus,* refers it to " *?Favia bertholleti* (Val.) . . . Perhaps only a thin-walled *F. favus* ". A number of museum specimens however, some previously undescribed, provide evidence that the relationship of the two species is more complex, and additional species (with at least one other genus) are involved. Thus the problem of *F. valenciennesii* has wider implications that was realized at first. The ecological and geographical abundance of both the genus *Favia* and the species *F. favus* moreover, provided an added interest to the present study. The physiological significance of the very deep intercorallite grooves and associated features, customarily taken to be typical of one facies of *F. valenciennesii,* was an additional problem.

There has been virtually no consideration of any of these points in previous published work. Edwards & Haime (1848, 1849), in describing their type of *Phymastrea valenciennesii* provided the first description of the deeply grooved structure, but evidently thought it was simply another mode of junction of corallites that happened to be less common than most. Duncan (1883) added little detail of importance to their description and took the same view of the structure's significance. Quelch (1886) thought that the passage openings between the corallites of his new species *Phymastraea aspera* might be those of worm tubes; his figure of the structure is oversimplified. Although Matthai (1914 : 79) gave no description of the structure at all, he made it clear that, contrary to Edwards & Haime, he believed the particular mode of junction of the corallites had no generic significance; but it would seem from his remark that he perhaps did not appreciate the very unusual nature of the grooves. Vaughan (1918) agreed with Matthai. Crossland's (1952) only specimen of *Leptastrea bottae* exhibits what he called " beams connecting the thecal walls " and he suggested comparison of his figure showing a longitudinal section (Crossland, 1952 : pl. 2, fig. 2) with the similar sectional view given by Edwards & Haime of their *P. valenciennesii* (1848, pl. 9, fig. 3a). Both show the presence of " tubercles " uniting adjacent corallites. Crossland felt that *F. valenciennesii* was "difficult to define ", having also commented in his 1941 paper that Matthai seemed hardly certain of the distinction between *F. favus* and *F. bertholleti,* in certain instances. Apart from these relatively brief references, made largely in passing, very little discussion has arisen on this subject, though these few remarks make it clear that there were certain difficulties which deserved attention. There has in fact even been a lack of good descriptions and figures of the various features first noted by Edwards & Haime.

The subject has been considered in three parts. The first concerns problems of synonymy, as a result of which various authors' original concepts have seemingly become blurred. The second involves the precise nature of the intercorallite structure currently taken to be diagnostic of *Favia valenciennesii,* and hence its systematic significance. (Detailed description of this structure has been given at this point in the following account, rather than in the systematics section, for convenience of comparison.) The third part concerns the physiological significance of this structure, although further study is required before anything more than generalized speculation can be made. Only hard parts have been studied, there being no material available at the time that possessed soft parts. It is here, perhaps, that future work might best concentrate.

II. CURRENT CONCEPT OF *F. VALENCIENNESII* (EDWARDS & HAIME)

Synonymy

A full synonymy based on the present currently accepted concept of the species *F. valenciennesii* is as follows:

?*Madrepora favus* Forskål, 1775 : 132 (part).
**Phymastrea valenciennesii* Edwards & Haime, 1848 : plate 9, figs. 3, 3a; Edwards & Haime, 1849 : 124; Edwards & Haime, 1857 : 500; Duncan, 1883 : 408; Yabe, Sugiyama & Eguchi, 1936: 31, pl. 23, figs. 3–5, pl. 24, fig. 5.
Favia valenciennesii: Matthai, 1924 : 14, pl. 4, fig. 1, pl. 11, fig. 2 (also pl. 1, fig. 2[1] pl. 2, fig. 9); Faustino, 1927 : 133, pl. 27, figs. 1–3; Crossland, 1952 : 126; Wells, 1954 : 485; Nemenzo, 1959 : 89.
Favia (*Phymastraea*) *valenciennesii*: Umbgrove, 1939 : 28, pl. 28, fig. 2.
* *Prionastrea rousseaui* Edwards & Haime, 1849 : 131 (part).
* *Prionastrea halicora* Edwards & Haime, 1851 : 102 (part) (non *Astraea halicora* Ehrenberg, 1834); Edwards & Haime, 1857 : 517 (part).
* *Parastrea bertholleti* " Valenciennes, MS " Edwards & Haime, 1857 : 431.
* *Favia bertholleti* Edwards & Haime, 1857 : 431; Matthai, 1914 : 94, pl. 7, fig. 2, pl. 22, fig. 7, pl. 23, figs. 4, 6, pl. 24, fig. 1.
* *Prionastraea australensis* Edwards & Haime, 1857 : 520.
Phymastraea irregularis Duncan, 1883 : 409, figs. 1, 2.
* *Phymastraea aspera* Quelch, 1886 : 105, pl. 4, figs. 1–1b.

Taxa asterisked were brought together by Matthai (1914) under the name *Favia bertholleti* (Valenciennes). Duncan's paper (1883) included a shortened redescription of *P. valenciennesii* based on Edwards & Haime's account, not, it would seem, from relevant specimens of his own. His new species, *Phymastraea irregularis*, was believed by Matthai (1924) to be *Favia valenciennesi*. *Madrepora favus* Forskål has been added here because Matthai was of the opinion that one of Forskål's types was possibly *F. bertholleti*, although he did not place the species in his synonymy, (see his caption to pl. 22, fig. 7). Vaughan (1918 : 100) regrouped Matthai's species of *Favia* and in the course of his discussion pointed out that Valenciennes' name *bertholleti* was invalid, as it was only known from a manuscript. He suggested that the next available name be used instead, this being *Phymastrea valenciennesii* Edwards & Haime. *Phymastrea* was rejected as a genus, because Vaughan (and Matthai) agreed that the mode of junction of the corallites, regarded by Edwards & Haime as a distinguishing factor in separating "astraeid" genera, was of doubtful significance.

Prionastrea rousseaui, according to Matthai, consisted of eight specimens, five of which he referred to *F. favus*, including the types, and the remainder of which he identified as *F. bertholleti*. Edwards & Haime (1851) referred their *P. rousseaui* (1849) to an earlier species of Ehrenberg's, *Prionastrea halicora*, hence Matthai cited their use of this species, in part, also. The species name *bertholleti*, was made valid by Edwards and Haime (1857), when they redescribed it presumably from Valen-

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[1] Plate printed upside down.

ciennes' original specimen. For reasons that will be clear below, it is convenient to continue to use this name as discussion is simplified. Two further species were included by Matthai in his synonymy, each consisting of one specimen only: *P. australensis* Edwards & Haime (with a query) and *Phymastraea aspera* Quelch.

Seven papers subsequent to Matthai (1914) have included descriptions or formal systematic reference to *Favia* (or *Phymastrea*) *valenciennesii*. This species name has always been used since Vaughan's revision in 1918, although Yabe, Sugiyama & Eguchi evidently did not agree with him on the use of the generic name. Apart from this change no revision has been suggested or implied by any other authors. It is clear from their synonymies that later authors' definitions of the species have always included Matthai's concept of *F. bertholleti*.

Skeletal morphology

Even though the valid name now in use is *F. valenciennesii*, consideration of Matthai's account of *F. bertholleti* shows that his concept of that species is based primarily on Edwards & Haime's specimen of the latter. It will be shown that the type of *F. valenciennesii* falls outside this delineation. From Edwards & Haime's type description, (a translation of which is given below under *F. favus* in the systematics section) and from Matthai's own account and specimens, the diagnostic characters of his *F. bertholleti* are the irregular or polygonal open calices, closely set corallites with adjacent walls united at the summits, or nearly so, weak columella and thin septa. Matthai divided the species into two facies or morphological forms (referred to by him as " varieties "):

> " (1) in which the adjacent corallite-walls are fused, the intercalicinal walls thus formed being not more than 1 mm. in thickness, often thinner; over these the septa are continuous in arches, the septa being thin; (2) thicker-looking in which the corallite-walls are distinct, separated on the surface by intercorallite grooves at the margins of which the exsert ends of the septa stop; the septa are thicker and rougher."

It is concluded from the phrase, " at the surface ", that deeply grooved forms, like *Phymastrea valenciennesii* were not considered typical of either of Matthai's two varieties, which provides at least one reason for doubting the validity of including them as *F. bertholleti*. However, if, as here, it is thought that some of these deep-grooved forms might only be variants of for example, *F. bertholleti*, there is a second more important reason for separating at least several of them from *F. bertholleti*—in particular, the type of *Phymastrea valenciennesii*. Comparison of the two relevant type descriptions (below) shows that in contrast to *F. bertholleti*, *P. valenciennesii* has smaller corallites and good paliform lobes. Edwards & Haime also state in their description of the genus that *Phymastrea* has extracalicular budding.

Matthai was aware that *P. valenciennesii* possibly did not belong with *F. bertholleti*: " The single small type of *Phymastraea valenciennesii* (an edge of a colony. . .) perhaps belongs with the present species, it has deep intercorallite grooves and coarse septal sides and may therefore be only an extreme case of var. 2, described above, but the principal septa have long teeth near their union with the columella." Had Matthai complemented his doubt in the text with a query in his synonymy, then Vaughan in making his revision, might conceivably have chosen the next available name after *P. valenciennesii* in Matthai's synonymy, this being appropriately *F. bertholleti* Edwards & Haime. The change would then only have required different authorship.

Further evidence that the deeply grooved forms are to be thought of as atypical within Matthai's *F. bertholleti* rather than typical, is given by the fact that apart from *P. valenciennesii* itself, only two other specimens in both Matthai's own material and that referred to in his synonymy exhibit these deep groves, as far as is known. The first of these is Quelch's type of *Phymastraea aspera* (" . . . which in all probability belongs here "), the second is a small fragment from Ceylon, which he figured (pl. 23, fig. 6, lower left). By reason of the change of name made by Vaughan, *valenciennesii*-forms have however become typical of the species, and *bertholleti*-forms atypical, so effecting a reversal of the previous situation.

Matthai's original two " varieties " were thought by him to intergrade, and his specimens and figures support this view. But subsequent authors have mistaken forms bearing deep grooves for his " var. 2 ", and it is here that intergradation has yet to be demonstrated. It is therefore convenient in the first instance to divide the current concept of *F. valenciennesii* into two groups of species: the first includes specimens which correspond to *F. bertholleti*, and the second, specimens which exhibit a similar structure to that of the type of *P. valenciennesii*. For the sake of brevity, the latter will be referred to here as " groove-and-tubercle forms " this term being based on Edwards & Haime's original description and has more implication than " deeply grooved ". A list of each group is given at the end of this section. Details of specimens examined are given in Table I.

As will be discussed in the systematics section, all gradation occurs between *F. bertholleti*-forms and specimens of *F. favus*. Since the latter name has priority, the former may be regarded as a facies of *F. favus*. This provides a solution to Matthai's difficulty in distinguishing the two species. Groove-and-tubercle forms however exhibit so wide a range of calicinal characters that affinity with any single species alone is improbable. Relevant museum material suggests that at least four species and two genera are involved, which is the principal reason for believing that the characteristic structure is not only of doubtful generic value, but of doubtful specific value also. This is further explained in the following section.

Forms broadly similar to *F. bertholleti* Edwards & Haime:

Madrepora favus Forskål, 1775 (part).
Favia bertholleti Edwards & Haime, 1857; Matthai, 1914 (non pl. 23, fig. 6, lower left).
Prionastrea rousseaui Edwards & Haime, 1849 (part); Edwards & Haime, 1857 (part).
Prionastraea australensis Edwards & Haime, 1857.
Favia valenciennesii: Faustino, 1927; Crossland, 1952; Wells, 1954.

TABLE I

Details of specimens examined.

PRESENT IDENTIFICATION	SPECIMEN NO. (B.M. Register and Great Barrier Reef Expedition)	LOCALITY	PREVIOUS IDENTIFICATIONS	REFERENCES AND FIGURES		REMARKS		
Favia favus (Forskål)	1927.5.4.89	Ceylon	*Favia bertholleti* (Valenciennes)	Matthai, 1914	—	Facies 3 Corallites small (c. 7 mm. diam.) and very close; rather smooth—spinules and prominent teeth absent.		Groove-and-tubercle structure absent
Favia favus (Forskål)	1927.5.4.165	Long Island, Seychelles	*Favia bertholleti* (Valenciennes)	Matthai, 1914	—	Facies 3 See description in text. Pl. 5, fig. 2; Pl. 6, figs. 2, 4.		
Favia favus (Forskål)	1927.5.12.6	Aldabra	*Favia bertholleti* (Valenciennes)	Matthai, 1914	pl. 24, fig. 1	Facies 2–3 On old label " *F. favus* " has been struck out and " *F. bertholleti* " substituted		
Favia favus (Forskål)	1927.5.12.49	Aldabra	*Favia bertholleti* (Valenciennes)	Matthai, 1914	—	Facies 3		
Favia favus (Forskål)	1927.5.12.67	Long Island, Seychelles	*Favia bertholleti* (Valenciennes)	Matthai, 1914	—	Facies 2–3		
Favia favus (Forskål)	1934.5.14.128 (GBRE 163)	Great Barrier Reef	*Favia valenciennesi* (Edwards & Haime)	Crossland, 1952	—	Facies 2–3		
Favia favus (Forskål)	1927.5.12.167	Delft, Ceylon	*Favia bertholleti* (Valenciennes)	Matthai, 1914	pl. 23, fig. 6 lower R.	Facies 3	Specimens more or less form morphological series in this order	
Favia favus (Forskål)	1927.5.12.165	Delft, Ceylon	*Favia bertholleti* (Valenciennes)	Matthai, 1914	pl. 23, fig. 6 upper R.	Facies 3		
Favia favus (Forskål)	1927.5.12.164	Point Pedru, Ceylon	*Favia bertholleti* (Valenciennes)	Matthai, 1914	pl. 23, fig. 6 upper L.	Facies 2–3		
Favia favus (Forskål)	1927.5.12.166	Delft, Ceylon	*Favia bertholleti* (Valenciennes)	Matthai, 1914	pl. 23, fig. 6 lower L.	Pl. 5, fig. 3		

Favia ?favus (Forskål)	1898.12.1.12	Singapore	*Favia bertholleti* (Valenciennes)	(previously undescribed) determined by?	Groove-and-tubercle structure present in most of colony, but transition to normal exothecal development. Corallites rather small for *F. favus* (see text) Pl. 8.	Groove-and-tubercle structure present
Favia speciosa (Dana)	1892.12.1.362	Great Barrier Reef	*Favia bertholleti* (Valenciennes)	(previously undescribed) " teste G.M." (label)	Compare corallites with those of B.M. 1895.10.9.133 (Pl. 7, fig. 1).	
Favia speciosa (Dana)	1892.12.1.594	Great Barrier Reef	*Favia bertholleti* (Valenciennes)	(previously undescribed) " fide G.M." (label)	Compare corallites with those of B.M. 1895.10.9.133 (Pl. 7, fig. 1) Pl. 7, fig. 2.	
Plesiastrea? valenciennesii (Edwards & Haime)	1886.12.9.151	Banda	*Phymastraea aspera*	Quelch, 1886 pl. 4, figs. 1-1b	See text Pl. 4, figs. 1–3.	
			Favia bertholleti (Valenciennes)	Matthai, 1914 —		
Leptastrea bottae (Edwards & Haime)	1934.5.14.444 (GBRE 407)	Great Barrier Reef	*Leptastrea bottae* (Edwards & Haime)	Crossland, 1952 pl. 1, fig. 4 pl. 2, figs. 2, 3	See text	
Favia favus (Forskål)	1934.5.14.166 (GBRE 166)	Great Barrier Reef	*Favites aspera* (Verrill)	Crossland, 1952 pl. 5, fig. 1	Facies 3 Originally identified by Matthai as *?Favia bertholleti* and also *Favites parvimurata*, according to labels. Walls absent in places.	
Favia favus (Forskål)	1927.5.4.158	Long Island, Seychelles	*Favia favus* (Forskål) " var. 1"	Matthai, 1914 pl. 20, fig. 2	Facies 2 (*cavernosa*-facies) Pl. 5, fig. 1; pl. 6, figs. 1, 3.	
Favia speciosa (Dana)	1895.10.9.133	Roebuck Bay, N.W. Australia	*Favia clouei* (Valenciennes)	(previously undescribed) determined by?	Compare Vaughan's Pl. 36, fig. 1 (1918) of Dana's type of *Astraea speciosa*. Pl. 7, fig. 1.	

Forms broadly similar to *P. valenciennesii* Edwards & Haime (i.e. Groove-and-tubercle forms):

Phymastrea valenciennesii Edwards & Haime, 1848, 1849, 1857; Yabe, Sugiyama & Eguchi, 1936.
Favia valenciennesi: Matthai, 1924; Nemenzo, 1959.
Favia (Phymastrea) valenciennesii: Umbgrove, 1939.
Phymastraea profundior Edwards & Haime, 1849, 1857.
Phymastraea irregularis Duncan, 1883.
Phymastraea aspera Quelch, 1886.
Favia bertholleti: Matthai, 1914 (part) pl. 23, fig. 6 lower left only.

also:

Leptastrea bottae: Nemenzo, 1959; Crossland, 1952.

III. NATURE OF THE GROOVE-AND-TUBERCLE STRUCTURE AND ITS SYSTEMATIC SIGNIFICANCE

Description

A translation of Edwards & Haime's description of *Phymastrea valenciennesii* in which this structure is described, is given below under *Plesiastrea? valenciennesii.* Duncan (1883) also described it for his species *Phymastraea irregularis*, later referred by Matthai (1924) to *Favia valenciennesi.* Duncan's description of the species, together with his further remarks are too lengthy to be quoted here in full, but those sections relating to groove-and-tubercle structure are given below.

There are six relevant specimens in the British Museum (Natural History), all of them Faviids. Three have not previously been described in any published account: B.M. (N.H.) Register Nos. 1892.12.1.362, 1892.12.1.594 and 1898.12.1.12. A fourth specimen (1886.12.9.151) has been described in some detail and figured by Quelch as his type of *Phymastraea aspera*; its unusual structure was only briefly referred to, however. A fifth, (1934.4.14.444), was figured and given a short description by Crossland as *Leptastrea bottae*; and the last specimen Matthai figured as an example of *Favia bertholleti* (1927.5.12.166).

Phymastraea irregularis Duncan[1] (= ? *Favia favus*). " The larger costae have nodules on their free edge placed in linear series, and often extending over an intercostal space and smaller costae to the next large one. These nodules join those of approximated costae of neighbouring corallites, and form short processes. Junction-processes occasionally do not correspond to costae. An epitheca exists over each corallite, especially low down; it covers the costae and inter-costal spaces and laps round the junction-processes; it is membranous-looking and has a few transverse and other ridges. A small amount of exotheca exists between the costae. . . .

" There is considerable distance between the corallites at the surface, amounting to 1 millim. and more, and this is crossed by the junction-processes. These are very variable in their size and distribution; some do not reach across, and others are constricted in the middle. Very broad ones are exceptional."

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[1] The section of Duncan's paper (1883) entitled " Remarks on the structure of *Phymastraea profundior* " should really refer to his own species *P. irregularis*. The list of contents of the paper, as well as its context indicate that the use of this name was a lapsus.

Favia speciosa B.M. (N.H.) Register No. 1892.12.1.594. At the margins of the corallum, corallites are up to 3 mm. apart, or more, and the intercorallite groove is, for the most part, a superficial feature as seen in most species of *Favia*. Occasionally however, small tubular passage openings are present, rising more or less vertically from the surface of the groove for about 0·5 mm., their diameter being somewhat less. The exothecal dissepiments in this part of the corallum are frequently more blistery and thinner than elsewhere, and bear fine lines, which are broadly concentric to the margins of the individual plates making up each dissepiment. In several instances, tubes may be seen rising up directly from these dissepiments; the fine lines on the plates do not continue up on to the outside of these tubes (Pl. 1, fig. 1).

Apart from the tubes, the structure is close to that typical of *Favia*, but the larger part of the corallum differs considerably, with gradations between the two conditions present within the same colony. In detail, the difference is essentially one of degree. For most of the corallum the intercorallite groove is up to 4 or 5 mm. deep, and, except at the uppermost margins of the corallites, about 1–1·5 mm. wide. The groove completely separates adjacent corallites: the costae of neighbouring corallites do not meet in the groove, although their spines may be united. At a depth greater than 5 mm., the groove continues downward at intervals, between which the corallites are united partially by exothecal material. Seen from above, the exothecal material, which is not solid, alternates with tube-like openings, similar to those already mentioned, but more frequent (1A, Text-fig. 1, and as in Pl. 4 which is a different specimen). The rims of the tube openings project above the level of the highest exothecal material by about 0·5 mm. (1C, Text-fig. 1). The openings themselves are often circular and generally less than 0·5 mm. in diameter. More often they are elongated along the length of the groove, though in many such instances, the openings may be seen passing downwards into more than one tube (IBc, Text-fig. 1). In all examples, the openings may either be turned inwards or outwards, (IB, 1C, Text-fig. 1) or even both, being the surface expression of a system of passages which surrounds each corallite. The walls of the tubes which are thin, bear very fine circumferential lines on the inside; but not, apparently, on the outside, though it is difficult to verify their external absence. The spacing of the openings along the grooves is irregular, as is the variation in their elongation.

Since this specimen is a complete colony, there are no longitudinal sections to be seen.

Structures in the grooves between new and parent corallites, differ from those already described and are taken to represent an early development of the latter. Until a complete partition is formed within the parent corallite, no visible difference can be seen between this and the same feature in corals without groove-and-tubercle structure. In instances where the new partition is complete, and the separated corallites have begun to develop exsert corallite margins on either side of the partition, the features shown in columns 3–6 of Text-fig. 1 may be observed. A sequence is inferred as follows:

(1) small plates form up to about 0·25 mm. in diameter, sometimes larger; these bear very fine, broadly concentric lines; the plates are generally concave uppermost. (Pl. 1, fig. 2, extreme right). In some instances, where a tube opening is situated

near the end of a new intercorallite groove, the actual opening develops a rim which becomes extended along the groove; this is also concave along its length, and bears concentric lines. (Pl. 2, fig. 1). These features are shown diagrammatically in column 3, Text-fig. 1.

(2) Continued growth of the plates and extended rims results in their becoming fused, (column 4, Text-fig. 1, and Pl. 1, fig. 2) to form trough-like plates.

(3) The margins curl upward and close over in part as in columns 5, 6 and 7. Points where the tubes are closed often correspond to positions of costae, particularly where costal spines are strongly developed (Pl. 2, fig. 1). Where the troughs remain only partly closed over, continued upward growth takes place at the margins of these openings so becoming vertical tubes (7D, 8D in Text-fig. 1). The tubes give the appearance of " finding their way " round the costal spines, and form a continuous system which is essentially rectilinear. Further details are better seen in the longitudinal sections found in other specimens, below.

Favia speciosa B.M. (N.H.) 1892.12.1.362. This specimen is not greatly different from that above, and again does not provide a sectional view, being a complete colony.

FIG. 1. Diagram showing sequence of development of groove-and-tubercle structure around newly formed corallites of *Favia*. The sequence is given by each successive column, as below.

Rows: A—general view of corallites; B—details (plan view) of structures in intercorallite grooves; C—longitudinal sections through corallites at right angles to newly formed corallite wall; D—longitudinal sections along newly formed corallite wall.

COLUMNS 1—A—corallite and neighbours before division, showing tube openings. Compare Pl. 4. B—details of tube openings. Unshaded areas are the outsides of tubes; areas with growth lines are the insides; black areas represent the insides of the tubes at a depth too great for details to be seen. C—section through corallite and exotheca; the tube system appears discontinuous because of its pattern (section at right angles to those seen in Pl. 3). Note the united costal spines and two different modes of tube opening corresponding to 1Ba and 1Bb.

2—Earliest formed partition is no different from that seen in most specimens of *Favia*.

3—First structures to appear are the plates, and extended rims of the existing tube openings. (Pl. 1, fig. 2 extreme right; Pl. 2, fig. 1)

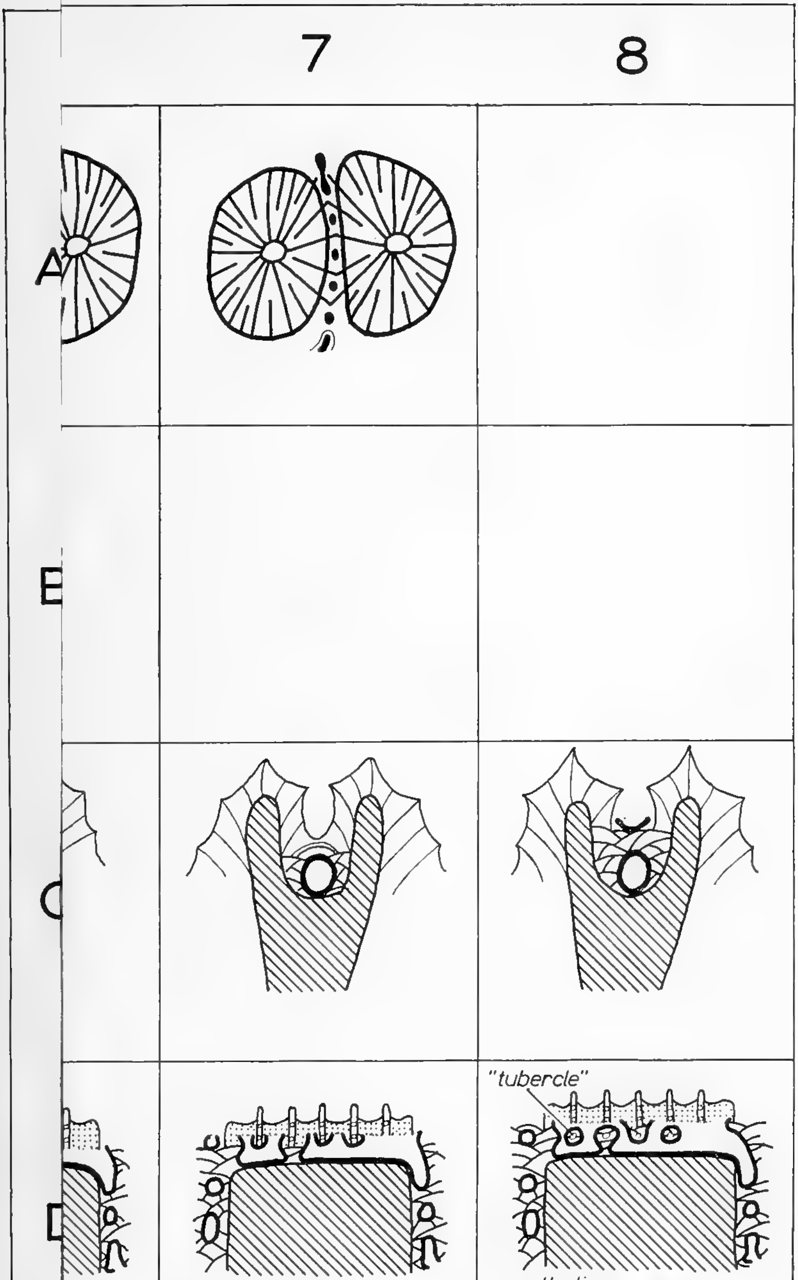
4—Fusion of plates follows, forming troughs (Pl. 1, fig. 2, centre and left).

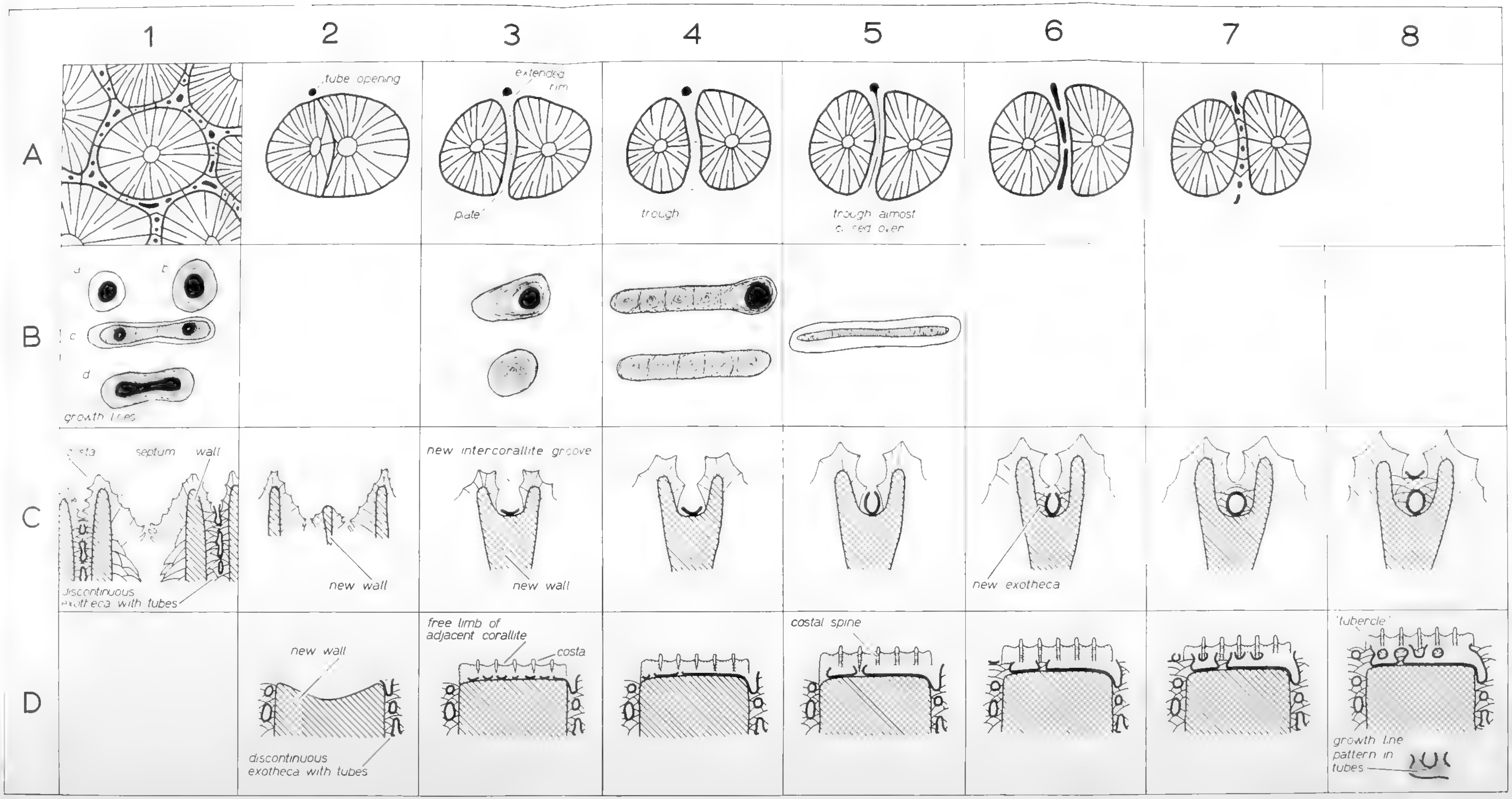
5—Longer margins of troughs curl upwards (out of the plane of the diagram in 5B, in which the unshaded area represents the underside, or outside of the trough).

6—Growth of exotheca obscures the outside of the trough and the structures now appear more like slots between the corallites.

7—Irregular upward growth results in the development of vertical tubes. 7C shows the original trough completely closed over beneath united costal spines. The position of this section corresponds to the first costa from left in 7D. 7D shows tubes " finding their way " round costal projections. View from above (7A) is now similar to that of parent corallite in 1A.

8—Continued upward growth extends the tube system. 8C represents a section corresponding in position to the first costa at left in 8D. (Pl. 3, fig. 1).


7
8
A
B
C
D
"tubercle"
growth line pattern in tubes


1
2
3
4
5
6
7
8
A
B
C
D
tube opening
extended rim
plate
trough
trough almost closed over
a
b
c
d
growth lines
costa
septum
wall
discontinuous exotheca with tubes
new wall
new intercorallite groove
new wall
new exotheca
new wall
discontinuous exotheca with tubes
free limb of adjacent corallite
costa
costal spine
'tubercle'
growth line pattern in tubes

The stages seen in columns 4 and 5 of Text-fig. 1 are better seen than in the previous specimen. In one instance there is a trough, almost closed in, which surrounds the corallite concerned for about a third of its circumference; the floor of the trough can be clearly seen to consist of the fused plates noted in the previous specimen; at either end the floor passes downward into tubes. This example thus combines most of the features already described.

Favia favus B.M. (N.H.) 1927.5.12.166. The grooves in this specimen are shallower than in the previous specimen (about 1 mm.), but not in this sense superficial. Apart from this the details of intercorallite structure as seen from above, do not differ in any fundamental way from those examples previously described. The specimen does however provide sectional views, which enable further details to be elucidated.

The surface along which the specimen was broken both passes through corallites and between them, and the view so given may be compared with the figure given by Edwards & Haime of their type of *Phymastrea valenciennesii* (pl. 9, fig. 3a, 1848). Where corallites have been broken through, the view is more or less that shown diagrammatically in 1C, Text-fig. 1: between corallite walls, sections through tubes alternate almost regularly with those through bridges of exotheca; the exothecal material consists of stereome with some development of small dissepimental plates. The bridges are thus not solid. Where the plane of the break passes between corallites, the view (Pl. 3, fig. 1) is really an upward extension of the section shown in 8D, Text-fig. 1; the bridges of exotheca are mostly cut through at right angles to the previous section and are seen to be circular to oval in shape. The outside of the corallite walls therefore give the impression of being covered by "tubercles" as described by Edwards & Haime. In this case however, they are less symmetrically arranged (see type description below, under *Plesiastrea? valenciennesii*).

Whatever the disposition of any part of the tube system, the trend of the fine lines on its inner surface is always broadly parallel to the surface of the corallum; in the second section above, the tubes are, of course, split along their length and so resemble discontinuous, rather curled epitheca; the lines are very fine and could not be counted—they are probably of the order 30–50 per mm. The tubes reach 0·5 mm. in diameter though they are often narrower; tubercles are wider, there being about 10 per cm. along the length of the corallite; they may be elongated circumferentially with respect to the corallites up to 5 mm. or so. The tube system remains entirely outside individual corallites; nowhere was there seen any hole or tube passing through a corallite wall. As already observed, tubercles seem to consist of stereome and some dissepimental plates; the stereome is often concentrated around the margins of the tubercle. Costal material is also taken to be contributory, particularly costal spines. Many tubercles seem to have formed around united costal spines of adjacent corallites (7C and D, 8C and D in Text-fig. 1), which would follow from the feature already noted, where the tubes give the appearance of " finding their way " between united costal spines. The overall pattern of the tubes and tubercles is reasonably regular.

In addition to the tubes which emerge between the corallites, there are several instances where larger tubes are to be found within them. Some of these are almost certainly serpulid tubes, (Pl. 5, fig. 3, extreme lower left) but in two adjacent corallites in the centre of the specimen, they more closely resemble the intercorallite tubes (Pl. 2, fig. 2). Both tubes are offset from the centre of the calices and become progressively wider upwards; they bear very faint circumferential lines on their inner surfaces and are about 3 mm. in diameter at the opening.

Favia ?favus B.M. (N.H.) 1898.12.1.12. The intercorallite grooves are about 3 mm. deep and the openings of tubes and slots somewhat narrower than in any of the above examples. Tubercles typically measure 0·5 mm. (vertical) × 1·5 mm., and as in the previous specimen, are approximately 10 per cm. In several places, the tubercles are much larger and can be seen to consist of rather irregularly arranged exothecal elements. There is further transition from this state to parts of the colony where the exotheca is almost continuous with only an occasional horizontal tube every 5 mm. or so along the corallite length (Pl. 3, fig. 2). The size of the tubes seems to remain constant. In yet other regions of the colony the tubes are absent.

Plesiastrea? valenciennesii B.M. (N.H.) 1886.12.9.151. This specimen shows no important differences from those already described. There is a larger proportion of exothecal material between the tubes than in most of the above specimens and the tubes, though frequent, seem to be more often vertical than horizontal.

Leptastrea bottae B.M. (N.H.) 1934.5.14.444. From above, the corallites are rounded and project irregularly; there is a narrow groove between them up 0·5 mm. across and 2 mm. deep. At a depth greater than 2 mm. adjacent corallites are seen to be united by discontinuous exothecal material. In contrast to all of the previous examples however, the spaces between the exothecal material are not occupied by tubes; that is, although the intervening spaces do constitute a tube system very similar to that described, the thin-walled, finely-lined tubes themselves are not present. A sectional view (Crossland, 1952 : pl. 2, fig. 2) shows the exothecal bridges to be the equivalent of the tubercles above; but here, they are solid, or very nearly so. They are more obviously circular, and measure 0·5–1·0 mm. in diameter. There are 10 per cm. Between these tubercles can be seen the slightly rough walls of the corallites themselves.

SUMMARY OF DESCRIPTIONS. In all specimens, the corallites are separated at the surface by a groove, often narrow and rather deep. An impression of greater depth is given by the exotheca being discontinuous. With a single exception, tubes are present in the intervening spaces and open into the grooves of all of the specimens and form a very broadly rectilinear intercommunicating system. If two adjacent corallites are broken apart the tubes are seen to be finely lined more or less horizontally, and the broken section of exotheca in between is found to correspond to Edwards & Haime's " tubercles ". The fine lines are similar to those seen on epitheca, and these broken sections of tubes are evidently what these authors meant by " epitheca ". Contrary to the impression gained from their description it is the tubes rather than the " tubercles " which are the positive feature, except in the one instance where a specimen has no tube system at all. This same specimen differs from the others in that exothecal material is solid or very nearly so.

At one extreme, adjacent corallites are united for only about 50 % of the maximum;

there is then all gradation, through corallites united by almost continuous exotheca (i.e. large " tubercles ") with some tube development, to those between which there are no tubes at all. The diameter of the tubes remains broadly constant throughout. This complete gradation is seen in only one specimen here, although Professor J. W. Wells also possesses an example in his own collection (personal communication).

From observing the details of grooves between newly-formed and parent corallites, a sequence in the development of the groove-and-tubercle structure can be inferred. This is summarized in Fig. 1.

Discussion

Edwards & Haime and Duncan believed that groove-and-tubercle structure was an essential part of the coral skeleton, diagnostic of the genus *Phymastrea*. Quelch was the only author to have stated the possibility of another organism being responsible, by suggesting that the openings along the grooves might be those of worm tubes. Since Matthai's revision of the " Astraeidae ", the structure has always been taken to be a variation associated with one particular species. In a sense, all three of these views are, in part, taken here.

The tube openings certainly do have a superficial resemblance to serpulid tubes, but the intercommunicating, broadly rectilinear system which they form round each corallite, and the character of the lines (see below) make this interpretation unlikely. Moreover, the " plates " and " troughs " described remain unexplained. The material of which the tubes consist resembles epitheca too closely for it to be likely that they were laid down by anything other than the coral itself. If, however, any external agency has been involved then it seems more probable that its presence would have induced the coral to grow in the manner described rather than it being directly responsible for the structure. If this interpretation is accepted that the structure is part of the coral skeleton, it is nevertheless an insufficient criterion for recognizing a distinct taxon or taxa if species are to be defined and recognized on a truly biological, rather than merely morphological basis. The evidence for believing this structure is induced is provided by at least two known specimens with complete gradation within their respective coralla from parts in which groove-and-tubercle structure is present, to parts where it is absent. Both Matthai and Vaughan considered that the structure had no generic significance and the evidence provided by these specimens not only corroborates their conclusion but also extends it as now it follows that it has no specific significance either. In addition there is the evidence that certain specimens exhibiting groove-and-tubercle structure may be identified with established species of *Favia* which lack this structure.

The tube material resembles epitheca as Edwards & Haime and Duncan pointed out. In particular, it bears very fine lines on a scale similar to the epithecal growth lines described and figured by Wells (1963) and Scrutton (1965). These lines within the tubes, seen also on the plates and troughs, are therefore taken to be growth lines. The direction of growth they indicate corresponds exactly with the sequence of groove-and-tubercle development inferred on other grounds. On the other hand, the apparent presence of epitheca around individual corallites in corals of plocoid habit, clearly requires explanation. Professor J. W. Wells has pointed out that dissepiments, when newly formed, exhibit growth lines (personal communication), an an observation borne out by Pl. 1, fig. 1. Rather than attempting to explain the structure in terms of true epitheca, it might be simpler, therefore, and more accurate, to regard the tube system as modified exothecal dissepiments particularly as in this same figure, the tube and dissepiment are seen to be entirely continuous.

By analogy, in specimen No. 1927.5.12.166, the presence within the corallites of two tubes similar to, but larger than those found surrounding the corallites, might equally represent unusual endothecal development. However, No. 1934.5.14.444, by possessing no tubes at all, may at first seem to provide conflicting evidence. But Crossland identified the latter specimen as *Leptastrea* (confirmed here) and the exothecal character of this genus is dense, consisting mostly of stereome without visible dissepiments. The absence of tubes is therefore to be predicted if the present interpretation is correct, and the Crossland specimen supplements, rather than contradicts the evidence.

The possibility of this structure reflecting phylogenetic divergence by reason of its great difference from all other features seen in this group of Scleractinia, has already been discussed as being improbable. On the other hand, to regard such a striking feature simply as a variation seems insufficient, though not necessarily incorrect if " variation " is understood in a wide sense. The possibility of there being a pathologic cause is discussed in the next section. If this proves to be the case, then it may be concluded that Edwards & Haime were right in believing the tubes to be part of the coral skeleton; Quelch was right in thinking another organism (or agency) might be involved; and Matthai and Vaughan correct in doubting the systematic significance of the structure.

IV. PHYSIOLOGICAL SIGNIFICANCE OF THE GROOVE-AND-TUBERCLE STRUCTURE

Adequate discussion of the physiological significance of this structure is not entirely valid without a study of the polyps, both preserved and living. It is convenient however, to discuss several points very briefly, in this section.

It is suggested above that the structure is essentially a modified dissepimental growth. With the possible exception of Matthai's figured specimen, it is the exothecal dissepiments that are involved, from which it may be taken that the coenosarc rather than the polyps themselves are affected. Perhaps the coenosarc in affected specimens does not form a continuous layer, as it usually does, and the material of the tubes is laid down at the edges of holes. Since these would be analogous to edge zone margin (Wells, 1956 : Fig. F 228), material similar to epitheca would be deposited. The earliest formed plates in new intercoralliate grooves could, in this way, correspond to the earliest formed holes in the coenosarc between new and parent polyps, each growth line marking successive stages in their deposition. Continued growth would then lead to the enlargement, and eventual coalescence of the holes in the coenosarc, reflected by the circumferential growth of the plates and their lateral fusion to form troughs. Subsequent upward growth would cause the material of these structures to be built up vertically, and the tube system would develop in the form observed according to the way in which the holes expanded and contracted, fused and separated, or generally changed their relative position during upward growth. That the direction of growth is always essentially upward, and not consistently parallel to the length of the tubes, is demonstrated by the attitude of the growth lines (alternatively another interpretation of the fine lines is necessary). A different explanation might be that instead of the coenosarc being absent in places, the cause might lie within it. For instance, the calicoblast layer may be incomplete or diseased. Anything more widespread within the coral, would not in the first place seem to explain the highly localized nature of the abnormal feature.

None of the foregoing provides any explanation of the prime cause of the structure, which may be a disease or the indirect result of an association with another organism. There is some evidence that the living corals were adversely affected in their overall growth which would be expected if they were diseased or hosts to a parasite. In the case of Crossland's *Leptastrea bottae,* the septal cycles are fewer and the general character less spinulose than is usual in this species; both features point to inhibited growth. The specimen figured by Matthai as *Favia bertholleti* also gives the same impression; but here the numerous serpulid worms which were evidently present in the living colony cannot be excluded as a possible cause affecting structure during growth. (They might equally be the result, having taken advantage of a coral colony made unhealthy by whatever caused the groove-and-tubercle structure.)

Whether a disease or an association is involved, and whatever the nature of the latter, it seems that some species are more prone than others. One species, here referred to as *Plesiastrea? valenciennesii* is known only from affected specimens, while *Favia favus* is occasionally affected, and *Leptastrea bottae* has provided just the single example so far. Obviously future work is likely to modify this picture, so that for instance unaffected *Plesiastrea? valenciennesii* specimens may be found.

V. SYSTEMATIC DESCRIPTIONS

The diagnoses given below are intended to outline only those characters which serve to distinguish the species from others within the genus. Supraspecific characters and diagnoses followed here, are to be found in Wells (1956) and Vaughan & Wells (1943). The taxonomic state of certain species is such that accurate diagnoses are difficult to provide.

Order SCLERACTINIA Bourne, 1900

Suborder FAVIINA Vaughan & Wells, 1943

Superfamily **FAVIICAE** Gregory, 1900

Family **FAVIIDAE** Gregory, 1900

Subfamily **FAVIINAE** Gregory, 1900

Genus ***PLESIASTREA*** Edwards & Haime, 1848

TYPE SPECIES. *Astrea versipora* Lamark, 1816 (by monotypy).

REMARKS. Two species are doubtfully referred to this genus. These correspond to Edwards & Haime's genus *Phymastrea*, which, according to these authors, shows extratentacular budding. In other respects specimens of the first of the species below are similar in appearance to *Favia* and they therefore seem to be positioned between the two genera. Duncan (1883) pointed out that Edwards & Haimes' description of the genus *Phymastrea* in their 1857 work, differed from those they gave previously, with respect to the nature of corallite increase. He concluded that the 1857 description ("calicular and submarginal") was incorrect, the true mode of increase being " extracalicular and subapical ". Quelch's specimen of *P. aspera*, (pl. 4, fig. 3) which closely resembles Edwards & Haime's *P. valenciennesii*, exhibits both methods, which might explain the " mistake ".

Plesiastrea? valenciennesii (Edwards & Haime, 1848)

(Pl. 4, figs. 1–3)

Phymastrea valenciennesii Edwards & Haime, 1848 : pl. 9, figs. 3, 3a, and 1849 : 124; Edwards & Haime, 1857 : 500 ; Duncan 1883 : 408 ; Yabe, Sugiyama & Eguchi, 1936 : 31, pl. 23, figs. 3–5, pl. 24, fig. 5.

Favia valenciennesii : Nemenzo, 1959 : 89, pl. 5, fig. 1.

Phymastraea aspera Quelch, 1886 : 105, pl. 4, figs. 1–1b.

Leptastrea bottae : Nemenzo, 1959 : 110, pl. 14, fig. 1 (non *Cyphastrea? bottae* Edwards & Haime, 1849).

MATERIAL. See accompanying table.

DIAGNOSIS. Corallites irregular, small to medium in size (5–10 mm.), strong costae, innermost septal teeth directed upwards as irregular, rounded paliform lobes.

DESCRIPTION.

B.M. (N.H.) Register No. 1886.12.9.151. (Type of *Phymastraea aspera* pl. 4, figs. 1–3).

Quelch's description of this specimen is excellent; it is quoted in full below:

> " Corallum massive, heavy, irregularly convex. Calicles rather large, very unequal and deep, polygonal, circular, oval or elongated, greatest width from about 9 to 11 mm., many calicles less, about 4 to 5 mm. deep; furrows between the calicles well marked, very narrow, with deep spaces between the connecting portions occupied by small tubes—apparently worm tubes—which preserve the intercalicinal spaces and keep them open during the growth of the colony; costae unequal, denticulate, those of opposite cups often coalescing. Septa not perforated, of five cycles, the last being very rudimentary, the fourth being small; those of the three first cycles are subequal, large and rather thick, much exsert, and roughly, unequally, and bluntly toothed; the innermost teeth are very distinct, large, long and paliform, not divided, surrounding a distinct deep and narrow depression, at the bottom of which is a small, subtrabeculate or papillose columella which is almost absent in a transverse section. Texture of the corallum very dense and hard."

The only important information lacking in this description concerns the mode of corallite increase. This and some additional details are given below:

One corallite near the margin of the corallum looks as if it has a new partition forming within it, suggesting unequal intratentacular budding (Pl. 4, fig. 3, left centre). Another has given rise to a young corallite which is circular and 1·5 mm. in diameter; the wall shared with the adult corallite is surprisingly substantial for an early growth stage of a corallite formed by intratentacular budding and is therefore thought to be extratentacularly formed (Pl. 4, fig. 3, upper right centre). Budding in such instances evidently takes place very close indeed to the corallite margin. Other corallites also give the impression of extratentacular formation, the only evidence of a partition forming within a calyx being the example already cited.

The corallum measures 7 × 5 × 3 cm. and is almost complete. It has at some time been partially killed off, but subsequently spread a new encrusting growth over most of the dead area.

The smallest corallites are usually completely united to adjacent (parent) corallites along their common wall, separated only by a superficial intercorallite groove 1 mm. or so deep, in which the low costae meet or almost meet. Between mature corallites, the intercorallite grooves are more prominent, the costae themselves do not meet, and the tube openings already described are seen along them.

On the free limb of the corallites, costae are about the same width as the septa in the theca, and bear one to three rough irregular teeth. They are exsert over the margin by about 2 mm. (i.e. relatively exsert); crests are rough and more or less horizontal. The upper half of the septal margins bear two to three rough, slightly lobate, spinulose teeth, of which the upper one to two are directed inwards, while the last is stronger and directed upwards as a rounded paliform lobe. The margin below the lobe is rough. The septa are thick in the theca (one half to one third of the width of the interseptal loculi) and taper towards the columella.

The groove-and-tubercle structure is described in a previous section.

Discussion. Of the species included in the synonymy which were not actually examined, the figure given by Nemenzo of his *Leptastrea bottae* shows that his specimen is very close indeed to that described above, even in the details of new corallite formation. The same is true of the specimens figured by Yabe, Sugiyama & Eguchi.

The type specimen itself was not seen, but Edwards & Haime's figures and description suggest that Quelch's specimen above is very similar. Quelch, however, thought otherwise, believing his specimen to differ

> ". . . by its convex mode of growth, by its more distinct and prominent calicles, which are also quite deep, by the much greater development of the septa, which are more exsert, numerous, and closely spaced, not perforated, with non-bifurcated and large paliform teeth, and by the slight development of columella ".

He also stated, on the other hand, that round the outer part of the corallum, "the cups become rather shallow and approach very closely to the form of those of *Phymastraea valenciennesii* ". Re-examination of Edwards & Haime's type is clearly desirable. For reference, a translation of their type description is given below. (Compare with that of *Favia bertholleti*, given under *F. favus*, below). Duncan's description is the only other in English and seems to be a shortened translation after Edwards & Haime.

" Corallum encrusting, (upper surface) subplanar. Calices penta- or hexagonal, separated by very pronounced grooves, where deep holes may be seen (from place to place) by which the intercalicinal spaces communicate with the exterior. (Fossa very slightly deep.) Columella well developed, dense in texture and subpapillose at the surface. Four complete cycles, but the last cycle is rudimentary in most systems. Septa close, subequal, slightly exsert, slightly thick; the faces bear numerous unequal granulations projecting only a little; the teeth are rather numerous and very strong, particularly the innermost one which is usually bifurcated and upright. In broken septa, small channels can be seen between the two septal plates. In longitudinal section, epitheca is seen to cover the entire walls. Each prism face of the corallites usually bears 2 vertical series of large verrucose tubercles, almost entirely solid in texture, rounded and elongated transversely, strongly uniting neighbouring corallites; the tubercles of one series alternate with those of the other series, and they are all covered by epitheca. The walls are thick. The septa are wide and are perforated only near the free edge. The columella is formed of upright trabeculae, very long, and very close. Dissepiments slightly irregular, very close together, but unevenly so, very slightly inclined, rather ramifying. Larger diameter of corallites, from 8 to 10 mm. (their depth scarcely 2)."

Passages in parentheses in the above translation denote those omitted from Edwards & Haime's 1857 work.

The species seems to be represented only by specimens with groove-and-tubercle structure, a point already discussed.

Occurrence. Banda; Honsyû, Sikoku, Kyûsyû, and Taiwan (after Yabe, Sugiyama & Eguchi); Philippines (after Nemenzo).

Plesiastrea? profundior (Edwards & Haime, 1848)

Phymastrea profundior Edwards & Haime, 1849 : 125 ; Edwards & Haime, 1857 : 500 ; Duncan 1883 : 408.

Material. Not seen (one specimen in Museum National d'Histoire Naturelle, Paris).

Description. (*Translation of type description*): " Corallum encrusting, convex overall. Calices polygonal: in the deep grooves which separate them, tubercles may be seen which unite their walls, and which are slightly granulose. (Calicinal fossa deep.) Columella poorly developed. In general three cycles, but some systems have just the three, while others sometimes have a further septum of a fourth cycle. Septa slightly close, slightly exsert, narrow above, rather thickened over the walls, thin within, at the edges unevenly divided. There is normally one tooth much stronger than the others adjacent to the columella. Secondary septa are almost equal to the primaries. Larger diameter of calyces 8 to 10 mm.; (their depth 5 or 6). "

Passages in parentheses are those omitted from Edwards & Haime's 1857 work.

Discussion. The affinities of this taxon are not known as it was not seen, has never been figured as far as is known and has not been included by another author in a synonymy. The presence of a strong tooth near the columella perhaps indicates affinity with *P? valenciennesii* above. Duncan's description was taken from Edwards & Haime; he stated that *P. profundior* differed from *P. valenciennesii* " by having deeper and smaller calices, a smaller columella, a lower septal number and slender junctions."

OCCURRENCE. Not known.

FAVIA Oken, 1815

TYPE SPECIES. *Madrepora fragum* Esper, 1795 (subsequent designation Edwards & Haime, 1848).

Favia favus (Forskål, 1775)

(pl. 5, figs. 1–3, pl. 6, figs. 1–4, ?pl. 8.)

Madrepora favus Forskål, 1775 : 132.
Favia favus : Wells, 1954 : 458 (synonymy).
Parastrea bertholleti " Valenciennes MS," Edwards & Haime, 1857.
Favia bertholleti Edwards & Haime, 1857 : 431 ; Matthai, 1914 : 94, pl. 7, fig. 2, pl. 22, fig. 7 (= *M. favus* Forskål type), pl. 23, fig. 4 (= *F. bertholleti* Edwards & Haime type), fig. 6, pl. 24, fig. 1.
Prionastraea halicora : Edwards & Haime, 1857 : 517 (synonymy : non *Astraea halicora* Ehrenberg, 1834).
Prionastraea australensis Edwards & Haime, 1857 : 520.
Phymastraea irregularis Duncan, 1883 : 409, figs. 1, 2.
Favia valenciennesi : Matthai, 1924 : 14, pl. 4, fig. 1, pl. 11, fig. 2 (also pl. 1, fig. 2[1], pl. 2, fig. 9) Faustino, 1927 : 133, pl. 27, figs. 1, 2, ?3; Crossland, 1952 : 126; Wells, 1954 : 458; (non *Phymastrea valenciennesii* Edwards & Haime, 1848).
Favites aspera : Crossland, 1952 : 132 (part), pl. 5, fig. 1 only (non *Goniastrea aspera* Verrill, 1866).

MATERIAL. See accompanying table.

DIAGNOSIS. Corallites medium to large in diameter (10–15 mm. typical); rims only slightly exsert if at all; intercorallite areas very variable in width; fission equal to subequal. Septa rough and irregularly dentate.

DESCRIPTIONS.

B.M. (N.H.) Register No. 1927.5.4.165 (pl. 5, fig. 2, pl. 6, figs. 2, 4).

Corallum measures 17 × 12 × 9 cm., massive, rounded, complete colony.

Corallites rounded to irregular, open, 1 mm. apart, diameter 10–12 × 5–8 mm., depth 5mm.

Calicular margins fine, exsert 1 mm., often united. Intercorallite area less than 1 mm. across, or absent; costae continue across intercorallite area.

Twenty-five to thirty septa of which about half reach the columella; some rudimentaries are present. Septa may curve to unite before reaching columella, but rarely more than in two's, thin (about one quarter, or less, width of the interseptal loculi), narrow for the upper one half to two thirds benched, and broader below.

Costae more or less equal; usually continue directly into costae of adjacent corallite, but may also end abruptly against neighbouring corallite margin; exsert over theca by about 0·5 mm., or less, rarely more than 1 mm.; margins horizontal and virtually entire, but may slope inwards. Septa poorly or irregularly toothed or lobed

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[1] Plate printed upside down.

above bench (up to 5); sometimes low rounded lobe on bench; a few slight teeth below bench. Septal faces covered with fine conical spinules.

Columella loose, trabecular, one quarter diameter of calice.

Fission intratentacular, subequal.

B.M. (N.H.) Register No. 1927.5.12.166 (pl. 5, fig. 3)

Fragment 4·5 × 5 × 4 cm. consisting of about twenty-five corallites only.

Corallites polygonal, 1 mm. apart, up to 13 mm. long and 7 mm. wide, 5 mm deep; margins rounded, 0·5 mm. thick, slightly exsert. Distinct intercorallite groove, narrow (less than 1 mm.), passing downwards into groove and tubercle system as described above.

About thirty septa of which twelve or so reach columella; some rudimentaries, thick in theca where they are of the same width as interseptal loculi, thinning just within; narrow for upper half, widening below to form a bench above columella.

Costae on free limbs often united by spines across intercorallite grooves, but spines usually limited to only one or two on each costa. Costae thick, separated only by narrow grooves; may alternate with rudimentary costae, slightly exsert over calicular margin where they are rough and generally without teeth or spines; up to six teeth on septal margins, often more pronounced above, sometimes poorly developed as lobes; bench usually marked by one or two larger lobes; two or three smaller teeth below bench; septal faces and costae bear fine spinules, often long and almost bristle-like.

Columella rudimentary, loose, one fifth to one quarter diameter of the calyx.

Fission not seen (intratentacular?).

Development of endothecal dissepiments gives corallites shallow appearance.

B.M. (N.H.) Register No. 1898.12.1.12 (identified here as *F. ?favus*) (pl. 8.)

Corallum measures 12 × 8 × 4 cm., almost complete.

Corallites rounded to slightly polygonal, up to 10 × 7 mm. in diameter, rarely less than 5 mm., 2–3 mm. apart, up to 5 mm. deep.

Free limb of corallites descends steeply or vertically to grooves 3 mm. deep, which pass downwards into groove-and-tubercle system described above, though not throughout the colony—absent in places, where groove is superficial.

Thirty-five to forty septa, of which fourteen usually reach the columella; some rudimentaries present. Septa are thick in theca, but otherwise thin (one third or less width of interseptal loculi), narrow above, upper two thirds either sloping towards centre or tracing concave outline to bench; lower one third vertical to columella or nearly so.

Costae equal in size, thicker than septa, but increase in thickness to meet thickened septa in theca; do not meet across intercorallite groove, bear seven or so good teeth with transversely flattened, upward-directed teeth which may either be pointed or slightly rounded, and occasionally unite with costal teeth of adjacent corallites to form arch over intercorallite groove; crests entire, sometimes with two or three smaller teeth, exsert above corallite margin by 1 mm. or so. Septal margins above bench bear up to eight usually five, inward-directed, irregular teeth, often stronger above; below bench, two or three more teeth, usually less pronounced, also inward-directed. The bench gives slight effect of palial crown, but no good lobes present. Septal faces finely spinulose.

Columella loose, poor, approximately one fifth diameter of calyx.

Fission seen in one corallite is unequal. In two others, nearer to subequal. New corallites at margins of corallum formed by unequal fission.

Discussion. The first of the above described specimens, like most of those referred by Matthai to *F. bertholleti* differs in no fundamental way from the very large suite of specimens he identified as *F. favus*. The principal differences are essentially superficial, with all transitions from these specimens to those of *F. favus*, mostly consisting of narrower intercorallite areas and rather smoother less dentate septa. Matthai's difficulty in distinguishing the two species has already been referred to (p. 325). For comparison a figure is also given here of one of Matthai's specimens of *F. favus*, collected from the same locality (pl. 5, fig. 1, pl. 6, figs. 1, 3). This author describes two facies for each of the species *F. favus* and *F. bertholleti*—" thick-walled " and " thin-walled ". Allowing for the apparent confusion that has arisen by which thick-walled forms of the latter have been mistaken for *Phymastrea valenciennesii*, and *vice versa* (see above) it is possible to define a broad morphological series thus: *F. favus* " var. 2 " (thick-walled)↔*F. favus* " var. 1 " (thin-walled)↔ *F. bertholleti* " var. 2 " (thick-walled)↔*F. bertholleti* " var. 1 " (thin-walled). The usefulness of being able to distinguish such forms in the genus *Favia* seems open to doubt (see, for example, Wells' remarks on *F. pallida*; 1954 : 458), but it might prove to be helpful in the future. The above series is accordingly regrouped, as follows:

(1) thick-walled, with enclosed corallites. e.g. Matthai's pl. 22, fig. 4 (one of Forskål's types), Matthai's pl. 20, fig. 4, Vaughan's (1918) pl. 39. figs. 1, 1a (Verrill's type of *F. danae*). This facies might referred to as " *danae*-facies ", and is the equivalent of Matthai's *F. favus* " var. 2 " (Wells, 1954).

(2) walls thinner—up to 3 mm. with calyces more open. Septa often benched and corallites often bear a resemblance to *F. speciosa* (i.e. Dana's type). e.g. Matthai's pl. 20, fig. 2, pl. 22, fig. 5 (Forskål's type of the synonym *Madrepora cavernosa*). This facies might be referred to as " *cavernosa*-facies ", and is the equivalent of Matthai's *F. favus* " var. 1 " and *F. bertholleti* " var. 2 " together.

(3) walls of adjacent corallites closely united to summits, or nearly so; septa often rather fewer, thinner and less rough. e.g. Matthai's pl. 22, fig. 7 (one of Forskål's types of *F. favus*). It would be convenient to refer to this facies as " *bertholleti*-facies " but the type of the species seems to fall within the above category, to judge by Matthai's figure of it (pl. 23, fig. 4); it is the equivalent of Matthai's *F. bertholleti* " var. 1".

Forskål's type of *F. favus* range across the facies and there is therefore no " typical " form in the strict sense, if the above division is made.

In addition to the three specimens above, all those that Matthai (1914) referred to *F. bertholleti*, and the single specimen of *F. valenciennesi*, Crossland, 1952 were examined, together with several others. With the exception of *Phymastraea aspera* Quelch, they are all referred here to *F. favus*. *Favites aspera*: Crossland belongs here also. Of species known only from the literature, two of the four included by Matthai in his synonymy of *F. bertholleti* are included here, those omitted being *Phymastrea valenciennesii* Edwards & Haime and *P. aspera* Quelch, as discussed above. Edwards & Haime's *Prionastrea rousseaui* (later *halicora*) was divided by Matthai between *F. favus* and *F. bertholleti*; none of the eight specimens could have displayed groove-and-tubercle structure or these authors would surely have referred them to their genus *Phymastrea*. Matthai's grounds for dividing this species are taken to be that some of the specimens had very narrow walls. Edwards & Haime do not often seem to have referred a group of specimens to one species, where most later authors have recognized several; more often the reverse has been true. Edwards & Haime's *Prionastraea australensis*, according to Matthai consists of one specimen only, whose corallites have " a meandering tendency ", but otherwise " resemble those of *F. bertholleti* ". *F. valenciennesii*: Faustino corresponds to facies 3 above, in the specimen figured in pl. 27, figs. 1 and 2; the third figure might belong elsewhere. *F. valenciennesii*: Wells would appear to be facies 3 also, from the description given, but there is no figure.

Duncan's species, *Phymastraea irregularis* was reidentified by Matthai (1924) as *F. valenciennesi* [sic], though he omitted it from his synonymy.

Two of the specimens described above exhibit the pathologic (?) groove-and-tubercle structure. B.M. (N.H.) 1927.5.12.166 has corallites which differ in no fundamental way from normal specimens of *F. favus*. The fragments given by Matthai in his same figure, do not possess this same structure, but otherwise are very close. B.M. (N.H.) 1898.12.1.12 likewise exhibits groove-and-tubercle, but it is less easy to be certain of the affinities of the corallites: they are somewhat small, and the fission seems to be unequal; the costae are noticeably dentate. The specimens figured by Matthai in his 1924 paper as *F. valenciennesi* also seem to be groove-and-tubercle forms of *F. favus*.

For convenience of reference, a translation of Edwards & Haime's type description of *F. bertholleti* is given below. The differences between this and that of their *Phymastrea valenciennesii* have already been stressed:

> " Corallum convex. Calices very close, rectangular, margins usually united or only separated by a weak groove. Columella very reduced. From 24 to 30 exsert septa, rather unequal, rather close, very thin within, with quite long teeth; the principals are thick near the wall. There are no distinct lobes. Size of calices 8 to 10 mm."

OCCURRENCE. Widespread Indo-Pacific species. " Red Sea and Indian Ocean eastward to the Fiji Islands, and Fanning Island." (Wells, 1954).

Favia speciosa (Dana, 1846)

(Plate 7, Figs. 1, 2.)

Astraea speciosa Dana, 1846 : 220, pl. 11, figs. 1–1d.
Favia speciosa : Wells, 1954 : 457, pl. 174, fig. 2 (synonymy).

MATERIAL. See accompanying table.

DIAGNOSIS. Distinct corallite margins; numerous thin fine septa, evenly dentate; fission subequal to unequal.

DESCRIPTIONS.

B.M. (N.H.) Register No. 1892.12.1.594 (pl. 7, fig. 2).

Corallum measures 9 × 8 × 6 cm., massive, hemispherical; complete.

Corallites polygonal, sometimes elongated or slightly rounded separated by deep intercorallite grooves 1 mm. in width. Mature corallites 10 × 15 mm. diameter, 7–10 mm. deep.

Groove between corallites up to 4 mm. deep. Free limbs of corallites bear spinulose costae which alternate regularly with rows of granulations which sometimes become rudimentary costae. Principal costae exsert up to 0·5 mm. relative to free limb surface. At a depth greater than 4 mm., most corallites are partially united by discontinuous exotheca, between which tube openings can be seen; margins of corallum tend to exhibit corallites joined more continuously, or even completely, by exotheca.

Forty to fifty septa of which about half reach the columella; some rudimentaries, which, together with slightly larger septa correspond to rows of granulations, or in some instances, rudimentary costae, between the main costae. Septa thin (one half to one third width of interseptal loculi), taper towards columella; narrow above, broadening out for lower one third to give bench.

Margins of costae bear numerous well developed spinulose teeth, lobed, sometimes forked, directed slightly upwards; absent over calicular margins, where costal margins are entire or irregular and horizontal. Septal margin vertical, concave, or convex to bench; up to twelve teeth which may be similar to costal teeth, or, when fewer than six, just irregular lobes; in some instances, comb-like set of very closely small teeth just below costal crest; septal teeth generally directed very slightly upwards; below bench, up to six teeth similar to those higher up; margin descends from bench vertically or nearly so. The septal bench gives slight appearance of palial-crown, but good lobes not developed. Septal faces finely granulose.

Columella loosely trabecular or spongy, up to one third diameter of calice.

Fission unequal to subequal.

B.M. (N.H.) Register No. 1892.12.1.362

Corallum measures 13·5 × 7 × 10 cm., massive, rounded, complete. Character of corallites virtually identical to specimen above, except that the general appearance is somewhat coarser. The thickening of septa over the calicular margin is more pronounced.

DISCUSSION. The principal difference between these specimens and most specimens of *F. speciosa* is in the presence of the groove-and-tubercle structure, identical to that seen in *Plesiastrea? valenciennesii*. For reasons already discussed, this feature is not believed to be of specific value. Comparison of the calicinal characters of these two specimens with those of a third Museum specimen without groove-and-tubercle structure, shows them to be very similar. (Pl. 7, fig. 1). This third specimen, not described at all before, is one of several that compare well with Vaughan's figure of Dana's type of *Astrea speciosa* (1918, pl. 36, fig. 1). It is on this basis that the present identification was made.

OCCURRENCE. Widespread Indo-Pacific species. " Red Sea generally eastward to Fanning Island northward to Honsyû " (Wells, 1954).

Subfamily **MONTASTREINAE** Vaughan & Wells, 1943

Genus ***LEPTASTREA*** Edwards & Haime, 1848

TYPE SPECIES. *Leptastrea roissyana* Edwards & Haime, 1848; subsequent designation Edwards & Haime, 1850.

Leptastrea bottae Edwards & Haime, 1848

Cyphastrea? bottae Edwards & Haime, 1849 : 115.
Leptastrea bottae : Vaughan, 1918 : 94, pl. 31, figs. 3, 4 (synonymy) ; Faustino, 1927 : 121, pl. 21, figs. 1–3; Wells, 1950 : 49; Crossland, 1952 : 116, pl. 1, fig. 4, pl. 2, figs. 2, 3.
Baryastrea solida Edwards & Haime, 1849 : 144.
Leptastrea solida : Matthai, 1914 : 69, pl. 17, figs. 8, 9, pl. 18, figs. 3–6, 8, pl. 19, figs. 5, 6 (synonymy).
non *Leptastrea bottae* : Yabe, Sugiyama & Eguchi, 1936 : 27, pl. 30, fig. 1 (= *Cyphastrea* sp) ; Nemenzo, 1959 : 110, pl. 14, fig. 1 (= *Plesiastrea? valenciennesii*).

MATERIAL. See accompanying table.

DESCRIPTION.

B.M. (N.H.) Register No. 1934.5.14.444.

Crossland's description of this specimen is as follows:

> " In the small crowded calyces of the more usual size, only the six thick primary septa reach the columella, or the secondaries may reach it deep down in the calyx, but generally they are small; tertiaries are just visible or are absent, but their costae, low and rounded like those of the other series, are generally present. Columella greatly reduced, but may bear vertical points, and septa often bear paliform lobes. As seems to be usual in this species, giant corallites are present; in these, numerous septa reach the tuberculated columella, which seems to block the bottom of the theca. Comparison with the other species and with an intermediate specimen in the København museum, indicates that these " giant " calyces are, in fact, nearer the normal form, and the more numerous and smaller being the farthest from the ancestral type.
>
> " A longitudinal section of this species has not yet been figured; it is remarkable for the beams[1] connecting the thecal walls, some solid, some hollow . . . Compare Milne Edwards and Haime's (1848) pl. 9, fig. 3a (for *Phymastrea valenciennesii*) ".

Additional information is as follows:

Corallum measures 6 × 5 × 4 cm., rounded, massive, not complete. Corallites circular, walls relatively thick (0·5 mm.); mature corallites 3 mm. diameter, 0·5–1·0 mm. apart; giant corallite 5·5 mm. diameter; separated by groove up to 1 mm. deep in which the corallites can be seen only partially united.

Giant corallite has one cycle of septa more than other corallites. Septa thick in theca where they are almost as wide as the interseptal loculi; taper fairly abruptly towards columella; broad; depending on cycle, exsert over calicular margin up to

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[1] Footnote by A. K. Totton in Crossland's text: " visible also at surface."

1 mm. Septal margin horizontal or sloping slightly inwards over calicular margin for about half the distance to the columella; entire at this point; sharp angle before margin descends vertically or nearly so to fossa, then sharp angle again and margin horizontal to columella. Septal faces spinulose.

Columella formed of upstanding lobes corresponding to each septum of the first cycle, joined by a few horizontal elements to form a crude circle; sometimes a few additional horizontal elements.

Extratentacular budding.

Discussion. The reduced columella, and less spinulose character would suggest some intergradation between *L. bottae* and *L. immersa*, the latter as described by Vaughan (1918 : 96, pl. 31, figs. 2–2b). Crossland believed that his sectional view of the specimen would be similar to that of other specimens of *L. bottae*, but this is not the case: in most instances, corallites are united by continuous exotheca, consisting almost entirely of stereome, as far as can be seen. The tubercles of his specimen are, moreover, not both solid and hollow, as he stated, but almost always solid: an illusion of their being hollow is given when the plane of the section passes slightly into the corallite wall, so allowing a view into the corallite cavity. Crossland's specimen has been interpreted here as abnormal by virtue of the discontinuous exotheca. It has been suggested above that it is essentially a groove-and-tubercle specimen, in which the absence of tubes seen in specimens of other species is explained by the absence of visible exothecal dissepiments in normal growth. The cause of this abnormality may be linked in some way with the cause of the rather atypical calicinal characters.

Nemenzo has described a specimen attributed by him to this species. In his figure, small tube openings can be seen in the intercorallite grooves. The calicinal characters are however totally different from those of *L. bottae* and the specimen is probably closer, if not the same as *Plesiastrea? valenciennesii* above.

Occurrence. Maldives, Chagos, Red Sea, Great Barrier Reef. French Somaliland, Cocos-Keeling, South and Central Philippines, Hawaii (after Vaughan).

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ADDENDUM

Genus *BARABATTOIA* Yabe & Sugiyama, 1941

Type species. *Barabattoia mirabilis* Yabe & Sugiyama, 1941.

Discussion. Yabe and Sugiyama described two species of this genus, *mirabilis* and *goroensis*, each represented by one specimen but *B. goroensis* is possibly only an example of *B. mirabilis* in a rather poor condition. None of the differences between the two original descriptions is usually found to be really significant in distinguishing other Faviid species. The nature of these differences is of the same order as those found for example, in the different facies of *Favia favus* as given above.

Barabattoia mirabilis Yabe & Sugiyama, 1941

Barabattoia mirabilis Yabe & Sugiyama, 1941 : 72, pl. 61, figs. 1–1e.

Diagnosis. Columella well developed, pseudo-pallial crown present, septa alternating.

Material. B.M. (N.H.) 1894.6.16.37 (King's Sound, Northwest Australia; W. Saville Kent's Collection).

Discussion. Yabe and Sugiyama's plates of the type specimen show clearly that groove-and-tubercle structure is absent. This is the only feature by which the present specimen differs from the type. Tube openings are not seen round every corallite however, nor are they as regularly developed as in some of the other described examples. Thus the specimen shows transition from one condition (taken to be normal) to the other (taken to be pathologic), the significance of which has been discussed above. The tubes themselves are not in any way significantly different from those already described.

This specimen is of great interest although it has been previously overlooked in the collections of the British Museum (Natural History). It was provisionally labelled "*Stylophora*" because, according to the label inscription, it bore a small encrusting growth of that genus 2 mm. in size but the supposed *Stylophora*, in fact, appears to be a bryozoan growth. The main body of the specimen, hitherto unidentified, is a small, complete colony of *Barbattoia mirabilis* Yabe & Sugiyama. It is almost certainly the only representative of this taxon in the collections of the British Museum (Natural History), and seems to be the first record of this rare genus and species since the type description. Of greater interest still in the present context, it exhibits groove-and-tubercle structure, so providing still further evidence that the occurrence of this feature is not restricted to either one species or one genus. The number of different genera in which groove-and-tubercle is known to occur is now 3 (possibly 4), all Faviids. It is therefore seems more than likely that still other related genera and species, both fossil and recent, may prove to be represented by such colonies.

OCCURRENCE. Yap Island in Palau Islands, King's Sound in Northwest Australia.

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PLATE 1

FIG. 1. View from above of an exothecal dissepiment in an intercorallite area near the margin of the corallum, showing growth lines on the dissepiment and a tube rising up from it. The tube is completely continuous with the dissepiment, and the growth lines are absent on the outside of the tube. × 80.

Specimen No. B.M. (N.H.) 1892.12.1.594, *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46286).

FIG. 2. View from above of a newly formed intercorallite groove showing (extreme right) a plate, and (centre and left) troughs. The pattern of the growth lines on the latter marks the original plates of which they are formed, now fused together. The longer margins of the trough are beginning to curve upwards. × 30.

Specimen No. B.M. (N.H.) 1892.12.1.594, *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46284).

1

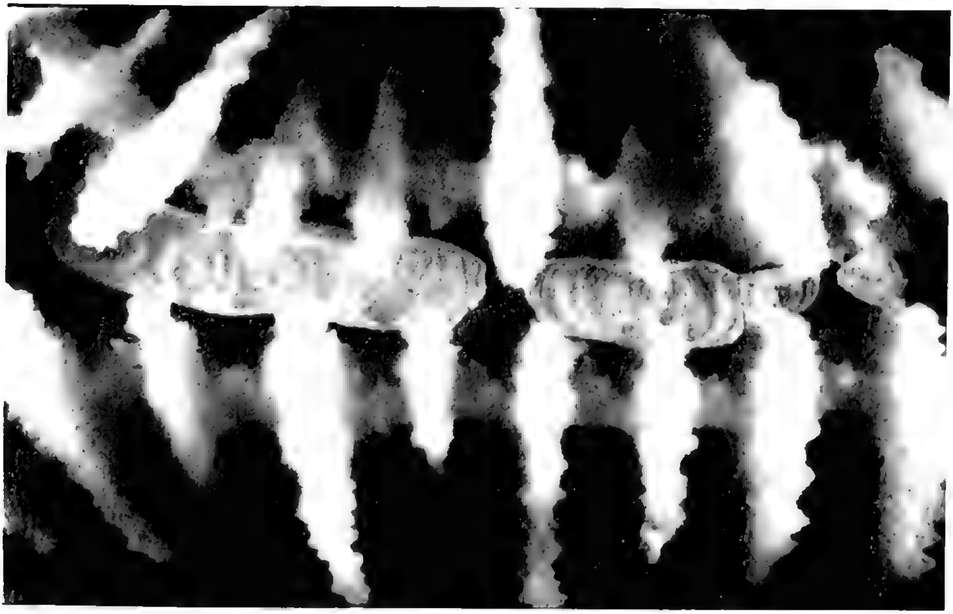

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PLATE 2

FIG. 1. View from above of a tube opening in an intercorallite groove, whose rim is extended along the groove. The margins are beginning to close over beneath pronounced costal projections. × 60

Specimen No. B.M. (N.H.) 1892.12.1.594 *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46281).

FIG. 2. View from above of a tube opening, within a corallite, similar to those found around corallites along grooves, but somewhat larger. This possibly represents an analogous structure to the latter which are more common. The two corallites in this specimen which contain tube openings may be seen in the centre of Pl. 5, fig. 3. × 27.

Specimen No. B.M. (N.H.) 1927.5.12.166, *Favia favus* (Forskål) (B.M. (N.H.) negative No. 46283).

1

2

PLATE 3

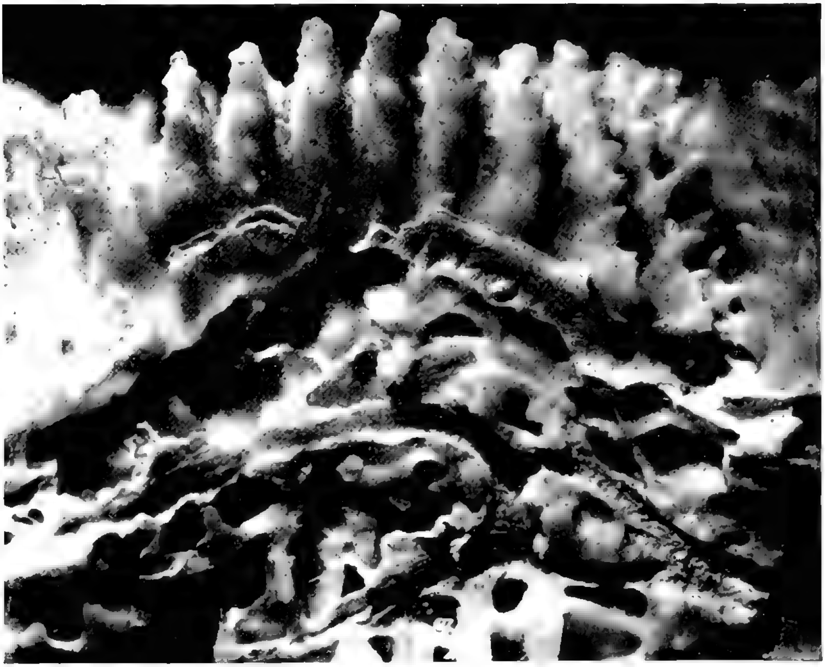
FIG. 1. Lateral view of a corallite wall showing " tubercles " surrounded by tubes seen in section, so appearing similar to epitheca. The " tubercles " can be seen to consist of stereome and exothecal dissepiments. Compare this view with those given by Edwards & Haime (1848) and Crossland (1952). × 17.

Specimen No. B.M. (N.H.) 1927.5.12.166, *Favia favus* (Forskål) (B.M. (N.H.) negative No. 46282).

FIG. 2. Lateral view of a corallite wall, comparable with Fig. 1, but showing much larger " tubercles ", clearly seen to consist of exotheca typical of *Favia*. Tube system is greatly reduced in amount. × 13.

Specimen No. B.M. (N.H.) 1898.12.1.12, *Favia ?favus* (Forskål) (B.M. (N.H.) negative No. 46285).

1



2

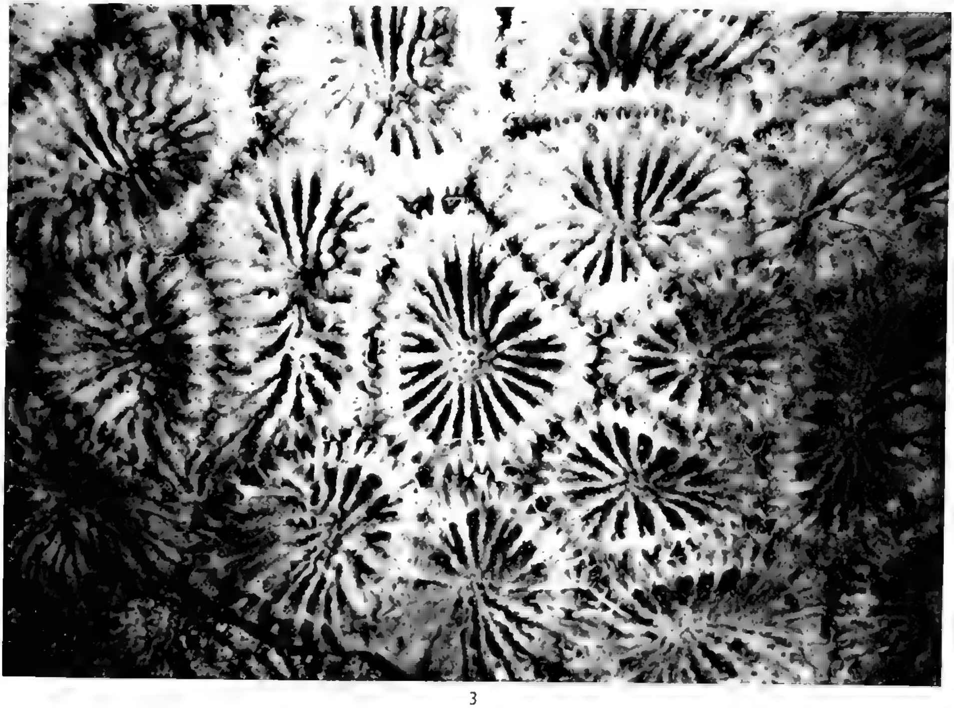
PLATE 4

FIGS. 1–3. *Plesiastrea? valenciennesii* (Edwards & Haime). Quelch's type of *Phymastraea aspera*. The intercorallite grooves contain tube openings. Note mode of corallite increase. (see text p. 341). × 8, × 8, × 4.6.

Specimen No. B.M. (N.H.) 1886.12.9.151. (B.M. (N.H.) negative Nos. 47572/29b, c, a).

1

2



3

PLATE 5

FIG. 1. *Favia favus* (Forskål), *cavernosa*-facies. This specimen was also identified by Matthai as this species; compare with fig. 2, and pl. 6, figs. 2, 4 which he referred to *F. bertholleti* (Valenciennes). × 2.

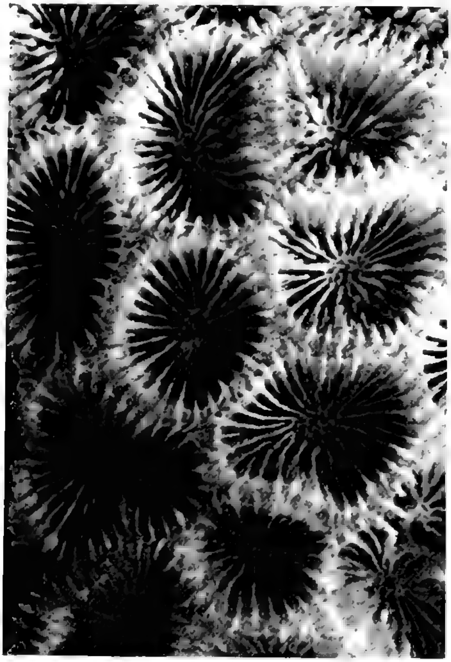
Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 47572/11a).

FIG. 2. *Favia favus* (Forskål), facies 3. This specimen was identified by Matthai as *F. bertholleti*; compare with fig. 1, and pl. 6, figs. 1, 3 which he referred to *F. favus* (Forskål) × 2.

Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 47572/12a).

FIG. 3. *Favia favus* (Forskål) with groove-and-tubercle structure. For enlarged views of certain details see pl. 2, fig. 2, pl. 3, fig. 1. The tube within the extreme lower left corallite is that of a serpulid. The two tubes in each of two central corallites appear to be analogous structures to the tubes which surround the corallites, i.e., modified dissepiments. × 2.2.

Specimen No. B.M. (N.H.) 1927.5.12.166.



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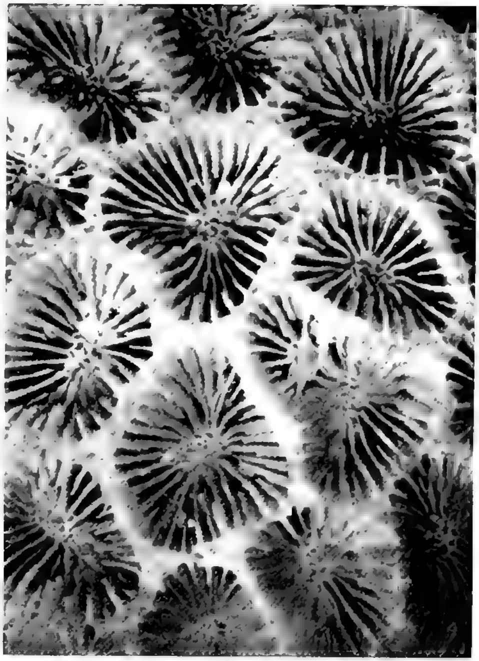

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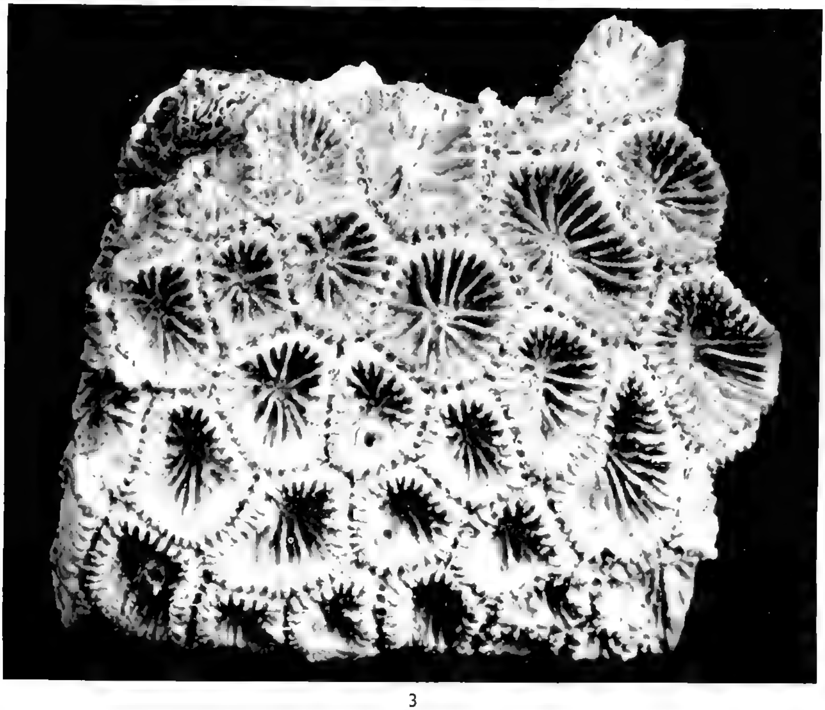


3

PLATE 6

FIG. 1. *Favia favus* (Forskål), *cavernosa*-facies. See caption to Pl. 5, fig. 1. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 47572/11b).

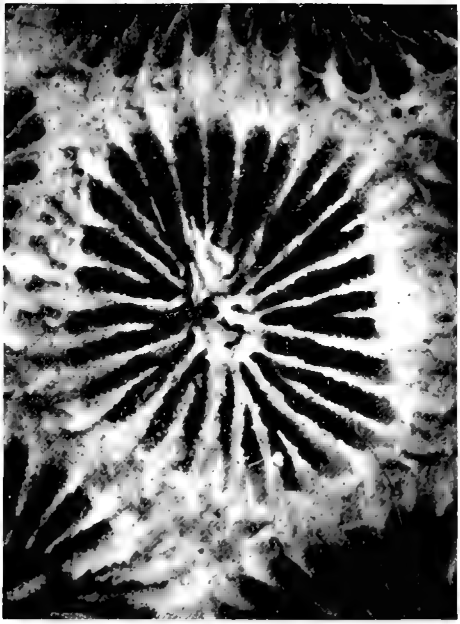
FIG. 2. *Favia favus* (Forskål, facies 3. See caption to Pl. 5, fig. 2. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 47572/12b).

FIG. 3. *Favia favus* (Forskål), *cavernosa*-facies. See caption to Pl. 5, fig. 1. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 47572/11c).

FIG. 4. *Favia favus* (Forskål), facies 3. See caption to Pl. 5 fig. 2. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 47572/12c).

3

1



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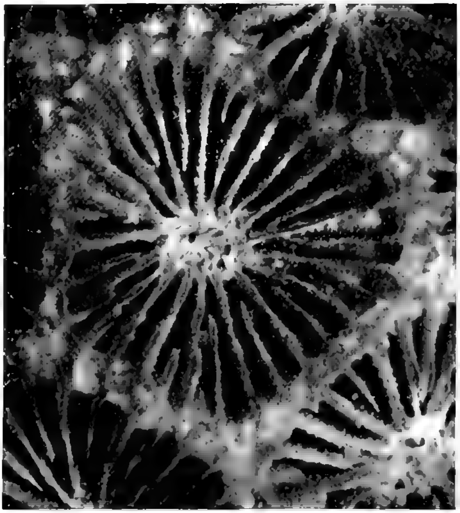
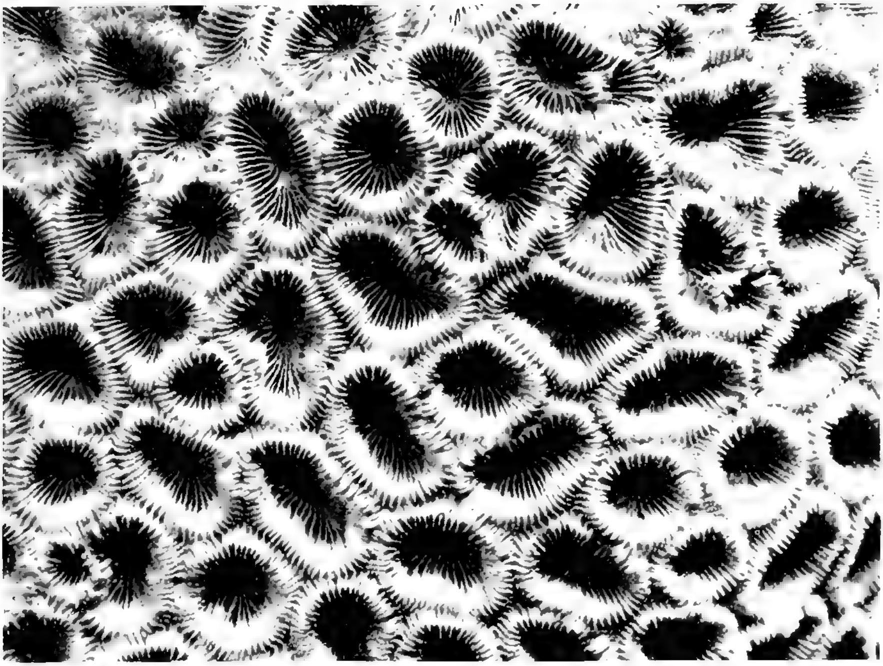


2

PLATE 7

Fig. 1. *Favia speciosa* (Dana). Compare Vaughan's (1918) figure of Dana's type. × 1.5.
Specimen No. B.M.(N.H.) 1895.10.9.133.

Fig. 2. *Favia speciosa* (Dana) showing groove-and-tubercle structure (not visible in photograph). For enlarged view of details see Pl. 1, and Pl. 2, fig. 1. × 1.3
Specimen No. B.M. (N.H.) 1892.12.1.594.



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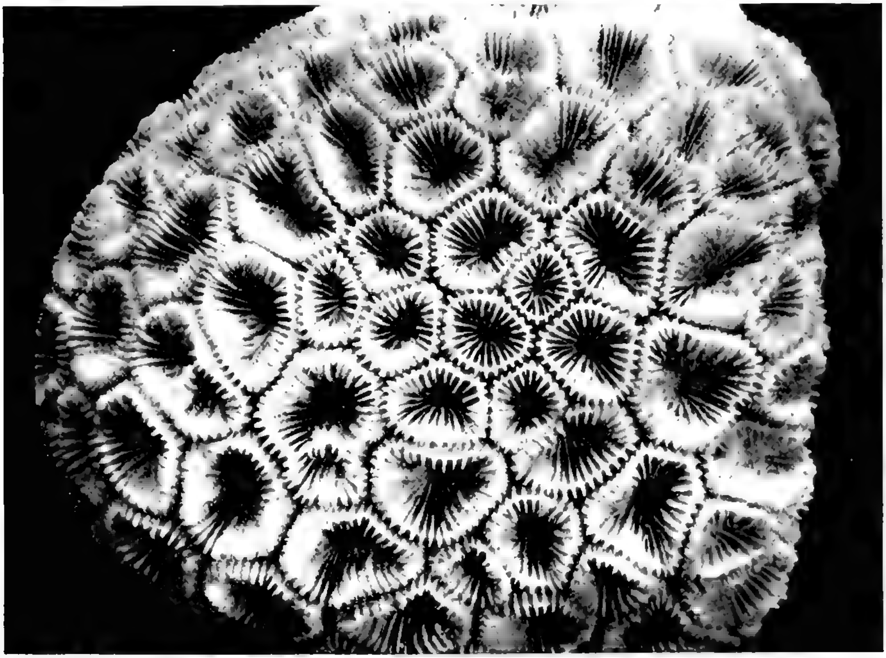
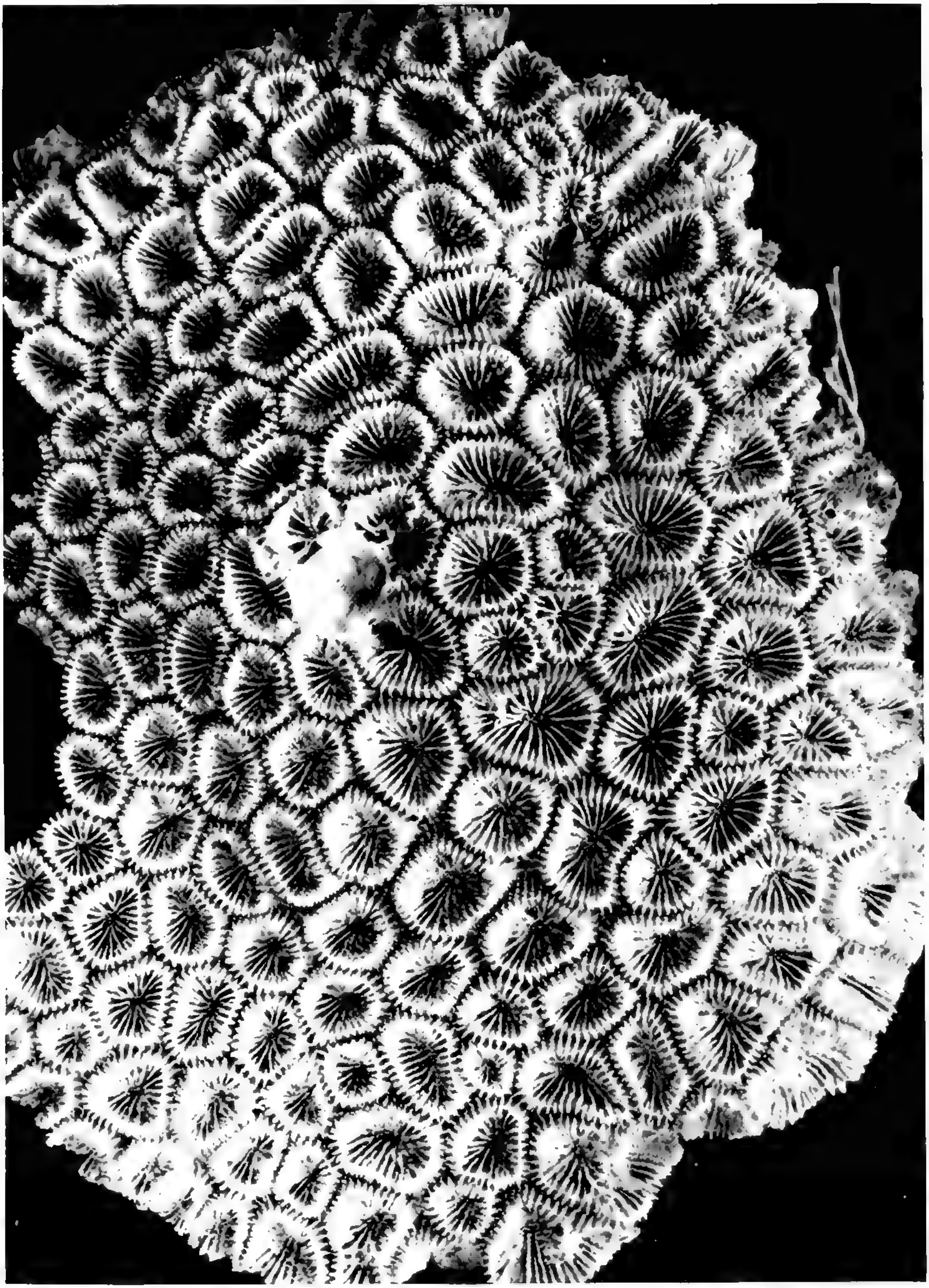


2

PLATE 8

Favia ?favus showing groove-and-tubercle structure (not visible in photograph). Corallites at the margins of the corallum (lower part of photograph) only partially exhibit the structure, as in Pl. 3, fig. 2, or do not do so at all. Elsewhere the structure is fully developed similar to that seen in Pl. 3, fig. 1. × 1.6.

Specimen No. B.M. (N.H.) 1898.12.1.12.



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SOME TYPE AND OTHER SPECIMENS OF SPECIES INVOLVED IN THE PROBLEM OF *STYLOPOMA* LEVINSEN (POLYZOA)

ANNA B. HASTINGS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 16 No. 9
LONDON: 1968

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BY

ANNA B. HASTINGS
28 Kew Gardens Road, Richmond, Surrey.

Pp. 353–364

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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SOME TYPE AND OTHER SPECIMENS OF SPECIES INVOLVED IN THE PROBLEM OF *STYLOPOMA* LEVINSEN (POLYZOA)

ANNA B. HASTINGS

CONTENTS

ABSTRACT

A lectotype is chosen for *Schizoporella errata* (Waters). *S. errata, S. longirostris* Hincks and the specimens referred to *Stylopoma spongites* by Levinsen are discussed The indications of identity given by Heller for his varieties of *Lepralia spinifera* Hassall are considered. The material to which Busk gave the manuscript name *Schizoporella spiculifera* belongs to *S. longirostris,* but Waters's publication of the name *S. spiculifera* appears to have made it an absolute synonym of *Stylopoma viride* (Thornely). Busk's specimen encrusts a sponge which was alive when collected. The specimens described by Levinsen as *Schizoporella* (*Stylopoma*) *spongites* have been examined. Large, acute avicularia, like those of *S. falcifera,* are present.

INTRODUCTION

HARMER's choice of type-specimen for *Eschara spongites* Pallas (which is strictly legal) has left problems about the status of the genus *Stylopoma* Levinsen (1909).[1]

The late Dr. H. Dighton Thomas and I prepared an application to the International Commission on Nomenclature which I have now submitted (Thomas & Hastings, 1967). It asks for suppression of all previous type-designations for *Eschara spongites* Pallas, and for the designation of Levinsen's two specimens from St. John, W. Indies (described below) as neotype and neoparatype. If these proposals be approved they will preserve the name *Stylopoma* in its currently accepted sense.

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[1] See Cheetham & Sandberg (1964 : 1031) whose statement of the type-species of *Stylopoma* Levinsen is wrong. Canu & Bassler (1920 : 359) chose: "*Stylopoma* (*Eschara*) *spongites* Pallas, 1766".

Schizoporella errata (Waters)

SYNONYMY (Mediterranean area only):
Eschara spongites Pallas, 1766 (partim) : 45.
Lepralia spinifera Busk, 1854 (partim) : 69, pl. XCI, figs. 1, 2. (Gibraltar).
Lepralia spinifera c) *L. serialis* Heller, 1867 : 104.
Lepralia spinifera d) *L. spongites* Heller, 1867 : 104.
Lepralia errata Waters, 1878, p. 11 (expl. pl.), pl. I, fig. 9.
Lepralia errata, stadium *Hemeschara* Waters, 1879 : 39, pl. X, fig. 5.
Schizoporella unicornis, Johnston : Waters, 1909 (partim) : 143, pl. XII, figs. 12, 13.
Schizoporella unicornis, var. Waters, 1909 : 144, pl. XII, fig. 11. (Synonymy in footnote, p. 145. Referred to *Eschara spongites* Pallas.)
Schizoporella unicornis (Johnston, 1847) var. *errata* Waters, 1879: Calvet, 1927 : 16.
Schizoporella unicornis Johnston: Hastings, 1927 : 336.
Schizopodrella errata. Waters, 1878 : Canu & Bassler, 1930 : 39. (*Synonymy*.)
Schizopodrella violacea. Canu & Bassler, 1930 : 40, pl. IV, figs. 1–14.
Schizoporella spongites (Pallas): Harmer, 1930 : 79, 80, pl. I, fig. 2.
Schizopodrella errata (Waters, 1878): Barroso, 1935 : 373, text-figs. 1, 2.
Schizopodrella violacea (Canu y Bassler, 1930): Barroso, 1935 : 374, text-figs. 3, 3a.
Mucronella soulieri Calvet 1902: O'Donoghue & de Watteville, 1939 : 28. (Not *M. soulieri* Calvet. See Hastings, 1966 : 75.)
Schizopodrella errata (Waters): Gautier, 1953 : 52.
Schizopodrella errata (Waters) 1879: Gautier, 1958*a* : 57.
Schizoporella errata Waters 1878: Gautier, 1958*b* : 106.
Schizoporella errata (Waters) 1878: Gautier, 1962 : 149, text-fig. 14.
Schizoporella errata (Waters): Ryland, 1965 : 64, text-figs. 31a, 31b.

DISTRIBUTION (in the Mediterranean and some neighbouring areas): E. and W. Mediterranean, Adriatic (including the Venetian lagoon), Suez Canal, Red Sea, Zanzibar.

There can be no doubt that *S. errata* has a much wider distribution than that given above, and, in particular, that some of the records of *S. unicornis* from the Atlantic coast of America are based on it, e.g.: *Schizoporella unicornis* Hastings, 1930 : 720, Colon; Marcus, 1937 : 83, Brazil; Maturo, 1957 : 49, Beaufort, N. Carolina; Shier, 1964 : 629 (part ?)[1], W. Florida.

I have examined extensive colonies on oysters collected at Charleston, S. Carolina on 24th May, 1954, lent to me by the Zoologisk Museum, Copenhagen, (labelled as *Schizoporella spongites* Pallas).

Osburn (1952 : 318, as *S. unicornis*) noted that it had not previously been recorded from " the Pacific coast of the Americas ", but he had found it to be a " rather common species in the bays where oysters from the Atlantic coast have been planted ", and that it was probably a recent introduction.

S. errata is a typical ship-fouling species (see Ryland, 1965; 1967 : 354), and records of *S. unicornis* in works on fouling are mostly based on it. In works on Polyzoan systematics it is noticeable that its growth in ports, on piles and other harbour structures, and on boats, rafts etc. is very frequently mentioned.

Dr. Ryland has drawn my attention to the fact that a figure by Marcus (1940 : 237,

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[1] Shier's description and measurements agree with *S. errata*, except that his account of large avicularia with " bulbous chambers which may be nearly as large as a zooecium " suggests an admixture of some other species.

text-fig. 121) represents *S. errata*, and has pointed out (MS) that it appears that the figure was not drawn from Danish material, and that only the form called by Marcus *S. unicornis* var. *ansata* (see Ryland, in press) is found in the Skagerrack (see Marcus, 1950 : 17).

LECTOTYPE, chosen here: H. 1186, Waters Collection, Manchester Museum. Naples 1875. One piece mounted on a slide after boiling in potash. Waters noted the absence of ovicells.

PARALECTOTYPES: Manchester Museum. Naples: two slides of chitinous parts.

OTHER WATERS MATERIAL: Two specimens mentioned by Waters in 1879 are in the British Museum. Not being mentioned in 1878, they are not syntypes. They are: 1899.5.1.1136. Specimen figured by Busk (Pl. 91, fig. 1) from the Bay of Gibraltar, the figure being cited by Waters.[1]

1955.7.20.1. Mediterranean. Specimen formerly exhibited without registered number, recognized later (and registered then) as the specimen described by Waters as " piece, about 2 inches high ".

MEASUREMENTS OF LECTOTYPE:

Basal layer.	Lz	0·43–0·60	average	0·50 mm.
	lz	0·30–0·49	,,	0·38 mm.
	Lo	0·13–0·18	,,	0·15 mm.
	lo	0·13–0·16	,,	0·14 mm.
Superficial layer.	Lz	0·55–0·80	average	0·65 mm.
	lz	0·45–0·53	,,	0·49 mm.
	Lo	0·14–0·18	,,	0·16 mm.
	lo	0·13–0·16	,,	0·14 mm.
Avicularia.	Lav.	0·12–0·16	average	0·14 mm.
	lav.	0·05–0·09	,,	0·07 mm.

These measurements, for which I am indebted to Miss Cook, are inevitably based on rather few (14) zooecia.

DESCRIPTION OF LECTOTYPE: The lectotype, kindly lent to me by the Manchester Museum, is an encrusting piece, measuring 9 × 10 mm. It consists of a regular layer of straight-sided zooecia over which two successive layers of superficial zooecia are spreading. The superficial zooecia are larger, irregular in shape and orientation, and more rounded in outline. The tremocyst in all layers has large pores, and the orifice has a broad, rounded sinus, and shows little variation in size. The avicularia are acute. They are of two kinds and sporadic in their distribution: (a) a small

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[1] Waters cited both Busk's figures (Pl. XCI, figs. 1, 2). Both figures were drawn from material from the Bay of Gibraltar (information from Busk's drawings). A specimen from the Bay of Gibraltar, McA. [McAndrew], (1899.5.1.1136, Hincks Coll., mounted by Busk) is recognizable as the original of fig. 1. It is not to be expected that the single zooecium shown in fig. 2 should be individually recognizable.

There are two other slides of Busk's Gibraltar material, both in his own collection: 1899.7.1.2413 (chitinous parts) and 1899.7.1.2392, McAnd. [McAndrew].

avicularium beside the proximal part of the orifice and directed outwards; (b) a somewhat larger avicularium, not situated in relation to a particular zooecium (Vicarious? Interzooecial? Only one seen). Unfortunately the lectotype has no ovicells.

The first superficial layer has a recognizable, though uneven, growing edge, and most of its zooecia are orientated towards this edge. Such irregularities as are present are of some interest. For example, a few zooecia are budded laterally and lie parallel to the general line of the growing edge instead of being directed towards it. Lateral budding from these has restored the normal orientation.

The second superficial layer is an irregular patch of disorientated zooecia, including two zooecia in linear series, without lateral neighbours.

Thus the lectotype shows the transition from a regular primary encrusting layer to an irregular, multilaminar encrusting growth.

OTHER MATERIAL: The erect zoarium (1955.7.20.1), cited by Waters, is similar to that figured by Gualtieri (see reproduction in Harmer, 1930, pl. I, fig. 2, and referred to *S. spongites* Pallas, see Thomas & Hastings (1967)). It is dull pinkish purple, paler towards the tips, massive and many-layered. The tubular branches may be cylindrical or flattened, sometimes widening and almost trumpet-shaped, and they branch and anastomose. Ovicells are present.

The Gibraltar specimens (particularly 1899.7.1.2392) appear superficially different, being encrusting and white, with long, straight-sided zooecia, but an incipient, irregular, superficial layer is present, with traces of pigmentation. The specimens do not differ in the shape of the orifice or the position of the avicularia, and the shape of the longer zooecia is evidently related to their forming the primary encrusting layer of a much younger colony than 1955.7.20.1.

The consideration of these type, and other, specimens examined by Waters confirms the interpretation of *Lepralia errata* given, with full descriptions, by Canu & Bassler and Gautier. It also confirms the inclusion of the species in *Schizoporella* Hincks, type-species *S. unicornis* (Johnston).

The differences between young, ancestrulate colonies of *S. unicornis* and *S. errata* are well shown in Ryland's figures (1965: text-figs. 31b and 32a; figured specimens now in British Museum, 1964.4.12.1) which conclusively settle the much debated question of whether *S. errata* is specifically distinct from *S. unicornis*.

Waters (1909 : 144) described material in which the zooecia of successive layers were exactly superimposed on those in the layer below (see also Waters, 1913 : 501–502, 504; 1918 : 15, pl. II, fig. 17; Calvet, 1927 : 18 (quoted by Canu & Bassler, 1930 : 39); Marcus, 1937 : 84; Gautier, 1958*b* : 107). This is well seen in some part of most of the multilaminar colonies of this species. There are large colonies from the Red Sea and Malta in the Museum which show it, as do material from the Suez Canal (see Hastings, 1927 : 337) and the erect specimen cited by Waters in 1879 (1955.7.20.1).

THE IDENTITY OF HELLER'S VARIETIES OF *LEPRALIA SPINIFERA*

Unpublished information from the Busk Drawings (see Hastings, 1943 : 303) has elucidated the names used by Heller (1867 : 103) for certain Mediterranean species, including *Schizoporella errata.* He recognized four forms (p. 104) and defined them as variations[1] of one species, *Lepralia spinifera* Johnston. Three of these he further defined by quoting figures by Busk and also (in two instances) by Johnston.

Heller's references are as follows:

a. *L. unicornis*, references to Johnston, [1847], pl. LVII, fig. 1, and Busk, [1854] pl. LXXX, figs. 5–7, pl. LXXXI, figs. 6–7.

Johnston's figure and the three figures on Busk's pl. LXXX were all drawn from the type-material of *L. unicornis* Johnston (Johnston Coll., 1847.9.16.174, 187, 194, Britain).

b. *L. aculeata*, references to Johnston, [1847], pl. LVII, fig. 6, and Busk, [1854], pl. LXXVI, figs. 2 and 3.

All three figures were drawn from Johnston's material of *L. spinifera* Hassall (Johnston Coll., 1847.9.16.49, Dublin Bay).

c. *L. serialis*, reference to Busk, [1854], pl. XCI, figs. 1, 2.

As noted above, under *Schizoporella errata*, these two figures were based on encrusting material of *S. errata* from the Bay of Gibraltar, and they were cited by Waters (1879 : 39) in discussing that species.

d. *L. spongites*, reference to Lamouroux, [1821], Expos. Méth., pl. XLI, fig. 3, and not to any figure by Johnston or Busk.

Heller's definition of this variety clearly indicates the massive, erect, often tubular, form, later described by Waters as *Lepralia errata*. Lamouroux's description (p. 2, *Cellepora spongites*) and figure are applicable to the same form. Heller's other varieties (a–c) are described as encrusting.

Schizoporella longirostris Hincks

Schizoporella unicornis, form *longirostris* Hincks, 1886 : 266, pl. X, fig. 2.
Schizoporella longirostris Hincks Levinsen, 1909 : 323, pl. XVIII, fig. 3a g (as *Schizoporella* (*Stylopoma*) *longirostris* Hincks in explanation of plate).
Schizopodrella longirostris Hincks 1886 Canu & Bassler, 1925 : 29.
Schizopodrella longirostris, Hincks, 1886: Canu & Bassler, 1930 ; 43, pl. IV, figs. 15–20, pl. V, figs. 1–19.
Schizoporella longirostris Hks: Marcus, 1950 : 18, text-fig. 4.
Schizopodrella longirostris (Hincks): Gautier, 1953 : 51, text-fig. 6.
Schizoporella longirostris Hincks 1886: Gautier 1962 : 151 (synonymy).
?*Lepralia ansata*, Johnst., var. *porosa*, Rss: Waters, 1879 : 32. (Not *L. ansata* var. *porosa* Reuss, 1874 : 158, pl. VI, fig. 13.)

DISTRIBUTION: Mediterranean (for details see Gautier); Atlantic coast of Morocco (Canu & Bassler); Scilly Isles (Brit. Mus.).

SPECIMENS IN HINCKS COLLECTION: Adriatic (1899.5.1.1107, as *S. unicornis* form *longicornis* [sic]; 1109, as *S. unicornis* form; 1112, as *S. unicornis* var.).

All these three slides agree with Hincks's description, and may be syntypes (Hincks often omitted to put the published name on his slides); but he stated in his

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[1] He called them " variationen " but did not treat them formally as varieties. Jelly (1889), however, lists them as such.

paper that he received his material from Pieper. The three slides were mounted by Jelly (evidence of style), and Pieper's name does not appear on them. I formerly regarded them as syntypes, and Cheetham and Sandberg (1964 : 1030), who examined the specimens, consequently referred to one of them as " holotype ". Specimens of Hincks's " normal " *S. unicornis* from the Adriatic are discussed below.

OTHER MATERIAL: Capri, 100 f. [fathoms[1]] (Bracebridge Wilson Coll., from Waters, 1897.5.1.775, as *Schizoporella unicornis*); Roche de la Madrague, Mediterranean, May, 1952 (Gautier Coll., 1960.11.2.18); Mediterranean (Gautier Coll., St. 187, 1965.9.4.11; St. 229, 1965.9.2.8; Busk Coll., as *Schizoporella spiculifera*, 4 slides as follows: 1899.7.1.2366, dry mount by Busk and preparation of chitinous parts from it by Waters; 1899.7.1.2367, from Alder; 1899.7.1.2368, preparation of chitinous parts by Busk, with a note that they were taken from " The thick massive specimen "); Naples, Gorgonian zone (Waters Coll., as *Lepralia ansata*, 1879.4.25.9); Mazarron, S. Spain (1891.5.29.4); No locality, on *Pinna rotundata* (Copenhagen Museum, as *Schizoporella spongites* Pallas. The Polyzoa are detached and no shell present). Porth Hellick, Scilly Is., 40 ft., 21st July, 1966 (University of London Subaqua Club, St. 230, 1967.8.2.17); off Great Britain Rock, Scilly Isles, 170 ft., 22nd July, 1966 (U.L. Subaqua Club, St. 288, 1967.8.2.16).

REMARKS: Gautier's description and material of *S. longirostris* agree with those of Hincks. There is some variation in the length of the sinus, reflected in the length of the tongue (vanna) of the operculum. Marcus's material had the sinus short (1950: text-fig. 4A). Further, the published figures are not consistent in the shape of the vanna (cf. Levinsen, 1909: pl. XVIII, fig. 3e; Canu & Bassler, 1930: pl. IV, fig. 18; Marcus, 1950: 17, text-fig. 4B). Levinsen's appears to be the truest representation. The shape shown in the other two figures is sometimes seen. It appears to be produced when the thinner part at the articulation has either been lost in teasing out the operculum, or become invisible in clearing and mounting.

The specimens from the Scilly Isles constitute the only record of this species from Britain. They show all the essential characters of the species, but are smaller in all dimensions than Mediterranean specimens, and more heavily calcified.

Waters (1879 : 32) recorded *Lepralia ansata* Johnston var. *porosa* Reuss from Naples. The specimen in the British Museum set of slides of Waters's Naples material (1879.4.25.9) is labelled *L. ansata* by Waters, without the varietal name. It proves to be a specimen of *Schizoporella longirostris*. As Waters did not include typical *L. ansata* in his paper, I have taken it that this slide represents his variety, and have tentatively included the name in the synonymy of *S. longirostris*. *S. ansata* sensu Hincks, as opposed to the Mediterranean species often called *S. ansata*, see Gautier (1962: 147 note; Ryland, in press), is a deep-water British form rather similar to *S. unicornis*. It is chiefly characterized by being only very obscurely porous (Hincks, 1880 : 239; Ryland, in press). Thus, the markedly porous wall of *S. longirostris* fully explains Waters's varietal name, *porosa*, for his supposed specimen of *S. ansata*.

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[1] Waters did not describe his collection from Capri as such, but he cited specimens from there in his papers, usually without stating the depth. Where I have found it given, it is in fathoms or in metres, and is considerably in excess of 100 feet. It is thus probable that here f. stands for fathoms.

The name *Schizoporella spiculifera* on the labels of some of Busk's Mediterranean slides was unpublished until Waters (1909 : 147) stated that one of these specimens belonged to *Schizoporella viridis* Thornely (1905 : 116; a species of *Stylopoma* redescribed by Harmer, 1957 : 1036). It could, perhaps, be argued that Waters's published statement made the name *spiculifera* an absolute synonym of *Stylopoma viride*, a species not known from the Mediterranean. Busk's specimens are distinct from *S. viride* (see Hastings, 1932 : 426), and clearly belong to *Schizoporella longirostris*. They encrust the surface of a sponge, and are multilaminar. The oscules of the sponge are clear of all débris, and are neatly bordered by the zooecia of the Polyzoan. Looking into the oscules the channel is also seen to be clear, and its brown spicular lining reaches to the surface of the Polyzoan colony, and ends neatly at the rim of the opening, thus having grown as successive layers of zooecia were added. In one, smaller, opening the spicular tissue projects slightly above the surface of the Polyzoan colony forming a rim, and tufts of spicules project obliquely over the opening as a bordering fringe. It is evident, from examination of the oscules and channels, that the sponge was alive when collected. The reason for Busk's choice of name is now obvious.

Hincks's supposed " normal " *S. unicornis* from the Adriatic is represented by two slides, 1899.5.1.1113 and 1114, labelled respectively *S. unicornis* and *S. unicornis* (normal); both mounted by Jelly. They certainly do not represent true *S. unicornis* (Johnston). 1899.5.1.1113 bears one piece of *S. errata*. The rest of the material (both slides) has the sinus broad and rounded, similar to that of *S. unicornis*, but the frontal avicularia are like those of *S. longirostris* in their shape and their variable position. The base of the avicularium is beside the sinus, and the mandible is directed laterally or obliquely proximally. In addition 1899.5.1.1114 has interzooecial avicularia with acute mandibles and extensive, convex tremocyst, similar to those of *S. longirostris*, but smaller. This specimen also has what looks superficially like a broad, rounded, spatulate avicularium. No opesia is, however, discernible proximally to the articulation of the supposed mandible. The tremocyst in these specimens is coarser and rougher than is usual in either *S. unicornis* or *S. longirostris*.

THE SPECIMENS DESCRIBED BY LEVINSEN AS *SCHIZOPORELLA* (*STYLOPOMA*) *SPONGITES*

The material under the name *Schizoporella spongites* in the Zoologisk Museum, Copenhagen, includes three specimens representing material mentioned in Levinsen's monograph (1909 : 324), and others that may have been examined by him. Those mentioned are:

1. St. Jean Bay, 10 Fv. [St. John, W. Indies, 10 fath.][1] Th. Mortensen. 19.12.05. Dry specimen.

2. St. Jean. [on] Arca. Spirit specimens.

3. Aor, [Malacca] Corneliussen legit. 1874. As suggested by Levinsen, this material represents a distinct species. It agrees with *Stylopoma duboisii* (Aud.), redescribed by Harmer, 1957 : 1033. Spirit specimen.

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[1] Levinsen gave the depth as 15–20 fath.

The specimen from Java, figured (operculum only) by Levinsen (1909: pl. XVIII, fig. 4d) is not in the Museum. The shape of the sinus is consistent with its having been a specimen of *Stylopoma parviporosum* Canu & Bassler (redescribed by Harmer, 1957 : 1035).

THE MATERIAL FROM ST. JOHN, W. INDIES: The dry specimen is an extensive colony on the surface of a shell. It is practically complete, with the growing edge largely intact, extensive areas of regular series of zooecia of the primary layer exposed, and a distinct development of the secondary, disorientated layer present. It has many ovicells and, in general, agrees with Levinsen's account, but has a second type of large avicularium, and rather few of the small ones. I have not seen small avicularia in any other position than beside the orifice and I have not seen any " tubercle-shaped projection proximally to the aperture".

In the primary layer, the spatulate avicularia arise as one of the paired zooecia at the start of a new series, but there are also instances when both members of the pair are autozooecia. The mandibles are a little longer in proportion to their width than that on the right in Canu & Bassler's figure (1928, pl. X, fig. 8). They are mostly directed distally, but I noted one directed proximally and one oblique mandible.

The second type of large avicularium resembles those figured in *Schizoporella falcifera* Canu & Bassler (1928: pl. X, fig. 2). It has a much raised chamber extending across two or more zooecia, and a long, slender, pointed mandible, which is strongly curved as it arches down towards the surface of the zoarium, with its point of attachment higher than its distal end. It is considerably more arched than those figured by Canu & Bassler.

The presence together of these two types of avicularia confirms Osburn's (1940 : 424) treatment of Canu & Bassler's two forms as conspecific. The agreement of the measurements given by Canu & Bassler should also be noticed.

The spirit material from St. John agrees in general with the dry. It has spatulate avicularia in both the regular and irregular layers, those in the regular layers being at the bifurcation of the series. Large, pointed avicularia have not been seen. Ovicells are present. The material is labelled " Arca ", presumably indicating the substratum, but it is now unattached. The largest specimen has basal irregularities which suggest loose attachment to an irregular surface. There are round openings through the zoarium which appear to have been caused by an underlying organism (possibly burrowing in the shell?).

The synonymy and distribution of " *Stylopoma spongites* " Levinsen are given by Cheetham & Sandberg (1964 : 1031).

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ADDENDUM

Part of the specimen of *S. errata*, 1955.7.20.1, is in the Department of Invertebrate Zoology, U.S. National Museum, catalogue number 9528.

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The page numbers of the principal references and the new taxonomic names are printed in **bold** type

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