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A.
D.

PRIMITIVE CRYPTOSTIGMATID
MITES FROM RHODODENDRON
FORESTS IN THE NEPAL HIMALAYA



J. G. SHEALS

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BY

J. G. SHEALS

British Museum (Natural History)

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Issued August, 1965

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PRIMITIVE CRYPTOSTIGMATID MITES FROM RHODODENDRON FORESTS IN THE NEPAL HIMALAYA

By J. G. SHEALS

INTRODUCTION

THIS report forms the first of a series on the soil- and litter-dwelling Acari collected by the British Museum (Natural History) Expedition to East Nepal 1961-62. A full account of this expedition with details of the localities examined is given by Sheals & Inglis (1965). In spite of the outstanding biogeographical interest of the Himalayan region as a complex transitional zone, very little attention has been paid to the soil and litter fauna of the area. In so far as the Acari are concerned, small collections were made in 1954 by the British Museum (Natural History) Expedition to West Nepal. Some of this material has been utilized in revisionary studies (Hyatt 1956, Evans & Hyatt 1958, 1960), but apart from these no account of the Himalayan free-living mites appears to have been published since the report on a collection of Oribatidae from the Sikkim Himalaya by Pearce (1906).

The present paper is concerned with the taxonomy of the *Oribatei Inferiores* from Rhododendron forest soil and litter in four localities in East Nepal: a large forest of tree Rhododendrons (mainly *R. arboreum*) on the slopes of the Milke Danra ridge, 27° 19' N 87° 31' E, altitude 9,300-11,000'; an area of dwarf Rhododendron at Topke Gola, 27° 38' N 87° 35' E, altitude 12,500-13,000'; an area of tree and bush Rhododendron (mainly *R. arboreum*) at Selap, 27° 38' N 87° 49' E, altitude 10,100-10,300' and thickets of bush Rhododendron (mainly *R. arboreum*) on the crest of the Singalila ridge near Sandakphu, 27° 06' N 88° 01' E, altitude 12,000'. The higher Cryptostigmata and other mites from these localities will be dealt with in later papers.

In the descriptions the setal nomenclature used in the later works of Grandjean has been followed except in the case of the Nothroidea where it is convenient to follow the system used by Sellnick & Forsslund (1955). The type material is deposited in the British Museum (Natural History).

Family **ACARONYCHIDAE** Grandjean, 1932

*Himalacarus chimalae*¹ gen. et sp. nov.

ADULT. The prodorsum (figs. 1 & 2) is approximately 160 μ long and 140 μ wide at the broadest point level with the sensilli. There is a prominent obliquely projecting rostral protuberance (the naso of Grandjean, 1958) below which a bilobed eye such as Grandjean (op. cit.) has noted for other members of this family can easily be discerned. The rostral setae (ro) are stout, prominent, quite smooth and about 80 μ in length while the lamellar setae (la) are barbed and about 95 μ in length. The interlamellar setae (in) and the exobothridial setae (xi) are barbed and about 130 μ in length, while the exobothridial setae (xs) are short (approx. 30 μ long), smooth

¹From the Nepali *chimal* - certain tree Rhododendrons

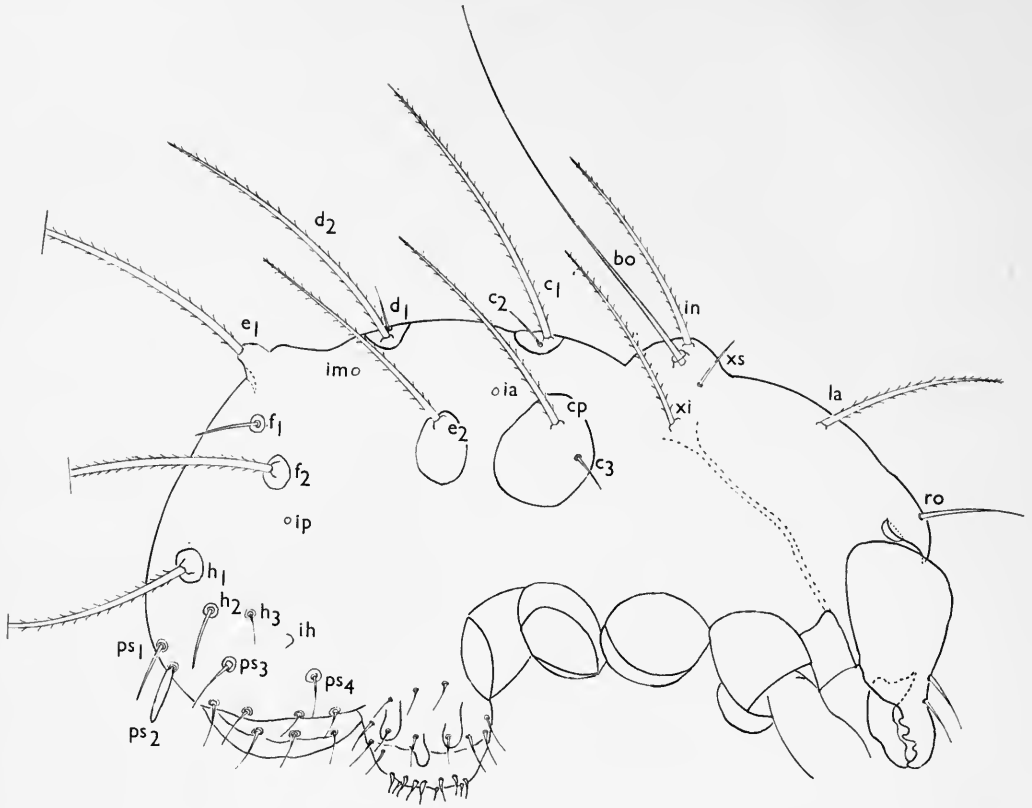
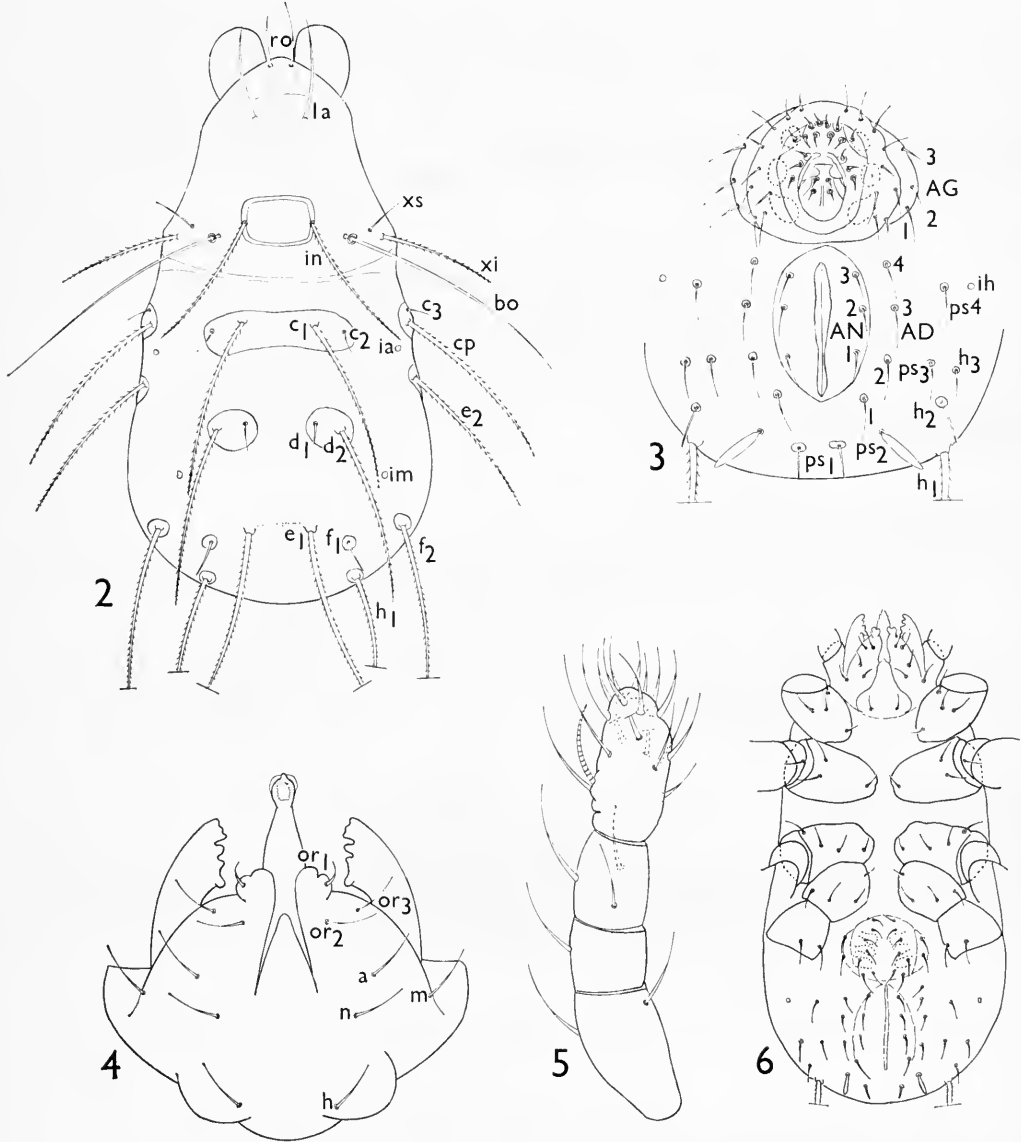


FIG. 1. *Himalacarus chimalae* gen. et sp. nov. Adult lateral.

and rather blunt. The sensillus (bo), 185–190 μ long, is quite smooth and tapers gradually to a fine point. A rectangular design evidently formed by a thickening of the cuticle can be discerned between the interlamellar setae; this is almost identical in form to the system of 'chitinous nervures' (false lamellae) described by Grandjean (1952) for *Stomacarus tristani*.

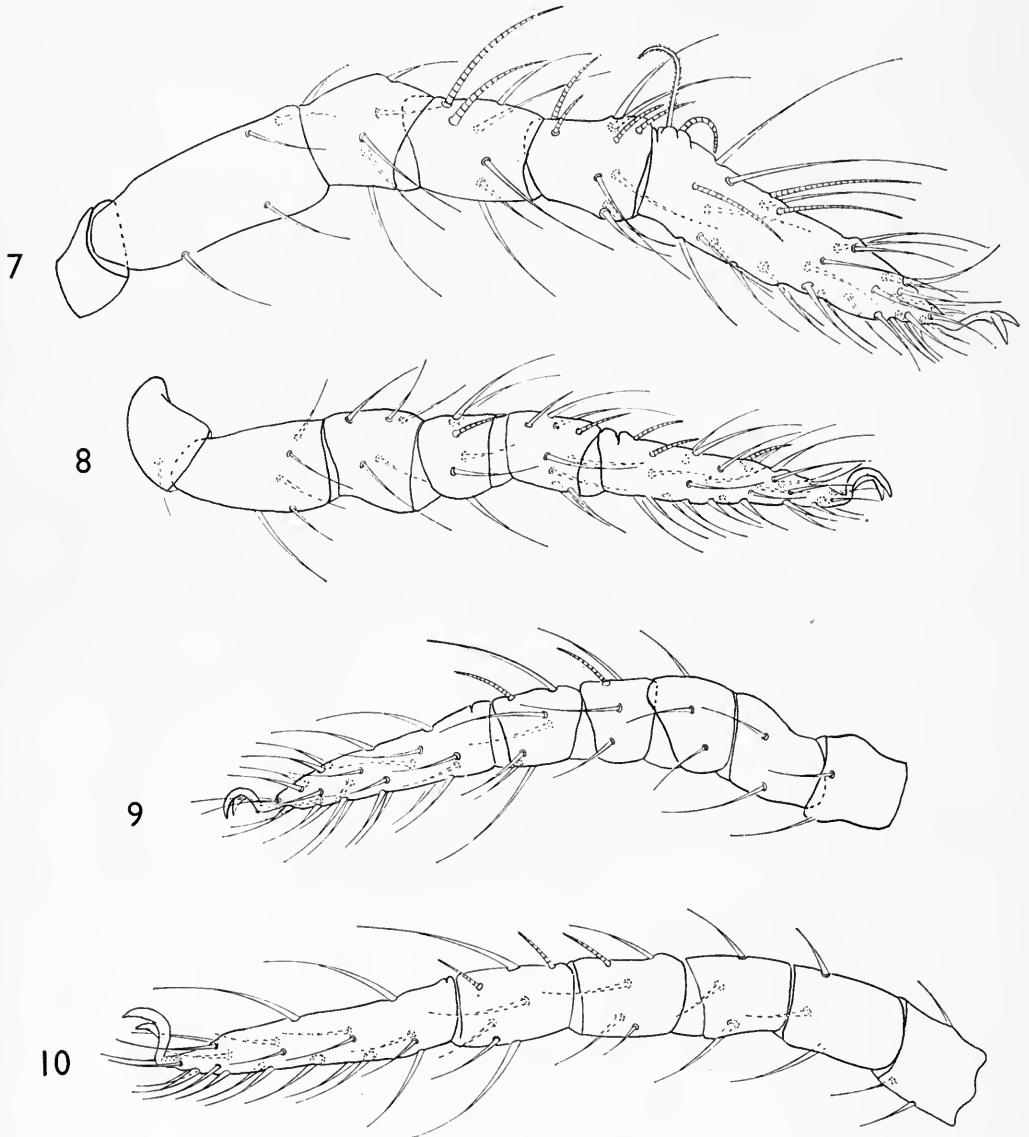
The hysterosoma is about 175 μ in length and approximately 170 μ wide at the broadest point level with setae e_2 . The 'asthenique zone' between the posterior border of the propodosoma and the median dorsal sclerite is very short. There are 17 pairs of setae in the gastronotal series. Setae c_1 , cp, d_2 , e_1 , e_2 , f_2 and h_1 are long, barbed, dark brown in colour and arise from tubercles, those of setae e_1 being particularly prominent. An internal thickening such as Grandjean (1952, 1952a, 1957) has observed for *Stomacarus*, *Archeonothrus* and *Andacarus*, respectively, can be seen below the tubercle of e_1 . Difficulty was experienced in securing specimens with completely undamaged setae but it would appear that the long barbed setae c_1 , c_2 , cp, d_2 and e_2 are about equal in length (i.e. about 170 μ) while the barbed setae f_2 and h_1 may be slightly longer than the total length of the idiosoma. Setae c_1 and the

short smooth c_2 lie together on a median dorsal sclerite, while setae d_2 and the short smooth d_1 lie together on paired sclerites. The remaining gastronotal setae, with the exception of e_2 , are borne individually on small sclerites. Setae f_1 and those of the ps and h series are short, smooth and simple, with the exception of setae ps₂ which are shaped like spear-heads. Setae ps₁ and h₂ are rather blunt.



FIGS. 2-6. *Himalacarus chimalae* gen. et sp. nov. Fig. 2. Adult, dorsum. Fig. 3. Adult, ano-genital region. Fig. 4. Adult, infracapitulum. Fig. 5. Adult, palp. Fig. 6. Tritonymph, venter.

The ano-genital region is shown in fig. 3. There are 3 setae in the anal series (AN) and 4 in the adanal (AD). All these setae lie individually on small sclerites. There are 9 pairs of genital setae and 3 pairs of aggenitals (AG). The 10 pairs of eugenital setae are all approximately similar in size and shape and it is suspected that all the adults collected were males. The coxisternal region is essentially similar to that of the tritonymph (fig. 6), the setal formula being (4-3-4-4).



FIGS. 7-10. *Himalacarus chimalae* gen. et sp. nov. Adult, legs.
 Fig. 7. Leg I. Fig. 8. Leg II. Fig. 9. Leg III. Fig. 10. Leg IV.

The infracapitulum is shown in fig. 4. There are four oral lips and in comparison with other members of the family the lower lip is particularly large and easily seen. The upper lip is also prominent and bears on its under surface a series of minute denticles forming an inverted U-shaped pattern. The three pairs of adoral setae are simple, the anterior pair (or_1) being shorter than the other two. The chelicerae have the characteristic 'ornithocephaline' outline common to other members of the family and carry two setae dorsally. Their fixed digits bear three prominent teeth and the movable digits only two ill-defined shallow projections. The five-segmented palp (fig. 5) has the setal formula (0-2-1-3-18). The solenidion of the palp-tarsus is borne on a prominence immediately distal to the lyriform fissure and of the 18 setae on this segment, 9 are eupathidia.

The legs (figs. 7-10) are relatively stout and robust, legs I and IV being markedly longer than II and III. All the femora are divided. The setal formulae are: I (0-[4-6]-5-6-31); II (1-[5-5]-5-7-27); III (2-[2-3]-3-6-26); IV (3-[3-3]-4-5-23), and the formulae for the solenidia are:— I(2-4-4); II (1-2-3); III (1-1-0) and IV (1-2-0). On tarsus I the famulus, which is slender and ciliated, lies on a small prominence between the lyriform fissure and the proximal solenidion. Of the 31 setae observed on this segment at least 9 can be distinguished as eupathidia. As in *Acaronychus*, only the pleural setae on tarsus II are eupathidial.

On all four legs the ambulacrum has two well-developed lateral claws. A minute blunt central element can also be distinguished but this is evidently very much less developed than in other *Acaronychid* genera.

TRITONYMPH. The number and disposition of dorsal setae are essentially similar to those of the adult. Ventrally (fig. 6) the anal and coxisternal regions are similar to those of the adult although in the figured specimen only 3 adanal setae were present on one side. There are 7 genital and 2 aggenital setae.

The setal formulae for the legs are I (0-(4-6)-5-6-27), II (1-(3-5)-5-7-21), III (2-(1-3)-3-6-21); IV (3-(1-3)-4-5-17). The formulae for the solenidia are the same as those for the adult.

OTHER STAGES. Unknown.

SYSTEMATIC POSITION

The Palaeacaroida, now comprising 11 genera, were first recognised as a group by Trägårdh (1932) who considered they should constitute a separate sub-order of the Acari—the Palaeacariformes. A few months later, however, Grandjean (1932) failed to confirm Trägårdh's observation of the presence of mandibulatory stigmata and concluded that the group should be incorporated with the Oribatei. In 1954, Grandjean considered the group should be regarded provisionally as a super-family—the Palaeacaroida—comprising three distinct families, the *Acaronychidae* (=Archeonothridae), *Palaeacaridae* and *Ctenacaridae*.

Himalacarus shows obvious affinities with the four genera, *Acaronychus*, *Stomacarus*,

Andacarus and *Archeonothrus* which comprise the family Acaronychidae in so much as it possesses all the family attributes listed by Grandjean (1954), namely:

1. A 'naso' and its associated inferior protuberance.
2. A gastronotal series of 34 setae, the long dorsal setae being darkly pigmented.
3. No large asthenique zone.
4. A short hysterostoma without large mediodorsal and pygidial shields.
5. Normal genital papillae and unmodified anterior genital setae.
6. Four oral lips.
7. The anterior adoral setae being much shorter than the other two pairs.
8. A large rounded palp tarsus with 16-19 setae of which 9 are eupathidia.
9. A mandible with an 'ornithocephaline' outline.
10. A first tarsus with a large erect famulus implanted close to the lyriform fissure.

Grandjean further recognised two sub-families, the Archeonothrinae for the 3 genera *Archeonothrus*, *Stomacarus* and *Andacarus*; and the Acaronychinae for the single genus *Acaronychus*. He separated the Archeonothrinae on the basis of their non-claviform famulus and normal female eugenital setae and on the presence of 2 aggenital setae, false lamellae and small internal apophyses at the bases of setae e_2 . The Acaronychinae were characterised by the absence of internal apophyses and false lamellae and by the presence of a dilated famulus, 3 aggenital setae and, in the female, swollen claw-like eugenital setae. However, Grandjean later (1957) observed that the female of *Stomacarus macfarlani*, the species which was subsequently made the type of *Andacarus* (Grandjean 1958a), had claw-like eugenital setae so that this feature had to be abandoned as a sub-familial character.

Although having 3 aggenital setae, *Himalacarus* shows greater overall similarity to the Archeonothrine genera than to *Acaronychus*, thus the number of aggenital setae must also be eliminated from the list of sub-familial features, and, with the reduction of the number of diagnostic sub-familial attributes to two, it might be preferable to consider the family as a single relatively homogenous group. In table 1, the condition of the genera in relation to the main characters which have been used in their classification is summarized.

Since the main part of this account was prepared, Balogh and Csiszár (1963) have published a description of *Stomacarus longicaudatus* from South Argentina. Judging by the figure of the dorsum this species appears to be very close to *H. chimalae* and is probably congeneric with it. It can be noted that in *S. longicaudatus* the dorsal setae d_1 and f_1 are comparatively long and barbed whilst in *H. chimalae* these setae are shorter and smooth.

MATERIAL. *H. chimalae* occurred only in the samples from the Milke Danra forest taken on 2nd December 1961. In all about 40 specimens were collected of which 15 were adult, apparently all males, the remainder being tritonymphs. The greater

TABLE I. THE DISTRIBUTION OF CHARACTER STATES IN THE ACARONYCHIDAE

	<i>Acaronychus</i>	<i>Stomacarus</i>	<i>Andacarus</i>	<i>Archeonothrus</i>	<i>Himalacarus</i>
Lower lip	Very small	Large	Large	Large	Very large
Famulus	Dilated	Slender	Slender	Slender	Slender
Internal apophyses of setae e ₁	Absent	Present	Present	Present	Present
False lamellae	Absent	Present	Present	Present	Present
No. of aggenital setae	3	2	2	2	3
Eugenital setae of female	Swollen, claw-like	Normal	Swollen, claw-like	Normal	?
Setae ps ₂	Spearlike	Slender	Slender	?	Spearlike
Median post-anal sclerite bearing setae h ₁ , h ₂ , ps ₁ & ps ₂	Absent	Absent	Absent	Present	Absent
Setae c ₁ , c ₂	c ₂ on separate paired sclerites	All on single median sclerites	All on single median sclerite	All on single median sclerite	All on single median sclerite
Setae e ₁ , f ₁ , f ₂ : number of associated paired sclerites	3	3	2 (f ₁) (f ₂ , e ₁)	1	3
Long dorsal setae	Barbed	Smooth	Barbed	Barbed	Barbed

part of the material was collected in the shallow litter layer but a few specimens were found in the underlying mineral soil.

Holotype (1964.5.27.1) and four paratypes (1964.5.27.2-5).

Family **PARHYPOCHTHONIIDAE** Grandjean, 1932

Parhypochthonius aphidinus Berlese

Parhypochthonius aphidinus Berlese, A. 1904. *Redia* 2: 25.

Parhypochthonius sp. Grandjean, F. 1934. *Bull. Mus. Hist. nat. Paris* (2) 6: 423.

The true identity of Berlese's *aphidinus* appears to be doubtful although it seems most probable that the *Parhypochthonius* species described in detail by Grandjean (op. cit.) is conspecific with this. A single specimen agreeing well with Grandjean's description was recorded from Selap.

Family **HYPOCHTHONIIDAE** Berlese, 1910

Hypochthonius rufulus Koch

Hypochthonius rufulus Koch, C. L. 1836. *Deutsch. Crust. Myr. Arach. Fasc.* 3 t.19.

This common species has a wide holarctic distribution having been recorded from Europe and North America (van der Hammen, 1959) and from Japan (Aoki, 1959). *H. rufulus* occurred in small numbers in the Topke Gola forest but was not recorded from the other localities.

Family **ENIOCHTHONIIDAE** Grandjean, 1947

Eniochthonius minutissimus (Berlese)

Hypochthonius minutissimus Berlese, A. 1904. *Redia* 1: 252.

Hypochthonius pallidulus, Michael, A. D. 1888. *British Oribatidae* 2: 536.

The type locality is Florence and Michael found this species at the roots of ground mosses in Epping Forest. *E. minutissimus* appears to be widely distributed in Europe and in Nepal was found in all localities except Sandakphu. It was most abundant in the Selap forest.

Family **COSMOCHTHONIIDAE** Grandjean, 1947

Cosmochthonius lanatus (Michael)

Hypochthonius lanatus Michael, A. D. 1885. *J. roy. micr. Soc.* (2) 5: 396.

The Nepalese material has been compared with specimens in the Michael collection. Tarsi I are bidactylous while tarsi II-IV are tridactylous and as van der Hammen (1952) has pointed out, Michael was in error when he figured the legs as being monodactylous. Michael collected most of his material from an old thatched roof in Cornwall and considered the species to be uncommon. However, it appears to be widely distributed in soil and litter in Europe and in Nepal was found in all the 4 localities sampled.

Family **PHTHIRACARIDAE** Perty, 1841***Phthiracarus robertsi*** sp. nov.

ADULT. The aspis (figs. 11 & 12) ranges in length from about 320–480 μ and is approximately 1.4 times as long as its greatest width immediately behind the sensilli. All the prodorsal setae are weak. The sensillus is distinctly elbowed near the base; proximally the basal portion is slender while at the elbow the sensillus thickens abruptly before tapering gradually to a fine point. There are distinct lateral ridges as well as a very pronounced broad median crest while behind the bothridium the integument is raised into a series of longitudinal corrugations.

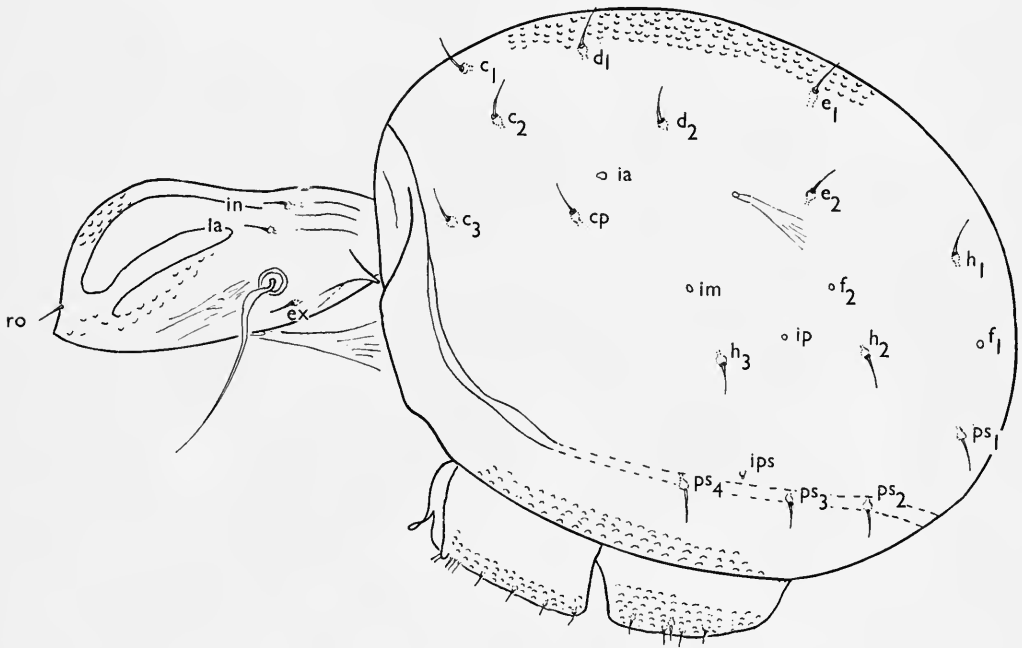
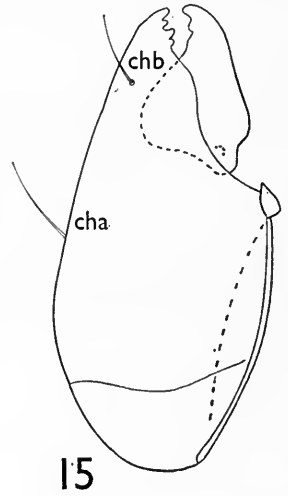
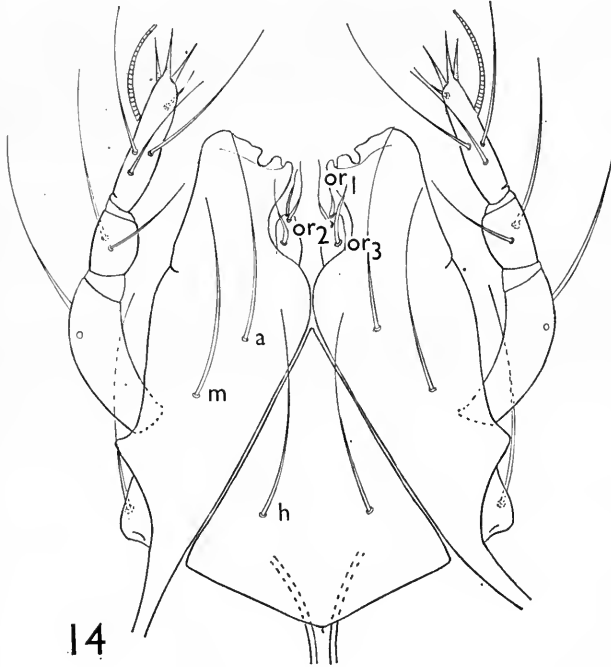
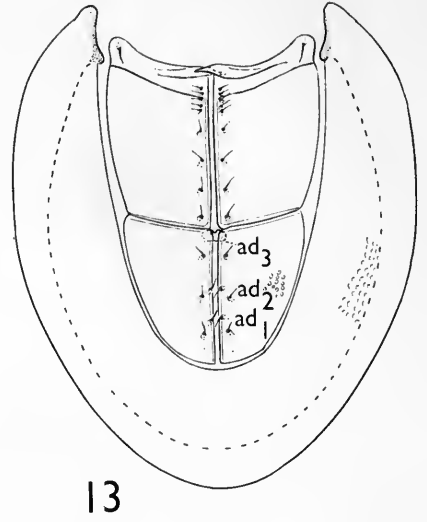
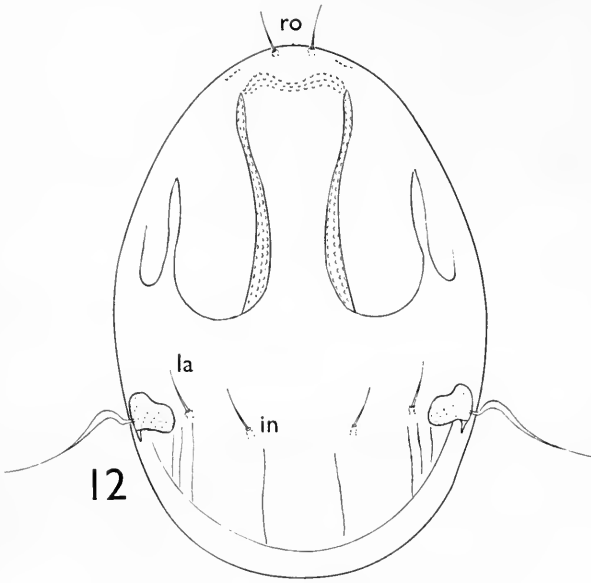
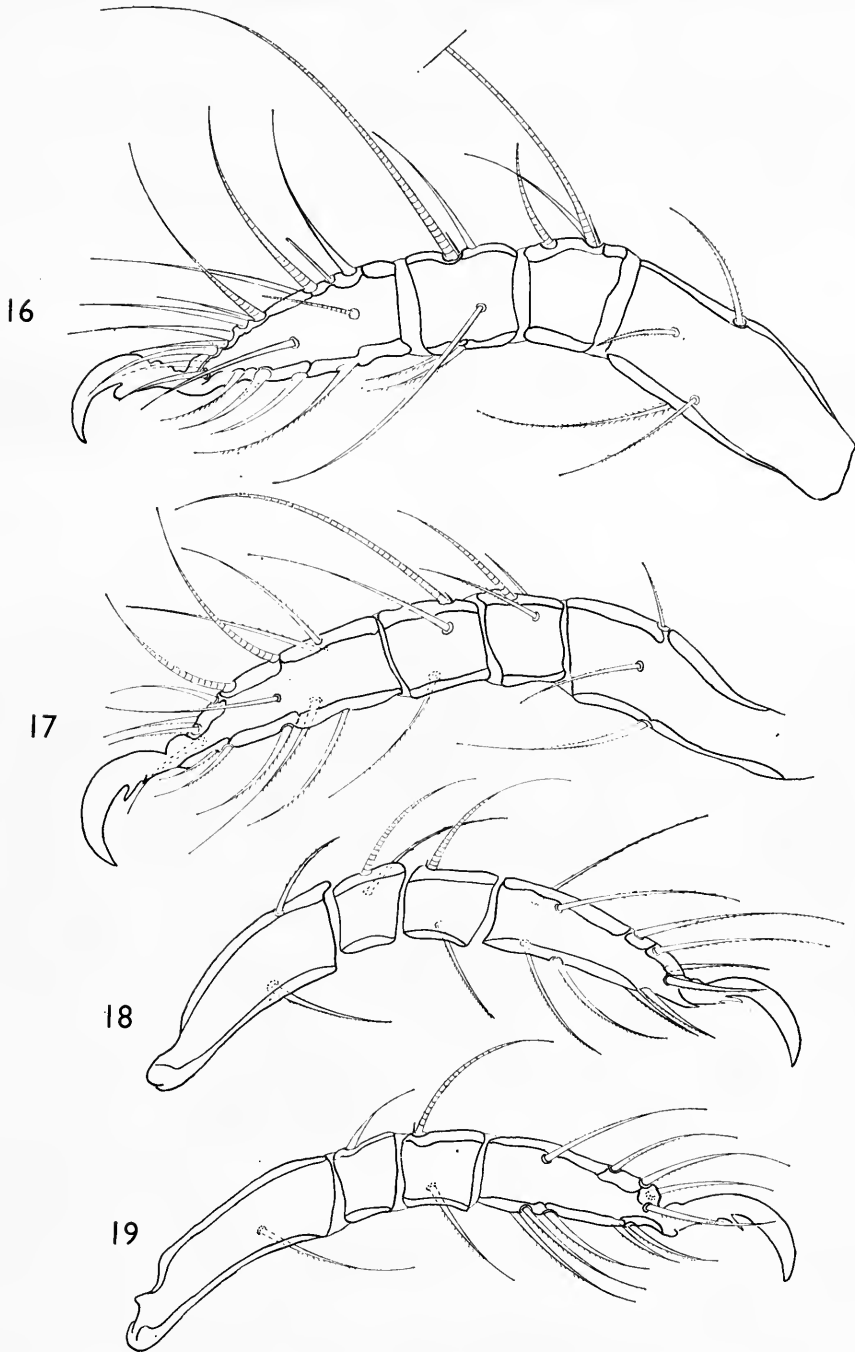


FIG. 11. *Phthiracarus robertsi* sp. nov. Lateral.

Along the line c_3 – h_1 the notogaster ranges in length from approximately 475–830 μ . It is highly arched and, excluding the vestiges of f_1 and f_2 , carries 15 pairs of very weak short setae. The fissures ia , ip and ips are well marked as also is the muscle insertion point anterior to seta e_2 . The notogastral integument is distinctly pitted. The ano-genital region is shown in fig. 13. There are five setae on each anal valve and of these, two, evidently belonging to the anal series, are quite distinctly located nearer the median border than the other three. All the anal and adanal setae are very fine but equally well developed—cf. van der Hammen (1963 a) for *P. laevigatus* (Koch). There are nine genital setae and a single aggenital seta. All the genital setae are marginal and the anterior five setae are inserted more closely together than the posterior four.



FIGS. 12-15. *Phthiracarus robertsi* sp. nov. Fig. 12. Aspis
 Fig. 13. Ano-genital region. Fig. 14. Infracapitulum. Fig. 15. Chela.



FIGS. 16-19. *Phthiracarus robertsi* sp. nov. Legs, excluding trochanters.
Fig. 16. Leg I. Fig. 17. Leg II. Fig. 18. Leg III. Fig. 19. Leg IV.

The infracapitulum is shown in fig. 14. The mentum is sub-trapezoidal in outline and carries a single pair of long smooth setae while each gena carries two pairs of similar setae. The three pairs of adoral setae are smooth and slightly sinuous. The three-segmented palp has the formula (2-2-7) and of the tarsal setae, three are eupathidia. The chelicerae are shown in fig. 15. The fixed digit has three teeth and the movable digit carries only a single tooth. Seta chb is located well down on the anti-axial face, while seta cha is dorsal.

The legs are shown in figs. 16-19. The solenidia of the tarsi are all free, while on each tibia the solenidion is coupled with a minute dorsal seta as also is the proximal solenidion on genu I. The solenidion on tibia 1 extends beyond the tip of the tarsus and the solenidion on genu 1 is about the same length as leg I. All the legs are mono-dactyl and the formulae for the setae and solenidia are as follows:—

I (1-4-2-5-15) and (2-1-3); II (1-3-2-3-12) and (1-1-2);

III (2-2-1-2-10) and (1-1-0); IV (2-1-1-2-10) and (0-1-0).

This species is of some interest as the arrangement of setae on the anal valves approaches the condition commonly associated with species of *Steganacarus*. This species is dedicated to Lt. Colonel J. O. M. Roberts M.C., formerly Military Attaché, British Embassy, Kathmandu, in appreciation of his assistance to the East Nepal Expedition.

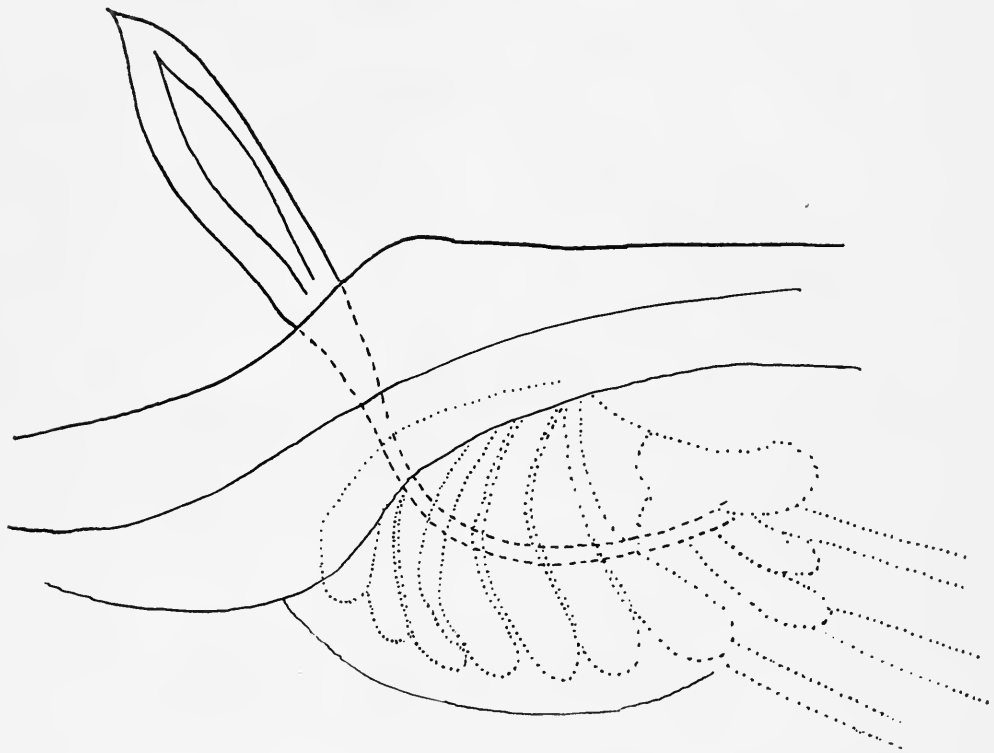


FIG. 20. *Phthiracarus* cf. *laevigatus* Koch. Sensillus of Nepalese specimen.

MATERIAL. Holotype (1964.6.19.1) and five paratypes (1964.6.19.2-6) Milke Danra, 24.xi.61. This species was not abundant and was recorded only from the Milke Danra forest.

***Phthiracarus* cf. *laevigatus* (Koch)**

Hoplophora laevigata Koch, C. L. 1841. *Deutsch. Crust. Myr. Arach. Fasc.* 38 t.16.

Phthiracarus laevigatus, van der Hammen, L. 1963. *Acarologia* 5: 704.

Six specimens evidently referable to this species were taken at Sandakphu. The material agrees reasonable well with van der Hammen's redescription but the form of the sensillus in the Nepalese specimens (fig. 20) appears to differ slightly. In the Nepalese material the first adoral seta is feathered, a feature not mentioned by van der Hammen.

***Hoplophthiracarus nepalensis* sp. nov.**

ADULT. The aspis (figs. 21 & 22) ranges in length from about 215-290 μ and is approximately 1-2 times as long as its greatest width immediately behind the sensilli. The rostral (ro), lamellar (la) and exobothridial (ex) setae are short and simple, while the interlamellar setae (in) are stout, feathered apically, nearly erect, and about three times as long as the rostrals. The sensilli are elbowed and taper gradually to a fine point with slight apical feathering. The prodorsal integument is coarsely pitted and behind the sensilli is raised into a series of low longitudinal ridges.

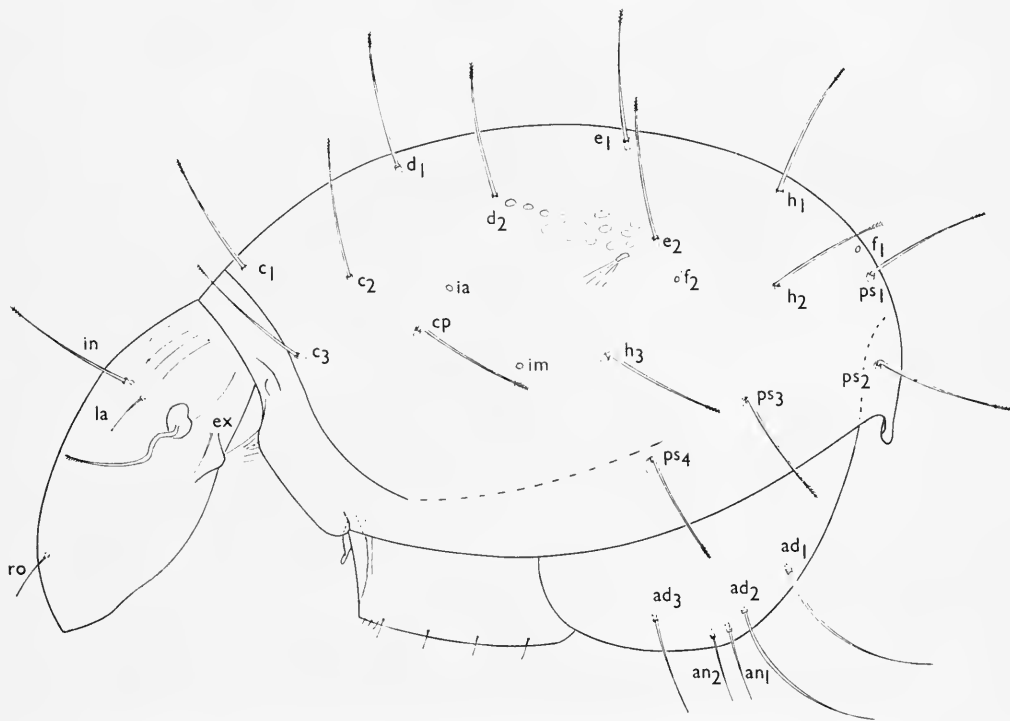
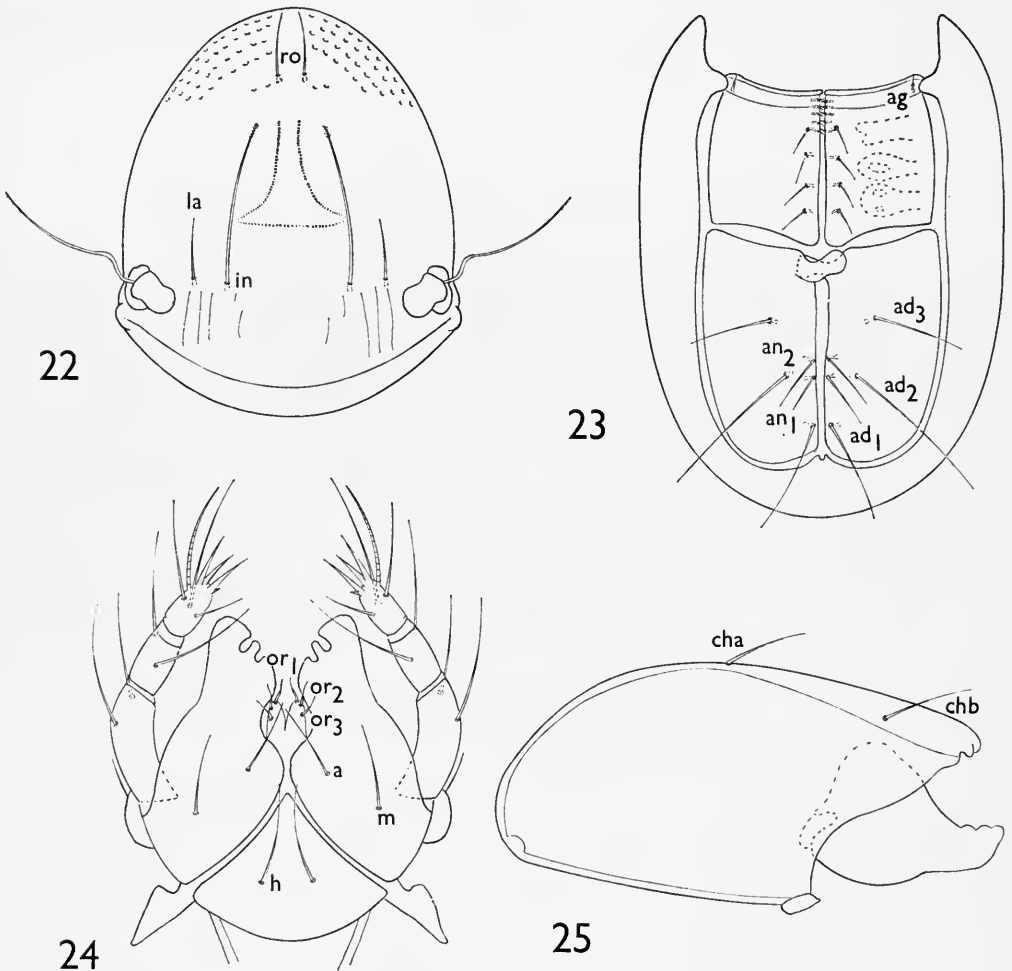
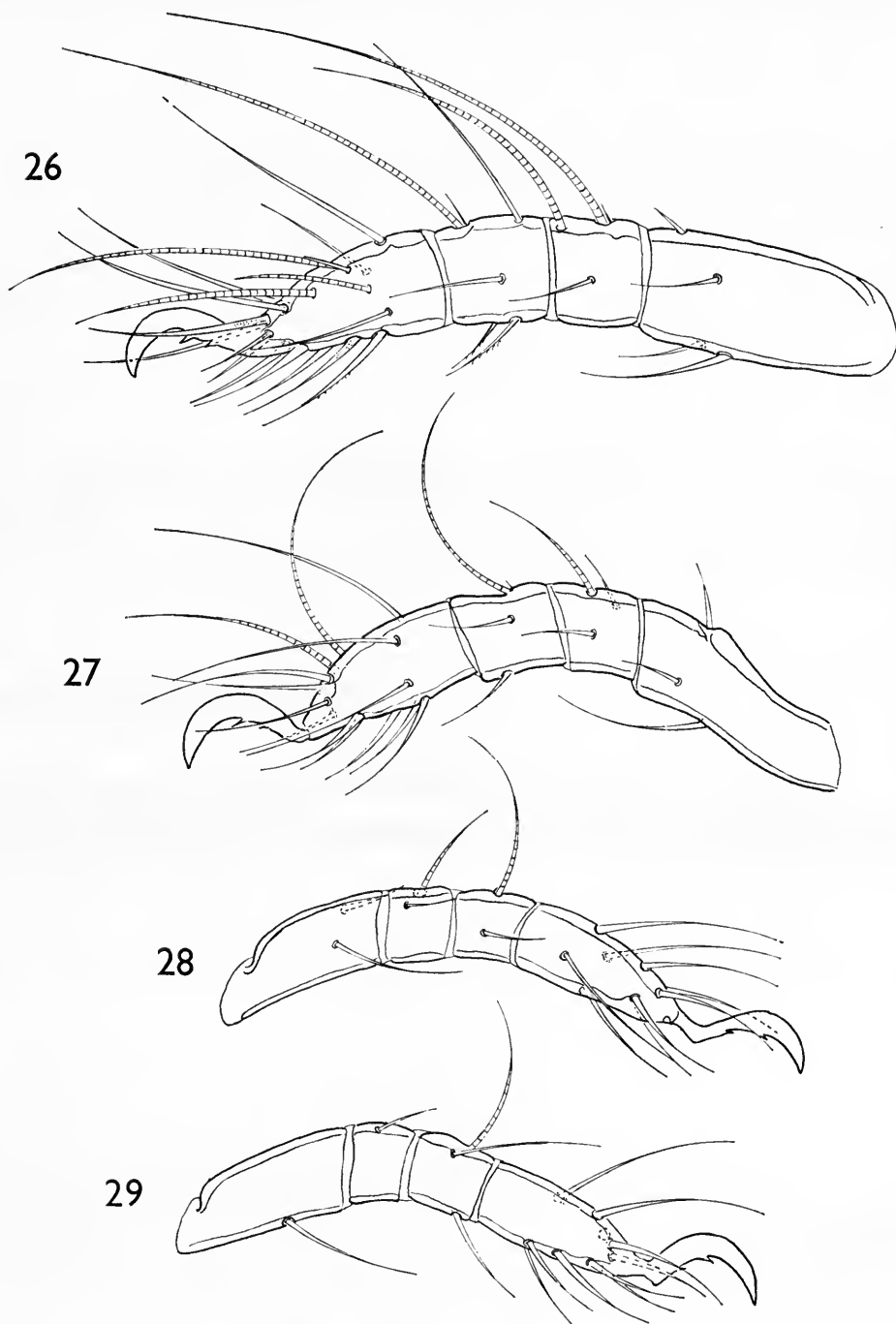


FIG. 21. *Hoplophthiracarus nepalensis*. sp. nov. Lateral.

Along the line c_3 - ps_1 , the notogaster ranges in length from about 330–500 μ , and, excluding the vestigial f_1 and f_2 there are 30 setae in the notogastral series. All the notogastral setae are strong, nearly erect, weakly feathered apically and about equal in length. Only the fissures ia and im could be discerned. The notogastral integument is coarsely pitted, the margins of the pits being irregular. Ventrally (fig. 23) the anal valves have prominent antero-median overlapping lobes, the right overlying the left. The two anal setae are marginal and comparatively long while the three adanal setae form an oblique row, the longest in the series being ad_2 , which is approximately 2–5 times as long as the anal setae. There are nine pairs of genital setae and a single pair of aggenitals. The posterior four pairs of genital setae are comparatively long and situated in a line somewhat remote from the margin, whilst the anterior five



FIGS. 22–25. *Hoplophthiracarus nepalensis* sp. nov. Fig. 22. Aspis. Fig. 23. Ano-genital region. Fig. 24. Infracapitulum. Fig. 25. Chela.



FIGS. 26-29. *Hoplophthiracarus nepalensis* sp. nov. Legs, excluding trochanters.
Fig. 26. Leg I. Fig. 27. Leg II. Fig. 28. Leg III. Fig. 29. Leg IV.

pairs are minute and marginal. There are three pairs of genital papillae, the anterior papillae being rather small (cf. van der Hammen 1963, p. 314 for *H. pavidus* Berlese which has only two pairs of genital papillae). The ornamentation of the integument of the genital and anal valves is similar to that of the notogaster.

The infracapitulum is shown in fig. 24. The mentum is subtrapezoidal in outline and carries a pair of long simple setae (h). The genae carry two pairs of setae (a & m); setae m being about 1.5—2 times as long as setae a. There are three pairs of simple adoral setae. The three-segmented palp has the setal formula (2-2-7) and at least three of the tarsal setae are eupathidial. The minute dorso-anterior seta appears to be discrete and may be eupathidial. The chelicerae are shown in fig. 25.

The legs are shown in figs. 26-29. It is interesting to note that the solenidion on genu I and the solenidia on tibiae I-III are coupled with minute dorsal setae, while the solenidion on tibia IV is free. This condition also appears to obtain in *H. pavidus* (Berlese), (van der Hammen 1963). All the legs are monodactyl and the formulae for the setae and solenidia are as follows:

I (1-4-2-5-15) and (2-1-3); II (1-3-2-3-12) and (1-1-2);
III (2-2-1-2-10) and (1-1-0); IV (2-1-1-2-10) and (0-1-0).

H. nepalensis appears to be very similar to *H. robustior* Jacot which was taken from second growth pine at Pensacola, Florida, U.S.A. Jacot (1933) did not figure the venter of *H. robustior* but noted that the anal and genital plates were 'scrolled' and not 'pock marked'. In *H. nepalensis* both the anal and genital valves are quite clearly pitted in the same way as the notogaster.

MATERIAL. Holotype (1964.6.24.1) and five paratypes (1964.6.24.2-6) Sandakphu, 12.xi.61. This species was common at Sandakphu but was not found in the other localities.

Steganacarus striculus (Koch)

Hoplophora stricula Koch, C. L. 1836. *Deutsch. Crust. Myr. Arach. Fasc. 2* t.10.

Steganacarus striculus, Feider, Z. & Suciú, I. 1957. *Stud. Cerc. stiint. Biol. Agric. Acad. R.P.R.* 8: 33.

The Nepalese material conforms closely to the redescription of this species by Feider and Suciú (op. cit.) and by Aoki (1958). In comparison with British material however the Nepalese specimens have rather stouter notogastral setae and the apical feathering of these setae is well marked i.e. as figured by Fieder & Suciú. *S. striculus* has a wide holarctic distribution and in Nepal was particularly abundant in the Milke Danra and Topke Gola forests. It was prominent in Selap but only a few specimens were taken at Sandakphu.

Family EUPHTHIRACARIDAE Jacot, 1930

Euphthiracarus inglisi sp. nov.

ADULT. The aspis (figs. 30 & 31) ranges in length from approximately 260-330 μ and is about 1.3 times as long as its greatest width at the level of the sensilli. The rostral setae (ro) are long and smooth and about 1.5 times the length of the lamellar

setae (la). Both the lamellar and the interlamellar setae (in) are slightly feathered apically and the latter are about 1.6 times the length of the former. There is a very pronounced scale below the bothridium, and the sensilli, which are elbowed, taper to a comparatively blunt point with very slight apical feathering. The prodorsal integument is coarsely pitted.

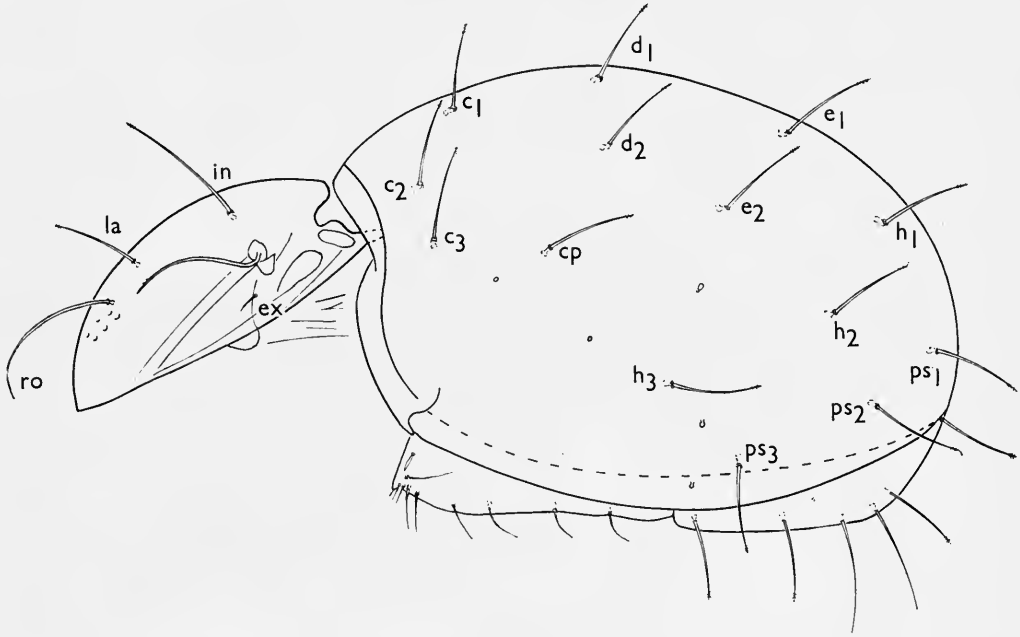
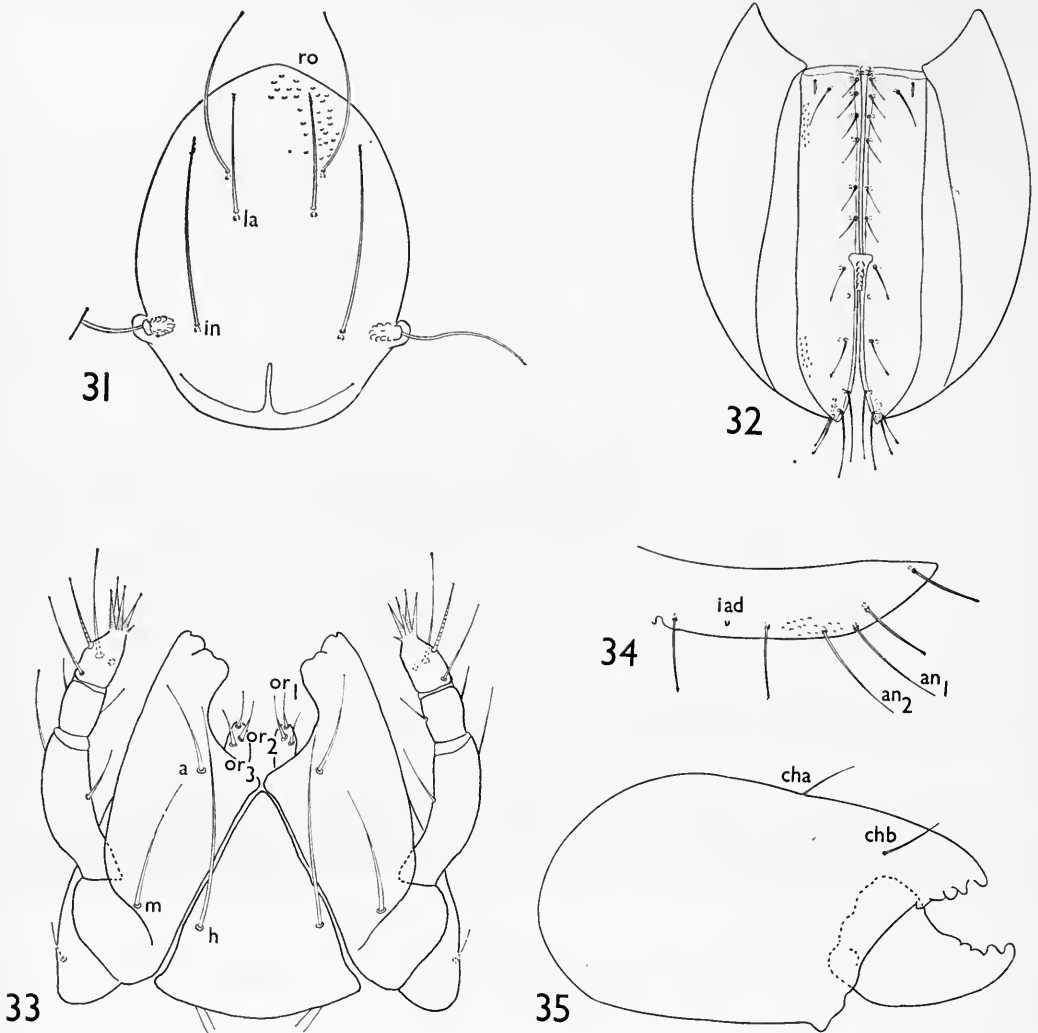


FIG. 30. *Euphthiracarus inglisi* sp. nov. Lateral.

At the level of seta h_2 the notogaster (fig. 30) ranges in length from 475 to 620 μ . The 14 pairs of setae in the notogastral series are all equal in length, erect and slightly feathered apically. The ornamentation of the notogastral integument, consisting of very weak pits, is barely discernible. Ventrally (fig. 32), the anal portion of the ano-genital valve carries six pairs of setae and a single pair of pores. Posteriorly the ano-genital plate is very much produced dorsally so that the position of the posterior setae is difficult to discern in the whole animal, but on dissection (fig. 34) the most posterior pair are seen to be inserted near the notogastral border. Of the six pairs of setae on the anal valves, two are marginal, quite smooth and distinctly longer than the other four. The latter are removed from the margin and slightly feathered apically as in the case of the notogastral setae. There are nine pairs of genital and two pairs of aggenital setae. The anterior pair of aggenital setae are short and narrowly lanceolate. The integument of the ano-genital region is distinctly pitted.

The infracapitulum is shown in fig. 33. The sub-triangular mentum carries a single pair of long setae (h). The genae carry two pairs of simple setae (a & m), seta m being rather longer than a, and there are three pairs of simple adoral setae. The three-segmented palp has the setal formula (2-2-8) and at least four of the tarsal

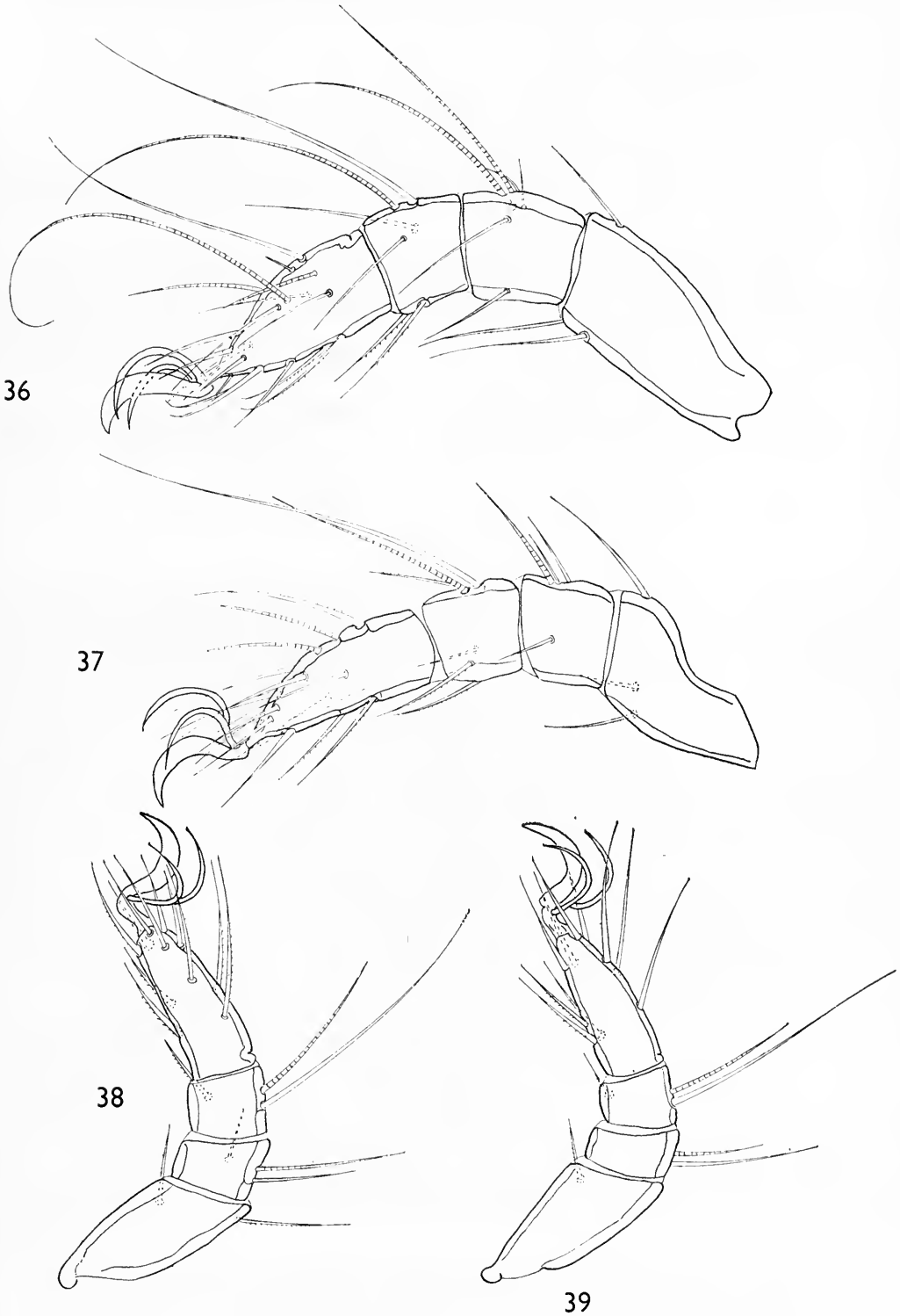


FIGS. 31-35. *Euphthiracarus inglisi* sp. nov. Fig. 31. Aspis. Fig. 32. Ano-genital region. Fig. 33. Infracapitulum. Fig. 34. Anal valve—dissected. Fig. 35. Chela.

setae are eupathidial. The minute dorso-anterior seta is discrete and has the appearance of being eupathidial. The chelicerae are shown in fig. 35. Seta cha is dorsal and seta chb is inserted well down on the anti-axial face. Each digit has four teeth.

The legs are shown in figs. 36-39. A noticeable feature is that on all the tibiae the dorsal seta is extremely long and on legs II-IV exceeds the tibial solenidia in length. All the tarsi are tri-heterodactyl and the formulae for the setae and solenidia are as follows:—

- I (1-3-4-5-16) and (2-1-3); II (1-3-3-5-14) and (1-1-2);
 III (2-2-2-2-11) and (1-1-0); IV (2-1-1-2-10) and (1-1-0).



FIGS. 36-39. *Euphthiracarus inglisi* sp. nov. Legs, excluding trochanters.
 Fig. 36. Leg I. Fig. 37. Leg II. Fig. 38. Leg III. Fig. 39. Leg IV.

E. inglisi is very similar to *E. flavus* (Ewing). However, an examination of a specimen of the latter collected in Illinois, revealed that, in contrast to *E. inglisi*, the notogastral integument is very heavily ornamented and the rostral setae are very much shorter than those of *E. inglisi*. Moreover, in *E. flavus* the distal third of the sensillus is distinctly feathered whilst in *E. inglisi* the feathering is slight and confined to the tip. This species is dedicated to my colleague on the East Nepal Expedition, Dr. W. G. Inglis.

MATERIAL. Holotype (1964.7.2.1) and five paratypes (1964.7.2.2-6), Sandakphu, 12.xi.61. *E. inglisi* was common at Sandakphu but was not found in the other localities.

Rhysotritia ardua (Koch)

Hoplophora ardua Koch, C. L. 1841. *Deutsch. Crust. Myr. Arach. Fasc. 32* t.15.

Pseudotritia loricata, Feider, Z. & Suci, I. 1957. *Stud. Cerc. stiint. Biol. Agric. Acad. R.P.R.* 8: 40.

Rhysotritia ardua, Märkel, K. & Meyer, I. 1959. *Zool. Anz.* 163: 341.

This species was extremely common in the Milke Danra and Selap forests. It occurred in small numbers at Topke Gola but was not found at Sandakphu. The Nepalese material has been compared with topotypic material from the Regensberg area kindly provided on loan by Dr. L. van der Hammen. The Nepalese specimens are generally larger and more heavily sclerotized than the topotypic material. Thus,

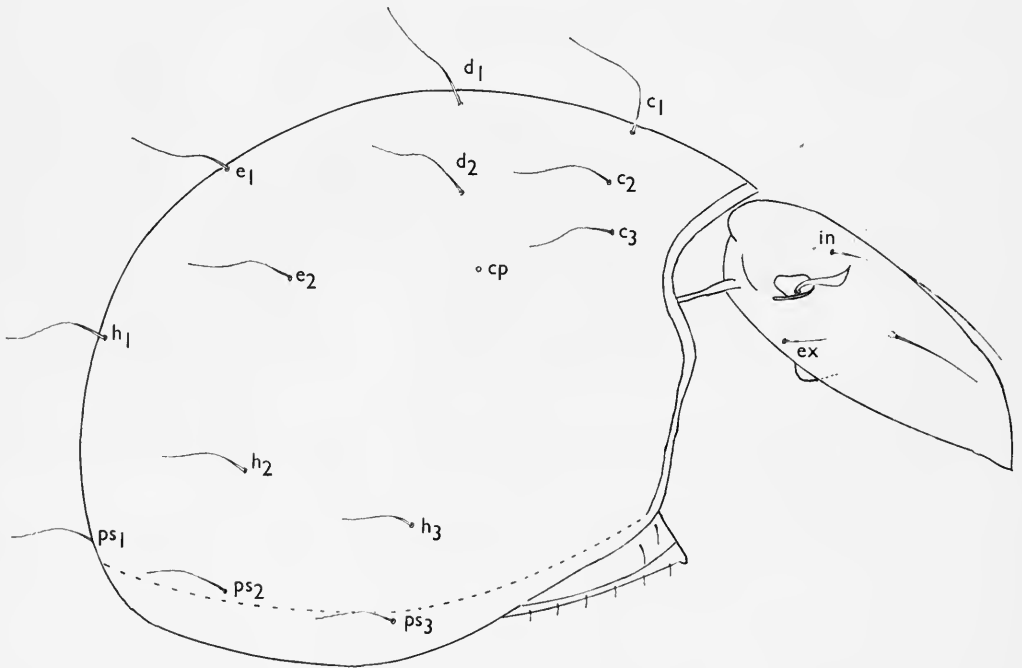
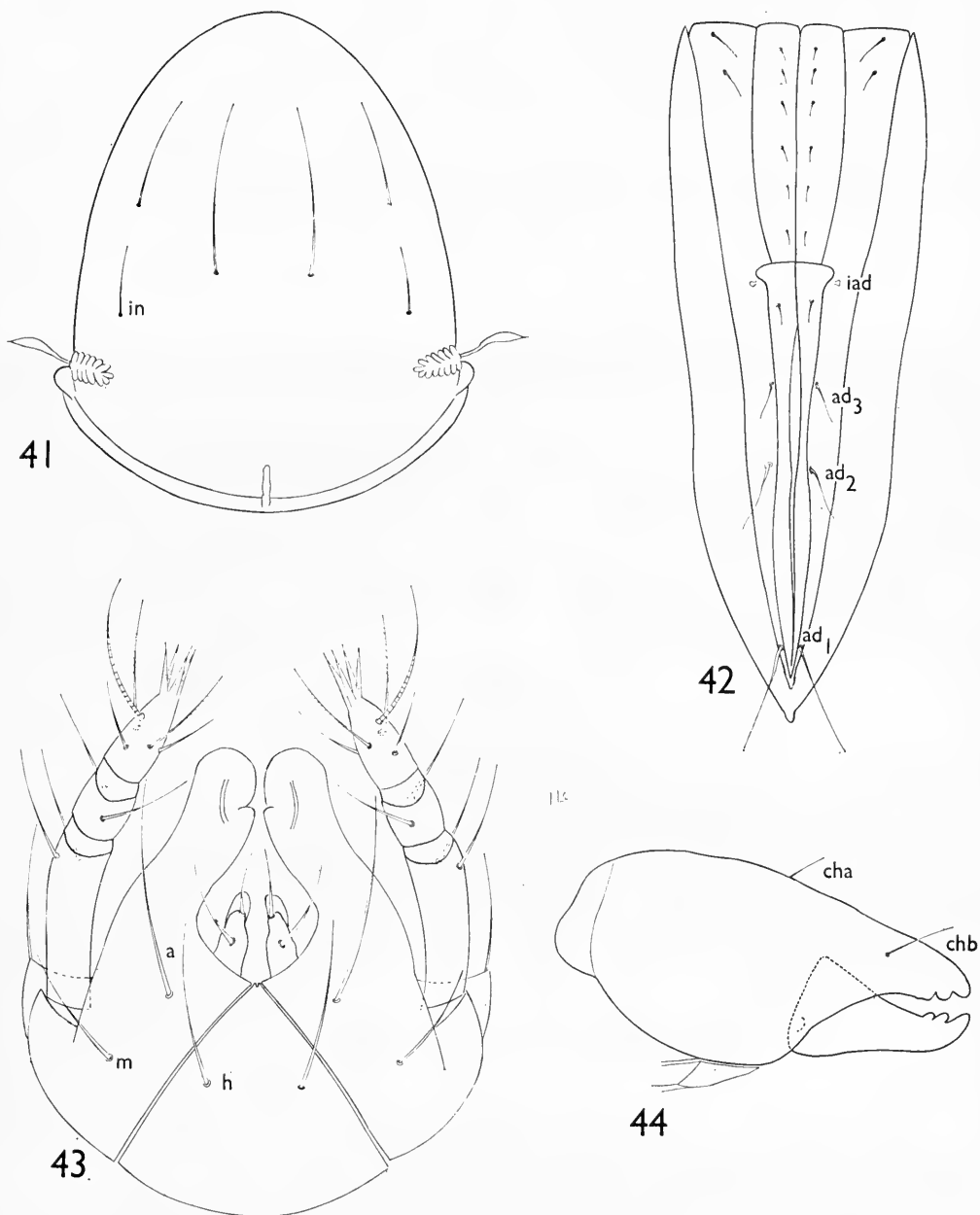


FIG. 40. *Mesotritia maerkeli* sp. nov. Lateral.

the length of the aspis in the Nepal material ranged from about 285–310 μ whilst in the six topotypes examined the length of the aspis ranged from about 215–250 μ . No other morphological differences could be detected.

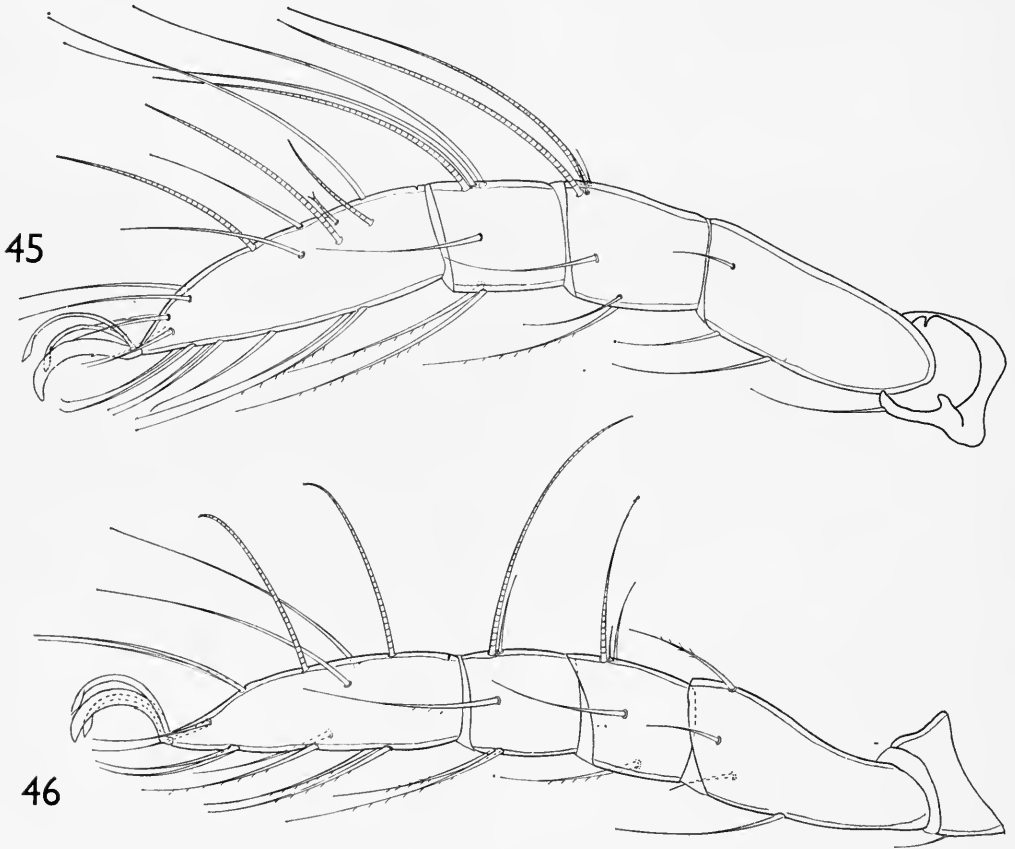


FIGS. 41–44. *Mesotritia maerkeli* sp. nov. Fig. 41. Aspis.
Fig. 42. Ano-genital region. Fig. 43. Infracapitulum. Fig. 44. Chela.

Mesotritia maerkeli sp. nov.

ADULT. The aspis (figs. 40 & 41) ranges in length from approximately 300–360 μ and is about 1.2 times as long as its greatest width at the level of the sensilli. The rostral setae which are inserted well behind the lamellar setae are long and smooth and about 1.6 times the length of the latter. Both the lamellar and interlamellar setae (in) are smooth. There is a very pronounced scale below the bothridium while the sensilli are short—about the same length as the interlamellar setae—and expanded sub-apically before tapering abruptly to a fine point.

At the level of seta h_1 , the notogaster ranges in length from approximately 550–600 μ . The 14 pairs of setae in the notogastral series are all approximately equal in length, slender and rather weak. The notogastral integument has no distinct ornamentation. Ventrally (fig. 42) the anal valve carries a single pair of setae and there are three pairs of setae in the adanal series. The adanal pore (iad) is located well in front of the anal seta. The genital valve is completely separated



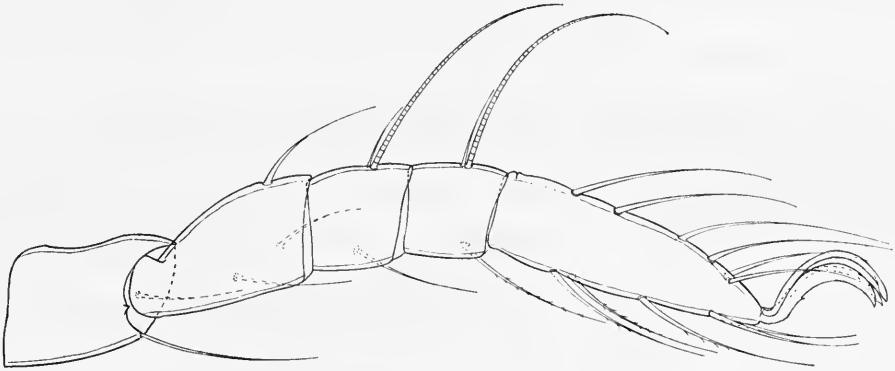
FIGS. 45–46. *Mesotritia maerkeli* sp. nov. Legs.
Fig. 45. Leg I. Fig. 46. Leg II.

from the aggenital plate by a distinct suture while the oblique fissure separating the aggenital from the adanal elements characteristic of *Oribotritia* is lacking. There are six pairs of genital and two pairs of aggenital setae.

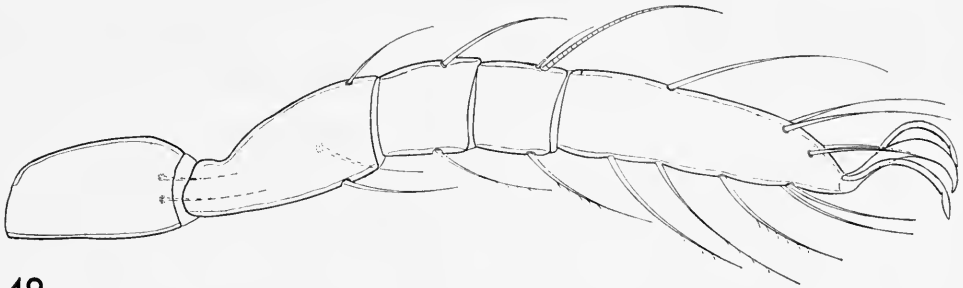
The infracapitulum is shown in fig. 43. The sub-triangular mentum carries a single pair of long simple setae (h). The genae carry two pairs of simple setae (a & m) seta a being about 1.7 times the length of seta m. Only two pairs of adoral setae could be discerned. The three-segmented palp has the setal formula (2-2-8) and four of the tarsal setae are eupathidial. The chelicerae are shown in fig. 44. Seta chb is situated well down on the anti-axial face and both the fixed and movable digits have two teeth.

The legs are shown in figs. 45-48. On leg I the famulus is forked and on all legs the solenidia of the tibiae and genua are coupled with dorsal setae, the dorsal setae on tibia I being particularly long. All the tarsi are triheterodactyl and the formulae for the setae and solenidia are as follows:—

- I (1-3-5-5-17) and (2-1-3); II (1-4-4-4-12) and (1-1-2);
 III (2-3-2-2-11) and (1-1-0); IV (2-3-2-2-10) and (0-1-0).



47



48

FIGS. 47-48. *Mesotritia maerkeli* sp. nov. Legs.
 Fig. 47. Leg III. Fig. 48. Leg IV.

I am indebted to Professor Konrad Märkel, to whom this species is dedicated, for information on the genus *Mesostritia*. Professor Märkel is currently preparing a revision of the Euphthiracaridae and for the present it is sufficient to note that while *M. maerkeli* has affinities with *M. testacea* Forsslund (Forsslund & Märkel 1963) it can be readily separated from the latter by reference to the position of the rostral setae and adanal pore.

MATERIAL. Holotype (1964.7.20.1) and one paratype (1964.7.20.2), Selap, 4.ii.62. Only four specimens were taken and all were found in the Selap Forest.

***Oribotritia berlesei* (Michael)**

Phthiracarus berlesei Michael, A. D. 1898. *Das Tierreich Lief* 3: 81.

Oribotritia decumana, Willmann, C. 1931. *Die Tierwelt Deutschlands Teil* 22: 193.

Oribotritia berlesei, Grandjean, F. 1933. *Bull. Mus. Hist. nat. Paris* 5: 309.

Eight specimens were taken from the Topke Gola forest, four from Selap and one from the Milke Danra forest.

Family **EPILOHMANNIIDAE** Oudemans, 1923

***Epilohmannia cylindrica* (Berlese)**

Lohmannia cylindrica Berlese, A. 1904. *Redia* 2: 23.

Lesseria szanisloi Oudemans, A. C. 1917. *Arch. Naturgesch.* 88A. (6): 79.

A single specimen agreeing well with Oudemans' description was recorded from Selap.

Family **EULOHMANNIIDAE** Grandjean, 1931

***Eulohmannia ribagai* Berlese**

Lohmannia (Eulohmannia) ribagai Berlese, A. 1910. *Redia* 6: 223.

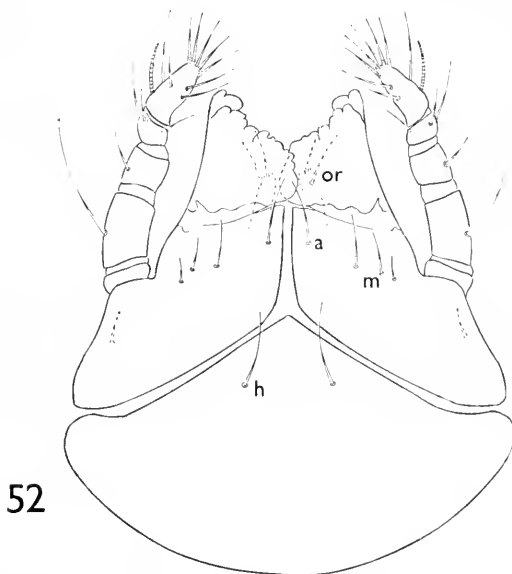
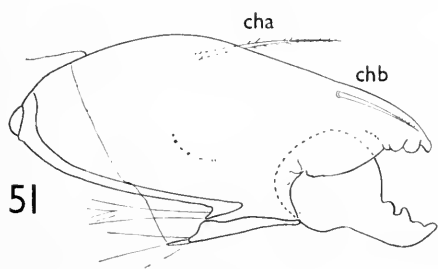
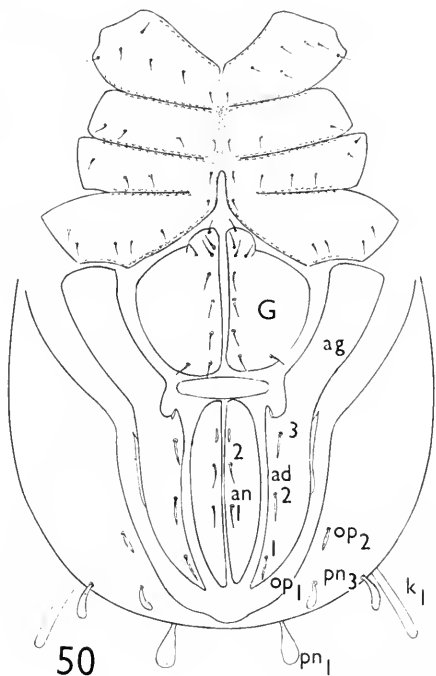
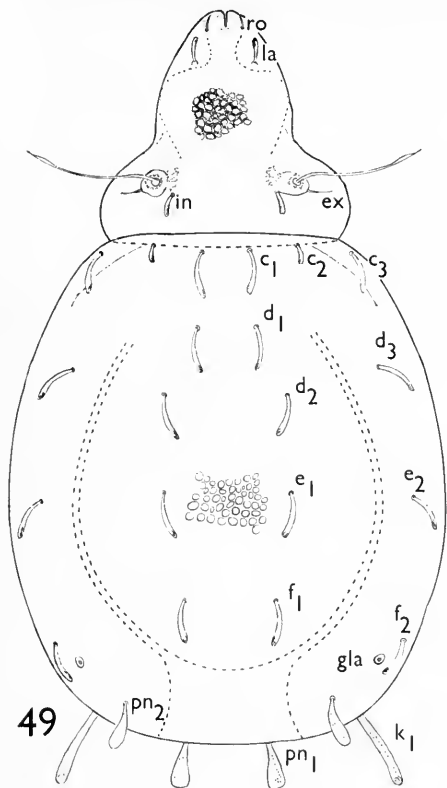
Arthronothrus biunguiculatus Trägårdh I. 1910. *Naturwissenschaftliche Untersuchungen des Sarekgebirges in Schwedisch-Lappland* 4: 544.

Generally regarded as a relict, this species has a wide holarctic distribution (Balogh 1961). In Nepal a small number of specimens was taken at Topke Gola and a single specimen was recorded from Selap.

Family **NOTHRIDAE** Berlese, 1896

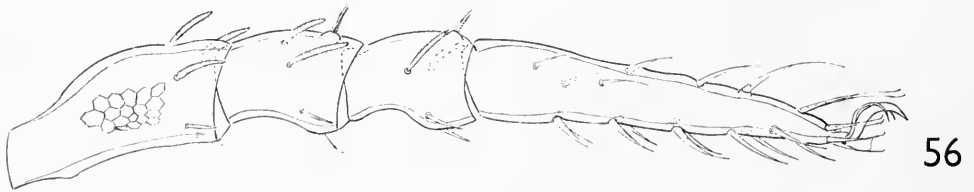
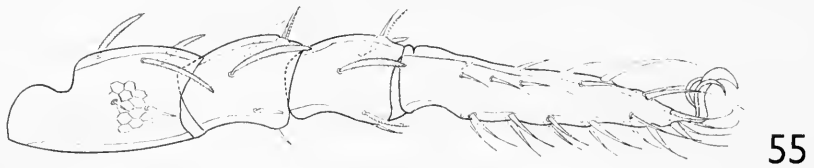
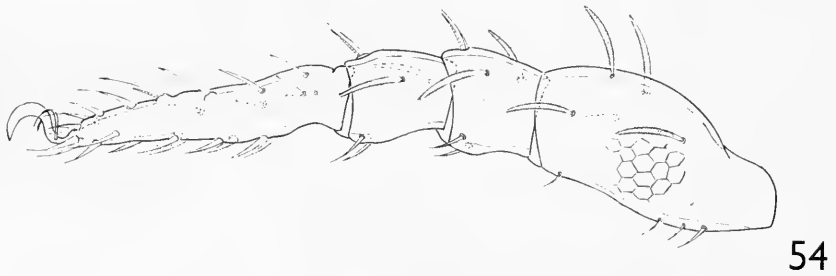
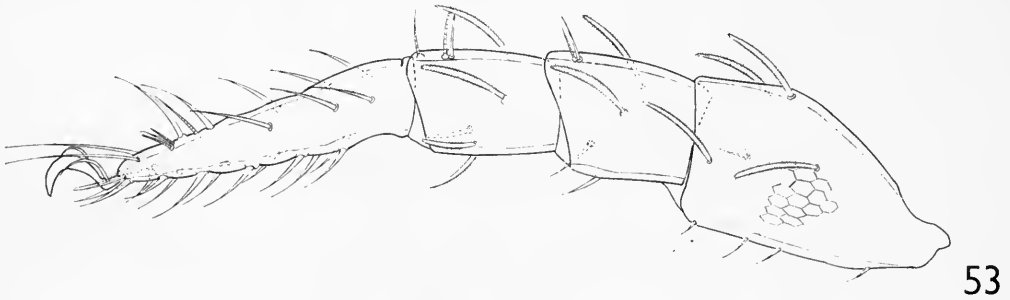
***Nothrus springsmythi* sp. nov.**

ADULT. The prodorsum (fig. 49) is approximately 350 μ long and 350 μ wide at the broadest point level with the interlamellar setae (in). The median rostral incision extends almost to the base of the rostral setae (ro) and the latter are short and simple while the lamellar (la) and interlamellar setae are narrowly spatulate and serrated apically. The exobothridial setae (ex) are simple. The sensilli are approximately 210 μ in length and slightly expanded in one plane subapically. A cluster of pseudotracheae can be discerned below the bothridia. The integument of the prodorsum is pitted and, centrally, the raised margins of the pits form a regular polygonal network.



FIGS. 49-52. *Nothrus springsmythi* sp. nov. Adult. Fig. 49. Dorsum.
Fig. 50. Venter. Fig. 51. Chela. Fig. 52. Infracapitulum.

The notogaster (fig. 49) is approximately 720μ in length and about 620μ wide at the broadest point near the level of setae e_2 . There are 16 pairs of notogastral setae, those in the c, d, e and f series being narrowly spatulate. Seta c_1 is about 2.5 times the length of c_2 and the insertion point of the latter is slightly closer to c_1 than to c_3 . The setae of the pn series are broadly spatulate and seta k_1 is about 1.9 times the length of pn_1 . All the setae of the pn and k series have a very prominent core of active chitin with ramifying branches near the tip. The integument of the central part of the notogaster is irregularly pitted, the margins forming a sub-circular pattern.



FIGS. 53-56. *Nothrus springsmythi*. Adult, legs excluding trochanters.
 Fig. 53. Leg I. Fig. 54. Leg II. Fig. 55. Leg III. Fig. 56. Leg IV.

Ventrally (fig. 50) there are two setae in the anal (an) and three setae in the adanal (ad) series. The latter are very narrowly spatulate. Owing to the granular nature of the integument of the epimera the setal bases are difficult to discern. However there appears to be considerable variation in the chaetotaxy of the intercoxal region and the arrangement is not always bilaterally symmetrical. The observed variation in epimera was as follows: I (6-7), II (3-4), III (5) and IV (5-7). This condition is evidently neotrichous, and, as Grandjean (1934) has noted for *Nothrus silvestris* (Nicolet), the 'abnormal' condition first becomes apparent in the protonymph (3-2-3-0), the formula for the larva (2-1-2) being normal (vide infra).

The infracapitulum is shown in fig. 52. The arrangement is 'stenarthric' (Grandjean, 1957a) and the rutella are basically of the *Camisia* type with large overlapping ventral lobes completely covering the adoral papillae. There are two pairs of long simple adoral setae and the four pairs of setae on the genae are arranged in a straight line. The five-segmented palp has the formula (0-1-1-3-9) and four of the tarsal setae are eupathidia.

The chelicera is shown in anti-axial view in fig. 51. It resembles the chelicera of *Camisia* figured by Grandjean (1947) although seta cha is longer and more posteriorly situated. The organ of Trägårdh is discernible only with difficulty.

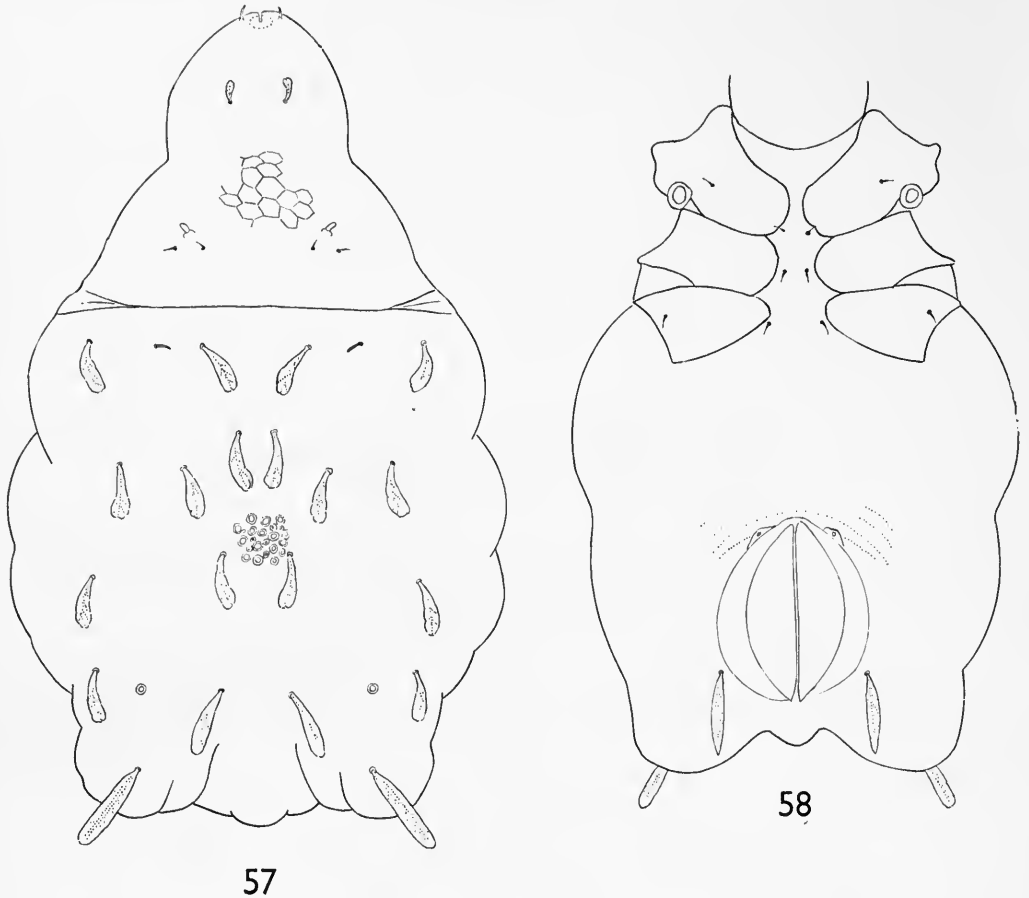
The legs are shown in figs. 53-56. Legs I and IV are much longer than II and III and the integument of trochanters II and IV as well as that of all the femora is sculptured with a distinct polygonal pattern. All the tarsi are tri-heterodactyl and the formulae for the setae and solenidia are as follows:—

I (1-9-5-6-27) and (1-2-3); II (1-9-5-5-24) and (1-1-1);
 III (3-5-5-5-25) and (1-1-0); IV (2-5-5-5-22) and (1-1-0).

LARVA. The prodorsum (fig. 57) is approximately 165μ long. The lamellar setae (la) are spatulate while the remaining prodorsal setae are simple. The sensilli are represented by short stumps. Along the mid-line the notogaster is approximately 260μ in length and the integument is tuberculate. With the exception of setae c_2 and k_1 , all the dorsal setae are broadly spatulate. Setae c_2 are simple but somewhat blunt and less than one third of the length of setae c_1 . Setae k_1 are narrowly spatulate and about twice the length of setae f_2 . Ventrally (fig. 58) seta pn_1 is spear-shaped and approximately the same length as k_1 . The structure of the ano-genital region is normal for the genus and the intercoxal formula is (2-1-2). The setal and solenidial formulae for the legs are as follows:

I (0-2-3-4-14) and (1-1-1); II (0-2-3-3-13) and (1-1-1);
 III (0-2-2-3-12) and (1-1-0).

PROTONYMPH. The prodorsum (fig. 59) is approximately 200μ in length and its integument is ornamented with a polygonal pattern. The lamellar (la) and interlamellar setae (in) are broadly spatulate, while the sensilli, approximately 260μ in length, taper to a fine point after bending sharply near the base. Along the mid-line the notogaster is approximately 380μ in length, its integument is tuberculate although this feature is not so well marked as in the larva. With the exception of seta k_1 , all the dorsal setae are broadly spatulate. Seta c_2 is about half as long as seta c_1



FIGS. 57-58. *Nothrus springsmythi* sp. nov. Larva.
Fig. 57. Dorsum. Fig. 58. Venter.

and seta k_1 is about six times the length of seta pn_1 . Ventrally (fig. 60) setae pn_1 and pn_3 are broadly spatulate, while the two pseudanal setae (op) are sub-lanceolate. There are no setae in the anal or adanal series and each crescent-shaped genital shield carries a single seta. The intercoxal formula is (3-2-3-0) and the setal and solenidial formulae for the legs are as follows:

I (0-3-5-5-15) and (1-1-2); II (0-3-5-5-13) and (1-1-1);
III (1-2-4-4-13) and (1-1-0); IV (0-0-0-0-7) and (1-1-0).

DEUTONYMPH. Along the mid line the prodorsum and notogaster are approximately 200 and 450 μ in length, respectively. The arrangement and form of the dorsal setae is essentially similar to that of the protonymph. Setae k_1 are about 180 μ long and 4-5 times as long as setae pn_1 . Ventrally (fig. 61) the pseudanal setae (op) have

become broadly spatulate, while three pairs of simple adanal and four pairs of genital setae have appeared. The setal and solenidial formulae for the legs are as follows:

I (1-7-5-5-19) and (1-2-2); II (1-7-5-5-17) and (1-1-1);

III (3-3-5-5-17) and (1-1-0); IV (1-2-4-4-13) and (1-1-0).

TRITONYMPH. Along the mid-line the prodorsum and notogaster are approximately 230 and 650 μ in length, respectively. The arrangement of dorsal setae is essentially the same as in the adult except that the spatulate setae are rather broader. Setae k_1 are about 240 μ long and about 3 times the length of setae pn_1 . Ventrally (fig. 62), the anal region differs from that of the deutonymph by the addition of 2 pairs of anal setae and a pair of anal pores. There are seven pairs of genital setae. The setal and solenidial formulae for the legs are as follows:

I (1-8-5-6-23) and (1-2-3); II (1-7-5-5-17) and (1-1-1); III (3-3-5-5-17) and (1-1-0) and IV (1-2-4-4-13) and (1-1-0).

Nothrus springsmythi appears to have affinities with *Nothrus biciliatus* C. L. Koch. However, European specimens of the latter kindly provided by Dr. K.-H. Forsslund had an overall length of 790-800 μ , whilst *N. springsmythi* is much larger ranging in length from 1070-1130 μ . Moreover, in *N. springsmythi* setae k_1 are much more slender although the form of these setae, as well as that of setae pn_1 , seems to vary considerably. An interesting difference can also be seen in the form of the setae on the tarsi. In *N. biciliatus* the three proximal latero-dorsal setae of the tarsi are markedly spatulate with a sickle-like curve, whilst in *N. springsmythi* these setae are much more slender and of the same type as the proximal ventral setae.

N. springsmythi also resembles two recently described South American species viz. *Nothrus oblongus* Hammer 1961, and *Nothrus macedi* Beck 1962. It differs from the latter in lacking the tubercle at the base of seta pn_2 , by having a smooth sensillus, comparatively smooth distal setae on the tarsi and also in the length, relative to the basal distance of setae f_1 . In comparison with *N. oblongus*, *N. springsmythi* is larger and stouter. In the former species the first adanal seta is described as being similar to the dorsal hysterosomal setae (narrowly spatulate) whilst in *N. springsmythi* all the adanal setae are very narrowly lanceolate. This species is dedicated to Major T. Le M. Spring Smyth in appreciation of his services to the East Nepal Expedition.

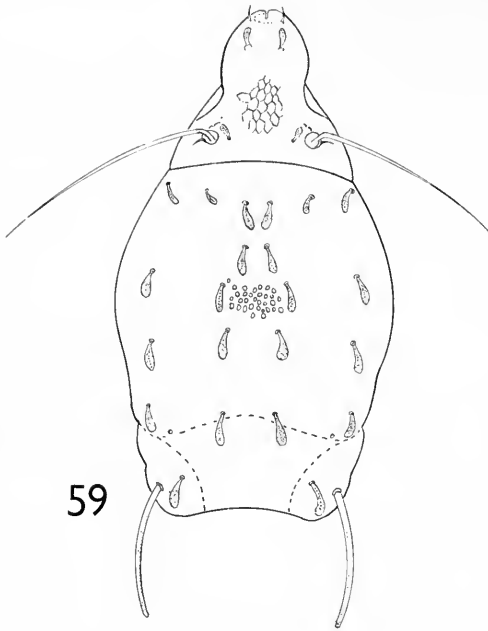
MATERIAL. Holotype adult (1964.6.15.1) and five paratypes comprising an adult and all four postembryonic developmental stages (1964.6.15.2-6), Selap, 4.ii.62. *N. springsmythi* was extremely common in the Milke Danra and Selap forests. It was particularly abundant in the latter locality and in one sample constituted 24% of the Cryptostigmatid population. It was less abundant at Topke Gola and was not found at Sandakphu.

Nothrus palustris Koch

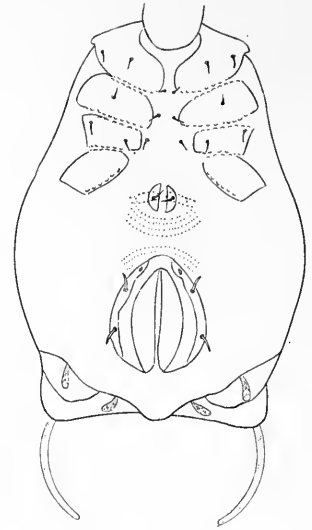
Nothrus palustris Koch, C. L. 1839. *Deutsch. Crust. Myr. Arach. Fasc. 29* t.13.

Nothrus palustris, Sellnick, M. & Forsslund, K.-H. 1955. *Ark. Zool.* 8: 498.

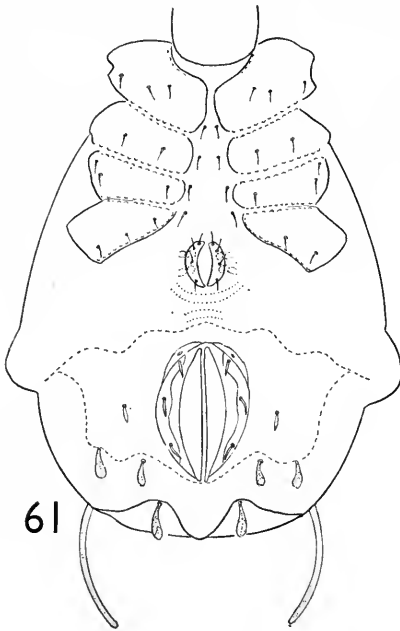
This species dominated the community at Topke Gola. It occurred in small numbers in the Milke Danra and Selap forests and a single tritonymph was recorded from Sandakphu.



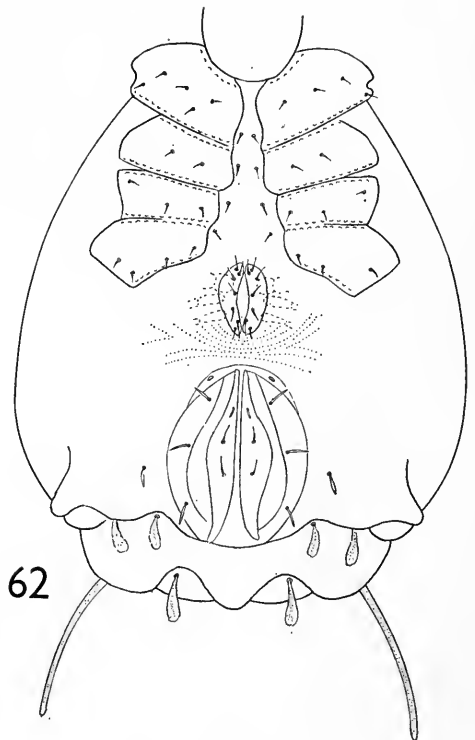
59



60



61



62

FIGS. 59-62. *Nothrus springsmythi* sp. nov. Fig. 59. Protonymph, dorsum. Fig. 60. Protonymph, venter. Fig. 61. Deutonymph, venter. Fig. 62. Tritonymph, venter.

Family **CAMISIIDAE** Oudemans, 1900***Camisia lapponica*** (Trägårdh)

Nothrus lapponicus lapponicus Trägårdh, I. 1910. *Naturwissenschaftliche Untersuchungen des Sarekgebirges in Schwedisch-Lappland* 4: 526.

Camisia lapponica, Sellnick, M. & Forsslund, K.-H. 1955. *Ark. Zool.* 8: 489.

According to Sellnick & Forsslund (op. cit.) this species has a wide holarctic distribution. It occurred in small numbers at Sandakphu.

Platynothrus peltifer (Koch)

Nothrus peltifer Koch, C. L. 1839. *Deutsch. Crust. Myr. Arach. Fasc.* 29 t.9.

Platynothrus peltifer, Sellnick, M. & Forsslund, K.-H. 1955. *Ark. Zool.* 8: 515.

This species, which has a wide holarctic distribution, was found in all four localities, but was most prominent in the Selap and Milke Danra forests. *P. peltifer* was amongst the species recorded from the Sikkim Himalaya by Pearce (1906).

Family **TRHYPOCHTHONIIDAE** Willmann, 1931***Trhypochthonius tectorum*** (Berlese)

Hypochthonius tectorum Berlese, A. 1896. *Acar. Myr. et Scorp. Ital. rep. Fasc.* 78 8.

Trhypochthonius tectorum, Willmann, C. 1931. *Die Tierwelt Deutschlands Teil* 22: 103.

The type material appears to have been collected from moss on roofs in Florence (van der Hammen, 1959). This species is widely distributed in Europe and the collections of the British Museum (Nat. Hist.) include three specimens from Pearce's Sikkim-Himalaya collection. This species was particularly common at Topke Gola but occurred in small numbers in all the localities sampled.

Family **MALACONOTHRIDAE** Berlese, 1916***Malacothrus monodactylus*** (Michael)

Nothrus monodactylus Michael, A. D. 1888. *British Oribatidae* 2: 528.

This species was common in the Milke Danra and Topke Gola forests and occurred in small numbers at Selap.

Family **NANHERMANNIIDAE** Sellnick, 1928***Nanhermannia nana*** auct.

Nanhermannia nana, Willmann, C. 1931. *Die Tierwelt Deutschlands Teil* 22: 96.

Nanhermannia nana, Strenzke, K. 1953. *Zool. Anz.* 150: 73.

Although rather larger, ranging in length from approximately 580–600 μ , the Nepalese specimens agree well with Strenzke's description. Van der Hammen (1959) has shown that Nicolet's *nanus* has been widely misinterpreted and is not identical with *nana* sensu Willmann, but he considered that the latter should not be renamed until detailed redescriptions of Banks' species had been made. This species was plentiful in the Milke Danra and Topke Gola forests.

SUMMARY

Twenty two species of *Oribatei Inferiores* were found in the soil and litter of Rhododendron forests in four localities in East Nepal. The following six species are considered to be new.

1. *Himalacarus chimalae* gen. et sp. nov. (p. 3)
2. *Phthiracarus robertsi* sp. nov. (p. 11)
3. *Hoplophthiracarus nepalensis* sp. nov. (p. 15)
4. *Euphthiracarus inglisi* sp. nov. (p. 18)
5. *Mesotritia maerkeli* sp. nov. (p. 24)
6. *Nothrus springsmythi* sp. nov. (p. 26)

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I am indebted by my colleague Mr. D. Macfarlane for advice on a number of problems and to Mrs. E. Hyatt for assistance with sorting the samples.

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JAPANESE AND OTHER OPHIUROIDS FROM THE COLLECTIONS OF THE MÜNICH MUSEUM

By

AILSA M. CLARK

THIS paper deals with some ophiuroids from the collections of the Zoologische Staatssammlung des Bayerischen Staates in München entrusted to me by Dr. H. Fechter, to whom I am deeply indebted, not only for the opportunity of studying such interesting material but also for permission to retain a proportion of the duplicate specimens for the British Museum collections.

Most of the material came from southern Japan (collected by Döderlein, Doflein and Haberer) or from the colder waters of the northern Japan Sea (Schmidt, Brashnikow and Domaschnew) but a number of other localities, ranging from the Mediterranean and West Indies to the Indian Ocean and western as well as eastern Pacific, are involved, including some specimens from the "Albatross" collections originating with the United States National Museum—the greater part of which has already been worked up by Koehler, Döderlein and others. Unfortunately some of the specimens were labelled only with collectors numbers or dates and in the case of the Japan Sea collections the details were often given only in almost illegible cyrillic script so that, in some instances, only an approximate transliterated version can be given where the name is untraceable in the atlases available. I am indebted to Mrs. H. Sabo for help in deciphering the labels.

The most interesting family represented is the Amphiuroidae, which has been the subject of a recent revision by Fell (1962), involving extensive dismemberment of the major genera *Amphiura*, *Amphiodia*, *Amphipholis* and *Amphioplus*. I am not convinced that the resultant groups form natural genera and accordingly am retaining the customary combinations of names in this paper.

A number of the species represented evoke no special comment; accordingly the records of these are simply listed at the end of the paper.

Family OPHIOMYXIDAE

Ophiobyrssa intorta (Koehler)

Ophiobyrssella intorta Koehler, 1922, 27–29, pl. iv, figs. 2–5, pl. xcii, fig. 4.

MATERIAL. "Albatross" station 5215, 12° 31' 30" N., 123° 35' 24" E. (Philippines), 1,105 metres, 3 specimens; station 5219, 13° 21' 00" N., 122° 18' 45" E., 970 metres, 2 specimens.

The type of *Ophiobyrsella intorta* was also taken in the Philippines by the "Albatross". The present specimens agree with Koehler's photographs and description of the type except that there is no row of median teeth up the apex of each jaw but simply multi-serial thorny-tipped tooth papillae throughout. The papillae altogether number about 20 on each jaw, including one or two almost superficial papillae lateral to the apex which might be termed oral papillae. The apical papillae deeper in the mouth are longer than the superficial ones. Koehler notes "Together with the tooth papillae the mouth (oral) papillae form a little bundle of short, slender and spinulose spines continuous with the teeth which are fairly regular in their arrangement and which have exactly the same form as these papillae." [My italics]. If the "teeth" are as narrow and spiniform as the papillae in the type it would be surprising if they formed only a single vertical row not flanked by other papillae. In view of the otherwise close correspondence between Koehler's description and figures and the present specimens, I think the only difference is one of terminology and accordingly am referring *intorta* to the genus *Ophiobyrsa*, characterized by the presence of few oral papillae, many tooth papillae and no proper teeth.

It should be noted that the type species of *Ophiobyrsa* is *O. rudis* Lyman, not *O. hystricis* Lyman as stated by Koehler.

In comparison with the holotype of *O. rudis* the present specimens differ notably in the much smaller oral shields with the adorals meeting proximal to them, the fewer and smaller disc platelets and spinelets and the absence of spinelets on the fragmented dorsal arm plates. *Ophiobyrsa synaptacantha* H. L. Clark, from south-west Japan differs in the separated adorals though it has similarly fragmented and spineless dorsal arm plates.

***Ophiobyrsa acanthinobrachia* H. L. Clark**

Ophiobyrsa acanthinobrachia H. L. Clark, 1911, 269-270, fig. 134; Matsumoto, 1917, 24.

MATERIAL. Doflein, no. 588, Yogashima, 150 metres, 31.x.1904, 1 specimen.

Murakami (1944) has described a species *Ophiobyrsa strictima*, from unknown locality, in his paper on the ophiuroids of Ogasawara and Yaeyama, the unique type having the disc diameter 23 mm. He notes that it is closely related to *O. acanthinobrachia*, which it resembles in having spinelets on the dorsal arm plates. The differences between them given by Murakami are that *strictima* has oval rather than rounded-triangular oral shields, narrower adoral shields, more compact disc scaling and the tooth papillae arranged in three rather than two vertical rows.

The type of *O. acanthinobrachia* is also large with the disc diameter 20 mm., whereas in the present specimen it is only 7 mm., the arms being about 45 mm. long, giving a ratio of 1:6.4 compared with 1:14 in the type of *O. acanthinobrachia*. The disc scales are slightly spaced and the tooth papillae are arranged in two vertical rows so I am referring the specimen to H. L. Clark's species. Besides the tooth papillae, which number about six in each vertical row with the longest ones highest in the oral slit, there is an irregular cluster of smaller papillae at the superficial end of the two rows as well as one slightly larger papilla lateral to the apex of the jaw each side,

which might be termed an oral rather than a tooth papilla. On the distal side of the superficial second oral tentacle there is an erect papilla or scale not mentioned by H. L. Clark, though his figure shows an oral papilla just proximal to the tentacle pore. The arm spines number up to five, as might be expected at this size, the type having seven proximally.

Family **OPHIACANTHIDAE**

Ophiacantha acanthinotata H. L. Clark

Ophiacantha acanthinotata H. L. Clark, 1911, 203-204, fig. 94; Matsumoto, 1917, 117; Murakami, 1942, 3.

MATERIAL. Döderlein, Enoshima 22, 1 specimen.

The disc diameter is 6 mm. and the basal arm segments have not more than nine arm spines each side in comparison with the type, in which there were ten or eleven spines proximally at a disc diameter of 9 mm. The two more distal oral papillae in each series of three are both rather paddle-shaped, the third one not the widest, unlike that of the type. Another slight difference is that a wedge-shaped area at the distal end of each radial shield is left bare.

Ophiacantha rhachophora H. L. Clark

Ophiacantha rhachophora H. L. Clark, 1911, 201-202, fig. 92; Matsumoto, 1917, 119-120, fig. 30; Murakami, 1942, 5-6; Djakonov, 1954, 41-42, fig. 10.

MATERIAL. Döderlein: Enoshima 22, 1 specimen; Enoshima 25, 14 specimens; Yogashima, 7 specimens; Yogashima, 2.xi.1881, 1 specimen; 7.xi.1881. III, 250 fathoms (457 metres), 2 specimens; 2.xi.1881. III, 1 specimen; no details, 2 specimens.

The number of oral papillae is variable in these specimens. As Matsumoto has shown, the distalmost and thorniest one arises vertically from the adoral shield. One or two of the other papillae are bifurcate dorso-ventrally at the tip but none are really thorny. In one specimen with disc diameter 5 mm. there are only three oral papillae each side of the apical one, including the clavate, thorny, adoral shield papilla, but usually the number is five, though six may be found in some series as on one side of the jaw figured by Matsumoto. The oral shields usually have a more prolonged and acute proximal angle than is shown in H. L. Clark's figure of the type.

The thorny tentacle scales and distalmost oral papilla as well as arm spines make this species easily recognizable from the sympatric *Ophiacantha pentagona*.

Ophialcaea congesta (Koehler)

Ophiacantha congesta Koehler, 1904, 103-104, pl. xxiv, figs. 1, 2.

Ophialcaea congesta: H. L. Clark, 1915, 217.

Ophialcaea congesta: Koehler, 1922, 85, pl. xv, figs. 6, 7.

MATERIAL. "Albatross" station 5119, 13° 45' N., 120° 30½' E. (Philippines), 721 metres, 1 specimen; station 5618, 0° 37' N., 127° 15' E. (Moluccas), 763 metres, 1 specimen.

As Koehler (1922) noted, only the basal dorsal arm spines are enlarged. In the case of the specimen from "Albatross" station 5618 this applies to the uppermost spines of the first three free segments; on the second and third segments these spines measure 1.9 mm. in length, whereas on the fourth segment the corresponding spine of each side is only 1.3 mm. long. The length of the basal segments is about 1.0 mm. These enlarged spines also differ in being distinctly clavate in shape. The disc diameter is *c.* 9.5 mm. but the disc is rather distorted. The arm length is *c.* 50 mm. There are four arm spines basally but the number increases to five beyond the thirteenth segment or thereabouts. The dorsal arm plates of at least the proximal half of the arm each have a row of minute thorns along the distal edge. Neither of these last two features was observed by Koehler in his material. This specimen also differs from his description in the apical oral papilla (or lowest tooth), which is much wider than the lateral papillae, not similar to them. The disc granules are conical (or at least appear so through the thin skin). The dorsal arm plates have the distal edge convex, unlike those of the type, which Koehler described as having parallel sides, but much like the specimen he figured in 1922.

Because of the thorns on the dorsal arm plates, this species runs down to *Ophiogema* in Fell's generic key (1960) but differs markedly from the type species, *Ophiogema punctata* Koehler, 1922, in having a coat of conical granules (or they could be called very short spinules) on the disc rather than "a rather stout pointed spine" on each disc plate; the ventral arm plates are also different, the dorsal arm plates have thorns rather than spinelets and in *Ophiogema punctata* the arm spines are more needle-like and numerous, seven in number, none of them are clavate and they are "finely echinulated" not smooth. With so many differences I have no doubt that the two species are generically distinct. The rib-like concealed radial shields give *Ophialcaea congesta* the appearance of a Euryalid rather than an Ophiacanthid.

The specimen from "Albatross" station 5119 is similar in size but only the first two free arm segments, especially the second, have the uppermost spine enlarged. The thorns on the dorsal arm plates are also less distinct.

Family OPHIACTIDAE

Ophiactis macrolepidota Marktanner-Turneretscher

Ophiactis macrolepidota Marktanner-Turneretscher, 1887, 298, pl. xii, figs. 12, 13; Döderlein, 1898, 484, pl. xxxvii, fig. 1; Matsumoto, 1917, 155-156, fig. 37; Murakami, 1942, 8; 1943, 167.

MATERIAL. Döderlein: Yogashima, 2 specimens; Kashiya, 1 specimen.

Whereas the largest specimen of *Ophiactis pteropoma* in the present collection has only three arm spines though the disc diameter is 4 mm., all three of these specimens, which are smaller, have four spines on the second free arm segment, though the following segments have only three; also the second from lowest spine differs in being somewhat squared at the tip.

I agree with Matsumoto and Murakami that such Japanese specimens are almost certainly conspecific with Döderlein's from Amboina but there is some doubt whether

this is also true of the holotype of *O. macrolepidota*. Not only was it supposed to come from "Sidney" (presumably Sydney, N.S.W.), a temperate locality (though a few tropical species do have their southern limit there) and one from which there are no later records, but also it was described as having the ventral side of the disc (rather improbably for an *Ophiactis*) covered with skin only. If Marktanner's description was wrong in this respect it is possible that his species is now known by another name, there being several nominal species of *Ophiactis* found in that part of Australia.

Family AMPHIURIDAE

Amphiura iridooides Matsumoto

Amphiura iridooides Matsumoto, 1917, 205-207, fig. 56.

Monamphiura iridooides: Fell, 1962, 11.

MATERIAL. Döderlein: nr. Yogashima, 1 specimen; Yogashima, 200 metres, 1 specimen; Enoshima 22 and 24, 5 specimens; no details, 1 specimen.

One of the two from Yogashima particularly approaches *Amphiura iris* Lyman in having the distal oral papilla thicker than is usual in *iridooides*, while on some jaws the papilla appears to have a double apex, being preserved in the erect position, since its thin cross-section is slightly bowed; when appressed the papillae appear leaf-shaped. There are six arm spines on one or two basal segments although the disc diameter is only about 3.5 mm., whereas Matsumoto's holotype of *A. iridooides* with disc diameter 4 mm. has only five arm spines. The type of *Amphiura iris* at a disc diameter of 5 mm. has only four spines although Matsumoto's largest specimen of *iris*, with diameter 5.5 mm., did have five spines. The Yogashima specimen also differs from *A. iris* in having the disc scaling very smooth and the dorsal arm plates not "humped", agreeing in these characters with *A. iridooides*. The radial shields are nearly three times as long as broad and distinctly divergent, whereas in the type specimen of *A. iris* they are relatively larger and are parallel in alignment.

Amphiura iris Lyman

(Text-fig. 1)

Amphiura iris Lyman, 1879, 23, pl. xi, figs. 302-304; 1882, 132, pl. xvi, figs. 4-6; Matsumoto, 1917, 204-205.

Monamphiura iris: Fell, 1962, 11.

MATERIAL. Enoshima, 230 fathoms (420 metres), 1 specimen.

The disc diameter is 5 mm. and the arm length 40 mm., a ratio of 1:8, whereas Matsumoto's specimen measured 5.5/25 mm. or 1:4.5. Unfortunately the holotype has all the arms badly broken and no estimate of their length can be made. The Enoshima specimen has the two infradental oral papillae of each jaw spaced from one another with a third papilla or tooth at the same level between them; on one jaw, however, the infradental papillae are placed asymmetrically. In the holotype

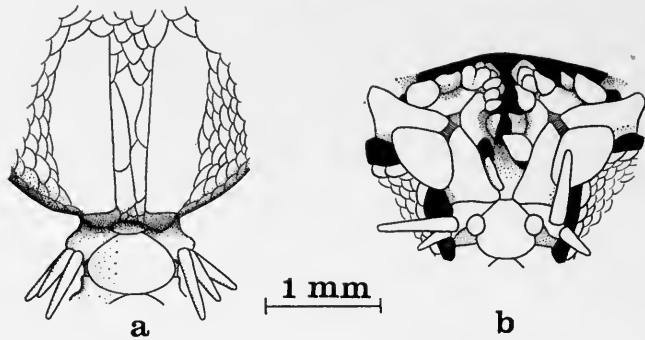


FIG. 1. *Amphiura iris* Lyman. Holotype, B.M. no. 82.12.23.104. (a) Dorsal and (b) ventral views of parts of the disc and oral area. In (a) the scales between the radial shields are very indistinct and some imagination has been used in showing their limits; nevertheless, they are certainly more numerous than shown in Lyman's figure, where only one row is drawn. In (b) one of the four distal oral papillae included is displaced and seen edge-on.

of *A. iris* the infradental papillae are closer together on three jaws, the small lowest tooth being just above and partially between them; a fourth jaw is damaged but the fifth has a cluster of terminal papillae almost like an *Ophiopsila*, though these too are damaged. In other respects the Enoshima specimen agrees with the type, that is in the disc scaling, long parallel radial shields, shapes of the arm plates (the dorsal ones slightly humped), the form of the distal oral papilla and the large single tentacle scale.

Amphiura trachydisca H. L. Clark

Amphiura trachydisca H. L. Clark, 1911, 149-150, fig. 60; Matsumoto, 1917, 201; Murakami, 1942, 19.

MATERIAL. Enoshima, 230 fathoms (420 metres), 1 specimen.

H. L. Clark's figure is rather misleading since the disc scales of this species do not so much bear tubercles as have their free edges thickened and erected. This is true not only of this specimen but also of the type, which I have examined in the U.S. National Museum.

Amphiura arcystata H. L. Clark

Amphiura acrystata (lapsus for *arcystata*) H. L. Clark, 1911, 145-148, fig. 58; Matsumoto, 1917, 203; Murakami, 1942, 11.

Amphiura arcystata H. L. Clark, 1915, 224; Djakonov, 1954, 74.

Hemilepis arcystata: Fell, 1962, 10.

MATERIAL. Döderlein, no details, 1 specimen.

In this specimen the disc is almost completely scaled above, though interradially the scales are obscured; the ventral side is quite bare. Beyond the base of the arm the middle spines become square at the tips and even slightly bihamulate but the tip is never very broad and the general impression given by most of the spines is that they

are tapering. The dorsal arm plates are ovate, as in the holotype, not rhombic as in the two other specimens figured by H. L. Clark.

Fell (1962) referred *Amphiura arcystata* to *Hemilepis*, which he characterized as having the disc scaled above but partly or wholly naked below. This move was evidently a compromise measure between the three specimens figured by H. L. Clark (1911, fig. 58, p. 146) under the name of *arcystata*, two of which (including the holotype) have more or less extensive skin on the dorsal side interradially and centrally, though the ventral side is quite naked, while the third specimen has a complete scale-covering on both sides of the disc. In fact the type of *arcystata* conforms more closely to the diagnosis of Fell's *Amphinephthys*, with type species *Amphiura crossota* Murakami from the Caroline Islands, which similarly has scales only around the radial shields. Matsumoto (1917) recorded some additional Japanese specimens as *arcystata*, noting that the larger ones have discs of the "*Ophinephthys*-type" (i.e. with scales only around the radial shields), implying that the smaller ones have more extensive scaling, as with H. L. Clark's "Albatross" specimens. Djakonov (1954) also found that some small specimens from the north-west Pacific have fine granuliform scaling on both sides of the disc in contrast to the more usual nearly naked condition.

Unless the station number was incorrect (as H. L. Clark suggested might be possible), the holotype of *arcystata*, together with the 25 "topotypes" from the same station, was from Californian waters, though, with a single exception of doubtful identity, all the other "Albatross" specimens were from Japan. However, in support of the correctness of the "Albatross" station given for the type there are further records from the eastern Pacific, notably by May, Nielsen and Ziesenhene. Although all the specimens of the two latter authors appear to have had mainly naked discs, May noted that specimens from Monterey Bay usually show this condition but sometimes have the disc completely scaled above.

If H. L. Clark, Matsumoto, Djakonov and May are right in considering specimens with more fully scaled discs as conspecific with others with reduced scaling, it seems to me inadvisable to set up generic distinctions based on the extent of the disc scaling alone, as Fell has done. Though very useful in reducing the large number of species of *Amphiura* to more manageable groups, the resultant subdivision is I think too artificial for these groups to be acceptable as genera (or even subgenera) without further limitation of characters. The second character used by Fell to delimit his new genera, namely the number of tentacle scales, is also of doubtful value at the generic level, in my view, but I hope to be able to examine this problem in the detail which it deserves before too long.

Amphiura sp. cf. *euopla* H. L. Clark

see *Amphiura euopla* H. L. Clark, 1911, 144-145, fig. 57; Matsumoto, 1917, 201-202, fig. 55; Murakami, 1944, 265-266.

Hemilepis euopla: Fell, 1962, 10.

MATERIAL. Döderlein, Kagoshima, 1 specimen.

This specimen has the disc diameter 5 mm. and differs from H. L. Clark's descrip-

tion of the type of *euopla* (d.d. 10 mm.) in having the disc finely scaled ventrally as well as dorsally, the radial shields just contiguous, the primary plates distinct, the oral shields with no distal lobes, the distal oral papilla more pointed and the second and third of the seven arm spines conspicuously bihamulate. However, Matsumoto and Murakami both refer specimens to *euopla* with disc diameter less than 6 mm. having the discs scaled ventrally, the primaries distinct, shorter oral shields and the middle arm spines not just blunt but thorny-tipped (some appearing almost hatchet-shaped in Matsumoto's figure while he uses the term "spur-shaped" to describe them). The difference in the radial shields may be illusory since I found on examination of the holotype that the scales only extend between the two radial shields of each pair for the proximal two-thirds of their length, beyond which they gape apart from each other, probably unnaturally. The artist has used his imagination in drawing scales between the distal ends of the shields, which I believe were originally contiguous as they are in this specimen. Even so, there are still so many differences between the type and this specimen, together with Matsumoto's smaller ones, that I am not convinced that they are conspecific. In addition to the characters already mentioned, H. L. Clark notes that a young specimen of *euopla* with disc diameter less than 4 mm. has only four or five arm spines, whereas this one at diameter 5 mm. has as many as seven spines.

In running down this specimen in Matsumoto's key to the Japanese species of *Amphiura* I found the key rather misleading. Both *A. euopla* and *arcystata* come within the section with two tentacle scales, a single distal oral papilla and five to seven arm spines, the last distinction being coupled with the nakedness of the disc at least ventrally, despite the fact that H. L. Clark has referred fully scaled specimens to *arcystata* and Matsumoto himself proceeds to do the same for *euopla*. Then the two species are supposedly distinguished from each other by four characters, according to Matsumoto. However, the first of these four is the thickness of the disc, said to be thick in *euopla* and thin in *arcystata*, and I think that the thickness is too liable to be influenced by abundance of food, seasonal conditions and preservation to allow its use as a specific character. The second point is the extent of the scaling on the disc; this is given as less extensive in *arcystata* but, in view of the variation in this character observed by both H. L. Clark and Matsumoto, this does not seem to provide a valid distinction. Thirdly, there is the shape of the radial shields, described as "short" in *euopla* but "long and rather narrow" in *arcystata*; although the type of *euopla* does have fairly short shields, in the larger, and to a lesser extent also the smaller, specimen figured by Matsumoto under the name of *euopla*, I would describe the shields as long and narrow (if the proportions shown are true). Also in the third specimen figured by H. L. Clark under the name of *arcystata* (the one with the disc fully scaled), the radial shields are much shorter than in the type and other specimen figured. Finally the shape of the arm spines is given as "spur-shaped and rough at the tip" in *euopla* as opposed to "conical, not rough" in *arcystata*; this may be a genuine difference but it should be pointed out that the single specimen in the present collection referred by me to *arcystata* does have the tips of the middle arm spines beyond the base of the arms slightly squared-off and there may even be a small thorn proximally and

distally, though this is quite inconspicuous in comparison with the much widened bihamulate tip of the second and third spines in the specimen from Kagoshima which I believe is conspecific with the smaller ones Matsumoto referred to *A. euopla*, if not with the type of *euopla*.

Another Japanese species with which the Kagoshima specimen has some affinity is *A. pachybacra* Murakami, 1942, from the Izu Peninsula. The latter similarly has the disc completely scaled, two tentacle scales and seven arm spines (at a disc diameter of 8 mm.) but the primary plates are not distinct (though this may well be expected at such a relatively large size), all the arm spines are square-tipped and the second to fifth of them are thorny-tipped without being distinctly bihamulate, the distal oral papilla is blunter (in this specimen it is spiniform), the dorsal arm plates are narrower and the oral shields have a flat distal side, their shape being broadly pentagonal. In fact, *A. pachybacra* is very similar to *A. ambigua* Koehler, 1905, of which a large specimen with disc diameter 11 mm. from Indo-China (identified by Mortensen) is in the British Museum collections. I have compared this specimen with the one from Kagoshima and find that it too has the middle arm spines modified with bihamulate tips, but these tips are much smaller, barely squared-off on the second and third spines and thus more like the corresponding spines in the specimen from the München collection which I have referred to *arcystata*. However, *A. ambigua* also has the disc fully scaled, two tentacle scales and divergent radial shields just contiguous distally, though it differs in having long distal lobes on the oral shields and the distal oral papilla shorter and blunter. In the specimen of *A. ambigua* figured by Koehler in 1922 (pl. 69, figs. 5 and 6) the oral shields appear to have a rather shorter distal lobe but it is still not as short as the lobe in this specimen, where the length : breadth ratio of the whole shield is 14.5 : 14 and the distal side has only a very obtuse angle.

Murakami compared *A. pachybacra* instead with *A. rapida* Koehler, 1930, which is a synonym of *A. poecila* H. L. Clark, 1915, according to H. L. Clark in 1946, the types of both originating in the waters of southern Australia. *A. poecila* has similar oral shields, distal oral papillae, tentacle scales, fully-scaled disc with primaries distinct and fan-shaped dorsal arm plates proximally, like the Kagoshima specimen but it differs in having the radial shields quite separate.

It is surprising that Murakami (1944) referred specimens with the disc fully-scaled to *A. euopla* rather than to his *A. pachybacra* without commenting on their inevitable resemblance to the latter.

Amphiura sp. juv. aff. *koreae* Duncan

see *Amphiura koreae* Duncan, 1879, 466, pl. x, figs. 18, 19; Matsumoto, 1917, 198-199, fig. 53.

MATERIAL. Döderlein, Kagoshima, 2 specimens.

Even the larger specimen has the disc diameter only 2.6 mm. It has two short distal oral papillae like *A. koreae* but differs from Duncan's type specimen in having the proximal end of the oral tentacle scale more nearly superficial and the two papillae of each infradental pair often spaced from each other with a conical tooth in between. Also the type of *koreae* has the inner distal oral papilla arising from the side of the

oral plate rather than from the adoral shield as it does here. However, Lütken and Mortensen (1899) and Matsumoto (1917) emphasize that the oral structure is very variable in the types of *A. diomediae*, which is generally considered to be a synonym of *koreae*.

I believe that *Amphilepis diastata* Murakami, 1942, may prove to be another synonym of *Amphiura koreae*. Although Murakami describes it as having only two oral papillae (i.e. one infradental and one distal) his figure shows two distal papillae, the inner one arising from the distal end of the oral plate where it joins the adoral shield.

The Kagoshima specimen also has some resemblance to *Amphiura confinis* Koehler, 1904, from the East Indies, especially in the superficial position of the oral tentacle scale. The same character allies it with the specimens named *Amphiura concolor* by Lyman from "Challenger" station 191 in the Aru Islands, which also have two distal oral papillae on the adoral shield and the infradental papillae often spaced, conical and with a cusped tooth between them. The "Challenger" specimens are much bigger, even the smallest of them having the disc diameter 6 mm. and their consecutive dorsal arm plates are quite separate from each other, also the radial shields are not contiguous at all distally; otherwise they are very like this specimen. I do not believe that they are conspecific with the type specimen of *A. concolor*, described by Lyman also in the "Challenger" report, since the type has rounded, closely-placed infradental papillae, the dorsal arm plates just contiguous, the disc scales thicker, the oral and adoral shields of different shapes and more numerous arm spines. Indeed, I believe that the Aru Island specimens should be referred to *A. confinis*, though they differ slightly in having the disc scales thinner and the disc as a result smoother than in the types of *confinis*.

Amphiura inepta Djakonov

Amphiura inepta Djakonov, 1954, 77-79, fig. 23.

Amphiura carchara: Djakonov, 1954, 80-81, fig. 25. [Non *A. carchara* H. L. Clark, 1911.]

Monamphiura inepta: Fell, 1962, 11.

MATERIAL. Brashnikow, no, 18, June, 1899, (northern Japan Sea) 2 specimens.

The larger specimen has the disc diameter 6 mm. and there are four spines on each side for the first 17 free arm segments on the only arm remaining attached. The smaller specimen has the disc diameter *c.* 4.5 mm. and has four spines on about 12 proximal segments. The discs of both have the ventral scales spaced from each other in transparent skin, some enlarged plates dorsally and centrally but not forming a regular rosette, the oral shields very blunt proximally, the adorals barely or not quite meeting and the dorsal arm plates oval or wide fan-shaped with a very obtuse proximal angle.

The type specimen of *A. inepta* has the disc diameter 14 mm., while in the type of *A. carchara* H. L. Clark it is 8 mm. Even at this relatively large size the latter has no more than three arm spines, also its primary rosette is not mentioned by H. L. Clark and so is probably indistinct, the disc skin is completely lacking in scales on the ventral side, the adorals are separate interradially and the orals have a proximal

angle. The specimen from the northern Okhotsk Sea figured by Djakonov under the name of *A. carchara* has the disc diameter 5.2 mm. but already has four arm spines proximally and also agrees with the present material in the shape of the oral and adoral shields and in the spaced scales of the ventral side of the disc. Djakonov himself recognized all these differences from the type of *A. carchara* but still did not compare the specimen with *A. inepta*. Although in his key he included *inepta* among the species with two tentacle scales proximally, rarely only one, the figure he gives of the species shows only one scale throughout; the two Brashnikow specimens similarly have no more than one scale. Djakonov's material of *A. inepta* came from La Perouse Strait (between Hokkaido and Sakhalin), southern Sakhalin and the north-east Okhotsk Sea.

Amphiura digitula (H. L. Clark)

(Text-fig. 2)

Amphiodia digitula H. L. Clark, 1911, 162-164, fig. 70.

Amphiura digitula: Matsumoto, 1917, 199-200, fig. 54; Djakonov, 1954, 71.

Amphiura leptopholida H. L. Clark, 1915, 226-227, pl. iv, figs. 11, 12 [Possibly recognisable as a distinct form of *digitula*.]

Diamphiodia digitula: Fell, 1962, 14.

MATERIAL. Döderlein: Enoshima 22, 1 badly damaged specimen; Enoshima 24, 3 specimens without discs; (?Doflein), Kachiyama, 5 specimens with discs, 6 without; Döderlein: Enoshima, 4 specimens of forma *leptopholida*.

The present material together with Matsumoto's observations and my drawings of the types of some of H. L. Clark's nominal species from Japan, made in 1953 in the U.S., suggest that *Amphiura digitula* tends to intergrade with *Amphioplus ancistrotus* (H. L. Clark). This is not so surprising as it may seem at first sight since the two genera are closely related and species of *Amphiura* with two distal oral papillae, such as *A. digitula*, need only the development of a single intermediate papilla to bridge the gap to *Amphioplus*. The species of both genera possess a first oral tentacle scale higher in the oral slit each side of the jaw, which is completely absent in *Amphiodia*, where the oral papillae are only numerically, not morphologically, intermediate between those of the type species of *Amphioplus* with four papillae and of *Amphiura* with two.

H. L. Clark in 1911 referred both *digitula* and *ancistrotus* to *Amphiodia* but when Matsumoto studied the homologies of the oral papillae of Amphiurids he recognized that, although *digitula* has two distal oral papillae, these are based on the adoral shield rather than the oral plate and an oral tentacle scale (additional papilla in Matsumoto's terminology) is present; accordingly the species should be referred to *Amphiura*. There are several comparable species of *Amphiura*, notably *A. koreae*, in which there are two distal oral papillae, similarly arising from the edge of the adoral shield (though the inner of the two may be based about the point of junction of the adoral shield and the oral plate). Even if Fell's *Diamphiodia* proves to be sufficiently natural for recognition as a genus distinct from *Amphiodia*, there is no question that

digitula could be referred to it since the type species of *Diamphiodia* has oral papillae similar to *Amphiodia*. Matsumoto also referred *Amphiodia ancistrotota* to *Amphioplus* because of its total of four (sometimes even five) oral papillae together with an oral tentacle scale.

Both these species have rather unusual paired digits outside the radial shields, which prompted the name *digitula*; also both have two tentacle scales of moderate size, somewhat similar arm plates and radial shields which are divergent and more or less narrow (the width is exaggerated in H. L. Clark's figure 69 (1911) of *A. ancistrotus* in comparison with the type specimen). The type of *Amphiura digitula* is distinguished particularly by the spiniform shape of the inner one of the two distal oral papillae and by the diastema between this papilla and the infradental one (characteristic of the genus *Amphiura* as opposed to *Amphioplus*) also by the fine, almost granuliform, scaling of the disc ventrally and marginally, contrasting with the smoother and larger dorsal scales. In the type of *Amphioplus ancistrotus* there are four rounded oral papillae in continuous series and the ventral disc scales are smooth and not extremely fine.

Between or close to one or other of these two extremes come two other Japanese amphiurids described by H. L. Clark in 1915 as the types of new species. One of these was referred to *Amphiura* and the other to *Amphioplus* (incidentally supporting Matsumoto's generic dispositions), so that Dr. Clark failed to compare them with either *digitula* or *ancistrotus* since he had left these both in *Amphiodia* in 1911.

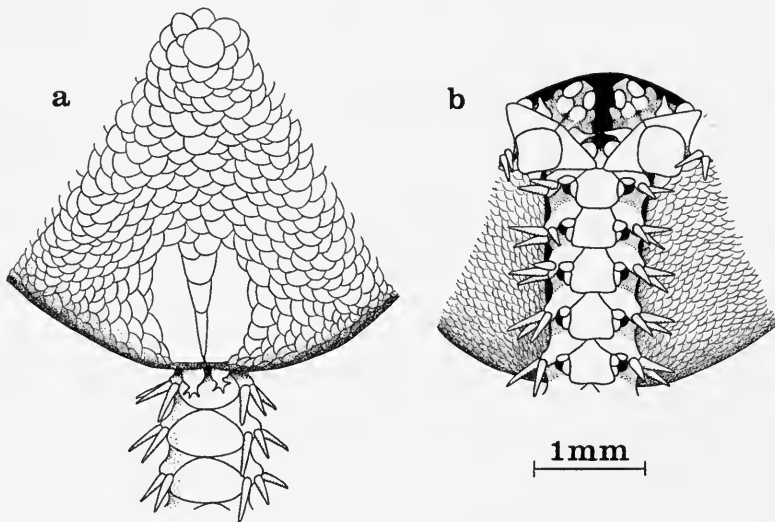


FIG. 2. *Amphiura digitula* forma *leptopholida* H. L. Clark. Holotype of *A. leptopholida*, M.C.Z. no. 1365. (a) Dorsal and (b) ventral partial views of disc and oral area.

The first of these nominal species (fig. 2), which he named *Amphiura leptopholida*, has oral papillae almost identical with those of the type of *digitula*, the inner of the two distal ones being spiniform; also it has pairs of digits outside the radial shields. The

only differences are that the ventral disc scales are not very small and granuliform but smooth and somewhat larger and the second from lowest of the four arm spines has a very slight terminal hook rather than a simple tip. The four specimens in the Munich collection from "Enoshima" differ from the complete specimens labelled "Enoshima 22" or "24" and the rest from Kachiyama (all of which are immediately recognizable as *digitula*) in having the ventral disc scales smooth, not granuliform, and the second arm spine distinctly hooked on the segments beyond the base of the arm. Since the disc is easily lost in this species, judging from the proportion of incomplete specimens in the present collection, it is possible that the difference in disc scaling at least is correlated with regeneration. Three of the four Enoshima specimens exceed by 2 or 3 mm. the 6 mm. disc diameter of the types of both *A. digitula* and *leptopholida*, so the presence of five rather than four arm spines basally is only to be expected; the fourth specimen, disc diameter 5 mm., has four spines basally.

The differences being of such small magnitude, I believe that the types of *digitula* and *leptopholida* are conspecific, nevertheless I think it worthwhile to distinguish specimens with smooth disc scales and hooked arm spines (if these characters prove to be consistently linked) as forma *leptopholida*, though such infrasubspecific taxa have no status in taxonomy, according to the Code of the International Commission.

The second nominal species of H. L. Clark, 1915, is *Amphioplus lobatodes*. Apart from minor differences in the proportions of the oral shields and lesser curvature of the second arm spine, there seems to me no reason why it should not be referred to the synonymy of *A. ancistrotus*.

The Munich collection also includes three Amphiuroids which, like *Amphiura leptopholida*, present an intermediate condition between *A. digitula* and *Amphioplus ancistrotus*. These are described under the heading of the latter species.

Amphioplus ancistrotus (H. L. Clark)

(Text-figs. 3 and 4)

Amphiodia ancistrota H. L. Clark, 1911, 161-162, fig. 69.

Amphioplus ancistrotus: Matsumoto, 1917, 171-172, fig. 43; Chang, 1948, 54-55, fig. 11, pl. viii, fig. 7; Djakonov, 1949, 54, fig. 69; 1954, 61; Fell, 1962, 17.

Amphioplus lobatodes H. L. Clark, 1915, 254-255, pl. vii, figs. 12, 13.

MATERIAL. No details, presumably southern Japan, 2 specimens; Haberer, Sagami Bay, 7. vii. 1904, 1 specimen of a distinct form; Döderlein, Enoshima 24, 2 specimens of the same form.

As mentioned under the heading of *Amphiura digitula*, I consider *Amphioplus lobatodes* to be a synonym of *A. ancistrotus*. The drawing of the type, which I made in 1954 when visiting the United States, shows no digits distal to the radial shields in the radius depicted. Unfortunately I omitted to notice whether this was also true of the other radii. H. L. Clark's brief description, largely comparative with *A. lobatus*, makes no mention of this feature. If digits are really absent, then it may be possible to distinguish *lobatodes* from *ancistrotus* but I doubt this.

In the two specimens with no detailed locality the oral papillae are all short and rounded. Although H. L. Clark's figure of the holotype shows the third (from innermost) papilla as conical and somewhat elongated, I found on examination of the holotype that the three inner papillae are all rounded, though subequal, while the third one is not erect (fig. 3a); in fact they are just as described by Dr. Clark, accordingly I have no doubt that these two specimens are conspecific with the type.

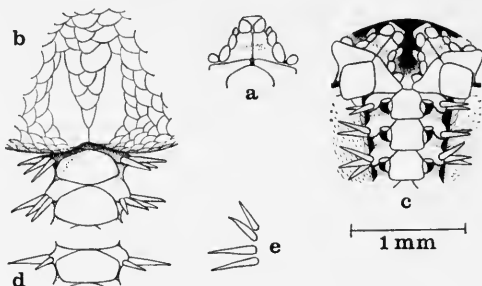


FIG. 3. *Amphioptus ancistrotus* (H. L. Clark). (a) Holotype of *Amphiodia ancistrotota* H. L. Clark, U.S.N.M. no. 25601, oral papillae. (b) to (e) holotype of *Amphioptus lobatodes* H. L. Clark, M.C.Z. no. 1480; (b) dorsal and (c) ventral partial views of disc and oral areas, (d) segment with twenty-second dorsal arm plate, (e) arm spines of twelfth free segment. In (c) the ventral scaling is in reality barely distinct, especially proximally where it is very tenuous and broken in most interradii.

The other three specimens in the Munich collection, however, have the third oral papilla, and to some extent the second also, erect and spiniform. Matsumoto's figures 43b and c both show these papillae as elongated and acute, but in Chang's drawing all the papillae are short and rounded as in the type of *Amphioptus lobatodes* (fig. 3b-e). (It should be noted that Chang's specimen has the disc naked ventrally so the identification may be incorrect, however the disc diameter was only 3 mm. and the small size might contribute to this deficiency.) In most other characters, namely the form of the arm plates, tentacle scales, hooked second arm spine and particularly the paired digits outside the radial shields, these three specimens agree with the first two mentioned but their oral papillae provide such a sharp contrast that I consider it worthwhile to designate this form with the two middle oral papillae erect and spiniform as forma *anisopapilla* of *Amphiura ancistrotus*. Although such infrasubspecific names are not recognized by the International Commission on Zoological Nomenclature and have no status in taxonomy, I think they still have their uses for the sake of comparison. The shape of the oral shields, the extent of contact of the adorals and the proportions of the radial shields all appear to be variable in *A. ancistrotus* and it is interesting that some of the shapes exhibited approximate to those found in *Amphiura digitula*. (It may be noted here that H. L. Clark's figure of the holotype of *Amphioptus ancistrotus* shows the radial shields shorter than they really are and therefore relatively too wide.) There are two minor differences between the specimen of forma *anisopapilla* figured and the type of *ancistrotus*, namely in the former the disc scales are particularly indistinct and the dorsal arm plates appear thinner and

more transparent. However, I doubt whether these differences are significant.

The two specimens of unknown locality, which may be designated as forma *ancistrotus*, have disc diameters of 9 mm. and 6 mm. In both of them the second from lowest arm spine is hooked but the larger specimen has five arm spines on the first four or five free segments, while the smaller one has no more than four basally.

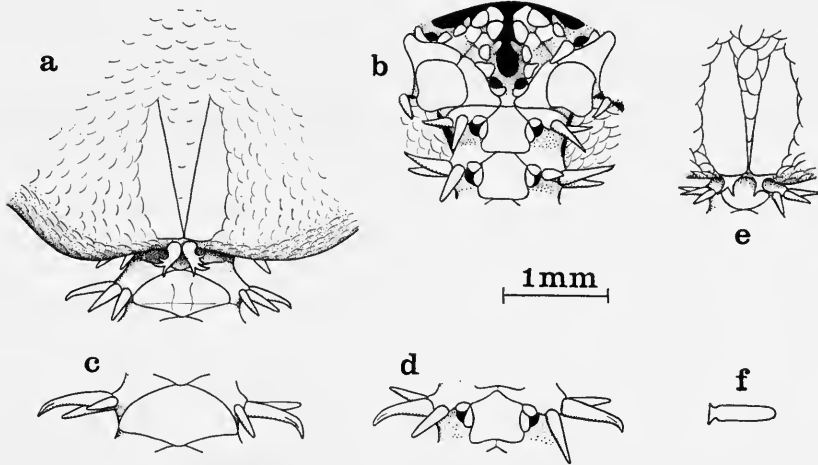


FIG. 4. (a) to (d) *Amphioplus ancistrotus* forma *anisopapilla* nov. Enoshima 24. (a) Dorsal and (b) ventral partial views of disc and oral area, (c) segment with fourteenth dorsal arm plate, (d) segment with twelfth ventral arm plate. (e) and (f) *Amphioplus conductus* Koehler, holotype, U.S.N.M. no. 41161, (e) a pair of radial shields with hyaline processes distal to them, (f) the second from lowest arm spine of a middle arm segment. In (a) the dorsal disc scales are very indistinct, also the dorsal arm plate is semi-transparent and the underlying ossicles are indicated below it. In (b) three of the third oral papillae shown are more or less fore-shortened, whereas the fourth has become appressed.

The larger Enoshima specimen of forma *anisopapilla* (fig. 4a-c) has the disc 7 mm. in diameter. The radial shields are 1.3-1.45 mm. long and 0.4 mm. in maximum width; the proximal angle is acute. The smaller specimen from the same locality has the disc 3 mm. across and differs in having the oral shields longer and more acute proximally. The Sagami Bay specimen has the disc diameter just over 7 mm. and, unlike the other two, has the primary rosette just distinct; its radial shields are smaller, with length : breadth 0.8 : 0.2 mm. and only the third oral papilla is spiniform.

There are a few species of *Amphioplus* which similarly have the middle oral papillae spiniform, but all of them have only a single tentacle scale. They include *A. dispar* (Koehler), 1897, from the Indian Ocean, *A. aciculatus* from off the Congo and *A. acutus* from the Antarctic, both species of Mortensen, 1936 (Discovery Report), also *A. gastracantha* and *notacantha* (Lütken and Mortensen), 1899, from the East Pacific, though the two last-named differ further in having a few disc spinelets so that they may not be referable to *Amphioplus* at all but to *Amphiacantha*.

Amphioplus ancistrotus is closely comparable with *A. diacritus* Murakami (1943, p. 225), the type of which has the disc diameter as much as 10 mm. The plates of

the primary rosette in *A. diacritus* are small but distinct, the radial shields appear to be longer and narrower than in *ancistrotus* and not so divergent, also the arm spines number only three even at this large size, the middle one the longest but evidently not hooked at the tip (though, as all the arms are said to be broken at the base, since specialized spines only develop further out on the arm, in most Amphiuroid species that have them, it is possible that all the segments with hooks have been lost). *A. diacritus* is possibly more closely related to *A. rhadinobranchius* H. L. Clark, another Japanese species with only three arm spines. It is noteworthy that in Murakami's figure of *A. diacritus* there are paired processes distal to the radial shields though none are mentioned in his description.

A few other species of Amphiuroids from the western Pacific have similar processes. One such is *Amphiacantha acanthina* (H. L. Clark), also from Japan, which has distal angles to the dorsal arm plates like *Amphioplus ancistrotus* but differs in having only three arm spines as well as in the generic character of possessing spines on the disc. A second species is *Amphioplus conductus* Koehler from the Philippines, in the holotype of which I found paired hyaline bifurcating digits distal to the radial shields (fig. 4d) not observed by Koehler. The only significant differences I can see between *conductus* and *ancistrotus* are that, at a disc diameter of 6 mm., *A. conductus* already has six arm spines on some basal segments and the second of these is not hooked but bifurcated; also the dorsal arm plates lack the marked distal angle.

***Amphioplus asterictus* H. L. Clark**

(Text-fig. 5)

Amphioplus asterictus H. L. Clark, 1915, 252, pl. vii, fig. 9-11.

MATERIAL. Haberer, Sagami Bay, 7.vii.1904, 1 specimen lacking the disc.

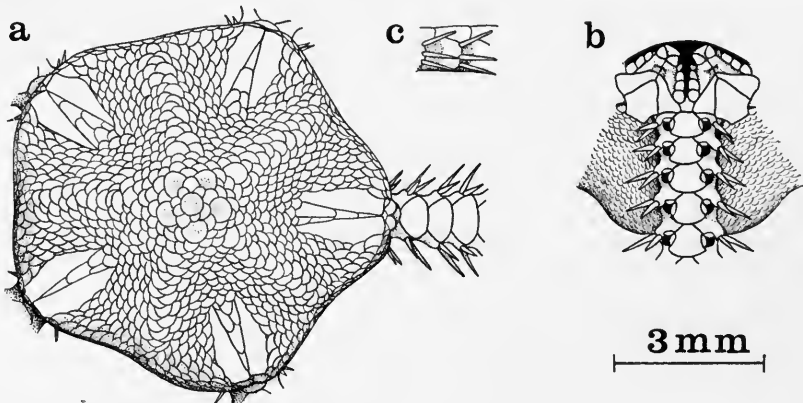


FIG. 5. *Amphioplus asterictus* H. L. Clark. Holotype, M.C.Z. no. 1486. (a) Disc and one arm base viewed dorsally, (b) two jaws and part of the disc viewed ventrally, (c) spines of two proximal segments. In (a) the primary disc scales are slightly hollowed, not thickened.

Since H. L. Clark published only photographs of the type, I give here a drawing of it which I was able to make at the Museum of Comparative Zoology, thanks to the kindness of Dr. Elisabeth Deichmann.

Amphioplus japonicus forma *parvus* (Matsumoto)

Amphioplus relictus (part), Koehler, 1922, 180, pl. lxxi, figs. 7, 8; Fell, 1962, 17. [Non *A. relictus* (Koehler), 1898].

Ophiophragmus japonicus var. *parvus* Matsumoto, 1941, 334-336, figs. 3, 4.

MATERIAL. Döderlein: Tango, 40 fathoms (73 metres), 1 specimen; Tango 4, 7 specimens; Kagoshima, 6 specimens; no details, 7 specimens.

The generic position of *Ophiophragmus japonicus* has been the subject of some controversy. Matsumoto (1915) included the species in *Ophiophragmus* because of the erect marginal scales, despite the fact that it has four oral papillae. Since the possession of only three papillae is partly diagnostic of *Ophiophragmus*, H. L. Clark (1918, p. 271) referred *japonicus* to *Amphioplus* noting that the erect "fence" of marginal scales is *not* homologous with the articulated marginal papillae or spinelets found in the other species of *Ophiophragmus*, including the type, *O. wurdemanni* (Lyman), 1860 (of which no good figures existed up to that time, Koehler (1914) having confused the issue by publishing photographs of *Amphiodia limbata* under the name of *Ophiophragmus "wundermanni"*). Likewise H. L. Clark referred *Ophiophragmus affinis* Duncan, 1887, to *Amphioplus* [where the name became invalid as a homonym of *A. affinis* (Studer)], noting that it is probably identical with *A. relictus* (Koehler), 1898. Matsumoto had considered Duncan's *affinis*, which came from the Bay of Bengal, to be a close relation of *japonicus* together with *Amphipholis andreae* Lütken, 1872, from Java, *Amphiura praestans* Koehler, 1905, from the Flores Sea and *Amphiodia periercta* H. L. Clark, 1911, from Alaska and Oregon, U.S. [The last-named of these is a true *Amphiodia* but the others are currently referred to *Amphioplus*.]

In 1922 Koehler also referred *affinis* Duncan, as well as his own *Amphiura relictus*, to *Amphioplus* on the grounds of differences in the internal structure in comparison with *Ophiophragmus wurdemanni*.

In 1941 Matsumoto noted that the additional oral papilla above the main series of superficial papillae (alternatively called the first oral tentacle scale) is absent in *japonicus* unlike the type species of *Amphioplus*, *A. tumidus* (Lyman). Accordingly he disagreed with H. L. Clark's transfer of the species to *Amphioplus* and retained it in *Ophiophragmus*. Having removed the three distal oral papillae of one series in a specimen from this collection, I can confirm that Matsumoto's observation is correct. However, in the closely related species *Amphioplus hastatus* (Ljungman) the oral tentacle scale may not be visible in some specimens, even when the overlying papillae are displaced, though its development is clearly variable since in others a small scale or papilla can be distinguished. *A. hastatus* may also have spinous projections on the uppermost row of ventral scales similar to those occurring in *japonicus*, as Mortensen (1940, Echinoderms from the Iranian Gulf) has shown.

Disc diameter (mm.)	Arm length (mm.)	A.l. : d.d. ($\times : 1$)	No. of scales across interradius	Radial shields Length Breadth (mm.)	Radial shields I : br ($\times : 1$)	Disc r (mm.)	R.s.l. : disc ($\times : 1$)
2.5	—	—	5-7	0.53 0.26	2.05	1.25	0.42
2.5	—	—	7	0.50 0.25	2.00	1.25	0.40
2.75	—	—	7-9	0.63 0.26	2.40	1.40	0.45
3.1	16	5.2	6.7	0.70 0.29	2.40	1.55	0.45
3.3	—	—	7-9	0.74 0.29	2.55	1.65	0.45
3.7	21	5.7	7-9	0.74 0.33	2.25	1.85	0.40
4.0	—	—	9	0.74 0.40	1.85	2.00	0.37
4.0	6.27	6.7	6.7	0.74 0.35	2.10	2.00	0.37
4.0	—	—	9	0.74 0.37	2.00	2.00	0.37
4.0	—	—	7 (8)	0.75 0.37	2.00	2.00	0.39
4.3	6.26	6.0	9	0.80 0.37	2.15	2.15	0.37
4.4	26	5.9	9	{ 0.74 0.34 0.80 0.40	2.20	2.20	{ 0.34 0.37
4.5	—	—	9 (11)	0.71 0.38	1.85	2.25	0.32
4.6	6.27	5.8	6.9	0.75 0.35	2.15	2.30	0.33
5.0	6.26	5.2	6.11	0.80 0.40	2.00	2.50	0.32
5.0	6.27	5.4	9-11	0.79 0.34	2.30	2.50	0.32
5.0	—	—	9	{ 0.82 0.42 0.87 0.50	1.95	2.50	{ 0.33 0.35
5.1	26+	5.1+	11	0.84 0.40	1.75	2.55	0.33
5.2	31.5	6.0	9	0.76 0.34	2.10	2.60	0.29
5.25	—	—	11	0.87 0.34	2.55	2.60	0.33
8.4	—	—	11	{ 1.00 0.53 1.10 0.55	1.90	4.20	{ 0.24 0.26
Range 2.5-8.4	16-31.5 +	5.2-6.7 : 1	5-11	0.53- 0.25- 1.10 0.55	1.75- 2.55 : 1	1.25- 4.20	0.24- 0.45 : 1
Mean		5.7 : 1			2.1 : 1		0.36 : 1

Amphioplus japonicus forma *parvus*. Some measurements and ratios of 21 specimens, three of them with varying proportions for the radial shields.

Accordingly, together with Fell (1962), I agree with H. L. Clark that *japonicus* is better referred to *Amphioplus*, although I believe that, together with *A. hastatus*, *depressus*, *relictus*, *andreae*, *laevis*, *praestans*, *megapomus*, *miyadaii* and some others, it may be possible to distinguish it as forming part of a subgenus marked off from *Amphioplus tumidus*, the type species of the genus, by the reduction of the oral tentacle scale coupled with linear arrangement of the oral papillae, contiguity of the radial shields and enlargement of the two tentacle scales of each arm pore.

The present specimens are referred to Matsumoto's forma *parvus*, of *A. japonicus* because none of them have the row of enlarged outermost dorsal disc scales shown by Matsumoto in his figures of *japonicus* itself. I have not seen any specimens of the latter and am unable to assess whether or not the forma is worth retaining.

The table given here shows some measurements of 21 specimens of *A. japonicus* forma *parvus*. It indicates that the relative size of the radial shields decreases as growth proceeds, from a maximum of just under half the disc radius at about 3 mm. disc diameter to a minimum of only a quarter when the diameter is over 8 mm. Since this ratio has been used to distinguish between related species belonging to this section of the genus *Amphioplus* it is clearly advisable that the total size of the disc should be taken into account when making such comparisons.

When describing *parvus* in 1941, Matsumoto commented that it is allied to *Amphioplus megapomus* H. L. Clark. Having examined the discless type specimen of *megapomus* I cannot agree with this. The dorsal arm plates of *megapomus* have a median distal peak, so appearing trilobed, and the arm spines are much more acute than in *japonicus*. In 1915, H. L. Clark noted that complete specimens of *A. megapomus* have relatively wide radial shields as in *A. japonicus*. Despite this, I believe that *A. megapomus* is more likely to prove conspecific with *A. miyadaii* Murakami, 1943, also of Japanese origin, since it agrees in the oral structure and in the distinctive trilobed dorsal arm plates. Regeneration of the disc in those species of *Amphioplus* which are particularly liable to shed it, such as *A. integer*, results at first in abnormally short radial shields, though their relative length increases as growth proceeds. If the specimens with discs studied by Clark in 1915 were regenerating, the shields would probably be abnormally short. However, another possibility is that these intact specimens were not conspecific with the types of *megapomus* since Clark noted that their arm plates were not identical. *A. miyadaii* is certainly more closely related to *A. laevis* (Lyman) and *praestans* (Koehler) with similarly elongated radial shields, than it is to *A. japonicus*.

In contrast to the type of forma *parvus*, the majority of the present specimens have the six primary plates distinct, if not by larger size then by a slight hollowing of their surface. In the smallest specimens the primaries are partly contiguous with each other, having interstitial scales only at their corners (as in Koehler's photograph of the small type of *A. hastatus* (1927), *Ark. Zool.*, **19**, pl. 3, fig. 2) but in larger specimens the primaries are more or less widely separated.

In 1922 Koehler referred sixty-four specimens from Kagoshima, Japan, as well as a number of Philippine specimens to *Amphioplus relictus*, noting that the relative width of the oral shields is variable and that some specimens (of which he figures one

from Kagoshima) have a distinct marginal row of erect disc scales. I have found that some of the specimens earlier (1905) identified as *A. relictus* by Koehler, at least those from "Siboga" stations 51 and 71 (Makassar and Molo Strait in the East Indies), have a distinct enlarged row of marginal disc scales contrasting with the uppermost row of smaller ventral scales, which are erect and project to form a scalloped edge to the disc, as in some specimens of *A. japonicus*. Nevertheless, I think that Koehler's Kagoshima specimens are more likely to be referable to *A. japonicus* than *relictus* since the ventral view of one (1922, pl. 71, fig. 7) suggests that the distal edge of the oral shields is simply convex as in all the present specimens, without having a distinct, more or less constricted, distal lobe, as occurs even in Koehler's Manila specimen (pl. 71, fig. 6) where the shields are particularly wide in comparison with those of most Philippine and East Indian examples of the species, in which the distal lobe is usually as long as the proximal angle. [In the Manila specimen the shape is very like that found in one of the syntypes of *A. andreae*, seen by me at the Museum of Comparative Zoology, and it is possible that it should have been referred to *andreae* and not to *relictus*.]

As these remarks indicate, the distinctions between *Amphioplus hastatus*, *depressus*, *relictus*, *andreae* and *japonicus* are very subtle and in need of further consideration when a true assessment of variation and growth changes can be made together with re-examination of the types.

Amphiodia craterodmeta H. L. Clark

Amphiodia craterodmeta H. L. Clark, 1911, 155-157, fig. 65; Matsumoto, 1917, 182; Djakonov, 1938, 463; 1949, 54, fig. 72; 1954, 62.
Diamphiodia craterodmeta: Fell, 1962, 14.

MATERIAL. Domaschnew, nos. 53 and 55, 20.vi.1900 and 27.vii.1900, 4 specimens; Brashnikow, no. 6, July, 1899, 2 specimens; Schmidt, nos. 9 and 10, Mauka, south-west Sakhalin, 46-47 sageses (c. 100 metres), 8.vi.1901, 19 specimens. (All N. Japan Sea).

Of the two specimens from Brashnikow's number 6, the larger has the disc diameter 8 mm. and the smaller 4.5 mm. The former has no distinct primary disc scales, the oral shields are very small with the distal lobe both sunken and constricted, also the infradental papillae are widely spaced and head the series of three oral papillae each side and the disc plates are all extremely well-defined. The smaller specimen from no. 6 differs in having the primaries much larger than the other scales.

In comparison with *Amphiodia fissa*, this species differs in having narrower (but still mainly contiguous) radial shields, entire dorsal arm plates, smaller oral shields and larger adorals, the primary disc scales not so different from the other scales, four arm spines proximally and the ventral tentacle scales longer.

Amphiodia fissa (Lütken)

(Text-fig. 6)

Amphipholis fissa Lütken, 1869, 12-13 (30-31).

Amphiodia rossica Djakonov, 1935, 465, figs. 7 and 8 ; 1938, 465-466, fig. 8 ; 1949, 55, fig. 71 ; 1954, 64, fig. 18.

Diamphiodia fissa and *rossica* : Fell, 1962, 14.

MATERIAL. Schmidt, nos. 3 and 5, Mauka, south-west Sakhalin, 20 and 15 sagues (42 and 31 metres), 3.vi.1901 and 4.ii.1901, 5 specimens ; no. 21, Posjet Bay, near the bay of Minanosok, 12 sagues (26 metres), 6.iv.1900, 4 specimens ; no. 81, entrance to the bay of Tshogu-tschien-dogu, 11 specimens.

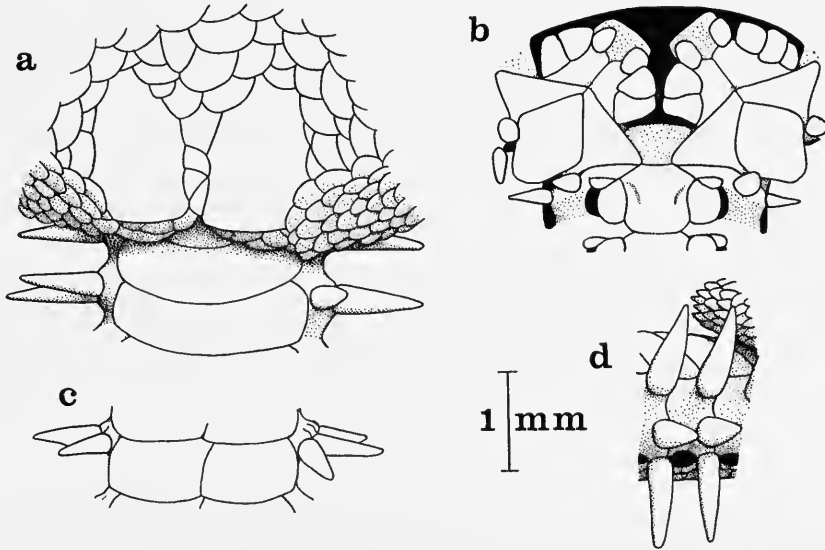


FIG. 6. *Amphiodia fissa* (Lütken). Specimen from Peter the Great Bay, M.C.Z. no. 4622, labelled as *A. rossica* Djakonov. (a) Dorsal and (b) ventral views of parts of the disc and oral area, (c) segment with fifteenth (split) dorsal arm plate, (d) lateral view of an arm base showing the individually projecting disc scales ; the middle arm spines fore-shortened.

NOMENCLATURE. Lütken described this species in Danish from material collected on the Amur coast (i.e. probably in the vicinity of Vladivostok), giving also a short latin diagnosis but no figures. The very unusual feature for an Amphiuroid of the subdivided dorsal arm plates, which gave the species its name, taken in conjunction with the peculiar erect marginal scales of the disc, leaves me in no doubt that *Amphiodia rossica* Djakonov (also from the Amur region), which shares these characters, was based on material of this same species. In his original description of *Amphiodia rossica* (1935) Djakonov made no mention of *Amphipholis fissa* but in 1954 he commented on the possible identity of the two ; however, with no published figure of the type of *A. fissa* in existence he evidently thought that sufficient doubt exists to justify the continued use of the name he had himself established.

Since Lütken's name *Amphipholis fissa* has remained in oblivion for well over 50 years, I submitted to the International Commission on Zoological Nomenclature a petition to obtain the suppression of the name *A. fissa* as a *nomen oblitum*. This case

is suspended in view of the controversy regarding *nomina oblita* in general raised at the last colloquium on nomenclature.

REMARKS. The smallest of the five specimens from Mauka has the disc diameter only 3.5 mm. and the proximal tentacle scale on the lateral plate is reduced or absent on all but the basal pores, though the scale on the ventral arm plate is quite large. The dorsal arm plates are nearly all split and fairly regularly so, also the marginal disc scales are erect. In another small specimen with disc diameter 3 mm. the ventral scale is also absent on segments beyond the tenth and sometimes as far proximally as the fifth. The larger specimens have the disc diameter about 10 mm.

Yet another small specimen, with disc diameter only 2.75 mm., has the dorsal arm plates fan-shaped and not split. It also has the plates of the primary rosette in direct contact with each other, whereas in specimens with disc diameter 5 mm. or more the primaries are all separated. The splitting of the dorsal arm plates seems to start with the distal plates and progress proximally, but even when the plates are not split the arms appear distinctly carinate. One specimen with disc diameter 4.5 mm. has the first five to seven plates entire; it also has three arms regenerating, each with a soft, worm-like tip, not yet distinctly segmented. There are two tentacle scales only to about the twentieth segment, then one.

Other variable characters include the erection of the marginal disc scales, which may be lacking, also the development of the distal lobe of the oral shields.

Since Djakonov's figures are unnatural with regard to the mouth parts and not quite in agreement with the specimens I have seen, it seems worthwhile to give here a figure of an oral angle drawn from a specimen presented by Djakonov to the Museum of Comparative Zoology, Harvard.

Family OPHIOTRICHIDAE

Ophiothrix sp. ?*eusteira* H. L. Clark

Ophiothrix eusteira H. L. Clark, 1911, 265-267, fig. 132; Matsumoto, 1917, 222-223, fig. 60.

MATERIAL. Döderlein, 7. xi. 1881. III, 170 fathoms (311 metres), 1 specimen.

The single specimen has the disc diameter 7.5 mm. The radial shields are large, c. 2.4 mm. long, and completely bare. The disc scales are clearly visible below the sparse covering of small, spaced, tapering stumps, though some have about three long thorns remaining on their tips. In the middle of the disc are a few short spines only, agreeing more with Matsumoto's figured specimen than with the holotype, which has the central spines very long. There is more resemblance to the specimen figured by Koehler (1922, pl. 45, fig. 6) under the name of *Ophiothrix koreana*, which I think would be better referred to *O. eusteira* in view of my observations (below) about the types of *O. koreana*.

This specimen is only doubtfully identified as *Ophiothrix eusteira* because it already has as many as nine arm spines on the second free segment, whereas the holotype, with disc diameter 1.5 mm. greater, has only six or seven spines, according to H. L. Clark.

Ophiothrix koreana Duncan

(pl. I, figs. 3 and 4.)

Ophiothrix koreana Duncan, 1879, 473-476, pl. xi, figs. 28-32; H. L. Clark, 1911, 257-262, figs. 127-128; Matsumoto, 1917, 220; Murakami, 1942, 20; 1943, 232-233; 1944, 267; Djakonov, 1954, 88.

MATERIAL. Döderlein: Yogashima, 3 specimens; Yogashima, 2.xi.1881, 3 specimens; Yogashima 2 & 3.xi.1881, 1 specimen; Enoshima 18, 183 metres, 8.xi.1881.II, 1 specimen; Tango, 73 metres, 2 specimens.

Duncan's figures of the syntypes of *Ophiothrix koreana* were not very good so I give here photographs of the upper surfaces of two of them. These show that, unlike the specimens figured under the name of *koreana* by H. L. Clark, which subsequent writers have taken as models of the species, their radial shields carry a number of thorny, mostly trifid, stumps at their distal ends as well as proximally, though the stumps appear more sparse on the shields than on the scales. The largest syntype, with disc diameter 8 mm., has about 30 stumps on each radial shield including four or five at the distal tip, while the smallest specimen, disc diameter 4.5 mm., has about 12 stumps on each shield. This smallest syntype, as well as one other out of the six, has some thorny disc spines in addition to the stumps but the remaining four have no spines and superficially resemble H. L. Clark's figure of *Ophiothrix hylodes* (1911, p. 263, fig. 130), which Matsumoto and subsequently Clark himself referred to the synonymy of *Ophiothrix marenzelleri* Koehler, 1904a. The type of *hylodes* has the disc stumps (or "stout, blunt, rough spines" in Dr. Clark's terminology) with irregular thorns along their lengths and at their tips rather than the trifid form found in the types of *O. koreana* and also in the specimens identified as *O. marenzelleri* by Koehler (1922). However, some of the specimens of the present collection also have "stumpy spines" of this kind, so the form of the stumps cannot be considered as diagnostic. H. L. Clark did not mention *O. marenzelleri* in his work of 1911, but commented that *O. hylodes* might be "only an extreme variety of *koreana*". Matsumoto repeated this supposition and noted that "the sublittoral form (of *marenzelleri*) approaches *O. koreana* more closely than the littoral form", this sublittoral form sometimes having a few long spines on the disc as well as the close covering of thorny stumps or tubercles. Matsumoto did not comment on the density of tubercles on the radial shields as being any less in the littoral form than in the sublittoral but Koehler (1904a, p. 104) noted that in the types of *O. marenzelleri* the radial shields are almost as closely covered with stumps as the rest of the disc.

In the present collection I have identified as *O. marenzelleri* specimens in which the stumps appear equally dense on the radial shields as on the rest of the disc and those with the radial shields distinctly barer I have named *O. koreana*. However, so close are the types of *O. koreana* to the form generally accepted as *O. marenzelleri* that I think the latter name might well be considered a synonym. Judging from the variation of *Ophiothrix fragilis* in the north Atlantic it is quite possible that the Japanese specimens hitherto designated as *koreana*, *marenzelleri*, *hylodes* and possibly even *eusteira* H. L. Clark, 1911, all represent a single very variable species. Alternatively the specimens with almost or completely bare radial shields such as those

figured under the name of *O. koreana* by H. L. Clark in 1911 might be referred to *O. eusteira*. A much larger collection than that available to me is necessary before a proper assessment of this problem can be made, so notorious is the genus *Ophiothrix* for its variability.

Ophiothrix stabilis Koehler

Ophiothrix stabilis Koehler, 1904a, 84-86, figs. 46-49; Matsumoto, 1917, 224; Murakami, 1944, 268.

Ophiothrix ciliaris: H. L. Clark, 1911, 257. [Non *O. ciliaris* (Lamarck), 1816.]

MATERIAL. Schmidt, 1901, Nagasaki, 3 specimens.

These three specimens were taken with one which I have referred to *Ophiothrix marenzelleri*. They are immediately distinguishable from it by the disc stumps which are shorter and better-termed tubercles than stumps; they also have a coronet of usually five to seven divergent points. Some disc spines are also present as in the holotype *O. stabilis* but there is a difference in the shape of the ventral arm plates. None of these have the distal edge markedly convex as Koehler describes it in the holotype (though his figure may not be reliable since it shows the ventral-most arm spines with their hooks directed inwards instead of outwards or proximally, when aligned perpendicularly, as in other species of *Ophiothrix* and in the three specimens of *O. stabilis* in the present collection).

Since Matsumoto used the convex or concave shape of the distal edge of the ventral arm plates as an important character in his key to the Japanese species of *Ophiothrix*, the identification of these three specimens as *O. stabilis* invalidates this particular dichotomy of his key. This dichotomy was already untrue for *O. eusteira*, included with *stabilis* as having convex edges to these plates, whereas only two proximal plates are so depicted in H. L. Clark's figure of *eusteira* and none at all in Matsumoto's own figure, where all the plates appear incurved in the middle of the distal side.

Ophiothrix panchyendyta H. L. Clark

Ophiothrix panchyendyta H. L. Clark, 1911, 264-265, fig. 131; Matsumoto, 1917, 219.

MATERIAL. Okinose Bay, 600 metres, 1 specimen.

The disc spines appear longer than shown in H. L. Clark's figure of the type. The disc diameter of this specimen is 10.5 mm. and the majority of the spines towards the centre of the disc are 1.7-2.0 mm. long. The length of the corresponding spines was not specified in the type. There are hardly any short stumps on the disc besides the spines. Close to the proximal interradial edge of each radial shield is a row of four to eight short, tapering thorny-tipped spines or stumps, but superficially the radial shields appear relatively large and very bare. There is no spine in the middle of the first dorsal arm plate, unlike the type of *O. panchyendyta*, but the arm plates are similarly conspicuously granular in surface texture. Although H. L. Clark suspected that neither of these last two characters might prove to be diagnostic, the latter at least holds good for this specimen.

***Ophiopsammium rugosum* Koehler**

Ophiopsammium rugosum Koehler, 1905, 116-117, pl. xiii, figs. 4-6; 1930, 197.

MATERIAL. Sprater, Gulf of Siam, 1910/4500, clinging to a pennatulid, 10 specimens.

The outlines of the radial shields are visible through the skin and granules. The disc spines are very variable in occurrence, even in different interradii of the same specimen; there may be just two widely separated spines right on the edge of an interradius or about 10 conical spines more or less inset or some shorter conical tubercles (all these with truncated tips). One specimen has two to four very short, thick, pointed tubercles in each dorsal interradius level with the tangent to the distal ends of the radial shields, then at the very edge of the disc or slightly towards the ventral side there are two separate clusters each of about four short conical spines. Another specimen has about 35 very large low granules in the central part of the disc and central interradiial areas, not projecting out of the skin.

The colour of the disc is pinkish dorsally and dark-red ventrally. There are also patches of intense black spots dorsally of varying extent and conspicuousness in the different specimens. One has particularly large spots in asymmetrical areas of the disc and arms, so that one pair of radial shields and one adjacent shield are covered with big spots and one pair with only fine spots, while the rest are parti-coloured. On the arms the spotted patches extend over about four segments. The tube feet are dark red.

These specimens appear to have been epizooic on the pennatulid, since they are well entwined within its branches. Possibly the peculiarities of the genus are correlated with this habit.

Family **OPHIODERMATIDAE*****Ophioconis permixta* Koehler**

Ophioconis permixta Koehler, 1905, 14-15, pl. ii, figs. 4 & 7 (5 in caption).

Ophiurodon permixtus: Matsumoto, 1915, 84; 1917, 315; Koehler, 1922, 352.

MATERIAL. Xenia reef, Dar-es-Salaam, Tanganyika, 3 specimens.

The use of the original generic name for this species results from a comparison between the three present specimens and two examples in the British Museum collections of *Ophioconis forbesi* (Heller), 1863, the type species of *Ophioconis* Lütken, 1869, one specimen from the Adriatic originating with Dr. Heller himself and the other from La Ciotat in the south of France. Unfortunately I have no material of *Ophioconis grandisquama* Koehler, 1904, the type species of *Ophiurodon* Matsumoto, 1915 but there are several examples in the British Museum collection of *Ophioconis cupidum* Koehler, which Matsumoto referred to *Ophiurodon* together with *Ophioconis cincta* Brock and *O. permixta* Koehler, all of which I consider to be congeneric with *Ophioconis forbesi*.

Matsumoto's restricted *Ophioconis* included only *O. forbesi* and *O. brevispina* Ludwig, 1880, both from the Mediterranean and neither known to Matsumoto at

first hand. He distinguished *Ophioconis* from *Ophiurodon*, *Ophiuroconis*, *Ophiurochaeta*, *Ophiolimna* and *Ophiarachna* by the arm spines, which he said are "very short, lying flat on the arm, hyaline". In fact the dorsal arm spines of the first two free segments on both specimens of *Ophioconis forbesi* seen by me are equal to or even slightly longer than the corresponding dorsal arm plates and in the better-preserved (French) specimen (pl. I, figs. 1 & 2) most of the spines are erect, only those of the distal parts of the arms having become flattened against the arms in preservation. In *Ophioconis brevispina* and in *O. vivipara* Mortensen, 1925, from Morocco, the arm spines are much shorter, only about half as long as the corresponding segments near the bases of the arms, judging from the figures, but it is *O. forbesi* which is the type species and criterion of the genus.

The three specimens of *O. permixta* in the Munich collection are all small, with the disc diameter little more than 3 mm. but their arm spines have very similar proportions and alignment to those of *O. forbesi* and, apart from the scattering of spinelets among the granules of the disc, there is little difference between them, certainly not enough to warrant a generic separation. Hertz (1927) has described a subspecies *nueva* of *Ophiurodon grandisquama* based on four specimens from Madeira. She maintains that these are very similar to a Japanese specimen of *O. grandisquama* which she has studied. Certainly the arm spines appear from her photographs to be relatively longer than those of *Ophioconis forbesi*, since most of the spines of the proximal half of the arm exceed or at least equal the segments in length. Nevertheless I can see no difference of sufficient magnitude to justify generic separation. If Hertz is right in asserting that *nueva* is closely related to *grandisquama* then *Ophiurodon* must be considered as a synonym of *Ophioconis*. However, this needs confirmation from a study of Japanese specimens. Certainly I do not think that the presence of disc spinelets in *permixta* warrants a generic distinction from *Ophioconis forbesi*, particularly as H. L. Clark (1938) has found the occurrence of such spinelets in the related species *Ophioconis cincta* Brock to be very variable. In eleven specimens from northern Australia he found that five had a distinct marginal fringe of disc spinelets, as in the type of *cincta*, while five others had these marginal spinelets poorly developed or absent and the last specimen had both marginal and dorsal spinelets, as in *O. permixta*. This last observation casts doubt on the validity of *permixta* as distinct from *cincta*, but much better sampling of these rather inconspicuous ophiuroids is needed before a true appreciation of the specific limits can be reached. *Ophiurodon cupidum* should also be referred to *Ophioconis*; having no disc spinelets it is the Indo-Pacific counterpart of the Mediterranean *Ophioconis forbesi*, the main difference being only of colour pattern.

In the small specimens of *O. permixta* the second tentacle scale is present for the first six to twelve segments, on one arm even to the seventeenth.

This record from East Africa provides a considerable extension of range for *Ophioconis permixta*, which was previously known only from the East Indian area.

Pectinura anchista H. L. Clark

Pectinura anchista H. L. Clark, 1911, 23-25, fig. 1; Matsumoto, 1917, 322.

MATERIAL. Haberer, no. 4168 (pt.), Sagami Bay, between Ito and Hatsushima Island, *c.* 150 metres, March 1903, 2 specimens.

Matsumoto thinks that *Pectinura anchista* may be a synonym of *P. cylindrica* (Hutton), 1872, from New Zealand. On morphological grounds it seems to me to be equally likely that *anchista* is synonymous with *P. aequalis* (Lyman), 1880 and on zoogeographical grounds *more* probable since the "Challenger" collected *aequalis* off New Guinea and it has since been recorded by Koehler (1904 and 1922) from the vicinity of Celebes and from the Philippines, while Murakami (1944) records it from Yaeyama, Japan. Murakami did not state the size of his specimens but Lyman's type of *P. aequalis* has the disc diameter 25 mm. and Koehler's Philippine specimens are equally large or larger still. The presence of 10 arm spines in Koehler's specimens, whereas these from Sagami Bay have only seven proximally, may be attributable to the much smaller size of the latter, the disc diameter being only 11 or 12 mm. The holotype of *P. anchista* also has seven arm spines; its disc diameter is 14 mm. I think that a direct comparison between Japanese and East Indian specimens of similar size will show the two to be indistinguishable.

Family OPHIURIDAE

Aspidophiura uniumbonata Murakami

Aspidophiura uniumbonata Murakami, 1942, 21-22, fig. 8.

MATERIAL. No details, presumably southern Japan, 1 specimen.

The disc diameter is 4.5 mm. and the longest stump of arm remaining attached is only 3.5 mm. long. There is a suggestion of a boss on the central disc plate as in the type of *Aspidophiura uniumbonata*. Two of the five primary radials are irregularly subdivided but the other three are regular and about equal in size to the radial shields. The oral shields are wider than in either *A. watasei* or *A. forbesi* but agree with those of the type of *uniumbonata*. The only difference from the type is that the uppermost arm spine of at least the first and second free segments is just longer than the segment and the middle arm spine too is relatively longer, almost equal to the segment in length. In the two other species the spines are shorter.

A number of other species were included in the collection for which no particular comment was elicited. They are as follows :

Southern Japan

Astrodermum sagaminum (Döderlein)

Haberer, no. 4118, Fukuura, Sagami Bay, *c.* 150 metres, 1-2. iii. 1903, 2 specimens.

Ophiacantha pentagona Koehler

Doflein, no. 320, Sagami Bay, 180 metres, 25.x.1904, 10 specimens; Döderlein: Enoshima 14, 1 specimen; Enoshima 22, 2 specimens; 2.xi.1881, IV, 1 specimen.

Ophiopholis mirabilis (Duncan)

Doflein: Yogashima (Misaki), 150 metres, 31.x.1904, 4 specimens; Sagami Bay, towards Boshu, 120 metres, 1.x.1904, 1 specimen; Haberer, Fukuura, Sagami Bay, March, 1903, 1 specimen; (Haberer?), no. 4356, Sagami Bay 7.vii.1904, 1 specimen.

Ophiopholis sp.? *brachyactis* H. L. Clark

Döderlein, Enoshima 18, 8.xi.1881, II, 1 specimen.

Ophiactis pteropoma H. L. Clark

Döderlein: Enoshima 25, 2 specimens; 2.xi.1881, III, 1 specimen.

Amphipholis sobrina Matsumoto

Döderlein, Enoshima 22, 1 specimen; Tango, 40 fathoms (73 metres), 1 specimen.

Amphiacantha acanthina (H. L. Clark)

Doflein, station 16, no. 22b, 3 specimens.

Ophiothrix marenzelleri Koehler

Schmidt, Nagasaki, 1901, 1 specimen; Haberer, no. 4356, Sagami Bay, 7.vii.1904, 1 specimen; Doflein, Yogashima (Misaki), 150 metres, 31.x.1904, 1 specimen; (Doflein?), Kachiyama, 1 specimen; Döderlein, 2.xi.1881, III, 2 specimens.

Ophiomastix mixta Lütken

Schmidt, Nagasaki, 1.iii.1901, 3 specimens.

Ophiarachnella gorgonia (Müller and Troschel)

Schmidt, Nagasaki, February–March, 1901, 1 specimen.

Ophioplocus japonicus H. L. Clark

Schmidt, Nagasaki, 1.iii.1901, 1 specimen.

Ophiura kinbergi (Ljungman)

Schmidt, Nagasaki, 1 specimen; Doflein, Tzushi (?), 130 metres, 11.xi.1904, 2 specimens; Döderlein, Tagawa (?), 7.xi.1881, II, 1 specimen; (Döderlein?), Tagawa, 1 specimen.

Ophiozonella projecta (Koehler)

Döderlein, Yogashima, 1 specimen.

Ophiozonella longispina (H. L. Clark)

Haberer : no. 4168 (pt.), Sagami Bay, between Iso and Hatsushima Island, c. 150 metres, March, 1903, 20 specimens ; Fukuura, Sagami Bay, March, 1903, 1 specimen ; Döderlein : Enoshima 22, 1 specimen ; 2.xi.1881, III, 1 specimen.

Stegophiura sladeni (Duncan)

Haberer : no. 4356 (pt.), Sagami Bay, 7.vii.1904, 1 specimen ; no. 4168 (pt.), Sagami Bay, between Ito and Hatsushima Island, c. 150 metres, March, 1903, 1 specimen ; Sagami Bay, 1900, 2 specimens.

Stegophiura vivipara Matsumoto

Doflein, no. 582, Uruga Channel, Sagami Gulf, 150 metres, 22.x.1904, 1 specimen ; (Döderlein?), Yogashima, 2 and 3.xi.1881, 4 specimens.

Ophioleuce charischema (H. L. Clark)

Döderlein : Enoshima 22, 1 specimen ; Yogashima 2 and 3.x.1881, 1 specimen ; no details, 1 specimen.

Amur-Sakhalin (Localities probably east of Vladivostok, unless Sakhalin included).*Ophiacantha adiaphora* H. L. Clark

Schmidt, no. 64, 19.v.1900, 1 specimen.

Ophiacantha bidentata (Retzius)

Schmidt : no. 57, 1 specimen ; no. 48, off Cape Povorotny, 230-196 metres ; 18 specimens.

Ophiopholis aculeata (Linnaeus)

Schmidt : no. 68, 24.v.1900, 1 specimen ; no. 46, Strelok Channel, 1 specimen ; Brashnikow : no. 7, June 1899, 1 specimen ; no. 14, June, 1899, 1 specimen ; no. 49, August, 1899, 4½ specimens ; nos. 19 and 14, 1899/1901, 11 specimens ; Domaschnew, no. 59, July, 1900, 1 specimen.

Amphiura lepidovaspis Djakonov

Schmidt, no. 10 (pt.), Mauka, S.W. Sakhalin, 46-47 sageses (c. 100 metres), 8.vi.1901, 1 specimen.

Amphiodia craterodmeta H. L. Clark

Domaschnew, no. 55, 20.vi.1900, 3 specimens ; no. 53, 27.vii.1900, 1 specimen ; Brashnikow, no. 6 (pt.), July, 1899, 2 specimens ; Schmidt, nos. 9 (pt.) and 10 (pt.), Mauka, S.W. Sakhalin, 46-47 sageses (c. 100 metres), 8.vi.1901, 19 specimens.

Amphioplus macraspis (H. L. Clark)

Schmidt, no. 81 (pt.), 1900, 2 discless specimens.

Stegophiura nodosa (Lütken)

Schmidt, no. 47, 95-100 (? sages), 9. v. 1900, 1 specimen.

Ophiura leptoctenia H. L. Clark

Schmidt : nos. 8, 9, Mauka, S.W. Sakhalin, 46-47 sages (c. 100 metres), 8. vi. 1901, 5 specimens ; no. 48 (pt.) off Cape Povorotny, 230-196 metres, 1900, 9 specimens ; no. 58, same locality, 200-132 metres, 3 specimens.

Ophiura quadrispina H. L. Clark

Schmidt, no. 48 (pt.), off Cape Povorotny, 230-196 metres, 1900, 1 specimen.

Ophiura sarsi Lütken

Schmidt : nos. 9, 10 (pts.), Mauka, S.W. Sakhalin, 46-47 sages (c. 100 metres), 8. vi. 1901, 16 specimens ; no. 11, "east facing Patrok Bay (?)," 22. iii. 1900, 1 specimen ; no. 30 (locality illegible), 17. iv. 1900, 1 specimen ; no. 48 (pt.), off Cape Povorotny, 230-196 metres, 1900, 2 specimens ; no. 69, between Askold and (?) Skriplev Islands, 55 sages (c. 115 metres), 24. v. 1900, 2 specimens : Brashnikow : no. 6 (pt.), July, 1899, 3 specimens ; no. 35, July, 1899, 2 specimens.

Ophiura sarsi vadicola Djakonov

Schmidt : no. 18, off Cape Povorotny, 3. iv. 1900, 11 specimens ; no. 24, Aniva Bay, S. Sakhalin, 13-14 sages (27-29 metres), 28. viii. 1901, 1 specimen ; no. 46, Strelok Channel, 48-42 (? sages), 8. v. 1900, 1 specimen ; no. 69 (pt.), between Askold and (?) Skriplev Islands, 55 sages (c. 115 metres), 24. v. 1900, 1 specimen ; Brashnikow, no. 35, 16. vii. 1899, 7 specimens.

Ophiura maculata (Ludwig)

Brashnikow : no. 15, June, 1899, 2 specimens ; no. 27, July, 1899, 1 specimen.

*Miscellaneous Localities**Asteronyx longifissus* Döderlein

Albatross st. 2892 (Santa Barbara Channel, S. California)	35
st. 2979 (Anacapa Island, S. California)	30
st. 3198 (off central California)	23
st. 2891 (Point Conception, Oregon)	26

Asteronyx loveni Müller and Troschel

Albatross st. 2923 (off San Diego, California)	1
st. 3787 (off Punta Gorda, N. California)	1
st. 5637 (Molucca Islands)	1

Asteroschema (or *Ophiocreas*) spp.

(Döderlein, 1927, regards *Ophiocreas* as hardly distinct from *Asteroschema* even at the subgeneric level, but Mortensen and Fell since consider *Ophiocreas* to be a distinct genus. Without the disc no distinction is possible).

Albatross st. 5621 (Molucca Islands) 1 arm

(Döderlein recorded *Asteroschema* (*Ophiocreas*) *gilolense* from this station).

Albatross st. 5634 (Molucca Islands) 1 arm

(Döderlein recorded *A. (O.) ambonesicum* from this station).

Amphiura chiajei Forbes

Villefranche. Dr. Neresheimer 1

Ophictais savignyi Müller and Troschel

Ceylon. Haeckel 1

Ophiactis simplex (Le Conte)

Academy Bay, Santa Cruz, Galapagos Islands
Foerster, 15.v.1959 2

Ophiothrix sp. prob. *fragilis* (Abildgaard)

44° 48' N : 13° 45' E (northern Adriatic)
36 metres, 26.ix.1895 1

Ophiothrix angulata (Say)

Kingston Harbour, Jamaica. Dr. Heitz, 30.xii.1903 c. 50

Macrophiiothrix hirsuta (Müller and Troschel)

Ras Mohammed, Red Sea. Dr. Hofer, 1892 1

Ophiothela danae Verrill

Thursday I. Regenerating 3 arms and half the disc 1

Ophiocoma scolopendrina (Lamarck)

Red Sea, Schadwan I. (? spelling), southside. H. Haas,
27.iii.1956 5

Mombasa, E. Africa, May, 1960, Papp 5

Washington Museum, no. 46985, Philippines, E. A. Mearns, 1912
2 (badly damaged)

Ophioderma cinereum Müller and Troschel

New Port, Curaçao. Dr. Hellmich, 24.1937 1

<i>Ophioderma longicauda</i> (Retzius)	
Tunis. Pet. Müller, 13. ix. 1960	1
<i>Bathypectinura conspicua</i> (Koehler)	
Albatross st. 5215	3
st. 5219	2
<i>Ophionereis albomaculata</i> E. A. Smith	
Academy Bay, Santa Cruz, Galapagos Islands, Foerster, 15. v. 1959	5
<i>Ophiurolepis gelida</i> (Koehler)	
German Südpolar-Expedition : 25. vi. 1902	4
17. iv. 1902, 385 m. (one infested with sponge <i>Iophon</i>)	9
12. viii. 1902 (largest with <i>Iophon</i>)	5
14. iv. 1902	2

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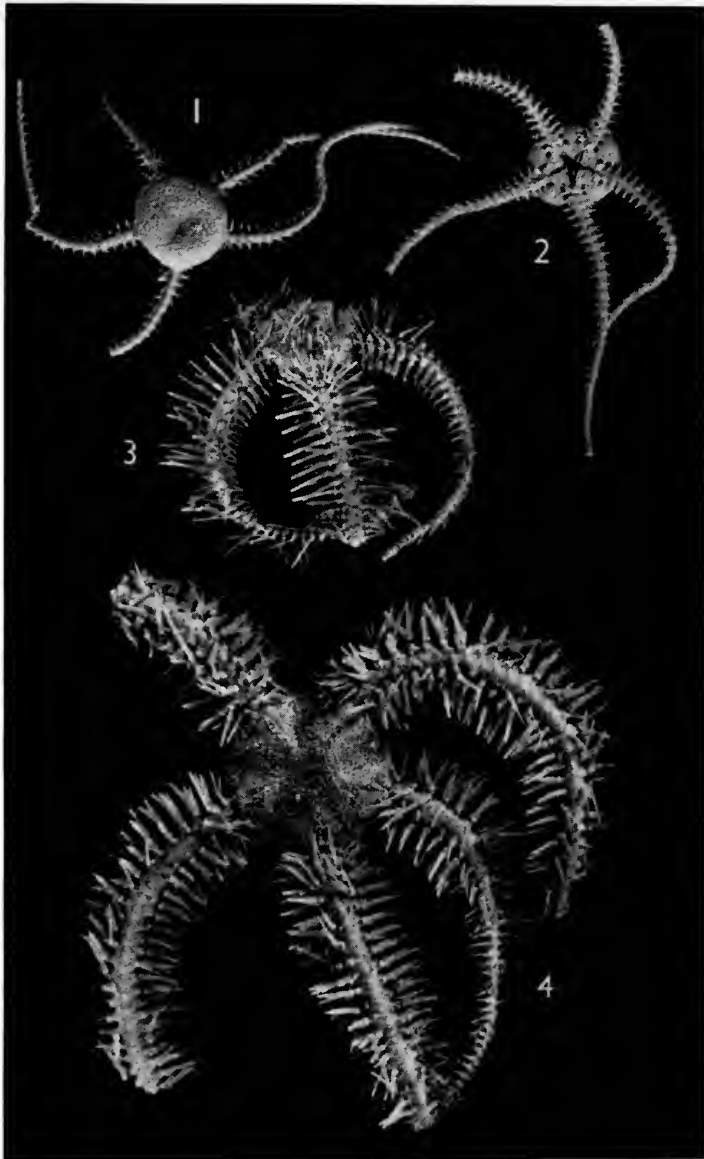
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PLATE 1

FIGS. 1, 2. *Ophioconis forbesi* (Heller). B.M. reg. no. 94.11.19.2, from La Ciotat, S. of France. $\times 3$.

FIGS. 3, 4. Two syntypes of *Ophiothrix koreana* Duncan, B.M. reg. no. 80.1.3.13, from the Korean Straits, 42 metres, both $\times 3$.





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THE FRESHWATER GASTROPOD MOLLUSCS OF WEST CAMEROON

By C. A. WRIGHT

SCHISTOSOMIASIS, the disease of man caused by blood-flukes of the genus *Schistosoma*, is commonly associated with the savannah and semi-arid regions of Africa and the Middle East. In 1953 a focus of infection with *S. haematobium* was reported by Zahra in two crater lakes in the rain-forest area of West Cameroon. In 1957 Mandahl-Barth (1957b) reported two species of *Bulinus* (one of them new) from one of these crater lake foci and, in reply to a request made to Dr. B. O. L. Duke of the Helminthiasis Research Unit at Kumba, I received a preserved sample of bulinid snails from the second of the two infected lakes reported by Zahra. In order to obtain living material of both snails and schistosomes from this unusual focus and to investigate the possible wider distribution of the disease in West Cameroon a short visit was made to the territory in October and November 1963. This paper reports the malacological results of the expedition.

I am greatly indebted to Dr. S. P. Tchoungui, Federal Minister of Health of the Republique Federale du Cameroun and to Colonel R. Aretas, Conseiller Technique at the Federal Ministry of Health for their encouragement and support. It is a pleasure also to acknowledge the facilities made available by Dr. G. G. Dibue, Director of Medical Services, West Cameroon and Dr. B. O. L. Duke, Director of the Helminthiasis Research Unit at Kumba. Special thanks are due to Mr. and Mrs. Peter Moore of the Helminthiasis Research Unit for their kindness and hospitality; it is largely due to their help that a series of minor disasters were overcome and the objectives of the expedition were achieved. Both in the field and subsequently in the laboratory I was assisted by Mr. M. S. Bennett. This work was made possible by grant No. AI-03650-03 from the U.S. Public Health Service.

TOPOGRAPHY OF WEST CAMEROON

The territory now designated West Cameroon was formerly the south-western part of the British Trusteeship territory lying between Nigeria and the French-administered Cameroun. In a number of scientific papers the same area has been referred to by different authors as West Cameroon, the Southern Cameroons and the North-western Cameroons. The region extends about 450 miles north-eastward from roughly 4°N., 9°E. on the coast of the Gulf of Guinea to about 9°N., 13°E. The country is mountainous with dense rain-forest in the south-western part and open grassland in the hills to the north-east; its geography and geology have been very fully described by Gêze (1943). The mountains are partly tectonic in origin but the majority are volcanic, forming a chain of which the Gulf of Guinea islands (Fernando-Poo, Principe, São Thomé and Annobon) are a south-western extension. Overlying the

pre-Cambrian bedrock of gneisses and gneissic granites are a sedimentary series of Cretaceous age which form a band running roughly parallel to the coast and there is another band in the Mamfe region. Overlying the Cretaceous deposits in the south-western part of the country is a thick sheet of basalt of volcanic origin. Gèze quotes evidence suggesting that volcanic activity in Cameroon began in the Cretaceous period but Reymont (1954) does not support this view and considers that the activity has been entirely post-Cretaceous. There are some sedimentary grits and sandstones of Tertiary age in the coastal area and Quaternary deposits are confined to the mangrove swamps which surround much of the coast. Volcanic activity resulting in extensive layers of tuffs in some areas has continued into recent times and the last eruption of Mount Cameroon occurred in 1954.

The crater lakes which were one of the major objectives of the present expedition are considered by Gèze to be the result of violent gaseous explosions of relatively recent origin. This opinion is based on the absence of igneous material associated with the craters, other than that of the older basalt sheet through which the eruptions occurred or demonstrably younger elements. These younger igneous elements include the island in Lake Barombi Kotto (the remains of a small volcano which appeared after the lake was formed) and the basalt stream on the north-east side of Lake Barombi Mbo. Evidence of the relatively recent origin of the craters is provided by the generally steep slope of their sides but in some this incline is less abrupt, suggesting a considerable variation in their age. Typically the lakes are roughly circular in outline and the internal slopes of the craters are thickly forested with dense vegetation extending down to and overhanging the water's edge. Hydrographic information is available for only the three main lakes in Kumba division, Barombi Mbo, Barombi Kotto and Soden ; the first and last of these are steep-sided and deep but the volcanic island in Barombi Kotto has filled a good deal of the lake, making it relatively shallow and creating a more gently sloping shore, particularly around the island. On the north-west side of Barombi Mbo the entering stream has created a small, swampy delta. The extension of this silt deposition has formed a shelf extending out into the lake about one hundred yards. The water depth over this shelf probably does not exceed ten feet and there is considerable growth of aquatic vegetation. Access to Lake Soden is difficult and the only point which was visited had a very steep slope and exceedingly dense, overhanging marginal vegetation. The fringing forest appears to be uninterrupted and it is not known if there are any shallow areas. Lake Ejaghem near Mamfe has less steep banks and forest clearing has resulted in some gaps in the marginal vegetation ; this lake and the three preceding ones have endemic fish populations which are utilized to varying extents by the local people. In Bamenda Division there are a number of lakes whose origin is uncertain but which have many of the characteristics of the craters in Kumba Division. Only three of these were visited, Lakes Bambuluwe, Bafeng and Wum ; the first two are small, steep-sided and with dense marginal vegetation while Lake Wum is open and has some areas with a gently sloping margin with aquatic vegetation. Fish have been introduced into Lake Wum and appear to be thriving but there is no natural fish population in either Bambuluwe or Bafeng and

information from inhabitants of the village at Oku indicated that there are no fish in Lake Oku either.

HISTORICAL

Cameroon has attracted a good deal of malacological attention as a result of its rich and interesting fauna of terrestrial species but, for a territory so well-endowed with rivers, streams and lakes, the records of freshwater species are poor. von Martens (1877) described a large West African collection made by Professor Bucholz and this included six species of fresh- and brackish-water prosobranchs from the coastal region, mostly in the neighbourhood of Victoria. In 1891 the same author reported on a collection made by Preuss in the area of the "Barombi-Station" and mentioned the two large species of freshwater prosobranchs still found in Lake Barombi Mbo and its tributary stream. d'Ailly's (1896) account based upon excellently documented collections made by the Swedish surveyor Dusén included nine species of prosobranchs and de Rochebrune (1898) gave a list of species received from Sjostedt, one of Dusén's colleagues, and mentioned two of the prosobranchs present in d'Ailly's material. O. Boettger (1905) published a list of Cameroons species based on material received from several collectors but here again the only freshwater gastropods noted were prosobranchs. Two small collections made by Dyke were reported upon by Spence (1925 and 1928) and included three species of prosobranchs, two of which were described as new. The first basommatophoran recorded was a planorbid, found on the northern slopes of Mount Cameroon and described by C. R. Boettger as *Australorbis camerunensis* (1941). A Swiss expedition in north-eastern Cameroon collected two freshwater prosobranchs not included in any of the earlier accounts (Forcart, 1951) and the Danish expedition to the French Cameroons in 1949-50 brought back only terrestrial species (Nøstvik, 1956). Mandahl-Barth (1957b) described *Bulinus camerunensis* and recorded *B. truncatus rohlfsi* from specimens collected by Mr. P. J. Moore in Lake Barombi Kotto. These two species together with Boettger's planorbid are the only basommatophoran pulmonates recorded from the area. The present account adds seven more planorbids, one lymnaeid and one ancylid to the list as well as an additional prosobranch not previously recorded.

Family PLANORBIDAE

Biomphalaria camerunensis (Boettger)

Australorbis camerunensis C. R. Boettger, 1941 : 121.

Biomphalaria camerunensis camerunensis Mandahl-Barth, 1957a : 1142.

MATERIAL : Bambalang, N'dop Plain, Bamenda Division, about 70 specimens collected from shallow water with thick mud bottom and scarcely any vegetation, heavily shaded by thickets of low-growing palm trees. 6th November, 1963.

Shell (Pl. I, figs. 16-23) : yellowish-brown, discoidal, flattened above with the centre slightly depressed ; Whorls weakly angled beneath, umbilicus wide ; well-developed spiral lines give marked granular microsculpture even on later whorls ;

larger shells irregularly rugose and patchily eroded. Nearly all shells up to 12.5 mm. diameter have apertural lamellae (Pl. I, fig. 23). The largest specimen collected had a maximum diameter of 17.3 mm., umbilicus 7.2 mm. and height 5.4 mm. The mean ratio maximum diameter/umbilicus diameter for 30 specimens of all sizes is 2.67 and for the ratio maximum diameter/height the value is 2.75.

Anatomy: male copulatory organ large, penis-sheath longer than preputium (Text-fig. 4), mean ratio penis sheath/preputium for a series of adult specimens is 1.42 (range 1.07–1.86), penis slightly shorter than the sheath; prostate long with 30 or more primary diverticula, all with secondary and many with tertiary branches. Albumen gland relatively small, oviduct and muciparous gland (the translucent white proximal part of the uterus) short but the distal, yellow oöthecal gland is long; vagina long, without marked dilatation, receptaculum seminis club-shaped (Text-fig. 4), vesicle about equal in length to duct. The pericardia of all specimens dissected were packed with metacercariae of an unidentified trematode and the gonad and part of the digestive gland of others were found to be completely destroyed by rediae of probably the same species of parasite.

Radula (Text-fig. 10): teeth small, tendency towards arrow-head shape of some lateral mesocones but majority triangular, ecto- and endocones roughly equal; six to eight tricuspid laterals in each half-row, about the same number of intermediates, division of the endocone starts at about tooth 15, most marginal ectocones undivided but some have outer edge serrated.

Biomphalaria camerunensis has so far been known only from the type series of shells collected at Mongonge on the northern slope of Cameroon Mountain. Mandahl-Barth (1957a) described a sub-species *B. c. manzadica* from a few localities in the Lower Congo and, on shell characters my material is closer to this sub-species than the nominate form in that the umbilicus diameter is greater than the height. However, the illustration of the type specimen of *B. camerunensis* shows that it differs from any of my specimens in that the aperture and terminal part of the body whorl are deflected downward, a character which gives a misleading increase in the height of the shell in very large specimens. All other members of the *Biomphalaria sudanica* species group have the umbilicus diameter greater than the shell height as in my material and it seems unwise to set *B. camerunensis* apart because this proportion is reversed in a single, large, possibly aberrant specimen. Anatomically the present material differs from all other members of the *B. sudanica* group (with the exception of *B. sudanica rugosa* Mandahl-Barth, 1960) in that the penis sheath is consistently longer than the preputium. The radula teeth conform to the general characters of the *sudanica* group. Three shells (B.M. (N.H.) coll. no. 1936-6-2-24-26) from the Batouri District of East Cameroon which compare well with my material were labelled "*Planorbis salinarum*" by Connolly in 1936 and there is no doubt that they bear a close resemblance to that species. However, the umbilical diameters and heights of the Cameroons shells are proportionately slightly higher than in the type series of *B. salinarum*. It is probable that snails reported from Yaounde in East Cameroon as *B. sudanica* by Gaud (1955) are also *B. camerunensis*.

The presence of apertural lamellae does not appear to have been noted before in

members of the *B. sudanica* species group. Smith (1881) originally described the form *tanganyicensis* (now considered by Mandahl-Barth (1957a) to be a sub-species of *B. sudanica*) as a member of the genus *Segmentina* but there is no trace of lamellae in any of Smith's specimens. The lamellae found in *B. camerunensis* do not differ from those reported in *B. pfeifferi* and in various Puerto Rican species by Richards (1963) who suggested that they may serve as supporting structures for the delicate aperture during aestivation. The unusually shallow and shaded habitat from which this sample was collected is most probably subject to desiccation in the dry season. The specimens brought alive into the laboratory showed a persistent tendency to crawl out of the water. Compared with Sudanese and Kenyan strains of *B. sudanica* kept in this laboratory *B. camerunensis* is an exceptionally slow-growing species and it has so far proved refractory to infection with strains of *Schistosoma mansoni* from Egypt and Liberia.

Biomphalaria pfeifferi (Krauss)

Planorbis pfeifferi Krauss, 1848 : 83, pl. 5, fig. 7.

MATERIAL : Lake Wum, Bamenda Division, on sparse aquatic vegetation in 2-3 feet of water. Six specimens. 7th November, 1963.

Shell (Pl. I, figs. 14-16) : light yellowish-brown, whorls without marked angulation, well-developed spiral lines intersect fine growth lines to give a strong granular microsculpture. The dimensions of the largest specimen in the sample were, maximum diameter 6.4 mm., umbilical diameter 1.8 mm., height 2.8 mm. The mean ratio for the whole sample of maximum diameter/umbilical diameter was 3.66 and of maximum diameter/height was 2.14.

Anatomy : the state of preservation of the sample was poor. The two largest specimens (6.4 and 5.5 mm. diameter) were dissected and found to be fully mature. The penis sheath is shorter than the preputium, the prostate has about 15 primary diverticula, most of them with secondary branches. In contrast to *B. camerunensis* the oviduct is strongly convoluted and the muciparous gland encloses more than half the uterus. The receptaculum is club-shaped and the vesicle is about equal in length to its duct. The pericardia of both specimens contained many trematode metacercariae.

Radula : the teeth are larger than in *B. camerunensis*, there are seven tricuspid laterals in each half-row, their mesocones are broad and spatulate and the marginal ectocones are divided.

Biomphalaria pfeifferi has an almost universal distribution in the Ethiopian region and its presence in Cameroon is to be expected.

Anisus coretus (de Blainville)

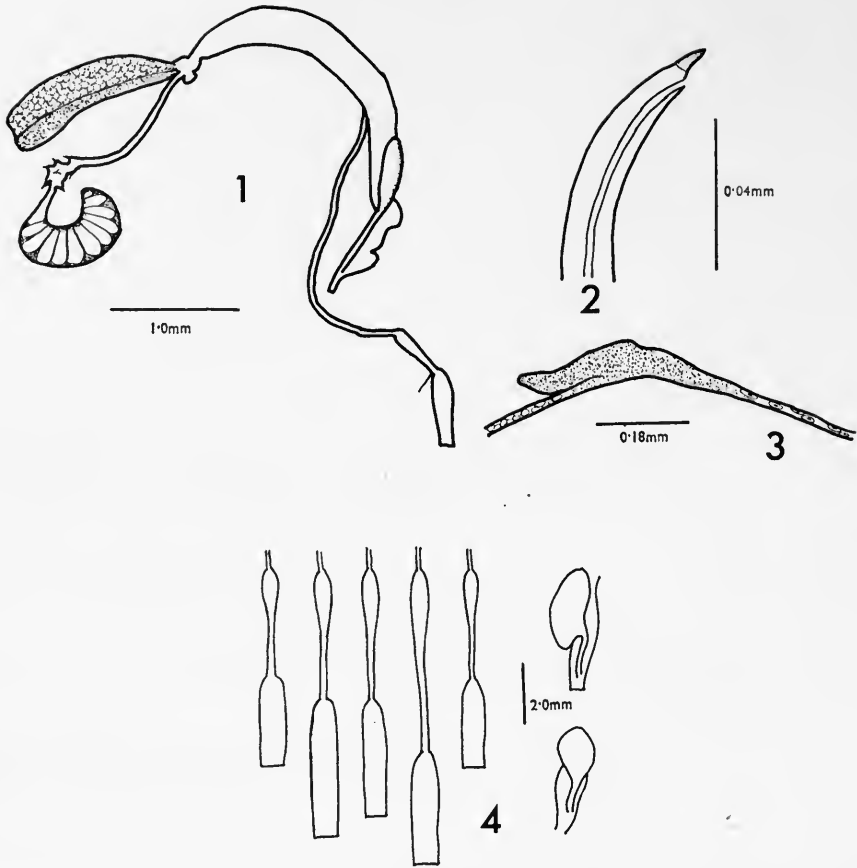
Le Coret, *Coretus* Adanson, 1757 : 7-10, pl. I, fig. 3.

Planorbis coretus Adanson, de Blainville, 1826 : 230.

non *Planorbis coretus* Adanson, Dautzenberg, 1890.

Coretus adansonii Gray, 1850 : 119, pl. 309, fig. 4.

Planorbis (Gyraulus) gibbonsi Nelson. Binder, 1957 : 120, fig. 17.



FIGS. 1-3. *Anisus coretus*. 1, Whole genital system. 2, Tip of male copulatory organ. 3, Prostate.

FIG. 4. *Biomphalaria camerunensis*. Male copulatory organs and receptacula.

MATERIAL: Lake Barombi Kotto, Kumba Division. Ten specimens and laboratory-bred material. 15th November, 1963.

Pamol Estate, Lobe, Kumba Division, in ditches, about 70 specimens. 15th November, 1963.

Shell (Pl. II, figs. 4-6): small, discoidal, flattened above, slightly concave beneath, whorls $3-3\frac{1}{2}$, rounded without angulation, sutures relatively deep, aperture rounded. The shells are glossy with fine growth lines, many of those from Lobe have a very fine spiral sculpture on the underside giving a wavy appearance to the growth lines. The largest specimen seen was laboratory bred and measured 2.7 mm. maximum diameter. The mean dimensions of five adult specimens from Lobe are 2.4 mm. maximum diameter, 1.24 mm. umbilicus diameter and 0.68 mm. height.

Anatomy (Text-fig. 1): the male copulatory organ is small with the penis sheath and preputium about equal in length and the preputium slightly greater in diameter

than the proximal dilatation of the sheath. The penis is usually a little longer than the sheath, there is a small claw-like stylet at its tip and the opening of the vas deferens is sub-terminal (Text-fig. 2). The prostate (Text-fig. 3) consists of a glandular part of the male duct with a single diverticulum. Examination by phase-contrast microscopy shows that the wall of the sperm-duct consists of irregularly rounded cells, the glandular prostatic part and the diverticulum are finely and densely granular and the vas deferens appears to be composed of connective tissue with sparse oval cells with well-defined nuclei. The seminal vesicle on the hermaphrodite duct is coiled and has small projections on its surface. The vagina is short and proximally dilated, the uterus is long, narrow and straight and the albumen gland is relatively large. The receptaculum seminis is ovoid and slightly shorter than its slender duct.

Radula (Text-fig. 16): teeth small and few in number, there are about eight tricuspid laterals, a single intermediate in which the ectocone is divided and a single five-cusped marginal in each half-row.

Anatomically this material does not differ significantly from Binder's (1958) description of *Gyraulus gibbonsi* from the Ivory Coast. The terminal stylet of the penis is similar in both forms and differs from the smooth cap-like structure of *Anisus misellus* (Morelet) from Angola (Wright, 1963). The single prostatic diverticulum of the Ivory Coast material is very much longer than in specimens from the Cameroons but this is probably a variable character in view of the occurrence of occasional individuals with a single diverticulum in *A. misellus*, a species which usually has a more normal prostate with several diverticula. Binder shows the seminal vesicle to be convoluted but smooth in his specimens and in this respect the Cameroon form resembles *A. misellus* which also has small projections from the surface of the vesicle.

Binder referred his specimens to *Gyraulus gibbonsi* on the basis of an illustration by Pilsbry & Bequaert (1927). *G. gibbonsi* was described by Nelson (1878) from Zanzibar but his illustration does not agree with his description in that it shows a shell completely flattened beneath and with a sharp basal angle while the description says that the aperture is rounded. The whereabouts of the type-specimen are unknown but Pilsbry & Bequaert examined material from Zanzibar and found that it agreed with specimens from the Congo with a rounded aperture. I have also examined topotype shell material and have found that it resembles the form from the Cameroons except that it lacks any trace of spiral sculpture and reaches a much greater size at the $3\frac{1}{2}$ whorl stage than does the West African form. There is, however, a very striking resemblance between my specimens and the description and photographs of Adanson's (1757) *Le Coret*, *Coretus*, published by Fischer-Piette (1942). Fischer-Piette pointed out that Adanson's species had never been rediscovered and that Dautzenberg's (1890) re-description of it from the type-locality at Podor, Senegal, certainly did not agree with the original specimens recovered later. Gray's (1850) species *Coretus adansonii* was based only on Adanson's original description as was the earlier *Planorbis coretus* of de Blainville (1828). Adanson emphasized the small size of this snail and reported copulation between individuals just over 3 mm. in diameter.

The relationships of *A. coretus* to other species are not yet readily determined.

A. misellus is obviously close and it is possible that some of the many species of small planorbids indifferently described by Germain (1907, 1909, 1911, 1917) from West Africa and the Lake Chad region are no more than local variations. de Azevedo *et al.* (1961) have recently described the anatomy of *A. natalensis* from Mozambique as having a single prostatic diverticulum, no penial stylet and a terminal opening to the vas deferens. These characters are in contrast to the normal prostate and sclerotized terminal part of the penis in *A. natalensis* from Ethiopia and Transvaal (Wright & Brown, 1962).

Gyraulus costulatus (Krauss)

Planorbis costulatus Krauss, 1848 : 83, pl. 5, fig. 8.

MATERIAL : Lake Wum, Bamenda Division. On dead leaves near the lake margin. 3 specimens. 7th November, 1963.

Shell (Pl. II, figs. 7-9) : small, discoidal, pale yellowish brown, strongly and regularly ribbed with a well-marked equatorial carination. The largest specimen was broken but probably had 3-3½ whorls ; an individual with 3 whorls measured 3.2 mm. diameter, 0.8 mm. umbilical diameter and 1.08 mm. high.

Anatomy : one specimen was aphyllid but the anatomy of the other two corresponded well with that described for this species from Angola (Wright, 1963). The penis papilla noted by de Azevedo *et al.* (1961) was observed but the Cameroon specimens had the penis relatively shorter with the stylet not reaching to the end of the sheath.

Radula (Text-fig. 18) : teeth small, 9-10 tricuspid laterals and about 6 five cusped marginals in each half-row. The cusps of the laterals are a little broader than those in Angolan specimens.

This species was probably more abundant than the number of specimens collected suggests but the samples obtained from Lake Wum were, for various reasons, inadequate. The largest of the three specimens was grossly infected with rediae of an unidentified trematode. This was probably the same species of parasite as the metacercariae found in the pericardia of the other two individuals and the *Biomphalaria pfeifferi* and *Segmentorbis angustus* from the same locality.

Segmentorbis angustus (Jickeli)

Segmentina angusta Jickeli, 1874 : 220, pl. 7, fig. 24.

Segmentorbis angustus (Jickeli), Mandahl-Barth, 1954 : 96.

MATERIAL : Lake Wum, Bamenda Division. On dead leaves and emergent grasses. About 50 specimens, also laboratory-bred material. 7th November, 1963.

Shell (Pl. II, figs. 1-3) : lenticular, flattened beneath, relatively sharp basal angle, translucent, pale yellowish-brown, wild specimens often thickly crusted with dark brown deposits, umbilicus narrow and very deep. There are usually two, rarely three sets of lamellae in the body whorl, the basal is well-developed, straight, about half the width of the whorl, the inner curves strongly over the parietal wall, the

outer is usually weak, often sub-divided and sometimes absent while the dorsal is rarely present (Text-figs. 5 and 6). The shell is smooth and shiny with a faint trace of spiral sculpture on the underside, visible only under high magnification.

Anatomy (Text-fig. 7) : penis-sheath about two-thirds the length and a quarter the width of the preputium, with a single, large, thin-walled flagellum attached to the proximal end of the sheath. There is a separate prostatic duct from which arise about fifteen unbranched diverticula. The seminal vesicle is widely dilated and convoluted with small surface protruberances. There is a slight dorsal dilatation of the vagina, the uterus is long and straight and the receptaculum seminis is clavate, about equal in length to its duct. Several specimens had heavy infections of trematode metacercariae in their pericardia.

Radula (Text-fig. 17) : the teeth are similar to those of *Anisus coretus* but they are smaller and more numerous. The first 7-9 laterals are tricuspid, the endocone is subdivided in the next six or seven and from about tooth fifteen outward the ectocone is also divided giving six to eight typical 5-6 cusped marginals.

S. angustus was originally described from Ethiopia and is known from many places in East and South Africa. A single small specimen was recorded from Kikondja in the Congo by Pilsbry & Bequaert (1927). Their illustration of the shell shows a greater number of basal lamellae (4) than are found in specimens of comparable size in the present material and the outer lamellae are even more degenerate in the Congo specimen. Mandahl-Barth (1954) notes that there is usually only a single set of septa but occasionally up to five sets are seen in this species in Uganda. He also mentions specimens of *Segmentorbis* with even larger numbers of septa in which the other shell characters do not differ from normal *S. angustus*. The form of the receptaculum seminis in the Cameroon specimens differs from that described by Mandahl-Barth (1954) for Uganda material and by de Azevedo *et al.* (1961) for specimens from Mozambique. Both of these authors show the vesicle to be small and spherical with a diameter only about a quarter the length of the duct. Even young specimens from Lake Wum have an elongate-ovoid receptaculum about equal in length to its duct and this form is similar to that in Ethiopian specimens (Brown, 1965).

Segmentorbis kanisaensis (Preston)

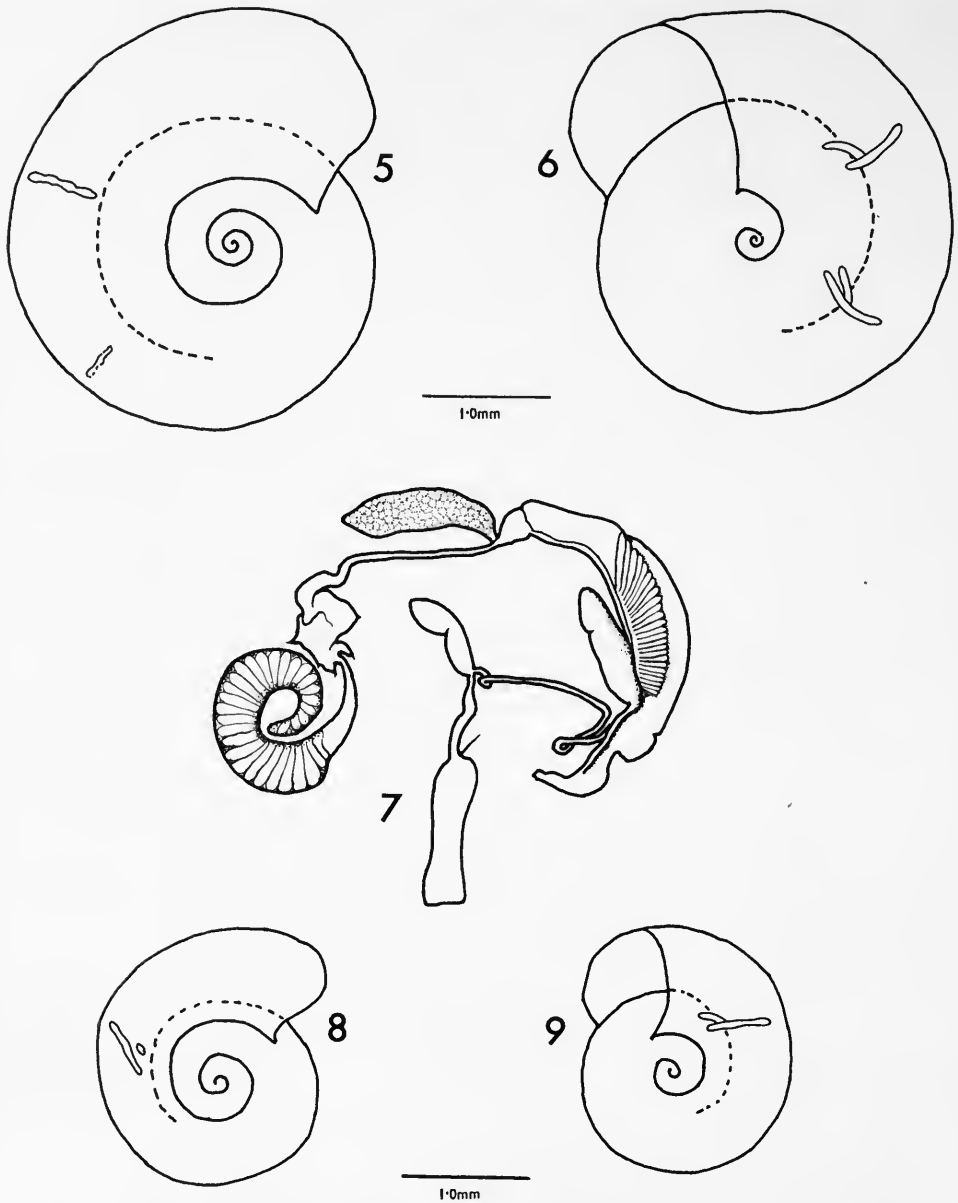
Segmentina kanisaensis Preston, 1914 : 265, pl. 18, figs. 17-19.

Segmentorbis (Carinorbis) kanisaensis ; Mandahl-Barth, 1954 : 98, fig. 45.

MATERIAL : Lake Barombi Mbo, Kumba Division. One specimen.

Shell : lenticular, flattened beneath, sharp basal angle ; translucent, yellowish-brown, fine growth lines and slight spiral microsculpture on the underside ; a single set of well-developed lamellae (Text-figs. 8 and 9), the basal about two-thirds the width of the whorl, the inner strong, curved, the outer long, oblique and the dorsal a pronounced dot-like structure. Dimensions of the single specimen were diameter 2 mm., umbilicus 0.5 mm., height 0.6 mm.

Anatomy : the specimen was immature but dissection showed the characteristic lack of a flagellum on the male copulatory organ.



FIGS. 5-7. *Segmentorbis angustus*. 5, Dorsal view of shell. 6, Ventral view of shell. 7, Whole genital system.

FIGS. 8, 9. *Segmentorbis kanisaensis*. 8, Dorsal view of shell. 9, Ventral view of shell.

Segmentorbis snails were relatively common on dead leaves in Lake Barombi Mbo near the mouth of the entering stream on the north-west shore. Unfortunately all

of the wild specimens were lost and the single individual reported here was later found in a tank in the laboratory containing leaf-litter from the lake. This species is common in low-lying areas of West Africa from the Gambia to Angola and is also found in East and South Africa.

Bulinus rohlfsi (Clessin)

Physa rohlfsi Clessin, 1886 : 349, pl. 49, fig. 7.

Bulinus truncatus rohlfsi ; Mandahl-Barth, 1957(b) : 29, pl. 20, fig. 18.

MATERIAL : Lake Barombi Mbo, Kumba Division. About 100 specimens received from Dr. B. O. L. Duke, 8th January, 1957 ; 20 specimens and laboratory-bred material, 14th November, 1963.

Lake Barombi Kotto, Kumba Division. About 40 specimens and laboratory-bred material, 31st October and 15th November, 1963.

Shell (Pl. I, figs. 7-10) : light yellowish-brown, spire short, no marked ribbing or other micro-sculpture ; columella more or less straight, columellar margin reflexed, closing the umbilicus. Adult specimens from Lake Barombi Kotto usually have the aperture margin reflexed giving to the shell a bell-mouth appearance ; this distortion occasionally occurs in younger individuals and, if followed by a period of normal growth, results in the formation of a marked ridge on the body whorl. Similar reflexion of the aperture margin has not been seen in wild specimens from Barombi Mbo but it occasionally occurs in laboratory colonies from the Mbo stock. The maximum size in the Kotto sample is length 11.2 mm., width 8.8 mm. and aperture length 8.9 mm. From Mbo the largest specimen is 7.7 mm. long, 5.1 mm. wide and has an aperture length of 5.1 mm. This disparity in maximum size between the two populations has been maintained in laboratory colonies bred from the stocks. The colony from Kotto is also remarkable for the number of distorted shell-forms which it produces. The mean ratio shell-length/aperture length for adult specimens of both populations is 1.2.

Anatomy : all specimens dissected from both populations were aphyllid ; in some there is a trace of sperm-duct and a vestigial prostate but in the majority there is no development of the male system. Specimens from Mbo have the uterine glands fully developed and apparently functional at shell-length 4.0 mm. while those from Kotto are less well-developed at 6 mm. The mantle in specimens from Kotto is pale grey with black spots and patches while in the Mbo samples the markings vary, as they do in the same species from Angola, from almost unmarked to strongly patterned.

Radula (Text-fig. 13) : teeth smaller than in *B. truncatus*, 3-5 tricuspid laterals, all with slightly arrowhead-shaped mesocones flanked by fine interstitial cusps, 13-18 marginals in which the mesocone is not so clearly dominant as it is in the next species.

Bulinus rohlfsi is the oldest name of a considerable number of species and varieties described from Lake Chad. Mandahl-Barth (1957b) treats *rohlfsi* as a sub-species of *B. truncatus* and there is no doubt about the close relationship of the two species. However, the sub-species concept has little real meaning in the Basommatophora

and I prefer to regard *rohlfsi* as a distinct species. The large number of names given to this species in Lake Chad is some indication of the great variability of its shell form. The distinctions observed here between the populations from the two Kumba lakes are further evidence of this polymorphism. In both lakes *B. rohlfsi* is acting as intermediate host for *Schistosoma haematobium*.

Bulinus tropicus (Krauss)

Physa tropica Krauss, 1848 :

Bulinus (Bulinus) hemprichii depressus Haas, 1936 : 28, pl. I, fig. 15.

Bulinus tropicus tropicus (in part) ; Mandahl-Barth, 1957b : 19, pl. 10, fig. 4.

MATERIAL : Babungo, N'dop Plain, Bamenda Division. On aquatic plants in a slow-flowing stream about 1 mile east of the village. 20 specimens, also laboratory bred material. 6th November, 1963.

Shell (Pl. I, figs. 11 and 12) : thin, translucent, yellowish-brown, spire flat, aperture wide, columella slightly twisted ; early whorls ribbed, body-whorl smooth with fine growth-lines. Dimensions of the largest specimen were—length 8.1 mm., width 6.9 mm. and aperture length 7.4 mm. In the laboratory shell-lengths in excess of 12 mm. have been achieved by mature individuals. The mean ratio shell-length/aperture-length for a series of juveniles is 1.03, a clear indication of the flatness of the spire. However, laboratory-bred specimens develop a prominent spire even in the first generation.

Anatomy : penis sheath about twice the length of the preputium, its proximal dilatation is a little wider than the distal part ; epiphallus short and without dilatation. The largest wild specimen (8.1 mm.) was protandrously mature with apparently functional copulatory organ and prostate but poorly differentiated uterine glands. The remainder of the sample were all juvenile but in all there were at least traces of rudimentary male genitalia and no potentially aphyllid individuals were seen. The mantle is light grey with sparse, well-defined black spots and patches.

Radula (Text-fig. 12) : teeth larger than in *B. rohlfsi*, 6–7 tricuspid laterals with sub-division of the endocone occurring in the seventh or eighth tooth ; lateral mesocones slightly arrow-head shaped, usually flanked by lanceolate interstitial cusps, inner edge of the endocones frequently corrugated. In the 20–22 marginals the mesocones remain undivided and are very prominent.

Wild specimens of this form closely resemble *Bulinus depressus*, described as a sub-species of “*B. hemprichii*” from a canal near Lake Bangweulu in Zambia. In an earlier paper (Wright, 1957) I suggested that *B. depressus* was no more than a juvenile of *B. globosus* but, in a private communication, Dr. Mandahl-Barth drew my attention to certain features of *depressus* which indicate that it is definitely not related to the *B. africanus* complex and he (1957b) included it in the synonymy of *B. tropicus tropicus*. Examination of the immature wild material from Babungo left me in some doubt as to whether it should be assigned to the *tropicus* or *truncatus* species groups. However, electrophoresis of the egg-proteins of the one living specimen brought back to London demonstrated without doubt that this form belongs to the

B. tropicus complex (Wright & Ross, in press). This record is probably near to the extreme north-west limits of the range of this species group for I am unable to agree with Mandahl-Barth on the inclusion of *B. guernei* from West Africa in the *tropicus* group; I have examined *B. guernei* from three of the four localities mentioned by Mandahl-Barth (1957b) and I have found a high proportion of apallid individuals and arrowhead shaped lateral mesocones, Smithers (1956) has also reported wild-caught specimens infected with *Schistosoma haematobium*. These three characters all indicate an affinity with the *truncatus* group and no other species with *tropicus* characteristics has been reported from West Africa. It is possible that the *B. strigosus* reported by Gaud (1955) from Bangui is *B. tropicus*.

Bulinus forskali (Ehrenberg)

Isidora Forskalii Ehrenberg, 1831 : 20.

MATERIAL : Ditches and streams on Pamol Estate, Lobe, Kumba Division. 36 specimens. 25th October, 1963.

Shell (Pl. I, figs. 5 and 6) : strongly turretted with well-marked shoulders and ribs on all whorls, distinct small spines on the shoulder of the third whorl where the ribs intersect the angle. Mean dimensions in millimeters of 14 adults (maxima in brackets) were length 5.4 (7.2), width 2.7 (3.2) and aperture length 2.7 (3.0).

Anatomy : male copulatory organ small and slender, penis sheath/preputium ratio about 3/2.

Radula (Text-fig. 15) : similar to that described for this species from Angola but few malformations present in this population; 5 or 6 tricuspid laterals and up to eighteen marginals.

B. forskali is probably the most widely distributed and variable species of freshwater snail in Africa and its presence in Cameroon was to be expected. It was recorded by Zahra (1953) from the stream flowing into the lake past Barombi Mbo village but it was not found there during the present visit despite repeated examination of the area.

Bulinus camerunensis Mandahl-Barth

Bulinus camerunensis Mandahl-Barth, 1957b : 31, pl. 22, fig. 21.

MATERIAL : Lake Barombi Kotto, Kumba Division. About 150 specimens, also laboratory-bred material. 31st October and 15th November, 1963.

Shell (Pl. I, figs. 1-4) : high-spired, translucent, yellowish-white, most specimens show some quite marked ribbing and in a few there is a weak shoulder on the second and third whorls; about half the shells examined show irregular spiral lines giving patches of reticulate sculpture. The mean dimensions in millimeters (maxima in brackets) for a sample of 50 wild adults are length 5.4 (6.9), breadth 2.9 (3.5) and aperture length 3.2 (4.0). Larger specimens, up to 11.5 mm. high have been bred in the laboratory. The mean value and range of the ratio shell-length/aperture-length is 1.65 (1.47-1.94). In only three out of the 50 wild snails measured was the breadth

of the shell greater than the aperture length. This is in contrast to the dimensions given in the original description.

Anatomy : male copulatory organ small and slender, sheath usually longer than the preputium and its proximal dilatation about equal in diameter to the distal part. The relative lengths of the two parts of the copulatory organ vary widely, the mean ratio of sheath-length to preputium is 1.43 but it ranges from about 1.0-2.0. The prostate is relatively small in all of the fully adult specimens examined. Mantle markings in wild specimens are irregular and somewhat diffuse black patches on a grey ground but laboratory-bred individuals have the mantle almost uniformly black.

Radula (Text-fig. 14) : teeth similar to those of *B. forskali* but slightly smaller and nearly all of the lateral mesocones are flanked by fine interstitial cusps. There are five or six laterals as in *B. forskali* but the number of marginals is greater (up to twenty-four) in *B. camerunensis*.

In his original description of this species Mandahl-Barth mentioned the possibility that *B. camerunensis* was no more than a local form of *B. forskali* but that it differed from that species by its smaller radula teeth. The contrast in shell-characters between *B. camerunensis* and the form of *B. forskali* collected a few miles away at Lobe is well-marked and the present species shows greater similarity to *B. beccarii* (Paladilhe) from Aden (Wright, 1963a) than to any other member of the *forskali* group. In the hope of finding further foci of this species six other crater lakes were visited but without success. Repeated attempts to infect *B. camerunensis* with the West Cameroon strain of *Schistosoma haematobium* have failed.

Family LYMNAEIDAE

Lymnaea natalensis Krauss

Limnaeus natalensis Krauss, 1848 : 85, pl. 5, fig. 15.

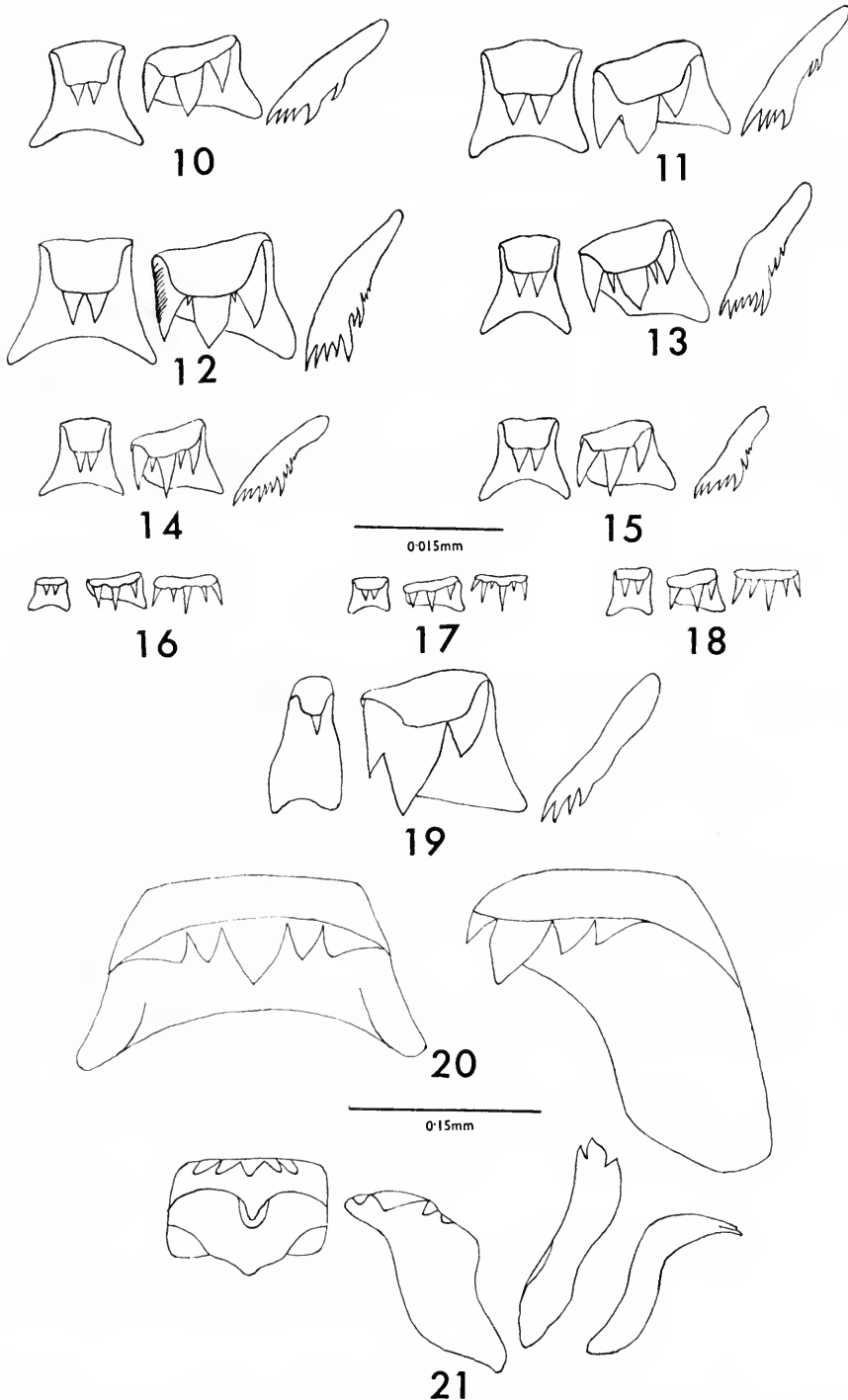
MATERIAL : Babungo, N'dop Plain, Bamenda Division. On aquatic vegetation in a slow-flowing stream about 1 mile east of the village. 12 specimens. 6th November, 1963.

Lake Wum, Bamenda Division. 6 specimens. 7th November, 1963.

Shell (Pl. I, fig. 13) : thin, shiny, elongate-ovoid, spire short and sharply pointed ; the only ornament is fine growth lines. Mean dimensions in millimeters (maxima in brackets) of four adult specimens from Babungo are length 8.4 (9.1), breadth 4.6 (5.6) and aperture length 6.4 (7.0).

Anatomy : penis-sheath approximately twice the length of the preputium, receptaculum seminis duct long with the receptaculum lying on the left side of the body. Two of the four adult specimens from Babungo had the accessory genital glands completely destroyed by an unidentified larval trematode but the other two had the characteristic distal dilatation of the prostate.

Radula (Text-fig. 19) : eight to ten tricuspid laterals in which the endocones and mesocones are fused together for over half their length ; fifteen to twenty marginals, transition from the laterals occurring by sub-division of the ectocone which almost



FIGS. 10-21. Radula Teeth. 10. *Biomphalaria camerunensis*. 11. *Biomphalaria pfeifferi*. 12. *Bulinus tropicus*. 13. *Bulinus rohlfsi*. 14. *Bulinus camerunensis*. 15. *Bulinus forskali*. 16. *Anisus coretus*. 17. *Segmentorbis angustus*. 18. *Gyraulus costulatus*. 19. *Lymnaea natalensis*. 20. *Lanistes libycus*. 21. *Potadoma freethi*.

disappears in the outer teeth which have only four or five cusps derived from the endo- and mesocones.

L. natalensis is widely distributed throughout Africa. The only feature of interest in the present material is the relatively small size at which maturity is reached.

Family ANCYLIDAE

FERRISSIA sp.

MATERIAL : Ditches on Pamol Estate, Lobe, Kumba Division. 5 specimens. 15th November, 1963.

Shell (Pl. II, figs. 10 and 11) : small, rectangularly ovoid, light yellow, apex striate, displaced to the right, smoothly rounded. The margin of all five specimens was of soft periostracum causing considerable variation in shell shape. The mean dimensions in millimeters (maxima in brackets) of four entire specimens are length 1.78 (1.92), width 1.2 (1.2), height 0.57 (0.64).

No preserved specimens were available for anatomical study. Small ancyliids were also found in Lake Wum and at Babungo, both in Bamenda Division but the material from both localities was lost. The small amount of material and lack of anatomical data do not permit an assessment of the affinities of this species but the proportions of the shell are similar to those of *F. eburnensis* Binder, 1957, from the Ivory Coast. Population variations in the outline of the shell from uniformly oval to rectangularly ovoid were noted by Binder.

Family AMPULLARIIDAE

Lanistes libycus (Morelet)

Ampullaria libyca Morelet, 1848 : 28, pl. 3, fig. 9.

Ampullaria bernardiana Morelet, 1860 : 190.

MATERIAL : Lake Barombi Mbo, Kumba Division. On stones and sandy bottom near canoe beach on north-east side of the lake. 40 specimens. 24th October, 1963.

Ditches on Pamol Estate, Lobe, Kumba Division. 12 specimens. 15th November, 1963.

Shell (Pl. III, figs. 9 and 10) : large, globose, low-spined, apex often eroded ; whorls with well-marked shoulder angle, distinctly flattened below the suture, moderate carination around the umbilicus. Specimens from Lake Barombi Mbo have the shell smooth with strong spiral bands of colour which appear brownish-red externally and purple internally, those from Lobe have the colour bands less well-marked but have strong spiral ridges of periostracum which persist on adult shells ; these ridges are present on some juveniles from the lake population. The largest specimen collected (from the lake) measured 27 mm. in height, 28 mm. in width and had an aperture length of 18 mm.

Radula (Text-fig. 20) : central tooth massive, median cusp flanked usually by two, sometimes three, smaller cusps all of which may be fused into a single transversely elongate blade ; lateral four-cusped and the two marginals bi-cuspid.

The type-locality for *L. libycus* is in Gaboon and the species has a wide distribution in West Africa. It has been reported from many places in the Cameroons by previous workers. The treatment of *L. bernardianus* as a variety of *L. libycus* was retained by d'Ailly (1896) because the large number of samples which he examined from Cameroon showed no intermediates between the two forms. However, the characteristic spiral ridges of *bernardianus* are confined to the periostracum and are easily rubbed off. This distinguishing character is therefore dependent on the nature of the substratum in the habitat. Binder (1957) has put forward a strong claim for the retention of the name *libycus* despite the recently demonstrated prior claim of *L. intortus* (Lamarck). In view of the confusion likely to be created by the use of Lamarck's name I am in entire agreement with Binder's argument.

Family BITHYNIIDAE

GABBIA sp.

MATERIAL : Lake Wum, Bamenda Division. 1 specimen. 7th November, 1963.

Shell (Pl. II, fig. 12) : pale yellowish-brown with three rounded whorls, a very faint spiral microsculpture intersects the fine growth lines but the general appearance of the shell is smooth and shiny. The umbilicus is narrowly open and the spiral nucleus of the operculum occupies about half its total width. The single specimen measures 2.32 mm. in height and width and has an aperture height 1.52 mm. and aperture width of 1.36 mm.

The genus *Gabbia* is mainly East and Central African in distribution, the only West African records being Frauenfeld's *B. africana* and Binder's (1955) *Bithynia* (*Gabbia*) *tournieri* from the Ivory Coast. Several species have been recorded from the Lake Chad region but the affinities of the present specimen appear to be nearest to *G. parva* Mandahl-Barth, 1954.

Family THIARIIDAE

Potadoma freethi (Gray)

Melania freethi Gray, 1831 : 11.

Melania nigritina Morelet, 1848 : 345 ; von Martens, 1877 : 270 ; von Martens, 1891 : 33 ; d'Ailly, 1896 : 121.

Melania (*Nigritella*) *nigritina* ; Boettger, 1905 : 181.

Thiara (*Melanoides*) *dykei* Spence, 1925 : 249.

Potadoma graptocomus Pilsbry & Bequaert, 1927 : 276, fig. 46a and pl. XX, figs. 10 and 11.

MATERIAL : Stream on Bai Rubber Estate, Kumba Division. 10 specimens. 25th October, 1963.

Stream on Pamol Estate, Lobe, Kumba Division. 10 specimens. 25th October, 1963.

Stream near Barombi Kotto Stranger Town, Kumba Division. 18 specimens. 15th November 1963.

Stream through Barombi Mbo village, Kumba Division. 20 specimens. 16th November 1964.

Shell (Pl. III, figs. 1-8) : large, solid, turreted, adults usually black and decollate, whorls flattened, suture shallow, aperture pear-shaped, pointed above, columella gently curved outward resulting in a slight expansion of the aperture at the junction of the basal and columellar margins. There is a well-marked spiral sculpture and on the later whorls fine growth lines are more accentuated and intersect the spiral lines to give a granular pattern. Young specimens have a marked basal angle on the body whorl (Pl. III, figs. 7 and 8) but this almost disappears in the adults. The usual black colour of adult shells results from a fine covering of silt which can be removed by ultrasonic cleaning to show the basic greenish-brown colour of the young shell with at least one dark purple-brown band. Specimens from habitats with sandy bottoms are often found in this clean condition.

Radula (Text-fig. 21) : central tooth complex with five small cusps on its anterior edge. The single lateral on each side is assymmetrically four-cusped and the two marginals are tricuspid.

The genus *Potadoma* is typically West African and more or less confined to the forested areas. The type locality for *P. freethi* is the island of Fernando Poo off the Cameroon coast, *Melania nigratina* was described from Gaboon, *P. dykei* from near Victoria in Cameroon and *P. graptoconus* from the Congo. All authors are in agreement concerning the identity of *P. freethi* and Morelet's *nigratina*. *P. dykei* was described without reference to *freethi*; a specimen of *dykei* identified by Spence (Pl. III, figs. 2 and 5) is in the collection of the British Museum (Natural History) and apart from being slightly more obese and having more well-marked cords around the columella it is not possible to separate it from large specimens of *freethi*. *P. graptoconus* was distinguished by Pilsbry & Bequaert because of its well-marked spiral sculpture without the granulation said to be characteristic of *freethi*. However, examination of numbers of specimens from West Cameroon indicates that this granulation is not always present and is somewhat irregular on the holotype of *freethi* (Pl. III, fig. 4).

P. freethi was always found in gently moving water and although it is present in the stream flowing into Lake Barombi Mbo live specimens were not found in the lake itself. This species is common as a sub-fossil in the area of Lake Barombi Kotto and near Bekondo on the route to Lake Soden.

DISCUSSION

The collections made during this expedition fall readily into two groups, those from the low-lying forested area of Kumba Division and those from open savannah country at 4-5,000 feet in Bamenda Division. No species has been found which is common to both areas and although the search in Mamfe Division which intervenes between Kumba and Bamenda was superficial no freshwater snails of any kind were found. This suggests that an effective barrier exists between the two areas. The broad differences between the two parts of the snail fauna are those typical of altitude

and correspond to the differences between the coastal plain and southern plateau regions of Angola (Wright, 1963b). The low-lying areas are characterized by an abundance of prosobranchs, the presence of *Anisus* and members of the *Bulinus forskali* group and *B. rohlfsi* while the highlands have *Biomphalaria*, *Gyraulus costulatus* and *Bulinus tropicus*. The presence of *Segmentorbis kanisaensis* in Lake Barombi Mbo is in keeping with its occurrence in the coastal plain of Angola and at low altitudes in the Ivory Coast and Gambia while *S. angustus* in Lake Wum corresponds with its distribution in higher crater lakes in Uganda. If the affinities of the species of *Gabbia* in the same lake have been correctly assessed it also points to a similarity with the Uganda fauna. Gèze (1943) mentions the occurrence of a number of East African elements in the insect fauna of the mountains in Cameroon and attributes this to a more extensive temperate connection with the east along the highland chain during the pluvial periods. Sram (1955) has even gone so far as to suggest that there is evidence of glaciation on Mount Cameroon and Mannengouba during this period. The type locality of *Biomphalaria camerunensis* on Mount Cameroon suggests that this is a relic population now isolated from the more general highland areas by the intervening tropical rain forest.

In Kumba Division the difference between the snail faunas of lakes Barombi Mbo and Barombi Kotto is interesting. The only species which they have in common is *Bulinus rohlfsi*, the two populations of which have distinctive characteristics. Trewavas (1962) has recently shown that the two lakes have no species of fish in common and that all but one of eight species in Barombi Mbo are probably endemic while Barombi Kotto has an endemic genus, two endemic species and one endemic sub-species out of a total of seven species. *Bulinus camerunensis* appears to be endemic to Barombi Kotto but the other snail species in both lakes have wide distributions in West Africa. The effluent from Barombi Kotto passes into the Meme River near the mouth of which lies Lobe. *Anisus coretus* is common to both the lake and the streams in the Lobe area while *B. camerunensis* in the lake, although closely related to *B. forskali*, is clearly distinct from the local form of that species at Lobe. Differentiation of the two populations of *B. rohlfsi* may be the result of the "founder principle" and does not necessarily imply any prolonged separation.

SCHISTOSOMIASIS IN WEST CAMEROON

Zahra's (1953) original report has remained virtually the only source of information on schistosomiasis in West Cameroon. de Azevedo (1958) included these data in a general report covering what was at that time the whole British Cameroons but did not add anything further. One of the objectives of the present expedition was to confirm the identity of the snails responsible for transmission of the parasite in the known foci and to investigate their wider distribution in the territory.

Wild specimens of *Bulinus rohlfsi* from Barombi Kotto were found to be shedding cercariae of *Schistosoma haematobium* (confirmed by exposure of hamsters with subsequent recovery of adult worms). Laboratory bred snails of this species from both of the Barombi lakes have been successfully infected by miracidia hatched from urine samples from Barombi Mbo. *Bulinus camerunensis* from Barombi Kotto

was not found naturally infected nor has it been successfully exposed to infection in the laboratory. Laboratory bred specimens of *Bulinus tropicus* from the N'dop plain were not susceptible to miracidia from Barombi Mbo. This is to be expected because so far no member of the *B. tropicus* complex has been demonstrated to act as an intermediate host for *S. haematobium*. *B. rohlfsi* has not been found in any of the other places investigated in West Cameroon so there is little chance of the disease spreading unless the snails become established in other areas.

The habitat for *B. rohlfsi* in both lakes is limited to shallow water with reasonable sun-exposure and the snails are found on dead leaves rather than on aquatic vegetation. It is remarkable that the focus in Lake Barombi Mbo has remained confined to the small area on the north-west side of the lake near to the beaches where fishing canoes from the village are drawn up since there is ample opportunity for distribution of the snails both on the canoes and on fish traps which are set daily in all suitable places around the lake margin. It is probable that shading of the water's edge by fringing vegetation is the most important factor in preventing the colonization of new areas and any major clearance of the marginal bush should be viewed with concern. It is probable that transmission in both lakes is partly seasonal; to judge from conditions in October and November it seems likely that maximum snail population densities occur in January–February and, allowing for development of the larval schistosomes there is probably a peak of transmission in February–March.

An interesting aspect of these lake foci is that schistosomiasis is almost confined to members of the Barombi tribe who fish both lakes. The Barombis appear to be the only local people who do not have a profound superstitious fear of the lakes and contact with the water by people of other tribes is relatively infrequent. Lakes such as Soden and Ejaghem are known to contain fish but this is not a sufficient attraction to draw people to them regularly. On Lake Soden there are not even any canoes and only poor tracks to the water's edge. The few cases of urinary schistosomiasis encountered outside the Kumba area are usually from Nigeria or the East but some are found in people who have lived in Barombi Kotto Stranger Town and visited the lake for washing.

Dissemination of *Bulinus rohlfsi* from the Barombi lakes might occur if development of fisheries in other lakes is undertaken using Barombi fish for stocking. There is also a slight possibility that *B. rohlfsi* from Barombi Kotto might gain access via the Meme river to the Lobe area where bush clearance has provided potentially good snail habitats in the streams and ditches. It seems that the West Cameroon foci of urinary schistosomiasis are effectively closed with little opportunity for spread and not much chance of importation of new strains. The strain in the Barombi foci is probably derived from the *B. rohlfsi*-borne form in Nigeria (Cowper, 1963). Snail control by molluscicides or habitat modification would not be practical in the lakes since the danger of damaging the fish population would be too great. The confined nature of the foci will probably lend themselves to control by drug treatment when suitable compounds are available.

There is little information available concerning *Schistosoma mansoni* in West Cameroon. It is perhaps significant that Gaud's (1955) distribution map of this

parasite shows the edge of a lightly endemic zone in the east coinciding exactly with the border between East and West Cameroon in the area of the N'dop plain. Enquiries in the area near Bambalang revealed that dysentery accompanied by passing of blood is common in the area but time did not permit a survey to be carried out. *Biomphalaria camerunensis* is a possible host for *S. mansoni* but limited infection experiments with laboratory-bred specimens have so far failed. Both an Egyptian and a Liberian strain of parasite have been tested. There is at present no evidence for the existence of *S. mansoni* in the Wum area despite the presence of the potential intermediate host *Biomphalaria pfeifferi* in Lake Wum.

In conclusion brief mention must be made of two other trematode diseases, paragonimiasis (lung-fluke) in man and liver-fluke in cattle. Zahra (1952) reported a widespread incidence of infection with *Paragonimus* in Victoria and Kumba Divisions. This distribution coincides with that of the snail intermediate host, *Potadoma freethi*, which is common in small streams throughout the area. The incidence of *Paragonimus* is said to be particularly high among the Bakossi people in the region of Mount Kupe up to a height of 5,000 feet. No published reports of the occurrence of *Fasciola gigantica* in cattle in West Cameroon have been seen. Inquiries through the sanitary inspectors responsible for meat inspection suggest that the few cases seen are in cattle brought from outside the territory. However, around Banso and Ndu (6-7,000 feet) the parasite is scarcely ever seen while in the N'dop plain where the intermediate host *Lymnaea natalensis* is found it is said to be of slightly more frequent occurrence. Most of the grazing area in Bamenda Division appears to be above the altitude limit for *L. natalensis* and examination of apparently ideal habitats near Oku failed to yield any snails.

ALPHABETICAL LIST OF COLLECTING PLACES

This list includes the major places visited but not a large number of minor streams and pools in which nothing was found.

1. Babungo, N'dop Plain, Bamenda Division. 6°02' N., 10°12' E. Altitude about 4,000 feet. Slow-moving, weed-choked stream about one mile east of the village. 6th November, 1963. *Bulinus tropicus*, *Lymnaea natalensis* and unidentified ancyliid.

2. Bafeng (Lake), near falls on Mencham River, about 12 miles south of Wum on Bafut road, Bamenda Division. 6°20' N., 10°02' E. Altitude unknown, probably between 5,000 and 6,000 feet. Small, very steep-sided crater lake with dense bush within the crater but surrounded by open grassland. 7th November, 1963. No snails found.

3. Bambalang, N'dop Plain, Bamenda Division. 5°52' N., 10°25' E. Altitude about 4,000 feet. Stagnant, shallow, marshy pools, heavily shaded by palm scrub. Thick, black mud bottom and mixed emergent vegetation. 6th November, 1963. *Biomphalaria camerunensis*.

4. Bambuluwe (Lake), south of Bamenda town, Bamenda Division. 5°50' N., 10°10' E. Altitude probably over 6,000 feet. Moderate-sized crater lake, slightly

irregular in shape, dense surrounding bush except near outlet of effluent stream where grassland runs down to lake shore. Few leeches and insect larvae seen. 4th November, 1963. No snails found.

5. Barombi Kotto (Lake), Kumba Division. $4^{\circ}29' N.$, $9^{\circ}20' E.$ Altitude about 350 feet. Large crater lake with less steep margins than most and a volcanic island in the centre on which stands the village. No snails found on the lake margin at canoe beach but numerous specimens collected from dead leaves and débris on gently sloping beaches of the island. 31st October and 15th November, 1963. *Bulinus rohlfsi*, *B. camerunensis* and *Anisus coretus*.

6. Barombi Mbo (Lake), Kumba Division. $4^{\circ}42' N.$, $9^{\circ}28' E.$ Altitude about 1,000 feet. Large crater lake, about two miles in diameter, very deep except on north-west side where entering stream has deposited a shelf of silt and gravel. Snails confined to this part of the lake. Visited six times in October and November, 1963. *Bulinus rohlfsi*, *Segmentorbis kanisaensis*, *Lanistes libycus* and *Potadoma freethi* (in entering stream).

7. Ejaghem (Lake), Mamfe Division. $5^{\circ}45' N.$, $8^{\circ}56' E.$ Altitude about 600 feet. Moderately large lake, shallow sloping surround with thick bush which has been cleared in patches. Natural(?) fish population but no snails found. 9th November, 1963.

8. Lobe, Pamol Estate, Kumba Division. $4^{\circ}37' N.$, $9^{\circ}01' E.$ Altitude, near sea level. Oil palm plantation on which most of the bush has been cleared and some water-management of small streams undertaken. 25th October and 15th November, 1963. *Bulinus forskali*, *Anisus coretus*, *Ferrissia* sp., *Lanistes libycus* and *Potadoma freethi*.

9. Soden (Lake), Kumba Division. $4^{\circ}45' N.$, $9^{\circ}16' E.$ Altitude, 1,500 feet. Moderately large, isolated crater lake with very steep, densely forested internal slope, difficult of access, very little human contact, no canoes, natural fish population. 28th October, 1963. No snails found.

10. Tiko, Victoria Division. $4^{\circ}5' N.$, $9^{\circ}20' E.$ Altitude, near sea level. Heavily polluted stream flowing through the edge of the town, visited at several points after hearing reports of urinary schistosomiasis in the area. Reports later proved to be without foundation. 12th November, 1963. No snails found.

11. Wum (Lake), Bamenda Division. $6^{\circ}28' N.$, $10^{\circ}02' E.$ Altitude about 5,000 feet. Moderate sized lake, gently sloping bank with patches of shallow marginal water and some aquatic vegetation. Lake open, surrounded by savannah, margins unshaded. 7th November, 1963. *Biomphalaria pfeifferi*, *Gyraulus costulatus*, *Segmentorbis angustus*, *Lymnaea natalensis*, *Gabbia* sp. and unidentified ancyliid.

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PLATE 1

- FIGS. 1-3. *Bulinus camerunensis*, Lake Barombi Kotto, $\times 8$.
FIG. 4. *Bulinus camerunensis*, laboratory bred, $\times 8$.
FIGS. 5, 6. *Bulinus forskali*, Lobe, $\times 8$.
FIGS. 7, 8. *Bulinus rohlfsi*, Lake Barombi Mbo, $\times 2.5$.
FIGS. 9, 10. *Bulinus rohlfsi*, Lake Barombi Kotto, $\times 2.5$.
FIGS. 11, 12. *Bulinus tropicus*, Babungo, N'dop plain, $\times 2.5$.
FIG. 13. *Lymnaea natalensis*, Lake Wum, $\times 2.5$.
FIGS. 14-16. *Biomphalaria pfeifferi*, Lake Wum, $\times 2.5$.
FIGS. 17-23. *Biomphalaria camerunensis*, Bambalang, N'dop Plain, $\times 2.5$.



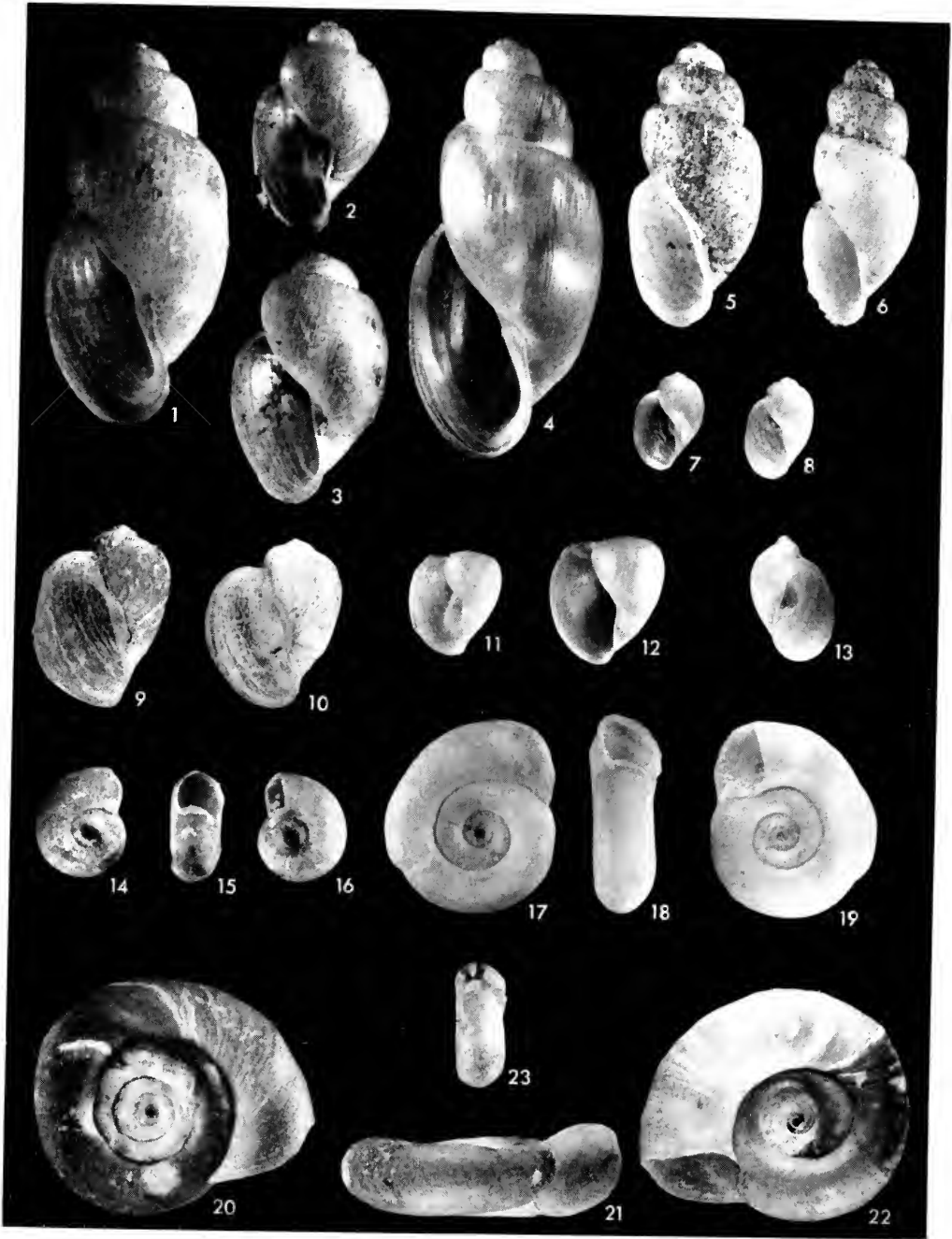


PLATE 2

FIGS. 1-3. *Segmentorbis angustus*, Lake Wum, $\times 14$.

FIGS. 4-6. *Anisus coretus*, Lobe, $\times 14$.

FIGS. 7-9. *Gyraulus costulatus*, Lake Wum, $\times 14$.

FIGS. 10, 11. *Ferrissia* sp., Lobe, $\times 14$.

FIG. 12. *Gabbia* sp. Lake Wum, $\times 14$.

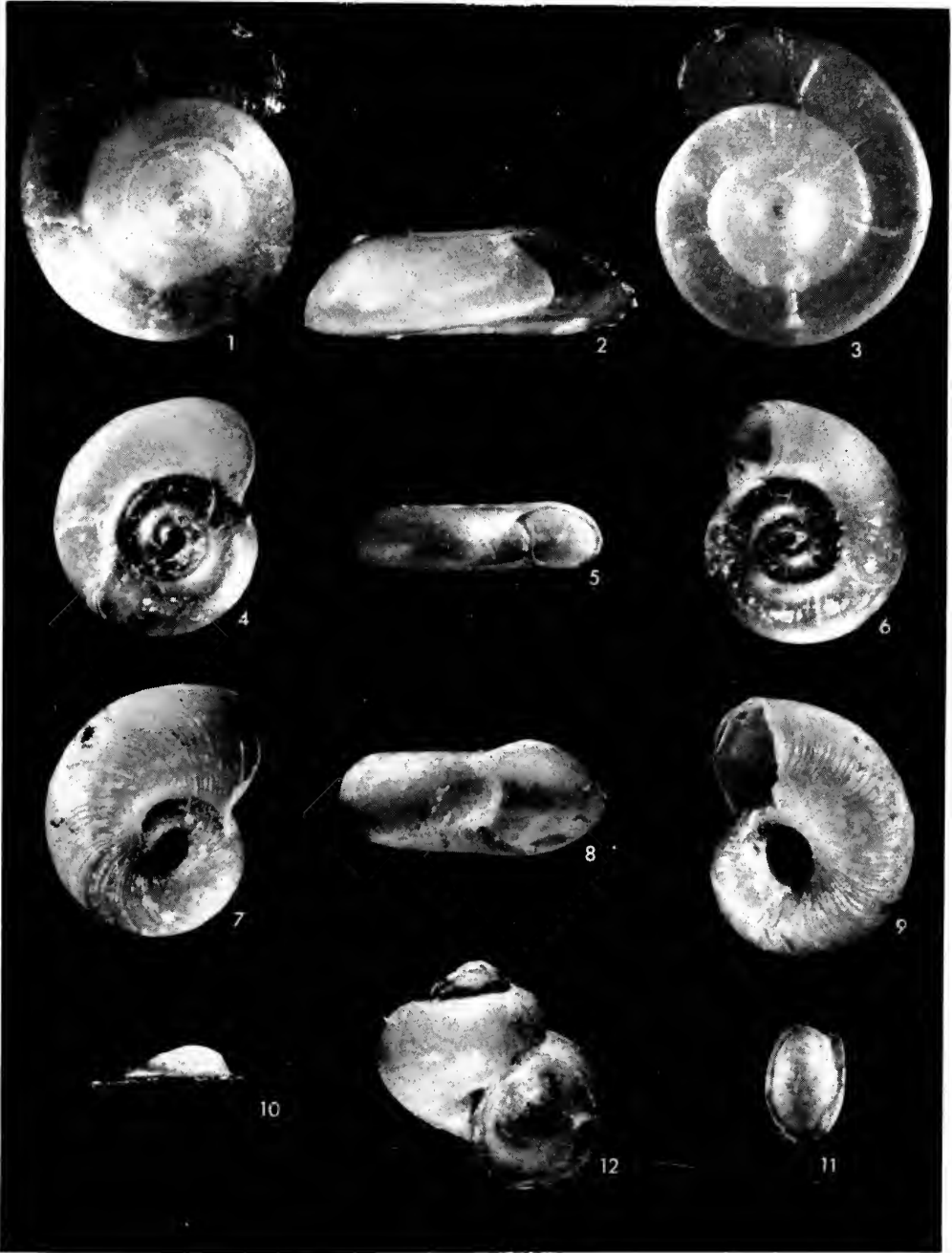


PLATE 3

Figs. 1-3 & 7-10 \times 1.6, Figs. 4-6 \times 6.5.

FIG. 1. *Potadoma freethi*, Fernando Poo, (Holotype).

FIG. 2. *Potadoma freethi*, (*P. dykei* Spence).

FIG. 3. *Potadoma freethi*, Barombi Mbo.

FIG. 4. Microsculpture of specimen in Fig. 1.

FIG. 5. Microsculpture of specimen in Fig. 2.

FIG. 6. Microsculpture of specimen in Fig. 3.

FIGS. 7, 8. *Potadoma freethi*, juveniles, Lobe.

FIG. 9. *Lanistes libycus*, Lake Barombi Mbo.

FIG. 10. *Lanistes libycus*, Lobe.



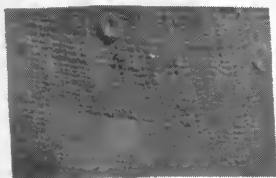
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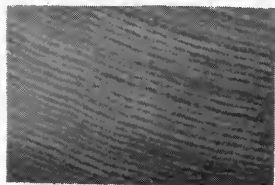
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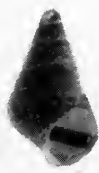
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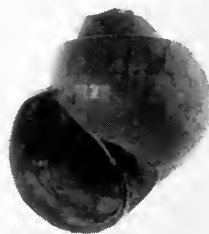
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BARBUS (PISCES, CYPRINIDAE)
OF THE VOLTA REGION

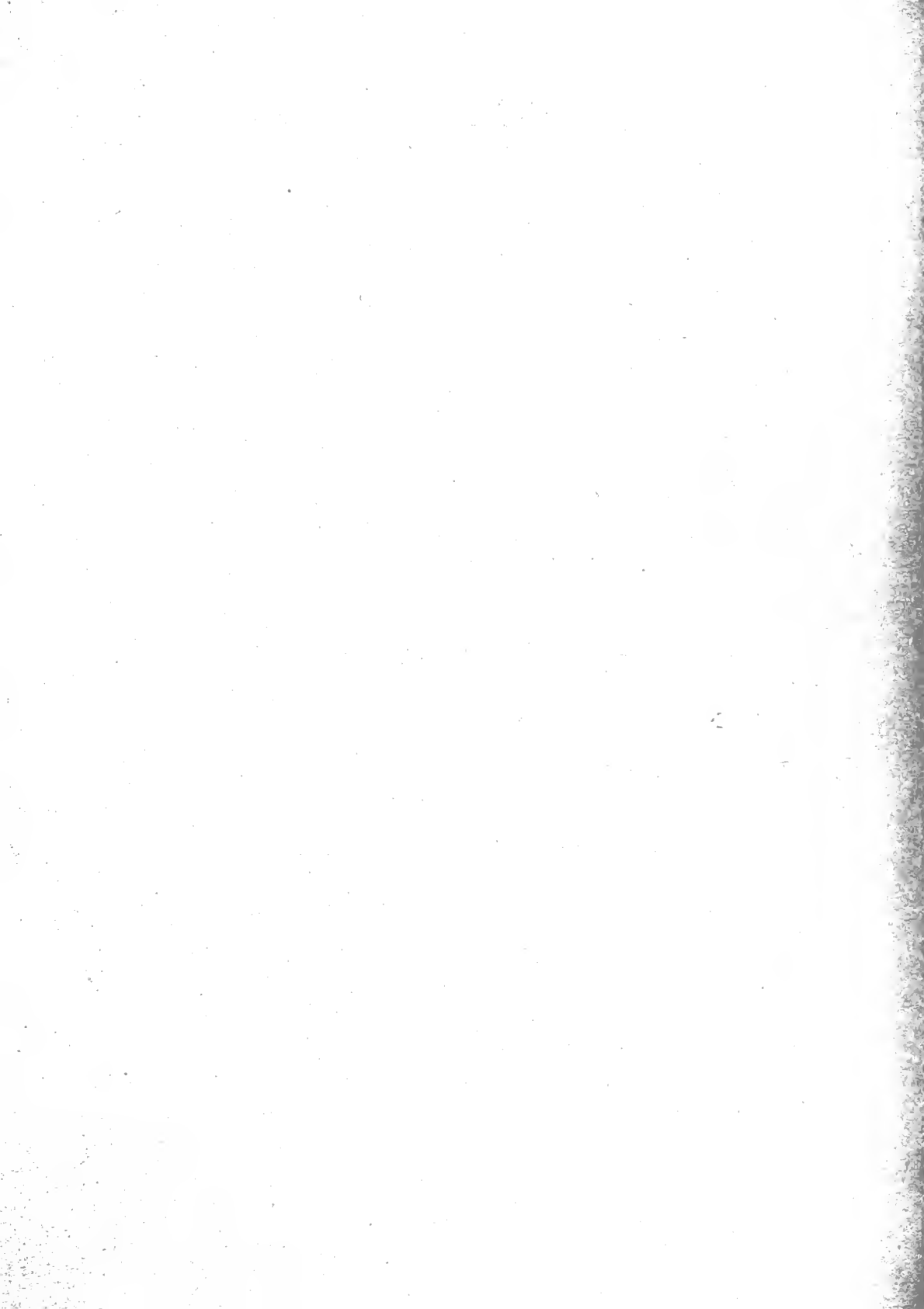


A. J. & J. HOPSON

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BARBUS (PISCES, CYPRINIDAE) OF THE
VOLTA REGION



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Pp. 99-149; 18 *Text-figures*

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BARBUS (PISCES, CYPRINIDAE) OF THE VOLTA REGION

By A. J. & J. HOPSON

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SYNOPSIS

Eighteen species of *Barbus*, collected recently in Ghana, are described and figured. Fifteen of the species were obtained from the Volta basin. The synonymy of West African *Beirabarus* is revised and four species of this subgenus are shown to occur in Ghana. *Barbus nigeriensis* is redescribed using the holotype augmented with new material. A key is given for voltaic species of *Barbus*.

INTRODUCTION

Barbus is one of the most specifically numerous genera of freshwater fish in Africa and well over 200 species have been described. The genus is well represented in West Africa and fifteen species were identified from a collection of fish which we made in the Volta basin, chiefly in northern Ghana, during 1961. Most of the species are widespread and common and *Barbus* forms an important and characteristic element in the fish fauna of all habitats. The present investigations deal chiefly with voltaic

species but observations are also made on three species of *Barbus* collected from the Prah basin in the forest region of southern Ghana :

- B. ablables* (Bleeker)
- B. trispilus* (Bleeker)
- B. subinensis* Hopson

Environmental conditions in the rivers of northern Ghana are comparable with those described by Blanc & Daget (1957) for Haute Volta and by Holden (1963) for the Sokoto River in Northern Nigeria which are indeed typical of the whole savannah region of West Africa. Flooding occurs during a short rainy season lasting from mid-May to mid-September followed by a rapid fall in water level with the onset of the dry season. By the end of December the output of the Black Volta in northern Ghana is greatly diminished and the White Volta is reduced to a mere trickle linking a chain of sandy pools. Smaller tributaries dry out completely before the onset of the rains in May. A more stable environment is found in permanent, well-vegetated oxbow lakes which are particularly characteristic of the valley of the White Volta. Relatively stable conditions are also found in dams constructed across seasonal streams for agricultural purposes ; these are now common in Ghana.

Previous observations on *Barbus* in Ghana have dealt almost exclusively with species occurring outside the Volta basin (Boulenger, 1911, 1916 ; Trewavas in Irvine, 1947). A detailed account of voltaic species was made only during the last decade by Blanc & Daget (*op. cit.*) who worked on material from Haute Volta. They recorded nine species of *Barbus* from the Volta basin :

- B. macrops* Blgr. (= *B. ablables*, *sensu* Blanc & Daget, 1957)
- B. parablables* Blanc & Daget
- B. voltae* Hopson (= *B. nigeriensis*, *sensu* Blanc & Daget, *op. cit.*)
- B. macinensis* Daget
- B. punctitaeniatus* Daget
- B. atakorensis* Blanc & Daget
- B. leonensis* Blgr.
- B. stigmatopygus* Blgr.

Most of these are widely distributed elsewhere in the savannah region of West Africa and all, with the exception of *B. parablables* and *B. atakorensis*, were shown by Blanc & Daget to be common to the Niger basin.

Six additional species were recorded from the Volta basin during the present survey :

- B. spurrelli* Blgr.
- B. hypsolepis* Daget
- B. nigeriensis* Blgr.
- B. lawrae* Hopson
- B. bawkuensis* Hopson
- B. pobeguini* Pellegrin

Of these, *B. hypsolepis*, *B. nigeriensis* and *B. pobeguini* also occur in the Niger basin.

In the course of the present investigations extensive use has been made of material

in the British Museum (N.H.) and in the Musée National d'Histoire naturelle, Paris. Comparisons were made with type material whenever possible. Most of our observations agree with Daget (1954) and Blanc & Daget (1957). We differ mainly in the synonymy of the subgenus *Beirabarus* and in the diagnosis of *B. nigeriensis*.

Four species of *Beirabarus* are shown to occur in Ghana: *B. ablakes*, *B. spurrelli*, *B. macrops* and *B. parablakes*. *Barbus deserti* of Daget (1954) and *B. ablakes* of Blanc & Daget (1957) are now regarded as misidentified examples of *B. macrops*, which proves to be widely distributed through the savannah regions of West Africa and the Chad basin. *Barbus ablakes* and *B. deserti*, with which *B. macrops* has been confused, are apparently restricted in distribution, *B. ablakes* to the forest rivers between south west Ghana and Liberia and *B. deserti* to the north central Sahara.

A redescription has been prepared for *B. nigeriensis*, based on the holotype, on material from Western Nigeria and on specimens recently collected in northern Ghana. The species described by Blanc & Daget (1957) as *B. nigeriensis* was misidentified. It has been shown recently to be a new species, *B. voltae* (Hopson, 1965).

Methods: the snout length was measured between the verticals to the tip and the anterior margin of the eye; the head length was taken to the posterior extremity of the bony operculum. Ledges of skin forming the dorsal margin of each orbit are included in the interorbital width. Perforated scales overlapping the base of the caudal fin are included in the lateral line count. Other data were obtained in accordance with standard practice.

All specimens were fixed initially in 5% formalin for three to four months. The material was then carefully washed and transferred to an 80% solution of alcohol for permanent preservation. It was found that this procedure satisfactorily exposes the underlying melanophores, the pattern of which is often of taxonomic importance.

The relationship of lateral line to horizontal myoseptum often provided characters of diagnostic value. Marked differences were noted among the *Barbus* under consideration in the degree to which the lateral line dipped below the myoseptum. In species of the subgenus *Beirabarus* and in *B. punctitaeniatus* for example the dip is slight whereas in *B. nigeriensis* and *B. lawrae* it is more pronounced. The maximum distance between horizontal myoseptum and lateral line has been expressed in terms of the depth of adjacent scale rows. The point at which the myoseptum and lateral line converge also varies interspecifically. In *Beirabarus* the point is usually above the base of the anal fin whereas in *B. perince* and in *B. wernerii* they converge near the tip of the caudal peduncle.

CEPHALIC PIT-LINES

Herre (1932) first drew attention to cephalic pit-lines in *Barbus palustris* (= *B. radiatus*, vide Greenwood, 1963) and considered them to be of sufficient importance to be the criterion for establishing a new genus, *Beirabarus*. Apparently unaware of Herre's work, Schultz (1942) described a new genus *Mannicthys* (*M. lucileae* Schultz = *B. macrops* Boulenger), on an identical basis. Johnels (1954) later showed that cephalic pit-lines were present in at least six West African *Barbus* and doubted

the advisability of using them as generic or subgeneric characters. Recently, Greenwood (1962) has given a detailed discussion on the occurrence of pit-lines in African *Barbus*. He upholds Herre's taxon *Beirabarb* at subgeneric level and recognizes two distinct patterns of pit-line distribution.

(a) Pit-lines of the *Beirabarb* type where the individual pits are small and very numerous, grouped tightly into lines like beads and raised above the surface as ridges. These lines sometimes branch and are present in a characteristic pattern on the side of the snout, the cheek, the operculum and on the dorsal surface of the head. On the basis of these characters, Greenwood referred the following species to the subgenus *Beirabarb* :

<i>B. abl</i>	<i>B. deserti</i> Pellegrin
<i>B. radiatus</i> Peters	<i>B. aurantiacus</i> Blgr.
<i>B. jae</i> Blgr.	<i>B. macrops</i> Blgr.
<i>B. aspilus</i> Blgr.	<i>B. spurrelli</i> Blgr.
<i>B. callipterus</i> Blgr.	

(b) The pits are relatively larger than in *Beirabarb* and much fewer in number. They are sometimes arranged in lines but with the pits always well separated from one another. The lines are never raised above the surface in ridges and are usually visible only on the cheek and operculum. Greenwood found this type of pit in fourteen species of *Barbus* :

<i>B. nigeriensis</i> Blgr.	<i>B. trispilomimus</i> Blgr.
<i>B. kessleri</i> (Steindachner)	<i>B. pumilus</i> Blgr.
<i>B. trispilus</i> (Bleeker)	<i>B. anema</i> Blgr.
<i>B. congicus</i> Blgr.	<i>B. svenssoni</i> Johnels
<i>B. pseudognathodon</i> Blgr.	<i>B. collarti</i> Poll
<i>B. pleuropholis</i> Blgr.	<i>B. leonensis</i> Blgr.
<i>B. urostigma</i> Blgr.	<i>B. cercops</i> Whitehead

Of the above species, only *B. kessleri* has a serrated last simple dorsal ray and all with the exception of *B. cercops* are West African in distribution.

Our own observations agree with Greenwood's. Cephalic pit-lines were noted in all of the eighteen species of *Barbus* described in the present work. Of these, four are referable to *Beirabarb* :

<i>B. abl</i>
<i>B. spurrelli</i>
<i>B. macrops</i>
<i>B. parabl</i> Blanc & Daget

The remaining fourteen species all had weakly developed pit-lines corresponding to the description under (b) above. They are as follows :

<i>B. hypsolepis</i> Daget	<i>B. voltae</i> Hopson
<i>B. nigeriensis</i> Blgr.	<i>B. atakorensis</i> Blanc & Daget
<i>B. lawrae</i> Hopson	<i>B. punctitaeniatus</i> Daget

<i>B. subinensis</i> Hopson	<i>B. bawkuensis</i> Hopson
<i>B. trispilus</i> (Bleeker)	<i>B. pobeguini</i> Pellegrin
<i>B. sublineatus</i> Daget	<i>B. stigmatopygus</i> Blgr.
<i>B. macinensis</i> Daget	<i>B. leonensis</i> Blgr.

Cephalic pit-lines were always most clearly seen in formalin-fixed specimens.

Barbus (Beirabarus) ablabes (Bleeker, 1863)

(Text-fig. 1)

Puntius (Barbodes) ablabes Bleeker, 1863, *Nat. Verh. Wet. Haarlem*, **23** : 114, pl. 23, fig. 1.

Barbus ablabes : Boulenger, 1911, *Cat. Afr. Fish.* **2** : 156, fig. 133.

Barbus ablabes : Pellegrin, 1923, *Les poissons des eaux douces de l'Afrique occidentale* : 134, Paris.

[*non Barbus ablabes* : Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 132, fig. 13, see p. 110 below].

SYNTYPES : two fish S.L. 64 and 66 mm. from Dabo Crom, Guinea in the Leyden Museum.

DESCRIPTION based on 30 fish, 31–53 mm. S.L. from the R. Weiwei, Kumasi, south Ghana supplemented with notes on the following material in the British Museum (N.H.) : 10 fish, 44–70 mm. S.L. from the Kotchwah River, south Ghana (reg. no. 99.12.22.46–55) ; 4 fish, 36–48 mm. S.L. from the R. Atesu, south Ghana (reg. no. 1903.4.24.94–97) ; 2 fish, 58–62 mm. S.L. from near Bunsu, south Ghana (reg. no. 1938.12.15.40–41).

Body moderately compressed. S.L. 3.1 to 3.7 times the maximum depth and 3.1 to 3.6 times the length of the head. Predorsal profile convex with a slight nuchal hump. Eyes inclined slightly upwards, the diameter 2.9 to 3.4 times in the length of the head and 1.05 to 1.2 times in the interorbital width. Snout bluntly pointed, 0.6 to 0.9 times the diameter of the eye. Mouth moderate, subterminal. Anterior barbel overlapping the base of the posterior barbel, 0.4 to 0.6 times the diameter of the eye. Posterior barbel extending well past the vertical to the centre of the eye, 0.6 to 0.9 times the eye diameter. Pit-lines of the *Beirabarus* type present on the side of the snout, the cheek, the operculum and on the dorsal surface of the head, between the eyes. Pectoral fin 0.6 to 0.8 times the length of the head, the tip just overlapping the pelvic origin in the four smallest individuals (31–37 mm. S.L.). Last simple dorsal ray smooth, flexible, 0.8 to 1.0 times the length of the head. Tip of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.29). Anal fin rays III 5. The pelvic origin lies between the verticals to the third simple and the first branched dorsal rays. Caudal peduncle 1.1 to 1.4 times as long as deep. The lateral line dips to a maximum of the depth of half a scale row below the horizontal myoseptum in the anterior third of the body ; the two converge at a point in the verticals to the last anal fin rays. Lateral line scales 22 to 27 (modal number 24). Three and a half scales between the lateral line and the dorsal origin, 3½ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and 2½ scales between the lateral line and the pelvic origin. Eleven (f.1) or 12 (f.29) scales round the caudal peduncle.

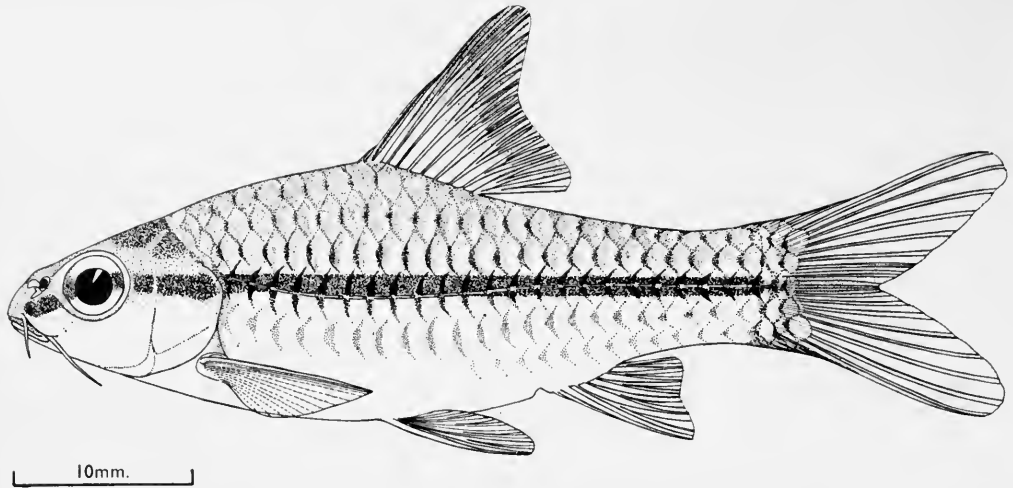


FIG. 1. *Barbus ablates*; N.B. in this and all following figures the caudal fin is simplified.

Summary of morphometric data based on 30 fish, 31–53 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	27.5–33.3	29.6	—
Length head	27.6–32.5	29.8	Negative
Diameter eye	8.5–10.2	9.4	Negative
Interorbital width	9.8–11.2	10.5	—
Length snout	6.2–8.7	7.6	—
Length anterior barbel	3.8–5.9	4.5	—
Length posterior barbel	6.2–8.9	7.4	—
Length pectoral fin	19.6–23.7	21.7	—
Length dorsal fin	25.4–30.2	27.7	—
Length caudal peduncle	17.4–21.4	19.7	—
Depth caudal peduncle	14.2–15.9	15.3	—

COLORATION: *in living specimens*, greenish-brown above, silvery on the sides, whitish below. A conspicuous dark mid-lateral band runs from the snout to the posterior end of the body; the band frequently shows a brilliant green iridescence. Dorsal and caudal fins are tinged basally with yellow which becomes more intense towards the distal margin to merge with a terminal band of orange-red. Anal fin orange-red with a colourless free margin. Paired fins yellow on the anterior rays; the pelvic fins are also tinged with orange in brightly coloured individuals. Iris, orange-red above. *In formalin fixed specimens* the dorsal surface is densely pigmented with fine melanophores free from a narrow zone near the margin of each scale; the pigment-free zone becomes wider on more lateral scales. Dorsal and lateral scales are outlined with larger and darker melanophores, more concentrated in a vertical bar on the pocket of each scale to form a regular pattern. These markings are heaviest on the lateral line scales each of which bears a narrow vertical

stripe in the shape of a cupid's bow. A black mid-lateral band, one third of a scale row in depth, runs from the side of the snout, across the operculum and along the body to the tip of the caudal peduncle. There are scattered melanophores on the pockets of the first and sometimes the second scale row below the lateral line but the ventral surface is generally pigment-free. The anterior margin of the dorsal fin appears greyish-black owing to a moderately heavy peppering of melanophores on the membrane between the second and third simple rays, along the anterior margin of the distal half of the third simple ray and to a lesser extent on the second simple ray and on the membrane between the third simple and first branched rays. Pigmentation on the remainder of the fin is restricted to scattered and inconspicuous melanophores chiefly on the distal parts.

DIAGNOSIS AND AFFINITIES: Dr. Greenwood recently compared the syntypes of *B. ablables* in the Leyden Museum with material from the Kotchwah River, south Ghana (Brit. Mus. (N.H.) reg. no. 99.12.22.46-55) which has been used to supplement the above description. He found (*pers. comm.*) that the two collections were identical in barbel length and in details of pigmentation not lost in preservation. There was no sign in the type specimens of particularly heavy pigment in the region of the second simple dorsal ray (a heavily pigmented second simple ray is characteristic of the closely related *B. macrops*).

Barbus ablables resembles *B. macrops* in morphometric details and in pigmentation. The most obvious difference is in the distribution of melanophores on the dorsal fin. In *B. ablables* moderately heavy pigment is distributed along the entire length of the second and third simple rays and the anterior margin thus appears uniformly grey; in *B. macrops* the second simple ray and the tips of the first to third branched rays are densely pigmented so that the dorsal fin has a broad black tip and a black streak down the lower half of the anterior margin. The part of the third simple ray lying between these two areas of dense pigment is almost clear of melanophores. The two species also differ in the form of the pocket pigment on the lateral line scales; in *B. ablables* the markings are relatively slender in the shape of a cupid's bow, whereas in *B. macrops* the markings are broader and triangular. *Barbus ablables* is readily separated from West African populations of *B. macrops* by the relatively longer posterior barbels (6.2-8.9 c.f. 2.5 to 5.1% S.L. in Ghanaian material). The relative length of the posterior barbel in *B. macrops*, however, varies geographically and a population from the Tibesti shows a slight overlap with *B. ablables* (5.1-6.6 in *B. macrops* c.f. 6.2-8.9% S.L.).

The relative diameter of the eye which Boulenger (1911) originally used to separate the two species is no longer of diagnostic value. This character also varies geographically in *B. macrops*, and in the Tibesti population the eyes are relatively smaller than in *B. ablables*.

The geographical distributions of *B. ablables* and *B. macrops* do not appear to overlap. *Barbus ablables* is recorded only from the forest rivers of south-west Ghana and Liberia whereas *B. macrops* is widespread throughout the savannah rivers of West Africa and the Chad basin.

Barbus ablables is easily distinguished from *B. spurrelli* by the dark mid-lateral band

and the denseness of the pocket pigment on the lateral line scales. In *B. spurrelli* the mid-lateral band is very faint and the pigmentation of lateral line scales is only slightly heavier than that of more dorsal scales.

Barbus ablabes is compared with *B. parablabes* in the description of that species.

DISTRIBUTION: in Ghana, common and widespread in forest streams and rivers in the southwest. Probably absent from the Volta Basin. Elsewhere, Dabo Crom, Guinea (type locality); Liberia (no locality given, Boulenger, 1911). The record of *B. ablabes* from the St. Paul basin, Liberia (Schultz, 1942) is doubtful; Dr. Weitzman of the Smithsonian Institution reports that the specimens appear to have no *Beirabarus* type cephalic pit-lines (*pers. comm.*). *Barbus ablabes* probably belongs to a faunal group restricted to the forest rivers of western Ghana, Côte d'Ivoire and Liberia. The group may also include *Alestes longipinnis* (Günther), *Petersius occidentalis* (Günther), *Nannocharax seiboldi* Schultz, *Barbus trispilus* (Bleeker) and *Eutropius mentalis* Blgr. among other species.

Barbus (Beirabarus) spurrelli Boulenger, 1913

(Text-fig. 2)

Barbus spurrelli Boulenger, 1913, *Proc. zool. Soc. Lond.*: 51, pl. 3, fig. 1; *Idem*, 1916, *Cat. Afr. Fish.* 4: 264, fig. 162.

Barbus ablabes var. *spurrelli* Pellegrin, 1923, *Les poissons des eaux douces de l'Afrique occidentale*: 135, Paris.

Barbus spurrelli: Daget, 1952, *Mem. Inst. France. Afr. Noire*, no. 19: 316, fig. 7.

LECTOTYPE: 67.8 mm. S.L., B.M. (N.H.) reg. no. 1911.11.27.1, from near Dunkwa (Prah Basin) south Ghana. We consider this fish to be the specimen illustrated in Boulenger, 1916, fig. 162.

DESCRIPTION based on 12 fish, 25–46 mm. S.L. from the River Azubone (Volta Basin), near Mpraeso, south Ghana. Body compressed. S.L. 3.25 to 3.5 times the maximum depth and 2.9 to 3.5 times the length of the head. Predorsal profile convex with a slight nuchal hump. Snout bluntly pointed, 0.85 to 1.1 times the diameter of the eye. Mouth moderate, subterminal. Anterior barbel 0.3 to 0.7 times the diameter of the eye, barely overlapping the base of the posterior barbel. Posterior barbel 0.6 to 0.95 times the diameter of the eye, the tip reaching the vertical to the posterior margin of the pupil. Eyes inclined slightly upwards, the diameter 3.25 to 3.85 times in the length of the head and 1.2 to 1.5 times in the interorbital width. Pit-lines of the *Beirabarus* type present on the side of the snout, the cheek, the operculum and on the dorsal surface of the head, between the eyes. Pectoral fin 0.6 to 0.75 times as long as the head, sometimes (f.3) overlapping the pelvic origin. Last simple dorsal ray smooth, flexible, 0.75 to 0.85 times the length of the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.11). Anal fin rays III 5. The pelvic origin lies between the verticals of the first and second branched dorsal rays. Caudal peduncle 1.2 to 1.55 times as long as deep. The lateral line dips to a maximum of the depth of slightly over half a scale row below the horizontal myoseptum in the anterior third of the body; the

two converge above the posterior anal fin rays. Lateral line scales 24 to 26 (modal number 25). Three and a half to $4\frac{1}{2}$ scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and 2 to $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Twelve scales round the caudal peduncle.

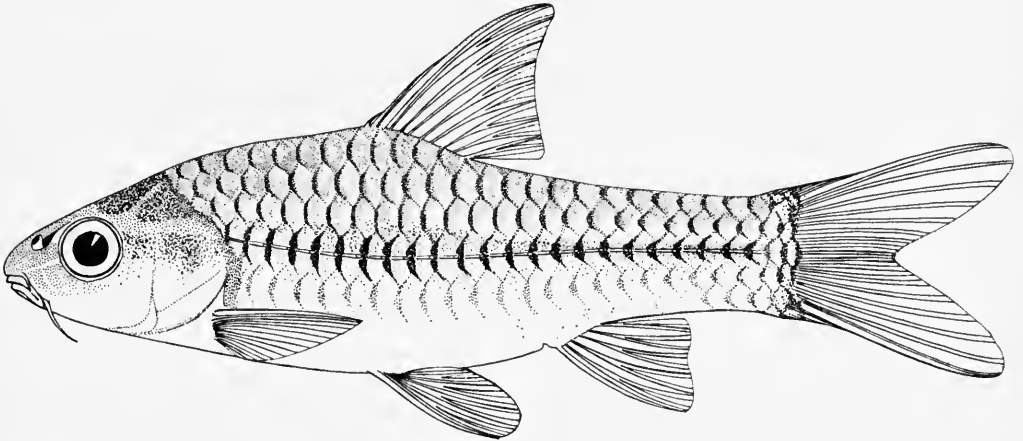


FIG. 2. *Barbus spurrelli*.

Summary of morphometric data based on 12 fish, 25 to 46 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	28.3-30.5	29.3	—
Length head	28.5-33.0	31.5	Negative
Diameter eye	7.4-9.6	8.9	Negative
Interorbital width	10.8-13.0	11.7	—
Length snout	7.8-8.8	8.2	—
Length anterior barbel	3.2-5.8	4.7	—
Length posterior barbel	5.7-7.9	7.2	—
Length pectoral fin	18.6-24.6	22.2	—
Length dorsal fin	22.6-28.1	25.8	—
Length caudal peduncle	18.5-23.3	20.8	—
Depth caudal peduncle	14.3-15.1	14.6	—

COLORATION: *in formalin fixed specimens* the dorsal surface is relatively heavily pigmented with fine melanophores absent only from a narrow zone near the margin of each scale. Dorsal and lateral scales are outlined with larger and darker melanophores; this pigment is more concentrated in a vertical bar on the pocket of each scale to form a regular pattern. Lateral line scales are marked with similar but slightly heavier pigment; each vertical bar is bisected horizontally by the lateral line pore. Diffuse melanophores form an indistinct band, approximately one third of a scale row in depth, running just below the horizontal myoseptum in the anterior half of the body; the two converge over the anal fin and run together onto the caudal

peduncle where the band ends in front of a small and inconspicuous terminal spot, overlapping the base of the caudal fin. A narrow black band runs obliquely downwards from the lateral line origin to the base of the pectoral fin. The ventral surface is generally pigment-free, with the exception of a few scattered melanophores on the pockets of the first and sometimes the second row of scales below the lateral line. The snout is marked with a dark lateral spot. The anterior margin of the dorsal fin is moderately peppered with melanophores which are slightly heavier on the free edge of the last simple ray. Melanophores are thinly distributed over the distal half of the branched dorsal rays.

DIAGNOSIS AND AFFINITIES: these data are in close agreement (allowing for allometry) with the type description. *Barbus spurrelli* is readily distinguishable from other *Beirabarus* occurring in West Africa either by the absence of a dark mid-lateral band or by the lack of a dark spot on or near the tip of the dorsal fin. Detailed comparisons with *B. ablakes* and *B. parablakes* are given in the descriptions of those species.

DISTRIBUTION: *Ghana*. The type locality of *B. spurrelli* is Dunkwa (Prah basin) in the forest region of south Ghana. Our material was collected from the R. Azubone near Mpraeso, a forest stream on the Volta side of the Prah-Volta watershed. *Elsewhere*, Sierra Leone (Pellegrin, 1923); Mount Nimba, French Guinea (Daget, 1952). The record of *B. spurrelli* from the St. Paul basin, Liberia (Schultz, 1942) is doubtful. Dr. Weitzman of the Smithsonian Institution has kindly re-examined the material and reports that no *Beirabarus* cephalic pit-lines are visible (*pers. comm.*).

Barbus (Beirabarus) macrops Boulenger, 1911

(Text-fig. 3)

Barbus macrops Boulenger, 1911, *Ann. Mag. nat. Hist.* (8) 7 : 374; *Idem*, 1916, *Cat. Afr. Fish.* 4 : 265, fig. 163.

Barbus deserti: Pellegrin, 1921 (Ennedi and Tibesti specimens only), *Mem. Soc. Sci. nat. Maroc*, (1) 2 : 143.

Barbus macrops: Pellegrin, 1923, *Les poissons des eaux douces de l'Afrique occidentale*: 136, Paris.

Barbus gambiensis Svensson, 1933, *Kungl. Sven. vet. Handl.* (12) 3 : 67, pl. 4, fig. 1.

Mannichthys lucileae Schultz, 1942, *Proc. U.S. Nat. Mus.* 92 : 321, pl. 35, fig. 3.

Barbus deserti: Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 192, fig. 62.

Barbus ablakes: Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 132, fig. 13.

LECTOTYPE: a fish of 45.0 mm. S.L. (Brit. Mus. (N.H.) reg. no. 1912.4.1.110), from above the rapids, Crobal River, Portuguese Guinea. We consider this to be the specimen illustrated in Boulenger, 1916, fig. 163.

DESCRIPTION based on 24 fish, 31 to 56 mm. S.L. from a tributary of the White Volta, 5 m. N. of Bawku, northern Ghana. Body moderately compressed. S.L. 3.3 to 3.9 times the maximum depth and 3.3 to 3.7 times the length of the head. Predorsal profile convex with a slight nuchal hump. Snout bluntly pointed, 0.7 to 0.85 times the diameter of the eye. Mouth moderate, sub-terminal. Barbels moderate, the anterior 0.1 to 0.35 times the diameter of the eye, the tip barely over-

lapping the base of the posterior barbel. Posterior barbel 0.25 to 0.6 times the eye diameter, the tip reaching the vertical to the centre of the eye in a few individuals. Eyes inclined slightly upwards, 2.85 to 3.1 times in the length of the head and 1.05 to 1.15 times in the interorbital width. Pit-lines of the *Beirabarus* type fully developed on the side of the snout, the cheek, the operculum and on the dorsal surface of the head between the eyes. Pectoral fin 0.65 to 0.8 times the length of the head, the tip always falling short of the pelvic origin. Last simple dorsal ray, smooth, flexible, 0.9 to 1.05 times the length of the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.23). Anal fin rays III 5. The origin of the dorsal fin lies between the verticals to the last simple and first branched dorsal rays. Caudal peduncle 1.3 to 1.6 times as long as deep. The lateral line dips to a maximum depth of slightly over half a scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the vertical to the last anal fin rays. Lateral line scales 24 to 28 (modal number 25). Three and a half scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the mid-ventral line immediately in front of the pelvic origin and $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Twelve scales round the caudal peduncle.

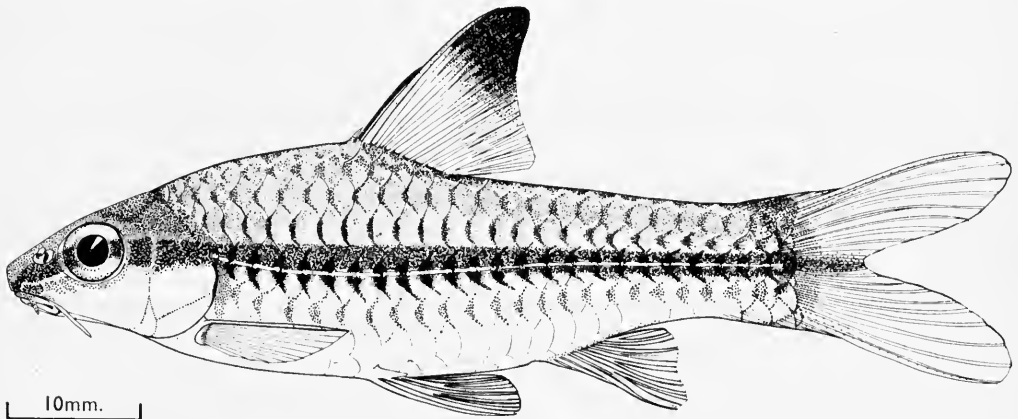


FIG. 3. *Barbus macrops*.

Summary of morphometric data based on 24 fish, 31 to 56 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	25.5-30.2	27.1	—
Length head	26.4-29.7	27.6	Negative
Diameter eye	8.3-10.2	9.1	Negative
Interorbital width	9.2-12.2	10.2	—
Length snout	6.3-7.3	6.8	—
Length anterior barbel	1.2-3.1	2.3	—
Length posterior barbel	2.5-5.1	3.5	—
Length pectoral fin	17.8-21.8	19.7	—
Length dorsal fin	25.2-28.8	26.6	—
Length caudal peduncle	18.1-21.1	19.9	—
Depth caudal peduncle	13.3-14.8	14.1	—

COLORATION: *in living specimens*, greenish-brown above, silvery on the sides, whitish below. A dark mid-lateral band extends from the snout to the tip of the caudal peduncle. Dorsal and caudal fins bright orange-red, the dorsal with a conspicuous black tip. The other fins are frequently tinted orange-yellow. Iris, bright orange-red above. *In formalin fixed specimens* the dorsal surface is densely pigmented with fine melanophores absent only from a narrow zone near the margin of each scale. Dorsal and lateral scales are clearly outlined with larger and darker melanophores which are more concentrated in a vertical line on the pocket of each scale to form a regular pattern. These markings are heaviest on the lateral line where each scale bears a relatively broad and triangular group of melanophores, bisected horizontally by the lateral line pore. A conspicuous black band, one-third of a scale row in depth, runs mid-laterally from the side of the snout, across the operculum and along the body to the end of the caudal peduncle. In some specimens an oblique dark stripe is noticeable between the origin of the lateral line and the base of the pectoral fin. The pattern of scale pocket pigment, described above for dorsolateral scales, is repeated more faintly on the first and sometimes the second scale row below the lateral line. The ventral surface is generally pigment-free. The apex of the dorsal fin bears a dense black spot extending over the distal third of the first four branched rays but heaviest on the tips of the first two. Dense pigment is also present in the vicinity of the second simple ray, particularly on the membrane between it and the third ray. The third simple ray is less heavily pigmented and closely packed melanophores are present only in the basal third along the anterior margin and near the tip; the central section of the third simple ray is almost pigment-free.

GEOGRAPHICAL VARIATION: during the present investigations, *B. macrops* were examined from most of the savannah region of West Africa, the Chad Basin, the Hoggar in the western Sahara and the Tibesti in the eastern Sahara. Details of pigmentation, particularly on the dorsal fin, proved to be constant throughout this wide area. Marked geographical variation was however noted in certain morphometric characters, especially eye diameter but also the relative length of the barbels as demonstrated below:

B. macrops: geographical variations in eye diameter (N.B.—negative allometry).

Locality	No. examined	Range S.L. (mm.)	Eye diameter expressed as % S.L.
Tibesti	24	43-55	6.2-7.6
Niger (N. Nigeria)	3	48-60	7.8-8.6
Sierra Leone	2	61	8.0-8.4
Volta (N. Ghana)	24	31-56	8.3-10.2
Volta (S. Ghana)	17	21-52	8.2-10.6
Hoggar	4	26-39	8.6-10.0
Chad Basin (Nigeria)	12	27-48	9.0-10.2
Port. Guinea	16	25-60	8.8-11.6

B. macrops: geographical variations in posterior barbel length.

Locality	No. examined	Range S.L. (mm.)	Length post. barbel expressed as % S.L.
Chad Basin (Nigeria) . . .	12	27-48	2.4-3.3
Volta (N. Ghana) . . .	24	31-56	2.5-5.1
Volta (S. Ghana) . . .	17	21-52	2.7-6.0
Hoggar	4	26-39	3.0-5.1
Port. Guinea	16	25-60	3.0-5.3
Sierra Leone	2	61	4.5-5.1
Niger (N. Nigeria)	3	48-60	4.8-5.4
Tibesti	24	43-55	5.1-6.6

Diagnosis and Affinities : there has been considerable confusion between *B. macrops* and *B. deserti* Pellegrin. This undoubtedly originated from the inclusion of *B. macrops* (localities Tibesti and Ennedi) in material used for a redescription of *B. deserti* (Pellegrin, 1921).

We have examined type material of *B. deserti* from the Tassili des Azdjers, central Sahara, both the syntypes in the Paris Museum (reg. no. 09.457-458) and a syntype in the British Museum (N.H.) (reg. no. 1909.12.9.7) on which Boulenger (1911) based his diagnosis. They all differ from *B. macrops* in the following details :

(a) In *B. deserti* there is no well-defined mid-lateral band running from the snout across the operculum to the tip of the caudal peduncle. *Barbus deserti* is marked only in the posterior half of the body with relatively faint dark pigment on the horizontal myoseptum.

(b) The lateral line scales are relatively narrower and deeper in *B. deserti* (cf. *B. parablabe*).

(c) The lateral line scale pockets of *B. deserti* are marked with narrow vertical stripes (cf. *B. parablabe*), never with broader triangular spots as in *B. macrops*.

(d) The second simple dorsal fin ray (always dense black in *B. macrops*) is only lightly pigmented.

(e) Further details of pigmentation of the dorsal fin in *B. deserti* are obscured by damage to the tip in all the type material. Pellegrin (1909) noted that the dorsal fin was tipped with black whereas Boulenger (*op. cit.*) records that a spot was present near the tip. It seems likely that Boulenger's description is the more accurate of the two. Three *Barbus* from the oasis of El Barkat, Fianferrari, Fezzan (within 500 miles of the type locality in the same region of the N. Central Sahara) in the British Museum (N.H.) (reg. no. 1937.7.8.4-6), similar to the types in every respect, bear a spot on the distal half of the last simple and first three branched dorsal rays, well clear of the distal margin. This should prove a trenchant character in distinguishing *B. deserti* from *B. macrops* where the black pigment extends to the tip of the anterior dorsal rays.

Comparisons of *B. macrops* with *B. ablabe* and *B. parablabe* are included in the descriptions of those species.

DISTRIBUTION AND HABITAT : in Ghana, restricted to the Volta basin where it is the most common and widespread species of *Barbus*. *Barbus macrops* occurs in rivers, well vegetated lakes and dams, over all substrates coarse and fine. Elsewhere,

distributed over most of the savannah area of West Africa and the Chad basin, extending into the Sahara in the Hoggar to the west and the Tibesti to the east: Portuguese Guinea (Boulenger, 1911, type locality); Gambia River (Svensson, 1933); L. Kwarko, Sierra Leone (Brit. Mus. (N.H.) reg. no. 1958.9.18.54-55); St. Paul and Bolor Rivers, Liberia (Schultz, 1942); Middle Niger (Daget, 1954); Arak Gorge, Hoggar (Brit. Mus. (N.H.) reg. no. 1932.5.6.5-11); R. Katagum (Chad Basin) N. Nigeria (Brit. Mus. (N.H.) reg. no. 1928.7.3.56-62); Sherda, Tibesti (Brit. Mus. (N.H.) reg. no. 1960.6.7.111-160).

LIFE HISTORY: in the White Volta, *B. macrops* spawns during the rains. Gonads start to mature during April and the majority of fish are ripe by mid-June when the first post-larvae appear in the river. Spawning is over by the end of July and the size-composition of samples taken in August suggests that most fish die at the age of one year. Juvenile fish have grown to a modal length of *c.* 35 mm. by November. Females, which ripen at a minimum S.L. of *c.* 50 mm, grow slightly larger than males. Maximum size, a female of 98 mm. S.L.

***Barbus (Beirabarus) parablabe* Blanc & Daget, 1957**

(Text-fig. 4)

Barbus parablabe Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50: 134, fig. 13.

HOLOTYPE: a fish 62 mm. S.L. from between Tanguieta and Natitingou, Volta basin, N. Dahomey, Paris Mus. reg. no. 56-108.

DESCRIPTION based on 24 fish, 39-52 mm. S.L. from the waterworks reservoir at Tamale (Volta basin), northern Ghana. Body moderately compressed. S.L. 3.3 to 3.9 times the maximum depth and 3.2 to 3.6 times the length of the head. Predorsal profile convex with a slight nuchal hump in the larger individuals (*c.* 45 mm. S.L. and over). Snout bluntly pointed, 0.6 to 0.8 times the diameter of the eye. Mouth moderate, subterminal. Barbels moderate, the anterior 0.25 to 0.4 times the diameter of the eye, its tip reaching the base of the posterior barbel. Posterior barbel 0.45 to 0.6 times the diameter of the eye, the tip extending to between the verticals to the anterior margin and the centre of the pupil. Eyes inclined slightly upwards, the diameter 2.95 to 3.35 times in the length of the head and 1.0 to 1.15 times in the interorbital width. Well developed *Beirabarus* type pit-lines on the side of the snout, the cheek, the operculum and on the dorsal surface of the head between the eyes. Pectoral fin rather long, 0.7 to 0.85 times the length of the head, the tip frequently overlapping the pelvic origin, particularly in smaller males. Last simple dorsal ray smooth, flexible, 0.9 to 1.0 times the length of the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.23). Anal fin rays III 5. The pelvic origin lies between the verticals to the last simple and first branched dorsal fin rays. Caudal peduncle slender, 1.4 to 1.8 times as long as deep. The lateral line dips to a maximum of slightly more than the depth of half a scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the vertical to the anal fin, usually over the anterior rays. Lateral

line scales 23 to 27 (modal number 25). Three and a half scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2-2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Nine (f.1), 10 (f.18) or 11 (f.5) scales round the caudal peduncle ; the odd row of scales, when present always lies along the mid-ventral line (N.B.—Daget records only 12 scales round the caudal peduncle in the type description).

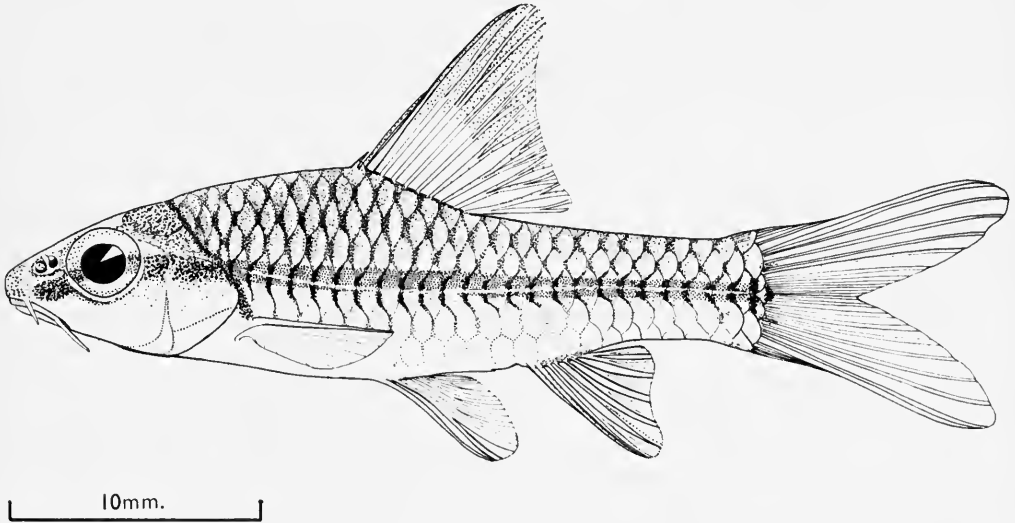


FIG. 4. *Barbus parablades*.

Summary of morphometric data based on 24 fish, 39 to 52 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth 25.8-29.6	27.5	—
Length head 27.3-30.7	28.9	—
Diameter eye 8.9-9.7	9.3	—
Interorbital width 8.9-10.4	9.8	—
Length snout 6.4-7.6	6.9	—
Length anterior barbel 2.5-3.6	2.9	—
Length posterior barbel 4.1-5.7	4.9	—
Length pectoral fin 21.2-24.7	23.0	—
Length dorsal fin 26.8-31.2	28.0	—
Length caudal peduncle 20.0-24.0	22.0	—
Depth caudal peduncle 13.1-14.4	13.7	—

COLORATION : *in living specimens*, dorsal surface greyish green, flanks silvery, whitish below. A greyish mid-lateral band is punctuated with short dark vertical streaks on the lateral line. Caudal and dorsal fins clear rose-pink, the dorsal less brightly coloured than the caudal ; all other fins colourless. Iris reddish above. *In formalin-fixed specimens*, dorsal surface with a moderately heavy scattering of fine melanophores, free from a narrow zone near the margin of each scale ; the clear zone becomes increasingly wide on the flanks. Dorsal and lateral scales are outlined

with larger and darker melanophores which are more concentrated in a vertical band on the pocket of each scale to form a regular pattern. Pocket pigment is particularly heavy on the lateral line where each scale is marked with a conspicuous crescent-shaped vertical stripe traversed by the lateral line pore. A well-marked band of diffuse melanophores, one third of a scale row in depth, runs mid-laterally from the side of the snout, across the operculum, to the tip of the caudal peduncle. The ventral surface is generally pigment free with the exception of scattered melanophores on the pockets of the first and sometimes the second row of scales below the lateral line. The dorsal fin is relatively lightly peppered with melanophores chiefly on the second simple ray and on the distal halves of the third simple and first three branched rays. This pigment is sometimes more concentrated towards the apex of the fin but never enough to form a definite spot. Fine lines of black pigment are frequently present on the anterior and posterior edges of the fin rays particularly in the basal half of the fin; this may produce a streaky appearance.

DIAGNOSIS AND AFFINITIES: *Barbus parablables* is readily distinguished from *B. macrops* (with which it usually occurs in North Ghana) by the absence of a heavy black spot at the tip of the dorsal fin, the relative lightness of the lateral band and the slender crescentic markings on the pockets of the lateral line scales (broader and triangular in *B. macrops*). The lateral line scales themselves are narrower and deeper in *B. parablables*. The caudal peduncle is more slender in *B. parablables*, and in northern Ghana the lower number of scales round the caudal peduncle (9-11 cf. 12 in *B. macrops*) is diagnostic. However, as noted above, 12 scales round the caudal peduncle were recorded in the type material of *B. parablables* from north Dahomey (Blanc & Daget, 1957). The pectoral fin is relatively longer in *B. parablables*, frequently overlapping the pelvic origin in the smaller males (never in *B. macrops*.) In living specimens the pale pink of the caudal fin is strikingly different to the bright orange red of *B. macrops*.

Most of the above characters also serve to distinguish *B. parablables* from *B. ablables*. Both species are, however, without a black tip to the dorsal fin and the stripes on the lateral line scale pockets are only slightly broader in *B. ablables* than in *B. parablables*. The shorter posterior barbel of *B. parablables* (4.9-5.7 cf. 6.2-8.9% in *B. ablables*) is diagnostic.

Compared with *B. spurrelli*, *B. parablables* has a shorter snout (6.4-7.6 cf. 7.8-8.8% S.L.), shorter posterior barbels (4.1-5.7 cf. 5.7-7.9% S.L.) and a narrower caudal peduncle (13.1-14.4 cf. 14.3-15.1% S.L.). The dark mid-lateral band is much heavier in *B. parablables* and the vertical lines of pigment on the lateral line scales are narrower and more emphasized; in *B. spurrelli* there is relatively little contrast between the pigmentation of the lateral line and more dorsal scales.

DISTRIBUTION AND HABITAT: in Ghana, widespread and common throughout the northern region in rivers, streams and dams. Occurs over all substrates though rarely in thickly vegetated habitats. No records from the south or from outside the Volta basin. *Elsewhere*, recorded from a tributary of the River Oti (Volta basin) in north Dahomey (type locality).

NATURAL HISTORY: *Barbus parablabe* spawns during the rains. Gonads start to mature during April and by mid-June the majority of fish are ripe. Juveniles appear in the rivers during July and by mid-August the larger mature fish have disappeared, suggesting that death occurs after breeding, at the age of approximately one year. Females grow larger than males. Maximum size: a female of 53 mm. S.L.

***Barbus hypsolepis* Daget, 1959**

(Text-fig. 5)

Barbus hypsolepis Daget, 1959, *Bull. Inst. France. Afr. Noire*, 21 (A), 2: 670, fig. 1.

DESCRIPTION based on 21 specimens 14–27 mm. S.L. from the Black Volta, 3 miles west of Lawra, north Ghana. Body moderately compressed. S.L. 3.65 to 4.15 times the maximum depth and 3.05 to 3.90 times the length of the head. Pre-dorsal profile smooth, convex. Snout somewhat pointed, 0.4 to 0.7 times as long as the diameter of the eye. Mouth moderate, subterminal and protrusible obliquely downwards. Weakly-developed pit-lines clearly visible on the cheeks. Anterior barbel 0.03 to 0.25 times the diameter of the eye, the tip overlapping the base of the posterior barbel only in the larger specimens. Posterior barbel 0.05 to 0.45 times the diameter of the eye, the tip extending in larger specimens beyond the vertical to the anterior margin of the pupil. Eyes large, inclined slightly upwards, 2.35 to 2.95 times in the length of the head and 0.85 to 1.05 times in the interorbital width. Pectoral fin 0.55 to 0.75 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.9 to 1.05 times as long as the head. Apex of dorsal fin pointed, distal margin concave. Dorsal fin-rays III 8. Anal fin-rays III 5. Origin of pelvic fin below the vertical to the last simple dorsal ray. Caudal peduncle slender, 1.55 to 1.9 times as long as deep. The lateral line scales are unusually deep, particularly below the origin of the dorsal fin. The lateral line dips to a maximum of the depth of a third of a scale row below the horizontal

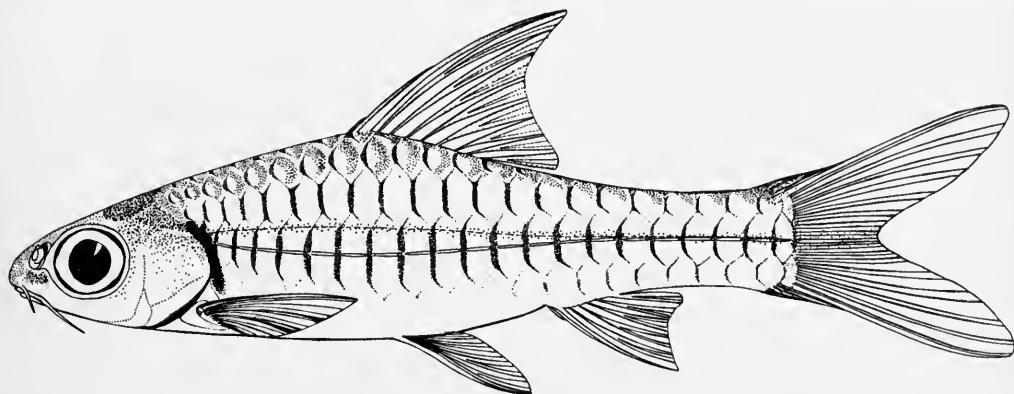


FIG. 5. *Barbus hypsolepis*.

myoseptum in the anterior third of the body; the two converge in the vertical to the base of the anal fin. Lateral line scales 22 to 24 (modal number 23). Two and a half scales between the lateral line and the dorsal origin, $2\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $1\frac{1}{2}$ scales between the lateral line and the pelvic origin. Eight scales round the caudal peduncle.

Summary of morphometric data based on 21 fish, 14 to 27 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	23.5-27.8	25.5	—
Length head	25.6-32.4	28.8	Negative
Diameter eye	9.7-12.8	10.7	—
Interorbital width	9.7-11.0	10.4	—
Length snout	4.7-7.1	5.8	—
Length anterior barbel	0.1-2.6	1.2	Positive
Length posterior barbel	0.6-4.6	2.4	Positive
Length pectoral fin	16.8-22.5	19.0	—
Length dorsal fin	25.8-30.4	27.3	—
Length caudal peduncle	19.6-23.9	21.4	—
Depth caudal peduncle	11.8-14.0	12.5	—

COLORATION: *in living specimens*, body nacreous silver with a pinkish flush on the dorsal surface. Scales clearly outlined with dark pigment. Dorsal and caudal fins pale pinkish-orange, anal and paired fins tinged with the same colour. Iris with an orange-red arc above. Daget (1959) noted that in *B. hypsolepis* from the Middle Niger, females are less brightly coloured than males and have a greyish dorsal fin. *In formalin-fixed specimens* scales of the lateral line and above are clearly outlined with dark pigment which is emphasized in a slender, vertical arc of melanophores on each scale pocket. A few scattered melanophores form an indistinct band on the horizontal myoseptum, more noticeable in the posterior half of the body. There is frequently a dark bar of pigment immediately behind the operculum, running obliquely downwards from the lateral line to the base of the pectoral fin. Daget (*op. cit.*) has observed that in *B. hypsolepis* this bar is present only in males.

DIAGNOSIS: these data agree closely (allowing for allometry) with the original description of material from the Middle Niger (Daget, *op. cit.*). Daget includes *B. hypsolepis* in the subgenus *Clypeobarbus* which differs from other *Barbus* in having exceptionally deep lateral line scales, particularly in the region below the origin of the dorsal fin. He observes that when more material becomes available it may be possible to consider *B. hypsolepis* as a subspecies of *B. pleuropholis*, a species occurring in the Congo basin.

DISTRIBUTION: *in Ghana* local and uncommon, known only from the Black Volta near Lawra and from the White Volta near Bolgatanga. *Elsewhere*, the Middle Niger (Daget, *op. cit.*).

Barbus nigeriensis Boulenger, 1902

(Text-fig. 6)

Barbus nigeriensis Boulenger, 1902, *Proc. zool. Soc. London*, 2 : 327, pl. 28, fig. 3. ; *Idem*, 1910 (type only), *Cat. Afr. Fish*, 2 : 154, fig. 130.

[*non Barbus nigeriensis* : Trewavas, 1947, in Irvine, *Fisheries and Fish of the Gold Coast*, London ; *non Barbus nigeriensis* : Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 135, fig. 14.]

DESCRIPTION based on 20 fish, 23 to 50 mm. S.L., from the White Volta and its tributaries near Bawku, northern Ghana. Body moderately compressed. S.L. 3.2 to 4.1 times the maximum depth and 3.2 to 4.1 times the length of the head. Pre-dorsal profile convex with a slight nuchal hump. Snout rather pointed, 0.65 to 0.9 times in the diameter of the eye. Mouth relatively large, subterminal. Barbels long, the anterior 0.65 to 1.2 times the diameter of the eye, and the posterior 0.8 to 1.4 times the diameter of the eye. In larger specimens the tip of the anterior barbel reaches the vertical to the centre of the eye and the tip of the posterior barbel extends beyond the posterior margin. Eyes inclined slightly upwards, relatively large, 2.5 to 3.2 times in the length of the head and 0.95 to 1.2 times in the interorbital width. Weakly-developed pit-lines are visible on the cheek and operculum. Pectoral fin 0.55 to 0.75 times the length of the head, the tip not reaching the pelvic origin. Last simple dorsal ray smooth, flexible, 0.8 to 1.0 times as long as the head. Apex of dorsal fin somewhat rounded, distal margin slightly concave. Dorsal fin rays III 8 (f.19) or III 9 (f.1). Anal fin rays III 5. The origin of the pelvic fin lies between the verticals to the first and third branched dorsal fin rays. Caudal peduncle 1.35 to 1.55 times as long as deep. The lateral line dips to a maximum of approximately one and a quarter scale rows below the horizontal myoseptum in the anterior third of the body ; the two converge in the vertical to the base of the anal fin. Lateral line scales 27 to 30 (modal number 29). Four and a half scales between the lateral lines and the dorsal origin, $3\frac{1}{2}$ to $4\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2\frac{1}{2}$ scales between the lateral line and the pelvic origin ; 12 scales round the caudal peduncle.

COLORATION : *in living specimens* greenish-brown above, silvery on the flanks and whitish below. A dark narrow mid-lateral band is present. Dorsal and caudal fins clear pale pink. The eye is marked with a red crescent over the pupil. *In formalin-fixed specimens* scales of the dorsal surface with dense melanophores, free from a narrow marginal band and less dense at the centre of each scale. This pattern, which is darkest on the scales at the base of the dorsal fin, fades out rather abruptly on the flanks. Dense melanophores lying over the horizontal myoseptum form a narrow dark band running the entire length of the body. The band is generally less than a scale row in depth, becoming slightly wider on the caudal peduncle and frequently more dense at the tip to form a vague spot. The band may be interrupted below the anterior rays of the dorsal fin but never enough to form distinct spots or streaks. The scale pockets of the lateral line are each marked with a compact group of melanophores bisected horizontally by the lateral line pore. Similar markings may appear

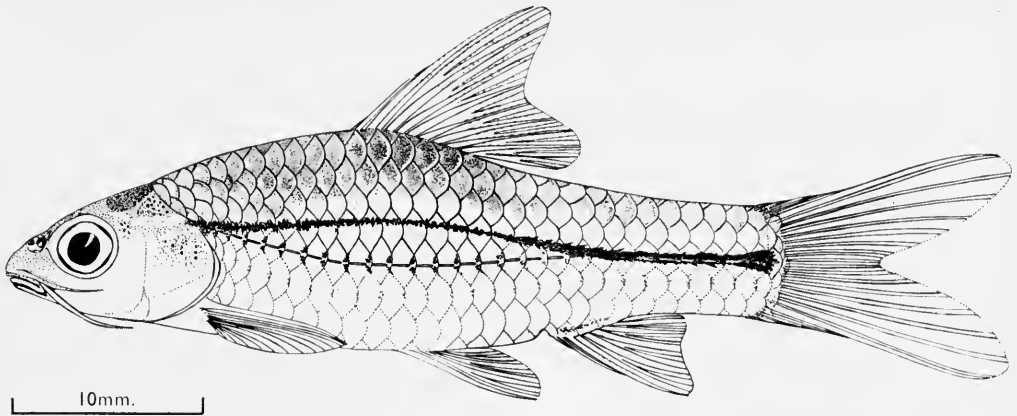
faintly on the scale row below the lateral line, but apart from an indistinct group of melanophores at the base of the anal fin the ventral surface is generally pigment-free.

DIAGNOSIS AND AFFINITIES: the original description of *B. nigeriensis* (*op. cit.*) was based on a poorly preserved holotype (Brit. Mus. (N.H.) reg. no. 1902.10.25.2) lacking any obvious pigment. We believe that Boulenger (1911) later mistook other superficially similar specimens for *B. nigeriensis*, resulting in his observations that the markings are a "broad black lateral band which may be broken up into a series of spots or streaks". Such a broken band is not characteristic of *B. nigeriensis* and the description has tended to confuse subsequent workers. *Barbus nigeriensis* material in the British Museum (N.H.) thus included examples of *B. wernerii* Boulenger, *B. laurae* and *B. sublineatus*. The holotype is now in poor condition. Pigment is restricted laterally to microscopic melanophores in a longitudinal line on the caudal peduncle, grouped closer together at the posterior end to suggest a spot. Allowing for features lost by deterioration, the holotype corresponds closely with our own material from northern Ghana. Three fish from the Ogun River, Western Nigeria (Brit. Mus. (N.H.) reg. no. 1956.9.6.57-59) must also be regarded as authentic *B. nigeriensis*; the pigmentation is identical with that of the specimens from Ghana. Data from the three collections are tabulated below. Measurements are expressed as percentages of the standard length. Means are given in parentheses.

	Holotype Agberi River, Lower Niger	Ogun River, S. Nigeria	White Volta, N. Ghana
Number of specimens . . .	1	3	20
Standard length (mm.) . . .	42	45-50	24-50
Maximum depth	25.2	32.2-35.0 (33.2)	24.5-29.7 (26.8)
Length head*	23.7	22.7-23.7 (23.4)	24.5-31.3 (28.7)
Diameter eye*	8.5	7.7-8.0 (7.8)	7.6-11.8 (9.9)
Length snout	5.7	5.6-6.0 (5.8)	6.4-8.3 (7.5)
Interorbital width	8.1†	9.3-9.8 (9.5)	9.3-11.8 (10.4)
Anterior barbel	6.4†	7.9-8.6 (8.2)	7.4-10.0 (9.1)
Posterior barbel	7.8†	10.6-11.0 (10.8)	8.5-12.0 (10.8)
Length pectoral fin	17.2	17.5-19.4 (18.6)	17.3-21.4 (19.6)
Length dorsal fin	—	22.6-22.8 (22.7)	23.0-27.9 (25.0)
Length caudal peduncle	20.1	17.9-20.0 (19.0)	17.8-20.5 (19.3)
Depth caudal peduncle	12.8	13.0-13.1 (13.0)	12.6-14.7 (13.7)
Number lateral line scales	c. 27	28-29	27-30
Scales lateral line to dorsal origin	4½	4½	4½
Scales lateral line to vent. mid-line.	3½	4½	4½

* Negative allometry; † somewhat shrivelled.

Barbus nigeriensis appears to have no close relatives. It resembles *B. chlorotaenia* Boulenger in pigmentation and barbel length but in that species the lateral line dips less markedly below the longitudinal myoseptum and the mouth is smaller and set more obliquely, with the lips folding characteristically round the base of the posterior

FIG. 6. *Barbus nigeriensis*.

barbel in the form of a socket. The combination of relatively large eyes, large mouth, long barbels and the narrow and continuous lateral band widening on the caudal peduncle should prevent the confusion of *B. nigeriensis* with other species.

HABITAT AND DISTRIBUTION: *in Ghana*, an uncommon species found in small numbers in the White Volta and its tributaries in north-eastern Ghana. All examples were from running water. *Elsewhere*, the Agberi River, a tributary of the Lower Niger (type locality) and the Ogun River, both in south Nigeria.

***Barbus lawrae* Hopson, 1965.**

(Text-fig. 7)

Barbus lawrae Hopson, 1965, *Rev. Zool. Bot. Afr.* 71 : 245.

HOLOTYPE: a female of 42 mm. S.L. from Lissa Dam on the Kamba River (a tributary of the Black Volta), 15 miles north-east of Lawra, north-west Ghana, 25.x.61, British Museum (N.H.) reg. no. 1964.9.8.1.

DESCRIPTION based on the holotype and 23 of the paratypes, 32–47 mm. S.L., from Lissa Dam. Body compressed, particularly near the dorsal surface. S.L. 2.95 to 3.65 times the maximum depth and 3.4 to 3.75 times the length of the head. Pre-dorsal profile convex with a slight nuchal hump. Snout rather pointed, 0.55 to 0.75 times the diameter of the eye. Mouth moderate, subterminal. Anterior barbel 0.1 to 0.4 times the diameter of the eye, the tip barely overlapping the base of the posterior barbel. Posterior barbel 0.3 to 0.8 times the diameter of the eye, the tip reaching the vertical to the posterior margin of the pupil in the largest individuals.

Eyes inclined slightly upwards, 2.75 to 3.1 times in the length of the head and 1.0 to 1.1 times in the interorbital width. Weakly-developed pit-lines visible on the cheeks. Pectoral fin 0.7 to 0.8 times as long as the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, rather long, 1.0 to 1.2 times the length of the head. Apex of the dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 8. Anal fin rays III 5. The origin of the pelvic fin lies between

the verticals to the first and second branched dorsal rays. Caudal peduncle 1.3 to 1.6 times as long as deep. The lateral line dips to a maximum of the depth of one and a third scale rows below the horizontal myoseptum in the anterior third of the body; the two converge in the centre of the caudal peduncle. Scales radially striated. Lateral line scales 28 to 31 (modal number 30). Four and a half to 5½ scales between the lateral line and the dorsal origin, 4½ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and 2½ scales between the lateral line and the pelvic origin. Twelve scales round the caudal peduncle.

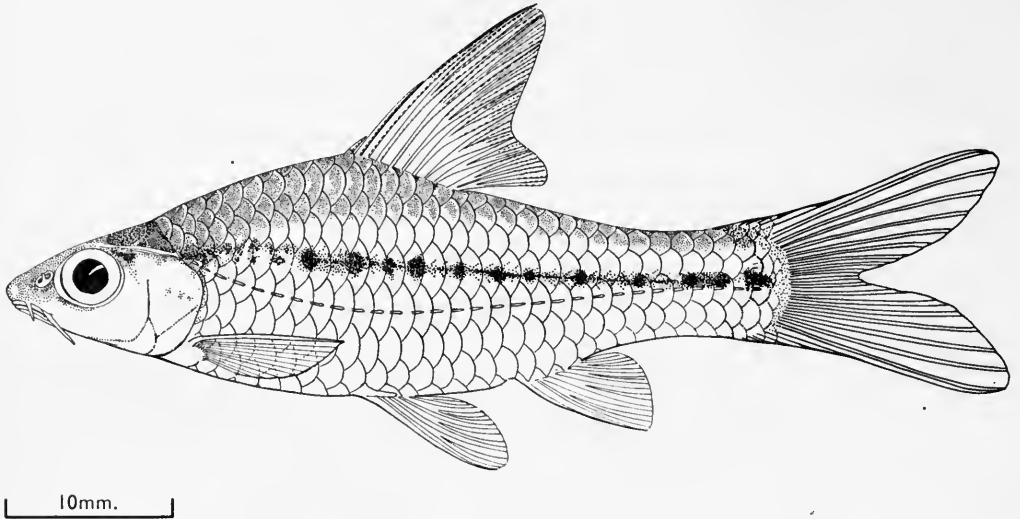


FIG. 7. *Barbus lawrae*.

Summary of morphometric data based on 24 fish, 32 to 47 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	27.2-33.3	30.3	—
Length head	26.6-29.3	27.6	Negative
Diameter eye	9.1-10.0	9.7	Negative
Interorbital width	9.4-10.9	10.1	—
Length snout	5.7-7.4	6.5	—
Length anterior barbel	1.2-3.9	2.2	—
Length posterior barbel	3.3-7.8	5.5	—
Length pectoral fin	19.5-22.4	20.8	—
Length dorsal fin	28.4-31.6	29.5	—
Length caudal peduncle	19.3-24.0	21.0	—
Depth caudal peduncle	13.9-15.8	14.6	—

COLORATION: *in living specimens* brownish above, silvery on the flanks and whitish below. A dark mid-lateral band, often broken up into spots or streaks is present. No conspicuous colour was noted on the fins. *In formalin-fixed specimens*

each scale of the dorsal surface is marked with a broad band of fine melanophores, free from a narrow marginal zone and from the centre of each scale. These markings fade away quickly towards the flanks and a broad zone above the mid-lateral band is more or less pigment-free. The mid-lateral band consists of heavy pigment, approximately one third of a scale row in depth, originating at the level of the sixth or seventh lateral line scale and running along the horizontal myoseptum to the tip of the caudal peduncle. The band is frequently broken up into a series of rounded spots or streaks, connected by more lightly scattered pigment. Spots, when present, are irregular in arrangement and number; only the first, at the level of the sixth or seventh lateral line scale, and the last, on the tip of the caudal peduncle, are fixed in position. A few scattered melanophores lie on the horizontal myoseptum anterior to the mid-lateral band. Each pocket of the anterior lateral line scales may bear a small group of melanophores, divided horizontally into two by the lateral line pore. There are several indistinct spots of black pigment at the base of the anal fin. Relatively dense pigment is present on the posterior margin of the second simple dorsal ray and on the distal half of the third simple ray. Scattered melanophores are present on the distal parts of all branched dorsal rays.

DIAGNOSIS AND AFFINITIES: material identified as *B. nigeriensis* from the R. Katagum (Chad basin), Northern Nigeria in the British Museum (N.H.) reg. no. 1952.4.28.136-144, is now referred to *B. lawrae*. The Nigerian specimens differ from the types in having slightly fewer lateral line scales (28 to 31, mode 29 cf. 29 to 31, mode 30) but are in other respects identical.

Barbus lawrae most closely resembles *B. weneri*, *sensu* Daget, 1954 (from the Middle Niger) but is more compressed laterally, has more lateral line scales (28 to 31, mode 29 and 30 cf. 25 to 29, mode 26 and 27) and much shorter barbels; in *B. lawrae* the anterior barbel barely extends beyond the base of the posterior barbel, whereas in *B. weneri*, *sensu* Daget, the tip reaches the anterior margin of the pupil. Furthermore, a heavier and more pronounced spot marks the tip of the caudal peduncle in *B. weneri*, *sensu* Daget.

During the present studies, specimens of *B. weneri*, *sensu* Daget, 1954 from the Middle Niger (Paris Museum reg. no. 51-246) were compared with a syntype of *B. weneri* Boulenger from Fashoda on the White Nile (Brit. Mus. (N.H.) reg. no. 1907.12.2.1333). They were found to be a distinct species. *Barbus weneri* Boulenger is easily distinguishable from *B. weneri*, *sensu* Daget, and from *B. lawrae* by the small terminal mouth, set very obliquely with the angle in front of the vertical to the nostril. In *B. weneri*, *sensu* Daget, and in *B. lawrae* the mouth is subterminal and set more horizontally with the angle overlapping the vertical to the nostril. *Barbus weneri* Boulenger is unusual in the form of the band of scattered melanophores on the line of the mid-lateral row of spots; the band veers upwards on the caudal peduncle to end slightly above the terminal spot. In *B. weneri*, *sensu* Daget, and *B. lawrae* the band merges horizontally with the terminal spot.

Barbus lawrae closely resembles *B. lepidus* in form and pigment pattern. The mouth of *B. lepidus* is however more terminal, the barbels relatively longer and the body less compressed laterally. In *B. lepidus* the lateral line dips further below the

horizontal myoseptum and the two converge near the tip of the caudal peduncle (cf. the centre of the caudal peduncle in *B. lawrae*). The lateral spots of *B. lepidus*, although variable in number, are always rounded and discrete; spots when present in *B. lawrae* are irregular and fragmented. The terminal spot in *B. lawrae* is never as pronounced as in *B. lepidus*.

Morphometrically, *B. lawrae* is also similar to *B. perince* with which it occurs in rivers of the Chad basin in Northern Nigeria (pers. record). *Barbus perince* is easily distinguished from *B. lawrae* by the three rounded, black, mid-lateral spots, one in the anterior third of the body, one below the last dorsal ray and one on the end of the caudal peduncle. *Barbus perince* also has longer barbels than *B. lawrae* (the anterior extending to the margin of the eye in *B. perince*) and the lateral line and horizontal myoseptum converge near the tip of the caudal peduncle (cf. the centre in *B. lawrae*).

DISTRIBUTION: in Ghana, probably rare and local; known only from the type locality in the Volta basin near Lawra. Elsewhere, rivers of the Chad basin in Northern Nigeria (pers. records).

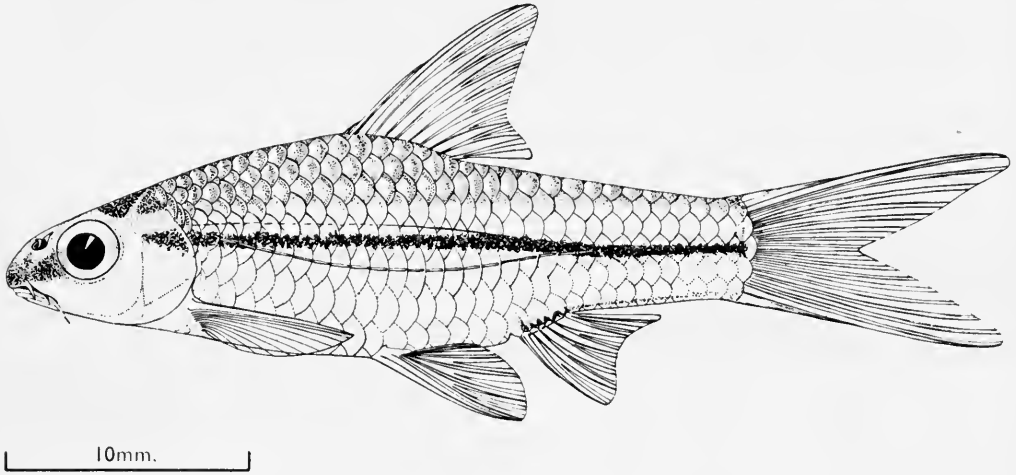
Barbus subinensis Hopson, 1965

(Text-fig. 8)

Barbus subinensis Hopson, 1965, *Rev. Zool. Bot. Afr.* **71**: 249.

HOLOTYPE: a female of 33 mm. S.L. collected from the River Subin (Prah basin), Juaso, south Ghana, 9.xi.61, British Museum (N.H.) reg. no. 1964.9.8.256.

DESCRIPTION based on the holotype and 19 paratypes, 25–34 mm. S.L. from the River Subin, Juaso. Body somewhat compressed. S.L. 3.1 to 3.9 times the maximum depth and 3.4 to 4.1 times the length of the head. Predorsal profile smooth, convex, becoming abruptly steep on the snout. Snout 0.6 to 0.75 times the diameter of the eye. Mouth moderate, subterminal. Barbels small, the anterior 0.1 to 0.3 times and the posterior 0.2 to 0.4 times the diameter of the eye. The tip of the anterior barbel falls short of the base of the posterior barbel which extends posteriorly slightly beyond the vertical to the anterior margin of the pupil. Eyes lateral 2.65 to 3.05 times in the length of the head and 1.03 to 1.16 times in the interorbital width. Weakly-developed pit-lines are visible on the cheeks and operculum. Pectoral fin 0.7 to 0.85 times the length of the head, the tip overlapping the pelvic origin in three smaller individuals. Last simple dorsal ray smooth, flexible, 0.95 to 1.1 times the length of the head. Apex of dorsal fin somewhat pointed, distal margin slightly concave. Dorsal fin rays III 8; anal fin rays III 5. The pelvic origin lies on the vertical to the last simple dorsal ray. Caudal peduncle slender, 1.45 to 1.9 times as long as deep. The lateral line dips to a maximum depth of one and a quarter scale rows below the horizontal myoseptum in the anterior third of the body; the two converge in the anterior half of the caudal peduncle. Scales radially striated, 27 to 30 (modal number 28) in the lateral line. Five and a half scales between the lateral line and the dorsal origin, 4 to 4½ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and 2½ between

FIG. 8. *Barbus subinensis*.

the lateral line and the pelvic origin. Nine (f.1), 10 (f.5), 11 (f.12) or 12 (f.2) scales round the caudal peduncle.

Summary of morphometric data based on 20 fish, 25 to 34 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	25.6-32.2	28.9	—
Length head	24.0-29.2	27.1	Negative
Diameter eye	8.5-10.4	9.4	—
Interorbital width	9.6-11.2	10.3	—
Length snout	5.9-7.4	6.4	—
Length anterior barbel	1.2-3.0	2.1	—
Length posterior barbel	2.0-3.9	3.0	—
Length pectoral fin	19.4-24.6	21.3	—
Length dorsal fin	25.0-30.0	27.0	—
Length caudal peduncle	21.0-25.0	22.5	—
Depth caudal peduncle	12.4-15.2	13.9	—

COLORATION : *in formalin-fixed specimens* a band of melanophores close to the margin of each scale forms a regular pattern over the dorsal surface of the body, fading abruptly on the flanks. A narrow continuous mid-lateral band of black pigment is always present. The band, which originates on the operculum runs below the myoseptum in the anterior half of the body ; the band and the myoseptum converge between the verticals to the last dorsal ray and the anal origin and run together onto the caudal peduncle. The ventral surface is pigment-free with the exception of a group of melanophores at the base of the anal fin which continues backwards as a narrow stripe along the ventral surface of the caudal peduncle. Snout with a conspicuous dark band running from eye to eye round the tip (cf. *B. punctitaeniatus*). Scattered melanophores noticeable on the anterior rays of the dorsal fin.

DISTRIBUTION : known only from the River Subin (Prah basin), near Juaso, south Ghana.

REMARKS : *Barbus subinensis* appears to have no close relatives. The lateral band and the markings on the snout recall *B. boboi* Schultz but the types of that species bear a large black spot on the caudal peduncle, have considerably longer barbels (anterior barbels 11.2–12.8 cf. 1.2–3.0% S.L. ; posterior barbels 11.8–13.0 cf. 2.0–3.9% S.L.) and only $4\frac{1}{2}$ scales above the lateral line compared with $5\frac{1}{2}$ in *B. subinensis*.

Barbus trispilus (Bleeker, 1863)

(Text-fig. 9)

Puntius (Barbodes) trispilos Bleeker, 1863, *Nat. Verh. Wet. Haarlam*, 23 : 113, pl. 23, fig. 3.

Barbus trispilus : Boulenger, 1910, *Cat. Afr. Fish.* 2 : 163, fig. 141.

Barbus trispilus : Daget, 1952, *Mem. Inst. France. Afr. Noire*, no. 19 : 314, fig. 4.

DESCRIPTION based on 24 fish, 27–65 mm. S.L. from the River Weiwei (Prah Basin), Kumasi, south Ghana. Body slightly compressed. S.L. 3.0 to 3.75 times the maximum depth and 3.3 to 3.85 times the length of the head. Predorsal profile convex with a slight nuchal hump in larger individuals (over c. 40 mm. S.L.). Snout rounded, 0.65 to 0.9 times the diameter of the eye. Mouth moderate, subterminal. Barbels relatively long, the anterior 1.05 to 1.55 times the diameter of the eye, the tip usually extending beyond the vertical to the posterior margin of the eye. Posterior barbel 1.5 to 1.8 times the diameter of the eye, the tip extending beyond the posterior margin of the preoperculum. Eyes inclined slightly upwards, the diameter 2.9 to 3.6 times in the length of the head and 1.15 to 1.65 times in the interorbital width. Weakly-developed pit-lines present on the cheek and operculum. Pectoral fin 0.6 to 0.85 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.75 to 0.95 times the length of the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 8. Anal

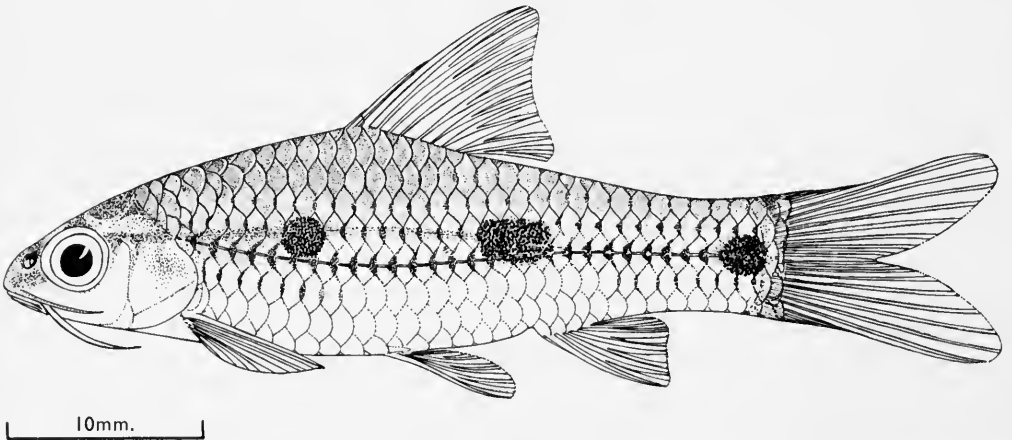


FIG. 9. *Barbus trispilus*.

fin rays III 5. The pelvic origin lies between the verticals to the last simple and first branched dorsal rays. Caudal peduncle 1.2 to 1.5 times as long as deep. The lateral line dips to a maximum of the depth of slightly over a scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the first third of the caudal peduncle. Lateral line scales 26 to 29 (modal number 28). Four and a half scales between the lateral line and the dorsal origin, $4\frac{1}{2}$ to $5\frac{1}{2}$ scales between the lateral line and the mid-ventral line, immediately in front of the pelvic origin and $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Twelve scales round the caudal peduncle.

Summary of morphometric data based on 24 fish, 27 to 65 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	26.2-32.9	29.3	—
Length head	25.8-30.0	27.7	Negative
Diameter eye	7.4-10.0	8.8	Negative
Interorbital width	10.2-12.0	10.8	—
Length snout	5.6-7.4	6.6	—
Length anterior barbel	9.8-12.7	11.1	—
Length posterior barbel	11.7-15.4	13.8	—
Length pectoral fin	18.5-23.4	20.5	—
Length dorsal fin	20.4-26.4	24.1	—
Length caudal peduncle	17.4-22.6	20.0	—
Depth caudal peduncle	13.6-15.6	14.8	—

COLORATION: *in formalin-fixed specimens*, dorsal surface with a dense peppering of fine melanophores, more scattered towards the centre and free from a narrow zone near the margin of each scale. The lateral line scale pockets are each marked with a small, dark, triangular patch bisected horizontally by the lateral line pore. Similar but lighter markings are present on most scale rows above the lateral line and on the anterior and posterior scales of the row below. Three round, black, mid-lateral spots are always present, the first at the level of the sixth or seventh lateral line scale, the second immediately behind the vertical to the last dorsal ray and the third on the tip of the caudal peduncle. The second spot is slightly larger than the first and last spots which are approximately the depth of a scale row in diameter. Slight elongation of the second and third spots was noted in a few specimens. Scattered melanophores form a faint band over the horizontal myoseptum between the spots. The base of the anal fin is marked with a few indistinct melanophores.

DIAGNOSIS: these data are in close agreement with previous descriptions of the species. *Barbus trispilus* is superficially similar to *B. perince* (from the Nile and Chad basins) which is also marked with three round mid-lateral spots. *Barbus trispilus* has, however, fewer lateral line scales (26-29 cf. 28-32 in *B. perince*), a lateral line which dips less markedly below the horizontal myoseptum (1 cf. $1\frac{1}{2}$ scale rows) and relatively longer barbels (the anterior reaching the posterior margin of the eye cf. the anterior margin in *B. perince*). The lateral spots are relatively larger in *B. trispilus*.

DISTRIBUTION : *in Ghana*, widespread and common in forest streams and rivers (notably the Prah basin) in the south-west. Probably absent from the Volta. *Elsewhere* Dabo Crom, Guinea (type locality); Sierra Leone (Norman, 1932); Bolor River, Liberia (Schultz, 1942); Mt. Nimba, Rep. Guinea (Daget, 1952).

***Barbus sublineatus* Daget, 1954**

(Text-fig. 10)

Barbus sublineatus Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 203, fig. 69.

Barbus sublineatus : Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 137, figs. 15 and 16.

DESCRIPTION based on 24 fish 28–40 mm. S.L. from a tributary of the White Volta, 5 miles north of Bawku, north Ghana. Body slightly compressed. S.L. 3·8 to 4·4 times the maximum depth and 3·4 to 3·85 times the length of the head. Predorsal profile convex with a slight nuchal hump. Snout rather pointed 0·6 to 0·8 times as long as the diameter of the eye. Mouth moderate, sub-terminal. Barbels relatively long, the anterior 0·5 to 0·95 and the posterior 0·75 to 1·12 times the diameter of the eye. The tip of the anterior barbel normally extends beyond the centre and the posterior barbel beyond the posterior margin of the eye. Eyes inclined slightly upwards, relatively large, 2·65 to 3·1 times in the length of the head and 1·03 to 1·17 times in the interorbital width. Weakly-developed pit-lines are present on the cheek and operculum. Pectoral fin 0·65 to 0·75 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0·75 to 0·95 times as long as the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 8; anal fin rays III 5. The origin of the pelvic fin lies between the verticals to the first and second branched dorsal rays. Caudal peduncle 1·35 to 1·7 times as long as deep. The lateral line dips to a maximum

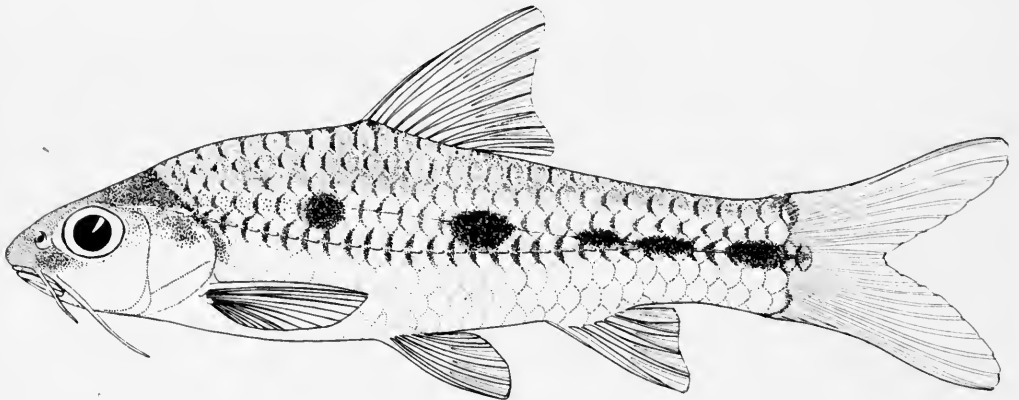


FIG. 10. *Barbus sublineatus*.

of approximately the depth of one scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the vertical to the posterior anal rays or in the anterior third of the caudal peduncle. Lateral line scales 27 to 31 (modal number 29). Four and a half scales between the lateral line and the dorsal origin, $4\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Twelve scales round the caudal peduncle.

Summary of morphometric data based on 24 fish, 28 to 40 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	22.5-26.3	24.5	—
Length head	25.8-29.2	27.4	—
Diameter eye	8.7-10.3	9.5	Negative
Interorbital width	9.7-11.5	10.5	—
Length snout	5.8-7.0	6.5	—
Length anterior barbel	5.3-9.1	7.3	—
Length posterior barbel	7.8-11.2	9.2	—
Length pectoral fin	18.7-20.3	19.5	—
Length dorsal fin	22.5-25.3	23.9	—
Length caudal peduncle	19.0-22.4	20.7	—
Depth caudal peduncle	12.0-14.3	13.8	—

COLORATION: *in living specimens*, yellowish fawn above, flanks silvery, belly whitish, the body marked laterally with a row of four or more dark spots. Rays of caudal fin with pale pink chromatophores, yellowish nearer the base; dorsal and pectoral rays with pale yellowish chromatophores; pelvic and anal fins clear. The iris is marked dorsally with an orange-red crescent. *In formalin-fixed specimens* dorsal surface finely peppered with melanophores free from the margin and thinning out towards the centre of each scale; the pattern fades out on more lateral rows. A basic series of four black rounded spots lies over the horizontal myoseptum, the first at the level of the seventh lateral line scale, the second below the last dorsal ray, the third starting above the last anal ray and the fourth on the tip of the caudal peduncle. The last three are usually slightly elongated. Additional spots up to four in number may occur, usually between the second and the fourth spot. Occasionally two or more of the posterior spots may coalesce to form a band. Each lateral line scale is marked on the pocket with a small compact group of melanophores. Similar pigment though less heavy is present on scales above the lateral line. The ventral surface is generally pigment-free with the exception of a faint dark spot at the base of the anal fin continuing backwards as a slender line along the ventral surface of the caudal peduncle.

DIAGNOSIS AND AFFINITIES: Blanc & Daget (1959) note variation in the pigmentation of *B. sublineatus*. Type specimens from the Middle Niger are marked with a dark continuous mid-lateral band. The band is represented in more recent material from the Volta and from the Haute Comoé (Blanc & Daget, 1957) by a series of spots comparable with the markings of the present material from Ghana. In other

respects our data agree closely (with allowances for allometry) with the type description. *Barbus sublineatus* is closely related to *B. lineomaculatus* Blgr. which occurs in East and South Africa. *Barbus lineomaculatus* is similarly marked with a series of lateral spots but never as few as four. In this species most of the first spot lies above the horizontal myoseptum whereas in *B. sublineatus* it is situated chiefly below. *Barbus sublineatus* also has relatively larger eyes, a narrower interorbital space and the dorsal fin is inserted more posteriorly.

HABITAT AND DISTRIBUTION: *in Ghana*, widespread in the north, *B. sublineatus* occurs sparingly in most of the rivers and larger streams over a substrate of gravel or sand. It is apparently absent from lagoons, pools and dams. *Elsewhere*, recorded from the Haute Comoé (Blanc & Daget, 1957) and the Middle Niger (Daget, 1954).

LIFE HISTORY: the occurrence of ripe females in June indicates that, as in other *Barbus*, spawning takes place during the rainy season. Females grow larger than males. Maximum size—a female of 74 mm. S.L.

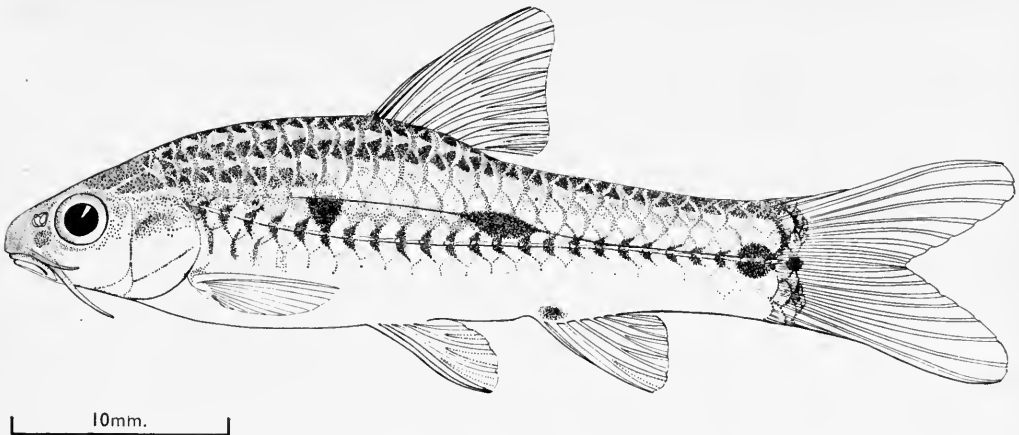
Barbus macinensis Daget, 1954

(Text-fig. 11)

Barbus macinensis Daget, 1954, *Mem. Inst. France. Afr. Noire*, no 36 : 200, fig. 67.

Barbus macinensis : Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 137.

DESCRIPTION based on 25 fish 26–32 mm. S.L. from the River Nahau, 5 miles north of Bawku, northern Ghana. Body slightly compressed. S.L. 3.75 to 4.6 times the maximum depth and 3.55 to 4.05 times the length of the head. Predorsal profile well humped; snout rounded, 0.65 to 0.8 times the diameter of the eye. Mouth moderate, subterminal. Anterior barbel 0.65 to 0.8 times the diameter of the eye, its tip reaching the vertical to the anterior half of the pupil. Posterior barbel 0.8 to 1.2 times the diameter of the eye, the tip usually extending beyond the vertical to the posterior margin. Eyes inclined slightly upwards, diameter 2.85 to 3.55 times in the length of the head and 1.2 to 1.35 times in the interorbital width. Head with weakly-developed pit-lines on the cheek and operculum. Pectoral fin 0.65 to 0.8 times the length of the head, its tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.8 to 1.0 times as long as the head. Apex of dorsal fin rounded, distal margin barely concave. Dorsal fin rays III 8; anal fin rays III 5. The origin of the pelvic fin lies between the vertical to the 1st and 2nd simple rays. Caudal peduncle rather stout, 1.15 to 1.5 times as long as deep. The lateral line dips to a maximum of slightly less than a scale row's depth below the horizontal myoseptum in the anterior third of the body. The two converge in the anterior half of the caudal peduncle. Lateral line scales 24 to 27 (modal numbers 25 and 26). Three and a half scales between the lateral line and the dorsal origin, $4\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Ten (f.1), 11 (f.15) or 12 (f.9) scales round the caudal peduncle.

FIG. 11. *Barbus macinensis*.

Summary of morphometric data based on 25 fish, 26 to 32 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	24.7-27.8	26.2	—
Length head	21.4-26.6	24.6	—
Diameter eye	7.8-9.2	8.4	Negative
Interorbital width	10.3-11.8	10.9	Negative
Length snout	5.7-6.7	6.2	—
Length anterior barbel	3.5-5.9	4.9	—
Length posterior barbel	6.8-10.3	8.4	—
Length pectoral fin	17.9-22.9	19.9	—
Length dorsal fin	22.4-26.3	24.3	—
Length caudal peduncle.	18.2-21.8	20.2	—
Depth caudal peduncle	14.4-15.9	15.1	—

COLORATION : *in living specimens*, dark brownish-yellow above, silvery on the sides, pearly white below. Body marked dorsolaterally with three dark longitudinal stripes. Three lateral spots are present and the lateral line bears a series of small black dots. Basal two-thirds of the caudal fin, the dorsal, pectoral and pelvic fins pale straw-yellow. Distal third of the caudal and the anal fin clear. The iris is marked dorsally with an orange-red crescent. *In formalin-fixed specimens* body marked dorsolaterally on each side with three dark bands running along the overlapping portion of adjacent scale rows and formed by a concentration of melanophores in the upper and lower third of each scale. The two upper bands extend along the entire length of their respective scale rows but the lowest, lying between the first and second rows of scales above the lateral line, ends in front of the vertical to the dorsal fin. The lowest band is frequently ill-defined and sometimes absent. One or two round dark spots are often present on the dorsal mid-line between the head and dorsal fin. Each scale of the lateral line, including the two overlapping the base of the caudal fin, is marked with a small but heavy concentration of melanophores, usually divided horizontally into two by the lateral line pore. Three conspicuous black spots

are constantly present on the horizontal myoseptum, the first at the level of the 7th lateral line scale, the second below the last dorsal fin ray and the third at the tip of the caudal peduncle. The second spot is somewhat elongated. Faint melanophores occasionally form a noticeable band between the second and the last spots. Scales of the row below the lateral line are often outlined with fine pigment and there is always a faint subepidermal group of melanophores at the base of the anal fin. The remainder of the ventral surface is pigment-free.

DIAGNOSIS AND AFFINITIES: stumpy and thick-set in appearance, *B. macinensis* should be easily distinguishable from other voltaic species by the characteristic pattern of pigmentation. Our data are in close accordance with the original description (Daget, 1954) based on specimens from the Middle Niger. *Barbus macinensis* has close affinities with the morphometrically similar *B. niokoloensis* Daget, 1959 from the Gambia River, which is also marked longitudinally with dark dorsolateral bands. That species, however, lacks the three lateral spots of *B. macinensis* and the lateral line scales bear a dark stripe, extending forward onto the operculum.

Barbus macinensis is superficially similar to *B. neefi* Greenwood (1962) from the Upper Zambesi which is also marked with dorsolateral stripes and lateral spots. *Barbus neefi*, however, has more than three spots and in addition, horizontal stripes below the lateral line. Compared with *B. neefi*, *B. macinensis* has fewer scales between the lateral line and the dorsal origin ($3\frac{1}{2}$ cf. $4\frac{1}{2}$ – $5\frac{1}{2}$), shorter barbels (anterior 3.5–5.9 cf. 6.0–10.3% S.L.; posterior 6.8–10.3 cf. 10.0–14.8% S.L. in *B. neefi*) and a stouter caudal peduncle.

A comparison is made between *B. macinensis* and *B. voltae* in the description of that species.

HABITAT AND DISTRIBUTION: in Ghana, *B. macinensis* is present in suitable localities throughout the northern regions. The distribution suggests a preference for coarse substrates and the species is particularly abundant in the sandy pools of dry season river beds. Dams are sometimes colonized if there is a sandy or gravelly bottom but the species is generally absent over muddy substrates and from areas of thick vegetation. *Elsewhere*, recorded from the Haute Comoé (Blanc & Daget, 1957) and from the Middle Niger (type locality). Blanc & Daget (*op. cit.*) note this species in the Volta basin, Haute Volta.

LIFE HISTORY: *Barbus macinensis* breeds during the rainy season. Ripe and ripening females were observed between May and August and the first juvenile stages appeared in the rivers during July. Growth seems to be more rapid in females than in males. All fish ripen at the end of their first year and few if any survive to spawn a second time. Maximum size, a female of 5.9 cm. S.L.

Barbus voltae Hopson, 1965

(Text-fig. 12)

Barbus voltae Hopson, 1965, *Rev. Zool. Bot. Afr.* 71: 251

Barbus nigriensis: Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50: 135, fig. 14.

HOLOTYPE: a female of 31 mm. S.L. from the River Nahau (tributary of the

White Volta), 5 miles north of Bawku, northern Ghana, 27.xi.61, British Museum (N.H.) reg. no. 1964.9.8.73.

DESCRIPTION based on the holotype and 23 paratypes, 27 to 33 mm. S.L. from the River Nahau, near Bawku. Unfortunately we have been unable to examine the material identified by Blanc and Daget (*op. cit.*) as *B. nigeriensis*. Body somewhat compressed. S.L. 3.3 to 3.7 times the maximum depth and 3.25 to 3.7 times the length of the head. Predorsal profile smooth, convex. Snout bluntly pointed, 0.55 to 0.7 times the diameter of the eye. Mouth small, subterminal, protrusible and opening obliquely downwards. Anterior barbel 0.1 to 0.25 times the diameter of the eye, the tip falling short of the base of the posterior barbel. Posterior barbel 0.15 to 0.4 times the diameter of the eye, the tip extending to between the verticals to the anterior margin of the eye and the anterior margin of the pupil. Eyes lateral, 3.35 to 3.7 times in the length of the head and 1.0 to 1.25 times in the interorbital width. Weakly-developed pit-lines present on the cheek and operculum. Pectoral fin 0.55 to 0.8 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray, smooth, flexible, 0.9 to 1.05 times as long as the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.23). Anal fin rays III 5. The origin of the pelvic fin lies in the vertical to the first branched dorsal ray. Caudal peduncle 1.35 to 1.55 times as long as deep. The lateral line dips to a maximum of slightly less than the depth of a scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the anterior third of the caudal peduncle. Scales radially striated, 25 to 29 (modal number 27) in the lateral line. Three and a half scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin, and 2 to $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Eleven (f.1) or 12 (f.23) scales round the caudal peduncle.

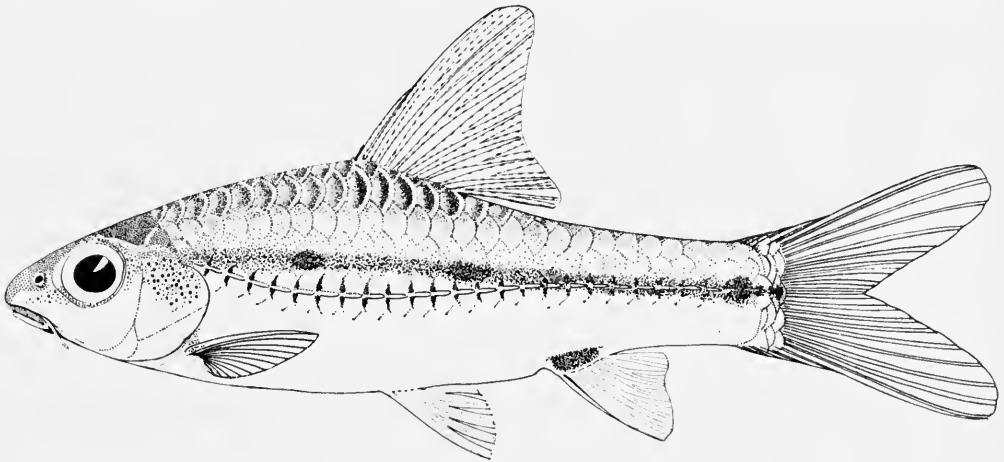


FIG. 12. *Barbus voltue*.

Summary of morphometric data based on 24 fish, 27 to 33 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	26.8-29.6	27.8	—
Length head	26.7-30.6	28.2	Negative
Diameter eye	9.4-11.1	10.0	Negative
Interorbital width	9.6-12.9	11.2	—
Length snout	5.8-7.3	6.4	—
Length anterior barbel	1.0-2.6	1.8	—
Length posterior barbel	1.6-3.7	2.6	—
Length pectoral fin	16.5-22.5	19.8	—
Length dorsal fin	25.3-31.1	27.7	—
Length caudal peduncle	20.0-25.0	21.5	—
Depth caudal peduncle	13.6-15.5	14.5	—

COLORATION : *in living specimens* brownish above, brilliant silver on the flanks, whitish below. The body is marked mid-laterally with three small black spots ; a fourth spot is present at the base of the anal fin. Caudal fin sandy-fawn, dorsal fin pinkish-fawn, base of pectoral fin rays pale yellow. The remaining fins are colourless. Iris, red above. *In formalin-fixed specimens* the dorsal surface is peppered with fine melanophores, free from the centre and margin of each scale. The pigment is heaviest on the scales at the base of the dorsal fin and fades away on the second row of scales above the lateral line. A moderately heavy band of melanophores, approximately half a scale row in depth, runs along the horizontal myoseptum from the operculum to end in a small, round, black spot on the tip of the caudal peduncle. Two other mid-lateral spots are always present. They are small, usually slightly elongated and lie within the lateral band, the first at the level of the sixth or seventh lateral line scale and the second below the last dorsal fin ray. Although the band varies in intensity and is sometimes broken into a series of irregular streaks, the three spots are always discernible. Each lateral line scale is marked on the pocket with a small but conspicuous group of melanophores, bisected horizontally by the lateral line pore. Similar but lighter markings often appear on the first and second row of scales above the lateral line. A conspicuous black spot is always present on the body at the base of the anal fin.

DIAGNOSIS AND AFFINITIES : *Barbus voltae* is the species described by Blanc & Daget (1957) as *B. nigeriensis*. *Barbus voltae* differs from *B. nigeriensis* Boulenger in a number of important details : fewer scales between the lateral line and the dorsal origin ($3\frac{1}{2}$ cf. $4\frac{1}{2}$ in *B. nigeriensis*), considerably shorter barbels (anterior 1.0-2.6 cf. 6.4-10.0% S.L. ; posterior 1.6-3.7 cf. 7.8-12.0% S.L. in *B. nigeriensis*), smaller eyes and a much smaller mouth. Furthermore, *B. nigeriensis* Blgr. has no trace of lateral spots which are always present in *B. voltae*.

Barbus voltae is superficially similar to *B. macinensis* with which it frequently occurs in the Volta basin. It is, however, easily distinguished by the smooth predorsal profile (humped in *B. macinensis*), shorter barbels (anterior 1.0-2.6 cf. 3.5-5.9% S.L. ; posterior 1.6-3.7 cf. 6.8-10.3% S.L.), a smaller mouth, larger eyes

(9.4-11.1 cf. 7.8-9.2% S.L. in *B. macinensis*) and a more obvious spot at the base of the anal fin. *Barbus voltae* also lacks the dorsolateral stripes of *B. macinensis*.

HABITAT AND DISTRIBUTION: in Ghana, common in rivers, streams and dams throughout the northern regions. Infrequent in well-vegetated situations. *Barbus voltae* is more plentiful over muddy than over sandy bottoms, indicating a preference for finer substrates. Elsewhere, recorded only from the Black Volta and its tributaries in Haute Volta (Blanc & Daget, 1957).

***Barbus atakorensis* Blanc & Daget, 1957**

(Text-fig. 13)

Barbus atakorensis Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 140, fig. 17.

DESCRIPTION based on 21 fish 27-36 mm. S.L., from Dahwenia Dam, 6 miles east of Tema, south Ghana. Body moderately compressed. S.L. 3.3 to 3.9 times the maximum depth and 3.5 to 4.0 times the length of the head. Predorsal profile convex with a slight nuchal hump. Snout somewhat pointed, 0.7 to 0.95 times as long as the eye diameter. Mouth moderate, subterminal. Anterior barbel 0.25 to 0.5 times the diameter of the eye, the tip extending beyond the base of the posterior barbel. Posterior barbel 0.6 to 0.95 times the diameter of the eye, the tip extending to between the verticals to the posterior margin of the pupil and the posterior margin of the eye. Eyes lateral, the diameter 3.2 to 3.6 times in the length of the head and 1.2 to 1.5 times in the interorbital width. Weakly-developed pit-lines visible on the cheeks and operculum. Pectoral fin 0.6 to 0.8 times as long as the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.8 to 0.95 times the length of the head. Apex of dorsal fin rounded, distal margin slightly concave. Dorsal fin rays III 7. Anal fin rays III 5. The origin of the pelvic fin

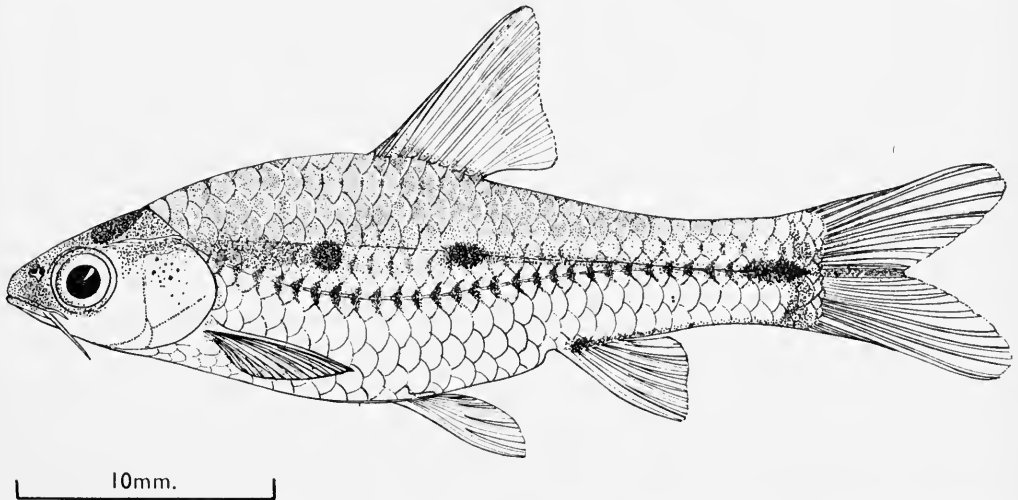


FIG. 13. *Barbus atakorensis*.

lies between the vertical to the first and second branched dorsal rays. Caudal peduncle relatively slender, 1.4 to 1.8 times as long as deep. The lateral line dips to a maximum of the depth of one and a half rows below the horizontal myoseptum in the anterior third of the body; the two converge in the anterior third of the caudal peduncle. Lateral line scales 27 to 32 (modal number 28). Four and a half to $5\frac{1}{2}$ scales between the lateral line and the dorsal origin, $4\frac{1}{2}$ to $5\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin, and $2\frac{1}{2}$ to 3 scales between the lateral line and the pelvic origin; 12 scales round the caudal peduncle.

Summary of morphometric data based on 21 fish, 27 to 36 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	26.5-30.5	28.2	—
Length head	24.9-27.5	26.0	Negative
Diameter eye	6.9-8.5	7.5	Negative
Interorbital width	9.7-10.9	10.3	—
Length snout	5.4-6.7	6.2	—
Length anterior barbel	2.1-3.3	2.7	—
Length posterior barbel	5.0-6.8	5.7	—
Length pectoral fin	17.8-20.4	19.3	—
Length dorsal fin	20.9-24.5	23.3	—
Length caudal peduncle	20.9-24.0	21.8	—
Depth caudal peduncle	13.2-15.0	14.1	—

COLORATION: *in living specimens* body greyish green, dark above, paler on the sides and whitish on the belly. Fins colourless. The colour pattern is best seen in *formalin-fixed specimens* where the dorsal surface is peppered with fine melanophores, less heavy in the centre of each scale and absent from the free margin. The pigmentation becomes lighter on the flanks and fades out on the second row of scales above the lateral line. Pockets of each lateral line scale are marked with a small group of dense melanophores split horizontally into two by the lateral line pore. Similar markings are repeated on the pockets of the first and sometimes the second row of scales above the lateral line. The horizontal myoseptum, appearing as a fine black line, is punctuated in most specimens with three black spots, the first at the level of the 7th lateral line scale, the second on the vertical to the last dorsal ray and the third at the tip of the caudal peduncle, partly overlapping the base of the caudal fin. The third spot, present in all specimens, is elongated and nearly twice as long as deep. The other two spots are variable in size and shape and one or both may be missing. Occasionally a fourth spot may occur immediately behind the vertical to the last anal ray. Scattered melanophores, usually heavier in the posterior half of the body, lie in a diffuse band over the horizontal myoseptum. Underparts unpigmented with the exception of a faint black spot at the base of the anal fin and a thin dark line along the ventral surface of the caudal peduncle.

DIAGNOSIS AND AFFINITIES: these data agree closely with the original description (Blanc & Daget, 1957) of material from the Volta basin in north Dahomey. We

found $5\frac{1}{2}$ as well as $4\frac{1}{2}$ scale rows below the lateral line and a higher maximum number of lateral line scales (32 cf. 29) although the modal number, 28, was the same. The two collections differ principally in coloration. Whereas our specimens normally have three lateral spots, the type material is characterized by a dark mid-lateral band, continuous from the operculum to the caudal peduncle. We noted, however, that in the Paris Museum paratypes the band is constricted on the caudal peduncle to form a rectangular terminal spot identical with the spot of our own specimens. Although *B. atakorensis* is superficially similar to numerous species of *Barbus* each with three lateral spots, we consider that it has no near relatives. The presence of only seven branched dorsal rays, the relatively high number of scales and the elongated spot on the slender caudal peduncle should prevent confusion with other species.

DISTRIBUTION : *in Ghana*, at present known only from dams on the Accra plains and from the River Azubone (Volta basin) in forest country near Mpraeso. The dams are on small coastal rivers draining directly into the sea. No specimens of *B. atakorensis* were collected in the northern regions of the country. *Elsewhere*, the upper reaches of the River Oti (Volta basin), in north Dahomey (type locality), the Ogun River, south-west Nigeria (personal observation), and the Kaduna River (Niger Basin), Northern Nigeria (B.M. (N.H.) reg. no. 1936. 11.24.27-29).

Barbus punctitaeniatus Daget, 1954

(Text-fig. 14)

Barbus punctitaeniatus Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 202, fig. 68.

Barbus punctitaeniatus : Blanc & Daget, 1957, *Mem. Inst. France. Afr. Noire*, no. 50 : 137.

DESCRIPTION based on 24 specimens 21-37 mm. S.L., 8 from tributaries of the White Volta near Bawku and 16 from the Black Volta near Lawra, northern Ghana. Body moderately compressed. S.L. 3.55 to 4.3 times the maximum depth and 3.55 to 4.1 times the length of the head. Predorsal profile convex with slight nuchal hump, more pronounced in the largest individuals. Snout bluntly pointed, 0.55 to 0.9 times the diameter of the eye. Mouth moderate, subterminal. Barbels relatively long, the anterior 0.4 to 0.85 times and the posterior 0.8 to 1.2 times the diameter of the eye. Tip of the anterior barbel extending to about the vertical to the centre of the eye and the posterior barbel extending beyond the posterior margin. Eyes lateral, 2.75 to 3.6 times in the length of the head and 1.0 to 1.35 times in the interorbital width. Cheeks and operculum with weakly-developed pit-lines. Pectoral fin 0.65 to 0.85 times the length of the head, the tip falling short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.8 to 1.0 times as long as the head. Apex of dorsal fin slightly rounded, distal margin concave. Dorsal fin rays III 7 (f.1) or III 8 (f.23). Anal fin rays III 5. The pelvic origin lies on the vertical to the first branched dorsal ray. Caudal peduncle 1.35 to 1.85 times as long as deep. The lateral line incomplete in all but the three largest specimens (28-37 mm S.L.) with 7 to 12 anterior scales perforated; total scales in the row 23 to 27 (modal number 25); this row dips to a maximum of slightly more than the depth of

half a scale row below the horizontal myoseptum in the anterior third of the body; the two converge at the anterior end of the caudal peduncle. Three and a half scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2-2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Nine (f.22) or 10 (f.2) scales round the caudal peduncle.

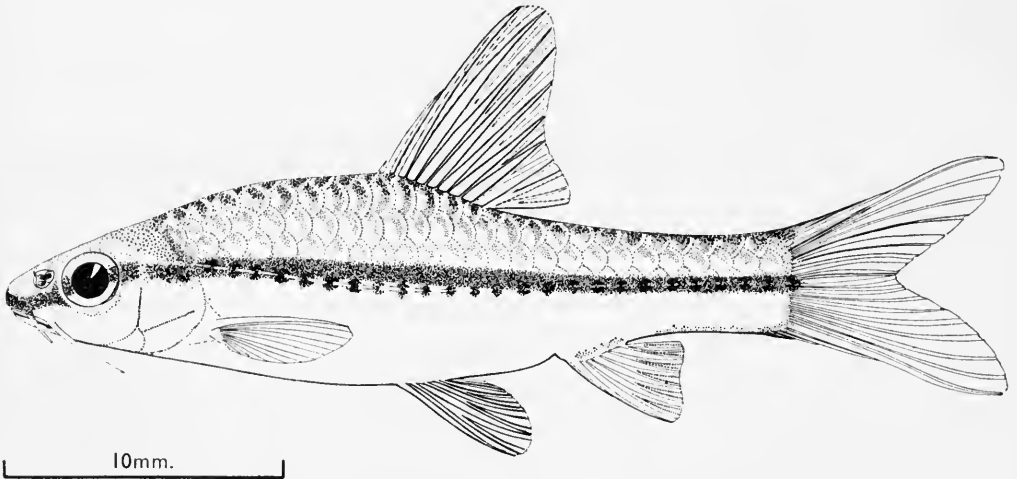


FIG. 14. *Barbus punctitaeniatus*.

Summary of morphometric data based on 24 fish, 21–37 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	23·1–28·1	25·5	—
Length head	24·2–28·0	26·3	Negative
Diameter eye	7·1–10·0	8·7	Negative
Interorbital width	8·3–11·0	9·8	—
Length snout	5·0–6·5	6·0	—
Length anterior barbel	3·2–6·4	4·6	—
Length posterior barbel	6·0–11·2	8·8	—
Length pectoral fin	18·2–24·2	19·7	—
Length dorsal fin	22·0–25·9	24·4	—
Length caudal peduncle	18·8–23·6	21·3	—
Depth caudal peduncle	12·1–15·0	13·4	—

COLORATION: *in living specimens* dorsal surface light fawn, silvery on the sides, whitish below. A narrow, dark mid-lateral band runs from the tip of the snout to the tip of the caudal peduncle. Yellow chromatophores are scattered over the dorsal surface, on the operculum and most noticeably in a narrow zone above the lateral band. Pectoral fins frequently tinged with yellow; all other fins colourless. The iris is marked dorsally with a yellow crescent. *In formalin-fixed specimens* pigment on the dorsal surface consists of a relatively slender band of dense melanophores near the margin of each scale fading abruptly on the flanks. A narrow black stripe

originating on the tip of the snout (i.e. continuous round the tip from eye to eye) runs obliquely upwards across the operculum and thence along the body. The stripe lies slightly below the horizontal myoseptum in the anterior half of the body but the two converge on the caudal peduncle. The stripe is intensified by small round spots of dense pigment on the pockets of all lateral line scales. Melanophores form a faint stripe at the base of the anal fin continuing backwards as a narrow line along the ventral surface of the caudal peduncle.

DIAGNOSIS: our data are in close agreement with the type description (Daget, 1954) based on specimens from the Middle Niger. We examined six of the syntypes in the Paris Museum and found that as in most of the material from Ghana, the lateral line is incomplete, a point which Daget did not observe.

Barbus punctitaeniatus is readily distinguished from most West African species by the black streak on the snout running without interruption round the tip. *Barbus boboi* and *B. subinensis* are similarly marked but both have higher scale counts and a pronounced dip in the lateral line; in *B. punctitaeniatus* the dip is unusually shallow. The differences between this species and *B. bawkuensis* are discussed in the description of that species below.

DISTRIBUTION: in Ghana, widespread and reasonably common in the northern regions, usually in rivers but occasionally in dams. Elsewhere, the Middle Niger (Daget, 1954), the Volta basin in Haute Volta (Blanc & Daget, 1957) and rivers of the Chad basin in Northern Nigeria (personal records).

LIFE HISTORY: the spawning season is probably restricted to the rains. Ripe females were noted in July and juveniles appeared in the rivers during September. Females grow larger than males. Maximum size 37 mm. S.L.

Barbus bawkuensis Hopson, 1965

(Text-fig. 15)

Barbus bawkuensis Hopson, 1965, *Rev. Zool. Bot. Afr.* **71**: 254

HOLOTYPE: a female of 26 mm. S.L. from the White Volta, Bazua Bridge, 10 miles west of Bawku, north Ghana, 28. vi. 61, British Museum (N.H.) reg. no. 1964.9.8. 278.

DESCRIPTION based on the holotype and 15 paratypes 20–29 mm. S.L. from the White Volta, Bazua and on 17 specimens 21–26 mm. S.L. from the River Morago, Nakpanduri, 45 miles south of Bawku. Body moderately compressed. S.L. 3.1 to 4.1 times the maximum depth and 3.55 to 4.2 times the length of the head. Predorsal profile convex with a slight nuchal hump. Snout rounded 0.65 to 0.95 times the length of the head. Mouth moderate, slightly protrusible and subterminal. Anterior barbel 0.25 to 0.7 times and the posterior barbel 0.6 to 1.1 times the diameter of the eye. The tip of the anterior barbel usually extends to the vertical to the anterior margin, and the tip of the posterior barbel beyond the centre of the eye. Eye moderate 2.85 to 3.8 times in the length of the head and 1.05 to 1.4 times in the inter-

orbital width. Weakly-developed pit-lines visible on the cheeks and operculum. Pectoral fin 0.6 to 0.8 times as long as the head, the tip falling well short of the pelvic origin. The last simple dorsal ray smooth, flexible, 0.9 to 1.1 times the length of the head. Apex of dorsal fin rather pointed, distal margin concave. Dorsal fin rays III 8; anal fin rays III 5. The pelvic origin lies between the verticals to the first and second branched dorsal rays. Caudal peduncle slender, 1.45 to 2.0 times as long as deep. Scales radially striated, 24 to 28 in the lateral line row (modal number 26). Lateral line incomplete, perforated scales usually consecutive, 4 to 9 in number at the anterior end of the row. In a few individuals, however, up to 21 perforated scales were noted; the additional scales were not arranged consecutively but were scattered irregularly amongst blank scales. The lateral line row dips to a maximum depth of half a scale below the myoseptum in the anterior third of the body. There are $3\frac{1}{2}$ scales between the lateral line and the dorsal origin, $3\frac{1}{2}$ scales between the lateral line and the ventral midline immediately in front of the pelvic origin and 2 to $2\frac{1}{2}$ scales between the lateral line and the pelvic origin. Eight (f.1), 9 (f.24) or 10 (f.6) scales round the caudal peduncle.

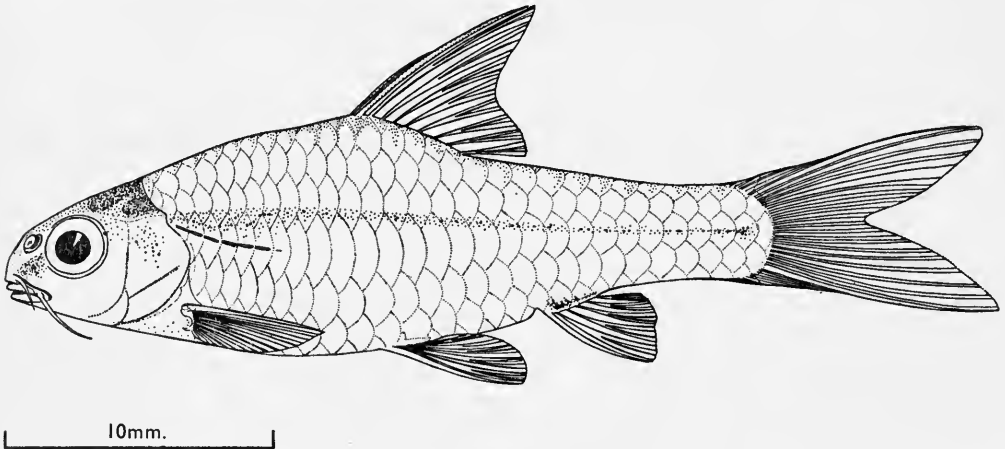


FIG. 15. *Barbus bawkuensis*.

Summary of morphometric data based on 33 fish, 20 to 29 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	24.4-31.1	27.7	—
Length head	23.8-28.5	25.9	—
Diameter eye	7.1-9.0	7.7	—
Interorbital width	8.9-11.5	9.9	—
Length snout	5.7-6.9	6.3	—
Length anterior barbel	1.9-4.6	3.0	—
Length posterior barbel	4.4-8.0	6.1	—
Length pectoral fin	15.5-21.2	18.3	—
Length dorsal fin	22.6-28.8	25.4	—
Length caudal peduncle	19.5-22.8	21.4	—
Depth caudal peduncle	12.0-14.0	12.8	—

COLORATION : *in formalin-fixed specimens* dorsal surface with a light scattering of melanophores near the margin of each scale. A narrow, diffuse band of melanophores runs mid-laterally from the operculum to the end of the caudal peduncle. An indistinct black spot lies at the base of the anal fin. The body is otherwise pigment-free. The snout is marked laterally with a dark streak which does not extend forwards onto the tip. Dark pigment is noticeable along the anterior margin of the dorsal fin.

DIAGNOSIS AND AFFINITIES : morphometrically, *B. bawkuensis* is very similar to *B. punctitaeniatus* differing only in the shorter barbels (anterior 1.9–4.6 cf. 3.2–6.4% S.L. ; posterior 4.4–8.8 cf. 6.0–11.2% S.L.) and in the slightly higher modal number (26 cf. 25) of lateral line scales. *Barbus bawkuensis*, however, lacks the black streak on the tip of the snout and the dark spots on the lateral line scales characteristic of *B. punctitaeniatus*. Other minor differences in the newly described species are heavier pigmentation on the last simple dorsal ray and a darker spot at the base of the anal fin. *Barbus bawkuensis* and *B. punctitaeniatus* are remarkable for their high variability in the number of perforated lateral line scales. This unusual feature has been noted previously in *B. anoplus* (Groenewald, 1958) where, as in *B. bawkuensis*, the lateral line is frequently interrupted, and also in *B. pobeguini* from Ksar Torchane, Mauritania (Daget, 1954) where some specimens had complete, others rudimentary lateral lines. *Barbus bawkuensis* and *B. punctitaeniatus* are unique among West African species in the combination of a incomplete lateral line and two pairs of relatively long barbels.

DISTRIBUTION : at present known only from the White Volta and its tributaries near Bawku, northern Ghana.

Barbus pobeguini Pellegrin, 1911

(Text-fig. 16)

Barbus pobeguini Pellegrin, 1911, *Bull. Soc. zool. France*, 36 : 187.

Barbus pobeguini : Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 205, fig. 71.

DESCRIPTION based on 24 fish 29–36 mm. S.L., from Dedoro Tankara Dam, 8 miles north-east of Navrongo (Volta basin), north Ghana. Body cylindrical, only slightly compressed. S.L. 3.7 to 4.3 times the maximum depth and 3.5 to 3.8 times the length of the head. Predorsal profile smooth, convex. Snout rounded, 0.85 to 1.0 times the diameter of the eye. Mouth moderate, subterminal. The single pair of short barbels 0.1 to 0.3 times the diameter of the eye. Eyes relatively small, inclined slightly upwards, the diameter 3.45 to 4.0 times in the length of the head and 1.35 to 1.7 times in the interorbital width. Weakly-developed pit-lines present on the cheeks. Pectoral fin 0.65 to 0.8 times the length of the head, the tip falling well short of the pelvic origin. Last simple dorsal ray smooth, flexible, 0.8 to 0.9 times the length of the head. Apex of dorsal fin rounded, distal margin slightly convex. Dorsal fin rays III 7 ; anal fin rays III 5. The pelvic origin lies within the verticals to the first or second dorsal rays. Caudal peduncle 1.45 to 1.75 times as long as deep.

The lateral line dips to a maximum depth of one scale row below the horizontal myoseptum in the anterior third of the body; the two converge in the first third of the caudal peduncle. Twenty-seven to 32 lateral line scales (modal number 29). Four and a half to $5\frac{1}{2}$ scales between the lateral line and the dorsal origin, $5\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $2\frac{1}{2}$ to 3 scales between the lateral line and the pelvic origin. Twelve (f.21) or 13 (f.3) scales round the caudal peduncle.

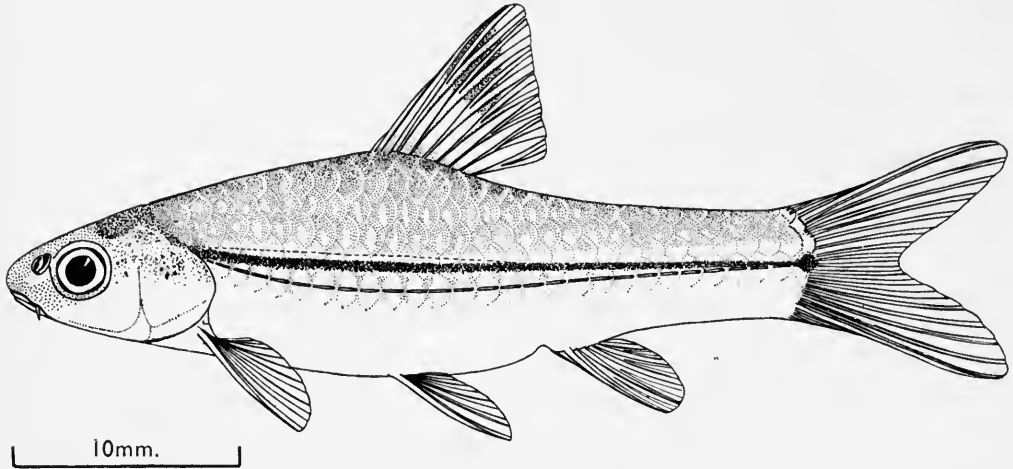


FIG. 16. *Barbus pobeguini*.

Summary of morphometric data based on 24 fish, 29 to 36 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	23.5-26.5	24.2	—
Length head	26.2-28.0	27.1	—
Diameter eye	6.8-8.7	7.2	—
Interorbital width	10.0-11.5	10.5	—
Length snout	6.3-7.2	6.8	—
Length barbel	0.7-2.2	1.4	Positive
Length pectoral fin	17.6-22.0	19.6	Negative
Length dorsal fin	21.5-25.5	23.4	—
Length caudal peduncle	21.8-24.1	22.7	—
Depth caudal peduncle	12.9-15.2	13.9	—

COLORATION: in *living specimens* silvery with a characteristic steel-blue iridescence. A dark lateral band ends in a small but pronounced spot on the caudal peduncle. There is an oblique black stripe on the distal half of the anterior rays of the dorsal fin. In *formalin-fixed specimens* dorsal surface well peppered with melanophores absent from a narrow zone close to the margin and thinning out towards the centre of each scale. Dark pigment fades out on the flanks, and scales below the lateral line are clear. Pockets of anterior lateral line scales each with a small black streak

divided horizontally into two by the lateral line pore. The upper halves of the streaks persist on more posterior scales. A narrow black lateral band slightly below the myoseptum extends backwards onto the caudal peduncle, stopping just short of a round black spot on the tip. The spot overlaps the base of the caudal rays. Dorsal fin with a narrow black stripe, parallel with the distal margin of the fin, on the upper halves of the last simple and first three branched rays.

DIAGNOSIS : these data are in close agreement with descriptions of *B. pobeguini* from the Middle Niger (Pellegrin, 1911 and Daget, 1954). *Barbus pobeguini* appears to have no close relatives in West Africa. The presence of a single pair of barbels, 7 branched dorsal rays and the distinctive colour pattern should prevent confusion with other species in the area. Pellegrin (*op. cit.*) has pointed out the similarity of this species with *B. afer* Peters from South Africa.

HABITAT AND DISTRIBUTION : in *Ghana*, rivers, streams and pools throughout the northern regions. The commonest *Barbus* in flood water ; often found in temporary streams after storms and one of the first colonizers of newly built dams. Never abundant in the larger rivers. *Elsewhere*, basins of the Niger (Daget, 1954) and Comoé (Blanc & Daget, 1957) and in Mauretania (Daget, 1954).

LIFE HISTORY : *Barbus pobeguini* apparently breeds during the rains. Ripening fish were observed in June and juvenile stages appeared in August. Growth is more rapid in females than in males. Maximum size, a female 50 mm. S.L.

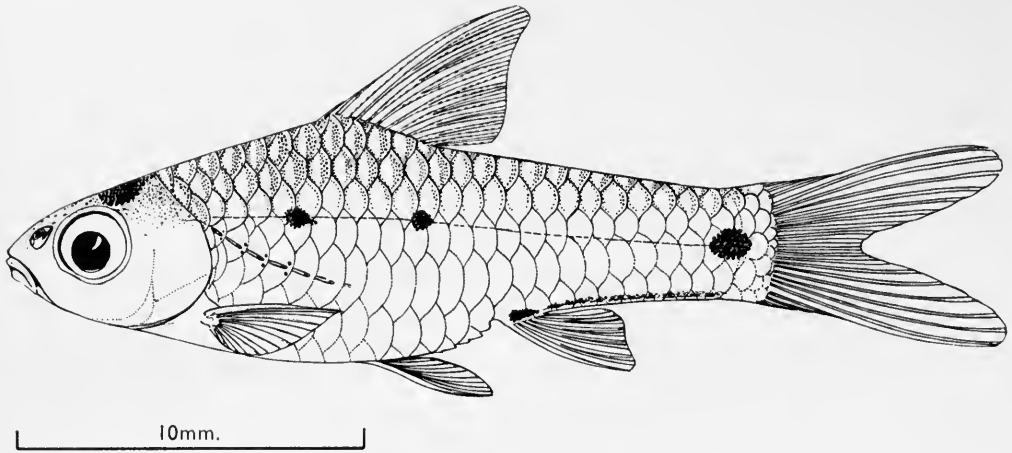
Barbus stigmatopygus Boulenger, 1903

(Text-fig. 17)

Barbus stigmatopygus Boulenger, 1903, *Ann. Mag. nat. Hist.* (7) 12 : 533 ; *Idem*, 1911, *Cat. Afr. Fish.* 2 : 185, fig. 163.

Barbus stigmatopygus : Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 210, fig. 75.

DESCRIPTION based on 24 fish, 16–19 mm. S.L. from the Black Volta, 3 miles west of Lawra, northern Ghana. Body compressed. S.L. 3.2 to 3.8 times the maximum depth and 3.45 to 3.95 times the length of the head. Predorsal profile convex. Snout short, bluntly pointed, 0.55 to 0.75 times in the diameter of the eye. Mouth terminal, small. Eyes lateral, relatively large, 2.45 to 2.8 times in the length of the head and 0.95 to 1.15 times in the interorbital width. A few weakly-developed pit-lines present on the cheek and operculum. Barbels absent. Pectoral fin 0.6 to 0.75 times as long as the head, its tip falling short of the pelvic origin. Last simple ray of dorsal fin smooth, flexible, 0.8 to 1.0 times the length of the head. Apex of dorsal fin rounded, distal margin concave. Dorsal fin rays III 8. Anal fin rays III 5. Origin of pelvic fin between the verticals to the last simple and first branched dorsal rays. Caudal peduncle 1.25 to 1.5 times as long as deep. Lateral line incomplete, only the first 4 to 7 scales in the row perforated. There are 23 to 25 (modal number 24) scales in the lateral line row, $4\frac{1}{2}$ scales between the lateral line and the dorsal origin, $2\frac{1}{2}$ scales between the lateral line and the mid-ventral line immediately in front of the pelvic origin and $1\frac{1}{2}$ scales between the lateral line and the pelvic origin. Nine (f.1) or 10 (f.23) scales round the caudal peduncle.

FIG. 17. *Barbus stigmatopygus*.

Summary of morphometric data based on 24 fish, 16 to 19 mm. S.L. ; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth	26.1-31.2	28.5	—
Length head	25.2-28.9	27.3	—
Diameter eye	9.5-11.2	10.3	—
Interorbital width	10.3-11.9	11.1	—
Length snout	5.8-7.4	6.7	—
Length pectoral fin	16.8-20.0	18.6	—
Length dorsal fin	22.1-27.6	24.9	—
Length caudal peduncle	17.6-21.2	19.9	—
Depth caudal peduncle	13.2-15.0	14.2	—

COLORATION: *in living specimens* dorsal surface finely patterned with yellow and black chromatophores, scales of the lateral line and below, silvery. A round black terminal spot on the caudal peduncle and a second spot at the base of the anal fin are always present. Two additional spots frequently occur on the horizontal myoseptum in the anterior half of the body. The fins are colourless. There is a yellow arc over the pupil of the eye. Specimens from clear water are frequently transparent with the vertebral column and viscera visible through the body wall. *In formalin-fixed specimens* the scales of the dorsal surface are outlined with a fine lacework of melanophores which fade away on the flanks. A small round black spot at the tip of the caudal peduncle is always present, as is a compact group of melanophores at the base of the anal fin, which continues backwards as a thin black line along the ventral surface of the caudal peduncle. Two further round black spots, smaller than the one on the caudal peduncle, usually occur on the horizontal myoseptum, the first at the level of the fifth lateral line scale, the second below the last ray of the dorsal fin. One or both of these may be absent. Pockets of anterior lateral line scales are frequently marked with a black dot above and below the canal.

DIAGNOSIS: these data correspond closely with previous descriptions of *B. stigmatopygus*. Despite careful examination of the material described here we can find no trace of the single pair of much reduced barbels which Dr. Trewavas recently observed in specimens from the White Nile and Lake No (*pers. com.*). *Barbus stigmatopygus* is easily distinguished by its markings from other small *Barbus* with similarly reduced lateral lines and barbels.

HABITAT AND DISTRIBUTION: *in Ghana*, judging from our records, *B. stigmatopygus* is a relatively rare and local species. With the exception of two fish from the River Nasia near Tamale all records are from backwaters and tributaries of the Black Volta in the Lawra district where it is not uncommon. The habitat is always deep, relatively still water, free from vegetation. *Elsewhere*, widespread in the Sudanese belt. Recorded from the White Nile (type locality), the Middle Niger (Daget, 1954), Haute Volta (Blanc & Daget, 1957) and the Geba River, Portuguese Guinea (Boulenger, 1911).

Barbus leonensis Boulenger, 1915

(Text-fig. 18)

Barbus leonensis Boulenger, 1915, *Ann. Mag. nat. Hist.* (8) 15 : 203 ; *Idem*, 1916, *Cat. Afr. Fish.* 4 : 273, fig. 167.

Barbus leonensis : Daget, 1954, *Mem. Inst. France. Afr. Noire*, no. 36 : 209, fig. 74.

DESCRIPTION based on 24 fish 27 to 33 mm. S.L. from the water-works reservoir, Tamale, north Ghana (Volta basin). Body somewhat compressed. S.L. 3.1 to 3.7 times the maximum depth and 3.2 to 3.7 times the length of the head. Predorsal profile smooth, convex. Snout pointed, 0.7 to 0.95 times the diameter of the eye. Mouth small, slightly subterminal. Eyes lateral, 2.9 to 3.35 times in the length of

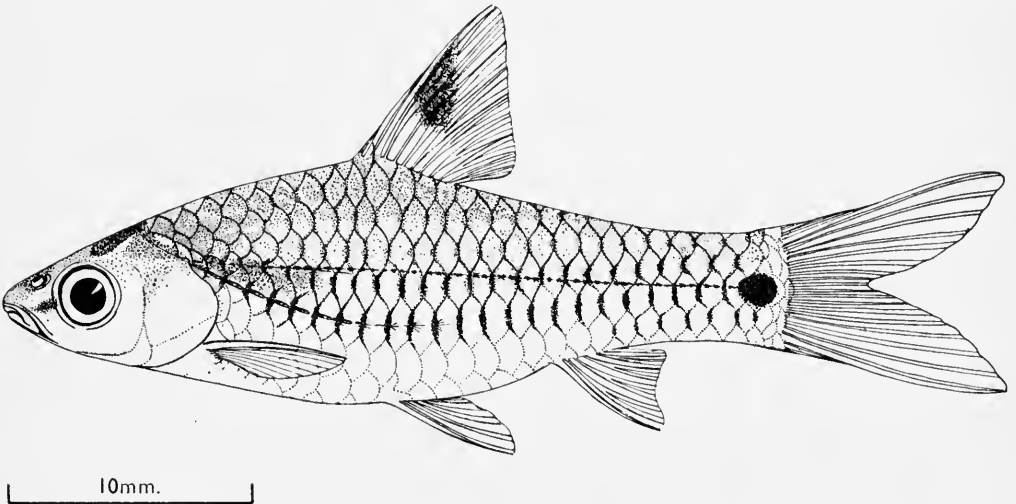


FIG. 18. *Barbus leonensis*.

the head and 1.15 to 1.4 times in the interorbital width. Barbels absent. A few weakly-developed pit-lines on the cheeks and on the operculum. Pectoral fin 0.55 to 0.7 times the length of the head, the tip falling short of the pelvic origin. The last simple dorsal ray is smooth, flexible, 0.75 to 0.95 times as long as the head. Apex of the dorsal fin slightly rounded, the distal margin straight. Dorsal fin rays III 7 (f.2) or III 8 (f.22). Anal fin rays III 5 (f.21) or 6 (f.3). The origin of the pelvic fin lies between the verticals to the first and second dorsal rays. Caudal peduncle 1.2 to 1.5 times as long as deep. The lateral line is always incomplete; 6 to 10 anterior scales are perforated. There are 22 to 26 scales (modal number 24) in the lateral line scale row, $4\frac{1}{2}$ to $5\frac{1}{2}$ scales between the lateral line and the dorsal origin, $2\frac{1}{3}$ scales between the lateral line row and the mid-ventral line immediately in front of the pelvic origin, and $1\frac{1}{2}$ scales between the lateral line and the pelvic origin. Eight (f.1), 9 (f.18) or 10 (f.5) scales round the caudal peduncle.

Summary of morphometric data based on 24 fish, 27 to 33 mm. S.L.; measurements are expressed as percentages of S.L.

	Range	Mean	Allometry
Maximum depth . . .	27.0-31.8	29.3	—
Length head . . .	27.5-30.3	28.6	—
Diameter eye . . .	8.2-9.6	8.9	—
Interorbital width . . .	10.4-12.8	11.5	—
Length snout . . .	6.6-8.2	7.3	—
Length pectoral fin . . .	16.6-21.0	18.6	—
Length dorsal fin . . .	23.0-26.0	23.8	—
Length caudal peduncle . . .	18.2-21.0	19.6	—
Depth caudal peduncle . . .	13.1-15.4	14.3	—

COLORATION: *living specimens* pale lemon yellow in colour with two rounded black spots, one on the caudal peduncle the other on the anterior rays of the dorsal fin. Yellow pigment brightest in an arc over the pupil of the eye and in the vicinity of the two black spots. *Living specimens* frequently transparent, the vertebral column and viscera clearly visible through the body wall. *In formalin-fixed specimens* dorsal surface with an even scattering of melanophores thinning out and disappearing on the flanks. Scales of the lateral line row and above lightly outlined with melanophores which are thicker in a vertical line on the pocket of each scale, thus forming a regular pattern over the dorsal surface of the fish. Traces of the pattern may persist on the row below the lateral line but the ventral surface is generally pigment-free. The black spot on the caudal peduncle is equal in diameter to the depth of one scale row and slightly overlaps the base of the caudal fin. The side of the snout is marked with a narrow, horizontal, band of melanophores touching the anterior margin of the eye. The spot on the dorsal fin lies between the last simple and the third branched ray at a point midway between the base and the apex of the fin.

DIAGNOSIS: these data correspond closely with the description of the types from Sierra Leone and also with data obtained by Daget (1954) from fish in the Middle Niger. We, however, record 9 as the modal number of scales round the caudal peduncle compared with 8 in the previous descriptions. *Barbus leonensis* is easily

distinguished from *B. anema* and *B. stigmatopygus* (both of which have incomplete lateral lines and no barbels) by the characteristic pattern of pigmentation.

HABITAT AND DISTRIBUTION : *in Ghana*, widespread in well-vegetated pools, oxbow lakes and dams throughout northern Ghana. Rare in rivers and streams. *Elsewhere*, recorded from much of the savannah zone of West Africa—Sierra Leone (type locality), Gambia River (Johnels, 1954), Niger basin (Daget, 1954), Comoé (Blanc & Daget, 1957), Haute Volta (Blanc & Daget, *op. cit.*) and Chad (Daget, *op. cit.*).

LIFE HISTORY : spawning is confined to the rainy season, June to September. All fish mature at the age of 8 to 10 months. Few individuals, if any, survive their first spawning season and the maximum life span is probably 15 months. Growth is slightly more rapid in females than in males. Maximum size, 33 mm. standard length.

KEY TO THE VOLTAIC SPECIES OF *Barbus*

- 1 Well-developed pit-lines present ; individual pits bead-like in appearance, forming parallel ridges on the side of the snout, the cheek, the operculum and on the dorsal surface of the head between the eyes subgenus ***Beirabarus*** 2
- Cephalic pits relatively few in number, sometimes orientated into lines, but with the individual pits well-separated from one another and usually visible only on the cheek and on the operculum 3
- 2 Apex and second simple ray of dorsal fin dense black ; heavy melanophores form a conspicuous mid-lateral band running from the side of the snout to the tip of the caudal peduncle ; pockets of lateral line scales with relatively broad, triangular spots ; 12 scales round the caudal peduncle ; the tip of the pectoral fin never overlaps the pelvic origin ; snout 6.3-7.3% S.L. ; caudal fin in living specimens orange-red ***B. macrops***
- No dense pigment patches on the dorsal fin ; mid-lateral band relatively light ; pockets of lateral line scales with narrow and crescentic vertical stripes ; usually 10 or 11 scales round the caudal peduncle ; the tip of the pectoral fin often overlaps the pelvic origin ; snout 6.4-7.6% S.L. ; caudal fin pale pink in living specimens ***B. parablabe***
- No dense black pigment patches on the dorsal fin ; mid-lateral band faint ; pockets of lateral line scales with relatively narrow vertical bars of pigment ; 12 scales round the caudal peduncle ; the tip of the pectoral fin sometimes overlaps the pelvic origin ; snout 7.8-8.8% S.L. ***B. spurrelli***
- 3 Lateral line scales markedly deep, over 2.7 times as deep as long ; dorsolateral scales outlined with melanophores which are concentrated in a vertical arc on the pocket of each scale ; mid-lateral band, if present, very faint ; an oblique black stripe often lies between the origin of the lateral line and the base of the pectoral fin : subgenus *Clypeobarbus* ***B. hypsolepis***
- Lateral line scales not markedly deep, under 2.4 times as deep as long ; pigment pattern consisting of lateral stripes or spots ; no black stripe between the origin of the lateral line and the base of the pectoral fin 4
- 4 Barbels present 5
- Barbels absent 13
- 5 Usually 8 branched dorsal rays 6
- Usually 7 branched dorsal rays 12

- 6 Body marked with three or more mid-lateral spots ; one in the anterior third of the body, one below the last dorsal ray and one on the caudal peduncle are nearly always present ; the spots are sometimes partly obscured by a dark mid-lateral band 7
 Body marked with a black mid-lateral band, sometimes broken into irregular spots or streaks 9
- 7 Body marked with three mid-lateral spots 8
 Body marked mid-laterally with four or more large rounded black spots . *B. sublineatus*
- 8 Dorsolateral surface with two or three dark longitudinal stripes ; barbels relatively long, the anterior clearly overlapping the base of the posterior ; mouth not protrusible obliquely downwards ; spot at the base of the anal fin relatively faint *B. macinensis*
 Dorsolateral surface without longitudinal stripes ; barbels short, the anterior barely overlapping the base of the posterior ; mouth small, protrusible obliquely downwards ; black spot at the base of the anal fin conspicuous *B. voltae*
- 9 Lateral line complete ; $4\frac{1}{2}$ or $5\frac{1}{2}$ scales between the lateral line and the dorsal origin 10
 Lateral line usually incomplete ; $3\frac{1}{2}$ scales between the lateral line and the dorsal origin 11
- 10 Mid-lateral band more or less continuous from the tip of the operculum to the end of the caudal peduncle ; mouth large, barbels long, the posterior extending to or beyond the posterior margin of the eye *B. nigriensis*
 Mid-lateral band, originating between the operculum and the dorsal fin, frequently broken into irregular spots or streaks ; mouth moderate in size ; barbels moderate, the posterior not extending past the vertical to the posterior margin of the pupil *B. lawrae*
- 11 Black pigment on the snout continuous round the tip from eye to eye ; conspicuous black spots on the scale pockets of the lateral line *B. punctitaeniatus*
 Black pigment on the snout confined to the sides ; scale pocket pigment of the lateral line inconspicuous *B. bawkuensis*
- 12 Two pairs of barbels ; mid-lateral pigmentation variable but three spots often present ; no spot on the dorsal fin *B. atakorensis*
 One pair of barbels ; a narrow continuous mid-lateral band ends in a spot on the tip of the caudal peduncle ; dorsal fin marked with a black streak across the distal half of the anterior rays *B. pobeguini*
- 13 Dorsal fin marked with a round black spot ; body with a single spot on the tip of the caudal peduncle *B. leonensis*
 No spot on the dorsal fin ; Body marked with two to four black spots, one at the base of the anal fin, the others on the horizontal myoseptum *B. stigmatopygus*

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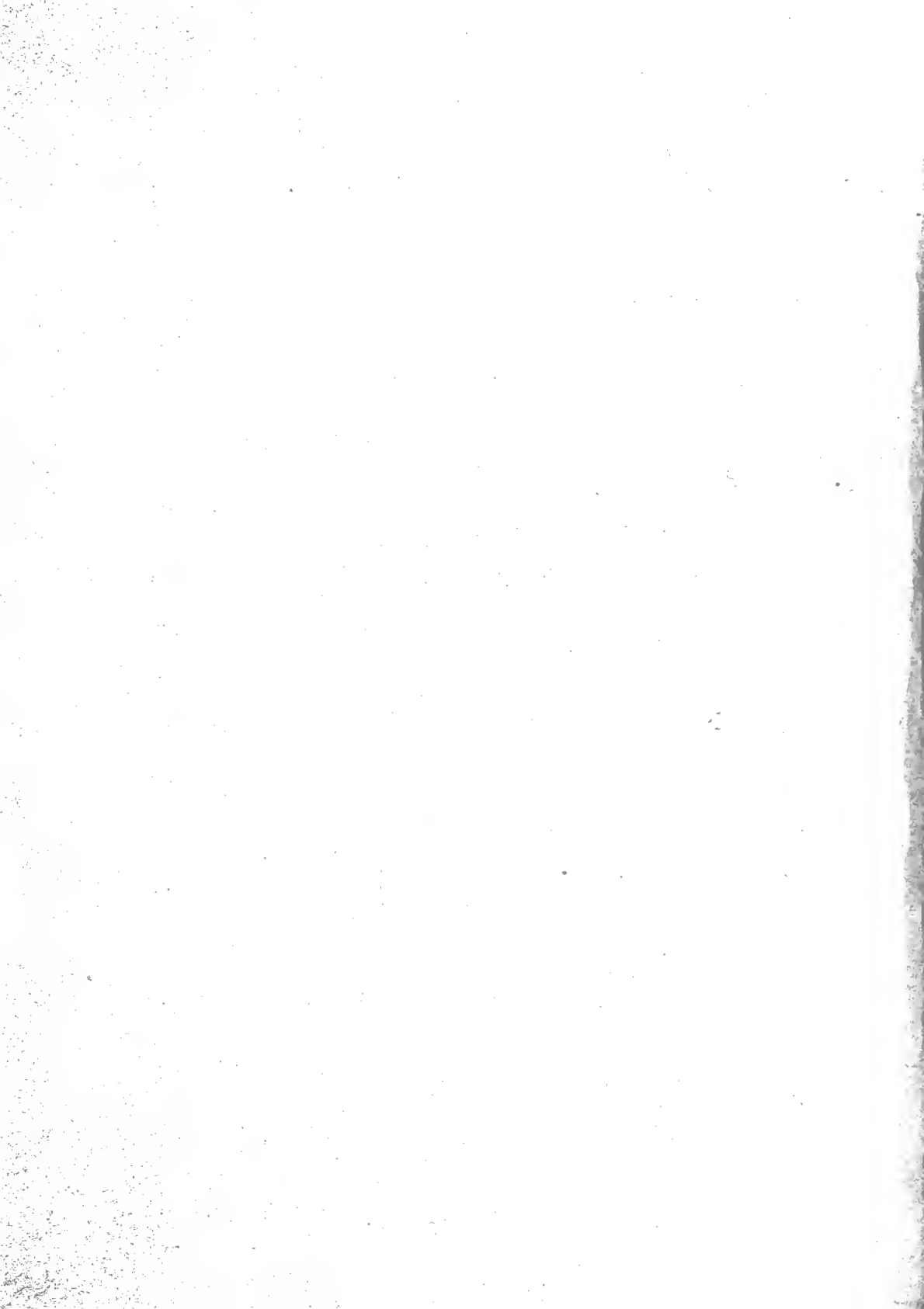
NOTES ON THE CUPULADRIIDAE
(POLYZOA, ANASCA)

PATRICIA L. COOK

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY

Vol. 13 No. 5

LONDON: 1965



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PATRICIA L. COOK

British Museum (Natural History)

Pp. 151-187 ; Plates 1-3 ; 6 Text-figures

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NOTES ON THE CUPULADRIIDAE (POLYZOA, ANASCA)

By PATRICIA L. COOK

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I INTRODUCTION

RECENT work on the rich west African fauna of species belonging to the Cupuladriidae, has led to an examination of other species and to a general review of the characters of the family. The following notes are an attempt to define the limits of variability of some of these characters, and to delimit groups of species which appear to be related.

Specimens in the Zoological Department of the British Museum are referred to by registered number thus, 1899. 7. 1. . . . ; in the Palaeontological Department thus, D 6474. Measurements of zooecial length have been made from the distal rim of one zooecium to that of the next succeeding radial zooecium, so including the vibraculum.

Measurements are given thus :

Length of zoecium	Lz	Length of operculum	Lo
Width of zoecium	lz	Width of operculum	lo
Length of vibracular opesia	Lvo	Length of zoecial opesia	Lop
Length of vibracular seta	Ls	Width of zoecial opesia	lop

DEFINITION OF TERMS USED. The majority of the terms used may be found defined by Lagaaij (1952 : 12) and Bassler (1953 : 7).

Horizontal cryptocyst lamina. A porous lamina, formed from fused cryptocyst denticles, extending from the descending cryptocyst across the opesia, parallel to, and below, the frontal membrane.

Vestibular arch. The distal, crescentic, raised portion of the aperture.

Vicarious vibraculum. A large vibracular individual, taking the place of a zoecium, and itself having a distal vibraculum.

2 CUPULADRIIDAE Lagaaij

Cupuladriidae Lagaaij, 1952 : 31.

Lagaaij defined the family to include only the genus *Cupuladria*. A series of species is now known to exist (Cook (in press)) which links the membraniporan forms such as *C. canariensis* (Busk) with the microporan forms like *Discoporella umbellata* (Defrance). Both genera have therefore been included in the Cupuladriidae, the diagnosis of which has been accordingly slightly modified.

DIAGNOSIS. Lunulitiform Anasca with vibracula alternating with zoecia in the same radial series. Cryptocyst variously developed. Ovicells absent. Ancestrula surrounded by seven zoecia and a distal vibraculum.

Lagaaij (1953 : 13) defined the term "lunulitiform" to include conical and discoid zoaria such as those of *Cupuladria*, *Discoporella*, *Lunulites* and *Selenaria*. For reasons given below, the term is here restricted to the first three of these genera, which all bud radially, although it is not assumed that the Cupuladriidae and *Lunulites* are closely related. The term "selenariiform" used by Harmer (1926 and 1957) for both Anaskan and Ascophoran conical colonies, is here restricted to zoaria with spiral budding, e.g. *Selenaria*, *Setosellina* and *Heliodoma*. The term "conical" is used here for all the remaining forms described by Harmer, some of which may be attached to the substrate by rootlets, e.g. *Conescharellina*.

It must be stressed that, whereas the combination of characters found in the Cupuladriidae is exclusive, and the limits defining the species are generally well marked, the division of the family into two genera, *Cupuladria* and *Discoporella*, is somewhat arbitrary, depending upon only one character, namely, the extent of the development of the cryptocyst. Until work can be done on the life-histories and breeding of the Cupuladriidae, the importance of this character in relation to, for example, the size of the eggs, the larvae, and the other zoecial structures, cannot be assessed, and *Discoporella* is therefore retained here.

3 STRUCTURE AND DEVELOPMENT OF THE ZOARIUM

Although many free-living colonies are similar in appearance, they differ considerably in structure and development. In the Cupuladriidae both the early astogeny and subsequent growth of the zoarium are distinct from that found in other lunulitiform, selenariiform or conical colonies.

a. *Early astogeny.* The ancestrular area is here defined as comprising the ancestrula and the primary circle of zooecia budded from it. The single ancestrula buds a distal vibraculum, a pair of proximal-lateral zooecia and then one proximal zoecium (see Marcus & Marcus, 1962 : 287). A pair of lateral zooecia follows, and a pair of distal-lateral zooecia is the last to be formed (see Text-fig. 1B). Lagaaij (1963a : 182, text-fig. 10) found that secondary proximal buds were developed before this last pair, but colonies seem to be variable in development at this stage. Evidence has been gained from very young colonies of *Cupuladria* sp. (Gulf of Mexico, 1959. 8. 20. 3, Lagaaij Coll.) and *D. umbellata* (Madeira, 1963. 2. 28. 9, and S. Africa, 1949. 11. 10. 668, Burrows Coll.). Waters (1926 : 426) described a double ancestrula in *C. canariensis*, but none have been seen in any of the many specimens examined, and I agree with Lagaaij (1963a : 184) that it is possible that Waters regarded the proximal bud as the second member of a paired ancestrula.

In one group (*C. canariensis*, group A, see p. 167), the entire ancestrular area may consist of vicarious vibracula (see Smitt, 1873, pl. 2, fig. 70 ; Hastings, 1930 : 714 ; Marcus & Marcus, 1962 : 289 ; Lagaaij, 1963a : 183 ; and Cook (in press)). Although vicarious vibracula in the ancestrular area may sometimes be the result of regeneration of a normal zoecium, most of those found in *C. biporosa* (Canu & Bassler) and *C. monotrema* (Busk) are budded primarily as vibracular individuals. The "special area" described by Canu & Bassler (1923 : 81, pl. 2, fig. 18) is not an ancestrular area, but the growing edge of a regenerating, broken fragment (see below).

The pattern of budding outside the ancestrular area appears to be variable. Another variable character is found in *C. pyriformis* (see 168) and a few colonies of *C. canariensis*, where the vibracular seta of the ancestrula, when closed, is directed towards the right side (viewed frontally) (see Text-fig. 1C). In all specimens of

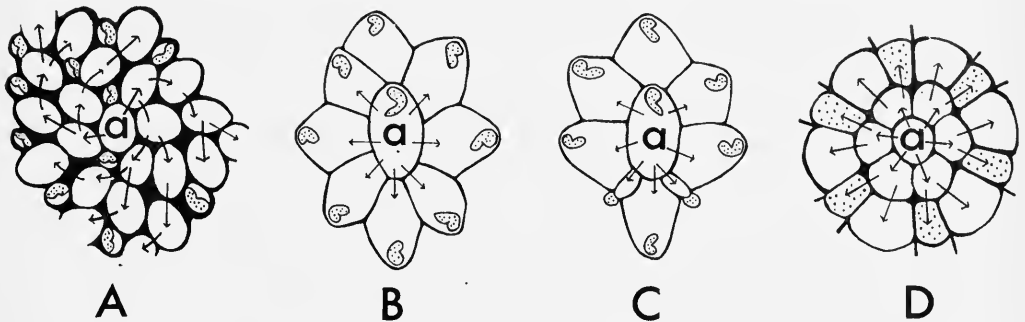


FIG. 1. Early astogeny. a, ancestrula ; vibracula stippled. A. *Setosellina*. Spiral budding. B. Cupuladriidae. Radial budding. C. *Cupuladria pyriformis* (Busk). 1st pair of zooecia aborted. D. *Lunulites*. Radial budding.

other species the seta is directed toward the left side, the seta of the zooecium budded from the proximal end of the ancestrula having the same orientation (see Text-fig. 1B). The seta of the right-proximal-lateral bud is directed to the right, that of the left-proximal-lateral bud to the left (see also Marcus & Marcus, 1962 : 297).

b. *Growth.* Each zooecium and vibraculum develops radially as a unit which arises as a common bud, the vibracular chamber being divided off from the cavity of the zooecium in the later stages of development. The relationship of the vibraculum with the zooecium distal to it is comparable with that of the "recumbent" ovicell of *Crepidacantha* (see Brown, 1954 : 244, footnote). Here the ovicell is fully formed before the development of the next distal zooecium, which grows round it from below. The vibracular chamber in the Cupuladriidae is not terminal and does not reach the basal surface of the zoarium. Thus, although apparently inserted between the zooecia at the frontal surface, the vibracula are not strictly interzooecial, nor are they adventitious or dependent.

The common bud is rarely present, even in specimens preserved in alcohol, as in its peripheral position it is particularly susceptible to damage when the colony is dead, and it is no longer protected by the extended peripheral vibracular setae (see Marcus & Marcus, 1962, and Cook, 1963). The bud arises between peripheral zooecia. The membranous ectocyst is closely applied frontally and basally to the neighbouring zooecia, but over the bud it is convex and free from the underlying structures. A line of demarcation occurs basally where the ectocyst is no longer in contact with the calcareous basal walls (see Text-fig. 2A). On the basal side the bud originates from the distal end of the proximal zooecium, below the vibracular chamber. On the frontal side the upper surface of the bud appears at the distal wall of the vibracular chamber. The membranous frontal part of the bud becomes the frontal membrane of the zooecium, the basal part the endocyst lining the zooecial cavity (see Marcus & Marcus, 1962, pl. 2, fig. 5). This can be seen in well-preserved specimens of *C. indica* (1899. 5. I. 267); *C. multispinata* (1949. II. 10. 617); *Discoporella umbellata* (MM I 39A); and *D. u. depressa*, (Terra Nova Coll., Stn. 42). The relationships of the young common bud have also been observed in living colonies of *D. umbellata* from Madeira.

As the bud enlarges and grows up between the two adjacent lateral zooecia, the basal wall is covered by a calcified lamina, which develops from the point of origin of the bud (see Text-fig. 2A, B). The polypide is first differentiated at the proximal end of the bud before it is completely covered basally by the lamina. As the lamina advances distally, the cryptocyst develops beneath the frontal membrane growing inward from the lateral walls. The lamina curves upward and inward, and the vibracular chamber develops as an inner compartment from the distal end of the bud. The walls of the chamber are thus double-layered laterally, with connecting bars of calcification. Large pores are present in the outer layer (= "chambers" of Marcus & Marcus, 1962 : 295). These calcify further, become smaller, and eventually communicate with the next distal-lateral zooecia to be developed. The vibracular chamber is connected with its proximal zooecium through a large pore in the dividing

wall. An uncalcified area, which is left in the lamina as it curves up sharply distally to the vibracular chamber, calcifies, but leaves a small pore which eventually communicates with the succeeding radial zoecium (see Text-fig. 2). Specimens clearly showing these structures are *C. multispinata* (S. Africa, 1949. II. 10. 94 B, Burrows Coll.) and *D. u. depressa* (Rio de Janeiro, Terra Nova Coll., Stn. 42).

Transverse sections of zoaria frequently show the stem-like extension of the zoecium, below the vibracular chamber of the previous zoecium. Each zoecium thus has a large distal pore communicating with the vibracular chamber, and 2-3 lateral pores communicating with the adjacent distal-lateral zoecia. No pores enter the vibracular chamber laterally, but it communicates with the next distal zoecium in a radial row. Specimens showing the interzoecial pores clearly are: *C. indica* (1899. 5. I. 267 pt.) and *C. canariensis* (section, 1929. 4. 26. 85 pt.); see also Marcus & Marcus, 1962, pl. 2, fig. 1.

Large colonies of *D. umbellata* (e.g. coast of Ghana, 50B, Achimota Coll.) and *C. canariensis* (Senegal, MM II 3) show rings of growth (see Harmer, 1926 : 267). Apparently these zoaria have grown evenly for a period and then ceased to grow. New budding has been resumed simultaneously all round the periphery, so that a series of concentric ridges may be seen on the basal side.

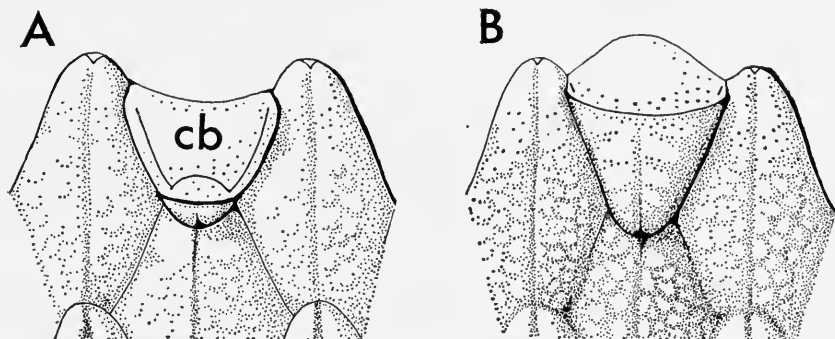


FIG. 2. Growth of the membranous common bud (*c.b.*) and calcareous basal lamina, viewed from the basal side. A. Transparent, membranous common bud developing between two peripheral zoecia. Note the uncalcified area in the distal wall of the vibracular chamber. B. Calcareous curved basal lamina developing over the growing common bud. Note the increased calcification of the previously developed proximal-lateral basal laminae, and the development of the radial median groove.

c. *Regeneration and deformation.* A large number of colonies are regenerated from broken fragments, and the budding by which a symmetrical colony is re-formed follows a characteristic pattern. Stach (1936a : 63-65) and Darteville (1933 : 70-72) have discussed the fragmentation of colonies, and the ecological significance of this form of regeneration. Darteville (1935 : 559-561) also described the form of budding in *C. canariensis*. He mentioned regeneration as occurring from "calcified zoecia" (see below), and examination of many colonies shows that these closed zoecia are, in fact, the primary buds regenerated from a broken edge of a fragment. The original fragment can usually be seen on the basal side of such colonies, as secondary

calcification at the centre does not seem to occur. The broken zooecia which were distal in position in a fragment regenerate zooecia distally, those which were proximal, regenerate zooecia proximally, in which the zooecial orientation is reversed. Zooecia growing from the lateral walls of old zooecia, are at right angles to the previous direction of growth of the fragment. Each broken zooecium produces one bud laterally from the mid-line of its basal wall, and another bud arises from beneath the vibracular chamber. These zooecia are wide and often slightly distorted (see p. 175). Subsequent budding of radial series, including intercalary rows, is exactly the same as in zoaria developing from an ancestrula. The usual radial alternation in the asymmetry of the vibracular opesia is established in the primary and secondary series of buds (see Text-fig. 3A). The colony of *C. elongata* Sakakura mentioned as distorted by Marcus & Marcus (1962 : 288) is, in fact, such a regenerating fragment.

Marcus & Marcus (1962 : 301) have described a second form of regenerative or "zoarial budding", in which small, fan-shaped zoaria are produced from a single zooecium at the periphery of the parent colony. This form of budding has been seen so far only in the *D. umbellata*-complex (e.g. Madeira, 1912. 12. 21. 1004, Norman Coll.) and in *C. multispinata* (Madeira, 1963. 1. 2. 3 and 4, Norman Coll.). Marcus & Marcus described the results of the fracture of the initial zooecium ("pseudoancestrula"), which frees the young zoarium from the parent colony. It then continues its development, eventually assuming a circular shape by the budding of intercalary series. Colonies arising in this manner have no central substrate present, e.g. a sand-grain or foraminiferan. They may also be recognized by the reversed orientation of the regenerated zooecium developed from the broken pseudoancestrula, and by their early fan-shaped budding.

The pseudoancestrula does not calcify fully on the basal side, and when still attached to the zoarium has been seen to fold frontally when its vibracular seta closes (see Cook, 1963 : 411). When fracture occurs, the basal lamina is detached with the new zoarial bud, but the proximal part of the cryptocyst remains with the parent colony (see Marcus & Marcus, 1962 : 302). The distal part of the pseudoancestrula then regenerates a zooecium orientated in the opposite direction. In the Madeiran material the fracture has not always occurred, and buds have continued to develop attached to the parent colony. Deformed colonies have resulted, some of which have been described as *C. lowei* by Busk (1854 : 99 = *D. umbellata*) and "*C. deformis*" by Waters (1921 : 413 = *C. multispinata*).

Other deformed zoaria, especially of these two species, originate from regenerating fragments, and here, deformation is the result of failure of development of one or more radial rows of zooecia. The cause is unknown, but in some cases it appears to be correlated with the growth of associated Sponges, belonging to the Plocamiidae, on the basal side of the Polyzoan colony. The Sponge appears to have inhibited growth at the origin of the chitinous zooecial bud, just below the penultimate series of vibracular chambers. The radial rows of zooecia adjacent to the affected zooecium or zooecia, produce intercalary series until the radial slit in the colony is closed when the two sides touch. Frequently, these zooecia are unable to form interzoecial connections, and a slit or furrow continues radially through the colony, which, as the

associated Sponge develops, becomes lined with spicules. No example of a spiral slit has been seen in deformed colonies of the Cupuladriidae, and the budding pattern should be compared with that of one deformed specimen of *Selenaria maculata* (Bass's Straits, 1899. 7. 1. 1497), where the slit is distinctly spiral (compare Text-figs. 3C, D). The basal surface of this zoarium also shows traces of a Sponge colony, and although it is possible that the Sponge is a secondary and unrelated growth, the correlation with this type of deformation is interesting.

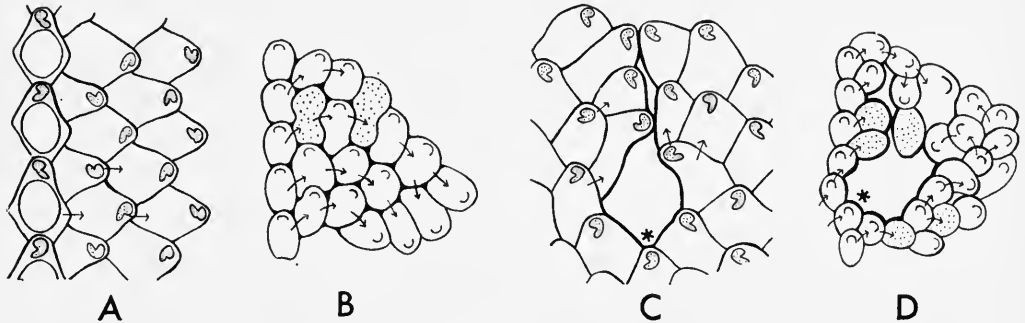


FIG. 3. Regeneration and deformation. Vibracula stippled. A. *Cupuladria*. Regeneration from lateral walls of a radial series. B. *Selenaria*. Spiral regeneration. C. *Discoporella*. Deformation (*), point where distal radial bud has not developed. D. *Selenaria*. Deformation (*), point where lateral distal bud has not developed.

4 CHARACTERS OF SYSTEMATIC VALUE

a. *The central area* is here defined to include the ancestrular area and the centre of the colony where the budding of intercalary radial rows is most frequent and closed zooecia are found. In all groups of species but one (group A, see p. 167), the opesia of the zooecia of the central area become occluded by secondary calcareous growth; these zooecia do not then contain polypides (see Harmer, 1926 : 267). Closed zooecia are often present even in fairly young colonies, and are also found in areas of rapid budding at the edges of regenerating fragments (see above).

In the membraniporan group B (see below) the lamina is formed as a thin sheet originating just below the level of the slight shelf formed by the descending cryptocyst. It develops in a proximal direction from the distal end of the opesia, later also growing out from the lateral walls. Although the lamina thickens it rarely approaches close to the frontal membrane. Irregular pores are left, especially at the lateral edges. In the denticulate forms (Group C, see p. 167), the lamina is formed by extension and fusion of the existing cryptocystal denticles and first develops proximally, spreading progressively to the sub-opercular region. It is closer to the frontal membrane in origin than the lamina in Group B, and when thickened by further deposition may almost obscure the mural rims of the central zooecia. In *Discoporella* where the opesia is restricted to a small sub-opercular area, the central cryptocystal pores calcify first, the opesia then becoming occluded by denticulate growth. The opesiules frequently remain uncalcified or only partially closed. The lamina in these

last two groups is rarely complete, irregular pores usually being present, but in contrast to the first group, no pores are present in the subopercular area.

The existence and type of central area closure may be evidence of the group to which a species belongs, and the association of closed zooecia with ancestrular and regenerative budding in groups B, C and D is comparable to the occurrence of vicarious vibracula in group A.

b. *The cryptocyst* is present in all species and, in well-preserved material, is a useful specific character, especially when its form can be correlated with other characters, such as those of the basal surface. Unfortunately, the cryptocyst is among the first structures to be damaged or worn, although there are usually one or two zooecia present in which it can be seen, even in fossil specimens.

The type of cryptocyst forms a series in the Cupuladriidae from the membraniporan *C. canariensis* to the microporan *D. umbellata*. In the *C. canariensis* and *C. guineensis* groups (see below), it is simple, though variously extensive. In the *C. owenii* group it is denticulate, the form and extent of the denticles being specific. In *Discoporella* it is so extensive that it has been regarded as a generic character. In development, however, the cryptocyst of *D. umbellata* shows great similarity to that of the *C. owenii* group, as it is formed from the fusion of irregular denticles (see Marcus & Marcus, 1962, pl. 1, fig. 4). In *Discoporella* the final development of the cryptocyst results in a pair of distal opesiules or opesiular indentations, through which pass a pair of muscles. Other opesiular pores are present, but the opesia is always limited proximally by a complete bar, formed by part of the cryptocyst.

c. *The opercula* of the majority of species of Cupuladriidae are similar to one another. They are membraniporan with a strong, curved distal sclerite. Their mean dimensions or proportions may give additional information toward the definition of a species, but generally their range of variation is large. Furthermore, opercula are absent not only in fossil specimens, but frequently from dead, Recent material which is a little worn.

Groups C and D (see below) each include species in which the operculum has a partial or complete proximal sclerite. In *C. doma* (Group C), the proximal sclerite is variable, and may be incomplete. Its presence may be useful in distinguishing small fragments from those of *C. owenii*, which may have similar zooecial characters, but the basal surface is here more certain as a determinant of the species. *Discoporella* (group D), has hitherto been distinguished by the possession of a proximal sclerite in the operculum, but there is evidence (Cook (in press)) that even in this group the opercula are not all of the same type and include at least one species in which they are without a proximal sclerite.

d. *The vibracula* are also similar in character in all species of the family. The opesia is auriform, with distinct condyles, which are alternately asymmetrical to right or left in each member of a radial row of zooecia. The vibracular setae are long and usually follow a sigmoid curve, they increase in length toward the periphery of the colony. The setae have an asymmetrical basal sclerite, to which are attached powerful muscles which fill the vibracular chamber. Although there are differences between the setae of various species, especially in the size and shape of the basal

sclerite, the variation within the colony is large and they appear to be of little use in specific determination. The basal sclerites of group A seem generally to be less tuberculate and robust than those of the other groups. The detailed morphology of the vibraculum was discussed by Marcus & Marcus (1962).

The seta is able to move in two directions and in one plane. Owing to its asymmetrical articulation and curvature, these movements cover nearly half of the frontal surface of the zooecia proximal and distal to any vibraculum. Live colonies examined by me have not been seen to use their setae like tweezers, as described by Marcus & Marcus (1962 : 299). The distribution of the setae, and their range of movement, is such that they rarely come into contact (see Text-fig. 4). Those near the centre of the colony may touch each other when closed, owing to the convergence of radial rows, but should any detritus be held between two setae in this position, they automatically lose all contact as soon as an opening movement begins. Particles on the frontal surface are dislodged by the movement of individual setae. They roll down the sloping surface of the colony, passing between the peripheral, supporting setae. The zoarium is thus kept clear of deposits settling upon it (see Cook, 1963 : 410).

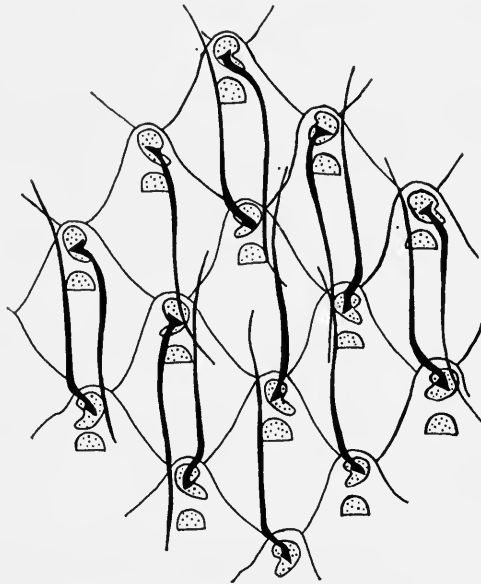


FIG. 4. Distribution of vibracular setae in *Discoporella umbellata*. Membrane of vibracular opesia and opercula stippled. Setae pointing distally are in the "open" position; those pointing proximally are in the "closed" position.

e. *The basal surface.* Lagaaij (1952 : 34, 1953 : 13) stressed the importance of the character of the basal surface in specific determination of fossil specimens, where the frontal surface may have suffered wear. In those groups (A and B below) in which rectangular or hexagonal sectors are present, the thickening consists of layers of

calcification, pierced by regular series of kenozoecial chambers, or by small pores. The shape and arrangement of the sectors, and the number of pores or chambers may be specific, within defined limits. For example, the basal sectors of *C. canariensis* s. s. consist of several layers of long irregular units, interspersed with occasional short sectors; whereas those of *C. monotrema* are single layered and invariably short and square. The sectors of *C. guineensis* (see Hastings, 1930: 714, and p. 170) may vary, especially in large colonies, from square to hexagonal. In the first case the characters of the basal surface are correlated with other distinguishing features, in the second, the variability of the character is found within a single colony, and is not correlated with any other character, and is therefore not specific. In the remaining groups the basal surface consists of a series of alternating radial grooves and ridges, the characters of which may also be specific, although they are variable, affected by wear, and similar forms occur in both *Cupuladria* and *Discoporella*.

The ridges and grooves are the result of the form of growth of the zooecia. Each curved basal lamina is grooved in the mid-line (see Text-fig. 2). As secondary calcification increases the groove may be filled in, and in some cases may be marked by a protuberant "thread" of heavier calcification. The tuberculation of the basal surface may increase with calcification, but may also become changed by wear. In some species, however, the form of tuberculation may be correlated with other characters, and be specific. For example, in *C. owenii*, the tubercles are consistently small and regular, and in *C. multispinata*, they are large, coarse, and coalescent (Cook (in press)).

5 THE EFFECTS OF ZOARIAL FORM ON CHARACTERS

The extreme variation in zoarial and zooecial characters of specimens attributed to *D. umbellata* has been discussed by several authors, and Silén (1942: 16) noted variation in the shape of zoarium of his specimens and grouped his material into localities where one type of zoarium was dominant. The type of zoarium appears to have little effect on the zooecial characters except where the form of the colony is the same as that found normally in *C. doma* (d'Orbigny) or that found in zoaria described as *C. peyroti* by Duvergier (1924: 19).

Doma-type zoaria occur in several species of Cupuladriidae (Cook (in press)) and perhaps correspond to the *Trochopora*-habit of *Lunulites* (see Lagaaij, 1953: 17). Specimens belonging to the *D. umbellata*-complex (see p. 175), frequently produce *doma*-type colonies, and before discussion of specific differences, the effects of form of growth must be considered.

The *doma*-type zoarium is small and usually high (diameter range 3-7 mm.) The zooecia are small, and the basal surface solid or nearly filled in by secondary calcification. In the majority of zoaria the peripheral zooecia are closed, and there may be from 1-3 rows of enlarged peripheral vibracula.

In all lunulitiform zoaria the angle of the axis of the polypide cavity approaches a right angle with the zoarial axis, and the planar intercept of the frontal of each zooecium is thus longer in flatter colonies than in the *doma*-type zoarium, where there is therefore a reduction of the zooecial dimensions usually found in the species, and

consequent changes in the development of the cryptocyst and the proportions of various other characters. The basal surface is also frequently non-typical, owing to the large amount of secondary calcification.

Canu & Bassler (1930 : 12) stated that specimens from abyssal depths of the Pacific reported in 1929 (p. 142), were stunted. Photographs of these specimens (1963. 3. 14. 14) show that they are not, however, either particularly small, or of the *doma*-type. Canu & Bassler also mentioned that colonies of " var. *conica* " had been found in the Helvetian of Touraine, but these colonies were not specifically mentioned by Canu (1909 : 448) in his description of the zoaria from this locality. Marcus & Marcus (1962 : 304) described colonies from the coast of Brazil as *D. umbellata* var. *conica* Canu & Bassler. These are certainly the same form as those listed below as *doma*-type zoaria (see p. 181).

The number of specimens examined of *doma*-type colonies is not at present sufficient to determine whether they should be considered a subspecies of *D. umbellata*. It appears more likely that they are a variant developed in response to specific, but unknown, ecological conditions. The specimens examined fall roughly into 3 groups, each corresponding to one of the 3 major forms in the *D. umbellata*-complex (see p. 176). The ecological factors involved in the occurrence of *doma*-type colonies are probably not simple. There is, for example, no correlation with depth in the material examined, although *C. doma* itself extends in distribution to greater depths than other species of the Cupuladriidae. One *doma*-type specimen from Cape Frio, off Angola, is the sole record from the south west coast of Africa, where the temperatures are lower than, for example, east of the Cape of Good Hope. At Möwe point, just south of Cape Frio, in 400 m., a temperature of 9° C. has been recorded (see Hart & Currie, 1960 : 173, text-fig. 29). The conditions producing *doma*-type growth may perhaps be related to temperature.

In the *D. umbellata*-complex the *doma*-type colonies are very small and the number of opesiules is reduced. The size of opesiæ and opercula are not, however, reduced in the same proportion. The peripheral zooecia are closed and the peripheral vibracula enlarged, as in *C. doma*. Generally, the effect is of a suppression of the characters normally separating the populations in the complex. In nearly all cases, however, the specimens retain traces of features consistent with those found in the larger, more normally developed colonies (see pp. 180, 182).

Peyroti-type growth is similar to *doma*-type growth, and may also be caused by ecological conditions at present unknown. Some colonies combine features of both forms of growth (see p. 180), but whereas *doma*-type zoaria occur in all 3 populations of the complex, Recent *peyroti*-type colonies are the characteristic form of one geographical area, namely the south-eastern coast of Africa. Duvergier (1924 : 19) described, as *Cupularia peyroti*, colonies similar in character to *Discoporella umbellata*, from the Miocene of France, in which the basal surface (described as " face superieur ", following Canu's theoretical orientation of lunulitiform and selenariiform colonies) was covered by kenozoecia and vibracula. Recent specimens from south and east Africa (see p. 177) show stages in the development of the same form of growth, which was briefly described by O'Donoghue (1924 : 39) and discussed by Hastings (1930 :

719), who doubted whether her south African specimens could be included in *D. umbellata*. The large number of colonies now available show that although the zoarial form is markedly different, the zooecial characters have much in common with *D. umbellata* s.s.

The modifications to a specific character produced by *peyroti*-type growth are principally in the appearance of the basal surface. Zoaria are usually large, unlike *doma*-type colonies, and have a smooth, slightly pitted base, which may be concave or solid. There is no sign of the tuberculate, grooved basal surface usually found in *D. umbellata*. In most zoaria the base is covered by a layer of kenozooecia and vibracula proliferated from the peripheral zooecia and vibracula (see Pl. 3, fig. 6). The vibracular opesia are as large as those of the peripheral vibracular zooecia but their setae are not as long. The kenozooecia have no polypides and resemble the closed zooecia of the frontal central area except that there are pores in the distal part of the lamina which in normal closed zooecia is the solid, sub-opercular region (see p. 160).

The peripheral frontal zooecia are also closed as in *doma*-type zoaria, but the peripheral vibracula are not greatly enlarged nor do several rows of them occur.

The basal vibracula presumably act in a similar manner to those at the periphery, and assist in stabilizing the zoarium and maintaining it just above the surface of the substrate (see Cook, 1963).

The conditions determining *peyroti*-type growth do not seem to be related to temperature, as similar ranges occur east of the Cape of Good Hope to those off west Africa (i.e. warm temperate to tropical, see Stephenson, 1947). No Cupuladriidae have been reported from the colder waters immediately to the west of the Cape of Good Hope.

6 COMPARISON WITH THE STRUCTURE OF OTHER FREE-LIVING ZOARIA

Silén (1942 : 1-22) examined many free-living zoaria and considered that their growth was spiral i.e. that the zooecia of each apparently radial row were budded from the nearest proximal-lateral, not proximal, zooecium. Examination of many lunulitiform, selenariiform and conical colonies has confirmed Silén's observations for *Setosellina*, *Setosella* (principally an encrusting form) and *Heliodoma*, and Stach's observations (1936a) for *Selenaria*, but has also shown that the method of growth in the Cupuladriidae and the genus *Lunulites* is entirely different. The evidence is summarized below.

a. In the spirally growing forms the ancestrula buds off both a distal and a proximal (or proximal-lateral) vibraculum, each with an adjacent zooecium. A good example was figured in *Vibracellina caribbea*¹ by Osburn (1947 : 11, pl. 1, fig. 2). Two spirals of zooecia and vibracula develop from these foci, so that although the ancestrula is eventually surrounded by zooecia, unlike that of *Lunulites* and the Cupuladriidae, it has not directly budded all of them (contrast Text-fig. 1A with Text-figs. 1B, C and

¹ Lagaaij (1963b : 172) also describes and figures the ancestrula region of this species, which he refers to *Setosellina goësi* (Silén).

D). The spiral budding is well illustrated in 5 zoaria of *Selenaria squamosa* (N. Zealand, 1947. 8. 16. 1), where the spiral is anti-clockwise. All colonies of other species seen are developed in a clockwise direction. In *Lunulites* the budding pattern is radial, not spiral, but differs from that of the Cupuladriidae in that the ancestrula buds 6 zoecia, each of which then gives rise to a zoecium and a vibraculum. The ancestrula does not therefore directly bud a vibraculum (see Text-fig. 1D).

b. Silén based his conclusions as to the spiral nature of the zoaria of the Cupuladriidae on the assumption that morphologically the vibraculum was the distal bud formed by each zoecium, and that a vibraculum could not bud off a zoecium distal to itself. The zoecium and vibraculum of the Cupuladriidae originate as a unit, and although there is evidence that the vibraculum is a modified zoecium (see Marcus & Marcus, 1962 : 298), it is produced within the confines of the common bud, and is not itself the product of distal budding. In spirally developed colonies (e.g. *Setosellina*), the vibracular chamber can be seen to reach the basal side of the zoarium, and the distal-lateral origin of the next zoecial bud can be seen.

c. In spirally developed colonies, the parent zoecium of an intercalary series forms the second bud consistently on the side opposite to the direction of spiral growth. In the Cupuladriidae the intercalary zoecia are produced from either distal-lateral wall of the parent zoecium, in a random manner. The vicarious vibracula in the *C. canariensis* group (see below) may be intercalary or may themselves produce intercalary zoecia or further vicarious vibracula. Their appearance is also entirely random, and has no spiral pattern. In *Lunulites* the radial rows of zoecia alternate with those of the vibracula. There is no direct lateral relationship between the budding of the types of individual, which are developed radially, not spirally. Successive vibracula enlarge in a series and finally one buds a distal zoecium. New intercalary rows of vibracula are produced from bifurcations of series distal to a zoecium, not a vibraculum. In the central area the first vibracular rows are all budded from the proximal zoecium in the same lateral relationship to the zoecial buds (see Text-fig. 1D). In subsequent bifurcations the vibracular bud arises to the right or left of the zoecial bud in a random manner.

d. The growing edge of *Selenaria bimorphocella* (off Adelaide, 1928. 9. 13. 81), shows no basal curved laminae, but a series of groups of young zoecia alternating with developing vibracula, similar in appearance to the growing edge of an encrusting colony. Similarly, the growing edges of colonies of *Setosellina* have no basal curved laminae. The peripheral zoecia of *Lunulites* arise in a similar manner to those in the Cupuladriidae and basal laminae have been seen. The resulting basal grooves mark the junction of the lateral walls and do not have the alternating pattern of the Cupuladriidae (see below). In Recent *Lunulites* the cavities of the vibracula reach the basal surface, in the fossil specimens described by Lagaaij (1953), they do not.

e. As in the Cupuladriidae, the regenerative budding in *Lunulites* is at right angles to the lateral walls of broken fragments. This is in contrast to colonies of *Selenaria* regenerated from fragments (New Zealand, Discovery Coll., Stn. 936), which show spiral budding from the lateral walls of old zoecia. Each new bud is consistently

distal-lateral, and no zoecium produces new zoecia at right angles to its long axis (see Text-fig. 3B). The budding of deformed colonies of *Selenaria* is also spiral (see p. 159)

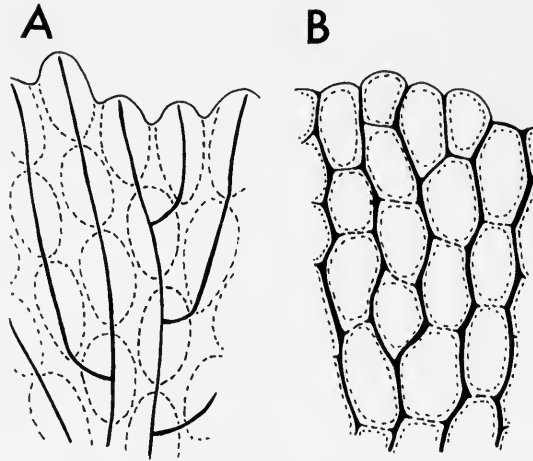


FIG. 5. Relationships of basal grooves. Broken lines indicate the position of the frontals of the zoecia on the upper surface. A. Cupuladriidae. Grooves running radially in the mid-line of the zoecia, branching at the beginning of an intercalary series. B. *Selenaria*. Grooves running between the zoecia, branching around the first zoecium of an intercalary series.

f. The basal radial threads and radial sector boundaries branch frequently. The origin of a branch may be traced and found to correspond exactly with the occurrence of the first zoecium of an intercalary row on the frontal surface. The budding of an intercalary row must be of the same nature as that of all other zoecia, and thus the radial nature of the threads and sector boundaries may also be presumed to reflect the radial development of the zoarium (see Text-fig. 5A). The formation of the basal surface in the Cupuladriidae is exclusive, but apparently similar forms are present in other families. An unnamed species of *Lunulites* described and figured by Lagaaij (1953 : 18, pl. 2, figs, 6a, b), has a basal surface superficially like that of *C. guineensis*, and specimens of *Lunulites radiata* show alternating tuberculate ridges and grooves similar to those of *C. owenii*. *Selenaria bimorphocella* (S. Australia, 1928. 9. 13. 80, and off Adelaide, 1928. 9. 13. 81, Siboga Coll.), shows radial undulating grooves with large pores, which are occluded at the centre of the zoarium, except beneath the vicarious vibracula, where they remain open. In section, these pores do not show the serial kenozoecial structure found in Group A of the Cupuladriidae (see below). The grooves exactly outline the position of the zoecia above them, and, at the periphery, show indications of distal and proximal links, which correspond in position to the distal and proximal walls of the zoecia. Thus the grooves are entirely different in nature to, and do not have the alternating relationships of, the grooves, threads, or radial sector boundaries of the Cupuladriidae, and are only secondarily radial in appearance (see Text-fig. 5B).

7 GROUPING OF SPECIES

The groups defined below do not include all the species which have been described, but formulate the correlation of various characters found to be common to some species. *C. pyriformis* and *C. indica* (see below) combine some of the characters of more than one of these groups.

The groups are arranged in order of increasing extent of cryptocystal development.

A. *C. canariensis* group. Cryptocyst simple, without denticles, central zoecia without closures by calcareous laminae. Vestibular arch absent. Basal surface consisting of rectangular sectors, with successive series of porous kenozoecial chambers. Vicarious vibracula sometimes present. (Examples: *C. canariensis* (Busk), *C. monotrema* (Busk), *C. bitorosa* Canu & Bassler).

B. *C. guineensis* group. Cryptocyst simple, without denticles, central zoecia closed by calcareous lamina developing proximally from below level of cryptocyst. Vestibular arch absent. Basal surface of hexagonal or quadrilateral sectors, with very small pores. Vicarious vibracula not present. (Examples: *C. guineensis* (Busk), *C. elongata* Sakaura².)

C. *C. owenii* group. Cryptocyst with denticles, central zoecia closed by lamina developing distally from fusion of denticles. Vestibular arch present. Basal surface with alternating ridges and grooves, tuberculate. (Examples: *C. owenii* (Busk), *C. haidingeri* (Reuss), *C. multispinata* (Canu & Bassler), *C. doma* (d'Orbigny), ? *C. misrai* (Tewari *et al.*³.)

D. *D. umbellata* group. Horizontal cryptocyst lamina complete proximally, with pores. Opesia with opesiules or opesiular indentations. Opesiae of central area closed by a complete lamina. Vestibular arch present. Basal surface with alternating grooves and ridges, or short grooves and lozenges, tuberculate. (Examples: *D. reussiana* (Manzoni), *D. umbellata* (Defrance), *D. umbellata* subsp. *depressa* (Conrad)).

There are two species which cannot be included in the groups defined above. Although superficially alike, they are probably not closely related. *C. pyriformis* has a similar cryptocyst to that found in groups A and B, but differs from both in the character of its basal surface, and in the possession of a distinct vestibular arch. *C. indica* is close to *C. guineensis*, but differs completely in the character of its basal surface; its geographical distribution is also distinct.

Cupularia capriensis Waters differs from the Cupuladriidae in important respects and is here referred to *Setosellina* (see p. 182).

² *Cupuladria elongata* Sakakura (1935: 6, pl. 1, figs. 1-3) was described with extremely elongated basa sectors, with small pores, from the Pleistocene of the Bôzô peninsula, Japan. Recent specimens from Japanese waters are all attributable to *C. guineensis*.

³ *Discoporella misrai* Tewari *et al.* (1958: 234, pl. 46, figs. 1-4, pl. 47 fig. 2), a Miocene fossil, was described to include specimens from Kutch, India, and those previously reported from the Miocene of Travancore as *Cupularia* spp. (Jacob & Sastri 1953: 348, pl. 14, figs. 5a, b, pl. 15, figs. 7a, b, pl. 16, figs. 10, 11). The specimens appear to have a denticulate cryptocyst and tuberculate basal surface.

8 *Cupuladria pyriformis* (Busk)

(Pl. 1, figs. 3, 4, Text-fig. 1C)

Cupularia pyriformis Busk, 1854: 100, pl. 124, St. Vincent (Windward Is.).*Cupuladria canariensis* (Busk): Silén (part), 1942: 14, pl. 4, figs. 15, 16, text-fig. 9, Anguilla, Leeward Is., 40-150 m. (not text-fig. 8).

LECTOTYPE, chosen here, specimen on slide B.M. 1840. 10. 23. 80 (figured by Busk, 1854, pl. 124, basal surface), St. Vincent.

LECTOPARATYPE, 1840. 10. 23. 81, on the same slide.

OTHER MATERIAL. Naturhistoriska Riksmuseet, Stockholm, FBD 533, Anguilla, Leeward Is., 45-150 m., Göes Coll., 1 specimen.

Zoarium small (3.5-4.5 mm. diameter). Cryptocyst without spines or denticles. Vestibular arch well developed. Opercula without proximal sclerite. One pair of circum-ancestrular zooecia aborted. Central zooecia closed by irregularly perforated lamina. Vibracula raised, with salient condyles. Basal surface with deep grooves and raised ridges, with very small tubercles.

DIMENSIONS. Lz 0.35-0.40 mm.; lz 0.20-0.30 mm.; Lop 0.12-0.17 mm.; lop 0.18-0.27 mm.; Lvo 0.09-0.12 mm.

C. pyriformis has been reported twice with certainty, and only 3 specimens are at present known to exist in Museum collections.

The zooecia are narrow, tapering distally, with a vestibular arch distinctly raised above the zoarial surface. The vibracula are also prominent, with narrow opesia and slightly hooked condyles. The central zooecia are closed by a thin, minutely granular lamina, originating just below the salient, shelf-like part of the cryptocyst. The lamina is perforated by 4-7 irregular pores, which in several cases are arranged parallel to the edge of the cryptocyst, but which may also be scattered.

In all 3 specimens the circle of zooecia budded by the ancestrula is unlike that of other Cupuladriidae in that pair No. 1 is nearly aborted. Each minute zoecium has a small distal vibraculum (see Text-fig. 1C). Silén (1942, text-fig. 9) showed only one abortive zoecium and did not clearly indicate its relationship to the ancestrula, but the figure shows the salient character of the vibracula.

The basal surface is deeply grooved, with sharp alternating ridges. The surface is finely tuberculate but not porous. Busk described *C. pyriformis* with basal pores, but the faint markings are in fact very small tubercles; his figure shows the other basal characters well, and they are the same in the specimen from Anguilla; unfortunately Silén's photograph does not show the ridges which are in fact present (see Pl. 1, fig. 4).

The position of the locality given by Busk for his material, "St. Vincent" ("St. Vincents" on the slide label), is open to several interpretations. Although much of the material from "St. Vincent" described in the 1854 Catalogue was from St. Vincent, Cape Verde Islands, the specimens registered as 1840. 10. 22 . . . and 23 . . . consist almost entirely of slides labelled "St. Vincents, W.I.". There is a St. Vincent Island off the west coast of Florida but the most likely locality is St. Vincent Island in the Windward Islands. This supposition is strengthened by the

occurrence of the one other specimen from the neighbouring Leeward Islands. Silén only doubtfully included this colony in *C. canariensis*, and examination of the specimen shows certainly that it belongs to *C. pyriformis*.

Studer (1889) listed specimens identified by Kirchenpauer from Madeira as *Cupularia pyriformis* Busk, on p. 7 and from near Cape Verde as *Cupularia pyriformis* Gray (sic), on p. 13. It is possible that Studer's specimens belonged either to *C. canariensis* or to *Cupuladria* sp. (Cook (in press)), which, superficially, have similar zooecial characters. Prof. E. Voigt (Geologische Staatsinstitut, Hamburg), has informed me that Kirchenpauer's specimens were almost certainly destroyed during the 1939-1945 war.

Lagaaij (1963a : 182, pl. 25, figs. 2a, b) mentioned a species of *Cupuladria*, probably related to *C. pyriformis*, from the Miocene of East Venezuela.

The character of the basal surface and the presence of a distinct vestibular arch indicate an affinity between *C. pyriformis* and the *C. owenii* group of species ; but the absence of denticles on the cryptocyst and the form of the central closures show a similarity with the *C. guineensis* group.

9 *Cupuladria indica* sp. n.

(Pl. 2, figs. 1, 2)

Cupularia umbellata Defrance : Hincks, 1887 : 125, Mergui Archipelago.

Cupuladria guineensis (Busk) : Hastings (part), 1930 : 714, 719 (specimens from Mergui, Burma).
Silén (part), 1942 : 8, pl. 4, figs. 13, 14 (specimens from locality 1, Gulf of Aden).

HOLOTYPE. Mergui, Burma, B.M. 1899. 5. 1. 23A, Hincks Coll.

PARATYPES, as above, 1899. 5. 1. 23B-H, 1899. 5. 1. 267, Hincks Coll.

OTHER MATERIAL. Mergui, 1963. 3. 18. 3, Anderson Coll.

" John Murray " Coll. (all specimens from a sandy or muddy substrate) : Stn. 80, S.E. of Muscat, 22° 13' 30" N., 59° 49' 42" E., 30.xi.33, 16-22 m., Z191A. Stn. 77, as above, 22° 13' 30" N., 59° 52' E., 421 m., Z196A. Stn. 178, N. of Somali Horn, 12° 00' 36" N., 50° 40' 06" E., 2.v.34, 91 m., Z201A (with *Anoteropora latirostris* Silén). Stn. MB I d, Hanish Is., Red Sea, 13° 39' 30" N., 42° 43' E., 17.ix.33, 29 m., Z146A and Z41E. Stn. Mb I b, as above, Z139A. Stn. MB II c, Khorya Morya Is., 17° 33' 30" N., 56° 01' 30" E., 28.x.33, 26 m., Z161A.

Naturhistoriska Riksmuseet, Stockholm, FBD 822, Gulf of Aden, 30 m. (with *Setosellina* sp.), photograph registered B.M. 1963. 3. 14. 1.

Zoarium frequently flattened, discoid, average diameter 7 mm. Cryptocyst simple, well developed laterally, descending gently, edge serrate but not denticulate. Operculum without proximal sclerite. Central zooecia closed by irregular denticles forming a lamina at the level of the cryptocyst. Basal surface with radial ridges and large, regular tubercles, no rectangular or hexagonal sectors or pores present.

DIMENSIONS. Lz 0.40-0.50 mm., av. 0.45 mm. ; lz 0.30-0.40 mm., av. 0.35 mm. ; Lop 0.25-0.30 mm., av. 0.28 mm. ; lop 0.16-0.21 mm., av. 0.19 mm. ; Lvo 0.12-0.15 mm. ; Ls 0.50-0.70 mm.

Hincks described his specimens as *C. umbellata* and his material in the British Museum was originally labelled as this species. Hincks noted that the majority of the zooecia showed "no trace of a lamina", but that the central zooecia were closed by one. The peripheral pores in the cryptocyst of the closed central zooecia in *C. indica* do somewhat resemble the opesiules of *D. umbellata*, as does the basal surface with its tuberculate ridges and grooves, of which Hincks gave a very full description.

The specimens show little variation; just over half of the zoaria are extremely flat, the remainder slightly more conical. The central closures differ from those of *C. guineensis* in that they are formed from denticles or laminae which appear to originate from the salient shelf-like edge of the descending cryptocyst, not just below it (see p. 159). This is particularly noticeable at the proximal edge of the opesia, which is the last part to be occluded. However, the later thickening results in a very similar appearance in both species. Young colonies, and those formed from regenerated fragments, have no closed zooecia. Generally, the cryptocyst is narrower than that of *C. guineensis*.

The basal surface shows little variation in the size of the tubercles, and the radial grooves are marked by a slight thread in all specimens, which distinguish *C. indica* from those specimens of *C. guineensis* which have heavy basal tuberculation.

The basal structure of *C. indica* is similar to that of the *C. owenii* group. There are no sectors, and no pores in the basal lamina, which is not thickened as in *C. guineensis*. In other respects, *C. indica* closely resembles *C. guineensis*, and its zooecial dimensions fall within the range of variation of *C. guineensis*; they are, however, consistently at the smaller end of that range.

The two species also appear to be allopatric, their geographical distributions being mutually exclusive. The occurrence of the conical *Anoteropora latirostris* and the selenariiform *Setosellina* sp. from the same stations as the lunulitiform *C. indica* illustrates the correlation between various types of free-living zoaria with a sandy or muddy substrate, as discussed by Harmer (1957 : 649).

10 *Cupuladria guineensis* (Busk)

(Pl. 1, figs. 1, 2, Pl. 2, figs. 3, 4, Text-fig. 6)

Cupularia guineensis Busk, 1854 : 98, pl. 114, figs. 1-5, New Guinea. Busk, 1884 : 206, pl. 14, fig. 6, N.E. Australia, 8 fath. Marcus, 1921 : 8, 2° 30' S., 107° 10' E., 15 Fd.

Cupularia stellata Busk, 1854 : 99, pl. 118, figs. 1-4, Philippines. Marcus 1921 : 8.

Cupularia canariensis Busk, Waters, 1885 : 308, Aldinga, Tertiary, S. Australia. 1887 : 201, Princess Charlotte Bay, N.E. Australia, 12 fath. 1921 (part) : 410. 1926 (part) : 426, pl. 18, fig. 10, Princess Charlotte Bay.

Cupuladria guineensis (Busk) Harmer, 1926 : 266, text-fig. 9, pl. 16, figs. 5-7, S. of Mindanau, 0-36 m. Canu & Bassler, 1929 : 74. Hastings, 1930 : 714 (not specimens from Mergui, = *C. indica*). 1932 : 412, Great Barrier Reef. Silén, 1938 : 366, pl. 17, fig. 119. 1941 : 61, East China Sea, 90 m. (cf. locality 7 in 1942). 1942 (part) : 8, text-figs. 5-6, pl. 3, figs. 10-12, localities 2-7 (not locality 1, pl. 4, figs. 13-14 = *C. indica*). Androsova, 1963 : 23, 39, pl. 1, fig. 3, S. China Sea.

Cupuladria intermedia Canu & Bassler, 1929 : 74. Hastings, 1932 : 412.

Cupuladria brevipora Canu & Bassler, 1929 : 74. Hastings, 1932 : 412.

- Cupuladria transversata* Canu & Bassler, 1929 : 74, 75, pl. 3, figs. 3, 4. Stn. D 5579, Borneo 175 fath., sand.
- Cupuladria dentifera* Canu & Bassler, 1929 : 74, 75, pl. 3, figs. 5-8, Stn. D 5230, Limasaua Is. 118 fath., sand.
- Cupuladria tuberosa* Canu & Bassler, 1929 : 76, pl. 4, figs. 1-4, Stns. D 5134, Sulu Archipelago, 25 fath., sand, and D 5144, Jolo, 19 fath., sand.
- Cupuladria grandis* Canu & Bassler, 1929 : 77, pl. 4, figs. 10-13, Stn. D 5161, Sulu Archipelago, 16 fath., sand.
- Cupuladria granulosa* Canu & Bassler, 1929 : 74, 78, pl. 4, figs. 5-9, Stn. D 5358, Jolo Sea, 39 fath., mud. Kataoka, 1961 : 224, pl. 30, figs. 2, 5, Pleistocene, Japan.
- Cupuladria hexagonalis* Canu & Bassler, 1929 : 74 (as *hexagona*) 78, pl. 5, figs. 1-4, Stns. D 5141, Jolo, 29 fath., sand, and D 5147, Sulu Archipelago, 21 fath., sand.
- Cupuladria microdenticulata* Kataoka, 1961 : 225, pl. 29, figs. 1, 2, Pleistocene, Japan.

HOLOTYPE, B.M. 1842. 11. 30. 14, New Guinea.

OTHER MATERIAL. Where the predominant type of basal sector present is hexagonal (see Text-fig. 6B), the specimens listed below are marked "A", where it is nearly square (see Text-fig. 6D), they are marked "B"; where pores have been seen, and where tubercles are present, the letters "P" and "T" are added.

British Museum. New Guinea 1842. 11. 30. 14 (APT). 1859. 2. 25. 11 (BP). S. of Mindanau, 15 fath. 1928. 3. 6. 74 (APT). Torres Straits 1862. 6. 5. 14 (BP), 10 fath., sand. 1882. 2. 23. 37-40 (BP). ?N. Australia 1855. 12. 27. 38 (APT), 1872. 6. 21. 21 (B). Holothuria Bank, N.W. Australia, 34 fath., 1892. 1. 28. 125 (BPT). 1963. 2. 2. 1 (BP), 1891. 12. 16. 1-4 (BP). Cossack Is., N.W. Australia, 8 fath., 1891. 12. 16. 31-37 (BP), Baudin Is., 15 fath., 1891. 12. 16. 21 (BP), 22 (BP), 23 + 24 (B + AP), 25-30 (BP + BPT), 1892. 1. 28. 128. 8-15 fath., (B + APT). Cape York N.E. Australia, 10° 30' S., 142° 18' E., 8 fath., sand, Chall. Stn. 186, 1887. 12. 9. 819 (BP). Low Is. off Port Douglas, Gt. Barrier Reef, 1932. 4. 20. 112 (BPT). Bass's Straits, S. Australia, 1899. 7. 1. 1269. Busk Coll. (BPT) Australia 1929. 5. 10. 1 (AP), 1899. 7. 1. 1252 Busk Coll. (labelled *C. stellata*). Philippines, 1854. 11. 15. 147 (type of *C. stellata*), 1899. 7. 1. 1231, Busk Coll. (AT). Philippines, Stn. D. 5161, 1931. 12. 30. 9 (AP) and Stn. D 5156, off Tinakta Is., 18 fath., 1931. 12. 30. 10 (AP) (topotypes of *C. grandis*), Canu & Bassler Coll. Sulu Archipelago, "Albatross" Stn., D5134, 1963. 3. 14. 2 (AP); Suluade Is., Stn. D 5147, 1963. 3. 14. 3 (APT); and Philippines, 26 fath., Stn. D 5181, 1963. 3. 14. 4 (AT), Bassler Coll. Photographs of type specimens from the Bassler Collection, United States National Museum, all $\times 20$. *C. transversata*, Holotype, 1963. 3. 14. 5 and paratypes, 1963. 3. 14. 6 (AP). *C. dentifera*, Cotypes, 1963. 3. 14. 7 (APT). *C. grandis*, Syntypes, 1963. 3. 14. 8 (AP). *C. granulosa*, Syntypes, 1963. 3. 14. 9 (APT). *C. hexagonalis*, Syntypes, 1963. 3. 14. 10 (APT). *C. tuberosa*, Syntypes, 1963. 3. 14. 11 (AP).

Manchester, Museum, Waters Coll. Princess Charlotte Bay, 12 and 13 fath., Australia, (BP).

Naturhistoriska Riksmuseet, Stockholm. Forty-five miles W.S.W. off Cap Jaubert, N.W. Australia, 100 m., FBS 157 (BPT), FBS 109 (BPT). S. China Sea, between Nagasaki and Hongkong 75 m., mud, FBS 904 (BPT). Malayan Archipelago, Java Sea, 2° 30' S., 107° 10' E., 27 m., FBS 639 (AT).

United States National Museum. The Museum was unable to lend material named by Canu & Bassler, but made available photographs of the type specimens (see above) and also unnamed specimens from various "Albatross" Pacific Stations, 2 of which were the same as those from which some of Canu and Bassler's species were obtained. D 5134 Sulu Archipelago, 6° 44' N., 121° 48' E., (APT) (Locality for *C. tuberosa*). D 5147 Suluade Is., Sulu Archipelago, 21 fath., (APT) (Locality for *C. hexagonalis*). D 5145, Jolo, 23 fath. (APT). D 5159, Philippines (AP). D 5181, Philippines 26 fath. (APT). D 5314, China Sea nr. Hong Kong, 122 fath. (AT).

Zoarium frequently very large (maximum observed diameter 24 mm.). Zoecia with broad tuberculate cryptocyst, opesia often almost rectangular. Operculum without a basal sclerite. Central area of zoecia closed by growth of a lamina from beneath the shelf-like salient part of the cryptocyst. Basal surface smooth or tuberculate, divided into quadrilateral or hexagonal sectors, variable. Pores present in peripheral sectors, becoming sunk in pits, occluded or hidden by tubercles.

DIMENSIONS. Lz 0.40–0.75 mm., av. 0.60 mm.; lz 0.30–0.50 mm., av. 0.40 mm.; Lop 0.30–0.40 mm., av. 0.35 mm.; lop 0.15–0.25 mm., av. 0.20 mm.; Lvo 0.12–0.20 mm.; Ls 0.5–1.5 mm.

C. guineensis was defined by Hastings (1930 : 714–5), who distinguished it from the *C. canariensis*-complex of species (Cook (in press)) by the nature of the basal surface and the extent of the cryptocyst. Of the 8 species introduced by Canu & Bassler (1929 : 74–9), two, *C. intermedia* and *C. brevipora*, were placed in the synonymy of *C. guineensis* by Hastings (1932 : 412), who also agreed with Marcus (1921 : 8) regarding *C. stellata* Busk as the young form of *C. guineensis*.

Before considering the remaining species introduced by Canu & Bassler, the characters of the material described by Busk in 1854 and 1884 must be re-examined. Two groups are evident in the large number of specimens available (see list above); these differ principally in the pattern of the basal sector boundaries, and fall very roughly, but not exclusively, into two areas of geographical distribution.

The first, more northerly form (A), is that originally described by Busk. The basal sectors are hexagonal, pierced by very small pores, which are frequently obscured by tubercles. Busk described the basal surface as "divided into hexagonal areas, each corresponding to a cell", and his fig. 3 showed irregular, tuberculate, hexagonal sectors; he did not mention the pores, which are, however, visible at the periphery of the holotype. The sectors, as described above (p. 162) do not, in fact, each correspond to a zoecium, but do have a definite relationship with the zoecia frontal to them (see Text-fig. 6). Busk's specimen from the Challenger Collection is of a second type (B), the basal sectors being quadrilateral, and the surface smooth. Pores are visible in the peripheral zoecia, which become immersed in pits and finally occluded toward the centre of the colony. The basal surface of his specimen was described by Busk "with shallow radial sulci, ridges quite flat, divided into moveable quadrangular areas, each of which has four or five shallow pits". Figure 6b showed these, and (p. 207) Busk mentioned that they might "represent occluded pores".

Busk's description of "moveable" areas may have referred to a dry, loose, basal ectocyst, which, like the calcareous surface, shows the sector boundaries, although his specimen from the Challenger Collection has no ectocyst present. However, it may perhaps have been a reference to the variation in shape of the basal sectors of other specimens Busk had examined.

Both types of basal sector may be modified by tuberculation which obscures the sector boundaries and pores. Zoaria of the B-type tend to be less tuberculated, and are also usually larger than the A-type. In several cases they show central areas with irregular and hexagonal sectors (e.g. 1891. 12. 16. 23 + 24 and 1892. 1. 28. 128).

The variation in zoecial size and proportion, the extent of the cryptocyst, and the shape of the zoecial and vibracular opesiae appear to include all the forms listed in the synonymy above. Canu & Bassler introduced *C. intermedia* for *C. guineensis* Busk, 1884, which they distinguished from the holotype by the possession of porous basal sectors. As noted above, pores are present in both A and B forms, and this is not a specific distinction. *C. brevipora* was introduced for *C. guineensis* Harmer, but the Siboga specimens are not distinct (see Hastings, 1932 : 412).

The remaining 5 species described by Canu & Bassler all have hexagonal basal sectors and are only distinguished from each other by the form of the opesiae and the degree of basal tuberculation. Silén (1942 : 8-9) remarked on the variations within the limits of the species and on the similarity of character given in Canu & Bassler's descriptions. One species was introduced on the evidence of one fragment of a zoarium (see Canu & Bassler 1929 : 75), and examination of photographs of the type specimens, and of unsorted Philippine material, shows that all 5 species fall within a continuous range of variability.

C. transversata, which was described from a single fragment, showed "a great variety of aspect of the inner face", and had a smooth basal surface with some peripheral tubercles, and pores. The figure shows a somewhat worn, moderately tuberculate colony, and photographs of the holotype (1963. 3. 14. 5, which comprises only 32 zooecia), show that it has characters extremely like those of the photographs of *C. hexagonalis*.

C. dentifera was described as differing from *C. stellata* in its tuberoso basal surface. Busk's fig. 3 shows *C. stellata* without basal tubercles, but one of the specimens numbered 1854. 11. 15. 147, is mounted on glass, and it may be seen that fine tubercles are present. Specimens from the type-locality of *C. tuberosa* show similar ranges of variation in size of colony, zooecia, opesiae and tuberculation of basal surface, as those from the type-locality of *C. hexagonalis*. Canu & Bassler's figure of the frontal surface of *C. hexagonalis* is of a worn specimen, and while some of the zoaria from Stns. D 5147 and D 5314 resemble it, others are very similar to the figures of *C. transversata*. Photographs of the cotype specimens of *C. dentifera* show that Canu & Bassler's figure (pl. 3, fig. 7) has been retouched, and that the irregular shape of the opesiae is due to the development of the cryptocyst laminae closing the zooecia.

C. granulosa, in which the sector boundaries were "scarcely visible", is an extremely tuberculated form. The specimen FBS 639 shows this type of development, but the

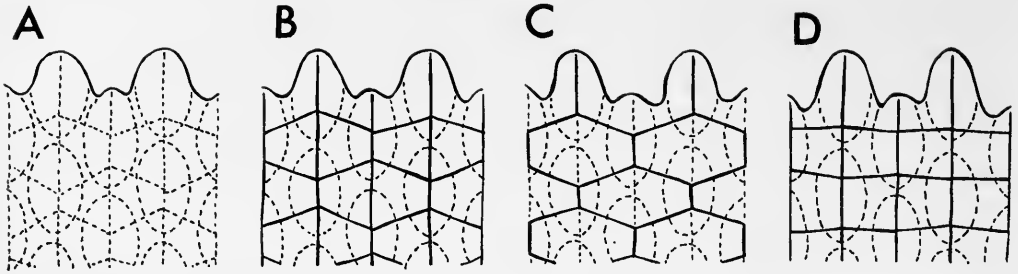


FIG. 6. Basal sectors in *Cupuladria guineensis*. Ovals in broken lines indicate the position of the frontals of the zoecia on the upper surface. A. "*C. dentifera*". Sector boundaries little developed. B. *C. guineensis*, "A" form. Hexagonal sector boundaries divided by radial boundaries. C. "*C. transversata*". Wide hexagonal sectors where the radial sector boundaries are intermittently obscured. D. *C. guineensis*, "B" form. Quadrilateral sectors.

sector boundaries may be seen at the periphery of the colony, and by lighting the surface obliquely. Heavily tuberculated variants of the *granulosa*-type are superficially similar to *C. indica*, but may be distinguished by the absence of any radial threads on the basal side (see above).

The features distinguishing *C. grandis* were its large zoarium and smooth basal surface. The largest zoaria of *C. guineensis* examined are all shallow, with square basal sectors; the topotypes of *C. grandis* are large, strongly domed, and have hexagonal sectors. Domed, B-type zoaria, of similar size (e.g. FBS 157, 18 mm.) and flatter, smaller, A-type colonies (e.g. 1928. 3. 6. 74) indicate that zoarial size and shape are not correlated with type of basal sector, although there is a tendency to reduction of tuberculation in large zoaria of both types. Canu & Bassler figured, but did not comment further on, two distinct forms of vibracular seta in *C. grandis*; "recurved" (text-fig. 13A) and "rectilinear" (text-fig. 13C). Two kinds of seta have been found in *C. canariensis* s.s., the differences in which are reflected in the calcareous parts (Cook (in press)). No sign of any such dimorphism has been seen in any of the many colonies with setae, or in the opesia of specimens of the topotypes of *C. grandis* and the other specimens attributed to *C. guineensis*. The seta in Canu & Bassler's text-fig. 13C somewhat resembles that of a regenerating seta figured by Marcus & Marcus (1962, pl. 2, fig. 7).

The variation in type and degree of calcification of the curved laminae may result in differing appearances of the basal surface. Where the hollows between the laminae are not filled in by secondary calcification, and where the pores are obscured, the surface is like that described in *C. dentifera* (see Text-fig. 6A). Where the radial sector boundaries are intermittently obscured, large, wide, hexagonal sectors are produced, as in *C. transversata* (see Text-fig. 6C). Differential development of tuberculation and pitted pores, together with the effects of wear, produce many other intermediate types of basal surface, but the characters of the zoecia are similar in all zoaria.

The specimens described as *C. granulosa* and *C. microdenticulata* by Kataoka (1961: 224, 5) appear to be referable to *C. guineensis*. The basal surface of both species had sectors, which were porous in *C. microdenticulata*, and the zooecia had the well-developed cryptocyst of *C. guineensis*.

The zoarium of *C. guineensis* attains a larger size than that of any other species in the Cupuladriidae. The largest colonies (Torres Straits 1862. 6. 5. 14 and S. China Sea FBS 904) are 24 mm. in diameter, and many of the other zoaria, especially those with square basal sectors, exceed 15 mm. in diameter.

The size of zooecia varies considerably, but the Lz does not seem to exceed 0.75 mm. and the lz 0.50 mm. The range of Lz given by Canu & Bassler for *C. transversata* includes the dimensions given for all the other species. Measurements taken from their figures indicate that the Lz for *C. dentifera*, *C. grandis* and *C. granulosa* may be as low as 0.50 mm., which is the figure given in the text for the Lz of *C. transversata*, *C. tuberosa* and *C. hexagonalis*. The opesia of these last 3 species are rectangular in contrast to the opesia of the first 3 species, which are often oval, but A-type zoaria having zooecia with both forms of opesia are present from Stn. D 5181, and B-type zoaria with the same degree of opesia variation from the Holothuria Bank 1963. 2. 2. 1, and Low Island, 1932. 4. 20. 112. Generally the more peripheral zooecia of the larger zoaria of both types tend to have more oval opesia and more steeply descending cryptocysts. Some zooecia have distinctly serrated cryptocysts.

As noted above, the vibracular setae appear to be of one kind, and are similar to those found in all other species of the family. Proportionately they are shorter than those of *Discoporella umbellata*, the larger zoaria of which approach those of *C. guineensis* in size.

Two forms of *C. guineensis* therefore exist, but the characters of each are not exclusively correlated and cannot be regarded as specific.

11 THE DISCOPORELLA UMBELLATA-COMPLEX

The characters defining species in the Cupuladriidae, where the common zoarial form determines similarity in the development of all structures, must of necessity be judged using fine criteria. To define a species adequately there must be a recognizable degree of correlation between each character considered, morphologically, geographically, and if possible, palaeontologically. In each of these respects it is possible to divide records of *D. umbellata* into two distinct groups. The problem is whether these groups are of specific or subspecific rank, and the principal criterion applied below is that of character-consistency throughout the time range of the group considered.

Canu & Bassler (1923, text-fig. 13) noted the variability of their material assigned to *D. umbellata*, and figured wide zooecia in Miocene material from Santo Domingo (pl. 2, fig. 18). The part of the zoarium figured showed the growing edge of a regenerating fragment, where the zooecia of all species are frequently wide and slightly distorted (see pp. 155, 158). Photographs of this material (1963. 3. 14. 12) show that subsequent zooecia are narrower. Canu & Bassler's figures (including fig. 17) emphasized the different appearance of Recent specimens from Oran (p. 76, text-

fig. 13A) and the increase in size of the zooecia compared with those of Miocene material from France (text-figs. 13B-C).

C. robertsoniae was introduced by Canu & Bassler for specimens named *C. canariensis* by Robertson (1908 : 314). Her figures showed narrow zooecia with 5-7 opesiules and were certainly referable to the *D. umbellata*-complex (see Hastings, 1930 : 719). In renaming Robertson's specimens Canu & Bassler were apparently aware of basic differences between "typical" *D. umbellata* and their Pleistocene material from the Pacific coast, which was included in *C. robertsoniae*, as they gave the narrow zooecia and large, proximally curved opesia as diagnostic characters. Comparison of Canu & Bassler's figures of their Pacific Pleistocene material (1923, pl. 34, figs. 5-7) with those they gave of West Indian Miocene specimens (1923, pl. 2, figs. 15-19, as *C. umbellata*) shows striking similarities and indicates a strong affinity between the two groups of specimens.

Osburn (1950 : 113) concluded that the wide range of variation found in American specimens justified their inclusion in one species with European *D. umbellata*, but apparently he did not compare his specimens with European material.

Generally, fossil material from the Miocene of Europe and America shows consistently correlated differences in character, which have become even more divergent in Recent specimens from the two areas (see Pl. 3, figs. 1-4). Applying the criteria used in defining the other species described above, the American fossils cannot be included in typical *D. umbellata*, and, as the Recent specimens differ still further, all American records have been separated here as *D. umbellata* subsp. *depressa* (Conrad).

The constant characters of the European material are the wide zooecia, the presence of a pair of opesial denticles, the proportionately large size of the vibracular opesiae, and the numerous small opesiules. There has been an increase in size in Recent specimens, where the proximal edge of the vibracular opesia is denticulate, and the smaller pores in the centre of the horizontal cryptocyst persist.

The constant characters of the American material are the narrow zooecia, the non-denticulate opesiae, with curved proximal edge, the relatively small size of the vibracular opesia, which is never denticulate, and the smaller number of large opesiules. Some fossil specimens have central cryptocystal pores, but these are rarely persistent in Recent material. In contrast to *D. umbellata*, the zooecia of fossil specimens of *D. u. depressa* are, on average, larger than those of Recent colonies.

It might be argued that the narrower zooecia of *D. u. depressa* themselves directly result in the smaller number of opesiules and the lack of central cryptocystal pores, but, as the two species exhibit similar ranges in size and shape of zoarium, there must be some inherent difference producing the narrower zooecia of *D. u. depressa*. The nature of the zooecial and vibracular opesiae are, however, not affected by conditions of growth or width of zooecia, and these are the most important features which show correlated character-consistency in the two forms.

When the *peyroti*-type zoaria listed below are included, records of *D. umbellata* show three separate mean types of population. These forms may overlap at the ends of their ranges of variation, but the Recent forms of each group are geographically distinct. By the application of a discriminant function technique to

further morphometric studies, it is intended to investigate the nature and degree of relationship of the members of this complex.

12 *Discoporella umbellata* (Defrance)

(Pl. 1, fig. 7; Pl. 3, figs. 1, 3, 5, 6; Text-fig. 4)

Lunulites umbellata Defrance, 1823: 361, pl. 47, figs. 1, 1a, 1b. "Lunulite en-parasol" de Blainville, 1834: pl. 72, fig. 1a, 1b.

Discoporella umbellata (Defrance) d'Orbigny, 1853: 473, pl. 717, figs. 1-5. Lagaaïj, 1953: 16, pl. 1, fig. 3, Miocene, Netherlands. Buge (part), 1957: 177, pl. 10, fig. 4, Miocene, S.W. France.

Discoporella berardana d'Orbigny, 1853: 474, Recent, Algeria, 14 m.

Cupularia lowei Busk, 1854: 99, pl. 116, figs. 1-6, Madeira. *C. lowei* Gray (sic) Norman, 1909: 290, pl. 37, figs. 7-12, Madeira 50-70 fath. Waters, 1921: 412, pl. 30, figs. 1-6, 26-29, Madeira.

Cupularia umbellata (Defrance): Manzoni, 1869: 26, pl. 2, fig. 16, Pliocene, Italy. 1875: 39, pl. 5, fig. 67, Miocene Italy. Calvet 1907: 393, Canaries, 80 m., and Cape Verde Islands, 1900 m. Canu, 1909: 448, pl. 16, figs. 16, 17, Burdigalien, Helvetien, Miocene, S.W. France. Waters, 1921: 414, Pliocene, Italy. Canu & Bassler, 1923: text-figs. 13A, Oran, Recent; B. C. D. E France Miocene, ?I Oran, Recent (as *C. multispinata*).

Peyroti-type zoaria: *Cupularia peyroti* Duvergier, 1921: 124. 1924: 19, pl. 1, figs. 6-10, Helvetien, Miocene, France.

Cupularia umbellata Defrance: O'Donoghue, 1924: 39, Cape St. Blaize, S. Africa.

Discoporella umbellata (Defrance) part Hastings, 1930: 719, specimens from S. Africa.

MATERIAL. British Museum. Bay of Funchal, 1892. 8. 6. 1 (type material of *C. lowei*). Madeira, 1911. 10. 1. 648, 1004 and 1963. 1. 16. 10 and 11, Norman Coll. Madeira, 1932. 8. 23. 1. Canaries, 1899. 7. 1. 1250, Busk Coll. Near Cape Frio, Angola, 12° E., 18° 30' S., 1899. 7. 1. 1241, Busk Coll. (*doma*-type zoarium).

Palaontology Dept. Coll. D. 25005, 25003, Burdigalian, L. Miocene, Bordeaux. D. 39047-96, Miocene, Reinbeck, Germany. D. 38947-9, Miocene, Beeringen. D. 39884-91 (pt), Albena, Bordighera, Pliocene, Italy.

Voigt Coll. Reinbeck, L. Miocene. Boring, Bockstedt, Middle Miocene (1 *doma*-type zoarium present).

Peyroti-type zoaria.

MATERIAL. British Museum. Cape St. Blaize, S. Africa, 1923. 7. 26. 9, O'Donoghue Coll. S. Africa, 1963. 1. 16. 9, O'Donoghue Coll. S. Africa, 34° 29' S., 21° 02' E., 26. 11. 59, 73 m., sand, SCD 114C, 1963. 1. 16. 6; 34° 29' S., 22° 18' E., 28. 8. 60, 106 m., sand, SCD 147D, 1963. 1. 16. 7; False Bay, 31. 1. 59, 50 m., FAL 341D (B), 1963. 1. 16. 8, Univ. Cape Town Ecological Survey Coll. Cape of Good Hope, 1842. 12. 2. 20, Belcher Coll. S. Africa, Cape Infanta N.E. by N½N, 13.5 miles, 43 fath., 1949. 11. 10. 618; Stalwart Point N.N.W. 9 miles, 53 fath., 1949. 11. 10. 652A; Nanquas Peak N. 46° E., 19 miles, 63 fath., 1949. 11. 10. 674A, and N.E. ¾N., 15 miles, 59 fath., 1949. 11. 10. 675 (including 2 *doma*-type zoaria), N.W. ¼N. 15 miles 49 fath., 1949. 11. 10. 668; Cape Infanta N.E. by N19 miles, 46 fath., 1949. 11. 10. 622A, 623A, N.E. by N¼N. 14.5 miles, 45 fath., 1949. 11. 10. 620; Cape St. Blaize N. 7.5 miles, 37 fath., 1949. 11. 10. 624A, 625A, 626A, 627A and 94A, N.E. ¾N. 11

miles, 40 fath., 1949. II. 10. 629; Tugela River mouth, N.N.W. 11.75 miles, 37 fath., 1949. II. 10. 644 (including 2 *doma*-type zoaria); Umtwalumi River mouth N. by W. 7 miles, 50 fath., 1949. II. 10. 651; False Island N. 8.5 miles, 53 fath., 1949. II. 10. 669A; Glendower Beacon N.½W. 6 miles, 39 fath., 1949. II. 10. 660, Burrows Coll. John Murray Coll. (all from sandy substrates). Stn. 103, 5° 39' 30" S., 39° 11' 30" E., N. of Zanzibar, II. 1. 34. 101 m., Z. 198 C. Stn. 104., 5° 37' 54" S., 39° 11' 36" E., II. 1. 34, 207 m. Z. 199A.

Zoarium usually large (maximum observed diameter 22 mm.). Zooezia often as wide as long. Opesia small, with straight proximal border with a pair of minute denticles. Operculum with a straight proximal sclerite. Descending cryptocyst wide, tuberculate, horizontal cryptocyst lamina with some small irregular central pores and 8-14 small opesiules, frequently slit-like. Vibracular opesia very large ($\times 1.75$ of Lop), finely denticulate proximally in Recent specimens. Basal surface with short grooves, pits and ridges, tuberculate, or smooth, with a layer of kenozooezia and vibracula encroaching from the frontal surface.

DIMENSIONS. Lz 0.50-0.70 mm.; lz 0.40-0.63 mm.; Lop 0.10-0.15 mm.; lop 0.12-0.20 mm.; Lo 0.10-0.11 mm.; lo 0.12-0.15 mm.; Lvo 0.18-0.25 mm.; Ls 0.6-1.45 mm.

The records of European Miocene and Pliocene specimens agree in describing and figuring *D. umbellata* with wide zooezia and a large number of opesiules. Although generally the zooezical measurements of fossils are smaller than those of Recent specimens, the proportions and general characters of the species seem constant, and are certainly distinct from those of *D. u. depressa*.

The majority of zooezia are as wide or occasionally wider than long, and the number of opesiules is most frequently between 8 and 10. DeFrance figured 8-9, d'Orbigny 10, de Blainville 8-9, and Manzoni (1869), 10-11, although the number given in 1875 was 7. In Recent specimens the number is often as many as 14, and the opesiules are slit-like. D'Orbigny described, as *D. berardana*, Recent specimens from Algeria with denticulate cryptocysts, transverse, semi-lunar orifices, and very large vibracular opesia. *D. umbellata* was figured by Canu & Bassler (1923, text-fig. 13A) from Oran, and it is possible that d'Orbigny's record referred to worn specimens of this species. Canu & Bassler's photograph of *C. multispinata* (1923, text-fig. 13I.) showed opesiules and a basal sclerite in the operculum, and is perhaps also of *D. umbellata*.

The specimens described as *C. lowei* were distinguished from *D. umbellata* by the deformation of the zoarium (see p. 158, and Marcus & Marcus, 1962 : 294).

The paired denticles on the proximal edge of the opesia are present in all well-preserved fossil and Recent material. Waters (1921 : 415) noted their occurrence, and Lagaaij (1953 : 16) included them in his diagnosis of the species.

The proximal edge of the vibracular opesia of Recent specimens is finely denticulate (see pl. 3, fig. 1), a character which has not been seen in fossil material. The vibracular opesia are extremely large, as noted by d'Orbigny (1853 : 474, in *D. berardana*), their length being significantly greater than that of the zooezical opesia.

The operculum is strongly flanged laterally, with a straight, robust, proximal sclerite.

The specimen from Cape Frio has a *doma*-type zoarium. The basal surface is solid and there are peripheral kenozoecia, but the zooecia are worn, and the character of the opesia cannot be clearly seen. However, the width of the zooecia (lz 0.3–0.48 mm.) and the number of the opesiules (5–7), are nearer the higher end of the range of variation than those of many of the corresponding *doma*-type specimens from the west Atlantic (see below), and thus reflect the differences found in zooecia of normal zoaria of the two forms. One fossil zoarium (Voigt Coll.) is also extremely worn, but shows two rows of peripheral vibracula and a basal surface almost filled by secondary calcification.

The development of the cryptocyst in the young peripheral zooecia shows the close relationship of *D. umbellata* both to *D. u. depressa* and to the denticulate species of *Cupuladria* (group C). Fine, irregular denticles grow first from the proximal and lateral edges of the cryptocyst and then develop progressively in a distal direction. At this stage the zooecia greatly resemble specimens of *C. owenii* and *C. doma*. Further calcification produces a distal bar cutting off the opesia, and, as the more proximal denticles fuse, leaving a series of denticulate, irregular opesiules, and a number of pores in the centre of the horizontal cryptocyst lamina thus formed (see also Marcus & Marcus, 1962, pl. 1, fig. 4). The appearance of the zooecia at this stage is then very similar to that of Miocene specimens of *D. u. depressa* from Oak Grove, Florida, where this type of development was the final stage. Other specimens of *D. u. depressa* from the Miocene of Cercado de Mao, Santo Domingo, show more complete calcification, with rounded opesiules and no central pores. The calcification of eastern Atlantic fossil and Recent specimens of *D. umbellata* is even greater, and the opesiules are further reduced.

The distribution of *D. umbellata* s.s. is now confined to the northern and north western coasts of Africa, and the neighbouring islands.

D. umbellata and *C. haidingeri* are frequently associated in samples from the European Miocene. When worn they are extremely difficult to distinguish from each other. The basal surface of *D. umbellata* is not as regularly grooved as that of *C. haidingeri*, and generally the zooecia of *D. umbellata* are wider. Even when the central part of the cryptocyst lamina is broken, the vestibular arch surrounding the distal part of the opesia is smaller and more incurved in *D. umbellata* than in *C. haidingeri*. At the edge of the central area of closed zooecia the most recent closed frequently show the straight bar, proximal to the opesia, which is absent in *C. haidingeri*.

Recent specimens from south and east Africa correspond almost exactly with *C. peyroti* as described by Duvergier. The dimensions he gave fall within the range of those now obtained from a large number of specimens, and the photograph shows kenozoecia exactly like those of the Recent material. In one respect, Duvergier's account may be confusing, as he followed Canu in describing the frontal, convex surface of the colony as basal, and the concave or planar kenozoecial surface as frontal. O'Donoghue mentioned the invasion of the basal surface by kenozoecia

and vibracula, and Hastings, who examined some of O'Donoghue's material, expressed doubt as to its inclusion in *D. umbellata* s.s. The Miocene specimen of *D. umbellata* figured by Buge shows a hollow basal surface covered by kenozoecia and vibracula. The specimens from south Africa show the complete range of development, those from east Africa, the young stages only. Young zoaria are flat, with a solid, smooth base, and older colonies are more domed, with the basal surface either concave (e.g. 1963. I. 16. 6-9, 1949. II. 10. 625A) or completely filled with secondary calcification (e.g. 1949. II. 10. 669A and 652A). In neither state is the surface ridged or tuberculate. The budding of the basal kenozoecia appears to be random and irregular, and the calcified cryptocyst is developed like that of the zoecia, from the fusion of irregular denticles.

The zoecial opesiae are often slightly curved proximally, and the denticles are often reduced or absent, but the opesiae are never sinuate as in *D. u. depressa*. The horizontal cryptocyst lamina differs from that of typical *D. umbellata* in the large number of frontal pores, which are often indistinguishable from the marginal opesiules. The operculum is like that of *D. umbellata*, and is flanged laterally, with a strong, straight proximal sclerite.

A few colonies combine some characters of both *doma*- and *peyroti*-type growth. They are small (diameter 2 mm.) and high, with solid, smooth bases. The peripheral zoecia are closed, but only one row of peripheral vibracula is present, and there is no invasion of the basal surface by kenozoecia. The zoecia are small, approximately half the length of zoecia in a normal colony, but the opesiae are not reduced in proportion, being about $\frac{3}{4}$ of the length of normal opesiae. The zoecia have an average of 8 opesiules and a number of irregular frontal pores in the cryptocyst. The proximal edge of some vibracular opesiae are finely denticulate. The *doma*-type colonies thus have many of the characters of the normal zoaria from the south east African coast. Their occurrence does not seem in this case to be correlated with low temperature, as all the records are confined to warm waters, extending from the warm-temperate zone, eastward to the subtropical zone, as described and discussed by Stephenson (1947 : 215).

As noted above (p. 163), no specimens of typical *D. umbellata* have been found from the south and east coasts of Africa, nor have *peyroti*-type zoaria been recorded from the west African coast. Specimens of *Cupuladria owenii* (Gray) and *C. multi-spinata* (Canu & Bassler), both of which also occur from these two areas, show no examples of *peyroti*-type growth.

13 *Discoporella umbellata* subsp. *depressa* (Conrad)

(Pl. 3, figs. 2, 4)

Lunulites depressa Conrad, 1841 : 348, Miocene, N. Carolina.

Discoporella denticulata (Conrad) Gabb & Horn, 1862 : 142, pl. 20, fig. 25, Miocene, New Jersey to S. Carolina.

- Cupularia umbellata* (Defrance) Smitt, 1873 : 14, pl. 3, figs. 75-80, Cape Fear River, N. Carolina, 7 fath. *C. umbellata* (Manz.) (sic) : Verrill, 1878 : 305. Canu & Bassler, 1918 : 118, pl. 53, figs. 2-4, 1919 : 85, pl. 1, figs. 5-7, pl. 2, figs. 17-21. 1923 : 68, pl. 2, figs. 15-19, text-fig. 10G, Lower Miocene, west Indies. 1928 : 64, pl. 7, figs. 1-3, Gulf of Mexico. 1929 : 142, pl. 15, figs. 5-11, text-figs. 35A-K (as *C. lowei*), between California and Hawaii, 2723 fath. 1930 : 11, Galapagos and Hawaii. Silén, 1942 (part) : 15, text-figs. 10-12, localities 1-17.
- Cupularia punctata* Canu, 1904 : 10, pl. 2, fig. 23, Miocene, Patagonia.
- Cupularia canariensis* Busk : Robertson, 1908 : 314, pl. 24, figs. 90, 91, California.
- Cupularia lowei* Busk : Osburn, 1914 : 194, Florida, 12 and 22 fath.
- Cupularia robertsoniae* Canu & Bassler, 1923 : 82, pl. 34, figs. 5-7, Pleistocene, California.
- Discoporella umbellata* (Defrance) Hastings, 1930 : 718, pl. 11, fig. 54, Gorgona, Galapagos, Balboa, 15-30 fath. Mcguirt, 1941 : 65, pl. 1, figs. 4, 7, 9-11, Miocene, Louisiana. Osburn, 1950 : 113, pl. 11, figs. 7-10, California to Ecuador, 5-100 fath. Soule, 1959 : 34, Gulf of California, 5-46 fath. Soule & Duff, 1957 : 99, Pleistocene, California. Marcus & Marcus, 1962 : 290, pl. 1, fig. 4, pls. 2-5, Brazilian coast, 4-150 m.

MATERIAL. British Museum. Gorgona, 1929. 4. 26. 102, 103, 106 ; Balboa, 1929. 4. 26. 104 ; Galapagos, 1929. 4. 26. 105. "St. George" Coll. Galapagos, 1933. 12. 10. 15, Canu & Bassler Coll. Abrolhos Bank, off Brazil, 1899. 7. 1. 1260, 1261 and 1265 (*doma*-type zoarium). Berbice, British Guiana, 25 fath. (21 zoaria, 4 of *doma*-type). "Terra Nova" Coll. Stn. 42, off Rio de Janeiro.

Palaeontological Dept., D 33911, D 33912, D 33916, D 33910, Miocene, San Domingo. D 41118, Bowden marl, Miocene, Jamaica. D 34392-409, Miocene, Duplin, S. Carolina.

Cheetham Coll. Miocene, Oak Grove, Okaloosa Co., Florida.

Philadelphia Academy Coll., Wilmington, N. Carolina.

Zoarium large (maximum diameter observed 18 mm.). Zooecia generally narrower than in *D. umbellata*, lateral cryptocyst descending more steeply. Horizontal cryptocyst lamina not usually porous at centre (in Recent specimens). Opesia large, curved proximally or slightly sinuate, denticles absent. Opesiules large, 3-9 in number. Operculum with delicate basal sclerite curved distally. Vibracular opesiae little larger than zoecial opesiae, not denticulate proximally. Basal surface tuberculate with grooves, or short furrows and pits.

DIMENSIONS. Lz 0.45-0.7 mm. ; lz 0.22-0.35 mm. ; Lop 0.11-0.13 mm. ; lop 0.12-0.14 mm. ; Lo 0.07-0.08 mm. ; lo 0.10-0.11 mm., Lvo 0.15-0.18 mm. ; Ls 0.60-1.10 mm.

Conrad's description of *L. depressa* mentioned that "many of the larger pores" (i.e. zooecia) were "filled with a minutely porous plate or diaphragm, solid in the centre". Specimens examined from the Miocene of Wilmington, N. Carolina, have narrow zooecia, with 7 large opesiules and an opesia with a curved proximal edge. A few central pores may be seen from the underside of the cryptocyst, but most of these are occluded by secondary calcification. Natural Well, the type locality, and Wilmington, are near the Cape Fear River, from which Smitt described the first Recent specimens from Pourtales's Collection. Canu's figure of *C. punctata* showed the frontal surface of a worn specimen ; it had the characters of *D. u. depressa*, with 3-7 opesiules, and a rounded opesia.

The magnification of some of the figures of *D. u. depressa* (as *D. umbellata*) given in

two of the works of Canu & Bassler is confusing. The same series of photographs were used throughout; but those of 1919 (pl. 2, fig. 17 (nat. size), figs. 18 ($\times 25$), 19, 20 and 21 ($\times 19$)) are smaller than those of 1923 (pl. 2, figs. 15, 16, 17, 18, 19) which are described as having the same magnification.

Osburn (1950) confirmed that Verrill's record (1878) of *D. umbellata* from Fort Macon, N. Carolina, was correct, as he had examined material from the same locality.

The zooecia of *D. u. depressa* are generally narrower than those of *D. umbellata*. The figures of American material all agree in showing narrow zooecia with large, rounded opesia and opesiules, and Soule & Duff described the zooecia as "elongate". The opesia is always curved proximally, and may be distinctly sinuate; denticles are absent. The bars between the opesiules are narrow. The proximal sclerite of the operculum is delicate and slightly curved in a distal direction. The vibracular opesia are never denticulate proximally, as in *D. umbellata*, and proportionately, they are smaller; the setae do not appear to attain the length of those of *D. umbellata*.

Most of the 7 *doma*-type colonies examined have large, rounded opesia and narrow zooecia (lz 0.20–0.35 mm.), with 2–7 opesiules, and are thus similar to more normal specimens of *D. depressa*. They differ from the *doma*-type colony of *D. umbellata* principally in their narrower zooecia and larger opesia.

14 CUPULADRIIDAE, GENERAL COMMENTS

The number of species of Cupuladriidae from the Pacific Ocean is thus two, *C. guineensis* and *D. u. depressa*, which last is confined to the eastern part. Two species occur in the Indian Ocean; *C. indica* in the north and west, and *D. umbellata* (*peyroti* form) in the south-west. Ten forms may be distinguished in the Atlantic Ocean (Cook (in press)), only the subspecies *D. u. depressa* occurring in both the Atlantic and Pacific.

The family is sharply defined, its principal characters being the distinctive astogeny, radial development and type of vibracula. Species in which any character shows a major discrepancy should be assignable to other families. This is demonstrated by examination of the characters of *Cupularia capriensis* Waters.

HINCKSINIDAE Canu & Bassler 1927

Hincksinidae Canu & Bassler, 1927: 3, Bassler, 1953: G 159, Lagaaij, 1963b: 171.

SETOSELLINA Calvet, 1906: 157

15 *Setosellina capriensis* (Waters)

(Pl. 1, figs. 5, 6)

not *Setosellina roulei* Calvet, 1907: 395, pl. 26, figs. 5, 6, Cape Verde Is., 1900 m., Capo Blanco, 2330 m.

"*Cupularia minima* (Busk MS)" Waters, 1921: 419, as *Heliodoma implicata* Calvet, specimens from the Aegean Sea. (not *H. implicata*, see below).

Setosellina roulei Calvet: Waters, 1925: 350, pl. 21, fig. 4, Capri, 50 fath.; Gautier, 1962: 69, Tunisia, 150 m., Rhone Delta, 120 m.

Cupularia capriensis Waters, 1926 : 432, pl. 18, figs. 8, 9, Capri.

Cupuladria capriensis (Waters) Marcus & Marcus, 1962 : 288.

LECTOPARATYPES, chosen here, Manchester Museum, Faraglione, Capri, 150 fath., Waters Coll.

OTHER MATERIAL. British Museum. Aegean Sea, 130 fath., 1899. 7. 1. 1253 and 5122 ; 100 fath., 1899. 7. 1. 1251, collected Spratt. Râs el-Amouch, 1899. 7. 1. 4701 ; Mediterranean, 30 fath., 1899. 7. 1. 1491, collected " Porcupine ". Busk Coll.

Zoarium small, selenariiform, free, growing on a sand-grain. Zooecia with oval opesia. Each zooecium with a distal interzooecial vibraculum, reaching the basal wall of the zoarium. Opesia of ancestrular and central area closed by a calcified lamina with a single central pore. Ancestrula with one distal and one proximal-lateral vibraculum, and surrounded by 6 zooecia, budded spirally.

DIMENSIONS. Lz 0.45-0.60 mm., av. 0.54 mm. ; lz 0.30-0.34 mm., av. 0.32 mm. ; Lop 0.32-0.35 mm., av. 0.33 mm. ; lop 0.17-0.20 mm., av. 0.19 mm.

Waters (1921) described, as *Heliodoma implicata* Calvet (1906 : 157, 1907 : 396, pl. 26, figs. 7, 10), some specimens from the Aegean Sea in the Busk Collection (1899. 7. 1. 1253). He particularly noted that the form of the zoarial spiral differed from that figured by Calvet. The zooecia of the ancestrular area of *H. implicata* are not occluded by a lamina, which is however, present in the specimens on slide 1899. 7. 1. 1253. These zoaria are identical with those from Capri described by Waters in 1926 as *Cupularia capriensis*, which has almost complete opesial closures in the ancestrular area, a small central pore only remaining open.

Waters does not at any time appear to have considered the Aegean specimens either as distinct from *H. implicata* or as identical with his new species, *C. capriensis*. His quotation of Busk's MS name for them in 1921 cannot therefore be regarded as a specific designation.

C. capriensis Waters is certainly referable to *Setosellina* Calvet. Calvet (1907 : 395) described *Setosellina roulei* with a salient calcareous lamina and figured (pl. 26, fig. 6) zooecia which were partially closed, with a small central pore. The early astogeny of specimens of *S. capriensis* was described (as *S. roulei*) by Waters (1925 : 350, pl. 21, fig. 4, Capri, 50 fath.). The budding is similar to that of *Otionella* and *Selenaria* figured by Stach (1936b : 64, text-figs. 1-7). The same type of spiral budding is found in *Setosellina constricta* (Borneo Bank, 1928. 3. 6. 75 and N. New Guinea, 1928. 3. 6. 76) described by Harmer (1926 : 264), and *S. goesi* (Silén) described by Lagaaij (1963b : 172). The basal surface of *S. capriensis* shows that the vibracular chambers are inserted between, and extend to the same depth as the zooecia. They are thus truly interzooecial, and completely unlike those found in the Cupuladriidae.

Gautier (1962 : 69) commented on the probable identity of *C. capriensis* Waters with *Setosellina roulei* Calvet. The dimensions of the abyssal specimens figured by Calvet are significantly smaller than those of *S. capriensis* given above. They average : Lz 0.36 mm. ; lz 0.25 mm. ; Lop 0.23 mm. ; lop 0.13 mm. Measurements taken from

Waters's figure of *S. roulei* from the Mediterranean (1925, pl. 21, fig. 4), combined with those given by Gautier, give a range of Lz 0.45-0.50 mm.; lz 0.32-0.35 mm.; Lop 0.25-0.28 mm.; lop 0.16-0.18 mm. These dimensions are far closer to those of *S. capriensis* given above than to those of *S. roulei* as originally described. The geographical and bathymetrical distributions of the two forms are also distinct; *S. roulei* occurring off the Cape Verde Islands at 1900 m., and off Capo Blanco at 2330 m. The larger *S. capriensis* has been recorded from the Mediterranean and Aegean only, at a greatest depth of 150 m. Until further material from both areas can be examined, all the Mediterranean records are here considered to be distinct and referable to *S. capriensis*.

S. capriensis differs from the Cupuladriidae in its early astogeny, and related to this, in the spiral development of the zoarium. The relationship of the vibracular chamber to the zooecium, and the type of opesial closure of the central zooecia, are also fundamentally different from those found in the Cupuladriidae.

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17 SUMMARY

The principal characters and mode of development of the Cupuladriidae are described and discussed, the family is defined, and groups of species with similar characters are listed. The effects of zoarial form of zooecial characters, and the occurrence and possible causes of abnormal zoaria similar to those found in *C. doma*, and those described as *C. peyroti*, are discussed. Descriptions are given of *C. pyriformis*, *C. indica* and *C. guineensis*. The complex of forms previously assigned to *D. umbellata* is examined in the light of character-consistency of fossil and Recent records. *Cupularia capriensis* Waters is described and referred to *Setosellina*.

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PLATE 1

Cupuladria, *Setosellina* and *Discoporella*

- FIG. 1. *Cupuladria guineensis* (Busk). Philippines, United States National Museum. Syntype of "*C. granulosa*", 1963. 3. 14. 9. Photograph by courtesy of the United States National Museum. $\times 14.5$.
- FIG. 2. *C. guineensis*. Philippines, United States National Museum. Cotype of "*C. dentifera*", 1963. 3. 14. 7. Photograph by courtesy of the United States National Museum. $\times 16$.
- FIG. 3. *C. pyriformis* (Busk). Anguilla, Naturhistoriska Riksmuseet, FBD 533, frontal surface. $\times 10$.
- FIG. 4. *C. pyriformis*. The same specimen, basal surface. $\times 10$.
- FIG. 5. *Setosellina capriensis* (Waters). Aegean, 1899. 7. 1. 1253pt., Busk Coll., frontal surface. $\times 17.4$.
- FIG. 6. *S. capriensis*. The same specimen, basal surface. $\times 17.4$.
- FIG. 7. *Discoporella umbellata* (Defrance). *Peyroti*-type zoarium, S. Africa, 1949. 11. 10. 94, Burrows Coll., basal surface, showing kenozoocia and vibracula growing over the basal surface. $\times 4.3$.

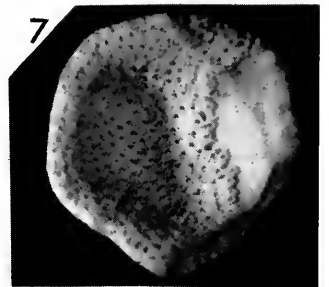
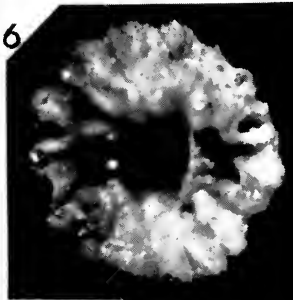
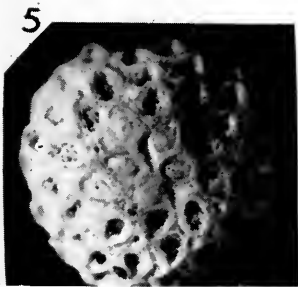
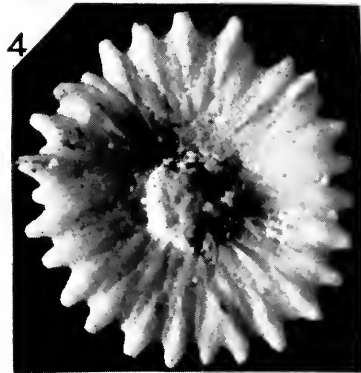
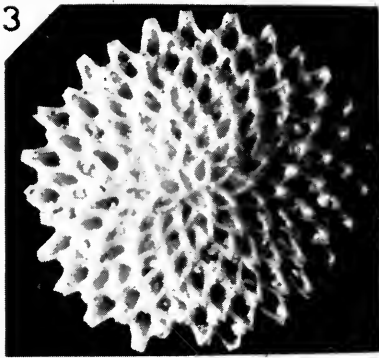
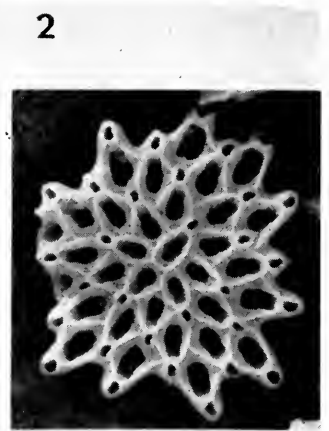
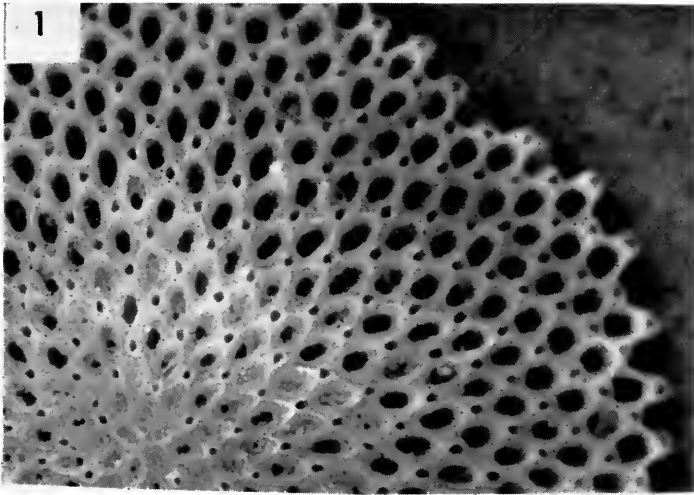


PLATE 2

Cupuladria indica and *C. guineensis*

- FIG. 1. *Cupuladria indica* n. sp. Burma, 1899. 5. 1. 267 pt., Hincks Coll., paratype, frontal surface. $\times 13.4$.
- FIG. 2. *C. indica*. The same specimen, basal surface. $\times 10.5$.
- FIG. 3. *C. guineensis* (Busk). Sulu Archipelago, 1963. 3. 14. 2, U.S.N.M. Coll. (from type-locality of "*C. tuberosa*"), frontal surface. $\times 9$.
- FIG. 4. *C. guineensis*. The same specimen, basal surface. $\times 9$.

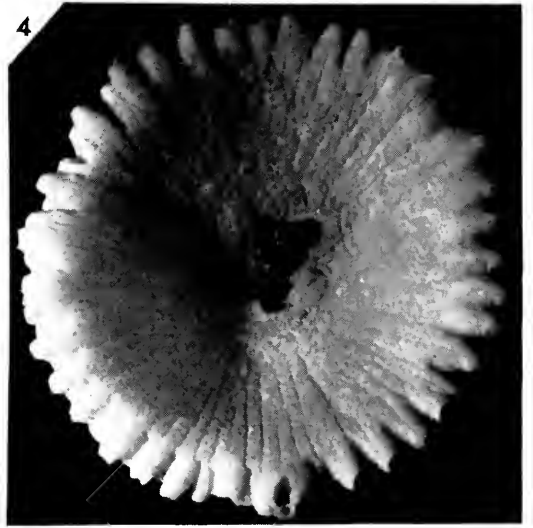
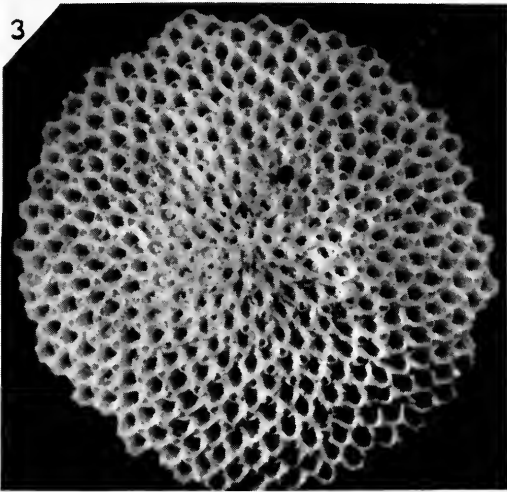
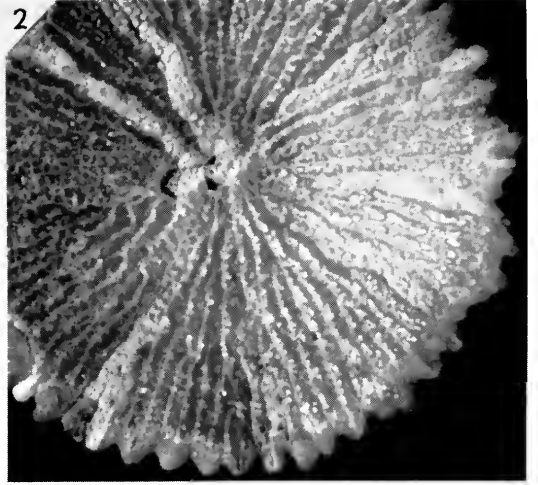
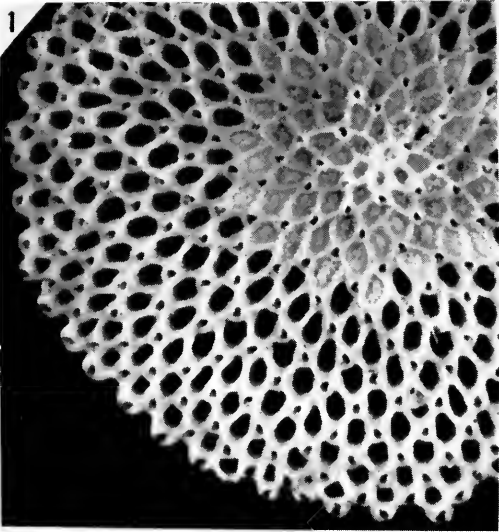
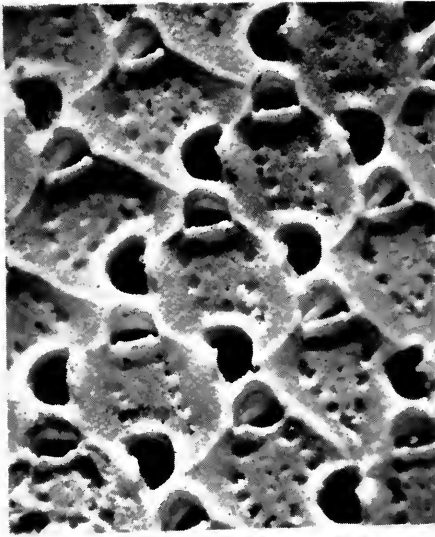


PLATE 3

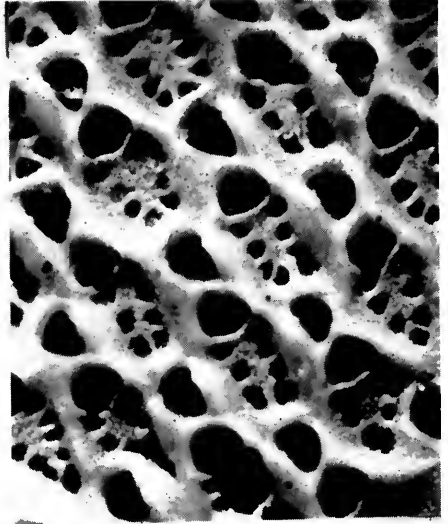
The *Discoporella umbellata*-complex

- FIG. 1. *Discoporella umbellata* (Defrance). Ghana, Achimota Coll., II, 7A. Zooecia and vibracula. $\times 40$.
- FIG. 2. *D. umbellata* subsp. *depressa* (Conrad). Rio de Janeiro, Discovery Coll., 879A. Zooecia and vibracula. $\times 55$.
- FIG. 3. *D. umbellata*. S.W. France, L. Miocene, D25003. Zooecia and vibracula. $\times 31$.
- FIG. 4. *D. umbellata* subsp. *depressa*. Florida, Miocene. Zooecia and vibracula. $\times 18.5$.
- FIG. 5. *D. umbellata*. *Peyroti*-type zoarium. S. Africa, 1949. II. 10. 94 pt., Burrows Coll. Zooecia and vibracula. $\times 43$.
- FIG. 6. *D. umbellata*. *Peyroti*-type zoarium. The same specimen, basal surface, showing kenozoecia and vibracula. $\times 37$.

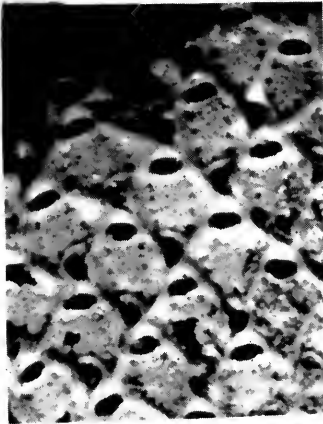
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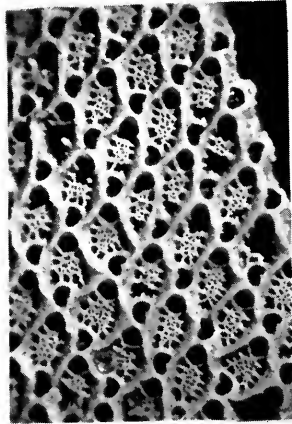
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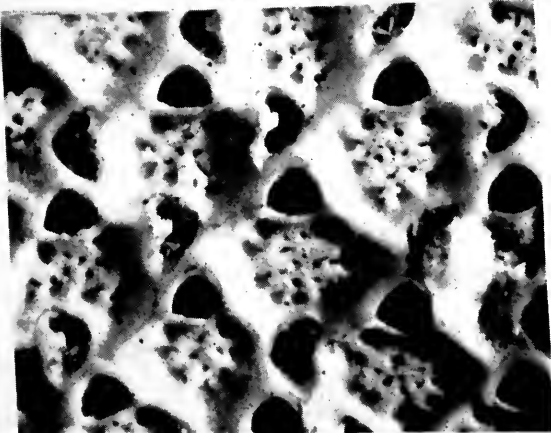
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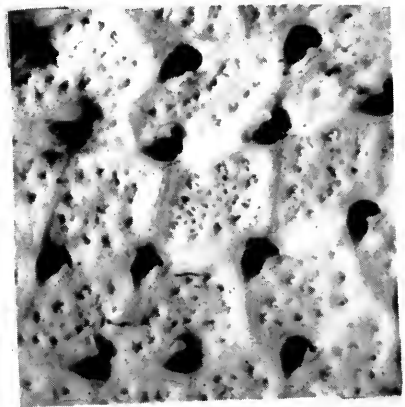
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POLYZOA FROM WEST AFRICA
THE CUPULADRIIDAE
(CHEILOSTOMATA, ANASCA)

PATRICIA L. COOK

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY

Vol. 13 No. 6

LONDON: 1965



POLYZOA FROM WEST AFRICA
THE CUPULADRIIDAE
(CHEILOSTOMATA, ANASCA)



BY

PATRICIA L. COOK

British Museum (Natural History)

Pp. 189-227 ; *Plates* 1-3 ; 4 *Text-figures*

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POLYZOA FROM WEST AFRICA

THE CUPULADRIIDAE

(CHEILOSTOMATA, ANASCA)

By PATRICIA L. COOK

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I INTRODUCTION

THE Collections from which the specimens originate have been described by Cook (1964 : 44) ; they comprise the " Calypso " Collections (Collection I from Senegal to the Bay of Biafra, Collection II from the Cape Verde Islands) ; the Marche-Marchad Collections (from Senegal) ; and the Achimota Collections (from Ghana). The Collections are rich in lunulitiform colonies belonging to the family Cupuladriidae ; 8 species occur round the west African coast, and it is estimated that approximately 2,000 colonies have been available for examination.

The lunulitiform and selenariiform types of zoarium are found among several unrelated genera of Polyzoa (see Harmer, 1926 and 1957, and Cook, 1965) ; they are both associated with sandy or muddy substrates, upon which other Polyzoa are usually unable to grow directly. Harmer (1957 : 649, 726, 885, 891 and 1009) discussed the correlation between substrate and selenariiform habit. A large number of the specimens in these Collections are known to be from a sandy or muddy bottom ; for example, those from the Achimota Collection are nearly all from stations close to, or included in, the " silty sand community " of Buchanan (1958 : 16, 26) and Bassindale (1961 : 492). Stations where the bottom is known to be of this type are marked with an asterisk in the lists of material examined. The lunulitiform zoarium

has been discussed by Waters (1921), Harmer (1926: 261 and 1957) and Lagaaij (1952: 31, 43; 1953; and 1963). Briefly it may be described as free, discoidal or subconical, with zooecia arranged in radial rows. In the Cupuladriidae each zooecium is associated with a distal vibraculum, which has a long seta.

METHODS. Colonies were treated with eau de javelle and fragments mounted dry. Others were decalcified in dilute acid, sometimes only partially, and stained to show the relationship of muscles to the calcareous parts, etc. Dry specimens were treated with trisodium phosphate solution to restore shape to shrunken chitinous parts before preparations were made.

The length of the zooecia were measured from the distal edge of the aperture to the distal edge of the next succeeding radial zooecial aperture, thus including the vibraculum.

The dimensions quoted give the range of variation of 50 measurements (where possible). Generally, measurements of the central area or of very young colonies have not been included. It is hoped to make a survey of measurements useful for specific determination, with a morphometric analysis of at least one population complex, in the near future.

The measurements made are :

Length of zooecium	Lz	Length of vibracula seta	Ls
Width of zooecium	lz	Length of vicarious seta	Lvs
Length of ancestrula		Length of operculum	Lo
(including vibraculum)	La	Width of operculum	lo
Length of vibracular opesia	Lvo	Length of opesia	Lop
Length of vicarious vibraculum	Lv	Width of opesia	lop

Definition of terms and symbols. The registration numbers of specimens in the British Museum (Zoology Department) are given thus: 1899. 7. 1 . . . ; (Palaeontological Department) thus: D 6764 . . .

Horizontal cryptocyst lamina. A porous lamina, formed from fused cryptocystal denticles, extending from the descending cryptocyst across the opesia, parallel to, and below, the frontal membrane.

Vestibular arch. The distal, raised portion of the aperture. Usually accompanied in the Cupuladriidae by a pair of distal cryptocystal denticles.

Vicarious vibraculum. A large vibracular individual, taking the place of a zooecium, and itself having a distal vibraculum.

In the lists of material examined, the presence of vicarious vibracula is indicated thus: (V); of Acrothoracid Cirripedes thus: (C), see p. 194; and of a sandy or muddy substrate thus: *.

2 CUPULADRIIDAE Lagaaij

Cupuladriidae Lagaaij, 1952: 31. Cook, 1965: 154.

The series of species described below links the membraniporan forms assigned to *Cupuladria* with the microporan forms represented by *Discoporella*, and both genera have therefore been placed in the family Cupuladriidae.

Diagnosis. Lunulitiform *Anasca* with vibracula alternating with zooecia in the same radial series. Ancestrula surrounded by seven zooecia and a distal vibraculum. Cryptocyst variously developed. Ovicells absent.

The systematic position of the two genera here included in the Cupuladriidae has been discussed by Canu & Bassler (1923 : 75), Harmer (1926 : 266), Hastings (1930 : 714, 717), Lagaaij (1952 : 32, and 1953), Marcus & Marcus (1962), and Cook (1965 : 154). Bassler (1953) placed *Cupuladria* in the Membraniporidae (p. G 156) and *Discoporella* in the Calpensiidae (p. G 171), but the small distinction between the membraniporan and microporan forms had already been indicated by Canu & Bassler (1923 : 75) who remarked "The union of spines is not a generic character. In fact it may be accidental (*Cupuladria denticulata*), partial (*Cupuladria reussiana*), almost complete (*Cupuladria umbellata*)". *D. ocellata* n. sp. links the irregular opesiular indentations and fused cryptocystal denticles typical of *D. reussiana* with the microporan *D. umbellata* (see p. 221).

3 GENERAL NOTES ON LUNULITIFORM COLONIES

a. *Budding*. The method of budding and development of lunulitiform colonies has been discussed by Silén (1942 : 7-13), Lagaaij (1963) and Cook (1965 : 155), and the regeneration of broken colonies by Dartevelle (1935 : 559-561). A large number of the colonies in these collections are regenerated from broken fragments; approximately 80% of *D. umbellata* in the "Calypso" Collection are of this type, as are many specimens of the other species. It is interesting that the drawings of *C. owenii* by Gray (1828, pl. 3, figs. 15a) and of *D. umbellata* by d'Orbigny (1853, pl. 717, figs. 3, 4) are of regenerated colonies.

b. *Sexual reproduction*. Ovicells are absent; large eggs ("about 0.5 mm. long"), were seen in *C. canariensis* and *C. doma* (as *C. johnsoni*) by Waters (1921 : 404 and 414), and smaller eggs, which may not have been fully developed, by Hastings (1930 : 726) in *D. umbellata depressa* (as *D. umbellata*). These eggs (Gorgona, 1929. 4. 26. 103 pt.), have an average diameter of 0.05 mm. (9% of Lz); those found in zooecia of *C. multispinata* (Stn. 299, Cape Verde Is., Discovery Coll.), have an average diameter of 0.30 mm. (45% of Lz). Eggs in *C. owenii disciformis* ("Calypso" Coll., C47A) average 0.20 mm. (60% of Lz), and one egg in *C. biporosa* ("Calypso" Coll., C49G) has a diameter of 0.20 mm. (50% of Lz). The date of breeding shows great variation and is probably dependent upon several unknown factors. Marcus & Marcus (1962 : 297) found no evidence of germ cells in material from the Brazilian coast collected in December, January, March, April, June and August. The "Calypso" specimen of *C. biporosa* was breeding on 26th May and that of *C. owenii disciformis* on 26th July, 1956. The Madeiran *C. doma* described by Waters was received from Norman, who collected in March and May (see Norman, 1909 : 275). The fertile *C. multispinata* from the Cape Verde Islands was collected on 4th September, 1927, and Hastings's *D. umbellata depressa* from Gorgona, was breeding in July, 1924. Specimens of *D. umbellata* collected in March, 1963, from Funchal, Madeira, were not breeding,

but one very young, recently settled, colony was found. This suggests that perhaps the breeding season here was in early spring.

Generally, the present evidence is that the eggs of the membraniporan and denticulate species are larger than those of the microporan species. This may be connected with the development of the cryptocyst and the size of the opesia, but until observations are made upon living, breeding colonies, the importance of these differences cannot be assessed. The relatively large size of some of the eggs may indicate that the larvae have a yolk and therefore a short free-living existence; but Lagaaij (1963 : 178) considered that the larval life may persist for some time. Settlement is upon a sand grain, small stone, or Foraminiferan shell, and the ancestrula buds one proximal, a pair of proximal-lateral zooecia, and a distal vibraculum. A pair of lateral zooecia follows, and the ancestrular area is later completed by a pair of distal-lateral zooecia (see Lagaaij, 1963, text-fig. 10; and Cook, 1965, text-fig. 1B).

c. *Mode of life.* The mode of life of lunulitiform colonies was virtually unknown, but living specimens have now been observed (Marcus & Marcus, 1962; and Cook, 1963). Their orientation is normally with the zooecial face upward. All the evidence at present available indicates that colonies belonging to the Cupuladriidae, at least, are not capable of free-swimming movement through the water, but are maintained by their peripheral vibracular setae in a position just above the surface of the substrate. The zooecia of the central area do not appear to have either a "hydrostatic" or "radicular" function (cf. Canu & Bassler, 1920 : 75, 1923 : 238, and 1929 : 144). The single instance of 9 colonies being taken at the surface was recorded by Silén (1942 : 13, in the Atlantic, 1881, 27° 16' N., 23° 21' W.), who commented on the lack of any similar occurrence. These specimens have been re-examined (see p. 207). All have vibracular setae and intact frontal membranes; the zooecia have polypides. They were therefore presumably alive when collected, but I agree with Silén, who later remarked (1947 : 10), "the free, swimming life of *C. canariensis* is not at present to be accepted as proved fact".

d. *Associated Cirripede.* West African Cupuladriidae are often hosts to individuals of an Acrothoracid Cirripede, the presence of which is indicated on the basal side of the colony by slightly thicker calcification, which in *C. canariensis* obscures the basal kenozoocial pores. On the frontal side a slit, surrounded by a calcified border, marks the opening through which the cirri of the Acrothoracid protrude for feeding (see Pl. 3, fig. 3). Members of this group of Cirripedes have been reported from localities including Cadiz and South Africa (see Utinomi, 1950 : 5), inhabiting barnacle plates and corals, and producing similar slit openings in these hosts. Most of the slits are found near the central area of the colony. The majority of Acrothoracid specimens have been found in large colonies of *C. canariensis* and *D. umbellata*, but they also occur in *C. multispinata*, *C. doma* and *D. reussiana*. Other conical zoaria with slits evidently made by similar Acrothoracids are those of *Selenaria maculata* Busk (Bass's Straits, 1854. 11. 15. 52, incinerated specimen) and *Stylopoma duboisii* (Audouin) (Holothuria Bank, 1892. 1. 28. 43, see Cook, 1965a, in press).

The majority of other Polyzoa of the silty sand community encrust the large Foraminiferan, *Jullienella foetida*, which has an argillaceous test. Neither these nor

the associated large, erect branching Polyzoan colonies of *Metrarabdotos unguiculatum* Canu & Bassler and *Cleidochasma oranense* (Waters), show any evidence of being inhabited by the Acrothoracid Cirripede.

Without observation of living specimens it is difficult to establish whether the association described above is one of symbiosis, commensalism or parasitism, but it should be noted that many of the zooecia surrounding the slit and thus directly overlying the cavity containing the Acrothoracid appear to be unaffected, and have well-developed polypides. The successful functioning of the Cirripede suggests that the Polyzoan zoarium has a degree of stability surprising in an unattached organism. Inhabited specimens are marked in the lists of material examined thus, (C).

e. *Epifauna*. The colony may provide a substrate for the settlement of larvae of species of Polyzoa which would otherwise not be able to establish themselves successfully in a sandy or muddy habitat. Osburn (1914 : 190) described *Beania cupulariensis* and (1950 : 176) *Membraniporella pulchra*, growing on the basal side of colonies of *Cupuladria*, and Soule (1959 : 22) reported *Chaperiella condylata* on *C. canariensis* and *D. umbellata*. *Smittipora levinseni* (Canu & Bassler) has been found on *C. canariensis* from the "Calypso" Coll. (C 72B), and a specimen of *Onychocella angulosa* (Reuss) budded from a central ancestrula completely covers the frontal surface of a colony of *C. biporosa* from the Canaries (1962. 10. 8. 7), the peripheral zooecia of which can be seen beneath the growing edge of the *Onychocella*.

The colonies are frequently the substrate for other groups, notably small barnacles, tube-worms, hydroids and sponges. The barnacles and worms are found on the basal side of zoaria with a well domed cavity, where there is presumably sufficient room for their cirri and branchiae to be protruded. Hydroid stolons are found on the frontal surface, running between the zooecia, and sponges on the basal side. Apparently these last may cause deformation of the zoaria, by the suppression of growth of one or more radial rows of zooecia. *C. multispinata* (see p. 210) was referred to by Waters (1921 : 413) under Busk's MS. name, *Cupularia deformis*, and specimens labelled "*C. deformis*" by Busk nearly all show fragments of sponges covering the area where the zooecia have failed to develop. Deformed colonies of *D. umbellata* were described as *C. lowei* by Waters, and his type-material and other specimens in the British Museum Coll. have sponge colonies on the basal side. Zoaria of *D. umbellata* ("Calypso" Coll. C56G and Marche-Marchad Coll. I 39D) are also covered basally with a sponge belonging to the Plocamiidae. Here the sponge appears to prevent the connection of the intercalary rows of zooecia produced on either side of the abortive row; the sponge eventually lines the radial slit thus produced. This may, of course, be a secondary effect, but the correlation of the occurrence of deformity and sponges is significant (see Cook, 1965 : 158).

The geographical, bathymetrical and palaeontological distribution of the Cupuladriidae is very wide. Recent specimens of *C. canariensis* have been found from the S.W. Mediterranean to the Gulf of Mexico; "*D. umbellata*" has been reported from a depth of 2,723 fathoms (Canu & Bassler, 1929 : 144); and the majority of the species have also been recorded from the Tertiary, *D. reussiana* and *D. umbellata* having originally been described as fossils.

4 KEY TO THE SPECIES OF CUPULADRIIDAE DESCRIBED BELOW

Note on the identification of worn specimens. Lunulitiform colonies are frequently found to be worn and identification under these conditions is extremely difficult. Lagaij (1952 : 34 and 1953 : 13) stressed the importance of the character of the basal surface, which is less susceptible to wear, and this is emphasized in the following key. Characters not found in fossil or worn specimens are placed in parentheses. All other features have been found to be present in a few zoecia at least of moderately worn Recent and fossil specimens examined.

- | | | |
|----|---|---|
| 1 | Basal surface divided by radial and tangential boundaries into sectors | 2 |
| - | Basal surface not divided into sectors | 4 |
| 2 | Basal sectors nearly always (95%) small, square, with 1-6 pores, vicarious vibracula frequently present (Operculum longer than wide). | 3 |
| - | Basal sectors irregular, majority (75%) long with 6-20 pores. Vicarious vibracula infrequent, zoecial vibracula of two kinds. (Operculum wider than long) | |
| | <i>C. canariensis</i> (p. 197) | |
| 3 | Basal sectors with 1-3 pores per sector, one layer only of basal kenozoecia, vicarious vibracula present throughout colony. (Operculum within a thickened area of the frontal membrane) | <i>C. monotrema</i> (p. 209) |
| - | Basal sectors with 1-6 pores per sector, basal surface frequently filled in by many layers of kenozoecia, vicarious vibracula near central area. (Operculum longer than wide) | <i>C. biporosa</i> (p. 203) |
| 4 | Colonies small (3-7 mm. diameter), steep-sided, solid basally, or with a small concavity lined with spinous tubercles. Peripheral zoecia closed, several rows of enlarged peripheral vibracula present. (Operculum with incomplete proximal sclerite) | <i>C. doma</i> ¹ (p. 216) |
| - | Colonies flatter, concave basally. Cryptocyst with denticles and spinules, or with horizontal cryptocyst lamina formed of fused denticles | 5 |
| 5 | Cryptocyst denticles fused to form horizontal cryptocyst lamina, with pores | <i>(Discoporella)</i> 6 |
| - | Cryptocyst denticles not fused to form horizontal cryptocyst lamina | 8 |
| 6 | Opesia small with a pair of closed opesiules | 7 |
| - | Opesia with a pair of opesiular indentations, trifoliolate. Zoarium high. Basal surface with large tubercles | <i>D. reussiana</i> (p. 219) |
| 7 | Opesia sinuate proximally, cryptocyst with a few large pores. Basal surface tuberculate with radial threads. (Operculum without a proximal sclerite) | <i>D. ocellata</i> (p. 220) |
| 8 | Opesia straight proximally with a pair of small denticles, basal surface tuberculate with pits and grooves. (Operculum with a proximal sclerite) | <i>D. umbellata</i> (p. 221) |
| 9 | Zoecia small Lz 0.37-0.47 mm., sides of vestibular arch convergent. Cryptocyst with large distal denticles. Basal surface with very small, regular tubercles, or smooth and glassy. (Operculum longer than wide) | <i>C. owenii</i> (p. 213) |
| - | Sides of vestibular arch straighter, distal denticles not well developed. (Operculum not longer than wide) | 9 |
| 10 | Zoecia large, Lz 0.55-0.76 mm., denticles spinulose. Basal surface with large, irregular tubercles and salient threads. (Operculum as long as wide) | <i>C. multispinata</i> (p. 210) |

¹ Small, *doma*-type zoaria may occur in *C. biporosa*, *C. owenii* and *D. umbellata* (see Cook, 1965 : 162). *C. biporosa* may be distinguished here by the basal surface (fork 1), *C. owenii* by the absence of closed peripheral zoecia and of a proximal sclerite in the operculum (fork 4), and *D. umbellata* by the presence of a complete horizontal cryptocyst lamina (fork 4).

- Zoarium flat, zoecia smaller, Lz 0.37–0.53 mm., denticles small, simple, few. Basal surface with small regular tubercles. (Operculum wider than long)

C. owenii subsp. *disciformis* (p. 215)

5 *CUPULADRIA* Canu & Bassler

Cupuladria Canu & Bassler, 1919 : 77, 1920 : 103. Hastings, 1930 : 718. Lagaaïj, 1952 : 32. Cheetham & Sandberg, 1964 : 1020.

TYPE SPECIES. *Cupularia canariensis* Busk, Madeira, Recent.

Zoarium lunulitiform. Zoecia with cryptocyst variously developed, frequently with denticles, which do not normally fuse. Vibraculum distal to each zoecium. Vicarious vibracula and basal sectors present in some species.

Vicarious vibracula have been found to occur only in the *C. canariensis* group of species (group A, Cook, 1965 : 167). They are marked in the lists of material examined thus : (V).

6 *Cupuladria canariensis* (Busk)

(Pl. 1, figs. 1A, B, Pl. 3, fig. 4, Text-figs. 1a–f)

Cupularia canariensis Busk (part), 1859a : 66 (not pl. 23, figs. 7, 8 = *C. biporosa* see p. 203), Madeira, Canaries.

Cupularia canariensis Busk : Manzoni, 1869 : 26, pl. 2, fig. 17, Pliocene, Italy. 1877 : 24, pl. 17, figs. 5a, b, c, Miocene, Austria and Hungary.

?*Membranipora canariensis* (Busk) Smitt (part), 1888 : 79, text-fig. 326, 120 fath. and over, Florida.

?*Cupularia canariensis* Busk : Angelis (part), 1899 : xxxiii, pl. B, figs. 7, 8, Pliocene, Spain (not fig. 6 = ?*C. biporosa*).

Cupularia canariensis Busk : Neviani 1891 : 130, Post Pliocene, Italy. 1895 : 101, Miocene, Italy.

?*Cupularia canariensis* Busk : Calvet (part), 1907 : 393, Canaries and Cap Blanc, 80–259 m.

Cupularia guineensis Busk : Norman (part), 1909 : 289, pl. 37, figs. 3 and 6, Madeira (not figs. 4, 5 = *C. biporosa*).

?*Cupularia guineensis* Busk : Osburn (part), 1914 : 195, Tortugas Islands, Florida, 10 fath.

?*Cupularia canariensis* Busk : Faura & Canu (part), 1916 : 133, Miocene, Spain (not pl. 3, fig. 8).

Cupularia canariensis Busk : Canu, 1917 : 137, pl. 3, figs. 4–6, Burdigalien, L. Miocene, France.

Cupularia canariensis Busk : Waters (part), 1921 : 410 pl. 30, figs. 11, 12 Liberia, (not pl. 29, fig. 15 = *C. biporosa*).

Cupuladria canariensis (Busk) : Canu & Bassler (part), 1928 : 16, pl. 1, figs. 7–9, Recent, Gulf of Mexico (not text-fig. 2 = *C. biporosa*).

Cupuladria canariensis (Busk) : Darteville, 1935 : 560, pl. 19, figs. 1, 2, Ràs el-Amouch, Algeria.

Cupuladria canariensis (Busk) : Silén (part), 1942 : 13, Pliocene, Italy ; Recent, Azores, West Indies (not text-fig. 8 = *C. biporosa* ; not text-fig. 9, pl. 4, figs. 15, 16 = *C. pyriformis*).

Cupuladria canariensis (Busk) : Lagaaïj, 1952 : 33, pl. 2, figs. 1a, b, Pliocene, Netherlands. 1953 : 15, pl. 1, fig. 1, Miocene, Pliocene, Netherlands.

Cupuladria canariensis (Busk) : Buge, 1957 : 139, pl. 9, fig. 5, Miocene, S.W. France (not pl. 10, fig. 3).

Cupuladria canariensis (Busk) : Gautier, 1962 : 53, Algeria, 100–300 m.

Cupuladria canariensis (Busk) : Lagaaïj, (part), 1963, pl. 25, figs. 1, 3–5, pl. 26, figs. 2, ?3.

Cupuladria canariensis (Busk) Annoscia, 1963 : 225, pl. 9, fig. 1, pl. 10, fig. 1, pl. 11, figs. 1a, 1b, pl. 12, figs. 1a, 1b, Quaternary, Italy.

Cupuladria canariensis (Busk) Cheetham & Sandberg, 1964 : 1021, text-figs. 11, 13, Quaternary, Louisiana.

MATERIAL. LECTOTYPE (chosen here), the top left-hand specimen on the slide B.M. 1899. 7. 1. 4697 (A), Busk Coll., M'Andrew, Canaries. Lectoparatypes, the top right-hand specimen on the same slide and 1962. 1. 24. 3, Busk Coll., M'Andrew, Canaries.

"Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C4F. Stn. 17*, 5° N., 5° 28' 30" W., 21.v.56, 27 m., C56J (C). Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49B (V). Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48B (V).

Coll. II. Stn. 24, 15° 16' 34" N., 23° 47' 44" W., 18.xi.59, 55-60 m., C86A. Stn. 26, Ile Sao Tiago, 15° 16' 30" N., 23° 47' 31" W., 18.xi.59, 50-65 m., C65G. Stn. 73, C72B (V).

Marche-Marchard Coll. I. Konakrey, Guinée Ise., 1F, 2E. Flor de la bouteille, Guinée Ise., 21.i.53, 8 m., 3B (V). Baie de Gorée, 1954, 46-48 m., 6B. Sud de Gorée, 27.x.53, 38-42 m., 7B (CV); and 24.ii.53, 40-41 m., 11H (CV). S.W. Madeleines, 15.ix.53, 48 m., 20B; 45-46 m., 26G; and 21.i.54, 46-48 m., 46E (V). Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 29A (CV), 33C (V). Baie de Seminoles, Gorée, 8.xii.53, 38 m., 39C (V).

Coll. II. Baie de Gorée, 9.ix.55, 190-220 m., 3A (V); and 210-220 m., 33A (V). S.W. large du Cap Vert, 9.ix.55, 100 m., 11A (V), 14E (V). Banque de Fagaque (Joal), 15.v.53, 5 m., 15A. S.W. Madeleines, 9.i.54, 47.5 m., 31D; and 15.ix.53, 48 m., 40A (V). Devant le Cap Manuel, Oct., 1952, 35 m., 37A (CV).

Coll. III. Sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1C (V). Sud de Gorée, 13.xi.53, 33-35 m., 9B; and 34-37 m., 17B. Either as above, 34-37 m., or S.W. Madeleines, 15.ix.53, 48 m., 16E. Dragage 1 "Gerard Freca" 18.ii.54, 23F, dragage 4, 97 m., 28G; dragage, 5, 15B. 27.xi.53, 33-34 m., 29C. No information 24G.

Achimota Coll. I, Stn. 69, Dredge haul No. 5, 22.i.51, 22 m., 90.III.C.

British Museum Coll. Madeira, 1912. 12. 21. 1002 (V), 1911. 10. 1. 647 (V) and 1962. 1. 28. 2 (V), Norman Coll. Bay of Funchal, Madeira, 1962. 1. 28. 1 (V), Norman Coll; 50 m., 1963. 2. 28. 10 Cook Coll., mud*. Tangier Bay, 35 fath., 1899. 7. 1. 1225-1229, Busk Coll. Râs el-Amouch, Algeria, 45 fath. and upward, "Porcupine", 1899. 7. 1. 84, 41 fath. 1226; 45 fath., 1222, 1264 and 1228; 4693 and 4694, Busk Coll. Mediterranean, 45 fath., 1899. 7. 1. 1223 and 1230, Busk Coll. Cape Rosa, Algeria, 95 fath., 1899. 7. 1. 1227, Busk Coll. Cape Sagraas, Portugal, 1899. 7. 1. 1221, Busk Coll. West Indies, "Blake", 1879, 1911. 10. 1. 1722, Norman Coll. Barbados, 73 fath., 9.iii.79, and 23° 13' N., 89° 10' W., 84 fath., "Blake" 1911. 10. 1. 644, Norman Coll. St. James Coast, Barbados, 1962. 1. 26. 2, Saunders Coll. Gulf of Mexico, 28° 58' N., 89° 9' W., mud lump SP 5, 1961. 11. 2. 49A, Cheetham Coll.

"Discovery" Coll., Stn. 279, off Cape Lopez, 10.vii.27, 58-67 m., mud and fine sand*, (CV).

Waters Coll. Manchester Museum. Four slides from Oran, 1 slide from "Post Pliocene", Pisa.

Naturhistoriska Riksmuseet, Stockholm Coll. (numbers in Silén, 1942: 13-14 in parentheses). St. Agata, Piemonte, Italy, Pliocene, FBD 737 (No. 2). Azores, off

Punta Delgada, FBS, 964 (No. 6). West Indies, 52 miles off Florida, 40 m., FBD 548, 1 specimen only (No. 16).

Specimens from Dr. R. Lagaaij. Beeringen, Netherlands, Miocene. Karsy, Poland, Miocene. Antwerp, Belgium, Pliocene. Gulf of Mexico "Atlantis" Stn. 161, 22 fath., Recent.

Specimens from Prof. Voigt. Rostej Banat, M. Miocene. Hamburg, Miocene. Pinneberg, nr. Hamburg. U. Miocene.

Zoarium frequently large (maximum diameter measured, 23 mm.). Cryptocyst narrow, descending steeply, finely tuberculate, not thickened in central zoecia. Operculum slightly wider than long with no proximal sclerite. Zoecial vibracula of two kinds, one with a short hooked seta. Vicarious vibracula sometimes present surrounding ancestrula, and in the central area, with a short, stout hooked seta. Basal surface divided into irregular rectangular sectors, the majority long, with from 4-20 pores (usually 6-12). Tentacles 17-19 (see p. 203).

DIMENSIONS. Lz 0.50-0.80 mm., lz 0.30-0.47 mm., La 0.45-0.60 mm., Lvo 0.12-0.19 mm., Lv 0.32-0.45 mm., Ls 0.70-1.50 mm., Lvs 0.17-0.30 mm., Lo 0.10-0.13 mm., lo 0.12-0.15 mm., Lop 0.35-0.47 mm., lop 0.21-0.32 mm.

Lagaaij (1952 : 33) first chose Busk's slide (B.M. 1899. 7. 1. 4697) as lectotype of *C. canariensis*, but did not indicate upon which of the 6 specimens present his description was based. The two specimens chosen above as lectotype and lectoparatype are definitely *C. canariensis* as described by Lagaaij, and as generally understood by European authors; although only part of Busk's description and neither of his magnified figures (1859a, pl. 23, figs. 7, 8) refer to this species. I have here followed the Recommendation 74A of the International Code of Zoological Nomenclature (1961 : 79), with regard to the "agreement with previous restriction" of the species.

Smitt² (1888 : 79, text-fig. 326) recorded *Membranipora canariensis* from 120 fathoms and over, from Florida. The figured colony is 18 mm. in diameter, and as *C. biporosa* does not appear to attain this size, is perhaps *C. canariensis*. Specimens sent to Norman by Smitt, from the "Blake" Collection from the West Indies, consist of a mixture of *C. canariensis* and *C. biporosa*, and presumably Smitt's record refers to both species, as perhaps does Osburn's from the Tortugas Islands, where some of the specimens were very large (0.75 in.). Calvet (1907 : 393) included "*C. guineensis* Kirkpatrick"³ (sic) in his synonymy; it may be presumed that part of his material, at least, was true *C. canariensis*.

Waters (1921 : 399) received material from Norman, whose figures (1909, pl. 37, figs. 3 and 6) are of *C. canariensis*. Norman's specimens from Madeira in the British Museum consist of a mixture of *C. canariensis* and *C. biporosa*.

The material described by Dartevelle is *C. canariensis* (Ràs el-Amouch, 1899. 7. 1. 84, Busk Coll.), and shows the method of budding of zoecia from a broken fragment particularly well.

² For Smitt's authorship see Agassiz, 1888 : xxi.

³ Kirkpatrick (1890 : 612) only listed *C. guineensis* from the Torres Straits, his record is certainly not *C. canariensis* (see Hastings, 1930 : 714).

Much of the material listed by Silén (1942 : 13-14) has been re-examined, namely specimens from localities 2, 6, 7, 8, 9, 10, 15, 16 and 18. Of these, specimens 2 and 6, and one of the zoaria from 16, are *C. canariensis*. The remaining specimens belong to three other species, *C. biporosa* and *C. owenii* (see pp. 203 and 213 below), and *C. pyriformis* (Busk). Silén expressed doubt as to the identity of specimen 18, from Anguilla, West Indies ; it is certainly referable to *C. pyriformis* (see Cook 1965 : 168).

The figures given by Canu & Bassler (1928) of specimens from the Gulf of Mexico are all of *C. canariensis* with the exception of text-fig. 2, of an operculum, which shows the elongated appearance typical of *C. biporosa*. Presumably their Recent material consisted of both species.

The figures of *C. canariensis* given by Manzoni (1869, Pliocene, Italy), Manzoni (1877, Miocene, Austria and Hungary) and Canu (1917, Lower Miocene, France) all show steeply descending cryptocysts and long basal sectors. Neviani (1895) recorded large colonies (2 cm. diameter) from the Italian Miocene, and (1891) had mentioned the elongated basal sectors with numerous pores of his post-Pliocene specimens. Both the specimens from the European Pliocene and Miocene lent by Dr. Lagaaij, and his description and figures (1952 and 1953) have the same consistent characters and thus contrast significantly with the figures of American Miocene specimens given by Canu & Bassler (see p. 206), all of which are attributable to *C. biporosa*. Buge (1957 : 177) stated that the figure of the basal side (as "face supérieure non zoéciale") of *D. umbellata* given by D'Orbigny (1853, pl. 717, fig. 4) was in reality of *C. canariensis*, and showed "secteurs radiaux avec pores". D'Orbigny's figure shows radial grooves typical of *D. umbellata*, and irregular tubercles, with no sign of tangential sector boundaries or biserial pores. It is, moreover, in outline, a mirror image of figure 3, which shows the frontal surface of *D. umbellata*, and the two figures were obviously drawn from the same colony with great attention to detail, as the budding pattern of the regenerated fragment from which the zoarium originates (see p. 193), may be seen to correspond on the frontal side, with the shape of the fragment visible on the basal side. D'Orbigny's explanation of pl. 717 (p. 473), however, gives the Plate number as "747" (which contains drawings of Cyclostomes only), and the descriptions of figures 2 and 3 have been interchanged. Buge found that d'Orbigny's material of *D. umbellata* contained one zoarium of *C. canariensis*. The frequent association of this pair of species has been noted, (see p. 209), and may have occurred in Buge's material from the Redonian, as his figure (pl. 10, fig. 3) of the frontal surface of his "*C. canariensis*" shows a well-developed vestibular arch and wide zooecia, and is perhaps a worn fragment of *D. umbellata* or *C. haidingeri* ; it has not the character of *C. canariensis*, but the basal surface of a specimen figured on pl. 9, fig. 5, has irregular sectors with 4-8 pores, and is similar to other Miocene specimens of *C. canariensis*.

The figure given by Faura & Canu (pl. 3, fig. 8) shows evidence of a worn denticulate cryptocyst in some zooecia and is not of a specimen of *C. canariensis*. Their text-figures 4a, b, are reproductions of those of Pliocene specimens given by Angelis (1899), and do not represent their own material. Canu & Lecointre (1925, pl. 3) figured *C. canariensis* from the Burdigalian of the Gironde, but the photographs have

been retouched (in fig. 11 sector boundaries have been drawn in through basal pores), and little of the character of the specimens can be deduced.

The measurements given by Gautier (1962 : 53) show that the zooecia of his specimens had wide opesiae. The zoaria were large (12.5 mm. in diameter), and were thus very probably of *C. canariensis*.

Lagaaij's extremely full and detailed study of *C. canariensis* (1963), includes a bibliography which combines references to both *C. canariensis* and to *C. biporosa*, as limited here.

Zoaria from west Africa are generally larger than those from the Gulf of Mexico, and of a flattened cone shape. In all the specimens examined the sides of the opesia are curved and the lateral cryptocyst descends steeply, and is so little salient that in cleaned specimens the pores in the lateral walls can be seen from a frontal view.

The ancestrula is frequently slightly larger than the zooecia of the primary circle budded from it (see Canu & Bassler, 1928, pl. 1, fig. 7), and the zooecia of the ancestrular area never show any thickening of the cryptocyst as in *C. biporosa* and *C. monotrema*. The zooecial vibracula of Recent specimens of *C. canariensis* are of two distinct kinds. The majority are similar to those found in all other species of the family; they have auriform opesiae, rounded proximally, and long vibracula setae. A proportion of between 1 : 10-1 : 30 individuals are small, have short, hooked setae, and more symmetrical opesiae, with prominent narrow rostra pointing proximally (see pl. 3, fig. 4). This kind of zooecial vibraculum has been found to occur in the lectotype, the majority of west African colonies, and in a few zoaria from the Gulf of Mexico. The occurrence thus differs from that of the vicarious vibracula with hooked setae (see below). No other species of Cupuladriidae has been seen in which two such types of vibracula occur. Canu & Bassler (1929 : text-fig. 13C) figured a second type of seta in *C. grandis*, but did not describe it. Their figure is somewhat similar to that of a regenerating seta in *D. umbellata* (subsp. *depressa*), given by Marcus & Marcus (1962, pl. 2, fig. 7). The opesiae of regenerated vibracula are not of the narrow, symmetrical type described above.

Vicarious vibracula are commonest in the central area of zoaria in which they occur, but may also be present among zooecia budded from a regenerating edge. They completely replace a zooecium and each has an ordinary small, distal vibraculum, like the zooecia. The opesia of the vicarious vibraculum of *C. canariensis* is quite unlike that of *C. biporosa*, which is auriform (see below). In *C. canariensis* a long, acute, raised, beaked rostrum protrudes proximally beyond the short gymnocyst. It supports a wide, short, strongly hooked seta, which is slung between the asymmetrical condyles. The basal sclerite differs slightly from that of the normal vibracular seta, but the individual is still basically a vibraculum (see Hastings, 1963 : 180).

The basal sectors of *C. canariensis* are unlike those of *C. biporosa*, being irregular in length and rarely square in outline. The majority are elongated rectangles, with 6-12 pores, and occasionally more (see Text-fig. 2f). Interspersed with these sectors are short wide ones with 3-6 pores, these occur at the origin of an intercalary row of zooecia. In basal view colonies of *C. canariensis* do not show the regular concentric series of sectors which is so striking in *C. biporosa*. At the growing edge, the minute

pores in the basal wall can be seen in the developing zoecia to be without any surrounding kenozoecial chamber. Further toward the centre of the colony, a crescent of calcification with the concavity pointing distally grows round the pore; when the arms of the crescent meet, this forms the first kenozoecial chamber. In young colonies the tangential divisions between the radial sector boundaries are not developed until at least 4 radial series of zoecia have been budded. Thus even young colonies

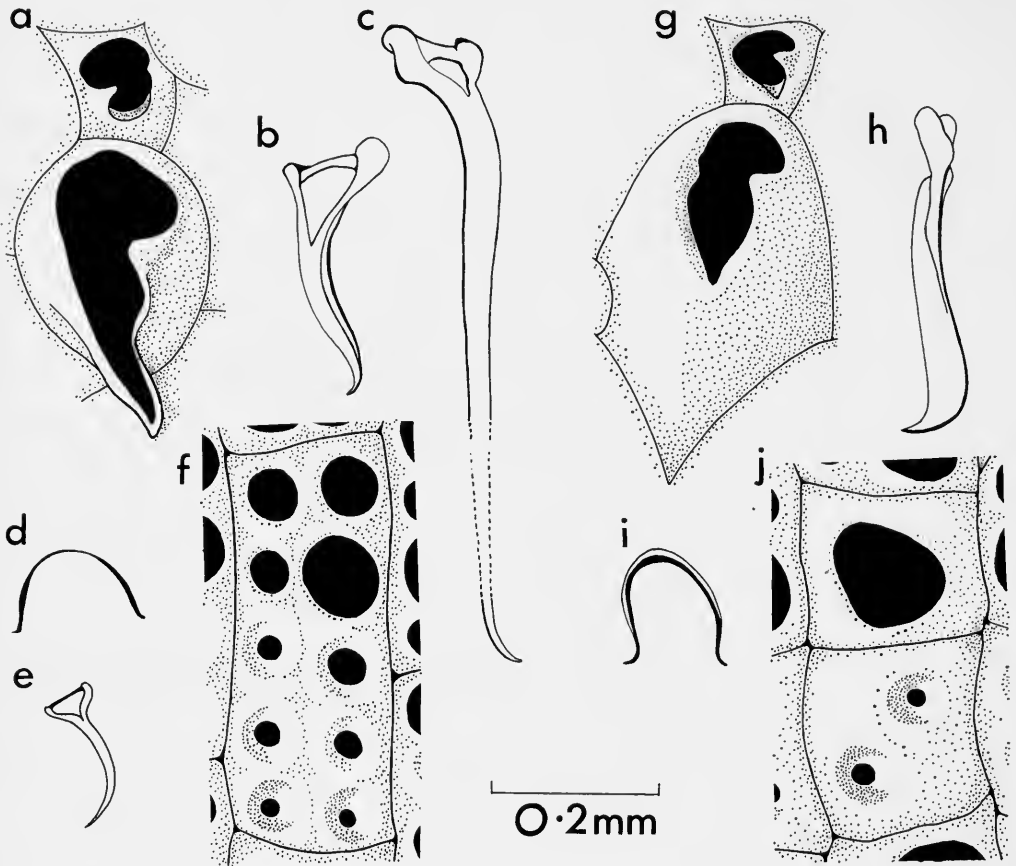


FIG. 1. *Cupuladria canariensis* and *C. biporosa*. a-f, *C. canariensis*. a. Vicarious vibraculum and normal distal vibraculum, treated with eau de javelle. Marche-Marchad Coll., I, 39 C. b. Hooked seta of vicarious vibraculum. c. Seta of normal vibraculum, central part omitted. d. Operculum. b-e, "Calypso" Coll., I, C 56 J. f. Basal surface, treated with eau de javelle, showing elongated sector with porous kenozoecial chambers. Marche-Marchad Coll., I, 39 C. g-h, *C. biporosa*. g. Vicarious vibraculum and normal distal vibraculum, treated with eau de javelle. 1962. I. 26. I. h. Scimitar-shaped seta of vicarious vibraculum, in lateral view. i. Operculum. j. Basal surface, treated with eau de javelle, showing small, square sectors with porous kenozoecial chambers. Marche-Marchad Coll., III, 24 G.

may be distinguished from those of *C. biporosa* where the tangential sector boundaries are seen as soon as the zoecia grow out beyond the original substrate.

Waters (1921 : 411) gave the number of tentacles as 14, but this is the number found in sections of *C. biporosa* (1929. 4. 26. 85 pt.). Waters's material included both *C. canariensis* and *C. biporosa*, and the number of tentacles in *C. canariensis* sections (MM II, 3A) is 17-19. *C. doma* (see Waters, 1921 : 411, and Cook, 1963 : 409) and the *D. umbellata*-complex (see Marcus & Marcus, 1962 : 295, and Cook, 1963 : 409) have 13-16 tentacles, and the same number has been seen in sections of *C. owenii disciformis* ("Calypso" Coll. C47A).

Thus *C. canariensis* differs from *C. biporosa* chiefly in the character of the basal surface, the cryptocyst, the number of tentacles, in the possession of two kinds of zoecial vibracula, and the form of the vicarious vibracula. The distribution of the two species also appears to have been completely distinct in the Miocene (see below). *C. canariensis* does not occur south of Barbados in Recent collections, all Brazilian records being of *C. biporosa* or *C. monotrema*.

7 *Cupuladria biporosa* Canu & Bassler

(Pl. 1, figs. 2A, B, 3A, B, 4A, B, 5, 6A, B, Text-figs. 1g-j)

Cupularia canariensis Busk (part) 1859a : 66, pl. 23, figs. 7, 8, Madeira and Canaries.

Cupularia canariensis Busk : Busk, 1859 : 87, pl. 13, figs. 2 a-e, Coralline Crag, Pliocene, Britain.
Membranipora canariensis (Busk) Smitt, 1873 : 10, pl. 2, figs. 69-71, 10-14 fath. Florida. (?part), 1888 : 79, 120 fath. and over, Florida.

?*Cupularia canariensis* Busk : Angelis (part), 1899 : 33, pl. B, fig. 6 only, Pliocene, Spain.

Cupularia canariensis Busk : Canu, 1908 : 275, pl. 5, figs. 8, 9, 10, Pampean, Pliocene, Argentina.

Cupularia guineensis Busk : Norman (part), 1909 : 289, pl. 37, figs. 4, 5, Madeira (not figs. 3, 6 = *C. canariensis*).

?*Cupularia guineensis* Busk : (part) Osburn, 1914 : 195, Tortugas Islands, Florida, 10 fath.

Cupularia canariensis Busk : Canu & Bassler, 1918 : 119, pl. 53, figs. 5-7, Miocene, Costa Rica and Jamaica.

Cupuladria canariensis (Busk) Canu & Bassler, 1919 : 78, pl. 1, figs. 8-10, Lower Miocene, Costa Rica, 1920 : 103, text-fig. 24D. 1923 : 28, pl. 1, figs. 7-9, Lower Miocene, Florida, Jamaica, Santo Domingo, Costa Rica ; Miocene and Pliocene, Florida.

Cupularia canariensis Busk : Waters (part), 1921 : 410, pl. 29, fig. 5, Madeira.

Cupuladria biporosa Canu & Bassler, 1923 : 29, pl. 47, figs. 1-2, Miocene, Santo Domingo.

Cupuladria canariensis (Busk) : Canu & Bassler, 1928 : 16, text-fig. 2, Pliocene Panama ; and Recent, Gulf of Mexico.

Cupuladria canariensis (Busk) : Hastings, 1930 : 714, pl. 8, figs. 38, 40, Gorgona, Colombia, 15-30 fath.

Cupuladria canariensis Busk (sic) McGuirt, 1941 : 46, pl. 1, figs. 1-3, 5-6, 8, Miocene & Pliocene, Louisiana.

Cupuladria canariensis (Busk) : Silén (part), 1942 : 13, text-fig. 8, West Indies.

Cupuladria canariensis (Busk) : Osburn, 1950 : 33, pl. 3, figs. 2, 3, Lower California to the Galapagos Islands, shallow water to 40 fath.

Cupuladria canariensis (Busk) : Soule, 1959 : 8, California, 7-40 fath.

Cupuladria canariensis (Busk) : Galopim de Carvalho, 1961 : 97, pl. 1, figs. 1-3, Pliocene, Portugal.

Cupuladria canariensis Marcus & Marcus, 1962 : 285, pl. 1, figs. 1-3, off Sao Paulo, 150 m., near Cabo Frio, 3 m., off mouths of the R. Amazon, 70 m.-71.5 m., dead.

Cupuladria canariensis (Busk) : Lagaij, part, 1963, pl. 26, figs. 4, 5.

Cupuladria sp. Cheetham & Sandberg, 1964 : 1021, Quaternary, Louisiana.

MATERIAL. Holotype U.S.N.M. 68425. (Photographs, B.M.N.H. 1963. 1. 2. 1, 2) Miocenè, Bowden Marl, Santo Domingo.

"Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C41(V). Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49G (V).

Coll. II. Stn. 26, 15° 16' 30" N., 23° 47' 31" W., 18.ii.59, 50-65 m., C65R. Stn. 75, 16° 04' 20" N., 22° 58' 10" W., 45 m., C109A.

Marche-Marchad Coll. I. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3E (V). Sud de Gorée, 27.x.53, 38-42 m., 7D. Sud de presque l'île de Cap Vert, 95 m., 33Q. S.W. Madeleines, 21.i.54, 46-48 m., 46G (V).

Coll. II. S.W. Madeleines, 9.i.54, 77.5 m., 31R.

Coll. III. Dragage 5, "Gerard Freca", 18.ii.54, 15I; Dragage 4, 97-98 m., 28K (V). 33-34 m., 27.ii.53, 29I (V). No information, 24R (V).

British Museum Coll. Canaries, M'Andrew, 1899. 7. 1. 4697B, Busk Coll. Canaries, M'Andrew, 1899. 7. 1. 4702, 1962. 1. 24. 4 and 5, Busk Coll. Madeira, 1879. 5. 28. 6. Bay of Funchal, Madeira, 1962. 1. 24. 6, 1963. 1. 16. 73, Madeira, 1962. 1. 24. 7, and 9 (V), Norman Coll; Funchal, 50 m., 1963. 2. 28. 6, Cook Coll., mud.* Râs el-Amouch, Algiers "Porcupine", 4 fath. and upwards, 1962. 1. 24. 1. Tangier Bay "Porcupine", 1911. 10. 1. 646, Norman Coll. Barbados, 73 fath., 9.iii.79, and 23° 13' N., 89° 10' W., 84 fath., "Blake", 1962. 1. 24. 8, Norman Coll. (V) West Indies, 1962. 1. 24. 2, Norman Coll (V). Gulf of Mexico, 91° W., 28° 6' 25" N., 37 fath., 1959. 8. 20. 3, Lagaaij Coll. (V). 89° 9' W., 28° 58' N., 1961. 11.2. 49B, Cheetham Coll. Gorgona, Colombia, 1929. 4. 26. 85. 86, 263 (V), 87 (V). St. James coast, Barbados, 1962. 1. 26. 1, Saunders Coll. (V). Miocene, Santo Domingo, 1899. 7. 1. 1259, Busk Coll. (V).

B.M. Palaeontological Dept. Coll. Coralline Crag, Pliocene, Britain, D 39968, 39969, D 6767, 6762, 6764, B 1624. Astigiana, Pliocene, Italy, 1848. 6. 12. 3-7.

U.S. National Museum Coll. Holotype, see above (V). 80747, Miocene, Bowden Marl, Jamaica (V).

Dr. A. Cheetham Coll. Forest Hill Clay, Alabama, L. Miocene. Oak Grove, Yellow River, Okaloosa County, Florida, L. Miocene. Cercado de Mao, Santo Domingo, L. Miocene (V). Tambo Trace, Shell Bed, nr. Talparo, Trinidad, L. Miocene (V). Manzanilla, Manzanilla coast, Trinidad, Miocene (V).

Dr. R. Lagaaij Coll. Miocene, Limestone Creek, Missouri. Miocene, Cubagua, Venezuela. Miocene, Bowden Marl (V), Jamaica. Pleistocene, Gulf of Mexico "Neptune" 1. Gulf of Mexico, "Atlantis" Stn. 163, 20 fath. (V).

Naturhistoriska Riksmuseet, Stockholm Coll. (Nos. in Silén, 1942: 13-14 in parentheses). Atlantic, 27° 16' N., 23° 21' W. at the surface, FBS 321 (No. 7). (One of the 9 specimens is *C. owenii* qv) West Indies, S.W. off Tortugas 40 m., FBD 239 (No 8) (V). As above, East Key, 20 m., FBD 258 (No. 9) (V). As above, nr. Rebecca shoal, 15 m., FBD 281 (No. 10) (V). Yucatan, 35 miles, N.N.E. off C. Catocla, 40 m., FBD 696 (No. 15) (V). 52 miles off Florida, 40 m., FBD 548 (No. 16) (V) (One colony of *C. canariensis* present).

C. biporosa is not present in the Achimota Collection.

Zoarium generally smaller than that of *C. canariensis*, not exceeding 16 mm. in

diameter, zooecia also smaller. Operculum frequently longer than wide with no basal sclerite. Cryptocyst descending gently, sides of opesia straight. Vicarious vibracula frequent, usually present in ancestrular area, occasionally throughout zoarium; seta straight, elongated, broad, slightly hooked, scimitar shaped. Basal surface divided into concentric series of small, nearly square sectors with 1-6 pores, usually 4. Basal concavity flattened and filled by many layers of kenozoecial chambers. Tentacles 14-15 (see above).

DIMENSIONS. Lz 0.40-0.65 mm., lz 0.25-0.35 mm., La 0.40-0.47 mm., Lvo 0.07-0.13 mm., Lv 0.45-0.55 mm., Ls 0.40-1.40 mm., Lvs 0.25-0.30 mm., Lo 0.10-0.11 mm., lo 0.09-0.10 mm., Lop 0.25-0.32 mm., lop 0.15-0.19 mm.

Dr. R. S. Boardman (*in litt.* 13.ii.1962) has found that the only specimen referred to *C. biporosa* in the U.S. National Museum Collection, is the holotype-fragment of which part was figured by Canu & Bassler (1923, pl. 47, figs. 1, 2). Enlarged photographs of the entire fragment show that one vicarious vibraculum is present, and that the opesiae of the zooecia in the published figure (fig. 1) have been enlarged by retouching of the photograph. This was presumably done to erase the image of detritus lodged in the opesiae, but has unfortunately given the impression that the cryptocyst descends more steeply than it in fact does.

Specimens of complete young zoaria labelled "*C. canariensis*", from the same horizon in Jamaica as the holotype (U.S.N.M. 80747) are strikingly similar in all characters to young Recent colonies from the West Indies (see pl. 1, figs. 4, 6).

Busk's description (1859a : 66) of the occurrence of 2-4 pores in the sectors on the basal side of his specimens, and his figures (pl. 23, figs. 7, 8) showing the small square basal sectors (fig. 7), and well-developed cryptocyst (fig. 8), are certainly of *C. biporosa*. The major part of the material from the Canaries collected by M'Andrew in the Busk Collection (see Busk, 1859a : 67) is also of *C. biporosa*, but specimens of *C. canariensis* are mixed with it, and it is probably these which Busk described as 0.5 in. in width, as none of his specimens of *C. biporosa* reach this size. The specimens on slide 1899. 7. 1. 4697 A + B, of *C. canariensis* and *C. biporosa*, are mounted on glass, and the distinctive characters of both surfaces of the colonies of the two species can be seen clearly.

Busk's figures of specimens from the British Crag (1859 : 87, pl. 13, figs. 2a-e), show typical *C. biporosa* characters, namely the straight sides of the opesiae and the gently descending cryptocyst. The figure of the basal side shows some irregular sectors, but specimen D 6764 has square sectors, with 4 pores, and many layers of kenozoecial chambers, as well as the frontal character of *C. biporosa*. Busk's specimens are particularly interesting as the only other records of *C. biporosa* from the Pliocene of Europe are from Spain, Portugal and Italy. Pliocene specimens from the Netherlands are all referable to *C. canariensis*.

Smitt (1873 : 10) described the "inner lamina" (i.e. cryptocyst) of his specimens as being similar to that of *Farcimia cereus* (p. 3, pl. 1, figs. 55, 56), which has a well-developed cryptocyst. His figure 69 shows the slightly elongated operculum, figure 70 the cryptocyst, and the vicarious vibracula in the ancestrular area (see Hastings, 1930 : 714). Figure 71 shows the basal sectors, some of which have 4

pores, although others are shown bearing more. The specimens listed by Silén (1942, Nos. 8, 9 and 10) have been examined; they include those described and figured by Smitt. No. 8 (FBD 239) is the original of figure 71 and the actual sectors have been recognized. The basal sectors are square and more regular than in Smitt's drawing and the long irregular sectors do not occur, but are composed of several smaller sectors. Figure 70 is also drawn from this specimen and confirms that the irregular opesia shown in the figure are those of vicarious vibracula. In fact, not only the ancestrular, but all the 7 individuals surrounding it are of this type. This development is not unusual in *C. biporosa* and also occurs in colonies from FBD 696, FBD 548, Dr. Lagaaij's specimen from the Gulf of Mexico, and 1962. 1. 26. 1. from Barbados. Specimen FBD 281 is the original of Smitt's figure 69; it is a large colony, 10 mm. in diameter.

The figures given by Angelis (1899, pl. B, figs. 7, 8) of the basal surface of his specimens from the Pliocene of Catalonia, show long irregular sectors, and are attributable to *C. canariensis*. Figure 6 (in which the zooecia are shown upside-down) has the appearance of *C. biporosa*, with a wide cryptocyst and straight-sided opesia. The figure is very similar in appearance to that of Busk's Crag specimens. Angelis's descriptions however, are taken from that of Manzoni (1877) and refers to *C. canariensis*. No fossil Spanish material has been seen, but specimens figured by Galopim de Carvalho (1961, pl. 1, figs. 1-3, Pliocene, Portugal) also show the straight-sided opesia and small basal sectors of *C. biporosa*. Pliocene material from Italy also consists of both *C. canariensis* and *C. biporosa*, (see pp. 198 and 204), and the correlation of the characters present is respectively consistent with the diagnoses of the two species.

The specimens figured from the Pliocene of Argentina by Canu (1908, pl. 5, figs. 8, 9, 10) were extremely worn, but figure 8 perhaps shows 2 vicarious vibracula (in the bottom right-hand corner).

Both Norman (1909, pl. 37, figs. 4, 5), and Waters (1921, pl. 29, fig. 5), who received his Madeiran material from Norman, show 2-4 pores on the basal sectors of their specimens. Examination of the plentiful Madeiran colonies in the Norman Collection shows that they, too, consist of a mixture of both *C. biporosa* and *C. canariensis*. Norman and Waters both stated that they considered *C. canariensis* and *C. guineensis* (Busk) to be synonymous. In view of the mixed nature of their material it should be noted that the salient lateral cryptocyst and small square basal sectors of *C. biporosa* are very similar to some specimens of *C. guineensis*, which was, however, distinguished and defined by Hastings (1930: 714).

The material from Costa Rica figured by Canu & Bassler (1918, 1919) as *C. canariensis*, belongs to *C. biporosa*. The same set of photographs was reproduced in both these papers and was again used to illustrate American fossil "*C. canariensis*" in 1920 and 1923. The photographs show 1) small colonies, natural size, with flattened bases; 2) zooecia with well-developed lateral cryptocysts, and with one vicarious vibraculum at the lower right-hand edge; 3) the basal sectors, each with 2-4 pores. The introduction of *C. biporosa* was illustrated by material from Santo

Domingo (1923). The fossils from the Gulf of Mexico region (1928), were illustrated by photographs of Recent *C. canariensis* from the same area.

The specimens described by Hastings (1930 : 714) from Gorgona, consist of colonies, the majority of which have regenerated from broken fragments. Where an ancestrula is present, the vicarious vibracula near it have smaller, more auriform opesia than those occurring elsewhere in the colony.

McGuirt (1941 : 46) mentioned the difficulty in distinguishing his Miocene material from Louisiana, attributed to *C. canariensis*, from *C. biporosa*. The specimens figured show vicarious vibracula (pl. 1, figs. 1, 3) and the small, square basal sectors (figs. 2, 5), and are certainly of *C. biporosa*. The zooecia in figure 8 have unusually narrow cryptocysts, and may have been worn.

Of the colonies collected at the surface of the Atlantic off the west coast of Africa (see Silén, 1942 : 13, specimen FBS 321 above, and p. 194), 8 colonies belong to *C. biporosa*. The ninth is a specimen of *C. owenii* (see p. 213).

Osburn's figure (1950, pl. 3, figs. 2, 3) shows small, square sectors with 1-3 pores (fig. 3), the zooecia in figure 2 have the well-developed lateral cryptocyst of *C. biporosa*, and Soule (1959 : 8) mentioned vicarious vibracula in his Californian material.

Marcus & Marcus (1962) gave a short description of the central vicarious vibracula, and, on pl. 1, fig. 2, illustrated the basal surface of one of their colonies with small segments arranged concentrically. Their material was collected from the northern and southern coasts of Brazil, no specimens being found in the intermediate area. The shallow depths at which some specimens occurred (3 m. near Cabo Frio) were at "sheltered localities", where there must have been little turbulence.

Lagaaij's figures (1963, pl. 26, figs. 4, 5) of material from the Gulf of Mexico are of *C. biporosa*, as is the unnamed species mentioned by Cheetham and Sandberg (1964).

The zoarium rarely attains a diameter of more than 10 mm.; fragments of large colonies estimated at 16 mm. diameter were found in fossil material from the U.S. Nat. Mus. Collection, 80747, and a colony of 11 mm. diameter, covered with 3 small colonies of *Onychocella angulosa* (Reuss) occurs in material from Madeira, 1962. I. 24. 7.

Unlike *C. canariensis*, the sides of the opesia are almost straight, and in the great majority of specimens the cryptocyst descends gently forming a salient lateral shelf and obscuring the pores in the lateral walls, which are not seen in frontal view as in *C. canariensis*. In some fossil specimens the cryptocyst descends more steeply, but this seems to be confined to zooecia of fragments of large zoaria, and does not occur in the smaller, whole colonies. The cryptocyst of the zooecia of the central area are sometimes slightly thickened by secondary calcification, but a lamina is never formed as is found in *C. guineensis* (see Cook, 1965 : 172); a similar thickening is found in *C. monotrema*.

The ordinary vibracula are of one kind only and vicarious vibracula are nearly always present, especially near the centre of the colony; their opesia are auriform, and there is a distinct, prominent gymnocyst. The setae of Recent specimens have the same type of basal sclerite and are similar to those of the ordinary vibracula (see also Hastings, 1930 : 714); they have no sigmoid curve, however, and in lateral view

they are broad, scimitar-shaped, and hooked at the tip (see Text-fig. 1h). They thus differ from the short, hooked setae of the vicarious vibracula of *C. canariensis*. Both Marcus & Marcus (1962 : 288, pl. 1, fig. 2) and Lagaaij (1963 : 183) described the vicarious vibracula of the ancestrular area as regenerated. Although the original zooecia may regenerate as vibracula in some cases, many specimens (notably those from Gorgona and the Gulf of Mexico), show that the vicarious vibracula are budded primarily as part of the normal development of a colony. Vicarious vibracula are often associated with areas of regenerating growth (see Cook, 1965 : 160), and here also, they are some of the first individuals to be budded, not the results of regeneration of the older zooecia.

The development of the basal porous sectors in *C. biporosa* differs from that of *C. canariensis* in that the chambers appear to develop more quickly, and large pores are rarely seen at the growing edges of young colonies. The tangential sector boundaries are always present on the basal side of the young peripheral zooecia, unlike *C. canariensis* (see above).

The layers of kenozoecial chambers are more numerous than *C. canariensis*, even in young colonies. They frequently conceal the original substrate, and in many colonies are so thick that the basal surface is flattened. In section these zoaria show successive rows of chambers up to 14 deep. A slide of sectioned colonies of *C. biporosa*, where the species is mounted with *C. guineensis* for comparison (1879. 5. 28. 6, Madeira + 1929. 5. 10. 1, Australia), was figured by Hastings (1930, pl. 8, fig. 38, as *C. canariensis*). The identity of the species in no way affects her description of the chambers as a distinction from *C. guineensis*, as those of *C. canariensis* are exactly the same in appearance, although they rarely reach a comparable number of layers, even in large colonies of this species.

One of the specimens from the Miocene of Santo Domingo (U.S.N.M. Coll.) shows a form of growth similar to normal colonies of *C. doma* (see Cook, 1965 : 162). The zoarium is small and high, the basal side is half filled by secondary calcification, and there are 3 rows of peripheral vibracula, the last of which encroaches on the basal side (see Pl. 1, fig. 5).

The geographical distribution of specimens of *C. canariensis* and *C. biporosa*, with and without vicarious vibracula, falls into distinct groups. The first, northerly area, consists of records from the S.W. Mediterranean, Spain, Portugal, and the Canaries ; no vicarious vibracula have been found in colonies of either species from these localities. Material of both species from Madeira, the Cape Verde Islands and the coast of Senegal has colonies both with and without vicarious vibracula ; whereas all the specimens from the southerly localities in the Gulf of Guinea and the Bay of Biafra have vicarious vibracula. Recent and fossil specimens of *C. biporosa* from the Gulf of Mexico are rarely without vicarious vibracula, whereas none have been found in the Recent colonies of *C. canariensis* from this area.

C. biporosa differs from *C. canariensis* consistently in the character of the basal surface, of the cryptocyst, in the number of tentacles, in the absence of a second kind of ordinary vibraculum, and in the form of the vicarious vibraculum. The fossil record shows whereas there are apparently no certain descriptions of *C. biporosa*

occurring before the Pliocene in south-western Europe, the only American records of *C. canariensis*, from the Gulf of Mexico and Florida, are Recent. The Miocene faunas of the eastern and western Atlantic were distinct.

C. canariensis and *C. biporosa* have similar geographical distributions, live in similar depths, under the same ecological conditions, and are thus frequently associated in Recent collections. There is a similar correlation between their occurrence and that of the *D. umbellata*-complex (see Canu & Bassler, 1918 : 119), and as many as 5 lunulitiform species occur together at Konakrey and Cape Verde, and Stn. 45, "Calypso" Coll. I, off Cape Lopez, in the Bay of Biafra.

The confusion between *C. canariensis* and *C. biporosa*, and the occurrence of vicarious vibracula in both species, make it advisable to compare them with the only other species with similar characters, namely *C. monotrema* (Busk).

8 *Cupuladria monotrema* (Busk)

Cupularia monotrema Busk, 1884 : 207, pl. 14, figs. 5, 5a, 5b, off Bahia, 10-20 fath.

Cupularia canariensis Busk : Waters, 1888 : 36, pl. 3, fig. 2, Bahia, 10-80 fath.

Cupuladria monotrema (Busk) Hastings, 1930 : 715.

MATERIAL. LECTOTYPE (chosen here), B.M., 1887. 12. 9. 820. British Museum Coll. Off Bahia, 10-20 fath., 1887. 12. 9. 820, 820A, Challenger Coll. (V). As above, 1944. 1. 8. 346, Busk Coll. (V). As above, 10-80 fath., 1889. 12. 12. 9 (V) Suppl. Challenger Coll. As above, 1890, 3. 22. 11 (V). Bahia and Pernambuco, 11° 45' S., 37° 15' W., 16-28 fath., 1890. 1. 30. 33-44 pt., and 13° 50' S., 38° 46' W., 32 fath., 1890. 1. 30. 33 pt. (VV).

British Antarctic Expedition Coll. Stn. 42, off Rio de Janeiro, 40 fath., 878A.

C. monotrema does not occur in any of the west African Collections.

Zoarium fairly large, maximum diameter 10 mm. Zooecia with cryptocyst descending quite steeply, lateral pores just visible in frontal view. Operculum opening within a strongly chitinized area of the frontal membrane, which is surrounded by a thickened band. Operculum frequently heavily chitinized, but proximal sclerite absent. Basal surface with only one layer of kenozoecia. Sectors small and square, with 1-3 pores. Vicarious vibracula numerous, nearly as large as the zooecia, with auriform opesia and long proximal gymnocyst. Vicarious vibracula often intercalary, reaching the penultimate peripheral circle of zooecia. Setae scimitar-shaped, similar to those of *C. biporosa*.

DIMENSIONS. Lz 0.40-0.50 mm., lz 0.26-0.37 mm., La 0.40-0.45 mm., Lvo 0.09-0.12 mm., Lv 0.35-0.45 mm., Ls 0.50-1.00 mm., Lvs 0.30-0.40 mm., Lo 0.10-0.11 mm., lo 0.12-0.13 mm., Lop 0.25-0.30 mm., lop 0.15-0.20 mm.

The opesiae of the zooecia of the central area are slightly reduced by secondary thickening as in *C. biporosa*. The vicarious vibracula are similar to those of *C. biporosa*, but are far more numerous. The opercular area is unlike that of other species, although the operculum itself is like that of *C. biporosa* in shape. Frequently its dark brown colour ends abruptly at the junction with the frontal membrane, giving the appearance of a curved proximal sclerite. In many colonies, a band of thickening

surrounds the distal part of the operculum and then extends proximally and across the frontal membrane. This whole area, with the operculum opening within it, is more heavily chitinized than the remaining frontal membrane surrounding it. It is particularly noticeable in dry specimens (such as those seen by Busk), that the area enclosed by the thick chitinous band shrinks differentially in relation to the rest of the frontal membrane, producing the "hippocrepian" shape described by Busk, who was thus misled into thinking that this part of the whole frontal area was the operculum. In his explanation of terms (p. xvi), Busk did not give a definition of "hippocrepian", but his "coarctate" form of orifice is similar to the lepra-lloid shape of the frontal area in *C. monotrema*. The chitinized band is not present in all specimens, nor in all zoecia of the zoaria in which it may occur.

As stated by Hastings (1930 : 715), *C. monotrema* is clearly distinct from *C. canariensis*. It is very similar to *C. biporosa*, and may indeed be synonymous, but until more material is available, it is distinguished by the opercular area, the more numerous vicarious vibracula, and the single layer of basal kenozoecial chambers.

Marcus & Marcus (1962 : 286) found no specimens of *C. monotrema* in collections ranging from São Paulo north to the mouths of the Amazon. *C. biporosa* was found only at the extreme North and South of the collecting area, not in the Bahia area.

9 *Cupuladria multispinata* (Canu & Bassler)

(Pl. 2, figs. 2A, B, Text-figs. 2d)

Cupularia owenii (Gray) Busk, 1884 : 207, St. Vincent, Cape Verde Islands, 11 fath., mud (not *C. owenii* (Gray) see p. 213).

Cupularia johnsoni Busk ; Norman part, 1909 : 290, pl. 38, figs. 5, 6, Madeira (not figs. 1-4 = *C. doma*, see p. 216).

Cupularia denticulata Waters, 1921 : 413, listing specimens labelled "*C. deformis*" by Busk, in the British Museum, from Portugal and the Mediterranean, 50 m. to 45 fath.

Cupularia multispinata Canu & Bassler, 1923 : 78, text-fig. 13H, Oran, 105 m. (not text-fig. 13 I = *D. umbellata*, see p. 221). 1928 : 22.

?*Cupularia haidingeri* (Reuss) : Canu & Bassler, 1923 : 77, pl. 1, figs. 13-17, Miocene, Europe (not *C. haidingeri* (Reuss) see Lagaaij, 1952 : 35).

Cupularia denticulata var. *multispinata* Waters, 1926 : 427, pl. 18, figs. 2, 4, 7, Oran (*C. denticulata* in the explanation of the plate).

Cupuladria owenii (Gray) : Silén, 1942 : 15, Madeira.

MATERIAL. "Calypso" Coll. I. Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m. C4E.

Coll. II. Stn. 26, 15° 16' 30" N., 23° 47' 31" W., 18.xi.59, 50-65 m., C65H.

Marche-Marchad Coll. I. Konakrey, Guinée Ise., 2E. S.W. Madeleines, 15.ix.53, 20A ; 9.i.54, 45-46 m., 26E. Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 33A. Baie de Seminoles, Gorée, 8.xii.53, 38 m., 39A (C) (+ *Hippoporina lacrimosa* Cook)

Coll. II. S. Baie de Gorée, 18.ii.54, 95 m., 30C. Baie de Seminoles, Gorée, 8.xii.53, 38 m., 36A.

Coll. III. Sud de Gorée, 13.ii.53, 33-35 m., 9C ; 34-37 m., 17C. Either S.W. Madeleines, 15.ix.53, 48., or Sud de Gorée, 13.ii.53, 34-37 m., 16G. Dragage 1 "Gerard Freca", 18.ii.54, 23G ; Dr. 4, 97-98 m., 28I ; Dr. 5, 27C. 33-34 m.,

27.ii.53, 29E. Mission Guinée Pte. 50, Parages des Fles de Los, Konakrey, 21.i.53, 19 m., 30C (C). No information, 24I.

British Museum Coll. St. Vincent, Cape Verde Islands*, 11 fath., mud, 1887. 12. 9. 82I, Challenger Coll. Port of Oratava, Canaries, 1899. 7. 1. 1224, Busk Coll. Bay of Funchal, Madeira, 1963. 1. 16. 4, Busk Coll; 50 m., 1963. 2. 28. 11. Cook Coll., mud*. Madeira, 1963. 1. 16. 2 and 3, Norman Coll. Mediterranean, 1899. 7. 1. 1236, and on 1223 with *C. canariensis*, "Porcupine", Busk Coll. Spain, 1899. 7. 1. 1239, Busk Coll. Cape Rosa, Algeria, 1899. 7. 1. 1233, Busk Coll. Ràs el-Amouch, Algeria, 45 fath., 1963. 1. 16. 1. Tangier Bay, 1890. 4. 15. 23. Cape of Good Hope, 1842. 12. 2. 19, Belcher Coll. South Africa, False Bay, 50 m., fine sand*, 1963. 1. 16. 5, Univ. Cape Town Coll. S. Africa, False Island N. 8.5 miles, 53 fath., 1949. 11. 10. 669B; Bakhoven Rock W., $\frac{1}{2}$ N. $\frac{3}{4}$ mile, 22 fath., 1949. 11. 10. 617; Cape St. Blaize, 7.5 miles N. 37 fath., 1949. 11. 10. 94B, 625B, 626B, 627B; Cape Infanta N.E. by N. 19 miles, 46 fath., 1949. 11. 10. 622B, 623B; N.E. by N. $\frac{1}{4}$ N., 45 fath., 1949. 11. 10. 621B; Stalwart Point, N.N.W. 9 miles, 53 fath., 1949. 11. 10. 652B; Nanquas Peak N. 46° E. 9 miles, 63 fath., 1949. 11. 10. 674B. Burrows Coll.

Discovery Coll. Stn. 299, 14.x.27, 7-11 m., Tarrafal, S. Antonio, Cape Verde Islands, 86A.

Naturhistoriska Riksmuseet, Stockholm, Madeira, FBD 36.

C. multispinata is not represented in the Achimota Collection.

Zoarium frequently large, (maximum diameter measure, 16 mm.), zoecia with a large range in size. Sides of vestibular arch straight, salient distal denticles absent. Operculum without a proximal sclerite. Descending lateral cryptocyst tuberculate, with 4-8 irregular denticles, themselves ending in fine spinules; proximal spinules infrequent. Central zoecia closed. Basal surface with large, irregular, coalescent tubercles and grooves frequently marked by a salient calcareous thread.

DIMENSIONS. Lz 0.55-0.76 mm., lz 0.32-0.47 mm., La 0.45-0.52 mm., Lvo 0.15-0.21 mm., Ls 0.60-1.90 mm., Lo 0.12-0.14 mm., lo 0.15-0.19 mm.

Busk's specimen from the Cape Verde Islands (Challenger Collection) differs slightly from the other west African specimens of *C. multispinata*. The colony is 7.5 mm. in diameter, but the peripheral zoecia are smaller than in other colonies of comparable size. The sides of the vestibular arch are straight, however, with no evidence of a distinct pair of distal denticles, as in *C. owenii*. The basal surface is worn, and almost smooth, but two areas show large irregular tubercles and faint threads marking the radial grooves. The specimen certainly belongs to *C. multispinata*.

Norman (1909: 290) remarked that specimens of *Cupularia oweni* (sic) were not found by him from Madeira. The Madeiran specimens which he referred to *C. johnsoni* are, however, a mixture of *C. multispinata* and *C. doma*. He included *C. reussiana* Manzoni and *C. doma* Smitt (sic) in his synonymy of *C. johnsoni* (= *C. doma* (d'Orbigny)). Part of the material which he referred to *C. lowei* (= *D. umbellata*, see p. 221), is also *C. multispinata*, as is the "variety" of *C. johnsoni* he described in which "the radiating ridges are greatly developed, and bear two rows of tubercles

regularly placed and of much larger size than those of the type". These specimens were figured on pl. 38, figs. 5, 6, and show the typical character of *C. multispinata*.

Waters (1921 : 413), in discussing *Cupularia lowei* (see p. 221), listed several British Museum specimens of another species, which had similarly deformed zoaria. He proposed to place these "under *denticulata*". Waters's publication of the manuscript name on the labels of Busk's specimens in the British Museum was not accompanied by a description, definition nor an indication (see International Code of Zoological Nomenclature, 1961, Articles 12 and 16). The specimens he listed are all identical with *C. multispinata*, as was suggested by Canu & Bassler (1923 : 78). Waters later (1926 : 427) confirmed this, and although in the explanation of pl. 18, on p. 432, he still referred to the species as *Cupularia denticulata*, he added the note "This is the *C. multispinata*, Canu & Bassler". On p. 427 he referred to it as "*Cupularia denticulata* var. *multispinata*". *C. denticulata* is a synonym of *C. owenii* (see below). The distribution of *C. multispinata* given by Canu & Bassler (1928 : 23) was derived from Waters's list of specimens given in 1921.

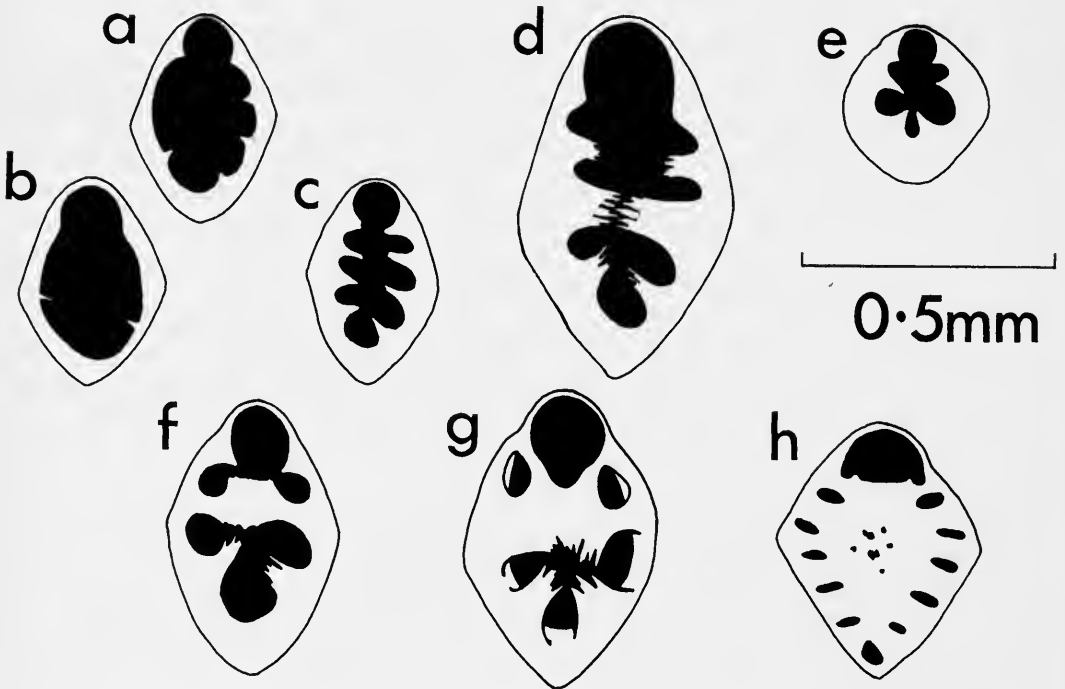


FIG. 2. Development of the cryptocyst in *Cupuladria* and *Discoporella*. Drawings semi-diagrammatic. a-e, *Cupuladria*. a, b, *C. owenii disciformis*. a. Form with vestibular arch with convergent sides, and several cryptocystal denticles. b. Form with vestibular arch with divergent sides, and very reduced cryptocystal denticles. c. *C. owenii*. d. *C. multispinata*. e. *C. doma*. f-h, *Discoporella* f. *D. reussiana*. g. *D. ocellata*. h. *D. umbellata*.

Nearly all the deformed colonies originate from regenerating fragments, and the irregularities are due to one or more radial rows failing to develop (see p. 195). Canu & Bassler's figure purporting to be of the frontal surface of *C. multispinata* with chitinous parts intact (1923, text-fig. 13 I) shows opercula with a strong basal sclerite and a horizontal cryptocyst with opesiules in one of the zooecia; it is almost certainly referable to *D. umbellata* (see p. 221).

Canu & Bassler (1923 : 77) described, as *C. haidingeri*, fossil specimens from Europe, in which the zooecia were large, like those of *C. multispinata*. *C. haidingeri* as defined by Lagaaij (1952 : 35) has small zooecia like *C. owenii*. Canu & Bassler gave a Lz of 0.60 mm., and measurements taken from their pl. 1, fig. 15 give an average length of 0.58 mm. It should be noted here that whereas the measurements given by Canu & Bassler for their *C. haidingeri* apparently include the vibraculum, those given for their *C. multispinata* are found (when compared with text-figure 13H), not to include it.

The specimens from Madeira referred by Silén to *C. owenii* have been re-examined, they belong to *C. multispinata*.

In west African collections where both *C. multispinata* and *C. owenii* are found, the basal surface of unworn colonies is so different that the two species may be distinguished by it even in young specimens.

The distribution of Recent specimens of *C. multispinata* is restricted to two areas: the northerly, from the south west Mediterranean to the coast of Senegal, and the southerly, off the the South African coast. Although there are differences between the two populations, the South African colonies being larger and more domed in shape, the characters of the zooecia are similar. *C. multispinata* has been recorded from depths of 7–105 m.

10 *Cupuladria owenii* (Gray)

(Pl. 2, figs. 3A, B, Text-fig. 2c)

Lunulites owenii Gray, 1828 : 8, pl. 3 figs. 15, 15a, 15b Coast of Africa.

Lunulites denticulata Conrad, 1841 : 348, Miocene, N. Carolina.

Lunulites denticulata Conrad : Lonsdale, 1845 : 503, text-figs. a, b, Miocene, N. Carolina.

Cupularia owenii (Gray) Busk, 1854 : 99, pl. 115, figs. 1–5, Coast of Africa.

Not *Cupularia denticulata* (Conrad) Busk, 1859 : 85 (= *C. haidingeri* (Reuss), see Lagaaij, 1952).

Cupularia denticulata (Conrad) Canu & Bassler, 1923 : 79, pl. 15, figs. 6–10, Miocene, N. Carolina and Florida, Pliocene, S. Carolina and Florida.

Lectotype, see Hastings (in press).

MATERIAL. "Calypso" Coll. I, Stn. 7*, 9° 40' N., 13° 53' W., 17.v.56, 18 m., C4H (C). Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C55G.

Marche-Marchad Coll. I. Konakrey, Guinée Ise., 2E (C). Flor de la bouteille, Guinée Ise, 2I.i.53, 8 m., 3A. S.W. Madeleines, 2I.i.54, 46–48 m., 46C.

III. Au sud de presque l'île du Cap Vert, 18.ii.54, 46–50 m., 1E. Mission Guinée Pte 50, Parages des Fles de Los, Konakrey, 2I.i.53, 19 m., 30A (C).

British Museum Coll. West coast of Africa, 1899. 7. 1. 4879, received from Gray,

Busk Coll. Canaries, M'Andrew, 1899. 7. 1. 1249, Busk Coll., and 1892. 6. 17. 1-4. Port of Oratava, Canaries, 1899. 7. 1. 1224, Busk Coll. South Africa, 1963. 1. 16. 12, O'Donoghue Coll. S. Africa, Cape Infanta N.E. by N. 19 miles, 46 fath., 1949. 11. 10. 622C, 623C, N.E. by N. $\frac{1}{2}$ N., 13 miles, 43 fath., 1949. 11. 10. 618B, N.E. by N. $\frac{1}{4}$ N., 14.5 miles, 45 fath., 1949. 11. 10. 621A; Great Fish River lighthouse N.E., 9 miles, 51 fath., 1949. 11. 10. 653A, Burrows Coll. Palaeontological Department, 2 miles S.W. Magnolia, S. Carolina, Duplin marl, Miocene, D 34410-18 and D 34419-30.

Naturhistoriska Riksmuseet, Stockholm. Atlantic, 27° 16' N., 23° 21' W., at the surface, FBS 312 part, (No. 7) (see p. 194).

Philadelphia Academy, Conrad Coll. Wilmington, N. Carolina.

U.S. Nat. Mus., Bassler Coll. Pliocene (Waccamaw marl), Waccamaw River, S. Carolina, No. 80710, Plesiotypes *C. denticulata*, fig'd. Canu & Bassler, 1923. Caloosahatchee marl, Pliocene, Florida.

C. owenii is not represented in the Achimota Coll.

Zoarium small (average diameter 5 mm.), zooecia small. Sides of vestibular arch curved, convergent, with a pair of well developed distal cryptocystal denticles. Operculum longer than wide, without a proximal sclerite. Descending cryptocyst finely tuberculate, with 4-6 denticles varying from wide, irregular denticles to narrow spinules. Central zooecia closed. Basal surface grooved, finely and regularly tuberculate or smooth and glassy.

DIMENSIONS. Lz 0.37-0.47 mm., lz 0.20-0.37 mm., La 0.32-0.35 mm., Lvo 0.08-0.13 mm., Ls 0.60-1.40 mm., Lo 0.07-0.09 mm., lo 0.09-0.10 mm.

The slide, 1899. 7. 1. 4879, which is labelled " West coast of Africa ", was received by Busk from Gray. It consists of two fragments, one of which was figured by Busk (1854, pl. 115, fig. 3), see Hastings (in press). The frontal of Gray's specimen is worn, but shows the small zooecia and convergent vestibular arch. The basal surface is smooth, glassy and grooved, a condition found in many specimens from the Marche-Marchad Collection. Specimens from the Achimota Collection have a finely tuberculate basal surface, but also show that the smooth type is not an effect of wear. Some colonies have the more central parts smooth and the later growth tuberculate; whilst in others the position of these types of surface is reversed.

The identity of *L. denticulata* Conrad with *L. owenii* Gray was suggested by Lonsdale (1845: 503), who also described the closed, central zooecia. Specimens of *C. denticulata* from Conrad's Collection, from Wilmington, N. Carolina, and from Bassler's Collection, from S. Carolina and Florida, agree in all respects with the type of *C. owenii* and thus extend its range in time and space to the Miocene and Pliocene of North America. The fossil material shows a similar range in variation of characters of both frontal and basal surface to that of Recent zoaria from west Africa. The specimens from the Caloosahatchee marl are small, the largest zoarium having a diameter of 4 mm., the smallest of 2 mm.; and those from the Waccamaw marl are generally larger and flatter. A few zoaria from Caloosahatchee have a growth form approaching that of *C. doma*; the basal concavity being nearly filled by secondary

calcification. However, the surface is still finely tuberculate, and there are no peripheral closed zooecia or enlarged vibracula (see below).

Generally, the small size of the zooecia distinguishes colonies of *C. owenii* from those of *C. multispinata*, even to the naked eye. In young colonies, the size of some of the zooecia may be similar, but the zoaria may then be separated by the basal surface (see above). In well preserved colonies of *C. owenii*, the strongly incurved vestibular arch, with the distinct distal denticles, is completely unlike that of *C. multispinata*, and resembles that of *C. doma*, from which *C. owenii* is distinguished by the absence of any trace of proximal sclerite on the operculum, the basal surface, and by the absence of peripheral kenozoecia or enlarged vibracula. *C. owenii* is very similar to the European fossil *C. haidingeri* (Reuss) (see Lagaaij, 1952 : 35, 1953), but differs in its finely tuberculate or smooth basal surface. A specimen of *D. owenii* (Marche-Marchad Coll. III, 30A) has a regenerated zoarium where many of the first zooecia budded from the edge of the fragment have become closed in the same manner as the ancestrular zooecia of other colonies.

The S. African zoaria are slightly larger and more domed than those from west Africa, and the distal pair of denticles is less well developed. The small zooecia and the glassy basal surface distinguish them from S. African colonies of *C. multispinata*.

The Recent distribution of *C. owenii* appears to be restricted to the African coast where it is known from the Canaries to the Bay of Biafra, and off S. Africa. It has not been found from depths of more than 95 m., and for this reason is unlikely to have been the species listed by Calvet (1907 : 393) from 1900 m., Cape Verde Islands, as "*Cupularia umbellata* . . . a la forme de *denticulata* de Conrad" (see p. 222).

II *Cupuladria owenii* subsp. *disciformis* n. subsp.

(Pl. 2, figs. 1A, B, Text-figs. 2a, b)

HOLOTYPE. Museum d'Histoire naturelle, Paris, C43A, pt.

PARATYPES. "Calypso" Coll. I. Stn. P1, entre Pta da Mina et I. S. Ana, 21.vi.56, 10-12 m., C44A. Stn. P7*, entre Pta da Mina et P. Novo Destino, 26.vi.56, 6 m., C47A. Stn. P8, I. S. Ana, 27.vi.56, 2-4 m., C43A.

C. owenii disciformis is not present in the Marche-Marchad nor the Achimota Collections.

Zoarium flattened, disc-like, average diameter 7 mm. Zooecia small, narrow, Cryptocyst descending steeply, with 2-4 small, simple denticles. Sides of vestibular arch not strongly convergent, distal denticles weakly developed. Central zooecia closed. Opercula wider than long. Basal surface with grooves and fine tubercles. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.37-0.53 mm., lz 0.20-0.35 mm., La 0.40 mm., Lvo 0.09-0.10 mm., Ls 0.60-0.90 mm., Lo 0.05-0.06 mm., lo 0.11-0.12 mm.

At first sight, this form is so unlike *C. owenii* that it might be thought to be a distinct species. Detailed examination of the colonies shows, however, that some zooecia have a vestibular arch with convergent sides, and more numerous cryptocystal

denticles, than others. These zooecia approach those of *C. owenii* in appearance. The vestibular arch varies in character in *C. owenii* (see above), and it is possible that a series of forms might be found linking the two extremes of variation.

This population was collected from one small area in the Bay of Biafra, from very shallow water. The zoaria all have polypides, and chitinous parts intact. They were associated with many specimens of *Caulibugula* sp., which were not, however, attached to the lunulitiform zoaria.

C. owenii disciformis is separated here because each of the large number of colonies examined (over 100), shows a high level of consistency of correlation of the characters distinguishing them from typical *C. owenii*. These characters are: the flattened shape; the slightly larger zooecia and coarser basal tubercles; the shallow opercula; and the reduction in cryptocystal denticles. In some zoaria, this reduction is such that the zooecia resemble those of *C. pyriformis* (Busk).

Studer (1889: 7, 13) listed *C. pyriformis* from west Africa, but it seems unlikely that it occurs anywhere in the eastern Atlantic (see Cook, 1965, 169). Although Studer's record may have belonged to *C. canariensis* or *C. biporosa*, it is also possible that the specimens were of *C. o. disciformis*, which, like *C. pyriformis*, has a ridged, finely tuberculate basal surface.

Five unnamed fossil specimens from France have similar characters to those of *C. o. disciformis*. Two zoaria are from the Burdigalian of Léognan (Lower Miocene, S. of Bordeaux, Gironde, D 25002 and 25004); they are very flat, regenerated fragments. The remaining three zoaria are from the Pliocene of Biot (near Antibes, D 49301-3); they are slightly more domed, and originate from ancestrula. The zooecia of all the specimens are slightly larger than those of *C. o. disciformis* (Lz 0.40-0.57 mm.), but like them, nearly all have a vestibular arch with divergent sides, and rarely more than 3 small lateral cryptocyst denticles. The basal surface of all the colonies is finely tuberculate. No reference has been found in the literature to this form, and further material would have to be examined before its relationship with *C. o. disciformis* could be established.

12 *Cupuladria doma* (d'Orbigny)

(Pl. 1, fig. 7, Text-figs. 2e, 3)

Discoflustrella doma d'Orbigny, 1853: 561, Recent, Algeria.

Cupularia johnsoni Busk, 1859a: 67, pl. 23, figs. 1-5, Madeira. Norman (part), 1909: 290, pl. 38, figs. 1-4, Madeira (not figs. 5-6 = *C. multispinata*, see p. 210). Canu, 1917: 139. Waters, 1921: 413, pl. 29, fig. 17, pl. 30, figs. 23, 30, 31, Oran, Madeira.

Cupularia doma (d'Orb.) Smitt, 1873: 15, pl. 3, figs. 81-84, Florida, 29 fath. Canu & Bassler, 1923: 77, pl. 1, fig. 15, pl. 15, figs. 1-5, Miocene, N. Carolina. 1928: 64, pl. 6, figs. 2-5, Florida, 56 fath. 1928a: 23, pl. 2, figs. 1-4, Cap Blanc, 20-30 m.

?*Cupularia reussiana* Manzoni: Neviani (part), 1895: 102, Recent, Algeria.

Discoporella doma (d'Orbigny) McGuirt, 1941: 64, pl. 2, figs. 1, 4, Miocene, Louisiana. Maturo, 1957: 41, figs. 48, 49, N. Carolina. Cheetham & Sandberg, 1964: 1022, text-fig. 15, Quaternary, Louisiana.

Cupuladria doma (d'Orbigny) Gautier, 1962: 54, Algeria, 75-80 m.

MATERIAL. "Calypso" Coll. I, Stn. 1*, 21° 05' N., 17° 14' W., 10.v.56, 43-45 m., C1H.

Marche-Marchad Coll. I, Konakrey, Guinée Ise, 2D. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3D. Sud de Gorée, 27.x.53, 38-42 m., 7A; 24.xi.53, 40 m., 8A; 39.5 m., 9F; 40-41 m., 11G. Baie de Seminole, 8.xii.53, 38 m., 39B. S.W. Madeleines, 15.ix.53, 48 m., 22A; 9.i.54, 45-49 m., 26F; 21.i.54, 46-48 m., 46D. Sud de presque l'île du Cap Vert, 18.ii.54, 95 m., 33B.

Coll. II. Alignment Gorée, Cap Manuel, hauteur de Madeleines, 19.x.56, 35-42 m., 9A. S.W. Madeleines, 9.i.54, 47.5 m., 31C. Baie de Seminole, 8.xii.53, 38 m., 36B.

Coll. III. Sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1F. Sud de Gorée, 13.xi.53, 33-35 m., 9D. Either as above or S.W. Madeleine, 15.ix.53, 48 m., 16H and 17D. Dragage 1 "Gerard Freca", 18.ii.54, 23H; Dr. 4, 97-98 m., 28F; Dr. 5, 15D, 27E. 27.xi.53, 33-34 m., 29F. No information, 24J.

British Museum Coll. Madeira, 1879. 5. 28. 6, and 1911. 10. 1. 649, 650, 1912. 12. 21. 1003, Norman Coll; Bay of Funchal, 50 m., 1963. 2. 28. 5, Cook Coll., mud*. Canaries, 1899. 7. 1. 1240, Busk Coll. Mediterranean, 1899. 7. 1. 1243, 152 fath.; 1242, 5-51 fath.; 1245, 151 fath., Busk Coll. Tangier, 1899. 7. 1. 1244, 164, Busk Coll. Râs el-Amouch, Algeria, 1899. 7. 1. 1247; 1245, 45 fath., Busk Coll. Oran, 1903. 3. 6. 1-4, and 1911. 10. 1. 645, Norman Coll. Gulf of Mexico, 28° 45' N., 85° 2' W., 30 fath., Stn. 2405, "Albatross", 1932. 3. 7. 102, Canu & Bassler Coll. S.S.W. John's Pass, Florida, 34 fath. 1959. 1. 6. 5, Lagaaij Coll.

C. doma is not represented in the Achimota Collection.

Zoarium small (average diameter 4.5 mm.), steep-sided, sometimes solid basally. Zooecia small, vestibular arch strongly curved, with well developed distal cryptocystal denticles. Operculum with a complete or partial proximal sclerite. Cryptocyst descending gently, with wide denticles which occasionally fuse proximally. Basal surface frequently solid, grooved or smooth, or with a small central cavity with elongated spiny tubercles. Central zooecia and those at the periphery closed in fully grown colonies. Peripheral vibracula enlarged, occasionally more than one series developed. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.34-0.42 mm., lz 0.30-0.37 mm., La 0.34-0.37 mm., Lvo 0.09-0.19 (peripheral) mm., Ls 0.50-1.70 mm. (peripheral), Lop 0.07-0.10 mm., lop 0.10-0.12 mm.

D'Orbigny's description of *Discofustrella* mentions the "Gros pore spécial" (= vibraculum) in front of each zooecium, and his specimens of *D. doma* were examined and their identity confirmed by Smitt (see below). D'Orbigny also described and figured *Discofustrellaria doma* (p. 509, pl. 722, figs. 6-10), a Cretaceous fossil, probably referable to *Lunulites* (see Waters, 1921: 408).

Unfortunately, Canu and Bassler (1923: 77) confused the two references and quoted "*Discofustrellaria doma* d'Orbigny, p. 561" in their synonymy, a combination followed by Gautier (1962: 54), and by Annoscia (1963: 227, as *Discofustrellaria* (sic)).

Smitt compared his specimens from Florida with Algerian material from Busk ; he also examined specimens in d'Orbigny's Collection (see Canu & Bassler, 1923 : 78), as did Canu (1917 : 139), who, nevertheless, still placed *C. doma* in the synonymy of *C. johnsoni*. There has been some confusion of *C. doma* with *Discoporella reussiana* (see below). Specimens labelled "*C. reussiana*", some from Levinsen (1903. 3. 6. 1-4), others in the Norman Collection (1911. 10. 1. 645), are referable to *C. doma*.

The west African material shows a range in development of the proximal opercular sclerite, which is, for example, complete in Marche-Marchad Coll. I 39B, but only partial, and absent centrally in Coll. II 9A.

The basal surface of *C. doma* may consist of a concavity, with long spinous tubercles, or be flat, and smooth or tuberculate. Although the solid state is apparently an effect of age, it is not correlated with growth in a simple manner, as very small colonies may have flattened bases, whereas in larger zoaria they may be concave. There seems, however, to be a correlation between the occurrence of peripheral kenozoecia and a flattened, solid basal surface, and presumably a colony at this stage does not grow further, as no zoarium has been found with new zooecia budding from closed peripheral kenozoecia. In these fully grown colonies, there may be several series of peripheral vibracula ; they are enlarged, and their setae may be much longer than those of the rest of the colony. The intervening kenozoecia are still present, but have become progressively smaller, until the zoarium has the appearance of possessing two or three rows of vibracula only at the periphery. A section through a zoarium shows that the cavity of each zooecium is present, but that the angle of its longitudinal axis in relation to the axis of the colony is such, that its projection on to the plane of the zoarial surface is very small. Thus, when the opesia is closed by calcification, the kenozoecial frontal is hardly noticeable, and the enlarged vibracular chambers appear to be adjacent to each other (see Text-fig. 3).

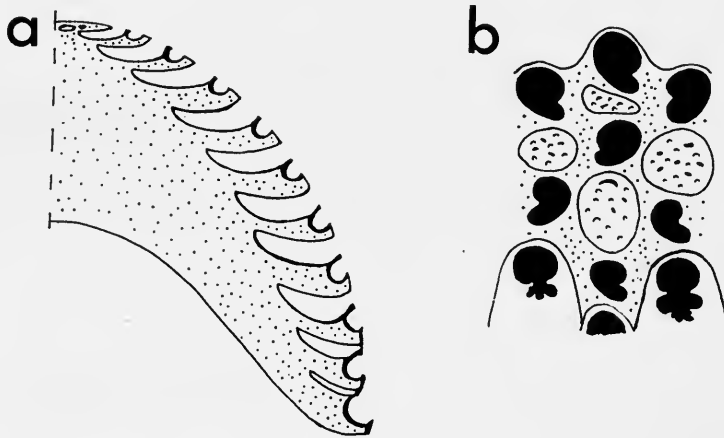


FIG. 3. *Cupuladria doma*, closed peripheral zooecia, drawings semi-diagrammatic. a. Section through a zoarium, $\times 20$. b. Frontal view of enlarged peripheral vibracula and closed peripheral zooecia, $\times 40$.

There may be some relationship between the presence of closed peripheral zooecia and the form of the zoarium. Although the closed zooecia are typical of *C. doma* they may also occur in specimens of other species which develop apparently aberrant small, high zoaria with a solid base (see Cook, 1965 : 162, and p. 208). Duvergier (1924 : 20) mentioned that some specimens of *C. porosa* Busk (= *C. haidingeri* (Reuss), see Lagaij, 1952 : 36) had two rows of peripheral zooecia.

C. doma is very similar in many features to *C. owenii*, which occasionally develops small high colonies (see p. 215), but it may be distinguished by its slightly smaller zooecia, its basal surface, and the presence of a proximal sclerite on the operculum.

The African distribution of *C. doma* is confined to the more northerly coasts from Algeria to Senegal, and includes the Canaries and Madeira, but not the Cape Verde Islands. It extends to greater depths than *C. owenii*, and has been recorded from 8–369 m.

13 *DISCOPORELLA* d'Orbigny

Discoporella d'Orbigny, 1852 : 472. Hastings 1930 : 718. Cheetham & Sandberg, 1964 : 1022.

TYPE-SPECIES *Lunulites umbellata* DeFrance, 1823, Miocene, France.

Zoarium lunulitiform. Zooecia with a well-developed vestibular arch. Horizontal cryptocyst lamina complete, formed of fused denticles. Opsiular indentations or closed opsiules present. Vibraculum distal to each zooecium. Vicarious vibracula absent. Basal surface grooved and tuberculate, not divided into sectors. Central zooecia closed.

14 *Discoporella reussiana* (Manzoni)

(Pl. 3, fig. 1, Text-fig. 2f)

Cupularia reussiana Manzoni, 1869 : 27, pl. 2, figs. 19, 19¹ (as 18, 18¹ in text), Tertiary, Italy. Waters, 1878 : 16, Pliocene, Italy. Canu & Bassler, 1923 : 78, pl. 1, figs. 19–22, Pliocene, Italy.

Cupuladria reussiana (Manzoni) Annoscia, 1963 : 226, pl. 9, fig. 2, pl. 10, fig. 2, pl. 13, fig. 1, pl. 14, figs. 1a, 1b, Quaternary, Italy.

MATERIAL. "Calypso" Coll. Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48D (C), with *Cleidochasma porcellanum* (Busk), C55L.

D. reussiana is not represented in the Marche-Marchad nor Achimota Collections.

Zoarium domed, sometimes higher than wide (average diameter 6 mm.). Zooecia wide, proximal part of vestibular arch strongly curved and flanged. Cryptocyst descending gently at first, coarsely tuberculate. Horizontal cryptocyst formed by fusion of wide, irregularly shaped denticles, with 2–4 pores. Distal pair of denticles forming a bar, with a wide tooth protruding distally into the opesia, forming two lateral opsiular indentations. Basal surface grooved with large tubercles, which obscure the slight threads marking the grooves in peripheral zooecia.

DIMENSIONS. Lz 0.48–0.60 mm., lz 0.30–0.42 mm., La 0.36 mm., Lvo 0.14–0.17 mm.

Norman (1909 : 290) included *C. reussiana* Manzoni in his synonymy of *C. johnsoni*, and Waters (1878 : 16) placed *C. doma* Smitt (sic) in the synonymy of *C. reussiana*. Neviani (1895 : 102) included *C. doma* in the distribution of *C. reussiana*, giving the localities of Recent specimens as Algeria and Florida.

There is no doubt that the "Calypso" specimens are referable to Manzoni's species, which has hitherto been described only from European Tertiary and Quaternary deposits. Manzoni's fig. 19 shows the large cryptocystal pores and the toothed distal bar which is not present in the majority of the zooecia figured by Canu & Bassler.

D. reussiana resembles *C. doma* and *C. owenii* in the strongly flanged vestibular arch, but the horizontal cryptocyst lamina is similar to that of *D. ocellata*, (see below) and forms a link in the series of species of which the end term is *D. umbellata*.

The specimens of *C. canariensis*, *C. owenii*, *D. reussiana* and *D. ocellata* from "Calypso" Stn. 45, in the Bay of Biafra, are all dark grey in colour, quite unlike those of the other west African localities, which are light brown. Those of *D. reussiana* have no chitinous parts and some are worn, but, as polypides are present in the zooecia of the majority of zoaria of the other 3 species, it is improbable that the specimens of *D. reussiana* are displaced fossils, and therefore it must be presumed that the species has existed continuously from Tertiary times.

15 *Discoporella ocellata* n.sp.

(Pl. 3, fig. 2, Text-fig. 2g)

MATERIAL. HOLOTYPE, Museum d'Histoire naturelle, Paris, C48C pt.

"Calypso" Coll. I, Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48C, C55K Lagaaij Coll., Nigeria D. 220.

D. ocellata is not represented in the Marche-Marchad nor Achimota Collections.

Zoarium fairly large (average diameter 8 mm.). Zooecia with lateral cryptocyst descending moderately at first, then salient, forming a narrow shelf. Horizontal cryptocyst lamina formed by fusion of wide, irregular denticles originating on the frontal side of the shelf. Vestibular arch with two curved flanges uniting centrally with each other below the orifice, and with the fused distal lateral denticles, forming a sinuate opesia with two closed lateral opesiules. Operculum without a basal sclerite. Basal surface grooved, grooves marked by a thread, not obscured by the irregular tubercles.

DIMENSIONS. Lz 0.55-0.63 mm., lz 0.36-0.42 mm., Lvo 0.10-0.14 mm., Ls 0.70-2.00 mm., Lo 0.10-0.12 mm., lo 0.12-0.15 mm.

The zoaria are more flattened than those of *D. reussiana*. In worn specimens of *D. ocellata* the proximal bar between the opesia and opesiules may be broken, producing a trifoliate opesia very similar to that of *D. reussiana*. The slope of the cryptocyst and position of the origin of the cryptocystal denticles are then the only features distinguishing the species on the frontal surface. In *D. ocellata* the cryptocyst descends moderately at first, then becoming salient, forming a shelf, which may be seen distally and below the horizontal denticles which originate above the angle produced by the change of slope (see Text-fig. 2g). In *D. reussiana* the descent of the

cryptocyst is at first gentle and then, after the origin of the horizontal denticles, steep, so that no shelf is visible below them (see Text-fig. 2f).

There is a superficial resemblance between *D. ocellata* and the photographs of *Cupularia bioculata* Canu (1904: 10, pl. 2, figs. 21, 22, Miocene, Patagonia). *C. bioculata* is shown with a sinuate opesia and a pair of opesiules. None of the zooecia has a distal vibraculum, and the occasional large individuals may be broken vicarious vibracula. The absence of small vibracula excludes it from the Cupuladriidae, and it is perhaps referable to *Selenaria*.

D. ocellata is related to both *D. reussiana* and *D. umbellata* and forms an important link between those species. It differs from *D. reussiana* in its closed opesiules and basal surface, and from *D. umbellata* in its sinuate opesia, basal surface, and operculum, which has no proximal sclerite.

16 *Discoporella umbellata* (Defrance)

(Pl. 3, fig. 3, Text-fig. 2h)

Lunulites umbellata Defrance, 1823: 361, pl. 47, figs. 1a, 1b, Miocene, France.

Cupularia lowei Busk, 1854: 99, pl. 116, figs. 1-6.

Discoporella umbellata (Defrance): Lagaij, 1953: 16, pl. 1, fig. 3, Miocene, Netherlands. Cook, 1965: 177, pl. 1, fig. 7, pl. 3, figs. 1, 3, 5, 6, text-fig. 4.

MATERIAL. "Calypso" Coll. I, Stn. 7*, 9° 40' N., 13° 53' 5" W., 17.v.56, 18 m., C4G. Stn. 17, 5° N., 5° 28' 30" W., 21.v.56, 27 m., C56G (C). Stn. 18, 5° 2' 5" N., 5° 24' 4" W., 21.v.56, 20-25 m., C5D. Stn. 19, 5° 2' 30" N., 5° 24' 40" W., 21.v.56, 21-27 m., C57I. Stn. 29*, 4° 3' N., 6° 12' E., 26.v.56, 32 m., C49A. Stn. 45*, 0° 25' N., 9° 0' E., 8.vi.56, 73 m., C48A (with *Labioporella dipla* Marcus and *Cleidochasma porcellanum* (Busk)), C55H. Stn. 63, 0° 20' N., 6° 47' E., 17.vi.56, 54-40 m., C28A. Stn. 77, 0° 25' 40" N., 6° 40' 10" E., 21.vi.56, 50 m., C45A. Stn. 90*, 1° 36' 55" N., 7° 22' E., 26.vi.56, 30 m., C37B. Stn. P14*, Dans l'axe de la Baie, Principe, 29.vi.56, 15 m., C59A.

Coll. II. Stn. 73, C72A. Stn. 88, 16° 15' N., 22° 56' 5" W., 26.xi.59, 54 m., C80A.

Marche-Marchad Coll. I. Konakrey, Guinée Ise, 1G, 2F. Flor de la bouteille, Guinée Ise, 21.i.53, 8 m., 3C. Sud de Gorée, 27.x.53, 38-42 m., 7C. S.W. Madeleines, 15.ix.53, 48 m., 20C; and 21.i.54, 46-48 m., 46F (C). Presque l'île du Cap Vert, 18.ii.54, 95 m., 33P (C). Baie de Seminoles, 8.xii.53, 38 m., 39D (C).

Coll. II, as above, 36C. Alignment Gorée-Cap Manuel, lantern de Madeleines, 19.x.56, 35-42 m., 9B (C), 20-25 miles au large de Saloum, 8.iii.55, 35-37 m., 26A (C).

Coll. III. Au sud de presque l'île du Cap Vert, 18.ii.54, 46-50 m., 1D. Either S.W. Madeleines, 15.ix.53, 48 m., or Sud de Gorée, 34-37 m., 13.xi.53, 16F. Dragage 4, "Gerard Freca", 97-98 m., 28H; Dr. 5, 18.ii.54, 15C, 27D. 33-34 m., 27.xi.53, 29D. Museum Guinée, parages de Flos de Los, Konakrey, 21.i.53, 9 m., 30B. No information, 24H.

Achimota Coll. I, Stn. 47*, Dredge Haul No. 1, 4.i.51, 44 m., 14d. Stn. 48*,

Dredge Haul No. 2, as above, 22C. Stn. 111*, Agassiz Trawl No. 2, 4.iv.51, 43 m., 49P. Stn. 132,* as above, 2.v.51, 44 m., 42E and 50B (C). Stn. 133*, Agassiz Trawl No. 3, as above, 51 m., 45H. Coll. II, Stn. 133*, see above, 7A. Stn. 111*, see above, 12A.

Zoarium frequently very large (maximum diameter measured, 30 mm.). Zooecia wide, opesia small, nearly straight proximally, with a pair of small denticles. Operculum with a stout proximal sclerite. Lateral cryptocyst descending gently, tuberculate, horizontal cryptocyst a complete lamina, with 8-14 small peripheral opesiules and small scattered central pores, which are frequently occluded. Vibracular opesia large, proximal edge denticulate. Basal surface with short grooves, irregular pits and tubercles. Tentacles 13-16 (see p. 203).

DIMENSIONS. Lz 0.60-0.70 mm., lz 0.45-0.65 mm., La 0.40-0.43 mm., Lvo 0.20-0.25 mm., Ls 0.90-1.65 mm., Lo 0.10-0.12 mm., lo 0.12-0.15 mm., Lop 0.13-0.15 mm., lop 0.15-0.20 mm.

C. lowei Busk differs from *D. umbellata* only in its deformed zoaria (see p. 195 and cf. *C. multispinata*, p. 212). The majority of the specimens from the Marche-Marchad Collections II and III are deformed, most of those from Collection I, the "Calypso" Collections, and the Achimota Collection, are not.

The tubules which extend from the basal wall of the cystid cavity to the basal surface of the zoarium have been described by Marcus & Marcus (1962 : 295, pl. 2, fig. 5). In decalcified specimens these appear as minute strands, and were first described by Waters (1921 : 412, pl. 30, figs. 3, 5, 6). Their presence in *D. umbellata* (subsp. *depressa*) was noted by Hastings (1930 : 719), and they are clearly seen in specimens from Rio de Janeiro (British Antarctic Expedition Coll., Stn. 42). The pore in the basal surface described by Waters is present in specimens of *D. umbellata* from Senegal (Marche-Marchad Coll. I 39D). It is present in all peripheral zooecia and remains open in the majority of zooecia of young colonies. In older colonies it becomes obscured by the increasing development of tuberculate secondary calcification. A short groove may be seen in peripheral zooecia running proximally and distally from the pore. As stated by Waters (who described them as muscles), the tubules appear to be inserted into the basal wall along or near the groove. Decalcified specimens from Rio de Janeiro show a small granular mass which corresponds in position to the basal pore.

Calvet (1907 : 393) recorded *D. umbellata* from Madeira (80 m.) and a specimen from the Cape Verde Islands (1900 m.) which was described as "à la forme de *denticulata* de Conrad". In view of the depth given, it seems unlikely to be *C. owenii* (see p. 213), which does not extend to great depths, and it may have been a colony of *D. umbellata*, in which the cryptocyst was worn away or damaged.

Specimens of *D. umbellata* from west Africa are consistent in character, and although larger, agree with the European fossil material. The wide zooecia, the nearly straight proximal edge of the opesia, with its two denticles, and the denticulate edge of the proximal vibracula opesia, are all features not found in the fossil and Recent specimens from the western Atlantic and eastern Pacific which have been separated

as *D. umbellata* subsp. *depressa* (Conrad) (see Cook, 1965 : 180). The development of the horizontal cryptocyst lamina in young peripheral zoecia, however, shows the close relationship of *D. umbellata* to both the subspecies *depressa* and to the denticulate species of *Cupuladria*.

The distribution of *D. umbellata* in these collections extends from Senegal to the Bay of Biafra, and includes the Cape Verde Islands. Recent specimens have also been recorded from Madeira and the Canaries. The recorded bathymetrical range is from 8–130 m.

Dr. R. Lagaaij (*in litt*) 20. x. 64 has drawn my attention to the two distinct species figured as *Lunulites rhomboidalis* by Münster (in Goldfuss, 1829 : 105, pl. 37, figs. 7a–c), from the German Tertiary deposits. Figure 7a greatly resembles a young colony of *Discoporella umbellata*, although no opesiules, and very few vibracula, are figured. Figures 7b and c are the frontal and basal views respectively of a regenerated fragment of a species of *Cupuladria*. Dr. Lagaaij remarks "Of the two localities mentioned on p. 106, that of Kassel is now considered the type locality of the Chattian (Upper Oligocene)" (see Drooger, 1964 : 372), "this would not fit with the presence of *D. umbellata* which first appears in the Aquitanian (Lower Miocene)". In this connection, it should be noted that neither Philippi (1844 : 3) nor Reuss (1865 : 685), who both listed *L. rhomboidalis*, had found specimens in their material.

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18 SUMMARY

Nine species belonging to the family Cupuladriidae are described, eight of which occur in west African waters.

Cupuladria canariensis is defined and distinguished from *C. biporosa*; *C. monotrema* is also described, and the occurrence of vicarious vibracula in the three species is discussed.

Three species with denticulate cryptocysts, *C. multispinata*, *C. owenii* and *C. doma*, are defined and distinguished, and a new subspecies, *C. owenii disciformis*, characteristic of very shallow waters in the Bay of Biafra, is described.

The genus *Discoporella* is defined, and three species are described, in which the development of the horizontal cryptocyst lamina is increasingly complex. *D. reussiana*, hitherto recorded as a fossil only, shows similarities with both the denti-

culate species of *Cupuladria* and with *D. umbellata*. *D. ocellata*, a new species, links the zoecial characters of *D. reussiana* and *D. umbellata*.

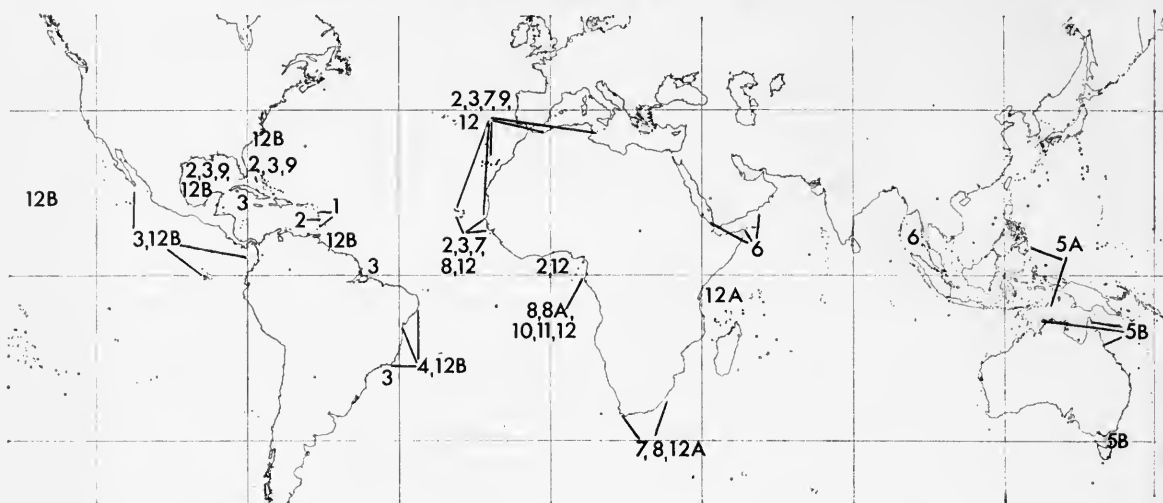


FIG. 4. Distribution of Recent Cupuladriidae. 1. *Cupuladria pyriformis*. 2. *C. canariensis*. 3. *C. biporosa*. 4. *C. monotrema*. 5. *C. guineensis*, A = A form, B = B form. 6. *C. indica*. 7. *C. multispinata*. 8. *C. owenii*. 8A. *C. owenii disciformis*. 9. *C. doma*. 10. *Discoporella reussiana*. 11. *D. ocellata*. 12. *D. umbellata*. 12A. *D. umbellata, peyroti*-type zoaria. 12B. *D. umbellata depressa*. (For notes on species 1, 5, 6, 12A and B, see Cook, 1965).

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PLATE I

Cupuladria, zoaria treated with eau de javelle

- FIG. 1. *C. canariensis* (Busk) Barbados, 1962. I. 26. 2. A. Frontal view. B. Basal view. $\times 7.4$.
- FIG. 2. *C. biporosa* Canu & Bassler. Barbados, 1962. I. 26. 1. A. Frontal view, showing zooecia with wide lateral cryptocysts, and large vicarious vibracula. B. Basal view. $\times 7.4$.
- FIG. 3. *C. biporosa*. Yucatan, Naturhistoriska Riksmuseet, No. FBD 696. A. Frontal view. B. Basal view, showing basal kenozoecia covering the original substrate, cf. *C. canariensis*, fig. 1B. $\times 7.4$.
- FIG. 4. *C. biporosa*. West Indies, Naturhistoriska Riksmuseet, No. FBD 548, a Recent specimen, cf. figs. 6A, B, of a Miocene colony. A. Frontal view. B. Basal view. $\times 7.4$.
- FIG. 5. *C. biporosa*. Jamaica, Miocene, Bowden marl, United States National Museum, No. 80747 pt. Colony with aberrant *doma*-type growth, basal view, showing rows of peripheral vibracula. $\times 7.4$.
- FIG. 6. *C. biporosa*. Jamaica, Miocene, Bowden marl, United States National Museum, No. 80747 pt., cf. figs. 4A, B. A. Frontal view. B. Basal view. $\times 8.1$.
- FIG. 7. *C. doma* (d'Orbigny). Senegal, Marche-Marchad Coll., I, 33 B. Lateral view, showing closed peripheral zooecia. $\times 12$.

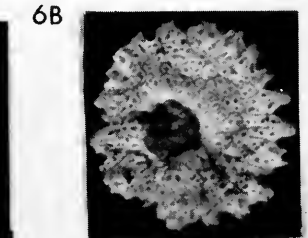
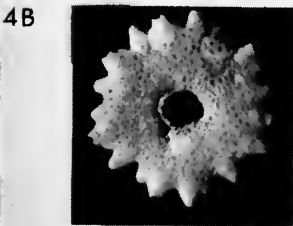
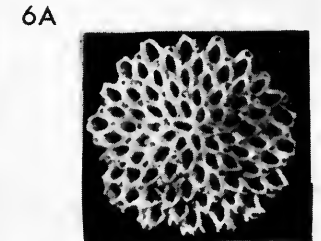
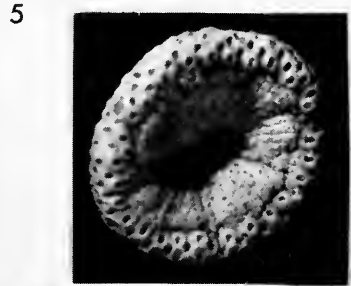
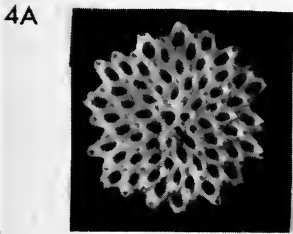
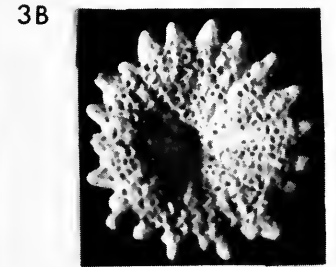
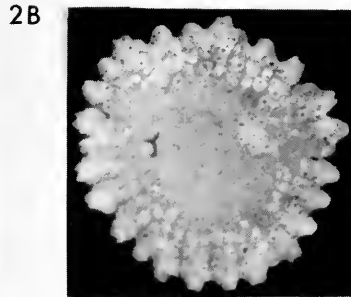
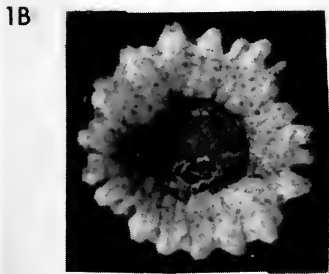
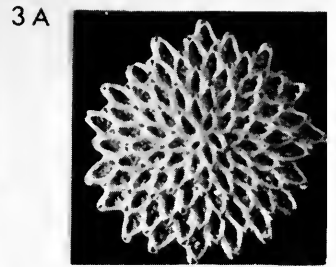
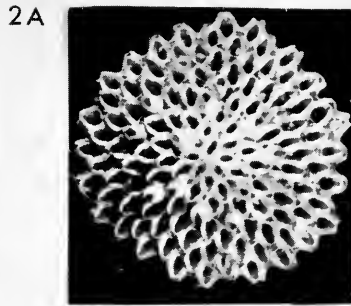
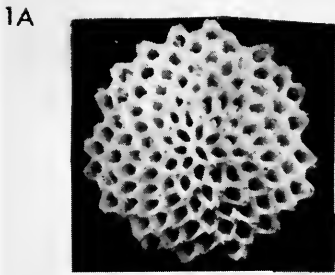


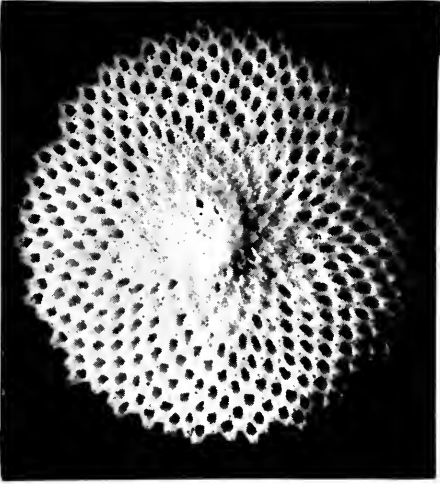
PLATE 2

Cupuladria, zoaria treated with eau de javelle

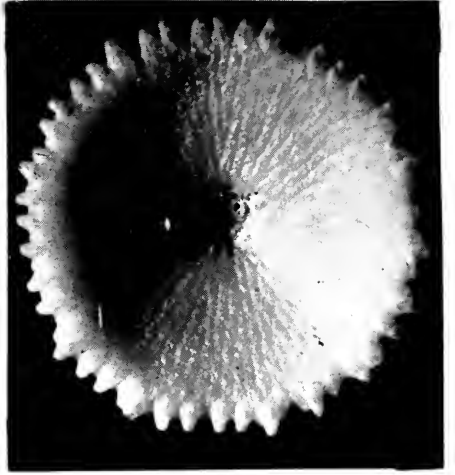
- FIG. 1. *C. owenii disciformis* n. subsp. Bay of Biafra, "Calypso" Coll., C47A. A. Frontal view, showing closed central zooecia, and reduced cryptocystal denticles of other zooecia. B. Basal view, showing fine tubercles. $\times 9$.
- FIG. 2. *C. multispinata* (Canu & Bassler). Senegal, Marche-Marchad Coll., I, 33 A. A. Frontal view, showing numerous cryptocystal denticles. B. Basal view, showing large tubercles and radial "threads". $\times 7.5$.
- FIG. 3. *C. owenii* (Gray). Senegal, "Calypso" Coll., I, C4H. A. Frontal view, showing closed central zooecia, and well-developed vestibular arches of other zooecia. B. Basal view, showing both smooth and finely tuberculate forms of basal calcification. $\times 10$.

N.B. Figures 2 and 3 are not reproduced at the same magnification, so that the marked difference in size between the zooecia of *C. multispinata* and *C. owenii* is not immediately apparent.

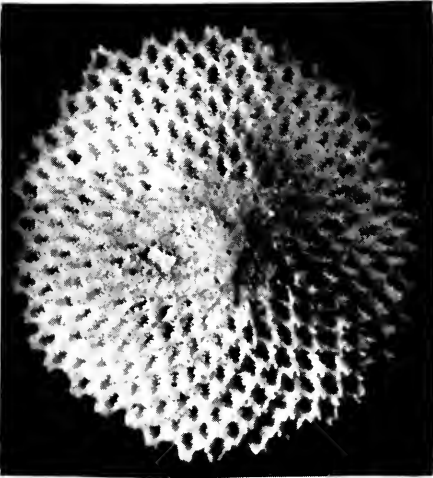
1A



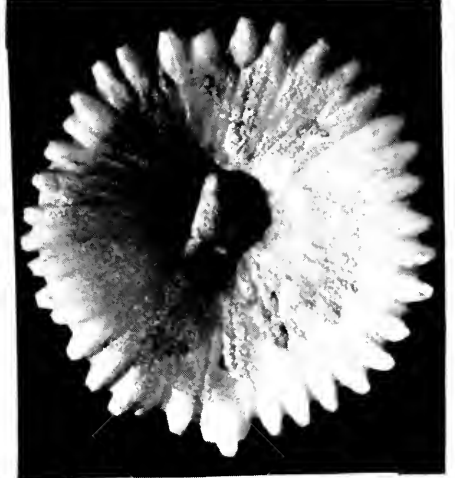
1B



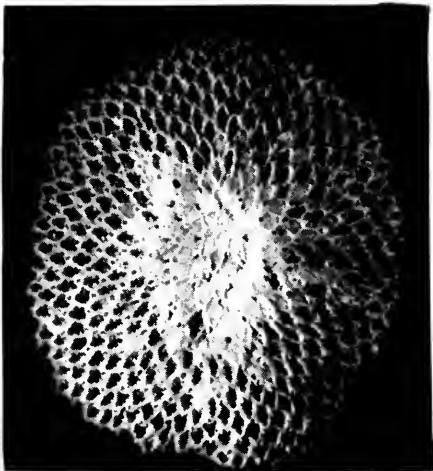
2A



2B



3A



3B

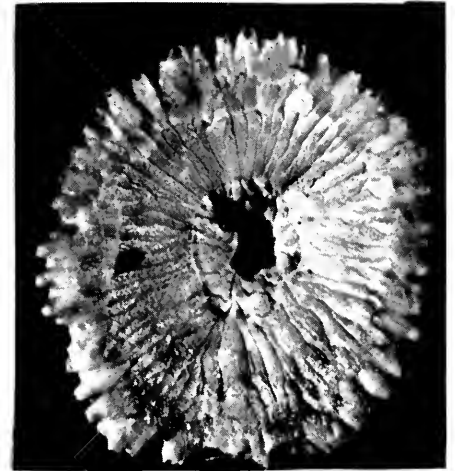
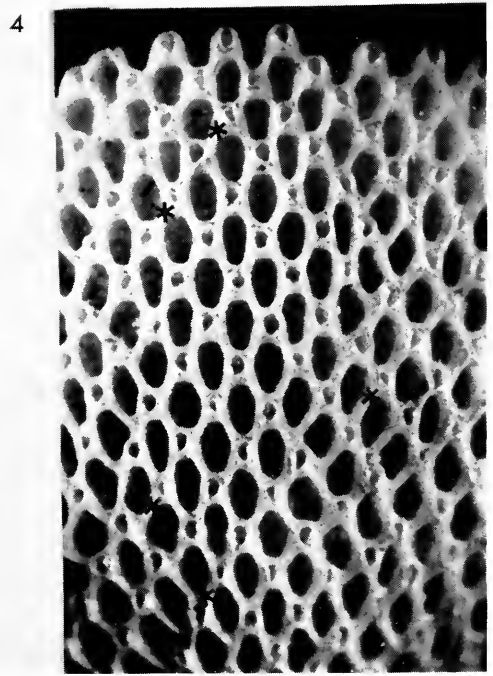
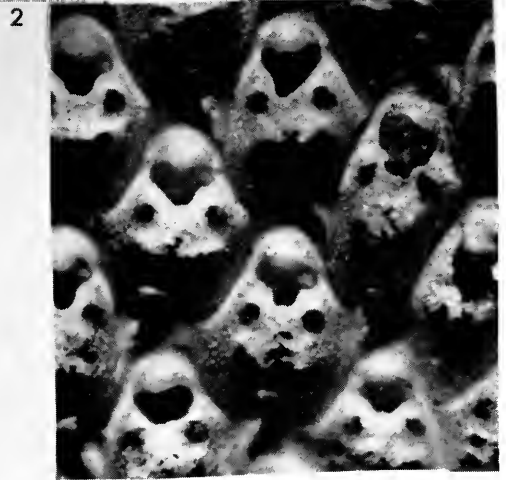
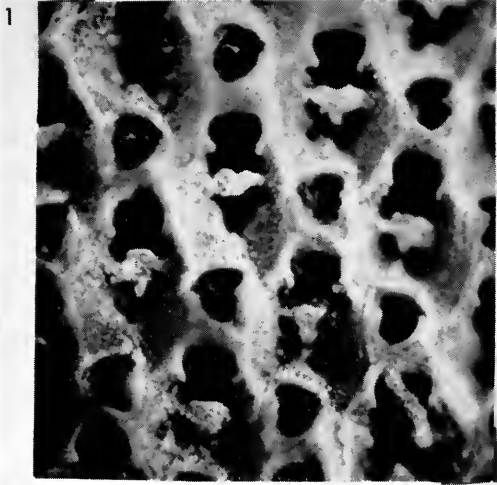


PLATE 3

Cupuladria and *Discoporella*, zooecia and vibracula treated with eau de javelle.


- FIG. 1. *D. reussiana* (Manzoni). Bay of Biafra, "Calypso" Coll., I, C48D. Zooecia showing toothed cryptocystal bar and opesiular indentations. $\times 49$.
- FIG. 2. *D. ocellata* n. sp. Bay of Biafra, "Calypso" Coll., C48C. Zooecia showing sinuate opesia and paired distal opesiules. $\times 53$.
- FIG. 3. *D. umbellata* (DeFrance). Ghana, Achimota Coll., II, 7A. Showing the slit indicating the former presence of an Acrothoracid Cirripede. $\times 32$.
- FIG. 4. *C. canariensis* (Busk). Senegal, Marche-Marchad Coll., II, 3A. Showing position of small, hooked vibracula thus: ***. $\times 24$.





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DESCRIPTIONS OF SOME
STRONGYLES (NEMATODA) FROM
MAMMALS IN EAST NEPAL: WITH
RECORDS OF OTHER PARASITIC
NEMATODES

WILLIAM G. INGLIS & COLIN G. OGDEN

BULLETIN OF
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ZOOLOGY

Vol. 13 No. 7

LONDON: 1965



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DESCRIPTIONS OF SOME STRONGYLES (NEMATODA) FROM MAMMALS IN EAST NEPAL: WITH RECORDS OF OTHER PARASITIC NEMATODES

By WILLIAM G. INGLIS & COLIN G. OGDEN

INTRODUCTION

ALTHOUGH the main zoological interest of the British Museum (Natural History) East Nepal Expedition: 1961-62 was in soil inhabiting invertebrates (Sheals & Inglis, 1965) the opportunity was taken, when possible, to collect helminth parasites. Among the nematodes collected are several new or rare species of Strongylina, which are described below, together with a list of the other species which were collected. Two new, non-strongyle species have been described elsewhere (Inglis & Ogden, 1965, 1965a).

List of All Species Collected

All host identifications were carried out by the staff of the British Museum (Natural History).

Felis bengalensis horsfieldi Gray, 1842. ♂. Hatia (27° 44' N., 87° 21' E.), Arun River, East Nepal. (22.xii.1961; 7,000 feet alt.).

Toxocara mystax (Zeder, 1800) ex small intestine.

Mastophorus muris (Gmelin, 1790) ex stomach.

Molineus (?) *patens* (Dujardin, 1845) ex stomach.

Molineus springsmithi sp. nov. ex small intestine.

Arthrostoma felineum Cameron, 1927 ex small intestine.

Arthrostoma tunkanati sp. nov. ex small intestine.

Callosciurus pygerythrus lokroides Hodgson, 1836. ♂. Popti La (27° 47' N., 87° 21' E.), Arun River, East Nepal. (22.xii.1961; 9,600 feet alt.)

Mastophorus sp. (♀♀ only) ex small intestine.

Rictularia dhanra Inglis & Ogden, 1965 ex intestine.

Brevistriata (?) *skrjabini* (Schulz & Lubimov, 1932) ex small intestine.

Longistriata gola sp. nov. ex small intestine.

Callosciurus maccllellandi maccllellandi Horsfield, 1839. ♀. Hatia (27° 44' N., 87° 21' E.), Arun River, East Nepal. (17.xii.1961; 7,500 feet alt.)

Citellina himalensis Inglis & Ogden, 1965 ex small intestine.

Brevistriata (?) *skrjabini* (Schulz & Lubimov, 1932) ex small intestine.

Longistriata (?) *gola* (♀♀, only) ex small intestine.

Suncus murinus caerulescens Shaw, 1800. ♀. Sanghu (27° 21' N., 87° 33' E.), Maewa Khola, East Nepal. (25.xi.1961; 6,500 feet alt.)

Capillaria minuta Chen, 1937 ex stomach.

Rattus rattus sikkimensis Hinton, 1919. juv. ♂. Sanghu (as above). (17.x.1961).

Nippostrongylus brasiliensis (Travassos, 1914) ex small intestine.

Rattus r. sikkimensis ♂. At same locality (6.xi.1961).

Nippostrongylus brasiliensis ex small intestine.

Rattus r. sikkimensis ♂. At same locality.

Heterakis spumosa (Schneider, 1866) ex caecum.

Rattus r. sikkimensis ♀. At same locality (21.x.1961).

Nippostrongylus brasiliensis ex small intestine.

Mastophorus muris ex stomach.

Heterakis spumosa ex intestine and caecum.

Rattus r. sikkimensis unsexed, at same locality (6.i.1962).

Heterakis spumosa ex caecum.

In addition two *Suncus m. caerulescens* and six *Rattus r. sikkimensis*, all caught at Sanghu between 7.xi.1961 and 5.iii.1962, were searched without finding any parasites.

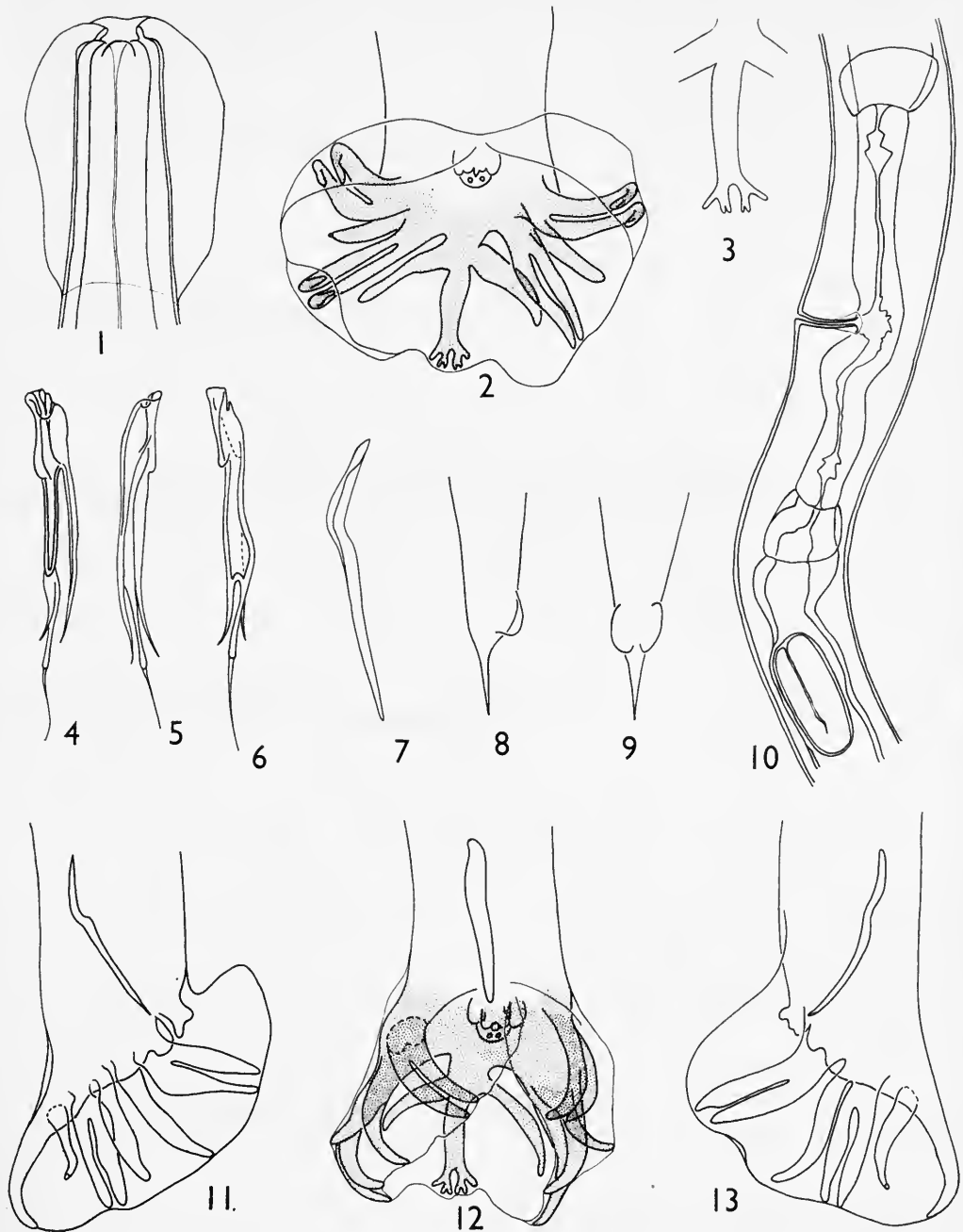
Descriptive Section

Molineus (?) *patens* (Dujardin, 1845)

MATERIAL STUDIED. 7 ♂, 3 ♀ ex stomach *Felis bengalensis horsfieldi*. Hatia, Arun River, East Nepal. B.M. (N.H.), Reg. Nos. 1965. 1-5.

MEASUREMENTS (in mm.). Males: Body length: 2.56; 2.64; 2.68; 2.78; 2.87; 2.91; 3.34. Body breadth: 0.053; 0.053; 0.055; 0.050; 0.051; 0.055; 0.054. Diameter of head: 0.022; 0.020; 0.017; 0.022; 0.022; 0.019; 0.023. Diameter of cephalic vesicle: 0.038; 0.030; 0.030; 0.034; 0.035; 0.031; 0.036. Length of cephalic vesicle: 0.060; 0.053; 0.054; 0.047; 0.051; 0.056; 0.054. Distance of cervical groove from anterior end of body: 0.153; 0.177; 0.159; 0.158; 0.188; 0.183; 0.177. Oesophagus length: 0.348; 0.347; 0.352; 0.366; 0.358; 0.298; 0.398. Length of spicules: 0.099; 0.107; 0.089; 0.100; 0.090; 0.103; 0.105. Length of gubernaculum: 0.051; 0.058; 0.047; 0.060; 0.046; 0.059; 0.064.

Females: Body length: 3.03; 3.55; 3.62. Body breadth: 0.063; 0.050; 0.072. Diameter of head: 0.023; 0.020; 0.022. Diameter of cephalic vesicle: 0.040; 0.030; 0.043. Length of cephalic vesicle: 0.056; 0.044; 0.060. Distance of cervical groove from anterior end of body: 0.160; 0.154; 0.201. Oesophagus length: 0.378; 0.316; 0.420. Length of tail: 0.064; 0.056; 0.068. Distance of vulva from posterior end of body: 0.588; 0.568; 0.622. Size of eggs: 0.054 × 0.027 to 0.075 × 0.031.



FIGS. 1-13. *Molineus* (?) *patens*. Fig. 1. Dorsal view of head showing the cephalic vesicle. Fig. 2. Ventral view of male bursa. Fig. 3. Detail of dorsal ray. Fig. 4. Spicule from the left. Fig. 5. Spicule from the right. Fig. 6. Dorso-lateral view of spicule. Fig. 7. Lateral view of gubernaculum. Fig. 8. Terminal region of female tail (lateral). Fig. 9. Terminal view of female tail (ventral). Fig. 10. Lateral view of vulvar region. Fig. 11. Lateral view of bursa from right-hand side (teratological). Fig. 12. Ventral view of bursa (teratological). Fig. 13. Lateral view of bursa from left-hand side (teratological).

The head bears the typical cephalic vesicle (Text-fig. 1).

The cuticle is marked by ten to twelve longitudinal ridges and the cervical groove is complete round the body although it is rather faint on the dorsal surface. No cervical papillae have been seen.

Male. The bursa is typical with the ventro-lateral and latero-ventral rays arising from a common base and the postero- and medio-laterals arising from a common base. The antero-lateral (or externo-lateral) ray does not reach the edge of the bursa. The externo-dorsal ray is given off some distance along the dorsal ray, and the latter ray bifurcates terminally twice with the internal small ray further divided just before the edge of the bursa (Text-figs. 2, 3 and 13).

The gubernaculum is fairly simple with a slight kink in its lateral outline (Text-figs. 7, 11 and 13) while the complex spicules are relatively slim and terminate posteriorly in three needle-like points, of which the median, and the longest, splits the spicule for about half its length (Text-figs. 4, 5 and 6). A small genital cone is present which carries two small papilla-like structures on its posterior edge (Text-figs. 2 and 12).

One teratological male is present in which there is an additional ray on the right-hand side of the bursa (Text-figs. 11 and 12) which arises between the typical externo-lateral and the pair of postero- and medio-laterals, and reaches the edge of the bursa (Text-fig. 11). The rays on the left-hand side are typical (Text-fig. 13).

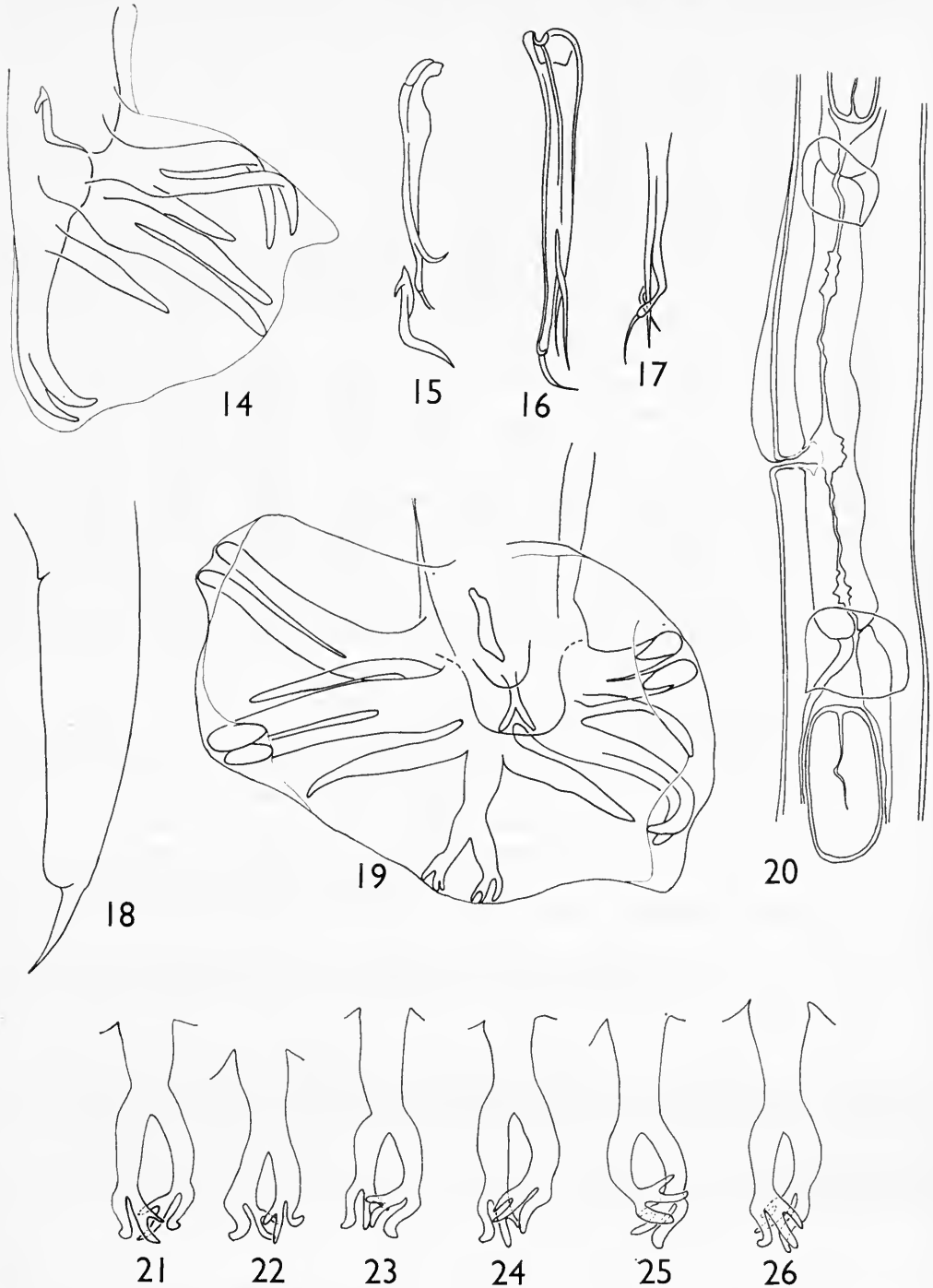
Female. The vulva, uterus and eggs are typical of the genus (Text-fig. 10) while the tail carries a pair of ventro-lateral swellings just anterior to the fine posterior terminal process (Text-figs. 8 and 9).

DISCUSSION. The specimens match the description of *Molineus patens* (Dujardin, 1845) Petrov, 1928 although they are smaller than any previously reported. Additional points of difference appear to be the lack of any small hooks or cuticular bumps on the inner surface of the bursa and the slightly elaborate genital cone. Comparison of the specimens described above with the descriptions of *M. patens* given by Petrov (1928), Zunker (1929), Leiper (1936), Travassos (1937) and Skrjabin *et al.* (1954) shows that the body is only half, the spicules two-thirds and the gubernaculum half the lengths of the corresponding dimensions for the smallest specimens previously recorded. Leiper (1936) observed that there appeared to be a tendency towards a host : parasite size relationship for specimens of *M. patens* recovered from the stoat and weasel in England, but Table 2 in Petrov (1928) shows that there are only slight variations between the measurements of specimens from five different hosts examined in the U.S.S.R.

As the relative proportions of the specimens we described above are in general agreement with those already reported and the structure of the spicules appears to be the same, we treat our specimens as *M. patens*, although with some reservations.

Molineus springsmithi sp. nov.

MATERIAL STUDIED. 6 ♂, 6 ♀ ex small intestine of *Felis bengalensis horsfieldi*. Hatia, Arun River, East Nepal. B.M. (N.H.), Reg. Nos. 1965. 6-25.



FIGS. 14-26. *Molineus springsmithi* sp. nov. Fig. 14. Lateral view of male bursa. Fig. 15. Lateral view of spicule and gubernaculum. Fig. 16. Detail of whole spicule. Fig. 17. Detail of posterior end of spicule. Fig. 18. Lateral view of female tail. Fig. 19. Ventral view of male bursa. Fig. 20. Lateral view of vulvar region of female. Figs. 21-26. Ventral views of dorsal rays showing variation of major bifurcation.

MEASUREMENTS (in mm.). Males. Body length: 2.27; 2.52; 2.63; 2.68; 2.69; 3.01. Body breadth: 0.054; 0.067; 0.044; 0.052; 0.046; 0.072. Diameter of head: 0.021; 0.022; 0.022; 0.022; 0.028; 0.025. Diameter of cephalic vesicle: 0.029; 0.040; 0.030; 0.028; 0.036; 0.033. Length of cephalic vesicle: 0.047; 0.042; 0.044; 0.045; 0.051; 0.044. Oesophagus length: 0.347; 0.353; 0.307; 0.381; 0.340; 0.397. Distance of cervical groove from anterior end of body: 0.125; 0.147; 0.141; 0.144; 0.139; 0.157. Length of spicules: 0.070; 0.065; 0.068; 0.068; 0.062; 0.065. Length of gubernaculum: 0.024; 0.024; 0.025; 0.021; 0.024; 0.021.

Females. Body length: 3.15; 3.52; 3.57; 3.79; 3.94; 3.95. Body breadth: 0.052; 0.057; 0.052; 0.054; 0.062; 0.057. Diameter of head: 0.023; 0.025; 0.024; 0.024; 0.025; 0.024. Diameter of cephalic vesicle: 0.032; 0.031; 0.032; 0.028; 0.033; 0.030. Length of cephalic vesicle: 0.041; 0.057; 0.047; 0.045; 0.046; 0.051. Oesophagus length: 0.298; 0.343; 0.374; 0.360; 0.422; 0.372. Distance of cervical groove from anterior end of body: 0.120; 0.155; 0.173; 0.154; 0.172; 0.172. Distance of vulva from posterior end of body: 0.592; 0.565; 0.522; 0.500; 0.532; 0.543. Length of tail: 0.068; 0.059; 0.048; 0.051; 0.072; 0.058. Size of eggs: 0.055 × 0.026 to 0.071 × 0.031.

The cuticle is marked by eleven to fifteen longitudinal ridges and the cervical groove is distinct completely round the body. No cervical papillae have been seen.

Male. The bursa is typical with the ventro-lateral and latero-ventral and the postero- and medio-lateral rays arising in pairs from common bases. The first bifurcation of the dorsal ray is rather deep while the terminal bifurcations, the inner one double, are somewhat variable (Text-figs. 21–26). The gubernaculum is small and slightly hooked anteriorly (Text-figs. 14–15) and the spicules are simple with three terminal processes. The major division of the processes extends only for about one third the length of the spicules (Text-figs. 15–17). The bursa is not divided into lobes and there is a small pre-cloacal supplementary membrane which is supported by an internal Y-shaped thickening (Text-fig. 19).

Female. The reproductive system is typical (Text-fig. 20) and the tail ends in a small spike (Text-fig. 18).

DISCUSSION. This species is very distinct in the extreme depth of the first bifurcation of the dorsal ray, the characteristic shape of the gubernaculum and the relative simplicity of the spicules.

Brevistrata ? *skrabini* (Schulz & Lubimov, 1932)

MATERIAL STUDIED. 2 ♂, 5 ♀ ex small intestine of *Callosciurus pygerythrus lokroides*. Popti La, Arun River, East Nepal. B.M. (N.H.) 1965. 26–28.

2 ♂, 7 ♀ ex small intestine *Callosciurus maccllellandi maccllellandi*. Hatia, Arun River, East Nepal. B.M. (N.H.) 1965. 29–31.

MEASUREMENTS (in mm.). In two groups separated by full stop. First group from Popti La sample. Males. Body length: 3.31; 3.73. 4.35; 5.32. Body breadth: 0.067; 0.063. 0.116; 0.116. Diameter of head: 0.020; 0.020. 0.028; 0.026. Diameter of cephalic vesicle: 0.030; 0.030. 0.040; 0.036. Length of cephalic vesicle: 0.042; 0.045. 0.046; 0.057. Oesophagus length: 0.347; 0.327. 0.314; 0.388. Length of spicules: 0.450; 0.442. 0.570; 0.548. Length of gubernaculum: 0.040; 0.044. 0.053; 0.060.

Females. Body length: 3.43; 3.98; 4.13; 4.39; 4.59. 4.63; 5.32; 5.33; 5.36; 5.40; 5.45; 5.59. Body breadth: 0.065; 0.065; 0.063; 0.065; 0.072. 0.089; 0.123; 0.109; 0.135; 0.098; 0.098; 0.104. Diameter of head: 0.022; 0.022; 0.023; 0.023; 0.025. 0.025; 0.029; 0.028; 0.025; 0.030; 0.030; 0.028. Diameter of cephalic vesicle: 0.026; 0.028; 0.023; 0.029; 0.027. 0.033; 0.038; 0.040; 0.032; 0.030; 0.030; 0.042. Length of cephalic vesicle: 0.042; 0.048; 0.042; 0.044; 0.044. 0.043; 0.050; 0.048; 0.047; 0.050; 0.048; 0.051. Oesophagus length: 0.300; 0.353; 0.335; 0.338; 0.322. 0.382; 0.436; 0.400; 0.410; 0.388; 0.378; 0.364. Length of tail: 0.049; 0.037; 0.042; 0.042; 0.044. 0.049; 0.049; 0.054; 0.040; 0.057; 0.051; 0.056. Distance of vulva from posterior end of body: 0.085; 0.094; 0.096; 0.093; 0.110. 0.098; 0.115; 0.107; 0.079; 0.112; 0.107; 0.117. Size of eggs: 0.055 × 0.033 to 0.076 × 0.040.

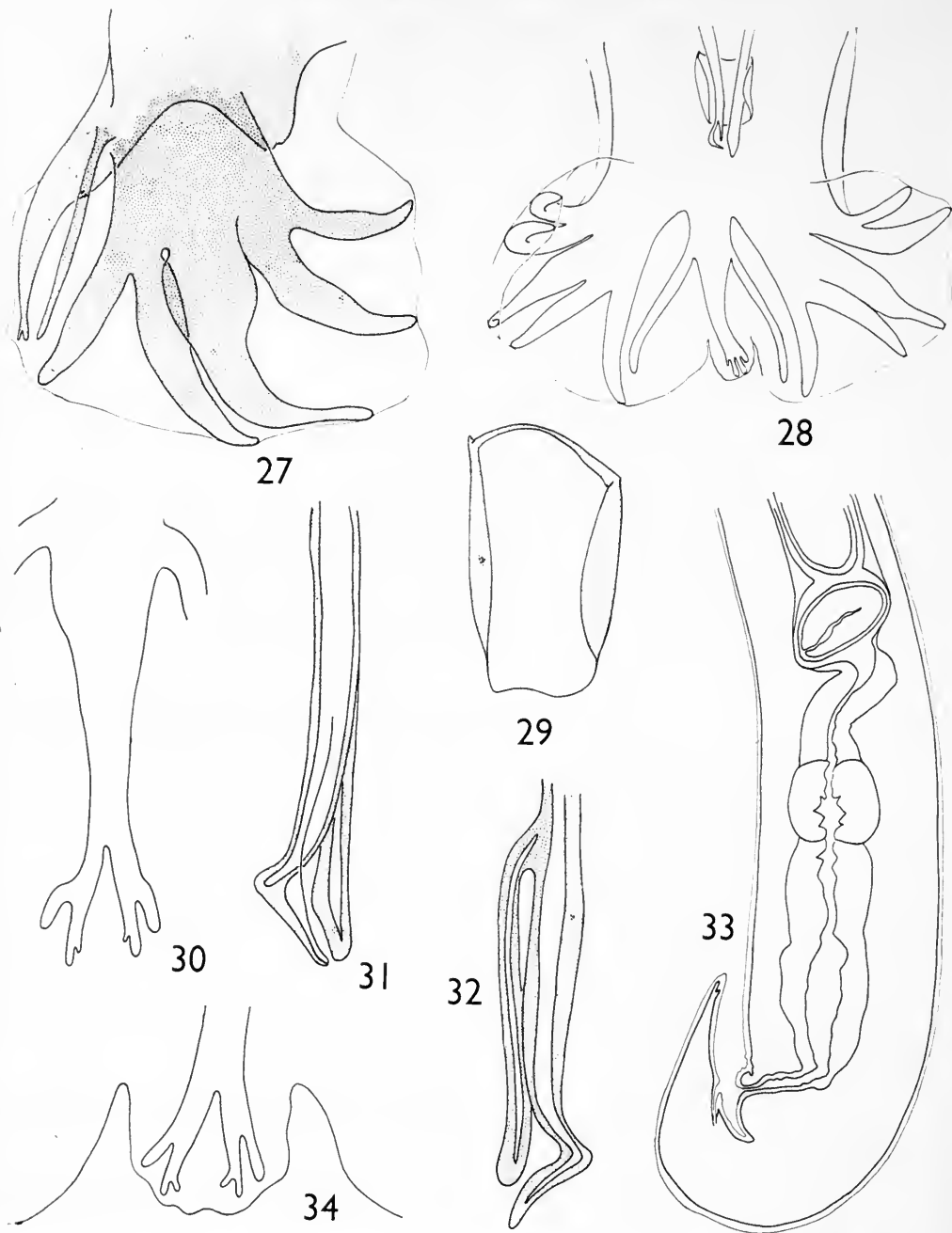
The worms are coiled into spirals with two or three turns. The head carries a small cephalic vesicle and the mouth is simple without any obvious cavity between it and the beginning of the oesophagus. The cuticle bears the typical broken longitudinal ridges which alternate down the body.

Male. The bursa has a small distinct dorsal lobe (Text-fig. 34). The ventral rays of the bursa arise together, as do the three lateral rays (Text-figs. 27 and 28). All these rays reach the edge of the bursa. The lateral rays differ in size with the stout externo- and medio-laterals lying close together, while the postero-lateral is much slimmer and is directed posteriorly away from the other two. The thin externo-dorsal rays arise some distance from the origin of the dorsal ray (Text-fig. 28). The dorsal ray bifurcates twice towards its posterior end with the inner branch of the final bifurcation bearing a further relatively small inner branch (Text-fig. 30).

The spicules are long and filiform with bifurcate posterior ends (Text-figs. 31 and 32). The main terminal branch of the spicules ends in a hook-like projection while the other branch is blunt. The gubernaculum is small and roughly square in outline when viewed from the ventral surface (Text-fig. 29).

Female. The single uterus and ojector open through the vulva which lies very near the anus (Text-fig. 33). The tail is relatively short and conical with the phasmids near the tip.

DISCUSSION. The three species currently referred to the genus *Brevistriata*: *B. skrjabini* (Schulz & Lubimov, 1932), *B. sinensis* Li, 1941 and *B. callosciuri* Supperer & Kutzer, 1963; all occur in Asian squirrels. Supperer & Kutzer (1963) tabulate what they consider to be the diagnostic characters for these three species.



FIGS. 27-34. *Brevistriata skryabini*. Fig. 27. Lateral view of male bursa. Fig. 28. Ventral view of male bursa. Fig. 29. Ventral view of gubernaculum. Fig. 30. Dorsal ray of bursa. Fig. 31. Ventral view of distal end of spicule from right. Fig. 32. Ventral view of distal end of spicule from left. Fig. 33. Lateral view of female tail showing vulva. Fig. 34. Detail of small dorsal lobe of bursa.

B. sinensis is characterized by extremely long spicules with non-bifurcate posterior ends and by the externo-dorsal rays arising about half-way along the length of the dorsal ray. *B. callosciuri* is unique in the extreme division of the caudal bursa into two distinct lobes, the spicules are bifurcate distally forming two, unequal pointed branches and the gubernaculum is complex.

The specimens described above are, however, in good agreement with the original description of *B. skrjabini* with the exception of the bifurcation of the spicules. Schulz & Lubimov (1932) state that the spicules are bifurcate "near the proximal end", but these structures are not figured and it would appear that "proximal" is an error for "distal". Travassos (1937) and Supperer & Kutzer (1963) state that the spicules are bifurcate distally although they apparently derive their data from the original description. The specimens described above agree with the original description in sufficient detail to warrant their reference, at least provisionally, to *B. skrjabini*.

Longistriata gola sp. nov.

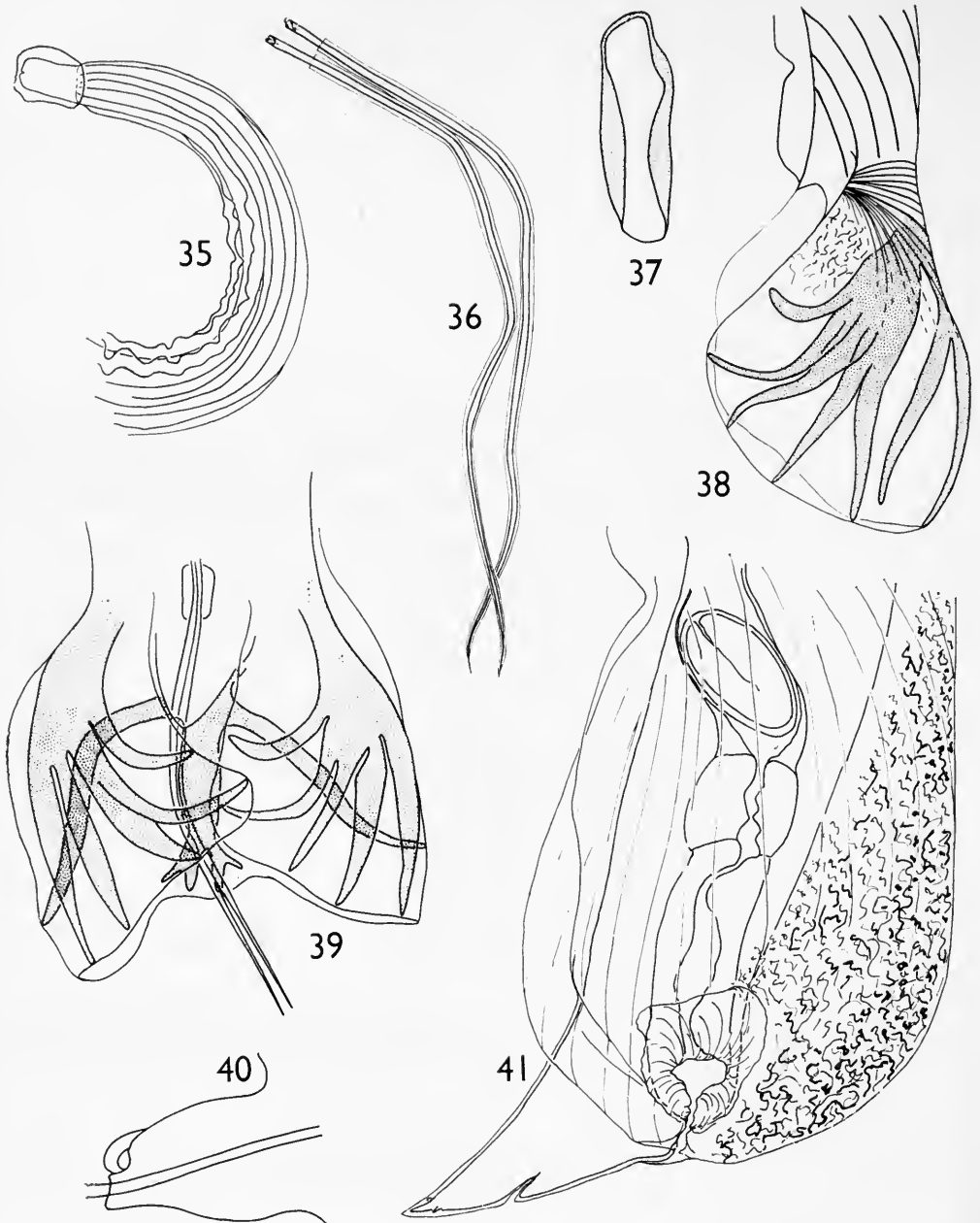
MATERIAL STUDIED. 4 ♂, 7 ♀ ex small intestine *Callosciurus maccllellandi maccllellandi*. Hatia, Arun River, East Nepal. B.M. (N.H.) Reg. Nos. 1965. 32-35.

MEASUREMENTS (in mm.). Males. Body length: 4.71; 4.97; 5.12; 5.51. Body breadth: 0.149; 0.128; 0.129; 0.137. Diameter of head: 0.027; 0.028; 0.028; 0.028. Diameter of cephalic vesicle: 0.042; 0.049; 0.055; 0.048. Length of cephalic vesicle: 0.051; 0.062; 0.055; 0.057. Oesophagus length: 0.351; 0.349; 0.367; 0.380. Length of spicules: 0.664; 0.692; 0.646; 0.661. Length of gubernaculum: 0.028; 0.034; 0.030; 0.036.

Females. Body length: 6.52; 6.73; 7.04; 7.21; 7.23; 7.32; 7.48. Body breadth: 0.120; 0.123; 0.131; 0.139; 0.129; 0.116; 0.148. Diameter of head: 0.032; 0.031; 0.030; 0.030; 0.031; 0.028; 0.039. Diameter of cephalic vesicle: 0.051; 0.050; 0.046; 0.044; 0.045; 0.049; 0.057. Length of cephalic vesicle: 0.058; 0.054; 0.055; 0.054; 0.056; 0.060; 0.058. Oesophagus length: 0.400; 0.425; 0.383; 0.373; 0.426; 0.443; 0.338. Length of tail: 0.048; 0.058; 0.050; 0.036; 0.052; 0.054; 0.057. Distance of vulva from posterior end of body: 0.121; 0.135; 0.171; 0.157; 0.168; 0.118; 0.108. Size of eggs: 0.072 × 0.044 to 0.054 × 0.032.

The body is coiled four or five times in a tight spiral. The head has the characteristic cephalic vesicle. The cuticle bears typical longitudinal ridges, twenty just posterior to the cephalic vesicle increasing to twenty-six at the mid-body region and diminishing in number posteriorly.

Male. The bursa is symmetrical and bilobed (Text-fig. 39). The ventral rays arise together from a common base as do the three lateral rays (Text-figs. 38 and 39), and all reach the edge of the bursa. The externo-dorsal rays arise close to the root of the dorsal ray but do not reach the edge of the bursa. The dorsal ray bifurcates at the extreme distal end to give two short branches which again bifurcate (Text-fig. 39). The genital cone is prominent and bears a pair of processes (Text-fig. 40)



FIGS. 35-41. *Longistriata gola* sp. nov. Fig. 35. Anterior end of female. Fig. 36. Spicules showing sheath. Fig. 37. Ventral view of gubernaculum. Fig. 38. Lateral view of male bursa. Fig. 39. Ventral view of male bursa. Fig. 40. Lateral view of genital cone showing process. Fig. 41. Lateral view of female tail showing vulvar and cuticular modification.

slightly ventral to the genital opening. The spicules are equal, long, thin, being finely pointed distally and enclosed in a sheath for most of their length (Text-fig. 36). The gubernaculum is small with the outer edges folded inwards to form a groove (Text-fig. 37).

Female. The tail is typical of the genus (Text-fig. 41), with the vulva situated just anterior to the anus. The extreme tip of the tail bears two small phasmids. The cuticle at the posterior end appears to be very loose and in some specimens completely surrounds the posterior end of the body, Mawson (1961) figures this in some detail.

DISCUSSION. Keys to the species of the genus *Longistriata* have been published by Dickmans (1935), Skrjabin, Shikhobalova & Schultz (1954) and Mawson (1961) in which the main criteria for specific separation are cuticular specialization (i.e. presence or absence of lateral alae) and the structure of the male caudal apparatus (symmetry of bursa and shape of the dorsal ray). Using these criteria more than half of the fifty-odd described species have no lateral alae and possess a symmetrical bursa as in *L. gola*. However, of these only five are similar to *L. gola* in the shape of the dorsal ray of the bursa, thus: *L. bathyergi*, *L. beta*, *L. leporis*, *L. schulzi* and *L. seurati*.

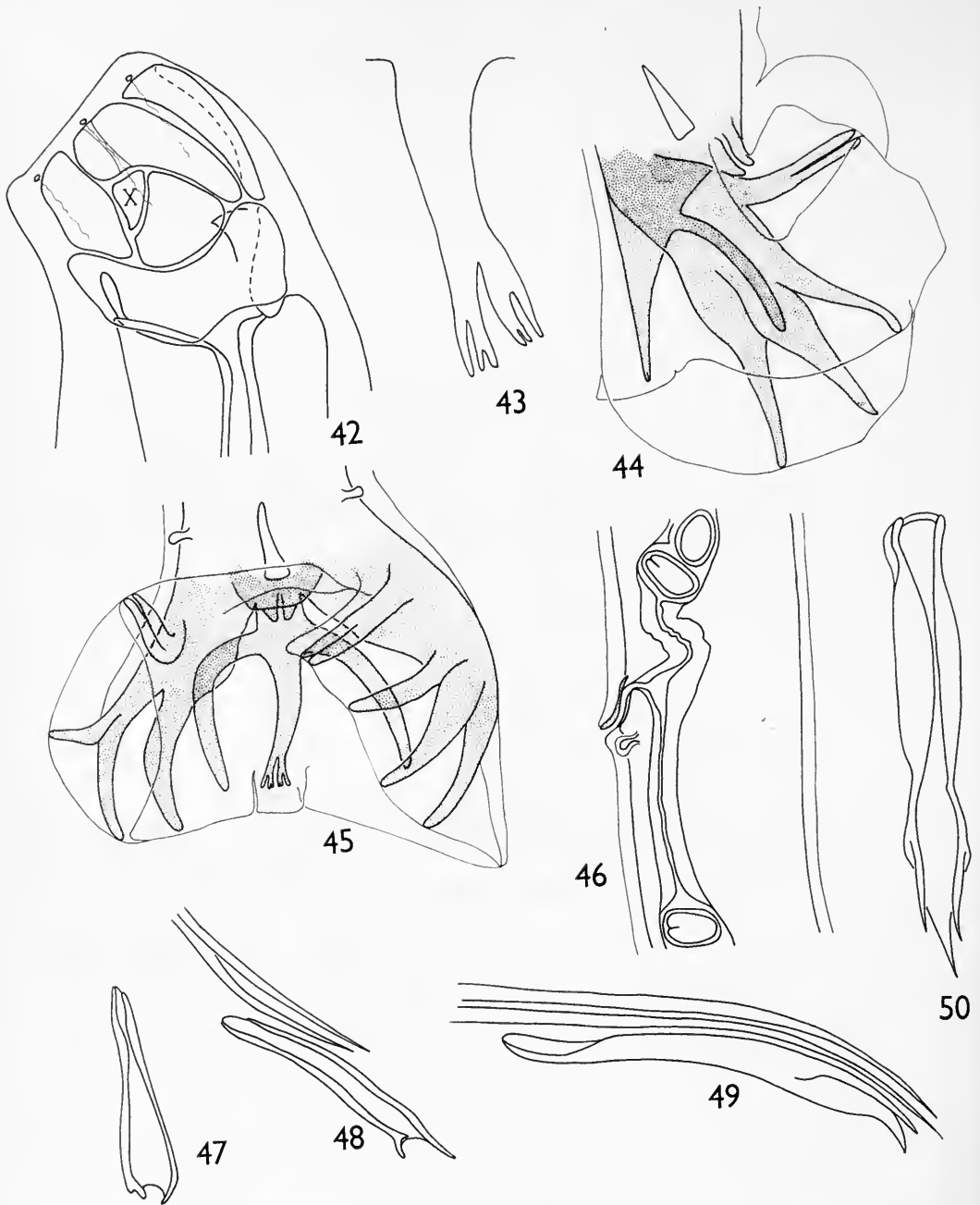
L. bathyergi Ortlepp, 1939 is similar to *L. gola* in overall size and the length of the spicules, but differs in having pre-bursal papillae, an indefinite gubernaculum, in the thickness of the dorsal rays and in the thickening at the tips of the spicules. *L. beta* (Travassos, 1918) differs in being only half the size of *L. gola*, in having smaller spicules and in the shape of the gubernaculum. *L. leporis* Schulz, 1931, and *L. schulzi* Schachnasarova, 1949 also have different spicules, those of the former being longer and distally bifurcate, whilst those of the latter are almost three times as long as those of *L. gola*. *L. seurati* Travassos & Darriba, 1929 differs in having only fourteen longitudinal ridges on the cuticle, in the spicules being united distally and in having an asymmetrical gubernaculum.

Arthrostoma tunkanati sp. nov.

MATERIAL STUDIED. 4 ♂, 7 ♀ ex small intestine. *Felis bengalensis horsfieldi*. Hatia, Arun River, East Nepal. B.M. (N.H.) Reg. Nos. 1965. 36-40.

MEASUREMENTS (in mm.). Males. Body length: 2.37; 3.23; 3.62; 3.74. Body breadth: 0.182; 0.145; 0.142; 0.163. Length of buccal cavity: 0.065; 0.074; 0.064; 0.080. Diameter of buccal cavity: 0.040; 0.061; 0.056; 0.053. Distance of excretory pore from anterior end of body: 0.327; 0.325; 0.293; 0.328. Oesophagus length: 0.438; 0.471; 0.483; 0.491. Breadth of oesophagus (maximum): 0.094; 0.068; 0.070; 0.095. Length of spicules: 0.270; 0.410; 0.383; 0.376. Length of gubernaculum: 0.054; 0.045; 0.040; 0.048.

Females. Body length: 2.46; 2.56; 2.90; 2.94; 3.85; 4.27; 4.28. Body breadth: 0.216; 0.205; 0.215; 0.211; 0.176; 0.192; 0.151. Length of buccal cavity: 0.063; 0.063; 0.070; 0.066; 0.086; 0.088; 0.074. Diameter of buccal cavity: 0.046; 0.045; 0.051; 0.045; 0.059; 0.056; 0.056. Distance of excretory pore from anterior end of body: 0.306; 0.276; 0.288; 0.308; —; 0.360; —.



FIGS. 42-48. *Arthrostoma tunkanati* sp. nov. Fig. 42. Lateral view of head, additional plate marked X. Fig. 43. Dorsal ray. Fig. 44. Lateral view of male bursa. Fig. 45. Ventral view of male bursa. Fig. 46. Lateral view of vulvar region of female showing papilla and cuticular flap. Fig. 47. Ventral view of gubernaculum. Fig. 48. Lateral view of gubernaculum and tips of spicules. Fig. 49-50. *Arthrostoma felineum*. Fig. 49. Lateral view of gubernaculum and tips of spicules. Fig. 50. Ventral view of gubernaculum.

Oesophagus length : 0.420 ; 0.503 ; 0.457 ; 0.477 ; 0.595 ; 0.567 ; 0.556. Breadth of oesophagus (maximum) : 0.094 ; 0.087 ; 0.097 ; 0.113 ; 0.102 ; 0.166 ; 0.091. Length of tail : 0.080 ; 0.086 ; 0.081 ; 0.098 ; 0.088 ; 0.083 ; 0.087. Distance of vulva from posterior end of body : 0.83 ; 0.81 ; 0.94 ; 1.01 ; 1.06 ; 1.15 ; 1.14. Size of eggs : 0.059 × 0.026 to 0.083 × 0.043.

Short narrow worms with the anterior end of the body bent dorsally. The lining of the buccal cavity is in the form of plates arranged in the same way as *Arthrostoma felineum* Cameron, 1927 but differing in the presence of an additional lateral plate (marked X in Text-fig. 42). That is, there are ten plates of which one forms a cone round the posterior of the buccal cavity, one triangular plate is ventral in position, and the remaining plates are paired, one large L-shaped pair ventro-lateral, one ovoid pair dorso-lateral and two pairs wholly lateral.

The mouth opening is ovoid without elaboration. The oesophagus is the typical club-shape.

Male : The bursa is very similar to that of *A. felineum* with prominent prebursal papillae, a distinct small dorsal lobe, small ventral rays which arise from a common base, large lateral rays which all arise from the same base. The externo-dorsal ray is markedly different from that of *A. felineum* in being narrow over its whole length and in arising some distance from the base of the dorsal ray. The dorsal ray also differs slightly in the terminal bifurcations, all of which reach the edge of the bursa (Text-figs. 43, 44 and 45). An unmodified genital cone is present.

The spicules are simple and needle-like. The gubernaculum is short, swelling slightly posteriorly where there are small ventro-lateral processes (Text-figs. 47 and 48). This is in marked contrast to the relatively larger gubernaculum of *A. felineum* in which the posterior end is sharply pointed with two lateral pointed processes (Text-figs. 49 and 50).

Female : The vulva is identical with that of *A. felineum* with a flap developed from the dorsal lip which is supported by dense cuticle (Text-fig. 46), and with a single papilla-like structure posterior and slightly lateral in position.

DISCUSSION. There are at present only two species referable to the genus *Arthrostoma*: *A. felineum* Cameron, 1927 and *A. cheni* Kou, 1958. These species are very similar but are distinguishable by the size of the spicules and the form of the gubernaculum in the males. Further the female of *A. cheni* has a wart-like projection just anterior to the vulva in addition to the usual single lateral papilla.

The species described above is similar to both those already referred to the genus but is very distinct in the additional plate in the head, in the size of the spicules and in the form of the gubernaculum.

Arthrostoma felineum Cameron, 1927

MATERIAL STUDIED. 2 ♂ ex small intestine *Felis bengalensis horsfieldi*. Hatia, Arun River, East Nepal. B.M. (N.H.) Reg. Nos. 1965. 41-42. 3 ♂, 3 ♀. Cameron's type specimens. B.M. (N.H.) 1928.9.27.1-6.

MEASUREMENTS (in mm.). Males. Body length: 4.23; 6.01. Body breadth: 0.166; 0.182. Length of buccal cavity: 0.068; 0.073. Diameter of buccal cavity: 0.044; 0.048. Distance of excretory pore from anterior end of body: —; 0.382. Oesophagus length: 0.619; 0.620. Breadth of oesophagus (maximum): 0.108; 0.120. Length of spicules: 1.07; 1.08. Length of gubernaculum: 0.083; 0.080.

Corrected measurements of Cameron's type material:

Males: Oesophagus length: 0.359; 0.360; 0.379. Breadth of oesophagus (maximum): 0.085; 0.094; 0.073.

Females: Oesophagus length: 0.420; 0.449; 0.456. Breadth of oesophagus (maximum): 0.100; 0.097; 0.089.

The two male specimens from Nepal are in good agreement with those described by Cameron (1927), with the exception of the length of the oesophagus and the description of the spicules. As the differences in length are more than can reasonably be attributed to differences in methods of fixation, in view of the otherwise close similarity between the Nepalese material and Cameron's description, the types of *Arthrostoma felineum* were re-examined (B.M. (N.H.) Reg. Nos. 1928.9.27.1-6).

The oesophagus in both sexes is much longer than originally stated by Cameron (see above) and the spicules do not form a single fine point (Text-fig. 49), but are quite separate posteriorly. The gubernaculum is distinct (Text-fig. 50).

A. felineum has now been reported from Sumatra (Cameron, 1927), Palestine (Witenberg, 1934) and Nepal.

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PART I EXTERNAL MORPHOLOGY

G. OWEN EVANS
AND
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BULLETIN OF
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PART I EXTERNAL MORPHOLOGY

By G. OWEN EVANS & W. M. TILL

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SYNOPSIS

The external morphology of the British representatives of the acarine family Dermanyssidae is reviewed with particular reference to the modifications in morphology associated with the adoption of a parasitic mode of life.

INTRODUCTION

THE family Dermanyssidae (including Laelapidae, Haemogamasidae and Macronyssidae) comprises free-living species inhabiting soil and humus as well as forms displaying various degrees of association with vertebrate and invertebrate animals. Associations with other animals range from predatory species living in the nests of insects, birds and mammals to facultative and obligatory ectoparasites of the nesting animal. At present the classification of the Dermanyssidae is largely based on the study of the parasitic forms whose economic importance as vectors or potential vectors of disease has overshadowed the taxonomic importance of their free-living relatives. Recent key works on the parasitic Dermanyssidae have been produced by Bregetova (1956), Strandtmann & Wharton (1958) and by Zumpt & Till (1961).

The British representatives of this family number about 75 species and these exhibit a wide range of structural and biological adaptations to the variety of ecological niches they have successfully colonized. This first contribution to a taxonomic revision of the British Dermanyssidae deals with the external morphology of the group.

* This study was supported, in part, by Research Grant No. E4656 from the National Institutes of Health, United States Public Health Service.

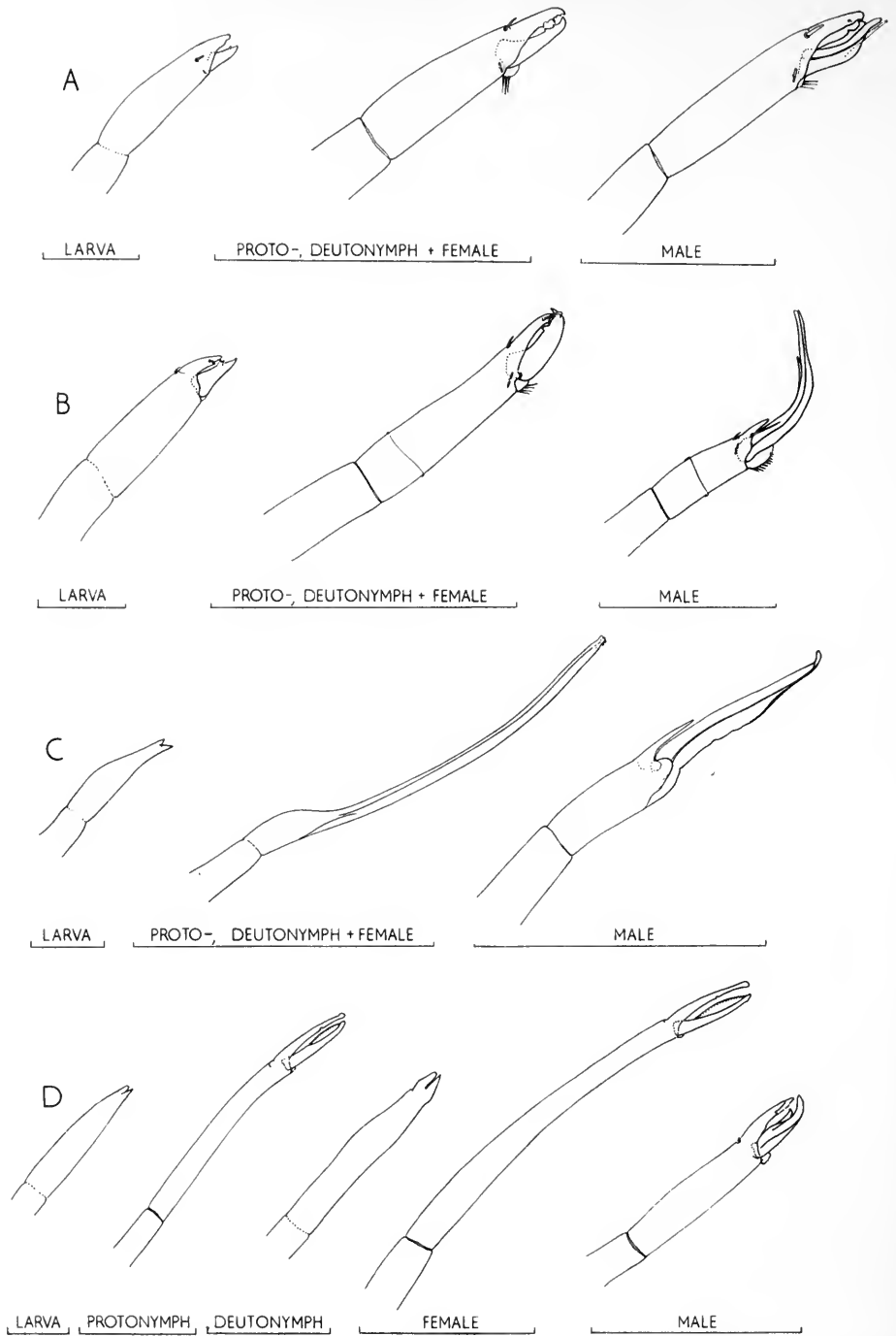


FIG. 1. Chelicerae of the immature and adult stages of: A. *Holostaspis vitathumi* (Womersley); B. *Laelaps echidnina* Berlese; C. *Dermanyssus gallinae* (Degeer); D. *Ornithonyssus bacoti* (Hirst).

EXTERNAL MORPHOLOGY

Gnathosoma

Chelicerae: The chelicerae, paired pre-oral trophic appendages, of the Dermanyssidae are three segmented (Text-fig. 1). The short proximal segment to which the cheliceral retractor muscles are attached is articulated to the longer second segment by a condylar process located on its internal (paraxial) face. Distally the second segment forms the fixed digit (*f. d.*) of the chelicera and the third segment or movable digit (*m. d.*) is articulated ventrally to the fixed digit by arthrodistal membrane and two condyles developed on the limb of the second segment which engage acetabula on the movable digit (Text-fig. 2E). The movable digit is operated by a pair of opposed muscles originating within the proximal segment and connected to the digit by a dorsal levator tendon and a ventral depressor tendon. The arthrodistal membrane at the base of the movable digit is usually produced into setiform processes.

In the free-living and the majority of the nest-inhabiting members of the family, the cheliceral shaft is of approximately equal diameter throughout its length and the ratio of the length of the first to the second segment is in the region of 1 : 1.5-3.5. The external (antiaxial) face of the chelicera bears a dorsal seta (*d. s.*), a lateral fissure (*lat. l. f.*) and a simple *pilus dentilis* (*p. d.*)¹, the latter being situated on the distal half of the fixed digit (Text-fig. 2A-B). A lyriform fissure (*d. l. f.*) associated with the dorsal seta occurs on the dorsal surface of the second segment at the origin of the fixed digit. In some forms this fissure extends to the lateral face of the segment. The fixed digit is provided with a variable number of teeth, but the movable digit in the nymphae and females is normally bidentate. In the male the movable digit, usually unidentate, carries on its external face a grooved spermadactyl (*sp.*). This process shows considerable diversity in form but its distal portion is invariably free (Text-fig. 2F-G). At the larval stage the chelicerae are well-developed and have a full complement of setae and fissures. The digits are weaker and less strongly dentate than in subsequent developmental stages since this stage is non-feeding (Text-fig. 1A). The chelicerae of the nymphae and female are essentially similar in form, the only differences being in their relative sizes and occasionally in the number of teeth on the fixed digit.

This basic type of chelicera, encountered in the polyphagous free-living forms, has become variously adapted for specialized feeding in the facultative and obligatory parasitic species of the family. Modifications are evident in the form of the cheliceral shafts, the digits and associated structures, and in the ontogenetic development of the chelicerae.

The form of the shaft (first and second segments) in the larva, nymphae and female of the facultative parasites, for example *Androlaelaps*, *Laelaps* and *Haemogamasus*, is fundamentally the same as in the free-living forms although in the males there is a tendency for a shortening of the second segment (Text-fig. 1B). In obligatory parasites the relative lengths of the first and second segments of the chelicera in the

¹ Van der Hammen (1964) has suggested replacing the term *pilus dentilis* by "cheliseta" since the former is "too long". To change such a well-established and universally accepted term for such a trivial reason is unwarranted!

non-feeding larva are similar to those in the same developmental stage of the free-living forms and facultative parasites but the distal half of the second segment generally shows some attenuation. The feeding nymphae and female, with few

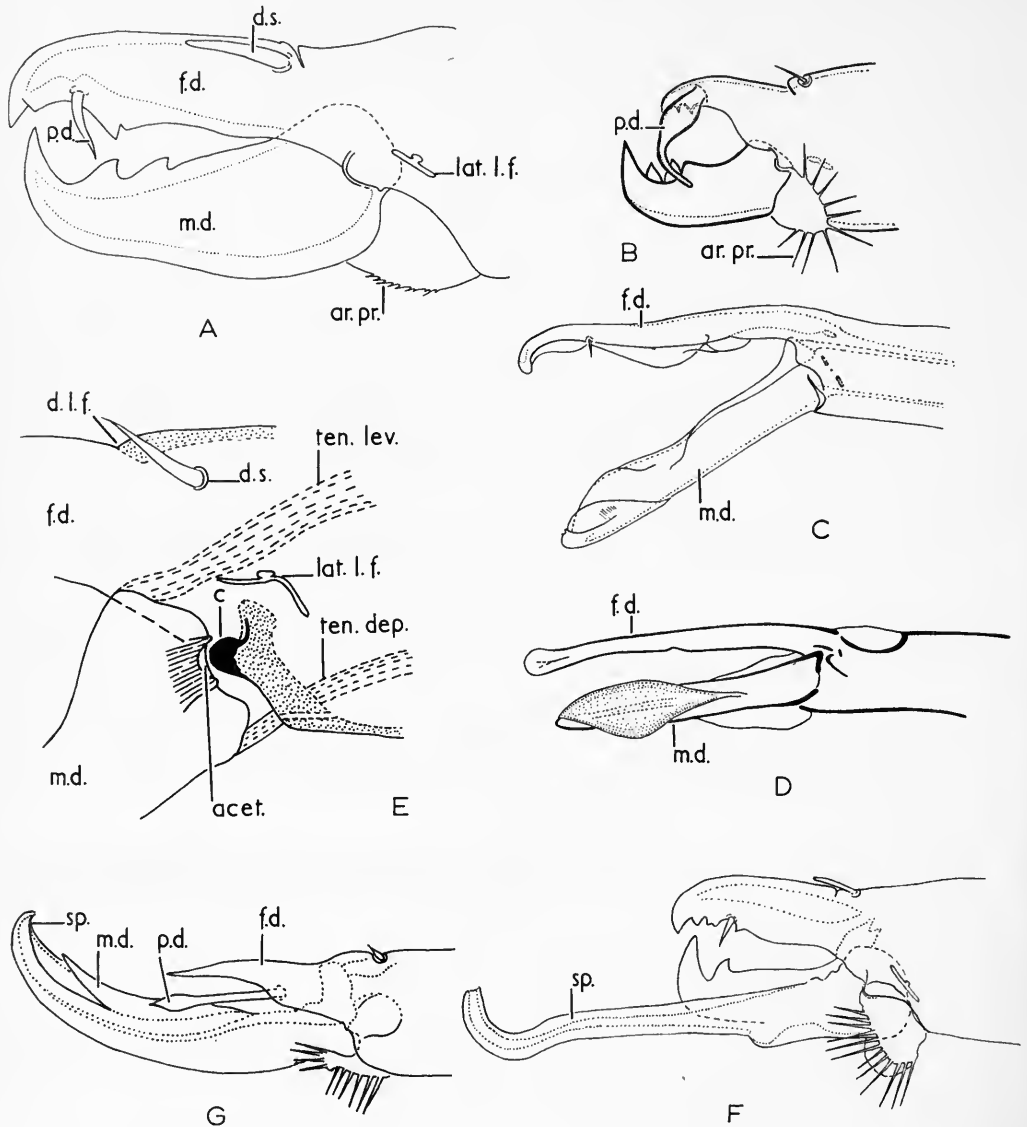


FIG. 2. Cheliceral digits of certain Dermanyssidae. A. *Eulaelaps stabularis* (Koch) female; B. *Androlaelaps fahrenheitzi* (Berlese) female; C. *Haemogamasus hirsutus* Berlese female; D. *Ornithonyssus bacoti* (Hirst) female; E. condylar articulation of the movable digit in a free-living Gamasine mite; F. *Hypoaspis (H.) krameri* (Canestrini) male; G. *Laelaps hilaris* Koch male.

exceptions, show a distinct lengthening of the second segment in relation to the first. Both nymphae and female of *Dermanyssus* have the second segment enormously elongated so that the chelicerae resemble stylets (Text-fig. 1C). A less spectacular elongation of this segment is also evident in the feeding stages of the Macronyssinae (Text-fig. 1D) in which the mesial surface of the segment is distinctly flattened. An interesting phenomenon in this group is the marked difference between the chelicerae of the feeding protonymph and the non-feeding deutonymph, the chelicerae of the latter reverting to the form in the non-feeding larva. Two main types of male chelicerae are present, one (*Dermanyssus*) in which the second segment is not more than twice the length of the first and the other (*Ornithonyssus*) in which the second segment is about three to four times the length of the first. This difference in the length of the second segment appears to be related to the length of the spermadactyl (see below).

The modifications of the digits and their associated structures are diverse and often complex. With few exceptions, the digits of the larva, nymphae and female of the facultative parasites retain their chelate-dentate form, the major specialization in this group being apparent in the degree of development and form of the setae, fissures and arthrodistal processes. The short slender *pilus dentilis* of the free-living forms is often enlarged and inflated as in post-larval stages of certain species of *Androlaelaps* (Text-fig. 2B), *Laelaps* and *Haemogamasus*. The dorsal seta is usually relatively short and simple, but may be lacking in certain *Androlaelaps*. In *Haemogamasus*, on the other hand, this seta is greatly enlarged and may be simple or spatulate. It tends to migrate ventrally onto the external face of the chelicera and in the male of *H. horridus* (Berlese) it has moved anteriorly onto the fixed digit. The arthrodistal processes may be simple and arranged in the form of a "coronet" as in the free-living species, but in certain members of the *Androlaelaps-Laelaps* complex there is a tendency for a reduction in the number of the processes accompanied by their elongation, for example in *Hyperlaelaps amphibia* Zachvatkin. Lyriform fissures are present in the normal position. Exceptions to the chelate-dentate form of the chelicerae occur in the nymphae and females of some species of *Androlaelaps* and *Haemogamasus*. In the ethiopian species *Androlaelaps cryptomia* (Radford), for example, the fixed digit is reduced to a weakly sclerotized, terminally unhooked process bearing a long *pilus dentilis*, whilst the movable digit is bipartite, comprising a strongly sclerotized, edentate, hooked digit with a less strongly sclerotized, dentate, digitiform process arising externally from its basal portion in much the same way as a spermadactyl on a male chelicera. Both digits in *Haemogamasus hirsutus* Berlese, on the other hand, are somewhat elongated and edentate, and the dorsal seta is lacking (Text-fig. 2C).

Two main types of chelicerae are present in the males of the facultative parasites. The least specialized form occurs in *Eulaelaps* and *Haemogamasus* in which the movable digit, usually unidentate, retains its hooked form and the grooved spermadactyl, free distally, rarely extends beyond the tip of the digit by more than one-third the length of the digit. Arthrodistal processes are reduced or lacking on the chelicerae of this sex. Considerably greater specialization is apparent in the second type which occurs in males of the *Androlaelaps-Laelaps* complex. These are characterized by

the reduction of the fixed digit to a relatively slender, distally tapering process bearing the enlarged *pilus dentilis* and by the size of the grooved spermadactyl which forms the greater part of the movable article of the chelicera (Text-fig. 2G). The typical form of the movable digit is lost although, in most species, its distal portion is recognizable as a slender pointed process protruding dorsally from the grooved spermadactyl. As in the *Haemogamasus*-type the arthrodial processes often show marked reduction in number and, rarely, the dorsal seta is lost.

As one would expect, the obligatory parasites feeding on the tissue fluids of their hosts show the highest degree of specialization of the chelicerae. The digits in the larva are small, subtriangular, edentate and functionless as trophic appendages. They lack setae and, apparently, fissures (Text-figs. 1C and D). With the exception of the Dermanyssinae, in which the digits are minute but dentate (Text-fig. 1C), the digits of the feeding nymphs and females are very weakly dentate or edentate and lose the hooked form typical of the polyphagous species. In the Macronyssinae, the fixed digit is generally slender and often terminates in a rounded hyaline boss whereas the movable article has an elliptical trough formed by cuticular outgrowths of the digit along its dorsal surface, the normal dentate surface of an unmodified chelicera (Text-fig. 2D). Both the digits are dorsoventrally flattened and grooved along their "cutting" faces in *Hirstionyssus*. We have been unable to see a *pilus dentilis* on the fixed digit although, in some species, a small depression occurs on the digit at the normal site of this sensory seta. The dorsal seta is reduced to a microseta or is lacking. There are no distinct arthrodial processes. The forms of the chelicerae in the males are comparable to the two types described for the facultative parasites. All macronyssines and *Hirstionyssus* have a relatively short spermadactyl showing varying degrees of fusion with the digit. In the dermanyssines, however, the fixed digit is strongly reduced and it is difficult to distinguish the movable digit from the proximal body of the elongated spermadactyl (Text-fig. 1C). Unlike the facultative parasites, the chelicerae of the males of the obligatory parasites lack a *pilus dentilis* and the dorsal seta, as in the female, is present as a microseta or is lost. The shortening of the second cheliceral segment in the forms with an extremely long spermadactyl (see above) has the effect of strengthening the shaft to counteract the increased weight of the movable digit and its appendage.

In those obligatory parasites (Dermanyssinae and *Hirstionyssus*) in which the two nymphal stages and the female are active and feeding the form of the digits is determined at the protonymphal stage and is retained by the deutonymph and female. In the macronyssines in which the deutonymph is relatively inactive and non-feeding, the specialized functional digits of the protonymph are not developed in the deutonymph whose chelicerae revert to the larval form. At the succeeding feeding female stage, however, the chelicerae resemble those of the protonymph.

Tectum capituli: The tectum², which forms the roof of the gnathosoma and

² At present the term *tectum* is also used to describe a shelf-like structure occurring below the vertex and forming the roof of the camerostome in some Uropodina. It is not a gnathosomal structure and appears to provide a supporting (and protective) shelf for the first pair of legs when the animal is at rest. As such, and to avoid confusion, it seems appropriate to re-name this structure *pedotectum-I* in the Uropodina.

overlies the chelicerae (Text-figs. 3, 4B and D), shows considerable variety in its degree of development and in the form of its anterior margin. In the free-living species and facultative parasites, with the exception of the *Eulaelaps-Haemogamasus* group, the anterior margin is smooth (*Melittiphis*), basically trispinate (*Pseudolaelaps*, Text-fig. 3B) or multidenticulate (*Hypoaspis*, Text-fig. 3A), and does not extend anteriorly to completely cover the hypostome and its associated structures (Text-fig. 4B). Members of the *Eulaelaps-Haemogamasus* group, however, have the free margin of the tectum

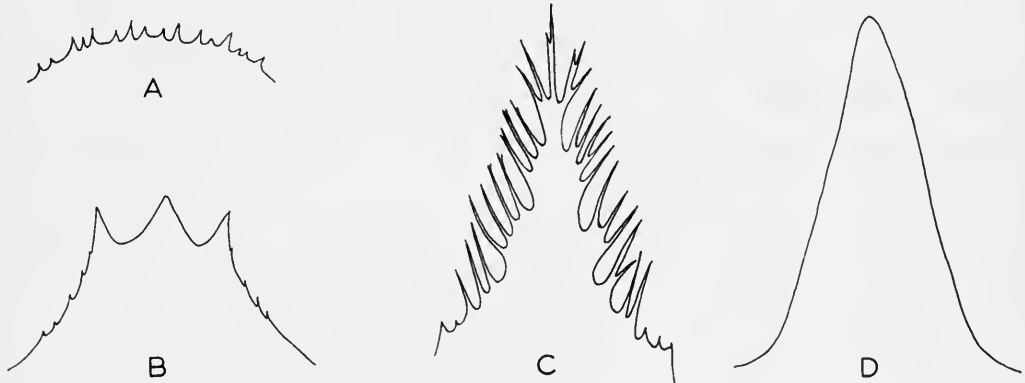


FIG. 3. Tectum capituli of: A. *Hypoaspis (Gaeolaelaps) praesternalis* Willmann; B. *Pseudolaelaps doderoi* (Berlese); C. *Haemogamasus ambulans* (Thorell); D. *Dermanyssus gallinae* (Degeer).

strongly fimbriated and considerably elongated so that it entirely covers the hypostome from above (Text-fig. 3C, 4D). This anterior extension of the tectum is also characteristic of the obligatory parasites (Dermanyssinae, Macronyssinae) and takes the form of a triangular lobe, smooth or denticulate at its tip, whose down-turned lateral margins overlap the lateral walls of a trough formed by the modified internal and external malae of the hypostome (Text-figs. 3D and 5C).

Basis capituli and hypostome: The *basis capituli* is formed mainly by the enlarged coxae of the pedipalps which are separated mid-ventrally by a shallow capitular groove whose floor is considered to represent the sternite of the pedipalpal segment (the *deutosternum*). A longitudinal series of antrose *deutosternal denticles* (*d. d.*) occurs on the floor of the capitular groove and the number and form of the denticles show little intraspecific variation (Text-figs. 4-5). Each member of the longitudinal series of denticles may be simple (one denticle) or comprise two to eight denticles arranged in a transverse row (Text-figs. 4-5). In free-living forms the larva appears to have a full longitudinal complement of denticles, but the number of denticles in each transverse row may vary in the succeeding developmental stages. Larvae of obligatory parasites, however, have the deutosternal denticles markedly reduced or absent and it is at the protonymphal stage that the full complement is determined. The number of denticles comprising the longitudinal series appears to be characteristic for certain groups of genera of the Dermanyssidae. Free-living forms and

members of the *Androlaelaps-Laelaps* groups have six, rarely seven, transverse rows of denticles/longitudinal series (Text-fig. 4A) with the number of denticles in the

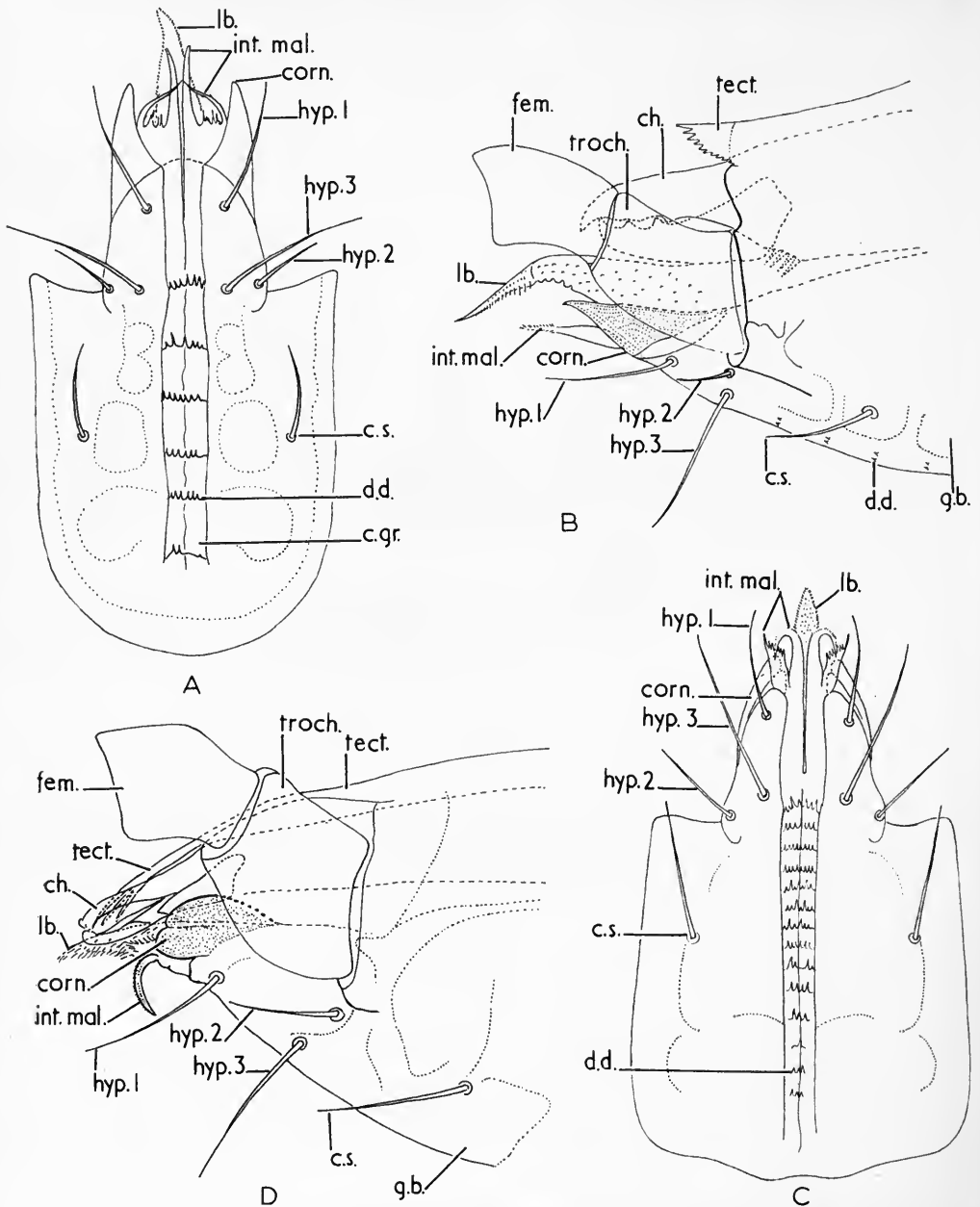


FIG. 4. A-B. Gnathosoma of female of *Cosmolaelaps claviger* (Berlese), A. ventral and B. lateral view. C-D. Gnathosoma of female of *Haemogamasus hirsutus* Berlese, C. ventral and D. lateral view.

transverse rows ranging from two to eight, the lower numbers being present in the facultative parasites of the *Androlaelaps-Laelaps* group. On the other hand, members of the facultatively parasitic *Eulaelaps-Haemogamasus* group always have more than seven transverse rows of denticles/longitudinal series, the usual number ranging between nine and fourteen (Text-fig. 4C). In the obligatory parasites the floor of the capitular groove contains about nine or ten small triangular denticles in a single longitudinal series; rarely, two denticles form a transverse row (Text-fig. 5). A similar longitudinal series of denticles occurs in *Melittiphis* and *Myonyssus* whose feeding habits are uncertain, but in these genera the corniculi (external malae) and the chelicerae do not show the marked modifications of the obligatory parasites (Dermanyssinae and Macronyssinae).

The *basis capituli* bears ventrally a pair of setae, the capitular setae, which first appear at the protonymphal stage (Evans, 1957).

The *hypostome*, divided mid-ventrally by the anterior extension of the capitular groove, bears three pairs of setae (*hyp.* 1, 2, 3) in the nymphae and adults. Setae *hyp.* 2 and 3 form a more or less transverse row of four setae (Text-figs. 4-5). At the larval stage only two pairs of setae are present on the hypostome (*hyp.* 1 and 2); the third pair (*hyp.* 3) first appears at the protonymphal stage. In the free-living forms and in the majority of the facultative parasites the hypostome bears anterolaterally a pair of large, horn-like structures (hypertrophied setae) termed *corniculi* (or *external malae*). The floor of the capitular groove in the region of the hypostome is considered by some acarologists to represent the sternite of the cheliceral segment and is referred to as the *protosternum*. It is divided into two parts by a longitudinal suture and anteriorly each part is produced into variously shaped process (Text-fig. 4) termed *internal malae* (or hypostomal processes).

The main external features of the hypostome in the obligatory parasites are its marked elongation (Text-figs. 5B, C and D) and the modification of the internal malae and corniculi to form a pre-oral trough. The corniculi, analogous structures to the *rutella* of the Cryptostigmata, already show certain deviations from their normal horn-like form in the facultative parasite *Haemogamasus hirsutus* Berlese, where they become modified into flat lobe-like structures (Text-figs. 4C and D). Further specialization of the corniculi results in the complex flange-like structures forming the lateral walls of the hypostomal trough in the obligatory parasites. The ventral floor of this trough in the protonymph and female is formed by the fusion of the internal malae along the longitudinal suture on the floor of the capitular groove (Text-fig. 5B). Owing to the complex nature of the internal malae and corniculi in these specialized parasitic forms, it is difficult to determine their homology with those in the free-living forms. At the non-feeding deutonymphal stage of *Ornithonyssus bacoti* (Hirst) fusion of the internal malae does not occur and although the internal malae and the corniculi are less complex than in the feeding stages it is still difficult to elucidate their homology (Text-fig. 5A). Two interpretations are possible, namely, one in which the short, pointed, internal process is homologous with the internal malae of the free-living forms and the two outer processes with the corniculus, and the second in which only the external article is homologous with the corniculus, the internal pair being

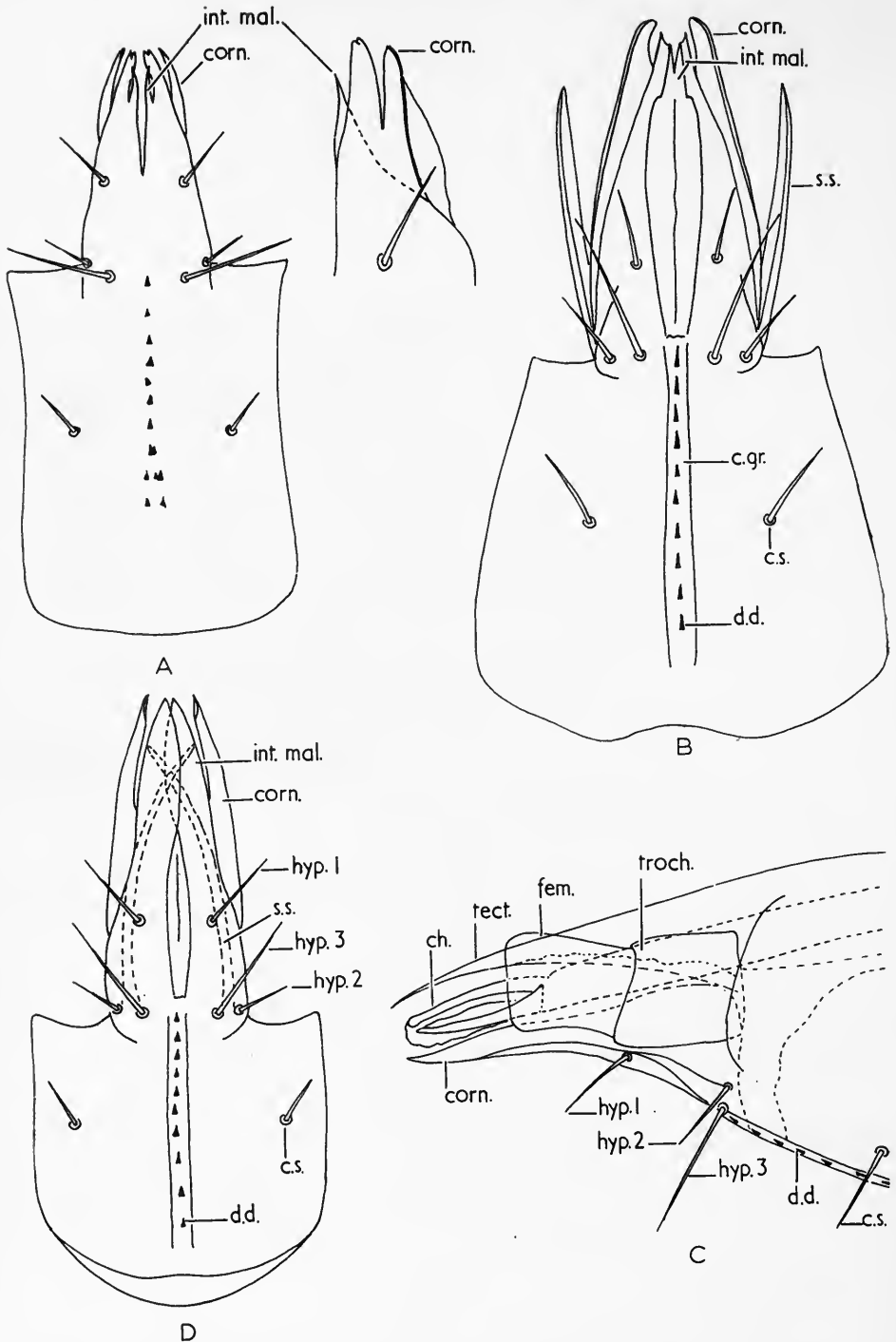


FIG. 5. Gnathosoma of *Ornithonyssus bacoti* (Hirst): A. female deutonymph, ventral and lateral views; B. female, ventral view; C. female, lateral view; D. male, ventral view.

the internal malae. In the male of *O. bacoti* the "internal malae" are in the form of two blades which overlap anteriorly and thus differ quite markedly from the form in the protonymph and female (Text-fig. 5D).

Labrum: The *labrum* (*epipharynx* of some authors), an extension of the dorsal-wall of the pharynx, appears as a long tapering structure between the corniculi and dorsal to the internal malae (Text-fig. 4). In the free-living forms and the facultative parasites the labrum projects beyond the tip of the hypostome but it is usually hidden by the elongated hypostome in the obligatory parasites. Its margin may be fimbriated and in the *Androlaelaps-Laelaps* group it has a distinct median longitudinal groove.

Salivary styli: The paired salivary styli lie laterally, immediately ventral to the chelicerae, and carry the ducts of the salivary glands located in the idiosoma. They are large and particularly well-sclerotized in the obligatory parasites (Text-figs. 5B and D).

In the forms having horn-like corniculi the salivary stylus lies in a lateral or dorsal channel along the length of the corniculus. Thus, the corniculi function as protective guides for the styli.

Pedipalps: The pedipalps have six free segments (trochanter, femur, genu, tibia, tarsus and apotele) of which the terminal segment, the apotele, is represented by a tined seta-like process at the inner basal angle of the tarsus (Text-fig. 6A). Weak condylar processes are present externally on the trochanter and dorsally on the distal margins of the femur and genu. A conspicuous lyriform fissure occurs proximally on the dorsal surface of the genu. These appendages have a well-defined chaetotaxy.

The normal ontogenetic sequence of development of the setae of the pedipalp has been defined by Evans (1964) and is characteristic of the free-living forms and of the majority of the facultative parasites of the Dermanyssidae. At the larval instar the trochanter lacks setae; the femur bears four (*al*, *d*₁, *d*₂ and *pl*), the genu five (*al*₁, *d*₁-*d*₃ and *pl*), the tibia 12 and the tarsus 11 setae. One seta (*v*₁) is added to the trochanter, and three setae to the tarsus at the protonymphal stage. A single seta is further added to the trochanter (*v*₂), femur (*d*₃) and genu (*al*₂), and two setae to the tibia at the deutonymphal stage. The deutonymphal chaetotactic pattern is retained by the adults. Thus the segmental formulae for the pedipalp (excluding the apotele which is present in all post-embryonic developmental stages) are: L. (0-4-5-12-11); P. (1-4-5-12-15); D. Ad. (2-5-6-14-15).

Deviations from the normal setal complement occur in both facultative and obligatory parasites as well as in certain myrmecophilous forms and are the result, in many cases, of the retention of the larval complement of setae on a segment in succeeding developmental stages. For example, in the adults of *Laelaspulus* the tibia retains the larval number of setae throughout ontogeny, with the result that the adult formula is (2-5-6-12-15), whilst *Hyperlaelaps amphibia* Zachvatkin retains the larval number on the femur and genu (Text-fig. 6B). In the latter the tibia is also

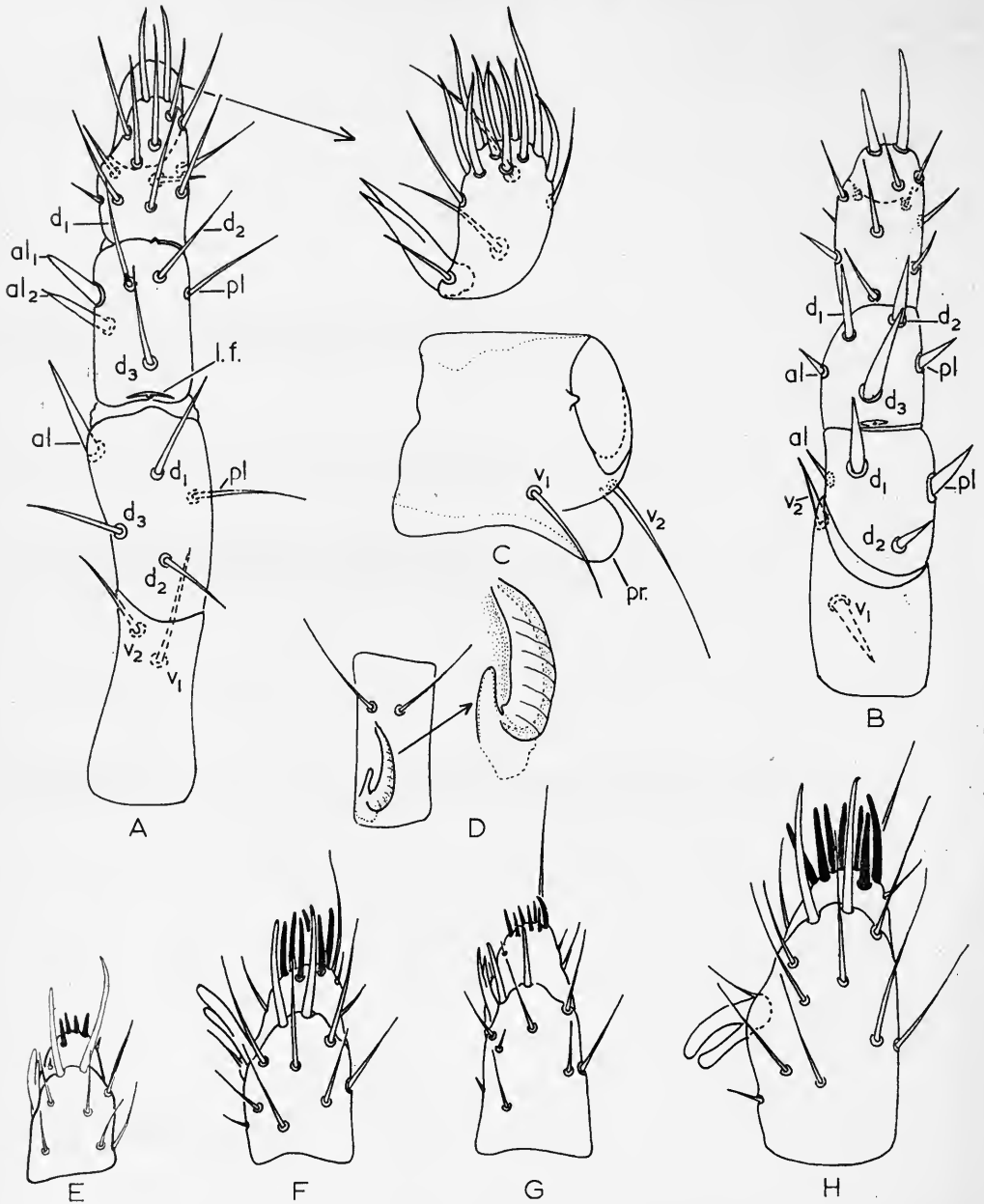


FIG. 6. A. Right pedipalp of *Hypoaspis (Gaeolaelaps) aculeifer* (Canestrini), dorsal view; B. right pedipalp of *Hyperlaelaps amphibia* Zachvatkin, dorsal view; C. palptrochanter of *Ornithonyssus bacoti* (Hirst) female, external (antiaxial) view; D. palptrochanter of *Eulaelaps stabularis* (Koch) female, ventral view; E-F. right palptibia and tarsus of *Ornithonyssus bacoti* (Hirst), larva (E), protonymph (F), deutonymph (G) and adult (H), in dorsal view.

unideficient in the deutonymph and adult (2-4-5-13-15). Amongst the macronyssines the normal pedipalpal chaetotaxy has been observed only in *Macronyssus*. Members of the other genera of this group show a deficiency in their tibial chaetotaxy. For example, *Sauronyssus*, *Steatonyssus*, *Ophionyssus* and the majority of the species of *Ornithonyssus* have only 13 setae on this segment. Some species of *Pellonyssus*, *Ornithonyssus* (*O. sylviarum*) and *Hirstionyssus* retain the larval complement of 12 in the nymphae and adults.

The greatest diversity in palpal chaetotaxy occurs in *Dermanyssus*. Only *D. intermedius* Evans & Till appears to have the normal number of setae. Deutonymphs and adults of the other species, except *D. alaudae* (Schrank), have the formula (2-4-6-12-15), indicating that the larval number has been retained on the femur and tibia. In *D. alaudae* the chaetotaxy of the four proximal segments is (2-4-5-7/8); thus, the femur and genu show no increase in setation from the larval condition whereas the tibia displays larval specialization, that is, the segment never bears the complete larval number.

The ontogenetic development of the pedipalpal chaetotaxy in the macronyssines follows the normal pattern on the trochanter, femur and genu only, that is L. (0-4-5), P. (1-4-5) and D. Ad. (2-5-6). At the larval stage of *O. bacoti*, for example, ten setae are present on the tibia and nine setae on the tarsus (Text-fig. 6E). There is an increase to the normal complement of 12 and 15 respectively on these segments in the protonymph whilst in the deutonymph, the protonymphal complement of 12 setae is retained on the tibia and the tarsus shows a regression to about 12 setae. In the adult 13 (unideficient) and 15 (normal) setae are present on the tibia and tarsus respectively. An interesting feature of the chaetotaxy of these distal segments is the reduction in the size and in the number on the tarsus of the hollow eupathidia-like setae in the non-feeding larva and deutonymph (Text-figs. 6E and G).

There is considerable variety in the form of the palpal setae (simple, pilose, leaf-like, spinose etc.) which provides stable taxonomic criteria. Hollow setae superficially resembling eupathidia occur on the tibia and tarsus, and are probably chemo-receptors. A pair is located dorsally on the distal margin of the tibia and a group of nine or ten on the distal half of the tarsus (Text-fig. 6A and H).

A median, longitudinal, keel-like process occurs ventrally on the trochanter of certain macronyssines (Text-fig. 6C). It appears to occur in females only of *Steatonyssus* s. str., some *Pellonyssus* and *Ornithonyssus*, but in both sexes and the protonymphs of *Macronyssus*. Its function is not known.

Both sexes of *Eulaelaps* have a unique organ of probable sensory function on the ventral surface of the trochanter (Text-fig. 6D). It was first observed by Fonseca (1935).

The apotele may be two or three-pronged. A three-pronged apotele occurs in the genera *Ololaelaps*, *Pseudoparasitus*, *Gymnolaelaps* and in some species (*H. hirsutus* and *H. pontiger*) of the genus *Haemogamasus*. The prongs may be slender with the proximal member small and relatively inconspicuous as in *Ololaelaps* and *Pseudoparasitus* or the three prongs may be large and spatulate as in some *Gymnolaelaps*. All the other species we have examined have a two-pronged apotele.

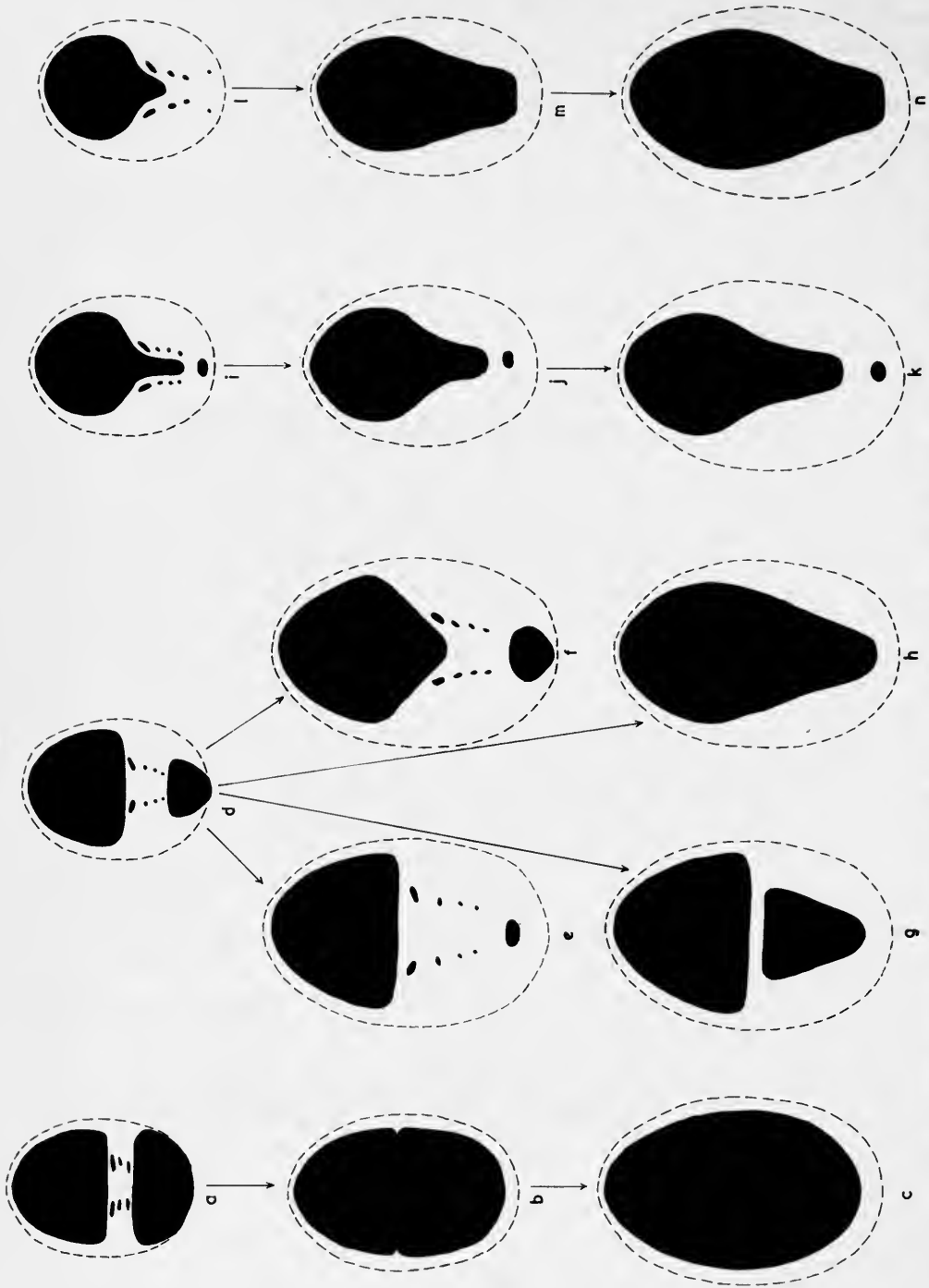


FIG. 7. Semi-diagrammatic representation of the dorsal sclerotization in: the protonymph (a), deutonymph (b) and adult (c) of a free-living or nest-inhabiting dermanyssid; the protonymph of an obligatory parasite of the Macronyssinae (d); females of *Ophionyssus natricis* (Gervais) (e); *Ornithonyssus aridus* Furman and Radovsky (f); *Steatonyssus* (g) and *Macronyssus* (h); the protonymph (i), deutonymph (j) and female (k) of *Liponyssoides sanguineus* (Hirst); the protonymph (l), deutonymph (m) and female (n) of *Dermanyssus gallinae* (Degeer).

Idiosoma

Dorsal sclerotization: The ontogenetic development of the sclerotization of the dorsum of the idiosoma in the free-living forms and in the facultative ectoparasites follows a definite and constant sequence. In the few larvae we have examined the dorsal sclerotization is relatively indistinct, the *podonotal shield* being the only one discernible (Text-fig. 8A). At the protonymphal stage a large anterior podonotal shield and a smaller posterior *pygidial shield* are always present, and on the striated cuticle between these two scutal elements lie a variable number of *mesonotal scutellae* (Text-fig. 7a). These scutal elements coalesce at the deutonymphal stage; presumably the pygidial shield and the mesonotal scutellae first unite and the resulting opisthonotal shield fuses with the podonotal shield except at its lateral margins to form a single dorsal shield with a pair of lateral incisions (Text-fig. 7b). Further fusion occurs at the adult stage resulting in the disappearance of the lateral incisions (Text-fig. 7c).

In order to allow for the expansion of the idiosoma which is necessary to accommodate the large quantities of tissue fluids taken during feeding, the obligatory parasites show a decrease in idiosomal sclerotization. This is first evident at the protonymphal stage by the reduction in the size of the pygidial shield (Text-fig. 7d). No distinct scutal elements are present in the larva (Text-fig. 8B). In the macro-nyssines the podonotal shield and the mesonotal scutellae of the protonymph resemble

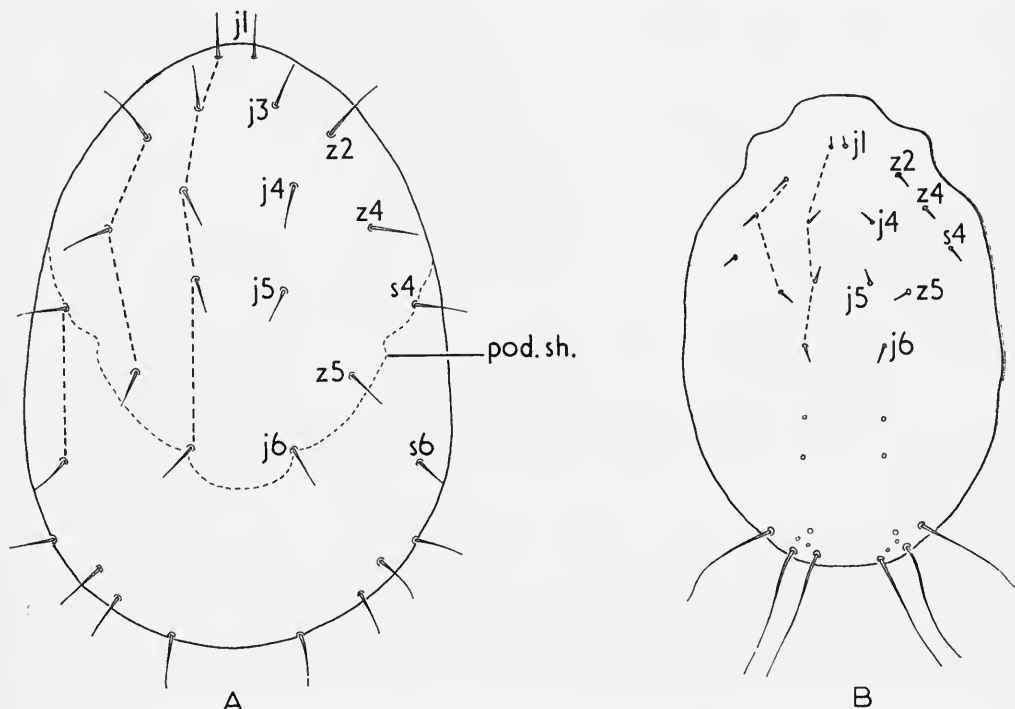


FIG. 8. Dorsal view of the larva of: A. *Holostaspis vitzhumi* (Womersley); B. *Ornithonyssus bursa* (Berlese).

the condition in the same instar of the free-living forms, but the pygidial shield is markedly reduced in size as is evident from its chaetotaxy (Text-figs. 10A and C). The non-feeding deutonymphal stages (male and female) of this group are very weakly sclerotized and it is difficult to differentiate the sclerotized area from the surrounding cuticle. It is probable that the extent of the weakly sclerotized areas is similar to that in their respective adult stages. All males, with the exception of *Steatonyssella*, which has two dorsal shields, have an entire dorsal shield formed as in the free-living species by the fusion of the podonotal, mesonotal and pygidial shields. This is also the condition in the female of *Macronyssus*, *Sauronyssus* and the majority of *Ornithonyssus* (Text-fig. 7h). The females of *Steatonyssus* and *Pellonyssus*, on the other hand, retain a distinct podonotal shield and have a smaller opisthonotal shield consisting of the pygidial and mesonotal elements (Text-fig. 7g). *Ornithonyssus aridus* Furman & Radovsky is exceptional amongst its congeners in retaining more or less the same form of dorsal sclerotization as the protonymph (Text-fig. 7f). The most specialized form occurs in females of *Ophionyssus* where distinct podonotal, mesonotal and pygidial elements are present and the pygidial shield shows a decrease in size in comparison with the protonymph (Text-fig. 7e).

Protonymphs of the Dermanyssinae show a further reduction of the pygidial shield (Text-figs. 7i and l). In the genus *Liponyssoides* the extremely small pygidial shield is either retained by the deutonymph and female as a separate scute (Text-figs. 7j and k) or fused with the remainder of the dorsal shield whilst in *Dermanyssus* the pygidial shield is lacking. The protonymphs of both genera have a strong posterior prolongation of the podonotal shield which extends between the mesonotal scutellae and serves as a more posterior attachment site for the retractor muscles of the greatly elongated cheliceral shafts. At the deutonymphal and adult stages of *Dermanyssus* an entire dorsal shield is usually present and this is probably formed by the posterior extension of the podonotal shield and its fusion with the mesonotal scutellae (Text-figs. 7m and n). Even within this genus there is a considerable variety in the dorsal sclerotization of the deutonymph and female, depending on the degree of development of the posterior prolongation of the podonotal shield. For example, in *D. scutatus* Krantz the posterior extension of the podonotal shield is very weak and bears only the first pair of dorsal opisthonotal setae, and the mesonotal scutellae are retained. The males of the Dermanyssinae have an entire dorsal shield.

Dorsal chaetotaxy: The dorsum of the idiosoma has a well defined chaetotaxy whose ontogenetic development is relatively stable. Deviations from the normal setal complement (the holotrichous condition) are relatively common in the specialized facultative and obligatory parasites and may be the result of hypo- or hypertrichy. The system of nomenclature adopted for the dorsal chaetotaxy in this work is that proposed by Lindquist & Evans (1965) and is a modification of the system used by Hirschmann (1957). In the adult holotrichous condition the dorsum is considered to bear 44 pairs of setae arranged in four longitudinal rows of 11 setae, a dorsal (*j*, *J*), a median (*z*, *Z*), a lateral (*s*, *S*) and a marginal series (*r*, *R*), on each side of the median longitudinal axis of the idiosoma, or alternatively in 11 transverse rows of eight setae.

The setae of the podonotal region are denoted by letters in lower case and those of the opisthonotum by capitals (Text-fig. 9c).

Van der Hammen (1964) has been extremely critical of the "artificial" (we should

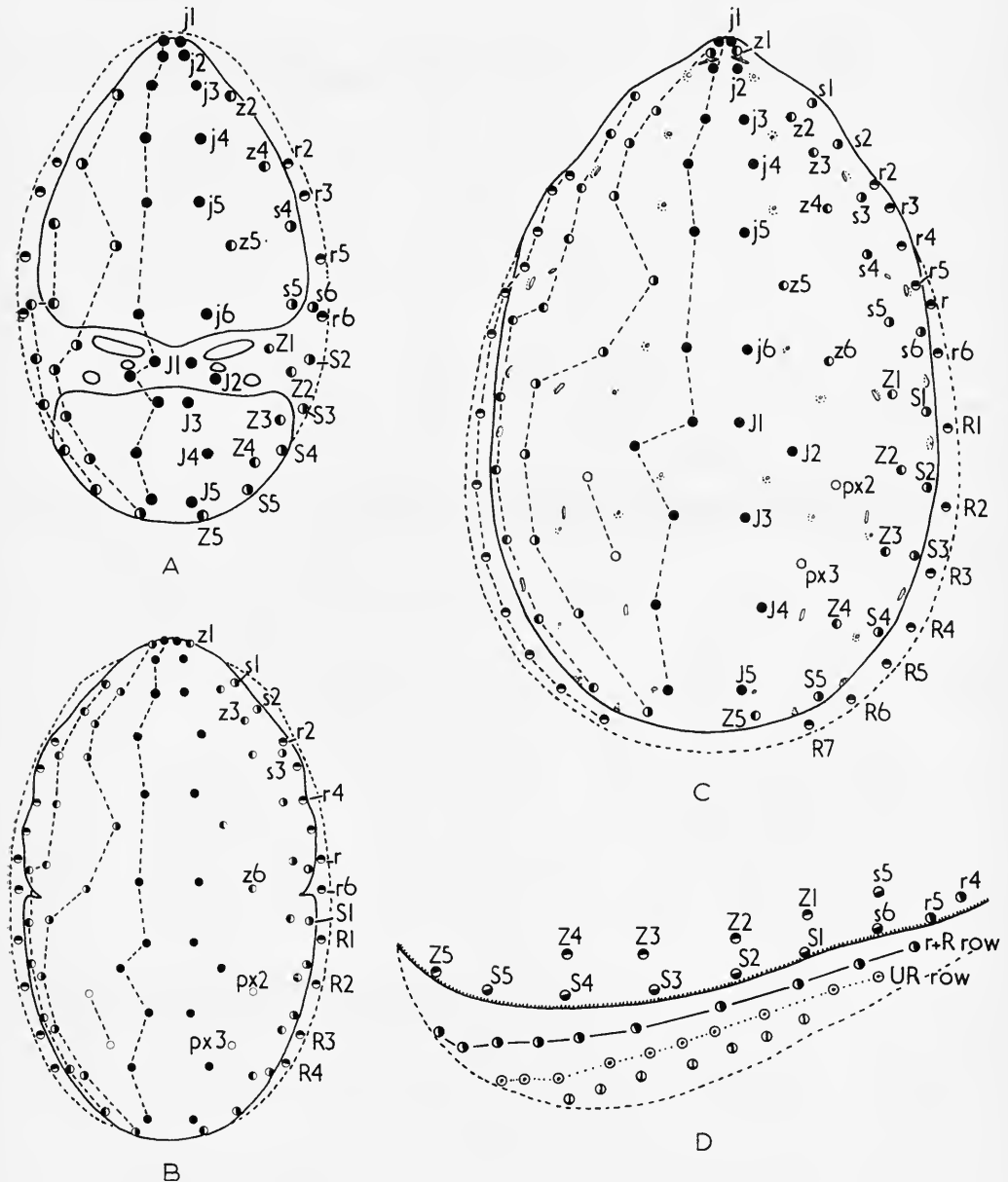


FIG. 9. Semi-diagrammatic representation of the dorsal chaetotaxy in the protonymph (A), deutonymph (B) and adult, dorsal (C) and lateral (D) view, of a free-living or nest-inhabiting dermanyssid (based on *Laelaps*).

prefer to call it "practical") system of setal nomenclature used in the Mesostigmata on the basis that the division of the idiosoma into two regions is probably artificial and useless for notation, since there is no evidence that the posterior margin of the podonotal shield and the anterior margin of the opisthonotal shield represent borders of tagmata. According to this author only a metameric arrangement of setae, that is in transverse rows, has phylogenetic value.

Theoretically, a metameric arrangement of setae would be ideal, but how is one to determine metamerism in a group which shows no evidence of idiosomal segmentation during post-embryonic development or for which there is, at present, no embryological evidence upon which to base metamerism? Certainly, the porotaxy of the dorsum shows such variability both in number and form of the "pores" as to be of doubtful value or significance, and we can see no basis for van der Hammen's statement that the "pores" show a metameric arrangement because their position corresponds to the borders of segments. In fact, any attempt to define metameric segmentation in the Mesostigmata on present evidence would be entirely speculative, and a system of setal terminology based upon it could be just as "artificial" as the system in current use. Such terms as "metameric arrangement" and "phylogenetic value" used at present in reference to a system of setal nomenclature in the Mesostigmata can only be classed as "red herrings" whose sole value is to add a pseudo-academic flavour to the text.

The main criterion for a system of setal nomenclature, in the absence of evidence of metamerism or of a primitive setal pattern, should be practicability. By this we mean that reference, for taxonomic purposes, can be made to individual setae and a comparison is possible between the setal patterns of related forms on the basis of "positional homology". The modified Hirschmann system of setal terminology proposed by Lindquist & Evans (1965) enables one to do this except in cases of extreme hypo- or hypertrichy of the dorsal chaetotaxy. This system retains the division of the chaetotaxy into a podonotal and an opisthonotal series since it is of practical value. The podonotal shield is a characteristic feature of the larval and protonymphal stages of the Mesostigmata and is retained as such (except for an increase in sclerotization laterally) in the deutonymphal and adult stages of many species. It can be readily defined by its chaetotaxy. No claim is made that the podonotal and opisthonotal shields define tagmata although it would indeed be surprising if the widespread occurrence of a division of the dorsal sclerotization of the idiosoma in the Mesostigmata at the podonotal-opisthonotal junction was without some functional significance.

Larvae of the Dermanyssidae are weakly sclerotized although it is usually possible in the free-living forms to define a podonotal shield which bears nine pairs of setae (j_1 , j_3 - j_6 , z_2 , z_4 , z_5 and s_4). A tenth pair of podonotal setae (s_6) occurs on the striated cuticle lateral to j_6 (Text-fig. 8A). The chaetotaxy of the opisthonotum is considerably less stable; for example, four pairs of setae are present in this region in some *Holostaspis* and seven pairs in some *Hypoaspis* s. lat. We have not attempted to name these setae. Few larvae of the obligatory parasites have been examined. In *Ornithonyssus bacoti*, for example, the podonotal region shows a deficiency of two

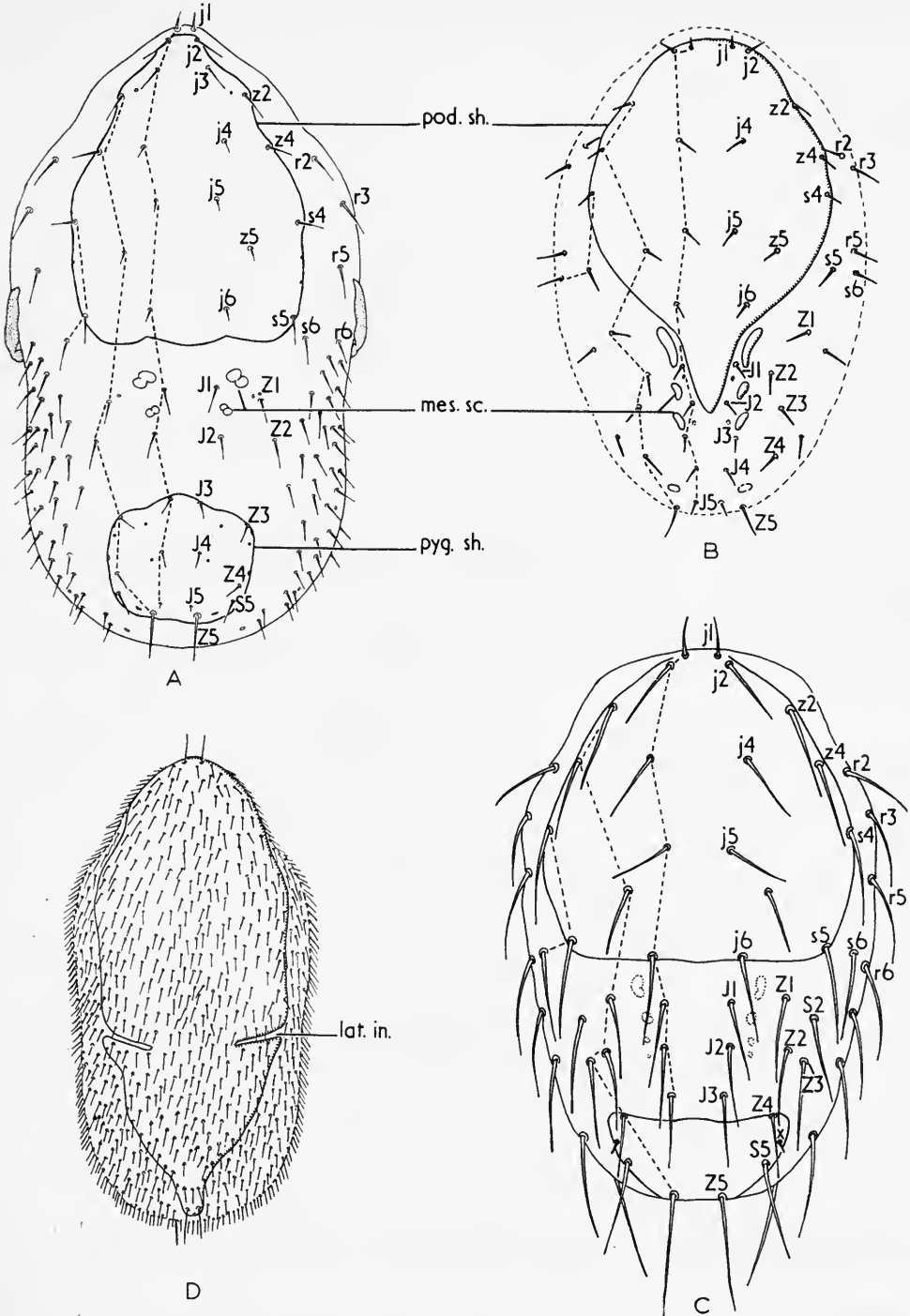


FIG. 10. Dorsum of: A. *Macronyssus flavus* (Kolenati) protonymph; B. *Dermanyssus gallinae* (Degeer) protonymph; C. *Ornithonyssus bacoti* (Hirst) protonymph; D. *Haemogamasus nidi* Michael, deutonymph.

pairs of setae (j_3 and s_6) and the opisthonotum bears only three pairs of long, slender setae. Setae j_3 , however, are present in some larvae of the Macronyssinae but the presence of only six opisthonotal setae appears to be characteristic for the group.

At the protonymphal stage of the free-living forms and the majority of the facultative parasites, the number of podonotal setae is increased to 16 pairs of which eleven pairs (j_2 and s_5 being additional to the nine pairs occurring on the shield in the larva) are situated on the podonotal shield and five pairs (r_2 , r_3 , r_5 , s_6 and r_6) on the cuticle lateral to the shield (Text-fig. 9A). Typically, the pygidial shield bears eight pairs of setae (J_3 - J_5 , Z_3 - Z_5 , S_4 and S_5) and the unsclerotized cuticle of the opisthonotum six pairs (J_1 , J_2 , Z_1 , Z_2 , S_2 and S_3) making a total of 14 pairs of opisthonotal setae and a dorsal complement of 30 pairs. In the facultative parasite *Eulaelaps stabularis* (Koch) the pygidial shield is reduced in size and bears only six pairs of setae (J_3 - J_5 and Z_3 - Z_5), setae S_4 and S_5 lying on striated cuticle. The total number of setae on the opisthonotum is sixteen pairs, an increase of two pairs over the normal. This may be the beginning of the hypertrichy of the dorsum which is so marked in the deutonymph and adult of this species. There is no hypertrichy of the podonotum at this instar. On the other hand, in the protonymphs of *Haemogamasus nidi* Michael there is marked hypertrichy of the lateral and marginal series in both the podonotal and opisthonotal regions.

The podonotal chaetotaxy of the protonymphs of the obligatory parasites is essentially the same as in the free-living forms (Text-fig. 10A). However, there is a tendency for hypotrichy of the j series by the suppression of j_3 , for example in some species of *Dermanyssus*, *Ornithonyssus* and *Pellonyssus*, or of j_3 and j_4 as in *Dermanyssus alaudae* (Schrank). Varying degrees of hypo- and hypertrichy are evident on the opisthonotum. In *Dermanyssus gallinae* (Degeer) the normal complement of J and Z series of setae is present but the S series is deficient, comprising only two pairs of setae (Text-fig. 10B). *O. bacoti* (Text-fig. 10C), on the other hand, shows a deficiency in the number of J setae (J_4 and J_5 being suppressed) whilst *Macronyssus flavus* (Kolenati) has the full complement of J and Z setae, and marked hypertrichy in the region of the S and R series. The widespread occurrence of hypo- and hypertrichy of the opisthonotum in the dermanyssines and macronyssines makes it difficult to use the relative positions of setae as a basis for comparing the chaetotaxy of this region with that of free-living forms, and we have restricted the naming of setae to those regions unaffected by these phenomena.

The full complement of dorsal setae is attained at the deutonymphal stage except possibly in some forms showing extreme hypertrichy (Text-figs. 9B-D). In the majority of the free-living forms and facultative parasites the dorsal, median and lateral series situated on the dorsal shield form six longitudinal rows of eleven setae (or eleven transverse rows of six setae). Setae added to these series at the deutonymphal stage are: z_1 , z_3 , z_6 , s_1 - s_3 and S_1 (Text-fig. 9B). The marginal series on the podonotum is fairly stable and comprises setae r_2 - r_6 (r_4 being added in the deutonymphal instar and r_6 remaining on the lateral integument) although in certain nest inhabiting forms (*Pneumolaelaps*) and facultative parasites (*Laelaps*) hypertrichy of this series is not uncommon. This series (R) and the submarginals (UR) are con-

siderably more variable on the opisthonotum and are commonly affected by hypo- or hypertrichy. *Hypoaspis praesternalis* Willmann, for example, has only one pair of *R* setae whilst in *Pneumolaelaps marginalis* Willmann both series are markedly hypertrichous and each comprises over 25 setae! Differences also occur in the number of opisthonotal marginal series (*R*) between the sexes of a given species and this is first evident at the deutonymphal stage, the male deutonymph and adult male having fewer setae in this series than the female deutonymph and adult female. Two further interesting features of the dorsal chaetotaxy are exhibited by the laelapines. The first is the appearance of a supernumerary row of setae between the *J* and *Z* series of the opisthonotum. This series, which is absent in *Stratiolaelaps*, some *Androlaelaps* and *Hyperlaelaps*, comprises a maximum of three setae/row, referred to as posterior accessories ($px1-3$) by Costa (1961). The maximum complement of px setae occurs in some *Androlaelaps*, but the usual number present is two pairs, $px2$ and $px3$ (Text-fig. 9c). Only one pair of the series ($px2$) is present in some *Hyperlaelaps*. The second feature is the tendency for hypertrichy to occur in the region of the *J* series in forms associated with other animals either as nest-inhabitants or facultative parasites. These unpaired setae show considerable intraspecific variability in number and in length. General hypertrichy of the podonotum and opisthonotum occurs at the deutonymphal stage of the *Eulaelaps-Haemogamasus* group and completely obscures the primary chaetotaxy (Text-fig. 10D).

Even within the free-living and facultative forms some hypotrichy of the dorsal and median series of setae is evident. For example, in *Ololaelaps* the deutonymphal setae $z1$ and $z3$ are suppressed and in *Ondatralaelaps*³ $j3$ and $z3$ are lacking on the podonotum and $J3$, $J4$ and $Z3$ on the opisthonotum. Rarely, in some *Androlaelaps*, a supernumerary seta occurs on the podonotal region of the dorsal shield lateral to $s4$ and has been referred to as an anterior accessory seta (*ax*) by Costa.

The dorsal chaetotaxy of the deutonymphs of the obligatory parasites is characterized by the tendency for the retardation in the development of the chaetotaxy of the podonotum and the occurrence of hypertrichy in the lateral and marginal series. Further, in the non-feeding deutonymphs of the macronyssines two distinct types of dorsal chaetotaxy are present, corresponding to the form in the adult male and female (Text-figs. 11A and C). Reference has already been made to the hypotrichy of the dorsal series at the larval and protonymphal stages of both dermanyssines and macronyssines, and those setae of the series which are suppressed at the protonymphal stage do not appear in subsequent developmental stages. However, the main feature of retardation in the development of the podonotal chaetotaxy in the deutonymphal stage is most apparent in the suppression of certain setae which normally first appear at this instar, for example, the paraverticals ($z1$), $z3$, $s2$ and, particularly in the male, $z6$ (Text-figs. 11A and C). The chief difference between the chaetotaxy of the male and female non-feeding deutonymphs of the macronyssines is seen in the greater hypertrichy of the idiosoma in the region of the lateral and marginal series of setae in the female.

In all the British members of the Dermanyssidae, the adults appear to retain the

³ *Ondatralaelaps* gen. nov. (type: *Laelaps multispinosa* Banks).

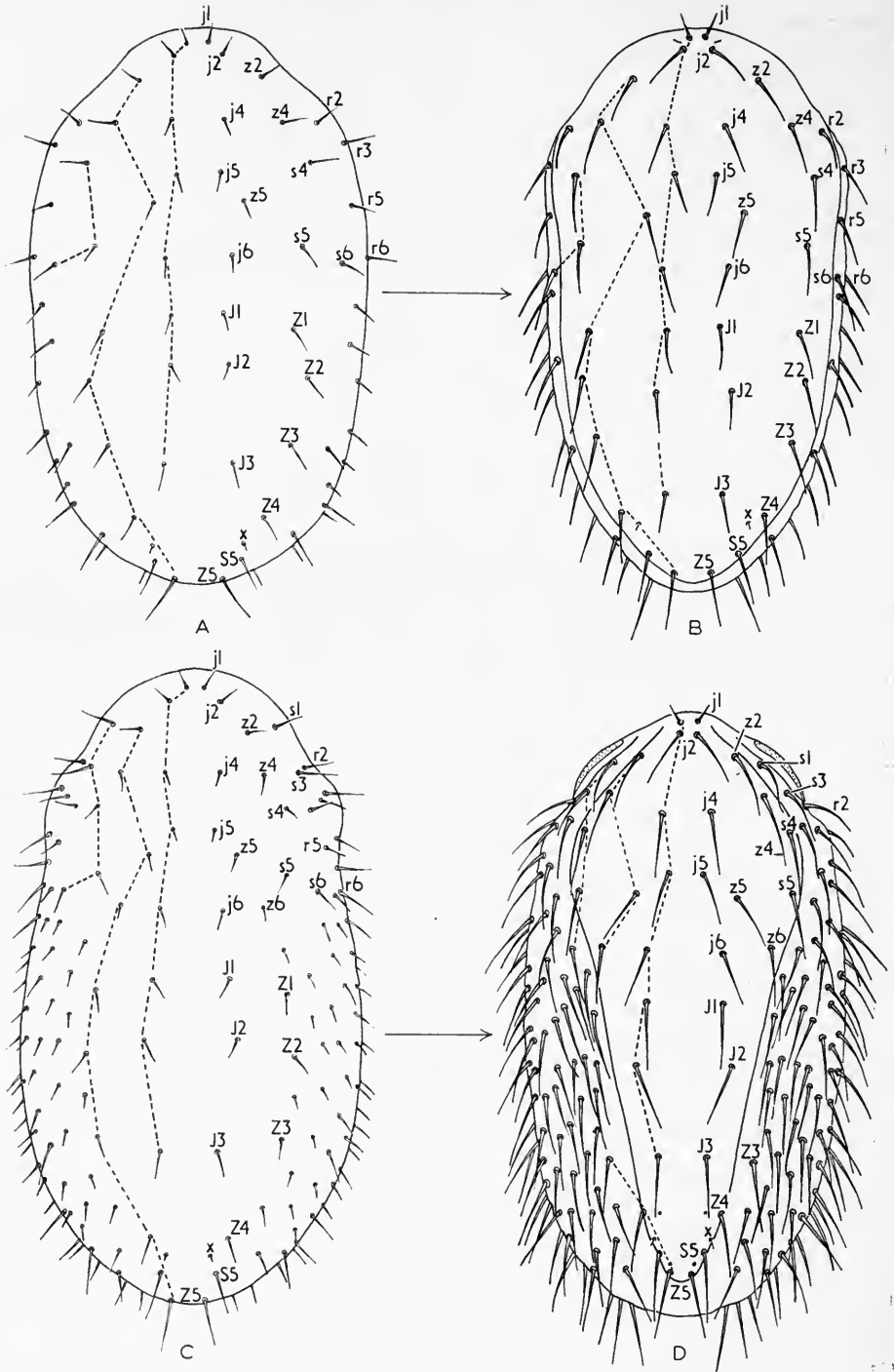


FIG. 11. *Ornithonyssus bacoti* (Hirst). Dorsum of A. male deutonymph ; B. male ; C. female deutonymph ; D. female.

dorsal idiosomal chaetotaxy of the corresponding male or female deutonymph. Males of the obligatory parasites show an increase in the area of dorsal sclerotization compared with the female with the result that certain of the r series and of the z series occurring on unsclerotized cuticle in the female are incorporated on the dorsal shield in the male (Text-figs. 11B and D).

An exception to the basic dorsal chaetotaxy of the Dermanyssidae occurs in the adults (the only known stages) of *Pseudolaelaps doderoi* (Berlese) whose systematic position is problematical. The dorsum is markedly hypotrichous, the podonotum bearing only 15 pairs of setae and the opisthonotum nine pairs.

Some intraspecific variability in the primary chaetotaxy of the opisthonotum is apparent in many obligatory parasites and in some facultative parasites and takes the form of the suppression of one seta of a pair or an asymmetrical arrangement of the setae of a pair. This is particularly evident in members of the genera *Dermanyssus* and *Ondatraelaps*.

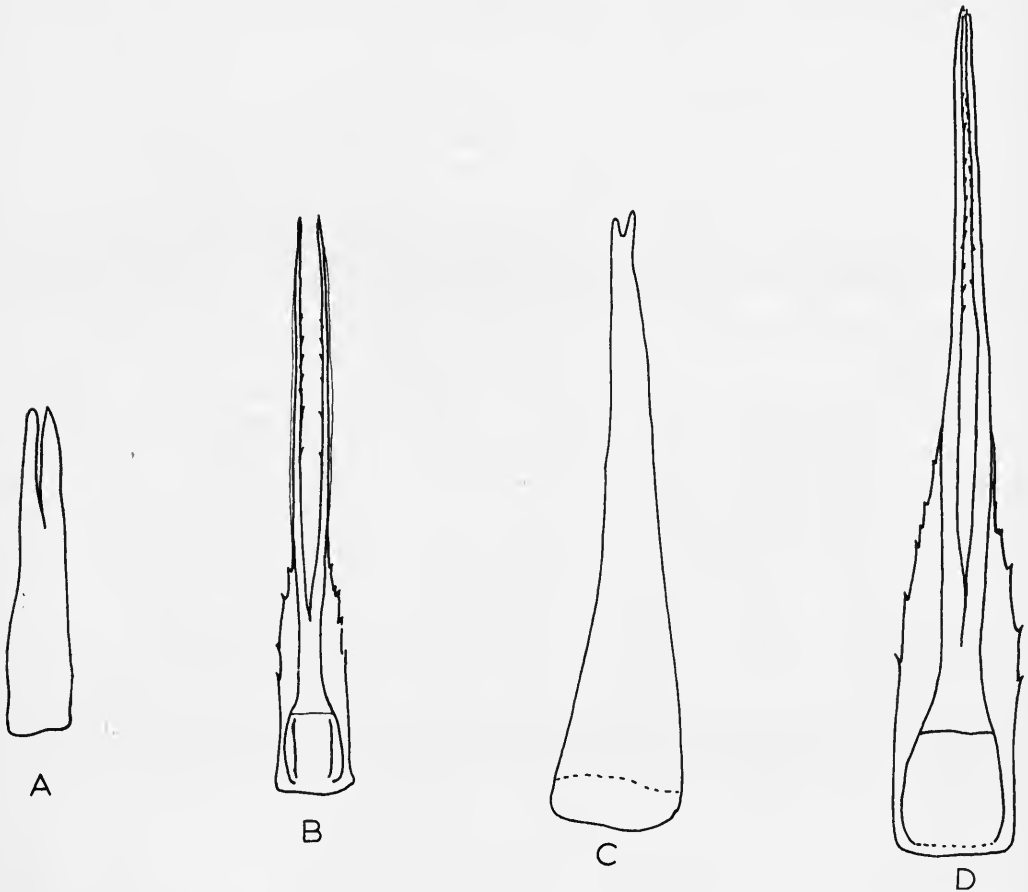


FIG. 12. *Ornithonyssus bacoti* (Hirst). Tritosternum of larva (A), protonymph (B), deutonymph (C) and adult (D).

The dorsal setae in the majority of the Dermanyssidae are slender and smooth or weakly pilose. Exceptions occur in the genera *Stratiolaelaps* and *Cosmolaelaps* where they tend to become leaf-like or spatulate, and in facultative parasites of the *Laelaps*-group in which they may be modified as short robust spines. The vertical setae (jI) sometimes differ in form from the other setae in the region of the vertex.

Dorsal porotaxy: The basic adult and deutonymphal complement of "pores" on the dorsum of the idiosoma appears to be 22 pairs (11 podonotal and 11 opisthonotal) and their distribution in *Laelaps* is shown in Text-fig. 9c. Considerable diversity occurs in the pattern and number of "pores" throughout the family and both hyper- and hypoporosity are not uncommon, particularly in the obligatory parasites.

Tritosternum: The tritosternum⁴ lies between coxae I on the venter of the idiosoma and is present as a biramous structure in all British Dermanyssidae (Text-figs. 12, 15, 16). Its function is unknown. In life, the laciniae lie along the capitular groove and the fine processes (pilae) along their margins possibly engage the denticles of the deutosternum. The basal portion of the tritosternum is longer than wide and the laciniae in the free-living and facultatively parasitic forms are invariably pilose. Many obligatory parasites (Dermanyssinae and Macronyssinae) have a transparent, marginally denticulate border to the tritosternum (Text-fig. 12D). The non-feeding larva and deutonymph of the Macronyssinae have the laciniae of the tritosternum markedly reduced (Text-figs. 12A-D).

Sclerotization and chaetotaxy of the venter: At the larval stage in the free-living forms and in most of the facultative parasites two sclerotized areas are present ventrally; a sternal shield, of varying degrees of sclerotization, inter-coxally and a subtriangular anal shield surrounding the anus which is provided with a pair of valves (Text-fig. 13A). The sternal shield carries three pairs of setae (*st.* 1-3) and the anal shield three setae, comprising a pair of paranals (*pan.*) and an unpaired postanal (*pon.*). There are no *euanal setae*, that is, setae situated on the anal valves. Four pairs of setae occur on the unsclerotized cuticle of the opisthogaster and, according to the system proposed by Lindquist & Evans (1965), these consist of three pairs of internal ventrals (*Jv*1, 2 and 5) and one pair of medio-lateral ventrals (*Zv*2) arranged as in Text-fig. 13A. Stigmata, peritremes and podal sclerites are not present in the larva. In the obligatory parasites there is a marked reduction in sclerotization to the extent that only rarely can one define distinct sternal and anal shields. However, the normal three pairs of sternal setae and the three setae associated with the anal

⁴ Van der Hammen (1964) has rejected the term tritosternum (for *furca*) on the ground that it is "no sternum at all, because a sternum is a distinct plate". However, he considers (without giving any evidence) that the small sclerite occurring in the normal position of a tritosternum in some of the *highly specialized* bat parasites of the family Spinturnicidae represents a "real sternal plate belonging to segment III"! The reason for this must be, by inference, that the structure is a "plate" although, even in this group, the tritosternum is not always a simple plate [cf. *Meristaspis jordani* (Radford)]. Perhaps the tritosternum in some Trachytidae (Uropodina) will also satisfy his "criterion" of a sternum? At present, the origin of the tritosternum is unknown but it seems unnecessary to change such a well-established term, certainly on the "evidence" presented by van der Hammen.

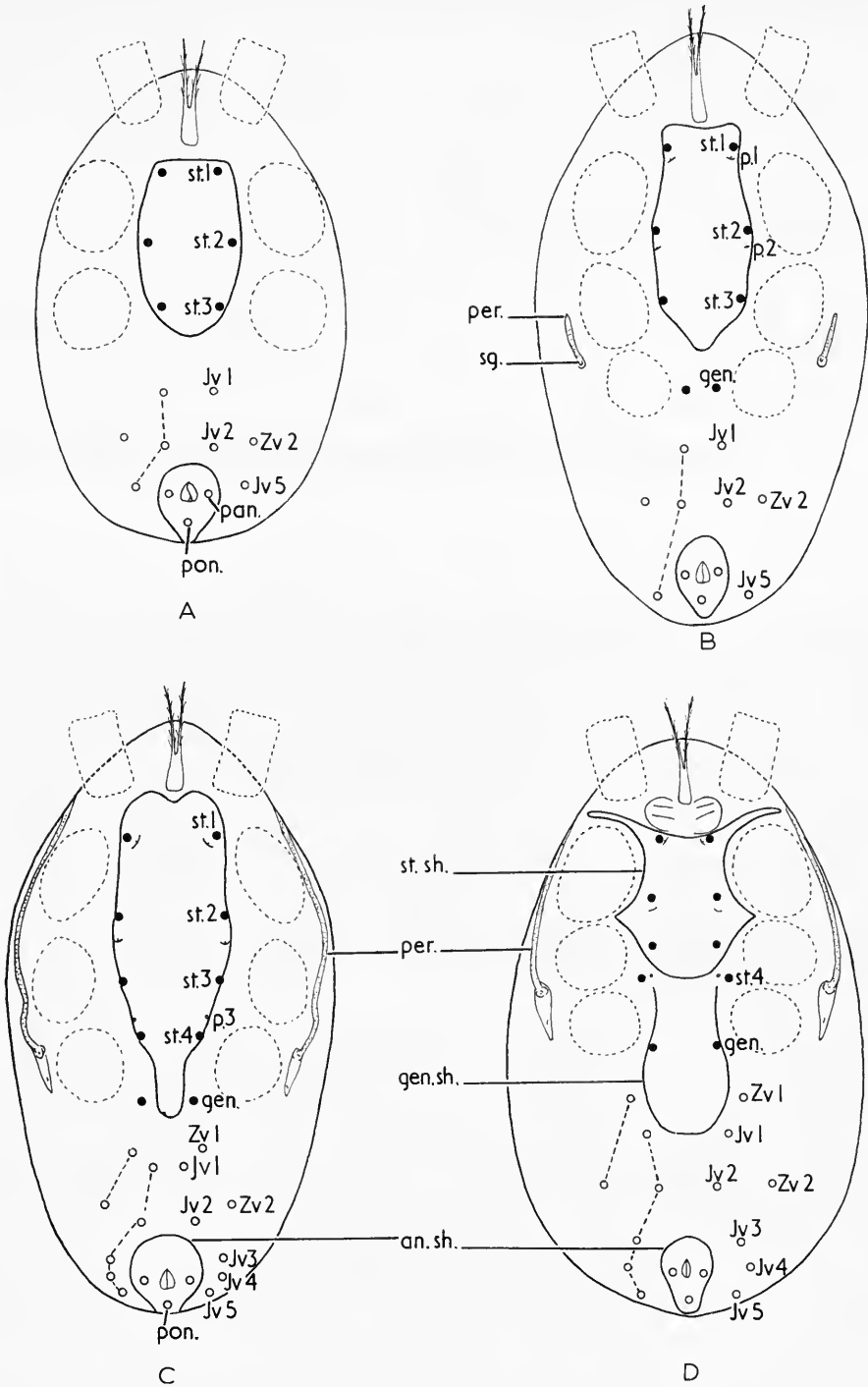


FIG. 13. Semi-diagrammatic representation of the venter of the larva (A), protonymph (B), deutonymph (C) and female (D) of *Hypoaspis (Gaeolaelaps) aculeifer* (Canestrini).

region are present, but there is a retardation in the development of the opisthogastric setae, only one pair (*Jv1*) being developed in some *Dermanyssinae* and two pairs (*Jv1* and 2) in the *Macronyssinae* (Text-fig. 14A).

The sternal and anal shields in the protonymph are generally well-defined and carry the same complement of setae as in the larva (Text-fig. 13B). A pair of genital setae (sometimes present as incipient setae in the larva) and two pairs of lyriform fissures (*p. 1* and *p. 2*) first appear at this instar. In the free-living forms the larval number of setae on the opisthogastric cuticle is retained, but in the obligatory parasites the larval deficiency in opisthogastric setae is rectified and the protonymph now acquires its full complement with the appearance of *Zv2* and *Jv5* (Text-fig. 14B). Hypertrichy of the opisthogastric region may occur at this stage in some *Macronyssinae*, for example, *Macronyssus flavus* (Kolenati). Stigmata with short, anteriorly directed peritremes never extending beyond the anterior margin of coxae III are present lateral to the third coxal interspace. No distinct podal shields occur at the protonymphal stage.

Increased sclerotization and setation of the venter are evident at the deutonymphal stage. The sternal shield, bearing the three pairs of setae and two pairs of fissures present in the protonymph and a fourth pair of setae, the metasternals (*st. 4*) with their associated pores, which first appear at this instar, occupies almost the entire

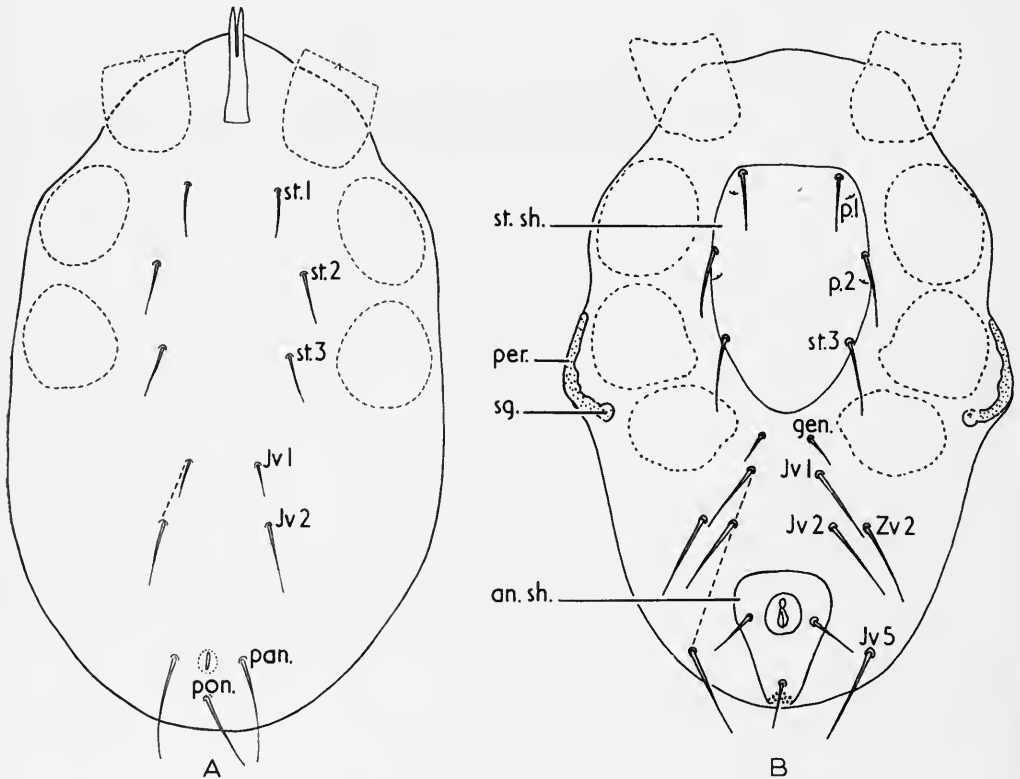


FIG. 14. *Ornithonyssus bacoti* (Hirst). Venter of larva (A) and protonymph (B).

length of the intercoxal region. Its tapered, posterior region extends between the genital setae (Text-fig. 13C). Hypotrichy of the sternal region has been observed in some obligatory parasites, for example, certain species of *Dermanyssus* and *Pellonyssus*, and this is characterized by the absence of the metasternal setae which fail to develop at their normal stage in ontogeny. Certain species of *Haemogamasus*, on the other hand, show a distinct hypertrichy of the sternal chaetotaxy, the secondary setae usually being shorter than the primary. The anal shield more or less retains the form present in the larva and protonymph.

Considerable variation occurs in the chaetotaxy of the opisthogaster in the deutonymph. Normally, the holotrichous condition for this region is seven pairs of setae (*Zv*₁, *Jv*₃ and *Jv*₄ added to the protonymphal complement) and this occurs in certain of the free-living forms, for example, some species of *Hypoaspis* s. lat., *Ololaelaps*, *Pseudoparasitus* and *Stratiolaelaps*. More commonly, however, the region shows some degree of hypertrichy, particularly in the *Eulaelaps*-*Haemogamasus* group and in the obligatory parasites. As in the case of the marginal setae of the dorsum, the male deutonymph often has fewer opisthogastric setae than the female deutonymph. Further, there may be considerable intraspecific variability in the number of opisthogastric setae in deutonymphs of the same "sexual phase". The stigmata are situated in the same position relative to coxae III and IV as in the protonymph, but in all free-living forms and the majority of the facultative parasites the peritreme is considerably longer and usually extends up to or beyond coxa I. Exceptions to this occur in certain of the obligatory parasites (*Dermanyssus*, *Steatonyssus*, *Pellonyssus*, *Ophionyssus*) where the protonymphal form of the peritreme may be retained at the deutonymphal stage. In the free-living forms a weakly developed peritrematal shield is also present and its post-stigmal portion bears a conspicuous pore (Text-fig. 13C). Podal shields are absent except for a weakly sclerotized strip along the posterior border of the coxal cavity of leg IV. Weakly sclerotized metapodalia may be present. An anal shield with the normal three setae is characteristic of the family although in densely hypertrichous forms (*Haemogamasus*) it may carry a number of secondary unpaired setae.

With the exception of the hypertrichous forms showing intraspecific variability of the opisthogastric setae, the adult setal complement of the venter is determined at the deutonymphal stage (male or female). The degree of sclerotization and the size and outline of the shields at the adult stage, however, show great diversity, greater in fact than within any other family of the Mesostigmata. In the female of the free-living forms and the facultative parasites the sternal shield normally bears three pairs of setae (*st.* 1-3) and two pairs of lyriform fissures (*p.* 1 and *p.* 2). It is fused laterally with the endopodal shields of coxae II. More rarely it bears, in addition, the metasternal setae (*st.* 4) and their associated pores (*p.* 3) as in *Ololaelaps* (Text-fig. 15D). The posterior margin of the sternal shield may extend as far as the level of the posterior margin of coxa III, as in *G. aculeifer*. Its anterior margin is often indistinct owing to the sclerotization of the cuticle immediately anterior to the shield. This pre-sternal area of sclerotization may be uniformly sclerotized and reticulated (Text-fig. 15B) or regionally more heavily sclerotized to form pre-endopodal sclerites (Text-

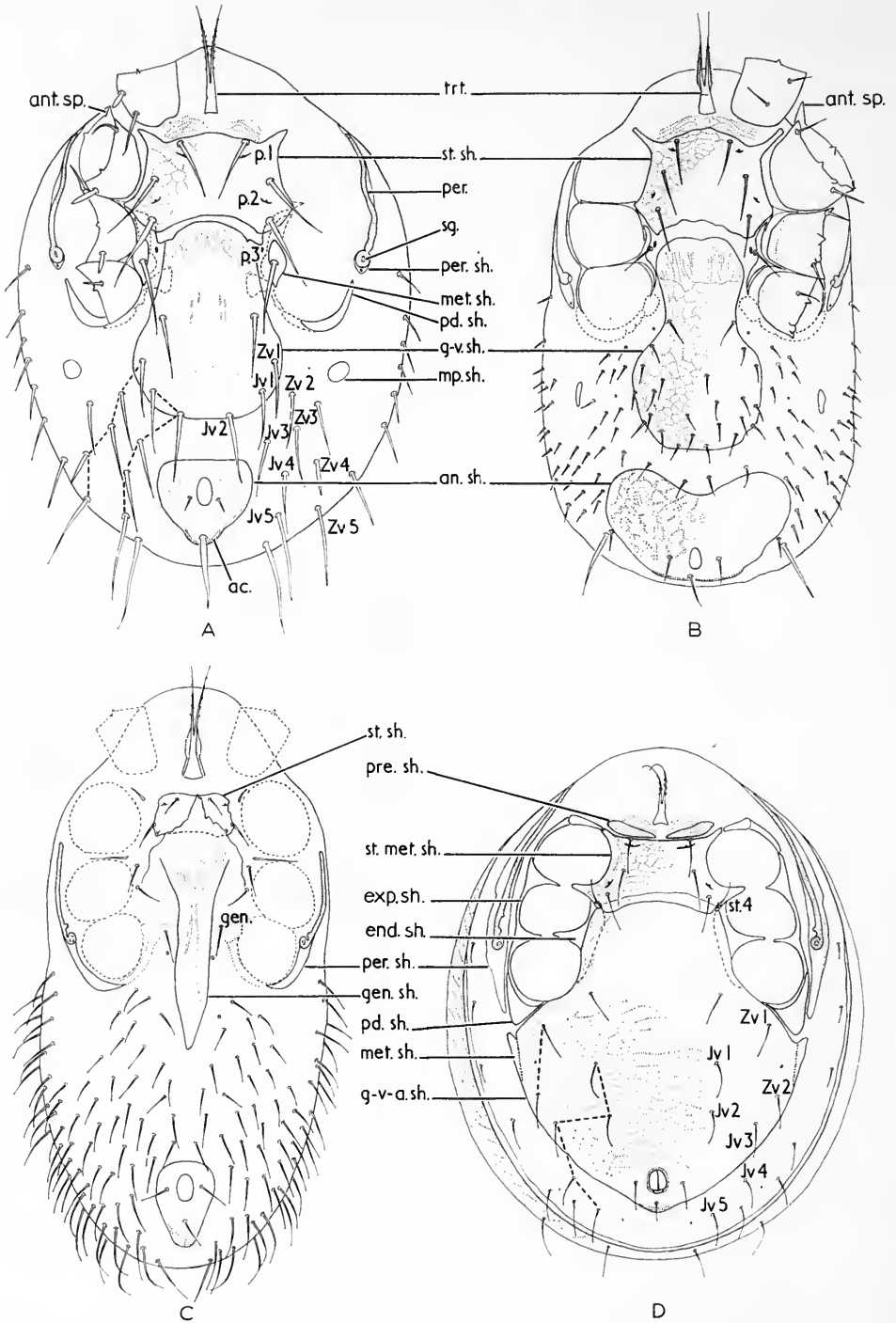


FIG. 15. Venter of female of : A. *Laelaps agilis* Koch ; B. *Myonyssus gigas* (Oudemans) ; C. *Ophionyssus natricis* (Gervais) ; D. *Ololaelaps placentula* (Berlese).

fig. 15D). We have not observed true jugularia in the British members of this family. The surface of the sternal shield is variously ornamented, the ornamentation being in the form of a reticulate pattern of lines, or punctate lines, or scattered punctures. The metasternal setae and pores are normally situated posterior to the sternal shield and lie on striated cuticle or on small metasternal shields which may be free or fused with the endopodal shields of coxae III. In the obligatory parasites the sternal shield is less well developed and rarely fused with the endopodal shields of coxae II. It may bear only two pairs of setae (*st.* 1 and 2) and pores (*p.* 1 and 2) or the normal three pairs of setae and two pairs of pores. In outline it is generally sub-rectangular but in some *Pellonyssus* it is reduced to a narrow, transverse, band-like sclerite. Subcircular "porose" areas occur between sternal setae 1 and 2 in some species of *Macronyssus*. The metasternal setae in this group are usually situated on striated cuticle. They are absent in the adults whose deutonymphs lack these setae.

The female genital orifice (with its apodemes) appears as a transverse slit at the level of the fourth coxae. Associated with this orifice, and extending posterior to it, is a characteristic genital shield bearing the genital setae. Anteriorly the shield has a hyaline flap of varying degrees of development. In its least specialized form the genital shield is more or less flask-shaped and bears only the genital setae (Text-fig. 13D) but, with the exception of the obligatory parasites, there is a general tendency for an increase in the size of the shield and the incorporation with it of a number of opisthogastric setae. Such a shield is termed *genito-ventral* (Text-figs. 15A-B). Marked hypertrichy of the genital shield occurs in *Eulaelaps*, *Haemogamasus* and *Myonyssus*. The genital shield shows some reduction in size in the obligatory parasites and tapers in its posterior half. In some macronyssines the reduction in size and the posterior tapering of the shield is very marked; the resulting shield is slender and does not carry the genital setae (Text-fig. 15C). The anterior hyaline flap is usually extensive in these obligatory parasites and its tapering anterior region may extend beyond the anterior margin of the sternal shield.

All the British dermanyssids have an anal shield bearing the three setae normally associated with the anus. It is typically sub-triangular or pear-shaped. An exception occurs in the genus *Myonyssus* (Text-fig. 15B) in which it is considerably broader than long. The region posterior and lateral to the postanal seta is invariably provided with aciculae. Secondary unpaired setae occur on the anal shield of some members of the genus *Haemogamasus*.

The ventral sclerotization of the female of *Ololaelaps* is exceptional in that there is a fusion of the genito-ventral, metapodal and anal elements to form a compound shield occupying almost the entire area of the opisthogaster (Text-fig. 15D).

The endo- and exopodal shields form a more or less complete framework enclosing coxal cavities II-IV in many of the free-living forms and facultative parasites. In *Pseudoparasitus*, *Ololaelaps*, *Laelaspulus* and some species of *Holostaspis* and *Gymnolaelaps*, the podal elements behind coxae IV become greatly enlarged (Text-fig. 15D). Varying degrees of reduction of the exopodal shields occur in the genera *Hypoaspis*, *Haemogamasus* and *Laelaps* and in the obligatory parasites only fragments of the podal shields remain, the most conspicuous being the one behind coxa IV.

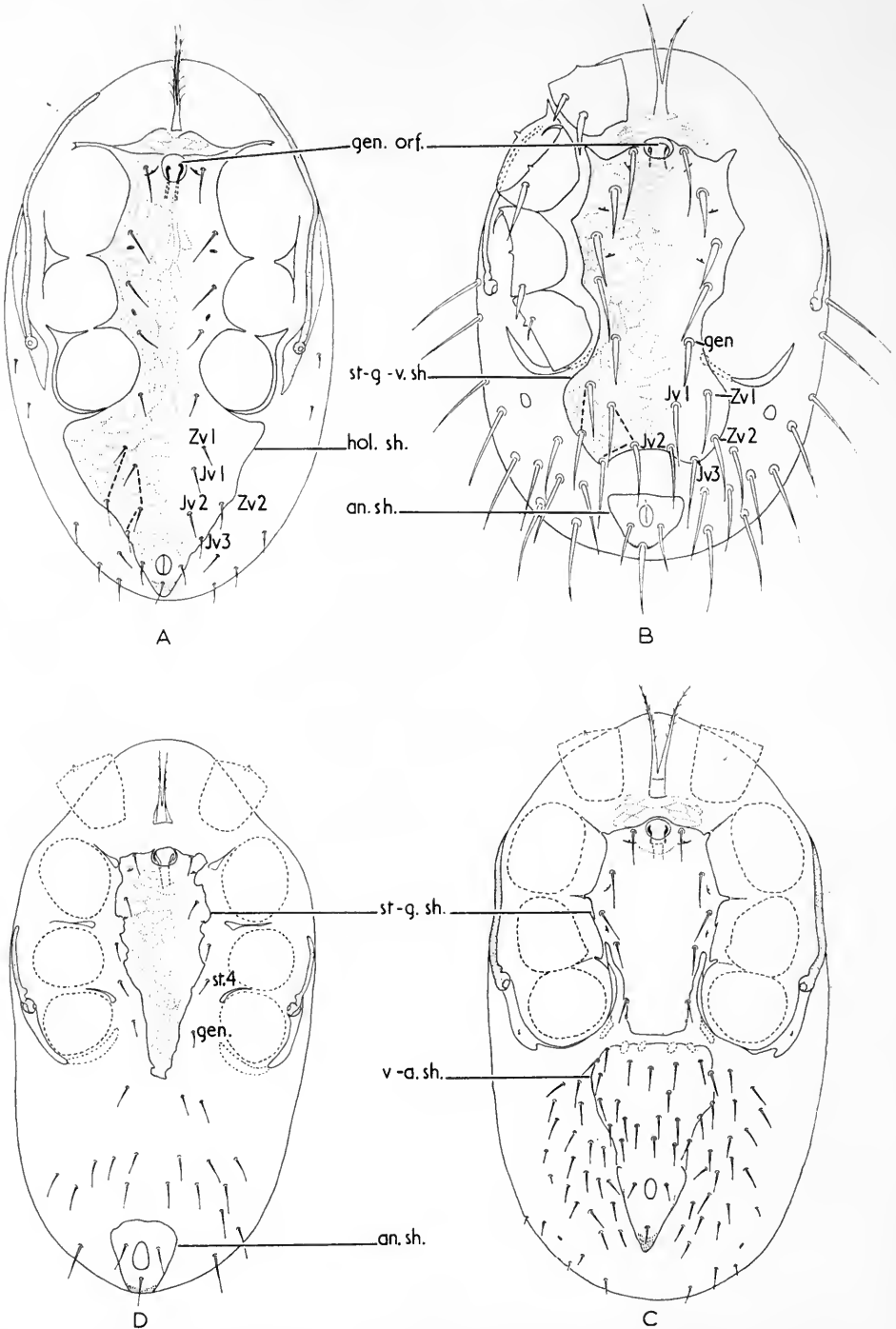


FIG. 16. Venter of male of: A. *Hypoaspis (Gaeolaelaps) aculeifer* (Canestrini); B. *Hyperlaelaps microti* (Ewing); C. *Macronyssus* sp.; D. *Ophionyssus natricis* (Gervais).

Metapodal shields are variable in form and number. In most free-living forms they are small, oval, elliptical or elongate bodies, but in *Eulaelaps* they become large subtriangular structures. Obligatory parasites usually have only one pair which is weakly sclerotized and difficult to discern. The metapodals may fuse with the genito-ventral shield as in *Ololaelaps* (Text-fig. 15D).

Stigmata and peritremes are of basically the same form as in the deutonymph. The peritrematal shield is fused with the dorsal shield anteriorly, except in some obligatory parasites. Posteriorly it may be free or fused with the podal shield in the region of coxa IV (Text-figs. 15A-C).

Typically, the males have a holovertral shield formed by the fusion of the sternal, metasternal, endopodal, genital, ventral and anal shields. It carries the four pairs of sternal setae, the genital setae, the three setae associated with the anus and a variable number of opisthogastric setae (Text-fig. 16A). In the free-living forms and the facultative parasites it is generally expanded posterior to coxae IV, but in some macronyssines it shows little or no expansion in this region. Deviations from the typical holovertral shield are apparent in some facultative and obligatory parasites. *Hyperlaelaps*, for example, has a compound sternito-genito-ventral shield and a separate anal shield (Text-fig. 16B). Further reduction of the ventral sclerotization occurs in *Ophionyssus natricis* (Degeer), the sclerotized areas comprising a sternito-genital and a separate anal shield (Text-fig. 16D). Certain species of *Macronyssus* show another variant in having a sternito-genital and a separate ventro-anal shield (Text-fig. 16C). The genital orifice, closed by a single valve, is always situated near the anterior margin of the "sternal shield" and is flanked by the first pair of sternal setae.

Legs

Segmental chaetotaxy: Without exception the legs are seven-segmented, the terminal segment being represented by the ambulacrum. The segments, from coxa to tarsus, have a well-defined chaetotaxy and the system of nomenclature and formulae for the segmental chaetotaxy follows that proposed by Evans (1963). This system, based on the observed ontogenetic development of the leg chaetotaxy in over 100 species of Gamasina and which has subsequently been found to be applicable to the Uropodina and Antennophorina, has been criticized by van der Hammen (1964) who, with little success, attempted to apply Grandjean's nomenclatural system for the leg chaetotaxy of the Oribatei and allied Actinochaeta to an adult macrochelid mite. His criticisms are: (a) that the existence of a basic whorl of setae on a segment was ignored; (b) that no attention was paid to the presence of the unpaired dorsal seta, *d*, and (c) that the segmental formulae are of little or no comparative value. Are these criticisms of the Evans system valid in the light of the observed segmental chaetotactic patterns on the legs of the Mesostigmata? In our opinion they are not, for the following reasons:

Grandjean (1940) considers the basic element of the segmental chaetotaxy to be a ring or whorl of setae consisting of a maximum of seven (oribatologists refer to this condition as "primitive"), namely, an unpaired dorsal, two pairs of laterals and one

pair of ventrals. The existence of a whorl of setae on the segment was not ignored by Evans and is implicit in his segmental formula

$$\left(al \begin{array}{c} \overline{ad} \\ \overline{av} \end{array}, \begin{array}{c} \overline{pd} \\ \overline{pv} \end{array} \overline{pl} \right)$$

which van der Hammen overlooked and instead based his criticism on a simpler formula

$$\left(al \begin{array}{c} \text{dorsals} \\ \text{ventrals} \end{array} \overline{pl} \right)$$

which was adopted only in those cases where the extreme non-cylindrical form of the segments (the femora and trochanters) made it impossible to distinguish the anterior and posterior members of the dorsal and ventral series. As regards the presence of an unpaired dorsal seta, there is no evidence from observed segmental patterns that such a seta exists on any leg segment (excluding perhaps tarsus I which has not been studied in detail) of the larva or any segments, excluding the tarsi, in subsequent developmental stages of the Gamasina and Uropodina. Van der Hammen's statement that Evans "did not pay attention to the definition of the unpaired dorsal seta *d*..." is contrary to the facts and one wonders whether the author has read

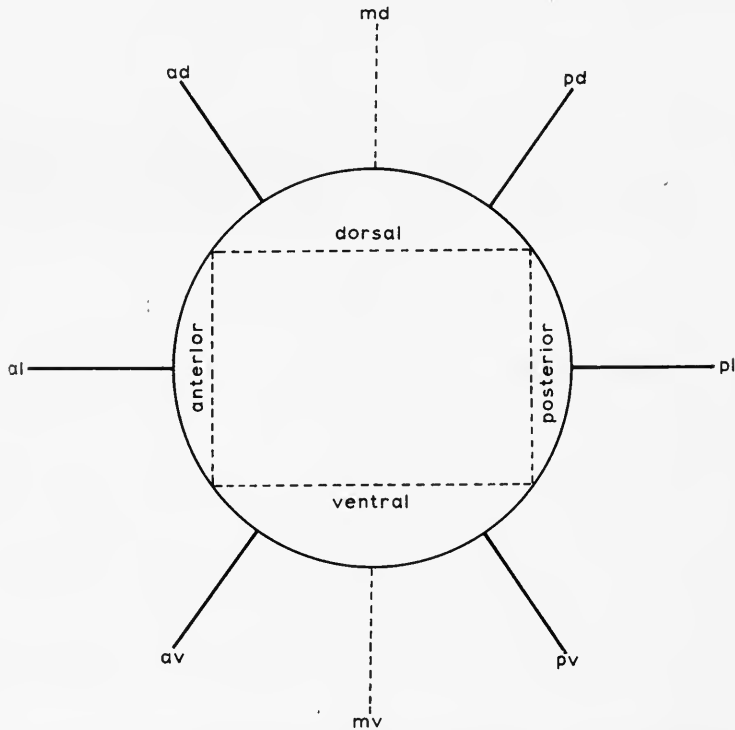


FIG. 17. Diagrammatic representation of the setal positions on a leg segment of a dermanyssid mite.

beyond the "introduction" in Evans' 1963 paper! In this paper attention is drawn to the appearance on tarsi II-IV of an unpaired dorsal and ventral seta at the protonymphal and deutonymphal stages respectively, and these are referred to as medio-dorsal (*md*) and medio-ventral (*mv*). If the observed position of these unpaired setae reflects their primary position on these segments, then the maximum complement of a segmental whorl in the Mesostigmata would be eight setae as shown diagrammatically in Text-fig. 17. Owing to a regression in the dorsal and ventral setae, the maximum complement of a whorl is apparently not present on other segments of the legs.

Van der Hammen's attempt to define the unpaired dorsal seta on the leg segments is characterized by such statements as "impossible to conclude whether the three plumose setae with a dorsal position are really *d*", "possibly dorsal plumose setae" and "probably dorsal setae". This uncertainty is inevitable and arises from an attempt to make the chaetotactic patterns fit a pre-conceived system. It is surprising that van der Hammen has used "probably dorsal setae" only in reference to certain setae on the dorsal surface of femur II, one of the segments showing an extreme non-cylindrical form which affects the primary chaetotactic pattern of the segment. In those forms which have a less specialized femur II, that is, the segment is more or less cylindrical, the longitudinal arrangement of the setae on its dorsal surface resembles that of genu II for which van der Hammen finds it impossible to define unpaired dorsal setae! The "migration" of setae from their normal (primary) position relative to other setae on a segment is common and is not only due to the asymmetrical development of the segment. More often the "migration" occurs as the result of the absence of one member of a "pair" of setae on the segment. The remaining seta often develops in an intermediate position along an imaginary line which would have connected the bases of the "pair". For example, four setae (*av*₁, *av*₂, *pv*₁, *pv*₂) whose bases form the corners of a rectangle often occur on the ventral surface of tibia I in the Gamasina, but in some groups *pv*₂ is lacking and the remaining member of the pair (*av*₂) may migrate to occupy a median position on the segment at the level of the line joining the bases of *av*₂ and *pv*₂ in the forms with four ventral setae. Such deviations from the normal distribution of setae on a segment add to the difficulty of applying any system of setal nomenclature based on "positional homology".

We reject van der Hammen's criticism of the segmental formulae which have proved to be of considerable practical value in referring to the segmental chaetotaxy. This author's alternative formula, which he considers "more logical" (?), depends on the recognition of unpaired dorsal setae and is completely impracticable.

It seems appropriate, in the present context, to refer to another fundamental difference between the system of nomenclature proposed by Evans and that used for the Actinochaeta. Although in both systems the positions of setae are defined in relation to certain faces of the segment, the lateral faces in the Grandjean system are defined according to the natural position of the limb relative to the longitudinal axis of the body, the anteriorly directed first two pairs of legs and the posteriorly directed legs III and IV having paraxial and anti-axial faces. In the system used in the Meso-

stigmata, on the other hand, the definition of the lateral faces (anterior and posterior) is not based on the natural, but on the artificial position of the limb, that is, when it is extended laterally at right angles to the longitudinal axis of the idiosoma. Adopting Grandjean's terminology for the lateral faces of the legs in the Mesostigmata would necessitate referring to the anterior and posterior faces of legs I and II as paraxial and anti-axial respectively, since these legs are directed anteriorly, retaining anterior and posterior for legs III which are directed laterally, and referring to the anterior and posterior faces of legs IV as anti-axial and paraxial respectively, since these limbs are directed posteriorly. In comparison with the existing system of setal terminology in the Mesostigmata, the advantages gained, if any, by basing the system on two (or three) different terminologies for the lateral faces of the limbs, would be at the expense of simplicity and practicability.

The segmental chaetotaxy of the legs in the larval dermanyssids we have examined is constant and normal for the Gamasina, as defined by Evans (1963). At the protonymphal stage one seta is added to the ventral surface of femur II and one medio-dorsal seta to each of tarsi II-IV, giving the following chaetotaxy :-

	I	II	III	IV
coxa . . .	2	2	2	I
trochanter . . .	$I-\frac{0}{2}-I$	$I-\frac{0}{2}-I$	$I-\frac{1}{2}-0$	$I-\frac{1}{2}-0$
femur . . .	$2-\frac{4}{2}-2$	$I-\frac{4}{2}-I$	$I-\frac{3}{1}-0$	$I-\frac{3}{0}-0$
genu . . .	$I-\frac{2}{1}, \frac{2}{1}-I$	$I-\frac{2}{0}, \frac{2}{0}-I$	$I-\frac{2}{0}, \frac{2}{0}-I$	$I-\frac{2}{0}, \frac{2}{0}-0$
tibia . . .	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$	$I-\frac{1}{1}, \frac{2}{1}-I$
tarsus ⁵ . . .	—	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{0}, \frac{3}{2}-3$

Genus IV in the protonymphs of *Ophionyssus* and *Sauronyssus*, is exceptional in having six setae ($I-\frac{2}{0}, \frac{2}{0}-I$).

The deutonymphal and adult⁶ segmental complements in the free-living forms, for example, *Ololaelaps*, *Pseudoparasitus*, some *Hypoaspis* s. lat. and *Cosmolaelaps* is extremely constant. The segmental chaetotaxy may be summarized as follows :-

	I	II	III	IV
coxa . . .	2	2	2	I
trochanter . . .	$I-\frac{1}{3}-I$	$I-\frac{0}{3}-I$	$I-\frac{1}{3}-0$	$I-\frac{1}{3}-0$
femur . . .	$2-\frac{5}{4}-2$	$2-\frac{5}{3}-I$	$I-\frac{3}{1}-I$	$I-\frac{3}{1}-I$
genu . . .	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{3}{1}, \frac{2}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-I$	$2-\frac{2}{1}, \frac{3}{0}-I$
tibia . . .	$2-\frac{3}{2}, \frac{3}{1}-2$	$2-\frac{2}{1}, \frac{2}{1}-2$	$2-\frac{1}{1}, \frac{1}{1}-I$	$2-\frac{1}{1}, \frac{3}{1}-2$
tarsus ⁵ . . .	—	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$	$3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$

Certain nest-inhabiting forms and facultative and obligatory parasites show considerable diversity in the segmental chaetotaxy of the legs at the deutonymphal and adult stages and these are discussed below. In the semi-diagrammatic representations of the segmental chaetotaxy in Text-fig. 18 the patterns marked (a) are considered to be the normal types for the family.

⁵ The chaetotaxy of tarsus I has not been studied in detail.

⁶ The deutonymphal complement of setae is invariably retained by the adult.

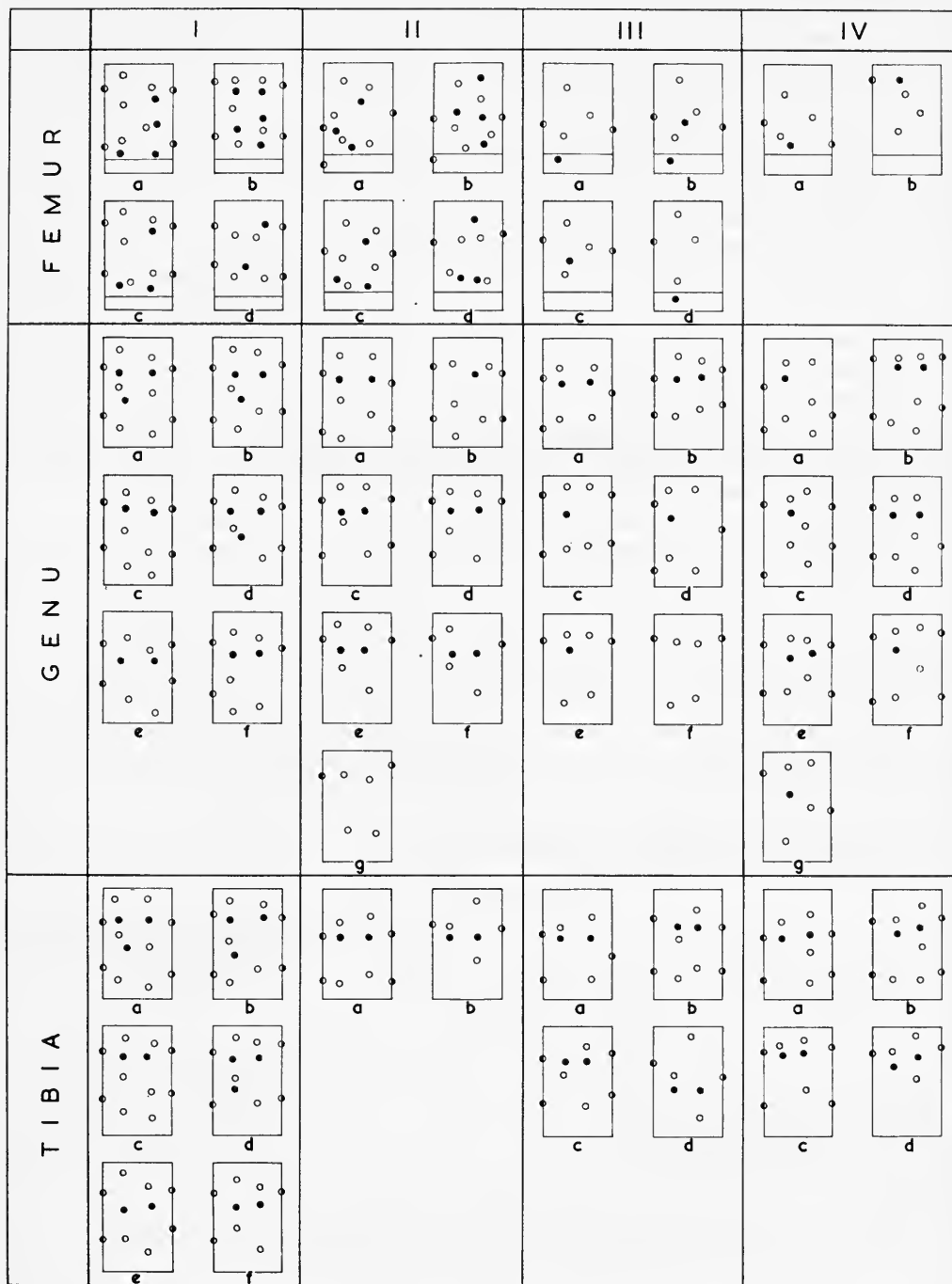


FIG. 18. Semi-diagrammatic representation of the chaetotaxy of selected segments of the legs of the Dermanyssidae.

Coxae I-IV: In the larva coxae I-III each carry two setae and this condition is retained in succeeding developmental stages. Coxa IV bears a single seta in post-larval instars. The coxal setae are normally simple but in many of the facultative parasites (*Laelaps*-group) certain of them, particularly on coxa I, become stout spines or spurs as the result of hypertrophy. Processes of non-setous origin may also occur on certain of the coxae. For example, in many facultative or obligatory parasites a stout, spine-like structure develops on the distal margin of the anterior face of coxa II (Text-figs. 15 A and B) and in *Hirstionyssus* stout spur- or ridge-like processes are present on coxae II and III and sometimes IV. The distal margin of the coxa is produced into a dorsal and a ventral condyle.

Trochanters I-IV: Trochanters I-III at the larval and protonymphal stages and trochanter IV in the protonymph each have four setae. In the deutonymphs and adults trochanter I normally carries six setae and trochanters II-IV five setae. An exception occurs in *Dermanyssus alaudae* (Schrank) which has only five setae ($1-\frac{0}{3}-1$) on trochanter I.

Femora I-IV (Text-fig. 18): Three variants of the normal complement of setae ($2-\frac{3}{1}, \frac{2}{3}-2$) of femur I have been observed. This segment (fig. b) in *Laelaspulus flexuosus* (Michael) shows an addition of one antero-ventral seta to the normal number, giving the formula ($2-\frac{3}{2}, \frac{2}{3}-2$). Many obligatory parasites [*Dermanyssus chelidonis* Oudemans, *D. hirundinis* (Hermann) and *D. quintus* Vitzthum, *Sauronyssus saurarum* (Oudemans) and *Ophionyssus natricis* (Deeger)] show a decrease in the number of ventral setae to three (fig. c) by the suppression of one postero-ventral seta ($2-\frac{3}{1}, \frac{2}{2}-2$). *D. alaudae* is exceptional in retaining the larval complement of setae ($2-\frac{2}{1}, \frac{2}{1}-2$) on this segment throughout ontogeny (fig. d). No setae occur proximal to the circumsegmental fissure.

Exceptions to the normal pattern ($2-\frac{3}{1}, \frac{2}{2}-1$) of femur II have been observed in *Haemogamasus hirsutosimilis* Willmann ($2-\frac{3}{1}, \frac{2}{3}-1$) which has an additional postero-ventral seta (fig. b), in *O. natricis*, *D. quintus* and *S. saurarum* which lack al_2 ($1-\frac{3}{1}, \frac{2}{2}-1$), fig. c, and in *D. alaudae* which differs from the latter group in having only two setae in the antero-dorsal series ($1-\frac{2}{1}, \frac{2}{2}-1$), fig. d. Seta al_2 , when present, is situated proximal to the circumsegmental fissure.

The normal complement of setae on femur III is six ($1-\frac{3}{1}-1$), of which the antero-ventral is situated proximal to the circumsegmental fissure. Although this number of setae also occurs on femur III in *Pellonyssus reedi* (Zumpt and Patterson) the ventral seta is situated distad of the fissure (fig. c). Two other types of chaetotaxy have been observed; in *H. hirsutosimilis* two ventral setae are developed ($1-\frac{3}{2}-1$) fig. b, whilst in *D. alaudae*, *chelidonis* and *hirundinis*, and in *S. saurarum*, the larval complement ($1-\frac{3}{1}-0$) is retained throughout ontogeny (fig. d).

The number of setae on femur IV is remarkably stable and the only exception we have found to the normal pattern ($1-\frac{3}{1}-1$) is in *D. alaudae* which has only five setae ($1-\frac{3}{1}-0$) fig. b.

Genua I-IV (Text-fig. 18): The apparent great diversity in the segmental chaetotaxy of the genera in the Dermanyssidae is somewhat misleading since the majority of the "variants", except on genu IV, occur in a single genus, *Dermanyssus*.

Exceptions to the normal chaetotaxy ($2-\frac{3}{2}, \frac{3}{1}-2$) of genu I are found, with the exception of *Pseudolaelaps doderoi* Berlese, only amongst the obligatory parasites. In *S. saurarum*, *O. natricis* and *D. chelidonis*, the setation is deficient in one postero-dorsal member ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. *b*) whilst in *P. doderoi* and in some populations of *O. sylviarum* an antero-ventral seta is lacking ($2-\frac{3}{1}, \frac{3}{1}-2$, fig. *c*). The remaining three types of chaetotaxy have been observed in *D. hirundinis* ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. *d*), *D. alaudae* ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *e*) and *D. quintus* ($2-\frac{3}{1}, \frac{2}{1}-1$, fig. *f*).

The normal pattern ($2-\frac{3}{1}, \frac{2}{1}-2$) of genu II occurs in all the British dermanyssids except *P. doderoi* and some species of *Dermanyssus*. In *P. doderoi* the antero-ventral seta is lacking ($2-\frac{3}{0}, \frac{2}{1}-2$) fig. *b*) whilst in *D. chelidonis* the antero-dorsal series is unideficient ($2-\frac{2}{1}, \frac{2}{1}-2$) fig. *c*). Further specializations are seen in *D. quintus* ($2-\frac{2}{1}, \frac{2}{1}-1$, fig. *d*) and in *D. alaudae* which retains the larval complement of setae ($1-\frac{2}{0}, \frac{2}{0}-1$, fig. *g*) throughout ontogeny. The chaetotaxy of this segment shows considerable intraspecific variation in *D. hirundinis* ($2-\frac{2}{1}, \frac{2}{1}-1, 1-\frac{2}{1}, \frac{2}{1}-1$, fig. *e* and $1-\frac{2}{1}, \frac{1}{1}-1$, fig. *f*).

Five different chaetotactic patterns have been observed on genu III, excluding the normal ($2-\frac{2}{1}, \frac{2}{1}-1$). Thus, members of the genera *Ophionyssus* and *Pellonyssus* and *Ornithonyssus bacoti* (Hirst) and *S. saurarum* have ten setae ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *b*) on this segment; *D. chelidonis* and *O. sylviarum* have nine setae, but differ from the normal form in lacking pv_1 and having two postero-laterals ($2-\frac{2}{1}, \frac{2}{0}-2$, fig. *c*); *Hyperlaelaps amphibia* Zachvatkin and *H. microti* (Ewing), and *P. doderoi* bear 8 setae ($2-\frac{2}{1}, \frac{2}{0}-1$, fig. *d*), *D. hirundinis* has seven setae ($1-\frac{2}{1}, \frac{2}{0}-1$, fig. *e*) and finally, *D. alaudae* retains the larval complement ($1-\frac{2}{0}, \frac{2}{0}-1$, fig. *f*).

Genu IV shows the greatest diversity in chaetotaxy of all leg segments in the British Dermanyssidae. In addition to the normal pattern ($2-\frac{2}{1}, \frac{3}{0}-1$), six other types of chaetotaxy have been observed, namely:—

fig. *b*, ($2-\frac{2}{1}, \frac{3}{1}-2$) in *Pellonyssus*, *Laelaps agilis* Koch, *O. bacoti* and *O. natricis*.

fig. *c*, ($2-\frac{2}{1}, \frac{3}{0}-2$) in *Laelaps echidnina*, *hilaris*, *muris*; *Hyperlaelaps amphibia* and *microti*; *Eulaelaps stabularis* and *nova*; *Androlaelaps casalis* and *fahrenheiti*; *Hypoaspis* (*G.*) *sardoa*; *Ondatraelaps multispinosa* and *Laelaspulus flexuosus*.

fig. *d*, ($2-\frac{2}{1}, \frac{3}{1}-1$) *Pneumolaelaps*, *Hypoaspis* (*G.*) *lubrica*; *Melittiphis alvearius*; *Macronyssus*; *Steatonyssus periblepharus* and *Ornithonyssus sylviarum*.

fig. *e*, ($2-\frac{2}{1}, \frac{2}{1}-2$) in *Sauronyssus saurarum*

fig. *f*, ($2-\frac{2}{1}, \frac{2}{0}-2$) in *Dermanyssus chelidonis*

fig. *g*, ($1-\frac{2}{1}, \frac{2}{0}-1$) in *Dermanyssus alaudae*, *hirundinis* and *quintus*.

Tibiae I-IV (fig. 18): With the exception of *P. doderoi*, deviations from the normal setal pattern of tibia I ($2-\frac{3}{2}, \frac{3}{1}-2$) have been noted only in the obligatory parasites. Three of the "variants" occur in the genus *Dermanyssus*, namely, ($2-\frac{2}{2}, \frac{2}{1}-2$, fig. *d*) in *D. chelidonis* and *hirundinis*; ($2-\frac{2}{1}, \frac{2}{1}-2$, fig. *e*) in *D. alaudae* and ($2-\frac{2}{1}, \frac{2}{1}-1$) fig.

f) in *D. quintus*. The remaining two types ($2-\frac{3}{2}, \frac{2}{1}-2$, fig. b) and ($2-\frac{3}{1}, \frac{3}{1}-2$, fig. c) have been found in *Pellonyssus*, *Sauronyssus saurarum* and *Ophionyssus natricis*, and in *P. doderoi* and some forms of *O. sylviarum*, respectively.

The only exceptions to the normal segmental chaetotaxy of tibia II ($2-\frac{2}{1}, \frac{2}{1}-2$) occur in *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus* which retain the larval complement of setae throughout ontogeny ($1-\frac{1}{1}, \frac{2}{1}-1$, fig. b).

In addition to the normal form ($2-\frac{1}{1}, \frac{2}{1}-1$), the following three types of chaetotaxy are found on tibia III :

fig. b, ($2-\frac{2}{1}, \frac{2}{1}-2$) in the ethiopian species *Steatonyssus tibialis* Till and Evans.

fig. c, ($2-\frac{1}{1}, \frac{2}{1}-2$) in *Pellonyssus*, *Steatonyssus* (except *tibialis*), *Ornithonyssus bacoti* and *sylviarum*; *S. saurarum*, *O. natricis*, *Melittiphis alvearius*, *Hypoaspis* (G.) *sardoa* and *Laelaspulus flexuosus*.

fig. d, ($1-\frac{1}{1}, \frac{2}{1}-1$) in *Hyperlaelaps amphibia* and *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus*. This is the larval pattern.

Only in the obligatory parasites have we observed variants of the normal chaetotaxy of tibia IV ($2-\frac{1}{1}, \frac{3}{1}-2$). *S. tibialis* has eleven setae on this segment ($2-\frac{2}{1}, \frac{3}{1}-2$, fig. b), *S. saurarum* nine setae ($2-\frac{1}{1}, \frac{2}{1}-2$, fig. c) and *Dermanyssus alaudae*, *chelidonis*, *hirundinis* and *quintus* have the protonymphal complement of seven setae ($1-\frac{1}{1}, \frac{2}{1}-1$, fig. d).

Tarsi I-IV : The chaetotaxy and the form of the distal sensory region of tarsus I have not been studied in detail in the present work. The ontogenetic development of the chaetotaxy of tarsi II-IV is extremely constant, the basic adult complement of eighteen setae ($3-\frac{3}{2}, \frac{1}{1}, \frac{3}{2}-3$) being present in the majority of the species. In the obligatory parasites there is a tendency for the reduction in the size of setae ad_1 and pd_1 which may be represented by microsetae or be lacking.

Ambulacra (Text-figs. 19A-D) : Little attention has been paid previously to the structure of the pretarsus and the ambulacrum in the Mesostigmata. The following account of the structure and mode of functioning of the ambulacral apparatus is based on that of *Haemogamasus hirsutus* Berlese.

The striated, sclerotized components of the pretarsus form a more or less rigid sheath. In the distal half of the pretarsus the sclerotized elements of the floor are thickened medially to form two slender, internal, longitudinal struts, the median *pretarsal apodemes* (*ptr. apod.*). Anterior to the apodemes lies a well-defined, dorsally directed U-shaped *basilar sclerite* (*bas. scl.*). It is pivoted by its base to the anterior processes of the pretarsal apodemes. A tendon (basilar tendon, Text-fig. 19D) is attached to the basal region of the basilar sclerite but its origin is difficult to trace in whole mounts of the tarsus and pretarsus. It appears to run ventrally through the tarsus and to be connected to a muscle originating in the tibia. A second unpaired sclerotized structure, the *pulvitractor sclerite* (*pulv. scl.*) is situated medially within the pulvillar mass immediately anterior and

dorsal to the basilar sclerite. In *H. hirsutus* it forms a dorsally directed hook-like process with a bifid base. Its basal limbs are movably articulated with the dorsally directed arms of the basilar sclerite. The paired lateral claws, each with a deep proximo-internal acetabulum, appear also to be articulated with the limbs of the pulvitractor and/or basilar sclerite. Lying dorsal to the apodemes and sclerites is a strong median tendon (*pulvitractor tendon*) connected distally with the pulvillus and by way of the pulvillus to the dorsal hook of the pulvitractor sclerite. It runs the entire length of the pretarsus and is connected to a strong retractor muscle originating within the basi-tarsus. Near the junction of the pretarsus and tarsus the tendon passes between the limbs of a dorsally directed Y-shaped apodeme (*pulvitractor guide*). The lateral elements of the pretarsal sheath are produced distally into denticulate lobes which Krantz (1962) has referred to in the Macrochelidae as the "laterodistal pretarsal elements". In view of their apparent function we propose renaming these lobes the *pretarsal opercula* (*ptr. op.*). The true form of the pulvillus

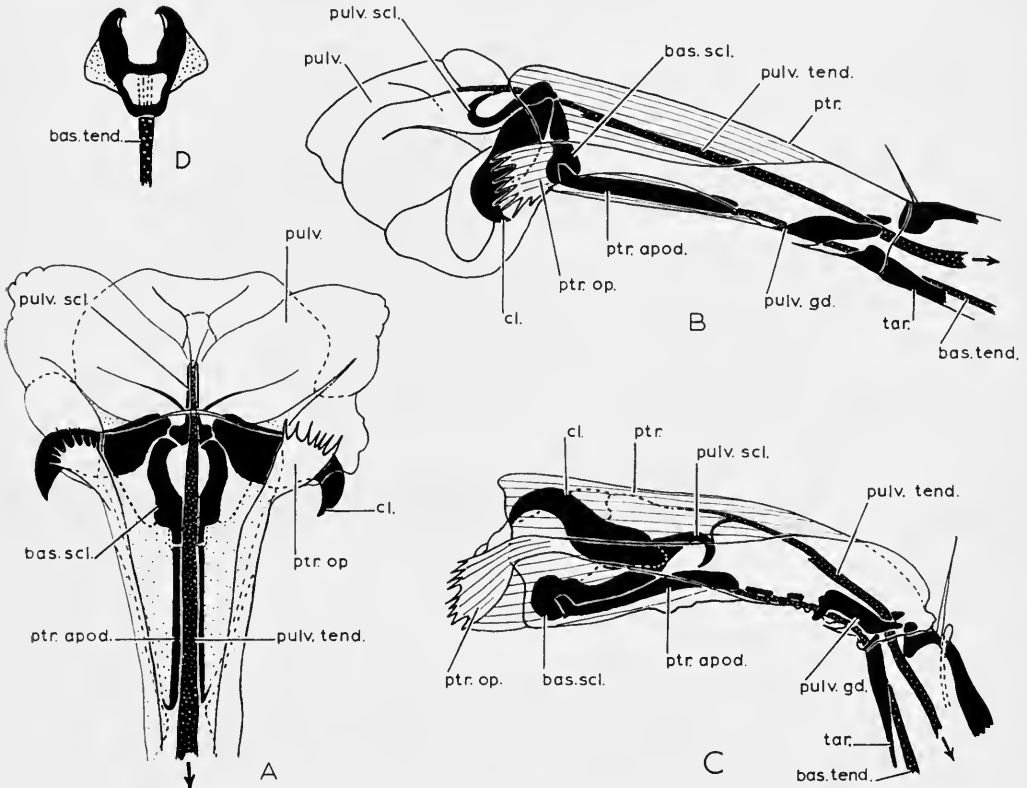


FIG. 19. Ambulacrum and pretarsus of *Haemogamasus hirsutus* Berlese. A. Dorsal view from a compressed preparation; B. partially retracted ambulacrum in lateral view; C. fully retracted ambulacrum in lateral view; D. Basilar sclerite with tendon.

is difficult to ascertain since it is invariably distorted during preparation for study. From compressed mounts it appears to comprise ventral, dorsal and lateral elements. It is provided with weakly sclerotized "veins" (Text-fig. 19A).

The function of the tarsal muscle and its tendon is to withdraw the ambulacrum into the pretarsal sheath and this is made possible by the nature of the articulations between the apodemes of the pretarsus and the basilar sclerite, and between the limbs of the basilar sclerite and the pulvitractor sclerite. As the muscle contracts the backwardly directed pull of the pulvitractor tendon on the pulvillus and on the pulvitractor sclerite causes the pulvillus and the claw-complex (basilar and pulvitractor sclerites and claws) to be retracted into the pretarsal sheath (Text-fig. 19B). At maximum retraction the basilar sclerite and the pulvitractor sclerite lie over the rigid median pretarsal apodemes with the hook of the pulvitractor sclerite directed ventrally and the claws directed anteriorly (Text-fig. 19C). Also at this stage the anterior margins of the pretarsal opercula meet and together form a protective "lid" to the pretarsal sheath.

The mode of extension of the ambulacral apparatus will remain somewhat problematical until the definite origin of the tendon of the basilar sclerite has been elucidated. If, as it appears, it is the tendon of a tibial protractor muscle, then contraction of this muscle would have the effect of pushing forward the basilar sclerite on its pivot when tension through the pulvitractor tendon is released. Thus, the ambulacrum would be operated by a pair of antagonistic muscles, the *pulvillar retractor* and the *basilar protractor*.

The ambulacral apparatus has this basic form throughout the Dermanyssidae although there is considerable diversity in the shape of the sclerotized structures, particularly the basilar and pulvitractor sclerites and the pretarsal opercula, and in the degree of the development of the claws. Normally in the dermanyssines paired claws are present on all legs and those of legs II-IV are usually stronger and larger than those of leg I which is chiefly sensory and not ambulatory in function. Claws are absent or strongly reduced on leg I of *Stratiolaelaps miles* Berlese and *Eulaelaps nova* Vitzthum and on legs I-IV of *Ondatratalaelaps multispinosa* (Banks) and *Laelaps muris* Koch.

Form of the leg setae: The leg setae are generally simple or pilose in form but throughout the family there is a tendency for certain setae, particularly the ventral setae of the femora, genua and tibiae of leg II and the distal setae of tarsi II-IV to enlarge and form stout spine- or spur-like structures (Text-fig. 20C). Hypertrophy of setae on leg II is not restricted to the male as is usual in the Gamasina. Seta av_1 on femur II in both sexes of certain *Androlaelaps* may be affected and, to a lesser extent, seta av_1 on the genu and tibia of this leg. In *Hypoaspis* (*Gaeolaelaps*) *nidicorva*, on the other hand, seta av_2 of femur II hypertrophies (Text-fig. 20A). On the tarsi, setae al_1 , pl_1 , av_1 and pv_1 usually show some enlargement in comparison with other tarsal setae and in *Eulaelaps nova* setae ad_2 , pv_2 and mv on tarsus II are also spur-like (Text-fig. 20B). Some members of *Hirstionyssus* have the tarsal setae av_1 and pv_1 developed into stout hook-like structures.

Certain coxal setae are often enlarged in the *Laelaps*-group and in many of the facultative parasites seta ad_1 and to a lesser extent, seta pd_1 on femur I and II are considerably stronger and longer than other femoral setae. The relative increase in

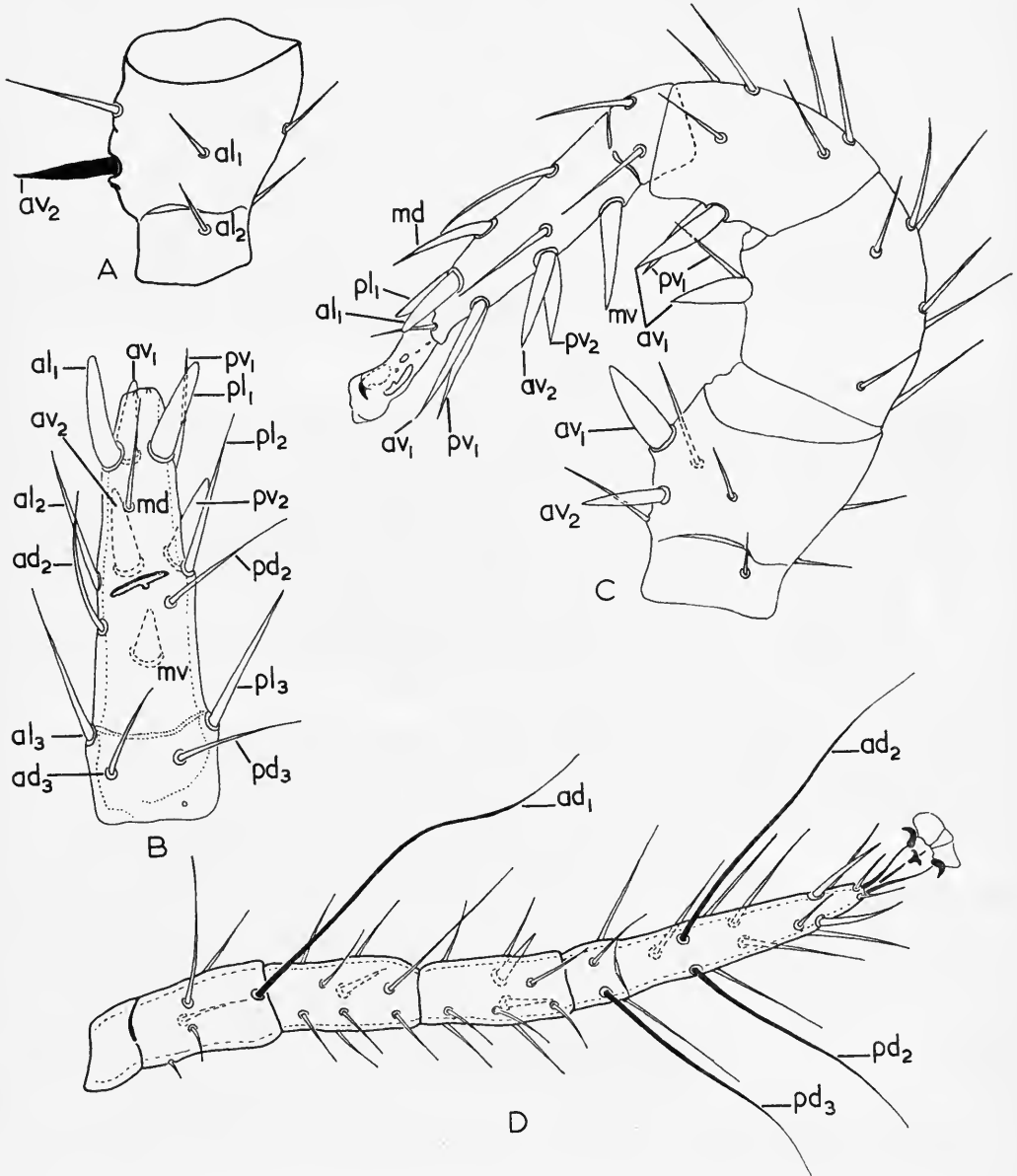


FIG. 20. A. Femur II, anterior view, of *Hypoaspis* (*Gaeolaelaps*) *nidicorva* sp. nov. female; B. dorsal view of tarsus II of *Eulaelaps nova* Vitzthum, female; C. anterior view of leg II (femur to tarsus) of *Hypoaspis* (*H.*) *krameri* (Canestrini) male; D. dorsal view of leg IV (femur to tarsus) of *Hypoaspis* (*H.*) *krameri* (Canestrini).

length of specific leg setae is also apparent in *Hypoaspis* (*H.*) *krameri*, for example, on leg IV seta ad_1 on the femur and setae ad_2 , pd_2 and pd_3 on the tarsus are long and whip-like (Text-fig. 20D).

Cuticular processes of non-setous origin: Reference has already been made to the occurrence of setiform or spiniform cuticular processes on the chelicerae at the junction of the second segment and the arthroidal membrane at the base of the movable digit. Such processes are by no means restricted to the trophic appendages but commonly occur at the distal margins of certain pedipalpal and leg segments. Generally, they are better developed on the basal segments of the appendages, particularly the coxae. The processes show considerable diversity in form and number. In their least specialized form (Text-fig. 21A), they appear as a more-or-less

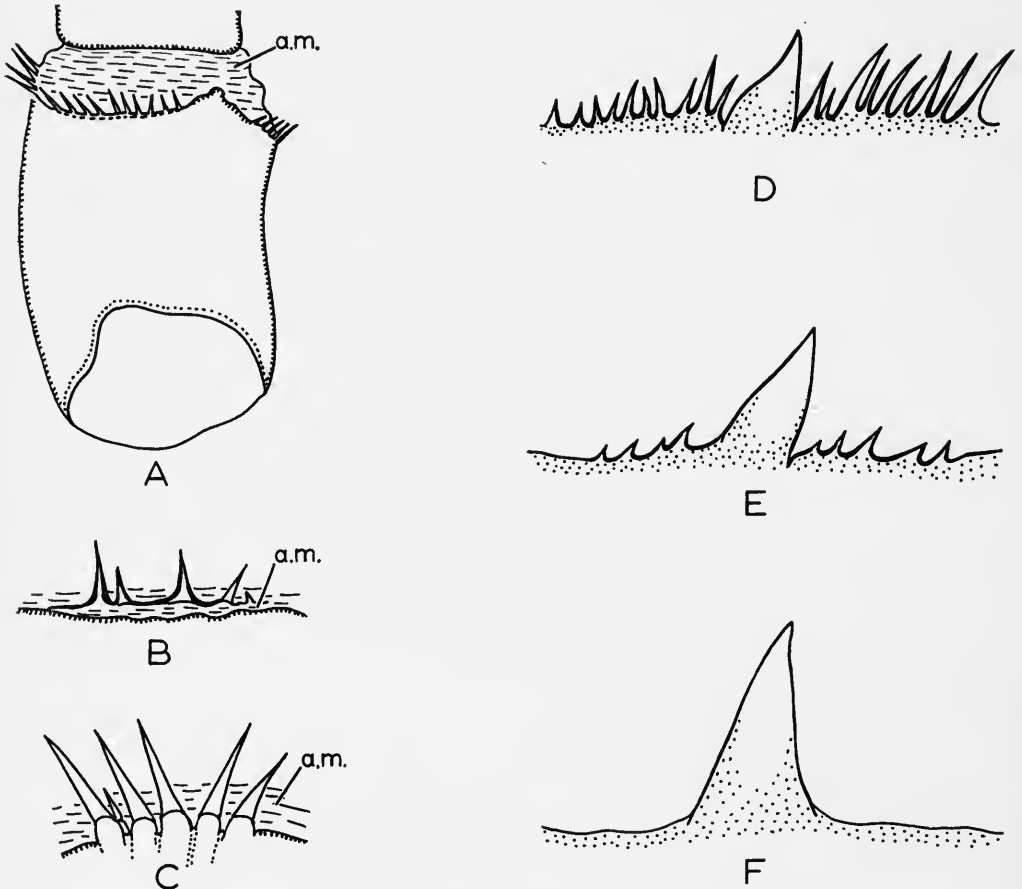


FIG. 21. A. Coxa I of *Haemogamasus hirsutus* Berlese, dorsal view, showing processes on distal margin of segment; B. processes free from distal margin of segment; C. processes fused with distal margin of segment; D-F. processes on distal margin of anterior (paraxial) face of coxa II in D. *Haemogamasus hirsutus* Berlese; E. *Laelaps agilis* Koch; F. *Macronyssus flavus* (Kolenati).

complete circumsegmental fringe of spines on the distal margin of the segment. The spines appear to have their origin on the arthrodistal membrane in close proximity to the distal margin of the segment (Text-fig. 21B), but by the sclerotization of the narrow strip of membrane between the segment and the processes, they become incorporated with the segment (Text-fig. 21C). Reduction in the number of processes is common to the extent that only one, two or three spines of the circumsegmental fringe remain and these are usually located on the anterior face of the limb. The remaining process (or processes) is better developed than the individual members of a circumsegmental fringe. It is possible to trace the regression in the number of marginal processes on the anterior face of coxa II in the Dermanyssidae. In free-living species, for example members of the genera *Ololaelaps* and *Pseudoparasitus*, the fringe is composed of spine-like processes of approximately equal size, but in certain of the facultative parasites a medial process of the fringe hypertrophies as in *Haemogamasus hirsutus* (Text-fig. 21D). A similar hypertrophy of a medial process occurs in *Laelaps agilis* but this is also accompanied by a reduction in the number and size of the remaining processes (Text-fig. 21E). Finally, in certain obligatory parasites (*Macronyssus* and *Steatonyssus*) only the hypertrophied medial process remains and this forms the stout anterior coxal spine (Text-figs. 15A and B, 21F).

Van der Hammen (1964) has referred to the cuticular processes on the distal margin of the external face of the *basis capituli* and on the antero-distal margin of coxa I as the latero-coxal setae and has unhesitatingly homologized them with the latero-coxal spines *e* and *e1* in the Actinochaeta. These are not setae and each represents a cuticular process originating from the junction of the segment and the arthrodistal membrane as described above. In many forms of Mesostigmata a fringe of spines occurs on the distal margins of the lateral face of the *basis capituli* to which the pedipalp trochanter is articulated and throughout the group there is a tendency for a reduction in the number of spines. To designate such a single process, which is rarely present in the group, a latero-coxal seta, seems unwarranted. There is no available evidence upon which to base the homology of the cuticular processes in the Mesostigmata with the latero-coxal spines of the Actinochaeta and we deprecate the application of the symbols *e* and *e1* to any of the cuticular processes associated with the pedipalpal "coxae" or the coxae of leg I, respectively.

Rows of spine-like cuticular processes also occur on the unsclerotized pre-sternal cuticle and regionally on the leg segments and *basis capituli* of many facultative parasites such as *Haemogamasus*. Spur-like structures, not hypertrophied setae, are present on certain of the coxae of *Hirstionyssus*. The functions of these various cuticular processes are not known.

Lyriform fissures: Fissures occur on the femora and tarsi of legs I-IV. Two lyriform fissures in the basal third of each femur are connected and form a complete or interrupted circumsegmental fissure which secondarily divides the segment into proximal and distal sections (Text-figs. 20A and C). The fissures on the basal third of the tarsi similarly divide these segments into two regions, but the circumsegmental fissure on tarsus I is usually less well developed than on the other tarsi. For example, in many obligatory parasites the fissure is interrupted dorsally and the isolated

proximodorsal fissure assumes the characteristic form of a lyriform fissure. A dorsal lyriform fissure, distinct from those forming the circumsegmental fissures, is also present on tarsi II-IV (Text-fig. 20B).

DISCUSSION

Members of the family Dermanyssidae show considerable diversity in morphology and biology largely as the result of the specializations exhibited by the parasitic forms which have become adapted to life in the great variety of niches afforded by their hosts. Within the family the free-living species, on the one hand, and the obligatory parasites, on the other, appear to form the extremes of a morphological continuum, the connecting link between them being provided by the morphological characteristics of nest inhabitants and facultative parasites. Species of these extreme groups have different morphological properties: the free-living forms show little diversity in morphology in comparison with the obligatory parasites which display marked morphological plasticity. This morphological plasticity is evident in the grades of specialization found amongst congeners, for example the degree of specialization of the gnathosoma in *Haemogamasus*, and in the higher incidence of intraspecific variability in morphological "characters".

The most spectacular morphological adaptations are associated with changes in feeding habits, and may be seen in the specialization of the trophic appendages and associated gnathosomal structures and in the reduction of idiosomal sclerotization in the monophagous obligatory parasites. Taxonomic characters based on these adaptive morphological structures have long played a dominant role in the suprageneric classification of the family. Less spectacular, but nevertheless of considerable taxonomic importance, are the differences in chaetotaxy between the free-living and parasitic forms. Deviations from the normal adult chaetotaxy, particularly of the segments of the pedipalps and legs, are due to a retardation in the normal ontogenetic development of the chaetotaxy. The retention of the larval complement of setae on a segment throughout ontogeny (localized neoteny) is not uncommon, although in most cases deficiency in adult chaetotaxy is due to the subnormal number of setae added to the protonymphal complement at the deutonymphal stage. Retardation in normal ontogenetic development also affects the dorsal idiosomal sclerotization in the obligatory parasites which tend to retain, to a greater or lesser degree, the form of the protonymphal scutal elements in succeeding developmental stages. In addition to the structural adaptations, many of the facultative and obligatory parasites show some degree of specialization of the life cycle. There is a general tendency for ovoviviparity and, more rarely, viviparity to occur and in the Macronyssinae the normally active, feeding, deutonymphal stage of the family is replaced by an inactive, non-feeding instar which shows considerable degeneration of the feeding and sensory organs.

The morphological and biological diversity displayed by the Dermanyssidae provides the taxonomist with numerous readily definable characters which are pre-eminently suitable for the practical differentiation of the taxa, that is, for a classification emphasizing differences between species. This is essentially the basis of the present classification of the family where the exaggerated importance given to one or

two morphological characters has resulted in a plethora of supraspecific taxa. Such a classification, which can be readily expressed in key form, serves a very useful purpose as a tool for identification. A more natural classification of the family requires emphasis to be made on resemblances rather than differences between its members, but in the elaboration of such a classification the considerable diversity in the morphology of facultative and obligatory parasites, resulting from variations in the degree of specialization of various parts of the body, not only between groups of species but also amongst closely related (congeneric) species, will inevitably add to the difficulty of defining distinct supraspecific categories.

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ABBREVIATIONS USED IN TEXT-FIGURES

a.m.	arthrodial membrane	bas. scl.	basilar sclerite
ac.	aciculae	bas. tend.	basilar tendon
acet.	acetabulum		
ad ₁₋₃	antero-dorsal setae		
al ₁₋₂	antero-lateral setae	c. gr.	capitular groove
an. sh.	anal shield	c. s.	capitular seta
ant. sp.	anterior spine	ch.	chelicera
ar. pr.	arthrodial processes	cl.	claw
av ₁₋₃	antero-ventral setae	corn.	corniculi

d ₁₋₃	dorsal setae	ptr.	pretarsus
d.d.	deutosternal denticles	ptr. apod.	pretarsal apodeme
d.l.f.	dorsal lyriform fissure	ptr. op.	pretarsal operculum
d.s.	dorsal seta of chelicera	pulv.	pulvillus
end. sh.	endo podal shield	pulv. gd.	pulvitractor guide
exp. sh.	expodal shield	pulv. scl.	pulvitractor sclerite
f.d.	fixed digit	pulv. tend.	pulvitractor tendon
fem.	femur	PV ₁₋₂	postero-ventral setae
g.b.	gnathosomal base	PX ₂₋₃	posterior accessory setae
g-v. sh.	genito-ventral shield	pyg. sh.	pygidial shield
g-v-a. sh.	genito-ventro-anal shield	r2-6	marginal series of podonotal setae
gen.	genital seta	R1-7	marginal series of opisthonotal setae
gen. orf.	genital orifice	s1-6	lateral series of podonotal setae
gen. sh.	genital shield	S1-5	lateral series of opisthonotal setae
hol. sh.	holoventral shield	s.s.	salivary stylus
hyp. 1-3	hypostomal setae	sg.	stigma
int. mal.	internal malae	sp.	spermadactyl
j1-6	dorsal series of podonotal setae	st. 1-3	sternal setae
J1-5	dorsal series of opisthonotal setae	st. 4	metasternal seta
Jv1-5	internal ventral setae	st-g. sh.	sternito-genital shield
l. f.	lyriform fissure	st-g-v. sh.	sternito-genito-ventral shield
lat. in.	lateral incision	st. met. sh.	sterno-metasternal shield
lat. l. f.	lateral lyriform fissure	st. sh.	sternal shield
lb.	labrum	tar.	tarsus
m. d.	movable digit	tect.	tectum capituli
md.	medio-dorsal seta	ten. dep.	depressor tendon
mes. sc.	mesonotal scutellae	ten. lev.	levator tendon
met. sh.	metasternal shield	troch.	trochanter
mp. sh.	metapodal shield	trt.	tritosternum
p. 1-3	pores	UR	submarginal series of opisthonotal setae
p.d.	pilus dentilis	v1-2	ventral setae
pan.	paranal seta	v-a. sh.	ventro-anal shield
pd1-3	postero-dorsal setae	x	supernumerary seta
pd.	podal shield	z1-6	median series of podonotal setae
per.	peritreme	Z1-5	median series of opisthonotal setae
per. sh.	peritrematal shield	Zv1-2	medio-lateral ventral setae
pl1-2	postero-lateral setae		
pod. sh.	podonotal shield		
pon.	postanal seta		
pr.	process on palp trochanter		



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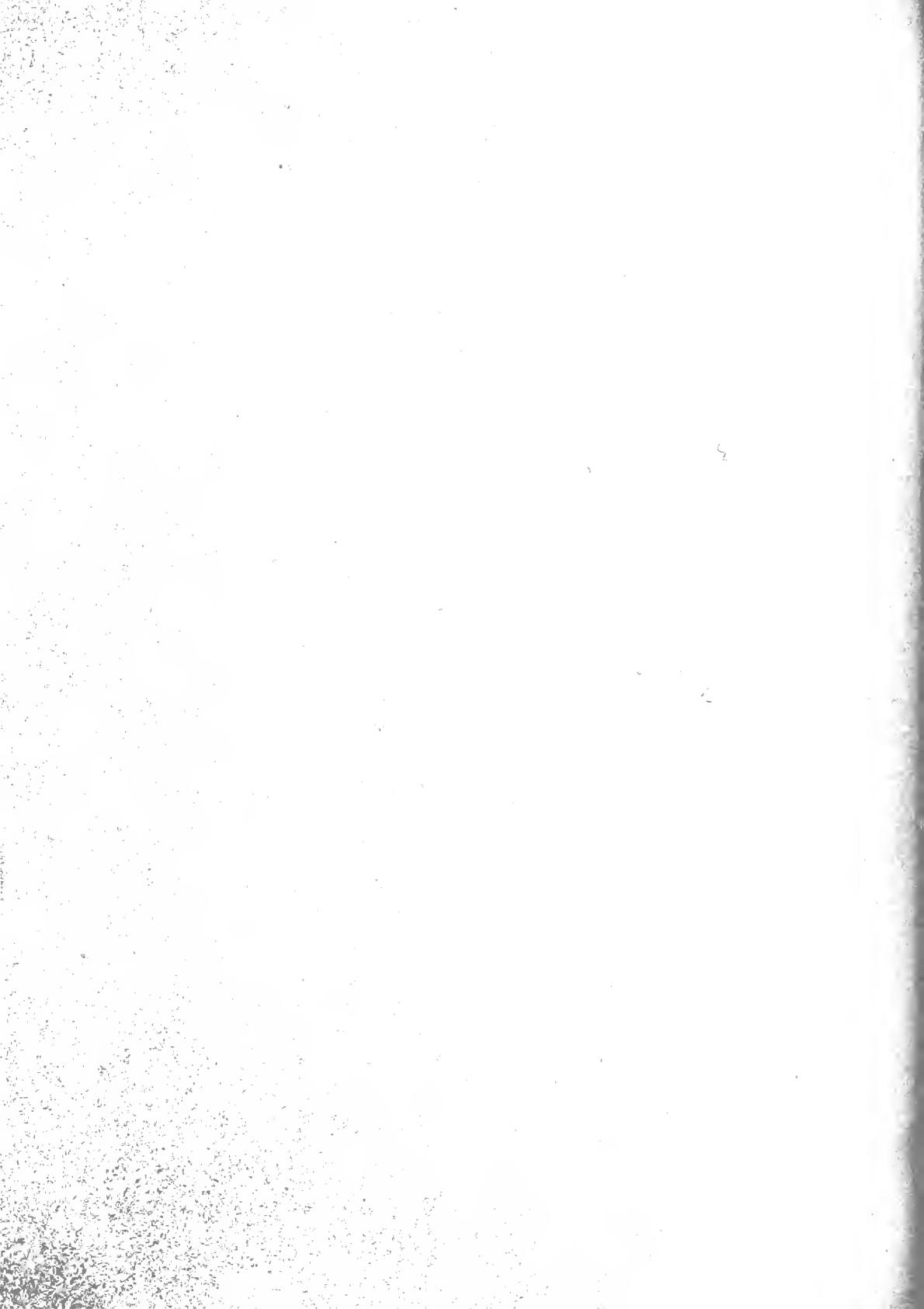


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A REVIEW OF THE MURIDAE
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By M. J. DELANY & B. R. NEAL

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INTRODUCTION

ALTHOUGH Uganda has an exceptionally rich mammal fauna, there has up to the present time been very little work published on the systematics and biology of these animals. Apparently, the only check list of Uganda mammals was that given by Oldfield Thomas in 1902 and published in Sir Harry Johnston's *The Uganda Protectorate*. The present work restricts itself to a review of the existing information on the murid rodents of Uganda. Thomas gave sixteen species occurring in the same general area (Uganda's boundaries have been changed since 1902) whereas the present list numbers forty-four. Even so, it is uncertain that this list is complete particularly in view of the fact that as recently as 1961 a new genus (*Delanymys*) was discovered in the south-west of the country and in 1963 a previously unrecorded genus (*Zelotomys*) was collected in Ankole. The main sources of information have been the collections in the British Museum (Natural History), the Coryndon Museum, Nairobi, published and unpublished literature and the collections made by Delany in 1961 and 1963. Of the unpublished, Hopkins manuscript entitled *The Known Wild Rodents of Uganda* has been particularly useful.

Descriptions of genera and species are given with keys to their identification. As we found it possible to identify almost every species without reference to cranial morphology or internal anatomy it has been decided to base the descriptions entirely on external characters. Such features as grooving of the incisors are included as their examination does not necessitate dissecting the animal in any way. Only in the identification of the species of *Otomys* has it been necessary to refer to other than external characters. All the measurements given in the text have been obtained from animals collected in Uganda. Animals that from their external measurements are obviously very young have been omitted.

The systematics include the reference to the original description of the genus and the name of the type species. The reference to the original description of each species is given together with the type locality. If the latter is outside Uganda the location follows the place name ; if it is in Uganda then the location appears in the

gazetteer. Synonyms based on material collected in Uganda are also included. We have not attempted any revisions of the systematics although in several cases they are clearly required. Subgeneric names have been avoided. Whether forms such as *Grammomys*, *Praomys*, *Myomys*, *Mastomys* or *Hylomyscus* are genera or subgenera seems a matter of constant debate. We have given them generic status in accordance with fairly general usage, but we fully appreciate that future and more extensive studies may show them to be of lower taxonomic rank. Furthermore, the paucity of information on the variation shown by individual species has prompted us to omit any reference to subspecies. Only very much more collecting from the whole country can reveal the nature of the subspecies, clines and variability that may be present.

In the following account we have used Simpson's (1945) definition of the Muridae. His classification of the Myomorph rodents recognizes three superfamilies. They are, the Muroidea which includes the rats, mice, voles, gerbils and lemmings; the Gliroidea containing the dormice, and the Dipodoidea containing the jumping "mice" and the jerboas. None of the third group occur in Uganda whilst the Gliroidea are represented by the genus *Graphiurus* Smuts. The dormice are easily recognized by their small size and very bushy tail; although normally grey in colour, brown and buff forms also occur.

The Muroidea are split into four families; the Muridae which are being considered in the present account, the Spalacidae or mole rats of the Mediterranean region, the Rhizomyidae which has only one species recorded from Uganda (*Tachyoryctes ibeanus* Thomas) and the Cricetidae in which group are included the gerbils. *Tachyoryctes*, one of the African mole rats, is easily recognized and not readily confused with the murids. It is highly adapted for burrowing. The limbs are very short and the front legs broad and slightly flattened for digging; external ears are almost completely absent and the eyes are very small. The fur is long, soft and dense and usually brown to black in colour. The tail is very short.

The gerbils are the forms most likely to be confused with the murids and can only be separated from them by a combination of several characters. The hind limbs are long in proportion to the fore limbs (not so obvious in *Tatera*), the feet have long claws, the fur is soft and dorsally sandy or buff in colour. The belly fur and the backs of the hands and feet are pure white and a patch of short white hairs occurs behind the ear. The tail is long and hairy and often tufted. The upper incisors are grooved but on occasion the grooving is so shallow as to make it hardly perceptible. Two genera (*Tatera* and *Taterillus*) have been recorded from Uganda.

Petter (1964) has recently suggested that the genera *Cricetomys* and *Saccostomus* should be placed in the Cricetidae.

In the sections on distribution the locality from which animals have been obtained is given with the District except in Buganda where the reference is to the Kingdom. The latitude and longitude of each locality appears in the gazetteer. In addition the distributions have been mapped; the location of Buganda and the Districts outside this Kingdom are shown in Text-fig. 1. The distribution records are undoubtedly inadequate as almost every species probably has a wider and more continuous distribution than is suggested from the maps. This can only be remedied by

considerably more collecting. Some distribution records are very vague and may refer to no more than a District; in which case the District is given in quotation marks. Various parts of Uganda appear to have been more rigorously collected than others with particularly large gaps occurring in Acholi, Busoga, east Toro and Ankole and in the north along the length of the Sudan border.

There is not a great deal of information available on the biology and breeding. Some data have been included from outside Uganda. However, there seemed little reason for including times of breeding of animals outside the country as this pheno-

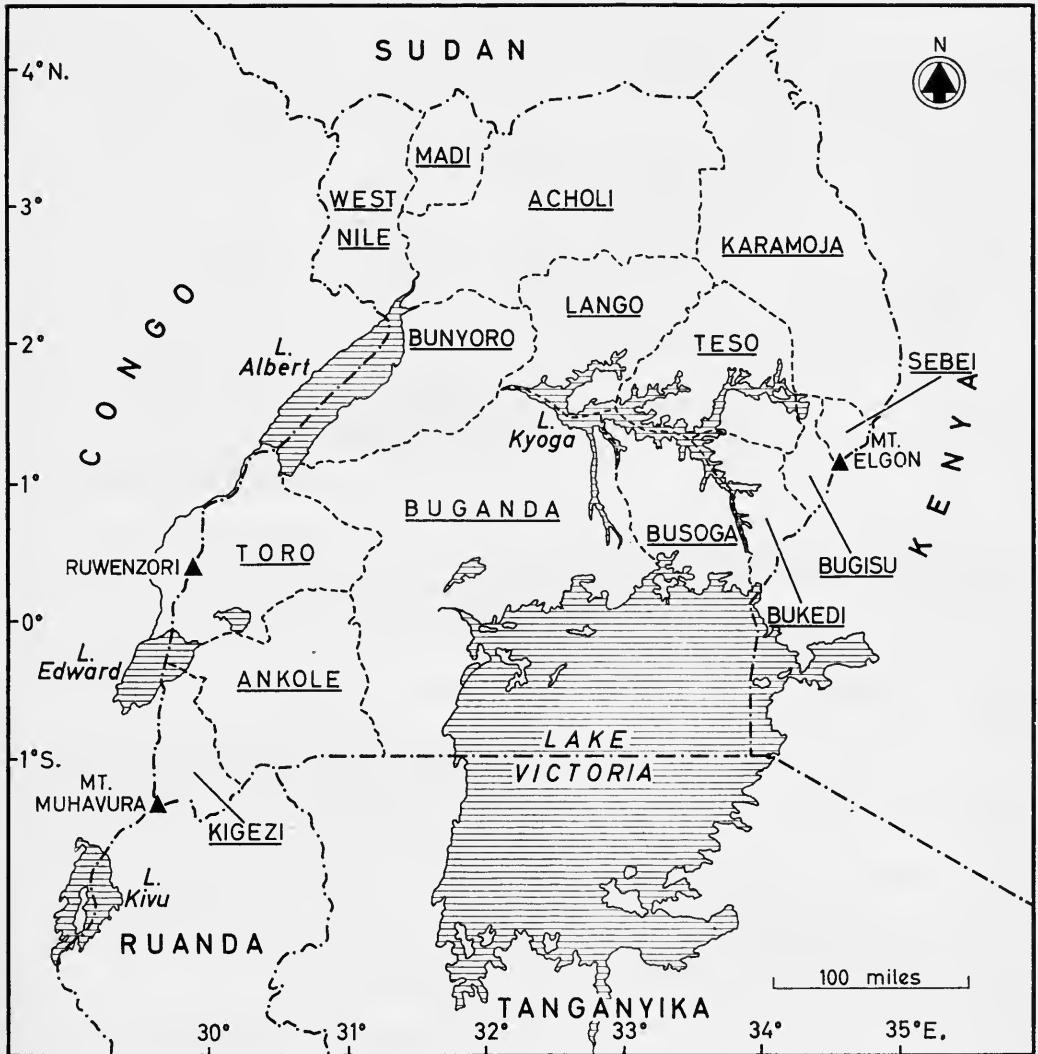


FIG. 1. Map of Uganda showing the location of the Kingdom of Buganda and the Districts outside the Kingdom (underlined).

menon is probably influenced by local climatic conditions. As these vary considerably from one part of Africa to another (as well as in Uganda itself) the inclusion of times of breeding from elsewhere could give an erroneous picture of when breeding took place in Uganda.

We are particularly indebted for the very considerable help Mr. R. W. Hayman of the British Museum (Natural History) has given us with this work. We are grateful to the Royal Geographical Society for assistance in tracing some of the localities. The collecting trips made by M. J. D. in 1961 and 1963 were financed by grants from the Royal Society, the Percy Sladen Memorial Fund and the University of Southampton.

ABBREVIATIONS

The following abbreviations have been used in the text :—

cm.	centimetres	Mt.	Mount
Co.	County	N.	North
E.	East	Q.E.P.	Queen Elizabeth National Park
g.	grams	S.	South
h. & b.	head-and-body length	strm.	stream
h. f.	hind foot length	W.	West
meas.	measured	wt.	weight
M.N.P.	Murchison Falls National Park	♂	male
m.	metre(s)	♀	female
mm.	millimetres		

Months have been abbreviated to their first three letters.

The number of records of the number of foetuses have been indicated in brackets; thus (2 × 1) signifies that two animals each had one foetus.

KEY TO THE GENERA OF UGANDA MURIDS

- 1 Large size (h. & b. 300–450 mm.). Long tail, distal portion white, proximal portion dark **CRICETOMYS** (p. 338)
Smaller with tail not showing this pattern of coloration 2
- 2 Dorsal fur either spiny or very bristly 3
Dorsal fur neither spiny nor very bristly 6
- 3 Fur modified into distinct spines along dorsal surface **ACOMYS** (p. 334)
Fur bristly but not spiny 4
- 4 Dorsal fur chestnut, bristly and stiff; tail about 1.5 times h. & b. **DEOMYS** (p. 343)
Dorsal fur stiff and brush-like, reddish-brown; tail approximately equal to or less than h. & b. 5
- 5 Backs of hands and feet brown or black; belly red-brown or buff **LOPHUROMYS** (p. 331)
Backs of hands and feet white, belly white **URANOMYS** (p. 336)
- 6 Either upper and lower incisors grooved or just the upper ones 7
Neither upper nor lower incisors grooved 11
- 7 Both upper and lower incisors deeply grooved; fur long and soft; tail appreciably shorter than h. & b. **OTOMYS** (p. 345)
Upper incisors at least faintly grooved; lower incisors not grooved 8

- 8 Large forms (h. & b. over 100 mm.) 9
 Small forms (h. & b. under 100 mm.) 10
- 9 Fur coarse and harsh; belly hairs dirty yellow-grey **PELOMYS** (p. 310)
 Fur thick and soft; belly hairs white at the tips and sharply demarcated from those
 at the flanks **MYLOMYS** (p. 305)
- 10 Tail very short, less than 40 mm. **STEATOMYS** (p. 342)
 Tail appreciably longer, over 60 mm. **DENDROMYS** (p. 339)
- 11 With red tip to snout in sharp contrast to rest of body **OENOMYS** (p. 305)
 Colour of snout neither bright red nor in sharp contrast with rest of body 12
- 12 Fur with metallic iridescent lustre 13
 Fur without metallic iridescent lustre 14
- 13 Fur rough and shaggy looking **DASYMYS** (p. 307)
 Fur closely applied to the body **AETHOMYS** (p. 317)
- 14 With at least one dorsal stripe 15
 Without stripes 17
- 15 A single black mid-dorsal stripe **HYBOMYS** (p. 316)
 Several stripes present 16
- 16 Four black stripes along back; mid-dorsal line pale **RHABDOMYS** (p. 315)
 Numerous pale stripes along back (may be composed of lines of spots); mid-dorsal
 line dark **LEMNISCOMYS** (p. 313)
- 17 Tail considerably longer than h. & b. 18
 Tail approximately equal to h. & b. or shorter 23
- 18 Tip of tail with small but distinct pencil of hairs 19
 Tip of tail without pencil of hairs 20
- 19 Hind foot relatively broad **THAMNOMYS** (p. 302)
 Hind foot not broadened **GRAMMOMYS** (p. 304)
- 20 Very small (h. & b. less than 60 mm.); tail relatively long (about 100 mm.)
 **DELANYMYS** (p. 343)
 H. & b. over 60 mm.; tail relatively not so long 21
- 21 Medium size (h. & b. 105 to 138 mm.) **PRAOMYS** (p. 321)
 Smaller size (h. & b. 71 to 107 mm.) 22
- 22 Hairs of belly with white tips and grey bases **HYLOMYSCUS** (p. 322)
 Hairs of belly pure white **MYOMYS** (p. 324)
- 23 Medium size (h. & b. 127 to 160 mm.); tail $\frac{1}{3}$ to $\frac{1}{2}$ h. & b. **SACOSTOMUS** (p. 337)
 Small or medium size; if the latter tail is not short 24
- 24 Hairs coarse, strongly annulated black on buff, producing a "pepper and salt" effect;
 tail shorter than h. & b. but never less than $\frac{2}{3}$ h. & b. length; ears hairy
 **ARVICANTHIS** (p. 309)
 Without "pepper and salt" effect 25
- 25 Medium size (h. & b. 133 to 171 mm.); tail about h. & b. length; hind feet very large
 (35 to 40 mm.) **MALACOMYS** (p. 327)
 Variable size but with appreciably smaller hind feet 26
- 26 Upper incisors pro-odont (projecting forwards) **ZELOTOMYS** (p. 327)
 Upper incisors not pro-odont 27
- 27 Small size (h. & b. less than 93 mm.) **MUS** (p. 329)
 Larger size (h. & b. over 90 mm.) 28
- 28 Texture of fur very soft; flanks brown, belly grey with clear demarcation between the
 two **MASTOMYS** (p. 325)
 Texture of fur coarse, dorsally brown to grey with a gradual transition in colour
 from back to belly with no sharp line of demarcation between flanks and belly
 **RATTUS** (p. 319)

SYSTEMATIC ACCOUNT

Family **MURIDAE** Gray

1821. Muridae Gray, *London Med. Reposit.* **15** : 303.

Subfamily **MURINAE** Murray

1866. Murinae Murray, *The Geographic Distribution of Mammals* : 359.

Genus **THAMNOMYS** Thomas. Thicket Rats

1907. *Thamnomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **19** : 121. Genotype *Thamnomys venustus* Thomas.

The genera *Thamnomys* and *Grammomys* are very similar. The tail is very long in both and with a pencil of hairs at its tip. The same is true of the gerbils but they can be separated from these two genera on other characters (p. 298). The hind foot of *Thamnomys* is broader than in *Grammomys*. Examination of the Uganda material shows differences in the colour of the belly fur in the two genera. In *Grammomys* the belly is pure white whilst in *Thamnomys* it is whitish washed with buff, or greyish with white tips. This character has not been found to hold good for all the specimens examined from other parts of Africa. We have recognized *T. kempi* as conspecific with *T. venustus*.

Hairs of belly white to bases, washed with buff	<i>T. rutilans</i>
Hairs of belly grey with white tips	<i>T. venustus</i>

Thamnomys rutilans (Peters)

1876. *Mus rutilans* Peters, *Monatsb. K. preuss. Akad. Wiss., Berlin* **1876** : 478. Lambarene, Gaboon [0° 45' S. 10° 15' E.].

DESCRIPTION. Only specimen examined from Uganda has a rich suffusion of buff to the white hairs of the belly.

DISTRIBUTION. Zika Forest, Buganda. Text-fig. 2.

MEASUREMENTS. One ♂ h. & b. 145 mm. ; tail 172 mm. ; h. f. 25 mm. ; ear 17 mm. ; weight 54 g.

BREEDING. No information available.

HABITAT. Typically a forest species.

BIOLOGY. No information available.

Thamnomys venustus Thomas

1907. *Thamnomys venustus* Thomas, *Ann. Mag. nat. Hist.*, (7) **19** : 122. Mubuku Valley, Toro.

1911. *Thamnomys kempi* Dollman, *Ann. Mag. nat. Hist.*, (8) **8** : 658. Buhamba, near Lake Kivu, Congo [1° 32' S. 29° 19' E.].

DESCRIPTION. Tips of belly hairs white, bases grey. Fur thicker and softer texture than *T. rutilans*.

DISTRIBUTION. Echuya Forest, Impenetrable Forest, Kigezi; Mihunga Swamp, Mubuku Valley, Toro. Text-fig. 2.

MEASUREMENTS. One ♂ h. & b. 125 mm.; tail 181 mm.; h. f. 25 mm.; ear 18 mm. Three ♀ h. & b. 151 mm., 131 mm., 141 mm.; tail 183 mm., 162 mm., 184 mm.; h. f. 26 mm., 26 mm., 28 mm.; ear 19 mm., 20 mm., 19 mm.; weights 66 g., 51 g., 56 g.

BREEDING. No information available.



FIG. 2. Distribution of *Thamnomys rutilans*, *T. venustus* and *Grammomys dolichurus*.

HABITAT. High altitude (including moist montane) forest.

BIOLOGY. Arboreal. Nocturnal (Allen & Loveridge, 1942).

Genus **GRAMMOMYS** Thomas. Tree Rats

1915. *Grammomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 16: 150. Genotype, by original designation, *Mus dolichurus* Smuts.

Separated, on external characters, from *Thamnomys* on the narrower hind foot. Long tail with a pencil of hairs at its tip. In the Uganda specimens examined the belly hairs are pure white without a buff suffusion. The dorsal fur is brown to grey-brown with, in some specimens, a buff line where flank and belly fur meet. Allen (1939) includes *Grammomys* as a subgenus of *Thamnomys*.

Grammomys dolichurus (Smuts)

1832. *Mus dolichurus* Smuts, *Enumerat. Mamm. Capens.*: 38. Type locality given as "near Cape Town", South Africa but this is of uncertain accuracy (see Ellerman, Morrison-Scott & Hayman, 1953).

1907. *Thamnomys dryas* Thomas, *Ann. Mag. nat. Hist.*, (7) 19: 123. Mubuku Valley, Toro.

1907. *Thamnomys macmillani* Wroughton, *Ann. Mag. nat. Hist.*, (7) 20: 504. Wouida, north of Lake Rudolf, Ethiopia.

1908. *Thamnomys surdaster* Thomas & Wroughton, *Proc. zool. Soc. Lond.* 1908: 550. Zomba, Malawi [15° 22' S. 35° 22' E.].

1910. *Thamnomys discolor* Thomas, *Ann. Mag. nat. Hist.*, (8) 5: 283. Kakamega Forest, Kisumu, Kenya [0° 19' N. 34° 51' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Maramagambo Forest, Ankole; Kalule, Kampala, Lialo, Nkyanuna, Buganda; Salalira, "south Bugisu", Bugisu; "Bukedi"; Kotido, Lotome, Moroto, Karamoja; Echuya Forest, Kumba, Nyalusanje, Kigezi; Serere, Teso; Ilumia, Mihunga, Mubuku Valley, Mweya, Wasa River, Toro; Rhino Camp, West Nile. Text-fig. 2.

MEASUREMENTS. Three ♂ h. & b. 120 mm., 98 mm., 126 mm.; tail 165 mm., 134 mm., 183 mm.; h. f. 23 mm., 22 mm., 27 mm.; ear 15 mm., 14 mm., 17 mm.; weights ?, 24 g., 51 g. ♀ h. & b. 113.9 mm. (8 meas., range 99 to 130 mm.); tail 173.7 mm. (8 meas., range 150 to 205 mm.); h. f. 23.6 mm. (8 meas., range 22 to 25 mm.); ear 16.2 mm. (8 meas., range 15 to 20 mm.); weight 41.2 g. (5 weighed, range 33 to 53 g.).

BREEDING. Foetuses (1 × 3), Mweya; (2 × 3) Moroto, Nov. In Zambia (3 × 4) (Ansell, 1960). Watson (1950) reports usually 3 young in a litter.

HABITAT. Scrub, bush and various types of forest.

BIOLOGY. Arboreal; nocturnal. Build nests in bushes and trees. Outer part of nest of coarse grass with a lining of finely chewed grass. Brown house snake (*Boaedon lineatus*) reported to prey on it (Allen & Loveridge, 1942). Vegetarian, including seeds.

Genus *OENOMYS* Thomas. Rusty-nosed Rats

1904. *Oenomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **13**: 416. Genotype, by original designation, *Mus hypoxanthus* Pucheran.

Medium sized rats easily recognized by their rusty-red nose. Upper surface brown or grey often with tinge of olive, this colour produced by the hairs having long buff or rufous tips and dark grey bases. Rump suffused with rusty-red colour. Backs of hands and feet pale brown. Flanks paler than back sharply demarcated from white of underside. Belly hairs white to roots. Tail grey-brown above, much paler below.

Oenomys hypoxanthus (Pucheran)

1855. *Mus hypoxanthus* Pucheran, *Rev. Mag. Zool.* **2**: 206. Gaboon.

1910. *Oenomys bacchante* Thomas and Wroughton, *Trans. zool. Soc. Lond.* **19**: 509. Mubuku Valley, Toro.

DESCRIPTION. As for genus.

DISTRIBUTION. Kampala, Buganda; Bubungi, Buyobo, Sipi, Bugisu; Fadjao, Bunyoro; Impenetrable Forest, Kigezi; Benet, Sebei; Bundibugyo, Bundimali, Ilumia, Kilembe, Kyatwa, Mihunga, Mubuku Valley, Sara, Toro. Text-fig. 3.

MEASUREMENTS. H. & b. ♂ 142.4 mm. (11 meas., range 105 to 167 mm.), ♀ 143.2 mm. (13 meas., range 131 to 159 mm.); tail ♂ 172.6 mm. (11 meas., range 150 to 205 mm.), ♀ 170.5 mm. (13 meas., range 135 to 187 mm.); h. f. ♂ 29.9 mm. (11 meas., range 24 to 33 mm.), ♀ 29.7 mm. (13 meas., range 28.5 to 31 mm.); ear ♂ 19.2 mm. (11 meas., range 18 to 21 mm.), ♀ 18.8 mm. (13 meas., range 17 to 21 mm.); weight ♂ 70 g. 90 g., ♀ 57 g., 76 g. (only four weighed).

BREEDING. Foetuses (5 × 3, 4 × 4) Kampala (Hopkins MS.); (1 × 3) in Congo (Misonne, 1963). Litter of three blind nestlings in Congo (Allen & Loveridge, 1942).

HABITAT. Tall grass bordering marshes and streams; swamps amongst *Cyperus latifolius* and fern.

BIOLOGY. Climbs easily and makes nests in grass.

Genus *MYLOMYS* Thomas

1906. *Mylomys* Thomas, *Ann. Mag. nat. Hist.*, (7) **18**: 224. Genotype, by original designation, *Mylomys cunninghamei* Thomas.

Medium sized rats with the dorsal surface a bright olive-gold, heavily lined with black; flanks with less black but sharply demarcated from the white of the underside. Tail generally a little shorter than the head-and-body length, black above, yellow buff or whitish below. Grooved upper incisors.

Mylomys cunninghamei Thomas

1906. *Mylomys cunninghamei* Thomas, *Ann. Mag. nat. Hist.*, (7) **18**: 225. East of Aberdare Mountains, Kenya [approximately 0°-1° S. 36° 45' E.].

1915. *Mylomys lutescens* Thomas, *Ann. Mag. nat. Hist.*, (8) **16**: 149. Nyalasanje, Kigezi.

DESCRIPTION. As for genus.

DISTRIBUTION. Paraa, Acholi ; Lutoto, north of Maramagambo Forest, Ankole ; Kampala, Mabira Forest, Buganda ; Walasi Bugisu ; Budama, Kidoko, Mulanda, Bukedi ; Kanaba, Kiduha, Nyalusanje, Kigezi ; Serere, Teso ; Butiti, Crater Track, Toro. Text-fig. 3.

MEASUREMENTS. H. & b. ♂ 154.3 mm. (20 meas., range 122 to 183 mm.), ♀ 153.1 mm. (21 meas., range 125 to 180 mm.) ; tail ♂ 141.4 mm. (20 meas., 104 to 180 mm.), ♀ 142.2 mm. (20 meas., range 119 to 156 mm.) ; h. f. ♂ 33.2 mm. (20 meas., range 29 to 36 mm.), ♀ 32.4 mm. (21 meas., range 30 to 35 mm.) ; ear ♂ 18.5 mm.



FIG. 3. Distribution of *Oenomys hypoxanthus* and *Mylomys cunninghamei*.

(17 meas., range 14 to 22 mm.), ♀ 18.8 mm. (20 meas., range 15 to 22 mm.); weight ♂ 103.1 g. (18 weighed, range 50 to 165 g.), ♀ 99.4 g. (20 weighed, range 46 to 160 g.).

BREEDING. Foetuses (1 × 3, wt. less than 1 g.), (1 × 5, wt. 18 g.) Jul. Crater Track. (1 × 5, wt. 1 g.), (1 × 4, wt. 4 g.) Aug. north of Maramagambo Forest. (1 × 3), (1 × 4 wt. 1 g.) Aug. Lutoto.

HABITAT. Typically thick grassland, heath and scrub.

BIOLOGY. Diurnal ? Herbivorous, eating grass leaves and stems.

Genus *DASYMYS* Peters. Shaggy Swamp Rats

1875. *Dasymys* Peters, *Mber. preuss. Akad. Wiss. Berl.* **1875** : 12. Genotype, by monotypy, *Dasymys gueinzii* Peters = *Mus incomtus* Sundevall.

Moderate sized rats with long, soft and untidy fur and sparsely haired tail. The animal has a flattened appearance. Dorsal hairs inconspicuously annulated black and buff giving the general effect of darkish grey tinged with brown or greyish brown. Backs of the hands and feet dark coloured, almost naked. Underside slaty grey with a greater or lesser amount of whitish admixture due to the pale tips of the hairs. Eyes small. Ears hairy. Ellerman (1941) and Hopkins (MS.) believe there is only one species of *Dasymys* in Uganda.

Dasymys incomtus (Sundevall)

1846. *Mus incomtus* Sundevall, *Öfvers. Vetensk. Akad. Förh. Stockh.* **3** : 120. "E. Caffraria prope Port Natal" (= Durban, Natal) [29° 53' S. 31° 00' E.].

1875. *Dasymys gueinzii* Peters, *Mber. preuss. Akad. Wiss. Berl.* **1875** : 13. Interior of "Port Natal" (= Durban, Natal).

1906. *Dasymys medius* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 143. Mubuku Valley, Toro.

1906. *Dasymys montanus* Thomas, *Ann. Mag. nat. Hist.*, (7) **18** : 143. Mubuku Valley, Toro.

1911. *Dasymys orthos* Heller, *Smithson, misc. Coll.* **56** : 13. Butiaba, Bunyoro.

DESCRIPTION. As for genus.

DISTRIBUTION. Asuya, Gulu, Acholi ; near Kagambah, Lutoto, Ankole ; Kakumiro, Kampala, Mengo, Buganda ; Budama, Bukedi ; Butiaba, Bunyoro ; Echuya Swamp, Ingezi, Kiduha, Kumba, Nyalasanji, Kigezi ; Moyo, Madi ; Amuria, Serere, Teso ; Mihunga, Mubuku Valley, Toro ; Rhino Camp, West Nile. Text-fig. 4.

MEASUREMENTS. H. & b. ♂ 154.9 mm. (13 meas., range 146 to 166 mm.), ♀ 145.0 mm. (11 meas., range 130 to 170 mm.) ; tail ♂ 132.5 mm. (13 meas., range 111 to 150 mm.), ♀ 127.4 mm. (11 meas., range 105 to 150 mm.) ; h. f. ♂ 29.9 mm. (13 meas., range 26 to 32.5 mm.), ♀ 28.8 mm. (11 meas., range 27 to 31 mm.) ; ear ♂ 20.6 mm. (13 meas., range 19 to 23 mm.), ♀ 20.4 mm. (11 meas., range 17.5 to 25 mm.) ; one ♀ weighed 59 g.

BREEDING. Foetuses (1×4 , 1×5) in Zambia (Ansell, 1960); (3×2 , 3×3) Hopkins (MS.). Usually 2 to 4 in a litter in South West Africa (Shortridge, 1934).

HABITAT. Typically swamps, reed beds and river valleys. Occurs at various elevations; recorded from boggy moss covered ground between 12,500 and 14,000 feet on Ruwenzori. Misonne (1963) has found this species in mixed savanna in the Congo.

BIOLOGY. Vegetarian. Nests made of grass on surface of the ground.



FIG. 4. Distribution of *Dasymys incommutus*.

Genus *ARVICANTHIS* Lesson. Unstriped Grass-mice

1842. *Arvicanthis* Lesson, *Nouv. Tabl. Regne Anim. Mammif.* : 147. Genotype, by monotypy and original designation, *Lemmus niloticus* Geoffroy, 1803 = *Hypudaeus variegatus* Lichtenstein, 1823 = *Arvicola niloticus* Desmarest, 1822.

1843. *Isomys* Sundevall, *K. svenska VetenskAkad. Handl.* 1842 : 219.

Medium sized animals, with fur composed of rather harsh hairs which are annulated with brown and buff in such a way as to produce a "pepper and salt" effect. The genus might be confused with *Mylomys* but *Arvicanthis* has a grisly coloured under-surface and upper incisors without grooves. The tail is usually distinctly shorter than the head and body.

Arvicanthis niloticus (Desmarest)

1822. *Arvicola niloticus* Desmarest, *Mammalogie* 2 : 281. Egypt.

1842. *Mus abyssinicus* Rüppell, *Mus. Senckenbergianum* 3 : 104. Entschetqab, Simen Province, Ethiopia [13° 15' N. 38° 20' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Kitgum, Acholi; Congo Road, north of Maramagambo Forest, Burumba, Kagambah, Mbarara, Ankole; Buruli, Entebbe, Kakumiro, Kampala, Kisingo, Mabira Forest, near Masaka, Nalweyo, Buganda; Budongo Forest, Bulisa, Butiaba, Hoima, Kibiro, Masindi, Bunyoro; Amudat, Anamuget, Bokora, Kamchuru, Kotido, Locihotome, Moroto, Moruita, Nabilatuk, Karamoja; Nyakabande, Nyalusanje, Kigezi; Kibusi, Lango; Ajeluk, Amuria, Serere, Teso; Bugoye, Bundibugyo, Crater Track, Hakitengya, Ilumia, Kamulikwezi, Kilembe, Kimara, Makoga, Mpanga Forest, Mubuku Valley, Mweya, south-east Ruwenzori, Toro; Adropi, Arua, Offude, Rhino Camp, West Nile. Kibandama, Patong. Text-fig. 5.

MEASUREMENTS. H. & b. ♂ 146.3 mm. (54 meas., range 120 to 184 mm.), ♀ 141.6 mm. (59 meas., range 120 to 167 mm.); tail ♂ 110.8 mm. (54 meas., range 83 to 134 mm.), ♀ 109.7 mm. (58 meas.; range 86 to 129 mm.); h. f. ♂ 28.5 mm. (55 meas., range 23 to 32 mm.), ♀ 27.9 mm. (58 meas., range 25 to 32.5 mm.); ear ♂ 16.7 mm. (52 meas., range 13 to 20 mm.), ♀ 16.3 mm. (57 meas., range 13 to 20 mm.); weight ♂ 80.0 g. (23 weighed, range 57 to 120 g.), ♀ 77.5 g. (33 weighed, range 50 to 101 g.).

BREEDING. Foetuses (1 × 4) Aug. Congo Road, (1 × 4) Sep. Kamulikwezi. Watson (1950) reports a possible maximum breeding season towards the end of the rains as they are very numerous during the early months of the dry season.

HABITAT. Typically a grassland species but also common in bush and cultivated land. May be found in native huts and grain stores.

BIOLOGY. Nocturnal and diurnal. Herbivorous, eating leaves and stems, especially of *Ameranthus polygamus*. The black-shouldered kite (*Elanus coeruleus*) has been reported to prey on this species. It digs burrows in which it nests, often in banks or rubbish heaps or at the foot of bushes, with tunnels leading through the thick grass from them. They are made of fine grass and often placed four or five together, forming a warren. Surface nests also occur, as well as burrows, but it is not

known in what circumstances they are used. The underground nests are usually 8 inches to 2 feet deep. The surface nests are usually in a thick tussock of grass.

Genus *PELOMYS* Peters. Creek Rats

1852. *Pelomys* Peters, *Mber. preuss. Akad. Wiss. Berl.* **1852**: 275. As a subgenus of *Mus* Linnaeus; genotype, by monotypy, *Mus. (Pelomys) fallax* Peters.

1910. *Desmomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **5**: 284. *Pelomys harringtoni* Thomas, valid as a subgenus.

1924. *Komemys* de Beaux, *Ann. Mus. Stor. nat. Genova* **51**: 207. *Komemys isseli* de Beaux, valid as a subgenus.



FIG. 5. Distribution of *Arvicanthis niloticus*.

The creek rats are medium sized rats. The colour of the dorsal surface rather resembles *Arvicanthis* from which they can be distinguished by the grooved upper incisors. They may or may not have a distinct dorsal stripe. The underside is dirty yellow, buff or greyish and not sharply demarcated from the dark coloured flanks. The relative length of the tail varies in the different species. *P. isseli* is included in the subgenus *Komemys* and the other two Uganda species in the subgenus *Pelomys*.

1	With very distinct black dorsal stripe	2
	Dorsal stripe absent	<i>P. fallax</i>
2	Tail about 1.5 times length of head and body	<i>P. isseli</i>
	Tail about as long as head and body	<i>P. hopkinsi</i>

Pelomys fallax (Peters)

1852. *Mus (Pelomys) fallax* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1852 : 275. Caya District, Zambezi River, Portuguese East Africa = Sena, Mozambique [17° 20' S. 35° 10' E.].

DESCRIPTION. Golden-yellow above, the hairs heavily annulated with black, giving a "pepper and salt" effect as in *Arvicanthis*; no dark dorsal stripe. Under-side olive buff. Tail just shorter than head-and-body length.

DISTRIBUTION. Kagambah, Mbarara, Ankole; Kiduha, Nyalasanje, Kigezi. Text-fig. 6.

MEASUREMENTS. H. & b. ♂ 142.3 mm. (6 meas., range 135 to 146 mm.), ♀ 147 mm. (1 meas.); tail ♂ 133.7 mm. (6 meas., range 127 to 137 mm.), ♀ 135 mm.; h. f. ♂ 29.7 mm. (6 meas., range 29 to 30 mm.), ♀ 29.5 mm.; ear ♂ 17.8 mm. (6 meas., range 17 to 18 mm.), ♀ 18 mm.; none weighed.

BREEDING. Foetuses, Ansell (1960) reports (1 × 9, 1 × 7); juveniles and sub-adults caught throughout the year suggests no fixed breeding season in Zambia.

HABITAT. Reported from swamps, reed beds, river banks and damp places.

BIOLOGY. Reported to be diurnal in South West Africa (Shortridge, 1934), but Ansell (1960) suggests that it is mainly nocturnal in Zambia. The South West African form of this species is reported to feed on reed shoots and other swamp vegetation, whilst in Tanzania it is stated to be destructive to grain crops. The species is a very able swimmer, and in Angola is reported to make deep burrows although no signs of any nests or holes have been found in other localities.

Pelomys isseli (de Beaux)

1924. *Komemys isseli* de Beaux, *Ann. Mus. Stor. nat. Genova* 51 : 207. Kome Island, Buganda.

DESCRIPTION. Upperside buff, sprinkled with black and with a very distinct black mid-dorsal stripe. Underside dirty whitish or buff. Tail nearly 1.5 times the length of the head and body.

DISTRIBUTION. Bugala Island, Kome Island, Buganda. Text-fig. 6.

MEASUREMENTS. Only two ♀ measured, h. & b. 100 and 106 mm. ; tail 143 and 148.5 mm. ; h. f. 29 and 29 mm. ; ear 16 and 18.5 mm. ; not weighed.

BREEDING. No information available.

HABITAT. No information available.

BIOLOGY. No information available.



FIG. 6. Distribution of *Pelomys* spp.

Pelomys hopkinsi Hayman

1955. *Pelomys hopkinsi* Hayman, *Rev. Zool. Bot. afr.* **52**: 323. Rwamachuchu, Kigezi.

DESCRIPTION. General appearance that of a small *Arvicanthis* with a distinct black mid-dorsal stripe. Underside generally buffy. Tail about as long as head and body.

DISTRIBUTION. Rwamachuchu, Kigezi. Text-fig. 6.

MEASUREMENTS. One ♂ meas., tail 135 mm.; h. f. 32 mm.

BREEDING. No information available.

HABITAT. Edge of papyrus swamp.

BIOLOGY. No information available.

Genus **LEMNISCOMYS** Trouessart. Striped Grass-mice

1881. *Lemniscomys* Trouessart, *Bull. Soc. Sci. Angers* **10**: 124. As a subgenus of *Mus* Linnaeus; genotype, by subsequent designation (Thomas, 1916, *Ann. Mag. nat. Hist.*, (8) **18**: 67), *Mus barbarus* Linnaeus.

The striped grass mice are characterized by the presence of a dark mid-dorsal line and numerous white dorsal and dorso-lateral stripes which may or may not be broken up into spots. The underside is pure white. The tail is hairy and as long as, or longer than the head and body. The fifth finger is shortened.

White dorsal and dorso-lateral stripes continuous	<i>L. barbarus</i>
White dorsal and dorso-lateral stripes broken into spots	<i>L. striatus</i>

Lemniscomys barbarus (Linnaeus)

1766. *Mus barbarus* Linnaeus, *Syst. Nat.* 12th ed., pt. 2, add. not paged. Morocco.

DESCRIPTION. Slightly smaller than *L. striatus*; continuous stripes along body.

DISTRIBUTION. Paraa, Acholi; Nabilatuk, Karomoja; Ajeluk, Malera, Serere, Teso; Rhino Camp, Wadelai, West Nile. Text-fig. 7.

MEASUREMENTS. H. & b. ♂ 105.7 mm. (7 meas., range 98 to 118 mm.), one ♀ 105 mm.; tail ♂ 107.3 mm. (7 meas., range 95 to 116 mm.), ♀ 118 mm.; h. f. 23.3 mm. (7 meas., range 22 to 25 mm.), ♀ 23 mm.; ear ♂ 12.9 mm. (7 meas., range 12 to 15 mm.), ♀ 12 mm.; weight ♂ 30.0 g. (6 weighed, range 23 to 36 g.), ♀ 41 g.

BREEDING. Foetuses (1 × 5) Oct., Nabilatuk.

HABITAT. Typically grass and scrub in dryer areas.

BIOLOGY. No information available.

Lemniscomys striatus (Linnaeus)

1758. *Mus striatus* Linnaeus, *Syst. Nat.* 10th ed., pt. 1: 62. "India" = Sierra Leone (Thomas 1911, *Proc. zool. Soc. Lond.* **1911**: 148).

1910. *Arvicanthis macculus* Thomas & Wroughton, *Trans. zool. Soc. Lond.* **19**: 515. Muhokya, Toro.

1919. *Lemniscomys macculus* Hollister, *Bull. U.S. nat. Mus.* **99**: 138.

DESCRIPTION. Slightly larger of the two species. The white stripes broken into spots which may be joined to each other.

DISTRIBUTION. Awack, Fort Patiko, Pamdero, Acholi ; Congo Road, Maramagambo Forest, north of Maramagambo Forest, between Rwempuno and Kaizi Rivers, Kagambah, Ankole ; Entebbe, Kabanyolo, Kabula, Kajansi, Kampala, Kasai Forest, Kisingo, Lunyo, Mabira Forest, Nabugabo, Buganda ; Lwakaka, Bugisu ; Tororo, Bukedi ; Busingiro, Hoima, Masindi, Bunyoro ; Moroto, Namalu, Karamoja ;



FIG. 7. Distribution of *Lemniscomys* spp.

Bugoye, Bundibugyo, Crater Track, Ilumia, Mihunga, Mpanga Forest, Mubuku Valley, Muhokya, Mweya, south east Ruwenzori, Tokwe, Toro; Rhino Camp, West Nile. Text-fig. 7.

MEASUREMENTS. H. & b. ♂ 111.7 mm. (27 meas., range 93 to 131 mm.), ♀ 113.9 mm. (24 meas., range 91 to 142 mm.); tail ♂ 119.4 mm. (25 meas., range 92 to 144 mm.), ♀ 124.2 mm. (18 meas., range 103 to 141 mm.); h. f. ♂ 24.2 mm. (28 meas., range 20.5 to 27.5 mm.), 24.4 mm. ♀ (24 meas., range 20.5 to 27 mm.); ear ♂ 15.3 mm. (21 meas., range 14 to 17.5 mm.), ♀ 15.8 mm. (15 meas., range 14 to 17 mm.); weight ♂ 36.7 g. (13 weighed, range 27 to 46 g.), ♀ 38.2 g. (12 weighed, range 18 to 68 g.).

BREEDING. Foetuses (1 × 5) Aug. Maramagambo Forest; Allen & Loveridge (1942) report (1 × 5) Dec. Kibale Forest, (1 × 5) Dec. Bundibugyo. Juveniles—4 nestlings Nov. Mabira Forest, 2 blind nestlings Jan. Mihunga, 2 young late Jan. Bugoye. Misonne (1963) reports litters of 3 to 6 in Congo.

HABITAT. Inhabits grassland, savanna, dense scrub and cultivated land. It is also apparently found in quite thick forest.

BIOLOGY. Nocturnal and diurnal. Omnivorous, observation of stomach contents showed leaf and stem remains, seeds and insects to be numerous. "Natives state that this species eats young shoots of grass, sweet potatoes, cassava and fallen maize cobs. The nest is often placed at the base of a tussock of tall grass, and is made from grass" (Hopkins MS.).

Genus *RHABDOMYS* Thomas. Four-striped Grass-mice

1916. *Rhabdomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 18: 69. Genotype, by original designation, *Mus pumilio* Sparrman.

Characterized by having four black stripes along length of body and a pale mid-dorsal line. Yellow to grey-brown ground colour. Tail black above, light brown below.

Rhabdomys pumilio (Sparrman)

1784. *Mus pumilio* Sparrman, *K. svenska VetenskAkad. Handl.* 1784: 236. Sitzicamma Forest, on Snake River, east of Cape of Good Hope, South Africa [33° 55' S. 23° 47' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Mudangi, Bugisu. Text-fig. 8.

MEASUREMENTS. H. & b. ♂ 106 mm., ♀ 103 mm.; tail ♂ 82 mm., ♀ 81 mm.; h. f. ♂ 22 mm., ♀ 20 mm.; ear ♂ 12 mm., ♀ 11 mm.

BREEDING. Foetuses (2 × 5, 1 × 3) in Kenya. From South West Africa 6 and 7 foetuses have been reported (Shortridge, 1934). Breed at 3 months.

HABITAT. In East Africa only recorded from high altitudes. In South West Africa frequent in bushy and semi-dry vleis country, mainly in scrub, long grass and forest edges (Shortridge, 1934).

BIOLOGY. Ground-dwelling but also, to a limited extent, arboreal. Makes burrows. Diurnal. Mainly vegetarian but also recorded as eating snails, insects and eggs and nestlings of birds.

Genus *HYBOMYS* Thomas. Back-striped Mice

1910. *Hybomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 5 : 85. Genotype, by original description, *Mus univittatus* Peters.

1911. *Typomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 7 : 382. Genotype, by original description, *Mus trivirgatus* Temminck. Synonym of *Hybomys* (Ingoldby, *Ann. Mag. nat. Hist.*, (10) 3 : 522).



FIG. 8. Distribution of *Rhabdomys pumilio* and *Hybomys univittatus*.

Medium sized rats characterized by having a rather indistinct mid-dorsal black line running from between the ears to the base of the tail. Upperside light brown, usually with a strong reddish tinge which is particularly well marked on the rump. Underside light buffy-grey contrasting sharply with the flanks. Scales of tail not at all obscured by the short hairs. Tail slightly shorter than head-and-body length. Hindfeet with long toes. Incisors not grooved.

Hybomys univittatus (Peters)

1876. *Mus univittatus* Peters, *Monatsb. K. preuss. Akad. Wiss. Berl.* 1876 : 479. Donghila, Gaboon [0° 12' N. 9° 44' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Kalinzu Forest, Maramagambo Forest, Ankole; Malabigambo Forest, Mpanga Forest, Buganda; Impenetrable Forest, Kigezi; Mpanga Forest, Mubuku Valley, north Ruwenzori, Toro. Text-fig. 8.

MEASUREMENTS. H. & b. ♂ 118.5 mm. (8 meas., range 103 to 128 mm.), ♀ 117.9 mm. (11 meas., range 108 to 127 mm.); tail ♂ 105.5 mm. (8 meas., range 85 to 116 mm.), ♀ 103.9 mm. (11 meas., range 86 to 115 mm.); h. f. ♂ 27.2 mm. (8 meas., range 26 to 29 mm.), ♀ 26.4 mm. (11 meas., range 24 to 28 mm.); ear ♂ 15.6 mm. (8 meas., range 15 to 17 mm.), ♀ 15.5 mm. (11 meas., range 14 to 17.5 mm.); weight ♂ 50.7 g. (6 weighed, range 46 to 61 g.), ♀ 49.4 g. (7 weighed, range 38 to 56 g.).

BREEDING. Foetuses (2 × 3) (1 lactating) Oct. Impenetrable Forest, (1 × 2) lactating Jul. Mpanga Forest (Buganda). Two ♀ lactating Sep. Maramagambo Forest. Misonne (1963) reports two embryos in Congo animals.

HABITAT. Apparently confined to forest being found in rain forest, transition forest and mountain forest but not bamboo forest. It has not been found in gallery forest. It is more abundant in secondary vegetation than in primary forest; apparently prefers the wetter parts of forest.

BIOLOGY. Reported by the Congo expedition to eat "the red fruit of a lily-like plant of which chimpanzees are so fond" (Hatt, 1940). Two stomachs examined by Delany (1964b) contained only vegetable matter. Apparently a good swimmer.

Genus *AETHOMYS* Thomas. Bush Rats

1915. *Aethomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 16 : 477. As a subgenus of *Epimys* Trouesart = *Rattus* Fisher; genotype, by original designation, *Epimys hindei* (Thomas).

Medium sized rats with tail usually a little shorter than head-and-body length. Incisor teeth ungrooved. Fur soft, smooth and tidy, but not silky and with a metallic lustre. Hairs of underside with pure white tips, with long slate grey bases, mottled when hairs displaced. The backs of the hands and feet are white.

Tail sparsely haired, nearly as long as, or occasionally slightly longer than head and body; dorsal pelage light brown in colour *A. kaiseri*
 Tail more hairy, barely longer than body without head; dorsal pelage rich warm brown *A. nyikae*

Aethomys kaiseri (Noack)

1887. *Epimys kaiseri* Noack, *Zool. Jb. Syst.* **2**: 228. Qua Mpala (Marungu), southern Congo [6° 46' S. 29° 32' E.].

DESCRIPTION. Tail sparsely haired; upper side dark brownish grey or brown; underside mainly white, grey bases of hairs show if the fur is ruffled.

DISTRIBUTION. Chua, Fort Patigo, Paraa, Acholi; Entebbe, Kabanyolo, Kabulamulero, Kakumiro, Kampala, Kikonda, Kisingo, Lialo, Nabugabo, Nkyanuna, Zika Forest, Buganda; Tororo, Bukedi; Hoima, Bunyoro; Moroto, Nabilatuk, Namalu, Karamoja; Ajeluk, Serere, Teso; Kimara, Wanka R., Wassa R., Toro; Nebbi, Ngal, Offude, Pakwach, Rhino Camp, West Nile. Text-fig. 9.

MEASUREMENTS. H. & b. ♂ 160.4 mm. (18 meas., range 140 to 184 mm.), ♀ 149.5 mm. (10 meas., range 135 to 169 mm.); tail ♂ 156.8 mm. (18 meas., range 140 to 186 mm.), ♀ 145.8 mm. (10 meas., range 121 to 180 mm.); h. f. ♂ 29.2 mm. (17 meas., range 26 to 32 mm.), ♀ 29.0 mm. (10 meas., range 26 to 32 mm.); ear ♂ 19.0 mm. (13 meas., range 17 to 21 mm.), ♀ 19.0 mm. (8 meas., range 16 to 23 mm.); weight ♂ 109.0 g. (10 weighed, range 62 to 150 g.), ♀ 82.4 g. (7 weighed, range 58 to 100 g.).

BREEDING. Foetuses (1 × 3) Sep. Kabanyolo, (3 × 3) Kampala (Hopkins MS.). Three large young observed attached to nipples of ♀ in Tanzania (Allen & Loveridge, 1942).

HABITAT. Open country, thick grassland. Southern & Hook (1963a) report finding this rat in the ground layer of seasonal forest, the swamp edge of lakeside forest and in deserted shambas at the edge of forest.

BIOLOGY. Occasionally enters houses (Hopkins MS.).

Aethomys nyikae (Thomas)

1897. *Mus nyikae* Thomas, *Proc. zool. Soc. Lond.* **1897**: 431. Nyika Plateau, northern Nyasaland [approximately 10° 30' S. 33° 52' E.].

1907. *Mus walambae* Wroughton, *Mem. Manchr. lit. phil. Soc.* **51**: 21. Msofu River, Rhodesia [close to 13° 30' S. 29° E.].

DESCRIPTION. Tail more hairy and the underside a darker grey than in *A. kaiseri*. Dorsal pelage a rich warm brown. Tail shorter in proportion to head-and-body length than *A. kaiseri*.

DISTRIBUTION. Kagambah, Mbarara, near Lake Nakivali, Ankole; Koki Co., Buganda; "Kigezi". Text-fig. 9.

MEASUREMENTS. Two ♂ h. & b. 159 mm., 162 mm.; tail 124 mm., 150 mm.; h. f. 28 mm., 28.5 mm.; ear 21 mm., 22 mm.; none weighed. ♀ h. & b. 167.9 mm. (7 meas., range 148 to 196 mm.); tail 138.4 mm. (7 meas., range, 131 to 151 mm.); h. f. 30.3 mm. (7 meas., range 28 to 33 mm.); ear 22.3 mm. (7 meas., range 20 to 24 mm.); none weighed.

BREEDING. Foetuses, in Zambia, (1 × 2), (1 × 4), (1 × 5) (Ansell, 1960).

HABITAT. In Zambia, usually in ant hills in woodland (Ansell, 1960).

BIOLOGY. No information available.

Genus *RATTUS* Fischer. House Rats

1803. *Rattus* [*sic*] Fischer, *Natmus. Naturg. Paris* 2 : 128. Genotype, by subsequent designation (Hollister, 1916, *Proc. biol. Soc. Wash.* 29 : 126), *Mus decumanus* Pallas = *Mus norvegicus* Berkenhout.

1881. *Epimys* Trouessart, *Bull. Soc. Sci. Angers* 10 : 117. As a subgenus of *Mus* Linnaeus ; genotype *Mus rattus* Linnaeus.



FIG. 9. Distribution of *Aethomys* spp.

Medium sized rats with incisor teeth ungrooved. Dorsal pelage not striped, rather long and slightly harsh ; varying shades of grey and brown. Underside varies in colour from creamy to dark slate, never pure white. No clear demarcation between flanks and belly. Tail usually longer than head and body, and uniformly dark coloured along length.

Rattus rattus (Linnaeus)

1758. *Mus rattus* Linnaeus, *Syst. Nat.*, 10th ed., 1 : 61. Uppsala, Sweden [59° 55' N. 18° 08' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Patiko, Acholi ; Gayoza, Kichwamba, Ankole ; Entebbe, Kampala, Mabira Forest, Masaka, Buganda ; Biso, Budongo Forest, Butiaba, Masindi Port, Bunyoro ; Iriri, Moroto, Namalu, Karamoja ; Nyakabande, Kigezi ; Kapiri, Serere, Teso ; Bundibugyo, Fort Portal, Isungu, Katwe, Mihunga, Muhokya, south east Ruwenzori, Toro ; Rhino Camp, West Nile. Probably occurs in all towns throughout Uganda. Text-fig. 10.

MEASUREMENTS. H. & b. ♂ 142.2 mm. (9 meas., range 109 to 193 mm.), 3 ♀ measured, 126 mm., 150 mm., 170 mm. ; tail ♂ 172.6 mm. (9 meas., range 148 to 198 mm.), ♀ 124 mm., 189 mm., 192 mm. ; h. f. ♂ 31.7 mm. (9 meas., range 31 to 33 mm.), ♀ 29 mm., ?, 33 mm. ; ear ♂ 21.3 mm. (9 meas., range 19 to 24 mm.), ♀ 21 mm., ?, 22.5 mm. ; weight ♂ 62.5 g. (5 weighed, range 47 to 92 g.), ♀ 58 g., 100 g., ?.

BREEDING. Breeding data from Kenya and Congo (Misonne, 1963) indicate that *Rattus* breeds throughout the year, with a peak during the long rains in the early part of the year and with a second smaller peak during the later rains. Breeding at a minimum during the dry seasons. The average number of foetuses in 54 pregnant females collected in Kampala was 6 (Hopkins MS.). Watson (1950) reports that the average number in a litter is 6 or 7 in Uganda. The young when born are blind with the external ears sealed down. The eyes open on the fourteenth day, weaning takes place about a month after birth. The gestation period is 21 days.

HABITAT. Essentially a dweller in huts and houses ; when found in open usually in close proximity to buildings. Generally found in thatch of huts, but occasionally may be found in the walls and floor.

BIOLOGY. Exclusively nocturnal. Omnivorous, food includes all kinds of grain, groundnuts, cotton seed, meat, potatoes etc. Competes with *Mastomys*, the other commensal rat, which it has now excluded from most towns. It is a vector of the flea *Xenopsilla* and there is no doubt that it is also the principle vector of plague in Uganda (Hopkins MS.). Allen & Loveridge (1942) report that predators include the owl (*Bubo africanus*), brown house snake (*Boaedon lineatus*), gaboon viper (*Bitis gabonica*), nose-horned viper (*Bitis nasicornis*) and the black-necked cobra (*Naja nigricollis*).

Genus *PRAOMYS* Thomas. Soft-furred Rats

1915. *Praomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 15: 477. As a subgenus of *Epimys* Trouessart = *Rattus* Fischer; genotype, by original designation, *Epimys tullbergi* (Thomas).

Similar to *Mastomys* with fur of silky texture; tail appreciably longer and only three pairs of mammae present. Tail almost naked. Fur brown to black dorsally, greyish white ventrally.



FIG. 10. Distribution of *Rattus rattus* and *Praomys morio*.

Praomys morio (Trouessart)

1881. *Mus morio* Trouessart, *Bull. Soc. Sci. Angers* **10**: 121. Cameroon Mountains [4° 13' N. 9° 10' E.].
 1897. *Mus jacksoni* de Winton, *Ann. Mag. nat. Hist.*, (6) **20**: 318. Entebbe.

DESCRIPTION. As for genus.

DISTRIBUTION. Maramagambo, Kalinzu Forests, Ankole; Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kisimbiri, Lunyo Forest, Malabigambo Forest, Mpanga Forest, Nabugabo, Zika Forest, Buganda; Budongo, Bugoma Forests, Bunyoro; Echuya, Impenetrable Forests, Kumba, Kigezi; Benet, Sebei; Bundibugyo, Bwamba, Kimara, Makoga, Mihunga, Mongiro, Mpanga Forest, Mubuku Valley, Wasa River, Toro. Text-fig. 10.

MEASUREMENTS. H. & b. ♂ 119.9 mm. (50 meas., range 97 to 140 mm.), ♀ 115.3 mm. (45 meas., range 95 to 135 mm.); tail ♂ 138.4 mm. (49 meas., range 121 to 160 mm.), ♀ 136.1 mm. (45 meas., range 94 to 160 mm.); h. f. ♂ 25.0 mm. (43 meas., range 22 to 27 mm.), ♀ 24.2 mm. (41 meas., range 21 to 27 mm.); ear ♂ 17.5 mm. (43 meas., range 15 to 20 mm.), ♀ 17.4 mm. (39 meas., range 15 to 19 mm.); weight ♂ 44.1 g. (40 weighed, range 21 to 57 g.), ♀ 37.0 g. (40 weighed, range 21 to 55 g.).

BREEDING. Foetuses (1 × 5 lactating) Oct. Echuya; (1 × 3) Sep. Chambura; (1 × 5), (1 × 4 lactating) Sep. Maramagambo. Three lactating, Mpanga (Buganda), May. Litters 2 to 6, normally 3 or 4 (Hopkins MS.). Foetuses (1 × 5) in Zambia.

HABITAT. Typically medium and high altitude forest.

BIOLOGY. Nocturnal. Omnivorous; plant and insect remains found in stomachs.

Genus *HYLOMYSCUS* Thomas. Climbing Wood-mice

1926. *Hylomyscus* Thomas, *Ann. Mag. nat. Hist.*, (9) **17**: 178. Genotype, by original designation, *Epimys aeta* Thomas.

The climbing mice are small with the tail always longer than the head-and-body length; they are very like *Praomys*. They differ from the latter in their smaller size and in the hind foot rarely attaining a length of 22 mm. whereas in *Praomys* it is always at least 22 mm.

Underside whitish grey with buff, flanks grey to dull brown	<i>H. denniae</i>
Underside white or silvery grey, flanks rich buff	<i>H. stella</i>

Hylomyscus denniae (Thomas)

1906. *Mus denniae* Thomas, *Ann. Mag. nat. Hist.*, (7) **18**: 144. Mubuku Valley, Toro.

DESCRIPTION. Dorsal surface grey to buff, the fur soft and rather woolly. Underside whitish grey touched with buff, well demarcated from the flanks. Tail longer than head and body.

DISTRIBUTION. Mpanga Forest, Buganda; Impenetrable Forest, Kigezi; Mubuku Valley, Toro. Kokanjiro. Text-fig. 11.

MEASUREMENTS. H. & b. ♂ 89.8 mm. (21 meas., range 71 to 103 mm.), ♀ 87.2 mm. (14 meas., range 76 to 99 mm.); tail ♂ 125.6 mm. (21 meas., range 84 to 154 mm.), ♀ 121.2 mm. (14 meas., range 97 to 145 mm.); h. f. ♂ 20.1 mm. (21 meas., range 18 to 22 mm.), ♀ 19.7 mm. (14 meas., range 18 to 21.5 mm.); ear ♂ 16.9 mm. (21 meas., range 13 to 21 mm.), ♀ 15.4 mm. (14 meas., range 13 to 20 mm.); weight ♂ 17.3 g. (12 weighed, range 8 to 24 g.), ♀ 20.0 g. (11 weighed, range 12 to 42 g.).

BREEDING. No data available. Large numbers of males with small testes suggesting large juvenile population in October in Kigezi.

BIOLOGY. No information available.



FIG. 11. Distribution of *Hylomyscus denniae*, *H. stella* and *Myomys fumatus*.

Hylomyscus stella (Thomas)

1911. *Rattus stella* Thomas, *Ann. Mag. nat. Hist.*, (8) 7 : 590. Between Mawambi and Avakubi, Ituri, E. Congo [between 1° 00' N. 28° 55' E. and 1° 18' N. 27° 32' E.].

DESCRIPTION. Slightly larger in size than *H. denniae*; upperside and flanks a bright ochraceous colour; underside a whitish or silvery grey colour well demarcated from the flanks. Tail longer than head and body.

DISTRIBUTION. Kalinzu Forest, Maramagambo Forest, Ankole; Mabira Forest, Malabigambo Forest, Mpanga Forest, Zika Forest, Buganda; Bwamba, Toro. Text-fig. II.

MEASUREMENTS. H. & b. ♂ 98.3 mm. (6 meas., range 89 to 104 mm.), ♀ 90.3 mm. (7 meas., range 85 to 101 mm.); tail ♂ 125.3 mm. (6 meas., range 121 to 133 mm.), ♀ 131.9 mm. (7 meas., range 111 to 140 mm.); h. f. ♂ 17.8 mm. (5 meas., range 17 to 19 mm.), ♀ 18.0 mm. (7 meas., range 17 to 20 mm.); ear ♂ 15.0 mm. (5 meas., range 14 to 16 mm.), ♀ 15.1 mm. (7 meas., range 14 to 16 mm.); weight ♂ 18.6 g. (6 weighed, range 16 to 23.5 g.), ♀ 17.4 g. (7 weighed, range 15 to 22 g.).

BREEDING. Hatt (1940) reports a female from the Congo containing three embryos.

HABITAT. Typically found in rain forest, especially around the bases of trees.

BIOLOGY. No information available.

Genus *MYOMYS* Thomas. African Meadow Rats

1915. *Myomys* Thomas, *Ann. Mag. nat. Hist.*, (8) 16 : 447. As a subgenus of *Epimys* Trouessart = *Rattus* Fischer; type, by original designation, *Epimys colonus* (Smith) = *Mus colonus* Brants.

The meadow rats have a similar dorsal coloration to *Mastomys* but are smaller in size; the tail is longer than the head and body; the underside is pure white.

Myomys fumatus (Peters)

1878. *Mus fumatus* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1878 : 200. Ukamba, Kenya [1°-2° S. 37°-38° E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Fort Patiko, Acholi; Kotido, Nakiloro, Karamoja. Text-fig. II.

MEASUREMENTS. H. & b. ♂ 98.0 mm. (5 meas., range 88 to 105 mm.), two ♀ 75 mm., 103 mm.; tail ♂ 126.4 mm. (5 meas., range 110 to 150 mm.), ♀ 97 mm., 130 mm.; h. f. ♂ 21.8 mm. (5 meas., range 21 to 24 mm.), ♀ 20 mm., 21 mm.; ear ♂ 16.2 mm. (5 meas., range 14 to 18 mm.), ♀ 13 mm., 14 mm.; weights ♂ 30.4 g. (5 weighed, range 24 to 35 g.), ♀ 12 g., 31 g.

BREEDING. No information available.

HABITAT. Dry savanna.

BIOLOGY. No information available.

Genus *MASTOMYS* Thomas. Multimammate Rats

1915. *Mastomys* Thomas, *Ann. Mag. nat. Hist.*, (8) **16** : 477. As a subgenus of *Epimys* Trouesart = *Rattus* Fischer ; type by original designation, *Epimys coucha* Smith = *Mus mariquensis* Smith, a race of *Mus natalensis* Smith.

The multimammate rats have no distinctive markings being very like *Praomys* in general appearance. The colour of the dorsal pelage is very variable, usually a grey-brown, but melanic specimens, entirely coal-black are common, especially in Kigezi. The underside is also of very variable colour ranging from a silvery grey to a pale grey touched with buff. The fur is distinctly soft and silky. Tail generally shorter than head and body. Female with teats in a continuous row, numbering up to 12 pairs, not divided into pectoral and inguinal sets.

Mastomys natalensis Smith

1834. *Mus natalensis* Smith, *S. Afr. quart. J.* **2** : 156. "About Port Natal" = Durban, Natal [29° 53' S. 31° 00' E.]. The nomenclature of this species is very confusing ; Swynerton & Hayman (1950) argue cogently in favour of the use of the specific name *coucha* Smith.

1836. *Mus coucha* Smith, *Rept, Exp. C. Afr.* : 43. 'The country between the Orange River and the Tropic' of Capricorn.

1897. *Mus ugandae* De Winton, *Ann. Mag. nat. Hist.*, (6) **20** : 377. Entebbe, Buganda.

1923. *Rattus somereni* Kershaw, *Ann. Mag. nat. Hist.*, (9) **11** : 594. Kaborini, Bukedi.

DESCRIPTION. As for genus.

DISTRIBUTION. Fort Fatiko, Gulu, Kitgum, Pamdero, Paraa, Acholi ; Burumba, Kichwamba, north of Maramagambo Forest, Ankole ; Chagwe, Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kikonda, Kisimbiri, Kisingo, Lialo, Mabira Forest, Mengo, Mubende, Buganda ; Kabaroni Camp, Mbale, Bugisu ; Busia, Tororo, Bukedi ; Fadjao, Hoima, Masindi, Bunyoro ; Isegero, Kama Island, Busoga ; Amudat, Irimi, Kamchuru, Kotido, Moroto, Nabilatuk, Nakiloro, Namalu, Karamoja ; Kumba, Kigezi ; Kacheba, Kibusi, Ngai, Lango ; Ajeluk, Serere, Teso ; Bundibugyo, Crater Track, Kamulikwezi, Kimara, Makoga, Mubuku Valley, Mweya, Wasa River, Toro ; Login, Rhino Camp, Vurra, Yumbe, West Nile. Usaga. Text-fig. 12.

MEASUREMENTS. H. & b. ♂ 122·8 mm. (57 meas., range 90 to 154 mm.), ♀ 125·1 mm. (53 meas., range 95 to 148 mm.) ; tail ♂ 112·3 mm. (57 meas., range 88 to 150 mm.), ♀ 114·0 mm. (52 meas., range 95 to 135 mm.) ; h. f. ♂ 23·7 mm. (59 meas., range 18 to 30 mm.), ♀ 23·3 mm. (49 meas., range 20 to 27 mm.) ; ear ♂ 16·6 mm. (58 meas., range 14 to 24 mm.), ♀ 16·8 mm. (50 meas., range 11 to 21 mm.) ; weight ♂ 48·0 g. (32 weighed, range 23 to 70 g.), ♀ 44·6 g. (34 weighed, range 20 to 60 g.).

BREEDING. Female with 2 or 3 embryos Jul., Murchison Falls National Park. Two females lactating Jun. and Jul. from Mweya and Tororo respectively. Hopkins (MS.) states that number of embryos varies between 3 and 12, but 16 has been recorded. First litters are usually small, young females frequently containing 2 to 4 foetuses. In Tanzania, Chapman, Chapman & Robertson (1959) note that the popu-

lation drops to a minimum at the end of the dry season and that breeding is at its maximum towards the end of the rains. Large catches from Uganda in the dry season and not in breeding condition confirm this.

HABITAT. Practically in all types of habitat including buildings, swamps and cultivation. It was formerly the prevalent hut-rat throughout Uganda until driven out by the invading *Rattus rattus*.

BIOLOGY. Nocturnal. Omnivorous, plant remains were the commonest material observed in the stomachs ; seeds and insects have been observed. The species is a



FIG. 12. Distribution of *Mastomys natalensis*.

good burrower and climber although less active than *R. rattus*. Nests in burrows. This species is a vector of the flea *Xenopsylla* and in the past has been an efficient vector of plague. The gaboon viper (*Bitis gabonica*) has been observed to prey on it (Allen & Loveridge, 1942).

Genus **MALACOMYS** Milne-Edwards. Swamp Rats

1877. *Malacomys* Milne-Edwards, *Bull. Soc. philom. Paris* 12: 10. Genotype, by original designation, *Malacomys longipes* Milne-Edwards.

The swamp rats are characterized by the great elongation of the hind feet. The metatarsals are loosely held together so as to splay out on soft ground. The tail is longer than the head and body; the underside of the body is greyish.

Malacomys longipes Milne-Edwards

1877. *Malacomys longipes* Milne-Edwards, *Bull. Soc. philom. Paris* 13: 9. Gaboon River, West Africa [approximately 0° 10' N. 10° 00' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Kalinzu Forest, Ankole; Kabanyolo, Mpanga Forest, Zika Forest, Buganda; Mpanga Forest, Toro. Text-fig. 13.

MEASUREMENTS. H. & b. ♂ 154.2 mm. (11 meas., range 120 to 172 mm.), ♀ 155.6 mm. (14 meas., range 127 to 183 mm.); tail ♂ 172.6 mm. (12 meas., range 158 to 190 mm.), ♀ 165.9 mm. (14 meas., range 151 to 186 mm.); h. f. ♂ 38.2 mm. (11 meas., range 35.5 to 40 mm.), ♀ 37.6 mm. (14 meas., range 35 to 40 mm.); ear ♂ 24.2 mm. (11 meas., range 21 to 29 mm.), ♀ 23.2 mm. (14 meas., range 19 to 28 mm.); weight ♂ 94.4 g. (9 weighed, range 65 to 120 g.), ♀ 93.3 g. (13 weighed, range 50 to 130 g.).

BREEDING. Foetuses (1 × 3) reported from Congo (Hopkins MS.); Ansell (1960) reports (1 × 3) from Zambia.

HABITAT. Wetter parts of forests.

BIOLOGY. Believed to be nocturnal. Omnivorous; food includes vegetable matter, insects, slugs and toads (Hopkins MS.). Makes a grass nest on the ground, also a climber (Misonne, 1963).

Genus **ZELOTOMYS** Osgood. Broad-headed Mice

1910. *Zelotomys* Osgood, *Publ. Field Mus. Nat. Hist., Zool.*, ser. 10, no. 2: 7. Genotype *Mus hildegardeae* Thomas.

Medium sized with distinctly pro-odont upper incisors. Dorsal pelage grey-brown, individual hairs with grey bases and brown tips. Backs of hands and feet brown. Tail covered in scales; hairs very sparse; appreciably shorter than length of head and body.

Zelotomys hildegardae (Thomas)

1902. *Mus hildegardae* Thomas, *Ann. Mag. nat. Hist.*, (7) 9: 219. Machakos, Kenya [$1^{\circ} 31' S.$ $37^{\circ} 15' E.$].

DESCRIPTION. As for genus.

DISTRIBUTION. Between Rwempuno and Kaizi Rivers, Ankole; Crater Track, Toro. Text-fig. 13.

MEASUREMENTS. Two ♂ h. & b. 124 mm., 120 mm., two ♀ 129 mm., 136 mm.; tail ♂ 89 mm., 86 mm., ♀ 92 mm., 90 mm.; h. f. ♂ 22 mm., 25 mm., ♀ 21 mm., 22 mm.; ear ♂ 15 mm., 13 mm., ♀ 15 mm., 13 mm.; weights ♂ 64 g., 57 g., ♀ 56 g., 64 g.



FIG. 13. Distribution of *Malacomys longipes* and *Zelotomys hildegardae*.

BREEDING. Foetuses (1 × 5) Jul., Crater Track.

HABITAT. *Imperata* grassland and scrub.

BIOLOGY. Examination of stomachs of four animals indicates an insectivorous diet.

Genus *MUS* Linnaeus

1758. *Mus* Linnaeus, *Syst. Nat.*, 10th ed. 1 : Genotype *Mus musculus* Linnaeus.

1837. *Leggada* Gray, *Charlesworth's Mag. nat. Hist.*, 1 : 586. Genotype *Leggada booduga* Gray.

The forms of this genus are all small mice (head-and-body length usually under 90 mm.), with the tail almost always shorter than the head and body. The fur is fairly soft but also quite crisp, falling back stiffly into place after being ruffled. We have included *grata* and *tenellus* with the species *minutoides*.

1	Underside grey or tinged with buff	2
	Underside pure white or nearly so; very small size	<i>M. minutoides</i>
2	Underside grey	<i>M. triton</i>
	Underside grey tinged with buff	<i>M. bufo</i>

Mus bufo (Thomas)

1906. *Leggada bufo* Thomas, *Ann. Mag. nat. Hist.*, (7) 81 : 145. Mubuku Valley, Toro.

DESCRIPTION. Large dark species with underside well washed with ochraceous-buff. Bases of belly hairs slate grey. General colour above dark coppery brown. Tail shorter than head and body.

DISTRIBUTION. Echuya Swamp, Echuya Forest, Impenetrable Forest, Kumba, Kigezi; Mihunga, Mubuku Valley, Toro. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 72.3 mm. (11 meas., range 68 to 79 mm.), ♀ 68.9 mm. (9 meas., range 61 to 73 mm.); tail ♂ 62.1 mm. (11 meas., range 53 to 69 mm.), ♀ 63.2 mm. (9 meas., range 56 to 68 mm.); h. f. ♂ 16.3 mm. (11 meas., range 15 to 18 mm.), ♀ 15.6 mm. (9 meas., range 13.5 to 16.5 mm.); ear ♂ 10.8 mm. (11 meas., range 9 to 12 mm.), ♀ 11.9 mm. (9 meas., range 10 to 13 mm.); weight ♂ 9.1 g. (8 weighed, range 7 to 12 g.), ♀ 9.3 g. (3 weighed, range 7 to 12 g.).

BREEDING. No data available.

HABITAT. Caught in bamboo, moist montane forest and at edge of sedge swamp.

BIOLOGY. No information available.

Mus minutoides Smith

1834. *Mus minutoides* Smith, *S. Afr. quart. J.* 2 : 157. Cape Town [33° 56' S. 18° 28' E.].

1910. *Leggada grata* Thomas & Wroughton, *Trans. zool. Soc. Lond.* 19 : 507. Mubuku Valley, Toro.

1911. *Mus tenellus* Heller, *Smithson. misc. Coll.* 56 : 6. Rhino Camp, West Nile.

1911. *Mus bellus* Heller, *Smithson. misc. Coll.* 56 : 8. Rhino Camp, West Nile.

1911. *Mus musculoides* Heller, *Smithson. misc. Coll.* 56 : 28. Kabulamuliro, Buganda.

DESCRIPTION. Small species with pure white underside.

DISTRIBUTION. Paraa, Acholi; Congo Road, Kalinzu Forest, Lutoto, Maramagambo Forest, north of Maramagambo Forest, Ankole; Kabanyolo, Kabulamuliro, Kampala, Kikandwa, Kikonda, Kisimbiri, Kisingo, Lunyo, Mpanga Forest, Nabugabo, Nkyanuna, Buganda; Butiaba, Hoima, Kajuia, Masindi, Bunyoro; Lotome, Moroto, Nabilatuk, Karamoja; Echuya Swamp, Kigezi; Crater Track, Mweya, Mihunga, Mubuku Valley, Toro; Rhino Camp, Wadelai, West Nile. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 60.6 mm. (13 meas., range 45 to 76 mm.), ♀ 60.8 mm. (11 meas., range 49 to 77 mm.); tail ♂ 43.8 mm. (12 meas., range 35 to 54 mm.), ♀ 45.5 mm. (11 meas., range 35 to 63 mm.); h. f. ♂ 13.1 mm. (10 meas., range 12 to



FIG. 14. Distribution of *Mus* spp.

14.5 mm.), ♀ 13.1 mm. (8 meas., range 12 to 14 mm.); ear ♂ 9.7 mm. (9 meas., range 8 to 11 mm.), ♀ 8.7 mm. (8 meas., range 7 to 10 mm.); weight ♂ 6.4 g. (7 weighed, range 4 to 10 g.), ♀ 5.9 g. (9 weighed, range 2.5 to 10 g.).

BREEDING. Foetuses (1 × 5) Jul. Mpanga, (1 × 4) Aug. Maramagambo Forest, (1 × 4) Nov. Moroto. Allen & Loveridge (1942) report (1 × 7) foetuses and groups of 3, 6, 7 and 8 blind nestlings in Tanzania. Ansell (1960) reports (1 × 3) well developed foetuses and groups of 4 and 5 juveniles from Zambia.

HABITAT. Very varied ranging from dry sandy ground to forest.

BIOLOGY. Nocturnal. Makes shallow burrows with a bed of grass in the bottom. Predators include the brown house snake (*Boaedon lineatus*), the burrowing viper (*Atractaspis bibroni*), mamba (*Dendraspis* sp.) and viper (*Atheris nischei*). Omnivorous, the stomachs containing leaves, seeds and insect remains.

Mus triton (Thomas)

1909. *Leggada triton* Thomas *Ann. Mag. nat. Hist.*, (8) 4: 548. Kirui, southern foothills of Mt. Elgon, Kenya [approximately 0° 45' N. 34° 40' E.].

DESCRIPTION. Differs from *Mus bufo* in the belly fur not being tinged with buff and the tail being appreciably shorter.

DISTRIBUTION. Kichwamba, Lutoto, north of Maramagambo Forest, Ankole; Entebbe, Kikandwa, Kisimbiri, Masaka, Buganda; Siroko Valley, Bugisu; Masindi Port, Bunyoró; Echuya Swamp, Ingezi, Kigezi; north Ruwenzori, Toro. Text-fig. 14.

MEASUREMENTS. H. & b. ♂ 78.3 mm. (11 meas., range 57 to 93 mm.), ♀ 73.8 mm. (10 meas., range 66 to 85 mm.); tail ♂ 48.5 mm. (10 meas., range 42 to 53 mm.), ♀ 46.8 mm. (9 meas., range 44 to 48 mm.); h. f. ♂ 15.4 mm. (11 meas., range 14 to 19 mm.), ♀ 14.9 mm. (9 meas., range 14 to 16 mm.); ear ♂ 10.6 mm. (9 meas., range 9 to 12 mm.), ♀ 10.7 mm. (9 meas., range 9 to 11 mm.); weight ♂ 11.4 g. (9 weighed, range 10 to 13 g.), ♀ 9.4 g. (9 weighed, range 7 to 13 g.).

BREEDING. No data available.

HABITAT. Found in grassland, heath and scrub principally in wetter areas.

BIOLOGY. Nocturnal. Makes nests of both fine and coarse rootlets and leaves of grass. Loveridge (1953) reports that the brown house snake (*Boaedon lineatus*) is a predator.

Genus *LOPHUROMYS* Peters. Harsh-furred Mice

1866. *Lasiomys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1866: 409. Genotype = *Mus sikapusi* Temminck. Not *Lasiomys* 1854, in Mammalia (Octodontidae).

1874. *Lophuromys* Peters, *Mber. preuss. Akad. Wiss. Berl.* 1874: 234. *Lasiomys afer* Peters = *Mus sikapusi* Temminck. To replace *Lasiomys* Peters, preoccupied.

The texture of the fur is very characteristic. It is smooth, sleek, stiff and brush-like. This is particularly obvious when the fur is stroked against the lie of the hairs.

Dorsally the fur is red to brown whilst the underside is rather paler in colour. Ellerman, Morrison-Scott & Hayman (1953) list two species of short-tailed *Lophuromys* both of which occur in Uganda. In addition, two species of long-tailed *Lophuromys* have been described from mountainous regions of western Uganda but as they are obviously very similar they are included here under *L. woosnami* which is the prior name.

1	Tail short, usually less than 80 mm.	2
	Tail long, usually more than 100 mm.	<i>L. woosnami</i>
2	Fur finely speckled	<i>L. flavopunctatus</i>
	Fur not speckled	<i>L. sikapusi</i>

Lophuromys flavopunctatus Thomas

1888. *Lophuromys flavo-punctatus* Thomas, *Proc. zool. Soc. Lond.* **1888**: 14. Shoa, Ethiopia (probably obtained at Ankober [9° 32' N. 39° 43' E.], Thomas, 1903, *Proc. zool. Soc. Lond.*, **1902**: 314).

1892. *Mus aquilus* True, *Proc. U.S. nat. Mus.*, **15**: 460. Kilimanjaro, Tanzania [3° 00' S. 37° 25' E.].

DESCRIPTION. Dorsal fur dark brown-red speckled with yellow or buff. Belly buff washed with red, overall effect buffy-pink.

DISTRIBUTION. Burumba, Lutoto, Kalinzu and Maramagambo Forests, between Rwempuno and Kaizi Rivers, Ankole; Entebbe, Kabanyolo, Kabulamuliro, Kampala, Kikonda, Kisingo, Lialo, Mabira Forest, Nabugabo, Nalweyo, Zika Forest, Buganda; Hoima, Bunyoro; Echuya Forest, Echuya Swamp, Impenetrable Forest, Nyakabande, Kigezi; Bundibugyo, Mihunga, Mpanga Forest, Mubuku Valley, Toro; Rhino Camp, West Nile. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 125.3 mm. (18 meas., range 117 to 141 mm.), ♀ 125.0 mm. (20 meas., range 112 to 144 mm.); tail ♂ 62.8 mm. (17 meas., range 46 to 69 mm.), ♀ 62.6 mm. (19 meas., range 55 to 94 mm.); h. f. ♂ 20.3 mm. (17 meas., range 19 to 21 mm.), ♀ 20.1 mm. (18 meas., range 18 to 21 mm.); ear ♂ 15.2 mm. (15 meas., 13 to 17 mm.), ♀ 15.5 mm. (18 meas., range 14 to 18 mm.); weight ♂ 52.0 g. (18 weighed, range 40 to 62 g.), ♀ 46.1 g. (18 weighed, range 36 to 56 g.).

BREEDING. Foetuses (2 × 3) Jun. Entebbe; (4 × 2) Sep. Echuya. Embryos near full term weigh 4-5 g. Ansell (1960) reports 3 embryos from Zambia. Litter size 1 to 4 (average 2.4) of 43 gravid females examined in Malawi (Hanney, 1964). Allen & Loveridge (1942) report foetuses (1 × 4) from Tanzania and (1 × 3) from Congo.

HABITAT. Moist situations in scrub and forest; recorded at altitudes up to 12,000 ft.

BIOLOGY. Diurnal and nocturnal. Omnivorous, mainly arthropods; slugs, snails, seeds, worms, frogs or toads and birds also recorded. Nests at base of grass tussocks (Hanney, 1964). Numerous scars on back of Mabira specimens.

Lophuromys sikapusi Temminck

1853. *Mus sikapusi* Temminck, *Esq. Zool. Cote de Guine* : 160. Dabacrom, Ghana [$7^{\circ} 40' N$, $2^{\circ} 58' W$].

1911. *Lophuromys pyrrhus* Heller, *Smithson, misc. Coll.* **56** : 10. Rhino Camp, West Nile.

DESCRIPTION. Dorsal fur a rich red-brown without any form of speckling. Underside usually a richer red than *L. flavopunctatus*. Tail short.

DISTRIBUTION. Kagambah, Kichwamba, between Rwempuno and Kaizi Rivers, Rutanda, Ankole ; Entebbe, Kampala, Mpanga Forest, Buganda ; Bubungi,



FIG. 15. Distribution of *Lophuromys* spp.

Lwakaka, Bugisu ; Butiaba, Bunyoro ; Jinja, Busoga ; Nyalasanje, Kigezi ; Moyo, Madi ; Serere, Teso ; Bwamba, Crater Track, Kamulikwezi Swamp, Fort Portal, Ruwenzori, Wasa River, Toro ; Rhino Camp, West Nile. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 133·1 mm. (27 meas., range 100 to 153 mm.), ♀ 136·6 mm. (16 meas., range 105 to 159 mm.) ; tail ♂ 71·6 mm. (26 meas., range 49 to 91 mm.), ♀ 72·7 mm. (16 meas., range 56 to 82 mm.) ; h. f. ♂ 23·0 mm. (27 meas., range 20 to 25 mm.), ♀ 22·8 mm. (16 meas., range 21 to 24 mm.) ; ear ♂ 14·8 mm. (23 meas., range 12 to 17·5 mm.), ♀ 14·1 mm. (13 meas., range 12 to 16 mm.) ; weight ♂ 76·8 g. (20 weighed, range 50 to 104 g.), ♀ 79·0 g. (14 weighed, range 43 to 100 g.).

BREEDING. Foetuses (1 × 2) Aug. Kichwamba. Two ♀ lactating Jul. Q. E. P. Usually 2 to a litter (Watson, 1950).

HABITAT. Heavily grassed bush country.

BIOLOGY. Diurnal and nocturnal. Examination of contents of 37 stomachs suggests that ants form major food. Insectivorous.

Lophuromys woosnami Thomas

1906. *Lophuromys woosnami* Thomas, *Ann. Mag. nat. Hist.*, (7) 18 : 146. Mubuku Valley, Toro.

1911. *Lophuromys prittieii* Thomas, *Ann. Mag. nat. Hist.*, (8) 8 : 377. Mufumbiro region, Kigezi.

DESCRIPTION. Easily separated from the other two species by its relatively long tail. The dorsal fur is not as richly coloured as in the other species tending to be rather more grey-brown. The speckling is sparse or absent. Underside without trace of pink or red and much more grey to brown.

DISTRIBUTION. Echuya Swamp, Impenetrable Forest, Muhavura, Kigezi ; Mihunga, Mubuku Valley, north Ruwenzori, Toro. Text-fig. 15.

MEASUREMENTS. H. & b. ♂ 118·0 mm. (5 meas., range 114 to 126 mm.), ♀ 107·2 mm. (11 meas., range 84 to 123 mm.) ; tail ♂ 113·0 mm. (5 meas., range 110 to 117 mm.), ♀ 107·1 mm. (11 meas., range 97 to 118 mm.) ; h. f. ♂ 23·6 mm. (5 meas., range 22 to 25 mm.), ♀ 23·1 mm. (11 meas., range 22·5 to 26 mm.) ; ear ♂ 19·0 mm. (5 meas., range 19 to 23 mm.), ♀ 19·1 mm. (11 meas., range 17 to 22 mm.) ; weight ♂ 45 g. (1 weighed), ♀ 36·5 g. (7 weighed, range 23 to 48 g.).

BREEDING. Foetuses (1 × 2) Sep. Echuya ; (2 × 2) Oct., Impenetrable.

HABITAT. Obtained in moist situations in scrub and forest at altitudes of 6,000 to 8,200 feet.

Genus *ACOMYS* Geoffroy. Spiny Mice

1838. *Acomys* Geoffroy, *Ann. Sci. nat. Zool.* 10 : 126. Genotype, by monotypy, *Mus cahirinus* Desmarest.

The spiny mice are small mice characterized by having the hair of the dorsal surface converted into coarse spines. They inhabit arid semi-desert country. Two species

have been collected in Karamoja from apparently similar types of habitat. Tail hard and scaly. Incisors ungrooved.

Dorsal pelage uniform grey-brown not speckled	<i>A. percivali</i>
Dorsal pelage speckled light and dark brown	<i>A. wilsoni</i>

Acomys percivali Dollman

1911. *Acomys percivali* Dollman, *Ann. Mag. nat. Hist.*, (8) 8: 126. Chanler Falls, N. Guaso Nyiro, Kenya [0° 47' N. 38° 03' E.].

DESCRIPTION. Dorsal pelage uniform grey-brown, tail relatively long, hind foot large.

DISTRIBUTION. Kotido, Namalu, Karamoja. Text-fig. 16.

MEASUREMENTS. Two ♂ h. & b. 82 mm., 94 mm.; tail 67 mm., 84 mm.; h. f. 15 mm., 15 mm.; ear 11 mm., ?; weights 19 g., 5 g. Two ♀ h. & b. 93 mm., 74 mm.; tail 79 mm., 48 mm.; h. f. 14 mm., 14 mm.; ear 12 mm., 11 mm.; weights 33 g., 11 g.

BREEDING. Foetuses (1 × 1) Nov. Kotido.

HABITAT. Dry savanna, semi-desert.

BIOLOGY. No information available.

Acomys wilsoni Thomas

1892. *Acomys Wilsoni* Thomas, *Ann. Mag. nat. Hist.*, (6) 10: 22. Mombasa, Kenya [4° 3' S. 39° 40' E.].

DESCRIPTION. Dorsal pelage annulated light and dark brown; annulations may tend to disappear posteriorly. Tail short; hind foot small.

DISTRIBUTION. Amudat, Kachere, Lorengikipi, Lotome, Manimani, Moroto Forest, Nabilatuk, Karamoja. Text-fig. 16.

MEASUREMENTS. Two ♂ h. & b. 87 mm., 83 mm.; tail 43 mm., 45 mm.; h. f. 12 mm., 13 mm.; ear 10 mm., 10 mm.; weights, 22 g., 21 g. Three ♀ 96 mm., 86 mm., 84 mm.; tail 48 mm., 47 mm., 41 mm.; h. f. 13 mm., 14 mm., 13 mm.; ear 12 mm., 10 mm., 10 mm.; weights 25 g., 27 g., 19 g.

BREEDING. Foetuses (1 × 2) Oct. Nabilatuk, (1 × 1) Nov. Moroto, (1 × 3) Nov. Amudat.

HABITAT. Dry savanna semi-desert. Watson (1950) only found it in less arid parts or alongside rivers.

BIOLOGY. No information available.

Genus *URANOMYS* Dollman

1909. *Uranomys* Dollman, *Ann. Mag. nat. Hist.*, (8) 4:155. Genotype *Uranomys ruddi* Dollman.

Texture of fur brush-like; hairs harsh and long measuring about 17 mm. Back grey-brown paling to buff on sides and on upper surfaces of limbs. Nasal region and head darker than back. Similar to *Lophuromys* but distinguished from it by the pure white backs to the hands and feet (in *Lophuromys* they are at least tinged with black or brown). In *Uranomys* the belly fur is white and in *Lophuromys* brown, orange, red or grey. Upper incisors are orthodont in *Lophuromys* and slightly proodont in *Uranomys*.



FIG. 16. Distribution of *Acomys percivali*, *A. wilsoni* and *Uranomys ruddi*.

Uranomys ruddi Dollman

1909. *Uranomys ruddi* Dollman, *Ann. Mag. nat. Hist.*, (8) 4: 552. Kirui, southern foothills of Mt. Elgon, Kenya [approximately 0° 45' N. 34° 40' E.].
1911. *Uranomys ugandae* Heller, *Smithson. misc. Coll.* 56: 12. Kikonda, Buganda.

DESCRIPTION. As for genus.

DISTRIBUTION. Kikonda, Buganda; Lwakaka, Bugisu; Budama, Bukedi. Text-fig. 16.

MEASUREMENTS. Two ♀ h. & b. 104 mm., 95 mm.; tail 50 mm., 66 mm.; h. f. 17 mm., 16 mm.; ear 15 mm., 13 mm.

BREEDING. No information available.

HABITAT. No information available.

BIOLOGY. No information available.

Genus *SACCOSTOMUS* Peters. Pouched Mice

1846. *Saccostomus* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* 1846: 258. Genotype, by monotypy, *Saccostomus campestris* Peters.

Medium sized with long, soft, silky fur and a relatively short tail. Cheek pouches present. Grey dorsally with brown tinge in some specimens; paler on flanks; belly hairs with white tips and slate bases. Ears small and hairy; tail dark above, paler below. Backs of hands and feet white. Ellerman, Morrison-Scott & Hayman (1953) believe there is only one species in this genus.

Saccostomus campestris Peters

1846. *Saccostomus campestris* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* 1846: 258. Tete, Portugese East Africa [16° 10' S. 33° 35' E.].
1936. *Saccostomus cricetulus* Allen & Lawrence, *Bull. Mus. comp. Zool. Harv.* 79: 100. South bank of Greek River, Sebei.

DESCRIPTION. As for genus.

DISTRIBUTION. Amudat, Lotome, Moroto, Nabilatuk, Karamoja; Greek River, Sebei. Text-fig. 17.

MEASUREMENTS. H. & b. ♂ 116.0 mm. (4 meas., range 94 to 130 mm.), ♀ 144.9 mm. (7 meas., 127 to 157 mm.); tail ♂ 45.3 mm. (4 meas., range 34 to 55 mm.), ♀ 53.9 mm. (7 meas., range 50 to 58 mm.); h. f. ♂ 21.0 mm. (4 meas., range 19 to 25 mm.), ♀ 21.9 mm. (7 meas., range 21 to 22 mm.); ear ♂ 18.3 mm. (4 meas., range 14 to 25 mm.), 18.3 mm. (7 meas., range 16 to 20 mm.); weight ♂, 2 weighed, 24 g., 34 g., ♀ 65.2 g. (6 weighed, range 41 to 84 g.).

BREEDING. Foetuses (1 × 7) Nov. Amudat. Ansell (1960) reports (1 × 7, 1 × 6) from Zambia and Shortridge (1934) (1 × 8) from South West Africa.

HABITAT. Dry savanna. Attracted to cultivated areas.

BIOLOGY. Nocturnal, very slow moving. From contents of cheek pouches food apparently largely of seeds, grain, fruits and also occasionally, insects. Lives in burrows.

Genus *CRICETOMYS* Waterhouse. Giant Rats

1840. *Cricetomys* Waterhouse, *Proc. zool. Soc. Lond.* 1840 : 2. As a subgenus of *Mus* Linnaeus ; genotype, by original designation, *Cricetomys gambianus* Waterhouse.

Very large rat with head-and-body length usually exceeding 300 mm. The tail is longer than the head and body ; it has a dark proximal portion and a white distal portion. Cheek pouches are present.



FIG. 17. Distribution of *Saccostomus campestris* and *Cricetomys gambianus*.

Cricetomys gambianus Waterhouse

1840. *Cricetomys gambianus* Waterhouse, *Proc. zool Soc. Lond.* **1840**: 2. River Gambia, West Africa [13° 30' N. 13° 30'–16° 40' W.].

DESCRIPTION. As for genus.

DISTRIBUTION. Aiago River, Fort Patigo, Acholi; Kampala, Mabira Forest, Malabigambo Forest, Buganda; "Bunyoro"; Jinja, Busoga; Moroto, Namalu, Karamoja; Mt. Sabinio, Kigezi; Mt. Elgon, Sebei; Ngora Rest House, Ongino, Serere, near Soroti, Teso; Bundibugyo, Mihunga, Mongiro, Mubuku Valley, Toro. Text-fig. 17.

MEASUREMENTS. Two ♂ h. & b. 350 mm., 350 mm.; tail 380 mm., 418 mm.; h. f. 70 mm., 72 mm.; ear 37 mm., 42 mm. Two ♀ h. & b. 335 mm., 330 mm.; tail 370 mm., 390 mm.; h. f. 66 mm., 66 mm.; ear ? mm., 42 mm.; weight 910 g., ?.

BREEDING. Foetuses (1 × 1) Mt. Sabinio (Hopkins MS.); (1 × 1) Congo (Misonne, 1963); (1 × 4) Zambia (Ansell, 1960).

HABITAT. Ubiquitous, being found in rain forest, mountain forest, gallery forest and very dry savanna.

BIOLOGY. Strictly nocturnal. Herbivorous, feeding mainly on seeds of trees. They live in deep burrows in the ground and do serious damage to agriculture. It is reported that they often climb trees and shrubs in search of fruit. Infected with an ectoparasitic Dermapteran (*Hemimerus talpoides* Walker) peculiar to itself.

Subfamily **DENDROMURINAE** Allen

1939. Dendromurinae Allen, *Bull. Mus. comp. Zool. Harv.* **83**: 349.

Genus **DENDROMUS** Smith. African Tree Mice

1829. *Dendromus* Smith, *Zool. J.* **4**: 438. Genotype, by original designation, *Dendromus typus* Smith = *Mus mesomelas* Brants.

1830. *Dendromys* Fischer, *Synop. Anim. Add.*: 658. Substitute for *Dendromus* Smith.

1916. *Poemys* Thomas, *Ann. Mag. nat. Hist.*, (8) **18**: 238. As a subgenus of *Dendromus* Smith; type, by original designation, *Dendromus melanotis* Smith.

Small mice. The fore feet have three well-developed digits only; hind feet narrow with very short hallux and fifth digit nearly as long as second. There is often a single dark, dorsal stripe along the length of the body. The upper incisors are grooved. Bohmann's (1942) revision of the genus has been adopted together with Ellerman, Morrison-Scott & Hayman's (1953) use of the specific name *mystacalis* in place of *pumilio*.

- | | | |
|---|--|----------------------|
| 1 | No dorsal stripe | <i>D. mystacalis</i> |
| | Dark dorsal stripe running the length of the body | 2 |
| 2 | Small size; dorsal stripe broken to form spot on the head; tail shorter than h. & b.; hind foot less than 18 mm. | <i>D. melanotis</i> |
| | Larger size; dorsal stripe not broken to form a spot on the head; tail longer than h. & b.; hind foot more than 19 mm. | <i>D. mesomelas</i> |

Dendromus melanotis Smith

1834. *Dendromus melanotis* Smith, *S. Afr. quart. J.* **2**: 158. Near "Port Natal" = Durban, Natal [29° 53' S. 31° 00' E.].

1911. *Dendromus spectabilis* Heller, *Smithson. misc. Coll.* **56**: 3. Rhino Camp, West Nile.

DESCRIPTION. Colour of upper parts light brown, gradually turning a grey-brown on the sides to a pale grey on the under parts. A wide black median dorsal stripe runs from the shoulders to the base of the tail, widest anteriorly and narrowing gradually posteriorly. A median black spot occurs on the forehead between the ears and eyes. At the anterior base of the ears are a few white hairs and a larger white patch just below the ear. Hind foot less than 18 mm.

DISTRIBUTION. Hoima, Bunyoro; Mweya, Toro; Rhino Camp, West Nile. Text-fig. 18.

MEASUREMENTS. Three ♂ h. & b. 67 mm., 73 mm., 61 mm.; tail 65 mm., 68 mm., ?; h. f. 16 mm., 17 mm., 16 mm.; ear 13 mm., 12 mm., 11 mm.; weight 5 g., 7 g., 6 g. Two ♀ h. & b. 91 mm., 56 mm.; tail 67 mm., 64 mm.; h. f. 16 mm., 16 mm.; ear 10 mm., ?; weight 8 g., 7 g.

BREEDING. Foetuses (1 × 3) Jul. Mweya. Ansell (1960) reports (4 × 3, 4 × 4, 1 × 5, 4 × 6) from Zambia.

HABITAT. Found in short herbs where *D. mystacalis* is uncommon. Typically in dry savanna.

BIOLOGY. Nocturnal. Herbivorous, although Ansell (1960) reports that they also eat insects. Apparently nest in burrows in the ground in Zambia but in the Congo, Misonne (1963) reports that they build nests in herbs at heights ranging from 10 cm. to 1 m. above the ground. (Further information under *D. mystacalis*.)

Dendromus mesomelas (Brants)

1827. *Mus mesomelas* Brants, *Het Geslacht der Muizen*: 122. "Near Zondags River" (Sundays River, just east of Port Elizabeth, Eastern Cape Province) [approximately 33° 45' S. 25° 45' E.].

DESCRIPTION. Colour of upper parts light brown, the sides not grey-brown as in *D. melanotis*. Dorsal stripe distinctly narrower than in *D. melanotis*. No white patch as base of ears. Tail longer than head and body. Hind foot longer than 19 mm.

DISTRIBUTION. Echuya Swamp, Kumba, Kigezi; Mubuku Valley, Toro. Text-fig. 18.

MEASUREMENTS. H. & b. ♂ 80.8 mm. (4 meas., range 76 to 87 mm.), ♀ 81.3 mm. (3 meas., range 78 to 87 mm.); tail ♂ 89.8 mm. (4 meas., range 86 to 93 mm.), ♀ 97.0 mm. (3 meas., range 93 to 102 mm.); h. f. ♂ 21.0 mm. (4 meas., range 20 to 22 mm.), ♀ 21.0 mm. (3 meas., all 21 mm.); ear ♂ 12.5 mm. (4 meas., range 11 to 15 mm.), ♀ 13.0 mm. (3 meas., range 12 to 14 mm.); weight ♂ 13.7 g. (3 weighed, range 11 to 15 mm.), ♀ two weighed, 13 g., 15 g.

BREEDING. Allen & Loveridge (1942) record litters of 3 and 4 young.

HABITAT. Found in swamp and associated vegetation in Kigezi.

BIOLOGY. Ansell (1960) reports that they feed largely on grass seeds but are to some extent insectivorous. Live in tall grass in which they are arboreal; also semi-terrestrial. Misonne (1963) claims that they are often caught around villages in the Congo. Apparently less communal than *D. mystacalis* and *D. melanotis*.



FIG. 18. Distribution of *Dendromus* spp.

Dendromus mystacalis Heuglin

1863. *Dendromus mystacalis* Heuglin, *Nova Acta Leop. Carol.* **30**, art. 2. suppl. : 5. Ifag, east of Lake Tana, Ethiopia [$12^{\circ} 15' N.$ $37^{\circ} 45' E.$].

1911. *Dendromus lineatus* Heller, *Smithson, misc. Coll.* **56** : 4. Rhino Camp, West Nile.

DESCRIPTION. No dorsal stripe running the length of the body. Tail about one and a third times length of the head and body.

DISTRIBUTION. Buligi, Kampala, Kawenge, Buganda ; Budadin Camp, Bugisu ; Hoima, Kajuia, Masindi, Bunyoro ; Kamchuru, Karamoja ; Sebei Camp, Sebei ; Bubukwanga, Bugoye, Bumatta, Bummaddu, Bundibugyo, Bundimali, Fort Portal, Humya, Kyabombo, Mihunga, Tokwe, Toro ; Rhino Camp, West Nile. Text-fig. 18.

MEASUREMENTS. H. & b. ♂ 69.2 mm. (20 meas., range 59 to 68 mm.), ♀ 61.7 mm. (6 meas., range 50 to 73 mm.) ; tail ♂ 90.4 mm. (20 meas., range 81 to 101 mm.), ♀ 86.0 mm. (6 meas., range 75 to 95 mm.) ; h. f. ♂ 16.6 mm. (21 meas., range 14 to 19 mm.), ♀ 16.2 mm. (6 meas., range 16 to 17 mm.) ; ear ♂ 12.8 mm. (21 meas., range 10 to 14 mm.), ♀ 12.3 mm. (6 meas., range 10 to 13 mm.) ; weight ♂ 8.7 g. (15 weighed, range 7.5 to 10.5 g.), ♀ 7.6 g. (4 weighed, range 6.5 to 9 g.).

BREEDING. Normally 3 in a litter, occasionally 4 (Hopkins MS.). Foetuses (1 × 5) in Zambia (Ansell, 1960). Three naked, blind nestlings, Jan. Mihunga ; 4 juveniles Jan. Bugoye. Seven naked nestlings and 4 furred with eyes open in Tanzania (Allen & Loveridge, 1942). Juveniles in Zambia : (5 × 4, 1 × 6) (Ansell, 1960).

HABITAT. Common in banana shambas where the nests are usually among the leaf-bases (Hopkins MS.). Also in grass and amongst herbage.

BIOLOGY. Nocturnal and herbivorous. Quarrelsome and aggressive animals. *D. mystacalis* and *D. melanotis* fight constantly when placed together ; in the course of the fighting the subordinate animal puts itself on its back and defends itself ; *D. mesomelas* is the less aggressive. *Dendromus* walks with the first and fifth digits at right angles. *Dendromus* dominates *Mus minutoides* and *M. triton* when they are together. They climb easily, the tail is prehensile and their light weight allows them to scale the lighter herbage, where they may construct nests.

Genus *STEATOMYS* Peters. Fat Mice

1846. *Steatomys* Peters, *Ber. Verh. preuss. Akad. Wiss. Berl.* **1846** : 258. Genotype, by monotypy, *Steatomys pratensis* Peters.

The fat mice are small with relatively short tails. Their plump appearance is due to a layer of fat beneath the skin. Upper incisors grooved. Fur of the back light brown-fawn ; sharp line of demarcation between flanks and belly ; hairs of the latter pure white. Hairs of back grey with brown tips. Backs of hands and feet white. Tail brown above, white below, moderately haired.

Steatomys parvus Rhoads

1896. *Steatomys parvus* Rhoads, *Proc. Acad. nat. Sci. Philad.* 1896: 529. Reshiat, Lake Rudolf, Ethiopia [approximately 4° 33' N. 36° 00' E.].

DESCRIPTION. As for genus.

DISTRIBUTION. Lotome, Nabilatuk, Napyananya, Karamoja. Text-fig. 19.

MEASUREMENTS. Two ♂ h. & b. 59 mm., 60 mm.; tail 37 mm., 35 mm.; h. f. 13 mm., 15 mm.; ear 10 mm., 13 mm.; weight 5 g., ?.

BREEDING. No information available.

HABITAT. Dry savanna, semi-desert.

BIOLOGY. No information available.

Genus *DEOMYS* Thomas

1888. *Deomys* Thomas, *Proc. zool. Soc. Lond.* 1888: 130. Genotype *Deomys ferrugineus* Thomas.

Similar to *Grammomys* with rufous upperside, white underside and pencilled tail 1.5 times head-and-body length. Differences include the presence of stiff fur along the back (soft in *Grammomys*), two faint grooves on the upper incisors (none in *Grammomys*), long and narrow snout of the skull (short and broad in *Grammomys*) and elongate feet (*Grammomys* short).

Deomys ferrugineus Thomas

1888. *Deomys ferrugineus* Thomas, *Proc. zool. Soc. Lond.* 1888: 130. Lower Congo.

DESCRIPTION. As for genus.

DISTRIBUTION. Bwamba Forest, Toro. Text-fig. 19.

MEASUREMENTS. One ♀ h. & b. 122 mm.; tail 191 mm.; h. f. 33 mm.; ear 24 mm.

BREEDING. Foetuses (2 × 2) in Congo (Hatt, 1940).

HABITAT. In the Congo typical of primary forest; does not penetrate *Cynometra* or transitional forest; rare (Misonne, 1963).

BIOLOGY. Eight stomachs examined of animals caught in the Congo contained grasshoppers, ants, termites and flesh resembling that of a rat (Hatt, 1940).

Genus *DELANYMYS* Hayman. Delany's Swamp-mice

1962. *Delanymys* Hayman, *Rev. Zool. Bot. afr.* 65: 129. Genotype, by original designation, *Delanymys brooksi* Hayman.

A very small mouse with a relatively long tail. Front feet very small, hind feet long and narrow. Tail thinly covered with short stiff hairs. Fur very dense and soft with stout guard hairs on dorsal surface. Basal two-thirds of dorsal and ventral hairs slate grey; dorsally, tips of hairs russet or hazel; ventrally, warm buff. Black patch between each eye and nostril.

Delanymys brooksi Hayman

1962. *Delanymys brooksi* Hayman, *Rev. Zool. Bot. afr.* **65**: 132. Echuya Swamp, Kigezi.

DESCRIPTION. As for genus.

DISTRIBUTION. Echuya Swamp, Kigezi. Text-fig. 19.

MEASUREMENTS. One ♂ h. & b. 57 mm. ; tail 100 mm. ; h. f. 17 mm. ; ear 10 mm. ; weight 5 g.

BREEDING. No information available.



FIG. 19. Distribution of *Steatomys parvus*, *Deomys ferrugineus* and *Delanymys brooksi*.

HABITAT. Sedge swamp in bamboo and montane forest. Occurs in similar habitat in the Congo (Hayman, 1962).

BIOLOGY. No information available.

Subfamily OTOMYINAE Thomas

1897. *Otomyinae* Thomas, *Proc. zool. Soc. Lond.* **1892**: 1017.

Genus OTOMYS Cuvier. Swamp Rats

1823. *Otomys* Cuvier, *Dents. Mamm.*: 168. Genotype, by subsequent designation (Sclater, 1899, *Ann. S. Afr. Mus.* **1**: 195), *Otomys irroratus* (Brants).

1918. *Anchotomys* Thomas, *Ann. Mag. nat. Hist.*, (9) **2**: 204. As a subgenus of *Otomys* Cuvier; type, by monotypy and original designation, *Euryotis anchietae* Bocage.

The genus *Otomys* is easy to identify as both upper and lower incisors are deeply grooved. The fur is long, thick and soft. A well haired tail appreciably shorter than head-and-body length. The ears are small and the face blunt. The colour is very variable. Swamp rat is probably a misnomer as they can occur in dry situations some distance from water. Many species of this genus have been described although according to Bohmann (1952) there are probably only three occurring in Uganda. In making specific identifications reference has to be made to the number of transverse laminae on the third upper molars. The systematics of this genus are in need of further investigation.

1	Lower incisors with two deep grooves	<i>O. typus</i>
	Lower incisors with a deep outer groove and a shallow inner groove	2
2	Five or six lamellae on third upper molar	<i>O. denti</i>
	Seven lamellae on third upper molar	<i>O. irroratus</i>

Otomys denti Thomas

1906. *Otomys denti* Thomas, *Ann. Mag. nat. Hist.*, (7) **18**: 142. Ruwenzori East, Toro.

1915. *Otomys kempi* Dollman, *Ann. Mag. nat. Hist.* (8) **15**: 152. Burunga, Mt. Mikeno, Congo [1° 28' S. 29° 25' E.].

DESCRIPTION. Dark coloured; dorsal surface brown-black speckled with copper buff. Backs of hands and feet blackish brown. Ventral surface slaty-black slightly speckled with buff. Tail black above and below. Lower incisor with a shallow inner groove, five or six transverse lamellae on third upper molar.

DISTRIBUTION. Mabira Forest, Buganda; Echuya Swamp and Forest, Kigezi; Kibale Forest, Mubuku Valley, Toro. Text-fig. 20.

MEASUREMENTS. Two ♂ h. & b. 170 mm., 150 mm.; tail 96 mm., 95 mm.; h. f. 26 mm., 27 mm.; ear 23 mm., 21 mm.; weight 125 g., ?. Three ♀ h. & b. 167 mm., 167 mm., 157 mm.; tail 94 mm., 94 mm., 89 mm.; h. f. 26 mm., 27 mm., 27 mm.; ear 23 mm., 25 mm., 21 mm.; weight 120 g., ?, ?.

BREEDING. Litters of two (Misonne, 1963).

HABITAT. Difficult to define in view of the limited number of records but apparently occurs in mixed vegetation and forest at various elevations.

BIOLOGY. Preyed on by harrier (*Circus macrourus*), grass owl (*Tyto capensis*) and leopard in Malawi (Loveridge, 1953).

***Otomys irroratus* (Brants)**

1827. *Euryotis irroratus* Brants, *Het Geslacht der Muizen* : 94. Uitenhage, Cape of Good Hope [33° 41' S. 25° 25' E.].

1915. *Otomys tropicalis* Dollman, *Ann. Mag. nat. Hist.*, (8) 15 : 157. Mt. Kenya, Kenya [0° 08' S. 37° 15' E.].

1915. *Otomys rubeculus* Dollman, *Ann. Mag. nat. Hist.*, (8) 15 : 161. Kagambah, Ankole.



FIG. 20. Distribution of *Otomys* spp.

DESCRIPTION. Colour variable but not usually as dark as *O. denti*. Distinguished from the other species on tooth characters.

DISTRIBUTION. Gulu, Acholi; Burumba, between Rwempuno and Kaizi Rivers, Ankole; Bugala Island, Kampala, Masaka, Mbanga Forest, Mubende, Buganda; Beelrunji, Bubungi, Likima, Mbale, Bugisu; "Bunyoro"; Echuya Swamp, Kiduha, Kumba, Kigezi; Fort Portal, Humya, Toro. Kasiba. Text-fig. 20.

MEASUREMENTS. H. & b. ♂ 168.1 mm. (18 meas., range 124 to 201 mm.), ♀ 164.7 mm. (14 meas., range 139 to 183 mm.); tail ♂ 93.0 mm. (18 meas., range 83 to 112 mm.), ♀ 84.4 mm. (14 meas., range 69 to 96 mm.); h. f. ♂ 29.5 mm. (18 meas., range 27 to 34 mm.), ♀ 28.3 mm. (14 meas., range 26 to 30 mm.); ear ♂ 22.0 mm. (18 meas., range 20 to 25 mm.), ♀ 22.0 mm. (13 meas., range 20 to 25 mm.); weight ♂ 95 g., 110 g. (only 2 weighed), ♀ 101.3 g. (6 weighed, range 60 to 120 g.).

BREEDING. Foetuses (1 × 2) Jul. Mbanga Forest; (1 × 2) between Kaizi and Rwempuno Rivers, Aug.; (1 × 1) Oct. Echuya Swamp. One ♀ from Echuya lactating in Sep. Two embryos obtained in August weighed 25 g. Apparently no fixed breeding season in Zambia (Ansell, 1960); litter size 2 to 3. Hair and incisors erupted at birth. Litter size 2 to 4 (never more) in South West Africa where the young have been found in rough grass nests in dense reed-growth (Shortridge, 1934).

HABITAT. Grassland, scrub where herbage is fairly dense. Has been obtained at relatively large distances from water.

BIOLOGY. Herbivorous; stomachs of nine animals contained leaves and stems.

Otomys typus (Heuglin)

1877. *Oreomys typus* Heuglin, *Reise in Nordost. Afrika* 2: 77. Highlands of Simyen, Ethiopia [13°-14° N. 38°-39° E.].

1891. *Otomys jacksoni* Thomas, *Ann. Mag. nat. Hist.*, (6) 7: 304. [Crater of] Mt. Elgon.

1906. *Otomys dartmouthi* Thomas, *Ann. Mag. nat. Hist.*, (7) 18: 141. Mubuku Valley, Toro.

DESCRIPTION. Similar to *O. irroratus* but separated on tooth characters.

DISTRIBUTION. Mudangi, Bugisu; Arugot (Mt. Elgon), Sebei; Mubuku Valley, Toro. Text-fig. 20.

MEASUREMENTS. H. & b. ♂ 142.3 mm. (4 meas., range 132 to 150 mm.), ♀ 140.0 mm. (4 meas., range 135 to 143 mm.); tail ♂ 91.0 mm. (4 meas., range 82 to 101 mm.), ♀ 80.5 mm. (4 meas., range 64 to 93 mm.); h. f. ♂ 26.3 mm. (4 meas., range 25 to 27 mm.), ♀ 24.6 mm. (4 meas., range 21 to 26.5 mm.); ear ♂ 24.3 mm. (4 meas., range 22.5 to 25 mm.), ♀ 23.7 mm. (3 meas., range 21 to 25 mm.). None weighed.

BREEDING. No information available.

HABITAT. Typically an animal of high altitudes occurring at over 11,000 feet on Mt. Elgon and over 12,000 feet on Ruwenzori. Occurs in *Senecio-Lobelia* zone (Misonne, 1963).

BIOLOGY. Apparently active in the early morning and evening. Does not dig burrows but lives in long tunnels under moss and *Sphagnum* (Misonne, 1963).

GAZETTEER

As much information as was obtained is given for places not located.

Adropi, West Nile	2° 48' N.	31° 15' E.
Aigo River, Acholi	2° 21' N.	31° 55' E.
Ajeluk, Teso	1° 30' N.	33° 50' E.
Amudat, Karamoja	1° 58' N.	34° 57' E.
Amuria, Teso	2° 01' N.	33° 38' E.
Anamuget, Karamoja	2° 25' N.	34° 30' E.
Arua, West Nile	3° 01' N.	30° 55' E.
Arugot, north-east Mt. Elgon, Sebei		not located
Asuya, Acholi	2° 57' N.	32° 36' E.
Awack, Acholi	2° 39' N.	33° 27' E.
Beelrungi, south Bugisu		not located
Benet, Sebei	1° 20' N.	34° 33' E.
Biso, Bunyoro	1° 45' N.	31° 25' E.
Bokora, Karamoja	2° 25' N.	34° 25' E.
Bubukwanga, Toro	0° 45' N.	30° 05' E.
Bubungi, Bugisu	1° 05' N.	34° 20' E.
Budadin Camp, Bugisu		not located
Budama, Bukedi	0° 40' N.	34° 03' E.
Budongo Forest, Bunyoro	1° 45' N.	31° 36' E.
Bugala Island, Buganda	0° 24' S.	32° 10' E.
Bugiongolo		not located
Bugoma Forest, Bunyoro	1° 15' N.	31° 00' E.
Bugoye, Toro	0° 17' N.	30° 07' E.
Buligi, Buganda	0° 27' N.	31° 53' E.
Bulisa, Bunyoro	2° 07' N.	31° 25' E.
Bumatta, Bwamba Co., Toro		not located
Bummaddu = Bumadu, Toro	0° 43' N.	30° 05' E.
Bundibugyo, Toro	0° 42' N.	30° 04' E.
Bundimali, Toro	0° 55' N.	30° 03' E.
Buruli Co., Buganda	1° 25' N.	32° 25' E.
Burumba, Ankole	1° 00' S.	30° 50' E.
Busia, Bukedi	0° 28' N.	34° 05' E.
Busingiro, Bunyoro	1° 44' N.	31° 28' E.
Butiaba, Bunyoro	1° 49' N.	31° 19' E.
Butiti, Toro	0° 39' N.	30° 32' E.
Buyobo, Bugisu	1° 10' N.	34° 17' E.
Bwamba Co., Toro	0° 55' N.	30° 03' E.
Bwamba Forest, Toro	0° 48' N.	30° 06' E.
Chagwe = Kyagwe Co., Buganda	0° 24' N.	32° 45' E.
Chua Co., Acholi	3° 20' N.	33° 05' E.
Congo Road (Q.E.P.) Ankole	0° 14' S.	29° 59' E.
Crater Track (Q.E.P.), Toro	0° 07' S.	29° 54' E.
Echuya Forest, Kigezi	1° 14' S.	29° 46' E.
Echuya Swamp, Kigezi	1° 14' S.	29° 46' E.
Elgon, Mt., Sebei	1° 08' N.	34° 33' E.
Entebbe, Buganda	0° 03' N.	32° 28' E.

Fadjao, Bunyoro	2° 15' N.	31° 40' E.
Fort Patiko = Baker's Fatiko, Acholi	3° 02' N.	32° 21' E.
Fort Portal, Toro	0° 40' N.	30° 18' E.
Gayaza, Ankole	0° 45' S.	30° 47' E.
Greek River, south bank, Sebei	1° 36' N.	34° 20' E.
Gulu, Acholi	2° 47' N.	32° 18' E.
Hakitengya, Toro	0° 45' N.	30° 05' E.
Hoima, Bunyoro	1° 25' N.	31° 21' E.
Humya = Humiya, Toro	0° 46' N.	30° 02' E.
Ilumia, Toro	0° 53' N.	30° 03' E.
Impenetrable Forest, Kigezi	1° 05' S.	29° 49' E.
Ingezi, Kigezi	1° 00' S.	29° 50' E.
Iriri, Teso	2° 06' N.	34° 12' E.
Isegero, Busoga	0° 50' N.	33° 35' E.
Isungu, Toro	0° 30' N.	30° 21' E.
Jinja, Busoga	0° 27' N.	33° 12' E.
Kabanyolo, Buganda	0° 27' N.	32° 36' E.
Kabaroni Camp, north Bugisu		not located
Kabula, Buganda	0° 22' S.	31° 10' E.
Kabulamuliro, Buganda	0° 42' N.	32° 13' E.
Kacheba, Lango		not located
Kacheri, Karamoja	3° 10' N.	33° 56' E.
Kagambah, Ankole	1° 00' S.	30° 15' E.
Kaizi River (Q.E.P.), Ankole	0° 25' S.	29° 51' E.
Kajansi, Buganda	0° 12' N.	32° 32' E.
Kajuia, Bunyoro		not located
Kakumiro, Buganda	0° 48' N.	31° 20' E.
Kalinzu Forest, Ankole	0° 22' S.	30° 07' E.
Kalule, Buganda	0° 38' N.	32° 32' E.
Kama Island, Busoga	0° 09' S.	33° 54' E.
Kamchuru, Karamoja	2° 40' N.	33° 35' E.
Kampala, Buganda	0° 19' N.	32° 35' E.
Kamulikwezi, Toro	0° 06' N.	30° 04' E.
Kamulikwezi Swamp, Toro	0° 05' N.	30° 09' E.
Kanaba Gap, Kigezi	1° 14' S.	29° 46' E.
Kapiri, Teso	1° 40' N.	33° 48' E.
Kasai Forest = Kasa Forest, Buganda	0° 13' N.	32° 02' E.
Kasiba		not located
Katwe, Toro	0° 08' S.	29° 52' E.
Kawenge = Kawempe, Buganda	0° 20' N.	32° 35' E.
Kibale Forest = Mpanga Forest, Toro	0° 33' N.	30° 24' E.
Kibandama, ? Kigezi		not located
Kibiro, Bunyoro	1° 41' N.	31° 15' E.
Kibusi = Kibuji, Lango	1° 53' N.	32° 23' E.
Kichwamba, Ankole	0° 14' S.	30° 06' E.
Kidoko, Bukedi	0° 52' N.	34° 07' E.
Kiduha, Kigezi	1° 15' S.	29° 41' E.
Kikandwa, Buganda	0° 37' N.	32° 07' E.

Kikonda, Buganda	1° 16' N.	31° 31' E.
Kilembe, Toro	0° 12' N.	30° 01' E.
Kimara, Toro	0° 50' N.	30° 15' E.
Kisimbiri, Buganda	0° 24' N.	32° 29' E.
Kisingo, Buganda	0° 45' N.	31° 57' E.
Kitgum, Acholi	3° 17' N.	32° 53' E.
Kokanjiro, Mt. Elgon		not located
Koki Co., Buganda	0° 43' S.	31° 20' E.
Kome Island, Buganda	0° 06' S.	32° 45' E.
Kotido, Karamoja	3° 01' N.	34° 06' E.
Kumba, Kigezi	1° 08' S.	29° 54' E.
Kyabombo, Toro		not located
Kyatwe, Toro	0° 27' N.	30° 13' E.
Lialo, Buganda	0° 53' N.	31° 57' E.
Likima, Bugisu		not located
Locihotome, Karamoja		not located
Login, West Nile		not located
Lorengikipi strm., Karamoja	2° 20' N.	33° 51' E.
Lotome, Karamoja	2° 24' N.	34° 31' E.
Lungo, Bukedi	0° 25' N.	34° 00' E.
Lunyo, Bugando	0° 03' N.	32° 28' E.
Lutoto, Ankole	0° 20' S.	30° 06' E.
Lwakaka = Lwakhakha, Bugisu	0° 48' N.	34° 22' E.
Mabira Forest, Buganda	0° 30' N.	33° 00' E.
Makoga, Toro	1° 01' N.	30° 22' E.
Malabigambo Forest, Buganda	0° 57' S.	31° 33' E.
Malera, Teso	1° 26' N.	34° 08' E.
Manimani, Karamoja	2° 19' N.	34° 39' E.
Maramagambo Forest (Q.E.P.) Ankole	0° 25' S.	29° 52' E.
Maramagambo Forest, north of (Q.E.P.), Ankole	0° 15' S.	30° 03' E.
Masaka, Buganda	0° 20' S.	31° 44' E.
Masindi, Bunyoro	1° 41' N.	31° 43' E.
Masindi Port, Bunyoro	1° 42' N.	32° 05' E.
Mbale, Bugisu	1° 04' N.	34° 11' E.
Mbanga Forest = Mpanga Forest, Buganda	0° 11' N.	32° 16' E.
Mbarara, Ankole	0° 37' S.	30° 39' E.
Mengo District, Buganda	0° 17' N.	32° 35' E.
Mfumbiro = Mufumbiro = Bufumbiro region, Kigezi	1° 22' S.	29° 39' E.
Mihunga, Toro	0° 22' N.	30° 03' E.
M.N.P. = Murchison Falls National Park in south-west Acholi and north west Bunyoro		
Mongi, Toro	0° 50' N.	30° 10' E.
Moroto, Karamoja	2° 33' N.	34° 39' E.
Moroto Forest, Karamoja	2° 33' N.	34° 44' E.
Mornita, Karamoja	1° 55' N.	34° 45' E.
Moyo, Madi	3° 39' N.	31° 42' E.
Mpanga Forest = Mbanga Forest, Buganda	0° 11' N.	32° 16' E.
Mpanga Forest = Kibale Forest, Toro	0° 33' N.	30° 24' E.
Mubende, Buganda	0° 35' N.	31° 23' E.
Mubuku Valley = Ruwenzori East, Toro	0° 22' N.	30° 01' E.
Mudangi, Bugisu	1° 10' N.	34° 29' E.

Muhavura Mt., Kigezi	1° 23' S.	29° 40' E.
Muhokya, Toro	0° 06' N.	30° 04' E.
Mulanda, Bukedi	0° 42' N.	34° 01' E.
Mweya, Toro	0° 11' S.	29° 54' E.
Nabilatuk, Karamoja	2° 03' N.	34° 35' E.
Nabugabo, Buganda	0° 22' S.	31° 53' E.
Nakiloro, Karamoja	2° 37' N.	34° 44' E.
Nakivali Lake, Ankole	0° 47' S.	30° 53' E.
Nalweyo, Buganda	1° 07' N.	31° 16' E.
Namalu, Karamoja	1° 49' N.	34° 38' E.
Napyananya, Karamoja	1° 52' N.	34° 35' E.
Nebbi, West Nile	2° 30' N.	31° 06' E.
Ngai, Lango	2° 30' N.	32° 29' E.
Ngal, West Nile	2° 26' N.	31° 29' E.
Ngora Rest House, Teso	1° 30' N.	33° 45' E.
Nkyanuna = Kyanuna, Buganda	0° 33' N.	32° 14' E.
Nyakabande, Kigezi	1° 18' S.	29° 43' E.
Nyalusanje, Kigezi	1° 00' S.	29° 58' E.
Offude, West Nile	3° 13' N.	30° 58' E.
Ongino, Teso	1° 33' N.	33° 59' E.
Packwack, West Nile	2° 27' N.	31° 29' E.
Pamdero (M.N.P.), Acholi	2° 22' N.	31° 40' E.
Paraa (M.N.P.), Acholi	2° 15' N.	31° 35' E.
Patiko = Baker's Fatiko, Acholi	3° 02' N.	37° 21' E.
Patong, River Naam		not located
Q.E.P. = Queen Elizabeth National Park in Kigezi, west Ankole and south Toro.		
Rhino Camp, West Nile	2° 58' N.	31° 24' E.
Rukiga Co., Kigezi	1° 05' S.	30° 02' E.
Rutanda (Q.E.P.), Ankole	0° 15' S.	30° 04' E.
Ruwenzori East = Mubuku Valley of British Museum		
Ruwenzori Expedition, 1906	0° 22' N.	30° 01' E.
Ruwenzori North, Toro	about 0° 40' N.	30° 10' E.
Ruwenzori South East, probably around Muhokya	0° 06' N.	30° 04' E.
Rwamachuchu = Rwamucucu, Kigezi	1° 10' S.	30° 02' E.
Rwempuno River (Q.E.P.), Ankole	0° 23' S.	29° 53' E.
Sabinio Mt., Kigezi	1° 23' S.	29° 36' E.
Salalira, Bugisu	1° 14' N.	34° 17' E.
Sara, Toro	0° 47' N.	30° 05' E.
Sebei Camp, Teso	1° 31' N.	33° 26' E.
Sipi, Bugisu	1° 20' N.	34° 14' E.
Siroko Valley, Bugisu	1° 21' N.	34° 14' E.
Soroti, Teso	1° 44' N.	33° 36' E.
Tokwe, Toro	0° 48' N.	30° 02' E.
Tororo, Bukedi	0° 41' N.	34° 10' E.
Usaga		not located

Vurra, West Nile	2° 53' N.	30° 53' E.
Wadelai, West Nile	2° 42' N.	31° 27' E.
Walasi, Bugisu	1° 11' N.	34° 13' E.
Wanka River, Toro	0° 51' N.	30° 16' E.
Wasa River, Toro	0° 47' N.	30° 15' E.
Yumbe, West Nile	3° 28' N.	31° 15' E.
Zika Forest, Buganda	0° 10' N.	32° 28' E.

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